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# Loss of larval parasitism in parasitengonine mites

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## ABSTRACT

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Larval Parasitengona are typically parasites, yet at least 29 species of water mites and one species of Trombidiidae forgo larval feeding and any association with a host. Species with non-feeding larvae are isolated cases within species groups or genera where the remaining species have parasitic larvae. Species without larval parasitism occur in at least 14 genera, eight families and four superfamilies of water mites; the loss of larval parasitism is presumably polyphyletic, having occurred at least 21 times. Lineages of water mites with non-feeding larvae frequently exist in parallel with almost identical populations or species that have parasitic larvae. Thus, there is tremendous potential for studies comparing the relative merits of the two life history strategies. Comparisons indicate that adults from lineages with non-parasitic larvae produce smaller numbers of larger eggs; the extra nutrition included in larger eggs permits the larvae to forgo feeding. Non-feeding larvae frequently have wider dorsal plates but reduced leg length, setal length and sclerotization when compared to parasitic larvae from sister lineages. The adults of lineages with non-feeding larvae are frequently smaller in comparison to adults of sister lineages with parasitic larvae. There is no apparent pattern in relation to habitat: lineages lacking larval parasitism occur in streams, temporary ponds and the littoral and planktonic regions of permanent lakes.

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## INTRODUCTION

The name 'Parasitengona' is a reference to larval parasitism and the typical life cycle that is the cohesive characteristic defining this taxon. In the majority of species the larval stage is parasitic, the prelarva, protonymph and tritonymph are quiescent and calyptostatic and the deutonymph and adult are free-living predators. However, there are a small number of species in which the larval stage does not feed and does not associate with a host. Mites may emerge from eggs as larvae or

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remain within eggs until after transformation into deutonymphs and, in some species, both the larvae and deutonymphs may appear to hatch from an individual clutch. Such exceptional cases were noted by early researchers (e.g. Claparède, 1868; Neuman, 1880; Kramer, 1891; Piersig, 1897–1900; Musselius, 1914) and caused confusion as to the typical life history of parasitengonine mites (Smith and Oliver, 1986).

The lack of a parasitic larval association is presumed to be apotypic, representing an evolutionary loss (Mitchell, 1957; Smith, 1976). The sparse distribution of species or populations lacking larval parasitism from a wide diversity of taxa and the apparent short duration of such lineages is consistent with this conclusion. Larvae that are not parasitic may resemble parasitic larvae or may have various degrees of morphological reduction.

The loss of larval parasitism, in the context of this paper, infers that larvae forgo parasitic feeding and do not associate with a host: sufficient nutrition is included in the egg to allow the larva to transform into the protonymph and, subsequently, the deutonymph without any additional energy and the larval mites forfeit host-mediated dispersal. Some terrestrial parasitengones have apparently become predators as larvae (e.g. *Johnstoniana rapax*, *Balaustium* spp. and some *Abrolophus* spp.; Witte, 1978; Wohltmann, 1998) and it is possible for a species to forgo larval feeding yet retain a host association (therefore, being phoretic in the strict sense), but I have not encountered any such cases. Facultative parasitism is also possible and could be an intermediate state in the evolutionary loss of parasitism, but the only documented case involves laboratory hybrids between populations or species exhibiting the two life histories (B. Smith, unpublished data). Presumably, if true phoresy and/or facultative parasitism occur during evolutionary loss of parasitism they are unstable and transitory states (see Hart (1996) for a discussion of the evolutionary loss of larval feeding in other taxa).

The reader should be aware of the bias in this presentation: I have conducted an extensive literature search of the Hydrachnidia only. However, loss of parasitism is not exclusive to just the water mites as is evident from a documented case reported among the Trombidiidae. Given that the life history has been examined for a small proportion of water mite species and an even smaller proportion of terrestrial Parasitengona, there are presumably many additional examples of species that forgo larval parasitism.

#### RECORDS OF LOSS OF LARVAL PARASITISM

Loss of larval parasitism has been recorded in at least 29 species, representing isolated cases from a diversity of taxa (Table 1). Some of the records are speculative (indicated by a question mark in Table 1), based upon the size of the eggs relative to the size of the adult female, association with interstitial (phreatic or hyporheic) habitats or the relative size of eggs and/or larvae in comparison to the same of species known to have typical parasitic larvae. Wainstein (1980) inferred

TABLE 1

Records of Parasitengona lacking larval feeding and host association

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Trombidioidea

  Trombidiidae

*Allothrombium* (C. Welbourn, personal communication)

Hydrachnidia (Mitchell, 1957; Böttger, 1972, 1976)

  Hydrovolvoidea?

    Hydrovolziidae?

      Acherontacarinae?

*Acherontacarus*?

*A. halacaroides*? (Cook, 1974; Smith and Oliver, 1986)

  Hydryphantoidea

    Hydryphantidae

      Thyadinae (Mitchell, 1957)

*Thyas*

*T. stolli* (Cook, 1959; Crowell, 1960, 1961; Böttger, 1972; Prasad and Cook, 1972; Smith and Oliver, 1986; Cook *et al.*, 1989)

  Hygrobatoidea

    Hygrobatidae (Mitchell, 1957; Proctor and Smith, 1994)

*Hygrobates*

*H. neoocroporus* (H. Proctor, personal communication)

*H. nigromaculatus* (Hezewijk and Davids, 1985; Ten Winkel, 1987; Ten Winkel *et al.*, 1989)

*H. longiporus* (Wainstein, 1980)

*Attractides* (Schwoerbel, 1961, 1967; Böttger, 1972)

*A. nodipalpis* (Wainstein, 1980)

  Unionicolidae (Mitchell, 1957)

*Unionicola*?

*Unionicola formosa*? (Paterson and MacLeod, 1979)

*Unionicola intermedia*? (Davids, 1973; Baker, 1989)

*Unionicola bonzi*? (Davids, 1973)

  Aturidae

    Notoaturinae?

*Taintaturus*?

*Taintaturus stoutae*? (Cook, 1991)

  Axonopsinae

*Brachypoda*

*Brachypoda versicolor* (Piersig, 1897-1900; Soar and Williamson, 1925; Müller-Liebenau, 1956; Crowell, 1960; Böttger, 1972; Smith and Oliver, 1986)

*Estellacarus* (L.M. Smith, personal communication)

  Aturinae?

*Aturus*? (M. 1954)

*A. scaber*? (Böttger, 1972; does parasitize according to Jones (1967))

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TABLE 1

*continued*

## Limnesiidae

*Limnesia* (Smith and Oliver, 1986; H. Proctor, personal communication)*Limnesia connata* (Piersig, 1897–1900; Soar and Williamson, 1925; Sokolow, 1925; Szalay, 1928; Böttger, 1972)*Limnesia undulata* (Neuman, 1880; Piersig, 1897–1900; Musselius, 1914; Soar and Williamson, 1925; Sokolow, 1925; Szalay, 1928; Sparing, 1959; Crowell, 1960; Böttger, 1972; Wainstein, 1980)*L. angustata* (Wainstein, 1980)*Limnesia fulgida?* (Wainstein, 1980)*Limnesia koenikei?* (Wainstein, 1980)*Limnesia maculata* (Böttger, 1972)*Physolimnesia**Physolimnesia australis* (Proctor, 1997)

## Pionidae (Proctor and Smith, 1994)

*Forelia* (Cook, 1955)*Forelia cookei* (Prasad and Cook, 1972)*Pionacercus* (Smith, 1976; Smith and Oliver, 1986)*Pionacercus leuckarti* (Lundblad, 1927; Böttger, 1972)*Piona* (Wainstein, 1966; Smith, 1976)*Piona, coccinea* group (Smith, 1976)*Piona alpicola* (= *Piona uncata*; Stout, 1953; Jones, 1967; Böttger 1972, Riessen 1982a; does parasitize according to Ellis-Adam and Davids (1970))*Piona, nodata* group (Smith, 1976)*P. nodata* (= *Piona fuscata*; Piersig, 1897–1900; Soar and Williamson, 1925; Lundblad, 1927; Böttger, 1962, 1972; Wainstein, 1980; Riessen, 1982a)*Piona annulata* (Wainstein, 1980)*Piona* n. sp., near *constricta* (Riessen, 1982a,b)*Piona, rotunda* group (Smith 1976)*P. pusilla* (= *Piona rotunda*; Piersig, 1897–1900; Wesenberg-Lund, 1904; Viets, 1924; Soar and Williamson, 1925; Crowell, 1960, 1961; Böttger, 1972; Prasad and Cook, 1972; Wainstein, 1980; Riessen, 1982a)*Piona, clavicornis* group*Piona clavicornis* (Lundblad, 1927; Motas, 1928; Ellis-Adam and Davids, 1970; Riessen, 1982a)*Piona, carnea* group*Piona carnea* (Lundblad, 1924; Wesenberg-Lund, 1939)*Piona, conglobata* group*Piona conglobata* (Lundblad, 1924; Wesenberg-Lund, 1939)

Ungrouped

*Piona novae-zealandiae* (Stout, 1953)

## Teutoniidae

*Teutonia**Teutonia cometes* (= *Teutonia primaria*; Piersig, 1897–1900; Böttger, 1972)

TABLE 1

*continued*

## Lebertioidea

## Sperchontidae

*Sperchon**Sperchon turgidus* (P. Martin, personal communication)

## Lebertiidae

*Lebertia* (Smith and Oliver, 1986; I. Smith, personal communication)*L. stigmatifera* (= *L. complexa* = *L. tau insignis*; Lundblad, 1924; Wesenberg-Lund, 1939; Sparing, 1959; Böttger, 1972; apparently needs host, P. Martin (personal communication))

## Arrenuroidea

## Arrenuridae

*Arrenurus**(Megaluracarus)**A. manubriator* (Cook *et al.* 1989; Proctor and Smith, 1994)*(Truncaturus)**A. rufopyriformis* (Cook *et al.*, 1989)*Arrenurus* n. spp. (B. Smith, unpublished data)

## Neoacaridae?

*Neoacarus?**N. hibernicus?* (Gledhill, 1969, 1985)

?, speculation.

the loss of larval parasitism in a number of species using the last-mentioned criterion and I expect that, in most cases, he was correct. While the other criteria make intuitive sense, predictions based on these are more likely to be erroneous. For example, Mitchell (1954, p. 351) noted that *Aturus* spp. (often incorrectly cited as reference to *Aturus scaber*, e.g. Böttger (1972) and Jones (1967)) produce eggs that are almost half the length of an adult female and stated that these probably hatch into deutonymphs. To date, all evidence indicates that *Aturus* spp. have parasitic larvae (Smith and Oliver, 1986) but it is still possible that non-feeding larvae exist in some species. There is much confusion regarding *Unionicola* spp.: it is clear that many species are parasitic on chironomid midges (see the discussions in Smith and Oliver (1986) and Edwards and Dimock (1995)) yet there are reports of species that can forgo larval parasitism (Paterson and MacLeod, 1979; Baker, 1989).

## EVALUATION OF POTENTIAL CORRELATES

*Phylogenetic*

The loss of larval parasitism has occurred sporadically among widespread taxa of Hydrachnidia. Species with larvae that are not parasitic occur within four (five?; the

number if speculative references are included) of seven superfamilies, eight (11?) of approximately 45 families,\* 14 (19?) of over 300 genera, representing 29 (38?) of over 5000 species and include species within six species groups of *Piona* plus two subgenera of *Arrenurus*. A conservative estimate is that the loss of larval parasitism has occurred independently at least 21 times. The trait is manifested repeatedly among species in the families Pionidae, Limnesiidae and Hygrobatidae, although the reason for this is not apparent. There are no species that lack larval feeding among the Hydrachnoidea or Eylaoidea: the trend in these superfamilies is towards an extended host association with extensive engorgement on a host (Smith, 1988).

There often appears to be either two forms of the same species or two closely related species, one with typical parasitic larvae and the other with non-feeding larvae. Crowell (1960) reported two types of *Thyas stollii* that were indistinguishable except for the size of their eggs and differences in their life histories, while Prasad and Cook (1972) suggested that *T. stollii* may represent two very closely related species which were being confused. Several authors have reported a loss of parasitism in *Lebertia stigmatifera* (= *Lebertia complexa*, = *Lebertia tau insignis*; Lundblad, 1924; Wesenberg-Lund, 1939; Sparing, 1959; Böttger, 1972), but the larvae in some populations apparently need to feed on a host (P. Martin, personal communication). Riessen (1982a,b) reported non-feeding larvae in *Piona constricta*, but I. Smith, personal communication) confirmed that this was actually a new species that was very similar to *P. constricta*. Wainstein (1980) recorded three occurrences of closely related species pairs (*Limnesia maculata* (parasitic larvae) and *Limnesia angustata* (non-feeding larvae), *Hygrobates longipalpis* (parasitic larvae) and *Hygrobates longiporus* (non-feeding larvae) and *Attractides spinipes* (parasitic larvae) and *Attractides nodipalpis* (non-feeding larvae)) and stated that the larvae of some of these pairs were almost impossible to tell apart. *Hygrobates neoocetopus* apparently lacks a parasitic larval association in at least some western Canadian populations (H. Proctor, personal communication), but has parasitic larvae in at least some eastern Canadian populations (I. Smith, personal communication). *Arrenurus manubriator* and *Arrenurus rufopyriformis* both occur in two forms, one with parasitic larvae and one with non-feeding larvae. In both cases the two forms maintain separate populations in nature, breed true in the laboratory and the two forms can be interbred with at least partial success (B. Smith, unpublished data). The two forms presumably represent either incipient or recently diverged species. *Piona nodata* is reported to lay two types of eggs: small eggs resulting in parasitic larvae are laid in spring, whereas large eggs resulting in non-feeding larvae are produced in summer (Piersig, 1897-1900); Lundblad, 1927; Böttger, 1962). While these reports suggest that there may be a seasonal change in

\* These figures probably underrepresent the proportion of species lacking larval parasitism: larval stages have been described for only 70 genera and 28 families (Smith and Oliver, 1986) and only a small proportion of the known species. A rough estimate would be that less than 5% of species in which the larvae have been studied lack larval parasitism.

reproductive tactics within a population, an alternative possibility is that cryptically similar species are involved. My own experience is with species in which lineages produce only one type of larva and which maintain separate populations in nature, but this does not preclude the occurrence of populations producing larvae of both lifestyles or of a given female producing both types of larvae. It appears that while there are numerous examples of the loss of larval parasitism, these represent recent evolutionary events involving divergent populations, incipient species or recently diverged species and lineages with this trait are not evolutionarily long-lived.

#### *Environmental*

While it would be intuitively logical to expect that the trait of forgoing larval feeding and host association would have correlations with the mites' ecology, there is no obvious trend. Species exhibiting these life history traits inhabit caves (*Allothrombium* sp.), the planktonic zones of lakes (*Piona* n. sp., near *constricta* and *Piona pusilla*), the littoral zones of lakes (*Hygrobates nigromaculatus*, *A. manubriator*, *Limnesia* spp. and *Piona* spp.), temporary ponds (*A. rufopyriformis* and *T. stolli*), streams (*H. neoocetopus*, *H. longiporus*, *A. nodipalpis* and *Lebertia* spp.) and interstitial habitats (*Taintaturus stoutae*?, *Neoacarus hibernicus*?, *Acherontacarus halacaroides*?, and *Arrenurus (Truncaturus)* n. sp.). In specific, mites inhabiting interstitial habitats can be buried several metres into the substrate (e.g. Cook, 1991) and a logical assumption would be that at least some of these species forgo larval parasitism. The loss of larval parasitism could reflect difficulty in obtaining hosts or at least that there would be a survival advantage since the larvae would be forgoing the risks associated with host association. However, a large proportion of a species' dispersal is presumably host mediated, so the persistence of loss of larval parasitism in a species should reflect stability of habitat over a long time scale. Although some species lacking larval parasitism and host association occur in temporary ponds, these habitats may be predictably seasonally present over many years. There is no detailed comparison of habitat association for closely related species or populations within species that represent the two larval lifestyles. My own experience with the two forms of *T. stolli* and *A. rufopyriformis* is that there is no apparent difference between temporary ponds inhabited by one form in comparison to temporary ponds inhabited by the other form. Furthermore, while both *T. stolli* and *A. rufopyriformis* co-occur in nature, there is no site-by-site correspondence in the loss of parasitism between the two species. I have also noted that large populations of appropriate hosts co-occur in temporary ponds with lineages of *A. rufopyriformis* lacking larval parasitism, but that these mites do not limit reproduction to times of year when hosts are available, unlike their parasitic counterparts.

#### *Reproductive*

For a larval mite to transform without feeding, the female mite would have to provide the offspring with an adequate amount of nutrients – presumably a greater

quantity than for larvae that require parasitic feeding. A reproductive trade-off between the size of eggs and number of eggs would therefore be expected: females from a lineage with non-feeding larvae would typically produce smaller clutches of larger eggs than females from a comparable lineage with parasitic larvae (Crowell, 1960; Böttger, 1962, 1976; Smith, 1976; Riessen, 1982a; Gledhill, 1985; Hezewijk and Davids, 1985; Ten Winkel, 1987; Cook *et al.*, 1989; Cook, 1991). For example, Crowell (1960) found that one form of *T. stolli* produced eggs with a mean diameter of 0.142 mm, with clutches of 74, 59 and 43 eggs and that the larvae required a host (type I). A second form of *T. stolli* (type II) produced eggs with a mean diameter of 0.24 mm and a mean clutch size of four eggs (range two to six eggs in 12 clutches). Böttger (1962) recorded that there were two types of *P. nodata*, one with large eggs (270  $\mu\text{m}$ ) that developed directly into deutonymphs and one with small eggs (190–195  $\mu\text{m}$ ) that had parasitic larvae. Hezewijk and Davids (1985) reported that female *H. longipalpis* laid a mean of 23 eggs per clutch with a mean diameter of 171  $\mu\text{m}$  (which produced parasitic larvae), *H. nigromaculatus* laid four to five eggs per clutch of a mean 194  $\mu\text{m}$  diameter (which produced non-feeding larvae) and *Hygrobatas trigonicus* laid two to three eggs of a mean 153  $\mu\text{m}$  diameter (which produced parasitic larvae). Cook *et al.* (1989) surveyed a diversity of *Arrenurus* species and reported that *A. rufopyriformis* and *A. manubriator*, the only two species which lacked larval parasitism, represented the extreme of a trend for smaller clutches with larger larvae (and eggs) that was the general pattern of *Arrenurus* species with larvae parasitic on Diptera.

### *Morphological*

Certain morphological traits may be associated with the loss of larval parasitism. The larvae may be very similar to typical parasitic larvae (e.g., *A. manubriator*) or they may have a wider dorsal shield (Böttger, 1962; Wainstein, 1980; Hezewijk and Davids, 1985; B. Smith, unpublished data), shorter legs (Wainstein, 1980; B. Smith, unpublished data) and reduced sclerotization and setation (B. Smith, unpublished data). The larvae of *Arrenurus (Truncaturus)* n. sp. are reduced to little more than membranous bags with very faint sclerotization, setae reduced to small pegs and legs reduced to about the length of the trochanter of larval *Arrenurus danbyensis*, its closest local relative (B. Smith, unpublished data). These traits are related to the likelihood that the larvae will hatch from eggs or remain within the egg until transformation to the deutonymph (B.A. Wainstein, 1980; and my personal observation).

Adults may also exhibit modifications associated with a loss of larval parasitism: while the adult may be virtually indistinguishable from individuals producing parasitic larvae (e.g. *Thyas stolli*; Crowell, 1960), they are frequently smaller (e.g. *Piona* spp. (Wainstein, 1980) and *A. manubriator* and *A. rufopyriformis* (personal observation)). Some species that lack an apparent relative population or species with parasitic larvae and, hence, probably have a longer history of loss of larval parasitism, frequently have very small adults (e.g., *Limnesia* sp. (H. Proctor,

personal communication), *Physolimnesia australis* (Proctor, 1997) and *Arrenurus (Truncaturus)* n. sp. (B. Smith, unpublished data)). In species with a well sclerotized idiosoma, the gonopore of adult females may be exceedingly large when the larvae of the species are non-feeding, which is correlated with the large size of the eggs necessary for the greater nutritional reserves (*A. manubriator*, *A. rufopyriformis* and *Arrenurus (Truncaturus)* n. sp. (personal observation)). It is apparent that changes in larval lifestyle can have profound effects on the other life history stages and probably alters the overall reproductive strategy of the species.

#### DISCUSSION

The loss of larval feeding among species of *Parasitengona* may at first appear to be highly unusual, but Hart (1996), in reference to aquatic invertebrates, described it as 'one of the most significant and widespread life-history phenomena known'. Indeed, it is known among at least ten phyla (Strathmann, 1978), with independent loss of feeding in many genera and families. Within the Echinodermata alone, it has occurred at least 15 different times (Strathmann, 1978; Hart, 1996). Most examples among marine invertebrates involve pleisiotypically planktonic larvae that give up both feeding and dispersal, closely paralleling the loss of parasitic feeding and dispersal among larval parasitengonines. The term 'lecithotropic' is applied to these non-feeding larvae, in reference to the dependency on the reserves provided in the eggs (Strathmann, 1978). Among marine invertebrates, the trait for non-feeding larvae is correlated with an increased investment per offspring, a faster rate of growth, a reduced risk to the larvae and a comparatively smaller adult size (Strathmann, 1985), as also appears to be true with this trait among Hydrachnidia.

While the loss of larval feeding appears to be a common trait in the animal kingdom, the loss of a parasitic lifestyle appears to be rare. As in the *Parasitengona*, loss of parasitism has occurred repeatedly among lampreys (see Youson and Beamish, 1991), although the mechanism is very different. Lampreys go through a filter-feeding larval stage, frequently followed by a parasitic juvenile phase, before becoming reproductively active during a non-feeding phase. However, accelerated sexual maturation results in a species forgoing parasitic feeding (Malmqvist, 1986; Youson and Beamish, 1991). Again, several important parallels exist with the loss of parasitic larvae in *Parasitengona*. Species with and without a parasitic phase appear to be paired (termed 'paired' or 'satellite' species in the lamprey literature) and are believed to arise from a common ancestor having parasitic juveniles (Youson and Beamish, 1991). The loss of parasitism is correlated with a smaller adult size, proportionately large eggs relative to the female body size, reduced fecundity and reduced dispersal (Malmqvist, 1986). While the presence or absence of a parasitic phase has been used as justification for distinguishing species of lampreys, there is some question as to whether divergent populations of one species could exhibit different life histories and whether individuals representing both life

histories could co-exist within one population (Beamish and Withler, 1986; Youson and Beamish, 1991). The pairing of forms or species also occurs frequently with the Hydrachnidia, as does the question of species distinction based primarily on differences in life history. Careful investigation involving interbreeding, estimates of gene flow or DNA analysis would be necessary in many cases to resolve such questions.

Paired species or even divergent populations with and without parasitic larval associations provide ideal situations for comparing these lifestyles. The apparently recent divergence would mean that differences in traits not related to the absence or presence of parasitism would be minimal. The parallel evolutionary loss provides ample opportunity for replication, while avoiding phylogenetic correlation.

Comparative studies between parasitic and free-living lifestyles have been conducted on other taxa (e.g. Copepoda (Poulin 1995), Nematoda (Wharton, 1986) and Platyhelminthes (Calow and Jennings, 1974)) but the comparisons represent at least generic- or family-level comparisons. Also, in these comparisons the parasitic lineages have evolved from free-living ones rather than the reverse, as seen in the loss of larval parasitism among Parasitengona. Parasitengonine mites provide ideal study organisms for extending the comparison.

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