The Human Vomeronasal Organ. V. An Interpretation of Its Discovery by Ruysch, Jacobson, or Kölliker, With an English Translation of Kölliker (1877)

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The vomeronasal organs (VNOs) of mammals are highly variable epithelial structures found bilaterally in the mucosa of the nasal septum. Whereas the discovery of the human VNO is traditionally ascribed to Frederick Ruysch (1703, 1724), the organ is named after Ludwig Levin Jacobson (1811, 1813) who described it in nonhuman mammals. We recently have pointed out controversies surrounding the incidence and structure of the enigmatic human VNO, and herein, we provide a historical analysis of its discovery. We present evidence that the honor of discovering the human VNO truly belongs to Kölliker (1877), and not to Ruysch. Ruysch illustrated the lateral view of a 2-year-old infant's nasal septum, and it is unclear whether the right nasal passage, the tubular VNO or its opening, or an unrelated duct is being indicated. Jacobson reported the VNO to be missing in humans. Its discovery in the human embryo can be related to later authors, such as Dursy (1869). Our reappraisal of the literature confirms that Kölliker was actually the first among these 18th–19th century investigators to provide evidence of the human VNO as a histologically identifiable structure in the fetus and the adult. Anat Rec (Part B: New Anat) 270B:4–15, 2003.

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KEY WORDS: Dursy; human; Jacobson; Kölliker; Ruysch; Sömmering; vomeronasal organ; VNO; history; translation; chemosensory

INTRODUCTION

Most mammals possess bilateral chemosensory structures found in the nasal septal mucosa, called vomeronasal organs (VNOs). These structures are exceedingly variable in primates (Smith et al., 2001a), and even humans possess a nonchemosensory homologue (Bhatnagar and Smith, 2001). Historically, Frederick Ruysch (1638–1721, Fig. 1a), a Dutch anatomist, has been universally and unquestionably associated with the discovery of the human VNO. In the human, the organ is quite unlike that in other vertebrates (see Bhatnagar and Meisami, 1998; Meisami and Bhatnagar, 1998). Instead of exhibiting clear evidence of chemosensory function seen in most other vertebrates, the human homologue of the VNO has no clear evidence for chemoreception (see Smith et al., 2001a, for definitions of the vomeronasal complex) and may have other unrelated functions (Bhatnagar and Smith 2001; Smith et al., 2001a).

The VNO of mammals in general (but not of humans) was discovered by Jacobson (1811, 1813). That the human VNO was discovered by Ruysch (1703), 108 years earlier, has been repeated to the present date (see Takami, 2002, p. 245) and never before questioned or investigated. More so, it is interesting that Ruysch himself did not give a name to the organ, which awaited its first description until 1811. Ruysch only presented the right lateral view of a 2-year-old child's nasal septum in an illustration with structures labeled (Figure 1b), several of which having no comparable morphological features to those on a septum we examined from the same age group (Figure 1d). To assign Ruysch as the discoverer of the human VNO misinterprets historical facts. We intend to set the record straight concerning discovery of the human VNO and to grant credit where credit is due.

There has been a distinguished list of authors who began to mention the human VNO, at least briefly, before and after its monographic treatment in mammals by Jacobson (1811, 1813). Ruysch (1703) and Sömmering...
(1809) each illustrated the lateral view of a human nasal septum in a child (Figure 1b) and adult (Figure 2b), respectively, although they did not show the VNO itself (which is submucosal in location, Bhatnagar and Smith, 2001). On the human condition, Jacobson (1811) clearly mentioned “...in the monkeys it becomes so small that we are prepared to see it vanish completely in man.” (See English translation by Bhatnagar and Reid, 1996, p 228.) Of interest, this statement is nearly accurate when relying on a gross observational perspective—VNOs can be quite small in anthropoid primates in general (Smith et al., 2001a) and are only visible by microscopy in humans (Bhatnagar and Smith, 2001). Gratiolet (1845) and Dursy (1869) made brief remarks about the human VNO. Finally, Professor Rudolf Albert von Kölliker (1877) provided the first detailed histological description of the human VNO in the fetus and adult. He offered 10 figures in two plates demonstrating the VNO. Kölliker’s contribution has been acknowledged by very few in the field. In our opinion, his monograph is as critical as the findings of Ruysch and Jacobson. Considering its importance, we are providing a verbatim translation of the original German text by Kölliker (1877) to make its availability within easy reach of English-speaking investigators.

As a postscript to Kölliker’s work, it took over a century for further serious enquiry into the human VNO, even though there are sparse considerations of the structure in the interim (e.g., Ishimitsu, 1958). The most detailed consideration of the development and adult structure of the human VNO has only occurred within the past two decades (Kreutzler and Jafek, 1980; Johnson et al., 1985; Ortmann, 1989; Smith et al., 1997; Smith and Bhatnagar, 2000; Trotier et al., 2000; Bhatnagar and Smith, 2001; Witt et al., 2002). In a series of papers, we have endeavored to provide a perspective on history (Bhatnagar and Reid, 1996), development (Smith and Bhatnagar, 2000), functional morphology (Bhatnagar and Smith, 2001), and topography (Bhatnagar et al., 2002) of the human VNO. Whereas this series began with a discussion of the well-known contributions of Ruysch and Jacobson, the present work discusses the lesser known but definitive discoveries by Kölliker (1877).

As of this writing, translations of relevant passages by Ruysch (1703, 1724), Jacobson (1811, 1813), and Kölliker (1877) are all available in English for learned scholars to reach their own conclusions. A partial time-line for the years between 1703 and 2002 is provided in Table 1. This details significant early findings on the human VNO and uses our contributions for a more recent perspective. This report analyzes the historical literature on the human VNO, encompassing the work that we have presented recently (see Table 1 and Bhatnagar and Reid, 1996). Our previous work on dissection of a nasal septum of a 2-year-old child was also compared with the same aged septa examined by Ruysch (1703), an important comparison, because our specimen has also been mapped by means of serial sections to relate to the gross morphology (Bhatnagar and Smith, 2001).

**OBSERVATIONS AND COMMENTS**

**Ruysch’s Contributions (1703, 1724)**

Ruysch (Figure 1a) published a description of his collections and preparations in a 10-volume set, *Thesaurus Anatomicus* (see Lindeboom, 1980). It
is quite probable that Ruysch’s preparations, including that of the now-famous nasal septum of an infant (Figure 1b), might still be available somewhere for inspection. His collection was purchased in 1717 by Peter the Great for 30,000 guilders (Lindeboom, 1980, p 41). Most certainly, Ruysch was the first to illustrate and remark on the nasal septum of a 2-year-old infant. The age of this cadaver is confirmed from Ruysch’s own writing and from a painting by Jurriaan Pool that is held in the collection of Museum Boijmans Van Beuningen, Rotterdam (Löwensteyn, 2000). The painting depicts Ruysch dissecting a child. A later, often repeated extrapolation states that Ruysch described the nasal septum of a soldier who received a facial wound (Kauer, 1969, cited in Monti-Bloch et al., 1998; Wysocki, 1979), but this is not related to his description of the nasal canals and is probably falsely attributed to Ruysch.

Ruysch’s illustration (1703, vol. 3, plate IV, Figure V, page 70; cf. Bhatnagar and Reid, 1996, p 224) of a “longitudinal dissection” (sagittal view, Figure 1b) of a nasal septum of a human infant and his brief description thereof are the only data related to discovery of the human VNO. The parts on the septum identified and labeled include the nasal septum, hairs set in the nasal canals, one of the nasal canals, oblique sulci, and unrelated labels. The six oblique sulci have no parallel to observations on young or aged septa by other authors (e.g., Potiquet, 1891; Bhatnagar and Smith, 2001).

<table>
<thead>
<tr>
<th>Year of Report</th>
<th>Relevant Findings</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1703</td>
<td>“Longitudinal dissection” through the nasal septal region of an infant</td>
<td>Ruysch (1703) as translated by Bhatnagar and Reid, 1996</td>
</tr>
<tr>
<td>1809</td>
<td>Lateral view of an adult human nasal septum showing a probe entering “Jacobson’s organ” (which was yet to be histologically identified)</td>
<td>Sommering (1809) as cited by Pearlman (1934)</td>
</tr>
<tr>
<td>1811</td>
<td>“...it is most developed in the rodents, next in the ruminants. The carnivores have less, and in the monkeys it becomes so small that we are prepared to see it vanish completely in man.”</td>
<td>Jacobson (1811), a report by Cuvier (translated by Bhatnagar and Reid (1996))</td>
</tr>
<tr>
<td>1838</td>
<td>Jacobson’s organ arises as an invagination of the olfactory mucous membrane, and the organ becomes differentiated from this invagination</td>
<td>Rathke (1838). See Bhatnagar and Reid (1996)</td>
</tr>
<tr>
<td>1845</td>
<td>This work has importance for the VNO in mammals in general, but the author does not specifically address the human VNO</td>
<td>Gratiolet (1845)</td>
</tr>
<tr>
<td>1869</td>
<td>Several human VNOs were examined; the author used the name “Jacobson’s organ” (sic), but there are no illustrations</td>
<td>Dursy (1869)</td>
</tr>
<tr>
<td>1877</td>
<td>Provided the histological description of the VNO, illustrated for the first time, in prenatal and postnatal humans; he called it Jacobson’s organ, and noted that it is homologous to that of other animals; he also named Jacobson’s (paraseptal) cartilages</td>
<td>Kölliker (1877)</td>
</tr>
<tr>
<td>2000a</td>
<td>Prenatal presence of the human VNO is examined from 33 days fertilization age to near-term; the VNO appears to lose receptor cells during early fetal development, and a nonsensory remnant persists during the remainder of prenatal development</td>
<td>Smith and Bhatnagar (2000)</td>
</tr>
<tr>
<td>2001</td>
<td>The consistent presence of the VNO is recorded as a homolog to that of other mammals, in a simplified duct-like form in the nasal septum; extremes of size variability, bilateral asymmetry, nonchemosensory pseudostatified ciliated epithelium is noted; serial histological sectioning is identified as the only means of locating and identifying the human VNO with absolute certainty</td>
<td>Bhatnagar and Smith (2001)</td>
</tr>
<tr>
<td>2002</td>
<td>Nasopalatine recess, nasopalatine fossa, septal mucosal pits, the VNO and VNO opening were histologically distinguished; it was emphasized that the human VNO can only be identified by serial sectioning</td>
<td>Bhatnagar et al. (2002)</td>
</tr>
</tbody>
</table>

aA gap in the literature from 1878 to 1999 is purposely left, for the sake of brevity, in which the presence vs. absence and homology of the human VNO is debated. For a more complete assessment of studies occurring between 1980 and 1999, see Smith and Bhatnagar (2000), Bhatnagar and Smith (2001), and Smith et al. (2001a).
Table 2. Arguments for and against the conclusion that Ruysch (1703, 1724) observed, described, and illustrated the human vomeronasal organ (VNO)

<table>
<thead>
<tr>
<th>Statement</th>
<th>For</th>
<th>Against</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. In the anterior and lower part of the septum</td>
<td>Correct location in general</td>
<td>—</td>
</tr>
<tr>
<td>2. Near the palate</td>
<td>—</td>
<td>VNO is positioned near above palate (Bhatnagar and Smith, 2001)</td>
</tr>
<tr>
<td>3. An opening or small mouth of some sort of duct appears</td>
<td>VNO has a similar type of communication</td>
<td>The particular opening indicated (Fig. 1b) appears too inferior and close to the palate (see 1d)</td>
</tr>
<tr>
<td>4. Concerning whose purpose or even existence, I have read nothing by other scholars</td>
<td>Correctly stated</td>
<td>—</td>
</tr>
<tr>
<td>5. I believe that it serves to expel mucus</td>
<td>Accurately surmised</td>
<td>There are numerous other openings that relate to mucus excretion.</td>
</tr>
</tbody>
</table>

2001). On the other hand, the nasal canals have retrospectively been interpreted (erroneously in our opinion) as the VNO. If Ruysch’s illustration is interpreted in a position 90 degrees rotated from Figure 1b, and drawn in coronal section (Figure 1c), the position of these canals is inconsistent with the VNO location. Based on our data from fetal to adult stages (Smith and Bhatnagar, 2000; Bhatnagar and Smith, 2001), the “nasal canals” are too close to the palate to represent the VNO (compare Fig. 1b with Fig. 1c,d). We must acknowledge the lack of an available scale in Ruysch’s illustration or, more definitively, histological series to verify our interpretation. But there is indirect evidence supporting our view.

The most comprehensive statement by Ruysch relating to the “nasal canals” is as follows: “In the anterior and lower part of the septum near the palate, an opening or a small mouth of some sort of duct appears, concerning whose purpose or even existence, I have read nothing by other scholars. I believe it serves to expel mucus.” (Plate IV, Figure 5, Letter E — translated from Latin). In our opinion, it is the above statement that has given rise to the notion that Ruysch was the discoverer of the human VNO. Table 2 presents a word-by-word analysis providing arguments for and against a relationship between the described opening and the VNO opening as understood by recent work (see Bhatnagar and Smith, 2001, for further discussion).

We are now left with making interpretations. Strictly speaking, the description by Ruysch was that of a septal mucosal pit, i.e., any externally visible opening on the septum (Bhatnagar et al., 2002). This structure in Figure 1b, pointed by a stylus (“D” — “hairs, set in the nasal canal”), could have corresponded to an opening for any number of mucosal structures—did it correspond to the true opening of the VNO? Two important thoughts lead to our following interpretation. First, some investigators have shown that the openings of the VNO are liable for misinterpretation, because other structures can create a similar aperture or surface depression (Bhatnagar et al., 2002; Jacob et al., 2000; Smith et al., 2001b). Second, the VNO is not synonymous with its surface opening. In other words, it is a tube found deep to the surface nasal septal epithelium, which cannot be observed grossly and, thus, must be viewed by serial sectioning (Bhatnagar and Smith, 2001; Bhatnagar et al., 2002). Based on these thoughts, we conclude as follows: (1a) The stylus in Ruysch’s Figure 5 (Figure 1b,c) appears to point to an opening in the septum as he described. However, it could only be the opening of the VNO and not the submucosal organ itself. (1b) Although the human VNO is rather variable in superoinferior location (Bhatnagar and Smith, 2001; Smith et al., 2001b), we believe the illustration indicates a position too close to the palate to indicate the true opening of the VNO. (2a) Ruysch effectively encouraged Sömmering, Jacobson, Gratiolet, and/or Dursy to explore the subject further, and (2b) this culminated in Kölliker’s (1877) definitive description of a histologically identifiable, submucosal, elongated epithelial tube in the nasal septum that comprises the human VNO. Kölliker (1877) thus described the actual organ itself, and not a surface opening of uncertain relations, for the first time.

Sömmering’s Contributions

Samuel Thomas von Sömmering’s (1755–1830) biographical note appears in the Dictionary of Scientific Biography (Hintzsche, 1980b). In 1809, he (Figure 2a) published a monograph on the human organ of smell. Here, we rely on Pearlman (1934) who presented an illustration from Sömmering (Figure 2b). This was a lateral view of the left side of the nasal septum in an adult and had a stylus entering an opening in the septal epithelium. The original text pertaining to this image remains unavailable to us, but the stylus was purported (retrospectively by Pearlman) to enter the VNO. The position of the opening is more in keeping with published findings on surface openings that were histologically verified to lead into the VNO (Johnson et al., 1985; Bhatnagar and Smith, 2001). The association of this opening in Sömmering’s illustration with the VNO cannot be verified with any certainty, and as noted above, a surface opening does not correspond to the organ itself. Thus, the portrayal of Sömmering as the second to describe the VNO (Pearlman, 1934) is inaccurate.
Ludwig Levin Jacobson’s Discoveries

In 1811, this now well-known monograph on the vomeronasal (Jacobson’s) organ of mammals appeared under Francois Cuvier’s name, which has been translated in its entirety by Bhatnagar and Reid (1996). It is notable that there are no illustrations in this work, and that most of it deals with Steno’s (nasopalatine) duct of mammals. The “Organ” as Jacobson (Figure 3) called it, was said to “vanish completely in man.” It is now clear that Ludwig Jacobson did not play a role in discovering the human VNO. Two years later, in 1813, Jacobson published a monograph in Danish, under his own name, on the “Anatomical description of a New Organ in the nose of the domesticated animals” (with illustrations). This text has been translated by Trotier and Døving (1998). To our knowledge, it shows the first coronal section of a VNO, from a horse, in Figure VI, Plate IV of this work. Jacobson, indeed, is the discoverer of the VNO in domesticated mammals, but not of the human VNO. Readers may obtain further historical perspective from Bhatnagar and Reid (1996) and Trotier and Døving (1998).

Other Relevant Contributions

Louis-Pierre Gratiolet (1815–1865, see Coleman, 1980) wrote a thesis on the VNO in animals. Even though he mentioned Steno’s canal in humans, a direct reference to the human VNO is missing. There are four plates of illustrations, none of which pertained to the human VNO. Gratiolet’s work has historical value on the mammalian VNO in general.

Emil Dursy (1828–1878, see Mörike, 1984) published a two-volume work on the human head. He examined several human embryos and recognized “Jakobson’schen Organe” (sic) and its cartilage. No illustrations accompanied this description.

Kölliker as the Discoverer of the Human VNO

Rudolf Albert von Kölliker (1817–1905; Figure 4a) was professor of histology at the University of Würzburg, Germany. A biographical note on him appears in Encyclopedia Britannica (1990) and the Dictionary of Scientific Biography (Hintzsche, 1980a).

Kölliker was aware of Dursy’s (1869) report on a blind sac in the human embryo, which emptied into the nasal cavity anteriorly, and which was interpreted by Dursy as the homolog of the mammalian VNO. Kölliker studied fetuses 4 months and older and noticed a round opening (what we know of today as a septal mucosal pit, cf. Bhatnagar et al., 2002). He showed the confluence of this opening with the tubular VNO, histologically (Figure 4b,c). The use of histology was of paramount importance without which the identity of the opening could not have been determined. Kölliker emphatically adds “From now on I will call (this structure) Jacobson’s Organ” (the VNO). He also recognized and named the bar-shaped cartilage below each VNO as Jacobson’s (paraseptal) cartilage. Kölliker also had examined newborns and children within 1 year of age. He mentions Ruysch as having correctly described and illustrated the emptying point of this organ. This statement by Kölliker was purely retrospective, because even if Ruysch has observed an opening, he did not know the relationship to the VNO. A VNO was observed in adults by Kölliker for which he provided measurements; by comparing this structure with that in other mammals, he noted many of its attributes missing in humans. He accepts his ignorance about the presence of sensory epithelium. Some remarks are made about the lack of a VNO in birds. In closing, Kölliker mentions derivation in the human from animal-like forms and that the human VNO is not an atrophied organ.

This monograph was supported by 16 footnotes, two plates bearing 10 figures, and figure explanations. His figures show complete consistency with more recent works on the general
morphology and anatomical position of prenatal (Kreutzer and Jafek, 1980; Smith et al., 1997; Smith and Bhatnagar, 2000) and postnatal (Johnson et al., 1985; Bhatnagar and Smith, 2001; Smith et al., 2001b) human VNOs. Some of his more specific microscopic observations, e.g., regarding communicating mucous glands, also were confirmed by later histochemical investigations (Roslinski et al., 2000; Bhatnagar and Smith, 2001). Considering Kölliker’s description complete in every respect, attribution of the discovery of the human VNO to Kölliker is well-deserved. His monograph, translated into English, is presented here as an appendix.

In conclusion, it is to be emphasized now that, when authors have attributed the “nasal canals” observed by Ruysch as being the human VNO, it has been a retrospective epiphany of sorts. Little was known of the microscopic nature of the human VNO until the second half of the 19th century, when Dursy (1869) commented on prenatal development and Kölliker (1877) described histological structure of the VNO in fetuses and adults. When histological observations such as these were first provided, a discrepancy between studies became clear for the first time—a discrepancy that continues to the present date. Studies that used gross structural landmarks to locate the VNO reported that the VNO may not be present in all adults (e.g., Potiquet, 1891). On the other hand, histological studies reported a universal presence of the VNO in prenatal and postnatal humans. When all data are examined and reconstructed, Kölliker stands out as the discoverer of the human VNO.

ACKNOWLEDGMENTS

We thank Dr. K. Lai Gauri, Professor Emeritus, Dept. Geosciences, University of Louisville, for translating Kölliker’s work; Dr. Robert D. Lugibill for translating page 26 from Ruysch (1724); and Dr. Bert Ph Menco who provided necessary help in harvesting the nasal septum communicating mucous glands, also attributed the “nasal canals” observed by Ruysch, in the magazine Kundschrift. We also thank the research librarians Felix Garza, Kathy Lynn Rogers, Michel Atlas, and Jane Bottoms for accessing the archival material for this study. Dr. Robert D. Acland, Professor of Surgery, provided necessary help in harvesting the nasal septum examined in the study.

LITERATURE CITED


Ruysch F. 1703. Thesaurus Anatomicus Ter tius. Amstelaedami: Joannen Wolters. p 48–49, 70; Plate IV. Fig. 5. (see English translation by Bhatnagar and Reid, 1996).


APPENDIX

UEBER
DIE JACOBSON’SCHEN ORGANE DES MENSCHEN
VON
A. KOLLIKER

MIT 2 TAFELN

ABOUT
THE JACOBSON’S ORGAN OF HUMAN BEINGS
BY
A. KOELLIKER

IN F. VON RINECKER, FETSCHRIFT. LEIPZIG:
WILHELM ENGELMANN. PP. 3-11 + EXPLANATION OF FIGURES + 2 PLATES.
BY A. KOLLIKER 1877

In 1869, Dursy¹ reported in human embryos from 8-20 ‘cm’ long, a small blind sac emptying in the nasal cavity in the lower frontal end of the nasal septum, and interpreted this as homologue of Jacobson’s organ in mammals. Strikingly, this concise definition of the structure did not find any further notice, at least no mention of it has been found in recent anatomical or embryological journals, and yet its occurrence is fully confirmed and can be demonstrated easily in every human embryo. Furthermore, it is found in the postembryonic period in children as well as in the adult. Without doubt these organs are equivalent to the mammalian Jacobson’s tubes (Jacobson’schen Rohren) and from now on it will not appear that they will be an insignificant addition, though rudimentary structures in humans.

I have looked at the human embryos older than four months and have found almost the same conditions in all of them. On the lower frontal portion of the nasal septum, somewhat before where the Stenson’s passages empty in the nose, and in a frontal plane passing through the incisors, one finds on both sides a small rounded opening which can be recognized with the naked eye in embryos older than six months, and at least with a hand lens in younger embryos. Vertical sections in this vicinity of the septum (Figs. 2 to 7) teach us that this opening leads into a cylindrical or laterally compressed canal, which runs approximately parallel with the floor of the nasal cavity, in which the mucous membrane that drapes the cartilaginous septum slightly extends backwards and then blindly.

¹ Dursy.
The Jacobson's organ occurs not only among children, but is also found in adults and is not different from that mentioned in short and partly in incomprehensible words by Meckel (J. Fr.) and illustrated by Sommering as the mucous membrane passage (Schleimhautgang) on nasal septum. I find this passage, that undoubtedly represents a further development of the Jacobson's organ of a child, in a large majority of cases that I have observed since I became aware of this organ (Figure 8), and stand by to characterize this as an organ of greater perpetual occurrence than Stenson's passage, even though it is easily possible that in the few cases in which I missed this organ one or both sides it was due to sickness that the mucous was wasted. My knowledge of the fine architecture of the Jacobson's organ in the grown ups is based on relationships due to scarcity of well-preserved specimens for study and I can only say that this passage does not mostly proceed backwards but is also at the same time somewhat pulled upwards, exceptionally it even runs steeply upwards, so that its situation is exactly the same as that in the embryos and in the children. Understandably, in adults the swelling that embraces the lower thick margin of the septal cartilage is much better developed and one does not always easily find the opening of the organ when one is directed toward this swelling and the Stenonian duct.

In 18 cases the measurements in adults are as follows:

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Endpoints</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance of the Jacobson's organ from surface</td>
<td>6.0–13.0 mm, in the middle</td>
</tr>
<tr>
<td>of the nasal cavity</td>
<td>8.5 mm</td>
</tr>
<tr>
<td>Width of the opening of Jacobson's organ</td>
<td>1.0–8.0 mm, in the middle</td>
</tr>
<tr>
<td>Distance of the same from Stenson's passage</td>
<td>5.0</td>
</tr>
<tr>
<td>Distance of the same from frontal nasal cavity</td>
<td>5.0</td>
</tr>
<tr>
<td>Distance of the same from upper edge of the</td>
<td>8.7</td>
</tr>
<tr>
<td>septum</td>
<td></td>
</tr>
<tr>
<td>Length of the canal</td>
<td>2.0–7.0 mm, in the middle</td>
</tr>
<tr>
<td>Width at the opening of the organ</td>
<td>1.0–1.6 mm, in the middle</td>
</tr>
<tr>
<td>Distance of the same from the Stenonian duct</td>
<td>1.0–8.0 mm, in the middle</td>
</tr>
<tr>
<td>Distance of the angle between the septum and the</td>
<td>21.0–29.0, in the middle</td>
</tr>
<tr>
<td>upper lip</td>
<td>24.0 mm</td>
</tr>
</tbody>
</table>

The only person who had seen this structure was RÜYSCH, as cited by J. Fr. Meckel and E. H. Weber, who had correctly described and illustrated in his "Thesaurus anatomicus" the emptying of the organ by introducing a probe (italics are ours). At the corresponding site where the organ is found in older embryos I have also found the organ without exception in the newborns (Figure 1) and children one year in age, which I had till then studied, allowing to affirm that at this age it is a normal occurrence. In support, I provide the following measurements in a newborn of few days with the long diameter of the head 16.3 cm and whose nasal septum was 1.65 cm high and 3.3 cm long (Figure 1), in an eight-month-old embryo with head length 8.5 cm, septum 2.2 cm high, and in an embryo of six months (septum 2 cm long and 1 cm high) on the side position.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Embryo 6 months</th>
<th>Embryo 8 months</th>
<th>Child of few days</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance of the Jacobson's organ from surface</td>
<td>1.5</td>
<td>3.0</td>
<td>2.5</td>
</tr>
<tr>
<td>of the nasal cavity</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Width of the opening of Jacobson's organ</td>
<td>0.5</td>
<td>0.7</td>
<td>0.33</td>
</tr>
<tr>
<td>Distance of the same from Stenson's passage</td>
<td>7.5</td>
<td>5.0</td>
<td></td>
</tr>
<tr>
<td>Distance of the same from frontal nasal cavity</td>
<td>5.0</td>
<td>8.0</td>
<td>9.5</td>
</tr>
<tr>
<td>Distance of the same from upper edge of the</td>
<td>8.7</td>
<td>9.0</td>
<td>14.2</td>
</tr>
<tr>
<td>septum</td>
<td></td>
<td></td>
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</tbody>
</table>

After I had found the Jacobson's organ on the ears of embryos in different ages, it was easier for me to search for these in postembryonic stages; yet I had only newborns and children within one year of age available to me at that time. The only person who had seen this structure was RÜYSCH, as cited by J. Fr. Meckel and E. H. Weber, who had correctly described and illustrated the emptying of the organ by introducing a probe (italics are ours). At the corresponding site where the organ is found in older embryos I have also found the organ without exception in the newborns (Figure 1) and children one year in age, which I had till then studied, allowing to affirm that at this age it is a normal occurrence. In support, I provide the following measurements in a newborn of few days with the long diameter of the head 16.3 cm and whose nasal septum was 1.65 cm high and 3.3 cm long (Figure 1), in an eight-month-old embryo with head length 8.5 cm, septum 2.2 cm high, and in an embryo of six months (septum 2 cm long and 1 cm high) on the side position.
That the Jacobson's cartilage occurs—whether perpetual is subject to further investigation—on both sides in adults in my experience on 1-3, was already mentioned and I further point out that recent studies, with the exception of Dursy, do not appear to recognize it. Taking this opportunity I present a condition, to my knowledge not yet reported, of the cartilaginous septum. The same always develops from its lower posterior edge as a 4–6 mm wide cartilage plate, which, more or less is completely enclosed and covered by the upper edge of vomer plate, pulls backwards and upwards along the lower edge of lamina perpendicularis of the Siebbein (some bone) and nearly reaches the rostrum sphenoidale, yet fuses with the same (Figure 9). This "processus sphenoidalis septi cartilagi-nei" as I call it, had possibly been seen by Schwegel, but his writing was so vague that this cannot be said with certainty.

I have also made observations on the oft mentioned Stenson's passage or the ductus nasopalatinae. I find the nasal junction of this passage open in most cases, but there are enough examples in which this is completely closed or disappears totally without any trace. Concerning its junction with the gum among adults, so far I have not seen any case in which the same condition existed, whereas it can be seen among children from the first year. Definite information however can be obtained by carefully preparing serial sections which I have been able to prepare only one of adults in which it showed that passage at the gums was closed. In this case the passage had, where there was a distinct clearing, a 53 μm thick flicker (flimmer) epithelium with cylindrical cells and so many grape-shaped mucous glands joining it, that they had completely overtaken the surrounding connective tissue. Near the nasal opening to about 1.28 mm long passage and the surrounding connective tissue (corresponding to the width of the bony canal), 5.13 mm, the structure, not considering the glands, looked almost cavernous due to the presence of numerous veins. Soon, the passage became narrower to 0.5 mm, then descending 0.22 mm it disappeared (Figure 10).

This is essentially what I have to convey about the Jacobson's organ among human beings. Now I wish to state concisely why I, like Dursy, place the organ in question without fail on the side of the Jacobson's organ of mammals, although many attributes of the last have not been observed in human beings, such as a cartilaginous capsule, the access from olfactory cilia, the opening into the Stenson's passage; the specific epithelium (S. C. Balogh in Wiener Sitzungsberichte, 1860) and the supply of nasopalatine region with fibers.

What first concerns the relationship to Stenson's passages or ductus nasopalatinus, so these are not original, because in very young mammalian embryos with still unformed palates, they merge freely into the Jacobson's organ simply on the frontal lower portion of the nasal septum. Thus among humans as well this primitive condition could exist, and it appears quite understandable that in him the Jacobson's organ from the beginning on has a higher position on the septum compared to that in animals, so they could not at all come in the area of the Stenson's passage.

From this higher position, it can be further explained why in humans the Jacobson's cartilage typically has a constant position on the lower septum. One could then argue that these cartilages extend much farther than the Jacobson's organ in mammals, and are not part of the floor of the nasal cavity. Such is truly the case with the Jacobson's organ.

With reference to the developed opinions in the last two paragraphs I further observe, that in human beings in certain cases the Jacobson's organ lies very close to the concerned cartilage.

Further, whether or not the Jacobson's organ of humans contains nerve fibers and possess sensory epithelium (sinnesepithel), is not known and therefore these points do not enter into this discussion. Because the olfactory fibers on the septum reach furthest to the area of Jacobson's organ, as also given by SCARPA, it does not seem implausible that these organs among humans by their specific construction offer indications of kinship to the mammalian organ. Even if it were not so, I would not find any hindrance to the above explanations that the organ of the mammalian embryos in the beginning also do not show any specific epithelium.

This is the place to discuss in detail the Jacobson's organ among animals, therefore, I observe the following.

First of all, much is yet to be learned about the extension and structure of this organ. With respect to mammals, I point to the hardly known knowledge in Germany of Gratiolet's work, and observe that after my studies on oxen, the cartilage of the organ and the inner epithelium are not thoroughly described, about which I will reserve my further comments. Among lower vertebrates the reptiles seem to have the Jacobson's organ (Rathke), Stannius, von Leydig, and perhaps also the amphibians (Gotte, Born) and the fishes (Winther). However, except that of v. Leydig, precise statements are yet not available on any of these classes.

Among birds Jacobson's organ is so far not known and my efforts on this have been fruitless. Nevertheless, it is striking that the exit passage of the nasal gland partly extends in a fashion as in humans. Because this passage in my knowledge has not been accurately described by any one, so I give for other's benefit a short description of its course in geese. From the upper edge of the eye cavity begins the passage of the nasal gland, under the frontal anterius and runs in a depression between these bones and the nasal bone at the upper surface of the ligamentous side portion of the nose. Somewhat behind the bony nasal cavity the passage perforates the ligament wall and runs on its underside, i.e., on the lateral wall, downwards towards the floor of the nasal cavity, where it enters the connecting fold, which the fore-chamber of shell (GEGENBAUR) meets with the septum, whereby it is endowed...
with a concave cavity directed towards the front. So, the passage reaches the septum and runs in it right and left of septal cartilage towards front, finally ending at a site, sharply defined in goose, with a small ending which is difficult to recognize. This point is found there, where the lateral margin of a fractured plate that makes the middle portion of the frontal section of the floor of the nasal cavity joins the septum. In a grown goose, the passage is nearly 4–5 mm in the septum and its ending is 5 mm from the frontal edge of the septum (at the site where both frontal pouches of the nasal cavity come together). On frontal sections across the septum lies the over 1 mm wide passage beneath a thickening of septal cartilage and above the strong nervi nasopalatini. However, I would not have described this situation in such a detail had this wide passage not reminded me of the human Jacobson’s organ by its position on the septum; perhaps, that portion of the organ lying in the septum is homologous with Jacobson’s organ. In the latter case, additional consideration is deserved, due to the fact that another small blind sac begins where this passage turns laterally, so that one may interpret it as the Jacobson’s organ, into which the nasal gland empties posteriorly. I note further, that at the junction of the passage, which I have also seen in hen and *Buteo vulgaris*, a pavement (flat) epithelium as seen in nasal frontal cavities, that in a young goose bears brown pigment granules, is found instead of the cylindrical epithelium that occurs inside.

Secondly I allow myself some remarks regarding the function of Jacobson’s organ in mammals. When one considers the short width of this organ and the narrowness of the passages through the Stenson’s canal, which are additionally closed near the mouth cavity in certain animals (in horse after Cuvier, in Cavia and in camel after Gratiolet), when one further thinks that the organ in question is enveloped by a rigid capsule and closed behind, then one is led to believe that it would be impossible to have the purpose to take air and olfactory materials from oral cavity through Stenson’s passage and thereby to distinguish harmful from harmless food products (Cuvier). So it remains, when one does not want to accept that Jacobson’s ducts are simply secretory organs–for which the indications come above all from their profusion of blood, their innumerable glands, and their richness on branches of nasopalatinus nerve, against which however speak the availability of innumerable olfactory fila and its sensory epithelium–nothing else can be assumed that they differentiate juices and substances from each other, which work on their specific nerves and so enable the organisms to somewhat directly obtain knowledge of chemical composition of their own secretions. Under this assumption the flicker (flimmerung) in the organ, which in my observations on calf produces current going from inside to outside, becomes understandable. Whether the organ is also secondarily to supply secretions which moistens the nasal cavity (Jacobson) or the snout, which can facilitate the intake of food or works on the nerves of tongue is possible. However, I do not want to close doors on these considerations and above all point out that possible physiological experiments could settle it on one or the other side.

In conclusion, I stress once again that through the Jacobson’s organ in humans the number of rudimentary, perhaps totally non-functional organs, will not just be increased by an insignificant feature. Undoubtedly this organ is inherited from an earlier, animal-related form, and appeared in humans in a way, which shows that this unlike the Meckel’s cartilage, the Muller’s passage in human form among others as atrophied, rather be considered only as an undeveloped embryonic feature, like the breast gland in man.

EXPLANATION OF FIGURES
ON PLATES I AND II

(Editor’s Note: The plates have been reproduced at about 50% of their original size.)

Fig. 1. Nasal dividing wall of a few days-old child with the opening of the Jacobson’s organ. Natural size.

Fig. 2. Frontal section through the frontal portion nasal cavity, the gums and the sacks of the inner incisor of human embryo of 4 months. The Jacobson’s organ sits deeper than normal and shows one of its junctions. The Jacobson’s cartilage appears on both sides closer to the septum in the form of three small bars, which are not continuation of each cartilage, as shown in Figs. 3 and 4. x 8.

Fig. 3. A similar section located somewhat posteriorly in another human embryo of 4 months. The Jacobson’s organs lie higher, the Jacobson’s cartilage are simple. The position of the inferior concha (Muschel) is clear as of both upper molars. x 8.

Fig. 4. A similar frontal section of a human embryo of 5 months. One sees the transverse sections of the Jacobson’s organ, the Jacobson’s cartilage, the position of 4 incisors, the upper molar, the inferior concha and centered within the gum a round epithelial mass, the overly grown mass formed by the growth of gum partition by the epithelium in the gum node of a primitive mouth cavity. x 8.

Fig. 5. Nasal septum of human embryo of 6 months, one Jacobson’s organ with opening, the other met obliquely. Jacobson’s cartilage of both sides represented by 3 small ligaments.

Fig. 6. Jacobson’s organ of embryo of Fig. 3 with the joining portion of nasal septum in high magnification. The opening is seen in one organ.

Fig. 7. The same organ towards its posterior end, here with clear connective tissue encapsulation.

Fig. 8. Nasal partitioning wall of an adult with the opening of Jacobson’s organ. Natural size.
Fig. 9. Cartilaginous and bony nasal septum of a grown up in natural size. a. cartilaginous septal sphenoidal process, exposed by removal of the lamella of upper frontal edge of the vomer bone. b. Jacobson’s cartilage (Pflugschaarknorpel, Huschke).

Fig. 10. Soft portion of an adult Canalis incisivus, approximately 19 times enlarged. a. Stenson’s passage with three joining glandular passages. b. artery. c. vein. d. nasopalatinus Scarpae. e. secretory glands.

FOOTNOTES
1. On the evolutionary history of the human head and of higher vertebrates. Tubingen 1869 with atlas. p. 135–139, Table VII, Fig. 6 c, Fig. 7; Table VIII, Fig. 2 c; Table IX, Fig. 6 c.
4. Thesaurus Anatomicus III. Amstelod. 1703. p. 49. “It appears in the anterior and inferior parts of the septum just above the palate, appearing literally along with its duct. I have read nothing from authors concerning Its use and its existence. I think it serves for mucus secretion. See Plate IV, Fig. 5, Thesaurus 3, Letter E.” (Authors’ note: see Bhatnagar and Reid, 1996, p. 223).
5. In Handb. Der Menschel. Anat. Bd. IV. 1820. p. 141. “On the lower edge of septal wall, a passage often runs posterior to front a narrow, blind on the back, which opens not too far behind the frontal edge; evidently about the Jacobson’s organ (Sic. ?) in this regard Ruysch and Jacobson l.s.c. are cited and should have been named "remainder of the Jacobson’s organ."
6. The illustration of the human organ of smell, Frankfurt 1809, Table II, Fig. 1, 9. “Opening of the perpetual mucous membrane canal, in which a probe has been introduced. Such a probe can be easily introduced in the canal for several unit length.”
8. In a sheep embryo of 2.7 cm I found in Jacobson’s organ cylindrical epithelium; contrary to this, in one embryo of 11 cm, already a differentiated epithelium on both sides is found in which the medial side was three or four times thicker as the lateral sides.
10. Developmental history of the viper. That Rathke describes as nasal gland is not different from Jacobson’s organ.
14. About the nasal cavities and tear passage in amphibians in Gagenbauer’s Morph. Jahrbuch, Vol 2, p. 577. Whether those written by Goette and Born as side sacs of nasal cavity be considered as Jacobson’s organ, is not yet proved. Born is against such explanation, because the organs in question open only in the nasal cavity and not also in the mouth cavity (p. 604. Anm.). Because same conditions are present in Jacobson’s organ of humans and few mammals (see below), so is this reason not adequate.
15. Fiskenes Ansigt, Forste Afsnit in Naturh. Tidsskrift. 3. R. X. vol. P. 185. Pl. I, Fig. 16, 18; Plate II, Figs. 1, 3, 5. Those parts indicated in young salmon by Winther are, less deep, front at snout at the outside between both nasal cavities, these depressions are not Jacobson’s organ. If this explanation is correct, so it can be said, that the Jacobson’s organ existed originally independently of nasal depressions, that also Dursy had in some sense tried to defend in the case of embryos of higher orders. (l.c.s. p. 132, u. Fig.).
16. Jacobson (Sur une glande conflomere a la cavite nasale in Nouveau Bulletin des sciences de la societe philomatique de Paris. T. III, VI. Annee. 1813, page 267) says, the gland joins at the frontal portion of the nasal cavity at the end of lower turbinate (Muschel). Also Nitsch had the site of nasal opening, that he found only in geese and in the Charadrius oedicnemus, not accurately described) (Meck. Archiv. VI. p. 234) and observes only “this ends in the nose apparently quite in front” (p. 248) and in Charadrius “the opening is found on the inner side of the outer nasal wall.”

TRANSLATOR’S COMMENTS
No attempt was made for a literary translation; instead it is mainly kept literal to maintain Kolliker’s ideas as expressed in the German text. Throughout the memoir, each page had its footnotes; in the translation, all 16 footnotes have been consecutively numbered and brought together.

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