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# Evolution and control mechanisms of air respiration organs in invertebrates

## Evolución y mecanismos de control de los órganos de respiración aérea en invertebrados

Sergio Pablo Urquiza[1*]

### Abstract

The conquest of the terrestrial environment required numerous adaptations, although aerial respiration was what allowed animals to become completely independent of aquatic environments. Here, we analyze the specialized organs for air respiration, describing lungs, tracheas and some modifications of these organs that have occurred in certain gastropods and arthropods. These organs have appeared independently on numerous occasions, even in closely related taxa, and have experienced frequent regressions. In some cases, as in the palaeal cavity of the snail, the organs evolved from homologous structures, but independently in different lineages, with specific areas of the nervous system always being responsible for their control. Although the neurons that perform these tasks are ancient and may have a common evolutionary history, homologous visceral control structures do not seem to exist in vertebrates, nor among invertebrate phyla. This situation is clearly a consequence of the fact that respiration has evolved independently on numerous occasions, even within the same phylum, so that specific organs may be lost, or equivalent organs may arise independently and secondarily. However, as they arise from common ancestral structures, there could be cases of deep homology.

*Keywords:* morphological evolution, invertebrate histology, deep homology, respiratory system

### Resumen

La conquista del ambiente terrestre requirió de numerosas adaptaciones, aunque la respiración aérea fue la que permitió a los animales hacerlo completamente e independizarse de los ambientes acuáticos. En esta revisión, se analizan los órganos especializados para la respiración aérea, describiendo pulmones, tráqueas y algunas transformaciones de los mismos en ciertos gasterópodos y artrópodos. Estos órganos han aparecido de forma independiente en numerosas ocasiones, incluso en taxones próximos, así como han experimentado frecuentes regresiones. En algunos casos, como ocurre con la cavidad paleal de los caracoles, los órganos evolucionan de estructuras homólogas, pero con independencia en distintos linajes, existiendo siempre áreas específicas del sistema nervioso encargadas de su control. A pesar de que las neuronas que realizan estas tareas, podrían tener una antigua historia evolutiva común, no parecen existir estructuras de control viscerales homólogas con los vertebrados, ni entre los filos de invertebrados. Esta situación claramente es consecuencia de que la respiración ha evolucionado en numerosas ocasiones en forma independiente incluso dentro del mismo filo, por lo que los órganos específicos pueden

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[1] Departamento de Diversidad Biológica y Ecología-Escuela de Biología - Facultad de Ciencias Exactas, Físicas y Naturales-Universidad Nacional de Córdoba, Córdoba, Argentina.

* Corresponding author: sergio.pablo.urquiza@unc.edu.ar

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perderse o surgir otros equivalentes en forma independiente y secundaria. Sin embargo, como surgen de estructuras ancestrales comunes podrían ser casos de homología profunda.

*Palabras clave:* evolución morfológica, histología de invertebrados, homología profunda, sistema respiratorio

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## INTRODUCTION

The conquest of the terrestrial environment seems to be particularly difficult and infrequent, while the opposite, the secondary return to the waters, is much more common (Vermeij & Watson-Zink, 2022). Despite the above, the number of terrestrial eumetazoan species significantly exceeds that of aquatic ones, although the number of taxa at class level or higher that show this type of respiration are comparatively few with respect to strictly aquatic taxa (Watson-Zink, 2021).

Moreover, except for some crabs and amphipods that colonized terrestrial environments in the Cenozoic (a little more than half a hundred million years ago), most of the animals that initiated such a transition did so quite early in their evolution, between the Cambrian and the Carboniferous, a little more than three hundred million years ago. The groups that did so are the same as those found today (Watson-Zink, 2021), having happened independently as many as a dozen times in the case of crustaceans (Krieger et al., 2021), and in gastropods on about 30 occasions (Vermeij & Watson-Zink, 2022).

In such an event, the accompanying microbiome of the animals would have played a decisive role, for example, as in crabs (Cannicci et al., 2020), which seems logical at least in the context of the holobiont hypothesis, especially thinking of invertebrates, in which various microorganisms could live intracellularly and potentially exchange genetic material with the host (Zilber-Rosenberg & Rosenberg 2021).

The conquest of land encompasses numerous adaptations, some very complex (van Straalen, 2021), although not always, as is the case in flatworms and annelids. Of all phyla, perhaps flatworms were the earliest to adapt to terrestrial environments (Sluys, 2019), probably through a single event. On the other hand, earthworms of the Crassiclitellata group also appear to have colonized terrestrial environments a single time from a freshwater ancestor, albeit quite late and much later than arthropods (van Straalen, 2021).

Although the number of higher-level taxa that respire in the aerial environment is small, the structures involved in this task present some very striking, yet somewhat different, adaptations. In the present article, we describe and compare the organs of the respiratory system in invertebrate phyla that have adapted to live in terrestrial ecosystems, with the exception of flatworms and annelids, since they generally do not exhibit particular respiratory adaptations for aerial life. This review deals with the structure of these systems, as well as those in charge of their control, which are part of the collectively termed visceral nervous systems. More or less recent reviews and books on these topics, with a fairly broad focus are: Harrison (2015); Perry et al. (2019) and Vermeij and Watson-Zink (2022) and the various articles and books by Maina (especially in Maina (2011) who provides a very interesting treatment of these problems). In order to write the present review, these works were consulted in the first instance, as well as others of a general nature, which were used to write a first text on which a more detailed study was made for each specific taxon/organ. For this second instance, various articles were selected that dealt in detail with a particular respiratory structure or a particular taxon. In some cases, the bibliography was abundant and it was possible to choose the most detailed and/or modern ones, while in other cases the bibliography was scarce and the subject could only be approached in a more limited way. In some cases, such as the "tracheal lungs" of certain gastropods, they were included because they seem to represent a structural variation far removed from that found in the majority of the members of the group. In total, about 200 papers were consulted, although 131 were considered for the writing of this review, according to the criteria mentioned above. As for the taxonomy of the animals studied, in each case, the taxonomic schemes followed in the article cited in particular are respected. However, from a more global point of view and for panarthropods we follow Giribet and Edgecombe (2020) and for mollusks Ponder et al. (2019).

The respiratory system acts, together with other organ systems, in the processing of food and nutrients, and together they are called nutritional systems. In vertebrates there are four, the digestive, respiratory, circulatory and excretory systems. However, respiratory functions are performed on numerous occasions by the integumentary system, which surely originated in the first instance in the first animal (Urquiza & Carezzano, 2018). But, although such a structure may be crucial in respiration, as it is not strictly adapted for gas exchange it cannot be considered as a specialized respiratory organ.

All animals breathe and, apparently, all can also perceive variation in oxygen levels (Gorr et al., 2006; Harrison, 2015). Thus, under suboptimal oxygen concentrations, the "hypoxic response" occurs, which in mammals includes increased ventilation, reduction or cessation of energetically demanding activities and, in the long term, an increase in certain ontogenetic processes that increase respiratory capacity (Harrison, 2015). In addition, some taxa can tolerate variable temporary periods of hypoxia, such as carp (*Cyprinus carpio*), which can spend entire seasons using alcoholic fermentation. Likewise, and although most invertebrate parasitic stages can tolerate varying levels of hypoxia, there do not seem to be notable genetic differences between aerobic and anaerobic lineages, as occurs, to some extent, in fungi or plants (Müller et al., 2012). When vertebrates lack sufficient oxygen, they produce lactate as the first product of anaerobic metabolism. Among non-vertebrates, however, other substances such as acetate, propionate or succinate are also released (Müller et al., 2012), in addition to lactate itself, as is the case with crustaceans. Also, among chelicerates this molecule is the main anaerobic by-product, being very likely that the basal state among arthropods is the utilization of lactate. In hexapods, although anaerobic metabolism is not very common, there are some secondary variations that utilize alanine and even ethanol (Harrison, 2015).

Tolerance to low oxygen tension is unequal among eumetazoans. Air (and oxygen) reach the interior of the body by different mechanisms, and the acquisition of oxygen from the outside, as well as the expulsion of carbon dioxide, is effected by ventilation, by which the animal artificially modifies the flow of water or air and brings the respiratory surfaces into contact with the environment. Depending on size, activity, phylogenetic position and environment, this exchange may take place in a very simple way through the integument (tegumentary respiration as in earthworms) or may require the help of specialized organs such as gills or lungs. Concomitantly, as animals became more voluminous and/or active, the circulatory system emerged to distribute gases, which may also possess respiratory pigments. Only diploblastic animals failed to develop specific organs (Schmidt-Rhaesa 2007). In addition, the transition to terrestrial environments, the third major evolutionary event after the emergence of life and multicellularity, was particularly challenging because the animal had to face osmotic stress and dehydration, since water molecules are smaller than those of gases. This is why respiratory membranes have been internalized during this evolutionary event (Selden, 2001), which occurred at different times in different taxa (Broly et al., 2013). However, the aeroterrestrial environment has the advantage of possessing a much higher oxygen concentration, so that the organism can decrease the ventilatory rate, although the blood carbon dioxide pressure increases. The latter is remedied by increasing the levels of strong ions capable of associating with bicarbonate. Therefore, animals that remained in water only have to control oxygen pressure, while those that adapted to terrestrial ecosystems must regulate, in addition to this variable, the amount of carbon dioxide and pH (Lee and Matthews, 2021).

Respiration can be effected mainly by four forms, which in turn depend on specific organs: tegumentary, gill, pulmonary and tracheal respiration. Although many respiratory organs present in different taxa have the same name, it should not be automatically assumed that they are homologous. However, there are situations where cases of deep homology may occur, such as when two structures are produced under the action of the same genetic program, even though morphologically these structures are very different and belong to phylogenetically distant organisms (Shubin et al., 2009). An example is what occurs in the formation of the appendages of arthropods and vertebrates, which develop under the direction of a very similar developmental program, although these limbs are clearly not homologous, being even very different (Panganiban et al., 1997).

Thus, tegumentary respiration occurs when respiration takes place directly through the body surface. If the integument has undergone evaginations in order to increase the exchange, we speak of gills, which always depend on the presence of water. If expansions occur as saccular invaginations, we speak of lungs, which are immersed in the body and are almost always associated with respiratory pigments. Tracheae, on the other hand, are tubular integumentary invaginations that carry air to the interior of the animal.

In most cases, the animal must be able to adapt the respiratory rate, or the amount of air or water exchanged or the frequency at which it does so, all actions that can be regulated and controlled by the visceral nervous system (VNS). This is a subdivision of the nervous system (NS) responsible for modifying, above all, respiration, digestion and circulation, which it does essentially by acting on the level of activity of the muscle and epithelium. In the first case it generally produces peristalsis, as in the intestine, while in the second it modifies the level of secretion of the glandular tissue (Selverston, 2007). In vertebrates, this control falls on the autonomic nervous system, which does not seem to have an exact morphological, physiological and histological correlate in non-vertebrates. However, certain regions with such functions can be observed, such as the aforementioned visceral nervous system (Jänig, 2013).

## THE RESPIRATORY SYSTEM OF MOLLUSKS

In this phylum respiration is primarily gill-breathing, with notable caveats, such as those seen in gastropods which are the only terrestrial ones, and that recorded in an air-breathing bivalve, perhaps even obligately (Perry et al., 2019). Gastropods may have gills, with gills and lungs (even if they are aquatic species), or only lungs but which may be present in both aquatic and terrestrial species (Mill, 1997). There are also aquatic species, such as limpets, tolerant to anaerobiosis (Heller, 2015). The basal stage corresponds to gill respiration, carried out by means of the ctenidium (primary gill), of which between one to eighty can be seen (Brusca et al.,2016). Beyond the possession of lungs in terrestrial and aquatic species, such organs seem to have already evolved in the aquatic environment (van Straaler 2021), although there are several lineages that have returned secondarily to the water.

### Distribution of respiration and systematics in gastropods

These mollusks include aquatic and terrestrial slugs and snails. Their systematics has been very unstable so the reader should be aware of this problem. Currently, and according to the classification adopted by Ponder et al., (2019), there are five infraclasses of gastropods: patellogastropods, vetigasteropods, cenogastropods, neritomorphs and heterobranchs. Only the last three have species with aerial respiration. According to a recent paper (Vermeij & Watson-Zink, 2022), these animals have independently colonized terrestrial environments on about 30 occasions, of which 14 correspond to marine groups and 12 to freshwater lineages. In turn, the most biodiverse groups (with more than 100 species) did so in tropical areas, before or during the Cretaceous and from fresh waters, being the terrestrial lineages derived from marine gastropods less diverse and emerged from the Cenozoic.

Of all infraclasses, cenogastropods, with about 157 families, are the most hyperdiverse, encompassing up to 60% of all species. Of those, only a few have undergone the process of limacization (conversion into slugs) or invaded the land (Ponder et al., 2019). The latter would have occurred in several independent events. These are animals that generally bear an operculum, are dioecious and are particularly abundant in the tropics (Pearce & Örstan, 2006).

On the other hand, the neritomorpha, formerly an infraclass, but now elevated to the level of a class, have undergone an evolutionary radiation that allowed them to conquer diverse environments, including terrestrial ones, beginning in the Cretaceous. Among their families, the Helicinidae and Hydrocenidae are exclusively terrestrial, and have probably colonized the land independently from freshwater lineages, with the Hydrocenidae probably being the oldest (Kano et al., 2002). In both cases the paleal cavity lacks osphradiae and gills, presenting a rich irrigation (Barker, 2001), since it serves as a lung (Kano et al., 2002).

The last infraclass, the heterobranchs, includes inland water lungworms and garden snails. Since they generally do not have gills, as cenogastropods do, they cannot inhabit deep waters. However, there are some, such as the planorbid pulmonates, which have developed a secondary gill (Strong et al., 2008). Among the pulmonates, aerial respiration capacity seems to have been achieved independently at least 9-10 times (Vermeij & Dudley, 2000). This is the precise point to warn the reader that the term "pulmonates" refers to a systematic category valid in different periods, but that many gastropods of other "non-pulmonate" taxa also possess lungs, such as apple snails (ampullarid cenogastropods). However, although these lungs are always found in the paleal cavity, they are not homologous.

The pulmonates do not bear an operculum and are usually hermaphroditic, they are a paraphyletic group, currently placed in Panpulmonata, comprising three lineages with terrestrial forms, the stylomatophores, sistellomatophores and ellobioids (van Straalen, 2021). The latter, and despite being probably monophyletic, would have colonized land in at least two independent events (Romero et al., 2016). However, regardless of the animals or respiratory systems involved, the latter are almost always found settled in the paleo complex (Lindberg & Ponder, 2001).

## Respiratory variants

### Cenogasteropods

It includes the apple snails (ampulariids). These maintain at least one ancestral gill and their lung develops as an invagination of the mantle cavity roof, not from the mantle cavity, so that organ and its pneumostome are not homologous with those of other gastropods (Rodriguez et al., 2021). In addition, members of the family exhibit a wide divergence in their independence from water, and both the gill and lung appear to be involved in various functional processes other than respiration, such as immunity, acid-base and ionic balance and/or excretion (Prieto, 2021). The lung is a cavity located in the mantle, with a roof and a floor lined by a richly irrigated respiratory lamina. Its walls are constituted by the mantle epithelium, a muscular layer on the roof and two on the floor, a vascular zone with storage tissue and the respiratory epithelium. The irrigation, very abundant and somewhat complex, presents a different pattern in the roof and floor of the lung (Rodriguez et al., 2021).

Prieto (2021) provides an exhaustive critique of a recent article by Mueck et al. (2020) on the respiratory structures of certain ampulariids, in which they mention the possibility of the existence of a kind of endothelium in the hemolymphatic vessels of the lung of *Pomacea maculata*, according to the data provided by the authors of the original article. It also refers to the mention by Rodriguez et al. (2021) of such a cell, which they call "like endothelial", observed in the lung of *P. canaliculata*. If it is really a permanent and more or less continuous lining cell, present in the blood vessels of these animals, it would be an outstanding fact, because the endothelium, in a strict sense of the term, is supposed to be an evolutionary innovation exclusive to vertebrates (Muñoz-Chápuli, 2011, Molnár et al., 2021). In any case, I have observed in samples from a giant earthworm the presence of coating cells in the vessels. However, it is not clear that they fulfill the functional role of the endothelium, nor that they present the structural characteristics of the endothelium.

Finally, among the cenogasteropods are the cyclophoroids, probably the first gastropods to conquer the land and perhaps the most diverse of all terrestrial gastropods, being particularly abundant in the southern hemisphere. They have lungs and have lost their gills and probably derive from a freshwater lineage (van Straalen, 2021). Their shells may have certain regions that serve as tubes to facilitate respiration (Páll-Gergely et al., 2017).

### Lung snails

In the well-known garden slugs and snails, gases are exchanged in two ways: by diffusion or by active ventilation (Ghiretti, 1966). These animals may have originated in water bodies with low dissolved oxygen and, as in vertebrates, the passage from the aquatic to the terrestrial environment is considered a crucial evolutionary event (Maina, 1989). In snails the lung is heavily irrigated and is located in the carapace spire (Lőw et al., 2016). Among the pulmonate gastropods, the Ellobiidae would be the ones that first colonized land and, as in the others, the lung is essentially a cavity formed in the mantle and communicated to the outside by the pneumostome (Barker, 2001), which would be an apomorphy of the pulmonates (Mordan & Wade, 2008) and consists of a muscular sphincter that prevents water loss in terrestrial forms (Ponder et al., 2020). The lung cavity itself would be homologous with the paleal cavity (Ruthensteiner, 1997). The latter and the pneumostoma would be one of three apomorphies of pulmonates, the other two being the forebrain and midbrain body in the central nervous system (Mordan & Wade, 2008). The lungs are located on the right side of the roof of the paleal cavity. However, in many shelled taxa (slugs), especially marine slugs, this cavity has been lost secondarily and respiration is essentially tegumentary. On the other hand, among the more derived eutineurid gastropods, a respiratory configuration more similar to the more basal gastropods can be found among the glacidorbids and pyramidelloids (Ponder et al., 2020), the former being a family of freshwater snails native to the southern hemisphere (Rumi et al., 2015).

Histologically in *Helix*, for example, the lung is a sac lined by simple flat epithelium with microvilli in which are also found, analogous to what is seen in vertebrates, surfactant-secreting cells. Underneath there is some connective tissue through which a large number of muscle fibers run in multiple directions. There are also large and numerous spaces representing the hemolymphatic vessels. Covering the whole is the epidermis (Dennis et al., 2021).

A highly diversified taxon is the Hygrophila or Lymnaeoidea, which contains only inland water snails. Among these are the Planorbidae and the Lymnaeidae, some of which have developed lungs and gills (Mordan & Wade, 2008). Finally, in stylomatophores that acquired the slug habit, the lungs were reduced because respiration is primarily tegumentary (Ponder et al., 2019). Although in certain pulmonate slugs, the Athoracophoridae, which would also breathe through the tegument, a series of very thin-walled, branched canaliculi are found in the paleal cavity leading to a circulatory sinus where they exchange gases (Burton, 1981). Because this structure is somewhat reminiscent of the trachea of insects, these animals are known as tracheopulmonates and are referred to as tracheal lungs (South, 1992). Vaginulids also do not have lungs, but breathe through the integument and through a series of invaginated tubules in the integument (Mordan &Wade, 2008).

## ARTHROPODS WITH EMPHASIS ON PANCRUSTACEANS

Arthropods, particularly chelicerates and myriapods, were the pioneers in colonizing the land, perhaps thanks to their exoskeleton, which provides support (along with their jointed legs) and facilitates osmoregulation. However, respiration does seem to have been a problem (Gueriau et al., 2020), although it has evidently not prevented the adaptation of these groups. Despite originating in waters, terrestrial lineages outnumber aquatic lineages by about 17 times in number of species (Dunlop et al., 2013).

However, several groups considered primarily terrestrial such as arachnids present numerous forms that can live associated with water to varying degrees, to which they returned secondarily. However, among these there are no clear morphological indications of this adaptation (Albin et al., 2022; Crews et al., 2019). Among aquatic insects, with more than 88,000 species distributed in 13 orders (Starr and Wallace, 2021) and secondarily adapted to water, the situation is quite different as gills may even be present (Lancaster & Downes, 2013).

As a phylum, arthropods present a great morphological disparity, being the most diverse animal taxon. They possess various morphological, physiological and biochemical adaptations for respiration, as they may have lungs, gills and trachea, as well as respiratory pigments (or not), and live underwater, on land or lead a more or less amphibious life. However, seven of its 19 clades present animals without specific respiratory organs, since they perform this task through the integument because they are very small. This respiration would probably be the ancestral state, independent of the secondary and parallel miniaturization observed in several lineages. On the other hand, among pancrustaceans (crustaceans plus insects), it is likely that oxygen levels are actively kept somewhat low so as not to generate high concentrations of reactive oxygen compounds, which would reflect the evolutionary history of early animals. In this sense, and particularly in insects, high oxygen concentrations are recorded in the hemolymph and tracheae, despite which such values in tissues are lower and equivalent to that found among crustaceans (Harrison, 2015). On the other hand, the tracheal system is highly dependent on the environment, to the point that perhaps the giant forms of protoodonates reached their large dimensions thanks to the exceptionally high oxygen content during such times (up to 30%). These organs are found in onychophorans, tardigrades and arthropods, although they would not be homologous (Bradley et al., 2009). Among arthropods in the strict sense tracheae can be found in myriapods and hexapods, having probably evolved independently in both and almost certainly in the terrestrial environment (Harrison, 2015). However, the ubiquity of this system and the structural similarities found in the different groups, would not be homologous in all cases, despite which perhaps in all or most taxa they would be produced according to the same developmental principles (Bradley et al., 2009). This, in the author's opinion, would constitute a case of deep homology.

Crustaceans, basal to insects, have a very different configuration from insects. Their respiratory system consists of gills or lungs, and is intimately associated with the circulatory system, which in crabs is practically closed. In addition, they possess oxygen-carrying molecules. The gills are not homologous throughout the taxon and are also frequently involved in osmotic balance and excretion (Wirkner et al., 2013a) and in general nearly always originate from the successes, external expansions of the appendages (Boxshall & Jaume, 2009). In insects the situation is different because there is usually a system of tubes, the tracheae, which communicate with the exterior from where they take in air. In these animals the circulatory system is normally open and although the possession of respiratory pigments is not very common, it is now known to be more frequent than was once believed (Harrison & Wasserthal, 2013). All in all, respiratory and circulatory systems do not usually possess a close functional association (Urquiza & Carezzano, 2018) and, despite what is sometimes believed, tracheae can transport up to ten times more oxygen than the blood capillary of a vertebrate (Maina, 2011). Some of their advantages are that they are lighter, allow a higher rate of oxygen diffusion and enable the action of flight muscles. They also act as respiratory reservoirs during times of hypoxia, although perhaps this same system would be the cause of the poor evolutionary success of insects in deep waters by giving them excessive buoyancy (Bradley et al., 2009). The first hexapods, although there is no certainty about their closest relatives, were undoubtedly flightless, terrestrial and fed on sporangia or carrion. They would possibly have been similar in appearance to certain apterygotes such as Zygentoma (Engel, 2015). A common structure throughout the phylum is the presence of the cuticle, which represents a hindrance to the free diffusion of gases. All in all, arthropods were the first animals to colonize emerged lands, a myriapod being the oldest terrestrial animal found so far (Lozano-Fernández et al., 2016), although perhaps the first panarthropod to do so, in the Silurian, was some form of onychophoran (Beutel et al., 2013). In addition to these two groups, breathing by tracheids (a term of dubious application to all cases) are arachnids (some forms) (Foelix, 2011) and certain isopod crustaceans (ball bugs) whose pseudotracheids exhibit a wide range of land-conquering adaptations (Hornung, 2011). As discussed, these organs are unlikely to be homologous, at least across taxa (Schmidt-Rhaesa, 2007). Even among springtails and proturans the tracheae are very different from those of insects, which has led certain authors to doubt their homology even within hexapods (Beutel et al., 2013). Functionally, among pancrustaceans, there seem to be certain differences regarding the response to long-term exposure to hypoxia, as insects respond by increasing the size and branching of the tracheae, while crustaceans may change the type of respiratory pigment or increase its concentration. There seems to be no evidence of morphological changes in the gills. On the other hand, in both crustaceans and insects, it is considered that there is greater tolerance to hypoxia in species exposed to severe hazards in oxygen supply (Harrison, 2015). Although tegumentary respiration was the first, as in other organisms, the first specialized respiratory organs as such would have been the book gills, from which the book lungs of arachnids would derive, which at least in principle, are diffusion lungs because they do not possess ventilatory mechanisms (Perry et al., 2019).

## Respiratory variants

### Onychophores

Onychophores are, together with tardigrades, considered part of the taxon Panartropoda, and present numerous spiracles in each segment, seated at the bottom of tegumentary sinks that communicate with the tracheal system (Nielsen, 2012). In opposition to insects, these ducts would not possess regulatory mechanisms (Pereira et al., 1985). In addition, at least some species possess hemocyanin, the same found in euarthropods, so this pigment probably preceded the separation of onychophores. This also suggests that at such times there were low oxygen tensions in the environment (Kusche et al., 2002). Although the oldest representatives of certain animals linked to the phylum date back to the Cambrian, fossils of the current terminal taxa have been placed in the Carboniferous, and they were most likely terrestrial and already showed tracheids (Garwood et al., 2016).

### Chelicerates with emphasis on spiders

Among these organisms may be found minute species with tegumentary respiration, such as certain mites or, very frequently, quite large animals with specialized respiratory organs such as spiders and scorpions. In these, the most common form of respiration is by means of book lungs, which is the only form in which amblypygids, uropygids, scorpionids and schizomids do it. Slightly more complex is the situation of most spiders, because they breathe through book lungs and tracheae. These lungs would be homologous to that of *Limulus*, an aquatic chelicerate, and Paleozoic scorpions (Selden & Edwards, 1989; Scholtz & Kamenz, 2006). In this sense, it is believed that chelicerates experienced only one event of conquest of the aeroterrestrial environment (Howard et al., 2020), although even extinct eurypterids would have been able to breathe, at least to some extent, in air, thanks to the possession of respiratory trabeculae in the gill chamber, as occurs in certain amphibian crabs (Lamsdell et al., 2020).

Likewise, and beyond their morphological and functional diversity, it is considered that pulmonary respiration is the basal state in chelicerates, and that from certain dorsal components of the epipodite the tubular tracheae and web spinnerets developed, which express certain molecular markers in common (Brunelli et al., 2015). Because of this, and although the relationships among taxa are debated, among arachnids monophyly is almost unanimously accepted, which is reflected by the configuration and distribution of their respiratory organs. This allows the formation of the taxon Tetrapulmonata, characterized by four lungs in a book (Howard et al., 2020).

In spiders in particular, book lungs, trachea and respiratory pigments can be observed, while much of their activity is carried out by anaerobic metabolism. The more basal spiders such as the migalomorph spiders or tarantulas and chick spiders exhibit two pairs of lungs while the more derived spiders, such as the Araneidae (web spiders), exhibit one pair of book lungs and tubular tracheae (Schmitz, 2016). Although their metabolism can, at least in part, be anaerobic when necessity dictates, they cannot run much longer than two minutes (Schmitz, 2013) and, along with crustaceans, exhibit little tolerance to hypoxia, very different from that recorded in myriapods and insects (Schmitz & Harrison, 2004). In any case, they are animals with a low metabolic demand because they possess venom for hunting, prolonged tolerance to lack of food and the fact that the extension of their legs occurs by increasing hydrostatic pressure and not by muscular action. Even in those that developed tracheae to increase oxygen supply, the mitochondrial mass in the appendicular muscles is markedly decreased (Schmitz, 2013). As will be seen later, this situation is very different from that in insects.

In some groups, such as the migalomorphs, and in the most basal of the araneomorphs, there are two pairs of lungs, while among the most derived of the latter there is only one pair since the other pair was lost and a tracheal system developed in its place. Likewise, there may be taxa in which there is a certain predominance of one or the other system, while in others both have an equivalent and integrated development. The factors that led to the appearance of tracheae are not very clear, although in general they exist in the most active animals.

In addition, those with lungs use hemocyanin for oxygen transport, while the tracheal forms deliver oxygen directly to the tissues through the aforementioned ducts. Finally, tracheae can also be transformed, in certain species, into tracheal lungs (Schmitz, 2013). Although spiracles may exist, they do not reach the degree of complexity seen in insects (Perry et al., 2019).

Book lungs are reminiscent of a radiator. Its name refers to the fact that it resembles a book, where each page would be a lamella filled with hemolymph, separated from the subsequent ones by an air chamber. In this way the oxygen from the air passes to the hemocyanin of the lamellar hemolymph. The set of lamellae and chambers form a well delimited and compact structure that communicates to the outside by an atrium, which allows the exchange of air. The atrium has a spiracle in its external opening and the blood circulates thanks to the cardiac work (Brunelli et al., 2015). The lungs, as mentioned above, act by diffusion and their spiracles are regulated by muscles (Schmitz, 2016).

At least in the genus *Cteniza*, a migalomorph, these lungs have a pyramidal and filter-like appearance. The hemolymphatic canals open on one side to the main lymphatic sinus while on the other side they are closed by a cell that separates them from the atrium. They have extremely thin walls formed by an epithelial layer on each side, lined by a thin cuticle on the side of the air channel. This also forms chitinous trabeculae, which extend between both walls through the latter, thus providing physical support. On the other hand, large, cubic, pillar cells that interdigitate with each other on both sides can be seen across the lumen of the hemolymphatic canal. They would also have a mechanical function (Brunelli et al., 2015).

As for the tracheae, despite the name, they are not very similar between spiders and insects. To begin with, those of spiders are hollow tubules along their entire length, while in insects there is a terminal cell. In addition, diffusion occurs along their entire length, very different from what occurs in insects, which occurs only at their termination. Also, in most cases, in spiders, oxygen is finally carried by the hemolymph. On the other hand, spider tracheae consist of a pair of tubes at the flanks, which are the modified lungs, and a pair of tubes located towards the middle zone, which are linked to the exterior, and derive from very specialized muscular junctions, the entapophyses. From this it is inferred that structurally, ontogenetically and evolutionarily these tracheae are completely different from those found in insects (Foelix, 2011; Lopardo et al., 2022). It has even been proposed that spider tracheae have evolved independently from book lungs on 6 different occasions (Ramírez et al., 2021).

## Myriapods

This taxon includes the well-known millipedes, centipedes and scolopendrons, plus some groups with few and unfamiliar species. In almost all cases they breathe by trachea and thrive in emerged lands (Hilken et al., 2011, 2015), although there are several species that would more or less regularly or intermittently inhabit flooded areas, which they would achieve either by decreasing their oxygen demand or by having specific structures such as the plastron (Adis & Junk 2002; Geoffroy, 2015). They probably derive from terrestrial chelicerates and, together with hexapods would have colonized land before vascular plants (Harrison, 2015), with eutycarcinoids being the first myriapods to do so, as early as the Cambrian (Gueriau et al., 2020).

Although chylopods breathe through tracheae, in some cases the tracheae were transformed into a sort of tracheal lung, as in the squaterigeromorphs (Lewis, 1981; Hilken et al., 2011, 2021), while millipedes (diplopods) have tracheae (Hilken et al., 2015). All in all, there is great disparity in the pattern of origin and branching of this system, making it difficult to point out characters common to all. Moreover, in some of them, such as the diplopods, for a long time the only studies carried out were from the 19th century and it was not until the 1990s that more complete studies were undertaken (Hilken et al., 2011). Histologically, all these organs are similar since the tracheae present a simple epithelium lined with a cuticle composed of the usual three layers and with the presence of helical ctenidia (Hilken et al., 2011, 2015). Despite the morphological variation mentioned above, the entire taxon would be monophyletic and would have invaded the soil only once (van Straalen, 2021). However, it is possible that the tracheal system evolved independently (Gueriau et al., 2020).

## Diplopods

Diplopods have spiracles, atria, tracheal pouches, tracheae (which may or may not be branched) and tracheoles. Branching is fairly uniform, segmental and anastomoses between neighboring tracheae are not usually found. Hemocyanin may be present in the larger species, a molecule that appears to be quite ancient but would have been lost independently in the various myriapod lineages (Hilken et al., 2015). Due to the presence of hemocyanin, at least part of the tracheal tree probably functions as a lung (Perry et al., 2019). The paired spiracles, ventral and seated in the vicinity of the leg bases (Koch, 2015), are varied in their morphology as they exhibit disparate sizes and hairs of different shape and size that function as filters. Regulation of their opening and closing is highly variable among taxa, and their nature is unclear. The tracheal pouches are almost always arranged in pairs and are usually quite sclerotized, serving as air reservoirs, filters and apodemes, and may have different extensions. Depending on the taxon, the truncal tracheae arise at different points in these pockets. Ventilation would occur mainly by passive diffusion, although it can also be active and, in some species, the spiracles can be closed (Hilken et al., 2015).

## Centipedes

With the exception of the squaterigeromorphs, which breathe through tracheal lungs and therefore belong to the group of notostigmophorans, all other centipedes breathe through tracheae and are grouped among the pleurostigmophorans, which will be discussed in more detail. In the former, the respiratory system consists of numerous tracheae of short length that are linked to the hemocoel. Here oxygen is transferred to hemocyanin, which transports this gas through the circulatory system (Hilken et al., 2011). On the other hand, although I will not go into detail, it should be mentioned that the distribution and nature of spiracles follows different patterns in taxa, and has systematic importance in many of the centipedes (Vahtera et al., 2012). In pleurostigmophores, meanwhile, the spiracles open on the flanks and have hairs, as well as the atrium, which act as hydrophobic barriers. Air normally enters by diffusion, although there are cases where there is active ventilation. Continuing to the atrium it is common to find tracheal pouches, which as in many diplopods also serve as apodemes, although it may lack them. From the pouches sprout the major tracheal tubes, which follow a very different branching pattern among taxa, there being some forms where there may be lateral asymmetry (Hilken et al., 2011). A reticuliform organization may be observed among scolopendrons, and there are even tracheae that connect opposite spiracles, or longitudinal branches, doing the same with contiguous ones. Large tracheae may resemble sinuses, and probably function as air reservoirs. In some species there is a perivisceral system that in turn gives rise to a subneural network that ventilates the nervous system (Lewis, 1981).

Beyond the aforementioned variants, the extinct euthycarcionoids, considered amphibians, seem to have inhabited shallow waters and to have possessed postabdominal air chambers with respiratory functions, different from the dominant tracheal system in the clade (Gueriau et al., 2020).

## CRUSTACEANS

Among crustaceans, only "terrestrial" crabs and isopods show aerial respiration. However, some basic notions of gills will be developed, an ancestral state of the taxon in aquatic forms, and which are retained in certain terrestrial forms.

Crustaceans have colonized land independently on at least 10 occasions. Life in this environment presents different degrees of adaptation to it, which has allowed it to be classified into five levels, being T5 the one where even reproduction is carried out independently of water (Krieger et al., 2021). In these organisms the circulatory and respiratory systems are integrated, which would be the basal stage of the phylum. Thus, the situation is similar to spiders, but very different from what occurs, at least in principle, with insects. However, the morphological and functional disparity is extreme, to the point that in some crabs there are lungs and gills, which may also be involved in electrolyte balance and excretion. It should be noted that in crustaceans that have gills, not all of them are homologous to each other (Wirkner et al., 2013b), which is also true for the lungs of isopods. In crustaceans, terrestrial or amphibious forms are found in isopods (Hornung, 2011), amphipods (Friend & Richardson, 1986) and decapods

(Watson-Zink, 2021), which show greater or lesser independence from water and different respiratory adaptations. On the other hand, some decapod malacrustaceans (crabs) have developed very complex organs and possess a circulatory system that is considered by some authors to be semi-closed. It should be noted that amphipods, which are semi-terrestrial, breathe through gills, as is the case of *Talitrus saltator*. The isopods, meanwhile, may have lungs or tracheae in the exopodite, or gills in the endopodite (Perry et al., 2019).

In this class the appendages are of great importance for their way of life, since they are involved in a multitude of functions in addition to locomotion. Thus, the biramous type have numerous portions that have followed different evolutionary paths, and have received different names, so their nomenclature is often complicated. In any case, one of these portions are the aforementioned successes, expansions that have frequently developed into gills. They may also be called epipodite or gill plate, among other names (Boxshall & Jaume 2009). Among malacrustaceans these gills are generally housed in a cavity, the gill plate, developed at the expense of the carapace and as a lateral extension of it, through which water circulates. It has inhalant and exhalant orifices between which is the gill, which divides the chamber into an inhalant and an exhalant section (Ruppert et al., 2004).

## Isopods

The isopods contain quite large marine forms, which can reach gigantism, although most of them are of small size (interstitial forms), in addition to terrestrial forms. They may have up to six pairs of gill-bearing respiratory pleopods, in which both the exopodite and the endopodite are involved in that task. Also, some portions of the appendages can be transformed into an operculum. Terrestrial species may possess simple lamellar gills, pseudotracheids and lungs, as well as gill chambers in their abdomen (Mill, 1997). There are about 3,700 terrestrial species or with some degree of adaptation to this environment (Sfenthourakis et al., 2020), with this group exhibiting the most water-independent lineages of all crustaceans (Krieger et al., 2021). The extreme has been documented in *Hemilepistus*, a desert form that exhibits brood care, social habits and lives in tunnels (Schmidt & Wägele, 2001). Although it was believed that all terrestrial isopods formed one clade and that the land invasion was a single event, there is increasing evidence that there were probably three independent lineages that became terrestrial and, although it is assumed that they came from marine ancestors, it is likely that there were freshwater intermediates (van Straalen, 2021). Therefore, it is accepted that respiratory organs have undergone several convergent evolutionary events in different isopod lineages and exhibit, in different species, an adaptive gradient according to environmental demands and particular phylogenetic position, ranging from very simple respiratory surfaces to highly elaborated organs and from animals that thrive in coastal marine areas to others that inhabit deserts. In addition, there are cases of secondary loss of all lungs while in other species there may be from one to five pairs of such organs, arranged in successive pleopods, which are the posterior appendages (Hornung, 2011). Even within certain taxa all morphological types can be found and of increasing complexity, arranged as if following a gradient from anterior to posterior in the aforementioned pleopods (Paoli et al., 2002).

The simplest case occurs when the ventral integument of the exopodite exhibits some folding to effect respiration, which varies among species. This initial level of complexity is followed by an intermediate one, when a covering of the respiratory area is added to these extensions. The most striking and extreme case is that where the entire structure is incorporated into the interior of the animal, acting as a "lung", which are quite diverse. In these cases, the epithelium is organized forming folds while presenting spiracles that, in addition, exhibit a certain tendency to decrease in size the greater the adaptation of the animal to the dry environment. The respiratory architecture is completed by the presence of several hemolymphatic spaces that cross the interior of the lung. The spiracles may be single or somewhat numerous, and their structure also varies among taxa, as they may present hydrophobic areas in the perispiracular zones surrounding this opening. In some species from very arid areas the spiracles may even be closed (Hornung, 2011). These openings communicate inwardly with the atrium, which is continued by a series of respiratory tubules of decreasing diameter, which in some animals may penetrate into the pleon and body cavity (Schmidt and Wägele, 2001). The lung is located in the pleon, and is formed by tegumentary expansions enclosing hemocoelomic spaces with which the air of the cavity exchanges gases. In the most complex cases this lung may consist of hundreds of such extensions, while in the most simplified cases it is just a relatively smooth exchange surface.

### Decapods

Decapods generally have complex gills contained in chambers that in some crabs, form lungs. This makes possible the existence of entirely aquatic, totally terrestrial or amphibious species. In amphibians, the adaptations are completely different from the first two. On the other hand, each of the eight thoracomeres (thoracic appendages) could carry up to four gills, although the theoretical maximum number of 32 is never reached, with 24 pairs being the largest number found (in a shrimp), while in lobsters there are up to 20. Marine brachyurans have between eight to nine pairs (Mill, 1997).

Crabs have colonized the land on at least 10 independent occasions. They arrived there from the sea through littoral zones or mangroves, or from fresh waters, through estuaries (Watson-Zink, 2021). Probably in some species this process would be facilitated by the presence of symbionts, which would help the animal by buffering its exposure to high levels of oxygen and in the utilization of new foods, such as nitrogen-poor vegetables, among other functions. The microbiome involved could be acquired either from the environment or from the mother (Wale et al., 2021).

The term crab can be applied to both brachyurans and other lineages that have undergone a folding in their ventral area, directing it towards the cephalic region (Scholtz, 2014). The lungs are highly vascularized areas of the gill chamber and are not always homologous with each other, and although this adaptation allows them to breathe in air, in several species the chamber holds some water (Luquet et al., 2000).

The respiratory possibilities of brachyuran crabs are very diverse; there can be found completely aquatic animals, as well as others that do not tolerate immersion for a long time, which are called terrestrial crabs. Species that inhabit intertidal zones can also be found, and they cope with periodic desiccation by means of two strategies. In one, the animals decrease their metabolism and their oxygen demand, while their gills collapse due to the lack of water. In the other, found in the so-called amphibious species, the animals maintain their activity at the usual levels and their gills usually recirculate some water because they are the only point for the expulsion of carbon dioxide (Luquet et al., 2000).

In addition, the gills can perform other functions, such as excretion, so they cannot be completely inactivated, because if they run out of water, they collapse or stick together, and can no longer function. This is why all crab species should always have their gills covered with at least some water. Of all, the coconut tree crab, *Birgus latro*, is perhaps the species that increased its lung capacity the most, while reducing its gills (Burggren & McMahon 1988).

Although there are respiratory surfaces in unusual areas, most commonly this function is performed in the gills or in the epithelium of the gill chamber, the branchiostegite, with cases where both types of respiration are performed at the same time. In species with bimodal respiration, three morphological characteristics are found in common: decrease of the gill surface, increase of the gill-stegite, and thinning of the air/blood barrier at the gill surface. Thus, in aquatic crabs, between 900 to 1,500 mm2 per gram of biomass can be found, while among terrestrial crabs this amount is between 12 to 500 mm2 (Henry, 1994). Hemolymph circulates in the gills to ensure oxygenation, following a similar pattern in both gill and land crabs. In terrestrial crabs there is also a capillary network in the gill chamber that serves as a lung. However, in order to adapt to situations of different water availability, the circulatory flow follows different patterns. In either case, oxygenation occurs both in the gills and in the lungs, where blood from the visceral sinuses passes through a capillary network that together flows from the respiratory structures to the pericardial gill sinus that carries blood to the pericardial cavity (Davie et al., 2015).

## HEXAPODS AND INSECTS

Hexapods include animals such as springtails, proturans and dipterans in addition to insects as the most diverse group, and although they were long considered equivalent taxa, they now belong to different groups (Bellini et al., 2023).

Insects probably colonized emerged lands about 480 million years ago from aquatic crustaceans, and their tracheal system would have originated during that event. However, given the lack of knowledge about many hexapods, some authors claim that it is still too early to decide on a possible evolutionary scenario (Dittrich & Wipfler 2021).

Almost all pterygotes have three main longitudinal tracheal trunks on each side, one dorsal, one lateral and one ventral. In general, the tracheae of consecutive segments are linked by connectors (Richards & Davies, 1997). Usually, the lateral trunks are the largest and are almost always present, while the ventral trunk is the smallest and is inconsistent (Snodgrass, 1993). The dorsal trunk carries gases from the dorsal musculature and integument and the heart, the lateral trunk carries gases from the fat bodies, intestine, Malpighian tubes and reproductive organs, and finally the ventral trunk carries gases from the ventral muscles and nerve cord (Beutel et al., 2013).

In apterygotes, the situation is quite complicated because there are no studies that include most of their groups, so it is difficult to draw very certain conclusions about the ancestral status of this system in hexapods (Dittrich & Wipfler 2021). As these are assumed to be derived from crustaceans, it is licit to assume that the earliest forms were aquatic. However, at present most of them are air-breathing, although they colonized secondarily the waters, mainly continental, and there are not many strictly marine insects. Despite the above, there are 15 orders of insects with aquatic forms, although only five present all or most of the species totally or mainly adapted to this environment (Thorp and O'Neill, 2015). In summary, and following Harrison (2015), it is likely that the various lineages of hexapods have derived their tracheal system independently of each other, and although this may have evolved on land, an intermediate amphibious stage cannot be ruled out. However, since no ancestral forms with gills have been found, it cannot be ruled out that tracheae and aeroterrestrial colonization occurred only once among hexapods. In this sense, it should also be mentioned that some authors defend the "tracheid" hypothesis, whereby hexapods and myriapods derive from an ancestral crustacean, and that tracheids originated only once when they colonized the land.

There is a possibility that the crustacean ancestor of the hexapods colonized fresh waters to conquer the land during two different events. In one, the "apterygotes" would have appeared, while in the other the other insects would have originated, except for the dermaptera and odonates, which remained in fresh waters. Then, several taxa returned to the waters in a secondary and independent way, because although they breathe by trachea or even by gills, they are not homologous with those of crustaceans (van Straalen, 2021).

The tracheae of insects form a system of ectodermal ducts separated from the exterior by spiracles, consisting of large multicellular branches that divide to generate thin unicellular tracheolae from which fine prolongations measuring only a few nanometers originate. Thus, these branches can even penetrate inside the myocytes of some flight muscles (Harrison & Wasserthal, 2013), in which each muscle cell possesses its own tracheole with prolongations up to 70 nm thick. Moreover, the tracheolar prolongations are lodged so close to the myocyte mitochondria that they are arranged around them, a pattern called "mitochondrial continuum" (Maina, 2011). But, although they appear to enter their cytoplasm, tracheolae and myocytes are always separate, although functionally these prolongations can be considered as intracellular (Klowden, 2013). Although there may be more tracheolae per unit area than capillaries in mammalian tissues, in very small species respiration is essentially tegumentary, while in some cases hemolymph is also involved in the transport of gases, as is the case in proturs and some springtails. Respiratory pigments, previously considered a rarity in hexapods, appear to be much more ubiquitous than previously thought. Tracheae may also serve as supports, as occurs in some myriapods (Harrison & Wasserthal, 2013). Inside the tracheae, except in the largest ones, there are thickened ctenidia that prevent their collapse. Histologically, from the lumen to the internal environment, they are composed of the cuticle, a flat epithelium of ectodermal origin and the basement membrane. Under the epicuticle a resilin lamina can be found. The thin tracheolae,

at the end of the tube, are closed by the tracheolar cell so that the end is blind, although in this area the tubes may anastomose with others. This end region does not molt with ecdysis and is within the terminal cell (Richards & Davies, 1997, Harrison & Wasserthal, 2013). Oxygen passes into the tissues in these extensions, while carbon dioxide can pass through the walls of the entire respiratory tree (Terblanche & Woods, 2018).
The tracheae communicate to the outside through the spiracles, which are essential for discontinuous respiration and unidirectional flow, typical of large flying insects. These organs are always actively closed, while their opening is mainly passive, although there are exceptions (Perry et al., 2019), and a maximum of ten can be found, always from the thorax backwards, as they never occupy the head, so tracheae originating from posterior segments reach the head. These openings present a wide morphological variation, although some common characteristics may be: the opening or pore, the peritreme, the atrium and the closing apparatus. The simplest situation is when there is only one opening, which in more complex cases is surrounded by a thickening, the peritrema. This is followed by the atrium, which may have hairs or roughness, which is followed, at least sometimes, by the closure apparatus, consisting of muscles and cuticular structures with the function of obliterating the pore, especially to prevent or reduce dehydration (Richards & Davies, 1997).

The closing apparatus operates thanks to the action of muscles linked to two neurons located in the same segment and innervating the spiracles of both flanks. On the contrary, when there are opening muscles, which are more unusual, they are independently innervated by different neurons. Likewise, inhibitory neurons may be found in both situations (Harrison & Wasserthal, 2013). In any case, in small or low-metabolism insects, the diffusion of oxygen through the tracheae covers the needs of the animal, which may nevertheless require ventilation movements if its activity increases (Maina, 2011). In addition, many forms may experience anoxia and then recover, suggesting that diffusion is sufficient to sustain minimal functional activity (Harrison & Wasserthal, 2013). In this sense, the rate of oxygen uptake is maximized and dehydration is minimized if the spiracles remain closed most of the time. In order to reach this result and take up oxygen, the spiracles open and close rapidly repeatedly for certain periods of time (Lawley et al., 2020).

To illustrate the possible evolution of the tracheal system of these animals, the simplest structural situation, found in some "apterygotes", can be discussed. In the archaeognaths we find the taxon of the machilids, which has a tracheal system with two spiracles in the thorax, whose trunks present anastomoses with each other and send branches to the head and anterior zones, and five spiracles in the abdomen. In the abdomen, each spiracle is linked to a segmental tracheal system that in some cases does not connect with adjacent ones. The last segments may have no tracheae in some species and the spiracles possess neither musculature nor control systems for closing or opening (Dittrich & Wipfler 2021). According to Ax (2000) and Perry et al., (2019), the basal plan of insects is one pair of spiracles in the mesothorax, another in the metathorax and eight pairs in the subsequent abdominal segments, which is concluded from those present in apterygotes. Likewise, there would have been no communicating tracheas between the spiracles, neither contralateral nor ipsilateral (Ax, 2000).

## THE NERVOUS SYSTEM AND THE REGULATION OF VISCERAL FUNCTIONS: THE CENTRAL GENERATORS OF MOTOR PATTERNS

The respiratory control of gastropods and insects, the most studied in this aspect of all invertebrates, except perhaps crustaceans, will be briefly discussed, so the structural, functional and evolutionary relationships of the nervous system in general and of the regions of the nervous system in charge of visceral control will be addressed. The latter is often carried out through the central pattern generators, neuronal ensembles particularly adapted for vegetative tasks.

From a traditional point of view, the nervous system has been classified into diffuse network nervous systems (apparently found only in xenoturbellids) and centralized nervous systems (CNS, clearly differentiated in vertebrates, arthropods, mollusks and annelids, to name only a few well-known animals). However, perhaps a third category should be created, that of ganglionated network nervous systems, found in cnidarians, which, classically and contrary to some evidence, were assumed to have simple and diffuse networks. As for their evolution, there is not complete agreement as to whether SNs and/or neurons are homologous in all cases, or whether they are homologous in some or most animal phyla. According to the latter possibility, the evolutionary origin of at least some taxa such as ctenophores could be independent (Urquiza, 2021).

There is another option, although in my opinion it does not solve the previous problem: that the first nervous system to appear was the enteric nervous system (which regulates the actions of the digestive system), and then this would have connected with the CNS, a hypothesis called "first brain" by Furness and Stebbing (2018). The vertebrate enteric nervous system (ENS), along with two other divisions, the sympathetic (SNS) and parasympathetic systems (SNPS) are part of the autonomic nervous system of these animals (Butler & Hodos 2005). As a whole, the Autonomic Nervous System (ANS) consists of gray nuclei located in the CNS and of nerves and ganglia in the PNS and governs in a generally involuntary and unconscious manner the activity of internal organs and viscera (Gabella, 2012) which could be defined as the contents of the cranial, thoracic, abdominal and pelvic cavities (Butler & Hodos, 2005).

Centralized nervous systems have a central region (CNS) and a peripheral region (PNS). In vertebrates, the former includes the brain and spinal cord. The PNS, meanwhile, consists of the nerves that emerge from the brain and spinal cord. Both regions comprise the Somatic Nervous System, responsible for voluntary actions (basically the mobility of the striated skeletal muscle), and the ANS, destined to control the functioning of the viscera. This classification dates back to the 19th century, which was applied to mammals, and in which the somatic branch would respond to the external environment while the autonomous division would regulate the internal environment, according to the conception established at the time by Claude Bernard. Despite the years that have passed since its formulation, this classification seems to be quite universal and could perhaps be applied to numerous animals, having appeared early in evolution, and would reflect the possible homology of at least part of these systems among the various phyla (Bertucci & Arendt, 2013), although this is something that is far from being agreed upon by all biologists (Copenhaver, 2007). The ANS not only regulates the three functions mentioned above, since together with the Neuroendocrine System (ENS), at least in mammals, it governs vital unconscious actions such as temperature, heartbeat, etc. Thus, both systems act on smooth muscle, exocrine and endocrine glands and adipocytes. Although their action is involuntary and unconscious, it is integrated with voluntary motor activities or specific moods (Kandel, 2021). In many non-vertebrate animals such as mollusks, annelids and insects, there is also a central, a peripheral and a visceral nervous system (iVNS) (Ponder et al., 2019; Purschke, 2016; Klowden, 2013). The latter is functionally equivalent to the vertebrate autonomic as it controls vegetative functions such as cardiac, respiratory, excretory, endocrine and digestive activity.

The ability to perceive the environment probably arose at the same time as life and, probably, the ability to detect osmotic changes was the first of all (Verkhratsky, 2021), obviously related to nutritional functions. The regulation of the viscera that act on circulation and feeding are carried out at the local or hormonal level thanks to the action of intrinsic, extrinsic and neuromodulatory neurons, through networks, plexuses and nerve ganglia or a combination of these locally connected. Networks are characteristic of the most basal animals, while ganglia would have formed at an early evolutionary stage in more modern taxa. Probably, in the early days of the emergence of this system, in many groups there would also have been giant axons that allowed muscle synchronization throughout the whole body or a very extensive region by connecting local circuits. Today, neuromodulators intervene at the local or systemic level in the form of hormones. On the other hand, as regards the structure of the vegetative organs themselves, the muscular layers of the hollow tubes are of the smooth type (except for arthropods and probably annelids) and are generally arranged in pairs, one longitudinally and the other circularly. This pattern is followed in several phyla such as cnidarians, annelids, mollusks and flatworms (Selverston, 2007). In fact, the aforementioned first brain hypothesis considers as evidence the existence of regulatory neural networks of these strata in phyla as diverse as annelids, mollusks and vertebrates (Furness & Stebbing, 2018).

In any case, and although all animal behavior is integrated with visceral activity, in invertebrates there is no autonomic system in the strict sense, if we speak in morphological, neurochemical and functional terms, as in vertebrates, but there is an iVNS, which regulates the activity of practically all the internal organs, although with an integrative activity of the CNS. In numerous animals these organs, which frequently perform repetitive movements, have served as study models because their controlling neurons constitute the "central pattern generators", such as the stomatogastric system of crustaceans, models in which particular neurons, sometimes very large and characteristic, can be specifically identified. On the other hand, the generation of such a contraction pattern can be either an emergent property of the network itself or due to the action of specific cells (Jänig, 2013). Central motor pattern generators (CMPGs) are involved in the production of repetitive movements such as swimming, locomotion or breathing (Marder & Bucher, 2001). They are generally small and autonomous neural networks, because they do not require the arrival of afferents for their firing action (Lodi et al., 2020). Although they have classically been associated with the generation of cyclic movements such as breathing or episodic movements such as locomotion, they could be involved in more complex ones that also include the possibility of learning (Berkowitz, 2019). Their oscillatory properties depend largely on the nature of the membranes of their constituent neurons, which can fire endogenously (pacemaker neurons), although they can also be associated with non-oscillatory neurons (Bucher et al., 2015).

Despite their relative functional independence, at least in some cases, rhythmic activity requires the presence of certain modulatory molecules in order to be initiated. On the other hand, some patterns that may be more or less similar, such as coughing, vomiting or breathing, may use the same neurons, although these intervene differently in each case. Moreover, in certain systems sensory afferents may be more necessary than in others to adapt the rhythm to the animal's demands (Marder & Bucher, 2001). In addition, although the properties of the neurons of these neural systems may be very similar, their functioning is often based on the intervention of very different ion channels (Bucher et al., 2015).

## EXAMPLES OF VISCERAL SYSTEMS AND BREATH CONTROL

### Mollusks

The CNS of these animals consists of a series of paired ganglia, usually four, called cerebral, pedal, pleural and buccal, scattered throughout the body, to which a fifth pair, the visceral, may be added. Whatever the case may be, the peripheral nerves emanate from them. These ganglia may aggregate in the form of a ring, constituting a circumesophageal ring (Urquiza, 2021). Among pulmonate gastropods, whether terrestrial or secondarily aquatic, a new ganglion appeared, called paleal or parietal (Chase, 2001) and, as in other snails, there is an SNVi as well as an enteric nervous system (Ponder et al., 2019). In addition, the cerebral ganglia of some of these animals have been divided into three, the forebrain, midbrain, and metabrain (Chase, 2000, 2001), terminology that is not always clarified and may confuse readers. Because they exhibit neurological and behavioral complexity intermediate between annelids and mammals or insects, they are considered excellent models in neurobiology. The number of neurons in these mollusks ranges from 4,000 to 200,000, some of which reach a large size, greatly facilitating experimentation (Chase, 2002).

Among these organisms, the regulation of visceral functions such as heartbeat, excretion or respiration is usually performed by the visceral ganglion, which can sometimes be fused to the parietal ganglion. Isolated neurons as well as peripheral ganglia may also participate in this task (Chase, 2002). However, in certain animals, such as in the genus *Aplysia*, the visceral ganglion does not exhibit a very obvious delimitation and seems to fuse to the abdominal ganglion, which is why it has been called the parietal visceral ganglion. This ganglion would be homologous to the right parietal ganglion found in the genus *Achatina*. In the genus *Helix*, it is called both visceral and abdominal ganglion (Kodirov, 2011).

The PNS includes numerous and varied neurons of a sensory nature, dispersed in different organs, which would outnumber those clustered in the central ganglia. They often form plexuses in the

walls of tubular systems such as the digestive, perhaps mediating the secretory and peristaltic response (Voronezhskaya & Croll, 2015).
It should be remembered that tegumentary respiration is executed in all gastropods, although frequently also gill and/or pulmonary respiration (Chase, 2002). On the other hand, cenogasteropods are oxygen conformers, while pulmonates are not, because they regulate oxygen consumption, along with their metabolism could be partially anaerobic (Pyron & Brown, 2015). Pulmonates of the genus *Lymnaea* possess a SN that can regenerate, with large and easily identifiable neurons (Dong et al., 2021), and that can be transplanted to another individual. In addition, they allow electrophysiological recording while the animal is breathing, and *in vitro*, they can even reconstruct the respiratory GPC (Taylor & Lukowiak, 2000). There are many reasons why this is a useful model. As its habitat periodically becomes hypoxic, preventing tegumentary respiration, the animal must emerge and begin lung ventilation. To perform this task, the pneumostoma is opened for about 20 to 30 seconds to expel the stale air. This action, which requires the contraction of three different muscle groups, contrasts with the complementary action, the entry of air into the lung, which apparently occurs by diffusion (Chase, 2002).

The motor pattern generating center involved in respiration would consist of three interneurons: one controls the initiation of the respiratory cycle and is located in the right dorsal pedal ganglion, another one expels air from the lung, because it acts on the motor neurons that innervate the muscles that open the pneumostoma and a third one completes the expulsion of air by closing the pneumostoma and is located in the dorsal visceral ganglion. Respiratory behavior is influenced by sensory afferents (Taylor & Lukoviak, 2000).

## Arthropods, with emphasis on crustaceans and insects

The SNVi in insects consists of a set of ganglia, mostly located towards the anterior region, which act on the buccal musculature and the anterior and middle portions of the digestive tract (Klowden, 2013). The various nervous regions vary greatly with the type of diet, with some structures being more developed in insects that feed on solid sources (Ayali, 2004). The VNSi consists of: an anterior stomatogastric system (SEG) or stomodeal system, the ventral odd nerve and the ventral sympathetic system or ventral caudal nervous system (Beutel et al., 2013; Wigglesworth, 1972).

In crustaceans and insects, ventilation is regulated by neuronal nuclei located in the thoracic ganglion, because this is where the central neurons that generate patterns sensitive to oxygen level are located. Sometimes this ganglion can reach the abdominal region. It should be noted that, although in panarthropods hypoxia stimulates ventilation, this is not the case in the genus *Limulus* and certain basal crustaceans, which reflect the initial situation, the response to hypoxia having arisen later within the phylum (Harrison, 2015).

In crustaceans, gill ventilation is carried out by the beating of the appendages, while aerial ventilation is carried out by the action of the scaphoid (Ruppert et al., 2004). In amphibians some can perform both types of respiration at the same time (Henry, 1994). Thus, in almost all cases crustaceans ventilate their gills thanks to the movement of more or less modified locomotor or mouth appendages (Harrison, 2015). In insects, gases progress into the tracheae by diffusion or, more generally, by diffusion and convection. These ventilatory movements, plus the opening and closing of the stigmata are jointly regulated by nerve centers of the CNS. The form of ventilation can be of three types, continuous, discontinuous or cyclic (Gefen & Mattehews, 2021) and, with few exceptions, it is carried out thanks to the action of intersegmental muscles located in the abdominal body wall, which they deform, thus producing a pumping action (Harrison & Wasserthal, 2013). This musculature, also found in crustaceans, has in them other functions and innervation, because it acts in posture or locomotion. Therefore, explaining how the change in the pattern of innervation occurred is a problem of utmost importance (Harrison, 2015). The regulation of respiration is effected by the action of muscles that actively close the two spiracles of each segment, which are in turn regulated by local neurons that innervate both openings at the same time. The opening of the spiracles is mainly passive. However, in cases where it is produced actively, it occurs because of the action of muscles that, unlike those of closure, are innervated independently on each side of the segment. A common point in both types of regulation is that inhibitory neurons may be involved (Harrison & Wasserthal, 2013).

## CONCLUSION

Aerial respiration was probably secondary to other adaptations such as osmotic regulation (van Straalen, 2021), and has arisen independently and followed multiple pathways in different phyla, as well as within phyla, which is evident from the multitude of times that snails, isopods or crabs invaded land and, in certain cases, secondarily returned to water. The situation of hexapods seems somewhat different, however, as they would not have independently emerged as many air-breathing or in lineages, despite which they represent the most hyperdiverse taxon. These events exemplify the plasticity and opportunism with which evolution operates, as tracheas or lungs have arisen independently and in parallel in related animals from the same or similar ancestral structures. In the case of the comparatively small number of aquatic insects, it also illustrates how morphological and/or functional constraints act.

On the other hand, the evolutionary relationships of the mechanisms of respiration regulation are not very clear, being an interesting point to clarify in the future, to what level they are shared among the different lineages that conquered the earth independently. That is, to deepen and clarify the evolutionary relationships between the neurons involved in the visceral control of respiration and other systems such as cardiac beating, peristalsis and other cyclic motor actions.

However, and in spite of the clear differences between respiratory organs of the same "type", which preclude seeing them as homologous, given certain similarities in the respiratory structures, as well as in those in charge of their control, it is perhaps not venturesome to think that they are examples of a special case of homology, deep homology. When compared with other visceral nervous systems, this seems to contrast sharply with, for example, the evolution of the enteric nervous system, which could be homologous (in the strict sense) in all animals. It is also curious that most of the animal biodiversity falls on a few bauplan adapted to aeroterrestrial life, although most of the phyla are found in the sea, but with a smaller total number of species. Nevertheless, the adaptive structures and mechanisms involved in aerial respiration are relatively similar and, in most cases, occurred in the same time period, even if they were independent colonizations of related lineages belonging to the same phylum or class. Reflecting on this, the study and understanding of the ecological and evolutionary processes of land conquest and, obviously, of the morphological transformations involved becomes more relevant. Among some of these mechanisms, the different pathways that led to symbiosis with microorganisms and that, according to the novel vision of the holobiont, would have allowed the conquest of the earth would be very attractive to clarify. Probably the interaction between microorganisms, enteric nervous system and brain would be an excellent model for comparison, especially if one thinks of the problem of the regulation of respiration and the evolution of visceral neurons.

To conclude, another interesting point to analyze in the future could be the in-depth comparison of the developmental programs of the tracheas and lungs of the different arthropod and gastropod taxa, assuming that at least in many of them, they are not homologous in a strict sense.

## CONFLICT OF INTEREST

The author declares that there are no conflicts of interest.

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