# Notes on the genus *Ilyocryptus* Sars, 1862 (Cladocera: Anomopoda: Ilyocryptidae). 6. South American I. *denticulatus denticulatus* Delachaux, 1919 and I. *denticulatus freyi* subsp.n.

# Заметки о роде *Ilyocryptus* Sars, 1862 (Cladocera: Anomopoda: Ilyocryptidae). 6. Южноамериканский I. *denticulatus denticulatus* Delachaux, 1919 и I. *denticulatus freyi* subsp.n.

# A.A. Kotov<sup>1</sup> & Pavel Štifter<sup>2</sup> А.А. Котов и П. Штифтер

<sup>1</sup> A.N. Severtsov Institute of Ecology and Evolution, Leninsky Prospect 33, Moscow 119071 Russia. E-mail: golokot2000@mail.ru Институт проблем экологии и эволюции им. А.Н. Северцова РАН, Ленинский проспект 33, Москва 117071 Россия. <sup>2</sup> Smetanova 25, Benatky nad Jizerou 29471 Czech Republic. E-mail: stifter@benatky.cz

KEY WORDS: Cladocera, Anomopoda, Ilyocryptus, morphology, systematics, South America.

КЛЮЧЕВЫЕ СЛОВА: ветвистоусые ракообразные, Cladocera, Anomopoda, *Ilyocryptus*, морфология, систематика, Южная Америка.

ABSTRACT. I. denticulatus denticulatus Delachaux, 1919 (Cladocera: Anomopoda: Ilyocryptidae), known to cladoceran investigators only from its first description, was redescribed based on the new material from highlands of northern Chile. It is a unique species among ilyocryptids in having of a large postero-lateral projection on the head shield and a very thick, ovoid process on the mandibular articulation. Also, a combination of large size, medial anus and not too numerous, exclusively single, straight and relatively small preanal teeth differentiates this species from all other known sordidus-like species. A new subspecies, I. denticulatus freyi subsp.n. found in few localities in southernmost portions of Chile and Argentina, differs from the nominotypical subspecies in having setules on the distal segments of basal lateral setae of antenna II three times or more longer than the diameter of its distal segment, and paired spines on their postabdomen markedly longer than the lateral setae. I. denticulatus denticulatus is found in a water body with salinity 8 ‰ (in the state of Tarapaca, Chile), which is the greatest recorded salinity for the genus.

РЕЗЮМЕ. *I. denticulatus denticulatus* Delachaux, 1919 (Cladocera: Anomopoda: Ilyocryptidae), который ни разу не находился со времени его первоописания, переописан по материалу из высокогорий Северного Чили. Это уникальный вид среди илиокриптид, имеющий большой задне-латеральный вырост на головном щите и широкий, округлый вырост мандибулярного сустава. Также, сочетание большого размера, медиального положения анального отверстия на постабдомене, и немногочисленных, исключительно одиночных, прямых и относительно небольших преанальных зубцов отличает его от всех остальных видов группы *I.* sordidus. Новый подвид, *I. denticulatus freyi* subsp.n. найден в нескольких водоемах с крайнего юга южноамериканского континента. Он отличается от номинативного подвида размером сетул на латеральных щетинках антенны II (которые в три раза больше диаметра дистального членика щетинки), и парными зубцами на постанальной части постабдомена (более длинными чем латеральные щетинки). *I. denticulatus denticulatus* найден в водоеме (в штате Тарапака, Чили) с соленостью 8 ‰, наибольшей из когда-либо отмечавшихся для представителей рода.

# Introduction

The *Ilyocryptus sordidus* species group is the most species-rich in the genus. While the European species have recently been revised [Stifter, 1988, 1991; Kotov, 1999], the taxonomy of non-European members remains confused [Kotov, 2001; Kotov et al., 2002a–c].

*I. sordidus* var. *denticulatus* Delachaux, 1919 was described from high altitude lakes (Huaron and Lavandera) in Peru. Although, the first description was reasonably detailed, no investigator of cladocerans has since recorded this species. Smirnov [1986] regarded this taxon as a subspecies of *I. sordidus* (Liévin, 1848) based on the author's description. Kotov [2001: 190] again analysed the first description and concluded that *I. denticulatus* Delachaux, 1919 is a valid South Amer-

ican species. Our recent analysis of samples from South America resulted in new records of this species, and description of its new subspecies from the southernmost portion of the South American continent.

# Methods

See previous communications of this series for methods, including scheme of measurements.

ABBREVIATIONS FOR COLLECTIONS. AAK — Personal collection of A.A. Kotov, Moscow, Russia; DGF — personal collection of D.G. Frey, now at USNM; MGU — Zoological Museum of Moscow State University ("Moskovskiy Gosudarstvenniy Universitet"), Moscow, Russia; NHM — The Natural History Museum, London, United Kingdom; RBINS — Royal Belgian Institute of Natural Sciences, Brussels, Belgium; USNM — The Smithsonian Institution Museum of Natural History, Washington, D.C., U.S.A.

## Results

#### Ilyocryptus denticulatus Delachaux, 1919

TYPE LOCALITY. Lakes Huaron and Lavandera (about 5140 m.a.s.l.), the Andes, Peru.

TYPE MATERIAL. Apparently lost.

EMENDED DIAGNOSIS OF PARTHENOGENETIC FEMALE. Body subovoid, dorsal margin slightly convex, postero-dorsal angle expressed, in anterior view, body thick, with a rudimentary dorsal keel, moulting incomplete. Head shield with a postero-lateral projection (with size varying between subspecies) in region of process of mandibular articulation, the latter massive, with wide, additional chitinised point of mandibular joint. Valves with six-seven anteriormost setae protruding sparsely, posteriorly to them, a bunch of four closely located setae. Each seta at posterior margin along one side basally with series of spine-like setules, and distally with fine setules, unmodified setules present or absent on base of seta depending on subspecies. Postabdomen with height maximal in postanal portion, anus opens somewhat closely to base than to distal extremity, numerous spinules on its internal wall. Preanal margin short, with 8-12 regularly located, straight teeth. Small, strong denticles near preanal teeth. Groups of similar denticles on lateral faces of postabdomen basally. Paired spines with size varying between subspecies start on postanal margin and continue up anal or to distal boundary of preanal margin, the proximalmost lateral seta is located on anal or distalmost portion of preanal margin. One to eight denticles of postabdominal claw ventrally, with size varying between subspecies. Two spines on base of postabdominal claw with relative size varying between subspecies. A group of long setules on claw base ventrally. Postabdominal seta longer than postabdomen, its basal segment with rarely possessing long hairs. Antenna I of medium length, relatively thin, its proximal segment with a distinct finger-like projection and low hillocks, distal segment without ridges or denticles, distal end with concentric row of hillocks. Coxal part of antenna II with numerous setules and two sensory setae of greatly different size. Distal sensory seta long, slender, distal burrowing spine somewhat shorter that distal seta. Apical swimming setae short, their distal segments with minute hooks on

tips, asymmetrically armed with short setules. Proximal and distal lateral swimming setae of unequal length, both setulated asymmetrically, but setules along one side markedly longer and sparser than those on apical setae (with size varying between subspecies), both with a minute hook on tip. Spine on second segment of exopod longer than half of third segment. A large seta on outer distal lobe of limb I with basal segment armed unilaterally with sparse setules, and distal segment armed bilaterally with dense setules, and a small, thin seta. A large, bisegmented, naked seta near ejector hooks; gnathobase I with a row of setules. Beating seta near gnathobase III. Four setae at inner-distal margin of limb IV of unequal size, similarly armed, a short sensillum near basal setae. Filter plate V with 6 setae. Limb VI with inner margin bearing continuous row of setules, separated by small incisions into six series, outer margin with series of setules. Size up to 1375 µm.

EPHIPPIAL FEMALE & MALE. Unknown for nominotypical subspecies.

DIFFERENTIAL DIAGNOSIS. Previous species differentiations were dubious. *I. denticulatus* was named due to presence of a slanting row of denticles at the base of postabdomen, unique for the genus according to Delachaux [1919]. In reality, these denticles are present in many species and were reported for the first time about 40 years before Delachaux's paper by Kurz [1878]. Also, numerous hairs and denticles on the coxa and antennal segments of antenna II are not unique; they are present in other South American species (e.g., *I. sarsi* see Kotov et al [2002a]).

*I. denticulatus* is a unique species among ilyocryptids in having of a large postero-lateral projection on the head shield and a very thick, ovoid (instead of triangular in other species) process of the mandibular articulation. Also, a combination of large size, medial anus and infrequent, exclusively single, straight and relatively small preanal teeth differs this species from all other known *sordidus*-like species. DISTRIBUTION. See two subspecies.

\*

Key for the subspecies of *Ilyocryptus denticulatus* 

- 1 (2) Setules on distal segment of basal lateral seta of antenna II two times longer than diameter of its distal segment, or less; paired spines on postabdomen shorter than lateral seta or approximately equal in length with these setae ...... *I. denticulatus denticulatus* Delachaux, 1919
- 2 (1) Setules on distal segment of basal lateral seta of antenna II three times or more longer than diameter of its distal segment; paired spines on postabdomen markedly longer than lateral setae ....*I. denticulatus freyi* subsp.n.

## Ilyocryptus denticulatus denticulatus Delachaux, 1919 Figs 1–46.

Iliocryptus sordidus var. denticulatus Delachaux, 1919: 26–27, Pl. 1: Figs 12–13.

Ilyocryptus sordidus subsp. denticulatus Delachaux in Smirnov, 1976: 49, Fig. 15 (after Delachaux [1919]).

*Ilyocryptus denticulatus* Delachaux in Kotov, 2001: 190, Figs 9–10 (after Delachaux [1919]).

#### TYPE LOCALITY, TYPE MATERIAL. See above.

MATERIAL. North Chile. Many parthenogenetic  $\Im$  from Lac Chungara (4520 m.a.s.l., salinity 0 ‰), and a small stream in wet prairie (4390 m.a.s.l., salinity 8 ‰), Parincota Region, State of Tarapaca (appr. 18°15'N, 69°10'W), collected in 06.xi.1991 by F. Billiet & B. Jadin, tubes AAK 2002-028, -030, -

South American Ilyocryptus denticulatus



Figs 1–10. *Ilyocryptus denticulatus denticulatus*, parthenogenetic  $\Im$  from Lac Chungara, Parincota Region, Tarapaca, N Chile, collected in 06.xi.1991 by F. Billiet & B. Jadin. 1, 2 — large adult  $\Im$  in lateral and anterior view; 3, 4 — head in lateral and dorsal view; 5 — projection in region of mandibular articulation; 6, 7 — setae in antero-ventral and ventral portion of valve; 9, 10 — setae at posterior margin of valve. Scale: 1000 µm (1, 2) and 100 µm (3–10).

Рис. 1–10. *Ilyocryptus denticulatus denticulatus*, партеногенетические ♀♀ из озера Чунгара, Тарапака, северное Чили, собранные 06.хі.1991 Ф. Биллетом и Б. Джарином. 1, 2 — большая ♀, вид сбоку и спереди 3, 4 — голова сбоку и спереди; 5 — вырост в задней части головного щита; 6, 7 — щетинки на переднебрюшном и брюшном крае створки; 9, 10 — щетинки на заднем крае створки. Масштаб: 1000 µm (1, 2) и 100 µm (3–10).



Figs 12–20. Ilyocryptus denticulatus denticulatus, parthenogenetic  $\Im$  from Lac Chungara, N Chile. 12, 13 — postabdomen; 13, 14 — its preanal portion; 15 — anus, inner view; 16, 17 — postabdominal claw; 18, 19 — its distal portion; 20 — antenna II. Scale 100 µm.

Рис. 12−20. *Ilyocryptus denticulatus denticulatus*, партеногенетические ♀♀ из озера Чунгара, северное Чили. 12, 13 — постабдомен; 13, 14 — его преанальная часть; 15 — анальное отверстие, вид изнутри; 16, 17 — постабдоминальный коготок; 18, 19 — его дистальная часть; 20 — антенна II. Масштаб 100 µm.

031. The sub-samples were obtained from the RBINS, where original samples have numbers D 983, 985 and 986.

DIAGNOSIS OF THE NOMINOTYPICAL SUBSPE-CIES. Postero-lateral projections on head shield relatively small, less developed that fornices; each seta at posterior margin of valves basally with spine-like setules and unmodified setules; paired spines shorter than lateral setae or equal in size with them; very fine denticles distally on postabdominal claw; two spines on base of postabdominal claw similar in size; distal segment of proximal lateral seta of antenna II with short setules (not more than 2 diameters of the segment). REDESCRIPTION. Adult parthenogenetic female. *General.* In lateral view body subovoid, of medium height for the genus (BH/BL = 0.77-0.87 in adults, 0.67-0.72 in juveniles), maximum height in posterior half (Fig. 1). Dorsal margin slightly convex, postero-dorsal angle expressed. In anterior view, body subovoid, thick (Fig. 2), BW/BL = about 0.6, with a rudimentary dorsal keel. Moulting incomplete, reticulation on head shield and valves very fine.

*Head* small (HL/BL = 0.25–0.28), its ventral margin in posterior part with prominent basis for antennae I, labrum base surrounded with a low fold (Fig. 3). In ventral view head shield triangular-ovoid, narrow (HW/BL = 0.35–0.37), with prominent fornices, and on each side with a posterolateral projection in region of process of mandibular articulation (Figs 4–5, arrows), the latter massive, with additional chitinized point of mandibular joint. Dorsal head pore located on a low prominence (Fig. 1, arrow). Compound eye of common size for genus (ED = about 30 µm), ocellus small, irregular in shape.

*Labrum* subquadrangular in lateral view, with a distinct medial projection in its basal portion (Fig. 3, arrow).

*Valves* subovoid, VL/BL = 0.76-0.82. Numerous setae along free margin (NE = 61-65), six-seven anteriormost setae protruding sparsely, following with a bunch (NB = 4) of closely located setae, which are only somewhat longer that following setae (AV/BL = 0.14-0.19), the first seta in bunch protruding posterior (Fig. 6, arrow). Setae in middle of ventral margin with long setules (Fig. 7), setae in posteroventral region not longer or slightly longer that the former (PV/BL = 0.17-0.20), each seta at posterior margin along one side basally with series of spine-like setules, and distally with fine setules, while its other side, including basal portion, supplied only with fine setules (Figs 8–10, arrows). Sometimes 1–2 setules immediately on the seta base strong (Figs 8, 10, arrows).

*Abdomen* dorsally with cross rows of setules, a long projection on the first segment (Fig. 11, arrow).

*Postabdomen* relatively short, PL/BL = 0.45-0.48, PH/ PL = 0.45-0.49, height maximal in postanal portion (Figs 11, 12). Preanal margin short (PR/PL = 0.40-0.45), with a row of regularly located, straight teeth (NT = 8-12) (Figs 13, 14). We regarded Delachaux' s [1919] figure with only 7 large teeth as having 8 teeth due to presence of eighth cluster of small denticles basally (Fig. 13, arrow). Small, strong denticles near preanal teeth. Groups of similar denticles on lateral faces of postabdomen basally. Anus small (AN/PL = 0.14-0.16), numerous spinules on its internal wall (Fig. 15). A row of relatively short paired spines (Figs 11–12, arrows) start on postanal margin (NP = 13-16). Large lateral setae (NL = 9-16) as long as paired spines, or longer; the proximalmost lateral seta small, located on anal or distalmost portion of preanal margin. On the distal part of postabdomen (Fig. 16), the row of lateral setae fluently transition into the group of middle-sized setae (NM = 2-8), the latter, more distally, – into group of rudimentary setae (NR = 9-15).

*Postabdominal claw* relatively long (CL/PL = 0.40-0.46), slightly bent. There are three pectens of setules along dorsal margin. One to four very fine denticles (indistinguishable without strong compression of the claw by cover slip) of claw ventrally (Figs 18, 19), it is difficult to assign these to distal and medial group as commonly for the genus. Two spines of unequal size on the base of each claw dorsally (DS/BS = 0.92-1.12). Long setules on claw base ventrally (Figs 16–17, arrow).

*Postabdominal seta* longer than postabdomen (SN/PL = 1.24-1.45), its basal segment shorter than distal one (BA/SN = 0.40-0.45), the latter with long, sparse hairs.

Antenna I of medium length for *Ilyocryptus* (AL/BL = 0.18-0.19), relatively thin (DA/AL = 0.13-0.15). Bases of antennae I not compressed against each other. Proximal segment relatively long for the genus (PS/AL = 0.19-0.22), with a well-expressed finger-like projection and low hillocks (Fig. 3); distal segment without ridges and denticles, distal end with concentric row of hillocks. Nine relatively short aesthetascs, two of them longer than the rest.

Antenna II relatively long for the genus (SL/BL = 0.40-0.52), coxal part with numerous relatively long setules (Fig. 20, arrows), and two sensory setae of greatly differing size (Figs 20, 21). Distal sensory seta on basal segment long, slender (Fig. 22), distal burrowing spine somewhat shorter than distal sensory seta, with long setules distally (Fig. 23). Antennal branches relatively elongated, on all segments, there are well-developed denticles around distal segment ends, and groups of similar denticles in middle part (Fig. 20). Swimming setae 0-0-0-3/1-1-3, spines 0-1-0-1/0-0-1. Apical swimming setae relatively short (SW/BL = 0.33-0.42), bisegmented, distal segments with very small hooks on tips (Fig. 33), asymmetrically armed with short setules (Figs 24, 27, 30). Proximal and distal lateral swimming setae unequal in size (PX/DI = 0.77-1.09), both setulated asymmetrically, but setules along one side markedly longer and distributed more sparsely than those on apical setae (Figs 25, 26, 28, 29, 31, 32), their tips also with minute hooks (Fig. 34). Apical spines on endopod (Fig. 35) and exopod (Fig. 36) unequal in size (AS/AP = 0.87-1.18). Spine on second segment of exopod longer than half of third segment (SE/TH = 0.57-0.72), with relatively long setules distally (Figs 37, 38).

*Limbs.* Very similar to those of *I. gouldeni*. A large seta on outer distal lobe of limb I with basal segment armed unilaterally with sparse setules, and distal segment armed bilaterally with dense setules (Fig. 39), and a thin seta approximately as long as this lobe, and with short setules on its distal segment (Fig. 40, arrow). A large, bisegmented, naked

Figs 21–46. Ilyocryptus denticulatus denticulatus, parthenogenetic  $\Im$  from Lac Chungara, N Chile. 21— sensory seta et coxal portion of antenna II; 22, 23 — distal sensory seta and distal burrowing spine on its basal segment; 24–26 — apical, proximal and distal lateral swimming setae of a female; 27–29 — the same of other female; 30–32 — the same of third female; 33, 34 — tip of apical and lateral swimming seta; 35, 36 — apical spine on endopod and exopod; 37, 38 — spine on second segment of exopod; 39–41 — limb I, its outer distal lobe and gnathobase; 42, 43 — inner-distal portion and gnathobase of limb III; 44 — four setae at inner-distal margin of limb IV; 45 — gnathobase of limb V; 46 — limb VI. Scale 100 µm.

Рис. 21-46. *Ilyocryptus denticulatus denticulatus*, партеногенетические ♀♀ из озера Чунгара, северное Чили. 21 — чувствительная щетинка на коксе антенны II; 22, 23 — дистальная чувствительная щетинка и дистальный шип на ее базальном членике; 24-26 — апикальная, проксимальная и дистальная латеральная щетинки одной самки; 27-29 — тоже у другой самки; 30-32 тоже у третьей самки; 33, 34 — концы апикальной и дистальной плавательных щетинок; 35, 36 — апикальные шипы на эндоподите и экзоподите; 37, 38 — шип на втором членике экзоподита; 39-41 — нога I, ее внешняя дистальная доля и гнатобаза; 42, 43 — внутреннедистальная часть и гнатобаза ноги III; 44 — четыре щетинки и сенсилла на внутреннедистальной части ноги IV; 45 — гнатобаза ноги V; 46 — нога VI. Масштаб 100 µm.



seta near ejector hooks (Fig. 39, arrow); a gnathobase I as a hillock with a row of setules (Fig. 41). On inner-distal margin of limb III, two soft setae of different length (Fig. 42, arrow); beating seta near gnathobase III (Fig. 43, arrow). Four setae at inner-distal margin of limb IV of unequal size, similarly armed, a short sensillum near basal setae (Fig. 44, arrow). Filter plate V with 6 setae (Fig. 45). Limb VI as a subovoid plate with inner margin bearing continue row of setules, separated by small incisions into six series, outer margin with series of setules (Fig. 46, arrows).

Ephippial female, male. Unknown.

SIZE. Parthenogenetic females from Lac Chungara 565–1375  $\mu$ m (n = 30). Size range is under-estimated, i.e., smallest females were of the third instar.

DISTRIBUTION. The subspecies is known from two localities in Peru, and two close localities in Chile, all these water bodies are located at high altitudes (4390–5140 m.a.s.l.). At the same time, this ilyocryptid was undetected in numerous samples from lowlands of Brazil at similar longitudes [Kotov, unpubl.]. So, we regard *I. denticulatus denticulatus* as an Andean endemic.

## Ilyocryptus denticulatus freyi subsp.n. Figs 47–85.

TYPE LOCALITY. An oxbow lake ("altwasser") in the foodplain of the Rio Coig, 46 km W of Esperanza, Santa Cruz, Argentina (appr. 50°58'S, 71°28'W). The type series was collected in 26.i.1989 by D.G. Frey. The original sample, labelled as DGF 89-88, was burrowed by PŠ during his visit of Prof. Frey in 1991. After the death of Prof. D.G. Frey, his collection was deposited to USNM, so, now this sample is there.

MATERIAL. *Holotype*. A large parthenogenetic  $\Im$ , 810 µm, in 95% alcohol, tube MGU Ml 37. Label of the holotype: *"Ilyocryptus denticulatus freyi* subsp. nov., 1 parth.  $\Im$  from foodplain of Rio Coig, Santa Cruz, Argentina, coll. by D. G. Frey, HOLOTYPE". *Allotype* an adult  $\Im$ , 840 µm, MGU Ml 38. *Paratypes*. Tubes: 15 parthenogenetic and pre-ephippial  $\Im$ , MGU Ml 39. 9 parthenogenetic and pre-ephippial  $\Im$ , AAK 2004-083. 3  $\Im$ , MGU Ml 40. 2  $\Im$ , AAK 2004-084. Slides: 2 exuvia, AAK-Sl-035. 1 parth.  $\Im$ , dissected, AAL-Sl-036. 1 eph.  $\Im$  k 1 parth.  $\Im$ , dissected, NHM 2005.162–163. 1 parth.  $\Im$ , NHM 2005.164. 1 ephippium, NHM 2005.165. 1  $\Im$ , NHM 2005.166. 1  $\Im$ , dissected, AAK-Sl-041.

OTHER MATERIAL STUDIED. Argentina. 2  $\Im$  from a marshy pond at the outskirts of Pta. Bandera on Lago Argentino, Santa Cruz (appr. 50°17'S, 73°00'W), coll. in 24.i.1989 by D.G. Frey, DGF 89-75. 1  $\Im$  from a pond (middle), E of Route E crossing of Rio MacLenan, Tierra del Fuego (appr. 54°08'S, 68°07'W), collected in 17.i.1989 by D.G. Frey, slide AAK Sl-042. *Chile.* 9  $\Im$  shallow channel in grossy meadow, N of turnoff to Monte Aymond, Magallanes (appr. 52°10'S, 69°30'W), collected 15.i.1989 by D.G. Frey, tube AAK 2004-077.

DIAGNOSIS. Postero-lateral projections on head shield (Figs 49–52, arrows) relatively large, better developed that fornices; each seta at posterior margin of valves basally with spine-like setules (Figs 53–54, arrows), but without unmodified setules; paired spines (Figs 55–56, arrows) markedly longer than lateral setae; well-developed denticles distally on postabdominal claw (Figs 60–63); distalmost spine on base of postabdominal claw longer that proximalmost spine (Figs 55, 56); setules on distal segment of proximal lateral seta of antenna II with long setules (3 diameters of the segment or more), decreasing in size distally (Figs 64, 66).

DESCRIPTION OF GAMOGENETIC SPECIMENS. Ephippial female. Body subovoid (Fig. 69) instead of triangular-ovoid in parthenogenetic female (Fig. 47), incision between head and valves deeper than in parthenogenetic female, dorsal margin of valves significantly prominent under head and additionally chitinized, postero-dorsal angle distinct. Central part of valve additionally chitinized, reticulation of this zone inflated, angles of polygons prominent above surface of shell, bearing well-developed, high column-like tubercles (Fig. 70), which were formed in preephippial female in incurved state (Fig. 71). Anterior and ventral valve portion, and region of posterior edge not modified in comparison with parthenogenetic female. No demarcation line between ephippium and rest of valve. Each of two studied females with eggs bears only one egg (other females lost eggs during fixation).

Male. Body triangular-ovoid (Fig. 72), less massive and more compressed laterally than in female. Head, eye, ocellus as female, labrum with reduced projection in its basal portion (Fig. 73). Abdomen with well-developed crossing rows of setules, projection on first segment small (Fig. 74, arrow). Postabdomen with gonopore opens near its base (Fig. 74, arrow), preanal teeth located with an acute angle with preanal margin, paired spines and lateral setae unequal in size, and very long postabdominal setae. Anus with spinules on internal wall (Fig. 75). Denticles in distal portion of postabdominal claw well-developed, distalmost spine on base of postabdomen somewhat longer than basalmost spine (Fig. 76). Antenna I thicker and more robust as compared with female, an additional male seta located in middle of distal segment (Fig. 73), this seta longer than half of the segment. End of antenna I with low hillocks and ten aesthetascs, five of them markedly longer than others (Fig. 77). In reality, one of these 'aesthetascs' (apparently larger members) is another additional male seta. Antenna II in general as in female (Fig. 78), distal sensory seta long (Fig. 79), but distal burrowing spine (Figs 78, 80) as long as this seta (in contrast to female). Distal (Fig. 81) and basal (Fig. 82) lateral seta with long setules along one side, and minute setules along other side. Spine on second segment of exopod (Fig. 83) as in female. Apical spines on exopod (Fig. 84) and endopod (Fig. 85) somewhat longer than in female, both significantly longer than apical segments. Limbs as in female, limb I not modified, as in all other studied species.

SIZE. parthenogenetic and pre-ephippial females from the foodplain of the Rio Coig 650–1030  $\mu$ m (n = 20), males 780–840  $\mu$ m (n = 5); parthenogenetic females from grossy meadow near Monte Aymond up to 1125  $\mu$ m. Range of sizes in female is clearly under-estimated, i.e., the smallest females were of the fourth instar.

DISTRIBUTION. *I. denticulatus freyi* subsp.n. is distributed in southernmost corner of the South American continent.

ETYMOLOGY. This subspecies is dedicated to the late Prof. David G. Frey, one of the most famous cladoceran investigators of the 20th century, who collected all material used for the present description.

#### Discussion

Among numerous *sordidus*-like species, there are the following members with medial anus: *I. sordidus* (Liévin, 1848) s.str., *I. bernerae* Kotov, Elías-Gutiérrez & Williams, 2002, *I. sarsi*-group, all with exclusively single preanal teeth, and a group of species with partly doubled teeth (*I. gouldeni* Williams, 1978, *I. cuneatus* Štifter, 1988, and *I. silvaeducensis* Štifter, 1988). But *I. sarsi*-group is the most specific *sordidus*-



Figs 47–59. *Ilyocryptus denticulatus freyi* subsp.n., parthenogenetic  $\Im$  from altwasser in the foodplain of the Rio Coig, 46 km W of Esperanza, Santa Cruz, Argentina, collected in 26.i.1989 by D.G. Frey. 47 — holotype, lateral view; 48 — head in lateral view; 49 — exuvium, lateral view; 50 — head shield in dorsal view; 51, 52 — postero-lateral projection on head shield, and mandibular articulation; 53, 54 — seta at posterior margin of valve; 55, 56 — postabdomen; 57 — its preanal portion; 58 — anus in inner view; 59 — basal segment of antenna I. Scale 100 µm.

Рис. 47-59. *Шуостурииs denticulatus freyi* subsp.n., партеногенетические ♀♀ из бассейна реки Коиг, Санта Круз, Аргентина, собранные 26.1.989 Д. Дж. Фраем. 47 — голотип, вид сбоку; 48 — голова сбоку; 49 — линочная шкурка, вид сбоку; 50 — головной цит, вид со спины; 51, 52 — постеролатеральный вырост на головном щите, и мандибулярный сустав; 53, 54 — цетинки на заднем крае створки; 55, 56 — постабдомен; 57 — его преанальная часть; 58 — анальное отверстие, вид изнутри; 59 — базальный членик антенны I. Масштаб 100 µm.



Figs 60–71. *Ilyocryptus denticulatus freyi* subsp.n., parthenogenetic (60–68), ephippial (69, 70) and pre-ephippial (71)  $\Im$  from foodplain of the Rio Coig, Argentina. 60–63 — distal portion of postabdominal claw; 64, 65 — proximal and distal lateral swimming seta of a female; 66, 67 — the same in second female; 68 — limb VI; 69, 70 — ephippial female and sculpture on its valve; 71 — incurved column-like projections. Scale: 1000 µm (69) and 100 µm (60–68, 70, 71).

Рис. 60–71. *Ilyocryptus denticulatus freyi* subsp.n., партеногенетические (60–68), эфиппиальные (69, 70) и преэфиппиальные (71) ♀♀ из бассейна реки Коиг, Санта Круз, Аргентина. 60–63 — дистальная часть постабдоминальнх коготков; 64, 65 — проксимальная и дистальная латеральная плавательные щетинки одной самки; 66, 67 — тоже у другой самки; 68 — нога VI; 69, 70 — эфиппиальная самка и скульптура ее створки; 71 — колонновидные выросты, ввернутые у преэфиппиальной самки. Масштаб: 1000 µm (69) и 100 µm (60–68, 70, 71).

like assemblage, all its species have (1) unusually small size, (2) very short setules dorsally on the base of the postabdominal claw, (3) seta at posterior margin supplied with only a single, large spine, (4) limb I lacking a large seta near the ejector hooks, *etc.* [Kotov et al., 2002a]. Among *sordidus*-like species with medial anus, *I. sordidus* s.str. is the most morphologically divergent from the other members, and closer to the species with a subdistal anus, for example *I. brevidentatus*, see Kotov et al. [2002c]. *I. bernerae* is also a very specific *sordidus*-like species [Kotov et al., 2002b]. After our examination of *I. denticulatus*, we are convinced that it is a close congener of species with partly doubled

preanal teeth, i.e. Palaearctic *I. cuneatus* and North American *I. gouldeni*, redescribed earlier [Kotov, 1999; Kotov et al., 2002b] (unfortunately, the third species with doubled teeth, *I. silvaeducensis*, lacks a recent detailed description). Combination of the medial anus and infrequent, straight and relatively small preanal teeth is characteristic both for this group and *I. denticulatus*. But we are unsure that these characters are synapomorphies (in contrast, some of them are apparent plesiomorphies) for the group. Among species with doubled teeth, *I. denticulatus* is maximally similar to *I. gouldeni*, with a different rate of doubled and single teeth between different populations. The two afore-

Figs 72–85. Ilyocryptus denticulatus freyi subsp.n., adult  $\bigcirc \bigcirc \urcorner$  from foodplain of the Rio Coig, Argentina, allotype (72) and paratypes (73–85). 72 — lateral view; 73 — head; 74–76 — postabdomen, anus in inner view and postabdominal claw; 77 — aesthetascs; 78–80 — antenna II, distal sensory seta and distal burrowing spine on its basal segment; 81, 82 — distal and proximal lateral swimming seta; 83 — spine on second segment of exopod; 84, 85 apical spines of exopod and endopod. Scale 100 µm.

Рис. 72–85. Ilyocryptus denticulatus freyi subsp.п., взрослые ♂♂ из Рио Коиг, Аргентина, аллотип (72) и паратипы (73–85). 72 — вид сбоку; 73 — голова; 74–76 — постабдомен, анальное отверстие и постабдоминальный коготок; 77 — эстетаски; 78– 80 — антенна II, дистальная чувствительная щетинка и дистальный шип на ее базальном членике; 81, 82 — дистальная и проксимальная латеральная плавательные щетики; 83 — шип на втором членике экзоподита; 84, 85 апикальные шипы на эндоподите и экзоподите. Масштаб 100 µm.





Figs 86–100. *Ilyocryptus gouldeni*, parthenogenetic  $\stackrel{\text{QQ}}{\stackrel{\text{def}}}\stackrel{\text{def}}{\stackrel{\text{def}}{\stackrel{\text{def}}{\stackrel{\text{def}}{\stackrel{\text{def}}{\stackrel{\text{def}}{\stackrel{\text{def}}}\stackrel{\text{def}}{\stackrel{\text{def}}{\stackrel{\text{def}}{\stackrel{\text{def}}{\stackrel{\text{def}}{\stackrel{\text{def}}{\stackrel{\text{def}}{\stackrel{\text{def}}{\stackrel{\text{def}}{\stackrel{\text{def}}}\stackrel{\text{def}}{\stackrel{\text{def}}}\stackrel{\text{def}}{\stackrel{\text{def}}}\stackrel{\text{def}}{\stackrel{\text{def}}}\stackrel{\text{def}}{\stackrel{\text{def}}}\stackrel{\text{def}}{\stackrel{\text{def}}}\stackrel{\text{def}}{\stackrel{\text{def}}\stackrel{\text{def}}}\stackrel{\text{def}}\stackrel{\text{def}}\\{\text{def}}\stackrel{\text{def}}\\{\text{def}}}\stackrel{\text{def}}\\{\text{def}}}\stackrel{\text{def}}\\{\text{def}}}\stackrel{\text{def}}\stackrel{\text{def}}\\{\text{def}}}\stackrel{\text{def}}\\{\text{def}}}\stackrel{\text{def}}\\{\text{def}}}\stackrel{\text{def}}\\{\text{def}}}\stackrel{\text{def}}\stackrel{\text{def}}\stackrel{\text{def}}\stackrel{\text{def}}\\{\text{def}}}\stackrel{\text{def}}\stackrel{\text{$ 

Рис. 86–100. *Ilyocryptus gouldeni*, партеногенетические ♀♀ из озера Монтебейо, Чиапас, Мексика, собранные 15.iv.2000 М. Элиасом-Гутиерресом. 86, 87 — головной щит и мандубулярный сустав; 88 — щетинки на переднебрюшном краю створки; 89, 91 — щетинки на заднебрюшном и заднем крае створки; 92, 93 — постабдомен и его преанальный край; 94–96 — апикальная, дистальная латеральная и дистальная проксимальная щетинки антенны II одной самки; 97, 98 — тоже у другой самки; 100 — шип на втором членике экзоподита антенны II. Масштаб 100 µm.

mentioned species are similar in having six setae in filter plate IV and additional bunches of setules on the external margin of limb VI, both characters are very rare among ilyocryptids but important for systematics [Kotov et al., 2002b]. If *I. cuneatus* is known only from the northern half of the continent, *I. gouldeni* is the most common *sordidus*like species in North America, found from temperate British Columbia to tropical Chiapas (from 16° to 57° N), although in Mexico present only in mountain regions (<1800 m.a.s.l.) (see Kotov et al. [2002b]). *I. gouldeni* (Figs 86–100) differs from *I. denticulatus* in (1) head shield lacking a postero-lateral projection, (2) a relatively narrow, triangular process of the mandibular articulation, (3) only five setae in front of the antero-ventral bunch of setae, (4) postabdomen without denticles or setules near preanal teeth (at least in its basal and middle portion), (5) reduced denticles at base of postabdomen, (6) distance between setules (strong) on basal lateral seta greater than diameter of distal segment of the basal seta. Of the two subspecies of *I. denticulatus, I. gouldeni* is more similar to *I. denticulatus freyi* subsp.n., having (1) setae at posterior margin lacking of setules on basal portion, and (2) large and sparse setules on the distal segments of lateral setae.

During the earlier Cretaceous, the zone of recent Andes and the southernmost corner of recent South America were probably parts of a proto-continent Pacifica, isolated from the South American continent, which appeared after a disruption of a proto-continent Gondwana [Briggs, 1995]. It is a remarkable fact that according to recent data, *I. denticulatus denticulatus* is distributed only in the "Peruvian Pacifica", while *I. denticulatus freyi* subsp.n. is present only in the "Magellanian Pacifica", two remainders of the Pacifica proto-continent, then joined with South America (cited from: Humphries & Parenti [1999]). Perhaps, differentiation of *I. denticulatus* took place in this proto-continent.

The southernmost portion of the South American continent, where *I. denticulatus freyi* subsp.n. occurs, is a unique biogeographical region of the world. So, our finding there of a new taxon was not surprising. In this region there are two other ilyocryptid species, *I. brevidentatus* and *I. cf. sordidus*. The latter must be revised in the future. Cladocerans of this region are well-studied, and commonly found to be endemic [Ekman, 1900; Frey, 1993; Kotov et al. 2002c].

Ilyocryptids are inhabitants of fresh water bodies, reports on their presence in brackish waters are extremely rare. Previously Chirkova [1984] mentioned ilyocryptids living in lakes of the Ural Mountains and the Kuban' River region with salinity up to 5 ‰. It is a remarkable fact that *I. denticulatus denticulatus* is found in a water body with salinity 8 ‰ (in State of Tarapaca, Chile). This salinity seems to be the highest known for the genus.

ACKNOWLEDGEMENTS. We are very grateful to Prof. N.N. Smirnov for help at different phases of our work, Prof. D. J. Taylor for editing of an earlier draft, Prof. F. Fiers for material from RBINS, and the late Prof. D.G. Frey for the material and help during visit of PS to U.S.A. This work is supported by the Russian Foundation for Basic Research (grant 03-04-48879 for AAK) and US National Science Foundation grant PEET (DEB-0331095). Examination of *I. gouldeni* was conducted by AAK in Mexico, during the visit supported by the Consejo Nacional de Ciencia y Tecnologia, special thanks to Prof. M. Elías-Gutiérrez for logistic help during this visit.

#### References

- Briggs J.C. 1995. Global biogeography // Dev. Palaeontol. Stratigraph. Vol.14. P.1–454.
- Chirkova Z.N. 1984. [Palearctic species of *Ilyocryptus* (Cladocera, Macrothricidae)]. Apatity: Publ. Murmansk Marine Biol. Inst. 105 pp [in Russian].
- Delachaux T. 1919. Cladocères des Andes Pèruviennes // Bull. Soc. neuchâtel. Sci. nat. T.43. S.18-38.
- Ekman S. 1900. Cladoceren aus Patagonien, gesammelt von der schwedischen Expedition nach Patagonien 1899 // Zool. Jahrb., Abt. Syst. Bd.14. S.62–84.
- Frey D.G. 1993. Species of *Pleuroxus* (Anomopoda, Chydoridae) from the subantarctic islands and southernmost South America: a partial unravelling of the *Pleuroxus aduncus* problem // Hydrobiologia. Vol.262. P.145–188.
- Humphries CJ., Parenti L.R. 1999. Cladistic biogeography. Second Edition: Interpreting patterns of plant and animal distribution. Oxford: Oxford University Press. 187 pp.
- Kotov A.A. 1999. Morphology and variability of *Ilyocryptus agilis* Kurz, 1878 and *Ilyocryptus cuneatus* Štifter, 1988 from Lake Glubokoe, Moscow Area, central Russia (Anomopoda: Branchiopoda) // Arthropoda Selecta. Vol.8. No.1. P.3–22.
- Kotov A.A. 2001. Analysis of some nominal species of sordiduslike *Ilyocryptus* (Anomopoda, Branchiopoda) // Artropoda Selecta. Vol.10. No.3. P.185–194.
- Kotov A.A., Dumont H.J., Van Damme K. 2002a. Redescription of *Ilyocryptus sarsi* Stingelin, 1913 // Hydrobiologia. Vol.472. P.207–222.
- Kotov A.A., Elías-Gutiérrez M., Williams J.L. 2002b. A preliminary revision of *sordidus*-like species of *Ilyocryptus* Sars, 1862 (Anomopoda, Branchiopoda) in North America, with description of *I. bernerae* n.sp. // Hydrobiologia. Vol.472. P.141–176.
- Kotov A.A., Paggi J.C., Elías-Gutiérrez M. 2002c. Redescription of *Ilyocryptus brevidentatus* Ekman, 1905 (Anomopoda, Cladocera, Branchiopoda) // Hydrobiologia. Vol.481. P.1– 18.
- Kurz W. 1878. Ueber limicole Cladoceren // Zeitschr. wiss. Zool. Bd.30B. (Suppl). S.392-410.
- Štifter P. 1988. Two new species of the genus *Ilyocryptus* (Cladocera, Crustacea) confused with *I. sordidus* Liévin // Vést. česk. Společ. Zool. Vol.52. P.290–301.
- Štifter P. 1991. A review of the genus *llyocryptus* (Crustacea: Anomopoda) from Europe // Hydrobiologia. Vol. 225. P.1–8.