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# Partial revision of the *aduncus*-like species of *Pleuroxus* Baird, 1843 (Chydoridae, Cladocera) from the southern hemisphere with comments on subgeneric differentiation within the genus

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## Abstract

The aim of this study is to revise the *aduncus*-like species of the genus *Pleuroxus* Baird, 1843 (Chydoridae, Cladocera) from the southern hemisphere and test the accuracy of subgeneric differentiation within this genus according to Frey (1993a). *Pleuroxus wittsteini* Studer, 1878 from the Kerguelen archipelago is re-examined with special attention to thoracic limbs. Forgotten *P. carolinae* (Methuen, 1910) from the mountains of South Africa is redescribed in detail; it is a species having nine to ten setae in filter plate II, and six to seven setae in filter plate IV, which is a plesiomorphic, non-oligomerized state. Brief descriptions are also provided for *P. scopuliferus* (Ekman, 1900) and *P. varidentatus* Frey, 1993. A new species, *P. hardingi* sp. nov., is reported from high altitudes of the Bolivian Andes; this species was previously misidentified as *P. aduncus* by Harding (1955). A key for identification of *aduncus*-like species in the southern hemisphere (except Australia and New Zealand) is proposed. Frey's (1993a) system for differentiation of the subgenera of *Pleuroxus* is found to be vulnerable in view of the new data. New studies, most probably using genetic methods, are needed for the construction of a consistent phylogenetic tree for the genus.

**Keywords:** *Anomopoda, Branchiopoda, Chydorinae, Crustacea, systematics, taxonomy*

## Introduction

Investigations of collections from the southern hemisphere revealed the presence of distinct species of the genus *Pleuroxus* Baird, 1843 characteristic of this part of the world (Frey 1991, 1993b). It was shown that, in contrast to all species of *Pleuroxus* from the northern hemisphere, some southern hemisphere species possess more numerous setae on the thoracic limbs, a plesiomorphic feature. In particular, all well-studied northern species are characterized by the gnathobasic filter plates of limbs II-III-IV-V consisting of 8-8-6-4

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setae, respectively. In *Pleuroxus foveatus* Frey, 1991 and *P. scopuliferus* (Ekman, 1900) the number of these setae is 8-9-6-4. *Pleuroxus*-like taxa from Australia with 10-10-7-5 setae were placed in the genus *Plurispina* Frey, 1991. In material from South Africa a *Pleuroxus*-like species with 10-10-8-3 setae was also referred to a special genus (Smirnov 2006).

In the course of our examination of material from the southern hemisphere we came across specimens from Bolivia which could not be identified as any of the known species, as the complex of characters did not fit any of them. They are described below as new species. Comments on some other species from the southern hemisphere, well-known or forgotten, are also included.

## Methods

Specimens were selected from preserved samples under a compound microscope, and studied under an optical microscope in toto in a drop of a glycerol–formaldehyde mixture. At least five parthenogenetic females from each locality (with the exception of the museum loan) were dissected under a stereoscopic microscope for the study of appendages and postabdomen. Drawings were prepared using a camera lucida attached to an Olympus CX41 compound microscope. A few females of *P. wittsteini* were lyophilized, mounted on an aluminium stub, coated with gold, and examined under a scanning electron microscope SEM CAMSCAN MB2300.

A system of enumeration for different setae on thoracic limbs proposed by Kotov (2000) for alonine chydorids (and then applied to other anomopods) is used.

The following abbreviations are used for the collections: AAK, personal collection of A. A. Kotov, Moscow, Russia; ALMG, Albany Museum, Grahamstown, USA; AM, Australian Museum, Sydney, Australia; GOS, Collection of G. O. Sars, Zoological Museum of the Oslo University, Norway; MGU, Zoological Museum of the Moscow State University, Moscow, Russia; NHM, The Natural History Museum, London, UK; NNS, personal collection of Prof. N. N. Smirnov, Moscow, Russia; SMNH, Swedish Museum of Natural History, Stockholm, Sweden; USNM, The Smithsonian Institution Museum of Natural History, Washington, DC, USA.

## Results

### *Pleuroxus wittsteini* Studer, 1878

(Figures 1–23)

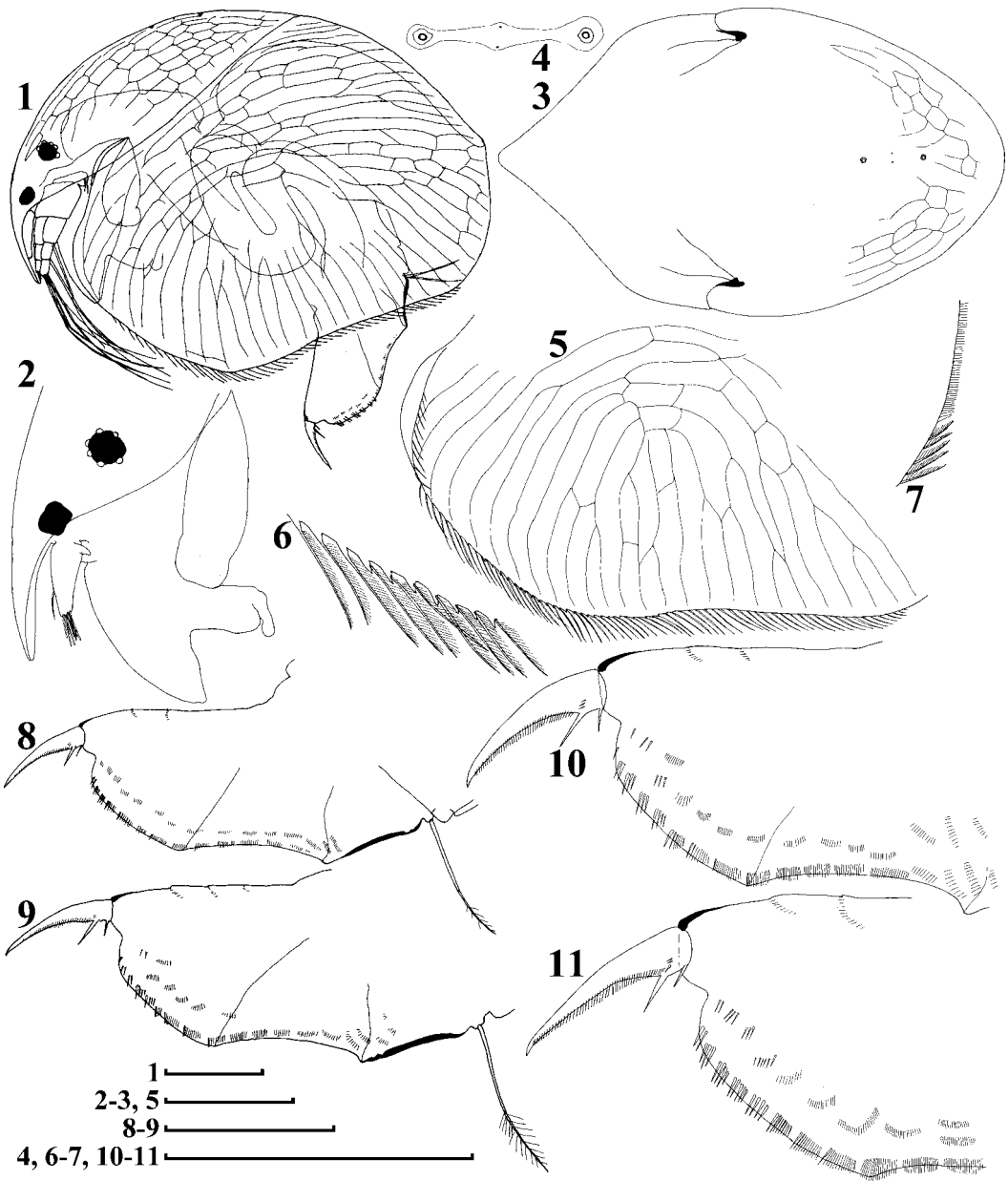
*Pleuroxus wittsteini* Studer 1878, p 109, Figure 4a, b; Rhe 1914, p 51–53, Figure 18a, b; Frey 1993b, p 148–157, Figures 3–49; Smirnov 1996, p 43–44, Figures 134–139; Hollwedel and Dartnall 1998, p 237–242, Figures 1–3, Plates 1–6; Pugh et al. 2002, p 1054 (in part).

*Pleuroxus aduncus wittsteini* Studer in Lofthouse 1967, p 142 (except Macquarie sample); Smith and Sayers 1971, p 363; Kok 1977, p 6.

See some other records in Pugh et al. (2002).

### *Type material*

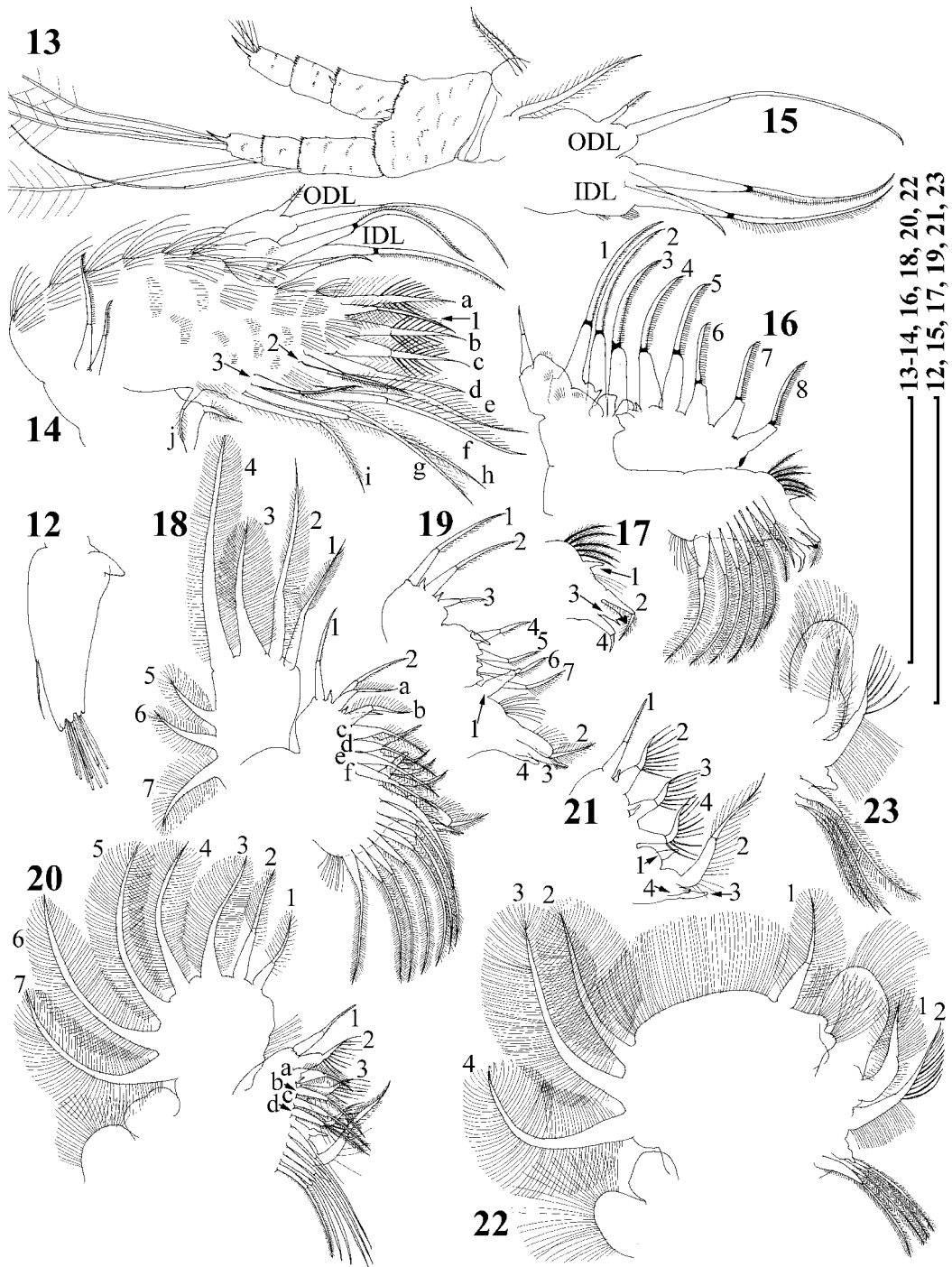
Apparently lost.



Figures 1–11. *Pleuroxus wittsteini*, parthenogenetic female from ponds near Port-aux-Français, Grande Terre, Iles Kerguelen. (1) Adult in lateral view. (2) Head, lateral view. (3, 4) Head shield and head pores. (5) Anterior half of valve. (6, 7) Armature of antero-ventral and posterior margin of valve. (8, 9) Postabdomen. (10, 11) Its distal portion. Scale bars: 0.1 mm.

*Type locality*

“Den zahlreichen Teichen in der Nähe der Station an Betsy Cove an der NW.-Küste”, Island of Grande Terre, Kerguelen archipelago.



Figures 12–23. *Pleuroxus wittsteini*, parthenogenetic female from ponds near Port-aux-Français, Grande Terre, Iles Kerguelen. (12) Antenna I. (13) Antenna II. (14, 15) Limb I and its inner distal lobe. (16, 17) Limb II and its gnathobase. (18, 19) Limb III and its inner portion. (20, 21) Limb IV and its inner portion. (22, 23) Limb V and its inner portion. Scale bars: 0.1 mm.

*Material*

Many parthenogenetic females from ponds 20 and 30 in De Smet (2001) near Port-aux-Français, Island of Grande Terre, Kerguelen archipelago, collected on 5 February 1998 by W. H. De Smet, sample AAK 2002-026-027.

*Short diagnosis*

Body dark brown, not transparent, no medial keel on dorsum, postero-ventral angle without denticles. Rostrum does not reach apex of labral keel. Head shield posteriorly widely rounded, anteriorly produced as a blunt rostrum,  $PP=1.4-1.8 ID$ . Head shield and valves with well-expressed reticulation, prominent under valve surface. All setae of valve ventral margin exactly marginal. Setules on posterior margin of valve exactly marginal. Postabdomen short and wide, strongly narrowing distally, with a widely rounded dorso-distal end, its anal margin clearly longer than preanal margin or postanal margin, anal teeth represented as series of small setules. Antenna I not reaching tip of rostrum, with a strong basal peg. On antenna II, one apical seta on both exopod and endopod shorter than other two setae. On limb I smallest ODL seta well-defined, distally with minute setules, two largest IDL setae subequal in size. On inner-distal portion of limb II scrapers 3–5 of subequal size, scrapers 6–7 of subequal size, setules on gnathobase plumose, filter plate II with eight setae. On exopodite III setae 1 and 3 subequal in length, filter plate III with eight setae. On inner portion of limb IV setae 2–4 with robust setules, filter plate IV with six setae. Exopodite V with two projections distally to distal seta 1.

*Redescription of parthenogenetic female*

See Frey (1993b), morphology of our specimens (Figures 1–13) fully agrees with this redescription.

*Description of thoracic limbs*

*Limb I* (Figures 14, 15). Accessory seta, or corm seta in Frey (1993b), present (not represented in Figure 14, because located on other side of limb corm), ODL relatively small, bears a long seta with naked distal segment and a short seta with short, setulated distal segment. IDL larger than ODL, series of setules; first IDL seta short, naked, second and third IDL setae subequal in size and similarly armed distally with short, fine setules (Figure 15). Endite 3 with three soft posterior setae (a–c) and stiff anterior seta 1 of similar length. Endite 2 with short seta anterior seta d, long setae e and f, and delicate posterior seta 2 armed with minute setules distally. Endite 1 with long, slender posterior setae g–i, a very short seta j, and anterior seta 3 similar to seta 2. Fascicles of thin setules on inner face of limb, plus bunches of longer thicker setules at ventral margin of limb. Two slender ejector hooks of remarkably different size. A short seta, a remnant of maxillar process, on limb base.

*Limb II* (Figures 16, 17). Exopodite subquadrangular, without a short seta. Inner portion of limb with eight scrapers, 1–2 specially long, 3–5 shorter, subequal in size, 3–8 shorter, also subequal in size. A series of small projections posteriorly to distal setae, and a small sensillum near scraper 4. Distal armature of gnathobase with a bunch of plumose setules, unique for the anomopods, and four setae (1–4). Filter plate II with eight setae, two distal

members subequal in size and shorter than the rest; basalmost seta of filter plate with inflated basal segment.

*Limb III (Figures 18, 19).* Exopodite sub-rectangular, with four distal setae (1–4), length of setae 1 and 3 equal, and three lateral setae (5–7). Distal endite with three anterior setae (Figure 19: 1–3), all with minute setules distally, of them two distal setae (1–2) long, basalmost seta (3) short. Small sensillae near bases of setae 2 and 3. Basal endite with four anterior setae (4–7), slightly increasing in size basally, armed with fine setules distally, small bottle-shaped sensillum near seta 4. On posterior surface, four soft setae (a–d) of similar size, bilaterally armed with sparse, fine setules. Gnathobase not clearly separated from basal endite. Distal armature of gnathobase with large, bottle-shaped sensillum (1), three setae (2–4), and a bunch of setules. Filter plate III with eight setae, distalmost seta shorter than the rest.

*Limb IV (Figures 20, 21).* Exopodite wide, subovoid, with seven setae of unequal size (Figure 20: 1–7). Inner-distal portion of limb IV with four marginal setae (Figure 21: 1–4). Distalmost seta (1) stout, with minute setules on distal segment, setae 2–4 with thick basal segments and slender, setulated distal segments, sensillae located near setae 2 and 3. On posterior surface, four soft setae (a–d), Gnathobase well-separated, its distal armature with four setae. Filter plate with six setae.

*Limb V (Figures 22, 23).* Exopodite large, subovoid, with a single distal seta 1 and three lateral setae (2–4), distally to seta 1 there are two projections bearing long setules. Inner limb portion as elongated, flat lobe, with setulated inner margin, supplied with setulated setae 1 and 2, the latter bears specially robust setules. Distal armature of gnathobase as a single projection, filter plate V with four long setae.

#### *Ephippial female*

Unknown.

#### *Male*

See Hollwedel and Dartnall (1998).

#### *Size*

Females from different localities 0.37–0.77 mm (Frey 1993b), males 0.55 mm.

#### *Comments*

The specimens investigated in the present case fully coincide with figures and description given for *P. wittsteini* from Kerguelen by Frey (1993b). In the key composed by Frey (1993b) there is a misleading formulation for *P. wittsteini*: its preanal margin is longer than the anal and postanal margins, which obviously contradicts his drawings (where the anal margin is the longest). In the same key couplet, there is a correct indication for brown *P. paraplesius* Frey, 1993 that “both anal and postanal sections much longer than preanal”. So there is no clear difference in this character (except the fact that in *P. wittsteini* the anal



margin is very wide). In *P. paraplesius* the postero-ventral angle of the valve is toothed, the shell is not pigmented brown. Our contribution to the study of *P. wittsteini* is the detailed redescription of its thoracic limbs.

#### *Distribution*

Kerguelen archipelago, Heard, Marion, Prince Edward Islands. Pugh et al. (2002) erroneously listed *P. scopuliferus* among junior synonyms of *P. wittsteini* and mistakenly referred localities of the former as belonging to the latter.

### ***Pleuroxus carolinae*** (Methuen, 1910)

(Figures 24–48)

*Pleuroxus inermis* Sars, 1896 in Sars 1916, p 342–343, Plate 41, Figure 2, 2a, b.

*Chydorus carolinae* Methuen 1910, p 157, Plate 16, Figure 44a, b; Methuen 1911, p 255.

#### *Neotype locality*

Small rockpools (28°40'43"S, 28°50'28"E) at 2050 m a.s.l. near Fika Patso, Qwaqwa, Freestate, Republic of South Africa. The sample was collected on 8 November 1996 by K. Martens, and marked as RSA/96/111.

The former type locality was "Lake Chrissie, the lake lies in the Carolina district due east of Pretoria near the borders of Swaziland" (Methuen 1910).

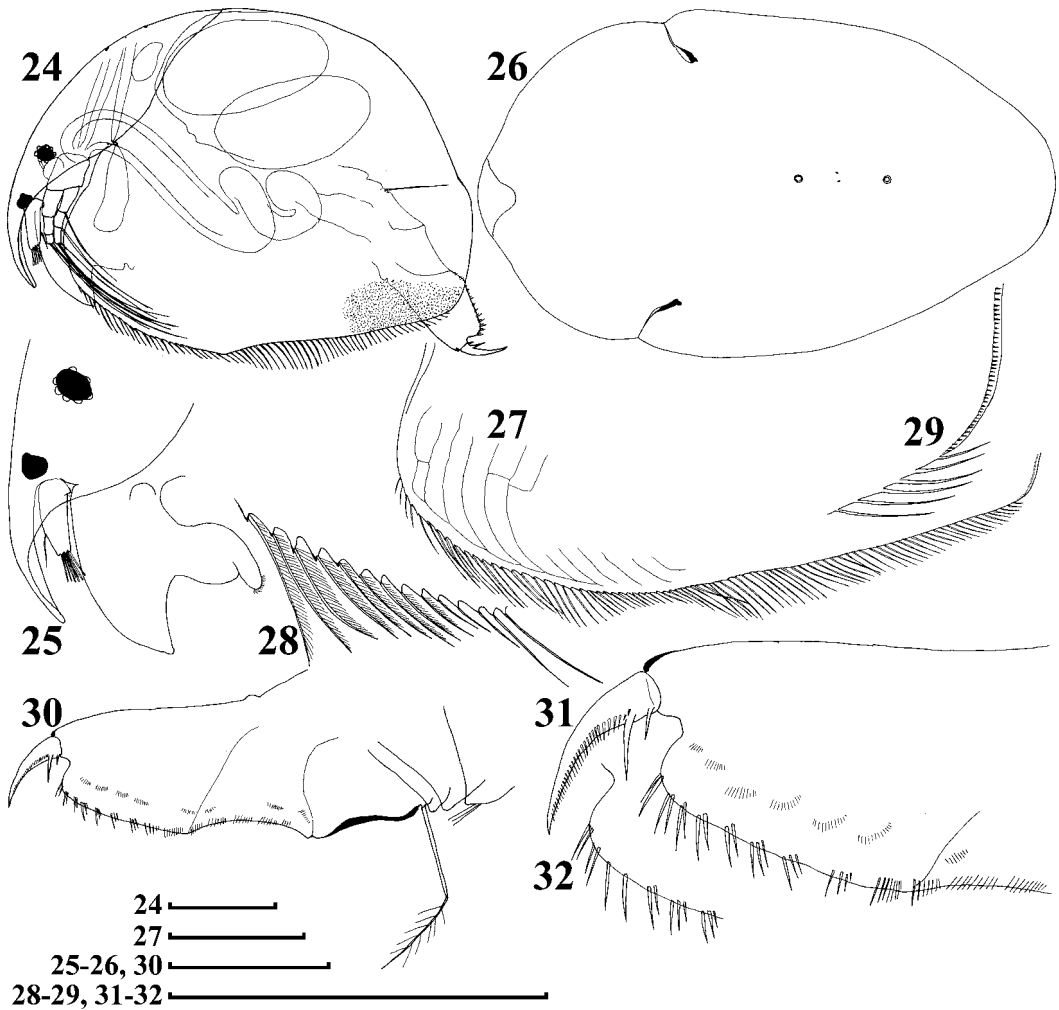
#### *Material examined*

Neotype: a parthenogenetic female in 96% alcohol, MGU MI 56. Author's type material is apparently lost.

*Other material examined.* Five parthenogenetic females from neotype locality (old number RSA/96/111); four females from Sani River pool 5 at 2890 m a.s.l. (29°34'32"S, 29°17'56"E), Sani Plateau, Lesotho, collected on 23 March 1995 by K. Martens, NNS 2002-073 (old number LES/95/026).

#### *Short diagnosis*

Body dark brown, not transparent, in anterior view dorsum as a smoothed angle, but true medial keel absent, postero-ventral angle without denticles. Rostrum does not reach apex of labral keel. Head shield posteriorly widely rounded, anteriorly makes a blunt rostrum, PP=1.5–2 IP. Obscure striation expressed only in antero-ventral and postero-ventral portions of valve. All setae of valve ventral margin exactly marginal. Setules on posterior margin of valve situated on inner side of valve, relatively far from the margin, so their tips do not reach it. Postabdomen relatively long, slightly narrowing distally, with rounded and slightly prominent dorso-distal angle, its anal margin as long as preanal margin and clearly shorter than postanal margin, anal teeth thin and rather long, organized in successive series of two to three, rarely solitary, slightly increasing in size distally. Antenna I not reaching tip of rostrum, with a strong basal peg. On antenna II, all apical setae subequal in size. On limb I smallest ODL seta rudimentary, two largest IDL setae unequal in size. On inner-distal portion of limb II, scrapers 1–3 with size decreasing basally, scraper 8 smaller than

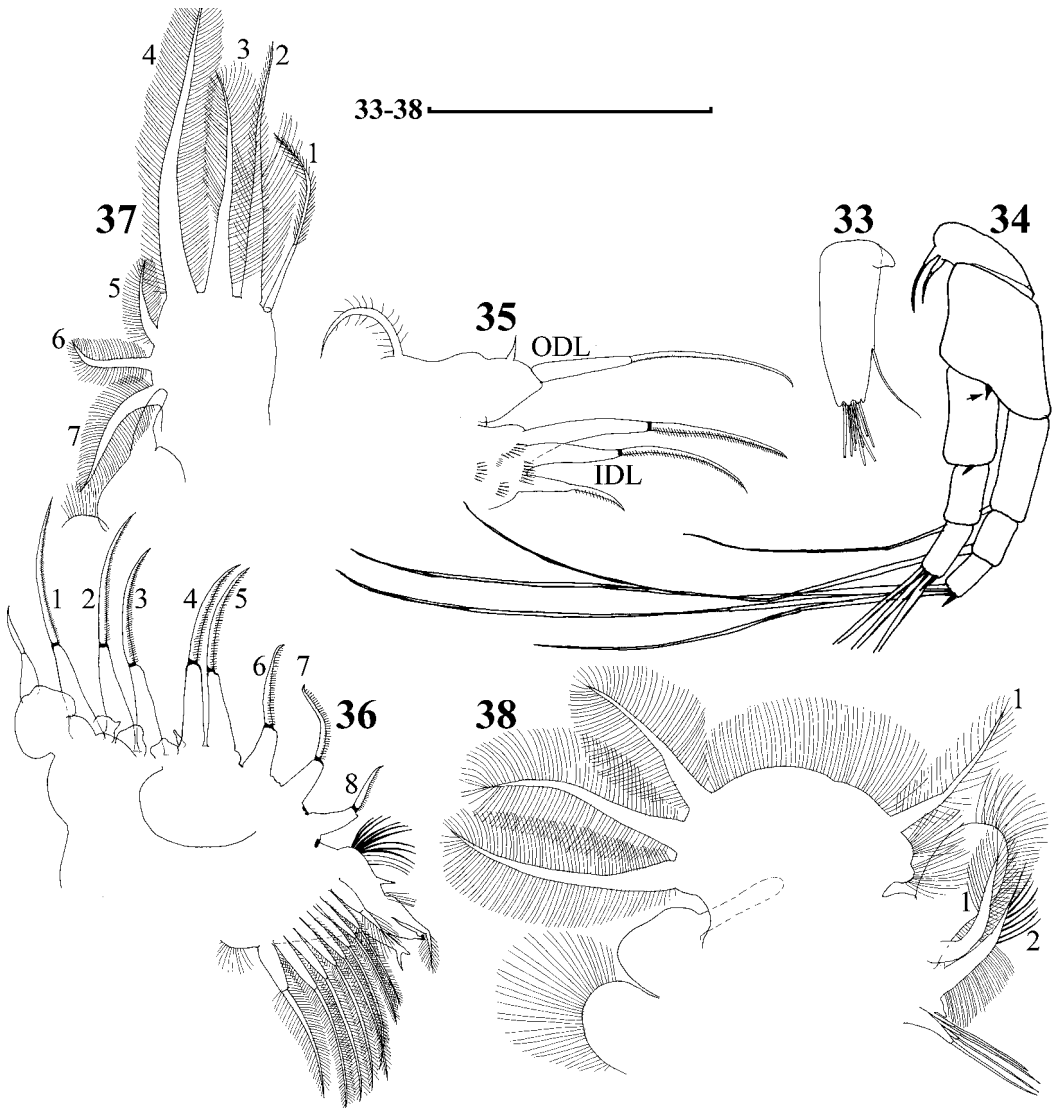


Figures 24–32. *Pleuroxus carolinae*, parthenogenetic female from small rockpools near Fika Patso, Qwaqwa, Freestate, Republic of South Africa. (24) Large adult, lateral view. (25) Head, lateral view. (26) Head shield. (27) Valve. (28, 29) Armature of antero-ventral and postero-ventral portion of valve. (30) Postabdomen. (31, 32) Its distal portion. Scale bars: 0.1 mm.

others; setules on gnathobase naked, filter plate II with nine, rarely 10 setae. On exopodite III seta 1 shorter than 3, filter plate III with eight setae. On inner portion of limb IV setae 2–4 with robust setules, filter plate IV with six to seven setae. Exopodite V with two projections distally to distal seta 1.

*Redescription*

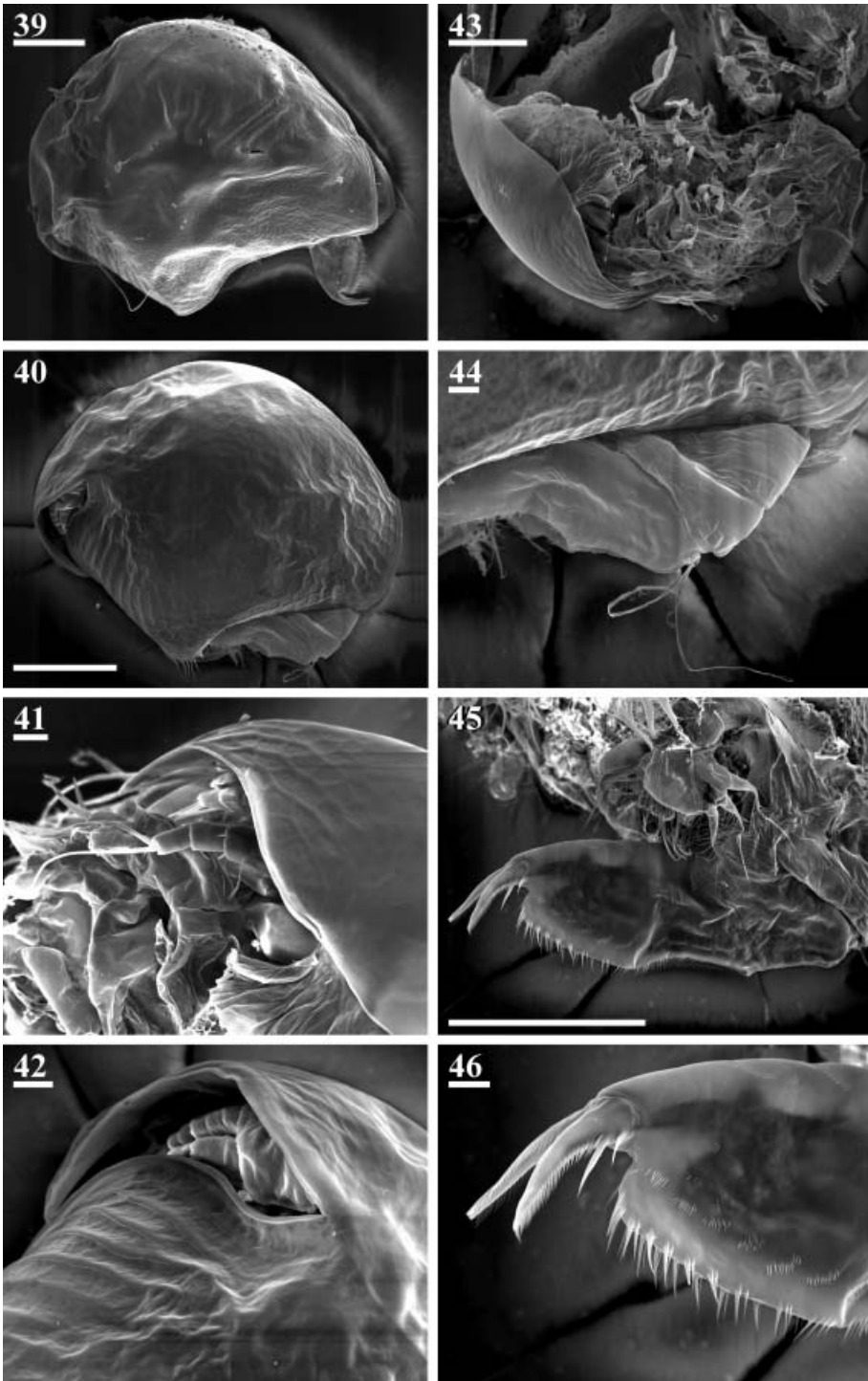
*Parthenogenetic female.* Body brown, not transparent. In lateral view body widely oval, high (body height/body length=0.74–0.80 in adults), maximum height in middle (Figures 24, 39, 40). Dorsal margin evenly arched from tip of rostrum to postero-dorsal angle, which is well-defined, posterior margin straight, postero-ventral angle broadly rounded, without teeth, ventral margin with a slight prominence in middle. Obscure striation expressed only



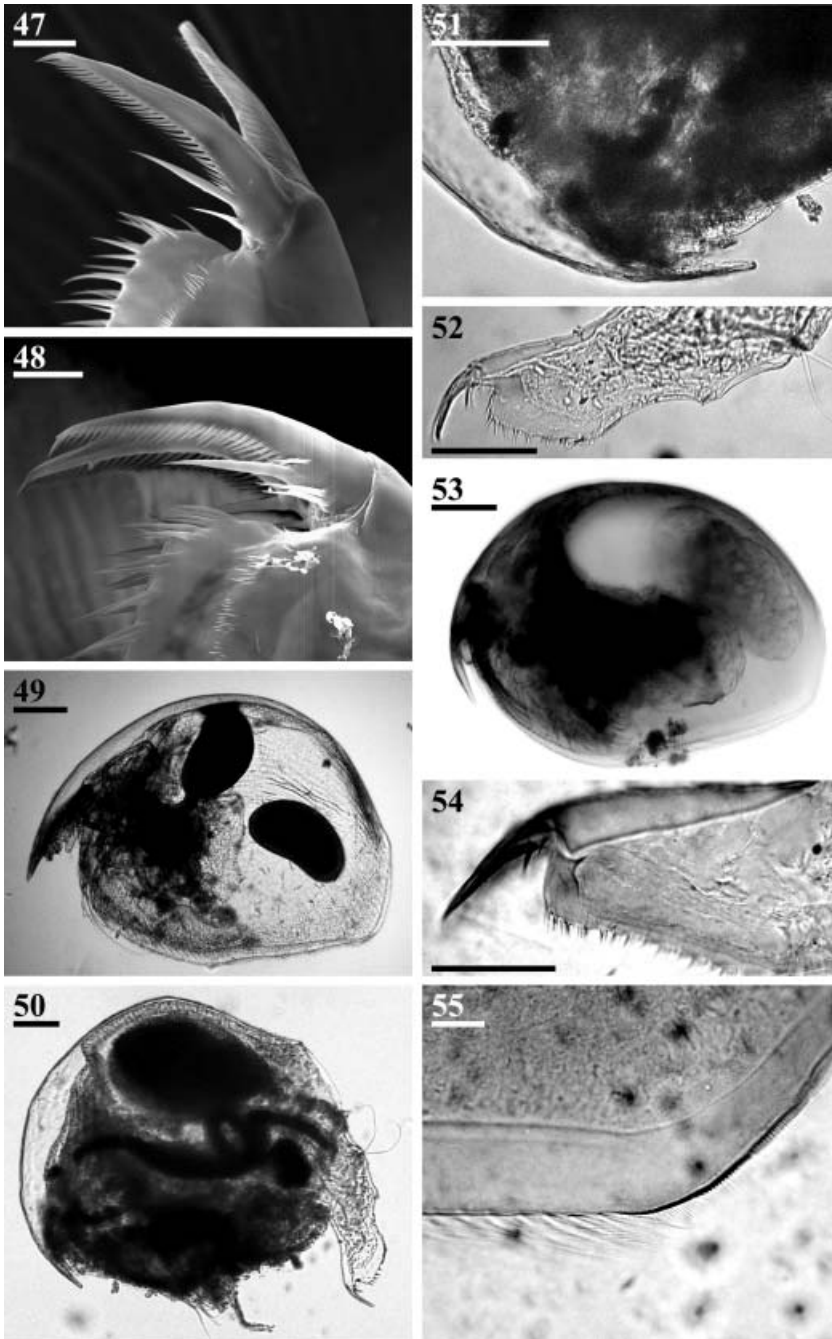
Figures 33–38. *Pleuroxus carolinae*, parthenogenetic female from small rockpools near Fika Patso, Republic of South Africa. (33) Antenna I. (34) Antenna II. (35) Distal portion of limb I. (36) Limb II. (37) Exopod III. (38) Limb V. Scale bars: 0.1 mm.

in antero-ventral (Figure 27) and postero-ventral portions of valve, while entire valve punctate (in Figure 24 this punctulation is represented only in postero-dorsal region). In anterior view body subovoid, with dorsum a smoothed angle, but dorsal keel absent.

Head with long rostrum, protruding downward and posteriorly (Figures 25, 41–43). Eye only slightly smaller than ocellus, distance from tip of rostrum to ocellus greater than that between ocellus and eye. Head shield elongated, with maximum width immediately behind mandibular articulation, its posteriormost extremity widely rounded (Figure 26). Two major head pores,  $PP=1.5-2$  IP. Lateral head pores minute, normally located asymmetrically to midline. Labrum with fleshy main body, small distal labral plate



Figures 39–46. *Pleuroxus carolinae*, parthenogenetic female from small rockpools near Fika Patso, Republic of South Africa. (39, 40) Lateral view. (41, 42) Head. (43) Specimen with removed valve. (44) Abdomen. (45, 46) Postabdomen and its distal portion. Scale bars: 0.1 mm (39, 40, 43, 45); 0.01 mm (41, 42, 44, 46).



Figures 47–55. Different species of *Pleuroxus* from the southern hemisphere. (47, 48) *Pleuroxus carolinae* from small rockpools near Fika Patso, Republic of South Africa, postabdominal claws. (49) *Pleuroxus scopuliferus* from unknown water body near Morro Chico, southern Chile, lectotype. (50–52) *Pleuroxus varidematus*, ehippial female from La Quinta, Argentina. (53–55) *Pleuroxus hardingi* sp. nov. from pools near the city of Cochabamba, Bolivia, general view, postabdomen and postero-ventral portion of valve. Scale bars: 0.01 mm (47, 48, 55); 0.1 mm (49–54).

(anterior plug in terms of Dumont and Silva-Briano 2000), and large medial labral keel, with well-defined apex projected significantly behind rostrum.

Valves large, ventral margin armed with numerous setae of different size in different regions, all plumose and located exactly marginally (Figures 27–29). A row of small setules situated on inner side of posterior valve margin, relatively far from the margin, so their tips do not reach it (Figure 29).

Postabdomen elongated, wide, its ventral margin almost straight (Figures 30, 45). Preanal margin slightly concave (Figure 44), as long as anal margin, preanal and postanal angle well-defined, postanal margin clearly longer than anal margin, dorso-distal angle widely rounded and slightly prominent distally, inflated basis of claws bordered from postanal margin by a distinct depression (Figures 31, 32, 46). Each side of postanal portion provided with a row of thin and rather long postanal teeth, organized in successive series of two to three, rarely solitary, slightly increasing in size distally. Series of postanal denticles evenly grading into five to six series of marginal setules on anal margin. Laterally to marginal denticles, a row of fascicles consisting of short, fine setules. Postabdominal seta relatively short, with basal segment approximately as long as preanal margin and distal segment as long as basal one, supplied with delicate setules. Postabdominal claw short (significantly shorter than preanal or anal margin), massive, evenly curved, with setules along ventral margin, and two basal spines, proximal one being half size of distal (Figures 46, 47), sometimes basalmost spine duplicated (Figure 48).

Antenna I not reaching tip of rostrum, slightly narrowing distally, with a well-defined basal peg (Figure 33). Antennular sensory seta slender, longer than half the antennule, arising at one-third of antennular length from distal directly from antenna I, without any prominences. Nine short aesthetascs of slightly differing size. Antenna II relatively short, coxal part with two sensory setae, basal segment robust, with a rudimentary distal spine (Figure 34, arrow). Antennal branches relatively elongated, exopod and endopod subequal in length, all segments cylindrical, antennal formula, setae 0-0-3/1-1-3, spines 1-0-1/0-0-1. Exopod and endopod apical swimming setae subequal in size. No chitinous insertions within distal segments. Basal lateral seta thinner and shorter than distal lateral seta. Spine on basal segment of exopod rudimentary.

Limbs very similar to those in *P. wittsteini*, but limb I with ODL smaller seta rudimentary, IDL second and third setae unequal in size (Figure 35), filter plate II (Figure 36) with nine, and rarely 10, setae; scrapers 1–3 on limb II with size decreasing basally, scraper 8 smaller than others; seta 1 on exopodite III shorter than seta 3 (Figure 37); filter plate IV with six to seven setae; seta 1 on exopodite V especially long, longer than seta 2 on inner limb portion and armed with rare setules (Figure 38).

#### *Ephippial female, male*

Unknown.

#### *Size*

Parthenogenetic females 0.42–0.47 mm in available material.

#### *Distribution*

Known from four high-altitude localities, our two localities plus those of Methuen (1910) and Sars (1916), on the Sani Plateau and the Cape Flats.

*Ecology*

Our specimens were collected from pools, at pH 7.4–7.9, conductivity  $142 \mu\text{S cm}^{-1}$ , 14.8–19.6°C, altitude 2050–2890 m a.s.l. The species occurs also in Lake Chrissie, a large and shallow high-altitude lake.

*Comments*

The taxon was reported by Sars (1916) as *P. inermis* from a pond in the Cape Flats; he said that his "*P. inermis*" was "without any obvious denticles" at postero-ventral angle, had reticulation only at anterior and posterior margins, and strong postanal spines. Then, Methuen (1910) established *Chydorus carolinae* as a new species. His too small and inadequate description was accompanied with quite realistic illustrations (Methuen 1910, Plate 16: Figure 44a, b). Keeping in mind that the type material was apparently lost, and that *aduncus*-like species of *Pleuroxus* from the southern hemisphere posed a difficult taxonomic problem, we selected the neotype of this species "to define the nominal taxon objectively" (International Commission on Zoological Nomenclature 2000, Article 75).

There are also other *aduncus*-like forms in Africa (Rühe 1914; Jenkin 1934; Chiambeng and Dumont 2004), but their status must be checked accurately.

***Pleuroxus scopuliferus* Ekman, 1900**

(Figure 49)

*Pleuroxus scopuliferus* Ekman 1900, p 78–82, Plate 4, Figures 25–29; Frey 1993b, p 163–171, Figures 69–99; Smirnov 1996, p 55–56, Figures 207–211; Kotov and Gololobova 2005, p 3063.

*Pleuroxus scopulifer* (Ekman) in Daday 1902, p 262–263; Olivier 1962, p 250–251, Plate 7: Figures 5, 6.

Not *Pleuroxus scopuliferus* Ekman in Pugh et al. 2002, p 1054.

See further synonymy in Frey (1993b).

Lectotype: a single parthenogenetic female, length 0.70 mm, with two eggs, SMNH 5846, selected by Kotov and Gololobova (2005). The "neotype" ZMU 21290a earlier selected by Frey (1993b) is rejected due to finding of original author's material (International Commission on Zoological Nomenclature 2000, Article 75.8).

*Type locality*

Unknown water body near Morro Chico, km. 146 of the 9, Punta Arenas-Puerto Natales, southern Chile (approximately  $52^{\circ}05'20''\text{S}$ ,  $71^{\circ}22'27''\text{W}$ ).

*Material examined*

A single female, the lectotype. The diagnosis below is based predominantly on Frey's (1993b) redescription.

*Diagnosis*

Body dark brown, not transparent, dorsum with medial keel, postero-ventral angle with one to two denticles. Rostrum long (Figure 49), projecting behind apex of labral keel. Head

shield pointed at posterior end, anteriorly makes a long rostrum, PP=3.7–4.8 IP. Well-expressed prominent striation on head shield and valve. Setae at posterior portion of valve ventral margin situated submarginally. Setules on posterior margin of valve situated exactly marginally. Postabdomen wide, significantly narrowing distally, with rounded and slightly prominent dorso-distal angle, its anal margin roughly as long as postanal margin and longer than preanal margin, anal teeth strong, solitary at dorso-distal angle, represented as series of two to four strong denticles in distal half of postanal margin, and then as series of fine setules in its basal portion. Antenna I not reaching tip of rostrum, with short, rounded basal peg. On antenna II, one apical seta on each branch shorter than two other setae. On limb I smallest ODL seta short, two largest IDL setae subequal in size. On inner-distal portion of limb II, scrapers 1–3 with size decreasing basally; setules on gnathobase naked, filter plate II with eight setae. On exopodite III setae 1 and 3 subequal in length, filter plate III with nine setae. Filter plate IV with six setae. Exopodite V with two projections distally to distal seta 1, distalmost projection especially large.

#### *Description*

See Frey (1993b).

#### *Distribution*

Southern portions of Chile and Argentina, see Frey (1993b).

### ***Pleuroxus varidentatus* Frey, 1993**

(Figures 50–52)

*Pleuroxus varidentatus* Frey 1993b, p 177–184, Figures 132–164; Smirnov 1996, p 46–47, Figures 151–156.

Holotype: a parthenogenetic female 0.62 mm long on a slide in glycerol jelly, deposited in the La Plata Museum, Argentina (Frey 1993b). Paratypes (slides): two females, ALMG GEN 951A; two females, AM P40973; two females, GOS 21292a; two females, NHM 1992.31–32; two females, USNM 251694. Paratypes (tubes): five females, ALMG GEN 951B; five females, AM P40974; five females, GOS 21292b; five females, NHM 1992.33–37; five females, USNM 251694.

#### *Type locality*

“A marshy channel alongside a small wooden church in Pta. Bandera, Santa Cruz Province, Argentina” (Frey 1993b).

#### *Material examined*

Twenty-three parthenogenetic females from “Arroyo agua caliente”, near San Salvador de Jujuy, Departamento de Cochino, Jujuy Province, Argentina, collected on 1 November 1901 by E. Nordenskiöld, SMNH Cladocera 24; one parthenogenetic and one ephippial female from “La Quinta” (Laguna La Quinta, 140 km from San Salvador de Jujuy), Jujuy Province, Argentina, collected on 1901 by E. Nordenskiöld, SMNH Cladocera 25.



*Short diagnosis*

Body (Figure 50) relatively light and transparent, dorsum without a medial keel, postero-ventral angle with one to three, rarely four denticles. Rostrum distinctly shorter than labral keel (Figure 51). Head shield with rounded posterior end, anteriorly makes a blunt rostrum, PP=3.0–3.6 IP. Striation on head shield and valve ill-defined. Setae at valve ventral margin situated exactly marginally. Setules on posterior margin of valve situated on inner face of valve submarginally. Postabdomen (Figure 52) long, slightly narrowing distally, with rounded and slightly prominent dorso-distal angle, its anal, preanal, and postanal portions roughly equal in length, anal teeth strong, solitary or in series of two to three in distal half of postanal margin, and as series of fine setules in its basal portion. Antenna I with a well-defined basal peg. On antenna II, one apical seta on each branch shorter than other two setae. On limb I smallest ODL seta short, two largest IDL setae greatly unequal in size. On inner-distal portion of limb II, scrapers 1–3 with size decreasing basally; setules on gnathobase delicate, naked, filter plate II with eight setae. On exopodite III setae 1 and 3 unequal in length, filter plate III with eight setae. Filter plate IV with six setae. Exopodite V with a single projection distally to distal seta 1 (according to Frey 1993b, Figure 164).

*Description*

See Frey (1993b).

*Distribution*

Our new findings change ideas on the distributional range of this species in South America, now, in addition to Frey's (1993b) single locality in the Province of Santa Cruz, it is found in Jujuy Province, in the northern part of the Argentinian Andes.

***Pleuroxus hardingi* sp. nov.**

(Figures 53–75)

*Pleuroxus aduncus* (Jurine) in Harding 1955, p 348–350, Figures 85, 86 (part); Uéno 1967, p 559–561, Figures 37–40.

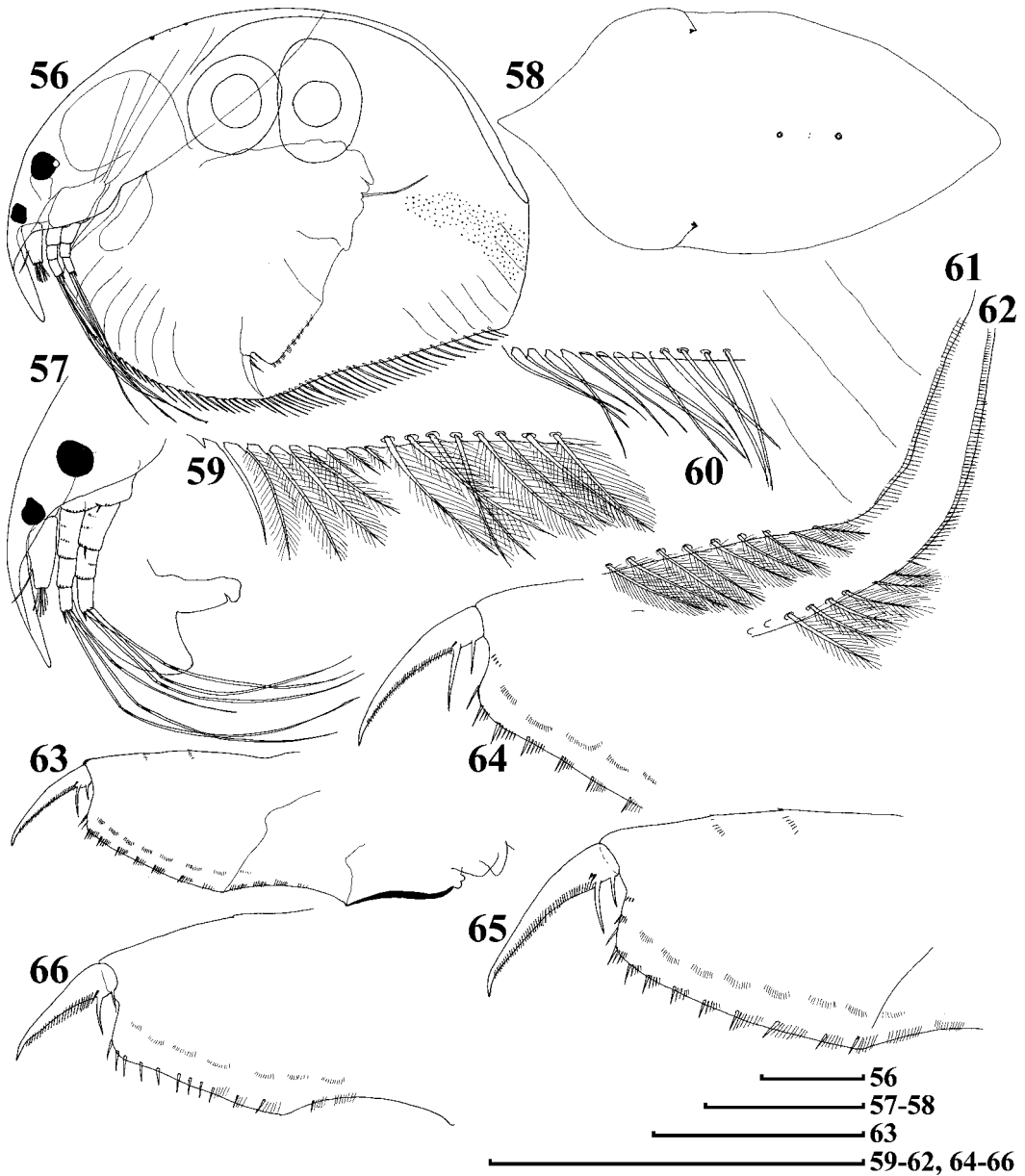
Holotype: parthenogenetic female 0.55 mm long, in 95% alcohol, MGU Ml 57. Label of the holotype: “*Pleuroxus hardingi* sp. nov., 1 parth. fem. from pools in the Cordillera del Tunari near the city of Cochabamba, Bolivia, HOLOTYPE”. Paratypes: five parthenogenetic females from the same sample, MGU Ml 58.

*Type locality*

Pools of the bofedal system in the cordillera del Tunari (part of the Cordillera Oriental) near the city of Cochabamba, Cercado Province, Bolivia (4000–4400 m a.s.l., 17°10'56"S–17°17'19"S, 66°07'62"–66°22'99"W). The type series was collected in February 2004 by J. S. Coronel, S. Declerck, and G. Crespo.

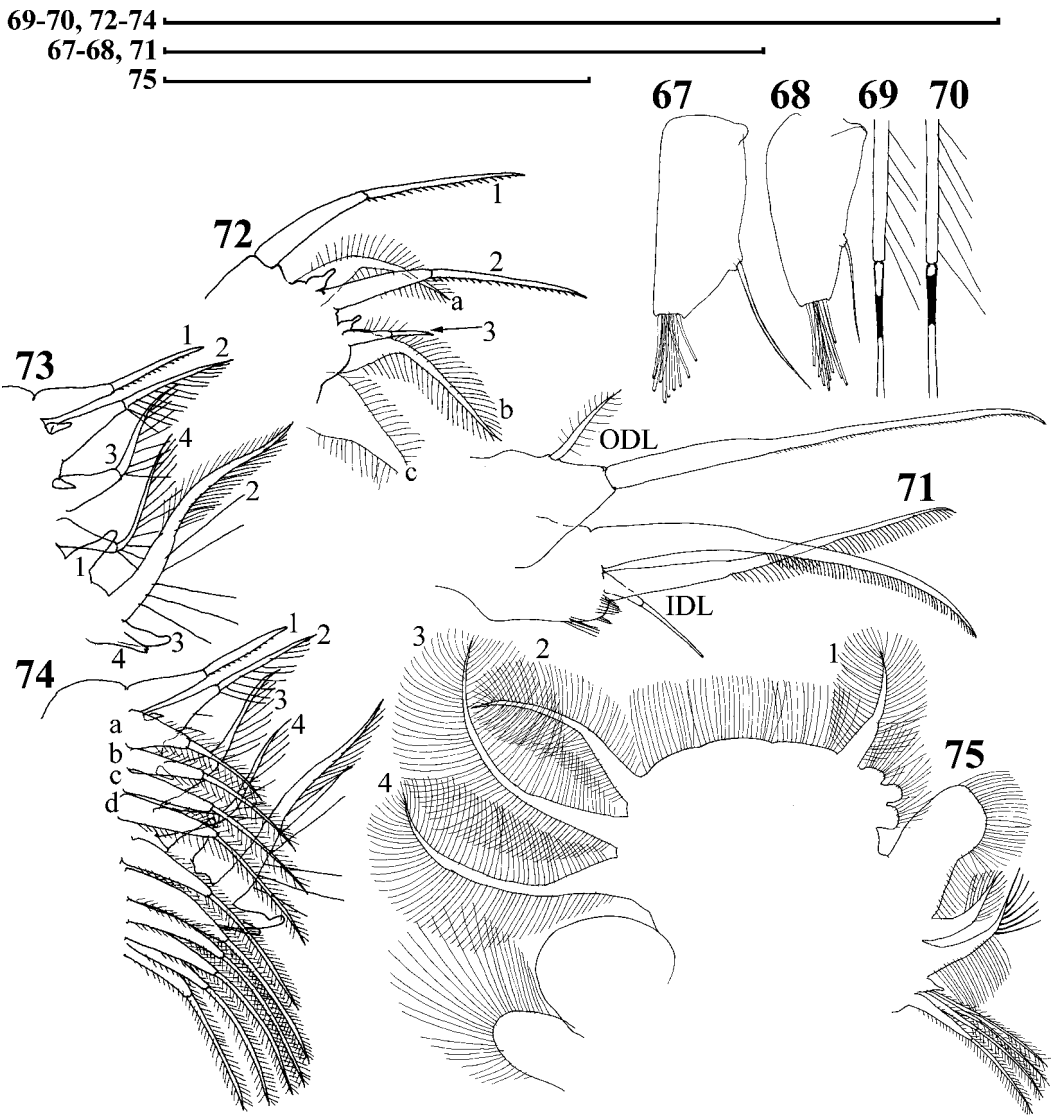
*Short diagnosis*

Body brown, not transparent, dorsum without a medial keel, postero-ventral angle without denticles. Rostrum not reaching apex of labral keel. Head shield with triangular-rounded



Figures 56–66. *Pleuroxus hardingi* sp. nov., parthenogenetic female from pools of the bofedal system in the cordillera del Tunari near the city of Cochabamba, State of Carrasco, Bolivia. (56) Large adult, holotype, lateral view. (57) Head. (58) Head shield, dorsal view. (59, 60) Setae at ventral margin of valve. (61, 62) Postero-ventral portion of valve. (63) Postabdomen of adult. (64, 65) Its distal portion. (66) Postabdomen of juvenile. Scale bars: 0.1 mm.

posterior end, anteriorly makes a blunt rostrum,  $PP=2.5-3$  IP. Striation on head shield and valve ill-defined. Setae at posterior half of valve ventral margin situated submarginally. Setules on posterior margin of valve situated on inner face of valve submarginally, but projecting behind the valve edge. Postabdomen long, slightly narrowing distally, with



Figures 67–75. *Pleuroxus hardingi* sp. nov., parthenogenetic female from pools near the city of Cochabamba, State of Carrasco, Bolivia. (67, 68) Antenna I. (69, 70) Apical setae of antenna II. (71) Distal portion of limb I. (72) Inner-distal portion of limb III. (73, 74) Inner portion and of limb IV in anterior and posterior view. (75) Limb V. Scale bars: 0.1 mm.

rounded and slightly prominent dorso-distal angle, its anal and preanal portion roughly equal in length, shorter than postanal portion, anal teeth represented in adults as series of setules. Antenna I with a rudimentary basal peg, sensory seta arises from a low prominence on antennular body. On antenna II, one apical seta on each branch shorter than two other setae. On limb I smallest ODL seta thin and armed with long setules, two largest IDL setae subequal in size. On limb II, scrapers 1–3 with size decreasing basally; setules on gnathobase naked, filter plate II with eight setae. On exopodite III setae 1 and 3 unequal in length, filter plate III with eight setae. Filter plate IV with six setae. Limb V with seta 1 of exopodite short and three projections distal to it.

*Description*

*Parthenogenetic female.* Body brown, not transparent. In lateral view body widely oval, high (body height/body length=0.72–0.76 in adults), maximum height somewhat anteriorly to middle (Figures 53, 56). Dorsal margin evenly arched from tip of rostrum to postero-dorsal angle, which is well-defined, posterior margin almost straight, postero-ventral angle well-defined, without teeth, ventral margin prominent in anterior half. Obscure striation expressed only in antero-ventral and postero-ventral portions of valve, while entire valve punctate, these dots smaller and sparsely located as in *P. carolinae* (Figure 56). In anterior view body subovoid, without traces of a keel.

Head with long rostrum, protruding downward and slightly posteriorly (Figure 57). Eye markedly smaller than ocellus, distance from tip of rostrum to ocellus greater than that between ocellus and eye. Head shield elongated, with maximum width anteriorly to mandibular articulation, its posteriormost extremity triangular-rounded (Figure 58). Two major head pores, PP=2.5–3 IP. Lateral head pores minute. Medial labral keel large, with well-defined apex projecting significantly behind rostrum.

Valves large, with ventral margin armed with numerous setae of different size in its different regions, located exactly marginally in anterior half of the margin (Figure 59), and slightly submarginally in its posterior half (Figures 60–62). A row of fine, relatively long setules situated on inner side of posterior valve margin, close to the margin, their tips projected behind it (Figures 55, 61–62).

Postabdomen elongated, distinctly narrowing distally, its ventral margin slightly convex (Figure 63). Preanal margin slightly concave, as long as anal margin or somewhat shorter than the latter, preanal and postanal angles well-defined, postanal margin clearly longer than anal margin, dorso-distal angle distinct, slightly prominent distally, inflated basis of claws bordered from postanal margin by a shallow depression (Figures 64, 65). Each side of postanal portion provided with successive series of marginal setules, size of setules increasing distally in each series. Series of setules continues in anal margin, but the size of setules in each series subequal. Laterally to marginal setules, a row of fascicles consisting of short, fine setules. Postabdominal seta relatively short (Figure 56). Postabdominal claw as long as anal margin, massive, slightly curved, with setules along concave margin, and two basal spines, proximal one being less than half length of distal (Figures 54, 64, 65). In juveniles postabdomen (Figure 66) with more pronounced angles, with shorter postanal portion and thin, sole postanal teeth instead of groups of setules in adults.

Antenna I not reaching tip of rostrum (Figure 57), slightly narrowing distally, with a rudimentary basal peg (Figures 67, 68). Antennular sensory seta slender, longer than half the antennule, arising at one-third of antennular length from distal end on a small projection of the antennular body. Nine short aesthetascs of slightly differing size. Antenna II relatively short (Figure 56), similar to than of *P. carolinae*, but among endopod apical swimming setae, one seta shorter than two others, and chitinous insertions present within distal segments of all setae (Figures 69, 70).

Limbs very similar to those in *P. wittsteini*, but smaller seta on ODL of limb I thin and armed with long setules, IDL first seta especially small and thin (Figure 71); limb III with especially thick, bottle-shaped sensillae near setae 2 and 3 (Figure 72); limb IV with thin setules on setae 2–4 and rare setules on basal segment of seta 2 of gnathobase distal armature (Figures 73, 74); limb V with seta 1 of exopodite short and three projections distal to it (Figure 75), instead of two projections in other species.

*Ephippial female, male*

Unknown.

#### Size

Parthenogenetic females 0.33–0.55 mm in available material.

#### Etymology

The species is named after J. P. Harding who recorded it from South America (as *P. aduncus*).

#### Distribution

It is known from the type locality (pools in the cordillera del Tunari), and from Lagunillas Pond (near Lake Titicaca), both from high altitudes in Bolivian Andes.

#### Ecology

The pools where the type series was collected are small, shallow with a layer of organic matter about 20–25 cm thick. About 30% of the pool surface was covered with aquatic plants and the rest was uncovered except for some algal mats. The physical parameters from the type locality at the time of collection were as follows: depth 18 cm, temperature 22.0°C, dissolved oxygen 8.4 mg l<sup>-1</sup>, pH 6.87. Other information in Coronel et al. (2005).

#### Comments

This taxon was first found by Harding (1955) and determined as *P. aduncus* (see Discussion). Then Uéno (1967) described specimens of brown colour, lacking denticles at the postero-ventral angle of the valve and with a peg on antenna I, apparently belonging to the same taxon. At the same time, quite typical *P. aduncus* was found in the Lake Titicaca region (Harding 1955, Figures 87–90; Smirnov 1996, Figures 179–185).

As our key below does not deal with Australian and New Zealand species, i.e. those described by Frey (1991), it is necessary to report their differences from a new species for accurate confirmation of its independent status. *Pleuroxus harding* sp. nov. differs from *P. helvenacus* Frey, 1991 in having postanal teeth on the postabdomen represented as a series of small setules, and having no tubercles on the valves; from *P. hastirostris* Sars, 1903, *P. foveatus* Frey, 1991, and *P. inermis* Sars, 1896 in having no teeth on the postero-ventral angle of the valve (the latter pair also bear strong postanal teeth). In addition, antenna I in all Australian forms are supplied with a peg.

### Key to species of the *Pleuroxus aduncus* group known from the southern hemisphere except Australia and New Zealand

- 1(2) Body with medial keel, rostrum protruding behind apex of labral keel, filter plate of gnathobase III with nine setae . . . *P. scopuliferus* (Ekman, 1900)

- 2(1) No medial keel, labral keel protruding behind tip of rostrum, filter plate of gnathobase III with eight setae
- 3(4) Filter plate of gnathobase II with 9–10 setae . . . *P. carolinae* (Methuen, 1910)
- 4(3) Filter plate of gnathobase II with eight setae
- 5(6) Antenna I with a rudimentary (if any) peg at the base, its lateral seta on elevation. Some of middle setae on ventral margin of valve submarginal . . .  
. . . . . *P. hardingi* sp. nov.
- 6(5) Antenna I with a well-developed peg at the base. All setae on ventral margin of valve exactly marginal
- 7(10) Brown, not transparent, valves with prominent reticulation, setules at posterior margin of valve exactly marginal
- 8(9) Postero-ventral angle of valve without teeth, postanal teeth on postabdomen as series of small setules . . . . . *P. wittsteini* (Studer, 1878)
- 9(8) Postero-ventral angle of valve with one or two teeth, postanal teeth on postabdomen strong, single . . . . . *P. paraplesius* Frey, 1993
- 10(7) Light in colour, valves with obscure reticulation, setules at posterior margin of valve submarginal
- 11(12) PP/IP about 2 . . . . . *P. macquariensis* Frey, 1993
- 12(11) PP/IP=3 or greater
- 13(14) Rostrum projects straight downward or even slightly forward, distinctly shorter than labral keel . . . . . *P. varidentatus* Frey, 1993
- 14(13) Rostrum curved backward or even slightly forward, only slightly shorter than labral keel . . . . . *P. aduncus* (Jurine, 1820)

## Discussion

Mainly with reference to the material from the northern hemisphere it was supposed for a long time (Richard 1897; Jenkin 1934; Harding 1955) that *Pleuroxus aduncus* is a highly variable taxon, and that there is a group of closely allied populations of this species. While partly this is probably so, investigations of a wider range of material, based on a wider assortment of characters, demonstrated that there are numerous, in part already - described species of this group. Harding (1955) was probably the last to use the concept of *Pleuroxus aduncus sensu lato*, as he did not separate the new species from vicinities of Lake Titicaca into a new taxon. In his Figures 83–92 he combined all *aduncus*-like forms, both with a basal peg on antenna I and without it, into *P. aduncus sensu lato*. More characters made separations of such different forms necessary. His specimen without a basal peg of antenna I from Lagunillas pond seems to be identical to our material. Harding found specimens without a peg at the base of antenna I also in four other water bodies. In contrast, some other animals represented in his illustrations apparently belong to other *aduncus*-like species occurring in this region, see also illustrations of Rey (1993) and Smirnov (1996).

Our examination of a relatively limited material from the southern hemisphere resulted in the discovery of a new species, redescription of forgotten *P. carolinae*, as well as new information on the distribution of *P. varidentatus*. It is possible that the fauna of this group is more diverse in the southern hemisphere. Particularly important regions for the discovery of new species are the highlands of South America and Africa, where, for example, several endemic ilyocryptids were found recently (Kotov and Štifter 2006).

Remarkably, our study of *P. carolinae* and *P. hardingi* sp. nov. revealed earlier unknown combinations of taxonomically important characters. As a result of this observation we

discovered that the systematics of the genus *Pleuroxus* is even more confused than was presumed.

It was known that *P. scopuliferus* has nine setae on filter plate III, and *P. foveatus* has a variable number (eight or nine) there. An exceptionally large number of setae on filter plate III was justifiably regarded as a plesiomorphy for the genus (Smirnov 2006). But we found that *P. carolinae* is unique among all species of *Pleuroxus* in having eight setae on filter plate III (like the majority of species), but nine or 10 setae in filter plate II, and a variable number of setae (six or seven) on filter plate IV; there are no doubts that this is also a plesiomorphy for the genus. Especially interesting is the fact that this number is not only large, but also variable. Evolution of seta number on anomopod limbs was described as oligomerization, from numerous and variable among individuals (and even among left and right limbs of a pair) to smaller and stable number (Smirnov 1971; Kotov 1997). *Pleuroxus carolinae* demonstrates just such an archaic, non-oligomerized state. So, *P. scopuliferus*, *P. foveatus*, and *P. carolinae* seem to be basal members of the phylogenetic tree of the genus *Pleuroxus*. At the same time, they are similar in many respects to other *aduncus*-like forms (e.g. in presence of the peg on antenna I which is an apparent apomorphy).

We found greater variability of some characters within the *aduncus*-like species than was described by Frey (1993a, 1993b). Among six characters of the female proposed by Frey (1993a, Table 1) for separation of subgenera of the genus *Pleuroxus*, three (postabdomen broad or tapered distally; presence/absence of the peg on antenna I; and marginal/submarginal setules at posterior margin) are questionable, first of all, because these are variable among *aduncus*-like species, placed by Frey (1993a) in his subgenus *Pleuroxus* (*Tylopleuroxus*). Two others (rostrum sharply pointed or bluntly pointed, and peculiarities of fine armature of the postero-ventral angle of valve) were not regarded as characters of generic rank for other chydorids (Smirnov 1971, 1996). Only two subterminal aesthetascs on antenna I of the *trigonellus* line is a good character, but it is an autapomorphy, a problematic item for the separation of a macro-taxon! So, Frey's (1993a) system for the differentiation of the subgenera is vulnerable to criticism. Earlier, in the most recent revision of the world fauna of Chydorinae, Smirnov (1996) supported only the genus *Picripleuroxus* Frey, 1993, but did not apply Frey's subgenera. Alonso (1996) also ignored Frey's (1993a) genera and subgenera.

Recently, Chiambeng and Dumont (2004) did not find any evidence for the separation of an independent genus *Picripleuroxus*. In contrast, they found that "*P. laevis* clusters with no other species in particular except perhaps the little known *unispinus*, while *P. denticulatus* and *P. similis* share a number of micro-characters, but *P. laevis* also shares with *aduncus*" (Chiambeng and Dumont 2004). So, elongated forms with elongated postabdomen ("*Picripleuroxus*") seem to have originated several times from different parts of the *Pleuroxus*-tree.

At present state of knowledge, a presumed phylogenetic tree of *Pleuroxus* seems to be a "bush" of *aduncus*-like species (subgenus *Tylopleuroxus*) with unclear topology, and with several of its branches marked as other "subgenera" or "genera" (*Pleuroxus* s.str., *Peracantha*, and *Picripleuroxus*). So, new studies, most probably using genetic methods, are needed for the construction of a consistent phylogenetic tree for the genus.

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