A toxinological argument in favour of the close relationship of the Vespidae and the Scoliidae (Hymenoptera)

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Abstract: It is generally assumed that the superfamily of Scolioidea is a polyphyletic group, and that one of the included families, viz. the Scoliidae, is closely related to the Vespidae. This view is supported by the findings of a special group of polypeptides, the so-called wasp kinins, in the venoms of both scoliid and vespid wasps, and their absence in the venoms of other aculeate Hymenoptera.

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Solitary wasp venoms, as is the case with so many venoms and toxins of animal origin, act on nervous systems. Contrary to the typical killing action of most of the animal venoms, including social wasp venoms, the solitary wasp venoms seem to be selected to paralyse the prey or change the prey's behaviour. Although only a few venoms have been studied in detail (Piek & Spanjer, 1986), it can be said with certainty that wasp venoms vary enormously in composition and in pharmacological action.

Studies in the last decennia reveal that venoms of Hymenoptera contain mixtures of agonists and antagonists for synaptic transmission, and solitary wasps make no exception to this rule. The limited information about the presence of agonists for synaptic transmission processes is presented in table 1. It shows a scattered distribution of some of the venom components among the different groups of the Hymenoptera, and the question arises whether the distribution of these agonists could contribute to the classification of aculeate Hymenoptera.

In his "Phylogeny and Classification of Aculeate Hymenoptera" Brothers (1975) based the association of the scoliid and vespid wasps on a number of characters, including the reduced pronotum (which is not freely movable against the mesothorax, but tightly appressed to it) as well as the reniform eyes, the dorsally produced clypeus, the sunken prosternum, and the membraneous pterostigma. Both of these taxa also possess highly muscular and similarly modified venom reservoirs with transversely running muscle fibres (Bordas, 1908; Pawlowsky, 1914; Robertson, 1968; for a review see Van Marle & Piek, 1986). The above combination of characters does not include the stinging behaviour, which is a very important and characteristic phenomenon within the group of aculeate Hymenoptera. Stinging priorities vary sharply among different wasps, even if they use the same kind of prey. This suggests alternative evolutionary solutions to similar or identical prey-related problems (Steiner, 1986). One of such prey-related problems is how the composition and pharmacological potency of the venoms may vary among the different groups of wasps. Today we are far from having a "comparative stinging behaviour" or a "comparative toxinology" of aculeate wasps, but occasionally we might be able to contribute to a classification of these groups of insects. Such a contribution is presented by table 1. In only two groups of aculeate Hymenoptera, wasp kinins have been found. These are the Vespidae and the Scoliidae.

Table 1. Agonists for the nervous system, in venoms of Hymenoptera (ACh = acetylcholine, Hist = histamine, Ser = serotonin, Glu = glutamate, Cat = catecholamines, Kin = wasp kinins, O = other agonists).

Family and genus	ACh	Hist	Ser	Glu	Cat	Kin	O
Scoliidae							
Megascolia	−	++	−			++	
Scolia	−	+++	−			+	a
Campsomeris	−	++	−			+	a
Pompilidae							
Anoplius	−	+	−			−	
Batozonellus	−	+	−			−	
Episyron	++	−	−			−	
Sphecidae							
Bembix	−	++	−			−	
Cerceris	−	+	−			−	
Mellinus	−	++	−			−	
Philanthus	++	−	−	++		−	
Sceliphron	−	++	−			−	
Palmodes	−	+++	−			−	
Vespidae							
Dolichovespula	−	+++	+++		+	++	
Vespula	−	+++	+++		+	++	
Vespa	+++	+++	+++		++	+	
Polistes	−	+++	+++			+++	
Polybia			+				
Rhopalidia		++	++		+		
Synoeca			+++				
Apidae							
Apis	−	+++	−		+++	−	b
Bombus	+++	+++	−			−	b
Xylocopa	−	++	−			−	b

− < 10 ng; + = 10-100 ng; ++ = 100-1000 ng; +++ > 1000 ng, per venom reservoir, per µl or per mg, which is roughly equivalent. (a) components causing contraction of the rat colon. (b) melittin or melittin-like muscle contracting substances. For references see Piek & Spanjer (1986) and Nakajima (1986).

In 1954 Jaques & Schachter identified a pain-producing bradykinin-like peptide in the venom of *Paravespula vulgaris* (Linnaeus), but the chemical structure of this wasp kinin has never been discovered. The first structural characterized wasp kinin is polisteskinin 3 (Pisano, 1968). At the moment 12 social wasp kinins have been characterized chemically (for a review see Nakajima, 1986). The first solitary wasp kinin has been found in the scoliid wasp *Megascolia flavifrons* (Fabricius) (Piek et al., 1983, 1984), and the chemical characterization of the two kinins present in this venom followed recently (Yasuhara et al., 1987). The question arises what role kinins may have as venom constituents. It is generally accepted, that social wasps benefit from their capability of producing pain in vertebrate predators, and that kinins are pre-eminently pain-producing substances. In a solitary wasp such a function is unlikely, although not impossible.

We have found in the venom of *M. flavifrons* five substances, including the two identified kinins, that block synaptic transmission in the insect central nervous system (Piek et al., 1987), indicating that they may be present in the venom in order to paralyse the prey. Therefore, kinins are obviously important constituents in the venom of vespid and scoliid wasps.

The presence of kinins, as a well defined group of polypeptide agonists (or antagonists) in the venom of both vespid and scoliid wasps supports the view by Brothers (1975) and Königsmann (1978) that the Vespidae and the Scoliidae may be closely related. It is now generally accepted that the Scoliidae form a monophyletic group, but the superfamily of Scolioidea (including also the Tiphiidae, Sapigidae and Mutili-

dae) must be regarded as a polyphyletic group (Brothers, 1975; Königsmann, 1978; Day, et al., 1981; Osten, 1982). As opposed to the previously commonly accepted seven families of the aculeate Hymenoptera, Brothers (1975) concluded that the Aculeata should be considered as comprising only three superfamilies: the Bethyloidea, the Vespoidea (including 12 families, the Scoliidae, Vespidae and Formicidae among them) and the Sphecoidea (17 families, divided among the Spheciformes and Apiformes). The monophyly of the Scoliidae and Vespidae is supported by the distribution of the kinin character as described in the present paper.

Venom composition, which is an important and characteristic phenomenon within the aculeate Hymenoptera, should be taken in consideration, while examining the phylogeny and classification of this group of insects.

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