Venom gland and reservoir morphology of the genus Pseudoyelicones van Achterberg, Penteado-Dias & Quicke (Hymenoptera: Braconidae: Rogadinae) and implications for relationships

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The venom apparatus of *Pseudoyelicones nigriscutum* van Achterberg, 1997 (Braconidae: Rogadinae) is described and illustrated. The venom apparatus morphology of *Pseudoyelicones* is closely related to that of *Bulborogas* van Achterberg. Therefore, we propose a sister group relationship between these two genera.

Introduction

The genus Pseudoyelicones van Achterberg, Penteado-Dias & Quicke, 1997, is a highly derived genus of rogadine parasitic wasps. It is only known to exist in the Neotropical region (Costa Rica and Brazil) and only five species are known (van Achterberg et al., 1997; Areekul & Quicke, in press). As the generic name implies, Pseudoyelicones species are morphologically very similar to those of another highly distinctive braconid wasp genus Yelicones Cameron, 1887. Consequently, they have often been confused with one another in collections. Species of both genera are robust wasps with swollen femora, shortened medial tarsal segments, and have a large triangular basal area of second metasomal tergite. However, the shape of the marginal cell of the hind wing allows distinguishing. In Pseudoyelicones species the marginal cell is wide medially with the widened area glabrous and distinctly corrugated, vein SR of the hind wing is distinctly curved medially and its medial and basal parts widened and not vein-like. In addition its mandibles are distinctly bidentate rather than tridentate as in Yelicones, the precoxal suture and the occipital carina are absent, the tarsal claws are not pectinate, vein M+CU of the fore wing is straight apically, vein 1r-m of the hind wing is vertical, vein 2-SC+R of the hind wing vertical and widened and vein m-cu of the hind wing is very short or indistinct (van Achterberg et al., 1997; Areekul & Quicke, submitted).

Given the similarities between *Pseudoyelicones* and *Yelicones* the question arises as to whether they are closely related to one another, or whether they are simply displaying a convergent set of characters as a result of selection to a particular way of life.

120 Areekul, Zaldivar-Riverón & Quicke. Venom gland of Pseudoyelicones. Zool. Med. Leiden 78 (2004)



Figs 1-4. Interpreted drawing of venom gland reservoir and gland intima. 1, *Pseudoyelicones nigriscutum* van Achterberg; 2, *Yelicones delicatus* (Cresson); 3, Y. spec. from Nepal; 4, *Bulborogas* spec. Figs 2 and 4 from Zaldivar-Riverón et al., 2004; and fig. 3 from Quicke et al., 1992; all with kind permission of Blackwell Publishing Ltd.

Similarly, the modified tarsi and the robust legs, for example, are known in several other groups of ichneumonoids, including in the Betylobraconinae (van Achterberg, 1995) and Metopiinae (Gauld et al., 2002). *Yelicones* and many Metopiinae attack lepidopteran larvae in silk retreats or leaf rolls and the modified legs in these groups may represent adaptations to gaining access to the hosts (Gauld et al., 2002).

The venom apparatus has provided many useful characters for the phylogenetic analysis of braconid wasps. Edson & Vinson (1979) first reported that there was considerable variation in the venom apparatus in the Braconidae with the cyclostome group subfamilies having a heavily muscularized reservoir whose intima is strongly spirally sculptured. However, at a lower level many more features have been found and it often indicates relationships between genera. The venom apparatus has now been extensively studied in many groups of the cyclostome braconid wasps: the Doryctinae (Quicke et al., 1992), the Opiinae and Alysiinae (Quicke et al., 1997) and most recently in the Rogadinae (Zaldivar-Riverón et al., 2004). Unfortunately, no specimens of *Pseudoyelicones* were available for dissection as until recently as only five specimens with only two females (both holotypes) being known. Recent examination of the INBio collection by DLJQ has revealed nine additional specimens representing P. nigriscutum van Achterberg, 1997, as well as two new species. As P. nigriscutum was represented by six specimens, we were able to make a venom apparatus preparation to help resolve the relationship of this genus. An abdomen was removed from a specimen of *P. nigriscutum* for dissection and the venom apparatus removed and mounted after staining in accordance with the protocol of Quicke et al. (1992).

Results and discussion

The venom apparatus of *P. nigriscutum* has a simple ovoid venom reservoir with the secondary venom duct inserted near its posterior end (fig. 1). The primary venom duct is spirally sculptured. The secondary venom duct is short, wide, unsculptured, rigid and has a small but distinct flange. Its insertion into the reservoir is not recessed. Internally there is a well-developed cone of filaments directed towards the venom reservoir (fig. 1). The tertiary ducts are tubular and strongly spirally sculptured. They differentiate very shortly beyond the flange of the secondary duct and each terminates into a bunch of about six shorter ducts that end in bulbous swellings. Importantly, the two tertiary ducts are very asymmetric in their length. In contrast, Yelicones has a flexible, sculptured, relatively long and undifferentiated secondary venom duct, with no internal filaments at its base and it lacks a flange. In the New World species, Y. delicatus (Cresson, 1872), the tertiary ducts are simple and tubular (fig. 2) as in most other rogadines, but in the three Old World species examined to date (Y. contractus Papp, 1991, Y. belokobylskiji Quicke, Chishti & Chen, 1997, Y. glabromaculatus Belokobylskij, 1993), they are medially expanded with evidence of ductules (fig. 3). In all cases the tertiary ducts are symmetric.

In the Rogadinae, a modified hard secondary venom duct with a flange and internal filaments defines a putatively monophyletic group of genera including *Bulborogas* van Achterberg, 1995; *Canalirogas* van Achterberg & Chen, 1996; *Colastomion* Baker, 1917; *Conspinaria* Schulz, 1906; *Cystomastacoides* van Achterberg, 1997; *Myocron* van Achterberg, 1991; *Macrostomion* Szépligeti, 1900; *Pholichora* van Achterberg, 1991; *Rectivena* van

122 Areekul, Zaldivar-Riverón & Quicke. Venom gland of Pseudoyelicones. Zool. Med. Leiden 78 (2004)

Achterberg, 1991; *Rogas* Nees, 1819; *Triraphis* Ruthe, 1855; *Spinaria* Brullé, 1846; *Bathoteca* Enderlein, 1905; and *Bathotecoides* Watanabe, 1958 (Zaldivar-Riverón et al., 2004). The absence of this structure in *Yelicones* suggests that this genus has a more basal origin in the subfamily. The venom apparatus morphology of *Pseudoyelicones* is in fact very similar to that of *Bulborogas* (fig. 4). They have a thickened, rigid and distinctly differentiated secondary venom duct with a distinct flange. Their tertiary venom ducts are distinctly asymmetric in their length. This character is not found in any other genera in the Rogadini which suggests that this character is a synapomorphic feature for these two genera. *Bulborogas* species are also robust wasps with swollen femora and with a large triangular basal area of second metasomal tergite and both *Bulborogas* and *Pseudoyelicones* lack an occipital carina or at least it is absent laterally, and both have vein M+CU1 of the fore wing straight.

Thus, the morphology of the venom apparatus provides strong evidence that the similarity of the external morphology of *Pseudoyelicones* and *Yelicones* is due to convergent evolution, and suggests a sister group relationship between *Pseudoyelicones* and *Bulborogas*. Further resolution of relationships between rogadine genera are likely to rely heavily on molecular data given the paucity of external morphological characters and obvious convergences.

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