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An anatomical study of the respiratory air sacs in ostriches

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ABSTRACT

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An accurate description of the number, location and relative position of the air sacs and their diverticula in the ostrich is essential for a better understanding of the pathogenesis of air sacculitis in this bird. The air sacs were studied in ten ostriches of varying ages by latex or silicone casting of the respiratory tract and dissection. Results revealed that the air sacs of the ostrich conform to the general pattern in birds. Cervical, lateral and medial clavicular, cranial and caudal thoracic, and abdominal air sacs are present. The left and right medial clavicular air sacs fuse with each other ventrally to the trachea to form a single, median compartment. A unique, large gastric diverticulum which covers the caudal aspects of the proventriculus and gizzard originates from the median compartment of the clavicular air sac. The lateral clavicular air sacs and their diverticula are similar to those of other bird species, with the exception that humeral diverticula are absent. Both abdominal air sacs are relatively small, with the left sac being the larger. Perirenal and femoral diverticula, similar to those found in other bird species, are present. However, the entire femur is aerated by the femoral diverticulum which also forms a large, subcutaneous division caudally and caudo-laterally to the femur. The presence of this subcutaneous part has practical implications for injury and intramuscular injections. The number and location of ostia connecting the air sacs to the bronchial tree are generally similar to those reported in other bird species.

Keywords: Air sacs, diverticula, ostriches, respiratory tract

INTRODUCTION

The structure and function of the respiratory air sacs of domestic bird species are well documented (for a review see King (1966) and Duncker (1971)) and some information on ratites has also been presented. Beddard (1886) gives a short description of the respiratory air sacs of the cassowary (*Casuarius uniappendiculatus*) while Huxley and Parker (quoted by Beddard 1886) report on the air sacs of species of kiwi and rhea, respectively. The presence of air sacs in the ostrich and their communications with the bronchial tubes was noted by Macalister (1864). Subsequently, the abdominal air sac of the ostrich was described by Roché (1888) and the connections between the bronchial tree and air sacs were described by Schultze (1908). Bezuidenhout (1981) noted that the clavicular air sacs communicated freely with each other above the heart. Schmit-Nielsen, Kanwisher, Lasiewski, Bretz & Cohn (1969) suggested that the air sacs of the ostrich play a role in maintaining a constant body temperature at high ambient temperatures by evaporative cooling.

The air sacs of birds in general are prone to infection. Under intensive commercial farming conditions air sacculitis in ostriches is a common condition. The presence or absence of air sacculitis at the time of slaughter is one of the criteria that is used to determine whether a carcass is suitable for human consumption or not. The condemnation of a carcass as unfit for human consumption represents a considerable financial loss to the farmer. In South Africa, air sacculitis in ostriches is responsible for a considerable loss of production. Nine percent of carcasses

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were condemned at slaughter during 1988 at the Oudtshoorn abattoir (Anon. 1988a), resulting in a loss of R250 000 to farmers (Anon. 1988b). It has also been observed that the different air sacs of ostriches are not affected at the same time or to the same degree in the progression of air sacculitis.

On evaluation of a carcass for air sacculitis, it is essential to know which of the air sacs are affected, which ones, if any, are more prone to infection and need to be examined more closely, what organisms affect the air sacs, and what the effects of infections are on the carcass. This implies that the inspector must know and understand the topographic anatomy of the air sacs and their diverticula. In most cases, however, little attention is paid to the exact limits of the different air sacs and a general diagnosis of "air sacculitis" is made.

In order to study the pathogenesis of air sacculitis, it is essential that an accurate description of the different air sacs and their diverticula be available and that researchers and inspectors become familiar with them. The existing literature contains no detailed anatomical descriptions of the air sacs of the ostrich (Macalister 1864; Beddard 1886; Roché 1888; Schultze 1908; Bezuidenhout 1981) and in some instances reflects generalizations that are not applicable to this species (see Duerden 1912; Fowler 1991). An accurate description of the normal macroscopic structure of the air sacs is thus essential for further investigation into the pathogenesis of air sacculitis.

MATERIALS AND METHODS

Ten ostriches of both sexes and of varying ages were used to study the macroscopic anatomy of the air sacs and their connections to the bronchial tree.

The birds were euthanased by intravenous injection of sodium pentobarbitone. After euthanasia the trachea was exposed in the middle of the neck, a polythene tube of suitable diameter was inserted into the trachea and tied in position with string. The tube was connected to a vacuum pump and the air in the lungs and respiratory air sacs was extracted. Following extraction of the air, the tube was clamped, disconnected from the vacuum pump and fitted with a funnel. In eight of the birds the funnel was filled with latex, the clamp removed and the latex allowed to fill the lungs and air sacs under gravitational force from a height of approximately 300 mm. The entire birds were then fixed by infusion of 10 % formalin via the right external jugular vein and immersion in 10 % formalin until the latex had set. The intestines were removed in order to visualize the abdominal air sacs. In cases where the abdominal air sacs and their diverticula did not fill completely, additional latex was injected directly into the air sac or its diverticula and allowed to set. In the other two birds the lungs and air sacs were filled with "Silastic S" (Dow Corning) silicon, using the same technique as for the latex. All the tissues surrounding the air sacs and their diverticula were then carefully dissected away to allow proper visualization of the casts. The specimens were photographed at various stages of the dissection using Ilford FP4, 125 ASA film.

RESULTS

Five pairs of air sacs were identified, namely cervical, clavicular, cranial and caudal thoracic, and abdominal air sacs.

To orientate the reader regarding the description of the relative positioning of the sacs and their ostia in the thorax, the following information applies: The thorax is bounded laterally, from cranial to caudal, by two pairs of a-sternal vertebral ribs (vertebral ribs 1 and 2) followed by five pairs of vertebral ribs with sternal counterparts (vertebral ribs 3–7) and caudally by two a-sternal vertebral ribs (vertebral ribs 8 and 9).

Abdominal air sac, *Saccus abdominalis*

Left and right abdominal air sacs were present. The left sac was appreciably larger than the right one. The two ostia leading to the air sacs originated from the terminal end of the primary bronchus (direct connection). They were located opposite the 8th vertebral ribs along the dorsal caudo-lateral borders of the lungs, just cranial to the cranial pole of the kidneys (Fig. 1). The openings were bounded ventrally and medially by the most caudal (6th) costoseptal muscles and laterally by the 8th vertebral ribs.

Caudomedially, the ostium of the right sac was bordered by the caudal vena cava, right adrenal gland and, in male birds, the epididymal region of the right testis. Each ostium opened into a funnel-shaped space situated between the costoseptal muscle and the thoracic wall, making visualization of the actual opening difficult. The funnel-shaped space communicated dorsally with the femoral and peri-renal diverticula of the air sac and caudally with the abdominal air sac proper. The left abdominal air sac (Fig. 4 and 5) extended caudally along the dorsolateral body wall, dorsally to the proventriculus and ventrally to the testis or ovary. It reached the middle third of the ischiopubic window opposite the caudal division of the kidney and extended somewhat across the midline to the right. The right abdominal air sac was smaller than the left one. It extended caudally along the dorsolateral body wall to reach the cranial part of the ischiopubic window opposite the middle division of the kidney. It was separated from the proventriculus by the medial wall of the left abdominal air sac and did not reach the midline.

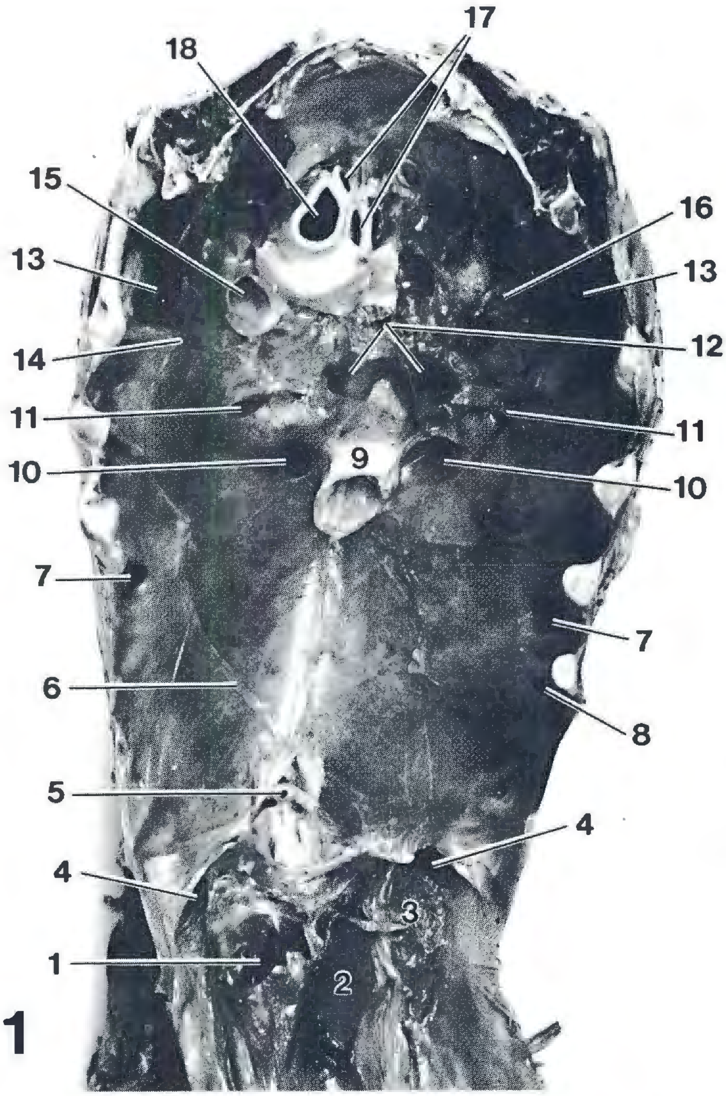
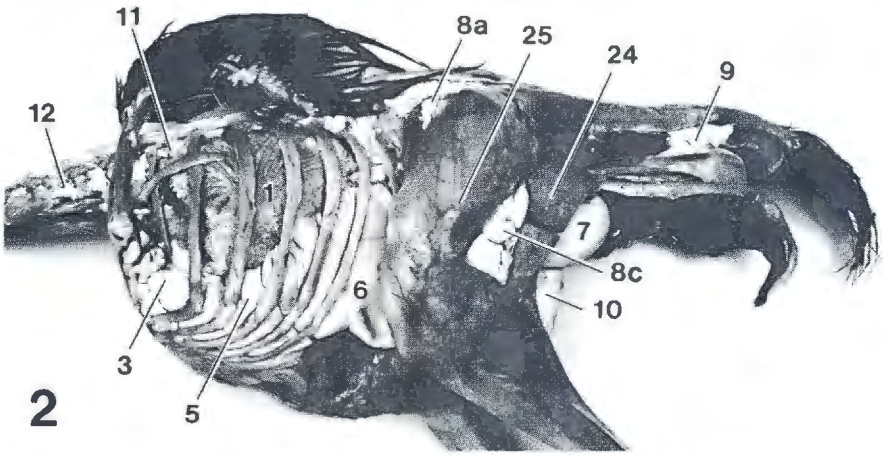


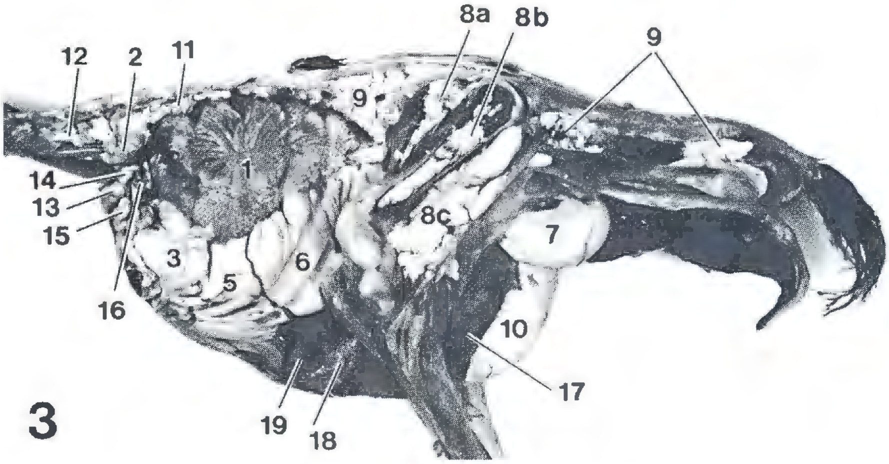
FIG. 1 A ventral view of the thoracic region of a 3 month-old ostrich indicating the various ostia leading to the air sacs after removal of the heart, proventriculus, gizzard and intestinal tract

1 Caudal vena cava
2 Adrenal gland
3 Kidney
4 Ostium to abdominal air sac
5 Coeliac artery
6 Septum between cranial and caudal thoracic air sacs
7 Ostium to caudal thoracic air sac
8 Additional ostium to caudal thoracic air sac
9 Oesophagus
10 Ostium to cranial thoracic air sac
11 Additional ostium to cranial thoracic air sac
12 Pulmonary vein
13 Ostium to lateral clavicular air sac
14 Septum between cranial thoracic and lateral clavicular air sacs
15 Right cranial vena cava
16 Left cranial vena cava
17 Pulmonary arteries
18 Aorta

KEY: Fig. 2–9

1 Lung
2 Cervical air sac
3 Clavicular air sac (lateral component)
4 Clavicular air sac (medial component)
5 Cranial thoracic air sac
6 Caudal thoracic air sac
7 Abdominal air sac
8 Femoral diverticulum of abdominal air sac—a around joint; b in femur; c subcutaneous
9 Perirenal diverticulum of abdominal air sac
10 Gastric diverticulum of clavicular air sac
11 Caudal vertebral division of the cervical air sac
12 Cranial vertebral division of the cervical air sac
13 Subcutaneous diverticulum of the clavicular air sac (extrathoracic)
14 Axillary diverticulum of the clavicular air sac (extrathoracic)
15 Sternal intrathoracic diverticulum
16 Cardiac diverticulum
17 Proventriculus
18 Gizzard
19 Liver
20 Spleen
21 Aorta
22 Oesophagus
23 Dorsal tube of the dorsal part of the supracardiac diverticulum
24 *M. ileofibularis*
25 *M. femerotibialis*
26 Trachea
27 Medial compartments of the clavicular air sacs
28 Lateral compartments of the clavicular air sacs





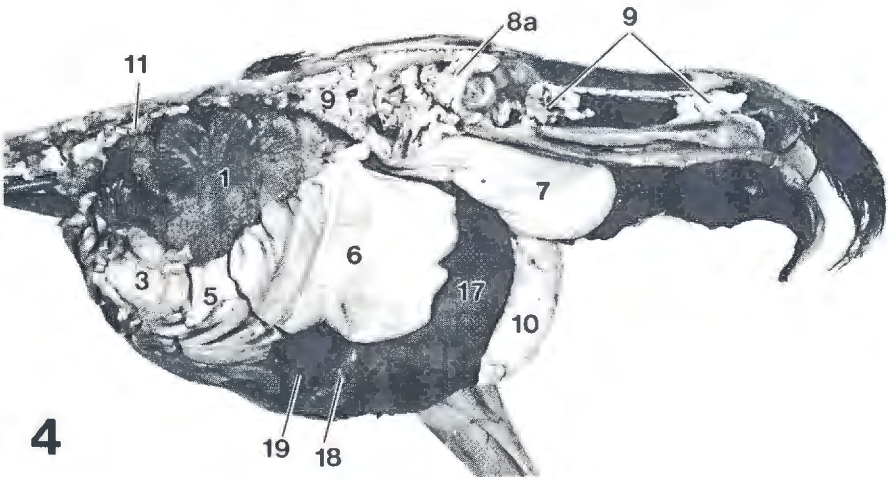
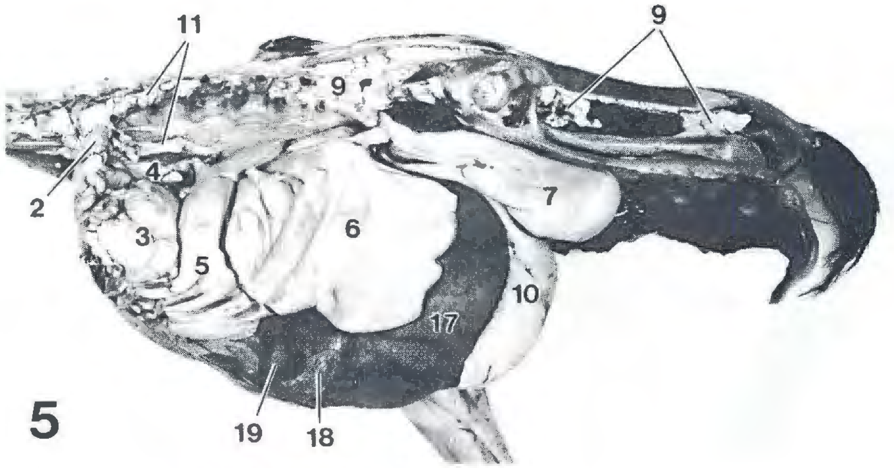


FIG. 2 Left lateral view of the lungs and air sacs (filled with latex) of a 3-month-old ostrich after removal of the skin, intercostal muscles and intestines

FIG. 3 Left lateral view of the lungs and air sacs (filled with latex) of a 3-month-old ostrich after removal of the pectoral limb, lateral body wall and laterally positioned thigh muscles. The femur has also been opened longitudinally to expose the air sac housed within the bone

[From Bezuidenhout (1999), reproduced with permission of CABI Publishing, Wallingford]

FIG. 4 Left lateral view of the lungs and air sacs (filled with latex) of a 3-month-old ostrich after removal of the thoracic wall, intestines and the left wing and limb



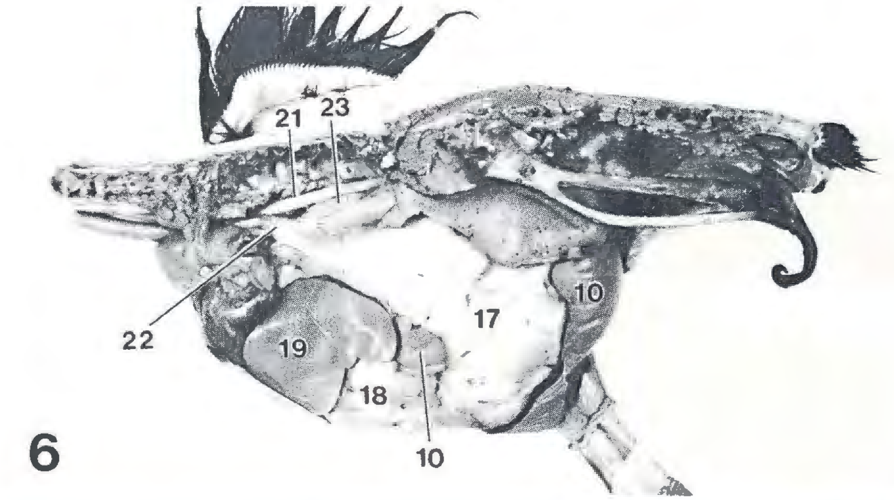


FIG. 5 Left lateral view of the lungs and air sacs (filled with latex) of a 3-month-old ostrich after removal of the thoracic wall, lungs, intestines and the left wing and limb

FIG. 6 Left lateral view of a 3-month-old ostrich specifically indicating the extent of the clavicular gastric diverticulum (filled with silicone)

FIG. 7 Caudal view of the left femur showing the opening for the femoral diverticulum (arrow head)

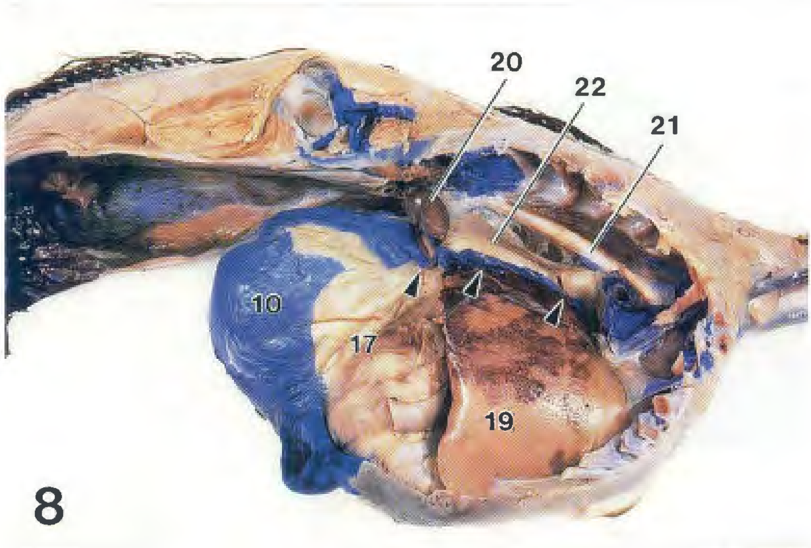


FIG. 8 Right view of a 3-month-old ostrich dissected to reveal the narrow ventral tube (arrowheads) between the dorsal supracardiac diverticulum of the median clavicular air sac and the gastric diverticulum

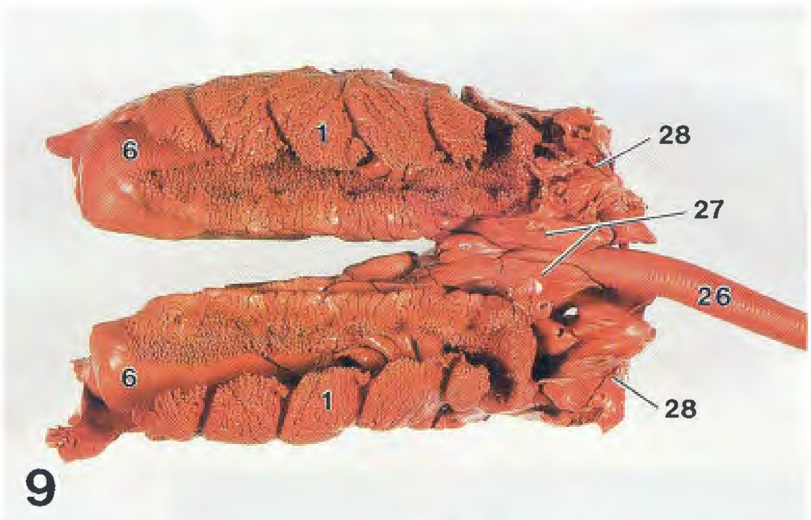


FIG. 9 Dorsal view of a silicone cast of the respiratory tract showing the medial and lateral compartments of the clavicular air sacs

Diverticula of the abdominal air sacs

Two diverticula, each with complex secondary extensions, originated from each abdominal air sac.

The femoral diverticula, *Diverticula femoralia*, extended dorsally from the funnel-shaped spaces immediately caudal to the ostia of the abdominal air sacs. Each diverticulum formed secondary diverticula that invaded the hip joint and surrounding tissues, and a diverticulum that passed through a pneumatic foramen on the caudal aspect of the femur (Fig. 7), just distal to the major trochanter, to aerate the femoral shaft as far distally as the femoral condyles (Fig. 3). The main part of the femoral diverticulum extended distally, between the *M. iliofibularis* and *M. femerotibialis*, to the level of the stifle (Fig. 2 and 3). In the femoral region it lay between the femur cranially and the ischiadic nerve caudally. At the femorotibial joint (stifle) it lay between the heads of the gastrocnemius muscle, with its distal end against the joint capsule (Fig. 3). An extensive part of the diverticulum was situated subcutaneously on the lateral surface of the limb, caudally to the stifle and bordered by the iliofibular and femorotibial muscles (Fig. 2). The perirenal diverticula, *Diverticula perirenalia*, extended cranially and caudally from the initial part of the femoral diverticulum (the two diverticula share a common origin from the funnel-shaped space at the beginning of the abdominal air sac). The cranial extension formed secondary diverticula that invaded the spaces between the heads and tubercles of vertebral ribs 7–9 and the corresponding thoracic vertebrae (Fig. 3, 4 and 5). These diverticula were related to the dorsal border of the lung. The caudal extension was situated dorsally to the kidney. It formed secondary diverticula that invaded the spaces between the synsacrum and ilium (Fig. 3, 4 and 5). Each perirenal diverticulum extended beyond the caudal pole of the kidney, forming a retroperitoneal air sac that extended caudally along the cloaca to reach the caudal limit of the abdomen.

Caudal thoracic air sac, *Saccus thoracicus caudalis*

Left and right caudal thoracic air sacs were present and of equal size. The ostia to the air sacs originated from the first lateroventral bronchus (direct connection) and were large, oval openings situated on the ventro-lateral surfaces of the lungs (Fig. 1). Each opening lay at the level of the uncinate processes, between the 6th and 7th vertebral ribs and was bounded cranially and caudally by the 3rd and 4th costoseptal muscles respectively. A variable second, smaller opening was present in some specimens (Fig. 1). This secondary opening, when present, lay between the 4th and 5th costoseptal muscles and originated from a parabronchus (indirect connection).

The caudal thoracic air sacs extended ventrally and caudally along the body wall, from the level of the 4th intercostal spaces to the lateral border of the sternum ventrally and to the level of the caudal thigh muscles caudally (Fig. 4 and 5). Each sac was bounded dorsally by the caudal half of the lung and abdominal air sac, laterally by the last five vertebral ribs and abdominal wall, medially by the liver, gizzard and proventriculus and cranially by the cranial thoracic air sac (Fig. 4 and 5). No diverticula were observed.

Cranial thoracic air sac, *Saccus thoracicus cranialis*

Left and right cranial thoracic air sacs were present and of equal size. The medial ostia originated from the 3rd dorsoventral bronchus (direct connection) and were located on the ventromedial surface of the lung, opposite the 5th vertebral ribs (Fig. 1). Each opening was bordered cranially by the pulmonary vein and medially by the oesophagus. Lateral ostia originating from parabronchi (indirect connection) were present craniolaterally to each main opening (Fig. 1).

The cranial thoracic air sacs were appreciably smaller than the caudal thoracic air sacs (Fig. 3, 4 and 5). They were triangular in outline and extended from the 4th to the 7th vertebral ribs (Fig. 2). The base of the triangle was ventrally directed and the apex displayed a cranio-caudal extension (Fig. 5). Each sac was bordered by the lung dorsally, medially by the liver, laterally by the body wall, cranially by the clavicular air sac, caudally by the caudal thoracic air sac and ventrally by the last (5th) sternal rib and the caudo-lateral process of the sternum (Fig. 4). In the latter region the air sac made contact with the ventral body wall. No diverticula were observed.

Clavicular air sac, *Saccus clavicularis*

The clavicular air sacs developed from four outgrowths of the bronchial tree, two medially (left and right medial clavicular air sacs) and two laterally (left and right lateral clavicular air sacs). The left and right medial clavicular air sacs fused with each other ventrally to the trachea, forming one large, median-positioned air sac that was flanked on either side by a lateral clavicular air sac (Fig. 9). Collectively, the clavicular air sacs extended from the thoracic inlet cranially, to the cranial thoracic air sacs caudally (Fig. 3–5), enveloping the oesophagus, trachea, syrinx, extrapulmonary bronchi and the large blood vessels dorsally and cranially to the heart. The ostia of the lateral clavicular air sacs originated from the first medioventral bronchus (direct connection) and were located on the craniolateral borders of the lungs, between the 3rd and 4th vertebral ribs (Fig. 1). Each opening was bordered by the first costoseptal muscle caudoventrally, the internal thoracic vein cranially and the 4th vertebral rib and intercostal muscles laterally. The ostia lay laterally to the cranial caval veins (Fig. 1). The ostia of the medial compartments originated from the second medioventral bronchus (direct connection) and were located immediately dorsolateral to the primary bronchi.

Diverticula of the clavicular air sacs

The clavicular air sacs gave rise to a number of intra- and extrathoracic diverticula, named after the region which they penetrated. The intrathoracic diverticula consisted of sternal, cardiac and supracardiac diverticula, while the extrathoracic diverticula consisted of axillary and subcutaneous parts.

Sternal diverticula, *Diverticula sternalia*, extended ventromedially from the cranial part of the lateral clavicular air sacs, invading the cranial aspect of the sternum as well as the spaces around the sternocostal articulations (Fig. 3).

Cardiac diverticula, *Diverticula cardiaca*, extended from the lateral clavicular air sacs into the spaces between the sternum and the heart (Fig. 3). The median compartment (combined medial clavicular air sacs) formed a large, unpaired supracardiac diverticulum between the dorsal body wall, oesophagus and trachea dorsally and the heart and large blood vessels ventrally. The dorsal part of the supracardiac diverticulum extended caudally along the dorsal and ventral borders of the oesophagus as two narrow tubes. The dorsal tube appeared to end blindly a short distance from its origin (Fig. 6). The ventral tube lay between the oesophagus and the right lobe of the liver (Fig. 8). It crossed the right surface of the oesophageal-proventricular junction, immediately ventral to the spleen (Fig. 8). At this point it communicated via a very narrow opening with an extensive gastric diverticulum.

The gastric diverticulum was a large, sac-like space that extended along the caudal border of the proventriculus (Fig. 3–6 and 8). At the distal end of the proventriculus it turned cranially to invade the space between the ventral body wall and the gizzard (Fig. 6). In some specimens it extended further cranially, occupying a position between the gizzard and left lobe of the liver (Fig. 6).

Subcutaneous diverticula, *Diverticula subcutanea*, extended from the lateral compartments into the subcutaneous tissue cranially to the coracoids and between the trachea and ventral neck muscles at the base of the neck (Fig. 3). Axillary diverticula, *Diverticula axillare*, invaded the spaces around the shoulder joint, but did not enter the humerus (Fig. 3).

Cervical air sac, *Saccus cervicalis*

The ostia of the paired cervical air sacs originated from parabronchi (tertiary bronchi) (indirect connection) of the first ventromedial bronchus. They were located at the craniodorsal border of the lungs, immediately dorsolateral to the tracheal part of the median clavicular air sac and lateral to the oesophagus. The primary cavities of the cervical air sacs were small, globular spaces, but they formed extensive caudal and cranial vertebral, as well as intramuscular, diverticula. The caudal vertebral diverticula extended caudally along the vertebral column, invading the spaces between the vertebrae and the vertebral ribs, and between the vertebrae and the oesophagus dorsally to the lungs, up to the level of the 6th vertebral ribs (Fig. 2–5). The cranial vertebral diverticula were tubular structures that accompanied the vertebral blood vessels through the transverse canal of the cervical vertebrae. They extended to the level of the axis (C2). Along the way they gave off supravertebral diverticula which lay around the articular processes and supramedullary diverticula that passed through the intervertebral foramina to form a continuous tube dorsally to the spinal cord. The intramuscular diverticula were small extensions that invaded the cervical muscles at the base of the neck (Fig. 3).

DISCUSSION

According to Duncker (1979), the abdominal air sacs in the ostrich and rhea are fused to the body wall only over a small area around the ostia of the sacs. In the present study the abdominal air sacs were found to have extensive areas of attachment along almost their entire lengths. In this study the abdominal air sacs were found to be fairly small and of about the same proportions as the caudal thoracic air sacs. Small abdominal air sacs appear to be a characteristic of ratites and Groebels (1932), as quoted by McLelland (1989), noted that these sacs are particularly small in *Casuarius* and *Apteryx*. A similar observation was made by Duncker (1971) in rheas. In kiwis the abdominal air sac is confined to the subpulmonary cavity (Duncker 1979). According to Schmidt-Nielsen *et al.* (1969) the largest air sacs of the ostrich are the post thoracic air sacs (caudal thoracic air sac—present study), followed in order of decreasing size by the interclavicular (unpaired)(medial clavicular air sac—present study), abdominal, prethoracic (cranial thoracic air sac—present study) and lateral clavicular air sacs. In the present study, the left abdominal air sac was found to be substantially larger than the right sac, possibly due to the large size and position of the proventriculus. This contrasts with the general position in most species of birds where the left abdominal air sac is smaller than the right sac (McLelland 1989). This is attributed to the asymmetry of the abdominal viscera as reported by various authors cited by McLelland (1989). The number and location of the various diverticula of the abdominal air sacs identified in the ostrich is in general agreement with those of other species as described by McLelland (1989). The presence of a large subcutaneous diverticulum caudally to the stifle in the ostrich, however, may have clinical implications in this species. Injuries to the lateral thigh can penetrate the diverticulum, and careless injections into the lateral and caudal thigh muscles may deposit the injected material into the air sac rather than into the muscle. This study has confirmed that the only pneumatized bone in the ostrich is the femur (accommodating a diverticulum of the abdominal air sacs) as has previously been reported for the ostrich and emu (Fowler 1991).

The thoracic, clavicular and cervical air sacs of the ostrich are similar in position and arrangement to those of other avian species as described by various authors quoted by McLelland (1989). A unique feature of the fused medial clavicular air sacs of the ostrich is the presence of two tube-like diverticula running along the dorsal and ventral surfaces of the oesophagus, the ventral one finally terminating in a very extensive gastric diverticulum. This diverticulum has not been described any other ratites. As the vagus nerve passes along the curvature of the proventriculus, it lies between the thin-walled air sac and the thick proventricular wall. In this position the nerve is potentially vulnerable should the diverticulum become infected. The role of the vagus nerve and gastric diverticulum in the development of gastric stasis (Huchzermeyer 1998) needs to be investigated. A small gastric diverticulum emanating from the left abdominal air sac and associated with the gizzard has been described in other bird species (McLelland 1989).

Roché (1888) and McLelland (1989) describe paired extensions of the vertebral diverticula of the cervical air sacs in the ostrich that extend caudally into the peritoneal cavity beyond the abdominal air sacs.

Although these extensions of the vertebral diverticula were not specifically identified in the present study, similar structures have been observed by the authors in post mortem material that was not part of the study.

The pattern of ostia leading to the various air sacs observed in the present study is in agreement with that described by Schultze (1908) for the ostrich. This study revealed direct connections between the clavicular air sacs and the first and second medioventral bronchi. This observation confirms the finding by Shultze (1908) that in the ostrich there is no connection with the third medioventral bronchus. In rheas (*Rhea americana*, *Pterocnemia pennata*) there is a direct connection of the clavicular air sac to the second medioventral bronchus (Duncker 1971). In bird species generally, the cranial thoracic air sac has direct medial and indirect lateral connections to the bronchi (Duncker 1971). The present study agrees with these findings. This is contrary to the situation in rheas where both medial and lateral openings to the cranial thoracic air sacs have direct connections to the bronchi (Duncker 1971).

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