



# How to stay on mummy's back: Morphological and functional changes of the pretarsus in arachnid postembryonic stages



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## ABSTRACT

A specific type of maternal care occurs in several groups of Arachnida: mothers carry their offspring on their back (pulli-carrying behaviour). In scorpions, whip scorpions and whip spiders it is the prenympal stage that settles on the mother. The prenympal is not yet fully developed for a free life and very limited in its mobility, but its feet are equipped with special adhesive organs (arolia) that become lost at the nymphal stage. Here we study the morphology, ultrastructure and mechanical function of the arolia. In scorpions (Scorpiones) the contact area between arolia and substrate and thus adhesion of the pad is controlled by the antagonistic work of hydrostatic pressure and muscular retraction. Arolia of whip scorpions (Thelyphonida) do not require muscular action for strong attachment. Arrays of long, branching fibres in the mesocuticle lead to high compliancy of the pad. In whip spiders (Amblypygi) the prenympal pretarsus is already equipped with sclerites and claws. Its arolium is retained in nymphs and adults in some taxa, but acquires a more complex structure. These results contribute to our knowledge on the postembryonic development of arachnids and to the understanding of attachment pad evolution among arthropods. Some of the described developmental, structural, and mechanical phenomena are not known from other animals and might be of potential interest for further biomimetic developments.

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## 1. Introduction

From hatching until maturity the growth and development of arthropods is not continuous but subdivided by several moulting events. These can be accompanied by a radical change in morphology and ecology, as during the metamorphosis in holometabolous insects and in some mites (Andre and Jocqué, 1986; Minelli et al., 2006). In most arachnids, however, morphological changes between two instars (stages between two moults) appear to be minimal. Yet, postembryonic development in Arachnida can be sub-divided in three different phases (Canard and Stockmann, 1993): 1. The postembryo is not fully developed for a free life, because cuticular structures, such as the mouthparts or sensory structures, are not fully developed. It feeds from yolk and its locomotion capabilities are rudimentary. This stage usually contains three instars: the immobile first and the second postembryo and the prenympal, also called pulli (singular: pullus) (Pavlovsky, 1924), larva (Millot and Vachon, 1949), pre- or pro-juvenile (Lourenço, 2000). 2. The following instars (nymphs) are free living, actively

feeding and usually of a rather similar morphology like the adults. 3. The adult stage is reached with sexual maturity (usually accompanied by the full development of copulatory organs). In some groups of Arachnida adults continue to grow and moult (female mygalomorph spiders, both sexes of Amblypygi (Weygoldt, 2000)).

As both the developing eggs and the (barely movable) post-embryonic stages are at a high risk of predation and parasitism, parental care is widespread among arachnids. Many spiders, harvestmen (males of some Laniatores) and solifuges guard and defend their clutch and young offspring. In some spiders, the mother even self sacrifices and is consumed by its offspring (matryphagy), such as in Eresidae (Schneider, 2002), Amaurobiidae (Kim and Horel, 1998) and Eutichuridae (Toyama, 2001). Mothers of scorpions (Scorpiones, Fig. 1A), whip scorpions (Uropygi: Thelyphonida, Fig. 1B, and Schizomida, Fig. 1C), whip spiders (Amblypygi, Fig. 1D) and wolf spiders (Araneae: Lycosidae, Fig. 1F) carry their eggs with them and the hatching offspring on the opisthosomal back. This behaviour is called *pulli-carrying* and the stage that attaches to its mother is often called the *pullus* (Canard and Stockmann, 1993).

Scorpions are viviparous: their eggs as well as the first and second postembryo develop within the genital tract of the mother (Lourenço, 2000). 'Birth' occurs during the moult into the

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**Fig. 1.** Maternal care in arachnids. Species of the Scorpiones (A, *Liocheles australasiae* Fabricius 1775), Thelyphonida (B, *Typopeltis crucifer* Pocock 1894), Schizomida (C, *Zomus bagnallii* Jackson 1908) and Amblypygi (D, *Phrynos marginemaculatus* C.L. Koch 1840) carry prenympths of their offspring on the opisthosoma. In the whip-spider *Sarax* sp. also the protonymphs stay on the mother occasionally (E). So-called pulli-carrying behaviour is also found among lycosid spiders (F, *Hogna radiata* Latreille 1817), with the difference, that here the prenympths stay in the egg sac and settle on the back of their mother as protonymphs. Photographs A., B. and E. by Siegfried Huber, C. by Heiko Bellmann with the kind permission of Tobias Bellmann, D. by Michael Seiter and F. by Arno Grabolle, with kind permission.

prenymp instar, which then actively climbs on the back of the mother. The protonymph leaves the mother's back, but is still closely associated with her. It feeds from the prey captured by the mother (Kästner, 1940).

In whip-scorpions and whip-spiders the carried eggs are attached to the ventral opisthosoma. In whip-scorpions the eggs are surrounded and clotted by a jellylike substance, forming two clusters (pers. obs.). In whip-spiders the eggs are surrounded by a filamentous viscous substance that hardens and forms a protective shell ('egg sac') (Weygoldt, 2000). The prenymp emerges from the egg sac and climbs onto the dorsal opisthosoma of its mother. After the moult into the protonymph it leaves the mother. However, in single cases the protonymph stays on the mother for a longer period of time, as reported for the whip scorpion *Thelyphonus* cf. *caudatus* (Weygoldt and Huber, 2013) and the whip spider *Sarax* spec. (Fig. 1E, pers. obs.).

While scorpions and whip scorpions usually stay rather inactive within a burrow during this period of maternal care, whip spiders and spiders maintain their free living lifestyle. In lycosid and trechaleid spiders the eggs develop in a silken cocoon that is attached to the anterior spinnerets by the means of glue-like piriform silk (Townley and Tillinghast, 2003). The post-embryo stays within this cocoon and it is the protonymph that climbs onto the back of its mother (Fig. 1F). In Trechaleidae and some Lycosidae, the hatching protonymphs (pulli) stay on the cocoon for some time, until they disperse (Dolejš, 2013). This may be an ancestral state of this brood care behaviour, from which pulli-carrying may have evolved, although the author states, that it is an adaptation to humid environments. Thus, pulli-carrying behaviour in wolf spiders differs fundamentally by its time point and mechanism to that of scorpions, whip scorpions and whip spiders.

In pseudoscorpions the mother also carries the first instars, but this mechanism is significantly different from pulli-carrying behaviour: The postembryo does not attach actively, but is embedded into a secretion pad ('brood sac') attached to the ventral side of the opisthosoma (Weygoldt, 1968). During this stage the postembryo absorbs nutrients from the brood sac (Weygoldt, 1968).

Pulli-carrying behaviour includes the demand of active, strong and durable attachment in the prenymp, in high contrast to the subsequent free living instars, which must be able to attach and detach quickly and to environmental substrates. Therefore there should be a radical change in foot morphology, including the development of special prenymp attachment organs. The scorpion prenymp lacks tarsal claws, but instead bears cushion-like adhesive pads on its feet, called *arolia* (sing.: *arolium*) (Millot and Vachon, 1949). The thelyphonid prenymp is still in a very embryo-like state and bears large 'suction discs' on its feet (Kästner, 1941). The foot of the amblypygid prenymp is equipped with two tarsal claws and a lobe-like pad, called the *pulvillus*, which is either retained ('Pulvillata') or becomes lost ('Apulvillata') in the subsequent instars (Quintero, 1975). In contrast, the riding protonymphs of wolf spiders do not possess adhesive pads and attach by interlocking their claws and spun silk with the hook-like microstructures of specialized opisthosomal setae of the mother: if the mother is shaved, the nymphs are unable to settle on their mother and stay on the egg sac (Rovner et al., 1973). Beside these scattered observations nothing is known about the morphology, function and mechanics of prenymp attachment organs and the change in pretarsal structures in the protonymph. This work aims to fill this gap by providing morphological, ultrastructural, behavioural and biomechanical data on prenympths of scorpions, whip scorpions and whip spiders.

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