Postembryonic development, life cycle, and diagnostic characters of the linyphiid spider Meioneta mossica Schikora, 1993 (Arachnida: Araneae)

Postembryonic development, life cycle, and diagnostic characters of the linyphiid spider *Meioneta mossica* Schikora, 1993 (Arachnida: Araneae)

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ABSTRACT   Contrib. Nat. Hist. 12: 1179–1206.

The postembryonic development of the linyphiid spider *Meioneta mossica* Schikora, 1993 is described in detail and information on life cycle, ethology and habitat of the species is provided. Additionally, a concise compilation of selected taxonomic characters is given, which should simplify a reliable determination, especially of female individuals, of *M. mossica*.

Introduction

A previously overlooked sibling species of the linyphiid spider *Meioneta saxatilis* (Blackwall, 1844) was described 16 years ago from pristine oligotrophic mire habitats in southern Sweden: *Meioneta mossica* (Schikora 1993). It could be shown that the distribution area of *M. mossica* apparently extends over most of the Northwest Palaearctic (Finland, Sweden, Norway, Great Britain, Germany, Kaliningrad region of Russia, Estonia) (Schikora 1993, 1995, 1997; additional finds from GB and N: e.g. Milner & Riddiford 1999, Harvey [no year], Merret 2000, Aakra 2000). In the meantime, *M. mossica* has also been reported from Poland (Kupryjanowicz & al. 1997, Staręga 2004), Lithuania (Koponen & al. 2001, Rėlys & Dapkus 2002, Rėlys & al. 2002), and Ireland (Nolan & McCormack 2004). Currently the citation of *M. mossica* in a checklist of Caucasian spiders (Otto 2006) falls somewhat beyond the chorological scope.

Regardless of its rather wide distribution within Northern and Central Europe, *M. mossica* belongs to the less common linyphiids in many regions. As in the majority of other small and uncommon spiders, detailed data about its biology were not available up to now. An improvement of that unsatisfactory situation along general lines belongs undoubtedly to the kind of toilsome task in arachnology appearing as "shoreless" in the meaning of Thaler

(2004). Nevertheless, the method of controlled *ex ovo*-breeding offers advantageous facilities to compile a vast range of basic biological information in many linyphiids, as it was already shown for *Wubanoides uralensis lithodytes* (Schikora 2004). In the present paper the postembryonic development of *M. mossica* is described in detail, and information on its life cycle, ethology and habitat will be given. Additionally, a concise compilation of selected taxonomic characters is provided, which should simplify a reliable determination, especially of female individuals, of *M. mossica*.

Materials and Methods

Materials

In the following the origin of mated females and juvenile specimens is indicated, both of which were caught alive in their natural habitat by direct hand-picking. The mated females permitted successful *ex ovo*-breedings. With the help of additional individuals questions regarding the life cycle of *M. mossica* under natural habitat conditions were investigated.

Origin of live specimens: N Germany, Lower Saxony, Rehbachmoor, Harz National Park, (705–750 m NN; Bog No. 908/7 in Schneekloth & al. 1983; Jensen 1990). A slightly sloped 0.14 km² (13.7 hectares), regenerating low mountain range bog (ombro-soligenous mire) with typical open ombrotrophic, fully growing *Sphagnum* expanses (Sphagnetum magellanici with *S. magellanicum, S. rubellum, S. papillosum*) in its north-western half (Fig. 22). Start of paludification about 9000 years before now, thickness of peat stratum 0.5 to 4 m. See Jensen (1990) for more detailed information.

15 June 2001: 4 adult females, 22 June 2004: 2 adult females ("mother spiders"; caught by hand-picking with the help of an aspirator); 18 September 2004: 1 subadult female, 3 subadult males (aspirator; reared to adulthood).

Methods

Ex ovo-breeding: Mated female spiders from the wild were kept singly in small glass vessels (25 ml; 1 cm charcoal-plaster layer). By way of trial a small head of peatmoss (*Sphagnum rubellum*) was added to each of the vessels in the beginning, but it was later found to be unnecessary. The vessels were covered with pieces of densely perforated airtight film. Plaster layer or peatmoss, respectively, were moistened very economically with some drops of water every now and then, and it proved to be essential to avoid excessively wet or damp conditions. After having built their small sheet webs, the spiders were fed almost daily with small arthropleonous or symphypleonous Collembola,

maximally measuring half a spider's body length. The spiders were maintained under normal room conditions (18–22°C).

Hatchlings from egg sacs were kept also singly in similar vessels to those described above. Except for the time around ecdysis, they were fed daily with minute Collembola, in size distinctly below the spiders' individual body lengths. All vessels with hibernating instars were transferred into a 20 x 37 cm plastic tub and placed onto a low wooden platform inside the tub. The bottom of the tub was then covered with a small amount of water. After protecting the tub against precipitation by a cover that was loose enough to allow free access of air, it was shelved in a shaded place on the balcony. Every day the temperature in the tub was recorded using a calibrated minimax thermometer. Once a week the well-being of the spiders or spiderlings was inspected, and at mild temperatures above 5°C prey was offered.

Measurements: Whenever possible, the growth of all raised spiders was monitored immediately after an individual moult event through recordings of selected body parameters. Measurements were taken on undisturbed, live spiders hanging upside down in their sheet webs in their glassy rearing vessels. The following characters were measured (LEICA MZ16 stereoscopic binocular microscope, magnification x40 to x115; calibrated ocular graticule with measuring pitches 12 mm : 120):
a) maximum diameter of the distal palp limbs,
b) sternum width between coxae II,
c) maximum width of opisthosoma,
d) total body length and
e) leg span.

The leg span was ascertained only in resting and totally relaxed specimens. The glass vessels were adjusted and stabilized using a small dish filled with sea sand before mensuration.

Courtship, mating behaviour: Recently moulted females were transferred into glass cuvets (2.7 x 2.7 x 7.6 cm), equipped with a 2 cm plaster-charcoal layer, where they were allowed to establish a sheet web. A single male was then introduced and continuous observations started until successful mating had occurred. The cuvets warranted the spiders' inspection at different perspectives without any disturbance, and they allowed photographic documentation.

Developmental stages: Two individuals, each of successive developmental stages and of both sexes, were fixed in 70% ethanol after killing them with carbon dioxide. Specimens just prior to, or shortly after a moult were not considered. Lateral prosoma views of all instars were drawn following dissection of the legs between coxae and femora.

Abbreviations:

GB   Great Britain
Lc   Lamella characteristica
N   Norway
OpW   maximum width of opisthosoma
Pc   paracymbium of male palp
PpD   maximum diameter of distal palpal limb
s.d.   standard deviation
StW   sternum width between coxae II
TL   total body length

Measures: Linear measures, if not otherwise indicated, are in mm.

Results

Chapter 3 is divided into four subchapters: (I) diagnostic characters of *M. mossica*, (II) postembryonic development, (III) reproductive behaviour, and (IV) life cycle and notes on the natural habitat.

I Diagnostic characters

Whereas males of *M. mossica* can be rather easily distinguished from those of *M. saxatilis*, the reliable determination of females can raise problems, especially for less experienced persons. Hence, a compilation of helpful clues to identify *M. mossica* (Tab. 1) shall be presented in the following. For all structures, which are only mentioned, but not illustrated here, see Schikora (1993, 1995). In order to check a specimen's chelicerae from the front, a layer of fine sea sand or fine glass beads in the bottom of the examination dish can hold the spider in the required position.

II Postembryonic development

The following information on the postembryonic development of *M. mossica* was exclusively derived from *ex ovo*-breedings in 2001/02 and 2004/05. It is based on a total of about 90 spiderlings, which were reared from 26 egg sacs. A successful rearing is possible for many generations as it was indicated by a second viable offspring generation in 2005.

The development of *M. mossica* is characterized by six postembryonic instars, five of which outside the egg sac (= free instars). The free instars need four moults to reach adulthood. According to the 2004 breeding attempt, which was the best documented, the sex ratio was skewed in favour of the

Meioneta mossica	Meioneta saxatilis
Colouration (both sexes)	
During growing season prosoma of living specimens usually bright amber-coloured, opisthosoma reddish brown (Figs. 24–25). Colouration becomes paler in preserved specimens, but still remains distinctive.	Prosoma commonly with a blackish tinge, clearly darker than in reproductive *M. mossica*.
Hibernating stages distinctively darker, sometimes pale brownish.	
Male palp	
Basis of Pc with only a single well defined pigmented tooth (Fig. 1).	Basis of Pc with two strong and neighbouring pigmented teeth.
Lc highly typical, but examination needs experience due to its three dimensional complexity.	Lc: neighbouring note also valid in this species.
Epigynum & Vulva	
Outer copulatory organ (epigynum; Fig. 2) not reliably different from that of *M. saxatilis*.	Outer copulatory organ (epigynum) not reliably different from that of *M. mossica*.
Vulval rectangle on average 1.8 times wider than high (Fig. 3).	Vulval rectangle rather flat, on average 2.2 times wider than high (Fig. 4).
Rectangle defined by distance between the outer edges of the receptacula (= width), and distance between anterior edges and outer edge of the posterior curvature of the copulatory ducts (= height).	
Chelicerae	
Male chelicerae highly characteristic when viewed frontally (Fig. 5). Distal cheliceral interstice roughly arciform, only 3 reduced cheliceral teeth each visible from in front, dentation not reaching down to distal end of inner margin (Fig. 5: arrows).	Male chelicerae with distal interstice almost equilaterally triangular (Fig. 6). 5 cheliceral teeth each visible from in front, dentation almost reaching down to distal end of inner margin (Fig. 6: arrows).
Female chelicerae with distal part of inner margin only gently curved (Fig. 7)	Female chelicerae with distal part of inner margin strongly curved, curvature meets the lateral margin almost at a right angle (Fig. 8).

Tab. 1. Brief aid to identification of *M. mossica* and the distinction from its sibling species *M. saxatilis*. For further diagnostic characters see Schikora (1993, 1995).

female sex (1 : 0.7; females 38, males 28). The unequivocal distinction of both sexes is possible already in the 2nd free instar by the ratio of sternum width and maximum diameter of the last (distal) palpus limb (Tab. 2, Fig. 9). In the assignment of live individuals of the 1st instar, however, remains some uncertainty due to the spiders' small size and inadequacies of the measurement procedure used (see Methods).

The progress of postembryonic development can be visualized by the measures of selected body characters for all instars, which have been compiled in Tab. 2. The data allow also the unequivocal classification of any juven-
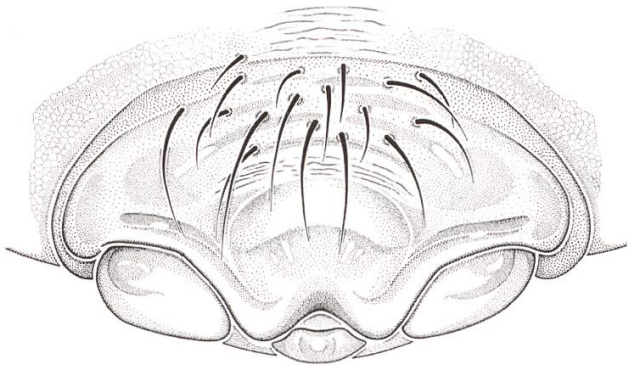
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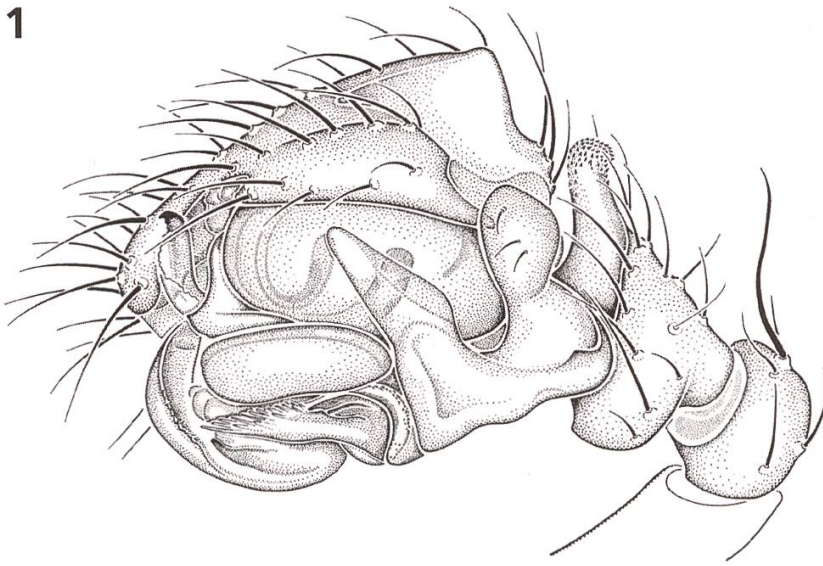
Figs. 1–2. Diagnostic characters of *M. mossica*.
– 1: Left male palp, lateral;
– 2: Epigynum, slightly from behind.
Scale line = 0.1 mm.

ile specimens to their stage of individual development. Here, the ratio of sternum width and total length is useful (Fig. 10). Certain measures in Tab. 2 show rather high s.d., which again should indicate inadequacies of the measuring method rather than variation.

Details on the duration of the complete postembryonic development are provided in connection with the adult stage (5th free instar).

Egg and egg sac (Fig. 29, 30): If reproductive females, ready for oviposition, could choose between the glass wall of the keeping vessel, the plaster layer at the bottom or the small heads of added peatmoss, the latter were clearly preferred for the establishment of egg sacs. Often the egg sac was somewhat hidden in the peatmoss whorl. The egg sac is densely coated with white silk and has an average diameter of 3.0 mm (fixing threads not included; n=7, range 2.2–3.7). Although the dense paddy coating of the egg sac usually interferes with the detection of its content, in four cases the diameters of the yellow mulberry-shaped egg bales (Fig. 30) could be measured and lay between 0.9 and 1.2 mm, depending on the egg number.
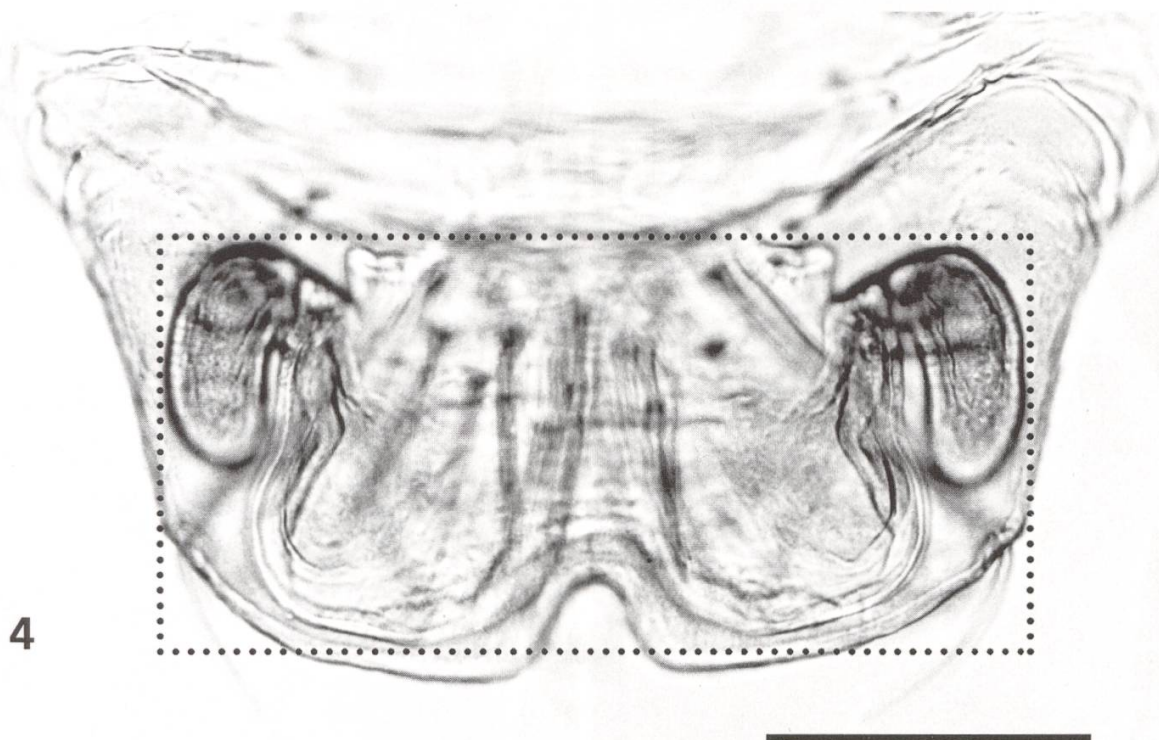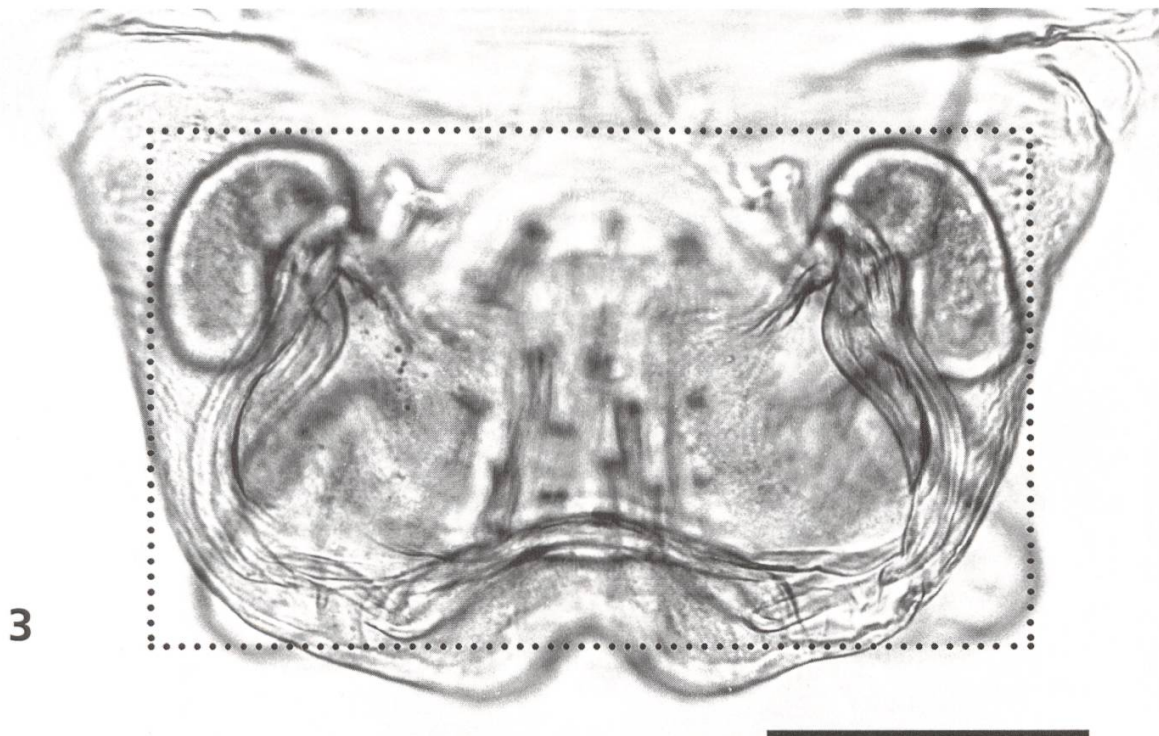
Figs. 3–4. Diagnostic characters of *M. mossica* and its sibling species *M. saxatilis*. – 3: Vulva of *M. mossica*, ventral view. KOH-treated and cleared, micrograph. Vulval rectangle dotted (width : height = 1.8 : 1; see Tab. 1); – 4: Vulva of *M. saxatilis*, ventral view. KOH-treated and cleared, micrograph. Vulval rectangle dotted (width : height = 2.2 : 1; see Tab. 1). Scale lines = 0.1 mm.

One of the *M. mossica* females, caught on 22 June 2004, produced a maximum number of 18 egg sacs between 29 June and 17 Nov. 2004 (Fig. 29). The last egg sac was merely rudimentary, and the female died on 19 Nov. 2004. In other females a total of 1–7 egg sacs were established within their lifespan. It
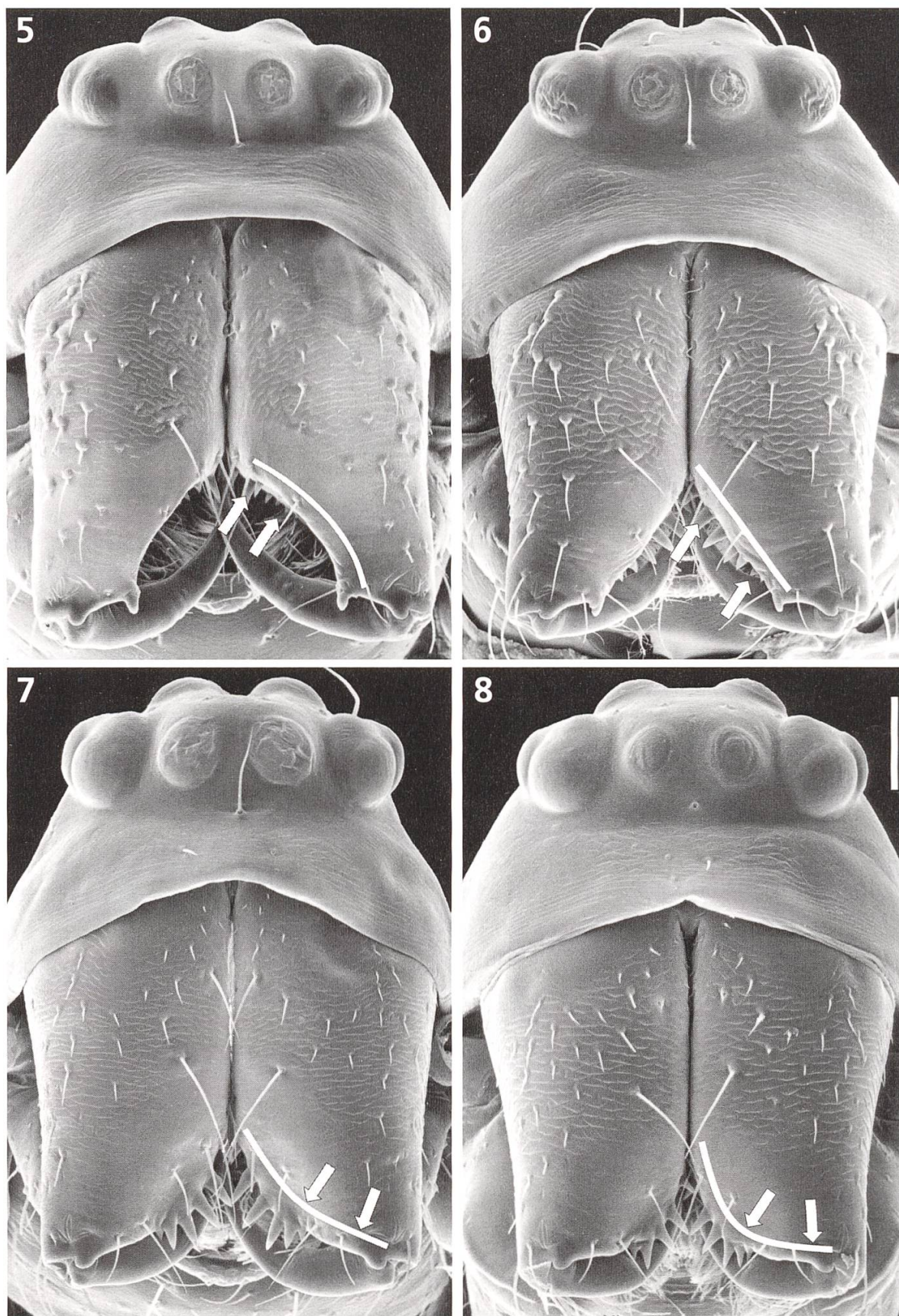
Figs. 5–8. Chelicerae of *M. mossica* and *M. saxatilis* (SEMs), frontal view. Important characters indicated (see Tab. 1 for explanations). – 5: *M. mossica* male; – 6: *M. saxatilis* male; – 7: *M. mossica* female; – 8: *M. saxatilis* female. Scale line = 0.1 mm.

1st free instar	Males (Fig. 12)	Females (Fig. 12)
Total length	0.70±0.02 (0.65–0.74; n=22)	0.71±0.04 (0.65–0.81; n=35)
Sternum width	0.24±0.01 (0.23–0.26; n=22)	0.24±0.01 (0.22–0.26; n=36)
OpW	0.27±0.03 (0.23–0.34; n=21)	0.27±0.04 (0.21–0.36; n=34)
Leg span	1.47±0.12 (1.19–1.68; n=20)	1.54±0.13 (1.30–1.90; n=29)
PpD/StW (1 : x)	5.47±0.57 (4.74–6.09; n=8)	5.68±0.46 (4.75–6.36; n=16)
2nd free instar	Males (Fig. 13)	Females (Fig. 14)
Total length	0.92±0.05 (0.83–1.01; n=26)	0.92±0.06 (0.79–1.05; n=34)
Sternum width	0.28±0.01 (0.25–0.30; n=25)	0.28±0.01 (0.26–0.30; n=34)
OpW	0.38±0.03 (0.32–0.44; n=26)	0.39±0.05 (0.33–0.52; n=34)
Leg span	2.03±0.15 (1.75–2.25; n=18)	2.03±0.12 (1.80–2.23; n=22)
PpD/StW (1 : x)	4.55±0.26 (4.00–4.89; n=14)	5.99±0.50 (5.38–7.33; n=25)
3rd free instar	Males (Fig. 15)	Females (Fig. 16)
Total length	1.16±0.06 (1.03–1.25; n=23)	1.14±0.07 (1.03–1.28; n=33)
Sternum width	0.32±0.01 (0.29–0.35; n=23)	0.33±0.01 (0.28–0.35; n=33)
OpW	0.46±0.02 (0.43–0.50; n=23)	0.47±0.05 (0.40–0.58; n=32)
Leg span	2.96±0.19 (2.60–3.25; n=14)	2.74±0.27 (2.05–3.35; n=26)
PpD/StW (1 : x)	2.71±0.13 (2.48–3.01; n=16)	6.18±0.64 (5.21–7.43; n=25)
4th free instar	Males (Fig. 17)	Females (Fig. 18)
Total length	1.42±0.08 (1.26–1.58; n=22)	1.41±0.08 (1.23–1.60; n=32)
Sternum width	0.38±0.02 (0.35–0.42; n=22)	0.38±0.01 (0.36–0.39; n=32)
OpW	0.57±0.05 (0.50–0.74; n=22)	0.57±0.04 (0.49–0.68; n=30)
Leg span	3.61±0.27 (3.05–4.10; n=14)	3.66±0.21 (3.35–4.15; n=25)
PpD/StW (1 : x)	1.55±0.08 (1.43–1.76; n=21)	6.05±0.42 (5.27–6.89; n=28)
5th free instar	Males (Fig. 19)	Females (Fig. 20)
Total length	1.76±0.09 (1.60–1.93; n=11)	1.70±0.09 (1.50–1.83; n=14)
Sternum width	0.44±0.02 (0.41–0.46; n=11)	0.43±0.02 (0.39–0.45; n=14)
OpW	0.69±0.06 (0.59–0.76; n=11)	0.68±0.06 (0.56–0.79; n=14)
Leg span	4.36±0.16 (4.15–4.60; n=7)	4.31±0.22 (4.00–4.60; n=9)
PpD/StW (1 : x)	1.79±0.05 (1.74–1.89; n=11)	6.96±0.79 (5.38–7.91; n=14)

Tab. 2. Measurements of selected body characters for all free developmental instars of *Meioneta mossica* according to *ex ovo*-rearing. All measurements refer to newly hatched (1st free instar) or recently moulted specimens. Measures as mean ± s.d. (range; sum of measured specimens.) 4th/5th instar = subadult/adult.

is to be expected that a female in the wild should be able to produce about 5–8 (10?) egg sacs under favourable habitat conditions. The first egg sac following mating was, on average, established 14 days later (n=7, s.d.=7.8, range 8–29). On the condition of a daily food supply, the next egg sacs, on average, followed 9.5 days later (s.d. 5.0, range 3–21, n=22). Egg diameters ranged from 0.41–0.50 mm (mean 0.46, s.d. 0.02, n=49). When the numbers of eggs could be ascertained in some of the egg sacs, they ranged from 5–10 (mean 6.6, s.d. 1.7, n=8).
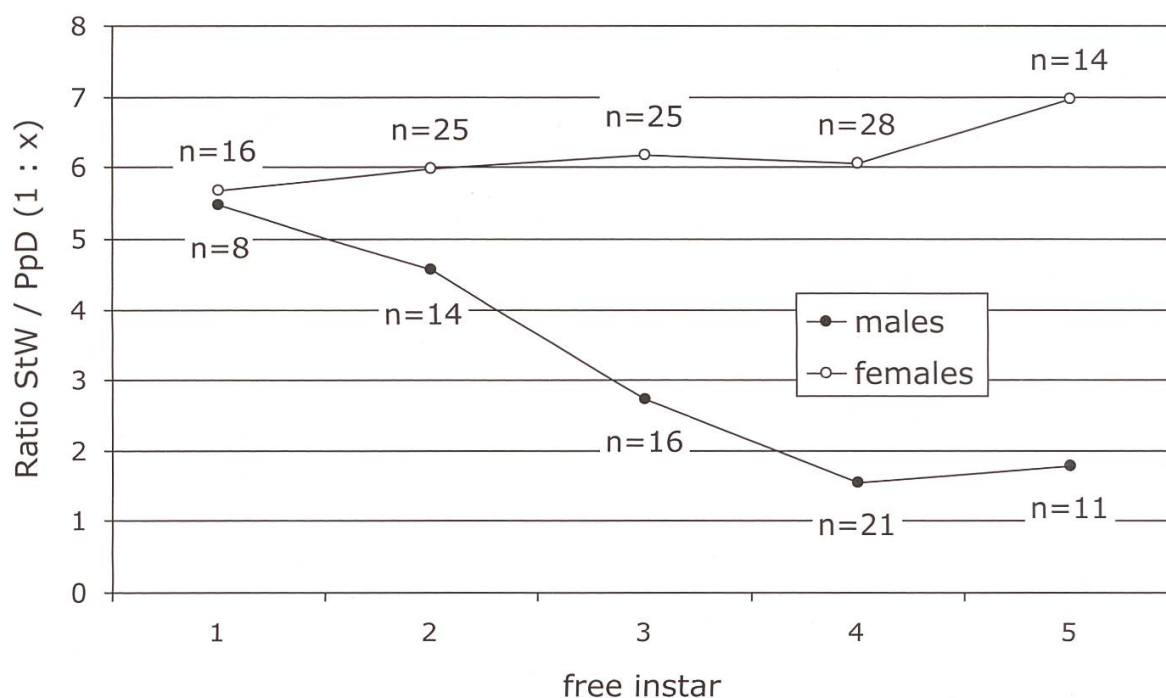
Fig. 9. Distinction of sexes during the postembryonic development of *M. mossica* by the ratio of sternum width (StW) and the max. diameter of the distal palpus limb (PpD).

First postembryonic instar (Fig. 31, 32): On 26 October 2004 an egg sac, lacking the dense paddy silk cover and containing 10 eggs, had been established by a *M. mossica* female. This circumstance enabled an undisturbed observation of the late embryogenesis, the hatching procedure as well as the first (incomplete) instar. 13 days after oviposition (8 Nov. 2004) the chorion layer of three eggs was ripped and the frontal appendages of the late embryos became visible (Fig. 30). On the next day two incomplete instars had hatched, and in the remaining eggs (except 3) embryos were now visible. On 12 November, five spiderlings had left the egg (Fig. 31). Remnants of a cuticle, which remained attached to the abdomen of two of the spiderlings for a while (Fig 31), indicated that the embryonic cuticle is shed in the course of hatching. The shedding of the embryonic cuticle would be the 1st moult, releasing the 1st postembryonic developmental instar. All 1st instar individuals lack eyes, but show pigmented eye spots instead (Fig. 32). Their compact appendages lack terminal claws but the tip of the tarsi has 3 straight and very short spines. The remaining limbs of the leg have a short minute dorsal spine (position approx. 0.25).

On 13 Nov. 2004, four days after hatching, the first two spiderlings moulted a second time, resulting in the 2nd instar (= 1st free instar). They left the rudimentary egg sac the next day. In total, 5 vital spiders emerged from the egg bale, 1 embryo and one 1st instar spiderling died, while three eggs remained undeveloped.
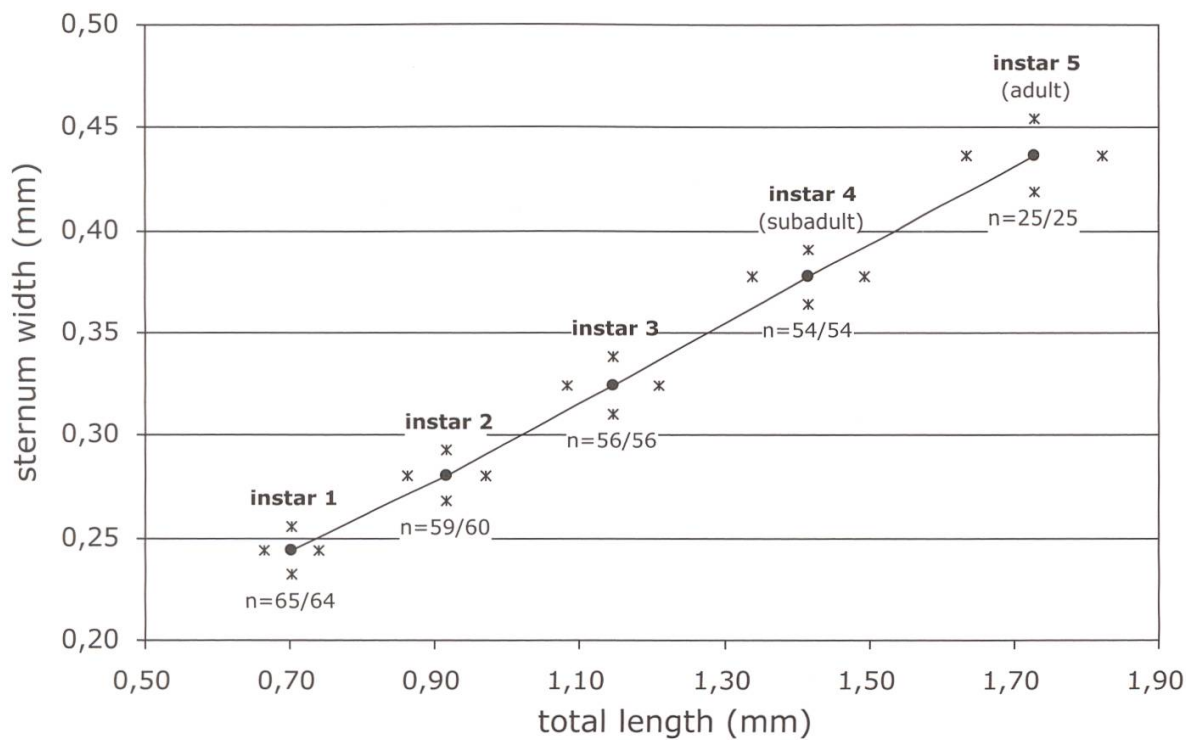
Fig. 10. Relationships between developmental stages (free instars) and sizes of selected body parameters (sternum width, total length), based on data from *ex ovo*-rearings. Shown are means (•) ± s.d. (x); n = number of measured male and female specimens (n StW/n TL).

Second instar (1st free instar) (Fig. 12, 33, 34): On average, the 1st free instars left the egg sac 19.9 days after its establishment (s.d. 5.8, range 12–30, n=54; Fig. 11) through an almost circular lateral hole in the silk layer. Frequently the spiderlings did not leave the egg sac simultaneously but within a time frame of 2–3 days. It was found occasionally that the mother spider had taken some of the 1st free instar spiderlings as prey.

Prosomata and legs of the 1st free instars are greyish and translucent, but the opisthosoma is yellowish (Fig. 33). The prosoma is characterized by a mid dorsal elevation (Fig. 12). After having established their sheet web shortly above ground (Fig. 34), the young spiders are able to seize prey, the size of which has to fall distinctly below their own body lengths. Early instars of Collembolans proved to be an ideal, readily accepted diet.

Twelve days on average after leaving the egg sac (mean 11.6, s.d. 4.3, range 6–23, n=59; Fig. 11) the spiders of the 1st free instar moulted a third time (= 2nd free instar).

Third instar (2nd free instar) (Fig. 13, 14, 35, 36): In the 2nd free instar the spiders' coloration starts to resemble that of the adults (Fig. 35, 36). Also, the differences between the two sexes become more distinct, as the young males
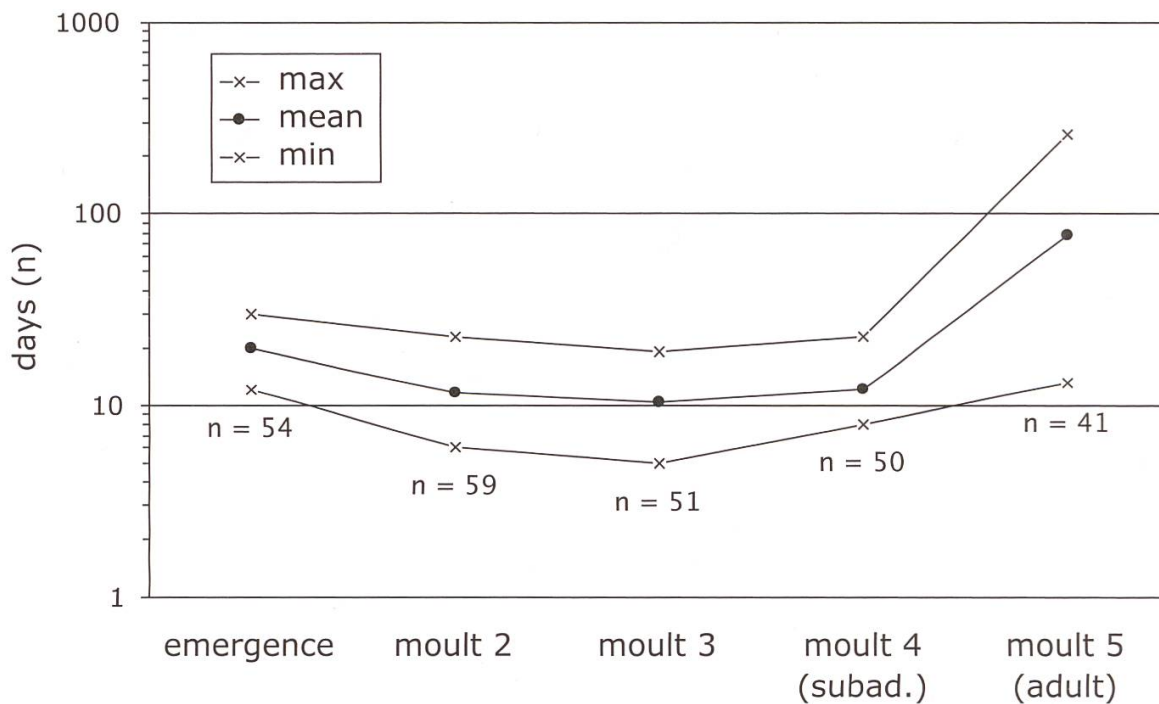
Fig. 11. Developmental rate of *M. mossica* from egg to adult according to *ex ovo*-rearing. n = number of observed specimens; max/min = observed range. Emergence = leaving the egg sac.

now show for the first time clearly thickened terminal palp limbs (Fig. 13 vs. 14). In both sexes the dorsal prosoma elevation, that had already been characteristic for the 1st free instar, continues to exist (Fig. 13, 14).

Approximately 10 days after the last ecdysis (mean 10.4, s.d. 3.1, range 5–19; n=51) the cuticle is shed again in the course of a 4th moult, leading over to the 3rd free instar (Fig. 11).

Fourth instar (3rd free instar) (Fig. 15, 16, 37): Individuals of the 3rd free instar (Fig. 37) have lost the mid dorsal prosoma elevation (Fig. 15, 16), which was typical for the preceding free instars. On average the 3rd free instar lasted 12 days (mean 12.1, s.d. 2.7, range 8–23; n=50) until the next moult followed, resulting in the 4th free instar (Fig. 11).

Fifth instar (4th free instar, subadult) (Fig. 17, 18, 38, 39): After their 5th moult the subadults (4th free instar) closely resemble the adult stage with regard to their coloration and general appearance (Fig. 17, 18, 38, 39). After having reached the subadult stage, most of the spiders soon exhibited clear indications of imminent hibernation. In 78% of the subadults (2004: 32 out of 41) development slowed down and the last moult did not occur. Only 9 spiders (22%) developed without a clear deceleration and became adult 13–24 days after their 5th ecdysis (5 Sep. – 6 Oct. 2004).

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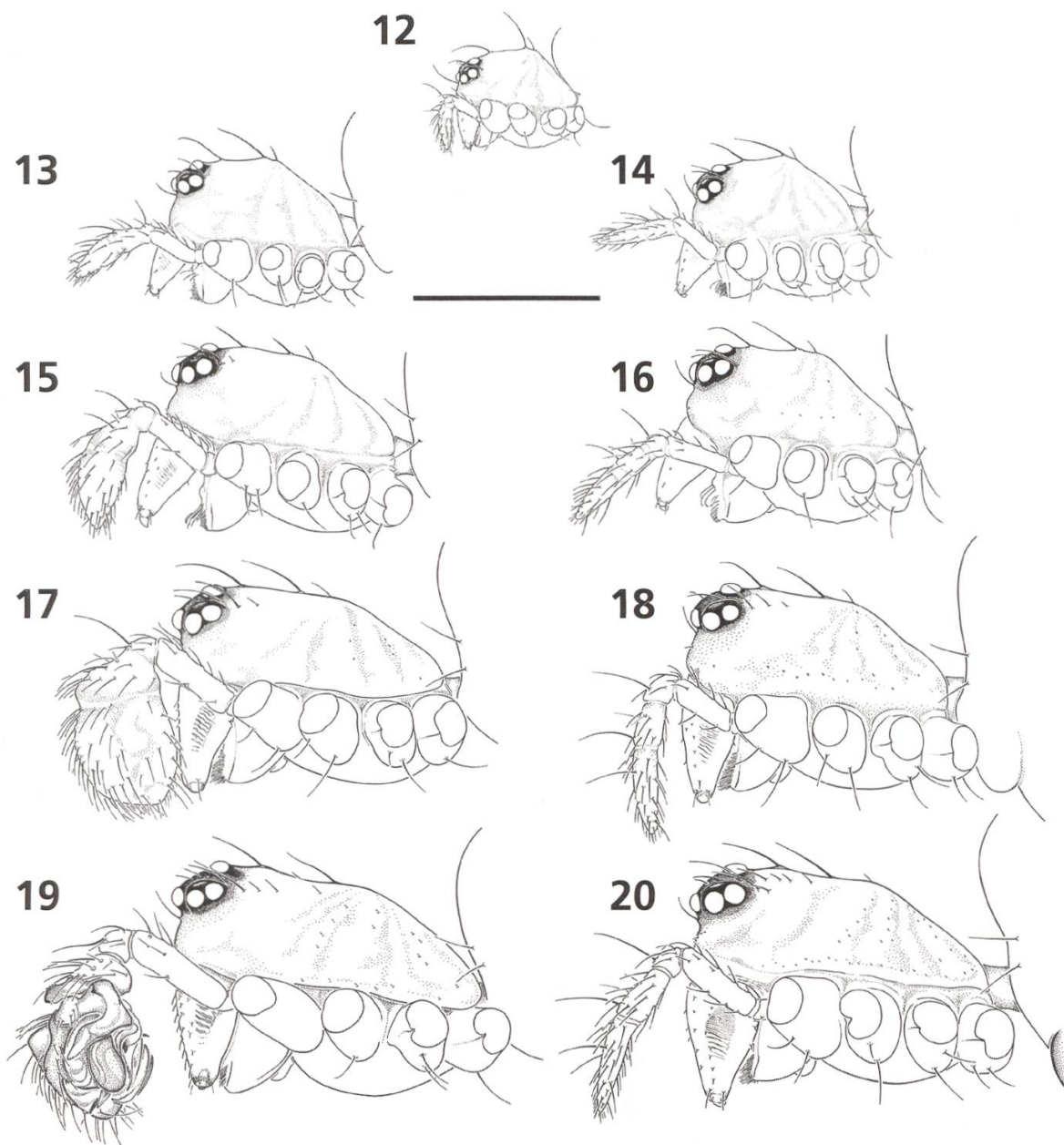
Figs. 12–20. Stages of postembryonic development in the linyphiid spider *M. mossica* according to *ex ovo*-rearing. Lateral prosoma views, legs dissected off. – 12: 2nd postembryonic instar (= 1st free instar), sex unknown; – 13, 14: 3rd instar male, female; – 15, 16: 4th instar male, female; – 17, 18: 5th instar male, female (subadult); – 19, 20: 6th instar male, female (= 5th free instar; adult). Scale line = 0.5 mm.

For overwintering, the remaining subadults were placed outdoors on the balcony on 23 September (see Methods). Under the given balcony conditions (Fig. 21) 21 further spiders (51% out of 41) reached maturity 26–64 days after their penultimate moult (12 Sep. 2004 – 5 Feb. 2005). In the 11 residual subadults (27%) the last moult occurred 102–260 days after their 5th ecdysis (12 Feb.–1 May 2005), with the majority becoming mature at the end of April. On average, the last moult occurred 77 days after the spiders' second shedding (mean 77.2, s.d. 79.1, range 13–260; n=41; Fig. 11). In most of the hibernating subadults the coloration of the prosoma turned into a pale brown.
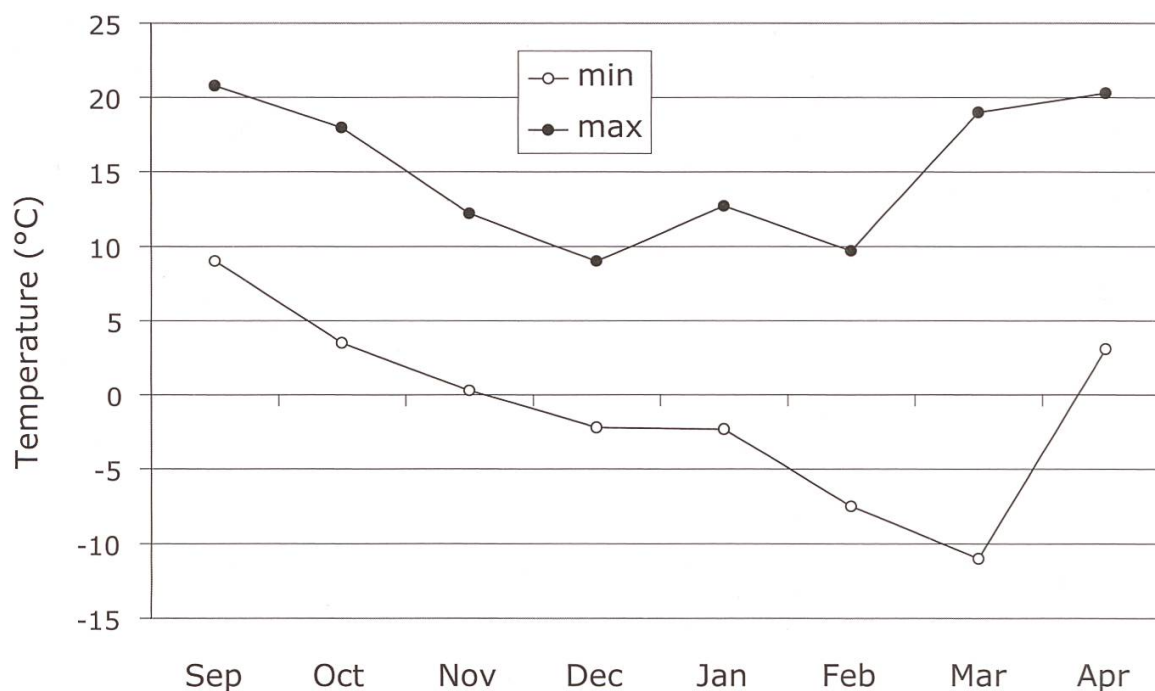
Fig. 21. Monthly minimum and maximum temperatures during hibernation of *M. mossica* outdoors under balcony conditions (Ritterhude near Bremen, N Germany, 2004/05).

Sixth instar (5th free instar, adult) (19, 20, 24, 25, 40, 41): The 6th instar is the adult stage (5th free instar; Fig. 19, 20). In most adult spiders, which had overwintered as subadults, their typical amber-like prosoma colour returned soon after the last moult (Fig. 24, 25, 41). Only in rare cases single specimens retained a more brownish prosoma (Fig. 40).

The duration of the complete development from egg to adult stage was 68 days at the shortest, and 306 days at the longest (mean 126.7, s.d. 74.7, n=35). In 2001/02, furthermore, the maximally possible life span was examined in a few individuals (from quitting the egg sac up to the death of the adult specimen). On average, female individuals reached an age of 395 days in captivity (range 382–411; n=4), while two males lived for 156 and 158 days. Assuming that the spiders of the 1st free instar occur at the end of June in the wild, and assuming that the adults will die at the latest during the end of July the following year, females could reach a maximum age of about 400 days under natural habitat conditions. According to these assumptions, one of the adult females, that was caught on 22 June 2004 in the wild (see Materials), and then died on 19 Nov. 2004 after 150 days in captivity, might have reached an age of about 500 days.

Fig. 22. Typical habitat of *M. mossica* in an ombro-soligenous bog (Harz Mountains). Fully growing Sphagnetum magellanici in the foreground.

III Reproductive behaviour

The reproductive behaviour of *M. mossica* allows the distinction of four major steps: (1) courtship, (2) pre-mating, (3) sperm web construction and (4) mating. It was observed in detail in six *M. mossica* couples (Dec. 2001 and May 2004), all springing from *ex ovo*-rearings (see Methods).

Courtship: In some cases the males paused almost motionless for several hours after having entered the web of an unmated female. When courting started, the males circled round their mate in a special, rather fast, courtship walk, reminiscent very closely of the jerk-like locomotion of an ant. The walk was accompanied by a jiggling of the opisthosoma. Additionally short phases of rapid stridulation occurred, recognizable by violent and alternating up-and-down movements of the palps. During short intervals of rest, the abdomen's jiggling continued and, in addition, the body was pushed jerkily to the front. Sometimes the female went towards the courting male with her chelicerae spread, trying to push the male away by means of her palps and both frontal pairs of legs.

Pre-mating (Fig. 26): After a while (up to 45 min) the male approaches the female, besetting her directly from the front by boisterous drumming move-
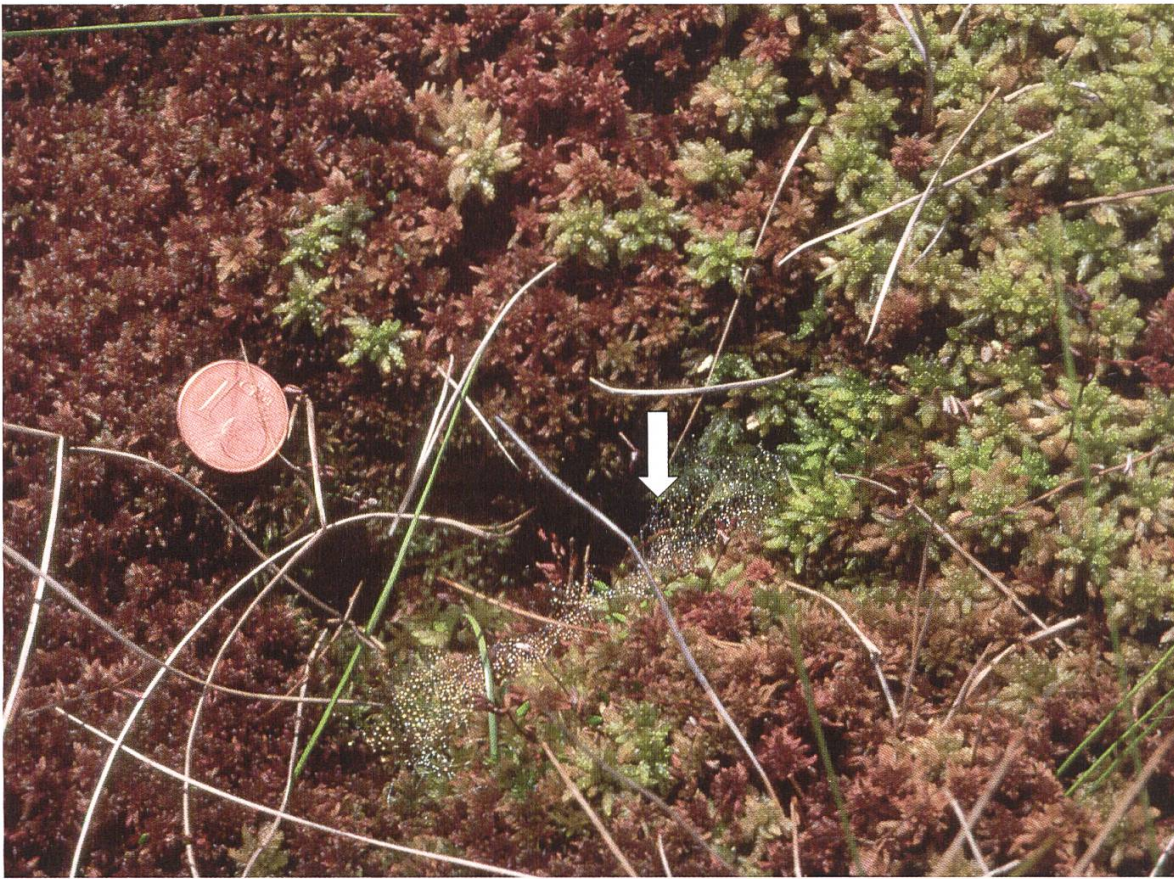
Fig. 23. Microhabitat of *M. mossica*. Sheet web in this case established below the margins of a roe deer footprint in the peatmoss cover.

ments with his forelegs. The male then pushes its prosoma underneath that of the female and immediately starts copulating by alternating insertions of the palps (Fig. 26). These copulations are here defined as "pre-mating", because at this moment the male has not yet transferred spermatozoa to the reservoir in the palpal organs.

The female displays a comparable mating position as has been described for the linyphiid spider *Wubanoides* (Schikora 2004). The female's epigynal mound is erected, sticking out almost vertically from the abdomen, and the scapus is somewhat protruding. The attachment of the palp to the epigynum, followed by a distortion of the palpal sclerites and the distension of the hae-matodochae, occurred so rapidly that details were hardly discernible. Anyway, the curved tibial apophysis of the male palp (Fig. 1) seems to serve as an ini-tial positioning device, and the paracymbium is attached to one of the lateral lobes of the epigynal basis (Fig. 2). In the course of the energetic palpal distort-ion, the epigynal scapus is torn forth and bent laterally. After almost each insertion, the male works on its palp tips with the chelicerae. From time to time some males left their mate, which remained in the mating position, strid-ulated, returned and started pre-mating activities again. The entire pre-mating

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Figs. 24–26. Adult instars of *M. mossica*, mating behaviour. – 24: Adult female from the wild; – 25: Adult male; – 26: Pre-mating activity without sperm transfer. Distended haematodochae of the male (right) visible.
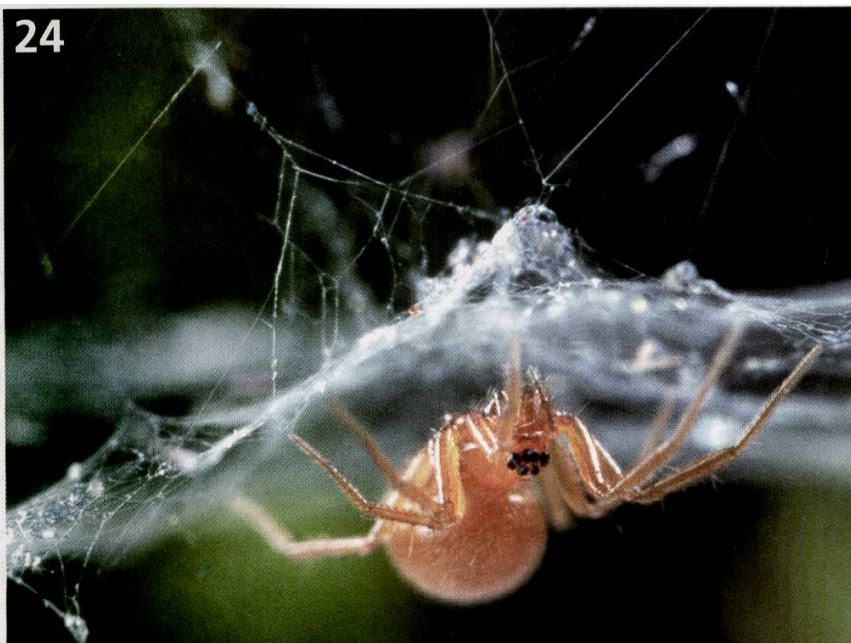
Figs. 27–29. Adult instars of *M. mossica*, mating behaviour and oviposition.
– 27: Sperm web (encircled) of the male;
– 28: Mating. Fully distended haematodochae of the right male palp visible during sperm transfer;
– 29: Female coating her egg sac with paddy silk.

process lasted for about 45–60 minutes; the palpal insertions were very short, and they were usually repeated every 2–3 seconds.

Sperm web construction (Fig. 27). At the end of pre-mating the male bites an opening into the female's web with erratic and rather hectic movements, with a diameter of about the male's body length. Inside the opening a small, roughly triangular sperm web is established (Fig. 27), and a small whitish sperm droplet is deposited. Moving to the under-surface of the sperm web the male takes up the sperm by rapidly dipping the palp tips alternatingly into the droplet from above. In the observed cases the whole procedure lasted less than 2 minutes. Sometimes a second sperm web was established by a male in the course of mating, and a further sperm transfer occurred.

Mating (Fig. 28). Immediately after the sperm transfer to the palpal organs, the male once again displays courtship behaviour for some seconds, returns to the female anew and starts mating *sensu stricto*. In contrast to the pre-mating activity each of the alternating palp insertions now lasts considerably longer (10–12 sec.), and the haematodochae remain distended for a longer time, showing pulsations (Fig. 28). Also, in the course of mating the male may leave the female temporarily, but usually returns quickly to continue. After 30–60 minutes of consecutive copulations the female spider initiates the separation. Often the mating procedure was repeated several times. Inclusive of short interruptions one *M. mossica* couple remained in a mating position for 325 minutes, and mating activities could be observed almost all the time.

Precociously mature individuals of both sexes, which had overwintered as adults, were also found to be able to mate successfully in spring and to produce viable offspring.

IV Life cycle and notes on the natural habitat
Life cycle

The following information is based on my own field data from South Sweden (Komosse and Store Mosse 1990; see Schikora 2003) and North Germany (Harz Mountains) as well as on the results of *ex ovo*-breedings under the climatic conditions of the North German lowlands (see Postembryonic development). Insofar, the ascertained data related to the life cycle of *M. mossica* might be predominantly valid for the geographical reference area defined above.

Without any doubt *M. mossica* belongs to the category of stenochronic, univoltine spiders, having only one period of maturity annually, ranging from mid April to mid July (Fig. 42). The occurrence of single, precociously mature males of the next generation already in autumn (Fig. 43) is, for the time being, regarded as exceptional.
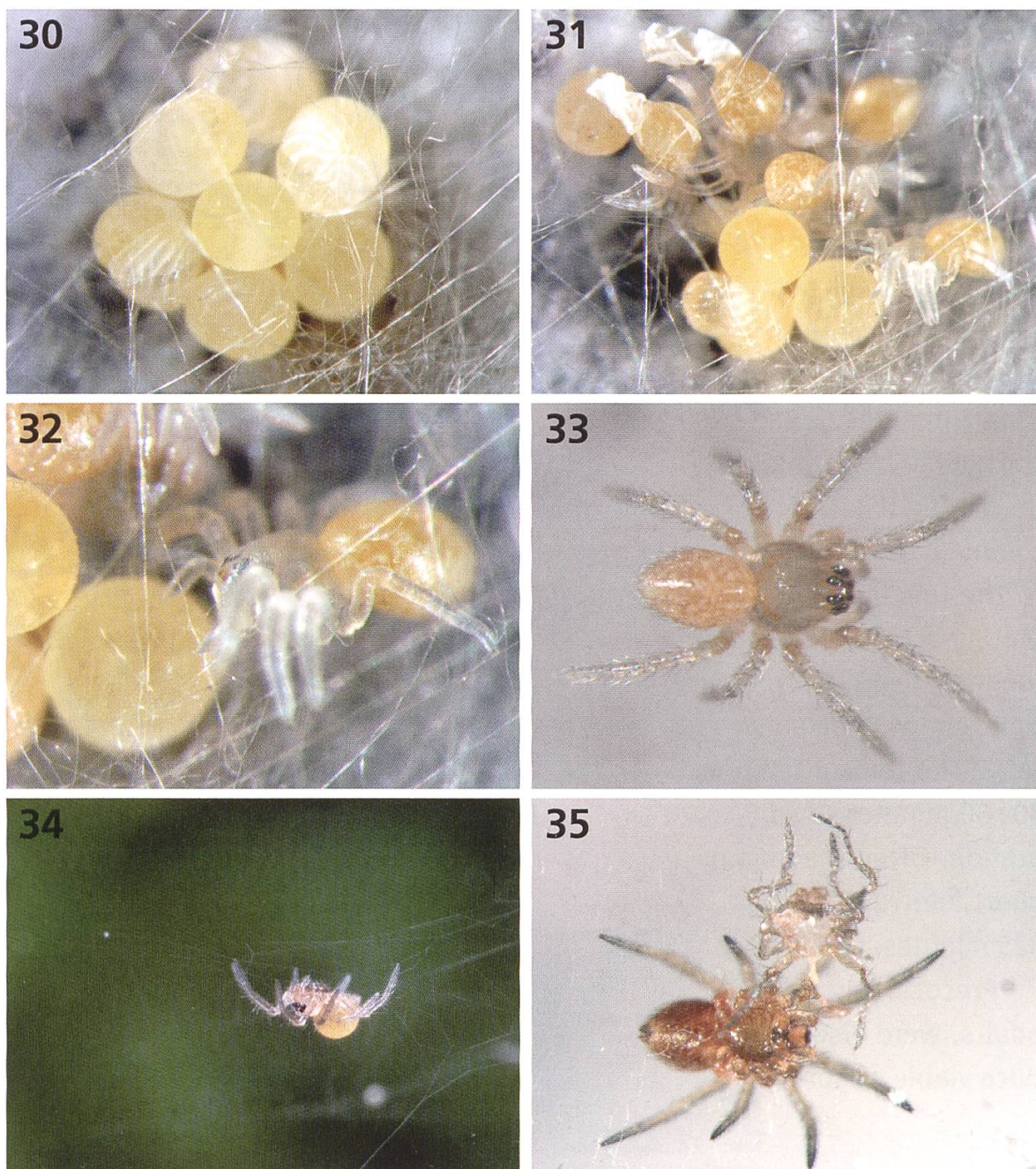
Figs. 30–35. Postembryonic development of *M. mossica* from egg to adult instar (*ex ovo*-rearing). – 30: Egg bale 12 days after oviposition (1.2 mm). Chorion of 3 eggs ripped, appendages of embryo visible; – 31: Hatching of 1st (incomplete) instars. Note cuticle remnants on the abdomen of the left spiderling, indicative of the 1st moult; – 32: 1st (incomplete) instar, pigmented eye spots visible; – 33: 2nd instar (= 1st free instar) after leaving the egg sac; – 34: 1st free instar spiderling in its sheet web; – 35: 2nd free instar male (ventral) after moult.

M. mossica seems to overwinter chiefly in the subadult stage (4th free instar) as is indicated also by finds of 4 subadult individuals at the end of the growing period in the Harz Mountains (see Materials). Precociously mature individuals are able to hibernate successfully just as well (see above). Precociously mature females, which were paired in captivity in autumn 2004, could also overwinter successfully and produce offspring in the following year. In

Figs. 36–41. Postembryonic development of *M. mossica* from egg to adult instar (*ex ovo*-rearing). – 36: 2nd free instar female (ventral) below remnants of prey; – 37: 3rd free instar female (ventral); – 38: 4th free instar male (subadult); – 39: 4th free instar female (subadult) after penultimate moult; – 40: 5th free instar male (adult), prosoma exceptionally somewhat darker that usual; – 41: 5th free instar female (adult), showing typical colouration.

one case a reproductive female, that had already established an egg sac in Sep. 04, overwintered and started reproduction again in spring 2005.

Hibernating individuals prefer to rest closely below small particles attached to their web, like old exuvia, dry remnants of prey or dead leaflets for example. They react to and take prey in temperatures down to about 5°C. In one case a reared hibernating subadult was observed feeding on a symphypleonous
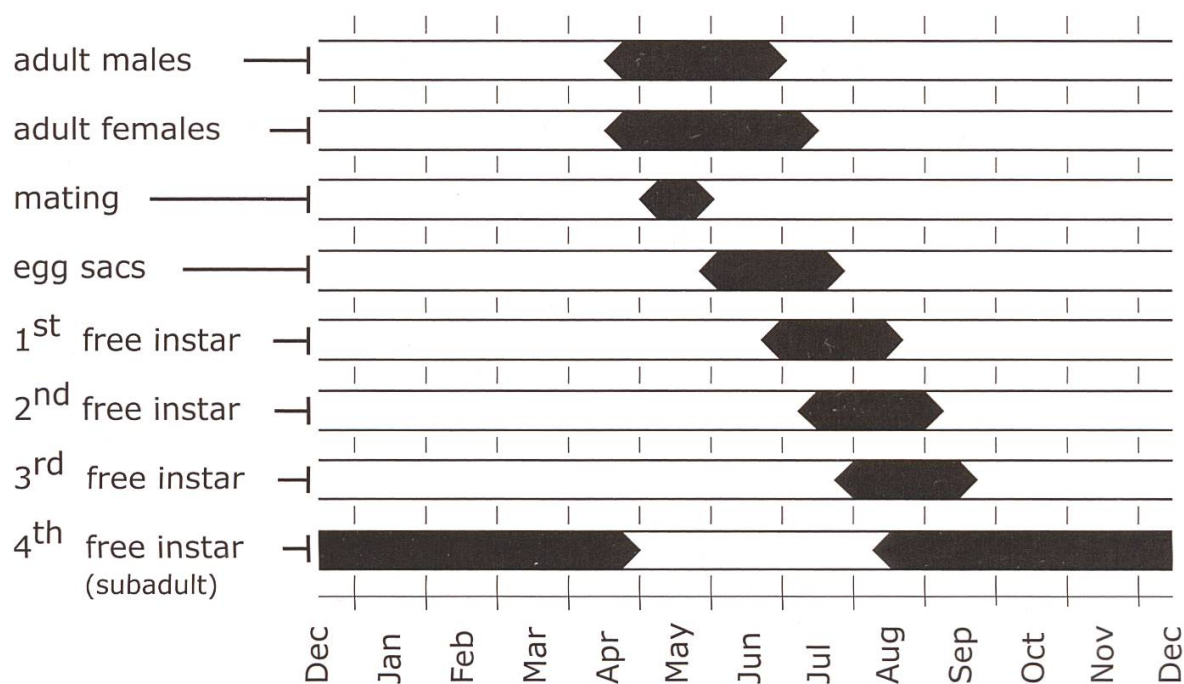
Fig. 42. Life cycle of *M. mossica* according to data from *ex ovo*-rearings and field data from S Sweden (Komosse, Store Mosse) and N Germany (Harz Mountains).

collembolan (Sminthuridae) at 2.5°C on 13 February. By chance it was observed that an over-wintering subadult, whose glass vessel accidentally had been completely flooded by rainwater, was encased in a small air bubble attached to the wall, where it survived without any ill effect. This incidental observation might give information about the species' behaviour in the course of flooding of its natural bog habitat after torrential rainfalls or during the thawing period (see habitat).

In Fig. 43 the phenology (numerical abundance, activity density) of *M. mossica* is shown according to pitfall trapping in the bog complex Komosse, S Sweden (65 traps, 30 Apr.–29 Oct. 1990, 14 day intervals, 95 adult individuals; details & method: Schikora 2003). The figure shows displaced peaks of seasonal occurrence for both sexes, with males reaching maximum frequency around the beginning of May and females peaking at the beginning of June. When compared with the quantitative abundance data for *M. mossica* from the same study site (Fig. 44), it becomes obvious that the difference in seasonal occurrence is merely due to different patterns of locomotor activity.

Habitat, microhabitat, abundance

The habitat of *M. mossica* has been described in detail elsewhere (Schikora 1993, 1995, 2003). Hence a brief synopsis of the most important facts should be sufficient here, which is consecutively supplemented with hitherto unpublished data from my own field studies. They refer to different bogs in the Harz
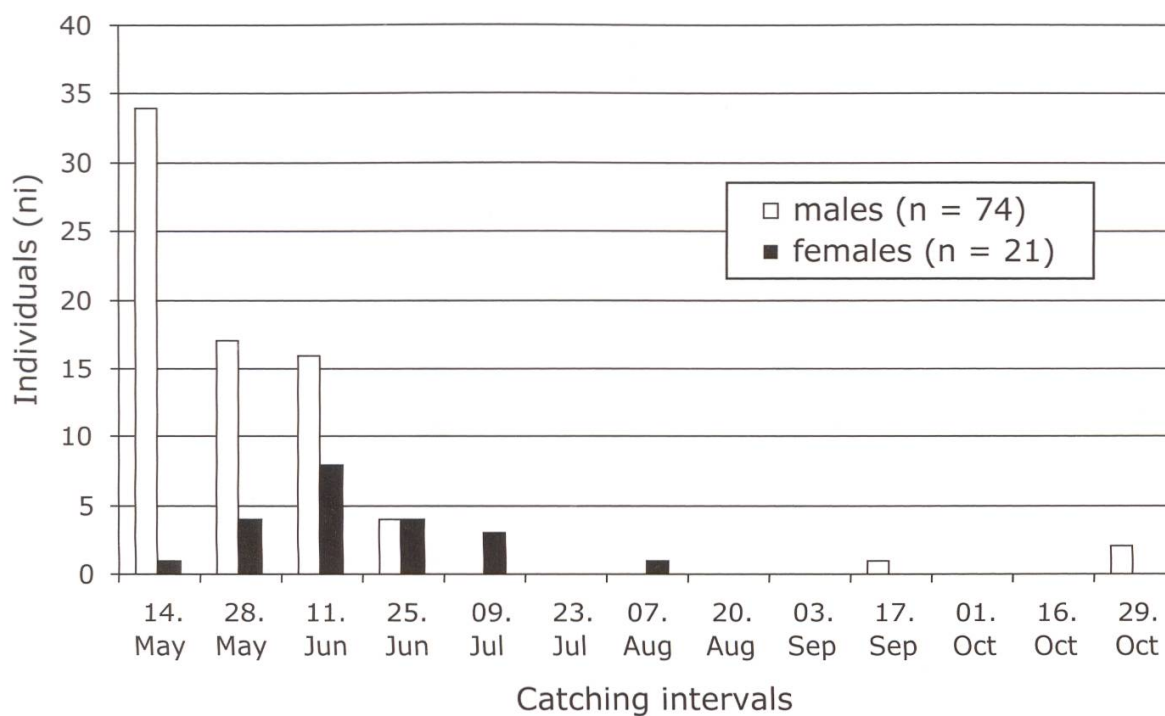
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Fig. 43. Numerical abundance ("activity density") of *M. mossica* according to pitfall trapping (bog complex Komosse/Ulricehamn, S-Sweden; 65 traps, 30. 04.–29. 10. 1990).

National Park, and to the south Swedish *locus typicus* of the species, the bog complex Komosse near Ulricehamn (see Schikora 1993).

Pristine or relatively unspoiled oligotrophic mires *sensu lato*, preferably bogs in the upland and low mountain ranges of northern and central Europe, are the typical habitat of *M. mossica*. Here, the spider colonises *Sphagnum*-expanses and -hummocks, belonging to the phytosociological order Sphagnetalia magellanici (class Oxycocco-Sphagnetea). In the most typical case the degree of *Sphagnum*-cover of the habitat is close to 100%, it is only sparsely overgrown by vascular plants, and it is fully exposed to the sunlight (Fig. 22). Such sites are characterized by pronounced dynamics of their biotic and abiotic ecofactors, both, short-termed and long-termed. They are subject to considerably changing degrees of moisture, and they usually show considerable daily temperature fluctuations in spring and summer. The habitat surface can dry out completely in summer so that even a high danger of fire is given, and it is frequently flooded almost completely after heavy rainfalls or during the thawing period at the end of winter. On sunny days the temperature can pass peak amplitudes of up to 32.5–35°C between minimum and maximum values (Schmeidl 1965, Schikora 2003). Floating or constantly wet mats of peatmoss are of negligible importance. Possibly the species is not so strictly dependent on oligotrophic mire habitats in the northernmost parts of its area, where sub-arctic climatic conditions prevail.
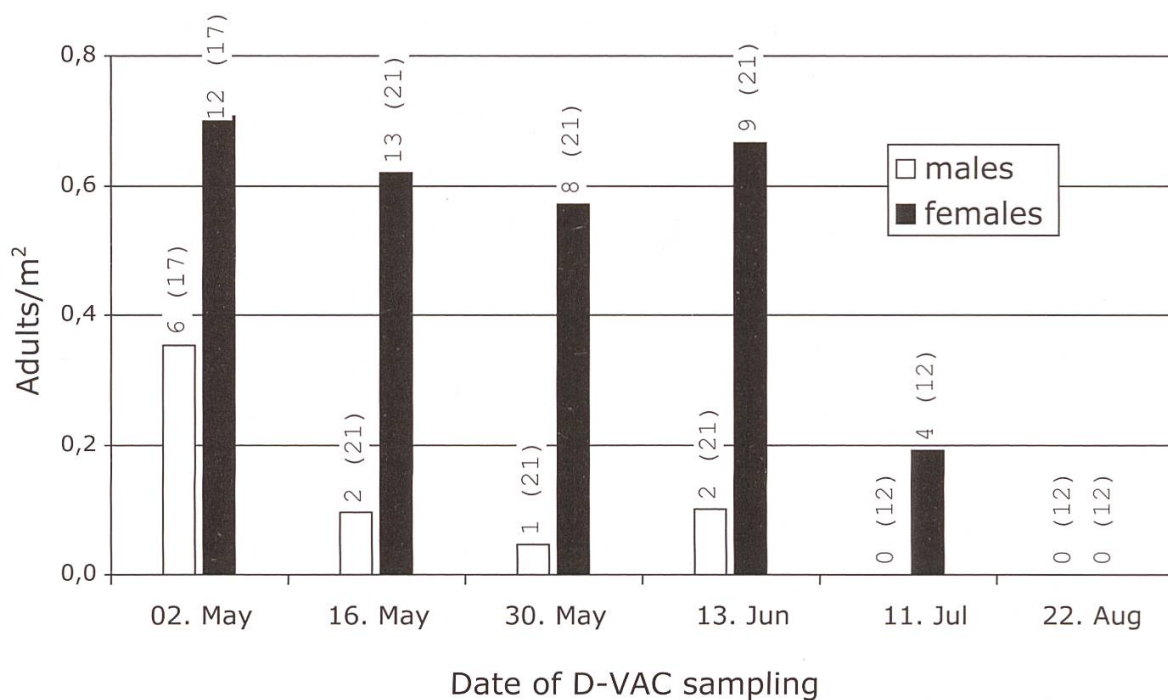
Sum: 11 males, 53 females

Fig. 44. Seasonal abundance of *M. mossica* according to D-VAC sampling (bog complex Komosse/ Ulricehamn, S Sweden 1990). x (y) = sum of caught individuals (sum of D-VAC samples of 1 m² each in May and June, and of 0.5 m² in July and August).

M. mossica may be quite abundant in its typical habitat. Up to 1.1 adults were found per m² at the beginning of May in the course of quantitative sampling using a D-VAC suction apparatus (Komosse, S Sweden, 1990; details & method: Schikora 2003) (Fig. 44).

Small depressions in the open peatmoss-layer are preferably used as a micro-habitat. Here, the inconspicuous sheet webs of *M. mossica* can be found (and those of other small spider species as well). In zones of its habitat, which are frequently crossed by game such as European red deer and roe deer, *M. mossica* likes to use their footprints left in the peatmoss-cover for the establishment of its web (Fig. 23). The webs are best discovered early on a damp morning at the end of April till the end of June, when they are more obvious on account of a fine cover of dew. An excellent alternative method for the detection of webs on drier days is the use of a plant mister. Also the late postembryonic instars can be found by the use of these methods.

As in other linyphiids the spider hangs upside down below the sheet web surface. Usually it is hidden below small particles attached to the web such as leaflets, exuvia or remains of prey. In most places studied, the webs were situated at locations where small ants of the genus *Myrmica* were abundant

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as well. Frequently these ants run across the spiders' sheet web without being caught up in it, and the spiders ignore the intruders. Under field conditions *M. mossica* is usually best distinguished from other linyphiids present in the same habitat (e.g. *Meioneta affinis* (Kulczynski, 1898) in the Harz Mountains) simply by its body coloration, appearing conspicuously light to the naked eye (Figs. 24, 25, 38–41).

Discussion

Except for the northern parts of its (conjectural) Northwest Palearctic area (N Fennoscandia, Baltic countries, eventually N England), *M. mossica* is a rarely found species (especially in the West of Central Europe). No finds have been reported so far e.g. from Denmark, the Netherlands, Belgium, France, the alpine countries or the Czech Republic. From Germany no further findings have been reported other than those which had been described in Schikora (1993, 1995). The latter dated from 1968–70 and referred to (former) bog habitats in N Germany (Lower Saxony: Esterweger Dose/Papenburg and Harz Mountains) and in the foreland of the Alps, S Germany (Bavaria: Rottauer Filz/Lake of Chiem, Mettenhammer Filz/Marquartstein, Sindelsbach Filz/Benediktbeuren). Merely the spider's occurrence in a bog in the Harz Mountains, cited in Schikora (1993, 1995) as "Torfhaus-Moor/Torfhaus", was verified again by Platen (1994). Apparently the Harz Mountains accommodate the last German populations of *M. mossica,* since the species was not (or could not be) confirmed again for any of the other places of its former occurrence.

M. mossica is beyond doubt a habitat specialist (see Habitat). The apparent rareness of the species especially in the western part of Central Europe may thus largely reflect the extent of habitat destruction in that region. Particularly in Germany, but also in most of the adjacent countries, unspoiled oligotrophic mire ecosystems, such as bogs, which formerly covered vast parts in certain areas, have for many decades belonged to one of the most endangered type of habitat (e.g. Schikora 1994). In northern Europe inclusive of the Baltic region, comprising rather sparsely populated countries, the situation of oligotrophic mires is currently still less precarious (see Schikora 1997), although many of them have also been, or still are, influenced by draining, peat extraction and subsequent cultivation.

According to present knowledge, *M. mossica* belongs to a small number of spiders, which may probably constitute specific (stenotopic) faunal elements of oligotrophic mires *sensu lato* (Schikora 2003). Bogs are an extremely nutrient poor subunit of oligotrophic mires and seem to represent the most pre-

ferred habitat of this spider. But which ecofactors can explain the spider's pronounced linkage to its habitat? Which ecological type of spider can *M. mossica* be assigned to? Unfortunately, both questions will have to remain unanswered for the time being as further research is needed. However, information stemming from *ex ovo*-breeding successes of the species (see Methods, Life cycle) and from my own field studies (see Habitat) suggest that simple systems of an ecological classification of spiders (e.g. Platen 1984) do not do justice to the ecological requirements of the species, which are apparently rather more complex. Surely *M. mossica* is not merely a hygrobiontic and photophilous spider, as had been suggested by Platen (1994). The key for a closer understanding of the habitat requirements of *M. mossica* probably depends on the microclimatic peculiarities of extensive *Sphagnum*-layers as well as the pronounced dynamics of the habitat conditions, which have been outlined above.

A further question that can only be insufficiently answered is that of the diet of *M. mossica* under natural conditions. During the course of rearing, the spiders were exclusively fed with collembolans as prey. Although collembolans clearly constitute an important group of invertebrates in pristine bogs, it remains uncertain if they actually play a major role in the spider's natural prey spectrum. Anyway, the fact that some spiders were found in captivity feeding on small predatory mites, or on their own young of the 1st free instar, indicates that their prey spectrum is certainly larger and not restricted to collembolans alone. *M. mossica* seems to have become specialized in hunting small organisms, in contrast to other linyphiids (e.g. *Wubanoides uralensis lithodytes*, *Bathyphantes simillimus buchari*), which attack and seize prey also considerably larger than themselves.

Acknowledgements

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