

Morphological comparison of bisexual and parthenogenetic  
*Polyxenus lagurus* (Linné, 1758) (Diplopoda, Polyxenidae)  
in Denmark and Southern Sweden, with notes on taxonomy,  
distribution, and ecology

by HENRIK ENGHOFF

*Abstract:* A morphological comparison of the bisexual and the parthenogenetic (thelytokous) form of *Polyxenus lagurus*, based on several metric and meristic characters, is presented. Both forms are rather variable, and cannot be separated from each other by the measured characters. A few samples are constituted by exceptionally large or small individuals. The two forms were distinguished entirely on the basis of sex ratio, which is not fully satisfactory, since it cannot be excluded that the thelytokous form produces a few males.

It is recommended to distinguish neither the thelytokous form nor the "giant" and "dwarf" populations as separate species or subspecies. On the other hand, *Polyxenus fasciculatus* Say may be a subspecies of *P. lagurus*.

The distribution of the two forms of *P. lagurus* in Denmark and southern-most Sweden is mapped, and new records from other countries are given.

No difference in choice of habitat between the two forms could be demonstrated. A parasitoid gallmidge, presumably *Chiliodiplosis vasta*, attacks both forms and is recorded for the first time from Denmark and Sweden.

#### INTRODUCTION

Parthenogenesis in *Polyxenus lagurus* has been studied by rather many authors. Vandel (1926, 1928) discussed the geographic variation in sex ratio and hypothesized that the rarity or lack of males in the northeastern parts of Europe might be attributed to *thelytoky* (i. e. parthenogenesis in which unfertilized females produce female offspring). Vandel's data were mapped by Udvardy (1969) who mentioned *P. lagurus* as an example of geographic parthenogenesis: the existence within one species or species-group of bisexual and thelytokous forms with different distribution areas. Schömann (1956) proved that the maleless form of *P. lagurus* actually is thelytokous, and gave a good general account of the biology of the species. Several others have commented on varying sex ratios in *P. lagurus*, see Enghoff (in press) for references.

Schömann (1956) noted a colour difference between the bisexual and the thelytokous form, and Duy-Jacquemin (1975, 1976) made a thorough biometrical comparison of the two forms.

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### MATERIAL

This paper is based on the collections of the Zoological Museum, Copenhagen, and the Natural History Museum, Gothenburg, Sweden. Most of the Copenhagen material was collected by myself or by friends, who collected at my request. Most of the Gothenburg material was collected by H. Lohmander. A few samples were borrowed from the collections of the Royal Veterinary and Agricultural College, Copenhagen.

In Table 1, the basis material is presented. With one exception, only samples of 10 or more individuals of stadia VII and later stadia (12 or 13 pairs of legs) are shown, although numerous smaller samples were studied. Only samples shown in Table 1 were used for sex ratio calculations and biometrical studies.

Although the sexes can be separated from stadium VI (10 pairs of legs) onwards, I have followed Meidell (1970) and have used stadium VII etc. only. Even with this restriction, it may be rather difficult to see whether an individual (especially if it is badly preserved) possesses penes (♂) or vulvae (♀). See illustrations in Schömann (1956).

### ACKNOWLEDGEMENTS

Material brought me by Kristian Arevad, Inge Bødker Enghoff, Peter Gjelstrup, Ole Lomholdt, Ole Martin and Ulrik Søchting was of great value.

S. L. Tuxen provided excellent working facilities at the Zoological Museum, Copenhagen. H. W. Waldén and N. Haarløv made the collections of the Natural History Museum, Gothenburg, and the Royal Veterinary and Agricultural College, Copenhagen, respectively, accessible to me.

M. Nguyen Duy-Jacquemin, Paris, M. Kane, Michigan, and A. Minelli, Padova, kindly let me use unpublished information.

Inge Bødker Enghoff perused the manuscript, and A. Volsøe corrected the text linguistically.

I extend my sincere thanks to these persons.

The investigation was made, while I received a graduate scholarship from the University of Copenhagen. "Japetus Steenstrups legat" provided economical support to travels in connection with the study.

### ANALYSIS OF THE SEX RATIO

The following analysis is based entirely on the material studied by myself and shown in Table 1. It is true that Vandel (1928) listed a large material from Sweden in a way that permits calculation of the sex ratio. Vandel, however, did not state his criteria for separating the sexes (cf. above). Therefore, his data have been left out for the sake of comparability.

Table 1. The material.

Locality	Province sensu Fauna ent. Scand., e. g. Lomholdt, 1976	Date	Habitat	♂♂	♀♀	♂♂+ ♀♀	♂-9/0	Thelyto- kous (T) or bisex- ual (B)
Denmark:								
Thyborøn	NWJ	27.6. 1935	house	4	153	157	2.5	T
Løvel	EJ	15.10. 1956	stone fence	0	43	43	0.0	T
Karup	WJ	6.9. 1956	stone fence	0	13	13	0.0	T
Hinge	EJ	24.4. 1974	under bark	0	10	10	0.0	T
Rønde	EJ	28.6. 1974	under bark	8	10	18	44.4	B
Malt	WJ	6.10. 1956	stone fence	0	18	18	0.0	T
Bov	SJ	19.6. 1936	?	3	10	13	23.1	B
Ore	F	25.5. 1937	?	1	13	14	7.1	?
Bederslev	F	17.5. 1937	stone fence	6	38	44	13.6	B
Turø	F	27.5. 1937	under bark	2	13	15	13.3	B
Tranekær	F	6.7. 1937	hollow tree	6	15	21	28.6	B
Sjællands Odde	NWZ	18.5. 1970	under stones	15	10	25	60.0	B
Sejerø	NWZ	seve- ral	under stones	40	32	72	55.6	B
St. Dyrehave I	NEZ	23.2. 1974	under bark	0	59	59	0.0	T
St. Dyrehave II	NEZ	12.9. 1975	under bark	0	60	60	0.0	T
Hellebæk	NEZ	June 1898	?	9	4	13	69.2	B
Gunderslevlille	SZ	22.10. 1974	under bark	0	12	12	0.0	T
Sundby	LFM	9.9. 1975	under bark	15	43	58	25.9	B

*Continued*

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Table 1, continued.

Locality	Province sensu Fauna ent. Scand., e. g. Lomholdt, 1976	Date	Habitat	♂♂	♀♀	♂♂+ ♀♀	♂- <sup>o</sup> / <sub>o</sub>	Thelyto- kous (T) or bisex- ual (B)
Marielyst	LFM	22.6. 1954	house	0	80	80	0.0	T
Åstrup	LFM	14.9. 1933	under bark	23	32	55	41.8	B
Møns Klint	LFM	6.9. 1933	under bark	8	23	31	25.8	B
Humledal	B	29.8. 1973	under bark	12	37	49	24.5	B
Gudhjem	B	26.10. 1930	salt marsh with pebbles	0	77	77	0.0	T
Bodilsker	B	24.10. 1930	under stones	205	279	484	42.4	B
Vestermarie	B	27.9. 1930	under bark	15	15	30	50.0	B
Hammeren	B	Sept. 1975	lichens on coastal rocks	14	22	36	38.9	B
Sweden:								
Lerbäck I	Nrk	30.7. 1954	stone fence	0	40	40	0.0	T
Lerbäck II	Nrk	19.6. 1954	stone fence	0	15	15	0.0	T
Bo	Nrk	28.7. 1954	stone fence	0	12	12	0.0	T
Bärbo	Sdm	5.6. 1954	stone fence	0	33	33	0.0	T
Bergshammar	Sdm	28.5. 1954	?	0	50	50	0.0	T
Nykyrka	Sdm	6.6. 1954	stone fence	0	13	13	0.0	T
Undenäs	Vg	20.6. 1954	?	0	16	16	0.0	T
Kisa	Ög	27.6. 1941	?	0	41	41	0.0	T
Kättilstad	Ög	28.6. 1941	?	0	36	36	0.0	T

*Continued*

Table 1, continued.

Locality	Province sensu Fauna ent. Scand., e. g. Lomholdt, 1976	Date	Habitat	♂♂	♀♀	♂♂+ ♀♀	♂-0/0	Thelyto- kous (T) or bisex- ual (B)
Krokek	Ög	11.6. 1954	?	0	28	28	0.0	T
Dörby	Sml	4.6. 1926	stone fence	5	189	194	2.6	T
Älmeboda	Sml	12.6. 1928	?	0	15	15	0.0	T
Bökeberg	Sk	17.8. 1975	under bark	0	54	54	0.0	T
Vollsjö	Sk	16.8. 1933	stone fence	0	24	24	0.0	T
Våmb	Sk	22.6. 1930	stone fence	0	15	15	0.0	T
Häckeberga	Sk	1.6. 1930	?	0	34	34	0.0	T
Bolshög	Sk	19.8. 1933	?	0	19	19	0.0	T
Simris	Sk	13.8. 1933	under moss on stones	3	6	9	(33.3)	(B)

Judged from Table 1, males are almost absent throughout southern Sweden. Only two out of 18 Swedish samples include males, and only one of these has males in a considerable proportion (Simris, Sk: 3 ♂♂ + 6 ♀♀). The rarity of males naturally raises the suspicion that most of the Swedish populations are thelytokous. It should be mentioned, however, that Vandell (1928) listed several male-rich besides many male-poor samples from southern Sweden (cf. above).

In Denmark, the sex ratio varies very considerably. A frequency diagram based on the Danish material (Fig. 1) shows this graphically. It is evident that there is no clear distinction between high and low male-percentages, except for the comparatively large number of all-female samples. It might be tempting to regard the all-female samples as representing the thelytokous form, and all the remaining ones, the bisexual form. This attitude is justified if one accepts Schömann's (1956) statement that the thelytokous form is purely thelytokous, i. e. it never produces males. However, several

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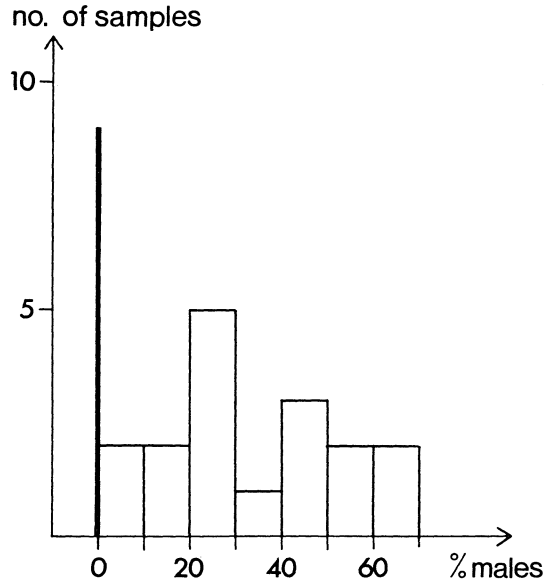


Fig. 1. Frequency distribution of the sex ratio in Danish samples of *P. lagurus*. Only samples consisting of 10 or more sexed individuals. The heavy vertical bar represents 9 all-female samples.

other thelytokous animals do produce a low number of (presumably often functionless) males (e.g. *Proteroiulus fuscus* (Diplopoda, Blaniulidae) (Rantala, 1974), to mention another millipede). *A priori*, it cannot be excluded that this is also the case in *P. lagurus*. Schömann (1956) may just have been “unfortunate” in not getting any fatherless males in his cultures.

The chromosomes of the male of *P. lagurus* were counted by Tuzet & Manier (1957), who reported  $2n = 20 + X$ . It is easy to suggest that the female has  $2n = 20 + XX$ , and fatherless “mistake-males” thus could be produced by loss of an X-chromosome during oogenesis in thelytokous females.

Schömann (1956) reported only modest fluctuations in the sex ratio for the bisexual form. Although somewhat wider seasonal fluctuations were reported by Condé & Duy (1971), although Vandel's (1928) data for the bisexual form in S. France indicate rather considerable seasonal fluctuations, and although very wide seasonal fluctuations in sex ratio have been recorded in some bisexual millipedes (e.g. Sahli, 1967), I find it more likely that e.g. the samples from Thyborøn, NWJ (4 ♂♂ + 153 ♀♀) and Dörby, Sml (5 ♂♂ + 189 ♀♀) represent the thelytokous form with a few

“mistake” males, than the bisexual form in an extremely male-poor phase. The fact that *P. lagurus* often lives for more than one year as an adult (Schömann, 1956) would tend to level out seasonal fluctuations in the sex ratio. I have had the opportunity to sample a bisexual population (Sejerø, NWZ) on three occasions. These samples (21.VI: 14 ♂♂ + 13 ♀♀; 30.VII: 14 ♂♂ + 13 ♀♀; 18.IX: 12 ♂♂ + 6 ♀♀), admittedly, cover only four months of the year, but the results indicate that the sex ratio of the bisexual form probably does not fluctuate so much that samples like these mentioned above from Thyborøn and Dörby would result. If the total material (Table 1) is considered, a seasonal trend in the sex ratio also cannot be detected.

Since no reliable morphological difference between the two forms is known (see below), the sex ratio is the only way to separate them. In the remaining part of this paper, a male percentage of less than 10% is taken as evidence that a sample represents the thelytokous form, incl. possible “mistake-males”. Male percentages higher than 10% represent bisexual populations in this interpretation. Of course, it cannot be excluded that the two forms may occur in mixed populations, as is the case in another millipede, *Nemasoma varicorne* (Blaniulidae) (Enghoff, 1976c) (cf. Schömann, 1956, p. 203), but with the above conventions, one would hardly record erroneously the occurrence of one of the forms, although one form might be omitted in spite of its presence. A single sample (Ore, F: 1 ♂ + 13 ♀♀, 7,1% ♂♂) is “dubious” (one male more would have raised the male percentage above the 10% limit), and I have left the question open, which form this sample represents.

#### INTRODUCTION TO THE MORPHOLOGICAL COMPARISON OF THE TWO FORMS

Schömann (1956) only found a colour difference between the two forms of *P. lagurus*. According to him, the bisexual form is characterized by three dark-coloured longitudinal bands on the dorsal side of the body. These bands, he stated, are only very faintly developed in the thelytokous form.

A careful morphological comparison of the two forms of *P. lagurus* and the American bisexual *P. fasciculatus* Say, 1821 was made by Duy-Jacquemin (1975, 1976). Apart from the colour difference (as to which she agreed with Schömann) Duy-Jacquemin studied the following characters:

The length of the tarsus of the first pair of legs ( $t_1$ ).

The sum of the lengths of the two segments of the tarsus of the last (13th) pair of legs ( $t_{13}$ ).

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The number of trichomes on the posterior part of the vertex (*tr*).

The number of sensillae on the gnathochilarial palp (*gn*).

The number of thin bacilliform sensillae on the sixth antennal segment (*a*VI).

The number of thin bacilliform sensillae on the seventh antennal segment (*a*VII).

$t_1$  and  $t_{13}$  were used as measurements of "body size". The total body length of an individual cannot be used as a measure, because the body may be more or less contracted. The width of the head was not measured by Duy-Jacquemin, because this measure is influenced by the pressure of the coverglass.

In order to make my measurements comparable with those of Duy-Jacquemin, I used the same characters as she, but added another, namely:

The width of the head (including the eyes) (*h*).

*h* was measured through the stereo microscope before the head was placed under a coverglass.

Duy-Jacquemin (1975) found that bisexual males are significantly smaller (tarsus lengths!) than bisexual females. I have not included males in my investigation, but compared the two types of females only.

It is evident from the results of Duy-Jacquemin (1976) that the morphological difference between bisexual *P. lagurus* and *P. fasciculatus* is rather inconclusive. In some places (N. Spain, Madeira) intermediate forms exist, which are referred to *P. lagurus*. There is, however, no indication that the thelytokous *Polyxenus* found in N. America is more similar to "fasciculatus" than to *lagurus*. Therefore, it may still be maintained that the thelytokous form of *P. lagurus* lives in N. America.

Measurements were taken on seven Danish and one South Swedish samples, namely: Thyborøn, St. Dyrehave I, St. Dyrehave II, Marielyst, Bøkeberg (thelytokous), and Sejerø, Sundby, Humledal (bisexual) (cf. Table 1). The results of the measurements are shown in Table 2, together with the relevant figures from Duy-Jacquemin (1976) for comparison. For the character *gn*, the range of the number of sensillae on each palp is shown, but the sum for the two palps (*sgn*) was used for statistical calculations. The characters *a*VI and *a*VII are treated analogously, but here, the sum total of thin bacilliform sensillae on antennal segments VI + VII on the two antennae (*a*) was used for the calculations (numbers of sensillae on segments VI and VII are positively correlated). I attempted to measure



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Table 2. Results of the morphological studies. Abbreviations: Orig.: original results; D-J: from Duy-Jacquemin (1976); n: number of individuals, palps, or antennae; s.d.: standard deviations; *b*: width of head ( $\mu\text{m}$ ); *t*<sub>1</sub>: length of tarsus 1 ( $\mu\text{m}$ ); *t*<sub>13</sub>: length of tarsus 13 ( $\mu\text{m}$ ); *tr*: number of posterior trichomes on the vertex; *gn*: number of sensillae on the gnathochilarial palp; *sgn*: sum of *gn* for the two palps of an individual; *a*VI: number of thin bacilliform sensillae on antennal segment VI; *a*VII: number of thin bacilliform sensillae on antennal segment VII; *a*: sum of *a*VI + *a*VII for the two antennae of an individual.

Thelytokous samples:		<i>b</i>	<i>t</i> <sub>1</sub>	<i>t</i> <sub>13</sub>	<i>tr</i>	<i>gn</i>	<i>sgn</i>	<i>a</i> VI	<i>a</i> VII	<i>a</i>
Thyborøn	n	20	19	19	17	34	15	40	39	19
Orig.	range	553-646	98-108	158-179	45-54	10-15	21-29	5-9	3-6	16-25
	mean	594	102.3	165.6	50.8	-	24.9	-	-	19.8
	s. d.	30	2.8	5.1	2.7	-	2.3	-	-	2.6
St. Dyrehave I	n	20	19	20	20	39	19	40	40	20
Orig.	range	544-646	96-114	160-175	48-61	9-12	21-24	5-10	3-6	21-28
	mean	597	103.6	165.1	52.9	-	23.4	-	-	24.0
	s. d.	34	3.8	3.8	3.7	-	1.0	-	-	2.4
St. Dyrehave II	n	19*	20	20	18	39	19	40	40	20
Orig.	range	536-612	96-108	155-166	44-51	8-12	20-24	4-6	2-5	13-20
	mean	567	102.2	160.0	48.3	-	23.6	-	-	15.5
	s. d.	22	3.3	3.1	1.6	-	1.1	-	-	1.9
Marielyst	n	20	20	19	20	40	20	39	38	18
Orig.	range	604-672	120-127	178-192	46-51	10-15	22-27	6-9	3-5	19-25
	mean	647	123.3	184.8	48.3	-	23.9	-	-	21.6
	s. d.	18	2.1	6.0	1.8	-	0.9	-	-	1.7
Bøkeberg	n	20	20	20	20	39	19	40	40	20
Orig.	range	510-655	93-108	148-169	46-57	8-13	20-25	4-7	3-5	15-21
	mean	573	101.7	160.1	50.1	-	23.2	-	-	18.1
	s. d.	30	3.0	6.0	2.9	-	1.6	-	-	1.3
France	n	-	-	-	-	47	-	26	24	-
D-J	range	-	88-106	137-170	42-62	9-13	-	5-6	3-5	-
	mean	-	96	155	50.4	-	-	-	-	-
	s. d.	-	3.9	6.3	3.6	-	-	-	-	-
USA	n	-	-	-	-	55	-	60	58	-
D-J	range	-	99-111	147-171	41-58	10-15	-	4-6	3-4	-
	mean	-	104.3	158.1	46.4	-	-	-	-	-
	s. d.	-	3.0	6.6	3.6	-	-	-	-	-

\*one individual with an exceptionally (teratologically?) narrow head (493  $\mu\text{m}$ ) not included in the calculations.

Continued

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Table 2, continued.

Bisexual samples		<i>h</i>	<i>t</i> <sub>1</sub>	<i>t</i> <sub>13</sub>	<i>tr</i>	<i>gn</i>	<i>sgn</i>	<i>a</i> VI	<i>a</i> VII	<i>a</i>
Sejerø	n	12	12	12	10	23	11	16	17	7
Orig.	range	544-604	93-110	148-169	42-53	9-14	18-27	4-9	3-5	17-24
	mean	571	99.4	156.7	46.8	-	23.3	-	-	19.3
	s. d.	22	3.9	6.1	3.6	-	3.0	-	-	2.6
Sundby	n	20	20	20	19	40	20	40	40	20
Orig.	range	553-646	96-112	157-173	48-59	9-15	21-29	5-8	2-4	16-22
	mean	574	101.2	163.3	53.8	-	24.3	-	-	18.4
	s. d.	29	4.6	4.6	2.8	-	1.7	-	-	1.7
Humledal	n	14	13	14	14	28	14	27	27	13
Orig.	range	553-629	96-108	158-176	45-57	10-13	21-25	4-6	2-4	14-19
	mean	586	103.6	167.3	51.0	-	23.4	-	-	16.9
	s. d.	26	2.9	5.6	3.3	-	1.1	-	-	1.5
France	n	-	-	-	-	55	-	30	30	-
D-J	range	-	96-112	156-180	52-62	11-15	-	5-10	3-5	-
	mean	-	104.6	169.7	54.7	-	-	-	-	-
	s. d.	-	4.1	5.5	2.9	-	-	-	-	-
Corfu,	n	-	-	-	-	15	-	17	16	-
Greece	range	-	99-111	159-173	44-54	13-15	-	5-6	3-4	-
D-J	mean	-	105.9	166.9	48.5	-	-	-	-	-
	s. d.	-	3.5	4.7	2.7	-	-	-	-	-
Gerona,	n	-	-	-	-	10	-	10	12	-
Spain	range	-	64-77	98-119	40-47	11-12	-	6-10	3-4	-
D-J	mean	-	69.9	106.7	42.5	-	-	-	-	-
	s. d.	-	4.1	5.1	2.7	-	-	-	-	-

20 fullgrown females (13 pairs of legs) from each sample. In many cases, the number had to be lower, either due to lack of specimens, or because e. g. one or both antennae of some specimens were broken, or because the sensillae were impossible to count due to inadequate position under the coverglass. Hence the varying numbers of measurements (n) in Table 2.

STATISTICAL TREATMENT OF THE MORPHOLOGICAL CHARACTERS

The statistical calculations are based on the eight original samples mentioned in Table 2. For each sample, all types of linear correlations between pairs of characters were worked out. Table 3 shows significant correlations

found. It is evident that the characters most frequently correlated with some other character are: width of head ( $b$ ), length of tarsus 1 ( $t_1$ ), length of tarsus 13 ( $t_{13}$ ), and number of the posterior trichomes on the vertex ( $tr$ ). This is not surprising, since the characters  $b$ ,  $t_1$ , and  $t_{13}$  all are measurements of body size, and since large heads can carry more trichomes than small heads.

If the sample means are used for inter-sample correlations (i. e. eight pairs of values for each correlation, corresponding to eight samples), only the "body size characters" show significant correlation between them. If, however, the extraordinarily large individuals from the Marielyst-sample are excluded, there is no significant inter-sample correlation between any pair of characters.

It may be noted that "nonsense" correlations (e. g. length of tarsus 1 / number of gnathochilarial sensilla) are more frequent in thelytokous samples than in bisexual ones. It is tempting to suggest that this may reflect decreased variability in the thelytokous form.

It is remarkable that some samples show no or very few correlations (e. g. Humledal), while others exhibit a considerable number of significant correlations (e. g. St. Dyrehave I).

Table 3. Correlation of characters. Only character combinations, which show significant linear correlation in one or more samples, are listed.

Symbols: +: positive linear correlations; -: negative linear correlation; x:  $p < 0.05$ ; xx:  $p < 0.01$ .

	$b/t_1$	$b/t_{13}$	$b/tr$	$b/a$	$t_1/t_{13}$	$t_1/tr$	$t_1/gn$	$t_{13}/tr$	$tr/a$	$gn/a$
Thelytokous samples:										
Thyborøn									- x	
St. Dyrehave I	+ xx		+ xx	+ xx	+ xx	+ xx		- x		+ xx
St. Dyrehave II	+ xx	+ x			+ xx					
Marielyst										+ x
Bøkeberg	+ x		+ xx	+ x	+ x	+ x				
Bisexual samples:										
Sejerø			+ x			+ x				
Sundby	+ xx	+ xx			+ xx					
Humledal										
All sample means	+ xx	+ xx			+ xx					
Do., Marielyst excluded										

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Table 4. Significances of added components of variance between samples.  
 Symbols: n. s.:  $p \geq 0.05$ ; x:  $p < 0.05$ ; xx:  $p < 0.01$ ; xxx:  $p < 0.001$ .

Character	<i>b</i>	<i>t</i> <sub>1</sub>	<i>t</i> <sub>13</sub>	<i>tr</i>	<i>gn</i>	<i>a</i>
Bisexual samples	n. s.	x	xxx	xxx	n. s.	x
Thelytokous samples	xxx	xxx	xxx	xxx	xx	xxx
Do., Marielyst excluded	xxx	n. s.	xxx	xxx	x	xxx
All samples	xxx	xxx	xxx	xxx	x	xxx
Do., Marielyst excluded	xx	x	xxx	xxx	x	xxx

The question whether there is any difference between the bisexual and the thelytokous form in the investigated characters was approached by means of a nested analysis of variance (Sokal & Rohlf, 1969). In this statistical method, three levels of variation are considered for each character. I: the variation *within each sample*, II: the variation *between samples* of one reproduction type, III: the variation *between reproduction types* (bisexual versus thelytokous).

If there is an added component of variation between samples of one reproduction type, it can be concluded that populations of *P. lagurus* are different from one another. If there is a further added component of variation between the bisexual versus the thelytokous samples, it can be concluded that the two forms are morphologically different.

Table 4 shows significances of added components of variance *between samples*. It is evident that there is a considerable variation between samples, both in the bisexual and in the thelytokous form. This is true, even if the exceptional Marielyst-sample is excluded from the calculations. It might appear that inter-sample differences are "more significant" in the thelytokous than in the bisexual form. It should, however, be remembered that more thelytokous than bisexual samples were investigated.

If all samples are considered together (simple analysis of variance), a picture similar to that obtained for thelytokous samples results.

It is of particular interest that in no characters is there any added component of variation *between reproduction types*, i. e. no difference between the bisexual and the thelytokous form can be demonstrated.

## DISCUSSION OF THE MORPHOLOGICAL CHARACTERS

*Width of head (h).*

As mentioned above, Duy-Jacquemin refrained from measuring the head. If unmounted specimens are available, the width of the head is, in my opinion, a more direct measurement of body size than the length of tarsi.

The thelytokous Marielyst-sample is clearly different from all the other samples, the Marielyst individuals having much wider heads. Among the remaining original samples, St. Dyrehave I and St. Dyrehave II, both thelytokous, and taken less than five kilometers from each other, have the largest, resp. smallest, mean head widths (seasonal variation?). There is no indication that bisexual females have larger heads than thelytokous females or vice versa.

*Length of tarsi ( $t_1$ ,  $t_{13}$ ).*

These "measurements of body size" are best considered together. Fig. 2 shows the mean values of the samples investigated by Duy-Jacquemin (1976) and myself. Two samples are clearly exceptional: The bisexual sample from Gerona, Spain, has much smaller mean values than the rest, and the thelytokous one from Marielyst has considerably larger mean values. The remaining samples form a quite compact cluster.

Duy-Jacquemin (1975, 1976) stated that the bisexual females of *P. lagurus* (those from Gerona excepted) are generally larger, i. e. have longer tarsi, than thelytokous females. This statement, based on two samples of each form, is clearly invalidated by the present measurements of tarsus lengths (and widths of head, cf. above).

*Number of posterior trichomes on the vertex (tr).*

My counts support the results of Duy-Jacquemin (1976): that there is no difference between the two forms in this character, although considerable differences exist between populations.

The "posterior trichomes" include two more or less regular, parallel rows across the vertex plus two, more rarely three, isolated trichomes situated caudally relative to the rows (Duy-Jacquemin, 1976: Fig. 2). The frequency of individuals with three "ultra-posterior" trichomes instead of two in my material varied from 0 in samples from Thyborøn, St. Dyrehave I, St. Dyrehave II (thelytokous) and Sejerø (bisexual) to 0.3 in samples from Bökeberg (thelytokous) and Humledal (bisexual).

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*Number of sensillae on the gnathochilarial palps (gn, sgn).*

Duy-Jacquemin (1976) stated that the two forms of *P. lagurus* differ in this character, the thelytokous females most frequently having 12 sensillae per palp, and bisexual females, except the small ones from Gerona, usually having more and exhibiting also a wider variation.

No such difference is present in my material, as is evident from Table 2. Twelve sensillae per palp is by far the commonest number both in the thelytokous (140 out of 191 palps) and the bisexual (58 out of 91 palps) form, and there is no difference between the forms as to mean number or variation (range, standard deviation). Admittedly, the "typical" number of 12 sensillae per palp is more frequent in the thelytokous form, but samples with high variability are present, both among the thelytokous (Thyborøn) and the bisexual (Sejerø) samples.

Often, the two palps of an individual have different number of sensillae. The difference may amount to 4 sensillae, although usually, the numbers are less different. Such asymmetries are a little more frequent in the bisexual form (26 out of 45 individuals) than in the thelytokous form (34 out of 92 individuals), but again, some thelytokous samples have a high frequency of asymmetries, e. g. Thyborøn: 10 out of 13 individuals.

*Number of thin bacilliform sensillae on the sixth and seventh antennal segments (aVI, aVII, a).*

The total number of thin bacilliform sensillae on the sixth plus seventh segments on both antennae (*a*) exhibits considerable inter-sample variation. It is remarkable that the largest and smallest sample means were found in the geographically close thelytokous samples St. Dyrehave I and St. Dyrehave II, respectively (cf. above, "width of head").

Duy-Jacquemin (1976) stated that the thelytokous form has fewer sensillae on the sixth antennal segment than the bisexual form. In the thelytokous samples studied by her, the numbers (*aVI*) ranged from 4 to 6. The present thelytokous material shows a much wider variation, the range being from 4 to 10 sensillae per sixth segment. Also, I have seen bisexual females with only 4 sensillae on the sixth segment, while Duy-Jacquemin found minimally 5 in her bisexual females.

The number of thin bacilliform sensillae on the seventh antennal segment also is more variable in my material (range of *aVII*: 2–6 in thelytokous, 2–5 in bisexual females) than in Duy-Jacquemin's (range of *aVII*: 3–5 in both forms).

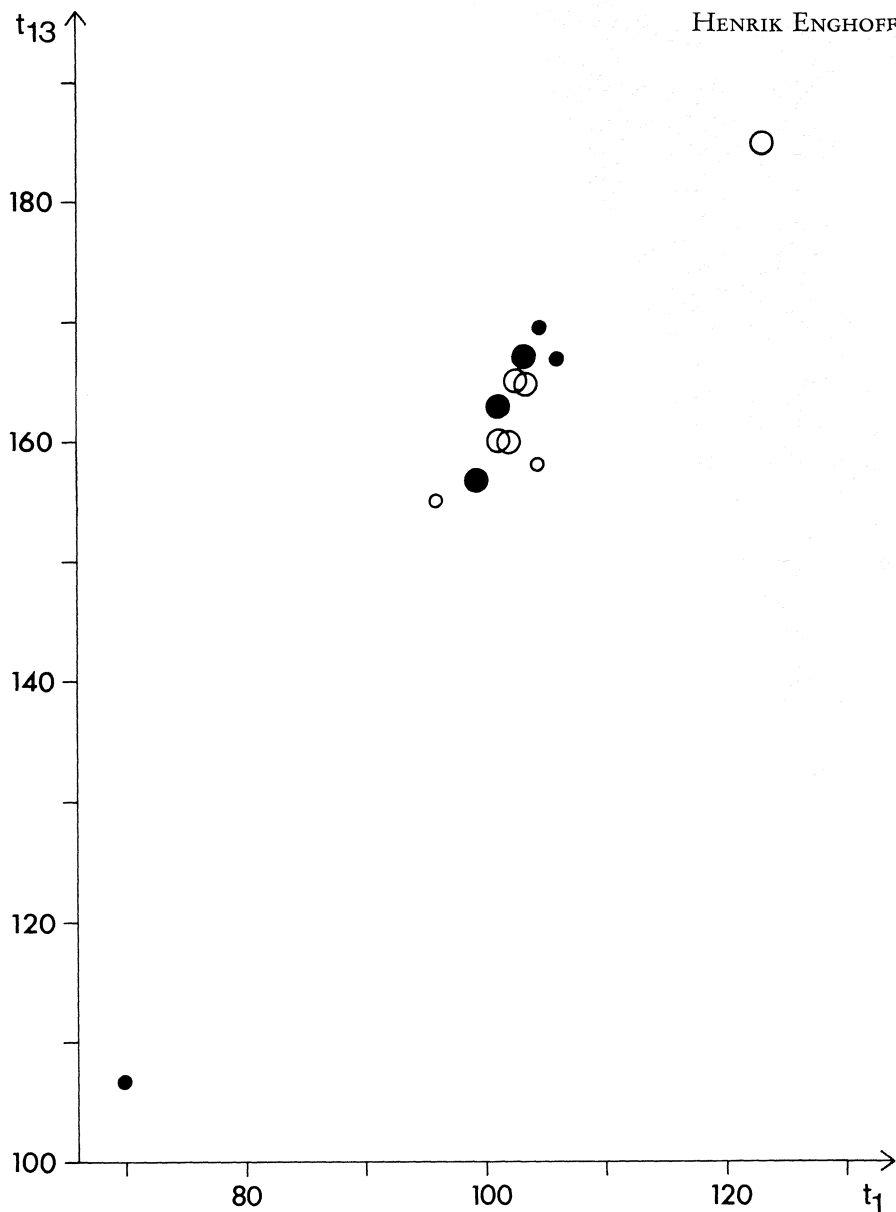


Fig. 2. Graphical representation of tarsus lengths in *P. lagurus*. Sample means of length of tarsus 1 ( $t_1$ ) and corresponding sample means of length of tarsus 13 ( $t_{13}$ ) are shown. Filled circles: bisexual form, open circles: thelytokous form. Large circles: original measurements, small circles: values from Duy-Jacquemin (1976). The isolated small, filled circle in the lower left part of the diagram represents the sample from Gerona, Spain. The isolated large, open circle in the upper right part of the diagram represents the sample from Marielyst, Denmark.

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As in the case of the sensillae of the gnathochilarial palps, asymmetries are frequently found in numbers of antennal sensillae. Although the difference between the two sixth or seventh segments of an individual is usually 0 or 1, differences of 2 (*a*VI) or even 3 (*a*VII) sensillae were found.

*Colour*

I have not been able to detect any colour difference between the bisexual and the thelytokous form of *P. lagurus*, and thus cannot agree with Schömann (1956) and Duy-Jacquemin (1976), who claim that such a difference exists (cf. above). Admittedly, the number of living or freshly killed specimens seen by me is modest, but at least thelytokous individuals from some localities have longitudinal bands quite as pronounced as bisexual individuals.

*The receptaculum seminis*

Tuzet & Manier (1957) gave an illustration of the receptaculum seminis in the bisexual form of *P. lagurus*. It is a spherical, rather large (about 0.2 mm in diameter) sac, connected via a short ductus to the oviduct near the genital pore.

A similar organ was described in the thelytokous form by Reinecke (1910). Although Reinecke was not sure, whether the cavity seen by him actually was a receptaculum (he found a gland in close connection with it, and proposed that the cavity might function as a reservoir of that gland), there is hardly any doubt that the thelytokous form of *P. lagurus* has retained the receptaculum, unlike another thelytokous millipede, *Nemasoma varicorne* (Enghoff, 1976 c).

Of course, careful studies of the receptacula of the two forms may reveal differences. It also cannot be excluded that some thelytokous populations of *P. lagurus* have lost the receptaculum, although others have retained it.

*General conclusions on morphology*

It can be concluded that the hitherto studied characters do not reveal any clear morphological difference between the thelytokous and the bisexual form of *P. lagurus*. Both forms seem to be more variable than assumed by previous authors. It is to be hoped that other characters will be found which can separate the two forms. Anatomical studies of the genitalia may reveal differences (cf. above) and so may caryological or biochemical approaches.

The "exceptional" populations (Gerona, Marielyst) are puzzling. Do



they represent adaptation to special environments? (the Marielyst population lived in a house). Or are they separate (sibling) species? (cf. below).

Another interesting question, which cannot be answered on the basis of the present investigation is, whether the inter-sample variation in the thelytokous form – if it is not purely phenotypic – is due to evolution which occurred after the acquisition of thelytoky, or to polyphyly of the thelytokous form (Enghoff, 1976 b, c, Lokki et al., 1975, Suomalainen & Saura, 1974).

#### TAXONOMIC STATUS OF THE TWO FORMS. SUBSPECIES OF *P. lagurus*?

Schömann (1956) could not accomplish crossings between the bisexual and the thelytokous form in his laboratory cultures. He concluded that this isolation, if it is really significant, would justify the recognition of the two forms as different species.

On the basis of morphological differences between the two forms, Duy-Jacquemin (1975) also thought that the thelytokous form could be separated as a different species.

The result of the present investigation, viz. that no morphological difference between the two forms apparently exists, constitutes a practical objection against separating the two forms as different species or subspecies. But there is also good theoretical reason for not separating them, namely the fact that a polyphyletic origin of the thelytokous form the bisexual form cannot be excluded (Enghoff, 1976 b).

Duy-Jacquemin (1976) suggested that the exceptionally small bisexual *P. lagurus* from Gerona might be separated as a subspecies. The existence of another exceptional population (large thelytokous individuals from Marielyst) clearly counterindicates such a splitting. Very probably, other exceptionally large and small populations remain to be discovered, and the erection of subspecies based on size difference demands a much more comprehensive knowledge of the geographic pattern of size variation in *P. lagurus*. It also should be emphasized that the subspecies concept is not at all applicable to thelytokous forms (Enghoff, 1976 b).

With our present knowledge, I also would find it unwise to designate the exceptional populations as separate (sibling) species.

A third problem is constituted by the North American *P. fasciculatus*, which may very well be found to be only a subspecies of *P. lagurus* (cf. above).

DISTRIBUTION OF THE TWO FORMS

The total distribution of the two forms of *P. lagurus* was mapped by Enghoff (in press). This map was based on literature references, on part of the material dealt with in the present paper, and on material from Soviet and Madeira, belonging to the Natural History Museum, Gothenburg. Since the map was compiled, a considerable amount of new information has accumulated: Duy-Jacquemin (1975, 1976) recorded the bisexual form from several new localities in France and from Corfu (Greece); the thelytokous form the recorded from Nancy (NE. France) and from Washington and New Jersey (USA). A. Minelli (personal communication) has found the bisexual form near Pisa (Italy). M. Kane sent me unquestionable *P. lagurus* from Michigan, stating that no males are present among large samples of this species from Michigan and Ohio (USA). In spite of this new information, the total distribution of the two forms is still far from being wellknown, and I do not find it necessary to present a new map here.

As far as Denmark and S. Sweden are concerned, sufficient information is now available for presenting a provisional map (Fig. 3). As mentioned above, the thelytokous form seems to be absolutely predominant in S. Sweden: there is only one sample (Simris, Sk: 3 ♂♂ + 6 ♀♀) which indicates the presence of the bisexual form in S. Sweden. (Note that not all S. Swedish samples are entered on the map, but only those from Scania (Sk), the southernmost province). As mentioned above, the material seen by me, to some degree, is in conflict with Vandel's (1928) results. A restudy of Vandel's material is desirable.

In Denmark, on the other hand, both forms are undoubtedly present. The map gives the impression that the bisexual form is restricted to the Danish islands plus SE. Jutland, while the thelytokous form occurs throughout most of the country. This is reminiscent of the distribution pattern in another bisexual/thelytokous millipede, *Nemasoma varicorne* (Enghoff, 1976 c), but the evidence in the case of *P. lagurus* is much weaker than in *N. varicorne*. Certainly, more information is wanted before definite conclusions can be drawn.

The similarity of the distribution patterns of *P. lagurus* and *N. varicorne* can be extended to S. Sweden, provided that Vandel's data (1928) are erroneous (cf. above). However, the total distribution of the two forms of *P. lagurus*, as far as known, is quite different from that of *N. varicorne* (cp. the maps of *P. lagurus* (Enghoff, in press, and new data listed in the present paper) and *N. varicorne* (Enghoff, 1976 c)).

Until a more complete distribution map of the two forms of *P. lagurus* is available, very little can be concluded, except that *P. lagurus* undoubtedly is an example of geographic parthenogenesis (Vandel, 1928, Udvardy, 1969). Vandel's (1928) generalization: that the male percentage decreases from SW. Europe towards NE. Europe must, however, be dismissed. The same is most probably true of Schömann's (1956) hypothesis, supported by Meidell (1970): that the bisexual form may be dependent on a humid (maritime) climate.

#### ECOLOGY OF THE TWO FORMS

Although Schömann (1956) thoroughly studied the ecology of *P. lagurus*, no investigations comparing the bisexual and the thelytokous form have so far been undertaken. Duy-Jacquemin (1976) found that the thelytokous form survived better in captivity than the bisexual form. This may be due

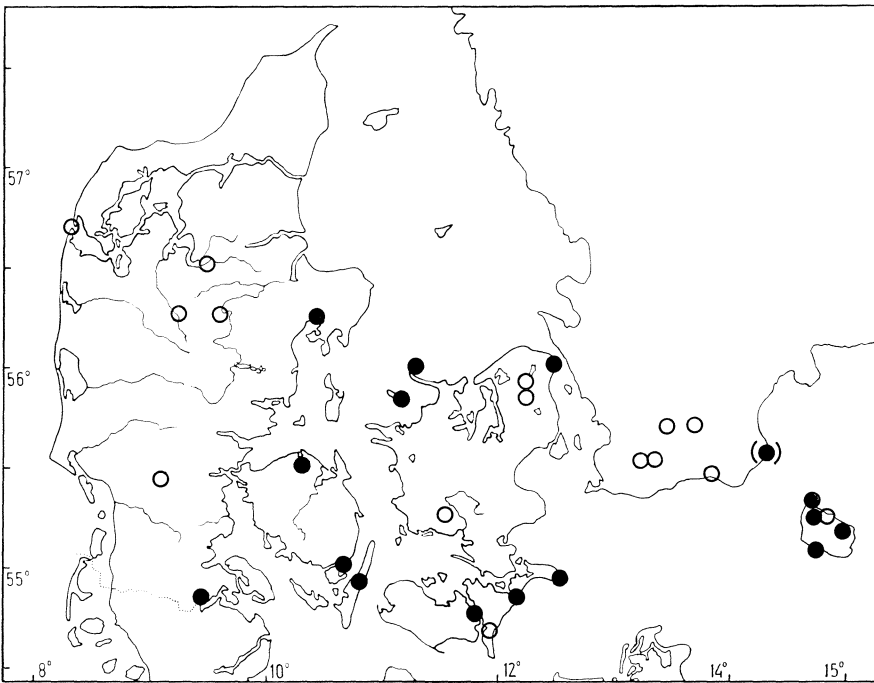


Fig. 3. Distribution of the two forms of *P. lagurus* in Denmark and the southernmost province in Sweden (Scania). Filled circles: bisexual form, open circles: thelytokous form. Many more thelytokous samples were seen from further north in Sweden (cf. Table 1). The filled circle in parentheses (SE. Scania) represents a sample of only 9 individuals.

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Table 5. Danish samples, arranged according to habitat.

	Bisexual samples	Thelytokous samples
Associated with trees (under bark etc.)	7	4
Associated with stones (stone fences etc.)	5	4
In houses	0	2

to lesser tolerance of males compared to females (as in *Nemasoma varicornis*, (Enghoff, 1976 c)) or of bisexual females compared to thelytokous (and possibly polyploid) females (as in the weevil (Coleoptera: Curculionidae) *Otiorrhynchus dubius*, (Lindroth, 1954)).

In an area, where the two forms live sympatrically, like Denmark, it could be imagined that their habitats were different (Enghoff, 1976 a). *P. lagurus* actually occurs in a wide range of habitats: on trees (under bark etc.), in forest litter, under stones, in houses etc. In Table 5, the Danish samples are arranged after habitat type. It is evident that the present material reveals no difference between the two forms with regard to choice of habitat. It would be interesting to get more samples from houses, since so far only the thelytokous form has been found in this habitat. One of the samples from houses is the Marielyst-sample, consisting of exceptionally large individuals.

Schömann (1956) found a parasitoid gallmidge (Diptera: Itonididae), *Chilodiplosis vasta* Möhn, 1955 on individuals from two thelytokous populations in W. Germany. Duy-Jacquemin (1976) recorded the parasitoid from bisexual populations in France. I have seen gall-midge larvae, presumably *C. vasta*, on individuals from Humledal, B (bisexual), Løvel, EJ (thelytokous) and Kisa, Ög (thelytokous). In all cases, only single larvae were present. Some of the larvae were found detached from the host, but others were attached to one of the lateral trichome bundles by their anterior ends. This is hardly a natural position of the parasitoid. Schömann (1956) stated that the young larvae of *C. vasta* sit between the segments of the host. Later, they may move to the ventral side of the host, which dies from the attack.

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### SAMMENDRAG:

En morfologisk sammenligning mellem biseksuelle og parthenogenetiske *Polyxenus lagurus* (Linné, 1758) (Diplopoda, Polyxenidae) i Danmark og Sydsverige, med bemærkninger om taxonomi, udbredelse og økologi.

Det har længe været kendt, at *Polyxenus lagurus* omfatter såvel en biseksuel som en parthenogenetisk – eller nøjagtigere: thelytok – form (thelytoki er den type parthenogenese, hvor ubefrugtede æg udvikles til hunner). Tidligere forfattere har hævdet, at de to former kunne skelnes morfologisk. I nærværende artikel påvises det, at begge former er mere variable end tidligere antaget og således *ikke* kan adskilles ved hjælp af de undersøgte karakterer (farvetegning, hovedbredde, længde af tarser, antal af trichomer og sensiller på forskellige legemsdele).

En af de undersøgte thelytoke populationer udmærker sig ved ekstraordinær stor størrelse og danner et modstykke til en tidligere beskrevet »dværg«-population af den biseksuelle form.

Da der således ikke kan påvises nogen morfologisk forskel mellem de to former, kan de i praksis kun adskilles ved hjælp af kønskvotienter i foreliggende materiale. Denne adskillelse besværliggøres af, at man ikke kan udelukke, at den thelytoke form kan producere nogle få hanner (dette kendes fra andre thelytoke dyr). De to former er blevet adskilt ved en han-procent på 10, hvilket naturligvis er en arbitrær grænse.

Det anbefales at undlade at betragte den thelytoke form som en særskilt art eller underart. Ligeledes bør de afvigende »kæmpe«- og »dværg«-populationer ikke udskilles som arter eller underarter. På den anden side findes der overgangsformer mellem *P. lagurus* og den nordamerikanske *P. fasciculatus*, som måske bør betragtes som en underart af *P. lagurus*.

Angående udbredelsesforhold gives der supplerende oplysninger til et andetsteds publiceret kort over de to formers totale udbredelse. Udbredelsen i Danmark og Skåne vises på et særskilt kort. Der kræves dog flere oplysninger, før udbredelserne kan gøres til genstand for velfunderede fortolkningsforsøg.

*Polyxenus lagurus* kan findes på mange forskellige habitater: under bark på døde eller syge træer, blandt vissent løv i skovbunden, under sten, i huse etc. Der synes dog ikke at være nogen forskel mellem de to former i habitatvalg (dog foreligger kun et ret ringe antal oplysninger – Tabel 5).

Fra Tyskland og Frankrig er beskrevet en parasitoid galmyg, *Chiliodiplosis vasta*, der har *P. lagurus* som vært. Galmyggelarver (givetvis *C. vasta*) er fundet på biseksuelle individer fra Bornholm og på thelytoke individer fra Østjylland og Østergötland.

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