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On the Evolution of Tracheae in Arachnids

Herbert W. Levi
and
William M. Kirber
Museum of Comparative Zoology,
Harvard University,
Cambridge, Mass. 02138, U.S.A.

Tracheae, respiratory tubes that carry air directly to tissues, have evolved independently several times in arachnids. A similar structure has evolved in certain terrestrial crustaceans, the isopods (woodlice). Petrunkevitch (1933) considered that the absence of booklungs, the more usual arachnid respiratory organs, and their replacement by tracheae, was a significant character for grouping families of spiders, and on the basis of this character erected the suborder Apneumonomorphae. Dipneumonomorphae, two-lunged spiders, he considered a less homogeneous group, including spiders with varied development of the tracheal system. However, both Forster (1959) and Levi (1967) have shown that the replacement of booklungs by tracheae is related more to habits than to phylogeny. It is a characteristic of the more active arachnids. Furthermore, Anderson (1970) has shown that spiders with high metabolic rates possess tracheae. It would seem that tracheae are more efficient than booklungs in supplying oxygen. An interesting exception are wolf spiders (Lycosidae) which have high metabolic rates but lack efficient tracheae (Anderson, 1970). Lycosid spiders are, however, limited in their activity by being nocturnal or confined to relatively moist areas.

The most elaborate tracheal systems are found in active desert animals such as wind-scorpions (solifugids) and also in small arachnids with body surface areas proportionately greater than volume (Levi, 1967). Possibly tracheae are an adaptation for the reduction of water loss, a matter of major importance for terrestrial invertebrates. But then, why should the aquatic spider, *Argyroneta aquatica,* require an elaborate tracheal system (Crome, 1966)? A completely different explanation for the evolution and adaptive significance of tracheae must be devised.

It has been shown (Cloudsley-Thompson, 1957) that the rapid fatigue observable in some spiders is due to a lack of oxygen. Also Stewart and Martin (1974) and Kirber (1974) showed that due to the hydraulic system of leg extension, activity in spiders may be accompanied by a blood pressure differential between the leg-bearing prosoma and the opisthosoma, containing the localized booklungs and the heart. This pressure differential may be sufficient to effectively block circulation of oxygenated blood from the opisthosoma to the prosoma, resulting in fatigue (Wilson and Bullock, 1973; Kirber, 1974). It would be of selective advantage to a spider to have a direct supply of oxygen to its prosoma, independent of the circulation of hydraulic fluids. A tracheal system could provide this supply, while booklungs and blood carrying oxygen could not. Active wolf spiders lack an efficient tracheal system and as far as we know they run in short spurts. Measurements of running endurance in spiders with and without tracheae might constitute a good test for this hypothesis. But for many arachnids continuous activity may not be of survival value and booklungs remain.

While minimized water loss, increased efficiency of oxygen uptake and delivery, and better supply of oxygen during activity of the hydraulic system, separately or combined, would be of sufficient adaptive value to explain the evolution of the tracheal system in arachnids, other advantages suggest themselves as well. Tracheae permit smaller body size, as they take less space than do localized booklungs. And, the tracheal system may be important in determining the centre of gravity in the aquatic spider, *Argyroneta aquatica.* Of course these are not alternative adaptations of tracheal systems; the system might be an adaptation to several factors.

Wigglesworth (1966, p. 23) has shown for insects that during growth and moulting, new tracheae and tracheoles grow out from the existing tracheal system, and the outgrowths are most abundant in regions deficient in oxygen supply. If this probably inherited characteristic is the case in arachnids also, then perhaps the tracheal system is in part a direct result of lack of oxygen in the prosoma, rather than a selected-for improvement. Experiments on arthropods' tissue cultures at different oxygen concentrations might provide a clue to the evolution of tracheae.

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Nomenclatural Note on *Argiope* Audouin

Opinion 1038 of the International Commission on Zoological Nomenclature ruled unanimously to validate the generic name *Argiope* Audouin, 1826 and to place it in the Official List of Generic Names in Zoology. The name *Argyope* has been placed, as an incorrect spelling, on the Official Index of Rejected and Invalid Generic Names in Zoology (*Bull.zool. Nom.* 32(2): 105-109, June 1975). The case was submitted to the Office of the Secretary of the Commission in March 1967.

H. W. Levi