

## A CT-based survey of supramedullary diverticula in extant birds

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Birds are unique among extant tetrapods in having pneumatic diverticula of the lungs and air sacs that pass among the viscera and muscles, under the skin, and into the skeleton. In addition to those well-documented diverticula, some birds also have supramedullary diverticula inside the neural canal, adjacent to the spinal cord. The anatomy of the supramedullary diverticula has only been documented in a handful of birds to date, including pigeons, turkeys, and ostriches. Using CT scans, we surveyed the morphology of the supramedullary diverticula in a phylogenetically broad sample of extant birds.

In taxa we have surveyed to date, supramedullary diverticula are present in *Anas* (Anseriformes), *Aphelocoma*, *Melozona*, *Psaltriparus* and *Turdus* (Passeriformes), *Bubo* (Strigiformes), *Buteo* and *Cathartes* (Accipitriformes), *Calypte* (Apodiformes), *Larus* and *Uria* (Charadriiformes), *Meleagris* (Galliformes), *Nycticorax* and *Pelecanus* (Pelicaniformes), *Phalacrocorax* (Suliformes), *Puffinus* (Procellariiformes), *Pyrrhura* (Psittaciformes), and *Zenaida* (Columbiformes). However, they are absent in *Dryobates* and *Melanerpes* (Piciformes), *Falco* (Falconiformes), *Aechmophorus* (Podicipediformes), and *Gavia* (Gaviiformes).

Although supramedullary diverticula are present in some small-bodied taxa such as hummingbirds and pigeons, the diverticula are typically larger and more complex in large forms such as ostriches and pelicans. Absence of these diverticula in loons and grebes is consistent with the lack of skeletal pneumatization in diving birds. Other absences, for example in the kestrel, are less explicable.

When present, the supramedullary diverticula are best developed in presacral vertebrae, but only occasionally present in the synsacrum, and rarely present in the free caudal vertebrae. In the presacral series, these diverticula tend to be larger and more continuous in cervicals. Typically they are developed as bilaterally paired tubes dorsolateral to the spinal cord. In most taxa we have surveyed, the diverticula are not continuous craniocaudally, but exist as separate segments extending fore and aft from each intervertebral joint, as documented by Müller for the pigeon.

Occasionally supramedullary diverticula communicate with interosseous diverticula through foramina in the wall or roof of the neural canal. These foramina are osteological correlates of supramedullary diverticula and allow the presence of these diverticula to be inferred in fossil organisms.

## Present

- Great horned owl (Bubo, Strigiformes)
- Red tailed hawk (Buteo, Accipitriformes)
- Anna's hummingbird (Calypte, Apodiformes)
- Turkey vulture (Cathartes, Accipitriformes)
- Western gull (Larus, Charadriiformes)
- Wild turkey (Meleagris, Galliformes)
- Black-crowned night heron (Nycticorax, Pelicaniformes)
- Brown pelican (Pelicaniformes)
- Ostrich (Struthioniformes)

## Absent

- Western grebe (Aechmophorus, Podicipediformes)
- American kestrel (Falco, Falconiformes)
- Pacific loon (Gavia, Gaviiformes)
- Acorn woodpecker (Melanerpes, Piciformes)
- Nuttall's woodpecker (Dryobates, Piciformes)