RECORDS OF POLYMORPHISM IN THE MITE FAMILY SCUTACARIDAE (ACARI, TARSONEMINA)

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ACARI, SCUTACARIDAE, POLYMORPHISME, PHORÉSIE, EXPÉRIENCES D'ÉLEVAGE

RÉSUMÉ : Chez les espèces de scutacarides *Archidispus minor* (Karafiat, 1959) et *A. magnificus* (Karafiat, 1959) un polymorphisme femelle inconnu jusqu'à présent a été découvert au cours d'expériences d'élevage. Chez chacune des deux espèces on a trouvé deux formes de femelle différentes, dont une se sert de cafards comme hôte-moyen de transport. Cette forme de femelle phorétique a des caractéristiques morphologiques et éthologiques adaptées au comportement phorétique qui la distinguent nettement de la forme non-phorétique. Les deux types de femelles sont capables de reproduire aussi l'autre type morphologique. Contrairement aux femelles, les mâles chez les deux espèces examinées ne sont que du type non-phorétique.

Les résultats d'élevage ainsi que les descriptions des deux types de femelles sont présentés.

ACARI, SCUTACARIDAE, POLYMORPHISM, PHORESY, BREEDING EXPERIMENTS

ABSTRACT : A previously unknown female polymorphism was found in breeding experiments in the scutacarid species *Archidispmus minor* (Karafiat, 1959) and *A. magnificus* (Karafiat, 1959). Both species have two different female morphs, one of which in each case uses beetles as transport hosts. This phoretic female differs sharply from the nonphoretic form as its morphological and ethological characteristics are adapted to the phoretic behavior.

Both females are capable of reproducing the other morphic type. Each of the species examined has only one nonphoretic male.

The breeding results and the descriptions of the two female forms are given.

ACARI, SCUTACARIDAE, POLYMORPHISMUS, PHORESIE, ZUCHTVERSUCHE

ZUSAMMENFASSUNG : Bei den Scutacariden-Arten *Archidispus minor* (Karafiat, 1959) und *A. magnificus* (Karafiat, 1959) wurde im Verlaufe von Zuchtversuchen ein bislang unbekannt gewesener Weibchen-Polymorphismus entdeckt. Bei beiden Arten treten zwei verschiedene Weibchenmorphen auf, wobei jeweils eine davon Käfer als Transportwirte benutzt. Diese Weibchenform besitzt morphologische und ethologische, an das Phoresieverhalten adaptierte Merkmale, durch welche sie sich scharf von der nichtphoretischen Morphe unterscheidet. Beide Weibchen sind in der Lage, auch den jeweils anderen Morphentyp zu reproduzieren. Jede der untersuchten Arten besitzt nur eine, nichtphoretische Männchenform. Es werden die Zuchtergebnisse sowie die Beschreibungen beider Weibchenformen vorgelegt.

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Introduction

The discovery of female dimorphism in species of the family Pyemotidae sensu Cross, 1965 by Moser & Cross (1975) was the main reason for further research on the polymorphism phenomenon in other groups of Tarsonemina as well. In the meanwhile, cases of female and occasionally male polymorphism in the families Pyemotidae, Pygmephoridae (among others Cross, Moser & Rack, 1981, Rack & Kaliszewski, 1985) and Dolychocybidae (Magowski, 1988) have been reported.

Only recently has experimental evidence become available on the existence of polymorphic species in the scutacarid family; a detailed description and discussion of these findings is being prepared (Ebermann in prep.).

The continued breeding experiments have led to the discovery of polymorphic species, two of which will be discussed here.

Material and methods

Material examined

a) Soil samples were collected from the following localities to obtain females :

" UPR " : Unterpremstätten (SW of Graz, Austria); Overgrown bank of a waterbearing clay pit, decaying grass cuttings on wet, firm mud.

" MU " : Muttendorf (SW of Graz, Austria); filled-in pond (former clay pit), decaying plant substrate, mainly stems and leaves of *Typha angustifolia*.

The samples were dried in modified Berlese-Tullgren funnels; the mites that fell through were caught as necessary in tapwater or 70 % alcohol.

b) Breeding material : females for breeding were placed in individual breeding vessels and left there until eggs had been laid. The breeding containers were cylindrical glass vessels with a diameter of 8 mm. The breeding procedure was according to Ebermann & Rack 1982.

c) Material for comparison was provided by the Hungarian Museum of Natural History, Budapest (HNHM), whom I should like to thank at this point.

d) Slides have been deposited in the Museum of Natural History (HNHM), Budapest, the Zoological Museum of the University of Hamburg (ZMUH) and in the author's collection.

e) The designations of the body setae and setae of extremities are based on Lindquist (1977, 1986).

Abbreviations :

astpl = anterior sternal plate
pstpl = posterior sternal plate
BL = body length
BW = body width
Fe = femur
Ge = genu
TiTa = tibiotarsus
Tr = trochanter
PrTa = pretarsus
LEI = The diagonal ridge of the anterior sternal plate running between the leg pairs II and III (after Karafiat 1959)
$\bar{x}$ = arithmetic mean
V = coefficient of variability
W = width

All measurements are given in µm.

Results

1) *Archidispus minor* (Karafiat, 1959)

Imparipes (Archidispus) minor : Karafiat 1959, 663, 671-672, Fig. 8a, 18 (vicinity of Bonn and Erlangen, FRG; type no longer exists, Karafiat pers. comm.); Mahunka 1965a, 358-359 (only key), Table 2, Figs. 7-8; 1971, 28 (India); 1972, 95 (only key), Table 50, Figs. E-G;

Imparipes minor : Sevastianov 1978, 53 (only key), Table 19, Fig. 142a-b; Niedbała *et al.* 1981, 124 (Poland); Niedbała *et al.* 1982, 248 (Poland);

Archidispus minor : Rack 1973, 325; Mahunka 1981, 346 (Hungary).

Breeding experiments

In the fall of 1988 I repeatedly took soil samples from locality UPR to obtain live *Archidispus* fe-

TABLE 1 : Number of F1 progeny of nonphoretic and phoretic strains of *Archidispus minor*.

		Progeny (F1)				
No.	parental-♀	nonphoretic-♀	phoretic-♀	intermediate-♀	males	total offspring
A/88/a	nonphoretic	2	6	—	4	12
b	nonphoretic	—	18	—	6	24
c	nonphoretic	1	1	—	1	3
d	nonphoretic	5	1	—	5	11
e	phoretic	3	3	—	3	9
f	phoretic	—	—	—	12	12
g	phoretic	1	3	—	8	12
h	phoretic	1	2	—	4	7
i	phoretic	—	2	—	1	3
j	phoretic	2	1	—	1	4
	total number	15	37	—	45	97

males. Of 25 females collected and used for breeding, 16 could be identified as *Archidispus minor*. Nine had to be classified for the time being as belonging to an as-yet undescribed species. Both forms were found together in some samples.

Six of the 16 *minor* females and 4 of the 9 unidentified animals could be induced to lay eggs.

FEMALE DIMORPHISM

After hatching of the f1 adults, it was seen that the two female forms did not belong to different species, but were only two phenotypically different morphs of one and the same species. Morphological comparison and additional observation of behavior showed that the typical *minor* female is a morph with a distinctive inventory of characteristics and behaviors that represent adjustments for phoretic behavior (see below). The second, previously unknown female form is a nonphoretic morph that differs significantly from the phoretic female both in phenotype and in behavior (see below).

The f1 generation almost always produced both nonphoretic and phoretic females ; only in one case did a nonphoretic mother produce exclusively phoretic f1 females (Table 1, breeding group A/88/b). The percentage of both female morphs was, as related to the total number of female f1 individuals, 24 % nonphoretic and 76 % phoretic for the offspring of nonphoretic females, and 39 % nonphoretic females and 61 % phoretic females for the offspring of phoretic females.

Detailed examination of the f1 females failed to show any intermediate forms.

A phoretic mother female (A/88/f) that was in all likelihood unmated produced only male offspring (arrhenotokous parthenogenesis, see EBERMANN 1982).

a) Differences in characteristics : The description of the two morphs includes a detailed report of the differences in characteristics that were found (see also Tables 2 and 3).

b) Difference in behavior : This concerns the appetitive behavior, which is related to phoresy and is produced only in the phoretic female as a response to adequate stimuli. In experiments, typical *minor* females (= phoretic females) could easily be induced, when touched with the tip of a fine needle, to stand on leg pair IV and to perform seesawing movements with the extended leg pairs I-III (" perching stance ", see BINNS 1979, EBERMANN & RACK 1982). If the needle tip was still offered, the animals tried at the slightest touch to run up it. When this happened, the females seemed very excited and it was difficult to get them back into the breeding vessel.

In the same test, the second morph, which was interpreted as being nonphoretic, never showed this behavior that was so typical for the phoretic female.

In behavioral experiments, these animals always tried to avoid the offered needle tip and to run away from it as quickly as possible.

Larvae and males

The larvae of both female forms are morphologically identical. The morphic type of the female larvae can only be determined in the last stage of larval development; at this point, the well developed adult can be seen in detail through the thin, transparent larval skin.

Both female morphs produce only one identical, monomorphic f1 male type. The first description of larvae and male will be the subject of a future publication.

Redescription of phoretic female of *Archidispus minor* (described by Karafiat 1959) (Fig. 1, 2, 4, 5)

Entire body surface finely stippled.

a) Dimensions see Table 2.

b) Dorsal side (Fig. 1 : a).

Free margin of the clypeus has pronounced stripes. Cupulae *ia* and *ip* large, round to oval. Tergit *H* with posteromedian tonguelike elongation. Setae *c*2 insert on the free margin of the clypeus and have a highly sclerotic hair tube; dorsal setae not modified.

Relative and absolute lengths of dorsal setae (Average values in parenthesis based on 14 measurements on each of 10 animals) : *c*1(29) = *c*2 (30) < *d*(39) < *e*(46) > *f*(38) < *h*1(68) = *h*2(65). The following variation was seen : *h*1(70) > *h*2(61). Distances between the dorsal setae (10 measurements) : *c*1-*c*1(55) < *d*-*d*(105) > *f*-*f*(55) > *h*1-*h*1(37). Distance *c*1-*c*1 > *c*1-*c*2.

c) Ventral side (Fig. 2 : a).

Setae 3*b* and 4*a* have a pronounced thickening at the base. Setae 4*b* and 4*c* also thickened, but narrow down uniformly over the length of the hair. There is a diagonal cuticular crevice on the aureols of the hairs 3*b*, 4*a* and 4*b*. Distance 4*a*-4*a* > 4*a*-4*b*. Apodemata I and II highly sclerotic, the latter with a distinctly lowered edge, the connecting ridge LEI is immediately adjacent and also has a lowered edge. Apodemata III reach to the edge of the sternal plate; apodemata IV highly sclerotic and extend to the insertion of 3*b*; apodemata V rudimentarily visible between the acetabulae IV and the insertion of 4*b*.

Posterior genital sclerite triangular, broader than long, with slight frontal indentation.

Table 2 : *Archidispus minor*; body and leg dimensions of 10 phoretic and 10 nonphoretic females.

phoretic female												
											$\bar{x}$	V
BL	212	219	194	212	179	209	184	159	172	214	195.40	10.66
BW	187	164	162	172	174	179	184	142	179	174	171.70	7.61
astpl (W)	57	54	52	55	55	69	60	49	59	55	56.50	9.59
pstpl (W)	112	106	100	105	98	109	109	90	109	106	104.40	6.33
leg I	67	69	61	62	62	68	67	57	61	66	64.00	6.10
TiTa I	37	36	34	36	36	36	37	31	35	37	35.50	5.18
leg II	87	80	75	77	81	80	87	71	87	81	80.60	6.66
Ta II	37	35	34	35	34	36	39	30	37	32	34.90	7.44
leg III	94	92	89	91	94	96	96	—	100	92	93.77	3.48
Ta III	37	40	36	36	40	42	40	—	42	40	39.22	5.94
leg IV	164	149	137	152	154	157	164	132	157	124	149.00	9.14
Ta IV	51	45	49	50	50	50	53	45	49	47	50.50	8.45
PrTa IV	26	21	21	21	24	26	26	20	27	22	23.40	11.42

nonphoretic female												
											$\bar{x}$	V
BL	237	276	234	217	179	276	219	212	187	217	225.40	14.27
BW	179	202	164	169	159	202	159	187	157	192	177.00	10.06
astpl (W)	50	51	46	47	44	54	46	50	47	50	48.50	6.16
pstpl (W)	96	106	89	92	86	107	89	97	89	94	94.50	7.60
leg I	74	71	66	66	60	76	64	70	59	69	67.50	8.26
TiTa I	37	40	34	35	31	40	34	35	29	36	35.10	9.88
leg II	81	85	72	72	70	87	70	87	69	79	77.20	9.61
Ta II	35	37	29	31	29	36	30	32	27	34	32.00	10.50
leg III	91	100	81	84	79	100	85	89	80	90	87.90	8.64
Ta III	39	42	30	35	31	40	36	35	31	37	35.60	11.40
leg IV	153	169	140	141	129	—	137	149	125	149	143.55	9.25
Ta IV	52	57	45	47	44	56	46	47	41	50	48.50	10.70
PrTa IV	21	22	21	19	17	—	20	22	17	22	20.11	10.07

d) Gnathosoma (Figs. 1 : a, 2 : a).

Length 22-23 (n=4); posterior width 19-20 (n=4); anterior width 17-18; solenidion 5 (n=4); dorsal with 3 pairs of setae : of these, *Gd*1 > *Gd*2, with both on the same line; *pp* tiny and insert at the side in front of *Gd*1. The ventral side has one pair

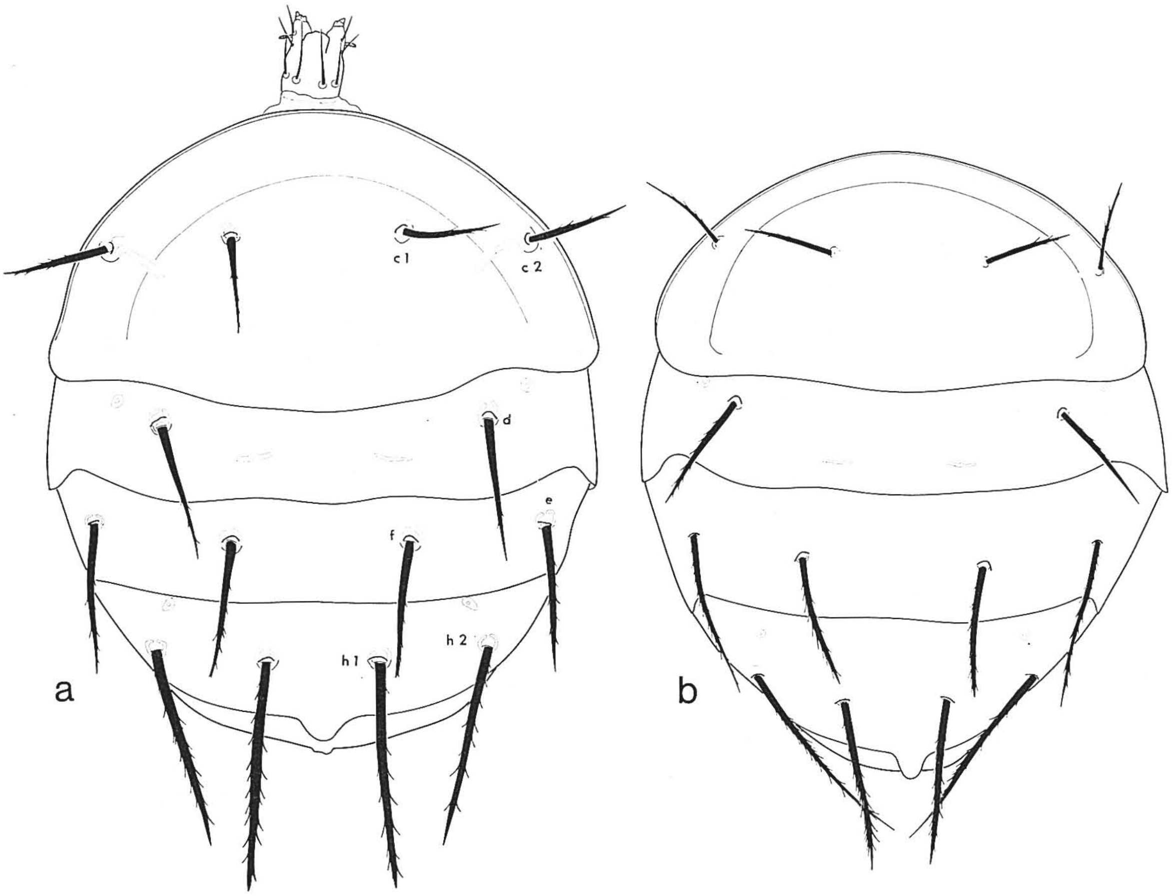

FIG. 1 : *Archidispus minor.*
a. — Dorsal view of phoretic female. b. — Dorsal view of nonphoretic female (body lengths : a = 210 µm ; b = 240 µm).

of setae. Palps with one pair of setae, ventral with a piston-like process, ventrolateral with one slender, thinly stemmed, diagonally striped solenidion each. Ventral gnathosoma base with an indentation shaped like an inverted U.

e) Trichobothrium.

Anterior trichobothrial seta longer and thicker than posterior. Trichobothrium with thin stem, distally round, with fine barbs.

f) Extremities.

Quantitative data. The values obtained from length measurements on the legs I-IV are summarized in Table 2 under " phoretic female ". The following lengths were measured : leg I from the base of the trochanter to the distal end of the longest tibiotarsal seta socket ; leg II-III from the base of the femur, leg IV from the base of the trochanter up to and including the claw socket of pretarsus ; similarly, measurements of the tibiotarsus or tarsus are made from their respective bases.

Leg lengths were measured on the extended leg ; thus, owing to the bending of legs II and III in the area of the trochanter-femur joint, the trochanters were not taken into consideration in order to obtain a more exact measurement.

On the average, leg II is 26 % longer than leg I, leg III 47 % longer and leg IV 133 % longer.

Description of the extremities (Figs. 4, 5). Leg I (Fig. 4 : a) : Setae formula : Tr1-Fe3-Ge4-TiTa16(4) ; femur and genu wider than long, tibiotarsus thickened, with a powerful distal claw whose basal opposing piece has a long, sharp tooth. The distal tibiotarsus has a long seta socket into which

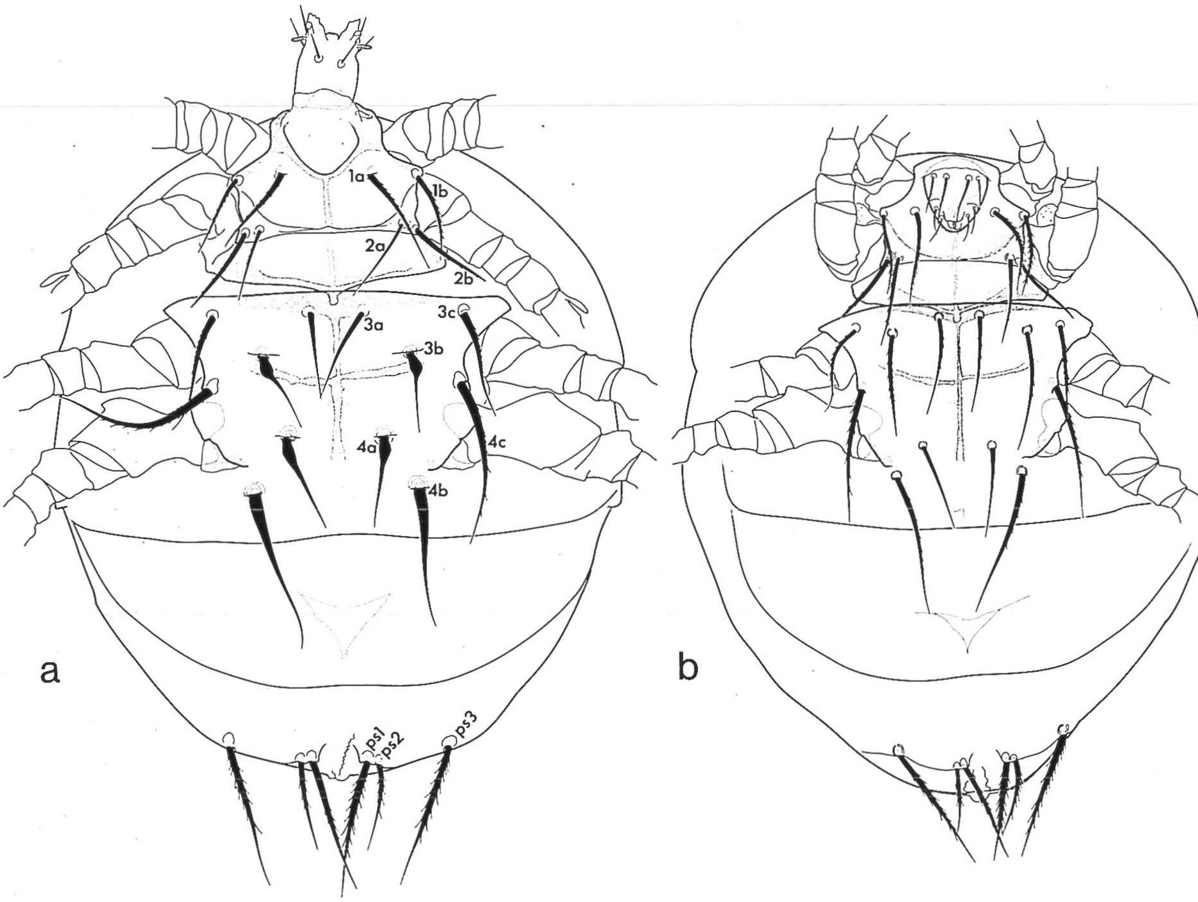

FIG. 2 : *Archidispus minor.*
a. — Ventral view of phoretic female. b. — Ventral view of nonphoretic female (for body lengths, see Fig. 1).

2 setae insert (probably the eupathidia *tc'* and *tc"*) and directly next to its base the solenidion ω2. The setae *u'* and *pv'* are the shortest tibiotarsal setae, *u'* < *pv'*. Solenidia ω2 > ω1 = φ2 = (>) φ1 ; ω2 is uniformly thin, extends above the seta socket ; ω1, ϕ2 and ϕ1 are thickened distally. Setae *dF* broad and leaflike with very fine barbs at the edge. Relation of length (x̄) leg I :

tibiotarsus (x̄) = 1 : 0.52 — 1 : 0.58 (x̄ = 1 : 0.55, n = 10).

Leg II (Fig. 4 : b) ; Setae formula : Tr1-Fe3-Ge3-Ti4(1)-Ta6(1) ; tarsus with stemmed, distally very broad empodium and two small claws of equal size. Solenidion ω slender, distally somewhat broader, origin near the base of the tarsus, does not extend to the insertion of *tc"* ; solenidion φ < ω.

Leg III (Fig. 5 : a) : Setae formula : Tr1-Fe2-Ge2-Ti4(1)-Ta6 ; empodium as for leg II ; two small claws of equal size ; solenidion φ short and club-shaped.

Leg IV (Fig. 5 : b) : Setae formula : Tr1-Fe2-Ge1-Ti3(1)-Ta6 ; tarsus with pretarsus and two very small claws, empodium extended and distally widened. Relation of tarsus length (x̄) : pretarsus length (x̄) = 1 : 0.42 — 1 : 0.55 (x̄ = 1 : 0.47, n = 10). Distance *tc'* — *tc"* = *pv'* — *pv"*. Setae *pl"* and *u'* very short ; seta *v"Ti* = *dTi* ; tibial solenidion φ short.

Material : 16 females from locality UPR (Sept.-Nov. 1988) : 37 bred females including 7 adults and 30 pharate females.

Distribution (literature data) : Europe, Asia. From soil samples and phoretically from different species of the carabid beetle genera *Acupalpus, Agonum, Amara, Anisodactylus, Calathus, Europhi-*

lus, Harpalus, Pardileus, Platynus, Poecilus, Pterostichus, and *Stenolophus*; on the connecting skin between head and prothorax as well as between thorax and abdomen, sometimes also on the other intersegmental skins.

First description of nonphoretic female of *Archidispus minor*.

Total body surface finely stippled.

a) Dimensions see Table 2.

b) Dorsal side (Fig. 1 : b).

Free margin of clypeus striped. Cupulae *ia* and *ip* roundish. Tergit *H* with posteromedian tongue-like elongation. Setae *c*2 insert on the free margin of the clypeus, with thin hair tube. Dorsal setae not modified.

Relative and absolute lengths of dorsal setae (average values in parentheses based on 14 measurements on each of 10 animals) : *c*1(34) = *c*2(35) < *d*(47) < *e*(71) > *f*(53) < *h*1(68) < *h*2(80). The setae lengths of a series often show considerable differences in length for one and the same animal, e.g. setae *d* 52, 43 ; setae *e* 52, 65 ; setae *h*2 79, 89.

Distances between dorsal setae (10 measurements) : *c*l-*c*l(57) < *d*-*d*(113) > *f*-*f*(65) > *h*1-*h*1(39). Distance *c*1-*c*1 > *c*1-*c*2.

c) Ventral side (Fig. 2 : b).

Ventral setae not modified. Setae aureoles of 3*b*, 4*a* and 4*b* without overlying cuticular crevice. 3*a* extend to apodemata IV ; 3*b* as long as or longer than 3*a*. Position of 4*a* and 4*b* as in phoretic female, distances 4*a*-4*b* variable (Fig. 3). 4*a* as long as or shorter than 3*a* and *ps*1 ; 4*b* as long as or longer than 4*c* ; *ps*2 more than half as long as *ps*1 ; *ps*1, *ps*2 and *ps*3 heavily barbed. *LEI* and apodemata as in the phoretic female ; edge of *LEI*, however, only slightly developed.

Posterior genital sclerite as in phoretic female.

d) Gnathosoma.

Length 22-25 ($\bar{x}$=23, n=7) ; posterior width 18-23 ($\bar{x}$=21, n=7) ; anterior width 15-19 ($\bar{x}$=17, n=7), solenidion 4-7 (n=7).

e) Trichobothrium as in phoretic female (Fig. 4 : e).

f) Extremities.

Quantitative data. " Nonphoretic female " in Table 2 summarizes the values obtained from length measurements on legs I-IV. Measured lengths are as for phoretic females. The legs II and III are on the average 14 % and 30 % longer than leg I, respectively ; leg IV is 113 % longer than leg I.

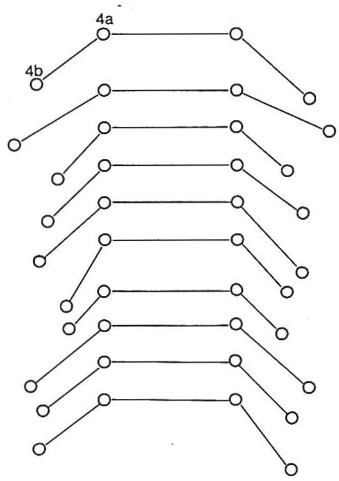

FIG. 3 : *Archidispus minor*, nonphoretic female, examples of the variability in the positions of setae 4*a* and 4*b* in relation to each other ; insertion of the respective animals are connected by lines.

Description of the extremities (Figs. 4-5). Leg I (Fig. 4 : c) : Setae formula : Tr1-Fe3-Ge4-TiTa16(4) ; femur and genu longer than wide ; tibiotarsus slender, no claw present, distal with a long seta socket into which two setae insert (probably the eupathidia *tc'* and *tc''*) and basally the solenidion ω2 ; seta *u'* > *pv'*.

Solenidion ω2 > (=) ω1 > φ2 = φ1 ; ω2 uniformly thin, ω1 finger shaped, φ2 slightly thickened, φ1 clubshaped. Seta *dF* with leaf like flattening as in phoretic female. Relation of length ($\bar{x}$) leg I : tibiotarsus ($\bar{x}$) = 1 : 0.49-1 : 0.56 ($\bar{x}$ = 1 : 0.52, n = 10).

Leg II (Fig. 4 : d) : Setae formula : Tr1-Fe3-Ge3-Ti4(1)-Ta6(1) ; tarsus with unstemmed, distally broadened empodium and two small claws of equal size. Solenidion ω slender, does not extend to the insertion of *tc''*, origin near base of tarsus ; solenidion φ < ω.

Leg III (Fig. 5 : c) : Setae formula : Tr1-Fe2-

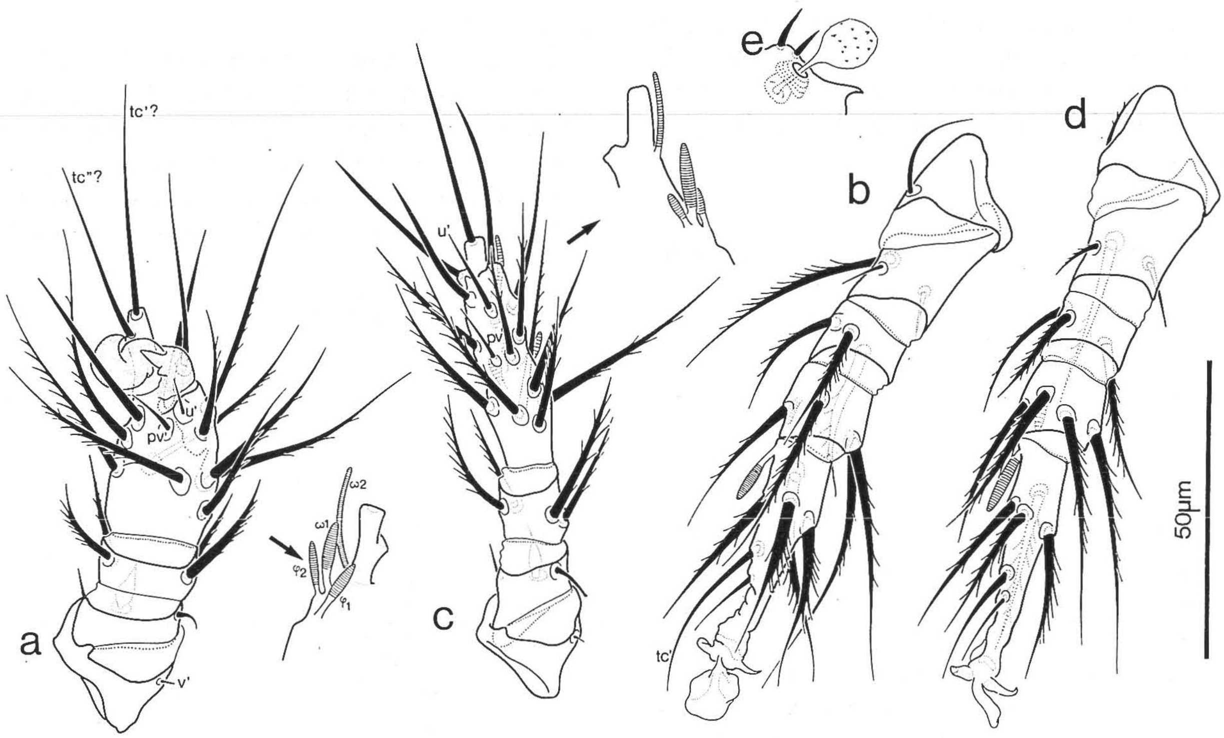

FIG. 4 : *Archidispus minor.*

a. — Phoretic female, leg. I. b. — *Idem*, leg II. c. — Nonphoretic female leg I. d. — *Idem*, leg II. e. — *Idem*, trichobothrium. (Solenidia are marked by arrows).

TABLE 3 : *Archidispus minor*, a comparison between phoretic and nonphoretic females, based on the breeding material shown in Table 1. Characteristics that are thought to have adaptational value for the phoresy are indicated by bold — face numbers.

phoretic female (a)	nonphoretic female (b)	common characteristics
1. Dorsal setae sometimes different from (b) in position and length		1. Dorsal setae not modified
2. Setae 3b, 4a spindle shaped, 4b, 4c thickened	Ventral setae not modified	2. Form of posterior genital sclerite
3. Position of 3b different from (b)		3. Position of 4a-4b
4. Integument thicker		4. Length ratio of ps1-ps2-ps3
5. Sternal plates wider		5. Proportions of gnathosoma and its solenidia
6. Apodemata more sclerotic		6. Form of trichobothrium
7. LEI with a distinct lowered edge	LEI only faintly present	7. Form of seta dF (leg 1)
8. Leg 1 shorter		8. Form of claws of legs II and III
9. Tibiotarsus I longer (cf. ratio leg/tibiotarsus)		9. Solenidion of tarsus II does not reach tc'
10. Tibiotarsus 1 thickened	Tibiotarsus 1 slender	
11. Tibiotarsus 1 with claw	Tibiotarsus 1 without claw	
12. Length of solenidia of leg 1 differs from (b)		
13. u' < pv' (tibiotarsus)	u' > pv'	
14. Femur and genu 1 wider than long	Femur and genu 1 longer than wide	
15. Legs II-IV longer		
16. Empodia II-III stemmed	Empodia II-III not stemmed	
17. Pretarsus IV longer (cf. ratio tarsus/pretarsus)		
18. Setae of leg IV sometimes differ from (b) in positions and lengths		
19. Appetitive behavior present	Appetitive behavior absent	

Ge2-Ti4(1)-Ta6 ; claws, empodium and solenidion φ as for leg II.

Leg IV (Fig; 5 : d) : Setae formula Tr1-Fe2-Ge1-Ti3(1)-Ta6 ; tarsus with pretarsus and two very small claws, empodium elongated, distally broader. Relation of tarsus length ($\bar{x}$) : pretarsus length ($\bar{x}$) = 1 : 0.38-1 : 0.46 ($\bar{x}$ = 1 : 0.41, n = 9). Distance $tc' — tc'' > pv' — pv''$. Setae $p1''$ and u' very short ; seta $v''Ti < dTi$; tibial solenidion φ as in phoretic female.

Material : 8 females from locality UPR (Sept.-Nov. 88) ; 3 females from site MU (Sept. 1987) ; 15 bred females including 7 adults and 8 pharate females.

Table 3 compares the diagnostically relevant individual characteristics and groups of characteristics of the two morphs.

NOTE :

The nonphoretic female of *A. minor* was discovered during breeding experiments and bears a striking similarity to *Archidispus haarloevi* (Karafiat, 1959), but for the time being the two species should not be considered to be identical. The normal *minor* female differs considerably in several characteristics from the original descriptions of *haarloevi.* These differences involve the setae lengths of the series $3a$-$3c$, $4a$-$4c$ and $ps1$-$ps3$ as well as the setae pv'' and tc'' of leg IV. If this should actually be a case of conspecificity (*i.e. A. haarloevi* should be the nonphoretic female form of *A. minor*), these differences would be due to intraspecific morphological variability or flaws in the description of *A. haarloevci.* I think it more likely that *A. haarloevi* is the nonphoretic female of an *Archidispus* species that is closely related to *A. minor* and may or may not have already been described. Breeding experiments with appropriate species are planned.

MAHUNKA (1971) published the finding of *A. minor* and *A. haarloevi* in India ; he found both species in the same soil samples (As-118, As-119). My followup examination of the female from sample As 118 identified as *A. haarloevi* provided the complete morphological agreement with the nonphoretic *minor* female morph that I had bred. There is no doubt that it is the first common finding in nature of the phoretic and nonphoretic (“ *haarloevi* ”-like) female morphs of *A. minor*.

2) *Archidispus magnificus* (Karafiat, 1959)

Imparipes (Archidispus) armatus magnificus : KARAFIAT 1959, 671, Fig. 17 (near Erlangen, FRG ; type no longer existent, KARAFIAT pers. comm.) ;

Imparipes (Archidispus) magnificus : BALOGH & MAHUNKA 1962, 512, Hungary ; MAHUNKA 1965a, 358-359 (only key), Table 2, Fig. 1-2 ; 1965b, 141 (Hungary) ; 1972, 370 (France) ;

Imparipes magnificus : SEVASTIANOV 1978, 53 (only key), Table 18, Fig. 138a-b (USSR) ;

Archidispus magnificus : RACK 1973, 322-323 (only key) ; MAHUNKA & ZAKI 1984, 77 (Hungary).

BREEDING EXPERIMENTS.

The examination of soil samples (locality UPR, June 1988) provided four live females of the phoretic type. Breeding experiments were begun immediately and it was possible to induce three females to lay eggs and to cultivate the larvae to the emergence of the f1 adults.

TABLE 4 : Number of F1 progeny of nonphoretic and phoretic strains of *Archidispus magnificus.*

		Progeny (F1)				
No.	parental-♀	nonphoretic-♀	phoretic-♀	intermediate-♀	males	total offspring
A/88	nonphoretic	1	19	—	7	27
B/88	nonphoretic·	17	11	1	3	32
C/88	nonphoretic	2	1	—	—	3
D/88	phoretic	3	4	—	1	8
E/88	phoretic	18	33	—	28	79
F/88	phoretic	—	1	—	—	1
	total number	41	69	1	39	150

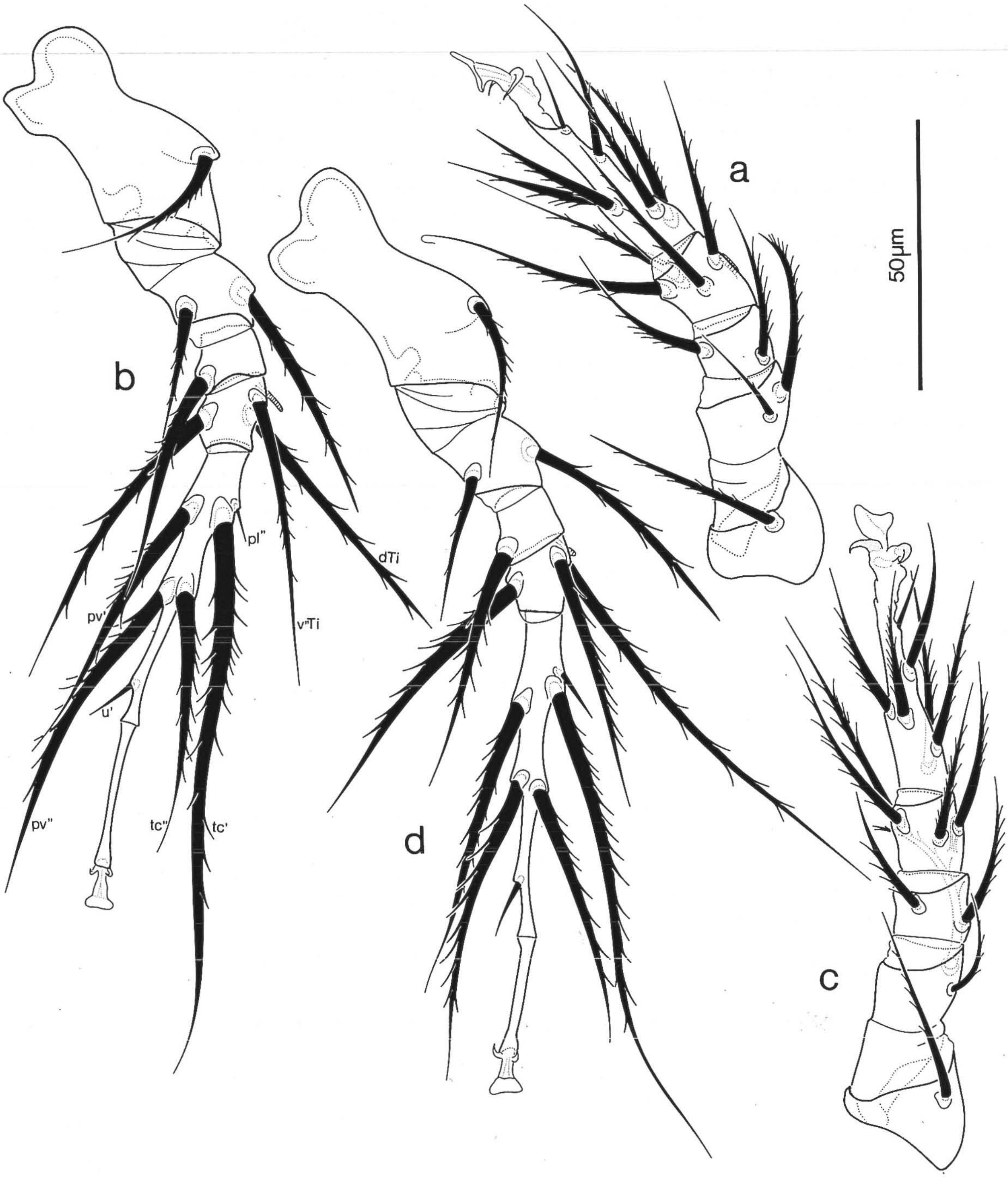

FIG. 5 : *Archidispus minor*.
a. — Phoretic female, leg III. b. — *Idem*, leg IV. c. — Nonphoretic female, leg III. d. — *Idem*, leg IV.

FEMALE DIMORPHISM.

When the f1 generation showed the appearance of phoretic females and nonphoretic females lacking claws on leg I, breeding experiments were also performed with nonphoretic f1 females. These experiments showed that nonphoretic females can also produce both female morphs (Table 4).

The percentages of female morphs — related to the total number of f1 individuals — produced by nonphoretic mother animals was 36 % nonphoretic females and 63 % phoretic females. The percentages for phoretic females was 38 % nonphoretic offspring and 62 % phoretic offspring.

Among a total of 111 f1 females there was only one animal with intermediate characteristics (see below).

Test of the appetitive behavior (perching stance) of both morphs showed the same results as were found in *Archidispus minor*.

Redescription of phoretic female of *Archidispus magnificus* (described by KARAFIAT, 1959) (Fig. 6-10).

Total body surface finely stippled.

a) Dimensions see Table 5.

b) Dorsal side (Fig. 6 : a).

Free margin of clypeus narrow, striping only weak. Cupulae *ia* and *ip* rounded. Tergit *H* with posteromedian tongue-like elongation. Setae *c*2 are not on the free margin of the clypeus; hair tube missing or short and stumpy. The dorsal setae are similar to those of *Archidispus armatus* (Karafiat, 1959), but in *magnificus* the setae *c*2 have the normal hair form.

Relative and absolute lengths of dorsal setae (averages in parentheses, determined from 14 measurements on each of 10 animals) : *c*1(21) < *c*2(29) = *d*(30) < *e*(40) > *f*(22) < *h*1(62) > *h*2(48). Distances between the dorsal setae (10 measurements) : *c*1-*c*1(56) < *d*-*d*(69) > *f*-*f*(48) > *h*1-*h*1(34). The distance *c*1-*c*1 is distinctly greater than that of *c*1-*c*2.

TABLE 5 : *Archidispus magnificus*; body and leg dimensions of 7 phoretic and 7 nonphoretic females.

	phoretic female								
								$\bar{x}$	V
BL	214	212	182	209	199	207	187	201.42	6.24
BW	155	157	142	162	164	164	122	152.28	5.03
astpl (W)	57	59	56	58	57	57	55	57.00	2.26
pstpl (W)	102	107	95	106	102	106	99	102.48	4.24
leg I	67	69	63	69	69	66	65	66.85	3.49
TiTa I	35	36	33	39	37	35	35	35.71	5.28
leg II	84	84	78	82	85	80	81	82.00	3.06
Ta II	34	34	32	35	35	34	32	33.71	3.62
leg III	91	94	87	97	96	94	92	93.00	3.61
Ta III	32	32	31	35	35	34	32	33.00	4.94
Leg IV	145	148	133	144	147	137	137	141.57	4.11
Ta IV	44	42	40	44	44	41	41	42.28	4.03
PrTa IV	21	21	19	20	21	20	19	20.14	4.41
	nonphoretic female								
								$\bar{x}$	V
BL	264	214	172	251	232	199	214	220.85	14.14
BW	187	162	170	175	169	170	162	170.74	5.01
astpl (W)	54	49	51	51	51	50	51	50.00	2.40
pstpl (W)	105	94	97	102	99	95	95	98.14	4.17
leg I	76	69	71	75	71	69	75	72.28	4.12
TiTa I	37	35	36	37	36	32	37	35.71	5.03
leg II	81	75	79	80	79	77	77	78.28	2.62
Ta II	30	31	30	32	30	30	29	30.28	3.16
leg III	94	85	86	90	89	89	87	88.57	3.37
Ta III	31	30	30	30	31	31	30	30.42	1.75
leg IV	144	131	131	143	140	126	132	135.28	5.15
Ta IV	46	41	41	44	44	39	41	48.28	5.74
PrTa IV	15	14	13	16	15	11	14	14.00	11.64

c) Ventral side (Fig. 7 : a).

Setae 3*b* are thicker and longer than 3*a* and reach the insertion of 4*b*. The basal swelling of the setae 4*a* and 4*b* is characteristic; 4*a* are spindle-shaped and insert far behind apodemata IV. Setae *ps*3 > *ps*1 > *ps*2. Apodemata I and II are highly sclerotic, the latter form a clearly dropped edge in the direction of the posterior sternal plate. Ridge *LEI* also has a lowered edge. Apodemata III highly sclerotic, apodemata IV reaches acetabulae III. Apodemata V rudimentary between acetabulae IV and the insertions of 4*b*.

Posterior genital sclerite is triangular and distinctly wider than long.

d) Gnathosoma.

Length 21-23 (n = 10); posterior width 16-19 (× = 18, n = 10); anterior width 17-19 (n = 10);

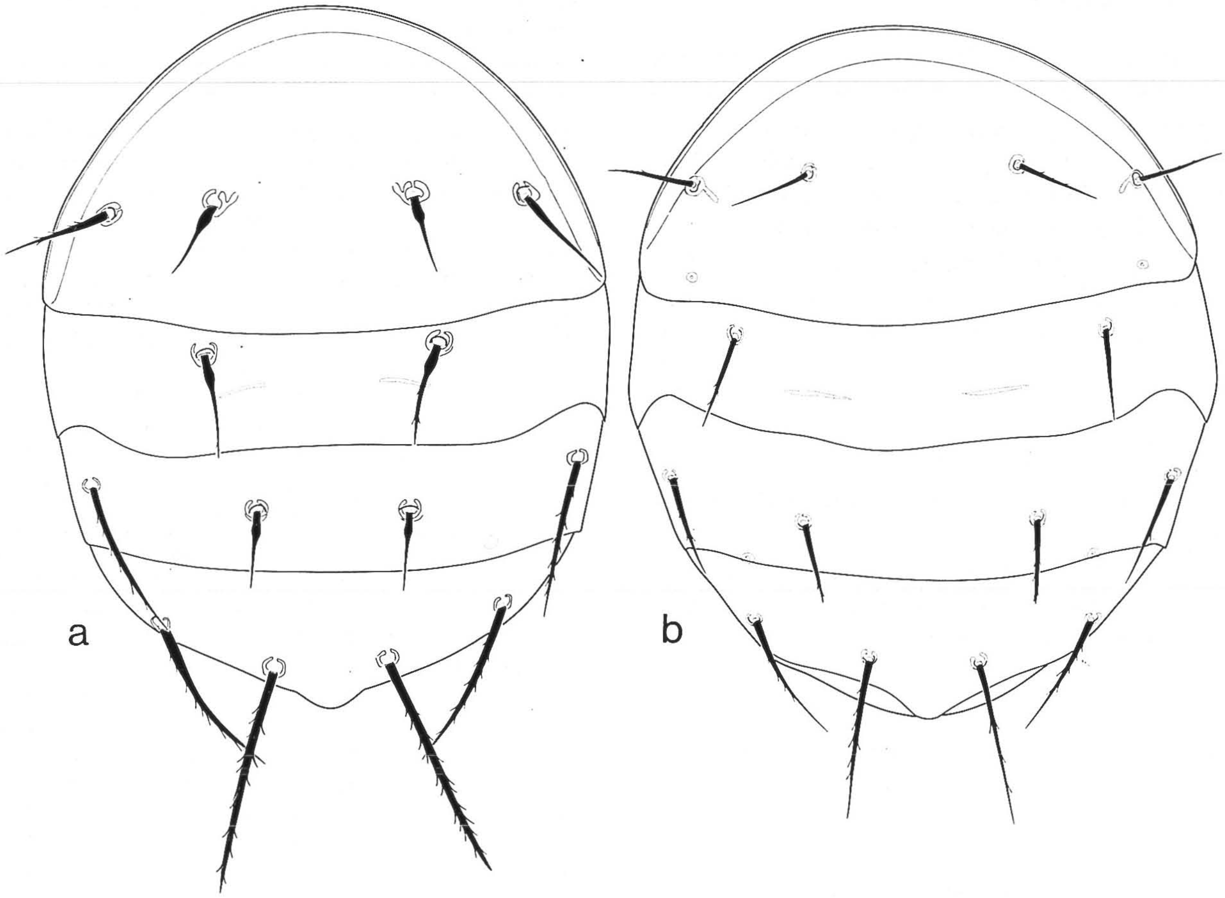

FIG. 6 : *Archidispus magnificus.*

a. — Phoretic female, dorsal view. b. — Nonphoretic female, dorsal view (body lengths for a and b = 200 μm).

length of solenidion 5-6 (n = 10). Ventral base with deep indentation shaped like inverted U. Dorsal with 3 setae : The median pair *Gd*1 is the longest ; *Gd*2 insert somewhat laterally before *Gd*1 and are shorter ; *pp* insert far before *Gd*2, tiny. Ventral side with one pair of setae, these insert at about the level of the middle of the gnathosoma. Palps with one pair of setae each, ventral with one piston-like process each, ventrolateral with one diagonally striped solenidion each, pointing forward. The contour of the gnathosoma without the palps is almost square, laterally it is sometimes slightly convex.

e) Trichobothrium (Fig. 9 : e).

The anterior trichobothrial seta much longer and thinner than the posterior one. The trichobothrium has a slender stem and is rounded distally ; it has irregular and very fine barbs.

f) Extremities.

Quantitative data. The data obtained from measurements of legs I-IV are summarized in Table 5 under " phoretic female ". Distances measured were as for *Archidispus minor*.

Legs II, III and IV are 47 %, 65 % and 112 % longer on the average than leg I, respectively.

Description of the extremities (Figs. 9-10). Leg I (Fig. 9 : a, b) ; Setae formula : Tr1-Fe3-Ge4-TiTa16(4) ; femur and genu wider than long ; tibiotarsus very thickened, distal with a powerful claw, whose basal opposing piece has a pointed, toothlike formation. Distally the tibiotarsus has two separate setae sockets, the longer of which

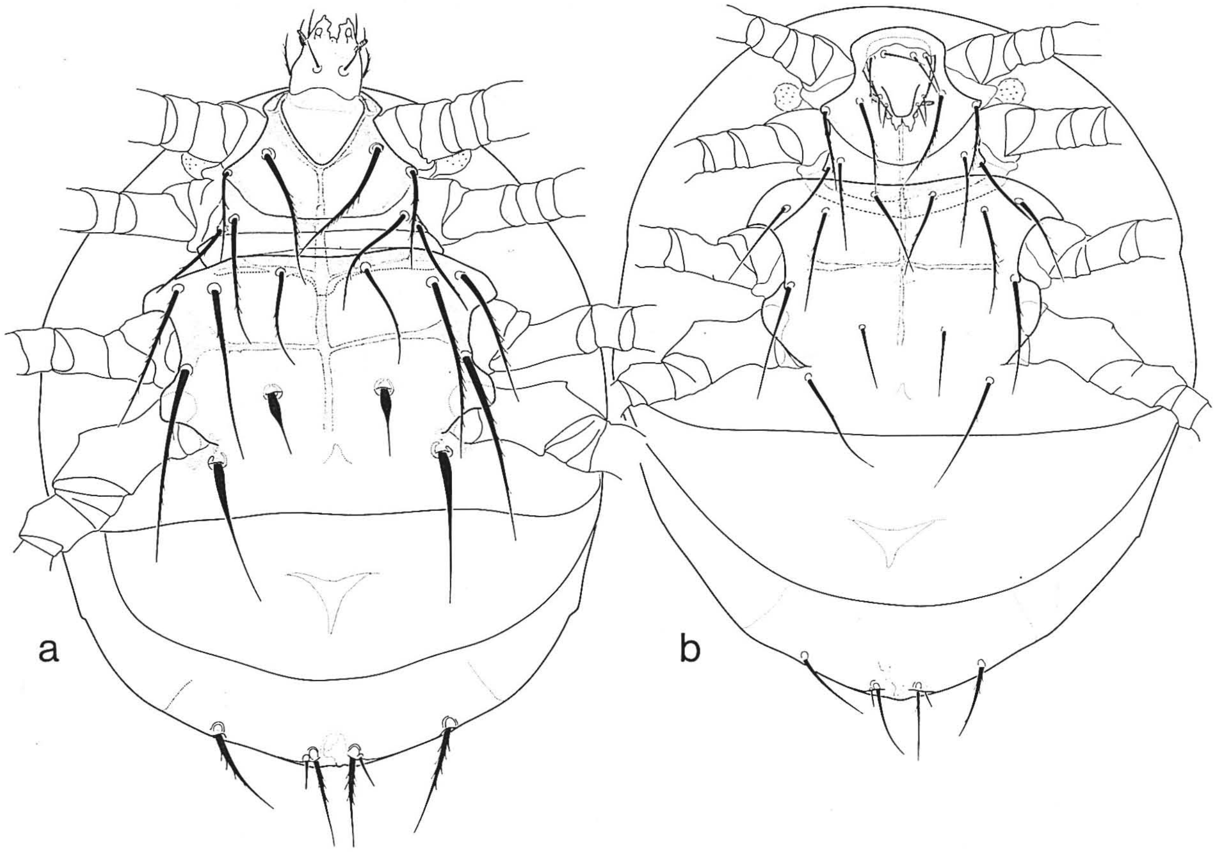

FIG. 7 : *Archidispus magnificus.*
a. — Phoretic female, ventral view. b. — Nonphoretic female, ventral view. (Body lengths as in Fig. 6).

bears 2 setae (probably the eupathidia *tc'* and *tc"*) as well as solenidion ω2 which inserts into its base. Setae *u'* and *pv'* are the shortest tibiotarsal setae, with *pv'* somewhat longer than *u'*. Solenidia ω2 > ω1 < (=) φ2 > φ1 ; ω2 and φ2 long and thin, ω1 finger shaped, φ2 club shaped. Seta *v'T* very short and peg-like ; seta *dF* leaf-like and flattened with fine lateral barbs. Relation of length ($\bar{x}$) of leg I : tibiotarsus ($\bar{x}$) = 1 : 0.52 — 1 : 0.56 ($\bar{x}$ = 1 : 0.53, n = 7).

Leg II (Fig. 9 : c, d) : Setae formula : Tr1-Fe3-Ge3-Ti4(1)-Ta6(1) ; tarsus with thinly stalked empodium with broad distal lobes. The anterior claw is twice as long as the posterior one. Solenidion ω originates on the base of the tarsus and does not reach the insertion of seta *tc"* (see " note ") ; ω > φ.

Leg III (Fig. 10 : a) : Setae formula : Tr1-Fe2-Ge2-Ti4(1)-Ta6 ; empodium as for leg II ; anterior claw more than twice as long as posterior. Solenidion φ slender and finger shaped.

Leg IV (Fig. 10 : b) : Setae formula : Tr1-Fe2-Ge1-Ti3(1)-Ta6 ; tarsus with pretarsus, two small claws and empodium with slender stem and broad distal lobes. Relation of tarsus length ($\bar{x}$) to pretarsus length ($\bar{x}$) = 1 : 0.45 — 1 : 0.50 ($\bar{x}$ = 1 : 0.47, n=7). Distance *pv'* — *pv"* = *pv"* — *u'*. Seta *v"Ti* > *dTi*. Solenidion φ thin and rod-like ; setae *pl"* and *u'* are the shortest tarsal setae.

NOTE :

In the small, poorly detailed illustration in the original description, the claws of legs II and III are shown as being equal in length ; the solenidion of leg IV is missing ; instead of the 6 tarsal setae of leg IV only 4 are shown ; seta *tc'* does not extend beyond the distal end of the pretarsus. These are probably errors in observation or reproduction on the part of KARAFIAT; with regard to the serious difference of length of setae *tc'*, however, intraspecific variability could play a role. As the type material for the species described by KARAFIAT is no longer available (KARAFIAT, pers. comm.), no definitive answer to this question can be expected.

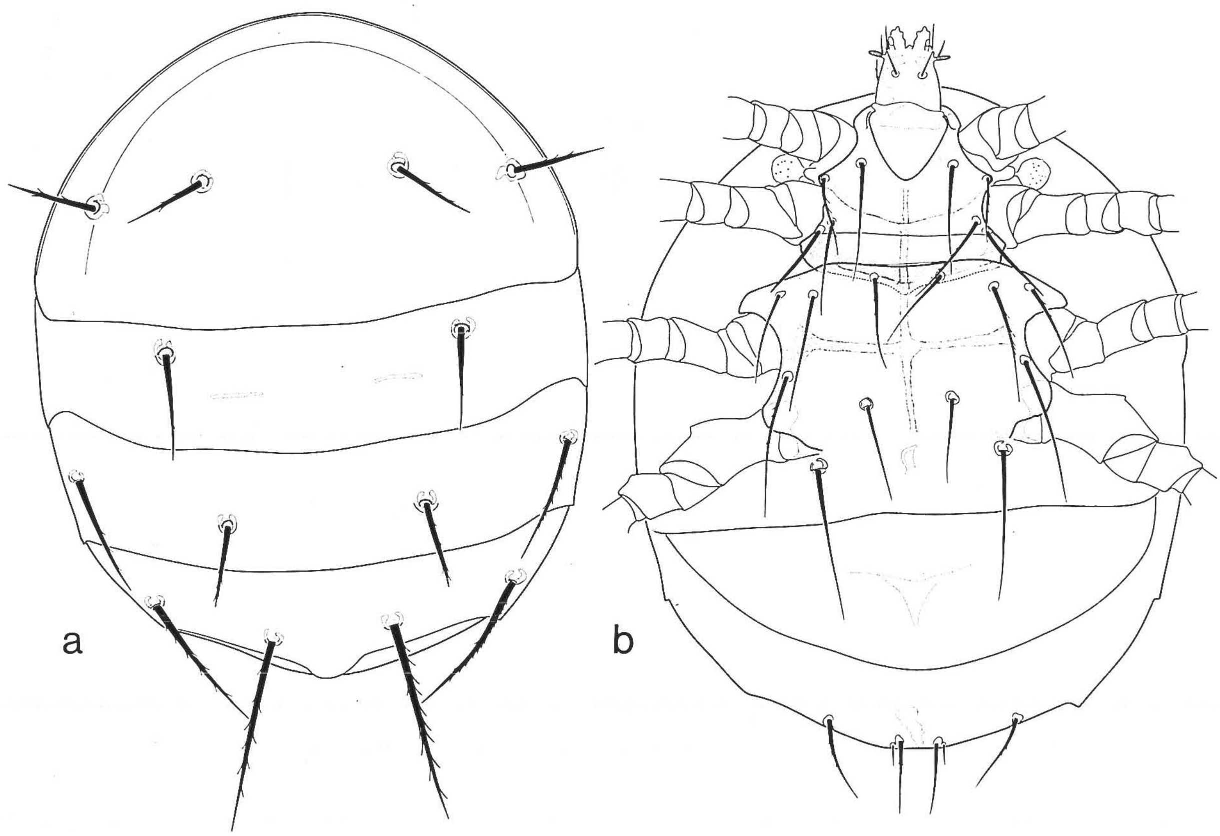

FIG. 8 : *Archidispus magnificus*.
a. — Female, intermediate form, dorsal view. b. — *Idem, ibid.*, ventral view. (Body length = 200 µm).

The problem of consistency of position and length of solenidion ω (leg II) will require further study. In all 37 bred phoretic f1 females, solenidion ω was as in the redescription and proved to be a constant characteristic of the phoretic female (cf. leg II, nonphoretic female). One phoretic *magnificus* female from Hungary (HNHM, T-151p-67) that I examined differed (only) in this respect from my natural and breeding material. In this animal, the solenidion ω inserts far from the tarsus base on the distal end of the first third of the tarsus; in comparison to the Austrian material, the solenidion is twice as long, extends far beyond the insertion of *tc'* and even reaches as far as the anterior claw (Fig. 9 ; d).

Material : Three females from locality MU (Sept. 1986, June 1987) ; four females from locality UPR (June 1988) as well as 16 adult females and 46 pharate females ; four adult f1 females were lost in the breeding experiments.

Distribution (literature data) : Europe. From soil samples and phoretic on the carabid beetle *Europhilus fuliginosus* ; under the elytra on the dorsal side of the abdomen.

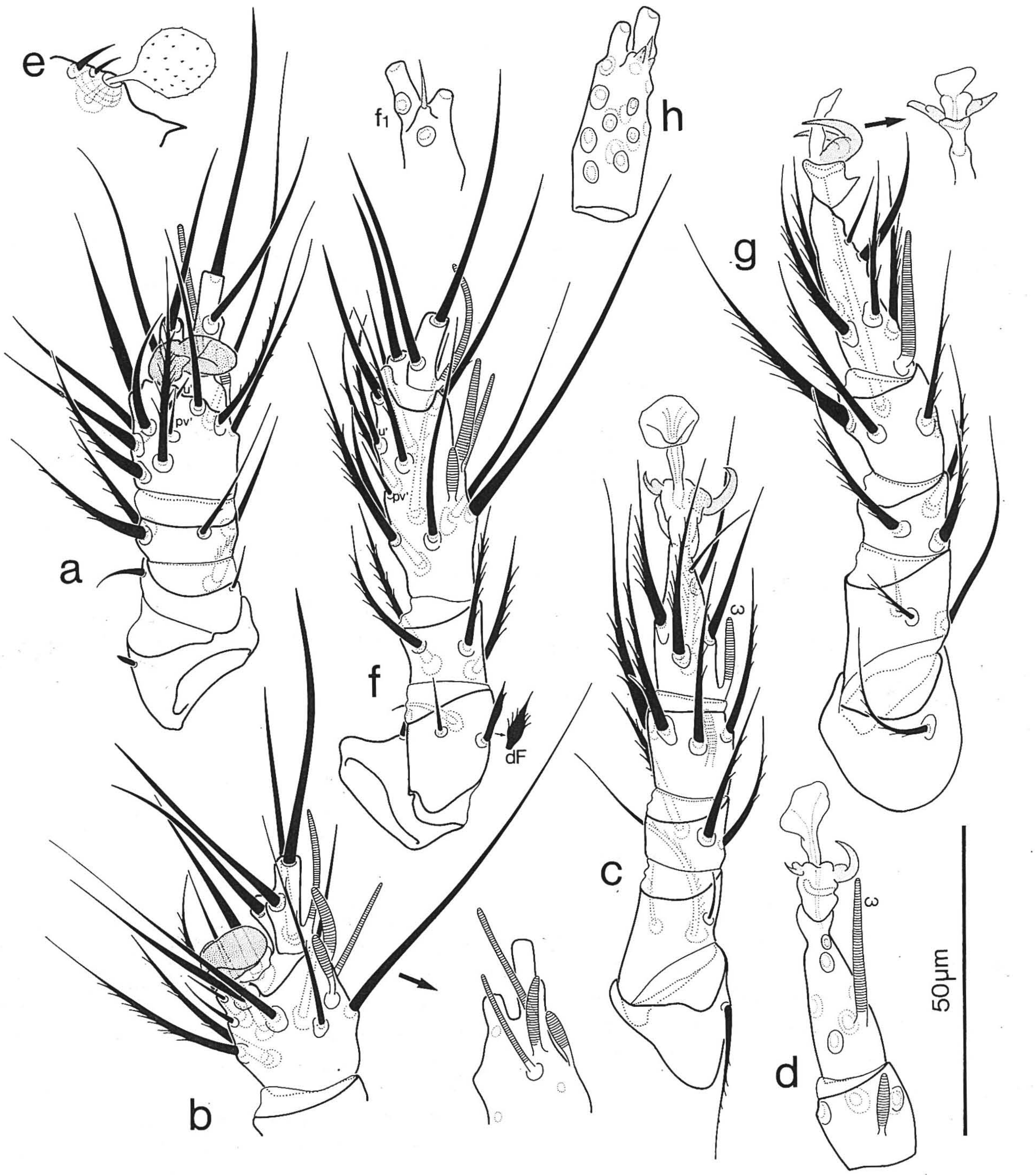

FIG. 9 : *Archidispus magnificus.*

a & b. — Leg I of phoretic female in different views (solenidia are marked by arrows). c. — Leg II of phoretic female. d. — *Idem*, with unusually long solenidion (specimen from Hungary, HNHM). e. — Trichobothrium of phoretic female. f. — Nonphoretic female, leg I. f1. — *Idem*, leg II, distal part of tarsus with seta arising from the top of rudimentary hair socket. g. — *Idem, ibid.* (empodium in ventral view marked by arrow). h. — Female, intermediate form, tibiotarsus I with rudimentary claw.

First description of nonphoretic female of *Archidispus magnificus*. (Fig. 6-10).

Entire body surface finely stippled.

a) Dimensions see Table 5.

b) Dorsal side (Fig. 6 : b).

Free margin of clypeus narrow, weakly striped. Cupulae *ia* and *ip* round to oval. Tergit *H* has a posteromedian tongue-like extension. Setae *c*2 insert on the free margin of the clypeus ; hair tube missing in weakly sclerotic animals, present in those that are larger and more sclerotic, but short. Dorsal setae are not modified.

Relative and absolute lengths of dorsal setae (average values in parentheses, calculated from 14 measurements on each of 10 animals, all values in μm) : $c1(28) = c2(29) = d(31) = e(31) > f(25) < h1(46) > h2(38)$.

Distances between the dorsal setae (10 measurements) : $c1\text{-}c1(63) < d\text{-}d(98) > f\text{-}f(68) > h1\text{-}h1(32)$. Distance *c*1-*c*1 is distinctly greater than distance *c*1-*c*2. Owing to the large distance between setae *d*, a line connecting *c*1, *d*, *f* and *h*1 curves towards the edge of the body.

c) Ventral side (Fig. 7b).

Ventral setae are not modified. Setae 3*b* are as thick as 3*a* but longer ; they do not reach the insertion of 4*b*. Position of 4*a* and 4*b* as in phoretic females. Setae *ps*1 and *ps*3 thin, smooth or weakly barbed, *ps*2 very short and thin, $ps3 > ps1 > ps2$. Ridge *LEI* between setae 2*b* usually not present, sometimes weakly developed, only rarely with a fine edge. All apodemata present as in phoretic female but, like the sternal plate edges, less sclerotic.

Posterior genital sclerite as in phoretic female.

d) Gnathosoma.

Length 22-25 ($\bar{x}=24$, $n=10$) ; posterior width 18-25 ($\bar{x}=23$, $n=10$) ; anterior width 15-20 ($\bar{x}=18$, $n=10$). Length of solenidion 4-6 ($n=10$). Contour of gnathosoma nearly trapezoid ; on its ventral base a flat indentation shaped like an inverted U. Setae as in phoretic female. Near the ventral palps one piston-like process each ; ventrolateral solenidion pair thickened, bent to the side or slightly backwards.

e) Trichobothrium : as in phoretic female.

f) Extremities.

Quantitative data. The data from measurements of legs I-IV are given in Table 5 under " nonphoretic female ". Distances measured were as for the phoretic female.

Legs II, III and IV are longer than leg I by 8 %, 23 % and 87 %, respectively.

Description of the extremities (Figs. 9-10). Leg I (Fig. 9 : f, f1) : Setae formula : Tr1-Fe3-Ge4-TiTa16(4) ; femur and genu longer than wide. Tibiotarsus slender, no claw present, two separate setae sockets distally ; two setae insert on the longer one (probably the eupathidia *tc'* and *tc"*) ; solenidion $\omega2$ originates on its dorsal base ; on its ventral base there is a soft-skinned, wart-like bump (rudiment of the claw socket). Setae *u'* and *pv'* are the shortest tibiotarsal setae with $u' > pv'$; *u'* barbed. Solenidion $\omega2 > \omega1 = (>) \varphi2 > \varphi1$; $\omega2$ and $\varphi2$ thin, $\omega1$ finger shaped, thinning distally, $\varphi1$ club shaped. Seta *v'T* very short, peg-like ; *dF* broad and leaf-like, with very fine lateral barbs. Relation of length ($\bar{x}$) leg I : tibiotarsus ($\bar{x}$) = 1 : 0.46-1 : 0.50 ($\bar{x}$ = 1 : 0,49, $n=7$).

Leg II (Fig. 9 : g) : Setae formula : Tr1-Fe3-Ge3-Ti4(1)-Ta6(1) ; tarsus with short stemmed, distally widened empodium which anteriorly is blunt or has a pointed extension ; anterior claw is only slightly larger than the posterior one ; solenidion ω is slender and becomes more so distally, extends beyond the insertion of *tc"*. Solenidion $\omega > \varphi$.

Leg III (Fig. 10 : c) : Setae formula : Tr1-Fe2-Ge2-Ti4(1)-Ta6 ; tarsus with unstemmed empodium, which is wider distally and is blunt anteriorly or has a pointed extension ; both claws are of the same size. Solenidion φ is slender.

Leg IV (Fig. 10 : d) : Setae formula : Tr1-Fe2-Ge1-Ti3(1)-Ta6 ; tarsus with pretarsus, two small claws and basally thin-stemmed, distally broadened empodium. Relation tarsus length ($\bar{x}$) : pretarsus ($\bar{x}$) = 1 : 0.28 — 1 : 0.36 ($\bar{x}$ = 1 : 0.33, $n = 10$). Distance $pv'\text{-}pv'' = 3 \times pv''\text{-}u'$. Setae $v''Ti < dTi$. Setae *pl"* and *u'* are the shortest tarsal setae. Solenidion φ thin and peg-like.

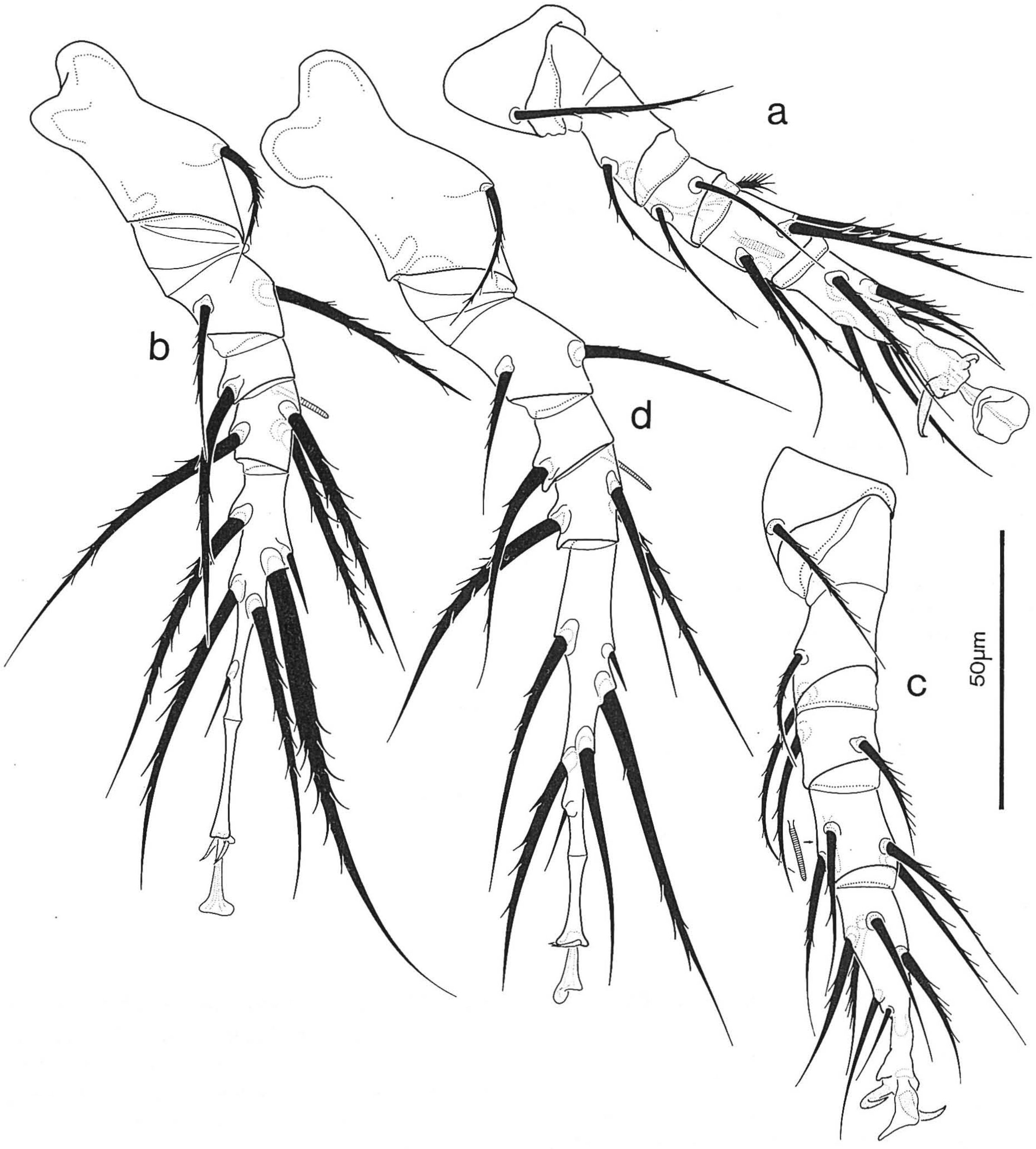

FIG. 10 : *Archidispus magnificus.*
a. — Phoretic female, leg III. b. — *Idem*, leg IV. c. — Nonphoretic female, leg III. d. — *Idem*, leg IV.

Material : 27 adult females and 11 pharate females, exclusively from breeding experiments; two adult females were lost in the breeding experiments.

Table 6 contrasts the diagnostically relevant individual characteristics and groups of characteristics of the two female morphs.

TABLE 6 : *Archidispus magnificus*, a comparison between phoretic and nonphoretic females, based on the breeding material shown in Table 4. Characteristics that are thought to have adaptational value for phoresy are indicated by bold-face numbers.

phoretic female (a)	nonphoretic female (b)	common characteristics
1. Setae *c*1, *d*, *f* modified	Dorsal setae not modified	1. Width of posterior sternal plate
2. Dorsal setae sometimes different from (b) in position and length		2. Position of 3*b*
3. Setae 3*a*, 3*b*, 3*c*, 4*b*, 4*c* longer		3. Position of 4*a*-4*b*
4. Setae 4*a* spindle shaped, 4*b* and 4*c* thicker	Ventral setae not modified	4. Form of posterior genital sclerite
5. Integument thicker		5. Form of trichobothrium
6. Anterior sternal plate wider		6. Form of seta *dF* (leg 1)
7. Apodemata more sclerotic		7. Length ratios of *ps*1-*ps*2-*ps*3
8. *LEI* highly sclerotic with a distinct lowered edge	*LEI* only faintly present or absent	
9. Proportions of gnathosoma and its solenidia differ from (b)		
10. Leg 1 shorter		
11. Tibiotarsus 1 longer (cf. ratio leg/tibiotarsus)		
12. Tibiotarsus I thickened	Tibiotarsus 1 slender	
13. Tibiotarsus 1 with claw	Tibiotarsus 1 without claw	
14. Length of solenidia of leg 1 differs from (b)		
15. $u' < pv'$ (tibiotarsus)	$u' > pv'$	
16. Femur and genu 1 wider than long	Femur and genu 1 longer than wide	
17. Legs II-IV longer		
18. Empodia II-III long stemmed, no tip	Empodia II-III short stemmed, anterior tip	
19. Anterior claw of leg II twice as long as posterior	Anterior claw of leg II only slightly longer than posterior	
20. Anterior claw of leg III more than twice as long as posterior	Claws of leg III equal in length	
21. Solenidion of tarsus II does not reach *tc'*	Solenidion of tarsus II extends beyond *tc'*	
22. Pretarsus IV longer (cf. ratio tarsus/pretarsus)		
23. Setae of leg IV sometimes differ from (b) in positions and lengths		
24. Appetitive behavior present	Appetitive behavior absent	

3. Female with intermediate phenotype.

The analysis of the f1 daughters of a phoretic breeding female (B-88) showed an animal that on the basis of its characteristics occupies an intermediate position and so cannot be classified as being one or the other of the two morphs.

Description (Fig. 8 : a, b : 9 : h).

Dimensions : length 200, width 162, anterior sternal plate 51, posterior sternal plate 96, leg I 67 total, TiTa 35 ; leg II (without Tr) 79, Ta 31 ; leg III (without Tr) 87, Ta 31 ; leg IV (with Tr) 131, Ta 44, PrTa 15. Relation of tarsus IV : pretarsus = 1 : 0.34. Leg II is 18 % longer than leg I, leg III is 30 % longer and leg IV 96 % longer.

The distribution of the diagnostically relevant characteristics is shown in Table 7.

Material : One female from breeding experiment B-88, 4 June 1988.

A nonphoretic female from the same breeding experiment has a 7 µm-long hair-like formation

TABLE 7 : *Archidispus magnificus* : Intermediate female showing proper characteristics as well as characteristics of nonphoretic and phoretic females.

Characteristics of		
nonphoretic female	phoretic female	intermediate female
Width of anterior sternal plate	Ridge *LEI*	
	Apodemata IV	
Structure and setation of leg I	Empodia and claws of legs II and III	Rudimentary claw of leg I
Solenidion ω (leg II) reaches seta *tc'*	Relative length of tibiotarsus I	Relative length of legs
Body setae except *c*1, *d*, 4*a*, 4*b*	*v"Ti dTi* (leg IV)	Form of setae *c*1, *d*, 4*a*, 4*b*
Relation Ta IV : PrTa	Gnathosoma	

unilaterally on the rudimentary claw socket of tibiotarsus I (Fig. 9 : f1).

DISCUSSION

Sixty-three percent of the characteristics of phoretic females listed in Tables 3 and 6 are apparently apomorphies which can be interpreted as adaptations to phoretic behavior ; they are shown as bold-face numbers in these two tables. Above all it is the extremities that show striking functional adaptations as are needed for climbing onto the transport host and holding on to it while on board. The chaetotaxic differences between the morphs are similarly striking. Tables 3 and 6 also show that the two morphs differ in 68 % (*A. minor*) and 77 % (*A. magnificus*) of the compared characteristics or groups of characteristics. The extent of difference between the two morphs thus goes far beyond what is normally required for the differentiation of two species. An objective recognition of the conspecificity of two such different morphs is not possible without breeding experiments. The consequences that this will have, especially in the area of museum taxonomy, cannot be estimated.

There are already a number of known scutacarid genera that show differing degrees of polymorphism (EBERMANN in prep.). This indicates that there is an even larger number of as-yet unknown polymorphic species which would have an even greater effect on the current systematics of scutacarids. In this context, one need only think of the numerous species of the *Variatipes* group, whose common characteristic is the lack of claws on leg pair I. At present we have no idea as to whether this group of species is a convolute of nonphoretic females whose phoretic females happen to be unknown, or whether this situation only applies to some of the described species, or, finally, whether the loss of the claw on leg I is due to other causes.

A comparative study of the phenomenon of polymorphism in scutacarids is being prepared.

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