Redescription of *Leydigia parva* Daday, 1905 and assignment to *Parvalona* gen. nov. (Cladocera: Anomopoda: Chydoridae)

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Abstract
A morphological investigation of *Leydigia parva* Daday, 1905 (Chydoridae: Anomopoda: Cladocera), based on specimens from Paraguay (type specimens) and Brazil, clarifies its position in the subfamily and prompts its assignment to a new genus, *Parvalona*. The affinity of this rare benthic chydorid with *Leydigia* Kurz, 1875 and *Alona* Baird, 1843, in which this taxon was placed earlier, is discussed.

Keywords: *Aloninae*, *Chydoridae*, *Cladocera*, morphology, *Parvalona* gen. nov., South America, systematics.

Introduction

*Leydigia parva* Daday, 1905 was described from specimens from two localities in Paraguay; the description (Daday 1905, p 186) was relatively detailed for the standards of that time, and accompanied by drawings. Besides a note by Goulden (1966), who (erroneously) mentioned the species from sediments of Lake Petenxil, Guatemala, it was never recorded again. Frey (1966), followed by Smirnov (1971), assigned this taxon to *Alona* Baird, 1843, but this giant, polyphyletic genus is currently under revision. Molecular phylogenetic analysis of the Aloninae supports the polyphyly of *Alona* s.l. as currently understood (Sacherová and Hebert 2003). Several species groups within this assemblage have already been reassigned to new or existing genera, based on thorough morphological research (Dumont and Silva-Briano 2000; Van Damme et al. 2003; Sinev 2004), but a number of further candidates await separation in the future (Kotov and Sanoamuang 2004). Here, we discuss a South American taxon that qualifies for re-evaluation at the genus level, *Leydigia parva* Daday, 1905.

Daday’s (1905) slide containing the lectotype and paralectotype is kept in the collection of Daday (DAD) at the Hungarian Museum of Natural History, Budapest; however, the
specimens are relatively poorly preserved and not sufficient for redescription. A recent finding of this rare taxon in NE Brazil now offers an opportunity to redescribe it and to elucidate its position within the subfamily Aloninae (Cladocera: Anomopoda: Chydoridae).

Material and methods

A slide with the lectotype and paralectotype was loaned from DAD; these two females could be studied only in toto. In addition, three specimens were picked from samples from a temporary pool in Mandacaru, Lençóis Maranhenses National Park, Maranhao, Brazil, collected by K. Van Damme and Dr D. Van Damme, 16 August 1996, kept at the University of Ghent (UG), Belgium. These animals were placed on slides in a drop of a glycerol–formaldehyde mixture, and two were studied under an optical microscope in toto. Two of the three parthenogenetic females were dissected for analysis of the appendages. Drawings of both A.A.K. (types) and K.V.D. were combined in the figures.

Enumeration of setae and other limb structures is done from the epipodite towards the gnathobase, without any suggestion of homology.

Results

Family CHYDORIDAE Stebbing, 1902 emend. Dumont and Silva-Briano, 1998
Subfamily ALONINAE Dybowski and Grochowski, 1894 emend. Frey, 1967
Tribe ALONINI Dybowski and Grochowski, 1894 emend. Kotov, 2000

Parvalona gen. nov.

Type (single) species. Leydigia parva Daday, 1905 = Parvalona parva (Daday, 1905).

Etymology

The name “Parvalona” is composed of the genus name Alona and parva- ("parvus" = "small") a prefix containing the epitheton of the type species.

Diagnosis

Parthenogenetic female. Body subovoid, high, postero-dorsal and postero-ventral angle rounded, ventral margin convex in posterior half and straight to concave in anterior half. Rostrum short and relatively blunt, eye and ocellus of similar size. Three major head pores with relatively narrow connection between them, no lateral head pores found.

Labrum with trapezium-shaped labral keel, lacking setulation. Valve with numerous, relatively long setae. Postabdomen remarkably widened in comparison to other alonines, with postanal portion four times as long as anal portion, and whole postabdomen larger than head of animal (in lateral view). Preanal margin somewhat longer than anus, straight to depressed, preanal and postanal angle well defined. Each side of postanal portion with row of successive clusters of relatively long marginal denticles. Medially to postanal denticles, numerous lateral groups of remarkably long lateral setules, distalmost setule of each group considerably large. Postabdominal claw approximately as long as preanal margin, or somewhat longer, slightly and evenly curved. Basal spine large, not adpressed to claw.
Antenna I short, with two to three transverse rows of setules at anterior face. Antennular sensory seta arising at distance of one-third of antenna I length from distal end. Nine aesthetascs of different size, longest as long as antenna I, projecting beyond tip of rostrum. Antenna II with branches relatively elongated, all segments cylindrical, with rows of stout setules. Antennal formula (exo/endo): setae 1-1-3/0-0-3, spines 0-0-1/1-0-1. Spine on first (basal) segment of exopod long, reaching or almost reaching tip of second segment.

Limb I without accessory seta, ODL with a long, naked seta, and a rudiment of the second seta. IDL with two relatively large setae of somewhat different size. Endite III with three posterior soft setae and an anterior stiff seta. Endite II with three soft setae of unequal size, anterior seta rudimentary. Endite I with three long soft setae, without a stiff seta. At ventral margin of limb, groups of short denticles. Low maxillar process with a single short seta supplied with a bunch of setules distally. Limb II with exopodite small, lacking setae. Eight scrapers, a series of hillocks posteriorly to scrapers. Gnathobase with prominent basal-ventral angle, distal armature of gnathobase with three elements, filter plate with six setae, two distalmost setae specially short. Limb III with exopodite supplied with two setae of different size distally, and three lateral setae. On inner limb portion, four posterior soft setae. Seven setae in filter plate III. Limb IV with exopodite supplied with six setae not differentiated into lateral and distal group. Three soft setae on inner limb portion. Filter plate with five setae. Limb V with exopodite supplied with a single distal seta and three lateral setae. Gnathobase a greatly reduced, simple projection, no filter plate found.

Size up to 0.60 mm.

Differential diagnosis

Among representatives of the tribe Alonini Dybowski and Grochowski, 1894 sensu Kotov (2000), Parvalona gen. nov. has a unique combination of characters: the postabdomen is conspicuously wide, consisting mainly of a large, evenly curved postanal portion armed with clusters of medium-sized marginal denticles and lateral groups of long, relatively stout setules, limb I with stout denticles instead of long setules on its ventral margin, limb III with unique morphology, with five exopodite setae of which the third is remarkably long and widely spaced from the fourth seta. Characteristic (although not unique) traits are long setules along the ventral margin of the valve, stout setules on segments of antenna II, ODL I with a relatively short seta and a rudimentary second seta, IDL with only two setae. Morphological differences from some closer relatives are reported in Table I.

Parvalona parva (Dayad, 1905) comb. nov.
(Figures 1–3)
Leydigia parva Dayad, 1905, p 186–187, Plate 11: Figures 20, 21.
Alona parva (Dayad) in Smirnov 1971, p 391, 393, Figure 471; Forró and Frey 1982, p 124.
Not Leydigia parva Dayad in Goulden 1966, p 101–103, Plate 3: Figures 3–5; Frey 1982, Table 1.
Not Leydigia glabra Smirnov, Garcia Ponce and Silva-Briano 2000, p 1–3, Figures 1–10.
Not Birgeia travassosi Bergamin 1939, Plate 2: Figure 5.
Not Alona sp. nov. in Brehm 1939, p 184, Plate 36: Figures 20, 21.
Table I. Main morphological differences between *Leydigia* Kurz, 1875, *Leydigia glabra* Smirnov et al., 2000, *Parvalona* gen. nov., and *Alona* s.l. (data from Kotov 2004, Smirnov et al. 2000 and personal observations).

| Character | *Leydigia* s. str. | *Leydigia* glabra | *Parvalona* gen. nov. | *Alona* s.l. |
|-----------|-------------------|------------------|----------------------|--------------|
| Labrum with setulated anterior margin | +                 | −                | −                    | −            |
| Postabdomen significantly wide | +                 | +                | +                    | −            |
| Lateral groups on postabdomen consisting of: | Stout setae | ?                | Strong setules | Fine setules |
| Limb I: ODL large, with extremely large seta | + | ? | − | − |
| Limb I: ventral margin with series of robust denticles | − | − | + | − |
| Limb I: maxillar process | − | ? | + | + |
| Limb II: distalmost scraper specially long and located on especial projection | + | + | − | − |
| Limb II: number of setae in filter plate of gnathobase | 7–8 | 7 | 6 | 6–7 |
| Limb III: exopodite specially elongated, with two large terminal setae | + | + | − | − |
| Limb III: number of setae in exopodite | 3–7 | 2? | 5 | 6–7 |
| Limb IV: number of soft setae on inner limb portion | 4 | ? | 3 | 0–4 |
| Limb V: inner-distal projection with a bunch of strong setules | + | ? | − | − |
| Limb V: number of setae in filter plate | 2 | ? | 0 | 0–3 |

**Type material**

**Type locality.** From Daday (1905, p 186, 228): “Curuzu-chica, toter Arm des Paraguayflusses; Estia Postillon, Lagune und deren Ergüsse”, Paraguay. For remarks, see “Distribution”.

Lectotype: parthenogenetic female, 0.47 mm from unknown locality in Paraguay, DAD D III-79: II/P-721. There are two females on this slide, the lectotype marked by an arrow on the slide; selected by D. G. Frey, July 1965 (Forró and Frey 1982). Paralectotype: parthenogenetic female on the same slide with the lectotype.

**Other material examined**

Three parthenogenetic females, on three slides, kept at UG: two dissected specimens, one complete, from a temporary pool in Mandacaru, coordinates 2°35’50”S, 42°42’46”W, Lençóis Maranhenses National Park, Maranhao, Brazil, collected by K. Van Damme and D. Van Damme, 16 August 1996, from samples at UG, Belgium, labelled Brazil 1996.014–1996.015 (SIII 1-2).

**Amended diagnosis**

See diagnosis of the genus.

**Redescription**

Parthenogenetic female. General: colour (after fixation) colourless to pale yellow (Daday 1905) to reddish brown. In lateral view body subovoid, high (body height/body length=0.65–0.73 in adults), with maximum height in middle (Figure 1A–C). In dorsal view, body strongly bilaterally compressed. Dorsal margin regularly arched from tip of rostrum to rounded postero-dorsal angle, posterior margin slightly convex, postero-ventral
margin widely rounded, ventral margin convex in posterior half and straight to concave in anterior half. In contrast to Daday’s (1905) description, no wide striation on the carapace was found. Granulate or dotted valves, resulting from internal structures. In the postero-ventral portion of the valve, these dots are organized in several bands along the valve margin, as marked by Daday (1905).

Head: relatively small, rounded-triangular in lateral view, with rostrum short and relatively blunt, in contrast to Daday’s (1905) description. Also, in Daday’s specimens (Figure 1A) the rostrum is truncated, but it seems to be an artefact of excessive compression of the specimens during slide preparation. Eye and ocellus of similar size, ocellus located approximately in middle of distance from eye to tip of rostrum. Head shield with mandibular articulation of alonine-type (see Frey 1967). Three major head pores (Figure 2C–E) with a relatively narrow connection between them, central pore of the same size as anterior or posterior one, or somewhat narrower (Figure 2D, E). Lateral head pores

Figure 1. Parvalona parva (Daday, 1905), parthenogenetic females from unknown locality in Paraguay (A, D, E) and temporary pool at Mandacaru, Lençóis Maranhenses dune field, Maranhao, Brazil, collected 16 August 1996 by K. Van Damme and D. Van Damme (B, C, F, G). (A) Lectotype; (B, C) two other females; (D) postabdomen of lectotype; (E) postabdomen of paralectotype; (F, G) postabdomens of other females. Scale bars: 0.1 mm.
were not seen. In one specimen (Figure 2D), a clear field around the pores was noted, demarcated by a thin line.

Labrum: labrum with a main body, small distal labral plate, and a large medial labral keel (Figure 2A, B). In lateral view, labral keel trapezium-shaped, without setulation. Ventral portion of labral keel with thickened ridge.

Figure 2. *Parvalona parva* (Daday, 1905), parthenogenetic female from unknown locality in Paraguay, lectotype (C, G, I, K) and temporary pool at Mandacaru, Lençóis Maranhenses dune field, Maranhao, Brazil, collected 16 August 1996 by K. Van Damme and D. Van Damme (A, B) Labrum; (C–E) head pores; (F, G) postero-ventral portion of valve; (H, I) antenna I; (J, K) antenna II; (L) exopod of antenna II; (M) mandible; (N, O) limb I in inner and outer view; (P) inner portion of limb I. Scale bars: 0.1 mm.
Figure 3. *Parvalona parva* (Daday, 1905), limbs of parthenogenetic female from temporary pool at Mandacaru, Lençóis Maranhenses dune field, Maranhao, Brazil, collected 16 August 1996 by K. Van Damme and D. Van Damme. (A) Endite 3 of limb I; (B) limb I; (C) limb II. (D) limb III; (E, F) exopod III; (G, H) inner portion of limb III in anterior and posterior view; (I) limb IV; (J, K) inner portion of limb IV; (L) limb V; (M) inner portion of limb V. Scale bars: 0.1 mm.
Valves: large, subovoid, with numerous (51; average of two specimens, Figure 1B, C), relatively long setae, located submarginally in posterior portion of margin bases (Figure 2F). Setae divisible in three groups, of which the most rostral group contains the largest setae, followed by a small group of shorter setae situated ventrally of the region between limbs I and III and a third and final group of larger setae. Posterior margin of valve with a row of numerous setules at some distance from one another, implanted on inner side of carapace (Figure 2G).

Postabdomen (Figure 1D–G): postabdomen with remarkably wide postanal portion, at least four times as long as anal margin. Ventral margin straight to slightly convex, with rows of minute marginal setules. Anal margin relatively short, shifted strongly to base of postabdomen. Preanal margin somewhat longer than anus, straight to depressed (there is a chance that it is deformed in Daday’s specimens), preanal and postanal angle well defined. Whole postanal margin as large arched curve. Inflated basis for postabdominal claws bordered from postanal margin by a distinct depression. Distally, each side of postabdomen provided with a row of 13–16 successive clusters of relatively long marginal denticles, with size increasing distally and each group consisting of mostly three to five denticles; these clusters continue into three to four groups of fine setules on anal margin. Medially to postanal denticles, 9–13 groups of long lateral setules, the distalmost of each group or row being the largest and thicker than the others.

Postabdominal seta: as long as anal plus preanal margin (Figure 1D).

Postabdominal claw: approximately as long as or little longer than preanal margin, slightly and evenly curved. Basal spine large, as marked by Daday (1905), length up to 1.5–2 times diameter of claw at base; basal spine stout, not pressed to claw. Small basal denticles present, proximally from basal spine (Figure 2F, G).

Antenna I: short (shorter in lectotype, Figure 2I), not reaching tip of rostrum, with two to three transverse rows of setules at anterior face (Figure 2H, I). Antennular sensory setae slender, as long as half of antenna I length, arising at distance of one-third of antenna I length from distal end. Nine aesthetascs of different size, longest as long as antenna I, projecting beyond tip of rostrum.

Antenna II: relatively short. Coxal part with two sensory setae (Figure 2J); basal segment robust, with transverse rows of numerous, fine, long setules, rudimentary distal spine and short setules at its distal margin. Antennal branches relatively elongated, exopod shorter than endopod, all segments cylindrical, with rows of four to seven long, stout setules, longest of which reaching up to half of following segment (Figure 2J, K). Antennal formula (exo/endo): setae 1-1-3/0-0-3, spines 0-0-1/1-0-1. Spine on first (basal) segment of endopod long, reaching or nearly reaching tip of second segment. Apical spines of exopod and endopod of similar length, markedly longer than apical segments (Figure 2J–L).

Mandible: elongated, with widened head (Figure 2M) bearing small ridges. Left and right mandibles asymmetrical.

Limb I: epipodite small, globular (Figure 2N). Accessory seta absent, ODL with a long, naked seta, and a rudiment of the second seta (Figure 2O, P). IDL of similar size as ODL, with two relatively large setae of somewhat different size, armed with small setules unilaterally in terminal half. Endite 1 with three posterior soft setae (Figures 2N, O, 3A: 2–4), with size increasing basally, all armed with short hairs bilaterally, and one anterior seta (1) long, stout, with short setules in second distal half. Endite 2 with three soft setae of unequal size (5–7): seta 5 short, armed bilaterally with short setules, seta 6 longest, asymmetrically armed with long setules proximally, seta 5 armed with short setules; two small elements anterior to seta 5, one of which (arrow) clearly a rudiment of a stiff seta on
endite 2. Endite 3 with three soft setae (8–10), of which one (8) naked and significantly larger than the rest, two other setae two-segmented, setulated along one side, seta 10 somewhat longer than seta 9. Two ejector hooks (eh) of equal size anteriorly on outer portion of limb corm. Also here, a series of long setules and groups of short denticles (Figure 3B). Low maxillar process with a single short seta supplied with a bunch of setules distally.

Limb II: exopodite a small, subovoid lobe with a row of setules. Eight scrapers (Figure 3C: 1–8), scrapers 1–3 with size slightly decreasing basally, scraper 4 short, scraper 5 longer that 4, scraper 5–8 again with size decreasing basally. A series of hillocks posteriorly to scrapers. Gnathobase with prominent basal-ventral angle, armed with short setules. Distal armature of gnathobase with three elements, filter plate with six setae, two distalmost setae markedly short.

Limb III: epipodite ovoid, exopodite flat, relatively small, with three lateral setae (Figure 3D–F: 1–3) and two setae of different size distally (Figure 3D, E: 4–5); exopodite setae 4 and 5 widely spaced from one another, their proximal bases (first fourth of seta) perpendicular to each other. Exopodite setae 1 and 2 sparsely setulated with long filter setules, longest exopodite seta 3 armed with long setules in distal half while proximal half bears shorter setules, pressed to the seta; exopodite seta 4, half the length of exopodite seta 3 (Figure 3D), bears short setules over complete length, while exopodite seta 5, one-quarter length of previous seta, is only setulated in distal half (note that setulation of exopodite setae can be described better on SEM photographs because of the three-dimensional nature which is represented less in a two-dimensional drawing). Distal endite armed with three stiff setae (Figure 3D, H: 1–3). Basal endite of similar size with distal endite, anteriorly with a sensillum and four, stiff setae (Figure 3H: 4–7). Four posterior soft setae (1′–4′), setulated bilaterally. Distal armature of gnathobase with four setae (Figure 3G: 1–4), one of them (1) a thick, bottle-shaped sensillum of middle size. Seven setae of similar size in filter plate III.

Limb IV: pre-epipodite relatively large, setulated; epipodite ovoid. Exopodite large, round, with six setae, not differentiated into lateral and distal group (Figure 3I: 1–6); exopodite setae 5 and 6 markedly smaller and more slender than the others. Marginally on inner limb face, a row of four stiff ("torch") setae (Figure 3J: 1–4), seta 1 longest, stout, naked, each of setae 2–4 armed with fine setules, sometimes seta 4 shortened (Figure 3K). Posteriorly, three soft setae (Figure 3I: 1′–3′). Distal armature of gnathobase with four elements (Figure 3K: 1–4): element 1 an ovoid sensillum. Filter plate with five setae of similar size.

Limb V: pre-epipodite small, bipartite and setulated; epipodite ovoid (Figure 3L). Exopodite large, ellipsoid, with a single distal seta (4) and three lateral setae (1–3). Inner marginal setae (1–2) on inner face of limb, distal member (1) larger, but not protruding behind distal projection. Gnathobase greatly reduced, as a simple projection, no filter plate was found.

Ephippial female, male. Unknown.

Size. Lectotype, parthenogenetic female 0.47 mm; parthenogenetic females 0.45–0.47 mm (n=2), up to 0.60 mm according to Daday (1905).

Ecology. Daday (1905) did not provide details about the localities from Paraguay. The Brazilian specimens were found in a shallow, temporary waterbody (dimensions:
1.5 m × 100 m × 80 m) between cerrado-fixed dunes in the Lencois Maranhenses, functioning as a drinking pool for cattle. The waterbody was rich in submerged vegetation, with a mean temperature of 31°C, pH 8.4, conductivity of 140 μS cm⁻¹ and oxygen level of 8.4 mg l⁻¹. Regarding faunistic elements, it was rich in aquatic insects (Hemiptera), molluscs (Ampullaria), frogs and fish. Most common branchiopods consisted of *Cyclostephia hislopi* Baird, 1859, *Leydigiopsis curvirostris* Sars, 1901, *Alona ossiani* Sinev, 1998 (*Alona affinis* group), *Ephemeroptera hybridus* (Daday, 1905), and *Chydorus ventricosus* Daday, 1898.

**Distribution.** This is a rare South American species. At present, it is known only from two (?) localities in Paraguay (Daday 1905) and now a single locality in NE Brazil (first record), both on the Atlantic Coast of the South American continent. It is important to note that although Daday (1905) mentions having studied in his work “several samples from Paraguay”, we were not able to pinpoint these two locations. The only current locality of which the name resembles Daday’s “Curuzu-chica” is Curuzu Cuatiá (coordinates 29°48' S, 58°02' W), a city situated east of the Paraná River in Corrientes Province, Argentina. Situated close to the border of Paraguay, and the Paraná River being a hydrological continuation of the Paraguay River, we believe it possible that this locality might actually be situated in Argentina. Note that all other Central and South American records (Bergamin, 1939; Goulden 1966; Frey 1982) in reality dealt with other species (see “Discussion”).

**Discussion**

*A confused synonymy*

Our redescription of *Parvalona parva* comb. nov. makes it clear that previous authors were confused about the identity of this taxon. Goulden’s (1966) remains of “*Leydigia parva*” from deposits of Lake Petenxil in Guatemala show a quite distinct armature on the postanal margin of the postabdomen. Smirnov (1971), who placed it in *Alona*, supposed that the taxon had been described earlier as *Birgeia travassosi* by Bergamin (1939) and as *Alona* sp. nov. by Brehm (1939) but we think that this is incorrect. Bergamin (1939) did not actually describe *Birgeia travassosi*, but offered figures which are quite realistic. The animal depicted has several traits distinguishing it from *parva*: (1) the body is too high, (2) the rostrum too long and curved, (3) marginal denticles on postabdomen too long, (4) antenna II too long. *Birgeia travassosi* therefore seems more similar to a juvenile *Leydigiopsis curvirostris* Sars, 1901 than to *Parvalona* gen. nov., *Alona* s.l. or *Leydigia*. Traits 2 and 3 are also characteristic for Brehm’s (1939) material, although the real status of this animal remains unclear.

Daday’s (1905) original description, here expanded, contains a few characters helpful for the identification of this animal: (1) body egg-shaped, both postero-dorsal and postero-ventral angles smooth; (2) rostrum short and pointed; (3) ventral margin of valves slightly convex; (4) short setules along whole ventral margin; (5) dorso-distal angle of postabdomen widely rounded; (6) armature of postanal margin of the postabdomen expressed as a series of setules (“hairs”); (7) series of setules (“hairs”) on sides of postabdomen; (8) anal margin depressed, postanal angle smoothed, while preanal margin prominent and pointed; (9) basal spine on the postabdominal claw well developed; (10) antenna I elongated; (11) relatively small size. Also, we can extract from the author’s Figures 20 and 21 that this animal had (12) a large labral keel and (13) a relatively wide postabdomen. Our
investigation of the lectotype and paralectotype revealed that suggestions 2, 5, 8, and 10 in Daday’s description were inadequate. In reality, the rostrum is relatively blunt; the postanal margin is armed with denticles instead of setules; the postanal angle is well defined; antenna I is relatively short. Helpful for a determination of its taxonomic status are also: (14) three major head pores with a narrow connection; (15) long setules on the body of antenna I; (16) long and stout setules on the basal segment, and on the first and second segments of the exopod of antenna II.

Daday’s (1905) placement of *L. parva* was supported only by his suggestion on the “characteristic shape” of its postabdomen. In fact, his animal has a series of traits, completely contradicting the diagnosis of the genus *Leydigia* according to Kotov (2004) (see Table I). In addition, the size of the adult females in *Parvalona parva* gen. nov. is significantly smaller than that of any *Leydigia*.

**Position of Parvalona gen. nov. within the Aloninae**

Clearly close to *Parvalona* gen. nov. in morphology of the postabdomen, is *Leydigia glabra*, described from Nicaragua by Smirnov et al. (2000). Although the status of this taxon needs to be investigated further, the morphology of the PIII suggests *L. glabra* to group within *Leydigia*. As seen in Table I, there are still a number of questions to be answered in this taxon.

Some species groups of *Alona* Baird, 1843, e.g. members of the *A. verrucosa* group, a candidate to be lodged in a separate genus (Kotov and Sanoamuang 2004), have relatively long setules in lateral groups on the postabdomen as well, with the distalmost setule of each group conspicuous and strong, as in members of the genus *Karualona*. However, the postabdomen in these taxa is not as massive and the exopodite of PIII not as elongated, separating them from *Parvalona* gen. nov. Long spines or spine-like setules on the endopod of the second antenna are also shared by *Parvalona* gen. nov., *Leydigia* and members of the *Alona verrucosa* group. Reduction of setae on the distal lobe of the first limb is also present in members of the *Alona verrucosa* group where the IDL consists of two setae, but we suggest that this reduction is an independent event in alonine phylogeny. The phylogenetic relationships between these taxa can be clarified once we have a better view of the detailed morphology of other Aloninae, in which a revision of the large and complex genus *Alona* Baird, 1843 will play a pivotal role. Most important differences between *Parvalona* gen. nov. and related taxa are given in Table I. The original confusion as to where to place this taxon (first *Leydigia*, then *Alona*) is understandable when outer features are considered, but the current study aims to clarify why it belongs to neither.

From a functional-morphological perspective, it is obvious that *Parvalona* gen. nov. is specialized for life in mud, with adaptations similar to those of the larger benthic inhabitants *Leydigia* Kurz, 1875 and *Leydigiopsis* Sars, 1901. Together, these three genera share characters separating them from other chydorids, qualified by Fryer (1968) for *Leydigia* as specializations for life in muddy substrates: (1) strong bilateral compression of the body; (2) presence of haemoglobin, indicated by a reddish colour (possible induction in Cladocera by environmental factors are not studied); (3) a large and wide postabdomen with strong lateral setules; (4) relatively large marginal setules on the valves; and (5) large exopodite surfaces of limbs IV and V. The specialization of these taxa is most obvious in the morphology of the first, second and third limbs, the main components in handling and scraping detrital particles during benthic feeding (Fryer 1968), and the same can be said for *Alona* Baird, 1843 as well. At the generic level, food handling in benthic environments is clearly one of the driving forces of alonine adaptive radiation.
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