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THE ZEBRA MUSSEL, *DREISSENA POLYMORPHA* (PALLAS), AS AN EPIZOON OF ANISOPTERAN LARVAE (ANISOPTERA: GOMPHIDAE, CORDULIIDAE, LIBELLULIDAE)

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A list of records of anisopteran larvae and final instar exuviae with attached zebra mussels is provided. It contains records of 29 specimens from 10 spp. with zebra mussels including 2 new records. The possibilities how this association between odonate larvae and zebra mussels comes into being are discussed. Considering the biology and the life history of the mussels, from a few of the recorded cases of this interaction it is assumed that the larval development of the Odonata involved is more variable than hitherto known.

INTRODUCTION

Aquatic stages of Odonata enter into numerous interactions with other aquatic organisms. Apart from various forms of predation and parasitism, commensal, phoretic or symbiotic associations, where aquatic invertebrates are attached to the cuticle of odonate larvae, are recorded. In German a fine distinction is made between these terms of interaction, and some kind of benefit for at least one partner of a "phoretic" association is required. As in most of these probably incidental cases a benefit is not clear, we follow the proposal of GRABOW & MARTENS (2000) and regard the attached animals without further assessment simply as epizoa.

The range of macroinvertebrates which are recorded attached to odonate larvae includes hydrozoan polyps (Hydrozoa; STOKS & DE BRUIN, 1996; GRABOW & MARTENS, 2000), moss animalcules (Bryozoa; WILDERMUTH, 2001), larvae

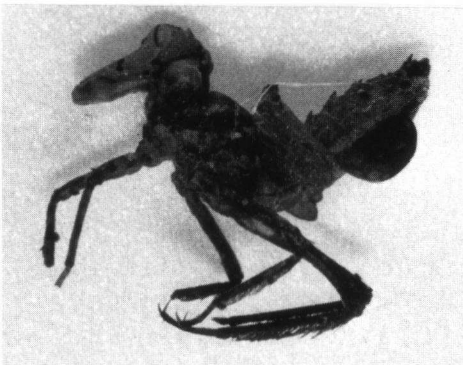

Fig. 1. Exuviae of *Cordulia aenea* (L.) with ventrally attached zebra mussel (side length = 4.4 mm), collected on 11-V-2000 at a gravel pit lake near Geisenfeld, Bavaria, Germany – [photograph by B. Golya and F. Weihrauch].

and pupae of caddisflies (Trichoptera; CORBET, 1962; WHITE & FOX, 1979), larvae and pupae of non-biting midges (Chironomidae; ROSENBERG, 1972; WHITE & FOX, 1979; WHITE et al., 1979; DUDGEON, 1989; HAWKING & WATSON, 1990; DE LA ROSA & RAMÍREZ, 1995; STERNBERG, 1999; WILDERMUTH, 2001), larvae of ceratopogonid midges (Ceratopogonidae; DUDGEON, 1989), pupae of blackflies (Simuliidae; CORBET, 1962) and sphaeriid mussels (Sphaeriidae; SOLDÁN et al., 1989). Most of these records are summarised by CORBET (1999, p. 613). We have recently found anisopteran final larval instar exuviae with attached zebra mussels *Dreissena polymorpha* (Bivalvia, Eulamellibranchiata: Dreissenidae) and this paper summarises and discusses the hitherto known records of zebra mussels attached to odonate larvae or exuviae.

METHODS AND NEW RECORDS

Apart from a literature search, we obtained unpublished records from personal communications, including several in response to a query sent to an international Odonata mailing-list on the Internet (URL: <http//:dragonflies.listbot.com>). The results are summarised in Table II. Details of our new records are as follows:

On 10-VI-1997, one exuviae of *Orthetrum cancellatum* (L.) (Libellulidae) was collected at a small channel that connects some ox-bows of the Lower River Rhine south-east of Rees, North Rhine-Westphalia, Germany (6°30′E, 51°42′N; S. Klostermann leg. & det.). The exuviae, which was found in the bank vegetation at a height of about 30 cm and 80 cm from the shore, carried one specimen of *D. polymorpha* attached to the dorsal side of the abdomen, covering segments 6-10. The shell length of the mussel is approximately 11 mm.

On 11-V-2000, one exuviae of *Cordulia aenea* (L.) (Corduliidae) was collected at a gravel pit lake north Geisenfeld, Upper Bavaria, Germany (11°37′E, 48°43′N; F. Weihrauch leg. & det.). The exuviae, which clung to the lower side of a leaf of *Carex* sp. at a height of 80 cm, 20 cm from the shore, carried one specimen of *D. polymorpha* attached to the ventral side of the abdomen, covering segments 6--8. The size of the mussel is 4.4×2.5×2.2 mm (Fig. 1).

DISCUSSION

Originating in the palaearctic Aralocaspian Basin, *D. polymorpha* has spread throughout Europe since the beginning of the 19th century, mainly by shipping (WALZ, 1973). In the mid-1980s it was also carried accidentally, most likely via ballast water from transoceanic vessels, to North America, where at the end of the 20th century it has infested the catchment areas of the Great Lakes and the Mississippi River, covering approximately one fourth of the nearctic region. Here the species is regarded as an aquatic nuisance species and a menace to native aquatic communities, especially to unionid mussels (for current information and distribution maps online on the Internet see the web site of the U.S. Geological Survey, URL: <http// :nas.er.usgs.gov/zebra.mussel/>).

By the use of its byssal threads, *D. polymorpha* is able to attach to a wide range of substrates. Apart from inorganic substrates and plants, *D. polymorpha* is well--known for the colonisation of the shells of other aquatic molluscs such as unionid mussels (e.g. SCHLOESSER et al., 1996) or snails (TUCKER, 1994). Even crustaceans as large as crayfish of the genus *Orconectes* (Cambaridae) are reported to be colonised heavily by zebra mussels (CARLTON, 1993; ANWAND, 1996; BRAZNER & JENSEN, 2000). During their life history, there are two main phases when zebra mussels settle on different substrates (ACKERMAN et al., 1994). The last larval stage, the pediveliger, can either swim using its velum or crawl using its foot (LEWANDOWSKI, 1982). Pediveligers preferentially select filamentous substrates such as aquatic plants, as well as the underside of various artificial substrates, where they undergo metamorphosis to become juvenile mussels (LEWANDOWSKI, 1982). The second phase involves the translocation of juvenile mussels to a suitable place for final settlement. This dispersal may be active (crawling up to 7 cm per night; SHEVCHENKO, 1949, cit. by ACKERMAN et al., 1994), or passive by floating, mostly on plant material (LEWANDOWSKI, 1982), or a combination of both. This final place of settlement is left by larger juveniles (> 3 mm shell length) or even adults only under extreme stress conditions, as it is linked to the complete loss of byssal threads and parts of the byssal gland (J. Borcherding, unpubl. observ.). Settlement on substrates on a large scale during both phases is more or less by chance (e.g. drift of larvae up to several hundred kilometers in a river, cf. BORCHERDING & DE RUYTER VAN STEVENINCK, 1992, or floating of small juveniles up to several kilometers on water plants which are detached from the bottom, cf. LEWANDOWSKY, 1982), which, concerning a small scale selection by the mussel, can be actively adjusted up to a few meters, e.g. in order to find some hard substrate in a muddy area. In cases of settlement of *D. polymorpha* on aquatic organisms, it must be assumed, that this "choice" depends not on a substrate attractiveness, but because these organisms may be the only suitable substrate in muddy or sandy areas.

Almost all of the dragonfly species in Table I are "spring species", i.e. species

Table I

Up-to-date list of records of dragonfly larvae or exuviae with attached zebra mussels *Dreissena polymorpha*

Family/Species	Record of	Collecting date	Mussel shell lengths	Location	Trophic state	Reference
Gomphidae						
Dromogomphus spinosus Sélys	1 exuviae	16-VI-2001	7.1 mm	Burt Lake, Cheboygan County, Michigan, USA	mesotrophic	O'BRIEN (2001), M. O'BRIEN (pers. comm.)
Gomphus pulchellus Sélys	1 exuviae	23-V/13-VI-1989	"small"	Kuhgrien gravel pit lake, Baden-Württemberg, Germany	mesotrophic?	FOIDL (1990)
Gomphus vastus Walsh	1 larva (F-1/0)	23-X-1993	15 mm + 16 mm	Mississippi River near Grafton, Jersey County, Illinois, USA	eutrophic?	TUCKER & CAMERER (1994)
Gomphus vulgatissimus (L.)	1 exuviae	?	?	River Spree, Brandenburg, Germany	eutrophic	H. Beutler (in litt.) in STÖCKEL (1987)
Gomphus vulgatissimus (L.)	exuviae	?	?	River Spree?, Brandenburg, Germany	eutrophic	BEUTLER (1991)
Gomphus vulgatissimus (L.)	2 exuviae	16-V-1992	ca. 10 mm/11 mm	Lake Wuckersee, Schorfheide, Brandenburg, Germany	mesotrophic	R. Mauersberger leg., R. Mauersberger (pers. comm.)
Gomphus vulgatissimus (L.)	1 exuviae	09-V-1997	9 mm	River Oder near Lebus, Brandenburg, Germany	eutrophic	O. Müller leg., O. Müller (pers. comm.)
Gomphus vulgatissimus (L.)	2 exuviae	14-V-1998	14.1 mm/5.3 mm	Gravel pit lake near Manching, Bavaria, Germany	mesotrophic	WEIHRAUCH (1999)
Gomphus vulgatissimus (L.)	1 exuviae	18-V-1998	5.5 mm	Gravel pit lake near Manching, Bavaria, Germany	mesotrophic	WEIHRAUCH (1999)
Gomphus vulgatissimus (L.)	1 exuviae	18-V-2000	3 mm	Datteln-Hamm-Canal near Hamm, North Rhine-Westphalia, Germany	eutrophic	POSTLER & POSTLER (2000), E. Postler & W. Postler (pers. comm.)
Gomphus vulgatissimus (L.)	1 exuviae	15-V-2001	11.1 mm	Datteln-Hamm-Canal, NSG Beversee, North Rhine-Westphalia, Germany	eutrophic	E. Postler & W. Postler leg., E. Postler & W. Postler (pers. comm.)
cf. *Hagenius brevistylus* Sélys	1 larva	07-IX-2000	10 mm	St. Croix National Scenic River, mile 7.5, Wisconsin, USA	mesotrophic	B. Karns & N. Rowse leg., B. Karns (pers. comm.)
Onychogomphus f. forcipatus (L.)	1 exuviae	06-VI-1982	"small"	Lake Müritz, Mecklenburg--Vorpommern, Germany	mesotrophic	STÖCKEL (1987)

Table I, continued

Family/Species	Record of	Collecting date	Mussel shell lengths	Location	Trophic state	Reference
Onychogomphus f. forcipatus (L.)	3 exuviae	15-VI-1997	ca. 1 mm/1 mm/1 mm	Lake Krummer Köllnsee, Schorfheide, Brandenburg, Germany	eutrophic	R. Mauersberger leg., R. Mauersberger (pers. comm.)
Onychogomphus f. forcipatus (L.)	1 larva (F-1)	21-X-2000	5 mm	Lake Helene-See near Frankfurt/O., Brandenburg, Germany	oligotrophic	O. Müller leg., O. Müller (pers. comm.)
Corduliidae						
Cordulia aenea (L.)	1 exuviae	11-V-2000	4.4 mm	Gravel pit lake near Geisenfeld, Brandenburg, Germany	eutrophic	F. Weihrauch leg.; (this paper)
Oxygastra curtisii (Dale)	1 exuviae	29-VI-2000	7 mm	Lake d'Annecy, Haute Savoie, France	oligotrophic	B. Bal leg., B. Bal, C. Deliry (pers. comm.)
Epitheca princeps Hagen	1 exuviae	1997	ca. 8 mm	Clear Lake near Peterborough, Ontario, Canada	mesotrophic	ANONYMOUS (1998)
Epitheca princeps Hagen	3 exuviae	17-VI-2000	8.5 mm/9.0 mm/10.0 mm	Clear Lake near Peterborough, Ontario, Canada	mesotrophic	K. Ness leg., C. Jones, D. Sutherland (pers. comm.)
Epitheca princeps Hagen	1 exuviae	17-VI-2000	9.2 mm + 4.8 mm	Clear Lake near Peterborough, Ontario, Canada	mesotrophic	K. Ness leg., C. Jones, D. Sutherland (pers. comm.)
Libellulidae						
Orthetrum cancellatum (L.)	1 exuviae	03-VII-1993	8 mm	Lake Jezioro Biale near Okunince, Central Poland	eutrophic	TONCZYK (1995), G. Tonczyk (pers. comm.)
Orthetrum cancellatum (L.)	1 exuviae	12-VI-1996	10 mm	Lake d'Annecy, Haute Savoie, France	oligotrophic	B. Bal, L. Delomez & P. Marigo leg., B. Bal, C. Deliry (pers. comm.)
Orthetrum cancellatum (L.)	1 exuviae	10-VI-1997	11 mm	Lower Rhine River ox-bow near Rees, North Rhine-Westphalia, Germany	eutrophic	S. Klostermann leg., (this paper)

that overwinter as F-0-larvae and then have a synchronised emergence in spring. Of the species listed, only *Onychogomphus forcipatus* is a "summer species" (SUHLING & MULLER, 1996). Secondly, the largest number of records are species regarded as "shallow burrowers" sensu CORBET (1999). Judging from the sizes of the mussels in the majority of the recorded cases, these relatively immobile dragonfly larvae were colonised either by veliger larvae of *D. polymorpha* in late summer or juvenile mussels in autumn, probably after the breakdown of aquatic plants, when numerous mussels are losing their primary places and must find a final place of settlement (cf. LEWANDOWSKI, 1982). However, this simple explanation for the colonisation does not work in all cases. For example, the mussel on one exuviae of *Gomphus vulgatissimus* with a side length of 14.1 mm (cf. WEIHRAUCH, 1999; Fig. 2) was too big for a life span of eight to ten months which passed at best between the assumed last molt of the dragonfly and its emergence. Considering the mesotrophic conditions of the gravel pit lake where the dragonfly developed, the minimal age of this mussel was 15 to 20 months, as the nutrients supply is the main limiting factor for growth (JANTZ & NEUMANN, 1998; J. Borcherding, unpubl. data). In this case the dragonfly larva was either colonised by an older mussel changing its place of settlement, an extremely rare phenomenon, or the *G. vulgatissimus*-larva spent a year or longer in F-0, a developmental pattern which to our knowledge has not been reported yet.

Larval development of *G. vulgatissimus* is highly variable and can be finished in Central Europe within two, three or four years, depending on the water type and not the climatic conditions or the geographical latitude (MÜLLER et al., 2000). As generally accepted, the larvae usually enter F-0 in September or October after the second, third or fourth summer of their life to pass the following winter in diapause, emerging synchronously in the following April or May. In a few cases F-0 larvae have been recorded in July (MÜLLER, 1995; KERN, 1999), which hitherto seemed to be the earliest time of year for this stage in Central Europe. Assuming that this mussel with a side length of 14 mm and an age of 15 to 20 months attached to the *G. vulgatissimus*-specimen as a veliger or juvenile, the F-0 stadium of the larva must have lasted a year or probably longer. Thus, either a larva which reached F-0 in autumn must have undergone another year of a possibly facultative dormancy, or it molted from F-1 to F-0 very early in spring to emerge more than a year later. Considering that it is extremely unlikely that an adult mussel changed its final place of settlement, as discussed above, these theories should be taken into serious consideration.

Similar difficulties exist in interpreting the record of a larva of *Gomphus vastus* from the Mississippi River with two attached mussels with side lengths of 15 and 16 mm late in October (TUCKER & CAMERER, 1994; cf. Tab. I), and with the record of an exuviae of *Orthetrum cancellatum* from Lac d´Annecy, an oligotrophic alpine lake, in mid-June carrying a mussel with 10 mm side length (B. Bal & C. Deliry, pers. comm; cf. Tab. I). This mussel specimen must be regarded to have had a minimal age of approximately 12 months. Anyhow, the discussion of these records possibly can offer a new approach for future research on anisopteran larval development.

The ventral attachment of *D. polymorpha* to *C. aenea* (Fig. 1) requires explanation. *Cordulia aenea* is a "sprawler" (CORBET, 1999; WILDERMUTH, 1998) with a "slow life style" with low activity (JOHANSSON, 2000). The larvae usually inhabit floating vegetation, such as *Ceratophyllum* spp. and moss carpets, or hide in the muddy, detritus-covered substrate of the littoral region (WESENBERG-LUND, 1913; MÜNCHBERG, 1932; ROBERT, 1959; WILDERMUTH, 1998). Sometimes, however, they can be found resting inverted on the underside of leaves in the upper layer of leaf litter (BROOKS et al., 1995, cit. in CORBET, 1999; H. Wildermuth, pers. comm.). Consequently, this case can most likely be explained by the attachment of a veliger or small juvenile mussel to an upside-down resting dragonfly larva.

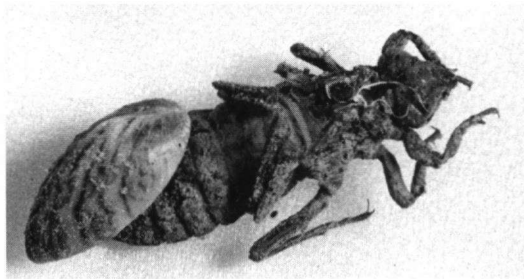

Fig. 2. Exuviae of *Gomphus vulgatissimus* (L.) with dorsally attached large zebra mussel (side length = 14.1 mm), collected on 14-V-1998 at a gravel pit lake near Manching, Bavaria, Germany – [from WEIHRAUCH, 1999; photograph by B. Golya and F. Weihrauch].

On 17-VI-2000, four exuviae of *Epitheca princeps* were collected from mesotrophic Clear Lake, Ontario, Canada with attached mussels, three of them carrying mussels with side lengths of 8.5 to 10.0 mm. The fourth exuviae carried two mussels with side lengths of 9.2 mm and 4.8 mm, respectively (C.D. Jones & D. Sutherland, pers. comm.; cf. Fig. 3). Obviously, under certain circumstances colonization rates can be high, for example, when there is both, a high number of veligers or small juvenile mussels and a shortage of other adequate substrates. If younger odonate larvae are chosen as a substrate which undergo at least one more larval molt, the soddened exuviae will decompose within short time and, due to their ability to crawl, the mussels have a second chance of settlement in the surrounding area. However, if F-0 odonate larvae are chosen which will not undergo another molt before leaving the water for emergence, this probably is the poorest choice because this substrate must be regarded as detrimental for the mussel. From the dragonfly's view, the association can be detrimental either when the larva is attached to another substrate by the mussel's byssal threads, as described by TUCKER & CAMERER (1994), or when the mussel is attached to the larva on the head or thorax along the preformed lines at which the cuticle will split during the molt and thus prevent the next larval stage or the imago from ecdysis. The only recorded case of such interference was an emerging *Gomphus vulgatissimus* observed at Lake Wuckersee, Brandenburg, Germany, on 16-V-1992 with a zebra mussel

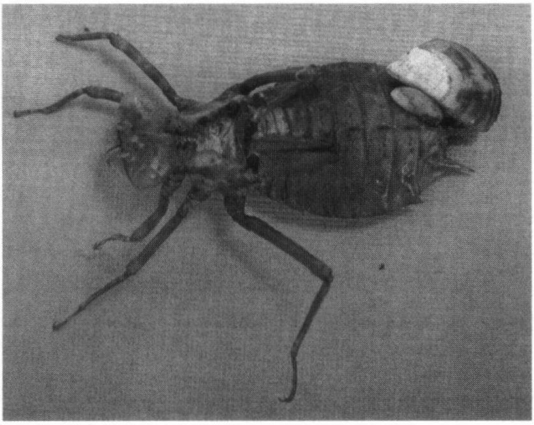

Fig. 3. Exuviae of *Epitheca princeps* Hagen with two dorsally attached zebra mussels (side lengths = 4.8 and 9.2 mm), collected on 17-VI-2000 at Clear Lake near Peterborough, Ontario, Canada – [photograph by C.D. Jones].

attached to the vertex of the head (cf. Tab. I): Although the imago had practically completely emerged from the exuviae, it was unable to release its head from the larval skin as the cuticular gap here was bolted by the mussel (R. Mauersberger, pers. comm.). In summary, this association between odonate larvae and *D. polymorpha* frequently seems to be without any deterious consequences for either the mussel or the dragonfly, except if the odonate larva leaves the water for emergence.

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Postscript

On 13-VI-2001, one larva (19 mm) *Didymops transversa* (Say) was collected at mesotrophic Otter lake, Michigan, USA, with 13 attached zebra mussels, their side lengths ranging from 4.3 mm to 10.3 mm. All mussels were attached to the dorsal side of abdomen and thorax, including the wing pads. On 27-VI-2001, at the same lake, the following records of exuviae with attached zebra mussels on abdomen were made: *Hagenius brevistylus* with two mussels (no measurement) on posterior ventral side; *Epitheca princeps* with one mussel (10 mm) on dorsal side; *E. princeps* with one mussel (11 mm) on dorsal side; *E. princeps* with three mussels (7 mm, 7 mm and 10 mm) on wingpad, posterior ventral and dorsal sides of abdomen. Special thanks to MARGRET ANN CHRISCINSKE, Ann Arbor, USA, for this personal communication.