A new pattern of parasitism in water mites (Hydrachnidia)? An insight into their relationships with pupae of caddisflies (Trichoptera)

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ABSTRACT

To date, relatively few data have been available regarding the parasitism of water mite larvae on caddisflies; most available information relates to the adult stadia, fewer to caddisfly larvae, with just single references to pupae. The present paper examines the occurrence (phoresy and parasitism) of Piona stjordalensis larvae (119 individuals) on the larvae and pupae of Mystacides longicornis. It is possible that water mite larvae exhibit a new type of parasitism on caddisflies, with two consecutive parasitic larval stadia: one on the pupa, the other on the imago.

1. Introduction

Water mites belong to the cohort Parasitengona (Actinedida), which is characterized by a complex life cycle that includes a parasitic larva (Wohltmann et al., 2007). The two most important benefits of such parasitism are (a) obtaining nutrition from the host’s body, and (b) a dispersive potential for species that are poorly mobile in other developmental stadia (Martin et al., 2010).

Larvae of Hydrachnidia parasitize members of most aquatic insect orders. Initially phoretic on the aquatic stadia of amphibiotic hosts (larvae and pupae), they only become parasitic on imagines inhabiting aerial-terrestrial environments (Böttger, 1976; Zawal, 2006; Baker et al., 2008; Zawal and Szlauer-Lukaszewska, 2012). This is also thought to be what happens in Trichoptera, but the relations of caddisflies with water mites – including the synchronization of the life cycles of host and parasite – are very poorly understood. Water mite larvae are usually found on the imagines of caddisflies, only occasionally on their larvae (Smith and Oliver, 1986; Fairchild and Lewis, 1987; Martin et al., 2010; Więcek et al., 2013; Martin and Tempelman, 2014). There are two records of water mites found on caddisfly pupae (Gerecke, 2000; Buczyńska et al., 2015) but only in one case was the parasitic phase definitely involved (Buczyńska et al., 2015). Now the pupal stadium is key, as it precedes the host’s adult stadium, by means of which the water mites are dispersed (Zawal, 2005a). The absence of data due to the rarity of the phenomenon itself means that it is difficult to interpret such information as to hand regarding the occurrence of water mite larvae on pupae. Here, we describe a very interesting new case, suggesting the possible existence of a hitherto undescribed pattern of parasitism between water mites and caddisflies.

2. Material and methods

The study site is a sand mine (Fig. 1) situated in Gardzienice Drugie (N 51.104155 E 22.841070), a village in eastern Poland c. 20 km E-SE of Lublin. This was one of ten localities explored in 2018 as part of a project to analyse the aquatic insect fauna in sand mine water bodies.

The sand mine in Gardzienice Drugie is situated in open country with a predominance of crop fields on the edge of the Giełczew river valley. The sand mine cover an area of 4.06 ha, within which there are three water bodies, of 0.56, 0.70 and 0.90 ha in area and with a depth of several metres in their centres, and also with a strip of shallow littoral (Fig. 1a). In all three cases, the bottom was sandy with an admixture of organic matter, the water was greenish and slightly turbid, but in the littoral zone transparent to the bottom. In the littoral zone, there was a...
narrow belt of emergent vegetation with predominant *Typha angustifolia* L., *Carex* sp. or *Phragmites australis* (Cav.) Trin. ex Steud. with some sections of bare shoreline. Patches of *Potamogeton natans* L. were floating on the water, while below the surface *Potamogeton crispus* L., *Potamogeton pusillus* L. and *Myriophyllum spicatum* L. were present (Fig. 1b and c). In summer there were small patches of filamentous algae.

The water in all three bodies was warm, with a pH of 7 or slightly higher, quite rich in oxygen and moderately fertile (Table 1).

The fieldwork was carried out once a month from April to October 2018. Samples were taken with a pond net from an area of c. 2.5 m². They were immersed in 96% ethanol, transported to the laboratory and sorted under a microscope. Water mites and the larvae and pupae of

![Fig. 1](image-url)

**Table 1**

Physical and chemical properties of the water bodies at the sand mine in Gardzienice Drugie. Min. – minimum, Max. – maximum, Av. – average.

| Parameter                  | Min.  | Max.  | Av.  |
|----------------------------|-------|-------|------|
| Temperature [°C]           | 12.3  | 27.4  | 22.1 |
| pH                        | 6.3   | 8.8   | 7.6  |
| Oxygen [%]                | 49.1  | 76.6  | 60.4 |
| Oxygen [mg dm⁻³]          | 4     | 6.2   | 5.1  |
| Conductivity [μS cm⁻¹]    | 50    | 162   | 111  |
| Total Dissolved Solids [ppm]| 25   | 81    | 55   |

![Fig. 1](image-url)

**Fig. 1.** a Water body at the sand mine in Gardzienice Drugie; b and c Microhabitats of the aquatic stadia of *Mystacides longicornis* infested by *Piona stjordalensis*: patches of *Potamogeton pusillus* and *Myriophyllum spicatum*. 
Caddisflies were preserved in 70% ethanol.

During each survey, an HI9828 Multiparameter Portable Meter (Hanna Instruments) was used to measure the following parameters of the water: temperature, pH, redox potential (ORP), concentration and saturation of dissolved oxygen, conductivity, resistance, total dissolved solids and salinity.

Water mite larvae were described as phoretic or parasitic on the basis of their body dimensions, unmistakable features showing them to be taking up food (spread-out coxal plates) and the strength of adhesion to the host. They were identified using the keys by Davids and Kouwets (1987) and Tuzovskij (2016).

The statistical analyses (Mann-Whitney U test, Kruskal-Wallis test) were performed in Statistica 13.0.

3. Results

A total of 76 larvae, 27 pupae and 58 empty larval cases or pupal exuviae of Trichoptera were collected. The most numerous were Mystacides longicornis (Linnaeus, 1758) (52.5% of the material) and Ecnomus tenellus (Rambur, 1842) (16.5%). 7 species achieved a percentage share from 7.5 to 1.0%; in order from the most to the least numerous, they were: Oecetis ochracea (Curtis, 1825), O. furva (Rambur, 1842), Athripsodes aterrimus (Stephens, 1836), Anabolia laevis (Zetterstedt, 1840), Phryganea bipunctata Retzius, 1783, Orthotrichia sp. and Oecetis lacustris (Pictet, 1834). Only single specimens of the following were obtained: Cyrnus crenaticornis (Kolenati, 1859), Leptocerus tineiformis Curtis, 1834, Triaenodes bicolor (Curtis, 1834) and Hydroptila sp.

Caddisflies carrying water mite larvae were found only in the sample taken on 30.07.2018. The species in question were Mystacides longicornis (5 larvae, 17 pupae, 26 cases) and Oecetis furva (2 cases).

The larvae of one species of water mite – Piona stjordalensis (Thor, 1897) (Fig. 2) – were found on 2 larvae and 17 pupae of one species of caddisfly – Mystacides longicornis (prevalence 40.0% and 94.4%, respectively; intensity of infestation: 1–19 and 1–30, respectively) (Table 2). The differences in intensity of infestation between the caddisfly developmental stadia were statistically not significant (Mann-Whitney U test: \( Z = 0.067101, p = 0.946501 \)).

All the water mite larvae (19 individuals) found on the larvae of M. longicornis were phoretic, but on the pupae 15 were phoretic and 75 parasitic (Figs. 3 and 4). Moreover, in one instance involving a case with a damaged pupa there were 10 free-swimming water mite larvae, 5 of which were phoretic and the other 5 parasitic (Table 2).

On the caddisfly larvae, the water mites were attached only to the abdomen, mostly its last segments (Table 3). On the pupae, they were found on all body parts, albeit with a clear preference for the abdomen (Fig. 5): the difference between the numbers of larvae attached to the abdomen and to other body parts was statistically significant (Mann-Whitney U test: \( Z = -1.99099, p = 0.046483 \)). On the pupal abdomen, the end segments were preferred (Table 4, Fig. 4b), but the differences were not statistically significant (Kruskal-Wallis test: \( H(10, N = 32) = 14.47664, p = 0.1523 \)).

| Table 2 | Occurrence of Piona stjordalensis larvae on Mystacides longicornis caddisflies. |
|---------|---------------------------------|
| Larvae  | Pupae  | Cases  |
| Prevalence | 40     | 94.4   | 9.1  |
| Intensity  | 1–19   | 1–30   | 10   |
| Average intensity | 10.0   | 7.0    | 10.0 |

Fig. 2. Larva of Piona stjordalensis; a ventral side; b first-leg tarsus; c excretory pore plate.
The body sizes of the water mite larvae found on the caddisfly larvae were small (348–397 μm, mean 383 μm), whereas the size range of those found on the caddisfly pupae was somewhat larger (342–568 μm, mean 426 μm) (Fig. 5). The smallest water mite larvae (342–396 μm, mean 376 μm) were phoretic, the larger ones (396–568 μm, mean 438 μm) were parasitic, with stylostomes observed (Figs. 4 and 5), although the difference between them was statistically not significant (Mann-Whitney U test: \( Z = -0.605959, p = 0.544542 \)).

4. Discussion

Although little information is available about the parasitism of water mite larvae on caddisflies, it is known that members of 15 genera exhibit such behaviour. Whereas most of these have been recorded on adult caddisflies, up to 5 genera have been found on their larvae (Smith and Oliver, 1986; Fairchild and Lewis, 1987; Gerecke, 2000; Martin, 2008; Martin et al., 2010; Martin and Tempelman, 2014; Buczyńska et al., 2015). But on their pupae just one, definitively identified species of water mite (Tiphys torris (Müll.)) has been recorded (Buczyńska et al., 2015), along with one other larva unidentified to species level and with an unspecified mode of occurrence (Gerecke, 2000).

It is interesting, and in our view significant, that the water mite species found earlier on a caddisfly pupa belonged to the same family (Pionidae) as the larvae of that species found in the present study, and
also that they affected a member of the same trichopteran family (Lep
toceridae) (Buczyńska et al., 2015). It is also significant that leptocerids
are mentioned more often than other families in the specialist literature,
e.g. the genus Hygrobates Koch was recorded on larvae of the genera
Nectopsyche Müll., Oecetis McL. and Ceraclea Steph., Unionicola Hald. on
larvae of Oecetis (including Oecetis furva), and Tiphys Koch on Triaenodes
bicolor (Fairchild and Lewis, 1987; Martin and Tempelman, 2014; Buc-
zyńska et al., 2015). This consistent record of different leptocerids as
host may indicate a kind of host specificity, a fact also emphasized by
Martin and Tempelman (2014).

The parasite species that we recorded (Piona stjordalensis) belongs to
a group of closely-related species – the Piona coccinea-complex, whose
close relationships have been confirmed by genetic research (Stålstedt
et al., 2013) – the other members of which (P. coccinea (Koch) parasitic
on Diptera, or their hosts (P. imminuta (Piersig)) are unknown (Sparing,
1959; Davids and Kouwets, 1987). Stryjecki et al. (2015) mentioned
parasitism of P. stjordalensis on Chironomini n.det., but the larva was
atypical and needs confirmation (Tuzovskij, 2016). The parasitism of
caddisflies by larvae of P. stjordalensis appears to be an interesting
example of an alternative adaptation among a group of closely-related
species, which in the long-distant past could have led to speciation.

But the most fascinating aspect of the data presented in this paper is
the model of parasitization by water mite larvae. Böttger (1976) already
described three types of behaviour among water mite larvae: 1. parasitization of insects that do not leave the water; 2. parasitization of insects whose imagines do leave the water; 3. no parasitization. Hitherto it was thought that type 2 applied to caddisflies, namely, that phoretic water mite larvae reached the adult insect via the latter’s larva (Odonata, Plecoptera) or pupa (Diptera, Trichoptera) (Böttger, 1976; Zawal, 2003a, 2004; Martin, 2008). But wherever water mite larvae have been recorded on caddisfly pupae, and especially in the present case, most of those larvae were in the parasitic (Figs. 3a and 4), not the phoretic phase (Fig. 3b), and the few phoretic larvae that were found had probably not yet entered the parasitic phase. Accordingly, it is

Table 4

Location of Piona stjordalensis larvae on various body parts of Mystacides longicornis. I-IX – numbers of abdominal segments.

| Body part | Head | Thorax | Wings | Legs | Abdomen | I | II | III | IV | V | VI | VII | VIII | IX |
|-----------|------|--------|-------|------|---------|---|----|-----|----|---|----|-----|------|----|
| prevalence | 11.8 | 11.8   | 11.8  | 5.9  | 100     | 17.6| 17.6| 22.5 | 17.6| 11.8| 5.9 | 5.9  | 52.9 |
| intensity  | 1    | 1-3    | 1-2   | 1    | 1-30    | 1-7 | 1-3 | 1-4  | 1-3 | 1-2 | 1   | 1    | 1-26 |
| average intensity | 1.0 | 2.0    | 1.5   | 1.0  | 5.9     | 3.3 | 1.7 | 2.0  | 1.7 | 1.5 | 1.0 | 1.0  | 5.6  |
highly probable that the parasitization of caddisflies by water mite larvae takes a different form (type 4 parasitism, respectively), namely, that there are two consecutive phases of parasitic larvae, first on the pupa and then on the imago (Fig. 6). One idea supporting this concept is that the pupal stadium in trichopterans lasts a long time, a period which phoretic water mite larvae would probably not be able to survive. If that were the case, it would have important implications for our understanding of the dispersal of water mite species parasitizing caddisflies: some of the larvae parasitizing pupae could pass into the deutonymph stadium, bypassing the parasitic phase on adult caddisflies and thus forming a more stable though less dispersive population. On the other hand, the larvae passing from the caddisfly pupae to the imagines would already have completed the first growth phase, and would therefore be in a better condition to survive the parasitic phase on adult hosts, which could much reduce their mortality. This would be of key significance, as the mortality of this phase in water mites is unusually high, perhaps as much as 70% (Zawal, 2002; 2003b, 2006).

Obviously, finding evidence to confirm the above hypothesis will require further study, because there could well be an alternative explanation. Such study must include cooperation between invertebrate specialist as well as pure luck in finding caddisflies, especially pupal stages, with water mites attached. To date, the only parasitic larvae found on trichopteran pupae have been Pionidae species (Piona stjordalensis and Tiphys torris), which normally parasitize dipterans. Instances are also known of parasitism, e.g. by members of the family Arrenuridae, on preimaginal stadia of insects, but here the rule is that the larvae are phoretic (Zawal, 2004, 2006).

The subject literature contains very little information regarding the prevalence and intensity of infestation of water mite larvae on caddisflies. Such data for trichopteran larvae are given by Fairchild and Lewis (1987), Martin and Tempelman (2014) and Buczyńska et al. (2015), for their pupae solely by Buczyńska et al. (2015), whereas for imagines only intensities of infestation are known (Nagasawa and Abe, 2014; Abe and Ito, 2021). The prevalence of Piona stjordalensis in the case we are describing here was high: in trichopteran pupae it far exceeded the values given in earlier reports, while in their larvae it achieved the highest levels. In contrast, the intensities of infestation in both larvae and pupae fell within the ranges given earlier. Since, however, we found parasitic larvae of Piona stjordalensis at only one locality and in just single sample, this high level of infestation does not have to be the rule: it could have been a coincidence, resulting from the coming together in one place of a large number of larvae and pupae of Mystacides longicornis and larvae of Piona stjordalensis. That this is possible emerges from the fact that water mite species from the family Pionidae lay large numbers of eggs in a single packet, particularly Piona coccinea, which is closely related to P. stjordalensis (Kłosowska et al., 2011; Dzierzgowska et al., 2011; Bankowska et al., 2016). The larvae and pupae of the trichopteran genus Mystacides Berth. often occur in large aggregations, their larval cases adhering one next to the other to aquatic plants (as we found here) or to solid substrates like stones or branches (Anderson, 1976). It is also

Fig. 6. A new type of parasitism (dashed line) against three basic types (solid lines) (Böttger, 1976) among aquatic insects. La – larva, Pu – pupa, In – insect, Ad – adult, Deut – deutonymph, phor – phoretic, par – parasitic, sw – swimming. Blue colour – water. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)
worth emphasizing that the larvae of *Piona sjordalensis* targeted the most dominant caddisfly species in a given water body. In contrast, *Fairchild and Lewis* (1987) as well as *Martin and Tempelman* (2014) found water mites on caddisfly species that were not dominant in the localities concerned; the explanation of the first-mentioned authors was that water mites preferred not the most numerous species but those with sufficient free space in their larval cases. In line with this explanation, the most desirable hosts for water mites should therefore be members of the families Limnephilidae and Phyrganeidae, but in fact they are not.

The preference of water mite larvae for the abdomens of caddisfly larvae and pupae is probably due to two causes: there is a large area available for attachment, and there is less danger of mechanical damage on emerging from the larval case. *Fairchild and Lewis* (1987), *Martin and Tempelman* (2014) and *Buczyńska et al.* (2015) all achieved similar results.

Phoretic larvae had the same size as freshly hatched larvae (*Davids and Kouwets*, 1987), whereas parasitic larvae were only c. 50% larger; they are thus far smaller than the adult forms (*Gerecke et al.*, 2016). Body size in caddisflies are therefore the greatest during the larval stadium parasitizing adult caddisflies or during the deutonymph stadium. Since most water mite species from the family Pionidae achieve their greatest growth rates in the deutonymph stadium, this latter possibility is the more likely one (*Baker et al.*, 1991; *Smith et al.*, 2001).

**Financial support**

The research was financed from the research subsidy of the Institute of Biological Sciences of the Maria Curie-Skłodowska University, Lublin.

**Ethical standards**

No experimentation was performed in this study.

**Declaration of competing interest**

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Paweł Buczyński reports financial support was provided by Maria Curie-Skłodowska University.

**Acknowledgements**

We thank Mr. Andrzej Pitucha for permission to conduct research on his property (a sand mine). We sincerely appreciate all valuable comments and suggestions of the Reviewers.

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