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'Anatomical Description of a New Organ in the Nose of Domesticated Animals' by Ludvig Jacobson (1813)

Didier Trotier and Kjell B. Døving[1]

Laboratoire de Neurobiologie Sensorielle, Ecole Pratique des Hautes Etudes, 1, Avenue des Olympiades, F-91305 Massy, France and [1]Avdeling for generell fysiologi, Biologisk Institutt, Universitetet i Oslo, PO Boks 1051, N-0316 Oslo, Norway

Correspondence to be sent to: Didier Trotier, Laboratoire de Neurobiologie Sensorielle, Ecole Pratique des Hautes Etudes, 1 Avenue des Olympiades, F-91305 Massy, France. e-mail: trotier@citi2.fr

Introduction

The vomeronasal organ was discovered by L. Jacobson (Figure 1) and described in detail in a publication in 1813. This article was printed with Gothic script and in Danish, so was, and still is, accessible to only a limited public. Jacobson's contribution to natural science was astonishing, considering the large number of studies carried out on the anatomy of different animals up to his time. The fact that a richly innervated organ was hidden in the nasal septum of mammals and had escaped the attention of a great many anatomists was naturally a surprise to many and a source of envy to other contemporary anatomists. The thoroughness of his anatomical observations, and the many reflections that Jacobson made on the function of the organ, are pertinent even for the scientist of today. In addition, he made a series of observations on the anatomy of the vomeronasal organ that have escaped the attention of later authors. Subsequent investigators sometimes have not even realized that Jacobson had previously described various structures, such as the relationship between the organ and the accessory olfactory bulb.

Unfortunately, when Jacobson was alive, the time was not ripe for a full understanding of the sensory function of the organ. These fascinating aspects of the vomeronasal organ began to be revealed only 100 years after Jacobson's death; interest in its function has increased considerably in recent years. Thus the time is now ripe to make Jacobson's original article available to the scientific community. This translation is intended to honour Jacobson's contribution to science. We hope that it will add to the estimation of his work and his findings, and will give scientists an opportunity to award his seminal article the credit it deserves.

The original drawings and the manuscript of the French article that Jacobson wrote are available at the library of the Agricultural University at Copenhagen. This article, together with a biography of Ludvig Jacobson and a translation of his original article into French, were published posthumously in 1950 by Danish scholars (unfortunately only in 150 copies). That publication contains facsimiles of a large number of his drawings. The French text has been compared with the Danish one for the present translation of this work.

Jacobson studied a large number of animals in order to determine if the 'new' organ was present also in species other than various domesticated animals. These animals included some that must have been 'exotic' in Copenhagen at that time, like the camel, tiger, antelope and buffalo.

It should be mentioned that the 'organ of Jacobson' has been renamed. When the scientific society 'Der Anatomische Gesellschaft' was founded in 1887 it established a Nomenclature Commission which, at the ninth meeting of the Society in Basel in 1895, proposed that the organ of Jacobson should be called: 'organon vomeronasale (Jacobsoni)' (His, 1895).

Ludvig Jacobson (1783–1843)

Ludvig Levin Jacobson was born in Copenhagen. His father was a jeweller at the Royal Court of Denmark. The young Jacobson studied medicine in Stockholm and Copenhagen, and was soon recognized as an eminent anatomist, zoologist and teacher. King Frederik VI of Denmark demanded that Jacobson follow the French army to gain experience about what medical services are needed in wartime. Jacobson obediently did as requested. He joined the French army, but at the battle at Leipzig in 1813 he was badly beaten up and robbed, and lost everything, even his clothes. He caught a fever and was hospitalized in Leipzig. There he was recognized as a scientist, and was promoted to physician in the English Hannoverian Legion until his return home to Copenhagen in 1814. Jacobson made a number of anatomical observations, including the description of the electroreceptors of rays (later known as the ampullae of Lorenzini) and the salt glands of birds. He also invented an instrument, called the lithoclast of Jacobson, to crush kidney stones. Jacobson had the honour to receive the

Figure 1 Reproduction of a lithograph of Ludvig Jacobsen by Em. Bærentzen & Co. produced in 1842 as a reproduction of a portrait painted by C.A. Jensen.

highly respected Montyon prize on two occasions. He was appointed professor by King Frederik VI, a decision opposed by the University because he was a Jew.

Jacobson was a pupil and admirer of George Cuvier, and referred to him as his spiritual father. Jacobson was greatly admired by many anatomists of his time and the Swede Anders Retzius (father of Gustav Retzius) studied at Jacobson's private laboratory around 1816, a stay which had a major impact on Retzius's career. In spite of Jacobson's industriousness and extensive investigations, he managed to publish, during his lifetime, only a single article, in Danish, on his findings concerning the vomeronasal organ (Jacobson, 1813). Among present day scientists there is still some confusion as to what Jacobson wrote and discovered. He sent an article written in French to George Cuvier for publication in a French journal, but this was not published until long after his death. Cuvier wrote a note about Jacobson's findings (Cuvier, 1811). It is this note that is frequently cited as 'Jacobson (1811)' by modern scientists when they want to honour Jacobson's contribution. In fact, it does not give much information; there are no drawings and only a superficial description of the organ of Jacobson in mammals. Alas, this note was not even written by Jacobson himself. His article was not widely known and, surprisingly enough, even contemporary anatomists did not refer to his work in Danish, but only to the note published by Cuvier in 1811. Jacobson caught typhoid fever and died on 29 August 1843.

Anatomical Description of a New Organ in the Nose of Domesticated Animals

I herewith have the honour to present to the Royal Veterinary Society an anatomical description of an organ discovered by myself in the mammalian nose. My purpose is to subject my work, in this way, to more detailed investigation by veterinary experts and ensure that it comes into the hands of persons who have the best opportunity to study this organ further, and extend our knowledge about it.

I have already submitted to the Royal Danish Academy of Science a comprehensive description of the said organ, which will at some time be published in its writings. Therefore my present wish is to give a brief description of this organ in general, and afterwards describe it as it exists in our most important domesticated animals, and finally to pose some questions, which if answered will provide much information about the object under discussion.

Before writing the description itself, I hereby beg permission to offer Knight and Professor Viborg my public thanks for the human and truly scientific manner in which he has encouraged and supported me in these investigations; I thank him for allowing me to use the, to the anatomist, so important collection that is in his care; it is to him I owe my investigation of several rare animals.

Mammals have a facial component which in humans is very small or not developed at all, namely the part which can be referred to by the general term snoot.[1]

This component is formed by the intermaxillary bone (ossa intermaxillaria) which constitutes the prolongation of the face or head which clearly distinguishes the four-footed mammals from man. It is in this part of the head, which is a part of the nose, that the organ I have discovered is located. We find it therefore in the foremost part of the nasal cavity, very close to the palate; in cases where the nasal cavity is small, or where the nasal cavity is lacking, it can be assumed that it must project further forward and eventually come to lie in the foremost part of the head, outside the above mentioned cavity.

This organ is closely associated with the intermaxillary bone (os incisivum), although it does not seem that the whole of this bone is there to serve the organ. The maxillary bone is found in several classes of animals in which I have, as yet, not been able to observe this organ, and it consists of several parts whose exact connection with the organ I am not yet fully acquainted with. But the parts of this bone which extend along the palate, and are called the palatine apophysis, are destined for this organ alone; this can be proved partly by their existence in all animals that possess the organ, and partly by the correspondence that exists between the size of the elongations and of the organ. Therefore, when these palatine apophyses are found, it can

also be assumed with certainty that the organ is present. From their size and shape it is also possible to determine the size and shape of the organ. It is to be hoped, therefore, that this discovery will lead us somewhat nearer to knowledge about the intermaxillary bone; a bone about whose function not the slightest likely hypothesis has been developed, in spite of its having been known for a long time.[2]

According to the investigations I have conducted so far, the organ exists in all mammals. It is located in the foremost part of the nasal cavity, in close contact with the nasal cartilage (septum), on the above-mentioned palatal elongations of the intermaxillary bone. It is so carefully concealed that it has avoided discovery by the very discerning eyes of several anatomists, so that nothing except the opening of its secretory duct has been discovered and described by our great Steno (Niels Steensen 1638–1686). What in particular has hidden this organ from the eyes of the observers is a cartilaginous capsule that surrounds the parts comprising the organ, namely a secretory apparatus, a receptacle and an exit duct. All these parts are usually enclosed in this capsule, although in some animals one finds that the secretory apparatus extends outside it and lies unattached on the nasal septum or on the side of the nose. This secretory organ is even more remarkable because it has its own large and specific nerves. The capsule consists of a flat sheet of cartilage, which is curled and therefore hollow in the middle. It has a sharp, free edge which turns upwards, a rounded one that turns downwards, extends into a distinct or less distinct tip at the posterior end, and forms several extensions at the anterior, namely one for the exit duct, one which stretches forwards on the nasal septum, and one to the outer wall of the nose (Figure 2).

These extensions are not always developed to the same degree; in some animals some of them are very large and in others they are lacking. The capsule has several small and two large openings, namely a longish opening at the posterior and a smaller, rounder opening at the anterior. In carnivores (Ferae) the capsule is not a complete tube, but forms just a half-cylinder which is open from above (Figures 3 and 4).

This capsule contains the receptacle, an elongated sac which ends in a fine, blind point at the posterior end; the middle part is of variable width and at the anterior opens in a duct that can be either short or long. The sac consists of two very strong membranes which enclose either the whole secretory apparatus or the greater part of it. This system consists of a glandular mass, which is distributed evenly among the membranes of the receptacle, though the greater part is found on its inside wall, where it not only becomes thicker but also extends right into the cavity of the sac. The glands are reddish in colour, very small and supplied with exit ducts which terminate along the outer side of the receptacle, where numerous narrow openings can be seen; in several animals, especially in the Gliridae [Rodentia] and in some Carnivora, the glandular tissue is so extensive that it stretches far out through the hindmost opening in the capsule and up to the wall of the nasal cavity. In the hare, it is reddish-brown in colour and very considerable (Figure 4, Figs IV & V).

In other animals (the pig) one also finds glands spread out along the capsule, which send their secretory exit ducts towards the receptacle. Another mass of a special structure, where the actual structure of the glands cannot be demonstrated, is found in particular in ruminants and in the horse. This lies on the anterior part of the wall of the nasal cavity, where it occupies a considerable area, passes through a slit in the foremost part of the capsule and becomes smaller on the receptacle; in Bovidae and Ovidae this union is clearly visible; in the horse, on the other hand, which also has this mass, no such communication with the receptacle could be demonstrated.

We now come to the exit ducts, which have been known for a long time, although incompletely.

These are, in fact, the Stenonii canals which run from the nose down to the mouth. Steno discovered these canals in some animals as long as 150 years ago, described them only briefly, and since that time they have not been studied much, so even the first anatomists either do not mention them at all or only repeat what Steno described.[3]

That there are two larger or smaller openings immediately behind the body of the maxillary bone has been known for some time. These openings are found consistently, from humans down to the very lowest mammals. They are of different sizes and of different structures, and scientists have long been uncertain about their function. Some have believed that they served only as a passageway for various blood vessels and nerves, or that their only function might be to connect the nose and the palate, to give it more strength, or lastly, which is the most correct, to serve as a passageway for a special duct that passes from the nose down to the mouth, and to thus lead fluids away from this cavity (Figure 4, Figs II & III).

The knowledge about these ducts is so incomplete that a more detailed description of them becomes necessary. Immediately behind the body of the intermaxillary bone is a depression extending down to the internal opening of a canal, canalis nasopalatinus, canalis Stenonii, canalis incisivus. But the structure of this canal varies; it is either fully developed, with one opening in the nose and another on the palate, or it is not fully developed, starting in the nose and ending blindly on the palate. The first is the most common; the last I have found only in the horse, but assume it is of the same nature in the other equine species, and in the genus *Trichecus*.

The fully developed canals are wide in the nose, and after becoming narrower pass through the opening in the bone, bend slightly at the anterior end and open down on the palate. Here their openings are concealed in a special way. Namely, behind the front teeth (incisors), or in animals which do not have front teeth, behind the bulge (gum) at the

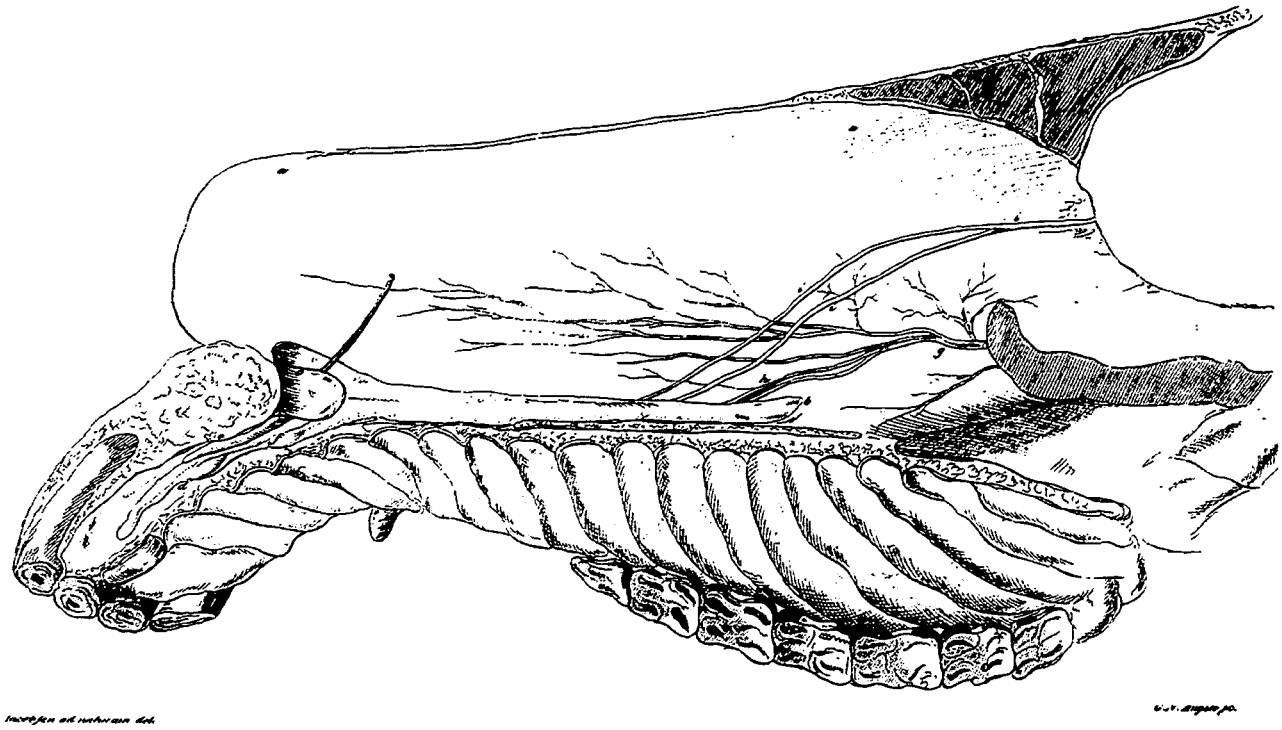

Figure 2 Tab. III [Medial view of the nasal septum of a hemisected snout of a horse]. (a) The nasal septum or the medial cartilage. (b) The cartilaginous elongation, where the organ is located. (c) The elongation of the capsule, turning outwards. (d) The elongation of the capsule towards the palate. (e) The Stenonii canal, with the hair in place. (f) The exit of the receptacle, which joins the Stenonii canal and ends blindly lower down. (g) Branches of the nasopalatine nerve (nervus nasopalatinus), running forward together with several blood vessels. (h) Branches of the nasopalatine nerve that go to the organ. (I) The specific nerves of the organ.

edge of the premaxilla, we find a papilla (tuberculum palatinum) which may be elongated, square, oval, round or heart-shaped, with its tip facing forwards or backwards. For a long time veterinarians have known this papilla, under the name of 'lampus' ([lit. 'the bean'], der Kern), as well as the canals concealed by its free edges. This papilla is found even in the horse, where the canal is not completely developed.

At the uppermost opening of the canal of Stenonii begins, in several animals, a half-tubular canal which is embedded in the nasal septum. This passes over the edge of the body of the intermaxillary bone and disappears at the lowest part of each nostril.

The exit duct of the organ ends in the canals (canales Stenonii) I have just described. Either the duct opens so high up that the opening comes to lie in the uppermost part of the Stenonii canal, so that, in fact, there is no continuation of the receptacle, which instead opens directly at the above-mentioned site; or otherwise a long cylindrical passage goes from the receptacle, runs along the internal side of the Stenonii canal and opens on its anterior wall. This occurs in most animals, the first, on the other hand, only in rodents (Gliridae). Both the exit duct and the Stenonii canal are surrounded in some animals by a cartilaginous-like capsule which is sometimes completely closed and sometimes not.

After having considered the structure of the organ, we now come to its blood vessels and nerves.

The arteries originate from a branch of the interior maxillary artery (arteria maxillaris interior). This branch passes into the nasal cavity through the hindmost lateral opening (foramen sphenopalatinum) and spreads to several parts of the nasal membrane. One of its main branches passes along the nasal septum, and this one is specifically destined for the organ. This artery follows the course of a nerve which will be described shortly, and is named, like the nerve, the nasopalatine artery (arteria nasopalatina); it first sends out branches to the nasal membrane, and branches to the mass of glandular tissue, if this is located outside the capsule, then branches into two, of which one branch enters the capsule and distributes to the glands and membranes; the other accompanies the nerve outside the capsule, divides into several branches which penetrate the capsule here and there and join the first-mentioned branch, and afterwards passes out through the opening in the bone belonging to the palate; it disappears after having given off branches to the membranes of the exit duct, partly in the palatine papilla and partly in the membrane of the palate (Figure 4, Plate III).

The veins are also large and follow the same course as the arteries.

The capillaries have not yet been discovered.

The nerves of the organ are very remarkable, partly because of their size, partly because of their origin. The

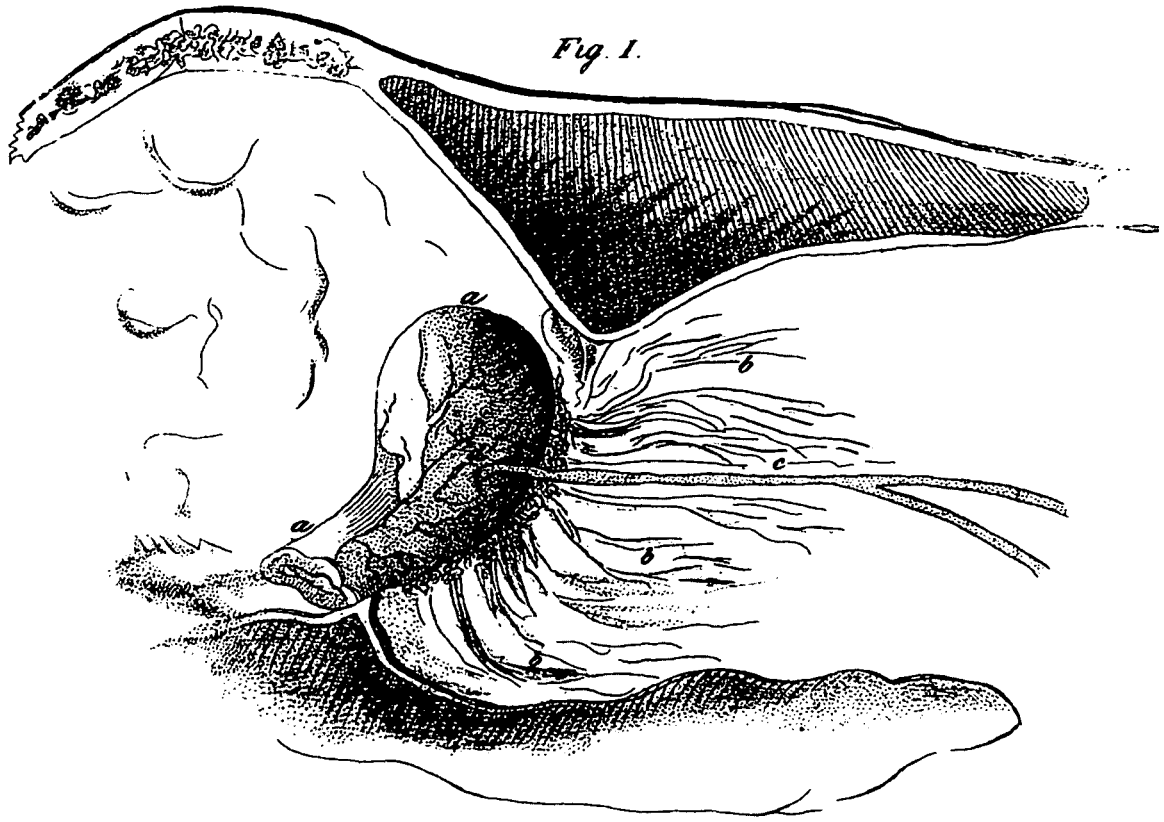

Figure 3 Tab. IV, Fig. 1. The origin of the specific nerve to the organ. (a) The olfactory bulb (bulbus nervi olfactori). (b) The olfactory bulb at the septum. (c) The site of origin of the main nerve to the organ. (d) The site where this nerve originates from the olfactory bulb.

organ is supplied, in fact, with two different nerve branches, namely with a branch from the olfactory nerve and with a branch from the 5th pair [trigeminal]. The former is destined for the organ alone, the latter runs up to the nasal membrane and the palate. Let us look at this first. It comes from the second branch of the 5th pair, branching either from the trunk itself or from the ganglion (ganglion meckeli), which is formed in the depression between the maxillary bone, the palate and the pterygoid bone (fossa sphenopalatina). The branch passes out through the hindmost opening from the nasal cavity (foramen sphenopalatinum), and is called, in conformity with this opening, nervus sphenopalatinus. It ramifies to the mucous membrane of the nose, but gives off an important branch that is intended exclusively for the organ. This nerve is Scarpa's naso-palatine nerve (nervus nasopalatinus scarpae), which usually originates from the above-mentioned branches, but is sometimes nevertheless seen branching from the Vidian nerve (n. vidianus) (Figure 4, Tab. III).

Scarpa's nerve (n. nasopalatinus), accompanied by the artery from the nasal septum, passes forward and downward, approaches the capsule, and after giving off some branches to the nasal membrane, divides into two branches, one of which passes into the capsule and ramifies in the membranes, the other passing either outside the capsule, or just a small distance into the capsule, where it passes out again and down to the palate along the same route as the artery; it disappears partly in the exit duct, partly in the palatine papilla, partly in the palatine cavity, immediately behind the teeth.

Branches of this nerve become fused together. On the other hand, no fusion can be found between these branches and the nerves of the organ itself.

The organ's peculiar nerves (nervi proprii organi) [ed.: the vomeronasal nerves] originate from a part from which no physiologist would immediately expect them to come from. The way in which they originate is specific. Their nature is distinct from that of most other nerves, and the regularity of their course and ramification attract the admiration of the investigator. They seem to originate from the olfactory nerve itself, namely from its upper surface, close to the inner and most important part of the bulb (tuberculum cinereum). This part of the bulb differs both in colour and texture from the rest of the nerves. It is yellowish in colour, is harder, looks like a ganglion and is round, compressed or heart-shaped in form; this body is sunk into the bulbus of the olfactory nerve itself, and in a few animals can be seen clearly, clearest of all in the horse, calf and sheep. The nerve

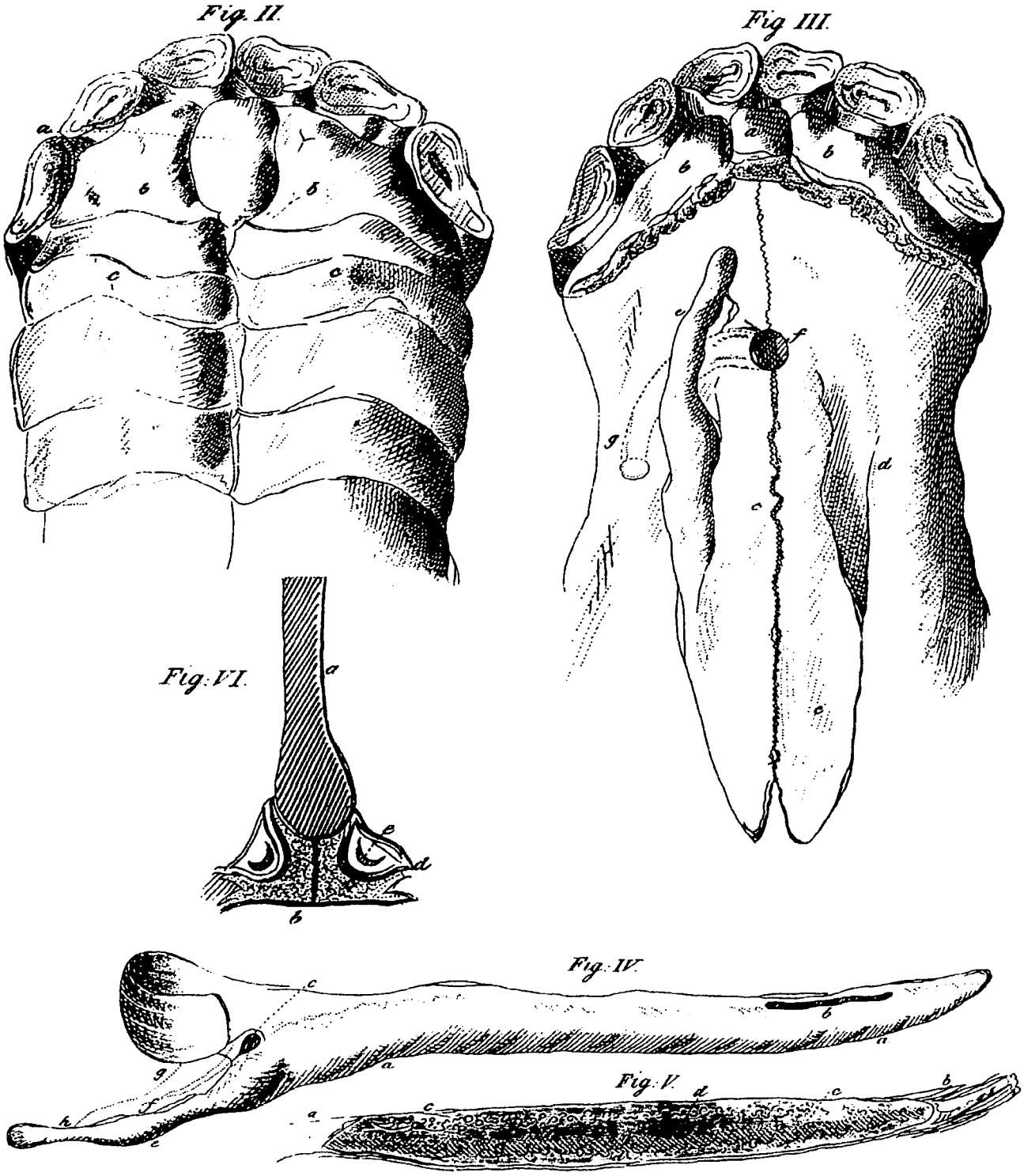

Figure 4 Tab. IV, Figs II–VI. **Fig. II**. The anterior part of the palate. (a) The papilla. (b) The lateral elongations. (c) The folds of the palate. **Fig. III**. The anterior part of the palate, with some of the soft tissue removed. (a) Part of the papilla. (b) Some of the lateral elongations. (c) Palate- or gum elongations of the medial maxillae or gum bones? (d) The anterior fissure of the palate. (e) The elongation of the capsule. (f) The hole for the palatine artery. (g) The palatine artery. **Fig. IV**. (a) The organ's cartilaginous capsule. (b) The posterior fissure. (c) The opening for the secretion. (d) The upcurled elongation of the capsule. (e) The palatine elongation of the capsule. (f) The exit. (g) Stenonii canals. (h) The point where they end blindly. **Fig. V**. The receptacle opened along its length. (a) The anterior part. (b) The posterior part for nerves, blood vessels etc. (c) The elongation found on the outer wall, which appears as a layer of glands between the walls. These glands send their secretory canals to the upper part of the receptacle, where they open at d. **Fig. VI**. Cross section of the anterior part of the nasal septum to show the position of the organ. (a) The nasal septum. (b) The elongation of the palatine. (c) The receptacle surrounding the organ. (d) The receptacle. (e) The lumen of the receptacle.

itself starts from this site as several roots which unite into a single trunk; this runs downwards and then forwards through an opening found in the inner edge of the cribriform plate (lamina cribrosa), after which it comes to lie on the nasal septum and divides into two main branches, a division which, in some species, already has taken place in the skull. These two branches then run forward and downward in an arch, and pass into the most posterior opening of the capsule. Along this path, which can be traced clearly in the vomer, they do not give off any branches at all to the nasal membrane, and only seldom divide into several branches until they are close to the organ itself. As soon they reach the organ, however, they pass to the membranes, where these large branches cling to one of the walls, and then give off numerous fine branches, which can be followed right up to the exit duct of the receptacle. They are accompanied in the membranes by the previously mentioned arteries. It is impossible to discover the slightest anastomosis between these and the above-mentioned nerves. These branches also have a very characteristic structure; they are almost flat, of a yellowish colour, very soft and decompose easily; striations are seen only when the nerves are fairly fresh. They possess all these properties in common with the nerves given off from a ganglion (Figure 4, Tab. IV & Fig. I).

The origin of these nerves is therefore very curious; they are so special that one does not dare to regard it as certain whether they arise from the olfactory nerve or from some other nerve, and their ganglion is merely hidden in the bulbus of the said nerve (bulbus). The nearest nerve is a branch of the first branch of the 5th pair, namely ramus nasalis, but it lies so far away from the mentioned nerve that it is impossible to see the smallest union between them. As yet, these nerves, like the branch of the nerve n. nasopalatinus that runs to the organ, have not been investigated or described in detail, although they have been seen in one animal (actually only in the sheep).

Such is the structure of the organ; and such has it developed in numerous mammals. Humans, however, possess only a rudiment of the organ; as for the situation in the whale, this I have not as yet had an opportunity to investigate. As far as size is concerned, it is most well developed in rodents (Gliridae) [Rodentia], ruminants ([Artiodactyla] Pecoræ) and pachyderms (Belluæ) [ed: Ungulata], namely the horse [Perissodactyla] and the pig [Suina], and is least among carnivores ([Carnivora] Feræ).

After having examined the structure of the organ, we should now decide what kind of organ it is. Its general structure confirms that it is a secretory organ; in addition, the receptacle is always filled with a viscous, clear and yellowish fluid. That fluid is regularly secreted can be proved, because pressing on the palate of a living animal evokes the release of a couple of clearly visible droplets from the opening of the organ, and this can be repeated frequently.

However, if we consider the exceptional number and size of the nerves with which this organ is provided, and compare these with the blood vessels, we find that the former predominate to such a degree that nothing similar is found among the other secretory organs. We must therefore assume the organ to have exceptional properties. The extensive nervous system with which the organ is provided causes one to assume either that the secreted fluid is of a special nature and/or the organ has a more important function, and that the secretion, as a secondary property, exists just to serve the nerves.

In the latter case, the organ is either a kind of sensory organ which is a sense about which human beings have no conception, or a sensory organ which may be of assistance to the sense of smell or may compensate for the sense of taste so often lacking in animals.

Smell and taste are senses of the same category, and could easily overlap; let the nerve branch in a different fashion, let the nerve come into contact with other media, and the sense of taste would become a sense of smell, or rather the olfactory organ would be demoted to a taste organ.

This hypothesis is supported by the anatomy of the organ, its nerves, its localization and its connection with the nasal and buccal cavities. However, nothing definite can yet be decided, partly because we still lack studies of the genus of animals which, according to some scientists, lacks an olfactory organ, namely the whale (Cete [Ungulata; Cetacea]), and partly because there is one animal, namely the horse, where this organ has no connection with the buccal cavity; however, this organ is so well enclosed that neither anything that enters the nasal cavity with the air nor anything from the mouth can easily come into contact with it, so it seems more likely that the organ is merely a secretory system which is provided with such special nerves that it can produce a unique secretion. It still remains to be investigated whether this secreted fluid, either by flowing to the nose or running down into the mouth, becomes an auxiliary factor for intensifying the sense of taste or smell, or whether it has a function of its own. Its effect on smell will be difficult to establish, its effect on taste easier.

The fluid secreted by the organ runs down to a point on the palate to which, with the tip of our tongue, we bring the particle we want to investigate, rub it against this point and, in this way, seem to bring forth its actual taste. Arguments against this suggestion are that some animals exist (horses) where this organ is very well developed but has no connection with the buccal cavity itself, and that humans, who possess a very well developed sense of taste, have only a rudiment of the organ.

It is likely that this organ has some influence on taste, but in the light of the above it follows that this cannot be its main function.

If we consider the location of the organ and its secretory ducts, it seems that the secretion is intended to reach the foremost part of the nose, namely either to just inside the

nostril and/or to the part which in structure and nervous system coincides with the same, and constitutes the snoot. We find, in fact, that in all animals with a naked snoot the organ has a duct that passes down to the buccal cavity, and this is sometimes an 'open' duct, actually a semi-circular groove, which is found in the nasal cavity and stretches, as described before, from the beginning of the Stenonii canals to the tip of the snoot. In this case the secretion, because of the hanging position of the head, flows down either to the tip of the snoot or to the palate. In the latter case it is received by the tongue, and the animal, by licking around the snoot, conveys the fluid to the whole of the external, soft tip of the snoot.

If the snoot of the animal is not as described above, then it can be assumed that the part that is analogous to the soft part of the snoot lies behind the nostrils on the foremost part of the nasal septum, which has the same structure and is supplied with the same nerves as the tip of the snoot. In these animals the organ has no connection with the buccal cavity, nor any semi-circular duct leading to the tip of the snoot. The wide upper opening of the Stenonii canal permits the secretion to flow along the foremost part of the nasal septum, whereby this is moistened. It appears that the function of the organ is definitely associated with this part of the head, and is of far greater importance in animals than previously assumed. This foremost part of the nasal septum is probably the site of a hidden sense about which we know very little as yet.

It would extend beyond the framework of this paper to elaborate on and prove what I believe we should look for at this site in animals. Nor can this reasonably take place, because I perceive there to be several facts which have to be ascertained, partly from studying such organs in a diseased condition, and partly by provoking them by experiment.

Let me therefore ask the veterinary experts the following questions:

1. What is the condition of the organ in those diseases associated with considerable discharge from the nose, in particular glanders and hydrophobia?
2. In those diseases associated with dryness of the nose and a dry snoot, is this organ found to be in any way unhealthy?
3. Some animals secrete a special substance from nose and mouth during the mating season, which in camels can be very considerable; perhaps the fluid comes from this organ, and are there any periodic changes in the organ?
4. Are there any diseases in which the palatine papilla (tuberculum palatinum) is very adversely affected, and what are the consequences for the animal?
5. Under what circumstances has it been found useful to cauterize horses on the papilla?
6. What circumstances cause accidental or intentional damage to this organ?

The last question requires various experiments, of which I have already carried out a number, but which I do not consider sufficient to explain what one is looking for.

In order to keep within the framework of the paper I now turn to a description of this organ, in particular in the ox, sheep, horse, pig and dog, which are the most important animals for veterinarians.

Ruminants*

In animals in this order, of which I have investigated several different species, this organ is very well developed, almost as highly developed as in rodents (Gliridae [Rodentia]). In these animals the intermaxillary bones are very large, even though they are not intended to house teeth. The palatine apophyses are large, and in these and in the premaxillae it is possible to see a clear trace of the organ, which has rested on these parts. A characteristic of several animals belonging to this order is the large openings in the palate, which are closed by a membrane, and allow the organ's secretory duct, the Stenonii canals and the branch of Scarpa's nerve (n. nasopalatinus) to pass through only at the foremost corner. The advantage of these large openings seems to be that the animal, by pressing the tongue against the palate, can exert an effect on the receptacle and thus induce secretion of the fluid. In the ox this is very likely, but not, on the other hand, in rodents which, it is true, do have large openings in the palate, but where the apophyses are developed in such a way as to totally surround the organ so that the organ cannot be influenced by any pressure through the palate.

We shall now consider the organ in the ox, which is very large. The capsule surrounding the organ is found on the above-mentioned apophysis of the palate and stretches towards the vomer, so that in an adult ox it may be three inches long. Its shape is somewhat triangular. One surface faces outwards, the second, which is round, downwards, and the third, of the same form, inwards; the last two overlap. Here, as in most cases, the upper edge is very distinct; it comes from the posterior end of the capsule, where it is attached to the vomer; this part is flat and pointed, and from here the edge appears like a pointed cartilaginous plate, which becomes larger in the middle, lies against the nasal septum and finishes at the anterior, where it disappears in one of the apophyses found near the foremost part of the capsule. Here, namely, the cartilaginous-like capsule forms three elongations, one of which turns forwards (or downwards when the head is in its normal position) and appears to end in the cartilage of the nose; another passes outwards, becomes wider and comes to lie on the outer surface of the nasal elongations of the intermaxillary bone, and to some extent closes the large openings in the palate; finally the capsule gives off still a third elongation, which passes downwards towards the palate and partly surrounds the organ's secretory duct and the Stenonii canals. The capsule has several openings at the posterior, for passage of blood vessels and nerves. At the anterior end is a longish fissure, whose function will soon be discussed.

The receptacle has a very strong natural structure, and its membranes are very firm. It is two inches long and two 'linie' wide [one 'linie' = 2.18 or 3.14 mm], it ends at the front in a narrow secretory duct which runs alongside the Stenonii canal and opens at the foremost and inner part of this. The Stenonii canals start immediately behind at the body of the intermaxillary bone, close to the nasal septum. This place is hollow and formed by an elongation of the capsule, which here seems to unite with the nasal septum. From this groove begins a half-tubular canal, embedded in the nasal cartilage, which stretches to the lowest and innermost part of each nostril. The openings of the Stenonii canals are found at this spot, and are fairly large (average one and a half 'linie'). Here the canals themselves become somewhat smaller and at the front pass out through the foremost corner of the large openings in the palate, accompanied by the receptacle's secretory duct and by Scarpa's nerve; they now bend slightly at the anterior, run towards each other and end at the front of the palate close to the papilla, which in these animals is heart-shaped in form, with the point facing backwards. The opening of the duct is concealed somewhat by the projecting edge of the papilla. The secretory apparatus can be found between the membranes of the receptacle described above, especially against the external wall. It is quite considerable, and consists of several reddish glands. The external wall thus gets a bulge, which is very prominent in the cavity of the receptacle. Beside this bulge, which stretches right up to the secretory duct, one can see the openings of the glandular ducts. Sometimes it is observed that this glandular mass stretches out of the receptacle, and lies on the vomer itself. Another mass of tissue with a distinct structure is also similarly connected with the receptacle, and without doubt belongs to the secretory apparatus. It lies at the foremost part of the nasal septum, occupies considerable space, stretches far forward and enters the capsule through a longish opening found in the foremost part of the same, and ramifies somewhat in the foremost part of the receptacle. This tissue is not exactly the same as what we refer to as glandular tissue. It has many blood vessels and some small reddish bodies, which are somewhat remotely similar to glands.

Let us now turn to the organ's blood vessels and nerves. The first come from the location described in the general account, and need not be described in more detail here.

Also nerves are found to follow the same course very closely, making it is necessary to describe only those that are specific for this suborder.

In the ox, Scarpa's nerve is very large; it gives off several important branches, although Scarpa has described only one. Afterwards it divides, close to the receptacle, into two almost equally large branches. The uppermost, which is somewhat smaller, enters the capsule itself and is intended for the organ alone; it ramifies mainly on the outermost wall and can be followed very far forward. The lower one, the actual continuation of the trunk, runs along the lower surface of the capsule, penetrates it, runs slightly forward, though without giving off any branches to the membranes, passes afterwards out of the capsule again, and stretches downwards on the foremost part of the large openings in the palate, through which it passes in order to branch out to the Stenonii canal and to the palate.

In the ox the organ's main nerves are very large. Their origin can be seen clearly, preferably in younger animals of this family. One finds, in fact, at the inner and uppermost side of the bulbus of the olfactory nerve, a harder part, which is heart-shaped, and from which the nerve, as described above, springs out in the form of several roots. In the ox it passes out of the skull by means of two trunks. These two trunks do not give off a single branch, nor do they divide, but enter the capsule at its upper edge and ramify in the membranes, mainly on the inside wall, and can be followed right up to the secretory duct.

Such is the structure of the organ in the ox, of which genus I have investigated only our inland animal; but from the traces and rudiments that I observed in a head of a buffalo, which is to be found in the collection at the Veterinary College, I can say with certainty that the organ is extremely large in this genus of the ox family.

In the sheep and the goat, the organ has the same appearance as in the ox.

Pachyderms (Belluae)**

This suborder, which covers such a variety of families of animals, contains two important domesticated animals, namely the horse and the pig.

The horse (Equus caballus) (Figure 2, Tab. III and Figures 3 and 4, Tab. IV & Figs I–VI)

The horse is unique, not only because in this animal the organ is very well developed, but also because of a special characteristic which I have not found as yet in any other animal; the horse, namely, does not have any openings for the Stenonii canals[4] in the palate itself. Actually we do find in this animal a palatine papilla, or the so-called lampus or 'bean [lit.]', which is large, square and surrounded by a groove, and without the least trace of palatine openings. In the horse the intermaxillary bones are very large; the body of the foremost part is very prominent, the elongations of the palate are very long, the openings in the palate are long and narrow, and about one and a half inches above them we find the openings through which passes the Scarpa nerve. In the bones intended to accommodate the organ we find visible precursors; the elongations of the palate have a longish furrow; the same can be seen in the pre-maxilla, and to some extent also in the vomer. This furrow becomes very deep and takes on the form of a half-tubular canal, since the hindmost edge of the nasal cartilage (septum), which presses on the pre-maxilla, is thicker and more prominent than the upper part of the said cartilage. This 'half-pipe' contains the capsule, which in a full-grown horse is more

than three and a half inches long. Its posterior part is attached to the lateral surface of the vomer, is flattened and is often somewhat pointed. The middle part has a smooth external surface and an internal surface that is distinctly arched, and lies against the palatine apophysis and the pre-maxilla. As soon as it nears the body of the inter-maxillary bone it ceases to be hollow and at this point an opening can be seen through which passes the organ's secretory duct. The capsule now produces two elongations, one of which runs downwards towards the body of the maxilla, the other towards the palate. The first is particularly large and thick, forms a depression in which the Stenonii canal begins, and stretches also to the external wall of the nose. The other elongation is thinner, starts further back from the inner surface of the capsule and passes out through the openings in the palate, where it is broad and has a furrow on its external side in which the said ducts are situated; it then stretches along the palate, is narrow and flattened, and turns inwards and under it by means of a blunt tip. The tips of these elongations are connected by ligaments. The receptacle is large, wide and has exceptionally strong membranes. The internal surface is very smooth. The bulge on the external wall is remarkably strong, and the openings for the gland are large and clearly visible; they lie mainly at the edge of this bulge, and are concealed by folds, created by the inner 'skin' at each of them. At the anterior part of the Stenonii canal the receptacle changes into a cylindrical canal which runs out of the opening at the foremost part of the capsule and passes along the inner elongation along the palate, almost to its tip, where it becomes united with the Stenonii canal, which in the horse is incomplete. These canals begin in the depression created by the foremost elongation of the capsule, which becomes much larger at the projecting part of the body of the inter-maxillary bone; here they are somewhat funnel-shaped, run down to the palate along the above-mentioned elongations of the capsule and end at their tips, where, as recently stated, they unite with the secretory duct of the receptacle. I have called these canals incomplete because they lack the lowest openings, and because there is no trace that indicates that they have in any way been united with the palatine papilla (Figure 4, Tab. IV, Figs II & III).

The secretory apparatus is exactly like the one found in the ox. The glands, however, are not as evident. Similarly, the horse has the special mass of tissue at the foremost part of the nasal septum; although this does not enter the capsule itself, but stretches over this towards the grooves where the Stenonii canals begin.

The blood vessels are particularly large in the horse; they give off numerous branches to the membranes, but also form a unique anastomosis, which is either not so complete in the other animals or cannot be seen so clearly. After the artery has supplied the membranes it gives off an important branch which runs along the lower surface of the capsule, gives off here and there some branches to the membranes, passes out together with the secretory duct and unites with the palatine artery; this is accompanied by a clearly visible vein or blood vessel. To this special mass of tissue situated at the foremost part of the nasal septum pass numerous large branches, all of them originating from a main trunk, the same one that the organ's other arteries originate from, namely the sphenopalatine artery, which is much larger in the horse than in any of the other animals species I have investigated. The blood vessels form two bundles of considerable size (plexus), of which the one, which spreads along the nasal septum, does not seem to be connected with the organ; from the other, which lies along the lowest part of the vomer, immediately behind the capsule, emerge on the other hand the blood vessels of the organ.

The organ's main nerve can be seen distinctly to end in several fine rootlets on the previously mentioned location, the olfactory bulb, though more towards the posterior than in most other animals (Figure 3, Tab. IV & Fig. I).

The site at which they emerge is of a yellowish colour, and much harder than the rest of the olfactory nerve. This part can be easily detached, in which case it is discovered that it consists of a small, flattened body, similar to a ganglion, and shaped like a lens.

After these fine rootlets have united to form one trunk, this passes out of the skull, accompanied by a fine artery; the trunk now runs along the nasal septum right up to the posterior part of the capsule. Along this course it divides into two to three branches, which join together, then pass through the opening in the upper edge of the capsule and ramify in the membranes. The other nerve that goes to the organ is, in the horse, similarly very large; its main trunk (nervus nasalis scarpa) gives off more branches to the nose in this animal than in any other. As soon as it reaches the nasal septum it gives off one or two branches, which run upward and forward, and ramify in the epithelium of the nasal septum; afterwards it gives off a very large branch, which runs forward and follows the course of the previously mentioned blood vessels along the nasal septum; it again gives off another branch to the epithelium of the nasal septum and finally the branch that goes to the receptacle. This branch originates directly from the main trunk, is very large and can be followed all the way to the receptacle's secretory duct. The continuation of Scarpa's nerve does not then give off any more branches to the organ; it becomes embedded in a deep furrow, located under the capsule in the foremost part of the jaw, passes through special apertures, which are found on the elongation of the palate, unites to some extent with the nerve from the other side, and finally disappears, partly in the olfactory bulb and partly in the palatal epithelium. All these parts can be easily identified in the horse. The distribution of the nerves is particularly clear, and in this case one can be sure of what I have stated above, that there is no connection between the main nerve to the organ and the Scarpa nerve.

The course and distribution of the blood vessels is very

clear, but, because of their large and extensive anastomosis, partial injection is seldom successful.

The horse is the only animal in which I have found the Stenonii canal to be incomplete. I have indicated the other animals which can be expected to be of the same nature.

However, the following question immediately arises: could it be that these canals are open in the horse in its natural wild state? Could it be that in an animal that has been subdued by man for such a long time they could have gradually disappeared, because they are perhaps only essential for the animal in its wild state, when it has to search for and select its own food? Could it be that this kind of degeneration can continue through several generations?

The pig (Sus scrosa)

A deep impression in the premaxilla and semi-cylindrical elongations of the palate in the intermaxillary region provide evidence of a large organ in this animal. Investigation of the healthy animal also confirms our assumption.

The capsule is one and a half inches long, strong and thick, and somewhat cylindrical. Its posterior end consists of a flattened cartilaginous plate which is attached to the vomer. Its upper edge is very prominent, and at the anterior end develops two large elongations down to the palate. One of these contains the Stenonii canal and secretory duct, and the other disappears down into the nasal cartilage. The latter also constitutes a part that contains part of those canals. Along the outer surface of the capsule can be seen a number of larger and smaller openings.

The receptacle is not much more than one inch in length. The membranes are extremely firm and strong, and between them, on both the outer and the inner wall, is found a large layer of glands, which are not connected with each other in any way. Most of the openings from the secretory apparatus are found on the outer wall.

The pig has, in addition, some glands belonging to this organ which are not found in other animals. Along the receptacle, in the nasal membrane, are found a large number of small reddish bodies collected into various clusters which constitute glands, which send their secretory ducts through the capsule and into the receptacle. Glands of the same nature and structure can also be found at the external wall of the nose, immediately under the anterior (bottom) end of the large ethmoid bone (concha inferior). I have not been able to trace in detail the course of their secretory ducts; but it looked as if they ran to the uppermost part of the Stenonii canals.

These canals are very large in the pig. Their upper opening is very wide, and close to them, on the nasal septum, starts a large and noticeable groove, which bends over the body of the maxilla and disappears at the lowermost and innermost niche of the nostril. The Stenonii canals pass out through the large openings in the palate found in the pig, and are surrounded by the previously mentioned elongation of the capsule. They now tend to run towards each other and finally end in large openings on the sides of the roundish palatine papilla (the lampus).

In this animal the nerves show nothing exceptional; they are clearly seen and are large, and can easily be traced far forward on the membranes. Normally, the main nerve of the organ forms three trunks, which are very long; the last applies in particular to Scarpa's nerve, which runs far forward on the septum before giving off fine branches. As regards the blood vessels, a slight peculiarity can be observed. Namely, the artery gives off some branches, which run along the outer surface of the receptacle and serve the gland located there.

Investigation of the dry bones of several species of pig has convinced me that the organ is of the same nature in all of them, but in the species *Sus babyrussa* it must be especially large.

Carnivora (Feræ)

In animals of this order the organ is clearly visible and fully developed, but is smaller than in the other animals. The palatine elongations of the intermaxillary bone, the openings in the palate and the depression in the premaxilla of every skull (cranium) of these animals provide convincing evidence of its existence. Of all the animals I have studied it is most obvious in the dog, which I have chosen as the subject of the following description.

The dog (Canis familiaris)

The palatine apophyses have a marked groove on their outer surface which extends from the foremost part of the jaw (premaxilla) to the vomer. The palatine openings are quite large, and from these runs a deep groove which stretches forwards toward the teeth. In all the carnivores the capsule is not completely closed, it resembles a curved cartilaginous plate, forming just a 'half-tube' that is open above and outwards. The wall which lies close to the nasal cartilage stretches furthest forwards, and forms a small elongation at the anterior end, which lies against the movable nasal septum of the snoot. The elongation which stretches out through the opening in the palate is a continuation of the capsule itself and is of the same shape and nature as this. It surrounds only part of the Stenonii canals above, and below, where it is smaller, the cartilage surrounds them completely. The receptacle is quite wide, but short; the membranes are very fine and are supplied with many blood vessels. The glands belonging to the secretory apparatus are located at the usual place, but in some varieties they stretch slightly upwards on the vomer.

The receptacle ends at the anterior end in a very long secretory duct, which does not join the Stenonii canal until far down on the palate. These canals begin in the deep groove found just behind the intermaxillary bone; at this site can be seen a large groove, which runs in the manner already described down to the tip of the snoot. After the canals have emerged from the holes in the palate, they turn towards each

other and end in the usual way close to the palatine papilla (the lampus), which is large, heart-shaped, has a forward-pointed tip, and is of a particularly firm structure. There is nothing distinctive as regards the source of the nerves and their course to the organ. The main nerve has two trunks, which divide into numerous branches before passing down to the membranes.

Scarpa's nerve has nothing special about it; the same applies to the blood vessels. Because the membranes of the receptacle are so thin, in no other animal can the distribution of the nerves in these tissues be seen so clearly as in the dog. They form, namely, a true plexus nervosus which can be followed with the naked eye right up to the secretory ducts, and one is thus clearly convinced that there is no union between these two separate nerves.

The same applies to the organ in all the other varieties of the dog that I have studied.

Similarly, the nature and structure of the organ is the same in the cat (*Felis domestica*).

Endnotes

[1]Let me be permitted to use this word, in order thus to describe the foremost part of the nose or the animal's face, since we only have a specific name for this part in the case of certain animals, for example, muzzle in bovine animals and snout in pigs.

[2]Even a well-known natural philosopher (Lorenz Oken, 1779–1851), who with great spirit and wit has interpreted the purpose of the cranial bones, admits that it is difficult to define the purpose of the intermaxillary bones. *Über die Bedeutung des Schädelknochen*, p. 14: 'Die Bedetung des Zwischenkiefers ist sehr schwer zu finden'.

[3]This applies to Scarpa, Harwood, Blomenbach and Cuvier.

[4]In the horse, the Stenonii canal is found behind the front teeth (incisors).

*Editor's note: The collection of animals listed as 'Ruminants', including sheep, goats, and cattle is no longer considered an order, but a family (Bovidae) in the suborder Ruminantia of the order Artiodactyla.

**Editor's note: Horses and pigs are no longer considered part of a single suborder, or even members of the same order of mammals. Horses, along with rhinos and tapirs, are of the order Perissodactyla, suborder Hippomorpha; pigs are of the order Artiodactyla, suborder Suina.

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