Gynandry and intersexuality in spiders

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Summary

After defining gynandry and intersexuality and suggesting an alternative method of classifying these abnormal forms, we have described nine examples with figures, and discuss these phenomena.

Introduction

If an adult spider is found in which parts of the body are female and parts are male, and if the female and male areas are each quite normally developed, then that spider is a gynandromorph. A good example of this is the case of *Pardosa monticola* (Clk) described by Mackie (1969), which has a normal male palp and male characters on one side, and a "normal" half epigyne and female characters on the other side (the half epigyne being "normal" if one allows for inevitable distortion in the midline).

The relative areas occupied by male and female tissues varies and a gynandromorph may be "regular" - in the sense that the male and female areas are clearly disposed either laterally, transversely, or quarterly, - or "irregular" - when the various parts are disposed more haphazardly, but still retain their individual normality (with reference to a normal specimen of the appropriate sex).

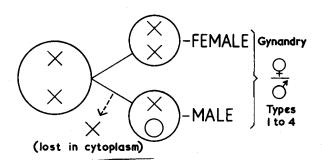


Fig. 1: Possible combinations of male and female characters giving rise to types of regular gynandromorphs.

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.

The "typing" of regular gynandromorphs in this manner was arbitrary and, although we recognize the fact that they are not, strictly speaking, different types (but variations on 3 themes), we feel that the discussion of cases will be made simpler by such a scheme.

It should be noted that type 4 would be impossible to detect in most cases, and that types 11 and 12 could easily be overlooked.

Whilst most authors refer to types 1 and 2 as lateral gynandromorphs, and to types 3 and 4 as transverse gynandromorphs, some would refer to, say, type 14 as a "mosaic gynandromorph with the male tissue occupying the anterior right quarter". We would refer to this as a regular (type 14) gynandromorph, and if we were to use the term "mosaic" would reserve it for cases with haphazard distribution – our "irregular" gynandromorphs.

However, cases occur in which, although parts of the spider may be predominantly female and other parts predominantly male, the divisions are less definite. Certain organs, such as palps and epigyne, may be very poorly developed; other areas, such as carapace and abdomen, may be intermediate in size, shape and colour between that for the normal male and female, and the greater the normal degree of sexual dimorphism, the more obvious will this intermediate state be. These cases are referred to as intersexes.

Gynandry and intersexuality might be mixed in a specimen and, in addition to this, further abnormalities could be produced by difficulties at ecdysis, injuries and faulty regeneration of lost appendages. Thus, in the case of a gynandromorph in which some areas are imperfectly developed, it may be difficult to tell whether the anomalies are due to coexisting intersexuality, or to injuries etc.

Description of cases

In the descriptions that follow, the terms "right" and "left" refer to the right and left sides of the spider viewed from above. Most of the drawings of the specimens, and all the epigynes, are of the ventral aspect. The length of each specimen is given and this is followed by the normal size range given by Locket & Millidge (1951 & 1953).

The material used in the following case descriptions has been deposited in the British Museum (Nat.Hist.) and accession numbers indicated in parenthesis after each species.

Theridion pallens Bl. (1973: 276) Figs 2 & 3

The specimen was beaten from a bush at Dobshill, Hawarden, Flintshire on 13 June 1971. (M.J.R.)

LENGTH: c. 1.6 mm (Normal: Females c. 1.75 mm; Males 1.25 - 1.5 mm) CARAPACE: Asymmetrical. Yellow, with cephalic and ocular areas dark brown; darker on the right side. ABDOMEN: Asymmetrical. Dorsally: left side light vellowish pink with white blotches; right side mottled densely with dark brown - black, and this extending round to involve half of the ventral aspect. STERNUM: Asymmetrical. Yellow, a wide light brown border on right side of the spider only. CHELICERAE: Right slightly larger and darker than left, particularly in the fang. LEGS: Tibiae and metatarsi darker on the right side and there are also slight differences in leg lengths between the two sides. PALPI: Left, normal female palp; right: normal male palp. EPIGYNE: Normal and perfectly symmetrical in every detail. The specimen was cleared in clove oil, when the vulva was also seen to be normal.

This specimen is a gynandromorph, as the male and female areas are all normally developed. Of our regular types it most closely resembles types 2 and 14 – but it is neither. For it to fit type 2 the epigyne would have to be only half developed – whereas in fact it is complete. Similarly, to fit type 14, the abdomen would have to be symmetrical and of a uniform light (female) colour. The specimen would, therefore, seem to be an irregular gynandromorph.

Entelecara flavipes (Bl.) (1973: 277) Figs 4 & 5

The specimen was beaten from undergrowth below trees, when many normal specimens of both sexes were also taken, at Happy Valley, Box Hill, Surrey on 1 July 1971. (J.R.P.)

LENGTH: c. 1.7 mm (Normal: Females 1.6 - 1.7 mm; Males 1.5 mm) CARAPACE: Symmetrical. Head elevation present, but not so pronounced as in normal male specimens. PALPI: Incompletely developed and

there are considerable differences between each. The apophyses of the palpal tibiae are no more than vestigial. ABDOMEN: Typical for the female sex. EPIGYNE: Symmetrical and typical for the female of the species.

The specimen would, at first sight, appear to be a regular (type 3) gynandomorph, but the carapace is intermediate between that for normal males and females and the palpi are underdeveloped (c.f. Locket & Millidge, 1953, p. 213, fig. 131 A & D). The incompleteness of the palpi could be explained by loss of, or injury to, both palps at some stage, with subsequent partial regeneration. But a similar argument could not apply to explain the intermediate state of the carapace. This specimen would therefore seem to exhibit intersexuality of the anterior half, with a normal posterior half.

Micrargus herbigradus (Bl.) (1973: 278) Figs 6, 7 & 8

The specimen was collected at ground level by Mr J. Crocker at Minsmere River Marsh, Suffolk, on 21 September 1972. Normal specimens of both sexes were also collected in the same area on the same day.

LENGTH: c. 1.6 mm (Normal: Females & males 2.0 mm) CARAPACE: Symmetrical. Very slightly elevated behind eyes, but holes and sulci behind posterior lateral eyes not so pronounced as usual. PALPI: Very incompletely developed, one more so than the other. ABDOMEN: Asymmetrical. EPIGYNE: Only developed on the left side of the spider.

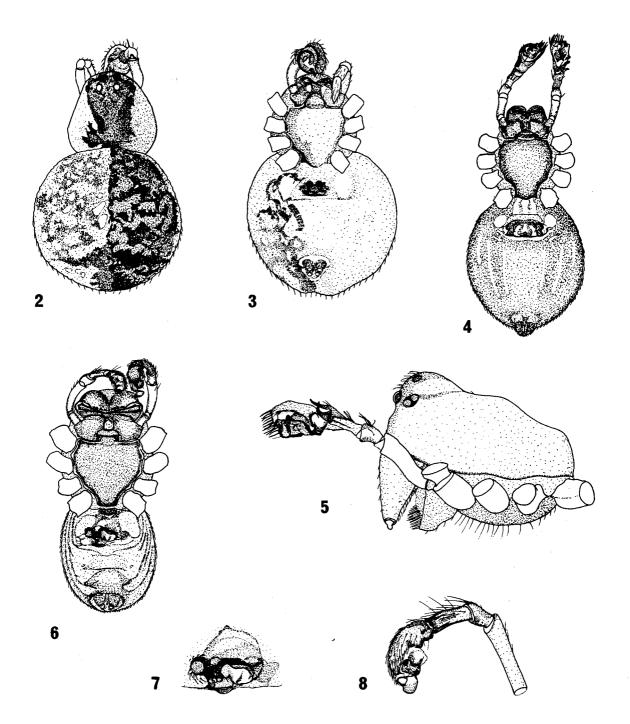
Again, if the palpi and carapace were normally developed, the specimen would be regarded as a regular (type 8) gynandromorph. However, it would seem to be a combination of intersexuality of the anterior half, with gynandry of the posterior half.

The following six specimens described are from the D. J. Clark collection in the British Museum.

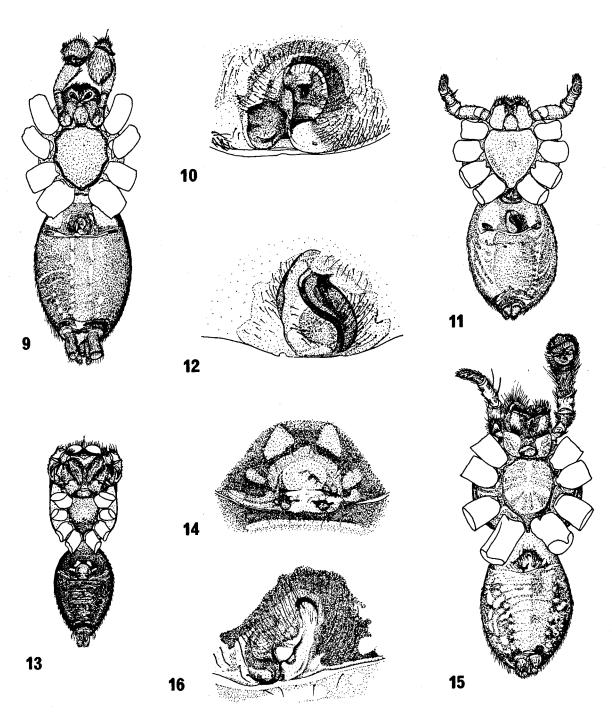
Zelotes pedestris (C. L. Koch) (1973: 279) Figs 9 & 10

The specimen was collected at Happy Valley, Box Hill, Surrey, on 28 May 1960. (D.J.C.)

LENGTH: c. 5.1 mm (Normal: Females c. 7 mm; Males 4.5 - 6 mm) CARAPACE, STERNUM & LEGS: Symmetrical and typical for the male of the species. ABDOMEN: Asymmetrical; female on the left of the spider and male on the right. There are also differences in the spinners. PALPI: Both normal for



Figs 2-8: Gynandromorphs/intersexes. *Theridion pallens* 2 dorsal aspect x 35; 3 ventral aspect: *Entelecara flavipes* 4 ventral aspect x 35; 5 lateral view of carapace and palp x 70: *Micrargus herbigradus* 6 ventral aspect x 35; 7 epigyne x 70; 8 left palp from outside x 70.



Figs 9-16: Gynandromorphs/intersexes. Zelotes pedestris 9 ventral aspect x 14.5; 10 epigyne x 70: Philodromus aureolus 11 ventral aspect x 14.5; 12 epigyne x 70: Heliophanus cupreus 13 ventral aspect x 14.5; 14 "epigyne" x 70: Lycosa hortensis 15 ventral aspect x 14.5; 16 epigyne x 70.

the male of the species. EPIGYNE: Only half developed (on the left of the spider).

This specimen is, therefore, clearly a regular (type 8) gynandromorph.

Philodromus aureolus (Clk) (1973: 280) Figs 11 & 12 The specimen was collected at Happy Valley, Box Hill, Surrey, on 8 July 1961. (D.J.C.)

LENGTH: c. 4 mm (Normal: Females 5 - 6 mm; Males 4 mm) The anterior part of this specimen is typical for the female of the species in every detail. The abdomen, however, is asymmetrical and exhibits differences in marking and colouration between the two sides, being male on the right and female on the left. There are also slight differences in the spinners. The epigyne is also only half developed (on the left side of the spider).

This specimen is therefore clearly a regular (type 11) gynandromorph.

Heliophanus cupreus (Walck.) (1973: 281) Figs 13 & 14

The specimen was collected at Woody Bay, Ventnor, Isle of Wight, on 22 July 1961. (D.J.C.)

LENGTH: c. 3.6 mm (Normal: Females 5 - 6 mm; Males c. 4 mm) This specimen appears to be a normal male of the species in all respects except one - it appears to have an "epigyne". This structure is difficult to evaluate as normal females usually have a rather poorly defined epigyne. Nearly all the females examined by us have the epigyne completely obscured by reddish processes. However, none of the males examined have anything like the structure in fig. 14 present. Two distinct reddish areas are visible, but whether or not these rudiments are homologous with those found in normal females, is not known. Possibly these processes are functional, rather than primarily structural, and therefore are rudimentary in a non-functioning epigyne. Another possibility is that of eversion of the epigastric fold, in a male spider, causing an artefact "epigyne". When the specimen was cleared in clove oil, however, it was seen to resemble the vulva of normal females, and to differ from the cleared epigastric region of normal males.

If we accept it as fact that the specimen has a normal epigyne, then it is an irregular gynandromorph. If we regard this "epigyne" as being abnormally or poorly developed (but nevertheless as having definite female elements), then the specimen is exhibiting a degree of intersexuality. However, if we consider the structure to be an artefact, then the s p e c i m e n m i g h t b e t e r m e d a "pseudogynandromorph".

Lycosa hortensis Thorell (1973: 282) Figs 15 & 16

The specimen was collected at Happy Valley, Box Hill, Surrey, on 5 April 1959. (D.J.C.)

LENGTH: c. 5 mm (Normal: Females 4.5 - 5.5 mm; Males 3.5 - 4.5 mm) This specimen is quite clearly a regular (type 1) gynandromorph.

Tarentula barpipes (Sund.) (1973: 283) Figs 18 & 19

The specimen was collected at Bloxworth Heath, Dorset, on 6 December 1957. (D.J.C.)

LENGTH: 9.3 mm (Normal: Females 8 - 12 mm; Males 7.5 - 9 mm) The colour and pattern of the carapace and abdomen appear midway between that for normal males and females, with a preponderance of maleness anteriorly and femaleness posteriorly. The ventral sides of tibiae and metatarsi I have a few black hairs, but much less than in normal males. The other legs are clearly marked with dark blotches and annulations. PALPI: Midway between that for normal males and females. A small alveolus is discernible, and a claw is present. EPIGYNE: Very poorly developed.

This specimen is therefore exhibiting complete intersexuality.

Trichoncus affinis Kulcz. (1973: 284) Fig. 17

The specimen was collected at Havergate Is., Suffolk, on 10 June 1960 (D.J.C.)

LENGTH: c. 2.3 mm (Normal Females 2.5 mm (from others in D.J.C. coll.); Males 2 mm) This specimen has the anterior half (including legs) male, and the abdomen female (with a normal epigyne). The left palp is normal for the male of the species, but the right is very rudimentary in the tibia (which has a minute apophysis) and tarsus. This specimen would seem most likely to be a regular (type 3) gynandromorph which has suffered loss of the terminal two segments of the right palp at some stage, with partial regeneration subsequently.

Discussion

In our introduction we put forward a system for classifying sexually anomalous spiders. This may stimulate some controversy and we would now like to attempt to justify it.

Kaston (1961) used Bonnet's basic scheme, with

additions, in placing the then 47 known cases in his classified list, as follows:

- 1. Typical lateral gynandry.
- 2. Lateral crossed gynandry.
- 3. Transverse gynandry.
- 4. Partial or mosaic gynandry.
- 5. Mixed gynandry & intersexuality.
- 6. Intersexuality.

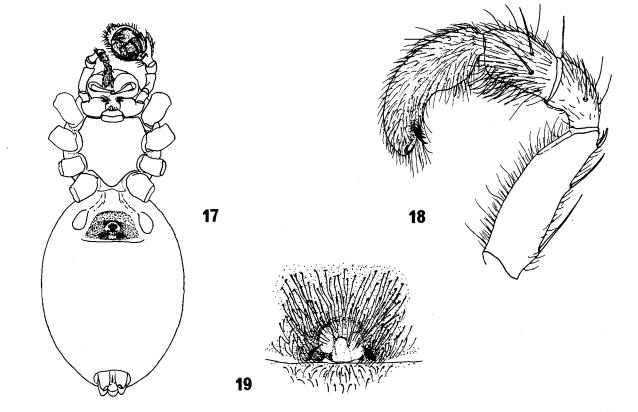
Our scheme, for comparison, appears thus:

- 1. Regular gynandry lateral – transverse – crossed (types 1-14)
- 2. Irregular gynandry.
- 3. Mixed gynandry & intersexuality.
- 4. Intersexuality.

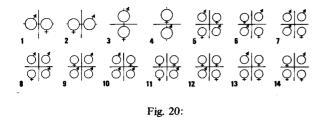
The term "regular" means simply that the specimen fits into one of our types 1 - 14. Whilst Kaston's scheme would regard, say, type 6 as a lateral

crossed gynandromorph, it would regard a type 14 as a partial or mosaic gynandromorph. If, instead of being a complete type 14, only part of the anterior right quarter were male (say, just the palp and chelicera), his scheme would *still* regard the specimen as a partial or mosaic gynandromorph.

The term "irregular" means that the specimen does not fit into our regular types, although each of the sexual components are normally developed. We would prefer to reject the term "partial" because (a) it can mean anything from minimal to almost total, (b) all cases of gynandry/intersexuality are in a sense "partial", and (c) in a specimen composed of, say, $\frac{1}{4}$ of one sex and $\frac{3}{4}$ of the opposite sex, one reasonably assumes the $\frac{1}{4}$ to be abnormal. But one cannot be certain that it is not the $\frac{3}{4}$ which has undergone sexual change — in which case the gynandry would be "almost total".



Figs 17-19: Gynandromorphs/intersexes. *Trichoncus affinis* 17 ventral aspect x 35: *Tarentula barbipes* 18 left palp from outside x 28.5; 19 epigyne x 70.



As regards the mechanism of production of gynandromorphs and intersexes, little is known, but there is much conjecture. In spiders, it is the male that is heterogametic, but the number of X chromosomes present varies from species to species. Thus, in some species, the female tissue cells contain XX and the male cells XO; in others the female cells have $X_1 X_2 X_1 X_2$ and the male cells $X_1 X_2 0$, and similarly females of other species have three pairs of X chromosomes.

If we assume the same mechanism as that known to occur in Drosophila to be responsible for gynandry in spiders, then production of a regular (type 1) gynandromorph in a genetically determined female spider, with one pair of X chromosomes, could be effected by the loss of one X chromosome at the first cleavage of the zygote. Fig. 20. If this happened at the second cleavage, then only ¼ of the resultant spider would be male. However, production of a type 8 gynandromorph from a genetically determined female would involve the loss of three X chromosomes at the first cleavage, or, one at the first and one at the second cleavage. This seems to be much less likely - the more so when one considers that most spiders seem to have 2 or 3 pairs of X chromosomes, and that to produce a type 1 would require, in these cases, loss of 2 or 3 X chromosomes, and to produce a type 8 would require loss of between 4 and 9 chromosomes. So we are obliged to search for some method of production of gynandry from genetically determined males. This would involve some means of addition, or rearrangement of sex chromosome material.

Intersexuality is equally difficult to explain, but we feel that, as gynandry is without doubt a genetic phenomenon, and that gynandry and intersexuality frequently coexist in one specimen, intersexuality also is most likely to have a genetic aetiology in some, if not all cases. Holm (1941) has suggested that parasitism by nematodes could account for some intersexes, by interfering with testicular development. However, (a) parasitism does not invariably cause intersexuality, (b) not all intersexes are parasitized, and (c) reduction of size, or even complete absence, of the testes does not always cause intersexuality.

Nevertheless, this raises another possible cause for cases of combined gynandry/intersexuality. For example, in the case of a juvenile type 3 gynandromorph, growing to maturity, could the posterior (female) part exert some sort of (?hormonal) influence on the growing anterior (male) part, preventing it from maturing normally? Or conversely, could the absence of testes have the same effect?

Apart from gynandry and intersexuality, many cases of other malformations, duplications and monstrosities have been recorded, and, in conclusion, it must be said that very little is known of the aetiology of any of these abnormal and very interesting forms.

Acknowledgements

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