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Occurrence and taxonomic significance of a palpal spine in larvae of *Enallagma* and other genera (Odonata: Coenagrionidae)

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Abstract

A small inconspicuous spine, first detected at the base of the distal-most seta on each labial palpus of early stadia of two species of *Enallagma*, is reported to occur in final-stadium (F-0) larvae of Palaearctic and Nearctic *E. cyathigerum*, in F-0 of 31 other Nearctic species of *Enallagma* and in F-0 of three other coenagrionid genera among 11 inspected for this character. The spine is absent from F-0 of eight other coenagrionid genera, including *Coenagrion* and *Ischnura*. It is also lacking from F-0 of the two species of Afrotropical *Enallagma* that we examined, a discovery that suggests the latter may not be closely related to Nearctic and Palaearctic species. In European populations such a spine occurs in the first few stadia of certain *Coenagrion* species but persists to F-0 only in *E. cyathigerum*. We re-emphasize the potential value of this spine as a means of distinguishing at least the last three stadia of *E. cyathigerum* from those of other coenagrionid genera in Europe, and very probably from *Coenagrion* and *Ischnura* everywhere.

Introduction

The genus *Enallagma*, as currently understood (e.g. Bridges 1994), is ill-defined taxonomically (May 1997) and enigmatic biogeographically, having strong, disjunct centers of diversity in eastern North America and sub-Saharan Africa, and a scattering of species in the Palaearctic and Oriental regions. Moreover, relationships among many of the North American and Palaearctic species are difficult to decipher (Westfall & May 1996; May 1997; Donnelly 1999; Brown et al. 2000). On a more practical level, although the adults are reasonably distinctive, identification to species of larvae of certain genera of Coenagrionidae, especially *Coenagrion*, *Enallagma*, and *Ischnura*, can

be difficult and sometimes impossible using known external morphological characters, especially if larvae are small and lack caudal lamellae. Since these three genera are all widespread, often abundant, and commonly co-occur as larvae, lack of such diagnostic characters remains a serious obstacle studies larval ecology and voltinism.

This paper reports a preliminary study of the incidence and possible taxonomic significance of a small spine on the upper surface of the labial palpus, immediately lateral to the tubercle of the primary (i.e. distal) palpal seta (Fig. 1). We call this structure the parasetal palpal spine (PPS). Although most published illustrations of this structure imply that it is articulated at the base, all examples we have examined lack a basal articulation and so must be regarded as true spines.

The first published descriptions of the PPS known to us are illustrations, presented without comment, by Wilson (1920) for stadium 2 *E. hageni* (p. 245) and *E. signatum* (p. 246). Reporting observations made in 1951, Corbet (1955) recorded the PPS in stadia 2 to 5 of *Coenagrion mercuriale* (Charpentier) (Fig. 2B) as did Gardner (1954a) in *C. hastulatum* (Charpentier). Gardner also remarked that in *C. hastulatum* and "the other British Coenagrions" PPS or a similar spine occurs in early stadia and appears to become "absorbed" by stadium 7 but that in *E. cyathigerum* the PPS persists to the final stadium (F-0). In his dichotomous key for identifying F-0 larvae of British Odonata, Gardner (1954b: 162, 170) used the presence of the PPS to separate *E. cyathigerum* from *Ischnura elegans* (Vander Linden), apparently being the first to recognise and use the spine's diagnostic value.

Parr (1970) noted that *E. cyathigerum* can be distinguished from *Coenagrion puella* (Linnaeus) and *I. elegans* by the presence of the PPS "in all" stadia and that, although small larvae of *C. puella* and *I. elegans* often possess a similar spine, this is never as well developed as in *E. cyathigerum*. In stadia 2-4, 6, 8 and 11 of *E. hageni* (Pilon & Masseau 1983: 128, 132), in stadia 2-5 and 7 of *Ischnura verticalis* (Say) (Pilon & Francini 1984: 555), and perhaps in stadia 10 and 11 of *E. ebrium* (Pilon & Fontaine 1980: 159) the PPS, or a very similar structure, has been illustrated without comment.

In a field study about to be published (Corbet & Chowdhury in prep.) the PPS was found to be well developed and distinct (Fig. 2A) in all of several hundred larvae assigned to *E. cyathigerum* on other characters (see Chowdhury & Corbet 1987), except for one F-1 larva that possessed a very small PPS on the right palpus (Fig. 2C) and none on the left. In F-0 larvae the PPS could be discerned with relative ease using a binocular microscope at a magnification of 20x and, in smaller larvae, a compound microscope at 40x. The smallest larva examined (head width 0.6 mm, i.e. ca stadium 4, or about F-11) possessed the spine.

These observations led Philip Corbet to investigate the occurrence of the PPS in North American representatives of *E. cyathigerum*, in which it was found to be present as well. Michael May has now surveyed a large number of *Enallagma* species, and representatives of other coenagrionid genera, to try to answer the following questions:

1) Is the spine present in *Enallagma* species besides *E. cyathigerum*?
2) Does the spine, by its presence or absence or degree of development, help to elucidate relationships among *Enallagma* species?
3) Is the spine present in other coenagrionid genera, or is it a unique synapomorphy of the species of *Enallagma*?

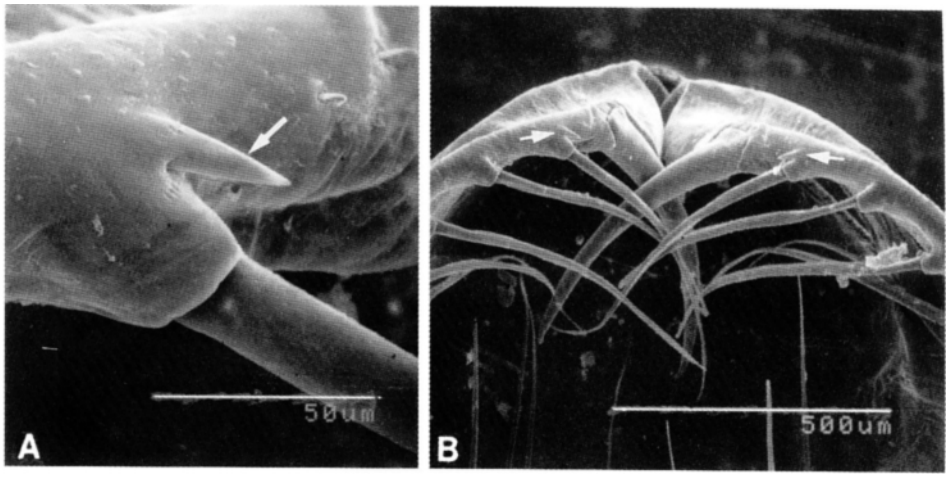

Figure 1. Scanning electron micrographs of *Enallagma aspersum* showing A, detail of PPS and B, location of PPS (indicated by arrows) on distal part of palpi. Scale bars (mm): A, 0.05; B, 0.5.

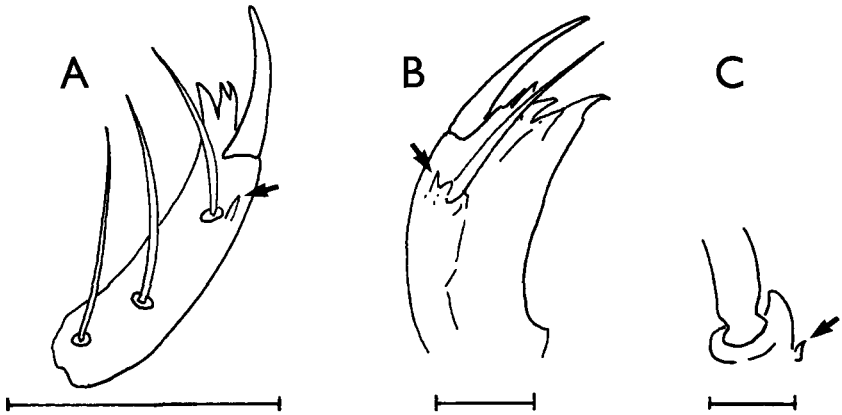

Figure 2. Appearance of PPS in stadia other than F-0: A, *Enallagma cyathigerum*, stadium ca F-9; B, *Coenagrion mercuriale*, stadium 2; and C, *E. cyathigerum*, stadium F-1 (aberrant condition on right palpus only). Scale bars (mm): A, 0.5; B, C, 0.04.

We have not attempted to address the question of the functional significance, if any, of the spine, although we note that any pointed structure facing away from the ecdysial line probably helps to maintain the ratchet movement characteristic of ecdysis.

Materials and methods

Specimens were obtained from our own collections, from the Florida State Collection of Arthropods (FSCA) and the International Odonata Research Institute (IORI), Gainesville, FL, USA, the National Museum of Zimbabwe (NMBZ), Bulawayo, and the collections of the Department of Biological Sciences, University of Montreal (DBS) and of Professor Michael Samways, Pietermaritzburg, South Africa. Whenever possible, exuviae of reared specimens were examined to eliminate the possibility of misidentification. Otherwise all larvae were in F-0 or late stadia. We have therefore not examined here the possibility that the PPS occurs in early stadia of the species examined from outside Europe.

Visual observations were made with various binocular and compound microscopes. Photographs of structural details were made by May using an Hitachi™ S510 scanning electron microscope after coating specimens with gold-palladium.

Results

The species examined and the distribution among taxa of the PPS are shown in Table 1. The PPS occurs in some individuals of all the North American *Enallagma* species examined and in all specimens of most of these species. In some species (e.g. *E. aspersum*, Fig. 1) it can be conspicuous, but in others, when it can be very small and appressed to the basal tubercle of the palpal seta (e.g. *E. signatum* and *E. sulcatum*, Fig. 3), it could probably sometimes be overlooked, though variably present, as in *E. sulcatum* (Figs 3B, C). We believe that the likelihood of our having mistakenly recorded the spine as being present is almost nil. May did not examine early larval stadia in this study but, as mentioned above, the PPS has been detected by Corbet and others in early stadia of certain other coenagrionid genera, including *Enallagma*.

Two species attributed to *Enallagma* from sub-Saharan Africa, *E. glaucum* and *E. nigridorsum*, lack any trace of the PPS in stadium F-0 (Fig. 4B, C). Somewhat to our surprise, however, a palpal spine not visibly distinct from the PPS of *Enallagma* was found also in F-0 larvae of species in the genera *Acanthagrion*, *Apanisagrion*, and *Hesperagrion*, and indeed it is larger in *Hesperagrion* than in any known *Enallagma* (Fig. 5).

Discussion

The intraspecific variability in occurrence and size of the PPS certainly reduces its utility as a means of discriminating or determining relationships among North American species of *Enallagma*. We have the impression that it is generally more likely to be absent, or smaller when present, in the yellow to red species closely related to *E. signatum* (Westfall & May 1996), but accurate use of the character for these purposes would require very painstaking examination, if indeed it can be done at all.

Table 1. Occurrence of a parasetal palpal spine in selected species of Coenagrionidae.

Genus	Species	Reared[1]	Spine[2]
Enallagma	*anna* Williamson	+	+
(North America)	*antennatum* (Say)	+	+
	aspersum (Hagen)	-	7/7
	basidens Calvert	+	+
	boreale Selys	+	+
	civile (Hagen)	+	5/7
	coecum (Hagen)	-	1/1
	concisum Williamson	+	+
	cyathigerum (Charpentier)[3]	+	>650
	daeckii Calvert	+	4/6
	davisi Westfall	+	4/4
	divagans Selys	+	+
	doubledayi (Selys)	+	+
	dubium Root	+	+
	durum (Hagen)	+	+
	ebrium (Hagen)	-	+
	exsulans (Hagen)	+	+
	geminatum Kellicott	+	+
	hageni (Walsh)	+	+
	laterale Morse	+	2/2
	novaehispaniae Calvert	-	+
	pallidum Root	+	8/8
	pictum Morse	+	6/7
	pollutum (Hagen)	+	+
	praevarum (Hagen)	+	+
	recurvatum Davis	+	6/6
	semicirculare Selys	+	+
	signatum (Hagen)[4]	+	+/-
	sulcatum Williamson	+	6/13
	traviatum Selys	+	+
	vesperum Calvert	-	4/5
	weewa Byers	+	+
Enallagma	*glaucum* (Burmeister)	+	0/5
(Africa)	*nigridorsum* Selys	+	0/5
Acanthagrion	*quadratum* Selys	+	3/3
Apanisagrion	*lais* (Selys)	-	3/3
Argia	*tibialis* (Rambur)	+	0/1
Chromagrion	*conditum* (Selys)	-	-
Coenagrion	*resolutum* (Selys)	-	-
Enacantha	*caribbea* Donnelly & Alayo	-	0/3

Table 1. Continued.

Genus	Species	Reared[1]	Spine[2]
Hesperagrion	*heterodoxum* (Selys)	+	4/4
Ischnura	*kellicotti* Williamson	-	-
	posita (Hagen)	+	0/3
	ramburii (Selys)	-	-
Nehalennia	*integricollis* Calvert	-	-
	irene (Hagen)	-	-
Neoerythromma	*cultellatum* (Selys)	+	-
Telebasis	*byersi* Westfall	-	0/2

[1] At least one of the specimens examined was reared (+) or none was reared (-).

[2] Palpal spine present (+) or absent (-). Numerals indicate the number of specimens with the spine present/number examined; thus for *E. sulcatum*, six had the spine and seven apparently did not. In all other cases at least three specimens were examined, there being no variation in occurrence except possibly in *E. signatum*.

[3] Data include >650 specimens from Britain and about 10 from North America, all possessing the palpal spine.

[4] At least five specimens of *E. signatum* were examined visually, but the spine was detected only in the single specimen examined using SEM because the spine is closely appressed to the basal tubercle; thus the frequency of occurrence is uncertain.

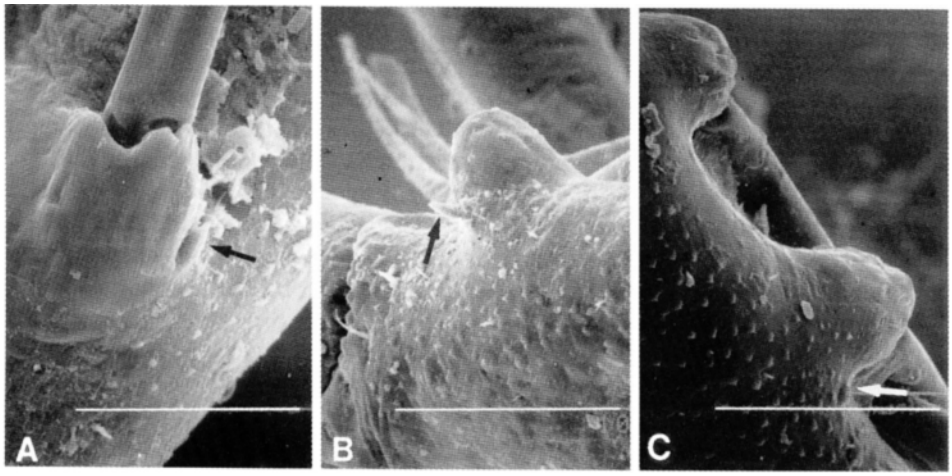

Figure 3. Scanning electron micrographs of A, *Enallagma signatum* and B,C, *E. sulcatum*, showing variation in development of PPS. Scale bars: 0.1 mm.

Among Palaearctic *Enallagma* we have examined only *E. cyathigerum*. These species appear to form a very closely related group (May 1997; Brown et al. 2000), however, of

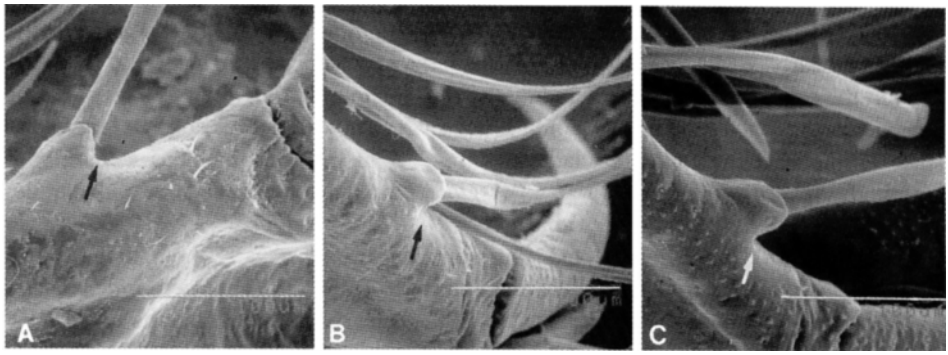

Figure 4. Scanning electron micrographs of A, *Coenagrion resolutum*, B, *Enallagma glaucum*, and C, *E. nigridorsum*, showing absences of PPS. Scale bars: 0.1 mm.

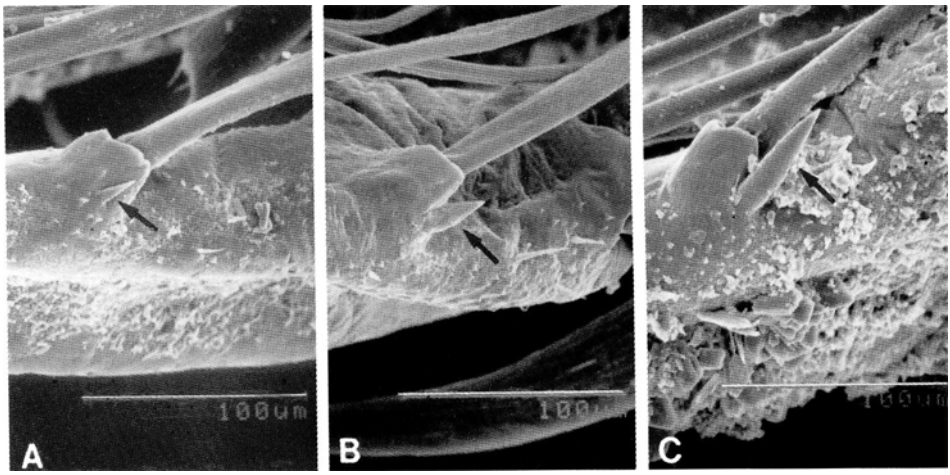

Figure 5. Scanning electron micrographs of A, *Acanthagrion quadratum*, B, *Apanisagrion lais*, and C, *Hesperagrion heterodoxum* showing presence of PPS. Scale bars: 0.1 mm.

which the North American member, *E. boreale*, as well as *E. cyathigerum*, display the PPS. Thus we predict with some confidence that other species within the *E. cyathigerum* group, such as *E. risi* Schmidt, *E. circulatum* Selys and *E. deserti* (Selys), also have the spine. On the other hand, its absence in sub-Saharan species (Fig. 4B, C) may support the suggestion that these species are only distantly related to the North American and Palaearctic *Enallagma* (Kennedy 1920; May 1997). We assume that loss of the PPS in late stadia is a plesiomorphy of Coenagrionidae because this condition is evidently characteristic of many apparently unrelated genera. If so, this argues that North American/Palaearctic species are a clade, with other African species excluded.

Alternatively, it is possible, since the PPS is commonly, and perhaps universally, present in early stadia, its loss by F-0 may be apomorphic. In that case, our data support the existence of a clade including the sub-Saharan *Enallagma* plus *Ischnura* plus *Coenagrion* but excluding the remaining *Enallagma*. This alternative appears less likely, since it implies either that the clade lacking PPS in F-0 also includes a variety of seemingly very disparate genera (e.g., *Argia*, *Chromagrion*) or that several parallel losses of the PPS have occurred (Table 1).

Acanthagrion, *Apanisagrion*, and *Hesperagrion* are not usually thought to be particularly close relatives of *Enallagma*, and Davies & Tobin (1984) placed *Apanisagrion* in a different subfamily. Nevertheless, the PPS is clearly present. Thus its occurrence in F-0 larvae is not an apomorphy unique to *Enallagma*. Whether its presence indicates a closer phylogenetic relationship among the genera possessing it than previously believed remains to be determined. It would be interesting to examine larvae of other New World genera, in particular, for a similar spine. Nevertheless, the PPS does appear to be reliable in distinguishing late-stadium larvae of *Enallagma* from those of *Ischnura* and *Coenagrion* (see Fig. 4A) and, although its detection often requires close examination, it seems at present to provide a useful tool for this purpose.

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References

Askew, R.R., 1988. The dragonflies of Europe. Harley Books, Colchester.

Bridges, C.A., 1994. Catalogue of the family-group, genus-group and species-group names of the Odonata of the world. 3rd edition. Urbana, Illinois, privately published.

Brown, J.M., M.A. McPeek & M.L. May, 2000. A phylogenetic perspective on habitat shifts in the North America *Enallagma* damselflies. Systematic Biology 49: 697-712.

Chowdhury, S.H. & P.S. Corbet, 1987. New external morphological characters for distinguishing larvae of *Enallagma cyathigerum* (Charpentier) and *Ischnura elegans* (Vander Linden) (Zygoptera: Coenagrionidae). Odonatologica 16: 375-378.

Corbet, P.S., 1955. The larval stages of *Coenagrion mercuriale* (Charp.) (Odonata: Coenagriidae). Proceedings of the Royal Entomological Society of London (A) 30: 115-126.

Corbet, P.S. & S.H. Chowdhury, in prep. Voltinism of *E. cyathigerum* in central Scotland, U. K.

Davies, D.A.L. & P. Tobin, 1984. The dragonflies of the world: a systematic list of the extant species of Odonata. Volume 1, Zygoptera, Anisozygoptera. Utrecht, S. I. O. Rapid Communications (Supplement) 3, 127 pp.

Donnelly, T.W., 1999. Intergradation between *Enallagma cyathigerum* and *vernale* in northeastern North America – widespread hybridization between sibling species with different habitat preferences.

International Congress of Odonatology, Colgate, New York. Abstracts of Papers and Posters: 5.

Gardner, A.E., 1954a. The life-history of *Coenagrion hastulatum* (Charp.) (Odonata: Coenagriidae). Entomologist's Gazette 5: 17-40.

Gardner, A.E., 1954b. A key to the larvae of the British Odonata. Part I. Zygoptera. Entomologist's Gazette 5: 157-171.

Kennedy, C.H., 1920. Forty-two hitherto unrecognized genera and subgenera of Zygoptera. Ohio Journal of Science 21: 83-88.

May, M.L., 1997. The status of some species of *Enallagma* (Odonata: Zygoptera: Coenagrionidae). Entomological News 108: 77-91.

Parr, M.J., 1970. The life histories of *Ischnura elegans* (van der Linden) and *Coenagrion puella* (L.) (Odonata) in south Lancashire. Proceedings of the Royal Entomological Society of London (A) 45: 172-181.

Pilon, J.-G. & R. Fontaine, 1980. Étude morphologique des larves de *Enallagma ebrium* (Hagen) (Zygoptera: Coenagrionidae). Odonatologica 9: 155-171.

Pilon, J.-G. & J. Franchini, 1984. Étude morphologique des larves de *Ischnura verticalis* (Say) élevées en laboratoire (Zygoptera: Coenagrionidae). Odonatologica 13: 551-564.

Pilon, J.-G. & M.J. Masseau, 1983. Morphologie externe des larves de *Enallagma hageni* (Walsh) (Zygoptera: Coenagrionidae). Odonatologica 12: 125-140.

Westfall, M.J. & M.L. May, 1996. Damselflies of North America. Scientific Publishers, Gainesville, Florida.

Wilson, C.B., 1920. Dragonflies and damselflies in relation to pondfish culture, with a list of those found near Fairport, Iowa. Bulletin of the United States Bureau of Fisheries 36: 181-264.