

Analysis of some nominal species of *sordidus*-like *Ilyocryptus* (Anomopoda: Branchiopoda)

Анализ некоторых *sordidus*-подобных номинальных видов *Ilyocryptus* (Аномопода: Branchiopoda)

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КЛЮЧЕВЫЕ СЛОВА: “Cladocera”, Аномопода, *Ilyocryptus*, систематика, синонимия.

ABSTRACT: *Ilyocryptus sordidus* (Liévin, 1848) is the type species of the genus *Ilyocryptus* Sars, 1862 (Branchiopoda, Anomopoda, Ilyocryptidae). Previously this species was regarded as cosmopolitan, but recently Štifter [1988], in the course of his revision of *sordidus*-like species in Europe, described two new species, which seemed to be quite “good”. But he did not conduct an accurate comparison of these with other forms described previously from Europe and other continents. This resulted in some uncertainty in the systematics of *sordidus*-like forms.

Types of the majority of these forms have been lost. I have analysed the first descriptions and pictures of all formal *sordidus*-like species and subspecies established before Štifter’s [1988] article: (1) *Ilyocryptus sarsi* Stingelin, 1913; (2) *Ilyocryptus sordidus* var. *longisetus* Arévalo, 1916; (3) *I. sordidus aequalis* Romijn, 1919; (4) *I. sordidus inaequalis* Romijn, 1919; (5) *I. silvaeducensis* Romijn, 1919; (6) *I. sordidus* var. *denticulatus* Delachaux, 1919; (7) *I. balatonicus* Hankó, 1926; (8) *I. sordidus sordidus* (Liévin, 1848) in Smirnov, 1976; (9) *I. gouldeni* Williams, 1978; (10) *I. alexandrinae* Negrea, 1987. Numbers 1, 5, 6, 9 are valid species, while 3, 7, 10 are junior synonyms of *I. sordidus*, and 2 is, most probably, a junior synonym of *I. agilis*. Now I can confidently say that *I. cuneatus* Štifter, 1988 is valid species. But there is a chance that *I. spinosus* Štifter, 1988 is a junior synonym of *I. inaequalis* Romijn, 1919. At this moment this question can not be resolved due to inadequate study of both *I. sordidus* and *I. spinosus*.

Smirnov [1976] subdivided *I. sordidus* into four subspecies: (I) *I. sordidus sordidus* (Liévin, 1848); (II) *I. sordidus inaequalis* Romijn, 1919; (III) *I. sordidus sarsi* Stingelin, 1913; (IV) *I. sordidus denticulatus* Delachaux, 1919. But Smirnov’s subspecies III & IV are, in actuality, good separate species, II is a questionable species, either junior synonym of *I. sordidus* or

separate species, but not a subspecies of *I. sordidus*. The name *I. sordidus sordidus* (Liévin, 1848) cannot be used now because, as this article demonstrates, there are no other subspecies of that taxon, but, if another subspecies is found later on, that name should be applied to the nominal subspecies.

РЕЗЮМЕ: *Ilyocryptus sordidus* (Liévin, 1848) — типовой вид рода *Ilyocryptus* Sars, 1862 (Ilyocryptidae, Аномопода, Branchiopoda). В прошлом он рассматривался как распространенный космополитически, но недавно Штифтер [Štifter, 1988] в ходе ревизии *sordidus*-подобных форм Европы описал 2 новых вида, кажущихся вполне “хорошими”. Но автор не провел аккуратного сравнения его видов с другими формами, ранее описанными из Европы и других континентов. Это стало причиной некоторой неопределенности в систематике *sordidus*-подобных форм.

Типовые материалы для большинства этих форм потеряны. Я проанализировал первоописания и рисунки всех формальных *sordidus*-подобных видов и подвидов, установленных до ревизии Штифтера, а именно: (1) *Ilyocryptus sarsi* Stingelin, 1913; (2) *Ilyocryptus sordidus* var. *longisetus* Arévalo, 1916; (3) *I. sordidus aequalis* Romijn, 1919; (4) *I. sordidus inaequalis* Romijn, 1919; (5) *I. silvaeducensis* Romijn, 1919; (6) *I. sordidus* var. *denticulatus* Delachaux, 1919; (7) *I. balatonicus* Hankü, 1926; (8) *I. sordidus sordidus* (Liévin, 1848) in Smirnov, 1976; (9) *I. gouldeni* Williams, 1978; (10) *I. alexandrinae* Negrea, 1987. Из них 1, 5, 6, 9 — валидные виды, в то время как 3, 7, 10 — младшие синонимы *I. sordidus*, и 2, скорее всего, — младший синоним *I. agilis*. Можно уверенно сказать, что *I. cuneatus* Štifter, 1988 — валидный вид. Однако, имеется вероятность того, что *I. spinosus* Štifter, 1988 — младший синоним *I. inaequalis* Romijn, 1919. Окончательное решение по этому вопросу не

может быть принято в настоящий момент, поскольку как *I. sordidus*, так и *I. spinosus* исследованы недостаточно.

Смирнов [1976] подразделил вид *I. sordidus* на 4 подвида: (I) *I. sordidus sordidus* (Liévin, 1848); (II) *I. sordidus inaequalis* Romijn, 1919; (III) *I. sordidus sarsi* Stingelin, 1913; (IV) *I. sordidus denticulatus* Delachaux, 1919. Но подвиды III и IV по Смирнову — это самостоятельные, валидные виды, а II — или младший синоним *I. sordidus* или отдельный вид, но никак не подвид *I. sordidus*. Название *I. sordidus sordidus* (Liévin, 1848)? настоящее время непригодно, но может быть применено, если другой новый подвид будет описан в будущем.

Introduction

Ilyocryptus sordidus (Liévin, 1848) is the type species of the genus *Ilyocryptus* Sars, 1862 (Branchiopoda, Anomopoda, Ilyocryptidae). Previously, this species was regarded as cosmopolitan, but recently Štifter [1988], in the course of his revision of *sordidus*-like species in Europe, described two new species that appear to be valid. He redescribed only *I. silvaeducensis* Romijn, 1919 [Štifter, 1984] and did not conduct an accurate comparison of his new species with other forms described later than Liévin [1848] from Europe (*I. sordidus* var. *longisetus* Arévalo, 1916; *I. sordidus aequalis* Romijn, 1919; *I. sordidus inaequalis* Romijn, 1919; *Ilyocryptus balatonicus* Hankó, 1926; *I. alexandrinae* Negrea, 1987), and from other continents (*I. sordidus sarsi* Stingelin, 1913; *I. sordidus denticulatus* Delachaux, 1919; *I. gouldeni* Williams, 1979).

Therefore, there is some uncertainty in the systematics of *sordidus*-like forms occurring in anywhere [Kotov, 1999; Kotov et al., 2001]. Only *I. alexandrinae* Negrea, 1987, which had been established using an ephippial female as a holotype, was subsequently regarded by Štifter [1991] as a junior synonym of *I. sordidus* (Liévin, 1848). This point of view was supported by Kotov & Timms [1998].

Because other forms were not analysed comparatively, there were some doubts about the validity of *I. cuneatus* Štifter, 1988 and *I. spinosus* Štifter, 1988, especially keeping in the mind the fact that some of traits applied by Štifter [1988] in his revision had already been used by Romijn [1919] for the separation of his *I. sordidus aequalis* and *I. sordidus inaequalis*. The aim of this communication is to resolve these doubts by means of an analysis of all formal *sordidus*-like species established before Štifter's [1988] article.

Methods

Only data from the literature are analysed here. Unfortunately, types of the majority of *ilyocryptid* forms have been lost, but the all previous descriptions (including some of the most recent publications!) do not comply with new taxonomic standards. In addition, many of these articles were published

in obscure proceedings, which are not easily accessible for contemporary investigators. My main idea was to extract from the old descriptions all the information that is really helpful for species determination according to present-day views. In the case of publications that are rarities now, I have reproduced the original author's description and pictures in full. But the names of all body parts are given here in contemporary [Kotov & Dumont, 2000; Kotov et al., 2001], rather than the original author's, terminology.

ABBREVIATIONS IN FIGURES: **aI** — antennule; **ans** — anus; **apr** — abdominal projection; **ape** — apical spine of endopod of all; **ase** — apical spine of exopod of all; **bsc** — more basal of basal spines on postabdominal claw; **dbs** — distal burrowing spine of basal segment of all; **dis** — distal lateral swimming seta; **dpb** — denticles on postabdomen base; **dsa** — distal segment of antennule; **dsc** — more distal of basal spines on postabdominal claw; **eye** — composed eye; **iml** — inner margin of limb VI; **flp** — finger-like projection on basal segment of aI; **lbc** — large bisegmented seta on corm of limb I; **lls** — large lateral setae; **ocl** — ocellus; **pcl** — postabdominal claw; **pom** — postanal margin of postabdomen; **prm** — preanal margin of postabdomen; **prr** — preanal teeth; **pse** — postabdominal seta; **psp** — paired large spines on postanal and anal part of postabdomen; **pvm**, posterior valve margin; **pxs** — proximal lateral swimming seta; **spm** — setae on posterior margin of valve; **sse** — spine on second exopod segment; **sws** — apical swimming seta.

Results: Analysis of nominal species

1. *Ilyocryptus sarsi* Stingelin, 1913

Sars, 1901: 42, Pl. VII: Figs. 11–13 (*Ilyocryptus sordidus*); Stingelin, 1913: 618 (*Ilyocryptus sordidus* var. *sarsi*); Smirnov, 1976: 49, Fig. 14 [after Sars, 1901] (*Ilyocryptus sordidus sarsi*); Paggi, 1992: 148 (*Ilyocryptus sarsi*)

? Harding, 1955: 340 (*Ilyocryptus sordidus*)

Non Harding, 1955: 341, Fig. 49 (*I. sordidus* var.)

Neotype: A parthenogenetic female, 4th instar, 409 µm, preserved in 96% alcohol, tube F18459a, redeposited in the G.O. Sars Collection in the Zoological Museum of Oslo, Norway by Kotov et al. [2001]. Stingelin's holotype was lost [Frenzel, 1987], but, according to paragraphs 72.4.1 and 72.4.2. of ICZN (2000), Sars's specimens are members of Stingelin's type series also.

Locality of neotype: Ipiranga, Paraná, Brazil. Former type locality: "Stumpfige Wiese, in geringer Entfernung von Laguna östl. oberhalb Medellin (westl. von Bogota) 2504 m ü. M.", Columbia.

Etymology: The species was named after the famous carcinologist G.O. Sars, who described previously this animal, but confused it with the European *I. sordidus*.

Comments: Stingelin [1913: 618] did not give any important comments on the species morphology, only referred to Sars' [1901] description, and said that this form (described as *I. sordidus*) is at least a new variation:

"Das in Frage kommende Tier habe ich in einem einzigen, bereits deformierten Exemplare in [F. 5] gefunden. Es ist leider im Laufe der Untersuchung noch vollends zu Grunde gegangen, so dass es mir unmöglich war, eine genaue Zeichnung des auffälligsten Körperteiles, des Postabdomens herzustellen. Dasselbe war sehr breit, wie bei *I. sordidus*. Die Serie der längeren, präanal Dornen bestand aber aus bedeutend kürzeren Elementen als bei der forma typica. Postanalzähne waren 9 vorhanden.

... Immerhin kommt dem *I. sordidus* SARS (1901!) mindestens der Wert einer neuen Varietät zu. Ich bezeichne sie darum nach ihrem Entdecker als *I. sordidus* var. *sarsi*.”

But, undoubtedly, Stingelin described a good new species [Paggi, 1992], relatively common in South America. The species was redescribed by Kotov et al. [2001].

2. *Ilyocryptus sordidus* var. *longisetus* Arévalo, 1916

Arévalo, 1916: 48, 50, Fig. 20; 1917: 142, Fig. 4.

Type material: lost.

Type locality: “la Albufera de Valencia”, Spain (in Spanish, albufera means a very shallow, slightly brackish, near-coastal lagoon).

Etymology: The author referred to the long postabdominal setae of this form.

Comments: The first description was lacked much helpful information [Arévalo, 1916: 48, 50]:

“Los escasos ejemplares que yo he podido recoger (solamente tres) distinguense de la forma típica por tener los ojos, y especialmente el compuesto, mucho más grandes; las cerdas dorso-caudales, sensiblemente más largas; así como por el mayor número de cerdas natatorias en el segundo par de antenas. Su tamaño parece también ser muy inferior en esta variedad. A pesar de que estos caracteres autorizarían para formar una nueva especie, yo me reservo el hacerlo para cuando haya estudiado mejor esta forma. Todos fueron recogidos en Noviembre.

Tamaño medio de hembras jóvenes: 0.40 mm.”

We can extract from the text the following information on characteristic traits of this form: (1) very large eye and ocellus; (2) very long postabdominal (= “dorso-caudal”) setae; (3) numerous swimming setae (3 apical and 2 lateral setae on both endopod and exopod in author’s Fig. 20); (4) shorter swimming setae than in *I. sordidus*, but this fact is questionable, according to the same figure; (5) very small size, about 0.4 mm. In addition, from the author’s figure 20 (reproduced here in Fig. 1), the animal has: (6) incomplete moulting; (7) preanal part of postabdomen shorter than postanal part; (8) relatively thin antennules; (9) very long apical spines of the second antenna and a very long distal burrowing spine on its basal segment.

Keeping in the mind features 1, 2, 5, 6, 8, 9, we can confidently say that a juvenile specimen of a species from the genus *Ilyocryptus* was described here. In the South American *I. sarsi* Stingelin, 1913, which is the one of the smallest in the world, 400µm is barely a minimal size of reproduction [Kotov et al., 2001], but no species with 400µm adults is known from Europe. Most probably, a juvenile of *I. agilis* Kurz, 1878 was described by Arévalo [1916]. Features 1, 2, 6, 7, 8, 9 are quite characteristic for both juveniles and adults of this species [Kotov, 1999]; earlier Smirnov [1976] also regarded *I. sordidus* var. *longisetus* as a junior synonym of *I. agilis*. The finding of some lateral setae on exopod of the second antenna (marked by thick arrows in Fig. 1) is undoubtedly a mistake made by the author, as all *ilyocryptids* have the same antennal formula.

3. *I. sordidus aequalis* Romijn, 1919

Romijn, 1919: 534, Fig. 2 (*Ilyocryptus*)

Type material: all Romijn’s materials were most probably lost; at least, they appear to be absent from museums in the Netherlands (Dr. Leentvaar and Dr. Pinkster, personal communication to Dr. P. Štifter).

Type locality: It was not specified clearly. Romijn [1919] had a material from a series of water bodies in Provinces Nordbrabant, Gelderland and Limburg, the Netherlands.

Etymology: The author made reference to the similar lengths of the preanal and postanal margins of the postabdomen, inferred from the length of the preanal margin relative to the total length of the postabdomen.

Comments: See section on “*I. sordidus inaequalis*” below.

4. *I. sordidus inaequalis* Romijn, 1919

Romijn, 1919: 534–535, Fig. 2 (*Ilyocryptus*)

Type material: most probably lost.

Type locality: It was not specified clearly. Romijn [1919] had a material from a series of water bodies in Provinces Nordbrabant, Gelderland and Limburg, the Netherlands. Only some of them were listed by the author, see below.

Etymology: The author referred to different lengths of the preanal and postanal margins of the postabdomen.

Comments: Discrimination of these two forms was based on only a single morphometrical feature, namely, the length of preanal margin of the postabdomen relative to the total length of the postabdomen [Romijn, 1919: 534]:

“... anders ist dies jedoch mit der Kurve 2, wobei der Quotient der Länge des Präanalstücks und des ganzen Hinterkörpers als Merkmal genommen ist. Es ergibt sich daraus, daß diese Zahl zwischen 0,40 und 0,78 schwankt. Die Frequenzkurve zerfällt jedoch in zwei Stücke. Der erstere Ast, der die große Mehrzahl der Beobachtungen enthält, hat seinen Gipfel bei 0,52 und erstreckt sich bis 0,59. Die hierher gehörigen Tiere möchte ich *I. sordidus aequalis* nennen.

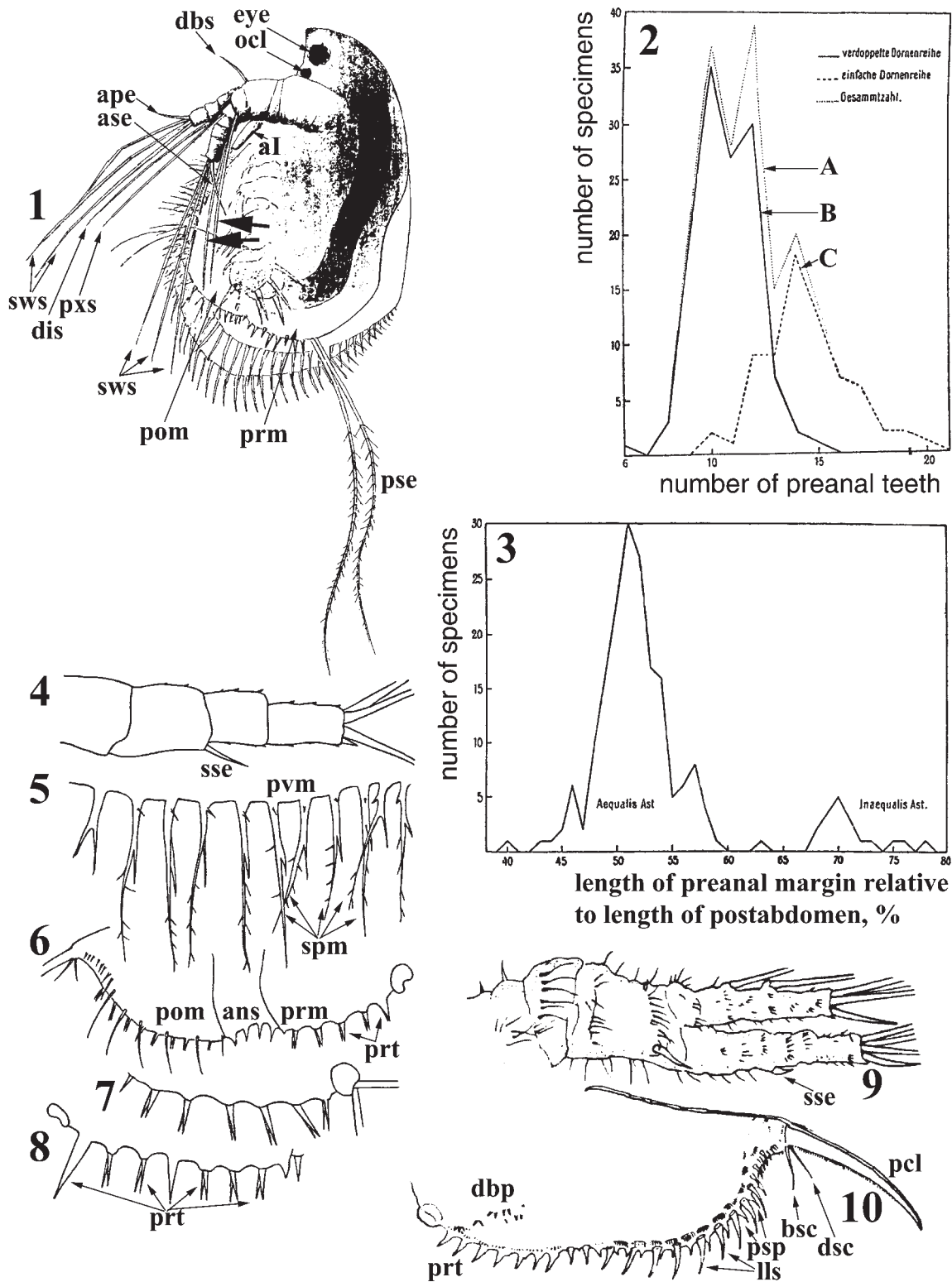
Nun folgt mit nur einer Unterbrechung ein zweiter Ast von 0,68 bis 0,78, der seinen Gipfel bei 0,70 hat und dem 18 Stück entsprechen, welche man dann auch *I. sordidus inaequalis* nennen muß. Die achtzehn Stück gehören zu den Tieren mit Dornenzahl von 13–19; doch gehen hohe Dornenzahl und langes Präanalstück nicht immer zusammen; so erreicht der Quotient bei dem einen Stück mit 20 Dornen nur 0,53, und bei den zwei mit 18 Dornen nur 0,48 bzw. 0,55.

An einer Stelle, in dem runden Teich auf dem Landgut „Zegenwerp” bei St. Michielsgestel, fand ich nur *I. sordidus inaequalis*. An anderen Stellen kamen die beiden Abarten zusammen vor, so in den Teichen des im Winter überfluteten Geländes bei Herzogenbusch.”

The author himself [Romijn, 1919: 535] had doubts in the status of the described forms. He represented many pictures of postabdomens of *I. sordidus*, but he did not mark the variety of each specimen in those figures; his discrimination was based only on his figure 2 (reproduced here as Fig. 3). According to his other graph, (author’s figure 1, reproduced here as Fig. 2), animals with few teeth more frequently bear partly doubled teeth. But he also stated that the number of preanal teeth was not closely connected with the relative length of preanal margin.

My present understanding of the systematics of *sordidus*-like European forms, based on Štifter’s [1988] revision and subsequent explanations [Štifter, 1991], leads me to regard both Romijn’s forms as artificial assemblages of different species.

Romijn [1919] completely subdivided all specimens of *I. sordidus* into two varieties with new names. This is an incorrect step in contemporary terms, because one of these “variations” (all trinomens described before 1961 are regarded as subspecies according to paragraph 45.6.4. of ICZN [2002]) must



Figs 1–10. Reproduced author’s illustrations from original descriptions of previously established *sordidus*-like forms of *Ilyocryptus*, somewhat modified using a computer graphical editor: 1 — *Ilyocryptus sordidus* var. *longisetus* Arvola, 1916, author’s Fig. 20, female in lateral view; 2–3 — *I. sordidus aequalis* and *I. sordidus inaequalis* Romijn, 1919, author’s graphs 1 and 2: A — total number of specimens studied, B — number of specimens with partly doubled preanal teeth; C — number of specimens with exclusively single preanal teeth; 4–8 — *I. silvaeducensis* Romijn, 1919, author’s pictures of antennal exopod, setae at posterior margin of valve, postabdomen and its preanal margin (after Smirnov [1976]); 9–10 — *Ilyocryptus sordidus* var. *denticulatus* Delachaux, 1919, author’s Figs 12–13, second antenna and postabdomen. No scale bars were presented by any authors.

Table 1. Some features of three closely related species of *Ilyocryptus* (according to data of Štifter, 1988; Kotov, 1999; Kotov et al, 2002).Таблица 1. Некоторые особенности родственных видов *Ilyocryptus* (по данным: Štifter, 1988; Kotov, 1999; Kotov et al, 2002).

Species	Preanal teeth	Number of preanal teeth	Length of preanal margin relative to length of postabdomen, %
<i>Ilyocryptus sordidus</i> (Lievin, 1848)	Only single	10–14	About 0.5–0.6
<i>Ilyocryptus cuneatus</i> Štifter, 1988	Partly single, partly doubled	8–12	0.43–0.53
<i>Ilyocryptus spinosus</i> Štifter, 1988	Only single	17–19	0.65–0.71

named “*I. sordidus sordidus*”. Just “*I. sordidus aequalis*” is this pseudo-monotypical taxon, and only a junior synonym of *I. sordidus*. It appears to be a disproportional mixture of *I. sordidus* and *I. cuneatus* in present-day terms, these species can not be discriminated using the length of the preanal margin (see table 1). We can see in Romijn’s Figure 1, that the bulk of his *aequalis* was represented by specimens of *I. cuneatus* as it presently is understood, but the author did not conduct any efforts to distinguish forms with exclusively single and partly doubled preanal teeth, two species in recent understanding!

“*I. sordidus inaequalis*” apparently was a mixture of:

(1) *I. spinosus*, this species with very long preanal margin and exclusively single preanal teeth formed the bulk of this assemblage;

(2) *I. cuneatus*, because some of specimens with long preanal margin had doubled preanal teeth, characteristic only for this species (but we can not also exclude a chance, that these specimens were inter-specific hybrids of *I. cuneatus* with either *I. sordidus* or *I. spinosus*, but any hybrids were never reported for any species of *Ilyocryptus* earlier)

(3) Probably, *I. sordidus*, because range of relative length of preanal margin seems to be underestimated now.

There is a chance, that Romijn regarded just “*I. spinosus*” (in present-day understanding) as type of his *I. inaequalis*, and the former is a junior synonym of the latter. But the main problem connected with both Romijn’s forms is the absence of types. I am not sure that types were selected. Only if types, and a clearly marked holotype, are found, which seems quite unlikely, can we return to a re-evaluation of the status of Romijn’s forms, surely confirm the priority of *I. inaequalis*, and regard *I. spinosus* as a junior synonym of the latter. This question is opened for further investigations, and, may be, needs to be resolved by special resolution of ICZN.

5. *I. silvaeducensis* Romijn, 1919

Romijn, 1919: 535, Taf. II: Figs. 25–32 (*Ilyocryptus*); Smirnov, 1976: 49–50, Fig. 16 (after Romijn, 1919); Štifter, 1984: 133–135, Figs. 1–10; Štifter, 1988: Table 1; Štifter, 1991: Figs. 2b, 3b.

Type material: lost [Štifter, 1984].

Type locality: It was not specified clearly, and only some of the water bodies studied in the Netherlands were listed (see the first description reproduced below).

Etymology: unknown exactly, but it undoubtedly referred to the localities where the species was found, some of

which were within some forests, *sylva* (L.) = forest. But no information about these forests was given in the text.

Comments: The author’s first description is reproduced below [Romijn, 1919: 535]:

“Zuerst in der Nähe von Herzogenbusch, später jedoch auch bei Valkenswaard und bei Grathem fand ich in Teichen oder Moortümpeln eine Ilyocryptusart, die von den bisher gefundenen etwas abweicht, und die auch nicht mit *I. longiremis* nach der Beschreibung von Sars (3) übereinstimmt. Ich nenne diese Art *Ilyocryptus silvaeducensis* n. s.

I. silvaeducensis, wovon ich bis jetzt nur Weibchen gefangen habe, ist 0,7–0,9 mm groß. Am meisten stimmt er mit *I. sordidus* überein. Wie diese wirft er beim Häuten die alte Schale nicht ab und sieht ihm deshalb oberflächlich sehr ähnlich. Der Hinterkörper ist ähnlich gebaut wie bei *sordidus*, nur schwankt die Dornenzahl zwischen 5 und 10 mit einer starken Höchstzahl bei 5, (16 von den 29 untersuchten Stücken). Die Dornenreihe ist stets, wenigstens zum Teil, verdoppelt. Während das Präanalstück bei *I. sordidus* und *agilis* meist ziemlich stark gebogen ist, ist es bei *I. silvaeducensis* zwischen den Dornen fast gerade. Die Haare auf der Hinterseite der Schale sind nicht so stark verästelt als bei *sordidus*. Die Farbe ist viel heller; man findet sogar und zwar am sandigen Grund von kleinen seeartigen Teichen ganz farblose Stücke. Der Dorn auf dem zweiten Glied des Außenastes der Ruderantenne ist etwa so lang wie das Ende dieses Gliedes breit ist.

I. silvaeducensis habe ich in vielen Moortümpeln mit *I. sordidus* zusammen gefunden. In den oben erwähnten seeartigen Teichen mit ihrem sandigen Grund kommt er jedoch allein vor. Er scheint also etwas reineres Wasser zu wählen als *sordidus*.”

The following information on this species can be extracted from the description: (1) large size; (2) incomplete moulting, (3) number of stout spines on setae at posterior margin of valve smaller than in *I. sordidus*; (4) 5–10 preanal teeth, and animals with 5 teeth are much more frequent; (5) these teeth are partly or fully doubled; (6) preanal margin straight; (7) small number of spines on posterior marginal setae; (8) spine on second segment of exopod long (length = diameter of the segment). In addition, the animal in Romijn’s figures 25–27 (partly reproduced here as Figs 4–8) has (9) a short preanal margin; (10) lateral setae greatly longer than paired spines; (11) relatively elongated segments of exopod.

There is no doubt about the validity of this species. More information on the morphology were represented by Štifter

Рис. 1–10. Воспроизведенные иллюстрации из первоописаний ранее установленных *sordidus*-подобных форм *Ilyocryptus*, обработанные с помощью графического редактора: 1 — *Ilyocryptus sordidus* var. *longisetus* Aréval?, 1916, авторский рисунок 20, самка сбоку; 2–3 — *I. sordidus aequalis* и *I. sordidus inaequalis* Romijn, 1919, авторские графики 1 и 2: А — общее число исследованных особей, В — число особей с частично двойными преанальными зубцами; С — число особей с одиночными преанальными зубцами; 4–8 — *I. silvaeducensis* Romijn, 1919, авторские рисунки экзоподита 2-й антенны, щетинок заднего края створки, постабдомена и его преанального края (по: Смирнов [1976]); 9–10 — *Ilyocryptus sordidus* var. *denticulatus* Delachaux, 1919, авторские рисунки 12–13, 2-я антенна и постабдомен. Авторы не привели масштабных линеек.

[1984, 1988, 1991]. But this species must be redescribed once again following Štifter [1984], because many new important features have been revealed in the course of present-day investigations of *Ilyocryptus* morphology, i.e. armature of apical and lateral swimming setae, structure of thoracic limbs [Paggi, 1992; Kotov, 1999, Kotov & Dumont, 2000]. Some ilyocryptids, similar to European *I. silvaeducensis* have been found also in Africa [Kotov, 2000], South America and Australia [Sars, 1896; Kotov, unpublished].

6. *Ilyocryptus sordidus* var. *denticulatus* Delachaux, 1919

Delachaux, 1919: 26–27, pl. I: Figs. 12–13; Smirnov, 1976: 49, Fig. 15 (after Delachaux, 1919).

Type material: most probably lost.

Type localities: Lakes Hyaron and Lavandera, in the Andes, altitude 5140 m, Peru.

Etymology: The author referred to the denticles on the sides of basal part of the postabdomen.

Comments: The first description was reasonably good [Delachaux, 1919: 12–13]:

“Nous avons trouvé un exemplaire jeune, ainsi que plusieurs postabdomen et plusieurs paires d’antennes d’exemplaires adultes d’*ilyocryptus*, et des ephippies que nous rattachons malgré quelques hésitations à *I. sordidus*. Par la forme générale du postabdomen, cette espèce ressemble plus spécialement à *I. sordidus* que SARS a décrit et figuré en 1901, provenant de l’Amérique du Sud [10]. STINGELIN, dans ses Cladocères de Colombie [8], retrouve cette forme et la décrit brièvement sous le nom de var. *Sarsi* et la compare à *I. brevidentatus* Ekman des Iles Falkland.

Nos exemplaires présentent le même raccourcissement des épines latérales qui sont au nombre de 11 à 12. Le bord préanal possède 7 dents simples légèrement dirigées en avant; le bord postanal en a 12 qui augmentent de longueur vers la partie distale du postabdomen. Le bord ventral n’est pas lisse, mais présente une série de crans. Les griffes terminales sont grandes, à courbure simple, finement ciliées avec deux longues soies secondaires. Tout le long du bord en dessous des grandes épines postanales se trouve une série de peignes secondaires qui deviennent plus nombreux près des griffes terminales. Dans la partie préanale, ces peignes sont remplacés par des groupes de denticules. Depuis la première dent préanale et se dirigeant en diagonale sur le post-abdomen se trouvent placées des épines plus fortes qui n’ont été signalées jusqu’ici chez aucune espèce.

Les antennules sont longues et étroites, très peu renflées en leur milieu (moins par exemple que dans les dessins de Sars); leur article basal possède un appendice digitiforme assez prononcé qui ne se trouve pas non plus dans les dessins des auteurs cités. L’antenne natatoire est robuste et trappue. Elle est garnie d’un grand nombre de soies et de spinules lui donnant un aspect hirsute que nous n’avons pas observé sur l’espèce type ni sur les autres espèces du genre.

Nous croyons donc l’introduction d’une nouvelle variété comme suffisamment justifiée pour une forme qui se rapproche de *I. sordidus* var. *Sarsi*, mais s’en distingue cependant nettement par la présence des groupes de denticules ornant les flancs du postabdomen.

Les ephippies contenant deux œufs n’ont été trouvés que dans le lac Lavandera et correspondent aux dessins qui donne S. Minkiewicz [12] pour l’ephippium d’*I. sordidus* à la figure 6 Pl. 11 de son élude.”

The following traits are important for the species discrimination: (1) 11–12 large lateral setae on postabdomen; (2)

only 7 simple preanal teeth forming an acute angle with the margin; (3) postabdominal claws large; (4) presence of numerous denticles on side of base of postabdomen; (5) antennules relatively long and thin; (6) finger-like projection on basal segment of the antennule well-developed; (7) second antenna short and robust; (8) second antenna with many bristles and hairs; (9) ephippium with two eggs. In addition, the animal in the author’s figures 12–13 (reproduced here as Figs 9–10) has: (10) more distal and more basal of spines at base of claw of similar size; (11) paired spines along postanal margin much shorter than lateral setae; (12) elongated segments of both branches of the second antennae; (13) distal burrowing spine medium-sized, reaching the distal border of basal segment; (14) length of spine from the second segment of exopod equal to half that of third segment.

Unfortunately, the author had only a single juvenile specimen in a complete state, and only fragments of other specimens, but recent systematics is based on features of adult females. The type of moulting was not explicitly reported, but most probably moulting was incomplete, with just the exuviae of the second antennae and postabdomen (which Delachaux reported finding) being discarded. The slanting row of denticles at the base of the postabdomen, which was suggested by the author as the most important diagnostic character of *I. denticulatus*, is not a unique trait among ilyocryptids [Kotov et al., 2001]. But the very small number of preanal teeth (7), which furthermore are also bent toward the base of postabdomen, distinguishes this animal from all other South American forms. Discrimination of *I. denticulatus* from *I. sarsi* Stingelin, 1913, the most common South American *sordidus*-like species, is explained by Kotov et al [2001]. Most probably, Delachaux, 1919 described a valid species, which was never reported after him because subsequent authors determined this taxon as *I. sordidus*. This species must be re-examined in the future.

7. *I. balatonicus* Hankó, 1926

Hankó, 1926: 102–111, Taf. II–III (*Ilyocryptus*).

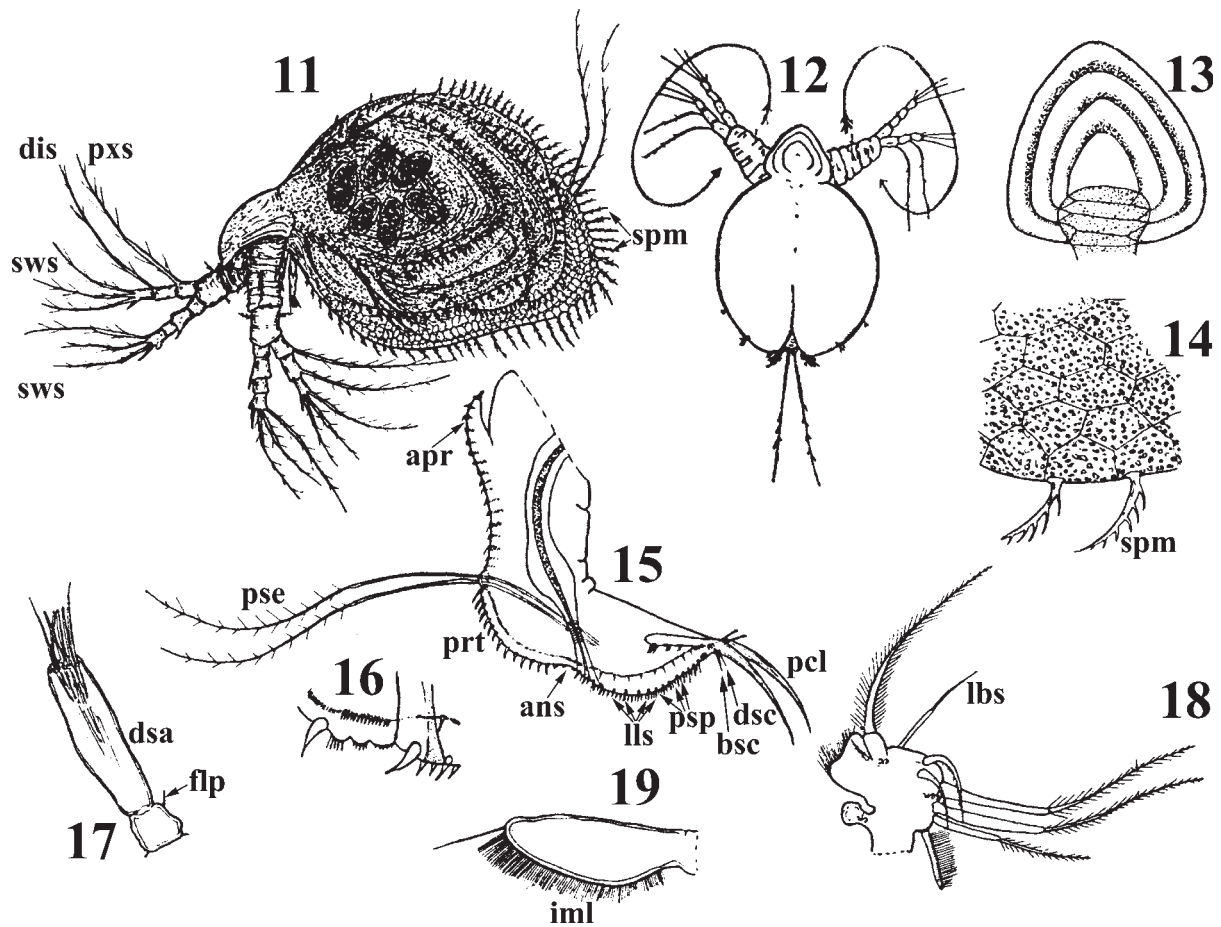
Type material: lost.

Type locality: Lake Balaton near Révfülöp, Hungary.

Etymology: The author named the species after Lake Balaton, where it was found.

Comments: The original description (in parallel in Hungarian and German) was relatively detailed; it is reproduced here without author’s expanded citations of Behning’s and Brehm’s suggestions on *Ilyocryptus* morphology and systematics [Hankó, 1926: 102–111]:

„Ausgewachsene Weibchen sind, von der Seite betrachtet, kurz und hoch, beinahe kugelig, von hinten betrachtet kugelig (Fig. 1). Schale fünf- und sechseckig gefeldert (Fig. 12). Schalenoberrand kurz, gleichmässig leicht konvex, und schwach gekielt. Einsenkung am Hinterkopf deutlich. Schalenhinterwand hoch, schwach konvex, oberer hinterer Winkel deutlich stumpf; der Hinterrand übergeht gleichmässig in den Unterrand; dieser schwach konvex. Hinter- und Unterrand mit groben, langen, gefiederten Borsten besetzt. Kopf klein, vorne mit stumpfer Spitze, sein Unterrand ausgebuchtet; Auge in der Mitte der Bucht, mit wenig Linsen. Der kurze und stumpfe Schnabel trägt die zweigliedrigen Vorderfüher (Fig. 3). Vorderfüher am Ende mit vier stumpfen, wie abgebrochen erscheinenden, und zwei spitzen, längeren Sinnesborsten, die zu diesen führenden Nerven sind im Fühler deutlich sichtbar; an der inneren Seite des kurzen Grundgliedes ein kleiner Stachel. Am Grunde des Vorderfühlers der viereckige Augenfleck.



Figs 11–19. Reproduced author's illustrations on *Ilyocryptus balatonicus* Hankó, 1926, somewhat modified using computer graphical editor: 11–12, female in lateral and dorsal view; 13 — head in dorsal view; 14 — posterior margin of valve; 15–16 — postabdomen and region of anus; 17 — antennule; 18 — limb I; 19 — limb VI. No scale bars were represented by the author.

Рис. 11–19. Воспроизведенные иллюстрации из первоописания *Ilyocryptus balatonicus* Hankó, 1926, обработанные с помощью графического редактора: 11–12, самка сбоку и сверху; 13 — голова, вид сверху; 14 — задний край створки; 15–16 — постабдомен и район ануса; 17 — антеннула; 18 — 1-я нога; 19 — 6-я нога. Автор не привел масштабных линеек.

Stamm der Hinter- (Ruder-) föhler gegliedert, äusserstes Glied mit zwei derben gefiederten Borsten, in der Mitte des Stammes eine dorsale gefiederte Borste, sonst an jedem Glied des Stammes kleine Borsten (Fig. 1). Das zweite Glied des viergliedrigen Aussenastes trägt einen

Stachel. Endglied mit einem derben Stachel, neben welchem sich ein fingerhutförmiger Höcker befindet, und drei langen, schwachgefiederten Schwimmborsten. Der dreigliedrige Innenast trägt an den beiden unteren Gliedern je eine lange, gefiederte Schwimmborste. Endglied mit drei langen, gefiederten Schwimmborsten und einem kurzen Stachel. Längste Schwimmborste so lang wie der Ruderföhler. Am Hinterrumpf ein langer spitzer, nach vorne gerichteter Rückenfortsatz (Fig. 2, a). Sowohl der Rückenfortsatz, als auch der dorsale Rand des Hinterkörpers bis zu den Schwanzborsten, mit in Querreihen geordneten, dichtstehenden, nach hinten gerichteten Borsten; ca 10–16 solche kurze Querreihen sind vorhanden. Äussere Hälfte der langen, auf vorspringenden Warzen stehenden Schwanzborsten, beiderseits gefiedert. Hinterkörper gross, seitlich stark komprimiert, dorsaler Rand konvex, in der Mitte mit einer deutlichen Bucht; vor dieser drei Stachelreihen; deren mittlere mit 11–17 derben, nach hinten gerichteten Stacheln,

die äusseren mit dichtstehenden, kurzen, dünnen Börstchen. Hinter der Bucht sechs Dornenreihen; die äussersten mit 6–9 kleinen, von einander gleich entfernt stehenden Stacheln, zwischen welchen kleine, dichtstehende, kurze Härchen sind; die mittleren Reihen führen 13–18 nach vorne gekrümmte, schlanke, grosse Dorne. Die Innersten Reihen mit kiemernden dichten Dornen besetzt. Der After mündet wie bei *I. sordidus*. In der Bucht, vor der Afteröffnung, sind drei kleine Höcker mit je fünf Börstchen vorhanden, von welchen die dem After am nächsten liegenden die kleinsten, die entfernt gelegenen die grössten sind (Fig. 2, b). Unter den Höckern stehen beiderseits 11–13 kleine Borsten kammförmig in einer Reihe.

Endkrallen gleichmässig gekrümmt, ungefähr so lang wie die grösste Breite des Hinterkörpers; am Grunde dorsal mit je zwei, ventral mit je einem geraden Stachel. Der Fortsatz, auf welchem die Endkrallen stehen, führt beiderseits in zwei Reihen feine Borsten und zwar in den inneren Reihen je 6–8, in den äusseren 8–12.

... habe ich jede Extremität des Tieres genau untersucht und habe mit Ausnahme der Maxille, welche keine typischen Artmerkmale aufweist, an allen übrigen Körperanhängen für unsere Art charakteristische Merkmale gefunden.

Statt einer langwierigen Beschreibung der einzelnen Extremitäten gebe ich deren genaue Zeichnung (Fig. 4–10), aus welchen alle typischen Details, sowie auch ersichtlich ist, dass selbe nicht mit den Extremitäten von *I. sordidus* übereinstimmen.

Bei der Häutung bleibt die alte Schale auf dem Tier sitzen, so dass je älter das Tier ist, um so mehr (bis 6) parallele Streifen an der Schale zu sehen sind, die alle mit grob gefiederten Borsten umrandet sind (Fig. 1). Im Brutraum, mitten am Rücken, mit meistens 6 Eiern, oder 6 Embryonen; manchmal auch 12, wovon auf die eine Seite 6 Eier, auf die andere 6 Embryonen fallen. Farbe des jungen Weibchens glasartig durchsichtig, ihre Körperform länglich, also weder von oben noch von hinten gesehen kugelförmig, sondern linsenartig. Jede neue Häutung verbreitert das Tier bis der Körper die kugelige Gestalt erreicht. Die alten Weibchen sind rot gefärbt, da ihr roter Körpersaft durch die lichtgelbe Schale hindurchschimmert. Die Schale ist von Schlammteilchen meistens völlig bedeckt, da die Schlammteilchen an den verzweigten Randborsten jedes Schalenrandes hängen bleiben.

Die Schale ist fünf- und sechseckig gefeldert (Fig. 12). Diese gefelderte Struktur ist bei jungen Tieren sehr auffallend, an älteren Tieren wird sie durch körnige Chitinverdickung und kleine Höcker, welche sich an der Schale bilden, getrübt, ist jedoch bei entsprechender Belichtung immer sichtbar. Diese gefelderte und durch kleine Chitinhöcker getrübt Schalenstruktur gleicht ein wenig der Schale von *I. verrucosus* DAD. aus Paraguay, doch ist sie mit dieser nicht identisch. Mit Höcker besetzt, jedoch nicht gefeldert ist auch die Schale von *I. tuberculatus* BREHM aus Zentral-Afrika. ...

Das Kopfschild ist nicht gefeldert, sondern zeigt eine gestreifte Struktur in welcher glatte und körnige Anwachsstreifen zu sehen sind (Fig. 11).

Das ausgewachsene Weibchen hat eine Länge von 1 mm und eine Körperbreite von 0,75 mm (der Rumpf ist bis zum Halseinschnitt ebenfalls 0,75 mm lang, also kugelig.)“

Helpful items, which can be extracted from it are the following: (1) size up to 1 mm; (2) incomplete moulting; (3) body of adult female very high, generally ovoid in lateral view, but dorsum only slightly convex; (4) body ovoid in lateral view, and with very low dorsal keel, visible in ventral view; (5) reticulation well-expressed in juveniles, but more obscure in adults; in the latter rough dots visible within each cell of reticulation; (6) ventral margin of head slightly concave; (7) setae of posterior margin long and with rough setules [=spines]; (8) small finger-like projection on basal segment of antennule; (9) lateral swimming setae of the second antennae relatively long, longer than apical setae, and feathered; (10) abdominal projection long; (11) postabdominal setae bilaterally setulated; (12) postabdomen with markedly convex dorsal margin, interrupted by anal depression; (13) 11–17 preanal teeth, bent towards distal part of postabdomen; (14) numerous lateral setae reaching anal margin of postabdomen (description of armature of postanal postabdomen part is very complicated and not clear); (15) postabdominal claws regularly bent, as long as depth of postabdomen. In addition, according to the author's pictures (partly reproduced here in Figs 11–19), this animal has: (16) preanal teeth exclusively single and of similar size; (17) lateral setae of postabdomen not too long, although longer than paired spines; (18) basal spines on claws of similar size; (19) long and sparsely located setules on postabdominal setae; (20) distal segment of antennule relatively short and lacking denticles; (21) setules on swimming setae of second antennae very long; (22) a large seta on limb I; (23) very dense setules on inner margin of limb VI.

Hankó (1926) only declared the dissimilarity of his animal and *I. sordidus*, but no differential diagnosis was given. In contrast to his opinion, no information on differences between two forms can be extracted from the description and pictures. In addition, the examination of his quite realistic pictures undoubtedly confirm an interpretation that Hankó dealt with typical *I. sordidus*. Each of features 9, 13, 16, 17, 20, 21, and, especially, their combination, is diagnostic of *I. sordidus* s. str. (see Štífler, [1988, 1991]; Alonso, [1996]). The name *I. balatonicus* was not accepted by subsequent investigators of Lake Balaton, which found only *I. sordidus* there [Sebestyén, 1948].

8. *I. sordidus sordidus* (Liévin, 1848) in Smirnov, 1976

Smirnov, 1976: 48, Figs. 11–13.

Type material: undoubtedly lost.

Type locality: “in einem kleinen Bruche mit torfigem Grunde und sehr klarem Wasser“ [Liévin, 1848], unknown water body in the vicinity of Gdańsk, Poland.

Etymology: *sordidus* (L.) is dirty, filthy [Brown, 1956].

Comments: The nominotypical subspecies was assigned within *I. sordidus* (Liévin, 1848) by Smirnov [1976], according to his understanding of the intra-specific organization of the species. See comments in “Discussion” section below.

9. *Ilyocryptus gouldeni* Williams, 1978

Williams, 1978: 673–676, Fig. 5

Holotype: an adult parthenogenetic female in the collection of the Smithsonian Institution Museum of Natural History, Washington, D.C., U.S.A., number USNM 170599.

Paratypes: 4 females from type locality, USNM 170602; 3 females from a pond in Orange, Texas, USNM 170601; 5 females from Tidemill Marsh, James River, Virginia, USNM 170600.

Type locality: Anacostia River, Maryland, near Washington, D.C., U.S.A. (appr. 38°50'N, 76°57'W) [Williams, 1978].

Etymology: This species was named after Dr. C.E. Goulden, a well-known U.S. investigator of the Anomopoda.

Comments: Undoubtedly a valid North American species, redescribed in detail by Kotov et al. [2002].

10. *I. alexandrinae* Negrea, 1987

Negrea, 1987: 107–110, Figs. 5–11.

Holotype: an ephippial female 0.54 mm long in formaldehyde, at the collection of the Museum ‘Grigore Antipa’ in Bucharest, Romania.

Paratypes: a gamogenetic and a parthenogenetic female (according to author's opinion), at the same museum.

Type locality: a spring at 30 m from the left bank of the river Desnatui upstream of the village Radovanu, 25 km SW of the city of Craiova, Romania.

Etymology: This species was named after author's wife and colleague, Dr. Alexandrina Negrea.

Comments: Although the description was relatively large, the only these characteristic traits, extracted from the diagnosis and description, are useful: (1) length 0.36–0.54 mm, smaller than in parthenogenetic females of *I. sordidus*; (2) body triangular; (3) dorsal margin of valves convex, with strong cervical incision; (4) postero-dorsal angle rounded; (5) each seta at posterior margin with 3–5 spines in its proximal third; (6) valves with projections of various size; (7) fornicies

developed; (8) eye small; (9) antennules long (a dubious thesis, keeping in the mind the author's pictures); (10) basal segment of antennule with hillocks; (11) anterior margin of distal antennular segment with 1–2 ridges basally; (12) spine on second segment of exopod not reaching tip of third segment [less than 0.5 of 3rd segment length in Fig. 6]; (13) postabdominal setae long; (14) anus opening in the middle of dorsal margin of postabdomen; (15) preanal margin arched, armed with 9–12 teeth, which slightly decrease in size distally, and 2–3 very small teeth near anus; (16) 9–10 lateral setae, row of these reaching anal margin; (17) 10–12 short paired spines; (18) size of both paired spines and lateral setae increasing somewhat distally; (19) postabdominal claws long, s-shaped; (20) both basal spines of similar size, about 40% of claw length; (21) ephippium with single egg. Additional information can be obtained from author's figures 5–11, which are not reproduced here: (22) complete moulting, not noted in the description; (23) preanal teeth slightly and regularly bent towards distal portion of postabdomen; (24) no denticles in distal portion of postabdominal claws; (25) setules on claws base ventrally very long; (26) segments of both antennal branches robust; (27) both distal sensory seta and distal burrowing spine relatively long.

The author specially remarked that the holotype was an ephippial female. He said that the parthenogenetic female was "generally similar to gamogenetic female. Dorsal margin of valves slightly convex and with a weak carina. Posterior margin with 23 + 24 long, spini-form setae; ventral margin with 31+33 long, barbed setae. Tubercles on valves smaller and less numerous than in gamogenetic female..." All these so-called differences are only a variability of ephippial females (note that the term "gamogenetic" is not accurate, because ilyocryptids very frequently lay ephippia with unfertilized, diploid eggs [Chirkova, 1984; Kotov & Dumont, 2000]). Without doubt, both the "gamogenetic" and parthenogenetic females of "*I. alexandrinae*" in the author's figures are really ephippial females of *I. sordidus*. Features 1, 3, 6, 21, 22 are characteristic for ephippial females of all species of the genus; none distinguishes *I. alexandrinae* from *I. sordidus* (see Lilljeborg [1901]; Štifter [1988, 1991]; Alonso [1996]). Negrea repeated a mistake of Daday [1905], who earlier described ephippial females of *I. spinifer* Herrick, 1882 as a separate species, *I. verrucosus* Daday, 1905 [Štifter, 1987; Kotov & Dumont, 2000].

Discussion

In the beginning-middle of the 20th century, all specimens of *Ilyocryptus* from different continents with incomplete moulting and a row of lateral setae not shorter than paired spines and reaching the anal margin were determined by most authors as *I. sordidus* [Sars, 1901; Daday, 1905; Harding, 1955; Flössner, 1972]. Smirnov [1976] subdivided *I. sordidus* into four subspecies: (I) *I. sordidus sordidus* (Liévin, 1848); (II) *I. sordidus inaequalis* Romijn, 1919; (III) *I. sordidus sarsi* Stingelin, 1913; (IV) *I. sordidus denticulatus* Delachaux, 1919. He made apparent the marked diversity of *sordidus*-like forms in the world fauna.

As I demonstrate above, Smirnov's subspecies III & IV are, actually, good separate species, II is a questionable species, either junior synonym of *I. sordidus* or separate species, but not a subspecies of *I. sordidus*. The

name *I. sordidus sordidus* (Liévin, 1848) cannot be used now because, as this article demonstrates, there are no other subspecies of that taxon, but, if another subspecies is found later on, that name should be applied to the nominal subspecies.

After recent significant progress in the study of ilyocryptids [Paggi, 1992; Kotov, 2000, Kotov & Dumont, 2000], it is absolutely clear that *I. sordidus* must be redescribed, and a neotype must be selected. Most probably, now only a single species is represented by this name in Europe and the northern parts of Asia. But this species is completely absent in, at least, Australia and South America, all previous authors having found other species superficially similar to *I. sordidus*. The status of African [Smirnov, 1976] and North American [Kotov et al., 2002] populations must be checked also.

I. cuneatus Štifter, 1988 is a valid species, studied well, we can regard it now as "valid" in terms of Korovchinsky [1996]. In addition, *I. cuneatus* is the most common species in Eurasia [Kotov, unpubl.], and present in the USA [Štifter, 1988] and Canada [Kotov et al., 2002]. But there is a chance, that *I. spinosus* Štifter, 1988 is a junior synonym of *I. inaequalis* Romijn, 1919. In any cases, now this question is opened for discussion, it is necessary to re-study *I. sordidus* and *I. spinosus* to resolve this problem, now both are not described adequately [Kotov, 1999; Kotov et al., 2002].

Presently, the European fauna of *Ilyocryptus* has been studied reasonably well, while those of many other territories are mysteries to investigators. Most probably, the validity of all former species described from Europe that are regarded now as junior synonyms of *I. sordidus*, with the exception of *aequalis-spinosus*, will not be restored as a result of any future revisions.

Conclusion

(valid species are marked by bold type)

- Ilyocryptus sarsi* Stingelin, 1913**, valid South American species.
- Ilyocryptus sordidus* var. *longisetus* Arévalo, 1916, junior synonym of *I. agilis* Kurz, 1878.
- I. sordidus aequalis* Romijn, 1919, jun. syn. of *I. sordidus* (Liévin, 1848).
- I. sordidus inaequalis* Romijn, 1919, questionable species.
- I. silvaeducensis* Romijn, 1919**, valid European species, status of any forms from other continents must be accurately investigated.
- I. sordidus* var. *denticulatus* Delachaux, 1919**, most probably a valid South American species, which must be re-examined.
- I. balatonicus* Hankó, 1926, jun. syn. of *I. sordidus* (Liévin, 1848).
- I. sordidus sordidus* (Liévin, 1848) in Smirnov, 1976, the name cannot be used now because there are no other subspecies of that taxon, but, if another subspecies is found later on, that name should be applied to the nominal subspecies..
- I. gouldeni* Williams, 1978**, valid North American species.
- I. alexandrinae* Negrea, 1987, jun. syn. of *I. sordidus* (Liévin, 1848).

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