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Original paper

Developmental and post-embryonic growth patterns in *Longidorus piceicola* Lišková, Robbins & Brown, 1997 and *L. intermedius* Kozlowska & Seinhorst, 1979 (Nematoda: Dorylaimida)

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Summary. Based solely on molecular markers, D-D3 28R rDNA and ITS1, *Longidorus intermedius* and *L. piceicola* share a high level of similarity. However, despite this molecular similarity, *L. piceicola* and *L. intermedius* significantly differ in morphometrics and ontogeny. Two key concepts in the development and growth of longidorid nematodes are developmental and growth patterns. Developmental patterns categorize longidorid nematodes according to whether they undergo four or three juvenile developmental stages (JDS) during post-embryonic development. Growth patterns refer to specific morphometric levels, which are more or less similar between species within a genus with the same developmental pattern. There are some differences between different populations of the same species, probably due to intraspecific variability and the environmental conditions in which they live. *Longidorus piceicola* undergoes four JDS, while *L. intermedius* undergoes three JDS. In the typical life cycle of longidorid nematodes, there are four or three molts, which occur between the four or three JDS, with the last molt preceding the fully sexually mature adult stage. The similarities and differences between these two developmental patterns are not well known. Growth patterns refer to changes in specific morphometric dimensions during the post-embryonic growth of a nematode, such as: body length, odontostyle and replacement odontostyle size, and body volume. Using these characteristics, a study was conducted to assess whether there are similarities or differences between selected populations of *Longidorus piceicola* (4 JDS) and *L. intermedius* (3 JDS). This paper presents results on the developmental and post-embryonic growth patterns of the species *Longidorus piceicola* and *L. intermedius*.

Keywords: developmental patterns, growth patterns, juvenile stages, Longidoridae, morphometrics, ontogeny.

INTRODUCTION

He et al. (2005), in a work dedicated to the phylogeny of the entire family Longidoridae, first noted that based on molecular markers, *Longidorus intermedius* shows great similarity to *L. piceicola*. Although this work was based only on the D-D3 28R rDNA marker, the authors did not add any additional comments. Subsequently, Kornobis (2013) and Groza et al. (2017) found that the difference between molecular markers (p-distance) was only 0.3% and 0.3-0.9%, respectively. Additionally, Kornobis (2013) found that the difference between the two species based on the ITS1 marker was 1.4%. Such low differences are usually interpreted as intraspecific variation, rather than as a unique feature of different species.

Despite their similarity based on comparison of specific molecular markers, *L. piceicola* and *L. intermedius* display significant morphometric and ontogenic differences. *Longidorus piceicola* undergoes four juvenile developmental stages (JDS) (Liskova et al. 1997, Barsi and Lamberti, 2001; Kornobis and Peneva, 2011; Groza et al. 2017; Barsi 2022), while

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L. intermedius undergoes three JDS (Peneva et al. 2001; Barsi and Lamberti 2004; Kumari et al. 2006; Susulovska and Tsaryk 2018).

During a typical life-cycle, longidorid nematodes undergo four or three molts, which occur between the four or three juvenile developmental stages (JDS), respectively, with the final molt preceding full sexual maturity (Halbrendt and Brown 1992, 1993; Halbrendt et al. 1997). Although the presence of four or three JDS is a characteristic of the two developmental patterns present in Longidoridae; similarities and differences between these two developmental patterns are not well known. Yeates and Boag (2002) used a volumetric base for comparison of the successive stages of Longidoridae, in order to define post-embryonic growth patterns in longidorid nematodes. They concluded that within the Longidoridae there was generally a larger increase in body volume between the first two juvenile stages. Unfortunately, their results do not give a clear picture of the basic similarities and differences between the two developmental patterns obviously present in Longidoridae.

Two important concepts in the development and growth of longidorid nematodes are developmental patterns and growth patterns (growth strategy). In longidorid nematodes, developmental patterns are dictated by the presence of either four or three JDS during post-embryonic development. Growth patterns are defined by specific morphometric levels, which are more or less similar between species within a genus with the same developmental pattern. There are some differences between different populations of the same species, probably due to intraspecific variability and the environmental conditions in which they live. Growth patterns describe the post-embryonic growth of a nematode, and defined as changes in certain measurable morphometric parameters, such as: body length, odontostyle and replacement odontostyle length, and body volume. Using these characteristics, a study was conducted to assess whether there are similarities or differences between selected populations of *L. piceicola* (4 JDS) and *L. intermedius* (3 JDS).

The present study presents results on the developmental and postembryonic growth patterns of the species *L. piceicola* and *L. intermedius*.

MATERIAL AND METHODS

The present study was based on published data for 6 populations of *L. piceicola* and 4 populations of *L. intermedius* (Table 1). For each population, the following data were used: mean body length, odontostyle and replacement odontostyle lengths and body diameter for each developmental stage (all in μm). Body length and body diameter were used to calculate the body volume at every stage, using the empirical equation of Andrássy (1956): $V = W^2 \times L/1.7$, where W is the body diameter and L is the body length in μm. These data were tabulated for each population/species, and used for further calculations.

A percentage method was used to ensure that the data sets are comparable between each other for every population of both species. Absolute data for females (body and odontostyle length in μm and calculated body volume in μm^3) were defined as 100%. The same data set for each juvenile stage was then compared to the female data set and expressed as a percentage. The only exception was the replacement odontostyle length; where the absolute value of the replacement odontostyle length in the pre-adult stage (J4 or JIII, respectively) was defined as 100% for the comparisons.

The percent values for each stage of each population/species were tabulated and the mean value, standard deviation, minimum and maximum values were calculated for

Table 1. List and sources of data for linear dimensions of 6 populations of *Longidorus piceicola* and 4 populations of *L. intermedius*.

Longidorus species	Reference
L. piceicola[1]*	[1]Montenegro, Durmitor [1]Barsi and Lamberti 2011
L. piceicola[2]	[2]Kopaonik [2]Barsi 2022
L. piceicola[3]	[3]Slovakia [3]Lišková et al. 1997
L. piceicola[4]	[4]Romania, Bran population [4]Groza et al. 2017
L. piceicola[5]	[5]Poland [5]Kornobis and Peneva 2011
L. piceicola[6]	[6]Romania, Cernica [6]Groza et al. 2017
L. intermedius[7]**	[7]Serbia [7]Barsi and Lamberti 2004
L. intermedius[8]	[8]Bulgaria, Dedevo-Rhodopi [8]Peneva et al. 2001
L. intermedius[9]	[9]Czech Republic [9]Kumari et al. 2006
L. intermedius[10]	[10]Ukraine, Ustia, [10]Susulovska and Tsaryk 2018

**Longidorus piceicola* has 4 juvenile developmental stages (JDS); ***L. interemdius* has 3 JDS.

each character studied. Also, using percent values for each stage, the relative increase in the analyzed morphometric characters between successive stages were calculated for each population/species.

Analyses were conducted at the species level (intra-generic), separately for the populations of *L. piceicola* and *L. intermedius*, respectively.

RESULTS AND DISCUSSION

A comparison of selected characteristics of 6 populations of *L. piceicola* with 4 JDS, and 4 populations of *L. intermedius* with 3 JDS, revealed the presence of specific basic similarities and differences between these two species.

The final data sets used in the present study are presented in Tables 2 and 3. Analyses of these data sets were conducted at the species (intra-generic) level. However, it must be strongly emphasized that these average values provide only an average picture of the relationships present between these species.

Body length (Fig. 1A, B)

Based on results for the analyzed data from the studied populations, it appears that in *L. intermedius*, body lengths for the JI, JII, and JIII stages are greater than the body lengths in the corresponding J1, J2, and J3 stages in *L. piceicola*. In general, in *L. intermedius,* the body length during JI is 1.2 times that of the body length of *L. piceicola* during J1, JII is 1.29 times that of J2, and JIII is 1.31 times that of J3, for *L. intermedius* vs. *L. piceicola*. -

Although inclusion of additional populations of both species would certainly affect the numerical values obtained, the trends would be expected to remain the same.

Using the percentage body lengths for each stage, the relative increase from stage to stage was calculated for each species (Tables 2 and 3). The sum of the relative increases between successive stages is lower in L. *intermedius* (4.42) than in *L. piceicola* (5.62). This also supports the observation that for *L. intermedius*, specimens in stages JI, JII and JIII generally have a longer body length than *L. piceicola* specimens in stages J1, J2 and J3. Therefore, *L. intermedius* nematodes can probably reach maturity more quickly, through only three molts.

Body volume (Fig. 2A, B)

It is known that *L. intermedius* reaches maturity through 3 JDS and *L. piceicola* through 4 JDS, which represent two different developmental patterns. Based on the results of the analyzed data from the studied populations, it appears that the body volumes during stages JI, JII and JIII in *L. intermedius* are larger than the body volumes in the corresponding stages J1, J2 and J3 in *L. piceicola*. In general, the body volume during JI for *L. intermedius* is 1.17 times the body volume during J1 for *L. piceicola*, while JII is 1.45 times the volume of J2, and JIII is 1.51 times the volume of J3 for *L. intermedius* vs. *L. piceicola*, respectively.

Body volume is a useful metric for describing processes during postembryonic development in nematodes, but it should be used with caution, especially when comparing different populations of the same species or other species, and for drawing conclusions. Body volume depends on body length and width. Unlike body length, body width may be more affected by flattening during the mounting process. Therefore, uncritical use of published data may lead to erroneous conclusions.

Including additional populations of both species would certainly affect the numerical values obtained, but the trends would be expected to remain the same.

Using percent body volumes for each stage, the relative increase from stage to stage was calculated for each species (Tables 2 and 3). The sum of the relative increases between successive stages was lower in *L. intermedius* (7.99) than in *L. piceicola* (8.84).

This also supports the results that *L. intermedius* specimens in stages JI, JII and JIII generally have a larger body volume than corresponding *L. piceicola* specimens in stages J1, J2 and J3.

Odontostyle length (Fig. 3A, B)

In *L. intermedus*, specimens in stages JI, JII and JIII generally have a 1.14, 1.12 and 1.11 fold longer odontostyle than corresponding *L. piceicola* specimens in stages J1, J2 and J3 (Fig. 3A). These JDSs are not directly comparable to each other (Tables 2 and 3). However, comparison of specimens in stages JI, JII, and JIII with specimens in stages J2, J3, and J4, respectively, reveals a very similar and comparable growth pattern (Fig. 3B).

The odontostyle in JI is 1.67% longer than in J2, while in JII it is 4.02% shorter than in J3 and in JIII it is 2.06% shorter than in J4. Due to its longer odontostyle in the JI stage, *L. intermedus* can probably reach its final odontostyle length more quickly after only three molts.

Including additional populations of both species would certainly affect the numerical values obtained, but the trends would be expected to remain the same.

Using percent odontostyle lengths for each stage, the relative increase from stage to stage was calculated for both species (Tables 2 and 3). The sum of the relative increases between successive stages was smaller for *L. intermedius* (3.43) than for *L. piceicola* (4.57).

This also supports the observation that *L. intermedius*

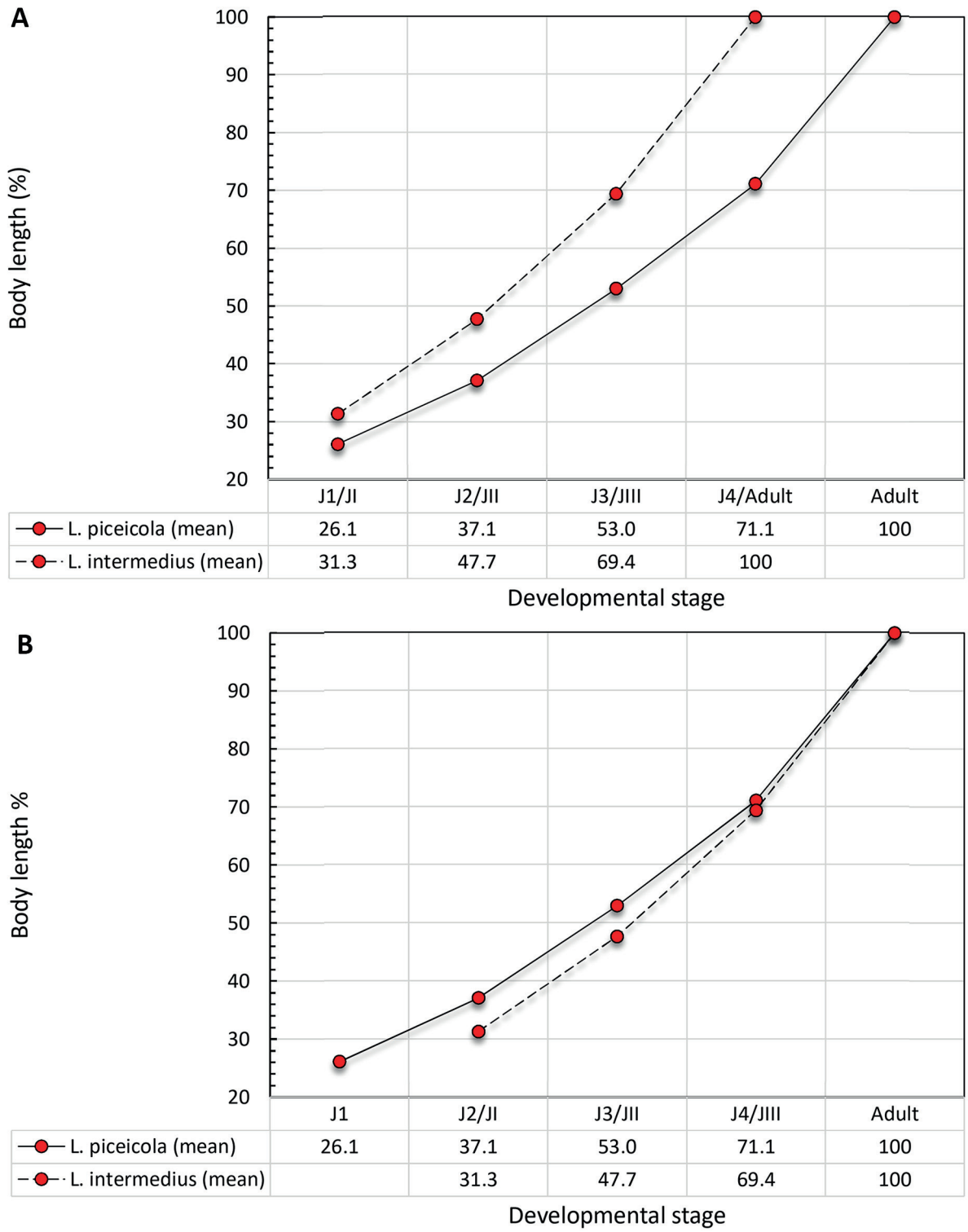


Fig. 1. Comparison of body length growth patterns in 6 populations of *Longidorus piceicola* and 4 populations of *L. intermedius*.

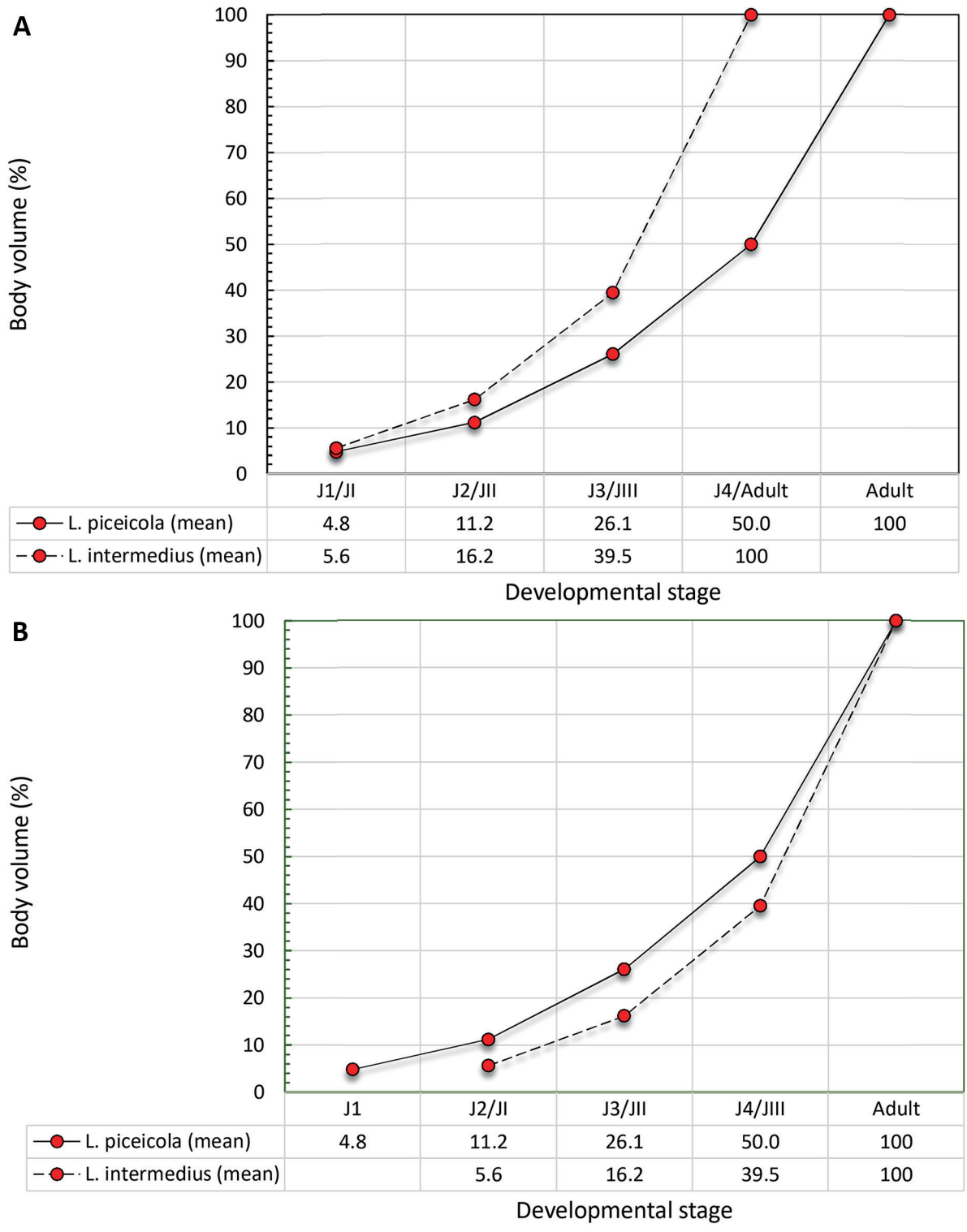


Fig. 2. Comparison of body volume growth patterns in 6 populations of *Longidorus piceicola* and 4 populations of *L. intermedius*.

Table 2. Growth patterns of the body length, body volume, odontostyle length and replacement odontostyle length and relative increase in the body length, body volume, odontostyle length and replacement odontostyle length between successive stages in six populations of *Longidorus piceicola**.

	Growing patterns						Relative increase				
L%	**J1**	**J2**	**J3**	**J4**	**F**	**L µm**	**J2/J1**	**J3/J2**	**J4/J3**	**F/J4**	**Sum**
L. piceicola[1]	26.2	38.7	55.7	79.0	100.0	5953	1.48	1.44	1.42	1.27	5.60
L. piceicola[2]	29.2	34.6	54.6	72.2	100.0	6332	1.18	1.58	1.32	1.39	5.47
L. piceicola[3]	28.9	45.5	57.8	72.3	100.0	5190	1.57	1.27	1.25	1.38	5.48
L. piceicola[4]	26.9	37.3	53.5	70.3	100.0	4900	1.39	1.43	1.31	1.42	5.56
L. piceicola[5]	22.3	32.7	44.5	65.6	100.0	6477	1.47	1.36	1.47	1.52	5.83
L. piceicola[6]	23.0	33.6	51.8	67.2	100.0	5880	1.46	1.54	1.30	1.49	5.79
Avg	26.1	37.1	53.0	71.1	100.0	5789	1.42	1.44	1.35	1.41	5.62
Min	22.3	32.7	44.5	65.6	100.0	4900	1.18	1.27	1.25	1.27	5.47
Max	29.2	45.5	57.8	79.0	100.0	6477	1.57	1.58	1.47	1.52	5.83
Stdev	2.9	4.7	4.6	4.7	0	625	0.13	0.11	0.08	0.09	0.15
V%	**J1**	**J2**	**J3**	**J4**	**F**	**V mm³**	**J2/J1**	**J3/J2**	**J4/J3**	**F/J4**	**Sum**
L. piceicola[1]	4.4	12.0	28.7	63.6	100.0	0.0115	2.73	2.39	2.22	1.57	8.91
L. piceicola[2]	7.4	10.1	29.6	50.2	100.0	0.0117	1.36	2.93	1.70	1.99	7.98
L. piceicola[3]	5.8	18.8	31.0	50.9	100.0	0.0096	3.26	1.65	1.64	1.97	8.51
L. piceicola[4]	4.4	10.3	23.5	47.6	100.0	0.0099	2.34	2.28	2.03	2.10	8.75
L. piceicola[5]	3.8	8.7	17.9	40.2	100.0	0.0129	2.29	2.06	2.25	2.49	9.08
L. piceicola[6]	3.1	7.6	25.9	47.6	100.0	0.0138	2.45	3.41	1.84	2.10	9.80
Avg	4.8	11.2	26.1	50.0	100.0	0.0111	2.41	2.45	1.94	2.04	8.84
Min	3.1	7.6	17.9	40.2	100.0	0.0096	1.36	1.65	1.64	1.57	7.98
Max	7.4	18.8	31.0	63.6	100.0	0.0129	3.26	3.41	2.25	2.49	9.80
Stdev	1.5	4.0	5.4	7.7	0.0	0.0016	0.69	0.47	0.28	0.33	0.43
O%	**J1**	**J2**	**J3**	**J4**	**F**	**O µm**	**J2/J1**	**J3/J2**	**J4/J3**	**F/J4**	**Sum**
L. piceicola[1]	61.1	68.0	79.0	89.6	100.0	178.2	1.11	1.16	1.13	1.12	4.52
L. piceicola[2]	57.3	65.5	79.2	88.2	100.0	175.6	1.14	1.21	1.11	1.13	4.60
L. piceicola[3]	57.5	61.9	74.4	83.1	100.0	160.0	1.08	1.20	1.12	1.20	4.60
L. piceicola[4]	61.6	68.8	76.1	88.9	100.0	155.5	1.12	1.11	1.17	1.12	4.52
L. piceicola[5]	59.0	66.5	78.3	85.8	100.0	153.9	1.13	1.18	1.10	1.17	4.57
L. piceicola[6]	55.9	64.0	75.9	88.0	100.0	155.4	1.14	1.19	1.16	1.14	4.63
Avg	58.7	65.8	77.1	87.3	100.0	163.1	1.12	1.17	1.13	1.15	4.57
Min	55.9	61.9	74.4	83.1	100.0	153.9	1.08	1.11	1.10	1.12	4.52
Max	61.6	68.8	79.2	89.6	100.0	178.2	1.14	1.21	1.17	1.20	4.63
Stdev	2.3	2.6	2.0	2.4	0.0	10.9	0.03	0.04	0.03	0.04	0.04
R%	**J1**	**J2**	**J3**	**J4**	**R µm**	**–**	**J2/J1**	**J3/J2**	**J4/J3**	**Sum**	**–**
L. piceicola[1]	66.4	77.4	88.9	100.0	177.6	–	1.17	1.15	1.12	3.44	–
L. piceicola[2]	66.4	76.0	88.6	100.0	176.7	–	1.14	1.17	1.13	3.44	–
L. piceicola[3]	62.7	77.2	77.3	100.0	158.0	–	1.23	1.13	1.15	3.51	–
L. piceicola[4]	67.9	75.6	90.2	100.0	152.7	–	1.11	1.19	1.11	3.42	–
L. piceicola[5]	65.2	76.8	86.7	100.0	151.5	–	1.18	1.13	1.15	3.46	–
L. piceicola[6]	60.8	69.9	86.9	100.0	157.3	–	1.15	1.24	1.15	3.54	
Avg	64.9	75.5	88.1	100.0	162.3	–	1.16	1.17	1.14	3.47	–
Min	60.8	69.9	86.7	100.0	151.5	–	1.11	1.13	1.11	3.42	–
Max	67.9	77.4	90.2	100.0	177.6	–	1.23	1.24	1.15	3.54	–
Stdev	2.7	2.8	1.4	0.0	11.8	–	0.04	0.03	0.02	0.04	–

**Longidorus piceicola*, a species with 4 juvenile developmental stages (JDS).
Sources: [1]Barsi and Lamberti 2011; [2]Barsi 2022; [3]Lišková et al. 1997; [4,6]Groza et al. 2017; [5]Kornobis and Peneva 2011.
L = body length; V = body volume; O = odontostyle length; R = replacement odontostyle length; F = female.

Table 3. Growth patterns of the body length, body volume, odontostyle length and replacement odontostyle length and relative increase in the body length, body volume, odontostyle length and replacement odontostyle length between successive stages in four populations of *Longidorus intermedius**.

		Growing patterns					Relative increase			
	L%	**JI**	**JII**	**JIII**	**F**	**L µm**	**JII/JI**	**JIII/JII**	**F/JIII**	**Sum**
L. intermedius[7]		32.1	44.6	68.2	100.0	4352	1.39	1.53	1.47	4.38
L. intermedius[8]		32.7	52.0	70.9	100.0	3759	1.59	1.36	1.41	4.36
L. intermedius[9]		31.1	48.6	69.9	100.0	3993	1.56	1.44	1.43	4.43
L. intermedius[10]		29.4	45.5	68.5	100.0	4220	1.55	1.51	1.46	4.51
Avg		31.3	47.7	69.4	100.0	4081	1.52	1.46	1.44	4.42
Min		29.4	44.6	68.2	100.0	3759	1.39	1.36	1.41	4.36
Max		32.7	52.0	70.9	100.0	4352	1.59	1.53	1.47	4.51
Stdev		1.4	3.4	1.3	0.0	261	0.09	0.07	0.03	0.07
	V%	**JI**	**JII**	**JIII**	**F**	**V mm³**	**JII/JI**	**JIII/JII**	**F/JIII**	**Sum**
L. intermedius[7]		7.0	14.8	37.7	100.0	0.0065	2.11	2.55	2.65	7.31
L. intermedius[8]		5.1	20.8	42.4	100.0	0.0062	4.08	2.04	2.36	8.48
L. intermedius[9]		4.9	13.9	38.4	100.0	0.0079	2.84	2.76	2.60	8.20
L. intermedius[10]		5.4	15.4	39.5	100.0	0.0071	2.85	2.56	2.53	7.95
Avg		5.6	16.2	39.5	100.0	0.0069	2.97	2.48	2.54	7.99
Min		4.9	13.9	37.7	100.0	0.0062	2.11	2.04	2.36	7.31
Max		7.0	20.8	42.4	100.0	0.0079	4.08	2.76	2.65	8.48
Stdev		1.0	3.1	2.1	0.0	0.0008	0.81	0.31	0.13	0.50
	O%	**JI**	**JII**	**JIII**	**F**	**O µm**	**JII/JI**	**JIII/JII**	**F/JIII**	**Sum**
L. intermedius[7]		65.4	73.9	86.4	100.0	112.9	1.13	1.17	1.16	3.46
L. intermedius[8]		67.6	75.2	86.5	100.0	111.0	1.11	1.15	1.16	3.42
L. intermedius[9]		68.2	73.6	84.5	100.0	110.0	10.8	1.18	1.18	3.41
L. intermedius[10]		66.5	73.4	84.4	100.0	111.2	1.10	1.15	1.18	3.44
Avg		66.9	74.0	85.5	100.0	111.3	1.11	1.15	1.17	3.43
Min		65.4	73.4	84.4	100.0	110.0	1.08	1.15	1.16	3.41
Max		68.2	75.2	86.5	100.0	112.9	1.13	1.17	1.18	3.46
Stdev		1.2	0.8	1.2	0.0	1.2	0.02	0.01	0.02	0.02
	R%	**JI**	**JII**	**JIII**	**R µm**	**–**	**JII/JI**	**JIII/JII**	**Sum**	**–**
L. intermedius[7]		74.4	86.3	100.0	111.2	–	1.16	1.16	2.32	–
L. intermedius[8]		77.6	89.3	100.0	107.0	–	1.15	1.12	2.27	–
L. intermedius[9]		74.3	83.5	100.0	109.0	–	1.12	1.20	2.31	–
L. intermedius[10]		72.1	86.1	100.0	112.6	–	1.19	1.16	2.36	–
Avg		74.6	86.3	100.0	110.0	–	1.16	1.16	2.32	–
Min		72.1	83.5	100.0	107.0	–	1.12	1.12	2.27	–
Max		77.6	89.3	100.0	112.6	–	1.19	1.20	2.36	–
Stdev		2.3	2.4	0.0	2.5	–	0.03	0.03	0.03	–

**Longidorus intermedius*, a species with 3 juvenile developmental stages (JDS).
Sources: [7]Barsi and Lamberti 2004; [8]Peneva et al. 2001; [9]Kumari et al. 2006; [10]Susulovska and Tsaryk 2018.
L = body length; V = body volume; O = odontostyle length; R = replacement odontostyle length; F = female.

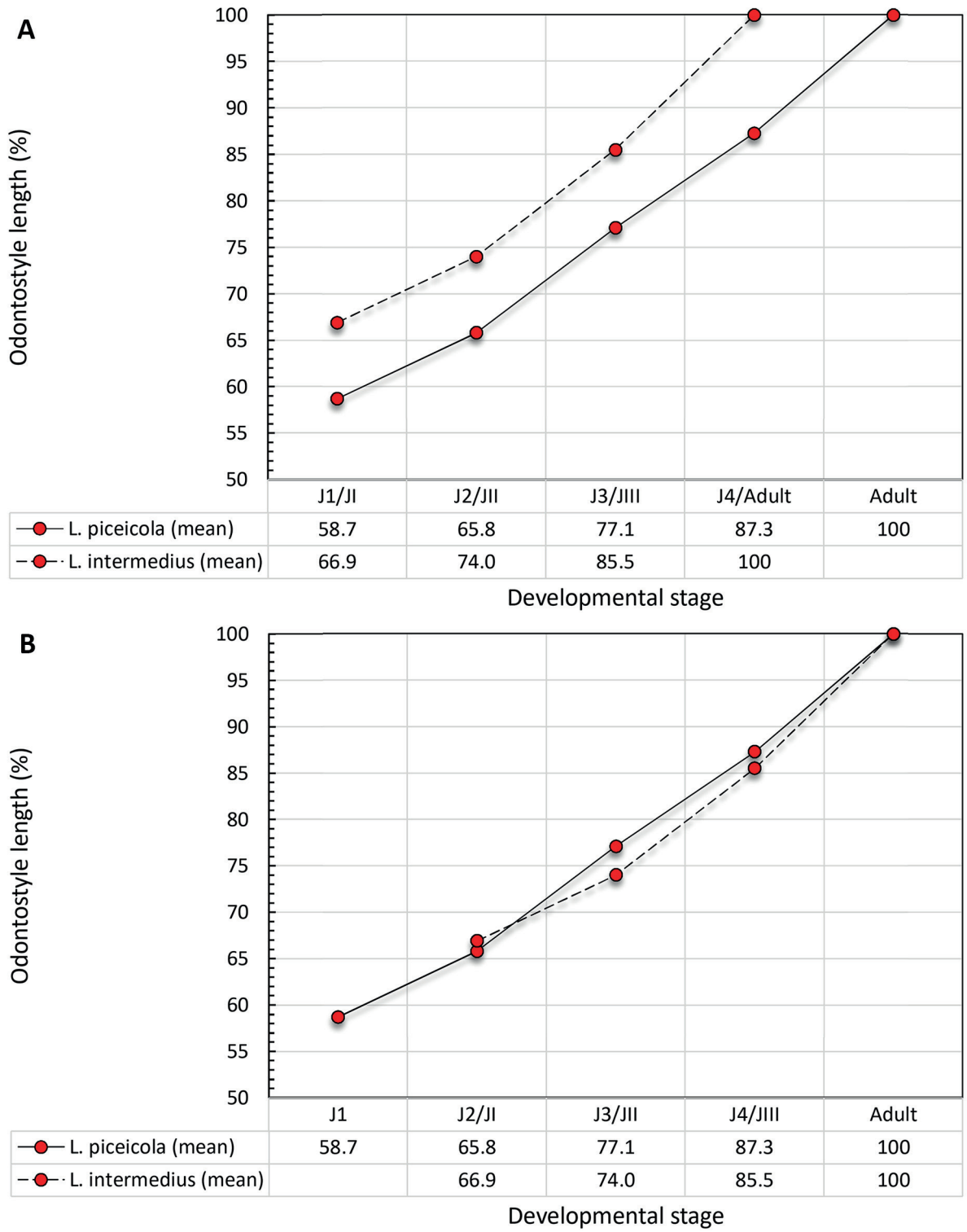


Fig. 3. Comparison of odontostyle length growth patterns in 6 populations of *Longidorus piceicola* and 4 populations of *L. intermedius*.

specimens in the JI stage generally have a longer odontostyle length compared to J1 stage specimens of *L. piceicola*. Therefore, they may likely reach maturity more quickly after only three molts.

Replacement odontostyle length (Fig. 4A, B)

Reminder: in the case of replacement odontostyle length, the absolute value of the replacement odontostyle

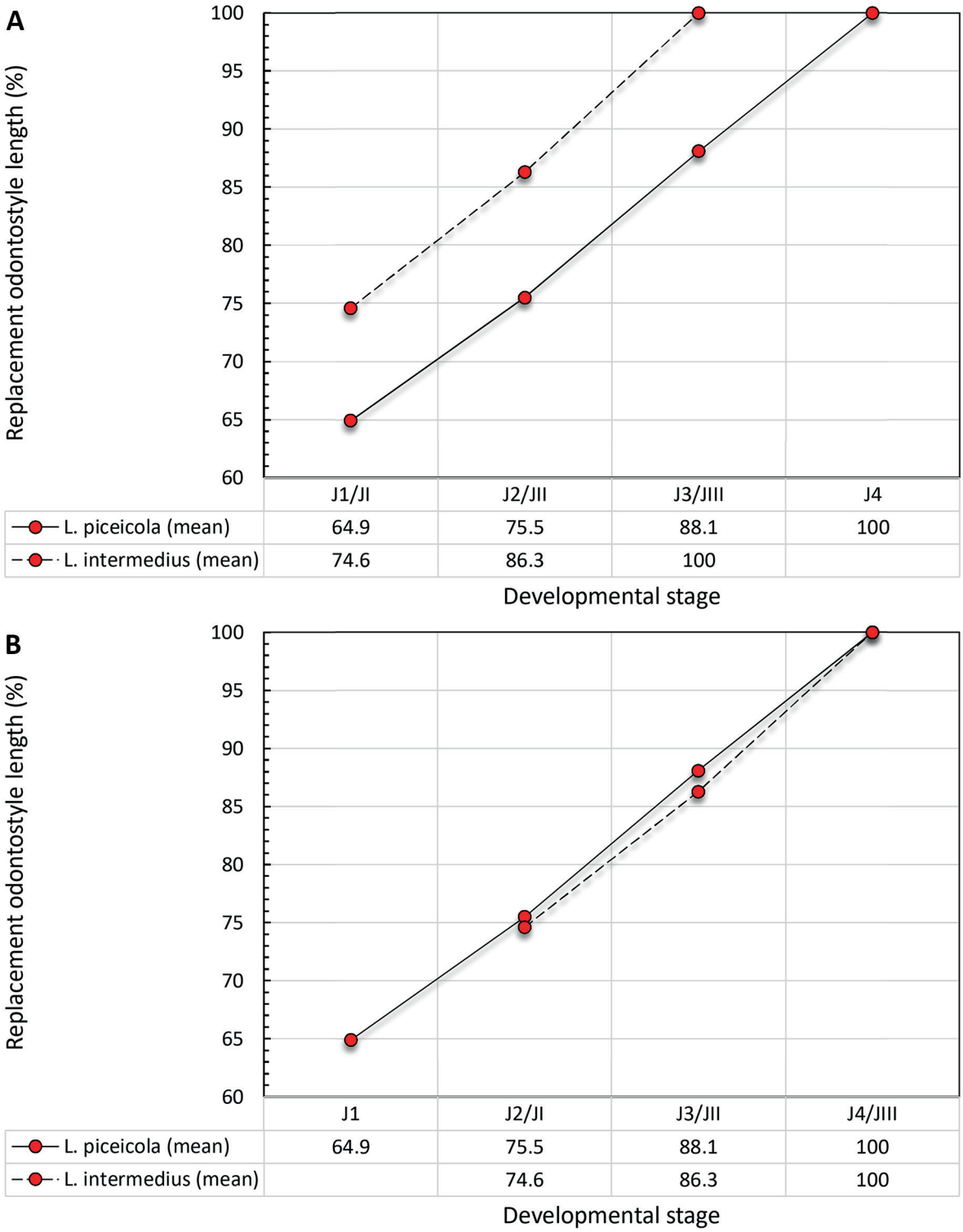


Fig. 4. Comparison of growth patterns of replacement odontostyle length in 6 populations of *Longidorus piceicola* and 4 populations of *L. intermedius*.

length in the pre-adult stage (JIII or J4, respectively) was used for comparison. and was defined to be 100%.

Longidorus intermedus specimens in stages JI and JII have generally 1.15 and 1.14 times longer replacement odontostyle than specimens of *L. piceicola* in the corresponding stages J1 and J2 (Fig. 4A). But a comparison of stages JI and JII with stages J2 and J3, respectively, reveals a very similar and comparable growth pattern (Fig. 4B). The replacement odontostyle in JI specimens is 1.19% shorter than in J2 specimens, and in JII it is 2.04% shorter than in J3.

Including additional populations of both species would certainly affect the numerical values obtained, but the trends would be expected to remain the same.

Using the percent replacement odontostyle lengths for each stage, the relative increase from stage to stage was calculated for both species (Tables 2 and 3).

The sum of the relative increases between successive stages was smaller in *L. intermedius* (2.32) than in *L. piceicola* (3.47). This also supports the results that in *L. intermedius*, stage JI specimens have generally longer replacement odontostyle lengths compared to stage J1 specimens in *L. piceicola*.

Therefore, they can probably reach maturity more quickly through only three molts.

Comparison of growth patterns of odontostyle and replacement odontostyle

A comparison of the growth patterns of the odontostyle and the replacement odontostyle in *L. piceicola* (Table 2) shows that the length of the replacement odontostyle during the J1 stage is similar to the length of the functional odontostyle in the J2 stage, and significantly greater than the length of the functional odontostyle in the J1 stage (Figure 5A). This situation is present between J2/J3, J3/J4 and J4/adults.

A comparison of the growth patterns of the odontostyle and the replacement odontostyle in *L. intermedius* (Table 3) shows that the length of the replacement odontostyle in the JI stage is similar to the length of the functional odontostyle in the JII stage, and significantly greater than the length of the functional odontostyle in the JI stage (Fig. 5B). A similar situation is present between JII/JIII and JIII/adult.

Notes on patterns of odontostyle and replacement odontostyle growth in the species *Longidorus piceicola* and *L. intermedius*

Generally, each juvenile specimen (if not in the molting stage) contains one functional odontostyle and one replacement odontostyle. The replacement odontostyle is longer than the functional odontostyle. The question is: how much longer? Unfortunately, it is not entirely clear from different publications because the mean values of the length of the odontostyle and replacement odontostyle can only give an average picture of their growth.

Another attempt should be made to obtain a more reliable picture of the patterns of odontostyle and replacement odontostyle growth. Intraspecific analysis is a good opportunity to obtain such a picture.

Tables 4 and 5 present individual data (body length, odontostyle length, and replacement odontostyle length and percentage increases) for specimens of *L. piceicola* in stages J1, J2, J3, and J4 from Mount Durmitor, Montenegro (Barsi and Lamberti 2011) and Mount Kopaonik, Serbia (Barsi 2022), respectively, and are illustrated in Figs 6 and 7.

Individual data for specimens of *L. intermedius* in stages JI, JII, and JIII from Obedska bara, Serbia (Barsi and Lamberti 2004), are presented in Table 6 and illustrated in Fig. 8.

It is clear that there is no uniform growth pattern for all specimens in the studied population. Some specimens within the same juvenile stage have the same odontostyle length (Tables 4, 5 and 6, boxed). In these specimens, the replacement odontostyles may be of different lengths (Tables 4, 5 and 6, boxed) or the same length (Tables 4, 5 and 6, boxed and bold). In contrast, in specimens with different odontostyle lengths, the replacement odontostyle may be the same length (Tables 4, 5 and 6).

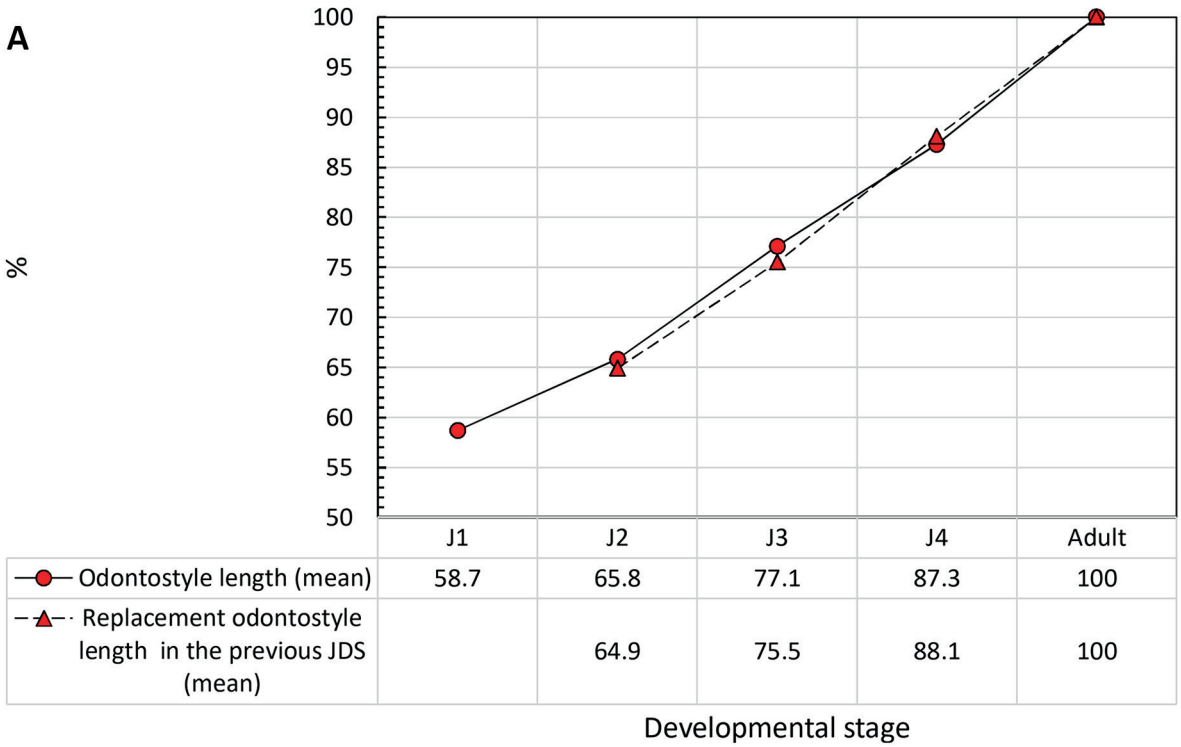
The percentage increase (the difference between the length of the replacement odontostyle and the length of the functional odontostyle) is variable within populations and juvenile stages.

CONCLUSIONS

Despite their molecular similarity, *L. piceicola* and *L. intermedius* differ greatly in morphometry and ontogeny. *Longidorus piceicola* and *L. intermedius* have different developmental patterns, the former with 4 JDS (which is the most common) and the latter with 3 JDS (less common, but probably more common than currently assumed).

The results presented in the present study indicate that for *L. intermedius*, individuals in stages JI, JII and JIII generally have a greater body length and a greater body volume compared to corresponding *L. piceicola* individuals in stages J1, J2 and J3. Therefore, they can probably reach maturity more quickly through only three molts.

Regarding the growth patterns of odontostyle and replacement odontostyle length, these results indicate that specimens of *L. intermedius* in the JI stage generally have longer odontostyle and replacement odontostyle lengths compared to specimens of *L. piceicola* in the J1 stage. At the individual level, it is clear that there is no single growth pattern for all individuals in a population. Some specimens in the same juvenile stage have the same odontostyle length. In these specimens, the replacement odontostyles may be



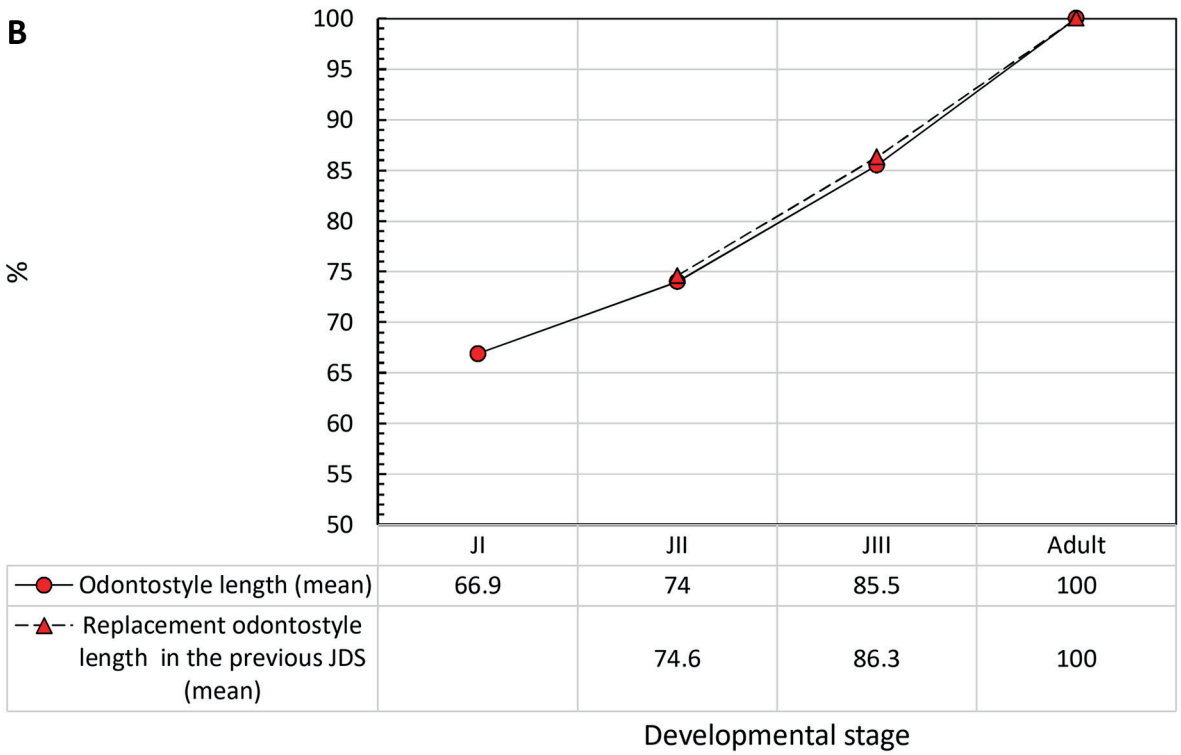


Fig. 5. Comparison of odontostyle length and replacement odontostyle length growth patterns in 6 populations of *Longidorus piceicola* (**A**) and in 4 populations of *L. intermedius* (**B**).

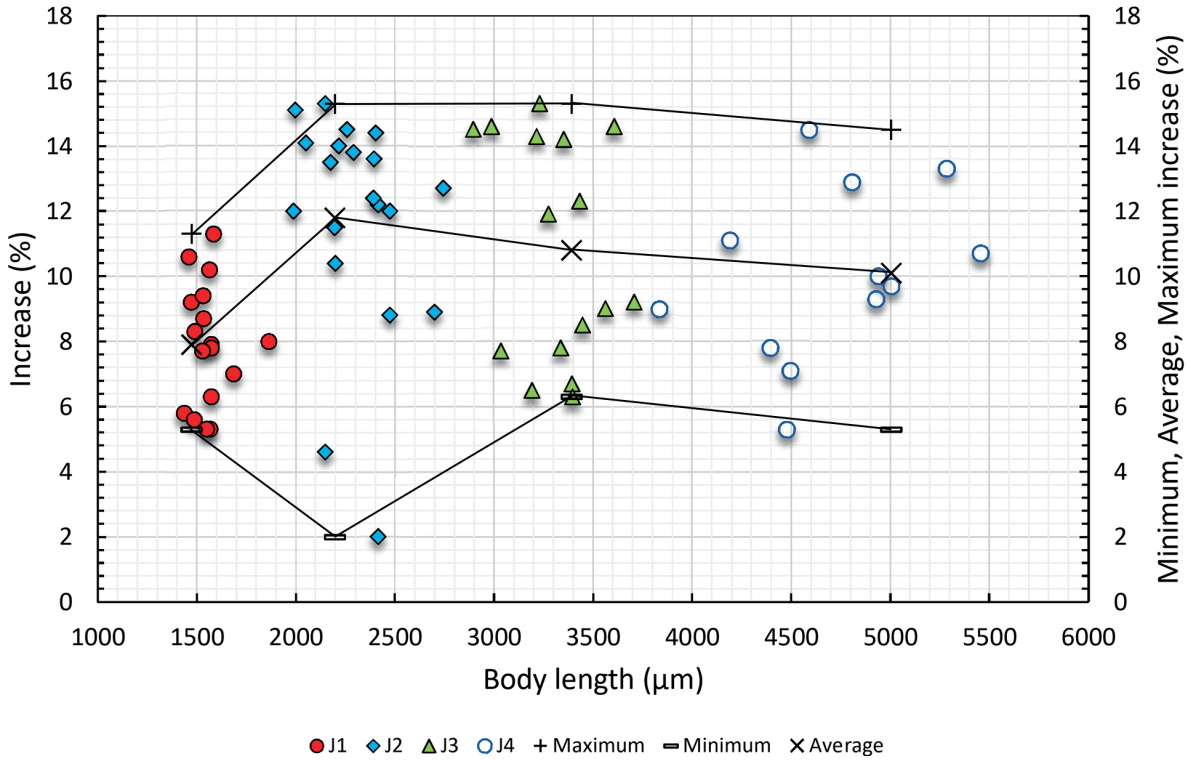


Fig. 6. *Longidorus piceicola*, Durmitor (Montenegro). Individual increase in the length of the replacement odontostyle relative to the functional odontostyle in individuals in 4 juvenile developmental stages; minimum, average and maximum individual increase.

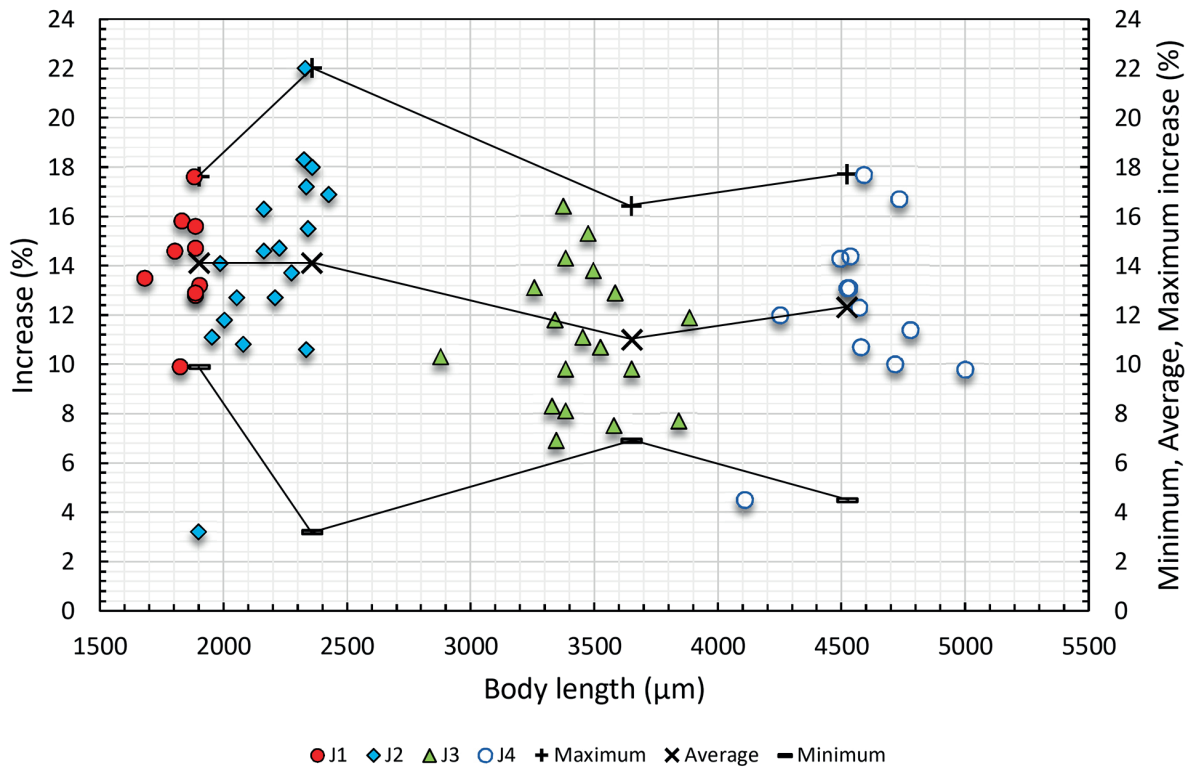


Fig. 7. *Longidorus piceicola*, Kopaonik Mt. (Serbia). Individual increase in the length of the replacement odontostyle relative to the functional odontostyle in individuals in 4 juvenile developmental stages; minimum, average and maximum individual increase.

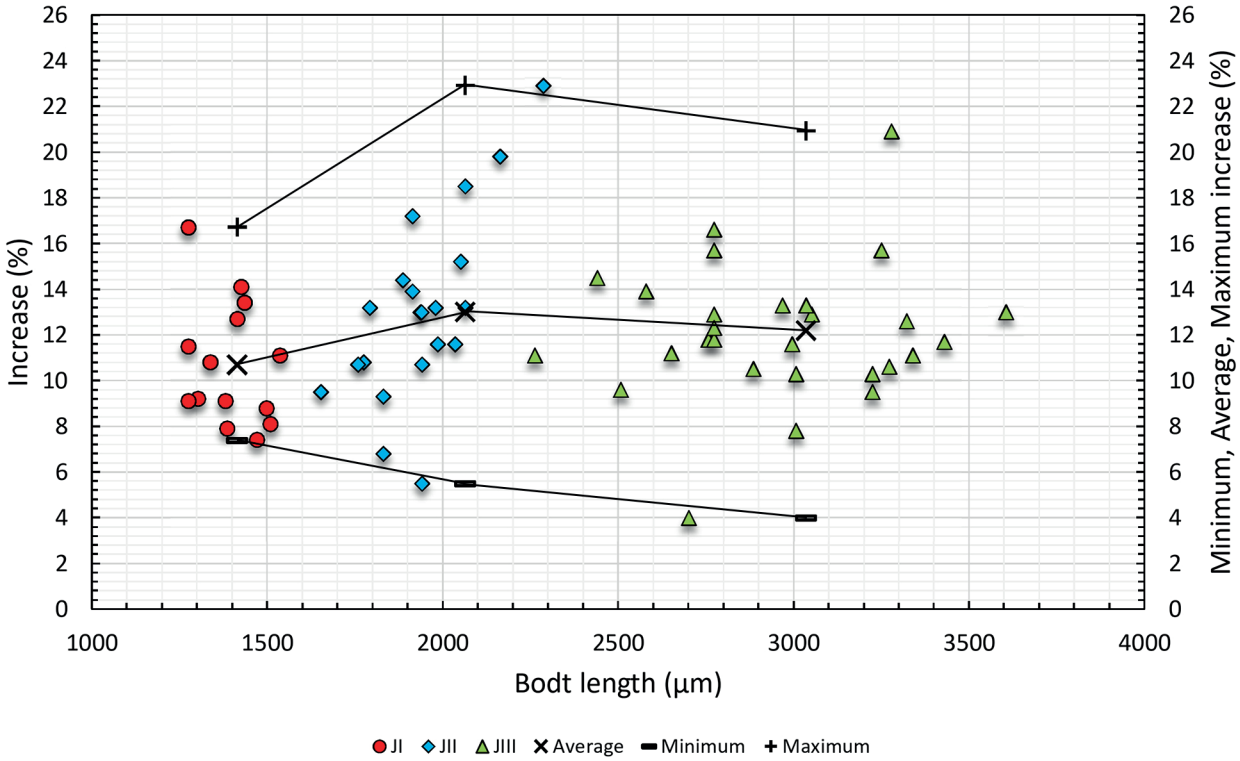


Fig. 8. *Longidorus intermedius*, Obedska bara (Serbia). Individual increase in the length of the replacement odontostyle relative to the functional odontostyle in individuals in 3 juvenile developmental stages; minimum, average and maximum individual increase.

of different lengths or the same length. Conversely, in specimens with different odontostyle lengths, the replacement odontostyle may be the same length.

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Table 4. Odontostyle and replacement odontostyle growth patterns in *Longidorus piceicola* (Durmitor Mt., Montenegro).

J1	L	O	R	O_R%	I%	J2	L	O	R	O_R%	I%
1	1573	103.7	112.5	92.2	7.8	1	1988	115.0	130.7	88.0	12.0
2	1490	103.7	113.1	91.7	8.3	2	2173	115.0	132.9	86.5	13.5
3	1473	104.4	115.0	90.8	9.2	3	2402	117.5	137.2	85.6	14.4
4	1461	105.0	117.5	89.4	10.6	4	2196	118.7	134.2	88.5	11.5
5	1527	105.0	113.8	92.3	7.7	5	2216	118.7	138.0	86.0	14.0
6	1533	105.0	115.0	91.3	8.7	6	2050	118.7	138.2	85.9	14.1
7	1487	106.2	112.5	94.4	5.6	7	2394	120.0	138.9	86.4	13.6
8	1530	108.7	120.0	90.6	9.4	8	2148	120.0	141.7	84.7	15.3
9	1436	108.7	115.4	94.2	5.8	9	2256	120.0	140.4	85.5	14.5
10	1584	108.7	122.5	88.7	11.3	10	2291	120.6	139.9	86.2	13.8
11	1564	110.0	122.5	89.8	10.2	11	1996	121.2	142.8	84.9	15.1
12	1573	111.2	120.7	92.1	7.9	12	2148	121.2	127.1	95.4	4.6
13	1567	**112.5**	**118.8**	94.7	5.3	13	2391	121.2	138.4	87.6	12.4
14	1550	**112.5**	**118.8**	94.7	5.3	14	2199	123.7	138.0	89.6	10.4
15	1573	113.7	121.3	93.7	6.3	15	2416	123.8	141.0	87.8	12.2
16	1862	115.0	125.0	92.0	8.0	16	2416	123.8	126.3	98.0	2.0
17	1684	116.2	125.0	93.0	7.0	17	2700	125.0	137.2	91.1	8.9
						18	2474	125.0	137.1	91.2	8.8
						19	2474	125.0	142.1	88.0	12.0
						20	2745	127.5	146.0	87.3	12.7
J3	L	O	R	O_R%	I%	J4	L	O	R	O_R%	I%
1	3352	132.1	153.9	85.8	14.2	1	4590	149.9	175.3	85.5	14.5
2	2986	133.4	156.2	85.4	14.6	2	4806	153.7	176.5	87.1	12.9
3	3191	134.6	143.9	93.5	6.5	3	3835	154.9	170.2	91.0	9.0
4	3231	135.5	160.0	84.7	15.3	4	4478	156.8	165.6	94.7	5.3
5	2894	136.5	159.6	85.5	14.5	5	4928	157.5	173.7	90.7	9.3
6	3034	137.2	148.6	92.3	7.7	6	4939	160.0	177.8	90.0	10.0
7	3274	141.0	160.0	88.1	11.9	7	4395	161.9	175.6	92.2	7.8
8	3606	141.0	165.1	85.4	14.6	8	4190	162.6	182.9	88.9	11.1
9	3214	142.0	165.6	85.7	14.3	9	5455	163.4	182.9	89.3	10.7
10	3392	142.2	152.4	93.3	6.7	10	5006	165.1	182.9	90.3	9.7
11	3563	142.2	156.2	91.0	9.0	11	5283	165.1	190.5	86.7	13.3
12	3397	143.5	153.2	93.7	6.3	12	4495	165.1	177.8	92.9	7.1
13	3337	144.8	157.1	92.2	7.8						
14	3432	144.8	165.1	87.7	12.3						
15	3706	149.9	165.1	90.8	9.2						
16	3446	151.1	165.1	91.5	8.5						

Note. Data sorted by odontostyle length.
J1-J4 = juvenile stages; L = body length (μm); O = odontostyle (μm); R = replacement odontostyle (μm); O_R% = odontostyle length in relation to replacement odontostyle length (%); I = increase of replacement odontostyle in relation to odontostyle length (%).

Table 5. Odontostyle and replacement odontostyle growth patterns in *Longidorus piceicola* (Kopaonik Mt., Serbia)

J1	L	O	R	O_R%	I%	J2	L	O	R	O_R%	I%
1	1903	98.7	113.7	86.8	13.2	1	2331	110.0	141.0	78.0	22.0
2	1887	98.7	116.9	84.4	15.6	2	2325	110.0	134.6	81.7	18.3
3	1682	100.0	115.6	86.5	13.5	3	2359	112.5	137.2	82.0	18.0
4	1831	100.0	118.7	84.2	15.8	4	2336	112.5	135.9	82.8	17.2
5	1881	100.0	121.3	82.4	17.6	5	2225	112.5	132.1	85.2	14.8
6	1887	101.2	116.2	87.1	12.9	6	1898	113.7	117.5	96.8	3.2
7	1887	101.2	118.7	85.3	14.7	7	2164	113.7	135.9	83.7	16.3
8	1826	102.5	113.8	90.1	9.9	8	2342	113.7	134.6	84.5	15.5
9	1887	102.5	117.5	87.2	12.8	9	2164	115.0	134.6	85.4	14.6
10	1804	102.5	120.0	85.4	14.6	10	2425	115.0	138.4	83.1	16.9
						11	1987	115.6	134.6	85.9	14.1
						12	2275	116.2	134.6	86.3	13.7
						13	2053	117.5	134.6	87.3	12.7
						14	1954	117.5	132.1	88.9	11.1
						15	2336	118.1	132.1	89.4	10.6
						16	2003	118.7	134.6	88.2	11.8
						17	2209	118.7	135.9	87.3	12.7
						18	2081	120.0	134.6	89.2	10.8
J3	L	O	R	O_R%	I%	J4	L	O	R	O_R%	I%
1	2880	132.1	147.3	89.7	10.3	1	4590	142.2	172.7	82.3	17.7
2	3258	134.6	154.9	86.9	13.1	2	4534	149.9	175.2	85.6	14.4
3	3496	134.6	156.2	86.2	13.8	3	4523	**152.4**	**175.3**	86.9	13.1
4	3374	135.9	162.6	83.6	16.4	4	4529	**152.4**	**175.3**	86.9	13.1
5	3585	137.2	157.5	87.1	12.9	5	4733	152.4	182.9	83.3	16.7
6	3347	137.2	147.3	93.1	6.9	6	4495	152.4	177.8	85.7	14.3
7	3385	137.2	160.0	85.8	14.3	7	4778	157.5	177.8	88.6	11.4
8	3524	138.4	154.9	89.3	10.7	8	4578	158.7	177.8	89.3	10.7
9	3341	138.9	157.5	88.2	11.8	9	4251	158.7	180.3	88.0	12.0
10	3652	**139.7**	**154.9**	90.2	9.8	10	4717	160.0	177.8	90.0	10.0
11	3385	**139.7**	**154.9**	90.2	9.8	11	4107	160.0	167.6	95.5	4.5
12	3330	139.7	152.4	91.7	8.3	12	5000	162.6	180.3	90.2	9.8
13	3885	141.0	160.0	88.1	11.9						
14	3474	141.0	166.4	84.7	15.3						
15	3580	141.0	152.4	92.5	7.5						
16	3385	144.8	157.5	91.9	8.1						
17	3841	152.4	165.1	92.3	7.7						

Note. Data sorted by odontostyle length.
J1-J4 = juvenile stages; L = body length (µm); O = odontostyle (µm); R = replacement odontostyle (µm); O_R% = odontostyle length in relation to replacement odontostyle length (%); I = increase of replacement odontostyle in relation to odontostyle length (%).

Table 6. Odontostyle and replacement odontostyle growth patterns in *Longidorus intermedius* (Obedska bara, Serbia).

JI	L	O	R	O_R%	I%
1	1426	68.7	80.0	85.9	14.1
2	1276	68.7	82.5	83.3	16.7
3	1338	71.9	80.6	89.2	10.8
4	1387	72.5	78.7	92.1	7.9
5	1276	72.5	81.9	88.5	11.5
6	1437	72.5	83.7	86.6	13.4
7	1415	73.1	83.7	87.3	12.7
8	1304	73.7	81.2	90.8	9.2
9	1382	75.0	82.5	90.9	9.1
10	1276	75.0	82.5	90.9	9.1
11	1537	75.6	85.0	88.9	11.1
12	1498	77.5	85.0	91.2	8.8
13	1510	78.1	85.0	91.9	8.1
14	1471	78.7	85.0	92.6	7.4

JII	L	O	R	O_R%	I%
1	1915	78.7	95.0	82.8	17.2
2	2164	78.7	98.1	80.2	19.8
3	2287	80.0	103.7	77.1	22.9
4	1793	**82.5**	**95.0**	86.8	13.2
5	2065	82.5	101.2	81.5	18.5
6	1981	**82.5**	**95.0**	86.8	13.2
7	1776	82.5	92.5	89.2	10.8
8	2065	**82.5**	**95.0**	86.8	13.2
9	2053	83.7	98.7	84.8	15.2
10	1759	**83.7**	**93.7**	89.3	10.7
11	1942	**83.7**	**93.7**	89.3	10.7
12	1654	83.7	92.5	90.5	9.5
13	1937	83.7	96.2	87	13.0
14	1987	85.0	96.2	88.4	11.6
15	1832	85.0	93.7	90.7	9.3
16	1915	85.0	98.7	86.1	13.9
17	1887	85.6	100	85.6	14.4
18	1831	86.2	92.5	93.2	6.8
19	1942	86.2	91.2	94.5	5.5
20	2037	86.2	97.5	88.4	11.6

JIII	L	O	R	O_R%	I%
1	3280	91.9	116.2	79.1	20.9
2	2509	93.7	103.7	90.4	9.6
3	2758	93.7	106.2	88.2	11.8
4	2775	93.7	106.2	88.2	11.8
5	2775	**93.7**	**111.2**	84.3	15.7
6	3252	**93.7**	**111.2**	84.3	15.7
7	2886	95.0	106.2	89.5	10.5
8	3324	95.0	108.7	87.4	12.6
9	2664	95.6	107.5	88.9	11.1
10	3052	96.9	111.2	87.1	12.9
11	2581	96.9	112.5	86.1	13.9
12	3225	**97.5**	**108.7**	89.7	10.3
13	3008	**97.5**	**108.7**	89.7	10.3
14	2775	97.5	111.9	87.1	12.9
15	2969	**97.5**	**112.5**	86.7	13.3
16	3036	**97.5**	**112.5**	86.7	13.3
17	2653	98.7	111.2	88.8	11.2
18	2775	98.7	112.5	87.7	12.3
19	2997	99.4	112.5	88.4	11.6
20	2442	99.4	116.2	85.5	14.5
21	3341	100.0	112.5	88.9	11.1
22	3607	100.0	115.0	87.0	13.0
23	3225	100.6	111.2	90.5	9.5
24	3274	100.6	112.5	89.4	10.6
25	2775	100.6	120.6	83.4	16.6
26	2703	101.9	106.2	96.0	4.0
27	3008	102.5	111.2	92.2	7.8
28	3430	103.7	117.5	88.3	11.7

Note. Data sorted by odontostyle length.
JI-JIII = juvenile stages; L = body length (µm); O = odontostyle (µm); R = replacement odontostyle (µm); O_R% = odontostyle length in relation to replacement odontostyle length (%); I = increase of replacement odontostyle in relation to odontostyle length (%).