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POSTLARVAL DEVELOPMENT OF *EUPOLYBOTHRUS TRANSSYLVANICUS* (LATZEL) (CHILOPODA: LITHOBIOMORPHA) FROM SERBIA

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Abstract — Criteria for delimiting larval stadia in different animal groups, the number of adult and hatchling leg-bearing trunk segments in the Chilopoda, and modes of centipede development (hemianamorphic and epimorphic) are briefly considered. Data are presented on variation during post-larval development in the following morphological characters of *Eupolybothrus transsylvanicus*: body length; body width; head length; head width; antenna length; length of the 14th and 15th legs; number of antennal articles, ocelli, teeth on the forcipular coxosternite, and coxal pores; projections on T.6, T.7, T.9, T.11, and T.13; spinulation on the last pair of legs; and the degree of development of the genitalia (gonopods). Key criteria for defining post-larval stadia in natural populations of *E. transsylvanicus*, the boundary between juvenile and adult stadia, and the number of post-larval stadia are also analyzed and discussed.

Key words: Chilopoda, Lithobiomorpha, *Eupolybothrus transsylvanicus*, larval stadia, hemianamorphosis, morphological characters, post-larval development, Serbia.

INTRODUCTION

Every animal, whether earthworm, eagle, beagle, or pseudoscorpion, passes through similar stages of development. The basic life cycle consists of fertilization, cleavage, gastrulation, germ layer formation, organogenesis, metamorphosis, adulthood, and senescence. In many species, the organism that hatches from the egg or is born into the world is not sexually mature. Indeed, in most animals, the young organism is a larva that may look significantly different from the adult (Gilbert, 2003).

Minelli (2003) recommended restricting the meaning of the term "larva" to those cases in which a real metamorphosis occurs. This means excluding the use of the term in the case of nematodes and many arthropods. "True" larvae are those of the holometabolous insects, those of many marine invertebrates, and those of many amphibians. Criteria for delimiting this stage, other than habitus differences between early and more advanced post-embryonic stages, include the lack of structures in the larva strictly related to reproduction, as well as dramatic changes in life-style, morphallaxis, and growth of subsequent stages from set-aside cells or at least the presence in early stages of parts that will be discarded later.

In chilopods with 15 leg-bearing trunk segments in the adult condition (Scutigeromorpha, Lithobiomorpha and Craterostigmomorpha), the organism that hatches from the egg has been called the larva by various authors. In hemianamorphic centipedes, a typically larval trait is the number of pairs of walking legs, which is always lower than in adults (Table 1).

These larvae are small and pale-colored forms whose legs are well-formed and whose tracheal system is functional (Lewis, 1981). The final complement of body segments and appendages is progressively reached through some larval molts (the anamorphic phase of post-embryonic development). Reproductive maturity, however, requires further post-larval molts without associated changes in segmentation (the epimorphic phase of post-embryonic development) (Minelli et al., 2000).

According to the evidence available to date (Verhoeff, 1902-25; Eason, 1964; Andersson, 1976, 1978a, 1978b, 1980, 1981, 1982, 1983, 1984a, 1984b; Kos, 1997), there are five larval stadia in the Lithobiomorpha, each preceded by a molt. The first and second larval stadia (L0 and LI) usually possess seven pairs of fully developed legs, the third (LII) – eight, the fourth (LIII) – 10, and the fifth (LIV) – 12. In post-larval development, each stadium has 15 pairs of legs; the number of these stadia can be different for different species. Between each stadium, there is a molt in which an increase occurs in size and the number of ocelli, antennal articles, coxal pores, spines, setae, etc. After attainment of sexual maturity, there are one or more further molts (Andersson, 1976).

In the present paper, we report variability in some morphological characters during post-larval development of the hemianamorphic species *Eupolybothrus transsylvanicus* (Latzel) and establish key criteria for defining post-larval stadia (including adults). These stadia are described in the same way as for *E. grossipes* (C. L. Koch), *E. litorallis* (L. Koch) (Eason, 1970), and *E. dolops* Zapparoli (Zapparoli, 1998).

Table 1. Number of adult and hatchling leg-bearing trunk segments and mode of centipede development (Edgecombe and Giribet, 2007).

	Adult	Hatchling	Development
Scutigeromorpha	15	4	Hemianamorphic
Lithobiomorpha	15	6–8 (7)	Hemianamorphic
Craterostigmomorpha	15	12	Hemianamorphic
Scolopendromorpha	21-23	21–23	Epimorphic
Scolopocryptopidae	23	23	Epimorphic
Others	21	21	Epimorphic
Geophilomorpha	27–191	27–191	Epimorphic
Mecistocephalidae	47–101	47–101	Epimorphic
Adesmata	27–191	27–191	Epimorphic

Eupolybothrus transsylvanicus is widely distributed in Serbia, Romania, Croatia, Bosnia and Herzegovina, Montenegro, Albania, Bulgaria, and Greece (Stoev, 1997, 2002; Mitić, 2001, 2002, 2005; Mitić and Tomić, 2002; Mitić et al., 2003, 2007; Zapparoli, 2002). Mitić and Makarov (2007) registered some morphological anomalies on antennae and tergites of *E. transsylvanicus* from Košutnjak, Belgrade. As far as we know, no description of sub-adult stadia of this species has been previously published.

MATERIAL AND METHODS

The centipede material analyzed in this study was collected by hand in leaf litter under stones or bark of decayed logs and fallen trees during the period from 2001 to 2007. The collected samples of *E. transsylvanicus* are from four sites in Serbia, the first of which was in a mixed oak forest in Košutnjak (Belgrade). The other sites were Čarapićev Brest (village of Beli Potok, Mt. Avala), Rapajlovača (village of Rošci, Mt. Kablar), and Dubočica (village of Miliće, Mt. Radočelo). The collected material is preserved in glass vials filled with 70% ethanol. Identification took place at the Institute of Zoology, Faculty of Biology, University of Belgrade.

Fig. 1.*Eupolybothrus transsylvanicus* (Latzel) – habitus, dorsal view.

The number of analyzed specimens was 1186, distributed in the following post-larval stadia – first post-larval stadium (PL1): six specimens (or 0.51%), second post-larval stadium (PL2): 44 specimens (or 3.71%), third post-larval stadium (PL3): 38 specimens (or 3.20%), fourth postlarval stadium (PL4): 101 specimens (or 8.52%), fifth post-larval stadium (PL5): 373 specimens (or 31.45%), and adult: 624 specimens (or 52.61%).

The morphological traits observed were: body length; body width; head length; head width; antenna length; length of the 14th and 15th legs; number of antennal articles; number of ocelli; number of forcipular teeth; number of coxal pores on the 12th to 15th legs; presence and status of posterior projections on T.6, T.7, T.9, T.11, and T.13; spinulation on the last pair of legs; and the degree of development of the genitalia (gonopods).

Body length was measured from the edge of the cephalic shield to the edge of the intermediate tergite, while body width was measured at T.10; head length and head width were measured according to Andersson (1978a). Ocelli were counted on both sides and antennal articles on both antennae because the number of ocelli and antennal articles can be different on the two sides. Spinulation on the 15th legs was recorded according to Eason (1964).

RESULTS

In the Lithobiomorpha, the number of post-larval stadia can be different for different species and is probably not fixed for any given species. Eason (1970) critically examined the type material of three species of the genus *Eupolybothrus* Verhoeff including immature stadia of two of them – *E. grossipes* (C. L. Koch) and *E. littoralis* (L. Koch) and separated six different stages of post-larval development. The description of a new species of the genus *Eupolybothrus* (*E. dolops* Zapparoli) from mainland Greece (Zapparoli, 1998) also included description of the fourth and fifth post-larval stadia. Our investigation is based on analysis of several natural populations of *E. transsylvanicus* resulting in the description of six post-larval stadia (including the adult stadium), which probably covers the complete post-larval life history.

The variation in body length, head length, head width, and number of antennal articles, ocelli, forcipular teeth, and coxal pores in different post-larval stadia of *E. transsylvanicus* is shown in Figs. 2-8.

Using all relevant literature data and comparative morphological analysis of four natural populations from different localities in Serbia, we here present a description of all post-larval stadia of *E. transsylvanicus* for the first time.

First post-larval stadium (PL1). Body length: 10.0–12.0 mm. Body width: 1.10–1.30 mm. Head length: 1.23–1.48 mm. Head width: 1.28–1.60 mm. Antennae: 6.0–9.0 mm long; number of antennal articles 22–26. Ocelli: 1+3 to 1+5 on each side. Prosternum: with 5+5 to 6+6 teeth. Tergites: approaching the shape found in adults – posterior angles of T.6 and T.7 with projections that are blunt, broad and short; those of T.9, T.11, and T.13 with triangular projections, much narrower than in adults. Coxal pores: 3–5 on each of the 12th to 15th coxae. 14th leg: 4.0 to 5.0 mm long. 15th leg: 6.0 to 7.0 mm long. Spinulation on the 15th legs: DpP, DpF; VmpP, VmF, VmT. Genitalia: undeveloped.

Second post-larval stadium (PL2). Body length: 12.0–16.0 mm. Body width: 1.30–1.60 mm. Head length: 1.54–1.84 mm. Head width: 1.62–1.98 mm. Antennae: 7.0–10.0 mm long; number of antennal articles 27–34. Ocelli: 1+5 to 1+8 on left side and 1+6 to 1+8 on right side. Prosternum: with 5+5 to 6+7 teeth. Tergites: posterior angles of T.6 and T.7 with projections that are blunt, broad, and short; those of T.9,

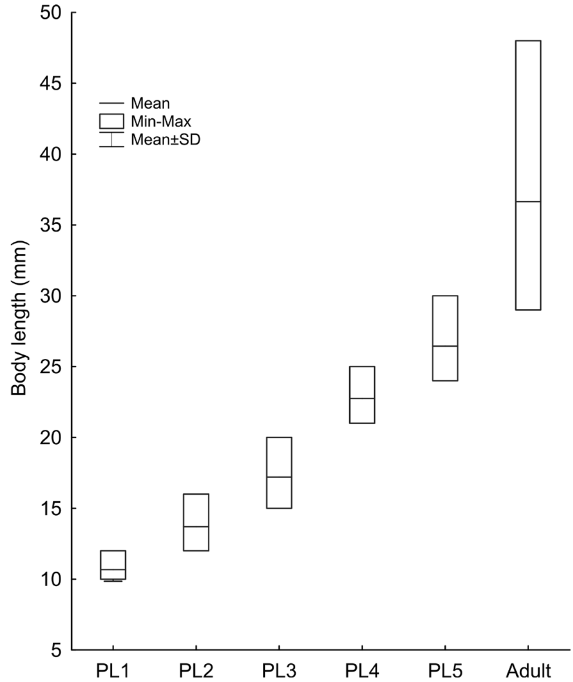

Fig. 2. Variation of body length in different post-larval stadia of *E. transsylvanicus*.

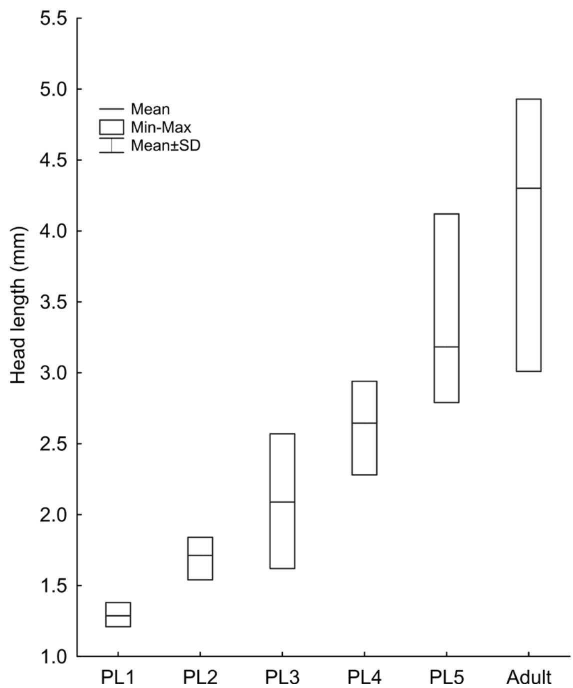

Fig. 3. Variation of head length in different post-larval stadia of *E. transsylvanicus*.

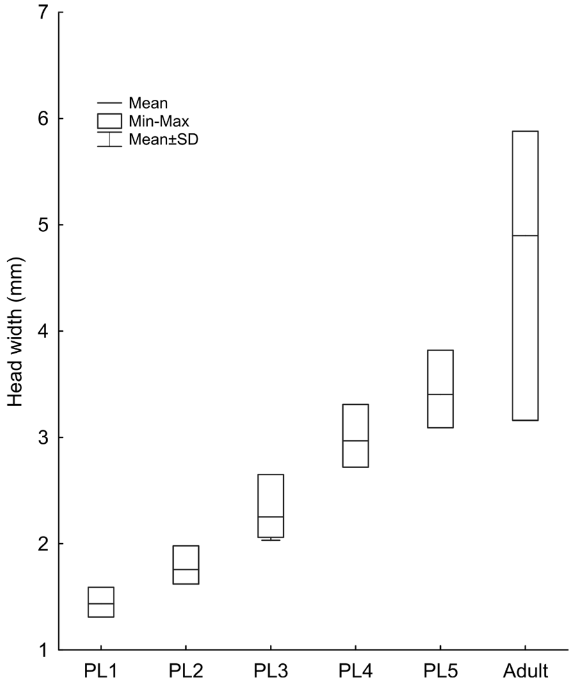

Fig. 4. Variation of head width in different post-larval stadia of *E. transsylvanicus*.

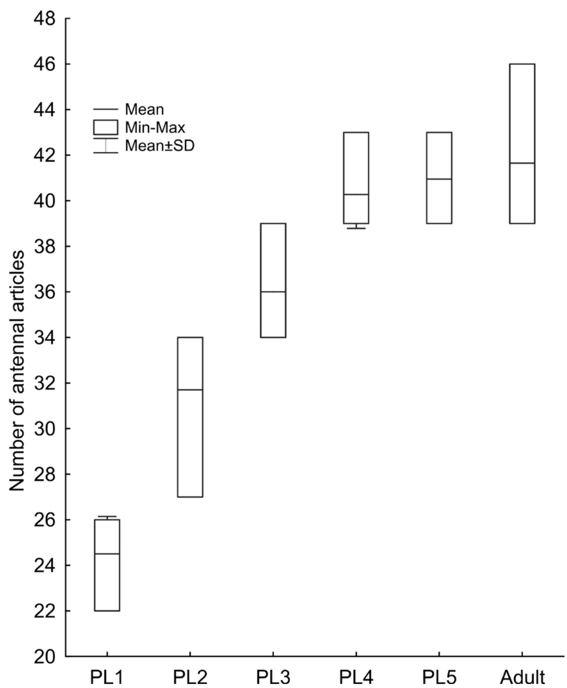

Fig. 5. Variation in number of antennal articles in different post-larval stadia *E. transsylvanicus*.

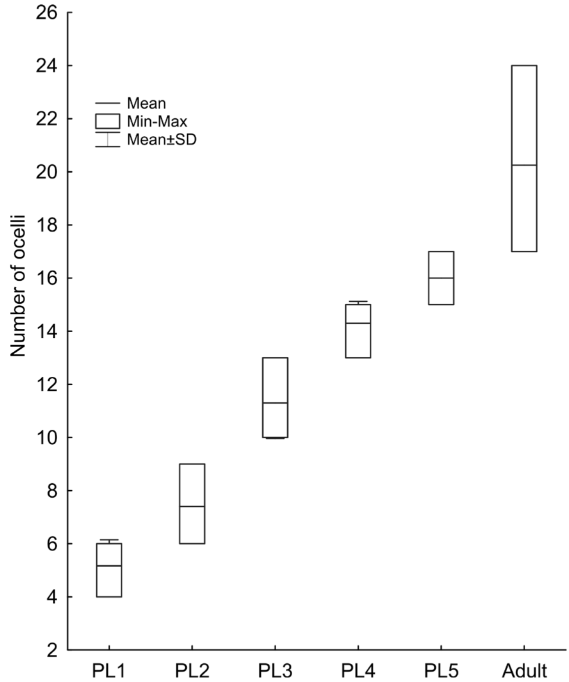

Fig. 6. Variation in number of ocelli in different post-larval stadia of *E. transsylvanicus*.

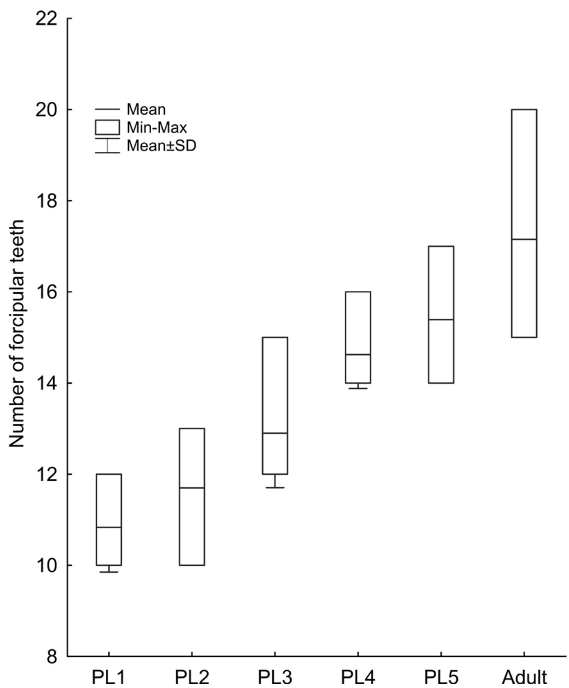

Fig. 7. Variation in number of forcipular teeth in different post-larval stadia of *E. transsylvanicus*.

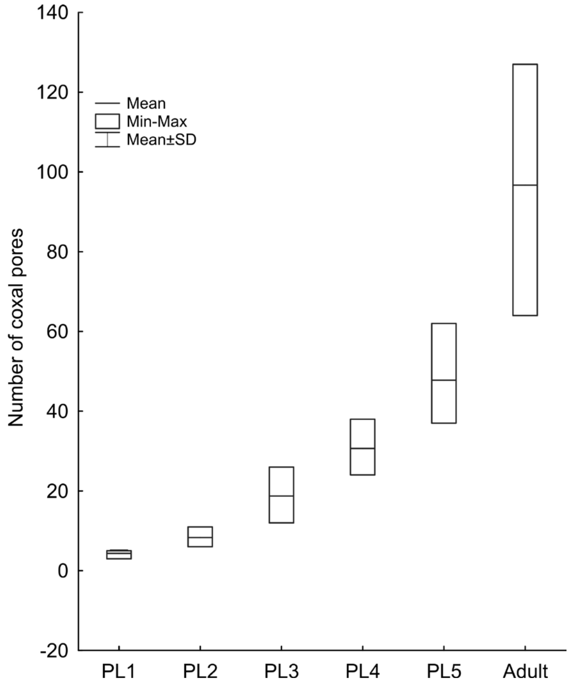

Fig. 8. Variation in number of coxal pores in different post-larval stadia of *E. transsylvanicus*.

T.11, and T.13 with triangular projections. Coxal pores: 6–11 on each of the 12th to 15th coxae. 14th leg: 5.0 to 7.0 mm long. 15th leg 8.0 to 9.0 mm long. Spinulation on the 15th legs: DaC, DampP, DpF; VaC, Vmt, VampP, VmF, VmT. Genitalia: the gonopods are discernible, but the sexes cannot be differentiated.

Third post-larval stadium (PL3). Body length: 15.0–20.0 mm. Body width: 1.70–2.60 mm. Head length: 1.62–2.65 mm. Head width: 2.06–2.65 mm. Antennae: 9.0–12.0 mm long; number of antennal articles 34–40. Ocelli: 1+9 to 1+12 on each side. Prosternum: with 6+6 to 7+8 teeth. Tergites: posterior angles of T.6 and T.7 with projections that are blunt, broad, and short; those of T.9, T.11, and T.13 with triangular projections. Coxal pores: 12–26 on each of the 12th to 15th coxae. 14th leg: 7.0 to 9.0 mm long. 15th leg: 9.0 to 12.0 mm long. Spinulation on the 15th legs: DaC, DampP, DpF; VaC, Vmt, VampP, VamF, VmT. Male genitalia: gonopods are unsegmented slender buds. Female genitalia: gonopods small with indefinite segmentation, with or without minute cylindro-conical spur, with a small claw.

Fourth post-larval stadium (PL4). Body length: 21.0–25.0 mm. Body width: 2.20–2.90 mm. Head length: 2.28–2.94 mm. Head width: 2.72–3.31 mm. Antennae: 10.0–13.0 mm long; number of antennal articles 39–43. Ocelli: 1+12 to 1+14 on each side. Prosternum: with 7+7 to 8+8 teeth. Tergites: posterior angles of T.6 and T.7 with projections that are blunt, broad, and short; those of T.9, T.11, and T.13 with triangular projections. Coxal pores: about 24–38 on each of the 12th to 15th coxae. 14th leg: 9.0 to 11.0 mm long. 15th leg: 11.0 to 14.0 mm long. Spinulation on the

15th legs: DaC, DampP, DpF, DpT; VaC, Vmt, VampP, VamF, VamT. Male genitalia: gonopods completely segmented with distal article about half as long as basal article. Female genitalia: gonopods fairly well-developed, with two small unequal spurs and small claw.

Fifth post-larval stadium (PL5). Body length: 24.0–30.0 mm. Body width: 2.60–3.40 mm. Head length: 2.79–3.46 mm. Head width: 3.09–3.82 mm. Antennae: 12.0 to 16.0 mm long; number of antennal articles 39–44. Ocelli: 1+14 to 1+16 on each side. Prosternum: with 7+7 to 8+9 teeth. Tergites: posterior angles of T.6 and T.7 with projections that are blunt, broad, and short; those of T.9, T.11, and T.13 with triangular projections. Coxal pores: about 40-62 on each of the 12th to 15th coxae. 14th leg: 11.0 to 13.0 mm long. 15th leg: 14.0 to 17.0 mm long. Spinulation on the 15th legs: DaC, DampP, DpF, DpT; VaC, Vmt, VampP, VamF, VamT. Male genitalia: distal article of gonopod as long as basal article. Female genitalia: gonopods with two unequal spurs; claw of gonopod sharp.

Adult. Body length: 29.0–48.0 mm. Body width: 3.10–4.90 mm. Head length: 3.01–4.93 mm. Head width: 3.16–5.88 mm. Antennae: 14.0–22.0 mm long; number of antennal articles 39–46 (usually 41–43). Ocelli: 1+16 to 1+23 on each side. Prosternum: with 7+8 to 10+10 teeth. Tergites: posterior angles of T.6 and T.7 with projections that are blunt, broad and short; those of T.9, T.11, and T.13 with triangular projections. Coxal pores: about 64–127 on each of the 12th to 15th coxae. 14th leg: 14.0 to 17.0 mm long. 15th leg: 18.0 to 22.0 mm long. Spinulation on the 15th legs: DaC, DampP, DpF, DpT; VaC, Vmt, VampP, VamF, VamT. Male genitalia: gonopods long, basal article as long as distal article. Female genitalia: two conical and equal spurs on each gonopod, with very occasionally a single or third spur on gonopod(s); claw of gonopod sharp.

DISCUSSION

The variation in morphological characters of adult specimens of *E. transsylvanicus* from Serbia seems to correspond closely to descriptions of the type specimens (Latzel, 1882) and material from the Romania (Matic, 1966).

Body length is not a reliable measurement, as it depends on the extent to which the body segments telescope into one another. However, body length was here measured for comparison with existing descriptions of this species. The variation in this character is very high (Fig. 2); in the samples we analyzed, the maximum length in adults is 48 mm, a value lower than reported by Matic (1966) (Table 2).

Because of the strong head capsule, head length or head width is much more reliable than body length. Head length and head width are also features which can be used in combination with others for stadium and species identification. On the other hand, length of the 14th and 15th pairs of legs is a very useful morphological trait for separating PL5 from the adult (Table 3). Length of the 15th pair of legs is probably a key criterion for defining the adult stadium of *E. transsylvanicus* (Table 4).

Only specimens with normal or completely regenerated antennae were analyzed.

Table 2. Variation in some morphological characters of adult specimens of *E. transsylvanicus* in previous publications and present study.

Character	Latzel (1882)	Matic (1966)	Present study
body length (mm)	28-38	30-50	29.0-48.0
body width (mm)	3.50-5.0	–	3.10-4.90
head length (mm)	–	–	3.01-4.93
head width (mm)	–	–	3.16-5.88
antenna length (mm)	–	–	14.0-22.0
number of antennal articles	40-47	39-47	39-46
number of ocelli	17-21	17-20	17-24
number of forcipular teeth	16-20	16-20	15-20
number of coxal pores	–	–	64-127
spinulation on the 15th legs	0,1,3,2,2	1,1,3,2,2	1,1,3,2,2
14th legs length (mm)	–	–	14.0-17.0
15th legs length (mm)	–	–	18.0-22.0
number of spurs (female)	2+2	2+2	2+2 (1+1-3+3)

There was no significant difference in the number of antennal articles between the left and right antennae, or between males and females. This character is important for distinguishing between the PL1 and PL2 stadia (Table 3).

It is noteworthy that we found adult specimens with 24 ocelli, representing the highest number of ocelli registered to date (Table 2). However, there is clear overlapping in the number of ocelli between post-larval stadia, so this trait cannot be used to separate the different stages (Table 3).

The number of forcipular teeth is not a reliable character for identification of post-larval stadia because their growth is also irregular and variable. The nature of posterior projections on T.6, T.7, T.9, T.11, and T.13 is not a useful trait because these projections are fully developed in PL2 (Table 3).

The number of coxal pores on each of the last four pairs of legs is a character that can be used for identification of early post-larval stadia (from PL1 to PL3), as well as for distinguishing between PL5 and adult specimens (Table 3).

Although there is a characteristic pattern of spinulation for each species, there is always considerable intra-specific variation, and exactly the same spinulation is rarely found even on both sides of the same specimen. Latzel's original description of this species did not indicate a VaC spine on the 15th pair of legs (Table 2), but one is present in both Romanian and Serbian material. Spinulation of the 15th pair of legs is a key criterion for defining the PL2 and PL3 post-larval stadia of *E. transsylvanicus* in nature (Table 4).

With some difficulty, it is possible to determine the sex as early as the PL3 stadium. No gonopods were found in the PL1 stadium, while in the PL2 stadium the gonopods are discernible, but the sexes cannot be differentiated. In the male,

Table 3. Variation in some morphological characters during the postlarval development of *E. transsylvanicus.*

Character	PL1	PL2	PL3	PL4	PL5	Adult
body length (mm)	10.0-12.0	12.0-16.0	15.0-20.0	21.0-25.0	24.0-30.0	29.0-48.0
body width (mm)	1.10-1.30	1.30-1.60	1.70-2.60	2.20-2.90	2.60-3.40	3.10-4.90
head length (mm)	1.23-1.48	1.54-1.84	1.62-2.65	2.28-2.94	2.79-3.46	3.01-4.93
head width (mm)	1.28-1.60	1.62-1.98	2.06-2.65	2.72-3.31	3.09-3.82	3.16-5.88
antenna length (mm)	6.0-9.0	7.0-10.0	9.0-12.0	10.0-13.0	12.0-16.0	14.0-22.0
14th leg length (mm)	4.0-5.0	5.0-7.0	7.0-9.0	9.0-11.0	11.0-13.0	14.0-17.0
15th leg length (mm)	6.0-7.0	8.0-9.0	9.0-12.0	11.0-14.0	14.0-17.0	18.0-22.0
number of antennal articles	22-26	27-34	34-40	39-43	39-44	39-46
number of ocelli	4-6	6-9	10-13	13-15	15-17	17-24
number of forcipular teeth	5+5-6+6	5+5-6+7	6+6-7+8	7+7-8+8	7+7-8+9	7+8-10+10
number of coxal pores	3-5	6-11	12-26	24-38	40-62	64-127
spinulation on the 15th leg	0,0,2,1,1	1,1,3,1,1	1,1,3,2,1	1,1,3,2,2	1,1,3,2,2	1,1,3,2,2
genitalia (gonopods)	undeveloped	developed	developed	developed	developed	developed

the gonopod is an unsegmented slender bud in PL3; it has two articles in PL4-PL5 and the adult. In the female, the gonopod has indefinite segmentation in PL3; it has three distinct articles and two cylindro-conical spurs from the PL3 stadium onwards. Although the degree of development of the genitalia as a morphological

Table 4. Postlarval stadia in natural populations of *E. transsylvanicus.*

Stadia	Approximate body lengths (mm)	Key criteria defining stadia
PL1	10.0-12.0	undeveloped genitalia (gonopods)
PL2	12.0-16.0	15th leg spinulation: 1,1,3,1,1
PL3	15.0-20.0	15th leg spinulation: 1,1,3,2,1
PL4	21.0-25.0	distal article of male gonopod about half the length of basal article
PL5	24.0-30.0	40-62 coxal pores
adult	29.0-48.0	15th leg length: 18.0-22.0 mm

character is not sufficient for separating the post-larval stadia of *E. transsylvanicus* due to extensive overlap, it can help in defining stadium PL1, in which the genitalia (gonopods) are undeveloped (Table 4).

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