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Developmental and other body abnormalities in the genus *Lepidurus* Leach, 1819 (Crustacea: Notostraca) from Serbia

Отклонения в развитии и другие нарушения строения тела в роде *Lepidurus* Leach, 1819 (Crustacea: Notostraca) в Сербии

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КЛЮЧЕВЫЕ СЛОВА: морфологические отклонения, *Lepidurus*, Сербия.

ABSTRACT. The occurrence of morphological abnormalities and the emergence of body defects are well-known phenomena in crustaceans and other groups of arthropods. They usually originate from genetic factors and are attributable to aberrations during the moulting process, but they can also be of exogenous origin. The aims of this study were to present the external body changes that occurred in large branchiopod crustaceans of the genus *Lepidurus* Leach, 1819 (Notostraca) sampled in Serbia and discuss their possible etiology. The majority of variations were identified on the carapace and limbs, followed by ones on the abdominal part of the body, telson with caudal lamina, and cercopods. As for potential causes, the observed variations can be attributed both to genetic factors and to non-genetic ones such as predatory stress and possible environmental disturbance. Certain deviations from the mean phenotype point to irregular development (or an unpatterned moulting process) and to a possible disease. Some of the body transformations observed here influenced symmetry and functional morphology of the individuals, and may have ecological and ethological implications.

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РЕЗЮМЕ. Проявление морфологических отклонений и появление дефектов тела хорошо известны у ракообразных и других групп членистоногих. Обычно они возникают благодаря генетическим факторам и относятся к изменениям в процессе линьки, но они могут быть и экзогенного происхождения. Цель настоящей работы — показать внешние изменения в строении тела у крупных ракообразных-бранхиопод рода *Lepidurus* Leach, 1819 (Notostraca), собранных в Сербии, и обсудить их возможную этиологию. Большинство изменений отмечены у карапакса и конечностей, а затем у брюшного отдела, тельсона с хвостовой долей и у церкоподов. Что касается потенциальных причин, наблюдаемые изменения могут вызываться как генетическими, так и негенетическими факторами типа пресс хищников и возможные нарушения природной среды. Определенные отклонения от нормального фенотипа указывают на неправильное развитие (или нарушенный процесс линьки) и, возможно, болезнь. Некоторые из наблюдаемых перемен повлияли на симметрию и функциональную морфологию животных и могут иметь экологические и поведенческие последствия.

Introduction

Atypical morphology in animals usually occurs as a result of developmental instability influenced by environmental and genetic stressors [Graham *et al*., 1993]. Gilbert [2000] defined abnormalities (defects) caused by genetic events as malformations, while the abnormalities due to exogenous agents he referred to as disruptions. Body defects can appear as visible morphological changes (phenodeviance), or in the form of subtle random deviations from perfect bilateral symmetry (assuming that symmetry is an ideal state of bilaterally paired characteristics) [Tomkins, Kotiaho, 2001]. Phenodeviance represents an unusual expression of a trait that essentially differs from the typical phenotype and usually appears in less than 4% of the population (according to Møller & Swaddle, 1997). Relatively large changes, expressed as complete or partial loss of certain body parts, may influence both body shape and symmetry. Further, the abnormal appearance of a trait may occur due to disruption of the moulting process or to disproportionate or incomplete regeneration after injury [Jagadeesan, Jyothibabu, 2016]. Also, post-mortem changes are common in specimens that have been fixed or preserved in alcohol. After preservation, some body parts may appear odd [Beladjal, Mertens, 1999; Järvinen *et al*., 2014], and normal life-colours may be lost or faded.

In the case of arthropods, the aims of many studies were to observe and define various malformations and discuss possible causes of their occurrence. In such studies, natural samples were examined or anomalies were induced in laboratory conditions using different genetic or environmental manipulations. Studies were conducted in many groups of insects (for a review see Yi *et al*., 2017), spiders [Napiórkowska *et al*., 2015a, b; Tomić *et al*., 2016], scorpions [Šarić, Tomić, 2016], pseudoscorpions [Lučić, 1995; Makarov, 1995], centipedes [Minelli, Pasqual, 1986], millipedes [Janssen, 2013] and crustaceans [Dias, 1999; Luppi, Spivak, 2007; Miličić *et al*., 2013; Melo *et al*., 2014].

The genus *Lepidurus* Leach, 1819 consists of large freshwater branchiopod crustaceans. As a member of the order Notostraca, *Lepidurus* is characterized by a shield-shaped carapace with a dorsal position. At the front of the carapace there are a pair of stalkless (sessile) compound eyes and the oval nuchal organ located in the midline between the eyes. The carapace has a longitudinal dorsal carina on the medial line, with a chitinized terminal spine. The carapace covers a large part of the body and provides protection. It also provides hydrodynamic advantages to individuals, and facilitates burrowing [Olesen, 2013]. The shape, size, and pattern of spines at the posterior margin of the carapace are species-specific characters. The thorax has 11 ring-like segments with leaf-like paired swimming appendages (phyllopodous limbs). In females, the exopodite of the 11th pair of thoracopods is rounded and modified into an egg sack for reproduction [Fryer, 1988]. The number of abdominal pairs of limbs is not fixed, and, as a rule, it is greater than the number of body segments (a feature common to Notostraca). The limbs gradually become smaller, leaving some body rings free of limbs toward the end of the abdomen. The abdomen is multi-segmented and not clearly differentiated from the trunk. Since no clear correlation between the chitinized body rings and the actual body segmentation could be distinguished, Linder [1952] suggested that the term "body ring" be used instead of the term "body segment". *Lepidurus* can also be recognized from the presence of a medial elongation projecting from the telson (caudal lamina, supra-anal plate) with a characteristic arrangement of spines on its dorsal side.

Lepidurus typically inhabits astatic water bodies and short-lived pools of small volume with dramatic changes in ecological conditions over the season, and even during a single day. Species of the genus have all biological attributes necessary to provide effective mechanisms for persisting under the harsh conditions in habitats of such an unpredictable nature. They are benthic inhabitants that mainly feed on detritus, plants, algae, and bacteria [Tasch, 1969; Miller, 1980]. *Lepidurus* can also prey on other invertebrates, even on injured members of the same species [Lakka, 2013]. On the other hand, temporary pools are not "enemy-free" [Brendonck *et al*., 2002] and several potential invertebrate and vertebrate predators live in the same habitats along with *Lepidurus*. Environmental stress and environmental contamination, together with the effect of predation, can contribute to different body defects reported in populations [Linder, 1952; Longhurst, 1958; Lakka, 2013].

Table. Body defects observed among specimens. N_A — number of individuals with a specific abnormality.
Таблица. Дефекты тела, наблюдаемые у образцов. N_A — число экземпляров с определенным отклонением.

Body defect	N_A	Proportion of affected individuals in the sample considered (%)
MALFORMATIONS		
Incomplete body rings	26	12.15
Spirally growing abdominal rings	2	0.93
Asymmetrically shaped caudal lamina	15	7.04
Incompletely developed cercopod	3	1.60
DISRUPTIONS		
Injuries of carapace	31	16.85
Injuries of limbs	41	23.70
Injuries of telson and caudal lamina	11	5.16
Injuries of cercopods	9	4.81
Granules in ventral head area	28	15.47

The aims of the present work were to give an overview of the body changes observed in individuals assigned to the species *Lepidurus couesii* Packard, 1875 from Serbia, describe the most representative examples, and discuss their possible etiology.

Material and methods

We investigated specimens sampled from ponds situated in the zone of the city of Belgrade. Samples were caught alive, using a hand-held mesh net, and immediately fixed in ethyl-alcohol. Only individuals that showed attributes of adults were used for analysis. During screening for body abnormalities, a total of 214 specimens were examined. Characters common to both sexes and sexually dimorphic characters [Šaganović *et al*., 2017] were observed in establishing the presence of morphological/structural variations and defects. The body rings of apodous segments (nomenclature following Longhurst, 1955) in ventral view of the abdomen were investigated and counted. The spiral-shaped body rings (after Linder, 1952) were also examined and assessed. Where it was appropriate, the body details of representative examples, including spiral-shaped abdominal rings, were photographed or illustrated. Each example of irregular development of the abdomen was presented using the formula (F) proposed by Linder [1952]: number of thoracic limbs (fixed at 11) + number of abdominal leg-bearing rings + legless rings + incomplete abdominal rings (*i*) or spiral-growth (*sp*), presented with the number of rounds of body rings (*r*). Orientation of the spirally growing body rings around the abdominal axis (right-handed – R/left-handed – L) was also taken into account.

In addition, each individual was investigated for possible qualitative changes in different body parts (physical deformations, injuries, lesions, changes in body colour, etc.), and for other types of abnormalities. The carapace, sulcal margin of the carapace, telson with the caudal lamina (after Rogers, 2001, supra-anal plate (after Linder, 1952) and most prominent parts of the body such as the furcal rami (cercopods) were also thoroughly investigated under a Carl Zeiss Stemi 2000 binocular dissecting microscope. Digital images were taken with a Sony DSC F828 digital camera (Sony Corp., Tokyo, Japan).

Results

Among all specimens examined, several body anomalies were observed on the carapace, abdomen, limbs, telson with caudal lamina, and cercopods (Table).

In *Lepidurus*, the dorsal medial carina divides the carapace longitudinally into the left half and the right half. In *L. couesii,* it is strongly chitinized and spineless. However, in more than one-third of the examined individuals (36.58%), we found solitary spines of tiny proportions or small rounded outgrowths lying along the carina (Fig. 1). In some individuals, we also observed irregularly arranged sulcal spines, especially in the area close to the terminal carina spine.

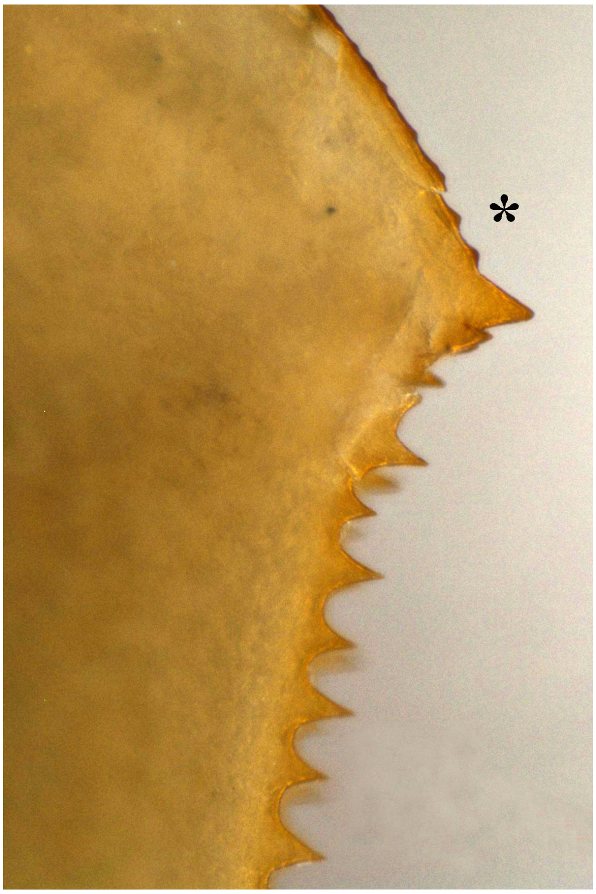

Fig. 1. Small spines and rounded outgrowths on the dorsal medial carina (asterisk).

Рис. 1. Мелкие шипы и округлые выросты на спинном срединном гребне (звездочка).

The abdomen of specimens was also subject to irregular development. Irregularities of the abdomen were usually manifested in the form of a discordant segmental pattern, even on the dorsal and ventral side of the same individual. In the same habitat, next to specimens with normal growth, we found individuals with the occurrence of shorter or incomplete (asymmetric) body rings showing a reduction (in some individuals, even half of the ring is missing (Figs 2a, 2c, and 2e). Some body rings exhibited partial atrophy in the form of a small ring residuum (scale) situated at the base of the telson (Fig. 2b). However, the typical spiral growth was rarely found in the sequence of rings (in only two specimens). One individual had a right-handed (R) spiral of little more than two rounds. In the other case, a left-handed (L) spiralization of two full rounds was noted (Fig. 2d).

Further analysis of the distal part of the body reveals the presence of many discrepancies between spines on the right and left sides of the telson. The mismatch in spine number was observed on both the dorsal and the ventral sides of the telson in almost all specimens.

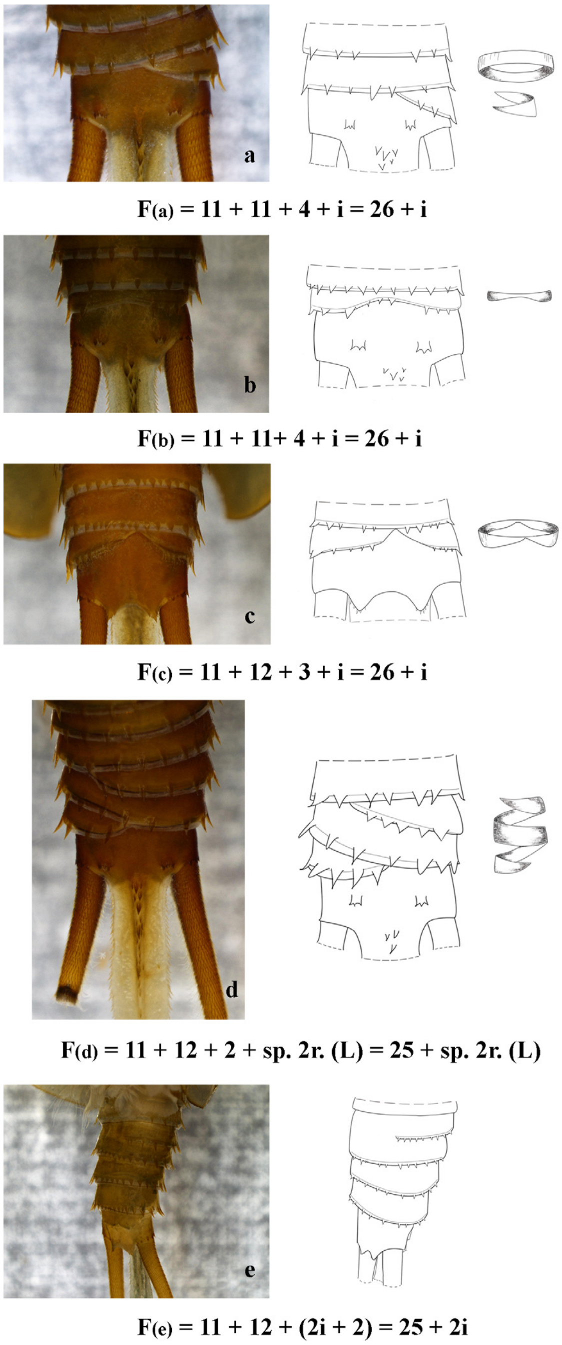

Fig. 2. Examples of incomplete and spirally growing abdominal rings, with original drawings (by I. Šaganović) of accurate structural changes represented by Linder's formula (F). Abbreviations: i — incomplete abdominal rings; sp — spiral growth; r — number of rounds of body rings; L — left-handed orientation of spirally growing body rings.

Рис. 2. Примеры неполных и спирально растущих брюшных сегментов, с оригинальными рисунками (выполнены И. Шагановић) аккуратных структурных изменений, представленными по формуле Линдера (F). Сокращения: i — неполные брюшные сегменты; sp — спиральный рост; r — число оборотов сегментов тела; L — левосторонняя ориентация спирально растущих сегментов тела.

In some individuals, we also found an asymmetrically shaped caudal lamina (clearly visible in 7.04% of individuals, Figs 3a and 3b) or an incompletely developed (shortened) cercopod of unusual morphology (Fig. 3d).

Disruptions of different origin (lesions, changes in body colour, parasite invasion, and tumour-like growths) were also visible on the body surface in some individuals. Those changes were manifested in the presence of altered morphology and/or chitinous darker edges, as well as in deposition of thickened dermal (callus) tissue in damaged animals. The most common were injuries of the carapace (in 16.85% of individuals considered) and limbs (23.70%), followed by damage to the telson with the caudal lamina (in 5.16% of individuals) and cercopods (injuries of the cercopods and considerable loss of cercopod length were observed in 4.81% of individuals). Only in two individuals did we find a serious injury (lack of) the 11th limb bearing the ovisac.

In some individuals, the carapace was developed incompletely, with partial reduction of the right or left side. It seems that those individuals failed to accomplish full development of this cuticular structure, a situation probably triggered by agents of different origin. Some carapaces exhibited holes or cracks, accompanied by reduction of the area covered by sulcal spines. To judge from shape of the fractures, it seems that these injuries were largely caused by attack from predators and/or conspecifics (Fig. 4). In some carapaces, we also observed a broken terminal carina spine.

Adults from our sample were usually brown to green in colour. However, we noted changes of standard body colouration in some individuals. We found rounded pale-yellow structures (granules) on the anteroventral side of the cephalic part of the carapace. Also, we noted zones with darker dots on the limbs, carapace, and telson. The observed granulations could be an indication of parasite infections (Figs 3c and 5).

In almost a quarter of considered individuals, we found a stage with the carapace and caudal lamina slightly raised to an upright position, indicating an ongoing moulting process.

Discussion

Up to now, many studies of body deformities have been focused on several groups of arthropods [Lučić, 1995; Makarov, 1995; Zanata *et al*., 2008; Martinelli-Filho *et al*., 2009; Fernandez *et al*., 2011; Feullassier *et al*., 2012; Tomić *et al*., 2016; Yi *et al*., 2017]. Morphological abnormalities were also documented and described in some large branchiopod crustaceans [Lakka, 2013; Miličić *et al*., 2013]. Body deformities are usually attributed to genetic factors [Zou, Fingerman, 2000]; alterations during the moulting process [Luppi, Spivak, 2007; Napiórkowska *et al*., 2015a] and predatory injury, disease, or regeneration after injury [Gregati, Negreiros-Fransozo, 2009].

Examinations of *Lepidurus* specimens from Serbia revealed the occurrence of several unpatterned forms,

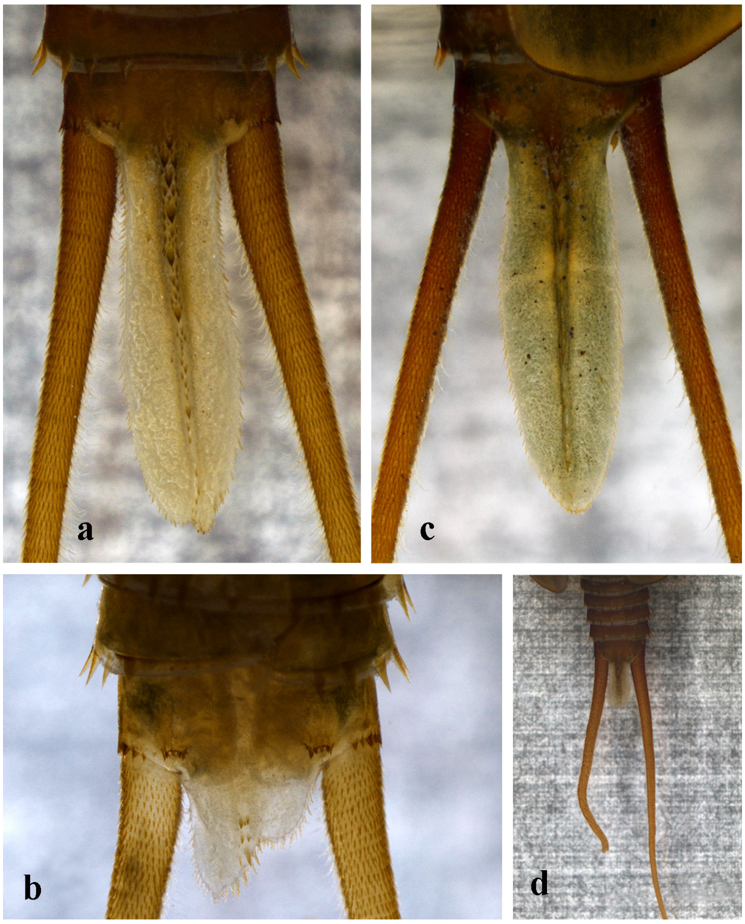

Fig. 3. Asymmetrically shaped caudal lamina (a), incompletely developed caudal lamina (b), caudal lamina with pigmentations (c), and incompletely developed cercopod (d).

Рис. 3. Асимметрично оформленная хвостовая доля (a), не полностью развитая хвостовая доля (b), хвостовая доля с пигментацией (c) и не полностью развитый церкопод (d).

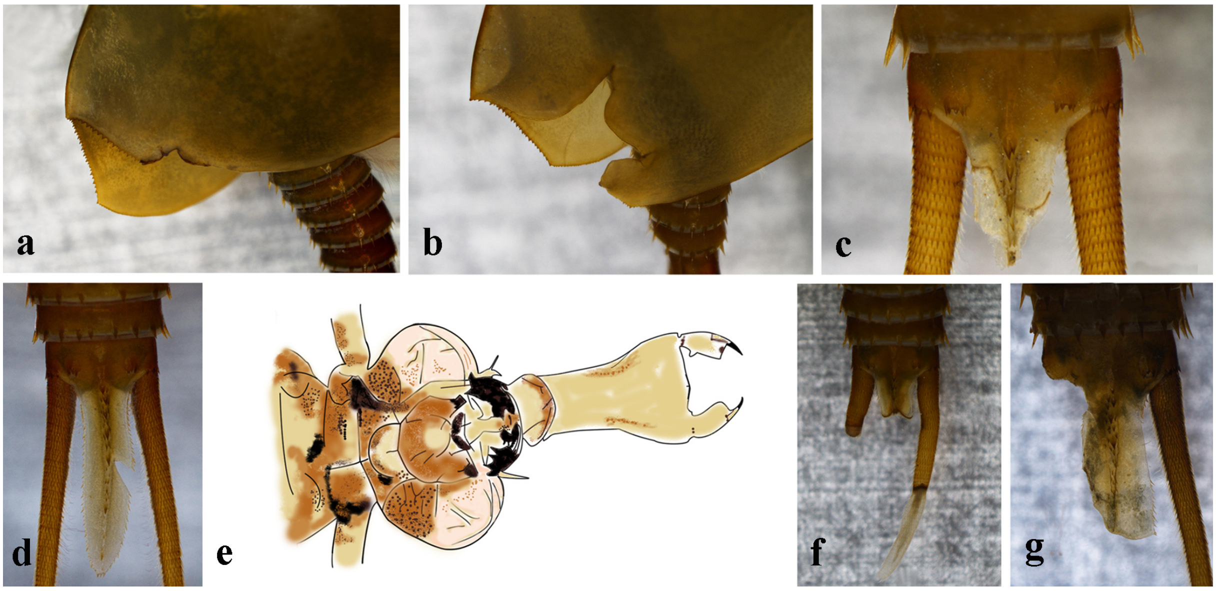

Fig. 4. Examples of injuries in different body parts: a, b — carapace injuries; c, d — caudal lamina injuries; e — drawing of Odonata larvae with extended mandibles (a potential predator in natural habitats, drawn by I. Šaganović); f, g — caudal lamina and cercopod injuries.

Рис. 4. Примеры повреждений различных частей тела: a, b — повреждения карапакса; c, d — повреждения хвостовой доли; e — рисунок личинок стрекоз с вытянутыми мандибулами (потенциальный хищник в естественных биотопах, выполнен И. Шагановић); f, g — повреждения хвостовой доли и церкоподов.

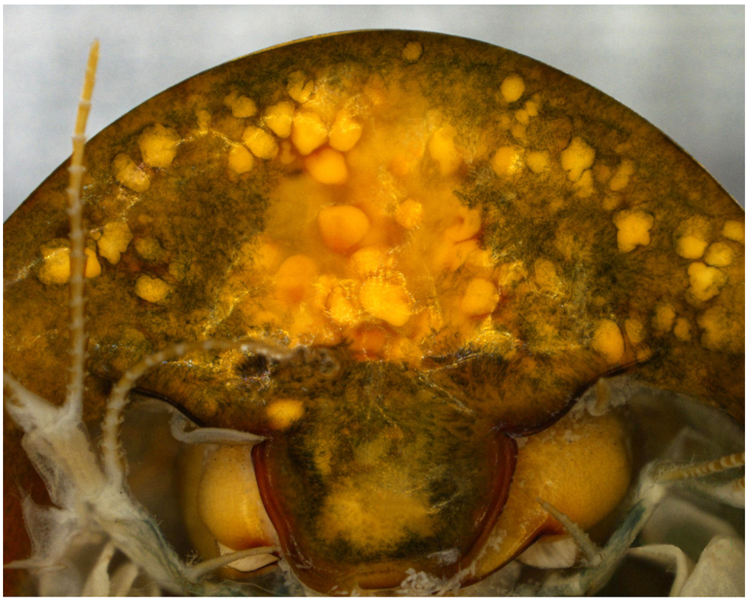

Fig. 5. Granules in ventral head area, most likely due to parasites.
Рис. 5. Гранулы в районе низа головы, скорее всего, это паразиты.

which could be attributed to both internal and external factors. The uneven body segmentation and irregular growth described in our study were manifested in the form of spiral growing, shortened body segments, or incomplete ring formation. In the past, they were usually considered to be developmental traits common to Notostraca [Bernard, 1929; Longhurst, 1958], but also to other major arthropod clades as well (for a review, see Leśniewska *et al*., 2009). This anomalous segmental pattern is referred to as 'helicomery' — a condition of segment structure in arthropods without discrete axial units (belts or segments) around the axis [Minelli, Pasqual, 1986]. According to recent investigations conducted on centipedes [Leśniewska *et al*., 2009], a helicomeric pattern should not be considered as a body anomaly on its own, but rather to be the result of a combination of several types of defects, mispairings, and sclerite arrangements during late-embryonic development and segmentation. A common feature of embryonic development in *Lepidurus* and other large branchiopod crustaceans is a period of dormancy, when the embryo is arrested in an early stage of organogenesis (at the gastrula stage). This dormant period is characterized by the absence of cellular multiplication and DNA replication [Dumont, Negrea, 2002]. Upon entry into cryptobiosis, only renewed hydratation, suitable osmotic pressure, or sufficient oxygen [Cleg *et al*., 1996] can initiate completion of development in the encysted gastrula. The period before hatching is characterized by increased cell activity [Olson, Clegg, 1978], and intense morphogenesis [Morris, Afzelius, 1967]. Growth of the abdomen is based on ectoteloblast proliferation and posterior segmentation (the sequential adding of segments from the posterior part of the growing embryo). As *Lepidurus* lives in temporary habitats (short-lived ponds) with high selection pressure on life history traits associated with rapid development, fast growth, and early maturity of individuals, it is important for individuals to mature quickly (in *L. apus* (Linnaeus, 1758) sexual maturity is reached in about 30 days [Miličić, Petrov, 1998]). The cost of fast growth and rapid maturation may be serious disruption of developmental processes, increased frequency of unpatterned morphogenesis, and malformations of organs and whole body regions. This could be a very promising area for further research, at least in large branchiopods.

It was previously noted that the number of ring-like segments ("body rings") may differ, even within the same population, in members of the genus *Lepidurus* [Linder, 1952; Longhurst, 1955]. Given that the number of apodous segments also varies in Notostraca, abdominal body parts were generally not considered to be good tools for species characterization [Korn *et al*., 2006]. Our study confirms that those characters can be variable even within a sample collected from the same pond.

Even though the dorsal carina is spineless, at least so in *L. couesii* (according to Lynch, 1972), in about 40% of Serbian samples we found individuals with the occurrence of minor sclerotizations in the form of small spines or rounded outgrowths arising smoothly along the dorsal surface of the carina. Since the carinal differences occur in a relatively high proportion of specimens, we can consider them to be a manifestation of intraspecific variation rather than a developmental malformation. It seems that some of the phenotypic traits observed in branchiopods appear as a plastic response to environmental heterogeneity rather than being a consequence of developmental instability [Miličić *et al*., 2017].

In Notostraca, the carapace is a characteristic body feature that extends from the head region and envelopes a large part of the body. The characteristic shape and structure of the carapace offer egg protection (only two specimens from our sample were missing a large part of the 11th thoracopod with the ovisac) and provide hydrodynamic streamlining of the animals.

In our sample, a damaged carapace was noted in several specimens. In most cases, the damage was externally induced, originating from injuries caused by predators and/or conspecifics. The shape of some holes and ruptures closely resembled morphology of the jaws of potential predators, mainly dragonfly (Anisoptera) and/or other aquatic insect nymphs. Some cut and crushed body areas may also be the result of intraspecific predation (cannibalism), which is widespread in Notostraca [Arnold, 1966; Lakka, 2013, 2015]. Damage was usually followed by partial regeneration, when new layers of chitin congregate in order to protect the broken cuticle. This is indicated by the occurrence of darkened areas, where the regenerated chitin was hardened via sclerotization. On the other hand, the most common injuries were noticed in limbs as the softest parts on the ventral side of the body (in almost a quarter of examined individuals), not protected by the carapace. The carapace offers many other advantages, such as ensuring proper feeding and respiration [Olesen, 2013].

Injuries to the telson and cercopods were also noted in the specimens observed in this study. Some individuals had a severely damaged and incompletely regenerated caudal lamina, usually half (or more than half) the length of the lamina of normal specimens, asymmetrical, and often with no marginal armature. The long and thin cercopods also differed in their morphology, even among individuals from the same pond. A few cercopods had a curled appearance, and in some cases the paired cercopods were intact, but of unequal length. On the other hand, the occurrence of darker areas in some cercopods indicated possible injuries, proved by the presence of rings of regenerated tissue. A highly flexible, narrow, and elongated structure of the tail in *Lepidurus* considerably enhances its swimming performance. Animals with abnormalities of the tail or lacking tails might have difficulties in achieving the force required to swim properly and overcome the water´s surface tension [Lakka, 2015].

The (cryptic) colouration of the animals may also have definite biological relevance. It likely depends on variations in the physical environment and conditions in temporary freshwater habitats [Rogers, 2001; Lakka, 2015]. Some specimens from our study diverged from the ”standard” colouration, showing an altered colour pattern of the carapace, legs, and telson, probably due to the presence of parasites attached to their surface. Since individuals with symptoms of disease can spread infection within the population and may display abnormal behaviour [Lakka, 2013], this certainly needs to be the subject of some further analysis.

The developmental and other deviations discussed here undoubtedly have ecological and ethological implications, since they affect behaviour and disable individuals in their (appropriate) response to the conditions of natural life. This assumes even greater importance when it is borne in mind that several potential predators (such as some amphibians and invertebrates) use the same habitats and represent significant biotic stressors in temporary pool communities [Brendonck *et al*., 2002]. The morphological changes and deformities mentioned above can also influence overall body shape and in the end contribute to altered symmetry of individuals. Defective or unusually changed sexually dimorphic traits, such as characteristics of the carapace, telson, caudal lamina, and cercopods (see Hessen *et al*., 2004; Lakka, 2015; Šaganović *et al*., 2017) might be under sexual selection and affect the fitness of individuals.

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