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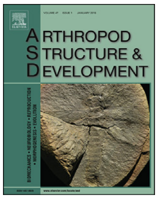

“Open access” growth histories in millipedes (Diplopoda)

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ABSTRACT

A unique pattern of missing defence glands on certain body rings is described for two species of the millipede family Mongoliulidae, order Julida: *Ussuriiulus pilifer* Golovatch, 1980, and *Koiulus interruptus* Enghoff et al., 2017. Based on the patterns of missing glands observed in recently collected samples of the two species, numbers of podous and apodous body rings in successive stadia of the postembryonic development can be inferred for each individual millipede, which in turn allows the reconstruction of pathways of anamorphosis in these species. The inferred numbers of body rings in developmental stadia are compared with actual numbers observed on additional samples, including the type series, of *U. pilifer*. The pattern of missing glands in the two mongoliulid species is compared with the pattern of missing glands typical of the entire millipede order Polydesmida.

1. Introduction

Although no millipede is known to have a thousand legs (Marek and Bond, 2006), high numbers of legs and segments are characteristic of this class of arthropods. However, hatching millipedes usually have only three pairs of legs, rarely four and exceptionally more (Enghoff et al., 1993; Frederiksen et al., 2012). During a series of moults, through a process known as anamorphosis, they acquire more and more segments and legs until a final number is reached (hemianamorphosis and teloanamorphosis), or the addition of segments and legs continues indefinitely until the millipede dies (euanamorphosis).

Enghoff et al. (1993) reviewed millipede postembryonic growth, anamorphosis, in great detail. The anamorphosis of several species has been studied in laboratory cultures, but in many cases it is possible to infer the course of anamorphosis indirectly from field-collected and preserved material. Most frequently used is the eyerow method which is based on the observation that many millipedes, especially those of the large superorder Juliformia (orders Julida, Spirobolida and Spirostreptida), add one row of eyes per moult. For example, in many species of the common European family Julidae, the hexapod stadium I has no eyes, stadium II has one eye on each side, stadium III has three (one “row” of one eye + one row of two), stadium IV has three rows (1 + 2+3) etc. By counting the eyerows one can therefore assign a specimen to a postembryonic stadium.

Several groups of millipedes, including the Juliformia, are characterized by considerable variation in the number of segments and hence the number of pairs of legs within a given postembryonic stadium. Others, e.g., the large order Polydesmida, show constancy in segment and leg numbers within each stadium.

In Juliformia and Polydesmida, tergites, pleurites and sternites belonging to each diplosegment are fused into complete *body rings*, and the two groups are collectively referred to as “ring-forming millipedes”. The anamorphosis of ring-forming millipedes follows the so-called “law on anamorphosis”. First formulated by Fabre (1855) the “law” states that the legless body rings (diplosegments) in front of the telson in a given stadium change into leg-bearing body rings in the next stadium. By counting numbers of leg-bearing (podous) and leg-less (apodous) body rings one may therefore obtain a general view of the course of anamorphosis in a species or population. The “law” is particularly useful for studies on the variable Juliformia. Examples of this approach are provided by, e.g., Voigtländer (1987) and Enghoff et al. (2009).

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Fig. 1. Examples of julid millipedes with clearly visible defence glands. Left: *Syrioiulus taliscius* (Attems, 1927), right: *Pachyiulus cattarensis* (Latzel, 1884). D. Antić phot.

Fig. 2. Example of a millipede with a "trans-segmental colour pattern". Dorsal (top) and lateral (bottom) views of a specimen of *Sagmatostreptus strongylopygus* (Attems, 1950) showing seven groups of dark-coloured body rings. Interpreting the posterior delimitation of the dark colour pattern elements as the limit between successive ring additions allows inferring part of the anamorphosis of the specimen. From Enghoff (2011). (For interpretation of the references to color/colour in this figure legend, the reader is referred to the Web version of this article.)

However, this approach does not allow to "read" the course of anamorphosis in each individual. In some cases, this information can be obtained by studying the row of paired defence glands which in Juliformia – with the rare exceptions described in this paper – extends from body ring five or six (in the small family Typhlobolellidae from ring three) until and including the last leg-bearing body ring. Especially in lightly pigmented species, and in young individuals of darker species, the glands shine through the cuticle as a row of dark, often reddish spots (Fig. 1). Often, the glands belonging to the row of rings added during a given moult differ in size from those in front and behind, and the number of body rings added during each moult can therefore be inferred. This "defence gland method" was first used by Halkka (1958) and later by Brookes (1963) and Biernaux (1972). However, in darker/older individuals the method fails because the defence glands are not or hardly visible through the cuticle; furthermore, in preserved individuals, the colour of the glands is frequently faded.

Most millipedes are of a rather dull coloration, but some possess contrastful colour patterns. A few of these show what Enghoff (2011) called "trans-segmental colour patterns". The patterns consist of an element extending over several body rings, repeated several times along the millipede's body, see, e.g., Fig. 2, where an element consisting of ca. three dark-coloured body rings occurs in seven places along the body. Enghoff (2011) found that in most cases these patterns agree closely with what is known and/or can be inferred about the anamorphosis in the species in question. Therefore, using the colour patterns, one may "read" at least part of the growth history of the individual. The specimen illustrated in Fig. 2, which has 53 podous rings (and no apodous rings as is normal in adults of the family Spirostreptidae to which it belongs) may serve as an example. By interpreting the posterior delimitation of the dark colour pattern elements as the limit between successive ring additions it can be inferred that the latter part of the anamorphosis of the specimen followed the following course:

stadium n: 24 podous + 5 apodous rings
stadium n + 1: 29 podous + 5 apodous rings
stadium n + 2: 34 podous + 5 apodous rings
stadium n + 3: 39 podous + 5 apodous rings
stadium n + 4: 44 podous + 4 apodous rings
stadium n + 5: 48 podous + 3 apodous rings
stadium n + 6: 51 podous + 2 apodous rings
stadium n + 7: 53 podous + 0 apodous rings (observed formula, no potential for adding more rings)

Comparing with the information on other species of Spirostreptidae mentioned by Enghoff et al. (1993) and Fontanetti and Zirondi (2000) n might equal 3 or 4. Because the colour pattern is only present in the posterior ca. 2/3 of the body, nothing can be said about the numbers of podous and apodous rings in the stadia preceding stadium n.

In connection with the description of a new species of the family Mongoliulidae, order Julida (Enghoff et al., 2017) a pattern of missing defence glands was discovered which provides an opportunity to "read" the course of anamorphosis of a preserved millipede specimen. Actually, the absence of defence glands on certain body

Fig. 3. A (subadult) female of *Ussuriiulus pilifer.* Arrows indicate body rings (nos. 7, 10, 14, 18, 23, 29) with missing defence glands. A. Illum phot.

rings was already noted by Golovatch (1980), who in his description of the mongoliulid *Ussuriiulus pilifer* Golovatch, 1980 (in Russian) noted that in this species the series of defence glands starts on body ring 6, but that glands are always missing from rings numbers 7, 10, 14, 18, 23, and certain subsequent rings (Fig. 3). This remarkable observation was neglected by subsequent authors writing about *U. pilifer* (Enghoff, 1981, 1991; Mikhaljova, 1998, 2004).

Based on newly acquired material of *U. pilifer* and the type material of *Koiulus interruptus* Enghoff et al., 2017, we here present analyses of the missing defence glands patterns under the main assumption that *the glandless body rings are the first in a series added during a moult*. The findings are compared with observations on two independent samples of *U. pilifer*, and the validity of the main assumption is discussed.

2. Material and methods

Four collections of millipedes, all preserved in 70% ethanol, were studied:

Collection A: *Ussuriiulus pilifer*, 20 entire specimens from RUSSIA (Far East), Primorskii Krai (southern), Shkotovskii distr., 5 km NE of Mt. Pidan (Livadiiskaya), and on the E slopes of the same mountain, Pryamoi Kluch river valley, 320–1350 m, 43.071–43.111°N, 132.695–132.729°E, mixed forest, fir dominated forest, and timber line, leaf litter, 15–18.v.2015, A. Solodovnikov, A. K. Hansen and M. Justesen leg. (kept in the Natural History Museum of Denmark).

Collection B: *Koiulus interruptus*, 46 entire specimens from the type material, from RUSSIA (Far East), Khabarovskii Krai (southern): Sikhote-Alin (Central) range, upper course of river Ko 47.037–47.074°N, 136.396–136.478°E, 400–800 m, mixed forest, fir-birch forest, (wet) leaf litter, river bank and flood debris, 22–26.v.2015, A. Solodovnikov, A. K. Hansen and M. Justesen leg. (kept in the Natural History Museum of Denmark).

Collection C: *U. pilifer*, 111 entire specimens from the type material, from RUSSIA (Far East), Ussurijskij Nature Reserve, 35 km NE of Chuguevka, G. F. Kurcheva & E. V. Mikhaljova leg. (kept in the Zoological Museum, Moscow University).

Collection D: *U. pilifer*, 81 entire specimens from RUSSIA (Far East), Primorskii Krai: Chuguevskii distr., Verkhne-Ussuriyskii Research Station, *Picea*, *Pinus* and *Ulmus* forests, litter, July–September 1975, 1978-1979, leg. E.V. Mikhaljova; Ussuriisky Nature Reserve, *Abies holophylla* forest, litter, 9.vii.1978, leg. E. V. Mikhaljova; Shkotovskii distr., near Anisimovka, Litovka mountain, 100 m a.s.l., coniferous forest, 28.IX.2006, leg. A. A. Rodionov (kept in Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok).

Numbers of podous and apodous body rings were counted on all specimens. On specimens from collections A and B the position of

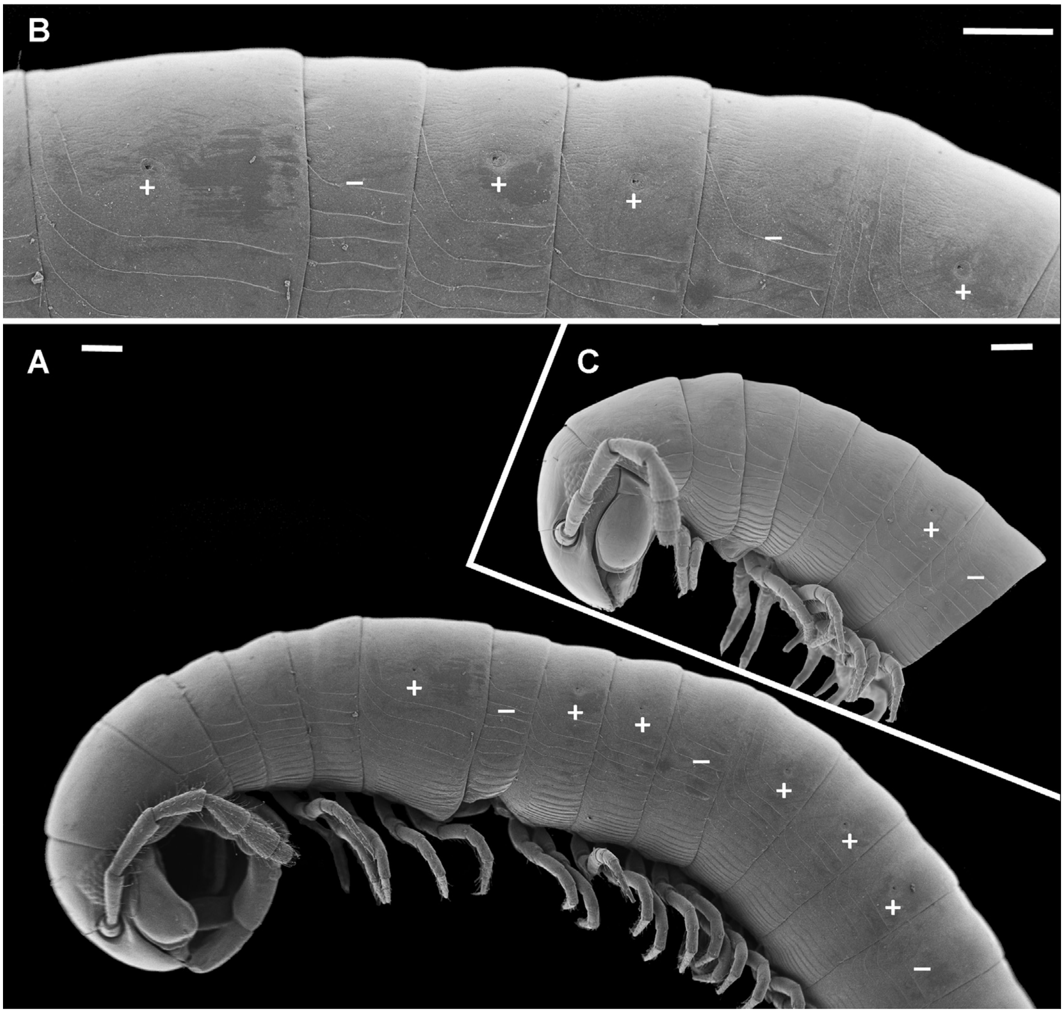


Fig. 4. *Ussuriiulus pilifer.* A. Anterior end of male, Gland openings (ozopores) present (+) on body rings 6, 8-9, 11-13, absent (−) on 1-5, 7 and 10. B. Close-up of body rings 6–11. C. Head and rings 1–7 of female, ozopores present (+) on ring 6, absent (−) on 1–5 and 7. (Absence of ozopores not indicated for rings 1–5 which always lack them). Scales 0.2 mm.

the defence-gland-less body rings was noted. This was easily done because these collections were freshly collected, and the defence glands were visible through the cuticle as dark spots (Fig. 3). Collections C and D had spent several years in alcohol, resulting in fading of the dark spots, and these collections were therefore only used for a comparison of numbers of podous and apodous body rings of *U. pilifer* as actually observed and as inferred by means of the missing glands.

Specimens for scanning electron microscopy (SEM) were transferred to 96% ethanol, then to acetone, air-dried, mounted on aluminium stubs, coated with platinum-palladium and studied in a JEOL JSM-6335F scanning electron microscope.

The validity of the assumption that glandless body rings are the first in each newly added series (henceforward: the main assumption) was examined semi-statistically by means of the chi-square statistic as implemented on https://www.graphpad.com/quickcalcs/contingency1.cfm.

3. Results

3.1. *The missing glands*

Fig. 3 clearly shows the absence of dark spots on certain body rings. In order to ascertain that defence glands are really missing, several body rings were dissected – no traces of glands were found. Study of body rings with scanning electron microscopy showed that not only the gland, but also the gland opening (ozopore) is actually missing from the body rings in question (Fig. 4, Enghoff et al., 2017: fig 4C).

3.2. *Growth history of Ussuriiulus pilifer*

Fig. 3 shows a specimen of *U. pilifer* with the glandless body rings indicated, and Table 1 lists the specimens in Collection A, their sex, their observable body ring formula, and the body rings from which the defence glands are missing.

In the material studied by Golovatch (1980), defence glands were missing from rings 7, 10, 14, 18, and 23. The new material, however, shows a more variable pattern. Glands are lacking from rings 7 and 10 in all specimens, but further back they are lacking from ring 13 *or* 14, from ring 17 *or* 18 *or* 19, from ring 22 *or* 23 *or* 24 *or* 25, and further back variability is even greater (Table 1).

According to our main assumption, viz., that the glandless body rings are the first in a series added during a moult, the series of numbers in Table 1 can be "translated" into inferred body ring formulae.

Using the female in the first row of Table 1 as an example we can argue as follows:

1. This specimen has 39 podous + 2 apodous rings and is missing defence glands on body rings 7, 10, 13, 17, 22, 27, 32 and 37.
2. Assuming that the early anamorphosis of *U. pilifer* follows the same course as in the vast majority of Julida (Enghoff et al., 1993), the first postembryonic stadium (Stadium I) will have has 4 podous + 2 apodous rings, and three pairs of legs because what is conventionally called the first podous ring paradoxically has no legs. (This assumption is supported by data from Collection D, see below).
3. Stadium II, in agreement with the "law of anamorphosis" will have 4 + 2 = 6 podous rings of which the 6th bears the first defence gland.
4. Invoking our main assumption, stadium III will have an additional 3 podous rings (nos. 7–9) of which the first (no. 7) has no defence glands. Stadium II will therefore (applying the law of anamorphosis in a reverse way) have 3 apodous rings, i.e., stadium II has the body ring formula 6 + 3.
5. Continuing arguing this way, stadium III will have 9 podous + 3 apodous rings.
6. Stadium IV will have 9 + 3 = 12 podous rings of which no. 10 is glandless, plus 4 apodous rings.
7. Stadium V will have 16 podous + 5 apodous rings, stadium VI will have 21 podous + 5 apodous rings, stadium VII will have 26 podous + 5 apodous rings, and stadium VIII will have 31 podous + 5 apodous rings.
8. Stadium IX will have 36 podous rings. Ring no. 37 is glandless, but since this is the last glandless podous ring, we cannot use the intervals between glandless rings to infer the number of apodous rings. However, since the specimen actually has 39 podous + 2 apodous rings we can infer that stadium IX will have had 3 apodous rings, and that the specimen when killed, was in stadium X.
9. Using the observed body ring formula 39 podous + 2 apodous rings (stadium X), stadium XI (which was never reached by this individual) would have had 39 + 2 = 41 podous rings.

Table 1
Ussuriiulus pilifer, collection A: missing gland patterns. Explanation by example: The female in the first row is missing defence glands on body rings nos. 7, 10, 13, 17, 22, 27, 32, and 37, and has 39 podous + 2 apodous rings.

Sex	Body rings with missing defence glands								Observed nos. of podous + apodous rings
♀	7	10	13	17	22	27	32	37	39 + 2
♂	7	10	13	18	23	29	35		39 + 2
♀	7	10	13	18	23				28 + 5
♀	7	10	14	17	22	28	33	39	41 + 2
♀	7	10	14	18					23 + 5
♀	7	10	14	18					22 + 5
♀	7	10	14	18	23				28 + 5
♂	7	10	14	18	23	28	33	38	40 + 2
♂	7	10	14	18	23	28	34		38 + 2
♀	7	10	14	18	23	29			34 + 5
♀	7	10	14	18	23	29			32 + 4
♀	7	10	14	18	23	29			33 + 5
♂	7	10	14	18	23	29	34	38	42 + 2
♂	7	10	14	18	23	29	34	39	41 + 2
♂	7	10	14	18	23	29	34	39	41 + 3
♂	7	10	14	18	24	30	35	40	42 + 2
♂	7	10	14	19	24	29	34	40	42 + 2
♀	7	10	14	19	24	29	35	40	42 + 2
♀	7	10	14	19	24	30	36	40	42 + 3
♂	7	10	14	19	25	31	37		40 + 4

Table 2 shows inferred body ring formulae for the same specimens as those in Table 1 (Collection A).

On Fig. 5, the *inferred* body ring formulae are compared with those observed on specimens in collections C and D. *Observed* formulae from collection A are not included in order to ensure independence of the two datasets. The agreement seems to be fine, which supports the main assumption. Ring formulae belonging (by inference) to the same developmental stadium are encircled. In order to test the assumption, the chi-square statistic was computed based on contingency tables comparing observed and inferred numbers of podous rings in stadia V-VIII (for these stadia, observed ring formulae for more than 20 individuals were available), assuming that the glandless rings are the first, second or third in a newly added series. Examples of the contingency tables are shown in Table 3, and the resulting chi-square values are shown in Table 4. The higher the chi-square value, the higher the probability that observed and inferred numbers differ. The entries in the contingency tables are generally too low for interpreting chi-square in terms of probability – therefore only the chi-square values themselves are shown. The values are always lowest for, and therefore support the main assumption. The opposite explanation (cf. comparison with the millipede order Polydesmida

Table 2

Ussuriiulus pilifer, collection A: body ring formulae inferred from missing gland patterns (from Table 1). Green shading: observed formula. Red bold numbers and pink shading: inferred from observed formula. Ranges of inferred numbers of body rings do not include the hypothetical stadia following the observed ones, nor the inferred numbers of apodous rings of the stadium preceding the observed ones.

inferred stadium:	II	III	IV	V	VI	VII	VIII	IX	X	XI
no. of podous rings observed	-	-	-	-	22-23	27-28	32-34	38-40	39-42	-
no. of podous rings inferred	6	9	12-13	16-18	21-24	26-30	31-36	36-39	41-43	42-45
no. of apodous rings observed	-	-	-	-	5	5	4-5	2-3	2-3	-
no. of apodous rings inferred	3	3-4	3-5	5-6	5-6	5-6	4-6	3-5	-	-
♀	6 + 3	9 + 3	12 + 4	16 + 5	21 + 5	26 + 5	31 + 5	36 + **3**	39 + 2	41 + ?
♂	6 + 3	9 + 3	12 + 5	17 + 5	22 + 6	28 + 6	34 + **5**	39 + 2	41 + ?	
♀	6 + 3	9 + 3	12 + 5	17 + 5	22 + **6**	28 + 5	33 + ?			
♀	6 + 3	9 + 4	13 + 3	16 + 5	21 + 6	27 + 5	32 + 6	38 + **3**	41 + 2	43 + ?
♀	6 + 3	9 + 4	13 + 4	17 + **6**	23 + 5	28 + ?				
♀	6 + 3	9 + 4	13 + 4	17 + **5**	22 + 5	27 + ?				
♀	6 + 3	9 + 4	13 + 4	17 + 5	22 + **6**	28 + 5	33 + ?			
♂	6 + 3	9 + 4	13 + 4	17 + 5	22 + 5	27 + 5	32 + 5	37 + **3**	40 + 2	42 + ?
♂	6 + 3	9 + 4	13 + 4	17 + 5	22 + 5	27 + 6	33 + **5**	38 + 2	40 + ?	
♀	6 + 3	9 + 4	13 + 4	17 + 5	22 + 6	28 + **6**	34 + 5	39 + ?		
♀	6 + 3	9 + 4	13 + 4	17 + 5	22 + 6	28 + **4**	32 + 4	36 + ?		
♀	6 + 3	9 + 4	13 + 4	17 + 5	22 + 6	28 + **5**	33 + 5	38 + ?		
♂	6 + 3	9 + 4	13 + 4	17 + 5	22 + 6	28 + 5	33 + 4	37 + **5**	42 + 2	44 + ?
♂	6 + 3	9 + 4	13 + 4	17 + 5	22 + 6	28 + 5	33 + 5	38 + **3**	41 + 2	43 + ?
♂	6 + 3	9 + 4	13 + 4	17 + 5	22 + 6	28 + 5	33 + 5	38 + **3**	41 + 3	44 + ?
♂	6 + 3	9 + 4	13 + 4	17 + 6	23 + 6	29 + 5	34 + 5	39 + **3**	42 + 2	44 + ?
♂	6 + 3	9 + 4	13 + 5	18 + 5	23 + 5	28 + 5	33 + 6	39 + **3**	42 + 2	44 + ?
♀	6 + 3	9 + 4	13 + 5	18 + 5	23 + 5	28 + 6	34 + 5	39 + **3**	42 + 2	44 + ?
♀	6 + 3	9 + 4	13 + 5	18 + 5	23 + 6	29 + 6	35 + 4	39 + **3**	42 + 3	45 + ?
♂	6 + 3	9 + 4	13 + 5	18 + 6	24 + 6	30 + 6	36 + **4**	40 + 3	43 + ?	

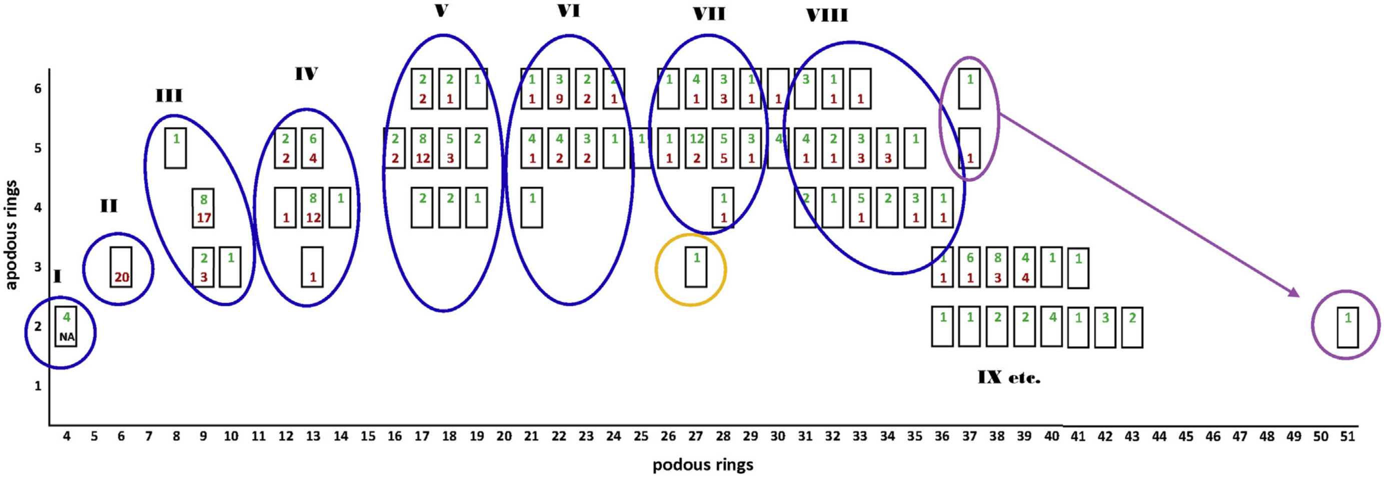


Fig. 5. *Ussuriiulus pilifer*, body ring formulae (horizontal axis: podous rings, vertical axis: apodous rings). Entries are numbers of individuals in which a given ring formula has been observed (green numbers, collections C and D) or inferred (red numbers, collection A). Example: The formula 22 podous + 6 apodous rings was observed in three individuals and inferred in nine. Formulae belonging to inferred stadia I-VIII are encircled in blue. "Outliers", encircled in purple or orange, are discussed in the text. (For interpretation of the references to color/colour in this figure legend, the reader is referred to the Web version of this article.)

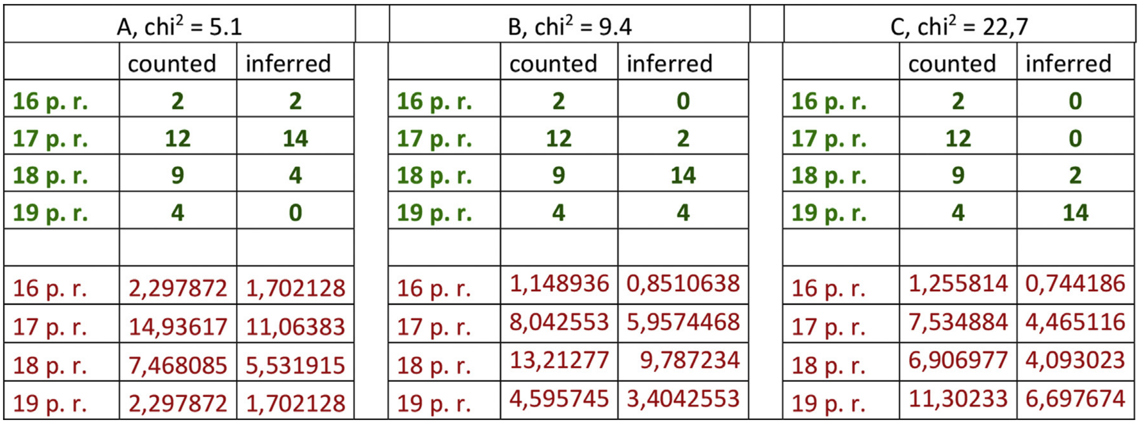
in discussion), viz., that the glandless rings are the *last* in a newly added series, would require that the last podous ring would be glandless which was never the case in any of the studied specimens in collections A (and B). Similarly, if the glandless rings would be the second-last in a series, we would accordingly expect always to find that the second-last podous ring would be glandless, which also was never seen.

No difference in observed and inferred numbers of rings between males and females was detected. In many julidan millipede species males do not undergo further moults after having attained sexual maturity, while females may continue moulting and thus reach higher body ring numbers. Whether this is true of *U. pilifer* is unknown, but the largest female in our material (51 + 2 rings) is not markedly larger than the holotype male which has 47 rings including apodous rings and possibly telson (the ring formula used by Golovatch (1980) is not quite clear about this). In any case, some of the body ring formulae of the form N + ? in Table 2, inferred to follow the observed formula by means of the law of anamorphosis, may never exist because the specimen used to infer them would have died without moulting.

A few specimens seem to fall outside the general pattern of formulae. There are two specimens with 37 podous + 5 (inferred) or 6 (observed) apodous rings which is more than normal for specimens with so many podous rings. These specimens serve to underline the high degree of variation in julidan anamorphosis – perhaps they would eventually have given rise to particularly large specimens, such as the one observed with 51 + 2 rings (Fig. 5)? A specimen with 27 + 3 rings may be an example of the opposite extreme. Some of the observed formulae in (inferred) stadium III (8 podous + 5 apodous rings, 10 podous + 3 apodous rings) lie outside the inferred range; however both these formulae would result in 13 podous rings in stadium IV, and this is the most frequently observed number of podous rings in that stadium.

In order to get a general overview over variations in the course of anamorphosis, as inferred by data from collection A, ring formulae for each individual have been combined in a branching

Table 3
Ussuriiulus pilifer, contingency tables comparing counted (collections C and D) and inferred (collection A) numbers of podous body rings in the range of 16–19 podous rings (inferred stadium V). "Counted" and "inferred" numbers (green, bold) are the "observed" values", "expected" values as used in the chi-square computation are shown in red. A. Assuming that glandless rings are the first in a newly added series (main assumption). B. Assuming that glandless rings are the second in a newly added series. C. Assuming that glandless rings are the third in a newly added series.



A, chi^2 = 5.1				B, chi^2 = 9.4				C, chi^2 = 22,7		
	counted	inferred			counted	inferred			counted	inferred
16 p. r.	**2**	**2**		**16 p. r.**	**2**	**0**		**16 p. r.**	**2**	**0**
17 p. r.	**12**	**14**		**17 p. r.**	**12**	**2**		**17 p. r.**	**12**	**0**
18 p. r.	**9**	**4**		**18 p. r.**	**9**	**14**		**18 p. r.**	**9**	**2**
19 p. r.	**4**	**0**		**19 p. r.**	**4**	**4**		**19 p. r.**	**4**	**14**
16 p. r.	2,297872	1,702128		16 p. r.	1,148936	0,8510638		16 p. r.	1,255814	0,744186
17 p. r.	14,93617	11,06383		17 p. r.	8,042553	5,9574468		17 p. r.	7,534884	4,465116
18 p. r.	7,468085	5,531915		18 p. r.	13,21277	9,787234		18 p. r.	6,906977	4,093023
19 p. r.	2,297872	1,702128		19 p. r.	4,595745	3,4042553		19 p. r.	11,30233	6,697674

Table 4
Ussurriiulus pilifer, values of chi-square computed from counted (collections C and D) and inferred (collection A) numbers of podous rings in inferred stadia V-VIII under the assumption that the glandless rings are the first in newly added series of podous rings, as well as under the assumptions that the glandless rings are the second or third in such series. Individuals with 25, 30 and 36 counted podous rings have been omitted, as these may belong to either of two stadia.

Range of podous rings	Inferred stadium	Number of specimens	Glandless rings = 1^{st} in series	Glandless rings = 2nd in series	Glandless rings = 3rd in series
16–19	V	27	5.1	9.4	22.7
21–24	VI	21	3.8	29.5	15.7
26–29	VII	30	5.6	15.1	8.3
31–35	VIII	28	3.8	7.2	5.7

diagram (Fig. 6) similar to those constructed by, e.g., Voigtländer (1987) and Enghoff et al. (2009). It is important to bear in mind, however, that the transitions from one stadium to the next (each transition corresponding to a moult) shown in Table 2 and Fig. 6 have all been inferred to occur in an actual specimen, whereas the diagram in Enghoff et al. (2009) is based exclusively on transitions inferred by matching ring formulae of different individuals, and the diagrams in Voigtländer (1987) are based on a combination of observations on individuals kept in captivity, and analysis of defence gland series in field-collected material.

In the diagram, Fig. 6, identical sequences of formulae have been combined, meaning that, unlike in Table 2, the history of each individual cannot be traced while on the other hand more than one observed formula may occur along a sequence. Notice that a given formula may result from different developmental histories. For example, the formula 17 + 5 may derive from 13 + 4 or from 12 + 5.

3.3. Growth history of *Koiulus interruptus*

Table 5 lists the specimens of *K. interruptus* in collection B, their sex, their observable body ring formula, and the body rings from which the defence glands are missing.

Glands are lacking from rings 7 and 11 in all specimens. This is a constant difference from *U. pilifer* where glands are always lacking

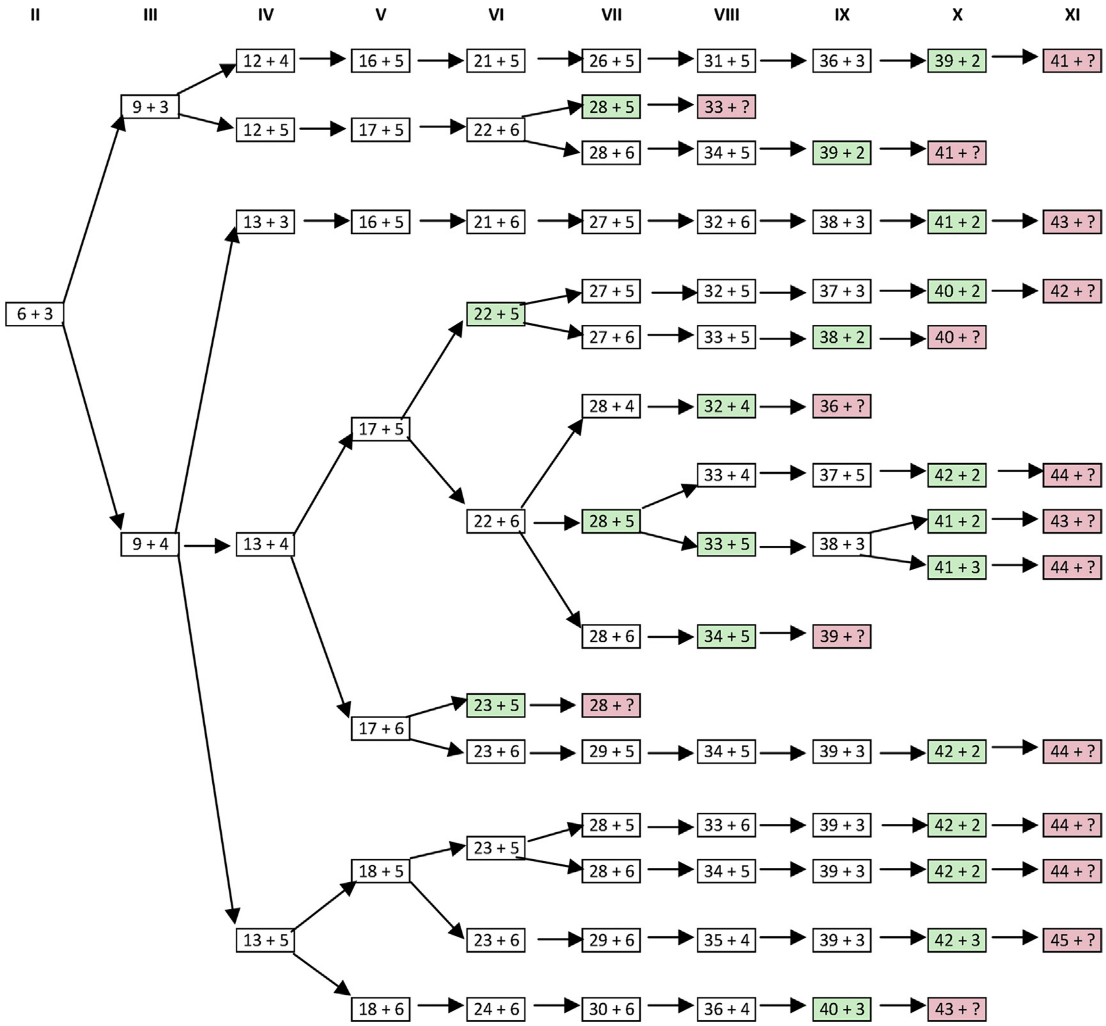


Fig. 6. *Ussuriiulus pilifer* (collection A), the course of anamorphosis as inferred by the missing gland method, combined with the law of anamorphosis. Formulae in boxes are number of podous rings + number of apodous rings. Green shading: observed formulae. Red shading: formulae of the form N + ? inferred by means of the law of anamorphosis. (For interpretation of the references to color/colour in this figure legend, the reader is referred to the Web version of this article.)

from rings 7 and 10. Further back on *K. interruptus* glands are lacking from ring 14 *or* 15, from ring 17 *or* 18 *or* 19 *or* 20, from ring 22 *or* 23 *or* 24 *or* 25 *or* 26, etc.

Based on the line of argument detailed above under *U. pilifer*, successive body ring formulae can be inferred from the patterns of missing glands. Table 6 shows the body ring formulae inferred through this approach for the same specimens as those in Table 5 (collection B). Fig. 7 illustrates the observed and inferred ring formulae in collection B; notice that in this case, observed and inferred formulae derive from the same specimens, unlike Fig. 5 (*U. pilifer*).

In the case of *K. interruptus* we had no independent samples to compare with; however, the body ring formulae observed in collection B seem to agree with the inferred ones from the same collection, just as well as in *U. pilifer* (compare Figs. 5 and 7).

No difference in observed and inferred numbers of rings between males and females was detected, and there is no marked difference in the maximum number of body rings in both sexes. In any case, some of the body ring formulae of the form N + ? inferred to follow the observed formula by means of the law of anamorphosis, e.g., 49 + ?, which is the highest inferred number, may never exist because the specimen used to infer them would have died without moulting.

Data from each individual have been combined in a branching diagram (Fig. 8), as for *U. pilifer* (Fig. 5). Also in *K. interruptus* a given formula may have different histories. For example, the formula 18 + 5 may derive from 13 + 5 or from 14 + 4.

4. Discussion

The analysis presented above is contingent upon the main assumption: that the glandless body rings are the first in a series added during a moult. Three lines of evidence support the main assumption:

1. There is agreement between observed and inferred body ring formulae.
2. The fact that the last (and second-last) podous rings are never glandless excludes the opposite hypothesis: that the glandless rings are the last (or second-last) rings in a series.

Table 5

Koiulus interruptus, collection B, missing gland patterns. Explanation by example: The juvenile male in the first row was missing defence glands on body rings nos. 7, 11, 14, 17, 22 and 26 and had 31 podous + 5 apodous rings.

Sex	Body rings with missing defence glands									Observed nos. of podous + apodous rings
juv. ♂	7	11	14	17	22	26				31 + 5
♀	7	11	14	18	22	28				33 + 4
♀	7	11	14	18	23	28	32	38		42 + 3
♀	7	11	14	18	23	28	33	38		40 + 2
♀	7	11	14	18	23	28	33			37 + 3
juv. ♂	7	11	14	18	23	28				33 + 4
♀	7	11	14	18	23	28				32 + 5
♀	7	11	14	19	23	27	32			36 + 4
♀	7	11	14	19	23	28				31 + 4
juv. ♂	7	11	14	19	23	29				34 + 4
♂	7	11	14	19	24	29	34			38 + 3
♂	7	11	14	19	24	29	34			38 + 4
juv. ♂	7	11	14	19	24	30	35			39 + 3
juv. ♂	7	11	14	19	24					27 + 5
♀	7	11	14	19	24					28 + 5
♀	7	11	15	19						25 + 5
juv. ♂	7	11	15	19	22	26	32	37		40 + 2
♀	7	11	15	19	23	28	34			38 + 4
♀	7	11	15	19	24	29	34	39		42 + 3
♂	7	11	15	19	24	29	34	39		43 + 2
♂	7	11	15	19	24	29	34	39		42 + 3
♀	7	11	15	19	24	29	34	38		41 + 1
♀	7	11	15	19	24	29	35			39 + 2
♀	7	11	15	19	24					29 + 4
juv. ♂	7	11	15	19	24					28 + 5
♂	7	11	15	19	24	30	36			40 + 2
juv. ♂	7	11	15	19	24	30				35 + 3
♀	7	11	15	19	25	31				36 + 4
♀	7	11	15	19	25					30 + 7
♀	7	11	15	20						24 + 5
♀	7	11	15	20	24	29	34	39		42 + 3
♀	7	11	15	20	24	28	33	38	43	45 + 1
juv. ♂	7	11	15	20	24					29 + 5
♀	7	11	15	20	25					30 + 4
♀	7	11	15	20	25	30	36	42		46 + 3
juv. ♂	7	11	15	20	25	30	36			40 + 4
♀	7	11	15	20	25	30	36			39 + 3
♀	7	11	15	20	25	30				35 + 4
♀	7	11	15	20	25	31				35 + 4
♂	7	11	15	20	25	31	36			40 + 3
juv. ♂	7	11	15	20	25	31				35 + 4
juv. ♂	7	11	15	20	25	31				35 + 4
♀	7	11	15	20	25	28				30 + 5
♀	7	11	15	20	25					29 + 5
♀	7	11	15	20	26	32				37 + 4
juv.	7	11								14 + 6

Table 6
Koiulus interruptus, collection B, body ring formulae inferred from missing gland patterns (From Table 5). Green shading: observed formula. Red bold numbers and pink shading: inferred from observed formula. Inferred numbers of body rings do not include the hypothetical stadia following the observed ones, nor the inferred numbers of apodous ring of the stadium preceding the observed ones.

inferred stadium:	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
no. of podous rings observed	-	-	14	-	24-25	27-30	31 - 37	36 - 40	40 - 46	45	
no. of podous rings inferred	6	10	13-14	16-19	21-25	25-31	31-35	36-41	42	-	
no. of apodous rings observed	-	-	6	-	5	4-7	3-5	2-4	1-3	-	
no. of apodous rings inferred	4	3-4	3-5	4-6	4-6	4-6	5-6	5	-		
juv. ♂	6 + 4	10 + 3	13 + 3	16 + 5	21 + 4	25 + **6**	31 + 5	36 + ?			
♀	6 + 4	10 + 3	13 + 4	17 + 4	21 + 6	27 + **6**	33 + 4	37 + ?			
♀	6 + 4	10 + 3	13 + 4	17 + 5	22 + 5	27 + 4	31 + 6	37 + **5**	42 + 3	45 + ?	
♀	6 + 4	10 + 3	13 + 4	17 + 5	22 + 5	27 + 5	32 + 5	37 + **3**	40 + 2	42 + ?	
♀	6 + 4	10 + 3	13 + 4	17 + 5	22 + 5	27 + 5	32 + **5**	37 + 3	40 + ?		
juv. ♂	6 + 4	10 + 3	13 + 4	17 + 5	22 + 5	27 + **6**	33 + 4	37 + ?			
♀	6 + 4	10 + 3	13 + 4	17 + 5	22 + 5	27 + **5**	32 + 5	37 + ?			
♀	6 + 4	10 + 3	13 + 5	18 + 4	22 + 4	26 + 5	31 + **5**	36 + 4	40 + ?		
♀	6 + 4	10 + 3	13 + 5	18 + 4	22 + 5	27 + **4**	31 + 4	35 + ?			
juv. ♂	6 + 4	10 + 3	13 + 5	18 + 4	22 + 6	28 + **6**	34 + 4	38 + ?			
♂	6 + 4	10 + 3	13 + 5	18 + 5	23 + 5	28 + 5	33 + **5**	38 + 3	41 + ?		
♂	6 + 4	10 + 3	13 + 5	18 + 5	23 + 5	28 + 5	33 + **5**	38 + 4	42 + ?		
juv. ♂	6 + 4	10 + 3	13 + 5	18 + 5	23 + 6	29 + 5	34 + **5**	39 + 3	42 + ?		
juv. ♂	6 + 4	10 + 3	13 + 5	18 + 5	23 + **4**	27 + 5	32 + ?				
♀	6 + 4	10 + 3	13 + 5	18 + 5	23 + **5**	28 + 5	33 + ?				
f	6 + 4	10 + 4	14 + 4	18 + **7**	25 + 5	30 + ?					
juv m	6 + 4	10 + 4	14 + 4	18 + 3	21 + 4	25 + 6	31 + 5	36 + **4**	40 + 2	42 + ?	
f	6 + 4	10 + 4	14 + 4	18 + 4	22 + 5	27 + 6	33 + **5**	38 + 4	42 + ?		
f	6 + 4	10 + 4	14 + 4	18 + 5	23 + 5	28 + 5	33 + 5	38 + **4**	42 + 3	45 + ?	
m	6 + 4	10 + 4	14 + 4	18 + 5	23 + 5	28 + 5	33 + 5	38 + **5**	43 + 2	45 + ?	
m	6 + 4	10 + 4	14 + 4	18 + 5	23 + 5	28 + 5	33 + 5	38 + **4**	42 + 3	45 + ?	
f	6 + 4	10 + 4	14 + 4	18 + 5	23 + 5	28 + 5	33 + 4	37 + **4**	41 + 1	42 + ?	
f	6 + 4	10 + 4	14 + 4	18 + 5	23 + 5	28 + 6	34 + **5**	39 + 2	41 + ?		
f	6 + 4	10 + 4	14 + 4	18 + 5	23 + **6**	29 + 4	33 + ?				
juv m	6 + 4	10 + 4	14 + 4	18 + 5	23 + **5**	28 + 5	33 + ?				
m	6 + 4	10 + 4	14 + 4	18 + 5	23 + 6	29 + 6	35 + **5**	40 + 2	42 + ?		
juv m	6 + 4	10 + 4	14 + 4	18 + 5	23 + 6	29 + **6**	35 + 3	38 + ?			
f	6 + 4	10 + 4	14 + 4	18 + 6	24 + 6	30 + **6**	36 + 4	42 + ?			
f	6 + 4	10 + 4	14 + 4	18 + 6	24 + **6**	30 + 7	37 + ?				
f	6 + 4	10 + 4	14 + 5	19 + **5**	24 + 5	29 + ?					
f	6 + 4	10 + 4	14 + 5	19 + 4	23 + 5	28 + 5	33 + 5	38 + **4**	42 + 3	45 + ?	
f	6 + 4	10 + 4	14 + 5	19 + 4	23 + 4	27 + 5	32 + 5	37 + 5	42 + **3**	45 + 1	46 + ?
juv m	6 + 4	10 + 4	14 + 5	19 + 4	23 + **6**	29 + 5	34 + ?				
f	6 + 4	10 + 4	14 + 5	19 + 5	24 + **6**	30 + 4	34 + ?				
f	6 + 4	10 + 4	14 + 5	19 + 5	24 + 5	29 + 6	35 + 6	41 + **5**	46 + 3	49 + ?	
juv m	6 + 4	10 + 4	14 + 5	19 + 5	24 + 5	29 + 6	35 + **5**	40 + 4	44 + ?		
f	6 + 4	10 + 4	14 + 5	19 + 5	24 + 5	29 + 6	35 + **4**	39 + 3	42 + ?		
f	6 + 4	10 + 4	14 + 5	19 + 5	24 + 5	29 + **6**	35 + 4	39 + ?			
f	6 + 4	10 + 4	14 + 5	19 + 5	24 + 6	30 + **5**	35 + 4	39 + ?			
m	6 + 4	10 + 4	14 + 5	19 + 5	24 + 6	30 + 5	35 + **5**	40 + 3	43 + ?		
juv m	6 + 4	10 + 4	14 + 5	19 + 5	24 + 6	30 + **5**	35 + 4	39 + ?			
juv m	6 + 4	10 + 4	14 + 5	19 + 5	24 + 6	30 + **5**	35 + 4	39 + ?			
f	6 + 4	10 + 4	14 + 5	19 + 5	24 + 3	27 + **3**	30 + 5	35 + ?			
f	6 + 4	10 + 4	14 + 5	19 + 5	24 + **5**	29 + 5	34 + ?				
f	6 + 4	10 + 4	14 + 5	19 + 6	25 + 6	31 + **6**	37 + 4	41 + ?			
juv	6+4	10 + **4**	14 + 6	20 + ?							

3. The chi-square statistic, in the case of *U. pilifer,* supports that the main assumption gives a better fit between inferred (collection A) and observed (collections C and D) numbers than assumptions placing the glandless rings as number 2 or number 3 in a series.
4. The inferred courses of anamorphosis for both analysed species agree with what is known from other julidan millipedes.
5. A correlation between ring increments and missing glands exists in another millipede order.

ad 4: no study on the anamorphosis of any mongoliulid species has previously been published. Our inferred "growth histories" for *U. pilifer* and *K. interruptus* can, however, be compared with published knowledge on other species of the order Julida. Enghoff et al. (1993) compiled such knowledge from many different sources and presented it in the form of 20 tables. The inferred course of anamorphosis for *K. interruptus* is particularly and remarkably similar to that of two species of Blaniulidae: *Blaniulus guttulatus* (Fabricius, 1798) and *Proteroiulus fuscus* (Am Stein, 1857), one species of Nemasomatidae: *Nemasoma varicorne* Koch, 1847, and one species of Julidae: *Brachyiulus pusillus* (Leach, 1815) (Enghoff et al., 1993: tables 29, 31, 33, 35). With (inferred) 6 + 3 rings in stadium II *U. pilifer* differs from almost all studied Julida. The exceptions are *N. varicorne* and *Nopoiulus kochii* (Gervais, 1847) (= *N. minutus* auct.) (Blaniulidae) in which individuals with 6 + 3 rings exist along with ones with 6 + 4 rings (Brookes, 1974); the 6 + 3 formula also occurs as a rare exception in *Choneiulus palmatus* (Němec, 1895) (Blaniulidae) in which Peitsalmi and Pajunen (1996) found 6 + 3 rings in 0.03% of the examined individuals. All other studied Julida invariably have 6 + 4 or 6 + 5 rings in stadium II. Apart from the 6 + 3 formula in stadium II, the inferred anamorphosis of *U. pilifer* is also fully compatible with what is known from the abovementioned other species of Julida.

ad 5: whereas a non-continuous series of defence glands is a rare exception in Julida, it is the rule in another millipede order, viz., Polydesmida. The by far most common pattern is that glands are present on rings 5, 7, 9, 10, 12, 13, 15–17(–19) (Enghoff et al., 2015). In Table 7 this gland pattern is compared with the numbers of podous rings in each postembryonic stadium of Polydesmida (Enghoff et al., 1993: table 26). It is seen that up to and including stadium V, defence glands are missing from the *last* newly added ring. As in *U. pilifer* and *K. interruptus* there is thus a correlation between gland absence and anamorphosis. It may be seen as disturbing that in Polydesmida it is the last added ring that lacks glands, not the first, but as argued above, our observations exclude the possibility that the glandless rings of the two mongoliulid species are the last in a series.

We therefore accept the main assumption: glandless body rings are the first in a series added during a moult. The "missing gland method" allows access to the growth history of each individual millipede, something that is possible otherwise only if individuals are reared, or (partly) when they have well-distinguishable series of defence glands or trans-segmental colour patterns. So far, however, the method is only applicable to *U. pilifer* and *K. interruptus*.

We have tested our assumption by comparing our inferred formulae with those observed in two large collections of *U. pilifer.* A further and stronger test would be to compare with observed formulae of successive stadia in reared individuals, but this has so far not been possible.

During the course of anamorphosis of a millipede, the number of new body rings (or leg-pairs) added during a moult normally shows an initial increase and then usually a gradual decrease as the animal grows older (Enghoff et al., 1993: fig. 35). Figs. 5 and 7 show that this is clearly the case in *U. pilifer* and *K. interruptus*. In *U. pilifer* (Fig. 5) the number of apodous rings converges on 2 towards the end of anamorphosis, as was found by Sahli (1972) in the Blaniulidae. In *K. interruptus* (Fig. 7) the pattern is less clear, 1, 2 and 3 apodous rings being all represented among the highest observed formulae.

Minelli (2015) reviewed what is known about developmental genetics of millipedes, but the genetic basis of millipede

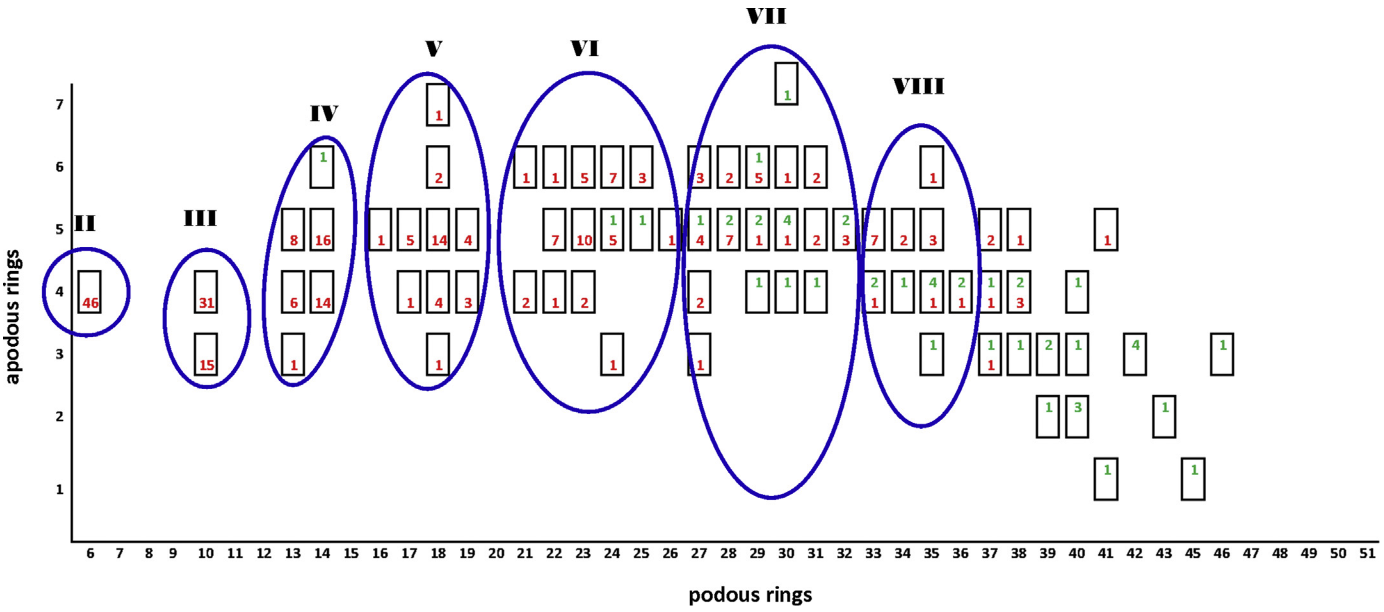


Fig. 7. *Koiulus interruptus*, collection B, body ring formulae (horizontal axis: podous rings, vertical axis: apodous rings). Entries are numbers of individuals in which a given ring formula has been observed (green numbers) or inferred (red numbers). Example: The formula 24 podous + 5 apodous rings was observed in one individual and inferred in five. Formula belonging to inferred stadia II-VIII are encircled in blue. (For interpretation of the references to color/colour in this figure legend, the reader is referred to the Web version of this article.)

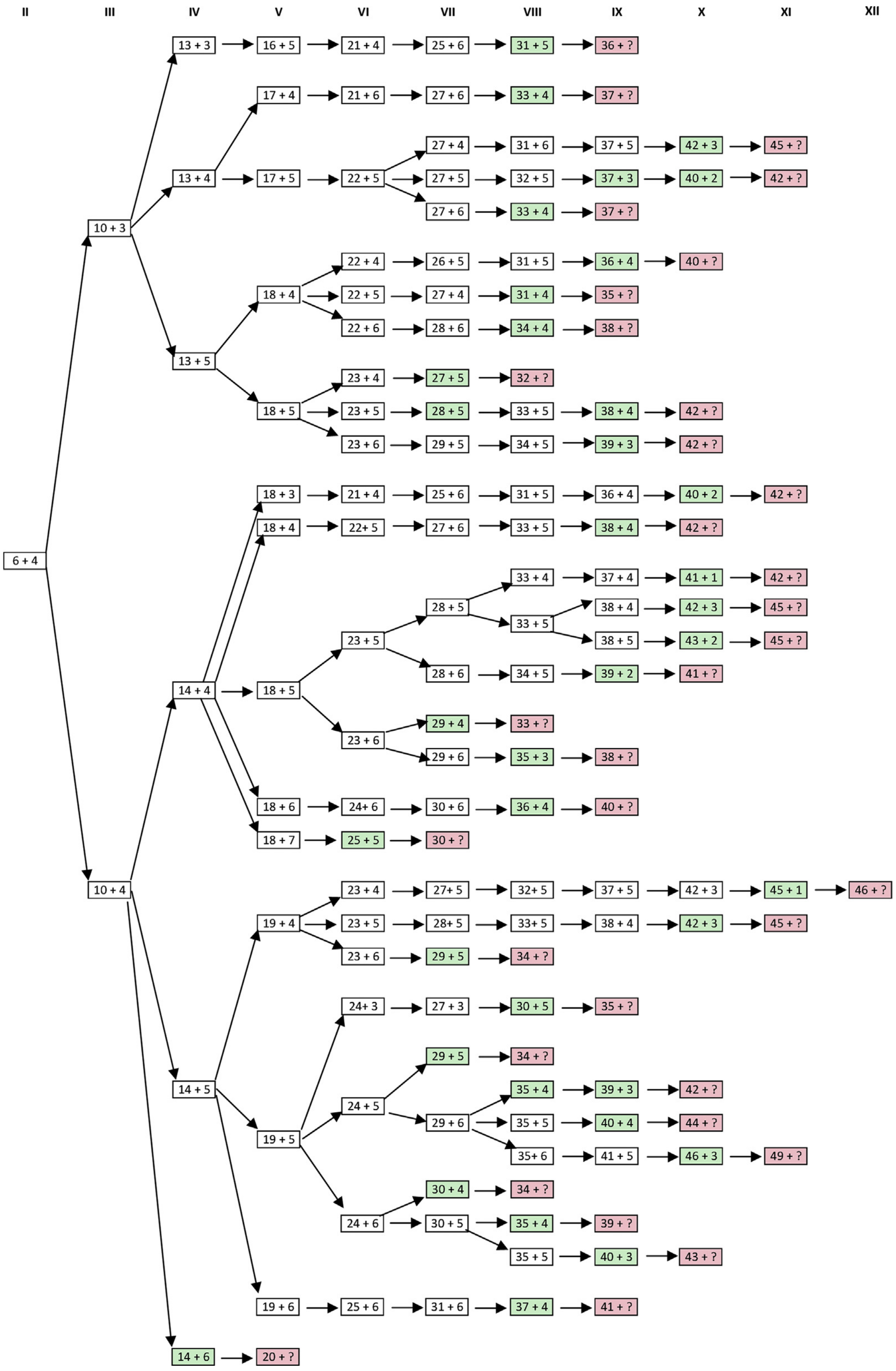


Fig. 8. *Koiulus interruptus* (collection B), the course of anamorphosis as inferred by the missing gland method, combined with the law of anamorphosis. Formulae in boxes are number of podous rings + number of apodous rings. Green shading: observed formulae. Red shading: formulae of the form N + ? inferred by means of the law of anamorphosis. (For interpretation of the references to color/colour in this figure legend, the reader is referred to the Web version of this article.)

Table 7
Comparison of defence gland sequences and ring increments in Polydesmida. Based on data from Enghoff et al. (1993, 2015). The table shows the by far commonest pattern in Polydesmida where the majority of species have 18 podous rings + 1 apodous ring.

Ring number	Defence glands	Last podous ring in series added in stadium N
1	missing	
2	missing	
3	missing	
4	missing	stadium I
5	+	
6	missing	stadium II
7	+	
8	missing	stadium III
9	+	
10	+	
11	missing	stadium IV
12	+	
13	+	
14	missing	stadium V
15	+	
16	+	stadium VI
17	+	stadium VII
18	+	stadium VIII

anamorphosis remains incompletely understood. Akkari et al. (2014) discussed a developmental model, developed by Minelli and Bortoletto (1988) and Minelli (2001), according to which the segmentation of arthropods is due to multiple duplications of segmental units; according to Akkari et al. (2014), this model can explain “discrete multisegmental patterns due to early positional markers”. The authors mentioned the trans-segmental colour patterns described by Enghoff (2011) as an example of such patterns. The “missing defence gland patterns” described in the present article is another example.

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