

Chapter 3

Tracheae in Spiders: Respiratory Organs for Special Functions

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3.1 Short Description of Respiratory Systems: Lungs or Tracheae

Many people do not know that spiders have a tracheal system. Even biologists often think that in spiders, lungs play the most important role in respiration. But nevertheless in most modern spiders a tracheal system has an important role, and it is still not exactly known why they have evolved tracheae and which purpose they are good for. This chapter wants to give a short overview over the morphology of tracheal systems in spiders and tries to give some explanations for evolution.

Spiders comprise a multifold equipment with respiratory organs. Basal spiders (Mesothelae, Mygalomorphae, and some Araneomorphae like Palaeocribellatae and some Austrochiloidea) possess two pairs of book lungs in the second and third opisthosomal (posterior) segments (see also Appendix, this volume). Most modern spiders (Araneomorphae), however, are bimodal breathers using a combination of lungs and tracheae (Weygoldt and Paulus 1979). Tracheae are invaginations of the body wall or originate from lungs or from other internal structures. Most often the second lung pair is reduced and replaced by tracheae. Moreover, the third opisthosomal segment is in many families stretched in the ventral part, whereby the tracheal spiracles lay at the end of the opisthosoma. This elongation happened as spiders developed their sophisticated webs which required special morphological adaptations. Mesothelae, in which original segmentation of the opisthosoma is still reflected by dorsal cuticular plates, possess the spinnerets directly behind the lung spiracles. Mygalomorph and araneomorph spiders, however, shifted the spinnerets at the end of the body to the tip of the opisthosoma. This is the best solution for web building, as far as possible distance from the legs, together with a high movability between pro- and opisthosoma because of the petiolus. As the spinnerets belong to

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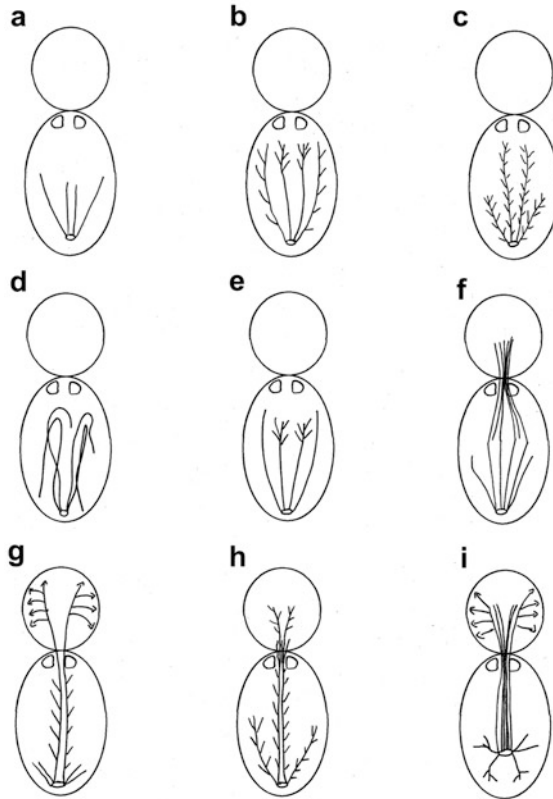


Fig. 3.1 (continued)

the opisthosomal segments 4 and 5, spiders elongated sternite 4 on the ventral side of the body. Most often also segment 3 is elongated thus repositioning the tracheal spiracle (Fig. 3.1).

Therefore in most modern spiders we have the situation with one pair of lungs in the second opisthosomal segment with an elongated third segment and one tracheal spiracle in this segment. Most often, the tracheal spiracles are single openings from which four tube-like tracheae originate. The outer two (primary or lateral) tracheae are remnants of lungs and can be connected to the lung extended lung atria. The inner two (secondary or median) tracheae, however, are new structures and are hollowed apodemes (entapophyses) elongated along the long axis of the spider (Purcell 1895; Lamy 1902; Purcell 1909, 1910; Levi 1967; Forster 1980; Ramirez 2000). True median tracheae are a synapomorphy of Entelegynae, as is the extreme posterior displacement and narrowing of the tracheal spiracle (Ramirez 2000).

In haplogyne spiders, tracheal spiracles are situated behind lung spiracles (e.g., Dysderoidea) (Ramirez 2000). In some species of this group also the first pair of respiratory organs is replaced by tracheae (e.g., Caponiidae, Telemidae). These are the so-called “sieve tracheae”. They look like a bundle of tubes, are probably

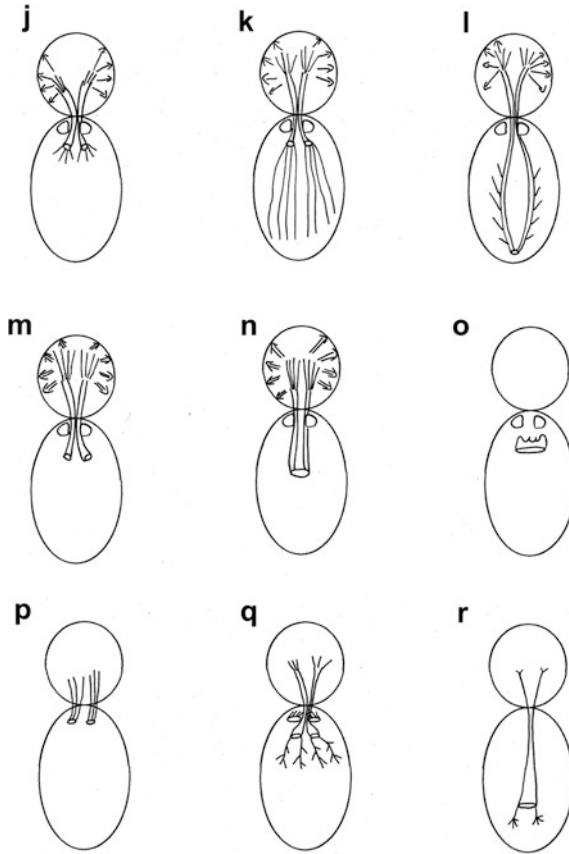


Fig. 3.1 Tracheae in different spider families. Bodies are schematized as two compartments. Lungs are given as simple *circles* in the frontal part of the opisthosoma. Legs are not given. (a) Lycosidae, Agelenidae, (b) Philodromidae, (c) Thomisidae, (d) Gnaphosidae, (e) Linyphiidae (Linyphiinae), (f) Linyphiidae (Erigoninae), (g) Uloboridae, (h) Salticidae, (i) Anyphaenidae, (j) Dysderidae, (k) Segestriidae, (l) Dictynidae, (m) *Argyroneta aquatica*, (n) Hahniidae, (o) Filistatidae, (p) Symphytognatidae, (q) Caponiidae, (r) Oonopidae

rounded derivatives of lung lamellae and occur exclusively in the second opisthosoma segment. In Oonopidae lungs are mainly reduced and tracheae take over the entire respiratory function. In other species, tracheae are completely lacking (e.g., Tetrablemmidae, Pholcidae, Diguetaeidae, Plectreuridae and Sicariidae) and the one pair of lungs is the only respiratory organ.

Also within the entelegyne spiders the first lung pair may be replaced by tube tracheae: in Symphognathidae spiders, the first lung pair may be replaced by tube tracheae while the third segment lacks respiratory organs. In some species, primary and secondary tracheae remain as tubes restricted to the opisthosoma. In others, however, highly branched tracheae also enter the prosoma via the petiolus and may penetrate the nervous system, muscles, or gut (Kästner 1929; Millot 1949; Bromhall

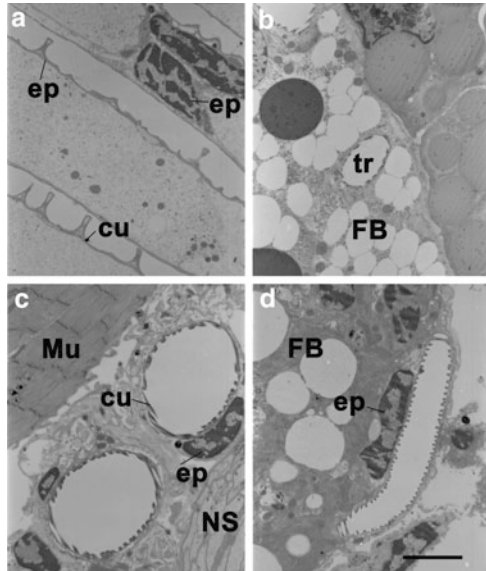
1987a, b; Schmitz and Perry 2000, 2001, 2002), examples include the water spider (*Argyroneta aquatica*) (Cybaeidae), hackled orb-weavers (Uloboridae), crab spiders (Thomisidae), tube dwelling spiders (Segestriidae), sheetweb weavers (Linyphiidae), jumping spiders (Salticidae) and woodlouse hunters (Dysderidae) (Blest 1976; Millidge 1986; Bromhall 1987a, b) (Fig. 3.1). In the families Dysderidae and Segestriidae and in *Argyroneta aquatica*, tracheae constitute the main respiratory system while lungs are poorly developed (Braun 1931). This is probably the reason why *Dysdera* sp. lost its hemocyanin completely (Burmester 2013).

In other families, e.g., wolf spiders (Lycosidae) and funnel web spiders (Agelenidae) lungs are the main respiratory organs, and in yet others lungs and tracheae complement one another. For example, tracheae are responsible for 25–30 % of total diffusing capacity of a jumping spider (Schmitz and Perry 2001). In hackled orb-weavers (Uloboridae) tracheae are less developed when lungs are well developed and vice versa. In Uloboridae species that use their legs actively for net monitoring an extensive tracheal system reaches into the legs. Thus, spider respiratory systems are highly versatile in meeting the O₂ demands of locomotion (Opell 1979, 1987, 1989, 1990, 1998; Opell and Konur 1992).

Lung lamellae pile up like the sheets of a book in which layers filled with haemolymph alternate with layers containing air. Epidermis lines the inner surface of the lung facing the haemolymph. Pillar cells prevent spaces from collapsing. The air space is lined with cuticle. Cuticular struts connect the dorsal and ventral part of the lamella over about one third of the lung area and spines also stabilize the air space. Ultrastructure of spider lungs has been measured in the theraphosid *Aphonopelma hentzi* (sub *Eurypelma californica*), in house spiders (*Tegenaria* sp.) and in wolf and jumping spiders. In house spiders, the diffusion barrier is twice as thick as in wolf and jumping spiders, resulting in a much lower morphological diffusing capacity (4–9 $\mu\text{l min}^{-1} \text{g}^{-1} \text{kPa}^{-1}$) than in the other two species (12–16 $\mu\text{l min}^{-1} \text{g}^{-1} \text{kPa}^{-1}$) (Strazny and Perry 1984; Schmitz and Perry 2001, 2002). Thus the flexibility of lung morphometrics in different spiders becomes clear. In *Aphonopelma hentzi*, epidermal and cuticular layers have similar thickness as in wolf spiders and jumping spiders (*Pardosa lugubris* and *Salticus scenicus*, each 0.05–0.5 μm thick) (Schmitz and Perry 2000, 2002). But dimensions of air (5–7 μm) and haemolymph spaces (60–70 μm) are much larger in *Aphonopelma hentzi* than in araneomorph spiders and the linear lung dimensions (length, width, interlamellar width) scale to the 0.2–0.35 power of body mass, i.e., a four- to eightfold increase in lung size over a 900-fold body size range (Moore 1976; Reisinger et al. 1990, 1991). Dimensions are 10–20 μm for the haemolymph space and 1–2 μm for the air space in the wolf spider *Pardosa lugubris* and the jumping spider *Salticus scenicus*, both about 20 mg in body mass (Schmitz and Perry 2000, 2002).

Ultrastructure of tracheae consists of an epidermal outer layer and a cuticular inner layer that builds hoop or spiral thickenings (taenidia) for stabilization (Fig. 3.2). Therefore spider tracheae look very similar to insect tracheae. Both cuticle and epidermis constitute about the same proportion of the tracheal walls: the walls of the smallest tracheae have about the same thickness as the lungs (Schmitz and Perry 2001, 2002).

Fig. 3.2 Examples of lungs (a) and tracheae (b–d) in *Salticus scenicus*, a salticid spider. In (b) and (d) tracheae (tr) can be found in the fat body (FB) while in (c) they are situated between muscles (Mu) and nervous system (NS). ep epidermis, cu cuticle



3.2 Functional Principles and the Evolution of Respiratory Organs

All lungs are so-called book lungs and they are diffusion lungs, convection is done by the haemolymph alone and the spiracles are diffusion regulators (Paul et al. 1987). Tracheae in spiders, however, can function as tracheal lungs or use terminal diffusion. Transitions between the two types are blurred and even within one animal, tracheae may function in the two general kinds. As tracheal lungs, their entire surface may be used as gas exchanger with haemocyanin within the haemolymph. Therefore, they considerably increase the effectiveness of respiration, last but not least because gas exchange is no longer restricted to the second and third opisthosomal segment. In terminal diffusion, proximal tracheae branches are grouped into bundles that run parallel through the body to create a thick diffusion barrier. O_2 loss is limited to the outer surface of those bundles. The terminal branches (tracheoles) reach into the epithelia of organs in which gas exchange takes place. Therefore the gas exchange is restricted to several places in the body.

Terrestrialization of arachnids especially influenced the evolution of the respiratory organs. Recent studies investigated the ultrastructure of lungs in arachnids (Scholtz and Kamenz 2006). It was concluded that arachnid lungs developed only once and therefore a common arachnid aquatic ancestor, at least for the lung breathers must be postulated. These ancestors might be the scorpions that in turn possibly stem from eurypterid-like ancestors (Weygoldt 1998). In this scenario, lungs were the first respiratory organs for air breathing and they have to be lost before tracheae could develop. Spiders, however, may have evolved from trigonotarbid-like ancestors, which were contemporaneous with aquatic scorpions

in the Devonian. First fossil records of terrestrial Mesothelae exist from late Carboniferous to early Permian around 295 million years ago (Selden 1996). Also other tracheal breathers might have evolved separately thus indicating that tracheae developed independently in all arachnid groups. One hint supporting this hypothesis is that number and position of tracheal spiracles being different in each group. First fossil records of tracheate arachnids are the harvestmen (Opiliones) appearing in the early Devonian 410 MYA, without any hint that this arachnid group stands in any evolutionary line with the lung breathers (Dunlop et al. 2003).

3.3 Potential Reasons to Develop Tracheal Systems

In the literature four hypotheses for the evolution of spider tracheae can be found (Ellis 1944; Levi 1967, 1976; Anderson and Prestwich 1975):

1. The first theory indicates that tracheae are an adaptation for the reduction of water loss. During evolution, spiders reduced body size and therefore are threatened by evaporation in low humidities. Unlike insects, spiders possess a relatively thin body cuticle and are threatened by evaporation in arid habitats. This hypothesis may not explain all tracheated spiders, as not all tracheal breathers are active during the day or in full sun. For example, the six-eyed spider *Dysdera erythrina* has highly developed tracheae and reduced lungs but is active only at dawn and night and rests under leaves or stones during the day.
2. The second theory indicates that spiders developed tracheae in response to increased local O₂ demand. Tracheae supply organs with high O₂ needs relative to surrounding organs. Two examples support this hypothesis. In jumping spiders that rely mainly on their eyes for prey capture and protection against predation, tracheae supply predominantly the prosomal nervous system. It was hypothesized that tracheae supply the highly energy consuming signal processing of the eyes by allowing a constant aerobic metabolism (Schmitz 2004, 2005). Orb-weavers (Uloboridae) actively monitor their nets with the third leg pair during prey capture, tracheal supply to the muscles of the third leg is better than that to the other legs (Opell 1987, 1990; Opell and Konur 1992).
3. Moreover, higher mass specific O₂ demands occur, for example, in free ranging hunters. Literature partly supports this hypothesis as jumping spiders have higher metabolic rates and better aerobic capabilities than spiders with a less developed tracheal system, e.g., wolf spiders (Prestwich 1983a, b; Schmitz 2004, 2005). However, also spiders breathing mainly with lungs may have increased metabolic rates compared to the average metabolism in spiders, e.g., araneid spiders that develop over only 1 year. Free ranging hunters such as wolf spiders and jumping spiders with different respiratory configurations may have similar metabolic rates, which are greater than in web hunters. Moreover, spiders possess haemocyanin, which is most effective with lung breathing. Highly effective tracheae serving increased metabolic rates would need a modified use of haemocyanin.

Comparison among tracheated spiders revealed a higher O_2 affinity and lower haemocyanin concentration in spiders with a well-developed tracheal system (Schmitz, unpublished). This point needs further investigation but indicates that haemocyanin is used for O_2 storage in tracheated spiders, even if it is better suited for O_2 transport and release at the tissues in non-tracheated spiders.

4. The fourth theory is related to the hydraulic type of leg extension in spiders (see Kropf 2013). This process is accomplished by high pressure in the prosoma generated by muscle contraction and supported by the separation of the prosoma from the opisthosoma. Therefore, breathing with book lungs alone will cause an O_2 lack in the prosoma, but tracheae reaching into the prosoma would solve that problem. As the tracheae are situated in the prosoma and in some species also in the legs, the O_2 support for the muscles is guaranteed. This hypothesis has been questioned because most spiders run in short spurts, which allows haemolymph exchange between pro- and opisthosoma during resting phases. Therefore, separation of those two body compartments is not complete. Moreover, not all walking or running spiders possess tracheae in the prosoma (e.g., wolf spiders) and vice versa not all spiders with prosomal tracheae are free ranging runners (e.g., crab spiders, Thomisidae).

3.4 Having a Double Respiratory System: Advantage or Disadvantage?

Resting metabolic rates of spiders are 50–80 % of that expected in poikilotherms (Anderson 1970, 1996; Greenstone and Bennett 1980; Anderson and Prestwich 1982) according to Hemmingsen's equation $V_{O_2} = 0.82 M^{0.75}$ (V_{O_2} in $\mu\text{l h}^{-1}$ and M in mg) (Hemmingsen 1960). This is because spiders are 'sit-and-wait' predators that have irregular access to prey and therefore a great ability to starvation accompanied with a reduction of metabolism (Anderson 1974), low energy needs in prey capture because of venom use and a high anaerobic capacity (Prestwich 1983a, b). In general, resting metabolic rates correlate with life style. Spiders that live longer or use webs for prey capture have lower metabolic rates than prey-stalking spiders or species that complete their life cycle within 1 year; the latter groups include araneid or theridiid spiders that have similar or higher metabolic rates than many poikilotherms (Anderson and Prestwich 1980; Anderson 1994). Bimodal breathers, e.g., jumping spiders, have higher resting rates than pure lung breathers, e.g., mygalomorph spiders (Anderson 1970). In spiders that lack tracheae or have poorly developed tracheae, e.g., mygalomorph and wolf spiders, resting rate is proportional to the respiratory surface area (Anderson 1970; Anderson and Prestwich 1982; Prestwich 1983a, b).

During food deprivation, metabolism is low but aerobic. During low activity, e.g. web building or egg production, the aerobic–anaerobic partition depends on ATP needs, species-specific respiratory and muscle capacities. During short phases

of high activity, anaerobic metabolism predominates. D-Lactate is the major anaerobic by-product, and the legs and prosoma are the main site of lactate accumulation (Prestwich 1983a, b). After anaerobic activity, O₂ debt is repaid during recovery. Most spiders are completely exhausted after 1–2 min of maximum activity, e.g. after being chased. The length of recovery depends on the duration of anaerobiosis and body mass. Complete lactate removal requires 30–45 min in small spiders and several hours in large species, e.g., mygalomorph spiders. Even free hunting species (such as wolf spiders or jumping spiders) use a sit-and-wait strategy and are dependent on anaerobic capacities for running in short spurts or jumping after slowly sneaking up on the prey. Such behaviour does not require prolonged high metabolic rates. In *Cupiennius salei*, mitochondria comprise only 0.1 % of leg muscle mass (Linzen and Gallowitz 1975) compared to 10 % in mammalian locomotive muscle. Therefore, anaerobic metabolism is the standard strategy of a spider and this seems to be not generally changed when animals developed tracheae.

Therefore, one of the most interesting questions regarding the respiratory biology of spiders is why these animals reduced the existing and well functioning lungs and developed tracheae. This evokes a conflict in gas exchange as lungs are designed to work together with the haemolymph and the haemocyanin herein and tracheae are most effective when used for terminal diffusion. In four- and two-lunged species, peak O₂ uptake occurs at submaximal activities that require lower haemolymph pressures and permit continuous circulation and O₂ exchange (Prestwich 1983a, b). Experiments that measured maximum O₂ uptake of spiders running on a treadmill show an aerobic scope of 3–10 in most species, but it can reach 17.8 times (McQueen 1980; Culik and McQueen 1985). Running increases the aerobic metabolic rate to its maximum and ATP needs are complemented by anaerobic pathways. At high or exhaustive speeds this leads to a considerable O₂ debt. This suggests that tracheae may have evolved in conjunction with higher aerobic needs (Prestwich 1988; Schmitz 2005). As already stated, the anaerobic partition in running not only depends on the velocity and the equipment with respiratory organs but also depends on the aerobic capabilities of the muscle tissue. For jumping spiders it was shown that tracheae support aerobic metabolism at highly intense activity (Prestwich 1988; Schmitz 2005).

Spiders have an open circulatory system without capillaries in which at least in the legs gas exchange has to take place along the open portion of the circulatory system. In four-lunged spiders, anterior and posterior circulation is separated, thus that haemolymph from the prosoma passes only through the anterior lung pair and haemolymph from the opisthosoma passes through the posterior lungs (Paul et al. 1989; Wirkner and Huckstorf 2013). Moreover prosomal perfusion is interrupted during fast locomotion, most likely caused by a muscular valve at the anterior end of the pedicel (Paul and Bihlmayer 1995). It was also measured in *Aphonopelma hentzi* that in resting animals the arterial O₂ pressure (P_{aO_2}) is 3.7 kPa, stays constant during walking, increases during the recovery phase and is maximum at the end of this phase (about 9.8 kPa) (Angersbach 1978). The crucial variable for O₂ transport in the haemolymph is the arterious-venous P_{CO_2} difference (P_{avO_2}). During rest,

spiracles are nearly closed and the P_{avO_2} is small. During recovery after an exhaustive run, spiracles are open and the P_{avO_2} increases because of an increase in P_{aO_2} . Together with an increase in heart rate, this results in a more intensive use of haemocyanin in respiration. In araneomorph spiders the correlation of heart rates and equipment with tracheae was tested. Spiders with prosomal tracheae have significantly lower maximum heart rates than spiders with tracheae limited to the opisthosoma. Return to normal heart rates in recovery phases after running are faster in spiders with prosomal tracheae (Bromhall 1987a, b). Other authors correlated the heart rate with life style and not with tracheal supply to the prosoma. In this study resting heart rates of spiders were found to be primarily a function of body size and can be used as a measure for metabolism. The less active an animal is, the lower is the resting heart rate, thus reflecting fundamental differences in foraging strategies among spiders. For example spitting spiders (Scytodidae) and brown spiders (Sicariidae) (both with low activity ranges) do not have lower metabolic rates but lower heart rates compared with salticid spiders which are more active for hunting prey (Carrel and Heathcote 1976; Greenstone and Bennett 1980; Carrel 1987). Sometimes both types of interpretation overlap as it is the case in salticid spiders that are more active, have prosomal tracheae and have a higher heart rate than other species.

3.5 Conclusions

Tracheae enable spiders to become more flexible in their respiratory behaviour. They can breathe more adapted to their individual needs even if this differs among all species. Spiders can use tracheae as a general increase in respiratory surface, but as most of them have lost their second lung pair this has not to be the main reason for developing tracheae. More convincing is the idea of using tracheae for local oxygen demands. Every family, or even species, can use the tracheae in an individual way. Some use them for delivering O_2 to their nervous system, e.g., jumping spiders, others to deliver O_2 to their legs, e.g., Uloboridae. So a tracheal system is a very flexible structure and so it is used in spiders.

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