



Gynandry and intersexuality in spiders: half a century onwards

Ginandria e intersexualidad en arañas: medio siglo después

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Abstract

A little over fifty years ago, Roberts and Parker (1973) advanced the knowledge of intersexual and gynandromorphic spiders. Those authors also provided a total of 14 categories for classifying gynandry in spiders. Seven new cases of gynandry and/or intersexuality are reported herein, in addition to a critical appraisal of all prior published literature available on this phenomenon and discussion on broader topics, such as a newly reported case of abnormal neoteny.

Keywords: Anomaly, Araneae, gynandromorph, sex, teratology.

Resumen

Hace poco más de cincuenta años, Roberts y Parker (1973) profundizaron en el conocimiento de las arañas intersexuales y ginandromórficas. Estos autores también proporcionaron un total de 14 categorías para

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clasificar la ginandria en arañas. Se reportan siete nuevos casos de ginandria y/o intersexualidad, además de una evaluación crítica de toda la literatura publicada previamente sobre este fenómeno y un análisis de temas más amplios, como un caso recientemente reportado de neotenia anormal.

Keywords: Anomalía, Araneae, ginandromorfo, sexo, teratología.

INTRODUCTION

Anomalies in the biological sex of animals has received much attention. In invertebrates, the most commonly reported form is commonly known as ‘bilateral gynandry’ – a striking phenomenon where the left and right side of the bodies are occupied by a different sex (e.g. Cavignato and Duarte, 2009; Martens and Wildermuth, 2021; de Souza Ribas *et al.*, 2021; Budrienè *et al.*, 2021).

Gynandry and intersexuality are uncommon anomalies in spiders, out of the countless numbers of spider specimens examined in taxonomic works in the last one hundred and fifty or so years only a comparatively small number of sexually anomalous specimens been reported. Gynandromorphic and intersexual arachnids have also been reported in the orders Opiliones (e.g. Blaszak, 1968; Suzuki, 1980; Tsurusaki, 1983; Chemini, 1984; Thaler, 2004), Ricinulei (Cokendolpher and Enríquez, 2004), Schizomida (Reddell and Cokendolpher, 1995), Scorpiones (e.g. Matthiesen, 1968; Francke, 1978; Maury, 1983; Armas, 1990; Mattoni, 2005), Solifugae (Delle Cave, 1979), and Thelyphonida (Teruel, 2017) on an even lesser degree. Sexual anomalies have not been reported in the Amblypygi, Palpigradi or Pseudoscorpiones (L. Prendini, M. Harvey, and M. Seiter pers. comm.). Hull (1918) noted that, at the time, he knew of no records of sexual anomaly in arachnids outside of the Araneae, except for one possible case in Acari.

Several studies have sought to develop typology for the classification of different types of gynandry and intersexuality in spiders (Hull, 1918; Bonnet, 1934; Exline, 1939; Kaston, 1961; Roberts and Parker, 1973). More than half a century has elapsed since the most classification by Roberts and Parker (1973) was proposed.

In this work, new cases of gynandromorphic and/or intersexual spiders are presented, in addition to a comprehensive compilation and appraisal of all available prior literature on this phenomenon in spiders. The present state of knowledge is thereby updated, and knowledge gaps identified for the benefit of future workers. Specimens first illustrated by Roberts and Parker (1973) and housed in the collections of the Natural History Museum, London have been relocated and photographs provided for the first time.

We report seven new cases of gynandry on the basis of material examined directly, and from the findings of other colleagues forwarded to us for publication; and describe in detail two cases which were previously under-documented by colleagues. We discuss the evolution of the five classification systems hitherto proposed for classifying sexually anomalous specimens, highlighting they were not cumulative nor agreed on key areas. Finally, we present the findings of our theoretical investigations which had the aim to improve on Roberts and Parker (1973) and allow for a more precise notation system for cases of irregular gynandry or mixed gynandry and intersexuality.

MATERIAL AND METHODS

Specimens directly studied were examined under a Leica MZ12.5Z stereomicroscope at NHMUK and Zeiss Stemi-2000C stereomicroscope at ISEA. Images were made using a Canon EOS 6D Mark II and Canon EOS 550D attached to the aforementioned microscopes respectively, with images stacked using Helicon Focus. Abbreviations: ISEA – Institute of Systematics and Ecology of Animals, Novosibirsk, Russia; NHMUK – Natural History Museum, London, United Kingdom; RGPC – Richard Gallon personal collection, United Kingdom; WPMPC – Wayne P. Maddison personal collection, Canada. Classification of [non-intersexual] gynandromorph spiders follows Roberts and Parker (1973). Recently, it has been demonstrated that with our improved knowledge of biological sex anomalies in animals, the distinct separateness of the categories of gynandromorphs and intersexes is not always possible (Fusco and Minelli, 2023). Nonetheless, for the purposes of this work, which relies entirely on interpretation of gross morphology, we have maintained the definitions for these two phenomena found in Roberts and Parker (1973).

RESULTS

A critique and history of the evolution of classification systems for sexually anomalous spiders

Several studies have sought to develop typology for the classification of different types of gynandry and intersexuality in spiders. Hull (1918) was the first to propose classification, proposing three so-called classes as follows “1. *One side male, the other female – sexual structures perfect except for the distortion resulting from the union of dissimilar halves on the median line.*”, “2. *As 1, but one side imperfectly developed before, the other behind.*” and “3. *One side perfectly female before and male behind, the other perfectly male in front and female behind.*”.

A newer typology was proposed by Bonnet (1934) in his review of gynandromorph spiders: typical transverse cases (cephalothorax male, abdomen female (reported) or vice versa (hypothetical/hard to spot)), typical lateral cases (wholly male on left side and female on right or vice versa), crossed lateral case(s) (reserved for one case he considered possibly interpreted, where the upper right of the cephalothorax was male whereas the right side of the abdomen was female), and partial cases (majority of tissue of spider with preponderance of one sex, with small amount present from the other). Some previously reported cases were so enigmatic that Bonnet (1934) cautiously refrained from assigning them to any of his categories.

Exline's (1938) classification system consists of interpreting an imaginary line dividing the specimen down the middle and another, through the pedicel, dividing the cephalothorax from the abdomen, allowing for the notation of the following types of gynandry: whole left male and whole right female; vice versa; male in upper left quadrant, both sexes in bottom left, female in both right; female in upper left and bottom right quadrants, male in bottom left and upper right; both upper quadrants mostly male but with some intersexuality (denoted by presence of female symbol in brackets) and vice versa in bottom quadrants; male in both left quadrants, mostly male with some intersexuality (again with female symbol in brackets) in upper right quadrant and female in bottom right; male with intersexuality (*ibid*) in both upper quadrants, female in both bottom; male in upper left quadrant, female in all other remaining quadrants; male in upper left quadrant; male with intersexuality (*ibid*) in upper right quadrant, female in both bottom quadrants; male with intersexuality (*ibid*) in all quadrants (proposed tentatively with question mark); male in both upper quadrants, and female with some intersexuality (denoted by male symbol in brackets) in both bottom quadrants (see Exline, 1938).

Exline (1938) introduced a morphometric relation factor, "leg index", to distinguish (implied wholly) male legs from female legs. Exline (1938) also dissected the female genitalia of all sexually anomalous specimens she examined, and produced meticulous drawings, still the only work of such detail. However, inevitably dissection of such a specimen removes the possibility of future workers having ever being able to examine the specimens and observe the genitalia as they were shaped and positioned on the specimens during their natural lives. She also made cross sections of tissue, not replicated by any future workers, including us, except Holm (1941). Later workers generally reverted to simply examining specimens externally, and we follow the same method. Nonetheless, this does not detract at all from Exline's work, which can be considered the most detailed ever done on sexually anomalous spiders. In a way, her work was superior to that of Roberts and Parker (1973) and of our own, as she was willing to take the extra step of dissection. Nonetheless, we must be respectful of the curatorial rules and decisions of collections we work in or loan from.

Kaston (1961) built on Bonnet's classification system and modified it somewhat, also classifying cases Bonnet (1934) did not under an expanded umbrella definition of his partial (mosaic) cases category. In addition to the categories of lateral, transverse, partial gynandromorphs, Kaston (1961) wisely recategorized the specimen which Bonnet (1934) had to classify as a lateral crossed gynandromorph as simple lateral gynandry, which had been misinterpreted by Hull (1918) (mis-referenced throughout Kaston (1961) as "Hull 1914"). Kaston also added the categories of intersex (building upon Rabaud and Millot, 1933), transverse gynandry mixed with intersexuality, and a holding category for four poorly described prior cases that he suspected were partial gynandromorphs, but for which, like Bonnet (1934), he was hesitant to confidently assign to one of Bonnet's categories. Kaston's tabulation of all 47 cases then-known-to-date is surmised at the end of his paper. It is very disappointing that Exline (1938) was given only the merest consideration in Kaston (1961), and we must consider whether this was due to social attitudes towards high-achieving women during this era.

Most recently, Roberts and Parker (1973) reported nine new cases of such anomalies, classified into two broad, often overlapping, categories: gynandry and intersexes. They considered gynandromorphic spiders to be those where the male and female parts were all "*quite normally developed*" and intersexes to be spiders which present intermediate morphologies in regard to characters such as the carapace, copulatory organs, body size, and colouration. Astutely, they noted that some specimens may be both gynandromorphs and intersexes, and that further deformities in so-called 'intermediate' anatomical parts could also sometimes be as a result of appendage regeneration, injuries during ecdysis, or injuries from other causes. They proposed a typology consisting of fourteen possibilities of gynandromorph combination in spiders: "*Of the regular gynandromorphs, 14 types are possible as shown in fig. 1, where the vertical lines represent the anterior/posterior axis of the spider, and the horizontal lines represent a transverse axis through the pedicle, the spider being viewed from above.*" and figure these possibilities, although "fig. 1" is a typographical error as the correct corresponding figure is fig. 20 on page 183.

Roberts and Parker (1973) note the 14 types are, arbitrarily, really just variations of three core themes: lateral, transverse, and crossed gynandry (= partial/mosaic gynandry in Bonnet (1936) and Kaston (1961)). As noted by those authors, some types of gynandry are easy to miss (e.g. types 11 and 12) or may not even be detectable based on morphology alone (e.g. type 4). Roberts and Parker (1973) also clarify that their use of the work 'mosaic' is synonymous with their 'irregular' gynandromorphs (i.e. where male and female tissue are more sporadically distributed within a specimen: cases which don't fit their 14 types of gynandry which assumes a given quadrant is unambiguously occupied by a single sex).

Later, they note that the classification system employed in Kaston (1961), itself adapted from Bonnet (1934), was inflexible, as its category of partial/mosaic so broad as not to precisely record cases where there may be atypical presentation (e.g. a type 14 gynandromorph where, hypothetically, only the palp and chelicera were male, the rest of the quadrant being female would be scored by Kaston as a partial/mosaic gynandromorph as equally as would a normal type 14 gynandromorph where each of the four quadrants is wholly of one sex, despite the clear differences in precise details between such cases).

However, whilst the system of Roberts and Parker (1973) was a significant improvement from the work of Kaston (1961), they themselves do not adequately develop their system to allow notation of irregular and mixed gynandromorphs, and putative cases of ‘absolute’ (not mixed with gynandry) intersexes. This is not to say they don’t recognise these limitations, indeed in their discussion they quite rightly reject Kaston’s use of ‘partial’ as this term is imprecise, theoretically superfluous, and because morphologically it cannot always be guaranteed that the smallest area of represented sex (i.e. the minority sex) is automatically the abnormal component. Broadly, Roberts and Parker (1973) outline their “scheme” later in the work as four categories: (1) cases that belong to their types 1–14 without any ambiguity, (2) irregular gynandry, (3) mixed gynandry and intersexuality, and (4) [assumed absolute] intersexuality. However, their notation system is given only for the first category (i.e. ‘regular’ gynandromorphs). They do not provide standardised nomenclature for how particularly cases of categories 2 and 3 should be recorded in a standardised way.

One common thread found in Kaston (1961) and Roberts and Parker (1973) is how little they discuss the work of Exline (1938), as in Roberts and Parker (1973) we find a complete absence of mentioning how pioneering her methods and results were. Given the significant sexism that has permeated arachnology since its inception, we can hardly conclude this was not a factor in the omissions by both later works.

New and expanded records of gynandromorphic and intersexual spiders

Baryphyma gowerense (Locket, 1965) (Linyphiidae) (Fig. 1A)

Material.— United Kingdom: Norfolk, Sutton Fen (TG37162359) [collector indicates National Grid Reference, coordinates: 52°45'28"N, 001°30'48"E], uncut fen, light phragmites, tussocks in 10 cm water, vacuum sampler (4 minutes), 23.IX.2024, R. C. Gallon (RGPC).

Remarks.— Our colleague Richard Gallon (Cofnod Records Centre, Wales) collected a possible type 1 gynandromorph with intersexuality of *B. gowerense*. The specimen is immature, so it is hard to say what exact type of gynandry is it and intersexuality is present or not.

Haplodrassus umbratilis (L. Koch, 1866) (Gnaphosidae) (Figs 2A–F)

Material.— Russia: Altai Krai, Kalmanka District, near Shtabka, c. 53°24'N, 83°48'E, summer 2020, M. S. Galyuta (ISEA).

Remarks.— We examined a type 14 gynandromorph with intersexuality of this species. The left side is female and the right predominately male, however the epigastric area has epigyne development on the right side, meaning it is not entirely male.

Mendoza canestrinii (Ninni in Canestrini, Pavesi 1868) (Salticidae) (Figs 3A–G)

Material.— Japan: Aichi Prefecture, Miyoshi City, Kurozasacho, Komochimatsu [= 35°08'15"N 137°06'03"E], abandoned field, 13.II.2024, N. Hagano [not deposited in a collection].

Remarks.— Noriko Hagano collected a type 2 gynandromorph alive. The abdomen is asymmetric and therefore abnormally shaped.

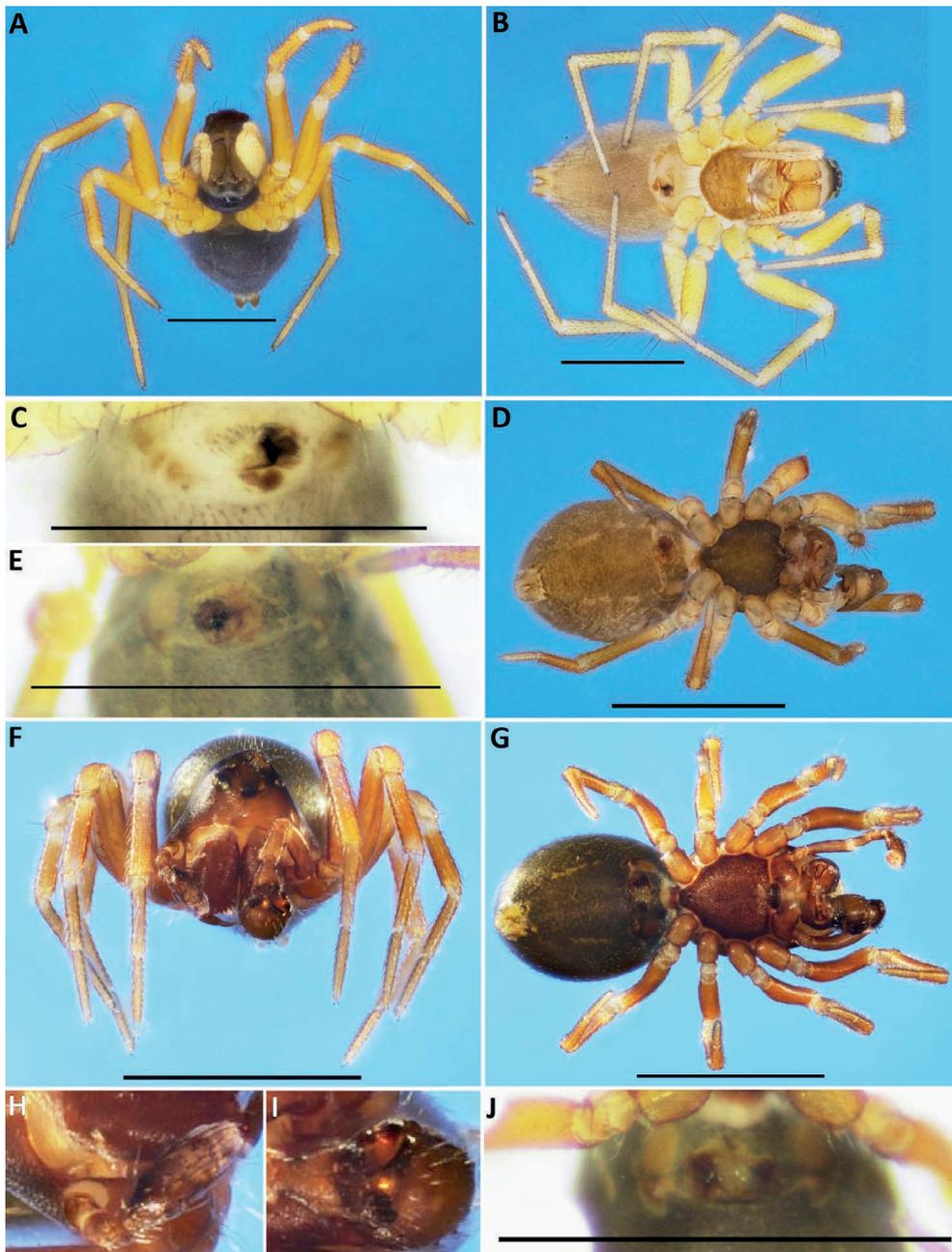


Figure 1. A) *Baryphyma gowerense* (Locket, 1965) type 1 gynandromorph with immaturity, dorso-lateral view. B) *Oedothorax fuscus* (Blackwall, 1834) type 11 gynandromorph, ventral view. C) Idem, epigyne, ventral view. D) *Pocadicnemis pumila* (Blackwall, 1841) type 1 gynandromorph with intersexuality, ventral view. E) Idem, epigyne, ventral view. F) *Troxochrus scabriculus* (Westring, 1851) type 13 gynandromorph with intersexuality, frontal view. G) Idem, ventral view. F) Idem, right palp, dorsal view. G) Idem, left palp, dorsal view. J) Idem, epigyne, ventral view. Scale bars = 1mm.

Figura 1. A) *Baryphyma gowerense* (Locket, 1965) ginandromorfo tipo 1 con inmadurez, vista dorsolateral. B) *Oedothorax fuscus* (Blackwall, 1834) ginandromorfo tipo 11, vista ventral. C) Ídem, epígino, vista ventral. D) *Pocadicnemis pumila* (Blackwall, 1841) ginandromorfo tipo 1 con intersexualidad, vista ventral. E) Ídem, epígino, vista ventral. F) *Troxochrus scabriculus* (Westring, 1851) ginandromorfo tipo 13 con intersexualidad, vista frontal. G) Ídem, vista ventral. F) Ídem, palpo derecho, vista dorsal. G) Ídem, palpo izquierdo, vista dorsal. J) Ídem, epígino, vista ventral. Barras de escala = 1 mm.

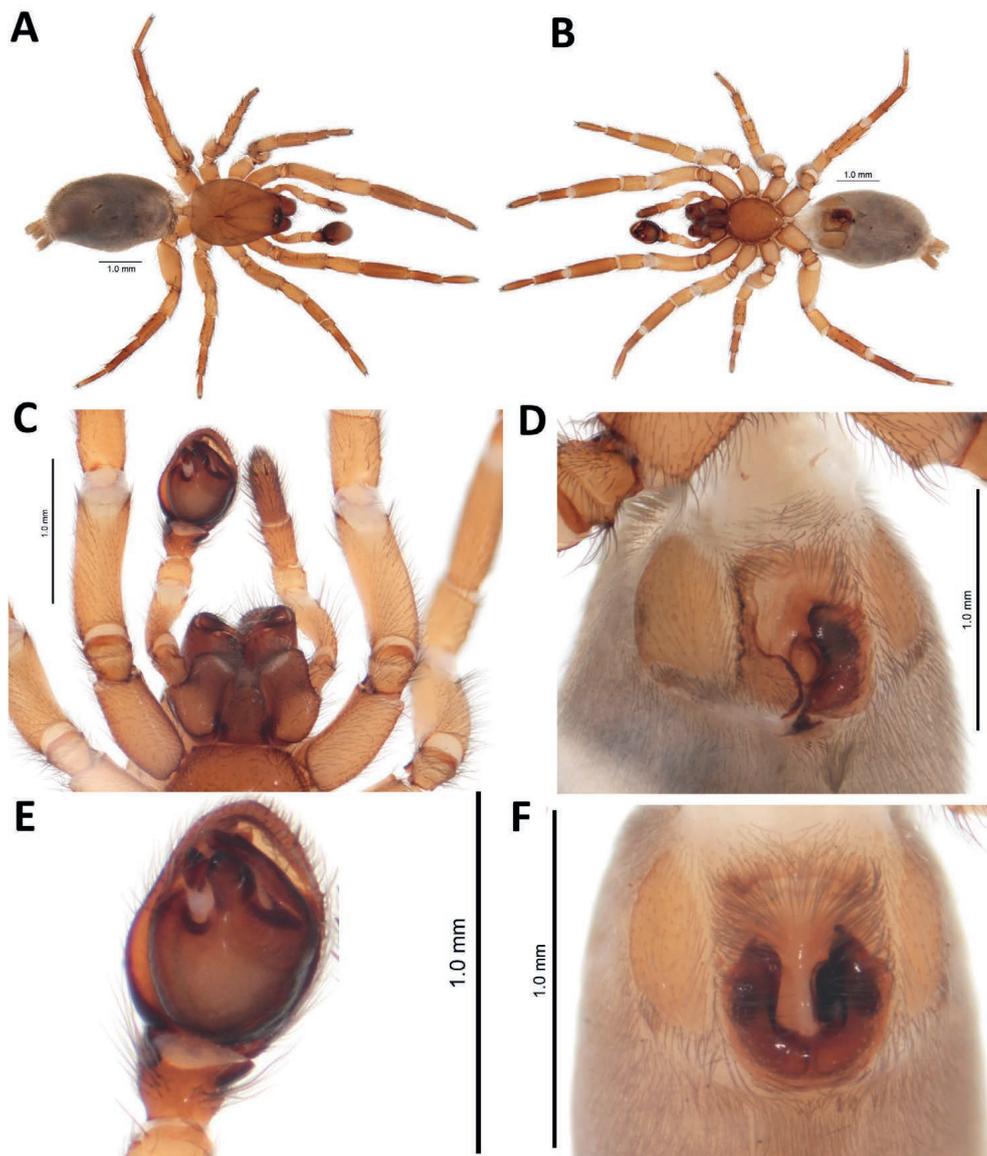


Figure 2. *Haplodrassus umbratilis* (L. Koch, 1866), A–E type 14 gynandromorph with intersexuality, F normal female. A) dorsal view. B) ventral view. C) close-up of both palps, ventral view. D) epigyne, ventral view. E) right palp, ventral view. F) epigyne, ventral view. Scale bars = 1 mm.

Figura 2. *Haplodrassus umbratilis* (L. Koch, 1866), ginandromorfo tipo 14 A–E con intersexualidad, hembra F normal. A) Vista dorsal. B) Vista ventral. C) Primer plano de ambos palpos, vista ventral. D) Epigino, vista ventral. E) Palpo derecho, vista ventral. F) Epigino, vista ventral. Escala de escala = 1 mm.

Notocosa bellicosa (Goyen, 1888) (Lycosidae)

(Figs 4A–E)

Material.— New Zealand: Canterbury Region, Christchurch, Bromley, 43°31'S, 172°41'E, inside human habitation, 9.V.2020, K. Curtis [deposited in Lincoln University, New Zealand].

Remarks.— Kate Curtis, a PhD student at Lincoln University collected a type 3 gynandromorph. Another of Cor's students is currently studying the prevalence of gynandry within populations of this lycosid (C. Vink pers. comm.), and we look forward to the publication of these results.

Oedothorax fuscus (Blackwall, 1834) (Linyphiidae)

(Figs 1B–C)

Material.— United Kingdom: Wales, Powys, Mynydd Illtyd (SN96372604) [collector indicates National Grid Reference, coordinates: 51°55'24"N, 003°30'30"W], stream margin, vacuum sampler (2 minutes), 16.IX.2021, R. C. Gallon (RGPC).

Remarks.— Our colleague Richard Gallon collected a type 11 gynandromorph of *O. fuscus*. The body of this specimen is wholly female, the left side of the epigyne is developed but epigynal structures are absent on the right side.

Pocadicnemis pumila (Blackwall, 1841) (Linyphiidae)

(Figs 1D–E)

Material.— United Kingdom: England, Cumbria, Meathop Moss (SD44288210) [collector indicates National Grid Reference, coordinates: 54°13'54"N, 002°51'23"W], raised bog, dry Sphagnum pools, vacuum sampler, 18.VI.2021, R. C. Gallon (RGPC).

Remarks.— Our colleague Richard Gallon collected a type 1 gynandromorph with intersexuality of *P. pumila*. The left palp is perfectly developed but the epigyne is slightly malformed.

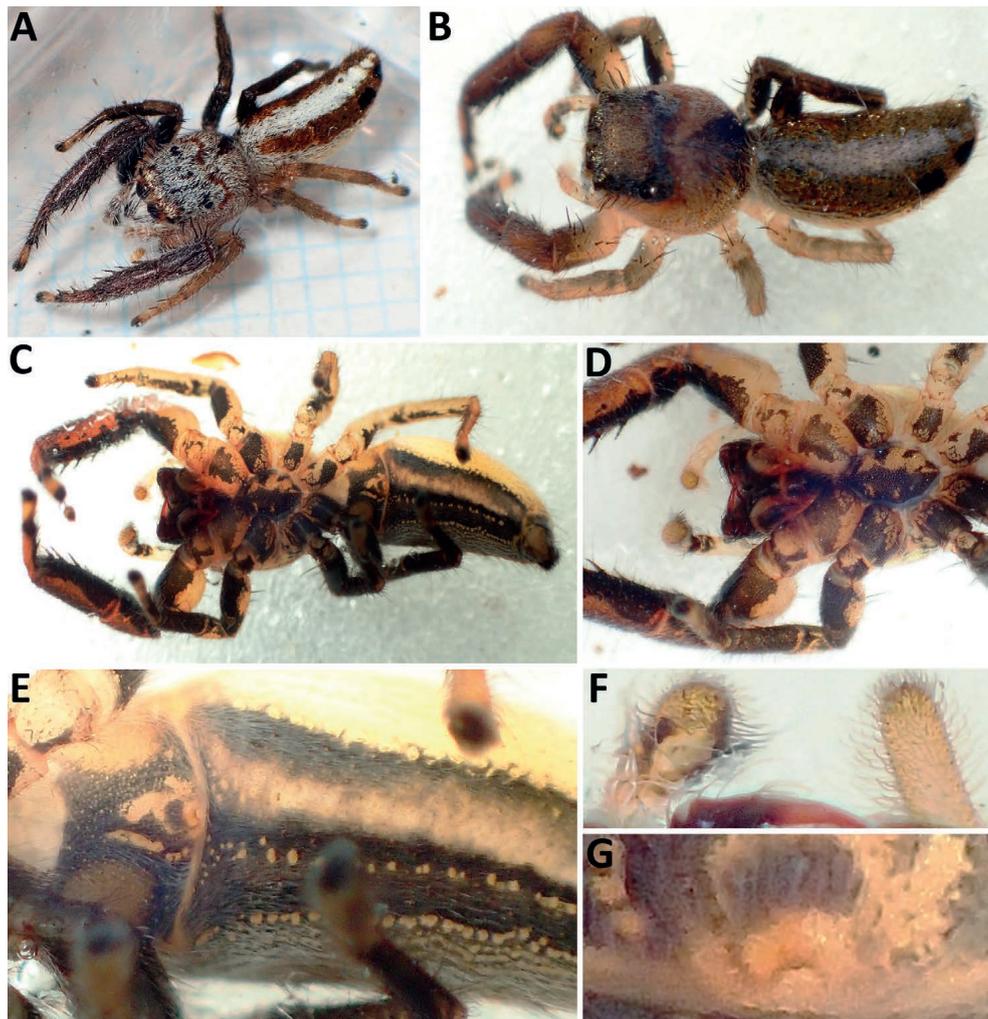


Figure 3. *Mendoza canestrinii* (Ninni in Canestrini, Pavesi 1868) type 2 gynandromorph. A) in life, dorso-lateral view. B) preserved, dorsal view. C) Idem, ventral view. D) Idem, close-up of sternum. E) Idem, close-up of abdomen. F) Idem, close-up of palps. G) Idem, close-up of epigyne. Photos courtesy of H. Hagano.

Figura 3. *Mendoza canestrinii* (Ninni in Canestrini, Pavesi 1868), ginandromorfo tipo 2. A) En vida, vista dorsolateral. B) Conservado, vista dorsal. C) Ídem, vista ventral. D) Ídem, primer plano del esternón. E) Ídem, primer plano del abdomen. F) Ídem, primer plano de los palpos. G) Ídem, primer plano del epígino. Fotos cortesía de H. Hagano.

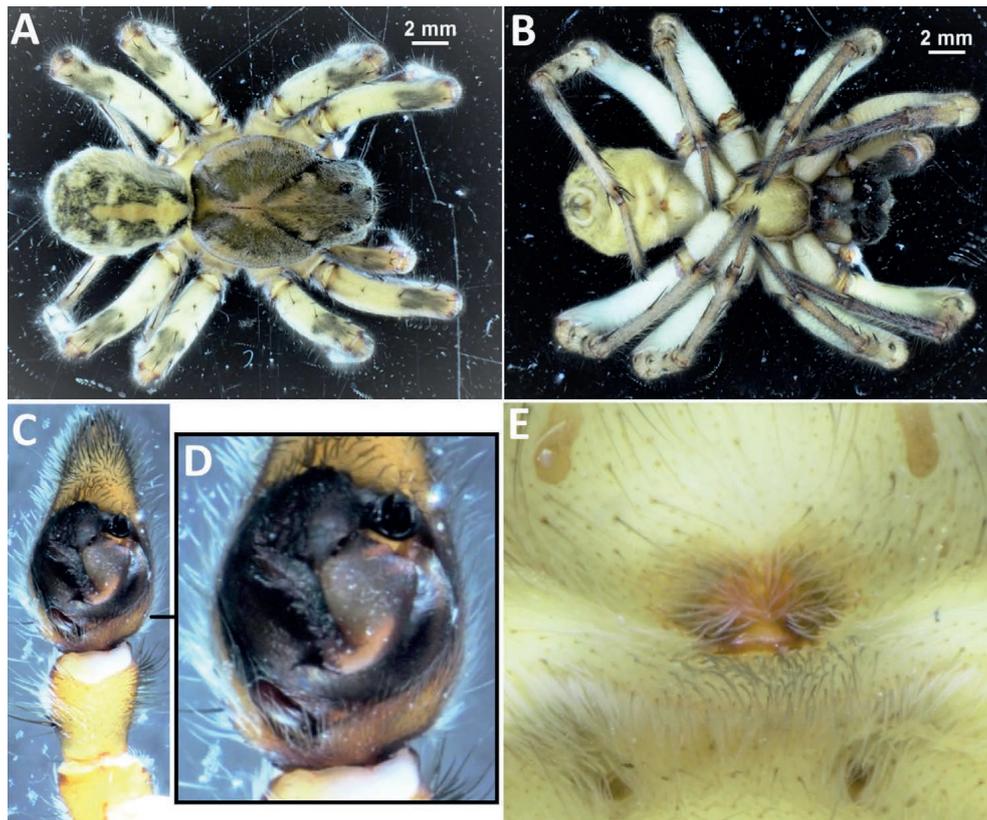


Figure 4. *Notocosa bellicosa* (Goyen, 1888) type 3 gynandromorph. A) dorsal view. B) ventral view. C) palp, ventral view. D) Idem, close-up. E) epigyne, ventral view. Photos courtesy of K. Curtis.

Figura 4. *Notocosa bellicosa* (Goyen, 1888), gindromorfo tipo 3. A) Vista dorsal. B) Vista ventral. C) Palpo, vista ventral. D) Ídem, primer plano. E) Epígino, vista ventral. Fotos cortesía de K. Curtis.

Thyene inflata (Gerstaecker, 1873) (Salticidae)
(Figs 5A-G)

Material.— Gabon, Moyen-Ogooué Province, Lambaréné, c. 0°42'S, 10°14'E, 2007, W. P. Maddison (WPMPC).

Remarks.— Our colleague Wayne Maddison (Beatty Museum, Canada) collected a type 1 gynandromorph with intersexuality. The left palp is mostly that of a normal male but the bulb and associated structures are malformed, indicating it is intersexual. The right palp is female. The epigastric area is mostly female, although only normally developed on the right side, the left being deformed and thus intersexual.

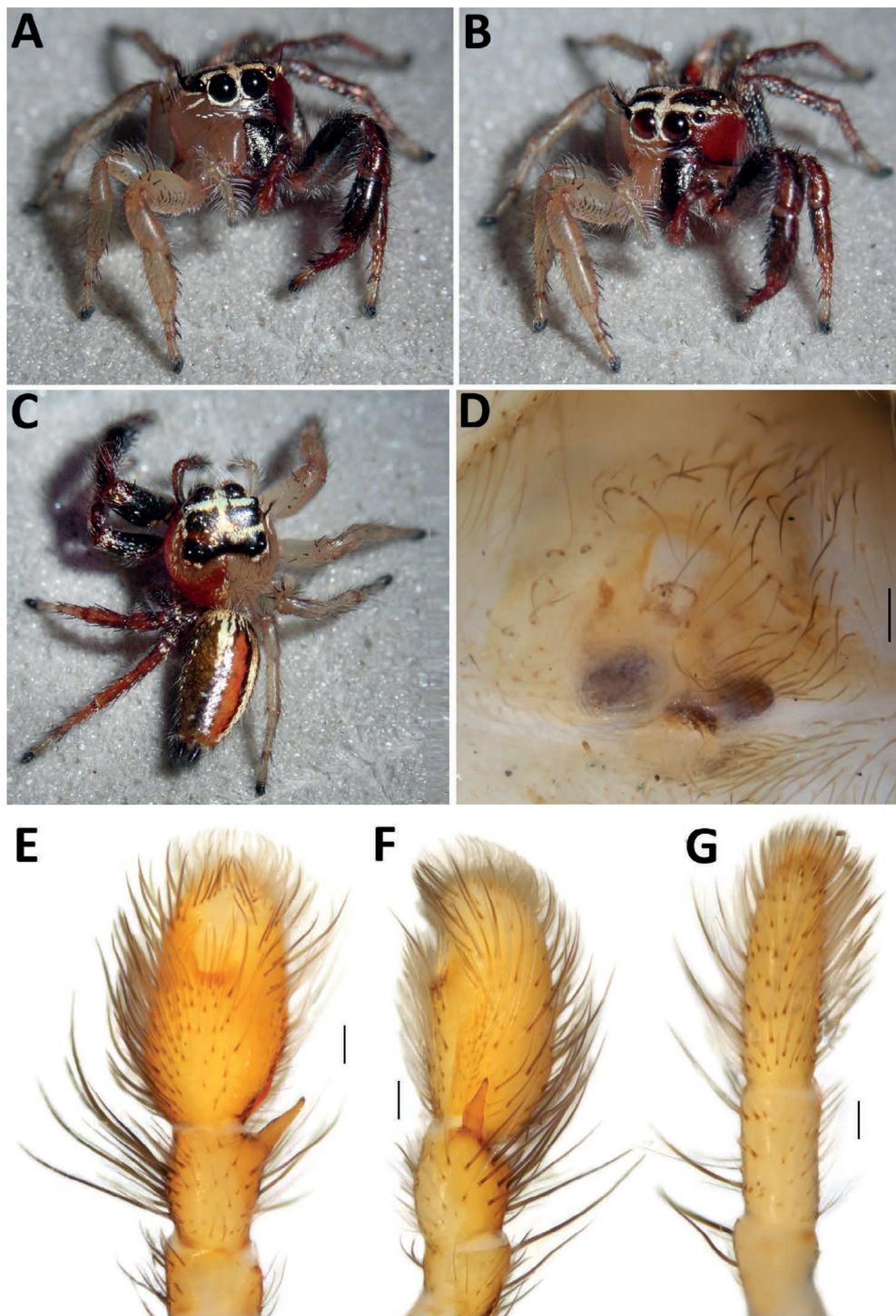


Figure 5. *Thyene inflata* (Gerstaecker, 1873 type 1 gynandromorph. A) in life, frontal view. B) Idem. C) Idem, dorsal view. D) epigyne, ventral view. E) left palp, ventral view. F) Idem, retrolateral view. G) right palp, ventral view. Scale bars (E-G) = 0.1mm. Photos courtesy of W. Maddison.

Figura 5. *Thyene inflata* (Gerstaecker, 1873, ginandromorfo tipo 1). A) En vida, vista frontal. B) Ídem. C) Ídem, vista dorsal. D) Epígino, vista ventral. E) Palpo izquierdo, vista ventral. F) Ídem, vista retrolateral. G) Palpo derecho, vista ventral. Barras de escala (E-G) = 0,1 mm. Fotos cortesía de W. Maddison.

Troxochrus scabriculus (Westring, 1851) (Linyphiidae)
(Figs 1F–J)

Material.— United Kingdom: England, Lancashire, Cabin Hill National Nature Reserve (SD28130478) [collector indicates National Grid Reference, coordinates: 53°32'05"N, 003°05'09"W], dense fixed dune marram, grubbing (10 minutes), 29.IV.2021, R. C. Gallon (RGPC).

Remarks.— Our colleague Richard Gallon collected a type 13 gynandromorph with intersexuality of *T. scabriculus*, briefly noted in a grey literature report (Gallon, 2022). The cephalic region on the left side is developed as in a male, the rest of the body as that of a female. The left palp is fully developed but the right palp is undeveloped, swollen and looks like that of an immature male. The right side of the epigyne is normally formed but the left side is slightly malformed.

Zodariellum schmidti Marusik and Koponen, 2001
(Zodariidae) (Figs 6A–G)

Material.— Mongolia: Ömnögovī Aimag, Bayandalai Somon, Zoden Uul Mt Range, 43°21'N, 103°11'E, 1700 m a.s.l., 27–30.V.1997, Y. M. Marusik (ISEA 001.9235).

Remarks.— Marusik, Koponen (2001) mentioned that one paratype of *Z. schmidti* was a so-called teratological male with one bulbus, the other palp as in a female. Infact, this paratype – which is extremely damaged – is a type 10 gynandromorph.

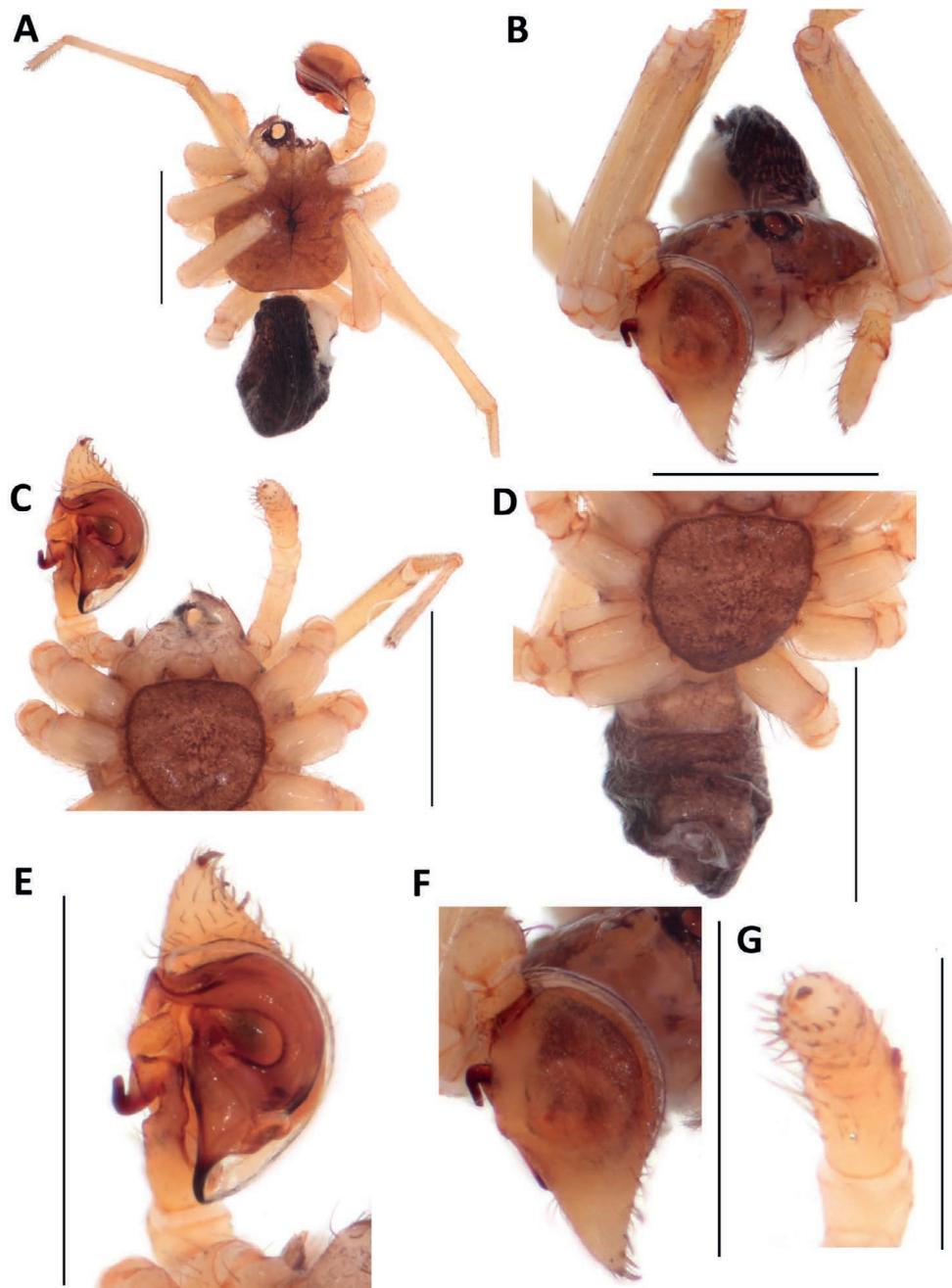


Figure 6. *Zodariellum schmidti* Marusik and Koponen, 2001 paratype type 10 gynandromorph (ISEA 001.9235). A) dorsal view. B) frontal view. C) close-up of palps, ventral view. D) sternum and abdomen, ventral view. E) right palp, ventral view. F) Idem, dorsal view. G) left palp, ventral view. Scale bars = 1mm.

Figura 6. *Zodariellum schmidti* Marusik y Koponen, 2001, paratipo tipo 10 gynandromorph (ISEA 001.9235). A) Vista dorsal. B) Vista frontal. C) Primer plano de los palpos, vista ventral. D) Esternón y abdomen, vista ventral. E) Palpo derecho, vista ventral. F) Ídem, vista dorsal. G) Palpo izquierdo, vista ventral. Escala de barras = 1 mm.

Can a practical solution be given for notation of spiders with mixed gynandry and intersexuality?

Earlier in this work, we alluded to the fact Roberts and Parker (1973) did not provide a notation system for cases of irregular gynandry nor mixed gynandry and intersexuality. A clue for the solution is given in how they refer to the hypothetical case which shows the limits of Kaston's definition of partial/mosaic gynandromorphs (i.e. that one can speak of the closest of type [of the 14 proposed] the specimen resembles, then explain its deviations). However, the approach given in the main text is not harmonious. For example, their case of *T. pallens* resembles the 'regular' types 2 and 14 but does not fit perfectly, so they classify it simply as an irregular gynandromorph. This is not technically incorrect, but the problem instead is by not having an extended framework that attempts, as far as possible, to typify irregular gynandry in as precise a way as 'regular' gynandry, then all atypical cases are lumped under a broad category, where any future worker who wants to examine these cases must individually review each one to see its particulars, since 'irregular' *sensu* Roberts and Parker (1973) and earlier workers is a wastebin category for anything that does not fit neatly with human-made 'boxes'. We propose that in fact these 'irregular' cases, although challenging, need a more extensive framework so that cases can be classified more consistently, and not lumped together.

It follows that within the four-quadrant system of gynandry that there exist 16 states where at least one quadrant is purely one sex, although we simplify this by lumping both combinations of bilateral gynandry into a single category each (i.e. male on both left quadrants and female on both right quadrants or vice versa) making for a total of 14 'types' as defined by Roberts and Parker (1973) (Fig. 7). Nonetheless, this simplification does not change the number of combinations for mathematical formulae, as this remains 16.

For the purposes of our work, we decided to consider all possibilities where one of the quadrants could be intersex, either biased to male or female or being comprised 50% of each sex and combine the range of possibilities for intersexuality in four quadrants with the pure sex quadrants of the 14 type "pure gynandry" framework of Roberts and Parker (1973). In a quadrant system with five possibilities for each of the four quadrants, we can easily calculate that $5^4 = 625$ possible combinations; a small sample of 32 possibilities, encompassing male-preponderance of one quadrant (Fig. 8) and equal-share intersexuality in one quadrant (Fig. 9) are illustrated.

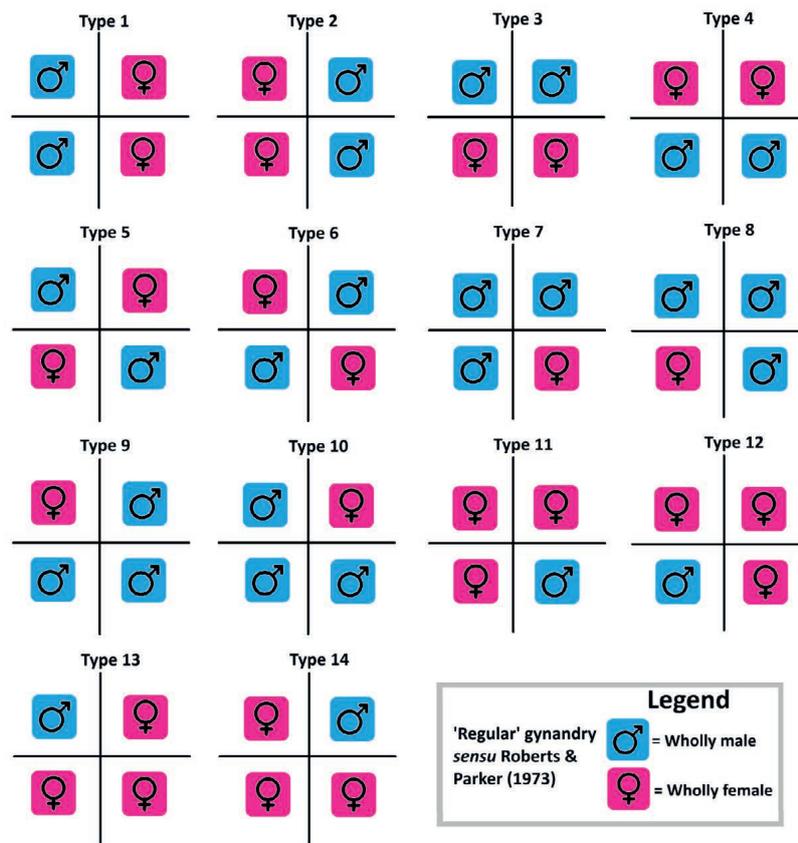


Figure 7. The 14 gynandromorph types of Roberts and Parker (1973) as defined by quadrants.

Figura 7. Los 14 tipos de ginandromorfos de Roberts y Parker (1973) definidos por cuadrantes.

This system is far too burdensome a classification system to incorporate in arachnology. Nonetheless, it shows the biological reality of the complexity of mixed gynandry and intersexuality, and it is important that future workers understand this. We therefore provide below a much more simplified way of classifying spiders with mixed gynandry and intersexuality which is still more precise and descriptive than the broad category given by Roberts and Parker (1973).

Thus, we propose that relating irregular cases towards the closest type(s) of regular gynandromorphs and then note its deviations, we can provide a clearer classification for these cases (i.e. using the established system so that at a glance it can be seen what conventional category it most closely resembles), at least as is possible within the constraints of morphology-only studies, which comprises almost all of the published investigations of sexually anomalous spiders to date.



Figure 8. A small number of possibilities of gynandry mixed with unequal intersexuality of quadrants.

Figura 8. Un pequeño número de posibilidades de ginandría mezcladas con intersexualidad desigual de cuadrantes.

We interpret, following examination of the specimen by DS, the *H. cupreus* case of Roberts and Parker (1973) as a type 3 gynandromorph with intersexuality. The reason for this is the epigyne is malformed, and the abdomen shape seems to be more elongated [male-type] than a typical female. However, the occupation of both bottom quarters by an abnormal epigyne gives little doubt that the dominant of the two sexes within these quadrants is female, otherwise this structure could not have been present on both sides. Evidently the shape of the abdomen and body size are what influenced Roberts and Parker (1973) to consider the specimen “entirely male” besides from the abnormal epigyne because those morphometrics were closer to normal male ranges than females, which exhibit some degree of sexual dimorphism.



Figure 9. A small number of possibilities of gynandry mixed with equal intersexuality of quadrants.

Figura 9. Un pequeño número de posibilidades de ginandría mezclada con igual intersexualidad de cuadrantes.

The abnormal body size and abdomen proportions may result from the intersexuality and associated endocrinological effects during ontogeny. Nonetheless, the abnormal form of the epigyne indeed does not make it a regular type 3 gynandromorph. By referring to it as a type 3 gynandromorph with intersexuality, we provide a more realistic classification, but at the same time break the artificial notion that the types 1–14 should only be used accommodate specimens with unambiguous sex for each quadrant. Intermediate morphology due to intersexuality should not be considered a ‘veto’ and instead should be viewed in its extent of presentation and this allowed to inform the decision of which type of gynandry the specimen should be associated (but not match completely) to.

Revisiting the case of *T. pallens*, we suggest it be considered a type 14 gynandromorph with intersexuality. The only reason Roberts and Parker (1973) do not assign it to this category is due to asymmetry of the abdomen and differences in colour to a regular female. However, these may not be sexual in origin and may instead be resultant from a non-sexual teratology, could involve pigmentation anomalies, or a combination of both.

It must nonetheless be remembered, for all sexually anomalous specimens, their classification is forever arbitrary when assessed only with morphology. It is becoming increasingly clear that the future of the field of research on spider sexual anomalies will rely on genetic approaches to further fine-tune the morphological categories established and refined over the last 90 years or so. An integrative classification should result in a more accurate and intuitive system in the distant future. One more comment must be made here, Roberts and Parker (1973) tentatively float the term “pseudogynandromorph” as a hypothetical category for the *H. cupreus* specimen, if one considers the epigynal structure to be artefactual in nature and not a “real” epigyne. However, this argument is illogical because there is no known mechanism that would produce epigyne-like artefactual anomalies (i.e. non-sexual teratological sclerotization) and we consider the chances that such “random” teratology would produce a structure that resembles an epigyne both inside and out (as is the case in *H. cupreus* discussed here) is infinitesimally low. Instead, the evidence of internal vulval structure in this specimen leaves us in no doubt that this specimen is a gynandromorph, and that the abnormality is simply explainable because the tissue is intersexual and not perfectly female.

Appraisal of the literature on gynandromorph and intersex spiders – 1867 to 2022

Blackwall (1867: 394) reported an adult of the pholcid *Crossopriza lyoni* (Blackwall, 1867) (*sub Pholcus lyoni*) that was “*united in the sexes*”, describing in the text a specimen that was likely a bilateral gynandromorph. He notes that the anterior legs were missing, thus Blackwall could not comment on whether these opposing legs showed characteristics of the respective sex. It is important to note that Blackwall (1867) also notes that this is the first case he has encountered of this phenomenon, deducing that it must thus be a rare occurrence. Unfortunately, the scarcity of information means it cannot be said which type of gynandromorph this specimen was *sensu* Roberts and Parker (1973).

Kulczyński (1885) reported a bilateral (type 1) gynandromorph of *Oedothorax fuscus* (Blackwall, 1834) (*sub Erigone fusca*) which showed no apparent intersexuality. Strand (1900) describes a gynandromorph of *Tetragnatha montana* Simon, 1874 (*sub Tetragnatha solandri* (Scopoli, 1763)) paying particular attention to differences in the cheliceral dentition, as the right chelicera was male and the left female. However, as details about the morphology of the genitalia were omitted it is not possible to be certain if it was a type 2 gynandromorph or another presentation of sexual anomaly.

Bertkau (1888) reported a type 3 gynandromorph of *Diaea dorsata* (Fabricius, 1777) briefly, whilst discussing sexual anomalies in invertebrates more generally. The next year, Bertkau (1889a) cites his own work a year prior and the work of Kulczyński (1885) as the two known examples of sexual anomaly in spiders. Bertkau (1889b, 1891) then newly reported a gynandromorph of *Pardosa* sp. (*sub Lycosa* in the 1889 work, which is an abstract of a talk he presented on the specimen) which had one immature male palp, an epigyne, and presence of malformed testicles and additional spinnerets. Bertkau (1891) gives a very detailed description of the morphology of this specimen but, as noted in both works, one palp is missing so it is not possible to classify with certainty to which type *sensu* Roberts and Parker (1973) the specimen belonged. He also cites previous cases, including that of Kulczyński (1885) (initially as *Erigone fusca*), and his further information about the specimen of *D. dorsata* allows us also to conclude it was an intersex as it had a malformed epigyne.

O. Pickard-Cambridge (1902) reported an intersex of *Hilaira excisa* (O. Pickard-Cambridge, 1871) which was male except for one palp. Based on the description, it is not possible to rule out that the spider was not also a type 9 or 10 gynandromorph, but O. Pickard-Cambridge also noted the caput was (entirely) male, which probably rules this out given the sexually dimorphic caput protuberance found in males of *H. excisa*. This specimen was also discussed Hull (1918) (see below) and the male caput mentioned in a list of the local spiders by Jackson (1907a).

Jackson (1907b) reports a specimen of *Porrhomma cambridgei* Merrett, 1994 (*sub Porrhomma oblongum* (O. Pickard-Cambridge, 1871)) stating: “I possess a gynandrous specimen taken at Hexham. It has one male palpus, one female palpus, and a distorted epigyne.” but not illustrating or discussing the specimen in any greater detail. Emerton (1907) reported a type 13 gynandromorph of *Drassodes neglectus* (Keyserling, 1887) which was predominately female but possessed a fully developed left male palp. Jackson (1909) reported a type 2 gynandromorph of *Palliduphantes pallidus* (O. Pickard-Cambridge, 1871) (*sub Lepthyphantes pallidus*), although it may also have been intersex given the abnormalities reported in the epigyne. Jackson (1909: 435) also stated: “This is the third gynandrous spider I have seen. The others were *Hilaria excisa* (Camb.) and *Porrhomma oblongum* (Camb.)”. At the time, the record of *H. excisa* remained without further discussion or publication.

Falconer (1910) reported two new cases of intersexuality, one in a specimen of *Oedothorax retusus* (Westring, 1851), and another in *Maso sundevalli* (Westring, 1851). The intersexual specimen of *O. retusus* has two male palps and an almost complete epigyne, but both palps and half of the epigyne are malformed, and the cephalothorax is intermediate. Similarly, that of *M. sundevalli* is intersexual, but has normal male left palp, slightly swollen right palp different from a female palp and a comparatively less malformed (but still so) epigyne. It is likely, but cannot be stated with certainty, that these intersexes were also type 3 gynandromorphs. Falconer (1910) also cites and discusses previous records by O. Pickard-Cambridge (1902 and, indirectly, 1867) and Jackson (1907 (as 1906), 1908). He overlooked the work of Blackwall (1867).

Hull (1911) reports a type 6 gynandromorph of *Micrargus herbigradus* (Blackwall, 1854) (*sub Lophomma herbigradum*), appearing to be the first of this type reported in the literature. O. Pickard-Cambridge (1913) simply states he examined a “hermaphrodite” of *Agroeca proxima* (O. Pickard-Cambridge, 1871) as noted by Hull (1918) (see below). Spassky (1914) reported a type 3 gynandromorph of *Agroeca cuprea* Menge, 1873 (*sub Agroeca chrysea* Chyzer and Kulczyński, 1897) which he observed had evidence of copulation within the fully developed (and presumably functional) female genitalia. The case is somewhat strange, leading us initially to consider if it may be a type 13 gynandromorph. However, the specimen was female ventrally, with a fully developed male palp on the left-hand and with the right palp swollen but undeveloped, as would be found in a subadult. Thus, this combination indicates it is best regarded as an intersexual type 3 gynandry.

Falconer (1917) reported an intersex of *Neon reticulatus* (Blackwall, 1853) which had a right male palp and female epigyne (presumably occupying both bottom quadrants) which were imperfectly formed. It is not clear from this account whether Falconer’s specimen had gynandry and intersexuality, but given no explicit evidence saying that the upper left quadrant was (apparently) wholly female, we prefer to interpret this case of being solely intersexuality. He also noted that prior to his reported case, sexual anomalies reported in spiders at that time were represented overwhelmingly by Linyphiidae.

Hull (1918) reviewed sexual anomalies in spiders, and proposed the first classification system (see Introduction). Hull (1918) gave a comprehensive review (and reproduction of some figures) of previously published reports he was aware of (note he did not cite Blackwall (1867), overlooking this reference as did Falconer (1910)), including an excellent English translation of Kulczyński (1885). Important discussion was also made on the intersexes described by Falconer (1910), and it was clarified the female of *H. excisa* mentioned in Hull (1911) was lost, hence why no full report of it was made in a previous publication.

Nonetheless, he classified it in his 'Class 2'. Hull (1918) tentatively placed the *O. retusus* reported by Falconer (1910) into his 'Class 3' but noted it was not entirely the same, showing exemplifying its intersexuality in a table (Hull, 1918: 178). He also recalls having seen a report of sexual anomaly in a lycosid by Tamerlan Thorell but was unable to specify where such a remark was made.

Deichmann (1920) reported a type 2 gynandromorph of *Hylyphantes graminicola* (Sundevall, 1830) (sub *Gongylidium graminicola*). Jackson (1924: 5–6) reported an intersex and probable type 3 gynandromorph of *Drassodes lapidosus* (Walckenaer, 1802). Braendegaard (1925) reported a type 1 gynandromorph of *Pardosa pullata* (Clerck, 1757) (sub *Lycosa pullata*).

Rabaud and Millot (1933) described an intersex (without gynandry) of *Argiope bruennichi* (Scopoli, 1772) which showed intermediate sexuality in essentially all parts of the body. As later noted by Kaston (1961), Rabaud and Millot (1933) were the first authors to consider their, and some previous cases, as probably being a combination of both conditions of sexual anomaly, and the first to dissect and examine precisely (otherwise) male organs affected by intersexuality. It is also worth noting that this was the first case to exceed differences in body proportion to the patterns observed by Hull (1918: 171) who stated "... none of the known instances of gynandry have occurred where the difference in size is unusually great; all the records are of species in which the total length of the female does not exceed that of the male by more than 15 per cent. of the latter.". The case of intersexuality in *A. bruennichi* is thus remarkable as the difference between males and females can easily exceed 30%.

Gertsch (1934: 29) reports in his material of examined specimens of *Neoantistea riparia radula* (Emerton, 1890) a single "hermaphrodite", without further comment, although this specimen was to be revisited later by Exline (1938) (see below).

Kolosváry (1935: 138) described a juvenile specimen of "*Micryphantes* sp." (the genus *Micryphantes* C. L. Koch, 1833 and all its species are now nomina dubia, see World Spider Catalog, 2025) which showed signs of gynandry in the palps (figured stylistically in the work), the left being that of a female and the right of a (immature) male. Unfortunately, given no further details are given, it is not possible to state conclusively if this was a type 2 gynandromorph or whether the specimen was another type and/or intersex. Balogh (1936) reported what was very likely a type 2 gynandromorph of *Philaeus chrysops* (Poda, 1761) but both palps were missing and thus could not be fully interpreted.

Exline (1938) discussed four cases (two new) of sexual anomaly – examining the specimens both internally and externally – provided a new morphometric method for visualising the leg differences between male and female spiders and summarized the prior literature she had at her disposal into a table. She redescribed in detail the type 2 gynandromorph of *Neoantistea agilis* (Keyserling, 1887) first reported (and misidentified) by Gertsch (1934) and the *D. neglectus* specimen first reported by Emerton (1907). For the former, her dissection of the epigyne allowed to correct the misidentification made by Gertsch, who had considered based on external morphology alone that it was a specimen of *N. riparia radula* (itself now a junior synonym of *Neoantistea magna* (Keyserling, 1887)). This pioneering work also allowed for histological examination of the four focal specimens.

Holm (1941) reports a probable type 5 gynandromorph with intersexuality of the linyphiid *O. retusus*: the cephalothorax is entirely male on the right quadrant, and the left is almost entirely male, save for abnormality in the palp and first leg, which indicate these areas are intersexual. The abdomen is symmetrical but the epigyne is present only on the right side of the specimen, and an internal dissection and histological evaluation of the tissues revealed the presence of both male and female organs in the abdomen. This confusing mix gives some uncertainty as to the status of the specimen, but we classify it as we do based on the following facts from Holm (1941): (1) the cephalothorax is typical for a male, (2) the right palp is entirely male but tarsus I looks like female (not thinner and “spiral-form”), (3) the left palp has a reduced tibial apophysis and undeveloped bulbus but tarsus I as in a normal male (“spiral-form” and thicker), (4) the abdomen slightly bigger than in males, (5) the right side of the abdomen presents with developed epigynal structure, the corresponding vulva contains both eggs and sperm with small part of testicles, and (6) the left half of the abdomen is typically male with only sperm and testicles. Holm (1941) also reports five cases of intersexual lycosid spiders which can be surmised as follows: a *Pardosa palustris* (Linnaeus, 1758) (*sub Lycosa tarsalis* Thorell, 1856) with female preponderance, with smaller epigyne compared to normal and abnormal ‘male’ palps resembling that of a subadult male; a *Pardosa sphagnicola* (Dahl, 1908) (*sub Lycosa riparia sphagnicola* Dahl, 1908) with male preponderance and presence of a malformed epigyne with developed receptacles, reduced testicles filled with sperm and swollen palps like in subadult male; a *Pardosa pullata* (Clerck, 1757) (*sub Lycosa pullata* (Clerck, 1757)) with male preponderance, a malformed epigyne, swollen palps smaller in size compared to subadult male, with testicles without sperm and undeveloped receptacles, and absence of evidence of parasites, and two cases of *Pardosa amentata* (Clerck, 1757) (*sub Pardosa saccata* (Linnaeus, 1758)) with male preponderance, with malformed palps, one of which had significantly enlarged and deformed sclerites on the male palp compared to other, both specimens have undeveloped epigyne and receptacles, and normally developed testicles with sperm.

All *Pardosa* specimens, except *P. pullata*, showed presence of significant incursion of *Mermis* parasites (but see Discussion) found in the abdomen.

Denis (1947) reported an adult of the linyphiid *Lasiargus hirsutus* (Menge, 1869) which can here be considered as both a 13 type gynandromorph and intersex, based on the significant deformity found in the male palp, and the intermediate somatic characters, namely the morphology of the carapace. Denis (1949) reported an intersex specimen of *Tenuiphantes tenuis* (Blackwall, 1852) (*sub Lepthyphantes tenuis*) which had a normally developed epigyne but a malformed and underdeveloped adult male palp on the left-hand side. Hadjissaranos (1951) reported an intersex (as a 'gynandromorph') of *Oxyopes heterophthalmus* (Latreille, 1804).

Machado (1951) reported an intersex of *Speocera vilhenai* Machado, 1951, surmising the origin of its intersexuality was likely due to parasitisation (see below). Hackman (1952) reported a type 1 gynandromorph of *Troxochrus scabriculus* (Westring, 1851), also hypothesising that gynandromorph spiders may occur when two separate sperms enter an egg, only one with sex chromosomes. Knulle (1954) reported a gynandromorph of *Prinerigone vagans* (Audouin, 1826) (*sub Erigone vagans spinosa* O. Pickard-Cambridge, 1872) which had some intermediate characteristics on the microsculpture and margins of the cephalothorax, but he did not consider there was any evidence to conclude the specimen was intersexual. However, it seems likely that it was, but that the overwhelming preponderance in the cephalothorax was that of male tissue.

Wiebes (1959) reported a type 14 gynandromorph and intersex of *Trochosa terricola* Thorell, 1857, also providing detailed histological observations. Indeed, it was through this that he was able to establish no male tissue was to be found in the abdomen, leading him to state there was "a male influence" (Wiebes, 1959: 89) to the right side of the abdomen but that overall it was female-preponderant.

Anderson (1961) describes a probable type 1 bilateral gynandromorph of *Xysticus ferox* (Hentz, 1847) (*sub Xysticus transversatus* (Walckenaer, 1837), now a *nomen oblitum*) but notes that the left palp (presumed to be male as was the rest of the left-hand side) is missing. The abdomen was also distorted.

Kaston (1961) made the next landmark publication in considering sexual anomalies in spiders, reporting ten new cases. Of these, a specimen of *Coelotes atropos* (Walckenaer, 1830) was a type 1 gynandromorph; those of *Dictyna coloradensis* Chamberlin, 1919 and *Xysticus ferox* (Hentz, 1847) (*sub Xysticus transversatus* (Walckenaer, 1837), now a *nomen oblitum*) are type 14 gynandromorphs, the latter apparently also intersex as the male quarter is imperfect; that of *Neoantistea magna* (Keyserling, 1887) (*sub Neoantistea radula* (Emerton, 1890)) is an intersex, being female everywhere except the right palp which is imperfectly male; *Scotinella pelvicolens* (Chamberlin and Gertsch, 1930) is an intersex showing intermediate morphology of both the epigyne and the two imperfectly male palps; *Hogna lenta* (Hentz,

1844) (*sub Lycosa lenta*) and *Hogna timuqua* (Wallace, 1942) (*sub* the incorrect subsequent spelling *Lycosa tumuqua*) are both intersexes with (immature) male palps only and normally developed epigynes; *Pelegrina flavipes* (G. W. Peckham and E. G. Peckham, 1888) (*sub Metahippidus flavipedes*, erroneously attributing the authorship solely to George Peckham) is an intersex with at least one male palp, partially adult and partially immature in morphology (unfortunately the left palp was missing); and two specimens of *Naphrys pulex* (Hentz, 1846) (*sub Habrocestum pulex*) were intersexes with normal female epigynes but imperfectly formed (immature) male palps. Kaston (1961) provided an updated classification of all contemporaneously known gynandromorphs and intersexes.

Yaginuma (1966) reported an intersexual specimen of *Neoscona scylloides* (Bösenberg and Strand, 1906) which was mostly male on both sides of the specimen but possessed (both male) anomalous palps and the presence of a pre-epigyne on the abdomen. Yaginuma and Arita (1967) report an intersexual *Xysticus insulicola* Bösenberg and Strand, 1906 which is female on the left-hand side and right-hand side, except for the genital plate which is female on both sides. This latter character precludes this specimen being a 'complete' type 2 gynandromorph but means instead it can be classified under the new framework as a type 2 gynandromorph with intersexuality. Mcheidze (1967) reported a type 3 gynandromorph and intersex of *Agelena labyrinthica* (Clerck, 1757) with fully developed male palps and deformed epigyne. Mackie (1969) reports a type 2 gynandromorph of *Pardosa monticola* (Clerck, 1757).

Waler (1970) reports a type 7 gynandromorph with intersexuality of *Walckenaeria karpinskii* (O. Pickard-Cambridge, 1873) (*sub Cornicularia karpinskii*). The specimen has a normal male left palp and severely malformed right palp, showing some but not all of the palpal structures of a typical male. He also notes the epigyne is incomplete, with development only on the right-hand side, and that the abdomen is malformed but that this "might be due to rough treatment, but might also be due to internal anomalies." (Waler, 1970: 5).

Nishikawa (1971) reports an intersex of *Oxytate striatipes* L. Koch, 1878. The specimen has numerous malformations, including both palps being intermediate, an asymmetrical abdomen, and a malformed (left side) and absent (right) epigynal structure. Tanaka (1971) reported a type 1 gynandromorph of *Plebs sachalinensis* (Saito, 1934) (*sub Zilla sachalinensis*) although the epigyne does exist on both the left and right sides of the specimen but undeveloped with only contour slightly larger on the right side, without developed internal structure on both sides.

Baert (1975) reported four cases of sexual anomaly in spiders: a type 3 gynandromorph with intersexuality of *Pocadicnemis pumila* (Blackwall, 1841); a type 5 gynandromorph with intersexuality of *Centromerus sylvaticus* (Blackwall, 1841); a type 12 gynandromorph of *Monocephalus fuscipes* (Blackwall, 1836), and an intersex of *Microneta viaria* (Blackwall, 1841) (restricted only to the two (immature) male palps).

Gack and Helversen (1976) discuss the behaviour of a specimen of *Alopecosa pulverulenta* (Clerck, 1757), a type 1 gynandromorph which has an almost bilateral gynandry, except for an intermediate right palp, indicating the specimen was also intersexual. Those authors were the first to report reproductive behaviour in gynandromorph spiders, detailing how the specimen made a non-viable egg sac but did not carry the egg sac in the usual way with the spinnerets. They also observed abnormal copulatory behaviour.

In their landmark paper discussed in detail elsewhere in this work, Roberts and Parker (1973) reported nine new cases (habitus of all specimens and complimentary genitalia views of some specimens, given in Figs 10–13), five of which are unambiguous: a type 8 gynandromorph of *Trachyzelotes pedestris* (C. L. Koch, 1837) (*sub Zelotes pedestris*), a type 11 gynandromorph of *Philodromus aureolus* (Clerck, 1757), a type 1 gynandromorph of *Pardosa hortensis* (Thorell, 1872) (*sub Lycosa hortensis*), an intersex *Alopecosa barbipes* (Sundevall, 1833) (*sub Tarentula barbipes*), and a likely type 3 gynandromorph (uncertainty due to absence of one palp due to damage) of *Trichoncus affinis* Kulczyński, 1894. The remaining cases do not neatly fit into a category – an irregular gynandromorph of *Paidiscura pallens* (Blackwall, 1834) (*sub Theridion pallens*), and intersexual and partly gynandromorph (i.e. not a perfect match for any of the 16 types) of *Entelecara flavipes* (Blackwall, 1834), *M. herbigradus*, and a type 3 gynandromorph with intersexuality of *Heliophanus cupreus* (Walckenaer, 1802) (see above for discussion of this specimen).

Cooper (1975) reports two sexually anomalous specimens: a probable type 1 gynandromorph of *Euophrys frontalis* (Walckenaer, 1802), and a type 1 gynandromorph with intersexuality of *Tenuiphantes zimmermanni* (Bertkau, 1890) (*sub Lepthyphantes zimmermanni*). Cooper (1975) noted that the gynandromorph of *E. frontalis* produced three eggs, which were unsuccessfully reared. Both specimens were also examined directly by the late Mike Roberts. Bednarz and Czajka (1975) reported a type 3 gynandromorph of *Oedothorax agrestis* (Blackwall, 1853).

Roberts (1976) reported that the holotype of *Centromerus parkeri* Cooke, 1967 was an intersexual specimen of *Centromerus prudens* (O. Pickard-Cambridge, 1873). Baert (1976) reported an intersex of *Gonatium rubellum* (Blackwall, 1841), which had no normal genital morphology. The predominately male areas were in the anterior half and female in the posterior, similar to a type 3 gynandromorph but not being so as none of the morphology was normally developed for either sex.

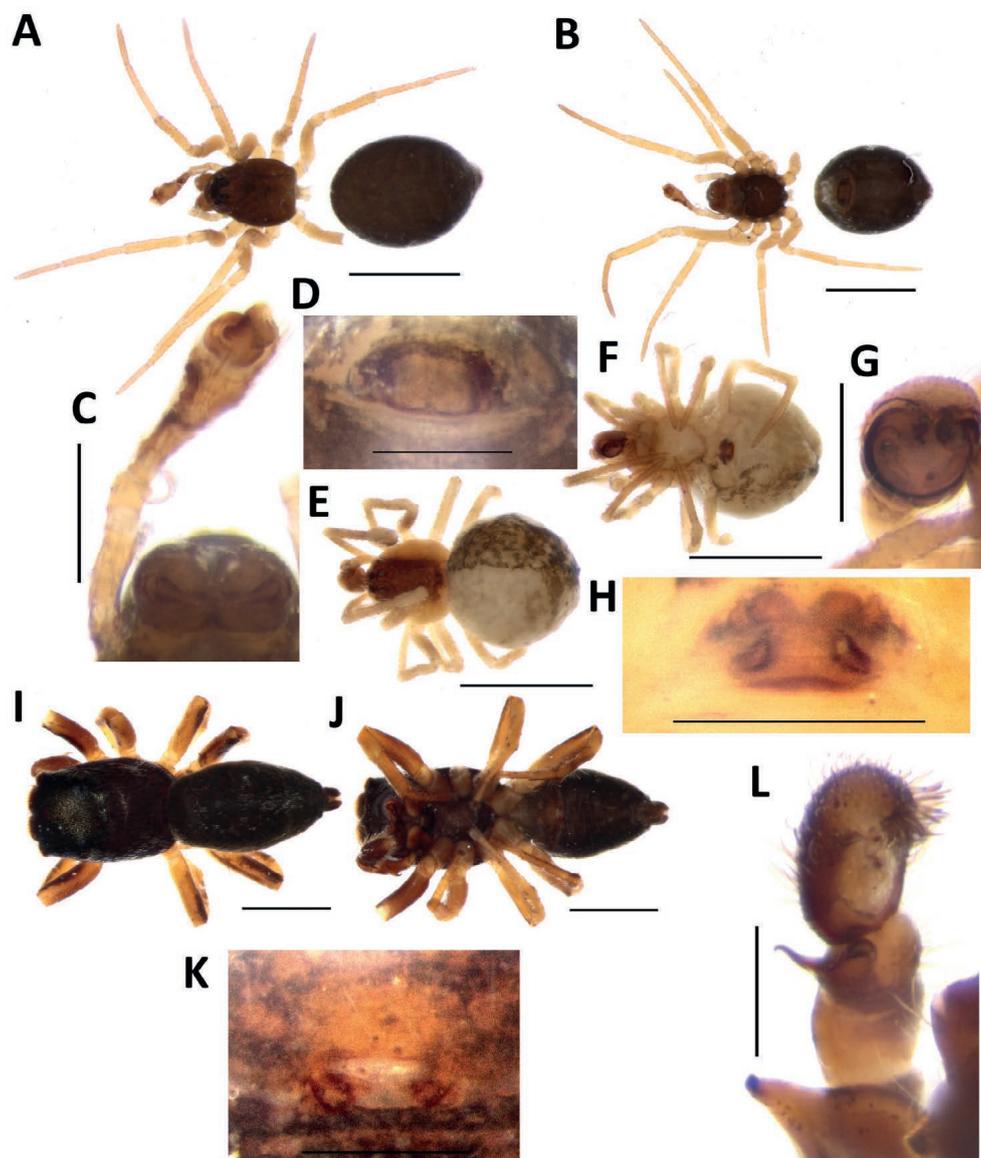


Figure 10. Complimentary photos of specimens reported by Roberts and Parker (1973) I. A–D *Entelecara flavipes* (Blackwall, 1834) irregular gynandromorph and intersex not fitting any neat categories (NHMUK 1973: 277); E–H *Paidiscura pallens* (Blackwall, 1834) irregular gynandromorph (NHMUK 1973: 276); I–L *Heliophanus cupreus* (Walckenaer, 1802) type 3 gynandromorph with intersexuality (NHMUK 1973: 281). A) habitus, dorsal view. B) habitus, ventral view. C) right palp, ventral view. D) epigyne, ventral view. E) habitus, dorsal view. F) habitus, ventral view. G) right palp, ventral view. H) epigyne, ventral view. I) habitus, dorsal view. J) habitus, ventral view. K) epigyne, ventral view. L) left palp, ventral view. Scale bars = 1 mm (A–B, E–F, I–J), 0.5 mm (C–D, G–H, K–L).

Figura 10. Fotos complementarias de especímenes reportados por Roberts y Parker (1973) I. A–D *Entelecara flavipes* (Blackwall, 1834) ginandromorfo irregular e intersexual que no encaja en ninguna categoría clara (NHMUK 1973: 277); E–H *Paidiscura pallens* (Blackwall, 1834) ginandromorfo irregular (NHMUK 1973: 276); I–L *Heliophanus cupreus* (Walckenaer, 1802) ginandromorfo tipo 3 con intersexualidad (NHMUK 1973: 281). A) habitus, vista dorsal. B) habitus, vista ventral. C) palpo derecho, vista ventral. D) epígino, vista ventral. E) habitus, vista dorsal. F) habitus, vista ventral. G) palpo derecho, vista ventral. H) epígino, vista ventral. I) habitus, vista dorsal. J) Hábito, vista ventral. K) Epígino, vista ventral. L) Palpo izquierdo, vista ventral. Escalas: 1 mm (A–B, E–F, I–J), 0,5 mm (C–D, G–H, K–L).

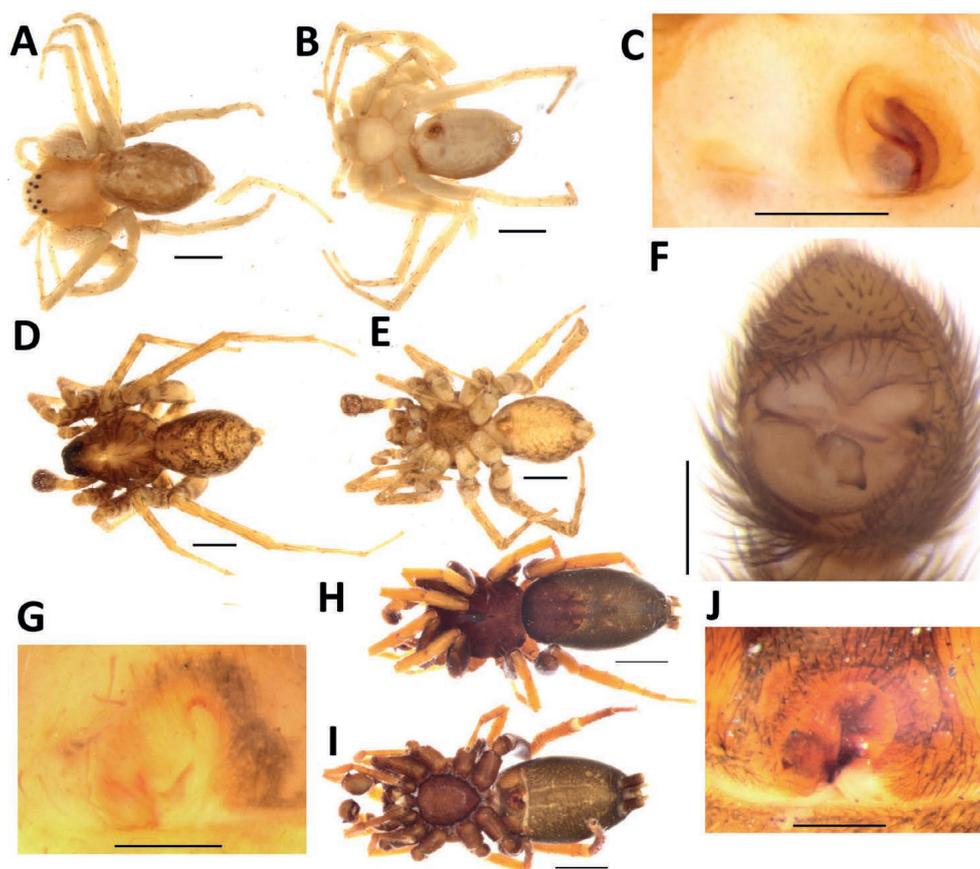


Figure 11. Complimentary photos of specimens reported by Roberts and Parker (1973) II. A–C *Philodromus aureolus* (Clerck, 1757) type 11 gynandromorph (NHMUK 1973: 280); D–G *Pardosa hortensis* (Thorell, 1872) type 1 gynandromorph (NHMUK 1973: 282); H–J *Trachyzelotes pedestris* (C. L. Koch, 1837) type 8 gynandromorph (NHMUK 1973: 279). A) habitus, dorsal view. B) habitus, ventral view. C) epigyne, ventral view. D) habitus, dorsal view. E) habitus, ventral view. F) left palp, ventral view. G) epigyne, ventral view. H) habitus, dorsal view. I) habitus, ventral view. J) epigyne ventral view. Scale bars = 1 mm (A–B, D–E, H–I), 0.5mm (C, F–G, J).

Figura 11. Fotos complementarias de especímenes reportados por Roberts y Parker (1973) II. A–C *Philodromus aureolus* (Clerck, 1757) ginandromorfo tipo 11 (NHMUK 1973: 280); D–G *Pardosa hortensis* (Thorell, 1872) ginandromorfo tipo 1 (NHMUK 1973: 282); H–J *Trachyzelotes pedestris* (C. L. Koch, 1837) ginandromorfo tipo 8 (NHMUK 1973: 279). A) hábito, vista dorsal. B) hábito, vista ventral. C) epígino, vista ventral. D) hábito, vista dorsal. E) hábito, vista ventral. F) palpo izquierdo, vista ventral. G) epígino, vista ventral. H) hábito, vista dorsal. I) hábito, vista ventral. J) Vista ventral de la epígina. Barras de escala = 1 mm (A–B, D–E, H–I), 0,5 mm (C, F–G, J).

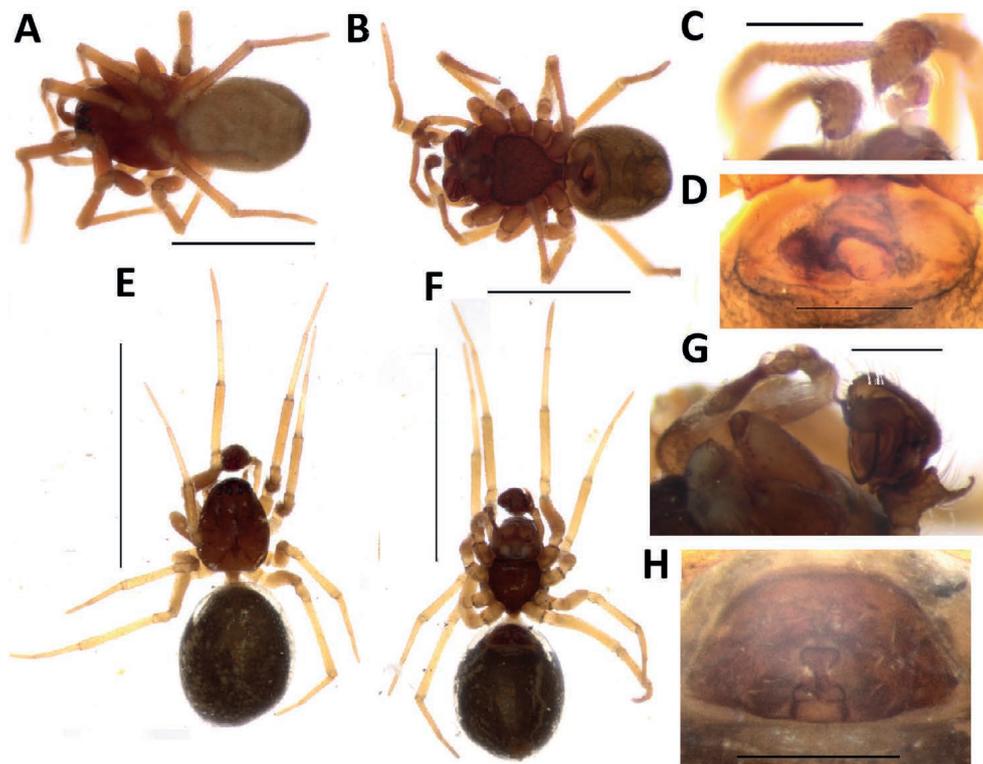


Figure 12. Complimentary photos of specimens reported by Roberts and Parker (1973) III. A–D *Micrargus herbigradus* (Blackwall, 1854) irregular gynandromorph and intersex not fitting any neat categories (NHMUK 1973: 278); E–H *Trichoncus affinis* Kulczyński, 1894 probable type 3 gynandromorph (NHMUK 1973: 284). A) habitus, dorsal view. B) habitus, ventral view. C) palps, ventral view. D) epigyne, ventral view. F) habitus, dorsal view. F) habitus, ventral view. G) right palp, ventral view. H) epigyne, ventral view. Scale bars = 1mm (A–B, E–F), 0.5mm (C–D, G–H).

Figura 12. Fotos complementarias de especímenes reportados por Roberts y Parker (1973) III. A–D *Micrargus herbigradus* (Blackwall, 1854) ginandromorfo irregular e intersexual que no encaja en ninguna categoría clara (NHMUK 1973: 278); E–H *Trichoncus affinis* Kulczyński, 1894 probable ginandromorfo tipo 3 (NHMUK 1973: 284). A) hábito, vista dorsal. B) hábito, vista ventral. C) palpos, vista ventral. D) epígino, vista ventral. F) hábito, vista dorsal. F) hábito, vista ventral. G) palpo derecho, vista ventral. H) epígino, vista ventral. Barras de escala = 1 mm (A–B, E–F), 0,5 mm (C–D, G–H).



Figure 13. Complimentary photos of specimens reported by Roberts and Parker (1973) IV. A–C *Alopecosa barbipes* (Sundevall, 1833) intersex (NHMUK 1973: 283). A) habitus, dorsal view. B) habitus, ventral view. C) right palp, prolateral view. Scale bars = 1mm.

Figura 13. Fotografías complementarias de especímenes reportados por Roberts y Parker (1973) IV. A–C *Alopecosa barbipes* (Sundevall, 1833) intersexual (NHMUK 1973: 283). A) Hábito, vista dorsal. B) Hábito, vista ventral. C) Palpo derecho, vista prolateral. Barras de escala = 1 mm.

Palmgren (1979) reported five new cases of sexual anomaly in as many species: type 1 gynandromorphs of *Tapinocyba pallens* (O. Pickard-Cambridge, 1873), *Tapinocyba bicissa* (O. Pickard-Cambridge, 1873), a type 1 with intersexuality of *Minyriolus pusillus* (Wider, 1834), a type 7 gynandromorph with intersexuality of *O. retusus*, and an intersexual specimen of *Meta segmentata* (Clerck, 1757). Palmgren (1979: 184) found an instance of around one sexually anomalous spider per 17, 000 specimens examined. Assmuth (1983) reported a type 6 gynandromorph of *Oedothorax apicatus* (Blackwall, 1850). Müller (1984) reported a type 3 gynandromorph with intersexuality (indicated by the malformed male palps) of *M. herbigrada* and an intersex of *Erigone* sp. which could not be identified to the species level.

Galiano (1985) describes a type 1 gynandromorph of *Phiale gratiosa* C. L. Koch, 1846 which is also intersexual, owed to the abnormal left-hand side colouration and the absence of any epigynal structure on the right (female) side of the specimen, in addition to an intermediate morphology of the maxillae. Kumada (1989) reports a type 1 gynandromorph with intersexuality of *Episinus nubilus* Yaginuma, 1960 which has a deformed and distended abdomen. In the text, the carapace is referred to as “uniform”, but the figures indicate a difference in size on either side of the specimen. Wright (1995) reported, vaguely in a single paragraph, a gynandromorph of *Bathyphyma trifrons* (O. Pickard-Cambridge, 1863). The specimen had an almost complete epigyne and a male right palp but details about the left palp are not stated, although he implies the carapace is male. It is thus possible this was a type 3 gynandromorph, but it is not possible to be certain.

Janssen (1987) reports a type 2 gynandromorph with intersexuality of *Peponocranium ludicrum* (O. Pickard-Cambridge, 1861), noting the carapace is slightly elevated in part and lacks the left sulci, thus being of intermediate morphology to normal exemplars of both sexes. Millidge (1991) reported a gynandromorph and intersexual specimen of *Meioneta proxima* Millidge, 1991 based on one of the paratype specimens. The specimen was almost entirely female except for one malformed male palp. However, it is not possible to classify which gynandromorph type it is as he does not specify which side presented the male palp.

Maekawa and Ikeda (1992) discuss the sexual behaviour of a type 2 gynandromorph of *Carrhotus xanthogramma* (Latreille, 1819). This specimen attempted to mate with a female using its right palp but displayed antagonistic behaviour towards males. However, when anesthetized the gynandromorph was placed again with a normal male which exhibited courtship behaviour towards the gynandromorph.

Wunderlich (1994) reported five new cases of sexual anomaly in spiders. Of these that of *Microneta viaria* (Blackwall, 1841) is a type 13 gynandromorph with intersexuality; *Centromerita concinna* (Thorell, 1875) is a probable type 9 gynandromorph; *O. fuscus* (sub *Oedothorax ?fuscus*) is a probable type 11 gynandromorph; *O. apicatus* is an intersex with characters not fitting perfectly with any of the 14 types of gynandromorph, and that of *M. herbigradus* is a type 8 gynandromorph. Interestingly, he also notes that the specimen of *O. apicatus* possesses a malformed metatarsus on the palp (!) and also notes he has seen more intersexual specimens not reported in the work. Vanuytven (1995) reported an intersexual specimen of *O. fuscus*, he notes the white stripe found on the dorsal abdomen in females is absent but that the epigyne is fully formed. Therefore, the gynandry is inferred here to likely be type 3.

Stratton (1995) reported a type 2 gynandromorph of *Schizocosa ocreata* (Hentz, 1844), also noting that based on her extensive experience rearing thousands of these spiders, this specimen was the only gynandromorph she encountered. Krumpalova (1999) reported a type 2 gynandromorph and intersex of *Phrurolithus festivus* (C.L. Koch, 1835) which was almost entirely male on the left side and female on the right. However, the epigyne is fully developed on both sides, meaning the specimen does not fit any of the categories of Roberts and Parker (1973) as noted by Krumpalova (1999) herself. This case mirrors the configuration found by Yaginuma and Arita (1967).

Gnelista (2005) reports two gynandromorphs from Ukraine, the first a type 12 of *Pocadicnemis pumila* (Blackwall, 1841), the second a type 14 gynandromorph of *Bathypantes gracilis* (Blackwall, 1841) with an incompletely developed and malformed male right palp. Simó *et al.* (2007) reported a type 1 gynandromorph of *Oxyopes salticus* Hentz, 1845. Ponomarev and Kovblyuk (2009) reported a type 3 gynandromorph of *Agroeca brunnea* (Blackwall, 1833), noting the right palp was that of an immature male whereas the left was that of an adult.

Rodrigues *et al.* (2012) report a type 2 gynandromorph of *Sphecozone personata* (Simon, 1894), this specimen is also presumably intersexual as the carapace did not show the modification found in normal males, as observed in two other cases (Denis, 1947; Janssen, 1987). Currie (2014) reported a type 13 gynandromorph of *Talavera aequipes* (O. Pickard-Cambridge, 1871). Breitling and Buckland (2015: 291) report a type 2 gynandromorph of *Archaeodictyna consecuta* (O. Pickard-Cambridge, 1872) and hypothesised that there may be a lateralisation in the sexual behaviour of spiders.

Baba *et al.* (2016) report a type 3 gynandromorph of *Allagelella opulenta* (L. Koch, 1878) with intersexuality, evident by the deformities of the epigyne. Laborda and Pérez-Miles (2017) reported a type 1 gynandromorph of *Pterinochilus murinus* Pocock, 1897 based on a captive raised specimen; after a post-maturation ecdysis the 'male' palp became malformed due to presumed non-intersexual causes (see below). Laborda and Pérez-Miles (2017) also cite the year of publication of Hackman (1952) as "1950–1951" (*sic*). Suzuki *et al.* (2019) report a type 2 gynandromorph of *Myrmarachne formicaria* (De Geer, 1778), which exhibited male sexual behaviour in captivity.

Sherwood (2020) reported a type 1 gynandromorph of *Theraphosa blondi* (Latreille, 1804) based on exuviae from a captive bred spider sent to her from a tarantula enthusiast, thus being the first ever work to discuss gynandromorphic morphology in spider exuviae. Those exuviae, originally intended to be deposited in the Natural History Museum, London, were instead eventually donated to the Manchester Museum where they are available for study (MMUE G7690.1). da Silva de Alvarenga *et al.* (2020) report an intersexual specimen of *Micrathena ruschii* (Mello-Leitão, 1945) which has all copulatory anatomy intermediate and severely deformed. Pewtress (2021) reported a type 2 gynandromorph of *Gonatium rubens* (Blackwall, 1833). Unfortunately, when the author DS contacted Pewtress to see if it was possible to deposit the specimen in a museum, she was informed that it had been discarded (!) following publication. Fortunately, the photographs in the original article leave no doubt as to the type of gynandromorph the specimen was and show no external (!) morphological signs of intersexuality.

Huber (2022) reported an intersexual specimen of *Crossopriza lyoni* (Blackwall, 1867). This specimen possessed a right palp of an immature male but other characters on the right-hand side were mostly female, except for the absence of epigynal structures on the right side of the epigynal plate. All structures on the left were female. Thus, this specimen does not perfectly match any of the types of gynandromorph of Roberts and Parker (1973) but was only the second report of sexual anomaly in pholcids, curiously being conspecific with the first gynandromorph spider reported (Blackwall, 1867).

Nadolny *et al.* (2022) report a type 1 gynandromorph of *Pardosa lapponica* (Thorell, 1872) which has a deformity to the male (left) palp; they also report individual cases of intersexes with male preponderance in four other lycosid species: *Arctosa tbilisiensis* Mcheidze, 1946, *P. lapponica*, *Pardosa proxima* (C. L. Koch, 1847), and *Piratula latitans* (Blackwall, 1841). Šestáková *et al.* (2022) reported a type 1 gynandromorph of *Haplodrassus bohemicus* Miller and Buchar, 1977.

Gallon (2022) reported two sexually anomalous spiders as gynandromorphs, the first was a preserved specimen of *Troxochrus scabriculus* (Westring, 1851) which is a type 13 gynandromorph with intersexuality. This specimen has one normal male palp and corresponding normally developed carapace with cephalic modification and setae present, the other upper quadrant however has a 'female' carapace and a weakly 'male' palp; the abdomen has a complete epigyne, but it is malformed on one side, thus it is clear there is intersexuality throughout the specimen, however the normal male palp also confirms the presence of gynandry. The second specimen reported by Gallon (2022) is a probable type 2 gynandromorph of the thomisid *Xysticus cristatus* (Clerck, 1757) found by a colleague at World Museum, Liverpool, but since the specimen was not preserved (R. C. Gallon pers. obs.), it is not possible to observe the genitalia to see if they were perfectly formed. Kunsete *et al.* (2025) report a type 1 gynandromorph with intersexuality of *Damarchus inazuma* Kunsete and Warrit, 2025 including photographs of the live habitus. Seropian (2025) reported an intersex of *Trochosa cachetiensis* Mcheidze, 1997.

DISCUSSION

Are *Mermis* spp. a source for gynandry and intersexuality in spiders?

Holm (1941) associated the four cases of lycosid intersexuality with infection from nematodes of the genus *Mermis* Dujardin, 1842 (Mermithida: Mermithidae). This idea was repeated by others such as Mackie (1969), but whilst undoubtedly *Mermis* sp. infestation can modify epigynes and cause intersexuality, we saw no evidence that they can cause *gynandry* and this has not been proven in any work. While not a complete synopsis of the existing literature, we present below some in-depth discussion on mermithid parasitism and its relevance to non-gynandromorphic and/or non-intersexual anomalies of spider genitalia.

It has been well established that parasitism by mermithid nematodes alters both primary and secondary sexual characteristics in spiders (e.g. Leech, 1966), often in addition to anomaly of non-sexual structures and, obviously, a distended or asymmetrical abdomen (e.g. Poinar, 1985).

Whilst spiders are the best-known arachnid group to be affected by these parasites, they are present in other groups such as Opiliones (see Poinar and Thomas, 1985) and Pseudoscorpiones (e.g. Harvey, 1982; Poinar and Ćurčić, 1992). Kostro-Ambroziak *et al.* (2024) recently showed the proportions, size, and symmetry of female genitalia in the lycosids *Alopecosa pulverulenta* (Clerck, 1757) and *Pardosa paludicola* (Clerck, 1757) were affected by mermithid parasitism. As noted by Poinar (1985), some workers confuse other types of parasites (“worms”) that are not true nematodes as being nematodes, something that continued later (e.g. Downie, 2006).

The interesting case of *Leptyphantès beckeri* Wunderlich, 1973 is perhaps the best known case of mermithid parasitism. Wunderlich (1973) described a new species based on a single specimen collected in Germany. A second specimen was reported by Crocker and Daws (1996), but, as noted by Nellist (1996), they discussed the possibility that both specimens were simply abnormal specimens of an existing species whose epigynes have been modified by some sort of abnormal process since both specimens were found to have mermithids in the abdomen. Harvey *et al.* (2002) also concurred that the species was likely not valid. Of note, Wunderlich (2008) agreed it was likely a junior synonym of one of two species sympatric at the type locality. Heimer (1978) recorded two females he tentatively placed as *L. beckeri* (overlooked by Nellist, 1996; Harvey *et al.*, 2002; Breitling *et al.*, 2015) but noted differences in the vulva. However, no mention of mermithid or other parasites is made; it is unclear if this is because they were not present or whether they were overlooked.

However, not all cases of mermithid parasitism result in abnormal development of the epigyne (e.g. Parker and Roberts, 1974; Allard and Robertson, 2003). Some other cases (e.g. Iida and Hasegawa, 2003; Košulić and Mašová, 2019) make no mention of whether or not the spiders had abnormal genitalia. Penney and Bennett (2006) reported parasitism of a juvenile linyphiid and thus genitalia could not be studied. Meyer (2014) discusses parasitism of a subadult female lycosid of the species, which would have had a pre-epigyne as opposed to an epigyne, but makes no comment on whether it appeared in any way ‘abnormal’ which would indeed be difficult to quantify. It is pertinent to note that, so far, no workers have reported on whether nematode parasitism affects the morphology of pre-epigynes [the normal morphology of which is itself chronically understudied], although presumably it does.

Equally, parasites affecting the form of the epigyne are by no means restricted to nematodes. Noordam (2021) demonstrated that lycosids of the species *Pardosa pullata* (Clerck, 1757) parasitised by the fly *Ogcodes* cf. *pallipes* Latreille in Olivier, 1812 (Acroceridae) had wider and shorter medium septa on the respective epigynes, showing that these parasites affect the normal development of the epigyne in adult female spiders. He theorised this prevented mating which would have adversely affected the parasites due to inevitable changes in the biomass of the spider.

The impact of sexual anomaly on the mating and reproductive behaviour of spiders

Only four studies to date have investigated the courtship and sexual behaviour of gynandromorph spiders. Gack and von Helversen (1976) recorded courtship and mating of their gynandromorphic intersex specimen with a non-anomalous female. Maekawa and Ikeda (1992) found similar courtship behaviour but also showed that the gynandromorph exhibited antagonistic behaviour when placed with a non-anomalous male. Suzuki *et al.* (2019) found identical results to Maekawa and Ikeda (1992) regarding the behaviours exhibited by their gynandromorph. In two out of three studies, the anomalous specimen was a salticid and showed bilateral gynandry and exhibited the behaviours expected of a male, in the exception (Gack and von Helversen, 1976) the specimen exhibited male behaviour despite the palp of the right (male) side being of intersexual composition. This suggests that even gynandromorphs with intersexuality likely have a dominant binary sex in the respective quarter(s) where both sexes are mixed, presumably to varying degrees. Genetic and further behavioural studies could shine light on how the interactions of classic gynandry and the complexity of intersexuality interact in the context of spider behaviour. For instance, given the only male palp of the lycosid in Gack and von Helversen (1978) was unable to perform its normal function, it is curious it acted in the same way a non-anomalous male would to a female. However, we hypothesise that females can likely detect that the ‘males’ are not normal specimens, hence their uniform rejection of sexually anomalous mates (Suzuki *et al.*, 2019). In contrast to the three aforementioned studies Laborda and Pérez-Miles (2017) noted that their gynandromorph with intersexuality of the theraphosid *P. murinus* did not exhibit any courtship behaviour, with normal females either ignoring it or, in one case, attacking the sexually anomalous specimen.

Post-maturation ecdysis and prior ontogenetic development in subadult ecdysis – two cases, endless new questions

Laborda and Pérez-Miles (2017) and Sherwood (2020) are the only authors to have reported post-maturation ecdysis in a sexually anomalous spider. Sherwood (2020) is the only author to have recorded the morphology of a sexually anomalous spider through its exuviae, in this case both a subadult exuvia and an adult exuvia. These unique cases are aided by the fact theraphosid spiders are long-lived, typically large, and their exuviae can (with care) be manipulated in such a way as to make observations of the internal genitalia. This case raises several tantalising questions: (1) the *T. blondi* specimen reported by Sherwood (2020) had part of a (abnormal) adult palpal bulb emerging through the cymbium prior to maturity: is this simply a case where the developing bulb accidentally broke through the

exoskeleton due to the bizarre circumstances of the specimen's morphology or was it some endocrinological anomaly which essentially caused an abnormal case of something to the opposite of abnormal neoteny? (2) for the same specimen, Sherwood (2020) considered it a type 1 gynandromorph and that the malformation of the genitalia was not due to intersexuality but rather from impacts (damage) of the ecdysial process(es), but what if there was also intersexuality detectable only with genetic approaches (not possible at the time, nor for this particular case in the present due to the fragility of the exuviae)?, and (3) Laborda and Pérez-Miles (2017) state that it must be a female-preponderance which drove post-maturation ecdysis (via endocrinological processes) in their specimen, but given that unambiguous male theraphosids without signs of sexual anomaly can also undergo post-maturation ecdysis (Sherwood, 2020), could it instead be the case that post-maturation ecdysis is triggered by another process entirely independent from anything tied to biologically female hormones? The answers to these, and other questions they spawn, are totally unknown to us, especially since phenomena such as post-maturation ecdysis in araneomorphs is (at least as far as we are aware) totally unknown and unreported, if it exists, and because any future genetic methods will not be able to assist in cases of specimens which are brittle, damaged, or perhaps too old for sequencing (noting also that many historical specimens are simply lost anyway and cannot even be re-evaluated morphologically for this reason). We find it unlikely that this research avenue can be realistically pursued with any other spider group except Theraphosidae, so it is hoped future workers may find new cases which can be more comprehensively documented.

The plot thickens – do abnormal neoteny and/or genital asymmetry contraindicate or accompany some cases of gynandry and/or intersexuality?

It must be noted that humans innately like to fit things into neat boxes and anomalies, be it of non-sexual or sexual teratology, with or without gynandry and/or intersexuality, this framework already presents several presentations that can be theoretically encountered: (A) non-genital teratology of a spider without sexual anomaly, (B) genital teratology of a spider without sexual anomaly, (C) non-genital teratology present in a spider with gynandry (never observed before), (D) genital teratology, not caused by intersexuality, present in a spider with gynandry, (E) non-genital teratology present in a spider with gynandry and intersexuality (never observed before), and (F) genital teratology of a spider with gynandry and intersexuality. Possibilities A, B and F have been reported, and presentations C, D, and E are theoretically possible, although would be hard to prove without genetic studies, unless the morphological anomaly was in an obvious non-sexual structure such as the eye(s).

Unfortunately, this is not the end of the complexity. Two previous works and one further new record from our dataset introduce an interesting third ‘comorbidity’ and make the above complexity more complex and expand the theoretical possibilities. Namely, the presence of evident morphological neoteny (e.g. Yaginuma, 1966; Baert, 1975), the retention of ontogenetic conditions of certain anatomical features of a specimen. These could theoretically occur or not occur with any of the other character states for sexual and non-sexual anomalies discussed above. As noted by Martin (2013), epigyne malformations may be a result of various origins such as teratology, injury, environmental (chemical) pollution, parasitism, hybridisation, or ‘malformed’ epigynes may simply be normal epigynes of undescribed species. Genital asymmetry is another interesting biological phenomenon, which in of itself is different from teratology and the processes of sexual anomaly described herein, although is sometimes mistaken for this (see discussion in Rivera-Quiroz *et al.*, 2020). Instead, genital asymmetry is a non-abnormal biological process, where normally developed genitalia of male spider palps and female genitalia (usually copulatory ducts and related structures) are simply not symmetrical (e.g. Huber *et al.*, 2007).

Yaginuma (1966) reports an interesting specimen of the agelenid *Coeolotes antri* (Komatsu, 1961) from Japan, he notes that it is undoubtedly a subadult male in regards to body length and proportions, and colouration, but that both palps are abnormally, and adult, male. The left palp is normal except for the bulb, which is malformed. This is resemblant of the condition found in some palps of non-sexually anomalous male spiders (Sherwood *et al.*, 2025). The right palp is much shorter and anomalous in all anatomical characters from the patella downwards. This condition of the anatomy also corresponds with a different grouping proposed for non-sexually anomalous spiders (Sherwood *et al.*, 2025). Yaginuma (1966: 23) postulates this “may be a kind of abnormal neoteny” but cautiously considers it formally just male palpal teratology. Without genetic studies, it is hard to ascertain rates and degrees of intersexuality in non-classical presentations of this biological phenomenon in spiders. However, the “what if” scenario is a slippery slope, and being overly cautious in considering intersexuality *possibly* present in all cases of profound abnormal male palp development with or without neoteny will almost certainly overestimate its true occurrence. Therefore, we propose that in cases of teratology without clear evidence of presence of tissue/quadrant(s) entirely or majorly comprised of the opposing sex, that these cases not be ascribed as gynandromorphs and/or intersexes until further genetic work clarifies our knowledge of their intersectionality, allowing us to improve upon the current classification system and make it more holistic with the reality of biology.

Okumura (2020) reports several anomalous agelenids of the genus *Coelotes* Blackwall, 1841, and mentions a case of genital asymmetry in the prior literature (Okumura, 2019). The latter case is not relevant here, nor are two of the cases presented in Okumura (2020), but the third and final case he presents is. Okumura (2020) reports a specimen of *Coelotes hataensis* Nishikawa 2009 from Japan where the specimen is either subadult or perhaps even more juvenile, and presents with a swollen (penultimate) left palp and an essentially unmodified right palp. There is no evidence of female development in the ventral abdomen, but Okumura (2020) recognises this may be due to the immaturity of the specimen. This case adds another layer of theoretical baggage. Without genetic studies, it could even be postulated that genital asymmetry may be present, whether directly resultant from or not, with sexual anomalies, which themselves may be comprised of solely gynandry, intersexuality, or a combination of both, themselves potentially present with further anomalies caused by non-sexual teratological processes. The matrix is both real and not real, the slippery slope must again be resisted.

The third case is new, and we hypothesise involves no gynandry and intersexuality, based on external anatomy, but furnishes discussion in the preceding two paragraphs regardless. An unusual pre-subadult (juvenile) specimen of the araneid *Neoscona adianta* (Walckenaer, 1802) (full data: (ISEA) Russia, Iskitim District, ca. 2 km SEE from Mayak Vill., c. 54°41'N, 83°10'E, 17.06.2025, leg. Novosibirsk State University students), was collected following an almost immediate prior ecdysis (Fig. 14). The right palp has the appearance of a normal palp of a subadult male, but the left palp is underdeveloped and minimally incrassate. No other differences between left and right half of the body are visible. Whilst it is tempting to consider the left palp may be female, it is more likely that it can be attributed to slower development after injury or the presence of genital asymmetry. The epigastric area does not show any evidence of female development, which probably rules out gynandry and/or intersexuality. Even if sexual anomaly is absent, either of the other above conditions could coexist with neoteny in theory. Unless genetic techniques can be utilised in the future, this case will remain enigmatic.

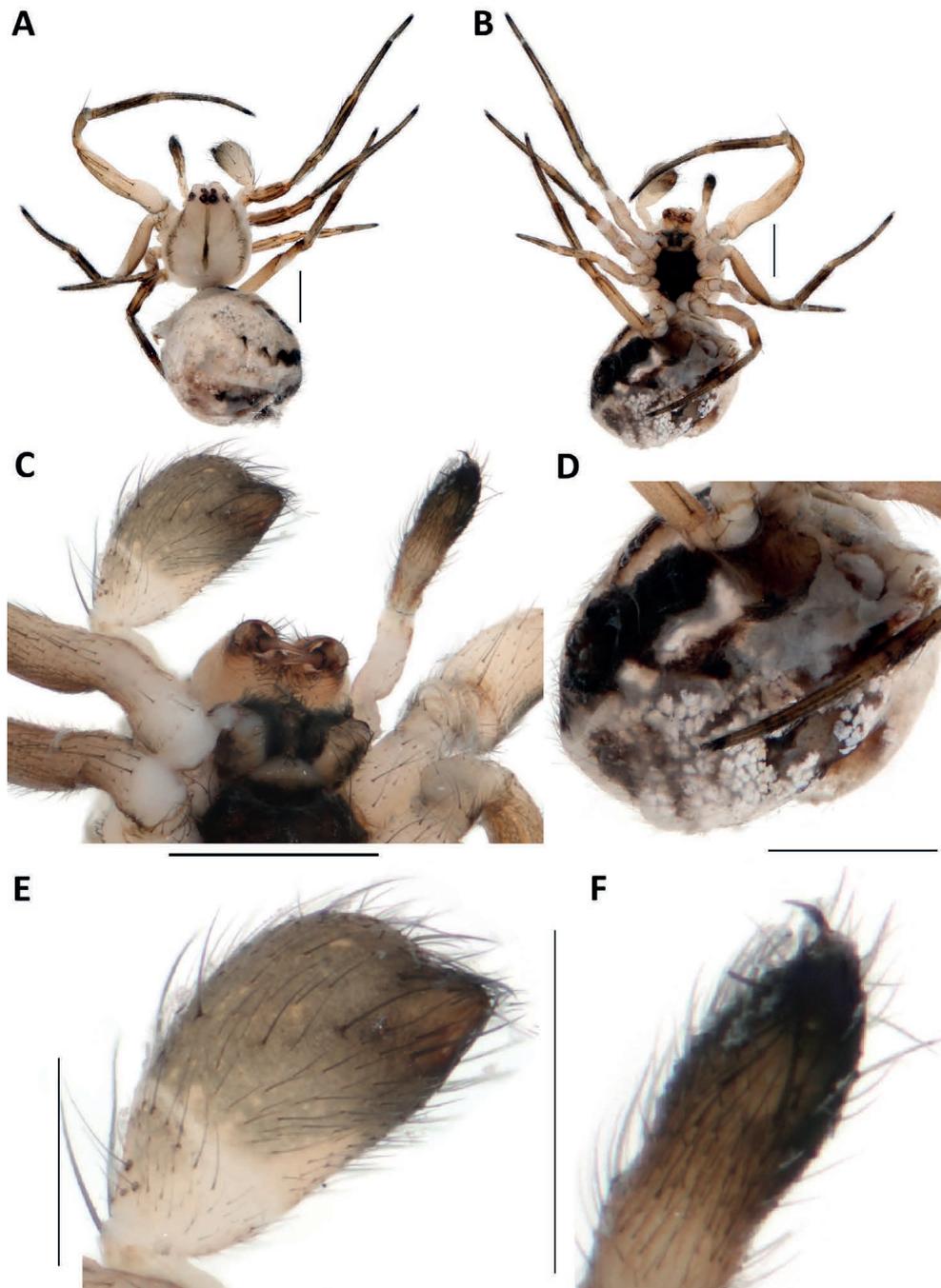


Figure 14. *Neoscona adianta* (Walckenaer, 1802) juvenile specimen with unusual characters, not easily morphologically ascribed to abnormal sexuality and possibly representing abnormal neoteny regardless. A) dorsal view. B) ventral view. C) close-up of palps, ventral view. D) close-up of abdomen, ventral view. E) right palp, ventral view. F) left palp, ventral view. Scale bars = 1 mm.

Figura 14. Ejemplar juvenil de *Neoscona adianta* (Walckenaer, 1802) con características inusuales, difícilmente atribuibles morfológicamente a una sexualidad anormal y posiblemente representando neotenia anormal. A) Vista dorsal. B) Vista ventral. C) Primer plano de los palpos, vista ventral. D) Primer plano del abdomen, vista ventral. E) Palpo derecho, vista ventral. F) Palpo izquierdo, vista ventral. Barras de escala = 1 mm.

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REFERENCES

- Allard, C., Robertson, M. W. (2003). Nematode and dipteran endoparasites of the wolf spider *Pardosa milvina* (Araneae, Lycosidae). *Journal of Arachnology*, 31, 139–141.
- Alvarenga, A. da S. de, Magalhaes, I. L. F., Fonseca, R. N. de, Pérez-González, A. (2020). Rectifying the identities of the males of two *Micrathena* species (Araneae: Araneidae), with report of the first case of intersexuality in the genus. *Zootaxa*, 4808(1), 151–164.
- Anderson, J. F. (1961). A gynandromorphic crab spider. *Bulletin of the Brooklyn Entomological Society*, 56, 100–102.
- Armas, L. F. de. (1990). Dos casos de anomalía sexual en escorpiones cubanos (Scorpiones: Buthidae). *Ciencias Biológicas*, 21–22, 173–175.
- Assmuth, W. (1983). Ein Fall von Gynandromorphismus bei *Oedothorax apicatus* (Blackwall) (Arachnida, Araneae). *Hessische Faunistische Briefe*, 3, 9–14.
- Baba, Y. G., Suguro, T., Naya, N., Yamauchi, T. (2016). A gynandromorph of the funnel-web spider *Allagelena opulenta* (Araneae: Agelenidae). *Acta Arachnologica*, 65(1), 11–13.
- Baert, L. (1975). Four gynandromorph and intersexual Linyphiid spiders for Belgium. *Biologisch Jaarboek Dodonaea*, 43, 58–62.
- Baert, L. (1976). Nieuwe intersexuele spin voor België: *Gonatium rubellum* (Blackw.). *Bulletin et Annales de la Société royale belge d'Entomologie*, 112, 203–207.
- Balogh, I. J. (1936). Über eine neue gynandromorphe Spinne, *Philaeus chrysoptus* (Poda). *Folia zoologica et hydrobiologica*, 9(1), 67–68.
- Brændegaard, J. (1925). A case of lateral hermaphroditism in a spider, *Lycosa pullata* Cl. . *Entomologiske Meddelelser*, 16, 13.
- Bednarz, S., Czajka, M. (1975). A case of gynandromorphism in *Oedothorax agrestis* (Blackwall, 1853) (Micryphantidae). *Zoologica Poloniae*, 24(3/4), 385–391.
- Bertkau, P. (1888). Zwitter von *Gastropacha Quercus* vor und berichtete über die Untersuchung von dessen Geschlechtsorganen. *Verhandlungen des naturhistorischen Vereines der preussischen Rheinlande*, 45, 68.
- Bertkau, P. (1889a). Untersuchungen der Geschlechtsorgane eines Arthropodenzwitters. *Verhandlungen des naturhistorischen Vereines der preussischen Rheinlande*, 48, 49–50.
- Bertkau, P. (1889b). Beschreibung eines Zwitters von *Gastropacha Quercus* nebst allgemeinen Bemerkungen und einem Verzeichnis der beschriebenen Arthropodenzwitters. *Archiv für Naturgeschichte*, 55(1), 7–116.
- Bertkau, P. (1891). Beschreibung eines Arthropodenzwitters. *Archiv für Naturgeschichte*, 57, 229–238.
- Blackwall, J. (1867). Description of several species of East Indian spiders apparently new or little known to arachnologists. *Annals and Magazine of Natural History*, 19(3), 387–394.

- Blaszak, C. (1968). Badania nad interseksami u kosarzy (Opiliones). *Polskie Pismo Entomologiczne*, 38(1), 9–27.
- Breitling, R., Lemke, M., Bauer, T., Hohner, M., Grabolle, A., Blick, T. (2015). Phantom spiders: notes on dubious spider species from Europe. *Arachnologische Mitteilungen*, 50, 65–80.
- Bonnet, P. (1934). La Gynandromorphisme chez les Araignées. *Bulletin Biologique de la France et de la Belgique*, 68(2), 167–187.
- Budrienė, A., Budrys, E., Orlovskytė, S. (2021). A bilateral gynandromorph of *Discoelius dufourii* (Hymenoptera, Vespidae, Zethinae): morphology and mating behaviour. *Journal of Hymenoptera Research*, 81, 23–41.
- Cavignato, T. C., Duarte, M. (2009). A bilateral gynandromorph of *Periga falcata* (Walker 1855) (Lepidoptera: Saturniidae: Hemileucinae). *Proceedings of the Entomological Society of Washington*, 111(1), 276–279.
- Chemini, C. (1984). Andromorphy in a female of *Nemastoma dentigerum* Canestrini (Opiliones) from northern Italy. *Newsletter of the British Arachnological Society*, 40, 56.
- Cokendolpher, J. C., Enríquez, T. (2004). A new species and records of *Pseudocellus* (Arachnida: Ricinulei: Ricinoididae) from caves in Yucatán, Mexico and Belize. *Texas Memorial Museum, Speleological Monographs*, 6, 95–99.
- Cooper, A. E. (1975). Further examples of gynandry and intersexuality in spiders. *Newsletter of the British Arachnological Society*, 15(6), 5–6.
- Deichmann, E. (1920). Note sur un cas de Hermaphroditisme lateral chez une Araignée. *Entomologiske Meddelelser*, 13, 181–182.
- Delle Cave, L. (1979). On a remarkable *Galeodes barbarus* (Lucas) from Ethiopia (Arachnida, Solifugae). *Bulletin of the British Arachnological Society*, 4(9), 396–397.
- Denis, J. (1947). Une curieuse anomalie sexuelle chez une araignée. *Bulletin de la Société Entomologique de France*, 52(3), 41–43.
- Denis, J. (1949). Un nouveau cas d'anomalie sexuelle chez une araignée. *Bulletin mensuel de la Société linnéenne de Lyon*, 18(6), 126–127.
- Downie, I. (2006). Parasitic hairworms and spiders. *Newsletter of the British Arachnological Society*, 105, 8.
- Emerton, J. H. (1907). A female spider with one male palpus. *Psyche*, 14, 40.
- Exline, H. (1938). Gynandromorph spiders. *Journal of Morphology*, 63(3), 441–475.
- Falconer, W. (1910). Abnormality in spiders. *The Naturalist*, 199–203, 229–232.
- Falconer, W. (1917). Abnormal spiders. *The Naturalist*, 232–233.
- Francke, O. F. (1978). Systematic revision of diplocentrid scorpions (Diplocentridae) from Circum Caribbean Lands. *Special Publications of The Museum of Texas Tech University*, 14, 1–92.
- Fusco, G., Minelli, A. (2023). Descriptive versus causal morphology: gynandromorphism and intersexuality. *Theory in Biosciences*, 142, 1–11.

- Gack, C., von Helversen, O. (1976). Zum Verhalten einer gynandromorphen Wolfspinne (Arachnida: Araneae: Lycosidae). *Entomologica Germanica*, 3, 109–118.
- Galiano, M. E. (1985). Un caso de ginandria combinado con intersexualidad en *Phiale gratiosa* Cl. L. Koch, 1846, (Araneae, Salticidae). *Revista de la Sociedad Entomológica Argentina*, 44(3/4), 399–402.
- Gallon, R. (2022). Spiders of mobile sand dunes on the Sefton Coast in 2021, with particular reference to *Rhysodromus fallax* and *Baryphyma maritimum*. World Museum Liverpool, 203 pp.
- Gertsch, W. J. (1934). Some American spiders of the family Hahniidae. *American Museum Novitates*, (712), 1–32.
- Gnelista, V. A. (2005). About abnormalities in the development of genitalia in Linyphiidae spiders. *Vestnik zoologii*, 39(5), 75–77. [In Russian]
- Hackman, W. (1952). A gynandromorph of the spider *Troxochrus scabriculus* Westr. *Memoranda Societatis pro Fauna et Flora Fennica*, 27, 67–69.
- Hadjissaranos, C. (1951). Sur une case d'araignée gynandromorphe. *Akademia Antheon Praktica*, 24, 296–303.
- Harvey, M. S. (1982). A parasitic nematode (Mermithidae) from the pseudoscorpion “*Sternophorus*” *hirsti* Chamberlin (Sternophoridae). *Journal of Arachnology*, 10(2), 192.
- Harvey, P. R., Nellist, D. R., Telfer, M. G. (2002). Provisional atlas of British spiders (Arachnida, Araneae), Volumes 1 and 2. Biological Records Centre.
- Heimer, S. (1978). Über bemerkenswerte Spinnenfunde im Kreis Eisenach (Arachnida, Araneae). Beiträge zur Spinnenfauna der DDR, III. *Faunistische Abhandlungen, Staatliches Museum für Tierkunde, Dresden*, 7, 19–22.
- Holm, Å. (1941). Über Gynandromorphismus und Intersexualität bei den Spinnen. *Zoologiska Bidrag från Uppsala*, 20, 397–415.
- Huber, B. A., Sinclair, B. J., Schmitt, M. (2007). The evolution of asymmetric genitalia in spiders and insects. *Biological Reviews of the Cambridge Philosophical Society*, 82(4), 647–698.
- Huber, B. A. (2022). Revisions of *Holocnemus* and *Crossopriza*: the spotted-leg clade of Smeringopinae (Araneae, Pholcidae). *European Journal of Taxonomy*, 795, 1–241.
- Hull, J. E. (1911). New and rare British spiders. *Transactions of the Natural History Society of Northumberland (N.S.)*, 4(1), 42–58.
- Hull, J. E. (1918). Gynandry in Arachnida. *Journal of Genetics*, 7(8), 171–181.
- Iida, H., Hasegawa, H. (2003). First record of a mermithid nematode emerging from the wolf spider *Pardosa pseudoannulata* (Araneae: Lycosidae). *Acta Arachnologica*, 52(2), 77–78.
- Jackson, A. R. (1907a). A contribution to the spider fauna of the county of Glamorgan. *Report and Transactions of the Cardiff Naturalists' Society*, 39, 63–77.

- Jackson, A. R. (1907b). The spiders of the Tyne valley. *Transactions of the Natural History Society of Northumberland, Durham, and Newcastle-upon-Tyne (N.S.)*, 1(3), 337–405.
- Jackson, A. R. (1909). On some rare arachnids obtained during 1908. *Transactions of the Natural History Society of Northumberland, Durham, and Newcastle-upon-Tyne (N.S.)*, 3(2), 418–439, plates 10.
- Jackson, A. R. (1924). On new and rare British Spiders. *Proceedings of the Dorset Natural History and Antiquarian Field Club*, 45, 101–120.
- Janssen, M. (1987). Een geval van gynandromorfie bij spinnen: *Peponocranium ludicrum* (O.P.-Cambridge) (Arachnida, Araneae, Erigonidae). *Natuurhistorisch Maandblad*, 76(6/7), 118–119.
- Kaston, B.J. (1961). Spider Gynandromorphs and Intersexes. *Journal of the New York Entomological Society*, 69, 177–190.
- Knulle, W. (1954). Gynandromorphie bei *Erigone vagans spinosa* Cambr. (Micryphantidae: Araneae). *Zoologischer Anzeiger*, 152, 219–227.
- Kolosváry, G. (1935). Die Spinnenbiosphäre des ungarländischen Pannonbeckens, III. *Acta Literaria Scientia Universalis Hungarica*, 5 (Acta biol., 3), 134–144.
- Kostro-Ambroziak, A., Jabłońska, U., Świsłocka, M., Wiśniewski, K., Kupyjanowicz, J. (2024). New mermithid nematode-spider associations, along with a molecular phylogeny of mermithids hosted in spiders. *European Zoological Journal*, 91(1), 590–600.
- Krumpalova, Z. (1999). A case of gynandromorph spider (Araneae, Licozanidae) in Slovakia. *Revue Arachnologique*, 13(4), 61–67.
- Kulczyński, W. (1885). Potworek Obojnakowy Pajaka *Erigone fusca* Blackw. *Rozprawy i Sprawozdania z Posiedzeń Wydziału Matematyczno-Przyrodniczego Akademii Umiejętności*, 14, 169–180.
- Kumada, K. (1989). A gynandromorph of the theridiid spider, *Episinus nubilus* Yaginuma, from Japan. In Y. Nishikawa and H. Ono (Eds.), *Arachnological Papers Presented to Takeo Yaginuma on the Occasion of his Retirement* (pp. 39–41). Osaka: Arachnologists' Group Osaka.
- Kunsete, C., Thanosing, C., Sivayyapram, V., Traiyasut, P., Warrit, N. (2025). New insights into *Damarchus*: a new species and gynandromorph description from Thailand (Araneae: Bemmeridae). *Zootaxa* 5696(3): 409–424.
- Laborda, A., Pérez-Miles, F. (2017). The first case of gynandry in Mygalomorphae: *Pterinochilus murinus*, morphology and comments on sexual behavior. *Journal of Arachnology*, 45, 235–237.
- Leech, R.E. (1966). The spiders (Araneida) of Hazen Camp 81°49'N, 71°18'W. *Quaestiones entomologicae*, 2(2), 153–208.
- Machado, A. de B. (1951). Ochyroceratidae (Araneae) de l'Angola. *Publicações Culturais da Companhia de Diamantes de Angola*, 8, 1–88.
- Mackie, D.W. (1969). A gynandromorph lycosid Spider. *Bulletin of the British Arachnological Society*, 1(3), 40–41.

- Maekawa, T., Ikeda, H. (1992). Sexual behaviour of a gynandromorphic spider of *Carrhotus xanthogramma* (Araneae: Salticidae). *Acta Arachnologica*, 41, 103–108.
- Martens, A., Wildermuth, H. (2021). Gynandromorphism and intersexuality in Odonata: a review. *Odonatologica*, 50(1–2), 65–80.
- Martin, D. (2013). Aberrante Epigynenbildungen bei der Wolfspinne *Pardosa palustris* (Araneae, Lycosidae). *Arachnologische Mitteilungen*, 46, 1–5.
- Marusik, Y.M., Koponen, S. (2001). Spiders of the family Zodariidae from Mongolia (Arachnida: Araneae). *Reichenbachia*, 34, 39–48.
- Matthiesen, F.A. (1968). On the male reproductive organs in some Brazilian scorpions. *Revista Brasileira de Pesquisas Médicas e Biológicas*, 1(5–6), 273–274.
- Mattoni, C.I. (2005). Tergal and sexual anomalies in bothriurid scorpions (Scorpiones, Bothriuridae). *Journal of Arachnology*, 33, 622–628.
- Maurý, E.A. (1983). Singular anomalía sexual en un ejemplar de *Brachistotermus pentheri* Mello-Leitão 1931 (Scorpiones, Bothriuridae). *Revista de la Sociedad Entomológica Argentina*, 42(1–4), 155–156.
- Mcheidze, T.S. (1967). A case of gynandromorphism of *Agelena labyrinthica* (CL.) (Agelenidae). *Zoologicheskii Zhurnal*, 46(2), 294–296. (in Russian).
- Meyer, M. (2014). New record of a parasitoid worm (Mermithidae, Nematoda) in a spider of the genus *Trochosa* (Lycosidae). *Arachnologische Mitteilungen*, 48, 13–15.
- Millidge, A.F. (1991). Further linyphiid spiders (Araneae) from South America. *Bulletin of the American Museum of Natural History*, 205, 1–199.
- Nishikawa, Y. (1971). A gynandromorph spider, *Oxytata striatipes* L. Koch from Japan. *Acta Arachnologica*, 23(2), 26–28.
- Noordam, A. (2021). European Acroceridae – new host records, modified epigynes and the British isolation. *Newsletter of the British Arachnological Society*, 150, 10–14.
- Müller, H.G. (1984). Gynandromorphismus und Intersexualität bei Spinnen und Insekten, mit einer Beschreibung von Genitalanomalien bei *Micrargus herbigradus* und *Erigone (atra?)* (Arachnida: Araneida: Linyphiidae). *Entomologische Zeitschrift*, 94(14), 199–208.
- Okumura, K. (2019). Unexpected pitfalls in spider identification. *Kishidaia*, 115, 95–96.
- Okumura, K. (2020). Examples of deformed specimens of coelotine spiders. *Kishidaia*, 117, 1–3.
- Palmgren, P. (1979). On the frequency of gynandromorphic spiders. *Annales Zoologici Fennici*, 16, 183–185.
- Parker, J.R., Roberts, M.J. (1974). Internal and external parasites of the spider *Pardosa hortensis* (Thorell) (Araneae: Lycosidae). *Bulletin of the British Arachnological Society*, 3(3), 82–84.
- Penney, D., Bennett, S.P. (2006). First unequivocal mermithid-linyphid (Araneae) parasite-host association. *Journal of Arachnology*, 34, 273–278.

- Pewtress, J. (2021). A gynandromorph *Gonatium rubens*. *Newsletter of the British Arachnological Society*, 150, 14–15.
- Pickard-Cambridge, O. (1903). On new and rare British Arachnida. *Proceedings of the Dorset Natural History and Antiquarian Field Club*, 23(1902), 16–40, pl. 1.
- Pickard-Cambridge, O. (1913). On new and rare British arachnids noted and observed in 1912. *Proceedings of the Dorset Natural History and Antiquarian Field Club*, 34, 107–136.
- Poinar, G. O. Jr. (1985). Mermithid (Nematoda) parasites of spiders and harvestmen. *Journal of Arachnology*, 13, 121–128.
- Poinar, G. O. Jr., Čurčić, B. P. M. (1992). Parasitism of pseudoscorpions (Arachnida) by Mermithidae (Nematoda). *Journal of Arachnology*, 20, 64–66.
- Poinar, G. O. Jr., Thomas, G. M. (1985). Laboratory infection of spiders and harvestmen (Arachnida: Araneae and Opiliones) with *Neoplectana* and *Heterorhabditis* nematodes (Rhabditoidea). *Journal of Arachnology*, 13, 297–302.
- Ponomarev, A. V., Kovblyuk, M. M. (2009). Gynandromorph specimen of spider *Agroeca brunnea* (Blackwall, 1833) (Aranei: Liocranidae) in Rostov region (Russia). *Vestnik Yuzhnogo Nauchnogo Tsentra RAN*, 5(4), 91–93.
- Rabaud, E., Millot, J. (1933). Anomalies sexuelles chez les Araignées. *Archives de Zoologie Expérimentale et Générale*, 75, 267–281.
- Reddell, J. R., Cokendolpher, J. C. (1995). Catalogue, bibliography, and generic revision of the order Schizomida (Arachnida). *Texas Memorial Museum, Speleological Monographs*, 4, 1–170.
- Rivera-Quiroz, F. A., Schilthuizen, M., Petcharad, B., Miller, J. A. (2020). Imperfect and askew: A review of asymmetric genitalia in araneomorph spiders (Araneae: Araneomorphae). *PLOS ONE*, 15(6), e0220354.
- Roberts, M. J., Parker, J. R. (1973). Gynandry and intersexuality in spiders. *Bulletin of the British Arachnological Society*, 2(9), 177–183.
- Roberts, M. J. (1976). *Centromerus parkeri* Cooke; an intersex of *Centromerus prudens* (O.P.-Cambridge). *Bulletin of the British Arachnological Society*, 3(7), 191–193.
- Seropian, A. (2025). Stuck in between: first case of transverse intersexuality in *Trochosa cachetiensis* Mcheidze, 1997 (Araneae, Lycosidae) from Georgia. *Caucasiana* 4: 153–161.
- Šestáková, A., Černecká, L., Naumova, M., Purgat, P., Szita, É., Gajdoš, P. (2022). A review of two very rare ground spiders from sandy habitats, new for Slovakia (Araneae: Gnaphosidae). *Arachnologische Mitteilungen*, 64, 14–24.
- Sherwood, D. (2020). On gynandromorphism evident in the exuviae of a theraphosid spider *Theraphosa blondi* (Latreille, 1804) (Araneae: Theraphosidae). *Arachnology*, 18(5), 473–476.

- Sherwood, D., Gonçalves, R. A., Peñaherrera-R., P., Jiménez, M.-L., Chamé-Vázquez, D., Sudhin, P. P., Sen, S., Azarkina, G. N., Caleb, J. T. D., Brescovit, A. D., Lucas, S. M. (2025). Palpal teratology in adult male spiders (Arachnida: Araneae): new cases and synopsis of the historical literature. *Invertebrate Zoology*, 22(3), 505–518.
- Simó, M., Lamborda, A., Falero, N. (2006). A case of gynandry in *Oxyopes salticus* Hentz, 1845 (Oxyopidae). *Revista Ibérica de Aracnología*, 14, 179–181.
- de Souza Ribas, N., Lopez, J. F. M., Lima, E. (2021). Description of a bilateral gynandromorph in *Spodoptera frugiperda* (Smith, 1797) (Lepidoptera: Noctuidae) from Brazil. *Revista Brasileira de Entomologia*, 65(2), e20200116.
- Spassky, S. A. (1914). Der Hermaphroditismus bei den Spinnen. *Izvestia Donskogo Politeknicheskogo Instituta*, 3(2), 98–99 + tab. III.
- Strand, E. (1900). Zur Kenntnis der Arachniden Norwegens. *Det Kongelige Norske Videnskabers Selskabs Skrifter*, 2, 1–46.
- Stratton, G. E. (1995). A gynandromorphic *Schizocosa* (Araneae, Lycosidae). *Journal of Arachnology*, 23(2), 130–133.
- Suzuki, S. (1980). An intersex of the harvestman *Gagrellula ferruginea* (Loman). *Acta Arachnologica*, 29(1), 43–46.
- Suzuki, Y., Kuramitsu, K., Yokoi, T. (2019). Morphology and sex-specific behavior of a gynandromorphic *Myrmarachne formicaria* (Araneae: Salticidae) spider. *Die Naturwissenschaften*, 106(7–8), 34.
- Tanaka, H. (1971). A gynandromorph of the spider *Zilla sachalinensis* (Saito) from Japan. *Acta Arachnologica*, 23(2), 23–25.
- Teruel, R. (2017). Una especie nueva de *Ravilops* Viquez and Armas, 2005 de República Dominicana, Antillas Mayores (Thelyphonida: Thelyphonidae). *Revista Ibérica de Aracnología*, 30, 15–20.
- Thaler, K. (2004). Ein Gynander des Fadenkankers *Nemastoma triste* (C. L. Koch) (Opiliones, Nemastomatidae). *Entomologische Nachrichten und Berichte*, 48, 64–65.
- Tsurusaki, N. (1983). Intersexuality and gynandromorphism in gagrellid harvestmen (Palpatores, Opiliones, Arachnida). *Acta Arachnologica*, 31(1), 7–16.
- Vanuytven, H. (1995). Een geval van gynandromorfie en intersexualiteit bij *Oedothorax fuscus* (Araneae, Linyphiidae). *Nieuwsbrief van de Belgische Arachnologische Vereniging*, 10(2), 27–28.
- Waalder, P. F. (1970). Spiders (Aranea) from Syd-Varanger, north Norway, with a note on a gynandromorph *Cornicularia*. *Rhizocrinus*, 1(5), 1–9.
- Wiebes, J. T. (1959). A gynandromorphous specimen of *Trochosa terricola* Thorell (Araneae, Lycosidae). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, 62(C), 84–89.

- World Spider Catalog (2025). *World Spider Catalog, version 26*. Natural History Museum Bern, online at <http://wsc.nmbe.ch>, accessed 19/10/2025
- Wright, J. (1995). A gynandromorph *Baryphyma trifrons* (O.P.-Cambridge) from the Isle of Man. *Newsletter of the British Arachnological Society*, 72, 13.
- Wunderlich, J. (1973). Zur Spinnenfauna Deutschlands, XV. Weitere seltene und bisher unbekannte Arten sowie Anmerkungen zur Taxonomie und Synonymie (Arachnida: Araneae). *Senckenbergiana Biologica*, 54, 405–428.
- Wunderlich, J. (1994). Fünf Gynandromorphe Baldachin-Spinnen aus Europa (Araneae: Linyphiidae). *Beiträge zur Araneologie*, 4, 471–477.
- Wunderlich, J. (2008). Differing views of the taxonomy of spiders (Araneae), and on spiders' intraspecific variability. *Beiträge zur Araneologie*, 5, 756–781.
- Yaginuma, T. (1966). Three anomalous spiders from Japan. *Acta Arachnologica*, 20(1), 21–23.
- Yaginuma, T., Arita, T. (1966). A gynandromorph of a crab spider, *Xysticus insulicola* Boes et Str. from Japan. *Acta Arachnologica*, 20(1), 18–20.