

Functional anatomy of the vomeronasal complex in the embryonic development of the pig (*Sus scrofa dom.*)

Angela WÖHRMANN-REPENNING and Ulrike BARTH-MÜLLER

Wöhrmann-Repennig A. and Barth-Müller U. 1994. Functional anatomy of the vomeronasal complex in the embryonic development of the pig (*Sus scrofa dom.*). Acta theriol. 39: 313–323.

The vomeronasal complex of 5 different aged pig embryos *Sus scrofa dom.* Linnaeus, 1758 with a total length (TL) of 330, 180, 75, 50 and 45 mm respectively were studied. In all cases the nasopalatal part surrounding Jacobson's organ was generally established. During the studied period of development the completion of details within the cartilaginous supporting structures were of primary interest. In the youngest embryo studied, ducts and furrows of the vomeronasal complex were blocked by fused epitheliums. Their dissolvment was completed in an embryo of 57 mm (TL). The elaborated vomeronasal complex of the oldest embryo allowed some further analyses. So it proved that all morphological peculiarities of the supporting structures, the nasopalatine ducts and the papilla palatina in pigs are an indication of their importance to a properly functioning vomeronasal complex. As pigs have no rhinarium or cleft snout of the kind found in most mammals, no philtrum communicates with the sulcus papillae palatinae and the nasopalatine ducts where Jacobson's organs merge into. Their flat snout is however provided with a distinct ventral groove which is obviously a substitute for the missing philtrum. Generally it was possible to classify the vomeronasal complex in *S. scrofa* from a phylogenetic point of view. As this anatomical system in placental mammals fundamentally reveals two differing construction types, classified as either primitive or progressive *S. scrofa* possesses a progressively developed vomeronasal complex.

Department of Zoology and Comparative Anatomy, University of Kassel, Heinrich-Plett-Str. 40, D-34109 Kassel, Germany

Key words: *Sus scrofa dom.*, Jacobson's organ, vomeronasal complex, functional anatomy

Introduction

Since Jacobson (1811) first described his observation of a paired organ in mammals situated in the nasal cavity, this organ, named after him, has been the centre of numerous publications under many different aspects (Herzfeld 1889, Broman 1920, Estes 1972, Johns 1978, Hofer 1982, etc.). Its histology soon showed it to be an accessory olfactory sense organ (Balogh 1891) while its biological function is still discussed frequently and controversially (Prescott 1977, Bailey 1978, O'Brien 1982, Hart 1987, etc.).

It was the merit of Broom (1898) to first recognize that this organ, belonging to a specially constructed part of the nose and rostral palate (called the vomeronasal

complex) follows two different construction types in mammals. They refer to the arrangement of the cartilaginous supporting elements which ensues from a differing relationship between Jacobson's organ and the nasopalatine duct. It follows that there are obviously two fairly well marked varieties of a vomeronasal complex within placental mammals. For that reason the knowledge of the morphological situation of the vomeronasal complex in mammals allows, to some degree, phylogenetic conclusions (Wöhrmann-Repenning 1984a, b). To increase the insight into these problems, it makes sense to study a broad variety of placental mammals. Besides previous studies have shown that each group of mammals and even each species has its own specialities concerning the arrangement of their vomeronasal complex (Wöhrmann-Repenning 1984b, 1987, 1993). This in turn is helpful in gaining a better understanding of the general situation. In addition, all the differing morphological details help to give a better understanding of the function of Jacobson's organ within the vomeronasal complex.

Up to now many papers have been published concerning the function of Jacobson's organ from a behavioural and physiological point of view for *Artiodactyla* (Jacobs *et al.* 1980, Ladewig and Hart 1980, Hart 1983, Melese-D'Hospital and Hart 1985, etc.). There are, however, very few studies describing its anatomical situation in relationship to its functioning. Therefore this paper will deal with the morphology of the vomeronasal complex in *Sus scrofa* under functional and phylogenetic aspects. It will be followed by other investigations on this subject for other artiodactyls.

Material and methods

For the present investigation series of cross sections of ten noses of different aged pig embryos (*Sus scrofa f. domestica* Linnaeus, 1758) were available. Their total length (TL), measured from the crown of the head to the curvature of the rump, was 45, 50, 57, 180 and 330 mm respectively. The embryos had been collected by the State Veterinary Research Center, Kassel and had been fixed by immersion in formol. The cross sections of 10 μ were stained mainly with azan and Delafield's hematoxilin and eosin. For a better understanding the description of a morphological situation of the vomeronasal complex in pig embryos will start with the oldest embryo studied.

Results

Embryo (TL 330 mm)

In a pig embryo with a total length of 330 mm the vomeronasal complex is already well arranged in details. Jacobson's organs are two distinct tubes, each completely encompassed by a paraseptal cartilage. Rostrally where Jacobson's organ merges into the nasopalatine duct, each paraseptal cartilage splits into a dorsal and a ventral branch. The dorsal part continues rostrally into the lamina transversalis anterior, while the ventral branch dorsally encircles the opening of Jacobson's organ (Fig. 1II, III).

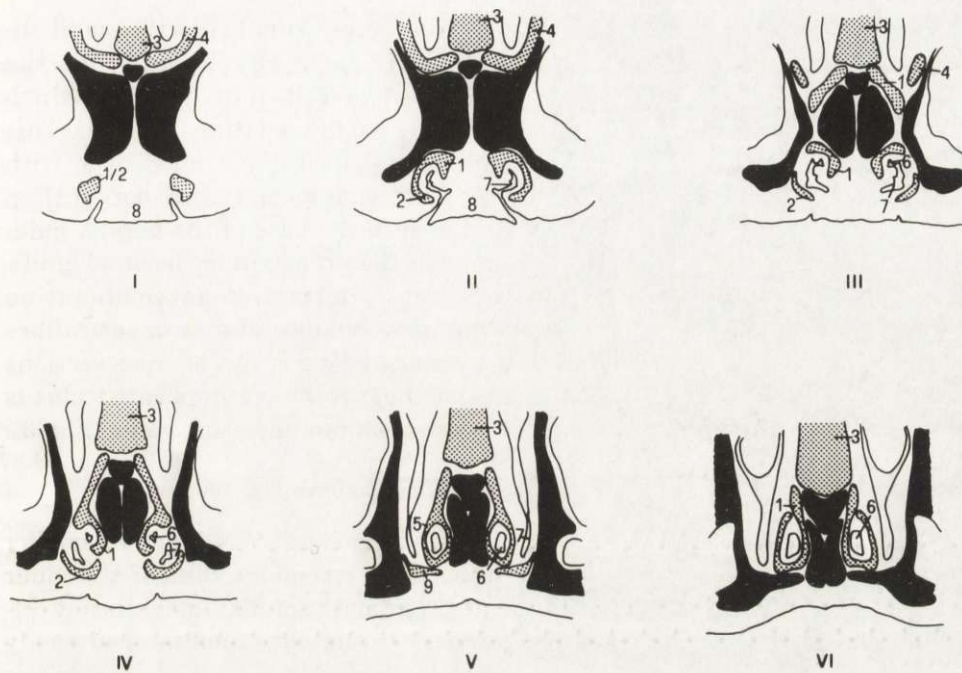


Fig. 1. Schematic representation of the rostral palate and the ventral half of the cavum nasi of *Sus scrofa* (Embryo, TL 330 mm) in six cross sections (I-VI). Black - bone, stippled - cartilage, 1 - cartilago paraseptalis, 2 - cartilago ductus nasopalatini, 3 - septum nasi, 4 - lamina transversalis anterior, 5 - outer bar of the cartilago paraseptalis, 6 - Jacobson's organ, 7 - ductus nasopalatinus, 8 - papilla palatina, 9 - cartilago palatina.

Caudally, directly adjacent to this branched area the paraseptal cartilage encloses the organ completely by forming a tunnel-like structure with an additional dorsal crest (Fig. 1V). This cartilaginous tube measures 2650 μm altogether. Further along the paraseptal cartilage remains a tunnel-like element but now with an extremely narrow dorso-lateral slit, which is just big enough to allow small bundles of nerves to leave the enclosed Jacobson's organ in a dorsal direction (Fig. 1VI).

In addition to the paraseptal cartilage rostrally some other cartilaginous elements are necessary to produce a functioning vomeronasal complex. One of these is a cartilago ductus nasopalatini, which forms a shallow groove supporting the nasopalatine duct ventrally. Rostral to the opening of Jacobson's organ it fuses with the ventral branch of the paraseptal cartilage. Caudally this element merges into the sturdy plate supporting the nasal floor of the cartilago palatina (Fig. 1III-V).

The nasopalatine ducts penetrate the rostral palate thus providing a connection between the nasal and the oral cavity. They pierce the gum at a slight angle (Fig. 1III-V) and continue as very narrow passages except for in the ventral part, where Jacobson's organ merges into them. Here their lumen increases to a kind of vesicle



Fig. 2. Cross section of the nasopalatine duct of *Sus scrofa* (Embryo, TL 330 mm). The vesicle-like part is amply supplied with small diverticles. 10 μ m Delafield's hematoxylin and eosin.

which is amply supplied with small diverticles (Fig. 2). On the oral side the ducts open laterally into the sulcus which forms the papilla palatina (Fig. 1II). This papilla is shaped like a mushroom with valve-like lobes along its oral border (Fig. 3). Between the base of the papilla palatina and the premaxillary bone a significant vessel formation in combination with nerve bundles of a stronger calibre are situated. The series of cross sections reveal them to be a complicated plexus of variably communicating veins (Fig. 3).

Embryo (TL 180 mm)

The vomeronasal complex of the smaller pig embryo resembles that of the older pig embryo in most details. Insignificant differences to the older embryo can easily be described. Almost all characteristic elements are present, even the suspicious vessel plexus at the base of the papilla palatina is extant. Only the cartilago palatina is still missing at this stage. The lateral supporting element of the naso-

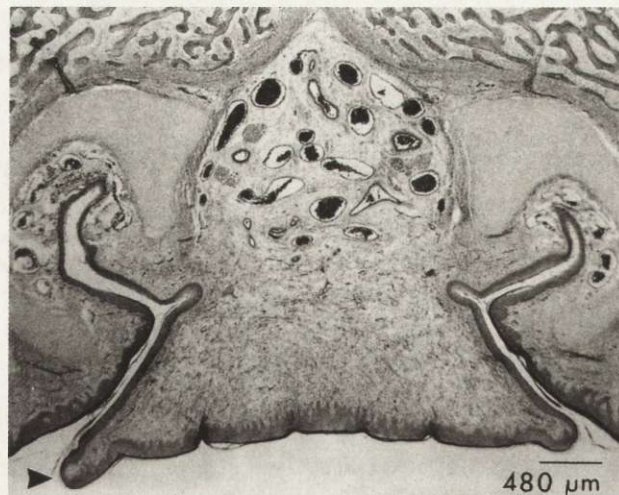


Fig. 3. Cross section of the papilla palatina of *Sus scrofa* (Embryo, TL 330 mm) with valve-like lobes (arrow) at its oral border. Between the papilla palatina and the premaxillary bone a conspicuous vein plexus is situated. 10 μ m Delafield's hematoxylin and eosin.

palatine duct, the cartilago ductus nasopalatini, is not yet present. Generally we can say that every detail of the vomeronasal complex in this early stage is still a bit compressed. It is obvious that the vomeronasal complex in the embryo with a length of 180 mm is generally complete and that it just needs to grow.

Embryos (TL 57 and 50 mm)

In embryos of *Sus scrofa* with a total length of 57 and 50 mm there are no significant differences present, concerning the morphology of their vomeronasal complex, so that they can be described together.

Jacobson's organs are already well developed and are embedded within the paraseptal cartilage. In contrast to the older embryos, however, it still has the form of a shallow groove and instead of a narrow gap there is a broad dorsal aperture. The cartilaginous components accompanying the very rostral part of Jacobson's organs, are up to this stage not fully developed. There is no outer

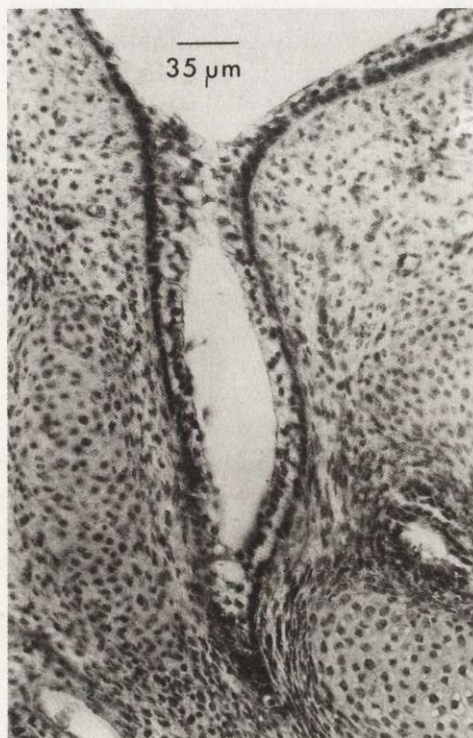


Fig. 4. Cross section of the nasopalatine duct of *Sus scrofa* (Embryo, TL 50 mm). The fused epithelial outlining is just about to split apart. 10 μ m Delafield's hematoxylin and eosin.

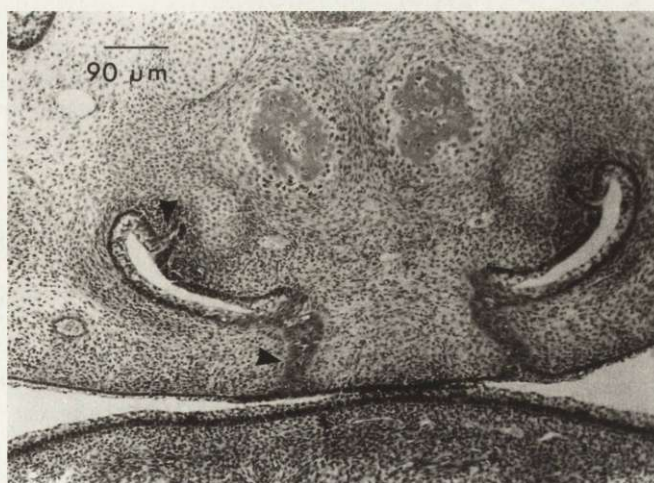


Fig. 5. Cross section of the mergences of Jacobson's organs (upper arrow) into the nasopalatine ducts of *Sus scrofa* (Embryo, TL 45 mm). The sulcus papillae palatinae is marked by fused epithelial sutures (lower arrow). 10 μ m Delafield's hematoxylin and eosin.

bar established yet. The cartilago ductus nasopalatini in both stages and the rostral part of the ventral branch of the paraseptal cartilage in the younger embryo are just marked by a small formation of densely agglomerated cells.

In the smaller pig embryo of 50 mm TL there are still fused epithelial outlings present along the nasopalatine ducts and the sulcus papillae palatinae. They are however obviously about to split apart (Fig. 4). In the older embryo of 57 mm TL they are largely dissolved.

Embryo (TL 45 mm)

Finally the vomeronasal complex of the youngest studied pig embryo with a total length of only 45 mm shall be described. To start with the subject ended in the chapter before: in the present case we still find extended parts of undissolved epithelial sutures. From this results a complete closure of nasopalatine ducts in their ventral parts where they mount into the sulcus papillae palatinae. The dorsal sections of these ducts are open while the mergence of Jacobson's organs are likewise closed here (Fig. 5). The supporting elements of the vomeronasal complex in this early stage are generally prearranged similar to that of the pig embryo of 50 mm TL. Accordingly along the rostral section of the vomeronasal complex some cartilaginous elements are just marked by dense cell formations.

In this young stage of 45 mm TL the epithelial outling of Jacobson's organ is already dimorphly developed. There is a thick epithelial layer of olfactory epithelium coating the medial half of the organ, while the lateral side is covered by a much lower indifferently structured epithelium (Fig. 6).

External anatomy of the nose and palate

The external anatomy of the rostral palate of a late pig embryo of 330 mm length reveals some interesting special morphological features. The conspicuously large papilla palatina is situated directly behind the place where the incisors are soon going to emerge (Fig. 7). Whereas often in mammals the sulcus papillae palatinae communicates rostrally with a median furrow, the philtrum, splitting

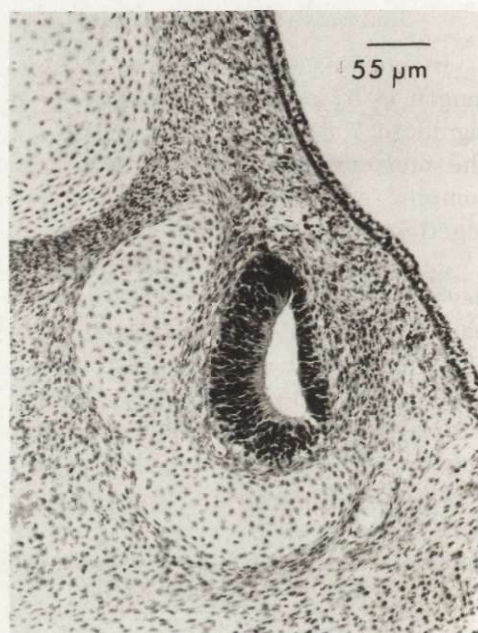


Fig. 6. Cross section of Jacobson's organ of *Sus scrofa* (Embryo, TL 45 mm). 10 μ m Delafield's hematoxylin and eosin.

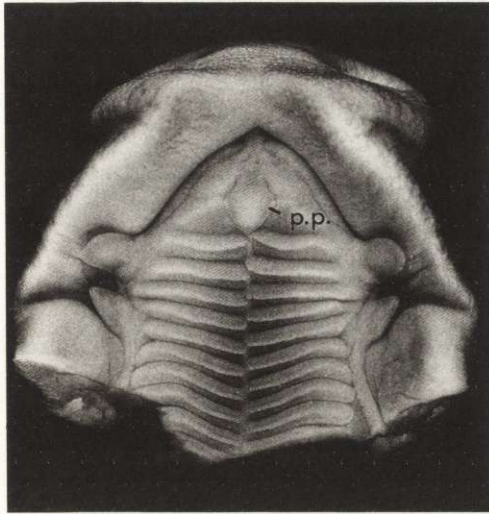


Fig. 7. Rostral view of the palate of *Sus scrofa* (Embryo, TL 330 mm). p.p. – papilla palatina.

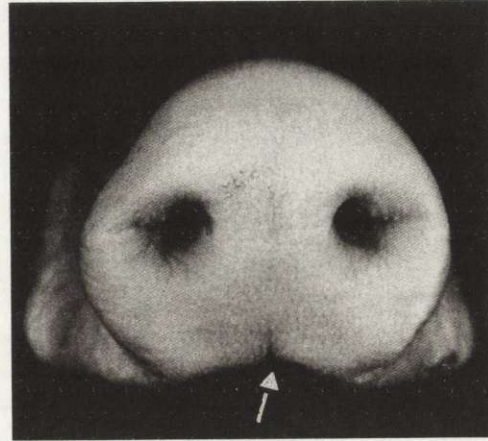


Fig. 8. Frontal view of the flat snout of *Sus scrofa* (Embryo, TL 330 mm). Note the median furrow parting the ventral side (arrow).

their rhinarium, in accordance with that, a deep cleft separates the upper lip in several artiodactyls (Keilbach 1954). In pigs however this is prevented by the well known special anatomy of their flat nozzle. Yet looking at their snout more closely, reveals a distinct median furrow parting the ventral side of their round nozzle (Fig. 8), thus establishing a communication path to the rostral palate where the papilla palatina is located and with it the entrance to Jacobson's organ.

Discussion

Developmental aspects

The vomeronasal complex of 5 different stages of embryos of *Sus scrofa* were studied under comparative aspects. It showed that even in the youngest embryo with a total length of 45 mm the nasal cavity was already properly formed and separated from the oral cavity by a complete secondary palate. As could be expected from former studies on other mammalian embryos (Wöhrmann-Repenning 1981, 1989) this developmental stage includes a vomeronasal complex which is fundamentally prearranged. In detail this means Jacobson's organ has attained its final form that of a caudally closed tube. Its epithelial outling is already distinctly dimorphously differentiated, a process which obviously takes place very early during mammalian development (Starck 1975, Wöhrmann-Repenning 1990). Eventually the skeletal elements of the vomeronasal complex become accentuated and completed during the following development phases. In *Sus scrofa* like in many other mammals (Peter 1902, Wöhrmann-Repenning 1989) this happens

during a certain time of their embryonic life where the epithelial outlinings of the ducts or furrows are fused together thus forming epithelial sutures where passages should be. With only a few exceptions, such as the rat for instance (Wöhrmann-Repenning 1981), the nasopalatine duct and the mergence of Jacobson's organ into it undergoes such a closure during ontogeny. Compared to other investigations by the author in *Galago crassicaudatus* and *Felis silvestris* (Wöhrmann-Repenning 1984b, 1989) where this phenomena of fused epitheliums is exhibited during the late embryonic life, this particular process in *Sus scrofa* takes place much earlier. The reason could be that the latter as a member of *Artiodactyla* is meant to lead an autonomous life immediately after birth, while cats and primates are much more dependent on the care of their mother for a longer postnatal period. This would mean that the phenomena of fused ducts of the vomeronasal complex in mammals could possibly be linked to early functional requirements. For a final conclusion further studies are needed which should necessarily include those mammals where fused epitheliums never occur.

Phylogenetic aspects

Comparative anatomical studies of the vomeronasal complex in mammals show two differently structured types, which are based on two diverging branches of development within placental mammals (Broom 1898, 1915, Wöhrmann-Repenning 1984a, b, 1987, 1993). While the majority of *Placentalia* have developed progressive features in this very special part of the nose, only a few groups have retained a primitively constructed vomeronasal complex as is typical for all *Marsupialia*. The most important criterion of a primitively constructed vomeronasal complex is a simple non-ramified paraseptal cartilage surrounding an organ of Jacobson whose opening is situated at the base of the nasal septum outside the nasopalatine duct. In comparison the progressive features are a rostrally branched paraseptal cartilage with Jacobson's organ merging into the nasopalatine duct inside the palate.

The present investigation proves doubtlessly that the vomeronasal complex in pigs belongs to the progressive line. Both, former results as well as personal experience with other mammals, indicate that this statement is of universal validity for all members of the *Artiodactyla*.

Functional anatomy

The anatomical situation of the vomeronasal complex in *Sus scrofa* reveals several functional aspects. It is apparent that all cartilaginous elements form a perfectly arranged system with two important characteristics. The first of these are skeletal elements that have to provide a completely protected area around the sensitive organs and at the same time have to guarantee the functionality of this system. The paraseptal cartilage is a good example for this: It surrounds and supports Jacobson's organ. The form best suited for this is that of a tunnel,

especially in those species such as pigs, whose snouts are subjected to a great deal of wear and tear. Actually the outer bar, an originally small strap in mammals with a primitively constructed vomeronasal complex (Broom 1898) has in pigs become elongated to form an enlarged tube-like element. For perfect protection it should continue like that, but due to the nerve bundles leaving the tube caudally, a narrow dorsal slit is present. This dorsal cleft of the paraseptal cartilage is rarely as narrow as in pigs.

The requirements for the arrangement of the cartilaginous elements of the vomeronasal complex around its rostral part are even higher. The mergence of Jacobson's organ inside the palate challenges the functionality while maintaining the protective features. In this region, where the ducts, accompanied by bundles of nerves and vessel formations fuse, the supporting structures are necessarily complicated. For this reason a vomeronasal complex of the progressive line, where the mergence of Jacobson's organ is situated inside the palate, produces a much more complex cartilaginous structure than that of the primitive line. In this situation, additional cartilage such as a cartilago ductus nasopalatini and a cartilago palatina gain in importance. Consequently, in a primitive vomeronasal complex, those skeletal elements – as far as they are present – are smaller and obviously less important. In the progressive vomeronasal complex however – the pig demonstrates it exemplarily – they tend to be broad and form extended layers. Like in the present case, they often fuse into one big cartilaginous element with two functions: While the cartilago ductus nasopalatini sustains the lateral side of the nasopalatine duct, the caudal cartilago palatina preserves a ventral closure of the osseus incisive window. Because of their complicated formation, the nomenclature of this rostral region is often very confusing (Spurgat 1896, Sturm 1936, and others), which naturally makes understanding the various elements and spotting homologies more difficult. Problems resulting from this have been discussed in detail (Wöhrmann-Repenning 1984b). In *Sus scrofa* the ventral branch of the paraseptal cartilage is sometimes confused with the cartilago ductus nasopalatini (Sturm 1936).

From a functional point of view also the morphology of the nasopalatine ducts in combination with the shape of the papilla palatina draws attention. The present investigation in pigs confirm the findings in other mammals (Wöhrmann-Repenning 1991). Generally those ducts are extremely narrow except for the region where Jacobson's organs merge into them. It is this part which is always somewhat widened. In addition in this region pigs have a great deal of diverticle-like folds. This confirms the suggested function of this vesicle as a reservoir for fluid samples meant for Jacobson's organ.

The papilla palatina in pigs is shaped like a mushroom which underlines its function as a plug. Supplementary folds along its ventral border are not unique to this species alone, but are also frequently present in other mammals (Wöhrmann-Repenning 1980). Their function as a kind of gasket has been previously discussed. The plug like motion of the papilla palatina is most probably induced by the

conspicuous vein formation located between the base of the papilla and the premaxillary bone (Wöhrmann-Repenning 1991).

Finally the functional side of the anatomical situation of the rostral palate and the snout in pigs should also be mentioned. In mammals the tip of the nose often shows the following situation: A medial philtrum splits the snout or a naked rhinarium. This philtrum ventrally communicates directly with the sulcus surrounding the papilla palatina. *Sus scrofa* does not have such a deep furrow splitting its nozzle. Its snout is flat and unfissured instead. A thorough inspection of it however reveals a distinct groove segmenting its ventral side. It is likely that this groove substitutes the missing philtrum in function. It should guarantee fluid samples a direct oral communication path towards Jacobson's organ.

Acknowledgements: We are very grateful to Drs W. Becker and K. Wagner (State Veterinary Center, Kassel) for providing us with the pig embryos and to Mr M. Westfall for kindly proofreading the English. Our special thanks is due to Mrs A. Scheuer for her skilful technical assistance.

References

- Bailey K. 1978. Flehmen in the ring-tailed lemur (*Lemur catta*). Behaviour 65: 309–319.
- Balogh C. 1891. Das Jacobsonsche Organ des Schafes. Sitz-Ber. Akad. Wiss. Wien, math.-nat. Kl. 42: 449–476.
- Broman I. 1920. Das Organon vomero-nasale Jacobsoni – ein Wassergeruchsorgan! Anat. Hefte 58: 137–191.
- Broom R. 1898. A contribution to the comparative anatomy of the mammalian organ of Jacobson. Trans. Roy. Soc. Edinburgh 39: 231–255.
- Broom R. 1915. On the organ of Jacobson and its relations in the *Insectivora*: Part II. *Talpa*, *Centetes* and *Chrysochloris*. Proc. zool. Soc. Lond. 1915: 347–354.
- Estes R. D. 1972. The role of the vomeronasal organ in mammalian reproduction. Mammalia 36: 315–341.
- Hart B. L. 1983. Flehmen behavior and vomeronasal organ function. [In: Chemical signals in vertebrates III. R. M. Silverstein and D. Müller-Schwarze, eds]. Plenum Press, New York: 87–103.
- Hart B. L. 1987. Roles of the olfactory and vomeronasal systems in behavior. Farm. Anim. Behav. 3: 463–475.
- Herzfeld P. 1889. Über das Jacobsonsche Organ des Menschen und der Säugetiere. Zool. Jb. Anat. 3: 551–574.
- Hofer H. O. 1982. Observation on the anatomy of the proboscis and of the ductus nasopalatinus and ductus vomeronasalis of *Solenodon paradoxus* Brandt, 1833. Gegenbaurs morph. Jb. 128: 826–859.
- Jacobs V. L., Sis R. F., Chenoweth J. P., Klemm W. R., Sherry J. C. and Coppock C. E. 1980. Tongue manipulation of the palate assists estrous detection in the bovine. Theriogenology 13: 353–355.
- Jacobson L. 1811. Description anatomique d'un organe observé dans les Mammifères. Ann. Mus. Hist. Nat. Paris 18: 412.
- Johns M. A. 1978. Urine-induced reflex ovulation in anovulatory rats may be an vomeronasal effect. Nature 272: 446–448.
- Keilbach R. 1954. Vergleichend anatomische Studien über die Säugernase mit besonderer Berücksichtigung des Knorpelskelettes. Wiss. Z. Univ. Greifswald. Math.-Nat. wiss. R. 3: 201–244.
- Ladewig J. und Hart B. L. 1980. Flehmen and vomeronasal organ function in male goats. Physiol. Behav. 24: 1067–1071.

- Melese-DHospital P. Y. and Hart B. L. 1985. Vomeronasal organ cannulation in male goats: Evidence for transport of fluid from oral cavity to vomeronasal organ during flehmen. *Physiol. Behav.* 35: 941–944.
- O'Brien P. H. 1982. Flehmen: Its occurrence and possible functions in feral goats. *Anim. Behav.* 30: 1015–1019.
- Peter K. 1902. Die Entwicklung des Geruchsorgans und Jacobsonschen Organs in der Reihe der Wirbeltiere. [In: *Handbuch der vergleichenden und experimentellen Entwicklungsgeschichte der Wirbeltiere*. Bd. 2/2. O. Hertwig, ed]. Fischer, Jena: 1–82.
- Prescott R. G. W. 1977. A mechanism for the presentation of chemical stimuli to the vomeronasal organ in the cat. *J. Anat.* 123: 244–245.
- Starck D. 1975. *Embryologie*. 3. Aufl. Thieme, Stuttgart: 1–693.
- Spurgat F. 1896. Beiträge zur vergleichenden Anatomie der Nasen- und Schnauzenknorpel des Menschen und der Tiere. *Morph. Arb.* 5: 555–612.
- Sturm H. 1936. Die Entwicklung des präcerebralen Nasenskeletts beim Schwein (*Sus scrofa domestica*) und beim Rind (*Bos taurus*). *Z. wiss. Zool.* 149: 161–220.
- Wöhrmann-Repenning A. 1980. The relationship between Jacobson's organ and the oral cavity in a rodent. *Zool. Anz.* 204: 391–399.
- Wöhrmann-Repenning A. 1981. Zur embryonalen und frühen postnatalen Entwicklung des Jacobsonschen Organs in Beziehung zum Ductus nasopalatinus bei der Ratte. *Zool. Anz.* 206: 203–214.
- Wöhrmann-Repenning A. 1984a. Phylogenetische Aspekte zur Topographie der Jacobsonschen Organe und der Ductus nasopalatini bei *Insectivora*, *Primates*, *Tupaia* und *Didelphis*. *Anat. Anz.* 157: 137–149.
- Wöhrmann-Repenning A. 1984b. Vergleichend anatomische Untersuchungen am Vomeronasal-komplex und am rostralen Gaumen verschiedener *Mammalia*. *Gegenbaurs morph. Jb.* 130: 501–530, 609–637.
- Wöhrmann-Repenning A. 1987. Zur Anatomie des Vomeronasalkomplexes von *Elephantulus rozeti* (Duvernoy, 1830). *Zool. Anz.* 218: 1–8.
- Wöhrmann-Repenning A. 1989. Beobachtungen zur frühen Entwicklung des Jacobsonschen Organs der Katze (*Felis silvestris*). *Gegenbaurs morph. Jb.* 135: 765–773.
- Wöhrmann-Repenning A. 1990. Zur frühen Entwicklung des Jacobsonschen Organs in der Nasenhöhle der Ratte vor Beginn der sekundären Gaumenbildung. *Gegenbaurs morph. Jb.* 136: 389–404.
- Wöhrmann-Repenning A. 1991. Functional aspects of the vomeronasal complex in mammals. *Zool. Jb. Anat.* 121: 71–80.
- Wöhrmann-Repenning A. 1993. The anatomy of the vomeronasal complex of the fox (*Vulpes vulpes* (L.)) under phylogenetic and functional aspects. *Zool. Jb. Anat.* 123: 353–361.
- Wöhrmann-Repenning A. and Ciba B. 1989. Zur spätembryonalen Entwicklung des Vomeronasalkomplexes der Katze (*Felis silvestris*). *Gegenbaurs morph. Jb.* 135: 917–927.

Received 11 April 1994, accepted 3 June 1994.