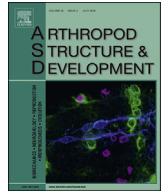




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## Review article

## Scorpions pectines – Idiosyncratic chemo- and mechanosensory organs

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## ABSTRACT

Scorpions possess specialised chemosensory appendages, the pectines. These comb-shaped limbs are located ventrally behind the walking legs. Like the antennae of mandibulate arthropods, they also serve a mechanosensory function. However, more than 90% of the sometimes well above 100,000 sensory neurons projecting from a pectine to the central nervous system are chemosensory. There are two primary projection neuropils. The posterior one, immediately adjacent to the pectine nerve entrance, has an intriguing substructure reminiscent of the olfactory glomeruli observed in the primary chemosensory neuropils of many arthropods and indeed of most bilaterian animals. There are further similarities, particularly to the antennal lobes of mandibulate arthropods, including dense innervation by a relatively small number of putative serotonergic interneurons and the presence of GABA immunoreactivity, indicative of inhibitory interactions. Scorpion idiosyncrasies include the flattened shape and broad size range of the glomerulus-like neuropil compartments. Further, these compartments are often not clearly delimited and form layers in the neuropil that are arranged like onion peels.

In summary, the pectine appendages of scorpions and their central nervous projections appear as promising study subjects, particularly regarding comparative examination of chemosensory representation and processing strategies. The possibility of combined, rather than discrete, representations of chemo- and mechanosensory inputs should merit further study.

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## 1. Introduction

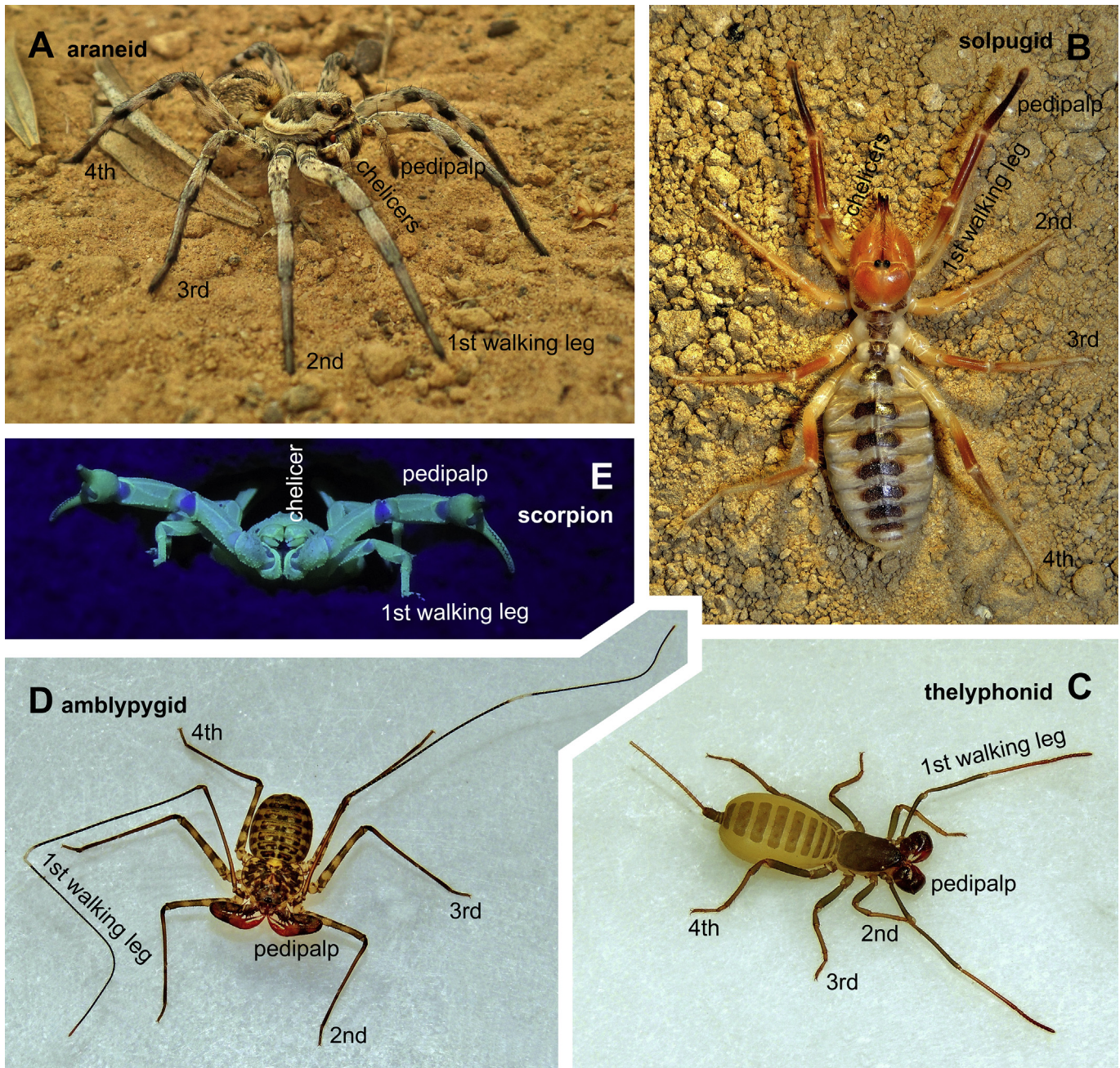
Scorpion pectines are mechano- and primarily chemosensory appendages (Brownell, 1988a,b; Hjelle, 1990; Polis, 1990; Gaffin and Brownell, 1997a) (Fig. 2). They are comb-shaped and in this way reminiscent of the antennae observed in many hexapods and crustaceans. The pectines are not located on the head, however, but ventrally behind the walking legs, and they are used for both, probing the substrate below and sensing airborne odorants (Alexander, 1959; Abushama, 1964; Hoffmann, 1964; Krapf, 1986; Gaffin and Brownell, 1992; Gaffin et al., 1992). Axons of the pectine sensilla on a pectine project to two neuropils in the central nervous system. The large posterior pectine neuropil has an

intriguing substructure (Brownell, 1991, 1998; Wolf, 2008) (Fig. 4) reminiscent of the glomerular organisation observed in the primary chemosensory neuropils not only of many other arthropods ((Loesel et al., 2013); crustaceans: (Schmidt, 2016); hexapods: (Galizia and Sachse, 2010); chilopods: (Sombke et al., 2011, 2012)) but of most bilaterian animals (Hildebrand and Shepherd, 1997; Eisthen, 2002; Chase and Tolloczko, 2004). Glomeruli are more or less spherical, dense synaptic neuropils that are delineated from the surrounding tissue and usually occur in larger groups. Boundaries between glomeruli are typically formed by glia, and the surrounding tissue consists of tracts formed by axons of the chemosensory afferents and of interneuron branches involved in further signal processing (Christensen and Hildebrand, 1987; Anton and Homberg, 1999; Strausfeld and Hildebrand, 1999; Homberg, 2005; Schmidt and Mellon, 2010). Further similarities between posterior pectine neuropil and olfactory neuropils of mandibulate arthropods concern innervation by putative serotonergic interneurons (Wolf and Harzsch, 2012) and the apparent presence of inhibitory neuronal interactions within the primary neuropil (Wolf,

Abbreviation: GABA, gamma-amino butyric acid.

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**Fig. 1.** Chelicerata and their appendages used for chemosensation. (A) Araneidae, *Alopecosa* spider (Tunisian species, probably *Alopecosa tunetana*); body length from chelicers to abdomen tip 24 mm. (B) Solifugae, *Galeodes arabs*; body length from chelicers to abdomen tip 43 mm. (C) Thelyphonida, *Typopeltis* spec.; body length from chelicers to abdomen tip (without “whip”) 21 mm. (D) Amblypygi, *Damon diadema*; larva, body length from chelicers to abdomen tip 16 mm. (E) Scorpiones, *Buthus occitanus*, fluorescence under UV illumination; body length from chelicers to stinger 61 mm. Note labelling of appendages (chelicers, pedipalps, walking legs, 1st to 4th).

2008). A second, smaller anterior pectine neuropil lacks conspicuous substructures.

Scorpion pectines and their neuropils thus merit comparison to insect and malacostracan antennae and their chemosensory neuropils (Wolf, 2016). The pectine appendages are located on the second metasoma segment and thus project to the ventral nerve cord, rather than to (supraesophageal) brain neuromeres as do the antennae of Mandibulata. This makes the similarities in central nervous organisation named above intriguing, and it begs the question of whether these similarities are due to convergence for functional reasons, or due to glomerular organisation being an

ancestral feature of primary chemosensory neuropils supplied by the arthropod appendage, or both. Finally, there are also characteristic differences between scorpion and Mandibulata primary chemosensory neuropils, including the arrangement and usually lobular rather than glomerular shape of the neuropil substructures, and their large size spectrum. This holds true despite exceptions to the (strictly) glomerular type of chemosensory projections, for instance, in archaeognaths and chilopods (Strausfeld and Reinman, 2009; Mißbach et al., 2011; Sombke et al., 2012). Structure and function of scorpion pectines shall be reviewed with the above aspects in mind, and relevant topics for future study shall be indicated.

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