9 Physiology of Olfaction
H. Altner

The human nose is capable of discriminating thousands of different odor substances, but this achievement is modest compared with the performance of other organisms. This relative lack of olfactory ability, combined with the dominant importance of our other sense organs, may well be one reason why people have had little interest in research on the olfactory system. Another is the difficulty of experiments on the sense of smell — with humans, certainly, but also with other animals. As a consequence, neither subjective nor objective criteria have permitted clear definition of odor qualities; there is little order in the bewildering variety of adequate olfactory stimuli. On the other hand, as this chapter will show, the olfactory pathway in mammals is well known. Structural and physiologic analysis has revealed a number of interesting properties of the system — for example, that the signals sent to the brain are under efferent control. Much has also been learned about the significance of the sense of smell in autonomic regulatory and emotional attitudes.

9.1 The Olfactory Mucosa; Peripheral Mechanisms of Olfactory Reception

The first subject of this section is the morphology of the olfactory organ and the cells it comprises. We shall then turn to the variety of stimulus substances; these cannot be classified as to quality, on the basis either of the sensations they elicit or of the responses of individual sensory cells.

**Location and cellular organization of the olfactory epithelium.** The nasal cavity is divided into two spaces, left and right, by a partition called the nasal septum. The surface area of each space is enlarged by folding to form ridges, the conchae, which project into the interior from the outside walls. As Figure 9–1 shows, in the adult human three conchae are arranged one above the other on each side. The entire nasal cavity is lined with a mucous membrane, but the olfactory sensory cells are restricted to a small area, the olfactory region (shown in red in Fig. 9–1). The olfactory region covers the whole of the upper concha and forms islands on the middle concha. There is also olfactory epithelium on the adjacent parts of the septum. The respiratory region — the part of the nasal mucosa that lacks olfactory cells — is a ciliated epithelium made up of two layers of cells, among them the goblet cells which produce the mucus.
In the human fetus, the mucosa on the septum contains closed tubules that appear to lead nowhere. These are rudiments of the vomeronasal (Jacobson’s) organ, an olfactory organ that plays an accessory, and in some cases important, role in many amphibians, reptiles, and mammals. It no longer exists in humans.

Figure 9–2 shows the structure of the olfactory mucosa, a several-layered epithelium with two predominant cell types, the olfactory cells and the supporting cells. As in the taste buds (cf. Chap. 8), basal cells are also present; these can develop into olfactory cells, and are thus immature sensory cells. The olfactory cells (unlike gustatory sensory cells) are primary sensory cells, sending out axons from the basal pole. These fibers form thick bundles beneath the sensory epithelium; these (also called fila olfactoria) run to the olfactory bulb.

At their apical poles the olfactory cells bear modified cilia, enclosed by the layer of mucus that covers the olfactory epithelium. The molecules of an odor substance must diffuse through part of this mucus layer before they reach the most peripheral part of the olfactory cells, the membranes of the cilia. The mucus is derived from three sources: 1. Bowman’s glands, 2. the goblet cells of the respiratory region, and 3. the supporting cells of the olfactory epithelium, which thus serve a dual function. The kinocilia of cells in the respiratory region act to control the flow of mucus.

Odor sensations are not mediated exclusively by the sensory cells in the olfactory region. The respiratory region includes, in addition to the cell elements already mentioned, free endings of sensory fibers of the fifth cranial nerve, the trigeminal;