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Redescription of two species of the genus *Leydigiopsis* Sars, 1901 (Branchiopoda, Anomopoda, Chydoridae)

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ABSTRACT: The two insufficiently known South American cladoceran species, *Leydigiopsis curvirostris* Sars, 1901 and *Leydigiopsis megalops* Sars, 1901, were redescribed from the type material. Detailed morphology of the trunk limbs of these species and morphology of male *L. megalops* were studied for the first time. Species of the genus *Leydigiopsis* combine clearly plesiomorphic characters — primitive morphology of head pores, male postabdomen similar to that in females, and apomorphic characters — long rostrum, antennules of unusual morphology, broad postabdomen with well developed postanal denticles. Analysis of morphology suggests that *Leydigiopsis* belongs to the group of the small tropical genera, like *Euryalona*, *Tretocephala*, long ago separated from the main trend of Aloninae and retain numerous plesiomorphic characters.

KEY WORDS: Cladocera, *Leydigiopsis,* morphology, systematics.

Переописание двух видов рода *Leydigiopsis* Sars, 1901 (Branchiopoda, Anomopoda, Chydoridae)

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РЕЗЮМЕ: С типового материала переописаны малоизученные южно-американские виды ветвистоусых раков *Leydigiopsis curvirostris* Sars, 1901 и *Leydigiopsis megalops* Sars, 1901. Впервые подробно исследовано строение грудных ног этих видов, описан ранее неизвестный самец *L. megalops*. В морфологии рода *Leydigiopsis* сочетаются явно плезиоморфные — примитивное строение головных пор, постабдомен самца не отличающийся от такового самки — и апоморфные признаки — длинный рострум, антенны необычного строения, широкий постабдомен с сильно развитыми постанальными зубцами. Анализ признаков показывает, что род *Leydigiopsis* принадлежит к группе малочисленных тропических родов, таких как *Euryalona*, *Tretocephala*, которые сравнительно рано отделились от основного ствола эволюции подсемейства.

КЛЮЧЕВЫЕ СЛОВА: ветвистоусые раки, *Leydigiopsis,* морфология, систематика.

Introduction

Recent taxonomic studies of the cladoceras of the subfamily Aloninae led to significant progress in the taxonomy of the group. Several genera were thoroughly revised (Smirnov, 1998; Hudec, 2000; Kotov, 2000a; Van Damme et al., 2003), several new genera were described (Ciros-Pérez, Elías-Gutiérrez, 1997; Dumont, Silva-Briano, 2000). Still, some genera remain insufficiently studied, like the genus*Leydigiopsis* Sars, 1901, one of most morphologically unusual genera of the subfamily Aloninae. Distinctive characters of this genus include long rostrum, broad postabdomen armed with very long marginal denticles, male postabdomen of same shape and armament as in female.

Sars (1901) had described two species, *L. curvirostris* and*L. megalops* from Brazil, neighborhood of Sao-Paolo. Both descriptions were quite detailed for that time, Sars even studied the trunk limbs morphology for*L. curvirostris*. After description, these species were rarely found. *L. curvirostris* was reported from Nicaragua (Smirnov, 1988). The exuvia of*L. megalops* were found in lake sediments in Venezuela (Goulden, 1966). Detailed morphology of these species remains unknown, and Korovchinsky (1996) did not list any of them among the adequately studied species.

Soon after that Daday (1905) described the third species of the genus, *L. ornata*, from Paraguay. This species differs from*L. curvirostris* by shorter rostrum, and from *L. megalops* by more broader postabdomen with a convex dorsal margin. The fourth species, *L. brevirostris* Brehm, 1938 was described from Brazil. An unusually short rostrum distinguishes it from other species. These two species have recently been revised,*L. ornata* by Rey et Vasquez, (1986) and *L. brevirostris* by Valdivia Villar (1984). While these works revealed additional unusual features of the genus, like leaf-shaped basal spine of the postabdominal claw, the overall level of knowledge of the *Leydigiopsis* morphology remains poor in comparison with other genera of Aloninae.

Until the end of the 20th century it was presumed that this genus is distributed in South and Central America only, but lately an occurrence of *Leydigiopsis* has been reported from Thailand (Sanoamuang, 1988). The taxonomic status of Asian *Leydigiopsis* is unclear.

Fortunately, several original Sars' samples and slides of *L. curvirostris* and *L. megalops* from the type localities were present among his collection of Cladocera deposited at the Zoological Museum of Oslo University. The aim of this research was to study detailed morphology of *L. curvirostris* and *L. megalops* and to analyse morphological characters of the genus Leydigiopsis and to determine its place within the subfamily Aloninae.

Material and methods

The studied material includes all samples and slides of *Leydigiopsis* species from G. O. Sars' collection, including the type samples for *L. curvirostris* and *L. megalops*. The animals were selected from samples under a binocular stereoscopic microscope, placed on slides (in a drop of a glycerol-ethanol mixture) and studied under an optical microscope in total. Several specimens were dissected for analysis of appendages. Measurements were conducted using an eyepiece-micrometer, all drawings were made using a camera lucida.

Results

Leydigiopsis curvirostris Sars, 1901

Sars, 1901: 44–46, Pl. VIII, fig. 1–11; Smirnov, 1971: 511, Fig 652–653.

Type locality: Brazil, Sao-Paolo, Ipiranda.

Lectotype: parthenogenetic ♀♀, Zoological Museum of Oslo University (ZMOU), sample F12379a.

Paralectotypes: over 50 parthenogenetic ♀♀, ZMOU, sample F12379; 3 parthenogenetic ♀♀, 1 ephipppial ?, 10♂♂, ZMOU, slide F9127; 3 dissected parthenogenetic ♀♀, ZMOU, slides F12379c–e.

Other material: over 200 parthenogenetic ♀♀, over 50 ephipppial ♀, over 50 adult and juvenile ♀♀, from Brazil, Sao-Paolo, ZMOU, samples F12386c and F12390d, slides F9127-

F9129; 4 dissected parthenogenetic♀♀, ZMOU, slides F12386j–m, dissected adult ♂, ZMOU, slide F12386n, dissected juvenile instar II ♂, ZMOU, slide F12386o, dissected juvenile instar I ♂, ZMOU, slide F12386p.

Diagnosis

Female: Rostrum very long, about three lengths of antennule, strongly curved, protruding backward. Postabdomen wide, of moderate length, with convex margins, length about 2.3 height. Ventral margin weakly convex. Dorsal margin weakly convex in postanal part and concave in the anal one, with distal part about 2.5 times longer than the preanal one, and with postanal portion 3 times longer than the anal one. Preanal angle clearly defined, postanal angle weakly defined. Antenna with seta arising from basal segment of endopod short and stout, little longer than middle segment. Size 0.52–0.84 mm.

Male: Rostrum short. Postabdomen of the same shape as in female. Size 0.59–0.63 mm.

Differential diagnosis: the main diagnostic feature of *L. curvirostris* is a very long, strongly curved rostrum. In other species of the genus length of rostrum varies from 1.5 to 2 lengths of antennule, and it is curved downward. Other distinctive character of the genus is a wide, relatively short postabdomen, in other species length of postabdomen is more than 2.5 maximum height. Additional difference of this species from *L. megalops* is a short seta arising from basal segment of endopod of antenna.

Description

Parthenogenetic female. Body moderately compressed laterally, in lateral view oval (Fig.1–2, 6), of moderate height in juvenile females (Fig. 1, A, B), high in adults (Fig. 1, C, D), maximum height at the middle of the body. In adults length about 1.4 times maximum height. Dorsal margin of valves strongly curved, posterior and ventral margins slightly convex. Postero-dorsal and postero-ventral angles broadly rounded. No setules at postero-ventral angle. A row of about 80 setules of uneven length along posterior margin at some distance from it on the inner side of carapace, these setules not organized into groups (Fig. 1, F). Ventral margin almost straight, with about 80 setulated setae, about 20 posteriormost setae especially broad and densely spaced (Fig. 1, G). Antero-ventral angle broadly rounded. Valves without any sculpture.

Head relatively small, triangle-round in lateral view (Fig. 2, A). Rostrum very long, about three lengths of antennule, strongly curved, extending posteriad. Ocellus larger than eye or equal to it . Distance from tip of rostrum to ocellus three times greater than that between ocellus and eye.

Head shield elongated, with maximum width behind mandibular articulation (Fig. 2, B, C). Rostrum long, pointed, evenly narrowing distally (Fig. 2, D). Posterior margin of head shield broadly rounded. Single major slot-shaped head pore, surrounded by broad rim. In females of juvenile instars pore significantly wider (Fig. 2, M), than in adults (Fig. 2, E). Distance from the end of the pore to posterior margin of head shield was 1.5–2 length of the pore in adult females, and only 0.8–1 in juvenile females. Lateral head pores located very close to major ones, about 0.1–0.2 length of the pore from the midline, almost at the middle of major head pore.

Labrum of moderate size (Fig. 2, F–I). Distal labral plate without setulation. In lateral view labral keel of moderate width, with apex in shape of narrow, pointed projection, which is not developed in most juveniles. Anterior margin of keel irregular, with a row of small setules in the middle, posterior margin convex, without any setules. In frontal view labral keel broad, wedge-shaped, not narrow like in most Aloninae, its apical projection more narrow than the keel itself.

Postabdomen wide, of moderate length, with convex margins, length about 2.3 height (Fig. 3, A,B). Ventral margin weakly convex. Inflated basis of claws separated from distal margin by clear incision. Distal margin convex, evenly passing into the broadly rounded dorso-distal angle. Dorsal margin weakly convex in postanal part and concave in the anal one, with distal part about 2.5 times longer than the preanal one, and

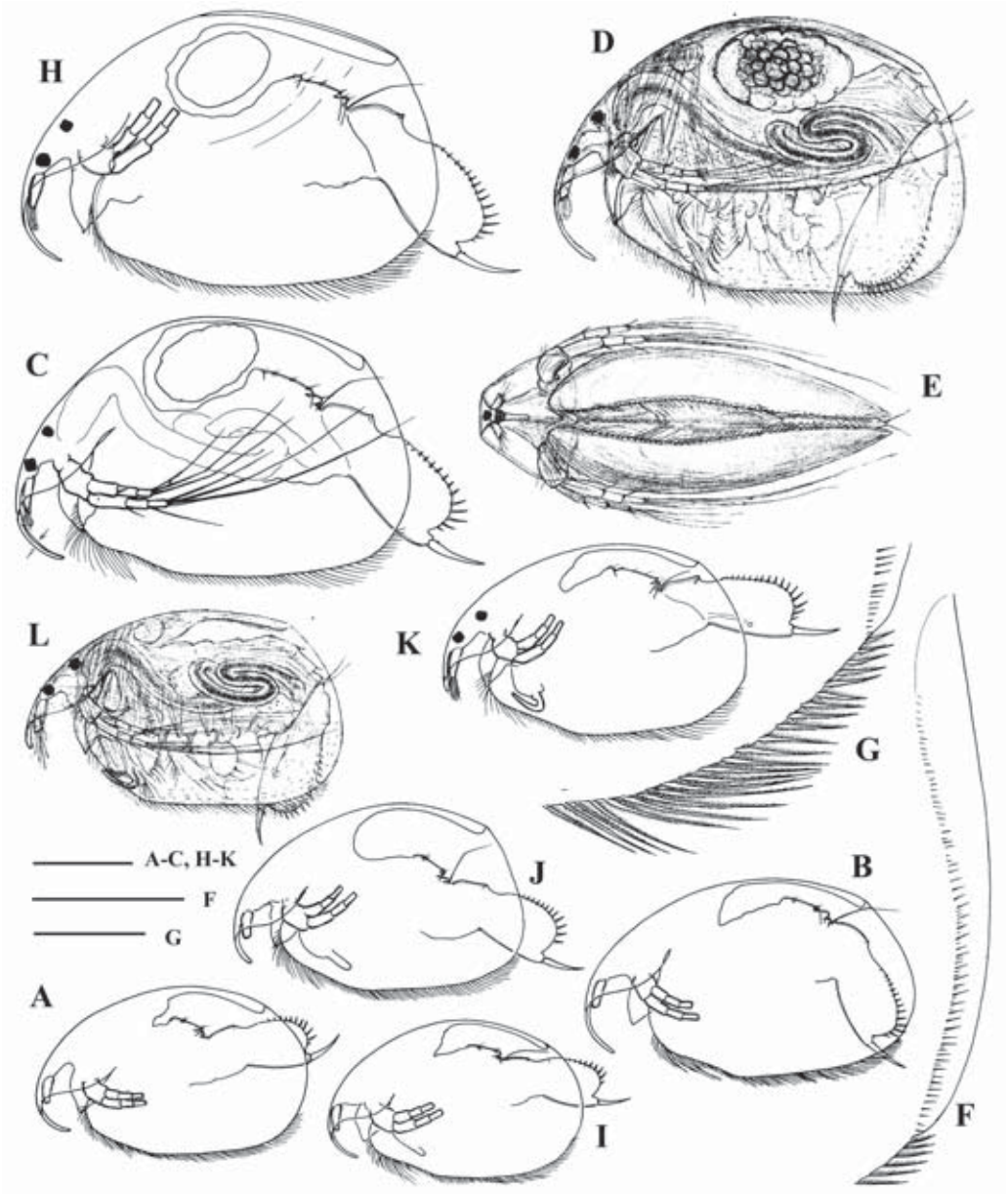

Fig. 1. *Leydigiopsis curvirostris* Sars, 1901 from Brazil, Saõ-Paolo.
A — instar I of juvenile female , B — instar II of juvenile female , C–H — parthenogenetic female: C–D — lateral view, E — ventral view, F — posterior margin of valves, G — posteroventral angle of valves; H — ephippial female, I — instar I of juvenile male , J — instar II of juvenile male , K–L — adult male [D, E, L — from Sars, 1901, other original]. Scale bar denotes 0.2 mm for A–C, H–K, 0.1 mm for F, 0.05 mm for G.

Рис. 1. *Leydigiopsis curvirostris* Sars, 1901 из Бразилии, Сан-Пауло.
А — ювенильная самка первого возраста, В — ювенильная самка второго возраста, С–Н — партеногенетическая самка: С–D — вид сбоку, Е — вид снизу, F — задний край створок, G — задне-нижний угол створок; Н — эфиппиальная самка, I — ювенильный самец первого возраста, J — ювенильный самец второго возраста, K–L — взрослый самец [D, E, F — по Sars, 1901, остальные оригинальные]. Масштаб 0,2 мм для А–С, Н–К, 0,1 мм для F, 0,05 мм для G.

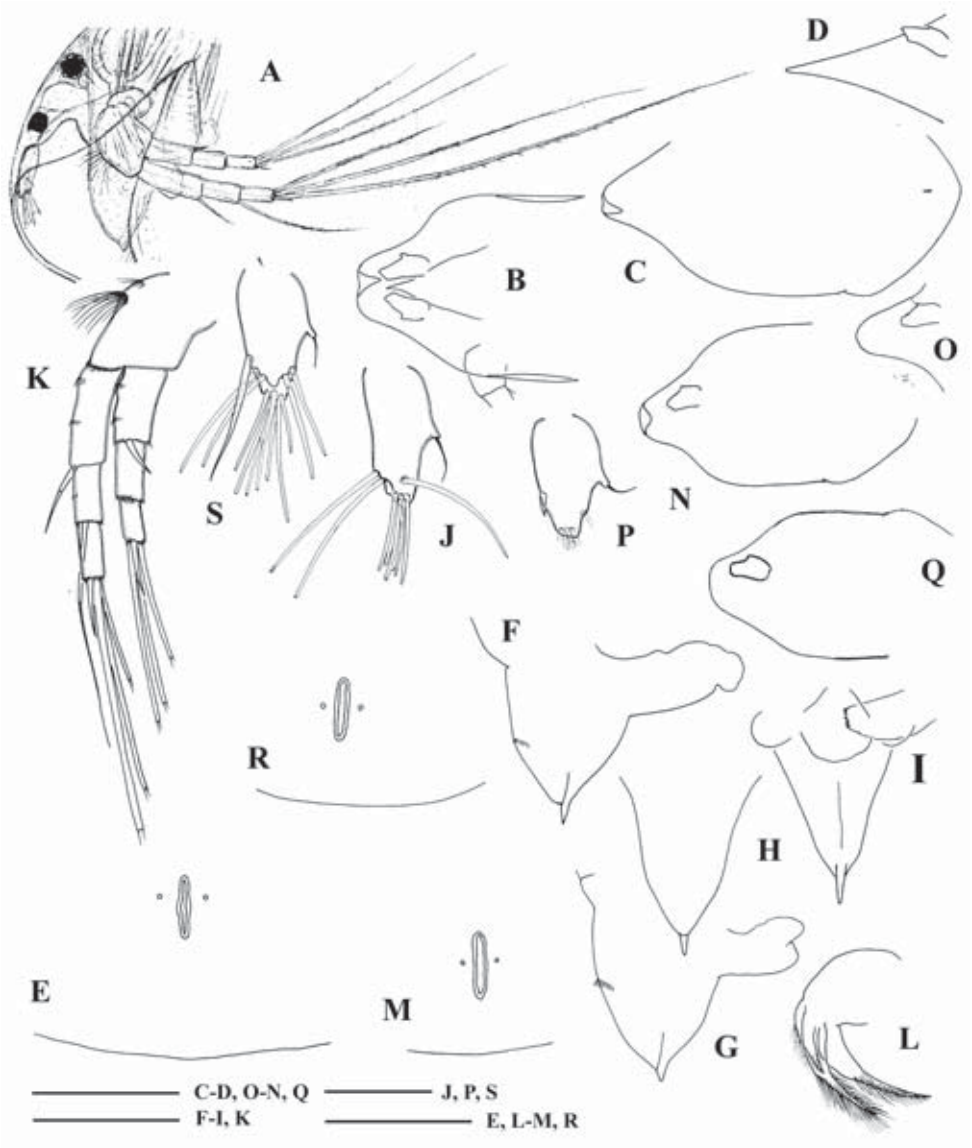

Fig. 2. *Leydigiopsis curvirostris* Sars, 1901 from Brazil, Saõ-Paolo.
A–L — parthenogenetic female: A — head, B–C — head shield, D — rostrum, E — head pores, F–G — labrum in lateral view, H — labrum in anterior view, I — labrum in posterior view, J — antennule, K — antenna, L — maxilla; M — head pores of juvenile female,instar I; N–P — juvenile male,instar II: N — head shield, P — rostrum, M — antennule; Q–S — adult male: Q — head shield, R — head pores, S — antennule [A — from Sars, 1901, other original]. Scale bar denotes 0.2 mm for B–D, N–P, Q, 0.1 mm for F–I, K, 0.05 mm for J, P, S and E, L–M, R.

Рис. 2. *Leydigiopsis curvirostris* Sars, 1901 из Бразилии, Сан-Пауло.
A–L — партеногенетическая самка: A — голова, B–C — головной щит, D — рострум, E — головные поры, F, G — лябрум сбоку, H — лябрум спереди, I — лябрум сзади, J — антеннула, K — антенна, L — максилла; M — головные поры ювенильной самки первого возраста; N–P — ювенильный самец второго возраста: N — головной щит, P — рострум, M — антеннула; Q–S — взрослый самец: Q — головной щит, R — головные поры, S — антеннула [A — из Sars, 1901, остальные оригинальные]. Масштаб 0,2 мм для B–D, N–P, Q, 0,1 мм для F–I, K, 0,05 мм для J, P, S и E, L–M, R.

with postanal portion 3 times longer than the anal one. Preanal angle clearly defined, postanal angle weakly defined. Preanal margin weakly convex.

Postanal margin with 16–20 long, sharp, slender marginal denticles (Fig. 3, C). All of them without any denticles on basal side. Longest denticles located on dorsodistal angle, their length about three width of postabdominal claw base. Anal margin with 3 rows of short marginal setules. Postanal part with 16–20 well-developed lateral fascicles of setules, 7–8 distal groups consisting of only 3–4 thick setules, posteriormost setae of each fascicle very thick, 3 times shorter than marginal denticles. Number of setules per fascicle increases anteriorly. Anal part with 4–5 lateral rows of short setules.

Postabdominal claw almost straight, longer than the preanal portion of postabdomen (Fig. 3, D). Basal spine in shape of small plate with spiked margin.

Antennule (Fig. 2, J) three times shorter than rostrum, narrowing distally, length about 3 times maximum width, without transverse rows of setules. Antennular sensory seta slender, three times shorter than antennule, arising at the middle of antennule from a well-defined tubercle. Three lateral aesthetascs subequal in length, about length of antennule itself, one projecting to the side of antennal seta, and two opposite to it. Five terminal aestetascs about half length of antennule.

Antenna of moderate size (Fig. 2, K). Antennal formula, setae 0–0–3/1–1–3, spines 1–0–1/0–0–1. Basal segment robust, with cluster of very long setules on its face above the base of endopod, exopod shorter than endopod. All segments slender, cylindrical, basal segments 1.5 time longer than apical ones. Seta arising from basal segment of endopod short and stout, little longer than middle segment. Setae of exopod strongly differentiated in thickness, setae of endopod of equal thickness. Seta arising from middle segment of endopod of similar size with shortest apical seta. Spine on basal segment of exopod about 2/3 length equal of middle segment. Apical spines slightly longer than segments bearing them.

Mandible of morphology usual for subfamily. Maxillae (Fig. 2, L) with three densely setulated setae pointed to its base.

Trunk limb I of moderate size (Fig. 4, A). Epipodite oval, without projection. Accessory seta absent. Outer distal lobe (ODL) with one long seta, and a conical hillock above it (Fig. 4, B). Inner distal lobe (IDL) with three setae, first IDL seta very slender, sharp, about 1/3 of third IDL seta, other two 2-segmented, with short setules in distal part, third IDL seta subequal to ODL seta, second IDL seta considerably shorter.

Endite 3 with four setae subequal in length, and additional small sharp conical element. Endite 2 with four setae, the longest of them subequal in length to ODL seta. Naked seta of endite 2 very short. Endite 1 with two 2-segmented setae, both setulated in distal part, straight narrow naked 1-segmented seta, and a naked setae on anterior face of limb, three times longer than naked seta of endite 2. A flat setulated seta pointed to the epipodite is not present. Ventral face of limb with cluster of 5–7 long setules basally, 11–14 very long and thick single setules in the middle portion, longest of these setules longer than most setae of endites, and several clusters of shorter and thinner setules distally. Two long, slender ejector hooks of similar size, slightly longer than setae of endite 3.

Trunk limb II subtriangular (Fig. 3, E). Exopodite narrow, elongated, of irregular shape, without seta, with clusters of short setules distally (Fig. 3, D). Inner portion of limb ("endopodite") with eight scraping spines, armed with small denticles. Spines 6–8 shorter, subequal in length, spines 1–5 long, increasing progressively in length distally. A portion of gnathobase bordering with "endopodite" with numerous hard setules. Distal armature of gnathobase with four elements. Filter plate with seven setae, the posteriormost member of same length as all other setae.

Trunk limb III. Epipodite oval, without any projection. Exopodite irregular, with seven setae (Fig. 4, C), setae 1–5 flattened, plumose, setae 6–7 slender, clearly two-segmented, without long setules. Seta 3 being the longest, length

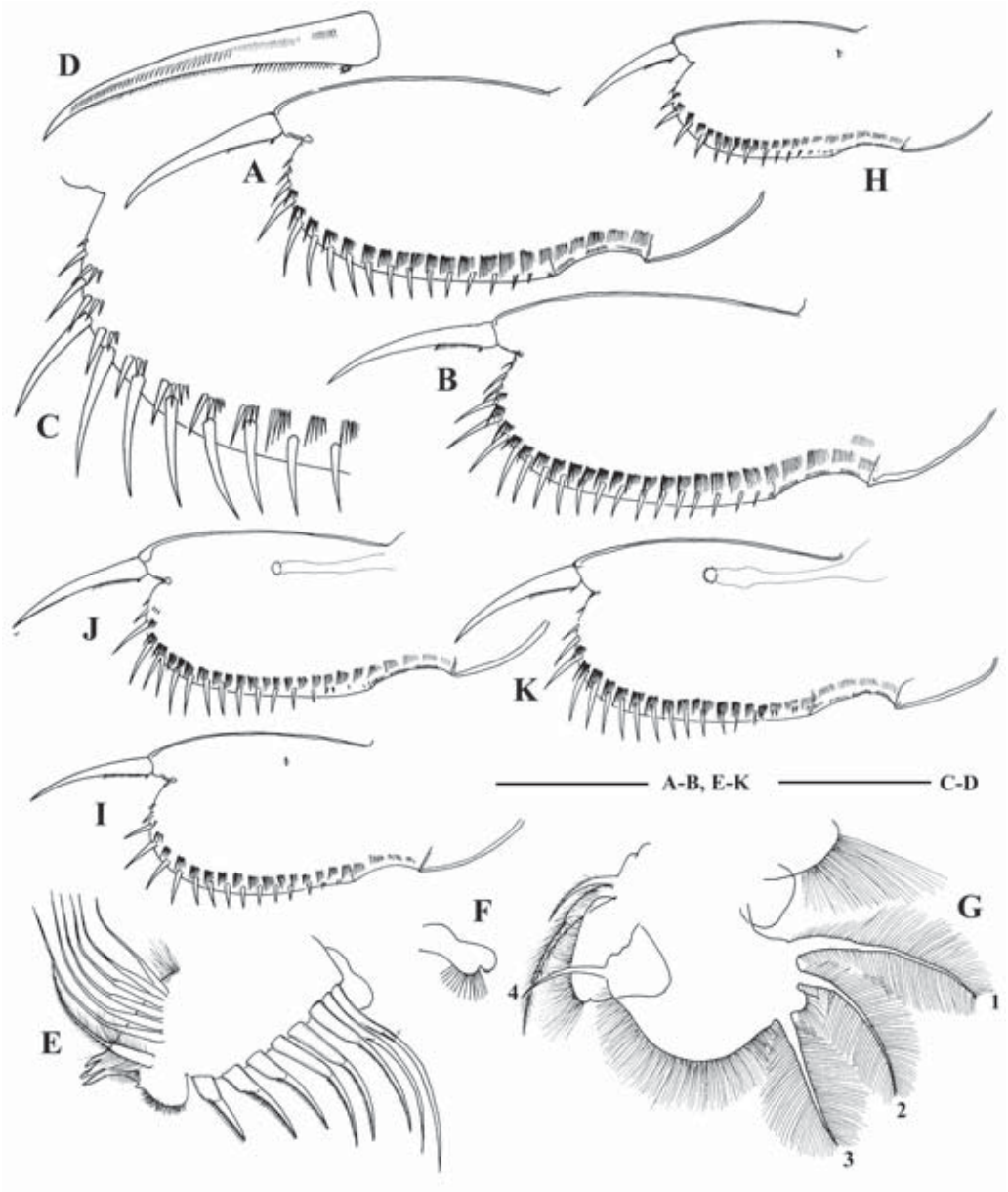

Fig. 3. *Leydigiopsis curvirostris* Sars, 1901 from Brazil, Saõ-Paolo.
A–G — parthenogenetic female: A–B — postabdomen, C — distal angle of postabdomen, D — postabdominal claw, E — limb II, F — exopodite of limb II, G — limb V; H — postabdomen of juvenile female, instar I, I — postabdomen of juvenile male, instar II, J–K — postabdomen of adult male. Scale bar denotes 0.1 mm for A–B, E–K, 0.05 mm for C–D.

Рис. 3. *Leydigiopsis curvirostris* Sars, 1901 из Бразилии, Сан-Пауло.
A–G — партеногенетическая самка: A–B — постабдомен, C — дистальный угол постабдомена, D — коготок постабдомена, E — нога II, F — экзоподит ноги II, G — нога V; H — постабдомен ювенильного самца первого возраста, I — постабдомен ювенильного самца второго возраста, J–K — постабдомен взрослого самца. Масштаб 0,1 мм для A–B, E–K, 0,05 мм для C–D.

of setae 1, 6, 7 and 2 about 2/3, 2/3, 1/2 and 1/3 of seta 3, respectively, setae 4–5 short, more than 4 times shorter than seta 3.

Distal endite with 3 slender setae with needle-like distal part, subequal in length, longer than setae 3–4 of exopodite (Fig. 4, D). Two distalmost setae armed with short setules: the basalmost setae somewhat similar to the flaming torch setae of limb IV, armed with about 10 long hair-like setules. Two sensillum-like elements of characteristic shape between them. Basal endite with 4 stiff, plumose setae, increasing in size in basal direction. Four soft setae increasing in size basally (Fig. 4, E), small sensillum located near the base of the distalmost seta, and two small conical sensillum-like elements between bases of setae. Gnathobase not clearly separated from basal endite. Distal armature of gnathobase with 3 elements. The first one an elongated, cylindrical sensillum, the second a geniculated seta, third a spine of characteristic shape, similar to the clawed finger. Filter plate III with seven setae.

Trunk limb IV (Fig. 4, F): pre-epipodite setulated; epipodite oval, with short finger-like projection. Exopodite elongated, of irregular shape, with six setae. Setae 1–4 (from epipodite) flattened, plumose, seta 3 being longest, others with length about s of seta 3. Setae 5–6 long, slender, clearly two-segmented, without setules. Seta 5 about half length of seta 3, seta 6 significantly shorter than seta 5. Inner portion of limb IV with four setae and sensillum (Fig. 4, G, H). Scraping seta very long, slender, with needle-like distal part, armed with short setules, flaming-torch setae with elongated, slender distal part, each armed with 7–10 long thin setules, longest of setules equal in length to setae bearing them. Sensillum elongated, slender. Additional small sensillum located between the bases of medium and basalmost flaming-torch setae. Three soft setae increasing in size basally. Gnathobase with a long 2-segmented seta and a long process distally. Filter plate with five setae.

Trunk limb V (Fig.3, G): pre-epipodite setulated. Epipodite oval, without any projection. Exopodite irregular, not divided into lobes, with four setae, setae 1–3 plumose, subequal in length, seta 4 significantly shorter and naked. Inner limb portion as wide subtriangular lobe, with long setules on the inner margin. At inner face, two densely setulated setae , the distal one long, equal to seta 2 of exopodite, the other 3 times shorter. Filter plate absent.

Trunk limb VI absent.

Ephippial female with body similar to that of the parthenogenetic female (Fig. 1, H), ephippium without developed egg locules, without prominent sculpture.

Male. Body of juvenile male of instar I (Fig. 1, I) similar to that of female of same instar, body of instar II juvenile (Fig. 1, J) and adult male (Fig. 1, K, L) similar to that of instar II juvenile female. In instar I rostrum the same as in female, in instar II rostrum shorter, about two length of antennule, with broadly rounded tip (Fig. 2, N, O), in adult male rostrum short and truncated, about 1.3 length of antennule (Fig. 2, Q). Head pores in both juveniles and adult similar to that of the juvenile females (Fig. 2, R).

Postabdomen in both juvenile instars (Fig. 3, H, I) and adult male (Fig. 3, J, K) of the same shape as in female, marginal denticles and postabdominal claw the same as in female. Gonopores located laterally near ventral margin, at the level of postabdominal claw base. In juvenile instars gonopores in shape of vertical slits, in instar I located near the base of ventral margin, in instar II at one third distance from its base. In adult gonopores large, round, in the middle of ventral margin.

Antennule: In instar I, the same as in female. In instar II (Fig. 2, P), antennule with anlage of male seta, with nine aestetascs spaced as in female; it was impossible to measure the length of aesthetascs due to their bad preservation. In adult male (Fig. 2, S), antennule slightly stouter than in female, with slender, long male setae longer than antennule itself arising about 1/3 length from tip. Four lateral aesthetascs, shorter than that of female, two of them projecting to the side of antennal seta, and two opposite to it, and eight terminal aestetascs longer than that of female.

Trunk limb I: In instar I (Fig. 4, I), copulatory hook short and stout, IDL of same structure as in female, ventral face of limb with 10 single large setules. In instar II (Fig. 4, J, K), copula-

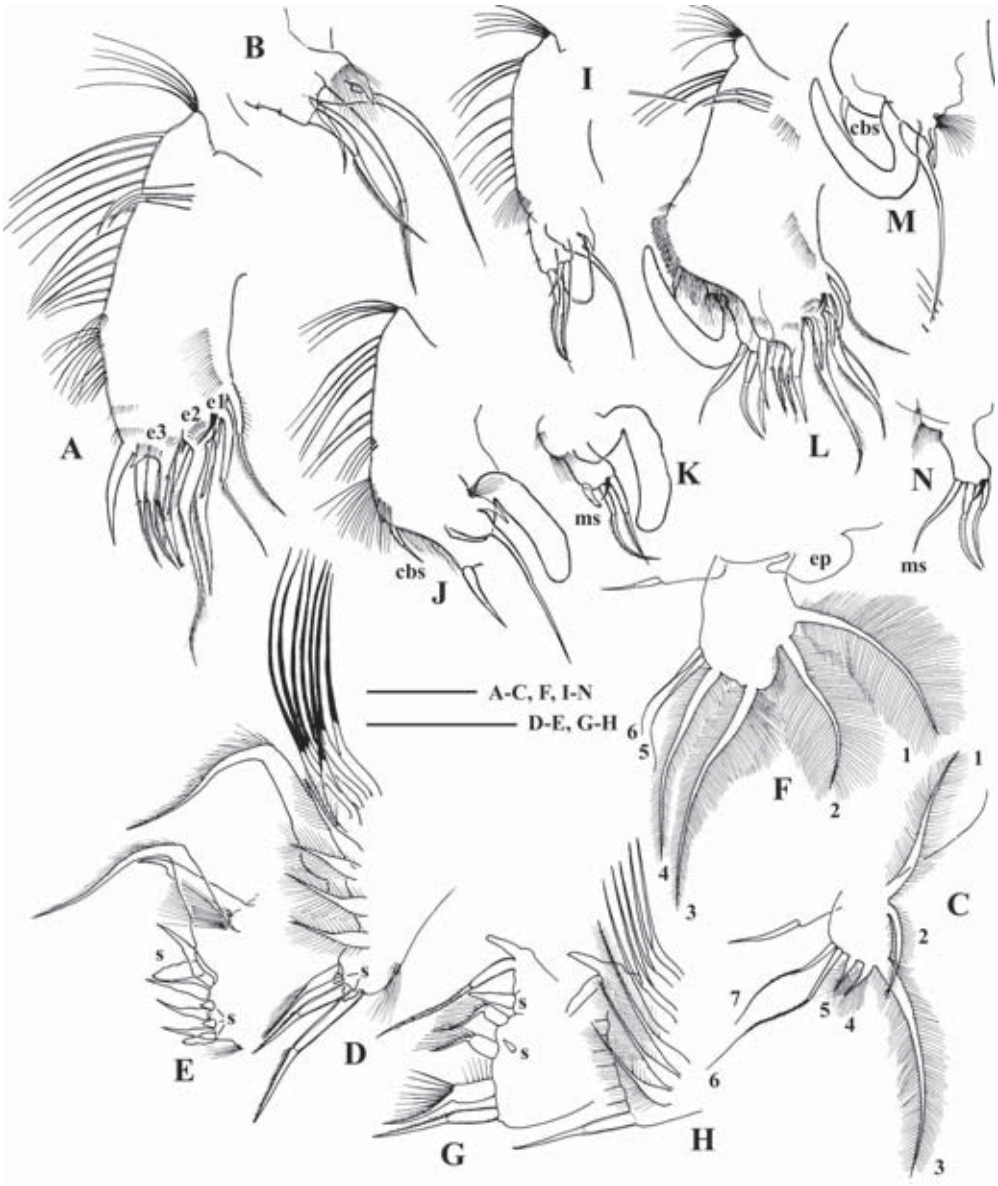

Fig. 4. *Leydigiopsis curvirostris* Sars, 1901 from Brazil, Saõ-Paolo.

A–H — parthenogenetic female: A — limb I, B — outer and inner distal lobes of limb I, C — exopodite of limb III, D–E — inner portion of limb III, F — exopodite of limb IV, G–H — inner portion of limb IV; I — limb I of juvenile female, instar I; J–K — limb I of juvenile male, instar II; L–N — adult male: L — limb I, M — copulatory hook and outer distal lobe of limb I, N — inner distal lobes of limb I; Abbreviations: cbs — copulatory brush seta, ep — epipodite, e1–e3 — endites 1–3, ms — male seta, s — sensillum; Scale bars denote 0.5 mm.

Рис. 4. *Leydigiopsis curvirostris* Sars, 1901 из Бразилии, Сан-Пауло.

A–H — партеногенетическая самка: A — нога I, B — внешняя и внутренняя дистальные доли ноги I, C — экзоподит ноги III, D–E — внутренняя часть ноги III, F — экзоподит ноги IV, G–H — внутренняя часть ноги IV; I — нога I ювенильного самца первого возраста; J–K — нога I ювенильного самца второго возраста; L–N — взрослый самец: L — нога I, M — копулятивный крюк и внешняя дистальная доля ноги I, N — внутреняя дистальная доля ноги I; Сокращения: cbs — щетинка копулятивной щетки, ep — эпиподит, e1–e3 — эндиты 1–3, ms — самцовая щетинка, s — сенсилла; Масштаб 0,5 мм.

tory hook curved, ventral face of limb copulatory brush setae of the same size as in adult and 7 single large setules. IDL with anlage of male setae, all IDL setae strongly reduced, second and third IDL setae being much shorter than the ODL seta. Rows of about 20 thin, hair-like setules on ventral face of limb under copulatory brush setae. In adult male (Fig. 4, L-N), trunk limb much stouter than in female and juvenile instars, with demicircular protrusion in distal part of ventral face bearing well developed copulatory brush. Ventral face of limb above copulatory brush with only three large single setules in distalmost part, and without clusters of large setules. Copulatory hook U-shaped, with free arm 1.5 times longer than base. Row of about 20 long, thin hair-like setules on ventral face of limb under copulatory brush. IDL setae similar to that of instar II, male seta long, subequal to second and third IDL setae, these setae lack setules in distal part, present in female and juvenile instars.

Size: In instar I juvenile females, length 0.52–0.54 mm, height 0.30–0.31 mm, in instar II, length 0.63–0.67 mm, height 0.39–0.42 mm. In adult female, length 0.69–0.84 mm, height 0.45– 0.55 mm. In single studied instar I juvenile male, length 0.5 mm, height 0.31 mm, in instar II males, length 0.56–0.61 mm, height 0.36–0.4 mm. In adult males length 0.59–0.63 mm, height 0.37–0.4 mm.

Distribution: Brazil, Nicaragua.

Leydigiopsis megalops Sars, 1901

Sars, 1901: 46–47, Pl. VIII, fig. 12–14; Goulden, 1966: fig. 376–377, pl. 4, fig. D–H; Smirnov, 1971: 511, Fig. 657.

Type locality: Brazil, Sao-Paolo.

Lectotype: parthenogenetic ♀, Zoological Museum of Oslo University (ZMOU), sample **F12383.**

Paralectotypes: 2 juvenile instar II ♀♀, 2 ♂♂ ZMOU, sample F12384a–f; dissected small parthenogenetic♀, ZMOU, slide F12384g; dissected adult ♂ ZMOU, slide F12384h.

Diagnosis

Female: Rostrum long, about two length of antennule, weakly curved, protruding downward. *Postabdomen* long, of moderate width, widening distally, length about 3 times height. Ventral margin weakly convex. Dorsal margin straight to weakly concave in postanal part and concave in the anal one, with distal part about 3 times longer than the preanal one, and with postanal portion 4.5 times longer than the anal one. Preanal angle clearly defined, postanal angle weakly defined. Antenna with seta arising from basal segment of endopod longer and thinner, almost reaching tip of apical segment, its first segment equal in length to middle segment. Size 0.56–0.79 mm.

Male: Rostrum short. Postabdomen of same shape as in female. Size 0.57–0.59 mm.

Differential diagnosis: the main diagnostic feature of *L. megalops* is the narrow, widening distally postabdomen. Other species have postabdomen with parallel or weakly convex margins, with length of postabdomen less than 2.7 maximum height. Rostrum of *L. megalops* is shorter than that of *L. curvirostris* (3 length of antenna), but longer than that of *L. brevirostris* (less than 1.5 length of antenna). Additional difference of *L. curvirostris* from *L. megalops* is long seta arising from basal segment of endopod of antenna.

Description

Parthenogenetic female. Body moderately compressed laterally, in lateral view subrectangular, of moderate height in juvenile females (Fig. 5, E, F), in adults high (Fig. 5, A, C, G), but lower than in previous species, maximum height at the third fourth of the body. In adults length about 1.5 times maximum height. Dorsal margin of valves weakly convex, posterior and ventral margins weakly convex. Postero-dorsal angle more or less defined, postero-ventral angle broadly rounded. No setules at postero-ventral angle. A row of about 80 setules of uneven length along posterior margin at some distance from it on inner side of carapace, these setules not organized into groups (Fig. 5, H). Ventral margin almost straight, with about 80 setulated setae, about 20 posteriormost setae especially broad and densely spaced. Antero-ventral angle broadly rounded. Valves without any sculpture.

Head relatively small, triangle-round in lateral view (Fig. 5, B). Rostrum long, about two length of antennule, weakly curved, protruding downward. According to Sars (1901), ocellus three times larger than eye. Distance from tip of rostrum to ocellus three times greater than the one between ocellus and eye. Head shield similar to that of the previous species, but with shorter and broader rostrum. Head pores same as in previous species (Fig. 5, I). In a single small adult female the distance from the end of the pore to posterior margin of head shield was about 0.8 length of the pore.

Labrum similar to that of the previous species, but apical projection of keel less developed (Fig. 5, J).

Postabdomen long, of moderate width, widening distally, length about 3 times height (Fig. 6, A, B). Ventral margin weakly convex. Inflated basis of claws separated from distal margin by clear incision. Distal margin convex, evenly passing into the broadly rounded dorso-distal angle. Dorsal margin straight to weakly concave in postanal part and concave in the anal one, with distal part about 3 times longer than the preanal one, and with postanal portion 4.5 times longer than the anal one. Preanal angle clearly defined, postanal angle weakly defined. Preanal margin straight.

Postanal margin with 16–19 long, sharp, slender marginal denticles. All of them without any denticles on basal side. Longest denticles located on dorsodistal angle, their length about two widths of postabdominal claw base. Anal margin with 3 rows of short marginal setules. Postanal part with 17–19 well-developed lateral fascicles of setules, 7–10 distal groups consisting of only 3–4 thick setules, posteriormost setae of each fascicle thick, 3 times shorter than marginal denticles. Number of setules per fascicle increases anteriorly. Anal part with 4–5 lateral rows of short setules. Postabdominal claw as in previous species.

Antennule (Fig. 5, K) two times shorter than rostrum, similar to that of the previous species. It was impossible to measure the length of aesthetascs due to their bad preservation.

Antenna (Fig. 5, L) similar to that of the previous species, but seta arising from basal segment of endopod longer and thinner, almost reaching tip of apical segment, its first segment equal in length to middle segment.

Trunk limb I (Fig. 6, C, D), *II* (Fig. 6, E, F) and *V* (Fig.6, J) same as in previous species. *Trunk limb III* (Fig. 6, G): similar to that of the previous species, but setae 1, 6 and 7 of exopodite subequal in length, about half length of seta 3. *Trunk limb IV* (Fig. 6, H, I): similar to that of the previous species, but epipodite oval, without any projection, setae 5 and 6 of exopodite subequal in length.

Trunk limb VI absent.

Ephippial female unknown.

Male. Body of adult male (Fig. 5, M) similar to that of instar II juvenile female, rostrum shorter, about 1.5 length of antennule. Head pores similar to that of juvenile females (Fig. 5, N).

Postabdomen (Fig 6, K) of same shape as in female, marginal denticles and postabdominal claw same as in female. Large, round gonopores located laterally at middle ventral margin, at the level of postabdominal claw base.

Antennule (Fig. 5, O) and *trunk limb I* (Fig. 6, L), similar to that of the previous species.

Size: Length of lectotype (adult female) 0.79 mm, height 0.50 mm, length of another studied adult female 0.64 mm, height 0.43 mm. In the two studied instar II juvenile females, length 0.56 and 0.61 mm, height 0.35 and 0.39 mm, respectively. In adult males length 0.57–0.59 mm height 0.33–0.39 mm.

Notes on material. According to Sars (1901), one of the distinctive characters of *L. megalops* is a denticle on the anterior margin of head shield, which is present on the lectotype on his drawings (Sars, 1901, VIII, 12–13, reproduced here as Fig. 5, A,B). Examination of this specimen reveals that its labrum was damaged (Fig. 5, D), all other specimens have normal labrum similar to that of the previous species. Due to the dissolution of soft tissue it was impossible to confirm the presence of the other distinctive feature of species — a very large ocellus.

Distribution: Brazil, Venezuela.

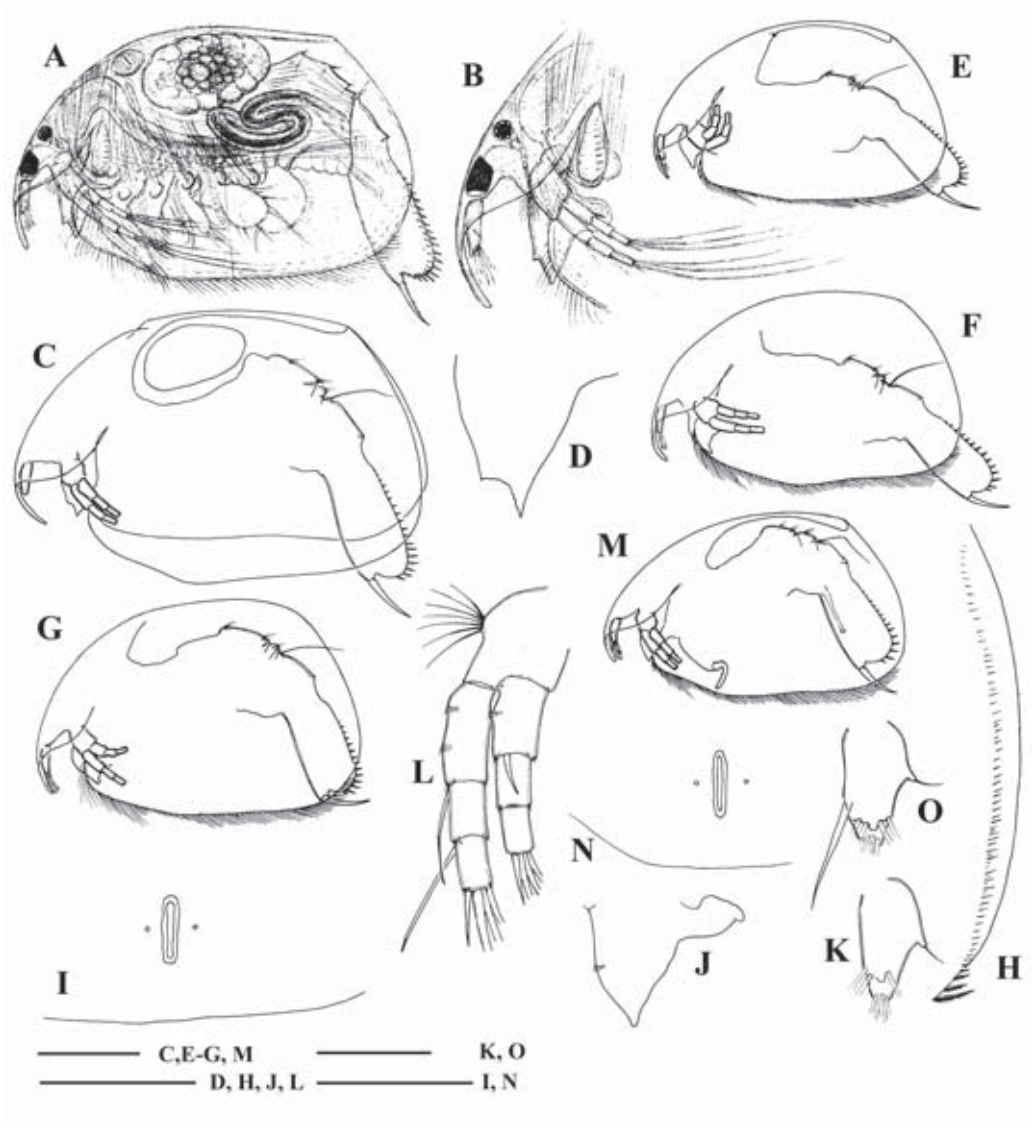

Fig. 5. *Leydigiopsis megalops* Sars, 1901 from Brazil, Saõ-Paolo.
A–D — lectotype, parthenogenetic female: A–B — lateral view and head as drawn by Sars (1901), C — lateral view in present conditions, D — labrum; E–F — juvenile female,instar II, G–L — small adult parthenogenetic female: G — lateral view, H — posterior margin of valves, I — head pores, J — labrum, K — antennule, L –antenna; M–O — adult male: M — lateral view, N — head pores, O — antennule [A–B — from Sars, 1901, other original]. Scale bar denotes 0.2 mm for C, E–G, Q, 0.1 mm for D, H, J, L, 0.05 mm for K, O and I, N.

Рис. 5. *Leydigiopsis megalops* Sars, 1901 из Бразилии, Сан-Пауло.
A–D — лектотип, партеногенетическая самка: A–B — вид сбоку и голова, рисунки Сарса (Sars, 1901), C — вид сбоку, современное состояние экземпляра, D — лябрум; E–F — ювенильная самка второго возраста, J–L — небольшая взрослая партеногенетическая самка: G — вид сбоку, H — задний край створок, I — головные поры, J — лябрум, K — антеннула, L — антенна; M–O — взрослый самец: M — вид сбоку, N — головные поры, O — антеннула [A–B — из Sars, 1901, остальные оригинальные]. Масштаб 0,2 мм для C, E–G, Q, 0,1 мм для D, H, J, L, 0,05 мм для K, O и I, N.

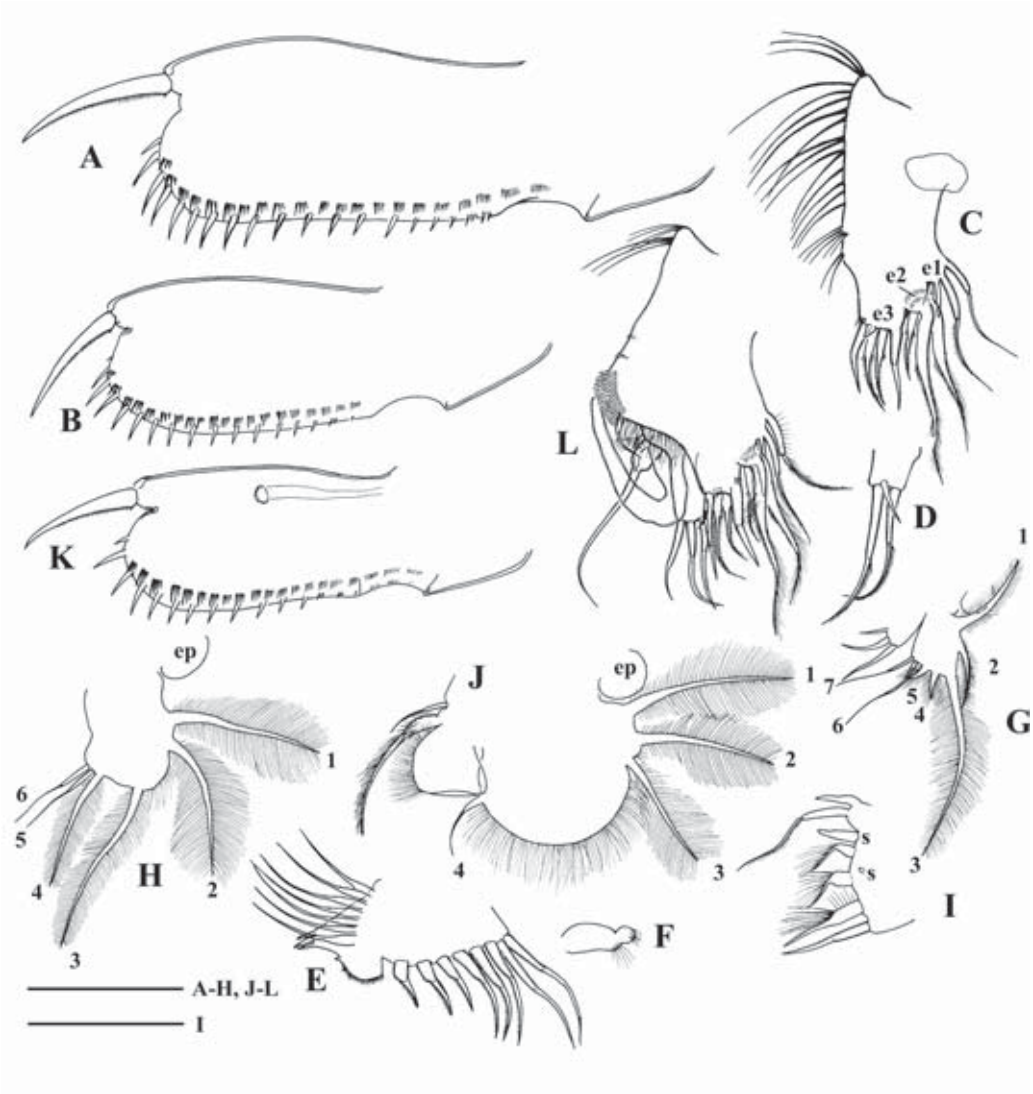

Fig. 6. *Leydigiopsis megalops* Sars, 1901 from Brazil, Saõ-Paolo.
A — lectotype, parthenogenetic female, postabomen; B–J — small parthenogenetic female: B — postabdomen, C — limb I, D — inner distal lobe of limb I, E — limb II, F — exopodite of limb II, G — exopodite of limb III, H — exopodite of limb IV, I — inner portion of limb IV, J — limb VI; K–L — adult male: K — postabdomen, L –limb I. Scale bar denotes 0.1 mm for A–H,J–L 0.05 mm for I.

Рис. 6. *Leydigiopsis megalops* Sars, 1901 из Бразилии, Сан-Пауло.
A — лектотип, партеногенетическая самка, постабдомен; B–J — небольшая взрослая партеногенетическая самка: B — постабдомен, C — нога I, D — внутренняя дистальная доля ноги I, E — нога II, F — экзоподит ноги II, G — экзоподит ноги III, H — экзоподит ноги IV, I — внутренняя часть ноги IV, J — нога VI; K–L — взрослый самец: K — постабдомен, L — нога I. Масштаб 0,1 мм для A–H,J–L 0,05 мм for I.

Discussion

Analysis of the morphology of *Leydigiopsis*

The general body shape of *Leydigiopsis* females is typical of the subfamily Aloninae, being similar to that of species of *Alona* Baird, 1843, *Oxyurella* Dybowski et Grochowsky, 1894 *Tretocephala* Frey, 1965 and other genera. Like the majority of genera, *Leydigiopsis* lacks keel or ridge on head shield and valves, which is present in the genera *Acroperus* Baird, 1843, *Camptocercus* Baird, 1843, *Celsinotum* Frey, 1991, and *Leberis* Smirnov, 1989. The lack of a prominent sculpture on valves and head shield is also characteristic of the subfamily. On the other hand, very long or even moderately long, as present in *L. brevirostris*, narrow rostrum, characteristic of the genus, is rare within the subfamily, similar rostrum is present only in the genera *Rhynchotalona* Norman, 1903 and *Kurzia* Dybowski et Grochowsky, 1894. With the exception of the rostrum, the shape of the head shield, with broadly rounded posteriormost extremity is the one of the most usual for the subfamily.

Single large major headpore surrounded by broad cuticular rim, according to Olesen (1996), is the initial type of major head pores ("neck organ") for Aloninae, the case of three small connected major head pores is deriving from it. A single elongated pore, like that of *Leydigiopsis*, is present only in two other genera: *Rhynchotalona* and *Tretocephala*. In *R. falcata* (Sars, 1862) the head pore is quite similar to that of juvenile females of *Leydigiopsis*, being only slightly wider and shorter (Alonso, 1996), in *R. kistarae* Roen, 1973 it is more broad, narrowing in the middle. In *T. ambigua* (Lilljeborg, 1900) the head pore is narrow, like that of adult *Leydigiopsis* females, narrowing in the middle (Alonso, 1996, Frey, 1965), in *T. colleti* (Sars, 1916) it is much broader, almost square (Frey, 1965). In contrast with these two genera, all studied species of *Leydigiopsis* have a quite similar major head pore, differences in its morphology between species not significant (see also Rey & Vasques, 1986, Valdivia Villar, 1984). The major head pore of *Euryalona* Sars, 1901, while of different shape, being round, is also quite large and surrounded by a circular rim, and in that similar to *Leydigiopsis*. It is quite interesting that in all the genera mentioned above lateral head pores are located very close to the major head pore. Such position of the lateral pores is also present in some Aloninae with three major head pores — in genera *Leydigia* Kurz, 1875, *Graptoleberis* Sars, 1862.

A labrum with a pointed apical projection of keel is unique for the subfamily, no such projection were found in any other genera. The most common shape of labral keel within the subfamily is oval, with rounded apex.

A relatively long, broad postabdomen is not common within the subfamily. The main trend of postabdomen evolution in Aloninae is elongation and narrowing of postabdomen, with its most extreme elongated postabdomen in *Camptocercus* and *Alonopsis*. Numerous genera of small-sized Aloninae have broad, but short postabdomen. Postabdomen of more or less similar shape are present in *Leydigia* and largest species of *Alona* (*A. quadrangularis* (O.F. Müller, 1785), species of *affinis*-group). Both *Alona* and *Leydigia* are quite distant from *Leydigiopsis* in most features, so such shape of postabdomen seems to be an outapomorphy of the genus.

Long and narrow single postanal denticles of the postabdomen are relatively rare within the subfamily, such denticles are present only within the genera *Euryalona* and *Oxyurella*. It should be noted that the denticles of this type are not homologous to the wide single denticles, as present in most species of *Alona*, *Camptocercus* and *Kozhowia* Vasiljeva et Smirnov, 1969. A groundpattern for the subfamily type of marginal denticles is a cluster of several relatively small marginal denticles or even setules. Denticles of the *Alona*-type were developed by the fusion of these denticles into a single structure. Such denticles are relatively broad and have several spinules on the anterior margin — the heads of former anteriour spines (see Alonso, 1996, Smirnov, 1998). The same process of fusion of setules, according to Dumont (1995), lead to the development of basal spine and

denticles on the posterodorsal corner of valves. The first step to the development of the *Leydigiopsis*-type denticles was the reduction of all anterior denticles in a cluster, followed by growth of the single remaining denticle. Such process is well illustrated by the denticles of *Oxyurella tennuicaudis* Dybowski et Grochowsky, 1894 (see Alonso, 1996) There are several clusters of denticles in the proximal part of postanal margin, small single denticles in the middle, each denticle is the same as the posteriormost denticle in clusters, and very long single denticles at the end of the postabdomen. The denticles of this type never have any spinules on the anterior margin.

The shape of basal spine of *Leydigiopsis* is unique for the subfamily, and seems to be an outapomorphy of the genus. In all other genera, the basal spine is a real spine, inflated laterally, and the completely different from the leaf-shaped spiked plate of *Leydigiopsis*. A homology between these two structures is doubtful. Postabdominal claw itself in *Leydigiopsis* is quite large and almost straight, postabdominal claws of similar shape are present mostly in genera with elongated postabdomen.

The shape of antennule is common to the subfamily. A well-defined tubercle at the base of antennal seta is present in several other genera (*Euryalona, Notoalona* Rajapaksa et Fernando, 1987, *Tretocephala*). Lateral aesthetascs in female are rare for the subfamily: a single lateral aesthetasc is present in genera *Tretocephala*, *Acroperus*, *Nicsmirnovius* Chiambeng & Dumont, 1999, and two of them in *Euryalona orientalis* (Daday, 1898), but other species of *Euryalona* lack them (Rajapacsa, Fernando, 1987a). Three long lateral aesthetascs are a unique feature of *Leydigiopsis*. Such length and placement of aesthetascs doubtless connected to the long rostrum and relatively short antennula of *Leydigiopsis*, which are not protruding beyond the border of the head shield. In two other genera with long rostrum, *Kurzia* and *Rhynchotalona,* antennules are long, in *Kurzia* with very long aesthetascs, in *Rhynhotalona* strongly protruding laterally, beyond the margins of rostum. Morphology of the antennae of *Leydigiopsis* is also common to the Aloninae, with the exception of the cluster of very long setules on basipodite, not present in other genera.

Reduction of accessory seta of limb I takes place in 8 genera of the subfamily (here and below used mostly data of Alonso, 1996, Kotov, 2000b and Smirnov, 1971). Such reduction of accessory setae seems to be a genus-level character, with no genera combining species with and without this seta. The morphology of ODL, IDL and endite 2 is common for the subfamily. IDL with three setae, the first being quite small, the two other armed with short setules in distal part seems to be initial for the subfamily.

Morphology of endite 1 is extraordinary. Usually, endite 1 of the Aloninae is armed with four setae — two 2-segmented setae, one naked seta on the anterior face of the limb, and one flat setulated seta pointing to the epipodite. *Leydigiopsis* lacks the last seta, but its reduction is frequently observed in the subfamily, for example in about half of *Alona* species, but possesses an additional narrow naked seta. This seta is absent in any other Aloninae. Ventral face of limb with long and thick single setules in the middle portion is a rare feature for the subfamily. Such setules are present in only one other species of the subfamily, *Alona quadrangularis*. In all other species of subfamily ventral face of limbs bear clusters of numerous shorter and thinner setules.

Limb II lacking an exopodite seta is present in 12 genera of Aloninae (Kotov, 2000b), some of them apparently quite distantly related (e.g. *Graptoleberis, Leberis, Oxyurella,* and *Tretocephala*), and species with and without this seta are present in some of them (*Leydigia, Notoalona*). Such reduction of exopodite II seta apparently had taken place more than once in the evolution of Aloninae, so this character is of limited value for the determination of relationships between genera. A similar morphology of limb II scrapers, as found in *Leydigiopsis*, seems to be the primitive state of this character, common to the subfamily, where strong differentiations between scrapers in length and size of denticles is quite rare and should be considered

as specialisations. Seven setae in filter plate II are the most common combination for the subfamily, but the distalmost seta is of the same length as other setae is present only in two other genera, *Euryalona* and *Notoalona*, (Rajapaksa, Fernando, 1987a,b), while in other genera these setae are significantly shorter.

There are two types of exopodite III present within the subfamily — with six and with seven setae, and the latter type, observed in *Leydigiopsis*, is the primitive state of this character. The unusual feature of exopodite III of *Leydigiopsis* is a very long seta 1, about two-third length of seta 3 and larger than other setae, such seta 1 is present in the genera *Tretocephala* and *Euryalona* (Kotov, 2000b; Rajapaksa, Fernando, 1987a). The inner part of the limb of *Leydigiopsis* is unusually rich in sensillae and sensillae-like elements. In the majority of studied species of Aloninae, there are three sensillae present — one on distal endite between the bases of distalmost setae, one near the base of distalmost soft seta, and one on the gnathobase. In addition to these elements, in *Leydigiopsis* there is a second sensillum on the distal endite, and two sensillum-like elements between the bases of soft setae. The morphology and number of setae on distal and basal endites, soft setae and filter plate III are common to the subfamily. The gnathobase of *Leydigiopsis* bears a peculiar long spine in the shape of clawed finger instead of two short spines, common for most Aloninae.

There are no unusual characters in morphology of trunk limb IV of *Leydigiopsis*, it has the usual number and morphology of setae. The shape of limb V of *Leydigiopsis* is common for the subfamily Aloninae. A reduction of the filter plate V is usual within the subfamily. Non-plumose seta 4 of exopodite V is a rare feature of the genus, such seta is present only in the genus *Euryalona* (Rajapaksa, Fernando, 1987a,) it is plumose in all other Aloninae. The lack of limb VI is also usual within the subfamily, this limb is present only in some species of *Alona, Acroperus, Camptocercus, Graptoleberis,* and *Parakozhowia* Kotov, 2000.

Males of *Leydigiopsis* demonstrate several outstanding features. Significant diminution of rostrum in instar II juvenile and adult male as it takes place in *Leydigiopsis* is not present in other Aloninae with a long rostrum. In *Kurzia* male rostrum remains of more or less the same size as in the female, and in *Rhynchotalona* it became larger and broader than in female.

Male postabdomen of same shape as in female, with well-developed postanal denticles, same as in female, and with lateral gonopores at the middle of postabdomen, as present in *Leydigiopsis*, is rare for the subfamily Aloninae. Such male postabdomen is present only in two genera — *Euryalona* and *Notoalona* (Rajapaksa, Fernando, 1987a,b). In these genera, gonopores are located more closely to the end of the postabdomen than in *Leydigiopsis*, only in one species, *Notoalona freyi* Rajapaksa & Fernando, 1987, they are located in the middle of ventral margin. In other genera with developed postanal denticles in female, clusters of short setules appears in their place in adult male. The shape of male postabdomen is never completely the same as in female, especially in genera with wide postabdomen, like *Leydigia* and *Alona,* where male postabdomen is more elongated and narrow than in female.

In the lack of changes in postabdomen morphology during male development these genera are quite similar to the family Eurycercidae (former subfamily Eurycercinae — see Dumont & Silva-Briano (1998)), most primitive family of superfamily Eurycercoidea. Also, in Euricercidae the gonopores of adult male are located in the middle of the ventral margin of postabdomen, not on its end. So, morphology of male postabdomen of *Leydigiopsis* in general seems to be very primitive, plesiomorphic character, representing the groundpattern for the subfamily Aloninae.

Stout trunk limb I with demicircular protrusion bearing a copulatory brush seems to be a unique character of the *Leydigiopsis* male. It can be speculated that the shape and armament of postabdomen and location of gonopores in *Leydigiopsis* male make the process of copulation quite awkward, particularly in achieving strong fixation of the females.

Place of the genus *Leydigiopsis* within the subfamily

Position of *Leydigiopsis* within Aloninae was previously discussed only by Smirnov (1971), who placed it between *Rhynchotalona* and *Oxyurella* in a phyletic tree of Chydoridae (Smirnov, 1971, fig. 182). It is clear that *Leydigiopsis* having a normal number of setae on all limbs, belongs to the tribe Alonini Kotov, 2000, not to Indialonini Kotov, 2000, where the number of limb setae is severely reduced (only 3 setae on the corm of limb I, 5, 4 and 3 setae on exopodites III–V respectively) (Kotov, 2000b).

A very long rostrum and a complex of characters connected to its morphology — female antennule with three lateral aesthetascs, reduction of rostrum in male, male antennule with aesthetascs shorter than in female and a very long male seta all seem to be outapomorphies of *Leydigiopsis*. While the rostrum of *Rhynchotalona* and *Kurzia* can be similar to those of *Leydigiopsis*, different morphology in the female and male antennule and lack of rostrum reduction in male shows that the development of the rostrum and the connected structures was independent in these genera. Other outapomorphies of the genus include a labral plate with apical process, large and broad postabdomen, basal spine of postabdominal claw in the shape of a spiked plate, and large single setules on the ventral face of limb I. On the other hand, the shape of major head pore, and shape and armament of male postabdomen are very primitive, plesiomorphic characters of the genus.

There are no reasons to doubt that the main tendency of limb evolution within the Chydoridae is a decreasing number and enhanced differentiation of setae (Smirnov, 1971 and others). In limbs of *Leydigiopsis* we see the combination of plesiomorphic (three IDL setae, morphology of scrapers and filter plate II, seven setae on exopodite III, typical morphology of inner parts of limb IV, numerous sensillae on the inner portion of limb III) and apomorhic characters (reduction of accessory seta of limb I, reduction of seta of exopodite II, lack of filter plate V and limb VI, unusual setae on ventral face of limb I), and only the last of the listed characters is an outapomorphy. It can be expected that the closely related genera should have more or less similar combination of these features, but not necessarily all of them.

A morphological analysis indicates that *Leydigiopsis* shares most similarities with another small genus of Alonini, *Tretocephala* (see Frey, 1965; Alonso, 1996; Kotov, 2000b). The synplesiomorphies between these genera include a large (for the tribe) size, high body without dorsal keel, the same type of major head pore, three IDL setae of same morphology, not differentiated scrapers of limb II, seven setae on exopodite III. Both genera have lateral head pores located extremely close to the major ones, and in my opinion it is also a synplesiomorphy, associated with more primitive type of major head pore (see above). The synapomorphies between them include antennule with antennal seta arising from tubercule, a very long seta 1 of exopodite III, lack of accessory setae on limb I, lack of exopodite seta on limb II, a very long seta 1 of exopodite 3, lack of gnathobase filter plate V and lack of limb V.

Also, *Leydigiopsis* shares several important characters with *Euryalona* (see Rajapaksa, Fernando, 1987a). The synplesiomorphies between these genera include shape and armament of male postabdomen similar to that of the female, single large major head pore surrounded by a circular rim (see above), lateral head pores located extremely close to the major ones, seven setae on exopodite III. The synapomorphies are mostly the same as between *Leydigiopsis* and *Tretocephala*: antennule with antennal seta arising from a tubercule, lack of accessory setae on limb I, lack of exopodite seta on limb II, a very long seta 1 of exopodite 3, lack of gnathobase filter plate V and lack of limb VI. One more synapomorphy in this pair is the same type of postanal denticles of postabdomen (see above). On the other hand, *Euryalona* differs from *Leydigiopsis* by morphology of trunk limb I, especially IDL, differentiated scrapers of limb II, and a more elongated postabdomen. Our data do not confirm close relationships between *Leydigiopsis* and *Oxyurella* and *Rhynchotalona*, proposed by Smirnov (1971).

The *Euryalona-Leydigiopsis-Tretocephala* clade seems to be one of the groups early separated from the main trend of Aloninae. It includes only small genera (four or five species in *Leydigiopsis*, three in *Euryalona*, two in *Tretocephala*), distributed mostly in tropical regions — only *T. ambigua* is a Palaeoarctic species. Its members retain several very primitive characters, not present in the majority of the subfamily. But the members of the clade are quite specialised genera and have unique apomorphies, so they should be quite different from the ancestral form of Aloninae.

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Literature

Alonso M. 1996. Fauna Iberica. Crustacea Branchiopoda. Madrid, Consejo Superior de Investigaciones Cientificas. 486 p.

Brehm V. 1938. Dritter Bericht über die von Dr. O. Schubart in Brasilien gesammelten Onychura // Zoolgischer Anzeinger. Vol.122. No.3/4. P.94–103.

Ciros-Pérez J., Elías-Gutiérrez M. 1997. *Spinalona anophtalma*, n. gen. n. sp. (Anomopoda, Chydoridae) a blind epigean cladoceran from the Neovolcanic Province of Mexico // Hydrobiologia. Vol.353. P.19–28.

Daday E., von. 1905. Untersuchungen über die Süsswasser Mikrofauna Paraguays // Zoologica, Bd.18. Heft. 44. Nr.3–6. P.1–374.

Dumont H.G. 1995. The evolution of the groundwater cladocera // Hydrobiologia. Vol.307. P.69–74.

Dumont H.J., Silva-Briano M. 1998. A reclassification of the anomopod families Macrothricidae and Chydoridae, with the creation of a new suborder, the Radopoda (Crustacea: Branchiopoda) // Hydrobiologia. Vol.384. P.119–149.

Dumont H.J., Silva-Briano M. 2000. *Karualona* n. gen. (Anomopoda, Chydoridae), with a description of two new species, and a key to all known species // Hydrobiologia. Vol.435. P.61–82.

Frey D.G. 1965. A new genus of Chydoridae (Cladocera) // Int. Rev. ges. Hydrobiol. Vol.50. No.2. P.153–168.

Goulden C.E. 1966. La aquada de Santa Ana Vieja: an interpretative study of the Cladoceran microfossils // Arch. Hydrobiol. Vol.62. No.3. P.373–494.

Hudec I. 2000. Subgeneric differentiation within *Kurzia* (Crustacea: Anomopoda: Chydoridae) and a new species from Central America // Hydrobiologia. Vol.421. P.165–178.

Korovchinsky N.M. 1996. How many species of Cladocera are there? // Hydrobiologia. Vol.321. P.191–204.

Kotov A.A. 2000a. Analysis of *Kozhovia* Vasiljeva & Smirnov, 1969 (Chydoridae, Anomopoda, Branchiopoda), and a description of *Parakozhovia* n. gen. // Hydrobiologia. Vol.437. P.17–56.

Kotov A.A. 2000b. Redescription and assigment of the chydorid *Indialona ganpati* Petkovsky, 1966 (Branchiopoda: Anomopoda: Aloninae), to Indialonini, new tribus // Hydrobiologia. Vol.439. P.161–178.

Olesen J. 1996. External morphology and phylogenetic significance of the dorsal/neck organ in the Conchostraca and head pores of the cladoceran family Chydoridae (Crustacea, Branchiopoda) // Hydrobiologia. Vol.330. P.213–226.

Rajapaksa R., Fernando C.H. 1987a. A redescription of *Euryalona orientalis* (Daday, 1898), with a consideration of the other species in the genus *Euryalona* (Cladocera: Chydoridae). // Hydrobiologia. Vol.150. P.75–90.

Rajapaksa R., Fernando C.H. 1987b. Redescription and assignment of *Alona globulosa* Daday, 1898 to a new genus *Notoalona* and a description of *Notoalona freyi* sp.nov. // Hydrobiologia. Vol.144. P.131–153.

Rey J., Vasquez E. 1986. Contribution à la connaissance des Cladocères néotropicaux: redescription de *Leydigiopsis ornata* Daday, 1905 (Crustacea, Cladocera) // Annls. Limnol. Vol.22. No.2. P.169–176.

Sanoamuang L. 1998. Contributions to the knowledge of the Cladocera of north-east Thailand // Hydrobiologia. Vol.362. P.45–53.

Sars G.O. 1901. Contributions to the knowledge of the fresh-water Entomostraca of South America, as shown by artificial hatching from dried material. 1. Cladocera // Archiv for Mathematik og Naturvidenskab. Christiana. Vol.23. No.3. P.1–102.

Smirnov N.N. 1971. [Chydoridae of the world fauna] // Fauna SSSR. Rakoobraznie T. 1. Vol.2. P.1–531 [in Russian].

Smirnov N.N. 1988. Cladocera (Crustacea) from Nicaragua // Hydrobiologia. Vol.160. P.63–77.

Smirnov N.N. 1998. A revision of the genus *Camptocercus* (Anomopoda, Chydoridae, Aloninae) // Hydrobiologia. Vol.386. P.63–83.

Valdivia Villar R.S. 1984 [On the morphology of Neotropical crustaceans of genus *Leydigiopsis* (Cladocera, Chydoridae] // Zoologichesky Zhurnal. Vol.63. No.10. P.1572–1575 [in Russian, with English summary].

Van Damme K., Chiambeng G., Maiphae S., Dumont H.J. 2003. New species in the rheophilous genus *Nicsmirnovius* Chiambeng & Dumont, 1999 (Branchiopoda: Anomopoda: Chydoridae), and reassigment of *Alona eximia* Kiser 1948 and *Alonella fitzpatricki* Chien, 1970 // Hydrobiologia. Vol.499. P.25–49.