THE ORGAN OF JACOBSON

By V. E. NEGUS
Ferens Institute, Middlesex Hospital, London

Although 250 years have passed since Ruysch (1703) described the structure now known as the organ of Jacobson (1811), the considerable volume of work devoted to the subject since then has not led to definite conclusions as to the organ's function. The bilateral organ in question is so beautifully designed that one cannot fail to ascribe a purposive function to it; it seems incredible that a carefully arranged system of specialized epithelium, with its own nerve supply, as described by Elliot Smith (1897), McCotter (1917) and others, with numerous glands emptying into it and with a duct communicating with the exterior by a more or less devious route, should not play some important part in the animal economy.

The object of this paper is, in part, to present certain observations on the anatomy of the organ in different groups of animals, but primarily to put forward ideas with regard to its possible role during life. The bibliography is extensive, but amongst general references are Klein (1880), Read (1908), Pearlman (1934), Romer (1949) and Allison (1953).

MATERIAL AND METHODS

The nasal region has been studied in the following animals: newt (*Triturus vulgaris*), toad (*Bufo bufo*), frog (*Rana temporaria*), slow worm (*Anguis fragilis*), guinea-pig (*Cavia porcellus*), rabbit (*Lepus cuniculus*), cat (*Felis domestica*) and dog (*Canis familiaris*).

Following intravital fixation and subsequent decalcification, serial sections were cut, of which every first, fifth, tenth or twentieth was stained, according to the complexity of structural detail. To supplement microscopic observation transparent reconstructions of the nose were prepared. In this way the nasal organ was reproduced as a three-dimensional model and studied either as a whole, or in parts, comprising as many sections as desired. The method of making the models was simply that of photographing the sections as negatives, which were then enlarged as half-plate or whole-plate positives according to size. Histological details were selectively tinted, the plates were then mounted serially in a rack and examined by transmitted illumination.

FINDINGS

Newt

A small lateral recess lined by epithelium of olfactory type, distinct from that of the nasal fossa itself, is present on each side. Communication with the exterior is indirect, via the nasal fossae and the anterior and posterior choanae. It is possible that this simple recess serves to retain odorous substances so that an after-smell is perceived when the air current has removed any olfactory substance from the nasal fossa itself; it would thus discharge a function assumed in other species by the specialized organ. The organ in various Amphibia was described by Seydel (1895).

Toad and frog

In these amphibians a separate recess, in the form of a tubular passage lined by olfactory epithelium, is found in communication with the nasal fossa through a narrow duct about 13·5μ in diameter (Pl. 1, fig. 1).* Connexion with the exterior is indirect, via the nasal fossa and through the anterior and posterior nares. Here again retention of odorous molecules may serve a useful purpose; it is clear, however, that with such a narrow channel of communication the volume of scent-laden air which can reach the organ of Jacobson must be very small, and its rate of passage very slow.

Slow worm

Amongst reptiles no distinct and isolated organ of Jacobson is found in the Crocodilia, nor in the Chelonia—tortoises and turtles (McCotter, 1917). Snakes and lizards are, however, so provided, but in them the organ opens directly on to the palate, without any communication with the nasal fossa (Pl. 1, fig. 2).

It has been reported that these reptiles touch substances in their path with their pronged tongues, the tips of which are then placed near the ducts of Jacobson's organ (Pratt, 1948). The nature of the object touched would then be perceived by the olfactory sense. However, the duct by my measurement is only 13·5μ in diameter (see footnote) and such a small size would necessitate extreme accuracy of tongue movement for any useful information to be derived. The epithelium, which is approximately 95μ in thickness, is symmetrically arranged in a concave crescentic form and appears to be of usual olfactory type. On the opposite wall of the organ the epithelium is ciliated and is about 15μ in thickness.

Mammals

The rabbit has been examined as a member of the order Lagomorpha. It has a beautifully arranged organ of Jacobson, paired and symmetrical. The epithelium is similar to that of the foregoing classes and its nerves are big and well defined; they are connected to the accessory olfactory bulb (Adrian, 1954). The duct from the tubular organ opens by a pore into the lower part of the nasal fossa; it is 27–31·5μ in diameter (Pl. 1, fig. 3). As in the Amphibia referred to above, communication with the exterior is indirect; it is, in the rabbit, into the nasal fossa, at some little distance from the nasal opening of the naso-palatine canal. Communication with the mouth is therefore indirect. The guinea-pig has a similar arrangement. Retention of after-smells would once again appear to be probable.

A well-marked organ is found in Carnivora; reconstructions of *Felis*, the domestic cat, and *Canis familiaris*, the domestic dog, have provided the opportunity for a clear study.

The structure of the organ is much like that of the rabbit, but its method of communication differs. Examination of consecutive serial sections shows that the organ opens directly into the naso-palatine canal (Pl. 1, fig. 4). The duct leading

* All measurements given are from prepared specimens after dehydration and embedding in celloidin. They are useful for comparison, but do not necessarily represent the state during life. For instance, the palatal opening of the naso-palatine canal in a rabbit will admit a tube of 700μ diameter, owing to stretching of the tissues.

from the anterior end of the organ in the cat is 30–40 μ or rather more in diameter and the opening on to the palate is about 50 μ.

It is found, therefore, that there are four types of communication: the first, as in Amphibia, opens into the nasal fossa; the second, as in the snake and lizard, has no connexion with the nasal fossa but opens directly on to the palate; the third, in the rabbit and guinea-pig, opens into the nasal fossa which itself is connected with the mouth by the naso-palatine canal; and the fourth, as in Carnivora, communicates both with the nasal fossa and with the mouth by opening into the naso-palatine canal.

The study of reconstructions and the measurement of the area of mucosa of olfactory type in Jacobson's organ give a rough estimate of relative areas in different animals. It appears that the actual surface area in the slow worm is less than that of the rabbit and still less than that of the cat.

On the other hand, a comparison of the olfactory areas in the organ of Jacobson and in the nasal fossa of mammals reveals a vast proportional increase of the latter as compared with the former.

The deduction is that while Jacobson's organ retains a position of importance in the mammals examined, yet the enormous increase of olfactory mucosa in their nasal fossae indicates a greatly increased reliance on olfaction in the nose as compared with the accessory organ.

The question of transference of odours to the olfactory region of Jacobson's organ presents considerable difficulty. Thus in the toad the communication between the organ and the nasal fossa is only 13·5 μ in diameter. This would make transference of air by diffusion a slow process.

Again, in the slow worm the palatal duct is still no more than 13·5 μ in diameter; there are no glands in the lumen of the organ, but cilia are present on the prominence facing the olfactory area (Pl. 1, fig. 2); and if these cilia were to carry in odorous secretion, it is difficult to see how it would be expelled.

In mammals the palatal duct is lined by thick squamous epithelium devoid of cilia (Pl. 1, fig. 4); in the olfactory part of the organ cilia are present, no doubt to expel secretion derived from the glands of Jacobson. These cilia were described by Kolliker (1877) and Mihalovics (1899).

It has been suggested that odorous secretions are forced upwards in those species where the duct opens through the palate; this would be possible in the cat or dog by pressure on the mushroom-shaped pad between the two orifices (Pl. 2, fig. 5), but it would only serve to propel a little fluid up the naso-palatine canal into the nasal fossa, since the organ of Jacobson is an air-locked tubule communicating laterally with the canal (Pl. 1, fig. 4). This observation can be confirmed experimentally. It would appear probable that the pad serves to prevent entrance of fluid.

It seems likely that olfactory molecules are carried in air rather than in fluid, and that a pumping action of the vascular spaces at the posterior end of Jacobson's organ draws in or expels air by alternate emptying and filling of these blood sinuses, as described by Hamlin (1930); the spaces are well seen in the guinea-pig and in the rabbit (Pl. 2, figs. 6, 7). Vascular spaces are absent in the slow worm (Pl. 2, fig. 8). The pump action was referred to by Broman (1920), but he thought that fluid and not air was the vehicle; Seydel (1895) was of the same opinion.

If the question of retention of olfactory molecules to give an after-smell is considered in relation to anatomical structure, it will be relevant to observe that in both the slow worm and toad there is no recessing of olfactory mucosa. The nasal fossae are more or less circular passages lined in part by specialized epithelium, and any olfactory molecules brought in through the anterior nares will pass down through the posterior nares unless they adhere to the epithelial surfaces. Consequently, when respiration is active, the exchange of air will be complete.

In Carnivora, on the other hand, there is very considerable recessing, a great part of the olfactory mucosa being tucked away in frontal or sphenoidal sinuses, or placed out of the direct respiratory stream above a sub-ethmoidal plate. After-smells will thus be retained, and the role of the organ of Jacobson as an after-smell device will thereby be rendered less important.

Why the organ should communicate with the nose alone in some animals and with the nose and mouth in others is less easy to explain.

SUMMARY AND CONCLUSIONS

1. Although the olfactory sense has progressed to an advanced state of acuity and discrimination in mammals, the organ of Jacobson is nevertheless retained and is of functional importance.

2. On anatomical grounds it appears probable that air and not fluid enters the tubule, and that it conveys odours or flavours connected with the diet of the animal.

3. The duct of Jacobson's organ is of such extreme narrowness, both relative to its length and absolutely, that the passage of air into it must take place slowly.

4. The most likely function of the organ would seem to be related to the after-smell of food rather than to its immediate detection. An associated role in connexion with the secretion of gastric juice is possible.

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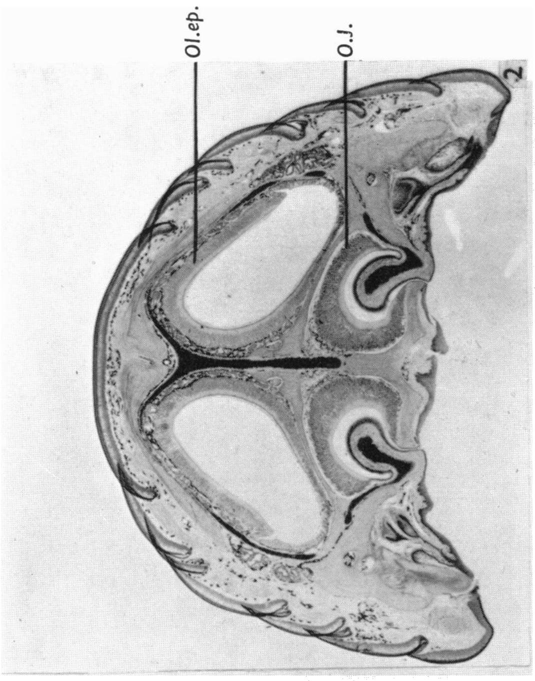

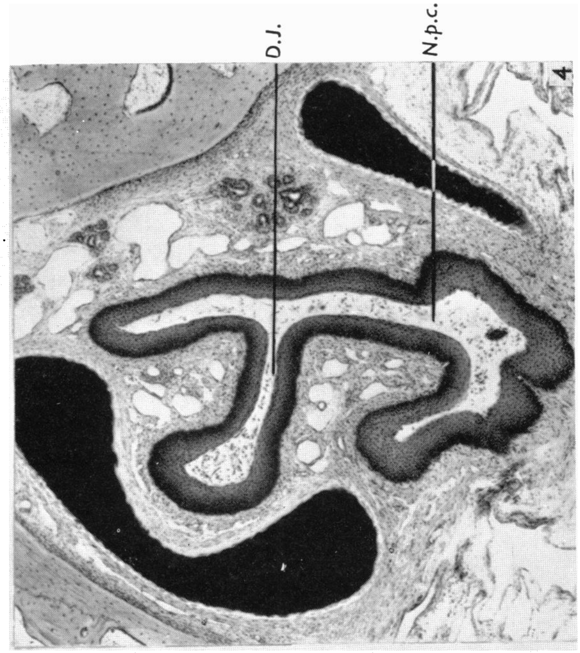

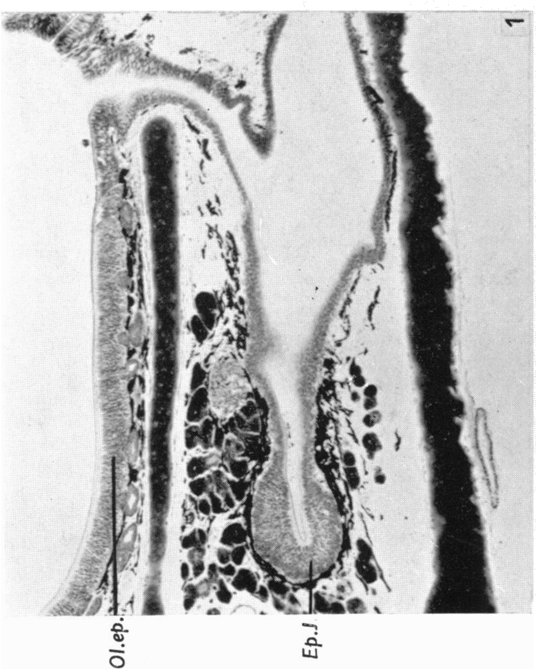

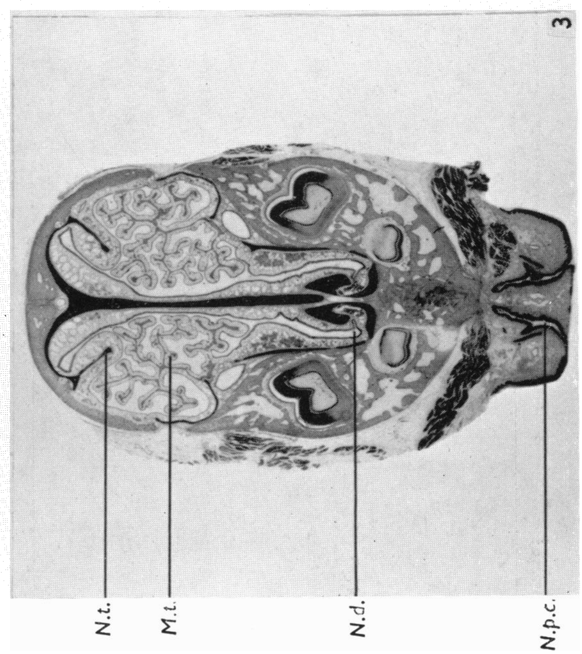

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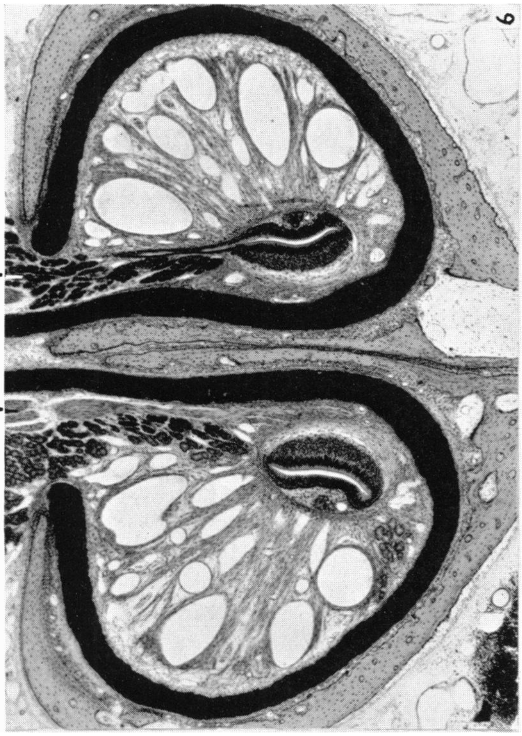
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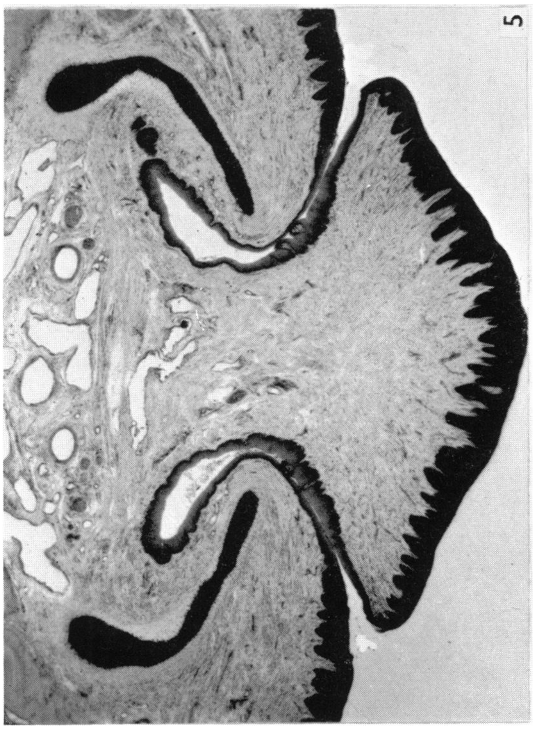
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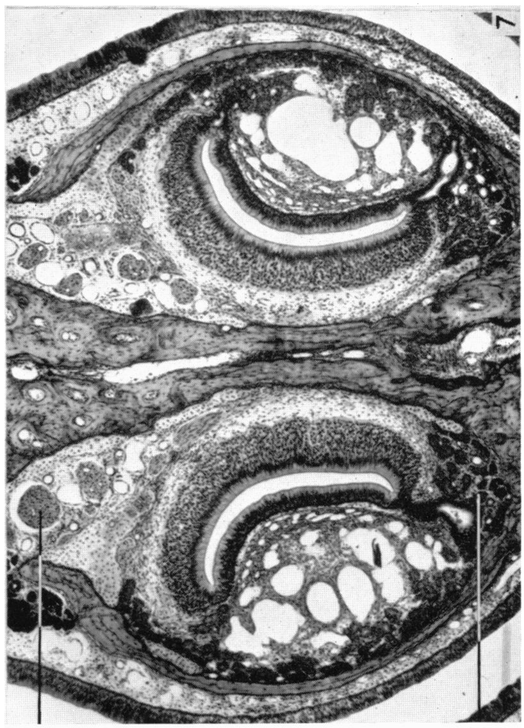
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KEY TO ABBREVIATIONS

D.J.	Duct of Jacobson's Organ.	*N.d.*	Nasål duct.
Ep.J.	Epithelium of Jacobson's Organ.	*N.p.c.*	Nasopalatine canal.
Gl.	Multicellular glands.	*N.t.*	Naso-turbinal.
M.t.	Maxillo-turbinal.	*Ol.ep.*	Olfactory epithelium of nasal fossa.
N.b.	Nerve bundles.	*O.J.*	Organ of Jacobson.

EXPLANATION OF PLATES

Plate 1

Fig. 1. Toad (*Bufo bufo*). The nasal fossa above communicates by a narrow channel with the organ of Jacobson below; the specialized epithelium of the latter is thicker than that of the former.

Fig. 2. Slow worm (*Anguis fragilis*). Transverse section to show the relative sizes of the nasal fossae and the paired organ of Jacobson; the epithelial lining of the latter is thick.

Fig. 3. Rabbit (*Lepus cuniculus*), showing the nasal duct of Jacobson's organ and also the commencement of the nasopalatine canal.

Fig. 4. Cat (*Felis domestica*). The duct of Jacobson opens into the medial wall of the nasopalatine canal; both are lined by squamous epithelium.

Plate 2

Fig. 5. Dog (*Canis familiaris*). The orifices of the two nasopalatine canals are protected by a mushroom-shaped flap.

Fig. 6. Rabbit (*Lepus cuniculus*). The olfactory part of the organ is contained in a cartilaginous capsule, within which are wide vascular spaces.

Fig. 7. Guinea-pig (*Cavia porcellus*). The olfactory part of the organ lies within a bony capsule and has wide vascular spaces on its outer side.

Fig. 8. Slow worm (*Anguis fragilis*). Posterior end of the organ with cells of the specialized epithelium cut across. There are no vascular spaces.