CHAPTER 2

GROSS MORPHOLOGY OF THE OROPHARYNGEAL CAVITY AND PROXIMAL OESOPHAGUS

2.1 INTRODUCTION

Despite numerous studies investigating the intestinal tract of ratites (Owen, 1841; Gadow, 1879; Pycraft, 1900; Mitchell, 1901; Herd, 1985; Bezuidenhoudt, 1999; Potter *et al*., 2006; Porchescu, 2007) there is very little comprehensive information available on the structure of the upper digestive tract (oral cavity, tongue, pharynx and oesophagus) of these birds. In contrast, the upper digestive tract of many other species of birds has been described in some detail (for a review of the earlier literature see Calhoun, 1954; Warner *et al*., 1967; McLelland, 1979).

The most comprehensively studied ratite in respect of the upper digestive tract is the ostrich and this region, or parts thereof, have been illustrated and described in a number of publications (Göppert, 1903; Faraggiana, 1933; Porchescu, 2007; Jackowiak and Ludwig, 2008; Tivane, 2008) with the most comprehensive work being that of Tivane (2008) who combined gross morphological descriptions with histology and scanning electron microscopy of the oropharynx and oesophagus. Descriptions, as well as illustrations of the ratite oropharynx or parts thereof have also been supplied for the greater rhea (Gadow, 1879; Pycraft, 1900; Faraggiana, 1933; Gussekloo & Bout, 2005), kiwi (Owen, 1879) and emu (Faraggiana, 1933, Bonga Tomlinson, 2000). No complete description of the emu oropharynx is currently available and the existing information, which records the structure of the tongue and laryngeal mound, is, in part, inaccurate or misleading (see Chapter 4).

The most complete comparative work on the ratite oropharynx is that by Cho *et al*. (1984) who noted that the shape of the tonsils, as with the tongue, varies between the ratites. The description is vague and open to interpretation, giving little information on the specific location or structure of the tonsils. The authors simply note that "The ostrich tonsils and tongue are smooth, blunt and U-shaped. In the Darwin's rhea both tongue and tonsils have simple, pointed V-shaped tips. The tonsils in the emu are similar to the rhea but have a small flap laterally" (Cho *et al*., 1984). It is clear from the existing literature on the topic that a comprehensive description of the upper digestive tract of ratites is sorely lacking, particularly in respect of the emu.

Emu farming in South Africa is a relatively new enterprise and efforts to place this emerging industry on a sound financial basis are hamstrung by a lack of basic knowledge on the biology of this bird. The upper digestive tract is of considerable importance considering that it is the first area for food selection and intake which is vital to the nutrition and growth of the animal and therefore its commercial viability. This chapter presents the first definitive macroscopic description of the oropharynx of the emu and reviews, consolidates and compares scattered information on the gross morphology of the ratite oropharynx available in the literature.

2.2 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.

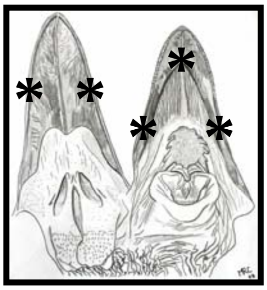
The specimens were rinsed in running tap water and each preserved head was used to provide information on the gross anatomical features of the oropharyngeal cavity. This was achieved by incising the right commisure of the beak, disarticulating the quadratomandibular joint and reflecting the mandible laterally to openly display the roof and floor of the oropharynx (Fig. 2.2). Relevant features were described and recorded using a Canon 5D digital camera with a 28-135 mm lens and a Canon Macro 100mm lens for higher magnification photographs.

The terminology used in this study was that of Nomina Anatomica Avium (Baumel *et al*., 1993).

2.3 RESULTS

The oropharyngeal cavity consisted of the oral (*Cavum oralis*) and pharyngeal (*Cavum pharyngis*) cavities (Figs. 2.1, 2.2), which could not be morphologically distinguished from each other. The oropharyngeal cavity was bounded laterally and rostrally by the tomia of the *rhamphotheca*, dorsally by the oropharyngeal roof, choana and pharyngeal folds, ventrally by the mandibular rhamphotheca and soft interramal region and caudally by the proximal oesophagus. The oropharyngeal cavity was dorso-ventrally flattened in the closed gape and housed the tongue and laryngeal mound. The oropharyngeal floor was triangular (Figs. 2.2, 2.7) and the oropharyngeal roof was pear-shaped (Figs. 2.2, 2.10).

2.3.1 Rhamphotheca



The mandibular rhamphotheca (Figs. 2.1, 2.2, 2.3, 2.7) was a dark brown/black colour in formalin fixed specimens and had a rubbery/leathery texture. Viewed from dorsally, it consisted of two long thin arms originating caudally from the fleshy angle of the mouth (mandibular rictus) which followed the contours of the mandibular rami and converged rostrally to meet and form a flattened plate overlying the mandibular rostrum (Figs. 2.1, 2.2, 2.3, 2.7). The rostral plate displayed a clear median sulcus which overlay the mandibular symphysis (Fig. 2.3). The sulcus was bordered on either side by a slight ridge and extended from the caudal edge of the mandibular nail (*Unguis mandibularis*) to the caudal edge of the rostral plate (Figs. 2.3). The rostral plate bore a series of transverse grooves extending the full width of the *rhamphotheca* (Figs. 2.3, 2.7). These varied in number and depth between the specimens.

The mandibular tomia (*Tomium mandibulare*) (the cutting edge of the *rhamphotheca*), were relatively wide caudally and presented a smooth and rounded surface forming a blunt cutting edge (Figs. 2.1, 2.2, 2.4, 2.7). The rostral third of the mandibular tomia bore serrations (*Lamellae rostri*) with rostrally pointing tips forming a sharp cutting edge (Figs. 2.3, 2.4). The right side (range: 18-27) almost always displayed a higher number of serrations than the left side (range: 19-26). The average total number of rostral lamellae for each bird was 44.6 (range: 38-52). The serrations were fairly uniform in profile for each specimen (Figs. 2.1, 2.3, 2.4, 2.7), but varied between the specimens, being prominent in some and less distinct in others. The serrations abutted the most rostral tip of the mandible, the mandibular nail, which was represented by a smooth, pointed, lightly pigmented thickening which formed a raised tip (Fig. 2.3). The mandibular nail was the most rostral extremity of the *gonys*, a thickened component of the external mandibular rhamphotheca (Fig. 2.4).

The left and right maxillary rhamphotheca extended from the rostral border of each maxillary rictus to the maxillary nail (*Unguis maxillaris*) where they merged to form a broad shelf (maxillary rostrum) similar to, but larger, than the rostral plate of the mandible (Fig. 2.10). It was similar in colour and texture to the mandibular rhamphotheca. The maxillary rostrum was concave and was indiscernible from the pigmented region of the roof. The maxillary tomia (*Tomium maxillare*) (Figs. 2.1, 2.2, 2.5, 2.6, 2.10) were smooth (non-serrated) and narrower than the mandibular tomia and formed a sharper cutting edge. The tip of the maxillary rostrum displayed a prominent maxillary nail (*Unguis maxillaris*) (Figs. 2.5, 2.6) which represented the most rostral tip of the *culmen*, a structure comparable to the *gonys*, but occurring on the maxilla (Fig. 2.5). The rostral tip of the unguis was lightly pigmented in most specimens (Fig. 2.5). In the closed gape the maxillary unguis projected rostral to and overlapped the mandibular unguis.

The *Rima oris* was formed by the maxillary and mandibular tomia. Caudally, in the closed position, the maxillary and mandibular tomia directly opposed each other. Rostrally, in the region where the serrations originated, the mandibular tomia lay medial to the maxillary tomia and the mandibular nail lay ventral and caudal to the maxillary nail. In lateral profile, the serrated part of the mandible had a slight ventral inclination from the origin of the serrations to the tip of the bill.

2.3.2 The floor of the oropharynx

The oropharyngeal floor was divided into the interramal region, consisting of a rostral pigmented and a caudal non-pigmented part, tongue (see Chapter 4) and laryngeal mound (Fig. 2.7).

2.3.2.1 Interramal region - Rostral pigmented part (Figs. 2.1, 2.2, 2.7)

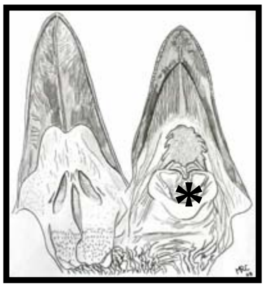
This region was situated rostral to the tongue and was bordered laterally and rostrally by the mandibular rhamphotheca. It represented the intra-oral tissue overlying the *mentum*. This region was triangular in outline with a rounded apex pointing rostrally and was dark ash-grey in colour. The base was clearly demarcated from the caudal non-pigmented region and had a scalloped outline. The median sulcus in the *rhamphotheca*, overlying the mandibular symphysis, continued caudally through this region as a smooth well defined light-grey line. The mucosa on either side of this line was divided into two columns composed of fine longitudinal folds (Fig. 2.2). The two medial columns were divided by and situated on either side of the obvious median smooth line, while the two lateral columns bordered the medial side of the *rhamphotheca*. The demarcation between the lateral and medial columns was not always well-defined, but was generally indicated by a thin light grey line. The lateral boundaries of the lateral columns tapered caudally onto the medial border of the *rhamphotheca*, ending by merging imperceptibly with the non-pigmented medial part of the mandibular rictus.

2.3.2.2 Interramal region - Caudal non-pigmented part (Figs. 2.1, 2.2, 2.7)

This region lay rostral and ventral to the body of the tongue and extended laterally around the tongue and laryngeal mound. The part situated in the midline and ventral to the tongue, was smooth and continuous caudally with the frenulum of the tongue. On either side of the smooth area, the tissue was thrown into longitudinal folds scattered with small raised nodules (Fig. 2.1). The folds followed the contours of the lateral sides of the laryngeal mound (medially) and the medial edge of the caudal mandibular rami (laterally), diverging from the smooth area ventral to the tongue, around the laryngeal mound, and converging caudal to the mound as they joined the origin of the oesophageal folds (Fig. 2.7). Two definite larger flat folds were identifiable, one on either side of the laryngeal mound, running medial to the rhamphotheca. They originated at the rostral border of the non-pigmented region and ended at the angle of the mouth. The folds lay flat on the floor with their free edge facing medially and enclosing a medially opening recess. These paired folds were also defined by a difference in colour, appearing slightly darker than the rest of the non-pigmented floor.

2.3.2.3 The tongue (see Chapter 4)

2.3.2.4 The laryngeal mound (*Mons laryngealis*) (Figs. 2.1, 2.2, 2.7, 2.8, 2.9)



The laryngeal mound projected dorsally from the floor of the oropharynx and was situated caudal to the tongue and rostral to the oesophagus. The lateral edges did not contact the mandibular rami. The laryngeal mound was supported by the circular cricoid cartilage, the paired dorsal arytenoid cartilages and the procricoid cartilage which connected the arytenoids caudally (Figs. 2.8, 2.9). The laryngeal fissure (glottis) (viewed dorsally) was wide rostrally and narrowed caudally. This was due to the lateral divergence of the arytenoid cartilages as they proceeded rostrally. The caudal protuberance of the tongue root (see Chapter 4) overlapped the rostro-medial part of the laryngeal fissure. Caudal to the tongue root and lying on the rostro-ventral floor of the larynx were 3-5 raised prominent, longitudinally plicated mucosal folds (Figs. 2.7, 2.8, 2.9). The middle fold was always the largest and longest. The mucosa supported by the arytenoid cartilages displayed a double fold separated by an intervening groove. The medial fold had a raised, sharp edge which terminated caudally as a bulbous protuberance. The medial folds formed the lateral edges of the glottis (*Rima glottis*) (Figs. 2.8, 2.9). The larger lateral folds presented gently rounded contours and merged caudally with the medial folds to form a single structure linked by the underlying procricoid cartilage. The mucosa covering the laryngeal mound was smooth and non-pigmented. Caudally, the mucosa merged with that of the oesophagus and became longitudinally folded.

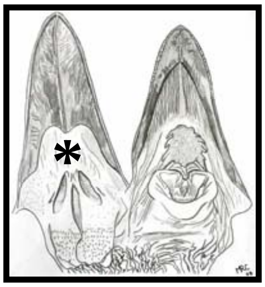
2.3.3 The roof of the oropharynx

The oropharyngeal roof consisted of a rostral pigmented region clearly demarcated from a caudal non-pigmented region which housed the *choana*, and two pharyngeal folds which extended caudally from the non-pigmented region (Fig. 2.10).

2.3.3.1 Pigmented region (Figs. 2.1, 2.2, 2.10)

The colour and texture of the pigmented region of the roof was similar to that of the *rhamphotheca* and it was difficult to clearly distinguish the two components (Fig. 2.10). It occupied approximately the rostral two thirds of the roof. Its shape was that of an arrow-head, with the tip pointing rostrally and the two elongated caudal arms extending to the rostral edge of the maxillary rictus. A prominent median palatine ridge (*Ruga palatina mediana*), bordered bilaterally by shallow sulci, extended from the maxillary unguis to the border of the pigmented and non-pigmented regions of the roof. The median sulcus of the rostral mandibular plate corresponded to the median palatine ridge of the maxilla, and the two ridges on either side of the mandibular sulcus corresponded to the sulci bordering the median palatine ridge.

2.3.3.2 Non-pigmented region (Figs. 2.1, 2.2, 2.10)



The outline of the non-pigmented region of the oropharyngeal roof (excluding the pharyngeal folds) was bell-shaped, with the base facing caudally. The rounded rostral border was indented caudally by the abrupt termination of the median palatine ridge at the junction of the pigmented and non-pigmented regions. The lateral borders extended to the maxillary rictus and ran parallel to the slits forming the choana (see below). The caudal border ended approximately level with the base of the choana, merging imperceptibly with the non-pitted surface of the pharyngeal folds. The maxillary rictus formed the most caudo-lateral extent of this region. The tissue had a lumpy uneven appearance and closer inspection revealed that the underlying tissue contained light-coloured doughnut-shaped structures, each with a dark, central spot (Fig. 2.11). Light microscopy confirmed each of the doughnut-shaped structures to be a glandular unit (see Chapter 3).

2.3.4 Choana (Figs. 2.1, 2.2, 2.10, 2.12, 2.13)

The choana was formed by paired, slit-like, oblique, oblong openings (the internal nares), resulting in a triangular-shaped choana. The paired slits originated rostro-medially and proceeded caudo-laterally, their line of direction being parallel to the border between the pigmented and non-pigmented regions of the roof. The two slits were separated by a wide raised ridge with a groove running down its midline and continuing to the infundibular cleft (*Rima infundibuli*). The infundibular cleft, housing the individual openings of the Eustachian tubes (McLelland, 1993), continued caudally as the separation between the two pharyngeal folds. In the most rostro-medial area between the two slits of the choana (the intervening ridge) were a few raised nodules which in the closed gape contacted the caudal point of the tongue root. On either side of the choana on the most caudo-lateral edge was a small fold of tissue (mucosal fold), concealing a small blind-ending pouch or recess, with its opening facing the choana.

2.3.5 Pharyngeal folds (*Plica pharyngis*) (Figs. 2.2, 2.10, 2.14, 2.15, 2.16, 2.17, 2.18, 2.19)

The pharyngeal folds were paired, U-shaped structures with the rounded free base facing caudally. They were divided into a smooth, attached rostral part and a pitted, free caudal part. The folds overlapped each other medially. The two pharyngeal folds formed the most caudal extent of the oropharyngeal roof and were connected laterally to the maxillary rictus. They originated caudal to the base of the choana and were separated rostrally by the infundibular cleft. The point where the pharyngeal folds were unattached was marked by a pitted horizontal line. Caudal to this line, the ventral surface of the folds displayed a deeply pitted surface in contrast to the dorsal surface that was smooth and free of large pits. Attached to the dorsal aspect of the caudo-lateral edge of each fold was a smooth rounded structure (caudo-lateral projection) that protruded beyond the margins of the fold. A blind-ending pouch or recess was formed between the ventrum of the protrusion and the dorsum of the pharyngeal fold (Fig. 2.14).

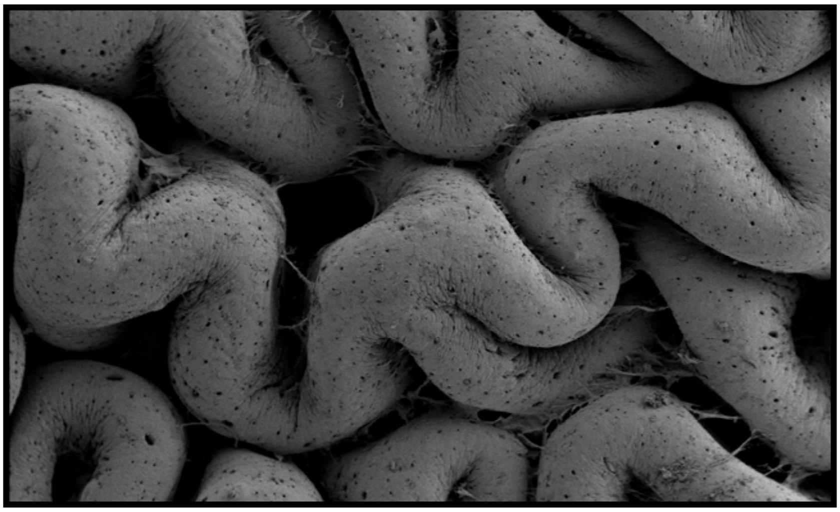
2.3.6 Proximal cervical oesophagus (*Oesophagus pars cervicalis*) (Figs. 2.2, 2.15, 2.19, 2.20)

The proximal oesophagus originated dorsal to the trachea and proceeded from the caudal end of the laryngeal mound caudally down the neck. It soon occupied a position lateral to the trachea and to its right. The oesophageal mucosa was non-pigmented and displayed a smooth surface thrown into prominent longitudinal folds. These folds proceeded from the oesophageal origin up to the end of the specimens studied. The proximal oesophagus of the emu was flaccid and wide in its natural state but appeared collapsed on itself in the preserved oesophagi which varied in cross-sectional shape from triangular to oval to circular.

The transition from oropharynx to oesophagus was not clearly demarcated on the oropharyngeal floor. The longitudinal folds on either side of the laryngeal mound converged caudal to the mound and merged with the longitudinal folds of the oesophagus. There was a raised transverse ridge caudal to the laryngeal mound, over which the longitudinal folds ran. This was not always as obvious in all specimens.

The transition from oropharyngeal roof to oesophagus was much more abrupt and clearly demarcated. The pharyngeal folds obscured the oesophageal origin. Their dorsal surface lay in contact with the oesophagus and formed a retropharyngeal recess, lined ventrally by the dorsal surface of the pharyngeal folds and dorsally by the longitudinally folded mucosa representing the origin of the oesophagus (Fig. 2.15).

In the fresh state, the longitudinally folded nature of the mucosa was not always apparent. However, following fixation the pattern of mucosal folds was prominent. The folds were raised off the floor, had rounded contours and were convoluted. Branching and anastomosing of the folds were also characteristic for this region (Figs. 2.15, 2.20). There were an average number of 16 folds in the proximal oesophagus (n=10) with a range of 14 – 26. The mucosa had a smooth appearance and was non-pigmented.



2.4 DISCUSSION

2.4.1 Oropharynx

In the emu the oral and pharyngeal cavities could not be morphologically distinguished from one another and therefore formed one combined cavity, namely, the oropharynx, a feature also noted in the ostrich (Tivane, 2008). As birds lack a soft palate (McLeod, 1939; Nickel *et al*., 1977; McLelland, 1975, 1979, 1990, 1993) and pharyngeal isthmus (McLelland, 1975, 1979, 1990, 1993) the occurrence of a combined oropharynx is typical of avian species (McLeod, 1939; Koch, 1973; Hodges, 1974; Nickel *et al*., 1977; King and McLelland, 1984; McLelland, 1975, 1979, 1990). The precise point where the oral and pharyngeal cavities join one another is impossible to determine (McLelland, 1975). However, some authors have named certain landmarks which they use to divide the oral and pharyngeal cavities, namely the last row of caudal pointing papillae on the palate (Koch, 1973; Hodges, 1974; McLelland, 1975) or the space between the choana and infundibular cleft (Hamilton, 1952; Nickel *et al*., 1977; King and McLelland, 1984). Lucas and Stettenheim, 1972 (cited by McLelland, 1993) using embryological evidence, note that the dorsal transverse boundary of the roof lies between the choana and infundibular cleft, stretching to the lateral angle of the jaws, while the ventral transverse boundary lies between the paraglossal and basihyal bones.

2.4.2 Rhamphotheca

The term *rhamphotheca* denotes the *Stratum corneum* of the epidermis covering the bill (Hodges, 1974; Clark, 1993). The *rhamphotheca* forming the most lateral limits of the oropharynx shows some special modifications in the emu. The most rostral extremity of both upper and lower bills display a distinct hook-like or nail-like structure, the mandibular and maxillary nail (*unguis*), a structure also evident in the ostrich (Tivane, 2008) and greater rhea (personal observation), but not in the kiwi (Roach, 1952). The mandibular and maxillary nails have been reported in procellariform, most pelecaniform (Clark, 1993) and anseriform birds (Berkhoudt, 1975; Nickel *et al*., 1977; Clark, 1993; Gussekloo, 2006).

The upper and lower beak function as prehensile organs (McLeod, 1939; Calhoun, 1954; Nickel *et al*., 1977); therefore these two structures would assist in the incomplete breaking down of food

(Nickel *et al*., 1977) as well as in its procurement and handling. Due to the absence of teeth in birds (McLeod, 1939; McLelland, 1975, 1979; Nickel *et al*., 1977; King and McLelland, 1984), these structures are replaced by the tomia (McLelland, 1975, 1979; Nickel *et al*., 1977; King and McLelland, 1984). The rostral mandibular tomia in the emu bear serrations (*Lamellae rostri*) and the maxillary tomia are narrow, strong and sharp. The rostral mandibular tomia of the ostrich revealed fine serrations (Tivane, 2008) whereas those of the greater rhea are entirely smooth (personal observation). The finding in the emu and ostrich contrasts with the statement by Gussekloo and Bout (2005) that the bill in ratites is relatively less adapted and non-specialised due to its sole function of holding food and that the tomia are blunt and rounded. Davies (1978) notes that the bill of the emu requires little strength due to their diet and that these birds only require the ability to ingest large objects. However, the nails of the bill together with the sharp and serrated tomia, present a formidable combination of tearing and pecking power.

2.4.3 Oropharyngeal floor

This study revealed the floor of the oropharynx of the emu to consist of four clearly discernable parts and structures, the interramal region, divided into rostral pigmented and caudal non-pigmented regions, the tongue (see chapter 4) and the laryngeal mound.

2.4.3.1. Oropharyngeal floor - Interramal region

Although the interramal region of the emu showed few remarkable features, in comparison to that of the ostrich (Göppert, 1903; Faraggiana, 1933; Porchescu, 2007; Jackowiak and Ludwig, 2008; Tivane, 2008) and greater rhea (Gussekloo and Bout, 2005; personal observation), the emu shows a more distinct demarcation between the rostral and caudal interramal regions. In the ostrich the entire interramal region is similar in colour (Porchescu, 2007; Jackowiak and Ludwig, 2008; Tivane, 2008) whereas in the emu the rostral region is pigmented in contrast to the non-pigmented caudal region. In the greater rhea, the lateral portions of the caudal interramal region display a pigmented surface in the form of small dark dots (personal observation). In the emu the surface of the rostral component displays a different pattern of folds (columns of fine longitudinal folds) to those of the comparable region in the ostrich. This area in the ostrich is characterised by irregular longitudinal folds, with a single or double larger fold, extending from the bill tip to the frenulum (Tivane, 2008). Although Tivane (2008), quoting Gussekloo and Bout

(2005) refers to folds in the interramal region in the greater rhea, this area is entirely smooth and displays no folds (personal observation).

The membranous floor of the oropharyngeal cavity is highly distensible in some groups of birds (Ziswiler and Farner, 1972), a similar feature also noted in the emu. The non-pigmented interramal area displayed a series of longitudinal folds which diverged around the laryngeal mound. The most lateral of those folds was large and conspicuous, a feature also illustrated in the ostrich (Göppert, 1903; Faraggiana, 1933; Porchescu, 2007; Jackowiak and Ludwig, 2008; Tivane, 2008) but not in the greater rhea (personal observation).

Two reasons can be advanced for the presence of folds in the caudal interramal region in the emu. In the ‘catch and throw’ feeding method employed by ratites (Gussekloo and Bout, 2005) the gape needs to be enlarged to allow the accelerated food particle/s to travel beyond the tongue and laryngeal mound into the proximal oesophagus. Yet, in the closed gape, the oropharyngeal cavity presents as a dorso-ventrally flattened structure. Thus enlargement of the cavity is necessary during eating. Gussekloo and Bout (2005) attribute the enlargement of the gape to depression of the tongue only. In the folded interramal region, depression of the tongue would allow for a greater enlargement of the gape than would a non-folded region. Tivane (2008) suggests that the folded nature of the ostrich oropharyngeal floor would allow food to be accumulated prior to swallowing, yet as seen from the feeding method described above ratites do not house food in the oral cavity prior to swallowing. Therefore this function of the distensible floor in the ostrich is questionable.

The second reason advanced for the presence of the folds in the interramal region would be for the process of fluid ingestion. During drinking in ratites (Gussekloo and Bout, 2005), the lower bill is inserted into the water and the head moved forward, using the lower bill as a scoop. Again, the folded nature of the oropharyngeal floor would allow the distensibility required to hold sufficient quantities of water to swallow as well as for the channelling of fluids around the laryngeal mound.

2.4.3.2. Laryngeal mound

The laryngeal mound of the emu is a prominent feature in the oropharynx and forms the most caudal structure of the oropharyngeal floor. This is in agreement with the general pattern in avians (Nickel *et al*., 1977; King and McLelland, 1984). In most birds the glottis, which is situated on the dorsal surface of the laryngeal mound, usually lies directly ventral to the caudal part of the choana (McLelland, 1979; Bailey *et al*., 1997). However, in the emu, which has an undivided choana (see discussion below), the glottis underlies the entire choana. This arrangement was also noted in the ostrich (Tivane, 2008) and greater rhea (personal observation) and appears to be the general pattern in ratites. The caudal margin of the laryngeal mound is sloped and the pharyngeal folds overlie this sloped area (Nickel *et al*., 1977), a feature also noted in the emu. This arrangement allows for closure of the oesophagus during respiration (Nickel *et al*., 1977). The illustrations of Porchescu (2007) and Tivane (2008) seem to confirm a similar situation in the ostrich.

The glottis in palaeognaths is relatively wider than in neognaths (Pycraft, 1900). The laryngeal fissure (glottis) in the emu is rhomboid-shaped (Faraggiana, 1933) and is wider rostrally than caudally. 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; Jackowiak and Ludwig, 2008; Porchescu, 2007; Tivane, 2008). It is of importance that the glottis is closed during swallowing (Kaupp, 1918; Nickel, *et al*., 1977; McLelland, 1990) to prevent the inhalation of anything except air. The respiratory route, during swallowing, is occluded by closure of the laryngeal fissure by the *M. constrictor glottides* (King, 1993). The positioning of the tongue root would appear to assist in sealing the rostral aspect of the larynx during closure of the glottis, almost assuming the role of an epiglottis. An epiglottis, however, is not present in birds (MacAlister, 1864; 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). Koch (1973) considers folds opposite the tongue base (i.e. tongue root) to be a form of rudimentary epiglottis. Indeed, it seems plausible that in birds with such a wide glottis (emu and ostrich) a structure would be necessary to assist in closure of the glottis. Owen (1879) describes a fold in the base of the kiwi tongue which can be retracted to cover the glottis. A fold or pocket has also been described at the base of the tongue body in the ostrich (see Chapter 4, Table 4.1). However, the only function attributed to this fold is the production of mucus (Tivane, 2008). Further studies will be required to determine whether the lingual pocket of the ostrich may perform a similar function to that of the kiwi (Owen, 1879).

A unique feature of the emu larynx is the presence of 3-5 raised folds situated immediately caudal to the tongue root. The function of these folds is unknown and their presence was not depicted in the illustration of the emu laryngeal entrance by Faraggiana (1933). The shape of the glottis of the emu observed in the present study differs from that depicted by Faraggiana (1933) and Bonga Tomlinson (2000). Whereas Faraggiana (1933) depicts the glottis with a constriction in the midline, Bonga Tomlinson (2000) shows the glottis as oblong and more similar to that of the ostrich (Bonga Tomlinson, 2000). None of these features were noted in the specimens studied. From the present observations the emu glottis is defined as being narrow caudally and widening rostrally as the arytenoid cartilages diverged. Reports in the literature indicate that the shape of the laryngeal mound and glottis differs between the ratites. These observations are compared with the results of the present study in Table 2.1.

Many bird species display papillae on the laryngeal mound caudal to the glottis (King and McLelland, 1984; Bailey *et al.*, 1997; McLelland, 1989). The laryngeal mound of ratites, however, is described as being smooth (McLelland, 1989), a feature also noted in the emu. Yet, as can be seen in the table below (Table 2.1), some of the ratites, namely the greater rhea and kiwis, possess papillae, even if ill-defined. Whether the lateral projections of the arytenoid cartilages in the ostrich (Tivane, 2008) can be considered as papillae remains debatable. The laryngeal mound is supported by the cricoid, two arytenoid (Kaupp, 1918; McLelland, 1989) and procricoid cartilages (totalling four) and their associated muscles, connective tissue and covering mucosa (McLelland, 1989). A similar situation is apparent in the emu (present study) and also in the ostrich (Tivane, 2008).

Though mainly associated and studied with the respiratory tract, the laryngeal mound of the emu fulfils both a respiratory and digestive function. In respect of its respiratory function, the laryngeal mound brings the glottis into contact with the choana allowing an open passage of air-flow directly from the external nares to the trachea and air sacs. The proximal oesophagus of the emu appears to lack an upper sphincter, in contrast to the situation in mammals, thus it is important that the oesophagus remains closed during respiration to prevent the movement of air into the digestive tract. The pharyngeal folds which overlie the caudal laryngeal mound (Nickel *et al.*, 1977) are reported to close off the oesophagus in birds during respiration. The substantial pharyngeal folds observed in the emu and also illustrated in the ostrich (Göppert, 1903; Porchescu, 2007; Tivane, 2008) would seemingly also fulfil this function.

Table 2.1 Comparative morphological features of the ratite laryngeal mound

Species	Shape of laryngeal mound	Shape of Glottis	Papillae on the caudal margin	Projections from the laryngeal cartilages
Emu (*Dromaius novaehollandiae*)	Raised, triangular with a flat rostral aspect[8]	Rhomboid-shaped[2] Wider rostrally and narrowing caudally[8]	No papillae on caudal edge[8]	Two small projections off the caudal arytenoid lips[8]
Ostrich (*Struthio camelus*)	Raised, oval, shield-shaped[6]	Wide, triangular[2], V-shaped[6]	Ill-defined papillae[2]	Arytenoids: Polygonal contours[2], three paired projections around the glottis[6]
Greater Rhea (*Rhea americana*)	Slopes caudally[2]	Thinner & longer than ostrich, triangular[2]	Three thick lobes on either side[2], Variable number[9, #]	Rounded, smooth contours, no projections[9]
Cassowary (*Casuarius casuarius*)	Raised, oval-shaped[7]	Short and narrow[7]	None[7]	Rounded contours, no projections[7]
Kiwi (*Apteryx australis mantelli*) [1,3]	Similar in outline to a Porcupine-fish swim-bladder[3]	Narrow[3]	Two elongate, square, smooth, thick, and apparently glandular folds or processes, the obtuse free margins face caudally[1]	-
(*Apteryx haasti*) [3]	Not as well-defined as above[3]	Large, with two 'glands' rostrally[3]	Two large, deeply divided, ovoid lobes, pits rostral to these structures[3]	-
(*Apteryx oweni*) [3]	Less defined than both above[3]	Partially obscured by caudal part of tongue[3]	Two fleshy, divided, oblong lobes with pitted surface[3]	-

(Underlined names indicate a sketch is supplied, bold indicates photographs.) [#]Extrapolated from 4, 5.

[1]Owen (1879), [2]Faraggiana (1933), [3]McCann (1973), [4]Bonga Tomlinson (2000), [5]Gussekloo and Bout (2005), [6]**Tivane** (2008), [7]Johnston (Personal communication), [8]**Present study**, [9]Personal observation.

In ratites the laryngeal mound also plays an important role in swallowing (digestive function) as it retracts, together with the tongue, during this process (Bonga Tomlinson, 2000; Gussekloo, 2006), a function which can also be attributed to the emu laryngeal mound. Furthermore, the tongue root and lips of the closed glottis fit neatly into the groove down the midline of the choana in the emu. During swallowing, when the tongue and laryngeal mound are retracted, these structures would be able to scrape food particles from the concavity of the choana and infundibular cleft thus cleaning this region and preventing the build-up of food particles which could possibly be inhaled or even occlude the internal nares.

2.4.4 Oropharyngeal roof

The oropharyngeal roof of the emu is divided into rostral pigmented and caudal non-pigmented regions, and two pharyngeal folds. The choana is situated in the non-pigmented region.

2.4.4.1 Pigmented and non-pigmented regions of the roof

The roof of the oropharynx in the emu is clearly divided into rostral pigmented and caudal non-pigmented regions. The caudal non-pigmented component housed the choana and infundibular cleft. Two distinct regions were also visible in the ostrich; however, in this species the entire roof was non-pigmented (Tivane, 2008). The transition between the two parts of the roof was abrupt in the emu (present study) and ostrich (Tivane, 2008). In the emu, a well-defined median palatine ridge ran the full length of the pigmented region, ending abruptly at the transition to the non-pigmented part. A median palatine ridge was also present in the ostrich (Tivane, 2008), represented a far more prominent structure than that of the emu, and ended abruptly between the two regions of the roof, as in the emu.

The rostral pigmented region of the roof of the emu was shown histologically to be aglandular (see Chapter 3), a similar finding to that in the comparable region in the ostrich (Tivane, 2008). The caudal non-pigmented region of the roof of the emu represented the glandular portion (see Chapter 3), which was again similar to the situation in the ostrich (Tivane, 2008). The caudal part of the roof of the greater rhea is also reported to be glandular (Feder, 1972).

The entire oropharyngeal roof in the emu was smooth and, with the exception of the median palatine ridge, showed no evidence of papillae or rugae. There were also no papillae or rugae present on the oropharyngeal roof of the ostrich (Tivane, 2008), greater rhea (Gussekloo and Bout, 2005) and kiwi (Owen, 1879). This is contrary to the situation in most birds were papillae and rugae are commonly present (see for example, Owen, 1879; Barge, 1937; Calhoun, 1954; McLelland, 1975, 1979, 1990; Bailey *et al*., 1997).

2.4.4.2 Choana

The choana of the emu was a triangular-shaped structure situated in the caudal non-pigmented region of the roof. In ratites, including the emu (present study) and ostrich (Göppert, 1903; Porchescu, 2007; Tivane, 2008), and in herons and ducks (Barge, 1937; McLelland, 1979) the choana is restricted to the caudal part of the roof and is short. In most other birds the choana is a longer structure consisting of a rostral slit and a wider caudal part (Barge, 1937; McLelland, 1975, 1979; Nickel *et al*., 1977; Bailey *et al*., 1997). The rostral slit is often closed off by the dorsum of the tongue (McLelland, 1975; Nickel *et al*., 1977; Bailey *et al*., 1997) whereas the caudal part overlies the glottis during respiration (Nickel *et al*., 1977).

The shape of the choana differs between the ratites and is compared in Table 2.2. The choana of palaeognaths is reported to be wide and triangular or cordiform while that of neognathous birds is slit-like (Pycraft, 1900). In the duck and goose however, the choana is a short wide oval (McLeod, 1939; Koch, 1973). Although the choana of ratites is divided by a septum (Pycraft, 1900) it appears that the grooved septum observed in the emu is unique.

The choana of the emu formed the communication between the nasal and oropharyngeal cavities as reported in other birds (Pycraft, 1900; Barge, 1937; Koch, 1973; King and McLelland, 1984; Bailey *et al*., 1997).

Caudal to the choana in the emu (as in other ratites), a cleft was formed between the pharyngeal folds, the infundibular cleft. This cleft was less obvious in its origin than that of the ostrich, although its origin in the greater rhea is also difficult to determine (see Table 2.2). In birds the infundibular cleft houses the common opening of the paired Eustachian tubes (Pycraft, 1900; McLeod, 1939; Ziswiler and Farner, 1972; McLelland, 1975, 1979; King and McLelland, 1984; Tivane, 2008) although in ratites each Eustachian tube is reported to open independently into the infundibulum (McLelland, 1993). This was not confirmed in the present study.

Table 2.2

Comparative features of the ratite choana, infundibular cleft and pharyngeal folds

Species	Choana	Infundibular cleft	Pharyngeal folds
Emu[5, 8] (*Dromaius novaehollandiae*)	Triangular – Two oblong slits following the lateral triangle edge, divided by a ridge with a median groove.[8]	Deep, grooved with no clear distinction from the groove in the midline of the choana.[8]	Two large overlapping U-shaped folds with rounded caudal edges and pitted ventral surfaces. Small projection on the caudo-lateral edge forming a pocket with the pharyngeal fold.[8] Similar to Darwin's rhea with small flaps laterally.[5]
Ostrich[3, 5, 6, 7] (*Struthio camelus*)	Bell/inverted V-shaped depression with prominent mucosal ridge in the midline[7, +]	Clear point of origin caudal to the choana.[+] Crater-like depression caudal to the crescent-shaped ridge of the choana.[7]	Two large folds with rounded caudal edges, pitted ventral surface.[+, 7] Blunt and U-shaped.[5]
Greater Rhea[2, 4, 9] (*Rhea americana*) Darwin's rhea[5] (*Pterocnemia pennata*)	Elliptical to teardrop-shaped with the median septum extending about half the length.[*, 9] -	Very wide, essentially forming the caudal half of the choana.[9] -	Rudimentary, very small, firmly attached and no free caudal edge. Caudo-lateral edge has a small indentation.[9] Pointed V-shaped tips[5]
Kiwi[1] (*Apteryx australis*)	Two linear slits, close together, parallel to the beak axis[1]	Straight, short and clearly defined.[#]	Two rectangular folds, with an undulating caudal free end.[#]

(Underlined names indicate a sketch is supplied, bold indicates photographs.) #Extrapolated from 1. *Extrapolated from 2, 4. +Extrapolated from 3, 6.

[1]<u>Owen</u> (1879), [2]<u>Pycraft</u> (1900), [3]<u>Göppert</u> (1903), [4]<u>Gussekloo and Bout</u> (2005), [5]Cho *et al*. (1984), [6]**Porchescu** (2007), [7]**Tivane** (2008), [8]**Present study**, [9]Personal observation.

2.4.4.3 Pharyngeal folds

The pharyngeal folds represented the most caudal structures of the oropharyngeal cavity in the emu. The comparative structure of the pharyngeal folds of ratites is described in Table 2.2. With the exception of the small ventro-lateral projection (see below), the pharyngeal folds of the emu most closely resemble those of the ostrich.

Cho *et al*. (1984) refer to the pharyngeal folds as tonsils and note that the shape of the tonsils differs between the ratites (see Table 2.2). The caudal edge of the emu pharyngeal folds is rounded yet Cho *et al*., (1984) describe the pharyngeal folds of Darwin's rhea as pointed and similar to that of the emu, yet no pointed tips were observed in any of the emu specimens studied. The emu pharyngeal folds seem unique amongst the ratites in that they possess an extra feature in the form of a small ventro-lateral projection which forms a pocket between its ventral surface and the dorsal surface of the pharyngeal fold.

2.4.5 Proximal cervical oesophagus

The proximal cervical oesophagus of the emu, after its origin dorsal to the trachea, soon occupied a position to the right of the trachea. This is similar to the finding in other ratites (Fowler, 1991), namely the ostrich (Bezuidenhout, 1999; Tivane, 2008), kiwi (Owen, 1879) and for birds in general (Pernkopf and Lehner, 1937; McLeod, 1939; Koch, 1973; McLelland, 1975, 1979; Nickel *et al*., 1977; King and McLelland, 1984; Bailey *et al*., 1997).

The avian oesophagus is a long distensible tube (Calhoun, 1954; Ziswiler and Farner, 1972; Koch, 1973; Hodges, 1974; Nickel *et al*., 1977; McLelland, 1979; King and McLelland, 1984; Bailey *et al*., 1997; Gussekloo, 2006) demonstrating a longitudinally folded mucosa (Pernkopf and Lehner, 1937; Warner *et al*., 1967; Ziswiler and Farner, 1972; Nickel *et al*., 1977; McLelland, 1979; King and McLelland, 1984; Bailey *et al*., 1997; Gussekloo, 2006). It is also apparent that longitudinal folds of the oesophageal mucosa are a feature of the ratite oesophagus and which is therefore also highly distensible (Gadow, 1879; Pernkopf and Lehner, 1937; Tivane, 2008 (ostrich); Gadow, 1879; Feder, 1972 (greater rhea); Owen, 1879; Pernkopf and Lehner, 1937 (kiwi); Meckel, 1829; Gadow, 1879 (cassowary)). As previously noted by Herd (1985), the lumen of the proximal oesophagus of the emu, exhibits a series of well-developed longitudinal folds. An average number of 16 folds were present in the emu oesophagus in comparison to 10-12 in the greater rhea (Feder, 1972) and 12 in the ostrich (Tivane, 2008).

The oesophagus transports food from the oropharynx to the stomach (Hodges, 1974; Davies, 1978) and performs an important storage function (Ziswiler and Farner, 1972). The avian oesophagus is generally greater in diameter (Ziswiler and Farner, 1972; McLelland, 1979; King and McLelland, 1984; Gussekloo, 2006) than that of mammals (McLelland, 1979; King and McLelland, 1984; Gussekloo, 2006). This is due to the limited ability of birds to break down their food orally (Gussekloo, 2006). The distensibilty of the oesophagus is particularly important in birds which swallow bulky food (Ziswiler and Farner, 1972; Gussekloo, 2006). A distensible oesophagus would be of great importance in the emu which employs the cranioinertial feeding method, as described by Bonga Tomlinson (2000). That the emu possess a distensible oesophagus is evident from the prominent folded mucosa it displays (see above) and also by virtue of the relatively large diameter of the proximal region. In the cranioinertial feeding method food is passed directly from the bill tips to the oesophageal entrance resulting in the oesophagus receiving completely unaltered food items and even stones in the case of the ostrich (Huchzermeyer, 1998) The proximal oesophagus is more distensible and folded than the distal parts in the ostrich (Tivane, 2008) and kiwi (Owen, 1879), possibly to accommodate the feeding method mentioned above. Another important adaptation of the oesophagus for swallowing large food items is that of lubrication (Ziswiler and Farner, 1972; Hodges, 1974). This is made possible in the emu by the ubiquitous presence of mucus-secreting glands in the lamina propria (Herd, 1985; Chapter 3). Thus the proximal oesophagus of the emu displays three main adaptations allowing it to receive and handle large, orally unaltered, food items: 1.) the diameter is relatively large, 2.) the mucosa is longitudinally folded allowing great distensibility and 3.) the numerous mucus-secreting glands provide copious amounts of mucus to lubricate the lumen and food for ease of transport.

2.5 REFERENCES

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2.6 FIGURES

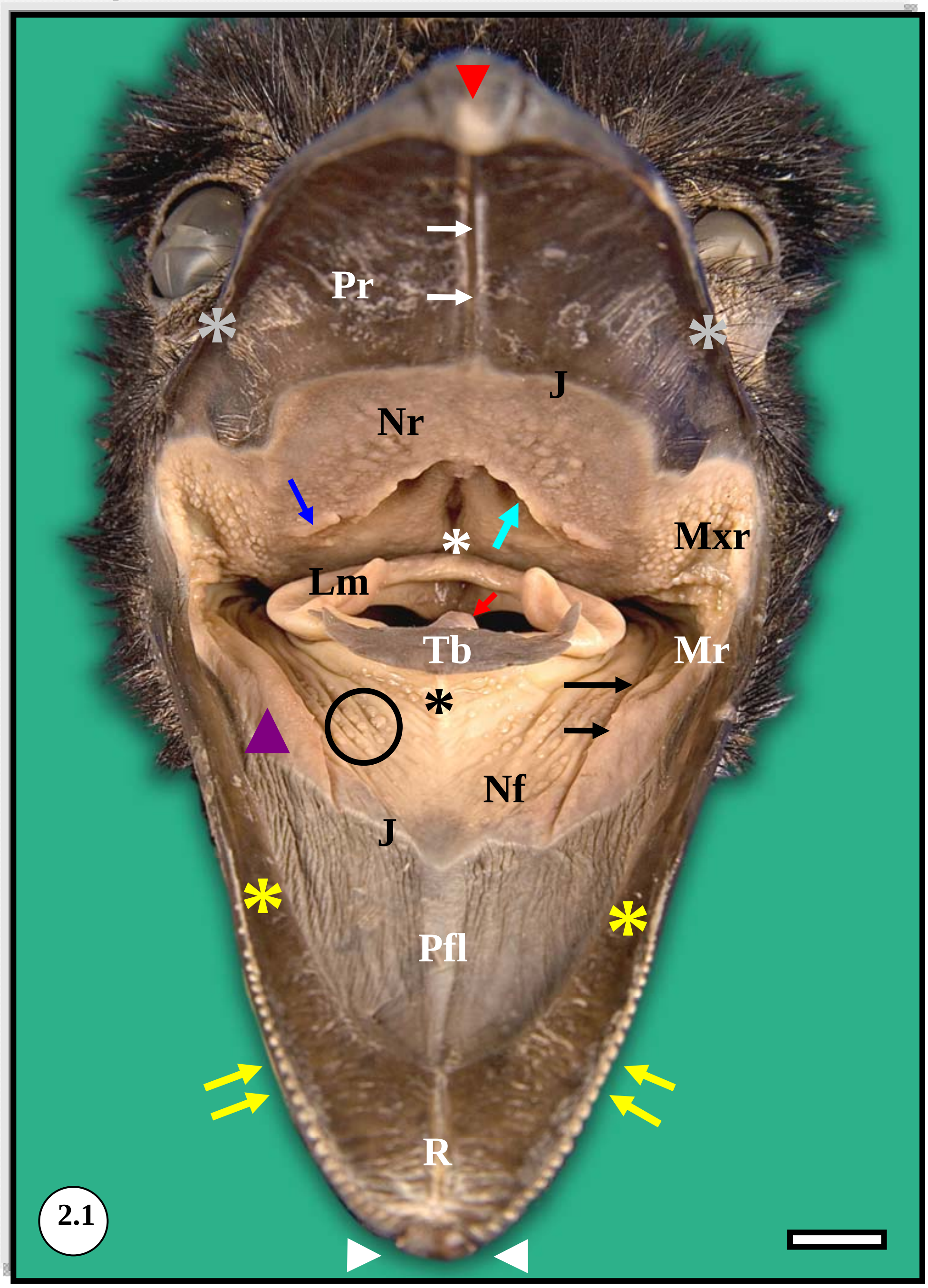


Figure 2.1: Rostral view of the full gape of the emu illustrating the major gross anatomical features visible. The oropharynx is divided into a rostral pigmented floor (Pfl) and roof (Pr) and caudal non-pigmented floor (Nf) and roof (Nr), bordered by the maxillary (grey *) and mandibular (yellow *) rhamphotheca. The serrations on the mandibular tomium are clearly visible (double yellow arrows) as are the junctions (J) between the pigmented and non-pigmented regions. Other noticeable features are the maxillary (red arrowhead) and mandibular (white arrowheads) nails, mandibular rostrum (R), large lateral mucosal fold (purple arrowhead) with associated medial facing groove or recess (black arrows), the tongue frenulum (*), body (Tb) and root (red arrow), nodules on the non-pigmented floor (encircled), laryngeal mound (Lm), mandibular (Mr) and maxillary (Mxr) rictus, median palatine ridge (white arrows), choana (turquoise arrow), small mucosal fold lateral to the choana (blue arrow) and infundibular cleft (white *). Bar = 5mm.

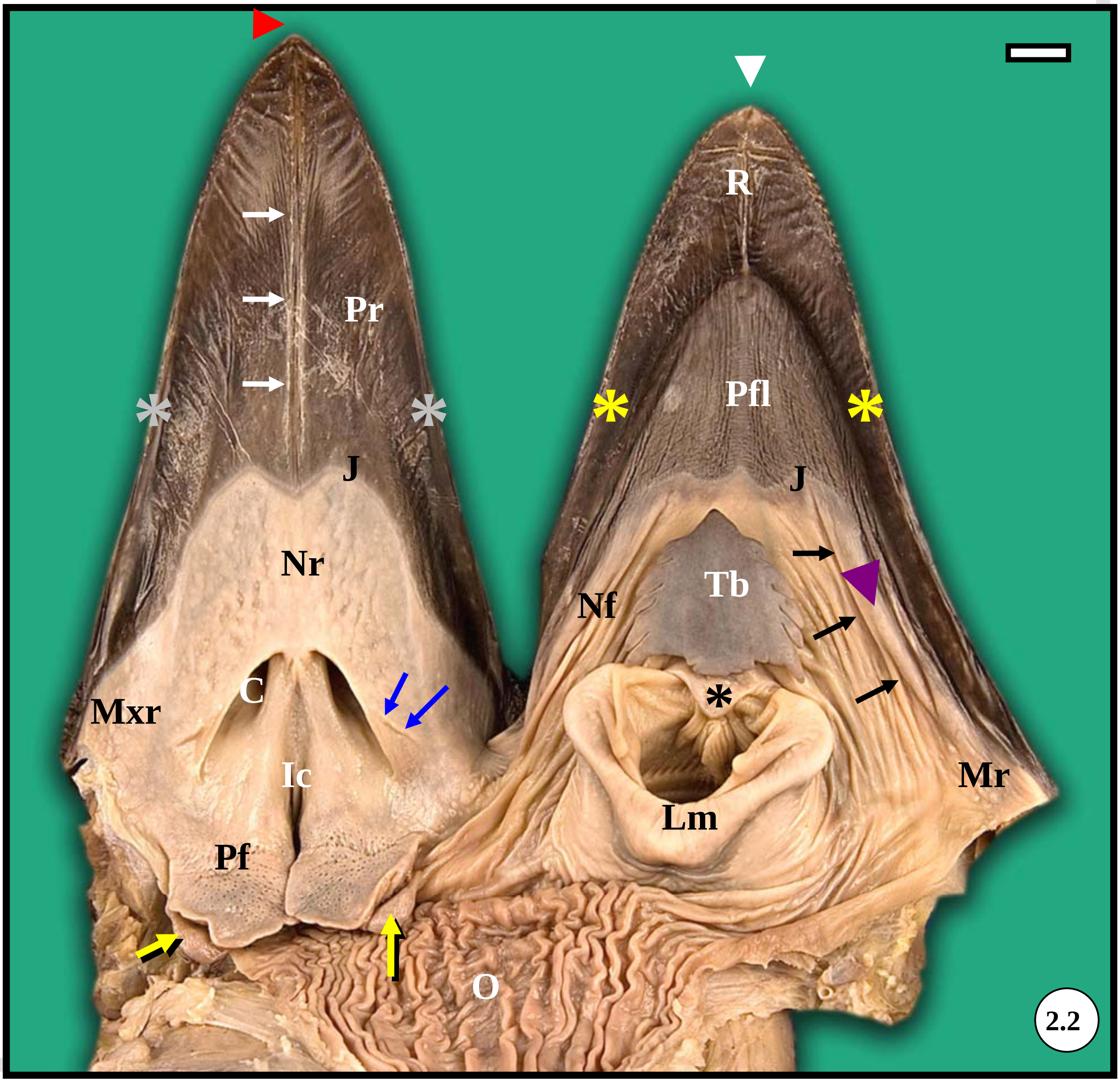


Figure 2.2: Gross anatomical features of the floor and roof of the emu oropharynx. The right commisure has been incised and the two components reflected. The oropharynx is divided into a rostral pigmented floor (Pfl) and roof (Pr) and a caudal non-pigmented floor (Nf) and roof (Nr), bordered by the maxillary (grey *) and mandibular (yellow *) rhamphotheca. Note the smooth rostral and pitted caudal components of the pharyngeal folds (Pf) with the caudo-lateral tissue projection (yellow arrows), and the convoluted longitudinal folds of the proximal oesophagus (O). Other noticeable features are the maxillary (red arrowhead) and mandibular (white arrowhead) nails, mandibular rostrum (R), junctions between pigmented and non-pigmented regions (J), large lateral mucosal fold (purple arrowhead) with associated medial facing groove or recess (black arrows), the tongue body (Tb) and root (black *), laryngeal mound (Lm), mandibular (Mr) and maxillary (Mxr) rictus, median palatine ridge (white arrows), choana (C), small mucosal fold lateral to the choana (blue arrows) and infundibular cleft (Ic). Bar = 5mm.

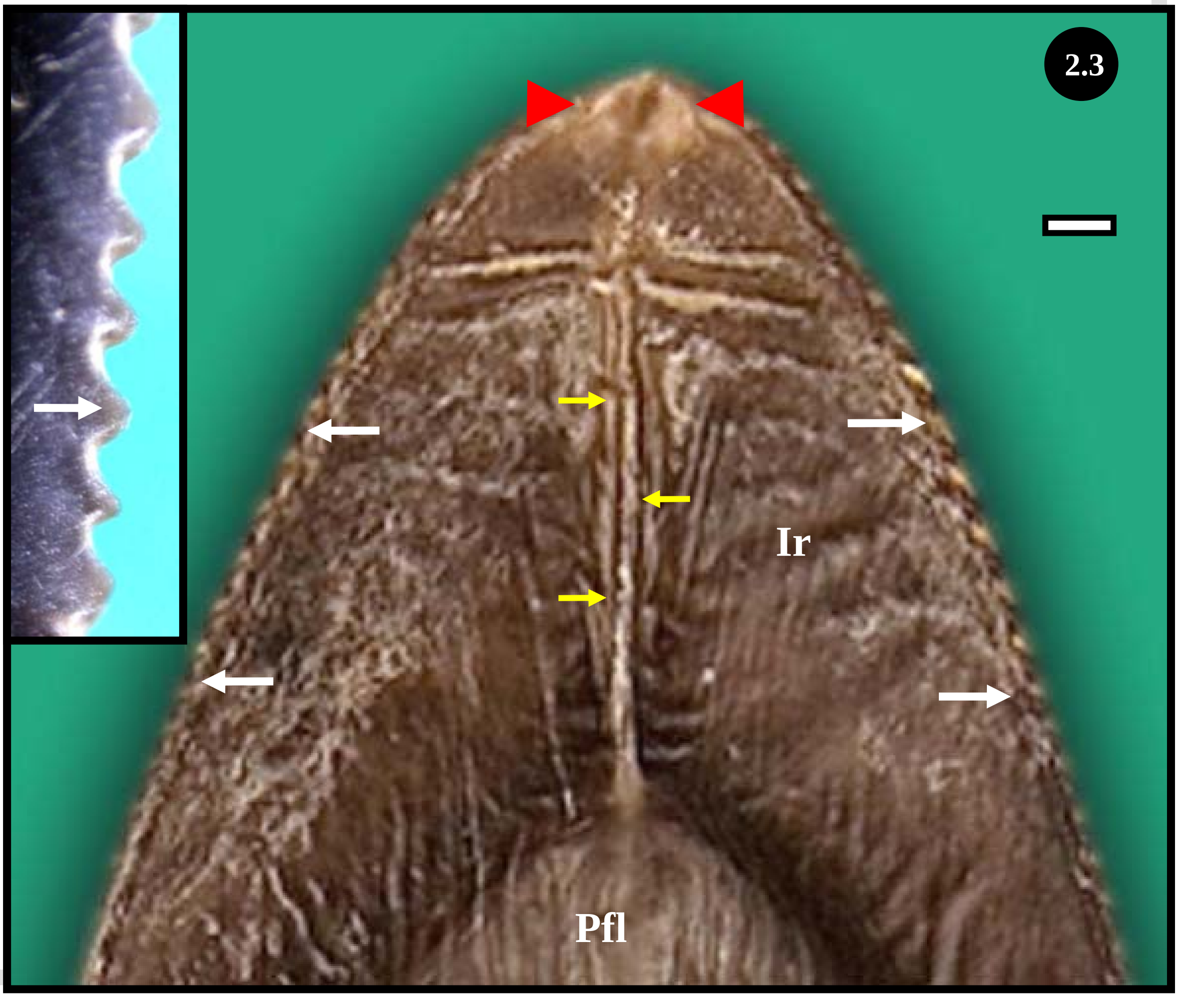


Figure 2.3: The flattened rostral plate formed by the internal rhamphotheca (Ir) overlying the mandibular rostrum. Note the median sulcus (yellow arrows) extending from the mandibular nail (red arrowheads) to the pigmented interramal floor (Pfl). Rostral lamellae (white arrows). Inset: High magnification of the rostral lamellae (white arrow) present on the mandibular tomium. Bar = 1mm.

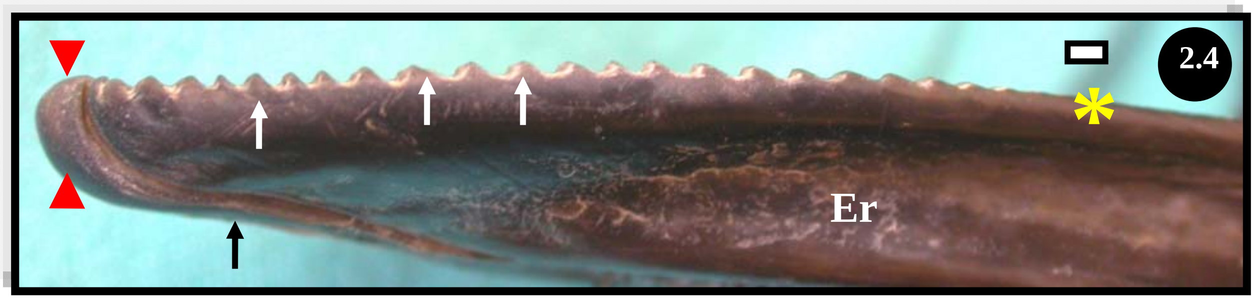
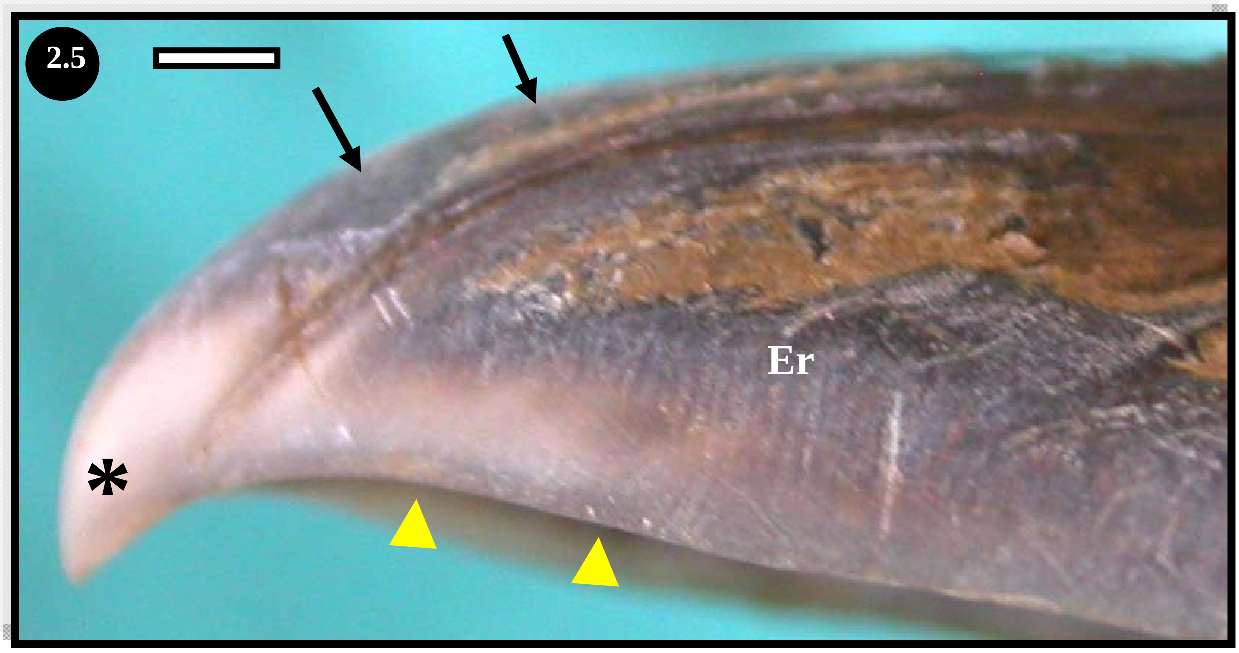


Figure 2.4: Lateral profile of the external mandibular rhamphotheca (Er) showing the smooth mandibular tomium (yellow *) proceeding rostrally to the serrated cutting edge (white arrows). Note how the *gonys* (black arrow) ends rostrally as the mandibular nail (red arrowheads). Bar = 1mm.



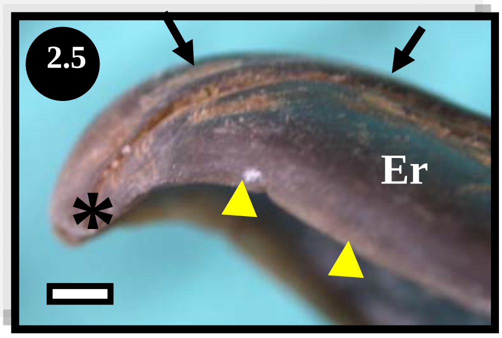


Figure 2.5: The external maxillary rostrum displaying the maxillary nail (*), the *culmen* (black arrows) on the dorsal surface of the beak and the sharp maxillary tomium (yellow arrowheads). External rhamphotheca (Er). Bar = 2mm.

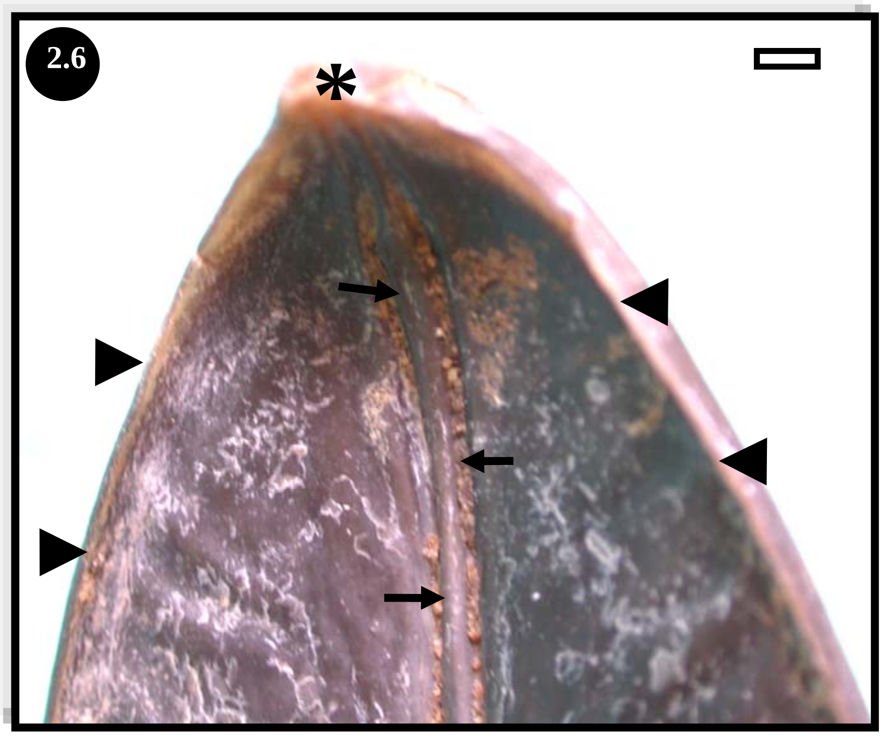


Figure 2.6: Maxillary rostrum, intra-oral view. The maxillary nail (*) can be seen projecting below the concavity (area between arrowheads) of the maxillary rostrum. Tomia (arrowheads) and median palatine ridge (arrows). Bar = 1mm.

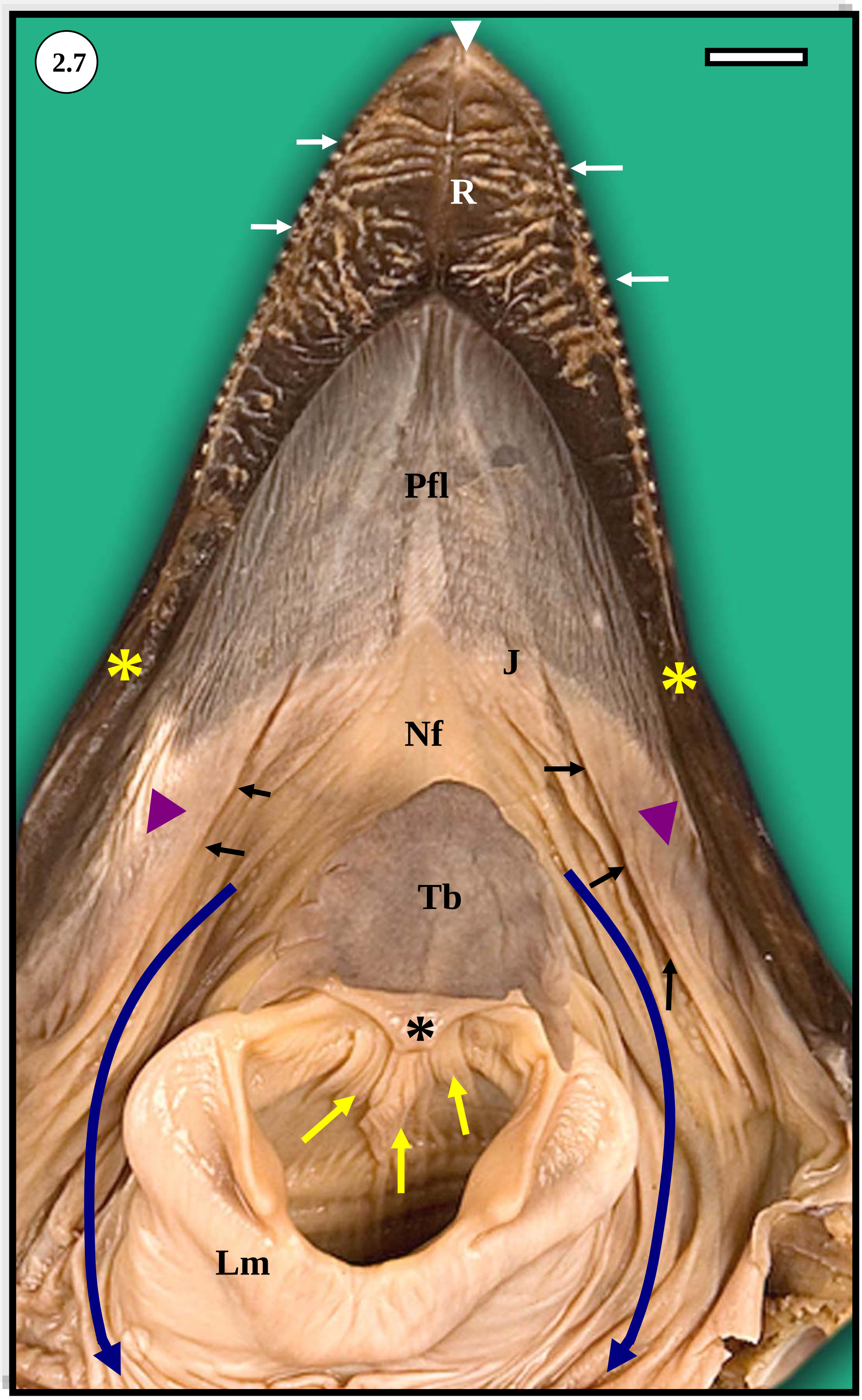
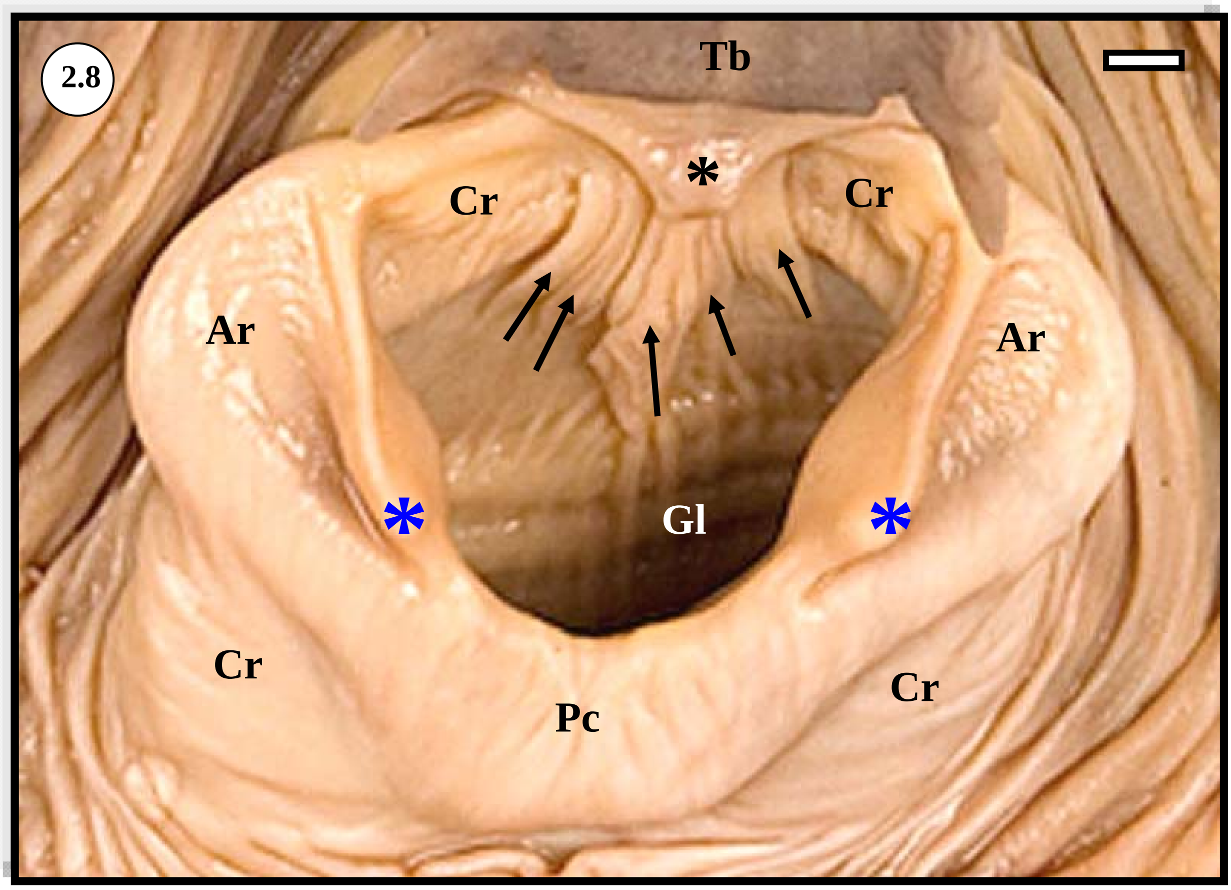


Figure 2.7: Gross anatomical features of the floor of the oropharynx. The interramal region is divided into a rostral pigmented (Pfl) and a caudal non-pigmented (Nf) part with a clear junction (J) marking the transition. The caudal region contains the tongue body (Tb) and root (*) and laryngeal mound (LM). The large lateral folds of the caudal floor are indicated (purple arrowheads) together with their associated medially opening groove or recess (black arrows). The smaller folds (blue arrows) follow the contours of the laryngeal mound. Mandibular rostrum with transverse ridges (R), mandibular nail (white arrowhead), rostral lamellae (white arrows) and smooth tomia (yellow *), mucosal folds at laryngeal entrance (yellow arrows). Bar = 5mm.



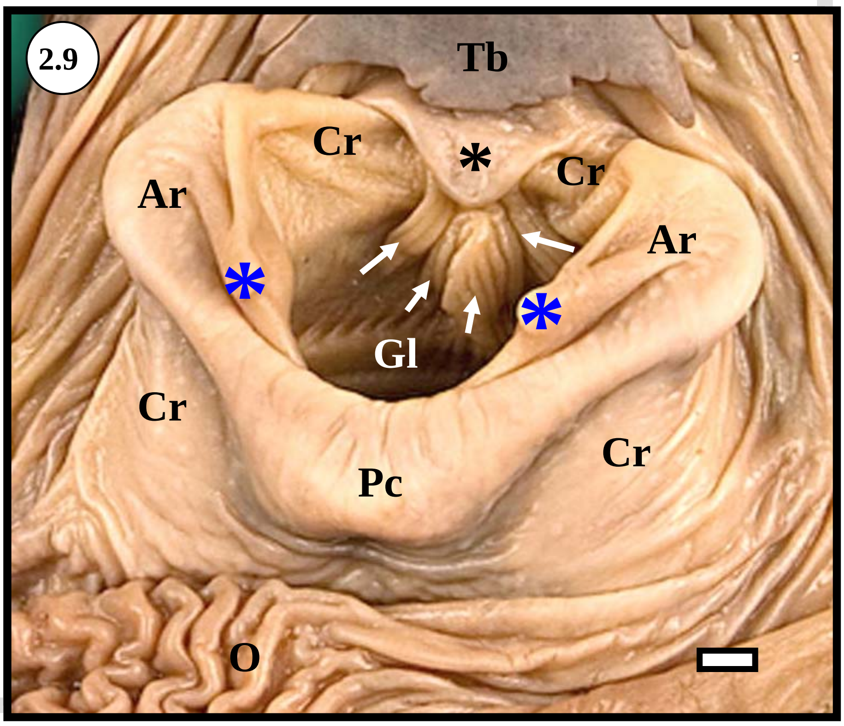


Figure 2.8 and 2.9: Dorsal view of the laryngeal mound of the emu showing the covering of smooth mucosa and the wide glottis (Gl). The circular cricoid (Cr), two dorsal arytenoid (Ar) and procricoid (Pc) cartilages support the larynx. Note the tongue root (black *) overlapping the glottis, the prominent mucosal folds (arrows) caudal to the root and the protuberances (blue *) projecting off the medial lips of the arytenoid cartilages. Tongue body (Tb), proximal oesophagus (O). Bar = 2mm.

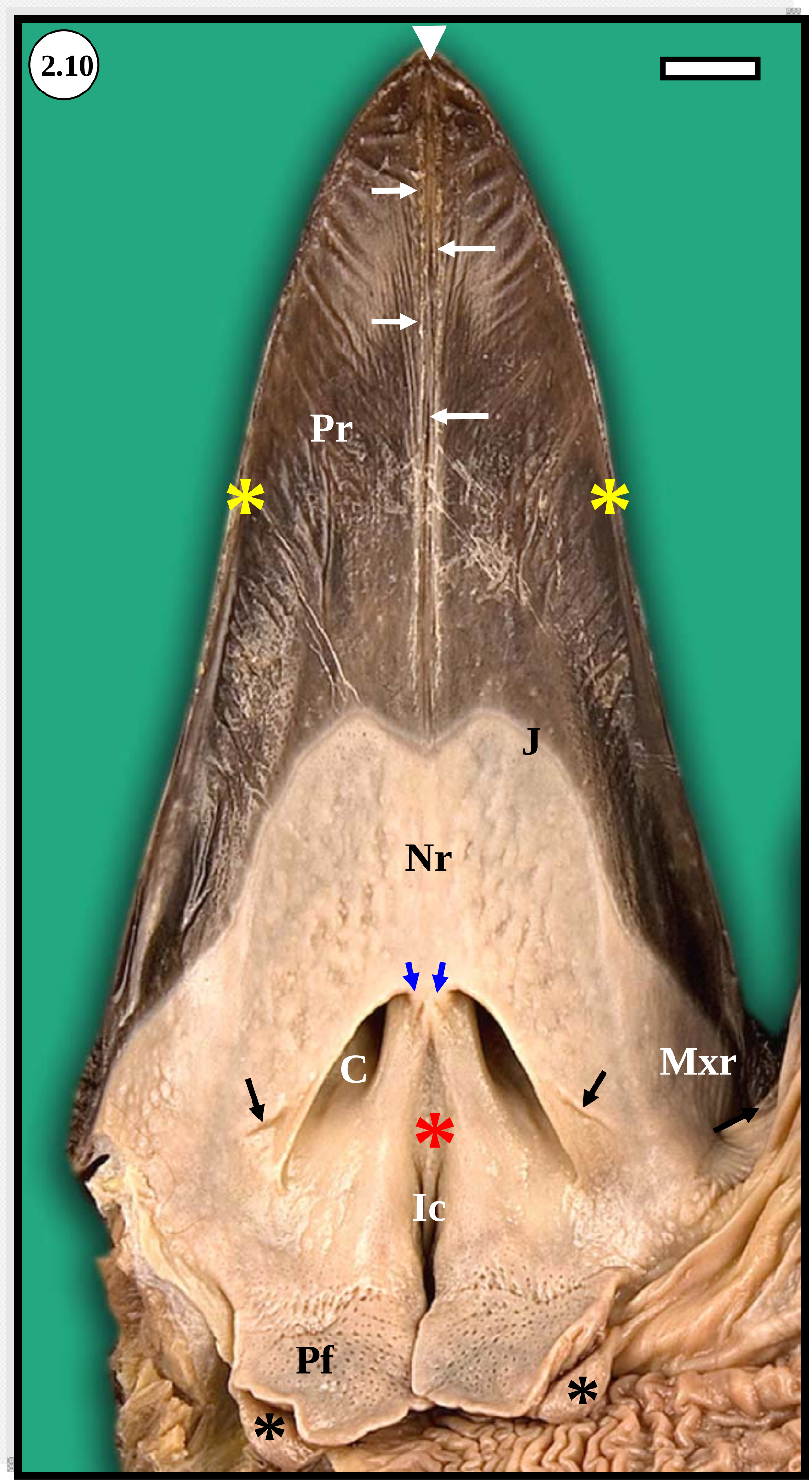


Figure 2.10: Gross anatomical features of the roof of the oropharynx of the emu. The junction (J) between the pigmented (Pr) and non-pigmented regions of the roof (Nr) is sharply demarcated. The pigmented roof is similar in colour to the maxillary rhamphotheca (yellow *) and displays a median palatine ridge (white arrows) down its midline. The division between the rhamphotheca and pigmented region is obscure. The choana (C) flanked by two small folds laterally (black arrows) and small raised nodules rostrally (blue arrows) is situated in the caudal non-pigmented roof. The pharyngeal folds (Pf) and their lateral projections (black *) are seen to form the most caudal extent of the oropharyngeal roof. Maxillary nail (white arrowhead), maxillary rictus (Mxr), median grooved septum (red *), infundibular cleft (Ic). Bar = 5mm.

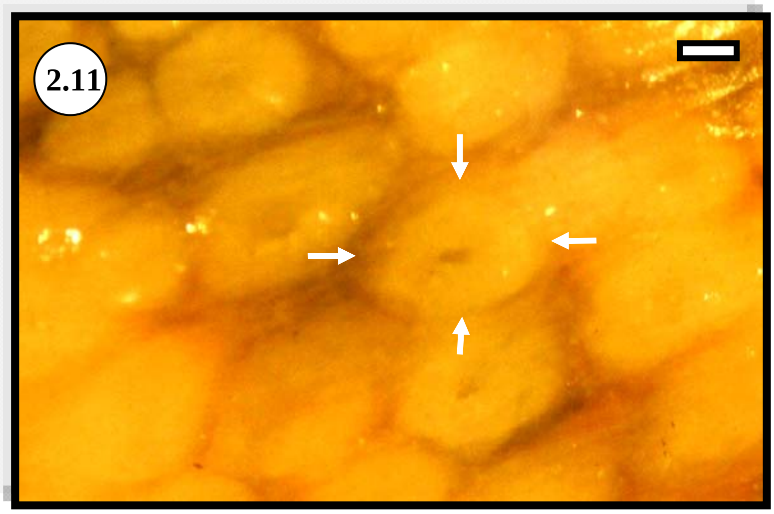


Fig. 2.11: High magnification of the doughnut-shaped structures lying beneath the mucosa of the non-pigmented roof. The outline of a single doughnut is shown by the white arrows and represents a glandular unit with the dark central spot indicating the gland opening. Bar = 200µm.

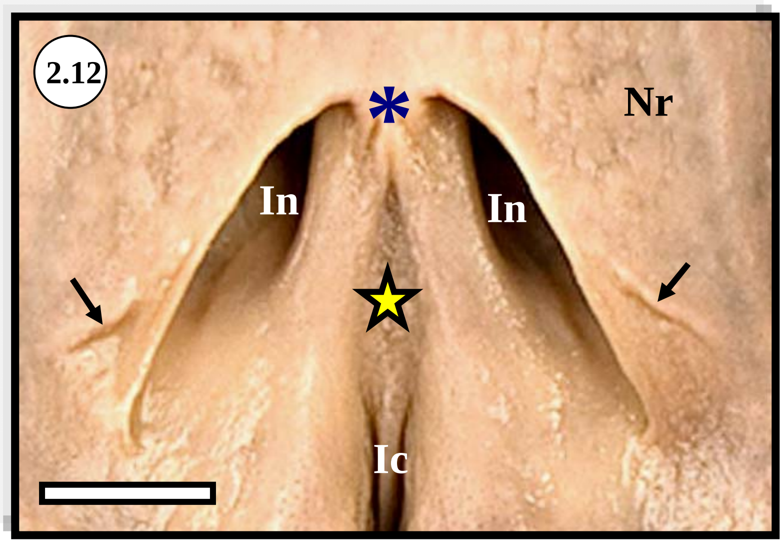


Fig. 2.12: The triangular choana of the emu with the two internal nares (In) separated by a median grooved septum (yellow star). The small nodules (blue *) are seen at the rostral choanal extremity. Non-pigmented roof (Nr) infundibular cleft (Ic), caudo-lateral mucosal folds (arrows). Bar = 5mm.

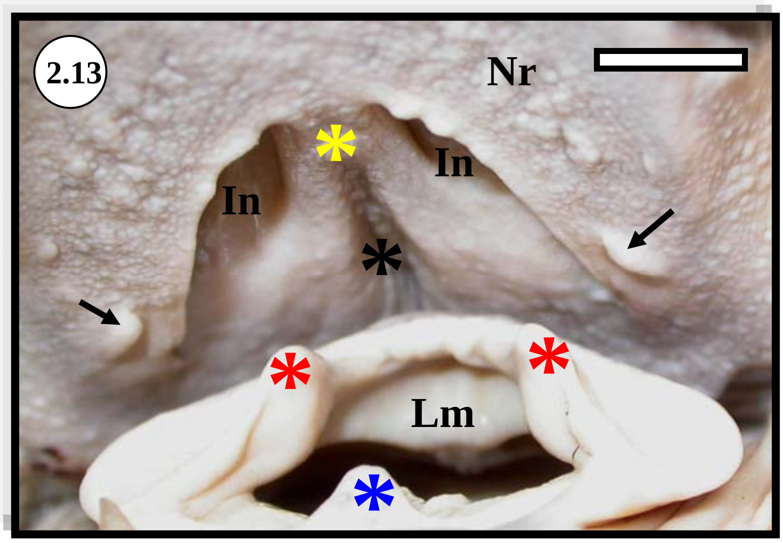


Fig. 2.13: Caudal view of the choana and laryngeal mound illustrating the functional relationship of the two structures. When the glottis is closed, the medial lips of the arytenoid cartilages (red *) and tongue root tip (blue *) align to move through the median grooved septum (black *) of the choana when the laryngeal mound (Lm) and the tongue (not shown) are retracted. Note the small mucosal folds (arrows) near the caudo-lateral edges of the choana. Non-pigmented roof (Nr), internal nares (In). Bar = 5mm.

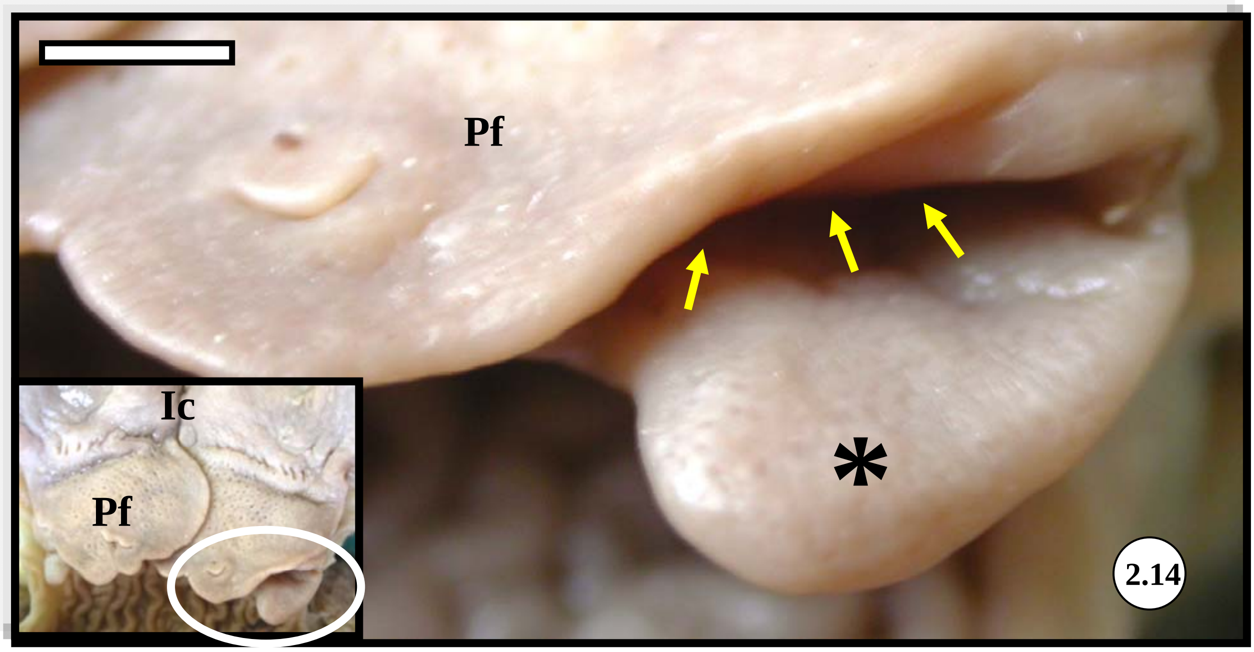


Figure 2.14: High magnification of the caudal pharyngeal fold (encircled area in inset). The caudo-lateral projection (*) forms a pocket or recess (yellow arrows) with the dorsal aspect of the pharyngeal fold (Pf). Note the medial overlapping of the free caudal aspect of the pharyngeal folds in the inset. Infundibular cleft (Ic). Bar = 1mm.

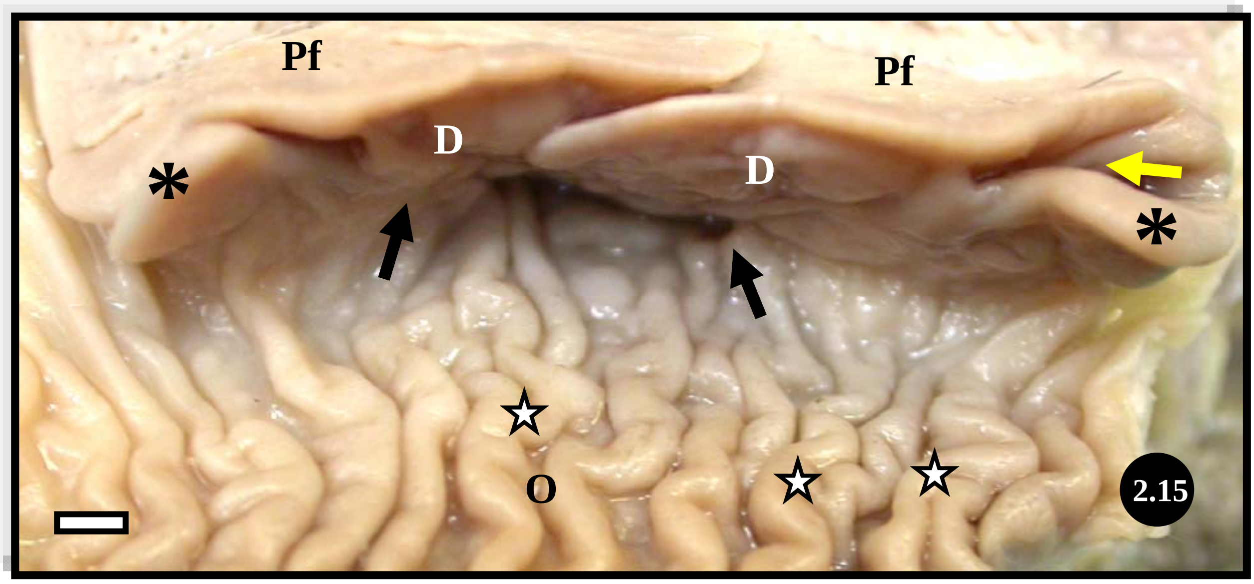


Figure 2.15: Caudal limit of the oropharynx showing the dorsal aspect (D) of the pharyngeal folds (Pf) forming a retropharyngeal recess (black arrows) where the mucosa of the folds is reflected and continued caudally as the proximal oesophagus (O). Note the wavy appearance of the oesophageal folds which branch and anastomose (starts). Lateral tissue projection (*), pocket or recess (yellow arrow). Bar = 1mm.

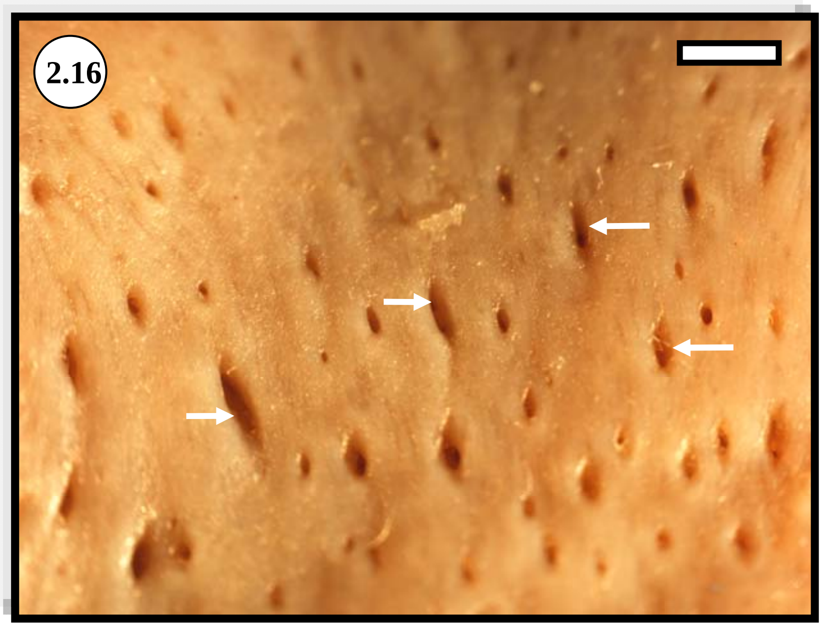


Fig. 2.16: The ventral surface of the caudal free part of the pharyngeal fold. The deeply pitted surface is made up of numerous large openings (white arrows) of underlying glands. Bar = 2mm.

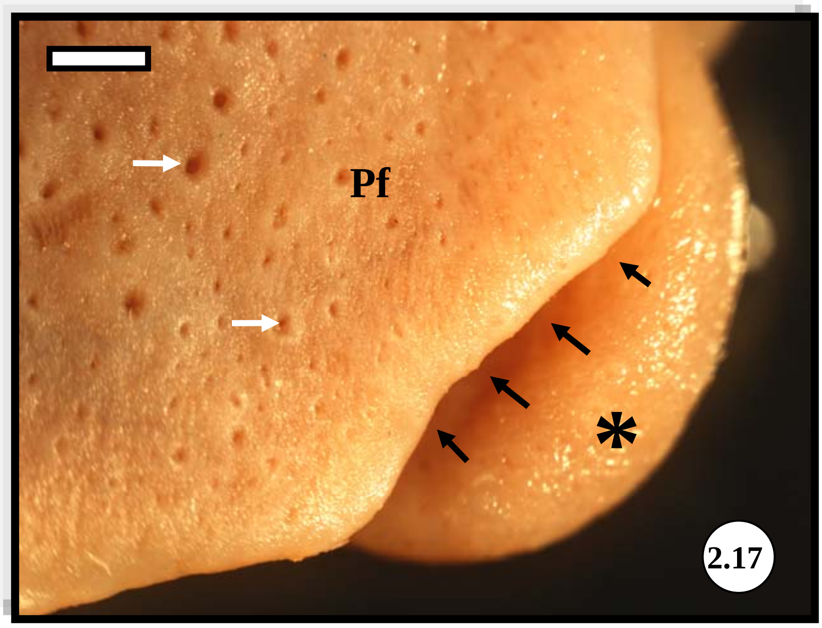


Fig. 2.17: Ventral view of the lateral projection (*) of the caudal part of the pharyngeal fold (Pf). A pocket or recess (black arrows) is formed between the fold and the projection. Gland openings (white arrows). Bar = 1mm

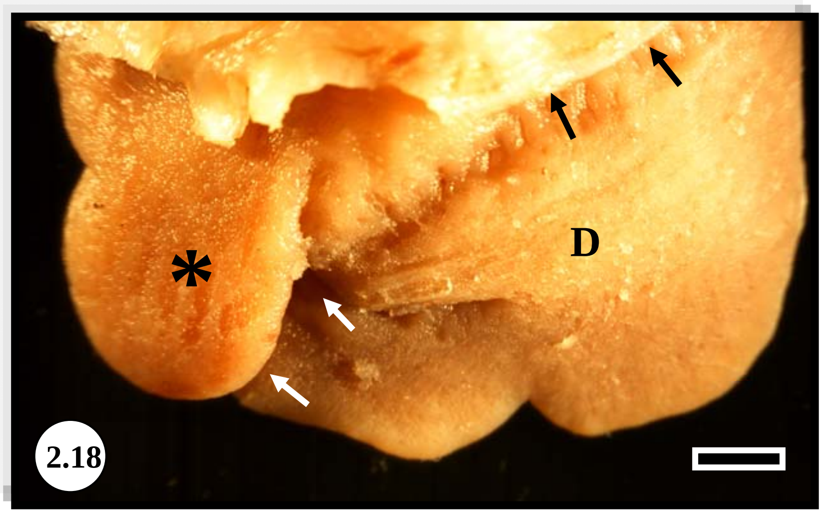


Fig. 2.18: Dorsal view (D) of the caudal part of the pharyngeal fold and projection (*). The pocket or recess is indicated by the white arrows and the reflection of the mucosa to form the retropharyngeal recess is indicated by the black arrows. Bar = 2mm.

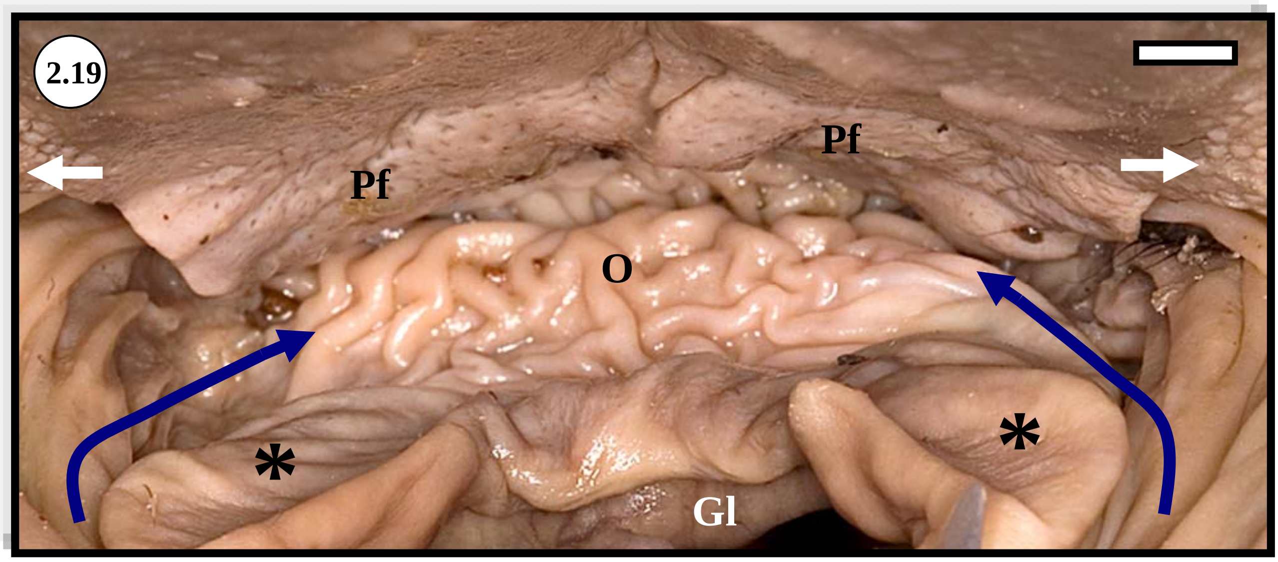


Figure 2.19: The entrance to the proximal oesophagus (O) seen from the gape of the emu (laryngeal mound depressed). The mucosal folds of the caudal oropharyngeal floor are indicated by the curved blue arrows. Pharyngeal folds (Pf), maxillary rictus with nodules (white arrows), arytenoid cartilages (*), glottis (Gl). Bar = 2mm.

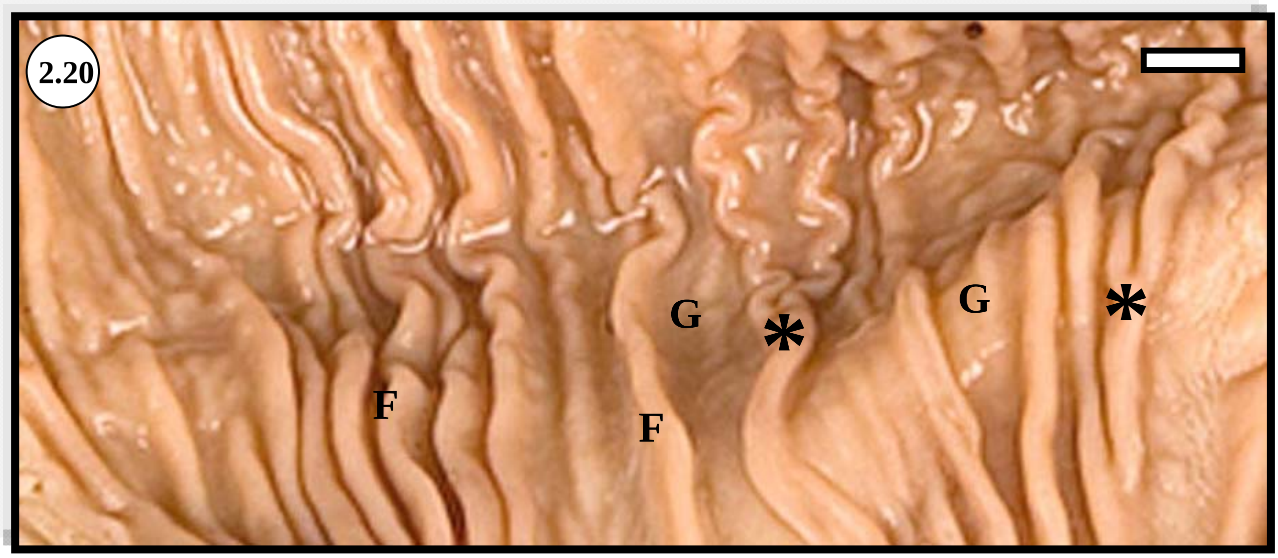


Figure 2.20: The proximal oesophagus showing the highly longitudinally folded nature of this region. Note the wavy appearance of the folds (F) and occasional branching and anastomosing (*). Intervening grooves (G). Bar = 2mm.