Acarologia

A quarterly journal of acarology, since 1959
Publishing on all aspects of the Acari

All information:
http://www1.montpellier.inra.fr/CBGP/acarologia/
acarologia-contact@supagro.fr

OPEN ACCESS

Acarologia is proudly non-profit, with no page charges and free open access

Please help us maintain this system by
encouraging your institutes to subscribe to the print version of the journal
and by sending us your high quality research on the Acari.

ON THE MORPHOLOGY AND PARASITISM OF *ARRENURUS GLOBATOR* (O. F. MÜLLER, 1776) (HYDRACHNIDIA, ACARI) A WATER MITE WITH AN UNUSUALLY EXTENSIVE HOST SPECTRUM

BY Klaus BÖTTGER [1] & Peter MARTIN [2]

ARRENURUS GLOBATOR
LARVAL MORPHOLOGY
PARASITISM
LIFE CYCLE
INSECT HOSTS
COLEOPTERA
DIPTERA-NEMATOCERA
HOST SPECIFICITY
HOST GENERALIST

SUMMARY: *Arrenurus globator* is a water mite distributed widely throughout Europe. The morphology of larval *A. globator* is described. The parasitological behaviour of the species turned out to be extraordinarily variable. The host spectrum is substantially broader than for the other well-known species of the family Arrenuridae. Observations made in the laboratory and in the field demonstrated that the parasitic stage can successfully be spent on nematocerous larvae and imagines as well as on the larvae of different coleopteran families. Depending on the host species, the life cycle of *A. globator* is either totally subaquatic or the larva goes through a supra-aquatic stage on an aerial host. The factors on which the host choice are dependent are still unknown. The known hosts of the species are reviewed. *Arrenurus globator* can be regarded as a host generalist.

ZUSAMMENFASSUNG : *Arrenurus globator* ist eine häufige, in ganz Europa verbreitete Wassermilbe. Die Larvalmorphologie von *A. globator* wird dargestellt. Das Verhalten der Larven von *A. globator* erweist sich bezüglich des Parasitismus als ungewöhnlich plastisch. Das Wirtsspektrum ist wesentlich größer als bei anderen bislang näher untersuchten Arten der Arrenuridae. Beobachtungen im Labor und Freiland zeigen, dass die parasitische Phase erfolgreich sowohl an Larven und Imagines von Nematocera als auch an Larven mehrerer Coleoptera-Familien durchlaufen wird. Der Entwicklungszyklus von *A. globator* verläuft somit in Abhängigkeit von der Wirtswahl entweder als ganzes subaquatisch, oder aber es wird eine supraaquatische Lebensphase an einem in der Luft lebenden Wirt eingeschaltet. Von welchen Faktoren die jeweilige Wahl des Wirtes abhängt, ist gegenwärtig noch unbekannt. Es wird ein Überblick über die bisher bekannten Wirte der Art gegeben. *Arrenurus globator* kann als Wirts-Generalist angesehen werden.

1. Teichgarten 12a, D-38300 Wolfenbüttel, Germany.
2. Christian-Albrechts-Universität, Zoologisches Institut, Olshausenstr. 40, D-24098 Kiel, Germany; e-mail: pmartin@zoologie.uni-kiel.de (corresponding author).

INTRODUCTION

Parasitology in general is marked by different degrees of host specificity; it may vary from a single host species up to several different suitable host species of different orders which can be parasitised from a single parasite species. The evolutionary factors influencing this specificity are various and depend mostly on the habits of free-living progenitors and the way in which the parasitic association arises (ADAMSON & CAIRA 1994).

Little is known about the extent of host specificity; observations are often derived from a single study on a selected parasite species, and some results turned out to be valid only on a regional scale. The number of known host species for a parasite and as a result the degree of host specificity directly depends on the number of studies on the parasite-host associations of the respective parasite species (POULIN 1998). Thus, a supposed host specificity of a species often only reflects the lack of information on the hosts.

As a rule, the water mite larvae as well as the whole parasitengonine mites are temporary ectoparasites. The two other free-living stages of the water mites, the (deuto-)nymph and the adult, are predators. Host associations of ancestral water mites are unknown, but were assumed to have been general and opportunistic as reflected by extant Hydryphantoidea which utilise a wide spectrum of hosts (SMITH & OLIVER 1986). Most "higher" water mites were seen as more or less host specialists which use single taxa in separated insect orders. Since accurate larval descriptions of water mites only exist for a fraction of this species-rich group, there are only few comprehensive studies on the complete host ranges of water mites. Thus, nearly nothing is known on water mite host specificity (DI SABATINO et al. 2002).

The present study deals with *Arrenurus globator*, a widespread species found in standing waters throughout Europe (see VIETS 1978). There are only insufficient descriptions of the larva of *A. globator*. This is regrettable because the species is one of the few water mites with a relatively well-known host spectrum which has been demonstrated in earlier studies to be extraordinarily broad (BÖTTGER 1962, STECHMANN 1975, 1980). The aim of the present study was to present an accurate description of the larva, and together with new data on its parasitology, to review the parasite-host associations of the species.

Material and methods, collecting site

The material examined derived from the littoral of a small pond near the city of Kiel (in Schleswig-Holstein, northern Germany): Larvae of Dytiscidae and Hydrophilidae were collected in early June 1997 from the reeds (predominately *Glyceria maxima*) of the littoral area of a small shallow lake (9°48′51″E, 54°16′35″N: Rümlandteich, 20 km west of Kiel). The coleopteran larvae were determined to the genus level according to KLAUSNITZER (1996). Only a few of the sampled coleopterans were uninfected by parasites. The species diagnosis of *A. globator* was made after the cultivation of the parasitic larvae to the adult stage. Cultivation took place in microaquariums (water temperature 22-24 ° C). The hatched nymphs were fed with ostracods (taken from different small ponds near the university).

When not otherwise indicated, the material examined for the larval description came from five larvae which had been removed from different hosts. For the method of measurement (all data are given in μm) and the abbreviations of the morphological characters see PRASAD & COOK (1972) and STECHMANN (1977a).

RESULTS

The results were divided into a morphological part (description of the larva) and in the parasitological part which includes some data on cultivation.

MORPHOLOGY

The larvae of *Arrenurus globator* are characterised by a large dorsal plate with setae Mh1, as found for all larvae of the water mite family Arrenuridae.

Idiosoma ovate (FIG. 1a). Dp covering about two thirds of the dorsal surface of idiosoma, even in engorged individuals. About one half of the ventral idiosoma covered by the coxal plates. Length of idiosoma (n=29) 216-328 (256), width 160-244 (206).
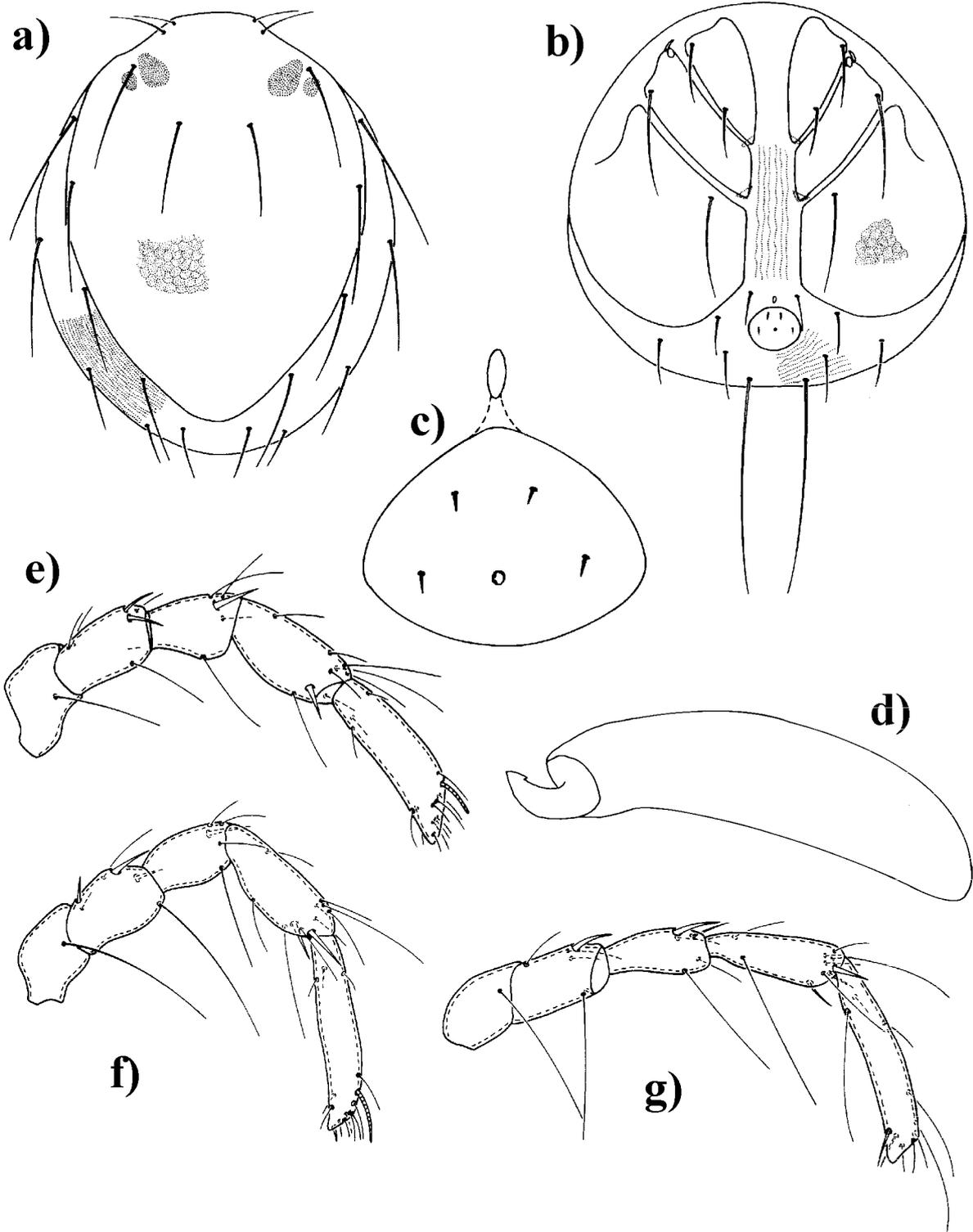
FIG. 1: Morphology of larval *Arrenurus globator*. a. — dorsal idiosoma, b. — ventral idiosoma, c. — area of the excretory pore plate, d. — chelicera, e. — IL lateral, f. — IIL lateral, g. — IIIL lateral.

Dorsal idiosoma: Dp with a scale-like pattern. Length of Dp 228-245 (233), width 165-190 (176). Mp2-Amdp 62-67 (65), Mp1-Mp1 47-54 (50), Mp2-Mp2 53-57 (55), Lp1-Lp1 57-65 (60), Lp2-Lp2 90-97 (94), Mp1-Lp1 5-7 (6), Mp2-Lp2 32-41 (36), Mp1-Mp2 54-61 (58), Lp1-Lp2 27-31 (29), Mh1-Mh1 150-163 (156), Mp1-Mh1 87-95 (90), Mp1 28-35 (31), Mp2 32-40 (36), Lp1 32-41 (36), Lp2 55-71 (61), Hu 75-95 (86), Mh1 65-78 (69), Mh2 58-62 (60), Mh3 54-57 (55), Mh4 35-39 (37), Lh1 88-92 (90), Lh2 50-52 (51), Lh3 18-25 (21).

Ventral idiosoma (Fig 1b): Cp with a scale-like pattern. CXI, CXII and CXIII completely separated. CXI with two pairs of setae, CXII and CXIII with one pair of setae each. Expp wide and rounded, with two pairs of short setae (FIG. 1c). Exp nearly round, lying in the centre of the Expp. Setae E1 and E2 short and E1 lying anterior and E2 lateral of Exp. Length CXI 67-70 (68), width CXI 42-47 (44), length CXII 37-40 (38), width CXII 63-69 (66), length CXIII 39-45 (43), width CXIII 94-98 (96), C1-C2 45-51 (48), C1-Mmcp 16-19 (18), C4-Pmcp 80-87 (84), C1-C4 43-52 (47), C1 38-54 (46), C2 52-63 (58), C3 77-83 (80), C4 59-71 (64), length of Expp 24-30 (27), width 33-38 (36), V1 26-31 (28), V2 32-38 (35), V3 58-65 (60), V4 93-112 (105).

Gnathosoma: base 74-85 (78), chelicere (FIG. 1d) 74-85 (80), chela 14-18 (16), length of P2 32-36 (34), height 25-29 (27), length of P3 26-28 (27), height 26-28 (27), claw 17-19 (18).

Legs (FIG. 1e-g, number of setae without eupathidia): Leg I: total length 211-223 (217), length IL1 (1 seta) 34-36 (35), IL2 (7 setae) 36-39 (37), IL3 (5 setae) 35-36 (35), IL4 (9 setae) 47-49 (48), IL5 (14 setae) 59-63 (61), height IL1 23-25 (23), IL2 23-25 (24), IL3 21-24 (22), IL4 19-24 (22), IL5 16-20 (18).

Leg II: total length 227-240 (233), length IIL1 (1 seta) 36-40 (38), IIL2 (7 setae) 37-40 (39), IIL3 (5 setae) 36-37 (36), IIL4 (11 setae) 51-55 (53), IIL5 (14 setae) 67-68 (68), height IIL1 24-26 (25), IIL2 25-27 (26), IIL3 21-23 (22), IIL4 20-25 (23), IIL5 17-19 (18).

Leg III: total length 235-250 (243), length IIIL1 (1 seta) 39-41 (40), IIIL2 (6 setae) 39-41 (40), IIIL3 (5 setae) 37-42 (39), IIIL4 (10 setae) 51-53 (52), IIIL5 (11 setae) 69-73 (72), height IIIL1 21-25 (23), IIIL2 22-24 (23), IIIL3 19-22 (20), IIIL4 19-23 (22), IIIL5 14-15 (15).

Cultivation and parasitological findings

The parasitised Dytiscidae larvae were of the four genera *Dytiscus*, *Hydaticus*, *Graphoderus* and *Laccophilus*; the parasitised larvae of Hydrophilidae were exclusively representatives of the genus *Hydrophilus*. The parasitism was not limited to the last larval stage of the host; larval moults could thus be observed in the laboratory several times. The larvae of *A. globator* which were shed during host moulting did not die, because they had already consumed enough food for successful further development.

The parasites were attached ventrally to the thorax and abdomen of the host, in the areas of the soft and less sclerotized intersegmental skins as well as to joints of the legs (see FIG. 2).

The intensity of infestation was low. Most host larvae carried between one and five parasites. The maximal infection was found on a *Hydrophilus* larva with 20 parasites; the larvae were preferentially attached near the caudal abdomen near the stigmata. The following cultivation data for the postlarval development of the parasites was recorded: First larvae entered the Postlarval Resting stage I two days after detaching from the host; this stage lasted three days. The duration of the deutonymph stage was about three weeks when food (ostracoda) was permanently present; afterwards they entered the Postlarval Resting stage II for a duration of four to six days. This data largely corresponds to the previous observations of BÖTTGER (1962). The cultivation of 40 adults resulted in 24 male and 16 female *A. globator* specimens.

DISCUSSION

THE LARVA OF *A. GLOBATOR*

There have been many descriptions of *Arrenurus globator* larvae (e.g. KOENIKE 1908, SPARING 1959, BÖTTGER 1962), presumably because of the wide distribution of the species. But even the most recent description (STECHMANN 1977a) is not up to the standard of the larval description given by PRASAD & COOK (1972). Therefore a new description of *A. globator* was given.

MÜNCHBERG (1937) and SPARING (1959) assumed that the *Arrenurus* larvae could not be differentiated taxonomically, but the work of e.g. STECHMANN
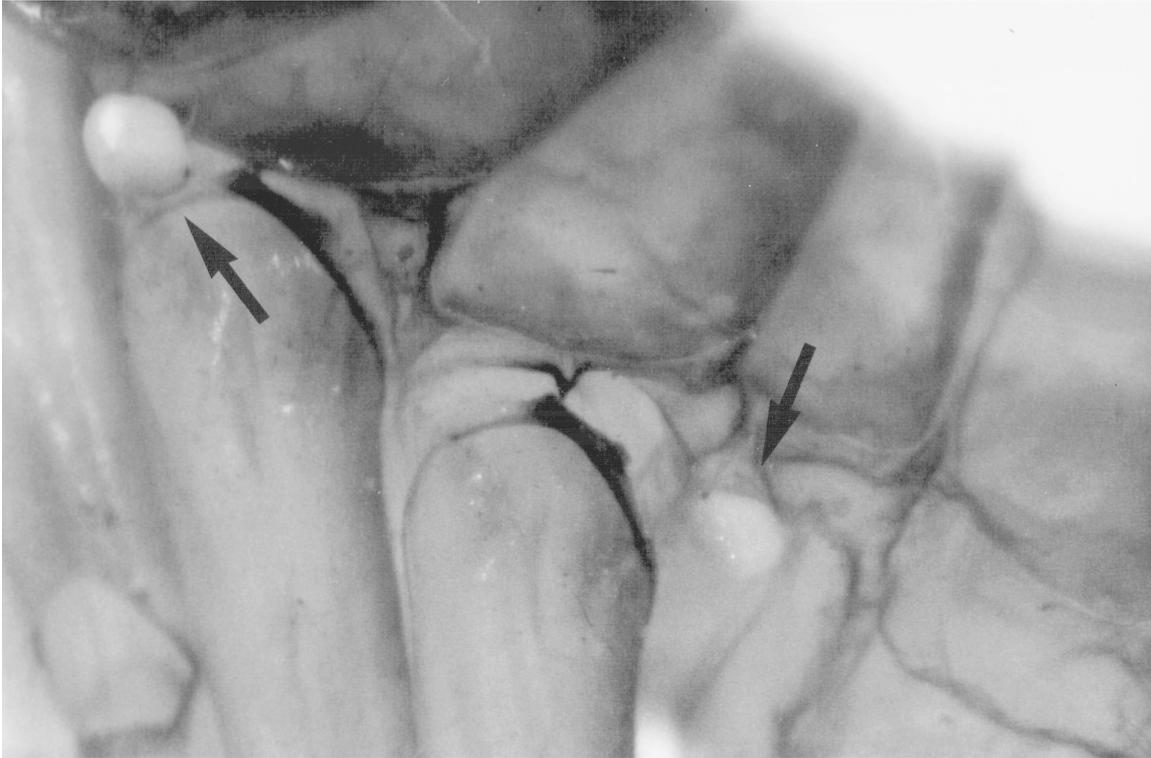
Fig. 2: Larva of *Dytiscus* sp. (left side of thorax) with two parasitic and distinctly engorged *Arrenurus globator* larvae. The parasitised host was collected in early June 1997 in the littoral vegetation of a small shallow lake (see text). The water mites lost their pigments during the preservation in ethanol and appear to be bright. Length of the water mite idiosoma about 250 μm.

(1977a) and B. P. Smith (1990) proved otherwise. It is still not possible to determine the larvae of the species-rich Arrenuridae to the species level because of the lack of detailed larval descriptions; only an increase in such larval descriptions could change this situation.

Stechmann (1977a) selected several morphological characters to distinguish nine *Arrenurus* species. Comparing his data for *A. globator* with data gathered in the present study (Tab. 1) reveals that there is only agreement on a few characters. The differences are possibly caused by certain morphological differences between freshly hatched larvae and larval exuviae (used by Stechmann) and engorged larvae (used in the present study). It is also possible that the number of measured individuals (five for each) was insufficient.

Böttger (1962) found an idiosomal length of 180-215 μm for larval *A. globator* after hatching. The range of idiosomal length of the engorged larvae in the present study lay between 216-328 μm (average 256 μm). Thus, the body length of larval *A. globator* increased by at least 150 % during the feeding.

	Stechmann (1977a)	present study
length of Dp	203-220	228-245
width of Dp	149-170	165-190
Mp1-Mp1	45-47	47-54
Mp2-Mp2	41-56	53-57
Lp1-Lp1	**55-59**	**57-65**
Lp2-Lp2	84-90	90-97
Mh1-Mh1	133-144	150-163
Mp1-Mh1	96-104	87-95
Mp1-Mp2	**55-69**	**54-61**
median length CXI	55-65	67-70
median length CXII	30-33	37-40
median length CXIII	31-35	39-45
C1-C2	**45-50**	**45-51**
C1-Mmcp	12-16	16-19

Tab. 1: Morphometrical data of *Arrenurus globator* larvae from Stechmann (1977a) compared with the results of the present study. Agreements are marked in bold.

Through the morphological characterisation and re-description of larval *A. globator*, determining specimens of this stage will be easier. However, due to the few recent larval descriptions of Arrenuridae which are sufficient for taxonomic work, the only practicable way to work on larval *Arrenurus* is the one which was applied in the present study: The parasitic larvae must be reared to adulthood.

THE PARASITISM OF *A. GLOBATOR*

Based on his observations of representatives of the genus *Arrenurus* (fam. Arrenuridae), MÜNCHBERG (1958) distinguished between "Odonata-Arrenuri" and "Nematocera-Arrenuri". The larvae of the former parasitise odonate imagines, the latter nematocerous imagines. In both cases the parasitic stage is spent on host imagines outside the aquatic environment. The water mite larvae reach these aerial imagines by infecting their juvenile stages: In the case of Odonata the larvae, and in the case of Nematocera the pupae. This phoretic stage is thus necessary for the switch to the host imago during the metamorphosis so that the parasitism can start.

Within the scope of his thesis, BÖTTGER (1962) worked with *A. globator*, which until then belonged to the "Nematocera-Arrenuri". He put the larvae and pupae of *Culex pipiens* (Culicidae) together with the larvae of *A. globator* in small aquariums to study the switching during host metamorphosis. The result, as reported in detail in BÖTTGER (1962), was quite unexpected: the larval water mites attached themselves to and fed upon the larval *Culex* and within 4-5 days had already taken in sufficient food for successful further development. The idiosoma of the parasites grew from 180-215 to 250-300 μm in length and from 165-200 to 225-290 μm in width. The preferred attachment sites were the caudal abdominal segments; i.e. those body regions of the midges which were first reached by the larval mites while the hosts hung underneath the surface of the water to breathe. If the midge larva shed its skin or metamorphosed before the parasite was fully engorged, the latter died; they became inactive and were unable to make the switch to the next developmental stage of the host.

In parallel experiments it was shown that the parasitic stage of *A. globator* was also able to survive successfully on the larvae of *Chaoborus* sp. However, infection of this representative of another nematocerous family (Chaoboridae) occurs less often than of *C. pipiens*, at least in the laboratory experiments.

BÖTTGER (1962) did not observe the second modus of larval parasitism of *A. globator*, i.e. the parasitisation of midge imagines, although it is described in the literature (MÜNCHBERG 1937). The mite larvae never infected pupae of *C. pipiens* in BÖTTGER's observation vials, and the hatching imagines of *C. pipiens* were always not parasitised.

It is still not clear just what influences the determination for one of the two modes of parasitism in natural environments. Whatever the cause, the modes lead to basic differences in the course of the developmental cycle of *A. globator*. If a larval midge is parasitised, its entire life is spent subaquatically and there is no danger of the mite not being able to return to the aquatic environment at the end of the parasitic stage. On the other hand, the mites which parasitise a midge pupa attach themselves during the phoretic stage to a midge pupa; a step necessary to ensure a successful switch during host metamorphosis. Although there is the danger of not being able to return to the water from the aerial host, this mode results in the chance of the species being distributed to other, new biotopes.

During his earlier studies, BÖTTGER (1962) repeatedly collected coleopteran larvae of the families Dytiscidae and Gyrinidae which had been parasitised by *A. globator* larvae. Species determination was possible after cultivating to the adult mites. BÖTTGER caught his specimens at the same time of year as in this study (late May/early June). One of the *Dytiscus* larva was parasitised by no fewer than 56 water mite larvae; the ventral side of the host seemed to be coloured red by the large number of parasites.

It was demonstrated that the parasitic stage of *A. globator* could be spent not only supra-aquatically on host imagines but also subaquatically on host larvae, and that representatives of two different orders (Diptera-Nematocera, Coleoptera) are possible for the latter mode. *A. globator* is so far the only representative of the genus *Arrenurus* for which this has been demonstrated.

Further studies on the parasitism of larval *A. globator* were made by STECHMANN (1977b, 1980), who confirmed the wide range of hosts of this mite by

observing water mite larvae parasitising the larvae and imagines of Nematocera as well as of larval Coleoptera. On the basis of his own observations and a critical examination of literature, STECHMANN listed the following hosts of *A. globator*:

1. subaquatic:
— larvae of *Culex pipiens* and *Aedes cantans* (both Nematocera, fam. Culicidae) and of *Chaoborus* sp. (Nematocera, fam. Chaoboridae)
— larvae of Dytiscidae and Gyrinidae (both Coleoptera)

2. supra-aquatic:
— imagines of two different species each of Dixidae and Culicidae (both Nematocera)

ARRENURUS GLOBATOR AS A TYPICAL HOST GENERALIST?

The host specificity of a species declines as the number of suitable host species increases; highly host-specific parasites are restricted to a single host species (POULIN 1998). Often parasites in communities were classified as being host generalists or as host specialists (BUSH et al. 2001). But the terms are not clearly defined and were used in a rather subjective manner.

The extension of the host range of *A. globator* through the use of different modes of parasitisation principally offers two interspecific advantages. The lower host specification and the wide host range reduce the necessity of parasite-host-synchronisation. That means that the probability of the presence of suitable hosts is higher and there are suitable hosts more or less throughout a major part of the year. Besides this temporal advantage, there is also a broadening of parasitisation effort in a spatial scale: The parasitisation of hosts occurring in different habitats could increase the chance of host-finding. Thus, *A. globator* could have advantages over water mite species with a high host specificity, a factor often found in connection with a short presence of larvae. Some water mites produce several larval generations over the course of a year. Consequently, *A. globator* larvae which parasitise different hosts simultaneously could belong to different generations, and the modes of parasitisation could reflect a temporal annidation. Larvae in springtime e.g. could be parasites of Culicidae larvae and later appearing larvae

could parasitise dipteran imagines and/or coleopteran larvae.

Considering the results of BÖTTGER (1962) and STECHMANN (1975, 1980) and also the accurate summary of the situation in MEYER (1985), it seems incomprehensible that SMITH & OLIVER (1986) only found the Arrenuroidea to be "parasites of the emergent aerial imagines" in their detailed review (p. 453) and do not mention the parasitism of pre-imaginal aquatic insect stages. SMITH & OLIVER (1986) mentions *A. globator* parasitising the larvae of Dytiscidae and Gyrinidae (Coleoptera) captured in the field, but they made an incorrect assessment. They wrote that the reports discussed "appear to be based upon accidental associations resulting from artificial laboratory conditions" (p. 455). Consequently, in subsequent overviews such as in SMITH et al. (2001), only Nematocera and Odonata were reported as hosts for the genus *Arrenurus*. Furthermore it is doubtful whether SMITH & OLIVER's rejections of reports on other *Arrenurus* larvae parasitising larval Hydrophilidae (see literature therein) are justified.

There are some reasons for being cautious when considering a parasite to be a host generalist (BUSH et al. 2001), something particularly true for water mites: As mentioned above, the known host spectrum depends on the number of studies. Thus, it is evident that the known hosts of the widespread *A. globator* are more frequent than those of rarer water mite species. Recent data indicates another interesting phenomenon: Not all hosts parasitised by water mite larvae, even when in great numbers, allow larval development to continue into the next stages (FORBES et al. 2002). Laboratory results of BÖTTGER (1962) demonstrate that this is not the case for the proved host taxa of *A. globator* (with the exception of nematocerous adults), but these results have to be kept in mind when interpreting host specificity. If one defines a host specialist as a species which is parasitic on only one host, then only few species of the water mite genus *Arrenurus* could be considered to be true host specialists. One example is the odonate parasite *A. cuspidifer* (Müller, 1776), which has only one known host species (*Ischnura elegans*) (MÜNCHBERG 1935). This may simply reflect a lack of knowledge, in that MÜNCHBERG's study is the only one which dealt with the hosts of *A. cuspidifer*. In contrast, e.g. *Arrenurus*

planus Marshall, 1908 was called a "host generalist" because it has been observed to parasitise different odonate species (Forbes et al. 1999). Of the *Arrenurus* species reported to parasitise nematocera, nearly all were found on more than one host species (e.g. Stechmann 1977b, 1980). These observations show that a proper assessment of the host specificity of *Arrenurus* species is still not possible. However, for all reported cases of parasitism in *Arrenurus* species, the hosts have been either in Odonata or Nematocera. In contrast to all other water mite species with known hosts, the parasitic larval stage of *A. globator* could be successfully finished either subaquatically on the larvae of several families of nematocerans and coleopterans or on the aerial imagines of several nematocerous families. In contrast to other *Arrenurus* species, the unusually wide host range of *A. globator* increases its chances for finding exploitable hosts. This species could therefore more justifiably be called a "host generalist" than e.g. a species which is parasite of two or three species of one genera.

A quantitative study of the distribution of *A. globator* larvae on the different hosts is necessary for a assessment of the importance of the different host groups and stages. However, only expensive studies on seasonal occurrence of host-parasite associations could clarify the importance of the different hosts for *A. globator*. Parallel studies of benthic and emergent host-parasite communities would be necessary to accomplish this. In view of the insufficient state of the larval descriptions, a collection site which has *A. globator* as the only *Arrenurus* species present would be desirable for such a study.

Since there is little faunistical knowledge on the *Arrenurus* species, a comparison of the distributions of parasite and host species has so far been impossible to make. In addition, *A. globator* is a locally rare species. Cassagne-Méjean (1966) found *A. globator* only rarely during his comprehensive five-year study on *Arrenurus* species near Montpellier. The distribution of a assumed host generalist may perhaps be restricted by the regional absence of the preferred host (e.g. single species of Culicidae). Further studies on the distribution areas of parasites and hosts could allow insights into constrains on coevolutionary aspects to be made.

The widespread water mite *Arrenurus globator* with its extraordinary wide host range could serve as a model organism of a true host generalist.

REFERENCES

Adamson (M. L.) & Caira (J. N.), 1994. — Evolutionary factors influencing the nature of parasite specificity. — Parasitology (Supplement), 109: S85-S95.

Böttger (K.), 1962. — Zur Biologie und Ethologie der einheimischen Wassermilben *Arrenurus* (*Megaluracarus*) *globator* (Muell.), 1776, *Piona nodata nodata* (Muell.), 1776 und *Eylais infundibulifera meridionalis* (Thon), 1899 (Hydrachnellae, Acari). — Zool. Jb. Syst., 89: 501-584.

Bush (A. O.), Fernandez (J. C.), Esch (G. W.) & Seed (J. R.), 2001. — Parasitism: The diversity and ecology of animal parasites: 566pp. Cambridge University Press, Cambridge.

Cassagne-Méjean (F.), 1966. — Contribution à l'étude des Arrenuridae (Acari, Hydrachnellae) de France. — Acarologia, 8 (Supplément): 1-183.

Di Sabatino (A.), Martin (P.), Gerecke (R.) & Cicolani (B.), 2002. — Hydrachnidia (water mites). — In Rundle, S. D., Robertson, A. L. & Schmid-Araya, J. M. (eds) *Freshwater Meiofauna: Biology and Ecology*: 105-133. Backhuys Publishers, Leiden, The Netherlands.

Forbes (M. R.), Muma (K. E.) & Smith (B. P.), 1999. — Parasitism of *Sympetrum* dragonflies by *Arrenurus planus* mites: maintenance of resistance particular to one species. — International Journal for Parasitology, 29: 991-999.

Forbes (M. R.), Muma (K. E.) & Smith (B. P.), 2002. — Diffuse coevolution: constrains on a generalist parasite favor use of a dead-end host. — Ecography, 25: 345-351.

Klausnitzer (B.), 1996. — Käfer im und am Wasser. — Die Neue Brehm-Bücherei, 567: 1-200. Westarp Wissenschaften, Magdeburg.

Koenike (F.), 1908. — Beitrag zur Kenntnis der Hydrachniden. — Abh. naturw. Ver. Bremen, 19: 217-266.

MEYER (E.), 1985. — Der Entwicklungszyklus von *Hydrodroma despiciens* (O. F. MÜLLER 1776) (Acari: Hydrodromidae). — Arch. Hydrobiol./Suppl., 66, 13 (3): 321-453.

MÜNCHBERG (P.), 1935. — Zur Kenntnis der Odonatenparasiten, mit ganz besonderer Berücksichtigung der Ökologie der in Europa an Libellen schmarotzenden Wassermilbenlarven. — Arch. Hydrobiol., 29: 1-122.

MÜNCHBERG (P.), 1937. — Über die an den Culicinae (Diptera) schmarotzenden *Arrenurus* - Larven (Hydracarina) II. — Intern. Rev. Hydrobiol. Hydrographie, 34: 353-372.

MÜNCHBERG (P.), 1958. —— Zur Infektion, Wirtswahl, Zoogeographie und angewandten Bedeutung des Parasitismus der Wassermilben-Larven (Hydrachnellae, Acari) an Luftinsekten. — Zool. Anz., 161 (5-6): 115-125.

POULIN (R.), 1998. — Evolutionary Ecology of Parasites. From individuals to communities. — Chapman & Hall, London: 212pp.

PRASAD (V.) & COOK (D. R.), 1972. — The taxonomy of water mite larvae. — Mem. Amer. Ent. Inst., 18: 1-326.

SMITH (B. P.), 1990. — Descriptions of larval *Arrenurus bartonensis* COOK, *Arrenurus birgei* MARSHALL, *Arrenurus neobirgei* COOK, and *Arrenurus rotundus* MARSHALL (Acari: Hydrachnidia; Arrenuridae). — Can. Ent., 122: 77-91.

SMITH (I. M.) & OLIVER (D. R.), 1986. — Review of parasitic associations of larval water mites (Acari: Parasitengona: Hydrachnida) with insect hosts. — Can. Ent., 118: 407-472.

SMITH (I. M.), COOK (D. R.) & SMITH (B. P.), 2001. — Water mites (Hydrachnida) and other arachnids. — In THORP, J. H. & COVICH, A. P. (eds) *Ecology and Classification of North American Freshwater Invertebrates*, Chapter 16: 551-659. 2nd edition. Academic Press, San Diego.

SPARING (I.), 1959. — Die Larven der Hydrachnellae, ihre parasitologische Entwicklung und ihre Systematik. — Parasitolog. Schriftenreihe, 10: 1-165.

STECHMANN (D.-H.), 1975. — Biologisch-ökologische Untersuchungen zum Entwicklungszyklus einheimischer *Arrenurus*-Arten (Hydrachnellae, Acari). — Ph.D. Thesis University of Kiel: 1-257.

STECHMANN (D.-H.), 1977a. — Zur Morphologie mitteleuropäischer *Arrenurus*-Larven (Hydrachnellae, Acari). — Acarologia, 18 (3): 503-518.

STECHMANN, (D.-H.), 1977b. — Zur Phänologie und zum Wirtsspektrum einiger an Zygopteren (Odonata) und Nematoceren (Diptera) ektoparasitisch auftretenden *Arrenurus*-Arten (Hydrachnellae, Acari). — Z. ang. Ent.: 349-355.

STECHMANN (D.-H.), 1980. — Zum Wirtskreis syntopischer *Arrenurus*-Arten (Hydrachnellae, Acari) mit parasitischer Entwicklung an Nematocera (Diptera). — Z. Parasitenkd., 62: 267-283.

VIETS (K. O.), 1978. — Hydracarina. — in: ILLIES, J. (ed.) *Limnofauna Europaea*, 532pp. G. Fischer, Stuttgart: 154-181.