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The female genitalic morphology of "micronetine" spiders (Araneae, Linyphiidae)

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Abstract Current knowledge of "micronetine" female genitalia is almost exclusively based on transmitted light microscopy data. As such, our understanding of the epigynal anatomy is incomplete and somewhat misleading, to the extent that it hinders comparative studies of linyphiid diversity. We used scanning electronic microscopy (SEM) to study the complex epigynal morphology of "micronetine" spiders. Enzymatic digestion of soft tissues allowed us to examine the internal chitinized structures in detail using SEM. A taxonomic sample of nine species was selected to represent the morphological genitalic diversity of female "micronetines" (including one member of the Erigoninae clade). Results reveal that the epigynum consists of a pair of grooves formed by integument folds (copulatory and fertilization grooves). The protruding epigynal region is divided into a ventral and a dorsal plate by the grooves; both plates can be modified to form an epigynal cavity and/or a scape. Our observations confirm the widespread occurrence of epigynal grooves, rather than ducts, in "micronetines". Epigynal grooves seem to be common in linyphioids and other spider groups.

Keywords Micronetinae · Erigoninae · Genitalia · Epigynal morphology · Groove complex · Epigynal cavity · Scape · Taxonomy · Systematics

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Introduction

One of the most remarkable aspects of animal diversity is the extraordinary array of structures used for copulation, which are collectively known as "genitalia" (see reviews in Eberhard 1985, 1996). Spiders (order Araneae) are one of the most species rich groups of terrestrial animals, with more than 40,000 species described so far (Platnick 2009) and many thousands still awaiting discovery and description. Unlike insects, whose copulatory appendages are located in the posterior abdominal segments, male spiders use special structures in appendages of the prosoma (the pedipalps) to transfer sperm into the female copulatory openings on the second opisthosomal segment (Foelix 1996). The astonishing diversity of male and female copulatory structures of spiders has provided one of the cornerstones of empirical data for the alpha-taxonomy of the group, ever since arachnologists realized that species that are similar in their somatic morphology can often be told apart by the details of their genitalic morphology (see Huber 2004 for a review).

Studies on the genital morphology of spiders have helped us to better understand many issues in evolutionary biology, such as sexual selection (e.g., Uhl 2000; Berendonck and Greven 2000, 2005; Eberhard 2004a; Huber 2005a, 2006) and male–female co-evolution (e.g., Eberhard 2004b; Huber 2005b; Ramos et al. 2005; Kuntner et al. 2009). Studies of genitalia have also provided a rich source of phylogenetic information for reconstructing evolutionary relationships (e.g., Álvarez-Padilla 2007; Agnarsson 2004; Coddington 1986, 1990, 2005; Coddington and Levi 1991; Hormiga 1994, 2000; Hormiga and Scharff 2005; Griswold et al. 1998, 2005; Kuntner et al. 2008; Miller and Hormiga 2004). However, in contrast with male palpal morphology, which has played a critical

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role in phylogenetic studies and often dominates character data matrices, very limited detailed information on female genitalia is available. Often female genitalic characters amount to less than a quarter of those of the male (e.g., Hormiga and Tu 2008).

Linyphiid spiders (Linyphiidae) are the second most diverse family within the order Araneae (Platnick 2009), surpassed in numbers of species only by the jumping spiders (Salticidae). "Micronetinae" is one of the largest groups among linyphiids (see Saaristo and Tanasevitch 1996) and particularly diverse in the Holarctic region. Recent cladistic work, based on both morphological characters and DNA sequences, suggests that the "micronetines" are not a natural group because they seem to include another large lineage, namely the erigonines (Erigoninae or dwarf spiders) (Arnedo et al. 2009). Whether a grade or a clade, "micronetines" share a remarkably complex male and female genitalia and a relatively uniform somatic morphology. In this paper we present some of the results of our studies on the female genitalic morphology of "micronetine" spiders.

In entelegyne spiders the female genitalia (epigynum) is characterized by a sclerotized plate on the ventral surface of abdomen, above the epigastric furrow. Internally a pair of sclerotized sacs, the spermathecae, serves as sperm storage organs. There are two pairs of internal ducts connecting to the spermathecae: one pair of copulatory ducts, connecting the spermathecae to the copulatory openings which are located on the epigynal plate, and one pair of fertilization ducts which connect the spermathecae to the uterus externus (Forster 1980; Sierwald 1989; Coddington and Levi 1991; Foelix 1996, Griswold et al. 2005; Millidge 1984, 1993; Uhl 2000; Wanless 1973; Berendonck and Greven 2005). The extraordinary anatomical diversity of epigyna in entelegynes rests on elaborations of this basic architecture, both externally and internally.

As typical entelegyne spiders, linyphiids have both copulatory and fertilization structures, often interpreted as ducts. However, several studies on linyphiine species, such as *Linyphia triangularis* (Clerck 1757) (Engelhardt 1910) and *Pityohyphantes phrygianus* (C. L. Koch 1836) (Blauvelt 1936; Uhl and Gunnarsson 2001), and "micronetine" species in the genera *Oreonetides* and *Maro* (Saaristo 1971, 1972) suggest that the so called ducts are in fact grooves (see also Saaristo 1975; Saaristo and Tanasevitch 1996; Uhl 2000). We agree with Uhl and Gunnarsson (2001: 371) in that "the spiral ducts described for linyphiid spiders will have to be re-examined. They may actually be grooves or folds and not proper ducts." Nevertheless, the term "duct" is more widely used in the taxonomic literature than "groove". It seems that most workers have preferred to take the described instances of grooves as special cases, rather than the rule, perhaps because for most species these structures really look like ducts when observed using transmitted light microscopy (e.g., Wanless 1973). The terms "epigynum" and "vulva" are often treated in the literature as if there were two separate systems: the epigynum referring to the external morphology and the vulva which would refer to the internal structures (Foelix 1996; Wanless 1972, 1973; Sierwald 1989; Millidge 1984, 1993). However, the fact is that since in some species the integument folds are misinterpreted as "ducts", the distinction between epigynum and vulva is often a simple nomenclatural convention, rather than an anatomical statement. This confusion often complicates comparative interpretations of the morphology of the female genitalia.

The epigynum of "micronetines" usually protrudes over the epigastric furrow and is different from the epigyna of other linyphiids. The epigynal plate (where the copulatory openings are usually located) is modified into an epigynal cavity and a posteriorly elongated scape which carries the grooves (ducts) and their openings. This scape is usually S-shaped and folded (Millidge 1984, 1993; Saaristo 1975; Saaristo and Tanasevitch 1996). There are many variations of this basic conformation across "micronetine" lineages. However, when observed under a transmitted light microscope the internal epigynal structures are no longer perceived as three dimensional and their spatial relationships may appear partially lost (Wanless 1973). Furthermore, external SEM images of the epigynum are less informative than those of male palp, because much of the variation is internal, as the spermathecae and the associated ducts and/or grooves lay hidden under the integument.

The goal of this study is to investigate the morphological basis of the female genitalia in taxa that have been ascribed to the Micronetinae (sensu Saaristo and Tanasevitch 1996). As we have mentioned, the current phylogenetic hypothesis on Linyphiidae implies that Micronetinae are paraphyletic with respect to Erigoninae (Arnedo et al. 2009). We refer to the Micronetinae (sensu Saaristo and Tanasevitch 1996) as "micronetine" and we use the informal label "micronetine-erigonine" to the clade proposed by Arnedo et al. (2009) that includes the "micronetines" and Erigoninae. We have used the methods described by Álvarez-Padilla and Hormiga (2008) to study external and internal epigynal morphology using a scanning electron microscopy (SEM). By integrating data both from SEM and transmitted light microscopy we can interpret the morphology of the epigynum in "micronetines". We have assessed the phylogenetic implications of epigynal morphology in the "micronetine-erigonine" clade based on comparisons across the species examined here and those described and illustrated from other linyphiid groups by previous studies (Millidge 1984, 1993; Hormiga 2000; Miller and Hormiga 2004; Miller 2007).

Materials and methods

Based on an ongoing study of "micronetines" in which we have examined more than 70 species representing 40 genera, we selected the following eight species to represent epigynal variation in "micronetines". *Lepthyphantes minutus* (Blackwall 1833), *Mansuphantes fragilis* (Thorell 1875) and *Meioneta rurestris* (C. L. Koch 1836) have a typical sigmoid scape, which is partly hidden in the basal epigynal cavity. *Arcuphantes arcuatus* (Roewer 1942) and *Bifurcia ramosa* (Li and Zhu 1987) have an exposed scape that is somewhat U-shaped. *Drapetisca alteranda* (Chamberlin 1909), *D. socialis* (Sundevall 1833) and *Helophora insignis* (Blackwall 1841) have a protruding epigynum without scape. In addition, *Erigone atra* (Blackwall 1833) was chosen for comparison as a representative of the Erigoninae lineage.

Specimens were examined using a Leica MZ16A stereomicroscope. Further details were studied using a Leica DM4000B transmitted light microscope. Digital images were taken with a Leica DFC 420 camera. Epigyna were cleared in methyl salicylate (Holm 1979) for examination under the microscope and temporarily mounted as described in Grandjean (1949) and Coddington (1983). Scanning electron microscope images were taken using a LEO 1430VP in the Department of Biological Sciences at The George Washington University and a Hitachi S-3400N scanning electron microscope at China Agriculture University. For SEM examination, the specimens were prepared as described in Álvarez-Padilla and Hormiga (2008). The non chitinous abdominal tissue was digested with SIGMA Pancreatin LP 1750 enzyme complex to expose the internal structures for examination.

Terminology for the epigynal structures follows Saaristo and Tanasevitch (1996).

Results

In the studied species the epigynum protrudes over the epigastric furrow to a varying degree (Figs. 1a, c, 4a, c), connecting to the abdomen through the epigynal base (Figs. 1a, 4a, 8a). In most "micronetines" a narrow epigynal scape extends posteriorly, carrying a pair of slits running through (Figs. 1d, 2c, 3c, 5a); a homologous scape is absent in *Drapetisca* spp. (Fig. 4), *Helophora insignis* (Fig. 7) and *Erigone atra* (Fig. 8). The basal part of the epigynum is usually depressed, forming the often large epigynal cavity, in which the scape can be partially hidden (Figs. 1c, 5b, 6a). No distinct epigynal cavity exists in *Arcuphantes arcuatus* (Fig. 2c), *Bifurcia ramosa* (Fig. 3b) and *Helophora insignis* (Fig. 7b) and thus the scape in both *Arcuphantes* and *Bifurcia* is exposed (Figs. 2b, 3a).

The slits on the dorsal surface of the epigynal integument divide the epigynum into a ventral and a dorsal plate (Figs. 2b, 3b, 4d, 7b, 9b). The dorsal plate curves inwards, close to the ventral plate and the two plates extend distally together (Figs. 2c, 3b), its proximal part dorsally forms the median plate (Figs. 1b, 2c, 3a, 4d, 5b, 8b). The median plate is absent in *Meioneta rurestris* (Fig. 6b). The dorsal plate can curve more deeply to form an inner lobe (IL) between the two spermathecae (as in *Mansuphantes fragilis*, Fig. 5c).

Epigynal cavity

The integument of the epigynal base is continuous with that of the abdomen above the epigastric furrow (Figs. 1a, c, 4a–c, 6a, 8a). The epigynal base may be deeply wrinkled, as in *Drapetisca* spp. (Fig. 4a–c). The epigynal cavity is a hollow area surrounded by a larger ventral plate and a smaller median plate (Figs. 1b, 4d, f, 5b, 8b). The later plate is smooth and lacks setae, and is located between the two lateral extensions of the ventral plate on the epigynal dorsal surface. The concave dorsal plate and the enlarged and mesally folded ventral plate form the epigynal cavity, which opens dorsally (Figs. 1b, 4d, f, 5b, 6b, 8b, 9b). In *Arcuphantes arcuatus* (Fig. 2c) and *Bifurcia ramosa* (Fig. 3b) the dorsal plate is depressed inwards, but the lateral extensions of the ventral plate are not mesally folded. In contrast, *Helophora insignis* (Fig. 7b) has the ventral plate extending and folding mesally, but the dorsal plate is almost flat. In both cases the epigynum lacks a distinct epigynal cavity.

Groove complex

Examination of the duct-like internal structures under the transmitted light microscope (e.g., Figs. 4e, 7c) and comparison to SEM micrographs of the same structures reveals that such "ducts" are not separated from the integument (Figs. 1e, 2e, 3g, 4g, 5c, 6c, 8d) and that they are not closed ducts (see the cross section of *Drapetisca socialis* in Fig. 4d). The micrographs of the dorsal and lateral views (e.g., Figs. 1d, 2c, 3b, 4d, 7b, 9b) show that the duct-like structures open on the epigynal surface, indicating that these are in fact integument folds (and hence are better interpreted as grooves). Ventral views of the digested epigyna with the outer layer of the epigynal wall removed reveal that in the examined species those structures traditionally recognized as "copulatory ducts" are copulatory grooves (Figs. 1e, 8c, d). The sinuous structures normally referred as "fertilization ducts" are the bottom of integument folds (Fig. 5b–d, see also Figs. 3h, 8e). Such fertilization grooves are present in all the species examined here. The copulatory grooves follow the length of the

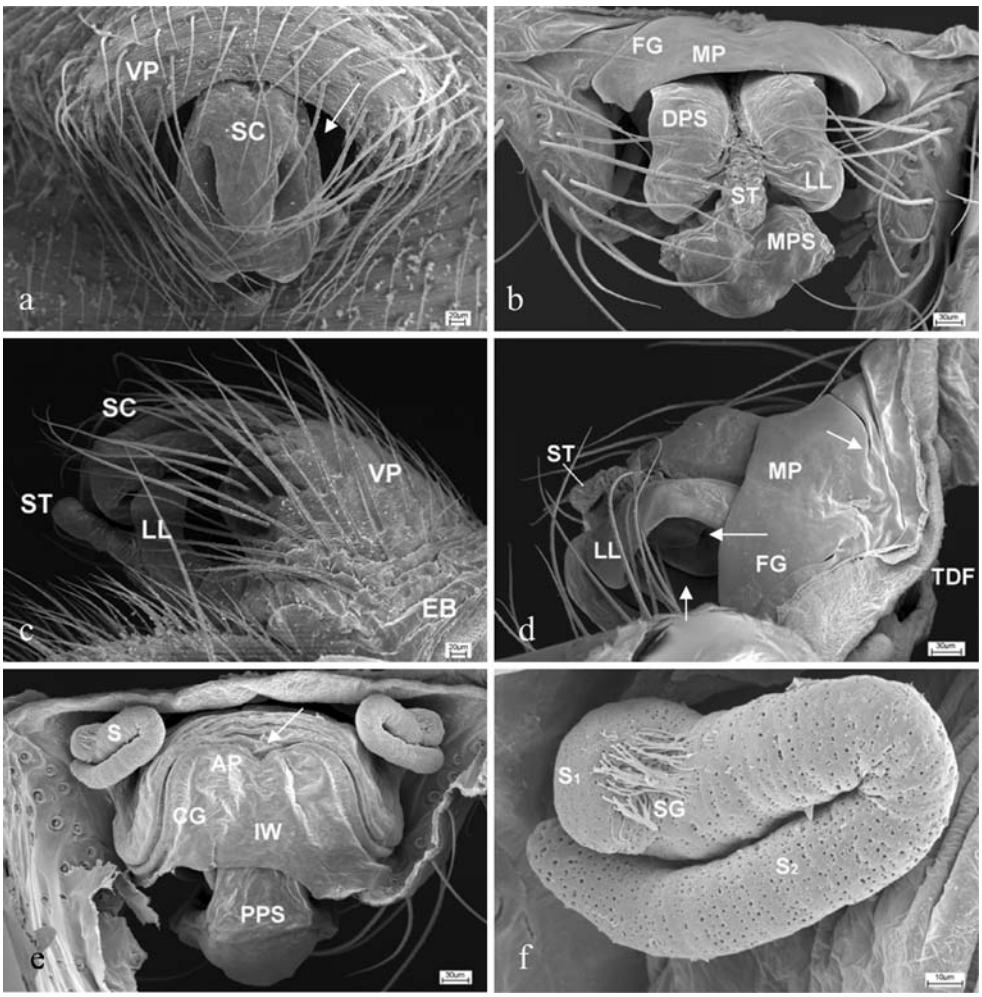

Fig. 1 Epigynum of *Lepthyphantes minutus*. **a** ventral view (*arrow* indicates epigynal cavity); **b** dorsal view; **c** lateral view; **d** lateral dorsal view (*upper arrow* indicates fertilization opening, *middle arrow* indicates bursa copulatrix, *lower arrow* indicates entrance groove); **e** ventral view with outer layer of epigynal wall removed and soft tissues digested (*arrow* indicates arising point of scape); **f** detail of **e**. *AP* arising point of scape, *CG* copulatory groove, *DPS* distal part of scape, *EB* epigynal base, *FG* fertilization groove, *IW* inner wall, *LL* lateral lobe, *MP* median plate, *MPS* median part of scape, *PPS* proximal part of scape, *S* spermatheca, S_1 upper chamber of spermatheca, S_2 lower chamber of spermatheca, *SC* scape, *SG* special gland, *ST* stretcher, *TDF* transversal dorsal fold, *VP* ventral plate

protruding epigynal plate (Figs. 2c, 3b, 7b, 8b; see also Figs. 3f, 4f, 5c, 6c) and can even extend into the scape and fold together with it (Figs. 1d, 2c, 3b, 5c, 6c).

The anterior views of the digested epigyna demonstrate that the groove runs uninterrupted from the proximal fertilization end to the distal copulatory opening, with the spermatheca located in between the two (Figs. 2e, 3g, 4g, 5c, 6c, 8e; see also Fig. 9a). However, the slit running along the epigynal surface is continuous and there is no discernable exterior evidence to show where the spermatheca is located along this groove (Figs. 4d, 7b, c). In all species examined here, except *Helophora insignis* (Fig. 7c), each spermatheca has two chambers, usually one of them is longer than the other (Figs. 1f, 2f, 3g, 4g, 5d). The presence of numerous pits scattered along the surface of the spermathecae suggests that the walls are equipped with many glands (Figs. 1f, 2f, 3g, 4g, 5d, 6d). Additional "special glands" (SG) are located on the boundary between the two spermathecal chambers (Figs. 1f, 2f, 3g, 4f, 5d, 6d, 8e). The lumina of these two chambers are continuous and the two chambers share a common basal part (Fig. 3e). The basal part of the spermatheca turns and connects with both the copulatory and the fertilization grooves from its dorsal side (Figs. 2f, 3h, 4g, 5d, 6c, 8e, 9d). The cross sections of the basal part show that the lumen of the copulatory and of the fertilization grooves are connected (Figs. 3c, e, f, 9c, d). We have used the term "groove complex" for the system of cuticular folds that includes (and connects) the copulatory and fertilization grooves and the spermathecae. This complex has been found in all species examined in the present study.

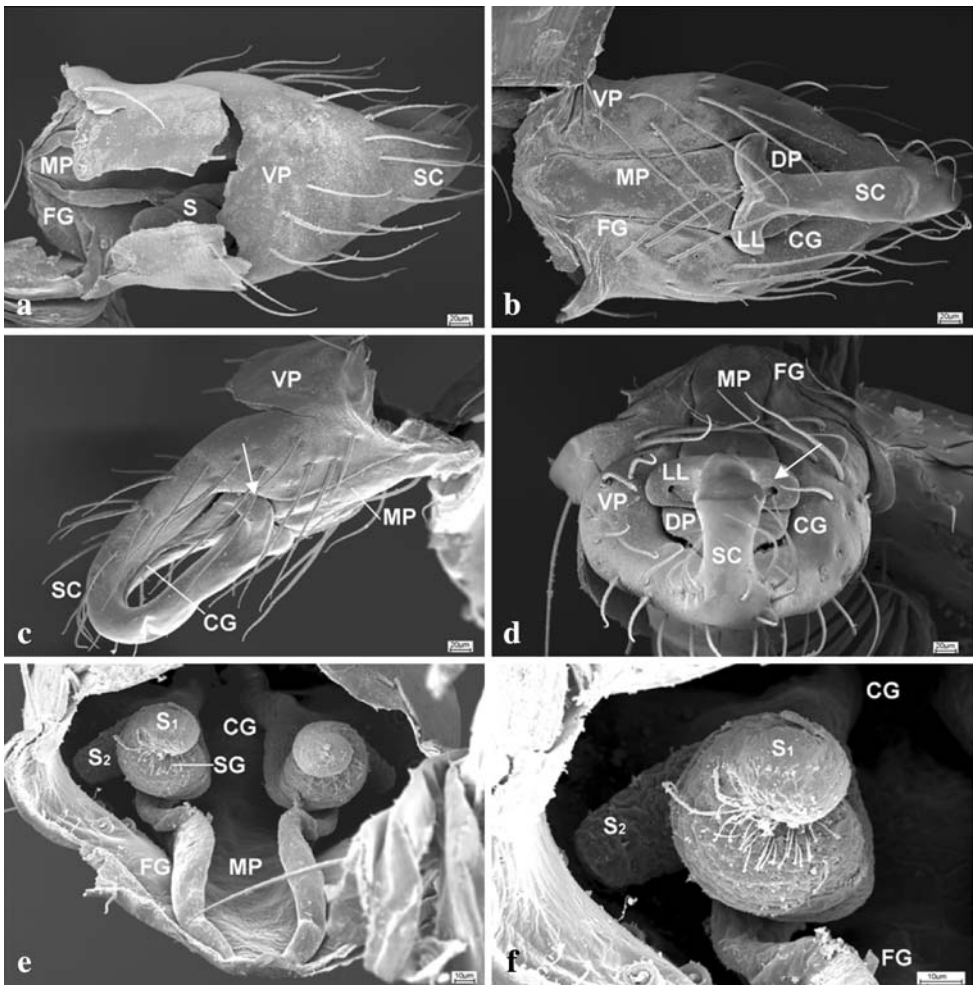

Fig. 2 Epigynum of *Arcuphantes arcuatus*. **a** ventral view with ventral plate broken; **b** dorsal view; **c** lateral dorsal view (*arrow* indicates the part where dorsal plate depressed); **d** caudal view (*arrow* indicates bursa copulatrix); **e** groove complex, anterior view with soft tissues digested; **f** detail of **e**. *CG* copulatory groove, *DP* dorsal plate, *FG* fertilization groove, *LL* lateral lobe, *MP* median plate, S_1 upper chamber of spermatheca, S_2 lower chamber of spermatheca, *SC* scape, *SG* special gland, *VP* ventral plate

Leaving the spermathecae, the copulatory grooves turn inwards from the dorsal to the ventral side of the spermathecae and then downwards (Figs. 2e, 3g, 4g, 5c, 6c, 8d). The copulatory openings (CO) are located at the distal ends of the copulatory grooves and in "micronetines" these openings are modified into a special structure known as bursa copulatrix (Figs. 2d, 3b, 4e). Both *Helophora insignis* (Fig. 7a) and *Erigone atra* (Fig. 8b) lack the bursa copulatrix. The fertilization grooves run anteriorly, and are to a varying degree associated with the median plate and can be tube-shaped (as in *Arcuphantes arcuatus*, Fig. 2b, e) or sinuous (as in *Mansuphantes fragilis*, Fig. 5b–d; see also Figs. 3f, g, 8e). In most "micronetines" the fertilization grooves end in, or close to but outside, the epigastric furrow (Figs. 1d, 2b, 3a, 4d, 5b, 7b, 8b), without extending internally (Figs. 1e, 2e, 3g, 4g, 5c, d, 8e). We have termed this conformation as the "*Lepthyphantes* type epigynum". In other "micronetines", such as *Meioneta rurestris*, the median plate is absent, the fertilization grooves are very short, and a tube-like structure arises from the basal part of each fertilization groove, extending towards the epigastric furrow (Fig. 6c). It is unclear whether this latter structure represents a true tube or the edge of the cuticular fold. We have termed this latter conformation as the "*Meioneta* type epigynum".

Scape

In "micronetines" the scape is part of the ventral wall of the epigynal cavity and it extends outwards distally (as in *Arcuphantes arcuatus*, Fig. 2a; see also Figs. 3a, 5a, 6a) or arises from the inner surface of the epigynal cavity (as in *Lepthyphantes minutus*, Fig. 1e). The scape may narrow abruptly (as in *Lepthyphantes minutus*, Fig. 1a; see also Fig. 5a) or gradually (as in *Arcuphantes arcuatus*, Fig. 2a; see also Fig. 3d). The protruding epigynum may be straight (as in *Helophora insignis*, Fig. 7a; see also Figs. 4c, f, 8a), U-shaped and folded (as in *Arcuphantes arcuatus*, Fig. 2c), or S-shaped and folded (as in *Lepthyphantes minutus*, Fig. 1c; see also Figs. 3b, 5a, b, 6a, b). All of these scapes share a pair of grooves running longitudinally (Figs. 1d, 2c, 3b, 7b). In the species with a sigmoid scape the grooves run along the dorsal side of the scape proximally but end ventrally. The grooves change

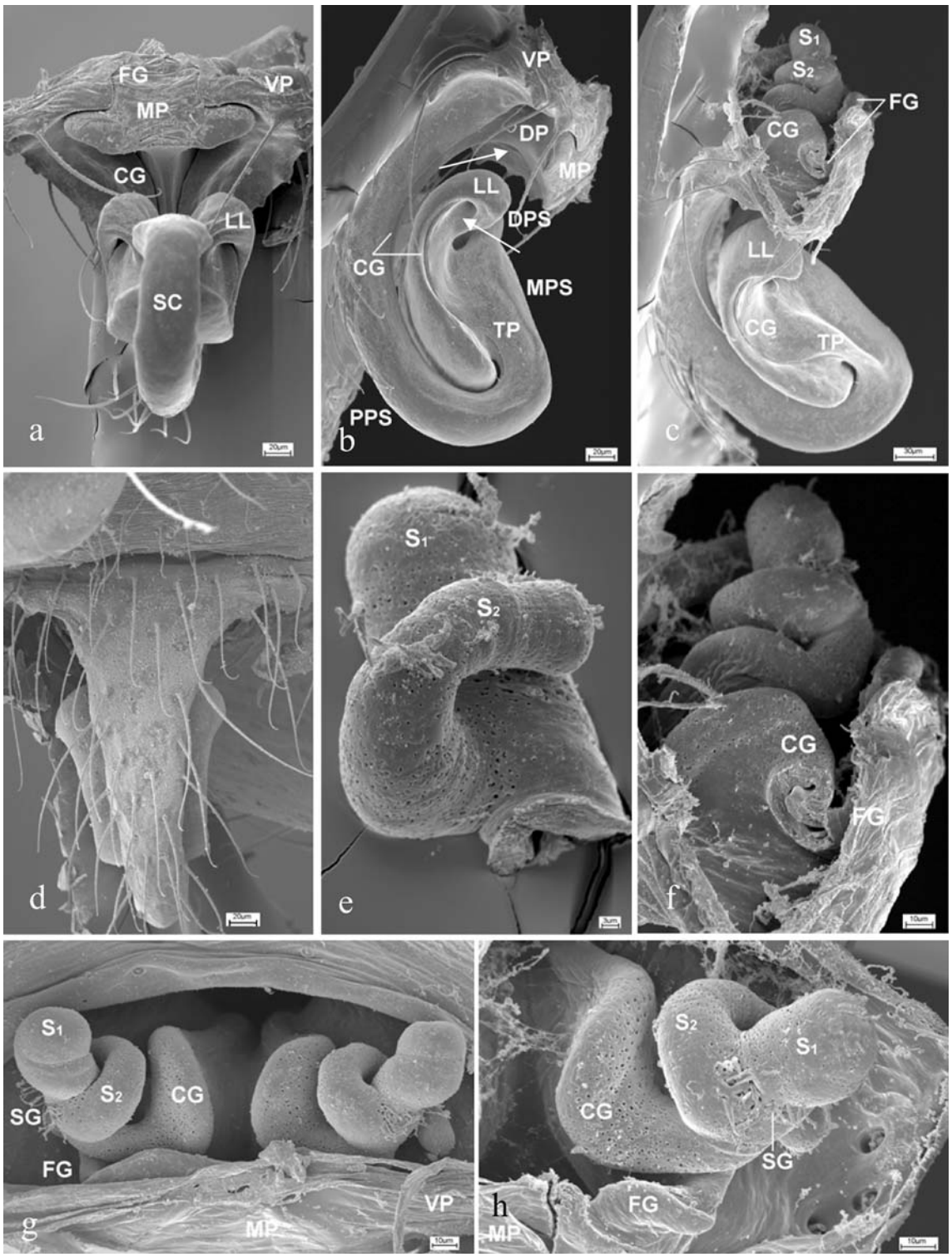

Fig. 3 Epigynum of *Bifurcia ramosa*. **a** dorsal view; **b** lateral view (*upper arrow* indicates the part where dorsal plate depressed; *lower arrow* indicates bursa copulatrix); **c** anterolateral view, right spermatheca removed to show the cross section of basal part of spermatheca; **d** ventral view; **e** right spermatheca, lateral view; **f** detail of **c**; **g** groove complex, anterior view with soft tissues digested; **h** detail of **g**. *CG* copulatory groove, *DPS* distal part of scape, *FG* fertilization groove, *LL* lateral lobe, *MP* median plate, *MPS* median part of scape, *PPS* proximal part of scape, S_1 upper chamber of spermatheca, S_2 lower chamber of spermatheca, *SC* scape, *SG* special gland, *TP* turning point, *VP* ventral plate

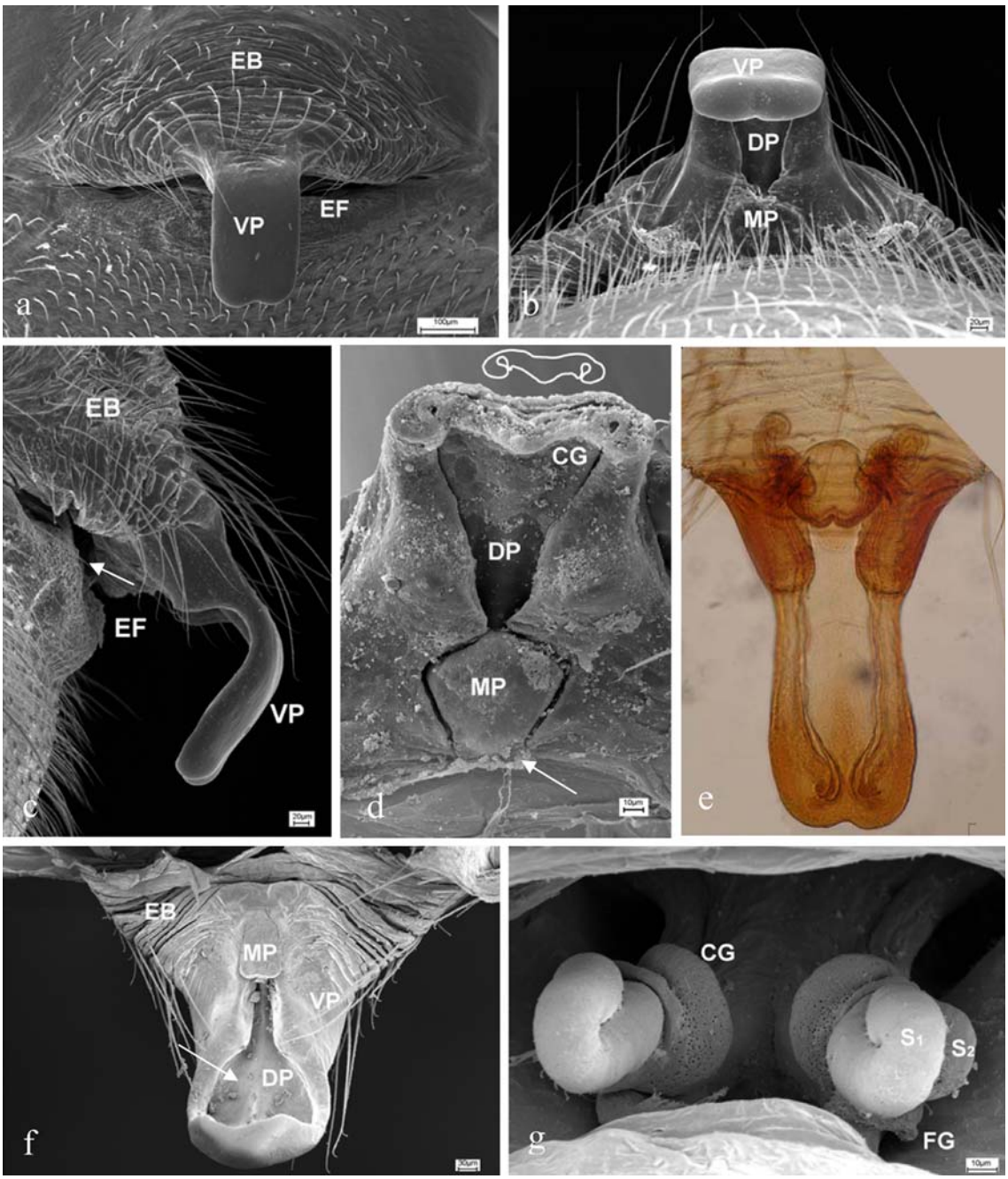

Fig. 4 Epigynum of *Drapetisca* spp. **a**–**e** *D. socialis*; **f**–**g** *D. alteranda*. **a** ventral view; **b** caudal view; **c** lateral view (*arrow* indicates epigastric furrow); **d** dorsal view with the distal part cut off (*line* drawing shows representation of cross section; *arrow* indicates the proximal end of fertilization groove); **e** dorsal view; **f** dorsal view (*arrow* indicates epigynal cavity); **g** groove complex, anterior view with soft tissues digested. *CG* copulatory groove, *DP* dorsal plate, *EB* epigynal base, *EF* epigastric furrow, *FG* fertilization groove, *MP* median plate, S_1 upper chamber of spermatheca, S_2 lower chamber of spermatheca, *VP* ventral plate

their paths at a turning point (TP) to let the grooves and the copulatory openings to orient ventrally at the distal part of the scape (as in *Bifurcia ramosa*, Fig. 3b, c). The scapes of both *Bifurcia ramosa* and *Arcuphantes arcuatus* are more or less U-shaped and folded (Figs. 2c, 3b); the former species differs from the latter in having a turning point in the copulatory groove. In some taxa the distal part of the scape is furnished with two lateral lobes (LL, Figs. 1b, 2d, 3a, 5b, 6a) and sometimes it has a finger-like stretcher (ST, Figs. 1b, 5b) with an apical pit. In *Meioneta rurestris* the pit is present but the stretcher is absent (Fig. 6a, b). When present, the pit, the stretcher and the lateral lobes are always located beyond the distal end of the copulatory grooves.

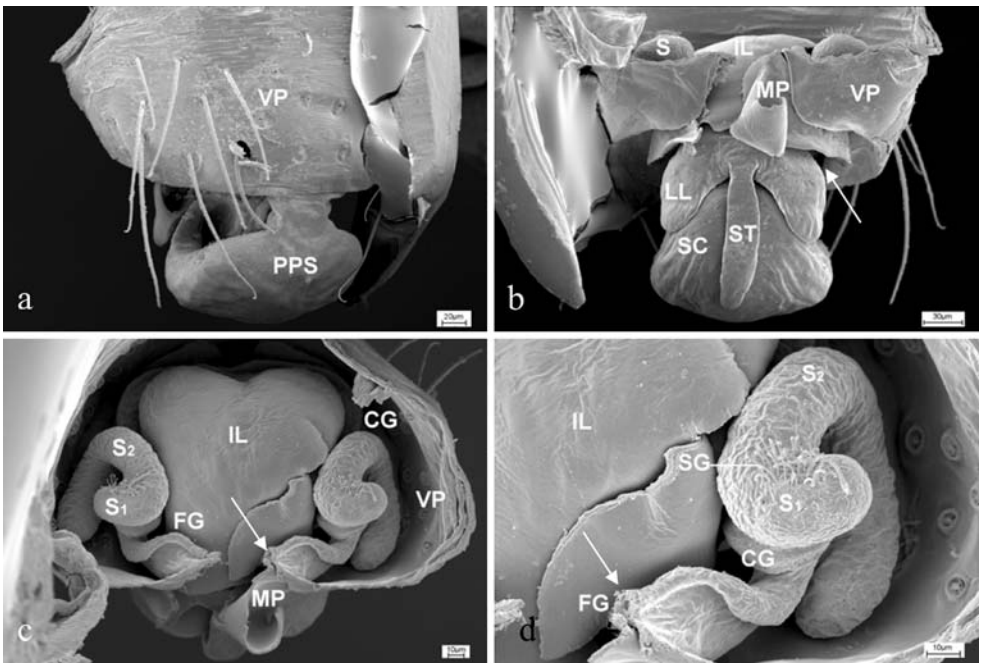

Fig. 5 Epigynum of *Mansuphantes fragilis*. **a** ventral view; **b** dorsal view (*arrow* indicates epigynal cavity); **c** groove complex, anterior view with soft tissues digested (*arrow* indicates fertilization groove); **d** detail of **c**. *CG* copulatory groove, *FG* fertilization groove, *IL* inner lobe, *LL* lateral lobe, *MP* median plate, *PPS* proximal part of scape, S_1 upper chamber of spermatheca, S_2 lower chamber of spermatheca, *SC* scape, *SG* special gland, *ST* stretcher, *VP* ventral plate

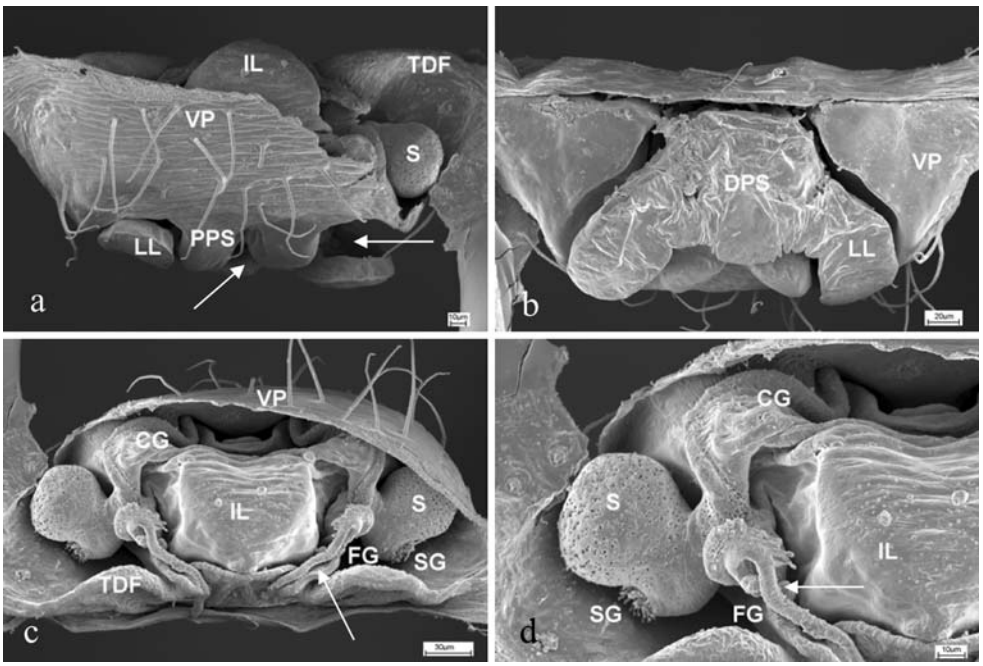

Fig. 6 Epigynum of *Meioneta rurestris*. **a** ventral view (*right arrow* indicates epigynal cavity; *left arrow* indicates pit on scape apex); **b** dorsal view; **c** groove complex, anterior view with soft tissues digested (*arrow* indicates the fine duct extending from fertilization groove); **d** detail of **c**. *CG* copulatory groove, *DPS* distal part of scape, *FG* fertilization groove, *IL* inner lobe, *LL* lateral lobe, *PPS* proximal part of scape, *S* spermatheca, *SG* special gland, *TDF* transversal dorsal fold, *VP* ventral plate

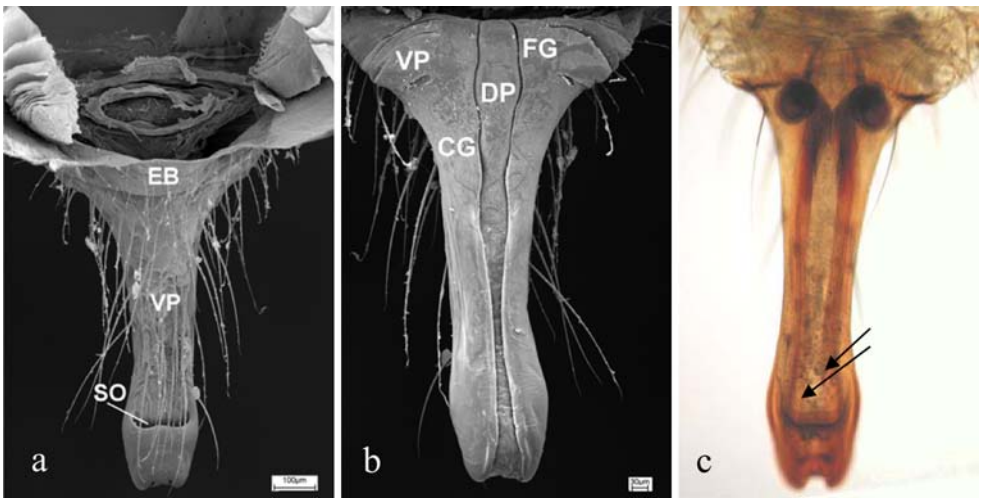

Fig. 7 Epigynum of *Helophora insignis*. **a** ventral view; **b** dorsal view; **c** ventral view (*arrows* indicate lateral extensions of ventral plate covering groove margins). *CG* copulatory groove, *CO* copulatory opening, *DP* dorsal plate, *EB* epigynal base, *FG* fertilization groove, *SO* socket, *VP* ventral plate

Discussion

Grooves

Our observations show that in the species of the "micronetine-erigonine" clade that we have examined, the epigynal structures that are often labeled as ducts in the literature (e.g., Hormiga 2000) are better interpreted as grooves derived from invaginations of the integument (Figs. 2c, e, 3b, g, 4d, e, 7b, c, 9b). The "bottom" of the groove is normally enlarged, leaving a slit on the integument surface and as a consequence the cross section of groove is shaped like a "comma" (e.g., Figs. 4d, 9b; see also Uhl and Gunnarsson 2001: Fig. 2a; Saaristo 1972: Fig. 17). A number of workers have rejected the interpretation of some of these epigynal structures as actual ducts (e.g., Engelhardt 1910; Saaristo 1971, 1972, 1977; Blauvelt 1936; Uhl and Gunnarsson 2001). Misinterpretation of a groove as a duct usually results from observations using transmitted light microscopy or clear (transparent) epigyna under the stereoscope. Such images often show a groove as consisting of several parallel lines representing the margins and the bottom (Figs. 4e, 7c, 9b). Slits (grooves) on the epigynal surface are common in linyphiids (Millidge 1984), however, they may not always represent the groove margins (see Figs. 4d, e, 7b). The lateral extensions of the ventral plate fold mesally to form the epigynal cavity, covering the slits so that the grooves may appear as internal structures (Figs. 7c, 9b). But at high magnification in transmitted light microscopy it is often not possible to discern that the "ducts" are in fact grooves (Figs. 4e, 7c, 9b; see also Millidge 1984: Fig. 84). A similar misinterpretation may occur, using transmitted light microscopy, when there are sinuous "fertilization ducts" at each side of the median plate (e.g., Fig. 5b–d; see also Figs. 3h, 8e–f).

Based on SEM data on the epigynal surface (e.g., Hormiga 2000; Miller 2007; Hormiga and Tu 2008), combined with data on the internal structures associated with the slits (e.g., Millidge 1984, 1993; Hormiga 1994, 2000; Miller 2007; Hormiga and Tu 2008), especially the sinuous fertilization ducts (grooves), as well as the histological evidence mentioned above, we infer that copulatory and fertilization grooves are more widespread than currently recognized in both Linyphiidae and its sister group, Pimoidae (Hormiga 1994, 2000). The slits on the epigynal surface and the internal structures are an integral part of the epigynum (Saaristo and Tanasevitch 1996). Accordingly, variations of the groove trajectory and morphology are related to variations in the dorsal plate morphology. For example, widening of the dorsal plate together with the ventral plate results in divergent groove margins (as in *Erigone atra*, Fig. 8c, d). At the turning point of a sigmoid scape, the dorsal plate becomes wider than the ventral plate that results in the groove running from the dorsal side proximally to the ventral side distally (as in *Arcuphantes arcuatus*, Fig. 2b).

The groove complex is distinctive in how the grooves and the spermathecae are connected and this complex is shared by all species examined in the present study, both "micronetines" and the erigonine (Figs. 1e, 2e, 3g, 4g, 5c, 6c, 8e). In that sense, the anatomical drawings of erigonine epigyna (e.g., Hormiga 2000) share a general the groove complex pattern with comparable illustrations of "micronetines" (e.g., Millidge 1984), especially the spiraling basal parts of the spermathecae and the sinuous fertilization ducts (grooves) associated with the lateral margins of the

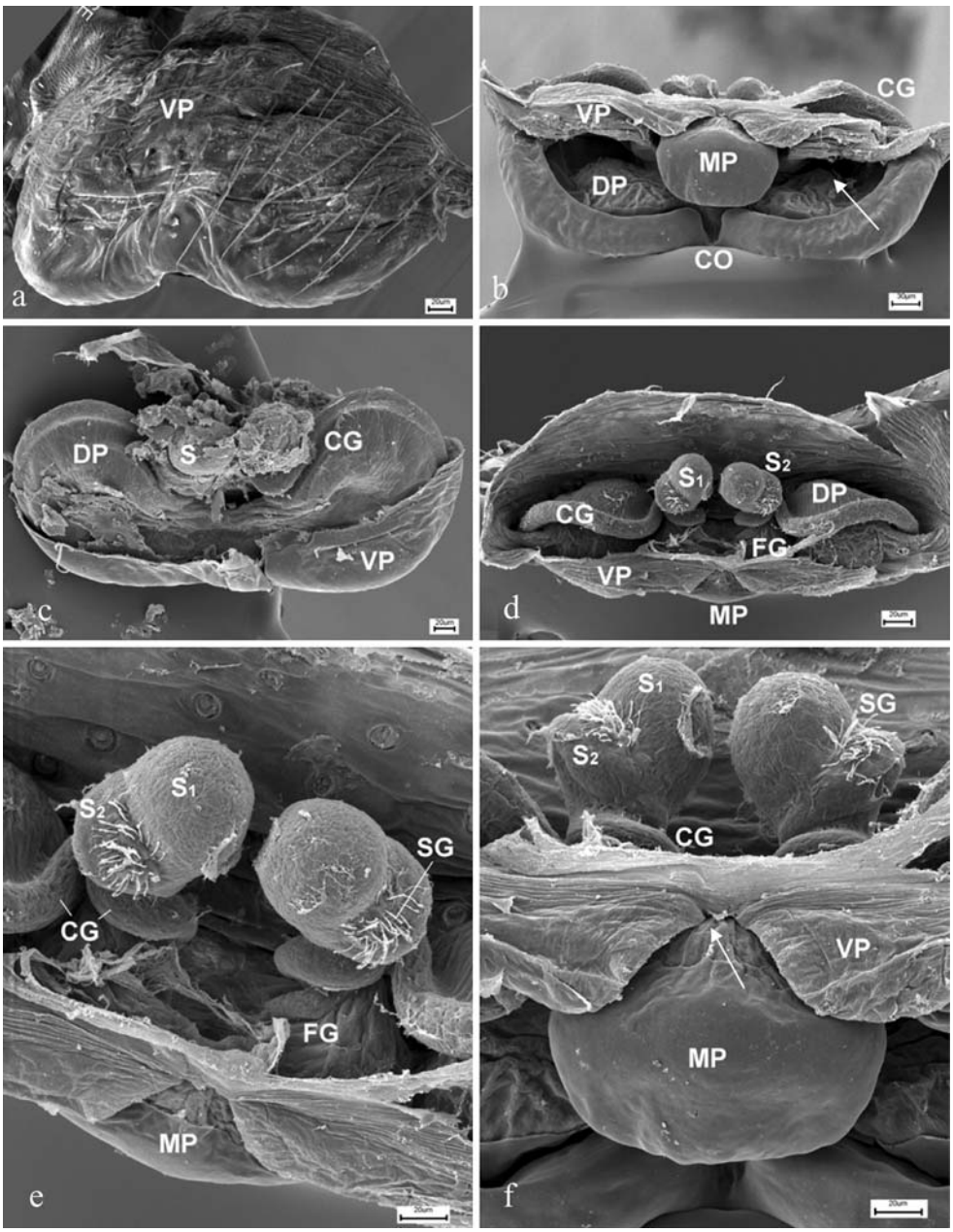

Fig. 8 Epigynum of *Erigone atra*. **a** ventral view; **b** dorsal view (*arrow* indicates the epigynal cavity); **c** ventral view with outer layer of ventral plate removed and soft tissues digested; **d** groove complex, anterior view with soft tissues digested; **e** detail of **d**; **f** detail of **b** (*arrow* indicates the proximal end of fertilization groove). *CG* copulatory groove, *DP* dorsal plate, *FG* fertilization groove, *MP* median plate, *S* spermatheca, S_1 upper chamber of spermatheca, S_2 lower chamber of spermatheca, *SG* special gland, *VP* ventral plate

dorsal plate (median plate). Furthermore, the illustrations of linyphiid vulvae provided by Millidge (1984, 1993) and those of *Orsonwelles* by Hormiga (2002) reveal that the basal part of the spermatheca is more or less spiraled with the copulatory and the fertilization ducts (grooves). Based on the strong support for the monophyly of Linyphiidae (Hormiga 1994, 2000; Miller and Hormiga 2004; Arnedo et al. 2009) combined with the widespread occurrence of the groove complex among the members of this family and the presence of a very similar structural pattern in many pimoids, such as *Pimoa* (see Figures in Hormiga 1994) and *Putaoa* (see Figures in Hormiga and Tu 2008), we can hypothesize that the groove complex is plesiomorphic for Linyphiidae.

Results of the present study suggest that in "micronetines" and erigonines the spermathecae, as the only connection between the copulatory and the fertilization grooves, may be partially derived from the groove itself

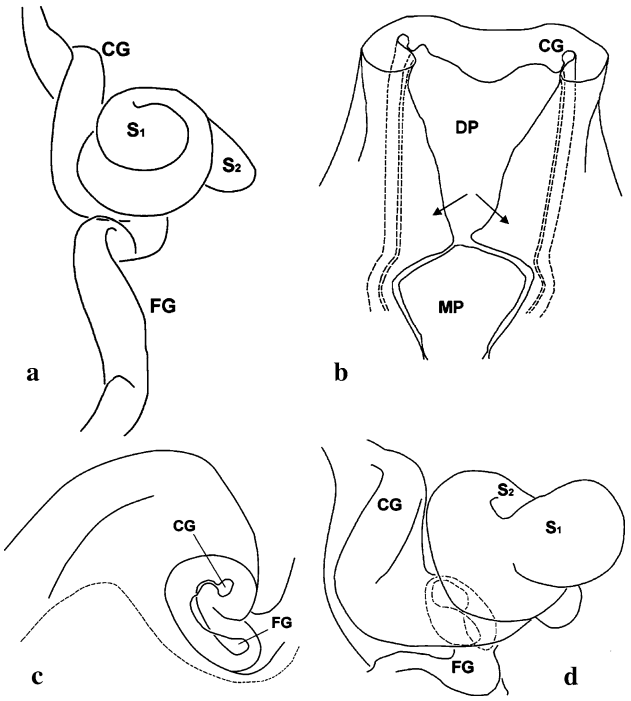

Fig. 9 **a** Groove complex of *Arcuphantes arcuatus*; **b** epigynum of *Drapetisca socialis*, dorsal view with distal part cut off (*broken lines* indicate margins and bottoms of grooves; *arrows* indicate lateral extensions of ventral plate covering groove margins); **c** cross section of basal part of spermatheca of *Bifurcia ramosa* (*broken line* indicates groove margin); **d** groove complex of *Bifurcia ramosa* (*broken line* indicates inner lumina of copulatory and fertilization grooves). *CG* copulatory groove, *DP* dorsal plate, *FG* fertilization groove, *MP* median plate, S_1 upper chamber of spermatheca, S_2 lower chamber of spermatheca

(Figs. 2e, 3g, 4g, 5c, 6c, 8e, 9a). The continuous groove margins (Figs. 2c, 3b, 7b) and the connected lumina of the copulatory and the fertilization grooves (Fig. 3e, f) lend to support to Saaristo's hypothesis (1971, 1975, 1977) that the spermathecae are bulged from the side of the integument fold. Presumably spermathecae in spiders develop as invaginations of the integument, at least in some groups, but a robust hypothesis of female genitalic evolution at the ordinal level has yet to emerge (see Forster 1980; Sierwald 1989 and references therein). In "micronetines" and erigonines the two chambers of the spermathecae share a common basal region, implying perhaps that one of them is branched from the other one (Fig. 3e; see also Saaristo 1971, 1975, 1977). So far divided spermathecae and the special glands at the boundary of the two chambers have been found only "micronetines" and some erigonines (Figs. 1f, 2f, 3g, 4g, 5d, 6d, 8e; see also Hormiga 2000: Figs. 22G, 29G) although similar two chambered spermathecae occur in other lineages such as *Pityohyphantes* (Blauvelt 1936; Uhl and Gunnarsson 2001).

In entelegyne spiders the spermathecae connect with the copulatory openings and the uterus externus via copulatory and fertilization ducts, respectively (Forster 1980). The epigynal grooves can be sealed by secretions so that such grooves may functionally be equivalent to ducts (Uhl 2000; Uhl and Gunnarsson 2001). In many spider groups the length of the male intromittent structure, the embolus, correlates well with the length of the copulatory duct/groove (e.g., Hormiga and Scharff 2005; Ruiz and Brescovit 2008). Such pattern of covariation suggests that during copulation the sperm can be deposited directly, or very close, into the spermathecae. However it is unclear how the sperm would travel from fertilization grooves that are at least partially external (e.g., as in *Drapetisca socialis*, Fig. 4d) into the uterus externus which is an internal structure.

Saaristo (1971) has suggested that in linyphiids the fertilization ducts which are U-shaped, converge and connect to the uterus externus by a common opening (see Saaristo 1971: Fig. 3). Based on her work on *Pityohyphantes*, Uhl (2000) stated that the fertilization groove ("fold" in her terminology) is the only connection between the spermatheca and the oviduct. This groove would have to function to transport the sperm into the epigastric furrow, where the opening of the oviduct is located. To some extent, the turning basal part of the spermatheca makes the grooves become closed, but the widespread occurrence of the fertilization grooves in the "*Lepthyphantes* type epigynum" (Figs. 1d, 2b, 3a, 4d, 5b, 7b, 8b) seems to support Uhl's conjecture. Intriguingly, in some species the fertilization grooves seem to end near but outside the epigastric furrow (see Figs. 1d, 4f), an observation of difficult interpretation in absence of histological sections. Nevertheless we should point out that in some "micronetines" the fertilization grooves have unchitinized parts (Saaristo 1971, 1975) which could be easily digested during specimen preparation and thus would be invisible to the methods of study used here. On the other hand, the "*Meioneta* type epigynum" has a fine tube like structure arising from the basal part of the short fertilization groove and extending towards the epigastric furrow (Fig. 6c, d). This observation partly supports the Saaristo's hypothesis, although there is no evidence to indicate that it connects with the uterus externus. Histological sections are clearly needed to better understand the nature of some these structure that we have described here.

As suspected by other workers (e.g., Uhl and Gunnarsson 2001) epigynal grooves, rather than ducts, may be more widespread than presently recognized. For example, SEM images of the internal structure of *Allende longipes* (Tetragnathidae, Álvarez-Padilla 2007: Fig. 6b, c) and *Coelotes atropos* (Amaurobiidae, Wang 2002: Fig. 40) show the presence of grooves. The histological sections of *Nesticus cellulanus* (Nesticidae, Huber 1993: Fig. 4a–d) also revealed structures that are better described as grooves

rather than ducts (Huber, personal communication). Furthermore, slits on the epigynal surface are commonly found in many spider groups (e. g. Saaristo 1975, 1977; Sierwald 1989; Griswold 1990; Griswold and Ubick 2001; Kuntner and Hormiga 2002) although detailed information on the corresponding internal structures is often not available. Nevertheless, it is also clear that true epigynal ducts exist in some taxa. For example, SEM images of *Cepheia longiseta* (Synaphridae, Lopardo and Hormiga 2007: Figs. 57, 59, 61) and of *Hyptiotes cavatus* (Uloboridae, Opell 1983: Figs. 2–6) indicate the presence of closed ducts. Although the epigynum is formed as an invagination of the integument, it often develops in different ways in different groups (Sierwald 1989; Uhl 2000). Much additional work is required to better understand the occurrence and distribution of epigynal grooves across spider lineages.

Morphology of "micronetine" epigyna

Grooves and folds divide the epigynal integument into a ventral plate and a dorsal plate. Modifications of the two plates can result in an epigynal cavity and a diversity of scapes. Epigyna may have a cavity (Figs. 1, 5, 6, 8) or not (Figs. 2, 3, 4, 7). The scape can be S-shaped (or sigmoid; see Figs. 1, 3, 5, 6), U-shaped (Fig. 2), although some species lack a scape altogether (Figs. 4, 7, 8). If we were to flatten the epigynum by opening the epigynal cavities from dorsal side and straighten the folded scapes, all the epigyna studied here would be similar in conformation to that of *Helophora insignis* (Fig. 7). This latter species has a protruding epigynum with a pair of grooves running through the dorsal surface (Figs. 2a–c, 3a–c, 4a, e, 7a–c). In this hypothetically "flattened epigynum" the spermathecae are located more proximally on the grooves, hence the copulatory grooves are much longer than the fertilization grooves (Figs. 2c, 3b, 4e, 7c); the depressed dorsal plate and the enlarged and mesally folded ventral plate form a dorsally-opening epigynal cavity (Figs. 4d, 9b). The longitudinally running copulatory grooves and the distal position of the copulatory openings suggest a double layer structure of the epigynal cavity and scape, both being comprised by the joining of the ventral plate and dorsal plates (Figs. 2c, 3b, 4e, 7c, 9b). The part of the inner wall between the two grooves comes from the dorsal plate; the area beyond the grooves comes from the ventral plate (Figs. 4d, 7b, 8c). Usually, the ventral wall of the epigynal cavity narrows down and further extends into a scape (Figs. 2a, 3d, 6a), however, sometimes the ventral plate (the outer layer of the ventral wall) is also folded up so that the scape appears as arising from the inner surface of the epigynal cavity (Fig. 1a, e).

Saaristo and Tanasevitch (1996) suggest that the turning point and the bursa copulatrix are two diagnostic characters of "Micronetinae". The turning point is also present in other linyphiids. For example, the epigynum of *Pityohyphantes phrygianus* shows that the groove running between the fertilization opening and the copulatory opening passes from the dorsal surface to the ventral surface, just like a compressed "micronetine" epigynum (Uhl and Gunnarsson 2001: Fig. 1a, d). In addition, the turning point is absent in the "micronetine" species with a U-shaped folded scape, such as *Arcuphantes arcuatus* (Fig. 2c) and those without scape, such as *Drapetisca* (Fig. 4e). On the other hand, the special morphology of the copulatory openings, the bursa copulatrix, has been described only in "micronetine" species (Figs. 2d, 3b, 4e), although in our study sample the bursa is absent in *Erigone atra* (Fig. 8b) and *Helophora insignis* (Fig. 7b).

Comparison of the epigynal morphology of *Erigone atra* (Fig. 8) to that of *Drapetisca* (Fig. 4) as well as other "micronetines" studied here shows that they have several characters in common that are not shared by other linyphiid groups. Both erigonines and "micronetines" have a similar conformation of the epigynal cavity (Figs. 4d, 8b, 9b). They also share spermathecae with two chambers (Fig. 8f), although in erigonines they are not as developed as that of *Drapetisca* (Fig. 4g). Hormiga (2000) and Miller and Hormiga (2004) reported divided spermathecae (two pairs) in two other erigonine species, but coded it as absent in all other linyphiid groups in their character matrices. In light of the observations reported here, it is clear that their character coding/scoring should be corrected-e.g., the erigonine *Tmeticus* should be coded as having the same state than *Tenuiphantes*, that is, two chamber spermathecae. Nevertheless, while some erigonines have two chamber spermathecae, it seems that most do not. The special glands at the boundary of the two spermathecal chambers are present in both "micronetines" and erigonines (Figs. 1, 2, 3, 4f, d, 6d, 8f), as reported here, but such glands seem absent in linyphiines (Uhl and Gunnarsson 2001, Fig. 1C; Hormiga and Scharff 2005, Fig. 18E). The special glands are not easily discernable using a transmitted light microscope, so reporting their presence/absence in other linyphiid groups it is often not possible using the study methods of standard taxonomic descriptions. Comparatively, among all linyphiid groups, the epigynal morphology of erigonines is the most similar to that of "micronetines", the former may be interpreted as a "compressed from" of the latter. Thus results of present study fit the phylogenetic hypothesis of Arnedo et al. (2009) which suggests that the "micronetines" are paraphyletic with respect to the erigonines, and that both form a lineage.

The term "scape" has been extensively used in different linyphiid groups (e.g., Hormiga 1994; Millidge 1984; Wanless 1972, 1973) as well as in other araneoid groups

(e.g., Griswold 1997; Scharff and Coddington 1997) to label a high diversity of epigynal structures. In "micronetines" the scape is a projection of the ventral wall (double layer) of the epigynal cavity and it is usually furnished with an apical pit which houses the suprategular apophysis of the male palp during copulation (Saaristo 1975, 1977; van Helsdingen 1965). Ventral plate scapes seem to have evolved independently more than once in linyphiids (Arnedo et al. 2009; Hormiga 2000; Miller and Hormiga 2004). In addition some linyphiids have a scape on the dorsal plate. Generally the "scape" of other linyphiid groups do not carry grooves and thus are different from the scape found in "micronetines". For example, in *Linyphia triangularis* the scape is derived from the dorsal plate (van Helsdingen 1969; Hormiga 2000: plate 8D) and thus non homologous to the scape of "micronetines". On the other hand, in some mynoglenines the scape is located on the ventral plate, beyond the distal end of the copulatory grooves (as in *Haplinis diloris*; Hormiga 2000: plate 4F) and it may be homologous to the stretcher of "micronetines".

Conclusions

The copulatory grooves, the spermathecae and the fertilization grooves comprise what we have described here as the groove complex which is found in many linyphiids and pimoids. Most of the variations of the epigynal morphology of "micronetines" can be equated to variations in the ventral plate, the dorsal plate and the system of grooves that connect to the spermathecae. Although some studies indicate the epigynal grooves may be functionally equal to ducts, the details of how the fertilization grooves connect to the internal gonoduct remain to be satisfactorily resolved. In addition, a growing empirical body suggests that in linyphioids and in some other spider groups epigynal grooves, rather than ducts, are more widespread than originally thought. Further studies on the epigynal morphology across a wide range of spider lineages are needed to understand the anatomy and the evolution of the female genitalia. Histological sections are essential for this endeavor to succeed since, as our paper illustrates, the methods traditionally used by taxonomists (such as SEM or examination of cleared specimens) are insufficient to address many of the questions pose by this wonderfully diverse system.

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Appendix

Specimen data of the species examined. Museum abbreviations: CNU—Capital Normal University, Beijing; IZCAS—Institute of Zoology, Chinese Academy of Sciences, Beijing; AMNH—American Museum of Natural History, New York.

Lepthyphantes minutus (Blackwall, 1833)—1 m and 1 fm, Finland, Sundholm, Houtskari, Aug. 24-Oct. 24, 1968, Lehtinen coll. (IZCAS)

Arcuphantes arcuatus (Roewer, 1942)—1 fm, USA, Oregon, Sixes (1 mile north), W124.30:N42.51, Sept. 30, 1959, Vincent Roth coll. (AMNH)

Bifurcia ramosa (Li and Zhu, 1987)—2 m and 3 fm, China, Prov. Sichuan, Count Tianquan, Erlangshan National Forest Park, July 8, 2004, Tu and Li coll. (IZCAS)

Drapetisca alteranda Chamberlin, 1909—4 m and 4 fm, USA, Ontario, Island 1024, Lake Temagami, W80.03, N46.59, Aug. 15–25, 1946, Gertsch coll. (AMNH)

Drapetisca socialis (Sundevall, 1833)—2 m and 2 fm, Finland, Mustfinnö, Parainen, Sept. 1968, Saaristo coll. (IZCAS)

Erigone atra (Blackwall, 1833)—2 m and 4 fm, China, Xinjiang Uygur Autonomous Region, Burgin County, Kirzlesu River, Alt. 469 m, E86.50, N47.41, Sept. 20 2007, Tu and Chen coll. (CNU)

Mansuphantes fragilis (Thorell, 1875)—1 m and 1 fm, France, Bishop coll. (no detailed locality and collecting data) (AMNH)

Meioneta rurestris (C. L. Koch, 1836)—2 m and 2 fm, Germany, Torfstgebiet, Haidgauer, Wurzacher Ried, MTB 8025, July 22, 1992, WJ coll. (IZCAS)

Helophora insignis (Blackwall, 1841)—2 m and 2 fm, Canada, Alberta, 10 miles N·W. of Whitecourt, W115.47, N54.15, Aug. 4, 1965, Ivie coll. (AMNH)

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