

Structure of the mandibular molar surface of  
*Lynceus dauricus* Thiele, 1907 and *L. brachyurus* O. F. Müller, 1776  
(Branchiopoda: Laevicaudata)

Строение жевательных пластинок мандибул  
*Lynceus dauricus* Thiele, 1907 и *L. brachyurus* O. F. Müller, 1776  
(Branchiopoda: Laevicaudata)

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КЛЮЧЕВЫЕ СЛОВА: Branchiopoda, “Conchostraca”, Laevicaudata, *Lynceus*, мандибулы, морфология, систематика.

ABSTRACT: The morphology of the mandibular molar surface of *Lynceus dauricus* Thiele, 1907 and *L. brachyurus* (O. F. Müller, 1776) (Crustacea: Branchiopoda: Laevicaudata: Lynceidae) was studied by optical and scanning electron microscopy (SEM). The following traits are characteristic of both right and left molar surfaces of *Lynceus*: full symmetry; elongation along the longitudinal axis; linear location of elements; absence of any special marginal elements along the dorsal and ventral margins; molar surface armed with 13–15 conspicuous transverse ridges, triangular in section and strongly prominent; a single posterior tooth; absence of any pores. A number of species-specific traits of the mandibles that may be used in the systematics of the genus *Lynceus* is revealed.

РЕЗЮМЕ: Морфология жевательных пластинок мандибул *Lynceus dauricus* Thiele, 1907 и *L. brachyurus* O.F. Müller, 1776 (Crustacea: Branchiopoda: Laevicaudata: Lynceidae) изучена при помощи оптической микроскопии и СЭМ. Для правой и левой жевательных пластинок *Lynceus* характерны: симметричность, вытянутость вдоль передне-задней оси, линейное расположение элементов на ней, отсутствие краевых элементов вдоль спинного и брюшного края, наличие 13–15 мощных поперечных складок и единственного зуба в задней части, отсутствие каких-либо пор на пластинке. Выявлен ряд признаков мандибул, имеющих значение для систематики *Lynceus*.

### Introduction

Mahoon [1960] presented sketchy pictures and un-detailed descriptions of lynceid mandibles. Martin [1989]

analysed the mandibular morphology of several “conchostracan” genera (in this communication, I follow the classification of Branchiopoda by Fryer [1987]), and revealed a basic dissimilarity in the morphology of the molar surfaces of Laevicaudata and Spinicaudata. Among the Lynceidae Stebbing, 1902, only the mandibles of *Lynceus gracilicornis* (Packard, 1871) have been investigated by SEM [Martin et al., 1986; Martin, 1989], but their descriptions are less detailed than those provided for other branchiopod mandibles (e.g. Edwards [1980]; Martin & Cash-Clark [1995]; Mura [1995, 1996]). As a consequence of this lack of information, no one has attempted to apply features of mandibular morphology to the systematics of the genus *Lynceus* (and all Laevicaudata), though this possibility was demonstrated earlier for other branchiopods: Anomopoda [Edwards, 1980; Kotov, 1999, 2000], Onychopoda [Meurice & Monoyer, 1984], and Anostraca [Mura, 1996].

This study attempts: (1) to describe in detail the molar surfaces of the mandibles of two species of the Laevicaudata common in Russia: the transbaikalian *Lynceus dauricus* Thiele, 1907 and the holarctic *L. brachyurus* O. F. Müller, 1776; (2) to analyse intra- and interpopulational variability of their morphology (including instar/size variability) using *L. brachyurus* as an example; (3) to ascertain the differences in morphology of the mandibles between the two species.

### Materials and methods

I studied samples from temporary ponds and pools from the following localities of Russia:

*Lynceus dauricus*: (1) flood plain of the Suyfun River, region of Vladivostok, Primorye Province,

28.09.56, collector unknown. Sample from the personal collection of T. I. Dobrynina.

***Lynceus brachyurus***: (1) right bank of the Yakot River near Rybnoye, Moscow Area, 15.05.67, coll. N. N. Smirnov; (2) right bank of the Moscow River near Novo-Shihovo, Moscow Area, 06.98, coll. A. Ju. Sinev; (3) vicinity of Borok on Ribinsk Water Reservoir, Yaroslavl Area, 1.06.1977, coll. A. V. Monakov & T. I. Dobrynina; (4) edge of road Yaransk-Tuzha, Kirov Area, 7.06.1991, coll. T. I. Dobrynina.

All samples were initially preserved in 4 % formaldehyde. A few animals (only females) were washed in distilled water, dried by lyophilization, and glued to aluminium stubs. The attached specimens were then dissected, the separated mandibles glued to the same stubs (members of a pair were placed near each other), sputtered with gold, and examined using a scanning electron microscope (JEOL-840A). I studied 5 left and right mandibles of *Lynceus dauricus*, and 10 right and left mandibles of *Lynceus brachyurus* from samples 1 and 3.

Material of *L. dauricus* was not abundant, and only the mandibles of *L. brachyurus* were studied morphometrically. For the study of size variability, a random subsample of 100 specimens from Yakot was studied. Body lengths (BL) were measured, then animals were divided into 3 size groups (< 2.5, from 2.5 to 3, and > 3 mm). Mandibles were dissected out, and the length (ML) and height (MH) of the molar surface, length of the single posterior tooth (TL), length of the gap between the latter and the closest element of the molar surface (LG), and number of transverse ridges (RN) were measured for left and right mandibles of each animal. Some other parameters (ML/BL, MH/ML, TL/ML, LG/ML) were calculated for each group independently. For the study of interpopulational variability, the same measurements and calculations were made for 20 animals larger than 3mm from each population.

## Results

### *Lynceus dauricus* Thiele, 1907 Figs 1–12.

The distalmost part of the corm of both mandibles is wrinkled near the molar surface (Figs. 1, 3, 5: wr), and this is not an artifact of the specimen preparation. In a ventral or dorsal view the molar surface of both mandibles

is slightly convex (Fig. 3). A single posterior tooth extends posteriorly (Figs 1–4: pt). In surface view, the molar surfaces of both mandibles are symmetrical, lancet-shaped, very narrow and long, length/width = 6-7/1. The dorsal edge of each molar surface is weakly convex, the ventral edge practically straight (Figs 1, 4–5).

Most of each molar surface of an adult female mandible is occupied by 13–15 transverse ridges (Figs 1–3: tr; arrow marks rudimentary 15th ridge on a left mandible in Fig. 2). In dorsal or ventral view, each ridge is triangular in section, with numerous minute nipple-shaped protuberances (term of Tyson & Sullivan, 1981) (Figs 7, 12). These elements are strongly effaced in the middle portion of the molar surface, apparently as a result of wear, but remain pointed in the anterior portion.

The anteriormost ridge (Figs 7–9; ar) is small or rudimentary, with a cluster of rather large spines on its anterior face (ac). The entire anterior-distal corner of the mandible, near the molar surface, is densely covered with fine setules, either solitary or organised in groups of 2 to 3 (Fig. 8–10: fs). Closer to the longitudinal axis of the molar plate, these setules gradually increase in size and merge with the above-mentioned anterior cluster of spines (Fig. 10). Isolated groups of setules are also present on wrinkles of the posterior-distal part of the mandible corm some distance from the molar surface (Fig. 11).

The distance between transverse ridges increases posteriorly, and there is an especially large gap between the two posteriormost ridges. In the posterior portion of the plate, the central part of each ridge is concave (Figs 5–6). The posterior corner of a molar surface is occupied by a single, rather high, conical tooth, located somewhat ventral to the longitudinal axis of the molar surface.

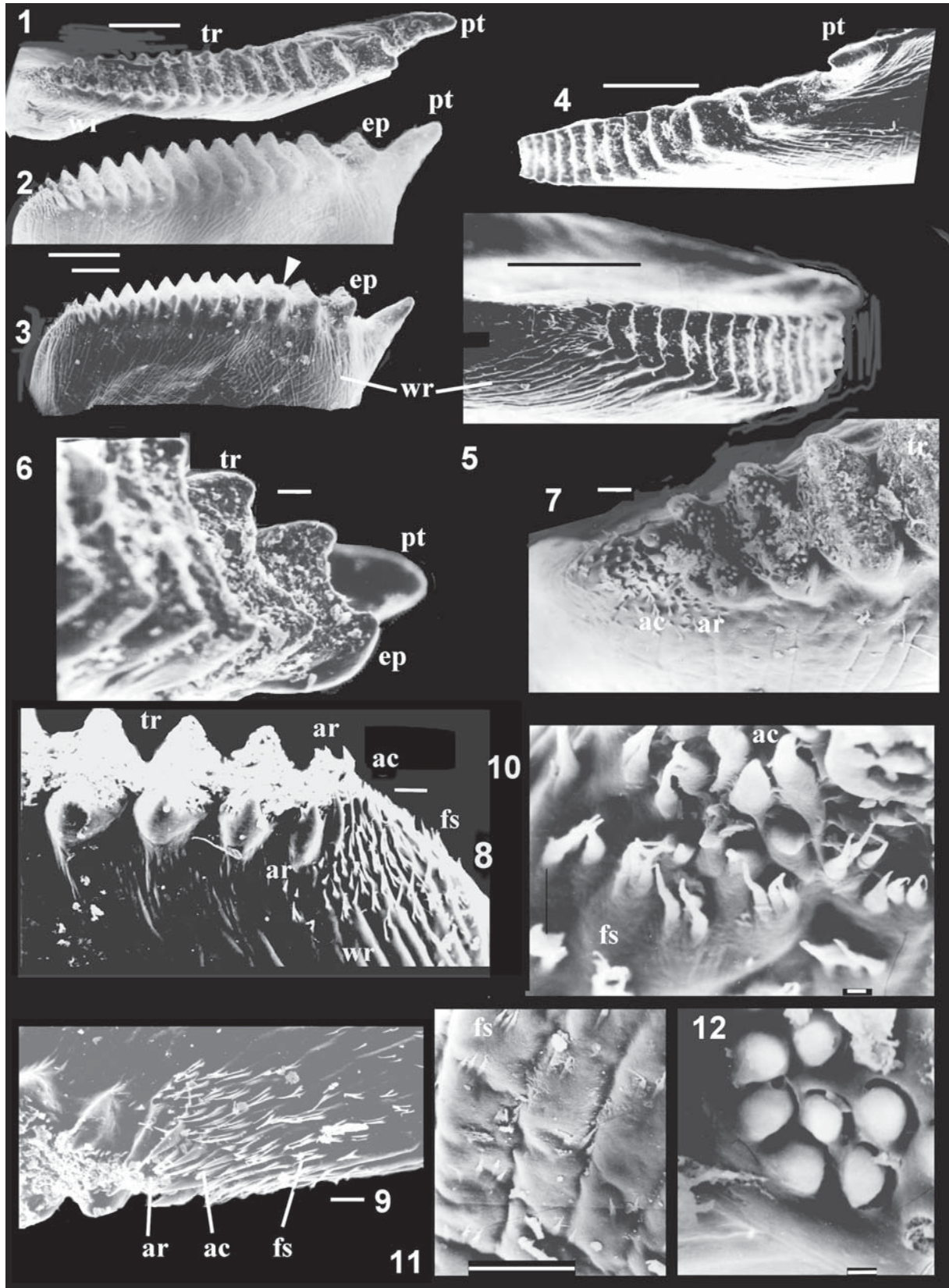
### *Lynceus brachyurus* O. F. Müller, 1776. Figs 13–25.

The form of the molar surface and its armature are rather similar in *L. brachyurus* and *L. dauricus*. In this short communication, I do not describe in detail the mandibular morphology in *L. brachyurus*, and only indicate the differences:

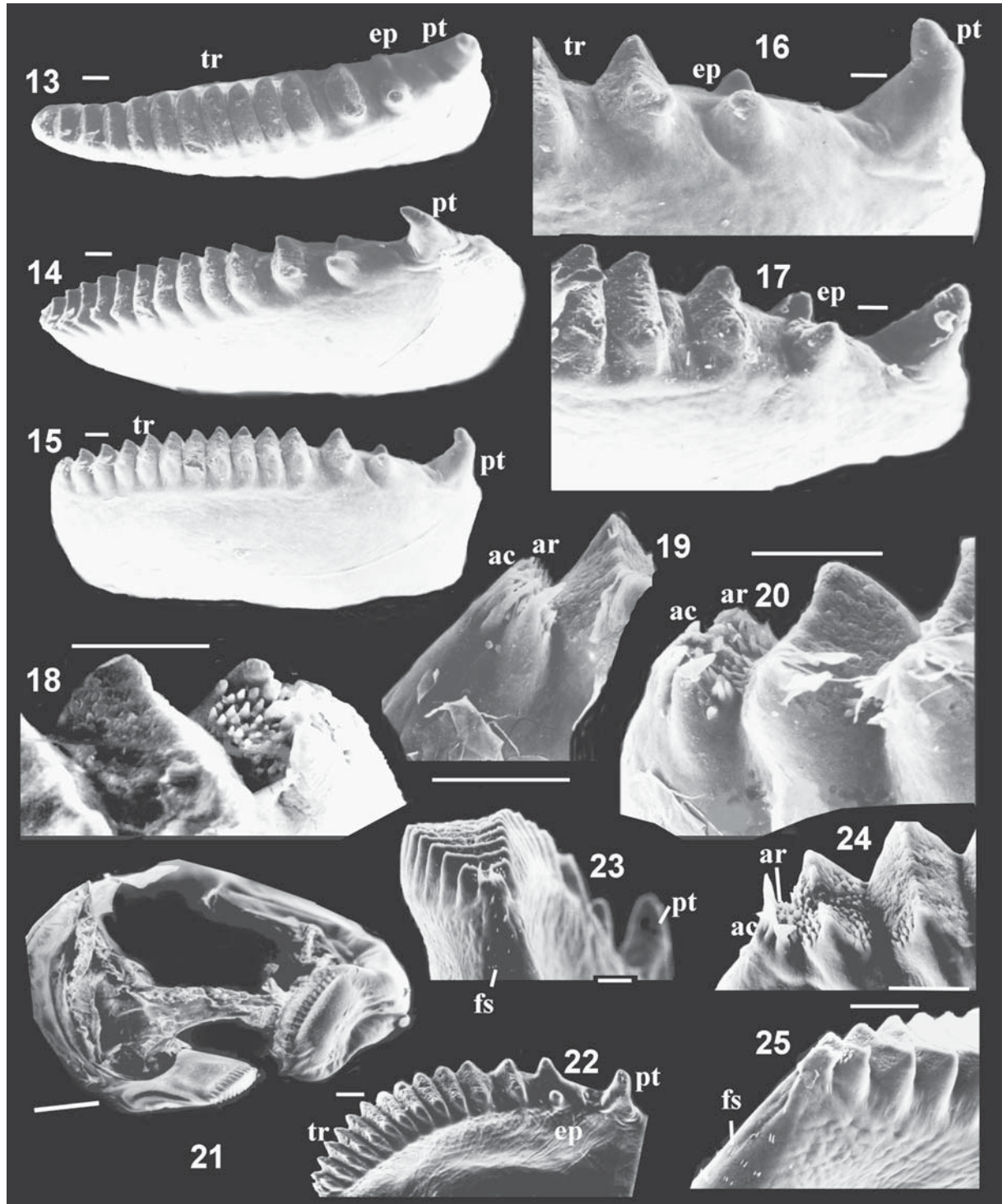
(1) In *L. brachyurus*, the element closest to the single posterior tooth is represented by two teeth, clearly separated from each other (Figs 13–17, 22: ep). In *L. dauricus* it is represented by a transverse ridge, concave in the central part and clearly continuing a line of more

Figs 1–12. *Lynceus dauricus*, mandibular molar surface: 1 — left mandible, surface view; 2–3 — dorsal view; 4 — posterior view; 5 — right mandible, anterior view; 6 — posterior portion of left mandible, anterior view; 7 — its anterior portion, surface view; 8–10 — anterior portion of left mandible, ventral, dorsal and anterior view; 11 — clusters of setules on wrinkles of posterior-distal part of the mandible corm; 12 — nipple-shaped protuberances on a transverse ridge. Scale bars: 100  $\mu$ m for 1–5; 10  $\mu$ m for 6–9, 11; 1  $\mu$ m for 10, 12. Abbreviations: ac — anterior cluster of spines; ar — anteriormost ridge; ep — element closest to single posterior tooth; fs — fine setules; pt — posterior tooth; tr — transverse ridge; wr — wrinkles on distal part of mandible corm.

Рис. 1–12. *Lynceus dauricus*, жевательные пластинки правой и левой мандибул: Рис. 1 — жевательная пластинка левой мандибулы, вид с поверхности; 2–3 — со спинной стороны; 4 — сзади; 5 — правая мандибула, вид спереди; 6 — задняя часть левой жевательной пластинки спереди; 7 — ее передняя часть; 8–10 — передняя часть жевательной пластинки левой мандибулы, вид с брюшной, спинной стороны и спереди; 11 — пучки зубчиков на задне-дистальной части тела мандибулы; 12 — сосковидные выступы на поперечной складке. Масштаб: 100  $\mu$ m для 1–5; 10  $\mu$ m для 6–9, 11; 1  $\mu$ m для 10, 12. Условные обозначения: ac — передние пучки зубчиков; ar — передние складки; ep — элемент, ближайший к одиночному заднему зубу; fs — тонкие сетулы; pt — задний зуб; tr — поперечные складки; wr — морщины на дистальной части тела мандибулы.







Figs 13–25. *Lynceus brachyurus*, molar surface of left (13–21) and right (21–25) mandibles: 13 — surface view; 14–15 — dorsal view; 16–17 — posterior portion; 18–20 — anterior portion, ventral and dorsal view; 21 — a pair of mandibles, 22–23 — distal part in ventral and anterior view; 24–25 — anterior portion of molar surfaces of two different mandibles. Scale bars: 100  $\mu\text{m}$  for 13–15, 21; 10  $\mu\text{m}$  for 16–20, 22–25.

Рис. 13–25. *Lynceus brachyurus*, жевательные пластинки левой (13–21) и правой (21–25) мандибул: 13 — вид с поверхности; 14–15 — со спинной стороны; 16–17 — сзади; 18–20 — передняя часть, вид с брюшной и спинной сторон; 21 — пара мандибул, 22–23 — дистальная часть пластинки с брюшной стороны и спереди; 24–25 — передняя часть пластинки двух разных мандибул. Масштаб: 100  $\mu\text{m}$  для 13–15, 21; 10  $\mu\text{m}$  для 16–20, 22–25.

Table 1. Measured and calculated parameters (average, and range in parentheses) of molar surfaces of *L. brachyurus*. See explanation of the abbreviations in the text, n — number of studied animals.  
Таблица 1. Результаты промеров (средние, в скобках — минимальное и максимальное значение) жевательных пластинок *L. brachyurus*. См. объяснения в тексте, n — число исследованных животных.

population	n	size, mm	ML, $\mu\text{m}$	ML/ BL	MH/ ML	TL/ ML	LG/ ML	RN
Yakot	23	2.2 (2–2.5)	242(240–253)	0.11 (0.10–0.12)	0.23 (0.21–0.27)	0.13 (0.10–0.17)	0.10 (0.9–0.10)	13.7 (13–14)
	63	2.9 (2.5–3)	286(250–300)	0.11(0.09–0.11)	0.24 (0.21–0.25)	0.14(0.12–0.16)	0.11 (0.08–0.13)	14.3 (13–15)
	14	3.2 (3–3.4)	312(303–321)	0.10 (0.10–0.11)	0.24 (0.20–0.28)	0.15 (0.11–0.18)	0.08 (0.07–0.10)	14.6 (14–15)
Shichovo	20	3.1(3–3.3)	309(290–317)	0.10(0.09–0.11)	0.23(0.22–0.24)	0.14(0.12–0.15)	0.09(0.07–0.11)	14.2(14–15)
Borok	20	3.4(3–3.8)	332(310–358)	0.11(0.09–0.11)	0.22(0.21–0.25)	0.15(0.13–0.17)	0.11(0.09–0.12)	14.6(14–15)
Yuransk	20	3.5(3–4.2)	341(316–385)	0.10(0.09–0.11)	0.23(0.21–0.25)	0.14(0.13–0.18)	0.10(0.08–0.14)	14.5(14–15)

anterior elements of the molar surface (Figs. 2–3, 4, 6). In all specimens of *L. brachyurus* the dorsal tooth is larger than the ventral. I believe that the situation in *L. dauricus* is the more primitive, and that in *L. brachyurus* the two teeth originated as a result of the further deepening of the depression in the central part of the posterior-most ridge. In my measurements I regarded this pair of teeth as another cross ridge of the molar surface.

(2) In *L. brachyurus* all the transverse ridges are weakly depressed and in the same manner (Figs 14–15, 20, 23), while in *L. dauricus* the more posterior and anterior ridges are more strongly incised (Fig. 6).

(3) In *L. brachyurus* the fine setules of the anterior-distal end of the mandible are scarce and located far from the anterior edge of the molar plate (Figs 23, 25), or are absent (Fig. 19, 24), whereas in *L. dauricus* they are numerous and gradually pass into the anterior cluster of spines (Figs 8–10).

All the aforementioned characters are not subject to size variability in adults (no information on larval and juvenile instars!). I could not find any significant differences in mandibular morphology either among populations or within a population, and morphometrics confirm this (Table 1). Only the number of ridges varies weakly from instar to instar; the majority of adults have 14 ridges on each mandible, but some of the smallest adults may have 13, and some of the largest 15.

## Discussion

Revealed species-specific traits are not subject to variation and provide a basis for using such mandibular features in systematics. They can be seen not only under SEM, but also by optical microscopy, and can be included in the diagnosis of species.

Morphometric analysis did not reveal any differences between the left and right mandible of an individual. Both molar surfaces of *Lynceus* are symmetrical, in contrast to various other branchiopods with a longer right molar surface: Spinicaudata [Mahoon, 1960], Anostraca [Ocioszyńska-Bankierowa, 1933b, Fryer, 1983], Anomopoda [Ocioszyńska-Bankierowa, 1933a; Fryer, 1963 and other papers; Kotov, 1998, 1999, 2000]. In the Anomopoda, Fryer [1963] showed how mandibular

asymmetry is accompanied by asymmetry of the transverse mandibular muscles which swing the right mandible through a greater arc than the left.

Unfortunately for purposes of this study, Martin [1989] published photographs showing only the lateral view of mandibles of *L. gracilicornis*, so various features are not seen. However, it is clear that the mandibles are very similar in all three species investigated at present. The characteristic features of the right and left molar surfaces of *Lynceus* are:

- 1) full symmetry;
- 2) elongation along the longitudinal axis;
- 3) linear location of elements on them;
- 4) absence of any special marginal elements along the dorsal and ventral edges;
- 5) presence of 13–15 powerful transverse ridges, which are triangular in section and strongly prominent above the molar surface (However, in *L. simiaefacies* Harding, whose mandibles are basically similar to those of the species described here, there are about 24 transverse ridges. These are, inevitably, smaller and more closely set than those described here. The difference is probably related to differences in the kinds of food collected (G. Fryer, personal communication);
- 6) presence of a single posterior tooth;
- 7) absence of any pores.

The transverse ridges of the mandibular molar surface of Laevicaudata probably are homologous with the diagonal or transverse ridges of the mandibles of recent Anostraca, Spinicaudata, Anomopoda, Ctenopoda and palaeozoic Lipostraca.

Branchiopod mandibles are the most primitive among crustaceans with grinding movements [Manton, 1977]. In the course of rotation the molar surfaces rub against one another. The function of diagonal ridges is the same in all branchiopods: they press and crush the food that penetrates a slit between the mandibles. Marginal elements prevent loss of food from between the mandibles. Such armature is scarcely represented in *Lynceus*. The posterodorsal zone of the molar surface is armed with powerful teeth which triturate large food particles. The morphology of this zone depends on the type of food in anomopods [Fryer, 1991; Kotov, 1998, 1999]. It was shown for anostracans that posterodorsal teeth are pow-

erful in facultative predators, and weakly developed in obligate planktophagous species, but in both categories of animals the anteroventral ridges are rather similar [Mura, 1995].

As in the case of other branchiopods, the anterior-most and posteriormost portions of the mandibles of the Lynceidae are of more systematic importance than the middle portion. The food of *Lynceus* is rather diverse: different authors refer to detritus, large benthic algae, and, probably, predatory tendencies in some cases, based on the presence of "arthropodal spines and cuticle" in gut contents (see review of Martin [1989]). However, this information is not systematised and the food preferences of individual species are not clear. It is probable that the differences between species, as revealed in this study, are a consequence of differences in their feeding habits.

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