2000. The Journal of Arachnology 28:23–28

MALE DIMORPHISM IN *OEDOTHORAX GIBBOSUS* (ARANEAE, LINYPHIIDAE): A MORPHOMETRIC ANALYSIS

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ABSTRACT. The linyphiid spiders *Oedothorax gibbosus* (Blackwall 1841) and *Oedothorax tuberosus* (Blackwall 1841) were formerly described as separate species due to marked differences in prosomal structures of the males. During the last decade it was demonstrated that they are two forms of a single species. However, it remained to be shown whether the former species represent two distinct morphs or extremes of a continuum of variation. A morphometric examination of 246 alcohol-preserved specimens revealed that individual spiders can clearly be assigned to one of two forms. No intermediates were found, demonstrating that there are two distinct morphs.

Keywords: Species status, polymorphism, morphometry, sexual selection, gustatorial courtship

Why individuals of some species occur in distinct varieties has been of considerable interest to evolutionary biologist (e.g., Clarke 1962). Dimorphism represents the simplest case of polymorphism, with two varieties maintained within the population. The most common case of dimorphism is the sexual dimorphism with males and females showing dimorphism in size (Anderson 1994). Behavioral or morphological dimorphism in one sex, usually occurring in the male sex, is known for a relatively large number of insects (Hamilton 1979; Thornhill & Alcock 1983; Danforth 1991; Alcock 1996; Eberhard & Gutiérrez 1991). To our knowledge, the only spider species investigated to date is the jumping spider, *Maevia inclemens* (Walckenaer 1837), in which the morphs show striking differences in body color and courtship behavior (Clark & Uetz 1992, 1993). Species with dimorphic males provide a unique opportunity to address questions about the importance of female choice (Gadgil 1972; Clark & Uetz 1992), male-male competition (Danforth 1991; Eberhard & Gutiérrez 1991), sensory exploitation (Clark & Uetz 1993), and alternative mating tactics with equal or unequal fitness (Austad 1984; Dominey 1984). However, it has yet to be shown that the varieties under consideration result from the expression of different developmental programs with a bimodal distribution, excluding the differences that are simply extremes of a continuum of variation.

The linyphiid spiders *Oedothorax gibbosus* (Blackwall 1841) and *Oedothorax tuberosus* (Blackwall 1841) were described as separate species due to differences in prosomal structures of the males. In *O. gibbosus*, the male prosoma is raised to form a marked protuberance in front of which lays a deep notch surrounded by long black hairs. Protuberances, notches, grooves and poreplates frequently found in male linyphiid spiders were shown to function as gustatorial courtship devices in several species (Lopez & Emerit 1981; Schaible et al. 1986; Schaible & Gack 1987). Males of *O. tuberosus* on the other hand, lack the marked protuberance, notch and hair. However, the division was doubted by several authors (Simon 1926; Locket & Millidge 1953; Wiehle 1960; Bosmans 1985; Roberts 1987) as neither the male pedipalps can be distinguished nor are there differences in female somatic and genitalic characteristics. Moreover, the two species almost always occur syntopically (Wiehle 1960; Roberts 1987; Maelfait et al. 1990). Roberts (1987) strengthened this view by stating that: ‘‘occasional specimens seem to represent an almost intermediate state’’ and by including a drawing of a tuberosus male with a slight notch. Not until a rearing study was undertaken by De Keer & Maelfait (1988) in which both male forms were reared from one egg-sac was it shown that *O. gibbosus* and *O. tuberosus* are two forms of one species. A more detailed rearing study supported this finding, demonstrating that the two forms are very likely determined by one major gene with a dominant and a recessive allele where the tuberosus phenotype is expressed in individuals carrying homozygotic recessive alleles (Maelfait et al. 1990). From this genetic system follows that the two forms must be discrete morphs which is incompatible with the supposed intermediate forms. In a morphometric analysis, we examine whether the *gibbosus* and *tuberosus* forms can be clearly distinguished on morphological grounds. This study provides the basis for the following investigations on female mate choice.

METHODS

Oedothorax gibbosus occurs in North-, West- and Central Europe (Wiehle 1960). It is restricted to low productive, wet grassland and marshes that are frequently flooded during winter and requires high water quality, resulting in a rather patchy distribution (De Keer & Maelfait 1989).

We examined 246 alcohol-preserved specimens from the Institut Royal des Science Naturelles de Belgique, Bruxelles, captured in pitfall traps from 1977 to 1991 at different locations in Belgium. We chose this collection for two reasons, 1) the most detailed study on the species was conducted in Belgium by Maelfait et al. (1990), and 2) this collection proved to be the largest one available, a prerequisite for a solid morphometric investigation.

An example of each male form is illustrated in Figs. 1–4. For the morphometric analysis we took the following measures (in μm)(Figs. 5–8): length of patella plus tibia of the first leg (a), height of the prosoma (b), width of the prosoma (c), length of the prosoma (d), dorsal line along the prosoma, when viewed from the side (e) and depth of the notch (f). To measure the height a perpendicular line was drawn from the highest point of the prosoma. The dorsal line is a measure that includes size and dimension of the notch and the hump. The height of the prosoma and the depth of the notch were measured additionally to examine both structures separately. The depth of the notch was measured by drawing a straight line over the notch from which a perpendicular was drawn to the deepest point of the notch. The width of the prosoma was measured at the widest part of the prosoma. To measure prosoma length, the length of a straight line from the front to the back of the prosoma, parallel to the sternum, was taken. The measure of patella plus tibia is frequently used as a measure of leg size and served as a measure independent of prosomal size.

The measures were taken with a macroscope (WILD M420) fitted with a CCD-camera (Pieper FK 5062), connected to a computer provided with the program NIH-Image (Version 1.60b7). SEM investigations were performed with a Hitachi S2460N using unsputtered alcohol material under low vacuum mode.

All statistical analyses were performed using SPSS for Windows95, Version 8.0.1. The level of significance was set at 0.05.

RESULTS

The data were tested for normal distribution: prosomal length, prosomal width, prosomal height and length of the first leg showed a normal distribution (Kolmogorov-Smirnov-one-sample-test: $n = 246$, (leg 1: $n = 243$), in all cases $P > 0.05$). The dorsal line of the prosoma ($n = 246$) and the depth of the notch ($n = 219$) were not normally distributed (K-S test, both $P < 0.01$).

In Principal Component Analysis using a correlation matrix and varimax rotation, two principal components with eigenvalues greater than 1 were extracted (Table 1). A clear separation of the two morphs was possible along PC1 which explains 48% of the variance. Characters highly correlated with this component are the dorsal line, the height of the prosoma and the depth of the notch, all characters whose presence is attributed to the *gibbosus* form (Figs. 1, 2). The scatterplot of PC-scores shows two distinct distributions (Fig. 9), the left cloud representing the *tuberosus* form and the right one the *gibbosus* form. No intermediate forms were found.

The character length of the dorsal line along the prosoma incorporates several prosomal measures. In order to exclude size effects, we used an index of the dorsal line relative to size as measured by prosoma length. The resulting histogram (Fig. 10) shows a clear bimodal distribution and confirms that there are no intermediate forms. Thus we can safely assume the existence of two distinct morphs in *O. gibbosus*.

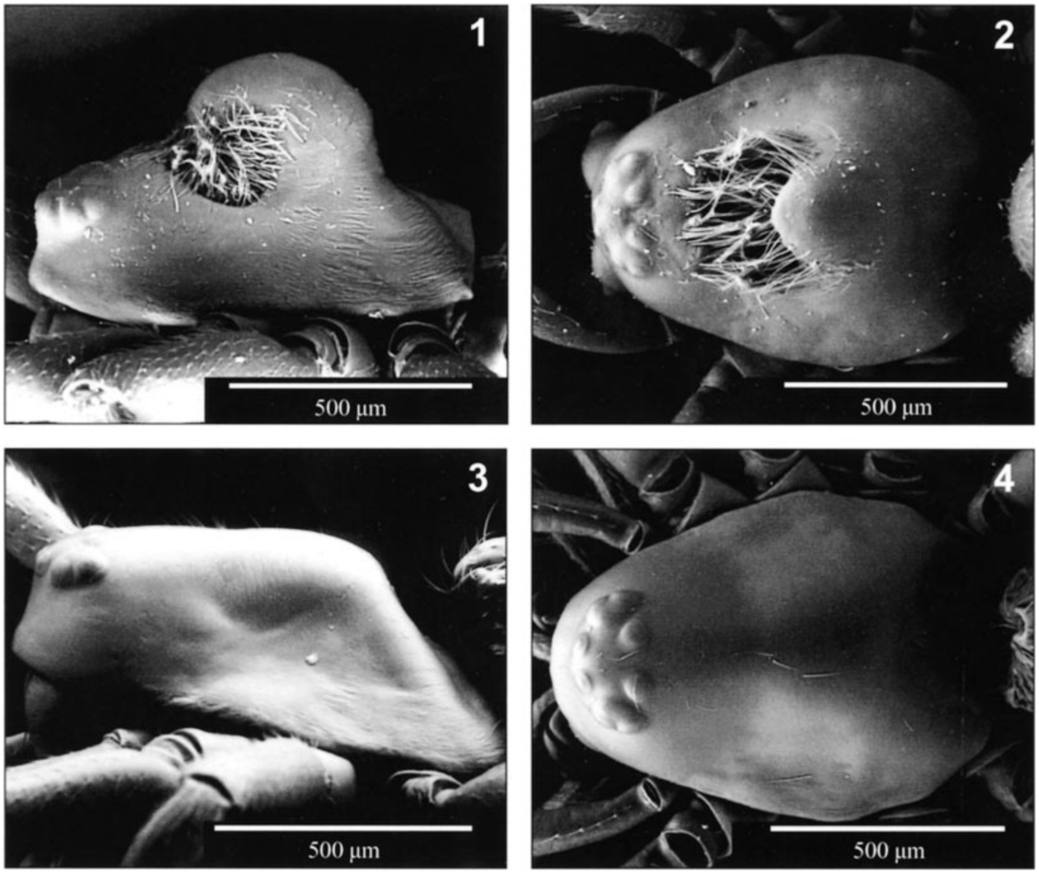
The mean of the dorsal line along the prosoma of the *gibbosus* morph ($\bar{x} = 1948$ μm,

Table 1.—Rotated component matrix resulting from Principal Component Analysis using eigenvalues greater than 1.

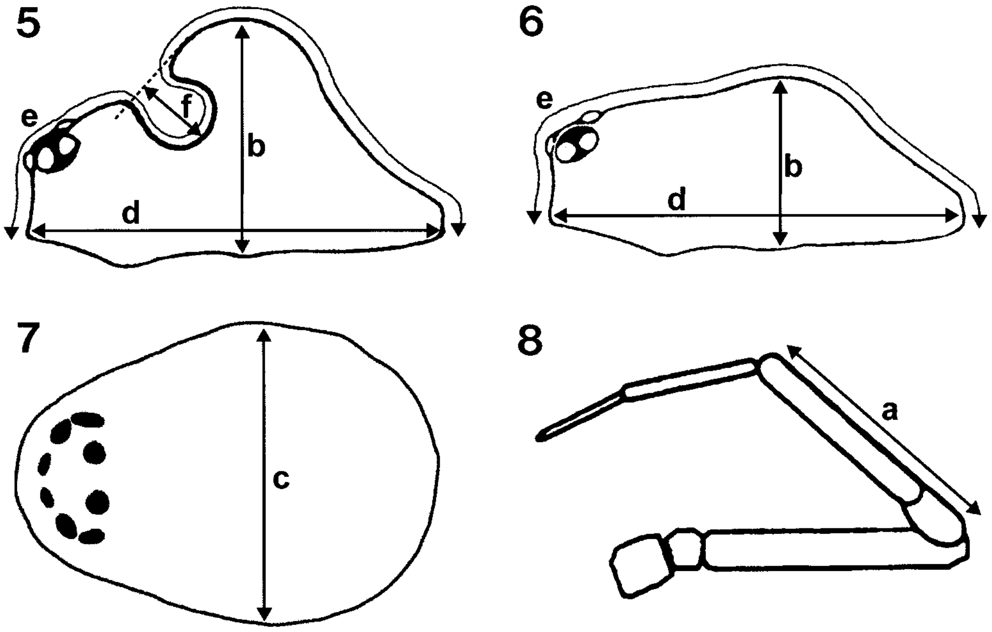
	PC1	PC2
Dorsal line along the prosoma	0.974	0.158
Prosomal notch	0.973	−0.025
Prosomal height	0.944	0.107
Prosomal width	0.317	0.751
Leg 1	0.001	0.802
Prosomal length	−0.341	0.863
Eigenvalues	2.89	1.99
Variance explained %	48.2	33.1

SD = 109) differs significantly from the one of the *tuberosus* morph ($\bar{x}$ = 1443 µm, SD = 71) (Mann-Whitney-*U*-Test, n_1 = 141, n_2 = 105, Z = 13.41, $P < 0.001$). The two morphs are significantly different in prosomal height, the prosoma of the *gibbosus* morph ($\bar{x}$ = 551 µm, SD = 41) being higher than the one of the *tuberosus* morph ($\bar{x}$ = 425 µm, SD = 43) (*t*-Test, $t = -23.35$, $df = 244$, $P < 0.001$).

Some males of the *tuberosus* morph showed a slight depression lacking hair on their prosoma. Comparison of depressions in the *tuberosus* morph ($\bar{x}$ = 14 µm, SD = 10) with the notches of the *gibbosus* morph ($\bar{x}$ = 199 µm, SD = 24) showed a significant difference (*U*-Test: n_1 = 114, n_2 = 105, Z = −12.781, $P < 0.001$). Furthermore, the prosoma of the *gibbosus* morph is significantly broader ($\bar{x}$ = 810 µm, SD = 34) as that of



Figures 1–4.—1. Lateral view of prosoma of the *gibbosus* form of *Oedothorax gibbosus*; 2. Dorsal view of the *gibbosus* form; 3. Lateral view of prosoma of the *tuberosus* form; 4. Dorsal view of the *tuberosus* form.



Figures 5–8.—Schematic representation of the characters measured. 5. Prosoma of *gibbosus* form, lateral view; 6. Lateral view of prosoma of the *tuberosus* form; 7. Dorsal view of prosoma of the *tuberosus* form; 8. First leg: a = length of patella plus tibia of the first leg, b = height of the prosoma, c = width of the prosoma, d = length of the prosoma, e = dorsal line along the prosoma, when viewed from the side, and f = depth of the notch.

the *tuberosus* morph ($\bar{x} = 793$ μm, SD = 34) (*t*-Test: $t = -3.68$, $df = 244$, $P < 0.001$). The width of the prosoma significantly correlates with its height (Spearman rank correlation, $r_s = 0.246$, $n = 246$, $P < 0.001$).

Although the *gibbosus* morph has a broader and higher prosoma than the *tuberosus* morph the difference in the length of the prosoma is only marginally significant (*gibbosus* morph: $\bar{x} = 1007$ μm, SD = 31, *tuberosus* morph: $\bar{x} = 1015$ μm, SD = 38; *t*-Test: $t = 1.85$, $df = 244$, $P = 0.066$). Interestingly, the two morphs do not differ in overall body size as measured by the leg character (*gibbosus* morph: $\bar{x} = 861$ μm, SD = 32, *tuberosus* morph: $\bar{x} = 865$ μm, SD = 32; *t*-Test: $t = 1.078$, $df = 241$, $P = 0.285$), although the leg measure significantly correlates with prosoma length ($r_s = 0.5$, $n = 243$, $P < 0.001$).

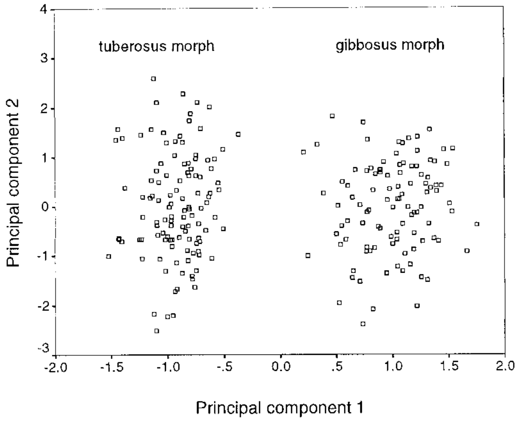


Figure 9.—Scatter plot of scores resulting from Principal Component Analysis.

Relative numbers of the two morphs are highly skewed towards the *tuberosus* morph in all of the four locations examined (Table 2).

DISCUSSION

The results of this work show that the *gibbosus* form and the *tuberosus* form represent two distinct morphs of *O. gibbosus,* thus corroborating the rearing experiments by Maelfait et al. (1990). We did not find any intermediate forms as supposed by Roberts (1987) although variation is considerable. This vari-

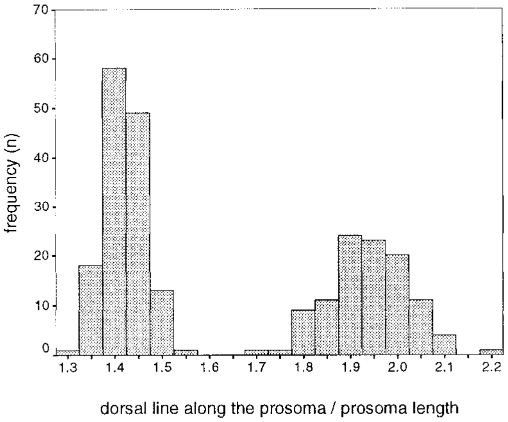


Figure 10.—Histogram of the indices of dorsal line of the prosoma and length of the first leg (n = 246).

Table 2.—Numbers of *Oedothorax gibbosus* and *tuberosus* morphs collected by pitfall trapping at different localities in Belgium (collection de l'Institut Royal des Science Naturelles de Belgique, Bruxelles).

	gibbosus	*tuberosus*	Rel. density
Moha (1977)	13	40	1 : 3.3
Moha (1979)	9	28	1 : 3.1
Virelles (1986)	9	16	1 : 1.8
Ethe (1981)	47	143	1 : 3.0
Antheit (1991)	18	52	1 : 2.9
Total	95	279	1 : 2.9

ation led Roberts to assume intermediate states, when he discussed the existence of both morphs with regard to their assumed species status. Seen in the light of the work by Maelfait et al. (1990) and our data, the intermediates supposed by Roberts are within the variability of the morphs: a slight notch was apparent in extremes of *tuberosus* morph males which can nevertheless easily be assigned to one distinct morph or the other, as confirmed by Roberts (*in lit.* 1999). The two morphs are clearly characterized by the presence or absence of a deep hairy notch and a hump on the prosoma.

Our results are based on individuals caught in pitfall traps from various places in Belgium in different years. Variations between populations whose characteristics may differ in time and location are thus included. Investigating individuals of one population from one location in one year should result in even stronger morphometric distinction of the two morphs.

It is a surprising finding that the *gibbosus* morph occurs in lower numbers compared to the *tuberosus* morph in all four locations we investigated (Table 2). The data given by Maelfait et al. (1990), however, show higher relative numbers of the *gibbosus* morph in two of seven additional locations. Thus, altogether, the *tuberosus* morph is predominant in 9 of 11 locations, although the *gibbosus* morph is genetically dominant. Different collection methods as an explanation can be ruled out, as all specimens were collected by pitfall trapping. Ecological factors seem to play an important role in determining the relative number of the two morphs. Examinations of the ecological demands and needs of both morphs may reveal a higher flexibility towards environmental changes of the *tuberosus* morph compensating for the genetic dominance of the *gibbosus* morph.

Sexual selection very likely also plays a role in balancing the dimorphism. Gustatorial courtship, the uptake of secretions by the female from a body part of the male during courtship is known for several linyphiid spiders (Lopez & Emerit 1981; Schaible et al. 1986; Schaible & Gack 1987). Indeed, SEM examinations of the notch revealed pores in the hair bases and ducts in the hairs of the *gibbosus* morph whereas no specializations were found in the prosoma of the *tuberosus* morph (Heinemann 1998). Preliminary investigation of courtship and mating behavior demonstrated that the chelicerae of the females contact the hairy notch of the *gibbosus* males (Heinemann 1998). If *gibbosus* males offer secretions to the female during courtship they should be sexually selected, i.e., females are expected to show preference for this morph.

Thus, we would expect the *gibbosus* morph to be sexually selected and the *tuberosus* morph to be naturally selected, possibly due to increased viability in comparison to *gibbosus* males. The role of gustatorial courtship, male mating behavior and female choice in combination with an investigation on ecological determinants need to be tackled to try to understand costs and benefits of the marked male dimorphism in *O. gibbosus*.

ACKNOWLEDGMENTS

We are indebted to Léon Baert (Institut Royal des Sciences Naturelles de Belgique) for the spider loan that made this work possible. The SEM photographs were taken at the Museum Koenig in Bonn. The comments of Gustavo Hormiga, Jean-Pierre Maelfait, Michael Roberts, Michael Schmitt, and the editor helped to improve the manuscript. Thanks are also extended to Ingo Nieschalke for help with computerized graphical presentation of the photographs.

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Manuscript received 30 April 1999, revised 25 August 1999.