

# The Cladocera (Crustacea: Branchiopoda) as a relict group

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According to the fossil record and DNA data, the Cladocera is an ancient crustacean group. Recent revisions make their taxonomy amenable to zoogeographical analysis. A bipolar (antitropical) disjunct distribution of faunal complexes and taxa (*Daphnia*, *Daphniopsis*, *Pleuroxus*, *Tretocephala*, etc.), the wide ranges of some species and narrow restriction of others, the presence of isolated populations and the concentration of endemics in the warm temperate – subtropical zone of both hemispheres are traits of cladoceran zoogeography. These enable us to compare them with better studied (both living and fossil) plants, invertebrates and vertebrates, and to analyse their faunal formation by the modern version of the concept of ‘ejected relicts’ instead of vicariance. This reveals the extant Cladocera as a relict group, whose taxa were widely distributed in the past. Tertiary climatic changes, primarily within the present tropical and boreal latitudes, resulted in mass extinction of their biotas, while the warm temperate – subtropical regions remained comparatively unchanged. Although most recent Cladocera have relict status, others such as the *D. pulex* and *D. longispina* species groups and the subgenus *Eubosmina* are evolutionary young and show recent speciation. © 2006 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2006, 147, 109–124.

ADDITIONAL KEYWORDS: antiquity – faunal formation – fossils – taxonomic composition – zoogeography.

## INTRODUCTION

The four orders of the cladocerans (Ctenopoda, Anopoda, Onychopoda, Haplopoda) are thought to be polyphyletic (Fryer, 1987a, b) or monophyletic (Olesen, 1998; Schwenk *et al.*, 1998; Taylor, Crease & Brown, 1999; Braband *et al.*, 2002), sometimes without the order Haplopoda (Negrea, Botnariuĉ & Dumont, 1999; Flössner, 2000; Dumont & Negrea, 2002). Whatever their taxonomic position, it is clear that their lineages have differentiated markedly (Fryer, 1987a; Smirnov, 1976, 1992a; Dumont & Silva-Briano, 1998; Negrea *et al.*, 1999; Dumont & Negrea, 2002) and reflect great antiquity. This is substantiated by Palaeozoic (Smirnov, 1970) and Mesozoic (Smirnov, 1971, 1992b; Fryer, 1991; Kotov & Korovchinsky, 2006) fossils.

Cladoceran taxonomy is imperfectly known (Frey, 1987; Korovchinsky, 1996, 1997; Dumont & Negrea, 2002), but has progressed significantly after revisions

of the Macrothricidae, Chydorinae (Smirnov, 1992a, 1996), Sididae and Holopediidae (Korovchinsky, 1992), predatory cladocerans (Rivier, 1998), and *Simocephalus* (Orlova-Bienkowskaja, 2001). Coupled with older monographs on the Moinidae (Goulden, 1968; Smirnov, 1976) and Scapholeberinae (Dumont & Pensaert, 1983), recent revisions of regional faunas (e.g. Smirnov & Timms, 1983; Hebert, 1995; Alonso, 1996; Flössner, 2000) and many current taxonomic papers, these form a major source of information on the geographical distribution of the Cladocera of the world.

Insufficient taxonomic and faunistic information of the Cladocera long hindered a zoogeographical analysis (Frey, 1987; Dumont & Negrea, 2002). Early attempts at analysis are of only historical interest (Richard, 1892; Brehm, 1908, 1955), or focus on particular taxa or geographical regions (e.g. Bayly & Morton, 1978; Dumont, 1980; Fernando, 1980a, b; Lieder, 1982; Smirnov & Timms, 1984; Korovchinsky, 1986). Their conceptual basis was the vicariance approach (Nelson & Platnick, 1980; Patterson, 1983; Bănărescu, 1990; Dumont & Negrea, 2002), which is currently

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under challenged from alternative methods. The aim of the present publication is to reconstruct the faunal formation of the Cladocera based on taxonomic, phylogenetic, palaeontological and zoogeographical data.

## APPROACHES AND METHODS

Fossils are scarce. For this reason, an indirect approach was used, i.e. a comparison of the geographical distribution of Cladocera with that of ancient plants, freshwater invertebrates (crustaceans, insects, molluscs) and vertebrates was performed. In accordance with Razumovsky (1971), Zherikhin (1978) and Eskov (1984, 2004) I restrict the term 'tropics' to tropical regions where the average temperature of the coldest month exceeds 18 °C. The subtropics are characterized by average temperatures of 7–18 °C.

Data on the 500+ currently recognized species of Cladocera have been used. The geographical preferences of widely distributed species have been estimated from the 'area of their primary distribution', excluding marginal 'areas of penetration' where few populations are on record (Bobrinsky, Zenkevich & Birshtein, 1946; Kryzhanovsky, 1976). Species known only from their *terra typica* or few nearby localities were attributed to the local geographical region. Taxa without clear preferences or known as presumably cosmopolitan (*Simocephalus serrulatus* Koch, *Graptoleberis testudinaria* Fischer, *Pseudochydorus globosus* Baird, *Paralona pigra* Sars, etc.) were excluded from the analysis.

## FOSSILS

Late Palaeozoic – Mesozoic fossils [*Archedaphnia*, *Propleuroxus*, *Prochydorus*, *Archeoxus*, ephippia of *Simocephalus*, *Daphnia* (*Ctenodaphnia*), *Ceriodaphnia*, *Moina*, Sididae gen. nov.] originate from disjunct regions (eastern Kazakhstan, Transbaikalia, Mongolia, southern Australia, Europe, China and North America), implying a wide palaeodistribution of the group (Smirnov, 1970, 1971, 1992b; Fryer, 1991; Kotov & Korovchinsky, 2006). They are diverse in morphology and taxonomic position and mostly belong to extinct groups. They show morphological, physiological and ecological continuity across major geological epochs (Frey, 1967; Fryer, 1991).

## GEOGRAPHICAL DISTRIBUTION

### BIPOLARITY

The absence of some cladoceran taxa from the tropics and southern hemisphere has often been noted (e.g. Brehm, 1955; Fernando, 1980a, b; Smirnov & Timms, 1983; Dumont, 1994a). The list includes taxa of order

(Haplopoda, Onychopoda), family (Acantholeberidae, Ophryoxidae, Eurycercidae, Dumontiidae, Holopediidae), tribe (Sidini, Indialonini) and genus rank [*Latona*, *Megafenestra*, *Parophryoxus*, *Wlassicsia*, *Bunops*, *Lathonura*, *Drepanothrix*, *Monospilus*, *Acroperus*, *Rhynchotalona*, *Estateroporus*, *Spinalona*, *Bosmina* (*Eubosmina*)], restricted to the Holarctic (or predominated here), including its subtropical borders (Table 1). In addition, *Picripleuroxus*, *Disparalona*, *Anchistropus*, *Camptocercus*, *Tretocephala* and *Bosmina* are mostly known from northern Eurasia and North America (Table 1).

By contrast, an assemblage of families, tribes (Neothricidae, Sayciidae, Australospilini) and genera (*Pseudomoina*, *Onchobunops*, *Cactus*, *Archepleuroxus*, *Plurispina*, *Planicirclus*, *Rak*, *Monope*, *Australochydorus*, *Rhynchochydorus*, *Celsinotum*, *Miralona*, *Armatalona*) is confined to the south of South America, Australia, Tasmania, and New Zealand (Table 1).

Numerous species are restricted to cold temperate – subtropical regions of the northern or southern hemispheres. These disjunct regions house partially complementary cladoceran assemblages of high taxonomic rank, dominated by anomopods.

The intermediate tropical zone is mostly characterized by a wide range of genera (*Latonopsis*, *Sarsilatona*, *Pseudosida*, *Diaphanosoma*, *Macrothrix*, *Grimaldina*, *Guernella*, *Moinodaphnia*, *Chydorus*, *Dadaya*, *Dunhevedia*, *Notoalona*, *Euryalona*, *Leydigia*, *Karualona*, *Nicsmirnovius*, *Bryospilus*, *Alona*, *Kurzia*, *Leydigia*, *Bosminopsis*) and species (in all 163) but exhibits a dearth of higher taxa (Tables 1, 3). Possibly *Indialona*, recently elevated to tribe status (Kotov, 2000) and inhabiting the border area between the subtropics and tropics in India, belongs to this assemblage, too.

Some taxa, such as *Daphnia* and *Daphniopsis*, show a bipolar (or antitropical, see Briggs, 1987, 1995) distribution (Dumont, 1980; Fernando, 1980a, b; Fernando, Paggi & Rajapaska, 1987). At present, 34 species are known from North America (Hebert, 1995), 24 from northern Eurasia (Glagolev, 1985; Korovchinsky *et al.*, 1995), 15 from Australia (Hebert & Wilson, 1994, 2000), about 20 from the non-tropical South America (Paggi, 1998; Kořinek & Villalobos, 2003; Adamowicz, Hebert & Marinone, 2004) and at least ten from South Africa (Harding, 1961; Hebert, 1978). Only six occur in tropical lowlands (Fernando *et al.*, 1987; Hudeč, 1991). Of other Daphniidae, *Simocephalus mirabilis* Orlova-Bienkowskaja and *Megafenestra aurita* (Fischer) live in the United States and Argentina and in the Palearctic and South Africa, respectively (Dumont & Pensaert, 1983; Orlova-Bienkowskaja, 2001).

Tropical species of *Moina* include *M. micrura* Kurz and infrequently *M. belli* Gurney, *M. hartwigi*

**Table 1.** Distribution of cladocerans over zoogeographical and geographical regions (endemic and dominant taxa)

	Worldwide	Holarctic	Paleartic (including Caspian Sea and Lake Baikal)	Nearctic	Tropics	Ethiopian	Indo- Malaysian	Australasian	Neotropical
<b>Order Ctenopoda (worldwide)</b>									
Families	Sididae	Holopediidae							
Genera	<i>Diaphanosoma</i>	<i>Sida</i> , <i>Latona</i>	<i>Limnosida</i>		<i>Latonopsis</i> , <i>Sarsilatona</i> , <i>Pseudosida</i>				
<b>Order Anomopoda (worldwide)</b>									
Families/ Tribes	Daphniidae, Moinidae, Macrothricidae, Ilyocryptidae, Chydoridae, Bosminidae	Acantholeberidae Ophryoxidae, Euryceridae		Dumontiidae			Indialonini	Neothricidae, Sayciidae, Australospilini	
Genera	<i>Daphnia</i> , <i>Simocephalus</i> , <i>Scapholeberis</i> , <i>Ceriodaphnia</i> , <i>Moina</i> , <i>Macrothrix</i> , <i>Chydorus</i> , <i>Alona</i> , <i>Alonella</i> , <i>Bosmina</i>	<i>Megafenestra</i> , <i>Wlassiczia</i> , <i>Bunops</i> , <i>Lathonura</i> , <i>Drepanothrix</i> , <i>Picripleuroxus</i> , <i>Disparalona</i> , <i>Anchistropus</i> , <i>Monospilus</i> , <i>Acroperus</i> , <i>Camptocercus</i> , <i>Rhynchotalona</i>	<i>Estateroporus</i> , <i>Tretocephala</i> , <i>Kozhowia</i> , <i>Parakozhowia</i>		<i>Grimaldina</i> , <i>Guernella</i> , <i>Moinodaphnia</i> , <i>Dunhevedia</i> , <i>Dadaya</i> , <i>Bryospilus</i> , <i>Notoalona</i> , <i>Euryalona</i> , <i>Kurzia</i> , <i>Leydigia</i> , <i>Leydigia</i> , <i>Nicsmirnovius</i> , <i>Bosminopsis</i>			<i>Pseudomoina</i> , <i>Archepleuroxus</i> , <i>Plurispina</i> , <i>Planicirculus</i> , <i>Rak</i> , <i>Monope</i> , <i>Australochydorus</i> , <i>Rhynchochydorus</i> , <i>Celsinotum</i> , <i>Miralona</i> , <i>Armatalona</i>	<i>Onchobunops?</i> , <i>Leydigia</i> , <i>Cactus</i>
<b>Order Onychopoda (Holarctic)</b>									
Families		Polyphemidae	Cercopagidae						
Genera			<i>Podonevadne</i> , <i>Cornigerius</i> , <i>Caspievadne</i>						
<b>Order Haplopoda (Holarctic)</b>									
Species		~ 250	160	77	163	19	14	94	95

Weltner, *M. minuta* Hansen, *M. reticulata* (Daday) and *M. oryzae* Hudeč. In the southern part of the Holarctic, *Moina* is prominently represented by 13 species. In the southern regions of Australia, Africa and South America the genus is represented by seven species. As examples of its characteristic distribution, *M. wierzeiskii* Richard is restricted to the southern part of North America and Argentina with a transitional locality in Haiti and *M. brachiata* (Jurine) to the Palearctic and South Africa (Goulden, 1968; Smirnov, 1976).

*Streblocerus serricaudatus* (Fischer) is predominantly Holarctic but also lives in south-east Australia, New Zealand, Chile and Argentina (Smirnov, 1992a; Paggi, 1998). *Bunops* (including *Onchobunops*, see Silva-Briano & Dumont, 2001) has related taxa in both hemispheres.

*Eurycercus*, specious in the Holarctic, has populations of uncertain status in the south of Brazil, Argentina and South Africa (Frey, 1971) and in mountainous areas of Colombia and Ecuador (H. J. Dumont, pers. comm.).

*Pleuroxus* and related genera (*Picripleuroxus*, *Archepleuroxus*, *Plurispina*, *Planicirclus*) show a similar pattern of distribution: rare in the tropics (Fernando, 1980a), but common in the Holarctic (13 species) and in South Australia, New Zealand and subantarctic islands (16 species). Of *Tretocephala*, *T. ambigua* (Lilljeborg) is common in the Palearctic while *T. colletti* (Sars) is restricted to South Africa.

#### CONCENTRATION OF ENDEMICS WITHIN THE WARM TEMPERATE – SUBTROPICAL ZONES

Cladoceran species richness does not change evenly with latitude but concentrates in the warm temperate – subtropical zone of both hemispheres (~ 25–30° to 50°, and elevated areas within the true tropics). Thus, in Mediterranean–Transcaucasian areas, Middle and Central Asia, and Northern–Central India, one genus (*Esteratorporus*), 53 species and two subspecies (including groundwater and cave species), mostly members of *Ephemeroporus*, *Alona*, *Moina* and *Daphnia* (*Ctenodaphnia*), occur as endemics. If Caspian onychopods are included (four genera, 24 species), the local endemism is even higher. At the same time, characteristic North Palearctic forms are absent or rare here: *Sida*, *Limnosida*, *Latona*, *Holopedium*, *Acantholeberis* and *Ophryoxus*. Locally, the difference may be even more striking: Alonso (1991, 1996) recorded endemism but also the absence of *Latona*, *Lathonura*, *Bunops*, *Bosmina* (*Eubosmina*), *Anchistropus*, *Kurzia*, *Pseudochydorus*, *Acroperus*, *Leptodora* and *Bythotrephes* from the Iberian fauna.

East Asia from eastern Mongolia to the Amur region and China are still poorly studied, housing 21 endemic

species and two subspecies, among which *Diaphanosoma* and *Bosmina* predominate. According to my data, East Asia is rich in endemics awaiting description.

The number of South Palearctic species (98) exceeds that of North Palearctic (55–60). In North America, the area embracing the United States, the Mexican plateau and the southern part of Canada is inhabited by many endemics, including one family (Dumontiidae), two genera (*Parophryoxus*, *Spinalona*), 77 known species and four subspecies, among which *Daphnia* and *Daphniopsis* (23 species) are prominent.

South Australia, Tasmania and New Zealand are rich in endemics of high taxonomic rank: one family (Sayciidae), one tribe (Australospilini), eight genera, and about 80 species and subspecies make up altogether most (~ 85%) of the Australian endemics. Only five species are shared with New Zealand, which itself has seven endemic species and subspecies. Tropical Australian endemic species are comparatively few (14). Some of them penetrate neighbouring areas, including New Guinea.

Endemics of the poorly studied South Africa seem to be few, comprising at the moment only *Tretocephala colletti* and *Leydigia microps* Sars, 1916. Sars (1916) and Harding (1961) listed about ten species of *Daphnia* but a local *Rak* species and an undescribed Chydorid genus should be added (Shiel & Dickson, 1995; N. N. Smirnov, pers. comm.).

Cladocerans of the subtropical and the temperate South America (western mountain edge and south of 20°S) include one endemic genus (*Cactus*) and 17 endemic species but recent investigations (Paggi, 1998; Kořinek & Villalobos, 2003; Adamowicz *et al.*, 2004) record about 20 species of *Daphnia*, ten of *Macrothrix* and some others. Thus, the species richness of the southern temperate – subtropical zone amounts to more than 100 endemic species.

#### ISOLATED TAXA AND POPULATIONS

Some species have populations that are isolated far from their primary range (Table 2). Of these, *Sida crystallina* (O. F. Müller), *Diaphanosoma brachyurum* (Lievin) *s.l.*, *Lathonura rectirostris* (O. F. Müller) and *Monospilus dispar* Sars display signs of bipolarity. Other examples are *Latona tiwarii* Biswas and *Sarsilatona fernandoi* (Rane) in North-Western and Central India (Korovchinsky, 1992), *Holopedium amazonicum* Stingelin, *Anchistropus ominusus* Smirnov and *Celsinotum* (or a similar form) in the Amazon region (Korovchinsky, 1992; Smirnov & Santos-Silva, 1995), '*Holopedium ramararmii*' in India (Rao, Naidu & Padmaja, 1998) and *Leydigiaopsis* in Thailand (Sanoamuang, 1998); these localities are distant from the primary ranges of these genera.

**Table 2.** Distantly isolated populations of some species (figures – number of localities, L – lowlands, M – mountains, ? – not specified)

Taxa	Primary range	Isolated populations	References	Notes
<b>Order Ctenopoda</b>				
<i>Sida crystallina</i>	Holarctic	Columbia – 1M, Peru – 1L 1M, Brazil – 2L, Argentina – 1L,	Stingelin, 1913; Olivier, 1962; Valdivia Villar, 1988; Elmoor-Loureiro, 1997	Record in Amazon region, (Koste, 1972) seems doubtful
<i>Diaphanosoma brachyurum</i> s.l.	Holarctic	Sumatra – 1M, Mali – 1L, Lake Victoria – 1L, Kenya – 1L, 1?, Zambia and Republic of South Africa – some localities?	Brehm, 1933; Harding, 1942; Kořinek, 1984; Korovchinsky, 2000b, unpubl. data	Similar forms from Central and South America certainly represent different undescribed species
<i>D. unguiculatum</i>	Southern and central Australia	Papua New Guinea – 1?	Brehm, 1959; Korovchinsky, 1992	
<i>D. excisum</i>	Palaeotropics	Uzbekistan – 1L	Korovchinsky & Mirabdullaev, 1994	
<i>D. sarsi</i>	Palaeotropics	Uzbekistan – some localities L	Korovchinsky & Mirabdullaev, 2001	
<i>Latonopsis australis</i> s.l.	Pantropics	Northern Italy L, Macedonia – L, Bulgaria – 1L, Uzbekistan – some localities L	Manfredi, 1932; Behning, 1938; Harding & Petkovski, 1961; Naidenov, 1969; Mukhamediev, 1986	This species is distributed up to Khorezm area in the north
<i>Pseudosida</i> cf. <i>szalayi</i>	Palaeotropics	South of Georgia – 1L	Rylov, 1933	In Italy and Macedonia possibly introduced with rice
<b>Order Anomopoda</b>				
<i>Lathonura rectirostris</i>	Holarctic	New Zealand – L	Chapman & Lewis, 1976	
<i>Moina macrocopa macrocopa</i>	Southern Palearctic	South-west India – ?, Sri Lanka – ?, Philippines – ?	Goulden, 1968; Smirnov, 1976	
<i>Disparalona leei</i>	North America	Iberian peninsula – ?	Alonso, 1991, 1996	
<i>Alonella nana</i>	Holarctic	Malaysia – ?, Papua New Guinea – ?, Argentina – ?	Fernando, 1980b; Smirnov & DeMeester, 1996; Paggi, 1998	
<i>Alona verrucosa</i>	Pantropics	Spain – L	Alonso, 1991	
<i>Monospilus dispar</i>	Holarctic	Tropical Africa and South Africa – ?, Venezuela – ?, New Zealand – ?	Smirnov, 1971, 1994; Chapman & Lewis, 1976	In Venezuela only a shell was found (Smirnov, 1994)

**Table 3.** Number of endemic, dominant and other taxa in tropical and subtropical-temperate-cold zones (STC) of both hemispheres

Taxa	Geographical zones								
	Tropical			STC (northern)			STC (southern)		
	End.	Dom.	Others	End.	Dom.	Others	End.	Dom.	Others
Orders	–	–	2	2	–	2	–	1	1
Families			9	6 (7*)	1	7	2	1	6
Tribes		1	–	2	–	1	1	–	1
Genera	9	9	21	20 (27*)	11	12	14	1	15
Species (total)		163			221 (250*)			110 (114†)	

\*Together with Caspian and Baikalian endemics.

†Together with the endemics of the Antarctic continent and subantarctic islands.

#### WIDE LATITUDINAL DISTRIBUTION

Some species are known only from a single water body, e.g. *Spinalona anophthalma* Ciros-Peres et Elias-Gutierrez in Mexico (Ciroz-Pérez & Elias-Gutierrez, 1997). Others have extensive distributions (especially if an 'area of primary distribution' and marginal 'areas of penetration' are taken into consideration) within one climatic zone (e.g. cold, temperate or tropical) of one or both hemispheres, or in two or three zones.

Thus, *Sida crystallina* is widely distributed throughout subarctic and temperate Eurasia and North America but it also reaches the southern United States, South America, China, Bangladesh, Thailand and South Vietnam (Thanh & Mien, 1979; Hossain, 1982; Korovchinsky, 1986; Sanoamuang & Saeng-arong, 2002). The ranges of *Diaphanosoma mongolianum* Ueno, *D. lacustris* Kořinek, and *D. dubium* Manuilova cover huge areas in Western and Eastern Eurasia, mainly at temperate and subtropical latitudes, but these species also penetrate equatorial Africa and South-East Asia (Korovchinsky, 1987, 2000a and unpubl. data). *Holopedium gibberum* Zaddach *s.l.* usually occurs north of 50°N or at high altitudes in the south (e.g. the Alps) but in Japan it reaches south of Honshu and the south Kyushu (~ 32°S) (Ueno, 1938; Miyamoto, 1953). Similarly, *Leptodora kindtii* (Focke), *Polyphemus pediculus* (L.) and *Eurycercus* spp. extend to Central and East India (Fernando & Kanduru, 1984; Sharma & Michael, 1987). North American *Oxyurella brevicaudis* Michael et Frey and *Disparalona leei* (Chien) (Michael & Frey, 1983, 1984), *Daphnia obtusa* Kurz (Hebert & Finston, 1996) and *Simocephalus rostratus* Herrick (Orlova-Bienkowskaja, 2001) occupy most of the continent. *Daphnia longispina* (O. F. Müller), *S. mixtus* Sars and *S. exspinosus* (De Geer), predominantly northern temperate, occur also far south in East Africa, subtropical and tropical Asia, and Australia (Dumont, 1980; Orlova-Bienkowskaja, 2001).

By contrast, certain tropical species reach temperate regions in North America, where *Latonopsis*, some moinids, chydorids and bosminids tend to press north (McNair, 1976; Frey, 1982b; DeMelo & Hebert, 1994a). A similar situation prevails in Central Asia (Behning, 1938; Mukhamediev, 1986; Korovchinsky & Mirabdul-laev, 1994, 2001).

#### ZOOGEOGRAPHICAL CONCEPTS

Disjunct ranges of plants and animals long attracted the attention of biogeographers, who initially used the 'theory of landbridges' to explain them. The alternative point of view is the 'theory of ejected relicts' (term of Geptner, 1936), which dates back to A. R. Wallace. This explains disjunct distributions as the result of extinction of taxa over most of their original range. The evolutionary process on the northern continents caused archaic taxa to be driven out by evolutionarily advanced forms, to the southern ends of continents, which were their 'last line of defence'. This resembles Darlington's (1957) concept of 'tropical pressure', according to which primary evolution takes place in the tropics but weak competitors are driven out to the south and north (see also Briggs, 1987, 1995).

At present, vicariant biogeography, including a simplified form termed 'mobilistic biogeography' (Eskov, 1984), is popular: (1) if a taxon is distributed on separated continents, its ancestors lived there at the time of their union; (2) the degree of affinity of 'sister groups' depends on the time since isolation; (3) a primitive 'sister group' persists close to the centre of origin of the group, i.e. relicts survive in the centre.

Many authors interpret these ranges as 'Gondwanian' or 'Laurasian' (e.g. Humphries, 1983; Patterson, 1983; Bănărescu, 1990; see also references in Eskov, 1984, 2004; Briggs, 1987, 1995) but ignore palaeontological evidence of regional extinction, the effect of eco-

logical (landscape, climatic) factors and the dispersal abilities of organisms. Intercontinental disjunctions resulting from continental drift are hard to separate from extinction, and molecular phylogenetic data do not offer strong support for the vicariant model (Taylor *et al.*, 1996).

The similarity of the biota of southern Australia, Africa and South America, with their concentration of relicts, may equally well be explained by the 'theory of ejected relicts' modified by Razumovsky (1971) and Zherikhin (1978, 1993). Both authors suggest that the view that a tropical biota is ancient (e.g. Fischer, 1961) is caused by the vagueness of the term 'tropics'. Restricting it to the regions where the average temperature of the coldest month exceeds 18 °C, it is seen that their biota almost lacks archaic traits. The bulk of primitive plants, insects and vertebrates occur outside the true tropics, while most tropical groups are evolutionarily young and of low taxonomic rank. Primitive taxa concentrate in the warm temperate – subtropical zone of both hemispheres.

Razumovsky and Zherikhin suggest that in Mesozoic – Early Tertiary times the position of land and sea favoured more intensive thermal exchange between low and high latitudes. As a consequence, the global climate lacked strong gradients and taxa had practically pancontinental ranges. The geological and climatic changes that began in the Tertiary established climatic gradients between tropical and boreal latitudes and led to mass extinction of Mesozoic and Early Tertiary taxa. Their best chance of survival was in regions (~ 30–50° of both hemispheres) where a warm temperate – subtropical climate, such as previously dominated worldwide, continued to prevail. Some pre-Eocene taxa could survive in the tropical and boreal regions, forming the present pantropical and bipolar ranges. Today's tropical and boreal communities, which originated in the Eocene or even later in the Miocene–Pliocene, became subject to intensive evolution and may be considered as evolutionarily the youngest.

## DISCUSSION

### ANTIQUITY OF THE CLADOCERA

Cladocera were widely distributed long ago and later suffered mass extinction, exactly as in the 'Conchost-raca' and Ostracoda (Novozhilov, 1960; Tasch, 1963; Martens, Horne & Griffiths, 1998; Dumont & Negrea, 2002). They lost taxa of species, genera and family rank (e.g. *Archedaphnia*, *Propleuroxus*, Prochydoridae) in the course of their very long evolution. These suggestions differ from those of Tasch (1963), which are clearly untenable. Despite assumptions of antiquity and stability (Frey, 1967), and the finding of

Palaeozoic–Mesozoic remains, the general perception was at odds with such evidence (e.g. see Potts & Durning, 1980). This is understandable given the high cladoceran species richness and abundance worldwide. The Anomopoda, the only cladoceran group recorded as fossils for a long time, are regarded as among the most successful recent freshwater animals (Fryer, 1985). This appears to disguise the evolutionary history of these microcrustaceans.

Judging from the presence of Cladocera, especially the representatives of some recent genera in the Mesozoic, it was suggested that their roots date back to the Palaeozoic (Frey, 1987; Kerfoot & Lynch, 1987; Fryer, 1995; Negrea *et al.*, 1999; Dumont & Negrea, 2002). Possibly, their appearance in continental waters coincided with the initial inland faunas in the Carboniferous. According to (Tsalolikhin, 1992) and several other authors (Hutchinson, 1967; Gray, 1988), the ancestral inland water forms subsequently diverged to family–order level, as exemplified by the Cladocera and its subordinate taxa (Ctenopoda, Anomopoda, Onychopoda, Haplopoda).

The antiquity and evolutionary stasis of Cladocera are also substantiated by zoogeographical and genetic data. According to these the differentiation of extant Chydrid genera occurred in the Mid Palaeozoic (Sacherová & Hebert, 2003), *Daphnia* species groups (*laevis*, *longiremis*, *pulex*, *longispina*) in the Late Mesozoic, and that the age of some species (*D. villosa*, *D. latispina*, *D. salina*, *D. laevis*, *D. dubia*) is Early or Mid Tertiary (20 to > 50 Mya) (Benzie, 1987; Colbourne & Hebert, 1996; Taylor *et al.*, 1996; Hebert, 1998; Taylor, Finston & Hebert, 1998). Colbourne & Hebert (1996) reported that sequence divergence of North American lineages of *Daphnia* suggest that the genus is more than 200 Myr old. These data are important because *Daphnia* spp. are considered advanced anomopods (Fryer, 1987a, 1995) and the age of many other cladoceran taxa should therefore be older. Judging from the antiquity of the Cladocera and the wide distribution of many genera, their origin seems at least of Pangean age (Late Palaeozoic – Early Mesozoic). Frey (1980) suggested that the primary macroevolution of Cladocera was completed by the Mid Tertiary, but probably this occurred earlier (Colbourne, Hebert & Taylor, 1997; Hebert, 1998). Despite the long evolutionary stasis of the group, some Holarctic *Daphnia* and *Bosmina* have speciated recently (Lieder, 1983; Colbourne *et al.*, 1997; Dufresne & Hebert, 1997; Little *et al.*, 1997).

### CLADOCERA AS A RELICT GROUP

The evidence for cladoceran antiquity and traits of their zoogeographical distribution coincide with those of archaic insects Megaloptera, Mecoptera, Plecoptera,

Peloriidae and Trichoptera, spiders, molluscs and primitive vertebrates used in the modern version of the 'theory of ejected relicts' (Razumovsky, 1971; Zherikhin, 1978; Eskov, 1984, 2004). All these have been well studied neontologically and palaeontologically. This also provides the possibility to reconstruct cladoceran faunal formation. Thus, I hypothesize that starting from the Late Palaeozoic – Early Mesozoic until the Early–Mid Tertiary (Eocene–Oligocene), probably all supraspecific taxa of Cladocera had a wide distribution throughout Pangea and later Laurasia and Gondwanaland. It is suggested that the cladoceran fauna of those epochs was probably richer than the extant fauna. I assume that its mass extinction was similar to that in 'Conchostraca' and Ostracoda. These changes resulted in a reduction of adaptive zones and ranges, especially in the present tropical and boreal regions, the climates of which became hotter and colder, respectively. The initial range reduction may have been variable (Eskov, 1984), and some species survived in a few localities. The remotely isolated species and populations (Table 2) testify to a wider distribution of these taxa in the past. Many cladocerans were ejected into the neighbouring regions retaining moderately high temperatures (warm temperate and subtropical regions of the five continents and New Zealand), which are inhabited now by most of the rare endemic taxa. Fewer taxa were able to adapt to the severe new conditions of the northern and southern hemispheres and true tropics.

Within the new climatic zones speciation and changing patterns of distribution appeared. Thus, the origin of *Holopedium amazonicum* with an age of 4–20 Myr (Hebert, 1998; Rowe, 2000), and the wide distribution of tropical forms such as *Daphnia lumholtzi* Sars (Benzie, 1987; Havel, Colbourne & Hebert, 2000), *Diaphanosoma excisum* Sars, *Moina micrura s.l.* and the *Ceriodaphnia cornuta* Sars species complex might reflect the Tertiary perturbations in the recent tropical zone. The northern temperate and cold regions were populated by complexes of evolutionarily young taxa of *Daphnia* (*longispina*, *pulex*, *obtusa*, *retrocurva*) and *Bosmina* with an estimated speciation time within the last 3 Myr (Lieder, 1983; DeMelo & Hebert, 1994b; Colbourne *et al.*, 1997, 1998; Dufresne & Hebert, 1997; Little *et al.*, 1997; Haney & Taylor, 2003).

The Cladocera qualify as relicts. Many extant representatives are morphologically primitive, highly specialized (Fryer, 1968, 1974, 1995; Korovchinsky, 1986; Mordukhai-Boltovskoi & Rivier, 1987), with restricted ranges and 'marginal' biotopes (temporal, acidic, saline, mountain, cave waters and even terrestrial environments). For example, 23 members of the family Sididae, comprising about a half the known species, may be considered rare. The same is true of

anomopod genera such as *Simocephalus*, *Chydorus* and *Alona*. Many sidids are highly specialized (*Sida*, *Latona*, *Pseudosida*, some *Diaphanosoma*) and narrowly restricted to specific localities (e.g. *D. australiensis* Korovchinsky, *Pseudosida australiensis* Korovchinsky in Australian coastal acid dune lakes, *D. senegal* Gauthier, *D. celebensis* Stingelin). Some Australian endemics occur exclusively in acid lakes (Smirnov & Timms, 1983, 1984), others only in granite pools (*Plurispina*) or in saline waters (*Celsinotum*, *Daphniopsis*). *Acantholeberis curvirostris* (O. F. Müller), *Alona rustica* Scott and some other anomopods are also specific to acid waters (Fryer, 1980). Species of *Daphniopsis* and *Daphnia* may be endemics of ephemeral spring pools, temporary waters of arid regions and high-altitude lakes (Hann, 1986; Schwartz & Hebert, 1987).

Species differ with respect to relict status: most of them probably have a considerable age and may be considered relicts, whereas others, common and widely distributed within their extensive primary ranges, possibly are not [e.g. *Sida crystallina*, *Diaphanosoma brachyurum s.s.*, *D. mongolianum*, *D. excisum*, *D. sarsi* Richard, *D. dubium*, *D. birgei* Kořinek, *D. spinulosum* Herbst, *D. fluviatile* Hansen, *D. breviceps* Sars, *Holopedium gibberum s.s.*, *Simocephalus vetulus* (O. F. Müller), *S. exspinosus*, *S. serrulatus*, *Scapholeberis mucronata* (O. F. Müller)]. This non-relict status is certainly also true of some northern *Daphnia* (*D. longispina*, *D. pulex* Leydig, *D. obtusa* Kurz, *D. retrocurva* Forbes species groups) and *Bosmina* (Lieder, 1983; Colbourne *et al.*, 1997, 1998; Dufresne & Hebert, 1997; Little *et al.*, 1997; Haney & Taylor, 2003).

The distribution of Cladocera has been explained in terms of vicariant biogeography (e.g. Bayly & Morton, 1978; Hebert, 1978; Lieder, 1982, 1983; Smirnov & Timms, 1983; Korovchinsky, 1986; Benzie, 1987; Fernando *et al.*, 1987; Bayly, 1993, 1995; Dumont & Negrea, 2002) with the origin of different groups treated as 'Gondwanian', 'Laurasian' or connected with particular parts of these supercontinents. Here, this idea is challenged (see also Hartmann, 1982; Briggs, 1987, 1995). Plate tectonics played only a secondary role, possibly in the diversification of taxa of species level. But extinction and the unique evolutionary histories of regional cladoceran faunas were of primary significance.

Suggestions regarding the relict nature of cladoceran species and populations (Dumont, 1980; Dumont & Verheye, 1984; Hann, 1986; Schwartz & Hebert, 1987; Benzie, 1988; Benzie & Bayly, 1996) or bipolar patterns of distribution (Smirnov & Timms, 1983, 1984) have been made, yet were mostly connected with the periods of glaciation and aridity in the Pleistocene. Certainly, these events affected distribution, but they



only followed great previous perturbations. Berg (1962) explained bipolarity as resulting from the glacial period, but assumed that in supraspecies taxa this phenomenon may be of older origin. Cladoceran bipolarity precisely concerns the latter taxonomic level (see above). Even for the species that are involved, their age is frequently pre-Pleistocene, as shown by DNA studies on *Daphnia* and *Holopedium* (Colbourne & Hebert, 1996; Taylor *et al.*, 1996, 1998; Hebert, 1998; Rowe, 2000).

High vagility may also account for bipolarity. However, the idea of successful long-distance dispersal has come under fire. Cladoceran resting stages may be well dispersed by different agents (e.g. Maguire, 1963; Proctor, 1964, 1967; Vilček, 1978; Jarnagin, Swan & Kerfoot, 2000), but that does not mean that colonization of particular habitats will be successful (Frey, 1972; Frey, 1986; Hebert & Finston, 1993; Hebert & Wilson, 1994; Jenkins & Underwood, 1998; De Meester *et al.*, 2002). Ecological barriers may often be more effective than physical barriers (Dumont, 1980; Eskov, 1984; Frey, 1986). Evidence of isolation is also provided by those species with extremely restricted distributions.

True Holarctic species in the southern hemisphere have not been substantiated well enough. Frey (1982a) suggested species rank for the isolated South American and South African populations of *Eurycercus*. South African representatives of '*Daphnia magna*' and '*Alona affinis*' differ from palearctic forms (A. A. Kotov & A. Y. Sinev, pers. comm.). Upon close examination, more and more populations of 'widely distributed species' appeared to be new, sometimes sibling species, for instance *Eurycercus longirostris* Hann and *E. vernalis* Hann (Hann, 1982), *Daphnia villosa* Kořinek et Hebert and *D. latispina* Kořinek et Hebert (Kořinek & Hebert, 1996). The Australian '*Moina mongolica*' (Smirnov & Timms, 1983, 1984) proved to be a true endemic, *M. baylyi* Forró (Forró, 1985), as were species of *Alona* and *Pleuroxus* on subantarctic islands (Frey, 1988, 1993).

#### REGIONAL FAUNAS

The Holarctic cladoceran fauna is rich and has representatives of all four orders, with the Haplopoda and Onychopoda endemic, four endemic families, and 21 endemic genera (including those of the Caspian Sea and Lake Baikal) (Table 1). Many taxa are primitive and phylogenetically divergent, monotypic or composed of few species. All these features stress the stochastic nature of the faunas, formed of representatives that survived. The great landmasses of the northern hemisphere has an effect on the evolutionary processes (Darlington, 1957; Anderson, 1994; Briggs, 1995). Their environmental diversity, and compara-

tively low predation pressure, also account for the preservation of the taxonomic diversity of the regional cladocerans.

It is significant that the northern cladoceran fauna includes archaic representatives (*Limnosida*, *Dumontia*, *Ophryoxus*, *Acantholeberis*, *Eurycercus*). At southern latitudes (< 50–55°N) these are absent or rare. This is in agreement with the predicted presence of primitive organisms in the Subarctic–Arctic, which is the 'periphery of the adaptive zone' for many taxa (Chernov, 1984, 1988).

Southern temperate and subtropical regions of the northern hemisphere (except Eastern Asia and Eastern North America) are mostly arid or mountainous. Semi-permanent, saline and turbid water bodies predominate. This determinates the specificity of the regional endemic cladoceran faunas, dominated by *Daphnia* (*Ctenodaphnia*), *Moina* and chydorids, many of which are restricted in distribution (Alonso, 1991; Hebert & Finston, 1993, 1996; Kořinek & Hebert, 1996). Probably the composition of this fauna was influenced by recent increased aridity and orogenesis (Dumont, 1978; Eskov, 1984; De Dekker, 1986; Krupp & Schneider, 1988).

In the southern hemisphere, cold-resistant cladocerans are represented by a few anomopods restricted to the southern end of South America, subantarctic islands and the Antarctic continent (Harding, 1941; Thomasson, 1955; Akatova, 1964; Frey, 1988, 1991, 1993; Paggi, 1998). Frey (1993) discussed the enigmatic source of the initial dispersal of specific subantarctic *Pleuroxus*, not related to their congeners from the neighbouring continents.

The Antarctic continent, fully glaciated in the Pliocene, has been a route of biotic dispersal and a stepping-stone between the southern continents (Eskov, 1984). Kerguelen Island and the young mountain areas of New Zealand were populated from the Antarctic continent. In Pleistocene/post-Pleistocene times these regions, along with the southern part of South America, were subjected to intense glaciations (Frey, 1988, 1993). Thus, Cladocera of the Antarctic continent and subantarctic islands represent remains of a fauna that earlier populated the Antarctic, subantarctic islands, New Zealand, Tasmania and the southern ends of the southern continents. A few species (*Daphniopsis studeri* Rühle, *Macrothrix* sp.) survived on the eastern and western edges of the Antarctic continent closest to Kerguelen, the Marion Islands and South America where they also occur.

Of the southern continents, Australia has the richest endemism at family, genus and species levels, concentrated in the south-east and south-west. All endemics are either monotypic or contain few species, which implies relict status. West Australia has its own set of endemic genera (*Plurispina*, *Planicirculus*) and

species (14), reflecting a long separation from eastern Australia in the Cretaceous (Benzie, 1987).

The Australian continent was affected by increased aridity and salinity since the Neogene (De Dekker, 1986; Bayly, 1993; Hebert & Wilson, 1994). This is probably the reason for the concentration of relicts in restricted localities (e.g. coastal acid lakes) and adaptations to saline waters (Williams, 1985; Sergeev, 1990; Hebert & Wilson, 2000). This also applies to South Africa and southern South America.

The faunal scenario of New Zealand is different. These islands have an impoverished fauna (45 known species, seven endemics) (Chapman & Lewis, 1976; Frey, 1991) but this poverty seems real because of the Pleistocene glaciations destroyed the thermophilic part of the biota (Eskov, 1984).

Discussion of the comparative species richness of tropical and temperate Cladocera is not lacking (Fernando, 1980a, b; Dussart *et al.*, 1984; Fernando *et al.*, 1987; Fernando, Tudorancea & Mengestou, 1990; Shiel & Williams, 1990; Dumont, 1994a; Fernando & Paggi, 1998; Dumont & Negrea, 2002) but it ignores the definition of the true tropics, which is usually confused with the subtropics. Thus, the species of each climatic zone have not been counted precisely: in particular, their number in non-tropical regions of the southern hemisphere has been underestimated.

Truly tropical taxa (*Sarsilatona*, *Grimaldina*, *Guernella*, *Moinodaphnia*, *Dadaya*, *Notoalona*, *Euryalona*, *Leydigiopsis*, *Nicsmirnovius*) are mostly of generic rank, possibly supplemented by one tribe, the Indiaronini. These taxa are phylogenetically divergent and monotypic or include few species, which implies relict status. Other genera are either largely tropical (*Latonopsis*, *Pseudosida*, *Dunhevedia*, *Bryospilus*, *Karualona*, *Kurzia*, *Leydigia*, *Bosminopsis*) or well represented in the tropics (*Diaphanosoma*, *Macrothrix*, *Chydorus*, *Alona*, *Ephemeroporus*). In general, the bulk of tropical species belong to widely distributed genera (21). Tropical species richness is currently estimated as 163, less than that of non-tropical zones of both hemispheres (Table 3) and of warm temperate – subtropical zones in particular. The northern non-tropical zone is highest in endemism and has a small fraction of widely distributed genera (12–15) (Table 3).

Many tropical species are known from one or a few localities: most are rare (Dumont, 1994a). Limnetic palaeotropical zooplankton (the situation in the neotropics is less clear) is dominated by a limited assemblage of species (*Diaphanosoma excisum*, *Ceriodaphnia cornuta s.l.*, *Moina micrura*) and sometimes *Diaphanosoma sarsi*, *Daphnia lumholtzi* and *Bosminopsis deitersi* (Fernando, 1980a, b; Timms & Morton, 1988). It contrasts with a more diverse northern limnetic zooplankton.

The causes of this limnetic impoverishment, especially the low number of *Daphnia*, have been much debated. Ecological variables include temperature and its direct and indirect effects, composition of the algal flora (Fernando, 1980a, b; Fernando *et al.*, 1987), relentless predation by fish and other predators, and the absence of a photoperiodic signal for sexual reproduction (Kerfoot & Lynch, 1987; Dumont, 1994a; Dumont & Negrea, 2002). But, additionally, events in the Tertiary caused a collapse at tropical and boreal latitudes, while warm temperate – subtropical regions remained comparatively unchanged. In tropical and boreal zones, respectively, *Daphnia* went extinct or underwent a recent burst of speciation (*D. longispina*, *D. pulex*, etc., phylogenetically young species groups).

#### OTHER INVERTEBRATES

Other inland water crustaceans show traits similar to the Cladocera. Thus, *Artemia*, *Branchinella*, *Streptocephalus* and other large branchiopods reach their highest species richness in the southern temperate – subtropical climates (Longhurst, 1955; Williams, 1968; Browne & MacDonald, 1982; Geddes, 1983; Martin & Belk, 1988; Brtek & Thiéry, 1995; Maeda-Martinez *et al.*, 1995; Brendonck & Riddoch, 1997; Triantaphyllidis, Abatzopoulos & Sorgeloos, 1998; Brendonck & Hamer, 1999). The same is true of ostracods (e.g. De Dekker, 1977, 1983). The genus *Boeckella* (Copepoda, Calanoida) provides a good example of bipolar distribution: restriction to the southern hemisphere but with one species in Mongolia (Bayly, 1992, 1995; Hebert & Wilson, 1994). Bipolarity is also characteristic of the Bathynellacea, while the Anaspidacea occur only in the south of the southern continents (Bănărescu, 1990). By contrast, the tropics host few of the above listed crustaceans, while *Cyclestheria*, some ostracods and diaptomids abound there (Timms, 1986; Little & Hebert, 1994; Boxshall & Jaume, 2000).

Additional examples of global distribution of Gymnolaemata (Bryozoa) (Abrikosov, 1959), molluscs (Starobogatov, 1970) and freshwater medusae (Dumont, 1994b) suggest that the proposed patterns may be applicable to other invertebrates of inland waters.

#### CONCLUSION

The Cladocera are at the same time one of the most successful groups in inland waters and a relict group, only a small part of which survives. They are 'living fossils' because probably many extant genera were alive in the Early Mesozoic or possibly earlier. According to the 'theory of ejected relicts' cladoceran faunas of present tropical and boreal regions suffered much extinction.

Many recent taxa, especially of supraspecies rank, have a relict status. Their taxonomic richness and ranges have decreased. Others (some *Daphnia*, *Bosmina*) appear to be evolutionarily young, and are still speciating. They are especially widely distributed in the northern hemisphere, but relict taxa may also be common and numerous here.

Thus, the Cladocera should be considered not only in terms of evolutionary progress and speciation but in terms of evolutionary stasis and extinctions. Only a few of them are involved in recent evolutionary development, but these are very active exponents of the process.

The occurrence of Cladocera in 'marginal' habitats (temporary, saline, acidic, cave, mountainous and groundwaters, ancient lakes and terrestrial habitats) is not a consequence of their recent diversification and dispersal but of relict status and specialization. Most representatives survived in refugia, to which they become adapted and where limited speciation occurred.

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