

Intraspecific variation in taxonomic characters, and notes on distribution and habitats of *Meioneta mossica* Schikora and *M. saxatilis* (Blackwall), two closely related spiders from northern and central Europe (Araneae: Linyphiidae)

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Summary

An outline of the intra- and interpopulation variation of taxonomic characters is presented for the recently described and previously overlooked spider *Meioneta mossica* Schikora and its close relative *M. saxatilis* (Blackwall). Information about distribution and habitat preferences is given for both species. In a large number of samples from northern and central Europe, negligible variational overlap was found for most of their geographical range. Both spiders remained as distinct species. The only exception was one of two locations of syntopic occurrence, where 11 specimens (both sexes) with intermediate characters were found. It is concluded that they are the result of local interspecific hybridisation.

Introduction

Differences between phenotypes may reflect either a species difference or intraspecific variation. The importance of taxonomic characters thus depends largely on their constancy in given taxa. Consequently the study of variation is one of the foremost tasks in taxonomy. The purpose of the present study has been to review the potential for individual and geographical variation of taxonomic characters in two spider species which are closely related morphologically. Specimens of the recently described and previously overlooked *Meioneta mossica* (Schikora, 1993), and reference collections of "*M. (Aprolagus, Agyneta) saxatilis* (Blackwall, 1844)" *sensu lato* from northern and central Europe were examined regarding the intra- and interpopulation variation of morphological characters which are of importance for identification. The study is based on 598 specimens of both species in both sexes, representing spot checks of 17 *M. mossica* and 45 *M. saxatilis* allotopic, and 2 syntopic populations/occurrences. The following structures were investigated: (1) lamella characteristica and (2) paracymbium of the male palp, (3) male chelicera, (4) epigyne and vulva.

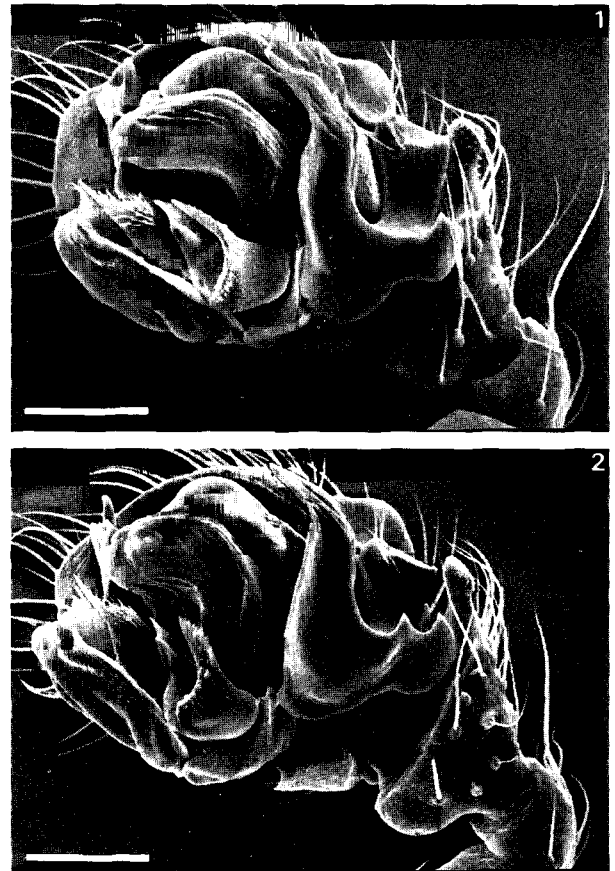
Abbreviations used: EG=epigyne, LC=lamella characteristica, PC=paracymbium. CHBS=author's collection; CPM=Merrett collection; IZBT=Institute of Zoology and Botany, Tartu; MHNP=Muséum national d'Histoire naturelle, Paris; NHMB=Naturhistorisches Museum, Basel; NHRS=Naturhistoriska Riksmuseet, Stockholm; RMSE=Royal Museum of Scotland, Edinburgh; SMF=Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt; ZMU=Zoological Museum, Uppsala; ZMT=Zoological Museum, Turku.

Methods

The characters of interest were examined at 80× with a stereoscopic microscope in every specimen. The results were documented by making notes and sketches according to a standardised scheme. From nearly all available samples of *M. mossica*, and from a large number of those of *M. saxatilis*, single specimens with both typical and deviant (or unclear) characters, were chosen. Their copulatory organs were dissected for a detailed examination.

The male palps were examined in detail by scanning electron microscopy (SEM), and the female genitalia by transmitted light microscopy (LM). The results were recorded photographically on Ilford PanF films (50 ASA).

For SEM and LM, material preserved in ethanol was used. The male palps to be studied with SEM were cleaned with short ultrasonic pulses, critical point-dried, then mounted on small graphite pillars and sputter-coated with gold (20 nm layer). Care was taken to make the mountings and adjustments in a comparable way on each palp. Owing to its three-dimensional complexity, the appearance of the LC in both species varies considerably with the angle of view which is chosen for investigation. This impedes morphological comparisons to a great extent. To enhance understanding of the LC



Figs. 1–2: Scanning electron micrographs. Orientation of left male palpus during SEM examination of lamella characteristica details. **1** *Meioneta mossica* Schikora; **2** *Meioneta saxatilis* (Blackwall). Origin of specimens: **1**: location 11; **2**: location 20 (see *Material*). Scale lines=0.1 mm.

details which are presented in this paper, the standardised orientation of the palps under SEM examination is shown in Figs. 1 and 2. SEM examination was carried out in an ISI-100B (International Scientific Instruments; Akashi Seisakusho Ltd.).

Female genitalia for LM were cleared in a 10% KOH solution at about 50°C and temporarily embedded in Hoyer's medium (water-soluble; Kraus, 1984) on microslides. The LM examinations were made at 200× with an Olympus BHS compound microscope equipped with an Olympus BH2-NIC differential interference contrast device and photographic unit.

Material examined

The study was carried out on 172♂ and 98♀ of *M. mossica*, and on 240♂ and 70♀ of *M. saxatilis*, representing respectively 18 and 46 different locations. The specimens originated from Norway (N), Sweden (S), Estonia (EST), Russia (RUS), Great Britain (GB) and Germany (D) for *M. mossica*, and from Sweden, Estonia, Great Britain, France, Switzerland, Austria and Germany for *M. saxatilis*. In one case, some specimens were found which appeared morphologically as intermediates between *M. mossica* and *M. saxatilis*. This sample is listed separately. The localities are indicated below by numbers in parentheses which are referred to in the figure legends, distribution maps and text.

Meioneta mossica Schikora, 1993 (all available material): (1) N, Nordland Fylke, N of Lake Iptojävi, 35 km SE Narvik, 1♂, 26 July 1992 (leg. HBS, CHBS). (2) S, Norrbotten, Stordalsmyren/Stordalen, 10 km E Abisko, Torne Lappmark, 1♀, 1970 (sub *M. saxatilis*, Coll. Svensson, ZMU 6765); 2♂, 15–17 June 1975 (sub *M. saxatilis*, Coll. Holm, ZMU 6763, 6764); 1♂, 5 June 1979 (sub *M. saxatilis*, Coll. Holm, ZMU 6761); 1♀, 3 July 1980 (sub *M. saxatilis*, Coll. Holm, ZMU 6762); 7♀, 16 July–19 September 1986 (leg. Främbs, CHBS). (3) S, Uppland, Ryggmossen/Uppsala, 2♂ 1♀, 2–24 June 1962 (sub *M. saxatilis*, Coll. Holm, ZMU 16067); 2♂, 21 May–15 June 1962 (sub *M. saxatilis*, Coll. Holm, ZMU 6758, 6759); 5♂ 2♀, 10–23 May 1964 (sub *M. saxatilis*, Coll. Holm, ZMU 6757); 16♂ 9♀, 5 May–4 August 1986 (leg. Främbs, CHBS). (4) S, Västermanland, Kulflyten/Fagersta, 7♂ 9♀, 2 May–14 August 1986 (leg. Främbs, CHBS). (5) S, Södermanland, 5 km SSW Eskilstuna, near Lake Skiren, 1♂, 5 June 1986 (sub *M. saxatilis*, Coll. Holm, ZMU 6760). (6) S, Västergötland/Småland, nature reserve Komosse (type locality; see Schikora, 1993), 20 km SE Ulricehamn (only specimens in good condition included in this study), 71♂ 20♀, 30 April–29 October 1990; 5♂ 2♀, 19 May 1993 (leg. HBS, NHRS, CHBS). (7) S, Småland, Store Mosse National Park, 18 km NW Värnamo, 11♂ 3♀, 5 May–18 September 1990 (leg. HBS, CHBS, CPM). (8) RUS, Kaliningrad region, Zehlaubruh, about 32 km SE Kaliningrad, 16♂ 22♀, 25 May–6 September 1994 (leg. HBS, CHBS). (9) D, Niedersachsen, Esterweger Dose, 17 km SE Papenburg, 1♂, 5 October 1969–20 May 1970 (leg. Mossakowski, CHBS). (10) D, Niedersachsen, Torfhaus-Moor/Torfhaus, Harz, 4♂ 3♀, 7 April 1968–28 May 1969 (leg. Mossakowski, CHBS). (11) D, Niedersachsen, Sonnenberger Moor/Sonnenberg, Harz, 13♂ 14♀, 4 May 1968–3 September 1969 (leg. Mossakowski, Coll. Schaefer, CHBS). (12) D, Bayern, Rottauer Filz, 2 km E Bernau, Lake of Chiem, 5♂, 26 March–2 July 1968 (leg. Mossakowski, CHBS). (13) D, Bayern, Sindelsbach Filz, 4 km W Benediktbeuern, 1♂ 2♀, 12 April–30 June 1968 (leg. Mossakowski, CHBS). (14) D, Bayern, Mettenhammer Filz near Marquartstein, 1♂, 13 April–14 September 1968 (leg. Mossakowski, CHBS). (15) GB, Scotland, Creag an Lochan, NW of Loch Tay, 1♀, 19 July 1993 (leg. HBS, CHBS). (16) GB, Scotland, Dun Moss/Alyth, 11 km NW Blairgowrie, 1♀, 21 July 1993 (leg. HBS, Coll. Roberts). (17) GB, Northumberland, Kielder Forest near border with Scotland, 6♂, 1988 (CPM). (29) EST, Bay of Matsalu,

Matsalu mets, 1♂, 5 June 1969 (sub *M. saxatilis*, Coll. Vilbaste, IZBT).

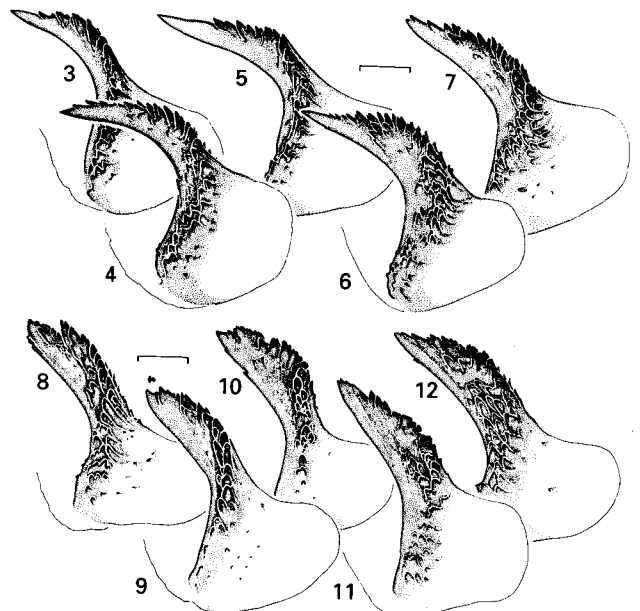
Meioneta saxatilis (Blackwall, 1844) (only material used for illustrations): (11) see above, 1♂, 1968–1969 (syntopic occurrence with *M. mossica*: leg. Mossakowski, Coll. Schaefer). (19) S, Uppsala, N Gottsunda, 2♂ 1♀, 20–22 June and 14–24 July 1969 (Coll. Holm, ZMU 6696, 6697). (20) S, Södermanland, Dammtorpssjön, Nacka, 39♂ 8♀, 13 June–3 July 1965 (Coll. Kronstedt, NHRS; see Kronstedt, 1968). (21) S, Skåne, Kullaberg, Ransvik, 50♂ 4♀, 13–27 June 1970 (Coll. Holm, ZMU 6766–6770; see Holm, 1977). (22) D, Schleswig-Holstein, Weisses Moor near Heide, 4♂ 2♀, 9 June–15 July 1965 and 1986–1987 (leg. Mossakowski, leg. HBS, CHBS; see Schikora, 1994). (23) D, Schleswig-Holstein, Kiel, Botanical Garden, 7♂ 1♀, 1970 (Coll. Schaefer; see Schaefer, 1973). (24) D, Hessen, vicinity of Kassel, 3♂ 3♀, June 1987 (leg. Stippich, CHBS). (25) D, Rheinland-Pfalz, Weissenseifen/Mürtenbach, near Prüm, Eifel, 5♂ 1♀, 31 May–16 August 1968 (leg. Mossakowski, CHBS). (26) D, Bayern, National Park Bayerischer Wald, 6♂ 2♀, 26 May–15 June 1992 (Coll. Weiss). (27) GB, Scotland, Tentsmuir, Fife, 1♂ 1♀, 1966 (CPM). (28) GB, Hampshire, New Forest, 2♂ 1♀, 1960 (CPM).

Meioneta sample, containing intermediate specimens: (18) GB, Derbyshire, Kinder Scout, E of Manchester, 14♂ 4♀, 1990 (CPM).

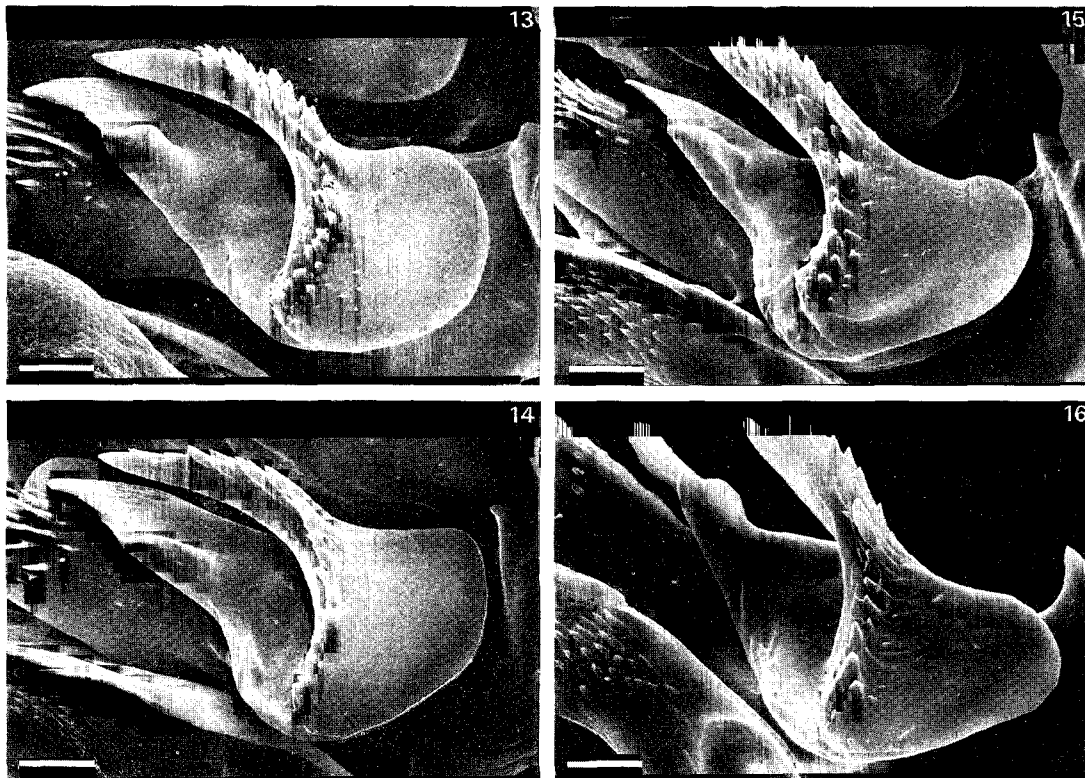
Intra- and interpopulation variation of taxonomic characters

Meioneta mossica (Figs. 1, 3–7, 13–14, 17–19, 23–25, 29–30)

Lamella characteristic: One basic (typical) LC phenotype was usually found predominating in local populations. The differences between individuals were, in general, slight and intergrading. Intrapopulation variation mainly affected the markedness and extent of teeth on the outer LC edge, and less frequently, the length of the pointed, needle- or beak-like, distal LC part (Fig. 3 cf. 14). Very rarely the pointed distal part of the LC on one palp was found to be broken off. Only slight



Figs. 3–12: Range of intraspecific variation in lamella characteristic. Left palp, lateral view, obliquely from the front and below (see Figs. 1–2). Terminal apophysis only suggested. 3–7 *Meioneta mossica* Schikora; 8–12 *Meioneta saxatilis* (Blackwall). Origin of specimens: 3–7: locations (in order of figure numbers) 12, 10, 3, 11, 17; 8–12: locations 25, 21, 23, 27, 24 (see *Material*). Scale lines=0.02 mm.



Figs. 13–16: Scanning electron micrographs. Typical phenotypes of lamella characteristica in northern- and southernmost populations investigated in this study. Lamella characteristica and posterior terminal apophysis of left palp, lateral view, obliquely from in front and below (see Figs. 1–2). **13–14** *Meioneta mossica* Schikora; **15–16** *Meioneta saxatilis* (Blackwall). Origin of specimens: **13–14**: locations 2, 12; **15–16**: locations 20, 26 (see *Material*). Scale lines=0.02 mm.

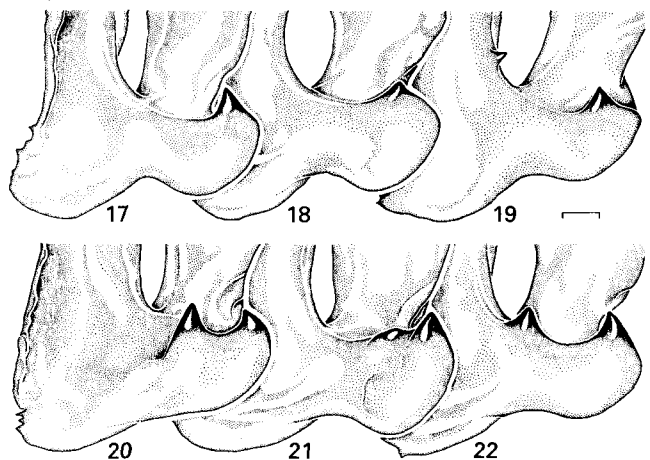
variation was found regarding the LC curvature. In rare cases, single males of a population differed from the remaining specimens by a stronger thickness or form of the basal curved LC part, appearing as the “neck” (Fig. 6 cf. 1). A rough review of intraspecific LC variation (total of intra- and interpopulation variation) is given by Figs. 3–7, with the most deviant LC (Figs. 3, 7) arranged at the sides. The most common LC phenotypes intergrade between the LC shown by Figs. 4 and 5.

With regard to geographical, i.e., interpopulation, variation, it was impossible to distinguish between specimens from Scandinavia and continental Europe by their LC with any certainty (Figs. 13–14). Only the distal LC part of single males from Lapland (2) was found to be more pronounced (Fig. 13). However, judging by the few available males from Northumberland (17), British specimens of *M. mossica* seem to differ markedly from those of all other European locations by their LC curvature, which appears comparatively weak (Fig. 7 cf. 3–6, 13–14).

Paracymbium: The general PC outline may show considerable morphological variation even within local populations. Mainly affected are the form and markedness of the processes of the lateral margin, basally of the ascending PC branch. As a common feature, the PC of all *M. mossica* males was characterised by a single pigmented tooth, marking the posterior PC pocket (see Schikora, 1993). Its range of variation in markedness is shown by Figs. 17–19. Occasionally — sometimes on only one of the two palps — a rather small and incon-

spicuous additional tooth was found on the basal third of the ascending PC branch (Fig. 19; locations 3, 6, 8, 17); 5–8% of all males were affected in the extensive samples from southern Sweden.

Male chelicera: The distinctive shape of the male chelicera in *M. mossica* (frontal view) proved to be a very reliable, and thus important, taxonomic character. General appearance and variation of the chelicera have already been shown in detail elsewhere (Schikora 1993: 159 and Figs. 5, 23).



Figs. 17–22: Range of intraspecific variation in paracymbium of male palp. Only basal part of paracymbium shown. Left palp, lateral view, somewhat from below. **17–19** *Meioneta mossica* Schikora; **20–22** *Meioneta saxatilis* (Blackwall). Origin of specimens: **17–19**: locations 4, 12, 3; **20–22**: locations 24, 28, 27 (see *Material*). Scale line=0.02 mm.

Epigyne and vulva: In females of *M. mossica*, no structures of the external EG seem to exist which would allow a reliable distinction from females of *M. saxatilis* in all cases. Such characters were, however, offered by the internal structures of the female copulatory organ (vulva): (1) In *M. mossica* the copulatory ducts which run anteriorly are distinctly curved outwards from the longitudinal axis (Figs. 23–25, 29–30 cf. 26–28, 31–32; see Schikora, 1993). The curvature can be described biometrically by the ratio between the distances x and y (for explanation see Fig. 24). Measurements, based on LMs from slide preparations ($n=10$; locations 2–4, 6, 12–14), showed x/y -values ranging from 0.65 (Fig. 25) to 0.82 (Fig. 23), with a mean of 0.76 (s.d.=0.05; Fig. 24). Clear indications of geographical variation were not found (Figs. 29–30). (2) The vulva (ventral view) roughly has the outlines of a rectangle that on average is 1.8 times wider than high (s.d.=0.1; sample and locations as above; Figs. 23–25, 30). The lengths of its sides are defined by (a) the distance between the outer edges of the receptacula (=width), and (b) the distance between their anterior edges and the outer edge of the posterior curvature of the copulatory ducts (=height). The vulval width of only one female from northern Sweden (2) was found to be slightly wider than usual ($a:b=2:1$; Fig. 29).

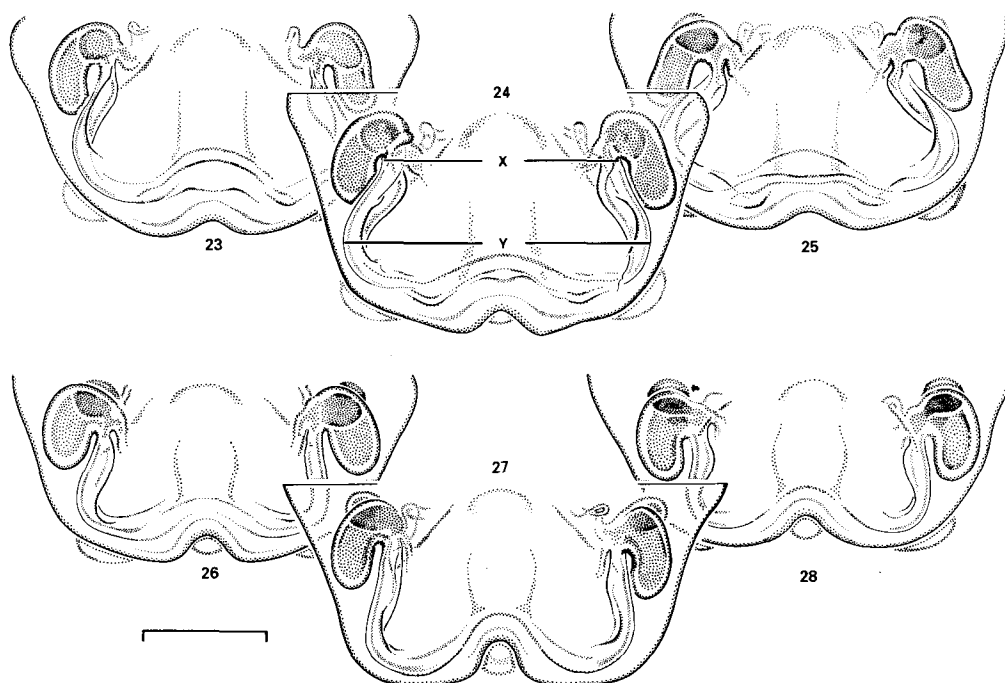
Meioneta saxatilis (Figs. 2, 8–12, 15–16, 20–22, 26–28, 31–32)

Lamella characteristic: As already shown for males of *M. mossica*, individual variation of the LC in *M. saxatilis* is mainly associated with the markedness and extent of the denticles on the outer LC edge (Figs. 8, 12 cf. 9–11, 15–16). Though somewhat variable, the LC

curvature was never as sharply bent as in *M. mossica*. A rough review of intraspecific LC variation is given by Figs. 8–12, with Figs. 9 and 10 constituting by far the most common types. The extremes are represented by Figs. 8, 11 and 12. Only exceptionally were single specimens found having the distal LC part markedly pointed (Figs. 11, 12). Judging by the specimens from Scandinavia, continental Europe and southern England, no special morphological variation related to the geographical situation became obvious (Figs. 15–16). It remains to be seen whether a pointed LC (Fig. 11) is possibly a peculiarity of specimens from northern UK. Only one male from that region was available for this study (27).

Paracymbium: Without exception two strong neighbouring pigmented teeth, marking the posterior paracymbial pocket, were present in the *M. saxatilis* males. Their markedness as well as the distance between them proved to be subject to some variation (Figs. 20–22). Only in one specimen each from New Forest, GB (28), and Vienna, Austria (Coll. Thaler; see Thaler & Steiner, 1993), the anterior PC tooth was somewhat reduced (Fig. 21). Usually both teeth are situated on a ridge, which is clearly separated from the base of the ascending PC branch (Fig. 20). However, in nearly all populations some specimens were found with the ridge and the anterior tooth in contact with the latter structure (Fig. 22). The general PC outline in *M. saxatilis* shows a similar extent of variation as already mentioned for *M. mossica*.

Male chelicera: The cheliceral shape (frontal view) was also found to be highly characteristic in males of *M. saxatilis* (see Schikora, 1993: Figs. 7, 25). The markedness of the cheliceral teeth (outer row) which, in contrast



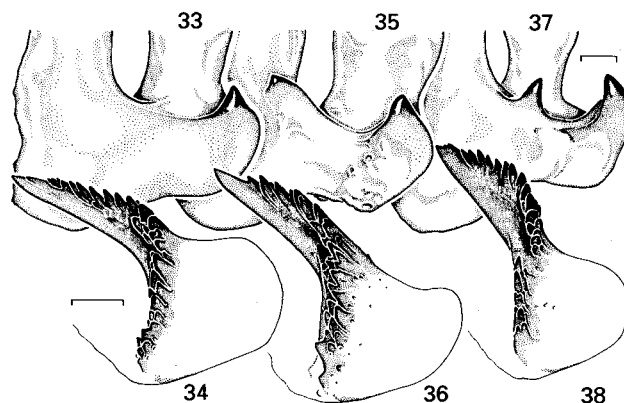
Figs. 23–28: Range of intraspecific variation in vulval structures. Ventral view, KOH-treated and cleared. **23–25** *Meioneta mossica* Schikora; **26–28** *Meioneta saxatilis* (Blackwall). X and Y indicate minimal and maximal distances between outer edges of copulatory ducts. Range of x/y ratios in *M. mossica*: 0.65–0.82 (mean 0.76; s.d. 0.05); in *M. saxatilis* 0.87–0.97 (mean 0.92; s.d. 0.03; see text). Origin of specimens: **23–25**: locations 11, 10, 4; **26–28**: locations 25, 20, 22 (see *Material*). Scale line=0.1 mm.

to *M. mossica*, always reached down almost to the conical process near the fang joint, was found to be somewhat variable. They were frequently stronger than those previously shown (1993: *ibid.*).

Epigyne and vulva: (1) In *M. saxatilis* females the copulatory ducts which run anteriorly are almost parallel or, at the most, only slightly curved outwards from the longitudinal axis (Figs. 26–28, 31–32 cf. 23–25, 29–30; see Schikora, 1993). The x/y ratios (for explanation see Fig. 24) ranged from 0.87 (Fig. 26) to 0.97 (Fig. 28), with a mean of 0.92 (s.d.=0.03; Fig. 27). As in *M. mossica*, these measurements are based on LMs from slide preparations ($n=16$; 12 different locations from S, GB and D). The means of x/y -ratios in both species were found to be significantly different ($t=9.54$, $p<0.001$; t -test according to Welch: Clauss & Ebner, 1982). (2) Generally the vulva (ventral view) has the outlines of a rather flat rectangle (Figs. 26–28, 31–32) that on average is 2.2 times wider than high (s.d.=0.15; sample and locations as above). This proportion proved to be significantly different from the respective proportion of the *M. mossica* vulva (means 1.8 vs. 2.2; $t=7.33$, $p<0.005$).

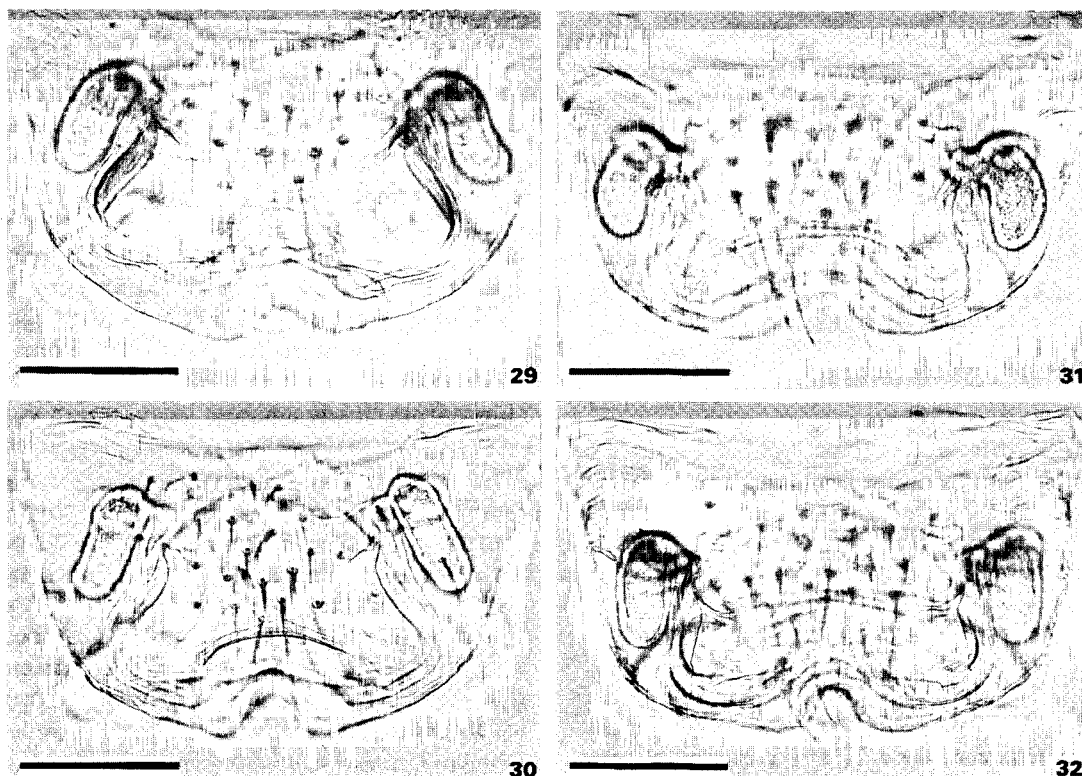
Specimens from Kinder Scout, Derbyshire (Figs. 33–41)

Lamella characteristica and paracymbium: The total range of different LC and PC phenotypes, which was found in the sample from Kinder Scout, Derbyshire, is shown in Figs. 33–38. Judging by the character combination, four males out of a total of 14 were in rather good accordance with *M. mossica* (Figs. 33–34), and one



Figs. 33–38: Range of different phenotypes of male palpal characters in sample from Kinder Scout, Derbyshire, GB. **33–34** *Meioneta mossica* Schikora; **35–36** Intermediate specimen; **37–38** *Meioneta saxatilis* (Blackwall). Each pair of figures are from same individual. **33, 35, 37** Basal part of paracymbium, lateral view; **34, 36, 38** Lamella characteristica, lateral view, obliquely from in front and below. Scale lines=0.02 mm.

with *M. saxatilis* (Figs. 37–38). Though resembling *M. mossica* more than the latter species, the remaining 9 specimens clearly showed intermediate characters (Figs. 35–36). This intermediate position was indicated by (1) the very weak LC curvature, (2) the shape of the distal LC part, and (3) the presence of a moderately strong second tooth (or at least its indication, or a bump) at the base of the ascending PC branch. Often this tooth appeared to be “fused” with the latter structure (Fig. 35). The PC cuticle basally of the posterior tooth appeared conspicuously wrinkled or gnarled in most of

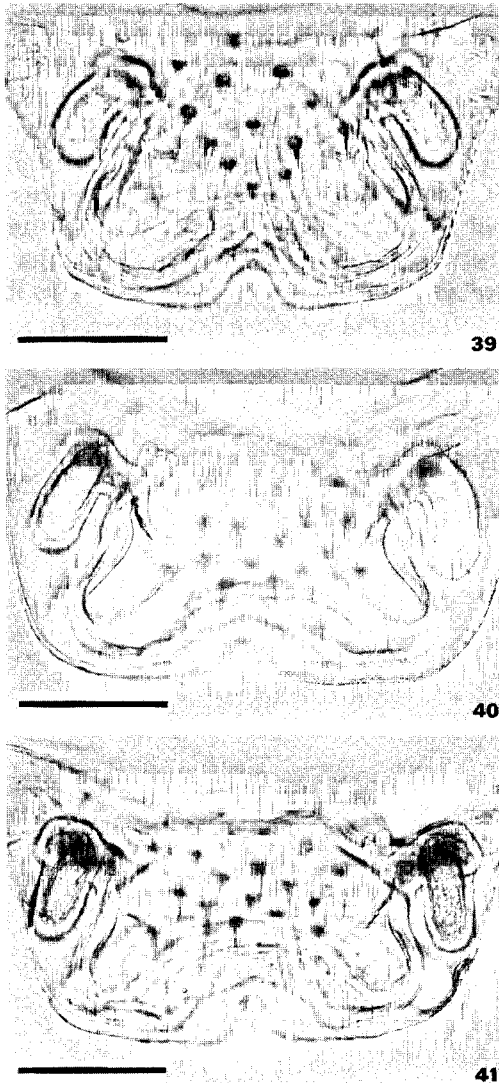


Figs. 29–32: Micrographs. Typical phenotypes of vulval structures in northern- and southernmost populations investigated in this study. Ventral view, KOH-treated and cleared. **29–30** *Meioneta mossica* Schikora; **31–32** *Meioneta saxatilis* (Blackwall). Origin of specimens: **29–30**: locations 2, 13; **31–32**: locations 19, 26 (see *Material*). Scale lines=0.1 mm.

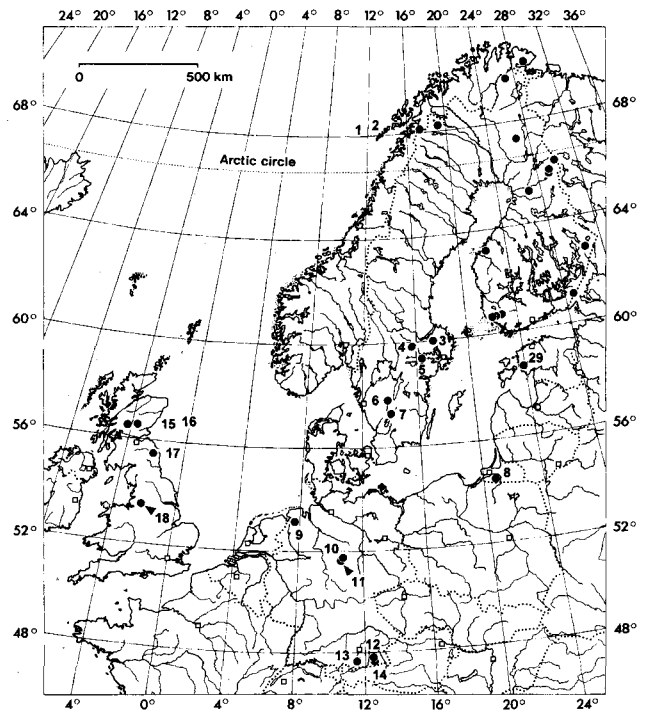
the intermediates (Fig. 35). The PC cuticle of the male which apparently belonged to *M. saxatilis* was sculptured in a similar way, and the PC teeth were unusually pronounced (Fig. 37).

Male chelicera: Judging by the cheliceral form, and position and number of the promarginal teeth, 5 of the 9 intermediates also had chelicerae showing intermediate characters. However, two each of the remaining 4 intermediates seemed to correspond either to *M. mossica* or *M. saxatilis*. Those 5 specimens which could be assigned to either species by their LC/PC combination, also appeared to have (more or less) typical chelicerae.

Epigyne and vulva: The EG from 3 out of the 4 available females from Kinder Scout were chosen for a detailed examination (Figs. 39–41). The following x/y ratios (see Fig. 24), cited in the order of the figure numbers, were found: 0.74, 0.76 and 0.90. The biometrical data suggest good accordance with *M. mossica* in the first two cases, and with *M. saxatilis* in the latter. But in the light of the vulval proportions (Figs. 39–41), indications of a fluid morphological transition became



Figs. 39–41: Micrographs. Range of different phenotypes of vulval structures in sample from Kinder Scout, Derbyshire, GB. Ventral view, KOH-treated and cleared. **39** *Meioneta mossica* Schikora; **40** Intermediate specimen; **41** *Meioneta saxatilis* (Blackwall). Scale lines=0.1 mm.



Map 1: Present known distribution of *Meioneta mossica* Schikora according to samples available for this study (numbered; see *Material*) and recently revised reference collections of *M. saxatilis sensu lato*. Closely adjacent locations are shown by only one symbol, syntopic occurrence with *M. saxatilis* (Blackwall) is indicated by arrows. Boundaries between countries or administrative areas are dotted. See text for detailed information.

apparent. One female (Fig. 40) seems to show intermediate characters.

Distribution (Maps 1–2)

The maps, showing the present known distribution of both species, are based on data from all samples which have been examined in the course of this study. Additionally, data are included from reference collections which have recently been revised by other persons (September 1993–November 1994; see Acknowledgements). All distribution data from Finland and NE Norway were provided by M. I. Saaristo (Coll. ZMT; in litt.). They are based on 16♂ and 16♀ from 20 sites for *M. mossica*, and on 4♂ from 3 sites for *M. saxatilis*. Finds from closely adjacent locations are shown by only one symbol in the maps, syntopic occurrence of both species is indicated by arrows.

***Meioneta mossica* (Map 1):** The present known distribution of this species extends from approximately 47° (southern Germany) to 70° N (northernmost Norway). In comparison with the data given in Schikora (1993), it should be noted that only two additional occurrences of *M. mossica* were recorded from continental Europe (location 8, Kaliningrad region of Russia; location 29, NW Estonia). Apart from the Derbyshire location (18), England, a second case of syntopy with *M. saxatilis* was found in Niedersachsen, Germany (location 11).

***Meioneta saxatilis* (Map 2):** The revised records indicate a distribution extending from 46° 33' N (CH:

Canton of Vaud, La vallée de Joux, 1040 m; G. Blandenier, in litt.) and 46° 47' N (A: East Tyrol, Lienz, 1100 m; see Thaler, 1983) to 61° N (southern Finland). Possibly the northernmost locations in Finland and Sweden roughly correspond to the northern distribution limit of this species. Specimens from France (MHNP 5002, 24709) are not shown on the maps, since no data about the sampling sites were available.

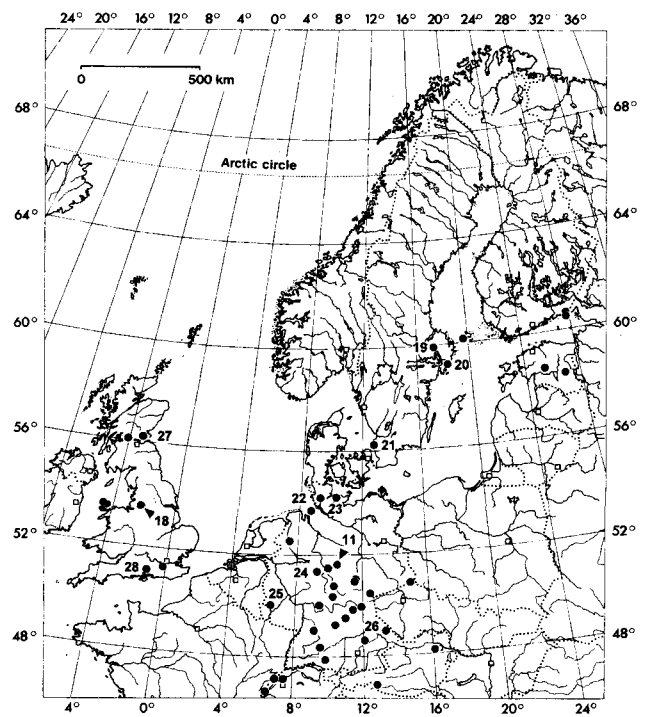
Habitats

Although the available habitat descriptions were frequently rather imprecise and more of a subjective nature, a compilation of such data nevertheless seems useful to indicate the range of ecological tolerances for both species. The data refer to my own habitat notes, tube labels from specimens of reference collections, and information provided by other arachnologists. My own descriptions are indicated by an asterisk (*), numbers in parentheses refer (1) to the total number of specimens and (2) to the respective number of sites; samples from different sites in one region (location 17; Kielder Forest) are listed successively and indicated by letters.

Meioneta mossica (all known finds; Jan. 1995)

Open plain (hummock-hollow mosaic, soaks) and adjoining periphery (e.g. open lagg-region) of pristine ombrogenous bogs* (270; 9); moist acidic mesotrophic fallow land on deep peat, adjacent to lagg-region of an ombrotrophic bog, dominated by e.g. *Carex nigra*, *Juncus filiformis*, *Poa angustifolia** (15; 1); hummock-hollow structures of pristine ombro-soligenous bogs in low mountain range* (34; 2); *Sphagnum* bog (1; 1); peat bogs (6; 3); bog (5; 3); regenerating part with abundant *Sphagnum* of a formerly drained bog-relict* (1; 1); sub-arctic palsa-* (12; 1), aapa- (1; 1) and mixed-mires* (1; 1); boggy *Sphagnum* area (1; 1); wet heath and bog on deep peat, characterised by *Calluna*, *Eriophorum*, *Deschampsia flexuosa* and *Sphagnum* (7; a), shaded riverside with deep peat and bryophytes (4; b), *Callunal* *Eriophorum* blanket mire with abundant *Sphagnum*, adjacent plantation and forest ride (2; c), wet roadside, dominated by *Calluna*, *Molinia*, *D. flexuosa* and *Vaccinium myrtillus* (2; d); *Sphagnum* on a boggy lake shore (9; 1); moorland, *Sphagnum* expanse of a boggy slope on poor rocky ground* (1; 1); *Sphagnum* (1; 1); *Sphagnum majus* expanses of a poor fen, sparsely overgrown with *Carex limosa*, *C. rostrata*, *Eriophorum angustifolium** (2; 1); fen (3; 3); edge of an open mire (4; 1); mire (1; 1); shore meadow (1; 1) no habitat details (2; 2).

The great majority of the finds of *M. mossica* refer to habitats which at present may be characterised best as "open oligotrophic mires". This term comprises ombrotrophic bogs (ombrotrophy as an extreme case of oligotrophy), boggy areas on wet poor grounds, as well as poor fens, which at least locally have such habitat structures in common as are preferred by the spider (see Schikora, 1993). The structural similarity refers to open *Sphagnum* expanses (type localities 6, 7: *Sphagnum*



Map 2: Present known distribution of *Meioneta saxatilis* (Blackwall) according to samples available for this study and recently revised reference collections. Numbers refer to material used for illustrations (see *Material*). Closely adjacent locations are shown by only one symbol, arrows indicate syntopic occurrence with *M. mossica* Schikora. Not shown are finds from France, since no information about sampling sites was available. Boundaries between countries or administrative areas are dotted. See text for further information.

tenellum, *S. cuspidatum*, *S. rubellum*, *S. magellanicum*, *S. papillosum*, *S. majus*, *S. balticum*, *S. imbricatum*), which are sparsely overgrown with dwarf shrubs or small tussocks (e.g. *Calluna vulgaris*, *Erica tetralix*, *Andromeda polifolia*, *Vaccinium oxycoccus*, *Eriophorum vaginatum*, *Carex rostrata*, *C. limosa*). In 1993, a small number of adult specimens were observed for the first time in the field (location 6). Their webs were situated in tiny depressions of the *Sphagnum* expanse adjacent to dwarf shrubs, or were fixed between the stems of dwarf shrubs close to the surface of the *Sphagnum* layer.

Meioneta saxatilis (examined samples and revised collections)

Oak wood (40; 1); deciduous wood and adjacent lake shore (47; 1); pine forest (1; 1); damp wood relicts (2; 1); forest edges (14; 2); grove on peat (1; 1); grove hill (2; 1); open meadows (15; 2); meadows along stream sides (11; 3); roadsides and banks (12; 2); bank- and shorelines (19; 1); embankment of a fishpond (6; 1); arable land (1; 1); field of winter wheat ("few"; 1); moss layer on clay in a park (2; 1); park (1; 1); botanical garden (8; 1); garden (2; 1); grassland (2; 1); wet mesotrophic fen with tussocky sedges (e.g. *Carex paniculata*) and adjacent moist meadow (17; 1); fen meadows (3; 1); rich fen (1; 1); *Sphagnum* bog (4; 1); ombro-soligenous bogs in pine wood area* (3; 2); open bog relict surrounded by arable land* (1; 1); very small bog relict surrounded

by pine forest (6; 1); *Empetrum nigrum*-*Eriophorum vaginatum* vegetation of a drained bog relict* (5; 1); spruce forest with *Calluna* and *Vaccinium uliginosum* on dry peat of excavated bog relicts (14; 2); wooded excavated bog relict (2; 1); *Empetrum nigrum* vegetation of a coastal dune area* (46; 1); sandy seashore (1; 1); area of sand dunes by the sea (2; 1); dry habitats (4; 1). No detailed information about specimen numbers (48; 10); edges of sparse mixed woods on limestone and chalk, dry and sparse hedge, wet shady undergrowth, herbaceous vegetation with open patches, herbaceous vegetation and bushes, open calcicolous fen (*Calthion*). No habitat details (43; 9).

The revised records of *M. saxatilis* refer to a great variety of rather contrasting habitats. However, judging by the frequency of its occurrence, the species shows a certain preference for ecotone habitats, ruderal places and meadows, and apparently tolerates shady conditions.

Meioneta specimens from Kinder Scout, Derbyshire

Kinder Scout, close to the city of Manchester, constitutes the highest moorland in the Derbyshire Peak District (610 m above sea level). By 1982, air pollution, over-grazing, accidental fires and erosion caused by huge numbers of visitors had turned it into one of the most damaged upland sites in Europe (P. Merrett, pers. comm.). The 18 *Meioneta* specimens available for this study (Figs. 33–41) were collected in 1990 in the course of an experiment which formed part of a 10-year restoration project. The spiders were caught with pitfall traps in each of 4 different vegetation types which were described as follows (P. Merrett, in litt.): (1) Fragile. Short *Deschampsia* grassland and bare ground, some *Nardus* and occasional *Vaccinium*; steep slope, stony. (2) *Eriophorum*. *E. vaginatum* and *E. angustifolium*, *Empetrum nigrum*; luxuriant vegetation cover on peat. (3) *Vaccinium*. Thick, tufty bilberry, growing vigorously, with about 30% cover *Nardus*; steep slope, stony. (4) *Nardus*. Very thick, tussocky *Nardus*, with about 5% other vegetation; *Juncus squarrosus*, *Vaccinium* and *E. vaginatum*.

It is not known which of the specimens (*M. mossica*, *M. saxatilis*, intermediates) came from which site, because the samples were not kept separately in their original tubes.

Discussion

The currently available information reveals different centres of distribution for each species (Map 1 cf. 2). The distribution of *M. mossica* seems focused mainly on Scandinavia and the northern parts of central Europe. *M. saxatilis* in contrast appears much more as a central European spider. The apparent distribution centres are connected by a broad zone of geographical overlap, ranging from about 48° N (southern Germany) to 61° N (southern Finland; Map 1 cf. 2). The spiders seem to be only exceptionally syntopic in areas where both species occur sympatrically.

Our present knowledge indicates that *M. mossica* is a rather specialised sibling species of the evidently eurytopic *M. saxatilis*. *M. mossica* seems to be mainly restricted to open oligotrophic mires, where it probably requires the special microclimatic conditions of sparsely overgrown *Sphagnum* expanses. Pristine ombrotrophic bogs, an extremely nutrient-poor subunit of oligotrophic mires, seem to constitute the optimal habitat. Today, after a period of industrial peat-exploitation and intensive cultivation, oligotrophic mire ecosystems have undergone great changes in central Europe (e.g. Schikora, 1994). In most countries they are now one of the most endangered habitats (e.g. Harms, 1984). The apparent rareness of *M. mossica* in that region may thus largely reflect the extent of habitat destruction. With regard to Germany, where unspoiled bogs have been absent for a long time in nearly all regions, the few known finds (which date from 1968–70) possibly constitute the last relicts of a formerly wider distribution. Though many reference collections of *M. saxatilis sensu lato* from Germany have been revised in the course of this study (Map 1 cf. 2), no further occurrences of *M. mossica* other than those already cited in Schikora (1993) were found. In contrast to *M. mossica*, *M. saxatilis* apparently tolerates shady conditions, and is frequently found in ecotone situations in a variety of different habitats.

Both taxa apparently remain as distinct species over most of their geographical range. In 98.2% of all available specimens (587 out of 598) the examined taxonomic characters permitted a reliable and definite assignment. Each character was found to be variable to some extent both individually and geographically. Often it was impossible to distinguish between intra- and interpopulation variation. Indications of noticeable geographical variation became obvious only in males of *M. mossica* from northern England and in males of *M. saxatilis* from Scotland. Judging by the relatively few available specimens from those regions, both species seem to differ markedly in their LC from males from all other European locations (Figs. 7, 11). It would be desirable to pursue this interesting phenomenon by subsequent investigations. Similar morphological differences have been mentioned by Grimm (1982: 174; 1985: 237) for *Zelotes apricorum* from England and central Europe.

No variational overlap (male chelicera, LC, vulva) or only slight overlap (additional PC tooth in *M. mossica*; Fig. 19) was apparent between the two species in most localities. The only exception was one of the two cases of syntopic occurrence, where some specimens were found which appeared to be intermediate (location 18; see *Specimens from Kinder Scout, Derbyshire*). In the second case of syntopy (location 11; 27 specimens of *M. mossica*, 1 of *M. saxatilis*), not the least indication of introgression was found.

Of course it can be only conjectured about the true nature of the specimens from Derbyshire. However, the relative constancy of their intermediate character combinations, and the presence of specimens in the same sample which could be (more or less reliably) assigned to either *M. mossica* or *M. saxatilis*, suggest that the intermediate specimens may be hybrids. This hypothesis

is possibly strengthened by the observed aberrations of the PC cuticle in intermediate males (Fig. 35), perhaps suggesting a certain genetic instability. Since only closely related species can hybridise successfully (Mayr & Ashlock, 1991), the existence of hybrids would emphasise the close relationships between both spiders.

It is well known from many animal species (vertebrates and certain groups of insects) that they occasionally exhibit local inconsistencies regarding their reproductive isolation from populations of other related species (e.g., Mayr, 1967; Mayr & Ashlock, 1991; Grant & Grant, 1992). In birds, for example, roughly one out of every ten species is known to have bred in nature with another species and produced hybrid offspring (Grant & Grant, 1992). It has recently been shown that hybridisation might even be evolutionarily effective under exceptional environmental conditions. Hybrid fitness was then found to be much enhanced (Grant & Grant, 1993). In contrast to vertebrates and insects, cases of (presumed) hybridisation of spiders in the wild have been only rarely reported (Merrett, 1980: 6; Grimm, 1982: 177; Oxford & Plowman, 1991: 295–296) or documented hitherto (Murphy & Platnick, 1986: figs. 9–13). Unequivocal spider hybrids seem to be much more frequently the result of “forced mating” under laboratory conditions (e.g. Gering, 1953; Stratton & Uetz, 1986; see there for further references). According to this study hybridisation of *M. mossica* and *M. saxatilis* appears to be a local and exceptional event. Since (presumed) hybrids were found in only 1 out of 64 different locations (1.6%), and their proportion is small (1.8% in a sample of 598), it does not invalidate the specific status of both taxa.

The apparent differences in ecological preferences between *M. mossica* and *M. saxatilis* (see *Habitats*) serve probably as an important part of their interspecific isolating mechanisms. In such cases human interference, causing considerable disturbance of the natural ecological balance in many habitats, could become significant (Mayr & Ashlock, 1991). There is strong evidence for the belief that anthropogenic influences may be regarded as a key factor in the case of Kinder Scout, Derbyshire (see *Habitats*).

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***Nyranytarbus*, replacement name for *Hemiphrynus* Frič, 1901 (Trigonotarbida: Eophryinidae)**

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The trigonotarbid genus *Hemiphrynus* Frič, 1901 was described for two species of fossil arachnid from the Upper Carboniferous Coal Measures of Nýřany, Czech Republic. These were placed in Araneae, and later Frič (1904) erected a monogeneric family, Hemiphrynidae, for them. Pocock (1910) transferred *Hemiphrynus* to Anthracomartida, and later Petrunkevitch (1953) placed the genus in the family Eophryinidae of the Trigonotarbida.

Since the name *Hemiphrynus* is preoccupied in the Coleoptera by *Hemiphrynus* Horn, 1889, it must be replaced. The name *Hemiphrynus* was also used by Pocock (1902) for an amblypygid genus from South America, which has since been replaced with *Paraphrynus* Moreno, 1940.

During the course of this work, it came to our attention that the date of Frič's (1901) paper is cited differently by various authors; Petrunkevitch (1953), for example, references the same paper twice, once as 1899, and again as 1902! Whilst the cover page of Frič's (1901) work has the data 1899 on it, Frič (1904) refers to it as having been published in 1901. Since this was a work published in parts over a number of years, presumably

the arachnid section appeared after the printing of the title pages. We have therefore taken the date cited by Frič (1904) as the correct year of publication of Frič (1901).

Genus *Nyranytarbus*, nom. nov.

Hemiphrynus Frič 1901: 57. Junior homonym of *Hemiphrynus* Horn, 1889 (Coleoptera). Type species *Hemiphrynus longipes* Frič, 1901, by subsequent designation (Petrunkevitch, 1913: 97).

Etymology: After Nýřany, Czech Republic, the locality from which all known specimens originate; and *tarbos*, Greek: terror, typical suffix for Trigonotarbida. Gender masculine.

Remarks: Only two species are included in the genus, *Nyranytarbus longipes* (Frič, 1901), comb. nov. and *Nyranytarbus hofmanni* (Frič, 1901) comb. nov., both from the Upper Carboniferous Coal Measures of Nýřany, Czech Republic.

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