POLSKA AKADEMIA NAUK
INSTYTUT ZOOLOGICZNY, ODDZIAŁ W KRAKOWIE

ACTA ZOOLOGICA CRACOVIENSIA

Tom II Kraków, 15 VIII 1957 Nr 3

M. J. DELANY (Glasgow)

Biologia i etologia *Thysanura*

Биология и этология *Thysanura*

Life histories in the *Thysanura*

[With 4 tables and 8 figures in text]

I. INTRODUCTION

The *Thysanura* is not an order of insects whose member have had their life histories widely studied. Nevertheless there has accumulated over the last half century a body of information which, apart from DÉNI'S excellent but short review in 1949, has not previously been collated. The Order contains five Families (REMINGTON, 1954) viz.: *Machilidae*, *Triassomachilidae*, *Meinertellidae*, *Nicoletiidae* and *Lepismatidae*. The *Triassomachilidae* are a fossil group. The *Nicoletiidae* are subterranean, myrmecophilous or termitophilous in their habits and together with the *Meinertellidae* have not had their life histories investigated. The vast majority of the work has been on the *Lepismatidae* and *Machilidae*.

At the beginning of the present century several important contributions appeared by HEYMONS (1897, 1906), HEYMONS and HEYMONS (1905), ESCHERICH (1903, 1904, 1906), VER-

HOEFF (1910 a, 1910 b) and BÄR (1912) which marked the initiation of systematic studies into the development, biology and life histories of the *Thysanura*. Between 1912 and 1930 papers on these topics were few and sporadic and it was not until later, with the publication of the works of ADAMS, DELANY, LINDSAY, RAFF, SAHRHAGE, SWEETMAN and WYGODZINSKY, that the life histories of the *Thysanura* were elaborated in detail.

Much work has centred around the two common pests of buildings — the silver fish, *Lepisma saccharina* L. and the firebrat, *Thermobia domestica* (PACK.). Economic considerations and relatively easy laboratory cultivation have probably influenced the quantity of work on these species. Contributions covering various aspects of the life history of *T. domestica* (PACK.) have been provided by ADAMS (1933 a, 1933 b, 1936 a, 1936 b, 1937), SAHRHAGE (1953), SPENCER (1930), SWEETMAN (1934, 1938, 1952) and SWEETMAN and WHITTEMORE (1937) whilst on L. *saccharina* L. the major papers have come from BACK (1931, 1937), CHARLTON (1921), CORNWALL (1915), GATENBY and MUKERJI (1930), MOHR (1923), MORITA (1926), SAHRHAGE (1953), STURM (1956), and SWEETMAN (1939, 1952). A third Lepismatid, *Ctenolepisma longicaudata* ESCH. has received attention from RAFF (1933) and LINDSAY (1940).

The Lepismatids may be either demestic or free-living in their habits with at least one species (*L. saccharina* L.) capable of living in both sets of conditions. It has been found under bricks and stones of broken down houses (WEIDNER, 1950) and in bird's nests (LEHNERT, 1933; EICHLER, 1937; KEMPER, 1938; WOODROFF and SOUTHGATE, 1951) in addition to its more common habitat of human dwellings. The *Machilidae* have no known members that are not free-living.

In contrast to the extensive studies on the *Lepismatidae*, the work on the *Machilidae* distinguishes itself for its brevity. Since VERHOEFF (1910 a, 1910 b), DELANY (1954, in press) is the only worker to have primarily directed his research to the study of field life histories of representatives (*Petrobius* LEACH and *Dilta* STRAND) of the Family. WYGODZINSKY (1941) made a number of observations on the bionomics of the *Machilidae* and other *Thysanura* of Switzerland.

II. THE EGG

HEYMONS first described the eggs of *Thysanura* in 1897 when making reference to the development of *Lepisma* L. and later (with HEYMONS H., 1905) when describing the embryology of *Trigoniophthalmus* VERH. GIARDINA (1900) also described the eggs of *Machilis* LATR.

The eggs of Thysanurans are comparatively large and, when first laid, are lighter in colour and possessing more flexible chorions than after exposure to the atmosphere for a few days. In *T. domestica* (PACK.) (SWEETMAN, 1938) the eggs are white and opaque at first and later become yellow in colour. *Petrobius* LEACH eggs (DELANY, in press) are initially bright orange; darkening takes place gradually until after two weeks have elapsed when they are black and vested with a thick shell. WYGODZINSKY (1941) reports *Machilis* LATR. and *Lepismachilis* VERH. as passing through a similar gradation of colours with the insertion in the former species of an intermediate dull red phase.

SAHRHAGE (1953) and SWEETMAN (1938) have measured the size of the irregularly oval eggs of *T. domestica* (PACK.); both sets of figures are in close agreement with sizes ranging from 1,0—1,2 mm × 0,70—0,87 mm. In all respects the eggs of *Ctenolepisma longicaudata* ESCH. (LINDSAY, 1940) are of similar structure. When comparing the size of *Thermobia* BERGR. eggs with those of *Lepisma* L., SAHRHAGE (1953) found the ones deposited by the latter to be slightly smaller, ranging from 0,77 mm — 1,01 mm × 0,72 mm — 0,78 mm. CORNWALL'S (1915) estimates for the same species are not in agreement with these figures as he maintained them to be of the order of 1,5 mm × 1,0 mm. The eggs of *Petrobius* LEACH are 1,0—1,3 mm long and 0,9 mm wide.

Machilis LATR., *Lepismachilis* VEHR., *Trigoniophthalmus* VERH. (WYGODZINSKY, 1941), *Thermobia* BERGR. (ADAMS, 1933 a; SWEETMAN, 1938) and *Petrobius* LEACH (DELANY, in press) are all able to have eggs of variable shapes. The variability has been attributed to the flexible nature of the chorion at the time of oviposition with the resulting ability of the egg to accomodate itself in variously conformed cavities.

Egg laying is for the most part restricted to a limited portion of the year although it is generally less marked in the domestic species where the period is frequently protracted. According to SAHRHAGE (1953), *T. domestica* (PACK.), living in bakehouses in Hamburg, lays most of its eggs from February to October and *L. saccharina* L. from mid-May to mid-August. *Ctenolepisma* ESCH. lays its eggs during the Australian summer months of September to March and the existing records for *Thermobia aegyptiaca* ESCH., in Egypt, are from July 9th—12th (ALFIERI, 1932). Amongst the *Machilidae*, *Trigoniophthalmus* VERH. oviposits in June with the period extending to September (WYGODZINSKY, 1941) and *Machilis* LATR. lays from June to winter. Three genera have restricted laying periods; *Lepismachilis* VERH. lays only in March and April (WYGODZINSKY, 1941), *Petrobius* LEACH in October and November (DELANY, in press) and *Dilta* STRAND in July and August (DELANY, 1954).

Estimates of fecundity have depended upon the use of two techniques. Either, the number of eggs females have laid in the laboratory have been counted for a given period, or counts have been made of the number of eggs in the ovarioles of gravid females. The latter method has only applied to species possessing a restricted breeding period. For all species the number of eggs laid by a female at one time falls within the range of 1—33. SWEETMAN 1938) gave 1—33 as the number of eggs laid at any one time by *T. domestica* (PACK.). BACK (1931, 1937) estimates *Lepisma saccharina* L. to produce 10—12 and SAHRHAGE (1953) gives 4—27 with an average of 10. LINDSAY (1940) suggests *Ctenolepisma* ESCH. deposits from 2—20. WYGODZINSKY (1941) states that *Trigoniophthalmus* VEHR. seldom lays more than 10 at a time, more generally 2—8, whilst *Machilis* LATR. varies its number with age. First year females lay from 3—8 and those of second and later years, 14—32. From the examination of gravid females DELANY (1954, in press) found *Dilta* STRAND to lay an average of 15 eggs and *Petrobius* LEACH from 5—25 with an average of 13.

Duration of the incubation period varies widely with environmental conditions. There exists no record of incubation

Table I

THE INCUBAT ION PERIOD OF THE GS OF *THYSANURA* UNDER THE CONDITIONS STATED

Species	Duration of incubation period (days)	Stated Conditions	% hatch	Authority
LEPISMATIDAE				
Ctenolepisma longicaudata Esch.	49	21°C	—	Lindsay, 1940
„	46	23°C	—	„
„	34	24°C	—	„
„	30	25°C	—	„
„	20	29,5°C	—	„
Lepisma saccharina L.	„several weeks“	—	—	Heymons, 1897
„	about 63	—	—	Mohr, 1929
„	45—60	18°—20°C	—	Cornwall, 1915
„	43	22°C	—	Sweetman, 1939
„	19	32°C	—	„
„	25—43	20°—25°C; R.H. 55%—65%	94	Sahrhage, 1953
Thermobia aegyptiaca Esch.	25—30	—	68	Alfieri, 1932
Thermobia domestica (Pack.)	44—48	27°C; R.H. 12%—100%	75	Sweetman, 1938
„	31—33	29°C; R.H. 32%—100%	85	„
„	20—22	32°C; R.H. 12%—100%	87	„
„	12—14	37°C; R.H. 12%—100%	91	„
„	10—11	40°C; R.H. 12%—100%	84	„
„	9—10	41°C; R.H. 32%— 96%	83	„
„	9—10	42°C; R.H. 12%—100%	73	„
„	7—10	44°C; R.H. 12%—100%	74	„
„	26—34	30°C; R.H. 35%—70%	65	Sahrhage, 1953
„	20—28	32°C; R.H. 35%—70%	72	„
„	12—16	37°C; R.H. 35%—70%	90	„
„	9—11	40°C; R.H. 35%—70%	86	„
„	8—10	43°C; R.H. 35%—70%	84	„
MACHILIDAE				
* *Dilta hibernica* (Carp.)	300—340	Moravia	—	Kratochvil, 1945
* *Dilta littoralis* (Wom.)	300—340	Southern England,	—	Delany, 1954
		west France	—	Argilas, 1939
Lepismachilis notata Stach	60—90	Switzerland	—	Wygodzinsky, 1941
* *Machilis* annulicornis Latr.	about 275	Switzerland	—	Wygodzinsky, 1941
* *Petrobius brevistylis* Carp.	160—190	[about 135 days in field 35—55 days at 7°—20,5°C]	29	Delany (in press)
„	180—215	[about 165 days in field 15—48 days at 7°—20,5°C]	35	„
„	180—240	[about 165 days in field 15—75 days at 11°—18,5°C]	43	„
„	200—240	Southern England	21	„
* *Petrobius maritimus* Leach	200—240	„	—	„
* *Trigoniophthalmus alternatus* (Silv.)	about 365	Switzerland	—	Wygodzinsky, 1941

* Species having eggs that overwinter.

lasting more than 63 days in the *Lepismatidae* nor less than 60 days in the *Machilidae*. Over-wintering of eggs is common in the latter Family and non-existent in the former. A full review of the incubation periods for the Order is given in Table I. Possibly correlated with the over-wintering habit is the very heavy mortality experienced in the *Machilidae*.

III. HATCHING

Normally, hatching is facilitated in a single operation although SWEETMAN (1934) has observed newly hatched nymphs of *T. domestica* (PACK.) (particularly in dry habitats) to retain the remains of the egg around the posterior of the abdomen until the completion of the first ecdysis. HEYMONS (1897) described a special hatching organ; he noted that in *L. saccharina* L. the shell was burst by a small pointed ridge on the frons. The hatching organ is characteristic of, and exclusive to, the first instar. HEYMONS observations on *Lepisma* L. have since been confirmed by SAHRHAGE (1953) who like SWEETMAN (1938) observed the structure in *T. domestica* (PACK.). The remaining record of a „hatching organ“ is in the first instar of *Ctenolepisma longicaudata* ESCH. (LINDSAY, 1940). Partial hatching followed by death may occur (SWEETMAN, 1938) in *T. domestica* (PACK.) when eggs have been deposited in unfavourable environments. Under such conditions the egg shell is fractured and the insect is capable of extracting only a portion of its body, varying from a single antenna to the whole head and thorax, before it dies.

IV. THE EARLY INSTARS

The determination of the number of instars a Thysanuran undergoes, as well as the morphological characters of each instar before attaining maturity has been found by most workers to be difficult to achieve. This is due to a combination of the comparatively large number instars passed through before maturity and the raletively slight changes in morphology between instars. Ideally, and this is generally more practicable with domestic species, the species under investigation should be reared under laboratory conditions where the course of development through successive ecdyses can be followed with precision. LINDSAY (1940) traced the development of *Ctenolepisma* ESCH. which she reared in the laboratory at 23°C. Sexual characters were fully developed after fourteen instars when the insects were 9,5 mm long, and in order to define the characters of each instar, LINSDSAY employed two techniques. Firstly, she measured the length of, the body, the terminal podite of the maxillary palp, the anterior edge of the metathoracic tibia, the styles of abdominal segments 8 and 9 (when present), the antennae, the cerci and the central caudal filament on five insects of each instar and secondly she described the more gross morphological changes seen at different instars. The application of a biometrical method in addition to the more orthodox morphological one adequately justified itself as LINSDAY subsequently discovered that there existed no recognisable morphological distinctions between certain instars. Thus, in *Ctenolepisma* ESCH. instars five, six and seven could only be isolated on the basis of statistical measurements. The first instar (body length 2,9 mm) is scaleless, light cream in colour and the possessor of relatively short appendages. The second instar has a small number of bristles. Darkening of the cuticle continues to the third instar when the characteristic silver-grey colour is attained. Two tarsal segments occur on each leg of the first instar, in the second instar a septum develops on the second tarsal segment of the third leg and in the third instar all tarsi have three segments. Scales first occur in the fourth instar as do the abdominal stylets on segment nine; the second pair of stylets, developing on segment eight do not appear until the ninth instar in the male and the eleventh in the female.

The genitalia first appear in both sexes, in instar eight, as small paired lobes ariging mid-ventrally from the intersegmental membrane between abdominal sterna eight and nine. The sexes can be separated in the eighth and successive instars from the shape of the ninth abdominal sternum. The female has a V-shaped cleft extending back to segment eight; the male's is more open, U-shaped and does not extend as far back. The genital lobes remain short in the male unti by the eleventh instar they are recognisably the shape of the penis. The reproductive system continues to develop and attains its full maturity by the fourteenth instar.

The lobes of the female steadily elongate and in the tenth instar a second pair appear arising anterior and ventral to the pair already present. The four lobes ultimately constitute the four valves of the ovipositor which by the twelfth instar is an abbreviated structure. The internal differentiation of the female reproductive system is completed by the thirteenth instar; the five pairs of ovarioles are fully formed and the spermatheca [Fig. 8] has assumed its characteristic shape.

The foregoing is largely based upon LINDSAY'S (1940) account of the early development of *Ctenolepisma longicaudata* ESCH. and is probably the most systematic treatment so far produced of the early instars of a Lepismatid. Other workers have described a smaller number of the early instars of alternative species of the Family but have generally lacked the thoroughness of LINDSAY. Their more limited findings generally conform to the developmental pattern of *Ctenolepisma* ESCH. ADAMS (1933 a) discussed the differences between the first instars of *T. domestica* (PACK.); he measured head width, metathorax width, body length, cercus length and caudal filament length and the number of annulations on the antennae, cerci and median caudal filament. SAHRHAGE (1953) made a large series of measurements (including weight) on the first five instars of *L. saccharina* L. and *T. domestica* (PACK.). As with *Ctenolepisma* ESCH. the scales and stylets do not appear before the fourth instar. They differ from *Ctenolepisma* ESCH. in the failure of the tarsi to have three podites before the fourth instar. WYGODZINSKY (1941) states that in *Ctenolepisma ciliata* DUFOUR the scales appear at the third instar.

In his description of the early instars of *T. domestica* (PACK.) SWEETMAN (1938) does not entirely agree with SAHRHAGE (1953) as he claims that the first stylets do not appear before the fifth instar, the second pair at the seventh or eight and the third pair (only in the females) at the tenth. The ovipositors then become visible. All authors are agreed that the first instar is a very inactive and sluggish stage. The body lengths (mm) of the first five instars of three species of Lepismatids are as follows:

Instar	*C. longicaudata* Esch. (Lindsay, 1940)	*T. domestica* (Pack.) (Sahrhage, 1953)	*L. saccharina* L. (Sahrhage, 1953)
1	2,9	1,89	1,89
2	3,4	1,98	1,99
3	4,4	2,56	2,44
4	4,8	3,06	2,64
5	4,8	4,23	4,07

Bär (1912) and Heymons (1906) briefly described some of the young forms of the *Machilidae* and Verhoeff (1910 a) attemted a systematic account of the different developmental „stages" (Larvenstufen) of *Machilis* Latr. More recently, Delany (in press) studying the life history of *Petrobius brevistylis* Carp. determined the number of instars a Machilid passed through in attaining maturity. As *Petrobius* Leach could not be reared beyond the fourth instar in the laboratory much of the data had to be obtained from field collected insects. In order not to omit any developmental stage (s) the habitats of the insects were visited at short intervals of time (1—3 weeks) from hatching in mid-May to the attainment of maturity in late September. Separation of individual instars necessitated the adoption of a character that could reasonably be assumed to alter with successive instars. Furthermore, a character would be preferred that involved the actual measurement of certain structures rather than one where changes of a structural nature were being followed. Close compliance with these prerequisites was obtained by counting the number of rings of scales on a lateral caudal cercus. The first two instars of *Petrobius* Leach are without scales and for them, segments have been counted. The caudal cercus was selected as it appeared to grow more rapidly than any other appendage. In *Petrobius* Leach, at the time of hatching the cerci were either absent or not more than one tenth of the length of the central filament whereas when the insect was fully adult they were between a half and a third its length. The rapid growth of the cerci was noted by Lindsay in *Ctenolepisma* Esch. Over the first fourteen instars the length of the cercus increases twelve-fold and for the same period the central filament, the antennae, the terminal podite of the maxillary palp and the anterior edge of the metathoracic tibia increased their lengths eleven-fold, nine-fold, three-fold and four-fold respectively.

In making the counts on *Petrobius* LEACH no selectivity was employed as far as the insects were concerned providing each has intact cerci. Scales and segments have collectively been spoken of as annuli and the results of the counts are displayed graphically in Figure 1 where they have been lumped together without any reference to the time of collection of the insects. It was possible, for the first four instars, to check the figures obtained from field collected insects against a small group of laboratory reared ones and as can be seen from Figure 2 the two sets of data are close agreement. Peaks are apparent at annulus counts of 1, 3, 6, 11, 19, 25, 37 and less obviously so at 46. The insects distributing themselves about a peak have been regarded as members of one instar. Although peaks are present beyond the annulus number, the distributions about them overlap so closely as to make the separation of instars very difficult. However, by the time the insects are of this size, they have passed through the major developmental stages and are approaching, if not already in, the reproductive stage. Thus, having separated the first eight instars on a biometrical character it was then possible to assign to each some diagnostic morphological characters. Their nature has been fully discussed by DELANY (in press); particular reference has been made to the presence or absence of scales, the development of the coxal vesicles and, on a more restricted scale, the external genitalia. The major characters have been summarized in Table II together with VERHOEFF'S Larvenstufen. When VERHOEFF (1910 a) was tracing the development of *Machilis* LATR. he made no attempt to correlate Larvenstufen with instar. TILLYARD (1932) found the first two instars of *Allomachilis* SILV. devoid of thoracic stylets.

Apparently the number of instars undergone before maturity is rather larger for the Lepismatids than the Machilids and such a difference cannot be attributed to the former Family being of a larger size at maturity. Comparison of LINDSAY'S (1940) and DELANY'S (in pres) data suggest a more accele-

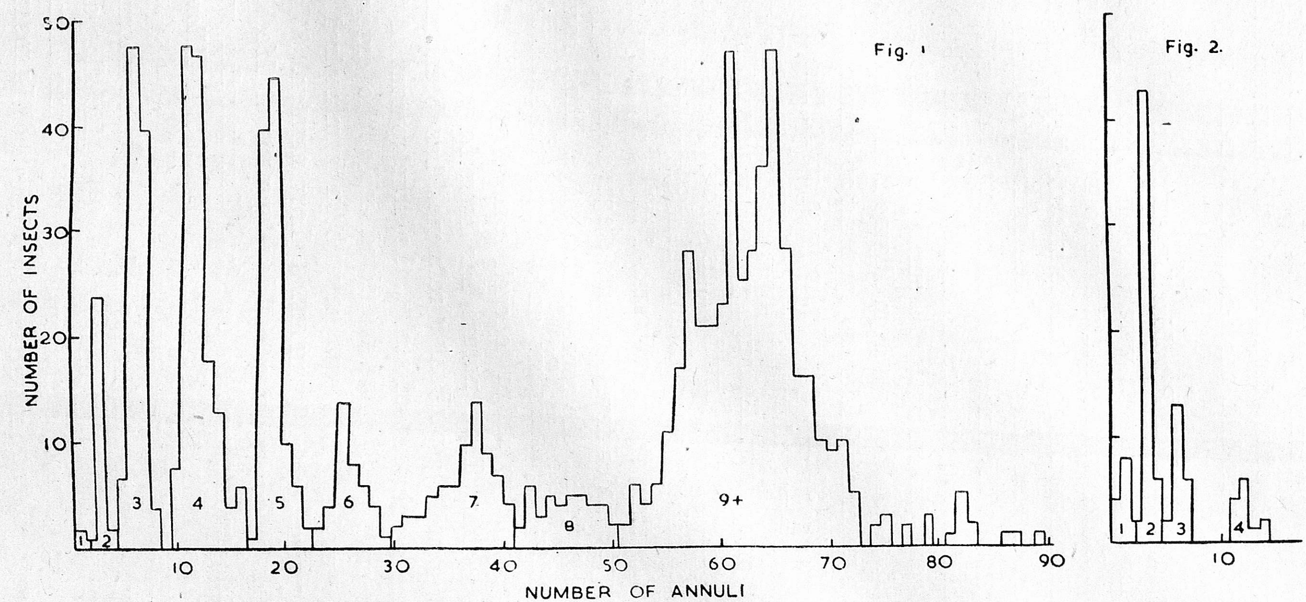

Fig. 1—2. The relationship between the number of annuli on the lateral caudal cercus of *Petrobius brevistylis* Carp. and the number of individuals observed with the specified number. Fig. 1 — Field collected insects. Fig. 2 — Laboratory reared insects. The histo-grams are separated and numbered, as far as possible, for individual instars.

Tabela II

MORPHOLOGICAL CHARACTERS OF THE FIRST EIGHT INSTARS OF *PETROBIUS BREVISTYLIS* CARP.

Instar	No. of Annuli	Thoracic Stylets	Scales	Coxal vesicles	External genitalia	Stage of VERHOEFF
1	0—2	Absent	Absent	One pair on Abd. I—VII	Not recognisable	pseudofoetus
2	2—4	,,	,,	,,	,,	larva II
3	5—8	,,	Present	,,	,,	
4	10—16	Vestigial	,,	,,	♀ valves: 2 pairs of protuberances ♂ penis: deeply cleft distally parameres absent	
5	17—22	Undeveloped, unscaled	,,	One pair on Abd. I—VII, development of processes for second pair on Abd. II—V	♀ valves: subequal not overlapping ♂ penis: cleft distally parameres present	larva III
6	23—29	Developed, unscaled	,,	One pair on Abd. I, VI, VII. Two pairs on Abd. II—V	♀ valves: subequel overlapping ♂ penis: cleft distally	immaturus
7	30—40	Developed, scaled	,,	,,	♀ valves: equal length not segmented ♂ penis: not cleft	praematurus
8	41—50	,,	,,	,,	♀ valves: equal length segmented	pseudomaturus

rated development by the Machilid. In *Ctenolepisma* ESCH. abdominal stylets are not present before the fourth instar, whereas in *Petrobius* LEACH they are present from hatching. The rudiments of the external genitalia appear four instars later in *Ctenolepisma* ESCH. (eight as compared with fourth) than in *Petrobius* LEACH and scales clothe the third instar of *Petrobius* LEACH and the fourth of *Ctenolepisma* ESCH.

Recognition of instars is further complicated by not all morphological structures assuming a characteristic form at a particular instar. SWEETMAN (1952) found the first pair of abdominal stylets in *Ctenolepisma quadriseriata* PACK. to invariably appear at the fifth instar; the second pair were less regular and may first show themselves at the tenth, eleventh or twelfth instars and the third pair were even less regular, appearing at the twelfth, thirteenth, fourteenth, fifteenth or twenty-first instar. The two pairs of stylets normally possessed by *L. saccharina* L. were equally irregular in appearing with the added complication that twelve of the twenty-three specimens SWEETMAN (1952) reared through a minimum of seventeen instars failed to produce any stylets at all. DELANY (in press) found it practicable to correlate exent of development of the extermal genitalia of *Petrobius* LEACH with instars four to eight.

V. GROWTH

Measurements of body length, or some other anatomical structure, at regular intervals over the life span of the insect will reflect its times and rates of growth. This simple procedure has only been adopted over a protracted period for four species of *Thysanura* viz.: *Thermobia aegyptiaca* ESCH. (ALFIERI, 1932), *Ctenolepisma* ESCH. (LINDSAY, 1940), *T. domestica* (PACK.) (SAHRHAGE, 1953) and *Dilta* STRAND (DELANY, 1954).

Growth is apparently influenced by insect age, sex and environmental conditions. In *Dilta* STRAND [Fig. 3] it is rapid during the summer of hatching and is followed by a static spell covering the winter months. Growth proceeds throughout the following summer with the females showing a greater increase in size during the early part of the summer than the males. *Dilta* STRAND is mature [Fig. 3] by the July of its second year and grown appreciably after this time. LINDSAY (1940) reared *Ctenolepisma* ESCH. at a constant temperature (23°C) and recorded rapid growth for the first sixty days.

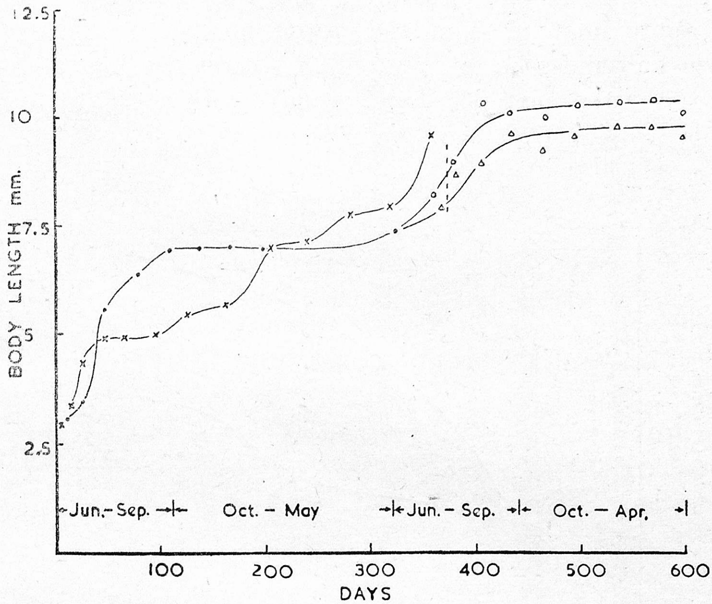

Fig. 3. Growth in relation to time of *Ctenolepisma longicaudata* ESCH. (after LINDSAY), represented by crosses, and *Dilta littoralis* (WOM.) (after DELANY). The young stages of *Dilta littoralis* (WOM.) are represented by solid circles and the adult males and females by triangles and open circles respectively. *Ctenolepisma longicaudata* ESCH. was maintained at 32°C. The time scale in months is applicable only to *Dilta littoralis* (WOM.) which was growing under field conditions. The broken vertical line indicates the approximate time of attainment of sexual maturity.

By this time the insects were 5 mm long. Following a thirty-day static period a long spell of two hundred days of steady growth ensued when body length increased steadily. Finally, at the thirteenth ecdysis growth was considerably accelerated with a size increase taking place of nearly 2 mm. Further measurements were sporadic and it was estimated that the maximum size attained after a further twelve months was 12,5 mm. Reproduction occurred six to seven months after the thirteenth instar.

Although ALFIERI (1932) reared, under unspecified conditions, specimens of *T. aegyptiaca* ESCH. from the egg to the adult his measurements of body length did not commence before the insects were seventy-nine days old. They were then 5,1 mm long and if it is assumed that their length at hatching was approximately 2 mm, the growth tor the first part of the life history must be fairly rapid. A steady size increase takes place over the next four hundred days with a slight but noticeable increase over the summer months.

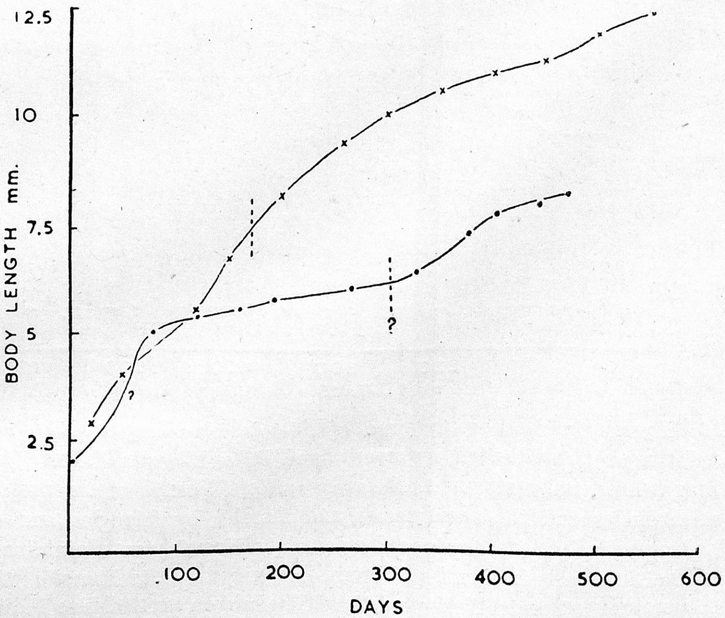

Fig. 4. Growth in relation to time of *Thermobia domestica* (PACK.), represented by crosses, at 37°C (after SAHRHAGE) and *T. argyptiaca* ESCH., represent by dots (after ALFIERI). The broken vertical lines approximate to the time of attainment of sexual maturity.

The growth curve of *T. domestica* (PACK.) [Fig. 4] (SAHRHAGE, 1953) differs appreciably in its shape from any of the three already considered. The specimens of *Thermobia*

BERGR. were maintained at a temperature of 37°C and a relative humidity of 35% — 45%. For the first three weeks of development growth is comparatively rapid; there then follows a long spell of approximately two hundred and thirty days with growth proceeding at a steady rate and lastly for a further two hundred and fifty days comes period when the rate of size increase is much reduced. The second growth phase is noteworthly for its constancy over a protracted period. The rate of growth under these conditions is slower than that of *Dilta* STRAND during the summer months and more rapid than *Ctenolepisma* ESCH. and *T. aegyptiaca* ESCH. *Thermobia* BERGR. varies its growth rate with climatic conditions.

The time of attainment of sexual maturity has been inserted, as far as possible, on figures 3 and 4 where it can be seen to take place considerably in advance of the insects reaching their maximum size. This is apparently a characteristic phenomenon in the *Thysanura*.

VI. ECDYSIS AND INSTAR DURATION

The first full description of ecdysis appeared in a short paper by BOYER in 1913 and has since been witnessed by ADAMS (1933 a), SWEETMAN (1938) and SAHRHAGE (1953) in *Thermobia* BERGR., CORNWAL (1915) and SAHRHAGE (1953) in *Lepisma* L., LINDSAY (1940) in *Ctenolepisma* ESCH., WYGODZINSKY (1941) in *Trigoniophthalmus* VEHR. and *Machilis* LATR. and DELANY in *Petrobius* LEACH.

The phenomenon is of the same basic pattern in all species of *Thysanura* studied. The insect about to moult, becomes motionless, arches the thorax, bends the head ventrally, expands and contracts the abdomen and ultimately splits the cuticle in a mid-dorsal line extending along the length of the thorax and epicranial suture. Emergence through the cleft is gradual process. The head and thorax make their appearance first, the antennae and legs are next withdrawn and finally the abdomen and its appendages. Extraction from the cuticle is facilitated through a series of undulatory movements. The linings of the crop, gizzard, hind intestine and spermatheca are also shed. *Petrobius* LEACH leaves its exuviae adhering to the substrate. *Machilis* LATR. and a number of Lepismatids have been reported (WYGODZINSKY), (1941); DENIS, (1949) to eat their shed exoskeletons. The loss of scales and the assumption of a colour darker than normal can generally be looked upon as indicative of approaching ecdysis.

Ctenolepisma ESCH. does not feed during the last third of each stadium. Such a period is assumed to give adequate time for the old chitinous lining of the alimentary tract to be discarded and a new one formed. Moulting is apparently a period of some physiological strain as many older Lepismatids (SWEETMAN, 1952) die through moulting difficulty.

A record of the number of instars a Thysanuran may experience in the course of its life history has been kept by SWEETMAN (1952) for males and females of *T. domestica* (PACK.), *C. quadriseriata* PACK. and *Lepisma* L. under a variety of environmental conditions. He reared fifteen specimens of *Ctenolepisma* ESCH. and found the number of instars from hatching to death to range from twenty-five to sixty-six. Seventeen specimens of *Thermobia* BERGR. reared at 37°C had from nineteen to fifty-eight instars whilst five individuals of the same species at 32°C had from six to fifty-seven instars.

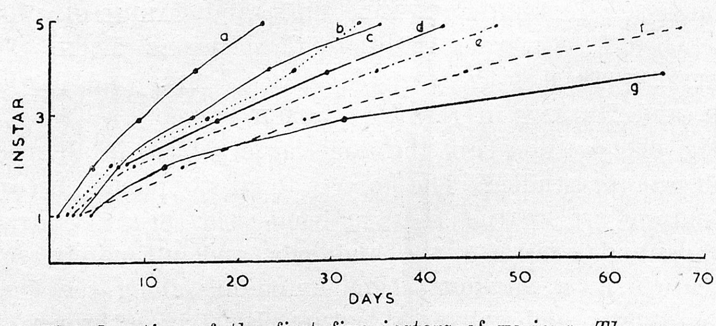

Fig. 5. The duration of the first five instars of various *Thysanura*. a — *Thermobia domestica* (PACK.) after SWEETMAN) at 37°C and 84°/₀ R.H.; b — *T. domestica* (PACK.) (after SWEETMAN) at 32°C and 84°/₀ R.H.; c — *T. domestica* (PACK.) (after SAHRHAGE) at 37°C and 35°/₀ R.H.; d — *Lepisma saccharina* L. (after SWEETMAN) at 27°C and 84°/₀ R.H.; e — *Ctenolepisma quadriseriata* PACK. (after SWEETMAN) at 27°C and 50°/₀ — 90°/₀ R.H.; f — *C. longicaudata* ESCH. (after LINDSAY) at 23°C; g — *L. saccharina* L. (after SAHRHAGE) at 22,5°C and 60°/₀ R.H.

Only one of the latter group underwent more than fourteen instars. Twenty-three individuals of *Lepisma* L. had between seventeen and forty-one instars. These data suggest instar numbers to be high in the *Thysanura*; an occurrence probably predictable from the previous observations on growth.

Instar duration and insect longevity are inextricably interlinked and very much influenced by environmental conditions, particularly temperature. SWEETMAN'S work is undoubtedly the most comprehensive although there have been a small number of less thorough investigations (LINDSAY, 1940; SAHRHAGE, 1953) covering early development. The result are displayed graphically in figures 5 and 6. Without exception the first two instars are short lasted, the later ones gradually increase their length and from the fifteenth last for fairly regular intervals of time. In the comparatively stable state ecdysis is far more frequent in *C. quadriseriata* PACK. (20—25 days) than in *Lepisma* L. (37—50 days) even though both species were kept at the same temperature (27°C). Two individuals approximating to the same longevity (1354 days for *Lepisma* L. and 1417 for *Ctenolepisma* ESCH.) were found to have totally different numbers of instars (forty-one in *Lepisma* L. and sixty-six in *Ctenolepisma* ESCH.). At 23°C *C. longicaudata* ESCH. had longer instars than any other species studied. In contrast *T. domestica* (PACK.) at 37°C had very short intervals (seven to thirteen days) but if the temperature was dropped to 32°C they were of similar magnitude to those of *C. quadriseriata* PACK. at 27°C. SAHRHAGE (1953) found the development of *Lepisma* L. for the first instars to be very much slower at 22,5°C than did SWEETMAN (1952) at 27°C. The latter temperature probably closely approaches the optimal for this species.

VII. MATURATION AND LONGEVITY

The time taken to mature and the maximum longevity of the *Thysanura* vary not only for different species but also for insects of the same species that have been living under diverse environmental conditions. The available data on these phenomena have been summarized in Tables III and IV.

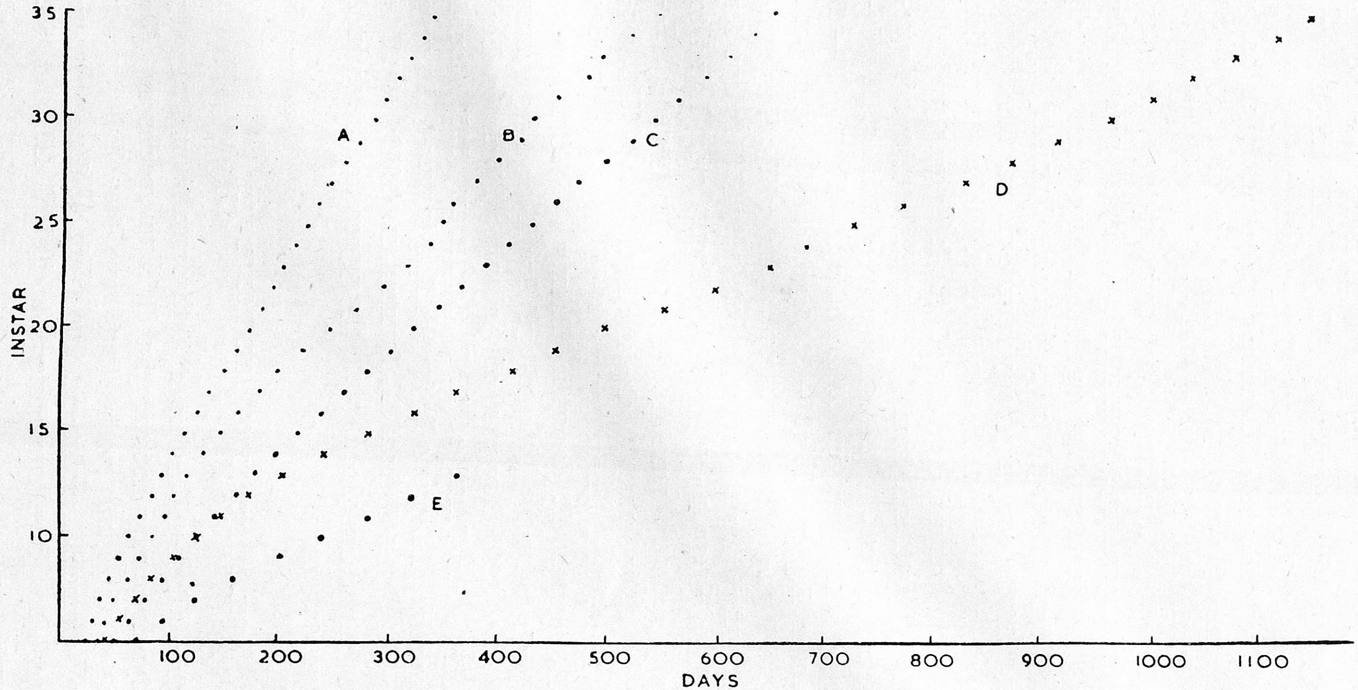

Fig. 6. Instar duration, covering the fifth to thirty-fifth instars, of: A — *Thermobia domestica* (PACK.) (after SWEETMAN) at 37°C and 84% R.H.,B. — *T. domestica* (after SWEETMAN) at 32°C and 84% R.H.,C —*Ctenolepisma quadriseriata* PACK. (after SWEETMAN) at 27°C and 50%—97% R.H., D — *Lepisma saccharina* L. (after SWEETMAN) at 27°C and 84% R.H. and E — *Ctenolepisma longicaudata* ESCH. (after LINDSAY) at 23°C.

Lepisma L. exemplifies a species displaying wide deviations in time taken to mature. Under optimal laboratory conditions development takes from three to four months whereas in the rather more natural conditions of a fluctuating environment it takes up to two years.

The most striking feature of Table III is the marked difference in the time the Lepismatids take to mature as compared with the Machilids. The much longer developmental period of the Machilids can possibly be associated with environmental factors and not necessarily with any inherent or fundamental difference in the two families. With the exception of *Lepisma* L. studied by SAHRHAGE (1953) and *Ctenolepisma* ESCH. reared by LINDSAY (1940) at room temperatures, the Lepismatids have been observed at temperatures of tropical and sub-tropical magnitudes. Furthermore, the constancy of the temperatures suggest a climate differing from a tropical one in the absence of a nocturnal cool spell. Contrasting these conditions with those under which the Machilids have been studied it can be seen that the two are vastly different. Work on the *Machilidae* has been restricted to species inhabiting various geographical regions of central and northern Europe where climatic conditions are distinctly temperate. The two Lepismatids mentioned earlier that have developed under conditions more closely approaching those of the *Machilidae* have a life history more characteristic of the latter Family. Before any rigid conclusions can be drawn in connection with the comparative lengths of time to maturation of the two families, it is felt that more research should be undertaken into the life histories of *Machilidae* from tropical regions or on non-domestic species of *Lepismatidae* from temperate ones.

Again, comparison of longevities [Table IV] in the two families is handicapped. Many of the Lepismatids were reared under ideal laboratory conditions, supplied with an adequate amount of food and protected from predators. In all cases the estimates of longevity in the *Machilidae* were made on natural populations whose members would be undergoing constant depredations in numbers. The general picture obtained is one of long life. The *Machilidae* appear capable of surviving for a minimum of two years and in many cases longer. *Lepisma*

Table III

DURATION OF THE DEVELOPMENT, UNDER THE STATED CONDITIONS, FROM HATCHING OF THE EGG TO THE FIRST OVIPOSITION IN VARIOUS SPECIES OF *THYSANURA*

Species	Time from hatching of egg to oviposition (months)	Stated conditions	Authority
Lepismatidae			
Ctenolepisma ciliata Duf.	11	—	Wygodzinsky, 1941
Ctenolepisma longicaudata Esch.	18	24°C	Lindsay, 1940
,,	30—36	Room temperatures	,,
Lepisma saccharina L.	21—24	[22,5°C for six months of year; 16°C for six months of year]	Sahrhage, 1953
,,	3—4	27°C; R.H. 84%	Sweetman, 1939, 1952
,,	about 24	—	Cornwall, 1915
Thermobia aegyptiaca Esch.	11 (?)	—	Alfieri, 1932
Thermobia domestica (Pack.)	2—2,5	37°C	Adams, 1937
,,	4,6	32°C	Sweetman, 1938
,,	2—4,5	37°C	,,
,,	5—6	37°C; R.H. 35%—40%	Sahrhage, 1953
,,	3,5—4,5	37°C; R.H. 70%	,,
,,	about 7,5	37°C; R.H. 90%—100%	,,
Machilidae		Moravia	Kratochvil, 1945
Dilta hibernica (Carp.)	11—12	Southern England; west France	Delany, 1954
Dilta littoralis (Wom.)	12—13		Argilas, 1939
Lepismachilis notata Stach	12	Switzerland	Wygodzinsky, 1941
Machilis annulicornis Latr.	7—9	low altitudes, Switzerland	,,
,,	18—20	high altitudes, Switzerland	,,
Petrobius brevistylis Carp.	5—6	southern England	Delany, (in press)
Petrobius maritimus Leach	5—6	,,	,,
Trigoniophthalmus alternatus (Silv.)	13—15	northern Switzerland	Wygodzinsky, 1941
,,	25—27	high altitudes, Switzerland	,,

Table IV

MAXIMUM ESTABLISHED LONGEVITIES, UNDER THE CONDITIONS STATED, OF VARIOUS SPECIES OF *THYSANURA*

Species	Maximum longevity (months)	Stated conditions	Authority
Lepismatidae			
Ctenolepisma longicaudata ESCH.	„Several years“	Room temperatures	LINDSAY, 1940
Ctenolepisma quadriseriata PACK.	47,2	27°C; R.H. 50%—90%	SWEETMAN, 1952
Lepisma saccharina L.	45	22,5°C for summer 16°C for winter	SAHRHAGE, 1953
„	44,8	27°C; R.H. 84%	SWEETMAN, 1952
Thermobia domestica (PACK.)	11,5—21,5	37°C; R.H. 35%—40%	SAHRHAGE, 1953
„	18,5—20	31°C; R.H. 40%—45%	„
„	18	37°C; R.H. 84%	SWEETMAN, 1952
„	33,5	32°C; R.H. 84%	„
Machilidae			
Dilta hibernica (CARP.)	23—24	Moravia	KRATOCHVIL, 1945
Dilta littoralis (WOM.)	22—24	southern England	DELANY, 1954
„	26—27	West France	ARGILAS, 1939
Lepismachilis notata STACH.	about 27	Switzerland	WYGODZINSKY, 1941
Machilis annulicornis LATR.	about 45	high altitudes, Switzerland	„
Petrobius brevistylis CARP.	18—20	southern England	DELANY, (in press)
Trigoniophthalmus alternatus (SILV.)	24	Switzerland	WYGODZINSKY, 1941

L. and *Ctenolepisma* ESCH. are also long-lived and in sharp contrast to *Termobia* BERGR. which only at lower temperatures has been recorded to live more than two years.

For the Machilids the winter months are periods of virtually complete inactivity. Growth is nearly, if not completely, at a standstill and mating, oviposition and hatching of eggs have not been recorded for this spell.

VIII. REPRODUCTION

Spermatogenesis has been described by CHARLTON (1921) and GATENBY and MUKERJI (1929) in *Lepisma* L., by ARGILAS (1939) in *Dilta littoralis* (WOM.) and by TUZET and MANIER (1954) in *Machilis tenuis* JAN. CARLTON observed males of *Lepisma* L. to contain most sperms during March, April and May. Corroborating CARLSTON'S observations, SAHRHAGE (1953) suggested April to mid-Summer as the breeding period of *Lepisma* L. The development of eggs is not seasonal in *Ctenolepisma* ESCH. (LINDSAY, 1940) as the ovarioles contain eggs in equal numbers at all time of the year.

The first record of mating appeared when SPENCER (1930) made brief reference to a „love dance" in *T. domestica* (PACK.). In 1938 SWEETMAN described mating in considerable detail in the same species and later still SAHRHAGE provided a rather fuller account of the production, structure and implantation of the spermatophore. The following account leans heavily on the findings of SWEETMAN and SAHRHAGE. Mating commences with the more active male facing the female and making frequent contacts of her antennae with his to which she responds slightly. The male next contacts the head of the female with his mouthparts; the female responds by lowering her head and arching the thorax. Contact may then be broken off, the male may move 1 cm — 2 cm from the female and rejoin her after a short rest. The male moves his head rapidly from side to side whilst not in contact with the female. The next development involves the „whirling" of the abdomen. The posterior portion of the abdomen is raised more or less vertically and slightly to one side and the head turned in the same direction as the abdomen. The male then rotates in a half or complete circle. Several „whirlings“ may take place and are interspersed with contacts with the female. Following contact of the head of the female, the male then touches her legs as he passes. After a time the female walkes forwards about 2 cm, turning her head from side to side and finally turns round and faces the male. The male repeats the gyrations described above and after a short spell of considerable agitation, deposits the spermatophore on the ground 1—2 cm, in front of the female. He then goes to the female, touches her head and legs and leaves her. The procedure lasts from 20—35 minutes up to the deposition of the spermatophore. The spermatophore is approximately 2,4 mm long and is composed of two sections [Fig. 7], a loose bag and a long slender neck. On being touched by the male the female walks over to, and straddles the spermatophore in such a way as to ensure that the neck passes into the spermatheca [Fig. 8], the storage receptacle for the sperms. Within 2—3 minutes of taking up the spermatophore the female starts to bite pieces off it until after 12—50 minutes no remains are left. SWEETMAN (1938) demonstrated through an exhaustive series of experiments that fertilization in *Thermobia* BERGR. was an essential prerequisite for egg-laying.

SAHRHAGE (1953) produced some interesting and anomalous results in connection with mating and fertilization in the same species. The spermatheca, being exoskeletal, is shed at ecdysis and if at that time it contains any sperms they would automatically be discarded with it. It would be expected that copulation would be followed by oviposition with ecdysis occurring last in the sequence. SAHRHAGE claims ecdysis to be interposed between implantation of the spermatophore and egg-laying with the result that theoretically fertilization could not take place. He is uncertain of the consequences of the phenomenon and tentatively suggests that either fertilization occurs whilst the ova are still in the ovarioles or, alternatively, sperms are stored in the oviducts which do not loose their lining at ecdysis.

The number of eggs produced per female is influenced in *C. longicaudata* ESCH. and *Thermobia* BERGR. by the numbers of males and females living together. Groups of two to four specimens of *Ctenolepisma* Esch. had a low productivity whereas if the same total number were placed in groups of ten to forty, the number of eggs deposited per female increased considerably. Sweetman (1938) found a significantly higher egg production per female if five females were placed with four males than if one female was placed with the same number of males.

Sturm (1952, 1956) has described mating in *Machilis* Latr. sp. and *L. saccharina* L. The process in *Machilis* Latr. is more elaborate than in *Thermobia* Bergr. and is initiated by the male rushing to the side of the female and drumming her on the anterior region of her body with his long maxillary palpi. The female responds by raising her abdomen vertically and the two insects then come to face each other, their maxillary palpi just making contact and their antennae extended forwards.

The male draws out from the penis a thread and the free end is attached to some arbitrary point on the substrate. The other end remains in contact with the penis. Throughout mating the position of the thread remains unaltered although the orientation of the insects to it change considerably. The male rotates through 90^0—180^0 and deposits three or four spermatophores on the thread. The male with its posterior abdominal segments raised vertically is by this time trembling considerably and is applying a lateral pressure to the female. A combination of the rotation of the body and the lateral pressure of the male, gradually revolves the female so that her body is parallel to and alongside the thread containing the spermatophores. The female's ovipositor is then moving actively. Finally, the male's antenna closer to the thread establishes contact between spermatophore and female genital orifice and thereby facilitates impregnation of the female. After a short resting phase the male once again becomes agitated and continues to rotate the female until the extended thread is ruptured. Mating is then complete having lasted about five minutes. In *Lepisma* L. a thread is formed by the male and used for the orientation of the female to the spermatophore which, as in *Thermobia* Bergr., is deposited on the ground.

Machilid and Lepismatid matings are involved processes with impregnation ensured by two methods. In the latter the female is orientated to the spermatophore as a culmination to a series of behavioural exchanges and finally takes up the deposited spermatophore of her own accord from the substrate. The male Machilid serves not only to orientate the female to the spermatophore but also uses one of its antennae as a medium of transport for the semen. In neither do the external genitalia of the two sexes come into contact.

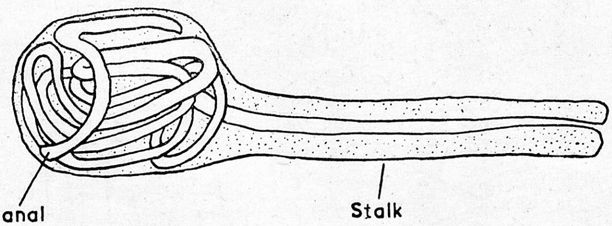

Fig. 7. The spermatophore of *Thermobia domestica* (PACK.) (after SAHRHAGE).

Oviposition behaviour varies with the habits of the species under consideration although generally these insects prefer to deposit their eggs in secluded cracks and crevices. WYGODZINSKY (1941) has described in detail the oviposition of *Machilis annulicornis* LATR. When ready to lay her eggs the female uses the ovipositor as a tactile organ moving it over the surface of the substrate until it finds a suitable site. She then anchors herself firmly to the ground with the aid of the abdominal styli and the claws on her walking legs. The ovipositor possesses digging claws at its tip and will, in the absence of suitable undulations, use them to dig a small hole. Periodically the ovipositor is withdrawn from the hole in order to remove the foreign bodies adhering to it. Having prepared the oviposition site the sternites of abdominal segments eight and nine become markedly arched and the egg is passed along the ovipositor as a stream of fluid. It leaves the ovipositor globular in shape and is gently pressed into position with the tip of the ovipositor. After laying, the aggs are covered with soil grains. Ovipositor length is reported to be shorter at lower altitudes than higher ones thereby enabling eggs to be deposited deeper from the surface in colder climatic localities.

Parthenogenesis has been proposed as a method of reproduction by Heymons and Heymins (1905) for *Trigoniophthalmus* Verh., Verhoeff (1010 a) for *Dilta* Strand, Bär (1912) for *Machilis* Latr. and Agrell (1944) for *Petrobius lohmanderi*

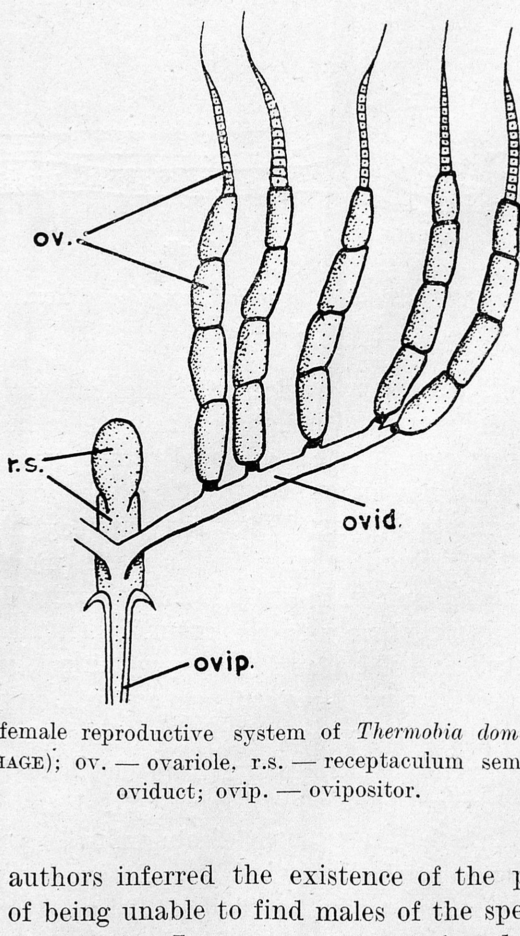

Fig. 8. The female reproductive system of *Thermobia domestica* (Pack.) (after Sahrhage); ov. — ovariole, r.s. — receptaculum seminis; ovid. — oviduct; ovip. — ovipositor.

Agr. The authors inferred the existence of the phenomenon as a result of being unable to find males of the species in question. More recently, Janetschek (1954) found for several species of *Machilis* Latr. from central Europe that males were either absent or in proportionally very small numbers.

IX. SUMMARY

1. The eggs are relatively large, of variable shape and when first laid have flexible chorions. Between one and thirty-three eggs are laid at a time. In the *Lepismatidae* the incubation period is less than sixty-four days and in the *Machilidae* invariably more than sixty and frequently over two hundred. The time and duration of the oviposition period is characteristic for each species.

2. Hatching is usually performed in a single operation with the aid of a „hatching organ".

3. The development of *Ctenolepisma longicaudata* Esch. and *Petrobius brevistylis* Carp. from hatching to maturity has been described. The former is not mature in less than fourteen instars whereas *Petrobius brevistylis* Carp. is ready to reproduce at the eight or ninth. The characters of individual instars can be determined by rearing the insects and/or by selecting some biometrical character that varies at each instar. In *Petrobius brevistylis* Carp. the number of rings of scales on the lateral caudal cercus has been found characteristic for each of the first eight instars.

4. Growth rates vary greatly with environmental conditions In the *Machilidae* no growth occurs over the winter months and is rapid during the summer. The laboratory reared Lepismatids grow at a far more even rate. Saxual maturity is reached before the insects are fully grown.

5. Ecdysis is performed by the insect splitting the cuticle in a mid-dorsal line along the length of the thorax and part of the head. The insect withdraws itself through the cleft. *Thermobia* Bergr. and *Ctenolepisma* Esch. may have more than fifty-six instars; the maximum number recorded for *Lepisma* L. is forty-one. The early instars of Lepismatids are shorter than the latter ones which may vary from seven to fifty days according to environmental conditions and the species.

6. Under optimal conditions the *Lepismatidae* take a short time (3—6 months) to attain sexual maturity. The only exception is *Ctenolepisma longicaudata* Esch. which takes eighteen months. The *Machilidae* may take from six to twenty-seven

months to mature. All *Thysanura* are apparently capable of surviving eighteen months. No records exist of them living more than four years.

7. The elaborate matings of *Thermobia* Bergr. and *Machilis* Latr. have been described.

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Department of Zoology, University of Glasgow, Scotland.

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Redaktor zeszytu: prof. dr J. Nast

Państwowe Wydawnictwo Naukowe — Oddział w Krakowie 1957

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