

PARASITISM, LIFE CYCLE AND PHENOLOGY
OF *LEPTUS TRIMACULATUS* (HERMANN, 1804)
(ACARI : PARASITENGONAE : ERYTHRAEIDAE)
INCLUDING A DESCRIPTION OF THE LARVA

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LEPTUS
TRIMACULATUS
LIFE CYCLE
PARASITISM
PHENOLOGY
LARVA

SUMMARY : To date, the taxonomy of most Erythraeidae (Parasitengonae) lacks clear correlations of deutonymph and adult stages with their conspecific parasitic larval instar. Hitherto, the taxonomy in almost all cases is based upon descriptions of isolated ontogenetical stages only. In controlled rearing experiments, all instars of *Leptus trimaculatus* (Hermann, 1804) (Erythraeidae : Leptinae), being formerly known as adult only, were reared. A description of the larva as well as data on parasitism, times of development, phenology, nutrition and habitat requirements of all instars are given. *L. trimaculatus* is an univoltine erythraeid, reproducing during late spring and hibernating in the adult instar. Unlike other Erythraeidae, the larva parasitizes a broad spectrum of arthropod hosts. Both postlarval active instars prey on immobile or slow moving arthropods. All stages of *L. trimaculatus* show a preference for humid and temperate habitat-conditions, although they may not be restricted to them. The results are discussed in comparison with other *Leptus* species.

LEPTUS
TRIMACULATUS
ENTWICKLUNGSSTADIEN
PARASITISMUS
PHÄNOLOGIE
LARVE

ZUSAMMENFASSUNG : Zum gegenwärtigen Zeitpunkt gibt es innerhalb der Erythraeidae (Parasitengonae) nur wenige eindeutige Korrelationen von Deutonymphen und Adulten mit ihren jeweiligen parasitischen Larvenstadien. Die Taxonomie basiert zumeist nur auf der Beschreibung einzelner Entwicklungsstadien. In kontrollierten Zuchtversuchen gelang es, alle Stadien von der bisher nur als Adultus beschriebenen Art *Leptus trimaculatus* (Hermann, 1804) (Erythraeidae : Leptinae) zu züchten. Die Larve wird beschrieben, weiterhin werden Daten zu Parasitismus, Entwicklungszeiten, Phänologie, Ernährung und Habitatansprüchen aller Stadien gegeben. *L. trimaculatus* ist eine univoltine Erythraeide, welche sich im späten Frühjahr fortpflanzt und als Adultus überwintert. Im Gegensatz zu anderen Erythraeiden, wird von der Larve ein breites Spektrum an Arthropoden parasitiert. Deutonymphe und Adultus ernähren sich von immobilen oder wenig aktiven Arthropoden. Alle Stadien von *L. trimaculatus* präferieren feuchte und gemässigte Lebensräume, scheinen aber nicht ausschliesslich darauf beschränkt zu sein. Die Ergebnisse werden im Vergleich zu anderen *Leptus* Arten diskutiert.

LEPTUS
TRIMACULATUS
CYCLE DE VIE
PARASITISME
PHENOLOGIE
LARVE

RÉSUMÉ : Jusqu'à présent, la taxonomie de la plupart des Erythraeidae se fait sans relation clairement établie entre stades deutonymphaire et adulte et stade larvaire parasite conspécifique. Dans la plupart des cas, la taxonomie est encore fondée seulement sur des descriptions de stades ontogénétiques isolés. Au cours d'expériences sur des élevages contrôlés, *Leptus trimaculatus* (Hermann, 1804) (Erythraeidae : Leptinae), connue auparavant uniquement par l'adulte, a été observée à tous les stades. Une description de la larve est apportée, ainsi que les données sur son parasitisme et sur les durées du développement, la phénologie, la nutrition et les exigences de l'habitat de tous les stades. *L. trimaculatus* est un erythraeide univoltin, se reproduisant à la fin du Printemps, et

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hibernant au stade adulte. Contrairement à d'autres Erythraeidae, sa larve parasite un large spectre d'hôtes arthropodiens. Les deux stades postlarvaires actifs chassent des proies arthropodes immobiles ou à déplacement lent. *L. trimaculatus* montre à tous les stades une préférence pour des habitats humides et tempérés, bien qu'elle ne soit pas limitée à de telles conditions. Ces résultats sont discutés en comparaison avec d'autres espèces de *Leptus*.

INTRODUCTION

For Europe, at least 12 species of the erythraeid genus *Leptus* Latreille, 1796, subfamily Leptinae Southcott, 1957 are described from their adult or deutonymph instar (OUDEMANS, 1913, WILLMANN, 1951, SCHWEIZER & BADER, 1963) and at least 12 species are described from the larva only (OUDEMANS, 1912, VITZTHUM, 1929, PAOLI, 1936, TURK, 1945, ANDRE, 1953, FEIDER, 1956, 1967, BERON, 1975). Because no correlations between these instars have ever been proved, the larvae and the adults all were denominated with different names. The only experimentally verified correlations between the heteromorphic parasitic larva and its free-living postlarval stages (the deutonymph and the adult), were carried out by TREAT (1974, 1975). Although the same author reports successful rearing of nymphs and an adult from moth-borne larvae in North-America, he did not give any definitive descriptions or determinations: "... several nine deutonymphal and one adult *Leptus*, collectively compromising three undetermined species" (TREAT, 1974, p. 301). Previous rearing experiments of EVANS (1910), BRYANT (1911) and FEIDER (1967) only resulted in correlations between larvae and deutonymphs. Unfortunately a description was only given by FEIDER (1967) in case of *Leptus galerucae* Feider, 1967.

This situation certainly is generally valid for the Erythraeidea since, according to SOUTHCOTT (1961) at least at that time only few published proofs for correlations of larval and adult forms had been recorded. The main problems of controlled rearing of all ontogenetic stages are: The larval host-specificity (1) is often unknown and if known, rearing is difficult to handle. Deutonymphs and adults (2) are often unknown for their specific nutritional requirements as mainly free-living predators.

OUDEMANS (1912) suggests from the erythraeid larva *L. ignotus* (Oudemans, 1903), that it could represent the larval form of *L. trimaculatus* (Hermann, 1804). This species is common in central Europe. His suggestions however, are exclusively based on form and colour of the idiosomal setae. In this paper, the successful rearing of *L. trimaculatus* under controlled conditions throughout all ontogenetic stages will be documented. Thus, a clear correlation of a distinct *Leptus* larva to its deutonymph and adult will be described. Moreover, data concerning parasitism, life cycle, phenology, nutrition and habitat requirements are given. So far, the knowledge on these points is rather fragmentary for the Leptinae in toto, except for its parasitism. Some of these data was obtained during ecophysiological investigations of *Anystis* spp. (Acari: Prostigmata: Anystidae) (OLOMSKI, in prep.) and several terrestrial Parasitengonae (WOHLTMANN, in prep.).

MATERIAL AND METHODS

Locality: The area of investigation is located on the campus of the University of Bremen. It lies close to a pond and shows three distinct zones (Fig. 1).

(1) Rush belt: Located adjacent to the pond, only a few meters in width. Moist to wet, humous and slightly shaded. Dominated by *Juncus effusus* L.

(2) Rough meadow: Approx. 30 m in width, slope 2-3°. Fresh to moderately dry, sandy and fully exposed. Dominated by *Agrostis tenuis* Sibth. Mowed once or twice a year (1989: 20.09.). In spring and in summer used to a great extent for recreational purposes.

(3) Rubble heap: Approx. 10 m in width, slope about 14°. Moist to moderately dry, rich in

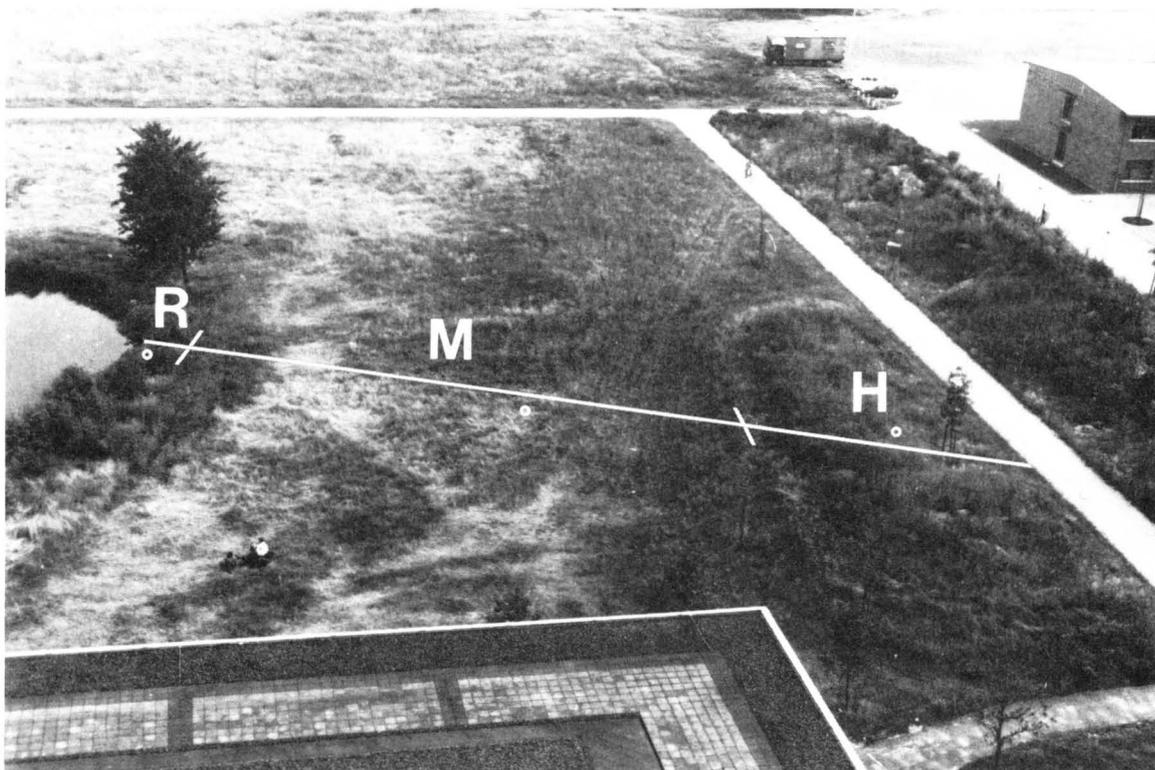


FIG. 1 : The area of investigation on the campus of the University of Bremen (FRG) on 26.06.1989.

Zones : rush belt (R), rough meadow (M), rubble heap (H). Symbols indicate points of microclimatic measurements in the respective zones.
Direction of view : south.

nutrients, fully exposed. Ruderal vegetation, dominated by *Cirsium arvense* (L.) Scop. and *Agropyron repens* (L.) P.B.

Periodically investigations were carried out in 1989 from May to September in intervals of two weeks and for the remaining time, monthly. During each date, animal samples and microclimatic data were obtained.

Capturing technique : A portable electric insect suction trap (Griesohn, D-7400 Tübingen) was used for quantitative analysis of the epibiotic fauna. For each date in each zone two samples of $5 \times 0.28 \text{ m}^2$ of the soil surface area were systematically exhausted. Additionally, sweepnet samples were evaluated sporadically. After mowing, mulch samples taken by hand were sorted out.

Microclimate : Parallel to periodical sampling, the following abiotic parameters were measured at defined sites within the zones between 11.00 a.m.

and 01.00 p.m. CET during the respective dates : Air temperature and air humidity (relative humidity = % RH), using a digital thermohygrometer with thin-layer detector (Kyberna FT 302.2, FT 311.2, D-6410 Bensheim) in heights of 0.05, 0.1, 0.5 and 1.0 m above the surface of the substratum.

Soil temperature, using a digital thermometer (Indunorm T 413, D-4000 Düsseldorf) connected to a NiCr/Ni piercing detector (Labomess 129k, D-4300 Essen) in depths of 0.05 and 0.1 m beneath the surface of the substratum.

The different ontogenetical stages of *Leptus trimaculatus* were reared in the following experiments :

(1) Eggs of a single clutch, oviposited by an isolated female the night after capturing (29.05.1989). The freshly emerged larvae were distributed over 10 rearing boxes, two to a box. Each box was supplied with one female anytid mite

(5 × *Anystis baccharum* (L.), 5 × *A. rosae* Oudemans.) as a host.

(2) Larvae (N = 4), captured parasitically in the field, attached to various hosts.

(3) Larvae (N = 3), captured freely in the field, fully engorged after parasitizing.

Rearing conditions : Rearing of the animals was carried out in plaster-charcoal filled polystyrene boxes (25 × 25 × 20 mm) in a lightthermostat at 20° C ± 1° C, with a 12h + 12h light-dark cycle. Intensity during light period : 3 klx ± 0.25 klx. Saturated air humidity was mediated by adding

water to the substratum, if required. The rearing of the deutonymph to the adult stage was performed under natural light conditions.

Determination and external morphology of the larva : Determination of adults was carried out referring to OUDEMANS (1913) and SCHWEIZER & BADER (1963). The description of the larva was attained by means of permanent mounts of some larvae cleared by lactate from the rearing experiment (1). Optic equipment : Dialux 20 EB (Leitz, D-6330 Wetzlar) with phase-interference contrast and camera lucida. The terminology follows SOUTH-COTT (1961).

RESULTS

Description of larva from mounted specimen P/E/LEP 891, supplemented by others (N=4) (Fig. 2 a,b,c and Fig. 3 a,b,c) :

All specimen unfed. Colour in life reddish. Idiosoma ovoid, length 263 µm, width 185 µm, total length from tip of gnathosoma to posterior pole of idiosoma 423 µm.

Dorsal surface of idiosoma : Dorsal scutum trapezoid, with rounded angles, all borders more or less straight. Surface smooth, with sclerites in shape resembling a crista. Two pairs of sensillae, these filiform with fine setules increasing in number distally. The anterior pair arising a little posterior to the level of the anterolateral scutalae. Two pairs of scoboscutalae. Standard data are given in Tab. 1. One eye on each side anterior to the level of the posterior sensillae. Lens circular, surrounded by a sclerite, 19 µm in diameter.

At the lateral edge of the idiosoma above coxae I one supracoxala on each side. Dorsum of idiosoma with 55 scobalae similar to scoboscutalae, arranged in irregular rows. All idiosomal setae dark in life.

Ventral surface of idiosoma : Sternalae I 28 µm long, parallel-sided, in the distal half tapering ; sternalae II similar, 35 µm long. Between area of coxae II and III one curved row of four scobalae, resembling the sternalae. About 24 scobalae at the level of and posterior to coxae III, the form

posteriad grading to the dorsal scobalae but more slender, 36 — 41 µm long.

Coxalae 1, 1, 1 : Coxalae I 54 µm long, thin and pointed ; coxalae II 23 µm long, blunt-ended ; coxalae III 38 µm long, pointed.

Legs normal ; lengths (including coxae and claws) I 498 µm, II 465 µm, III 522 µm. Scobalae of legs normal, increasing in number proximally.

CHARACTER	MEAN	RANGE	SD	N
AW	57	55 - 59	1.87	5
PW	69	67 - 70	1.22	5
SBa	8	8 - 9	0.40	5
SBp	13	11 - 14	1.14	5
ASBa	23	22 - 24	1.40	2
ISD	53	49 - 56	2.90	5
L	78	71 - 84	6.50	3
W	76	71 - 82	5.70	3
A - P	12	11 - 16	1.80	5
AL	42	38 - 48	3.05	5
PL	55	53 - 56	1.03	5
ASE	37	35 - 41	1.85	5
PSE	66	61 - 76	4.70	4
DS	-	40 - 52	-	3

TAB. 1 : Standard data of larval *Leptus trimaculatus* (Hermann, 1804). All lengths in µm. Abbreviations according to SOUTH-COTT (1961).

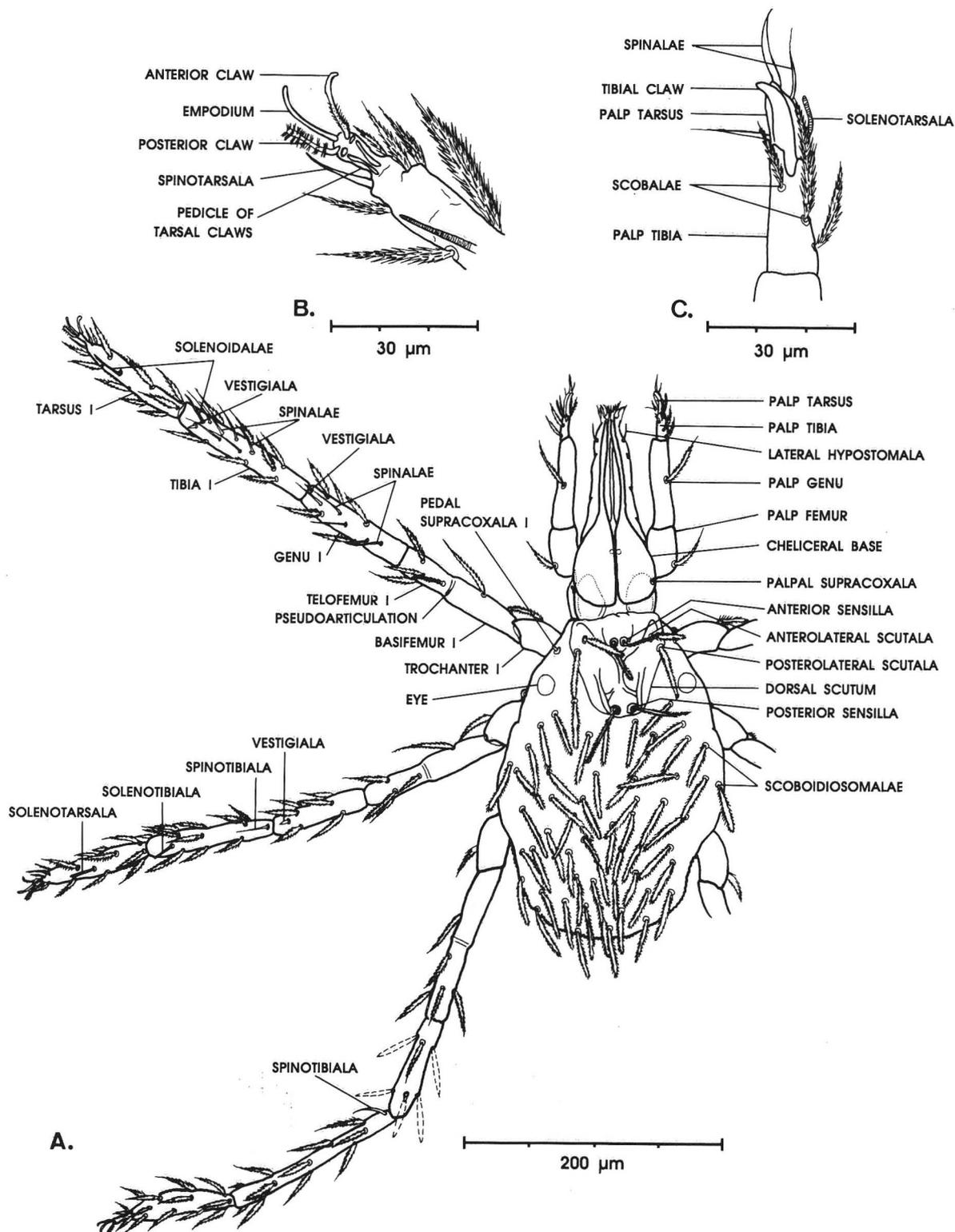


FIG. 2 : *Leptus trimaculatus* (Hermann, 1804), larva P/E/LEP 891, dorsal aspect.

A. — General habitus, right legs omitted beyond trochanters, damaged setae indicated by broken lines. B. — Distal part of the left tarsus I. C. — Tibia and tarsus of the right palpus.

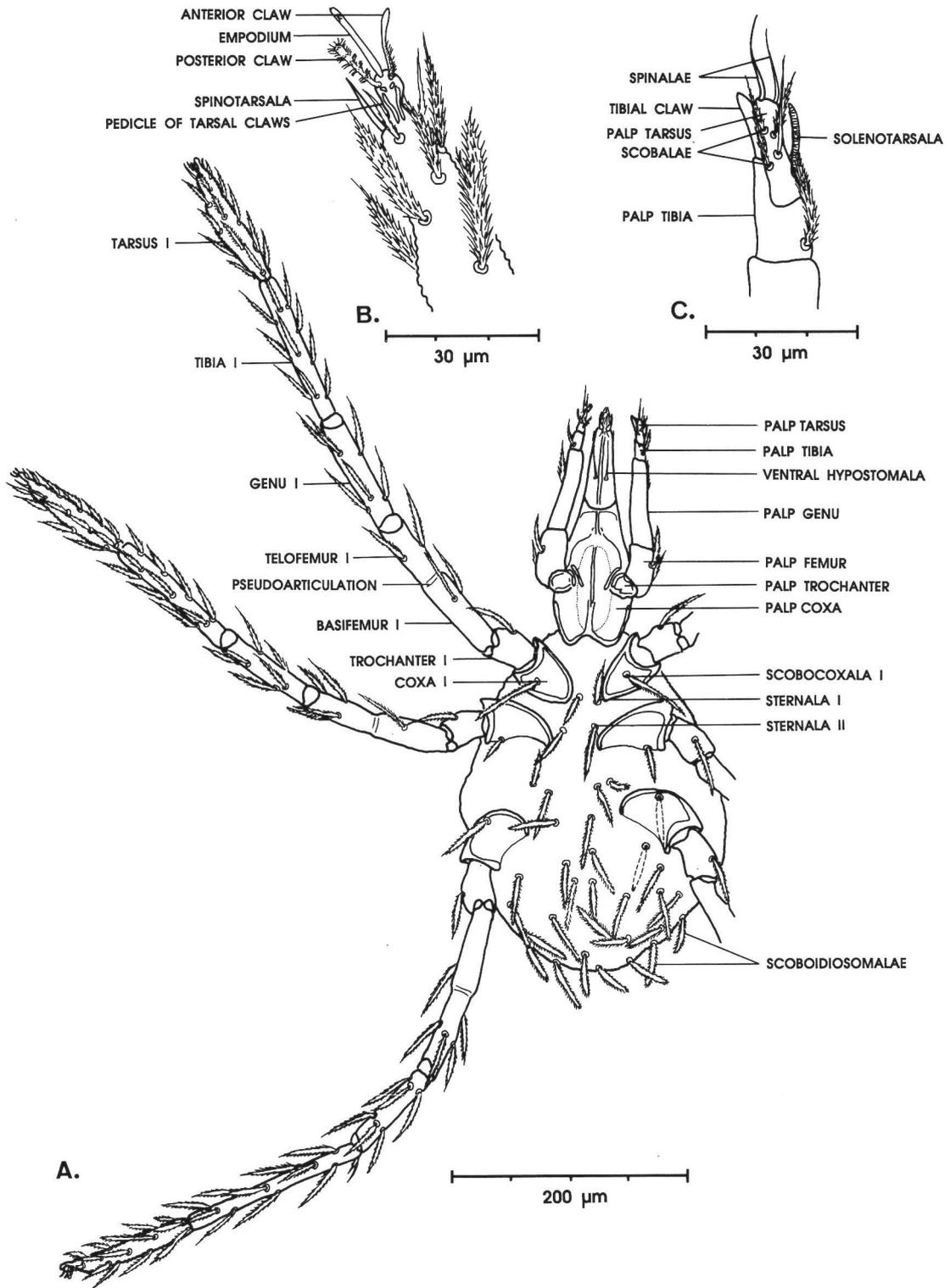


FIG. 3 : *Leptus trimaculatus* (Hermann, 1804), ventral aspect.

A. — General habitus, left legs omitted beyond trochanters, damaged setae indicated by broken lines. B. — Distal part of the right tarsus I. C. — Tibia and tarsus of the left palpus.

Leg specialized setae as follows (terminology see SOUTHCOFF, 1961, lengths in μm in parentheses).

Leg I : SpGeI.15d(29), SpGeI.22d(27), SpGeI.49d(28), SpGeI.59d(27), SpGeI.80d(28), VsGeI.90d(6), SpTiI.44d(31), SpTiI.52d(25), SpTiI.58d(35), SpTiI.69ad(31), SpTiI.69pd(29), SpTiI.79d(35), SoTiI.82d(31), VsTiI.87d(7), SoTaI.57d(32), SpTaI.99p(13).

Leg II : VsGeII.90d(6), SpTiII.05d(26), SoTiII.83d(17), SoTaII.51d(19), SpTaII.100p(15).

Leg III : SpTiIII.03ad(30), SpTaIII.100p(12).

Tarsal claws : Anterior claw distally smooth, falciform, in the proximal half with faint setules ; empodial claw longer, more slender, falciform, completely smooth ; posterior claw slender, slightly broadened distally, with fine setules arranged in coronal groups, arising approximately rectangular from the claw (Fig. 2b, 3c).

Gnathosoma : The cheliceral bases showing an abrupt transition from a rounded posterior part to a slender anterior part, each of about the same length, surface porose and with delicate longitudinal striations, length $150 \mu\text{m}$, maximum width of a single chelicera $84 \mu\text{m}$. One pair of lateral (length $33 \mu\text{m}$) and ventral (length $14 \mu\text{m}$) spinohypostomalae respectively. The lateral arising about $31 \mu\text{m}$

and the ventral about $52 \mu\text{m}$ from the tip of the gnathosoma.

Palpal setal formula 0 : 0 : 2 : 1 : 3 : 7. Palpal femorala, genuala and tibiala all pointed scobalae. Palpal tarsala see Fig. 2c and 3c. Palpal supra-coxala present, $4 \mu\text{m}$ long. Tibial claw smooth, falciform with a single tip.

Observations on parasitism : In the field, the larva of *Leptus trimaculatus* was found to be parasitizing upon prostigmatic mites as well as various pterygote and apterygote insects (Tab. 2, Fig. 4 a,b). In most cases, only one larva had attached itself firmly to its host. They did not prefer distinct body regions. As shown in Tab. 2, the anystids were the most parasitized of all captured hosts within the area of investigation. A quantitative analysis of sweepnet samples revealed infestation rates of 10.8 % (24.06.89), 12.5 % (26.06.89) and 14.8 % (27.06.89) for *Anystis baccharum* (N= 89).

Observations on life cycle : From the eggs of rearing experiment (1), larvae hatched after 38-39 days (Tab. 3). During light phase, they hid in small cavities of the rearing substratum. In several cases, it was observed that these larvae were attacked and even preyed upon by *Anystis*. However, after 3-4 days for three cases attachment to the *Anystis* —

HOSTS	ATTACHMENT SITES ON HOSTS	NUMBER OF HOSTS WITH N NUMBER OF LARVAE					
		N = 1	2	3	4	5	6
Acari: Anystis baccharum (L.) AD A. rosae Oudem. TN, AD Abrolophus sp. AD	idiosoma, legs idiosoma, legs opisthosoma	10 5 1	1 1	1			
Collembola: Arthropleona Symphypleona	thorax, abdomen thorax, abdomen, legs	8 4	1				
Homoptera: Aphididae LA	intersegmental integument head - thorax	1					
Hymenoptera: Tenthredinoidea LA	abdomen				1		1
Diptera: Chironomidae AD	thorax	1					

TAB. 2 : Parasitic associations of larval *Leptus trimaculatus* (Hermann, 1804). The data were obtained from field records. Abbreviations : larva (LA), tritonymph (TN), adult (AD).

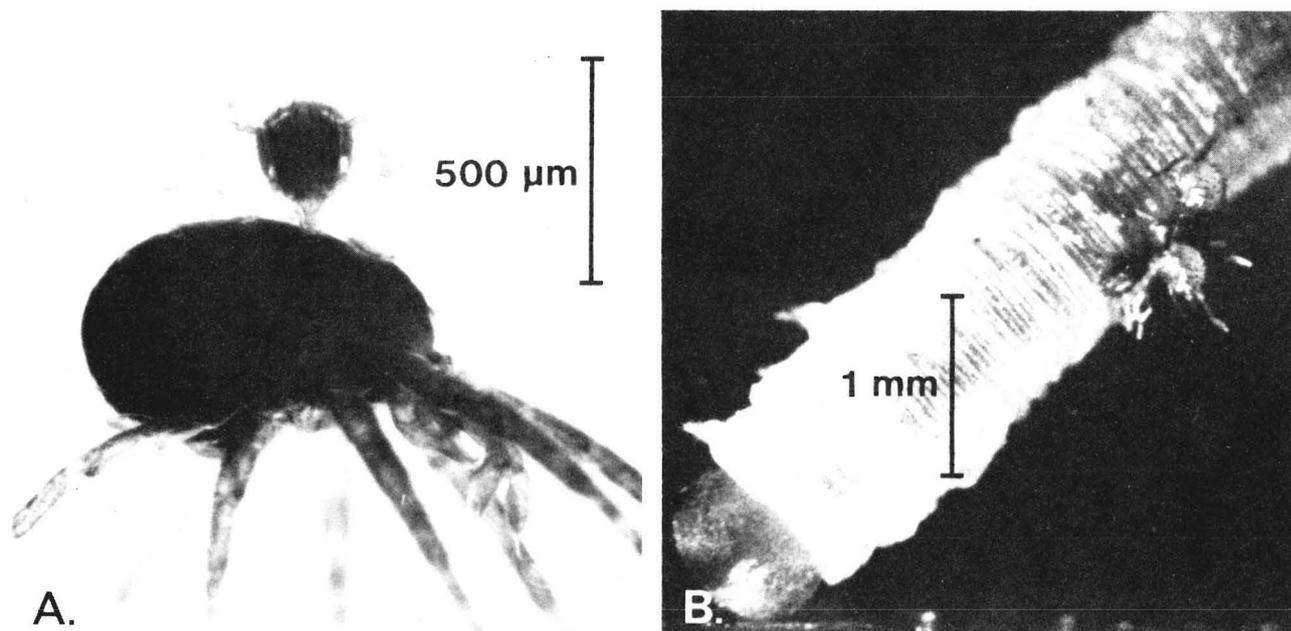


FIG. 4 : Larvae of *Leptus trimaculatus* (Hermann, 1804), infesting, an adult *Anystis baccharum* (L.) (A), a larval Tenthredinoidea (B).

ONTOGENETIC STAGE	DEVELOPMENTAL TIME (DAYS)	N
egg + prelarva	38 - 39	21
larva	10 - 12	3
1. preparasitic phase	3 - 4	3
2. parasitic phase	5 - 6	3
3. postparasitic phase	1 - 4	5
protonymph (calyptostatic)	13 - 18	8
deutonymph	17	1
tritonymph (calyptostatic)	21 - 22	1

TAB. 3 : Developmental time of the ontogenetic stages of *Leptus trimaculatus* (Hermann, 1804) in the rearing experiments. The mites were reared in a light thermostat at $20 \pm 1^\circ \text{C}$, with a 12h + 12h light-dark cycle. The intensity during the light period was $3000 \pm 250 \text{ lx}$.

host occurred ($2 \times A. rosae$, $1 \times A. baccharum$). In one case, the time of attachment could definitively be determined for the dark phase. The parasitic bonding lasted 5-6 days. Thereafter the larvae detached, and after a further 1-4 days, they turned into calyptostasis (protonymph). Once again, they preferred cavities in the substratum in order to undergo the calyptostatic protonymph. For all experiments the free living deutonymph emerged after 13-18 days. In two cases, a larva of rearing experiment (1) was successfully raised to the deutonymph and in the case of rearing experiment (3) an adult was derived. In the latter, the deutonymph

was active for 17 days. During this time it was fed on ant eggs and larvae. The adult emerged from the calyptostatic tritonymph after 21-22 days. The adult too was fed on ant eggs and larvae. It died after 44 days.

Observations on phenology : In the field, the larva of *L. trimaculatus* was found from the end of June to the middle of August (Fig. 5), the greatest abundance being found in July. 68 % from a total of 148 larvae were captured in the rush belt (R), 20 % on the rough meadow (M) and 12 % on the rubble heap (H). The deutonymph was found in July and August, 6 individuals in R and 2 on M. The adult was found during late spring and autumn only in R (N = 4). The microclimate data (Fig. 5) characterize R as humid (82-100 % RH), and compared to the other areas as quite temperate ($0.5- 21.5^\circ \text{C}$) in the annual periodicity. In contrast, M shows a broad fluctuation in temperature ($-1.5- 42^\circ \text{C}$) and humidity (41-100 % RH) over the year. This is particularly valid for the vertical gradients during summer (Fig. 6), when M is characterized by high temperatures and low humidities in the vegetation close to the surface. At the same time, reversed conditions are found in R. In winter, both zones show similar vertical gradients.

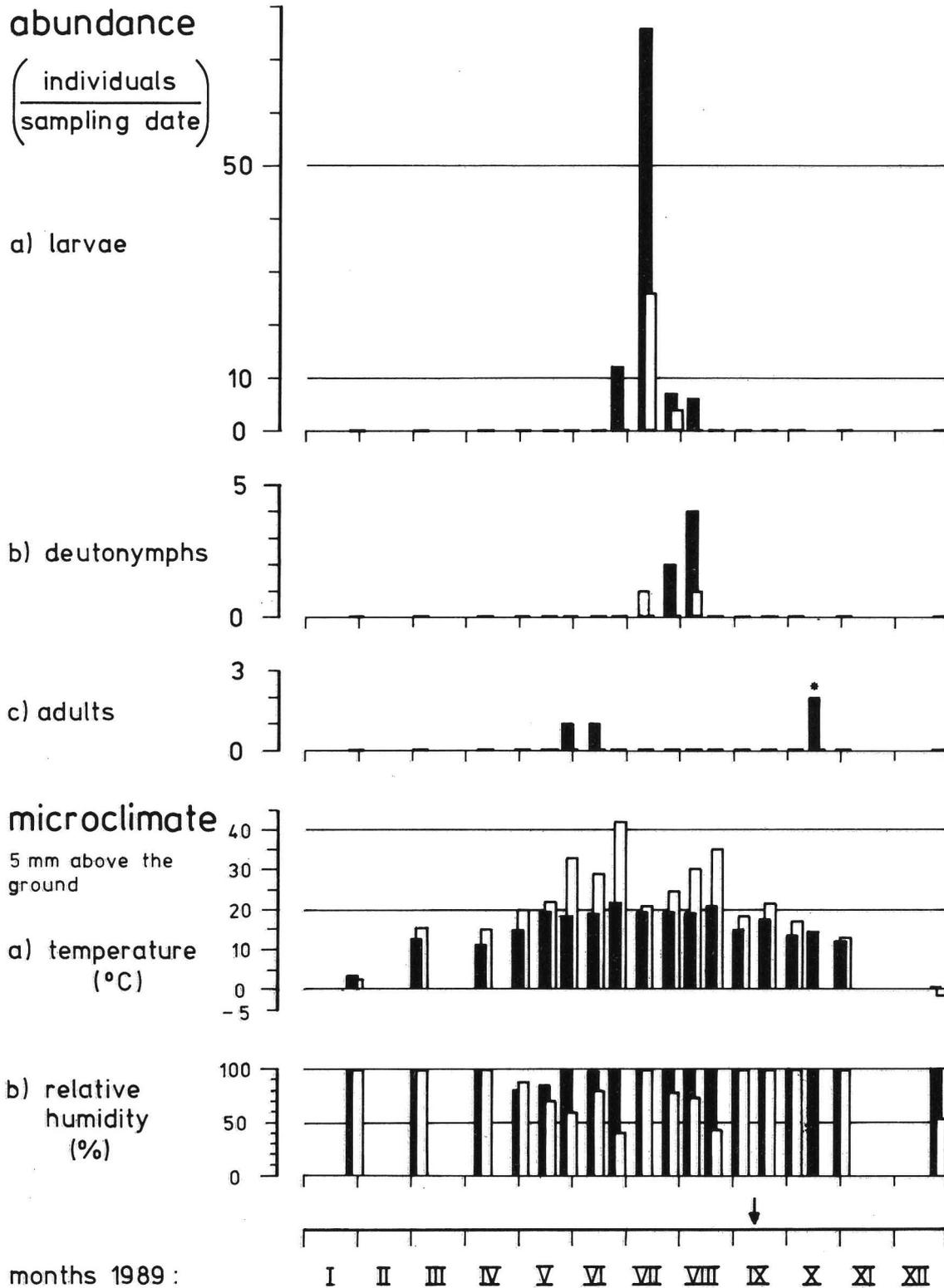


FIG. 5 : Phenology of *Leptus trimaculatus* (Hermann, 1804) and the microclimate at the area of investigation.

Zones : a) rush belt (solid columns), b) rough meadow (open columns ; the date of mowing is indicated by the arrow on the abscissa). All samples were taken by an insect suction trap, except “*”, which was taken by a sweepnet. Measurements of the microclimate were carried out between 11.00 a.m. and 01.00 p.m. CET about 5 mm above the ground.

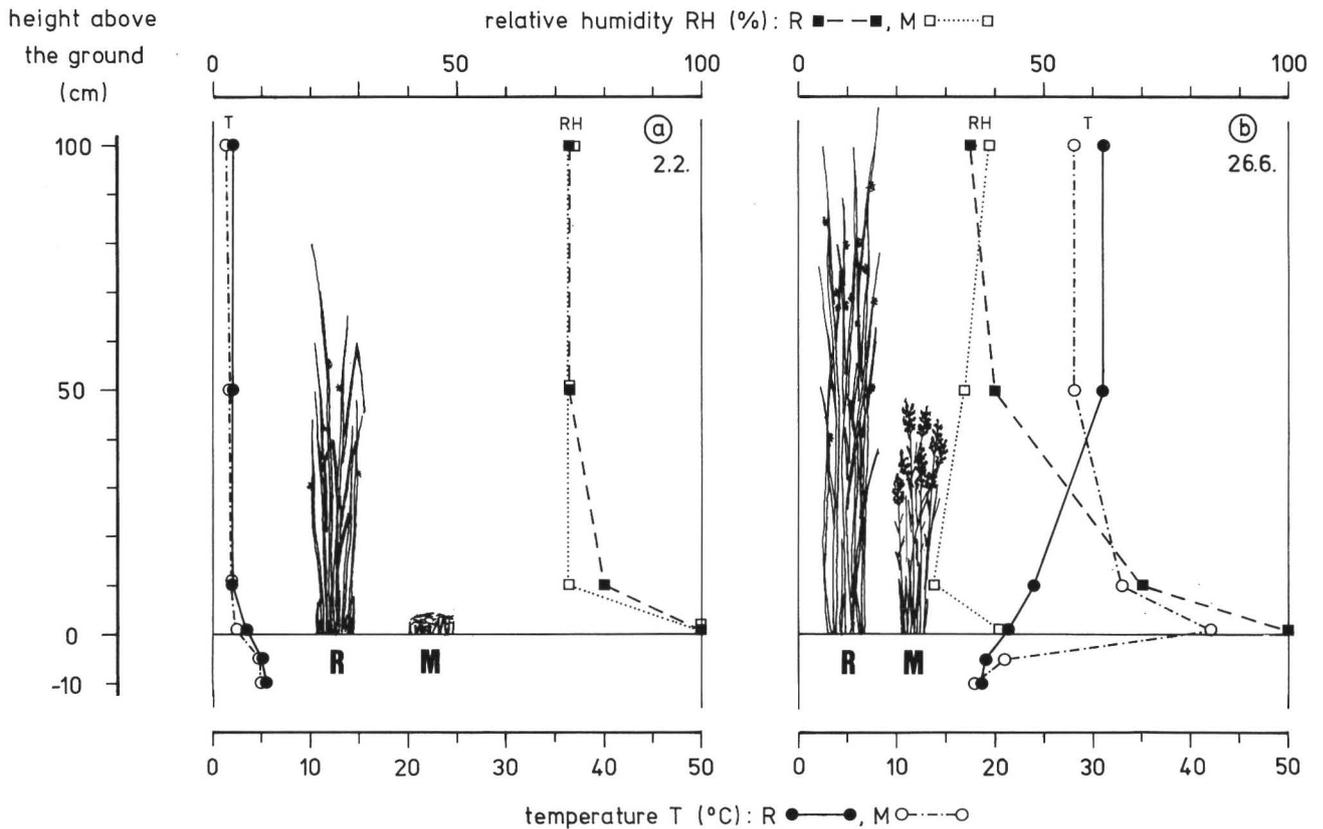


FIG. 6 : Vertical gradient of temperature and humidity at the area of investigation on 02.02.1989 (a) and on 26.06.1989 (b). Zones : rush belt (R), rough meadow (M). The measurements were carried out between 11.00 a.m. and 01.00 p.m. CET. The illustrated plants show the developmental stage of the vegetation.

DISCUSSION

Morphology : The larva we reared from an adult of *Leptus trimaculatus* is consistent with the general diagnosis of the monogeneric subfamily Leptinae given by SOUTHCOTT (1961). Compared to the descriptions of OUDEMANS (1904) we suggest that the larva of *L. trimaculatus* is not identical to his *L. ignotus* (Oudemans, 1903). This is true at least for the figures he gave concerning the number of dorsal setae (OUDEMANS, 1904, Tab. XII, Fig. 74) and the number of coxalae II. Furthermore, we believe that for *L. ignotus* more than one species are included because of the great variability OUDEMANS (1912) mentioned for the number of dorsal setae, length of legs, form of scutalae and the broad seasonal occurrence of the larva. But we can not wholly exclude the possibility that the larva of *L. trima-*

culatus lies somewhere between the larvae combined by OUDEMANS (1912) as *L. ignotus*. The larva, BERON (1975) provisionally identified and described as *L. ignotus* (Oudemans, 1903) is distinctly different to that of *L. trimaculatus*. This regards (*L. ignotus* sensu BERON) the higher number of dorsal idiosomatae, as well as the form of the posterior sensillae being ciliated only terminally. *L. ignotus* (sensu BERON) wears one spinala on genu I (*L. trimaculatus* : 5) and two spinalae on tibia I (6).

Compared to the descriptions of other european *Leptus* larvae for which sufficient data is available (ANDRE, 1953, FEIDER 1956, 1967, BERON, 1975), *L. trimaculatus* resembles more closely *L. echinopus* Beron, 1975 and *L. southcotti* Beron, 1975. Concerning the hosts, only these two species as well as *L.*

trimaculatus were found to be parasitizing upon collembolans. The scutal standard data of *L. echinopus* can be regarded as being closest to those of *L. trimaculatus* in nearly all dimensions. Furthermore, the overall leg dimensions and the lengths of single leg articles of *L. echinopus* all fit within the ranges of the respective *L. trimaculatus* data. A high number of spinae on genu I (both 5) and on tibia I (*L. echinopus* : 5, *L. trimaculatus* : 6) is a common feature of these two species. Additionally, the shape of the crista — like sclerites on the scutum are nearly identical (BERON, 1975, Fig. 18). These facts considered, *L. echinopus* might be synonymous to *L. trimaculatus*.

Parasitism : The larva of *L. trimaculatus* is found to be parasitizing upon a wide spectrum of arthro-

pods (Tab. 2). This is in contrast to other trombidian larvae, which in a majority of cases obviously are restricted to distinct groups of hosts. The overall host-spectrum previously cited for several *Leptus* larvae (Tab. 4) qualitatively is consistent with our observations on *L. trimaculatus*. Parasitizing upon prostigmatic mites other than Parasitengonae and on hymenopteran larvae is new, although adult hymenopterans as hosts have been recently described for two american *Leptus* species (SOUTHCOTT, 1989a, 1989b). According to our field investigations we can, for this species, to a certain degree of certainty exclude parasitism for cicadas, araneids and opilionids, the latter usually being parasitized by several other *Leptus* species (Tab. 4). The only recorded *Leptus* larva with a comparati-

LEPTUS SPECIES	LEPTUS HOSTS													SOURCE	
	ARACHNIDA				INSECTA										
	Scorpiones	Araneae	Opiliones	Acari	Collembola	Odonata	Dermoptera	Orthoptera	Homoptera	Heteroptera	Coleoptera	Hymenoptera	Diptera		Lepidoptera
<i>L. dubius</i> (Paoli, 1937)								■					■		PAOLI (1937)
<i>L. echinopus</i> Beron, 1975					■										BERON (1975)
<i>L. galerucae</i> Feider, 1967											■				FEIDER (1967)
<i>L. gracilipes</i> (Kramer, 1897)									■						KARPPINEN (1958)
<i>L. ignotus</i> (Oudemans, 1903)			■												BERON (1975)
			■	■		■		■	■	■	■		■		MÜNCHBERG (1936) OUDEMANS (1912)
<i>L. josifovi</i> Beron, 1975										■					BERON (1975)
<i>L. killingtoni</i> Turk, 1945						■									TURK (1945)
<i>L. meloidarum</i> Beron, 1975											■				BERON (1975)
<i>L. orthopterarum</i> Beron, 1975								■							BERON (1975)
<i>L. phalangii</i> (De Geer, 1778)		■	■								■	■			BRYANT (1911)
			■	■											VITZTHUM (1929)
<i>L. phyllotretae</i> Feider, 1956											■				FEIDER (1956)
<i>L. pyrenaeus</i> Andre, 1953	■														ANDRE (1953)
<i>L. slivovi</i> Beron, 1975														■	BERON (1975)
<i>L. southcotti</i> Beron, 1975						■									BERON (1975)
<i>L. trimaculatus</i> (Hermann, 1804)				■	■				■			■	■		present investigation

TAB. 4 : A list of larval *Leptus* described from Europe and their parasitic relations to different arthropod hosts (main groups). Solid squares : parasitism proved. Supposed synonyms are : BRYANT (1911) : *L. phalangii* (De Geer, 1778) = *L. nemorum* (Koch) = *L. ignotus* (Oudemans, 1903). KARPPINEN (1958) : *L. gracilipes* (Kramer, 1897) = *L. ignotus* (Oudemans, 1903) non *L. gracilipes* (Oudemans, 1912). For further taxonomic discussion see SOUTHCOTT (1961), pp. 514-521.

vely broad host spectrum is *L. ignotus* (OUDEMANS, 1912, MÜNCHBERG, 1936, BERON, 1975). But since we regard this species as a combined taxon (see above), evaluations of the host range of distinct species within *L. ignotus* are difficult to judge.

All of the larvae were firmly attached to their hosts on sclerotized as well as soft body regions. Thus, in the case of *L. trimaculatus*, we cannot confirm the statements of TREAT (1975) and SOUTHCOFF (1989a), that *Leptus* larvae prefer the more densely sclerotized sites of their hosts.

Nearly all of the proved hosts of *L. trimaculatus* are at very least active or even highly active during daytime. One of them, *Anystis spp.*, potentially preys upon this larva. We think that host-attachment of *L. trimaculatus* occurs preferably during night time. This behaviour of *L. trimaculatus* might be supported by the following facts : In one of our observations, attachment (1) could definitely be determined for the dark phase. The larva (2) shows no positive phototaxis. Under laboratory conditions (3) animals hide in available cavities of the rearing substratum during the light phase.

Life cycle : Compared to other Parasitengonae, *L. trimaculatus* belongs to those species of mites which develop rather quickly from the egg to the adult. None of the immature instars lasted more than three weeks and obviously the adult is the only stage which survives winter time (Tab. 3). Our data of *L. trimaculatus* correspond well with the results TREAT (1974) found for the *Leptus* species he examined. The only exception is one of TREAT's protonymphs (serial no. 73A-11) which stayed 36 days in this stage, i.e. more than twice as long as the respective instar of *L. trimaculatus*. Then it was kept in a refrigerator for about 8 months, the deutonymph hatched 12 days after leaving the refrigerator. BRUYANT (1911) also observed a larva he identified as *L. ignotus* (Oudemans, 1903), which stayed several months as a protonymph. EVANS (1910) described a *Leptus* species which stayed for one month as a calyptostatic protonymph until the deutonymph emerged. Unfortunately all authors cited above gave no details about the light and temperature conditions during rearing. Comparable data of ROBAUX (1971) for some Trombidioidea show that it is necessary to keep the mites under

controlled temperature conditions in order to get reproduceable times of development, at least concerning the calyptostatic instars. Nevertheless the prolonged protonymphal stages of TREAT's serial no. 73A-11 and the mite BRUYANT (1911) examined, are probably expressions of a different kind of life cycle with the protonymph as hibernating stage.

Concerning the diet of the adult and the deutonymph, in *L. trimaculatus* both stages prey on the same food. This is consistent with the data of TREAT (1974) concerning some other *Leptus* species. In contrast to the results of TREAT no collembolans or other fast moving arthropods were preyed, although many attempts were done. At least for *L. trimaculatus*, the prey obviously consists of immobile or only slow moving arthropods.

Phenology : There obviously is only one period of oviposition in *L. trimaculatus*, most probably during spring. This is evident by the occurrence of the larva in the field exclusively from June to August, and by the female, which deposited eggs in the night after capture on 29.05.1989.

The successive appearance of the active instars in the field (Fig. 5) synchronizes well with the time they needed to develop in our rearing experiments (Tab. 3). However, the small number of deutonymphs and adults in the samples only confirm assumptions about their phenology. Arising onto this, the phenomenon that deutonymphs could only be collected over a limited period in summer and adults only in autumn and spring, may indicate that the development of *L. trimaculatus* is completed by the autumn of the same year during which the eggs have been deposited. Only the adult stage seems to hibernate. This corresponds with the results of the rearing experiments, in which the deutonymphs either died before winter or transformed to adult. Nevertheless, the data does not exclude the possibility that a part of the deutonymphs bury themselves until they transform into adults during the spring of the following year. The disappearance of adults in the summer may be the effect of a dying out of the adult population when the reproduction period ends in late spring.

Conclusively, *L. trimaculatus* seems to be an univoltine erythraeid, which reproduces in spring,

completes its development until autumn, hibernates in the adult instar, and dies after it has reproduced. This result largely corresponds with the data TREAT (1974) obtained from his rearing experiments with a different *Leptus* species. He caught the larva parasitizing upon noctuid Lepidoptera in July, the deutonymphs emerged in August, and the only adult emerged in September (serial no. 73A-2). As mentioned above, this obviously is not the only life cycle strategy in *Leptus* species.

The abundance of *L. trimaculatus* in the three zones of our area of investigation reveals a preference for the humid and temperate rush belt (Fig. 5 : R). This is very obvious in the case of the larva, which decreases in abundance with increasing distance from the rush belt. As mentioned above the small amount of collected deutonymphs and adults does not constitute reliable evidence. However, this data corresponds with that of the larva. In contrast to our results of the year 1989, we also found some adults in spring 1990 on the dried rough meadow (M). Thus, *L. trimaculatus* obviously is not restricted to permanent humid and temperate conditions.

Previous records of *L. trimaculatus* adults (WILLMANN, 1951, SCHWEIZER & BADER, 1963) came from humid habitats but also from more xeric ones (WITTE, 1975 and pers. comm.).

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