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# Do large house spiders *Tegenaria gigantea* and *T. saeva* (Araneae, Agelenidae) hybridise in the wild? – A multivariate approach

**G. S. Oxford** and **A. Plowman**
Department of Biology,
University of York,
York YO1 5DD

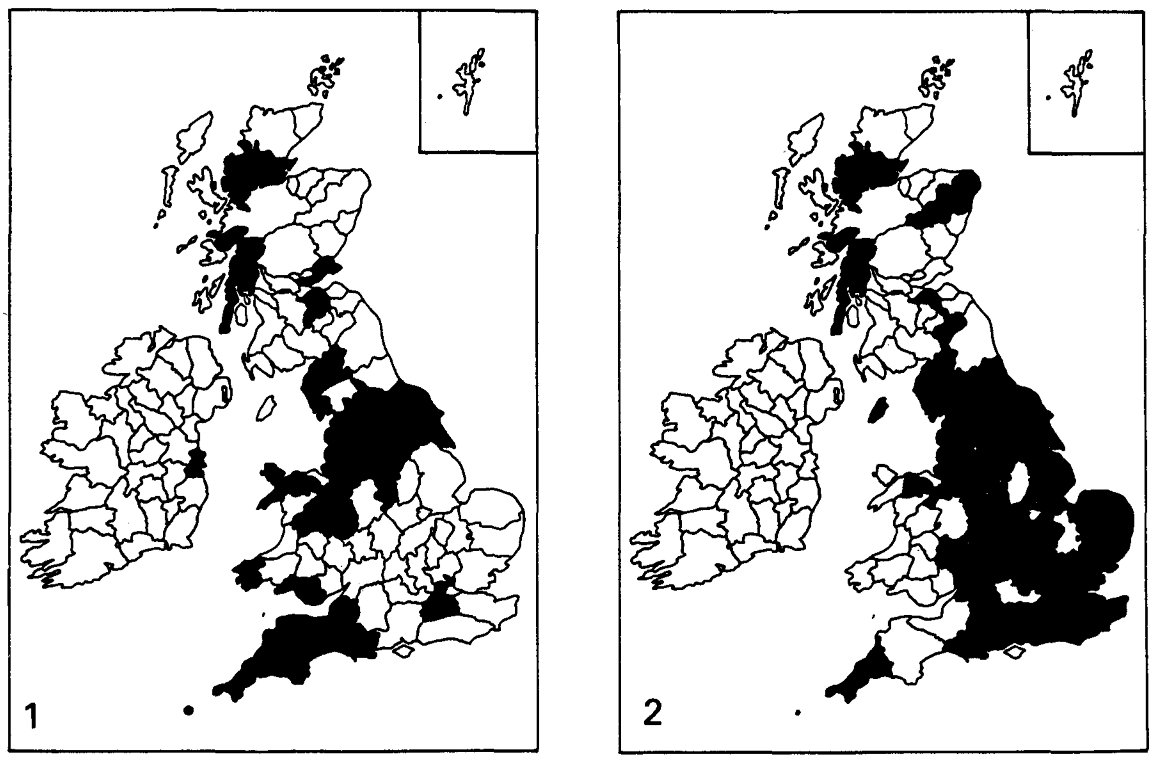

## Summary

A large number of morphological characters were measured on male large house spiders, *Tegenaria saeva* and *T. gigantea,* from the York area. The data were subjected to linear discriminant function analysis to identify those characters which, in combination, separated the species most clearly. These characters were then used to clarify the status of individuals previously identified as being in some ways intermediate between the species. Nine of these 'intermediates' proved to be *T. gigantea* while the other nine fell between the species clusters. It is concluded that the latter nine (all males) are the products of interspecific hybridisation. No intermediate females have been identified. The identification of a small proportion of hybrid males (3% in a sample of 643) does not invalidate the specific status of *Tegenaria gigantea* and *T. saeva.*


## Introduction

In 1980, Merrett clarified the diagnostic characters and the distribution of large house spiders in the *Tegenaria atrica* group. The two widespread representatives in Britain, *Tegenaria gigantea* Chamberlin & Ivie, 1935 and *T. saeva* Blackwall, 1844, were only recognised as distinct species in 1975 (with *T. gigantea* described as *T. propinqua*) (Locket, 1975), and consequently their distribution was rather poorly known when Merrett wrote in 1980. The information then available suggested that *T. saeva* is a more westerly species, with *T. gigantea* predominating throughout eastern and central regions. Subsequent distributional information (Merrett, 1982, 1989; O'Connor & Higgins, 1986, and unpublished county records) confirms this general pattern (Figs. 1, 2) although there is a considerable degree of overlap, particularly in the northern parts of England and Wales, and in Scotland. There are, in addition, indications from county records that both *Tegenaria* species have expanded their ranges in the recent past (Parker, 1984; Smith, 1985). For example, large house spiders were first recorded in Yorkshire in the mid-1960s (Smith, 1985). A detailed survey in 1984 and 1985 (Oxford & Smith, 1987) showed that both species are now widespread in the county with *T. gigantea* generally the commoner of the two. However, on a more local scale, particularly in York city and surrounding villages, *T. saeva* can reach frequencies of over 75%.

One consequence of an expansion, and possibly an increasing overlap, in the ranges of the species is that there might now be greater opportunity for interspecific hybridisation than in the past. A small number of male specimens examined by Merrett (1980) had palp characters intermediate between those of *T. gigantea* and *T. saeva,* and he suggested they might be hybrids. Similarly, Oxford & Smith (1987) found 43 of 643 males (6.7%) to be intermediate, both with respect to palp morphology and relative palp dimensions. They, too, thought that these individuals could be interspecific hybrids, a conclusion strengthened by the fact that all but one were found at sites containing both putative parent species. No intermediate females have yet been identified, a deficiency which is statistically significant (Oxford & Smith, 1987). Evidence that the two species *can* hybridise successfully comes from




Figs. 1-2: Distribution of *Tegenaria saeva* (1) and *Tegenaria gigantea* (2) in the British Isles, based on pre-1974 county boundaries.

artificial crosses in the laboratory (Kennett & Dalingwater, 1986), although it is not known whether these hybrids are fertile. The question is, do *T. gigantea* and *T. saeva* hybridise in the wild, and are the males with intermediate palp morphology the products of hybridisation?

An attempt to analyse this situation using electrophoretic enzyme markers was unsuccessful because diagnostic loci could not be found (Oxford, unpub.). This in itself suggests that the species are very closely related. In this paper we describe an approach using linear discriminant function analysis (LDFA) on morphological data.

## Materials and Methods

All spiders used were preserved in 70% alcohol and came from the collection made by Oxford & Smith (1987). Measurements were made on twenty randomly selected males of each of *Tegenaria gigantea* and *T. saeva,* and on eighteen males deemed 'intermediate' by Oxford & Smith. For comparison, ten *T. saeva* and six *T. gigantea* females were also examined – all the female specimens available. A total of 50 measurements were attempted on each male, and 43 on each female. In males these comprised 6 on the cephalothorax, 4 on the opisthosoma, 16 on the legs, 7 on the eyes and 17 on the palp. In females, measurements comprised 6 on the cephalothorax, 5 on the opisthosoma, 16 on the legs, 5 on the eyes and 11 on the epigyne. Measurements were made using a Vickers dissecting microscope fitted with an eyepiece graticule. Raw data (in mm) were subjected to LDFA using the Minitab package on the University of York VAX system. The robustness of the technique was assessed by cross-validation. Data from single individuals of *T. saeva* or *T. gigantea* were withheld from the analysis and the discriminant function calculated. Using this function the identity of the withheld individual was tested. In all cases, test individuals were assigned to the correct species.

(a) **Males**

- + 245.23 Distance between anterior median eyes
- + 187.08 Maximum conductor width [a]
- + 175.75 Sternal pattern [f]
- + 162.86 Conductor length [b]
- + 129.84 Tegulum width [h]
- + 81.68 Cymbium depth [d]
- − 95.99 Maximum embolus width [g]
- − 105.37 Anterior spinner length (left)
- − 140.50 Maximum tegulum + conductor length [c]
- − 291.98 Ectal tibial apophysis width (proximal end) [e]

(b) **Females**

- + 1330.62 Maximum apophysis width (right) [j]
- + 586.20 Minimum epigyne width [i]
- + 69.27 Epigyne to pedicel distance
- − 449.27 Epigyne length [l]
- − 611.91 Sternal pattern [f]
- − 3390.80 Seminal receptacle width (right) [k]

Table 1: Characters and their coefficients used in the final discriminant functions. The coefficients shown for each sex are derived by subtracting for each character the coefficient for *T. saeva* from that for *T. gigantea*. The constants are ignored. The score for an individual is obtained by multiplying each measurement (in mm) by the appropriate coefficient and summing over all characters. Letters in [ ] refer to measurements shown in Fig. 4 (a-h) and Fig. 6 (i-l).

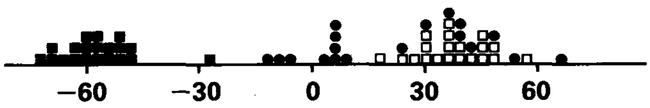



Fig. 3: Plot of scores from the discriminant function analysis for males: *Tegenaria saeva* (■), *T. gigantea* (□) and the 'intermediate category (●). Scores derive from the linear function given in Table 1a and are shown here after subtraction of the mean.

## Results

### *Males*

Discriminant functions were derived from information from individuals unambiguously assigned to *T. gigantea* or *T. saeva*. Data from legs were not used because (1) individual legs were often missing and (2) leg measurements were too highly correlated for the analysis to be performed. The discriminant function derived from the remaining 34 variables showed a very clear separation between *T. gigantea* and *T. saeva,* with a squared distance ($r^2$) between the groups of 365.6. To shorten the function, variables which contributed little to the separation, and those that were difficult to measure reliably, were eliminated. This left 23 variables and a discriminant function giving an $r^2$ value of 124.0. The number of variables was reduced even further by stepwise regression on a dummy variable (group membership) using backward elimination, and by a 'best subsets' regression technique. The final function of ten variables ($r^2$ = 93.8) is set out in Table 1a and individual values for *T. gigantea, T. saeva* and also the intermediate spiders, are plotted in Fig. 3. Eight of the ten measurements involved in this discriminant function are shown in Fig. 4; the other two are self-explanatory.

### *Females*

Fewer females were available for analysis and none of them was considered 'intermediate'. As with the males, leg measurements had to be excluded because of missing values. Most of the other 27 female characters were too highly correlated to perform LDFA directly. Instead, LDFA was applied to principal components derived from these data and then the original variables recovered. The discriminant function produced a wide separation between the species, with an $r^2$ value of 51,349. Only 14 variables were sufficiently uncorrelated for LDFA to be applied directly, yet even these gave excellent separation ($r^2$ = 619.7). These 14 characters were subjected to a stepwise regression technique with backward elimination to identify the best six; any less than six caused a large drop in $r^2$. The resulting function is given in Table 1b and plotted in Fig. 5, and yields a distance between the groups of 287.8. The six measurements made on females are shown in Figs. 4 and 6.

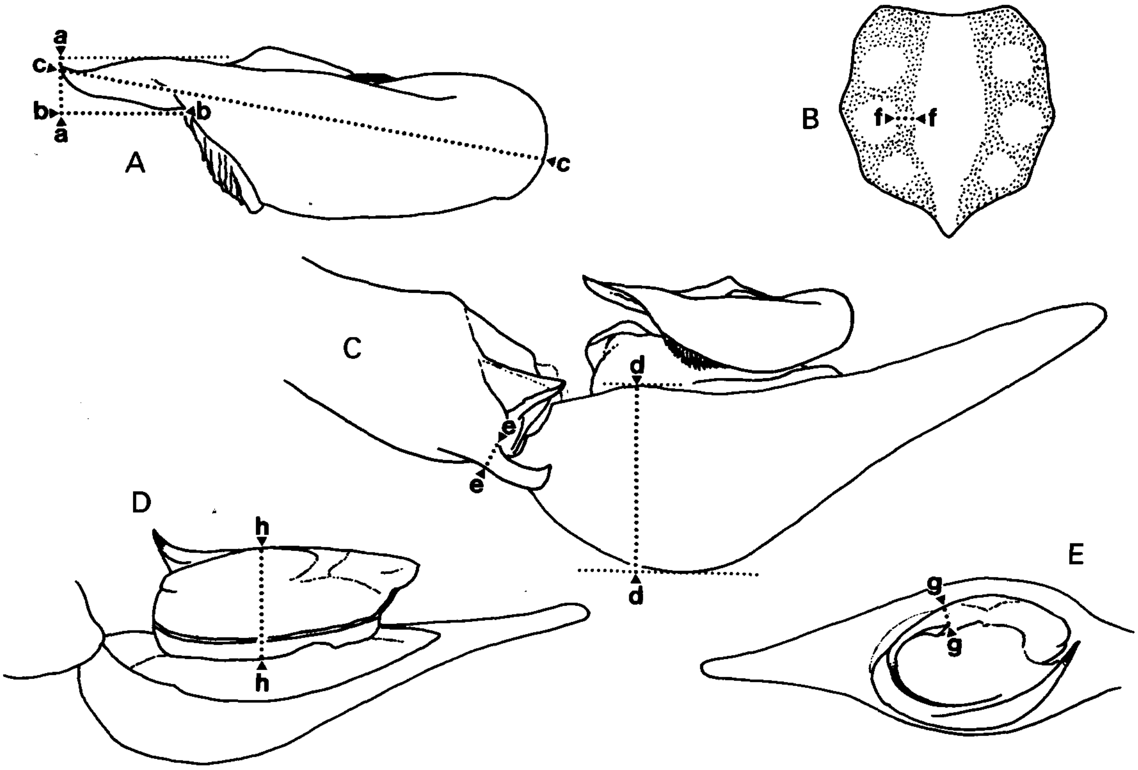



Fig. 4: Eight of the ten male characters used in the final discriminant function. **a** = maximum conductor width; **b** = conductor length; **c** = maximum tegulum + conductor length; **d** = cymbium depth; **e** = ectal tibial apophysis width (proximal end); **f** = sternal pattern. Diagrams **A**, **C**, **D**, **E** are of male palp; **A** and **C** viewed from outside, ventral side uppermost, **D** viewed from inside, ventral side uppermost, **E** ventral view. **B** is ventral view of sternum.

## Discussion

In males, a clear discrimination between *T. gigantea* and *T. saeva* was achieved using just ten variables. Seven of these measurements are of components of the palp (Table 1). Of the remaining three, the basal width of the ectal tibial apophysis was suggested as being of diagnostic importance by Locket (1975). However, later workers either ignored this character (Merrett, 1980) or concluded that it is unreliable (Roberts, 1985). This study suggests that the tibial apophysis does contain diagnostic information, at least in combination with other characters. It is also of interest that an aspect of the sternal pattern is diagnostically important in both males and females (Table 1). Locket (1975: 85) dismissed this character as being "so variable in both species that it is useless", but in combination with other characters, sternal pattern clearly does show species-specific variation.

The application of the discriminant function derived from unequivocally assigned males to those suspected of being hybrids yielded two fairly distinct groupings (Fig. 3). Nine of the values were solidly within the range of *T. gigantea*, while the other nine fell between the *T. gigantea* and *T. saeva* clusters, although biased slightly towards *gigantea*. It should be remembered that assignment of males to one or other species, or to the 'intermediate' category, was made initially on the basis of a subjective assessment of the shape of components of the palp (Oxford & Smith, 1987). It is not unlikely, therefore, that certain individuals were placed in the wrong category. The present data suggest that these characters in *T. gigantea* might be more variable, in the *saeva* direction, than was allowed for in the initial diagnosis. However when quantitative data are used in multivariate analyses, those *T. gigantea* individuals in the 'intermediate' category are now correctly assigned.

This leaves nine specimens with scores from the discriminant function which fall between those of the two species clusters. Both sexual and non-sexual

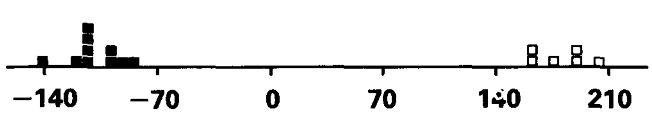



Fig. 5: Plot of scores from the discriminant function analysis for females: *Tegenaria saeva* (■) and *T. gigantea* (□). Scores derive from the linear function given in Table 1b and are shown after subtraction of the mean.

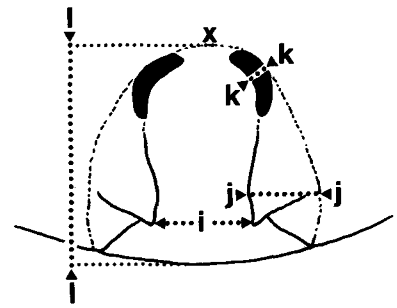



Fig. 6: Four of the six female characters used in the final discriminant function. **i** = minimum epigyne width; **j** = maximum apophysis width (right); **k** = seminal receptacle width (right); **l** = epigyne length. The distance from epigyne to pedicel was measured from point **x**.

characters are included in the function and they are uncorrelated with one another. They are likely, therefore, to be under independent genetic control. Intermediate discriminant function values suggest strongly that these individuals have arisen via interspecific hybridisation. An intermediate score could arise because an individual has intermediate characters or because it has some 'good' *T. gigantea* features while others are 'good' *T. saeva.* Which is the case will depend on the nature of the genetic control of a character, and whether individuals are first or subsequent generation hybrids. Inspection of raw measurements suggests that in the hybrids, spinner length is more like that of *T. saeva,* proximal tibial apophysis width and maximum conductor width are more like those of *T. gigantea,* while sternum pattern and maximum embolus width lie between the two. However, with data on only nine putative hybrids, patterns of this sort could appear by chance. An obvious and conclusive test of the hybridisation hypothesis would be to rear offspring from *gigantea* × *gigantea, gigantea* × *saeva* and *saeva* × *saeva* under laboratory conditions and repeat the analyses reported here. These known hybrids would also provide some information on the dominance relationships of the characters used.

To date, no female has been recognised, on any criterion, as being intermediate between the two species. This might be because of the nature of the characters used to separate females (Oxford & Smith, 1987). It might also be a result of chance. The original analysis (Oxford & Smith, 1987) assumed that the 'intermediate' male category was homogeneous whereas the present results show this is not the case. If only half the 'intermediate' males were of hybrid origin the apparent deficiency of 'intermediate' females is no longer significant ($\chi^2_{(1)} = 3.03$, $p > 0.05$). The discriminant function analysis shows that measurements on only six characters can produce a wide separation between the species. Interestingly, only three of these six are concerned with the epigyne. The laboratory hybridisation experiment mentioned above would indicate whether hybrid females assessed on these six characters generate scores intermediate between those of the pure species or whether they closely resemble one or the other. Indeed, hybrid females might be inviable.

Of the 18 'intermediate' individuals analysed here, nine had character combinations consistent with their being of hybrid origin. If this proportion is representative of the 'intermediate' category recognised by Oxford & Smith (1987), then the incidence of such males in the York area is about 3%. A further 3%, scored as being 'intermediate', were almost certainly *T. gigantea.* Thus, 94% of males (sample size, 643) and 100% of females (sample size, 86) could be easily assigned to one species or the other. Clearly, the identification of a very small proportion of interspecific hybrids does not invalidate the specific status of *T. gigantea* and *T. saeva.* It will be of interest to monitor the incidence of individuals with intermediate characters if the ranges of the two species continue to expand and overlap.

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**References**

KENNETT, J. A. B. & DALINGWATER, J. E. 1986: A progress report on using aspects of reproduction as criteria for distinguishing two closely related British *Tegenaria* species. *In* W. G. Eberhard, Y. D. Lubin & B. C. Robinson (eds.), *Proc. 9th int. Congr. Arachnol., Panama 1983:* 139-142. Smithsonian Institution Press, Washington.

LOCKET, G. H. 1975: The identity of Blackwall's *Tegenaria saeva* (Araneae, Agelenidae). *Bull. Br. arachnol. Soc.* **3:** 85-90.

MERRETT, P. 1980: Notes on the variation, identification and distribution of British species of the *Tegenaria atrica* group (Araneae, Agelenidae). *Bull. Br. arachnol. Soc.* **5:** 1-8.

MERRETT, P. 1982: New county records of British spiders. *Bull. Br. arachnol. Soc.* **5:** 332-336.

MERRETT, P. 1989: Twelve hundred new county records of British spiders. *Bull. Br. arachnol. Soc.* **8:** 1-4.

O'CONNOR, J. P. & HIGGINS, D. G. 1986: Some records of *Tegenaria saeva* Blackwall (Araneae) from the Dublin area. *Ir.Nat.J.* **22:** 115-116.

OXFORD, G. S. & SMITH, C. J. 1987: The distribution of *Tegenaria gigantea* Chamberlin & Ivie, 1935 and *T. saeva* Blackwall, 1844 (Araneae, Agelenidae) in Yorkshire. *Bull. Br. arachnol. Soc.* **7:** 123-127.

PARKER, J. R. 1984: Synanthropic spiders and other things – Part 2. *Newsl. Br. arachnol. Soc.* **39:** 1-2.

ROBERTS, M. J. 1985: *The spiders of Great Britain and Ireland,* **1:** 1-229. Harley Books, Colchester.

SMITH, C. J. 1985: The distribution of the larger *Tegenaria* spider species (Agelenidae) in the York area. *Newsl. Br. arachnol. Soc.* **42:** 5-6.