Arthropoda Selecta 14 (2): 103–109

Notes on the genus *Ilyocryptus* Sars, 1862 (Cladocera: Anomopoda: Ilyocryptidae). 3. Interspecific hybrids *I. spinosus* x *cuneatus* from Ireland

Заметки о роде *Ilyocryptus* Sars, 1862 (Cladocera: Anomopoda: Ilyocryptidae). 3. Межвидовые гибриды *I. spinosus* x *cuneatus* из Ирландии

Alexey A. Kotov[1] & Pavel Štifter[2]
А. А. Котов и П. Штифтер

[1]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.
[2]Smetanova 25, Benatky nad Jizerou 29471 Czech Republic. E-mail: stifter@benatky.cz.

KEY WORDS: Cladocera, Anomopoda, *Ilyocryptus*, hybridisation, morphology, systematics, Europe.

КЛЮЧЕВЫЕ СЛОВА: ветвистоусые ракообразные, Cladocera, Anomopoda, *Ilyocryptus*, гибридизация, морфология, систематика, Европа.

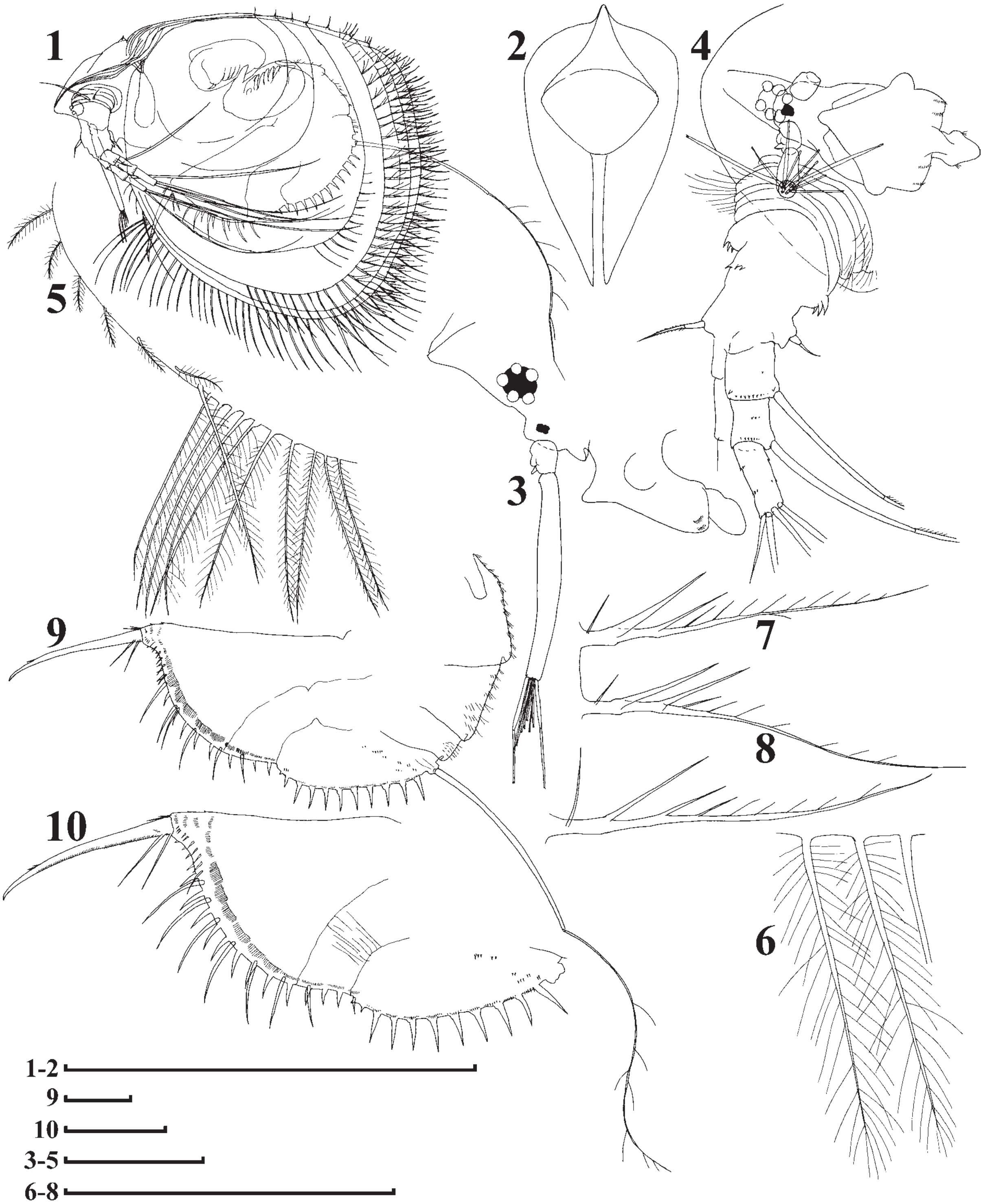
ABSTRACT. Natural interspecific hybrids have been proposed for daphniid and bosminid cladocerans, but little evidence exists for hybrids occurring in other cladoceran families. Kotov [2001], however, did suspect the existence of hybrids in the genus *Ilyocryptus* Sars, 1862 (Cladocera: Anomopoda: Ilyocryptidae), referring to Romijn's [1919] pictures. In present article, we provided evidence for natural hybridisation between *I. spinosus* Stifter, 1988 and *I. cuneatus* Stifter, 1988 in Lough Atorick, Ireland. Specimens from this lake shared diagnostic morphological characters with both *I. spinosus* and *I. cuneatus.* The chimeric nature of the morphology of the Lough Atorick specimens is unique among numerous *Ilyocryptus* populations examined. We propose that these peculiarities are reflections of a hybridisation. Although the proposed parent taxa do co-occur in some waters, we did not detect their co-occurrence in Lough Atorick.

РЕЗЮМЕ. Межвидовые гибриды найдены у представителей различных групп ветвистоусых ракообразных как при анализе из морфологии, так и с помощью генетических методов, а также получены экспериментально. Но никто из предыдущих исследователей рода *Ilyocryptus* Sars, 1862 (Cladocera: Anomopoda: Ilyocryptidae) не опубликовал описаний особей, в которых можно было бы заподозрить межвидовые гибриды, за исключением Ромийна [Romijn, 1919], что было отмечено Котовым [Kotov, 2001]. В данной статье мы сообщаем о находке гибридов *I. spinosus* Stifter, 1988 и *I. cuneatus* Stifter, 1988 в озере Лох Аторик, Ирландия. Особи из этого озера были сходны с *I. spinosus* по большей части признаков, но имели преанальный край постабдомена заметно более короткий, чем это отмечено для последнего вида, и гораздо меньшее число преанальных зубцов, к тому же, у некоторых особей 1–2 зубца были двойными. Эти особенности — отражение родства этой популяции с *I. cuneatus*. Оба исходных вида не были найдены в том же озере.

Introduction

F. E. Ruhe (1888–1915) was the first investigator who discovered interspecific hybrids in cladocerans, but his results were not published because he was called up into the army and killed in action in Belarus on September 21 of 1915 [Lieder, 1988]. Agar [1920] obtained hybrids among *Daphnia* in experiments. Later, natural hybrids between different species of the families Bosminidae, Daphniidae and Chydoridae (Anomopoda) were proposed [Lieder, 1956, 1983; Brooks, 1957; Hebert, 1985; Taylor & Hebert, 1992], or obtained experimentally [Shan Kuo-cheng & Frey, 1983].

Romijn [1919: Pl. 2] illustrated postabdomens of many specimen of *Ilyocryptus* cf. *sordidus* from the Netherlands, and some of them can be possibly interpreted as interspecific hybrids of *I. cuneatus* (with partly doubled preanal teeth on postabdomen) and *I. spinosus* or *I. sordidus* (with exclusively single preanal teeth) [Kotov, 2001: 189]. However, despite examination of many samples of *Ilyocryptus* from Europe since Romijn [e.g., Štifter, 1988, 1991; Kotov, 1999, 2001], cases of hybridisation have been unap-



Figs 1–10. *Ilyocryptus spinosus* x *cuneatus*, hybrid ♀ from Lough Atorick, W of Lough Derg, County Clare, Ireland, collected in 12.x.1985 by D. G. Frey: 1, 2 — adult in lateral and anterior view; 3, 4 — head in lateral and ventral view; 5, 6 — setae at antero-ventral and ventral portion of valve; 7, 8 — setae at posterior margin of valve; 9, 10 — postabdomen. Scales: 1000 μm (1, 2), 100 μm (3–10).

Рис. 1–10. *Ilyocryptus spinosus* x *cuneatus*, гибридная ♀ из Лох Аторик, графство Кларе, Ирландия, собранная 12.x.1985 Д. Фраем: 1, 2 — взрослая самка, вид сбоку и спереди; 3, 4 — голова, вид сбоку и с брюшной стороны; 5, 6 — щетинки на передне-брюшном и брюшном крае створки; 7, 8 — щетинки на заднем крае створки; 9, 10 — постабдомен. Масштаб: 1000 μm (1, 2), 100 μm (3–10).

parent. Recently, we (P. Štifter from deceased Prof. D.G. Frey) obtained putative hybrids between *I. spinosus* Stifter, 1988 and *I. cuneatus* Stifter, 1988 from a single locality in Ireland.

Material and methods

74 hybrid females were found in a sample from Lough Atorick, W of Lough Derg, County Clare, Ireland, collected in 12.x.1985 by D.G. Frey. Three females were dissected and not saved, 71 females are kept in the personal collection of AAK.

See the first communication of this series [Kotov & Štifter, 2005] for methods, including the scheme of measurements.

Results

Ilyocryptus spinosus x *cuneatus* hybrids

DESCRIPTION. PARTHENOGENETIC FEMALE. *General*: In lateral view body triangular-ovoid to subovoid (Fig. 1) (BH/BL = 0.71–0.78 in adults, 0.66–0.71 in juveniles), dorsal margin slightly convex, postero-dorsal angle rounded. In anterior view, body rhomboid-ovoid (Fig. 2), BW/BL = about 0.45, with a low, but relatively thin dorsal keel. Moulting incomplete, carapace reticulation fine.

Head of medium size for the genus (HL/BL 0.27–0.31), a fold surrounded base of labrum (Fig. 3), ocellus smaller than half of eye diameter. In ventral view head shield relatively narrow (HW/BL = about 0.35), with prominent fornices (Fig. 4).

Labrum subquadrangular in lateral view, with a distinct medial projection in its basal portion. In ventral view, labrum wide, with lateral projections on each side in medial portion, a row of setules on each side in its distal portion, latero-distal angles smooth.

Valves subovoid, VL/BL = 0.77–0.85. Numerous setae along free margin (NE = 63–71), six anteriormost setae short, protruding sparsely, posteriorly to them, a bunch of closely located setae (NB = 5–6; AV/BL= 0.18–0.23), the first seta in bunch protruding posterior, crossing following setae (Fig. 5). Setae at ventral margin shorter, plumose (Fig. 6), setae at postero-ventral region somewhat longer (PV/BL = 0.14–0.20), each seta at posterior margin (NS = 28–31) with a series of spine-like setules in basal half, and rare, fine setules distally (Figs. 7–8).

Abdomen with a well-developed projection on the first segment (Fig. 9).

Postabdomen large, PL/BL = 0.47–0.51 (Figs 9, 10), relatively narrow for the genus (PH/PL = 0.42–0.46), height maximal at level of distal portion of preanal margin. Preanal margin only slightly longer than postanal one (PR/PL = 0.46–0.49), with evenly-spaced straight teeth (NT = 9–13). Most of preanal teeth single (Figs 9, 10), but in some individuals there are 1, rarely 2 teeth doubled, specially this is characteristic for juveniles (Figs 11–14). Series of small denticles near each preanal tooth (Figs 15, 16). Series of fine spinules on lateral sides of postabdomen. Anus of middle size (AN/PL = 0.17–0.19), fine spinules on its internal wall (Fig. 17). A row of small and numerous paired spines starts on postanal margin and finishes on anal margin, sometimes at distal boundary of preanal margin (NP = 10–13); large lateral setae (NL = 6–8) markedly longer than paired spines, the proximalmost lateral seta located on anal margin. On the distal part of postabdomen, a group of middle-sized setae (NM = 4–7), more distally group of rudimentary setae (NR = 4–10).

Postabdominal claw relatively short and thick (CL/PL = 0.39–0.42), slightly bent. One-two denticles in distal portion of claw, and 3–5 fine setules in its middle portion (DD=1–2, AD=3–5) (Figs 18, 19), two spines on its base dorsally of similar length (DS/BS = 0.95–1.05). A group of long setules on claw base ventrally (Fig. 18, arrow).

Postabdominal seta long (SN/PL = 1.50–1.80), basal segment short (BA/SN = 0.38–0.42), regularly feathered with long, rare hairs.

Antenna I long, thin (AL/BL = 0.21–0.23; DA/AL = 0.12–0.14), slightly bent in transversal plane. Bases of antennae I not compressed against each other (Fig. 4). Proximal segment relatively short (PS/AL = 0.14–0.16), with a well-developed finger-like projection and distinct, low hillocks (Figs 20, 21). Distal segment without denticles, its distal end truncated, with nine aesthetascs of unequal length, two largest aesthetascs located at inner side of antenna I (Fig. 22, arrows).

Antenna II of medium length, SL/BL = 0.31–0.39, coxal part with two sensory setae greatly differing in lengths (Fig. 23). Distal sensory seta on basal segment relatively long (Fig. 24), distal burrowing spine somewhat shorter than the latter, with short setules (Fig. 25). Antennal branches relatively elongated, apical swimming setae of medium size for the genus (SW/BL = 0.44–0.50), distal segments without hooks on tips, asymmetrically armed with short setules (Fig. 26). Proximal lateral swimming seta shorter than distal one (PX/DI = 0.61–0.69), both with asymmetrically setulated distal segments (Fig. 27). Spine on apical segment of exopod (Fig. 28) longer than that on endopod (Fig. 29), AS/AP = 1.14–1.28. Spine on second segment of exopod longer than half of third segment (SE/TH = 0.75–0.87), setulated distally (Figs 30, 31).

Limb I: outer distal lobe with a large seta, and a small, thin seta (Figs 32, 33). Two ejector hooks of slightly different size, a large bisegmented seta near them. A gnathobase I as naked mound.

Limb II: typical for genus (Fig. 34).

Limb III: exopodite with five distal setae, differing in length and setulation (Fig. 35), and three lateral setae (not pictured here), typical for the genus. Distal endite with two soft, relatively short setae of different size, and three large, bisegmented setae of different size. Basal endite with four bisegmented setae of similar size, and a curved sensillum near border with distal endite (Fig. 36). A thin beating seta near gnathobase. Four differently armed setae in distal armature of gnathobase, filter plate with eight setae.

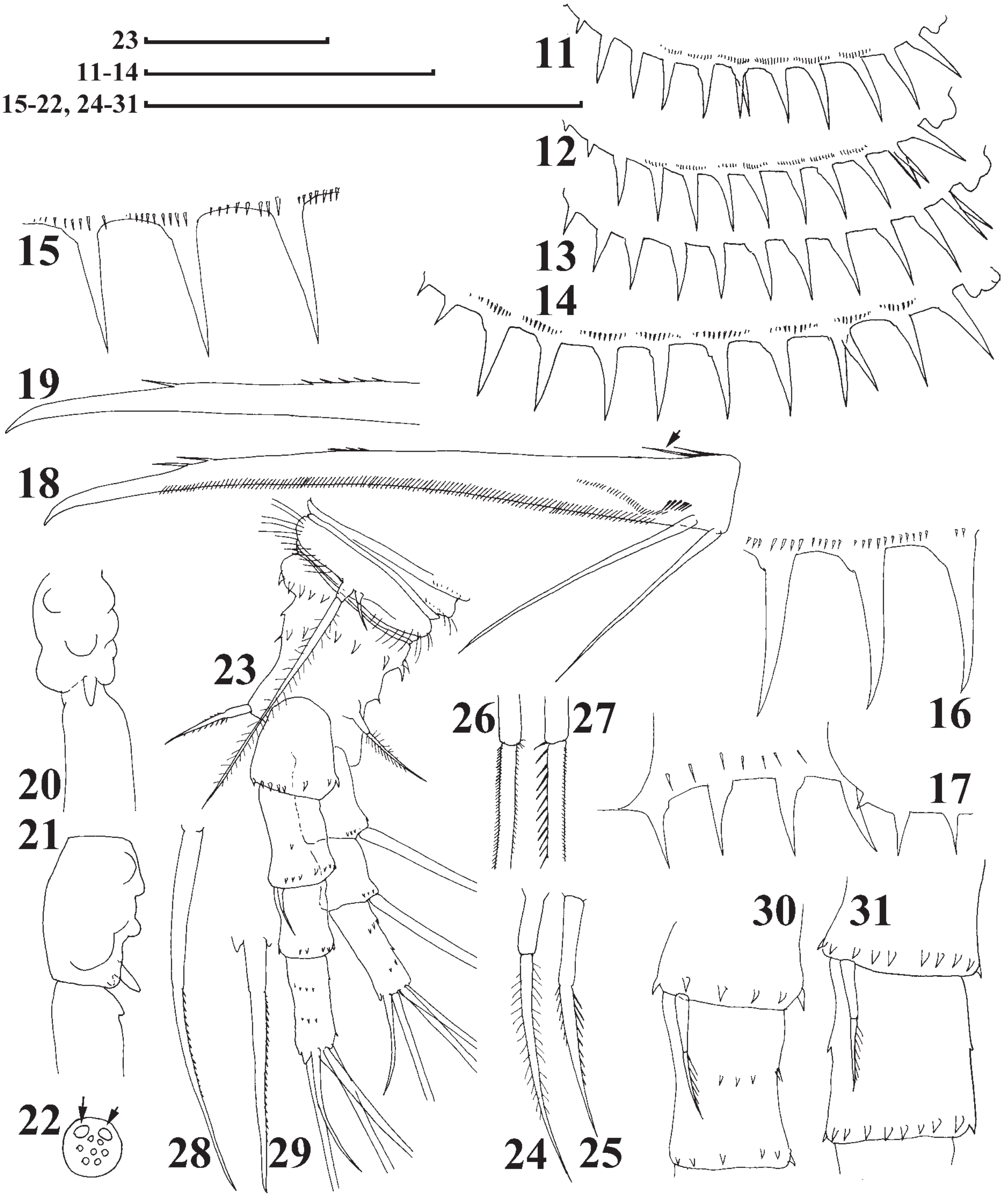
Limb IV: exopodite with 8 setae typical for the genus (not pictured). Inner-distal portion as a small lobe, with four thin setae (Fig. 37, arrows), distalmost seta with short setules, while three other setae with long setules, a short sensillum near basalmost seta. Basally and medially, five long, bilaterally setulated setae. Distal armature of gnathobase with four elements, filter plate with 8 setae.

Limb V: typical for genus, filter plate with 5 or 6 setae (Fig. 38).

Limb VI: small plate with continuous row of long setules along inner margin, subdivided into six bunches by small incisions on the margin (Fig. 39).

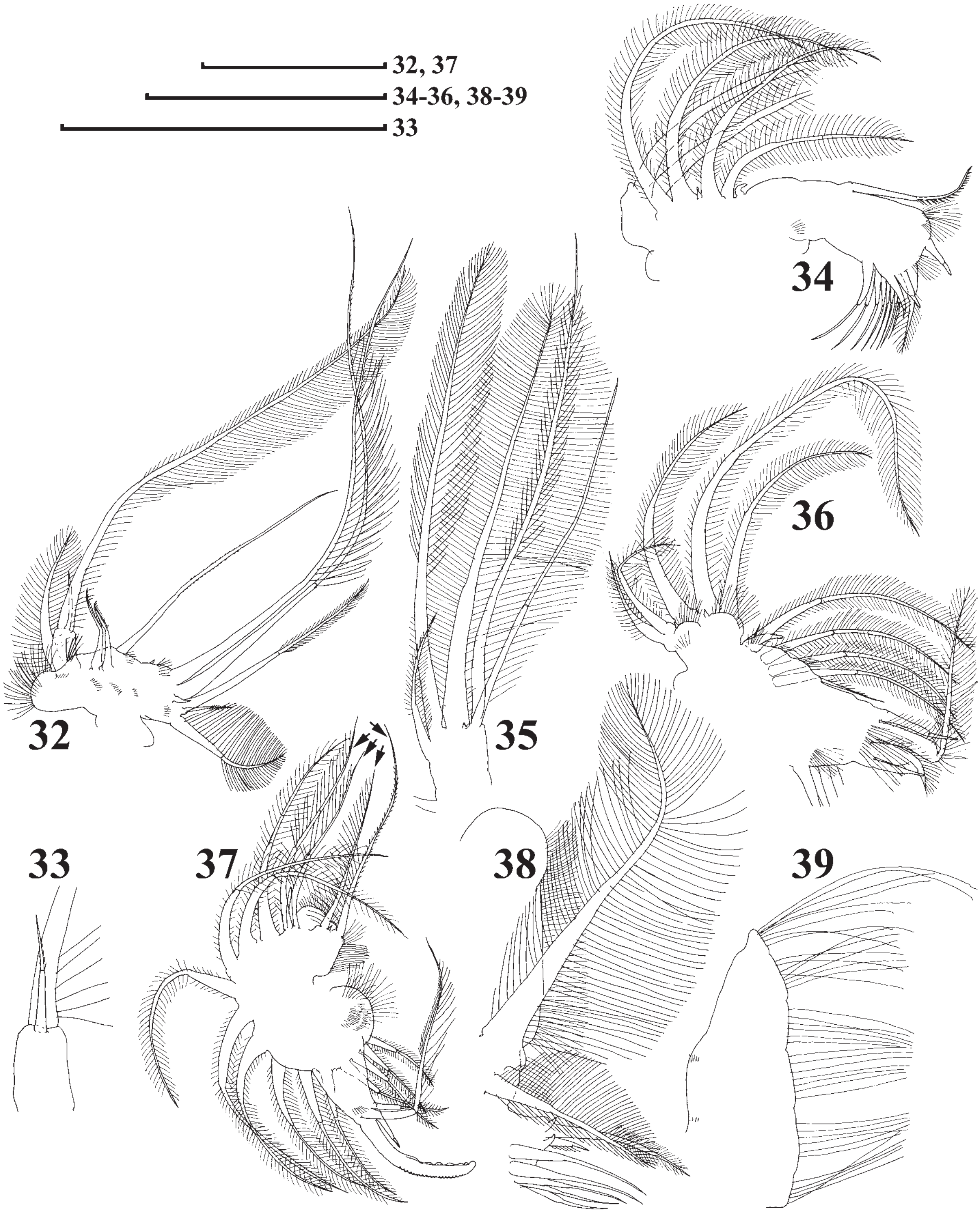
EPHIPPIAL FEMALE, MALE. Not found.

SIZE. Parthenogenetic females 510–1100 µm (*n* = 50). Minimal female size in this population was smaller, because females of the first instar were not found.



Figs 11–31. *Ilyocryptus spinosus* x *cuneatus*, hybrid ♀ from Lough Atorick, Ireland: 11–13 — preanal portion of postabdomen of juveniles; 14 — the same in adult; 15, 16 — preanal teeth; 17 — anus; 18, 19 — postabdominal claw and its distal portion; 20, 21 — basal portion of antenna I in anterior and lateral view; 22 — antenna I in distal view; 23 — antenna II; 24, 25 — distal burrowing spine and distal sensory seta of basal segment; 26, 27 — apical and lateral swimming seta; 28, 29 — apical spine on exopod and endopod; 30, 31 — spine on second segment of exopod. Scale 100 μm.

Рис. 11–31. *Ilyocryptus spinosus* x *cuneatus*, гибридная ♀ из Лох Аторик, Ирландия: 11–13 — преанальная часть постабдомена ювенильных самок; 14 — тоже у взрослой самки; 15, 16 — преанальные зубцы; 17 — анус; 18, 19 — постабдоминальный коготок и его дистальная часть; 20, 21 — базальная часть антенны I, вид спереди и сбоку; 22 — антенна I, вид с дистального конца; 23 — антенна II; 24, 25 — дистальный шип и дистальная щетинка базального членика; 26, 27 — апикальная и латеральная плавательная щетинка; 28, 29 — апикальные шипы экзоподита и эндоподита; 30, 31 — шип на втором членике экзхоподита. Масштаб 100 μm.



Figs 32–39. *Ilyocryptus spinosus* x *cuneatus*, limbs of hybrid ♀ from Lough Atorick, Ireland: 32, 33 — limb I and its outer distal lobe; 34 — limb II; 35, 36 — exopodite and inner portion of limb III; 37, 38 — inner portion of limb IV and V; 39 — limb VI. Scale 100 μm.

Рис. 32–39. *Ilyocryptus spinosus* x *cuneatus*, гибридная ♀ из Лох Аторик, Ирландия: 32, 33 — нога I и ее внешняя дистальная доля; 34 — нога II; 35, 36 — экзоподит и внутренняя часть ноги III; 37, 38 — внутренняя часть ног IV и V; 39 — нога VI. Масштаб 100 μm.

Table 1. Characters of *I. spinosus*, *I. cuneatus* and hybrid population between these two species found in Ireland.
Таблица 1. Признаки *I. spinosus*, *I. cuneatus* и гибридной популяции, найденной в Ирландии.

Character	*I. spinosus*	*I. cuneatus*	*I. spinosus* x *I. cuneatus* hybrid
A spinule on base on each seta et posterior margin	±	-	+
PR/PL	0.65-0.71	0.43-0.53	0.46-0.49
NT	16-19	8-12	9-13
Preanal teeth partly doubled	-	+	±
Spinules near each preanal tooth	+	-	+
Denticles on base of postabdomen	few, robust or absent	few, robust	numerous, small
NP	6-7	9-12	10-13
Spine on second segment of antennal exopod long	+	-	+
One among four seta on inner-distal margin of limb IV with short setules	+	-	+
Number of setae in gnathobase V	4	6	5-6

Discussion

In Europe, there are four *sordidus*-like species: *I. sordidus* (Lievin, 1848), *I. silvaeducensis* Romijn, 1919, *I. cuneatus* Štifter, 1988, and *I. spinosus* Stifter, 1988 (see Štifter [1988, 1991]). Of these species, *Ilyocryptus* from Lough Atorick is the most divergent from *I. sordidus,* which possesses a postabdominal claw lacking denticles in the distal portion, the basal segments of the lateral swimming setae are supplied with additional long setules, *etc*. The Lough Atorick population is also divergent from *I. silvaeducensis*, which possess a short preanal margin supplied with 5–8 doubled (mostly) teeth (see Štifter [1991]). Specimens from Ireland are similar to *I. spinosus* in most diagnostic features (see descriptions of Stifter [1988] and Kotov et al. [2002]), but the putative hybrids have a preanal margin significantly shorter than that minimally recorded for *I. spinosus*, and a significantly smaller number of preanal teeth than *I. spinosus* (see Table 1). Note that, unlike the defensive carapace structures that have been used to identify bosmind and daphniid hybrids, the ilyocryptid morphological characters studied here lack significant variation within species [Kotov, 1999; Kotov et al., 2002]). We propose that these two peculiarities of Irish specimens, as well as presence of 1–2 doubled members among preanal teeth, small and relatively numerous paired spines on postabdomen (not characteristic of *I. spinosus*) are reflections of their hybrid status, namely, evidence of a relationship with *I. cuneatus*. Nevertheless, the numerous small spinules on the sides of the postabdomen at its base are characteristic of neither *I. spinosus* nor *I. cuneatus*. These spinules are a likely recapitulation to a primitive state for the genus. We believe that the ancestral *Ilyocryptus* had spinules on the postabdomen sides which were very numerous and not different from setules near preanal teeth. Apparently, all elements of the armature of the preanal (preanal teeth, setules near them and on post-absomen base) and postanal (paired spines, lateral setae and setules near them) margin originated from uniform small spines, which covered the entire surface of the postabdomen (as in the most primitive anomopods *Acantholeberis* and *Eurycercus* [see Smirnov, 1976; Kotov, 2000].

The Irish population was apparently comprised entirely of hybrids, as no parent species were detected. Dominance of a lake by hybrid lineages has been proposed for other cladocerans [Lieder, 1956; Taylor & Hebert, 1992]. This new example of a hybrid cladoceran population existing as a separate race ("morphological personality" in terms of Lieder [1983]) is the first cladoceran case outside of Daphniidae, Bosminidae and Chydoridae. In contrast to the relatively rare *I. spinosus*, *I. cuneatus* is probably the most common ilyocryptid species in the Palearctic [Štifter, 1988]. Although *I. cuneatus* frequently co-occurs with other *sordidus*-like animals, we have never found evidence of hybridisation in other Palearctic populations. Possibly, interspecific hybridisation in benthic ilyocryptids is less common than in the pelagic daphniids or bosminids.

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, and to the late Prof. D.G. Frey for the sample with this hybrid population. 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).

References

Agar W.E. 1920. The genetics of a *Daphnia* hybrid during parthenogenesis // J. Genetics. Vol.10. P.303–330.

Brooks J.L. 1957. The systematics of North American *Daphnia* // Mem. Conn. Acad. Arts Sci. Vol.13. P.1–180.

Hebert P.D.N. 1985. Interspecific hybridization and cyclic parthenogenesis // Evolution. Vol.39. P.216–220.

Kotov A.A. 1999. Morphology and variability of *Ilyocryptus agilis* Kurz, 1878 and *Ilyocryptus cuneatus* Stifter, 1988 from Lake Glubokoe, Moscow Area, central Russia (Anomopoda: Branchiopoda) // Arthropoda Selecta. Vol.8. No.1. P.3–22.

Kotov A.A. 2000. Morphology and variability of *Eurycercus lamellatus* (O. F. Muller, 1776) (Branchiopoda: Anomopoda: Eurycercidae) from Lake Glubokoe, Moscow Area, central Russia // Arthropoda Selecta. Vol.9. No.3. P.159–173.

Kotov A.A. 2001. Analysis of some nominal species of *sordidus*-like *Ilyocryptus* (Anomopoda, Branchiopoda) // Artropoda Selecta. Vol.10. No.3. P.185–194.

Kotov A.A., Štifter P. 2005. Notes on the genus *Ilyocryptus* Sars, 1862 (Cladocera: Anomopoda: Ilyocryptidae). 1. *Ilyocryptus plumosus* sp. nov., a primitive Neotropical member of the *I. spinifer*-group // Arthropoda Selecta (in press)

Kotov A.A., Elías-Gutiérrez M., Williams J.L. 2002. 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.

Lieder U. 1956. Introgressive Hybridisation als Evolutionsfaktor bei den Gattungen *Bosmina* und *Daphnia* (Crustacea, Cladocera) // Naturwissenschaften. Bd.43. S.207.

Lieder U. 1983. Introgression as a factor in the evolution of polytypical plankton Cladocera // Inter. Rev. ges. Hydrobiol. Bd.68. S.269–284.

Lieder U. 1988. Das Lebenswerk F.E. Rühes und seine Beiträge zur Cladocerologie // Mitt. Zool. Mus. Berlin. Bd.64. H.2. S.269–297.

Romijn G. 1919. Das Geschlecht *Ilyocryptus* G.O. Sars // Int. Rev. ges. Hydrob. Hydrogr. Bd.8. H.5. S.529–539.

Shan R. Kuo-cheng, Frey D.G. 1983. *Pleuroxus denticulatus* and *Pleuroxus procurvus* (Cladocera, Chydoridae) in North America: distribution, experimental hybridization, and the possibility of natural hybridization // Can. J. Zool. Vol.61. P.1605–1617.

Smirnov N.N. 1976. [Macrothricidae and Moinidae of the Worid fauna] // Fauna SSSR, n. ser., Rakoobraznye T.l. №.3, Leningrad, "Nauka" Publ. 237 p. [in Russian].

Štifter P. 1988. Two new species of the genus *Ilyocryptus* (Cladocera, Crustacea) confused with *I. sordidus* Lievin // Vést. česk. Společ. Zool. Vol.52. P.290–301.

Štifter P. 1991. A review of the genus *Ilyocryptus* (Crustacea: Anomopoda) from Europe // Hydrobiologia. Vol. 225. P.1–8.

Taylor D.J., Hebert P.D.N. 1992. *Daphnia galeata mendotae* as a cryptic species complex with interspecific hybrids // Limnol. Oceanogr. Vol.37. P.658–665.