AIR SACS OF RESPIRATORY ORIGIN IN SOME PROCELLARIIFORM BIRDS

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The purpose of this paper is to present details of the air-sac system in three species of the order Procellariiformes—the Laysan Albatross, *Diomedea immutabilis*; the Wedge-tailed Shearwater, *Puffinus pacificus*; and the Christmas Island Shearwater, *Puffinus nativitatis*. The air sacs of respiratory origin, *i.e.*, those arising from the lung, are described in detail for *D. immutabilis*, and differences from this pattern are expressed for *P. pacificus* and *P. nativitatis*.

Bignon (1889) described some of the air spaces in the head and neck of *Diomedea fuliginosa*, and Ulrich (1904) emphasized in his work the body sacs in *D. exulans* and *D. fuliginosa*. But we have been unable to find an account of any part of the system in *D. immutabilis*.

A general list of the parts of the air-sac system and their diverticula, as used in this study, is given below in an attempt to reduce the confusion of the rather widely divergent names found in the literature. For the most part, the names we use follow those of Ulrich (1904) and Müller (1908); "D" indicates diverticulum.

Interclavicular sac (single)
- A. Medial chamber
  1. D. claviculare
  2. D. esophago-tracheale
  3. D. subcordale
- B. Lateral chambers
  1. D. subpectorale (pt. D. axillare) and
     D. propatagale (pt. D. sternale)
  2. D. subdeltoidea (pt. D. axillare)
  3. D. subscapulare
  4. D. suprahumerale

Cervical sacs (paired)
- A. Intervertebral diverticula (D. supravertebrale)
- B. Intravertebral diverticula (D. supramedullaria)

Anterior thoracic sacs (paired), with D. postcardiale

Posterior thoracic sacs (paired, no diverticula)

Abdominal air sacs (paired)
- A. D. femorale
- B. D. renale
- C. D. dorsale

METHODS AND MATERIALS

In past years we have experimented with several different techniques in attempts to obtain molds that reflected accurately the detail and relative sizes of the sacs and their many diverticula and interconnections and which at the same time were durable enough for handling. Further, we desired an apparatus with components that could be easily boxed and carried into the field.

These requirements eliminated use of the techniques of Tompsett (1957) and Braun (1965), which require evacuation chambers large enough to contain the bird. Then, too, in our experience the Tompsett method using Marco resin 26C

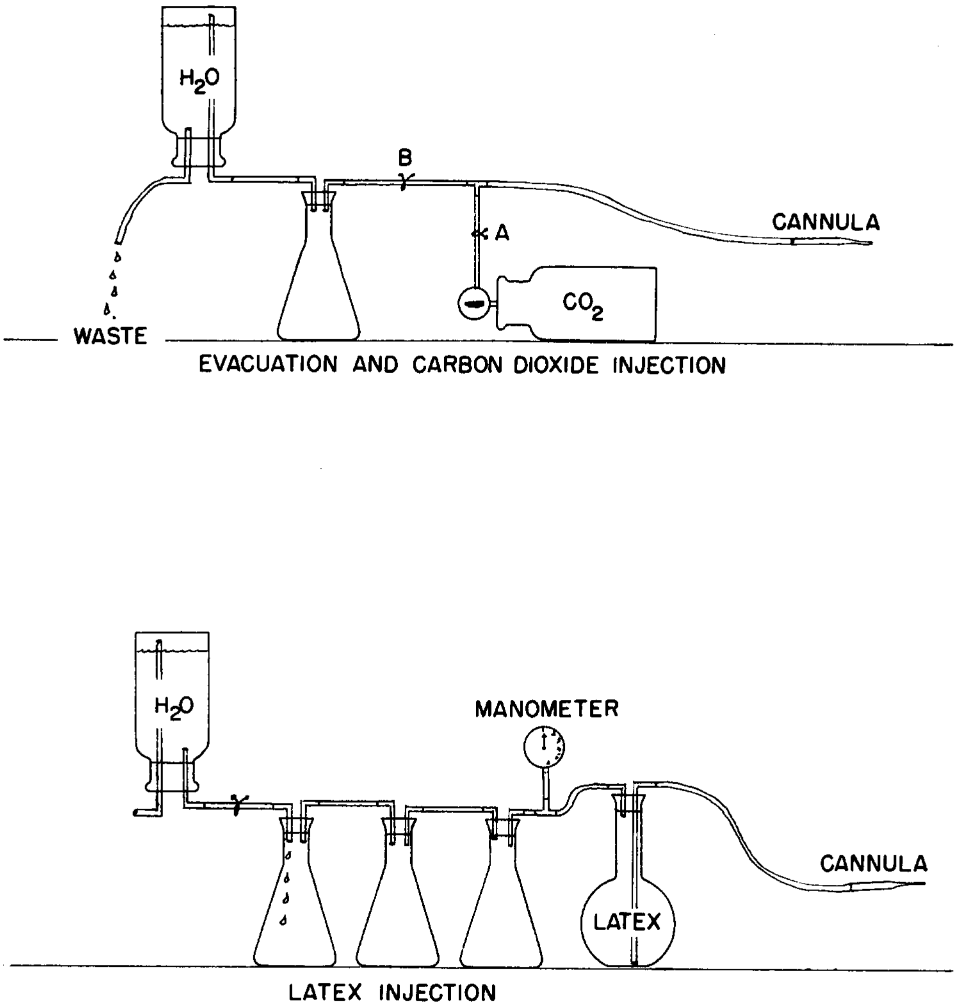

Figure 1. Apparatus for removal of air and injection of latex.

and birds dead for 24 hours produced fragile casts of air spaces that were badly and differentially distended by the gases of decomposition. The silicone foam used by Braun did, in our experience, form durable molds, but the porosity of the resulting "sponge casts" sometimes confused the identification of the smaller ostia and occasionally allowed breakage of small but important details. The primary difficulty with the method of Taylor *et al.* (1962), using methyl methacrylate, was failure of infusion into the finer tubules of the system.

Our procedure, devised several years ago and retained after trials of some more recently described practices, is to evacuate the air, inject carbon dioxide, evacuate the carbon dioxide, and inject latex with the simple apparatus shown in figure 1. The gentle increase in vacuum produced by the water bottle causes no collapse of cavity walls if the rate and level of the vacuum are watched carefully. Since the desired degree of vacuum varies with the species of bird, repeated trials and experience are necessary.

The process is as follows: Insert the cannula in the trachea of the freshly killed bird, close clamp A, and open clamp B. The resulting vacuum slowly produces a slight collapse of the body. Close clamp B and open A to inject carbon dioxide. The evacuation and subsequent injection of carbon dioxide should be repeated several times. Pinch the trachea to prevent the entrance of air and remove the cannula after the final evacuation. Insert the cannula for latex injection through the pinched trachea; do not allow air to be drawn in and be certain the latex is flowing in the cannula. Continue injection until a constant back pressure occurs and is maintained for at least 10 minutes. Tie the trachea below the cannula. Slight body distention and turgidity are the best means of judging whether or not the injection is complete.

The latex and moist tissues absorb small amounts of carbon dioxide in a short time. This absorption causes latex to flow into the remote and minute extensions of the air sacs.

After the injection of the latex the bird is manipulated gently but firmly to facilitate even distribution of the latex. The wings are moved in a manner similar to flight, and the bird is shaken as the body is held. It is then placed on its dorsal surface with the wings in whatever position they naturally fall. The head and neck are flexed and extended several times.

After 12 to 24 hours 10 per cent formalin (pH between 5 and 6) is injected into the esophagus and vent. This speeds up the hardening of the latex. After 24 hours the muscle masses are injected with the same solution, care being taken not to penetrate any of the air sacs, and the specimen is immersed in the solution. The larger the bird and the greater the volume of the air sacs the longer the hardening process, but a bird the size of a chicken or an albatross is ready for dissection in approximately one week. To determine if the latex has hardened sufficiently, a large hypodermic needle may be plunged into the region of the posterior thoracic sac. If latex flows out the needle, replace the bird in the acidic bath and repeat the test at a later time.

Hardening the latex in the absence of air causes little if any shrinkage, and the molds represent approximately fully distended air sacs. Once the casts are freed of tissue by dissection, they are sprayed at short intervals with a synthetic resin (Alvar, Shawinigan Chemicals Ltd., Montreal) to harden them and to fill minor porosities.

In the present study the muscle masses were dissected after the birds were skinned. The sacs were described as encountered, those of the pectoral region being first. After removal of the pectoral girdle, sternum, ribs, and muscle layers, the major sacs and diverticula were studied. It was most convenient to remove the posterior thoracic sac first and work anteriorly to the interclavicular air sac. Then the abdominal sacs, lungs, and cervical sacs were removed. Bone pneumatization was checked last.

Four specimens of each species were used.

OBSERVATIONS ON *DIOMEDEA IMMUTABILIS*

INTERCLAVICULAR AIR SAC

The origin of the interclavicular air sac from the lungs lies just dorsal to the entrance of the primary bronchi. The sac extends anteriorly, broadens dorsally, and has a centrally located portion; ventrolateral chambers are also present. The lateral portions lie on each side of and dorsal to the heart and are united dorsoanteriorly in a flattened, centrally located portion. These lateral expansions give rise to the paired external diverticula and pneumatize the sternal ribs, coracoid, and the spaces between the ends of the sternal ribs, along with D. subcordale. The lateral lobes envelop the primary bronchi, the pulmonary arteries and veins, and the major blood vessels and

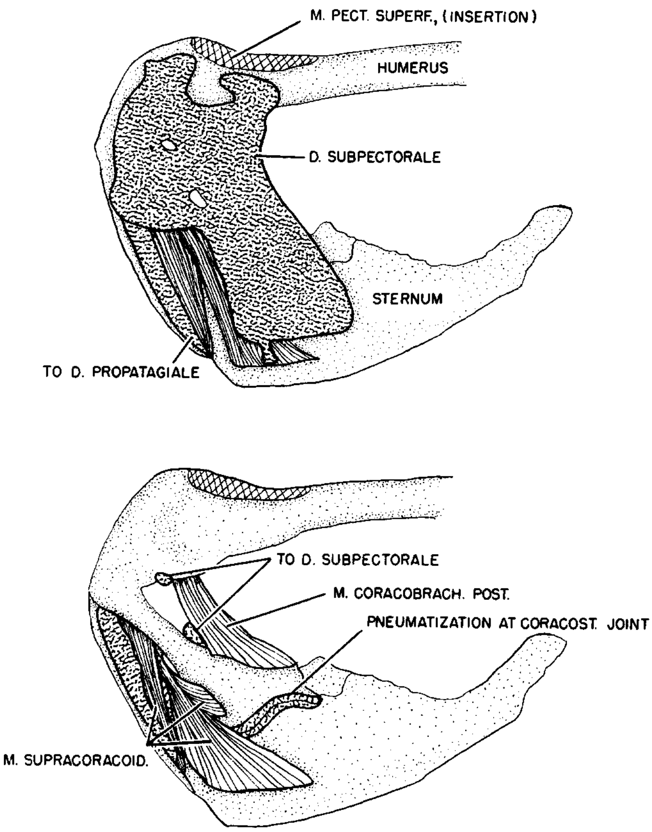

Figure 2. Lateral view of pneumatization of pectoral area in the Laysan Albatross: *top*, after removal of major breast muscles; *bottom*, after removal of D. subpectorale.

nerves of the brachial region. The limit of the posterior extension of the interclavicular sac is difficult to determine since the interclavicular and the anterior thoracic sacs appear to be fused in *D. immutabilis.* Ulrich (1904) did not describe them as being fused in *D. exulans* and *D. fuliginosa.* A deep fissure extends dorsoventrally between the sacs and almost separates them.

Diverticulum claviculare (Fig. 5). Removal of the skin of the neck reveals this arch-shaped sac consisting of two portions joined ventrally and filling the interclavicular fossa. Dorsal to this arch and progressing through it is D. esophagotracheale. Both D. claviculare and D. esophago-tracheale are separated anteriorly by thin, membranous tissue in the sagittal plane. The chambers are not connected; the diverticula simply lie next to each other.

Diverticulum esophago-tracheale (Fig. 5). D. esophago-tracheale is a bulblike form created by the union of the lateral chambers with the centrally located chamber. It projects craniad beyond the arch formed by D. claviculare and separates the trachea from the esophagus.

Diverticulum subcordale (Fig. 5). D. subcordale arises from the medial chamber of the interclavicular sac. This broad, flattened diverticulum dorsal to the sternum

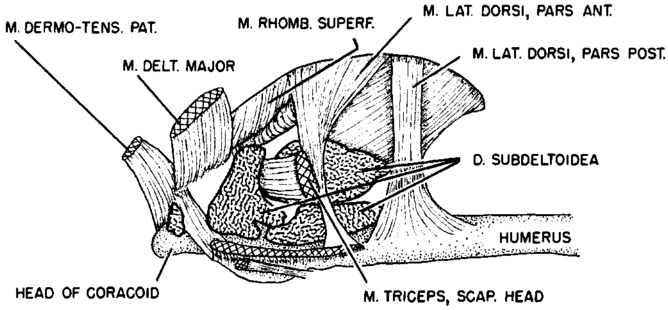

Figure 3. Dorsal view of pneumatization of the shoulder of the Laysan Albatross.

covers the ventral wall of the heart and extends posteriorly to the caudal tip of the heart. It may at times be united along its lateral border with the other portions of the interclavicular sac. This sac pneumatizes both the keel and the lateral borders of the sternum.

Diverticulum subpectorale (Fig. 2). By separating the deep layer of M. pectoralis superficialis and M. dermo-tensor patagii, the anterior lateral portion of D. subpectorale can be seen at a point anterior and ventral to the head of the humerus, deep to the inserting part of M. pectoralis superficialis. Small portions of this diverticulum perforate the keel origin of M. pectoralis superficialis, but the posterior extension is limited by the origin of M. pectoralis superficialis (deep layer) from the sternal plate. Raising the body of the sac reveals that small branches enter the capsule of the coracosternal joint. Others pass anteriorly around the clavicular part of M. supracoracoideus. Still another branch, more caudad, extends between the sternal and clavicular heads of this muscle. These two channels unite deep to M. supracoracoideus and form a flattened portion bounded by the sternoclavicular membrane.

Diverticulum propatagiale (Fig. 2). D. propatagiale arises from D. subpectorale and extends through the triosseal canal along with the tendon of M. supracoracoideus. It is small and lies along the anteroventral aspect of the head of the humerus, but extends ventrally anterior to the coracoid.

Diverticulum subdeltoidea (Fig. 3). D. subdeltoidea arises from the lateral chamber of the interclavicular sac and lies deep to the posterior edge of M. deltoid major. This diverticulum extends craniad to the region of the head of the humerus laterally, deep to M. deltoid major and between the anterior margin of M. triceps (scapular portion) and the origin of the humeral head of M. triceps. It courses around the anterior border of M. triceps (scapular head), forms a flattened portion deep to M. latissimus dorsi and its tendon, and then extends between the scapular head of M. triceps and M. dorsalis scapulae and M. proscapulohumeralis. A finger-like portion lies on the posterior marginal head of the humerus and extends distally along the shaft, ventral to the insertion of M. latissimus dorsi and superficial to M. triceps (humeral head). This portion covers D. suprahumerale. D. subdeltoidea courses deep to M. dorsalis scapulae beneath M. proscapulohumeralis. At this point, another lobe extends caudad, deep to M. dorsalis scapulae and along its ventral border. D. subdeltoidea exits from the body cavity anterior to the brachial nerve complex and subsequently develops the other lateral diverticula (D. subpectorale, D. subscapulare, and D. suprahumerale) of the interclavicular air sac, which are located outside the body cavity.

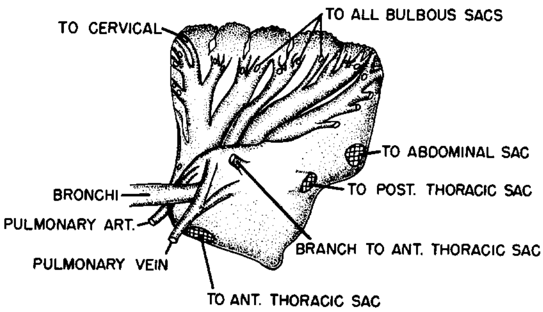

Figure 4. Medial view of surface features of the right lung of the Laysan Albatross.

Diverticulum subscapulare (Fig. 5). This diverticulum, forming with D. subpectorale, D. subdeltoidea, and D. suprahumerale, the axillary extension of the lateral chamber of the interclavicular sac, can be seen upon removal of Mm. rhomboideus superficialis and profundus. D. subdeltoidea and D. subscapulare are united between M. proscapulohumeralis and M. coracobrachialis posterior. D. subscapulare courses along the muscles attached to the scapula and extends only a short distance above the arch of the scapula. Posteriorly, it ends approximately halfway distad on the medial side of the scapula and anterior to D. claviculare. The lateral border is on the scapula and on the muscles attached to the underside of the scapula but lateral to M. serratus profundus.

Diverticulum suprahumerale. D. suprahumerale arises from D. subdeltoidea and extends into the humerus through the foramen in the pneumatic fossa near the head of the humerus.

Cervical Air Sacs

Cervical air sacs (figs. 4, 5) arise from ostia on the anterodorsal edge of the lung. There are also numerous other ostia and small air sacs along this anterior edge. The number of these diverticula varies from side to side and from bird to bird. They form irregularly shaped small sacs which tend to confuse the description of the cervical sacs proper. We limit the term "cervical sac" to the dorsalmost extension which courses craniad and deep to the cervical muscles and which pneumatizes the vertebrae. The other sacs might be considered as extensions of bronchi. There is one pair of these bronchial extensions, which Ulrich (1904) described as cervical sacs, but this description does not fit present-day nomenclature. The members of this pair arise at approximately the same position on either lung. Each sac extends dorsally over the muscles of the neck and between the scapula and body wall. Although Ulrich described it as a cervical sac, in the albatross it would more appropriately be termed an auxiliary diverticulum, deep to M. rhomboideus superficialis. In our four specimens the left side is larger than the right and gives rise to a small, arrow-shaped diverticulum superficial to the ventral cervical muscles, which sometimes unites the right and left auxiliary diverticula. There are also numerous small diverticula between the two lungs and ventral to the vertebrae. They vary in number, size, and origin from bird to bird.

The cervical sacs extend anteriorly, and posteriorly, to fill the intervertebral spaces and to pneumatize the vertebrae as far anteriorly as the axis. The atlas is not

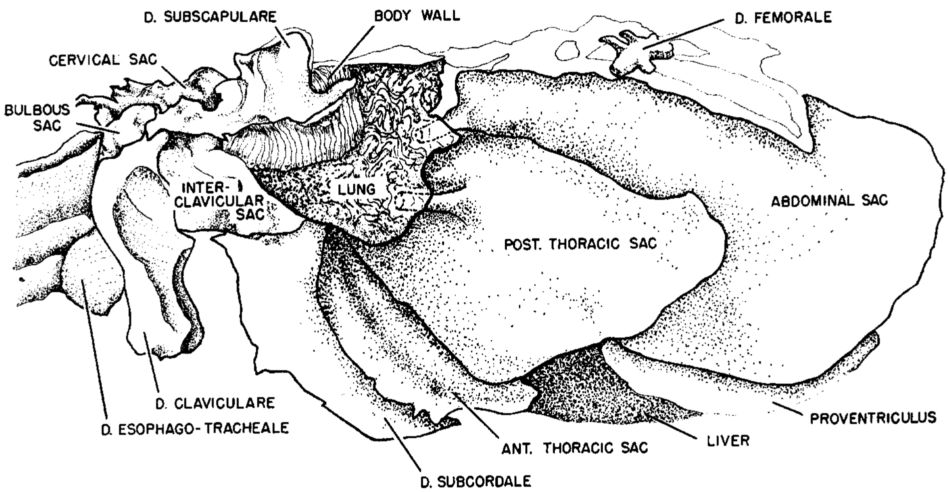

Figure 5. Major air sacs of the Laysan Albatross as seen from left side. All muscles and bones, except the synsacrum, have been removed.

pneumatic. The vertebrae are pneumatized as far posteriorly as the last sacral vertebra; the coccygeal vertebrae and pygostyle are not pneumatic. On each side of the curve of the neck, there occur four irregularly shaped diverticula which lie dorsal to the pre- and postzygapophyses of the vertebrae and deep to M. longus colli posterior.

Anterior Thoracic Sacs

Each sac arises from three points (figs. 4, 5), two from enlarged ostia on the ventralmost edge of the lung and the other from a curious branch on the medial surface of the lung. This branch is less than one centimeter long, extends to the sac and back to the lung, and passes across the pulmonary vein, which is at right angles to it, at its dorsalmost extent. The anterior thoracic sac is bordered anteriorly by the interclavicular sac, caudally by the posterior thoracic sac, laterally and ventrally by both the sternum and the ribs, and dorsally by the lungs. It fills the anterior medial depression in the surface of the lungs. The heads of the sternal ribs are embedded in this sac, and they may be pneumatized as previously mentioned. The other diverticulum from each anterior thoracic sac is a medial one and is larger from the left side; on the right side it is much reduced, existing only as a small, irregular sac. Ulrich (1904:326) described this sac and diverticulum as part of the interclavicular sac, but we believe it should be separated into anterior thoracic and interclavicular sacs. He described the diverticulum as the postcardiale, and we find no reason for modifying the name, although he stated that it arises from the interclavicular sac. The D. postcardiale arises from the left anterior thoracic sac equidistant from the dorsal and ventral and lateral margins of the body. There are two portions: one immediately against the posterior dorsal surface of the heart, between the heart and the anterior lobes of the liver; the second one is more dorsad, much larger, and expands posteriorly as far as the caudal point of the posterior thoracic sac. This larger diverticulum lies between the entire length of the lobes of the liver. Both diverticula lie between the liver and stomach.

Posterior Thoracic Sacs

Each posterior thoracic sac arises from a single ostium in a cleft midway between the dorsal and ventral tips of the posterior edge of the lung (figs. 4, 5). The anterior wall lies against the anterior thoracic sac, the anterior medial surface against the proventriculus and liver, and the posterior medial surface adjoins the lateral wall of the abdominal sac. Laterally, the posterior thoracic sac is next to the abdominal muscles. In lateral view the sac is triangular, with its apex directed posteriorly. In the ventral view the sac is "S" shaped with the lung lateral to the anterior portion and the abdominal sac lying against the posterior, medial surface. It fills the posterior, concave portion of the surface of the lungs. There are no diverticula.

Abdominal Air Sacs

The abdominal air sacs arise from numerous ostia halfway between the origin of the posterior thoracic sac and the dorsal tip of the lung (figs. 4, 5). Some of these ostia may be recurrent bronchi (Müller, 1908). The sac forms from a necklike projection which broadens posteriorly to form one of the two largest sacs in the body. Along this narrow neck portion are diverticula which pneumatize the thoracic, lumbar, and sacral vertebrae, and the ribs. There are also dorsal projections (D. dorsalia) from this neck which spread out between the synsacrum and the kidneys and reproductive organs and a portion which extends through the ilio-ischiadic foramen. The abdominal sacs themselves are large and occupy most of the abdominal cavity. The left sac completely envelops the intestine, and its volume would necessarily be controlled by the size of the digestive tract. Some of the coils of the intestine lie against the right abdominal sac, causing it to have a grooved appearance, but in no case does it envelop the intestine as does the larger and more bulbous left sac. The proventriculus and ventriculus form a groove on the ventral surface of the left sac.

Diverticulum femorale (Fig. 5). This diverticulum arises from the D. dorsale above the kidneys and passes from the body cavity along with the femoral artery. There are four lobes—three anterior and one posterior to the head of the femur. The most anterior lobe lies between M. iliotrochantericus medius and M. psoas. The largest anterior lobe is superficial to M. vastus medialis and deep to M. extensor iliotibialis lateralis. The most posterior lobe of the anterior group is found between M. ambiens, M. psoas, and M. vastus lateralis.

The diverticulum posterior to the head of the femur passes medial and posterior to the shaft of the femur to lie ventral to the insertion of M. flexor ischiofemoralis, posterior to the proximal end of the origin of M. vastus lateralis, and deep and posterior to the belly of M. extensor iliotibialis lateralis.

Diverticulum renale. D. renale is a flattened projection between the kidneys and the synsacrum. It may cushion the kidneys and reproductive organs.

Pneumatization of the Sternum, Coracoid, and Ribs

The sternum appears to be pneumatized in three regions: along the keel and along the line of the articulation of the ribs on either side. The sternal ribs are pneumatized either by D. subcordale via the lateral foramen by way of the sternum or by the diverticula of the lateral chambers of the interclavicular sac itself. The thoracic ribs are pneumatized by diverticula from the intervertebral spaces. The coracoid is pneumatized by way of the expansion of the lateral chambers of the interclavicular sac in the sternocoracoid joint. The diverticulum extends inside the coracoid to the distal end, where it appears to form a pad for the articulation of the scapula or, if not to pad it, to lie against the head of the scapula. There are small sacs lying between the sternum and the coracoid which appear to pad this joint also (fig. 2).

COMPARISONS WITH SHEARWATERS

Wedge-Tailed Shearwater

The structure and relationships of the air sacs in this species are similar to those in the Laysan Albatross, with the following exceptions.

The interclavicular air sac arises from numerous points around the entrance of the primary bronchi into the lung. Diverticulum subdeltoidea is not as extensive. The portion of D. subpectorale that extends deep to M. supracoracoideus does so at the angle of the articulation of the furculum and humerus. It does not course between the clavicular and sternal heads of M. supracoracoideus as it does in *D. immutabilis*, and it does not expand deep to the origin of M. pectoralis superficialis. Diverticulum esophago-tracheale is absent in *P. pacificus* and is one of the two major variations noted between these two species. The anterior thoracic and interclavicular sacs unite in only one area in this species.

Diverticulum femorale is not four-lobed in *P. pacificus*, but it possesses one anterior lobe which lies between M. iliotrochantericus and M. vastus lateralis. A very small diverticulum extends deep to the origin of M. ambiens on the posterior medial side of the femur. Both abdominal sacs envelop the intestine, and the left sac does so to an even greater extent than in *D. immutabilis*. The abdominals are not the largest sacs as they are in *D. immutabilis*; the posterior thoracic sacs have the greatest volume in this species.

The ribs are not pneumatic. The coracoid is not pneumatic from the sternum, and the coracosternal joint does not contain "air cushions." The sac dorsal to the kidneys does not pneumatize the synsacrum as it does in *D. immutabilis*.

Christmas Island Shearwater

The air sacs in this species are very similar to those of *P. pacificus*, and mostly differ in the same way from the arrangement in the Laysan Albatross. Some additional deviations from the situation in the Laysan Albatross are described below. Diverticulum subpectorale does not lie deep to M. supracoracoideus. D. subdeltoidea is small and does not course between M. deltoid major and M. triceps (scapular head). D. subcordale pneumatizes the sternum at its anteriormost point beneath the keel. D. postcardiale is as large on the right as on the left side; the smaller lobe is not present. D. femorale appears relatively larger than in *P. pacificus*; the posterior medial extension is present in this species but absent in *P. pacificus*. D. femorale itself lies between M. ambiens and M. extensor iliotibialis anterior.

SUMMARY

Only minor variations in the air sacs were found among three members of the Order Procellariiformes, including the Laysan Albatross, the Wedge-tailed Shearwater, and the Christmas Island Shearwater. Variations such as the absence of pneumatization of the ribs and coracoid are due, we believe, to the smaller size of the bird. Absence of the Diverticulum esophago-tracheale in *P. pacificus* and *P. nativitatus* may indicate a major variation between the families Diomedeidae and Procellariidae.

An interesting point in the three species is that the heart, liver, kidneys, testes, ovaries, and intestines are completely surrounded by air sacs. These air chambers appear to form a cushion or shock absorber around each organ. This is especially true of the kidneys, reproductive organs, and heart.

There is little individual variation indicated by our specimens. No sexual variation was noted as a constant feature, but the volume of the air sacs, particularly the abdominal, was much less in a female that contained a large egg.

The only pair of sacs that would be satisfactory for volumetric study is the posterior thoracic. If pressure remained constant, the comparative volumes would be valid, since the structures surrounding these sacs are fairly rigid and constant in position.

ACKNOWLEDGMENTS

We wish to thank the Office of Naval Research (Contract 3479 (00)) for partial support of this study, as part of a major investigation of the Laysan Albatross, and the Graduate School of Southern Illinois University for additional funds.

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