

## Postembryonic development of *Strigamia maritima* (Leach, 1817) (Chilopoda: Geophilomorpha: Linotaeniidae) with emphasis on how to separate the different stadia

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### Abstract

Our argumentation for the epimorphic status of *Strigamia maritima* (Leach, 1817) has led to questions on how we separated the stadia. Several measurements and counts, including character plots, were made in an effort to find the easiest and most accurate way of separating the postembryonic stadia. The measurements and counts are presented in tables and diagrams. Especially the presentation of the width of the forcipular coxosternite on probability paper indicated 6 stadia. The last stadium, Postmaturus, only comprised 0.5 to 0.8 % of the 1430 specimens investigated (Adolescens I and older). The most reliable single character seems to be the number of setae on the coxae of the last pair of legs. Another increase of setae through the stadia, here presented on the 10th sternite, shows an evolving pattern that could be of great help in allocating the specimens to the stadia.

**Keywords:** epimorphy, character development, probability paper, metasternite setation, postmaturus, eggtooth

### 1. Introduction

The results here presented are based on the premier author's thesis (Horneland 1984). At the 5th International Congress of Myriapodology in Virginia (USA), we showed that a statistically significant increase in number of segments, from the foetus to the maturus senior stadium, for a supposed epimorphic geophilomorph, *Strigamia maritima* (Leach, 1817) could be explained by the higher longevity of the more numerous segmented females as opposed to the more abundant younger stadia of lesser segmented males with a shorter lifespan (Horneland & Meidell 1986). Since then we have periodically been asked how we separated the stadia.

Lewis (1981) discusses several possible character sets for separating stadia among geophilids. From his work on *Strigamia maritima* (Lewis 1961), we selected the following characters for our analysis:

1. The width of the forcipular coxosternite (measured from the ventral side).
2. Mean number of pores on the coxae of the last pair of legs (i.e. the sum of pores is divided by two).

3. Numbers of setae (hairs) on the 1st genital sternite.

We have added:

4. Number of setae (hairs) on the coxae of the last pair of legs.

Several other morphological characters, like sensory sensilla on the antennae and development of the mouthparts, were investigated. Among these, only one character set seemed promising:

5. The pattern of growth of setae on the metasternites.

## 2. Materials and methods

The collection site and the period for sampling at the coast north of Bergen have been published earlier (Horneland & Meidell 1986). There we emphasised how important it is to separate the sexes as early as possible to get a clear picture from the data collected. From the several thousand specimens collected, either by hand or by flotation (Börseth 1969), 1504 were selected for character studies (Tab. 1). Further 53 microscopic slides were made of eggs/embryos and 68 of the peripatoid stadium. By using a microscope and observing the male gonopods, we were able to separate the sexes down to the Adolescens I stadium (Fig. 13).

Tab. 1 The number of specimens selected for the analysis of stadia. Further 53 eggs/embryos and 68 specimens of the peripatoid stadium were investigated.

	Foetus	Adol. I	Adol. II	Adol. III	Matr. jr.	Matr. sn	Sum
Males		84	209	239	134	52	718
Females		56	171	239	164	82	712
Sum	74	140	380	478	298	134	1504

The measurement and counting of Character 1 to 3 above were made under a stereomicroscope, while the counting of setae on the coxae of the last pair of legs (Character 4) was done under a microscope. Between 10 and 15 specimens of each stadium and sex were mounted on slides for examination and drawing. Also scanning-electron microscopy was used to make a basis for drawings of mouthparts/forcipular segment, genitalia region and sternal setation of the 1st to the 15th segment. As an expression of head width, the width of the forcipular coxosternite was measured from the ventral side. Strong chitinisation, due to the movement of the forcipules, made this a relatively well-defined measure (Fig. 1).

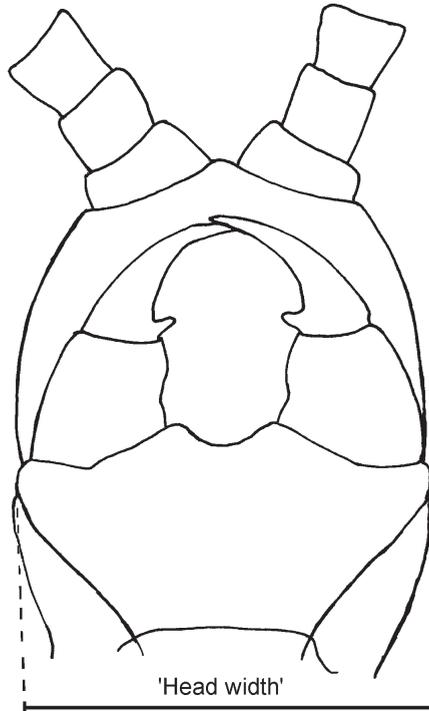


Fig. 1 'Head width', measuring the width of the fornicular coxosternite.

### 3. Results

The width of the fornicular coxosternite for both males and females (Character 1) is summarised in Tab. 2 and shown in Fig. 2. For both sexes a polymodal distribution with at least 5 'stadia' is indicated. The measurements were then transferred to Hazen's probability paper (Harding 1949, Lewis 1961), as width of fornicular coxosternite plotted against the cumulative percentage of the measured individuals. The percentage scale on the paper is so constructed that a normal distributed set of data produces a straight line. Five points of inflections in the curve for females indicate 6 stadia (straight lines) starting from Adolescens I (Fig. 3). Similar results can be shown for the males.

In accordance with Lewis (1961) we kept the following 'stadia' separate:

Egg/embryo – Peripatoid – Foetus

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Adolescens I – Adolescens II – Adolescens III – Maturus junior – Maturus senior – Postmaturus (?)

The line indicates the border between the stadia where the sexes could be separated (lower part) and could not be separated (upper part). The question mark at the last stadium relates to the fact that the last part of the curve (Fig. 3), indicating the 6th stadium, only relies on 0.5 to 0.8 % of the material. That is 7 to 11 individuals among the 1430 measured, counted and sexed specimens.

Tab. 2 Characters measured and counted, distributed on stadia and sex. Character 1: Width of the forcipular coxosternite in mm; Character 2: Mean number of pores on the coxae of the last pair of legs (i. e. sum of pores from both legs divided by two); Character 3: Numbers of setae on the 1st genital sternite; Character 4: Number of setae on one of the coxae of the last pair of legs.

		Adol. I	Adol. II	Adol. III	Mat.jr	Mat.sen	Post mat.
Character 1	Male	0.38–0.44	0.44–0.53	0.53–0.65	0.62–0.73	0.71–0.85	0.83–0.91
	Female	0.38–0.44	0.44–0.55	0.54–0.67	0.66–0.78	0.71–0.85	0.89–0.97
Character 2	Male	1	3.5–4.5	5.0–9.5	7.0–11.5	7.5–14.0	9.0–15.0
	Female	1	3.5–4.5	5.0–11.5	7.0–13.0	11.0–16.0	13.0–17.0
Character 3	Male	2	13–15	19–28	28–40	38–48	43–54
	Female	2	6–8	8–14	12–17	14–20	18–22
Character 4	Male	2	7–9	19–30	69–82	123–146	151–164
	Female	2	7–9	13–19	20–27	29–36	38–48

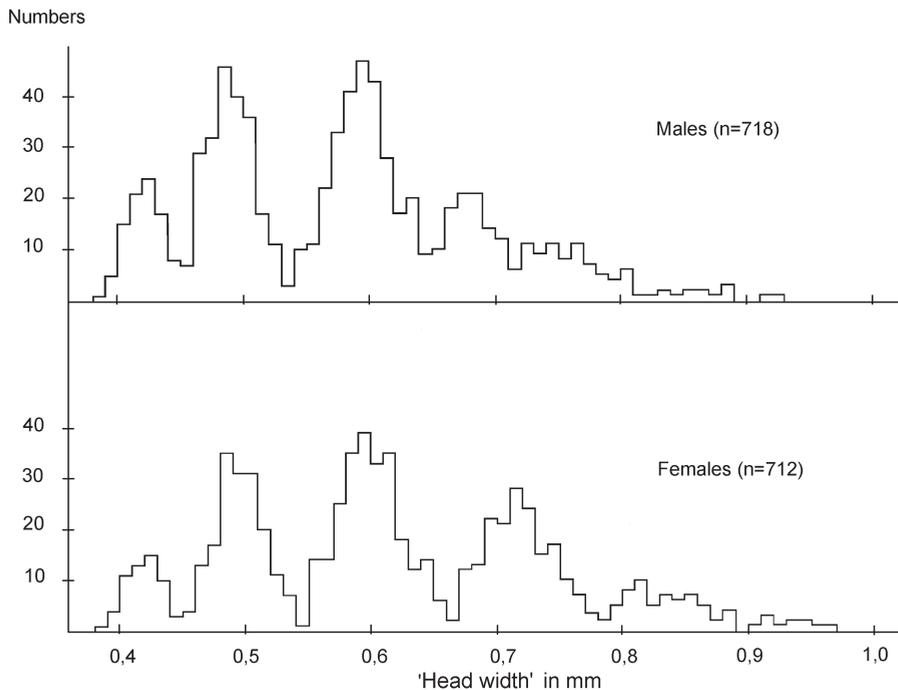


Fig. 2 Distribution of the width of the forcipular coxosternite ('head width') for males and females.

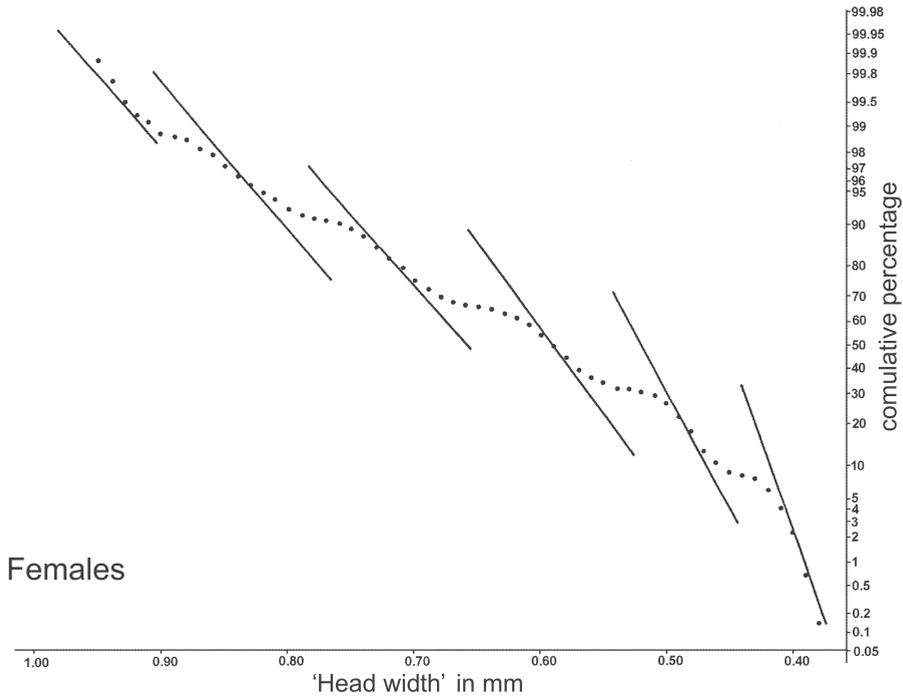


Fig. 3 A plot of cumulative percentage (Y-axis) of female individuals against 'head width' (X-axis) on Hazen's probability paper. The six straight lines indicate normally distributed sub-populations (stadia) within the material.

Lewis (1961) discusses the use of different characters and character-combinations for separating the stadia of *S. maritima*. In his Fig. 7, he gives a plot of head width against the number of 'hairs' on the first genital sternite. From this he obtained 'a fairly good separation' of the stadia Adolescens III through Maturus senior. Later (1981) he admitted that his counts were based on the sternite of the intermediate segment, the segment that lies in front of the first genital segment. This intermediate sternite is hard to see on the females, so only males were counted. This does not alter his conclusion.

Our counting is based on the 1st genital sternite as beautifully pictured by Lewis (1981, Fig. 10). A presentation of our counts from the males, plotted against the width of the forcipular sternite, from stadium Adolescens III on, is given in Fig. 4. The separation between the stadia seems at least as well defined as that of Lewis using the intermediate sternite. The more diffuse end of our plot could indicate a possible Postmaturus stadium. The 1st genital segment for the females was also counted and gave similar results. Results for both sexes are presented in Tab. 2 (Character 3).

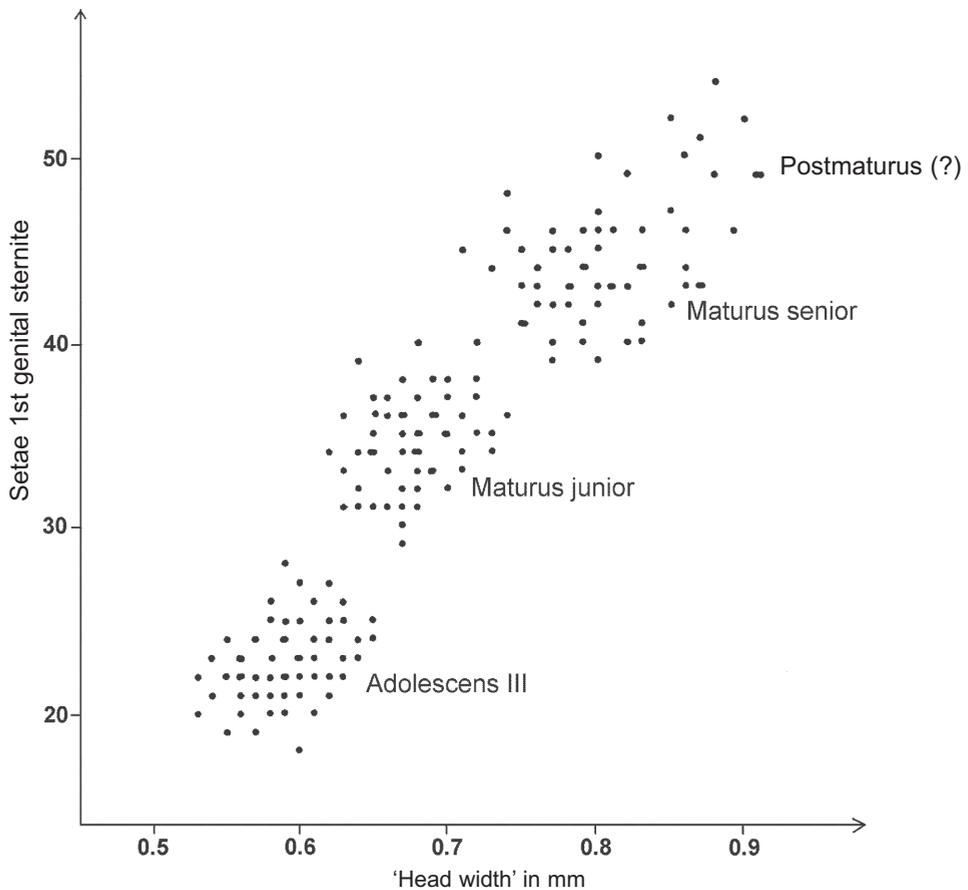


Fig. 4 Numbers of setae on 1st genital sternite (Character 3, Y-axis) plotted against 'head width' (Character 1, X-axis). Only Adolescens III and older stadia are included. This stadium and Maturus junior are well defined. Further investigations will clarify if the Maturus senior plot includes Postmaturus specimens.

Two other characters investigated are the number of pores (Tab. 2, Character 2) and the number of setae (Tab. 2, Character 4) on the ventral part of the coxae of the last pair of legs (Fig. 5). The number of pores separates stadium Adolescens I and Adolescens II from the rest. The numbers here (Tab. 2, Character 2) are the sum of the pores on the coxae divided by two. This makes the numbers comparable with those presented by Lewis (1961, Tab. 2). The number of setae (Character 4) seems to be a good character to separate all stadia except against the possible Postmaturus stadium. This character was also the hardest to count, but modern computer-techniques should be of great help for future investigations on this character.

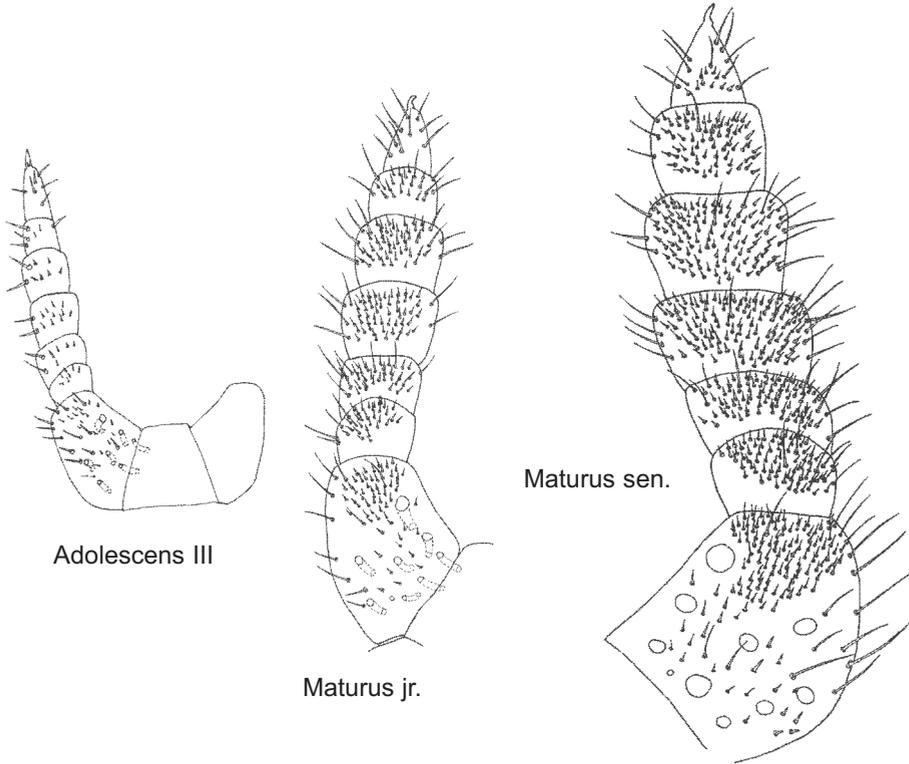


Fig. 5 Last pair of legs from male Adolescens III, Maturus junior and Maturus senior showing pores on its coxa (Character 2) and setation of the same (Character 4).

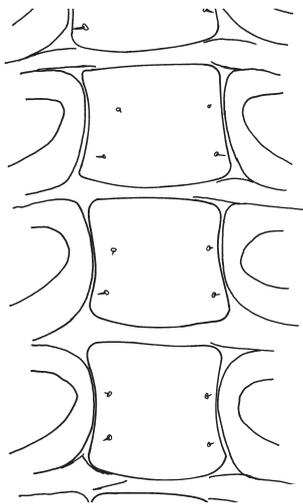


Fig. 6 The foetus stadium. Sternites showing 4 setae.

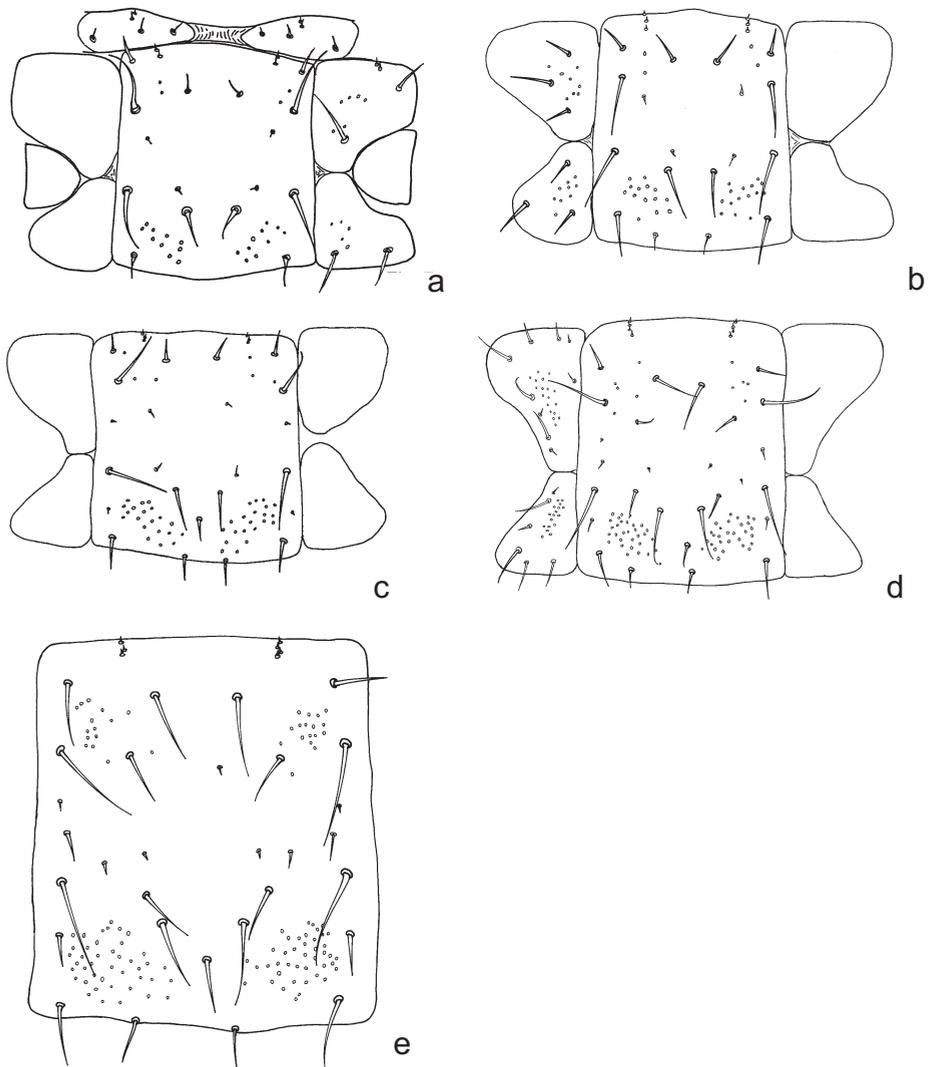


Fig. 7 a–e Number and arrangement of setae on the 10th sternite in different stages: a: Adolescens I: 16 setae; b: Adolescens II: 18 setae; c: Adolescens III: 23 setae; d: Maturus junior: 27 setae; e: Maturus senior: 30 setae.

Concerning the pattern of growth of setae on the metasternites, sternite number 10 was chosen for analysis/description. The foetus stadium is characterised by having 4 setae on most sternites, two along each side (Fig. 6), missing only on the last 4 to 8 segments. Going through the stadia up to Maturus senior the number of setae on each half sternite increases from 2 to 14 as well as they grow in size. In addition there are 2 median ones. The sternites are pictured in Fig. 6 to 11. The key to the increase, as positions for the setae, is given in Fig. 8. It proceeds like this: In Adolescens I setae no 3 to 8 are added, in Adolescens II no 9 is added and in Adolescens III no 10 and 11 plus the posterior median setae (square) are added. Finally in Maturus junior setae no 12 and 13 are added and in Maturus senior no 14 and the anterior median setae (square) completes the picture.

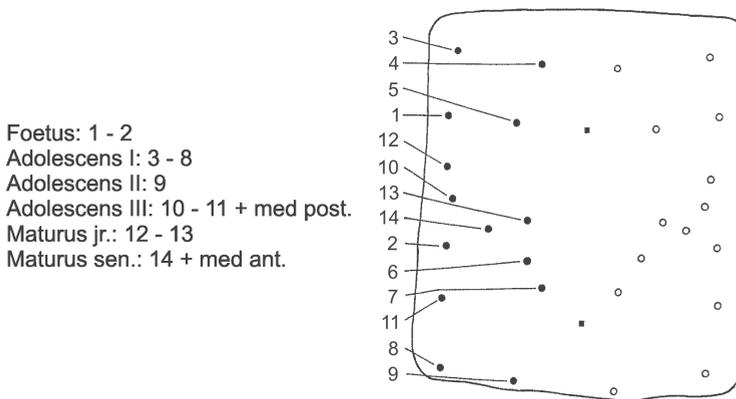


Fig. 8 Key to the increase of setae on the 10th sternite. The setae of the right half of the sternite are numbered. The two median setae are marked as squares (anterior up, posterior down).

In some specimens of Adolescens III seta no. 10 and 11 might be missing. Similar at the Maturus junior, seta no. 12 and 13 might be missing. When in doubt, both right and left side of the sternite should be checked.

At the front end of the sternum there are two rows, each of 3–4 small sensory sensillae, one row in each half. These are not to be confused with the setae.

To make it easier to identify the stadia by observing the pattern of setae that is developing, a greyscale presentation is given (Fig. 9a–f). In each of the six parts of the figure, representing stadia from Foetus to Maturus senior, all potential setae positions are shown. Those filled with grey or black are possessing setae at the given stadium. Newcomers, setae positions that are new to a stadium, are grey, compare Fig 9a with Fig. 10. In later stadia, newcomers are grey while those setae ‘inherited’ from stadia passed, are black.

The Foetus stadium is easily recognised with its four setae (Fig. 9a).

In the first free-living stadium, Adolescens I, there are four setae along each side and two rows of four setae in the frontal part of the sternite. The beginning of a V-like pattern in the middle posterior part of the sternite is also visible (Fig. 9b).

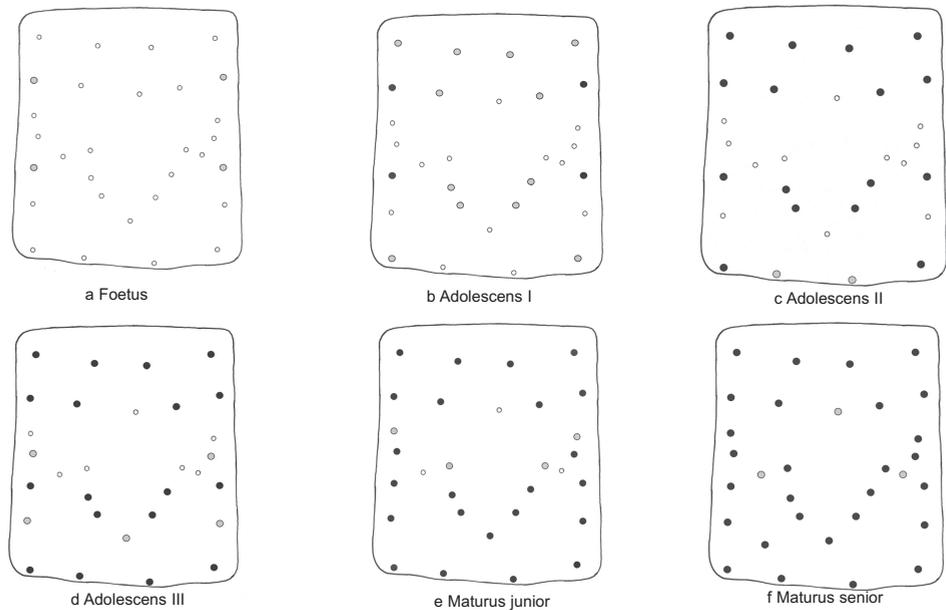


Fig. 9 a–f The increase of setae from foetus (a) up to Maturus senior (f). Grey circles indicate setae appearing in a given stadium. Black circles are setae accumulated up to a given stadium.

Adolescens II is characterised by a single transverse line of four setae, at the rear part of the sternum (Fig. 9c).

At the Adolescens III the sides of the sternum now counts 6 setae. The appearance of the posterior median seta makes the V pattern more complete (Fig. 9d).

At the Maturus junior stadium all 7 setae on the side rows are there and the V is made of 7 setae (Fig. 9e).

At the Maturus senior, the anterior median seta is there, together with a seta on each side ‘connecting’ the V-form to the lateral rows (Fig. 9f).

#### Short comments on the stadia:

Embryo (Fig. 10a, b)

The eggs are spherical, measuring 0.88 to 1.11 mm in diameter. The colour is changing from yellow to whitish yellow as the embryo develops. The goal for this investigation was not to make a full description on the embryogenesis of *S. maritima*. Here, based on 53 microscopic slides, we only present two illustrations of early cleavage (Fig. 10a, b) and the position of the egg teeth (rupta ovi) (Fig. 10a, c) which have a peculiar position. On both sides, in the area where the mouthparts are developing, just behind what is to be the antenna, parts of the embryonic cuticle is facing outwards as apposed to the other visible structures which are ‘curled’ towards the ‘ventral’ side of the embryo. Near the tip of these structures chitinised egg teeth are developed (Fig. 10c), which eventually helps the animal splitting the egg shell (Fig. 10d).

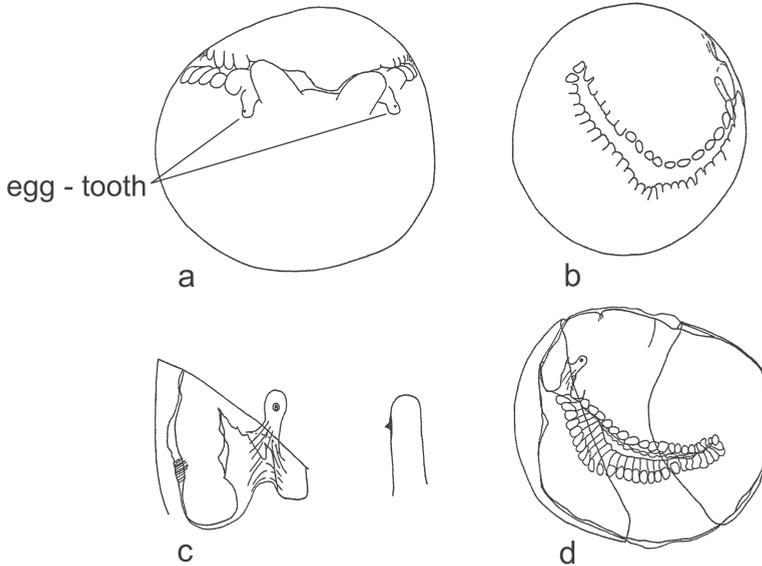


Fig. 10 a–d Evolving embryo. a: Frontal view with egg-tooth positioned just behind the developing antennae; b: side view; c: egg-tooth details; d: splitting of egg-shell.

#### Embryo to peripatoid (Fig. 11)

As the egg teeth, helped by the increase of yolk in the front part, break the egg-shell the last embryonic stadium appears (Fig. 11b–f). This ends up in the peripatoid stadium (Fig. 11g). Here, of the extremities, only the antenna are segmented (14 segments), the rest are paired sack-like evaginations along the body, clearly related to each sternite. At the end of the peripatoid stadium, both the pre- and the metatergites are formed and the embryonic cuticle is only attached at the rear end. Our observations are based on 68 microscopic slides.

#### Foetus stadium (Fig. 12)

Seventy four specimens were investigated. The body has got its 'normal' dorso-ventral flattening. The extremities are segmented and the male gonopods are not developed. The width of the forcipular coxosternite is measured to 0.34 to 0.41 mm. The number of setae is extremely low as compared to the coming stadia. The setation of the sternites is dealt with elsewhere (p. 381 and Fig. 6). As observed by Lewis (1961), the animals are nearly not moving. When doing so, the movement is nematode like.

#### Adolescens I (Fig. 13)

In this stadium most characters of the mature animal are apparent, but the numbers of seta, sensory sensilla and coxal glands are increasing through the stadia to follow. It is possible to separate the sexes using a microscope (see male gonopods, Fig. 13a). Evolving of intentional movement, which eventually leads to the seashore (feeding grounds), is described by Lewis (1961). Of major importance is the development of the tracheal system, which also marks the border between foetus and Adolescens I. It must be the survival factor for animals sporadically submerged in (salt) water, either surviving the submerging or being washed ashore by the same principle as we used in collecting by flotation.

## Adolescens II through Postmaturus

The characters used to describe these stadia are given in Tab. 2 and Figs 8–13.

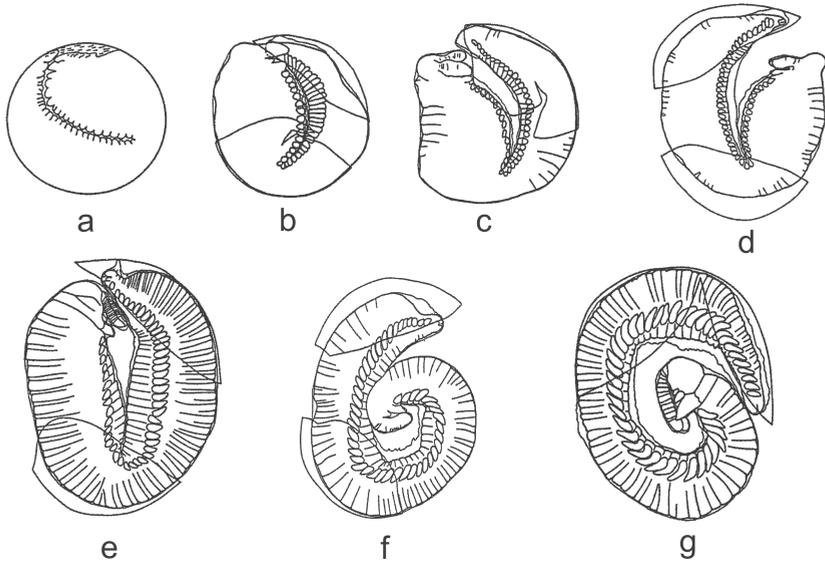


Fig. 11a–g The evolving of the peripatoid stadium. a: Germ band formation; b: last embryonic stadium breaks the egg-shell; c–f: development towards the peripatoid stadium; g: peripatoid stadium with segmented antennae but still within parts of the egg-shell and embryonic cuticle.

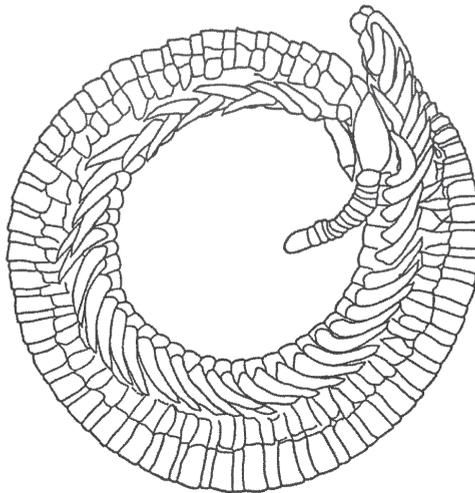


Fig. 12 The foetus stadium.

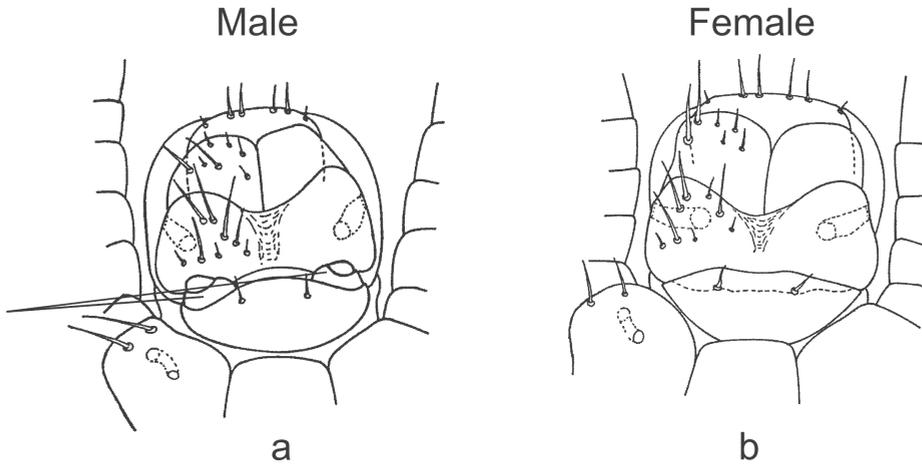


Fig. 13 a, b The Adolescens I stadium, here represented by a ventral view of the genital region of a: a male and b: a female. Lines point at the male gonopods. Characters 2–4 from Tab. 2 could easily be verified.

#### 4. Discussion

Lewis (1961) discussed many characters and he showed several diagrams of characters combined separating the specimens into groups/stadia. In our effort to characterise the different stadia we have looked at the front part, i.e., mouthparts including clypeus and antenna. Likewise we described the terminal segments in great detail.

Here we will focus on the usefulness of Characters 1 to 5 in separating the stadia.

The width of the forcipular coxosternite, as presented in Fig. 2 and Tab. 2 (Character 1), makes the ordering of most specimens to stadium easy. Only the demarcation against the following stadium has to be observed. Character 2 (mean number of coxal pores on last legs), Character 3 (number of setae on 1. genital sternite) and Character 4 (number of setae on coxae of last pair of legs) all easily separates Adolescens I from Adolescens II. The same set of characters easily separates Adolescens II from Adolescens III, except Character 3 for females. Here a quick inspection of Character 4 should settle the question. To separate Adolescens III from Maturus junior is easy based on Character 4 for males, but the females is not so clearly separated. The same character is also the one that separates Maturus junior from Maturus senior.

The most helpful single character set, together with setation on the coxae of the last pair of legs, was the pattern of increase in number and location of the setae on the 10th metasternites (Fig. 6–9).

The measurements for Postmaturus are given (Tab. 2) to challenge further research in this area. Whether they represent a minimal part of the normal population or a 'stadium' appearing sporadically, due to climatic coincidences or the like, is not yet clear.

### Addendum

At the turn of the century *Strigamia maritima* became a 'model' organism for studying early development and segment formation. Several papers have been published; here we will just refer to Chipman et al. (2004) as an interesting article and a source for further references on the subject.

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