

The biogeography of littoral *Lecane* Rotifera

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Abstract

Little is known on the biogeography of Rotifera, particularly regarding the littoral taxa. Here, the biogeography of the most specious group of littoral Rotifera, *Lecane*, is discussed based on a recent revision of the group, and considering only verified records.

Only 41.3% of all 167 *Lecane* morphospecies are widely distributed. Of these, 21 (12.6%) are cosmopolitan (*sensu strictu*), 26 (15.6%) are Tropicopolitan. There are 6 (3.6%) Arctic-temperate and Pantropical taxa. These categories of widely distributed taxa are not clear-cut, as differences in latitudinal distribution are largely gradual. Ten taxa have odd distributions. Most of these are insufficiently known and some may be recent introductions.

All the major zoogeographical regions have their share of endemic taxa, with endemism rates varying from 6.5% to 21.8%. Thirteen Holarctic, one widespread Eastern hemisphere, eleven Palaearctic, six Palaeotropical, one Australasian and five widespread Western hemisphere taxa have circumscribed ranges encompassing more than one region. The Palaeotropical and Holarctic components are particularly noteworthy, and may result from relatively recent faunal exchange between the Palaearctic and Nearctic, and between the African, Oriental and Australian regions. The different orientation of the major mountain chains of the Eastern and Western hemisphere, and the presence of extensive arid regions in Northern Africa, Arabia and Asia may explain the difference in faunal similarity between the tropical and temperate faunas of the Eastern and Western hemispheres. Ornithochoric dispersal and human introductions may have played a role in the exchange of faunas.

The analysis of pairs or groups of closely related taxa only rarely reveals a causal relation between tectonical events and phylogeny. Most vicariant distributions are readily explained by climatological rather than by tectonical considerations. The ranges of some closely related taxa indicate that they have different capacities of dispersal.

When compared to pelagic Rotifera, littoral *Lecane* exhibit a relatively wide variety of distribution patterns, and relatively many have restricted distributions. This may be a consequence of, either or both, their lower abundance, or be related to the littoral habitat which, being less predictable, implies more specific adaptations. *Lecane* is tropic-centred, which may be a consequence of avoidance of competition and/or predation by 'Cladocera' and, eventually, Ostracoda.

The most striking feature in rotifer chorology is the large range of many morphospecies. As such, the group's biogeography is more similar to that of freshwater algae than to that of other freshwater zooplankton. The likely explanations for this are the group's great ability for passive dispersal, combined with a short life-cycle and high fecundity, which are consequences of their parthenogenetic reproduction. So, relatively recent long-distance dispersal defines the ranges of the morphospecies. Vicariance plays a role in the distribution of Rotifera, but its importance is generally subordinate to that of dispersal. However, insufficient taxonomic resolution may be responsible for the apparently large ranges of some morphospecies.

Introduction

Zoogeography of Rotifera is a field that has remained underdeveloped. At the initial stage of descriptive

work on Rotifera, it became apparent that many morphospecies occurred in collections of diverse origins. From this emerged the idea that 'the Rotifera enjoy a cosmopolitan distribution which is not limited to

continents' (Rousselet, 1909; see also de Beauchamp, 1907; von Hofsten, 1909). Any species was expected to be found wherever the conditions necessary for its existence occurred, leading to the conclusion that *all* Rotifera are potential cosmopolites (Jennings, 1900; Haring & Myers, 1928; Pourriot, 1980; Ruttner-Kolisko *in* Dumont, 1980a). Examples of cosmopolitan Rotifera are, indeed, common (e.g., see Green, 1972).

However, many cases of taxa with restricted distributions are documented. Ahlstrom (1940, 1943) mentioned species with local distributions in his revisions of the genera *Brachionus* and *Keratella*. Green (1972) recognised four major distributional groups of planktonic Rotifera, viz. Cosmopolitan, Cosmotropical, Arctic-temperate and American. As in the Cladocera, another group consisting of cyclic parthenogens, the suspicion arose that the apparent cosmopolitanism was due more to inadequate knowledge rather than to reality (Pejler, 1977a; Dumont, 1980a; 1983; Frey, 1986; 1987; Koste & Shiel, 1989; Nogrady *et al.*, 1993).

Studies dealing with the distribution of selected rotifer taxa (e.g., Kutikova, 1970; Pejler, 1977b; De Ridder, 1981a, b; Dumont, 1983), or with rotifer distribution globally (Green, 1972), or regionally (e.g., Shiel, 1981; Shiel & Koste, 1986; Chengalath & Koste, 1987; 1989) have recently become available. Apart from De Ridder (1981a, b), who demonstrated complex distribution patterns in some littoral taxa, the above-cited authors deal mainly with planktonic Rotifera. The more diverse littoral and benthic groups are generally neglected, or even eliminated from analysis (e.g., Green, 1972; 1994). Only general statements exist, claiming that some littoral/benthic rotifers are endemic and most cosmopolitan (Dumont, 1983). Information on bdelloid Rotifera is even more scarce (Ricci, 1987). This is mostly because our knowledge of their taxonomy is of an even lesser standard than that of planktonic taxa (Dumont, 1983; Segers *et al.*, 1991, 1992, 1994). A fuzzy taxonomy and the questionable nature of published records are major constraints on zoogeographical analysis (Pejler, 1977a, b; Koste & Shiel, 1989; Segers & Dumont, 1993a; Segers & De Meester, 1994).

The purpose of this work is to contribute to chorology of littoral Rotifera, by studying the distribution of taxa in the specious genus *Lecane*. The analysis is largely based on a taxonomic revision of the genus (Segers, 1995a), and considers only verified records. In a first part, the need for such a rigorous approach

is illustrated, and coverage evaluated. The diversity of extant distribution patterns in this group of Rotifera is illustrated. A preliminary comparison is made between the relations in some groups of sister taxa, with the ranges of these taxa. Distribution patterns in *Lecane* are compared with those in other Rotifera, and, finally, with those in some other groups of freshwater organisms.

Material and methods

The zoogeographical analysis of *Lecane* is based on the taxonomic treatment of the genus as in Segers (1995a), supplemented by the additions in Segers (1994b), Segers *et al.* (1994b) and Segers & Dumont (1995). As a result, a total of 167 morphospecies is considered here.

Only verified records are taken into account. The majority of these concern published records, either identified or verified by myself, or verified by examining the original drawings accompanying the record. Some of the records by C. R. Russell could be verified by examining figures in his original notebooks, copies of which were provided by Dr R. J. Shiel. A number of unpublished records are also included in the analysis. The records considered are listed in Segers (1995d). At the scale of the resulting distribution maps, one symbol may represent several individual records.

To evaluate latitudinal variation, map records were grouped according to their latitude, with intervals of 10 ° starting from the equator to the poles. The *Lecane* fauna of the six major zoogeographical regions, as recognised by Cox & Moore (1993), was compared by a cluster analysis following the Average linkage method (see Wilkinson, 1990), and based on the Sørensen similarity index (Sørensen, 1948) between the regions. The analysis of phylogenetic relations between sister taxa follows cladistic principles (see Forey *et al.*, 1992).

Comments on methodology

Only verified records are included in the present analysis. The obvious disadvantage of this approach is that the majority of existing records is discarded, and, hence, a lot of information is not used. The following examples illustrate the need for such a critical approach.

Both *L. depressa* and *L. galeata* are listed here as Holarctic taxa, although Koste (1978) described both as cosmopolitan (*L. depressa* as *L. brachydactyla* (Stenroos), *L. levistyla* f. *depressa* and *L. tudicola* Harring & Myers). Admittedly, *L. depressa* has been recorded from Africa and the Australian region. The relevant drawing of the African record (Madagascar: Bērziņš, 1982b) shows an animal with a lorica like that of *L. mitis*, but with toes bearing pseudoclaws. Neither the lorica nor the toe shape conform to the description of *L. depressa*, suggesting that this record is a misidentification. Moreover, I do not know of any named *Lecane* that has the particular set of characters described, so the record may concern a new species. The Australian records are not illustrated. One of them (Chatham Islands: Russell, 1953; sub. *L. tudicola*) seems to be a misidentified *L. herzigii*, judging from a sketch in Russell's notebook (confirmed by R. Shiel, *in litt.*). Two more Australian records (Queensland, Victoria: Shiel & Koste, 1979; as *L. brachydactyla* and *L. tudicola*, respectively) concern unconfirmed records (R. Shiel, *in litt.*). Similarly, illustrated records of *L. galeata* from Africa and India are now thought to be misidentifications (Thomasson (1960) (sub. *L. pygmaea* (Daday), Zambia): *L. obtusa*: anterior margins are coincident and slightly convex; Bērziņš (1982b) (Madagascar): *L. arcuata*, see Segers, 1992; Wulfert (1966) (India): not *L. galeata*: dorsal plate anteriorly narrower than ventral plate, probably an incompletely contracted and compressed *L. lunaris*). Virtually all illustrated Western hemisphere records of *L. decipiens* are misidentified *L. hamata* (see Segers, 1995a).

Clearly, misidentifications are common in *Lecane*, which is not surprising considering that Nogrady *et al.* (1993) regard *Lecane* 'notoriously difficult'. Most illustrated records are included in taxonomic papers, or reports on faunistic peculiarities. It is unlikely that misidentifications would be more common in these papers than in contributions of ecological interest, or in routine faunal inventories.

The rigorous approach raises the need to consider the extent of coverage. The distribution map of *L. closteroerca* (Map 1), probably the commonest *Lecane*, illustrates to what extent the different zoogeographical regions are covered. Although records from most continents are available, large gaps are evident. These are the Australian continent, the Asian part of the Palearctic region, the North-East of North America and many regions of Africa. This may seem surprising as far as Australia is concerned, as considerable work has recently been done there by W. Koste, R. J. Shiel

and collaborators (e.g., Koste, 1979; Koste & Shiel, 1980; 1990; Koste *et al.*, 1983; 1988; Shiel & Koste, 1985). However, as these papers do not contain original illustrations of the taxa reported, they could not be considered. Other regions have been only superficially explored for littoral rotifers. This is illustrated by several undescribed taxa, especially from the regions mentioned above (e.g., Australia: Figure 12.1 in Koste & Shiel, 1990; Bolivia: Segers *et al.*, 1994; Nigeria: Segers *et al.*, 1993; Norway (Bjørnøya): *Lecane* sp., De Smet, 1988; Thailand: Segers & Sanoamuang, 1994). Map 1 also indicates that records from regions such as Europe, India, the North East of the USA, the Amazon Basin in South America as well as from some localities in Africa (e.g., river Niger floodplain) and Asia (North-East Thailand) are abundant. These regions may therefore be considered adequately studied, to the extent that the absence of records of a taxon here becomes meaningful. Moreover, there is no doubt that authors more readily illustrate rare than common taxa. The map of *L. closteroerca* may therefore even represent an underestimation of coverage.

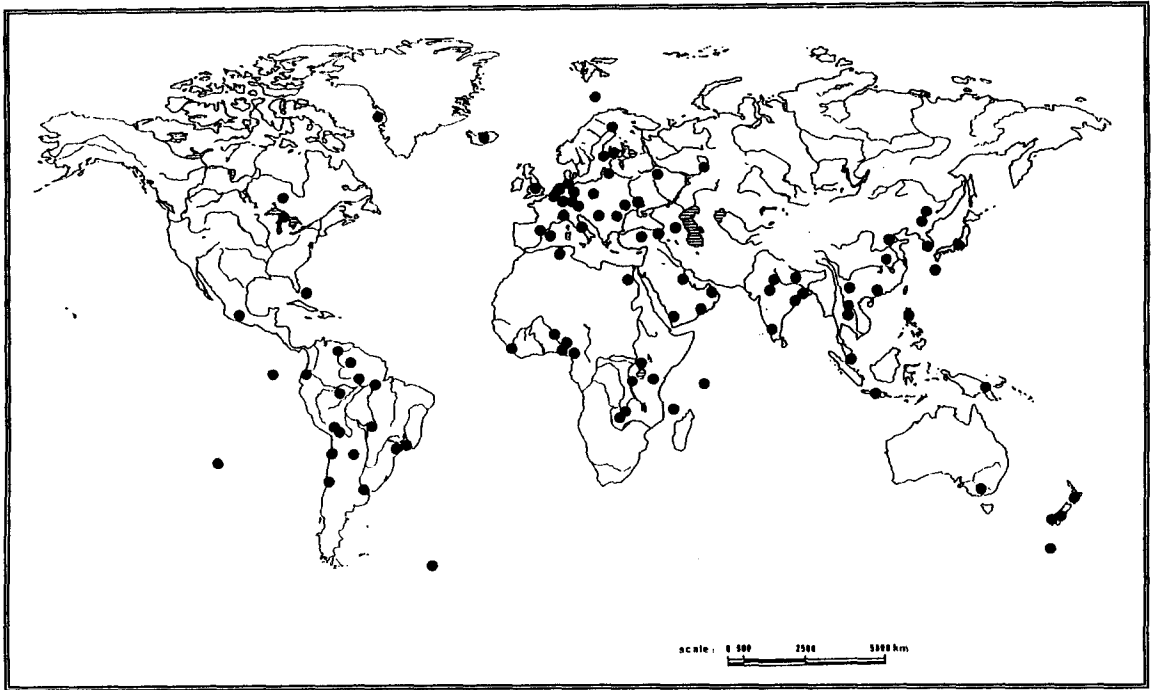
Although the dearth of records from a number of regions hampers detailed zoogeographical analysis, the coverage is such that it allows some generalisations to be formulated on the distribution of taxa. On the other hand, it is probably premature to analyze the fauna of transition zones between zoogeographical regions, or to attempt characterisation of subregions.

Distribution patterns in *Lecane*

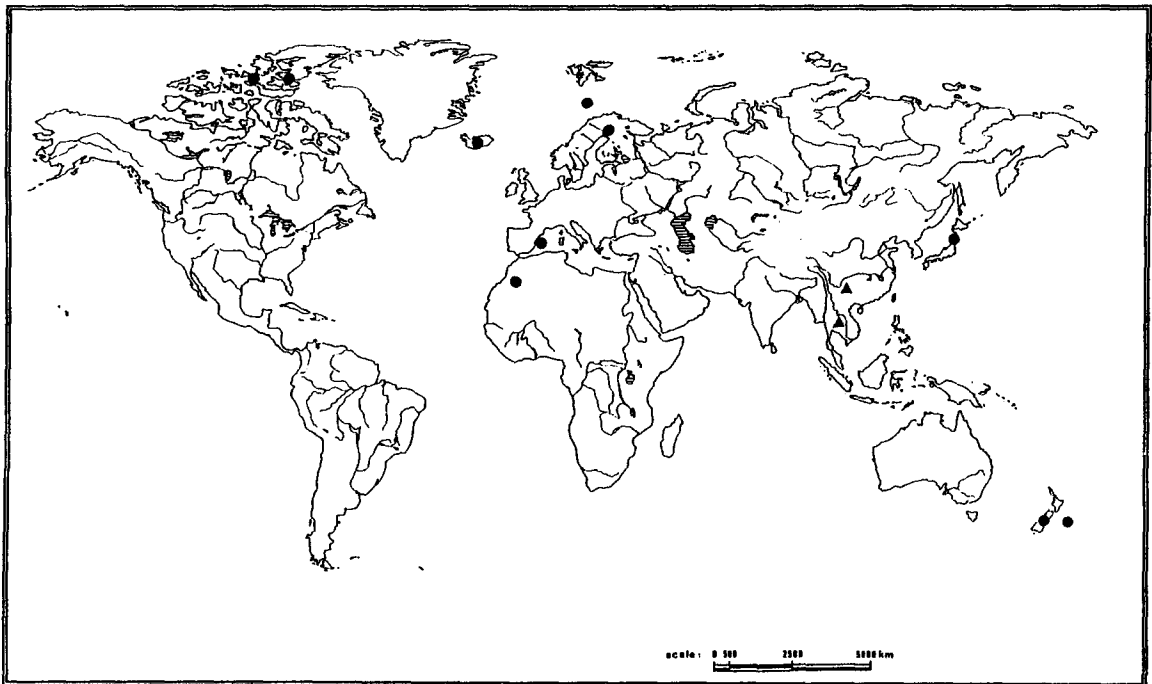
Widely distributed taxa

Considering that cosmopolitanism was inferred for all rotifers, it no surprise that many taxa have ranges spanning most, or large parts of the earth. A total of 69 taxa, or 41.3% of all *Lecane*, occur in both the Eastern and Western hemisphere, without being restricted to the Holarctic region (Figure 1). Here, four distinct groups are defined as follows (Table 1):

- **Cosmopolitan taxa** (*sensu strictu*): occur both in the Eastern and Western hemisphere, and under tropical as well as temperate climatic conditions;
- **Arctic-temperate taxa**: occur in regions with arctic or temperate climatic conditions, not necessarily restricted by latitude;
- **Tropicopolitans**: occur in tropical and subtropical latitudes, but can occasionally be found in suitable habitats in temperate regions;



Map 1. Distribution map of *L. closterocerca* (Schmarda)



Map 2. Distribution map of *L. latissima* Yamamoto (●) and *L. thailandensis* Segers & Sanoamuang (▲)

Table 1. Widely distributed taxa

Cosmopolitan taxa (sensu strictu)	
<i>L. agilis</i> (Bryce, 1892)	<i>L. ludwigii</i> (Eckstein, 1883)
<i>L. arcuata</i> (Bryce, 1891)	<i>L. luna</i> (O.F. Müller, 1776)
<i>L. aspasia</i> Myers, 1917	<i>L. lunaris</i> (Ehrenberg, 1832)
<i>L. bifurca</i> (Bryce, 1892)	<i>L. nana</i> (Murray, 1913)
<i>L. bulla</i> (Gosse, 1851)	<i>L. pyriformis</i> (Daday, 1905)
<i>L. clara</i> (Bryce, 1892)	<i>L. quadridentata</i> (Ehrenberg, 1832)
<i>L. closteroerca</i> (Schmarda, 1859)	<i>L. stenroosi</i> (Meissner, 1908)
<i>L. flexilis</i> (Gosse, 1886)	<i>L. stichaea</i> Harring, 1913
<i>L. furcata</i> (Murray, 1913)	<i>L. tenuiseta</i> Harring, 1914
<i>L. hamata</i> (Stokes, 1896)	<i>L. unguata</i> (Gosse, 1887)
<i>L. inermis</i> (Bryce, 1892)	
Arctic-temperate taxa	
<i>L. latissima</i> Yamamoto, 1955	<i>L. rhopalura</i> (Harring & Myers, 1926)
<i>L. ligona</i> (Dunlop, 1901)	<i>L. scutata</i> (Harring & Myers, 1926)
<i>L. perpusilla</i> (Hauer, 1929)	<i>L. subulata</i> (Harring & Myers, 1926)
Tropicopolitan taxa	
<i>L. aculeata</i> (Jakubski, 1912)	<i>L. monostyla</i> (Daday, 1897)
<i>L. aeganea</i> Harring, 1914	<i>L. myersi</i> Segers, 1993
<i>L. arcula</i> Harring, 1914	<i>L. obtusa</i> (Murray, 1913)
<i>L. crepida</i> Harring, 1914	<i>L. papuana</i> (Murray, 1913)
<i>L. curvicornis</i> (Murray, 1913)	<i>L. pertica</i> Harring & Myers, 1926
<i>L. donneri</i> Chengalath & Mulamootil, 1974	<i>L. punctata</i> (Murray, 1913)
<i>L. doryssa</i> Harring, 1914	<i>L. pusilla</i> Harring, 1914
<i>L. grandis</i> (Murray, 1913)	<i>L. rhenana</i> Hauer, 1929
<i>L. haliclysta</i> Harring & Myers, 1926	<i>L. rhytida</i> Harring & Myers, 1926
<i>L. hastata</i> (Murray, 1913)	<i>L. signifera</i> (Jennings, 1896)
<i>L. hornemanni</i> (Ehrenberg, 1834)	<i>L. subtilis</i> Harring & Myers, 1926
<i>L. inopinata</i> Harring & Myers, 1926	<i>L. thalera</i> (Harring & Myers, 1926)
<i>L. leontina</i> (Turner, 1892)	<i>L. undulata</i> Hauer, 1938
Pantropical taxa	
<i>L. decipiens</i> (Murray, 1913)	<i>L. sola</i> Hauer, 1936
<i>L. elegans</i> Harring, 1914	<i>L. syngenes</i> (Hauer, 1938)
<i>L. ruttneri</i> Hauer, 1938	<i>L. thienemanni</i> (Hauer, 1938)
odd cases	
<i>L. climacois</i> Harring & Myers, 1926	<i>L. lamellata</i> (Daday, 1893)
<i>L. copeis</i> (Harring & Myers, 1926)	<i>L. nelsoni</i> Segers, 1994
<i>L. cornuta</i> (Müller, 1786)	<i>L. tabida</i> Harring & Myers, 1926
<i>L. dumonti</i> Segers, 1993	<i>L. uenoi</i> Yamamoto, 1951
<i>L. elsa</i> Hauer, 1931	<i>L. venusta</i> Harring & Myers, 1926

– **Pantropical** taxa: chiefly restricted to the tropical belt, as delimited by the tropics of Cancer and Capricorn.

Only 21 cosmopolitan *Lecane* could be identified, which is 12.6% of the total number of recognised mor-

phospecies. An example is *L. closteroerca* (Map 1). The largest proportion of wide-spread *Lecanes*, 26 taxa or 15.6%, are Tropicopolitans (e.g., *L. leontina* (Map 7); see Figure 2, De Ridder, 1981a). There are only few Pantropical taxa (6 or 3.6%; *L. ruttneri*:

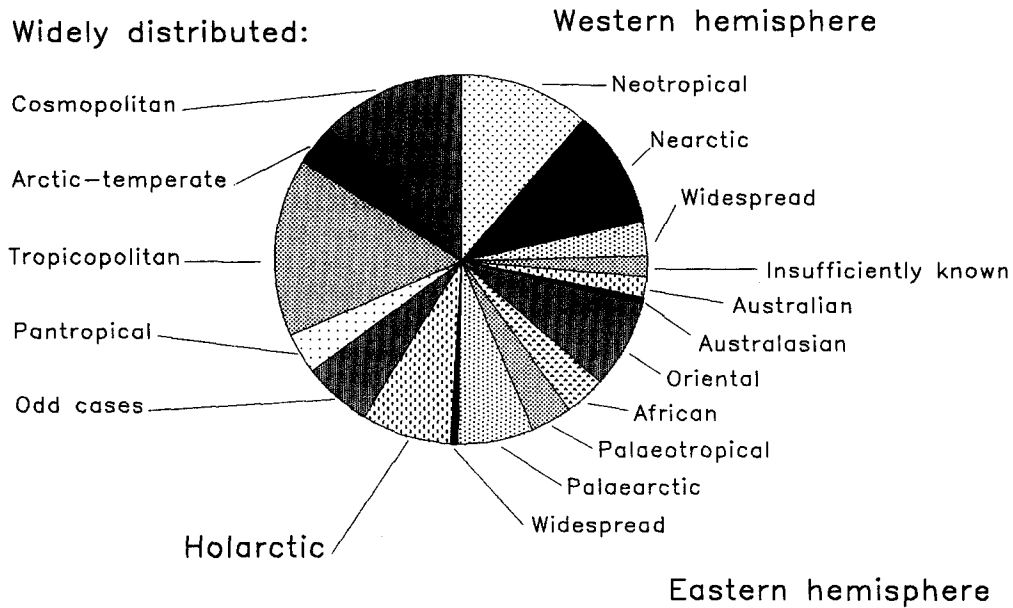


Figure 1. Proportional occurrence of distribution patterns in *Lecane*.

Figure 2). Six Arctic-temperate taxa could be identified. Their records are mainly from temperate regions, but they also occur on high altitudes at (sub)tropical latitudes, and/or they have an antitropical distribution, i.e. occurring in both the Northern and Southern temperate and cold climate zones. Examples of such taxa are *L. latissima* (Map 2), recorded predominantly from high latitudes in both the Northern and Southern hemisphere, and *L. ligona*, whose Venezuelan record concerns a capture at 2425 m a.s.l. (Zoppi de Roa *et al.*, 1990). Similarly, an African record of *L. perpusilla* is from Mount Kilimanjaro (De Smet & Bafort, 1990). The tropical-latitude populations of these Arctic-temperate taxa may represent glacial relicts.

A latitudinal gradient in the distribution of planktonic Rotifera was suggested by Green (1972), and was further documented by Pejler (1977b), De Ridder (1981a), Dumont (1983) and Green (1994). It should be kept in mind that latitude tends to reflect climate, blurred by the effect of altitude (see *L. ligona*, *L. perpusilla*; Pejler, 1977b; Green, 1990, 1994; Segers *et al.*, 1994b). A latitudinal gradient appears to exist in *Lecane* as well. In Figure 2, the relative abundance per latitudinal zone of different taxa is plotted. It can be appreciated that latitude-related differences in occurrence are indeed gradual. Clearly, the distinction of different groups of widely distributed taxa is artificial, but

it is practical, as it is an easy way of providing information on a taxon's distribution. Taxa with a well-defined preference may occur in isolated locations outside the climatic zone with which they are normally associated when environmental conditions are favourable. Examples are the occurrence of *L. papuana* in thermally polluted waters of the River Loire, France (Lair, 1980), and of *L. monostyla* in the Moscow region (Kutikova, 1970; both non-illustrated records). Some occurrences of *L. inermis* at higher latitudes are from habitats with relatively higher temperature than the ambient (e.g., thermal springs: De Ridder, 1981a; Pax & Wulfert, 1941). The best-documented case is probably that of the brachionid *Keratella tropica* Apstein. It is common in tropical regions, but can be found in temperate regions during hot summers (Leentvaar, 1980; De Ridder, 1981a; unpublished record from the River Schelde, Wetteren, Belgium, July 1994). Apart from *L. inermis* and *L. stichaea*, our 'ranking' from cold- to warm-water preference as in Figure 2 conforms to that of Bērziņš & Pejler (1989), for the few taxa that are common to both analyses (*L. flexilis*, *L. closteroerca*, *L. hamata*, *L. luna*, *L. bulla*).

Several taxa cannot be placed satisfactorily. Most concern animals of which only two records from widely separated localities are available. These cases probably indicate lack of knowledge, rather than having any zoogeographical relevance. However, there are some

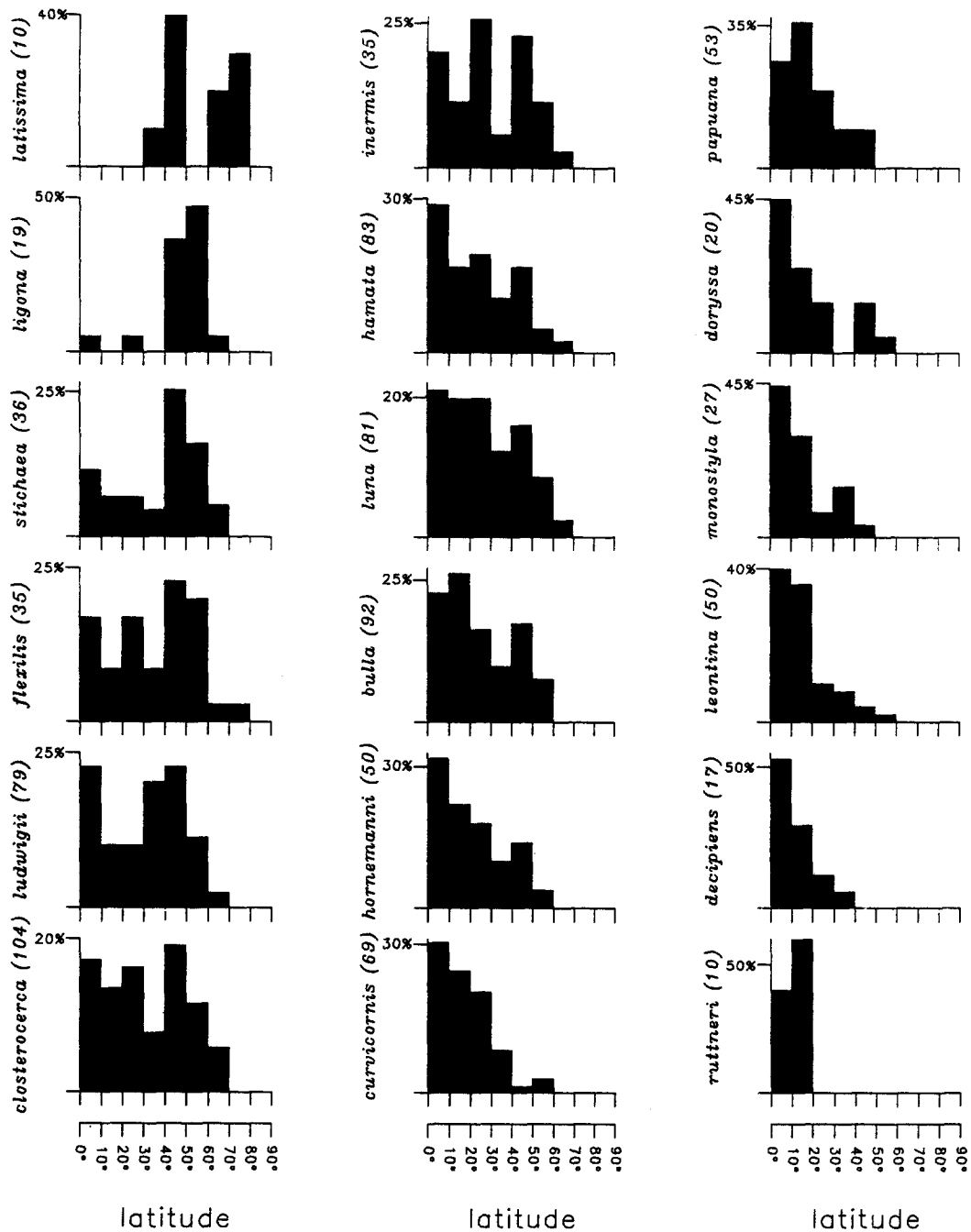
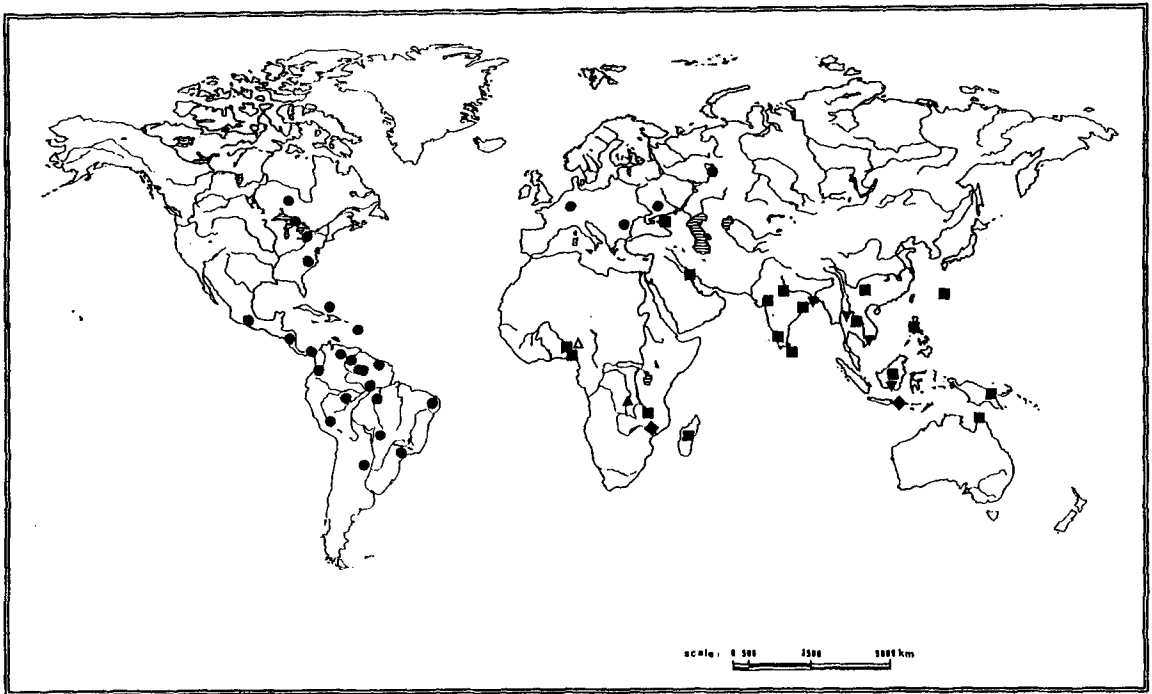


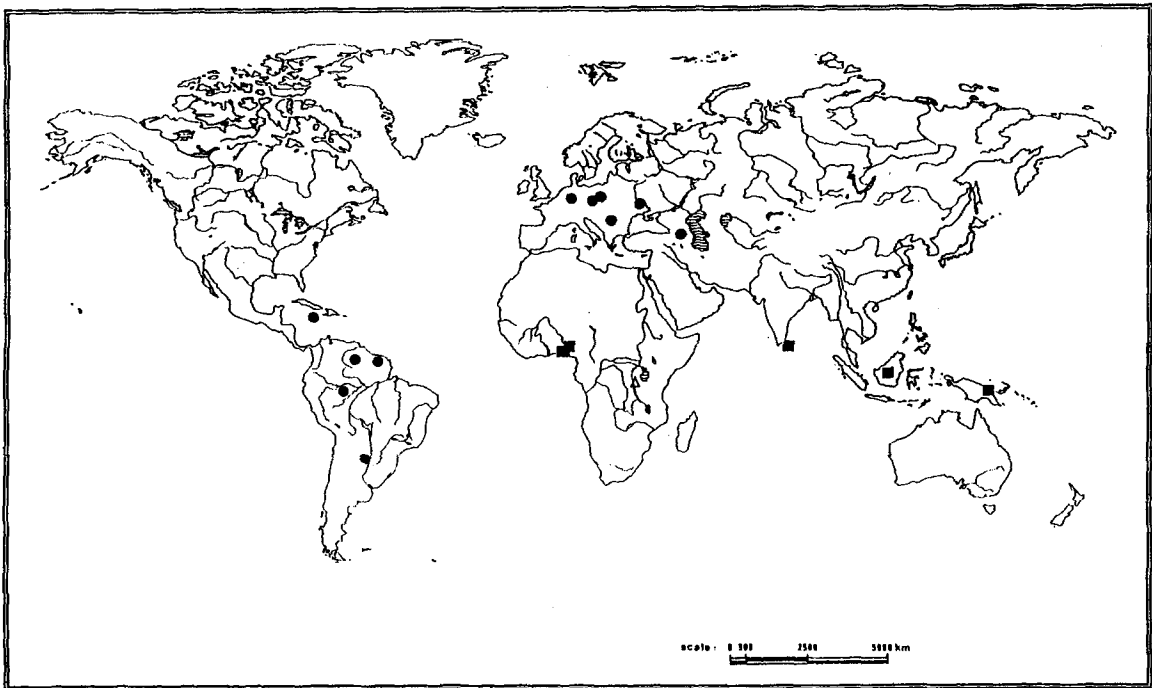
Figure 2. Frequency distribution of some widely distributed *Lecane* taxa relative to latitude. Taxa are ordered according to their distribution from Arctic-temperate to Pantropical, from top to bottom and from left to right. Number of records follows the name of the taxon.

taxa that have peculiar, disjunct distribution patterns. One is *L. cornuta* (Map 3). It is relatively common in the Western hemisphere, but rare in Europe. Only few non-illustrated records from the African, Oriental

and Australian regions exist. The only two illustrated records from these regions (Lake Kariba, Zambia: Thomasson, 1965; Okinawa, Japan: Sudzuki, 1992) both concern *L. unguitata*. *L. cornuta* is also easily



Map 3. Distribution map of *L. cornuta* (Müller)(●), *L. blachei* (Bērziņš)(▼), *L. nwadiaroi* Segers (△), *L. stephensae* (Hutchinson)(◆), *L. symoensi* (De Ridder)(▲), *L. unguitata* (Fadeev)(■)



Map 4. Distribution map of *L. elsa* Hauer (●) and *L. braumi* Koste (■) (△: undescribed Burundian relative)

confused with the cosmopolitan *L. lunaris*. *L. cornuta* and *L. unguitata* are two apparently little related, but superficially similar taxa with regard to size and ecology. Their ranges are remarkably complementary, and non-overlapping. The two may occupy a similar ecological niche in the Western, respectively Eastern hemisphere. *L. copeis* is a similar case, as there are several illustrated records from the Western hemisphere, but only a single illustrated (Romania: Rudescu, 1960), and a few non-illustrated records from the Eastern hemisphere. Another taxon with a disjunct distribution is *L. elsa* (Map 4). It is relatively common in the Neotropics and in Europe, but is absent from North America. *L. elsa* has as close relatives the Palaeotropical *L. braumi* Koste, and one undescribed Burundian taxon (Segers & Baribweguire, in press). Neither in *L. cornuta* nor in *L. copeis* are similar close relatives known.

The rare occurrence of *L. cornuta* and *L. copeis* in the Eastern hemisphere probably results from dispersal from the Western hemisphere to the Palaearctic. This conforms well with the general results on *Lecane* zoogeography, that indicate an important faunal exchange between the regions of the Holarctic (see further). Such a hypothesis is less satisfactory in the case of *L. elsa*: the absence of *L. elsa* from the Nearctic and the existence of close Palaeotropical and African relatives argue against it. The present disjunct distribution of *L. elsa* and relatives may result from the breakup of an ancestral range. In this connection, it would be rewarding to examine the taxonomic relation between the European and South American populations of *L. elsa* more closely. External morphology does not permit a separation of these two. An additional set of characters (trophi morphology) will have to be considered, or different approaches (experimental and/or molecular) applied.

Only the Nicaraguan record of *L. lamellata* falls outside the Holarctic region. As most records of this taxon are from warm-temperate regions of the Holarctic, it can hardly be considered an Arctic-temperate. The Nicaraguan record may represent a recent expansion of the taxon's range.

Another peculiar case of widely distributed taxa is that of *L. decipiens*. It is strikingly more common in the Neotropical region than in the Eastern hemisphere tropics, where a rare sister taxon of unresolved status, *L. serrata*, occurs. There are more cases where taxonomic constraints remain the major hinderance to a sound zoogeographical analysis (e.g., *L. lunaris*).

Holarctic *Lecane*

Of the 116 taxa reported from the Northern temperate region, thirteen (11.2%) are endemic (Table 2). Examples are *L. depressa* and *L. galeata* (Map 5). While comparing the distribution of *L. depressa* with that of its close relative *L. ligona*, it is striking that only two records of *L. ligona* from outside the Holarctic region motivate its appurtenance to the group of Arctic-temperate, rather than to that of Holarctic taxa. This illustrates that some of the latter will probably turn out to belong to the former group, as future studies dealing with cold habitats at tropical latitudes may reveal. Contrarily, *L. lamellata* may be primarily Holarctic (see above).

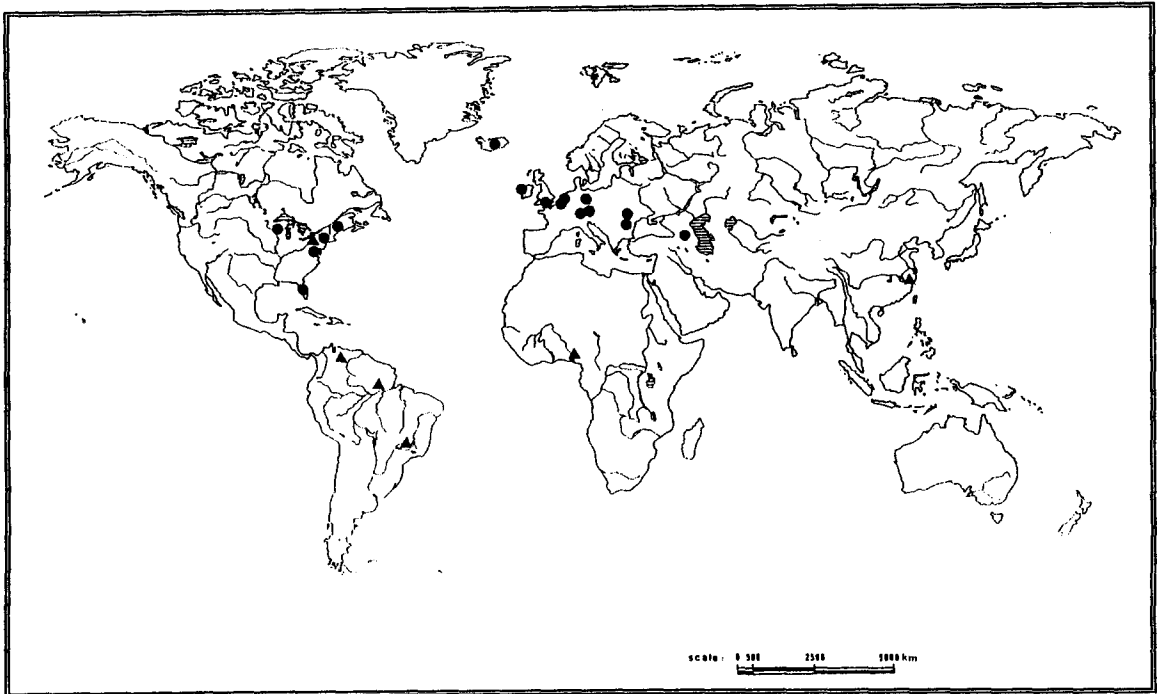
The distribution of *L. satyrus* is remarkable. Of this well-characterised taxon, a single record from Japan (Yamamoto, 1960) is available, whereas records from the East of North America are relatively frequent. Apart of the Japanese record, its range is strikingly similar to that of the Nearctic *L. mucronata* (Map 6). The taxon may be originally Nearctic, and may have extended its range recently to Japan either naturally across the Bering Strait, or by accidental introduction.

Eastern hemisphere taxa

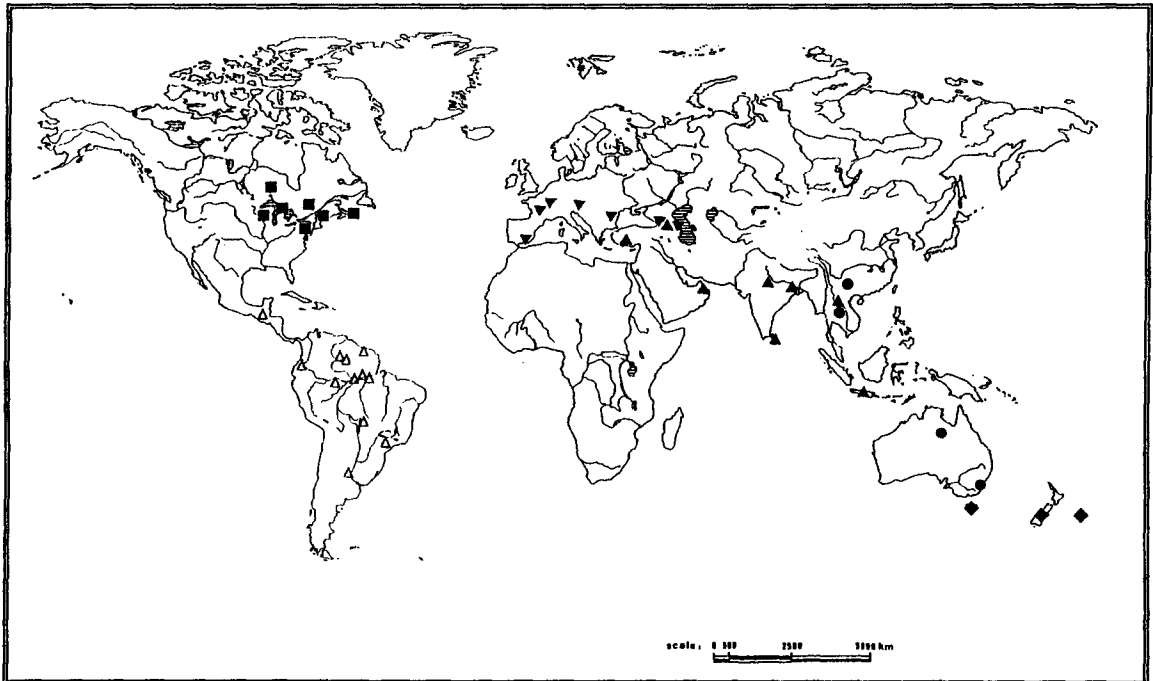
Forty-four *Lecane* (34.9% of the 126 taxa reported) are restricted to the Eastern hemisphere (Table 3). A single taxon, *L. pumila*, has been recorded from diverse regions of the Eastern hemisphere (France, Germany, Indonesia, Tanzania, Tasmania). Considering that the Tanzanian record is from Mount Kilimanjaro (De Smet & Bafort, 1990), whereas one of the Indonesian is from 1100 m a.s.l. (Hauer, 1937; 1938), *L. pumila* may be a cold-water taxon. The range of three taxa cannot be classified satisfactorily, due to the scarcity and scatter of records. They illustrate once more that the assignment of taxa to a zoogeographical category should be interpreted with caution, especially in cases where few records are available.

Palaearctic taxa

Most records from the Palaearctic region are from Europe; little or no information is available on the Asian part of the region. Eleven taxa (12.4% of the 89 reported) are restricted to the Palaearctic. Several have circumscribed ranges: e.g., *L. psammophila* and *L. fadeevi* are Central and Eastern European. Records of *L. ivli* are centred on the Balkan region, *L. kluchor*



Map 5. Distribution map of *L. galeata* (Bryce)(●) and *L. myersi* Segers (▲)



Map 6. Distribution map of *L. batilifer* (Murray)(●), *L. bifastigata* Hauer (▲), *L. eutarsa* Harring & Myers (△), *L. eylesi* Russel (◆), *L. kluchor* Tarnogradski (▼), *L. mucronata* Harring & Myers (■)

Table 2. Holarctic taxa

16 taxa reported; 13 endemics (11.2%):	
<i>L. depressa</i> (Bryce, 1891)	<i>L. levistyla</i> (Olofsson, 1917)
<i>L. elasma</i> Harring & Myers, 1926	<i>L. mira</i> (Murray, 1913)
<i>L. elongata</i> Harring & Myers, 1926	<i>L. niothis</i> Harring & Myers, 1926
<i>L. galeata</i> (Bryce, 1892)	<i>L. opias</i> (Harring & Myers, 1926)
<i>L. infula</i> Harring & Myers, 1926	<i>L. satyrus</i> Harring & Myers, 1926
<i>L. intrasinuata</i> (Olofsson, 1917)	<i>L. tryphema</i> Harring & Myers, 1926
<i>L. lauterborni</i> Hauer, 1924	

(Map 6) occurs in the European mountains, including the Caucasus. Some are point endemics (e.g., *L. bryophila*: Tatra Mountains, *L. donyanaensis*: Southern Spain, *L. inconspicua*: coastal lagoons in North East Arabia, *L. margalefi*: Balearic Archipelago). Only the saline-water *L. paradoxa* is widely distributed. Three taxa, *L. fadeevi*, *L. ivli* and *L. psammophila*, are psammobionts.

L. psammophila has also been recorded from the Nearctic (Myers, 1942). This record can not be confirmed, judging from a drawing of the relevant specimen (in Philadelphia Academy of Natural Sciences, USA) kindly provided by P. N. Turner. The radiation of *Notholca* in lake Baikal (Kutikova, 1970; Pejler, 1977b) has no counterpart in *Lecane*.

Palaeotropical taxa

Quite a few *Lecane* occur throughout the tropics and subtropics of the Eastern hemisphere, including the tropical part of the Australian region. The commonest of these is *L. unguitata* (Map 3). Records of *L. unguitata* from the Western hemisphere are noticeably rare. An illustrated record (Ahlstrom, 1938) does not concern *L. unguitata* (see Segers, 1995a). One of the few non-illustrated records of this taxon from South America (Turner & Da Silva, 1992) could not be confirmed (Turner, *in litt.*). A close relative, *L. stephensae*, is recorded from Mozambique and Indonesia (Bali). It is remarkable that *L. stephensae* and *L. unguitata* have relatives endemic to the Oriental (*L. blachei*) and African (*L. nwadiaroi*, *L. symoensi*) regions.

Four more Eastern hemisphere tropical *Lecane* exist. Three of these may have been confused with other taxa: *L. lateralis* resembles *L. luna*, *L. braumi* is closely related to *L. elsa*, and *L. simonneae* is similar to *L. rhytida*. Only *L. serrata* is readily distinguished, but its taxonomic relation with *L. decipiens* needs revision.

There are several more examples of rotifers that are Eastern hemisphere tropical. Apart of many rare ones,

Keratella javana Hauer (see Dumont, 1983), *Lepadella discoidea* Segers and *L. vandenbrandei* Gillard (see Segers *et al.*, 1993a; Segers & De Meester, 1994), are all relatively common species occurring in tropical latitudes in Africa, Asia and Australia. All these are part of a Palaeotropical component of the fauna.

African taxa

All but one of the six African taxa have been found only once. The endemics represent 9% of the 67 taxa reported, which is much higher than the 0.5% endemicity reported by De Ridder (1987). Only *L. sylviae* has been seen on more than a single occasion. One taxon, *L. gillardi*, is Malagasy. The West African (Nigeria) *L. nwadiaroi* (Map 3) and *L. nigeriensis* are close relatives of the Oriental *L. blachei* (Map 3), and the Amazon endemic *L. amazonica*, respectively. *L. blachei* is also related to the East African *L. symoensi*. That the present number of African endemics is an underestimation is clear from the fact that many unnamed taxa exist.

An additional example of an African (West African), littoral rotifer is *Lepadella berzinsi* Segers, known from Nigeria, Zambia and Zaire (Segers, 1993; Segers *et al.*, 1993a). *Keratella reducta* (Huber-Pestalozzi) is remarkable, as it is restricted to the South African subregion (Pejler, 1977b). The validity of some endemic genera, *Vanoyella* (Africa), *Repaulania* and *Veltae* (Both Madagascar; see De Ridder, 1981b; Dumont, 1983) is doubtful (Segers, 1992). The monotypic *Vanoyella* is a contracted *Notommata*, judging from the figure accompanying its description (Evens, 1949).

The Malagasy rotifer fauna was considered unique because of its high level of endemicity (Dumont, 1983). However, the majority of the numerous endemics reported by Bērziņš (1982) are doubtful, and poorly described (Segers, 1992).

Table 3. Eastern hemisphere taxa

- Widespread: *L. pumila* (Rousselet, 1906)

- Insufficiently know:

L. abanica Segers, 1994

L. sympoda Hauer, 1929

L. paxiana Hauer, 1940

Palearctic taxa

89 reported, 11 endemics (12.4%):

L. bryophila Koniar, 1957

L. kluchor Tarnogradski, 1930

L. donyanaensis Mazuelos & Segers, 1994

L. margalefi De Manuel, 1994

L. fadeevi (Neiswestnowa-Shadina, 1935)

L. paradoxa (Steinecke, 1916)

L. gwileti (Tarnogradski, 1930)

L. psammophila (Wiszniewski, 1932)

L. inconspicua Segers & Dumont, 1993

**L. urna* Nogrady, 1962

L. ivli (Wiszniewski, 1935)

Palaeotropical taxa

L. braumi Koste, 1988

L. simonneae Segers, 1993

L. lateralis Sharma, 1978

L. stephensae (Hutchinson, 1931)

L. serrata (Hauer, 1933)

L. unguitata (Fadeev, 1925)

African taxa

67 reported, 6 endemics (9.0%):

L. gillardi (Bērziņš, 1960)

**L. stichoclysta* Segers, 1993

L. nigeriensis Segers, 1993

L. sylviae Segers, 1993

L. nwadiaroi Segers, 1993

**L. symoensi* De Ridder, 1981

Oriental taxa

70 reported, 13 endemics (18.6%):

L. acanthinula (Hauer, 1938)

L. pawlowskii Wulfert, 1966

L. bifastigata Hauer, 1938

**L. schraederi* Wulfert, 1966

L. blachei Bērziņš, 1973

**L. shieli* Segers & Sanoamuang, 1994

L. eswari Dhanapathi, 1976

**L. solfatara* (Hauer, 1938)

L. jaintiaensis Sharma, 1987

**L. spiniventris* Segers, 1994

L. junki Koste, 1975

L. thailandensis Segers & Sanoamuang, 1994

L. minuta Segers, 1994

Australasian

L. batillifer (Murray, 1913)

Australian taxa

46 reported, 3 endemics (6.5%):

L. boorali Koste & Shiel, 1983

L. herzigi Koste, Shiel & Tan, 1988

L. eylesi Russell, 1953

*: known from a single locality only.
126 taxa reported

Oriental taxa

Thirteen taxa (18.6% of the Oriental *Lecane* fauna) are endemic to the region. Seven of these have been recorded only once. Of the remaining, two are restricted to India (*L. eswari*, *L. pawlowskii*), one is Indo-Chinese (*L. thailandensis*: Map 2) and one is Oriental *sensu strictu* (*L. blachei*: Map 3). Two widespread taxa are interpreted as primarily Oriental, although their range is extended beyond the classical limits of that zoogeographical region: *L. acanthinula* occurs in the South East of the Arabian peninsula, and *L. bifastigata* (Map 6) reaches Anatolia and the Caucasus as North East limits of its distribution, and the South East of Arabia. *L. acanthinula* may have been confused with the common, cosmopolitan *L. furcata*, but such can hardly be suspected for the unmistakable *L. bifastigata*. It is likely that more Oriental taxa exist (e.g., *Lecane* sp. after Segers & Sanoamuang, 1994).

Endemic genera are the Indo-Chinese *Architesudinella* and the Indian *Pseudoeuchlanis*. Both are monotypic, especially the latter needs confirmation (an incompletely contracted *Dipleuchlanis*?).

Australasian taxa

Only *L. batillifer* (Map 6) is Australasian. Although few records are available, its range is considered reliable considering that the taxon is unmistakable. Several more examples of Australasian taxa exist in other rotifer genera (*Macrochaetus danneeli* Koste & Shiel: Segers & Sarma, 1994; several *Brachionus* spp.: Sanoamuang *et al.*, 1995; Koste & Shiel, 1987).

Australian taxa

Remarkably few Australian *Lecane* are known, in contrast to the large number of endemics in other rotifer groups (Shiel & Koste, 1986). This is not surprising, considering that only 46 *Lecane* have been reported from Australia. There is only a single Australian endemic *Lecane*, *L. boorali*, which is known from its type locality only. Two others, *L. eylesi* (Map 6) and *L. herzigii* occur on Tasmania and New Zealand (the latter also on the Chatham Islands), where they live in similar habitats (Sanoamuang & Stout, 1993). They have not been recorded from the Australian mainland. The identity of *L. herzigii*, relative to the Floridian endemic *L. ordwayi* requires clarification (Koste & Shiel, 1990; Segers, 1995a). There are indications that several undescribed Australian *Lecane* exist.

Western hemisphere taxa

A total of 41 taxa (30% of the 126 *Lecane* reported) are restricted to the Western hemisphere (Table 4). Five are known from both the Nearctic and Neotropical regions. All, however, are relatively rare. Well-known examples of Western hemisphere taxa are known in other rotifer genera (Pejler, 1977b), e.g., *Brachionus satanicus* Rousselet, *B. havanaensis* Rousselet and *Keratella americana* Carlin. The latter two have recently been recorded from the Eastern hemisphere, possibly as accidental introductions by man (Segers *et al.*, 1993a; Segers, unpublished).

Nearctic taxa

Seventeen (18.9% of 90 reported) taxa have so far been recorded from the Nearctic region only. Some of these are well-documented cases, with circumscribed ranges. An example is the Laurentian *L. mucronata* (Map 6; see also *L. satyrus*). Few records are available, however, for the majority of Nearctic *Lecane*. Of other Rotifera, several *Keratella* are restricted to the Nearctic (Pejler, 1977b; Dumont, 1983).

The number of Nearctic *Lecane* is relatively large when compared to that of the Palaearctic region. A possible explanation for this is that research on psammophilous habitats was most intensive in North America: seven of the taxa listed were described from such biotopes. Moreover, Harring & Myers' (1926) studies on *Lecane* from acid waters in the North-East of the USA were of a thoroughness seldomly attained by subsequent researchers.

Neotropical taxa

Nineteen *Lecane* are Neotropical endemics (21.8% of 87 taxa reported). Many of them have been illustrated on several occasions. Distinction can be made between local endemics such as *L. amazonica* (a common Brazilian taxon; also: *L. melini*, *L. proiecta*), *L. boliviana* (known only from its type locality and, probably, Lake Titicaca in the Andes), and *L. margarethae* (Caribbean), and widespread Neotropical taxa such as *L. eutarsa* (Map 6) and the brackish-water *L. spinulifera*. Three of the Brazilian endemics are closely related to each other and to three non-endemic relatives, *L. signifera*, *L. pertica* and *L. nelsoni*. These are *L. deridderae*, *L. melini* and *L. rudescui*. This group probably radiated in the Amazon region (Segers, 1995a). As such, it is a remarkable counterpart of the Eastern hemisphere tropical/subtropical *L. unguitata*-group.

Table 4. Western hemisphere taxa

- Widespread taxa (known from both the Nearctic and Neotropic):

<i>L. calcaria</i> Harring & Myers, 1926	<i>L. sagula</i> Harring & Myers, 1926
<i>L. mitis</i> Harring & Myers, 1926	<i>L. whitfordi</i> (Ahlstrom, 1938)
<i>L. palinacis</i> Harring & Myers, 1926	

Nearctic taxa

90 reported, 17 endemics (18.9%):

<i>L. candida</i> Harring & Myers, 1926	<i>L. pelatis</i> Harring & Myers, 1926
<i>L. dysoarata</i> Myers, 1942	* <i>L. pideis</i> (Harring & Myers, 1926)
<i>L. flabellata</i> Edmondson, 1936	* <i>L. pustulosa</i> Myers, 1938
<i>L. formosa</i> Harring & Myers, 1926	<i>L. pyrha</i> Harring & Myers, 1926
<i>L. inquieta</i> Myers, 1936	<i>L. rhacois</i> Harring & Myers, 1926
<i>L. leura</i> Myers, 1942	* <i>L. tabulifera</i> Edmondson, 1936
<i>L. mitella</i> (Myers, 1936)	* <i>L. tenua</i> Myers, 1936
<i>L. mucronata</i> Harring & Myers, 1926	<i>L. verecunda</i> Harring & Myers, 1926
<i>L. ordwayi</i> Bienert, 1986	

Neotropical taxa

87 reported, 19 endemics (21.8%):

<i>L. amazonica</i> (Murray, 1913)	<i>L. marchantaria</i> Koste & Robertson, 1983
<i>L. armata</i> Thomasson, 1971	<i>L. margarethae</i> Segers, 1991
<i>L. asymmetrica</i> (Murray, 1913)	<i>L. melini</i> Thomasson, 1953
<i>L. boettgeri</i> Koste, 1986	<i>L. proiecta</i> Hauer, 1956
<i>L. boliviana</i> Segers, 1994	<i>L. remanei</i> Hauer, 1964
<i>L. braziliensis</i> Segers, 1993	<i>L. robertsonae</i> Segers, 1993
<i>L. broaensis</i> Segers & Dumont, 1995	<i>L. rudescui</i> Hauer, 1965
<i>L. deridderae</i> Koste, 1972	<i>L. rugosa</i> (Harring, 1914)
<i>L. eutarsa</i> Harring & Myers, 1926	<i>L. spinulifera</i> Edmondson, 1935
<i>L. kutikowa</i> Koste, 1972	

*: known from a single locality only.
126 taxa reported

Not only *Lecane*, but also *Brachionus* and *Keratella* contain a high proportion of Neotropical endemics (Dumont, 1983; Pejler, 1977b). The genus *Paranuraeopsis* is endemic to the Neotropical region. Several possible causes may account for this, viz. the abundance and high diversity of its aquatic habitats, and the zoogeographical isolation of the region during past geological periods. However, there is also the fact that the region, especially the Amazon basin, is the most intensively studied of all tropical regions. Consequently, some of the rarer endemics may eventually be found elsewhere. Illustrative in this respect are *L. dumonti* and *L. nelsoni*. These taxa were first seen in collections from Nigeria, but turned up later in material from Brazil. Similar examples exist in other groups

of littoral rotifers, e.g. *Trichocerca abilioi* Segers & Sarma. It can at present only be inferred whether or not these distribution reflect the zoogeographical relations between the tropical faunas of South America and Africa (Fittkau, 1969).

Species introductions

Species introductions blur the extant distribution patterns of taxa. Several examples of introductions in Rotifera (*Kellicottia*, see further; De Ridder, 1981a; Dumont, 1983; Pejler, 1977b) and other zooplankton groups (freshwater medusae: Dumont, 1994a; Copepoda: S. Maas, pers. comm.) are documented. A candidate in *Lecane* is *L. satyrus*, whose Japanese record

is the single illustrated record outside its main distribution centre, the East of North America. The same may hold for the above-treated *L. copeis* and *L. cornuta*. The distribution of two more taxa in which introductions were suggested (Segers *et al.*, 1993: *L. decipiens*, *L. rhytida*), can probably best be explained by the scarcity of reliable records. Apparently, species introductions by human activities do occur in *Lecane* as well.

A comparison of the regional Lecane faunas

Taxa, endemic to all of the major zoogeographical regions could be registered, with endemism rates varying from 6.5% to 21.8% (Table 5). The lowest of these figures should not be attributed much weight, as it concerns the insufficiently known Australian *Lecane* fauna. In those regions where more than 50% of the total number of *Lecane* has been recorded, endemism stands at 12.4% (Palearctic region), 18.9% (Nearctic region) and 21.8% (Neotropical region). Some of the endemics will surely turn up in more regions, but many more await discovery, even in well-studied regions. The above figures are far higher than the maximum endemism of 5–8% reported by Dumont & De Ridder (1987) for remote continents (e.g., South America) and major islands. The latter figures, however, also include pelagic taxa, in which endemism appears to be rarer than in littoral groups. It is noticeable that the divergence of the Lecanidae fauna in different regions has only reached the level of the morphospecies. Similarly, there are only few rotifer genera restricted to a single major zoogeographical region, and the taxonomic validity of some of these is even questionable. This either indicates a slow rate of evolution in rotifers, or intense exchange of fauna elements.

The similarity between the *Lecane* faunas of the six major zoogeographical regions is represented in Figure 3 (see Table 6). The overall level of similarity is relatively high, which reflects the abundance of widely distributed taxa in the group. However, the fauna of the Eastern hemisphere tropics is fairly homogeneous. The same holds, to a lesser degree, for the fauna of the Northern temperate regions. The Neotropical region has a well-characterised *Lecane* fauna, with affinities to that of the Northern temperate regions. This pattern of similarities may result from recent exchange of fauna elements. Migration of taxa between the tropical and temperate regions appears to be more important in the Americas than in the Eastern hemisphere. This is also illustrated by the ranges of many Tropicopolitan

Table 5. Summary of distribution patterns in *Lecane*

Widely distributed taxa: 69 (41.3%)	
-	Cosmopolitan (<i>sensu strictu</i>) taxa: 21 (12.6%)
-	Arctic-temperate taxa: 6 (3.6%)
-	Tropicopolitan taxa: 26 (15.6%)
-	Pantropical taxa: 6 (3.6%)
-	Odd cases: 10 (6%)
Holarctic taxa: 13 (7.8%)	
Eastern hemisphere taxa: 44 (26.3%)	
-	Widespread: 1 (0.6%)
-	Palaeartic taxa: 11 (3*, 6.6%)
	Widespread: 1 (0.6%)
	Widespread European: 5 (3.0%)
	point endemics: 5 (3*, 3.0%)
-	Palaeotropical taxa: 6 (3.6%)
-	African taxa: 6 (5*, 3.6%)
	Malagasy subregion: 1 (*, 0.6%)
	West African subregion: 4 (3*, 2.4%)
	East African subregion: 1 (*, 0.6%)
-	Oriental taxa: 13 (7*, 7.8%)
	Widespread: 3 (1.8%)
	Indian subregion: 4 (2*, 2.4%)
	Indo-Chinese subregion: 3 (2*, 1.8%)
	Indo-Malayan subregion: 3 (3*, 1.8%)
-	Australasian taxa: 1 (0.6%)
-	Australian taxa: 3 (1*, 1.8%)
	West Australia: 1 (1*, 0.6%)
	Tasmania, New Zealand: 2 (1.2%)
-	Insufficiently known: 3 (1.8%)
Western hemisphere taxa: 41 (24.6%)	
-	Widespread taxa: 5 (3.0%)
-	Nearctic taxa: 17 (10*, 10.2%)
	Widespread: 2 (1.2%)
	Alleghany subregion: 15 (10*, 9.0%)
-	Neotropical taxa: 19 (3*, 11.4%)
	Widespread: 5 (2.4%)
	Brazilian subregion: 13 (2*, 7.8%)
	Chilian subregion: 1 (1*, 0.06%)

(x*: number of taxa, known from a single locality)

Total number of taxa recognised: 167 (100%)

taxa (e.g., *L. aeganea*, *L. crepida*, *L. myersi* (Map 5), *L. leontina* (Map 7), *L. monostyla*) which have been recorded from the Nearctic, but not or only rarely from the Palearctic region. In the Americas, the North-South orientation of the Rocky Mountains and Andes chains makes their mountain ranges ineffective as barriers for warm-water, and effective as a corridor for cold water taxa during migration from the Neotropical

Table 6. Occurrence of Lecane in the major zoogeographical regions

	P	Af	O	Au	Na	Nt		P	Af	O	Au	Na	Nt
<i>L. abanica</i>	x	x		?			<i>L. fadeevi</i>	x					
<i>L. acanthinula</i>	x		x				<i>L. flabellata</i>					x	
<i>L. aculeata</i>	x	x	x	x		x	<i>L. flexilis</i>	x	x	x	x	x	x
<i>L. aeganea</i>	x		x	x	x	x	<i>L. formosa</i>					x	
<i>L. agilis</i>	x	x			x	x	<i>L. furcata</i>	x	x	x	x	x	x
<i>L. amazonica</i>						x	<i>L. galeata</i>	x				x	
<i>L. arcuata</i>	x	x	x	x	x	x	<i>L. gillardi</i>		x				
<i>L. arcula</i>	x	x	x		x	x	<i>L. grandis</i>	x				x	x
<i>L. armata</i>						x	<i>L. gwiletti</i>	x					
<i>L. aspasia</i>	x		x		x	x	<i>L. haliclysta</i>	x	x	x	x	x	x
<i>L. asymmetrica</i>						x	<i>L. hamata</i>	x	x	x	x	x	x
<i>L. batillifer</i>			x	x			<i>L. hastata</i>	x	x	x	x	x	x
<i>L. bifastigata</i>	x		x				<i>L. herzigii</i>				x		
<i>L. bifurca</i>	x	x	x	x	x	x	<i>L. hornemanni</i>	x	x	x	x	x	x
<i>L. blachei</i>			x				<i>L. inconspicua</i>	x					
<i>L. boettgeri</i>						x	<i>L. inermis</i>	x	x	x	x	x	x
<i>L. boliviana</i>						x	<i>L. infula</i>	x				x	
<i>L. boorali</i>				x			<i>L. inopinata</i>	x	x	x	x	x	x
<i>L. broaensis</i>						x	<i>L. inquieta</i>					x	
<i>L. braumi</i>		x	x	x			<i>L. intrasinuata</i>	x				x	
<i>L. braziliensis</i>						x	<i>L. ivli</i>	x					
<i>L. bryophila</i>	x						<i>L. jaintiaensis</i>			x			
<i>L. bulla</i>	x	x	x	x	x	x	<i>L. junki</i>			x			
<i>L. calcaria</i>					x	x	<i>L. kluchor</i>	x					
<i>L. candida</i>					x		<i>L. kutikowa</i>						x
<i>L. clara</i>	x	x			x	x	<i>L. lamellata</i>	x				x	x
<i>L. climacois</i>	x				x		<i>L. lateralis</i>		x	x	x		
<i>L. closterocerca</i>	x	x	x	x	x	x	<i>L. latissima</i>	x			x	x	
<i>L. copeis</i>	x				x	x	<i>L. lauterborni</i>	x				x	
<i>L. cornuta</i>	x				x	x	<i>L. leontina</i>	x	x	x	x	x	x
<i>L. crepida</i>	x	x	x	x	x	x	<i>L. leura</i>					x	
<i>L. curvicornis</i>	x	x	x	x	x	x	<i>L. levistyla</i>	x				x	
<i>L. decipiens</i>	x	x	x			x	<i>L. ligona</i>	x		x		x	x
<i>L. depressa</i>	x				x		<i>L. ludwigii</i>	x	x	x	x	x	x
<i>L. deridderae</i>						x	<i>L. luna</i>	x	x	x	x	x	x
<i>L. donneri</i>	x	x	?		x		<i>L. lunaris</i>	x	x	x	x	x	x
<i>L. donyanaensis</i>	x						<i>L. marchantaria</i>						x
<i>L. doryssa</i>	x	x	x	x		x	<i>L. margalefi</i>	x					
<i>L. dumonti</i>		x				x	<i>L. margarethae</i>						x
<i>L. dysoarata</i>					x		<i>L. melini</i>						x
<i>L. elasma</i>	x				x		<i>L. minuta</i>			x			
<i>L. elegans</i>		x	x			x	<i>L. mira</i>	x				x	
<i>L. elongata</i>	x				x		<i>L. mitella</i>					x	
<i>L. elsa</i>	x				x	x	<i>L. mitis</i>					x	x
<i>L. eswari</i>		x				x	<i>L. monostyla</i>	x	x	x	x	x	x
<i>L. eutarsa</i>						x	<i>L. mucronata</i>					x	
<i>L. eylesi</i>				x			<i>L. myersi</i>		x	x		x	x

Table 6. Continued.

	P	Af	O	Au	Na	Nt		P	Af	O	Au	Na	Nt
<i>L. nana</i>	x	x	x	x	x	x	<i>L. schraederi</i>			x			
<i>L. nelsoni</i>		?				x	<i>L. scutata</i>	x		x		x	
<i>L. nigeriensis</i>		x					<i>L. serrata</i>		x	x	x		
<i>L. niothis</i>	x				x		<i>L. shieli</i>			x			
<i>L. nwadiaroi</i>		x					<i>L. signifera</i>	x	x	x	x	x	x
<i>L. obtusa</i>	x	x	x	x	x	x	<i>L. simonneae</i>		x	x			
<i>L. opias</i>	x					x	<i>L. sola</i>			x			x
<i>L. ordwayi</i>					x		<i>L. solfatara</i>			x			
<i>L. palinacis</i>					x	x	<i>L. spiniventris</i>			x			
<i>L. papuana</i>	x	x	x	x	x	x	<i>L. spinulifera</i>					x	x
<i>L. paradoxa</i>	x						<i>L. stenroosi</i>	x	x	x	x	x	x
<i>L. pawlowskii</i>			x				<i>L. stephensae</i>		x	x			
<i>L. paxiana</i>	x	x					<i>L. stichaea</i>	x	x			x	x
<i>L. pelatis</i>					x		<i>L. stichoclysta</i>		x				
<i>L. perpusilla</i>	x	x			x		<i>L. subtilis</i>	x	x			x	x
<i>L. pertica</i>		x	x		x	x	<i>L. subulata</i>	x				x	x
<i>L. pideis</i>					x		<i>L. sylviae</i>		x				
<i>L. proiecta</i>						x	<i>L. symoensi</i>		x				
<i>L. psammophila</i>	x						<i>L. sympoda</i>	x	x				
<i>L. pumila</i>	x	x	x				<i>L. syngenes</i>		x	x	x		x
<i>L. punctata</i>	x	x	x		x	x	<i>L. tabida</i>		x			x	
<i>L. pusilla</i>	x	x	x	x		x	<i>L. tabulifera</i>					x	
<i>L. pustulosa</i>					x		<i>L. tenua</i>					x	
<i>L. pyriformis</i>	x	x	x	x	x	x	<i>L. tenuiseta</i>	x	x	x	x	x	x
<i>L. pyrrha</i>					x		<i>L. thailandensis</i>			x			
<i>L. quadridentata</i>	x	x	x	x	x	x	<i>L. thalera</i>	x		x			x
<i>L. remanei</i>						x	<i>L. thienemanni</i>		x	x	x		x
<i>L. rhacois</i>					x		<i>L. tryphema</i>	x				x	
<i>L. rhenana</i>	x		x			x	<i>L. uenoi</i>	x					x
<i>L. rhopalura</i>	x				x	x	<i>L. undulata</i>	x	x	x	x	x	x
<i>L. rhytida</i>		x		x	x	x	<i>L. unguitata</i>	x	x	x	x		
<i>L. robertsonae</i>						x	<i>L. ungulata</i>	x	x	x	x	x	x
<i>L. rudescui</i>						x	<i>L. urna</i>	x					
<i>L. rugosa</i>						x	<i>L. venusta</i>	x				x	
<i>L. rutmeri</i>		x	x		x		<i>L. verecunda</i>					x	
<i>L. sagula</i>					x	x	<i>L. whitfordi</i>					x	x
<i>L. satyrus</i>	x					x							

Pa: Palaearctic region, Af: African region, O: Oriental region, Au: Australian region, Na: Nearctic region, Nt: Neotropical region.

to the Nearctic region, and *vice versa*. The East-West oriented mountain chains between the temperate and tropical regions of the Eastern hemisphere are probably more effective in preventing the exchange of taxa (e.g., Darlington, 1957; Cox & Moore, 1993). It is likely that the extensive arid regions of Northern Africa, Arabia and Asia are also effective in diminishing the North-South exchange of Rotifera in the Eastern hemisphere.

The similarity between the *Lecane* fauna of the different regions in the Holarctic and Palaeotropics argues against the relevance of ornithochoric transport (See De Ridder, 1981a; Dumont, 1983). Ornithochoric dispersal can hardly account for it, as most migratory routes of birds follow a N-S direction. In conjunction to this, it is noteworthy that Schuster (1983) finds it unlikely that animals, especially birds, play a

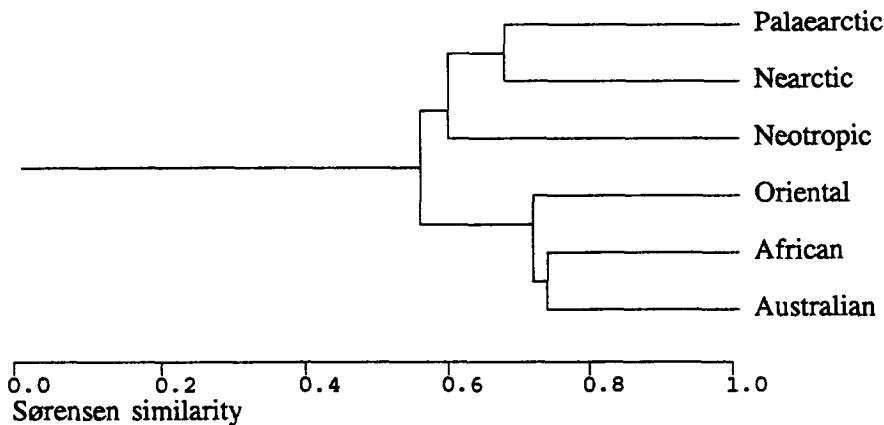


Figure 3. Dendrogram based on the species similarity between the major zoogeographical regions.

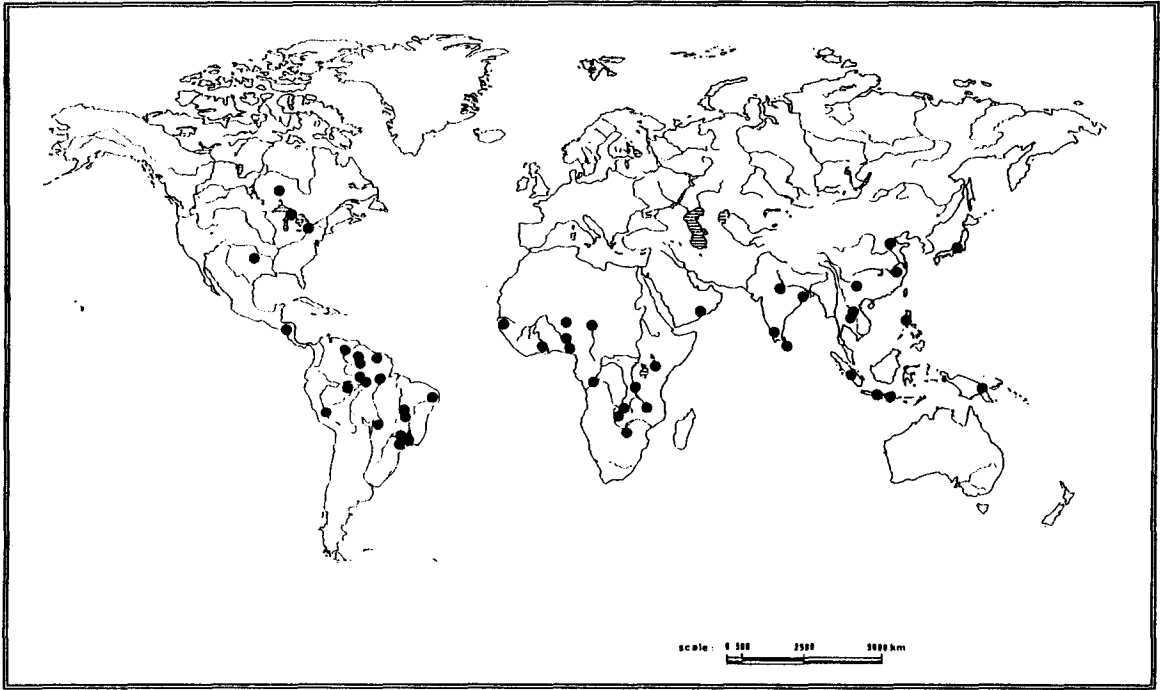
major role in the long-distance dispersal of bryophytes, another group of organisms with passive dispersal by resistant stages. However, wind migration is considered to play a minor role in desmids (Brown *et al.*, 1964). The difference in faunal similarity between the Northern, temperate and the tropical regions of both the Eastern and the Western hemisphere, may be related to bird migration. Similarly as for freshwater algae (Proctor, 1966; Atkinson, 1972; 1981), birds may transport rotifer propagules externally or in the digestive tract (Proctor, 1966; Dumont, 1979), although the effectiveness is reduced by the short passage time in the latter case. Bird migration is considered most effective over medium-long distances (Proctor, 1966; Coesel *et al.*, 1988). In the Americas, migratory birds follow an almost continuous series of water bodies, that act as stepping-stones for the migration of freshwater plankton species. Contrarily, the presence of extensive arid areas in Northern Africa and Asia, and of the East-West oriented mountain chains of the Eastern hemisphere imposes long, continuous flights or coastal routes including estuarine waters to migrating birds (Coesel *et al.*, 1988). Probably, the effectiveness of dispersal of freshwater organisms by migrating birds is relatively lower in the latter case. Thus, in similarity with desmids, northward migration of warm-water rotifer taxa carried by waterfowl can be expected to be more important in the Americas than from the tropical to the temperate zones of the Eastern hemisphere. It remains necessary, however, to assess the relative importance of birds in this respect, as the above-mentioned mountains and arid regions may also act as barriers for dispersal by wind.

Notes on sister taxa

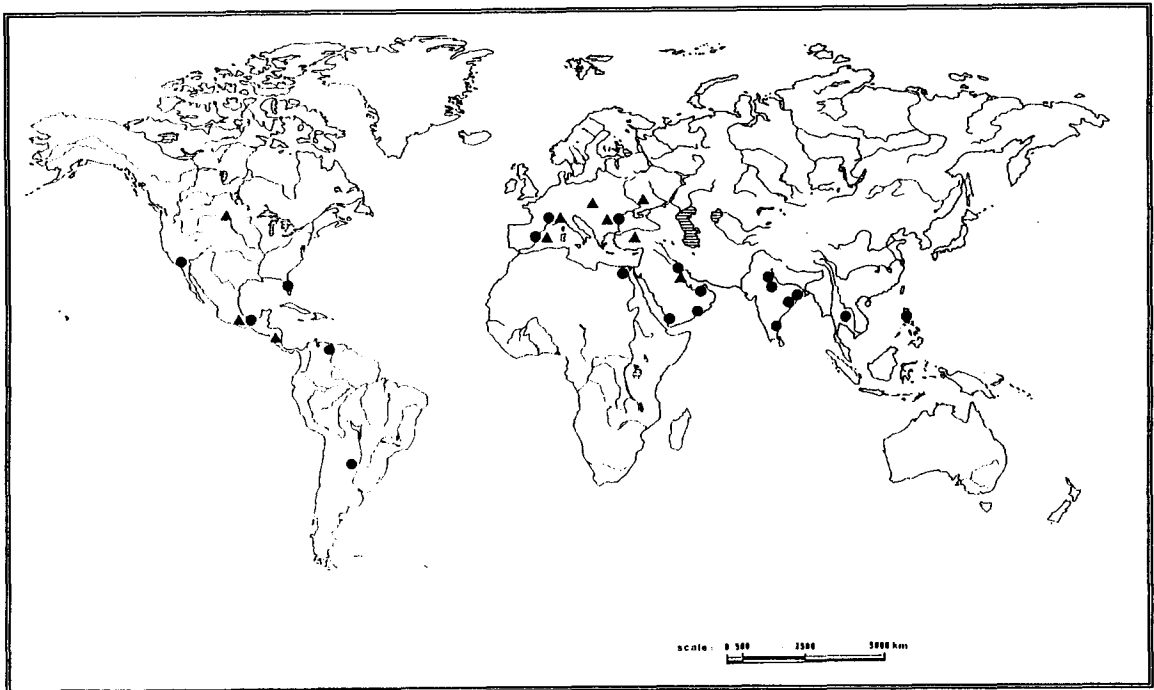
In biogeography, comparisons between the distribution and phylogeny of taxa are most rewarding. Examples of such studies are Brundin (1966, 1981) for chironomid midges, and Rosen (1978, 1979) for Poeciliid fish. The fact that Rotifera have passive dispersal mechanisms and are often widespread makes it difficult to derive relationships between geographical areas from them (see Ball, 1976; Platnick & Nelson, 1978). Moreover, the near-absence of a fossil record (e.g., Southcott & Lange, 1971) hampers a phylogenetic analysis. However, comparing the phylogeny and the distribution of taxa may be interesting even in groups like Rotifera when closely related taxa with restricted distributions are considered. Although the present state of knowledge of *Lecane* is still fragmentary, there are a number of groups or pairs of sister taxa in *Lecane* in which a comparison between distribution and phylogeny, following cladistic principles (see Forey *et al.*, 1992) is possible.

The *L. hornemanni*-group

In the *L. hornemanni*-group, the closely related *L. latissima* and *L. thailandensis* are of special interest. The phylogenetic relation between them follows from a comparison with taxa in the related *L. signifera*-group. A strongly ornamented lorica as in *L. thailandensis* does not occur in any taxon of that group. Such a lorica is found in only a few other, unrelated *Lecane*. So, the Oriental *L. thailandensis* can be considered a derived taxon when compared to the antitropical, Arctic-temperate *L. latissima* (Map 2). *L. thailandensis* may have originated from the adaptation of (a) relict



Map 7. Distribution map of *L. leontina* (Turner)



Map 8. Distribution map of *L. lamellata* (Daday)(▲) and *L. thalera* Haring & Meyers (●)

population(s) of *L. latissima* to a tropical environment, during the course of past climatic changes. As such, this case may be an example of vicariant, allopatric speciation, probably connected to the Pleistocene glaciations.

The L. ungulata-group

The cosmopolitan *L. ungulata* has a close relative, the point-endemic *L. donyanaensis*, living in temporary ponds in Southern Spain (Gallindo *et al.*, 1995). A posterior projection on the foot plate is absent in *L. ungulata* and in the related *L. curvicornis*-group (including *L. curvicornis*, *L. elsa*, *L. braumi*), but present in *L. donyanaensis*. Hence, it may concern an apomorphic addition. *L. donyanaensis* may have originated from a population of *L. ungulata* that specialised to extreme environmental conditions. It is unlikely that Southern Spain (the region of *L. donyanaensis*) was till recently outside, or at the edge of the range of the cosmopolitan and ubiquitous *L. ungulata*. Consequently, the two may not have been geographical separated at the time *L. donyanaensis* evolved, and the contact between *L. donyanaensis* and *L. ungulata*, by a continuous inflow of resting eggs of the former in the habitat of the latter, may not have been interrupted. Hypothetically, sympatric speciation could have occurred in this case.

The L. lamellata-group

Similarly as in the *L. ungulata*-group, the Tropicopolitan *L. thalera* and primarily Holarctic (Map 8; see above) *L. lamellata* differ by, respectively, the absence (plesiomorphic) or presence (apomorphic) of a posterior projection on the foot plate. Character polarity is ascertained by comparison with the *L. lunaris*- and *L. cornuta*-groups, and in analogy with the *L. ungulata*-group.

The taxonomic separation between *L. lamellata* and *L. thalera* is weak (Segers, 1995a). Their ranges, however, differ markedly. The case may concern two originally parapatric, vicariant taxa. Probably, *L. lamellata* is adapted to a warm-temperate, *L. thalera* to a tropical environment. It is noteworthy that morphological intermediates between the two have been recorded, but so far only from the zone in the Eastern hemisphere where the ranges of both taxa overlap. This agrees with the hypothesis that these intermediate forms could be hybrids (Segers, 1995a).

The L. unguitata-group

The *L. unguitata*-group comprises six taxa which are separated by the degree of fusion of their toes and pseudoclaws: *L. papuana* (two toes), *L. blachei* (toes fused basally), *L. nwadiaroi* (toes fused up to medially), *L. unguitata* (toes completely fused, pseudoclaws long and separate), *L. stephensae* (toes completely fused, pseudoclaws short and separate) and *L. symoensi* (toes totally fused, no pseudoclaws reported). Fusion of the toes and (pseudo)claws occurred independently in several groups of *Lecane*. Complete separation of the toes is considered the most plesiomorphic character state, while complete fusion corresponds to the apomorphic state.

The most primitive group member, *L. papuana*, is a common Tropicopolitan. *L. blachei* and *L. nwadiaroi* differ only little, but they have distinct, vicariant distributions. Whereas *L. blachei* is Oriental, *L. nwadiaroi* is Nigerian. *L. unguitata* and *L. stephensae* are also similar, but more evolved taxa. Both are Palaeotropical. *L. symoensi* is a point-endemic, known only from a lake near Lubumbashi, Zaire (Map 3).

Under the above hypothesis on the phylogeny of the group members, the ranges of some apparently older, primitive taxa (*L. blachei* and *L. nwadiaroi*) are much smaller than, and are encompassed by those of more evolved ones (*L. unguitata* and *L. stephensae*), whereas the range of the most evolved one (*L. symoensi*) is, again, small. This may indicate a different dispersal capacity in the taxa concerned.

The L. obtusa-group

The *L. obtusa*-group (diagnosis: single toe with claws, stiff lorica with consistently wider dorsal than ventral plate) comprises two subgroups, one (A, diagnosis: parallel, straight head aperture margins) with three morphospecies (*L. obtusa*, *L. psammophila* and *L. whitfordi*) and a second subgroup (B, diagnosis: ventral head aperture margin broadly sinuate) with two morphospecies (*L. galeata* and *L. myersi* Segers; Map 5). Character polarity within each subgroup is ascertained as follows:

1. Toe shape: a bulged toe occurs only in *L. psammophila*, and not in subgroup B. This character state is considered apomorphic in subgroup A.
2. Antero-lateral spines occur only in *L. whitfordi*, not at all in subgroup B. Hence, this represents the apomorphic character state in subgroup A.

3. Only *L. myersi* has an ornamented lorica. This represents the apomorphic character state in subgroup B.

Thus, both the Palaearctic psammophile *L. psammophila* and the Eastern hemisphere *L. whitfordi* seem to be derived from the Tropicopolitan *L. obtusa* (subgroup A), and the Tropicopolitan *L. myersi* may be derived from the Holarctic *L. galeata* (subgroup B). *L. psammophila* has a specialised ecology, which is less so for *L. obtusa*. *L. psammophila* could have originated through specialisation of some population of *L. obtusa*, living in conditions that are extreme for that taxon. *L. obtusa* and *L. fadeevi* have non-overlapping ranges, so allopatric speciation may be inferred. Little is known about *L. whitfordi*, but the range of this taxon is encompassed by that of *L. obtusa*.

The case of *L. galeata* and *L. myersi* is strikingly similar to that of *L. latissima* and *L. thailandensis*, and a similar hypothesis may apply. However, whereas *L. thailandensis* occupies a relatively small range, *L. myersi* is Tropicopolitan. The diagnosis of these two taxa relies on the same character (lorica ornamentation), and is probably a case of convergent evolution. When a similar rate of dispersal in both taxa is assumed, *L. myersi* would be much older than *L. thailandensis*, considering the time needed to expand its range to its present Tropicopolitan distribution. This implies that *L. myersi* has a conserved morphology, without additional change since it became established. The alternative, that the two have different dispersal capacities, appears more realistic.

The L. closterocerca-group

The diagnostic characters in this group are similar to those in subgroup (A) of the *L. obtusa*-group. Here, character polarity is assessed by comparison with the *L. arcuata*- and *L. hamata*-groups. The *L. closterocerca*-group contains *L. boliviana*, *L. closterocerca* and *L. fadeevi*. *L. closterocerca* is probably the commonest, cosmopolitan *Lecane*. *L. fadeevi* is a psammobiont in Central European rivers. It differs from *L. closterocerca* by having a bulged toe, whereas the toe is parallel-sided in *L. closterocerca*, and in all taxa of the *L. arcuata*- and *L. hamata*-groups. Thus, the apomorphic character state is as in *L. fadeevi*, which is therefore considered the derived taxon. The presence of antero-lateral spines diagnoses the Andean *L. boliviana*. Antero-lateral spines are equally present in the *L. arcuata*- and *L. hamata*-groups. However, if character polarity is inferred in analogy to subgroup (A) of

the *L. obtusa*-group, then also *L. boliviana* is derived from *L. closterocerca*. *L. boliviana* probably has a specialised ecology, as it is restricted to an Andean habitat.

There exist other than the above parallels between the *L. closterocerca*-group and subgroup (A) of the *L. obtusa*-group. Both *L. fadeevi* and *L. psammophila* have a bulged toe. Also their ecology is similar, as both are psammophilic. In fact, they have long been considered synonyms (Segers, 1994b). Here again, it can be assumed that the derived morphospecies evolved through adaptive specialisation to a habitat that is only marginally suitable to the ancestral taxon. The fact that *L. closterocerca* is probably the most ubiquitous and widespread of all *Lecane*, casts doubt on the possibility of allopatric speciation in this case.

The L. hamata-group

This group contains the cosmopolitan *L. hamata*, Pantropical *L. thienemanni*, Australasian *L. batillifer* (Map 6), Indian *L. pawlowskii*, and Neotropical *L. marchantaria*. All restrictedly-distributed taxa co-occur with the common *L. hamata*. The polarity of diagnostic features is inferred by a comparison with the *L. closterocerca*- and *L. arcuata*-groups. A posterior projection is present in *L. batillifer*, but not in the outgroups. The situation here is analogous to that in the *L. unguata*-group. *L. pawlowskii* has a unique collar around the head aperture. *L. thienemanni* has strong antero-lateral spines, whereas such are present, but less well-developed in the other members of the *L. hamata*-group. Antero-lateral spines are absent or small in the outgroups. Hence, the distinguishing characters are in the apomorphic state in *L. batillifer*, *L. pawlowskii* and *L. thienemanni*. These three taxa are all derived from *L. hamata*. The relation between the three cannot be ascertained, as they are all diagnosed by a single yet different character in the apomorphic state. The situation is not clear in *L. marchantaria*. The ranges of three derived taxa are strikingly different in size. Whereas *L. pawlowskii* is an Indian endemic, *L. batillifer* occurs in China, Thailand and Australia, and *L. thienemanni* is Pantropical. This difference probably results from a different dispersal capacity of the three or from a different age of the taxa.

Other cases

There are many more cases of groups or pairs of closely related taxa in *Lecane*. Some additional cases are mentioned below. They are not treated in detail, as the relation between the taxa can only be inferred in

analogy with some of the above-treated groups in these cases, and/or as their ranges overlap largely.

(1) *L. arcuata* (Cosmopolitan) and *L. opias* (Holarctic): anterolateral spines are absent (plesiomorphic) in *L. arcuata*, present (apomorphic) in *L. opias* (compare with *L. obtusa*-*L. whitfordi*).

(2) *L. arcula* Haring and *L. aculeata* (both Tropicopolitan, but *L. arcula* more ubiquitous than *L. aculeata*): the antero-lateral spines are more elongate in *L. aculeata* and *L. arcula*. None of their relatives has the elongate antero-lateral spines of *L. aculeata*, spines with a length as in *L. arcula* are common throughout the genus.

(3) *L. depressa* (Holarctic) and *L. ligona* (Arctic-temperate): a posterior projection on the foot plate is absent (plesiomorphic) in *L. depressa*, present (apomorphic) in *L. ligona* (compare with *L. hamata*-*L. batillifer*).

(4) *L. furcata* (cosmopolitan, freshwater) and *L. acanthinula* (Oriental, in more or less saline water): anterolateral spines are absent (plesiomorphic) in *L. furcata*, present (apomorphic) in *L. acanthinula* (compare with *L. obtusa*-*L. whitfordi*).

(5) *L. lunaris* (cosmopolitan) and *L. rhopalura* (Arctic-temperate): the toe is parallel-sided (plesiomorphic) in *L. lunaris* and bulged (apomorphic) in *L. rhopalura* (compare with *L. obtusa*-*L. psammophila* and *L. closterocerca*-*L. fadevi*).

In cases (1) and (5), the ancestral taxon is an ubiquitous cosmopolitan, whereas the derived one is restricted to a cold-water environment. Case (4) is similar, as it may also concern an ubiquitous, cosmopolitan taxon from which evolved a specialised taxon with a more restricted distribution. These cases are reminiscent of the *L. ungulata*- and *L. closterocerca*- groups.

Cases (2) and (3) concern sister taxa with largely overlapping ranges. By their similar range, it is difficult to interpret them in the light of vicariance or evolutionary biogeography. The well-documented case of *Kellicottia longispina* (Kellicott) and *K. bostoniensis* (Rousselet) (Brachionidae) is particularly illustrative in this context. Here, the presence of six anterior spines is considered the plesiomorphic character state, following a comparison with the related genus *Keratella*. Hence, the commonest of the two, the Arctic-temperate *K. longispina*, may be the most primitive. The originally Nearctic *K. bostoniensis* has recently been introduced to the Eastern hemisphere (Arnemo *et al.*, 1968; Pejler, 1977b; Balvay, 1994). Pejler (1977b) concluded that allopatric speciation could lay at the origin of the sister taxa. He argued that, whereas it is nowadays

common there, old records of *K. longispina* from the Western hemisphere are noticeably rare. This may indicate that the species reached the Western hemisphere only in historical times. Apparently, the sympatry of the closely related sister taxa is secondary here, and is due to long-distance dispersal. Also, dispersal of *K. longispina* is faster than of *K. bostoniensis* under this hypothesis.

Discussion

Quite a few examples exist of sister taxa in which climatological or ecological factors explain the present-day vicariant distribution of the taxa concerned. This is illustrated by the *L. hornemanni*-group, and by the *L. obtusa*-*L. psammophila* and *L. galeata*-*L. myersi* pairs of the *L. obtusa*-group. It may also apply to the *L. lamellata*-group. Similar cases were identified by De Ridder (1981a), who calls them 'ecological vicariants'. Sister taxa with vicariant distributions that can be related directly to ancient tectonic events are rare. Only the case of *L. blachei* and *L. nwadiaroi* is a clear example. Allopatric speciation may lay at the origin of the diversity of *L. signifera*'s Neotropical relatives.

Sister taxa having sympatric distributions occur in the *L. ungulata*-group and the *L. closterocerca*-group, and in the *L. hamata*-group (e.g., *L. batillifer* and *L. pawlowskii* versus *L. hamata*). Here, the range of the ancestral taxon encompasses that of (a) derived one(s). The assumptions necessary to conform some of these cases to a hypothesis of exclusive allopatric speciation are such, that this is an unlikely possibility. Sympatric speciation can be surmised here. It can also be inferred in cases (1), (4) and (5). However, there are pairs of sister taxa (case (2) and (3)) that concern taxa with similar ranges and ecology, as far as can be ascertained. The sympatry in these pairs may be secondary, and a result of allopatric speciation followed by expansion of the ranges of both taxa. These examples further illustrate the fact that biogeography of *Lecane* taxa is largely defined by passive dispersal. Analysis of the patterns is, moreover, hampered by the fact that dispersal capacity (different rate of dispersal or susceptibility to barriers) may differ between morphospecies. This may indicate a different effectiveness of resting eggs of different taxa to survive adverse conditions.

Distribution patterns in *Lecane* compared with other Rotifera

The proportion of widely distributed *Lecane* amounts to 41.3% of the total. There are, however, only 21 true cosmopolitans. There are relatively fewer widely distributed taxa in *Lecane* than in the pelagic Brachionidae (see Dumont, 1983; Pejler, 1977b). Two, not mutually exclusive, explanations are suggested to account for this. Firstly, littoral taxa are never found in such high numbers as pelagic animals (Nogrady *et al.*, 1993). Males and resting eggs are known in many pelagic, but only in a few littoral rotifers (see for example Koste, 1978). So, the possibility that sexuality and resting egg production occurs less frequently in these taxa, as suggested by Dumont (1983), should be considered. A lower abundance of littoral than pelagic rotifers, combined with, probably, a lower frequency of resting egg production results in a relative rarity of resting eggs of littoral taxa. If so, and assuming equal effectiveness to dispersal, the long-distance transportation of resting eggs will be less frequent in littoral than in pelagic rotifers. Secondly, littoral habitats are more unstable than pelagial ones, as they are more susceptible to adverse conditions such as desiccation and freezing. This lower predictability implies that recolonisation is more frequently required in littoral than in pelagic habitats. Moreover, the higher species diversity in the littoral indicates a higher heterogeneity of the biotope. Similar microhabitats will occur scattered in space. Hence, the probability to arrive in a suitable habitat after dispersal is relatively low for littoral taxa, and successful colonisation of new habitats is therefore likely to occur less frequently. Consequently, producing resting eggs that remain within the same habitat will probably be more advantageous to littoral than to pelagic taxa.

Of the 167 *Lecane* recognised, 77 or 46% are confined to (sub)tropical regions, as opposed to 50 (30%) that occur in temperate or arctic regions. It had already been noticed that *Lecane* is dominant in terms of species diversity in tropical acid waters (Fernando, 1980; Dussart *et al.*, 1984; Segers & Dumont, 1995), where over 40 taxa can be found in a single locality (Segers *et al.*, 1993a). The same holds true for *Brachionus* (Pejler, 1977b; Dumont, 1983) and for the much less species-rich, but equally littoral Scaridiidae (Segers, 1995b). There are, so far, no reports on predominantly temperate groups of littoral Rotifera, but these may exist. A possible example is *Cephalodella* (Notommatidae). This genus contributed the largest

number of taxa to a study on Swedish rotifers (Pejler & Bērziņš, 1993; 1994). A possible Gondwanan origin of *Lecane*, as was suggested by Dumont (1983) for the equally 'tropic-centred' (Pejler, 1977b) *Brachionus*, is unlikely. Considering that Rotifera are necessarily an evolutionary 'old' group, it may not be possible to trace the origin of taxa of generic or suprageneric rank. The present-day 'tropic-centred' character of Lecanidae and some other rotifer groups may be secondary.

There is a marked temperate and Arctic-subarctic component in *Lecane*. This component offers an additional argument against a Gondwanian origin of the genus. In Brachionidae, such a component is represented by the genera *Notholca*, *Synchaeta* and some *Keratella* (Pejler, 1977b; Dumont, 1983). A Southern hemisphere cold-temperate and Antarctic fauna, as treated by Brundin (1966, 1972, 1981; see also Platnick, 1991) is represented by several *Notholca* species (e.g., Battistoni, 1992; Dartnall & Hollowday, 1985) and a few *Keratella* (Dumont, 1983; Pejler, 1977b). No clear examples are found in *Lecane*, although the peculiar Tasmanian and New Zealand *L. eylesi* and *L. herzigii* may represent such taxa.

Green (1987) suggests that competition and predation play a role in the distribution of Rotifera. Rotifera are particularly susceptible to interference competition with large Cladocera (Gilbert, 1988a, 1988b; MacIsaac & Gilbert, 1989, 1991; Conde-Porcuna *et al.*, 1994) whose distribution, in turn, is strongly influenced by fish predation (Kerfoot & Lynch, 1987). Large Cladocera are predominantly temperate, as a result of more intense fish predation in the tropics (Dumont, 1980b, 1994b; Lazarro, 1987; Fernando, 1994). The 'tropic-centred' distribution of many rotifer groups may be linked to the relatively low abundance of Cladocera in tropical waters. This hypothesis is, however, not supported by the predominantly temperate *Keratella* (Pejler, 1977b; Dumont, 1983). It is especially the experimental work with *Keratella* that produced most evidence for the susceptibility of rotifers to competition with large Cladocera. Moreover, also genera like *Synchaeta* and *Cephalodella* are predominantly temperate. *Synchaeta* is illoricate and *Cephalodella* soft-loricated, hence they are even more vulnerable than loricate Rotifera (Jamieson, 1980; Williamson, 1983; Stemberger, 1985; Roche, 1987; Gilbert, 1988a). On the other hand, *Synchaeta* is most abundant during autumn, winter and early spring. This may also be an adaptation to avoid contact with large Cladocera, as these are scarce during this period.

Temperature and food quality (phytoplankton: see Pourriot, 1965) have been inferred as key features determining the occurrence of Rotifera by Pejler (1977b) and Green (1972). Also salinity (De Ridder, 1981a; Green & Mengistou, 1991; Segers & Dumont, 1993a), and pH (Harring & Myers, 1928; Dussart *et al.*, 1984) are cited in this respect. Regarding littoral Rotifera, it may be rewarding to examine the possible impact of Ostracoda on the occurrence of Rotifera. Ostracoda are rare in acid waters, a consequence of their calcified shells. Rotifer diversity, on the other hand, is highest in the littoral of such habitats (Harring & Myers, 1928). An adverse relation as between pelagic Rotifera and Cladocera seems likely, but requires substantiation.

General features of rotifer chorology

When compared to other groups of animals, *Lecane*, and Rotifera in general, is exceptional by the generally large ranges of morphospecies, and the high number of widely distributed taxa. The differentiation into faunas endemic to specific regions is relatively weak, and ancient plate tectonic events appear hardly, if at all, reflected in the relation between the regional *Lecane* faunas. Illustrative is that in other freshwater organisms, large-scale biogeographical considerations are on the family (fishes: see Darlington, 1957) or genus level (Copepoda: see Lewis, 1984; Dussart & Defaye, 1995) with little or rare cosmopolitanism at the morphospecies level. On the other hand, Round (1981) reports between 50 to 70% cosmopolitanism in freshwater algae.

Two hypotheses can account for the wide ranges of Rotifera. Either they are old, and predate the existing zoogeographical barriers between the continents, or they are more recent, and colonised their present range through dispersal (see Platnick & Nelson, 1978). It appears unrealistic to assume that the present-day cosmopolitan morphospecies would predate the breakup of Pangea, taking into account that the group's predominant mictic parthenogenesis can produce as much genetic variation in rotifer populations as sexual reproduction (see King, 1980). The group's high ability to passive dispersal favours the second hypothesis. A rotifer propagule can consist of a single, draught-resistant resting egg or anhydrobiotic specimen (Gilbert, 1974; Pourriot & Snell, 1983; Ricci, 1987). These are small (few have a diameter over 100 μm), hence easily transported (see Tibell,

1994). Resting eggs remain present in sediments for a long period (Pourriot & Snell, 1983; May, 1987), and have been known to hatch after 20 years of dormancy (Nipkow, 1961). Successful colonisation can start from a single individual, that can initiate a new population by parthenogenetic reproduction. The short life-cycle of rotifers (a few days from egg to adult) and high fecundity add to their colonisation capacity. Transportation by wind (e.g., as in algae: Round, 1981) is most likely responsible for long-distance dispersal of rotifer resting eggs. Although being effective, this dispersal strategy also has its limits, as illustrated by the species-poor rotifer assemblage on the isolated Easter Island (Segers & Dumont, 1993b). Transport by human activities and ornithochoric dispersal may also be important (see Dumont, 1979, 1994a; De Ridder, 1981a). However, an additional factor should be taken into account. The apparent high proportions of widely distributed taxa may be connected to the insufficiency of taxonomic resolution (e.g., see Round, 1981). In this respect, Rotifera are strikingly similar to the equally cyclic parthenogenetic 'Cladocera': a generalised cosmopolitanism was inferred for this group, until detailed taxonomical studies falsified this view (Frey, 1986; 1987). The flaws of a purely morphology-based taxonomy remain a major stumbling-block to the interpretation of distributional data (see Koste & Shiel, 1989; Ruttner-Kolisko, 1989). This is particularly relevant in a group like Rotifera, which is notorious for a wide, often environmentally induced variability in morphological characters. As far as could be ascertained, nothing is known on phenotypical plasticity and polymorphism of the lorica in *Lecane*, although these phenomena are documented in other rotifer genera (e.g., *Brachionus*, *Keratella*). Morphology-based taxonomic studies are further impeded by the consequences of the group's cyclic parthenogenesis and the possibility of hybridisation. The taxonomy of the genus *Daphnia* ('Cladocera') can serve as an example, illustrating the possible extent of confusion (e.g., *D. longispina*-group: see Wolf & Mort, 1986; Wolf, 1987; Schwenk, 1993; Taylor & Hebert, 1992; 1993). There are strong indications that the taxonomy of some rotifer genera such as *Asplanchna*, *Brachionus* and *Keratella* is similarly confused (King, 1977; Snell, 1977, 1989; e.g., *Brachionus plicatilis* (O. F. Müller): see Segers, 1995c). Several authors admit to their failure to satisfactorily resolve relations within or between certain taxa with only morphological data at hand (e.g., in *Keratella*, *Notholca*: Pejler, 1977b; *Lecane lunaris*: Segers, 1995a). This uncertainty can only be resolved

by an experimental (e.g., inducibility of variants in morphological traits, hybridisation) and/or molecular (e.g., enzyme electrophoresis, study of nucleic acids) approach, and lays a heavy burden on the biogeographical analysis.

Conclusions

In Rotifera, the degree of cosmopolitanism and endemism varies between groups as reflected in the contributions by Green (1972, 1994), Pejler (1978), De Ridder (1981a) and Dumont (1983).

(1) Compared to the pelagic Rotifera (Brachionidae: see Pejler, 1977b; Dumont, 1983), littoral *Lecane* exhibit a wide variety of distribution patterns. More than 50% of the *Lecane* have restricted distributions, ranging from point endemics to ranges encompassing several major zoogeographical regions. All regions have their share of endemic taxa, which, for some well-studied regions, varies from ca. 13 to 22% of the total morphospecies reported. This may be (1) a consequence of either or both their lower abundance and lower rate of mictic reproduction, or be (2) related to the littoral habitat, being less predictable and implying more specific adaptations.

(2) *Lecane* is tropic-centred. This is so for the widely distributed taxa, in which a majority of taxa is Tropicopolitan or Pantropical. The latitudinal variation in the distribution of widely distributed taxa as reported by Green (1972, 1994) for pelagic Rotifera, is equally evident in littoral *Lecane* rotifers. Similarly, the majority of taxa with restricted distributions are confined to tropical or subtropical regions. The tropic-centred distribution of *Lecane* and of some other groups of Rotifera is most likely secondarily. It may be a consequence of adaptations to avoid competition and/or predation by Cladocera.

(3) The faunal affinities between the major zoogeographical regions indicate the existence of a well-developed Holarctic and, especially, a Palaeotropical component in *Lecane*. These components probably result from relatively recent faunal exchange between the Palaearctic and Nearctic, and between the African, Oriental and Australian regions. The different orientation of the major mountain chains of the Eastern and Western hemisphere, and the presence of extensive arid regions in Northern Africa, Arabia and Asia seem to

have caused a difference in faunal exchange between the tropical and temperate faunas of the Eastern and Western hemisphere. The similarities between faunas of the different regions indicate that ornithochoric dispersal probably does occur, although it may not be of primordial importance.

(4) The analysis of pairs or groups of closely related taxa only rarely enables correlation between phylogeny and past geographical phenomena. Most vicariant distributions may be explained by climatological rather than by tectonical considerations. The ranges of some closely related taxa indicate that they have different capacities to dispersal, which may result from a different effectiveness of their resting eggs. Sympatric speciation can be surmised in some of the analyzed sister-taxa. Speciation through adaptation of local populations to environmental conditions that are marginal for the ancestral taxon may have occurred in such cases.

A congruent, final conclusion can be drawn from the analysis of the faunal similarity between the major zoogeographical regions, and of the relation between distribution and phylogeny between closely related taxa. In Rotifera, long-distance dispersal largely defines the ranges of morphospecies. As such, rotifer distribution patterns are more similar to those of freshwater algae than to freshwater fishes or copepods. Vicariance incontestably plays a role in the distribution of Rotifera, but its importance is generally subordinate to that of long-distance passive dispersal. The relative importance of these two factors varies according to the group considered. However, the biogeographical treatment of *Lecane* and of other groups is severely burdened by the flaws of an almost exclusive morphological approach to their taxonomy.

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