Universiteit Gent
Fakulteit van de Wetenschappen

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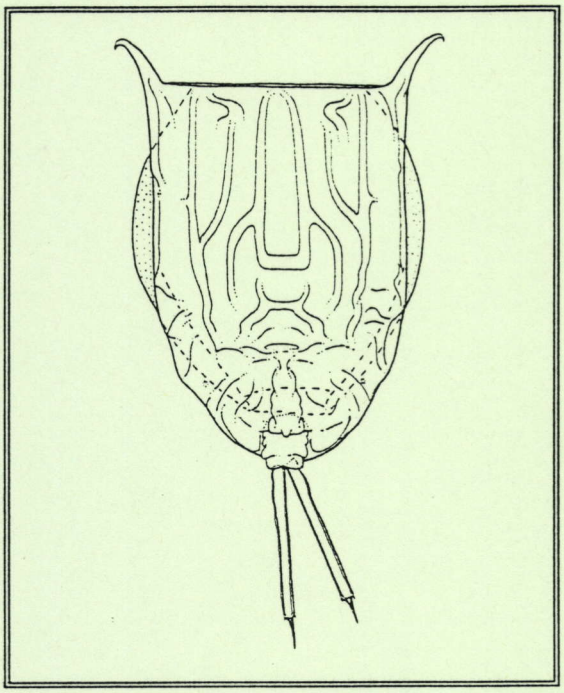
Zoogeography of littoral Rotifera, with special reference to the Lecanidae

Part I

by

Hendrik SEGERS



Proefschrift ingediend tot het
behalen van de graad van
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Promotor
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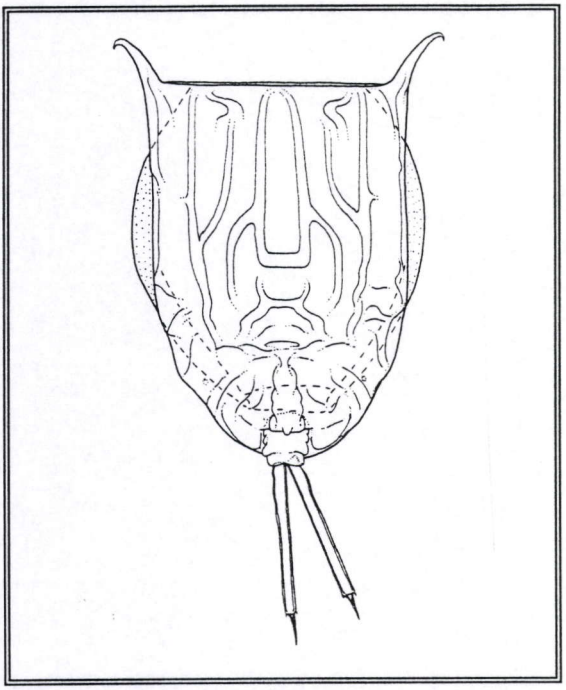

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Part I.

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SAMENVATTING

Weinig is geweten over de biogeografie van Rotifera. Dit is zeker het geval voor littorale taxa. De belangrijkste hinderpalen voor een zoögeografische studie van raderdieren zijn de beperkte taxonomische kennis en verwarring veroorzaakt door de vele verkeerde determinaties. Van alle littorale raderdieren kunnen Lecanidae als een bruikbare representatieve groep beschouwd worden. De groep is de meest soortenrijke van alle Rotifera. Determinatie van *Lecane* was tot op heden uitsluitend gebaseerd op de morfologie van de gespecialiseerde lorica. Hierdoor is het mogelijk gepubliceerde meldingen te verifiëren, voor zover deze vergezeld zijn van een originele afbeelding. Door enkel met dergelijke meldingen rekening te houden, is het mogelijk fouten, veroorzaakt door verkeerde determinaties te omzeilen.

Een eerste voorwaarde om tot een geldige zoögeografische analyse van de verspreidingspatronen bij *Lecane* te komen, is het uitvoeren van een revisie van de morfologie en de taxonomie van het genus. De resultaten van deze revisie werden gepubliceerd in een determinatiewerk (Deel II). Enkele aanvullingen en commentaren hierbij werden gevoegd bij deel I (hoofdstuk II).

De **morfologie** van *Lecane* (deel II) werd bestudeerd met behulp van licht- en rasterelectronenmicroscopie. Wat de lorica aangaat, wordt een nieuwe interpretatie van de voetstructuur voorgesteld. De term *pseudo*segment wordt gebruikt, daar het hier een groep van acoelomate dieren betreft. Slechts één voetpseudosegment wordt hier erkend. Het draagt twee gescheiden, deels of volledig vergroeide tenen. Ervoor, en het deels bedekkend is een prepedale vouw. Hiervan bestaan twee types, waarvan het voorkomen verbonden lijkt met het type van transversale vouw op de ventrale plaat van de lorica. Verschillende structuren (pedale lob, bijzondere accessorische klauwtjes, aanwezigheid van minuscule doorntjes op het hoofd) worden toegevoegd aan de lijst van loricakenmerken in *Lecane*. De detailstructuur van de trophi in *Lecane* wordt beschreven, en een vergelijking gemaakt tussen de trophi van een aantal soorten. Trophikenmerken worden voor het eerst gebruikt in de taxonomische analyse van een aantal *Lecane* morphospecies.

Wat betreft **taxonomie** wordt een aangepaste generische diagnose van *Lecane* voorgesteld. Deze nieuwe diagnose is gebaseerd op de unieke voetstructuur in deze groep, en is aangevuld met trophikenmerken. De drie voorheen onderscheiden (sub)genera worden in één taxon samengevoegd. Argumenten voor deze synonymie zijn, dat twee van de drie taxa gebaseerd zijn op één enkel kenmerk in de plesiomorfe toestand, dat twee ervan polyfyletisch zijn, en dat de intraspecifieke variabiliteit binnen een aantal morphospecies de afbakening van de drie (sub)genera overschrijdt.

In totaal worden 167 valide morphospecies behandeld, en 44 soortnamen nieuw als synoniem erkend. Veel van deze laatste betreffen inadequaat gefixeerde individuen of individuen die verkeerd geïnterpreteerd werden door een onjuiste inschatting van de intraspecifieke variabiliteit. Waar nodig, worden specifieke kommentaren toegevoegd en soortdiagnoses aangepast. In noten wordt een aantal taxa waarvan slechts één enkel individu gekend is, behandeld.

De betrouwbaarheid van een aantal kenmerken, gebruikt in de diagnose van *Lecane* morphospecies wordt bekommentariëerd. Aandacht wordt besteed aan de vorming van artefakten door onjuiste behandeling van studiemateriaal. Een aantal kenmerken wordt voor de eerste maal (type van prepedale vouw, dispositie van de dorsale ten opzichte van de ventrale loricaplaat), of voor de eerste maal consistent (aan- of afwezigheid van (pseudo)klauwtjes, vorm van het voetpseudosegment, ontwikkeling van de laterale sulci) aangewend in de taxonomische analyse.

Bijzonder belang wordt gehecht aan het aanpassen van soortnamen bij *Lecane* aan de geldende internationale regels voor zoölogische nomenclatuur.

De huidige staat van het taxonomisch onderzoek naar Rotifera wordt geëvalueerd door het totaal aantal en het aantal namen van valide taxa op en beneden het soortniveau, gecreëerd per decade, te vergelijken in de genera *Brachionus*, *Cephalodella* en *Lecane*. Taxonomisch onderzoek blijkt het meest intensief geweest te zijn gedurende de laatste decades van de 19de en de eerste decades van de 20ste eeuw en startte met de behandeling van pelagische dieren. Het recentelijk aantal gecreëerde namen per decade blijft hoog. De kwaliteit van het taxonomisch onderzoek, zoals blijkt uit het aandeel van de geldige namen op het totaal aantal gecreëerde namen, is echter relatief laag. Dit is zeker het geval voor het recente onderzoek. Dit kan het resultaat zijn van de proliferatie en verspreiding van relevante litteratuur. De kombinatie van een hoge intraspecifieke variabiliteit in raderdieren met een typologische benadering van hun taxonomie en een zwakke taxonomische opleiding spelen eveneens een rol.

In het eerste deel van het hoofdstuk over **zoogeografie** (hoofdstuk III) wordt de noodzaak om alle niet verifiëerbare meldingen weg te laten, geïllustreerd door het aanwijzen van enkele gepubliceerde verkeerde determinaties. De mogelijkheid om niettegenstaande onze strikte gegevensselektie, toch voldoende meldingen te verzamelen om tot betrouwbare verspreidingspatronen te komen, wordt geëvalueerd aan de hand van de verspreidingskaart van de waarschijnlijk meest algemene *Lecane*. Deze geeft aan dat de behandeling van verspreidingspatronen op grote schaal mogelijk is, alhoewel gegevens van een aantal belangrijke regio's ondervertegenwoordigd zijn.

Uit de analyse van verspreidingspatronen blijkt dat 41,3% van alle *Lecane* een wijde verspreiding hebben. Hieronder zijn slechts 21 (12,6%) kosmopolieten (*sensu strictu*), 26 (15,6%) zijn wijd verspreide tropische taxa. Er zijn 6 (3,6%) Arctisch-gematigd en evenveel Pantropische taxa. Niet al te veel belang moet toegeschreven worden aan de classificatie van taxa in categorieën van wijd verspreide taxa, daar breedtegraadgebonden verschillen in verspreiding grotendeels

gradueel zijn. Tien taxa vertonen een rare verspreiding. De meeste hiervan betreffen taxa met onvoldoende gedocumenteerde arealen, enkele kunnen het resultaat zijn van recente introducties. In één geval is een onvoldoende taxonomische kennis de meest plausibele verklaring.

Voor alle zoögeografische regio's konden endemieën vastgesteld worden, met een endemieratio variërend tussen 6,5% en 21,8%. Arealen variëren van lokaal, in het geval van puntendemieën, tot arealen die verschillende regio's omvatten. Dertien taxa met Holarctische verspreiding, één met wijde verspreiding op het Oostelijk halfrond, elf Palaearctische, één Australasisch en vijf met wijde verspreiding op het westelijk halfrond hebben welomschreven arealen die meer dan één regio omvatten. De Afrikaanse, Orientaalse en Australische *Lecane* fauna's vertonen een opmerkelijke overeenkomst, en vormen een Palaeotropische component. Een Holarctische component is vertegenwoordigd door gelijkende faunas in de Palaearctische en Nearctische regio's. De Palaeotropische en Holarctische componenten zijn mogelijkerwijze het resultaat van relatief recente uitwisseling van fauna-elementen tussen de Palaearctische en de Nearctische, en tussen de Afrikaanse, Oriëntaalse en Australische regio's. De verschillende oriëntatie van de belangrijkste gebergteketens van het oostelijk en westelijk halfrond, en de aanwezigheid van uitgestrekte ariede gebieden in Noord-Afrika, Arabië en Azië kunnen aan de basis liggen van het verschil in overeenkomst tussen de fauna's van de tropische en de gematigde streken van het oostelijk en het westelijk halfrond. Dispersie via trekvogels en introdukties door menselijke aktiviteiten spelen mogelijkerwijze eveneens een rol.

De analyse van paren of groepen van nauwverwante taxa laat slechts zelden toe een causaal verband te herkennen tussen tectonische verschijnselen en fylogenie. De meeste vicariante verspreidingen zijn eerder te verklaren door klimatologische dan door tectonische factoren. Uit de distributie van enkele nauwverwante taxa blijkt dat deze een verschillende dispersiecapaciteit hebben. Dit kan het gevolg zijn van een verschillende effectiviteit van hun rusteieren.

In vergelijking met pelagische raderdieren vertonen de littorale *Lecane* een relatief hoge diversiteit aan verspreidingspatronen. Bovendien heeft een groot aantal *Lecane* een beperkte verspreiding. Dit kan een gevolg zijn van hun lagere abundantie en, wellicht, een zeldzamer voorkomen van mictische reproductie. Hun minder voorspelbaar en meer specifieke adaptaties vereisend biotoop speelt hierin waarschijnlijke eveneens een rol. Net zoals *Brachionus* is *Lecane* voornamelijk tropisch, wat waarschijnlijk secundair is. Het kan het resultaat zijn van een adaptatie om competitie en/of predatie door Cladocera en, eventueel, Ostracoda, te voorkomen. Hierbij moet opgemerkt dat enkele hoogstwaarschijnlijk meer kwetsbare groepen een voornamelijk arctisch-gematigde verspreiding lijken te hebben.

Van alle zoetwaterdieren hebben Rotifera, en *Lecane* in het bijzonder, opmerkelijk grote arealen. Veel morphospecies zijn wijd verspreid en de differentiatie in regionale fauna's is relatief zwak. Hierdoor is de biogeografie van

deze groepen gelijkaardig aan die van zoetwateralgen. De meest voor de hand liggende verklaringen voor de wijde verspreiding van veel raderdieren zijn hun groot potentiëel voor passieve dispersie, gecombineerd met een korte levenscyclus en hoge fertiliteit, gevolgen van hun parthenogenetische reproductie. Dus, lange-afstandsdispersie bepaalt de arealen van de morphospecies. Vicariantie speelt zeker een rol in de verspreiding van deze dieren, maar is hoogstwaarschijnlijk van minder belang dan dispersie. De onvoldoende taxonomische resolutie kan echter mede verantwoordelijk zijn voor de grote arealen. Mogelijkerwijze faalt de hedendaagse taxonomie in het onderscheiden van oppervlakkig op elkaar lijkende soorten, daar ze bijna uitsluitend op morfologische kenmerken gebaseerd is.

SUMMARY

Little is known on the biogeography of Rotifera. This is particularly true for littoral taxa. The major hinderance to a zoogeographical study of Rotifera is the insufficient level of taxonomic knowledge, and frequent misidentifications obscuring extant distribution patterns. Of littoral Rotifera, Lecanidae is considered a suitable representative group. Firstly, it is the most specious genus of Rotifera. Secondly, the fact that identification of *Lecane* has so far only been based on morphology of its highly specialised lorica enables verification of illustrated published records. Including only verified records in the zoogeographical analysis makes it possible to overcome the consequences of incorrect identifications.

A prerogative to a sound zoogeographical analysis of distribution patterns in *Lecane* was the revision of the taxon's morphology and taxonomy. Results regarding these aspects are published in an identification guide (Part II). Some additions and comments are added in part I (chapter II).

The **morphology** of *Lecane* (Part II) is examined using light- and scanning electron microscopy. Regarding lorica morphology, an alternative interpretation of the structure of the foot is proposed. The term *pseudo*segment is used, as the group concerned is acoelomatic. Here, only a single foot pseudosegment is recognised. It bears two separate, partly or totally fused toes. It is preceded, and partly covered by a prepedal fold. Two types of prepedal fold are distinguished, which appear connected to the type of transverse fold on the ventral plate of the lorica. Several structures (pedal lobe, peculiar accessory claws, presence of minute spicules on the head) are added to the list of lorica characters in *Lecane*. The fine structure of the trophi in *Lecane* is described, and a comparison made between trophi of several species. For the first time, trophi features are considered in the taxonomic analysis of a number of *Lecane* morphospecies.

Regarding **taxonomy**, an emended generic diagnosis of *Lecane* is proposed. The new diagnosis refers to the unique foot structure in the group, and is supplemented by features of the trophi. Three previously existing (sub)genera are grouped in a single taxon. Arguments for the synonymy are, that two of the three taxa are defined on a single character in the plesiomorphic condition, that they are polyphyletic, and that the intraspecific variability within certain morphospecies surpasses the limits of their diagnosis.

A total of 167 valid morphospecies is dealt with, and 44 names newly recognised as junior synonyms. Many of these concern inadequately fixated specimens, or specimens that were incorrectly placed due to an inadequate assessment of intraspecific variability. Specific comments are added and diagnosis adjusted, whenever necessary. A number of taxa whose description was based on a single specimen is treated briefly in notes.

The reliability of a number of characters used in the diagnosis of *Lecane* morphospecies is commented upon. Attention is focused on the formation of artifacts following from inadequate specimen treatment. A number of features is used for this for the first time (type of prepedal fold, disposition of dorsal versus ventral lorica plate) or for the first time consistently (presence or absence of (pseudo)claws, foot pseudosegment shape, development of lateral sulci) in the taxonomic analysis.

An effort is made to conform *Lecane* nomenclature to the regulations of the International Code on Zoological Nomenclature.

The state of taxonomic research in Rotifera is evaluated by comparing the total number, and number of valid names established per decade in the genera *Brachionus*, *Cephalodella* and *Lecane*. Apparently, taxonomic research was most intense during the last decades of the 19th and the first decades of the 20th century, and originally focused on pelagic animals. In recent decades, the number of names established remains high. The quality of taxonomic research, evidenced by the fraction of valid names to all names established, is relatively poor, especially during the last decades. This is interpreted as a result of the proliferation and scatter of relevant literature. The combination of high intraspecific variability in Rotifera with adherence to a typological approach to their taxonomy, and neglected taxonomic education may also be relevant.

In the first section of the **zoogeography** chapter (chapter III), the relevance of our policy of discarding all non-verified records is illustrated by pointing several misidentifications that could blur distribution patterns. The approach is evaluated by considering the distribution map of the probably commonest *Lecane*. The results indicate that the level of coverage is sufficient to enable large-scale comparisons, although some important regions are under-represented in the data set.

The analysis of distribution patterns reveals that 41.3% of all *Lecane* are widely distributed. Of these, only 21 (12.6%) are cosmopolitan (*sensu strictu*), 26 (15.6%) are Tropicopolitan. There are 6 (3.6%) Arctic-temperate and Pantropical taxa. The classification of taxa in categories of widely distributed taxa should not be given too much weight, as differences in latitudinal distribution are largely gradual. Ten taxa have odd distributions. Most of these concern taxa with insufficiently documented ranges, some odd distributions may result from recent introduction. Insufficient taxonomy is inferred in one case.

Taxa, endemic to all of the major zoogeographical regions could be registered, with endemicity rates varying from 6.5% to 21.8%. Areas range from local, in the case of point endemics, to ranges, encompassing several major zoogeographical regions. Thirteen Holarctic, one widespread Eastern hemisphere, eleven Palaearctic, one Australasian and five widespread Western hemisphere taxa have circumscribed ranges encompassing more than one region. The African, Oriental and Australian *Lecane* faunas show a marked similarity, and constitute a Palaeotropical component. A Holarctic component is evidenced by the similar faunas of the Palaearctic and Nearctic regions. The Palaeotropical and Holarctic

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 may be the cause of 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 phylogeny and tectonical events. 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 to dispersal. This may result from a different effectiveness of their resting eggs.

When compared to pelagic Rotifera, littoral *Lecane* exhibit a relatively wide variety of distribution patterns, and a relatively large fraction of *Lecane* have restricted distributions. This may be a consequence of, either or both, their lower abundance and, eventually, lower rate of mictic reproduction, or be related to the littoral habitat, being less predictable and implying more specific adaptations. As in *Brachionus*, *Lecane* is tropic-centred, which is most likely secondary. This may be a consequence of an adaptation to avoid competition and/or predation by 'Cladocera' and, eventually, Ostracoda, although some groups which are likely more vulnerable to these factors do appear to be predominantly Arctic-temperate.

Amongst freshwater animals, Rotifera, and *Lecane* in particular, have relatively large ranges. Many morphospecies are widely distributed, and regional faunas are weakly differentiated. As such, the group's biogeography is most similar to that of freshwater algae. The likely explanations for the wide ranges of Rotifera are the group's high ability to passive dispersal, combined with a short life-cycle and high fecundity, consequences of their parthenogenetic reproduction. So, relatively recent long-distance dispersal defines the ranges of the morphospecies. Vicariance incontestably plays a role in the distribution of Rotifera, but its importance is generally subordinate to that of dispersal. However, insufficient taxonomic resolution may, at least partly, be responsible for the large ranges. Contemporary taxonomy may fail to distinguish between superficially similar species, as it is based almost exclusively on morphological criteria.

I. Introduction

I. INTRODUCTION

Zoogeography of Rotifera is a field that has remained underdeveloped. Until recently, Rotifera were classified as potential cosmopolites (Ruttner-Kolisko *in* Dumont, 1980), although already at that time many cases of taxa with restricted distributions were documented (Green, 1972; Pejler, 1977b; De Ridder, 1981). 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, 1980; 1983; Frey, 1986; 1987; Koste & Shiel, 1989; Nogrady *et al.*, 1993).

Regarding Rotifera, studies dealing with the distribution of selected taxa (e.g., Kutikova, 1970; Pejler, 1977b; De Ridder, 1981; 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. Most of these studies deal with pelagic organisms. The rotifer groups living in the more diversified littoral have been much neglected, 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). Most previous studies admit that poor taxonomic knowledge and frequent misidentifications strongly hinder zoogeographic analysis (Pejler, 1977b; Koste & Shiel, 1987; Segers & Dumont, 1993; Segers & De Meester, 1994).

Lecanidae was selected as a test group for a zoogeographical study of littoral Rotifera, because of the following considerations. First, the group is relatively diverse. Its single genus, *Lecane*, is the largest of the Rotifera: Koste (1978) lists 120 valid species and subspecies (286 names cited), and 'only' 88 of *Cephalodella* (206 names cited), the second most diverse rotifer genus. By considering a species-rich group, it is more likely to find examples of even the rarest distribution patterns. Also, the relative importance of the different distribution patterns can be more precisely assessed in this case. Second, identification of *Lecane* is based on the morphology of its highly specialised lorica. Consequently, and in contrast to most illoricates, it is often possible to verify illustrated literature records. Relatively many such records of *Lecane* are available, in contrast to other groups of littoral Rotifera. This is especially advantageous in our attempt to overcome the above-mentioned unreliability of published records. Thus, it was decided to consider only verified records, whether previously published or original, rather than including all available records. In a group judged 'notoriously difficult' (Nogrady *et al.*, 1993), the advantage of reliability outweighs the disadvantage of eliminating large numbers of records. The apparent taxonomic confusion in the group imposed a revision of the morphology and taxonomy of *Lecane*, prior to the zoogeographical analysis.

The morphology and taxonomy aspects of this research were included in a work, conceived as an identification book, and published in the Rotifera series (editor: T. Nogrady; editorial committee: R. Chengalath and R. Shiel) of the 'Guides to the Identification of the Microinvertebrates of the Continental Waters of the World' (editor: H.J. Dumont; see Part II).

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II. Morphology and Taxonomy

II. Morphology and Taxonomy

II.1. Introduction

To date, studies on the morphology and taxonomy of *Lecane* had only been performed using light microscopy. Trophi morphology had largely been neglected. In an initial stage of this work, it became apparent that this hiatus needed addressing. A study of the external and trophi morphology using scanning electron microscopy (SEM) was performed, prior to the taxonomic treatment of individual *Lecane* species. Results on morphology and taxonomy of *Lecane* are presented in Part II (Segers, 1995a), together with comments relevant to specific cases. Part II contains only preliminary reports on the distribution of *Lecane* taxa. References to figure and page numbers in the following refer to that work. Here, some recent additions to *Lecane* taxonomy are included, and some general considerations formulated.

Previously, the most complete coverage of the genus was by Koste (1978), who treated 120 valid species and subspecies (50 additional 'varieties' and 'forms'), from a total of 286 names cited. Harring & Myers (1926) had included only 109 valid species in their historical revision. In Part II, 163 valid morphospecies from 433 names are treated, and an additional four morphospecies are added here.

II.2. Material and methods

The material examined consisted of living or, mostly, preserved animals, the latter contained in formaldehyde (4%)-treated samples from various regions of the world. For light microscopy, animals were picked out under a Wild M10 dissection microscope and transferred to a glycerine - formaline mixture in glass slides. These were sealed with glyceel or DePeX mounting medium (prod. 36125, Gurr®). This method is quick, and has the advantage that specimens can be recovered easily from the slide. It is also safe, as could be judged from examining the condition of similar slides, made by F. Myers in the 1930's. A reference collection of such slides is kept in the laboratory. This collection also contains paratypes of recently described species and, additionally, a number of slides by J. Hauer, some of which also contain type specimens. Other type material could be traced in few cases only (see Part II). Specimens were examined under high magnification (1000x, oil immersion) using a Kyowa Medilux 12 or an Olympus CH2 microscope. Drawings were made with a camera lucida.

Scanning electron microscopy was performed on complete specimens, after dehydratation of the material in alcohol, critical point drying, and sputter-coating with gold. A technique, similar to that of Sanoamuang & McKenzie (1993), was developed in an attempt to use SEM of trophi in the taxonomic analysis. Selected animals are washed with distilled water and moved to a circular cover slide (diameter 0.8 or 1 mm). Trophi are then isolated by adding a small drop of NaOCl, and washed five to ten times with distilled water, by subsequently adding and removing liquids with a micropipette. The entire procedure is performed under a Wild M10 dissection microscope. The preparation is then left to dry overnight, sputter-coated with gold and examined with a JEOL JSM-840 Scanning electron microscope. The technique proved little efficient in the case of *Lecane*, due to the difficulty of extracting trophi from the lorica and the generally large similarity of *Lecane* trophi (see figs 34-61, 519-522 in Part II; figs 531-532, 539-540, 543-544, 547-548; but see further). It was applied successfully in the analysis of *Itura* and *Scaridium* (Segers, 1993; 1995b; Segers & De Meester, 1994; Segers *et al.*, 1994b) and of Brachionidae genera (Segers *et al.*, 1993a).

II.3. Results and Discussion

II.3.1. *Morphology*

Morphology of *Lecane* has been inadequately studied. Especially, the structure of the foot has been misinterpreted (Harring & Myers, 1926; Voigt, 1957; Koste, 1978; Koste & Shiel, 1990). As can be seen in figure 21 (also figs 20-28: Part II), the foot consists of a single pseudosegment (fp) bearing the toe(s). It is preceded and partly covered by an elongate region, the prepedal fold (pf). Lateral to the foot pseudosegment are coxal plates (cp) and extracoxal folds (ef). Most authors, starting with Harring & Myers (1926), discern two foot segments: a first, fused to the ventral plate (here: prepedal fold), and a second, mobile one. Koste & Shiel (1990) even recognize three foot segments.

Firstly, since Rotifera are acoelomatic, one cannot speak of true segments. A more appropriate term is pseudosegments. That not two, but only a single foot pseudosegment is present in *Lecane* can be appreciated from figs 20-25. The coxal plates and prepedal fold have a surface structure which is similar to that of the ventral plate. They are not separated from this ventral plate, in contrast to the mobile foot pseudosegment which is clearly distinct and lacks the surface ornamentation, if any, of the ventral plate. Thus, it is more likely that the prepedal fold is a specialised region of the ventral plate, rather than being part of the foot. It should be noted that, under this interpretation, the position of the pore(s) (fig. 23, see further; of the pedal gland?) is quite unique: in other Rotifera, openings of the pedal glands are reported to be situated terminally on the foot, near the basis of the toes. Adjusting our interpretation of foot structure to conform to that would imply that the toe consists of a single basal part and a pair (totally or partly fused or separate) of terminal, elongate parts. The pedal lobe (fig. 33) is situated dorsally near the insertion of the toes. This is similar to its position in other genera where it has been recorded (*Encentrum* of Dicranophoridae (Wulfert, 1950; 1960; Althaus, 1957), *Proales* of Proalidae and some *Notommata* species (Notommatidae. Jersabek, 1994). Its function has so far only been inferred.

Two types of prepedal fold are distinguished: The first type (e.g., fig 23) has a narrow and elongate fold, with a single, superficial pore; the transverse fold is always incomplete and, mostly, longitudinal folds are present (fig. 8). The second type (fig. 24) has a broad and posteriorly rounded prepedal fold, with a pair of covered pores. Here, the transverse fold is either complete, lunate (fig. 1) or incomplete, but longitudinal folds are never present. Only in few taxa could the prepedal fold type not be ascertained, due to observation difficulties. As this difference divides *Lecane* in two groups, without any apparent intermediates and without exhibiting any noticeable variability, it was used successfully as a diagnostic feature.

The presence of a pedal lobe (figs 27, 33) in all taxa, that of some, or of a fringe of accessory claws in taxa such as *L. arcula* Harring (fig. 29) and *L. eutarsa* Harring & Myers (fig. 30-31), and of a row of minute spicules on the head (*L.*

palinacis Harring & Myers: fig. 78, *L. dumonti* Segers: figs 336-338, *L. bifurca* (Bryce): fig. 353) had not been reported before.

II.3.2. *Taxonomy*

II.3.2.1. Introduction

Relying largely on morphological data in conducting a taxonomic study imposes limitations. It is clear that conclusions on the relation between presumed conspecific populations are tentative to a certain extent. 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 confuse (King, 1977; Snell, 1977, 1989; e.g., *Brachionus plicatilis* (O.F. Müller): see Segers, 1995c). Some of these problems have been discussed on several occasions (e.g., Pejler, 1977a; Dumont, 1980; Koste & Shiel, 1989; Ruttner-Kolisko, 1989). The confuse taxonomy is illustrated by the frequent use and misuse of the subspecific and of infrasubspecific categories for taxa that are diagnosed solely on morphological criteria (see Pejler, 1977a; Segers, 1993, Part II). 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*: see Pejler, 1977b; *Lecane lunaris* (Ehrenberg): see p. 166-168: Part II). 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.

On the other hand, the present state of knowledge in rotifer taxonomy is so confused that it is often even difficult to delimit relevant taxa on which such experimental approach would yield further insight into the phylogenetic relations. This especially applies to a group like *Lecane*, which contains a large number of taxa, many of which are inadequatly described. The morphological approach taken here intends to enlarge and refine our knowledge on morphology, morphological variability and diversity within this complex and largely unexplored group. It is a prerogative for a zoogeographical analysis (see chapter III). The relevance of this approach is illustrated by our attempt towards an evaluation of taxonomic research on Rotifera (see below, II.5.).

It should be stressed that all of our comments are restricted to characters of the female. This is merely because too little is known about male lecanids. These are reported in few taxa only (figs 62, 508-516, and *L. leontina* (Turner); see Part II). Male *Lecane* rotifers are rare, and, when found, only with difficulty associated with the corresponding female. They have a strongly reduced morphology, and no lorica, specialised foot or trophi. The degree of fusion of the toes does seem to correspond between the sexes (Sudzuki, 1964). Similarly, resting egg morphology has not been considered. This is again due to the fragmentary nature of the available knowledge, resulting from the fact that resting eggs are rarely found, especially in association with the corresponding female.

I.3.2.2. Family Lecanidae

According to Bartoš (1959), Koste (1978) and Nogrady *et al.* (1993), who borrow from Harring & Myers (1926), the taxon is diagnosed principally by having a stiff lorica. Additional diagnostic features mentioned are the partial fusion of the toe with the ventral lorica, a trend towards fusion of the toes (Koste, 1978), and the presence of lateral sulci and of a foot, projecting through the ventral plate (Nogrady *et al.*, 1993). Koste & Shiel (1990) record an undivided lorica and a foot with three 'segments'.

A diagnosis referring to the presence of a stiff lorica is not widely applicable, considering the existence of illoricate *Lecane* (see Voigt, 1957). A trend towards fusion of the toes is also present in some Colurellidae (e.g., the 'subgenus' *Xenolepadella* in *Lepadella*, some *Colurella* species). Lateral sulci are occasionally absent, even in many loricate taxa. The foot can be said to project through the ventral plate in other rotifer taxa, e.g. Mytilinidae, *Lepadella*, but hardly in *Lecane*. The inadequacy of the generic diagnosis caused severe confusion, and resulted in the incorrect assignment of some illoricate taxa (e.g., *L. longidactyla* (Edmondson, 1948)) or badly contracted specimens (e.g., *L. namibiensis* (Koste & Brain, 1993)) to the related Proalidae. These considerations and the present revision of *Lecane* morphology lead to a new diagnosis of *Lecane*, based on to the structure of the foot and supplemented by trophi morphology (Part II).

The family contains a single genus. A subdivision in three subordinate taxa, whether of generic (e.g., Harring & Myers, 1926; Bartoš, 1957; Koste & Shiel, 1990) or subgeneric (Koste, 1978) rank is rejected (see Segers, 1993; also Edmondson, 1935; Wiszniewski, 1954; Part II).

II.3.2.3. Trophi morphology

Although of primary importance in the taxonomy of illoricate rotifers, trophi morphology had hardly been considered in loricates like *Lecane*. Little information on *Lecane* trophi was available (e.g., De Smet & Bafort (1990) on *L. pumila*

(Rousselet); Koste (1983) on *L. leontina*; Koste & Robertson (1990) on *L. clara* (Bryce)). An attempt is here made to incorporate trophi characteristics in the diagnosis of taxa at the morphospecies level, using SEM and light microscopy. For this, the trophi of sixteen taxa were examined (figs 34-61, 519-522, 531-532, 545-551). The trophi structure of all taxa examined exhibits a large overall similarity. Some closely related taxa share peculiarities of trophi structure, not found in other congeners. Examples are the shape of antero-median projections of the preuncinal plate in *L. latissima* Yamamoto and *L. thailandensis* Segers & Sanoamuang (Segers & Sanoamuang, 1994), and the presence of a terminal, dorsad projection on both manubria in *L. closterocerca* (Schmarda), *L. boliviana* Segers and *L. fadeevi* (Neiswestnowa-Schadina)(see II.3.2.5., figs 546-551; Segers, 1994b). Minor differences in trophi morphology between closely related congeners could be observed (Segers, 1994a), although no attempt was made to assess intraspecific variability of these structures. Even in groups where trophi morphology is commonly applied taxa has variability in trophi characters been documented in few cases only (e.g., Notommatidae: *Cephalodella gracilis* (Ehrenberg): see Donner, 1970; Dicranophoridae: *Dicranophorus kostei* Pourriot & Zoppi de Roa: see Segers & Sarma, 1994). Major constraints hindering the use of throphi characters in the taxonomy of *Lecane* are their small size and fragility, and the fact that small differences in observation angle strongly hamper the interpretation of the features.

II.3.2.4. Lorica morphology

II.3.2.4.1. *Influence of treatment and formation of artifacts*

As mentioned in the general introduction, taxonomy of *Lecane* is based on the specialised and stiff lorica of most representatives of the group. However, the integument in some taxa 'can not by any stretch of the imagination be called a lorica' (Harring & Myers (1926), on *L. bifurca*). Consequently, diagnosing such illoricate taxa by body shape (see Koste, 1978; Koste & Shiel, 1990; e.g., see *L. clara*: figs 70-73) is inadequate, although some similarity in body shape is seen in contracted conspecific specimens. (Harring & Myers, 1926; e.g., figs 76-78; 79-82, 298-300, 350-353). Only foot and toe morphology are left as basis for a diagnosis in such forms.

The lorica and, especially, head aperture shape have been applied widely in the diagnosis of *Lecane* taxa (Harring & Myers, 1926; Koste, 1978; Koste & Shiel, 1990; Voigt, 1957). The lorica consists of flexible plates connected by soft membranes. Its precise shape is dependent on the quality of the material (e.g., whether dead or live specimens were collected), but also on the treatment of the samples (e.g., fixative and/or preservative used). The misinterpretation of differences in shape resulting from varying quality or treatment of the material is probably the most important source of confusion in *Lecane* (Koste, 1978). Illustrative of this is the comparison of figures 237-238 with figure 239, and 390, 391 with 392,

representing well-contracted versus incompletely contracted specimens of *L. flexilis* (Gosse) and *L. furcata* (Murray), respectively. Here, the relative length of the lorica and head aperture shape differ noticeably. In both cases, differently contracted specimens were named as separate species (*L. glypta* Harring & Myers and *L. mologensis* (Bogoslovsky), respectively; see also *L. hastata* (Murray): p. 86-88; *L. hornemanni* (Ehrenberg): figs 90-97, Segers, 1992; *L. pyriformis* (Daday): Segers *et al.*, 1992; *L. subtilis* Harring & Myers: see p. 84; *L. stichaea* Harring: p. 119-120, ...). That this difference indeed results from a difference in degree of contraction was confirmed by observing living *L. flexilis*. The body and lorica of these can be seen to extend and contract while the animal moves around. It should be noted, however, that relative width of the lorica was confirmed as a feature adding to the differentiation between *L. aculeata* (Jakubski) and *L. arcula* (compare figs 264-265 and 266-267; Segers & Dumont, 1993; see also differentiation of *L. braziliensis* Segers and *L. inopinata* Harring & Myers: p. 130-133).

The shape of the head aperture margins is another character that, although widely considered of taxonomic importance, is dependent on contraction. More or less drastic differences can be seen in cases where the lorica is distorted (e.g., *L. mira* (Murray): see Pawłowski, 1938; *L. undulata* Hauer: figs 322-326). Small changes in degree of retraction of the head aperture margins occur frequently (e.g., from slightly convex to straight, from straight to slightly concave,... see figs 478-481), as well as differences in relative position of the ventral and dorsal head aperture margins (e.g., figs 188-189, 195-196). The cases of *L. lunaris* and *L. hamata* (Stokes) are especially illustrative: head aperture shape is reported to be the most important character distinguishing taxa around *L. lunaris* (Figs 421-428, 438), together with toe length and size. However, the extant variability is of such magnitude, that no reliable diagnosis can at present be formulated. On the other hand, whereas head aperture shape varies in *L. hamata* (figs 489-501), the character appears relatively constant in some closely related taxa. Hence, head aperture shape can be part of their diagnosis: in *L. thienemanni* (Hauer)(figs 502-504), the antero-lateral spines are noticeably and constantly more pronounced than in *L. hamata*. The distinction between *L. hamata* and *L. marchantaria* Koste & Robertson (fig. 505) is less satisfactory; here, however, additional information is required before any taxonomic change can be justified.

Fixation and contraction appear to have only a marginal effect on the shape of special formations on the head aperture margins: shallow lobes (e.g., *L. papuana* (Murray): figs 191-194; *L. arcuata* (Bryce): figs 478-481) or antero-lateral spines (e.g., *L. curvicornis* (Murray): figs 226-230; *L. satyrus* Harring & Myers: figs 259-260, *L. boettgeri* Koste: figs 261-263; *L. aculeata* and *L. arcula*: figs 264-267) retain their general shape, and remain recognisable in diversely contracted specimens. Their position relative to the dorsal plate can vary (see *L. papuana*: p. 78). The diagnostic value of such traits can therefore be confirmed (e.g., differentiation of *L. sympoda* Hauer and *L. inopinata*; *L. furcata* and *L. acanthinula* (Hauer); *L. closterocerca* and *L. boliviana*). An exception is the *L. leontina* specimen of figure 219. It lacks the antero-lateral spines of the animals drawn in

figures 217-218. In *L. obtusa* (Murray), minute antero-lateral spicules may occasionally be present (figs 375-377; Hauer, 1938). Cases in which the shape or inclination of the antero-lateral spines was found to vary are rare, but do exist (e.g., *L. ludwigii* (Eckstein): fig. 157; *L. climacois* Harring & Myers: fig. 214).

The variability in lorica ornamentation (e.g., *L. signifera* (Jennings): compare figs 122 with 123 and 125; *L. curvicornis*: figs 228 and 229; *L. furcata*: figs 390 and 391) has also been ascribed to differences in contraction, at least as far as the ornamental folds are concerned (e.g., Koste, 1978; Koste & Shiel, 1990). That this is indeed likely is illustrated by figures 7, 8 and 13. These ornamented specimens are more strongly contracted (critical point dried) than the remaining, non-ornamented specimens in the sample from which they were extracted (compare fig. 8 with 391 and fig. 11 with 460-461). A single sample may contain both ornamented and non-ornamented specimens of taxa such as *L. curvicornis* (e.g., figs 227-228) or *L. leontina* (e.g., fig. 217). These ornamented and non-ornamented specimens received the same treatment. The origin of this variation is not known (resulting from a different reaction to the same treatment in different, co-occurring subpopulations?). The feature varies independantly of some other variable characters in the two morphospecies concerned. Hence, they are treated as variable taxa, following Koste (1978).

In some cases, on the other hand, have pairs of taxa been retained in which lorica ornamentation is an important diagnostic feature. These are *L. latissima* and *L. thailandensis* (figs 46-49, 177 and 517-525, respectively), *L. galeata* (Bryce) and *L. myersi* Segers (figs 371-372 and 373-374) and *L. decipiens* (Murray) and *L. serrata* (Hauer)(figs 506 and 507). The ornamentation here not merely consists of folds (e.g., as in figs 523-524), but of peculiar structures (e.g., fig. 523) that are present in one, and absent in the other taxon. Additional differences in ecology and range (*L. latissima* an Arctic-temperate, *L. thailandensis* a warm-water, Oriental taxon; *L. galeata* Holarctic, *L. myersi* Tropicopolitan) and toe shape (armed with minute spines in *L. thailandensis*; relatively elongate in *L. galeata*), and differences in trophi morphology between *L. latissima* and *L. thailandensis* (see Segers & Sanoamuang, 1994), further support the separation of the taxa concerned. The case of *L. decipiens* and *L. serrata* may be similar, but here the situation is more confuse. Only the presence or absence of ornamentation separates the two. They appear to have overlapping ranges, and co-occur occasionally (Segers *et al.*, 1993b).

Differences in degree of contraction are also inferred as a source of variation regarding position of the foot pseudosegment relative to the ventral plate. It may project beyond the posterior margin of the foot plate, or not. The taxonomic relevance of this easily assessed character had hardly been questioned. Yet in borderline cases where the foot pseudosegment reaches the posterior edge of the foot plate, specimens may be found in which the structure does project (e.g., *L. jaintiaensis* Sharma: see p. 55-57; *L. stichoclysta* Segers: compare fig. 256 and 257; *L. closterocerca*: figs 471-477).

II.3.2.4.2. *Comments on some characters of inconsistent taxonomic relevance*

It is striking that a number of features may exhibit negligible variability in one taxon, while their variability may be considerable in others. This is so for some of the characters treated above, but is also evident in other traits. Some illustrative cases concern the structure of the foot and toe(s). These features are widely used in the diagnosis of *Lecane* taxa, as they are relatively easy to assess (but see *L. remanei* Hauer: p. 46, *L. proiecta* Hauer: p. 73; *L. haliclysta* Harring & Myers: figs 280-285), and relatively stable. In some taxa, however, has considerable variability been observed in otherwise stable features:

- **Foot pseudosegment shape** is constant and, hence, diagnostic in *L. rhytida* Harring & Myers and relatives (see figs 115-121), *L. sagula* (Harring & Myers)(figs 206-207), *L. eutarsa* (fig. 276-277), *L. kutikowa* Koste (278-279), *L. haliclysta* (280-285), and many others. It is surprising that the character had been cited only rarely in the diagnosis of taxa before (in *L. sola* Hauer, *L. rhytida*, *L. sagula*, *L. kutikowa*: see Koste, 1978). On the other hand, the lateral margins of the foot pseudosegment are variable in *L. hamata* and relatives (figs 484-505), *L. closterocerca* (figs 536-543) and a few others. The foot pseudosegment is relatively simple in these cases. The observed variability may result from a difference of retraction of the toe into the foot pseudosegment.

- **Toe shape** serves as main the diagnostic feature for the separation of *L. obtusa* (figs 375-377) and *L. psammophila* (figs 368-369), *L. lunaris* (figs 421-428, 438) and *L. rhopalura* (Harring & Myers)(figs 436-437), *L. closterocerca* (figs 10, 471-477) and *L. fadeevi* (figs 538-540), and *L. gwileti* (Tarnogradski)(fig. 400) and *L. asymmetrica* (Murray)(figs 398-399), but is not considered in *L. stenroosi* (Meissner)(figs 455-457), and the toes are variably swollen in *L. paradoxa* (Steinecke)(figs 308-311). The diagnosis of the two latter taxa, however, is based on easily interpreted characters of the lorica. Regarding *L. stenroosi*, there are at present no data casting doubt on the hypothesis by Wulfert (1966), supported by Koste (1978), that this variability is of infrasubspecific relevance only. That toe shape is variable is *L. paradoxa* follows from our material from Saudi Arabia (Segers & Dumont, 1993), and from a comparison of relevant published drawings (see Part II).

- The **degree of fusion of the toe** separates taxa in the groups of *L. pusilla* Harring (figs 200-201), *L. undulata* (figs 322-326), *L. inopinata* (figs 327-329) and *L. furcata* (figs 333, 390-392); *L. kluchor* Tarnogradski (figs 302-303) and *L. syngenes* (Hauer)(figs 304-305); *L. minuta* Segers (figs 306-307) and *L. pyriformis* (figs 466-470); *L. nwadiaroi* (figs 348-349), *L. blachei* Bērziņš (figs 345-347), *L. stephensae* (Hutchinson) (figs 453-454), *L. symoensi* De Ridder (fig. 483) and *L. unguitata* (Fadeev)(figs 451-452). Some variability was observed in a few cases only (e.g., figs 304-305; 390-391). *L. blachei* is particularly noteworthy here, as its

toe was recorded to be fused both basally and distally, leaving a median fissure (Bērziņš, 1973; Koste, 1978; Koste, 1988; Sarma, 1988a). Close examination, however, reveals that the distal part of the toes is not fused, but only touches together (figs 345, 347). The toes spread when some pressure is applied to the specimens (fig. 346).

- The **fusion of the pseudoclaws** is always complete in *L. quadridentata* (Ehrenberg)(figs 366, 367), *L. lamellata* (Daday)(fig.408) and *L. thalera* (Harring & Myers)(fig. 409), but the (pseudo)claws are always separate in *L. furcata* (figs 390-392) and *L. lunaris* (figs 421-428); they are either fused or separate in *L. bulla* (Gosse)(figs 358-362), *L. cornuta* (Müller)(figs 439-443) and *L. stenroosi* (figs 455-457). The interpretation of this variability in *L. bulla* and *L. cornuta* as taxonomically irrelevant is tentative, as literature records of this character are particularly unreliable (see Dartnall & Hollowday, 1985) due to observation difficulties.

Interpreting the presence or absence, and difference in shape of a posterior projection on the foot plate (see fig. 19) has long been problematic. Here, distinction is made between cases in which such a projection is either absent or present, and cases in which it is always present, but variable in shape. Examples of the first are *L. batillifer* (Murray)(figs 484-485) and *L. hamata* (e.g., fig. 486), and *L. donyanaensis* Mazuelos & Segers (fig. 526) and *L. ungulata* (Gosse)(fig. 221). In both these pairs, the first-listed taxon is with, the second is without posterior projection. Moreover, the first-listed both pairs is rare and has a restricted distribution, whereas the second is a common cosmopolitan. *L. thalera* and *L. lamellata* are interpreted similarly, although they have overlapping ranges. Rare intermediate forms between these two are preliminarily interpreted as interspecific hybrids (see Pejler, 1956; Nogrady *et al.*, 1993; III.4.7.3., Part II). Some variability in shape of posterior projection is noticeable in those taxa in which it is present (figs 484-485). A variable posterior projection is always present in *L. ligona* (Dunlop), *L. ludwigii* and *L. leontina* (e.g., figs 146-153, 154-174, 217-220). That the variability in shape of the posterior projection represents mere intraspecific variability was previously accepted for *L. leontina* only (Koste, 1978). In *L. ligona* and *L. ludwigii*, taxa were recognised and named in sometimes remarkable and, especially in *L. ludwigii*, ever changing combinations of the species, subspecies, and different infrasubspecific ranks (Koste, 1978; Koste & Shiel, 1990; Koste & Böttger, 1992). The case of *L. depressa* (Bryce) and *L. ligona* combines both possibilities: a posterior projection in absent in *L. depressa* (figs 132-135), and present but variable in *L. ligona* (146-153).

II.3.2.4.3. *Other comments*

The existence of two types of prepedal fold had not been recognised before, ant this character is here newly used. The same holds for the patterns of folds on the ventral lorica. Bērziņš (1982) was the first to mention completeness of the transverse fold in a diagnosis, although it is likely that he misinterpreted the material before him. Koste (1988) used the character successfully in the distinction between *L. elsa* Hauer and *L. braumi* Koste. The feature appears to be invariable, and is applied consistently here. The confusion between *L. braumi* and *L. elsa*; *L. lunaris* and *L. cornuta* (complete versus incomplete transverse fold), and *L. furcata* and *L. scutata* (Harring & Myers)(longitudinal folds present or absent, respectively) in literature probably results from the fact that the relevance of the above-mentioned character was not recognised.

The relative width of the ventral and dorsal plates was cited by Wang (1961) as a diagnostic feature in his *L. hornemanni* (misidentified *L. thailandensis*, see Segers & Sanoamuang, 1994), and was mentioned for *L. obtusa* by Koste (1978). The character is constant in all loricate *Lecane*. However, confusion has arisen from uncareful examination (e.g., see *L. rudescui* Hauer: p. 47). Compression of the material may result in a widening of the domed dorsal plate (less of the already flat ventral plate), hampering the appreciation of the character. Using it permitted the formulation of a more reliable diagnosis in many taxa (e.g., *L. uenoi* Yamamoto (figs 312-314) versus *L. rugosa* (Harring & Myers)(figs 393-395; *L. paradoxa* (figs 308-311) versus *L. inconspicua* Segers & Dumont (figs 339-340)), and to unravel the taxonomy of *L. depressa*, *L. mitis* Harring & Myers and *L. levistyla* (Olofsson)(see pp. 58, 61, II.3.2.5.), and of *L. fadeevi* and *L. psammophila* (see II.3.2.5.).

The lateral margins of the dorsal plate may or may not reach the head aperture. Although variable in a few taxa (e.g., *L. elsa*: fig 195-196), the character appeared useful in the diagnosis of such taxa as *L. curvicornis* (figs 226-233), and *L. lamellata* and *L. thalera* (figs 208-209). The distinction of *L. hamata* (figs 486-501) and *L. decipiens* (fig. 506) now relies on this character, rather than to the head aperture margins being coincident or not (Koste, 1978; Koste & Shiel, 1990). Most illustrated records of *L. decipiens* turned out to be misidentified *L. hamata*.

The lateral sulci can be superficial or deeply invaginated. This depends slightly on contraction and, probably, state of the specimens, but was nevertheless found useful in the distinction of taxa such as *L. hornemanni* (90-97) and *L. nelsoni* Segers (figs 103-104), and, especially, the commonly confused *L. furcata* (figs 390-391) and *L. scutata* (figs 429-431).

The presence or absence of lateral antennae (see fig. 16) was listed by Koste (1988) in the original diagnosis of *L. braumi*, differentiating this taxon from *L. elsa*. This can not be confirmed, as these antennae appear to be present not only in both these taxa but, in fact, in all *Lecane*.

II.3.2.5. Additions

Recent additions to the knowledge of *Lecane* are as follows. Species and figure numbers follow on from, and conventions are as in Part II.

150. *Lecane broaensis* Segers & Dumont, 1995
Figs 529-532

Segers & Dumont 1995 figs 21-24

Type locality and types
Broa reservoir, São Paulo, Brazil. Holotype and paratype in the KBIN, paratype in RUG.

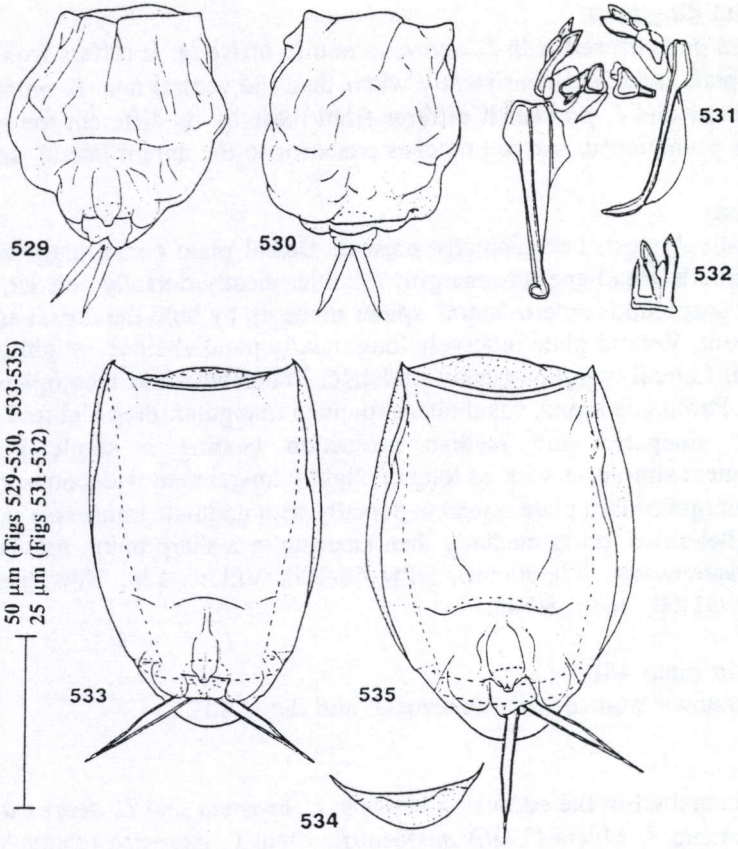
Differential diagnosis
L. broaensis is one of the few illoricate *Lecane* species. It is characterised by the shape of its parallel-sided toes bearing weakly separated, eccentrically inserted and curved claws, its foot pseudosegment with weak lateral lobes and by the presence of rounded coxal plates.

The species can be confused with *L. nana* (Murray) by their similar foot pseudosegment and toe shape. The absence of a stiff lorica distinguishes the species easily. *L. broaensis* keys out to *L. inermis* (Bryce), *L. elegans* Harring and *L. margalefi* De Manuel, but it can hardly be confused with any of these.

Description
Body soft, slightly longer than wide. Anterior margins more or less straight, precise body shape variable. Prepedal fold narrow, elongate, with median projection. Coxal plates rounded. Foot pseudosegment with weak lateral projections, covered or projecting. Toes parallel-sided, fused basally, mobile. Claws weakly separated bilaterally, inserted eccentrically and curved. Trophi: see figs 531-532.

Measurements: Lo l. 64-71, Lo w. 54-63, toe l. 18-20, claw l. 5-6. Trophi: manubrium l. 14, uncus l. 6, incus w. 7, fulcrum l. 3.

Distribution
Known from the type locality only.



Figs 529-532: L. broaensis Segers & Dumont. 529: ventral view; 530: dorsal view; 531: trophi, ventral view; 532: right uncus, anterior view.
Figs 533-535: L. mitis Harring & Myers. 533, 535: ventral views; 534: posterior part of foot plate, dorsal view.
(529-535: after Segers & Dumont, 1995).

151. *Lecane mitis* Harring & Myers, 1926

Figs 533-535

L. depressa after Harring & Myers (1926)
L. levistyla depressa after Zoppi de Roa *et al.* (1990)

Harring & Myers 1926 p. 329 plate 11 figs 3-4; Segers & Dumont 1995 figs 25-27.

Type locality
Gravelly Run, near Atlantic City, New Jersey, U.S.A.

Differential diagnosis

L. mitis can be confused with *L. depressa* and *L. levistyla*. It differs from these by its dorsal plate, which is consistently wider than the ventral one. *L. mitis* keys out to *L. signifera* and *L. pyrrha*. It differes from these by its different toe shape, and absence of pronounced, smooth notches posterior to the antero-lateral spines.

Description

Lorica relatively soft, but distinctly present. Dorsal plate consistently wider than ventral, smooth. Head aperture margins flexible, mostly dorsally convex, ventrally concave. Conspicuous antero-lateral spines made up by both the dorsal and ventral plates present. Ventral plate relatively long, nearly parallel-sided, slightly wider in distal third. Lateral margins weakly undulate. Transverse fold incomplete. Lateral sulci deep. Foot plate broad, coxal plates rounded triangular. Prepedal fold relatively broad but elongate, with median projection bearing a single pore. Foot pseudosegment simple, as wide as long or slightly longer than wide, non-projecting. Posterior margin of foot plate rounded, dorsally with undulate transverse ridge; Toes short, parallel-sided up to medially then tapering to a sharp point, no claws.

Measurements: DPl. 90-110, DPw. 66-100, VPl. 95-130, VPw. 64-80, head aperture w. 51-60, toe l. 30-45.

Distribution (map 46)

L. mitis is known from Brazil, Venezuela, and the U.S.A.

Comments

L. mitis succumbed in the confusion between *L. levistyla* and *L. depressa* by most authors. Harring & Myers (1926) misidentified real *L. depressa* (characterised by the dorsal plate being consistently narrower than the ventral one, see figs 132-135) as *L. brachydactyla*, and described it as new under the name *L. tudicola*. A similar misfortune happened to the real *L. levistyla* (with an anteriorly narrower, medially wider dorsal than ventral plate, figs 138-141), probably due to the poor original description of this species. It was described as new under the name *L. scobis*. A third species was recognised (dorsal plate consistently wider than the ventral, see figs 533-535). This third species was misidentified as *L. depressa*, and described as new under the name *L. mitis*.

Most subsequent workers followed the identifications by Harring & Myers (1926). As a result, *L. brachydactyla* and *L. tudicola* became the commonly used names for real *L. depressa*. The synonymy of *L. levistyla* and *L. scobis* was established by Wiszniewski (1934). The latter author also established the synonymy of *L. depressa* and *L. mitis* (as *L. depressa mitis*), probably based directly on Harring & Myers' (1926) figures. Records of *L. depressa* and *L. mitis* from the following period are few.

Koste (1978), too, followed Harring & Myers' (1926) and Wiszniewski's (1954) identification of *L. brachydactyla*, *L. tudicola* and *L. levistyla*, although the identity of the latter was further confused by his (Koste, 1972) misidentification of

a weakly ornamented *L. signifera* (different toe and head aperture shape) as *L. levistyla*. Moreover, he synonymised *L. depressa* with *L. levistyla*, incorrectly giving priority to the junior synonym, *L. levistyla*, in the combination *L. levistyla* f. *depressa*. *L. mitis* was only mentioned in his list of species that were excluded from the key.

Segers & Dumont (1995), finally, reestablished *L. mitis* as a valid species. The large variability in lorica morphology (compare figs 533 and 535), most likely resulting from differences in contraction, confirms the opinion of Wiszniewski (1954), that this *L. mitis* and Harring & Myers' (1926) *L. depressa* belong to the same species.

152. *Lecane fadeevi* (Neiswestnowa-Shadina, 1935)

Figs 538-540, 550-551

Synonym: *L. fadeewi* (Wiszniewski, 1954) Voigt, 1957

L. closterocerca after Pawłowski (1956, 1958), partly.

Neiswestnowa-Shadina 1935 p. 561-562 figs 7, 8 (*Monostyla fadeevi*); Wiszniewski 1954 p. 69 (*Monostyla fadeewi*); Voigt 1957 p. 238; Kutikova 1970 p. 469 (*Monostyla fadeevi*); Koste 1978 p. 245 (*M. fadeewi*); Segers 1994b p. 235-238 figs 1-5 (*Lecane fadeevi*)

Type locality

Oka River near Murom, European Russia.

Differential diagnosis

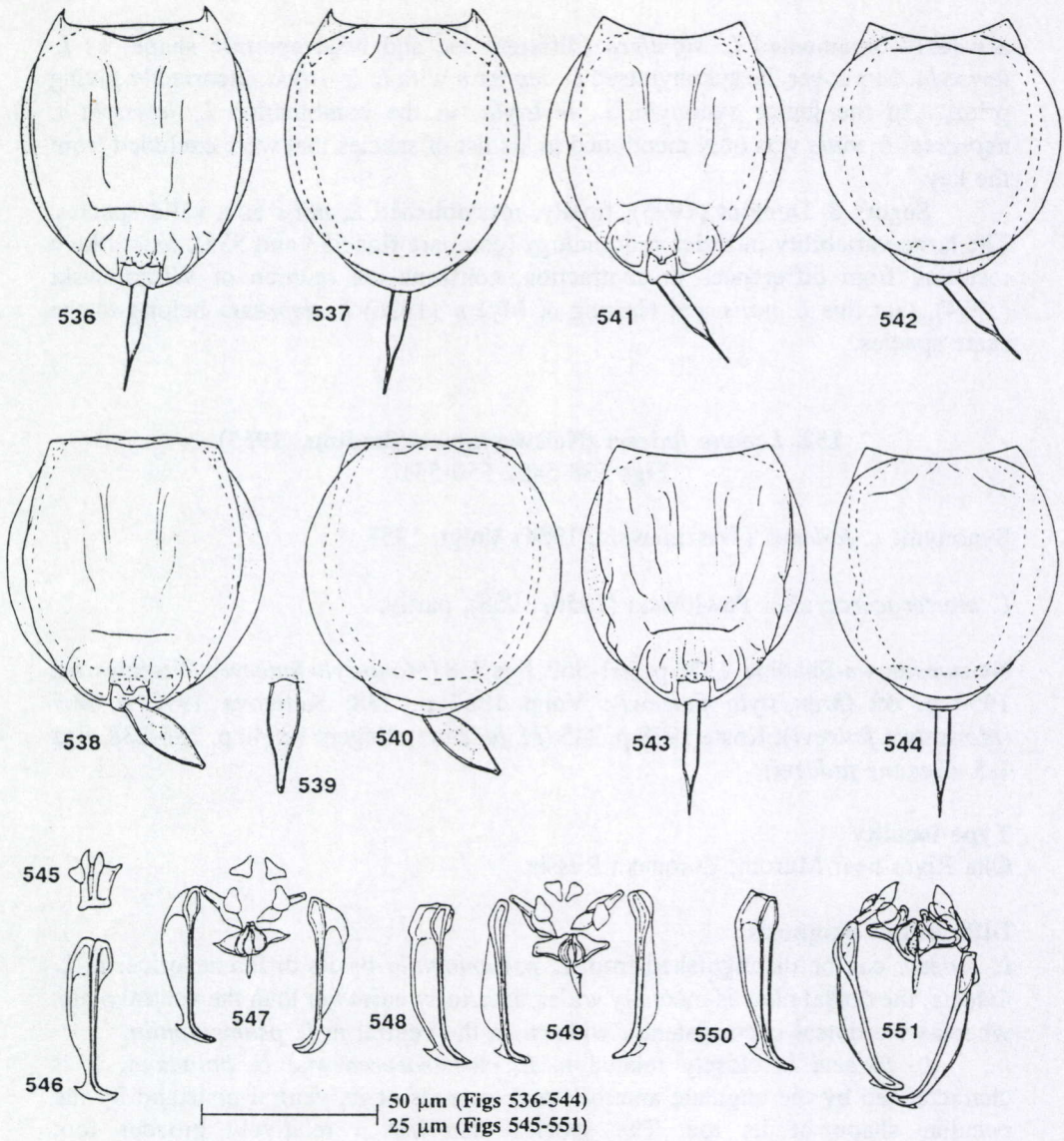
L. fadeevi can be distinguished from *L. psammophila* by its different lorica: in *L. fadeevi*, the dorsal plate is medially wider, anteriorly narrower than the ventral plate, whereas the dorsal is consistently wider than the ventral in *L. psammophila*.

L. fadeevi is closely related to *L. closterocerca* and *L. boliviana*. It is characterised by the angulate antero-lateral corners of its ventral plate,and by the peculiar shape of its toe. The species also has a relatively broader foot pseudosegment than *L. closterocerca*.

L. fadeevi keys out to *L. closterocerca* and *L. arcuata*. It can be distinguished from those by its bulging toe.

Description

Lorica stiff, smooth or slightly ornamented. Dorsal plate anteriorly narrower, medially wider than ventral plate. Head aperture margins nearly coincident, slightly concave or straight. Antero-lateral corners angulate. Lateral edges of dorsal plate scarcely reach anterior edge. Ventral plate longer than wide, with incomplete trans



Figs 536-527, 545-547: L. boliviana Segers. 536: ventral view; 537: dorsal view; 545: left uncus, anterior view; 546: right manubrium, lateral view; 547: trophi, ventral view.
Figs 538-540, 548-549: L. fadeevi (Neiswestnowa-Schadina). 538: ventral view; 539: toe; 540: dorsal view; 548: right manubrium, lateral view; 549: trophi, ventral view.
Figs 541-544, 550-551: L. closterocerca (Schmarda). 541, 543: ventral views; 542, 544: dorsal views; 550: right manubrium, lateral view; 551: trophi, ventral view.
(536-537, 543-549: after Segers *et al.*, 1995; 538-542, 550-551: after Segers, 1994).

verse and weak longitudinal folds. Lateral margins smooth or irregularly folded, slightly curved. Lateral sulci deep. Foot plate short, with rounded triangular coxal plates. Prepedal fold narrow, elongate, posterior margin with median projection. Foot pseudosegment simple, slightly wider than long, scarcely projecting. Toe single, distinctly bulging in the proximal half, then tapering to point. A short, scarcely visible terminal fissure present, no claw. Trophi: see figs 550-551.

Measurements: DPl. 75-74, DPw. 66-74, VPl. 75-90, VPw. 60-64, head aperture w. 45-46, toe l. 27-32, width 9-10. Trophi l. 29-32, manubrium l. 24-25, uncus l. 9-10, incus w. 14.

Distribution

Known from European Russia and, probably, Poland. The species lives in the interstices of coarse sands. It is also found in the littoral of rivers.

Comments

Although the different toe shape presents a reliable distinguishing characteristic between *L. fadeevi* and *L. closterocerca*, some intraspecific variability regarding this feature is apparent. In the common *L. closterocerca*, the basal part of the toe is normally parallel-sided, specimens with broadly constricted toe (see figs 474, 477; *L. closterocerca* after Murray (1913a), partly) can occasionally be encountered. Additionally, the toe tip is sharp and spiniform in *L. closterocerca*, and has a short terminal fissure in *L. fadeevi*. Small differences in head aperture shape are taxonomically irrelevant, as they result from a different degree of contraction of the specimens. The interpretation of internal structures in the toe as canals and reservoirs for some adhesive gland, as suggested by Neiswestnowa-Shadina (1935), remains speculative.

The subtlety of the characters distinguishing the two taxa may raise doubts on the separate identity of the two, although similar pairs of congeners (e.g., *L. rhopalura* and *L. lunaris*) exist. However, as both *L. closterocerca* and *L. fadeevi* co-occur, and as *L. fadeevi* is being recorded again after an interval of 57 years, and, hence, appear morphologically stable, it can at present but be concluded that they do represent different species.

The trophi structure of *L. fadeevi* does not differ significantly from that of *L. boliviana* or *L. closterocerca* (compare with figs 545-547 and 548-549, respectively). The three have in common that their manubria have dorsal hooks distally, a character previously reported in the unrelated *L. pumila* only (right manubrium only: see De Smet & Bafort, 1990).

Similarly as for *Lecane kutikowa* (p. 116), an objective synonym of *L. fadeevi*, *L. fadeewi* was created by Wiszniewski, 1954.

153. *Lecane boliviana* Segers, 1994
Figs 536-537, 545-547

Segers *in* Segers *et al.*, 1994 p. 228-231 figs 2a-d

Type locality and types
Kothia Lagoon and surroundings, near La Paz, Bolivia. Holotype and paratypes in the KBIN, paratypes in RUG and in the Universidad Mayor de San Simón, Cochabamba, Bolivia.

Differential diagnosis
Lecane boliviana is closest to *L. closterocerca*. They differ by the antero-lateral corners of their lorica being provided with sharp spines in *L. boliviana*, and being angulate in *L. closterocerca*. Subtle differences in trophi morphology also exist (compare figs 545-547 with 548-549). *L. boliviana* keys out to *L. opias*. *L. boliviana* has a distinctively rounded lorica and a characteristic pattern of longitudinal folds on the ventral plate.

Description
Lorica stiff, weakly ornamented. Dorsal plate anteriorly narrower, medially wider than ventral plate. Head aperture margins nearly coincident, ventral slightly concave, dorsal nearly straight. Antero-lateral corners with sharp projections. Ventral plate longer than wide, with incomplete transverse and weak longitudinal folds. Lateral margins smooth, slightly curved. Lateral sulci deep. Foot plate short, with rounded triangular coxal plates. Prepedal fold narrow, elongate, posterior margin with median projection. Foot pseudosegment simple, not or distinctly projecting. Toe single, parallel-sided in the proximal two thirds, then tapering to point, no claw. Trophi: see figs 545-547.

Measurements: DPl. 74-81, DPw. 65-72, VPl. 77-81, VPw. 58-61 head aperture w. 38-41, ant. spine l. 3.5-5, toe l. 33-36.

Comments
L. boliviana is a close relative of the common, cosmopolitan *L. closterocerca*. The decisive character differentiating between them, viz. presence or absence of antero-lateral spines, has proved to be one of the most reliable in the genus. Moreover, both these species were found in abundance and co-occurring: one of the samples contained hundreds of specimens of both species.

A similarity of the new species with *L. opias* is only superficial, as their general lorica shape is different. In fact, whereas *L. boliviana* is close to *L. closterocerca*, *L. opias* is close to *L. arcuata*. Considering this, the non-illustrated record of *L. opias* from Lake Titicaca by De Beauchamp (1939), which is the only record of this species from South America, may be *L. boliviania*.

II.4. Nomenclature

Nomenclature in Rotifera is confused, partly as a consequence of the frequent use of ranks below the species level, but also of an apparent lack of knowledge on the subject. A special effort was made to conform names in *Lecane* to the International Code of Zoological Nomenclature.

Corrections were required in many cases. These concern errors in the erroneous use of brackets (e.g., '*L. eupsammophila* (Koste, 1991)': see *L. copeis*), citation of author and date in taxa, originally established at infrasubspecific rank and elevated to subspecies or species rank (e.g.,'*L. ungulata australiensis* Koste & Shiel, 1990'), misspellings (e.g., '*L. aegana*', '*L. stichoides*', '*L. stichea*',... : Koste, 1978), incorrect terminations (e.g., '*L. deridderi* Koste', '*L. ludwigi* (Eckstein)') and alternative transliterations of Cyrillic names (see *L. kutikowa* Koste, 1972 and *L. kutikova* Koste, 1978: Part II; *L. fadeevi* (Neiswestnowa-Shadina, 1935) and *L. fadeewi* (Wiszniewski, 1954): Segers, 1994b).

Priority had been incorrectly assigned in several cases:

- *L. amazonica* (Murray, 1913) and *L. murrayi* Hauer, 1956 by Hauer (1956) and Koste (1978): see further.

- *L. aspasia* Myers, 1917 and *L. stichaeoides* Hauer, 1938 by Koste & Robertson (1983). The synonymy of the two is erroneous. *L. aspasia* represents a valid taxon, different from *L. stichaeoides* which is a junior synonym of *L. haliclysta* Harring & Myers (1926).

- *L. depressa* (Bryce, 1891) and *L. levistyla* (Olofsson, 1917) by Wiszniewski (1954) and Koste (1978). These are not synonymous (Segers & Dumont, 1995; see Part II, II.3.2.3).

- *L. sibina* Harring, 1914 and *L. rhenana* Hauer, 1929 by Koste (1978). That priority was awarded incorrectly was recognised and corrected by Michelangelli *et al.* (1980). However, the two are not synonymous (Part II).

Most alterations followed from the synonymy of the genera *Lecane*, *Monostyla* and *Hemimonostyla*, and represent unresolved cases of homonymy, although the synonymy of *Lecane* and *Monostyla* was first proposed by Edmondson (1935). Some of the homonyms remain unaltered, as they concern long established junior synonyms (e.g., *L. appendiculata* (Daday) non (Skorikov) nec (Levander) or inadequately described taxa (e.g., *L. ungulata* (Mola) non (Gosse)), and do therefore not threaten stability. Proposing *nomina nova* for these cases would only add to the confusion, considering the already large number of existing names in *Lecane*. Nomenclature was adjusted in the following cases.

- The name *amazonica* was found in several instances. The senior, *L. amazonica* (Bryce, 1913), designates a valid morphospecies, which was incorrectly listed as a synonym of *L. murrayi* Hauer, 1956 (see further). *L. closterocerca amazonica* Koste, 1972 represents a taxon of infrasubspecific rank, and, hence, is listed as a synonym. *L. aspasia amazonica* Koste & Robertson, 1983 was found to denote a separate, valid taxon at the species level. The name *L. robertsonae* was proposed for it (Segers, 1993). *L. stichaea* var. *amazonica* Koste, 1978 was recognised as a valid taxon at the species level and renamed *L. amazoniana* by Koste & Robertson, 1983 and, again, *L. amazonica* by Koste & Böttger (1992). The name *L. eutarsa* Harring & Myers, 1926 figures as synonym of *L. stichaea* var. *amazonica* in Koste (1978). Segers (1993) reestablished *L. eutarsa* as the senior synonym of *L. amazoniana* and *L. amazonica* Koste & Böttger non (Bryce).

- *L. deridderi* Koste, 1972 and *L. deridderae* De Paggi, 1989: Irrespective of the incorrect termination by Koste (1972), these two names are primary homonyms. Segers (1991) proposed *L. margarethae* as replacement name for the junior homonym.

- *L. murrayi* Hauer, 1965 was proposed as a *nomen novum* for *L. amazonica* (Murray, 1913), without a valid motivation. Apparently, *L. murrayi* (Korde, 1927), a junior synonym of *L. subtilis* Harring & Myers, 1926, had passed unnoticed. The situation was resolved by reestablishing *L. amazonica* (Murray, 1913) as the valid name for the taxon (Segers, 1993).

- By the reallocation of *Proales longidactyla* Edmondson, 1934 to *Lecane*, as a junior synonym of *L. clara* (Bryce, 1892), the name *L. longidactyla* Arora, 1965 became a junior homonym. No replacement name was proposed, considering the synonymy of Arora's species with *L. curvicornis* (Murray)(Segers, 1993).

- *L. ornata* (Harring & Myers, 1926) non (Daday, 1901): the name *L. myersi* was proposed as a *nomen novum* (Segers, 1993).

- *L. rotundata* (Olofsson, 1918) non (Jakubski, 1914): the junior homonym was replaced by the name of its oldest, junior synonym, *L. latissima* Yamamoto, 1953.

- *L. truncata* Yamamoto, 1953 non (Leissling, 1914) nec (Turner, 1892): both Yamamoto's and Leissling's species turned out to be junior subjective synonyms of *L. depressa* (Bryce) (Segers, 1993; Part II).

II.5. An evaluation of taxonomic research on Rotifera

II.5.1. *Introduction*

Many of the major identification- and text books on Rotifera (e.g., Ruttner-Kolisko, 1974; Koste, 1978; Nogrady *et al.*, 1993), but also works treating general problems of taxonomy or zoogeography (Pejler, 1977a, 1977b; Dumont, 1980, 1983; Koste & Shiel, 1989; Ruttner-Kolisko, 1989, 1993; Shiel & Sanoamuang, 1993; Segers & Dumont, 1993), complain about contemporary rotifer taxonomy. The most illustrative statement in this respect is that of Koste (*in* Dumont, 1980), that 'we are today witnessing the stone age of rotifer taxonomy'. On the other hand, rotifer taxonomy has remained reasonably stable for the last 30 years or so, with minor shifts at higher taxonomic levels (Nogrady *et al.*, 1993), and new taxa are only rarely described (e.g., only six new species, and four new subspecies listed in Zoological record, 1991/1992). That this stability is misleading is illustrated by the work of Markevich (Markevich, 1989, 1990; Markevich & Kutikova, 1989), who suggested a new scheme for rotifer systematics, and of Segers *et al.* (1993) and Segers (1995b), in which taxonomic changes at the genus or family rank are proposed regarding well known taxa.

The above criticisms emerged from general experience of researchers. Actual support for them is given by Ruttner-Kolisko (1989) and Snell (1989), who comment on the problems inherent to the work on parthenogenetically reproducing, highly variable and morphologically simple Rotifera. However, few attempts of critical analysis highlighting the actual state of taxonomic research on Rotifera have been made, although some studies dealing with the development of rotifer research (e.g., Hussey, 1980; Sarma, 1988b; Koste & Hollowday, 1993; Nogrady *et al.*, 1993) provide critical analysis of rotifer studies on a local basis. Here, such an analysis is attempted by evaluating, primarily, the taxonomy in the genus *Lecane*, and comparing the results with the situation in *Brachionus* and *Cephalodella*.

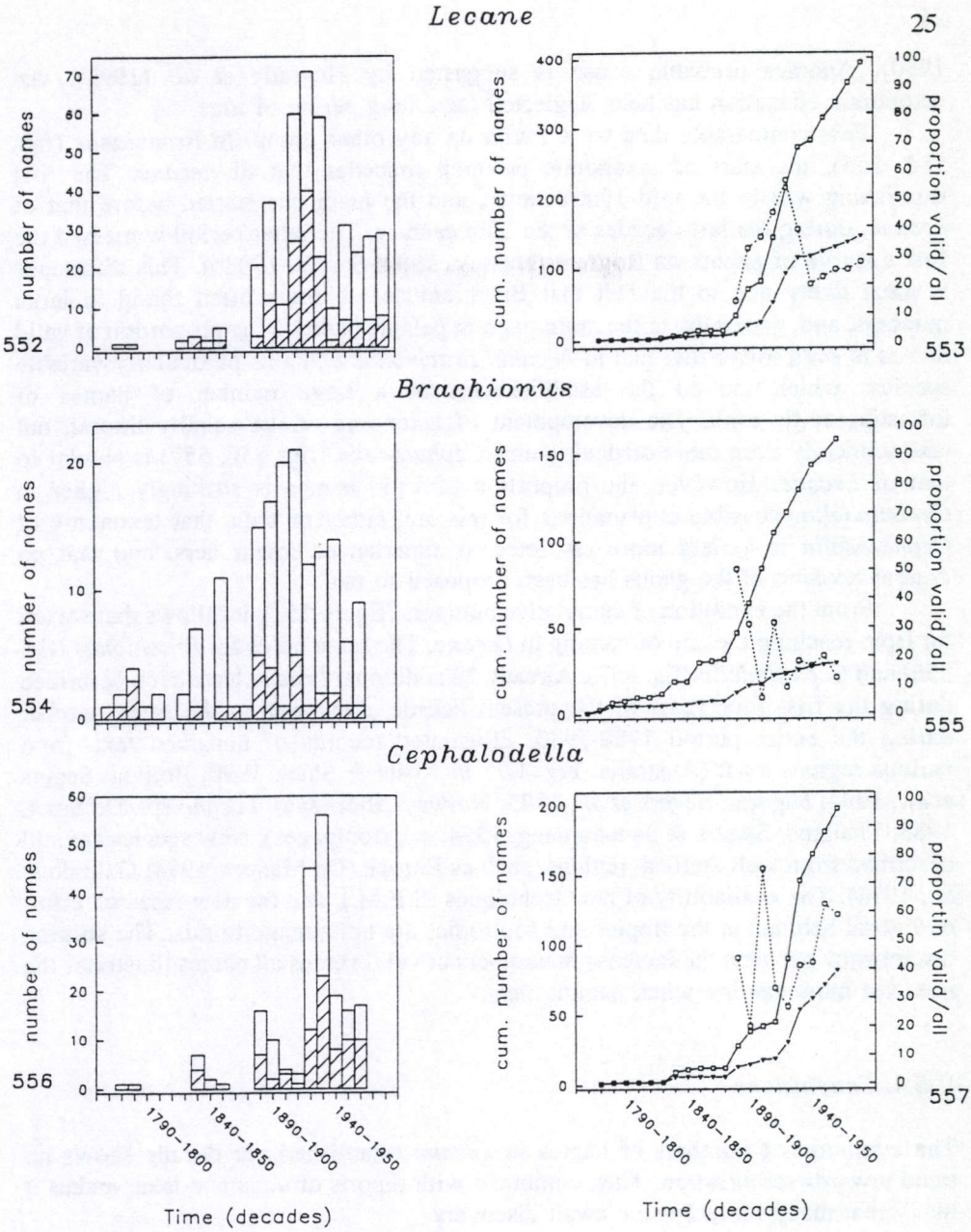
II.5.2. *Material and Methods*

The analysis is based on the 'check-list of names and synonyms in *Lecane*' in Part II, and the changes proposed by Segers (1994b), Segers & Dumont (1995) and Segers *et al.* (1994)(see II.3.2.5.). Counts were made of all available names (in the sense of the International Code of Zoological Nomenclature; *nomina nuda* excluded), established for taxa at and below the species level, per complete decade starting from 1780. Distinction is made between names now considered to denote valid (sub)species, and others (e.g., junior synonyms; including names of invalid subspecies, or names, presently considered to denote taxa of infrasubspecific rank). The proportion of valid names to all names established per decade was calculated from 1870-1880 onwards. A similar analysis, based on Koste's (1978) work, was

performed on two other species-rich rotifer genera. One is predominantly pelagic (*Brachionus*), the other, *Cephalodella*, contains littoral, soft-loricate taxa. Here, however, have unavailable names for taxa of infrasubspecific rank been included in the counts, as most of these are treated as representing valid taxa by Koste (1978).

II.5.3. *Results and Discussion*

Taxonomic research on *Lecane* started in the 18th century (figs 552, 553), by the establishment of *Cercaria luna* Müller, 1776 and *Trichoda cornuta* Müller, 1786. That these names are still in use, now in combination with the generic name *Lecane*, has everything to do with tradition rather than with accuracy of their description. Illustrative for this is Hauer's (1929) discussion on *L. cornuta*. The number of named taxa began to increase rapidly during the last two decades of the 19th century. During that period works by D. Bryce (Bryce, 1891; 1892), E. Daday (Daday, 1897; 1898) and, especially, C.T. Hudson and P.H. Gosse (Hudson & Gosse, 1886; Gosse, 1887a, b, c) were published. Unfortunately, many of the descriptions therein are unrecognisable due to the limited optics available at that time. The period from 1910 to 1940 was rich in species descriptions, with as most noticeable contributors J. Murray (Murray, 1913a, b, c), J. Hauer (Hauer, 1924, 1925, 1929, 1931, 1935a, b, 1936a, b, 1937, 1938, 1940), and, particularly, H.K. Harring and F.J. Myers (Harring, 1913, 1914, 1921; Harring & Myers, 1926; Myers, 1936a, b, c, 1937, 1938). This 'golden age' not only refers to quantity, but also to quality: a peak of over 50 per cent of names that are still considered valid was reached in the 1920's, the decade during which Harring & Myers' (1926) revision of the genus was published. This high proportion of valid names probably resulted from the fortuitous combination of early work (high probability of encountering unnamed taxa), with the availability of adequate optics, enabling accurate descriptions and recognisable drawings. After a short interval of reduced activity during the 1940's, the number of names established per decade increased at a steady pace from 1950 onwards. Not only more authors than before contributed to the taxonomy of *Lecane* (e.g., M. De Ridder, J. Hauer, W. Koste (and collaborators), K. Wulfert, and the following), but also authors living in nearly unexplored regions (e.g., B.K. Sharma: India; R.J. Shiel: Australia; M. Sudzuki and K. Yamamoto: Japan). The number of papers published by these authors is high, as can be appreciated from Part II. The proportion of valid names established, however, drops to 20% in 1940-1950, and increases only slowly to 28% in 1980-1990. Especially in a genus as large as *Lecane*, the proliferation and scatter of relevant literature resulted in duplications. Moreover, the combination of large intraspecific variability with a typological approach should be held responsable for the relative scarcity of valid names established. That this is so, is illustrated by the fact that quite a few of the invalid names established during this period were originally given to taxa of subspecific or infrasubspecific rank (see also Hussey,



Figs 552-557. Left: numbers of all (□), and valid (▨) names established per decade; Right: Cumulative numbers of all (—□—), and valid (—▾—) names established, and proportion of valid names (-- ○--) established per decade.
Figs 552-553: Lecane (based on Part II), *554-555: Brachionus* and *555-556: Cephalodella* (based on Koste, 1978).

1980). Another probable cause is suggested by Nogrady *et al.* (1993), viz. taxonomic education has been neglected for a long period of time.

Few comparable data were found on any other group. In *Brachionus* (figs 554, 555), the start of taxonomic research precedes that of *Lecane*. The first flourishing was in the mid 19th century, and the main one started before that of *Lecane*, during the last decades of the 19th century. The latter period witnessed the first upsurge of papers on Rotifera (Hussey, 1980; Sarma, 1988b). This difference is most likely due to the fact that Brachionidae are more often found in large numbers, and, generally, in the more popular pelagic habitat. The proportion of valid names is even lower that that in *Lecane*. *Brachionus* contains particularly variable species, which led to the establishment of a large number of names of infrasubspecific rank. The development of taxonomy of the equally littoral, but taxonomically even more difficult genus *Cephalodella* (figs 556, 557) is similar to that of *Lecane*. However, the proportion of valid names is strikingly higher in *Cephalodella*. Possible explanations for this are, either or both, that taxonomy of *Cephalodella* is a field more restricted to experienced researchers, and that no critical revision of the genus has been proposed so far.

From the evolution of cumulative numbers (figure 553), it follows that we are far from reaching the end of naming in *Lecane*. The same holds for *Brachionus* (fig. 556) and *Cephalodella* (fig. 557). Already 29 additional *Lecane* have been described during the first four years of the present decade, compared to the same number during the entire period 1980-1990. Illustrated records of unnamed taxa from various regions exist (Australia: Fig. 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; see frontpages). New species are still described from well-studied regions, such as Europe (De Manuel, 1994; Galindo *et al.*, 1994). The availability of new techniques (S.E.M.), and the new research effort on littoral habitats in the tropics and subtropics are not strange to this. The striking discrepancy between the increase in numbers of valid versus all names illustrates the need for more caution when naming taxa.

II.5.4. *Conclusions*

The evolution of numbers of names in *Lecane* established per decade shows no trend towards stabilisation. This, combined with reports of unnamed taxa, makes it likely that many more *Lecane* await discovery.

Only about 20 to 30 per cent of the names established during the last decades can be considered valid, against the 55 per cent valid names of the 1920's. The large number of taxa in the genus, scattered literature, the application of a typological methodology to a group exhibiting a wide morphological variability and poor taxonomic education are inferred as probable causes for this. More diligence is urged when naming taxa, not only in *Lecane*, but especially in genera such as *Brachionus*, that contain variable taxa.

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III. Zoogeography of Lecane

III. ZOOGEOGRAPHY OF *LECANE*

III.1. Introduction

Already 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 wherever on earth the conditions necessary for its existence occur, leading to the conclusion that all Rotifera are potential cosmopolitans (Jennings, 1900; Harring & Myers, 1928; Pourriot, 1980; Ruttner-Kolisko *in* Dumont, 1980a).

Examples of cosmopolitic Rotifera are indeed common. In contrast, 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. Pejler (1977b), De Ridder (1981a, b), Dumont (1983) and Ricci (1987) further added to rotifer chorology, by identifying more groups of species with restricted distributions. Except De Ridder (1981a, b), 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; Green, 1994). De Ridder (1981a) demonstrated complex distribution pattern in some littoral taxa. Information on bdelloid Rotifera is even more scarce (Ricci, 1987). The purpose of this work is to contribute to the chorology of littoral Rotifera, by studying the distribution of taxa in the specious genus *Lecane*.

A fuzzy taxonomy and the questionable nature of published records are major constraints towards a zoogeographical analysis (Pejler, 1977a, b; Koste & Shiel, 1989; Segers & Dumont, 1993a; Segers & De Meester, 1994). The present analysis is based on a taxonomic revision of the genus *Lecane* (see Part II: Segers, 1995a), and considers only verified records. In a first part, the need for such a rigorous approach is illustrated, and coverage evaluated. Considering the preliminary nature of our knowledge on littoral Rotifera, we focus on illustrating the diversity of extant distribution patterns in this group of Rotifera. 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 other groups of freshwater organisms.

III.2. Material and Methods

The zoogeographical analysis of *Lecane* is based on the taxonomic treatment of the genus as in Part II, supplemented by the additions in Segers (1994b); Segers *et al.* (1994b) and Segers & Dumont (1995)(see II.3.2.3.).

Only verified records are taken into account. The majority of these concern published records (see Appendix 1), either identified or verified by myself (Chiambeng *et al.*, 1992; Dumont *et al.*, 1994; Galindo *et al.*, 1994; Maas *et al.*, 1995a; Moreno *et al.*, 1992; Sanoamuang *et al.*, 1995; Segers, 1991, 1992, 1993, 1994a, 1994b; Segers & De Meester, 1994; Segers & Dumont, 1993a, 1993b, 1995; Segers & Sanoamunang, 1994; Segers & Sarma, 1994; Segers *et al.*, 1991, 1992, 1993a, 1993b, 1994a, 1994b, 1994c, 1995), or verified by examining the original drawings accompanying the record. Some of the records by Russell (see Appendix 2) 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 (Appendix 3). These are from Algeria, Belgium, Brazil, Burundi, China, Egypt, Ethiopia, Finland, India, Indonesia, Laos, Malawi, Malaysia, Mexico, New Zealand, Nigeria, Peru, the Philippines, Russia, Surinam, Tanzania, Uganda and Vietnam, and concern material collected by researchers of the Institute of Animal Ecology or, mostly, by trainees of the B.A.D.C. International Training Course: 'Zooplankton: a Tool in Lake Management'. Only preliminary accounts on the distribution of *Lecane* taxa are provided in Part II. A number of distribution maps, additional to the ones listed below is as in appendix 4 (maps 10-51). Note that, at the scale of the maps, one symbol may represent several individual records.

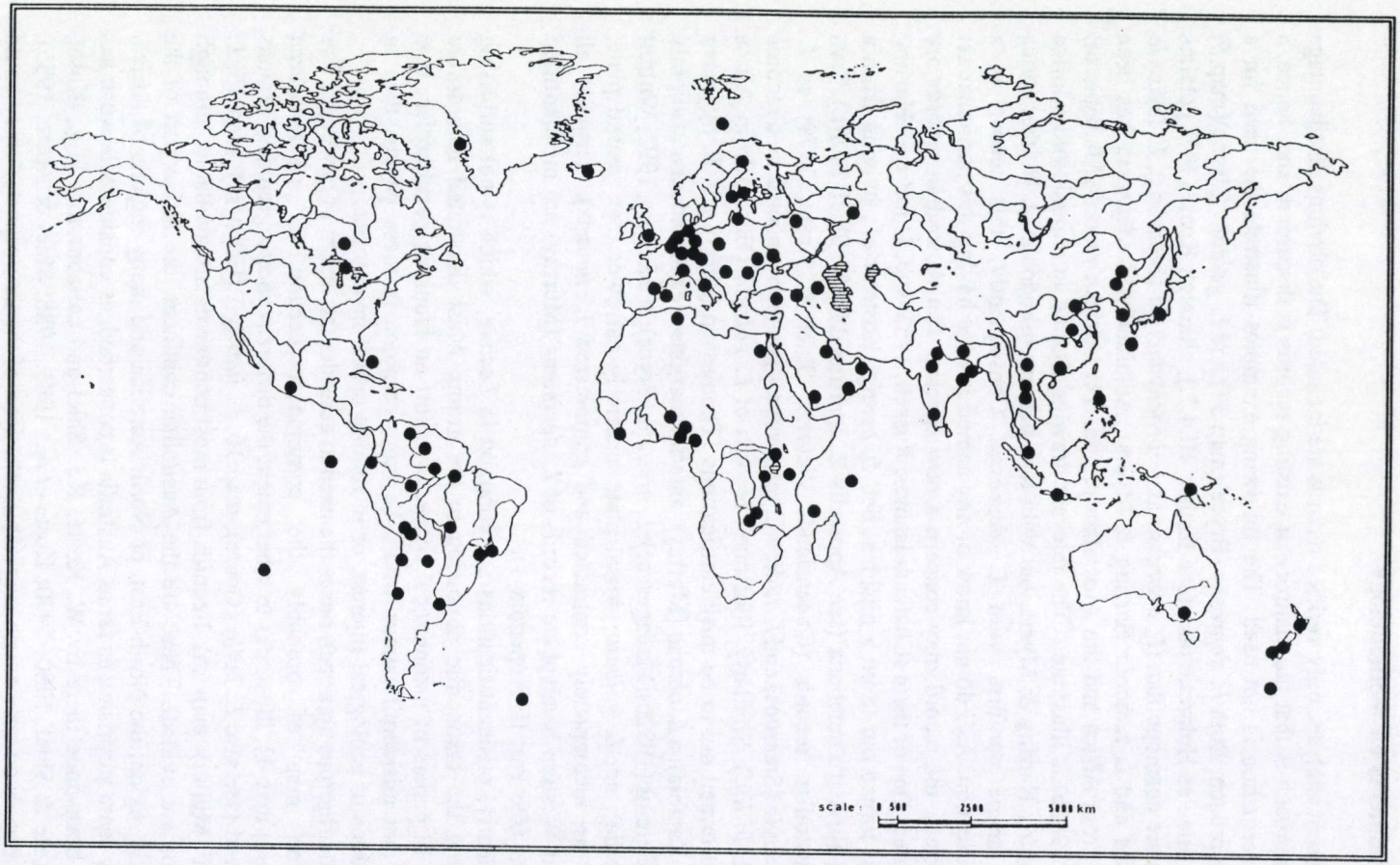
To evaluate latitudinal variation, map records were grouped according to their latitude, with intervals of 10° starting from the equator to the poles. The *Lecane* fauna of the six major zoogeographical regions, as recognised by Cox & Moore (1993), was compared by a cluster analysis following the Average 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).

III.3. Comments on methodology

In the present analysis, only verified records are included. 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 a critical approach. Both *L. depressa* (Bryce)(map 37) and *L. galeata* (Bryce)(map 5) are here listed as Holarctic taxa (see further, III.4.2.), although Koste (1978) claims that both are 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 African record (Madagascar: Bērziņš, 1982b) is illustrated. The relevant drawing figures an animal with a lorica as in *L. mitis* Harring & Myers, but with toes bearing pseudoclaws. Neither lorica nor toe shape conform with *L. depressa*. Consequently, this record is a misidentification. As I do not know of any named *Lecane* having this particular set of characters, the record may concern a new species. The Australian records are unillustrated. One of them (Chatham Islands: Russell, 1953; sub. *L. tudicola* Harring & Myers) turned out to be a misidentified *L. herzigi* Koste *et al.*, judging from a sketch in Russell's notebook (see Appendix 2, confirmed by R. Shiel, *in litt.*). Two more Australian records (Queensland, Victoria: Shiel & Koste, 1979; as *L. brachydactyla* (Stenroos) and *L. tudicola*, respectively) concern unconfirmed records (R. Shiel, *in litt.*). Similarly, illustrated records of *L. galeata* (Bryce) from Africa and India turned out to be misidentifications (Thomasson (1960)(sub. *L. pygmaea* (Daday), Zambia): a *L. obtusa* (Murray): anterior margins are coincident and slightly convex; Bērziņš (1982b)(Madagascar): *L. arcuata* (Bryce), 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* (Murray) are misidentified *L. hamata* (see Part II; Appendix 1).

Clearly, misidentifications are common in *Lecane*, which is not surprising considering the taxonomic confusion in the group. Most illustrated records are included in papers of taxonomical scope, or report 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.

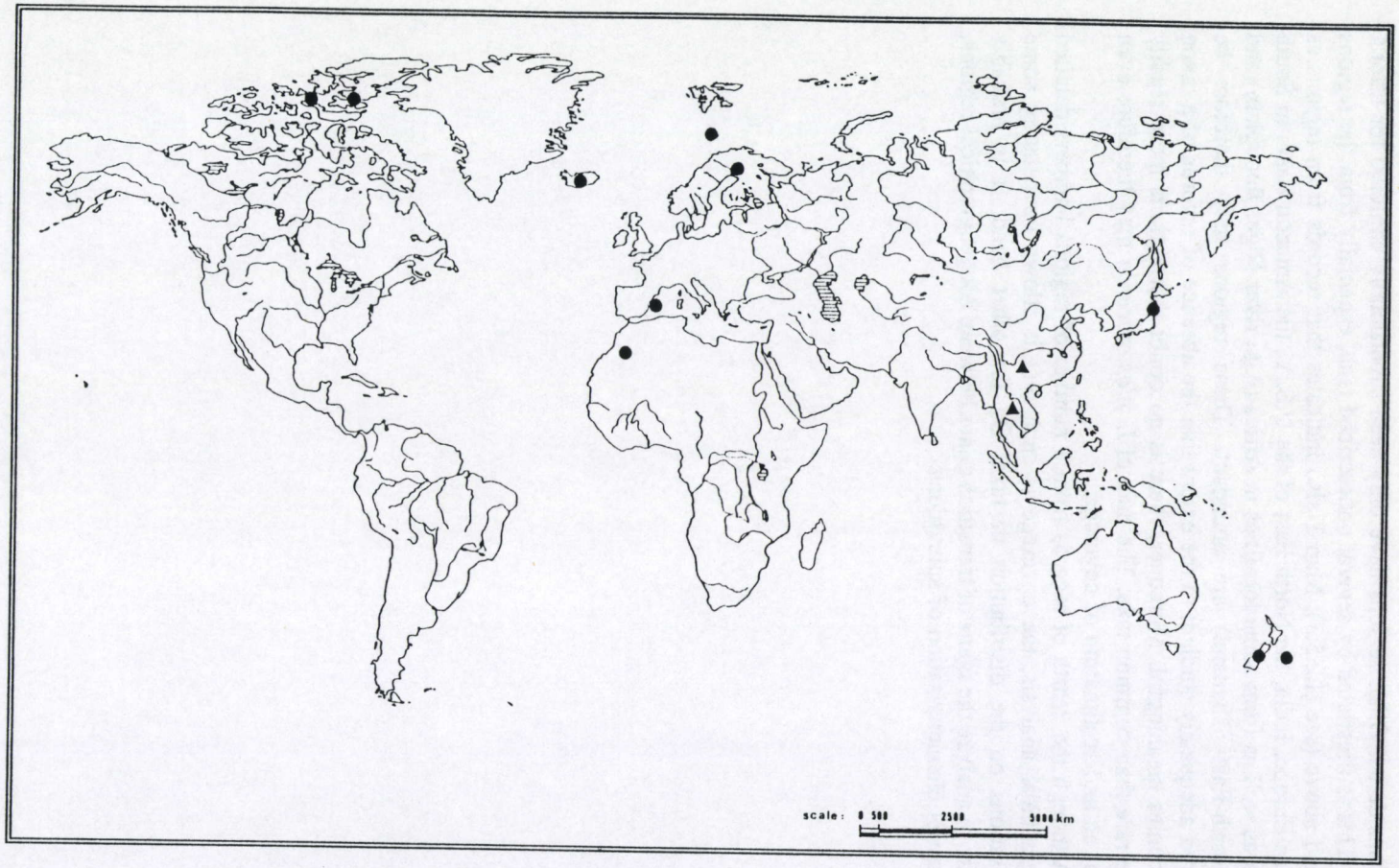
The rigorous approach raises the need to consider the extent of coverage. The distribution map of probably the commonest *Lecane*, *L. closterocerca* (Schmarda)(map 1), illustrates to what extent the different zoogeographical regions are covered (see also *L. bulla* (Gosse): map 10, *L. ludwigii* (Eckstein): map 15, *L. luna* (O.F. Müller): map 16). Records from most continents are available, although large gaps are evident. These are the Australian continent, the Asian part of the Palaearctic 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). As these papers do not contain original illustrations of the taxa reported, they could



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

not be considered. Other regions have only been superficially explored for littoral rotifers. This is illustrated by several undescribed taxa, especially from the regions mentioned above (see II.2.5.3). Map 1 also indicates that records from regions as diverse as Europe, India, the North East of the U.S.A., 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. closterocerca* 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 formulating some generalisations 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.



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

III.4. Distribution patterns in *Lecane*

III.4.1. *Widely distributed taxa*

Considering that cosmopolitanism was inferred for all rotifers, it no surprise that many taxa indeed have ranges spanning most, or large parts of the earth. A total of 68 taxa, or 40.7% of all *Lecane*, occur in both the Eastern and Western hemisphere, without being restricted to the Holarctic region (figure 558). Distinction is here made between four groups (Table 1). As the relevant terminology is sometimes hazy, I adhere to the following definitions:

- **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;
- **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 morphospecies. An example is *L. closterocerca* (map 1). The largest proportion of wide-spread *Lecane*s, 26 taxa or 15.6%, are Tropicopolitans (e.g., see De Ridder, 1981a; see fig. 559: *L. hornemanni* (Ehrenberg)(map 29), *L. leontina* (Turner)(map 7), *L. monostyla* (Daday)(map 30)). There are only few Pantropical taxa (6 or 3.6%; e.g., *L. ruttneri* Hauer (map33): fig. 559). 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. Illustrative are *L. latissima* Yamamoto (map 2), recorded predominantly from high latitudes in both the Northern and Southern hemisphere, and *L. ligona* (Dunlop)(map 18), whose Venezuelan record concerns a capture at 2,425 m a.s.l. (Zoppi de Roa *et al.*, 1990). Similarly, an African record of *L. perpusilla* (Hauer) 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 is only an approximative representative of 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 559, the relative abundance per latitudinal zone of different taxa is plotted. It can be

Table 1. Widely distributed taxa

Cosmopolitan taxa (sensu strictu)

L. agilis (Bryce, 1892)
L. arcuata (Bryce, 1891)
L. aspasia Myers, 1917
L. bifurca (Bryce, 1892)
L. bulla (Gosse, 1851)
L. clara (Bryce, 1892)
L. closterocerca (Schmarda, 1859)
L. flexilis (Gosse, 1886)
L. furcata (Murray, 1913)
L. hamata (Stokes, 1896)
L. inermis (Bryce, 1892)
L. ludwigii (Eckstein, 1883)
L. luna (O.F. Müller, 1776)
L. lunaris (Ehrenberg, 1832)
L. nana (Murray, 1913)
L. pyriformis (Daday, 1905)
L. quadridentata (Ehrenberg, 1832)
L. stenroosi (Meissner, 1908)
L. stichaea Harring, 1913
L. tenuiseta Harring, 1914
L. ungulata (Gosse, 1887)

Arctic-temperate taxa

L. latissima Yamamoto, 1955
L. ligona (Dunlop, 1901)
L. perpusilla (Hauer, 1929)
L. rhopalura (Harring & Myers, 1926)
L. scutata (Harring & Myers, 1926)
L. subulata (Harring & Myers, 1926)

Tropicopolitan taxa

L. aculeata (Jakubski, 1912)
L. aeganea Harring, 1914
L. arcula Harring, 1914
L. crepida Harring, 1914
L. curvicornis (Murray, 1913)
L. donneri Chengalath & Mulamoottil, 1974
L. doryssa Harring, 1914
L. grandis (Murray, 1913)
L. haliclysta Harring & Myers, 1926
L. hastata (Murray, 1913)
L. hornemanni (Ehrenberg, 1834)
L. inopinata Harring & Myers, 1926
L. leontina (Turner, 1892)
L. monostyla (Daday, 1897)
L. myersi Segers, 1993
L. obtusa (Murray, 1913)
L. papuana (Murray, 1913)
L. pertica Harring & Myers, 1926
L. punctata (Murray, 1913)
L. pusilla Harring, 1914
L. rhenana Hauer, 1929
L. rhytida Harring & Myers, 1926
L. signifera (Jennings, 1896)
L. subtilis Harring & Myers, 1926
L. thalera (Harring & Myers, 1926)
L. undulata Hauer, 1938

Pantropical taxa

L. decipiens (Murray, 1913)
L. elegans Harring, 1914
L. ruttneri Hauer, 1938
L. sola Hauer, 1936
L. syngenes (Hauer, 1938)
L. thienemanni (Hauer, 1938)

odd cases

L. climacois Harring & Myers, 1926
L. copeis (Harring & Myers, 1926)
L. cornuta (Müller, 1786)
L. dumonti Segers, 1993
L. elsa Hauer, 1931
L. lamellata (Daday, 1893)
L. nelsoni Segers, 1994
L. tabida Harring & Myers, 1926
L. uenoi Yamamoto, 1951
L. venusta Harring & Myers, 1926

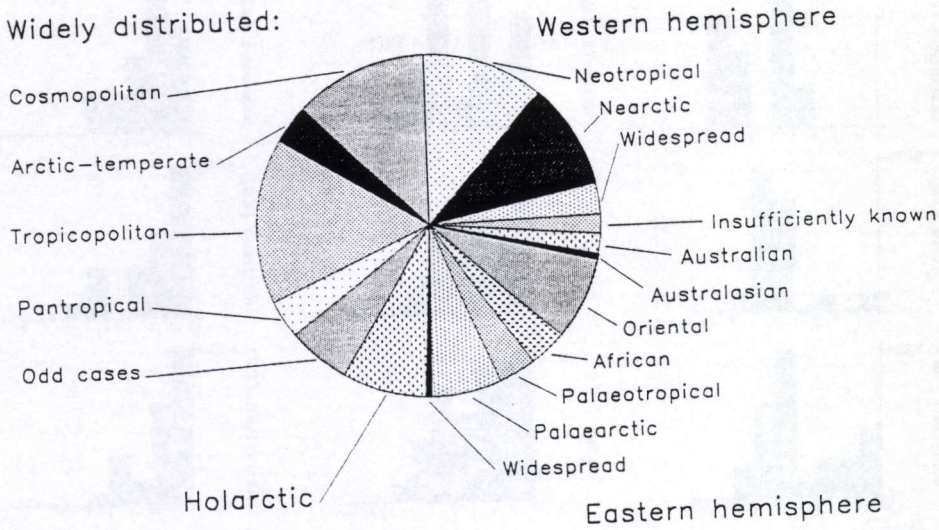


Fig. 558: Proportional occurrence of distribution patterns in *Lecane*.

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, point-wise, occur outside the climatic zone with which they are normally associated when environmental conditions are favourable. Examples are the occurrence of *L. papuana* (Murray) (map 31) 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* (Bryce)(map 14) at higher latitudes are from habitats with relatively higher temperature that 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). Except for *L. inermis* and *L. stichaea* Harring (map 17), our 'ranking' from cold- to warm-water preference as in figure 559 conforms to that of Bērziņš & Pejler (1989), for the few taxa that are common to both analyses (*L. flexilis* (Gosse), *L. closterocerca*, *L. hamata* (Stokes), *L. luna*, *L. bulla*).

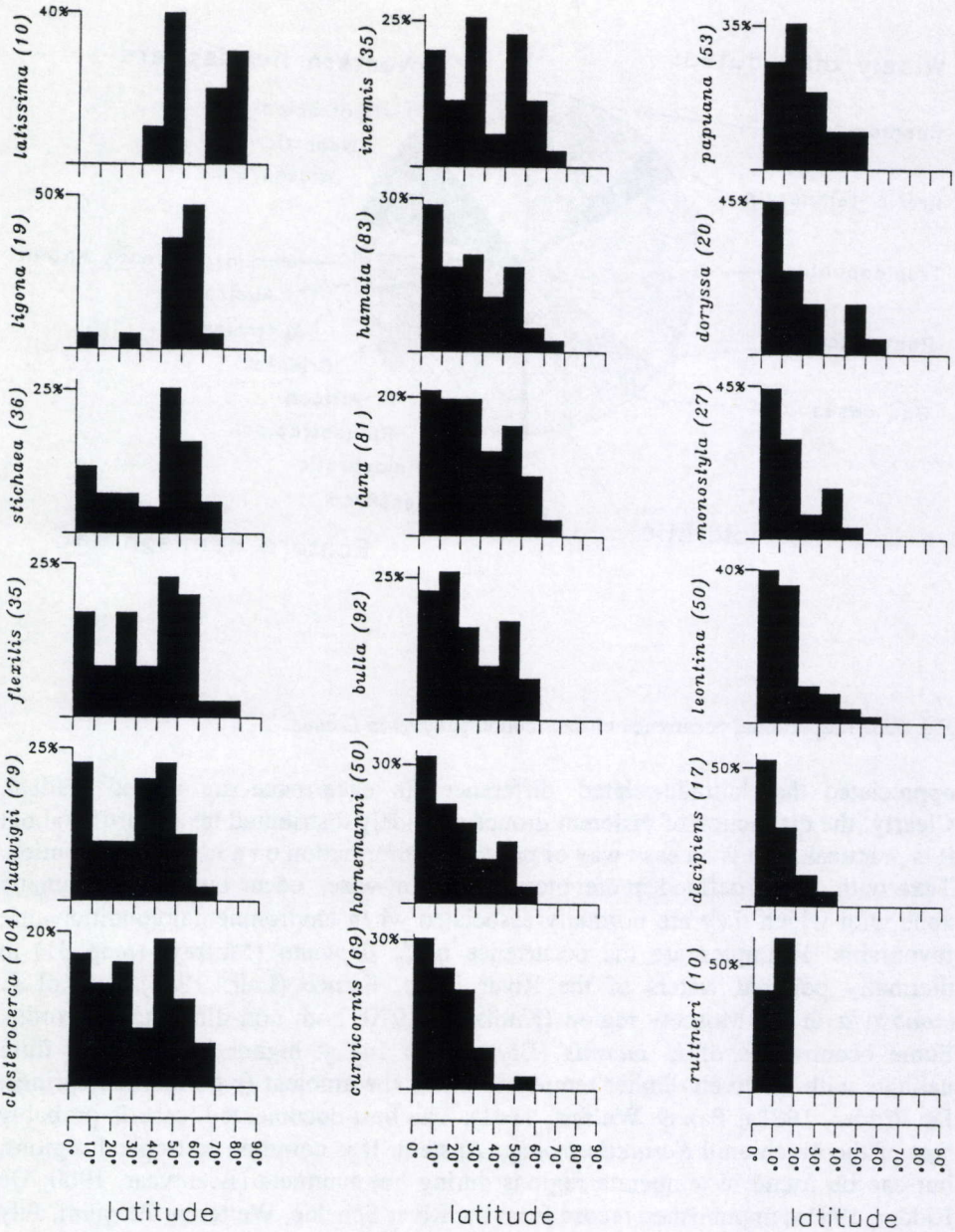


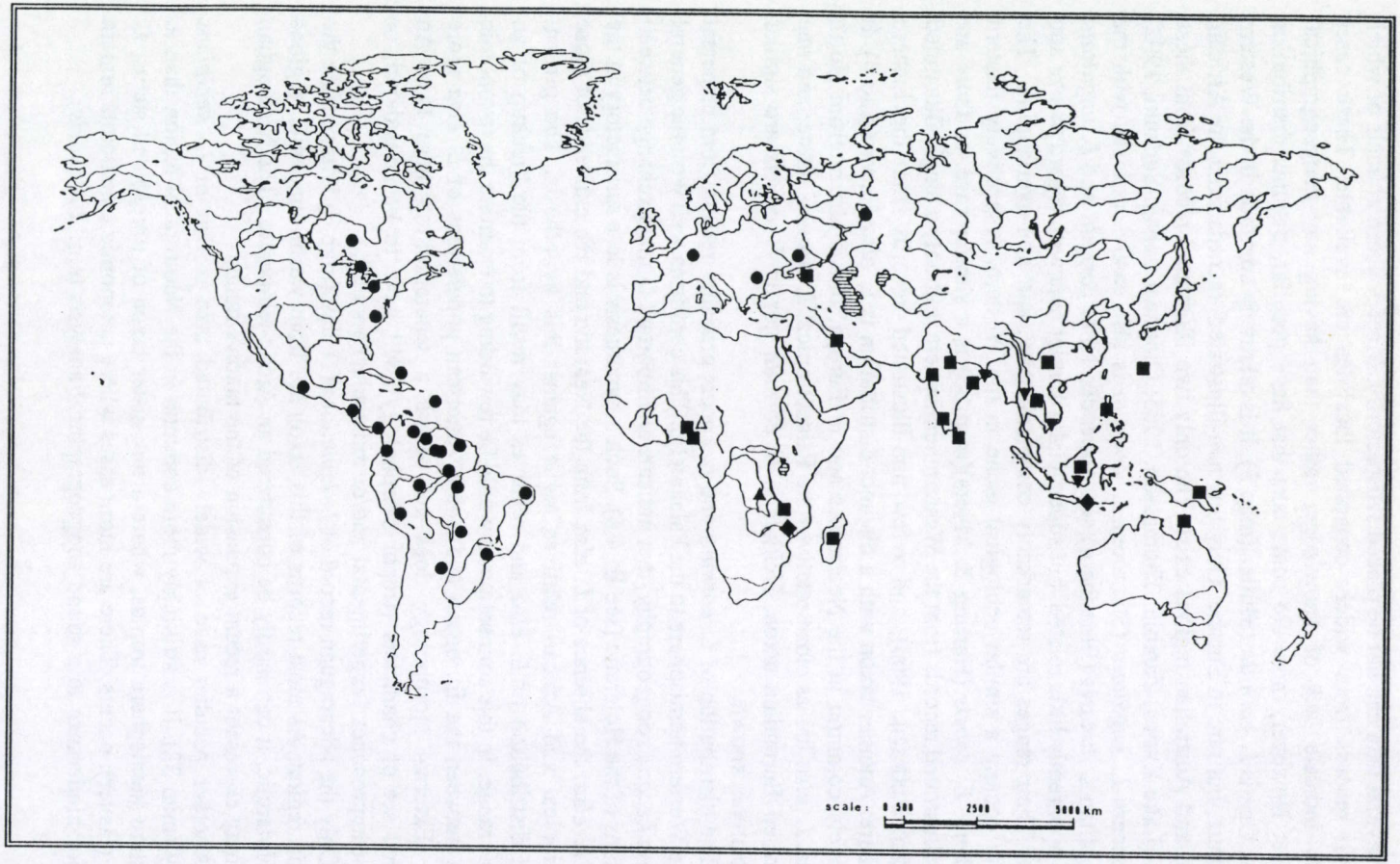
Fig. 559: Frequency distribution of some widely distributed *Lecane* taxa relative to latitude. Taxa are ordered according to their distribution from Arctic-temperate to Pantropical, from top to bottom and from left to right. Number of records follows the name of the taxon.

Several taxa can not 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 taxa that have peculiar, disjunct distribution patterns. One is *L. cornuta* (Müller)(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* (Stenroos). *L. cornuta* is also easily confused with the cosmopolitan *L. lunaris* (Ehrenberg)(see Appendix 1). *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* (Harring & Myers)(map 36) 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* Hauer (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. Neither in *L. cornuta* nor in *L. copeis* are similar close relatives known.

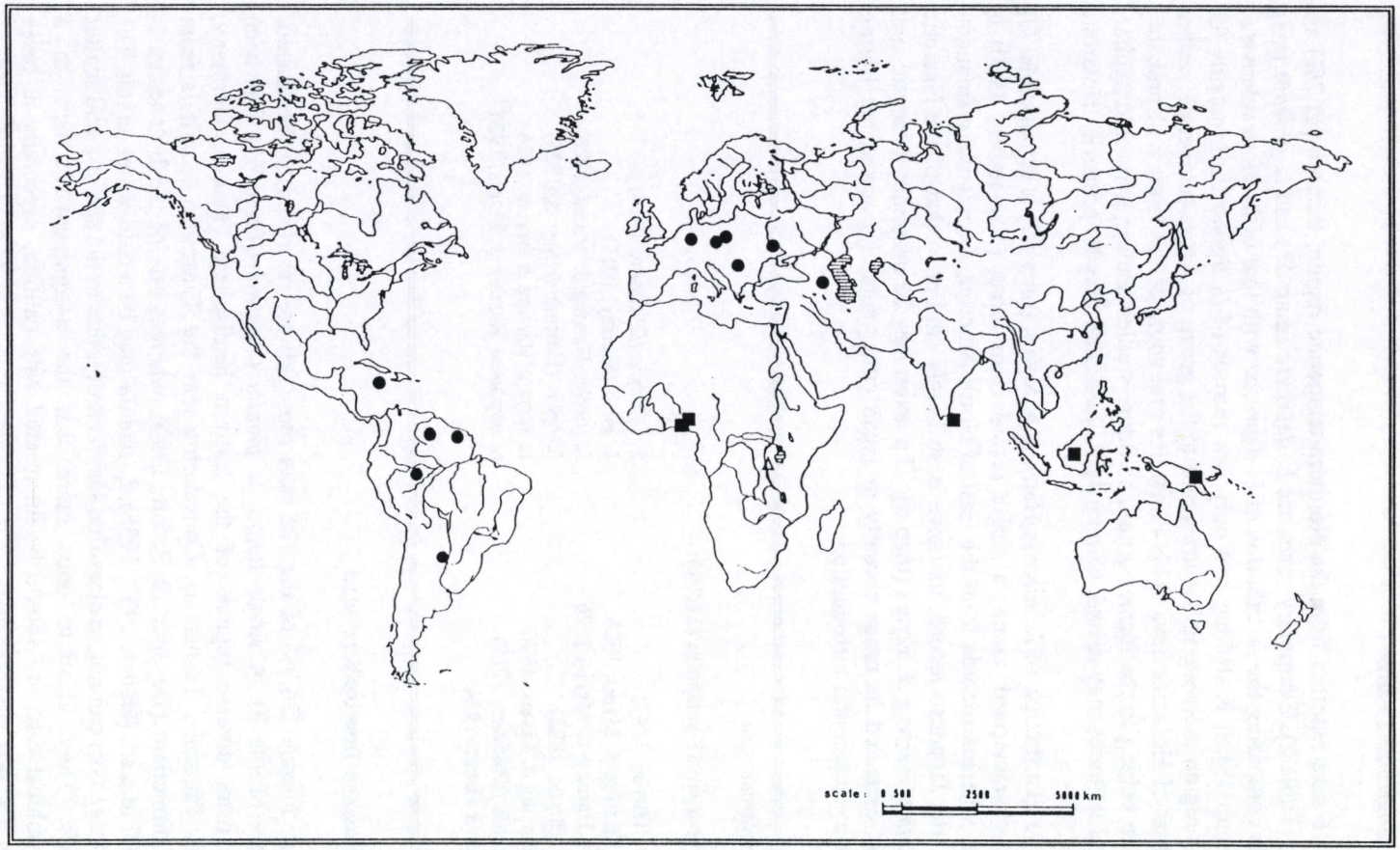
The distribution of *L. cornuta* and *L. copeis* probably results from dispersal from the Western hemisphere to the Palaearctic. This conforms well with the general results on *Lecane* zoogeography, that indicate an important faunal exchange between the regions of the Holarctic (see III.4.6). Such a 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 this hypothesis. 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* (Daday)(map 8) 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* (Murray)(map 32). 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* (Hauer), occurs. There are more cases where taxonomic constraints remain the major hinderance to a sound zoogeographical analysis (e.g., *L. lunaris*).



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)

III.4.2. *Holarctic* Lecane

Of the 116 taxa reported from the Northern temperate region, thirteen (11.2%) are endemic (Table 2). Exemplary cases are *L. depressa* (map 37) and *L. galeata* (map 5). While comparing the distribution of *L. depressa* with that of its close relative *L. ligona* (map 18), 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 III.4.1.).

The distribution of *L. satyrus* Harring & Myers (map 40) 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* Harring & Myers (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.

Table 2. Holarctic taxa

116 taxa reported; 13 endemics (11.2%):

L. depressa (Bryce, 1891)
L. elasma Harring & Myers, 1926
L. elongata Harring & Myers, 1926
L. galeata (Bryce, 1892)
L. infula Harring & Myers, 1926
L. intrasinuata (Olofsson, 1917)
L. lauterborni Hauer, 1924
L. levistyla (Olofsson, 1917)
L. mira (Murray, 1913)
L. niothis Harring & Myers, 1926
L. opias (Harring & Myers, 1926)
L. satyrus Harring & Myers, 1926
L. tryphema Harring & Myers, 1926

III.4.3. *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* (Rousselet)(map 41), 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 1,100 m a.s.l. (Hauer, 1937; 1938), *L. pumila* may be a cold-water taxon. The range of three taxa can not 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.

Table 3. Eastern hemisphere taxa
*: known from a single locality only.
126 taxa reported

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

L. abanica Segers, 1994
L. paxiana Hauer, 1940
L. sympoda Hauer, 1929

Palaearctic taxa

89 reported, 11 endemics (12.4%):

**L. bryophila* Koniar, 1957
**L. donyanaensis* Mazuelos & Segers, 1994
L. fadeevi (Neiswestnowa-Shadina, 1935)
L. gwileti (Tarnogradski, 1930)
L. inconspicua Segers & Dumont, 1993
L. ivli (Wiszniewski, 1935)
L. kluchor Tarnogradski, 1930
L. margalefi De Manuel, 1994
L. paradoxa (Steinecke, 1916)
L. psammophila (Wiszniewski, 1932)
**L. urna* Nograd y, 1962

Palaeotropical taxa

L. braumi Koste, 1988
L. lateralis Sharma, 1978
L. serrata (Hauer, 1933)
L. simonneae Segers, 1993
L. stephensae (Hutchinson, 1931)
L. unguitata (Fadeev, 1925)

African taxa

67 reported, 6 endemics (9.0%):

**L. gillardi* (Bērziņš, 1960)
**L. nigeriensis* Segers, 1993
**L. nwadiaroi* Segers, 1993
**L. stichoclysta* Segers, 1993
L. sylviae Segers, 1993
**L. symoensi* De Ridder, 1981

Oriental taxa

70 reported, 13 endemics (18.6%):

L. acanthinula (Hauer, 1938)
L. bifastigata Hauer, 1938
L. blachei Bērziņš, 1973
L. eswari Dhanapathi, 1976
**L. jaintiaensis* Sharma, 1987
**L. junki* Koste, 1975
**L. minuta* Segers, 1994
L. pawlowskii Wulfert, 1966
**L. schraederi* Wulfert, 1966
**L. shieli* Segers & Sanoamuang, 1994
**L. solfatara* (Hauer, 1938)
**L. spiniventris* Segers, 1994
L. thailandensis Segers & Sanoamuang, 1994

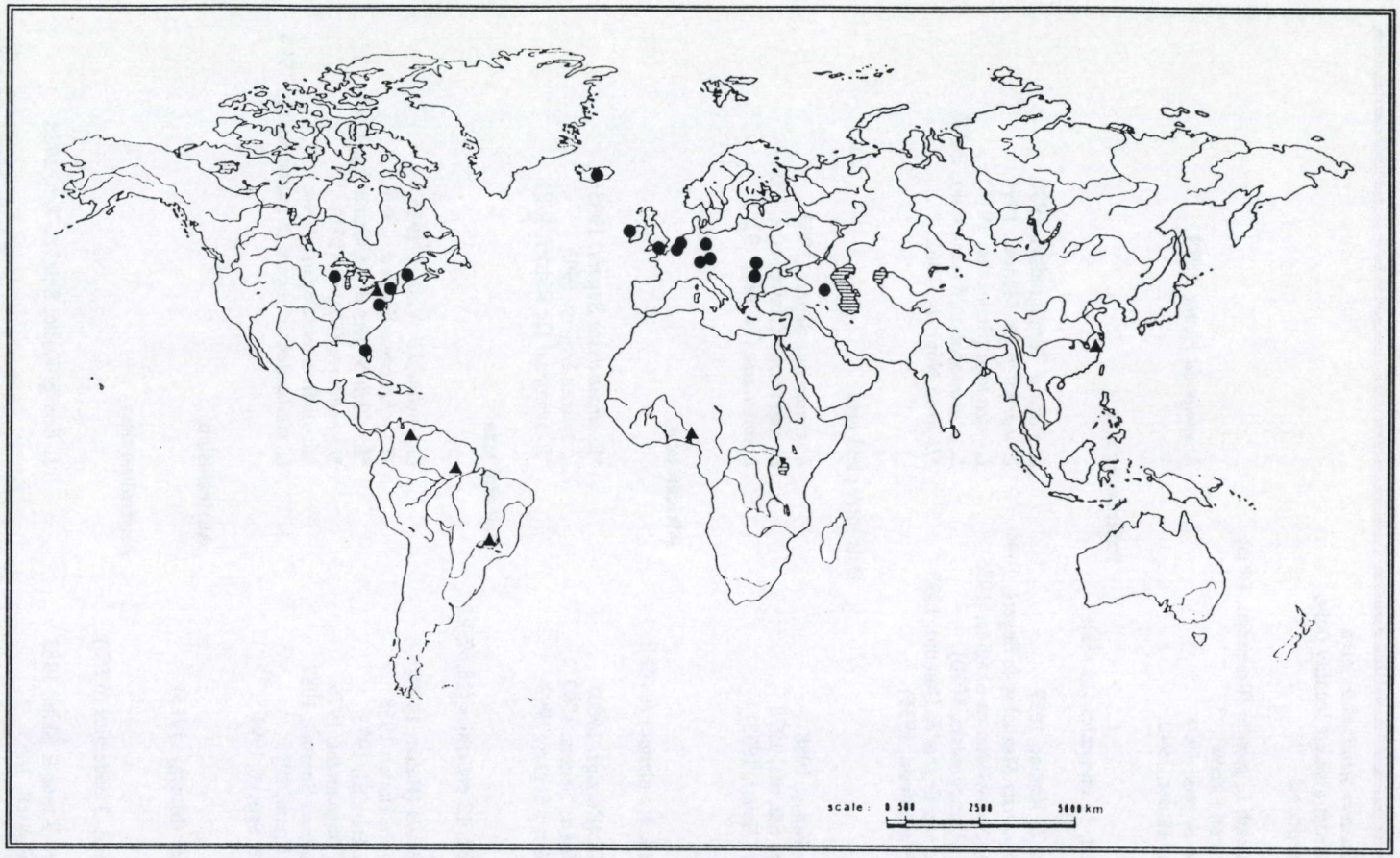
Australasian

L. batillifer (Murray, 1913)

Australian taxa

46 reported, 3 endemics (6.5%):

**L. boorali* Koste & Shiel, 1983
L. eylesi Russell, 1953
L. herzigi Koste, Shiel & Tan, 1988



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

III.4.3.1. 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* (Wiszniewski) and *L. fadeevi* (Neiswestnowa-Schadina) are Central and Eastern European. Records of *L. ivli* (Wiszniewski)(map 42) are centred on the Balkan region, *L. kluchor* Tarnogradski (map 6) occurs in the European mountains, including the Caucasus. Some are point endemics (e.g., *L. bryophila* Koniar: Tatra Mountains, *L. donyanaensis* Mazuelos & Segers: Southern Spain, *L. inconspicua* Segers: coastal lagoons in North East Arabia, *L. margalefi* De Manuel: Balearic Archipelago). Only the saline-water *L. paradoxa* (Steinecke)(map 43) is widely distributed. Three taxa, *L. fadeevi*, *L. ivli* and *L. psammophila*, are psammobionts.

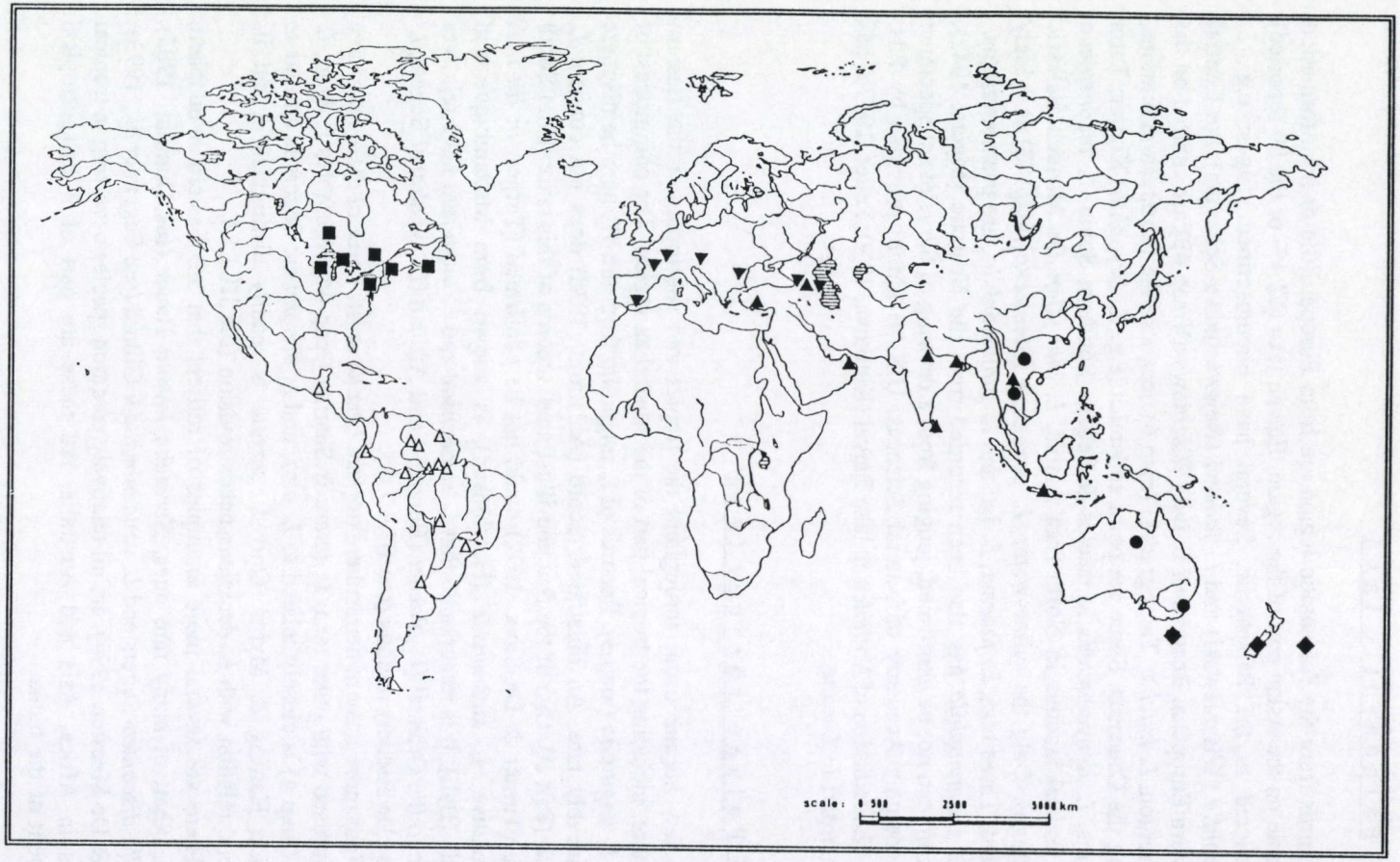
L. psammophila has also been recorded from the Nearctic (Myers, 1942). This record can not be confirmed, judging from a drawing of the relevant specimen (in Philadelphia Academy of Natural Sciences, U.S.A.) kindly provided by P.N. Turner. The radiation of *Notholca* in lake Baikal (Kutikova, 1970; Pejler,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

III.4.3.2. 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* (Part II). 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* (Hutchinson), is known from Mozambique and Indonesia (Bali). It is remarkable that *L. stephensae* and *L. unguitata* have relatives endemic to the Oriental (*L. blachei* (Bērziņš)) and African (*L. nwadiaroi* Segers, *L. symoensi* De Ridder) regions (see III.4.7.4.).

Four more Eastern hemisphere tropical *Lecane* exist. Three of these may have been confused with other taxa: *L. lateralis* Sharma (map 44) resembles *L. luna*, *L. braumi* (map 4) is closely related to *L. elsa*, and *L. simonneae* Segers is similar to *L. rhytida* Harring & Myers. Only *L. serrata* is readily distinguished, but its taxonomic relation with *L. decipiens* needs revision (see III.4.1.).

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.



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

III.4.3.3. 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* Segers has been seen on more than a single occasion. One taxon, *L. gillardi* (Bērziņš), is Malagasy. The West African (Nigeria) *L. nwadiaroi* (map 3) and *L. nigeriensis* Segers are close relatives of the Oriental *L. blachei* (map 3), and the Amazon endemic *L. amazonica* (Murray)(map 48), 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 (see Segers *et al.*, 1993; sub. *L. depressa in* Bērziņš, 1982b, see III.3.; III.4.1.: *L.* sp. near *elsa* (Appendix 3)). 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).

III.4.3.4. 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* Dhanapathi, *L. pawlowskii* Wulfert), one is Indo-Chinese (*L. thailandensis* Segers & Sanoamuang: 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* (Hauer)(map 45) occurs in the South East of the Arabian peninsula, and *L. bifastigata* Hauer (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* (Murray), 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 *Architestudinella* and the Indian *Pseudoeuchlanis*. Both are monotypic.

III.4.3.5. Australasian taxa

Only *L. batillifer* (Murray)(map 6) is Australasian. Although few records are available, its range is considered reliable considering that it 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).

III.4.3.6. 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* Koste & Shiel, which is known from its type locality only. Two others, *L. eylesi* Russell (map 6) and *L. herzigi* Koste *et al.* 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. herzigi*, relative to the Floridian endemic *L. ordwayi* Bienert requires clarification (Koste & Shiel, 1990; Part II). There are indications that several undescribed Australian *Lecane* exist (*L.* sp. near *bulla*, *L.* sp. near *rhenana*: see Appendix 3; fig. 12.1 in Koste & Shiel, 1990).

III.4.4. *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 (e.g., *L. mitis* Harring & Myers: map 46). 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).

III.4.4.1. 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*: see III.4.2.). 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 psammon 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 U.S.A. were of a thoroughness seldomly attained by subsequent researchers.

Table 4. Western hemisphere taxa
*: known from a single locality only.
126 taxa reported

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

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

Nearctic taxa

90 reported, 17 endemics (18.9%):

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

Neotropical taxa

87 reported, 19 endemics (21.8%):

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

III.4.4.2. 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: map 48; also: *L. melini* Thomasson (map 50), *L. proiecta* Hauer), *L. boliviana* Segers (known only from its type locality and, probably, Lake Titicaca in the Andes), and *L. margarethae* Segers (Caribbean: map 49), and widespread Neotropical taxa such as *L. eutarsa* Harring & Myers (map 6) and the brackish-water *L. spinulifera* Edmondson (map 51). Three of the Brazilian endemics are closely related to each other and to three non-endemic relatives, *L. signifera* (Jennings), *L. pertica* Harring & Myers and *L. nelsoni* Segers. These are *L. deridderae* Koste, *L. melini* and *L. rudescui* Hauer. This group probably radiated in the Amazon region (Part II). As such, it is a remarkable counterpart of the Eastern hemisphere tropical/subtropical *L. unguitata*-group.

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* Segers and *L. nelsoni*. These taxon 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 and *Lepadella minoruoides* Koste & Robertson. 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).

III.4.5. *Species introductions*

Species introductions blur the extant distribution patterns of taxa. Several examples of introductions in Rotifera (see *Kellicottia*: III.4.7.8.; 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 (see III4.2.). 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. The same may hold for the above-treated *L. elsa* and *L. cornuta* (see III.4.1.). Apparently, species introductions by human activities do occur in *Lecane* as well.

III.4.6. *A comparison of the regional* Lecane *faunas*

Taxa, endemic to all of the major zoogeographical regions could be registered, with endemicity 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, endemicity stands at 12.4% (Palaearctic 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 endemicity 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 is rarer than in littoral groups (see III.5.). 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 questionable. This either indicates a slow rate of evolution in rotifers, or intense exchange of fauna elements through long-distance dispersal (see III.6).

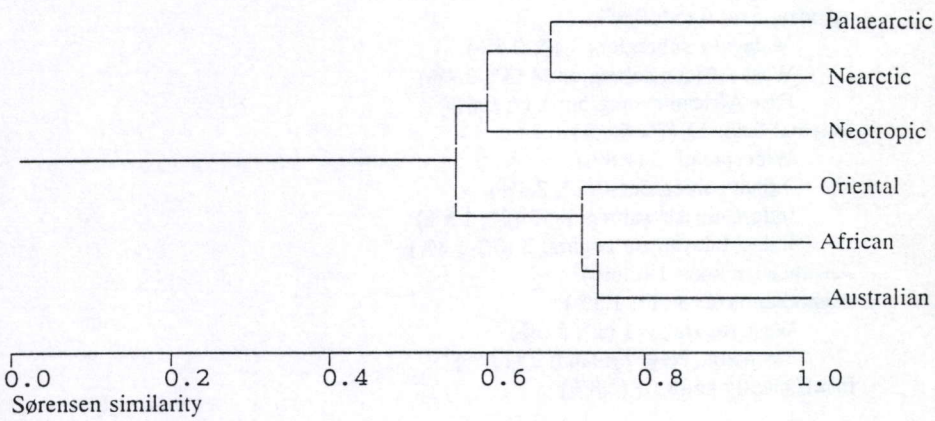


Fig. 590: Dendrogram based on the species similarity between the major zoogeographical regions

The similarity between the *Lecane* faunas of the six major zoogeographical regions is represented is Figure 560 (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

Table 5. Summary of distribution patterns in Lecane
(x*: number of taxa, known from a single locality)
Total number of taxa recognised: 167 (100%)

Widely distributed taxa: 69 (41.3%)

- Cosmopolitan (*sensu strictu*) taxa: 21 (12.6%)
- Arctic-temperate taxa: 6 (3.6%)
- Tropicopolitan taxa: 26 (15.6%)
- Pantropical taxa: 6 (3.6%)
- Odd cases: 10 (6%)

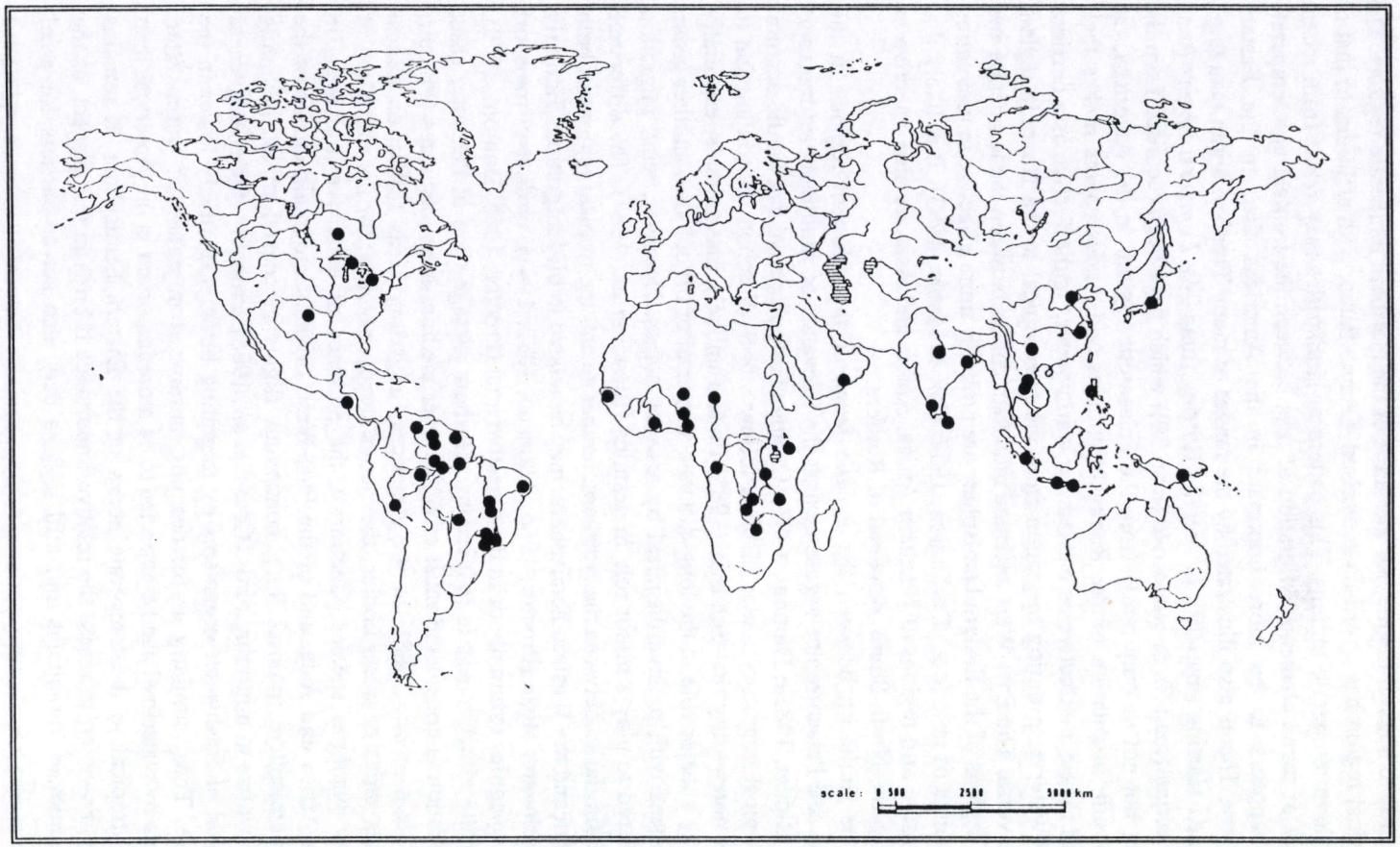
Holarctic taxa: 13 (7.8%)

Eastern hemisphere taxa: 44 (26.3%)

- Widespread: 1 (0.6%)
- Palaearctic 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 know: 3 (1.8%)

Western hemispere 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%)



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

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 taxa (e.g., *L. aeganea* Harring (map 22), *L. crepida* Harring (map 24), *L. myersi* Segers (map 5), *L. leontina* (map 7), *L. monostyla* (map 30)) which have been recorded from the Nearctic, but not or only rarely from the Palaearctic 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 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 as barriers to the North-South dispersal of Rotifera.

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 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, similarly as for desmids, northward migration of warm-water rotifer taxa 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 if birds in this respect, as the above-mentioned mountains and arid regions may also act as barriers for areal dispersal.

III.4.7. *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 interresting 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.

III.4.7.1. 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 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.

III.4.7.2. The *L. ungulata*-group

The cosmopolitic *L. ungulata* (Gosse) has a close relative, the point-endemic *L. donyanaensis*, living in temporary ponds in Southern Spain. A posterior projection on the foot plate is absent in *L. ungulata* and in the related *L. curvicornis*-group (including *L. curvicornis* (Murray), *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

Table 6. Occurrence of Lecane in the major zoogeographical regions

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

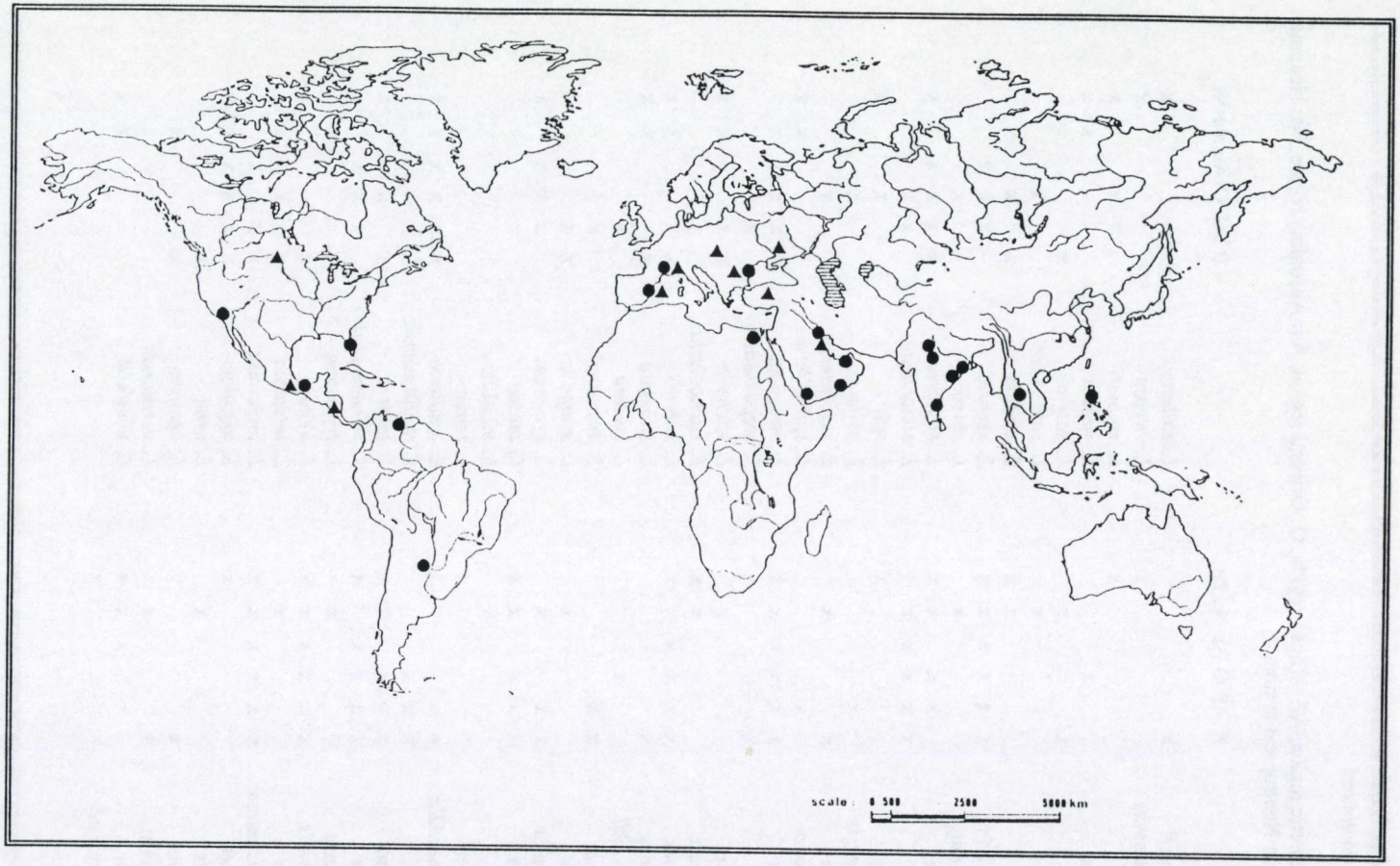
	P	Af	O	Au	Na	Nt
L. abanica	x	x		?		
L. acanthinula	x		x			
L. aculeata	x	x	x	x		x
L. aeganea	x		x	x	x	x
L. agilis	x	x			x	x
L. amazonica						x
L. arcuata	x	x	x	x	x	x
L. arcula	x	x	x		x	x
L. armata						x
L. aspasia	x		x		x	x
L. asymmetrica						x
L. batillifer			x	x		
L. bifastigata	x		x			
L. bifurca	x	x	x	x	x	x
L. blachei			x			
L. boettgeri						x
L. boliviana						x
L. boorali				x		
L. broaensis						x
L. braumi		x	x	x		
L. braziliensis						x
L. bryophila	x					
L. bulla	x	x	x	x	x	x
L. calcaria					x	x
L. candida					x	
L. clara	x	x			x	x
L. climacois	x				x	
L. closterocerca	x	x	x	x	x	x
L. copeis	x				x	x
L. cornuta	x				x	x
L. crepida	x	x	x	x	x	x
L. curvicornis	x	x	x	x	x	x
L. decipiens	x	x	x			x
L. depressa	x				x	
L. deridderae						x
L. donneri	x	x	?		x	
L. donyanaensis	x					
L. doryssa	x	x	x	x		x
L. dumonti		x				x
L. dysoarata					x	
L. elasma	x				x	
L. elegans		x	x			x

	P	Af	O	Au	Na	Nt
L. elongata	x				x	
L. elsa	x				x	x
L. eswari			x			
L. eutarsa						x
L. eylesi				x		
L. fadeevi	x					
L. flabellata					x	
L. flexilis	x	x	x	x	x	x
L. formosa					x	
L. furcata	x	x	x	x	x	x
L. galeata	x				x	
L. gillardi		x				
L. grandis	x				x	x
L. gwileti	x					
L. haliclysta	x	x	x	x	x	x
L. hamata	x	x	x	x	x	x
L. hastata	x	x	x	x	x	x
L. herzigi				x		
L. hornemanni	x	x	x	x	x	x
L. inconspicua	x					
L. inermis	x	x	x	x	x	x
L. infula	x				x	
L. inopinata	x	x	x	x	x	x
L. inquieta					x	
L. intrasinuata	x				x	
L. ivli	x					
L. jaintiaensis			x			
L. junki			x			
L. kluchor	x					
L. kutikowa						x
L. lamellata	x				x	x
L. lateralis		x	x	x		
L. latissima	x			x	x	
L. lauterborni	x				x	
L. leontina	x	x	x	x	x	x
L. leura					x	
L. levistyla	x				x	
L. ligona	x		x		x	x
L. ludwigii	x	x	x	x	x	x
L. luna	x	x	x	x	x	x
L. lunaris	x	x	x	x	x	x
L. marchantaria						x

Table 6, continued

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

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



Map 8: Distribution map of *L. lamellata* (Daday)(▲) and *L. thalera* Harring & Myers (●)

of the former in the habitat of the latter, may not have been interrupted. Hypothetically, sympatric speciation could have occured in this case (see also III.4.7.6.).

III.4.7.3. The *L. lamellata*-group

Similarly as in the *L. ungulata*-group, the Tropicopolitan *L. thalera* Harring & Myers and primarily Holarctic (map 8; see III.4.1.) *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.

L. lamellata and *L. thalera* are hardly taxonomically separated (see Part II). Their ranges, however, differ. The case may consern 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 (see part II).

III.4.7.4. 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 occurs independently in several groups of *Lecane*, and does not occur in the related Proalidae (Segers, 1993; part II). Hence, 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.

III.4.7.5. 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* (Ahlstrom)) 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 (see also III.4.7.1).

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*. A hypothesis similar as for the latter two (see III.4.7.1.) may apply to them as well. 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.

III.4.7.6. 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 (see 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.

III.4.7.7. The *L. hamata*-group

This group contains the cosmopolitan *L. hamata*, Pantropical *L. thienemanni* (Hauer)(map 35), Australasian *L. batillifer* (map 6), Indian *L. pawlowskii*, and Neotropical *L. marchantaria* Koste & Robertson. 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. ungulata*-group (see III.4.7.2.). *L. pawlowskii* has an 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 can not 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 is 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 (see also III.4.7.3.).

III.4.7.8. 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; map 9) and *L. opias* (Harring & Myers) (Holarctic): anterolateral spines are absent (plesiomorphic) in *L. arcuata*, present (apomorphic) in *L. opias* (compare with *L. obtusa-L. whitfordi*).

(2) *L. arcula* Harring (map 23) and *L. aculeata* (Jakubski)(map 21; 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)(map 37) and *L. ligona* (Arctic-temperate)(map 18): 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: map 12) and *L. acanthinula* (Oriental, in more or less saline water: map 45): 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* (Harring & Myers)(Arctic-temperate: map 19): 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. fadeevi*).

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 interprete 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.

III.4.7.9. 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 (see III.4.4.2.).

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 susceptability to barriers) may differ according to the morphospecies. This may indicate a different effectiveness of resting eggs of different taxa to survive adverse conditions.

III.5. 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 here 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 (see also III.4.1.). 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. herzigi* 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-loricate, 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 antagonistic relation as between pelagic Rotifera and Cladocera seems likely, but requires substantiation.

III.6. 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, many Tardigrada are cosmopolitic (see Ramazzotti & Maucci, 1983), and 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, considering 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 100μm), 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. Athough 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; III.4.6.).

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). The flaws of a purely morphology-based taxonomy remain a major stumbling-block to the interpretation of distributional data (see II.3.2.1; Koste & Shiel, 1989; Ruttner-Kolisko, 1989). In this respect, Rotifera is 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).

III.7. 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). Little is known on littoral Rotifera; only De Ridder (1981a) illustrated some cases. This study intended to report on the distribution patterns in a group of littoral rotifers, and to assess the relative importance of dispersal and vicariance in explaining extant distribution patterns. Our conclusions are as follows.

(1) As 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, although some groups which are likely more vulnerable appear to be predominantly Arctic-temperate.

(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 recent 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 is 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, probably predominantly by wind, 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 mostly by the flaws of an almost exclusively morphological approach to their taxonomy.

III.8. References

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Appendices

APPENDIX 1. VERIFIED PUBLISHED RECORDS OF LECANIDAE

Records are listed alphabetically, by political or geographical units (names abbreviated according to the Times Atlas) for continental records, or by the name of the island or archipelago. The appropriate locality or region(s) is(are) indicated in cases of records from large units, or general information on species' distribution in such units cited.

L. abanica Segers, 1994

Madagascar (sub. ?*L. rotundata*. Segers, 1992)
Saudi Arabia: North-East part (Segers, 1994a)

L. acanthinula (Hauer, 1938)

India: Delhi region (Segers *et al.*, 1994c)
Indonesia: Java (Hauer, 1937; 1938)
Oman: Dhofar region (Segers & Dumont, 1993b)
Thailand: North-East part (Sanoamuang *et al.*, 1995)

L. aculeata (Jakubski, 1912)

Caribbean Islands (De Ridder, 1977)
China: Zhejiang Province (sub. *L. arcula*. Wang, 1961)
India: West Bengal (Sharma, 1978a)
Indonesia: Sumatra, Java (Hauer, 1937; 1938)
Italy: near Venice (sub. *L. stichaea*. Braioni & Gelmini, 1983)
Japan: Kyoto Prefecture (sub. *L. curvicerata*. Yamamoto, 1951; Yamamoto, 1952)
Madagascar (Segers, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Jabal Al Akhdar region, Dhofar region (Segers & Dumont, 1993b)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Senegal (Bērziņš, 1959)
Seychelles (Maas *et al.*, 1995)
Singapore (Karunakaran & Johnson, 1978)
Spain: Albufera de Valencia (Wiszniewski, 1932a)
Taiwan (Sudzuki, 1991a)
Tanzania: Usangu savanna (Jakubski, 1912)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
Zaïre: Lubumbashi region (De Ridder, 1981)

L. aeganea Harring, 1914

Argentina: Rio Paraná, Resistencia region (sub. *L. tenuiseta*. Martinez & José de Paggi, 1988)
Bahamas Islands: New Providence (Segers *et al.*, 1995)
Panama (Harring, 1914)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
U.S.A.: New Jersey (Harring & Myers, 1926)
Yemen: North (Segers & Dumont, 1993b)

L. agilis (Bryce, 1892)

Austria: Hohen Tauern (Jersabek & Schabetsberger, 1992a)
Brazil: Broa reservoir, São Paulo (Segers & Dumont, 1995)
Germany: Schwarzwald region (Hauer, 1929); Würzburg, Bayern (Hauer, 1958a); Düben, Sachsen-Anhalt (Wulfert, 1960a)
Jamaica (Koste *et al.*, 1993)
the Netherlands: 'Grote Huisven', Oisterwijk (de Graaf, 1956)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Romania (Rudescu, 1960)
Russian Federation: Karatschaevo, Caucasus region (Tarnogradski, 1961a)
U.S.A.: not specified, 'rare' (Harring & Myers, 1926)
U.K.: Eppin Forest (Bryce, 1892)

L. amazonica (Murray, 1913)

Brazil: River Amazon (Murray, 1913a); Rio Negro, Manaus (sub. *L. murrayi*. Hauer, 1965a; 1965b); Lago Jurucui, Amazonas (sub. *L. murrayi*. Thomasson, 1971); Amazonas (sub. *L. murrayi*. Koste, 1972)
Ecuador: Jatun Cocha (sub. *L. murrayi*. Koste & Böttger, 1992)

L. arcuata (Bryce, 1891)

Austria: Hohen Tauern (Jersabek & Schabetsberger, 1992a)
Brazil: Rio de Janeiro (Murray, 1913a)
Canada: Little Cornwallis Island, Northwest Territories (sub. *L. piepelsi*. De Smet & Bafort, 1990a)
Comoro Islands (Segers, 1992)
Easter Island (Segers & Dumont, 1993a)
Galápagos Archipelago (De Smet, 1989a)
Hungaria: Belső Tó, Tihany (Varga, 1937)
Iceland (De Ridder, 1969)
Italy (sub. *L. closterocerca*, partly. Braioni & Gelmini, 1983)

Japan: Southwestern Islands around Okinawa (sub. *Monostyla* sp. Sudzuki, 1992b)
Kenya: Mount Kenya (De Smet & Bafort, 1990c)
Madagascar (sub. *L. galeata*. Bērziņš, 1982b)
New Zealand: Canterbury (Russell, 1954)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Norway: Svalbard (sub. *L. piepelsi*. De Smet, 1993)
Romania (Rudescu, 1960)
Spain: Albufera de Valencia (Wiszniewski, 1932a)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
U.S.A.: 'fairly common' (Harring & Myers, 1926)
U.K.: Epping forest (Bryce, 1891)
Yemen: North (Segers & Dumont, 1993b)

L. arcula Harring, 1914

Argentina (Murray, 1913a)
Antilles: Guadeloupe (sub. *L. aculeata*. Pourriot, 1975)
Belgium: Genk (Schepens, 1960)
Brazil: (Murray, 1913a); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Canada: Ontario (Chengalath & Mulamoottil, 1974)
Chile (Murray, 1913a)
China: Xinjiang Province (sub *L. flexilis*. Wang, 1961)
Comoro Islands (Segers, 1992)
Germany: near Karlsruhe (Hauer, 1935a); near Bersenbrück, Niedersachsen (Koste, 1962)
India: Madras (sub. *L. methoria*. Pasha, 1961); Ajwa reservoir, near Baroda, Gujarat (Wulfert, 1966); West Bengal (Sharma, 1978a)
Indonesia: Sumatra, Java (Hauer, 1937; 1938)
Latvia (sub. *L. strandi*. Bērziņš, 1943)
Nepal (Daems & Dumont, 1974)
Nicaragua (Moreno *et al.*, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Dhofar region (Segers & Dumont, 1993b)
Panama (Harring, 1914)
Poland: Białowieża forest (Pawłowski, 1938)
Russian Federation: Caucasus region (Tarnogradski, 1961b)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Sri Lanka (sub. *L. verecunda*. Chengalath & Fernando, 1973)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
U.S.A.: common ... everywhere in the United States (Harring & Myers, 1926)
Yemen: North (Segers & Dumont, 1993b)
Yugoslavia: Danube river (Živković, 1987)
Zambia: Lake Bangweulu (Wulfert, 1965)

L. armata Thomasson, 1971

Brazil: Lago Jurucui, Amazonas (Thomasson, 1971); near Santarém (sub. *L. gillardi armata*. Koste, 1974)

L. aspasia Myers, 1917

Argentina: Rio Paraná, Resistencia region (sub. *L. stichaeoides*. Martinez & José de Paggi, 1988)
?Canada: Ontario (sub. *L. verecunda*. Chengalath & Mulamoottil, 1974)
Hungary: Lake Balaton (Varga, 1939)
India: Delhi region (Segers *et al.*, 1994c)
Indonesia: Sumatra (Hauer, 1937; 1938)
Russian Federation: Moskow region (Bogoslovski, 1935)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
U.S.A.: California (Myers, 1917)

L. asymmetrica (Murray, 1913)

Guyana (Murray, 1913a)
Jamaica (sub. *L. janetzkyi*. Koste *et al.*, 1991)

L. batillifer (Murray, 1913)

Australia: Sydney (Murray, 1913b); Northern Territoriy (Bērziņš, 1982a)
China: Zhejiang Province (Wang, 1961)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)

L. bifastigata Hauer, 1938

India: West Bengal (Sharma, 1979)
Indonesia: Java (Hauer, 1937; 1938)
Oman: Jabal Al Akhdar region (Segers & Dumont, 1993b)
Russian Federation: Caucasus region (Tarnogradski, 1961b)
Sri Lanka (Chengalath *et al.*, 1974)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
Turkey : Lake Beşehir (Segers *et al.*, 1992; Segers & Dumont, 1993b)

L. bifurca (Bryce, 1892)

Australia: Victoria (sub. *L. bifurca entome*. Bērziņš, 1982a)

Austria: Hohen Tauern (sub. *L. furcata*. Jersabek & Schabetsberger, 1992a)
Brazil: Broa reservoir, São Paulo (Segers & Dumont, 1995)
Canada: Laurentides National Park, Quebec (sub. *L. fusilis*. Myers, 1936c)
Easter Island (Segers & Dumont, 1993a)
Galàpagos Archipelago (Segers, 1991)
Germany: Bad Wilstein (sub. *L. crypta*. Hauer, 1940)
India: Yamuna river (Sarma, 1988)
Indonesia: Sumatra, Java (sub. *M. crypta*. Hauer, 1937; 1938)
Madagascar (Bērziņš, 1982b)
Nepal: Khatmandu (Turner, 1987)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Dhofar region (Segers & Dumont, 1993b)
Romania (Rudescu, 1960)
Russian Federation: Northern Caucasus (Tarnogradski, 1930); Caucasus region (Tarnogradski, 1961b)
Spain: Minorca (De Manuel, 1990b; De Manuel, 1994)
Sweden: Aneboda region (Carlin, 1939)
U.S.A.: not rare (Harring & Myers, 1926)
U.K.: Sandown (Bryce, 1892)

L. blachei Bērziņš, 1973

Cambodia: Mekong delta (Bērziņš, 1973)
India: Calcutta (Sarma, 1988)
Indonesia: Borneo (Koste, 1988a)
Thailand: North-East part (Sanoamuang *et al.*, 1995)

L. boettgeri Koste, 1986

Paraguay: near Concepción (Koste, 1986)

L. boliviana Segers, 1994

Bolivia: Kothia Lake, near La Paz (Segers *et al.*, 1994b)

L. boorali Koste & Shiel, 1983

Australia: southwest Western Australia (Koste *et al.*, 1983)

L. braumi Koste, 1988

Indonesia: Borneo (Koste, 1988a)

Nigeria: River Niger floodplain (sub. *L. elsa*. Segers *et al.*, 1993a)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
?Sri Lanka (sub. *L. elsa*. Chengalath *et al.*, 1974)

L. braziliensis Segers, 1993

Brazil: Roraima, Pantanal region (Segers *et al.*, 1993b); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)

L. broaensis Segers & Dumont, 1995

Brazil: Broa reservoir, São Paulo (Segers & Dumont, 1995)

L. bryophila Koniar, 1957

Slovakia: Tatra mountains (sub. *L. spec.* Koniar, 1955; Koniar, 1957)

L. bulla (Gosse, 1851)

Argentina: Buenos Aires (Olivier, 1965); Santa Fe province (sub. *L. bulla styrax*. José de Paggi & Koste, 1988)
Austria: Thaya River region (Donner, 1954)
Belgium (De Ridder, 1961a); Gent (Segers *et al.*, 1991)
Brazil: Rio de Janeiro (Murray, 1913a); lower Rio Nhamundá (sub. *L. lunaris lunaris*, *L. bulla styrax*. Brandorff *et al.*, 1982); Suape Laguna, Pernambuco (Neumann-Leitão, 1990); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Cameroon: western part (Chiambeng *et al.*, 1991)
Canada: Ontario (Chengalath & Mulamoottil, 1974)
Caribbean Islands (sub. *L. styrax*. De Ridder, 1977)
China: Jiangsu, Zhejiang Province (Wang, 1961)
Comoro Islands (Segers, 1992)
France: Camargue (De Ridder, 1961b)
Germany: Sachsen-Anhalt (Althaus, 1957); Düben, Sachsen-Anhalt (sub. *L. physalis*. Wulfert, 1960a); near Bersenbrück, Niedersachsen (Koste, 1962); Lake Stechlin (Koch-Althaus, 1963)
India: Lake Sholavaram, Madras (sub. *M. bulla* f. *diabolica*. Hauer, 1936b); Madras (Pasha, 1961); Ajwa reservoir, near Baroda, Gujarat (Wulfert, 1966); Andhra Pradesh (sub. *M. styrax*. Dhanapathi, 1976a); West Bengal (Sharma, 1978a); Jammu and Kashmir region (Jyoti & Sehgal, 1980); Gwalior, Madhya Pradesh (Saksena & Kulkarni, 1986)
Italy (Braioni & Gelmini, 1983)

Japan: Hateruma Jima, Taketomi Jima, Okinawa Jima (sub. *M. bulla constricta* and f. *triangulata*., *M. bulla dentata*. Sudzuki, 1992a); Southwestern Islands around Okinawa (incl. *Monostyla* sp. Sudzuki, 1992b)
Kenya: Ahero (Segers *et al.*, 1994a)
Korea, South (Song & Kim, 1989; Chung *et al.*, 1991)
Latvia (sub. *M. ozolini*. Bērziņš, 1943)
Madagascar (Segers, 1992)
Moldavia (incl. *L. bulla kutikovi*, *L. goniata*. Naberezhniyi & Irmasheva, 1975)
Myanmar: Kinda reservoir (Koste & Tobias, 1990)
Nepal (Daems & Dumont, 1974); Kathmandu Valley (Sarma & Ghimire, 1990)
Nicaragua (Moreno *et al.*, 1992)
Nigeria: River Sokoto (Green, 1960); River Niger floodplain (Segers *et al.*, 1993a)
Oman: Jabal Al Akhdar region, Dhofar region (Segers & Dumont, 1993b)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Peru: Ucayali dept., Amazon region (sub. *M. quadridentata*. Samanez, 1988)
Philippines (Mamaril & Fernando, 1978)
Poland: River Grabi basin (Pawłowski, 1958)
Romania (Rudescu, 1960)
Russian Federation: Dagestan (sub. *L. bulla diana*. Abdullaev, 1989); Moskow region (sub. *M. goniata*. Bogoslovski, 1935; Segers, 1994b)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Senegal (Bērziņš, 1959)
Seychelles (Maas *et al.*, 1995)
Spain: Minorca (De Manuel, 1990b)
Taiwan (Sudzuki, 1991a)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)
Turkey: Akgöl, Selçuk- İzmir (Ustaoğlu & Balik, 1987); Central and East Anatolia (Segers *et al.*, 1992)
U.S.A.: Lake Erie, South Bass Island (Jennings, 1900); 'abundant everywhere' (Harring & Myers, 1926); Laurentian Great Lakes (Stemberger, 1979)
Venezuela: Lago de Valencia (Infante, 1980)
Yemen: North (Segers & Dumont, 1993b)
Yugoslavia: Danube river (Živković, 1987)
Zaïre: Lubumbashi region; Lake Mwero, Kiwa (De Ridder, 1981)
Zambia: Lake Bangweulu, Luapula regions (De Ridder, 1981)

L. calcaria Harring & Myers, 1926

Ecuador: 'Laguna Grande' (Koste & Böttger, 1992)
U.S.A.: New Jersey (Harring & Myers, 1926)

L. candida Harring & Myers, 1926

U.S.A.: Wisconsin (Harring & Myers, 1926)

L. clara (Bryce, 1892)

Brazil: Maracá Island, Roraima (Koste & Robertson, 1990); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Germany: Schwarzwald region (Hauer, 1931); Dieksee, near Plön (Wszniewski, 1934b)
Madagascar (Bērziņš, 1982b; Segers, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Poland: Lake Wigry, Suwalki region (Wiszniewski, 1934)
Romania (Rudescu, 1960)
Russian Federation: Caucasus region (Tarnogradski, 1961b)
U.S.A.: New Jersey, Washington D.C. (Harring & Myers, 1926); Michigan (sub. *Proales longidactyla*. Edmondson, 1948)
U.K.: Sandown (Bryce, 1892)

L. climacois Harring & Myers, 1926

Nigeria: River Niger floodplain (Segers, 1993; Segers *et al.*, 1993a)
U.S.A.: Florida, Maryland, New Jersey (Harring & Myers, 1926)

L. closterocerca (Schmarda, 1859)

Antarctica: South Georgia Island (Dartnall & Hollowday, 1985)
Argentina: Buenos Aires (Murray, 1913a; sub. *L. lunaris*. Olivier, 1965); North East Provinces (José de Paggi, 1989)
Australia: Victoria (Bērziņš, 1982a)
Austria: Donau region (Donner, 1964; Donner, 1978); Hohen Tauern (Jersabek & Schabetsberger, 1992a)
Bahamas Islands: New Providence (Segers *et al.*, 1995)
Belgium (De Ridder, 1961a); Gent (Segers *et al.*, 1991)
Bolivia: Lake Titicaca (Murray, 1913a); Kothia Lake, near La Paz (Segers *et al.*, 1994b)
Brazil: Rio de Janeiro (Murray, 1913a); Amazonas (sub. *L. wulferti*, incl. *Lecane* sp. Koste, 1972); near Santarém (Koste, 1974); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Cameroon: western part (Chiambeng *et al.*, 1991)
Canada: Ontario (Chengalath & Mulamoottil, 1974)
Chile: Valparaiso, Antofagasta (Murray, 1913a)
China: Manchuria (Hada, 1938); Guangdong, Hubei Provinces (Wang, 1961)
Comoro Islands (Segers, 1992)
Ecuador: Quito (Schmarda, 1859)
Easter Island (Segers & Dumont, 1993a)
Finland: Helsinki region (sub. *M. cornuta*. Levander, 1894); Tvärminne archipelago (Björklund, 1972)
France: Camargue (De Ridder, 1960; 1961b)

Galápagos Archipelago (De Smet, 1989a; Segers, 1991)
Germany: Oldesloe, Holstein (sub. *L. cornuta*. Hauer, 1925); Sachsen-Anhalt (Althaus, 1957); Near Ludwigsburg, Baden-Württemberg (Klement, 1959); Düben, Sachsen-Anhalt (Wulfert, 1960a, b)
Greenland: Disko (sub. *L. quennerstedti*. Bergendal, 1892)
Iceland (De Ridder, 1972)
India: Rajasthan (Nayar, 1968); West Bengal (Sharma, 1978a)
Italy (Braioni & Gelmini, 1983)
Japan: Mount Fuji (Sudzuki, 1978); Southwestern Islands around Okinawa (Sudzuki, 1992b)
Korea, South (Chung *et al.*, 1991)
Latvia (sub. *M. latvica*. Bērziņš, 1943)
Moldavia (incl. *L. beningi*, *L. punctata*. Naberezhniyi & Irmasheva, 1975)
the Netherlands: Oisterwijkse vennen (de Graaf, 1960)
Nepal (Daems & Dumont, 1974); Kathmandu Valley (Sarma & Ghimire, 1990)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Norway: Bjørnøya (De Smet, 1988)
Oman: Jabal Al Akhdar region, Dhofar region (Segers & Dumont, 1993b)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Philippines (Mamaril & Fernando, 1978)
Poland: river Grabi basin near Łódź (partly. Pawłowski, 1956; 1958)
Romania (Rudescu, 1960)
Russian Federation: Ural mountains, Perm region (Oparina-Charitonova, 1928); Caucasus region (Tarnogradski, 1961b); Moskow region (Segers, 1994b)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Seychelles (Maas *et al.*, 1995)
Sierra Leone: Lake Sonfon (sub. *L. wulferti*. Green, 1979)
Singapore (Sudzuki, 1991a)
Spain: Los Marismas (De Ridder, 1962); Minorca (De Manuel, 1990b); Majorca (De Manuel, 1994)
Sweden: Lappland (Pejler, 1962)
Tanzania: Mount Kilimanjaro (De Smet & Bafort, 1990b)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)
Turkey: Central and East Anatolia (Segers *et al.*, 1992)
U.K. (sub. *L. cornuta*. Bryce, 1891)
Ukraine (sub. *L. arcuata*. Ovander, 1980a)
U.S.A.: 'abundant everywhere' (Harring & Myers, 1926); Laurentian Great Lakes (Stemberger, 1979)
Venezuela: Laguna Mucubaji (Hauer, 1956)
Yemen: North (Segers & Dumont, 1993b)
Yugoslavia: Danube river (Živković, 1987)
Zaïre: Lubumbashi region; Lake Mwero, Kilwa (De Ridder, 1981)
Zambia: Luangwa river region (De Ridder, 1981)

L. copeis (Harring & Myers, 1926)

Brazil: Amazonas (sub. *L. obtusa*, cf. *L. acanthinula*. Koste, 1972); Mato Grosso do Sul (Turner & Da Silva, 1992)
Ecuador: 'Costa', 'Oriente' (sub. *L. eupsammophila*. Koste & Böttger, 1992)
Romania (Rudescu, 1960)
U.S.A.: Colorado, Wisconsin (Harring & Myers, 1926)

L. cornuta (Müller, 1786)

Antilles: Guadeloupe, Marie Galante (sub. *Lecane* sp. 2. Pourriot, 1975)
Argentina: Rio Paraná, Resistencia region (Martinez & José de Paggi, 1988)
Brazil: Lago Maica, Amazonas (Thomasson, 1971); Lake Jurucui, Belterra, Tapajoz (Gillard, 1967); Suape Laguna, Pernambuco (Neumann-Leitão, 1990); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Canada: Ontario (Chengalath & Mulamoottil, 1974)
Caribbean region: Hispaniola (sub. *M. rotunda*. Edmondson, 1934)
Colombia: Baranquilla (incl. var. *oidipus*. Hauer, 1956)
Germany: near Karlsruhe (Hauer, 1929)
Nicaragua: Lake Nicaragua (Segers, 1995)
Panama (Harring & Myers, 1926)
Peru: Ucayali dept., Amazon region (Samanez, 1988)
Romania (Rudescu, 1960)
Russian Federation: vicinity of Kharkov, Lopan River, Uda River (sub. *M. rotunda*. Fadeev, 1927); Ural mountains, Perm region (sub. *M. rotundata*. Oparina-Charitonova, 1928)
U.S.A.: Lake Erie, South Bass Island (Jennings, 1900); 'abundant ... in the United States (Harring & Myers, 1926); North Carolina (Ahlstrom, 1938); Laurentian Great Lakes (incl. *M. stenroosi*. Stemberger, 1979)
Venezuela: Laguna Taiguaiguai, near Barrancas (incl. var. *oidipus*. Hauer, 1956); Lago de Valencia (var. *oidipus*. Infante, 1980); Mantecal (sub. *Lecane* species. Michelangelii *et al.*, 1980); Mantecal, Rio Urama, Yaracuy, Aroa (var. *rotunda*. Zoppi de Roa *et al.*, 1994)

L. crepida Harring, 1914

Argentina: North East Provinces (José de Paggi, 1989)
Bahamas Islands: Grand Bahama (Nogrady, 1983)
Brazil: Lake Maica, Varzea Santarém (sub. *Lecane* sp. Gillard, 1967); Rio Madeira (sub. *L. crepida longidactyla*. Koste, 1972); near Santarém (Koste, 1974); Boa Vista region, Roraima (Segers & Sarma, 1994)
Canada: Ontario (Chengalath & Mulamoottil, 1974)
China: Zhejiang Province (Wang, 1961)

India: Madras (Pasha, 1961); Ajwa reservoir, near Baroda, Gujarat (incl. *L. neali*. Wulfert, 1966); West Bengal (Sharma, 1978a; sub. f. *bengalensis*. Sharma, 1979; sub. *L. vasishti*. Sharma, 1980)
Indonesia: Sumatra, Java (Hauer, 1937; 1938); Borneo (Koste, 1988a)
Madagascar (Segers, 1992)
Nepal (Daems & Dumont, 1974)
Nicaragua (Moreno *et al.*, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Dhofar region (Segers & Dumont, 1993b)
Panama (Harring, 1914)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Peru: Ucayali dept., Amazon region (Samanez, 1988)
Philippines (Mamaril & Fernando, 1978)
Singapore (Sudzuki, 1991a)
Spain: Albufera de Valencia (Wiszniewski, 1932a)
Sri Lanka (Chengalath & Fernando, 1973)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)
U.S.A.: South Bass Island (sub. *D. gissensis*. Jennings, 1900); Maine, Wisconsin (Harring & Myers, 1926); Laurentian Great Lakes (Stemberger, 1979)

L. curvicornis (Murray, 1913)

Argentina: Rio Paraná, Resistencia region (Martinez & José de Paggi, 1988)
Brazil: Rio de Janeiro (incl. *C. nitida*. Murray, 1913a); Lago Maica, Lago Jurucui, Amazonas (incl. *L. curvicornis nitida*. Thomasson, 1971); Paraná de Xiborena, Amazonas (Hauer, 1965b); Maranhão State (incl. f. *lofuana*, *L. curvicornis nitida*. Reid & Turner, 1988); Suape Laguna, Pernambuco (Neumann-Leitão, 1990); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (incl. f. *nitida*. Segers & Dumont, 1995)
Canada: Ontario (Chengalath & Mulamoottil, 1974)
Caribbean region: Hispaniola (sub. *L. bondi*. Edmondson, 1934)
Ethiopia: Lake Zwai (sub. *L. zwaiensis*. Bryce, 1931)
China: Heilongjiang, Jiangsu, Zhejiang Provinces (Wang, 1961)
Czechia: Silesia (sub. *L. ungulata curvicornis*. Dvorakova, 1960a)
Germany: Donaueschingen (Hauer, 1931)
Guatemala (Harring & Myers, 1926)
India: Nagpur (sub. *L. curvicornis* var. *padespares*, *L. tesselata*, *L. curvilinealis*, *L. longidactyla*. Arora, 1965); Ajwa reservoir, near Baroda, Gujarat (var. *nitida*. Wulfert, 1966); West Bengal (incl. var. *miamiensis*. Sharma, 1978a); Gwalior, Madhya Pradesh (Saksena & Kulkarni, 1986); Megalaya, Northeast region (sub. var. *nitida*. Sharma, 1987)
Indonesia: Sumatra (sub. *L. curvicornis nitida*. Hauer, 1937; 1938)
Italy: near Venice (Braioni & Gelmini, 1983)
Japan: Hyogo Prefecture (sub. *L. triloba*. Yamamoto, 1951)
Korea, South (Song & Kim, 1989; Chung *et al.*, 1991)

Nicaragua (Moreno *et al.*, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Dhofar region (Segers & Dumont, 1993b)
Panama (Harring & Myers, 1926)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Philippines (incl. var. *miamiensis*. Mamaril & Fernando, 1978)
Russian Federation: Lake Khanka (sub. *L. chankensis*. Bogoslovski, 1958); Ural mountains, Perm region (sub. *L. acronycha*. Oparina-Charitonova, 1928); Caucasus region (Tarnogradski, 1961b)
Senegal (sub. *L. ungulata curvicornis*. Bērziņš, 1959)
Singapore (sub. *L. curvicornis lofuana*, *L. curvicornis nitida*, *Lecane* sp. 2. Sudzuki, 1991a)
Sri Lanka (incl. var. *miamiensis*. Chengalath & Fernando, 1973)
Tanzania: Lake Tanganyika (sub. *L. lofuana*. Murray, 1913c)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)
U.S.A.: Arkansas, California, Maine, New Jersey, Texas, Wisconsin, Lake Erie (incl. *L. acronycha*. Harring & Myers, 1926); Florida (sub. var. *miamiensis*. Myers, 1941)
Venezuela: Mantecal (sub. *L. luna* var. *presumpta*. Zoppi de Roa *et al.*, 1994)
Zaïre: Lake Mwero, Kilwa; Lubumbashi region (incl. var. *nitida*. De Ridder, 1981); Bas-Zaïre (De Smet, 1989b)
Zambia: Lake Bangweulu, Luapula regions (incl. var. *nitida*. De Ridder, 1981)
Zimbabwe: Lake Kariba (Thomasson, 1965)

L. decipiens (Murray, 1913)

Brazil: Rio de Janeiro (Murray, 1913a); Ilha de Marchantaria, Amazonas (Koste & Robertson, 1983); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Galàpagos Archipelago (Segers, 1991)
Jamaica (Koste *et al.*, 1991)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Panama (Harring & Myers, 1926)
Peru: Ucayali dept., Amazon region (sub. *M. hamata*. Samanez, 1988)

L. depressa (Bryce, 1891)

Canada: Ontario (sub *L. tudicola*. Chengalath & Mulamoottil, 1974); Québec (sub. *L. brachydactyla*. Nogrady, 1976)
Germany: Plön (sub. *Distyla truncata*. Leissling, 1914); near Karlsruhe (sub. *L. tudicola*. Hauer, 1935a); Luckenwalde, Brandenburg (sub. *L. tudicola*. Wulfert, 1940); near Bersenbrück, Niedersachen (sub. *L. tudicola*. Koste, 1962); Bayern: Donau region (sub. *L. tudicola*. Donner, 1972)
Italy: near Venice (sub. *L. tudicola*. Braioni & Gelmini, 1983)

Japan: Honshu (sub. *L. brachydactyla*. Yamamoto, 1952); Ozegahara (sub. *L. truncata*. Yamamoto, 1953a)
Korea, North (sub. *L. brachydactyla*. Yamamoto, 1953b)
Latvia (Kutikova, 1959)
Poland: Gdansk (Danzig: sub. *L. brachydactyla*. Rousselet, 1912; Murray, 1913c); Silesia (sub. *L. brachydactyla*. Sachse, 1915)
Russian Federation: Caucasus region (sub. *L. brachydactyla*, *L. tudicola*. Tarnogradski, 1961b); St-Petersburg region (sub. *L. tudicola*. Kutikova, 1962); Karelian lakes (sub. *L. brachydactyla*. Kutikova, 1965)
Sweden: Dalarö (sub. *L. tudicola*. Carlin-Nilsson, 1934)
Ukraine (sub. *L. brachydactyla*. Ovander, 1980a)
U.S.A.: Maine, New Jersey, Wisconsin, St. Paul, Pribilof Islands, Alaska (sub. *L. brachydactyla*, incl. *L. tudicola*. Harring & Myers, 1926); Laurentian Great Lakes (sub. *L. tudicola*. Stemberger, 1979)
U.K.: River Lea (Bryce, 1891)

L. deridderae Koste, 1972

Brazil: Amazonas (Koste, 1972)

L. donneri Chengalath & Mulamoottil, 1974

Canada: Ontario (Chengalath & Mulamoottil, 1974)
?Indonesia: Borneo (sub. *L. lauterborni*. Koste, 1988a)
Madagascar (sub. *L. lauterborni*. Segers, 1992)
Oman: Dhofar region (Segers & Dumont, 1993b)

L. donyanaensis Mazuelos & Segers, 1994

Spain: Doñana National Park (Galindo *et al.*, 1994)

L. doryssa Harring, 1914

Brazil: near Santarém (Koste, 1972); lower Rio Nhamundá (Brandorff *et al.*, 1982)
China: Liaoning Province (Wang, 1961)
Guatemala: Puerto Barrios (Harring & Myers, 1926)
India: Megalaya, Northeast region (Sharma, 1987); Calcutta (Sarma, 1988)
Indonesia: Sumatra (Hauer, 1937; 1938); Borneo (Koste, 1988a)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Panama (Harring, 1914)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Russian Federation: Northern Caucasus (Tarnogradski, 1930); Caucasus region (Tarnogradski, 1961b)

Seychelles (Maas *et al.*, 1995)
Sweden: Aneboda region (Carlin, 1939)
Thailand: North-East part (Sanoamuang *et al.*, 1995)

L. dumonti Segers, 1993

Brazil: Roraima (Segers *et al.*, 1993b; Segers & Sarma, 1994)
Nigeria: River Niger floodplain (Segers, 1993; Segers *et al.*, 1993a)

L. dysoarata Myers, 1942

U.S.A.: Northeastern Pennsylvania (Myers, 1942)

L. elasma Harring & Myers, 1926

Germany: Schwarzwald region (Hauer, 1929); near Bersenbrück, Niedersachsen (Koste, 1962)
the Netherlands: 'Grote Huisven', Oisterwijk (de Graaf, 1956)
Romania (Rudescu, 1960)
U.S.A.: D.C., New Jersey, Wisconsin (Harring & Myers, 1926)

L. elegans Harring, 1914

Argentina: Rio Paraná, Resistencia region (Martinez & José de Paggi, 1988)
Brazil: near Santarém (Koste, 1974)
Indonesia: Borneo (Koste, 1988a)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Panama (Harring, 1914)
Philippines (Mamaril & Fernando, 1978)

L. elongata Harring & Myers, 1926

Poland: Tatra mountains (Pawłowski, 1938)
Romania (Rudescu, 1960)
Russian Federation: Dagestan (sub. *L. lebedevae*. Abdullaev, 1989)
U.S.A.: New Jersey (Harring & Myers, 1926)

L. elsa Hauer, 1931

Argentina: Rio Paraná, Resistencia region (partly. Martinez & José de Paggi, 1988)
Brazil: Paraná de Xiborena, Amazonas (Hauer, 1965b); Amazonas (Koste, 1972)

Czechia: Silesia (Dvorakova, 1960a)
Germany: near Karlsruhe (Hauer, 1931)
Jamaica (Koste *et al.*, 1993)
Poland: River Grabi basin (Pawłowski, 1958)
Russian Federation: Caucasus region (sub. *L. luna* var. *presumpta*. Tarnogradski, 1961b)
Ukraine (Ovander, 1980a)
Yugoslavia: Danube river (sub. *L. presumpta*. Živković, 1987)

L. eswari Dhanapathi, 1976

India: Andhra Pradesh (Dhanapathi, 1976b)

L. eutarsa Harring & Myers, 1926

Argentina: Santa Fe province (sub. *L. amazoniana*. José de Paggi & Koste, 1988)
Brazil: Arapuns, near Manaus (sub. *L. rhytida*, *Lecane* sp. 1. Hauer, 1965b); Amazonas (sub. *L. rhytida*. Koste, 1972); Ilha de Marchantaria, Amazonas (sub. *L. amazoniana*. Koste & Robertson, 1983); Boa Vista region, Roraima (Segers & Sarma, 1994)
Ecuador: 'Oriente' (sub. *L. amazonica*. Koste & Böttger, 1992)
Guatemala: Puerto Barrios (Harring & Myers, 1926)

L. eylesi Russel, 1953

New Zealand: Chatham Islands (Russel, 1953a); near Greymouth (sub. *L. tasmaniensis*. Sanoamuang & Stout, 1993)
Tasmania (sub. *L. tasmaniensis*. Shiel & Koste, 1985)

L. fadeevi Neiswestnowa-Schadina, 1935

?**Poland:** River Grabi basin (sub. *L. closterocerca*, partly. Pawłowski, 1956; 1958)
Russian Federation: Moskow region (Neiswestnowa-Schadina, 1935; Segers, 1994b)

L. flabellata Edmondson, 1936

U.S.A.: Maine (Edmondson, 1936)

L. flexilis (Gosse, 1886)

Austria: Hohen Tauern (Jersabek & Schabetsberger, 1992a)
Belgium: Gent (incl. *L. glypta*. Segers *et al.*, 1991)

Bolivia: Kothia Lake, near La Paz (Segers *et al.*, 1994b)
Brazil: Rio de Janeiro (Murray, 1913a); Ilha de Marchantaria, Amazonas (sub. *L. aculeata*. Koste & Robertson, 1983); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Canada: Ontario (Chengalath & Mulamoottil, 1974)
China: Yunnan Province (sub. *L. glypta*. Wang, 1961)
Denmark: Faroër Islands (De Smet *et al.*, 1988)
France: Camargue (De Ridder, 1960; 1961b)
Germany: In cold sulpur and thermal springs (Pax & Wulfert, 1941); Düben, Sachsen-Anhalt (incl. *L. glypta*. Wulfert, 1960a); Lake Stechlin (Koch-Althaus, 1963)
India: West Bengal (Sharma, 1978a)
Italy (Braioni & Gelmini, 1983)
Korea, South (Chung *et al.*, 1991)
Nepal: Kathmandu Valley (sub. *L. tudicola*. Sarma & Ghimire, 1990)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Norway: Bjørnøya (De Smet, 1988)
Panama (incl. *L. compta*. Harring, 1914)
Romania (Rudescu, 1960)
Russian Federation: Caucasus region (Tarnogradski, 1961b); Moskow region (Segers, 1994b)
Spain: Minorca (De Manuel, 1994)
Sweden: Aneboda region (Carlin, 1939); Lappland (Pejler, 1962)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
U.K.: England (Harring & Myers, 1926)
U.S.A.: common ... everywhere in the United States (incl. *L. glypta*. Harring & Myers, 1926); Laurentian Great Lakes (Stemberger, 1979)
Yugoslavia: Danube river (Živković, 1987)

L. formosa Harring & Myers, 1926

U.S.A.: Wisconsin (Harring & Myers, 1926)

L. furcata (Murray, 1913)

Belorussiya: Pinsk region (Wiszniewski, 1930)
Brazil: Rio de Janeiro (Murray, 1913a); Amazonas (sub. *L. scutata*, sub. *L. rugosa*. Koste, 1972); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Canada: Ontario (Chengalath & Mulamoottil, 1974)
Chile (Schmid-Araya, 1991)
China: Manchuria (Hada, 1938); Heilongjiang, Zhejiang Provinces (incl. *L. elachis*, *L. tethis*. Wang, 1961)
France: Camargue (sub. *L. vanoyei*. De Ridder, 1960; 1961b)
Germany: near Karlsruhe (Hauer, 1929); Sachsen-Anhalt (Althaus, 1957); near Bersenbrück, Niedersachsen (Koste, 1962)

Guatemala: Puerto Barrios (Harring & Myers, 1926)
India: Ajwa reservoir, near Baroda, Gujarat (sub. *L. elachis*. Wulfert, 1966); Andhra Pradesh (sub. *M. tethis*. Dhanapathi, 1976a); West Bengal (Sharma, 1979); Megalaya, Northeast region (sub. *L. scutata*. Sharma, 1987)
Indonesia: Sumatra, Java (incl. *M. elachis*, *Monostyla* sp (*rugosa*?). Hauer, 1937; 1938); Borneo (sub. *L. rugosa*. Koste, 1988a)
Italy (Braioni & Gelmini, 1983)
Japan: Southwestern Islands around Okinawa (Sudzuki, 1992b)
Latvia (sub. *M. rugosa*. Kutikova, 1959)
Moldavia (incl. *L. rugosa*. Naberezhniyi & Irmasheva, 1975)
Myanmar: Kinda reservoir (Koste & Tobias, 1990)
Nicaragua (Moreno *et al.*, 1992)
Nigeria: River Niger floodplain (incl. f. *elachis*. Segers *et al.*, 1993a)
Oman: Jabal Al Akhdar region (Segers & Dumont, 1993b)
Panama (Harring & Myers, 1926)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Romania (Rudescu, 1960)
Russian Federation: Ural mountains, Perm region (sub. *M. tethis*. Oparina-Charitonova, 1928); Northern Caucasus (Tarnogradski, 1930); Moskow region (sub. *M. mologensis*, *M. tethis*. Bogoslovski, 1935); Caucasus region (Tarnogradski, 1961b)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Spain: Minorca (De Manuel, 1990b); Majorca (De Manuel, 1994)
Sri Lanka (incl. *L. scutata*. Chengalath *et al.*, 1974)
Sweden: Aneboda region (Carlin, 1939); Lappland (Pejler, 1962)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)
Turkey: Central and East Anatolia (Segers *et al.*, 1992)
Ukraine (sub. *L. elachis*. Ovander, 1980a)
U.S.A.: common ... in the United States (incl. *M. elachis*, *M. tethis*, Harring & Myers, 1926)
Yemen: North (Segers & Dumont, 1993b)
Yugoslavia: Danube river (incl. *L. elachis*. Živković, 1987)
Zaïre: Bas-Zaïre (De Smet, 1989b)

L. galeata (Bryce, 1892)

Austria: Salzburg (Pax & Wulfert, 1942); Hohen Tauern (Jersabek & Schabetsberger, 1992a)
Belgium: Postel (Segers, 1995)
Germany: Schneeberg, Brandenburg (sub. *M. pygmaea*. Wulfert, 1940)
Iceland (De Ridder, 1969)
Ireland: Clare Island (sub. *M. turbo*. Murray, 1913c)
Moldavia (sub. *L. rylovi*. Naberezhniyi & Irmasheva, 1975)
the Netherlands: 'Grote Huisven', Oisterwijk (de Graaf, 1956)
Romania (sub. *L. pygmaea*. Rudescu, 1960)
Russian Federation: Caucasus region (incl. *L. beningi*. Tarnogradski, 1961b)

U.S.A.: D.C., Florida, Maine, New Jersey, Wisconsin (sub *M. pymaea*. Harring & Myers, 1926)
U.K.: Sandown (Bryce, 1892)

L. gillardi (Bērziņš, 1960)

Madagascar (Bērziņš, 1960)

L. grandis (Murray, 1913)

Argentina: Rio Paraná, Resistencia region (Martinez & José de Paggi, 1988)
Brazil: Rio de Janeiro (Murray, 1913a), Pernambuco (Neumann-Leitão, 1986)
Caribbean Islands (De Ridder, 1977)
Oman: Dhofar region (Segers & Dumont, 1993b)
Romania (Rudescu, 1960)
Russian Federation: Novorossiysk, Black Sea Coast (Fadeev, 1925)
Spain: Minorca (De Manuel, 1994)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
U.A.E. (Segers & Dumont, 1993b)
U.S.A.: New Jersey (Harring & Myers, 1926)

L. gwileti (Tarnogradski, 1930)

Germany: near Karlsruhe (sub. *L. kieferi*. Hauer, 1931)
Russian Federation: Northern Caucasus (Tarnogradski, 1930); Caucasus region (Tarnogradski, 1961b)

L. haliclysta Harring & Myers, 1926

Brazil: Paraná de Xiborena, Amazonas (Hauer, 1965b); Ilha de Marchantaria, Amazonas (sub. *L. stichaeoides*. Koste & Robertson, 1983); Boa Vista region, Roraima (Segers & Sarma, 1994)
France: Etang de Pommerau, Loire-et-Cher (Tassigny *et al.*, 1970)
Germany: Düben, Sachsen-Anhalt (Wulfert, 1960a)
India: Megalaya, Northeast region (Sharma, 1987)
Indonesia: Sumatra (sub. *L. stichaeoides*. Hauer, 1937; 1938)
Nigeria: River Niger floodplain (sub. *L. stichaeoides*. Segers *et al.*, 1993a)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Singapore (sub. *Lecane* sp. 1. Sudzuki, 1991a)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
U.S.A.: Maine, New Jersey, Wisconsin, Lake Erie (Harring & Myers, 1926)

L. hamata (Stokes, 1896)

Antilles (Pourriot, 1975)
Australia: Victoria (sub. *L. hamata victoriensis*. Koste & Shiel, 1980; Bērziņš, 1982a)
Austria: Thaya River region (Donner, 1954); Hohen Tauern (Jersabek & Schabetsberger, 1992a)
Argentina: Nahuel Huapi National Park (Thomasson, 1959); Buenos Aires (Olivier, 1965); Rio Paraná, Resistencia region (Martinez & José de Paggi, 1988)
Bahamas Islands: New Providence (Segers *et al.*, 1995)
Belgium (De Ridder, 1961a)
Brazil: Rio de Janeiro (Murray, 1913a); Amazonas (Koste, 1972); Ilha de Marchantaria, Amazonas (Koste & Robertson, 1983); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Cameroon: western part (Chiambeng *et al.*, 1991)
Canada: Ontario (incl. *L. fernandoi*, *L. decipiens*. Chengalath & Mulamoottil, 1974)
Caribbean Islands (sub. *L. arcuata*. De Ridder, 1977)
China: Manchuria (Hada, 1938); Shanghai (Wang, 1961)
Comoro Islands (Segers, 1992)
Easter Island (Segers & Dumont, 1993a)
Germany: Bad Landeck, Bad Schallerbach (Pax & Wulfert, 1941)
Hungary: near Budapest (sub. *L. decipiens*. Nogrady, 1962)
Iceland (De Ridder, 1972)
India: Madras (Pasha, 1961); Ajwa reservoir, near Baroda, Gujarat (incl. *L. arcuata*, *L. sinuata*. Wulfert, 1966); West Bengal (incl. *L. decipiens*. Sharma, 1978a); Jammu and Kashmir region (sub. *L. decipiens*. Jyoti & Sehgal, 1980)
Indonesia: Sumatra (sub. *M. sinuata*. Hauer, 1937; 1938)
Italy (Braioni & Gelmini, 1983)
Jamaica (Koste *et al.*, 1991)
Japan: Southwestern Islands around Okinawa (incl. *M. hamata* ssp. Sudzuki, 1992b)
Korea, South (incl. *L. arcuata*. Chung *et al.*, 1991)
Madagascar (Segers, 1992)
Moldavia (Naberezhniyi & Irmasheva, 1975)
Nepal (Daems & Dumont, 1974); Kathmandu Valley (sub. *L. decipiens*. Sarma & Ghimire, 1990)
Nicaragua (Moreno *et al.*, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Jabal Al Akhdar region, Dhofar region (Segers & Dumont, 1993b)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Philippines (sub. *L. decipiens*. Mamaril & Fernando, 1978)
Romenia: Bucegi Mountains (sub. *L. arcuata*. Godenau, 1970; Rudescu, 1960)
Russian Federation: Moskow region (Segers, 1994b)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Singapore (Sudzuki, 1991a)
Spain: Minorca (De Manuel, 1990b); Ibiza (De Manuel, 1994)
Sweden: Lappland (sub. *L.* cf. *decipiens*. Pejler, 1962)
Tanzania: Mount Kilimanjaro (sub. *L. arcuata*. De Smet & Bafort, 1990b)

Thailand: Bong Borapet, Central Thailand (sub. *L. arcuata*. Koste & Robertson, 1983); North-East part (Sanoamuang *et al.*, 1995)
Turkey: Central and East Anatolia (Segers *et al.*, 1992)
U.S.A.: South Bass Island (Jennings, 1900); 'common everywhere' (Harring & Myers, 1926); Oklahoma (sub. *M. lunaris*. Taft, 1932)
Yemen: North (Segers & Dumont, 1993b)
Yugoslavia: Danube river (Živković, 1987)
Zaïre: Lubumbashi region (incl. *L. arcuata*. De Ridder, 1981); Bas-Zaïre (sub. *Lecane* sp. De Smet, 1989b; 1990)

L. hastata (Murray, 1913)

Argentina: Northwestern Buenos Aires Province (Modenutti & Claps, 1988); Santa Fe province (José de Paggi & Koste, 1988)
Brazil: Rio de Janeiro (Murray, 1913a); near Bôa Vista (Koste, 1972)
Caribbean Islands (sub. *L. plesia*. De Ridder, 1977)
India: Ajwa reservoir, near Baroda, Gujarat (Wulfert, 1966); West Bengal (Sharma, 1979)
Japan: Hegura Island (sub. *L. hegurensis*. Yamamoto, 1951); Southwestern Islands around Okinawa (Sudzuki, 1992b)
Moldavia (incl. *L. plesia*. Naberezhniyi & Irmasheva, 1975)
Namibia: Namid Desert (sub. *Proales namibiensis*. Brain & Koste, 1993)
Oman: Dhofar region (Segers & Dumont, 1993b)
Papua New Guinea: Madang Province (Segers & De Meester, 1994)
Philippines (Mamaril & Fernando, 1978)
Romenia (Godenau, 1961b)
Russian Federation: Caucasus region (Tarnogradski, 1961b); Dagestan (sub *L. jana*. Abdullaev, 1989)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Spain: Majorca (De Manuel, 1990a); Majorca (De Manuel, 1994)
Sri Lanka (incl. *L. kahouteki*. Chengalath *et al.*, 1974)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)
U.A.E. (Segers & Dumont, 1993b)
U.S.A.: Louisiana, New Jersey, Virginia, Washington D.C. (Harring & Myers, 1926); New Jersey (sub. *L. plesia*. Myers, 1936b)
Yemen: North (Segers & Dumont, 1993b)

L. herzigi Koste, Shiel & Tan, 1988

New Zealand: near Greymouth (Sanoamuang & Stout, 1993)
Tasmania (Koste *et al.*, 1988)

L. hornemanni (Ehrenberg, 1834)

Australia: Victoria (sub. *L. nodosa*. Bērziņš, 1982a)
Brazil: Rio de Janeiro (Murray, 1913a); Amazonas (sub. *L. nodosa*. Koste, 1972); lower Rio Nhamundá (incl. *L. nodosa*. Brandorff *et al.*, 1982); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Bolivia: Lake Titicaca (Murray, 1913a)
Canada: Ontario (Chengalath & Mulamoottil, 1974)
Chad: Lake Chad (Pourriot, 1968)
China: Zhejiang Province (sub. *L. nodosa*. Wang, 1961)
India: Madras (Pasha, 1961); Ajwa reservoir, near Baroda, Gujarat (incl. *L. nodosa*. Wulfert, 1966); Andhra Pradesh (Dhanapathi, 1976a)
Indonesia: Sumatra, Java, Bali (incl. *L. nodosa*. Hauer, 1937; 1938); Borneo (sub. *L. nodosa*. Koste, 1988a)
Italy: Trentino (Braioni & Gelmini, 1983)
Japan: Nagono Prefecture (Yamamoto, 1952); Southwestern Islands around Okinawa (partly. Sudzuki, 1992b)
Madagascar (incl. *L. camptica*, *L. lamiranoensis*. Bērziņš, 1982b; Segers, 1992)
Nicaragua (Moreno *et al.*, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Dhofar region (Segers & Dumont, 1993b)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Philippines (incl. *L. ceylonensis*. Mamaril & Fernando, 1978)
Romania (Rudescu, 1960)
Russian Federation: Caucasus region (Tarnogradski, 1961b)
Singapore (sub. *L. nodosa*, *L. ruttneri*. Sudzuki, 1991a)
Spain: Albufera de Valencia (Wiszniewski, 1932a)
Sri Lanka (incl. *L. ceylonensis*. Chengalath & Fernando, 1973)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)
U.S.A.: New Jersey, Maine, Washington D.C., Wisconsin (Harring & Myers, 1926)
U.K.: England (Murray, 1913a)
Zaïre: Lubumbashi region (sub. *L. nodosa*. De Ridder, 1981)
Zambia: Luapula region (sub. *L. nodosa*. De Ridder, 1981)

L. inconspicua Segers & Dumont, 1993

Saudi Arabia: North-East part (Segers & Dumont, 1993b)

L. inermis (Bryce, 1892)

Austria: Thaya River region (Donner, 1954)
Brazil: Broa reservoir, São Paulo (Segers & Dumont, 1995)
China: Jiangsu Province (Wang, 1961)
Easter Island (Segers & Dumont, 1993a)

Germany: In cold sulpur and thermal springs (Pax & Wulfert, 1941); Near Ludwigsburg, Baden-Württemberg (Klement, 1959); Düben, Sachsen-Anhalt (Wulfert, 1960a); Lake Stechlin (Koch-Althaus, 1963)
Iceland (De Ridder, 1972)
India: Megalaya, Northeast region (Sharma, 1987); Delhi region (sub. *L. althausi*. Sarma, 1988)
Italy (sub. *L. supinoi*. Manfredi, 1929)
Japan: Southwestern Islands around Okinawa (sub. *Lecane* sp. Sudzuki, 1992b)
Nicaragua (Moreno *et al.*, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Nepal (Daems & Dumont, 1974)
Oman: Jabal Al Akhdar region (Segers & Dumont, 1993b)
Panama (sub. *L. amorpha*. Harring, 1914)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Romania (Rudescu, 1960)
Russian Federation: Northern Caucasus (sub. *L. tenuiseta*. Tarnogradski, 1930); Moskow region (Segers, 1994b)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Seychelles (Maas *et al.*, 1995)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
Turkey: Central Anatolia (Segers *et al.*, 1992)
U.S.A.: Common everywhere (Harring & Myers, 1926); Laurentian Great Lakes (Stemberger, 1979)
U.K.: Sandown (Bryce, 1892)
Yugoslavia: Danube river (Živković, 1987)

L. infula Harring & Myers, 1926

Japan: Nagono Prefecture (Yamamoto, 1960)
Russian Federation: Olenyi Island (Fadeev, 1927)
U.S.A.: Maine (Harring & Myers, 1926)

L. inopinata Harring & Myers, 1926

Brazil: Boa Vista region, Roraima (Segers & Sarma, 1994)
China: Hubei, Sichuan, Zhejiang Province (sub. *L. sympoda*. Wang, 1961)
Colombia: Barranquilla (Hauer, 1956)
Comoro Islands (sub. *L. sympoda*. Segers, 1992)
France: Lake Pazac, Dept. Nîmes (De Ridder, 1958)
India: Ajwa reservoir, near Baroda, Gujarat (sub. *L. sympoda*, partly. Wulfert, 1966); Andhra Pradesh (Dhanapathi, 1976a); West Bengal (incl. *L. sympoda*. Sharma, 1978a)
Indonesia: Sumatra, Java (sub. *L. sympoda*. Hauer, 1937; 1938)
Italy: near Alto Adige, Lazio (Braioni & Gelmini, 1983)
Japan: Southwestern Islands around Okinawa (sub. cf. *inopinata*. Sudzuki, 1992b)
Madagascar (Bērziņš, 1982b; sub. *L. sympoda*. Segers, 1992)

Myanmar: Kinda reservoir (sub. *L. inopinata sympoda*. Koste & Tobias, 1990)
Nepal (Daems & Dumont, 1974)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Jabal Al Akhdar region, Dhofar region (sub. *L. sympoda*. Segers & Dumont, 1993b)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Philippines (Mamaril & Fernando, 1978)
Russian Federation: Caucasus region (sub. *L. sympoda*. Tarnogradski, 1961b)
Senegal (Bērziņš, 1959)
Spain: Albufera de Valencia (sub. *L. sympoda*. Wiszniewski, 1932a); Ibiza (De Manuel, 1994)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
U.S.A.: Wisconsin (Harring & Myers, 1926); Laurentian Great Lakes (Stemberger, 1979)
Zaïre: Lubumbashi region (sub. *L. sympoda*. De Ridder, 1981)
Zambia: Lake Bangweulu (sub. *L. sympoda*. Wulfert, 1966)

L. inquieta Myers, 1936

U.S.A.: New Jersey (Myers, 1936a)

L. intrasinuata (Olofsson, 1917)

Canada: Ontario (sub. *L. methoria*. Chengalath & Mulamoottil, 1974)
Norway: Alexandrovsk, mouth of Kolafjord (Oloffson, 1917)
Russian Federation: Caucasus region (Tarnogradski, 1961b)
U.S.A.: Maine, New Jersey, Wisconsin (incl. *L. mylacris*. Harring & Myers, 1926)

L. ivli (Wiszniewski, 1935)

Hungary: Budapest (sub. *M. vargai*. Török, 1935)
Italy: near Venice (Braioni & Gelmini, 1983)
Macedonia: Lake Ohrid (Wiszniewski, 1935)
Yugoslavia: Danube river (Živković, 1987)

L. jaintiaensis Sharma, 1987

India: Megalaya, Northeast region (Sharma, 1987)

L. junki Koste, 1975

Thailand: Bong Borapet, Central Thailand (Koste, 1975)

L. kluchor Tarnogradski, 1930

Austria: Hohen Tauern (Jersabek & Schabetsberger, 1992a)
France: Puy-de Dôme (Francez & Pourriot, 1984)
Germany: Schwarzwald region (sub. *L. diadema*. Hauer, 1931; Hauer, 1935b)
Romania (Rudescu, 1960)
Russian Federation: Northern Caucasus (Tarnogradski, 1930); Caucasus region (Tarnogradski, 1961b)
Spain: Sierra Nevada (Morales-Baquero, 1987)

L. kutikowa Koste, 1972

Brazil: Cururú Mission, Amazonas (Koste, 1972)

L. lamellata (Daday, 1893)

France: Camargue (De Ridder, 1960; 1961b)
Hungary: Halas, Pest-Pilis-Solt-Kiskun (Daday, 1893)
Mexico: San Cristobal (Harring & Myers, 1926)
Nicaragua (Moreno *et al.*, 1992)
Romania: Black See Coast (Rodewald, 1940; Rudescu, 1960)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Spain: Majorca (De Manuel, 1994)
Turkey: Central Anatolia (Segers *et al.*, 1992)
Ukraine: near Kharkov (Skorikov, 1898)
U.S.A.: Devils Lake, North Dakota (Bryce, 1924)

L. lateralis Sharma, 1978

India: West Bengal (Sharma, 1978b)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Thailand: North-East part (Sanoamuang *et al.*, 1995)

L. latissima Yamamoto, 1955

Canada: Ellismere Island, Northwest Territories (Nogrady, 1989); Little Cornwallis Island, Northwest Territories (De Smet & Bafort, 1990a)
Iceland (sub. *L. kostei*. De Ridder, 1972)
Japan: Taka-numa pond, Shimokita Penninsula, Aomori Prefecture (Yamamoto, 1955)
Morocco: Lake Ifni (Coussement & Dumont, 1980)
Norway: Bjørnøya (De Smet, 1988)
Spain: Majorca (De Manuel, 1994)

Sweden: Lappland (sub. *L. rotundata*. Pejler, 1962)

L. lauterborni Hauer, 1924

Austria: Hohen Tauern (Jersabek & Schabetsberger, 1992a)
Germany: Schwarzwald region (Hauer, 1924)
Romania (Rudescu, 1960)
Russian Federation: Ural mountains, Perm region (Oparina-Charitonova, 1928); Karatschaevo, Caucasus region (sub. *L. muscicola*. Tarnogradski, 1961a)
Slovakia: Tatra mountains (Koniar, 1955)
Sweden: Lappland (Pejler, 1962)
U.S.A.: Maine (Harring & Myers, 1926)

L. leontina (Turner, 1892)

Brazil: Rio de Janeiro (Murray, 1913a); Lago Maica, Amazonas, (Thomasson, 1971); Suape Laguna, Pernambuco (Neumann-Leitão, 1990); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Canada: Ontario (Chengalath & Mulamoottil, 1974)
Chad: Lake Chad (Pourriot, 1968)
China: Hubei, Zhejiang Provinces (Wang, 1961)
Gambia (Bērziņš, 1957)
India: West Bengal (Sharma, 1978a)
Indonesia: Sumatra, Java (Hauer, 1937; 1938)
Japan: Honshu (Yamamoto, 1952)
Kenya: Sangoro (Segers *et al.*, 1994a)
Nicaragua (Moreno *et al.*, 1992)
Nigeria: River Sokoto (Green, 1960); River Niger floodplain (Segers *et al.*, 1993a)
Oman: Dhofar region (Segers & Dumont, 1993b)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Peru: Ucayali dept., Amazon region (Samanez, 1988)
Philippines (Mamaril & Fernando, 1978)
Sri Lanka (Chengalath & Fernando, 1973)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)
U.S.A.: Lake Erie, South Bass Island (Jennings, 1900); common all over the United States (Harring & Myers, 1926); Oklahoma (Taft, 1932); Laurentian Great Lakes (Stemberger, 1979)
Venezuela: Lago de Valencia (Infante, 1980); Mantecal (Zoppi de Roa *et al.*, 1994)
Zaïre: Lake Mwero (Evans, 1949); Lake Tanganyika (Gillard, 1957); Lubumbashi region (De Ridder, 1981); Bas-Zaïre (De Smet, 1990)
Zambia: Lake Bangweulu (incl. *L. thomassoni*. Wulfert, 1965); Luapula region (De Ridder, 1981)
Zimbabwe (Rousselet, 1906)

L. leura Myers, 1942

U.S.A.: Northeastern Pennsylvania (Myers, 1942)

L. levistyla (Olofsson, 1917)

Canada: Bernard harbour, N.W. Territories (sub. *L. scobis*. Harring & Myers, 1926)
Germany: Lake Stechlin (Koch-Althaus, 1963)
Poland: Lakes in the Suwalki region (Wiszniewski, 1934)
Romania (Rudescu, 1960)

L. ligona (Dunlop, 1901)

Canada: Yukon Territory, near New Rampart House (sub. *L. jessupi*. Harring, 1921); Ontario (Chengalath & Mulamoottil, 1974); Park Mont Tremblant (sub. *L. jessupi*. Nogrady, 1980)
Germany: Plön region (Voigt, 1904); Schwarzwald region (incl. *L. abnobensis*. Hauer, 1929)
the Netherlands: 'Grote Huisven', Oisterwijk (de Graaf, 1956)
India: West Bengal (Sharma, 1979)
Japan: Hokkaido (Yamamoto, 1959)
Romania (Rudescu, 1960)
Russian Federation: Ural mountains, Perm region (sub. *L. scobis*. Oparina-Charitonova, 1928)
Sweden: Aneboda region (incl. *L. jessupi*. Carlin, 1939)
U.K.: Arran Island, Scotland (Dunlop, 1901); Fort Augustus, Scotland (Murray, 1913c)
U.S.A.: Alaska, Maine, New Jersey, Wisconsin (incl. *L. jessupi*, *L. pycina*. Harring & Myers, 1926); Laurentian Great Lakes (Stemberger, 1979)
Venezuela: Rio Churun (sub. f. *abnobensis*. Zoppi de Roa *et al.*, 1990)

L. ludwigii (Eckstein, 1883)

Afghanistan (sub. *L. ichthyoura*. Bērziņš, 1961)
Argentina: Santa Fe province (sub. *L. ludwigi abrupta*. José de Paggi & Koste, 1988)
Belgium: Genk (sub. *L. stokesii*. Schepens, 1960)
Brazil: Rio de Janeiro (Murray, 1913a); Amazonas (Koste, 1972); near Santarém (incl. *L. ludwigi ercodes*. Koste, 1974); Suape Laguna, Pernambuco (Neumann-Leitão, 1990); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Canada: Ontario (incl. *L. ohioensis*, *L. stokesi*. Chengalath & Mulamoottil, 1974)
Czechia: Elbe region (Dvorakova, 1961)
China: Soochow, Jiangsu (Harring & Myers, 1926); Guangxi, Heilongjiang, Jiangsu, Zhejiang and Yunnan Provinces (incl. *L. ohioensis*. Wang, 1961)

Ecuador: 'Oriente', 'costa' (sub. *L. ludwigi laticaudata*, *L. ludwigi lacinulata*. Koste & Böttger, 1992)
Finland: Helsinki region (sub. *C. appendiculata*. Levander, 1894); Tvärminne archipelago (sub. *L. ohioensis*. Björklund, 1972)
France: Camargue (sub. *L. appendiculata*. De Ridder, 1960; 1961b)
Galápagos Archipelago (sub. *L. ohioensis* f. *ichthyoura*. De Smet, 1989a)
Germany: Oldesloe, Holstein (sub. *L. ichthyoura*. Hauer, 1925); near Karlsruhe (sub. *L. stokesii*. Hauer, 1929); Berlin region (Wulfert, 1956); near Bersenbrück, Niedersachen (Koste, 1962); Lake Stechlin (Koch-Althaus, 1963)
Hungary: Belső Tó, Tihany (sub. *L. ichthyoura*. Varga, 1937); Lake Balaton (Varga, 1945); Budapest (sub. *L. ichthyoura*. Kertész, 1955)
India: Andhra Pradesh (Dhanapathi, 1976a); West Bengal (incl. several formae, *L. ohioensis*. Sharma, 1978a; sub. *L. stokesi*, *L. ludwigii ercodes*. Sharma, 1979); Jammu and Kashmir region (Jyoti & Sehgal, 1980); Gwalior, Madhya Pradesh (Saksena & Kulkarni, 1986)
Indonesia: Sumatra, Java (incl. several formae. Hauer, 1937; 1938); Borneo (incl. *L. ichthyoura*. Koste, 1988a)
Italy: Sicilia (sub. *L. ohioensis*. Bērziņš, 1954); near Venice, Trentino, Sardegna, Lazio (incl. *L. ohioensis* f. *ichtyoura*. Braioni & Gelmini, 1983)
Japan: Mount Fuji (Sudzuki, 1978); Southwestern Islands around Okinawa (Sudzuki, 1992b)
Korea, South (Chung *et al.*, 1991)
Latvia (sub. *L. ohioensis*. Kutikova, 1959)
Madagascar (Segers, 1992)
Moldavia (sub. *L. ohioensis*., incl. var. *jorroi*. Naberezhniyi & Irmasheva, 1975)
Nepal (sub. *L. ohioensis*. Daems & Dumont, 1974)
Nigeria: River Niger floodplain (incl. *L. ohioensis*. Segers *et al.*, 1993a)
Panama (sub. *L. ercodes*, *L. marshi*. Harring, 1914)
Papua New Guinea: Madang Province (Segers & De Meester, 1994)
Peru: Ucayali dept., Amazon region (sub. *L. ercodes*. Samanez, 1988)
Philippines (Mamaril & Fernando, 1978)
Poland: Parczew region (sub. *L. ohioensis*. Radwan, 1974)
Romenia (sub. *L. ohioensis* var. *jorroi*. Godenau, 1961b: sub. f. *typica*, incl. f. *lacinulata*, *L. ohioensis*. Rudescu, 1960)
Russian Federation: Caucasus region (sub. *L. ohioensis* var. *jorroi*. Tarnogradski, 1961b)
Saudi Arabia: North-East part (incl. *L. ohioensis* f. *ichthyoura*. Segers & Dumont, 1993b)
Singapore (Sudzuki, 1991a)
Spain: Albufera de Valencia (sub. *L. ohioensis* var. *jorroi*. Wiszniewski, 1932a); Minorca (De Manuel, 1990b; sub. *L. ohioensis*. De Manuel, 1994)
Sri Lanka (incl. *L. ohioensis*. Chengalath & Fernando, 1973)
Taiwan (Sudzuki, 1991a)
Tasmania (sub. *L. ohioensis appendiculata*. Koste & Shiel, 1986)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)
Turkey: Central and East Anatolia (sub. *L. ohioensis* f. *ichthyoura*. Segers *et al.*, 1992)

U.S.A.: Lake Erie, South Bass Island (incl. *L. ohioensis*, *L. stokesii*. Jennings, 1900); D.C., Florida, Maine, New Jersey, Wisconsin, Virginia; widely distributed in the United States, common everywhere (incl. *L. ohioensis*, *L. stokesi*, *L. ichthyoura*, *L. ercodes*. Harring & Myers, 1926); Oklahoma (sub. *Distyla ohioensis*. Taft, 1932); Laurentian Great Lakes (incl. *L. ohioensis*, *L. stokesi*. Stemberger, 1979)
Venezuela: North East (incl. *L. ludwigi ercodes*, f. *laticaudata*. Lópes, 1993)
Yugoslavia: Danube river (incl. *L. ludwigi brevicaudata*, *L. ludwigi abrupta*, *L. ohioensis*. Živković, 1987)
Zaire: Lake Tanganyika (Gillard, 1957)

L. luna (O.F. Müller, 1776)

'occurs in abundance in weedy ponds all over the world and is without doubt one of the commonest of all rotifers' (Harring & Myers, 1926)
Afghanistan (Bērziņš, 1961)
Austria: Thaya River region (Donner, 1954); Hohen Tauern (Jersabek & Schabetsberger, 1992a)
Argentina: Nahuel Huapi National Park (Thomasson, 1959)
Belgium (De Ridder, 1961a); Gent (Segers *et al.*, 1991)
Brazil: Rio de Janeiro (Murray, 1913a)
Cameroon: western part (Chiambeng *et al.*, 1991)
Canada: Ontario (partly. Chengalath & Mulamoottil, 1974)
China: Qinghai Province (Wang, 1961)
Chile: Punta Arenas (Murray, 1913a)
Comoro Islands (Segers, 1992)
Finland: Helsinki region (Levander, 1894)
France: Camargue (sub. *L. submagna*. De Ridder, 1960; 1961b)
Galápagos Archipelago (De Smet, 1989a)
Germany: Sachsen-Anhalt (Althaus, 1957); Near Ludwigsburg, Baden-Württemberg (Klement, 1959); Düben, Sachsen-Anhalt (Wulfert, 1960a); Lake Stechlin (Koch-Althaus, 1963)
Hungaria: Lake Balaton (sub. *L. luna* f. *balatonica*. Varga, 1945)
Iceland (sub. *L. magna*. De Ridder, 1969)
India: Nagpur (sub. *L. dorsicalis*. Arora, 1965); Rajasthan (Nayar, 1968); West Bengal (incl. f. *doricalis*. Sharma, 1978a); Gwalior, Madhya Pradesh (Saksena & Kulkarni, 1986)
Iraq: Shat-el-Arab region (sub. *C. affinis*. Voronkov, 1907)
Italy: 'present in all, and varied biotopes' (Braioni & Gelmini, 1983)
Japan: Southwestern Islands around Okinawa (Sudzuki, 1992b)
Kenya: Ahero (Segers *et al.*, 1994a)
Korea, South (Chung *et al.*, 1991)
Madagascar (sub. *L. luna intermedia*. Bērziņš, 1982b; Segers, 1992)
Moldavia (sub. *L. luna balatonica*. Naberezhniyi & Irmasheva, 1975)
Nepal: Kathmandu Valley (Sarma & Ghimire, 1990)
Nicaragua (Moreno *et al.*, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)

Oman: Jabal Al Akhdar region, Dhofar region (Segers & Dumont, 1993b)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Philippines (Mamaril & Fernando, 1978)
Romania (incl. f. *balatonica*. Rudescu, 1960)
Russian Federation: Moskow region (sub. *L. grandis*. Bogoslovski, 1935)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Seychelles (Maas *et al.*, 1995)
Singapore (Sudzuki, 1991a)
Spain: Minorca (De Manuel, 1990b); Majorca (De Manuel, 1994)
Sri Lanka (Chengalath & Fernando, 1973)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)
Turkey: Görëme, Central Anatolia (Dumont & De Ridder, 1987); Akgöl, Selçuk-İzmir (Ustaoğlu & Balik, 1987); Karataş and Beyşehir (Emir, 1991); Central and East Anatolia (Segers *et al.*, 1992)
Ukraine (sub. *L. luna balatonica*. Ovander, 1980a)
U.S.A.: Lake Erie, South Bass Island (Jennings, 1900); Oklahoma (Taft, 1932); Laurentian Great Lakes (Stemberger, 1979)
Venezuela: Lago de Valencia (Infante, 1980)
Yemen: North (Segers & Dumont, 1993b)
Yugoslavia: Danube river (Živković, 1987)
Zaïre: Lake Mwero (Evans, 1949)
Zambia: Lake Bangweulu (Thomasson, 1960); Lake Bangweulu, Luapula regions (De Ridder, 1981)

L. lunaris (Ehrenberg, 1832)

Antarctica: South Shetland Island (José de Paggi, 1982); Signy and South Georgia Islands (Dartnall & Hollowday, 1985)
Austria: Hohen Tauern (incl. *L. acus*. Jersabek & Schabetsberger, 1992a)
Argentina: Buenos Aires (Murray, 1913a); Argentina: Santa Fe province (sub. *L. lunaris perplexa*. José de Paggi & Koste, 1988)
Australia: Sydney (sub. *Monostyla* sp. Murray, 1913b); Victoria (sub. *L. lunaris australis*. Bērziņš, 1982a)
Austria: Donau region (Donner, 1964; partly, incl. *L. perplexa*. Donner, 1978)
Belgium: Linkhout (sub. *L. galeata*. De Maeseneer, 1980); Gent (Segers *et al.*, 1991)
Bolivia: Kothia Lake, near La Paz (Segers *et al.*, 1994b)
Brazil: Rio de Janeiro (Murray, 1913a); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Cameroon: western part (Chiambeng *et al.*, 1991)
Canada: Ontario (incl. *L. crenata*. Chengalath & Mulamoottil, 1974)
Caribbean Islands (sub. *L. crenata*. De Ridder, 1977)
China: Hubei, Yunnan, Zhejiang Provinces (incl. *L. crenata*. Wang, 1961)
Finland: Helsinki region (Levander, 1894)
Germany: Schwarzwald region (incl. *M. crenata*. Hauer, 1929); Sachsen-Anhalt (Althaus, 1957); Near Ludwigsburg, Baden-Württemberg (incl. *L. crenata*. Klement,

1959); near Bersenbrück, Niedersachsen (sub. *L. perplexa*. Koste, 1962); Düben, Sachsen-Anhalt (incl. *L. acus*. Wulfert, 1966)
Hungary: Lake Balaton (sub. *M. crenata*. Varga, 1939)
Iceland (sub. *L. cornuta*. De Ridder, 1969)
India: Ajwa reservoir, near Baroda, Gujarat (incl. *L. galeata*, *L. perplexa*. Wulfert, 1966); West Bengal (incl. *L. crenata*. Sharma, 1978a)
Italy: near Venice (incl. *L. crenata*, *L. psammophila*. Braioni & Gelmini, 1983)
Japan: Ozegahara (sub. *L. acus*. Yamamoto, 1953a); Southwestern Islands around Okinawa (sub. *M.* cf. *perplexa*. Sudzuki, 1992b)
Korea, North (incl. *M. crenata*. Yamamoto, 1953b)
Korea, South (Chung *et al.*, 1991)
Madagascar (sub. *L. lunaris arthrodactylus*. Bērziņš, 1982b; Segers, 1992)
the Netherlands: 'Grote Huisven', Oisterwijk (sub. *M. crenata*, *M. constricta*. de Graaf, 1956)
New Zealand: Mount Cook (sub. *Monostyla* sp. Murray, 1913b); Canterbury (sub. *M. crenata*. Russell, 1945)
Nepal (Daems & Dumont, 1974); Kathmandu Valley (Sarma & Ghimire, 1990)
Nicaragua (Moreno *et al.*, 1992)
Nigeria: River Niger floodplain (incl. *L. perplexa*. Segers *et al.*, 1993a)
Oman: Jabal Al Akhdar region (Segers & Dumont, 1993b)
Panama (sub. *M. virga*. Harring, 1914)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Poland: Gdansk (Danzig: sub. *M. constricta*. Murray, 1913c)
Romenia (sub. *L. perplexa*; Godenau, 1961a; incl. *L. acus*, *L. crenata*. Rudescu, 1960)
Russian Federation: Caucasus region (sub. *L. crenata*. Tarnogradski, 1961b); Moskow region (incl. f. *crenata*, *perplexa*. Segers, 1994b)
Spain: Majorca (De Ridder, 1967b); Ibiza (De Manuel, 1994)
Sri Lanka (Chengalath & Fernando, 1973)
Sweden: Aneboda region (incl. *M. crenata*, *M. constricta*, *M. perplexa*. Carlin, 1939); Lappland (incl. *L. constricta*, *L. scutata*. Pejler, 1962)
Tanzania: Mount Kilimanjaro (incl. f. *perplexa*. De Smet & Bafort, 1990b)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)
Turkey: Central and East Anatolia (Segers *et al.*, 1992)
Ukraine: Kharkov region (sub. *M. virga*. Fadeev, 1924; incl. *L. constricta*. Ovander, 1980b)
U.S.A.: Lake Erie, South Bass Island (Jennings, 1900); 'Abudant ... all over the world'. Arkansas, D.C., Florida, Louisiana, Maine, Mississippi, New Jersey, Texas, Wisconsin (incl. *L. crenata*, Harring & Myers, 1926); North Carolina (sub. *M. perplexa*. Ahlstrom, 1939); Laurentian Great Lakes (sub. *M. crenata*. Stemberger, 1979)
Yemen: North (Segers & Dumont, 1993b)
Yugoslavia: Danube river (incl. *L. cornuta*. Živković, 1987)
Zaïre: Lubumbashi region; Lake Mwero, Kilwa (De Ridder, 1981)
Zambia: Lake Bangweulu, Luapula regions (De Ridder, 1981)

L. marchantaria Koste & Robertson, 1983

Brazil: Ilha de Marchantaria, Amazonas (Koste & Robertson, 1983)
Peru: Panguana (Koste, 1988b)

L. margalefi De Manuel, 1994

Spain: Majorca (De Manuel, 1994)

L. margarethae Segers, 1991

Caribbean Islands (sub. *L. punctata*. De Ridder, 1977)
U.S.A.: Florida (sub. *L. punctata*. Ahlstrom, 1934)

L. melini Thomasson, 1953

Brazil: Rio Negro, Manaus (Thomasson, 1953); Lago Jurucui, Lago Maica, Amazonas (Thomasson, 1971); Paraná de Xiborena, Amazonas (Hauer, 1965b); Lake Rio Preto da Eva (sub. *Lecane* sp. Gillard, 1967)

L. minuta Segers, 1994

Brunei (Segers, 1994a)

L. mitis Harring & Myers, 1926

Brazil: Broa reservoir, São Paulo (Segers & Dumont, 1995)
U.S.A.: New Jersey; "widely distributed" (incl. *L. depressa*. Harring & Myers, 1926)
Venezuela: Rio Churun (sub. *Lecane levistyla depressa*. Zoppi de Roa *et al.*, 1990)

L. mira (Murray, 1913)

Austria: Hohen Tauern (Jersabek & Schabetsberger, 1992a)
Germany: Schwarzwald region (Hauer, 1929); Bayern: Donau region (Donner, 1972)
Iceland (sub. *L. islandica*. De Ridder, 1967a)
Italy: Trentino (Braioni & Gelmini, 1983)
the Netherlands: Oisterwijkse vennen (de Graaf, 1960)
Poland: Huculszczyzna region (Pawłowski, 1938)
Sweden: Aneboda region (Carlin, 1939), Lappland (Pejler, 1962)
U.S.A.: Arkansas, D.C., Florida, Louisiana, Maine, New Jersey, Texas, Wisconsin (Harring & Myers, 1926); Laurentian Great Lakes (Stemberger, 1979)

L. mitella (Myers, 1936)

U.S.A.: New Jersey (Myers, 1936a)

L. monostyla (Daday, 1897)

Brazil: Amazonas (Koste, 1972); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Korea, South (Chung *et al.*, 1991)
India: Kerala State (Segers *et al.*, 1994c)
Indonesia: Sumatra (Hauer, 1937; 1938)
Jamaica (Koste *et al.*, 1991)
Japan: Mount Fuji (Sudzuki, 1978)
Nicaragua (Moreno *et al.*, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Papua New Guinea: New Guinea (Daday, 1897); East Sepik Province (Segers & De Meester, 1994)
Seychelles: Praslin (De Ridder, 1987; Maas *et al.*, 1995)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
U.S.A.: D.C., Florida, Maine, New Jersey, Wisconsin (Harring & Myers, 1926)
Zaïre: Katanga, Dembo river region (Gillard, 1959); Lubumbashi region (De Ridder, 1981); Bas-Zaïre (De Smet, 1989b)
Zambia: Lake Bangweulu region (Thomasson, 1960; De Ridder, 1981)

L. mucronata Harring & Myers, 1926

Canada: Ontario (Chengalath & Mulamoottil, 1974); Park Mont Tremblant (Nogrady, 1980); Cape Breton island (Chengalath & Koste, 1988)
U.S.A.: Maine, New Jersey, Wisconsin (Harring & Myers, 1926); Laurentian Great Lakes (Stemberger, 1979)

L. myersi Segers, 1993

Brazil: lower Rio Nhamundá (sub. *L. ornata*. Brandorff *et al.*, 1982)
China: Zhejiang Province (sub. *L. ornata*. Wang, 1961)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
U.S.A.: New Jersey (sub *M. ornata*. Harring & Myers, 1926)
Venezuela: Rio Churun (sub. *Lecane* sp. Zoppi de Roa *et al.*, 1990)

L. nana (Murray, 1913)

Argentina: North East Provinces (José de Paggi, 1989)
Bolivia : Lake Titicaca (Murray, 1913a)

Canada: Ontario (Chengalath & Mulamoottil, 1974)
Comoro Islands (Segers, 1992)
Easter Island (Segers & Dumont, 1993a)
Finland: Tvärminne archipelago (Björklund, 1972)
Hungaria: Belső Tó, Tihany (Varga, 1937)
Germany: Oldesloe, Holstein (Hauer, 1925); Sachsen-Anhalt (Althaus, 1957)
Iceland (De Ridder, 1972)
India: Ajwa reservoir, near Baroda, Gujarat (sub. *L. sola*. Wulfert, 1966); West Bengal (Sharma, 1978a)
Italy: Sardegna (sub. *L. paxiana*. Braioni & Gelmini, 1983)
Japan: Southwestern Islands around Okinawa (Sudzuki, 1992b)
Latvia (Kutikova, 1959)
Madagascar (Segers, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Jabal Al Akhdar region, Dhofar region (Segers & Dumont, 1993b)
Panama (Harring & Myers, 1926)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Romania (Rudescu, 1960)
Russian Federation: Donetz River near Zmiev (Fadeev, 1927); Moskow region (Bogoslovski, 1935); Ural mountains, Perm region (Oparina-Charitonova, 1928); Caucasus region (Tarnogradski, 1961b)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Seychelles (Maas *et al.*, 1995)
Spain: Minorca (De Manuel, 1990b); Formentera (De Manuel, 1994)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
Turkey: Central Anatolia (Segers *et al.*, 1992)
U.S.A.: D.C., Florida, Maine, New Jersey, Wisconsin (Harring & Myers, 1926)
Yemen: North (Segers & Dumont, 1993b)
Yugoslavia: Danube river (Živković, 1987)
Zambia: Lake Bangweulu, Luapula regions (De Ridder, 1981)

L. nelsoni Segers, 1994

Brazil: Boa Vista region, Roraima (Segers, 1994a; Segers & Sarma, 1994)
?Nigeria: River Niger floodplain (sub. *Lecane* sp. Segers *et al.*, 1993a; Segers, 1994a)

L. nigeriensis Segers, 1993

Nigeria: River Niger floodplain (Segers, 1993; Segers *et al.*, 1993a)

L. niothis Harring & Myers, 1926

China: Zhejiang Province (Wang, 1961)
U.S.A.: Maine (Harring & Myers, 1926)

L. nwadiaroi Segers, 1993

Nigeria: River Niger floodplain (Segers, 1993; Segers *et al.*, 1993a)

L. obtusa (Murray, 1913)

Caribbean Islands (De Ridder, 1977)
Brazil: Rio de Janeiro (Murray, 1913a); Boa Vista region, Roraima (Segers & Sarma, 1994)
India: West Bengal (Sharma, 1979)
Indonesia: Sumatra, Java (Hauer, 1937; 1938)
Jamaica (Koste *et al.*, 1993)
Madagascar (Segers, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Dhofar region (Segers & Dumont, 1993b)
Panama (Harring & Myers, 1926)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Philippines (sub. *L. perpusilla*. Mamaril & Fernando, 1978)
Russian Federation: Ural mountains, Perm region (Oparina-Charitonova, 1928)
Spain: Albufera de Valencia (Wiszniewski, 1932a)
Sri Lanka (Chengalath & Fernando, 1973)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
U.S.A.: Louisiana, Maine, Massachusetts (incl. *M. vastita*. Harring & Myers, 1926)
Yemen: North (Segers & Dumont, 1993b)
Zambia: Lake Bangweulu (sub. *M. pygmaea*. Thomasson, 1960; Wulfert, 1965)

L. opias (Harring & Myers, 1926)

Germany: Würzburg, Bayern (Hauer, 1958a); near Bersenbrück, Niedersachsen (Koste, 1962)
Iceland (De Ridder, 1969)
Poland: Białowieża forest (Pawłowski, 1938)
Romania (Rudescu, 1960)
Russian Federation: Kharkov region (Fadeev, 1927)
U.S.A.: D.C., Wisconsin (Harring & Myers, 1926)

L. ordwayi Bienert, 1986

U.S.A.: Ross Lake, Florida (Bienert, 1986)

L. palinacis Harring & Myers, 1926

Galàpagos Archipelago (Segers, 1991)
U.S.A.: Massachusetts, Washington D.C. (Harring & Myers, 1926)

L. papuana (Murray, 1913)

Brazil: Amazonas (Koste, 1972); Suape Laguna, Pernambuco (Neumann-Leitão, 1990)
Caribbean Islands (De Ridder, 1977)
China: Sichuan Province (Wang, 1961)
Comoro Islands (Segers, 1992)
Guatemala: Puerto Barrios (Harring & Myers, 1926)
India: Madras (Pasha, 1961); Yamuna river (sub. *L. yamunensis*. Novotná-Dvořaková, 1963); Ajwa reservoir, near Baroda, Gujarat (Wulfert, 1966); Andhra Pradesh (Dhanapathi, 1976a); West Bengal (Sharma, 1978a)
Japan: Southwestern Islands around Okinawa (Sudzuki, 1992b)
Kenya: Ahero (Segers *et al.*, 1994a)
Korea, South (Chung *et al.*, 1991)
Madagascar (Segers, 1992)
Mauretania: Adrar mountains (Coussement & Dumont, 1980)
Moldavia (incl. *L. luna* var. *presumpta*. Naberezhniyi & Irmasheva, 1975)
Morocco: Cavagnac reservoir (Coussement & Dumont, 1980)
Nicaragua (Moreno *et al.*, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Panama (Harring & Myers, 1926)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Philippines (Mamaril & Fernando, 1978)
Romenia (sub. *L. luna* var. *presumpta*. Godenau, 1961b)
Russian Federation: Northern Caucasus (Tarnogradski, 1930); Caucasus region (Tarnogradski, 1961b)
Spain: Albufera de Valencia (Wiszniewski, 1932a)
Sri Lanka (Chengalath & Fernando, 1973)
Taiwan (Sudzuki, 1991a)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)
Turkey: Central Anatolia (Segers *et al.*, 1992)
U.S.A.: Florida (Harring & Myers, 1926), North Carolina (sub. *L. luna* var. *presumpta*. Ahlstrom, 1938)
Venezuela: Lago de Valencia (Infante, 1980)
Yemen: North (Segers & Dumont, 1993b)
Zaïre: Lubumbashi region (incl. *L. luna* var. *presumpta*. De Ridder, 1981)
Zimbabwe: Lake Kariba (Thomasson, 1965)

L. paradoxa (Steinecke, 1916)

France: Camargue (sub. *L. hoffmanni*. De Ridder, 1960; 1961b)
Germany: 'Westpreuβen' (sub. *M. lunaris* f. *paradoxa*. Steinecke, 1916)
Japan: Ozegahara (sub. *L. ozensis*. Yamamoto, 1953a)
Romania: Lake Agigea (Rodewald-Rudescu & Godenau, 1961)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)

L. pawlowskii Wulfert, 1966

India: Ajwa reservoir, near Baroda, Gujarat (Wulfert, 1966); West Bengal (Sharma, 1978a)

L. paxiana Hauer, 1940

Czechia: Elbe region (Dvorakova, 1960b)
Germany: Bad Wilstein, thermal spring (Hauer, 1940; Pax & Wulfert, 1941)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)

L. pelatis Harring & Myers, 1926

U.S.A.: Maine, New Jersey, Wisconsin (Harring & Myers, 1926)

L. perpusilla (Hauer, 1929)

Austria: Sengsengebirges (Jersabek & Schabetsberger, 1992b)
Germany: near Freiberg (Hauer, 1929)
U.S.A.: Northeastern Pennsylvania (sub. *L. brevita*. Myers, 1942)
Russian Federation: Northern Caucasus (Tarnogradski, 1930)
Tanzania: Mount Kilimanjaro (De Smet & Bafort, 1990b)

L. pertica Harring & Myers, 1926

Brazil: Lake Jurucui, Tapajoz (sub. *Lecane* sp. Gillard, 1967); Amazonas (Koste, 1972); Boa Vista region, Roraima (Segers & Sarma, 1994)
India: Megalaya, Northeast region (Sharma, 1987)
Indonesia: Sumatra (Hauer, 1937; 1938)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
U.S.A.: Florida, Maine, New Jersey, Wisconsin (Harring & Myers, 1926)
Venezuela: Rio Churun (Zoppi de Roa *et al.*, 1990)

L. pideis (Harring & Myers, 1926)

U.S.A.: Maine (Harring & Myers, 1926)

L. proiecta Hauer, 1956

Brazil: Lake Maica, Amazonas (Gillard, 1967; Thomasson, 1971); Itugui, Lago rotondo, Lago Tefé, Amazonas (Hauer, 1965b); Maranhão state (Reid & Turner, 1988)
Venezuela: Orinocco Laguna Barrancas (Hauer, 1956)

L. psammophila (Wiszniewski, 1932)

Germany: Plöner See, Plön (Wiszniewski, 1934)
Poland: Lake Wigry (Wiszniewski, 1932b); Lakes in the Suwalki region (Wiszniewski, 1934)
Romania (Rudescu, 1960)

L. pumila (Rousselet, 1906)

France: 'Pyr. Orient.' (Segers, 1995)
Germany: Lake Garren, Holstein (Hauer, 1936a)
Indonesia: Sumatra, Java (Hauer, 1937; 1938)
Romania (Rudescu, 1960)
Tanzania: Mount Kilimanjaro (De Smet & Bafort, 1990b)
Tasmania (Koste & Shiel, 1986)
U.K.: Scotland (Rousselet *in* Murray, 1906)

L. punctata (Murray, 1913)

Argentina: North East Provinces (José de Paggi, 1989)
Brazil: Rio de Janeiro (Murray, 1913a; incl. *L. harringi*. Turner, 1990)
Caribbean Islands (sub. *L. harringi*. De Ridder, 1977)
Egypt: Lake Etku (sub. *L. harringi*. Hauer, 1963)
France: Camargue (sub. *L. aguessei*. De Ridder, 1960; 1961b)
India: Ajwa reservoir, near Baroda, Gujarat (sub. *L. harringi*. Wulfert, 1966)
Iraq: Shat-el-Arab region (sub. *M. ovata*. Voronkov, 1907)
Oman: Dhofar region (Segers & Dumont, 1993b)
Russian Federation: Caucasus region (Tarnogradski, 1961b)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Spain: Albufera de Valencia (Wiszniewski, 1932a); Minorca (De Manuel, 1990b); Ibiza (De Manuel, 1994)
Turkey: Central Anatolia (Segers *et al.*, 1992)

U.S.A.: New Jersey (Harring & Myers, 1926); Florida (sub. *L. harringi*. Ahlstrom, 1934; Turner, 1990)
Venezuela: Laguna Taiguaiguai. (sub. *L. harringi*. Hauer, 1956)
Yemen: North (Segers & Dumont, 1993b)
Zaïre: Bas-Zaïre (De Smet, 1989b)

L. pusilla Harring, 1914

Brazil: Broa reservoir, São Paulo (Segers & Dumont, 1995)
Ecuador: 'Costa' (Koste & Böttger, 1992)
India: West Bengal (Sharma, 1978a)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Panama (Harring, 1914)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Sri Lanka (Chengalath & Fernando, 1973)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
Yugoslavia: Danube river (Živković, 1987)
Zaïre: Bas-Zaïre (De Smet, 1989b)

L. pustulosa Myers, 1938

U.S.A.: New Jersey (Myers, 1938)

L. pyriformis (Daday, 1905)

Austria: Donau region (Donner, 1978)
Bahamas Islands: New Providence (Segers *et al.*, 1995)
Belgium: Gent (Segers *et al.*, 1991)
Brazil: Rio de Janeiro (sub. *M. truncata*. Murray, 1913a); Rio Cururú (Koste, 1972); near Santarém (Koste, 1974); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Cameroon: western part (Chiambeng *et al.*, 1991)
Canada: Ontario (Chengalath & Mulamoottil, 1974)
China: Sichuan Province (Wang, 1961)
Comoro Islands (Segers, 1992)
Easter Island (Segers & Dumont, 1993a)
Germany: near Karlsruhe (Hauer, 1929); Near Ludwigsburg, Baden-Württemberg (Klement, 1959)
India: West Bengal (Sharma, 1978a)
Jamaica (Koste *et al.*, 1991)
Japan: Mount Fuji (Sudzuki, 1978)
Korea, South (Chung *et al.*, 1991)
Madagascar (Bērziņš, 1982b)
Myanmar: Kinda reservoir (Koste & Tobias, 1990)

Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Dhofar region (Segers & Dumont, 1993b)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Philippines (Mamaril & Fernando, 1978)
Romania (Rudescu, 1960)
Russian Federation: Moskow region (Segers, 1994b)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Senegal (Bērziņš, 1959)
Singapore (sub. *M. paraclosterocerca*. Sudzuki, 1991a)
Sri Lanka (Chengalath *et al.*, 1974)
Spain: Minorca (De Manuel, 1990b; De Manuel, 1994)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
Turkey: Central Anatolia (Segers *et al.*, 1992)
U.S.A.: 'not rare' (Harring & Myers, 1926); Maine (sub. *L. pomiformis*. Edmondson, 1938); N-Wisconsin (sub. *L. paraclosterocerca*. Pennak, 1939); Kentucky (sub. *L. paraclosterocerca*. Bērziņš, 1984)
Yemen: North (Segers & Dumont, 1993b)
Yugoslavia: Danube river (Živković, 1987)
Zambia: Luangwa river region (De Ridder, 1981)

L. pyrrha Harring & Myers, 1926

Canada: Park Mont Tremblant (Nogrady, 1980); Cape Breton island (Chengalath & Koste, 1988)
U.S.A.: Florida (Ahlstrom, 1934); Maine, New Jersey, Wisconsin (Harring & Myers, 1926); Laurentian Great Lakes (Stemberger, 1979)

L. quadridentata (Ehrenberg, 1832)

Argentina: Buenos Aires (Olivier, 1965)
Australia: Victoria (Bērziņš, 1982a)
Bahamas Islands: Grand Bahamas (Segers *et al.*, 1995)
Brazil: Rio de Janeiro (Murray, 1913a); Suape Laguna, Pernambuco (Neumann-Leitão, 1990); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Canada: Ontario (Chengalath & Mulamoottil, 1974)
China: Manchuria (Hada, 1938); Zhejiang Province (Wang, 1961)
Germany: Sachsen-Anhalt (Althaus, 1957)
Hungaria: Lake Péteri (Kertész, 1960)
India: West Bengal (Sharma, 1978a); Gwalior, Madhya Pradesh (Saksena & Kulkarni, 1986)
Indonesia: Borneo (Koste, 1988a)
Italy (Braioni & Gelmini, 1983)
Japan: Southwestern Islands around Okinawa (Sudzuki, 1992b)
Korea, South (Song & Kim, 1989; Chung *et al.*, 1991)
the Netherlands: Oisterwijkse vennen (de Graaf, 1960)

Nepal (Daems & Dumont, 1974)
Nigeria: River Sokoto (Green, 1960); River Niger floodplain (Segers *et al.*, 1993a)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Peru: Ucayali dept., Amazon region (Samanez, 1988)
Philippines (Mamaril & Fernando, 1978)
Romania (Rudescu, 1960)
Russian Federation: Caucasus region (Tarnogradski, 1961b); Moskow region (Segers, 1994b)
Spain: Los Marismas (De Ridder, 1962); Minorca (De Manuel, 1990b); Majorca (De Manuel, 1994)
Sri Lanka (Chengalath & Fernando, 1973)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
Turkey: Akgöl, Selçuk- İzmir (Ustaoğlu & Balik, 1987); Central Anatolia (Segers *et al.*, 1992)
U.S.A.: Lake Erie, South Bass Island (Jennings, 1900); 'one of the commonest rotifers in ... the United States' (Harring & Myers, 1926); Oklahoma (Taft, 1932); Laurentian Great Lakes (Stemberger, 1979)
Yugoslavia: Danube river (Živković, 1987)
Zaïre: Ruki river near Eala (sub. *M. sexidentata*. Van Oye, 1926); Lake Tanganyika (Gillard, 1957); Lubumbashi region (De Ridder, 1981); Bas-Zaïre (De Smet, 1990)
Zimbabwe: Lake Kariba (Thomasson, 1965)

L. remanei Hauer, 1964

Brazil: near Manaus, Amazonas (Hauer, 1964; 1965b); Lago Jurucui, Amazonas (Thomasson, 1971)

L. rhacois Harring & Myers, 1926

U.S.A.: Washington D.C., Wisconsin (Harring & Myers, 1926)

L. rhenana Hauer, 1929

Brazil: Boa Vista region, Roraima (Segers & Sarma, 1994)
Germany: near Karlsruhe-Daxlanden (Hauer, 1929)
Indonesia: Borneo (Koste, 1988a)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994; Sanoamuang *et al.*, 1995)

L. rhopalura (Harring & Myers, 1926)

Bolivia: Kothia Lake, near La Paz (Segers *et al.*, 1994b)
Canada: Cape Breton island (Chengalath & Koste, 1988)

Russian Federation: Lake Baikal (sub. *L. aspersa*. Kutikova & Arov, 1985)
U.S.A.: Maine, Michigan, New Jersey, Wisconsin, Lake Erie (Harring & Myers, 1926); ?Laurentian Great Lakes (sub. *M. lunaris* Stemberger, 1979)

L. rhytida Harring & Myers, 1926

Argentina: Rio Paraná, Resistencia region (Martinez & José de Paggi, 1988)
Brazil: Ilha de Marchantaria, Amazonas (Koste & Robertson, 1983)
Madagascar (sub. *L. lauterborni*. Bērziņš, 1982b)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
U.S.A.: Maine, New Jersey (Harring & Myers, 1926)

L. robertsonae Segers, 1993

Brazil: Ilha de Marchantaria, Amazonas (sub. *L. aspasia amazonica*. Koste & Robertson, 1983)

L. rudescui Hauer, 1965

Brazil: Tarumaõ (Hauer, 1965b); Ilha de Marchantaria, Amazonas (Koste *et al.*, 1984)

L. rugosa (Harring, 1914)

Panama (Harring, 1914)

L. ruttneri Hauer, 1938

Brazil: Amazonas (Koste, 1972); Boa Vista region, Roraima (Segers & Sarma, 1994)
India: Kerala State (Segers *et al.*, 1994c)
Indonesia: Sumatra (Hauer, 1937; 1938)
Madagascar (Segers, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Dhofar region (Segers & Dumont, 1993b)
Thailand: North-East part (Sanoamuang *et al.*, 1995)

L. sagula Harring & Myers, 1926

U.S.A.: Maine, Wisconsin (Harring & Myers, 1926)
Venezuela: Rio Churun (Zoppi de Roa *et al.*, 1990)

L. satyrus Harring & Myers, 1926

Canada: Park Mont Tremblant (Nogrady, 1980); Cape Breton island (Chengalath & Koste, 1988)
Japan: Nagono Prefecture (Yamamoto, 1960)
U.S.A.: Florida, Maine, Maryland, New Jersey, Wisconsin (Harring & Myers, 1926)

L. schraederi Wulfert, 1966

India: Ajwa reservoir, near Baroda, Gujarat (Wulfert, 1966)

L. scutata (Harring & Myers, 1926)

Austria: Donau region (sub. *L. furcata*. Donner, 1978)
Germany: near Freiburg i. B., Schwarzwald region (Hauer, 1931); near Plön (Wiszniewski, 1934)
Hungary: Budapest (sub. *M. stroeszneri*. Török, 1935); Lake Balaton (Varga, 1957)
India: West Bengal (Sharma, 1979)
Korea, North (sub. *M. furcata*. Yamamoto, 1953b)
Poland: Lakes in Suwalki region (Wiszniewski, 1934); River Grabi basin (Pawłowski, 1958)
Romania (Rudescu, 1960)
Russian Federation: Ural mountains, Perm region (sub. *M. copeis*. Oparina-Charitonova, 1928)
Sweden: Lappland (sub. *L. perplexa*. Pejler, 1962)
U.S.A.: Wisconsin (Harring & Myers, 1926); Laurentian Great Lakes (sub. *M. copeis*. Stemberger, 1979)
Yugoslavia: Danube river (Živković, 1987)

L. serrata

Indonesia: Java (Thienemann, 1933; Hauer, 1937; 1938); Borneo (Koste, 1988a)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)

L. shieli Segers & Sanoamuang, 1994

Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994)

L. signifera (Jennings, 1896)

Argentina: Rio Paraná, Resistencia region (Martinez & José de Paggi, 1988)

Brazil: Lago Jurucui, Amazonas (sub. *L. ploenensis*, incl. *L. saginata*, *L. lauterborni*. Thomasson, 1971); Amazonas (sub. *L. levistyla*. Koste, 1972); near Santarém (sub. *L. signifera ploenensis*. Koste, 1974); lower Rio Nhamundá (Brandorff *et al.*, 1982); Boa Vista region, Roraima (Segers & Sarma, 1994); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Canada: Ontario (incl. *L. ploenensis*. Chengalath & Mulamoottil, 1974)
Chili: Villarica region (sub. *L. aquila*. Hauer, 1958b)
China: Zhejiang Province (Wang, 1961)
Germany: Plön region (sub. *D. ploenensis*. Voigt, 1904); Luckenwalde, Brandenburg (sub. *L. ploenensis*. Wulfert, 1940)
India: West Bengal (sub. *L. ploenensis*. Sharma, 1978a); Megalaya, Northeast region (Sharma, 1987)
Indonesia: Sumatra, Java (sub. *L. ploenensis*. Hauer, 1937; 1938)
Japan: Okinawa (Sudzuki, 1991b)
Madagascar (Segers, 1992)
the Netherlands: Oisterwijkse vennen (de Graaf, 1960)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Dhofar region (Segers & Dumont, 1993b)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Philippines (Mamaril & Fernando, 1978)
Singapore (sub. *L. signifera glandulosa*. Sudzuki, 1991a)
Sri Lanka (sub. *L. ploenensis*. Chengalath & Fernando, 1973)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
U.S.A.: D.C., Florida, Maine, New Jersey, Wisconsin; Abundant ... everywhere in the United States (incl. *L. aquila*, *L. ploenensis*. Harring & Myers, 1926); Laurentian Great Lakes (Stemberger, 1979)
U.K.: Scotland (sub. *L. ploenensis*. Murray, 1913c)
Yemen: North (Segers & Dumont, 1993b)
Zaïre: Bas-Zaïre (De Smet, 1990)
Zambia: Lake Bangweulu region (De Ridder, 1981)
Zimbabwe: Lake Kariba (sub. *L. ploenensis*. Thomasson, 1965)

L. simonneae Segers, 1993

India: Kerala State (Segers *et al.*, 1994c)
Nigeria: River Niger floodplain (Segers, 1993; Segers *et al.*, 1993a)

L. sola Hauer, 1936

Brazil: Boa Vista region, Roraima (Segers & Sarma, 1994)
India: ?Ajwa reservoir, near Baroda, Gujarat (sub. *L. nana*. Wulfert, 1966); Lake Almati, Madras (Hauer, 1936b)
Indonesia: Borneo (Koste, 1988a)
Myanmar: Kinda reservoir (Koste & Tobias, 1990)
Thailand: North-East part (Sanoamuang *et al.*, 1995)

L. solfatara (Hauer, 1938)

Indonesia: Sumatra (Hauer, 1937; 1938)

L. spiniventris Segers, 1994

Brunei (Segers, 1994a)

L. spinulifera Edmondson, 1935

Bahamas Islands: Grand Bahama (Nogrady, 1983)
Brazil: Rio de Janeiro (Turner, 1990)
Caribbean region: Hispaniola (sub. *M. spinifera*. Edmondson, 1934)
U.S.A.: Everglades National Park, Florida (Nogrady, 1983)

L. stenroosi (Meissner, 1908)

Austria: Thaya River region (Donner, 1954)
Brazil: Rio de Janeiro (sub. *M. bicornis*. Murray, 1913a)
Canada: Ontario (Chengalath & Mulamoottil, 1974)
China: Soochow, Jiangsu (Harring & Myers, 1926); Hubei, Jiangsu Provinces (Wang, 1961)
Czechia: Elbe region (Dvorakova, 1961)
Germany: near Bersenbrück, Niedersachsen (Koste, 1962)
Hungary: Lake Balaton (Varga, 1939)
India: Ajwa reservoir, near Baroda, Gujarat (Wulfert, 1966); Andhra Pradesh (Dhanapathi, 1976a); West Bengal (Sharma, 1978a)
Iraq: Shat-el-Arab region (sub. *M. bicornis*, partly. Voronkov, 1907)
Italy (Braioni & Gelmini, 1983)
Japan: Southwestern Islands around Okinawa (incl. *Monostyla* sp. Sudzuki, 1992b)
Korea, South (Chung *et al.*, 1991; Kim *et al.*, 1991)
Madagascar (Segers, 1992)
Moldavia (Naberezhniyi & Irmasheva, 1975)
Myanmar: Kinda reservoir (Koste & Tobias, 1990)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Dhofar region (Segers & Dumont, 1993b)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Philippines (Mamaril & Fernando, 1978)
Poland: Silesia (sub. *M. bicornis*. Sachse, 1915); River Grabi basin (Pawłowski, 1958)
Romania (Rudescu, 1960)
Russian Federation: Moskow region (Bogoslovski, 1935; Segers, 1994b); Caucasus region (Tarnogradski, 1961b)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Spain: Albufera de Valencia (Wiszniewski, 1932a)

Sri Lanka (Chengalath & Fernando, 1973)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
Turkey: Akgöl, Selçuk- İzmir (sub. *M. cornuta*. Ustaoğlu & Balik, 1987)
U.S.A.: California (Harring & Myers, 1926); Florida (Ahlstrom, 1934)
Venezuela: North East (Lópes, 1993)
Yugoslavia: Danube river (Živković, 1987)
Zaïre: Bas-Zaïre (De Smet, 1989b)
Zambia: Lake Bangweulu (Wulfert, 1965)

L. stephensae (Hutchinson, 1931)

Mozambique: Lake Matsume (Hutchinson, 1931)

L. stichaea Harring, 1913

Austria: Hohen Tauern (Jersabek & Schabetsberger, 1992a)
Argentina: Rio Paraná, Resistencia region (Martinez & José de Paggi, 1988)
Brazil: Lago Maica, Amazonas (sub. *L. methoria*. Thomasson, 1971); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Canada: Yukon Territory, Old Crow river flats (sub. *L. ephestra*. Harring, 1921)
Denmark: Faroër Islands (De Smet *et al.*, 1988)
France: Etang de Pommerau, Loire-et-Cher (Tassigny *et al.*, 1970)
Germany: Schwarzwald region (incl. *L. intrasinuata*. Hauer, 1935b); Luckenwalde, Schneeberg, Brandenburg (sub. *L. intrasinuata*. Wulfert, 1940); Würzburg, Bayern (Hauer, 1958a)
Hungaria: Hoverla mountain (Varga, 1962)
Japan: Honshu (sub. *L. haliclysta*, *L. intrasinuata*. Yamamoto, 1952)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Poland: Pabjanice region (sub. *L. saginata*. Pawłowski, 1938)
Romania (incl. *L. intrasinuata*. Rudescu, 1960)
Russian Federation: Kharkov region (sub. *L. muscicola*, *L. methoria*. Fadeev, 1927); Caucasus region (sub. *L. methoria*. Tarnogradski, 1961b); Karelian lakes (sub. *L. intrasinuata*. Kutikova, 1965)
Sweden: Aneboda region (Carlin, 1939); Lappland (Pejler, 1962)
U.S.A.: D.C. (Harring, 1913); Florida, Maine, Maryland, New Jersey, Wisconsin, Virginia (incl. *L. methoria*, *L. saginata*: Harring & Myers, 1926); Laurentian Great Lakes (incl. *L. intrasinuata*? Stemberger, 1979)
Venezuela: Rio Churun (sub. *Lecane* sp. Zoppi de Roa *et al.*, 1990)

L. stichoclysta Segers, 1993

Nigeria: River Niger floodplain (Segers, 1993; Segers *et al.*, 1993a)

L. subtilis Harring & Myers, 1926

Brazil: Broa reservoir, São Paulo (Segers & Dumont, 1995)
Germany: Schwarzwald region (Hauer, 1929)
Italy: near Venice, Trentino, Friuli (Braioni & Gelmini, 1983)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Romania (Rudescu, 1960)
Russian Federation: Ural mountains, Perm region (Oparina-Charitonova, 1928); Northern Caucasus (Tarnogradski, 1930); Caucasus region (Tarnogradski, 1961b)
U.S.A.: Wisconsin (Harring & Myers, 1926)
Yugoslavia: Danube river (sub. *L. apatinensis*. Živković, 1987)

L. subulata (Harring & Myers, 1926)

Chili: Villarica region (Hauer, 1958b)
Germany: Schwarzwald region (Hauer, 1929); Germany: Würzburg, Bayern (Hauer, 1958a); Düben, Sachsen-Anhalt (sub. *L. gwileti*. Wulfert, 1960a)
the Netherlands: 'Grote Huisven', Oisterwijk (de Graaf, 1956)
Russian Federation: Northern Caucasus (Tarnogradski, 1930); Karatschaevo, Caucasus region (Tarnogradski, 1961a; 1961b)
U.K.: Eppin Forest (Harring & Myers, 1926)
U.S.A.: 'fairly common' (Harring & Myers, 1926)

L. sylviae Segers, 1993

Nigeria: River Niger floodplain, Owena river Basin (Segers, 1993; Segers *et al.*, 1993a)

L. symoensi De Ridder, 1981

Zaïre: Lake north of Lubumbashi (De Ridder, 1981)

L. sympoda Hauer, 1929

Germany: near Karlsruhe (Hauer, 1929)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)

L. syngenes (Hauer, 1938)

Brazil: Amazonas (Koste, 1972)
India: West Bengal (Sharma, 1979)
Indonesia: Sumatra (Hauer, 1937; 1938)
Jamaica (sub. *L. kluchor syngenes*. Koste *et al.*, 1993)

Nigeria: River Niger floodplain (sub. *L. kluchor* f. *syngenes*. Segers *et al.*, 1993a)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Sri Lanka (Chengalath *et al.*, 1974)

L. tabida Harring & Myers, 1926

Sierra Leone: Lake Sonfon (Green, 1979)
U.S.A.: Maine (Harring & Myers, 1926)

L. tabulifera Edmondson, 1936

U.S.A.: Maine (Edmondson, 1936)

L. tenua Myers, 1936

U.S.A.: New Jersey (Myers, 1936a)

L. tenuiseta Harring, 1914

Australia: Victoria (Bērziņš, 1982a)
Austria: Sengsengebirges (Jersabek & Schabetsberger, 1992b)
Belgium: Lake Donk (Coussement, 1977)
Cameroon: western part (Chiambeng *et al.*, 1991)
Caribbean Islands (De Ridder, 1977)
China: Zhejiang Province (Wang, 1961)
Easter Island (Segers & Dumont, 1993a)
Germany: Lake Stechlin (Koch-Althaus, 1963)
Italy: near Venice (Braioni & Gelmini, 1983)
Japan: Southwestern Islands around Okinawa (sub. *Lecane* sp. Sudzuki, 1992b)
Korea, South (Chung *et al.*, 1991)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Jabal Al Akhdar region, Dhofar region (Segers & Dumont, 1993b)
Panama (Harring, 1914)
Romania (Rudescu, 1960)
Russian Federation: Tambov region (sub. *L. aeganea*. Fadeev, 1924); Ural mountains, Perm region (sub. *L. aeganea*. Oparina-Charitonova, 1928); Caucasus region (incl. *L. aeganea*, f. *punctata*. Tarnogradski, 1961b)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Spain: Minorca (De Manuel, 1994)
Sweden: Skåne, Närke, Kalarna (sub. *L. punctata*. Carlin-Nilsson, 1934); Aneboda region (Carlin, 1939)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
Ukraine: Kharkov region (sub. *L. aeganea*. Fadeev, 1924)

U.S.A.: common ... all over the United States (Harring & Myers, 1926)
Yemen: North (Segers & Dumont, 1993b)
Yugoslavia: Danube river (Živković, 1987)
Zambia: Luapula region (De Ridder, 1981)
Zaire: Lake Tanganyika (sub. *Lecane* sp. Gillard, 1957)

L. thailandensis Segers & Sanoamuang, 1994

China: Zhejiang Province (Wang, 1961)
Thailand: Sakon Nakhon province (Segers & Sanoamuang, 1994)

L. thalera (Harring & Myers, 1926)

Argentina: North East Provinces (José de Paggi, 1989)
Egypt: Lake Edku (Hauer, 1963)
France: Camargue (De Ridder, 1960; 1961b)
India: Lake Sholavaram, Madras (sub. *M. conspicua*. Hauer, 1936b); Rajasthan (sub. *M. paradecipiens*. Nayar, 1968); West Bengal (Sharma, 1978a); Delhi region (sub. *L. lamellata thalera*. Sarma, 1988)
Iraq: Shat-el-Arab region (sub. *M. hamata*. Voronkov, 1907)
Mexico: San Cristobal (Harring & Myers, 1926)
Oman: Dhofar region (sub. *L. lamellata*. Segers & Dumont, 1993b)
Philippines (sub. *L. lunaris*. Mamaril & Fernando, 1978)
Romania: Black See Coast (Rodewald, 1940; Rudescu, 1960)
Spain: Albufera de Valencia (Wiszniewski, 1932a)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
U.A.E. (sub. *L. lamellata*. Segers & Dumont, 1993b)
U.S.A.: California (Harring & Myers, 1926), Florida (Ahlstrom, 1934)
Venezuela: lake Valencia, Laguna Taiguaiguai (Hauer, 1956)
Yemen: North (sub. *L. lamellata*. Segers & Dumont, 1993b)

L. thienemanni (Hauer, 1938)

China: Zhejiang Province (Wang, 1961)
India: Ajwa reservoir, near Baroda, Gujarat (Wulfert, 1966); West Bengal (Sharma, 1979)
Indonesia: Sumatra, Java (Hauer, 1937; 1938); Borneo (Koste, 1988a)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Philippines (Mamaril & Fernando, 1978)
Venezuela: Rio Yaracuy, Urama (sub. *M. hamata* var. *thienemanni*. Zoppi de Roa *et al.*, 1994)

L. tryphema Harring & Myers, 1926

Austria: Hohen Tauern (Jersabek & Schabetsberger, 1992a)
Germany: Schwarzwald region (Hauer, 1929)
the Netherlands: 'Grote Huisven', Oisterwijk (de Graaf, 1956)
Romania (Rudescu, 1960)
U.S.A.: Maine, New Jersey, Wisconsin (Harring & Myers, 1926)

L. uenoi Yamamoto, 1951

Brazil: near Santarém (sub. *L. rugosa*. Koste, 1974); São Paulo, Roraima (Segers *et al.*, 1993b); Broa reservoir, São Paulo (Segers & Dumont, 1995)
Japan: Kyoto Prefecture (Yamamoto, 1951)

L. undulata Hauer, 1938

Canada: Ontario (sub. *L. sympoda*. Chengalath & Mulamoottil, 1974)
Galápagos Archipelago (sub. *L. inopinata* f. *sympoda*. De Smet, 1989a)
India: Ajwa reservoir, near Baroda, Gujarat (sub. *L. sympoda*, parlty. Wulfert, 1966)
Indonesia: Java (Hauer, 1937; 1938)
Madagascar (Segers, 1992)
Myanmar: Kinda reservoir (sub. *L. inopinata undulata*. Koste & Tobias, 1990)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Oman: Dhofar region (Segers & Dumont, 1993b)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)
Philippines (Mamaril & Fernando, 1978)
Russian Federation: Caucasus region (sub. *L. sympoda*. Tarnogradski, 1961b)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
Yugoslavia: Danube river (sub. *L. sympoda*. Živković, 1987)
Zaïre: Lake Tanganyika (Gillard, 1957); Lake Mwero, Kilwa (De Ridder, 1981)

L. unguitata (Fadeev, 1925)

Australia: Cape York, Queensland (Shiel & Koste, 1985)
China: Zhejiang Province (Wang, 1961)
India: Ajwa reservoir, near Baroda, Gujarat (Wulfert, 1966); West Bengal (Sharma, 1978a)
Indonesia: Borneo (Koste, 1988a)
Iraq: Shat-el-Arab region (sub. *M. bicornis*, partly. Voronkov, 1907)
Japan: Southwestern Islands around Okinawa (sub. *M. cornuta*. Sudzuki, 1992b)
Madagascar (Segers, 1992)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Papua New Guinea: East Sepik, Madang Provinces (Segers & De Meester, 1994)

Philippines (Mamaril & Fernando, 1978)
Russian Federation: Krasnodarsk (Fadeev, 1925)
Sri Lanka (Chengalath & Fernando, 1973)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
Zimbabwe: Lake Kariba (sub. *L. cornuta*. Thomasson, 1965)

L. ungulata (Gosse, 1887)

Argentina: Santa Fe province (José de Paggi & Koste, 1988); Rio Paraná, Resistencia region (Martinez & José de Paggi, 1988)
Australia: Alexandra, Victoria (sub. *L. ungulata var. australiensis*. Koste, 1979)
Brazil: Broa reservoir, São Paulo (Segers & Dumont, 1995)
Canada: Ontario (Chengalath & Mulamoottil, 1974); Québec (Nogrady, 1976)
Caribbean Islands (De Ridder, 1977)
Chad: Lake Chad (Pourriot, 1968)
China: Zhejiang, Hubei Provinces (incl. *L. sibina*. Wang, 1961)
France: Camargue (De Ridder, 1960; 1961b)
Germany: Luckenwalde, Brandenburg (sub. *L. magna*. Wulfert, 1940); near Bersenbrück, Niedersachsen (Koste, 1962); Lake Stechlin (Koch-Althaus, 1963)
India: Ajwa reservoir, near Baroda, Gujarat (Wulfert, 1966); Andhra Pradesh (incl. *L. donnerianus*. Dhanapathi, 1976a); West Bengal (Sharma, 1978a)
Italy: near Venice (Braioni & Gelmini, 1983)
Kenya: Sangoro (Segers *et al.*, 1994a)
Korea, South (Song & Kim, 1989)
Madagascar (sub. *L. fracida*. Bērziņš, 1982b; Segers, 1992)
Moldavia (Naberezhniyi & Irmasheva, 1975)
Nigeria: River Niger floodplain (Segers *et al.*, 1993a)
Papua New Guinea: East Sepik Province (Segers & De Meester, 1994)
Philippines (Mamaril & Fernando, 1978)
Poland: Silesia (sub. *C. minnesotensis*. Sachse, 1915); River Grabi basin (Pawłowski, 1958)
Romania (Rudescu, 1960)
Russian Federation: Caucasus region (Tarnogradski, 1961b); Moskow region (Segers, 1994b)
Saudi Arabia: North-East part (Segers & Dumont, 1993b)
Singapore (Sudzuki, 1991a)
Spain: Los Marismas (De Ridder, 1962)
Sri Lanka (Chengalath & Fernando, 1973)
Sweden: Lappland (Pejler, 1962)
Thailand: North-East part (Sanoamuang *et al.*, 1995)
U.S.A.: Lake Erie, South Bass Island, Ohio (Jennings, 1900); Florida (sub. *L. sverigis*. Ahlstrom, 1934); very common and widely distributed (Harring & Myers, 1926); Laurentian Great Lakes (Stemberger, 1979)
Yugoslavia: Danube river (sub. *L. magna*. Živković, 1987)
Zaïre: Lake Mwero (Evans, 1949); Lake Tanganyika (Gillard, 1957); Lubumbashi region (De Ridder, 1981); Bas-Zaïre (De Smet, 1990)

Zambia: Lake Bangweulu, Luapula regions (De Ridder, 1981)
Zimbabwe (Rousselet, 1906)

L. urna Nogrady, 1962

Hungary: near Budapest (Nogrady, 1962)

L. venusta Harring & Myers, 1926

Italy: near Venice (Braioni & Gelmini, 1983)
U.S.A.: Ottman Lake, Wisconsin (Harring & Myers, 1926)

L. verecunda Harring & Myers, 1926

U.S.A.: Maine, Wisconsin (Harring & Myers, 1926)

L. whitfordi (Ahlstrom, 1938)

Argentina: North East Provinces (sub. *L. obtusa*. José de Paggi, 1989)
U.S.A.: North Carolina (Ahlstrom, 1938)

APPENDIX 2. VERIFIED RECORDS OF *LECANE* BY C.R. RUSSELL

Records could be verified by comparison of sketches in C.R. Russell's notebooks. Copies of these were provided by Dr R.J. Shiel. The notebook records are, whenever possible, connected to records in Russell's publications. No drawings of Russell (1947, 1950 and 1952) were present.

New Zealand

* Canterbury (Russell, 1945): *Monostyla crenata* = *L. lunaris*; (Russell, 1954): *Monostyla arcuata* : one figure unrecognisable, one correct, one *L. closterocerca; L. hamata* = *L. closterocerca*
* Westland (Russell, 1951): *L. pomiformis* = incompletely contracted *L. closterocerca*.
* West Canterbury (Russell, 1953a): *L. hornemanni*: not recognisable
* Lake Katrine (Russell, 1953a): *Lecane perplexa* = *L. lunaris*
* Notornis Valley (Russell, 1954): *Monostyla rugosa* = unrecognisable, not *L. rugosa*.
* Fiordland district (Russell, 1956c): *L. tenuiseta*: unrecognisable; *L. glypta* f. *nuda* = *L. flexilis*; *Monostyla opias*: unrecognisable, not *L. opias*; *Monostyla styrax* = *L. bulla*.
* Dunedin and Wellington (Russell, 1957b): *Lecane inopinata* = *L. undulata*; *L. verecunda*: unrecognisable, not *L. verecunda*.
* Campbell Island (Russell, 1958): *Lecane closterocerca*: correct.
* Buller (Russell, 1959): *Monostyla pyriformis*: correct

Gilbert Islands (Russell, 1957a)

L. acronycha = *L. curvicornis*; *Monostyla punctata*: correct

New Hebrides (Russell, 1957a)

L. crepida = *L. hastata*; *Monostyla punctata*: correct.

Fiji (Russell, 1957a)

L. luna: correct; *L. pusilla*: unrecognisable, not *L. pusilla*.

Chatham Islands

* Russell, 1953b: *L. bulla*; *L. eylesi*; *L. gissensis*: non-contracted, unrecognisable specimen; *L. hamata*; *L. hornemanni* = *L. latissima*, *L. lauterborni*: unrecognisable, not *L. lauterborni*; *L. lunaris*; *L. palinacis*: unrecognisable, not *L. palinacis*; *L. styrax* = *L. bulla*; *L. tudicola* = *L. herzigi*.
* Russell, 1956b: *L. rhacois*: unrecognisable; *L. tenuiseta*: unrecognisable, not *L. tenuiseta*; (*Monostyla bulla*: no drawing); *Monostyla crenata* = *L. lunaris*.

Gold Coast (Ghana: Russell, 1956a)

L. calcaria = *L. inermis*; *L. curvicornis*; *L. leontina*; *L. pyrrha* = *L. signifera*; *L. sibina* = *L. curvicornis*; *L. verecunda* = *L. signifera*; *Monostyla hamata*: unrecognisable; *Monostyla truncata* = *L. arcuata*;

In notes only (unpublished): *L. curvicornis*: one figure unrecognisable, on correct; *Monostyla closterocerca*: correct; *Monostyla decipiens* = *L. hamata*; *L. luna*: correct; *L. papuana*: correct; *Monostyla quadridentata*: correct; *Monostyla styrax* = *L. bulla*.

APPENDIX 3. UNPUBLISHED RECORDS OF *LECANE*

The following unpublished records are identified or, at the least, verified by me; most of them consern results of the A.B.O.S. International Training Course: 'Zooplankton: a Tool in Lake Management'. The Australian records were kindly provided by Dr R.J. Shiel.

List of localities

Algeria (leg. & det. B. Samraoui)

1. Several localities in the El Kala wetlands, N.E. Algeria, 28 V 1993 - 12 VII 1993
2. Idem, Guerbes-Senhadja wetlands, N.E. Algeria, 24 V 1993 - 5 VII 1993

Australia (leg. R.J. Shiel)

1. Darling River Anabranch floodplain, National Parks and Widlife Service, NSW. coll. J. Hillman
2. Lake Angove, South West West Australia, 18 II 1993, coll. S. Halse
3. Lake Moates, South West West Australia, 18 II 1993, coll. S. Halse
4. Long Spring Swamp, West Australia, 18 II 1993, coll. S. Halse
5. Lake Gregory, North West West Australia, 19 VIII 1993, coll. W.D. Williams
6. Ryan's #3 billabong, an ephemeral roadside pool, Bonegilla, Victoria, 15 VII 1994
7. Dune Lake, Cape York Peninsula, Queensland, coll. B.V. Timms
8. Ormiston Gorge, Northern Territory, 22 II 1994, coll. M. Lawton
9. Ellery Big Hole, Northern Territory, 21 II 1994

Belgium

1. Oostkamp, Leiemeersen, 15 IV 1991, leg. K. De Kleer
2. Gent, tap water, 5 V 1991
3. Neerpelt, Hageven, 1 June 1992
4. Postel, Ronde Put, 2 June 1992

Brazil

1. 10 Stations in the Paraguai River and its tributaries neal Corumba, mato Grosso de Sul, 25-30 VI 1983 (Mitamura *et al.*, 1985). Coll. A.L. de Oliveiro-Neto

2. Lago do Prato, Rio Negro, Anavilhanas, Amazon State, 17 IV 1992. Coll E.N. dos Santos-Silva
3. Rio Jatapu, close to confluence with Rio Uatumá, Amazon State, 27 III 1987. Coll E.N. dos Santos-Silva
4. Lago Jacundá, Rio Tapajós, Alten do Chão, Pará State. 20 XII 1987. Coll E.N. dos Santos-Silva
5. Ilha de Maraca, Roraima State, 24 IX 1987. Coll E.N. dos Santos-Silva & B. Robertson
6. Pond near Lobo Reservoir, SP, 3 I 1990.
7. Prairie pond on road to Broa, ca 5 km from station SP, 3 I 1990.
8. Bonito pond, Brasilia (Federal district), 1991 (leg. & det. F.L. de Rêgo Monteiro Starling).
9. Formosa pond, Goias State, near Planaltina de Goias, 1991 (leg. & det. F.L. de Rêgo Monteiro Starling).

Burundi

1. Freshwaters in Bujumbura province, 1990 (leg. H.J. Dumont, det. D. Baribwegure)

China

1. Li- river, Yuangshuo SSE of Guilin, Zizhiqu province, 24°48'N - 110°26'E, 19 VII 1989 (leg. H.J. Dumont)
2. Yuangshuo, rice field. 24°48'N - 110°26'E, 19 VII 1989 (leg. H.J. Dumont)
3. Yuangshuo, pond. 24°48'N - 110°26'E, 20 VII 1989 (leg. H.J. Dumont)
4. Yuangshuo, eutrophic pond. 24°48'N - 110°26'E, 20 VII 1989 (leg. H.J. Dumont)
5. Yuangshuo, pond near cave. 24°48'N - 110°26'E, 20 VII1989 (leg. H.J. Dumont)
6. Er Hoi lake, near Dali, Yunnan provice, 25°39'N - 100°11'E, 23 VII 1989 (leg. H.J. Dumont)
7. Pond near Er Hoi lake, 25°39'N - 100°11'E, 23 VII 1989 (leg. H.J. Dumont)
8. between Dali and Lijang, ditch. 25°50'E - 100°11'E, 24 VII 1989 (leg. H.J. Dumont)
9. between Dali and Lijang, pond. 25°50'E - 100°11'E, 26 VII 1989 (leg. H.J. Dumont)
10. Taihu lake, Jiangsu province. 30°55'-31°33'N, 119°53'-120°36'E, IX 1993 (leg. & det. G. Xiaoming)
11. Lake Wudalianchi, Heilongjiang province, 20 V 1992 (leg. & det. Q. Wang)

Ecuador (leg. H.J. Dumont)

1. Lago de Cuicocha, 29 X 1993
2. Lake Yahuarcocha, 30 X 1993

Egypt (leg. & det. G.M. El Shebrawy Mohammed)

1. Wadi El-Raiyan, El Fayoum
2. River Nile near El Fayoum
3. Abbasa fish farm, El Sharkia
4. Irrigation canal, El Fayoum
5. Fish pond in Shakshouk research station, El Fayoum

Ethiopia (leg. & det. S. Bekelie)

1. Lake Awasa (7°03'N-38°36'E), 6 III 1993
2. Lake Chelelaqua (8°46'N-38°59'E), 14 IX 1994

Finland

1. Onkilampi pond, Joensuu region, IX 1993 (leg. & det. M. Rahkola)
2. Lake Saimaa, VI and VIII 1992 (leg. & det. M. Rahkola)
3. Kangaslampi pond, Kuopio, IX 1993 (leg. & det. K. Hyvönen)

India

1. Lake Kollera, 9 III 1974. leg. Y. Ranga Reddy
2. Temporary pond, near Guntur, 8 I 1980. leg. Y. Ranga Reddy
3. Roadside ditch, Nagamalai, near Madurai, Tamil Nadu, 1991 (leg. & det. G. Murugan)
4. Several localities (± 50) in Kerala state, 1991-1992 (leg. & det. F.K. Kakkassery)
5. Several localities in the Delhi region (leg. & det. S.S.S. Sarma, leg. & det N. Iyer)

Indonesia

1. Ponds (freshwater and brackish) in Jepara, Central Java, 25 IX 1992 (leg. & det. A. Erlina)
2. Lake Lido, West Java, 11 XI 1990 (leg. & det. Y. Retnaning-Widyastuti)
3. Taman Ayun, temple pond, Bali, 22 I 1995 (leg. Y. Kobayashi)
4. Lake Buyan, Bali, 22 I 1995 (leg. Y. Kobayashi)

Laos

1. ponds near Vientiane, 8-11 IX 1994 (leg. & det. S. Phanousith)

Malawi (leg. & det. V.E. Mushi)

1. Pool at Salima, 26 VII 1991
2. Senga Bay, Hippo pool, 28 VII 1991
3. Nteheu Mzimba, Pa dam, 31 VII 1991
4. Lithipe river, 31 VII 1991

Malaysia

1. Lake Kenyir, 22 XI 1990 (4°40'N, 102°40'E)(leg. & det. C.H. Peng)

Mexico

1. Lake Chapala, between state of Jalisco and Micoacan, Sept. 1990- Sept. 1991 (leg. & det. R. Rico-Maritnez)

New Zealand

1. Roadside pools, between Kumara and Greymouth. 19°C, pH 4.5 (leg. & det. L. Sanoamuang)
2. Travis Swamp, Christchurch, 10 VI 1993 (leg. R.J. Shiel & J.D. Green)
3. Rotootuauru, 7 II 1994, lake on North Island (leg. R.J. Shiel & J.D. Green)
4. Humuhumu Lake, 7 II 1994, North Island (leg. R.J. Shiel & J.D. Green)
5. Horsham Downs Pond, 24 VI 1993, North Island (leg. R.J. Shiel & J.D. Green)
6. stock dam, Cleaseby Hill, 6 II 1994, North Island (leg. R.J. Shiel & J.D. Green)
7. dune lagoon, 7 II 1994, North Island (leg. R.J. Shiel & J.D. Green)
8. Phoebe's lagoon, 7 II 1994, North Island (leg. R.J. Shiel & J.D. Green)

Nicaragua

1. Lake Nicaragua, littoral on Northern shore. Granada, 13 VII 1991

Nigeria

1. Abadaba lake, Imo State (leg. & det. S.N. Umeham)
2. Agbada swamp, Rivers State (leg. & det. S.N. Umeham)
3. Akika lake, Imo State (leg. & det. S.N. Umeham)
4. Nnenmiri lake, Imo State (leg. & det. S.N. Umeham)

5. Umu-Oseriche lake, Imo State (leg. & det. S.N. Umeham)
6. Yenagoa river, Rivers State (leg. & det. S.N. Umeham)
7. Asa lake, Ilorin Kwara State (4°30'E-8°26'N, leg. & det. S.I. Ovie)
8. Shiroro lake, Niger State (6°15'E-9°55'N, leg. & det. S.I. Ovie)
9. Fish pond, Kainji lake region, Niger State (leg. & det. S.I. Ovie)
10. Rivers in Ondo State, 1981-1983 (leg. I.F. Adeniyi, det. A.O. Ayayi)

Peru (leg. & det. M.A. Paliza)

1. Fish pond, near Rio Huallaga, Ahuashiyacu, 1991
2. Yarinacocha lagoon, near Rio Ucayali, 1991
3. Hemimarsh near Rio Madre de Dios, 1991

Philippines

1. Artificial pond in Los Banos, Laguna, Luzon, 28 IX 1990 (leg. & det. S.B. Torralba)
2. Rice research Institute reservoir, Los Banos, Laguna, Luzon, 28 IX 1990 (leg. & det. S.B. Torralba)
3. Swamp at Consolacion, Cebu, 4 I 1991 (leg. & det. S.B. Torralba)
4. Laguna de Bay, Luzon (leg. & det. A.C. Rivera)
5. Bataan, Luzon, IX 1994 (leg. & det. M.V. dela Cruz Camacho)
6. Talisay, Batangas, Luzon, 22 VII 1994 (leg. & det. M.V. dela Cruz Camacho)
7. Ilaguen river, Isabela, Luzon, VI 1994 (leg. & det. M.V. dela Cruz Camacho)

Russia

1. Lake Glubokoe, 31 VII - 8 VIII 1992
2. Pond near lake Glubokoe, Terehovo, 2 VIII 1992
3. Pond near lake Glubokoe, Ordino, 4 VIII 1992
4. Pond near lake Glubokoe, Novo-Gorbovo, 8 VIII 1992
5. Pond near lake Glubokoe, along road to village, left. With *Calla palustris* and *Sphagnum* sp., 8 VIII 1992
7. Pond near Andreevskoe, 10 VIII 1992

Surinam

1. Ponds around Paramaribo, Lake Brokopondo, IX 1994 (leg. & det. A. Haripersad)

Tanzania

1. Ponds in the Usangu plain, 1993 (leg. & det. N.L. Mchome)
2. Zanzibar, IX 1994 (leg. & det. S.M. Yussuf)

Thailand

1. Pratumthanee, near Bangkok (leg. & det. J. Wongsanoon)

Uganda

1. Lake Wamala, 1990-1991 (0°15'-0°25'N, 31°45'-32°0'E)(leg. L. Mwebaza-Ndawula, det. D.R. Mbaga)

Vietnam

1. Lakes in Hanoi City, 1993 (leg. & det. L.T. Kim Cuc)

Records

Numbers behind the country name refer to the sample(s) number as listed above.

L. acanthinula (Hauer): India 5
L. aculeata (Jakubski): Brazil 5, China 7; Ecuador 2; India 4, 5; Nigeria 5, 7
L. aeganea Harring & Myers: Brazil 1; India 5
L. amazonica (Murray): Brazil 3, 5
L. arcuata (Bryce): Belgium 1; Nicaragua 1
L. arcula Harring: Brazil 1, 5, 6; Egypt 1; India 4, 5; Nicaragua 1
L. aspasia Myers: India 5; Russia 1
L. bifurca (Bryce): India 4
L. braumi Koste: Nigeria 3, 5
L. bifastigata Hauer: India 5
L. bifurca (Bryce): Ecuador 2; Russia 1, 5
L. bulla (Gosse): Algeria 1, 2; Australia 3, 4, 5, 8, 9; Brazil 1, 2, 3, 4, 5, 6 (incl. f. *styrax*), 7 (f. *styrax*), 8, 9; Burundi 1; China 1, 3, 4, 5, 6, 7, 8, 9, 10, 11; Ecuador 1, 2; Egypt 1, 2, 4; Ethiopia 1; India 1, 2, 4, 5; Indonesia 2, 3, 4; Laos 1; Malawi 1, 3, 4; Malaysia 1; New Zealand 3, 4, 6, 8; Nicaragua 1; Nigeria 5, 7, 10; Philippines 3, 5; Russia 1, 2, 5, 6; Surinam 1; Tanzania 1, 2; Thailand 1; Uganda 1; Vietnam 1
L. clara (Bryce): Algeria 1; Brazil 3, 5; Belgium 3; Finland 2; Russia 1
L. closterocerca (Schmarda): Algeria 1, 2; Belgium 1, 4; Brazil 1, 2, 5; Burundi 1; China 6, 7, 8, 9, 11; Ecuador 2; Egypt 1; India 4, 5; Indonesia 1; Laos 1; Mexico 1; New Zealand 4, Nigeria 3, 5, 9, 10; Philippines 6; Russia 1, 2, 3, 4, 5, 6; Tanzania 2; Uganda 1
L. copeis (Harring & Myers): Brazil 1, 4
L. cornuta (Müller): Brazil 1 (incl. f. *rotunda*), 3, 5; Mexico 1; Surinam 1
L. crepida Harring: Brazil 1; India 4, 5; Indonesia 3; Philippines 7
L. curvicornis Murray: Australia 4, 7; Brazil 1, 2, 6, Burundi 1; Ethiopia 2; India 1, 2, 4, 5; Laos 1; Nicaragua 1; Nigeria 1, 5, 9, 10; Philippines 3; Surinam 1; Tanzania 2; Vietnam 1
L. decipiens Murray: Algeria 1; Brazil 1, 2, 5; Nicaragua 1; Philippines 5; Surinam 1
L. depressa (Bryce): Finland 1; Russia 5
L. deridderae Koste: Brazil 4
L. dumonti Segers: Brazil 5
L. doryssa Harring: Brazil 1, 5, 6; India 4; Peru 3
L. elegans Harring: Brazil 1, 2, 5, 7
L. elsa Hauer: Brazil 5; Surinam 1
L. eswari Dhanapathi: India 5
L. eutarsa Harring & Myers: Brazil 1, 2, 3, 4, 5, 6; Surinam 1
L. eylesi Russel: New Zealand 1

L. flexilis (Gosse): Brazil 1, 2, 5; Belgium 2; China 9; Indonesia 3; New Zealand 4; Russia 1

L. furcata (Murray): Algeria 1; Brazil 2, 3, 5; Burundi 1; China 3 (var. *elachis & thetis*), 6, 10; Ecuador 2; India 4, 5; New Zealand 7; Nicaragua 1; Nigeria 3, 5; Philippines 1; Russia 1, 2, 5, 6; Surinam 1

L. grandis (Murrray): Egypt 1, 5; Indonesia 1

L. gwileti (Tarnogradski): Belgium 1

L. hamata Stokes: Algeria 1, 2; Belgium 2; Brazil 2, 3, 5; Burundi 1; China 4, 6, 8, 9, 10; Ecuador 2; Egypt 1; 4; India 1, 2, 4, 5; Indonesia 2, 4; Mexico 1; New Zealand 7; Nicaragua 1; Nigeria 3, 5, 7, 10; Philippines 3; Russia 1, 2, 3, 4, 5, 6; Surinam 1; Tanzania 1, 2; Uganda 1

L. haliclysta Harring & Myers: Brazil 1, 2, 5; Nicaragua 1

L. hastata (Murray): Brazil 1; China 3, 5; India 4, 5; Nigeria 10; Philippines 5

L. hornemanni (Ehrenberg): Australia 5; Brazil 2, 6, 7; China 5; India 2, 4, 5; Indonesia 2, 3; New Zealand 3, 4, 8; Nigeria 7; Tanzania 2

L. inermis (Bryce): Brazil 1, 5; China 6; Nigeria 7; Philippines 5

L. inopinata Harring & Myers: Algeria 1; Brazil 1, 6; India 4, 5; Philippines 2, 7

L. intrasinuata (Olofsson): Belgium 2

L. kutikowa Koste: Brazil 3

L. lateralis Sharma: Burundi 1; China 9; India 1, 2, 5; Nigeria 8

L. latissima Yamamoto: New Zealand 1

L. leontina (Turner): Brazil 1, 2, 3, 4, 5, 6, 8, 9; China 10; India 1, 2, 4, 5; Indonesia 3; Laos 1; Malawi 2; Nicaragua 1; Nigeria 1, 2, 3, 4, 5, 6, 7; Surinam 1

L. ludwigii: Algeria 1; Australia 1, 5; Brazil 1 (incl. f. *ercodes*), 2, 5 (incl. f. *ohioensis*); 6 (incl. near f. *ohioensis*), 7; China 3 (f. *lacinulata*), 4, 6 (incl. f. *laticaudata*), 10; India 4, 5; Nigeria 5, 7; Peru 3 (f. *ohioensis*); Russia 1

L. luna (O.F. Müller): Algeria 1, 2; Australia 3, 4, 5; Brazil 1; Burundi 1; China 4, 6, 7, 9, 10; Ecuador 2; Egypt 1, 2, 3, 4; Ethiopia 2; India 1, 2, 4, 5; Indonesia 2, 3; Mexico 1; Malawi 1; New Zealand 3, 4, 6, 8; Nicaragua 1; Nigeria 7, 10; Philippines 7; Russia 1, 3; Surinam 1; Tanzania 2; Thailand 1

L. lunaris (Ehrenberg): Algeria 1, 2; Australia 3, 4, 5; Belgium 2 (f. *perplexa*), 3 (incl. f. *crenata*), 4 (f. *constricta, crenata*); Brazil 1, 2, 3, 4 (incl. f. *crenata*), 5 (incl. f. *crenata)*, 6, 7, 8 (incl. f. *crenata*), 9 (f. *crenata*); Burundi 1; China 6, 7, 8, 9, 10; Ecuador 2; Egypt 3; Finland 1, 3; India 4, 5; Indonesia 2; Mexico 1; New Zealand 1 (incl. f. *crenata*), 2, 4, 5, 7; Nigeria 1, 3, 5, 7, 10; Philippines 7; Russia 1 (incl. f. *perplexa*), 2, 3, 4, 5 (incl. f. *crenata*), 6; Thailand 1

L. marchantaria Koste & Robertson: Brazil 1

L. melini Thomasson: Brazil 1, 2, 3

L. mira (Murray): Belgium 4; Russia 5

L. monostyla (Daday): Brazil 1, 2, 3, 5; India 4; Nicaragua 1; Peru 3

L. myersi Segers: Brazil 6

L. nana (Murray): Algeria 1; Burundi 1; Ecuador 2; Egypt 1, 4; India 5; Nicaragua 1; Russia 2; Surinam 1
L. obtusa (Murray): Brazil 1, 4, 5; India 4, 5; Nigeria 7; Surinam 1
L. opias (Harring & Myers): Belgium 1
L. papuana (Murray): Australia 9; Brazil 1; China 2; Egypt 3, 4; India 1, 2, 3, 4, 5; Indonesia 3; Laos 1; Malawi 1; Nicaragua 1; Nigeria 1, 6, 7; Peru 1, 2, 3; Philippines 1, 3, 4, 5; Surinam 1; Tanzania 1, 2
L. pertica Harring & Myers: Brazil 1, 2, 3, 5, 6, 8, 9; India 4
L. proiecta Hauer: Brazil 1, 4
L. punctata (Murray): India 5
L. pusilla Harring: India 4, 5; Russia 1
L. pyriformis (Daday): Algeria 1; Brazil 1, 4, 5; India 4, 5; Mexico 1; Nicaragua 1; Nigeria 7, 9; Russia 6; Uganda 1
L. quadridentata: Algeria 1, 2; Australia 4, 5; Brazil 1, 3, 5; China 1, 3, 10; India 4, 5; Indonesia 2, 3; Nicaragua 1; Nigeria 5, 10; Peru 3; Philippines 3; Russia 3; Surinam 1
L. remanei Hauer: Brazil 3
L. rhenana Hauer: Burundi 1
L. rhopalura (Harring & Myers): Russia 1
L. rhytida Harring & Myers: Brazil 1, 5, 6; New Zealand 7; Nicaragua 1
L. robertsonae Segers: Brazil 1, 5, 6;
L. rudescui Hauer: Brazil 3
L. rugosa (Harring): Brazil 6
L. ruttneri Hauer: Brazil 5, 6, 7; India 4; Philippines 2
L. scutata (Harring & Myers): Russia 1
L. signifera (Jennings): Brazil 1, 2, 3, 5, 8, 9; India 4, 5; Indonesia 1, 3; New Zealand 7; Nicaragua 1; Nigeria 1, 5, 7; Philippines 5, 7; Surinam 1
L. simonneae Segers: India 4
L. sola Hauer: Brazil 1
Lecane **sp. near** *bulla*: Australia 2
Lecane **sp. near** *elsa*: Burundi 1
Lecane **sp. near** *rhenana*: Australia 1
L. spinulifera (Edmondson): Jamaica (Koste, *in litt.*)
L. stenroosi (Meissner): Burundi 1; China 6, 8; India 1, 2, 5; Indonesia 4; Philippines 7
L. cf. *stephensae* (Hutchinson): Indonesia 3
L. stichaea Harring: Brazil 1, 3, 5, 6; Belgium 3, 4; Finland 1; Nigeria 1, 7; Russia 1, 5
L. subtilis Harring & Myers: Brazil 3, 6
L. subulata (Harring & Myers): Burundi 1
L. sylviae Segers: Nigeria 10
L. syngenes Hauer: Brazil 6
L. tenuiseta Harring: Algeria 1; Brazil 1; India 4; Russia 1, 4
L. thalera (Harring & Myers): India 1, 5; Philippines 2

L. thienemanni Hauer: Brazil 1; Philippines 5, 7
L. tryphema Harring & Myers: Belgium 3
L. uenoi Yamamoto: Brazil 5, 6
L. undulata Hauer: Burundi 1; Ecuador 2; India 5; Nigeria 2; Thailand 1
L. unguitata (Fadeev): India 1, 2, 4, 5; Nigeria 7, 10; Philippines 5
L. ungulata (Gosse): Algeria 1; Australia 6; Brazil 1, 5; Burundi 1; China 10; India 1, 2, 4, 5; Indonesia 4; Malawi 2; Nigeria 1, 2, 3, 5, 6, 9, 10; Philippines 4; Russia 1; Tanzania 2

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Distribution Maps

LIST OF DISTRIBUTION MAPS OF SOME REPRESENTATIVE *LECANE*

Widely distributed taxa

Holarctic taxa

Eastern hemisphere taxa

Western hemispere taxa

Distribution Maps

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Widely distributed taxa

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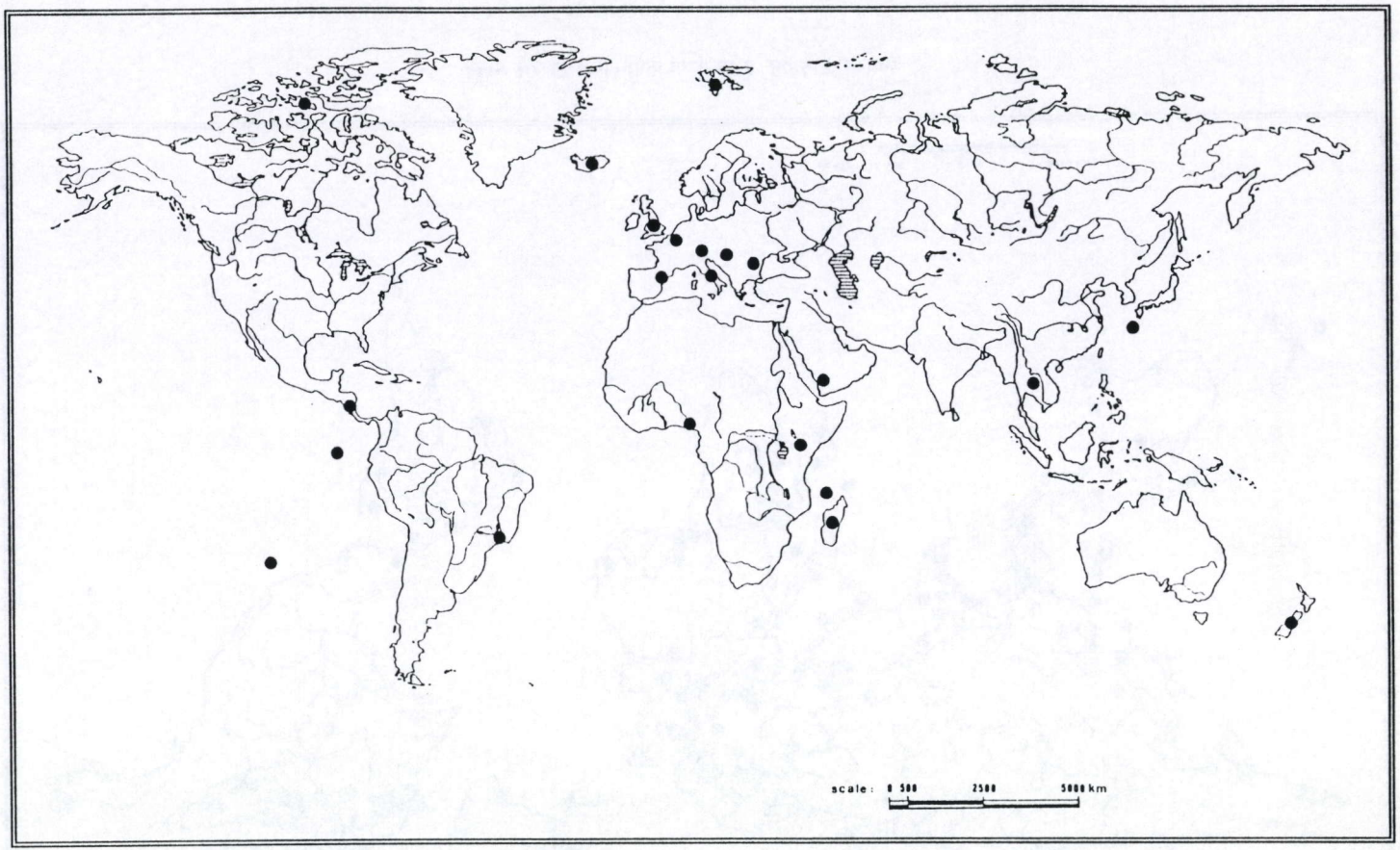
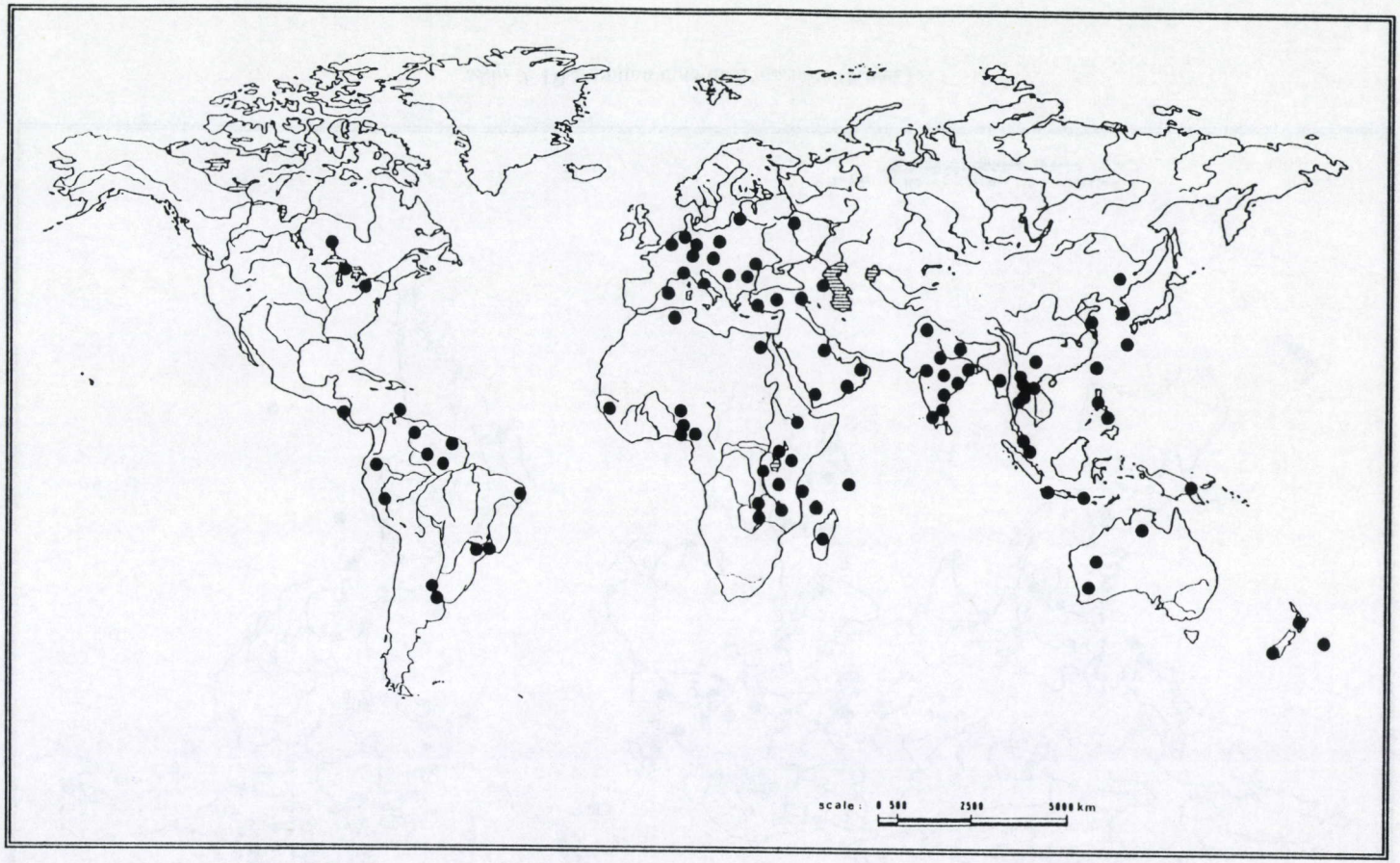
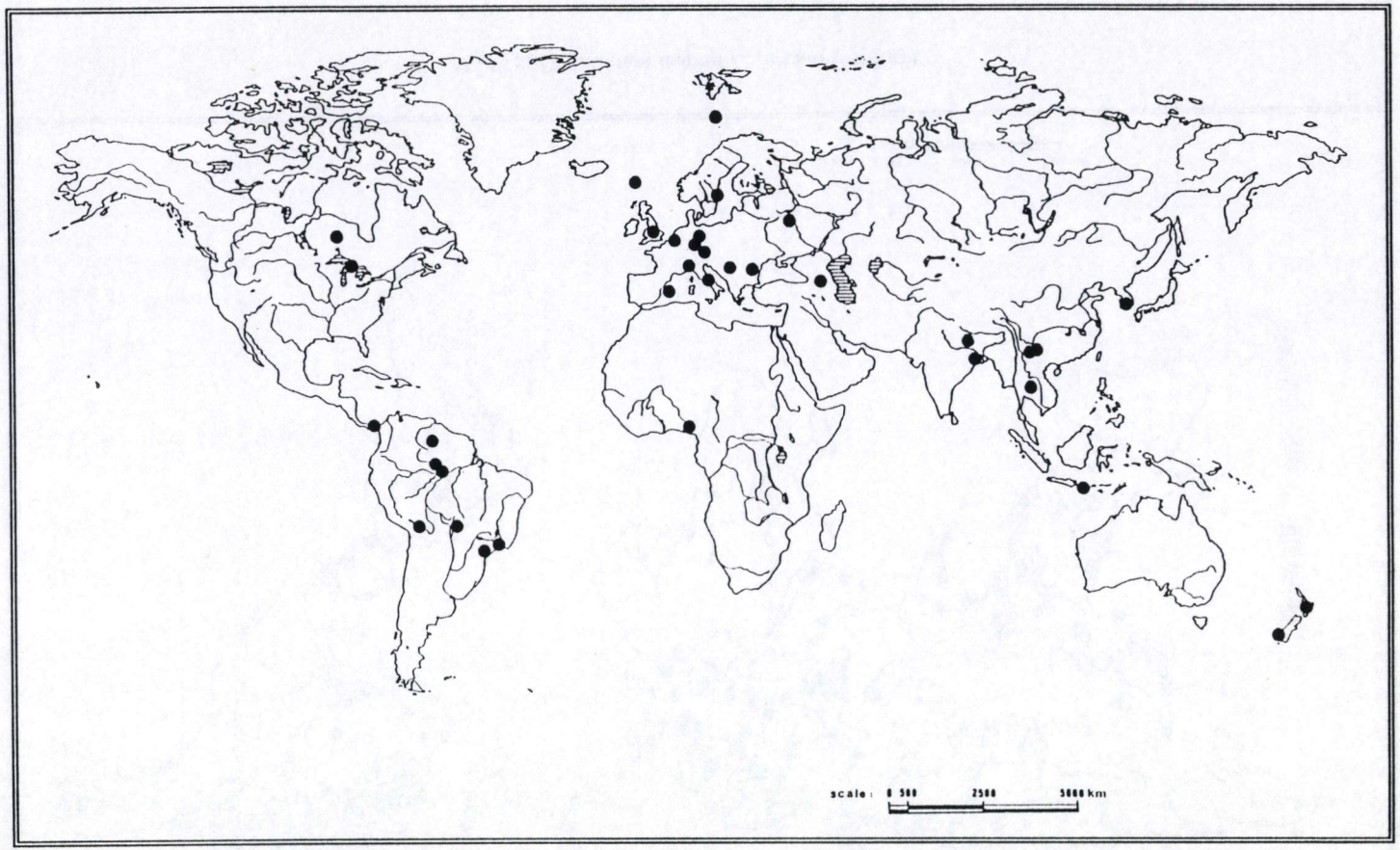


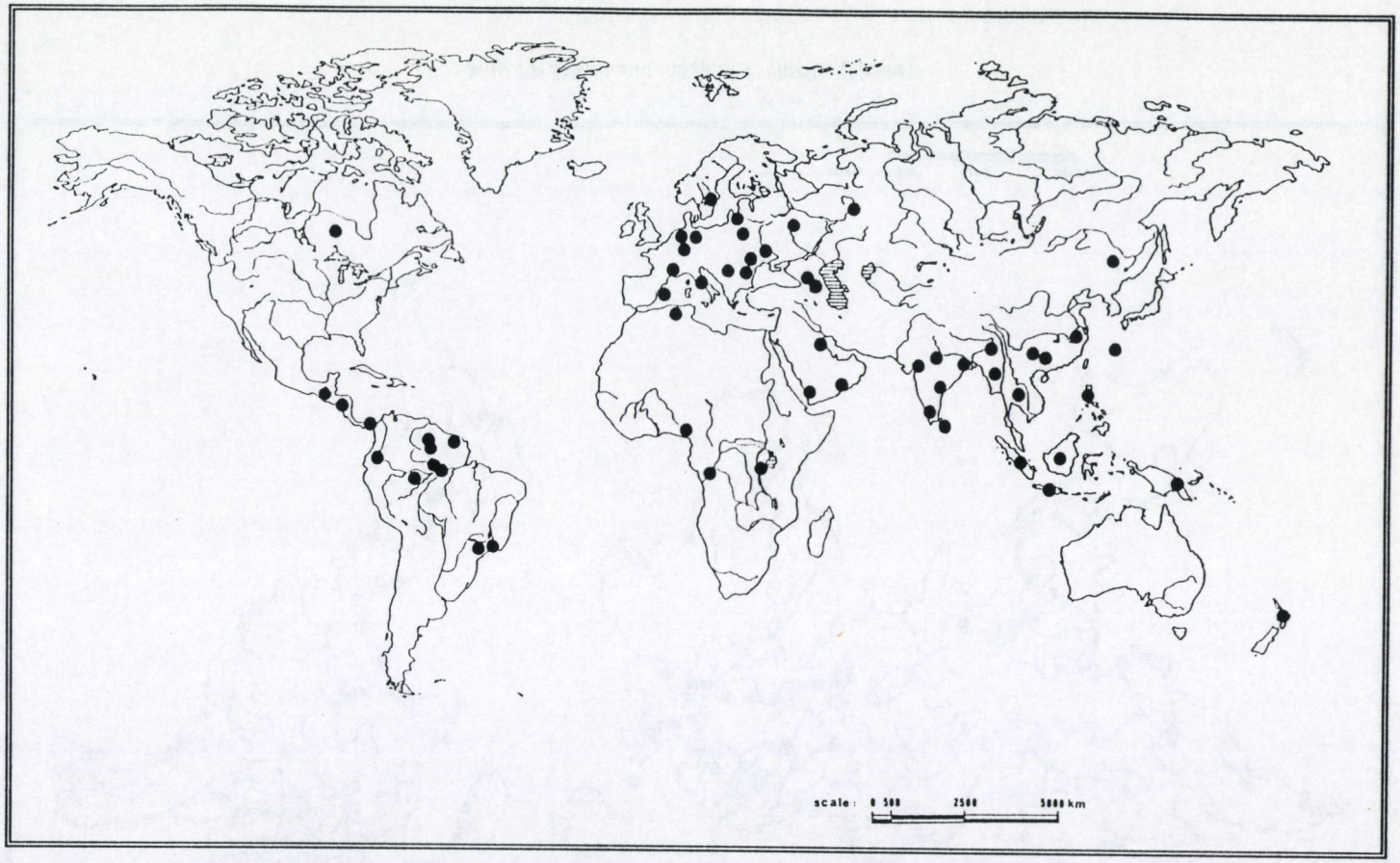
Map 9: Distribution map of *L. arcuata* (Bryce)



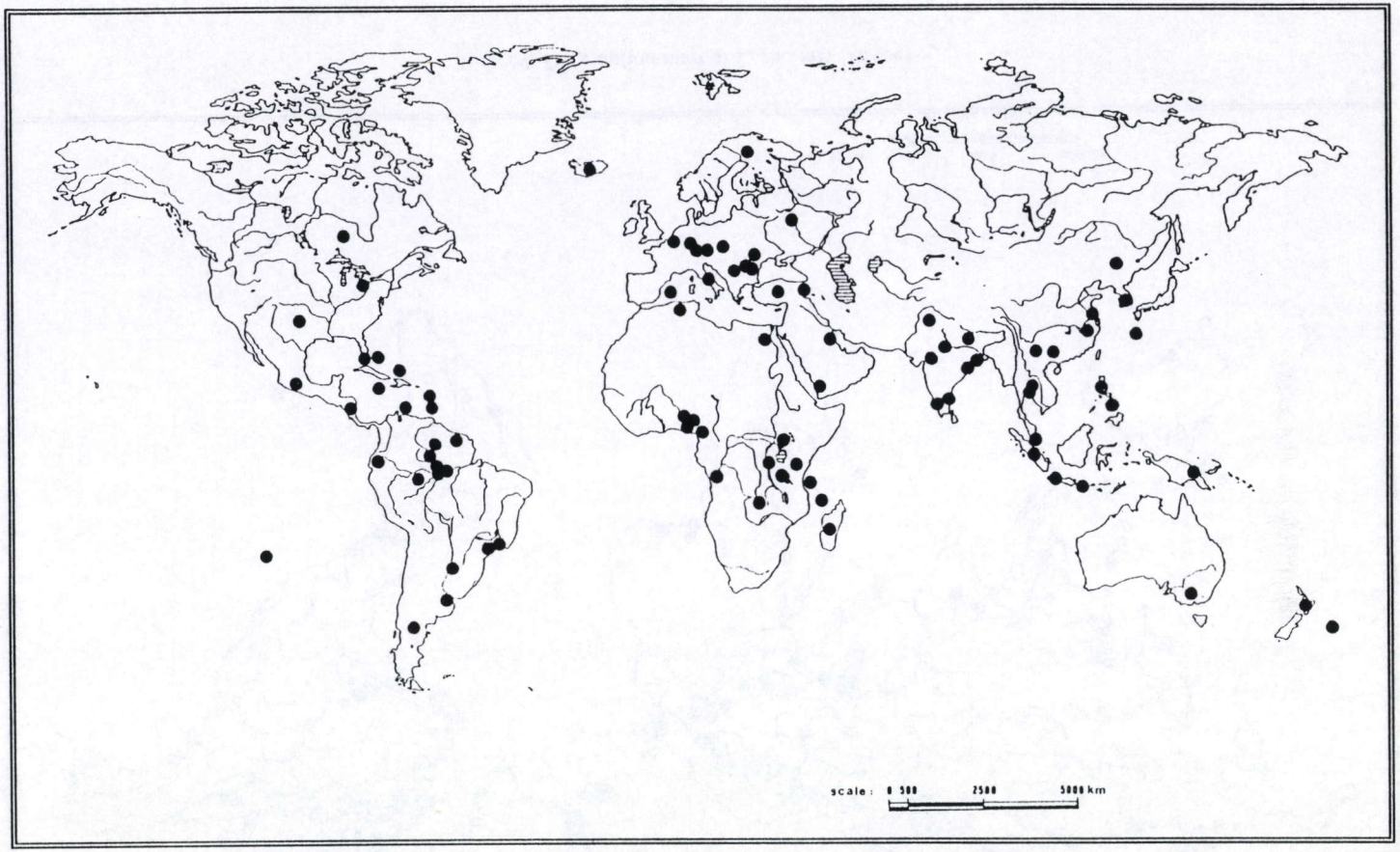
Map 10: Distribution map of *L. bulla* (Gosse)



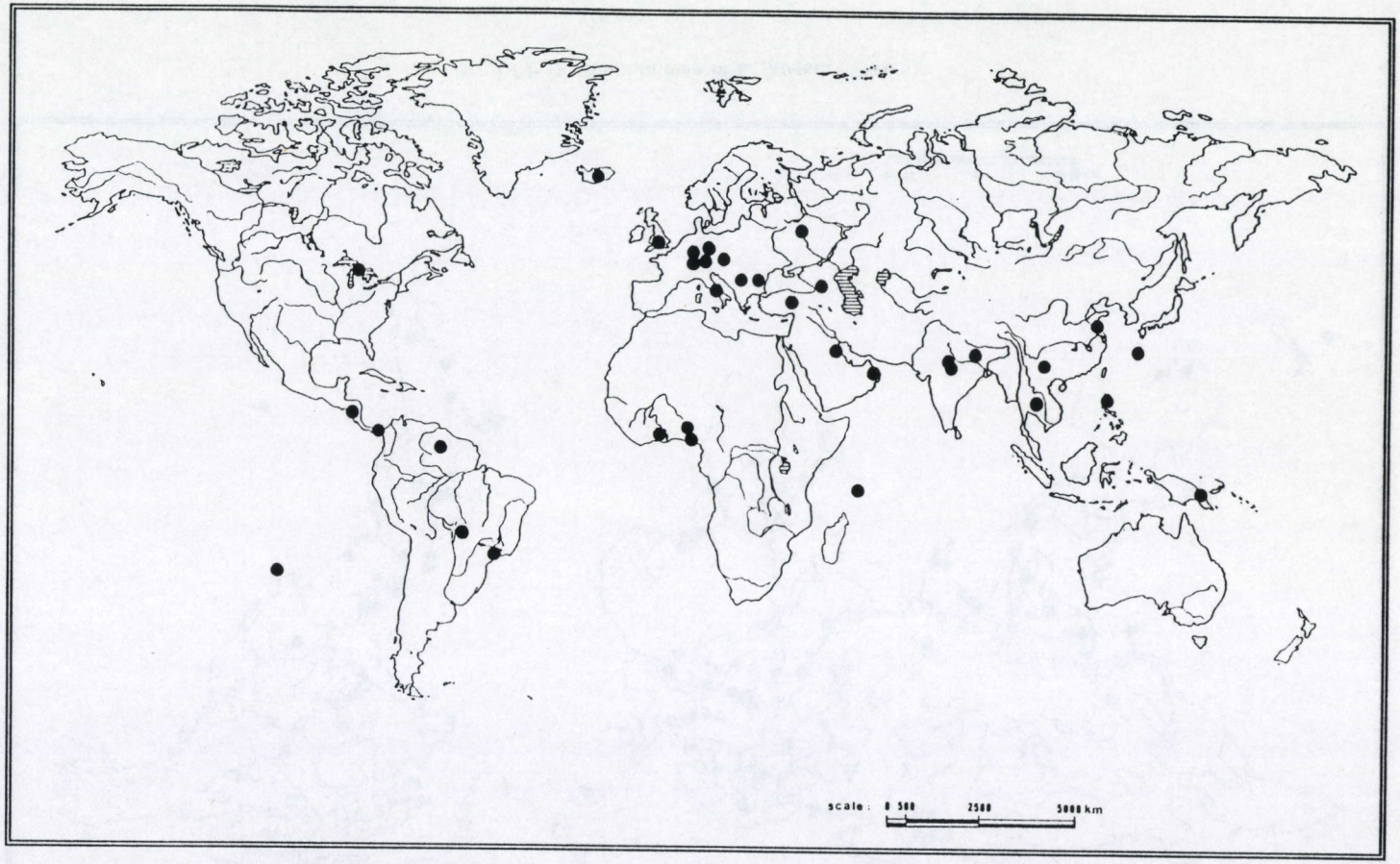
Map 11: Distribution map of *L. flexilis* (Gosse)



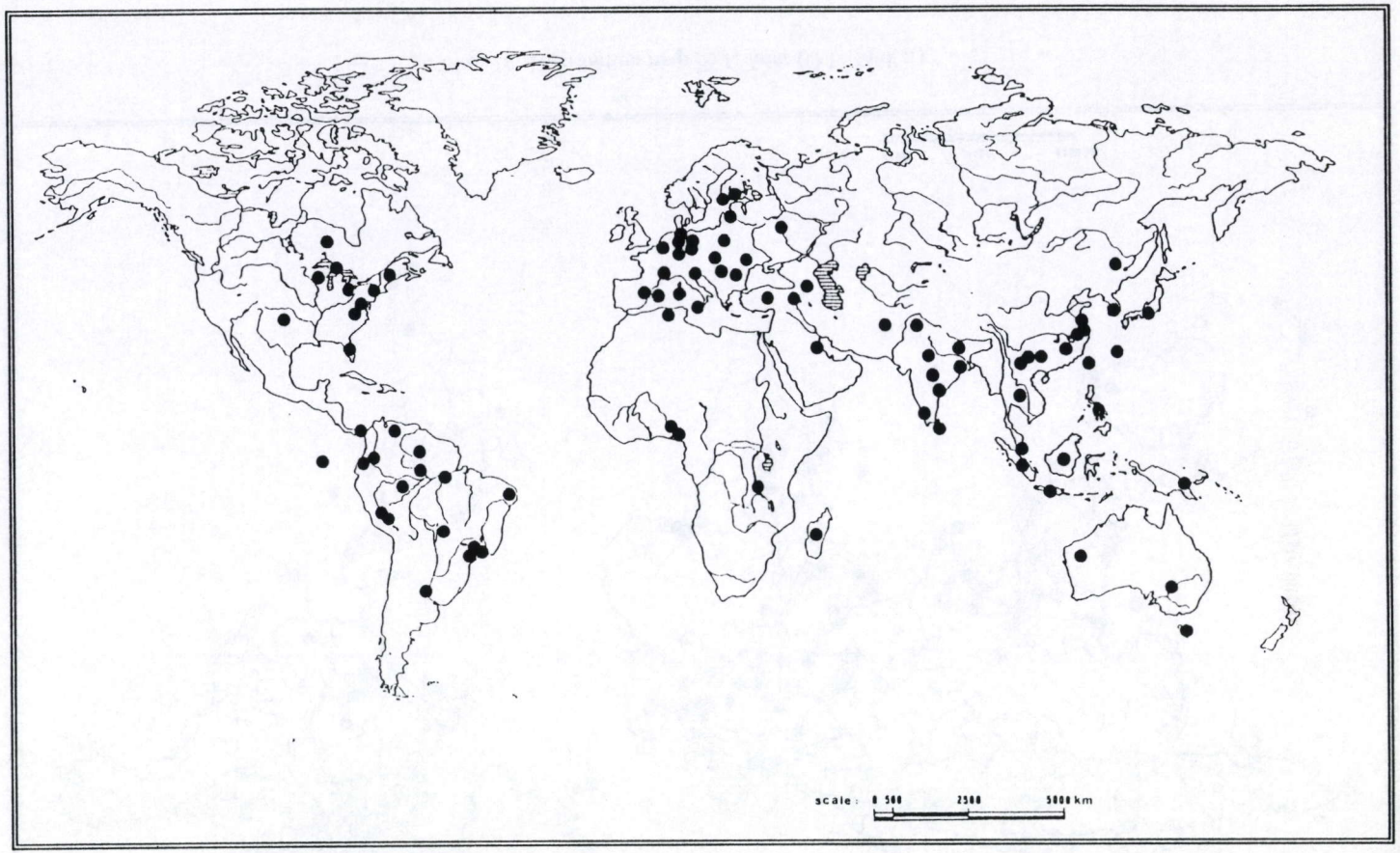
Map 12: Distribution map of *L. furcata* (Murray)



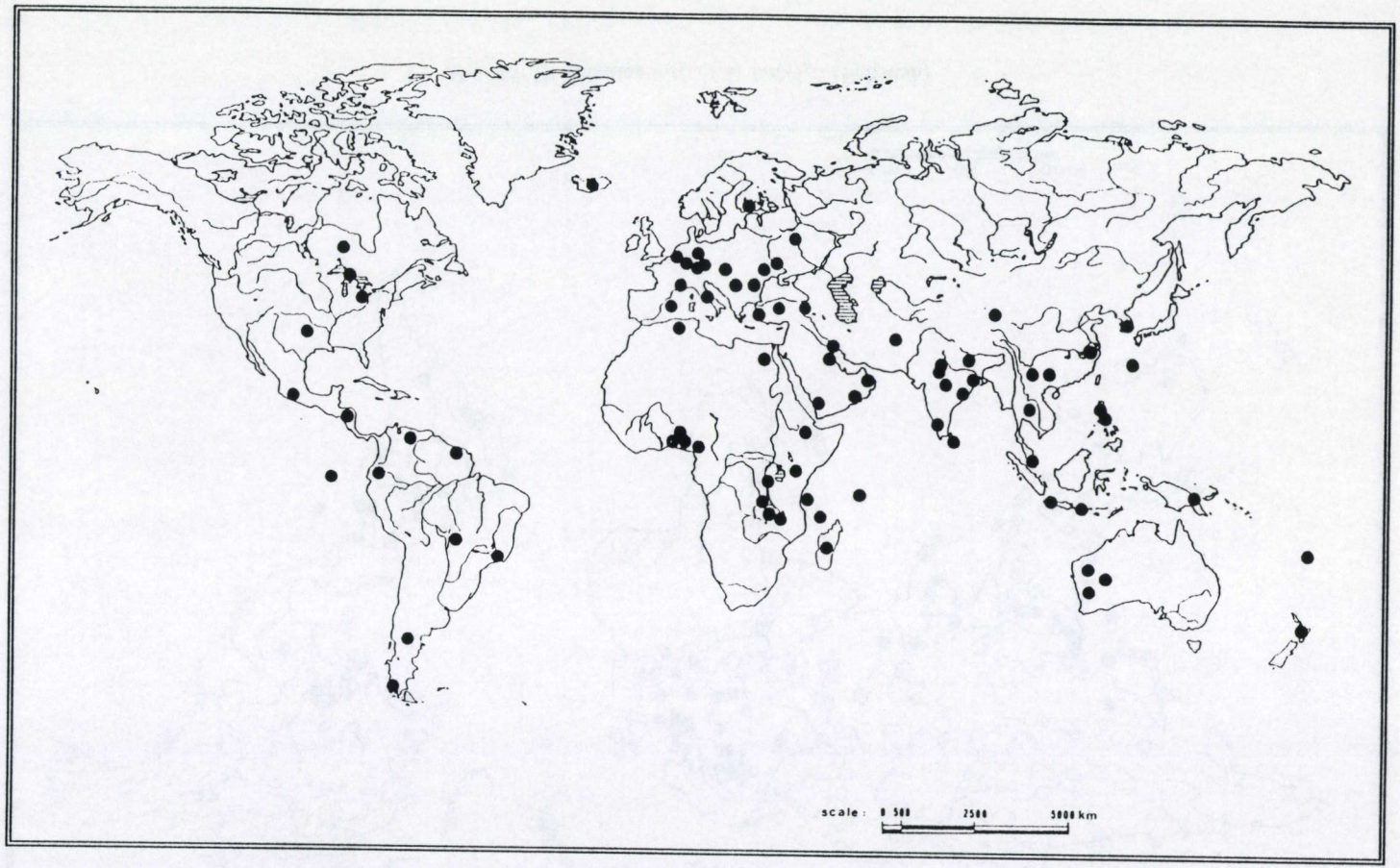
Map 13: Distribution map of *L. hamata* (Stokes)



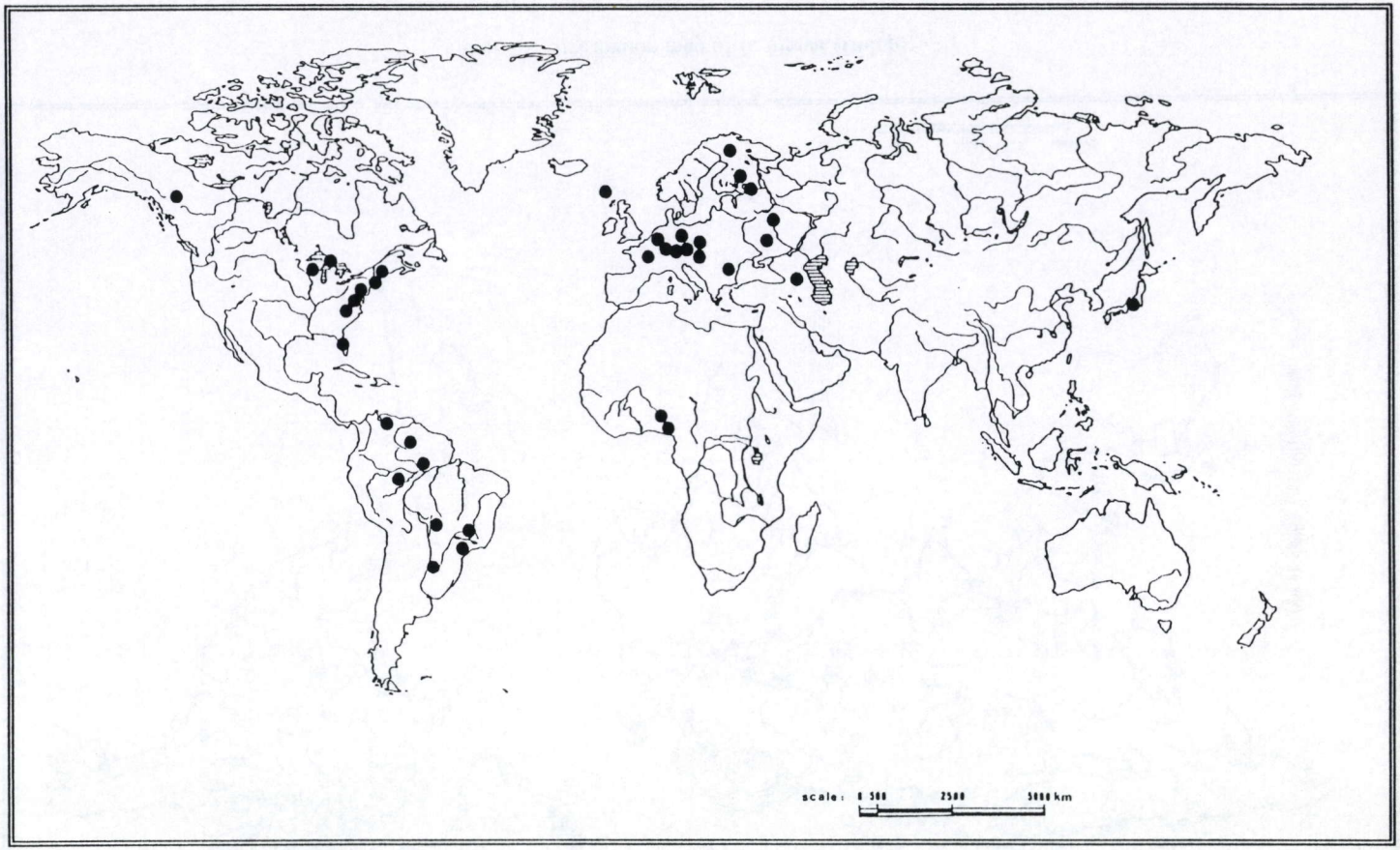
Map 14: Distribution map of *L. inermis* (Bryce)



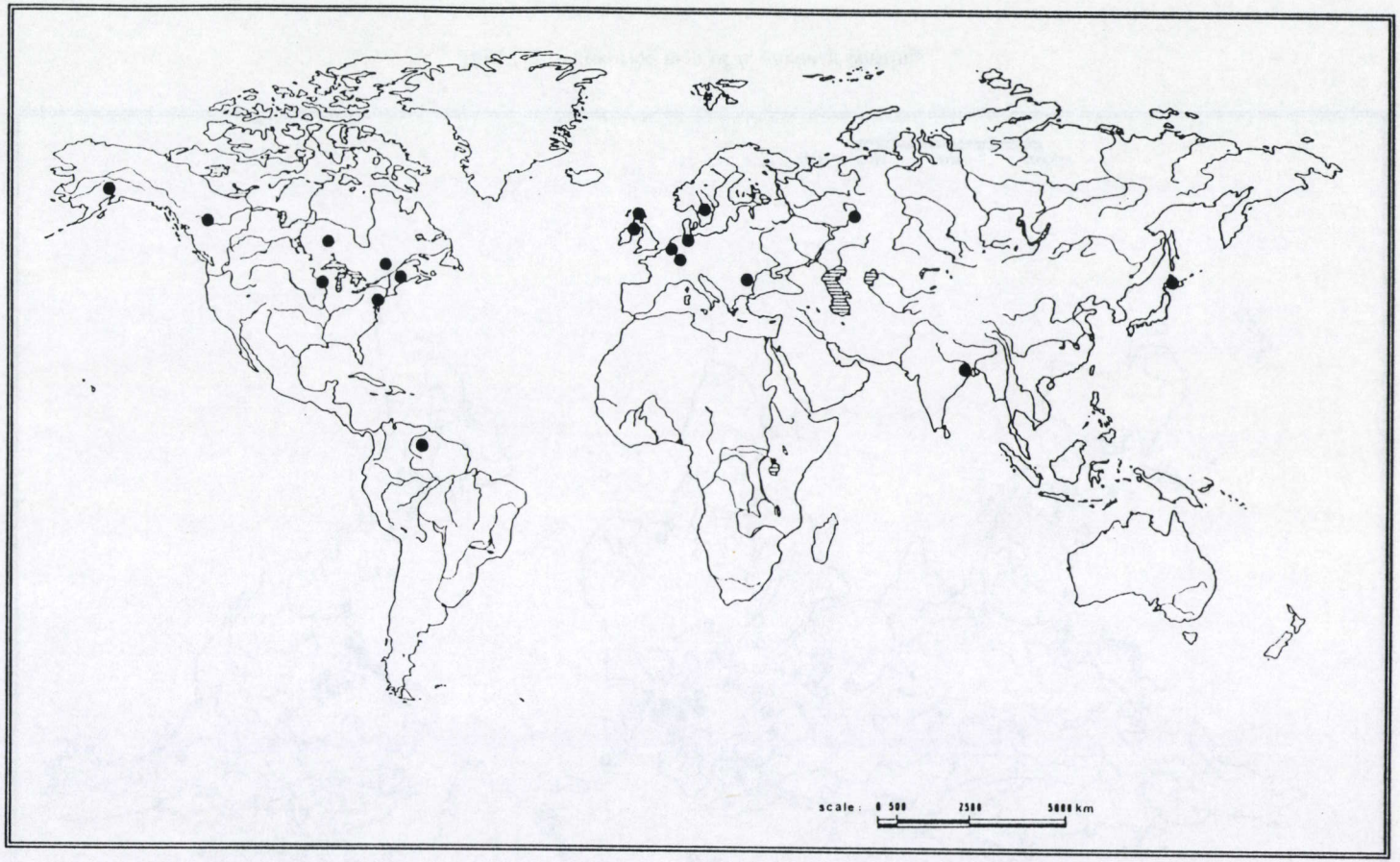
Map 15: Distribution map of *L. ludwigii* (Eckstein)



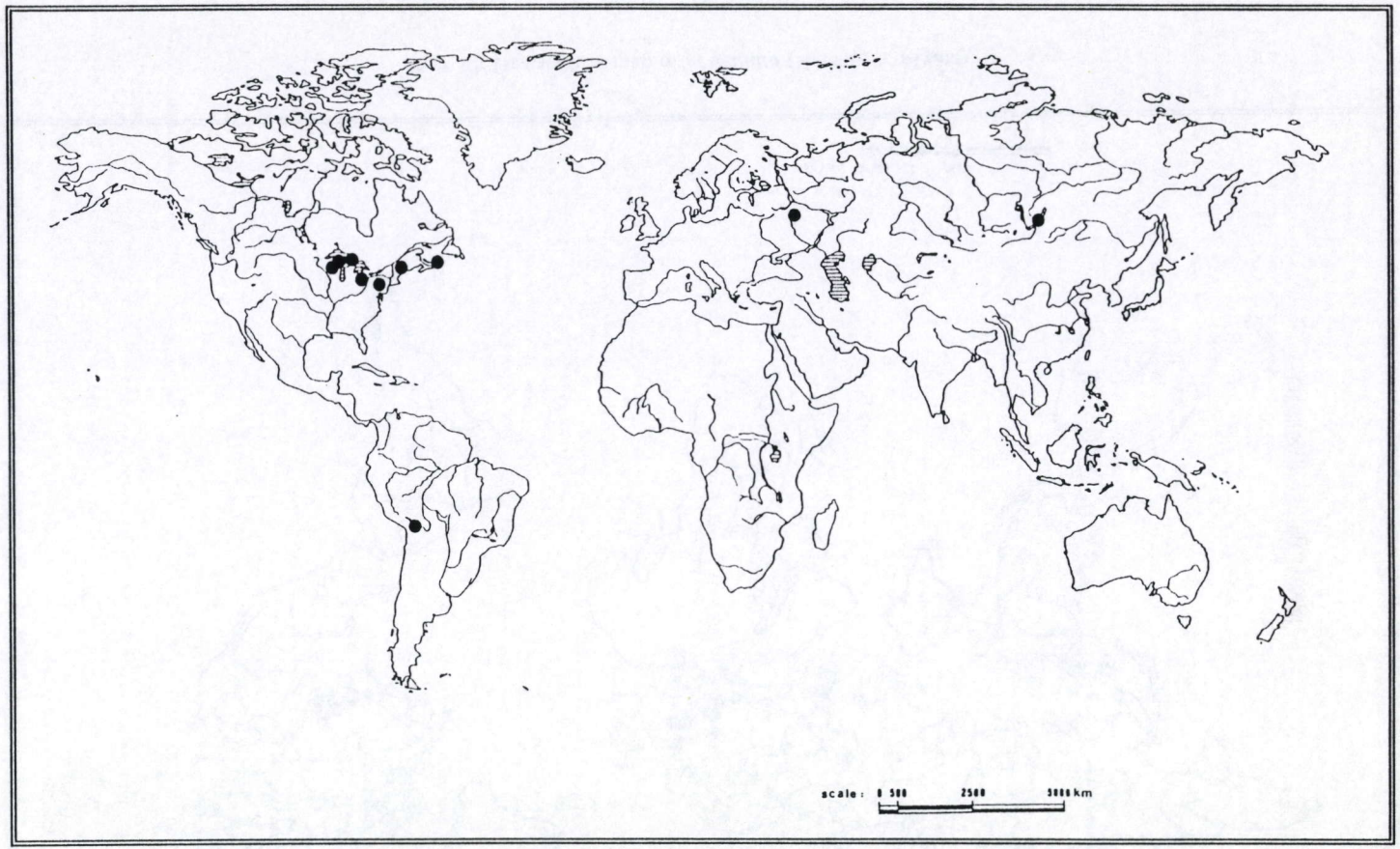
Map 16: Distribution map of *L. luna* (O.F. Müller)



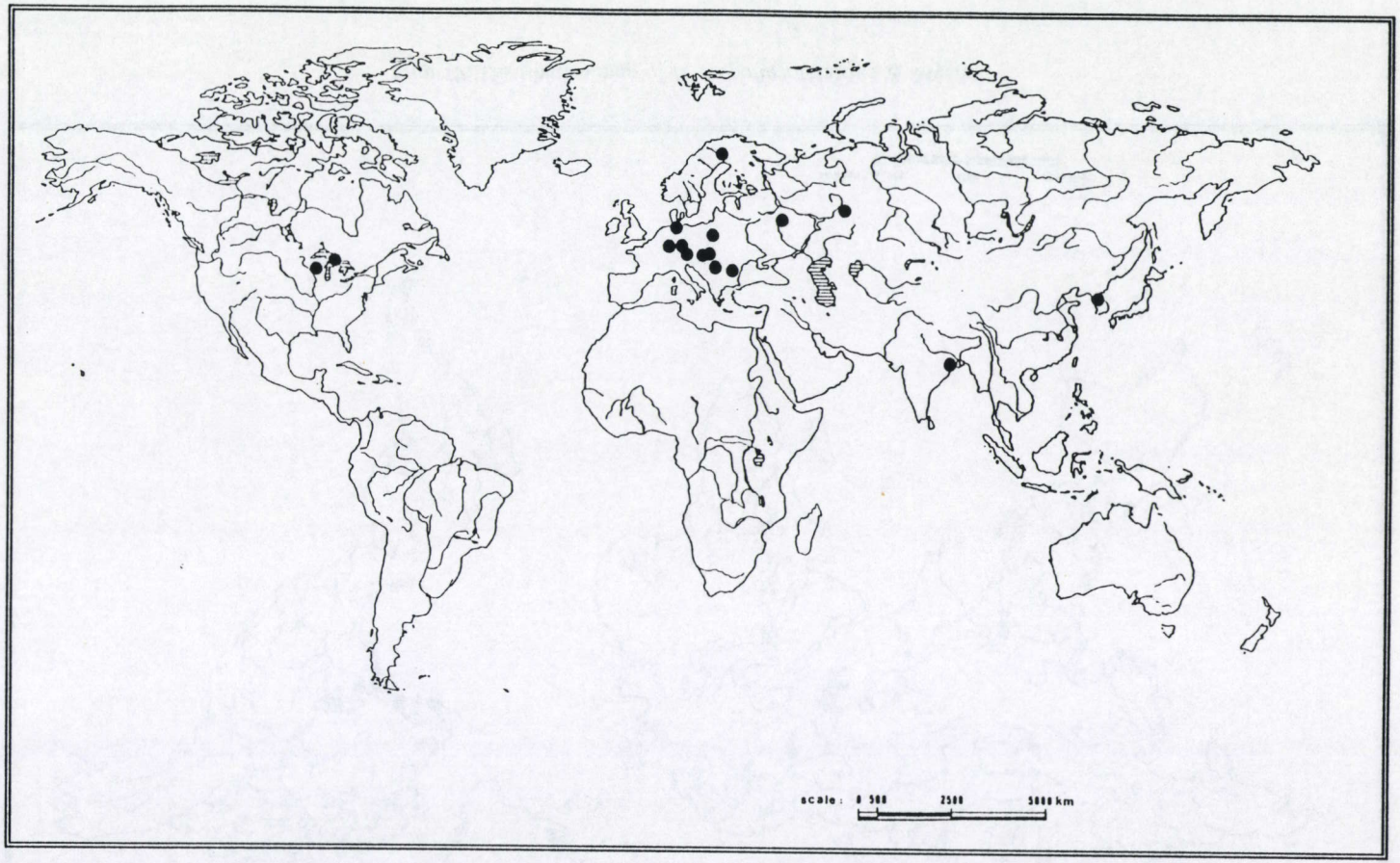
Map 17: Distribution map of *L. stichaea* Harring



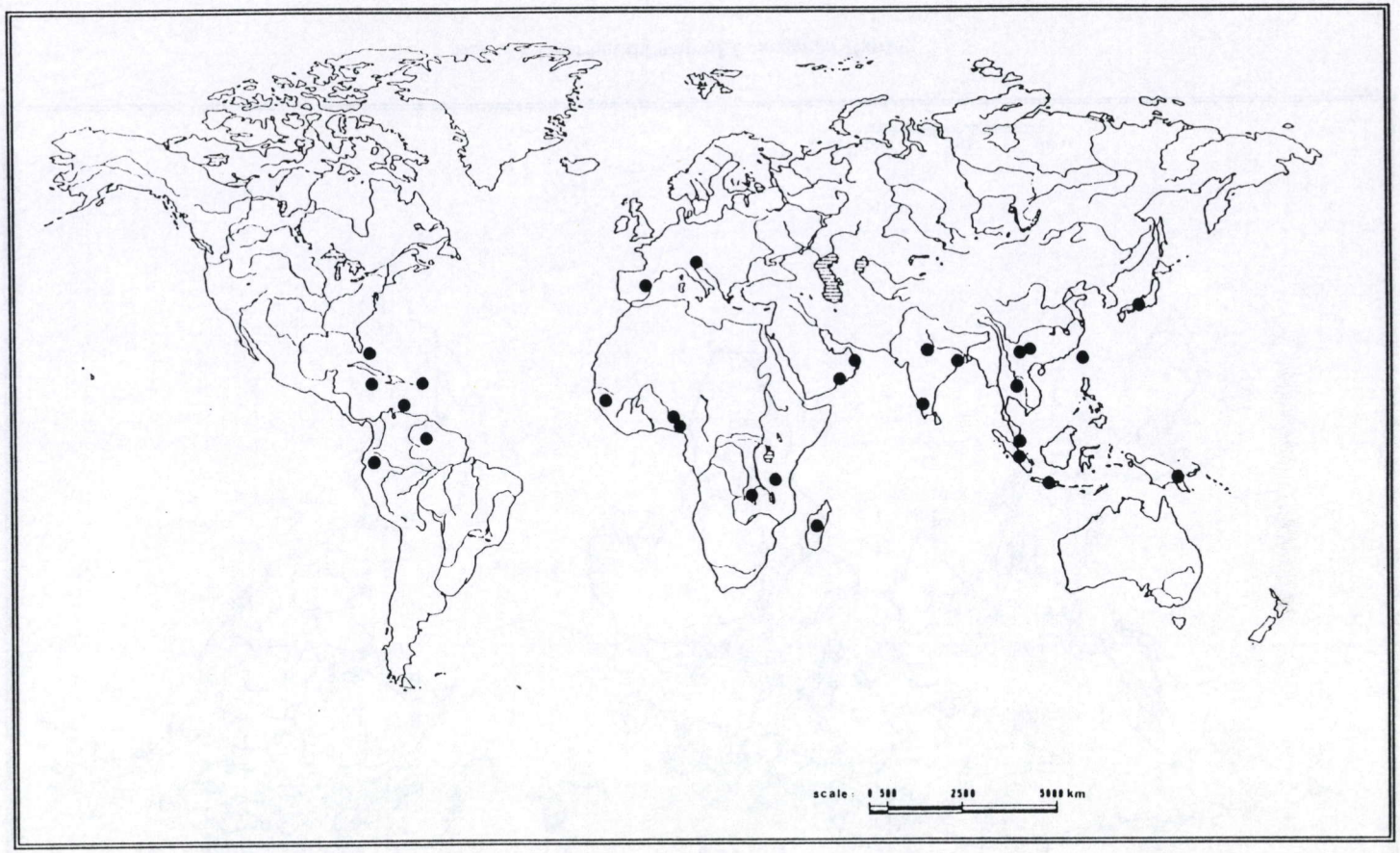
Map 18: Distribution map of *L. ligona* (Dulop)



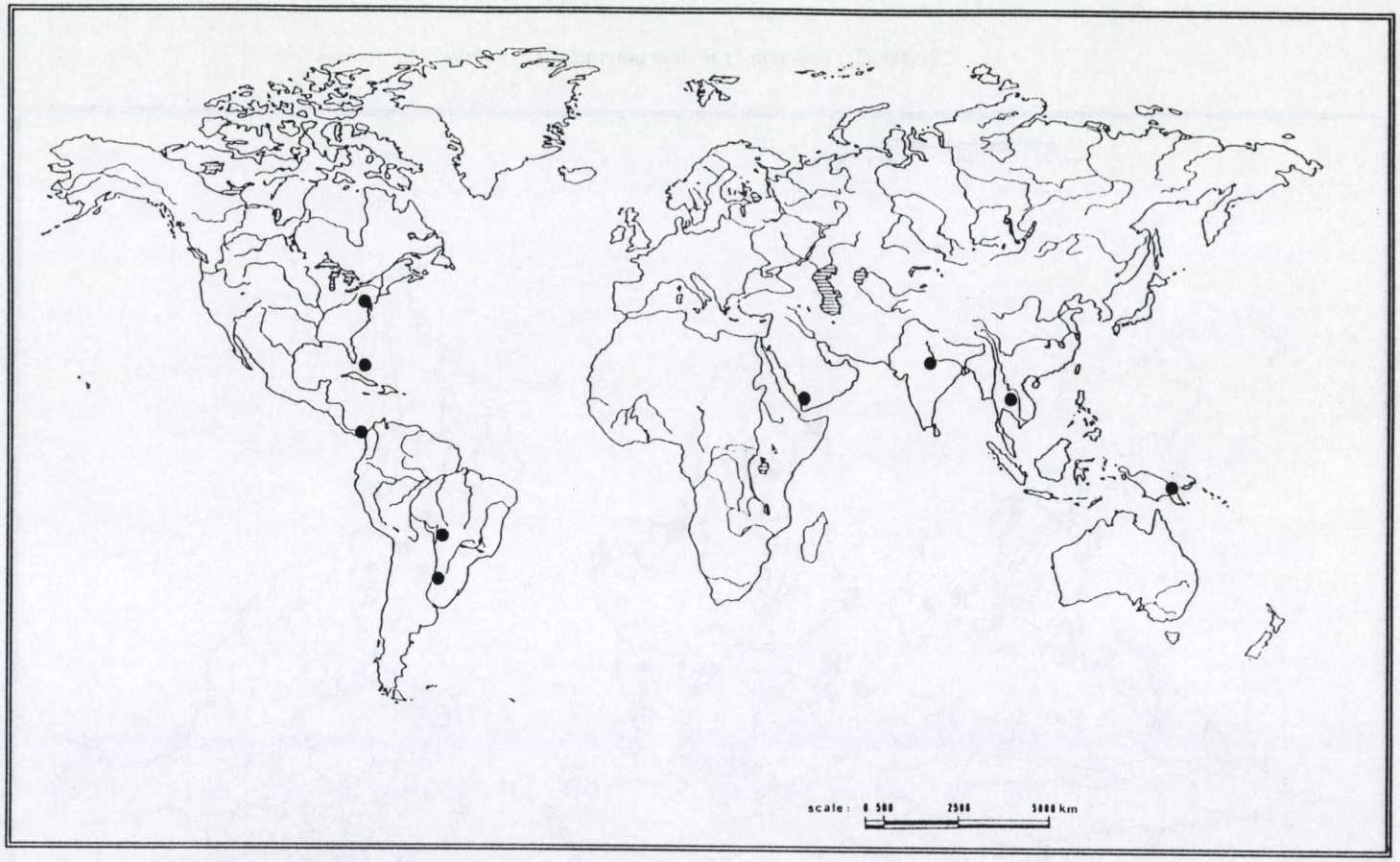
Map 19: Distribution map of *L. rhopalura* (Harring & Myers)



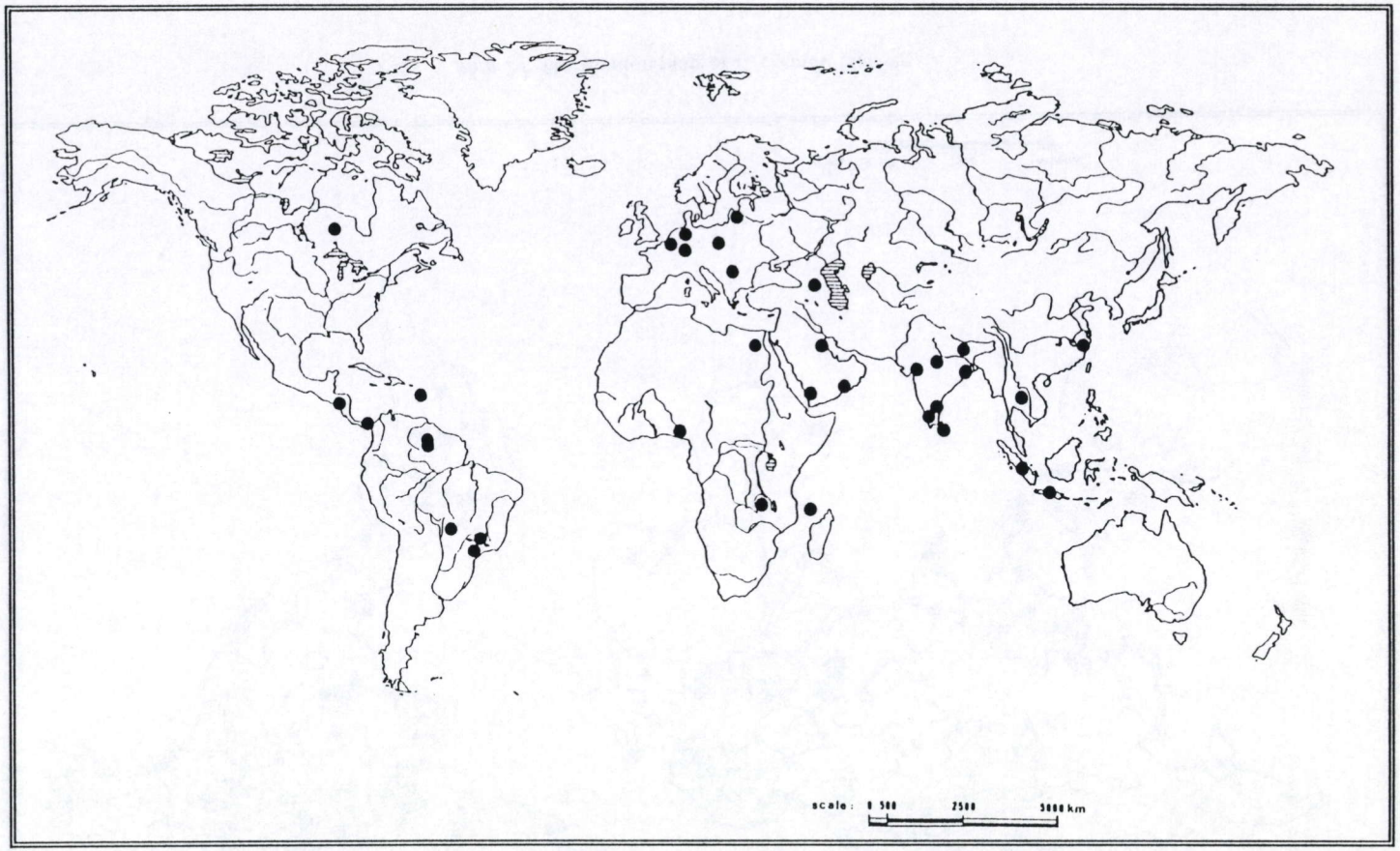
Map 20: Distribution map of *L. scutata* (Harring & Myers)



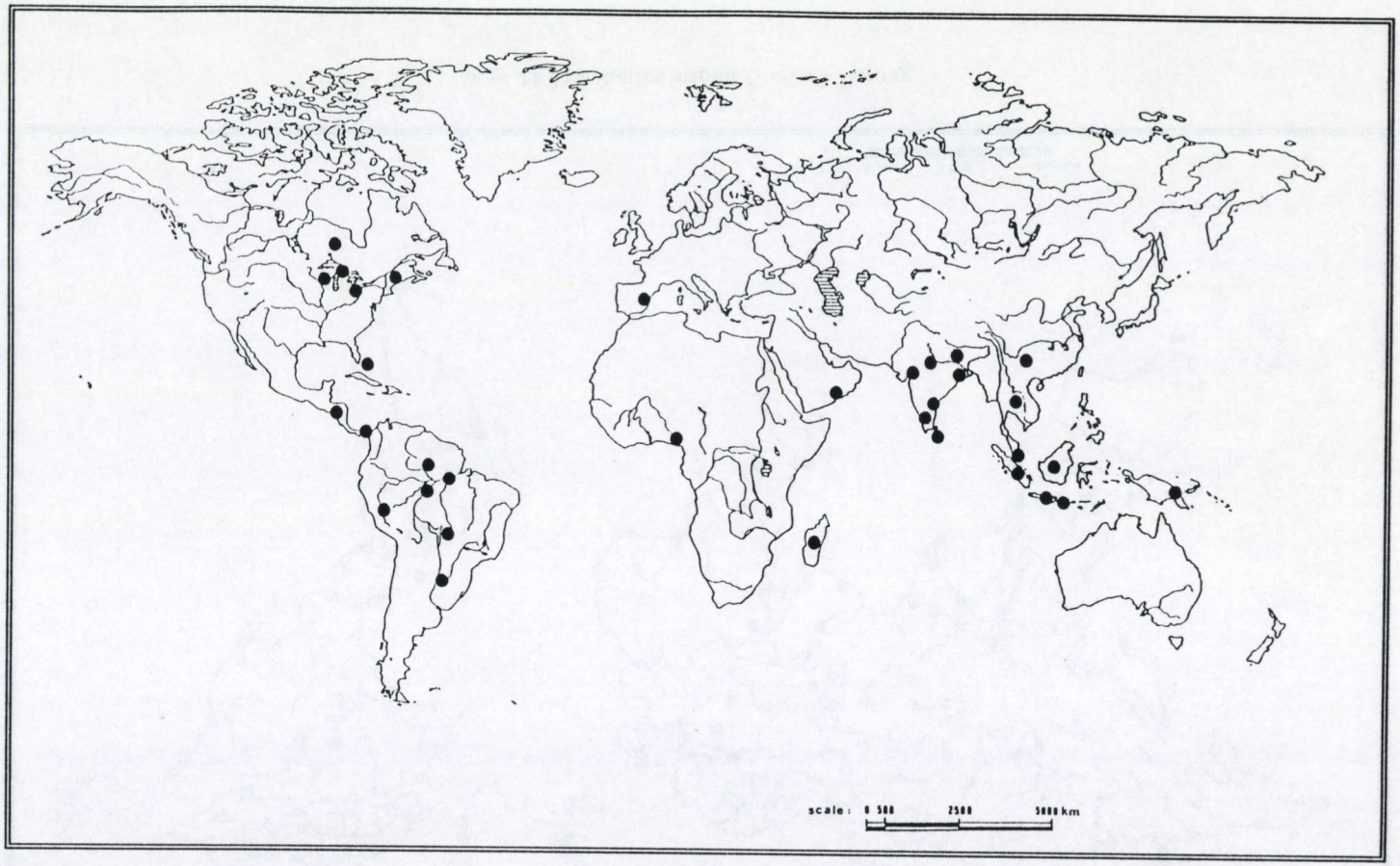
Map 21: Distribution map of *L. aculeata* (Jakubski)



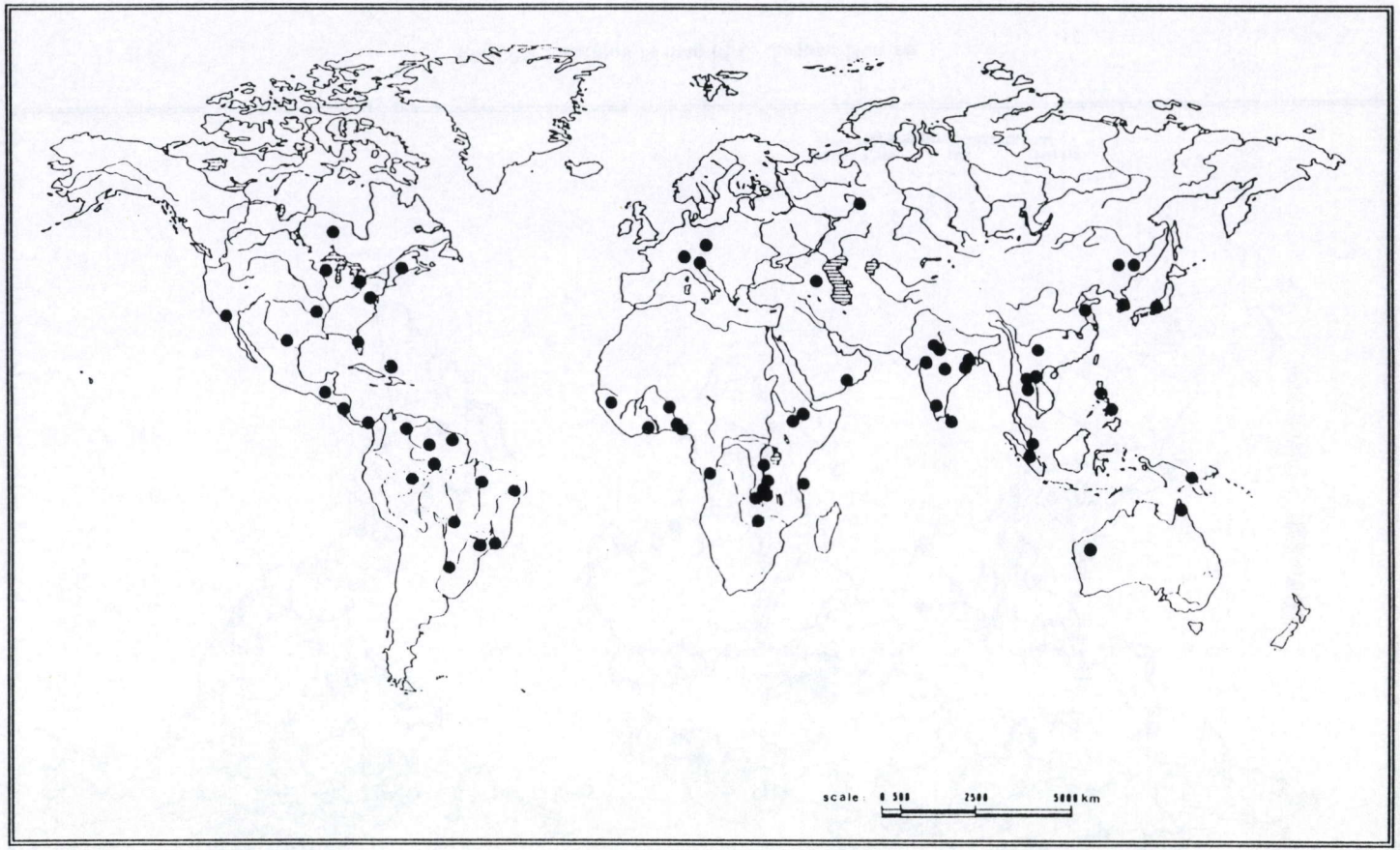
Map 22: Distribution map of *L. aeganea* Harring



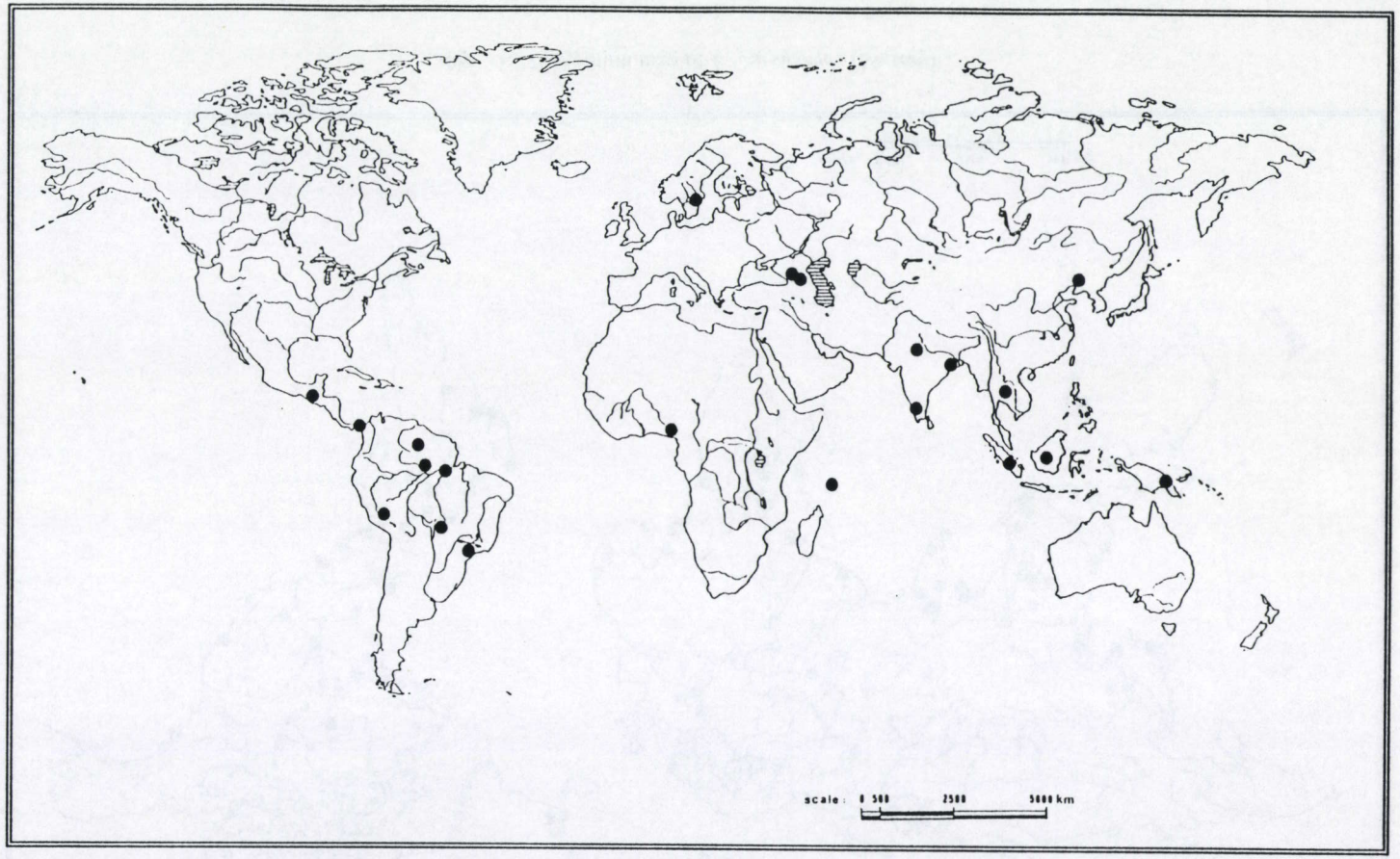
Map 23: Distribution map of *L. arcula* Harring



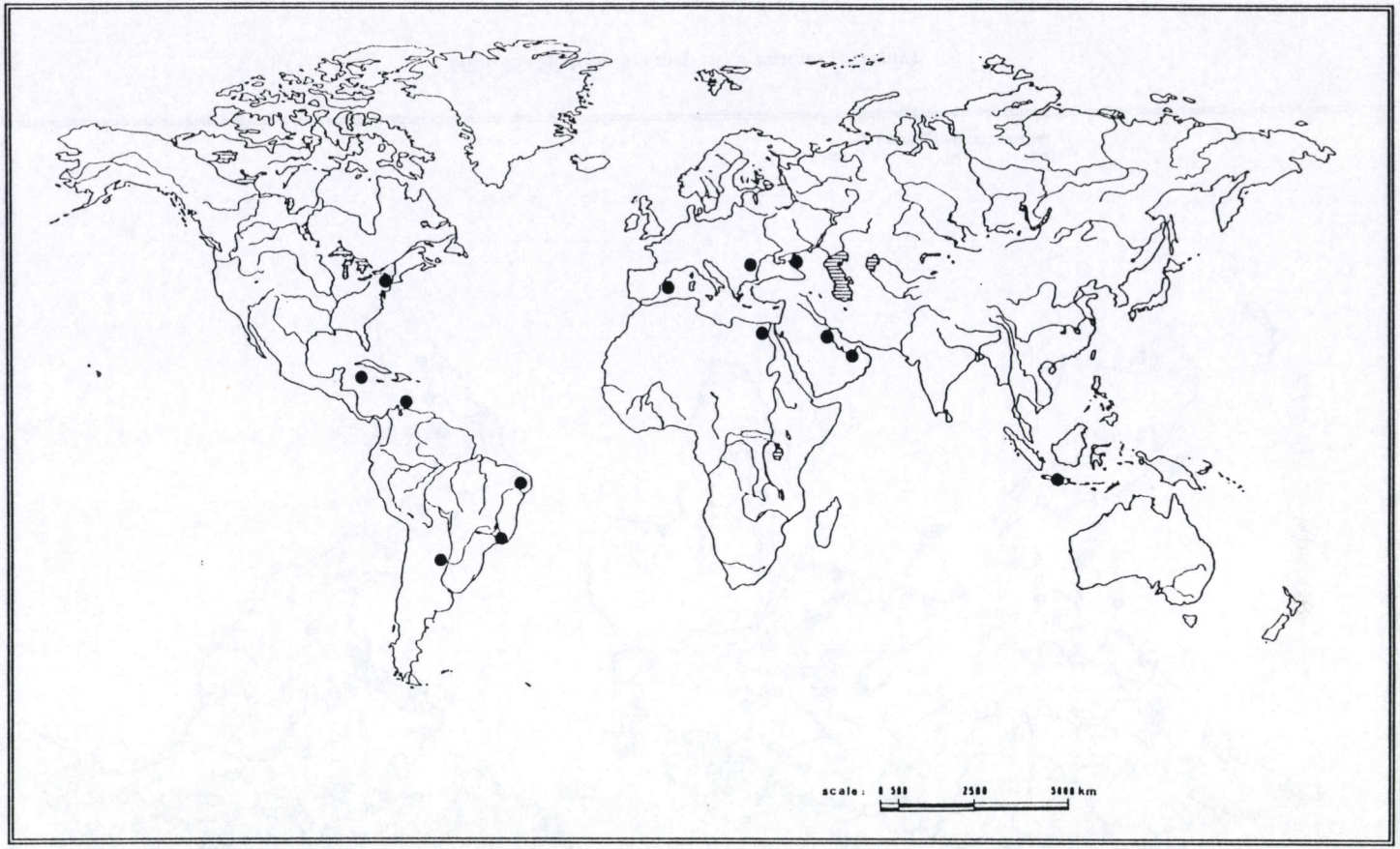
Map 24: Distribution map of *L. crepida* Harring



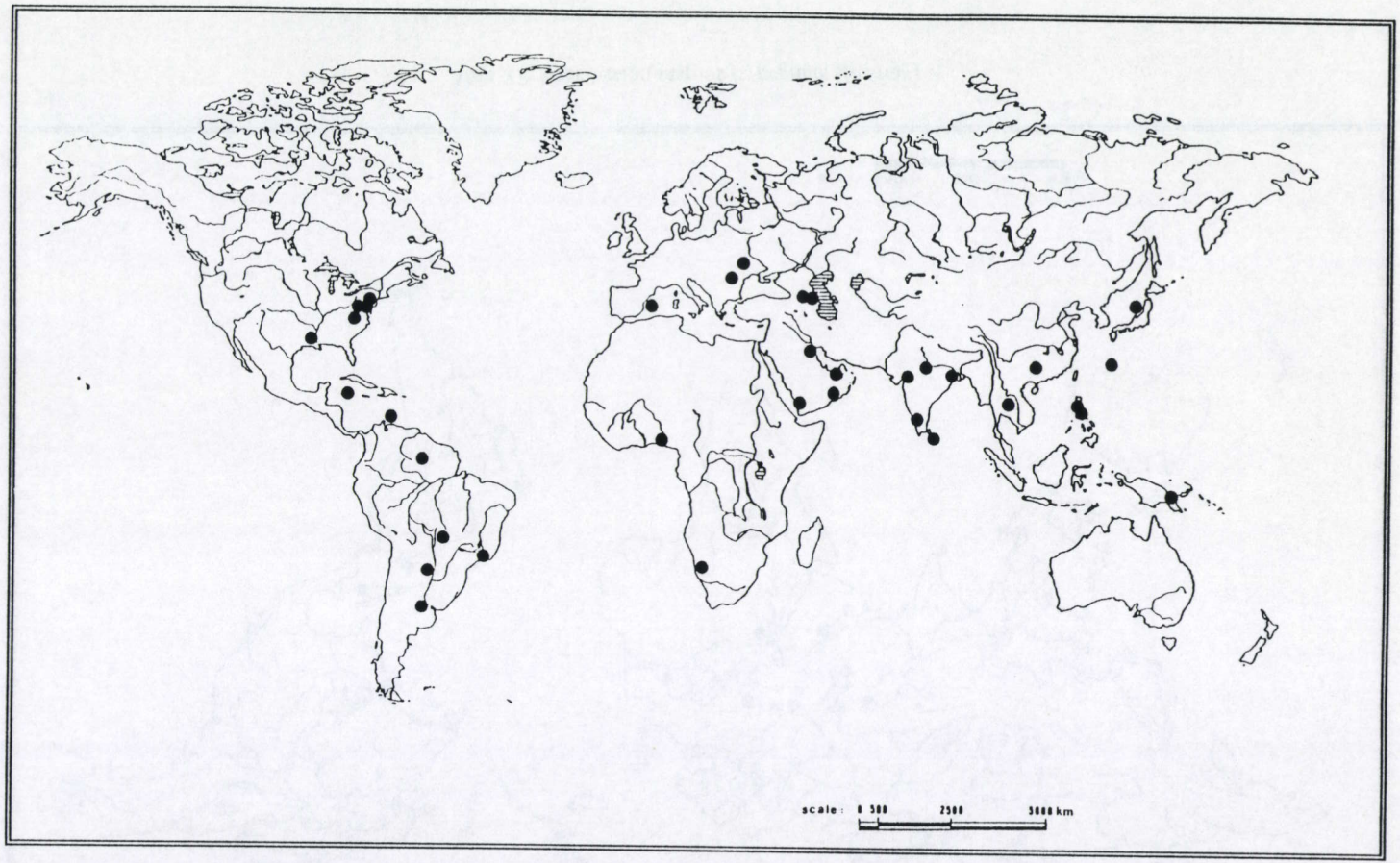
Map 25: Distribution map of *L. curvicornis* (Murray)



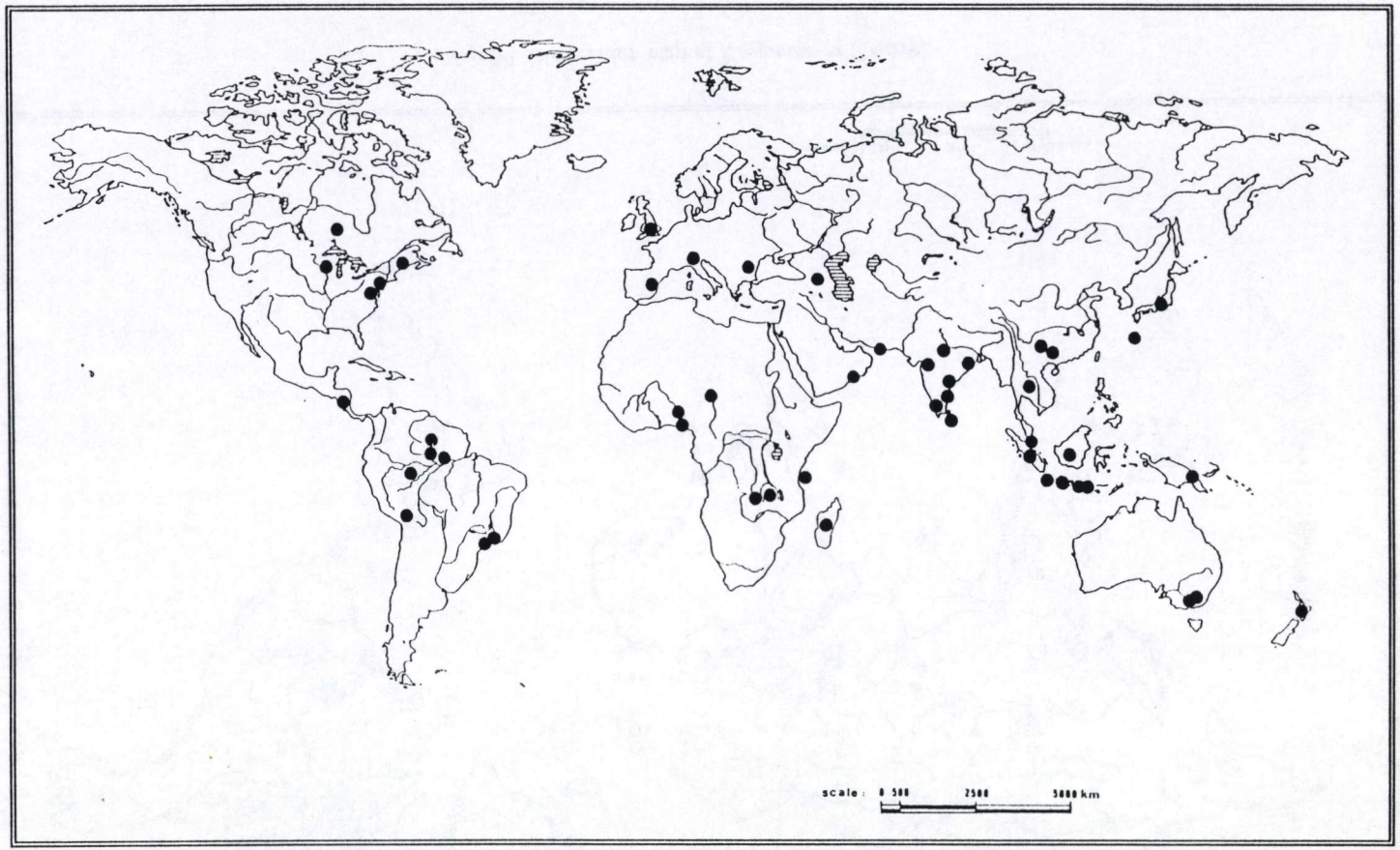
Map 26: Distribution map of *L. doryssa* Harring



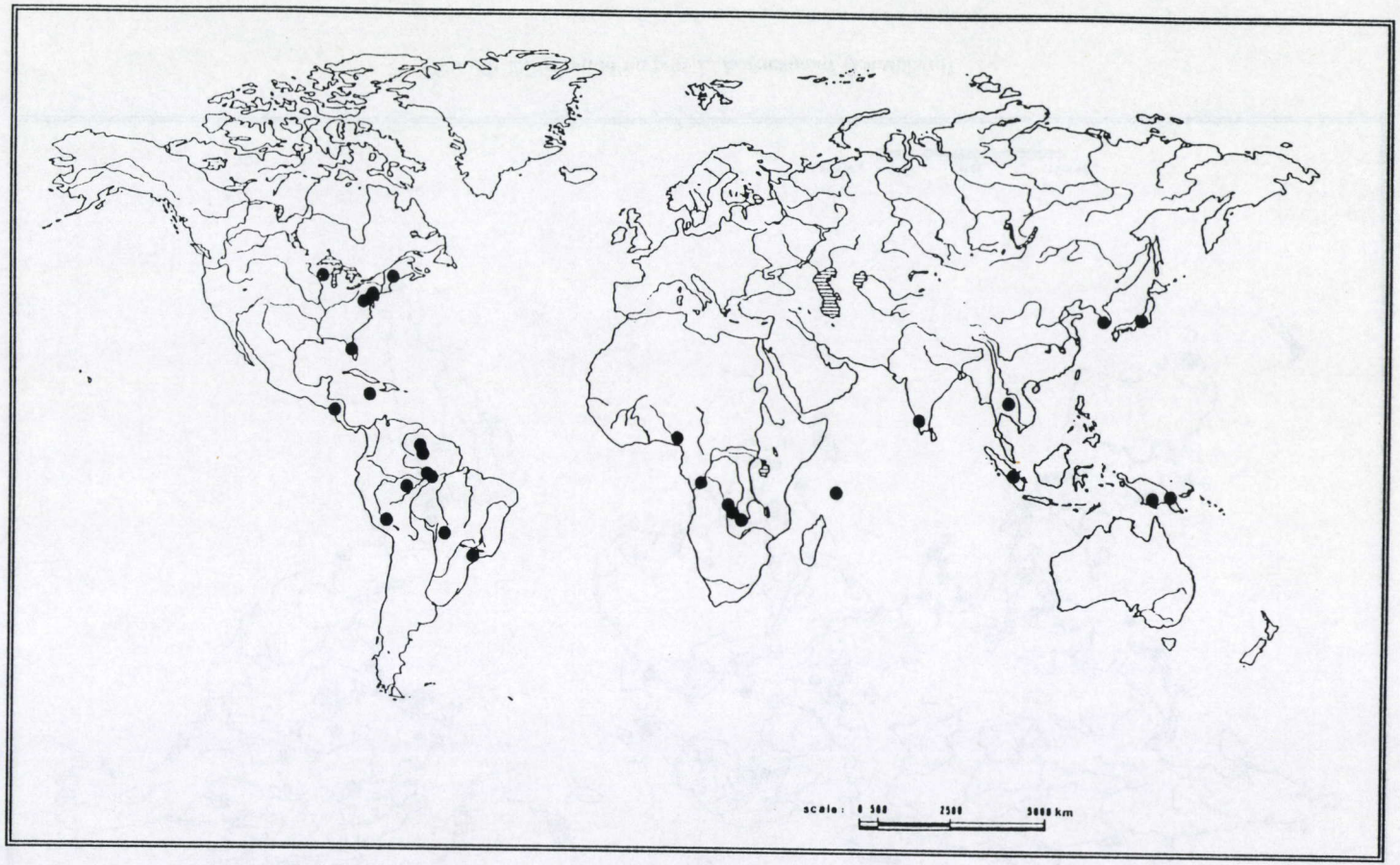
Map 27: Distribution map of *L. grandis* (Murray)



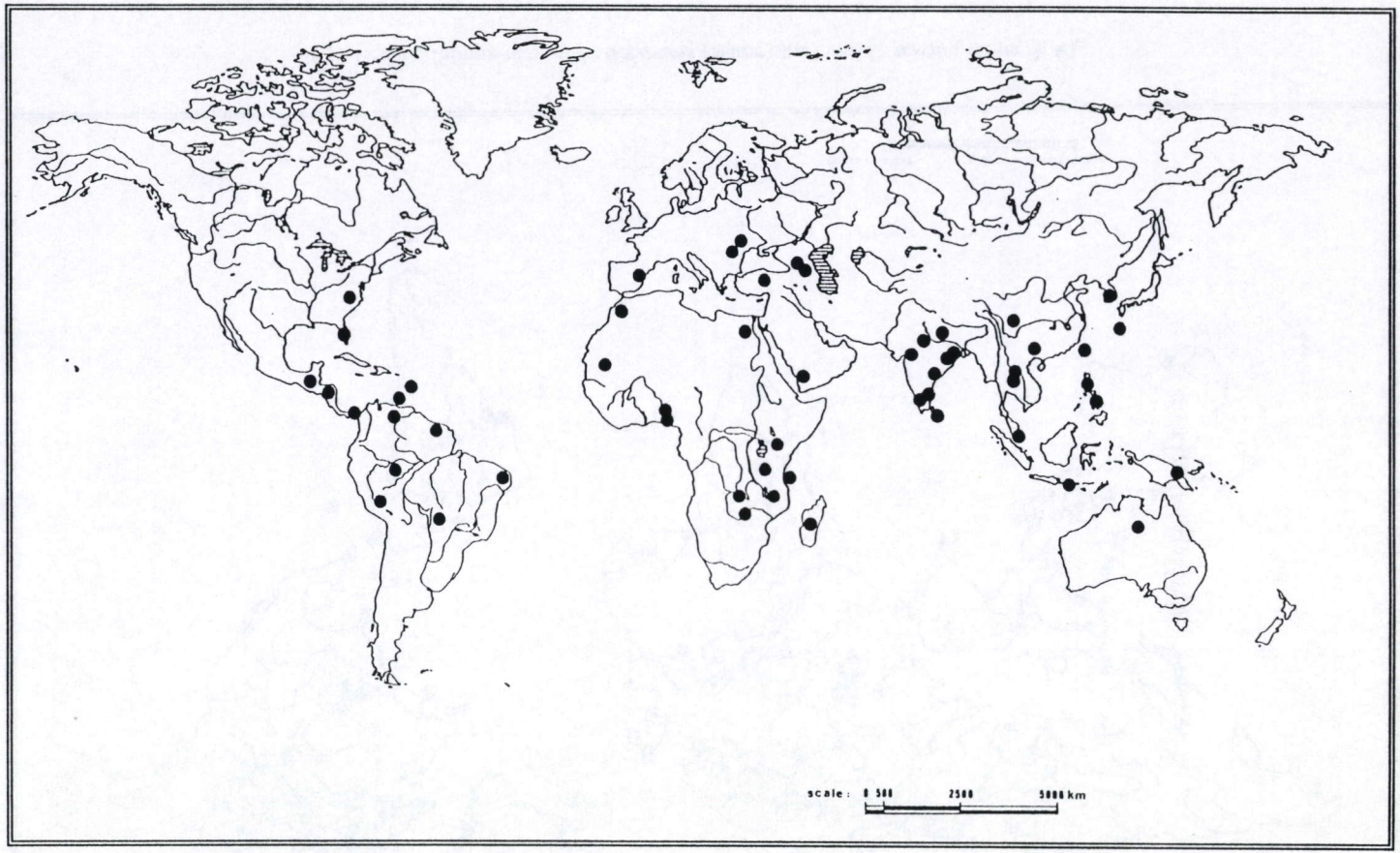
Map 28: Distribution map of *L. hastata* (Murray)



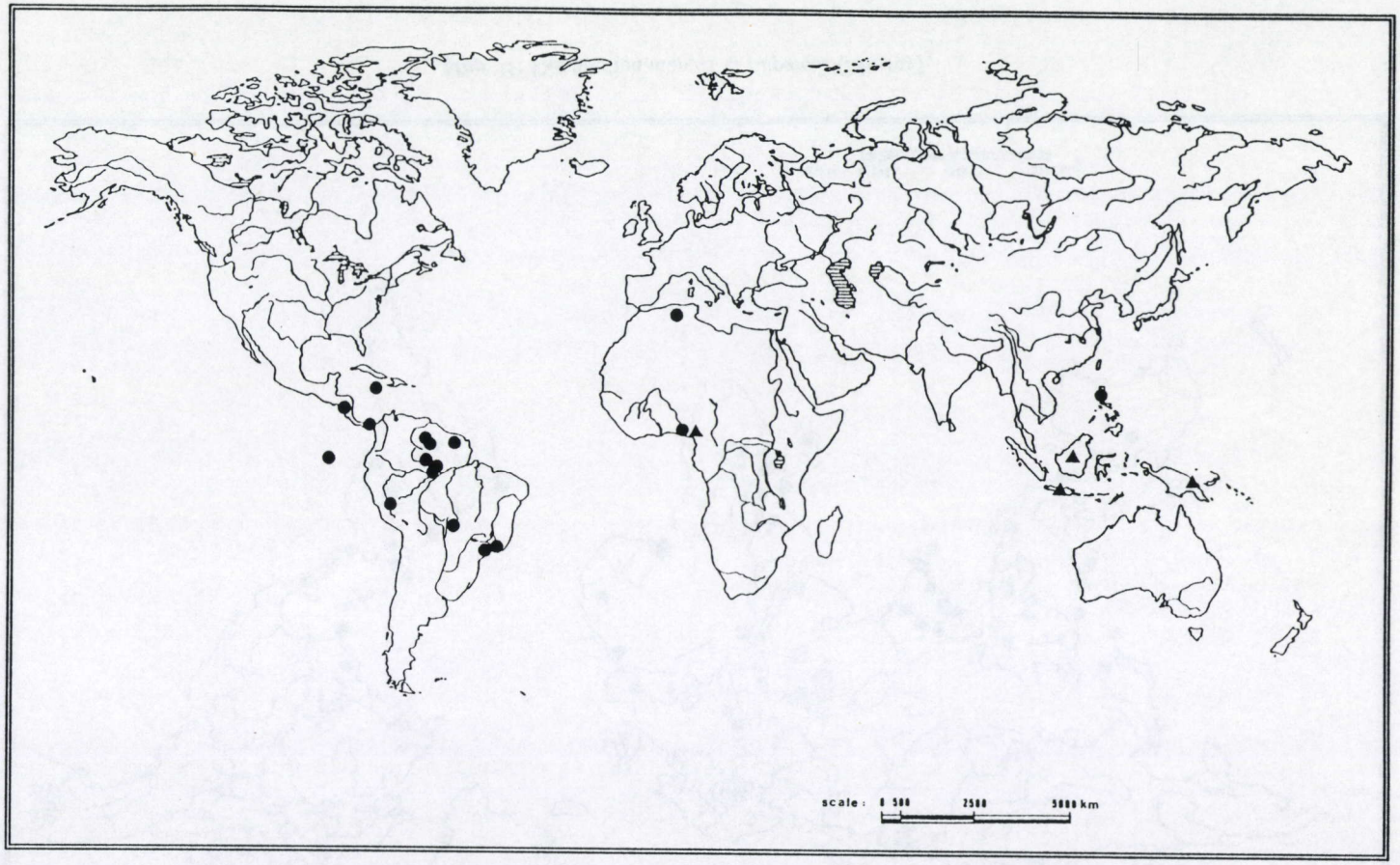
Map 29: Distribution map of *L. hornemanni* (Ehrenberg)



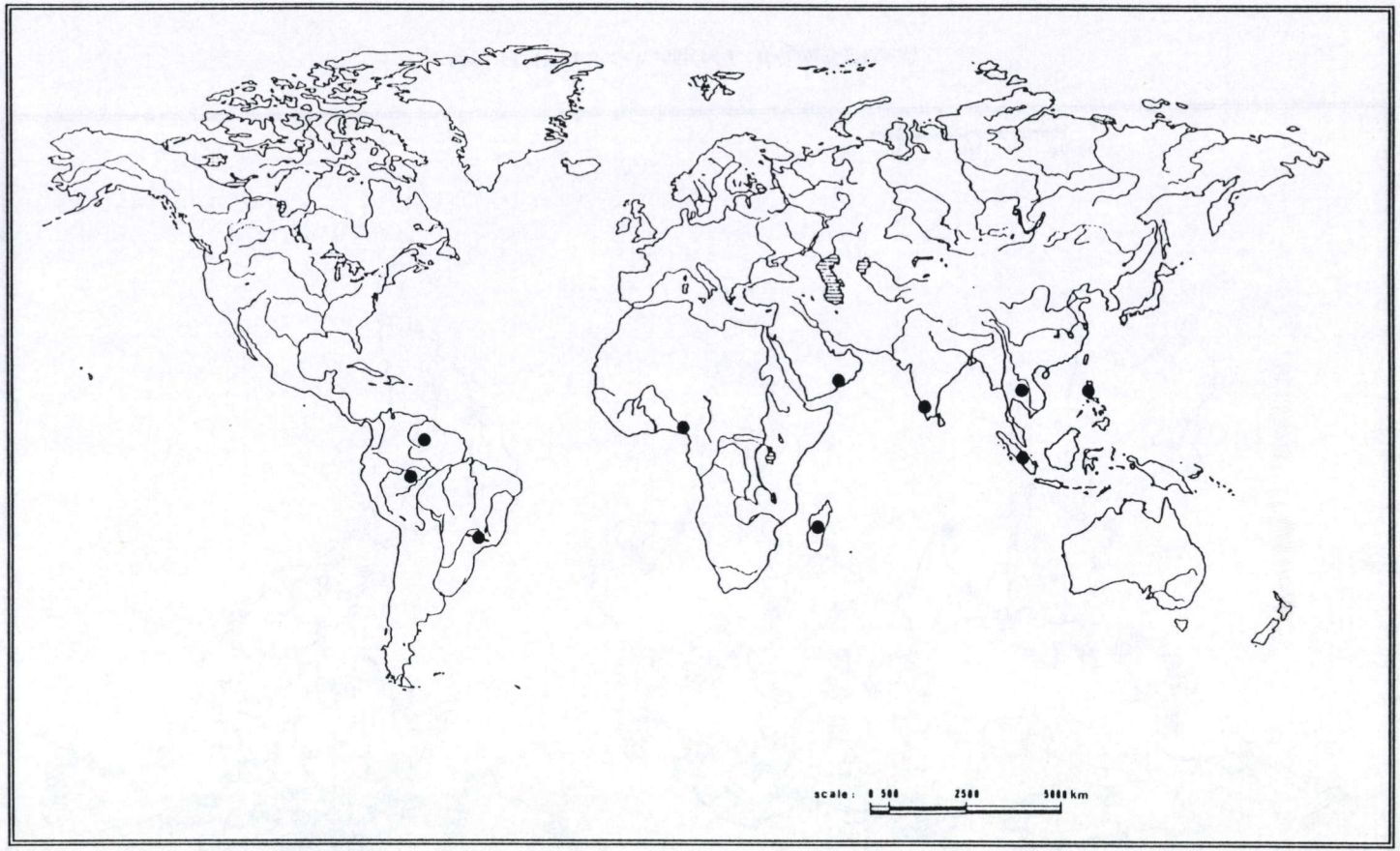
Map 30: Distribution map of *L. monostyla* (Daday)



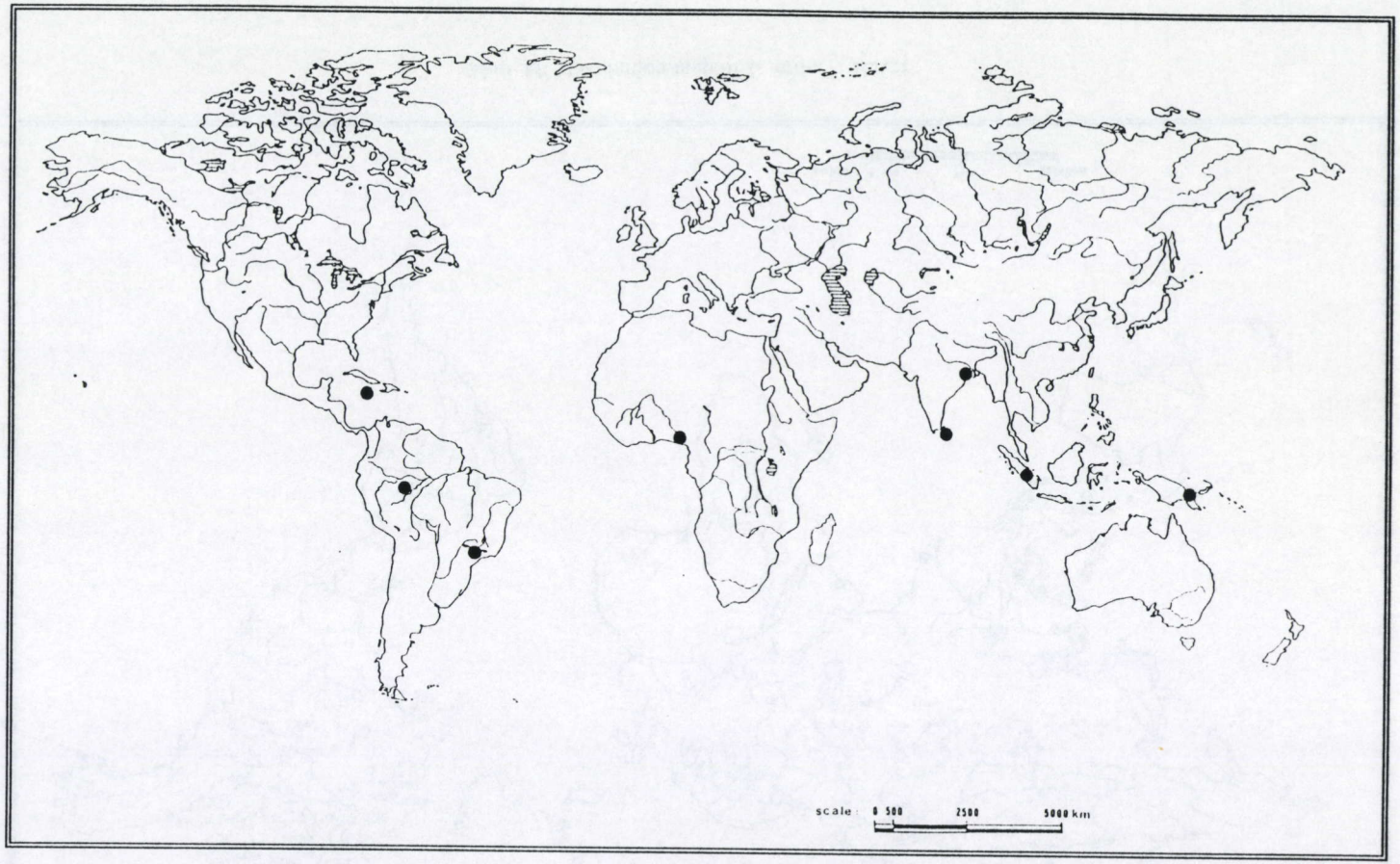
Map 31: Distribution map of *L. papuana* (Murray)



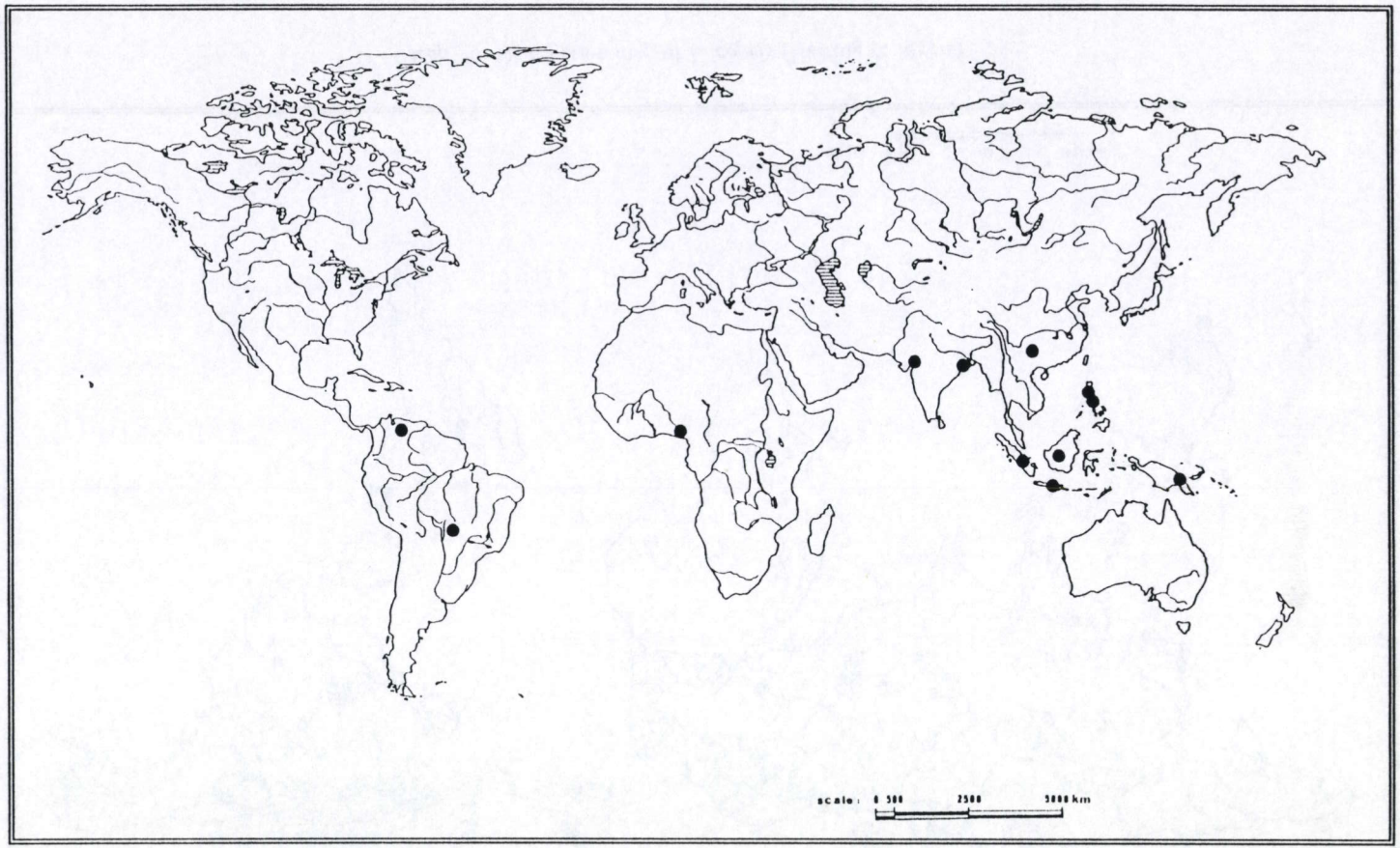
Map 32: Distribution map of *L. decipiens* (Murray)(●) and *L. serrata* (Hauer)(▲)



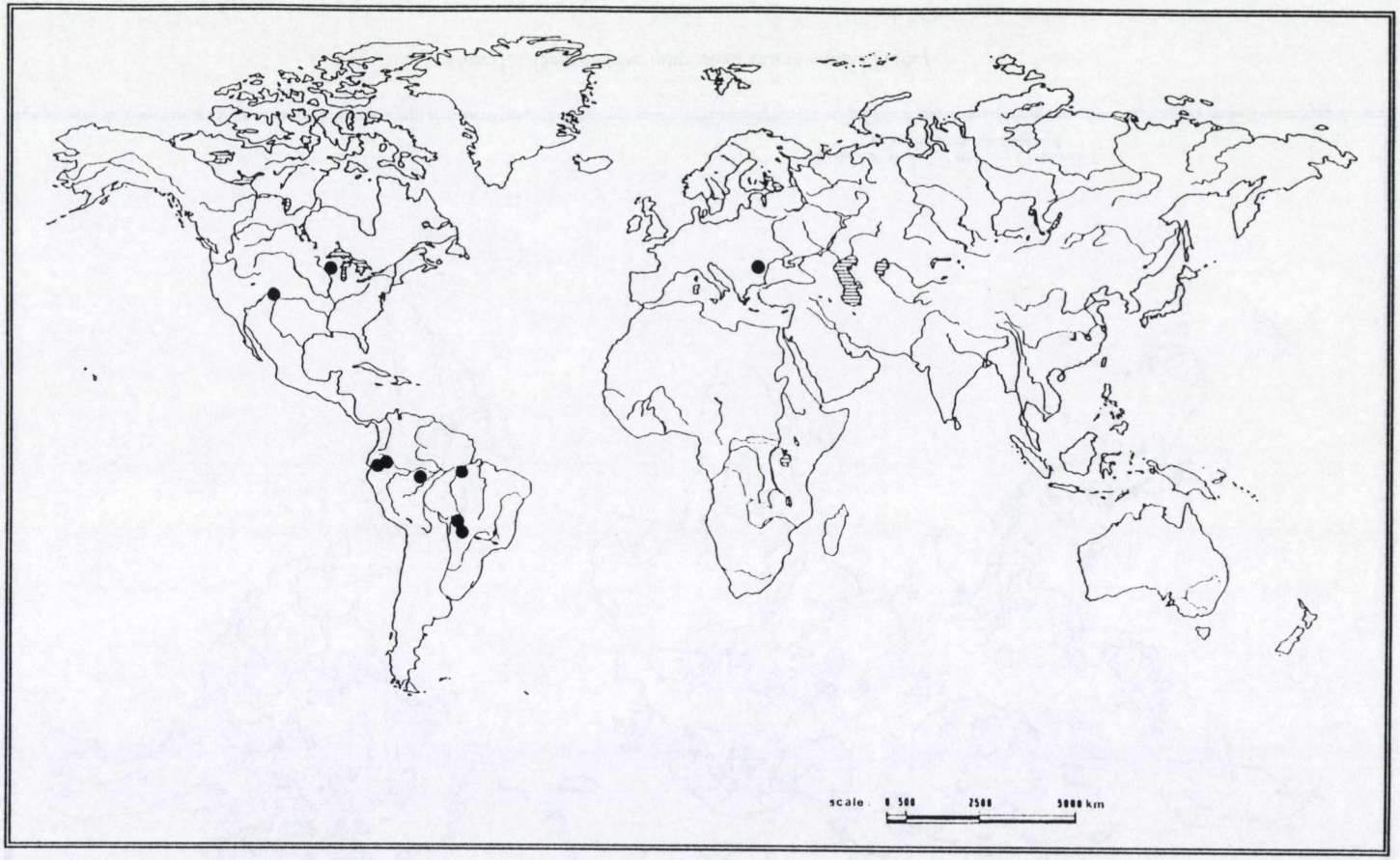
Map 33: Distribution map of *L. ruttneri* Hauer



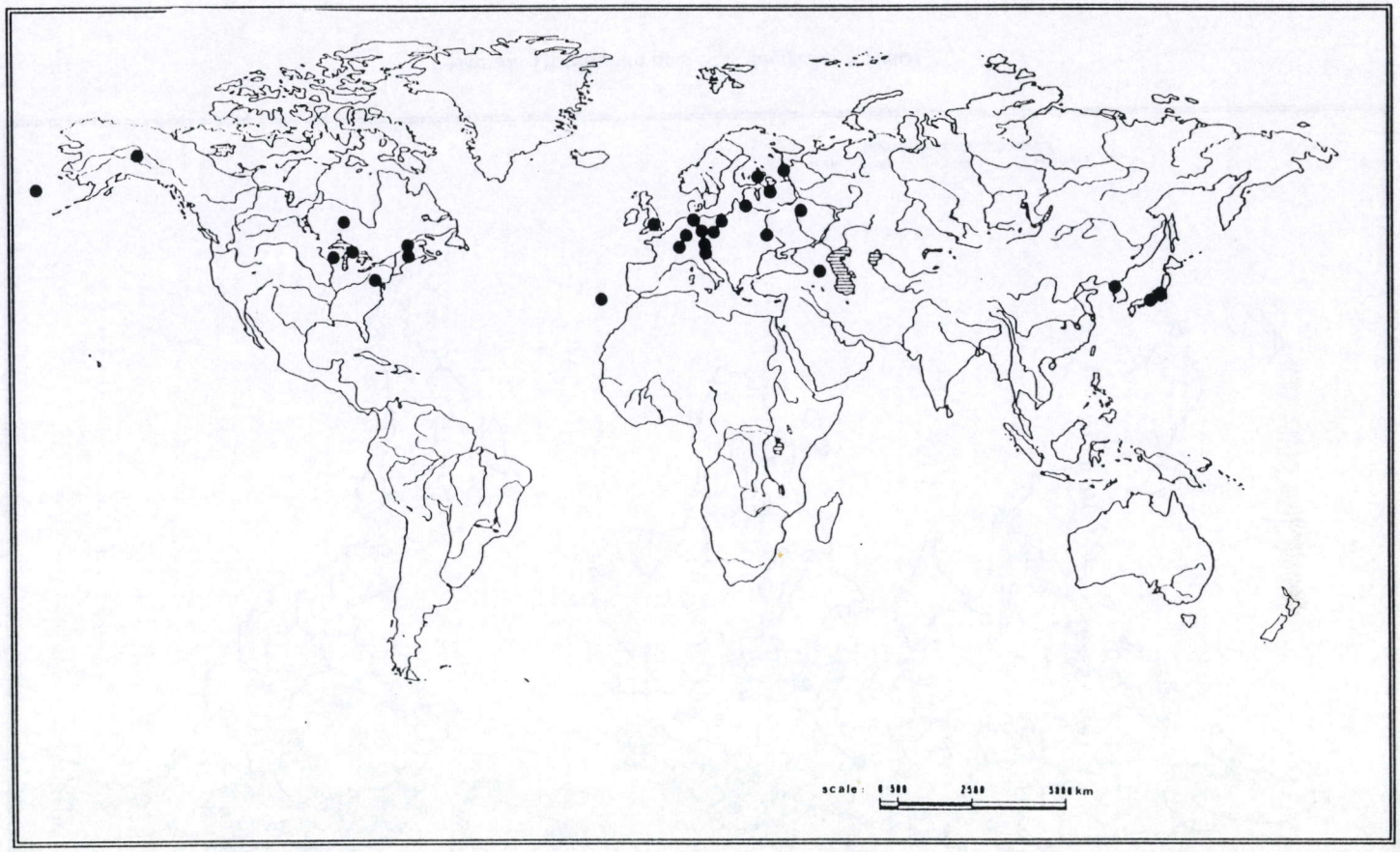
Map 34: Distribution map of *L. syngenes* (Hauer)



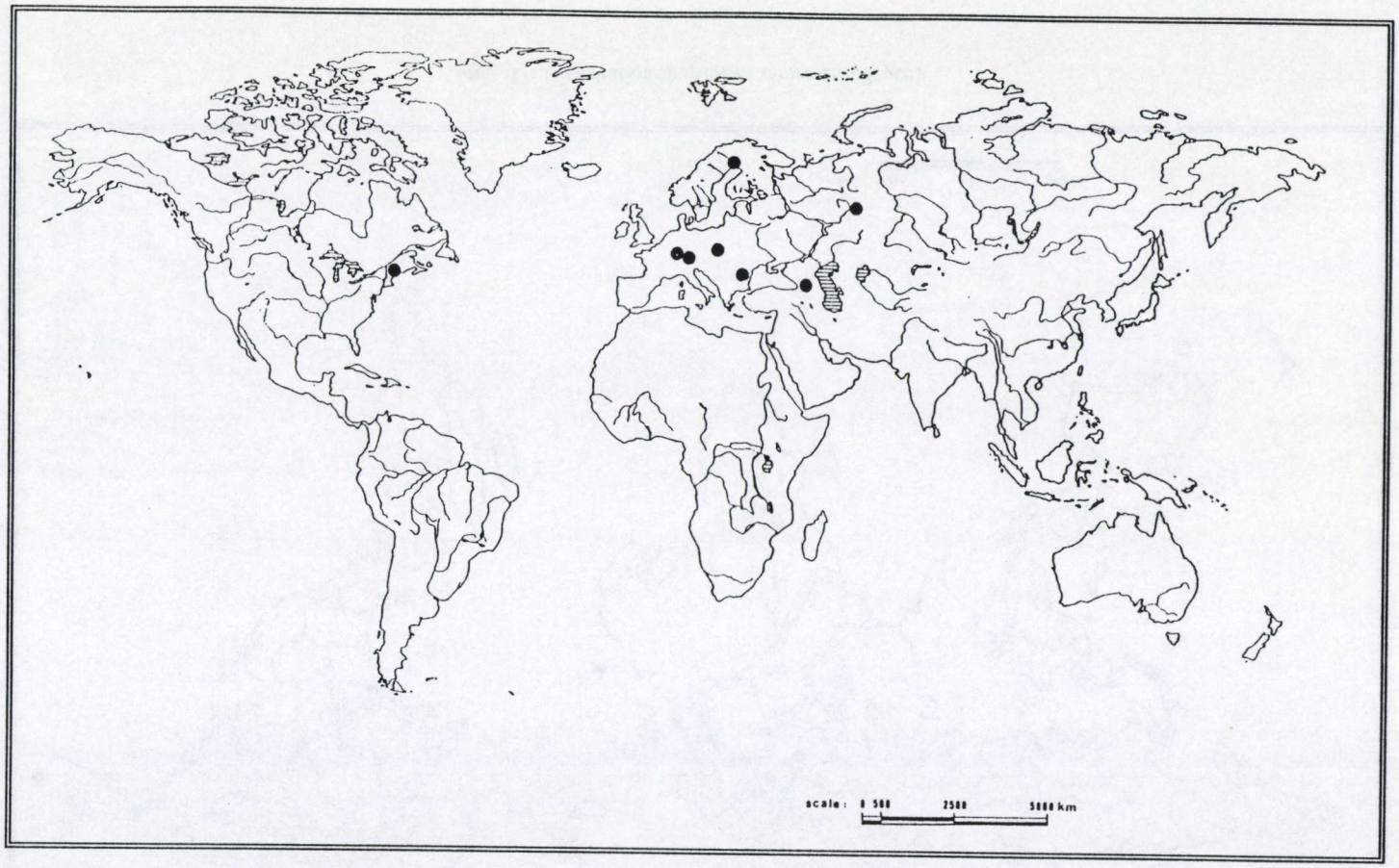
Map 35: Distribution map of *L. thienemanni* Hauer



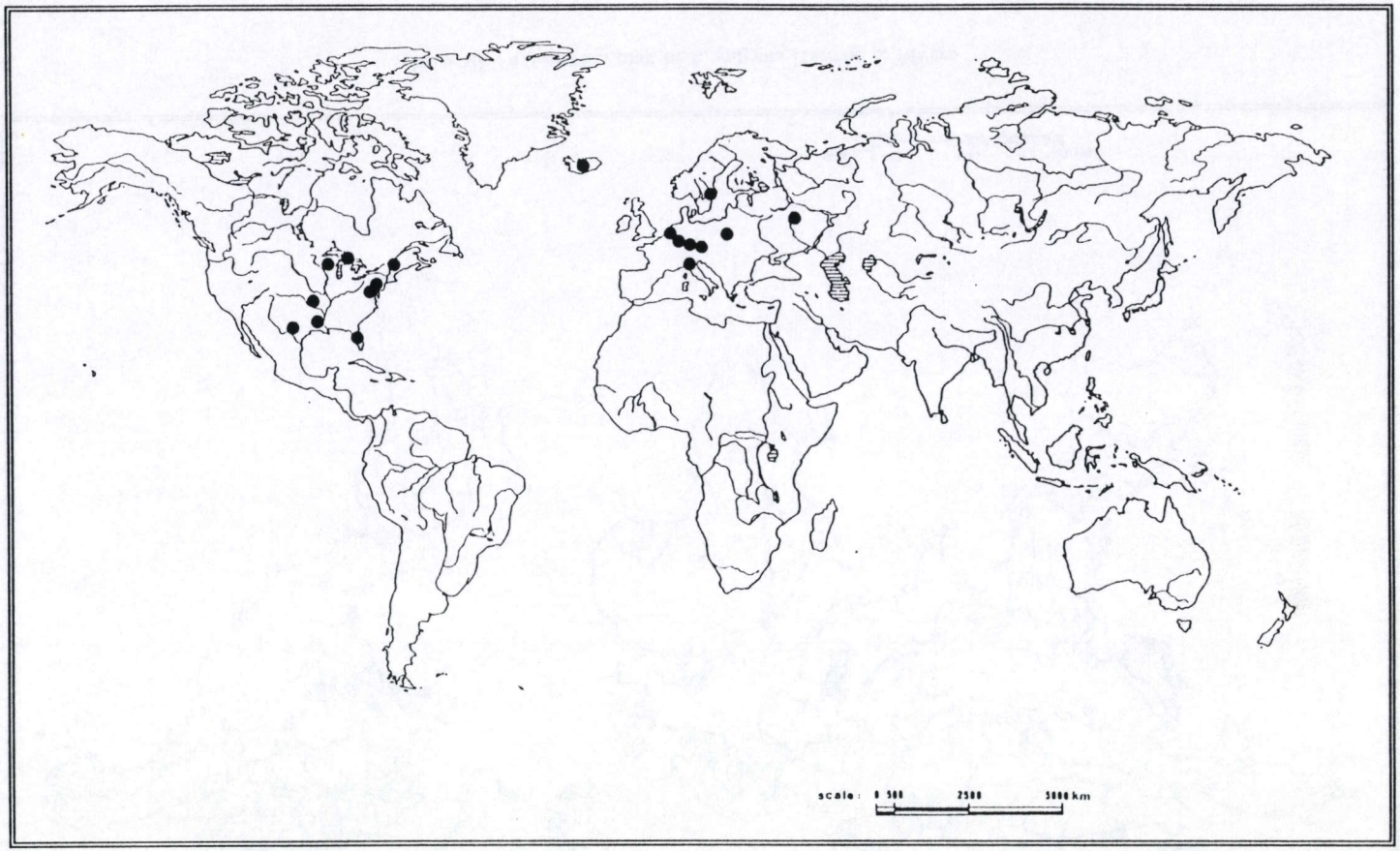
Map 36: Distribution map of *L. copeis* (Harring & Myers)



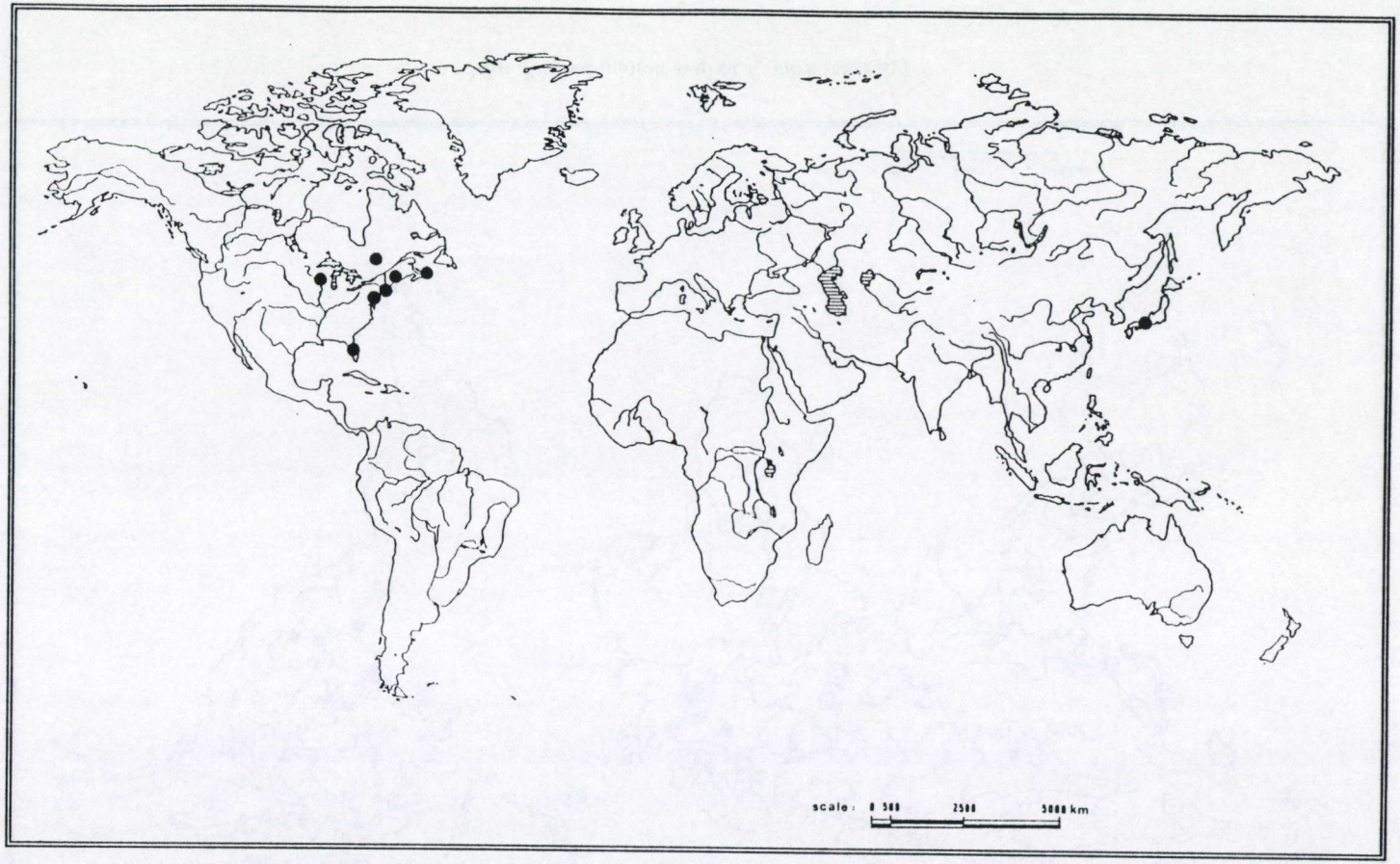
Map 37: Distribution map of *L. depressa* (Bryce)



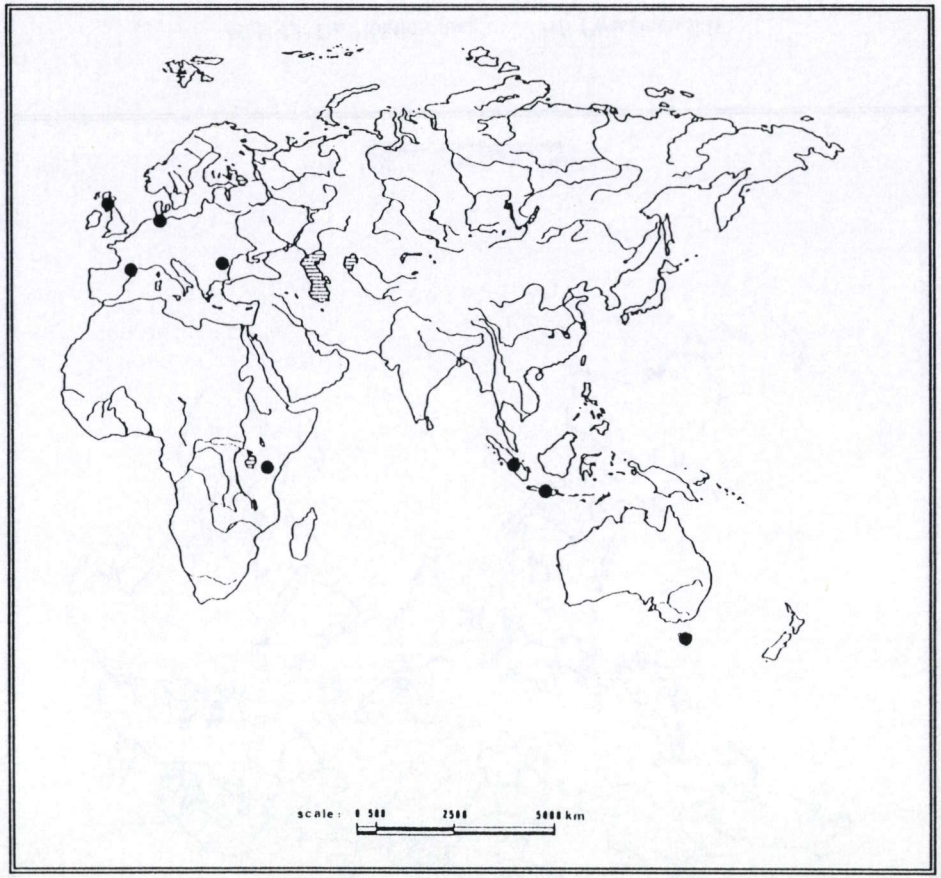
Map 38: Distribution map of *L. lauterborni* Hauer



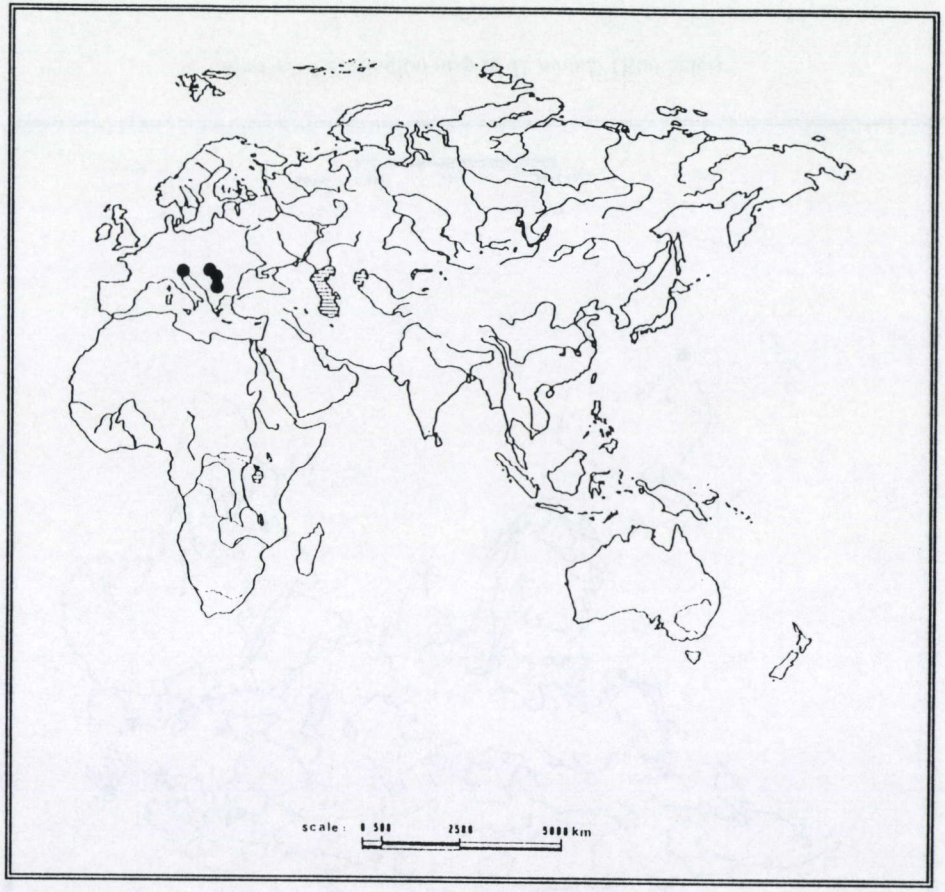
Map 39: Distribution map of *L. mira* (Murray)



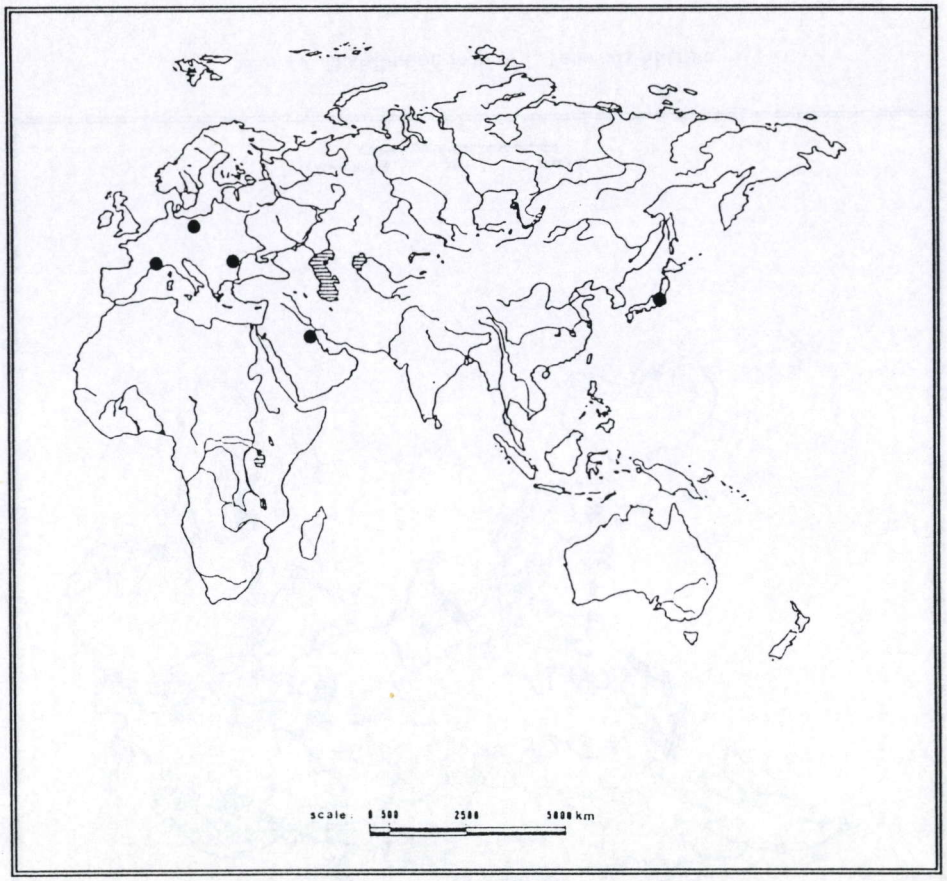
Map 40: Distribution map of *L. satyrus* Harring & Myers



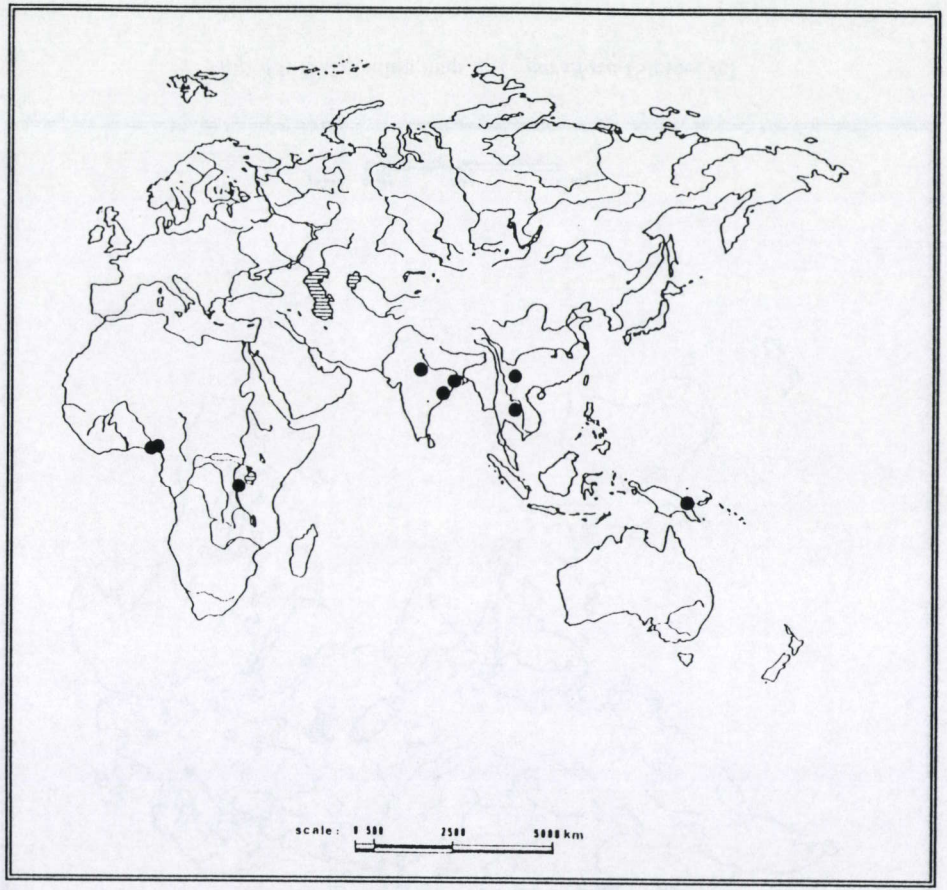
Map 41: Distribution map of *L. pumila* (Rousselet)



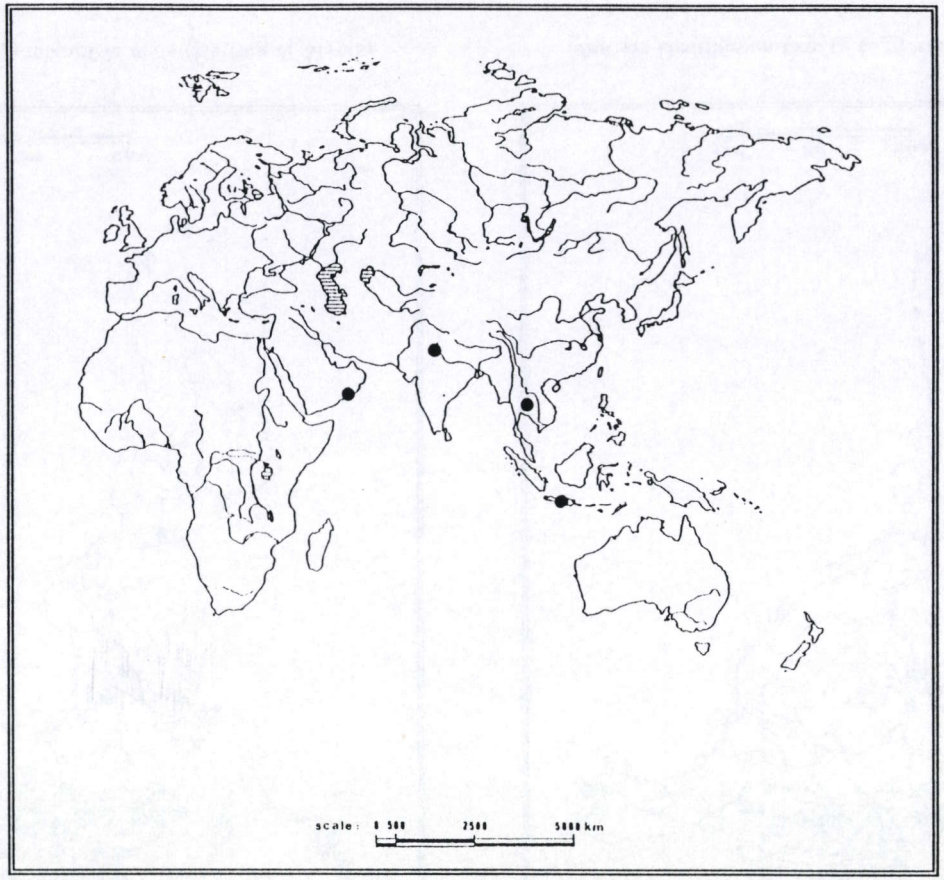
Map 42: Distribution map of *L. ivli* (Wiszniewski)



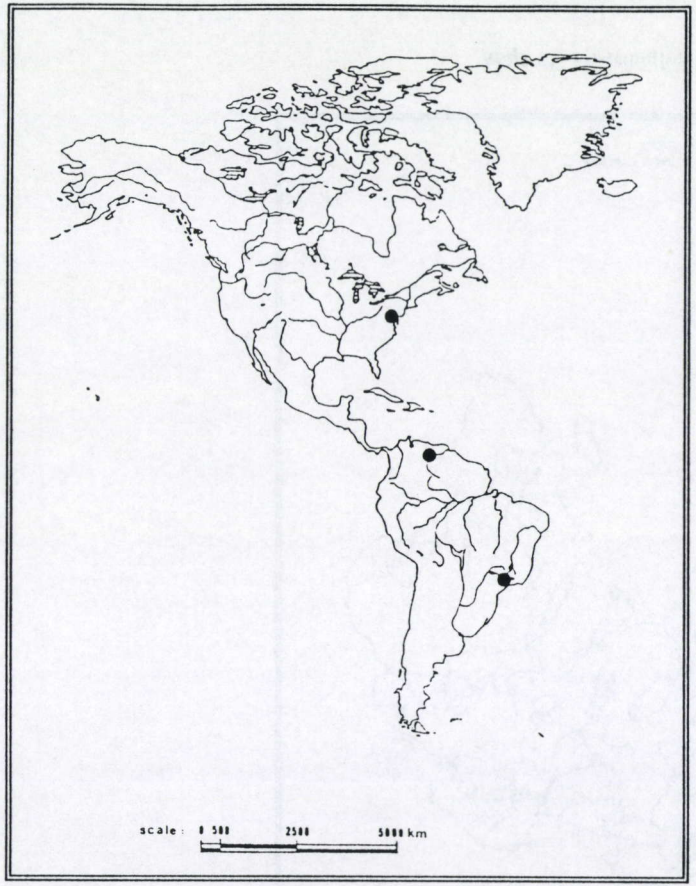
Map 43: Distribution map of *L. paradoxa* (Steinecke)



Map 44: Distribution map of *L. lateralis* Sharma

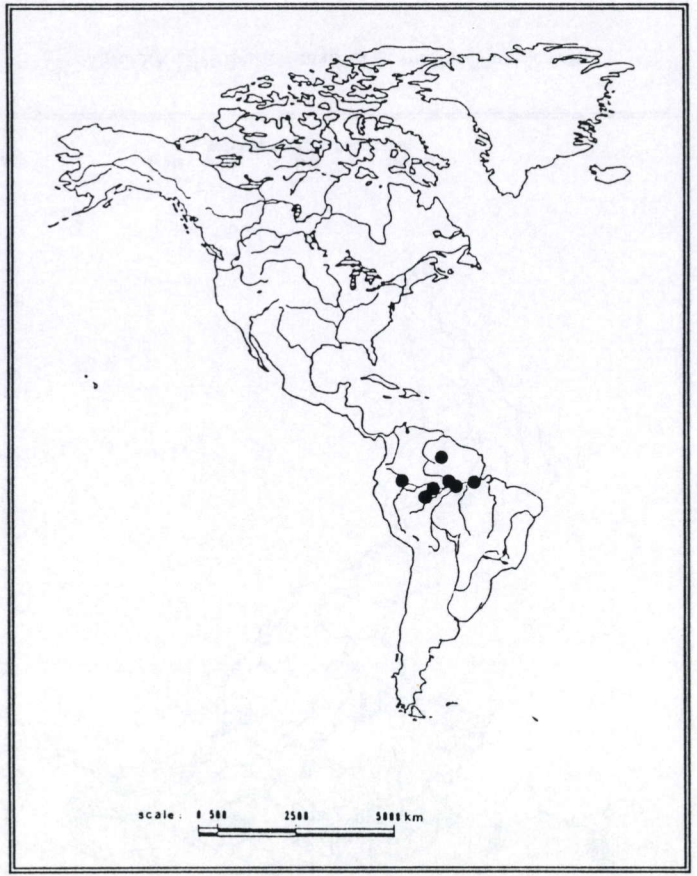


Map 45: Distribution map of *L. acanthinula* (Hauer)

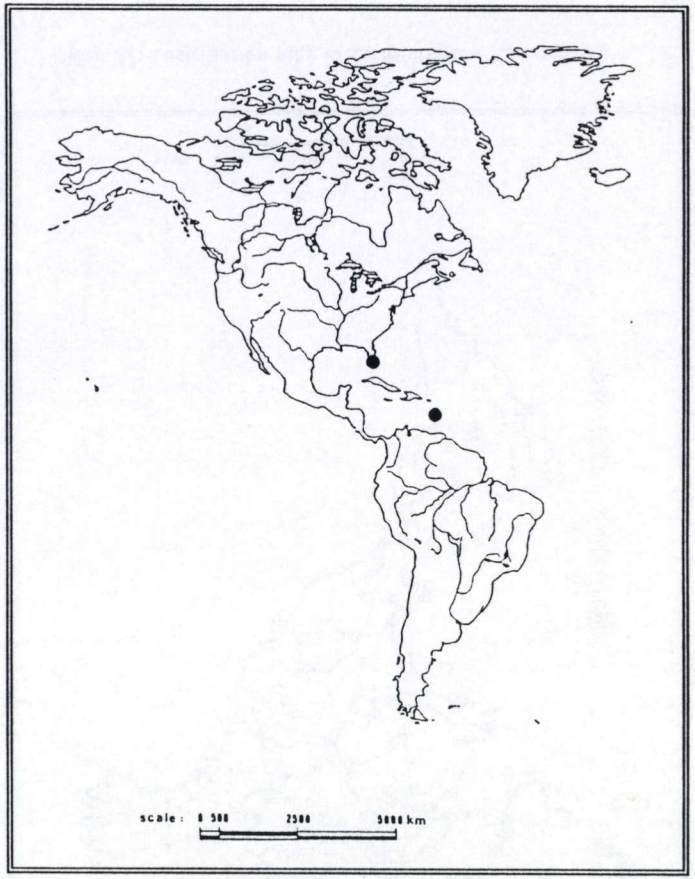


Map 46: Distribution map of *L. mitis* (Harring & Myers)

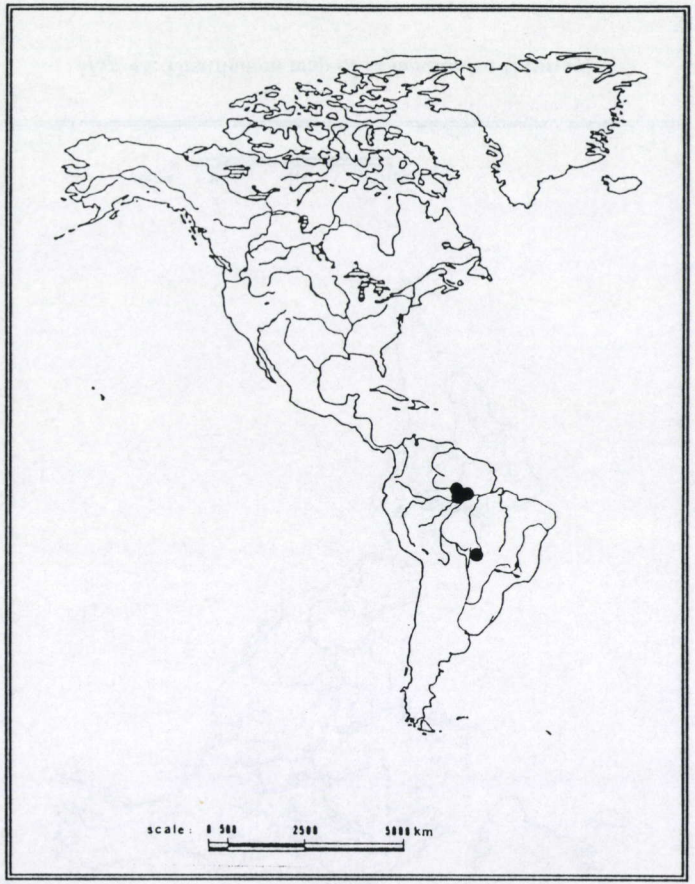
Map 47: Distribution map of *L. pyrrha* Harring & Myers



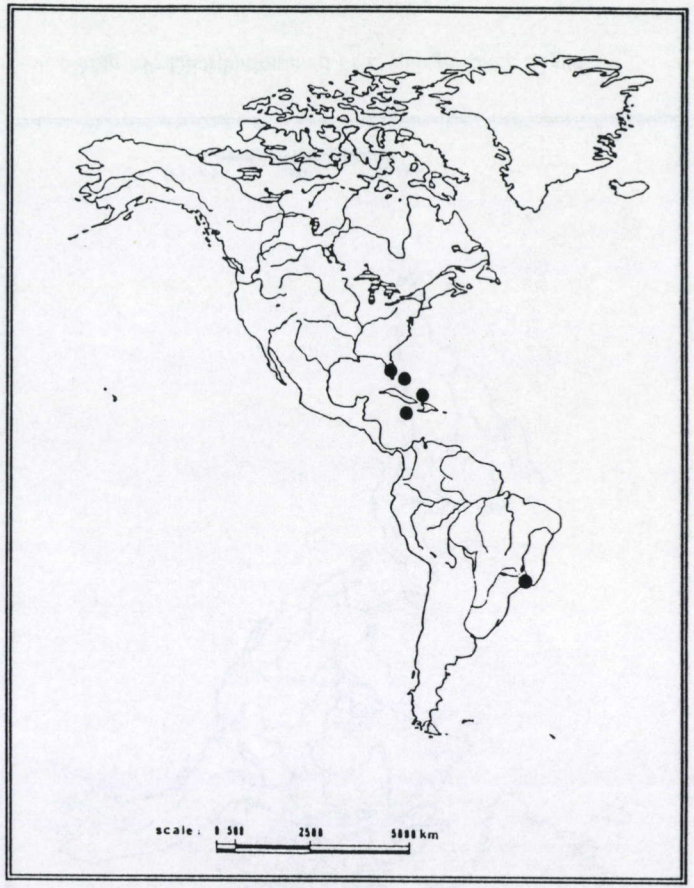
Map 48: Distribution map of *L. amazonica* (Murray)



Map 49: Distribution map of *L. margarethae* Segers



Map 50: Distribution map of *L. melini* Thomasson



Map 51: Distribution map of *L. spinulifera* Edmondson