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The occurrence and position of the "connecting sac" in the nasal tract complex of small odontocetes (Mammalia, Cetacea)

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ABSTRACT

The aspects of the "connecting sac" are studied in *Lagenorhynchus albirostris, Lagenorhynchus obliquidens, Lagenorhynchus acutus, Tursiops truncatus, Delphinus delphis, Phocoena phocoena, Sotalia guianensis, Stenella coeruleoalba* and *Stenella frontalis.*

Comparing the development of the connecting sac in the various species it is found that there are great variations. These variations are also found in the various individuals of the same species. For this reason the importance of this structure in sound-production is open to doubt.

The development of the connecting sac seems to be related to the development of the posterior part of the naso-frontal sac in such a way that, when a large and well developed posterior part of the naso-frontal sac is present, the connecting sac is small. The extreme situation is found is *Phocoena phocoena* where the posterior part of the naso-frontal sac is very large, while the connecting sac is often found to be reduced or completely absent.

In their paper on the functional anatomy of the delphinid nose, Lawrence & Schevill (1956) describe the complex nasal tract of *Tursiops truncatus* (Montagu, 1821) in which they distinguish four pairs of airsacs in the part of the nasal canal between the blowhole and the bony nares. When exploring the nasal canal from the blowhole one finds a pair of "vestibular sacs", situated lateral to the nasal passage. Beneath this level a pair of "tubular sacs" surrounding the nasal canal in two pneumatic semicircles which are blind diverticulae of the upper nares. This part of the nasal canal is situated above the level of the nasal plugs which can seal this part from the more deeply lying part of the nasal canal between the plugs and the larynx.

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Beneath the plugs, a pair of rostral extensions of the nasal canal, the "premaxillary sacs", cover a part of the premaxillary bones rostral to the bony nares. The dorsal wall of the premaxillary sacs are overlaid by the nasal plug muscles that originate on the premaxillary bones rostral to the airsacs and insert in the connective tissue of the plugs.

A fourth pair of airsacs described by Lawrence & Schevill (loc. cit.) are the "connecting sacs". They are extensions of the posterior wall of the nasal canal just ventral to the entrance to the tubular sacs.

Lawrence & Schevill found that these sacs could form a connection between the parts of the nasal canal above and beneath the plugs when the latter seal the passage.

Murie (1871) describes in *Grampus rissoanus* (= *Grampus griseus* G. Cuvier, 1812) seven airsacs, three being on the left and four on the right side of the nasal canal. The fourth sac on the right side can be seen as the anterior part of the naso-frontal sac (is "tubular sac" after Lawrence & Schevill, 1956). In his work on *Lagenorhynchus albirostris* (Gray, 1846), Murie describes only three pairs of airsacs.

Gruhl (1911) found in *Tursiops truncatus* and *Lagenorhynchus albirostris* in addition to the major pairs of airsacs an extra pair of "Blindsäcke" lying just beneath the level of the "Haupthöhle" (is "tubular sacs" after Lawrence & Schevill, 1956).

Evans & Prescott (1962) concur with the idea of Lawrence & Schevill that the connecting sacs provide the only direct passageway for air from the tubular sacs into the premaxillary sacs. In their opinion a connection like this is necessary because they think the source for noises of high frequency lies in this part of the nasal canal and not in the larynx were no structures as vocal cords or vocal folds can be found. In their opinion this is the only way the sound source can work without interfering with the tight sealing of the blowhole.

Rawitz (1900) describes four pairs of airsacs in *Phocoena phocoena* (Linnaeus, 1758). He does not mention, however, a pair of connecting sacs.

All investigators mentioned above, describe the connecting sacs as being blind ending sacs. This is not strange as all the airsacs in the nasal tract are blind diverticulae.

Dudok van Heel (1970) describes a bulb-like structure as a diverticulum in *Orcinus orca* (Linnaeus, 1758) with tube-like connections distally towards the premaxillary sacs below the level of the plugs and proximally to the tubular sacs above this level (see figure 1). He suggests that this type of "connecting sac" (which would be a real connecting structure) was found in other species such as *Lagenorhynchus obliquidens* Gill, 1865, *Lagenorhynchus albirostris* and *Tursiops truncatus*. In his book he does not mention any other connection to the nasal tract except these two tubes.

The material for the present study consisted of several individuals of *Phocoena phocoena*; three specimens *Lagenorhynchus albirostris*; two *Tursiops truncatus*; three *Delphinus delphis* Linnaeus, 1758; one *Sotalia guianensis* (P. J. van Beneden, 1864) from Surinam; one *Stenella coeruleoalba*

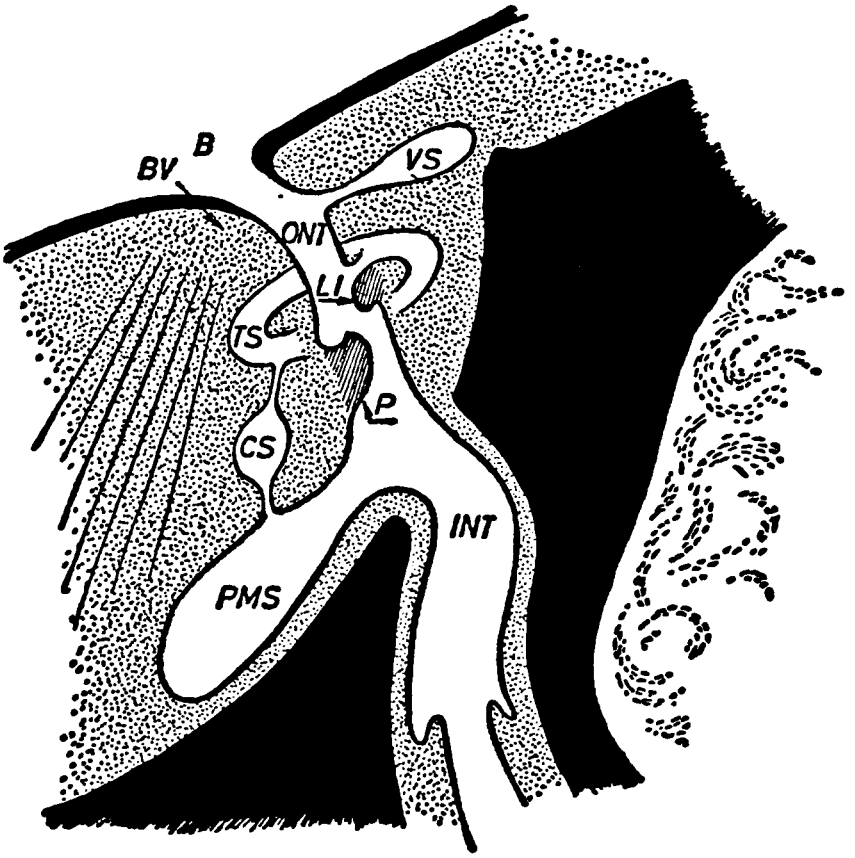

FIG. 1. Diagram of the nasal tract after Dudok van Heel (1970 : 66). CS = connecting sac, TS = tubular sac, PMS = premaxillary sac, P = nasal plug.

(Meyen, 1833); one *Lagenorhynchus acutus* (Gray, 1828); and two *Stenella frontalis* (G. Cuvier, 1829) from off the Ivory Coast. All this material was fresh or nearly fresh, and deepfrozen until there was an opportunity for precise examination. Only one head of a *Stenella frontalis* was preserved in formalin, which gave me the possibility to dissect the diverticulae while keeping them in their natural shape and position.

This is important to show the interposition of the different parts of the nasal tract.

Of all these heads the nasal canal, the diverticulae and the intrinsic muscles were examined. All the skulls are now in the Institute of Taxonomic Zoology (Zoological Museum), University of Amsterdam, with the exception of the skeletons of *Stenella coeruleoalba* and *Lagenorhynchus acutus*, which belong to the Rijksmuseum van Natuurlijke Historie, Leiden.

In most cases nothing like a connecting sac or other structure like a blind ending sac was found in *Phocoena phocoena*. Only in two heads there was a

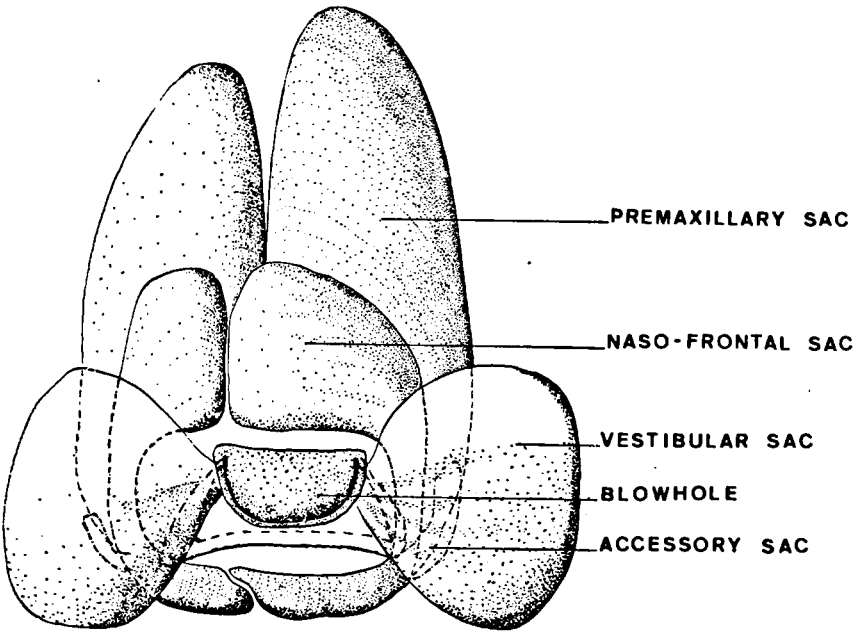

FIG. 2. Diagram of the dorsal view of the nasal tract and its diverticulae in *Lagenorhynchus albirostris.*

very small (length = 7 mm, diameter = 3 mm) sac-like structure in the right part of the nasal tract and an even smaller one on the left side.

In correlation to the asymmetrical development in the narial region in cetaceans in which the right side is always larger than the left (see figure 2), the smaller size of the connecting sac is quite normal. Both diverticulae were found just ventral to the most lateral part of the naso-frontal sac or tubular sac of Lawrence & Schevill (loc. cit.) (see figure 3).

We prefer the name which Murie (1871) and Huber (1934) used because this air chamber is not always tubular.

In all the other species of odontocetes examined I found structures described as "Blindsäcke" by Gruhl (1911) and as "connecting sacs" by Lawrence & Schevill (1956). In all these species the diverticulum on the right side of the nasal canal was far larger than that of the left side. This difference can be considerable as I found in *Tursiops truncatus,* in which the right sac had a length of about 3 cm while that on the left side was just a few mm in length. These structures were extensions of the wall of the nasal canal with its entrance just ventro-caudal to the entrance of the naso-frontal sac but above the level of the diagonal membrane that forms the dorsal limit for the movements of the plugs (Lawrence & Schevill, loc. cit.).

In *Lagenorhynchus albirostris* the difference in size of the diverticulae of both sides is less (left = 2 cm, right = 3.5 cm). One finds the same situation in other species of this genus.

The opinion of Evans & Prescott (1962) that the connecting sacs play an

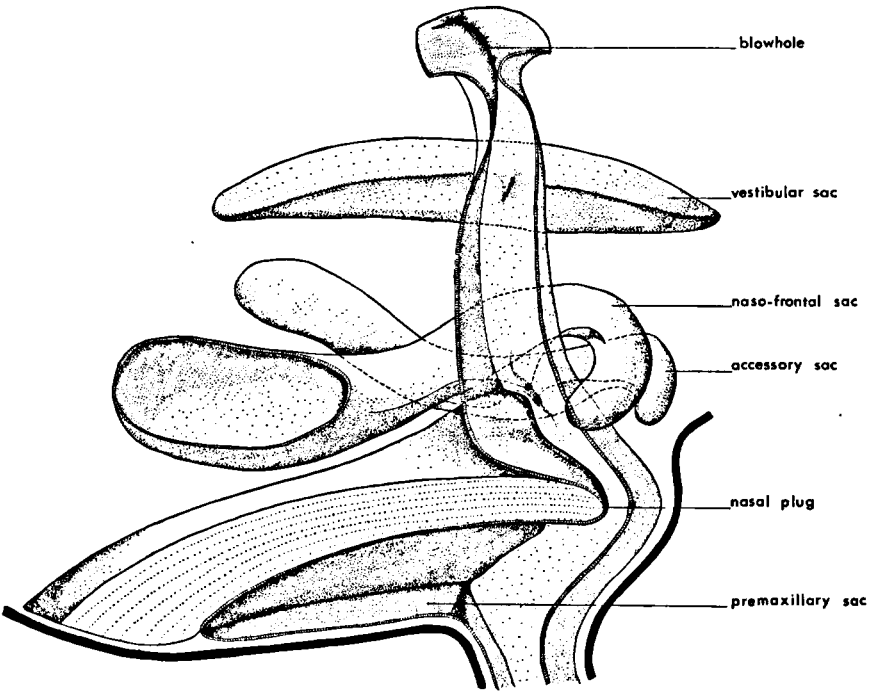

FIG. 3. Diagram of the medial view of the right part of the nasal tract and its diverticulae in *Lagenorhynchus albirostris*.

important role in sound production seems not to be realistic, for in most specimens of *Phocoena phocoena*, which make noises of the same character as in other odontocetes, no structures that can be related to a connecting sac were found. Moreover, I found a great difference in the development of airsacs in animals of one species, and an even greater variety in animals from different species. Therefore, it would seem that the name accessory sac will be a better name as this sac does not connect parts of the nasal canal diverticulae when the plugs are lying in their closed position.

Air may slip from below to the naso-frontal sacs only along the edges of the plugs and for this purpose, a structure like an airsac is not necessary. When examining the nasal canal from the accessory sac, an extension of the lateral margin of the plug can be seen in some cases protruding into the entrance of the accessory sac (see figure 3). Air can pass along this structure but it is not certain whether the plugs are in closing position when this happens.

If air does pass, the accessory sac can only be seen as a safety air reservoir in the event that there is a need for some more air in the uppermost part of the nasal tract between the plugs and the blowhole. It is improbable that a specialised structure like this diverticulum is provided for passing some air,

because it is easier to slip some air along the median lining of the plugs. Moreover one wonders how this important role is served in cases were no special airsacs consist.

In *Lagenorhynchus albirostris* the accessory sac is well developed and consists of two parts; one anterior part lying anterior to the entrance to the nasal canal with a length of about 3.5 cm and a diameter of about 1 cm. On the left side I found an anterior part only with a length of about 2 cm.

The small entrance from the nasal canal to the accessory sac was placed on the edge formed by the maxillary and premaxillary bones, just above the level of the caudo-lateral margin of the nasal plug but somewhat caudo-ventral to the entrance to the naso-frontal sac.

In other species like *Lagenorhynchus obliquidens, Lagenorhynchus acutus, Delphinus delphis, Stenella coeruleoalba, Stenella frontalis,* and *Sotalia guianensis* I found the same structure, though there was a great variation in development of the anterior part of the accessory sac while the posterior part in many cases was poorly developed.

In *Tursiops truncatus* the accessory sac on the right side had a size comparable to that found in *Lagenorhynchus albirostris,* but on the left side I found only a very small extension of the wall lining the nasal canal.

In *Stenella coeruleoalba,* the accessory sac was even bigger than in *Lagenorhynchus albirostris,* while the length of the skull was about half its size.

I have the impression that the development of this air chamber depends on the size of the posterior part of the naso-frontal sac in such a way that the larger the latter is, the smaller is the accessory sac.

In *Phocoena phocoena* for example, where structures like an accessory sac are found in a few examples, the posterior part of the naso-frontal sac is so large that it even consists of two parts behind each other, while in *Stenella coeruleoalba* the posterior part of the naso-frontal sac is a tiny tubular structure.

This relation can be important for keeping the nasal canal in place when the blowhole is sealed by air-pressure, because these airsacs are lying between the nasal tract and the narial bones and act as a buffer.

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