

1 Evolution of the Chemical Communication and Olfactory 2 System in Animal Kingdom

3
4 *Chemical signals transmit a large amount of information about the*
5 *environment, enabling animals to identify desirable elements (such as food) or*
6 *dangers to avoid (such as predators) and to locate mating partners.*
7 *Considering the wide range of different chemicals, it is not surprising that*
8 *organisms, living in different contexts, use an important repertoire of receptors*
9 *and signaling pathways to probe their environment. The aim of this work was to*
10 *describe the major stages in the development of the olfactory organ during the*
11 *course of evolution. The few cells on the body surface of primitive organisms*
12 *gave way to an individualised organ, at first rudimentary and then increasingly*
13 *complex and efficient.*

14 15 16 Introduction

17
18 Animals used a wide variety of methods to locate vital environmental
19 information or communicate with each other, the most common modes being
20 visual, auditory and chemical communication systems. Until recently, research has
21 focused on the visual and auditory systems, but recent improvements in chemical
22 analysis methods have shown that chemical signals are involved in communication
23 between a large number of organisms in a multitude of contexts (Müller-Schwarze
24 and Silverstein, 1980; Bradbury and Vehrencamp, 2011). Chemical signals have
25 several advantages over audible and visual signals : they are effective in darkness,
26 around obstacles, and are relatively persistent over time, even in the absence of the
27 transmitter (Alberts, 1992). Odiferous molecules are transported by the external
28 environment (air, water) or by the organisms themselves. Some chemicals have no
29 spontaneous informative, appetitive or aversive, value. However, a value can be
30 associated with them through learning. These chemical cues served as a guide for
31 locating environmental information essential for survival, such as detection of
32 food or sources of danger (Table 1) (Ache and Young, 2005). Other chemicals
33 have an intrinsic signal value. This is the case for the semiochemicals, which elicit
34 a biological response in individuals of the same species (pheromones) or different
35 species (allelochemicals) (Bakthavatsalam, 2016). Pheromones elicit a specific
36 reaction, such as a stereotyped behavior or a developmental process in congeners.
37 Allelochemicals are involved in interspecific communication. Some allelochemicals
38 are beneficial to the emitter of the signal (allomones), others to the receiver
39 (kairomones), or to both the emitter and the receiver (synomones) (Table 1)
40 (Sbarbati and Osculati, 2006). All these chemical substances present a great
41 structural and functional diversity, requiring the decoding of information by a
42 specialized system. Each animal group, whether invertebrate or vertebrate, has its
43 own chemical signal detection system adapted to its living conditions, which
44 requires a high discrimination power on part of the receiver, in order to allow
45 distinction of an odor among others, and allows it to respond appropriately to
46 chemical environmental information (Wyatt, 2014). In addition, chemicals are
47 often produced intermittently, making it difficult for animals to decipher the odor

1 signal. Indeed, animals are subjected to turbulence in the air or water, which
 2 disrupts the diffusion of odors and gives rise to highly discontinuous odor plumes.
 3 Finally, odors are rarely single compounds, but a combination of molecules,
 4 whose treatment is more complex. These different characteristic aspects of
 5 olfactory signal decoding give rise to certain organisational similarities between
 6 olfactory systems of phylogenetically different species. (Krieger, 1999; Ache and
 7 Young, 2005). The aim of this review was to describe the different ways in which
 8 olfactory signals are detected and processed in the animal kingdom.

9
 10 **Table 1.** *Chemicals signals involved in animal interaction (invertebrates and*
 11 *vertebrates)*

Chemical substances	Effects produced	Types		Examples of biological roles
Chemical cues	Non intentionnel effects	Physico-chemical parameters of the environment as guide to future action		Assess food or water, avoid fire
Semiochemicals	Interspecific effects	Allelochemicals	Kairomones: chemicals that benefit the receiver but not the emitter of the signal	Predation, parasitism
			Synomones: chemicals that favor both the emitter and the receiver of the signal	Mutualism
			Allomones: chemicals that benefit the emitter but not the receiver of the signal	Defence secretions
	Intraspecific effects	Pheromones	Releasers: initiate immediate behavioral responses Primers: causes physiological, morphological changes	Identity of individuals, social status, social group

13 **The Chemosensation in Invertebrates**

14
 15 Most invertebrates use olfaction as their main sensory modality and have a
 16 highly evolved olfactory system that enables them to reach an important level of
 17 sensitivity and specificity.

1 *In cnidarians*

2

3 In most cnidarians, vision is absent and prey is captured by an extraordinarily
4 sensitive chemodetection. Most of studies have focused on jellyfish. Chemicals
5 present on or originating from prey are detected by receptors located on
6 specialized epidermal cells, that activate the cnidocyte mechanoreceptors and the
7 discharge of nematocysts into the prey. The mechanoreceptors and
8 chemoreceptors are neutrally connected and cover most of the exterior surface
9 (Watson and Hessinger, 1989; Albert, 2011). Archdale and Anraku have shown
10 that other chemoreceptors are located in the lateral tracts of the *Aurelia sp.*
11 jellyfish oral arms, whose function is to select captured objects according to their
12 taste (Archdale and Anraku, 2005).

13

14 *In flatworms (platyhelminths)*

15

16 Chemoreceptors are found in multi-sensory structures, the auricles, located
17 near the anterior of the animal, behind the photoreceptors. The auricles contain
18 nerve cells, whose dendritic region in contact with the external environment is
19 ciliated and permits sensitivity to touch and certain chemicals. The
20 chemoreceptors allow the detection of prey and ensure the orientation towards
21 food sources (Mori et al., 2019). For example, *Platydemus manokwari* locates
22 snail slime trails, sometimes even in trees (Yamaura, 2008).

23 *In nematodes*

24 The free-living *C. elegans* can modulate its behavior by reacting to at least 50
25 odorous substances over a wide range of concentrations. Its olfactory organs
26 consist on the symmetric amphid sensilla in the head and composed of a small
27 number of interconnected neurons, gland cells and supporting cells. Each olfactory
28 sensory neuron expresses many different olfactory receptors and is polymodal
29 (dedicated to several sensory modality). Similarly, the parasitic worms use
30 olfactory cues to find and infect hosts. Studies have demonstrated that their
31 olfactory behaviors are specific to each species, despite the fact that sensory
32 neuroanatomy is approximately conserved across the different nematode species
33 (Rengarajan and Hallem, 2016).

34

35 *In annelids*

36

37 The chemoreception is involved in the behaviors of annelids. In polychaetes,
38 the chemicals are detected by the nuchal organs, including ciliated supporting
39 cells, bipolar primary sensory cells and a retractor muscle. Other structures, such
40 as the sensory cells of the parapodial cirri in errantia or the sensory cells of the
41 feeding palps in sedentaria have a chemoreception function in response to specific
42 chemicals signals (Lindsay, 2009). In clitellates, the majority of primary sensory
43 cells are located in the body wall. Earthworms perceive diverse environmental
44 chemicals, mainly through chemoreceptor tubercles in the prostomium and
45 anterior segments and through sensory cells in the mouth region. Receptors
46 covering the body respond specifically to salt and pH (Laverack, 1960). Their

1 nervous system is made up of a chain of ganglia that are highly sensitive to any
2 change in the environment, enabling them to identify both food resources and
3 harmful environments (Knapp and Mill, 1971; Kiszler et al., 2012; Syed et al.,
4 2017).

5
6 *In molluscs*

7
8 Chemical system is well developed, as indicated by the large number of
9 neurons which it contains, compared to the rest of the nervous system. It
10 compensates for the poorly developed visual system and is used to detect
11 odoriferous molecules at a great distance, providing the animal with information
12 about habitat selection, food finding, interactions with conspecifics, defense, or
13 mating (Emery, 1992).

14 Gastropods are by far the largest class of molluscs (accounting for around
15 80% of all species) and include between 40,000 and 150,000 species. The sensory
16 perception of terrestrial animals has been relatively well studied. They have two
17 olfactory pathways (Ito et al., 2000). The main pathway involves the perception of
18 olfactory information during long-distance orientation. It is provided by the
19 posterior tentacles. The second pathway, provided by the anterior tentacles, seems
20 to be essentially devoted to contact chemoreception. These two olfactory pathways
21 are structurally very similar, the main differences being their size and the presence
22 of eyes in the posterior tentacles (ommatophores) (Ito et al., 2000). Different
23 studies have shown that structure of the olfactory system of molluscs is very
24 similar to that of arthropods and vertebrates (Chase and Tolloczko 1993; Eisthen,
25 2002). Described in terrestrial animals, it consists of a sensory epithelium, a
26 tentacular ganglion and a tentacular nerve connecting the tentacular ganglion to
27 the procerebral lobe of the central nervous system by the. The procerebral lobe is
28 directly connected to the buccal and pedal ganglia, respectively the center of
29 feeding and locomotion. It should be noted that the olfactory epithelium contains
30 both lipid glands and protein glands. The nature and location of the latter suggest
31 that they are involved in the secretion of binding proteins associated with the
32 transport of odor molecules to the membrane receptors, as in insects and mammals
33 (Chase and Tolloczko 1993).

34 Movement and orientation are closely linked to the perception of olfactory
35 stimuli (Gervais et al., 1993). The orientation of terrestrial gastropods towards an
36 odorous source involves different forms of locomotor response. In trail following,
37 the animal uses its anterior tentacles to follow a mucus trail left by itself, a
38 conspecific or an animal of another species. Anemotaxis is involved in homing
39 behavior, courtship and sometimes foraging. In the presence of an air current,
40 orientation is made possible by a single posterior tentacle sampling the air at
41 different times during movement. However, in a calm environment with no air
42 currents, orientation follows a concentration gradient and requires the use of both
43 posterior tentacles (Chase and Croll, 1981).

44 To guide their navigation behaviour, aquatic gastropods also use chemical
45 cues detected by contact chemoreception or chemoreceptors sampling the water.
46 In this case, odors are transported by advection or diffusion and the aquatic snails

1 and slugs rely on odor-gated rheotaxis and/or chemotaxis to navigate (Wyeth,
2 2019). In addition to tentacles (rhinophores), the primary olfactory organs can be
3 the lips or potentially a single fused oral veil over the mouth. The osphradium,
4 located in the water entrance of the pallial cavity, in front of the gills, is also
5 chemosensory but it is not certain that it is involved in controlling the direction of
6 movement relative to the odorous sources. It would be used to modulate
7 physiology depending on the presence or the concentration of chemical cues in the
8 environment (Wedemeyer and Schild, 1995; Kamardin et al., 1999; Simone, 2021;
9 Wyeth, 2019).

10 11 *In arthropods*

12
13 Cuticular outgrowths, called sensillae, are sensory organs mediating tactile,
14 gustatory or olfactory modalities. They are consisting of bipolar sensory cells,
15 enveloping cells and a cuticular structure. In decapod crustaceans, aesthetascs are
16 the specialized chemosensory sensilla containing chemosensory neurons, other
17 sensillum types containing mechano- and/or chemosensory neurons., Aesthetascs
18 occur on the lateral flagellum of the first antennae (Steullet et al., 2002; Schmidt,
19 2007). Each aesthetasc includes a large number of primary olfactory receptor
20 neurons (40-500 neurons), that allows aesthetacs to provide the many information-
21 coding channels, needed to adapt to a complex odor environment. The afferent
22 projections of the olfactory receptor neurons transit in the antennular nerve before
23 reaching the olfactory lobe in the brain (Gleeson et al., 1996).

24 Olfaction is a remarkably sensitive and selective sense for most insects, which
25 used it in a wide range of intraspecific and interspecific communication modes.
26 Pheromonal signals guide many insects to conspecific mating partners and social
27 behaviors. For example, in mulberry bombyx (*Bombyx mori*), bombykol is emitted
28 by the females to specifically attract males. In honey bees, pheromones organize
29 the defense of the hive, recruit foragers and reinforce the primacy of the queen
30 (Paoli and Galizia, 2021). Ants used a diversity of volatile substances in different
31 behaviors, such as navigation, alarm or courtship (Jackson and Châline, 2007;
32 Hölldobler and Wilson, 2009). Pheromones are also necessary for interspecific
33 communication. Odors emitted by host plants attract phytophagous insects, and
34 those emitted by animal hosts attract hematophagous or parasitoid insects. Often,
35 these odors are made up of a mixture of compounds in very specific proportions.
36 specific proportions (Martin et al., 2011).

37 Despite the great diversity of insect behaviors associated with their olfactory
38 environments, the olfactory system is relatively simple. Olfactory sensilla are
39 mainly located on the antennae, but also sometimes in other parts of the body, such
40 as the maxillary palps in flies (Hansson and Stensmyr, 2011). The number of
41 sensilla for pheromone detection is about thousands to tens of thousands among
42 the species (more than 60,000 in *Manduca sexta*) and they show a variety of
43 shapes, but a common structure (architecture). Each sensilla responds specifically
44 to a chemical molecule or a family of chemical molecules, which explains the
45 great morphological diversity. Based on their chemosensory specificity
46 (pheromones *versus* general odorants), various types of olfactory sensilla are

1 described. Sensilla house olfactory sensory neurons (OSN), generally between 2
2 and 5, although in exceptional cases, the OSN number can be very high, as in the
3 ant *Camponotus japonicus*, where 130 neurons have been recorded (Keil, 1999;
4 Nakanishi et al., 2010).

5 Odorant molecules penetrate through the cuticular pores of the sensilla hair,
6 are dissolved in the aqueous sensilla lymph by Olfactory Binding Proteins (OBPs)
7 and transported to specific receptors expressed in the dendritic membrane of the
8 OSNs (Plettner et al., 2000; Hansson and Stensmyr, 2011). The OBPs are then
9 rapidly degraded, contributing to the dynamics of the responses. Binding of
10 odorant substance to the receptor initiates ionotropic or metabotropic mechanisms,
11 allowing chemical signal transduction into an electric response in the OSN. The
12 sequence of action potentials is then transmitted to primary olfactory brain, the
13 antennal lobe, subdivided into glomeruli. Each glomerulus received the afference
14 of the OSNs with the same receptor type. The output of glomeruli is carried to
15 higher brain centers, in particular the mushroom bodies and the lateral
16 protocerebrum, where odor perception and learning take place (Szyszka and
17 Galizia, 2015).

18 Even if the literature on chelicerate chemical communication is not as
19 extensive as for insects, it is known that the chemical sense of arachnids is well-
20 developed and that many of their behaviors depend on chemical signals
21 (chemotactile or/and olfactory pheromones) (Barth, 2001; Uetz and Roberts,
22 2002). For example, jumping spiders (family Salticidae) used, despite their good
23 eyesight, olfactory pheromones to species and sex identification (Cerveira and
24 Jackson, 2013). Whip spiders return to their home refuge despite structurally
25 complex tropical environment using the sensory input from the antenniform legs
26 (modified anterior walking legs) (Bingman et al., 2017). In fact, spiders may use
27 chemical signals to avoid predator or locate prey, to recognize congener or sexual
28 partner (Uetz and Roberts, 2002). Most of the sensory organs of arachnids are
29 located on their extremities, due to the absence of antennae. The pedipalps and the
30 anterior legs particularly carry chemoreceptors (Foelix, 1985).

31 Studies on the olfactory system in the Myriapod *Scutigera coleoptrata* have
32 shown that its primary olfactory center is well developed, allowing good odor
33 recognition and discrimination (Sombke et al., 2009). It is interesting to note that
34 the shape of the olfactory neuropils (olfactory glomeruli) is distinct from that in
35 Hexapods and malacostracan Crustacea, suggesting an independent evolution of
36 the olfactory sense in these two phylogenetically separate clades of arthropods
37 (Sombke et al., 2011).

38 39 *In echinoderms*

40
41 Echinoderms are slow-moving animals, who rely on waterborne chemical
42 signals to adapt their behavioral responses. Sea urchins can precisely orient
43 themselves towards chemicals emanating from potential food source or from
44 conspecifics, and away from those emanating from nearby predators or crushed
45 conspecifics. They use chemicals to enable external fertilization (Lawrence, 2013).
46 Different studies have shown that the activation of the spines, the tube feet and the

1 pedicellariae, equipped with a high number of chemoreceptors, permit a
2 sophisticated chemosensory response (Campbell, 1983; Solari et al., 2021). The
3 sea stars can also respond to chemicals and their orientation path is guided by the
4 stimulus field. They possess sensory tentacles on the tips of each arm, enabling
5 them to detect ambient odors and odor plumes (Moore and Lepper, 1997; Garm,
6 2017; Motti et al., 2018).

7 8 *In protochordates (Cephalochordate and Tunicate)*

9
10 Sensitivity to external chemical substances has been demonstrated in the non-
11 vertebrate chordates, but it does not always seem to play a role in their behavioral
12 repertoire. In the cephalochordate Amphioxus (*Branchiostoma lanceolatum*),
13 epithelial cells located at the front end of the body enable it to react to various
14 chemical substances (Lacalli, 2004). These scattered olfactory cells are
15 homologous to the olfactory epithelium found in vertebrates. In fact, it has been
16 shown that amphioxus has orthologs of vertebrate olfactory receptors, which
17 demonstrates that the vertebrate receptors evolved at least 550 million years ago
18 (Satoh, 2005; Churcher and Tylor, 2009).

19 It has not been clearly established that Tunicates are chemosensitive.
20 However, cells that can act as olfactory sensors, are located in the region around
21 the lips in the class Thaliacea (doliolida and salpa), and in the ventral organ, under
22 the lower lip in the class Appendicularia (*Oikopleura*) (Mackie and Burighel,
23 2005).

24 25 26 **The Chemosensation in Vertebrates**

27
28 The main olfactory system of vertebrates shares many characteristics with that
29 of nematodes, molluscs, or arthropods. In general, the olfactory receptor cells
30 detecting the odoriferous molecules are bipolar neurons with a dendrite that
31 protrudes into the fluid medium. The dendrite is covered with cilia and/or
32 microvilli, where are localized the membrane-bound odorant receptors, whose
33 genes are members of a large superfamily. At the opposite pole of the neuron, the
34 axon projects directly into glomeruli of the main olfactory bulb. A third layer of
35 neurons forms the superior olfactory center, involved in multimodal sensory
36 integration (Holley et al., 2013; Eisthen, 2002).

37 However, although vertebrates and invertebrates share commonalities in their
38 strategies to recognize and discriminate odors, differences exist in the olfactory
39 signaling mechanism (odorant receptors and olfactory transduction). In particular,
40 vertebrate olfactory receptors (main olfactory epithelium) are metabotropic
41 receptors, generally belonging to the G protein-coupled receptor family, whereas
42 insect receptors are ionotropic receptors, which of course has major implications
43 for the temporal coding of odors and feedback mechanisms. Moreover, the
44 vertebrate olfactory receptor repertoire is considerably largest (for most of them,
45 300-1300 olfactory receptor genes) than that of insects (50-160 olfactory receptor
46 genes). A large fraction of the receptor genes in the vertebrate genome are

1 pseudogenes (12% in zebrafish – 52% in humans); the fraction of pseudogenes is
2 low, or non-existent in insects (Nei et al., 2008; Kaupp, 2010).

3 Observation of the olfactory epithelium of various vertebrates has enabled it
4 to be classified into two types: a fish-type olfactory epithelium, observed in flatfish
5 and lungfish, and a mammal-type olfactory epithelium, observed in amphibians,
6 reptiles, birds and mammals (Taniguchi and Taniguchi, 2014).

7 In addition to the main olfactory system, an accessory olfactory system, the
8 vomeronasal system, is present in most amphibia, reptiles and terrestrial mammals,
9 although absent in birds, many bats and catarrhine Old-World monkeys (Brennan,
10 2001). It consists of the peripheral vomeronasal organ, the accessory olfactory
11 bulb and its projections to distinct cerebral zones. Depending on the species, the
12 vomeronasal organ communicates with the nasal or the oral cavity to uptake
13 odoriferous molecules, which may be pheromones or non-pheromonal social
14 chemical signals (Halpen, 1987; Silva and Antunes, 2017). It should be noted that
15 the histological structure of the vomeronasal sensory epithelium is different in
16 snakes, and bears no resemblance to the other vertebrate species (Taniguchi and
17 Taniguchi, 2014).

18 In the primitive vertebrates, the olfactory organ is unique and opens outwards
19 through a single nostril. Then in the course of evolution, the olfactory cavity is
20 formed and communication is established between the olfactory organ and the oral
21 cavity. With the appearance of the Amphibians, the first land animals, the
22 respiratory function was added to the sensory role. Thus, in Tetrapods, the
23 olfactory organ is associated with the respiratory organ, whereas in fish, it is
24 independent of it (Salesse and Gervais, 2013).

25 26 *In agnatha (cyclostomata)*

27
28 The jawless vertebrates have a well-developed olfaction. The olfactory system
29 of the sea lamprey is particularly efficient in the orientation toward prey fish
30 during the parasitic stage and in the migration behavior for spawning (Kleerekoper
31 and Mogensen, 1963; Li et al., 1995). It has been shown that migratory mature
32 adults use odors from conspecific larvae to select the best streams for spawning.
33 The larvae produce and release unique bile acids into the water, that function as
34 migratory pheromones that adults specifically recognize at very low detection
35 thresholds (10^{-12} - 10^{-13} M) (Li et al., 1995). Hagfish exhibit positive chemotactic
36 behavior in response to specific decay-related chemo-attractants (Glover et al.,
37 2019).

38 The olfactory organ consists on an unpaired structure, composed of the nasal
39 duct, the nasal sac and the nasopharyngeal pouch. The nasal tube opens externally
40 as a single nostril localized on the dorsal head surface in the lamprey and above
41 the mouth in the hagfish. A valve of the nasal tube of the adult lamprey's olfactory
42 organ is used to introduce and expel water in the nasal sac recovered with lamellar
43 folds, each fold being lined with the olfactory epithelium. The particularity of the
44 hagfish, compared to the lamprey, is that the nasal sac receives a continuous flow
45 of water from the nostril to the gill openings, the nasopharyngeal duct being open
46 to the pharynx. Moreover, it should be noted that hagfishes have specialized

1 chemosensory structures named the Schreiner organs, in addition to the olfactory
2 system. They are distributed all over the body epidermis (Poncelet and Shimeld,
3 2020).

4 In *Petromyzon marinus*, from the olfactory sac run two olfactory nerves to the
5 ipsilateral olfactory bulb (Kleerekoper and Erkel, 1960). The nasopharyngeal
6 pouch, close to a gill opening, is subject to the rhythmic contractions of the gill
7 chamber due to its soft walls. It allows water to be sucked in or expelled
8 synchronously with gill respiration, enabling water to circulate through the
9 olfactory organ. The olfactory organ is therefore independent of respiration, and
10 evolutionarily we have the first fully individualized olfactory organ (Dawson,
11 1905; Romer and Parsons, 1986; Janny, 2011).

12 13 *In fish*

14
15 Olfactory is involved in the regulation of most of behavioral patterns, as
16 feeding, spawning, parental defensive, migration, kin recognition and territorial
17 behaviors (Kasumyan, 2004; Maximino et al., 2019; Keller-Costa et al., 2015).
18 Fishes have high sensitivity to a wide spectrum of chemical stimuli, they can
19 detect very low threshold concentrations of chemical substances and can
20 differentiate the smell of conspecific individuals from that of other population or
21 species. The olfactory system is characterized by slow adaptation to the olfactory
22 substance, enabling fish to identify an odor source from a great distance (many
23 dozens or even hundreds of meters) (Hara, 1992; Kasumyan, 2004).

24 The olfactory organ consists on a paired structure. The anterior nostril brings
25 water into the nasal cavity, and the water flows out of the posterior nostril.
26 Respiratory movements of the gills activate the circulation of water in the
27 olfactory sac. Olfactory lamellae, covered by the olfactory epithelium, are located
28 at the bottom of the nasal cavity. Some fish have accessory olfactory cavities,
29 primarily used for the ventilation of the nasal cavity, but also to produce olfactory
30 mucus. The olfactory cavity is not linked with the pharynx in most fish, but is
31 linked in Dipnoi or Anguilliformes. Generally, the olfactory organ shows an
32 important diversity, reflecting the ecological habitats (Hara, 1994; Kasumyan,
33 2004).

34 35 *In amphibians*

36
37 Amphibians are the first land living emerging vertebrates, and most species
38 combine an aquatic larval stage with a more or less water-independent adult stage.
39 This habitat change requires important adaptations also of the sensory systems.
40 During metamorphosis, anatomical and physiological transformations, cellular and
41 molecular modifications of the olfactory system, make the transition from aquatic
42 olfaction in tadpoles to semi-aquatic or airborne olfaction in adults (Wells, 2007;
43 Reiss and Eisthen, 2008).

44 In most anuran amphibian tadpoles, the waterborne odor detection is
45 performed by a dual olfactory periphery, consisting of the main sensory epithelium
46 in the principal cavity (PC) and the vomeronasal organ (VNO). During

1 metamorphosis, a three communicating cavities system appears, consisting of the
2 PC, a newly formed middle cavity (MC) lined with a non-sensory epithelium in
3 most species and the VNO. In adults, the aerial olfaction is provided by the
4 sensory epithelium of the PC. The VNO is connected to the PC by a lateral nasal
5 groove (Reiss and Eisthen, 2008; Jungblut et al., 2020).

6 Unlike the most anuran amphibians, the African clawed frog *Xenopus laevis*
7 is almost completely aquatic: excursions overland occur occasionally (Measey,
8 2016). Adult *Xenopus* possess the three typical nasal cavities, as in other terrestrial
9 frogs, but the MC contains a well-developed sensory epithelium. Different studies
10 have shown that the PC is used for the detection of airborne odors and the MC for
11 the detection of aquatic odors: a flap valve directs air or water to one or the other
12 cavity according to the external medium (Altner, 1962; Hansen et al., 1998). The
13 olfactory epithelia of both PC and MC show significant differences in histological
14 and molecular levels. Ultrastructurally, the epithelium of the PC contains ciliated
15 sensory neurons, while those of the MC contain both ciliated and microvilli
16 sensory cells, as in the epithelium in larval PC. At the molecular level, each cavity
17 differentially expresses several markers. The adult MC is similar so that of the
18 larval PC and express class I olfactory receptors (found in aquatic vertebrates).
19 The class II odorant receptors, expressed in the PC, are the receptors found in
20 airborne mammals (Mezler et al., 2001; Jungblut et al., 2021). There is evidence
21 that important remodeling occurs during metamorphosis to reorganize the
22 olfactory epithelium in the PC. Massive cell death, replacement of the olfactory
23 neurons and changes in olfactory expression patterns of olfactory receptors are
24 involved (Gascuel and Amano, 2013; Dittrich et al., 2016).

25 In the gymnophiona, all burrowing animals, the olfactory and vomeronasal
26 systems are nearly completely separated; a small connection between the olfactory
27 cavity and the VNO. Chemoreception in the VNO is facilitated by the tentacle. In
28 fact, the VNO is associated with the tentacle, because the tentacular ducts open
29 into it. This association makes olfaction possible, even when the main nasal cavity
30 is closed during burrowing or swimming (Schmidt and Wake, 1990; Exbrayat,
31 2000). This system is probably an adaptation to a burrowing life and allows these
32 animals to capture molecules from the environment while keeping their nostrils
33 and mouth closed.

34 35 *In reptiles*

36
37 The position and presence of the vomeronasal organ is extremely variable in
38 reptiles. In crocodylians, the VNO exists during early embryonic development and
39 then regresses to be absent in adults (Weldon et al., 1990; Weldon et Ferguson,
40 1993). In turtles, it is not individualized (Parsons, 1970). In squamate reptiles
41 (lizards and snakes), the vomeronasal chemosensory system is an important
42 sensory mode, involved in many behaviors, such as foraging, feeding or
43 reproduction (Graves, 1993). In these animals, the VNO is anatomically and
44 functionally distinct of the main olfactory system; the airborne odorant
45 information is collected by the tongue and transmitted to the tiny vomeronasal
46 openings on the palate (Schwenk, 1995).

1 There is no functional vomeronasal system in crocodylians, but the olfaction is
2 well developed and crocodylians can locate prey at great distances (Weldon et al.,
3 1990; Weldon et Ferguson, 1993). These semi-aquatic animals are able to breathe
4 through the nostrils, which emerge from the water, while the mouth can remain
5 open underwater. The nasal structure is thus particularly complex, with anatomical
6 dissociation of the respiratory and olfactory noses (Janny, 2011). Each nostril acts
7 as a valve, which is closed with a muscular flap during submersion. This prevents
8 the olfactory cavity from being flooded and protects the airways. Olfaction is not
9 employed under water. Another respiratory valve, the buccopharyngeal valve, is
10 formed by the support of the elongated soft palate on the gular fold, which
11 protrudes from the back of the mouth. The inspired air is channeled through the
12 nasopharyngeal duct. With this flap, the animal can open its mouth underwater
13 without water rushing into the internal nares and the trachea (Weldon and
14 Ferguson, 1993; Fleming, 2014). Crocodylians can increase their olfactory capacity
15 by gular pumping, which consists of movements of the pharyngeal floor with the
16 glottis and buccopharyngeal valve closed (Pooley and Gans, 1976). This
17 mechanism has similarities with the buccal pump phenomenon in amphibians, but
18 the movements are pharyngeal rather than buccal, and the musculature of the
19 nostril is involved during these olfactory cycles (Janny, 2011).

20

21 *In birds*

22

23 Birds do not exhibit specific behaviors indicative of dependence on olfactory
24 cues, and it has long been thought that they don't smell very well. However, many
25 recent studies have demonstrated that birds are equipped with a functional
26 olfactory system (paired nasal olfaction chambers, olfactory epithelium, olfactory
27 nerves, and olfactory bulbs) that allow them to detect odors in a variety of
28 ethological contexts (Roper, 1999; Caro and Balthazart, 2010; Corfield et al.,
29 2015). For orientation, homing pigeons and other birds can smell atmospheric
30 gases in trace amounts to find their way back home after moving passively over
31 hundreds of kilometers of unknown terrain (Papi, 1989; Wallraff, 2005). For
32 foraging, it can be noted that various species of procellariiform seabirds (petrels,
33 albatrosses and shearwaters) are attracted by indirect cues such as dimethylsulfide
34 (DMS) associated with their prey. The DMS is effectively emitted by
35 phytoplankton when ingested by zooplankton, and it indirectly indicates to birds
36 the presence of fish feeding on zooplankton (Bonadonna et al., 2006). In fact, a
37 large number of bird species can use olfaction to foraging, as the great tit *Parus*
38 *major*, which can differentiate a caterpillar-infected tree from and uninfected one
39 on the basis of volatile emissions (Amo et al., 2013). For communication,
40 olfaction is used in a variety of social contexts. The uropygial gland of birds
41 produces an odoriferous secretion, that birds spread over their feathers. This preen
42 oil is used in intraspecific contexts, such as species discrimination, sexual mate
43 distinguishing or kin recognition (for review, Grieves et al., 2022). In the context
44 of reproduction, olfaction is involved in the choice and synchronization of
45 partners, the selection of nesting materials and the care of eggs and offspring (Caro
46 et al., 2015). In addition, it has been shown that olfaction of birds is well

1 developed *in ovo*: chicken embryos can perceive olfactory stimuli through the
2 shell pores and memorize this chemosensory information. So, the mother's diet can
3 generate specific odorant properties in the egg yolk and guide the feeding behavior
4 of the young chicken after hatching (Bertin et al., 2010; Bertin et al., 2012;
5 Aigueperse et al., 2013).

6
7 *In mammals*

8
9 The mammalian olfactory system is an evolved sensory system, enabling
10 most species to detect a very large number of chemical molecules necessary for
11 survival and reproductive success (Wilson and Stevenson, 2006). However,
12 significant differences in olfactory abilities characterize species. For example,
13 Cetaceans and Pinnipeds, which are aquatic mammals, have reduced olfactory
14 faculties and their olfactory organs have regressed (Pihlström, 2008). In contrast,
15 Ungulates, Carnivora or Rodents are microsmatic animals, with an extremely
16 acute sense of smell (Wackermannová et al., 2016).

17 Most mammalian species possess the two parallel circuits, the vomeronasal
18 system and the main olfactory system, to process olfactory information. In some
19 species, there are two additional olfactory subsystems, the septal olfactory organ,
20 described in several placental and marsupial species, and the Grueneberg ganglion,
21 particularly well developed in mice (Taniguchi et al., 1993; Storan and Key,
22 2006).

23 The vomeronasal system is specialized to the pheromone detection, which
24 provide information about the social or sexual status of other individuals in the
25 species. However, recent data suggest that the vomeronasal system also responds
26 to certain non-pheromonal chemical signals, at least in rodents. Furthermore,
27 evidence shows that the main olfactory system also detects a range of volatile
28 odorants that function as pheromones to facilitate reproduction (Brennan and
29 Keverne, 2004; Baum and Cherry, 2015). In humans, the VNO has regressed and
30 is no longer a sensory organ, as evidenced by the absence of neurons and nerve
31 bundles (Trottier et al., 2000).

32 The main olfactory system detects a wide variety of environmental odorant
33 molecules. It seems to play a key role in food detection, in social recognition, in
34 maternal behavior and in offspring recognition at birth (Popik et al., 1991; Keller
35 and Lévy, 2012). For example, infants rapidly recognize their nursing mother by
36 her odor signature, or distinguish between a pleasant smell (such as vanillin) and
37 an unpleasant one (such as butyric acid) (Romantshik et al., 2007). The high
38 olfactory capacity of most mammals is clearly linked to the significant
39 development and the complexification of the nasal cavities. The surface area of the
40 olfactory mucosa is particularly increased in mammals by the presence of
41 ethmoturbinals arising from the ethmoidal bone. Interspecies variations in the
42 number and shape of ethmoturbinals could easily be linked to differences in the
43 animal's sense of smell (Smith et al., 2015). In anthropoid primates, as the brain
44 increases in size and the eyes are brought closer together for a better vision, the
45 nasal cavity is both reduced and modified. The number and size of the
46 ethmoturbinals are reduced, resulting in a smaller olfactory surface. In fact, it is

1 likely that the arboreal life characteristic of primates has distanced individuals
2 from the many chemical stimuli present on the ground (food, various olfactory
3 trails) and has therefore made the olfactory system less necessary for survival. So,
4 the olfactive surface area in humans is estimated at between 2.5 and 4 cm² (by
5 comparison in dogs, it is 150 cm²) and represent only 1,25% of the total nasal
6 mucosa (Stoddart, 1980).

7 The human olfactory epithelium accommodates approximatively 6 million of
8 sensory neurons, each of them expressing a single type of receptor. Around 340
9 human genes encoding potentially functional receptors have been identified. This
10 number is much lower than in rodents (around 1000 genes) or dogs (870 genes),
11 which are animals with a highly developed olfactory sense. Nevertheless, the
12 number of human receptors is sufficient to recognize over 10,000 different
13 odorants. Recent studies even put the number at 1000 billion (Bushdid et al.,
14 2014). The odorous molecules are perceived using a combinatorial coding, in
15 which one olfactory receptor is able to recognize several odorants, while different
16 odorants are recognized by different combinations of olfactory receptors. In
17 addition, an odorant can act both as an activator of certain olfactory receptors and
18 as an inhibitor of others, making olfactory coding even more complex. So different
19 odorants, or different concentrations of the same odorant, active unique sets of
20 olfactory receptors and generate a specific response (Kurian et al., 2021).

21 The sensitivity and quality of human olfactory perception varies greatly from
22 one individual to another. This variability is linked to significant genetic
23 polymorphism in ORs (mutations, single nucleotide polymorphisms, copy number
24 variations, pseudogens), associated with a gene segregation in different human
25 ethnic groups. The fact that each individual has a specific repertoire of functional
26 genes and that certain genes are more frequently invalidated in one population than
27 in another suggests that different selection pressures have shaped chemosensory
28 repertoires in distinct populations (Menashe et al., 2003; Hasin-Brumshtein et al.,
29 2009; Ferdenzi et al., 2016).

30 Scents are powerful stimuli that can evoke emotional states and promote
31 learning and memory. The singularity of the anatomy of the olfactory pathway
32 explains the strong connection between odor and emotional memory. Indeed, the
33 olfactory information does not pass through the thalamus to the cortex, but is
34 relayed directly to the limbic system, which is the region of the brain typically
35 associated with emotional process and memory (Soundry et al., 2011). This gives
36 olfaction a powerful and unique ability to influence mood, cognitive mobilities,
37 and the learning of new elements related to the environmental context. The odors
38 can modulate complex behaviors and lead the animals to adjust their survival
39 decisions (Sullivan et al., 2015). These adjustments involve brain plasticity
40 phenomena, modifying the number or efficiency of neuronal synapses and creating
41 new neurons (Ming and Song, 2005). In humans, odors are also essential for
42 learning about situations, and they constitute efficient cues for recalling episodic
43 emotional memories (Livermore and Laing, 1996; Wilson and Stevenson, 2003).
44 Existence of connection between odor, emotion and memory explains why odors
45 are increasingly used for therapeutic purposes, for example to bring back

1 memories and emotions, or to free up the speech of patients who have suffered
2 memory or speech trauma.

3 4 5 **Conclusions**

6
7 All living organisms have senses that enable them to interact with their
8 environment, with other organisms of the same or different species, or with
9 physical objects. These senses have diversified over the course of biological
10 evolution, becoming important adaptation factors directly linked to the lifestyle of
11 each organism.

12 Olfaction is one of the most important senses in the animal kingdom. It
13 appears very early in biological evolution and the broad role for odors appears
14 highly preserved across species. Olfaction is heavily involved in survival
15 behaviors, such as foraging, danger detection or communication between
16 individuals of the same or different species. Olfaction based on the reception of
17 chemical molecules is reminiscent of certain aspects of communication in bacteria,
18 protists or archaea (Miller and Bassler, 2001; Lami and Teysedre, 2019). In these
19 unicellular organisms, there is a key mechanism for cooperative behaviour, the
20 quorum sensing, which is based on the emission and detection by the cells of small
21 signal molecules. The concentration of these chemicals in the external
22 environment increases with that of the unicellular organisms, and above a certain
23 concentration threshold in the external environment, the cells switch to a different,
24 cooperative mode of functioning.

25 In addition to the functions mentioned above, the sense of smell can be a
26 source of pleasure and well-being for humans. Among odorous molecules,
27 perfumes have multiplied since their origin at the discretion of perfumers, who
28 offer constantly renewed, complex scents with proven emotional effects. Some
29 molecules, such as essential oils, can have therapeutic effects. The hedonic value
30 that humans attach to certain scents and the pleasurable or spiritual activities with
31 which they are associated contribute to their well-being. Indeed, the loss of the
32 sense of smell affects a number of physiological parameters, including emotions,
33 reminding us of the importance of another sense, hearing, and the effects of sounds
34 and music (Brun and Exbrayat, 2022). The study of the senses, at the interface of
35 science and art, also shows the immense possibilities and plasticity of living
36 beings.

37 38 39 **References**

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