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Diversity of the subgenus *Disparalona* (*Mixopleuroxus*) Hudec, 2010 (Crustacea: Cladocera) in the New and Old World

Anna N. Neretina\(^a\), Petr G. Garibian\(^a\), Artem Y. Sinev\(^b\) and Alexey A. Kotov\(^{a,c}\)

\(^a\)Laboratory for ecology of aquatic communities and invasions, A.N. Severtsov Institute of Ecology and Evolution, Moscow, Russia; \(^b\)Department of Invertebrate Zoology, Biological Faculty, Lomonosov Moscow State University, Moscow, Russia; \(^c\)Laboratory of Paleoclimatology, Paleoecology, Paleomagnetism, Kazan Federal University, Kazan, Russia

**ABSTRACT**

During the last three decades, strong progress was made in the taxonomy of the family Chydoridae (Crustacea: Cladocera), and the results of these revisions have become a valuable confirmation of the non-cosmopolitanism in the cladoceran distribution. But, to date, delineation between several chydorid genera (*Pleuroxus* Baird, 1843, *Picripleuroxus* Frey, 1993, *Alonella* Sars, 1862 and *Disparalona* Fryer, 1968) has been intuitive rather than based on careful diagnostics. *Disparalona* is a cladoceran genus with a complicated and confused taxonomy. We compiled a checklist of all formal taxa belonging to this genus in current understanding. Our study comprises a taxonomic revision of the North American, African and East Asian populations of *D. cf. hamata* with the aim of clarifying their species and generic status. We redescribe *D. hamata* (Birge, 1879) based on material from North America and *D. chappuisi* (Brehm, 1934) based on material from Africa. The latter is common in tropical–subtropical Asia, with a distribution range reaching the Far East of Russia. The second taxon from Africa is provisionally identified as *D. cf. striatoides* (Šrámek-Hušek, 1946), which was described initially from the Czech Republic. Further comparison is needed for a final conclusion on conspecifity of European and African populations provisionally placed to this taxon. At the current level of knowledge *Mixopleuroxus* Hudec, 2010 must be accepted as a subgenus of the genus *Disparalona*. The diagnoses of *Disparalona* and *D. (Mixopleuroxus)* are provided. *Disparalona* s. str. includes *D. ikarus* Kotov and Sinev, 2011, *D. leei* (Chien Shing-ming, 1970), *D. rostrata* (Koch, 1841) and *D. smirnovi* Sinev, 2015, while *D. (Mixopleuroxus)* includes *D. hamata*, *D. chappuisi* and *D. striatoides*. *D. leptorhyncha* (Daday, 1905) and *D. caudata* Smirnov, 1996 are not described adequately, but they also probably belong to the latter subgenus. The status of *D. acutirostris* (Birge, 1879) must be clarified in the future.

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**CONTACT**

Alexey A. Kotov alexey-a-kotov@yandex.ru

Laboratory for ecology of aquatic communities and invasions, A.N. Severtsov Institute of Ecology and Evolution, Leninsky Prospect 33, Moscow, 119071, Russia

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Introduction

The Cladocera (Crustacea: Branchiopoda) is among the most intensively studied groups of microcrustaceans in continental water ecosystems (Dumont and Negrea 2002; Kotov 2013). During the last three decades, especially strong progress was made in the taxonomy of the family Chydoridae (Rajapaksa and Fernando 1986, 1987a, 1987b; Sinev 1997, 2015; Van Damme and Dumont 2008; Van Damme et al. 2010, 2011). Gradual accumulation of knowledge of chydorid morphology led to changes of our ideas on their diversity, and numerous discoveries of new taxa (e.g. Van Damme and Dumont 2008; Sinev and Elmoor-Loureiro 2010; Kotov and Sinev 2011; Neretina and Kotov 2015; Sinev et al. 2016; Sousa and Elmoor-Loureiro 2017). Also, some forgotten and poorly known species were recently redescribed to modern standards of morphological analysis (e.g. Van Damme et al. 2005, 2011; Sinev et al. 2007, 2016; Kotov 2009; Van Damme and Sinev 2013; Sinev 2015; Sousa et al. 2015; Neretina and Sinev 2016).

Results of these studies confirmed the non-cosmopolitanism concept of cladoceran distribution which is now an important basis for inventories of global chydorid diversity. This concept was proposed initially by Prof. D.G. Frey (Frey 1982, 1986, 1987). It is based on the fact that, although branchiopod resting eggs are easily dispersed by different vectors (including water birds) (e.g. Dumont and Negrea 2002; Kotov 2013; Incagnone et al. 2014; Rogers 2014), it is difficult for them to form stable populations in new habitats already occupied by other taxa. As a result, no mixing of different faunas is observed (e.g. Frey 1987; De Meester et al. 2002). In the frame of the non-cosmopolitanism concept, all species of chydorid taxa with a very broad or cosmopolitan distribution range and considered as ‘species’ are likely to be groups or complexes which need careful taxonomic revision. Although many taxonomic studies on discrimination of sibling chydorid species have been carried out via both morphological (e.g. Rajapaksa and Fernando 1986, 1987a, 1987b; Kotov 2009; Van Damme et al. 2011; Sinev and Kotov 2014; Sinev 2015; Sousa et al. 2015, 2016a, 2016b) and genetic (e.g. Belyaeva and Taylor 2009; Sharma and Kotov 2015; Kotov et al. 2016; others) approaches, there are still many unrevised groups.

The genus *Disparalona* Fryer, 1968 is a potentially interesting model for detailed revision, but the taxonomy of this genus is complicated and confused (Smirnov 1996a, 1996b). Most species of this genus were found to be continental endemics by Smirnov (1996a): *D. rostrata* (Koch, 1841) is distributed in the Palaeartic, *D. acutirostris* (Birge, 1879) in the Nearctic, *D. leptorhyncha* (Daday, 1905) in the Neotropics, and *D. caudata* Smirnov, 1996 in Australia (Fryer 1971; Michael and Frey 1984; Smirnov 1996a, 1996b). Our understanding of a ‘real’ distribution of *D. leei* (Chien Shing-Ming 1970) is more complicated: this taxon was described initially from the Nearctic zone (Chien Shing-Ming 1970) and then found to be present (although rarely) in some regions of Europe (Hudec 2010) and Asia (Klimovsky et al. 2015). Recent revisions of East Asian cladocerans revealed two more taxa, *D. ikarus* Kotov and Sinev, 2011, distributed from the Amur basin (Kotov and Sinev 2011) to Hainan Island (Sinev et al. 2015) and North-East Thailand (Sinev, unpublished), and *D. smirnovi* Sinev, 2015; to date known only from Yakutia (Klimovsky et al. 2015).

In this genus, only *D. hamata* (Birge, 1879) is regarded as a very widely distributed taxon, preferring warm regions of different continents: North and South Americas, tropical parts of Asia and Africa (Smirnov 1996a; Kotov et al. 2013a). It has not been
recorded from Australia (Shiel and Dickinson 1995; Smirnov 1995). Such wide distribution does not comply with Frey’s non-cosmopolitanism concept (Frey 1982, 1987) and could indicate existence of a species complex, as was already found in many other Chydorinae. Note that similar taxa, Pleuroxus chappuisi Brehm, 1934 and P. vulcanicus Brehm, 1951, were described from Africa, but subsequently regarded as junior synonyms of D. hamata (Smirnov 1996a), although such conclusions need to be checked based on new standards of morphological analysis.

Populations of D. cf. hamata from different continents are very similar in their habitus. But even analysing previous descriptions we could already conclude that there are differences in the labral keel length between populations from geographically distant localities. Also, it became obvious to us that males from the USA (described by Kiser 1950) are different in the postabdomen shape and structure from Chinese males (Chiang and Du 1979). Moreover, Sinev and Sanoamuang (2011) studied the males from Thailand and also revealed their rather strong differences from American males in morphology of their rostrum and postabdomen. Based on such observations, Sinev and Sanoamuang (2011) concluded that East Asian populations of D. cf. hamata are not conspecific with American D. hamata s. str.

Hudec (2010) proposed a new genus, Mixopleuroxus Hudec, 2010, for a single taxon, M. striatoides (Srámek-Hušek, 1946), which was placed initially in the genus Pleuroxus Baird, 1834 by its author (Srámek-Hušek 1946). Our analysis of the first description of Mixopleuroxus, which is quite detailed, led us to conclude that the latter taxon is a member of the D. hamata group as proposed by Smirnov (1971, 1996a). Combining the aforementioned literature data and our original results, we found that at the current level of knowledge, the D. hamata group could be placed in a special taxon at the rank of subgenus of the genus Disparalona, namely D. (Mixopleuroxus) Hudec, 2010.

This study aims to revise the North American, African and East Asian populations of D. cf. hamata, and to clarify their species and generic status on a morphological level.

Materials and methods

A set of samples containing specimens provisionally identified as D. hamata or D. cf. hamata from different regions of the Old and New Worlds were investigated under a stereoscopic binocular microscope LOMO (Open Joint-Stock Company, Russia). Disparalona specimens were selected from them via a small plastic pipette and transferred individually to drops of glycerol-formaldehyde or glycerol-ethanol mixture on separate slides. General morphology of all found individuals was studied in toto under an Olympus BX41 (Olympus Corporation, Japan) light microscope. Then some individuals were dissected using tungsten needles electrolytically sharpened in 10% NaOH (see Frey 1986; Kořínek 1999). Each dissected body part was transferred individually by the aforementioned needles to a new drop of glycerol on a separate slide, covered by a cover slip and investigated in details under an immersion lens. Figures of all individuals were made using camera lucida according to common techniques.

Several Disparalona individuals were dehydrated in increasing ethanol series (30, 50, 70, and twice in 96%), transferred to 100% acetone (40 min in each series), then, finally, to hexamethyldisilazane (40 min), and dried overnight (Laforsch and Tollrian 2000). Dried specimens were attached to stubs, coated by a platinum-palladium...
mixture in an IB-3 Ion Coater (Giko Engineering, Co., Ltd., Japan) or by gold in an S150A Sputter Coater (Edwards, UK) and studied under Jeol JSM-6380 or Jeol JSM 840-A (JEOL Ltd., Japan) scanning electron microscopes in secondary electron mode.

For morphological descriptions we used the terminology summarized by Kotov (2013).

**Abbreviations.** **Personal collections** (kept at A.N. Severtsov Institute of Ecology and Evolution, Moscow, Russia and represented in a single database): AAK, personal collection of Dr A.A. Kotov; ANN, personal collection of A.N. Neretina; AYS, personal collection of Dr A.Y. Sinev; NMK, personal collection of Dr N.M. Korovchinsky; NNS, personal collection of Prof. N.N. Smirnov. **Museum collections**: DGF, Collection of D.G. Frey, Support Center of the Smithsonian Institution Museum of Natural History in Suitland, MD, USA; HNHM, Hungarian Natural History Museum, Budapest, Hungary; NNS MGU, slides of Prof. N.N. Smirnov officially deposited to the collection of Zoological Museum of M.V. Lomonosov Moscow State University, Moscow, Russia; YUNN, samples from Yunnan Province at Jinan University, Guangzhou, China.

**Illustrations and text**: I–V = thoracic limbs I–V; e1–e5 = endites 1–5 of thoracic limbs; ejh = ejector hooks on limb I; epp = epipodite; ext = exopodite; IDL = inner distal lobe of limb I; ODL = outer distal lobe of limb I; pep = preepipodite.

**Results**

**Order ANOMOPODA** Sars, 1865  
**Family CHYDORIDAE** Dybowski and Grochowski, 1894 emend. Frey, 1967  
**Subfamily CHYDORINAE** Dybowski and Grochowski, 1894 emend. Frey, 1967  
**Genus Disparalona** Fryer, 1968

**Checklist of the formal taxa described to date (valid taxa are marked by bold type)**

2. **Lynceus griseus** Fischer, 1854 – junior synonym of *D. rostrata*, see Smirnov (1971, 1996a)).
3. **Pleuroxus hamatus** Birge, 1879 – valid species of the subgenus *Disparalona* (*Mixopleuroxus*).
4. **Pleuroxus acutirostris** Birge, 1879 – valid species, but its taxonomic position is not clear to date.
7. **Pleuroxus hamulatus** Birge, 1910 – junior synonym of *D. hamata* (see Smirnov 1971).
9. **Pleuroxus chappuisi** Brehm, 1934 – valid species of the subgenus *Disparalona* (*Mixopleuroxus*).
(10) *Pleuroxus striatiodes* Šrámek-Hušek, 1946 – valid; type species of the subgenus *Disparalona* (Mixopleuroxus).


(13) *Disparalona caudata* Smirnov, 1996 – valid species, most probably belonging to the subgenus *Disparalona* (Mixopleuroxus). But its differences from *D. (M.) striatoides* need to be specially formulated.

(14) *Disparalona adyiodii* Subhashbabu and Thomas, 2007 – junior synonym of *D. chappuisi* (as it was previously regarded as a junior synonym of *D. hamata* by Chatterjee et al. 2013).


Subgenus *Disparalona* Fryer, 1968 s. str.

**Type species**

*Lunceus rostratus* Koch, 1841 = *Disparalona rostrata* (Koch, 1841) now. Explicitly designated by the taxon author (Fryer 1968) (case 67.5 of the ICZN 2000).

**Emended diagnosis**

Parthenogenetic female. Middle-sized Chydorinae, length of adult parthenogenetic female up to 0.5 mm. In lateral view, body oval, low (especially in the posterior part), with maximum height almost at the middle. Height/length ratio about 0.60. In dorsal and ventral view body moderately compressed laterally, in some species lateral processes on valves present. Head small, with relatively long rostrum (distance between centre of eye and ocellus is two times shorter than distance between centre of ocellus and tip of rostrum). Dorsal and posterior margins of valves convex, posterodorsal angle expressed, posteroventral and anteroventral angles broadly rounded. Posteroventral angle of valve with or without denticle. Inner side of valve posterior margin covered by a row of numerous fine setules located quite close or far from the edge of margin, setules decreasing in size distally. Sculpture of valves and head strongly developed. Sculpture of posterior and anterior portion of valves is represented by parallel sometimes anastomosing lines and polygons. Surface between them may be covered by additional fine striation, represented by more short lines. Surface of head in some species also with parallel long lines. Structure of head pores are typical for the subfamily Chydorinae: two major bordered pores and two minute pores between them located slightly asymmetrically to midline, closer to anterior major pore than to posterior one. Surface between pores without ornamentation. Labral keel relatively long with drawn tip or short with rounded tip. Postabdomen relatively short (postanal margin almost subequal in size to anal margin or slightly longer). Postanal margin slightly convex. Distal angle of postabdomen is broadly rounded. Postanal margin is armed by composite
denticles, decreasing in size proximally. Anal margin and lateral surface of postanal margin are covered by bunches of fine setules. Postabdominal claw is long, subequal in length to anal margin, with two basal spines of different size. Antenna I typical for chydorids, antennular sensory seta slender, arising subdistally, subequal in length to antennular body. Antennal formula: setae 0–0-3/1–1-3, spines 1–0-1/0–0-1. Antenna II with massive, long spine on proximal exopod segment (this spine longer than the middle exopod segment). Five thoracic limbs. The number of setae on thoracic limbs is typical for subfamily Chydorinae. Inner distal lobe of thoracic limb I with three thin setae of different length, the largest seta hook-like or not. Two lateralmost setae covered by short setules on exopodite of limb IV are relatively long, subequal in size. 

**Ephippial female** is similar with parthenogenetic female in lateral view. Ephippium is not specially bordered from the rest of valves, brownish, contains single egg.

**Male.** In lateral view, body oval, elongated, up to 0.36 mm in length. Armature of valves and ornamentation similar to parthenogenetic female. Postanal margin of postabdomen of different shape (almost straight, convex or concave). Postabdominal claw with one or two basal spines. Gonopores open laterally or ventrally near claw bases. Antenna I with male seta located almost at the middle of antennular body near sensory seta. Limb I with massive copulatory hook.

**Subgenus Disparalona (Mixopleuroxus) Hudec, 2010**

**Type species**

*Mixopleuroxus striatiodes* (Šrámek-Hušek, 1946). Type species was fixed by Hudec (2010) by monotypy (International Commission on Zoological Nomenclature (ICZN) 2000, case 68.3).

**Emended diagnosis**

**Parthenogenetic female.** Middle-sized Chydorinae, length of adult parthenogenetic female up to 0.63 (0.80 according to Hudec 2010) mm. In lateral view, body elongated-subovoid, with maximum height almost at the middle. Height/length ratio about 0.60. In dorsal and ventral view body moderately compressed laterally, lateral processes on valves absent. Head relatively small, with a relatively long rostrum, distance between centre of eye and ocellus subequal in length to distance between centre of ocellus and tip of rostrum or significantly (two or three times) larger than it. Dorsal and posterior margins of valves convex, posterodorsal angle expressed; posteroventral and anteroventral angles broadly rounded. Posteroventral angle of valve without any denticles. Inner side of valve posterior margin covered by a row of numerous fine setules located quite close to the margin, these setules decreasing in size posteriorly. Sculpture of valves and head strongly developed. Sculpture of posterior and anterior portion of valves as long parallel sometimes anastomosing lines. Outer surface between them covered by additional fine striation, represented by more short lines. Head shield reticulation with short and relatively long parallel lines. Structure of head pores typical for the subfamily Chydorinae: two major pores and two minute pores between them at head shield midline, located slightly asymmetrically to midline, closer to anterior major pore than to posterior one. Labral keel relatively long, with a drawn tip, or short, with a rounded tip. Postabdomen subrectangular, postanal margin almost subequal in size to anal margin or
almost in two times longer. Postanal margin almost straight. Distal angle of postabdomen almost right. Postanal margin armed with composite teeth, decreasing in size proximally. Anal margin and lateral surface of postanal margin covered by bunches of fine setules. Postabdominal claw long, subequal in length to anal margin, with two basal spines of different size. Antenna I typical for chydorids, antennular sensory seta slender, arising subdistally, its length subequal to antennular body length. Antenna II with a very short spine on proximal exopod segment (shorter than 1/4 of next exopod segment). Five thoracic limbs. Number of setae on thoracic limbs typical for subfamily Chydorinae. Inner distal lobe of thoracic limb I with two thin setae of different length and one thick, hook-like seta. Two lateralmost setae on exopodite of limb IV covered by short setules, unequal in size, lateralmost seta almost two times shorter than nearest seta. Ephippial female similar with parthenogenetic female in lateral view. Ephippium not bordered from the rest of valves, brownish, contains a single large egg.

**Male.** In lateral view, body oval, elongated, up to 0.48 mm in length. Armature of valves and ornamentation of valves and head shield as in parthenogenetic female. Dorsal side of postabdomen almost straight or strongly concave. Postabdominal claw with two basal spines. Gonopores open laterally or ventrally almost near claw bases. Antenna I with male seta located almost at middle of antennular body, near sensory seta. Limb I with a massive copulatory hook, that only slightly thicker than hook-like seta on IDL.

**Differential diagnosis.** *D. (Mixopleuroxus)* differs from the nominotypical taxon in (1) a very short spine on proximal exopod segment of antenna II; (2) distal angle of postabdomen is almost right; (3) two thin setae unequal in size and one long thick hook-like seta on inner distal lobe of thoracic limb I; (4) two thin setae covered by short setules in length on exopodite IV, lateralmost seta is almost two times shorter than nearest seta. In contrast, *Disparalona* s. str. has: (1) a massive and long spine on proximal exopod segment of antenna II; (2) distal angle of postabdomen is broadly rounded; (3) two long thin setae subequal in size and one short seta on inner distal lobe of thoracic limb I; (4) two thin setae covered by short setules are subequal in size on exopodite IV.

Other features (proportions of labral keel, armature of posteroventral angle and posterior margin of valve, its ornamentation; presence of lateral processes on valves; length of basal spines on postabdominal claw; ratio between setae on IDL of thoracic limb I; characteristics of adult males) are important for discrimination of certain species within each subgenus. A further detailed comparison of considered species confirms our observation (*Table 1*). Below we analyse in detail populations of *Disparalona (M.) hamata* species group based on original data and available references.

### Disparalona (Mixopleuroxus) hamata species group

1. **Disparalona (M.) hamata** (Birge, 1879)  
   (Figures 1–5)

**Synonymy**

*Pleuroxus hamatus* Birge, 1879, pp. 22–23, pl. 2: figures 13, 14; Herrick 1884, pp. 110–111, pl. h: figure 1
Table 1. Comparison of known to date *Disparalona* species (mainly after Frey 1961; Michael and Frey 1984; Smirnov 1996a; Hudec 2010; Van Damme and Dumont 2010; Kotov and Sinev 2011; Klimovsky et al. 2015; our data).

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<tbody>
<tr>
<td>Distribution</td>
<td>Palaeartic zone</td>
<td>Nearctic zone</td>
<td>Neotropics</td>
<td>From Central America to Canada</td>
<td>From Africa to South-East Asia and southern part of Russian Far East</td>
<td>To date known only from Central Europe</td>
<td>Neartic, some regions of Europe and Asia</td>
<td>Australia</td>
<td>From Amur Basin to Hainan island and North-East Thailand</td>
<td>Endemic to Yakutia</td>
</tr>
<tr>
<td>Habitat</td>
<td>Lakes, rivers, oxbows</td>
<td>Lakes, rivers, oxbows, phytotelmata</td>
<td>Lakes, ponds, wetlands, rivers, creeks</td>
<td>Lakes, ponds, wetlands, rivers, creeks</td>
<td>Rivers</td>
<td>Rivers</td>
<td>Mudderneti Lagoon</td>
<td>Rivers</td>
<td>Oxbow of river Lunkebey</td>
<td></td>
</tr>
</tbody>
</table>

1. Parthenogenetic female

<table>
<thead>
<tr>
<th>Maximum length</th>
<th>0.52 mm</th>
<th>0.39 mm</th>
<th>0.50 mm</th>
<th>0.58 mm</th>
<th>0.8 mm</th>
<th>0.46 mm</th>
<th>0.60 mm</th>
<th>0.42 mm</th>
<th>0.37 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Labral keel</td>
<td>Relatively long, distal angle is acute</td>
<td>Short, distal angle is obtuse, rounded</td>
<td>Short</td>
<td>Relatively long, distal angle is acute, with drawn tip</td>
<td>Short, distal angle is acute</td>
<td>Relatively long, distal angle is acute, with drawn tip</td>
<td>Relatively long, distal angle is acute</td>
<td>Relatively long, distal angle is acute, with drawn tip</td>
<td>Short, distal angle is obtuse, somewhat rounded</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Posteroventral angle of valve</th>
<th>With denticle</th>
<th>Without denticle</th>
<th>Without denticle</th>
<th>Without denticle</th>
<th>Without denticle</th>
<th>Without denticle</th>
<th>Without denticle</th>
<th>Without denticle</th>
<th>With denticle</th>
</tr>
</thead>
<tbody>
<tr>
<td>Armature of posterior margin of valve</td>
<td>A row of numerous setules located close to the edge of posterior margin</td>
<td>Not studied</td>
<td>Not studied</td>
<td>A row of numerous setules located close to the edge of posterior margin</td>
<td>A row of numerous setules located close to the edge of posterior margin</td>
<td>A row of numerous setules located close to the edge of posterior margin</td>
<td>Not studied</td>
<td>A row of numerous setules located close to the edge of posterior margin</td>
<td>A row of numerous setules located from the edge of posterior margin</td>
</tr>
<tr>
<td>Ornamentation of valve</td>
<td>Polygons, parallel and anastomosing lines (outer surface between them with short, sometimes wavy lines)</td>
<td>Hexagons, with striation within cells</td>
<td>Parallel and anastomosing lines (outer surface between them with short, sometimes wavy lines)</td>
<td>Parallel and anastomosing lines (outer surface between them with short, sometimes wavy lines)</td>
<td>Parallel and anastomosing lines (outer surface between them with short, sometimes wavy lines)</td>
<td>Polygons, parallel and anastomosing lines (outer surface between them with short, sometimes wavy lines)</td>
<td>Polygons, parallel and anastomosing lines</td>
<td>Polygons, parallel and anastomosing lines (outer surface between them with short, sometimes wavy lines)</td>
<td>In posterior part of body ornamentation of valves represented by polygons, in other parts – by anastomosing lines</td>
</tr>
<tr>
<td>Lateral processes on valves</td>
<td>Present (?)</td>
<td>Absent</td>
<td>Not studied</td>
<td>Absent</td>
<td>Absent</td>
<td>Present</td>
<td>Absent</td>
<td>Present</td>
<td>Absent</td>
</tr>
<tr>
<td>Spine of proximal exopod segment</td>
<td>Massive, long (longer than the middle exopod segment)</td>
<td>As long as half of next segment length</td>
<td>Very short (shorter than 1/4 of the middle exopod segment length)</td>
<td>Very short (shorter than 1/4 of the middle exopod segment length)</td>
<td>Very short (shorter than 1/4 of the middle exopod segment length)</td>
<td>Very short (shorter than 1/4 of the middle exopod segment length)</td>
<td>Massive, long, slightly longer than the middle exopod segment</td>
<td>Massive, long (slightly longer than the middle exopod segment)</td>
<td>Massive, long (subequal in length to the middle exopod segment)</td>
</tr>
<tr>
<td>Postanal margin of postabdomen</td>
<td>Slightly convex</td>
<td>Almost straight</td>
<td>Almost straight</td>
<td>Almost straight</td>
<td>Almost straight</td>
<td>Almost straight</td>
<td>Slightly convex</td>
<td>Almost straight</td>
<td>Slightly convex</td>
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(Continued)
Table 1. (Continued).

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<tbody>
<tr>
<td>Distal angle of postabdomen</td>
<td>Rounded</td>
<td>Almost right</td>
<td>Almost right</td>
<td>Almost right</td>
<td>Almost right</td>
<td>Almost right</td>
<td>Almost right</td>
<td>Rounded</td>
<td>Rounded</td>
<td>Rounded</td>
</tr>
<tr>
<td>Basal spines on postabdominal claw</td>
<td>The longest spine is almost subequal in length to the claw diameter and four times longer than the smallest basal spine</td>
<td>The longest spine is almost subequal in length to the claw diameter and two times longer than the smallest basal spine</td>
<td>The longest spine is almost subequal in length to the claw diameter and two times longer than the smallest basal spine</td>
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<td>The longest spine is almost subequal in length to the claw diameter and two times longer than the smallest basal spine</td>
</tr>
<tr>
<td>Limb I: IDL setae</td>
<td>Two long thin setae subequal in size and one short setae</td>
<td>Two thin setae subequal in size, and one long thick hook-like seta</td>
<td>Two thin setae subequal in size, and one long thick hook-like seta</td>
<td>Two thin setae subequal in size, and one long thick hook-like seta</td>
<td>Two thin setae subequal in size, and one long thick hook-like seta</td>
<td>Two thin setae subequal in size, and one long thick hook-like seta</td>
<td>Two thin setae subequal in size, and one long thick hook-like seta</td>
<td>Two thin setae subequal in size, and one long thick hook-like seta</td>
<td>Two thin setae subequal in size, and one long thick hook-like seta</td>
<td>Two thin setae subequal in size, third seta is not found</td>
</tr>
<tr>
<td>Limb IV: exopod setae</td>
<td>Two thin setae subequal in length, covered by short setules</td>
<td>Two thin setae subequal in length, covered by short setules</td>
<td>Two thin setae subequal in length, covered by short setules</td>
<td>Two thin setae subequal in length, covered by short setules</td>
<td>Two thin setae subequal in length, covered by short setules</td>
<td>Two thin setae subequal in length, covered by short setules</td>
<td>Two thin setae subequal in length, covered by short setules</td>
<td>Two thin setae subequal in length, covered by short setules</td>
<td>Two thin setae subequal in length, covered by short setules</td>
<td>Two thin setae subequal in length, covered by short setules</td>
</tr>
<tr>
<td>2. Adult male</td>
<td>Postanal margin of postabdomen</td>
<td>Slightly concave</td>
<td>Slightly concave</td>
<td>Slightly concave</td>
<td>Strongly concave</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td></td>
<td>Position of gonopores</td>
<td>Laterally near claw bases</td>
<td>Laterally near claw bases</td>
<td>Lateral at short distance from claw bases</td>
<td>Ventrally at short distance from claw bases</td>
<td>Ventrally at short distance from claw bases</td>
<td>Ventrally at short distance from claw bases</td>
<td>Ventrally at short distance from claw bases</td>
<td>Ventrally at short distance from claw bases</td>
<td>Ventrally at short distance from claw bases</td>
</tr>
<tr>
<td></td>
<td>Basal spines on postabdominal claw</td>
<td>Absent or at most uncertainly present</td>
<td>A very strong distal and small, fine proximal spine</td>
<td>Two prominent short spines are unequal in length</td>
<td>Two prominent short spines are unequal in length</td>
<td>Two prominent short spines are unequal in length</td>
<td>Two prominent short spines are unequal in length</td>
<td>Two prominent short spines are unequal in length</td>
<td>Two prominent short spines are unequal in length</td>
<td>Two prominent short spines are unequal in length</td>
</tr>
<tr>
<td>3. Ephippial female</td>
<td>Ephippium</td>
<td>Dark brownish</td>
<td>Unknown</td>
<td>Dark brownish</td>
<td>Unknown</td>
<td>Dark brownish</td>
<td>Unknown</td>
<td>Dark brownish</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
</tbody>
</table>
Figure 1. Disparalona (M.) hamata (Birge, 1879), parthenogenetic female from Sunset Lake, NC, USA. (a) Adult parthenogenetic female, lateral view; (b) adult parthenogenetic female, lateroventral view; (c) adult parthenogenetic female, dorsal view; (d) head; (e–f) head pores and ornamentation of head near them; (g–h) posterodorsal portion of valve, outer view. Scale bars 0.1 mm for a–d, 0.01 mm for e–h.
Figure 2. Disparalona (M.) hamata (Birge, 1879), parthenogenetic female from Swan Pond, Long Island, New York, USA. (a) Adult parthenogenetic female, lateral view; (b) head; (c) head pores and ornamentation of head near them; (d) labrum; (e) valve; (f) armature of posteroventral portion of valve, inner view; (g) armature of ventral portion of valve, inner view; (h) armature of anterior portion of valve, inner view; (i) ornamentation of posteroventral portion of valve, outer view; (j) ornamentation of central portion of valve, outer view; (k) ornamentation of anterior portion of valve, outer view; (l) ornamentation of rostrum. Scale bars 0.1 mm.
Pleuroxus hamulatus Birge 1910, p. 1052; Birge 1918, p. 728, figures 1142, 1143; Kiser 1950, pp. 245–247, pl. 2: figures 1–4

Alonella hamulata (Birge) in Frey 1961, p. 138

Disparalona hamata (Birge) in Elias-Gutiérrez et al. 2008, p. 90, figure 30(3–6)

? Pleuroxus chappuisi Brehm in Brehm 1937, pp. 507–509, figure 4

? Alonella hamulata (Birge) in Rey and Vásquez 1986, p. 150, pl. 5: figures 13–20; Zoppi de Roa and Vásquez 1991, p. 56, figure 10

**Type material**

Most probably lost. Samples and slides of E.A. Birge were incorporated into the collection of David G. Frey at Indiana University and gifted to the Smithsonian Institution’s National Museum of Natural History (accession number 403,774) upon Frey’s death (Berner 1997; Kotov and Ferrari 2010). Several dried semi-permanent slides (e.g. numbers A-2–1, A-2–2, A-2–5, A-2–10, A-2–11, A-2–12, A-2–20) labelled as Pleuroxus hamatus or P. hamulatus are present in E.A. Birge’s metal file cabinet with slides, but all these slides are dated as 1903 or 1917 years; therefore they could not belong to type series of the taxon published in 1879. Liquid samples of E.A. Birge are also incorporated into D.F. Frey

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**Figure 3.** Disparalona (M.) hamata (Birge, 1879), parthenogenetic female from Swan Pond, Long Island, New York, USA. (a) Postabdomen; (b) distal portion of postabdomen and postabdominal claw from outer view; (c) antenna I; (d) antenna II, general view; (e) exopod and endopod of antenna II; (f) corm of limb I; (g) outer distal lobe of limb I; (h) inner distal lobe of limb I. Scale bars 0.1 mm.
collection, but there is no detailed inventory of them, e.g. with the animal identifications by Birge. There is a chance that any individuals of *D. hamata* could be found in the samples of 1879, but whether they can be regarded as belonging to the type series will be problematic: they were not separated by the author from the total samples, and most probably were not seen by him.

**Type locality**

‘Southampton, Mass.’, USA (Birge, 1879).
Figure 5. *Disparalona* (M.) *hamata* (Birge, 1879), ephippial female and adult male from Jordan Harbor, Ontario, Canada. (a) Ephippial female, lateral view; (b) adult male, lateral view; (c) labrum of adult male; (d) postabdomen of adult male; (e) antenna I of adult male; (f) antenna II of male; (g) limb I of adult male; (h) juvenile male of II-nd instar male, lateral view; (i) postabdomen of juvenile male II; (j) antenna I of juvenile male II; (k) antenna II of juvenile male II; (l) limb I of juvenile male II. Scale bars 0.1 mm.

**Material examined.**

Diagnosis
Parthenogenetic female. Species of typical size for the genus (length of adult parthenogenetic female up to 0.6 mm). In lateral view, body regularly ovoid, dorsal keel is not developed. Head with relatively long rostrum (distance between centre of eye and ocellus is two times shorter than distance between centre of ocellus and tip of rostrum). Posteroventral angle of valve without denticles. Posterior margin of valve bears a row of numerous fine setules located quite close to the edge of its margin. Sculpture of valves and head strongly developed. Outer surface of posterior and anterior portion of valves is covered by long parallel sometimes anastomosing lines, between them short sometimes wavy lines are located. Central portion of valves and head are covered only by short lines. Structure of head pores are typical for the subfamily Chydorinae: two major bordered head pores and two lateral pores (sensu Kotov 2013) between them. Surface between pores is also covered by short lines. Labral keel short, its anterior margin is straight or slightly convex, distal angle is acute. Postabdomen relatively long (postanal margin two times longer than anal margin). Postanal and ventral margin are rather convergent, although the ventral margin is clearly convex whereas the dorsal margin is straight. Distal angle of postabdomen is almost right. Postanal margin is armed distally by composite denticles, decreasing in size proximally, proximal half of margin with groups of denticles of decreasing length proximally in each group, anal margin is covered by bunches of fine setules. Also, bunches of fine short setules cover lateral surfaces of these margins. Postabdominal claw is long, subequal in length to anal margin, with two basal spines. The longest basal spine is slightly longer than the base of claw and two times longer than the smallest spine. Antenna I typical for chydorids, antennular sensory seta arising subdistally, almost subequal to antennular body. Antenna II with a very small spine on proximal exopod segment, it shorter than 1/4 length of the middle exopod segment. Five thoracic limbs. The number of setae on each thoracic limb as for genus. Inner distal lobe of thoracic limb I with two thin setae are unequal in size, and one long thick hook-like seta. Exopodite of limb IV with two thin setae covered by short setules are unequal in length, lateralmost seta is almost two times shorter than nearest seta. Ephippial female is similar with parthenogenetic female. Ephippium dark brownish with single egg. Male. Body ovoid, elongated, up to 0.48 mm in length. Armature of valves and ornamentation similar to parthenogenetic female. Dorsal side of postabdomen straight or slightly concave. Two spines are unequal in length on postabdominal claw. Gonopores open laterally at short distance from claw bases. Antenna I with male seta located at the middle of antennular body near sensory seta. Limb I with massive copulatory hook.

Redescription
Parthenogenetic female (Figures 1–4). In lateral view body oval (Figures 1(a), 2(a)), relatively elongated (body height/length ratio about 0.58 both for adults and juveniles), maximum height almost at the middle of body. Body moderately compressed laterally (Figure 1(b, c)), dorsal keel and lateral processes on valves absent (Figure 1(c)). Dorsal margin uniformly curved, depression between head and rest of body absent (Figures 1(b, c)).
(a), 2(a)). Posterodorsal and posteroventral angles rounded (Figures 1(a), 2(a)). Posterior margin slightly convex (Figures 1(a), 2(a)). Sculpture of valves and head strongly developed (Figures 1(a–h), 2(a, c, e, i–k)).

Head small, not keeled, triangular (Figures 1(d), 2(b)), its dorsal margin broadly rounded. Rostrum long, protruding downward. Compound eye larger than ocellus, distance between centre of eye and ocellus two times shorter than distance between centre of ocellus and tip of rostrum. Head shield elongated, with a maximum width immediately behind mandibular articulation, its posteriormost extremity triangular (Figure 2(c)). Structure of head pores are typical for the subfamily Chydorinae (Kotov 2013): two major head pores at body midline, PP = 0.6–0.8IP (Figures 1(e, f), 2(c)). Minute pores located slightly asymmetrically to midline, closer to anterior major pore than to posterior one. Surface of head between pores with ornamentation represented by short lines (Figure 2(c)), same with rostrum (Figure 2(l)).

Labrum large (Figure 2(d)). Distal labral plate densely setulated. Labral keel short, triangular, its anterior margin is straight or slightly convex, distal angle is acute.

Valve subovoid (Figure 2(e)). A row of numerous fine setules located quite close to posterior margin, these setules gradually increasing in size to posteroventral angle (Figure 2(e, f)), anterior setae located exactly at the valve margin and clearly not articulated, posterior setae internally articulated. Ventral margin convex, covered by densely pubescent setae of different size (Figure 2(f–h)). Anteroventral angle broadly rounded (Figure 2(k)). Outer surface of posterior and anterior portion of valves covered by long parallel sometimes anastomosing lines, with short sometimes wavy lines between them (Figure 2(e), 2(i)). Ornamentation of central portion of valves represented by short lines only (Figure 2(j)).

Thorax long (Figure 2(a)), abdomen relatively short (Figure 2(a)). Postabdomen subrectangular, postabdomen length/height ratio about 2.5 (Figure 3(a)). Ventral margin straight to slightly convex. Preanal and anal margins almost equal in length, postanal margin is about two times longer than preanal and anal margins. Preanal and postanal angles well expressed. Postanal margin almost parallel to ventral margin and straight. Distal angle of postabdomen almost straight, somewhat rounded (Figure 3(b)). Each side of postanal portion provided with a row of thin and rather long postanal composite teeth, increasing in size distally. Row of postanal denticles evenly turned into a row of bunches of fine setules on anal margin. Bunches of fine short setules cover lateral surfaces of postanal and anal margins. Postabdominal claw massive and long (subequal in length to anal margin), slightly curved (Figure 3(b)). Dorsal edge of claw armed with a pecten of fine setules decreasing in size distally. Two basal spines on each claws. Distal basal spine long (slightly longer than the base of claw). Proximal basal spine relatively short (two times shorter than distal spine). Postabdominal seta relatively long, about times longer than preanal margin. Its distal segment supplied with delicate setules.

Antenna I not reaching tip of rostrum, slightly narrowing distally. Antennular sensory seta slender, almost subequal to antennular body, arising subdistally (Figure 3(c)). Nine short aesthetascs, subequal in size.

Antenna II relatively short (Figure 3(d, e)). Antennal formula: setae 0–0-3/1–1-3, spines 1–0-1/0–0-1. Coxal part folded, with two sensory setae. Basal segment robust, with a rudimentary distal spine between exopod and endopod. Antennal branches relatively
elongated, subequal in length, all their segments cylindrical, proximal exopod segment slightly longer than proximal endopod segment. Apical setae long, unequal in length, with chitinous insertions in their distal segments. Seta arising from proximal endopod segment thin and relatively long (subequal in size to endopod branch with apical spine). Seta of the middle endopod segment long, reaches tips of longest apical setae. Spine of proximal exopod segment very short (shorter than 1/4 of the middle exopod segment length). Spines on both apical segments long. Endopod apical spine slightly longer than exopod spine.

Thoracic limbs: five pairs.

Limb I large. Accessory seta short (not represented in Figure 3(f), because located on other side of limb corm), ODL conical, relatively small, bears a long seta with setulated distal segment and a short seta with bilaterally setulated distal segment (Figure 3(g)). IDL thicker than ODL, the former supplied by series of setules; first IDL seta short, setulated in distal portion, second IDL seta long, armed distally with short, fine setules and long third seta represented by thick, strongly curved hook, its concave side supplied by a series of minute spinules in its third quarter (Figure 3(h)). Limb corm almost rectangular in lateral view. Endite 4 (Figure 3(f: e4)) with three soft posterior setae (Figure 3(f: a–c)) and a stiff anterior seta 1. All these setae subequal in size. Endite 3 with a short posterior seta d, very long setae e and shorter seta f, and a stiff anterior seta 2. Endite 2 with three posterior long setae (g–i) and short seta j, and anterior stiff seta 3. Three robust long setules located between seta 2 and 3. Endite 1 with a short seta, a remnant of maxillar process (Figure 3(f: e1)). Fascicles of thin setules on inner face of limb, plus bunches of longer thicker setules at ventral margin of limb. Two slender long ejector hooks unequal in length (Figure 3(f: ejh)).

Limb II triangular-rounded. Exopodite (Figure 4(a: ext)) ovoid, with a long seta (with length of 3–4 exopodite body lengths). Inner portion of limb with eight scrapers (Figure 4(a: 1–8). Among them scrapers 1–3 especially long, scrapers 4–5 shorter, subequal in size, 6–8 even shorter, also subequal in size. A series of small projections posteriorly to distal setae, and a large sensillum between scraper 3 and 4. A shallow incision between endite 2 and endite 1. Distal side of gnathobase (=endite 1 sensu Kotov, 2013; Figure 4(a: e1)) with rows of fine, short and especially long setules. Distal armature of gnathobase with four elements, one of them represented by minute sensillum. Filter plate with eight setae, increasing in size proximally.

Limb III with ovoid densely setulated preepipodite (Figure 4(b: pep)) and ovoid epipodite (Figure 4(b: epp)). Exopodite (Figure 4(b: ext)) subrectangular, its width about half of its length, with three bilaterally setulated lateral setae and four distal setae differing in size and armature. Among them two setae covered by long setules and two setae covered by short stiff setules. Distal endite (in terms of Kotov 2013) with three anterior setae (1, 2, 3 in Figure 4(b, c)): setae 1 and 2 subequal in size and significantly longer than seta 3. Proximal endite with four small anterior setae and a very small sensillum. Six soft setae on posterior face of limb (Figure 4(c: a–f)). Distal armature of gnathobase with four elements (thick bottle-shaped sensillum and three small setae) and a bunch of long setules. Filter plates with eight setae subequal in length.

Limb IV with ovoid densely setulated preepipodite (Figure 4(d: pep)) and ovoid epipodite (Figure 4(d: epp)) with a small finger-like projection. Exopodite (Figure 4(d: ext)) rounded, bears seven setae of different length. Among them five setae covered by long
setules and two setae covered by short setules, the latter unequal in length, lateralmost seta almost two times shorter than next seta. Inner distal portion of limb IV with four setae (Figure 4(e: 1–4)): distalmost seta 1 stout, with short setules; three other setae (2–4) with inflated bases and long setules on distal segments. Four soft setae (a–d) on posterior face of limb IV. Distal armature of gnathobase with four elements: three sensillae and a long bisegmented seta. Filter plate with six setae subequal in length.

Limb V with ovoid densely setulated preepipodite (Figure 4(f: pep)) and ovoid epipodite (Figure 4(f: epp)) supplied by a small finger-like projection. Exopodite large (Figure 4(f: ext)), oval, with a single, short distal seta and three long lateral setae. Inner limb portion as elongated, flat lobe, with setulated margin, supplied with setae 1 and 2 (distal segments of both setae covered by especially robust setules). Distal armature of gnathobase as a small elongated projection. Filter plate with four long setae (longest as long as seta 2).

**Ephippial female.** Shape as in parthenogenetic female, no demarcation line of ephippium and rest of valve, ephippium region dark brownish (Figure 5(a)). Ephippium carries a single large egg.

**Adult male.** Body elongated, rectangular-oval in the lateral view, height/length ratio about 0.55. Maximum height at first third of body (Figure 5(b)). Dorsal margin slightly convex, posterodorsal angle expressed, posteroventral angle broadly rounded. Ventral margin almost straight. Head relatively large, narrow (Figure 5(b)). Rostrum shorter as compared with female, its tip pointed posteriorly. Compound eye slightly larger than ocellus. Distance from tip of rostrum to centre of ocellus somewhat larger than distance between centres of ocellus and eye.

Labrum with a short, triangular labral keel, its apex rounded (Figure 5(c)).

Postabdomen long and narrow, not curved, narrowing distally (Figure 5(d)), postabdomen length/height ratio about 4. Ventral margin in general straight, but somewhat undulated in postanal portion. Preanal margin straight, anal and postanal margins slightly concave. Postanal margin 1.5 times longer than preanal margin and 2 times longer than anal margin. Postanal and preanal angles smooth. Distal angle expressed, but rounded. Postanal margin armed by bunches of setules of similar size through all the margin length, following by clusters of short setules on anal margin. Bunches of fine setules on lateral surfaces of postanal and anal margins. Postabdominal claw almost straight, subequal in length to anal margin, with a thin basal spine subequal in length to claw diameter at base, and a minute second basal spine. Gonopores open laterally at a distance from claw bases.

Antenna I cylindrical, with nine terminal aesthetascs (Figure 5(e)). Male seta thick, long, located at middle of antennular body near sensory seta. Antenna II relatively short, basal segment robust, with a rudimentary spine (Figure 5(f)). 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. Apical spine on endopod longer than apical spine of exopod.

Limb I of moderate size, copulatory hook U-shaped (Figure 5(g)). Copulatory brush seta short, slender. IDL with four setae: setae 1–2 slender, of unequal length, seta 3 as a massive hook; male seta slender, curved in distal portion, about 2/3 length of seta 1.
**Juvenile male of instar II.** Body shape subovoid (Figure 5(h)) as in juvenile female of same instar. Postabdomen broad, with a rounded distal angle and composite teeth substituted by clusters of setules (Figure 5(i)). Antennas I and II as in female (Figure 5(j, k)). On limb I copulatory hook short, slightly curved, IDL with three setae, while male seta not yet developed (Figure 5(l)).

**Size.** Maximum length of adult parthenogenetic females up to 0.63 mm, maximum height 0.40 mm (therefore females could be larger than previously reported by Birge (1879) – 0.45 mm and Smirnov (1971) – 0.6 mm). Maximum length of ephippial females up to 0.56 mm, height 0.30 mm. Maximum length of adult males up to 0.48 mm, height 0.29 mm.

**Variability.** No significant variability between investigated individuals was found.

**Distribution and ecology.** *D. hamata* is widely distributed in the New World (from North America to Central America). It occurs in stagnant and rheophilic habitats (lakes, ponds, rivers and oxbows). In an arid zone of Mexico specimens morphologically similar to *D. hamata* (and wrongly identified as Picripleuroxus cf. quasidenticulatus) were found in bromeliads (Romero et al. 2011). In this case bromeliads seem an important refugium for aquatic organisms during the dry season (Jocque et al. 2013).

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2. **Disparalona (M.) chappusi** Brehm, 1934  
(Figures 6–15)

**Synonymy**

*Pleuroxus hamatus hamatus* Birge in Smirnov 1971 (as description was based on African specimens), pp. 241, 238 (after Brehm 1934)  
*Alonella cf. hamata* (Birge) in Dumont 1981, p. 105, figure 4  
*Disparalona hamata* (Birge) in Smirnov 1996, p. 81–83, figures 296–300  
**Asia.** *Pleuroxus hamulatus* in Uéno 1927, pp. 295–296, pl. 28, figure 27(a–d); Chiang and Du 1979, pp. 244–245, figure 170(a–e) (not f, which is after Kiser 1950)  
*Alonella hamulatus* (Birge) in Idris and Fernando 1981, pp. 241–242, figures 34–37  
*Pleuroxus hamatus* Birge in Du 1973, p. 77, figure 83; Yoon 2010, pp. 140–141, figure 76  
*Disparalona cf. hamata* in Sinev and Sanoamuang 2011, pp. 53–54, figure 5; Kotov et al. 2012, p. 74, figure 20; Jeong, 2013, pp. 72–73, figure 60  
*Disparalona hamata* (Birge) in Kotov et al., 2013b, p. 98, figure 19

**Type material**

Brehm’s type material is lost.
Figure 6. Disparalona (M.) chappuisi Brehm, 1934, parthenogenetic female from Dura River, Ethiopia. (a) Parthenogenetic female, lateral view; (b) head, lateral view; (c) head, dorsal view; (d) head pores and ornamentation of head near them; (e) labrum; (f) valve; (g) armature of posterodorsal portion of valve, inner view; (h) armature of ventral portion of valve, inner view; (i) armature of anterior portion of valve, inner view; (j) ornamentation of posterodorsal portion of valve, outer view; (k) ornamentation of central portion of valve, outer view; (l) ornamentation of anterior portion of valve, outer view; (m) ornamentation of rostrum; (n) ornamentation of the edge of head shield. Scale bars 0.1 mm.
Type locality
‘Km 43 der Straße Odienné Touba, Bächlein mit bemoosten Steinen’, Côte d’Ivoire (Brehm 1934, p. 69), although Smirnov (1996a) erroneously reported on another locality – a tributary of the Dwangwa River near Katete, West Africa (Malawi now).

Material examined


Figure 8. Disparalona (M.) chappuisi Brehm, 1934, parthenogenetic female from Dura River, Ethiopia. (a) Limb II; (b) limb III; (c) limb IV; (d) exopodite of limb IV; (e) gnathobase and filter plate of limb IV; (f) limb V. Scale bars 0.1 mm.
Figure 9. Disparalona (M.) chappuisi Brehm, 1934, parthenogenetic female from Loeng Yai reservoir, Khon Kaen area, Thailand. (a) Parthenogenetic female, lateral view; (b) parthenogenetic female, ventral view; (c) parthenogenetic female, dorsal view; (d) head shield; (e) head pores and ornamentation of head near them; (f) labrum; (g) valve; (h) armature of ventral portion of valve, inner view; (i) armature of posteroventral portion of valve, inner view; (j) postabdomen; (k) antenna II. Scale bars 0.1 mm.

**Figure 10.** *Disparalona* (M.) *chappuisi* Brehm, 1934, parthenogenetic female from Loeng Yai reservoir, Khon Kaen area, Thailand. (a) Limb I; (b) limb II; (c) limb III; (d) gnathobase of limb III; (e) limb IV; (f) limb V. Scale bar 0.1 mm.
Figure 11. Disparalona (M.) chappuisi Brehm, 1934, parthenogenetic female from a small lake near bridge across the River Pir, right side of the highway Khabarovsk – Komsomol’sk-na-Amure, Khabarovsk Area, Russia. (a, b) Parthenogenetic female, lateral view; (c) head, dorsal view; (d) ornamentation of central portion of valve, outer view; (e) head pores and ornamentation of head near them; (f–g) postabdomen; (h) distal portion of postabdomen and claw from outer view. Scale bar 0.1 mm for a–c, 0.01 mm for d–h.

M-2100; many parthenogenetic females from Bak Sil Ji 1 (large lake in wetland) (N 35.5418°, E 128.1209°), coll. 16 May 2010 by H.G. Jeong, AAK M-1862 and AAK M-1863; 3 parthenogenetic females from Si Mock Ri (N 35.6076°, E 127.7756°), coll. September 2011 by A.A. Kotov and H.G. Jeong, AAK M-2108; many males, ephippial
Figure 12. *Disparalona* (M.) *chappuisi* Brehm, 1934, parthenogenetic and ephippial females from Il'inskoe Lake, region of Lake Khanka, Primorsky Territory, Russia. (a) Parthenogenetic female, lateral view; (b) parthenogenetic female, ventral view; (c) parthenogenetic female, dorsal view; (d) head, lateral view; (e) head pores and ornamentation of head near them; (f) labrum; (g) valve; (h) armature of ventral portion of valve, inner view; (i) armature of posteroventral portion of valve, inner view; (j) ephippial females, lateral view. Scale bars 0.1 mm.

Russia (Far East). Five parthenogenetic females from the Amur River near mouth of the Zeya, region of Blagoveshchensk (N 50.2300°, E 127.2900°), Amur Area, coll. in 2005 by N.G. Sheveleva, AAK 2006–022; 1 parthenogenetic female from Zeya Water Reservoir near dam (N 53.7767°, E 127.2842°), Amur Area, coll. August 2006 by N.G. Sheveleva, NMK 2617; 3 parthenogenetic females from Lake Khasan, the plain of Zeya river (N 53.4870°, E 126.9428°), Amur Area, coll. 20 July 2006 by N.G. Sheveleva, NNS 2009–036; 5 parthenogenetic females from an oxbow lake of Tunugska River, 54 km of hw Khabarovsk-Birobidzhan, Jewish Autonomous Area, coll. 10 September 2007 by N.M. Korovchinsky, NMK 2806; 3 parthenogenetic females from a large puddle 1 near hw Khabarovsk-Birobidzhan before Nikolaevka, Jewish Autonomous Area, coll. 10

Figure 13. Disparalona (M.) chappuisi Brehm, 1934, parthenogenetic female from Il’inskoe Lake, region of Lake Khanka, Primorsky Territory, Russia. (a) Postabdomen; (b) distal portion of postabdomen and postabdominal claw, outer view; (c) antenna I; (d) exopod and endopod of antenna II. Scale bars 0.1 mm.
September 2007 by N.M. Korovchinsky, NMK 2795; 1 parthenogenetic female from a mine lake, 62 km of hw Khabarovsk-Birobidzhan, Jewish Autonomous Area, 10 September 2007 by N.M. Korovchinsky, NMK 2807; 1 parthenogenetic female from an oxbow lake 1 of Tunguska River, after the village of Partizanskaya, Jewish Autonomous Area, coll. 10 September 2007 by N.M. Korovchinsky, NMK 2802; 5 parthenogenetic females from a lake near bridge at Birobidzhan hw. (N 48.5066°, E 134.9271°), Jewish Autonomous Area, coll. 2 September 2007 by A.A. Kotov and N.M. Korovchinsky, NMK 2756; 1 parthenogenetic female from River Simmi at Cheremshinniy Kordon (N 49.5920°, E 136.1261°), Khabarovsk Territory, coll. 19 August 2016 by E.S. Certoprud, AAK M-3907; many parthenogenetic females from a small lake near bridge across the River Pir, right side of the highway Khabarovsk-Komsomol’sk-na-Amure (N 48.9835°, E 136.4107°), Khabarovsk Territory, coll. 7 September 2007 by A.A. Kotov and N.M. Korovchinsky, NMK 2780; 1 ephippial female from an oxbow lake near bridge through the Melgunovka River (N 44.5913°, E 132.1743°), Primorski Territory, coll. 23 October 2016 by A.A. Makhrov, AAK M-3751; 1 parthenogenetic female from a tributary of Khanka Lake (N 44.6547°, E 132.5608°), Khankaisky Reserve, Primorski Territory, coll. 16 September 2009 by N.M. Korovchinsky, AAK M-1287; 5 parthenogenetic females from a small bay,

Figure 14. Disparalona (M.) chappuisi Brehm, 1934, parthenogenetic female from Il’inskoe Lake, region of Lake Khanka, Primorsky Territory, Russia. (a) Limb I; (b) limb II; (c) limb III; (d) limb IV; (e) limb V. Scale bar 0.1 mm.
Figure 15. Disparalona (M.) chappuisi Brehm, 1934, ephippial female and adult male from Chuksan Reservoir, South Korea. (a) Ephippial female, lateral view; (b, c) adult male, lateral view; (d) labrum of adult male; (e–g) postabdomen of males; (h) antenna I of male; (i) exopod and endopod of antenna II of male; (j) limb I of adult male. Scale bars 0.1 mm.

Khanka Lake (N 44.6608°, E 132.5750°), Primorski Territory, coll. 16 September 2009 by N. M. Korovchinsky, AAK M-1289; 3 parthenogenetic females from a ditch near Khanka Lake (N 44.6679°, E 132.5089°), Primorski Territory, coll. 25 June 2012 by Y.V. Deart, AAK M-2525; 12 parthenogenetic females from Ilyinskoe Lake 1, region of Khanka Lake (N 44.9211°, E 131.9642°), Primorski Territory, coll. 10 September 2009 by N.M. Korovchinsky, NMK 2948; 25 parthenogenetic females from Ilyinskoe Lake 4, region of
Khanka Lake (N 44.9247°, E 131.9617°), Primorski Territory, coll. 11 September 2009 by N. M. Korovchinsky, NMK 2962–2967; 5 parthenogenetic females from a canal with filamentous algae, area of Lake Khanka (N 44.9305°, E 131.9764°), Primorski Territory, coll. 11 September 2009 by N.M. Korovchinsky, AAK M-1277; 1 parthenogenetic female from a canal with Scirpus sp. and Typha sp. near Khanka Lake (N 44.9419°, E 131.9541°), Primorski Territory, coll. 11 September 2009 by N.M. Korovchinsky, AAK M-1275 and NMK 2968.

**Diagnosis**

**Parthenogenetic female.** Species of typical size for the genus (length of adult parthenogenetic female up to 0.6 mm). In lateral view, body regularly ovoid, dorsal keel absent. Head with a long rostrum (distance between centre of eye and ocellus is two times shorter than distance between centre of ocellus and tip of rostrum). Posteroventral angle of valve without denticles. Posterior margin of valve bears a row of numerous fine setules located quite close to the edge of its margin. Sculpture of valves and head strongly developed. Outer surface of posterior and anterior portion of valves is covered by long parallel sometimes anastomosing lines, between them short sometimes wavy lines are located. Central portion of valves and head are covered only by short lines. Structure of head pores are typical for the subfamily Chydorinae. Surface between pores is also covered by short lines. Labral keel relatively long, distal angle is acute, with drawn tip. Postabdomen relatively long (postanal margin in two times longer than anal margin). Postabdomen subrectangular. Distal angle of postabdomen is almost right. Postanal margin is armed by composite denticles, decreasing in size proximally, anal margin is covered by bunches of fine setules. Also, bunches of fine short setules cover lateral surfaces of these margins. Postabdominal claw is long, subequal in length to anal margin, with two basal spines unequal in size. Antenna I typical for chydorids, antennular sensory seta arising subdistally, almost subequal to antennular body. Antenna II with very small spine on proximal exopod segment, shorter than 1/4 length of the middle exopod segment. Five thoracic limbs. The number of setae on each thoracic limb as for genus. Inner distal lobe of thoracic limb I with two thin setae unequal in size, and one long thick hook-like seta. Exopodite of limb IV with two thin setae covered by short setules unequal in length, lateralmost seta is almost two times shorter than nearest seta. **Ephippial female** is similar with parthenogenetic female. Ephippium dark brownish with single egg. **Male.** Body ovoid, elongated, up to 0.44 mm in length. Armature of valves and ornamentation similar to parthenogenetic female. Dorsal side of postabdomen strongly concave. Two spines are unequal in length on postabdominal claw. Gonopores open ventrally at short distance from claw bases. Antenna I with male seta located at the middle of antennular body near sensory seta. Limb I with massive copulatory hook.

**Redescription**

**Parthenogenetic female (based on African specimens).** In lateral view, body regularly oval, elongated (body height/length ratio about 0.58–0.60 both for adults and juveniles), maximum height anterior to body middle (Figure 6(a)). In dorsal and anterior view body moderately compressed laterally, dorsal keel absent, lateral processes on valves absent. Dorsal margin evenly arched from anteriormost extremity to a distinct posteroventral...
angle, posterior margin almost straight, posteroventral angle broadly rounded, without any denticles, ventral margin with a slight prominence anterior to middle (Figure 6(a)). Head small, with a long rostrum, protruding downward and sometimes posteriorly (Figure 6(b)). Compound eye clearly larger than ocellus, distance from tip of rostrum to ocellus greater than that between ocellus and eye. Head shield posteriormost extremity triangular-rounded (Figure 6(c)). Two major head pores, minute pores located slightly asymmetrically to midline, closer to anterior major pore than to posterior one (Figure 6(d)).

Labrum large, with a fleshy main body, setulated distal labral plate and especially long distal labral keel (Figure 6(e)). Distal labral plate densely setulated. Labral keel relatively long, distal angle is acute, with a drawn tip.

A longitudinal striation expressed in outer faces of head shield, anteroventral and posterodorsal portions of valve (Figure 6(d, f-m)). Short, sometimes wavy lines between them. Surface of central portion of valves and head also covered by short lines.

Thorax long (Figure 6(a)), abdomen relatively short (Figure 6(a)).
Postabdomen subrectangular, with armature (Figure 7(a, b)) as in previous species.
Antenna I not reaching tip of rostrum, slightly narrowing distally (Figure 7(c)), with morphology as in previous species.
Antenna II (Figure 7(d, e)) as in previous species, but seta arising from proximal endopod segment somewhat longer (about 30% longer than branch including the apical spine).

Thoracic limbs: five pairs, principally similar with previous species (Figures 7(f), 8(a–f)).

**Parthenogenetic females from Asia.** No differences from African populations were found (Figures 9–14).

**Ephippial female from Asia.** Shape as in parthenogenetic female, no demarcation line of ephippium and rest of valve, ephippium region additionally pigmented, dark brownish (Figures 12(j), 15(a)). A single large egg in ephippium.

**Adult male from Asia.** In lateral view, body elongated oval, height/length ratio about 0.5 (Figure 15(b, c)). Maximum height at first third of body. Dorsal margin convex, posterodorsal angle expressed, posteroventral angle broadly rounded. Ventral margin of valves slightly concave in middle (Figure 15(b, c)).

Head large, narrow. Rostrum more strongly curved as compared with female, its tip pointed posteriorly. Compound eye slightly larger than ocellus, distance from tip of rostrum to ocellus somewhat larger than distance between ocellus and eye.

Labrum with a relatively long labral keel having a strongly convex anterior margin (Figure 15(d)).

Armature and ornamentation of valves as in parthenogenetic female.
Postabdomen long and narrow, not curved, narrowing in its postanal portion (Figure 15(e–g)), postabdomen length/height ratio about 3.5. Ventral margin straight. Preanal margin straight, anal margin concave, preanal angle distinct, postanal angle smooth. Postanal margin concave, postanal portion in two times longer than preanal one and 1.4 times longer than anal one. Distal angle massive, rounded. Postanal margin with cluster of setules having different size, long setules on distal part and
short one through all the margin length, followed by clusters of short setules on anal margin. Lateral bunches of setules similar with female. Postabdominal claw curved, about 1.3 length of preanal margin, with a thin basal spine about 0.3 length of claw and a minute second basal spine. Gonopores open ventrally at short distance from claw bases.

Antenna I cylindrical, with nine terminal aesthetascs of different size (Figure 15(h)). Male seta thick, longer than antennular body, located at the middle of antennular body near sensory seta. Antenna II relatively short, basal segment robust, with a rudimentary distal spine (Figure 15(i)). 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. Apical spine of exopod about two times shorter than distal spine of endopod.

Limb I of moderate size, copulatory hook U-shaped (Figure 15(j)). Copulatory brush seta short, slender. IDL with four setae: setae 1–2 slender, unequal in length, seta 3 as a massive hook; male seta slender, curved in distal portion, about 1.4 length of seta 1.

**Size.** Maximum length of adult parthenogenetic females up to 0.60 mm, height 0.35 mm. Maximum length of ephippial females up to 0.43 mm, height 0.28 mm. Maximum length of adult males up to 0.44 mm, height 0.23 mm.

**Distribution and ecology.** *D.chappuisi* is widely distributed in the Old World (from Kenya and Ethiopia to South East Asia and south part of Russian Far East). Like *D. hamata*, it occurs both in stagnant and in rheophilic habitats.

3. **Disparalona (M.) cf. striatoides** (Šrámek-Hušek 1946) in Africa (Figures 16–18)

**Synonymy**

**Europe.** *Pleuroxus striatoides* Šrámek-Hušek, 1946, p. 232, figures 1(b, d, e), 2(a–b)
*Pleuroxus chappuisi* in Šrámek-Hušek et al., 1962, pp. 374–375, figure 140(g–l)
*Alonella hamulata* in Floessner, 2000, pp. 283–285, figure 106(a–h) (not i–j!)
*Disparalona hamata* in Kotov et al., 2010, p. 263, pl. 150: figure 1–2
(?) *Disparalona hamata* in Illyová and Hudec, 2004, pp. 287–288, figure 1

**Material examined from Africa.**


Short diagnosis

Fine details of morphology completely correspond with *D. hamata* and *D. chappuisi* redescribed above. Found differences concern: (1) body shape (presence of prominent dorsal keel); (2) shape of rostrum (dorsal edge of rostrum and head form broadly

Figure 16. Disparalona (M.) cf. striatoides (Šrámek-Hušek, 1946), parthenogenetic female from Dura River, Ethiopia. (a) Adult parthenogenetic female, lateral view; (b) adult parthenogenetic female, dorsal view; (c) head; (d) head pores and ornamentation of head shield; (e) labrum; (f) valve; (g) armature of posteroventral portion of valve, inner view; (h) armature of ventral portion of valve, inner view; (i) armature of anterior portion of valve, inner view; (j) ornamentation of posteroventral portion of valve, outer view; (k) ornamentation of central portion of valve, outer view; (l) ornamentation of anterior portion of valve, outer view. Scale bars 0.1 mm.
rounded portion, while in *D. hamata* and *D. chappuisi* they form more or less narrowly rounded portion).

**Distribution**

We are not fully sure of the identity of African and South European populations. To date, *striatoides*-like forms are detected through all Africa (from the Republic of South Africa to Ethiopia) and Europe (Czechia and Slovak Republic). Šrámek-Hušek et al. (1962) synonymized *P. striatoides* with *D. chappuisi* and concluded that European populations appear as a result of anthropogenic introduction. But we found that such synonymization was wrong, i.e. the opinion of a human-mediated introduction must be specially checked: European populations in reality could belong to an endemic indigenous taxon.

**Taxonomic comments**

We found a significant difference between African populations in the rate of the dorsal keel development and concluded that there are two species in Africa, *D. (M.*) chappuisi* and *D. (M.*) cf. striatoides*. But we note that identification based only on shape of body (due to differences in the keel development) may be controversial, confusing and useless for discrimination of sibling species, as already shown for some other chydorids (e.g. Sinev 2009; Sinev and Elmoor-Loureiro 2010; Sinev et al.)

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**Figure 17.** *Disparalona (M.*) cf. striatoides* (Šrámek-Hušek, 1946), parthenogenetic female from Dura River, Ethiopia. (a) Postabdomen; (b) distal portion of postabdomen and postabdominal claw, outer view; (c) antenna I; (d) antenna II, general view; (e) exopod and endopod of antenna II; (f) limb I. Scale bars 0.1 mm.
Further investigations of African, South European and Australian populations described as *D. caudata* (Smirnov, 1996a, 1996b), including description of gamogenetic females and males and genetic comparison, are desirable in order to clarify the status of all *striatoides*-like forms.

In Ethiopian samples AAK 2009–118 and AAK M-1442 we found both species (identified here as *D. chappuisi* and *D. cf. striatoides*) without any transitional forms; this may be a sign of their reproductive isolation. Note that where only deformed specimens or exuvia (Figure 19) are found in samples, identification of these two Old World taxa, at least in Africa, is very difficult, or even impossible.
Discussion

(1) Our preliminary inventory of the genus *Disparalona* Fryer, 1968; the subgenus *Mixopleuroxus* (Hudec, 2010)

To date, delineation between genera *Pleuroxus* Baird, 1843, *Picripleuroxus* Frey, 1993, *Alonella* Sars, 1862 and *Disparalona* Fryer, 1968 has been rather intuitive and depends on convention, rather than careful diagnostics, perhaps understandable for a wide range of ecologists and hydrobiologists. Smirnov (1996a) placed the four genera (*Pleuroxus*, *Picripleuroxus*, *Alonella* and *Disparalona*) next to each other in his identification key. According to Smirnov, the most important differences between these chydorid genera are:

1. Proportions of body: ‘height of posterior margin of valve about one third body height or slightly more’ for *Pleuroxus* and *Picripleuroxus*; ‘height of posterior margin of valve about half body height’ for *Alonella* and *Disparalona*; in lateral view the body of *Alonella* is ‘oval, short’ and the body of *Disparalona* is ‘elongated oval’.

2. Proportions of postabdomen: postabdomen of *Picripleuroxus* is ‘long and slightly bent’, postabdomen of *Pleuroxus* is ‘comparatively short’.

![Figure 19. *Disparalona* (*Mixopleuroxus*) sp.?, parts of exuvium of a parthenogenetic female from Botanical Gardens Dam, Grahamstown, Eastern Cape, the Republic of South Africa. (a) Labrum; (b) exopod and endopod branches of antenna II; (c) limb I; (d) IDL of limb I; (e) limb II. Scale bars 0.1 mm.](image-url)
Although for *Alonella* Smirnov added description of head pores in the key (indeed, all species from this genus have a very small postpore distance); the other three genera were delineated based only on body proportions (see Smirnov 1996a, p. 13), which seems to be a rather subjective step. Some other characters could be taken into consideration for discrimination of *Alonella, Disparalona* and *Pleuroxus*, such as the shape of the posterior portion of head shield (triangular in two former and rounded in the latter), the presence of a basal peg on antenna I (only in a part of *Pleuroxus* taxa, but never in other genera), but resolving this problem requires further studies.

However it is well known that in some cases fine features are much more important for discrimination between similar cladoceran groups, and even not only of the species (Frey 1991; Sinev 2015; Sinev et al. 2016), but also for subspecies (Rajapaksa and Fernando 1987a; Van Damme et al. 2011), and even for subgenera (Bekker et al. 2012; Kotov and Bekker 2016) and genera (Dumont and Silva-Briano 2000; Smirnov 2007; Van Damme and Dumont 2008; Van Damme et al. 2010, 2011; Sinev 2015; Sousa et al. 2016a, 2016b). For example, after an examination of thoracic limbs of *Pleuroxus* taxa, Chiambeng and Dumont (2004) came to the conclusion that there is no reason to separate the genus *Picripleuroxus*, although analysis of other numerous species are desirable for a final decision.

The first description of the genus *Disparalona* by Fryer (1968, pp. 286–287), considered this genus as:

Chydoridae of subfamily Chydorinae, of more or less elongated form. Carapace with a broadly rounded postero-ventral corner with or without one or more denticles, and either striated or reticulated. Ventral margins of carapace with a narrow flange showing no elaboration in the region of the ill-defined embayment, and fringed over the whole of their length by setae of more or less uniform types, which show little differentiation among themselves on the basis of function. Flange on anterior margin of carapace widened dorsally. Headshield drawn out into a distinct, sometimes markedly elongated rostrum, and with head-pores showing the arrangement found in several chydorid genera (*Alonella, Dunhevedia, Chydorus, Pleuroxus, Peracantha, Anchistropus*), namely two major pores between which are situated two close-set minor pores. Antennae with seven natatory setae and three stout scrambling spines, one on the distal segment of the endopod and one each on the basal and distal segments of the exopod. Five pairs of trunk limbs. Trunk limb 3 in almost constant, active motion in life, with a fine gnathobasic filter plate and a coarse outer sieve, and with a large sweeping seta arising at posterior dorsal corner of the gnathobase and directed forward along the food groove. Post-abdomen with sharply pointed marginal denticles and minute lateral setules but no lateral squamae. Alimentary canal with rectal caecum. Type species: *Lynceus rostrata* Koch, 1841.

In Fryer’s description we would like to pay special attention to: (1) variability in the number of denticles on posteroventral angle of valves; (2) a rate of developing (massive and long) of the spine on the basal exopod segment; (3) a structure of the thoracic limb III. Nowadays variation in the number of denticles on posteroventral angle was shown in some chydorids (e.g. Smirnov 1996a, 1996b; Van Damme and Dumont 2008; Sinev 2009; Sinev and Elmoor-Loureiro 2010; Sinev et al. 2012; Neretina and Kotov 2015; Sousa et al. 2015). This feature may be used for a species or subspecies discrimination with some caution, because the number of denticles may vary even between different valves of the same individual. Of course, absence or presence of denticles on the posteroventral angle should be added to the genus
diagnosis, but identification of a generic status of poorly known and rare taxa only based on this feature is dubious or completely impossible. Also, a structure of the thoracic limb III is not unique for *Disparalona*, and basically its thoracic limbs are similar with those in *Pleuroxus* sensu lato (e.g. Alonso 1996; Chiambeng and Dumont 2004; Smirnov et al. 2006). At the same time, structure of antenna II seems to be an important feature for discrimination between *Disparalona* versus *Pleuroxus* s. l. and *Alonella*, although Fryer (1968) did not focus on this character.

Hudec (2010) created a special genus *Mixopleuroxus* for a single species *P. striatiodes*, but this step was not supported in subsequent taxonomic and faunistic works. This could be explained by: (1) the rarity of records of this taxon in Europe (mainly due to its specific ecology: *M. striatiodes* is present in oxbows of rivers with stony bottom, see Hudec 2010), this zone is rarely investigated intensively as compared with pelagic zone of lakes; (2) the regional status of his book (the descriptions were published in Slovak, and the taxonomic position of numerous non-European taxa related to *M. striatiodes* was not discussed).

The description of *Mixopleuroxus* by Hudec (2010) was incomplete and contained several apparent mistakes, concerning the structure of thoracic limbs. In fact, general structure of thoracic limbs in *Mixopleuroxus* conforms to the typical description for subfamily Chydorinae (e.g. Kotov 2013), i.e.: (1) thoracic limb I has a full number of setae (Hudec 2010 lacks information about setae i and j); (2) the filter plate of limb II has eight setae (in Hudec 2010 nine setae are shown, which, based on our observations, is a mistake, although nine to 10 setae were observed in *P. carolinae* (Methuen, 1910) by Smirnov et al. (2006)); (3) the filter plate of limb III has eight setae (in Hudec 2010 seven setae were described); (4) the exopodite of limb IV has seven setae, the lateralmost of them is very short (in Hudec 2010 six setae were shown); (5) the filter plate of limb V has four setae (in Hudec 2010 three setae were shown), as well as some other minor mistakes, which do not seem to be variable between populations and different species. Despite mistakes in the first description, we accepted *Mixopleuroxus* as a subgenus of *Disparalona*, amended its diagnosis (see above) and expand its volume.

The identification key of Hudec (2010) delineates much better the genus *Disparalona* from genera *Alonella* and *Pleuroxus* (Hudec 2010, p. 357) as compared with Smirnov (1996a), but it is based on a shape and proportions of body and postabdomen as well and partially ignores fine morphological features (such as length of spine on proximal exopod segment of antenna II and structure of IDL of thoracic limb I), although they are discussed in the description of genera and in the final comparative table (Hudec 2010, pp. 494–495) (see discussion below).

For our revision we accepted the genus *Disparalona* in the volume offered by Smirnov (1996a) (i.e. *sensu lato*) and took into account subsequent comment of Hudec (2010). Species considered as members of *Disparalona* from Table 1 were split into two groups: taxa with a massive long spine on the proximal exopod segment of antenna II, the subgenus *Disparalona* s. str. (*D. ikarus*, *D. leei*, *D. rostrata*, *D. smirnovi*) and taxa with a very short spine, the subgenus *D. (Mixopleuroxus)* (*D. hamata*, *D. chappuisi*, *D. cf. striatiodes*). Although this feature is not documented in *D. leptorhyncha* and *D. caudata*, we may assume that these two species also possess a very short spine on the proximal exopod segment of antenna II. Moreover, some other features of these taxa suggest that they are more closely related to *D. hamata* and *D. chappuisi* than to *D. ikarus*, *D. leei*,...
D. rostrata and D. smirnovi. In contrast, D. acutirostris has a developed spine (with length as half of the next segment length) on antenna II proximal segment according to Frey (1961), while Smirnov (1996a) did not illustrate any spine. It may be that Frey (1961) and Smirnov (1996a) dealt with different taxa from North America. This means we need to revise the acutirostris-like populations in the Americas. Unfortunately, nobody has described the IDL of this taxon.

However, Pleuroxus s. l. (including Picripleuroxus) and Alonella also have a very short spine on the proximal exopod segment. Thus, based on the characters of antenna II, D. hamata, D. chappuisi, D. leptorhyncha and D. caudata are closer to the genera Pleuroxus s. l. and Alonella, than to ‘true’ Disparalona. This could be easily explained as a symplesiomorphy. In fact, a convention to consider species without a massive long spine on the proximal exopod segment of antenna II among members of Disparalona arose due to Smirnov (1996a), although some authors accepted the genus Phrixura P.E. Müller, 1867 as valid and placed D. rostrata and D. leei within it, while a position of other taxa described to that time was not discussed at all (e.g. Alonso 1996). However, we agree with the synonymization of Phrixura (see Smirnov 1996).

Taking into account the facts discussed above, we may preliminarily estimate a volume of the genus Disparalona and emend the diagnosis of its nominotypical subgenus, see above. We considered four taxa as belonging to the subgenus Disparalona s. str. The type species, D. rostrata, is distributed in the Palaeartic and carefully redescribed by Michael and Frey (1984). Description of North American D. leei, prepared by these authors, seems complete (Michael and Frey 1984); findings of D. leei from some European localities need careful re-examination (e.g. Alonso 1996; Hudec 2010). Descriptions of D. ikarus and D. smirnovi are not complete, as the morphology of gamogenetic females and males is undescribed. Other species (D. hamata, D. chappuisi, D. leptorhyncha and D. caudata, and maybe D. acutirostris) should be excluded from Disparalona s. str. The majority of them, if not all, are members of D. (Mixopleuroxus).

The significance of fine features, discussed by us above for separation of Disparalona s. str., was noted by Hudec (2010) and used in his description of Mixopleuroxus. Hudec marked special features for separation of Mixopleuroxus in his key: (1) posteroventral angle of valve without denticles; (2) distal angle of postabdomen is rectangular (Hudec 2010: p. 357 – Slovak version, p. 454 – English version), but, in fact, the most prominent features of this genus versus Pleuroxus and Alonella were discussed only in the description in Slovak (Hudec 2010, pp. 408–411). They concern: (1) specific structure of valve; and (2) armature of IDL of limb I is presented by two thin setae are unequal in size and one long thick hook-like seta. The second feature seems the most prominent and important for separation of Mixopleuroxus versus Pleuroxus and Alonella. Although some members of Pleuroxus and Alonella have no denticles on posteroventral angle of valve (e.g. Smirnov 1996a; Alonso and Kotov 2017) or this feature is variable, they never have thick hook-like seta on IDL of thoracic limb I.

We propose that D. hamata, D. chappuisi and D. cf. striatoides, carefully examined by us, can be considered members of the subgenus Disparalona (Mixopleuroxus). Also, other poorly described taxa (D. leptorhyncha and D. caudata) could be transferred to this subgenus. In the future: (1) a reinvestigation of D. striatoides from the type locality is urgently needed; (2) a detailed re-examination of D. caudata is desirable and the non-
conspecifity of this species to *D. cf. striatoides* must be checked; (3) a re-examination of material on *D. leptorhyncha* is required (according to figures and description in Smirnov (1996a) it seems to be a species with unique combination of features: a very long rostrum and a reduced labral keel with prominent lateral processes); (4) the status of *D. acutirostris* must be carefully verified, because its morphology is not described adequately, and according to size (Smirnov 1996a) this taxon is closer to the genus *Alonella* than to *Pleuroxus* s. l.

The delimitation of chydorid genera based exclusively on morphological features seems to be complicated. As sometimes happens, delineation between close cladoceran genera requires investigation of fine features. Some of them (such as structure of antenna II and thoracic limbs) are useful; others may be controversial (such as the number of denticles on posteroventral angle of valves and ornamentation of valves). Probably, the prominent ornamentation (combination of parallel and anastomosing lines, polygons and short wavy lines between them) might have arisen in *Alonella, Disparalona* s. str. and *D. hamata, D. chappuisi* and *D. cf. striatoides* independently as adaptations to extreme conditions, or it may be a synapomorphy at least for some taxonomic groups. Preliminary genetic investigations have shown that members of *Alonella, Disparalona* and *Pleuroxus* s. l. are located quite close to each other (Sacherová and Hebert 2003).

Especially interesting is the position of *D. acutirostris* (with a developed, but not as long spine on antenna II): it was combined with *Alonella excisa* (Fischer, 1854) and *A. exigua* (Lilljeborg, 1853) with relatively high support, while a group of these three taxa is clustered with *D. leei* with a moderate support (Sacherová and Hebert 2003; Figure 3(a)). There is no doubt that the topology of such trees may be significantly changed after insertion of more species and populations following analysis, as well as after using more genes and their combinations. However observed patterns are intriguing and, undoubtedly, can attract more attention to taxonomy and phylogeny of the subfamily Chydorinae, which is not well developed to data compared with subfamily Aloninae Frey, 1967 (see e.g. Van Damme et al. 2010 and other publications).

(2) Morphological differences between taxa of *Disparalona (Mixopleuroxus)*

Morphology of parthenogenetic females is basically similar in all taxa (Table 1). In general, the shape of the labral keel is the most prominent feature for discrimination between populations of *Disparalona (Mixopleuroxus)* from the New and Old World based on morphology of parthenogenetic females (Figure 20). Populations from the New World have a short labral keel, its distal angle is acute (Table 1, Figure 20) and here we identified them as *D. hamata*. All investigated populations from the Old World have a relatively long labral keel, its distal angle is acute, with a drawn tip (Table 1, Figure 20). Here we identified all specimens without dorsal keel as *D. chappuisi* and those with prominent dorsal keel as *D. cf. striatoides*. Diversity of ecological conditions (stagnant and reophilic water bodies), in which populations of investigated species were found, may signal that, in fact, we are dealing with species complexes both in the New and Old Worlds. But at the level of parthenogenetic female morphology it is not possible to distinguish them. Moreover, shape of the labral keel is also useful for discrimination between males and ephippial females (where they are available).
At the current level of knowledge, traits of labrum are considered among the most important diagnostic traits for many other chydorids (Rajapaksa and Fernando 1986, 1987b; Smirnov 1996a, 1996b; Neretina and Kotov 2015; Neretina and Sinev 2016). Discrimination of sibling cladoceran species from the Old and New Worlds is usually based on few reliable features of parthenogenetic females (e.g. Rajapaksa and Fernando 1986, 1987a, 1987b; Kotov 2009; Sinev and Elmoor-Loureiro 2010; Neretina and Sinev 2016; Neretina and Kotov 2017); the same is characteristic even for the largest cladocerans, euryercids (Bekker et al. 2012; Kotov and Bekker 2016). But as discussed above, morphological differences are not varied strongly among investigated populations; the diagnostic characters are consistent for species. We may consider them as useful for taxonomy on a morphological level, even if they are so fine-scale.

In contrast, we find stronger and more numerous morphological differences between adult males of *D. hamata* and *D. chappuisi* (Table 1). But, unfortunately for taxonomists, chydorid males are not common in tropical samples. Despite intensive sampling in Ethiopia and some other African countries, we have no information on morphology of the African males. Thus traits of the adult males are more useful for special taxonomic studies instead of a taxon routine identification in the course of hydrobiological and ecological studies, which are dealing mainly with the parthenogenetic females.

In the course of our study, we found that the rate of the dorsal keel development and rostrum relative length are important characters for discrimination between sibling species and even genera, as was found previously (Smirnov 1996a; Sinev and Atroshenko 2011). But it is necessary to take into consideration that in some cases the latter character varies strongly in some other chydorid macrotaxa and has even been found to be useless for taxonomy (e.g. Sinev 2009; Sinev et al. 2012). Moreover, development of the dorsal keel could be caused by environmental factors, which is much better understood for planktonic daphniids, than for chydorids to date. Finally, a perception of an animal shape may vary between researchers and depends on

![Figure 20. Comparison of labrum of females from different populations of *Disparalona hamata* species group.](image)

- (a) Head of *D. hamata* from USA;
- (b) head of *D. chappuisi* from Africa;
- (c) labrum of *Disparalona* from USA;
- (d–g) labrum of investigated *Disparalona* specimens from Africa:
  - (d) *D. cf. striatoides* from Dura River, Ethiopia;
  - (e) *D. chappuisi* from Dura River, Ethiopia;
  - (f) *Disparalona* sp.? from the Republic of South Africa;
  - (g) *D. cf. striatoides* from the Republic of South Africa.

Scale bar 0.1 mm.
preservation of the specimen, orientation in the glycerol drop in the course of drawing preparation, etc. (see Kotov 2013, colour table 1, fig. B). Populations described by Smirnov (1996a) as *D. caudata* will be revised in the future for the presence/absence of such keel. The Old World apparently hides more species of the *D. (M.) hamata* group, but genetic investigations are needed to make a comprehensive revision of the Old World populations (see also taxonomic remarks for *D. (M.) cf. striatoides*). Species differentiation between the Old World and Australia and presence of several sibling species in South East Asia was shown for some chydorids (e.g. Sinev 1997; Sinev et al. 2007; Neretina and Sinev 2016) and the continental endemism concept could suggest that Australia may be inhabited by other sibling species of *Disparalona*.

A similar difficult situation was recently investigated in detail for another group of subfamily Chydorinae, namely *Chydorus sphaericus* species complex (Belyaeva and Taylor 2009; Klimovskiy and Kotov 2015; Kotov et al. 2016). Step-by-step revisions may be the simplest solution to such difficulties. It seems much easier to find genetic differences between investigated populations, mark separate clades and delineate precisely their distribution ranges; then, only after preliminary genetic investigations, to search purposefully for males and ephippial females in natural populations, or obtain them specifically from laboratory cultures. On the example of *Chydorus sphaericus* species complex, a relatively recent speciation was detected (Kotov et al. 2016). The same situation probably took place in the diversification of *Disparalona (Mixopleuroxus)* inside the New and Old Worlds, when species divergent not only geographically, but also ecologically, although this divergence does not concern morphology of parthenogenetic females. Still, we know that *Chydorus sphaericus* is represented by a complex of sibling species, but ‘final’ morphological criteria for their discrimination are not drawn clearly. It is unlikely that such results on the *C. sphaericus* species complex will be widely used in applied ecological and palaeoecological works.

Unfortunately, modern genetic works on chydorids are not as numerous as are studies of the genus *Daphnia* O.F. Mueller, 1785: for some members of the latter genus genetic data are already in good accordance with the results of morphological analysis (e.g. Hebert and Finston 1993; Kořínek and Hebert 1996), and just male characters are found to be more helpful for species discrimination as compared with females (Kotov 2015; Popova et al. 2016). Male characters are found to be more valuable for species discrimination in other cladoceran groups (Goulden 1968; Smirnov 1971, 1976).

After estimation of diversity of *Disparalona* s. l. we may formulate a preliminary identification key for its members known to date based on parthenogenetic female morphology (taking into account that not all taxa are equally well described).

**(3) Key for species of the genus *Disparalona***

1. A massive and long spine on proximal exopod segment of antenna II (length ≥ middle segment) .................................................................................................................................................................................. 2
   - A short to rudimentary spine on proximal exopod segment of antenna II (not longer than half the length of the middle segment) .......................................................... 5
2. Rostrum long (comparable with length of antenna II) and strongly curved backwards, labral keel very small (height less than thickness of labrum body). *D. smirnovi* Sinev, 2015
   - Rostrum relatively short (half of antenna II length), labral keel large (height significantly larger that thickness of labrum body) .................................................. 3
3. No lateral keels on valves, few denticles at posteroventral portion of.......... .......................... D. rostrata (Koch, 1841)
   - Lateral keels on valves present, no denticles at posteroventral portion of valve........ 4
4. Lateral keels very strong (width of each keel about 1/4 of body width), postanal margin of postabdomen two times longer than anal margin.................................................. 6
   - Lateral keels low (width of each keel about 1/8 of body width), postanal margin about 1.5 times longer than anal margin................. 7
5. Rostrum long (comparable with length of antenna II), remarkably curved posteriorly ...................................................................................................................... 6
   - Rostrum relatively short (shorter than antenna II), directed ventrally............. 9
6. Labral keel absent.................................................. 7
   - Labral keel present ......................................................................................... 7
7. Distal angle of postabdomen projected ........................................... D. acutirostri (Birge, 1879)
   - Distal angle of postabdomen almost straight ............................................. 8
8. Labral keel large (its height larger than labrum body height)............. 7
   - Labral keel small (its height apparently smaller than labrum body height) .................................................. D. hamata (Birge, 1879)
   - Body and postabdomen relatively short .................................................. D. striatoides (Šrámek-Hušek, 1946)

(Note that discrimination of the last pair is based on conventional practice, and a final conclusion must be made only after a comprehensive revision of *D. caudata*).

**4) Sibling species of Disparalona in the New and Old Worlds: hypothesis for explanation of current distribution patterns**

Although in the New World *D. (M.) hamata* is detected in the Great Lakes basin – a northern area with humid continental (in its southern part) and subarctic (in its northern part) climate, in the Old World its sibling species occurs predominantly in tropical and subtropical regions, and only rarely found in more northern areas (such as Southern Europe (Illyová and Hudec 2004) or Amur Basin (Kotov et al. 2010; our data)). Traditionally, differentiation between the *Disparalona (M.) hamata*-group taxa from the New and Old Worlds may be considered in the light of several biogeographical scenarios: (1) ancient proto-continent breakup events (such as the Gondwana breakup); (2) Boreotropical migration; and (3) later long-distance dispersal events. Although the Cladocera is considered a group of a great geological age with a Paleozoic origin (Frey 1987; Dumont and Negrea 2002; Korovchinsky 2006; Kotov and Korovchinsky 2006), Chydoridae itself seems to be the youngest family among the cladocerans.
based on both genetic (Sacherová and Hebert 2003) and palaeontological data (Kotov 2013; Van Damme and Kotov 2016).

The estimated age of the Chydoridae origin (at least Mesozoic, even taking into account absence of palaeontological findings from that time) allows us to consider Gondwana breakup (and subsequent colonization of northern areas in the New World) among potential reasons for differentiation between the Disparalona hamata group species from the Old and New World. In this case we may consider the small number of morphological differences between Disparalona taxa from Old and New Worlds as a result of the morphological stasis over millions of years (see review in Van Damme and Kotov 2016). Indeed, the Gondwana breakup hypothesis was proposed to explain the current distribution patterns for many tropical organisms all around the World (see examples in Eskov 1984), and cladocerans are not an exception from this rule (see review of Korovchinsky 2006). This approach was based mainly on morphological similarity/differences between different taxa of investigated groups. A Gondwanan vicariance scenario (or a potential ‘Gondwana signature’) was shown via a comprehensive modern approach (combination of morphological and genetic data and palaeontological findings) only for few groups (e.g. scaly tree ferns in Korall and Pryer 2014; Darwin’s stag beetle in Kim and Farrell 2015; diving beetles in Toussaint et al. 2017a; giant water scavenger beetle in Toussaint et al. 2017b). This scenario was found to be applicable for the freshwater crayfish diversification pattern (Crandal et al. 2000).

There are many more examples of a later differentiation for tropical plants, fungi and animals (during the warming period in the Oligocene). For the chydorid genus Leydigiopsis Sars, 1901 the differentiation via Boreotropical migration or long-distance dispersal events is continued to be considered only as a speculation (Van Damme and Sinev 2013). Indeed, the chance of finding some direct palaeontological records confirming such scenarios is very small. For some terrestrial and freshwater organisms, one of these hypotheses or a combination of both of them are well supported by genetic data and by palaeontological records (e.g. BM+LDD) for vascular plants from families Melastomataceae and Memecylaceae in Renner et al. 2001; for Cinnamomum group in Huang et al. 2016; for ectomycorrhizal fungi Amanita section Caesarea and its allies in Sánchez-Ramírez et al. 2015; for pond skater genus Limnogonus in Ye et al. 2017; LDD for leafy liverwort in Scheben et al. 2016; for some ferns from family Athyriaceae in Wei et al. 2015; for grammitid ferns in Bauret et al. 2017; and for vascular plants from the genus Paederia L. in Nie et al. 2013). The Gondwanan vicariance is not supported in aforementioned studies. Among the crustaceans, a Gondwanan origin was not confirmed for freshwater shrimps (Page et al. 2005), prawns (Murphy and Austin 2005) and crabs (Daniels et al. 2006).

If we consider differentiation between sibling species of Disparalona as a relatively young event (via Boreotropical migration or long distance dispersal models), the smallest number of morphological differences may be explained via a short period of time after separation of the taxa. But careful genetic investigations and more palaeontological records are necessary. To date the role of Boreotropical migration and later long distance dispersal for speciation in the chydorids needs to be revised. Climate changes starting in the Oligocene apparently influenced the fresh water ecosystems where the chydorids occur (Korovchinsky 2006).
Application of new methods for phylogenetic reconstructions leads to a new perspective on current distribution patterns of many tropical organisms. During the last decade, studies based on a combination of molecular, morphological and palaeontological data have promoted interest in biogeographical reconstructions. The Gondwanan vicariance model (or other proto-continent disruption) is not regarded now as the most probable one. For each group of organisms the biogeographical schemes should be supplied by genetic and palaeontological data in a combination with morphology. Detailed explanations of the biogeographical patterns in chydorid species (as well as for other cladoceran groups) are still waiting for their investigators, and experts in the Cladocera could contribute to such works with great enthusiasm.

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