

Descriptive anatomy of the subcutaneous air diverticula in the Northern Gannet *Morus bassanus*

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Abstract

Northern Gannets *Morus bassanus* typically forage by diving from high above the water surface. Their subcutaneous (s-c) tissues are invested by an elaborate system of air diverticula that presumably function in cushioning the impact of their entry into the water. The anatomical details of this system were studied by dissection and latex injection in 15 carcasses of these birds. The s-c air diverticula consist mainly of two independent systems of intercommunicating compartments that are bilaterally symmetrical, cover the ventral and lateral regions of the trunk and the proximal portions of the wings and legs, and communicate with the ipsilateral region of the clavicular respiratory air sac. This communication, which opens into the axillary region, is through a narrow gap between the subcoracoideus and coracobrachialis caudalis muscles. Two other, smaller, independent systems of s-c air diverticula, also bilaterally symmetrical, may contribute to cushioning the Northern Gannet's body during its dives: one at the thoracic inlet, which communicates with the corresponding side of the clavicular air sac, and the other along the neck, which communicates with the nasal cavities and the choanal opening. Further work is required to define more precisely the function of these extensive air diverticula and air circulation within them.

Introduction

The avian respiratory system is the most efficient among those of all air-breathing vertebrates and is unique in its basic structure (King & McLelland 1984). Its extensive system of air sacs allows a near-continuous flow of fresh air through the pulmonary air capillaries at countercurrent to the blood circulation and throughout the respiratory

Footnote: Definition of terms used in the text for anatomical orientation: cranial, toward the head; caudal, toward the tail; ventral, toward the front of the body; dorsal, toward the back of the body; proximal, closer to the centre of the body; distal, farther from the centre of the body; medial, closer to the body's midline; lateral, farther from the body's midline; rostral, toward the beak or tip of the beak.

cycle. Most avian species have four paired air sacs (cervical, cranial thoracic, caudal thoracic, abdominal) and one unpaired air sac (clavicular). Depending on the species, some of these air sacs can project complex systems of diverticula between muscles and into the subcutis and pneumatic bones of the trunk, pectoral and pelvic girdles, and limbs (McLelland 1989; O'Connor 2004). Some members of the order Pelecaniformes have an elaborate and extensive system of subcutaneous (s-c) air diverticula. Northern Gannets *Morus bassanus*, which typically forage by diving from heights of up to 30 m above water and reaching speeds of up to 100 km/h on impact with water, are thought to use these s-c air diverticula as a means of cushioning this impact (Montagu 1813; Gurney 1913; Nelson 1978). It is not known, however, whether these diverticula are inflated voluntarily prior to diving or whether air is simply prevented from exiting them as the bird hits the water. Regardless, an efficient communication is likely needed between the respiratory tract and the system of s-c air diverticula and among the various compartments of this system. Subcutaneous air diverticula were described, albeit only partially, many years ago in the Northern Gannet (Montagu 1813; Gurney 1913) and in the Brown Pelican *Pelecanus occidentalis* (Richardson 1939). According to the study of the Brown Pelican by Richardson (1939), the communication between the respiratory system, specifically the clavicular air sac, and the s-c air diverticula is located caudolaterally to the head of the coracoid bone and below the head of the humerus, 'primarily between the M [muscle] coracobrachialis posterior and the M subcoracoideus'. Similarly, in his study of the Northern Gannet, Gurney (1913), quoting C. B. Ticehurst, states that the s-c air diverticula communicate with the respiratory system by way of a passage just outside the coracoid bone and close to the tendon of the 'pectoralis minor muscle' ('M coracobrachialis posterior', according to Richardson (1939)). These authors also briefly describe the distribution of the s-c air diverticula along the ventral region of the trunk and down the thighs and wings and the separation of these diverticula between left and right sides of the body. The description of s-c air diverticula that they offer is, however, insufficient to fully understand the exact pattern of air flow among their various compartments.

The objective of this study was to provide a more detailed description, complemented by photographs, of the anatomy of the s-c air diverticula in the Northern Gannet than is currently available in the literature. More specifically, we describe the distribution of s-c air diverticula along the body and the communication between the system of s-c air diverticula and the respiratory system in this species. We also hypothesise that the wings' position may alter this communication as it changes from extended away from the body while flying and soaring to flexed against the body when diving. More specifically, we predict that wing flexion against the body closes the communication between the two systems, thus preventing air from escaping the s-c air diverticula, thus ensuring a firm cushion on impact.

Materials and Methods

Fifteen carcasses of Northern Gannets in a good state of preservation (ten adult, one immature and three full-grown hatch-year based on their plumage, one of undetermined age; six male, four female, five of undetermined sex) were dissected in the course of this study. The carcasses were of wild birds that had drowned in fishing nets, had died of emaciation/starvation, or had been euthanized because of a broken

limb. Two carcasses were refrigerated until used a few days later, whereas the 13 other carcasses were frozen at minus 20°C for a period varying between three weeks and 19 months (average, six months) prior to use. In 13 carcasses, a solution of either red or blue latex (Carolina Biological Supply, Burlington, NC, USA) was injected in various locations in order to make casts of the different cavities under study, i.e. respiratory air sacs and/or s-c air diverticula. Injection sites included: intrachoanal; intratracheal (via a small incision of the skin and tracheal wall in the mid-cervical region); and perihumeral, axillary, ventral, subclavicular and cervical regions of s-c air diverticula (via small skin incisions). In five instances, intratracheal injection was carried out while one wing was extended away from the body and the other flexed (folded) against the body. In each of these 13 cases, the carcass, if frozen, was completely thawed (over a period of 48h); latex was injected into the selected location, being allowed to settle strictly by gravity; and the carcass was frozen again for c.48h, in order to promote polymerisation of the latex solution (Tompsett 1970), and subsequently thawed for dissection. The amount of latex injected varied among the locations selected and was largest when latex was injected intratracheally, in which case up to 550 ml were used in order to adequately fill some of the respiratory air sacs. Within 48h following the start of dissection, the carcass (minus abdominal viscera) was immersed in a solution of 10% formalin in order to prevent decomposition. It was possible to make casts into two different locations in the same bird by using a latex solution of one colour, freezing the carcass for c.48h and thawing it in order to inject latex of the other colour. Two carcasses were dissected without prior latex injection in order to better examine the sites of origin and insertion of muscle masses particularly relevant to the anatomy of the s-c air diverticula. George & Berger (1966), Vanden Berge (1975), and Nickel *et al.* (1977) were consulted for muscle identification and terminology.

Results

Anatomical observations on the 15 Northern Gannets used in this study were consistent among all birds, with one exception pertaining to the possible role of wing flexion in air circulation (see below). According to these observations, the s-c air diverticula of this species consist mainly of two independent systems of intercommunicating compartments that extend from the respiratory tract, are bilaterally symmetrical along the cranio-caudal midline of the trunk and cover its ventral and lateral regions. Latex injected into the trachea easily fills most of the volume of the respiratory air sacs and their diverticula within the thoracic cavity. Latex further flows from what are interpreted as the left and right ventrolateral regions of the clavicular air sac into the axillary regions of the ipsilateral s-c air diverticula through a narrow gap between the subcoracoideus and coracobrachialis caudalis muscles (Figures 1 & 2). Both muscles are located immediately caudal to the coracoid bone. The subcoracoideus muscle originates on the inner (ventral) surface of the cranial region of the scapula and on the medial surface of the cranial region of the coracoid bone and inserts on the medial surface of the proximal humerus. The coracobrachialis caudalis muscle originates on the caudal region of the coracoid bone, primarily its lateral surface but with some fibres originating on its dorsal and ventral surfaces, and it inserts on the medial surface of the proximal humerus, proximal to the pneumatic foramen and distal to the insertion of the subcoracoideus muscle.

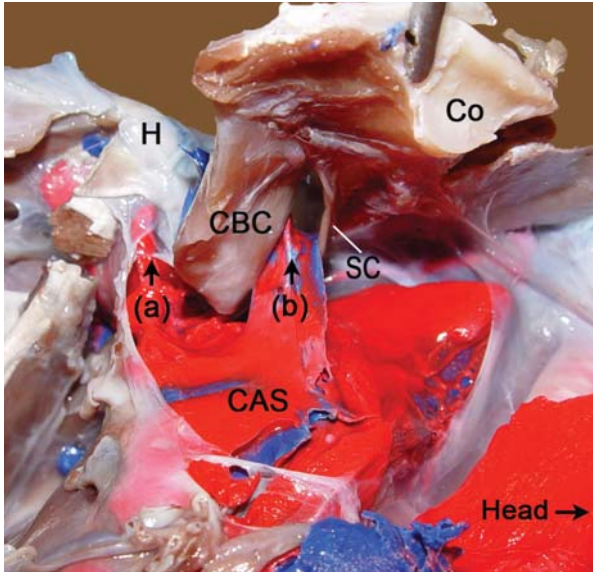


Figure 1. Right lateral view of the thoracic cavity of a Northern Gannet *Morus bassanus*. The head is directed to the right side of the Figure. Red latex injected via the trachea filled the clavicular air sac (CAS) and extended (a) into the pneumatic foramen of the right humerus (H) and (b) between the coracobrachialis caudalis muscle (CBC) and subcoracoideus muscle (SC) into the axillary region of the right subcutaneous (s-c) air diverticulum. (Blue latex had previously been injected into both axillary regions, and small amounts of it had reached the clavicular air sac.) Co, caudal end of coracoid bone detached from its insertion onto the sternum.

Latex emerges from the clavicular air sac into the left and right axillary regions, located laterally between the sternum and corresponding pectoralis muscle (Figure 2). In three of five instances in which intratracheal injection was carried out while one wing was flexed and the other extended, flow of latex into the axillary region occurred on the extended side, but not on the flexed side. Latex also flows from the clavicular air sac into the pneumatic foramen of the right and left humeri through a separate communication located immediately caudal to the corresponding coracobrachialis caudalis muscle (Figure 1). This flow of latex into the humerus occurred whether or not the wing was flexed.

From the axillary region, the air diverticulum extends ventrally between the sternum and the pectoralis muscle and caudally along the lateral side of the trunk and along the medial side of the leg down to the distal region of the tibia (Figure 2). No communication was found between the region of the s-c air diverticulum along the leg and the ipsilateral abdominal air sac.

Immediately caudal to the axilla, the diverticulum originating from the axillary region also extends dorsally and then cranially, dorsal to the scapulohumeralis muscle and ventral to (underneath) the latissimus dorsi muscle (Figure 2). The diverticulum emerges subcutaneously dorsal to the shoulder, curves around the cranial region of the shoulder, and opens caudally into a large compartment that covers the whole ventral surface of the pectoralis muscle and extends slightly caudal to it (Figure 3). The lateral region of this ventral compartment is subdivided into approximately six pockets that communicate widely with each other ventrally and are formed by thin transparent membranous partitions extending about 3–4 cm from the lateral wall of the compartment and attached to the skin along their outer border and to the pectoralis muscle along their inner border. The lateral wall of this ventral compartment, also consisting of a thin transparent membrane, separates it from the portion of the air diverticulum originating from the axillary region; this lateral wall extends along the

lateral side of the trunk and down the medial side of the leg. The ventral compartment is separated from the contralateral side by a thin transparent membranous partition which is continuous along the ventral midline from the cranial extremity of the keel to the vent and is attached to the skin along its outer border and to the keel and, more caudally, the abdominal muscle wall along its inner border. Thin bands of fibrous tissue and small blood vessels and nerves course through these various membranous partitions and may thus reinforce them (Figure 3).

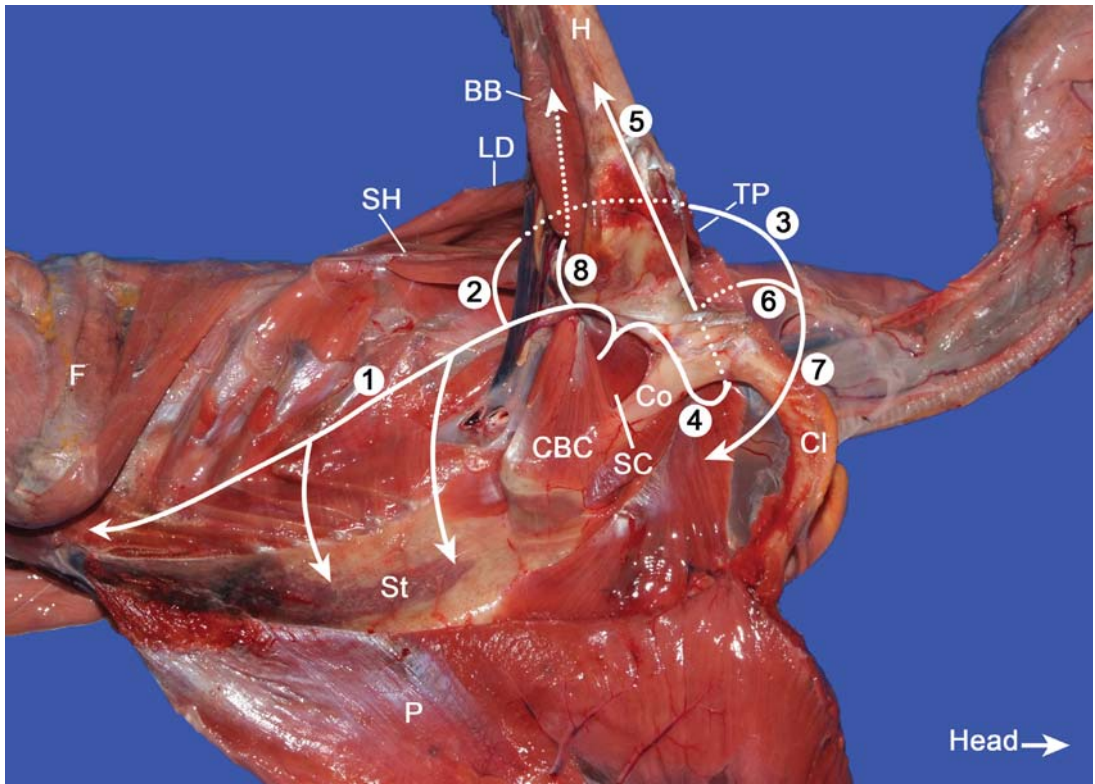


Figure 2. Right lateral view of the trunk of the skinned carcass of a Northern Gannet *Morus bassanus*. The head is directed to the right side of the Figure. The arrows show the communication among compartments of the right s-c air diverticulum, starting in the axillary region with its origin from the (intrathoracic) clavicular air sac between the subcoracoid muscle (SC) and coracobrachialis caudalis muscle (CBC) and spreading between the sternum (St) and ribs medially and the pectoralis muscle (P, reflected away from the sternum) laterally (1). The diverticulum continues caudally along the trunk and the medial side of the leg. Caudal to the axillary region, it passes dorsally and then cranially between the scapulohumeralis muscle (SH) and latissimus dorsi muscle (LD) (2) to emerge subcutaneously at the level of the shoulder (3). From underneath the pectoralis muscle, the diverticulum also passes cranially and then dorsally over the proximal end of the coracoid bone (Co) (4), emerges underneath the tensor proptagialis muscle (TP) to extend along muscles of the proximal portion of the wing (5), and also joins the compartment that emerges subcutaneously from underneath the latissimus dorsi muscle (6) (see Figures 4 & 5). The diverticulum then proceeds ventrally and caudally between the pectoralis muscle and skin (7) (see Figure 3). In addition, the diverticulum extends from the axillary region along the humerus between the muscle biceps brachii (BB) ventrally and the muscle triceps brachii dorsally (8) (see Figure 6). A third compartment of the diverticulum extending along the wing, besides (5) and (8), originates from the portion of the diverticulum as it emerges from underneath the latissimus dorsi muscle (see Figure 5) (hidden from view in this Figure). Cl, clavicle; F, femur; H, humerus.

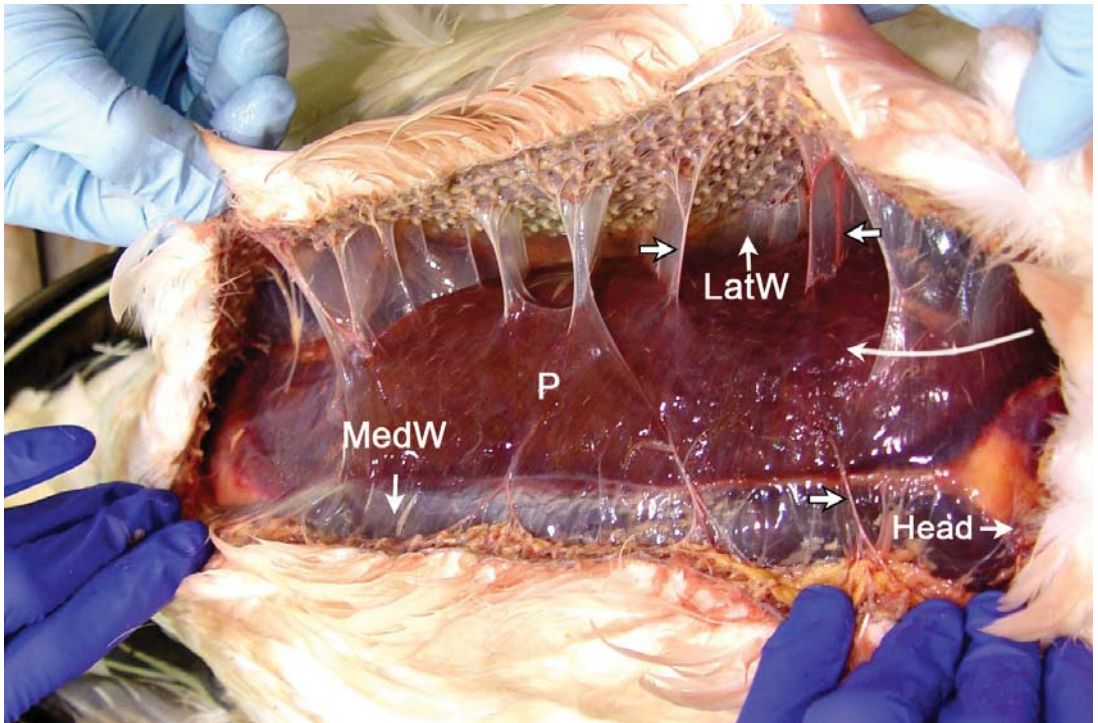


Figure 3. Ventral view of the trunk of a Northern Gannet *Morus bassanus*. The head is directed to the right side of the Figure. The skin has been partly reflected, revealing the large ventral compartment of the right s-c air diverticulum. The lateral region of this compartment is partly subdivided into individual pockets by thin transparent membranous partitions. Its lateral wall (LatW), also consisting of thin transparent tissue, separates it from the axillary region of the diverticulum, whereas a median wall (MedW) separates it from the ventral compartment of the left diverticulum. Thin bands of fibrous tissue and small blood vessels and nerves course through these various membranous partitions (thick arrows). The long arrow on the right shows the wide communication over the shoulder between this ventral compartment of the diverticulum and its dorso-lateral region (see Figure 1, point 7). P, pectoralis muscle.

From the axillary region, and in addition to extending ventrally and caudally between the sternum and pectoralis muscle, the diverticulum also extends through a narrow canal dorsally over the cranial end of the coracoid bone and spreads distally underneath the tensor proptagialis muscle (the origin of which is partly on the cranial end of the coracoid bone) toward the distal end of the humerus (Figures 4 & 5). From underneath the tensor proptagialis muscle, this portion of the diverticulum is continuous via a narrow opening with the portion of the diverticulum that emerges subcutaneously from underneath the latissimus dorsi muscle (Figure 5).

Air diverticula extending along muscles of the proximal portion of the wing are supplied from at least three sources. One, just described, originates from underneath the tensor proptagialis muscle (Figures 4 & 5). Another, which proceeds distally from underneath the deltoideus major muscle, originates from the portion of the diverticulum that travels beneath, and emerges subcutaneously cranial to, the latissimus dorsi muscle (Figure 5). A third source originates directly from the axillary

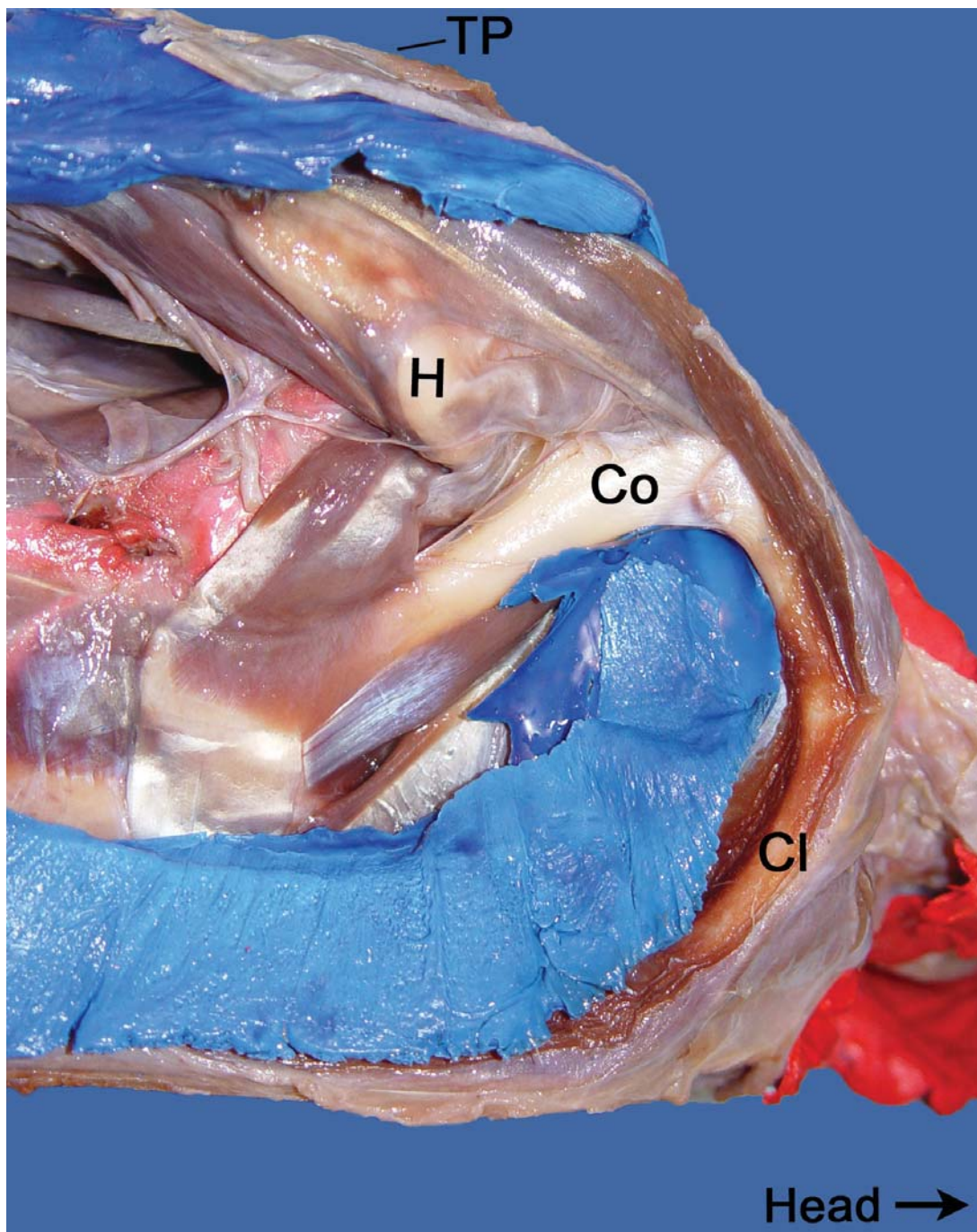


Figure 4. Right shoulder of a Northern Gannet *Morus bassanus* in lateral view. The head is directed to the right side of the Figure. Blue latex injected subcutaneously along the distal region of the right humerus spread underneath the tensor proptagialis muscle (TP) and, through a narrow canal running dorsally around the cranial end of the coracoid bone (Co), reached the axillary region of the s-c air diverticulum, located between sternum and pectoralis muscle (removed). Cl, clavicle; H, proximal end of humerus.

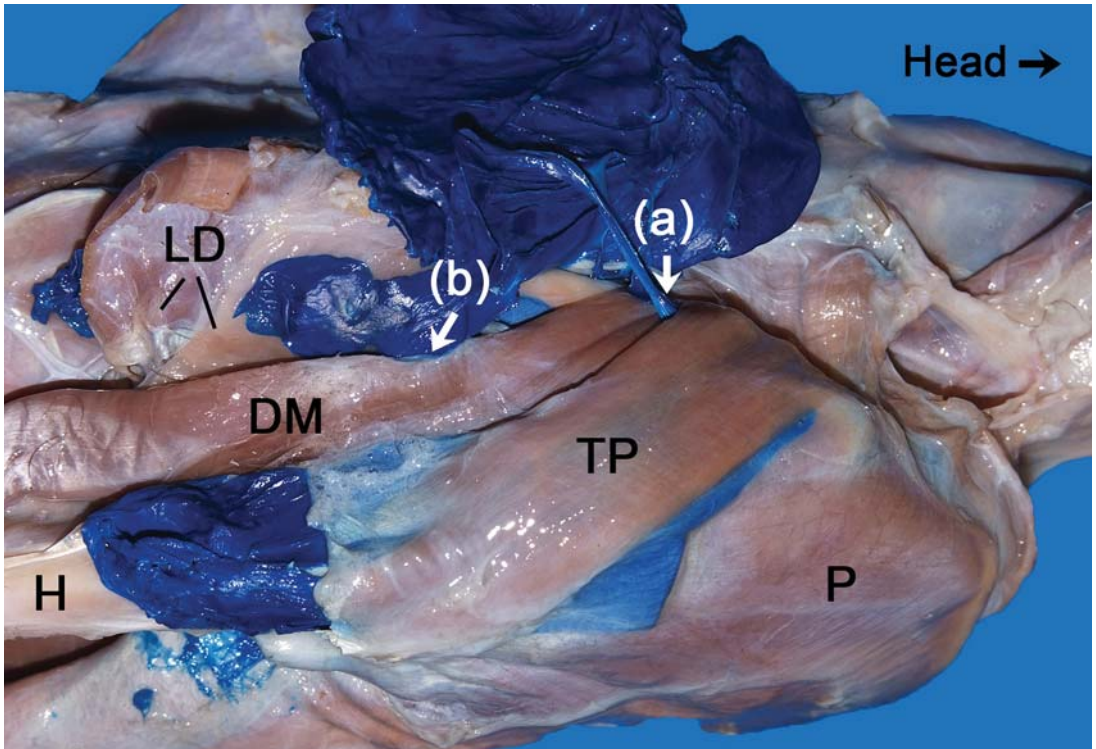


Figure 5. Right shoulder of a Northern Gannet *Morus bassanus* in lateral view. The head is directed to the right side of the Figure. Blue latex was injected into the axillary region, between sternum and pectoralis muscle (P). After having travelled dorsally around the cranial end of the coracoid bone, the latex solution extended underneath the tensor proptagialis muscle (TP) and further distally along the humerus (H). It also partly filled, through a narrow opening (a), the portion of the s-c air diverticulum that would normally emerge subcutaneously from underneath the latissimus dorsi muscle (LD, cranial and caudal heads). Some of the latex in the latter portion also extended underneath the deltoideus major muscle (DM) (b) distally along muscles of the proximal region of the wing.

region and proceeds between the biceps brachii muscle ventrally and the triceps brachii muscle dorsally (Figure 6).

In addition to the large systems of air diverticula covering the ventro-lateral region of the trunk, two other, small, bilaterally symmetrical, independent systems may contribute to cushioning the gannet's body during dives: one at the thoracic inlet and another along the neck. Air diverticula located at the thoracic inlet on either side of the cranio-caudal midline lie cranial to the main compartment of the respiratory clavicular air sac and internal and cranial to the corresponding clavicle (Figure 7). Each of these subclavicular air diverticula communicates with the corresponding side of the clavicular air sac via a tubular channel along the lateral wall of the thoracic cavity. Large s-c air diverticula, each possibly composed of a number of interconnecting compartments, lie ventrally along either side of the neck (Figure 8). Each of these two cervical s-c air diverticula communicates with the nasal cavities and the choanal opening through a small aperture along the roof of the pharynx. No communication was found between these cervical s-c air diverticula and the ipsilateral cervical respiratory air sacs.

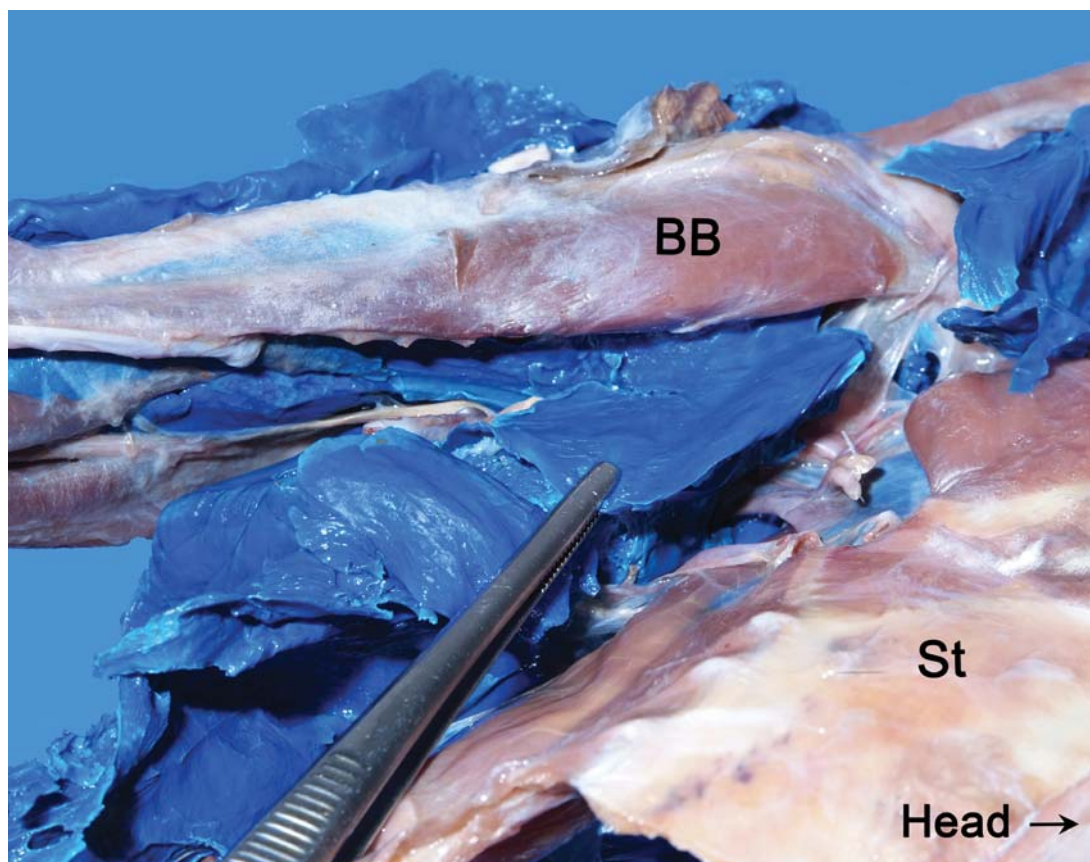


Figure 6. Ventral view of the right axilla and humerus of a Northern Gannet *Morus bassanus*. The head is directed to the right side of the Figure. Blue latex injected via the trachea extended into the axillary region and, from there, along the humerus between the biceps brachii muscle (BB) ventrally and the triceps brachii muscle dorsally. St, sternum, from which the pectoral muscle has been removed.

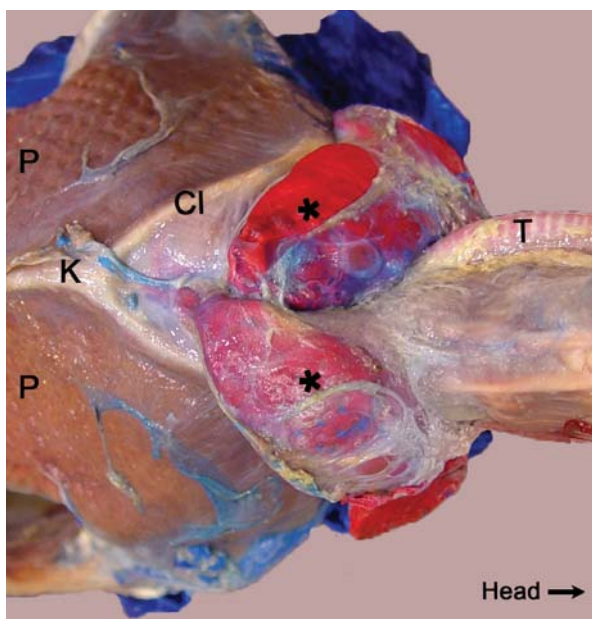


Figure 7. Ventral view of the thoracic girdle of a Northern Gannet *Morus bassanus*. The head is directed to the right side of the Figure. Red latex injected via the trachea (T) has filled the left and right subclavicular air diverticula (stars) via their communication with the clavicular air sac. (Blue latex had previously been injected into both axillary regions, and small amounts of it had reached the clavicular air sac and, subsequently, both subclavicular air diverticula.) Cl, clavicle; K, keel of the sternum; P, left and right pectoralis muscles.

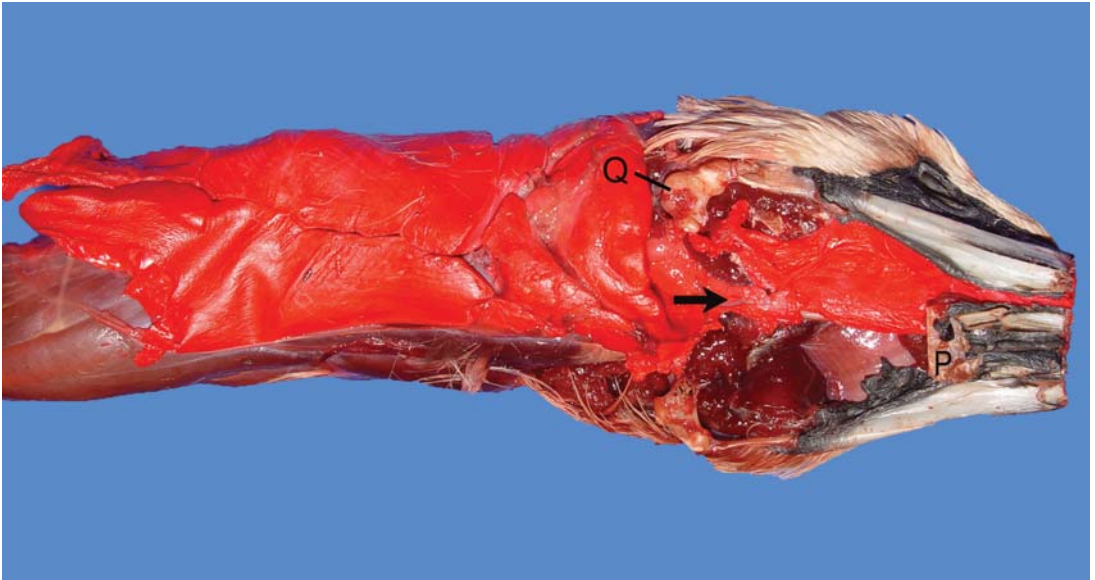


Figure 8. Ventral view of the neck and head of a Northern Gannet *Morus bassanus*. The head is to the right; the rostral portion of the upper beak was cut off. The mandible and caudal region of the palate (P) were removed in order to exposed the nasal cavities. Red latex injected directly into the right cervical s-c air diverticulum extends through a small opening (arrow) into the right nasal cavity. Q, quadrate bone, which articulates with the mandible.

Discussion

The results of this study confirm and expand upon earlier observations of the anatomy of s-c air diverticula in the Northern Gannet. Assuming that air flow among the various compartments of these diverticula can be inferred from that of latex, their distribution, more specifically their voluminous size along the ventral surface of the neck and trunk and their paucity along the back, supports their putative function in cushioning the impact of entry into the water as the bird dives from high above the water surface. We had originally hypothesised that flexion of the wings against the body at the start of a dive could close the communication between respiratory air sacs and s-c air diverticula of the trunk, thus allowing the air trapped in these diverticula to provide an efficient cushion against the impact of entry into the water. This was demonstrated in three of five instances. It is possible that, in the two birds in which latex could flow from the clavicular air sac into the axillary region of the s-c air diverticulum on the side of the flexed wing, incomplete flexion of the wing against the body and/or postmortem stiffness of the tissues could have prevented complete closure of the communication. Alternatively, during a dive, a gannet lays its wings back, flat against the body but fully extended rather than flexed (Elphick *et al.* 2001), and this position might better close the communication between respiratory air sacs and s-c air diverticula of the trunk. The hypothesis proposed above therefore requires further testing. More cranially, escape of air from inflated cervical air diverticula (via the nasal cavities) and inflated subclavicular air diverticula (via the clavicular air sac and into the lungs and trachea) could be prevented by complete closure of the Northern Gannet's mouth, as the nostrils are permanently closed by an overgrowth of epithelial cells in this species (King & McLelland 1984).

Our localisation of the communication between respiratory air sacs and s-c air diverticula of the trunk is as described in general terms in the Northern Gannet by Gurney (1913) and more precisely in the Brown Pelican by Richardson (1939), namely between the subcoracoideus and coracobrachialis caudalis muscles. Richardson (1939) assumed, based on the work of others, that this communication comes from the clavicular air sac and 'probably corresponds to the axillary diverticulum' of this air sac. We make a comparable assumption, i.e. that the s-c air diverticulum along the trunk on each side of the cranio-caudal midline represents a massive extension of an extrathoracic diverticulum originating from the ipsilateral (paired) lateral chamber of the clavicular air sac as described by King (1975) and McLelland (1989). The only other possible alternative would be a communication between the s-c air diverticula and the cranial thoracic air sacs. These air sacs were not visualised in this study, as it was not our intent to provide a detailed description of the system of respiratory air sacs in the Northern Gannet. However, whereas the clavicular air sac typically has several intra- and extra-thoracic diverticula, including a humeral diverticulum aerating the humerus in some species (as was found in our birds), the cranial thoracic air sacs are not known to have diverticula in any species (King 1975; Nickel *et al.* 1977; McLelland 1989), although they may aerate some bones (sternal ribs, sternum) in some species (e.g. Psittaciforms) (Evans 1996). King (1975) describes three diverticula of the lateral chamber of the clavicular air sac in the chicken (pectoral, humeral, and axillary), whereas McLelland (1989), citing Groebbels (1932), describes in general five such diverticula (subscapular, axillary, subpectoral, suprahumeral, and a fifth diverticulum under the latissimus dorsi muscle) but adds that 'considerable interspecific variation in development of the diverticula appears to exist'. We did not attempt to ascribe the s-c air diverticula along the trunk of the Northern Gannet to an extension of any one or more of the diverticula mentioned above. Bezuidenhout *et al.* (1999) describe diverticula originating from the abdominal air sacs and extending among muscles and under the subcutis of the legs in the Ostrich *Struthio camelus*. No such communication was found between the region of the s-c air diverticula along the legs of Northern Gannets and the ipsilateral abdominal air sacs.

The location of what we describe as the subclavicular air diverticula in the Northern Gannet corresponds to that of the craniolateral diverticulum of the median chamber of the clavicular air sac as described in the chicken by King (1975) and in general by McLelland (1989) and of the left and right cranial parts of the clavicular air sac as described in the chicken by Nickel *et al.* (1977). What we describe as cervical s-c air diverticula represent a greatly expanded cervicocephalic system of air sacs, as there was a clear communication between these diverticula and the nasal cavities. According to Richardson (1939), there is in pelicans 'sometimes a connection between the air cavities of the pharyngonasal system of the head region and the pulmonary cavities of the neck', but no further description is provided. Walsh & Mays (1984) described in psittacine birds a s-c cervicocephalic air sac with a cephalic portion situated caudodorsally to the skull and a cervical portion extending bilaterally dorsolaterally along the neck; this sac communicates with the infraorbital sinus cranially, but not with the respiratory air sacs. According to McLelland (1989), the cervical respiratory air sacs make 'an especially large contribution to the subcutaneous diverticula [along the ventral surface of the neck] in the

Gannet'. This author added, however, that 'extensions of the vertebral diverticula [of the cervical respiratory air sacs] penetrate between the neck diverticula of the cervicocephalic system of air sacs', suggesting that two independent systems of cervical s-c air diverticula are present in this species. We were unable in this study to find a distinct communication between the cervical s-c air diverticula and the cervical respiratory air sacs.

Several unanswered questions remain regarding the function of s-c air diverticula and air circulation within them. Within the six families of the order Pelecaniformes, all sulids (boobies and gannets) forage by plunge-diving, but among the other five families, only Brown Pelicans and Neotropic Cormorants *Phalacrocorax olivaceus* habitually do so (del Hoyo *et al.* 1992). We are not aware of a detailed description of s-c air diverticula in species of the order Pelecaniformes that do not plunge-dive. Such information could help to elucidate the evolution of s-c air diverticula in plunge-divers and might offer alternative explanations for their function. Bignon (1889) suggested a number of possible functions for the cervicocephalic air diverticula in birds besides that of cushions, including heat retention, buoyancy control, and head support during flight. Control mechanisms for inflation and deflation of the different s-c air diverticula are also incompletely understood. Although s-c air diverticula of the trunk and the subclavicular s-c air diverticula can be inflated voluntarily via the respiratory tract, it is less clear whether or how a bird can voluntarily inflate the cervical s-c air diverticula via the choanal opening. Owen (1866) suggested that birds (pelicans and gannets) may voluntarily expulse air from s-c air diverticula 'when the bird is about to descend, in order to increase its specific gravity, and enable it to dart with rapidity upon a living prey'; he added that this can be done through the action of those muscles that are connected to the skin by membranous partitions and bands of fibrous tissue, blood vessels and nerves.

In conclusion, the subcutis of the ventral region of the trunk and neck of the Northern Gannet is invested by an elaborate air mattress that may be related to the particular foraging behaviour of this species. Further work is required, however, to describe in more detail the numerous peripheral extensions of this system of s-c air diverticula and the potential anatomic variation in these extensions among individual birds and, particularly, to define more precisely its functional adaptation.



Figure 9. Northern Gannet *Morus bassanus*, Quendale Bay, Shetland, 2 September 2007 © Hugh Harrop.

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