N°47-48 1990

CYTHERISSA
THE DROSOPHILA OF PALEOLIMNOLOGY

bulletin de l'institut de géologie du bassin d'aquitaine
## ERRATA

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Le BULLETIN est une revue semestrielle qui peut être obtenue soit par échange, soit par abonnement. Sa vocation première est la publication de Travaux de Recherches réalisés au sein du Laboratoire de Géologie et Océanographie de l’Université de Bordeaux I, mais il peut être ouvert à des publications de travaux extérieurs au Laboratoire portant sur des sujets de recherches comparables. Chaque manuscrit n’est accepté qu’après avis favorable de deux rapporteurs.

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CYTHERISSA
THE DROSOPHILA OF
PALEOLIMNOLOGY

1990

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bulletin
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du bassin d’aquitaine
Je ne saurai prévoir mais
je saurai fonder. Car l'avenir, on
le bâtit.

I shall not know the outcome,
but I shall be able to lay the
foundations one builds for the
future.

A. de Saint-Exupery
Citadelle
This volume is dedicated to three outstanding ostracodologists:

N. GREKOFF, who contributed to our knowledge with regard to Mesozoic ostracods and their exciting implications for the continental paleogeography;

K. KOLLMANN, who offered new insights on the Neogene ostracods of the Paratethys, especially, on the Cytherideidae

Z.S. BRONSHTEIN, the specialist who described the extraordinary Cytherissa species of Lake Baikal.

N. GREKOFF and K. KOLLMANN demonstrated through their ostracod studies how basic research can have important applications especially in the oil exploration. The work of Z.S. BRONSHTEIN stimulates now a new generation of ostracodologists to continue the exploration of Lake Baikal in order to study its remarkable fauna.
CYTHERISSA (OSTRACODA) - THE DROSOPHILA OF PALEOLIMNOLOGY

CYTHERISSA (OSTRACODA) - LA DROSOPHILE DE LA PALEOLIMNOLOGY

(Scientific results of a multidisciplinary project on recent and fossil Ostracoda)

D. L. DANIELOPOL - P. CARBONEL - J.P. COLIN (Editors)

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The volume presents a collection of papers dealing with *Cytherissa lacustris* (Ostracoda, Cyprideidae) and related taxa, completed between 1983 and 1989. Two topics are especially explored:

1- the evolutionary pathways of the *Cytherissa* species and the causes which determined partly or fully the extinction of some of them;

2- how extensive can we the informations provided by the carapace morphology of *Cytherissa* for the reconstruction of paleoenvironments.

In the case one understands the external causes which produced the extinction of some *Cytherissa* species one could use these taxa as indicators of environmental deterioration.

The various contributions can be grouped within three main headings:

a) morphology and phylogeny,

b) historical biogeography,

c) ecology and paleoecology.

A supplementary section deals with the auxiliary products of the "Cytherissa project" i.e. with the description of sampling and laboratory devices as well as with methods of to processing samples.

Each paper has its own autonomy but in some way it contains connections to the other papers and reflects like in a "holographic" picture the general topics mentioned above. The volume will be of interest to those dealing with non-marine facies and biota either directly specialized on ostracod studies or on related fields of research like sedimentology, ecostratigraphy, paleoclimatology and where the Ostracods are just a research tool.

The scientific results presented here under the general title The "Cytherissa Project" are in fact the product of various students involved in several projects which ran independently since 1983. It is through a permanent cooperation and scientific communication of these students coming from Austria, France and F.R.G. that the various projects can be presented within one framework that we called also metaphorically "Cytherissa the Drosophila of Limnology". A synthesis of the various papers is presented at the end of the volume which should evaluate the meaning of the data, their practical applications and the feasibility for further developments.

At the end of this preface, we wish to acknowledge the Foundation for the Advancement of Sciences: "Fonds zur Förderung der wissenschaftlichen Forschung" to the core project, i.e. "The selective extinction of *Cytherissa lacustris* in Mondsee" (project no. 5614), as well as the financial support offered by the Ministries of Science and Foreign Affairs of Austria and France which enabled several students (D.L.Danielopol, W.Geiger, M.Tölderer-Farmer, C.Lété, M.N.Terrat) to travel and work in Mondsee and Bordeaux, respectively.

We are much indebted to our colleagues who helped to prepare this volume: Prof.J.W. Neale (Univ.of Hull), R. Coley (London), Mrs.D. Morel (Pessac) reviewed some of our papers; Mrs.A-M .Henning and Mrs. Gradl in Mondsee and Mrs.E .Dufour and Mrs F. Vinçon in Talence typed and edited most of our manuscripts; Dr. O. Bouchta (M.S.H.A. Pessac) helped with the computer programs. Miss M.H. Caralp, Chief-Redactor of the *Bulletin de l'I.G.B.A.*, is thanked for the permanent support during the production of this volume.
Préface

Ce volume contient une série d’articles élaborés à partir de recherches effectuées entre 1983 et 1989 sur *Cytherissa lacustris* (Ostracoda, Cyprideidae) et les taxons proches. Deux thèmes ont été abordés:

1- les modalités évolutives des espèces de *Cytherissa* et les causes responsables totalement ou en partie de l’extinction de celles-ci;
2- jusqu’où on peut utiliser les informations données par la morphologie de la carapace de *Cytherissa* pour la reconstitution des paléoenvironnements.

Dans le premier cas, la compréhension des causes externes qui produisent l’extinction de plusieurs *Cytherissa* peuvent conduire à utiliser ce groupe en tant qu’indicateur de détériorations de l’environnement.

Les différentes contributions peuvent être groupées selon trois axes:

- a) Morphologie et phylogénie,
- b) Biogéographie historique
- c) Ecologie et Paléoécologie

Un chapitre complémentaire a été construit avec les "produits annexes" du "projet Cytherissa ", par exemple, la description de procédés d’échantillonnage ou de protocoles de laboratoire ou de traitement d’échantillons.

Chaque article a son originalité propre, mais se trouve toujours en connexion avec d’autres articles de manière à donner une image "holographique" du thème général défini précédemment. Ce volume intéressera aussi bien les thématiques concernées par les problèmes d’environnement et de faune non-marine que celles plus spécialisées sur les ostracodes ou encore, celles reliées à des domaines de recherche comme la sédimentologie, l’érostratigraphie la paléoclimatologie et d’une manière générale à tous les domaines où peuvent intervenir les ostracodes.

Les résultats scientifiques présentés ici sous le titre général "le projet Cytherissa " sont en fait ceux obtenus par divers chercheurs et étudiants impliqués au départ dans plusieurs projets indépendants depuis 1983. C’est grâce à une coopération et des échanges scientifiques permanents entre ces chercheurs, originaires d’Autriche, de France, d’Allemagne ou d’autres pays que les résultats de ces différents projets ont pu être fédérés et rassemblés sous le titre "Cytherissa, la Drosophile de la paléolimnologie". Une synthèse de ces travaux est présentée à la fin de ce volume, synthèse qui fait une discussion sur la valeur des résultats. Leurs applications pratiques et les champs d’investigations futurs sont présentés à la fin de ce volume.

A la fin de cette préface, nous tenons à remercier la Fondation pour l’Avancement des Sciences "Fonds zur Förderung der Wissenschaftlichen Forschung" pour le soutien au projet "Extinction sélective de *Cytherissa lacustris* dans le Mondsee (projet n° 5614)", ainsi que le support financier accordé par les Ministères des Affaires Etrangères français et autrichien qui ont permis à plusieurs étudiants (D.L. Danielopol, W. Geiger, M. Farmer, C. Létée, M. N. Terrat) de séjourner et de travailler à Mondsee et à Bordeaux.

Nous n’aurions pu mener à terme l’édition de ce volume sans l’aide de nos collègues que nous remercions très sincèrement: Professeur J.W. Neale (Université de Hull), R. Coley (Londres), Madame D. Morel (Talence) ont relu la plupart des textes, Mesdames A.M. Hennings et J. Gradl à Mondsee, Mesdames E. Dufour et F. Vinçon à Talence ont effectué la frappe et la mise en page des manuscrits ; Monsieur O. Bouchta (M.S.H.A. Pessac) a grandement facilité la résolution les problèmes informatiques. Nous remercions particulièrement Mademoiselle M. Caralp, Rédacteur en Chef du Bulletin de l’I.G.B.A. pour son soutien permanent tout au long de l’élaboration de ce volume.
I - INTRODUCTION

I - INTRODUCTION
Abstract: The interest of *Cytherissa lacustris* for paleolimnology is emphasized. A historical review of the beginning of the investigations carried on in Vienna at the Limnological Institute is presented.

Résumé: L'intérêt que présente *Cytherissa lacustris* pour la paléolimnologie est mis en relief. Il est fait un rappel historique des recherches commencées à Vienne à l'Institut de Limnologie.

This volume is devoted to findings on the cytherid species *Cytherissa lacustris*. Dan Danielopol asked me to write an introduction (which he could have done in a most professional manner by himself). His reason for this request was based on the fact that by chance, in the early sixties, I realized the usefulness of this ostracod species for paleolimnology. At that time ostracods were practically neglected by paleolimnologists. - Dr.Delorme in Canada being one of the few exceptions. Anyone could have recognized the immense value of that crustacean group, as had the oil industry long ago.

It all started by coring different parts of Lake Constance (Loffler,1969). The extinction of *Cytherissa lacustris* was found to be an ideal indication of the onset of eutrophication. This was confirmed by the sudden mass appearance of certain diatoms like *Synedra acus* and *Melosira islandica helvetica*. In this context, the special properties of *Cytherissa lacustris* should be mentioned. *Cytherissa lacustris*, with the highest specific gravity among European ostracod species, is a predatory benthic ostracod. The increase of ooze caused by eutrophication therefore, becomes a limiting parameter for the existence of *Cytherissa lacustris* (Powell, 1976).

*Cytherissa lacustris* and its larval stages are also limited to cool water and rarely occur at temperatures above 18°C. Therefore in Central Europe the species is presently restricted to alpine or deep lakes which provide an appropriate climate. During the late Pleistocene, however, the species was abundant in shallow lakes of the Pannonian region, and is also indicative of that period in the Neusiedlersee. Recent investigations of the *Phragmites* belt reveal its occurrence in the lowest section of the lake sediment. In this context it is important to point out that *Cytherissa lacustris* is most likely to be the longest-lived of all European ostracod species. Although its life-span is not yet known, at least two years can be taken for granted. Thus, unlike more short-lived species, *Cytherissa lacustris* cannot avoid unfavourable seasons.

These peculiarities of *Cytherissa lacustris* have in combination contributed to evaluation of the development and the evolution of Austrian meromictic lakes which arrived at this stage during the late Pleistocene. The most significant events include the extinction of *Cytherissa lacustris* and simultaneous immigration of species of *Chaoborus*. In addition to this, and in combination with algal pigments, they allow us to define the onset of meromictic conditions and avoid any confusion with the impact of eutrophication.

*Cytherissa lacustris* has, however, one disadvantage whenever it is used as an ecological indicator. In contrast to the large variety of bisexual Baikalian species, the holarctic *Cytherissa lacustris* is parthenogenetic.
and, therefore, certainly represents different genotypes. Consequently, one of the foremost tasks in the study of *Cytherissa lacustris* is research which includes embryology, physiology, shell structure and chemistry. Though I see no pressing reason for comparing the importance of *Cytherissa lacustris* with *Drosophila*, I am optimistic that this peculiar ostracod species will contribute to the solution of palaeolimnological problems and questions in the near future.

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THE CYTHERISSA PROJECT: (PALEO)LIMNOLOGY AND (PALEO)OCEANOLOGY

LE PROJET CYTHERISSA: (PALEO)LIMNOLOGIE ET (PALEO)OCEANOLOGIE

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Key-Words: Cytherissa project, paleoenvironments, interdisciplinarity

Abstract

The interconnexion between limnologic and oceanologic problems is indicated. The interdisciplinary aspect is showed

It was only a few years ago when D. Danielopol and P. Carbonel started exchanging their views on two problems that did not seem at first to be directly connected. While the former was engaged in comprehending the causes and mechanisms responsible for the extinction of Cytherissa lacustris in the lake of Mondsee and of other species in genera, the latter was involved in the understanding of the part played by the environment on the morphology of the ostracod carapace.

The common point in both scientific goals was the environment, capable of accounting not only for the extinction of Cytherissa lacustris but also for the polymorphism of the carapaces. Biologists and paleobiologists were thus grouped together to study, experiment and quantify the fauna/environment relationship under a project which enabled them to explain and argue about a present-day phenomenon and its temporal dynamic evolution. This project came to be known in 1983 as the "Cytherissa Project".

One of the advantages of the project was to have selected as study-zone the Lake of Mondsee, north of Austria where one can find the Limnological Institute of the Austrian Academy of Sciences. In addition to the facilities offered by the Institute the Lake itself served as a life-sized laboratory that was sufficiently deep to show the superposition of water masses, to identify several physical, chemical and trophic parameters, to inventory living, dead or fossil fauna as well as to locate changes in space and time.

The "Cytherissa Projectical" attracted a great many researchers of varying disciplines and horizons and subsequently led to diversified research dealing with domains such as morphology, genetics, phylogeny, biogeography, ecology, paleoecology and statistics. The researchers involved in the project tried to understand the modes of evolution and the causes for the extinction of a certain number of species. They also tried to assess the impact of the environment on the form of the Cytherissa carapace. In fact, research went beyond the phylogenic relations of Cytherissa with other Cytherideidae were set off under the responsibility of J.P. Colin.
This volume groups and synthesizes all research work carried out since 1983 in the frame of the "Cytherissa Project". It emphasizes the interdisciplinary contribution of one group working within a particular study area. The results here presented and commented by all participants are of great common interest because they can be applied in other general situations. In fact, this work is fruitful for several reasons:

- research: results obtained on life, evolution and speciation are of great interest to the scientific community. The part played by the environment on life, survival, reconquest of species and the way carapaces translate changes in the environment can give rise to paleoenvironmental investigations. As such, the Cytherissa tests can serve as markers not only for limnic environments but also for the chemistry of water. Furthermore, the methods used can be applied in brackish as well as marine environments.

- education and training through research: this project allowed students to be acquainted with research work and to successfully complete thesis projects;

- new technologies: new technologies were put into effect and adapted to the goals set.

The success of the "Cytherissa Project" is due to the contribution of its participants, and above all to the active and tenacious part played by D. Danielopol, P. Carbonel and J.P. Colin as animators of the project and editors of the volume.

The "Cytherissa Project" is indeed a perfect example of pluridisciplinary research.
Je ne saurai prévoir mais j'aurai fonder. Car l'avenir, on le bâtit.

I shall not know the outcome, but I shall be able to lay the foundations one builds for the future.

A. de Saint-Exupéry
Citadelle
This volume is dedicated to three outstanding ostracodologists:

**N. GREKOFF**, who contributed to our knowledge with regard to Mesozoic ostracods and their exciting implications for the continental paleogeography;

**K. KOLLMANN**, who offered new insights on the Neogene ostracods of the Paratethys, especially, on the Cytherideidae

**Z.S. BRONSHTEIN**, the specialist who described the extraordinary Cytherissa species of Lake Baikal.

**N. GREKOFF** and **K. KOLLMANN** demonstrated through their ostracod studies how basic research can have important applications especially in the oil exploration. The work of **Z.S. BRONSHTEIN** stimulates now a new generation of ostracodologists to continue the exploration of Lake Baikal in order to study its remarkable fauna.
CYTHERISSA (OSTRACODA) - THE DROSOPHILA OF PALEOLIMNOLoGY

CYTHERISSA (OSTRACODA) - LA DROSOPHILE DE LA PALEOLIMNOLoGY

(Scientific results of a multidisciplinary project on recent and fossil Ostracoda)

D. L. DANIELOPOL - P. CARBONEL - J.P. COLIN (Editors)

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The volume presents a collection of papers dealing with *Cytherissa lacustris* (Ostracoda, Cyprideidae) and related taxa, completed during 1983 and 1989. Two topics are especially explored:

1-the evolutionary pathways of the *Cytherissa* species and the causes which determined partly or fully the extinction of some of them;

2-how extensive can we use the informations provided by the carapace morphology of *Cytherissa* for the reconstruction of paleoenvironments.

In the case one understands the external causes which produced the extinction of some *Cytherissa* species one could use these taxa as an indicator of environmental deterioration.

The various contributions can be grouped within three main headings:

a) morphology and phylogeny,

b) historical biogeography,

c) ecology and paleoecology.

A supplementary section deals with the auxiliary products of the "*Cytherissa* Project " i.e. with the description of sampling and laboratory devices as well as with methods to process samples.

Each paper has its own autonomy but in some way it contains connections to the others papers and reflects like in a "holographic" picture the general topics mentioned above. The volume will be of interest to those dealing with non-marine facies and biota either directly specialized on ostracod studies or on related fields of research like sedimentology, ecostratigraphy, paleoclimatology and where the Ostracoda are just a research tool.

The scientific results presented here under a general title the "*Cytherissa* Project" are in fact the product of various students involved in several projects which have been running independently since 1983. It is through a permanent cooperation and scientific communication of those students coming from Austria, France and F.R.G. that the various projects can be presented within one framework that we called also metaphorically "Cytherissa the Drosophila of Limnology". A synthesis of the various papers is presented at the end of the volume which should evaluate the meaning of the data, their practical applications and the feasibility for further developments.

At the end of this preface, we wish to acknowledge the Foundation for the Advancement of Sciences: "Der Fonds zur Förderung der wissenschaftlichen Forschung" to the core project, i.e. "The selective extinction of *Cytherissa lacustris* in Mondsee" (project n° 5614), as well as the financial support offered by the Ministries of Science and Foreign Affairs of Austria and France which enabled several students (W.Geiger, M.Tölderer-Farmer, C.Lété, M.N.Terrat) to travel and work in Mondsee and Bordeaux, respectively.

Ce volume contient une série d'articles élaborés à partir de recherches effectuées entre 1983 et 1989 sur *Cytherissa lacustris* (Ostracoda, Cyprideidae) et les taxons proches. Deux thèmes ont été plus spécialement abordés:

1- les modalités évolutives des espèces de *Cytherissa* et les causes responsables, totalement ou en partie, de l'extinction de celles-ci;

2- jusqu'à où on peut utiliser les informations données par la morphologie de la carapace de *Cytherissa* pour la reconstruction des paleoenvironnements.

Dans le premier cas, la compréhension des causes externes qui produisent l'extinction de plusieurs *Cytherissa* peuvent conduire à utiliser ce groupe en tant qu'indicateur de détériorations de l'environnement.

Les différentes contributions peuvent être groupées selon trois axes :

a) morphologie et phylogénie,

b) biogéographie historique,

c) écologie et paleocéologie.

Un chapitre complémentaire a été construit avec les "produits annexes" du "projet *Cytherissa*", par exemple, la description de procédés d'échantillonnage ou de protocoles de laboratoire ou de traitement d'échantillons.

Chaque article a son originalité propre, mais se trouve toujours en connexion avec d'autres articles de manière à donner une image "holographique" du thème général défini précédemment. Ce volume intéressera aussi bien les thématiques concernées par les problèmes d'environnement et de faune non-marine que celles plus spécialisées sur les ostracodes ou encore, celles reliées à des domaines de recherche comme la sédimento-
logie, l'écostratigraphie, la paleoclimatologie et d'une manière générale à tous les domaines où peuvent intervenir les ostracodes.

Les résultats scientifiques présentés ici sous le titre général "le projet Cytherissa" sont en fait ceux obtenus par divers chercheurs et étudiants impliqués au départ dans plusieurs projets indépendants depuis 1983. C'est grâce à une coopération et à des échanges scientifiques permanents entre ces chercheurs, originaires d'Autriche, de France, d'Allemagne ou d'autres pays que les résultats de ces différents projets ont pu être fédérés et rassemblés sous le titre "Cytherissa, la Drosophile de la paleolimnologie". Une synthèse de ces travaux est présentée à la fin de ce volume, synthèse qui ouvre une discussion sur la valeur des résultats. Leurs applications pratiques et les champs d'investigations futurs sont présentés à la fin de ce volume.

A la fin de cette préface, nous tenons à remercier la Fondation pour l'Avancement des Sciences "Der Fonds zur Förderung der wissenschaftlichen Forschung" pour le soutien au projet "Extinction sélective de Cytherissa lacustris dans le Mondsee (projet n°5614), ainsi que le support financier accordé par les Ministères des Affaires Étrangères français et autrichien qui ont permis à plusieurs étudiants (W.Geiger, M.Farmer, C.Lié, M.N.Terrat) de séjourner et de travailler à Mondsee et à Bordeaux.
I - INTRODUCTION
Cytherissa lacustris - An Introduction

Cytherissa lacustris: Introduction

by

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Key-words: Cytherissa, ostracods, ecology, paleolimnology

Mots-clés: Cytherissa, ostracodes, écologie, paléolimnologie

Abstract:

The interest of Cytherissa lacustris for paleolimnology is emphasized. A historical review of the beginning of the investigations carried on in Vienna at the Limnological Institute is presented.

Résumé:

L'intérêt que présente Cytherissa lacustris pour la paléolimnologie est mis en relief. Il est fait un rappel historique des recherches commencées à Vienne à l'Institut de Limnologie.

This volume is devoted to rich findings on the cytherid species Cytherissa lacustris. Dan Danielopol asked me to write an introduction (which he could have done in a most professional manner by himself). His reason for this request was based on the fact that by chance, in the early sixties, I realized the usefulness of this ostracod species for paleolimnology. At that time ostracods were practically neglected by paleolimnologists. - Dr. Delorme in Canada being one of the few exceptions. Anyone could have recognized the immense value of that crustacean group, as had the oil industry long ago.

It all started by coring different parts of Lake Constance (Löffler, 1969). The extinction of Cytherissa lacustris was found to be an ideal indication of the onset of eutrophication. This was confirmed by the sudden mass appearance of certain diatoms like Synedra acus and Melosira islandica helvetica. In this context, the special properties of Cytherissa lacustris should be mentioned. Cytherissa lacustris, with the highest specific gravity among European ostracod species, is a predatory benthic ostracod. The increase of ooze caused by eutrophication therefore, becomes a limiting parameter for the existence of Cytherissa lacustris (Powell, 1976).

Cytherissa lacustris and its larval stages are also limited to cool water and rarely occur at temperatures above 18°C. Therefore in Central Europe the species is presently restricted to alpine or deep lakes which provide an appropriate climate. During the late Pleistocene, however, the species was abundant in shallow lakes of the Pannonian region, and is also indicative of that period in the Neusiedlersee. Recent investigations of the Phragmites belt reveal its occurrence in the lowest section of the lake sediment. In this context it is important to point out that Cytherissa lacustris is most likely to be the longest-lived of all European ostracod species. Although its life-span is not yet known, at least two years can be taken for granted. Thus, unlike more short-lived species, Cytherissa lacustris cannot avoid unfavourable seasons.

These peculiarities of Cytherissa lacustris have in combination contributed to evaluation of the development and the evolution of Austrian meromictic lakes which arrived at this stage during the late Pleistocene. The most significant events include the extinction of Cytherissa lacustris and simultaneous immigration of species of Chaoborus. In addition to this, and in combination with algal pigments, they allow us to define the onset of meromictic conditions and avoid any confusion with the impact of eutrophication.

Cytherissa lacustris has, however, one disadvantage whenever it is used as an ecological indicator. In contrast to the large variety of bisexual Baikalian species, the holarctic Cytherissa lacustris is parthenogenetic.
and, therefore, certainly represents different genotypes. Consequently, one of the foremost tasks in the study of *Cytherissa lacustris* is research which includes embryology, physiology, shell structure and chemistry. Though I see no pressing reason for comparing the importance of *Cytherissa lacustris* with *Drosophila*, I am optimistic that this peculiar ostracod species will contribute to the solution of palaeoimnological problems and questions in the near future.

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*Ph. D. Thesis*, Univ. Vienna, 122 pp., Vienna.
THE CYTHERISSA PROJECT: (PALEO)LIMNOLOGY AND (PALEO)OCEANOLOGY

LE PROJET CYTHERISSA: (PALEO)LIMNOLOGIE ET (PALEO)OCEANOLOGIE

by

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Key-Words: Cytherissa project, paleoenvironments, interdisciplinarity
Mots-Clés: Projet Cytherissa, paleoenvironnements, interdisciplinarité

Abstract
The interconnexion between limnologic and oceanologic problems is indicated. The interdisciplinary aspect is showed.

Résumé
La connexion entre problèmes limnologiques et océanologiques est mise en évidence. L'aspect interdisciplinaire du projet Cytherissa est souligné.

It was only a few years ago when D. Danielopol and P. Carbonel started exchanging their views on two problems that did not seem at first to be directly connected. While the former was engaged in comprehending the causes and mechanisms responsible for the extinction of Cytherissa lacustris in the lake of Mondsee and of other species in genera, the latter was involved in the understanding of the part played by the environment on the morphology of the ostracod carapace.

The common point in both scientific goals was the environment, capable of accounting not only for the extinction of Cytherissa lacustris but also for the polymorphism of the carapaces. Biologists and paleobiologists were thus grouped together to study, experiment and quantify the fauna/environment relationship under a project which enabled them to explain and argue about a present-day phenomenon and its temporal dynamic evolution. This project came to be known in 1983 as the "Cytherissa Project".

One of the advantages of the project was to have selected as study-zone the Lake of Mondsee, north of Austria where one can find the Limnological Institute of the Austrian Academy of Sciences. In addition to the facilities offered by the Institute the Lake itself served as a life-sized laboratory that was sufficiently deep to show the superposition of water masses, to identify several physical, chemical and trophic parameters, to inventory living, dead or fossil fauna as well as to locate changes in space and time.

The "Cytherissa Projectical" attracted a great many researchers of varying disciplines and horizons and subsequently led to diversified research dealing with domains such as morphology, genetics, phylogeny, biogeography, ecology, paleoecology and statistics. The researchers involved in the project tried to understand the modes of evolution and the causes for the extinction of a certain number of species. They also tried to assess the impact of the environment on the form of the Cytherissa carapace. In fact, research went beyond the phylogenetic relations of Cytherissa with other Cytherideidae were set off under the responsibility of J.P. Colin.
This volume groups and synthesizes all research work carried out since 1983 in the frame of the "Cytherissa Project". It emphasizes the interdisciplinary contribution of one group working within a particular study area. The results here presented and commented by all participants are of great common interest because they can be applied in other general situations. In fact, this work is fruitful for several reasons:

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- **education and training through research**: this project allowed students to be acquainted with research work and to successfully complete thesis projects.

- **new technologies**: new technologies were put into effect and adapted to the goals set.

The success of the "Cytherissa Project" is due to the contribution of its participants, and above all to the active and tenacious part played by D. Danielopol, P. Carbonel and J.P. Colin as animators of the project and editors of the volume.

The "Cytherissa Project" is indeed a perfect example of pluridisciplinary research.
ON THE INTEREST OF THE "CYTHERISSA" PROJECT 
AND ON THE PRESENT STATE OF RESEARCHES 

L'INTERET DU PROJET "CYTHERISSA" ET L'ETAT 
ACTUEL DES RECHERCHES 

by 

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Key-Words : Cytherissa, species extinction, ostracoda, evolution, paleoecology 
Mots-Clés : Cytherissa, extinction d'espèce, ostracodes, évolution, paléoökologie 

Abstract 
An historical review of the way the "Cytherissa project" developed is presented. The initiator of the project was H. Löffler and his group in Vienna. An important part of the project was carried out at the Limnological Institute in Mondsee. The ostracodologists of the University of Bordeaux inspired and developed a part of the studies on the carapace polymorphism and carapace chemistry. Finally a group of sedimentologists from the Technical University of Munich developed an intensive programme on the stable isotopes in the carapace of Cytherissa lacustris. 

Résumé 
Nous présentons ici un historique des étapes du projet "Cytherissa". L'initiateur du projet a été H. Löffler et son groupe viennois. Une part importante du projet a été élaborée à l'Institut de Limnologie à Mondsee. Les ostracodologistes de l'Université de Bordeaux ont inspiré et développé une partie des études sur le polymorphisme des carapaces et sur la composition chimique de celles-ci. Enfin, un groupe de sédimentologistes de l'Université de Technologie de Munich ont développé un programme intensif d'analyse des isotopes stables dans les carapaces de Cytherissa lacustris. 

INTRODUCTION 
In recent years we assisted in the tremendous expansion of paleolimnology. This field of research deals with the paleoecology of limnic or nonmarine aquatic environments. Many, if not most, of its practitioners are involved in studies of Quaternary lacustrine deposits which still have close relationships to modern lakes. However, limnic facies and their biota can be recognized in pre-Quaternary deposits (beginning in the Middle Paleozoic). In this latter case it is generally more difficult to reconstruct the limnic paleoenvironments. One possibility is to use the information that one can extract from fossilized remains of organisms. Limnic Ostracoda are extremely useful for this purpose since abundant and diverse records exist (Carbonel et al. 1988). 

Cytherissa represents a group of ostracods belonging to the family Cytherideidae and is known from the Tertiary to Recent times. Species of this genus nowadays live in cold lakes, but they also occur in some Quaternary and Late-Tertiary facies. Intensive studies of Cytherissa in recent years, especially on the species Cytherissa lacustris (Sars) represented (fig. 1, A-D) by both living and fossil populations, showed us that it is possible to use this species for the reconstruction of the paleoenvironment from Quaternary to Recent
Fig. 1 - Cytherissa lacustris (Sars) from Mondsee, Recent, polymorphic valves.
A - right valve, juvenile, 7th stage, strongly ornate phenotype, displaying 7 well formed tubercles and heavy reticulation. B, C - right valves, adult female, moderately ornate phenotype, note the well developed node 7 (arrow). D - left valve, adult female, weakly ornate phenotype, note the postero-ventral node (arrow) poorly developed.

Fig. 1 - Cytherissa lacustris (Sars) du Mondsee, Récents, valves polymorphes.
times. It is our hope that some of the experience we obtained on this species can be extrapolated to other Cytherissa species or other related ostracod taxa of pre-Quaternary age. This would subsequently allow better reconstruction of other limnic paleoenvironments.

The fruit fly Drosophila became the paradigmatic animal for genetic research during this century. Many laboratories intensively investigate morphological and genetic traits, as well as ecological and biogeographical aspects, of species belonging to this group, although the principal species used is Drosophila melanogaster. Through these intensive studies various fields of genetics developed including population genetics, ecological genetics etc. By analogy, we believe that our multidisciplinary studies on Cytherissa carried out in recent years could help the development of research in paleolimnology in various directions.

In the following we present a brief historical review of the researches which led to the present volume. For the sake of convention we have divided our presentation into four sections that we call metaphorically: 1- the Vienna Center; 2 - the Mondsee crossroad; 3 - the Bordeaux connection and 4 - the Munich stop.

**THE VIENNA CENTER**

![Map of the Ager drainage basin](image)

*Fig. 2 - The Mondsee as part of the Ager drainage basin (simplified from Nagl, 1976).*

*Fig. 2 - Le Mondsee dans l'ensemble du bassin de drainage de l'Ager (d'après Nagl 1976, simplifié).*

It was Heinz Löffler from the University of Vienna who firmly demonstrated during the 60's and 70's (e.g. see his papers of 1969, 1972, 1975, 1978), through his paleolimnological research, that Cytherissa lacustris disappeared in many prealpine lakes before the onset of chronic eutrophication of the water bodies. Beside the observations on the local extinction of this species in modern times due to anthropogenic eutrophication (e.g. Löffler, 1972) this author tried to explain the earlier causes of this process, too. For instance, he suggested that the decrease of the oxygen concentration at the water sediment interface and the changes in the sediment texture (Löffler, 1975a) could create a catastrophic stress on the ostracod populations determining their gradual disappearance. Powell (1976) and Newrkla (1985), Löffler's students, investigated
experimentally *Cytherissa lacustris* in order to ascertain the magnitude of the negative impact of the oxygen and the sediment texture on the life style of this species. Powell (op.cit.) showed that *Cytherissa* cannot move in organogenic sediments and Newrkla (op.cit.) stressed the critical limits of oxygen respiration for this species. However, neither Löffler nor his students produced a comprehensive model for the extinction of *Cytherissa lacustris* because at that time there was not enough information from the prealpine lakes on the ecology of this species. If one could have such a model, it would be theoretically possible to use this ostracod species as an ecological or paleoecological indicator for specific environmental stress situations. At the beginning of the 70's Löffler founded the Limnological Institute which is affiliated with the Austrian Academy of Sciences. One of his objectives was to have the head quarters of this Institution located close to a lake area. This was achieved 1981 when the Institute moved from Vienna to Mondsee. The Salzkammergut area, in Upper Austria, is famous for its large and deep lakes, and Mondsee is one of the most beautiful and limnologically interesting lakes (see below). Another famous lake belonging to the same drainage basin (Fig. 2) is Attersee, intensively studied by Löffler's group during the 70's (review in Dudzinski et al. 1985).

**THE MONDSEE CROSSTROAD**

The transfer of the Limnological Institute head quarters from Vienna to Mondsee also required significant changes in the scientific programmes of the various research teams. Dan L. Danielopol was put in charge of the laboratory benthos studies. Fritz Schiemer and Peter Newrkla, the benthologists of Löffler's group in Vienna, did not move to Mondsee. It was decided to concentrate the activities of the Institute in Mondsee on the autecology of deep lake organisms. The present author chose as a research topic *Cytherissa lacustris*, its ecological distribution in Mondsee and the further elucidation of the gradual disappearance of this species from Mondsee. In this way we could make the benthos studies laboratory operational in a short period of time. We could use the know-how already existing in the Institute and could also contribute to a modern subject of evolutionary ecological research i.e. the selective species extinction problem. On this latter topic Raup (1986: 1529) commented: "Biological selectivity in extinction is poorly studied and little understood. This is perhaps the most crucial area for future research with rigorous
comparisons among extinction events having highest priority. A full understanding of selectivity is the most promising route to discovering the environmental stress that causes extinction. Evolutionary ecology is a modern field of research (Stearns, 1982) which studies, inter alia, how organisms developed biological adaptations which allow them to avoid extinction in environments which remain far from equilibrium for most of the time. Studying problems of selective extinction implies understanding how some of the morphological and biological characteristics of a species do not always succeed in integrating the organisms into new environments (Fowler and Mac Mahon, 1982). It also implies understanding how some aspects of the environment (e.g. the geographic area of a species) play an important role in the survival of a species or the recovery of a population after major environmental stress (Simberloff, 1985). For our evolutionary ecological project we combined within an actualistic approach, ecological and paleoecological data from Mondsee. To them we added biogeographical data, too. Figure 3 summarizes our conceptual framework.

During the first period of research we tried to get a feeling for the organism we studied i.e. we observed and described carefully the morphology of *Cytherissa lacustris* (see this volume), its movement on and within the sediment and we observed its life cycle. Paradoxically, with time, this type of work became the strongest argument for the subsequent researches and for our communication with other colleagues. Between 1982 - 1985 we mapped the distribution of *Cytherissa lacustris* in Mondsee (Danielopol et al. 1985, 1988). Students from Austria (W. Geiger) and guest students (C. Orellana-Newrka, L. Casale, C. Lété, M. Tölderer-Farmer, Y. Yin; from Costa Rica, France, Burundi, P.R. China and Brasil) participated in this intensive work. We tried to relate the presence or absence of this ostracod species to the sediment qualities. In particular the organic content and the oxygen concentration at the sediment water interface were analyzed (Danielopol et al. 1985). Parallel to this, the sediment accumulation rate in various parts of the lake was investigated (Irlweck and Danielopol 1985, Irlweck 1989). We discovered that *Cytherissa lacustris* disappeared from large areas of the deeper part of the lake durin the last 40 - 50 years. As a working hypothesis we explored the negative effect of the flocculent sediment organically enriched during the acme of the eutrophication period of the lake in the 60's and 70's (Danielopol et al. 1988). With time it became apparent that other key parameters had to be considered, namely the dissolved oxygen within the sediment and the water temperature. From the very beginning we tried to obtain a better understanding of the life cycle characteristics of the species, which is a prerequisite for any approach dealing with selective extinction. Alternative suggestions for the possible cause of extinctions were also considered. Löfler (in Carbonel et al. 1988) suggested that an ostracod fauna can be affected by the strong predation of fishes. Mbahinzireki et al. (1990) and Danielopol and Casale (1990) explored this possibility for *Cytherissa lacustris* too, and proved that this is an implausible scenario. The negative effect of high sulfide compounds and carbon dioxide were also investigated in a series of observations carried out mainly by Breda Rogulj (Univ. of Zagreb).

A strange situation developed during our intensive investigation of the Mondsee *Cytherissa lacustris*. As in human affairs, when one begins to have closer relationships with another person, ones interest in knowing more about their origin and history increases. In the same way, knowing more about the ecology of *C. lacustris*, we became involved in the reconstruction of the origin of modern *Cytherissa* species and their phylogenetic relationships with other Cytherideidae. R. Olteanu (Geological Institute in Bucharest), J-P. Colin (Esso-Rep. in Bègles), P. Carbonel (University of Bordeaux), J. Tétart (Univ. of Grenoble) and myself contributed to this subject (see this volume). It was of special interest to understand the relationships between the *Cytherissa lacustris* widely distributed in the cold waters of North and Central Europe and North America and the endemic living *Cytherissa* species from Lake Baikal and the Tertiary species from Eastern Parathetys which lived in a brackish water environment and during a much milder climate than that experienced by the palearctic *C. lacustris*.

The analysis of morphological polymorphism between *Cytherissa* species and *Cyprideis* suggested that some of the biological characteristics of *Cytherissa* could be similar to those of other Cyprideidae and therefore some of our knowledge on *Cytherissa* could be extrapolated to other Recent and fossil Cyprideidae taxa. This is a problem that will be discussed here mainly by P. Carbonel and J-P. Colin.

During the project in Mondsee we developed new sampling devices and new techniques of subsampling fossil Ostracoda, which is further developed by Danielopol and Casale (1988), and C. Wimmer and M. Handl (1990). R. Niederreiter (Limnological Institute in Mondsee) produced several efficient sampling devices that we described in the last section of this volume.
As a satellite project we also initiated the study of *Leucocythere mirabilis*. This is an ostracod species belonging to the Limnocytheridae which behaves ecologically very similarly to *Cytherissa lacustris*. Danielopol, Martens and Casale (1990) produced a monograph of this group dealing with systematics, evolutionary morphology, biogeography and ecology.

One could ask what makes Mondsee so attractive for ecological studies? We consider this lake a natural laboratory unique in its genre because of its habitat diversity where natural experiments can be observed in time and space. The advantage for natural experimental studies has been stressed by Diamond (1986). Mondsee is situated at 431 m and has a surface of 14.21 km², a maximal depth of 69 m, a mean depth of 6 m. The theoretical retention time is 1.7 ya and the mean discharge of 9.2 m³.s⁻¹. The lake is fed by three main streams (Achen in German) the Zeller, the Fuschler and the Wangauer and discharges into the Attersee through the Seeache (Fig. 2).

During the 60th and the 70th the Mondsee became strongly eutrophied due to massive discharges of untreated sewage waters (Findenegg, 1969; Jagsch & Megay, 1982).


In the last ten years an intensive programme for the study of lake sediments and their biota was undertaken. Five zones have been especially investigated (Fig. 4). The zones nr. 1 to 3 are situated in the northern basin which is more shallow and was stronger eutrophicated than the zones 4-5 (these latter areas belong to the central and the southern basin). The area nr. 1 was chosen as representative for a stressed zone due to the touristic activities of the Mondsee community. Zone 2 is located around the discharge pipe of the sewage treatment plant. Zone 3 contains a natural marker represented by gravel sediments deposited during the construction of the nearby highway. It also represents the deepest zone of the northern basin (see Danielopol et al., 1985; Irleweck and Danielopol, 1985 etc.). Zone 4 represents a transect directed towards the deepest place of the lake, within the central basin (Mooswinkel bay, transect MO-7). The sediments are partly unaltered by lake eutrophication and partly (the deepest zone) organically loaded. During the summer stagnation the deepest part of this area becomes anoxic. Finally, the 5th zone is located in the southern basin represented by shallow water and sandy sediments discharged by the surrounding streams. Sedimentologists and geochemists from the University of Göttingen under the supervision of Prof. J. Schneider thoroughly investigated these zones and data are presented by Horsthemke (1986), Helbig (1987) and Welzel (1988). Ecophysiological studies on the meiobenthos of zones 1 and 3 have been undertaken by Newrkla (Univ. of Vienna). The sedimentological as well as the meiobenthological studies have been financially supported by the "Austrian Forschungsfonds" (projects nr. P.5381 and P.5387). Beside this group, colleagues from the Limnological Institute in Mondsee investigated paleolimnologically different topics like the Recent and fossil diatoms (Schmidt in Klee and Schmidt 1987), the paleopigments (E.Schultze, 1985) and the Cladocera remains (Nauwerck, 1988).

The surrounding geology of the lake is remarkable (Tichy 1985, Nagl 1976). On the south-eastern side limestone cliffs dominate the lake, while on the north and north-eastern sides the flysch and the morainic material dominate. This diversity of geologic situations has an impact on the water and sediment chemistry of the various habitats and can play a role for the *Cytherissa* morphology (see Carbonel et al. (1990). It is this diversity of ecological situations of Mondsee within which one finds various morphotypes of *Cytherissa lacustris* (Fig. 1) which attracted the interest of P. Carbonel and his associated.

**THE BORDEAUX CONNECTION**

During 1982 P. Carbonel visited the benthos laboratory in Mondsee and discussed with D. Danielopol the possibility of a joint project on the polymorphism of *Cytherissa lacustris*. Peypouquet (1977) and Carbonel (1980) developed attractive models on the environmentally cued polymorphism of both brackish and marine ostracods, inter alia those of *Cyprideis torosa*, a species related to *Cytherissa*. In a series of papers (see review in Peypouquet et al. 1988) the Bordeaux group elaborated scenarios which explained the production of carapace nodations and of heavy walled and sculptured valves through the impact of the ionic composition of the water. Carbonel's idea was that it would be much easier to control the environmental parameters of the ostracod morphology in a limnic system with reduced dimensions instead of those occurring in open marine basins.
Fig. 4 - The Mondsee, general bathymetric map; 1-5 - The main areas investigated during 1983-1989 within a multidisciplinary framework.

Fig. 4 - Carte bathymétrique du Mondsee ; 1-5 : les principaux sites étudiés dans un cadre pluridisciplinaire entre 1983 et 1989.
Mondsee, with its diversity of the environmental situations and, still, a rich record of Cytherissa living and/or fossil populations was thought an ideal place of research.

In the next years the Bordeaux group (Carbonel, Tölderer-Farmer and Lété) visited Mondsee repeatedly and worked intensively (Tölderer-Farmer, 1985; Carbonel & Tölderer-Farmer, 1988 (1990). Especially interesting are their data on the chemical composition of the Cytherissa carapace which could be used as paleoecological indicator (see also this volume). One of the active discussions in the ostracodological literature is the problem of the environmentally cued nodation of the carapace (see for a review, Peypouquet et al. 1988, Reyment 1988). The data accumulated by the Bordeaux group suggest that the development of large nodes is determined by the chemical composition of the water or the sediments where Cytherissa lives. Genetical and biometrical investigations presented by T. Sywula (Univ. of Gdansk) and W. Geiger point out in this issue to a strong genetical determinism and less evidence for an environmental influence. This makes the present debate exciting and a synthesis on the state of affairs will be presented at the end of this volume. It is especially important to understand how one can use the Cytherissa nodation as paleoecological indicator for a given environmental situation.

THE MUNICH STOP

It was unexpected when Dr. U. Grafenstein (Technical University of Munich) contacted us at the beginning of 1988, in order to learn to identify Ostracoda. Grafenstein and his associates, as sedimentologists, are involved in the paleoenvironment reconstruction of several bavarian lakes. They intended to use ostracod carapaces for the indentification of oxygen and carbon stable isotopes in order to reconstruct the paleohydrology of these lakes and the surrounding paleotemperature. The Mondsee group was happy to transfer the know-how on Cytherissa lacustris, and this species appeared to be an excellent object for paleoecological studies of the bavarian group.

The advantage of Cytherissa lacustris as compared to other ostracod species is that it has thick carapace walls and one can accurately measure the stable isotopes using one or few valves for each sample.

For the Mondsee group, the Cytherissa project of the Munich group related to the oxygen and carbon isotopes is of paramount significance. First it was a confirmation that Cytherissa like Drosophila will be more and more used by various researchers. Secondly, the location of Grafenstein's group and the research area are not far away from Mondsee. Many observations from Salzkammergut in Austria can be compared to those of the bavarian prealpine lakes. Finally scientific communication functions well and both sides have mutually profited. We expect therefore that other scientific groups reading our reports will in the near future embark on Cytherissa research.

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II - MORPHOLOGY & PHYLOGENY

II - MORPHOLOGIE ET PHYLOGENIE
CARAPACE MORPHOLOGY OF CYTHERISSA LACUSTRIS (CYTHERIDEIDAE): ITS INTEREST FOR THE SYSTEMATICS AND THE PHYLOGENY OF THE GROUP

MORPHOLOGIE DE LA CARAPACE DE CYTHERISSA LACUSTRIS (CYTHERIDEIDAE): SON INTERET POUR LA SYSTEMATIQUE ET LA PHYLOGENIE DU GROUPE

by

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Mots-Cles: Ostracodes, morphologie de la carapace, systématique, phylogénie

Abstract:

Within the subfamily Cyprideinae, Cytherissa appears as an independent lineage, different from the Cyprideidini. The carapace morphology of the Cytherissini as compared to that of the Cyprideidini, displays primitive traits like those of the hinge and advanced traits like those of sieve plates.

An overview on the peculiarities of the carapace shape and structure of the ostracod Cytherideidae and Limnoocytheridae as well as on the calcification process is presented.

The basic functional morphological characteristics of the carapace are illustrated with the valves of Cladarocythere esphygmena. Brief descriptions of the carapaces and valves of Cytherissa lacustris from Mondsee, of C. sernovi and C. tuberculata from Lake Baikal, of C. bogatschovi bogatschovi, C. plana tuberculata, C. triformis tuberculata and C. laevata from the Paratethys, mainly from the Dacic Basin follow. Finally, data on Romecytheridea and Cyprideis sp. from Lake Tanganyika are presented.

Four groups of species within the genus Cytherissa are differentiated, i.e. C. lacustris, C. sernovi, C. tuberculata and C. bogatschovi. C. lacustris appears to be more closely related to C. bogatschovi group.

Résumé:

Au sein de la sous-famille Cyprideinae, Cytherissa apparaît comme une lignée indépendante, différente des Cyprideidini. La morphologie de la carapace des Cytherissini, comparée à celle des Cyprideidini, montre à la fois des caractères primitifs, comme la charnière et des caractères évolutés comme les zones de cibles.

Nous présentons une revue des particularités de la forme et de la structure de la carapace des ostracodes des familles Cytherideidae et Limnoocytheridæ ainsi que des processus de calcification.


1 - INTRODUCTION

The ostracod species now assigned to the genus *Cytherissa* Sars have heavy calcified carapaces of subtriangular or rectangular shapes (fig. 1, 2). The morphological differences among the various *Cytherissa* species are in some cases important, in others very minute. One can wonder about the origin of the morphological peculiarities of the *Cytherissa* carapace. Generally, many of the carapace traits are genetically cued and reflect the phylogeny of the group. Practically, nothing is known on this topic considering *Cytherissa*. Other traits could be ecophenotypical reactions to the environment in which the ostracods developed (Carbonel et al., 1990). An analysis of the functional morphology of the *Cytherissa* carapace will allow us to describe the complex of traits which could further help the reconstruction of the phylogenetical relationships between *Cytherissa* species. At present, there are three groups of species with quite different ecological characteristics and geographical distributions (Danielopol et al., 1990a). In the first group, we have *Cytherissa lacustris*, a parthenogenetic species, living in the Holarctic. A second group is formed by fossil and recent species living in the Eastern Paratethys and the present-day, Caspian Sea. Finally, one finds a rich endemic *Cytherissa* fauna in the Lake Baikal. These groups of species are ill-defined, and it is not clear what kind of relationships exist between them. Also, the position of the genus *Cytherissa* within the Cytherideidae is not precisely decided. Is *Cytherissa* closely related to the Cyprideidini as Kollmann (1958) and Hartmann and Puri (1974) consider or does it form an independent phylogenetical lineage within the Cytheracea as considered by Huang (1985). In the following, we shall try to see what kind of information we can extract from the carapace morphology in order to answer such questions.

The originality of some of the *Cytherissa* morphological traits can be revealed by comparing the carapace of various species of this group with those of other Cytherideidae (e.g. *Cyprideis*, *Romecytheridea* and related genera) and Limnocytheridae (e.g. *Cladarocyclythere* species).

We shall start our analysis with an overview of the carapace structure and its function. We shall take as paradigmatic example the carapace of *Cladarocyclythere esphygmena*. Further on, we shall describe briefly the peculiarities of the valves of *Cytherissa lacustris* from Mondsee, of *C. sernovi* and of *C. tuberculata* from Lake Baikal, of *C. bogatschovi*, and of *C. plana* from the Paratethys. Information regarding several other *Cytherissa* species which are interesting from the evolutionary and (paleo)ecological point of view are also presented.

2 - MATERIAL

Living and fossil material of *Cytherissa lacustris* was collected between 1983 and 1988 in Mondsee, especially at sites MO7, Mooswinkl and MO4, See (for location, see Danielopol et al., 1985). Here, we use mainly the carapaces of living specimens. One of us (D.L.D.) received from Prof. H. Löffler several specimens of *Cytherissa sernovi* and *C. tuberculata* (adults and juveniles) collected in Lake Baikal, in front of Selenga river, 20m deep (for an approximate location, see Kozhov, 1963). The material of this species is remarkable because it is represented by both males and females. Commonly *Cytherissa* species are known only through parthenogenetic forms.

*Cladarocyclythere esphygmena* is a limnic fossil species which was collected by Gorthner (Tübingen) at Steinheim am Albuch (Württemberg). This limnocytherid species was very abundant at the Phariongrube in the *G. trochiformis* layers dated as Upper Miocene (for a precise location see Bajor, 1965; Mensink, 1984). One of us (C.L.) extracted from the samples 6 to 8, collected by Gorthner more than hundred valves, adults and juveniles of *C. esphygmena*. The material used here comes from the sand pit Pharion (pers. comm.Gorthner to D.L.D.).

Two valves of *Romecytheridea* sp. from the Lake Tanganyika identified by Mondeguer (1984) as *Cytherissa* sp. were obtained from LeFèvre (Pau). The material was obtained from the Bujumbura basin at 52m deep, during the cruise 35 and it is a subfossil or recent ostracod. A specimen of "*Cyprideis*" sp. collected by Prof.H.Löffler (Vienna) near Bujumbura was also used for this study.

Material of *C. bogatschovi bogatschovi*, *C. triformis tuberculata* and *C. plana tuberculata*, adults and juveniles, from the Lower and Upper Dacian of the Dacic Basin, (Paratethys), was collected by one of us (R.O.), in cores from the Moesian Plain, around Alexandria, south of Bucharest.

Finally, one of us (R.O.) received from Vekua (Tbilissi) several specimens of *C. laevatula* from the Lower Maeotian of the Euxinic Basin in Abkhazia near Suchumi.
3 - THE OSTRACOD CARAPACE, GENERAL CONSIDERATION

Benson (1975) documented that an ostracod carapace is a homeostatic structure with redundant elements. These are produced through evolutionary changes and are genetically fixed. Other morphological traits are environmentally cued and are not genetically fixed. Within the ostracod as a whole animal, the carapace represents an important functional module. Its main role is to protect the animal limbs; it helps also to integrate the animal within the environment through the sensorial setae and pores which exist on the carapace. At a lower level of integration one discovers that the carapace, as an organized structure, is composed of several complexes of traits or submodules. One of them is the dorsal hinge, an other is the marginal zone of the valves (see for general description, van Morkhoven, 1962). There are other morphological characters of the carapace, which have not necessarily a functional role e.g. the ornamentation. However, the fine relief of the outer side of the valves or the various tuberous productions of the Cytherideidae carapaces are dependent on both organismic processes and environmental impacts. Long years of experience with various ostracod groups showed us that these traits can be used either for phylogenetical analysis, or for paleoecological reconstructions.

The carapace of an ostracod has shape and structure (1). The geometric form of the carapace changes during the post-embryonal development (see here fig. 6, 13). The internal shape of the carapace is inter alia related to the functional accommodation of the soft body and limbs. For us, the carapace, with its two valves, is a holistic structure. Stresses in one part of the framework determines reaction pathways and reajustments in the whole complex edifice (see below the Cidarocycythere esphygmena example). From an architectural point of view, the carapace of the benthic Cytherideidae and those of the Limnocytheridae (the two ostracod groups that we shall discuss here) could be compared to an arch beam (we follow Benson, 1975, 1981, for the classification of the architectural types of ostracod carapaces). In every day life we see the arch beam type realized in form of bridges. As d'Arcy Thompson (1917) showed (we used the 1961 edition, see p. 248):

"the essential function of a bridge is to stretch across a certain span, and carry a certain definite load, and this being so, the chief problem in the designing of a bridge is to provide due resistance to the bending moments which result from the load". In our case, the bridge is represented by the carapace and the load is represented by the soft body of the ostracod which hangs on the dorsal margin. Because many Cytherideidae and most of the Limnocytheridae have an elongated shape, the dorsal bending moments will be severe in the middle. One of the solution to avoid the bending in the central zone is either to reinforce it through a convex central arch, or to reinforce the peripheric cardinal zones instead of increasing the mass and the strength of the pillars. One of the famous specialists for building such type of bridges was Perronet (1708-1794) followed by many other students issued from the "Ecole des Ponts et Chaussées in Paris" (see for a historical review Heinrich, 1983). Later on we shall see that the analogue of the bridge with its loaded beams and pillars in an ostracod carapace is the hinge on the dorsal side and at the peripheric side, the calcified marginal zone. Shearing stresses in the carapace wall originate from the action of the valve adductor and limb muscles which are inserted on the inner side of the calcified lamella (fig. 2B). In order to maintain the carapace edifice intact, the valves are calcified, through the activity of epidermal cells. The external ornamentation of the ostracod reflects the activity of the various epidermal cells (Okada, 1981).

The carapace edifice of Cytherideidae or Limnocytheridae ostracods can be decomposed in several structural submodules for analytical purposes. The latter are represented by a complex of morphological traits playing a definite functional role.

We recognized the following submodules:

1 - the hinge to which one could sometimes add dorsal calcified ridges of one of the valves. The hinge complex is formed by the cardinal teeth with their sockets and the median bar and groove;
2 - the carapace external wall;
3 - the marginal zone, represented by the flange, the selvage, the inner calcified lamella. Through the integrated role of these complexes of traits the whole carapace edifice maintains its integrity of shape (i.e. it avoids to break or to deform);
4 - the carapace has also a complex of sensorial structures which help the animal to recognize its external environment. This is represented through various types of sensillae which traverse the carapace wall.

Beside these structures with definite roles, one can find a series of structures with unknown functions. These are for instance the dendritic structures which open at the surface of the carapace through pores disposed in a sieve plate and small chitineous pseudochaetae produced by the epicuticle (fig. 5E, F).

The process of calcification of a carapace follows the molting of the animal. The calcification starts from the periphery to the center of the valves. If the calcification process stops before complete calcification,

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(1) We use here these terms more or less following Benson (1982). Note that we shall not make a distinction between shape and form as did Benson (op.cit.)
especially the central part of the valves, around the muscular scars, deform (fig. 2A, 3, and other data in Danielopol, 1980).

The process of calcification for each epidermal cell consists of production of calcite crystals which are laid out within the chitineous polygonal matrix, from the periphery of the valve toward the center. Several possibilities exist:

1. Calcium carbonate is homogeneously produced within the whole cell, the external aspect of the valves wall is more or less smooth (fig. 4F);
2. Carbonates are deposited only at the periphery of the polygonal matrix, the external wall appears with pits or fossae (fig. 1, 4D, E);
3. The calcification fills in excess the periphery of the cell, the valve becomes ornated with polygonal ridges (fig. 2A).

The overdeposition of carbonates, especially at the periphery of the valves, determines an agradation state. From an undercalcification one can get valves with thin walls and large fossae. This is the case sometimes when the aquatic environment has a low Mg/Ca ratio (Fasbinder, 1912, Peyposquet, 1977, Honigstein, 1986), or/and mainly when the carbonate equilibrium at the water-sediment interface varies (Carbonel et al., 1988, Peyposquet et al., 1988). Environments which strongly fluctuate or which deviate strongly from the normal conditions in which the ostracods live produce physiological stresses. This can be expressed through a dysfunction of the normal morphogenesis of the carapace. One can find poorly calcified or deformed carapaces. Nodation in the case of many Cyprideidae could be due to such causes.

4 - THE CARAPACE OF CLADAROCYTHERE ESPHYGMENA

The morphology of this species represents a paradigmatic example for the ideas here expressed. Figure 3 presents the valves of females, males and juveniles of this species. The material here used for this Limnocytheridae species with very thin valves belongs to animals which lived in a shallow lake where the water had low Ca/Mg concentration (Bajor, 1965). The shape of the valves for both females and juveniles (fig. 3A, B, D) especially the right valves are dorsally deflected. The latero-ventral margin is externally plicated and forms a ventral concavity in the central part. The valves of the males (fig. 3F, G, R, S) are less subject to these deformations. They follow the general model of a typical limnocytherid carapace shape (e.g. Limnocythere sancti-patricii in Danielopol et al., 1989) i.e. the dorsal margin is straight. The dorso-anterior side of the valves has laterally two grooves which correspond to the muscular area (fig. 3A, D, M, S). The movement of the limbs produces a very strong pressure on the carapace wall (e.g. the apical point of the mandibular gnathobasis can erode the inner side of the calcified wall through its movement during the feeding activity (fig. 3J).

The hinge structure of Cladarocythere esphygmena is represented by cardinal teeth on the right valve with general cusps which fit in shallow sockets (fig. 3 I-O) of the left valve. The latter presents a strongly crenulate bar; especially the extremities of the bar have larger teeth (fig. 3 K, L). The females and juveniles which have a deflected dorsal margin (fig. 3 O, P) have as a compensatory structure on the right valve a dorsal ridge which is better developed at the peripheral sides than in the middle of the stretch (fig. 3 A, B, M, N, O). This type of functional solution recalls the static engineering solution of the Peronet's bridges, exposed above. The male's valves which have a straight dorsal margin do not develop a ridge on the right valve (fig. 3 E, R). Therefore we consider that through an insufficient calcification and heavy load from the soft body and strong strain, the valves did deform not only on the dorsal side but reajusted also on the ventral side (fig. 3 A-D). Well-calcified valves like those from fig. 3 G do not show such deformations.

The ornamentation of the carapace (fig. 3 A-P) represents a reticulation with thin ridges which reflect the pattern of the epidermal cells (see fig. 3 S for the internal side). Fig. 3 M-S show the well-developed inner calcified lamella which reinforce the peripheral zone of the valves and prevents further deformations. In the box-frame class of valves (Benson, 1975; 1981), the outer ridges of the carapace ornamentation represent abutments which can help the maintenance of the geometric shape of the valve without an increase in the thickness of the wall. In the present case the, thin reticulation does not apparently play any functional role.
5 - CYTHERISSA LACUSTRIS

5 - 1. Shape and size (fig. 1, 2, 4, 6, 7)

Left and right valve have the same general shape (e.g. fig. 6 A, B), valves elongated, anterior third larger than the posterior one. Maximal height at the anterior cardinal corner representing 2/3 of the total length. The ventral side slightly concave. Size for the Mondsee population, adult female, between 880-960 μm. Local differences in size length exist between the deme in Mondsee or between different lakes (See Sywula and Geiger, 1990).

5 - 2. Carapace structure (fig. 2 B, 4 A, B, 5 A-D)

Hinge merodont with cardinal teeth on the right valve: the latter are elongated; the anterior one slightly crenulated, the posterior, smooth. Cardinal sockets are elongated and opened. Figures 5 A,B show a strange bar X which closes the socket. A unique specimen displayed this structure which should lock the opposite tooth in the socket of the left valve. The intercardinal bar is more strongly developed at the extremities; this is reflected also on the right valve in the central groove. It follows the engineering solutions used in the bridge constructions discussed above.

The marginal zone (fig. 2 B, 4 A, B): on the right valve, the selvage and the flange, slightly developed, run together. The fused zone is small. The free inner calcified lamella is minimally developed. The left valve (fig. 4 A) with the fused zone, slightly bent, in which fits the selvage of the right valve. The selvage on the ventral side slightly departs from the flange. The calcified lamella is thick. On the inner side the muscular scars and the pores position are well visible (fig. 2 B). This position can be easily mapped on the inner side (Carbonel unpubl.). The external surface of the valves is variable (fig. 2 A, C-E). One can recognize well-calcified valves with a peripheral agradation forming a reticulate pattern within which are foveolae. In other morphs belonging to the same Mondsee population, the valves are completely smooth (fig. 4 F). In less well calcified valves, the fossae are larger deeper and a dorso-lateral sulcus becomes visible (fig. 2 A). A variable nodation is visible (fig. 2 A, 4 C-E). Seven nodes are present in some cases. They are here numbered (fig. 2 A) in an arbitrary way. The node nr.7 is equivalent in position to those of Cyprideis torosa of Sandberg (1964). This is the most frequent and well developed node for this species. It is better developed on the right valve (see also Carbonel et al., 1990 and Sywula and Geiger, 1990). On the surface of the carapace, at the living specimens, one sees minute chitineous pseudochaetae (fig. 5 E, F). The marginal pore canals are simple, straight, short and reduced in number (10-12) on the anterior side. Normal setae are sparsely dispensed on the valves. Around them, one finds 2-6 sieve pore areas (fig. 5 E, F). One of us (P.C.) tried to map these sieve plate areas and to calculate their surface in order to see if there are differences between individuals which live in the littoral habitats (12m deep) and those living in the deep parts (40m) of the Mondsee. No significant differences could have been found up to present.

5 - 3. Post-embryonal development

Figures 6 and 8 show the valve shapes of the juveniles from stage 4 to the adult. The general shape remains more or less the same. The adult stage of the valves recall those of the juvenile. We have here a case of paedomorphosis. Some of the individuals especially in the early stages present ventro-posteriorly, a minute denticle (fig. 6 D, J). Tubercles are visible already in the 4th stage (up to 7 tubercles), their number and size are less well expressed in the last juvenile stage (the 8th) and the adult. Well-developed pore areas are visible in the last four stages (fig. 7 A-E). Interesting enough the early stages (3-5) do not penetrate deep into the sediment. If the sieve pore areas have a respiratory function then this could explain why the small juveniles are less fit to use the deeper layers of sediments as compared to the older juvenile stages and the adult (see also Geiger, 1990b ; Danielopol et al, 1990b).
5 - 4. Carapace morphology; ecological and geographical differences

Sywula and Geiger (1990) showed significant differences in carapace size and the expression of node 7 between local populations of Mondsee and between those of Mondsee and Attersee in Upper-Austria. Carbonel et al. (1990) found ecophenotypical differences in the node 7 expression which is interpreted as a reaction to the local chemical environment. Kemle (pers. comm. to D. L. D.) found in the Eemian Interglacial deposits from Quackenbruck, south from Oldenburg, in Germany, a local population of C. lacustris having denticles on the anterior and posterior margin of the valves. We saw that the Mondsee individuals (juveniles stages) have only a posterior minute denticle.

5 - 5. Discussion

Bronshtein (1947) described two subspecies of Cytherissa lacustris, i.e. C. lacustris baikalensis and C. lacustris dubitabilis. The former is represented by amphigonic populations. The valves of the males are more elongated than those of the females. The valves of the female are widely bent in the anterior and posterior parts. C. lacustris dubitabilis belongs to the Cytherissa sernovi group, because the left valve has cardinal reinforcement plications.

6 - CYTHERISSA SERNOVI

6 - 1. Carapace shape and size (fig. 8 A-G)

Left valve larger and asymmetrical as compared to the right one in both sexes. General shape of the carapace more or less rectangular. Posterior margin slightly smaller than the anterior one. Dorsal margin with an arched plication on both valves in the central part (more strongly developed on the right valve, fig. 8 F, G). Cardinal angles reinforced with a calcareous plication. Left valve better developed on the ventral side, overlapping the right valve (fig. 8 C, D). Size in the examined specimens was between 900 and 1100 μm long. Height in both valves represents about 2/3 of the length. The right valve in the posterior part slightly more acuminated than the opposite valve (fig. 8 A, B). Valves of the male slightly more elongated than those of the female (fig. 8 A, G), which has more rectangular valves more rectangular (fig. 8 B-E). The carapace does not show a paedomorphic shape.

6 - 2. Carapace structure

Strong cardinal teeth on the right valve, both slightly crenulated. The posterior one with a convex external margin (fig. 8 H, 9 A, B); the anterior one elongated. The cardinal sockets on the left valve are large and anteriorly opened. The intercardinal bar and groove strongly developed on the anterior third; they become slender in the middle and redevelop in the posterior third. The functional solution for strengthening the dorsal margin recalls the two solutions of the bridge constructions, i.e. lateral reinforcement, this is visible in the hinge elements and the cardinal plication, and a central convex arch, i.e. the dorso-central plication. Marginal zone represented by a well-marked demarcation between selvage on the ventral side (fig. 8 F, G). The fused zone is narrow, without visible vestibulum. Sparse setae cover surface of the valves; the sieve plates around the setae are very large (fig. 8 A-C, 9 C, D) as compared to those of C. lacustris (fig. 5 E, F) and Cytherissa plana tuberculata (fig. 12 I). Carapace ornamentation with minute foveolae; an aggregation of the valves visible on the peripheral zone (fig. 8 C). The pseudochaetae, very long, resembling to a seta, are visible on the sieve plates (fig. 9 C, D). No nodes have been observed on the specimens dissected, and because of the very strong calcification, no sulcus forms in the adductor muscle area.

6 - 3. Discussion

The following species described by Bronshtein (1947) appear closely related to C. sernovi, Cytherissa lacustris dubitabilis, C. sernovi ornata, C. elongata, C. paralella, C. truncata, C. interposita, C. sinistrodentata and C. cytheriformis. The latter two species have a reverse hinge. Some of the species like C. sinistrodentata and C. elongata have an unique tubercle on the ventro-posterior part of the valves. This
Carapace morphology of *Cytherissa*

position is much lower than the position of node 7 of *C. lacustris*, but resembles those of *Cyprideis* sp. from Lake Tanganyika (fig. 15 D)

### 7 - CYTHERISSA TUBERCULATA

7 - 1. Carapace shape and size (fig.10A-D,F,G)

Valves with a very high asymmetry between the anterior and the posterior side. Maximum height at the anterior cardinal angle represents about 3/4 of the length. Dorsal margin straight without convex plication. Size, 950 to 1100 μm long; slight dimorphism between the male and the female valves. It seems that the male has a more elongated valve contrary to Bronshtein's data (1947). The shape of the adult resembles that of the juvenile (fig. 10 A, B, C,D,F) pointing out to the strong paedomorphic state of the carapace.

7 - 2. Carapace structure (fig.10 E, 11 D, E)

The hinge strongly developed. The right valve has large cardinal teeth of rounded shape, slightly crenulated. The anterior one is stronger than the posterior tooth. The intercardinal bar and groove are much similar to those described for the previous species, but appear better developed. Small reinforcement plications exist above the cardinal sockets of the left valve. These are less developed than in the *C. sernovi* group. The marginal zone has a well developed outer margin on the left valve which does not run parallel to the selvage on the ventral side (fig. 10 B). Sieve pores placed in large fossae seems, to be of moderate size (fig. 11 A, B). The ornamentation represented by large fossae (fig. 10 A, C, 11 C). Only five large tubercles are visible (fig. 10). The largest one is the ventral node, situated in the central third of the valve. It has an elongated shape. This position and the shape differ from those of node 7 in *C. lacustris* and of the postero-ventral node of *C. sernovi*. The dorso-posterior and dorso-anterior nodes are very large and round-shaped (fig. 11 C). The pseudochaetae are slender and short (fig. 11 A, B).

7 - 3. Discussion

Several species described by Bronshtein (1947) resemble *C. tuberculata*. These are: *C. pterygota*, *C. mirabilis*, *C. triangularis* and *C. lata*.

The size of those species varies between 900 to 1500 μm long. The variability of the length of *C. tuberculata* mentioned by Bronshtein (1947) is surprisingly high.

### 8 - CYTHERISSA PLANA TUBERCULATA

Olteanu (1990) described this subspecies from the Upper Dacian of the Eastern Paratethys in the Dacian Basin. Here, we add some comments in order to better compare the Paratethyan taxa with the other *Cytherissa* species.

8 - 1. Carapace shape and size.

Right and left valves with a slight asymmetry. The adult carapace shows a paedomorphic shape (fig. 12 E, F). There is a sexual dimorphism between what we consider to be a male valve (fig. 12 E) and a female one (fig. 12 F). The former is more elongated, the latter is more roundly shaped in its posterior part. The length of the adult valves varies between 600 and 800 μm.
8 - 2. Carapace structure

The hinge is represented by thin lamellar cardinal teeth on the right valve, in some cases slightly crenulated (fig. 12 G, H, 14 F- H). The intercardinal hinge groove is narrow, uniformly developed. No reinforcement of the cardinal zone of the dorsal margin is visible. The marginal zone is narrow, the selvage and the flange on the right valve are separated by a groove; however they run more or less parallel as compared to C. sernovi and C. tuberculata. An anterior well-developed vestibulum is visible in some of the specimens of this subspecies. The number of anterior marginal pore canals is reduced (9-11).

The outer lamella is thin. Most of the surface smooth. There are few fossae in which are located minute sieve plates (fig. 12 D). Only one posterior node is developed; which can have a variable expression.

9 - CYTHERISSA BOGATSCHOVI BOGATSCHOVI

9 - 1. Carapace shape and size (fig.13)

The valves are elongated. The anterior margin is only moderately higher as compared to the posterior one. The carapace displays a paedomorphic shape. The dorsal margin does not display plicate (reinforcement) structures.

9 - 2. Carapace structure

The hinge with the anterior cardinal tooth of the right valve is well crenulated and lamellar shaped. The posterior one is slightly bent and crenulated. The intercardinal groove is well and uniformly developed on the whole length. The left valve (fig. 13 E-G) has a lamellar intercardinal bar which is not reinforced at its extremities. An elongated socket is visible anteriorly, and a shorter and largely bent one posteriorly. The marginal zone has no visible vestibulum on the left valve (fig. 13 E). The right valve has well-developed selvage which does not follow the flange on the ventral side. The sieve plates minute, their number is reduced as compared to those of C. lacustris. The ornamentation of the valves is represented by well-developed tubercles (more than one).

The juveniles present up to seven nodes. The shape of those tubercles is different from those of C. lacustris. When well-developed, they are more robust and divided in 2-3 apical cusps. The fossae variously are large. A reticulation develops in some of the well-calcified carapaces.

9 - 3. Post-embryonal development

The post-embryonal development is here presented from the third stage to the adult. One notes that already in the early stages, all the nodes (7) occur. Then, strength and size decrease at the later juvenile stages. C. bogatschovi bogatschovi with well nodated morphotypes occurs mainly in the mesohaline water having more than 8-10%, while C. plana tuberculata with smooth valves occurs in the Dacian basin in a paleoenvironment with about 6% salinity.

10 - COMPARATIVE DATA ON CYTHERISSA TRIFORMIS TUBERCULATA (fig.14 B) AND C. LAEVATULA (fig.14 I-M)

10 - 1. Description

A description of the former subspecies is presented in Olteanu (1990). The main difference as compared to C. triformis triformis is the presence of a posterior node. The valves have a higher density of fossae as compared to C. plana tuberculata. Cytherissa laevatula has no nodes, the valves are reticulated. The cardinal teeth of the right valve are very elongated and thin. The intercardinal groove
uniformely thin too (fig. 14 K). *C. triformis tuberculata* has a much smaller size (500-600 μm long) as compared to the nominate subspecies which is 800 μm long.

The number of the marginal pore canals increases from the Upper Pontian to the Upper Dacian (from 11 to 15).

Compared to the variability of *Cytherissa lacustris*, in respect to the nodation and reticulation one should as alternative hypothesis, consider the possibility of a morphological plasticity of the ornamentation of the valves, in respect to the strong environmental fluctuation (especially of the salinity changes to which these ostracods were submitted in the Paratethys).

10 - 2. Discussion

The following species can be included in the *Cytherissa bogatschovi* group: *C. bogatschovi, C. plana, C. triformis, C. laevatula, C. naphtatscholana, C. duabica*.

11 - COMPARATIVE DATA BETWEEN CYTHERISSINI AND CYPRIDEIDINI

Figures 15 A, B represent the so-called *Cytherissa* sp. identified by Mondeguer (1984). The hinge and the general shape of the carapace are characteristic for the Cyprideidini. We place this taxon in the *Romecytheridea* Wouters. As compared to the Cytherissini, the Cyprideidini have more complex hinges (fig. 15 A, C) but less developed sieve pores. There are parallel evolutionary trends in the developement of the ornamentation, both with regards the production of the reticulation and the nodation. A dorsal plication, arch-shaped, develops in the central area of the valves where the intercardinal stretch of the hinge is the least developed (fig. 15 C). These data suggest that *Cytherissa* belongs to a different phylogenetical lineage one can call the tribe Cytherissini Huang, *Cyprideis* and *Romecytheridea* belong to the Cyprideidini Kollmann.

12 - CONCLUSIONS

1 - A review of the main morphological traits of the carapace of the Cytherideidae and Limnocytheridae show that the complex traits of the valves, especially the hinge and the dorsal margin offer important taxonomical criteria to identify several groups of species: *Cytherissa lacustris, C. sernovi, C. tuberculata* and *C. bogatschovi*.

2 - The *Cytherissa lacustris* group is characterized by the paedomorphic shape of the valves, by thin lamellar teeth and moderately high anterior side. A strong ornamentation and nodation variability is visible.

3 - The *Cytherissa sernovi* group has species with no paedomorphic valves besides those taxa which are paedomorphic. Carapaces are strongly calcified, with a reduced nodation and no visible variability of the reticulation. The dorsal margin has reinforcement plications above the cardinal sockets of the left valve. A central convex plication exists on both valves. The cardinal teeth are strongly developed, more elongated. The sieve-pores are very large and the pseudochaetae very long.

4 - The *Cytherissa tuberculata* group has marked paedomorphic carapaces. The anterior part is very high compared to the posterior part. The hinge has a strong tooth on the anterior side and a moderately developed one located posteriorly. No convex plication exists on the dorsal margin. Slight reinforcements above the cardinal sockets of the left valve exist. The nodation type is different from that occurring in the previous species groups i.e. there are only 5 nodes, the ventral one being very elongated. The ornamentation is very strong, with deep fossae. The pseudochaetae are small.

5 - The *Cytherissa bogatschovi* group has polymorphic species. The paedomorphic shape of the adult carapace is less well expressed. The cardinal teeth are slender elongated and crenulated. The intercardinal bar and groove uniformly large on the whole stretch. A sexual dimorphism is visible on the adult valves: the male has more elongated valves than the female. The sieve plates ( pores) are very small. An anterior vestibulum is visible especially on the left valve.

6 - One can see closer relationships between *Cytherissa lacustris* and *C. bogatschovi* and no related affinities with *C. sernovi* and *C. tuberculata*. 
7 - As compared to the two Cyprideidae species of the lake Tanganyika i.e. *Romecytheridea* sp. (initially identified as *Cytherissa* sp.) and *Cyprideis* sp., the *Cytherissa* valves has a primitive hinge and a better developed sieve pore area. The presence of pseudochaetae on the *Cytherissa* valves is a peculiarity of this group. No Cytherideidae group has such structures. We consider *Cytherissa* and *Cyprideis* as members of two phylogenetical lineages, the Cytherissini and the Cyprideidini (see also Danielopol and Tetart, 1990).

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**Fig. 1** *Cytherissa lacustris*, adult female, left valve, Recent (Mondsee, site MO-4 See)

*Fig. 1:* *Cytherissa lacustris*, femelle adulte, valve gauche, Récent (Mondsee, site MO-4 See)
Fig. 2: *Cytherissa lacustris*, adult female, right valve, Recent (Mundsee, site MO-4 See)

A: External and internal sides / Côtes intérieure et extérieure.
Fig. 3: **Cladarocythere esphygmena**, Upper Miocene (Steinheim am Albuch, Phariongrube, *G. trochoïdīs* layers), adult and juvenile valves.

**Fig. 3**: **Cladarocythere esphygmena**, Miocène supérieur (Steinheim am Albuch, Phariongrube, niveau à *G. trochoïdīs*), valves adultes et juveniles.


J: Central area (detail from I) / Zone centrale (détail de I) - L: Hinge (details from I) / Charnière (détails de I) - P: Hinge (details from O) / Charnière (détails de O)
Fig. 4: *Cytherissa lacustris*, adult female, Recent (Monsee, Site MO-7, Mooswinkl)

Fig. 4: *Cytherissa lacustris*, femelle adulte, Récent (Monsee, Site MO-7, Mooswinkl)

A,B: left valve, internal side / valve gauche, vue interne - C: smooth valve, slightly noded / valve lisse, faiblement nodée - D,E: reticulated valve, moderately noded / valve réticulée, moyennement nodée - F: smooth valve / valve lisse.
Carapace morphology of *Cytherissa*

Fig. 5: *Cytherissa lacustris*, adult female, Recent (Mondsee, Site MO-7)

Fig. 5: *Cytherissa lacustris*, femelle adulte, Récent (Mondsee, Site MO-7)

A-D: Hinge / Charnière - A,B: left valve, anterior socket / valve gauche, dent antérieure (X-transversal calcified lamella) / valve gauche, dent antérieure (X-lamelle transversale calcifiée) - C,D: right valve, anterior and posterior cardinal teeth / valve droite, dents cardinales antérieure et postérieure - E,F: sieve plates (arrows point to pseudochaetae, S= normal seta) / zones criblées (les flèches indiquent les pseudochaetae, S= soie normale).
Fig. 6: Cytherissa lacustris, larval stages and adult valves, external side, Recent (Mondsee site MO-7, 12m deep)

Fig. 6: Cytherissa lacustris, stades larvaires et valves adultes, vue externe, Récents (Mondsee, site MO-7, 12m de profondeur).

A, B: adult; C, D: 8th stage; E, F: 7th stage; G: 6th stage, left valve; H: 5th stage, left valve; I, J: 4th stage, right valve.
Fig. 7: *Cytherissa lacustris*, larval stages, internal side. Recent (Mondsee, site MO-7)

A: 8th stage / *stade* 8; B: 7th stage / *stade* 7; C: 6th stage / *stade* 6; D,E: 5th stage / *stade* 5; F: 4th stage / *stade* 4.
Fig. 8: Cytherissa sernovi, adult, Recent (lake Baikal, in front of Selenga river, 20m deep)

Fig. 8: Cytherissa sernovi, adulte, Récent (lac Baikal, en face de la rivière Selenga, 20m de profondeur).

A, F, G: male / mâle - A: right valve, external side / valve droite, vue externe; F, G, H: left and right valves, internal sides / valves gauche et droite, vues internes; B-E, H: female / femelle - B: left valve / valve gauche; C: carapace, right side / carapace, côté droit; D, E: left and right valves / valves droite et gauche; H: detail from D / détail de D.
Carapace morphology of *Cytherissa*

Fig. 9: *Cytherissa sernovi*, adult, Recent (Lake Baikal, in front of Selenga River, 20m deep)

Fig. 9 *Cytherissa sernovi*, adulte, Récident (lac Baikal, en face de la rivière Selenga, 20m de profondeur).

A, B: right valve, anterior and posterior third of the hinge, details from fig. 8. II / valve droite, tiers antérieur et postérieur de la charnière, détails de la fig. 8. II

C, D: sieve plates (arrow points to a pseudochaeta, s= normal seta), details from fig. 8, C) plages criblees (la flèche indique la pseudochaeta, s= soie normale)
Fig. 10: Cytherissa taberculata, Recent (Lake Baikal, in front of Selenga river, 20m deep), juveniles and adult valves.

Fig. 10: Cytherissa taberculata, Récent (lac Baïkal, en face de la rivière Selenga, 20m de profondeur), valves juvéniles et adultes.

A, B: juveniles, left and right valves / juvéniles, valves droite et gauche; C-F: adult male, left and right valves / mâle adulte, valves gauche et droite; E: detail from C of posterior tooth, right valve / détail de C, de la dent postérieure de la valve droite; F: external side, right valve / vue externe, valve droite; G: adult female, right valve, external side / femelle adulte, valve droite, vue externe.
Fig. 11: *Cytherissa tuberculata*, Recent (lake Baikal, in front of Selenga river, 20m. deep).

A, B: sieve plates, detail from fig. 10, F (S = seta, arrow in B points to a pseudochaeta) / plages cribées, détail de la fig. 10, F (S = seta, flèche indique une pseudochaeta)

C: carapace, juvenile / carapace, juvénile

D: anterior cardinal tooth, right valve, detail from fig. 10, C / dent cardinale antérieure, valve droite, détail de la fig. 10, C

E: detail from D / détail de D.
Fig. 12: Cytherissa plana tuberculata Olteanu, Pliocene, Upper Dacian (Moesian plain, borehole around Alexandria)

Fig. 12: Cytherissa plana tuberculata Olteanu, Pliocène, Dacien supérieur (plaine moesienne, forage près d'Alexandria) A-C: juvenile, 8th stage / juvénile, stade 8.
Carapace morphology of *Cytherissa*

Figure 13: *Cytherissa hogalschovi* hogalschovi Upper Getian, Moesian Plain, Alexandria, southern Romania

A: stage 3; B: stage 4; C: stage 5; D: stage 6; K, L: stage 7; H, I, J, M: stage 8; E, G, N, adults; F, G, I, J, hinge, details of anterior and posterior cardinal areas from the valves E and H (leg, det. and prep. for SEM: R. Olteanu).
Figure 14: Paratethyan Cytherissa species. A, C, N: Cytherissa bogatschovi bogatschovi Upper Dacian, Moesian Plain, Alexandria; A: stage 6, N: stage 7, C: stage 8; B: Cytherissa triformis tuberculata Upper Dacian, Moesian Plain, Alexandria; D-H: Cytherissa plana tuberculata Upper Dacian, Danube Delta, Pardina; D: stage 7, E,F: stage 8, G, H, details of the hinge from F; I-M: Cytherissa laevatula, Maeotian, Georgia (leg Vekua); I, K, adults; J, L, M: details from I and K (det. and prep. for SEM: R.Oteanu).

Figure 14: Cytherissa paratethysienes. A, C, N: Cytherissa bogatschovi bogatschovi Dacien supérieur, plaine de Moesie, Alexandrie, A: stade 6, N: stade 7, C: stade 8; B: Cytherissa triformis tuberculata Dacien supérieur, plaine de Moesie, Alexandrie; D-H: Cytherissa plana tuberculata Dacien supérieur, delta du Danube, Pardina; D: stade 7, E,F: stade 8, G, H, détails de la charnière de F; I-M: Cytherissa laevatula, Maeotien, Géorgie (leg Vekua); I, K, adultes; J, L, M: détails de I et K (déet. et prép. pour le MEB: R.Oteanu).
Figure 15: Ostracodes from lake Tanganyika. A, B: *Romerocytheridea* - A: right valve; B: detail of anterior part of the hinge C-F: *Cyprideis* - C: right valve, internal view; D: right valve, external side; E: right valve, detail of the anterior tooth; F: sieve-pore.

Figure 15: Ostracodes du lac Tanganyika. A, B: *Romerocytheridea* - A: valve droite; B: détail de la partie antérieure de la charnière. C-F: *Cyprideis* - C: valve droite, vue intérieure; D: valve droite, vue externe; E: valve droite, détail de la dent antérieure; F: pore en taniis.
MORPHOLOGY OF CYTHERISSA AND CYPRIDEIS: SUPPLEMENTARY DATA ON THE APPENDAGES AND THE CARYOTYPE

MORPHOLOGIE DE CYTHERISSA ET DE CYPRIDEIS DONNEES SUPPLEMENTAIRES SUR LES APPENDICES ET LE CARYOTYPE

by

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Abstract
The appendages of females of Cytherissa lacustris from Mondsee and males of Cytherissa sernovi from Baikal lake as well as Cyprideis torosa from the Arcachon Bay are described. Comparative data are presented for the male of Cytherissa tuberculata from Baikal. It is suggested that within the family Cyprideidae a sexual dimorphism of the limbs developed parallelly within at least two phylogenetic lineages the Cytherissa and the Cyprideis. The detailed morphology of the male copulatory organ and the caryotype of the Cytherissa representatives is for the first time described. It is noted that the antenna and the copulatory complex of Cytherissa species display primitive traits as compared to Cyprideis. The caryotype of Cytherissa lacustris has many similarities with those of Cyprideis torosa described by Tétart (1978).

Résumé

1 - INTRODUCTION
The representatives of the family Cytherideidae Sars 1925 live(d) in both marine and continental waters. Hartmann and Puri (1974) noted that there is difficult to group the various genera of this family in taxa which should reflect phylogenetical relationships because of a lack of informations on their morphology especially on the peculiarities of the body appendages. Therefore, they restricted their discussion to one subfamily, the Cytherideinae Sars with living and fossil representatives and noted that two other subfamilies: Schulerideinae Mandelstam and Cuneocyttherinae Mandelstam could be distinguished for exclusively fossil taxa.
Cytherissa Sars and Cyprideis Jones are two of the most important genera of Cytherideinae. Other genera with living representatives are Cytheridea Bosquet, Heterocyprideis Elofson, Neocytheridea Rome, etc (Hartmann and Puri, 1974).

Kollmann (1958) in his monograph of the Cytherideinae and Schulerideinae of the Paratethys in Austria proposed the division of the Cytherideinae in several supergeneric groups, the Haplocytherideini, the Cyprideidini and the Eucytherideini. Cytherissa could not be located in any tribes by Kollmann (op. cit.). In the Hartmann and Puri (1974) system the Eucytherini are considered a family Eucytheridae Puri.

Recently, Huang (1985) proposed a new family, the Cytherissidae, to accommodate the representatives of the genus Cytherissa. The author does not give any arguments why should be Cytherissa such an important phylogenetical lineage comparable to the Cytherideidae and the Limnocytheridae. This arbitrary decision points out to the necessity to examine in a carefully way the phylogeny of the Cytherideidae. To achieve such a goal it is important to describe or reexamine not only the morphology of the carapace but also those of the appendages and even the caryotype of various cytherideid groups.

There are two other arguments to look to the appendages of the Cytherideidae. Representatives of this family live on/in various substrates from fine grained sediments to coarse sand. It is interesting to see if some of the appendages specialised to the various types of sediment. Finally some of the appendages like the male copulatory organ are for most of the Cytherideinae unknown or poorly described. Recent progress in the description of the Limnocytheridae appendages (Colin and Danielopol, 1980, Danielopol et al., 1989, Martens, 1990) demonstrated that especially the copulatory organ and the fine structure of the chaetotaxy offer invaluable informations for phylogenetical reconstructions. The same could apply to the study of cytherideid caryotypes. One of us (J.T.) described the chromosomes of Cyprideis torosa. It is interesting now to compare their structure and number with those of Cytherissa lacustris in order to see how large are the differences of these structures between the two groups.

In the present contribution we redescribe the morphology of the limbs and those of the chromosomes of Cytherissa lacustris using the population of Mondsee. Sars (1925) gave a good illustration of the appendages of C. lacustris from Norway. As compared to the latter description we present here supplementary informations on the chaetotaxy which could be of interest for further comparative studies e.g. in taxonomy. Also the present data are useful for functional morphology.

The description of Cytherissa sernovi Bronshein, Cytherissa tuberculata Bronshein and the comparative data of Cyprideis torosa will help us to better understand the morphological structure of the male copulatory organs and the phylogenetical relationships between the two genera within the Cytherideidae. The analysis and the interpretation of the caryotypes of Cytherissa and Cyprideis was completed by J.T. while the senior author studied the morphology of the appendages of these two groups.

2 - MATERIAL AND TERMINOLOGY

Cytherissa lacustris from Mondsee, the site MO-7 (Mooswinkl) 12 and 18 m depth, adult females and juveniles where used for this description of the limbs and the caryotype. For C. sernovi and C. tuberculata one of us (D.L.D) examined males, females and juveniles from lake Baikal collected in front of the Selenga delta (Selengiskoie melkovodie, 20 m depth). The material was offered to D.L.D. by Prof. H.Löffler (Univ. Vienna). Cyprideis torosa males and females were collected by Carbonel (Univ. Bordeaux) and Geiger (Limnol. Inst., Mondsee).

The terminology for the limbs description adopted in this paper is those already used by Danielopol et al. (1989) Athersuch et al. (1989), Martens (1990). Some minor differences exist e.g. we use the term copulatory tube for what Martens (1990) called copulatory process. The terminology of the setae is those proposed by Broodbakker and Danielopol (1982).

The study of the caryotype of Cytherissa lacustris has been accomplished on 52 specimens collected during three sampling cruises in Mondsee (October, 1985, February and June 1986) The method that was previously used for the study of cypridid caryotypes (Tétart, 1978), consisting in stopping the mitosis which occur spontaneously in the intestinal epithelium did not give any result with this material. It was therefore possible in these parthenogenetic crustaceans to examine only meiotic prophases of the ovocytes.
Cytherissa and Cyprideis morphology

Fig. 1 - A-J: Cytherissa lacustris, female; K: Cytherissa tuberculata; A: antennula; B, C: antenna: detail from B, the aesthetasque Y and adjacent setae; D: mandibular palp; E: maxillule; F: hypostome; G-I: thoracic legs (P1-P3); J: posterior part of the body; K: maxillular palp; GM, Gm1, Gm2: distal claws of the antenna; B: Ext: dorsal extremity with caudal seta; Fu: furca; f1, f2: furcal setae; Ge: genital process; O: vaginal opening; Ov: ovocytes; ps: pseudochaetae; I-IV: segments; +: fusion of segments.

Fig. 1 - A-J: Cytherissa lacustris, femelle; K: Cytherissa tuberculata; A: antennule; B, C: antenne (C - détail de B, aesthésique Y et soies adjacentes; D: palpe mandibulaire; E: maxillule; F: hypostome; G-I: pattes thoraciques (P1-P3); J: partie postérieure du corps; K: palpe maxillulaire; GM, Gm1, Gm2: griffes distales de l'antenne; B: extrémité dorsale avec soie caudale; Fu: furca; f1, f2: soies de la furca; Ge: processus genital; O: ouverture vaginale; Ov: ovocytes; ps: pseudochètes; I-VI: segments; +: fusion de segments.
3. RESULTS

3.1. CYTHERISSA LACUSTRIS SARS

Antennula (fig. 1 A) - most of the setae are smooth; the seta II p, papose, IIa, plumose. 2nd segment with anterior and posterior long pseudochaetae (ps). The aesthetasc Ya fused to a distal seta.

Antenna (fig. 1 B, C) - the first two endopodial segments with long ps on the anterior side. The distal endopodial claws represented by GM, Gm1, Gm2, all are smooth; other setae, plumose, aesthetasc Y, long; the exopodite short. Spineret gland small, of globular shape.

Mandible (fig. 1 D) - the gnathobase with 7 teeth, DI, conical shaped, D2-D6, lamellar shaped, with 3 distal points. The palp, 4 segmented; the first 2 segments with plumose setae; 3rd segment in the middle, with 7 setae on the external side and 2 on the inner one.

Maxillule (fig. 1 E) - endite 1 with 2 strong plumose setae. Palp 2-segmented, the proximal one having on the external side 2 plumose and 2 simple setae, on the inner side with 2 smooth setae; the distal segment subapically inserted, with 3 simple setae, the internal one fused to the distal margin of the segment. For comparative purposes we show here also the maxillar palp of C. tuberculata, male (fig. 1 K). One can see a similar structure.

Mandible (fig. 1 D) - with long pseudochaetae; posterior part, acuminate.

Thoracic legs, PI - P3 (fig. 1 G - I) - PI with plumed setae, the distal claw spiky serrate; P2 and P3 with 5 rows of short ps on the 1st endopodial segment. The distal setae of the protopodite and the 1st endopodial segment of P1, plumose, instead of papose for P2 and P3. The sclerified support rami of the P1 - P3 short.

Furca (fig. 1 J) - with 2 short papose setae.

The genital process (fig. 1 J) - tubular shaped, the vaginal opening (o) unsclerified.

The dorsal extremity of the body without sclerified bars, but with a small caudal seta.

Ovary with many oocytes of various size.

The genital lobe, simple, widely bent.

The successive apparition and development of the limbs from the 4th post-embryonal stage up to the adult stage is visible in fig. 6.

3.2. CYTHERISSA SERNOVI BRONSHTEIN

The morphology of the female appendages are similar to those of C. lacustris (see also Bronshtein, 1947). Here we describe the morphology of the male’s limbs.

Antennula (fig. 2 F) - as compared to the females of C. lacustris the setae are longer and better sclerified.

Antenna (fig. 2 G) - GM, spiky serrate, aesthetasc Y longer than in C. lacustris.

Brush like organ (fig. 2 H) - small and tubular shaped.

Thoracic limbs, PI - P3 (fig. 2 I - N) - the right side: PI with only one endopodial segment, curved, with a well developed papose seta and a distal smooth claw; P2 with a reduced endopodial segment and a minute distal spine, no pseudochaetae, visible; P3 of normal type with many tiny ps, papose setae and a long serrate claw, poorly sclerified. The left side: P1 - P3 normally developed. P3 symmetric with those of the right side, P1 with the anterior endopodial seta and the distal claw serrate while the homologue structures of P2 are smooth.

Furca (fig. 3, 5) - peniferum with a triangular distal lobe; its proximal extremity has a small finger shaped process. On the medial side 2 elongated lobes called lal (lateral lobe) and ml (medial lobe). The distal part of the ml, finger shaped and largely curved. A proximal lobe, globular shaped is visible near the basis of medial lobe. The vas deferens opens in a globular vesicula seminis, from where starts a strongly sclerified copulatory tube; this one forms two coils and it presents an external extrusion. Ductus ejaculatorius is very large in the proximal part and becomes narrow at the distal part. No structured glans visible. The erection is produced through the peniferal muscles mu1 - mu4 inserted on the sclerified rami, the lateral ones Ir1, Ir2, the caudal ramis cr1, cr2, the medial ramus mr. The opening of the distal lobe and the projection forward of the copulatory tube is done through the changes in the position of the sclerified bar X, the ventral ramis vr1, vr2 and the contraction of the muscle mu3.
Fig. 2 - A-E: Cyprideis torosa male; Cytherissa sernovi, male: A, F: antennula; B, G: antenna; C-E: thoracic legs side; H: brush like organ; I-N: thoracic legs; I-K: right side; L-N: left side.

Fig. 3 - Cytherissa sernovi, hemipenis; A: lateral side; B: medial side; C: distal lobe; D: copulatory tube; E: lateral and medial lobes; F: vesicula seminis and adjacent structures; dl, ml, lal, pl: distal, medial, lateral, proximal lobes; Ir, mr, cr, vr, x: lateral, medial, caudal, ventral and x rami; mu1 - mu4: muscles; ct: copulatory tube; de: ductus ejaculatorius; ve: vesica ejaculatoria; vas deferens; Ex: excrescence of copulatory tube; pf: proximal finger.

Fig. 3 - Cytherissa sernovi, hemipenis; A: vue latérale; B: vue médiale; C: lobe distal; D: tube copulateur; E: lobes latéral et médian; F: vésicule séminale et structures adjacentes; dl, ml, lal, pl: lobes distal, médian, latéral, proximal; Ir, mr, cr, vr, x: branches latérale, médiane, caudale, ventrale et x; mu1, mu4: muscles; ct: tube copulateur; de: tube ejaculatorius; ve: vesica ejaculatoria; tube déférent; Ex: excroissance du tube copulateur; pf: doigt proximal.
Fig. 4 - A-D: *Cytherissa tuberculata*, male, hemipenis; E-G: *Cyprideis torosa*, male, thoracic limbs (P1-P3), right side; A - general view, medial side; B: medial and lateral lobes; C: distal lobe, medial side; D: copulatory tube.

Fig. 4 - A-D: *Cytherissa tuberculata*, mâle, hémipenis ; E-G: *Cyprideis torosa*, mâle, pattes thoraciques (P1-P3), côté droit ; A - vue générale, côté médian ; B : lobes latéral et médian ; C : lobe distal, côté médian ; D : tube copulateur.
Fig. 5 - Cytherissa vernoi, male, hemipenis, S.E.M. microphotographs: A: general view, lateral side; B: details of the copulatory tube; C: details of the hemipenis and furca, medial side; D: details of the medial and lateral lobes. Other symbols like in fig. 1 and 3.
3.3 CYTHERISSA TUBERCULATA BRONSHTEIN, COMPARATIVE DATA

The general morphology of both the female and the male's appendages are similar to those described for *C. lacustris* and *C. sernovi* (see also Bronshtein, 1947). There are surprisingly only minor differences in the hemipenis structure between *C. sernovi* and *C. tuberculata* (fig. 3,5 and 4,A-D). This latter has longer pf on the distal lobe, the copulatory tube has no conspicuous extrusion (Ex) on its outer side.

3.4. CYPRIDEIS TOROSA (JONES), COMPARATIVE DATA

We shall describe here briefly, the male's limbs (see also Sars, 1925).

Antennula and antenna (fig. 2, A, B) - as compared to *Cytherissa*, *Cyprideis* differs in the presence of a seta on the antennular segment IV+V (see arrow) and the lack of one of the Gm claws.

Thoracic legs, P1 - P3 (fig. 2, C, D, 3, E-G). The left side: P1 with a smooth endopodial seta and a distal claw. P2 with a plumed endopodial seta and a smooth distal claw. P3 normally developed, with long ps on the 1-st endopodial segment. The right side: P1 with a well developed endopodite. The en-I with a strong simple seta bearing a long ps. The distal claw are visible. P3 is similar to its homologue of the left side.

Hemipenis with a strongly sclerified medial lobe which is crenulated on one margin. The ml is protected apparently by the distal lobe. The lateral lobe completely separated from the medial one. The copulatory tube with a complex distal part which could be a glans.

3.5. COMPARATIVE DATA BETWEEN THE CARYOTYPES OF CYTHERISSA LACUSTRIS AND CYPRIDEIS TOROSA

The chromosomic formula of *Cytherissa lacustris* is composed of 12 pairs of homologous chromosomes. Although we did not observe any somatic metaphase, it appears that these chromosomes have a very small size, less than 2 microns, during the stage of maximum condensation. They are all acrocentric. Homologous pairs form a series of regularly decreasing size, in which however, the size difference between the largest and the smallest chromosomes is rather small. In young ovocytes, in which the meiotic prophase has started (aberrant prophase attributable to the parthenogenesis, in which the combination in pairs of homologous chromosomes does not occur normally), the decondensation of the chromosomes allows an interesting analysis of their morphology. They all present a positive centromeric heteropycnosis. In spite of the small size difference between the extreme elements of the formula, we could distinguish seven pairs of "large" and "middle" size chromosomes, for which the centromeric heterochromatine is not very abundant. Their chromatids present two to three condensations. The caryotype is completed by five pairs of slightly smaller chromosomes, the chromatids of which possess only one condensation or none.

In the studied samples, no variation of the number of chromosomes has been observed, nor a noticeable variation of their morphology.

It is interesting to compare the caryotype of *Cytherissa lacustris* with the one of *Cyprideis torosa* (which formula has been previously studied by Téart, 1983) because of the various affinities existing between those two species. The material studied in both cases does not allow a fully satisfactory comparison because the origin of the studied cells was not exactly the same. In the first species the ovocytes were examined, whereas in the second species, chromosomic formulas were obtained from spermatocytes. Furthermore, bivalent chromosomes do not form in identical conditions in these two species. We could however notice the apparent absence of division of the intestinal epithelium. This could suggest a very slow metabolism lowering the frequency of mitosis, or the presence of a barrier opposing to the action of colchicine on intestinal cells. On the other hand, the idiogram of both species shows very strong similarities: same number of chromosomes, same size, same distribution, most probably chromatidian condensations.

Amongst the smaller chromosomes of *Cytherissa lacustris* some are probably the equivalent of the chromosome X of the male formula of *Cyprideis torosa*. Finally, in both cases, no variation of the formula has been observed.

This comparison should however be made with some caution, because of the lack of data concerning the chromosomic formula of the cytherid ostracods in general and therefore of the fresh-water cytherids. The similarities noticed could well be restricted not only to the two studied species, but could apply to the entire group, the caryotype of which could in fact present a great uniformity.
4. DISCUSSION

Two types of questions will be emphasized in this section: 1. the adaptive value of the morphological traits displayed by the antennae and the thoracic legs.; 2. the usage of selected morphological characters for phylogenetical reconstructions.

4.1. THE ADAPTIVE VALUE OF THE MORPHOLOGICAL TRAITS OF THE ANTENNAE AND THE THORACIC LEGS

_Cytherissa lacustris_, _C. sernovi_ and _Cyprideis torosa_ live mainly on / in silty, silty -sand sediments (informations in Danielopol et al., 1990, Bronshtein, 1947 and Carbonel, 1980). These species show some interesting peculiarities which can be considered good solutions for living on/in fine grained substrates. The distal claws of the antennae especially of the last two segments are strongly developed. This allows to move or to dig into the substrate. Long pseudochaetae exist on the anterior side of the antennae and the walking legs. This help to avoid the fixation of fine sediment on the limbs. A cleaning role could be played by the strong posterior seta of the walking legs. The antennal exopodite is shorter than in the case of phytophilous Cytheracea. This morphological structure called also spineret seta helps to fix on solid substrates the animal through the fine glueproduced by an antennal. As _Cytherissa_ commonly does not live in high energetic environments and solid (hard) substrates a strong development of this organ is not needed. Hence the exopodite is poorly developed.

The polymorphism of the walking legs of _Cytherissa_ and _Cyprideis_ representatives is remarkable. While the females display the common pattern, i.e. a slightly differenciated type of P1 - P3 legs, the male presents a strong asymmetry between the right and the left side and important differences between the three thoracic legs. One could ask if the reduced and/or transformed endopodites are the result of a sexual selection process. From a functional point of view one could question what makes the advantage to have asymmetric limbs. The reduced endopodites of the P1 and P2 are certainly unefficient clasping organs in order to fix or stimulate the female during the matting process. From these observation one conclude that the polymorphic legs of the males in both _Cytherissa_ and _Cyprideis_ are non-adaptive or at most a poor adaptive solution for the accuplation. Figure 6 presents diagramaticaly the post-embryonal development of the limbs for _Cytherissa lacustris_. If one compares the P1 and P2 of the right side described here for _Cytherissa sernovi_ it will be obvious that these structures represent a limb which stopped its development during the 5th stage. _Cyprideis torosa_ suffered also an evolution of the two walking legs (P1, P2) on the right side which are equivalent with the 6th post-embryonal stage of a normaly developing cytherid. One of us (D. L. D) considers that the assymetrical and paedomorphic thoracic legs of the chytherideid males presented here are due to unusual genetical and/or epigenetical processes as discussed for _Leucocythere mirabilis_ in Danielopol et al. (1989) and for other animal groups, e. g. _Drosophila_, by Arthur (1984).

4.2. PHYLOGENETICAL RELATIONSHIPS BETWEEN CYTHERISSA AND CYPRIDEIS.

In the following we shall examine what kind of information gives us the morphology of the limbs and of the caryotype for a better understanding of the phylogenetical relationships between _Cytherissa_ and _Cyprideis_ within the family Cyprideidae.

We are confronted with the following alternative scenarios pertaining to the origin and the evolution of these two ostracod groups: a1 - _Cytherissa_ and _Cyprideis_ belong to the same phylogenetic lineage; a2 - these two groups belong to different phylogenetic lineages but having a common origin; a3 - _Cytherissa_ and _Cyprideis_ are two remotely related groups without a common origin. Taxonomically the a1 variant implies that the two genera will be grouped either in one tribus e.g. Cyprideini or one subfamily Cyprideinae : the a2 alternative implies the location in different tribes e.g. the tribus Cyprideini for _Cyprideis_ and Cytherissini for _Cytherissa_ ; the variant a3 will opt for the separation of the two genera either in two different subfamilies of the Cyprideidae or in two families, the Cytherideidae and Cytherissidae. Various authors as discussed in the introduction opted for one of these scenarios e.g. Hartmann and Puri (1974) inter alia for the a1 hypothesis, Kollmann (1958) for the a2 variant and Huang (1985) for the alternative a3.

Five complexes of characters will be considered for our phylogenetical analysis i.e.:

1) the antennae traits; 2) the polymorphic structures of the male's thoracic legs; 3) the diverse morphology of the hemipenis; 4) the extremity of the female's body; 5) the caryotype.
If one compares the general limbs morphology of Cytherissa and Cyprideis species described here with those of the representatives of another inland water group, the Limnocytheridae (see e.g. Danielopol et al., 1989; Martens, 1990) one can see important differences. The peculiar structure of the thoracic legs with their sexual dimorphism, the general structure of the hemipenis without claspers organs but with an well-developed erection system. The presence of a female tubular genital process without sclerified vaginal openings and a furca with only two setae show that Cytherissa: and Cyprideis belong to a group that one can call Cytherideidae which differs obviously from the reference group used here the Limnocytheridae. Hypothesis a1 is corroborated while the a3 variant has to be abandoned. We consider here that Cytherissa: and Cyprideis belongs to two distinct phylogenetic lineages that one could call tribus Cyprideidini Kollmann and tribus Cytherissini (Huang) which have a common origin. Arguments for this latter is given by the caryotypes similarities by the presence of the same evolutionary trends, i.e. the realisation of asymmetrical and sexual dimorphic structures on the thoracic limbs.Cytherissa: has some more primitive structures comparing to Cyprideis: i.e. the antenna has two Gm claws, the hemipenis has slightly developed medial and lateral lobes, the copulatory tube has not a well-developed glans.Cyprideis: as compared to Cytherissa, has on the antennula one seta in the middle of the 4+5 segment which normaly exist in most of the Cytheracea on the posterior side of the distal margin of the 4th segment. Cyprideis has an extremely elaborated male copulation organ and the extremity of the female's body is on the dorsal side transformed in a brood pouch.

In conclusion, the comparative morphology of Cytherissa: and Cyprideis confirms in an exemplary way the Kollmann's (1958) concept on the Cytherideinae which were based mainly on carapace morphology and paleoecological criteria, i.e. within the family Cyprideidae there several lineages one cancel the Cyprideidini, Cytherissini, etc. The lineages of Cytherissa: and Cyprideis separates from a common Cyprideinae stock and evolved parallelly. The Cytherissini appear to be less morphologically evolved as compared to the Cyprideidini.

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Prof. H.Löffler (Univ.Vienna) offered the Cytherissa of the lake Baikal.; P.Carbonel (Univ.Bordeaux) and W.Geiger (Limm.Institut, Mondsee) collected the Cyprideis torosa; K.Maier (Limm.Institut, Mondsee) was in charge for sampling the Cytherissa lacustris used for this study; A.Loser (Univ.Vienna) produced the SEM photomicrographs. Discussions with K.Martens (Musée Royal des Sciences Naturelles, Bruxelles) and P.Carbonel are greatly appreciated. One of us (J.T.) is indebt to J-P.Colin (ESSO-REP, Bègles) who translated his manuscript; G.Cucu (Constanta) and H.Ployer (Mondsee) helped with the production of the figures.

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GENETIC AND MORPHOLOGICAL POLYMORPHISM IN
THE FRESHWATER OSTRACOD CYTHERISSA LACUSTRIS
(SARS) OF MONDSEE AND ATTERSEE (AUSTRIA)

POLYMORPHISME GENETIQUE ET MORPHOLOGIQUE
CHEZ L'OSTRACODE D'EAU DOUCE CYTHERISSA
LACUSTRIS (SARS) DES LACS MONDSEE ET ATTERSEE
(AUTRICHE)

by

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Key-Words: Cytherissa lacustris, genetic polymorphism, electrophoresis, morphometry, ostracods.
Mots-Clés: Cytherissa lacustris, polymorphisme génétique, électrophorèse, morphométrie, ostracodes

Abstract

Genotypic and phenotypic polymorphism of the parthenogenetic freshwater ostracod Cytherissa lacustris were studied within a lake and between two lakes of the same drainage basin.

Using electrophoretic techniques, enzymograms of 4 enzyme systems were obtained. Three of them proved to be monomorphic (Ldh, Ao, Lap) and one (Gpi) polymorphic. Seven Gpi-genotypes could be differentiated. These genotypes were common to all stations but differed considerably in their relative frequency.

Differences between adults and juveniles are caused by selection, whereas within lake differences are explained as the combined effects of recurrent bottleneck situations and subsequent selection. Between lake differences were based on a higher number of genotypes, but could not be fully explained by selection alone.

In addition to the described genetic polymorphism, considerable morphological polymorphism was found concerning carapace size and nodation.

No relationship could be established between selected environmental parameters such as depth, temperature, organic matter, grain size and mineralogic composition and the morphometric data.

The influence of variably acting genetic determination on the nodation pattern has to be taken into account when paleo-ecological conclusions are to be drawn.

Résumé

Le polymorphisme génotypique et phénotypique de l'ostracode parthénogénétique d'eau douce Cytherissa lacustris a été étudié à l'intérieur d'un lac, puis dans deux lacs appartenant au même système de drainage.

Les enzymogrammes de 4 systèmes d'enzymes ont été obtenus au moyen d'électrophorèses. Trois d'entre eux se sont avérés monomorphiques (Idh, Ao, Lap) et un (Gpi), polymorphe. 7 génotypes Gpi ont pu être différenciés. Ces génotypes sont communs à toutes les stations mais diffèrent considérablement dans leurs fréquences relatives.

Les différences entre adultes et juvéniles sont dues à une sélection alors qu'à l'intérieur d'un lac, les différences sont explicables par une action conjointe de situations de bottleneck récurrent et de la sélection consécutive. Entre les lacs, les différences étaient basées sur un plus grand nombre de génotypes, mais n'ont pu être entièrement expliquées par la seule sélection.

En plus du polymorphisme génétique décrit, il a été constaté un polymorphisme morphologique considérable concernant la taille de la carapace et la nodation.

Aucune relation n'a pu être établie entre les paramètres de l'environnement tels que profondeur, température, matière organique, granulométrie ou composition minéralogique et les données morphométriques.

Lorsque l'on fait des interprétations paléoécologiques, on doit tenir compte de l'action variable de déterminisme génétique de la nodation.
INTRODUCTION

The existence of genetic polymorphism in parthenogenetically reproducing Crustacea is a commonly observed phenomenon (Hebert and Crease, 1980; Carvalho, 1988; Rossi and Menozzi, 1990).

The genetic diversity within parthenogenetic populations is a result of the coexistence of genetically different clones (Hebert and Crease, 1980). There is evidence from the literature for a differential response of clones of a given species to various environmental parameters such as salinity (Weider and Hebert, 1987), temperature (Rossi and Menozzi, 1990) and oxygen concentration (Weider and Lampert, 1985). Seasonal cycles in the frequency of occurrence of clones are related to differential survival and fecundity in response to temperature variations (Carvalho, 1987; Carvalho and Crisp, 1987).

Small scale geographical differences in clonal composition were found in arctic tundra ponds which varied in size, relative age and location (Weider, 1989) and even within the bays of a single lake (Jacobs, 1989).

Studies on ostracods are few, but agree well with the above mentioned findings (Rossi and Menozzi, 1990; Sywula and Lorenc, 1982; Sywula et al., 1985; Havel and Hebert, 1989; Chaplin and Ayre, 1989).

There is an ongoing discussion in the ostracod literature whether and to what extent, some of the features of the ostracod carapace such as size and ornamentation (e.g. nodation) are genetically or environmentally cued (Peyiouquet, et al, 1988; Carbonel and Tolderer-Farmer, 1988, Broodbakker, 1983; Pfau, 1982; Reyment, 1988).

In the present study, the allozyme pattern of *Cytherissa lacustris* (Sars), a parthenogenetic, slowly developing freshwater ostracod species, has been investigated in order to assess its genetic variability within a single lake and between two lakes of a single lake complex. An attempt has been made to relate phenotypic variability (size and nodation pattern) to genotypic differences and selected environmental factors.

*Cytherissa lacustris* has been the object of intensive study in the past few years (see related papers in 1990) and therefore more information about its autecology and paleoecological distribution is available than for other European freshwater ostracod species. Considering the obligatory parthenogenetic mode of reproduction of *Cytherissa lacustris* (with the exception of in Lake Baikal, where males occur, Bronstein, 1947)*, its endobenthic mode of life, its slow development (Geiger, 1990) and its main distribution in the profundal zone of deep lakes (a rather stable environment) limited genetic variability should be expected. The present work tries to evaluate the amount of genetic and morphological differentiation within a lacustrine system (Mondsee) and between two closely located lakes belonging to the same drainage system (Mondsee and Attersee, Fig.1) as well as to discuss the possible underlying mechanisms.

MATERIAL AND METHODS

1) STUDY AREA:

The two lakes belong to the Ager drainage basin (Moog, 1982; Fig.1) and are connected by a stream of 3km length. In the Late-Glacial they formed a single lake. Separation occurred at the beginning of the Post-Glacial (Janik,1969).

Animals were collected at three stations in September 1987: Mondsee station 1 (fig.1,A): Bay of Mooswinkl (station MO-7 in Danielopol et al., 1988). Samples were taken at two depths (12m and 40m). The 12m site is located within the bay, whereas the 40m site reflects a typical open lake situation. The bay itself is sheltered, has no major influents and can be separated from the open lake as regards abiotic parameters (Hermann and Geiger, in prep.). In this part of the lake a continuous population of *Cytherissa lacustris* has existed since the Atlanticum (Handl, 1989).

*Danielopol (pers. comm.) doubts, that *Cytherissa lacustris baikaliensis* is closely related to *Cytherissa lacustris* from Europe and most probably represents a valid species.*
Genetic polymorphism of *Cytherissa lacustris*

Mondsee station 2, at 12m depth, is in the vicinity to the outlet (Seeache stream) (fig. 1.B). This part of the lake is characterized by rapidly fluctuating sedimentological conditions due to the geomorphological situation with periods of high input of coarse, clastic sediments, transported by streams discharging into the area (Horsthemke, 1986). Colonization by *Cytherissa lacustris* most probably began later than at station 1 and the population has been subjected to periodic disturbances (Handl, 1989).

Attersee station 3 is located between Zettelmühle and Stockwinkel (fig. 1,C) at a depth of 20m. This site is physiographically similar to station 1-40m (open lake situation). For a more detailed description of the lakes and the sampling stations, see Danielopol et al., 1988 (Mondsee) and Müller, 1979 (Attersee).

2) ELECTROPHORETIC ANALYSIS

During August and September 1987, 743 specimens of *Cytherissa lacustris* both adult parthenogenetic females and juveniles in the last larval stage were examined. After 12-18 hours starvation at 12°C, single specimens were homogenized in a drop of distilled water and electrophoresed in horizontal starch gel slabs ("Sigma" starch).

Two buffer systems were used: a continuous system (A) - gel buffer 0.009M Tris-0.003M citric acid, pH 7.1, electrode buffer 0.155M Tris-0.043M citric acid, pH 7.1 - and a discontinuous system (B) - gel buffer 0.077M Tris-0.0055M citric acid, pH 8.6, electrode buffer 0.3M boric acid-0.06M sodium hydroxide, pH 8.6. After electrophoresis the gels were sliced horizontally into 2mm-thick slabs and stained appropriately. 23 enzyme systems were studied (Table 1). All electrophoretic techniques followed those described in Sywula et al, 1985.
<table>
<thead>
<tr>
<th>Enzyme system</th>
<th>Buffer system</th>
</tr>
</thead>
<tbody>
<tr>
<td>α-glycerophosphate dehydrogenase (α-Gpdh)</td>
<td>A</td>
</tr>
<tr>
<td>Sorbitol dehydrogenase (Sdh)</td>
<td>B</td>
</tr>
<tr>
<td>Lactate dehydrogenase (Ldh)</td>
<td>B</td>
</tr>
<tr>
<td>Malate dehydrogenase (MDH)</td>
<td>A</td>
</tr>
<tr>
<td>Malic enzyme (Me)</td>
<td>A</td>
</tr>
<tr>
<td>Isocitrate dehydrogenase (NAD) (Idh(NAD))</td>
<td>A</td>
</tr>
<tr>
<td>Isocitrate dehydrogenase (NADP) (Idh (NADP))</td>
<td>A</td>
</tr>
<tr>
<td>Glucose 6-phosphate dehydrogenase (G-3-pdh)</td>
<td>B</td>
</tr>
<tr>
<td>Aldehyde oxidase (Ao)</td>
<td>A,B</td>
</tr>
<tr>
<td>Glyceraldehyde-3-phosphate dehydrogenase (G-3-pdh)</td>
<td>B</td>
</tr>
<tr>
<td>Xanthine dehydrogenase (Xdh)</td>
<td>A</td>
</tr>
<tr>
<td>Glutamate dehydrogenase (Gdh)</td>
<td>B</td>
</tr>
<tr>
<td>Superoxide dismutase (Sod)</td>
<td>B</td>
</tr>
<tr>
<td>Glutamic-oxalacetic transaminase (Got)</td>
<td>B</td>
</tr>
<tr>
<td>Hexokinase (Hk)</td>
<td>A</td>
</tr>
<tr>
<td>Adenylate kinase (Ak)</td>
<td>B</td>
</tr>
<tr>
<td>Phosphoglucomutase (Pgm)</td>
<td>B</td>
</tr>
<tr>
<td>Esterase (Est)</td>
<td>A,B</td>
</tr>
<tr>
<td>Alkaline phosphatase (Aph)</td>
<td>B</td>
</tr>
<tr>
<td>Acid phosphatase (Acph)</td>
<td>B</td>
</tr>
<tr>
<td>Leucine aminopeptidase (Lap)</td>
<td>B</td>
</tr>
<tr>
<td>Cis-aconitase (cis-Aco)</td>
<td>B</td>
</tr>
<tr>
<td>Glucose-6-phosphate isomerase (Gpi)</td>
<td>A</td>
</tr>
</tbody>
</table>

Table 1: Survey of enzyme systems examined

Table 1: Liste des systèmes d'enzymes examinés.

The statistical significance of differences between materials from separate samples was tested using the G-test with all its restrictions. Firstly, phenotypes represented in the material by 5 or fewer specimens were pooled. Secondly, when the frequency of a given phenotype was 1-5% in one of the two samples being compared and over 5% in the other one, the inequality: lower phenotype frequency less than higher frequency minus its triple standard error was tested instead of the G-test (samples were considered significantly different if this inequality criterion was satisfied).

3) MORPHOMETRIC DATA

Samples were taken from the same locations as for the electrophoretic analysis in August and September 1987. Sampling dates at each individual site were the same to avoid the possibility of differences due to seasonal variations. At station 1, two different depths were chosen (12m and 40m) to investigate a possible influence of temperature on shell size. From each station 40 to 50 specimens were taken and maximum shell length and height were recorded. The carapace of living Cytherissa was measured to the nearest 5 μm under a microscope (Reichert Diavar, 100x magnification), subfossil shells (taken from the first 3cm of the sediment column) by using a stereo - microscope (Wild, 50x). Differences between right and left valve were negligible. Data were normally distributed and therefore no transformation was necessary. Values are compared using ANOVA and subsequent series of Scheffe-tests. The influence of environmental variables was checked using simple linear regression models (Sokal and Rohlf, 1981).
Genetic polymorphism of *Cytherissa lacustris*

4) NODATION

The nodation pattern of *Cytherissa lacustris* is described in Tölderer-Fanner, 1985. The most persistent node on the ventro-posterior side was taken and its occurrence or non-occurrence recorded (fig. 2). Only subfossil material was analyzed.

**RESULTS**

1) ALLOZYME VARIATION

Enzymograms of 6 enzyme systems were obtained. Three of them - Ldh, Ao, and Lap proved to be monomorphic in all samples (buffer system A was appropriate in the case of Ao). Two further enzyme systems - Mdh and NADP-dependent Idh were polymorphic. However, their activity was relatively low and varied from specimen to specimen, thus the enzymograms were so incomplete that there was no possibility of analyzing them on a genotypic or even phenotypic level.

Only the Gpi-system was suitable for studying population genetics of *Cytherissa lacustris*.

In fig. 3, the 7 different electrophoretic phenotypes and their genetic interpretation are presented. The Rf (relative mobility) of bands was estimated by comparison to the fastest one, the mobility of which was taken to be 1. It appears that dimeric proteins are being coded by a series of multiple alleles at one locus. The numbers of adults (ad.) and juveniles in the 8th larval stage (juv.) examined with regard to their Gpi genotype are given in Table 2. In the case of the Attersee population, specimens with(tub.) and without (nontub.) node have been treated separately.

![Fig. 2 - Right valve of adult *Cytherissa lacustris* showing the position of the ventro-posterior node.](image)

![Fig. 3 - Electrophoretic phenotypes and their genetic interpretation](image)
There are no differences between adults and juveniles except for the frequency of Gpi 1.0/1.0 and Gpi 0.94/1.0 genotypes. Statistical analysis confirms such an assumption. Applying the G-test to genotypes Gpi 0.86/0.86, Gpi 0.86/1.0, Gpi0.94/0.94 & 0.95/0.95 and Gpi0.86/0.95 gives a value of G = 0.67121, whereas G0.05 for 3 degrees of freedom is 7.815. On the other hand, there is a statistically significant difference in the proportion in adults and juveniles of the two genotypes which could not be included in the G-test, namely Gpi1.0/1.0 and Gpi0.94/1.0 (0.01869 < 0.04114 and 0.03597 < 0.05808 respectively). The effect of depth was studied at sampling station 1. No statistically significant differences in the frequency of particular Gpi genotypes were found at a depth of 12 m and 40 m (G(all genotypes) = 6.86148, 3 degrees of freedom). Between station 1 and 2, only the difference in the frequency of genotype Gpi1.0/1.0 proved to be statistically significant (0.01124<0.03025). This gives rise to the supposition that this difference may be the result of the above mentioned differences between adults and juveniles, as the material from station 2 contained a higher proportion of adults than the material from station 1. However, even when only the adults from both stations are compared, this difference is still significant (0.02273< 0.04025). Differences in frequency of Gpi-genotypes between the populations from Mondsee and Attersee are highly significant for Gpi0.86/0.86, Gpi0.86/1.0, Gpi0.94/0.94 & 0.95/0.95, and Gpi0.86/0.95 (G = 44.42573; 2 d.f.; P < 0.001) as well as for genotype Gpi0.94/1.0 (0.03004 < 0.04144). The frequency of genotype Gpi1.0/1.0 was the only one not being statistically different (0.01852 > 0.01339). The results of the comparison of all sampling stations are shown in Table 3:

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Station 1</th>
<th>Station 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0/1.0</td>
<td>0.001 n.s.</td>
<td>0.05 n.s.</td>
</tr>
<tr>
<td>0.86/0.86</td>
<td>0.001 n.s.</td>
<td>0.05 n.s.</td>
</tr>
<tr>
<td>0.94/0.94</td>
<td>0.001 n.s.</td>
<td>0.05 n.s.</td>
</tr>
<tr>
<td>0.95/0.95</td>
<td>0.001 n.s.</td>
<td>0.05 n.s.</td>
</tr>
<tr>
<td>0.86/0.95</td>
<td>0.001 n.s.</td>
<td>0.05 n.s.</td>
</tr>
<tr>
<td>0.94/1.0</td>
<td>n.s. 0.01</td>
<td>n.s. 0.01</td>
</tr>
</tbody>
</table>

Table 3 : Statistically significant genotype differences

Between lake variability was found to be significant for a higher number of genotypes than within lake Mondsee. Finally, highly significant genetic differences between tuberculated and non tuberculated specimens were detected. This refers to genotypes Gpi0.86/0.86, Gpi0.86/1.0, Gpi0.94/0.94 & 0.95/0.95,Gpi0.86/0.95 (G=22.809; 2 d.f.; p < 0.001) and genotype Gpi1.0/1.0 (0.01724 < 0.01844),but not to genotype Gpi0.94/1.0 [0.00862 >(- 0.00989)].
2) MORPHOMETRIC DATA

The mean size of the carapace of adult specimens varied between the three locations. The smallest type of shell was found in station 2 (mean length = 870 μm) followed by station 1-40m (mean length = 885 μm), station 1-12m (mean length = 890 μm) and station 3 (mean length = 910 μm). The differences are significant for all stations except at station 1-12m and station 1-40m indicating that there is no variation in shell size with depth. (Table 4).

<table>
<thead>
<tr>
<th>Station</th>
<th>Mean length (μm)</th>
<th>S.E. (μm)</th>
<th>N</th>
<th>Coeff. of variation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-12M</td>
<td>890</td>
<td>5.47</td>
<td>40</td>
<td>4.2 %</td>
</tr>
<tr>
<td>1-40M</td>
<td>885</td>
<td>3.92</td>
<td>47</td>
<td>3.2 %</td>
</tr>
<tr>
<td>2</td>
<td>870</td>
<td>4.83</td>
<td>40</td>
<td>3.9 %</td>
</tr>
<tr>
<td>3</td>
<td>915</td>
<td>4.1</td>
<td>42</td>
<td>3.9 %</td>
</tr>
</tbody>
</table>

Table 4: Mean carapace length, Standard error (S.E.) Number of specimens (N) and Coefficient of variation of living, adult, *Cytherissa lacustris*.

The data from the subfossil populations do not confirm the above findings. Size differences between the stations could not be detected. This may be due to post-mortem mixing of the shells or to inappropriately large sample intervals (1 cm covering several years, for sedimentation rates see Irlweck, 1990). By comparing subfossil and recent material from deeper stations the influence of the sedimentation conditions on the size distribution of the shells could be shown, but in lake Mondsee, sufficient numbers of specimens can not be found deeper than 40 m.

No correlation of carapace length with any of the measured environmental parameters was found (Table 5), with the exception of total phosphorus ($r^2 = 0.54$). This may reflect the influence of the different nutritional situation or the impact of eutrophication, but sample size (n=4) and the significance of the relationship are too small to allow firm conclusions.

<table>
<thead>
<tr>
<th>Station</th>
<th>Calcite %</th>
<th>Dolomite %</th>
<th>Quartz %</th>
<th>C-org %</th>
<th>P(tot) ppm</th>
<th>Sand % dw</th>
<th>Silt % dw</th>
<th>Clay % dw</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-12M</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.0</td>
<td>437</td>
<td>21.0</td>
<td>41.0</td>
<td>38.0</td>
</tr>
<tr>
<td>1-40M</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2.4</td>
<td>579</td>
<td>0.0</td>
<td>62.0</td>
<td>37.0</td>
</tr>
<tr>
<td>2</td>
<td>51.7</td>
<td>10.5</td>
<td>12.5</td>
<td>3.0</td>
<td>594</td>
<td>4.0</td>
<td>77.0</td>
<td>19.0</td>
</tr>
<tr>
<td>3</td>
<td>59.0</td>
<td>4.0</td>
<td>11.0</td>
<td>2.1</td>
<td>279</td>
<td>6.3</td>
<td>49.7</td>
<td>44.0</td>
</tr>
</tbody>
</table>

Table 5: Selected sediment parameters used for regression analysis.

3) NODATION

The nodation pattern of *Cytherissa lacustris*, based on occurrence (=nodated) or non-occurrence (=smooth) of the ventro-posterior node gave the following results: The population of station 3 (Lake Attersee) showed the highest number of smooth shells (40.6%), followed by station 1-12m (32.9%), station 1-40m (23.9%) and station 2 (17.4%). Of the seemingly clear differences in the percentages of smooth shells,
only three proved to be significant (Table 6). As in the allozyme pattern, between lake differences are more strongly expressed than those within a single lake.

<table>
<thead>
<tr>
<th></th>
<th>Station 2</th>
<th>Station 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Station 1</td>
<td>( G = 5.34 )</td>
<td>( G = 5.42 )</td>
</tr>
<tr>
<td></td>
<td>( p &lt; 0.05 )</td>
<td>( p &lt; 0.05 )</td>
</tr>
<tr>
<td>Station 2</td>
<td>-</td>
<td>( G = 13.05 )</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>( p &lt; 0.001 )</td>
</tr>
</tbody>
</table>

Table 6: G-values and significance level for nodated and smooth shells (1 degree of freedom).

There is no indication of a possible influence of temperature (depth) nor of any of the measured variables on the nodation pattern. Furthermore, the few laboratory experiments revealed that smooth specimens of older juveniles (VIIth and VIIIth instars) always molted into smooth ones and nodated into nodated ones.

**DISCUSSION**

Table 7 gives a summary of all statistically significant differences found by comparing the stations under investigation, combining the results of the allozyme pattern, length measurements and nodation analysis.

<table>
<thead>
<tr>
<th></th>
<th>Station 2</th>
<th>Station 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Station 1</td>
<td>1N; 1S; 1G</td>
<td>1N; 1S; 5G</td>
</tr>
<tr>
<td>Station 2</td>
<td>-</td>
<td>1N; 1S; 5G</td>
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<tr>
<td></td>
<td></td>
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<tr>
<td>Station 1-12 m</td>
<td>1N;</td>
<td>1N; 1S; 1G</td>
</tr>
<tr>
<td>Station 1-40 m</td>
<td>-</td>
<td>1S; 1G</td>
</tr>
</tbody>
</table>

Table 7: Number of statistically significant items (1-5)

As can be seen from table 7, the number of statistically significant items is considerably higher within the two lakes than within the Mondsee. Within lake variability is based on carapace size differences, differences in the expression of the nodes (at least for the stations of similar depth), but the genotype frequency differs only in genotype Gpi1.0/1.0. This particular genotype and genotype Gpi0.94/1.0 proved to be good markers of gene complexes under differential selection, depending on differential survival. According to studies on the life cycle of *Cytherissa lacustris* (Geiger, 1990), the ontogenetic development takes more than one year and adults from different years live and propagate side by side. Therefore the Gpi1.0/1.0 genotype can be seen as a marker of a gene complex associated with greater, the Gpi0.94/1.0 genotype as one with lower survival.
It may be argued, that the statistically highly significant difference in the frequency of the marker genotype Gpi1.0/1.0 observed in the Mondsee at sampling station 1 and 2 results from the specific ecological situation at station 2. Paleolimnological data (Handl, 1989) show, that the Cytherissa-population from station 2 was frequently reduced to low numbers, due to local sedimentological disturbances. These changes in population density might have been severe enough to create a bottleneck situation; subsequent recolonization from the adjacent areas and eventual differential selection in the modified environment could be responsible for the observed pattern.

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Allele frequency differences within a single lake were found by Jacobs (1989) and Weider (1984) for partially parthenogenetic planktonic daphnids and are partly explained as a response to environmental parameters. Our results for the Gpi-locus are similar to these results, even if the underlying mechanisms may not be the same, due to differences in the mode of reproduction (cyclic versus obligatory parthenogenesis); in the habitat properties (pelagic versus benthic zone), and in development time (a few week in daphnids and more than one year in Cytherissa lacustris).

The differences between the two lakes (Mondsee and Attersee) in terms of significantly different items (genotype frequency, carapace size and nodation) are considerably higher than is the within lake variability. During the Late-Glacial period (after the retreat of the Würmian glacier) Mondsee and Attersee formed a single lake. Since the beginning of the Post-Glacial (9000 - 10,000 years B.P) they have been separate (Janik, 1969), the only connection between them being the Seecache stream making the active migration of specimens from one lake to the other improbable. Nevertheless, as can be seen from our results, all the identified genotypes are common to both populations. This finding supports the possibility of passive dispersal of Cytherissa lacustris hypothesized by Sywula (1990), although, as far as the polymorphic Gpi locus is concerned, the relative frequencies of particular genotypes are significantly different.

As the history of the Attersee population is not known, the differentiation process between the two populations cannot be fully explained. One of us (T.S.) proposes the following two possibilities: 1) the eutrophication process differentially advanced in each lake (Jagsch and Megay, 1982; Moog and Megay, 1982) is the selective agent; 2) we might not be dealing with the differential effects of selection but with an area effect, possibly connected with some kind of genetic deviation of large, old parthenogenetic populations (see also Hebert, 1984; Lynch, 1984; Mort and Wolf, 1986). To verify these hypotheses, further studies including more enzyme loci and sampling stations are needed.

In addition to the genetic polymorphism, we noted considerable morphological polymorphism in Cytherissa lacustris, expressed as differences in carapace size and in the extent of nodation. Size differences in ostracods are related to temperature (Van Morkhoven, 1962; Pfau, 1982), food conditions (Keen, 1971), environmental stability (Kaesler and Lohmann, 1976) or to the succession of genetically different clones bearing the potential to react differentially to temperature (Rossi and Menozzi, 1990).

Our data (see table 5), yielded no visible indication of a direct influence of a number of environmental parameters on size. The effect of temperature is expressed as higher variability in shell size in the littoral (fluctuating temperatures) as compared to the profundal (stable temperatures). The observed differences in size within small geographic ranges are therefore most probably based on clonal differentiation and its effects on growth.

Polymorphism in the nodation pattern of ostracods was discovered as early as 1912 by Fassbinder and his observations were found to be valid for many groups of both fossil and recent fresh- and brackish-water species (Carbonnel, 1975; Carbonel and Peypouquet, 1983; Triebel, 1941; Keen, 1971; Tölöder-Farmer, 1985; Reyment, 1988). It is generally assumed that the position of the nodes is genetically fixed (Vesper, 1975; Kilenyi, 1972) and that their expression is stronger in juveniles than in adults (Tölöder-Farmer, 1985).

Ostracodologists were attracted to the study of the nodation pattern, because of its potential application in ecological and paleoecological studies. If the formation of nodes is in some way influenced by environmental parameters, it could be used as bio- or paleoecological indicator to reconstruct the environmental situation (Peypouquet et al., 1988). In the case of Cytherissa lacustris in Attersee, some Gpi genotypes are non-randomly more frequent in specimens with a smooth carapace and others in specimens with a nodated carapace (see table 4). Moreover, there are significant differences in the percentage of smooth shells between stations with similar ecological conditions. Molting experiments under laboratory conditions, where nodated specimens of VIIth and VIIIth instar always molted into nodated ones and similarly unnodated specimens...
remained unnodated, suggest that genetic mechanisms determine to a great extent the expression of the nodes. As demonstrated by Kilenyi (1972) for the sexually reproducing ostracod *Cyprideis torosa* the presence or absence of nodes can be seen as the expression of a differential genetic response (transient and balanced genetic polymorphism) towards changing environmental conditions (marine - brackish - limnic).

In *Cytherissa lacustris*, juveniles up to the 3rd larval stage are nodated. During the ontogenetic development, some of them become smooth. It may be argued, that there is clonal variability in the genetically determined range of the reaction norm for tuberculation. In response to some still unknown environmental stimuli older larvae with a broad reaction norm can eventually become smooth, but specimens with a narrow reaction norm cannot. Depending on the clonal composition of each population, the proportion of individuals with broad and narrow reaction norms can vary considerably in time and space. The above mentioned variability in the response to environmental factors and in the clonal composition of populations should be carefully considered in further paleoecological studies.

**ACKNOWLEDGEMENTS**

We would like to express our thanks to Miss Barbara Mayer and Dipl. Ing. Margot Kaiser (Mondsee) for the measurements of the subfossil material, to Univ. Doz. Dr. Dan L. Danielopol for offering the opportunity to realize this work and many useful discussions, to Dr. Valeria Rossi (Parma) for her valuable assistance in some of the investigations and to Raymond Colley (London) for carefully correcting our manuscript. This research was partly financed by the Austrian Fonds zur Förderung der wissenschaftlichen Forschung, Projekt P 5614.

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PHYLOGENETICAL AFFINITIES OF CYTHERISSA WITH OTHER CYTHERIDEINAE
(VERNONIELLA, FABANELLA, NEOCYPRIDEIS, CYPRIDEIS)
A PALEONTOLOGICAL APPROACH

AFFINITES PHYLOGENETIQUES DE CYTHERISSA AVEC LES CYTHERIDEINAE VOISINS
(VERNONIELLA, FABANELLA, NEOCYPRIDEIS, CYPRIDEIS)
APPROCHE PALEONTOLOGIQUE

by

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Key-words: ostracods, Cytherideinae, phylogeny, evolution
Mots-clés: ostracodes, Cytherideinae, phylogénie, évolution

Abstract
The differentiation of the genus Cytherissa is the end-product of a long story, beginning at the Early Mesozoic with some tribulations. We reconstruct here the evolutionary lineage of the group of the Cytherideidae to which Cytherissa is related from the Jurassic genus Fabanella and Vernoniella to the Cenozoic genus Cyprideis.

Résumé

1-INTRODUCTION

The Cytherissa group has been included by taxonomists in the Cytherideidae family, Cytherideinae sub-family (Hartmann & Puri 1974), Cyprideidinae incertae tribus (Kollmann 1958) often in an isolated part of the taxonomy of the group for various reasons. We must know the diverse lineages of the group to understand the evolution of Cytherissa, very poorly represented during the Paleogene of Mongolia (Su De Ying 1984) and suddenly developing in the Pliocene.

2-THE ORIGIN OF THE CYPRIDEIDINI:

According to Babinot and Colin (1976), the genus Fabanella (Martin, 1961), present since the Lower Jurassic and up to at least the Aptian in the Lower Cretaceous, is at the origin of the Cyprideidini tribe (Kollmann, 1958) of the Cytherideinae sub-family, in which probably belongs the genus Cytherissa.
In the Middle Jurassic (Bajocian: Bate, 1965), appears a new genus, *Vernoniella* (Oertli, 1957) which shows very close morphological characteristic with *Cytherissa*. This genus, known in Western Europe is a possible ancestor of *Cytherissa*, which splits from the ancestral group during this period.

**THE GENUS **FABANELLA**: DIAGNOSIS**

The carapace is sub-oblong in lateral view, rounded anteriorly and posteriorly. The dorsal margin is straight and the ventral margin sinuous or slightly concave. The carapace is normally heavily calcified and large, often around or above 1.0 mm. long. The greatest height of the valves is often in the posterior half. The valves surface is smooth, weakly reticulate or punctate, rarely noded (*Fabanella tuberculata* Brenner). The ventral surface is often finely striate with four to five faint longitudinal ridges in each valve (Pl.1, figs.7, 8). Denticles on the posterior end are sometimes present (Pl.1, Fig.5). There is a clear ocular swelling on the antero-dorsal angle (Pl.1, figs. 1, 7, 10). The valves are equal in size and no overlap occurs apart from that at the hinge-line. Adductor muscle scars are of *Cytheridea* type, e.g. a sub-vertical row of four with two separate scars in front of the row, one in line with the first and second, the other below the fourth (fig.1c). The hinge is antimerodont with weakly crenulate cardinal elements of equal length and anterior element slightly larger than the posterior one (Pl.1, figs.2, 3). There is no accommodation groove. The inner lamella is narrow with a well developed selvage. The inner margin and the line of concrescence do not coincide; there is a narrow vestibulum (fig.1a-b). Normal pore-canals are of sieve-type (Pl.1, fig. 5). Radial pore canals are spindle-shaped, thick in their middle part, thinning at each end; about twenty anteriorly and ten posteriorly in the Early Cretaceous species *Fabanella boloniensis* (according to Kilenyi and Allen, 1968); only 16 anterior radial pore canals have been observed in the Middle Jurassic species *Fabanella sarda* by Malz, 1985).

The sexual dimorphism is well pronounced. Males are more elongated (about 15% longer than females in *Fabanella boloniensis*), and females posteriorly swollen, developing a brood-pouch.

**3-EVOLUTION OF THE GROUP DURING THE MESOZOIC: FROM FABANELLA TO NEOCYPRIDEIS**

The genus *Fabanella* s.s probably disappeared toward the end of the Lower Cretaceous period, during the Aptian (Colin et al., 1990).

During the Middle Cretaceous (Cenomanian-Turonian), it differentiated into two main lineages (fig.2).

**THE NEOCYPRIDEIS LINEAGE** (pl 2, fig 1-4)

This lineage still owns primitive characters of the genus *Fabanella*. The main characteristics of this lineage are:
- Carapace laterally ovate to subrectangular. Postero-dorsal cardinal angle well marked (left valve mainly). Valves smooth or very finely pitted. Sometimes, with more or less numerous nodes;
Phylogenetical affinities

- crenulate tripartite hinge showing a progressive asymmetry of the cardinal elements and increasing crenulation (fig.3) - narrow marginal zones (getting wider in Miocyprideis); few marginal pore canals: from about 15 in the primitive forms (Neo­cyprideis vandenboldii Gerry and Rosenfeld, 1973), to about 35 for Neocyprideis and even more in Miocyprideis (van Morkhoven, 1963). In Neogene forms, bifurcate pore canals have been observed; - up to 50 sieve-type normal pore canals in Neocyprideis are known since the Cenomano­Turonian (Grékooff and Deroo, 1956; Gerry and Rosenfeld, 1973) and Miocyprideis appears at the Oligo­Miocene boundary (Kollmann, 1958; Moyes, 1965).

THE SARLATINA-CYPRIDEIS LINEAGE (pl.3, fig 1-8)
This second lineage, originating with the genus Sarlatina in the Cenomanian, is essentially characterized by:
- strongly crenulate hinge with v-shaped teeth, tripartite in Sarlatina (fig. 4 a-c) to quadripartite in Cyprideis (fig. 4d-f)
- relatively wide marginal zone;
- numerous sinuous marginal pore canals: about 60 for Sarlatina; numerous, in variable number for Cyprideis (Sandberg, 1964);
- numerous sieve-type normal pore canals: 50 to 60 for Sarlatina, 60 to 110 for Cyprideis.

True species of Cyprideis are not known before the Miocene although possible ancestors of this genus were reported and illustrated by Liebau (1971) in the Upper Maastrichtian of Northern Spain..

THE VERNONIELLA-CYTHERISSA LINEAGE
This lineage, originates in the Middle Jurassic (Bajocian,) marine to brackish-water genus Vernoniella (Bate, 1965).

Vernoniella is characterized by:
- a triangular to elliptic outline. Surface of the valves smooth (V. sequana) or reticulate (V. caletorum), sometimes noded (V. polymorpha);
- hinge: teeth with 5-6 crenulations, median element smooth to slightly crenulate;
- marginal pore canals simple, straight, few (8). Sexual dimorphism strong.

Cytherissa is characterized by:
- a thick often reticulate carapace;

Fig. 2 - Phylogeny and hinge evolution in the Cyprideini tribe (modified after Babinot and Colin, 1976).
Fig. 2 - Phylogénie et évolution de la charnière des tribus de Cyprideini (d'après Babinot et Colin 1976).
- phenotypic nodes may be present in variable number on one or both valves;
- hinge merodont/lophodont with smooth teeth and smooth or finely crenulate median element;
- normal sieve-pores often arranged in groups.

The morphological characteristics of the genus *Cytherissa* will be detailed in another paper (Danielopol et al., 1990; Danielopol and Tétart, 1990).

**4-THE GROUP DURING THE CENOZOIC: NEOCYPRIDEIS-MIOCYPRIDEIS and CYPRIDEIS**

During the Cenozoic, both lineages defined in the Mesozoic continue their expansion. They, progressively colonize all the brackish and limnic environments.

![Fig. 3 - Internal characters of Neocyprideis-Miocyprideis groups. a: Neocyprideis apostolescui, left valve (after van Morkhoven, 1963). b: Neocyprideis williamsoniana, right valve (after Keij, 1957). c: Miocyprideis janoscheki, left valve (after Kollmann, 1960).](image1)

![Fig. 3 - Caractères internes du groupe Neocyprideis-Miocyprideis. a: Neocyprideis apostolescui, valve gauche (d’après van Morkhoven, 1963). b: Neocyprideis williamsoniana, valve droite (d’après Keij, 1957). c: Miocyprideis janoscheki; valve gauche (d’après Kollmann, 1960).](image2)

**THE NEOCYPRIDEIS-MIOCYPRIDEIS LINEAGE**

Very widespread during the Paleogene, *Neocyprideis* appears not to have persisted until the present-day: the last occurrence being in the Pliocene of Portugal (Guemet and Lauverjat, 1986) However, a whole recent group with closely related morphological characters occurs in the lake Tanganyika (pl.2, fig. 9-10).

The genus *Miocyprideis* (pl. 2, fig. 5-8) is characterized by:
- a quadrangular shape, with strong ventral overlap of the left valve over the right (Kollmann, 1958);
Phylogenetical affinities

- conspicuous anterior and posterior marginal denticles;
- valves smooth or finely pitted (Moyes, 1965);
- hinge elements crenulate. The central element has about half the length than the anterior.

Posterior elements are less crenulate than the anterior (Kollmann, 1958).

Miocyprideis, which appeared towards the end of the Oligocene, continues to occur during the Pliocene (Carbonel, 1980) and perhaps until now in the coastal zones of equatorial seas under the name of Clithrocytheridea. The possible parenthood between these two genera will not be discussed here.

THE SARLATINA-CYPRIDEIS LINEAGE

Whereas the genus Sarlatina disappears in the Late Senonian, the first Cyprideis appears, following some authors, at the end of the Cretaceous. Most likely, this genus started its development in the Neogene: First, in relation with progressive isolation of the Paratethys, then probably, with the decline of Neocyprideis replaced by Cyprideis which colonized its biotopes.

5-DISCUSSION and CONCLUSION

The group, which appeared in the Lower Jurassic, evolved without major morphological and ecological changes nor noticeable diversification during the following 100 M.Y. However, in the Middle Jurassic, applies the Vernonrella lineage (hypothetical direct ancestor of Cytherissa). This genus origina es in shallow marine waters and since the Jurassic/Cretaceous boundary, is adapted to brackish-freshwater environments.

In the Middle Cretaceous, the group, suddenly diversified in two lineages which still exist today: Neocyprideis/Miocyprideis on one side, Sarlatina/Cyprideis on the other side. The first group dominated from the beginning until the end of the Cretaceous with very morphologically stable species. On the contrary, with the onset of the Paleogene, the Neocyprideis/Miocyprideis lineage became very polymorph, essentially with regards nodation. At the Paleogene-Neogene boundary, Neocyprideis progressively disappeared and was replaced by Miocyprideis and Cyprideis, in more euryhaline biotopes.

The second group, less widespread at the beginning (Colin et al 1990) is characterized by a strict monomorphism in the genus Sarlatina (Babinot and Colin, 1976). This genus, which disappeared at the end of the Cretaceous, is replaced by Cyprideis only in the Neogene. The absence of intermediate forms is probably due to lack of data. From the Middle Miocene onwards, one can observe a real explosion of the genus Cyprideis, mainly during the closure of the Paratethys (generalization of "caspibrackish" facies).

Therefore, the evolution of the whole group based on Fabanella appears to have started in single direction, connected with the periodicity of the occurrences observed during this period for all ostracods (Whatley, 1988). With the high rates of turnover of taxa, i.e. during the Middle Cretaceous, the group splits in two lineages, which evolved parallally. From the beginning of its history, the group found its ecological preferendum in which it continues to thrive until now. It is difficult to determine with accuracy when the genus Cytherissa split from the ancestor, probably Vernonella, because of the absence of record between the Berriasian (last occurrence of Vernonella) and the Paleogene (first occurrence of Cytherissa in China. The history of the genus shows a parallel evolution more complete than in the Fabanella-Cyprideis group: Vernonella in the Berriasian is marked by a strong polymorphisme, especially, the presence of nodation. The polymorphisme coincides with its adaptation to brackish-freshwater environments Although it is impossible to determine with accuracy when the genus Cytherissa split from the ancestral phylum, the history of the genus shows a strictly parallel evolution.

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PLATE 1 / PLANCHE 1

1. carapace, right lateral view (x 70) / carapace, vue latérale côté droit (x70);
2. left valve, internal view (x 70)/valve gauche, vue interne (x70);
3. anterior element of the hinge, L.V. (x 600) / élément antérieur de la charnière, V.G. (x600);
4. posterior element of the hinge, R.V. (x 600) / élément postérieur de la charnière, V.D. (x600)
5. sieve-type pore canal (x 2000)/canal de pore en tamis (x2000).

6. Carapace, female, right lateral view (x100) / femelle, carapace, vue latérale droite (x100);
7. carapace, male, right lateral view (x100) / mâle, carapace, vue latérale droite (x100)
8. carapace, female, ventral view (x100) / femelle, carapace, vue ventrale (x100)
9. carapace, male, ventral view (x100) / mâle, carapace, vue ventrale (x100)
10. carapace, female, dorsal view (x100) / femelle, carapace, vue dorsale (x100)

Fig. 11. *Fabanella boloniensis* (Jones, 1882). Lower Cretaceous of Spain. Carapace, right lateral view (x100)
*Fabanella boloniensis* (Jones, 1882). Crétacé inférieur d'Espagne. Carapace, vue latérale droite (x 100)
PLATE 2 / PLANCHE 2

Fig. 1: **Neocyprideis sp.**, Upper Maastrichtian, Peyrecave, R.V. x 78 / *Maastrichtien terminal*, *Peyrecave*, *V.D.*x 78
Fig. 2: **Neocyprideis sp.**, Danian, Mont-Aimé, R.V. x 60 / *Danien*, *Mont-Aimé*, *V.D.*x 60
Fig. 3: **Neocyprideis grandinatus**, Upper Thanetian - Lower Ierdiien, Pradals, noded form, dorsal view x 130 / *Thanétien supérieur - Ierdiien inférieur*, *Pradals*, *forme nodée*, *vue dorsale* x 130
Fig. 4: **Neocyprideis durocortoriensis**, Thanetian, Ain. / *Thanétien*, *Ain*
   a- Right valve, internal view x 70 / *vue interne* x 70
   b- R.V. detail of the posterior element of the hinge x 400 / *V.D. détail de l'élément postérieur* x 400
   c- L.V. internal view x 70 / *vue interne* x 70
Figs. 5 - 7: **Miocyprideis janoschecki**, Saratian, Gleisdorf / *Sarmatien*, *Gleisdorf*
   5: Left valve x 100 / *Valve gauche* x 100
   6: Right valve x 105 / *Valve droite* x 105
   7: Details of the hinge / *Détails de la chéneau*:
   a- Left valve x200 / *Valve gauche* x200
   b- Right valve x 240 / *Valve droite* x 240
Figure 8: **Vernoniella sequana**, Upper Oxfordian, Paris Basin / *Oxfordien supérieur*, *Bassin de Paris*
   a- Right valve, x 100 / *Valve droite*, x 100
   b- Dorsal view x 100 / *Vue dorsale*, x 100
Figure 9: **Vernoniella caletorum**, Upper Oxfordian, Paris Basin / *Oxfordien supérieur*, *Bassin de Paris*
   a- Left valve, x 100 / *Valve gauche* x 100
   b- Right valve, x 100 / *Valve droite*, x 100
   c- Dorsal view x 100 / *Vue dorsale*, x 100
PLATE 3 / PLANCHE 3

Figs. 1-2: *Sarlatina merlensis*, Cenomanian, Portugal / Cénomanien, Portugal
1: Right valve x 70 / Valve droite, x 70
2: Dorsal view x 70 / Vue dorsale, x 70

Figs. 3-4: *Sarlatina merlensis*, Cenomanian, Dordogne / Cénomanien, Dordogne
3: Left valve / Valve gauche
   a-Internal view x 70 / Vue interne x 70
   b-Detail of the hinge, anterior alveole, x 500 / Détail de la charnière, fossette antérieure, x 500
4: Right valve / Valve droite
   a-Internal view x 60 / vue interne x 60
   b-Detail of the hinge, anterior tooth x 500 / Détail de la charnière, dent antérieure x 500
   c- Detail of the hinge, posterior tooth x 600 / Détail de la charnière, dent postérieure x 600

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7: Left valve female, internal view x 72 / Valve gauche, femelle, vue interne x 72
8: Right valve male, internal view x 75 / Valve droite, mâle, vue interne x 75
III - HISTORICAL BIOGEOGRAPHY

III - BIOGEOGRAPHIE HISTORIQUE
PRESENT AND PAST GEOGRAPHICAL–ECOLOGICAL DISTRIBUTION OF CYTHERISSA (OSTRACODA, CYTHERIDEIDAE)

DISTRIBUTION GEOGRAPHIQUE ET ECOLOGIQUE ACTUELLE ET PASSEE DE CYTHERISSA (OSTRACODA, CYTHERIDEIDAE)

by

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Mots-Clés: (Paleo)biogéographie, (paleo)écologie Cytherissa Ostracoda

Abstract:
A review on the (paleo)biogeography and (paleo)ecological distribution of the Cytherissa group from the Paleogene to the Recent is presented. The oldest Cytherissa species occurs in limnic environments from Eastern China (C. tumula). During the Pliocene, the group was already widely dispersed in various continental water bodies in Asia, Eastern Europe and North America. Several species colonized the Eastern Paratethys during the Lower Pliocene. The group diversified during the Upper Pliocene in the Dacian, Euxinian and Caspian basins. The freshening of these basins and the formation of the modern Black and Caspian seas determined the extinction of the endemic Paratethyan taxa from most of their areas. The Pleistocene Cytherissa are represented mainly by one species, C. lacustris with a Holarctic distribution. The species lived in both cold and warm phases during this period. The Recent distribution of the Cytherissa group is mainly marked by the continuation of the wide distribution of C. lacustris and a large number of endemic taxa living in Lake Baikal. The history of the Cytherissa group and especially of C. lacustris points out to a group with wide ecological tolerances to temperature and salinity fluctuations. These characteristics helped these ostracods to spread fast over large geographical areas during various periods of time.

Résumé:
Nous présentons ici une revue de la distribution (paleo)biogéographique et (paleo)écologique du groupe Cytherissa du Paléogène à la période actuelle. La plus ancienne Cytherissa connue est apparue dans des environnements limniques de l’est de la Chine (C. tumula). Au cours du Pliocène, le groupe était déjà largement dispersé dans diverses eaux continentales d’Asie, d’Europe de l’Est et d’Amérique du Nord. Plusieurs espèces ont colonisé la Paratéthys orientale au cours du Pliocène inférieur. Le groupe s’est diversifié pendant le Pliocène supérieur dans les bassins dacien, euxinien et caspien. L’adoucissement des eaux de ces bassins et la formation de la Mer Noire et de la Mer Caspienne ont provoqué l’extinction des espèces endémiques de la Paratéthys de la plus grande partie de leur aire de distribution. Les Cytherissa pliostocènes sont représentées principalement par une espèce, C. lacustris avec une distribution holarctique. A cette période, l’espèce vivait aussi bien pendant les phases chaudes que pendant les phases froides. La distribution actuelle du groupe Cytherissa est caractérisée par la conservation de la large répartition de C. lacustris ainsi que par un grand nombre d’espèces endémiques du lac Baïkal. L’histoire du groupe Cytherissa et spécialement de C. lacustris met en relief un groupe à large valence écologique vis à vis des variations de la température et de la salinité. Ces caractéristiques ont aidé le groupe à conquérir rapidement de larges aires géographiques à plusieurs moments de son histoire.
Fig. 1 - Distribution of the *Cytherissa* group during the Pliocene and the Recent (see text and figs. 2 and 3 for additional information); star (P) = Pliocene records; dot (R) = Recent records.

*Fig. 1 - Répartition du groupe *Cytherissa* au Pliocène et à l'Actuel (cf. texte et fig. 2 et 3 pour d'autres informations); étoiles (P) = présence au Pliocène; points (R) = présence au Récen.*
1-INTRODUCTION

The group of *Cytherissa* is known over more than hundred years (review in Bronshttein, 1947). Especially *Cytherissa lacustris* (Sars, 1863) which can be easily identified, is the most quoted Cytherissini species. It is known in North America and Eurasia with living and fossil (Tertiary) representatives. It is believed that *Cytherissa* occurs also at the present time in Lake Tanganyika (Mondeguer, 1984). This very wide geographical distribution and also its long time range (representatives of this genus are known since the Paleogene), invite to reconstruct the biogeographical history of this group. It would be of interest to know if *Cytherissa* has its origins in a marine ancestor, and how representatives of this group spread over the whole Eurasia and North America. This is especially the case of *C. lacustris*. The cosmopolitanism of this species is impressively contrasted, with a rich endemic fauna (16 *Cytherissa* species and subspecies in lake Baikal (Bronshtein, 1947). Of course, one could ask too how this Baikalian species flock originated. Beside Baikal, there is another interesting geographic zone, the Eastern Paratethys, where *Cytherissa* developed during a long period of time, i.e. during the second part of the Tertiary and the beginning of the Quaternary (see below). *Cytherissa* belongs to a family with marine representatives the Cytherideidae (cf. Colin and Carbonel, 1990). One could ask (as Bronshtlein, 1939) if the caspibrackish environment of the Paratethys sea was not one of the centers of origin or at least a possible way of penetration of the "Cytherissa" ancestors from the marine realm into the inland freshwaters. The type of questions we mentioned here belong to the classical topics of the historical biogeography (cf. for a review Thiennemann, 1950, but also the scenarios proposed by Kaufmann, 1896 and Zschokke, 1911). The present contribution represents the first (paleo)biogeographical review of the *Cytherissa* ostracods. Because of the heterogenous information existing in the literature, we considered useful to present our topic under four heads, each having its own special interest when integrated within the modern (paleo)biogeographical debates. These subtopics are:

- the distribution of the limnic *Cytherissa* during the Tertiary;
- the colonization of the Paratethys sea; rise and fall of the *Cytherissa bogatschovi* group;
- the history of *Cytherissa lacustris* from the Quaternary to the present-day;
- *Cytherissa* species in the old Lakes Baikal and Tanganyika.

2-DISTRIBUTION OF THE LIMNIC *CYTHERISSA* DURING THE TERTIARY

The oldest record of *Cytherissa* species is that of Keij (1957) from the Eocene of Belgium and Su (1984) from the Paleogene of the inner Mongolia in China. Keij (op.cit.) mentions *Cytherissa spatheacea* (Lienenklaus). Unfortunately, this species does not belong to a Cytherideidae genus, but to Cladarocythere Keen (Limnocytheridae). Therefore, *Cytherissa tumula* described by Su (1984) appears to be the oldest *Cytherissa* known. Kazmina (1975) encounters in the Western Siberian plain between Petropavlosk and Tomsk (fig.1) *Cytherissa hyalina* Schweyer and *Cytherissa bogatschovi plana* Klein. The former species was found in the Lower, Middle and Upper Pliocene deposits around Omsk. *Cytherissa bogatschovi plana* is reported from the Middle and Upper Pliocene in the following regions, Omsk, Novosibirsk and Tomsk. Menshikov (1982) mentions *C. hyalina, C. lacustris* and *C. bogatschovi* in Central Asia, Kazakhstan, the latter one also in Ural. One of us (R.O.) considers *C. hyalina* as a Leptocythere. All these *Cytherissa* taxa from Asia occur in freshwater lacustrine facies. However one should note that the two species mentioned by Kazmina (op.cit.) have a wider ecological and geographical distribution as they are known also from the Eastern Paratethys in the Aralo-Caspian zone (see below). Gramm (1965) mentions *Cytherissa lacustris* in the Upper Pliocene and Quaternary limnic deposits located about 80 km west from Lake Baikal in the Tunkinsky Basin. Gramm (op.cit.), in the same way as Bronshtein (1939) before him, believed that the center of origin of *Cytherissa* was the Paratethys area, but Lake Baikal was colonized by *Cytherissa* species from the surrounding areas e.g. the Tunkinsky Basin) during the late Tertiary. Lütting (1967) found *Cytherissa lacustris* in the Upper Pliocene deposits of the Megalopolis Basin in southern Greece and Brouwers (written comm. to D.L.D.) identified this species in Upper Pliocene deposits of the Northern Alaska. This demonstrates that even during the Tertiary, *C. lacustris* had already a wide geographical distribution (fig. 1, 4). The interest of these data is that as
Fig. 2: Distribution of the Cytherissa group in the Eastern Paratethys during the Late Neogene (The paleogeographic reconstructions after Gillet, 1961; Olteanu and Vekua, 1989, redrawn with modification).

Fig. 2: Répartition du groupe Cytherissa dans la Paratéthys orientale au cours du Néogène supérieur. (Reconstructions paléogéographiques modifiées d'après Gillet (1961); Olteanu et Vekua (1989).)
mentioned above, if we integrate them into the large debate about the origin of the Baikal endemic fauna and on the origin of the modern European fauna with boreo-alpine disjunction (Kozhov, 1963; Thienemann, 1950). Several alternative hypotheses try to explain the origin of some of its fauna i.e.:

a) from the Paratethys during the Upper Tertiary;

b) from the Arctic during the Quaternary;

c) from Eastern Asia, the main center beings in China (the Berg's scenario, see Kozhov, 1963).

The Recent fauna displaying a boreo-alpine disjunction was considered to be of recent Quaternary origin, resulting from the glaciation history in the Holarctic realm (see Zschokke, 1911, Thienemann, 1950; Segerstræle, 1962). The alternative hypothesis was that many of the glacial relicts of the European fauna are much older, having sometimes their origin in a Tertiary asian fauna (see e.g. the Scharf's scenario in Thienemann, 1950, but also Holmquist, 1966). The Cytherissa data presented here support the existence of such an old and widely spread limnic fauna with a wide distribution in Eurasia and North America during the Upper Tertiary, when the climate was less contrasted in comparison to later periods.

3-THE COLONIZATION OF THE PARATETHYS SEA; RISE AND FALL OF THE CYTHERISSA BOGATOSCHOVI GROUP *

The Paratethys sea and its fauna continues to fascinate us as much as it fascinated several previous generations of paleontologists. Rögl and Steininger (1983) synthetized from a large number of information the paleogeographical evolution of this sea. For our Cytherissa (paleo)biogeographic topic, the Eastern Paratethys during the late Neogene forms the general frame. The first fossil Tertiary Cytherissa were described by Livental (1929). Later on even Cytherissa lacustris, the widely distributed Recent living species, was mentioned as fossil in Upper Tertiary deposits of various basins (e.g. the Dacic Basin) of the Eastern Paratethys (Hanganu and Papaianopol, 1976).

During the time at least ten species and subspecies of Cytherissa have been mentioned to live in this sea, starting with the Upper Maeotian (about 8 M.Y.ago) and continuing to the present-day in the Caspian Sea. This situation raises the following questions:

(i) what is the origin of these Cytherissa species;

(ii) where did they exactly live;

(iii) what kind of environment did they prefer;

(iv) why most of them disappeared during different periods of time?

Here, we shall try to reconstruct the history of the Cytherissa group which lived for a long period of time in a sea with low and/or fluctuating salinities (see below). Olteanu (1989a) observed that the changes in the ostracod assemblages in the Paratethys (e.g. in the eastern part of the Pannonian Basin and/or in the Dacic Basin) display some recurrent cyclic patterns. For the period which interest us, Olteanu (1989a) mentions (p.127): .."Having this in view, one can accept the two major cycles in the evolution of the post-Badenian ostracods - the Sarmatian-Maeotian and the Pontian cycles - which also continue today in the remanant basins of the Paratethys, the Black Sea and the Caspian Lake."

Kojumdgieva (1983) showed that during the latest Chersonian (about 10,3 M.Y. ago), the Eastern Paratethys (being isolated from the Pannonian Basin) suffered a short desiccation event in the Euxinian Basin. On its margins almost desalinized places existed. In this basin, water chemistry was dominated by high concentrations of magnesium carbonate. An important extinction event also in ostracod fauna was noticed by Stancheva (1981). A new marine-brackish transgression started in the Early Maeotian (9-10 M.Y. ago) embraced the Dacic and the Euxinian basins. The salinity of this sea at the beginning approached 20 %0 and later gradually decreased especially on the margins of the basins (Kojumdgieva op.cit.). In the Dacic area, Olteanu (1989b) noted that the Upper Maeotian (8 M.Y. ago) is characterized by the "Congeria navicula " layer or the freshwater layer with ostracod marls. It is during the Lower Maeotian at the south-eastern side of the Euxinic Basin, in Abkhazia near Sukhumi (Vekua, pers. comm. to R.O.) that the first Cytherissa species (C. laevatula) was found several times by Imnadze (1974) and Popkhadze (1978) in the Upper Maeotian of Georgia. It is a species which will continue to live until the Pleistocene in the Caspian Lake. During the Lower and Middle Pontian (fig.2 A) Cytherissa occurs in Azerbaijan and Georgia (Sheidæva-Kulieva, 1966 and Vekua, pers. comm. to R.O.). The dotted line in figure 2A marks approximately the western limit of

* This section contain many written informations communicated by R.O. to D.L.D. during 1984-1989
Fig. 3 - Distribution of the *Cytherissa* group mainly *C. lacustris*, from the Pleistocene to Recent. (open circles = Pleistocene records, dots = Recent ostracods; see text for additional information).

Fig. 3 - Répartition du groupe *Cytherissa*, principalement *C. lacustris*, du Pléistocène au Récént; (cercles: présence au Pléistocène , points: présence au Récént .cf. texte pour d'autres informations)
the area occupied by Cytherissa during the Pontian stages 1 and 2 (Olteanu unpubl.). It is interesting to emphasize the lack of Cytherissa in the Pannonian and Dacic basins during these periods. During the Late Pontian, which is in Rögl and Steininger (1983) coeval with the Messinian (dated at about 6,5 M.Y.), the Pannonian, the Dacic-Euxinian and the Caspian provinces became isolated lakes. Cytherissa naphatscholchana occurred in the Caspian lake (Agalarova et al., 1961). In the Upper Pontian (P3), or the Bosphorian, one can find Cytherissa species in the Dacic Basin, in the Fore-Carpathian zone and in the Moesian Plain (e.g. Papaianopol and Olteanu, 1979). These observations point out that the origin of Cytherissa (e.g. Cytherissa bogatschovi) has to be looked in Asia.

During the Dacian and Kimmerian (about 5,5 to 3,7 M.Y. ago), the Dacian and the Euxinian basins communicated, with the water continuing to desalinize especially along the northern margin of the sea (fig. 2B). In the Dacic Basin during the Bosphorian, the salinity fluctuated around 8 % while in the Upper Dacian, the water had only 5 to 6,5 % salinity. This basin which very restricted because of an extremely high sedimentation rate in the Fore-Carpathian zone, became a predominantly freshwater body during the Romanian (3,8-1,8 M.Y. ago). Cytherissa seems to have found its maximum of development in the Dacic and the Euxinian Basins during the Dacian. Cytherissa bogatschovi bogatschovi which occurs during the Bosphorian will reach here high abundances in the Lower Dacian (= Getian) and will slowly decrease in importance during the Upper Dacian (= Parsovian). In the Upper Pontian of the two basins, beside Cytherissa bogatschovi which has strongly developed nodes, one of us (R.O.) found commonly Pontoniella excellents, Amphlocypris aff. dorsobrevis, Leptocythere (Euxinocythere) bosquetii, L. (E) cornutocostata, L. (E) andrussovi dacica, Loxoconcha bicostata, L. ludica, L. petasa, Tyrrenocythere filipesca, Bakunella aff. dorsoarcuata. Because the environment fluctuated markedly, the associations and the abundances of the different species varied in time and space.

During the Parsovian in the Dacic Basin, Cytherissa bogatschovi diminishes in importance, while Cytherissa plana dominates. At the end of the Parsovian, C. bogatschovi disappears and C. plana becomes extinct in the Romanian deposits. The only place where Cytherissa continued to exist was at the contact zone of the Dacian with the Euxinian basins which continued to have saline waters like the area which in the present-day is occupied by the Danube delta. In the last part of the Parsovian, one finds for the first time classic linnic ostracod taxa which are common in our present-day water bodies, i.e. Candona neglecta, Pseudocandona compressa, Ps. albicans, Ilyocypris sp., Cyprinotus sp., Darwinula sp. Beside these species one has to remember the presence during the Dacian of abundant populations of Cyprideis.

It is worthwhile mentioning that in the southern Fore-Carpathian, the Dacian deposits are very important (about 800 m thick), while in the Moesian Plain the sedimentation was low; one finds deposits of 30-50 m thick. Cytherissa built low density populations in the Fore-Carpathian zone as compared to very abundant populations in the latter zone. This is due to completely different environments. While in the former zone high turbulent water, rich in detritic sediment and allochthonous organic matter accumulated from the surrounding drainage basin, in the latter zone shallow and calm waters, well-oxygenated and with macrophytes dominated. Strangely enough one does not find Cytherissa during the Dacian stage in the North-Eastern Bulgaria (Stancheva, 1981).

In the Euxinian Basin, the equivalent of the Dacian and the Romanian are the Kimmerian and the Kujalnikian (see details in Olteanu and Vekua, 1989). While the former basin slowly freshened and colmated, inducing also the extinction of the Cytherissa species, the latter continued to exist. The basin freshened only on its northern margins (fig. 2B). Vekua (1975) studied the Upper Pliocene fauna of Abkhazia. She noted the presence of Cytherissa bogatschovi during the whole Kummerian and Kujalnikian. Beside, three other species were found: Cytherissa plana, C. duabica and C. galeata.

The Akchagylian transgression (fig. 2C) allowed the Euxinian basin to communicate with the Caspian domain which then extended on more than 3000 km northward as well as expanded eastward (fig. 2C). This domain had a brackish-marine salinity which continued also until the Apsheron stage when the sea started to regress (Gillet, 1961). Several Cytherissa taxa are mentioned in Akchagylian and Apsheronian deposits from Azerbaijan, Turkmenistan, around the Aral Sea and along the Volga plain in the Fore-Ural, up to Ufa (Shweijer, 1949; Mandelshtam et al., 1962; Sheidaeva-Kulieva, 1966; Karmishina, 1969; Rozjeva, 1966, Popova-Lvova, 1977 ). The most quoted species are Cytherissa naphatscholchana, C. bogatschovi and C. lacustris (= C. cascusa). Other species are C. ovatula, C. articulata, C. uralica, C. lacustriformis.*

During the Pleistocene (fig. 3), Cytherissa species continued to exist along the north-western margin and in the central part of the Euxinian Basin (around the present-day Danube delta, Crimea, southern Bessarabia, around Tiraspol and the Prut valley (Negađaev-Nikonen, 1974; Kovalenko and Negađaev-Nikonen, 1982; Olteanu, 1982 and unpubl. data). Two species are commonly mentioned, Cytherissa bogatschovi

* The morphology of those species is poorly known and their revision is needed. For instance, it would be important to know if C. cascusa is a synonym of C. lacustris, as mentioned by Menshikov (1982)
Fig. 4 - Distribution of *Cytherissa lacustris* in North America (open circles = Pleistocene records, dots = Recent records; see text for additional information).

Fig. 4 - Répartition de *Cytherissa lacustris* en Amérique du Nord (cercles : présence au Pléistocène, points : présence au Récent. cf. texte pour d'autres informations)
and *C. plana*. In the northern part of the basin during the last part of the Quaternary the margin of the Black Sea transformed in freshwater isolated lakes (limans) fed by important rivers like the Danube, Prut, Dniestr. From this desalinized habitats, practically freshwater, *Cytherissa* disappeared. In other parts (see data in Olteanu, 1982), *Cytherissa* survived even in the Neo-Euxinian phase of the Black Sea (about 22000 to 8000 years ago). Here still occurred classic Paratethyan species like *Casiolla gracilis*, accompanied by typical freshwater species which supported low salinities, e.g. *Darwinula stevensoni, Ilyocypris* sp., or by marine mesohaline species belonging to the genera *Loxoconcha, Leptocythere and Cyprideis*.

During the Old Black Sea phase (8000 to 3000 years ago), the Bosphorus strait opened and marine waters from the Aegean flowed into the Euxinian basin. The salinity increased to values similar to those of the present-day, e.g. 18 ‰, along the western coast. This increased salinity eliminated the last *Cytherissa* from the Black Sea.

This group continued to exist in the Caspian Sea also after the end of the Aps hernonian stage (about 1 M.Y. ago) until now (Faradzhov, 1966, Hofman, 1966, Naidina, 1970).

These authors mentioned isolated local populations in the central part of the Caspian Sea as well as along the western side around Aps hernon cape. The following species were mentioned: *Cytherissa naphtatscholana, C. inornis, C. bogatschovi and C. lacustris (= C. cas cus*). The salinity where these species were found does not exceed 13,5‰, the substrates are sandy, silty sands and sands. Naidina (1970) mentions that the highest densities of *Cytherissa* were found in habitats with salinities varying between 9 and 13 ‰ Hofman (op.cit.) found most of her *Cytherissa* material at depths not exceeding 150 m. The maximal abundances occur at 10-50 m deep. However, none of the authors who mentioned Recent Caspian *Cytherissa* species described the limbs of these. Naidina (1970) criticized the data of Hofman (1966), and suspected that much of the Recent material collected by him do not belong to living populations, but are subfossil or fossil material.

At the end of this section, it is interesting to come back to the results of Karmishina (1969). She noted that in the Euxinian and Caspian domains, two different morphotypes of *Cytherissa* alternated and/or dominated depending on the environmental salinities. During caspibrackish salinity-phases in the Akchagylian and Aps hernonian *Cytherissa bogatschovi* with several well-developed tubercles, were more abundant, while in periods with freshened water, e.g. in the northern part of the Caspian Sea during the end of the Akchagylian-Aps hernonian, less tuberculate *Cytherissa* developed abundantly. Therefore, Karmishina (op.cit.) divided the genus *Cytherissa* in two subgenera: *Bogatschovia* for the former type (e.g. *C. bogatschovi*) and *Cytherissa* for the latter group (which includes *C. lacustris, C. uralensis, C. fuchsiarenensis*). This observation is much similar to that previously made here by one of us (R.O.), when dealing with Upper Pontian and Dacian. *Cytherissa* specialized during the Upper Tertiary and the Quaternary to live in oligo-to mesohaline waters of the various basins of the Eastern Paratethys. The various *Cytherissa* species cooperated efficiently with the frequent salinity changes of these basins but disappeared when the salinity either decreased toward the freshwater type or increased toward meso- to polyhaline values. The local populations of the *Cytherissa* from the Paratethys domain seem to have developed osmoregulatory mechanisms similar to those recently described by Aladin (1989) for *Cyprideis torosa*. The populations from the Ponto-Caspian seas and the Baltic sea display an amphiosomatic regulation while the typical marine populations from the White Sea are confohyperosmotic. Aladin (op.cit.) proposed two subspecies for the two eco-physiologically differentiated *C. torosa*.

A similar situation could have existed with *Cytherissa lacustris* mentioned in the Caspian Sea. If ostracods with morphologically similar carapaces to those of the *C. lacustris* from Europe, but physiologically different from the populations described by Sars, really exist, then the name *C. cas cus* proposed by Mandelshtam et al. (1962) should be used. In fact this is the option used by several Russian specialists (Hofman, 1966; Naidina, 1970, etc.).

In conclusion, *Cytherissa* flourished during a very long period (millions of years) on a wide area in the Paratethys. The last representatives in the Caspian Sea should be protected in order to allow us to reconstruct their biological and morphological characteristics.

### 4-THE HISTORY OF CYTHERISSA LACUSTRIS FROM THE QUATERNARY TO THE PRESENT-DAY

At the turn of the century, there was an important discussion about the origin of the fauna which showed Boreo-alpine disjunctions. Zschokke (1911) and Kaufmann (1896) suggested that this type of limnic fauna belonged to groups with a marine origin. These authors favored mainly the idea of an Arctic marine fauna which adapted to the freshwater environment during the Quaternary and which advanced southward during phases of cold climate. The present-day psychrophilic animals in these areas are the relics of this glacial fauna widely spread during the Late Quaternary. Data presented here on the Tertiary distribution of *Cytherissa lacustris* do not support this scenario. Later on, we shall examine the geographical distribution of *Cytherissa lacustris* and some of its ecological requirements from the Quaternary to the modern times. Illies (1983) who
reviewed some of the recent biogeographical literature, proposed several rules, or principles, which should be used as a theoretical framework for the interpretation of present-day distribution of organisms. Two of Illies' biogeographical principles (Illies, op.cit., p. 402) are relevant to our \textit{C. lacustris} topic:

1. "The spread of some animal species can take place quickly and surmount serious barriers and may involve active migration or passive transport".

2. "Species that were widespread originally can be forced into one or more relictual areas (refugia) by environmental events".

\textit{Cytherissa lacustris} has a very scattered geographical distribution. The species lives mainly in cold waters from Central and North Europe, as well as in the northern part of North America (fig. 1, 3, 4). In the Lower Pleistocene, the species is already known from southern Europe in Megalopolis Basin in Greece during warm phases (Lütting, 1967), and in Northern Alaska (E. Brouwers, pers. comm. to D.L.D.). In south-eastern Europe, \textit{C. lacustris} belongs to the Middle and Upper Pleistocene in Yugoslavia, the Dinaric coast around the Crude locality (Sokac, 1975, 1979), in the eastern Slavonia e.g. at Andrijasevici (Sokac, 1976), in western Croatia around Zagreb (Sokac, 1978), in north-western Slovenia near Gorica (Sokac, 1979), in Croatia, north of Belgrade and near the boarder with Hungary (Krstic, pers. comm. to D.L.D.). In Croatia and Serbia during the Middle Pleistocene, \textit{Cytherissa lacustris} was found abundantly with littoral species which live in a moderate warm climate as those of the Mindel-Riss Interglacial and develop well during the summer period e.g. \textit{Candonopsis kingslei}, \textit{Cypridopsis vidua}, \textit{Metacypris cordata} (Sokac 1979; Krstic, pers. comm. to D.L.D.). In Slovenia, the \textit{Cytherissa lacustris} lived during the cold Russian stage (Sokac, 1979). In Central Italy, \textit{C. lacustris} is recorded by Devoto (1965) in the Liri Valley, around Cassino, about 100 km south of Rome. The Pleistocene lacustrine deposits in which our cytherid species occur are typical for a shallow lake with cold waters which existed during the Russian Glacial (about 350 000 years ago). The accompanying fauna is represented by \textit{Herpetocypris reptans}, \textit{Prionocypris zenkeri}, \textit{Fabiocyptra domestica}, \textit{Candonopsis angulata}, \textit{C. candida}, \textit{Darwinula stevensoni}, \textit{Leptocythere (A.) fallax}, etc... (Devoto, 1965). On the northern side of the Alps, \textit{Cytherissa lacustris} was found by Ohmert (1972) in Riss–Würm Interglacial lacustrine sediments during a warm climatic phase, near Laufen, and at Eurach, Bavaria (Ohmert, 1979) and at Mondsee (close to Salzburg).

The ostracod species which accompany \textit{Cytherissa} at Laufen indicate a littoral-sub-littoral habitat (presence of \textit{Cypridopsis vidua}, \textit{Metacypris cordata}), and \textit{Limmocythere sancti-patricii} indicates that the water is moderately warm, less than 20°C during summer. In the eastern part of Austria, Kollmann (1958) and Löffler (1975b, 1978) mentioned \textit{C. lacustris} in Upper Pleistocene lacustrine facies around the present-day Neusiedlersee and near Einsenstadt. Löffler assumed (op.cit.) that shallow lake located around Neusiedl had cold waters, as few species occur and \textit{C. lacustris} was associated to \textit{L.sancti-patricii}. There are several data indicating the presence of \textit{C. lacustris} in Northern Germany during both cold and warmer phases (Pietrzeniuk, 1987). Here we present several examples: around Berlin, Diebel and Pietrzeniuk (1975) found \textit{C. lacustris} in the Holstein and Eemian interglacial facies which are indicative of a warm phase. Kempf (1967) found our cytherid at Tönisberg near Krefeld also in deposits dated Holstein Interglacial. One should mention also Triebel (1941) who quoted this species from the Paludinenbank deposits at Furstenberg on the Oder. Scharf (1984) discussed the presence of \textit{C. lacustris} during a cold climatic phase of the Upper Pleistocene (Weichsel stage) in the western part of Germany at Meerfelder Mar in Eifel. Our cytherid occurs still today in Laacher Lake in oligotrophic and sublittoral habitats.

The most detailed ecotaxonomical distribution of \textit{Cytherissa lacustris} occurring from Middle Pleistocene (Holstein Interglacial) to the Holocene (Atlanticum) are those of Mania (1967) who studied the deposits of the Ascherlebener paleolake in the Fore-Harz mountains, west of Berlin. \textit{C. lacustris} occurs with few interruptions in cold and warm lacustrine waters mostly in a shallow lake which changed from oligotrophic to an eutrophic phase during the Holocene.

In Great Britain, there is a long tradition in the study of \textit{C. lacustris}: Brady, 1868) Brady et al. (1874), Brady and Norman (1889), and more recently, Robinson, Whatley and Kaye (1971), studied the occurrence of \textit{Cytherissa} at the Pleistocene and Holocene sites. Especially interesting is the discovery of Whatley and Kaye (1971) who recorded this species in Eemian Interglacial deposits from Selsey, Sussex.

\textit{Cytherissa lacustris} occurs in Western Siberia in the Kurganskij and Bulmaevskij zone, respectively east and west of Petropavlosk (Lyuvinova et al., 1960), and in the Sanggan Valley (Middle Pleistocene), near Beijing, China (Huang, 1985).

In the northern part of North America, \textit{Cytherissa lacustris} occurs throughout the Pleistocene and the Holocene on the northern slope of Alaska in the Arctic coastal plain, e.g. Ilkkipuk area, Gubik formation (Swain, 1961; Brouwers, pers. comm. to D.L.D.), in Yukon (Delorme, 1968), Illinois (Staplin, 1963), Manitoba (Klassen et al., 1967) and in Ontario near Toronto (Poplawski and Karrow, 1981). Most of the sites with \textit{Cytherissa lacustris} in the Pleistocene deposits of North-America are known to have had cold waters typical of subarctic or temperate climate. The facies condition are those of shallow oligotrophic lakes.
Alaska, Brouwers found it also in small pond facies. Staplin (op.cit.) reported in the Chicago-Michigan lake area deposits belonging to facies of Lower and Upper Pleistocene in the Aftonian and Wisconsin stages indicating cool alkaline lacustrine waters. Poplawski and Karrow (1981) mentioned, in the Sangamon Interglacial, *C. lacustris*, in very cold and/or temperate climate and oligotrophic conditions.

*Cytherissa lacustris* continued during the Late Glacial and the Holocene to have a large geographical distribution. Lusted (1986) found this species in North-Africa (Morocco), south of Rabat in the Middle Atlas, at an altitude of 1626 m. Cytherissa occurred in sub-Recent sediments (1200 Y BP) of a lake.

In Northern Italy, Garofalo and Pugliese (in press) found the species in the Friuli Fore-Alps (Rio Vodizza basin) in a shallow oligotrophic lake, sublittoral facies with aparently cold waters, as indicated by the presence of a psychrophilous species *Cavernocypris subterranea*, and the quantitative and qualitative structure of the ostracod-assemblage. One of us (H.L.) studied intensively the paleolimnology of various lakes in Central Europe. *Cytherissa lacustris* is one of the first species to colonize the alpine and pre-alpine lakes, after the deglaciation in the Late Glacial. The most frequent species found together with *C. lacustris* are: *Candona neglecta*, *C. candida* and *Limnocythere sancti-patricii*.

At the end of the Pleistocene and the first part of the Holocene, *Cytherissa* disappears from many lakes in the Alpine area and concurrently, *Chaoborus flavicans* starts to increase in number. This is interpreted as the onset of a meromictic phase in the lakes history: anoxic conditions prevail at the bottom of the lake in the deep (profundal) zone. This colonization and local extinction patterns was described for small shallow lakes in Austria and Switzerland, e.g. Kleineisee in Carinthia, Lobingensee in Switzerland (Löffler, 1983, 1986). Here the extinction occurred during the Bølling (13000 Y BP), while in deeper and larger lakes it occurred later in the Subatlanticum (about 2500 Y BP), e.g., lake Bled in Yugoslavia, Langsee and Klopeninersee, during the Allerød, 12000 Y BP (Löffler, 1978, 1984). The extinction of *C. lacustris* in Lake Bled in Subatlanticum seems to be due to deforestation during the Bronze-Age. In still deeper and larger lakes, like Lake Constance or Mondsee, *Cytherissa lacustris* disappeared in Recent times during the anthropic eutrophication, with changes in the lake sediment texture and anoxic conditions (Löffler, 1969, 1972; Handl, 1989; Geiger, 1990a; Danielopol et al., 1990).

Other Holocene deposits where *C. lacustris* was found are in Germany: Weissensee in Bavaria (Absolon, 1973), Laacher lake in the Eifel area (Kempf and Scharf, 1980), Baltic Sea in the Mecklenburger Bay (Diebel, 1965). In this latter case, the ostracod assemblages are formed by typical freshwater species, living in a shallow habitat of a Prelittorina lake. In the Netherlands, Wagner (1957) mentions the species in Holocene sediments. In North-America, Benson and Mc Donald (1964) and Karrow et al. (1975) found this cytherid in shallow habitat of a Prelittorina lake. In the Netherlands, Wagner (1957) mentions the species in Holocene sediments. In North-America, Benson and Mc Donald (1964) and Karrow et al. (1975) found this cytherid in Holocene deposits of Great Lakes (Erie and Algonchin). Delorme (1971) reports it in a pond (Holocene sediments near Somerset, Manitoba). The present-day distribution shows that *C. lacustris* lived or still lives in many lakes in Italy. In Italy, the species is known to occur in Lago di Bracciano, north of Rome, Lago Maggiore, L. Lugano, L. Como (Zschochke, 1911). There are many pre-alpine and alpine lakes in Switzerland with living *Cytherissa*. In Vierwaldstättersee, this species occurs at a depth of 210 m (Zschockke, op.cit.) while in the Lüner lake, a high alpine lake, *C. lacustris* lives in the littoral zone at a depth of 1m. Schmassmann (1924) considering this occurrence suggested that *C. lacustris* is a cold stenothermic species which does not live in Central European shallow lakes. The Pleistocene data as well as information on the north-european sites contradicts this assertion and confirms the assumption by one of us (H.L.) that *C. lacustris* has a wide tolerance to temperature (Geiger 1990b). In Austria, *C. lacustris* lives in Carinthia, in Kloopen/ersee (Löffler, 1971) in the Salzkammergut lake area, Mondsee, Wolfgangsee, Attersee, etc. (Kaufmann, 1896; Graf, 1938; Löffler, 1975a, 1983...). In these lakes, *C. lacustris* lives from the sublittoral, 2-3 m deep to the profundal zone, 150 m deep (e.g. in Attersee).

The highest densities seem to occur in oligo-mesotrophic lakes and at depths between 12 and 40m (cf. for Mondsee, data in Geiger, 1990a; Danielopol et al., 1990).

In Germany, the species lives in the Eifel moraine lake area, e.g. Laacher lake (Scharf, 1980) in northern part of Germany, Zensee in Brandenburg (Zschochke, 1911), and in the Kiel area near the Schlei (Delling, 1981). This pond (Hemmelsmark, 1990) is especially interesting because *Cytherissa* lives in 1.5 m deep in slightly saline waters (0.5-1.5%) and in an environment with strongly annual temperature fluctuations during the year (20°C differences between winter and summer). Two typical ostracods living in brackish water occur also in this pond, *Cyprideis torosa* and *Cytheromorpha fusca*.

In Poland, Sywula (1977) mentions this species in one of the Konnin lakes (the Mikorzynskie lake at 20m deep). The species occurs in the Szczecin area, in Miedwie, Morzycko and Wielkie Pelcko lakes as well as in the Mazurian lakes area (Sywula, 1990).

In Soviet Union, one finds this species in several Karelian lakes (e.g. Onega lake) at depths varying between 2.8 m and 105 m, as well as in the Rubinsk reservoir (Akatova and Yarvekyulg, 1965) and in the large lakes of Sevan and Telets (Bronshtein, 1947).
Cytherissa lacustris in Scandinavia is rather well known. Sars (1925) mentioned it in several large lakes from Norway, living on soft bottom (e.g. in Mjøsøen, Tyri fjord, Aarangen, etc..) as well as in mountain lakes like Afsjø on the Dovre Plateau. There are a large number of records in Sweden mentioned by Ekman (1914), and Alm (1915).

In lake Vettern, Cytherissa lives at 13 to 120m deep, in Nömen-see, between 6-17m, other lakes are Iføsjøen, Mälaren, Vettern, etc.. The northeast record is Geautasjøen (Lappland). An extremely interesting record is the presence of this ostracod in a swamp near Uppsala. From such shallow habitats, Cytherissa can be passively transported by birds and other animals to other lakes and ponds (Absolon, 1975).

In Southern Finland, Holopainen and Paasivirta (1977) studied the quantitative distribution of Cytherissa in Lake Päljärvi, where it occurs from 2 to 65 m deep: up to 16000 ind.m-2 occur at 14m deep.

In Great Britain, recent Cytherissa occurs in Loch Leven, and a canal near Morningside as well as in Glasgow and Paisley canals (Brady and Norman, 1889).

In Northern Ireland, Brady and Norman (1889) found it in Loch Neagh.

Two interesting records are those of Poulsen (1939) in Southern and Western Iceland. The origins of the present-day aquatic fauna of Iceland is controversial, one hypothesis is that it was introduced by drift ice during the Post-Glacial. One should note that no peat or lacustrine sediments from the Late-Glacial time exist (Einaron and Albertson, 1988).

In Northern America, Delorme (1970) noted that Cytherissa is common in deep lakes of the boreal forests of Canada at sites deeper than 3m. In lake Erie, the species is now restricted to relicual areas due to the eutrophication of the lake which occurred in the last fifty years (Delorme, 1978). Other localities are lake Mendota in the U.S.A., where it occured on gyttja sediment, and as fossil, it is known from Great Slave lakes.

Brehm (1927), mentioned the species from the Hokkaido in Japan, occurring in the lake Aokiko at 832m above the sea level. The annual mean temperature around the lake is 8°C with maximum in July (22°C) and a minimum in January (-2°C).

ChingHai lake in Nan-Shan area in China, at more than 3000m altitude contains Cytherissa lacustris (Huang, 1984). This lake is 104 km long and 62 km wide. The water is alkaline, pH: 9,4, the salinity of 12-13‰ and the maximal depth is 29m. The water temperature at the bottom varies between summer and winter from 9,5 to 3,3°C. Note that this area was glaciated during the Pleistocene.

In conclusion, Cytherissa lacustris from the Quaternary to the Recent always had a very wide (Holarctic) geographical distribution. The species is certainly eurytherm (however prefering cold waters), which entailed the rapid colonization of many habitats in the northern hemisphere dominated by cool or cold climate. The rapid recolonization of areas which were formerly glaciated is due to its capacity to live in oligotrophic lacustrine environments and most probably to its capacity to resist during passive dispersal.

The history of Cytherissa lacustris confirms the first principle of Illies (1983) mentioned at the beginning of this section. No evidence exists that Cytherissa lacustris follows the second principle of Illies which resembles the Rouch and Danielopol’s scenario (1987) called “The refugium under constraint model”, and which was one of the most accepted explanations for the origin of the subterranean fauna. It was refuted by Rouch and Danielopol (op.cit.). Cytherissa lacustris appeared to be an excellent colonizer of the septentrional cold areas of the Holarctic, being an eurythermic species with preferences for cold waters.

It is our impression that within the wide geographical range of this species are their populations which adapted to the local conditions (e.g. the population from lake ChingHai living in saline waters, or the C. lacustris populations from Northern Alaska, etc...). The alpine area was not probably colonized for the first time during the Late Glacial by septentrional populations. C. lacustris could have existed in these areas even earlier as this species had a Holarctic distribution since the Upper Tertiary. These data are more in accord with ideas of Holmquist (1966) and concord with the (paleo)biogeographical data concerning other ostracod groups like Leucocythere (Danielopol et al., 1989) and Cavernocypris (Marmonier et al., 1989).
5-THE CYTHERISSA OF BAIKAL AND TANGANYIKA

Baikal and Tanganyika lakes have several peculiarities in common: they are old lakes which originated in the Tertiary, they are very deep and large, e.g. the present-day Lake Baikal has a maximum depth of 1620m and 636 km long, they, harbour a very rich endemic fauna represented by species flocks of various animal groups (Brooks, 1950; Kozhov, 1963). The presence of Cytherissa in these lakes has a biogeographical and evolutionary interest.

How and when did this ostracod group colonize these lakes; how did it evolve later on?

Bronshtein (1930, 1947) described 13 species and 3 subspecies of Cytherissa, all endemic taxa from the Baikal; Mondeguer (1984) mentioned Cytherissa sp. in the northern part of the lake Tanganyika. It is well known that this latter lake harbours a very rich endemic fauna of Limnocytheridae and Cytherideidae (cf. e.g. Rome, 1962). A close examination of the "Cytherissa" material from the Mondeguer collection (cf. Danielopol et al., 1990a) showed us that this is a wrong identification i.e. the valves figured and studied by Mondeguer belong to Romecytheridea, a Cyprideidini group and not to Cytherissini. A closer examination of the cytherideids from the lake Tanganyika by one of us (P.C.) showed us remarkable analogies between the endemic species flocks of "Cyprideis" and Romecytheridea with the Cytherissa flock from the Baikal.

In a previous section, we noted that the origin of the Baikalian fauna was the subject of many discussions. The origin of the endemic Cytherissa has to be looked for in a pre-Quaternary widely spread limnic fauna. Here, we shall examine the ecological distribution of the Cytherissa species flock in the Baikal lake.

The 16 taxa belong to three groups of species, i.e. C. lacustris (one species with 2 subspecies), C. servoni (8 species, 1 subspecies) and C. tuberculata (5 species). These species have been found in the lake Baikal from 1.5m to 149m deep, the most frequent and the highest densities occur between 3 and 50m depth. Such species like C. lata or C. tuberculata live on a very wide type of substrate from fine grained silty sediments to coarse sand, gravel and between stones. The temperature tolerance for the littoral species is high e.g. C. tuberculata in the zone of the Maloje Sea is submitted to annual temperature fluctuations of more than 10°C (Bronshtein, 1947, Kozhov, 1963). The origin of the endemic taxa in this lake is attributed to the slow subsidence of the bottom and the gradual appearance of new habitats in which the lacustrine old fauna gradually speciated during a long period of time (Kozhov, 1963). It is interesting to mention that the widely distributed species in the Holarctic, Cytherissa lacustris, is closely related with at least one endemic taxon i.e. C. lacustris baikalensis. * The other two groups have no known relatives outside the Baikal and the morphological data suggest not very closely phylogenetical relationships. This implies that the lake was colonized by the Cytherideidae at different times independently; maybe the representatives of C. servoni and C. tuberculata in more remoted times followed at a later time by C. lacustris. If one accepts the intralacustrine speciation model dependent on the appearance of empty places and looks to the wide bathymetric range within which some of the Cytherissa species are distributed, than one has to accept the existence of important migrations outside the original habitats where the speciation occurred. For instance, C. servoni was found on the northern side of the lake at the Maloje Sea at the following depths: 1.5, 25, 39 and 75 m and one of us (H.L.) have material from a remoted site about 80 km. far on the southern side in front of the Selenga delta.

Maybe, the ecological tolerance of some of these Cytherissa species explains this wide spatial distribution, as well as that within the three groups of species, C. lacustris, C. servoni and C. tuberculata, the speciation rate is not very high (see above) as compared, for instance, to the ostracod species flocks from other lakes like the Tanganyika (Rome, 1962; Carbonel and Rouxel, unpubl.; Wouters, unpubl.). The exact mechanism of speciation of the Cytherissa in Lake Baikal remains a problem for future studies.

In conclusion, we believe that new ecological and zoogeographical information is needed to explain the origin and the present-day distribution of the endemic Baikalian Cytherissa...

* One of us (D.L.D.) considers C. lacustros baikalensis a valid species because of differences in the chaetotaxy of the antennula e.g. the distal setae of the IV + V segment are much longer in the baikalian taxon as in the nominate C. lacustris species (Bronstein, 1947; Danielopol and Téart, 1990)
6-CONCLUSIONS

1-The present *Cytherissa* taxa belong to an old limnic group with a marine origin, most probably known since the Paleogene in Eastern Asia.

2-This group had a widely distribution during the Upper Tertiary with records in Eurasia and even North America.

3-During the Pliocene, limnic *Cytherissa* from Asia colonized the Eastern Paratethys and adapted to oligo- and/or mesohaline waters. The Paratethyan *Cytherissa* disappeared either due to the freshening of various basins, or to an increase of the salinity. This happened repeatedly in the Dacian, the Euxinian and the Caspian basins.

4-*Cytherissa lacustris* is a generalist species known since the Pliocene in the Holarctic. It is an eurythermic species with preferences for cold waters. It existed in Southern Europe already in the Lower Pleistocene. During the Middle and Upper Pleistocene in both cold and warm climatic stages, *C. lacustris* dispersed widely.

5-In Europe, there is no indication of a directionnal migration from the northern cold zones towards southern areas during this period. The Alpine zone did not serve as a refuge to *C. lacustris*.

6-The Lake Baikal, one of the deepest and oldest freshwater bodies, contains 16 endemic *Cytherissa* taxa which live in both shallow and deep lake habitats over a wide area. For some of these species the ecological tolerance seems to be wide considering the substrate and the thermic requirements.

7-In the old Lake Tanganyika, instead of *Cytherissa*, a diverse endemic fauna of Cyprideidini occur.

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A REVIEW ON THE PALEOBIOGEOGRAPHY AND PALEOECOLOGY OF THE CLOSEST GROUPS OF CYTHERISSA: FROM THE MESOZOIC FABANELLA AND VERNONIELLA TO THE CENOZOIC CYPRIDEIS

PALEOBIOGEOGRAPHIE ET PALEOECOLOGIE DES GROUPES LES PLUS PROCHES DE CYTHERISSA : DES FABANELLA ET VERNONIELLA MESOZOIQUES AUX CYPRIDEIS CENOZOIQUES

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Mots-Clés : ostracodes, paléobiogéographie, Jurassique-Crétacé, Tertiaire-Actuel.

Abstract:
The distribution of the closely related Cytherideinae groups of Cytherissa is herewith demonstrated since its differentiation in the Lower Jurassic. Ecological and paleoecological data are also given.

Résumé:
Nous donnons la répartition des groupes de Cytherideinae les plus proches de Cytherissa depuis leur différenciation au Jurassique inférieur. Les données écologiques et paleoécologiques sont également fournies.

1 - INTRODUCTION

It is a well-established fact (Colin and Carbonel, 1990), that the genus Cytherissa evolved within a very diversified group, that is largely represented and which colonized many different types of environments. In order to understanding better its recent geographical distribution - very dispersed - it is necessary to study the geographical distribution of the entire group since its origins. To this effect, the distribution of each of the main genera of the group (Fabanella, Vernoniella, Sarlatina, Neocyprideis, Cyprideis and Cytherissa) are presented here on paleogeographical maps at different geological periods.
Fig. 1: Distribution of *Fabanella* during Lower Jurassic (about 180 M.Y.) (Maps after Smith and Briden, 1977)
Répartition de *Fabanella* au Jurassique inférieur (environ 180 M.A.) (Cartes d’après Smith et Briden, 1977)

Fig. 2: Distribution of *Fabanella* and *Vernoniella* during Middle Jurassic (about 160 M.Y.)
Répartition de *Fabanella* et de *Vernoniella* au Jurassique moyen (environ 160 M.A.)
THE ORIGINS: THE GENUS **FABANELLA** IN THE LOWER JURASSIC (fig. 1)

Until very recently, the genus *Fabanella* which is considered to be at the origin of the Cyprideidini tribe (Babinot and Colin, 1976; Colin et Carbonel, 1990), was thought to have started in the Middle Jurassic. Recently, Rosenfeld et al., (1988b), described the oldest known species of the genus, *Fabanella ramonensis* Rosenfeld and Honigstein, in the Ardon Formation, of Early Jurassic, probably Pliensbachian age of Israel. *Fabanella ramonensis* is associated with both non-marine genera such as *Darwinula* and *Theriosynoecum (Bisulcocypris auct.)* and the shallow-marine genera *Cytherella* and *Ektyphocythere*.

THE SECOND STEP: THE MIDDLE JURASSIC (fig. 2).

During the Middle Jurassic (Bajocian-Bathonian), the genus *Fabanella* displays a much wider geographical distribution. It is especially well represented in Europe, particularly in France (Oertli in Bernard et. al., 1957; Depêche, 1969; Rohr, 1976), in Great-Britain (Bate, 1967) and in Sardinia (Malz, 1985). It was recorded in different types of environments. In the Bathonian Upper Estuarine Series of Great-Britain, it occurs in great numbers, dominating an assemblage of shallow-marine genera: *Glyptocythere. Progonocythere. Fastigatocythere, Schuleridea* (Malz, 1985). In Sardinia, Malz (1985), found *Fabanella sarda* in monotypic assemblages associated with numerous charophyte oogonia and in other levels associated with both non-marine genera (*Theriosynoecum, Darwinula, Timiriasevia*) and marine forms (*Kinkelinella, Pontocyprella, Progonocythere...*). In the Bathonian of southern France, Depêche (1969) observed an inverse relationship between the abundance of *Fabanella bathonica* and Charophyta.

The genus is also reported in the Bathonian of the Georges Bank-Scotian Basins offshore Eastern Canada (Ascoli, 1988).

The genus *Vernoniella*, possible ancestor of *Cytherissa* (Colin and Carbonel, 1990), appears in the Bajocian of Great Britain in shallow marine sediments (Bate, 1965).

FROM EXPLOSION TO EXTINCTION: UPPER JURASSIC-LOWER CRETACEOUS (fig. 3).

The genus *Fabanella* became especially common in the Upper Jurassic and Lower Cretaceous non-marine "Purbecko-Wealden facies" of northern and western Europe, which ended toward the end of the Barremian.

It is still present in the geographical area in which it was already known in the Middle Jurassic: Sardinia (Colin et al., 1984), France (Oertli, 1963; Colin and Oertli, 1985) and Great-Britain (Anderson, 1967; Anderson and Bazley, 1971).

During the Middle Jurassic, its geographical distribution increased tremendously. It has been reported, represented by a number of species, the most common being *Fabanella ansata* (Jones, 1855) and *Fabanella boloniensis* (Jones, 1882), in northern Europe (Denmark and Sweden: Christensen, 1963), the Netherlands (Sung, 1955), Germany (Martin, 1961; Wienholz, 1968), Poland (Bielecka, 1975), the Celtic Sea offshore Ireland (Colin et al., 1981), Switzerland (Bartenstein and Burri, 1954), Romania (Olteanu unpublished), and in southern Europe such as in Spain (Brenner, 1976) and Portugal (Rey et al., 1968).

The genus is also sporadically known in the African continent: Tunisia (Glintzboeckel and Magné 1959), Algeria (Benest et al., 1977) and Ethiopia (unpublished).

In North America, various species attributed to the genus *Fabanella* have been reported in the Early Cretaceous from the East Coast of the U.S.A. (Swain and Brown, 1972).

The occurrence of *Fabanella* is still unknown in the Soviet Union, China (Su, 1986), Equatorial Africa and South America, although thick deposits of non-marine Jurassic-Lower Cretaceous sediments exist in these areas.

During the Upper Jurassic and Lower Cretaceous, the genus *Fabanella* probably lived in the same types of environments as those related to the recent *Cyprideis*. It is commonly accepted as characterizing brackish water paleoenvironments. It certainly had a very wide tolerance and was probably able to live under hyperhaline and oligohaline conditions (Kilenyi and Neale, 1978). Neale (1988) gives a salinity range for *Fabanella* of 5 to 22% and characterizes it as a meso-polyhaline genus. During the dominantly freshwater environments of the Purbecko-Wealden dominated by the cypridid genus *Cypridea*, the presence of the genus *Fabanella* amongst other genera (*Sternebergella, Miocytheridea, Schuleridea, Hutsonia...*), is a reliable indicator of marine influences (S, saline and E, hypersaline phases of Anderson, 1967) (Kilenyi and Allen, 1968).
Fig.- 3: Distribution of Fabanella and Vernoniella from Upper Jurassic to Lower Cretaceous (about 120 M.Y.)
Répartition de Fabanella et de Vernoniella du Jurassique supérieur au Crétacé inférieur (environ 120 M.A.)

Fig.- 4: Distribution of Sarlatina and Neocyprideis during Upper Cretaceous (about 80 M.Y.)
Répartition de Sarlatina et Neocyprideis au Crétacé supérieur (environ 80 M.A.)
In the Purbeck beds of Southern England, species of *Fabanella* are generally the only species found in the gypsum bearing strata (Anderson and Bazley, 1971). Barker (1963) showed that the size of *Fabanella boloniensis* (Jones) was linked to salinity; euryhaline forms being smaller, marine forms larger.

In the Oxfordian / Kimmeridgian, *Vernoniella* is known from shallow-water marine deposits in Great-Britain (Kilenyi, 1978), Germany (Glashoff, 1964), France (Oertli, 1957, 1958) and Switzerland (Oertli, 1959).

In the Berriasian, the genus adapts non-marine environments ("Purbeckian facies") and is known from Spain (Brenner, 1976). At the same time, it develops a strong polymorphism mainly marked by appearance of clear nodation.

**5 - THE RELAY: SARLATINA AND NEOCYPRIDEIS: MIDDLE AND UPPER CRETAceous** (fig. 4)

As shown by Babinot and Colin (1976) (see also Colin and Carbonel, 1990), the genus *Fabanella* which disappeared in the late part of the Lower Cretaceous with the end of the "Purbecko-Wealden" facies, gave birth during the Middle Cretaceous (Cenomano-Turonian) to two lineages: the *Sarlatina* and the *Neocyprideis* lineages.

**SARLATINA**

The genus *Sarlatina* probably originated during the Cenomanian. During this period, it occurred mainly in south-western France and Portugal (Babinot and Colin, 1976) within brackish-water environments. The genus has been also found in Algeria (Grêkoff, 1968) and possibly the Niger Republic (unpublished). It locally persisted during the Early Senonian in the southern part of the Soviet Union (*Neocyprideis leguminiformis* Andreev, 1971) and the Niger Republic (unpublished). A related genus from the Cenomanian of the Coast of the U.S.A. is *Fossocytheridea* (Swain and Brown, 1964).

In all these areas, *Sarlatina* occurs in monospecific populations or associated with shallow-marine ostracods.

**NEOCYPRIDEIS**

The genus *Neocyprideis*, which has origins back to the Cenomano-Turonian, really started to diversify during the Paleogene.

As well represented in the Late Paleocene of southern France (Tambareau, 1972), the Late Paleocene-Eocene of the Anglo-belgo-parisian basin (Keen, 1977, 1978; Keij, 1957; Ducasse et al., 1985), the Eocene of Hungary (Monostori, 1985), the genus persists up to the Oligocene of England with *N. williamsoniana* (Bosquet), and into the lower Miocene with *N. aquitanica*. Kollmann & Moyes, 1963 of south-western France, Portugal and Turkey, (Carbonel, 1985; Nascimento, 1988; Bassiouni, 1979), and of Germany with *N. enkheimensis* (Malz,1973).

The diversification of the genus during the Paleogene in southern England, allowed Keen (1978) to propose a zonation for the brackish environments based on the succession of five species of *Neocyprideis*.
Fig. 5: Distribution of Neocyprideis during the Paleogene (about 40 M.Y.)
Répartition de Neocyprideis au Paleogène (environ 40 M.A.)

Fig. 6: Distribution of Neocyprideis, Miocyprideis and Cyprideis from Neogene to Quaternary (20 last M.Y.)
Répartition de Neocyprideis, Miocyprideis et Cyprideis du Neogène au Quaternaire (20 derniers M.A.)
The youngest fossil representative of the genus, *N.lusitanicus*, was found in the Pliocene of Portugal (Guernet and Lauverjat, 1986).

Beside Europe, *Neocyprideis* is located in the lower Eocene of Senegal (Carbonnel, 1989: *N.priani*). The author suggested a migration from southern Europe with a strongly hypothetical relay in Morocco. It has also been reported from the Paleogene of India (McKenzie, 1972; Guha, 1983), and in the Lower Eocene of Khazakhstan in U.S.S.R. (Nikolaeva, 1989).

Recent forms of *Neocyprideis* are unknown. But, some species, identified as "*Cyprideis s.I." from the lake Tanganyika (Le Fèvre 1985 unpubl., Carbonel and Rouxel 1987, 1988, unpubl.) are likely to be strongly related (Colin and Carbonel, 1990).

Paleoecologically, the genus *Neocyprideis* was sometimes found in lacustrine-lagoonal environments (salinity from 0.5 to 5\%), associated with *Kovalevskienia, Candonopsis, Paralimnocythere* (Carbonel et al., 1986) often, in estuarine-lagoonal environments (brackish waters with salinity from 3 to 16.5 \%) and in monospecific assemblages or with few species as *Kovalevskiella, Cytheromorpha, Cladarocythere, Hemicypredes, Vetustocytheridea* and in polyhaline environments (salinity 16.5 to 33 \%) in more diversified associations with *Cladarocythere, Cyamocytheridea, Haplocytheridea, Hemicypredes*. (Keen, 1978).

**MIOCYPRIDEIS**

This genus (we consider only the Neogene species, because the recent forms are probably to be related to the genus *Clithrocytheridea* as suggested by the paper of Kollmann, 1958), which is different from *Neocyprideis* (Colin and Carbonel, 1990), inhabited brackish to coastal environments by the end of the Oligocene in south-western France (Moyes, 1965; Carbonel, 1985), in the Tejo basin, Portugal (Nascimento, 1988), in Italy (Moos, 1962), in Germany (Dexbl et al., 1972), in the Vienna basin, Austria (Kollmann 1958), in Turkey (Bassioni 1979), in Morocco (Carbonel, 1980), and in India, (McKenzie, 1972).

**CYPRIDEIS**

This genus appears in the Late Miocene and within a very short time,becomes largely distributed: in the Tethyan and Paratethyan paleoenvironments (Krstic, 1968; Krstic and Ulianova, 1970; Mehes, 1908; Zalanyi, 1944; Gramann, 1969; Agalarova et al.,1961; Bassioni, 1979, Carbonnel,1978), in southern Spain (van Harten, 1974, 1980). Simultaneously, the genus appears in America (Van den Bold, 1963).

During the Pliocene, *Cyprideis* always lives in Europe (South Europe :van Harten, 1974, Ruggieri, 1952; North Europe: Jones, 1856) and occurs also in North Africa (Carbonel, 1980), in East Africa (Carbonel and Peypoquet, 1979; Peypoquet et al 1983), in Asia (Mandelstamm et al., 1962) and in Caribbean (Van den Bold, 1976).


Africa in all regions:
- N.Africa (Carbonel and Pujos, 1982; Carbonel, 1983; Lusted, 1986; Gasse et al, 1987),
- Central and East Africa (Lindroth, 1956; Carbonel and Peypoquet 1979; Peypoquet and Carbonel 1980; Carbonel and Rouxel, 1987-1988, unpublished; Cohen, 1986); Le Fèvre, unpublished; Wouters, 1988).
- Western Africa: (Carbonel and Pinson, 1979; Dubar, 1988; Carbonel, 1989);
- America: (Sandberg, 1964; Mc Kenzie, 1967).

The cosmopolitan distribution of *Cyprideis* is probably due to a "passive dispersion" by migratory birds (Sandberg, 1964; Mc Kenzie, 1967).

**7 - CONCLUSIONS.**

*Vernoniella*, apparently ancestor of the *Cytherissa* lineage, originally restricted to the north-western Europe during the Middle and Late Jurassic, extends its area of distribution to South-Western Europe at the
base of Cretaceous. The first known true Cytherissa appears only in the Paleogene in China (Danielopol et al., 1990)

Groups closely related to Cytherissa show a very large and rapid distribution based mainly on an apparently unique ancestral genus, Fabanella, which originated in the Early Jurassic. However, its evolution slows down considerably to attain explosion in the Tertiary. The first representatives of the group lived at the beginning in brackish waters and later on adapts sometimes to freshwater, but mineralized environments, namely in large, ancient inland lakes such as Tanganyika or Titicaca.

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THE DISPERSAL ABILITY OF CYTHERISSA LACUSTRIS

L'APTITUDE A LA DISPERSION DE CYTHERISSA LACUSTRIS

by

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Key-Words: ostracods, Cytherissa genetics, dispersal ability, biogeography.
Mots Clés: ostracodes, génétique de Cytherissa, aptitude à la dispersion, biogéographie.

Abstract

On the basis of electrophoretic studies on esterase polymorphism in Cytherissa lacustris (Sars) from lakes belonging to different drainage-basins it is argued that its populations inhabiting separate lakes are only slightly isolated from one another. The important part that birds play in dispersing C. lacustris specimens is suggested.

Résumé

A partir d'électrophorèses sur le polymorphisme des estérases chez Cytherissa lacustris (Sars), de lacs appartenant à des systèmes de drainage différents, il est discuté que les populations habitant des lacs séparés sont seulement faiblement différentes les unes des autres. La part importante que jouent les oiseaux dans la dispersion de C. lacustris est évoquée.

INTRODUCTION

Cytherissa lacustris (Sars) is an ecologically specialized lacustrine species. It avoids the littoral and must be classified among the rheophobes. During its whole life-cycle it is unable to swim i.e. to move away from the bottom sediment. Thus it may be expected that a local population of such an ostracodes, limited approximately by the upper boundary line of the profundal of a given lake, is largely isolated from local populations inhabiting even neighbouring lakes linked by a stream or a channel.

The present investigations were undertaken in order to verify the above assumption. They were carried out in the eastern part of the Masurian Lake-District (NE Poland) where several large and deep lakes are still not too eutrophicated. C. lacustris proved to be common in that area. It was found living in Lakes Hancza, Szelmont Wielki, Galadus, Wigry, Birole Wigierskie, Serwy, Rospuda, Rajgrodzkie and Lasmiady, all within a radius of 50 kilometers of Suwalki (in many other lakes of that region it is present only in the subfossil state).
MATERIAL AND METHODS

Five local populations of *C. lacustris* inhabiting lakes belonging to different drainage-basins were chosen: from lakes Hancza and Serwy (Czarna Hancza-Nemunas drainage-basin), Lake Szelment Wielki (Szeszupa-Nemunas drainage-basin), Lake Galadus (Biala Hancza-Nemunas drainage-basin) and Lake Rospuda (Vistula drainage-basin) (Fig. 1). Quite large samples were taken from lakes Hancza, Szelment Wielki and Rospuda, whereas only a few specimens could be obtained from Lake Serwy and, in particular, Lake Galadus.

The material was collected in the second half of August 1989. An idea of the variation of local populations was acquired by means of starch gel electrophoresis of single specimen homogenates, following procedures described by Sywula et al. (1985). Owing to the scarcity of material only one buffer system was used. In the case of Masurian specimens of *C. lacustris*, the best zymograms were obtained for leucine aminopeptidase and esterases; as the same buffer system is suitable for both these enzymes, they were the ones chosen for study.

RESULTS

Leucine aminopeptidase proved to be monomorphic but the esterases were highly polymorphic. As many as 11 different esterase phenotypes were observed (Fig. 2). Each of these phenotypes occurred in at least two lakes. Table 1 gives a general account of the results.

DISCUSSION

The genetic interpretation of the esterase phenotypes observed is uncertain. It is certainly very probable that we are dealing with the products of two gene loci. However, verifying such a hypothesis is now almost impossible in this parthenogenetic species. Nevertheless it is obvious that we have succeeded in distinguishing as many as 11 genetically determined classes of specimens (clones). If the differences in phenotype frequencies between the lakes are uninterpretable due to the uncertain genotypic background, the qualitative analysis of the pattern of phenotype distribution among the lakes is wholly justified. Using the similarity index $s = \frac{w}{a+b-w}$ (Marczewski & Steinhaus, 1959), where $a$ is the number of phenotypes in the one and $b$ that of the phenotypes in the other of the pair of lakes being compared, and $w$ the number of phenotypes shared by the two lakes, we obtain the values given in Table 2.
As can be seen from the raw data and from Table 2, the distribution pattern of esterase phenotypes is unclear. In particular, no correlations between the distribution of separate phenotypes and the course of watersheds are noticeable. Even the main watershed (Vistula/Nemunas) does not constitute a barrier to the separate clones of *C. lacustris*. Thus the assumption that local populations of *C. lacustris* from different lakes are largely isolated from one another is not confirmed.

It is scarcely possible to arrive at any explanation of the pattern observed other than on assuming the importance of birds in dispersing *C. lacustris* specimens. Of course, in the Masurian Lake-District there are no birds which could carry (on the body surface or in the alimentary tract) these profundal ostracodes taken directly from the environment. However, there are birds which feed on fish and/or macrobenthic invertebrates which are potentially in a position to prey on *C. lacustris*. These are the diving ducks from the genus *Aythya* Boie, the Goldeneye *Bucephala clangula* (L.), the mergansers *Mergus* L., the cormorant *Phalacrocorax carbo* (L.), the grebes *Podiceps* Lath. and the divers *Gavia* Forst. The possibility cannot be excluded that *C. lacustris* owes its ubiquity in young postglacial lakes to these birds, at least in the region studied.

The possibility that shallow-water ostracodes could be transported by birds has been suggested by de Deckker (1977). Now such a suggestion is put forward with respect to profundal species.
<table>
<thead>
<tr>
<th>Phenotype No</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake Rospuda</td>
<td>3</td>
<td>-</td>
<td>4</td>
<td>10</td>
<td>43</td>
<td>2</td>
<td>9</td>
<td>1</td>
<td>7</td>
<td>-</td>
<td>1</td>
<td>80</td>
</tr>
<tr>
<td>Lake Hancza</td>
<td>4</td>
<td>1</td>
<td>-</td>
<td>41</td>
<td>5</td>
<td>2</td>
<td>5</td>
<td>-</td>
<td>-</td>
<td>3</td>
<td>-</td>
<td>61</td>
</tr>
<tr>
<td>Lake Szelment</td>
<td>17</td>
<td>6</td>
<td>7</td>
<td>6</td>
<td>1</td>
<td>-</td>
<td>12</td>
<td>18</td>
<td>3</td>
<td>11</td>
<td>3</td>
<td>84</td>
</tr>
<tr>
<td>Lake Galadus</td>
<td>1</td>
<td>-</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td>Lake Serwy</td>
<td>5</td>
<td>-</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>5</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>17</td>
</tr>
</tbody>
</table>

Table 1 - Numbers of esterase phenotypes in material from different lakes
Tabl. 1 - Nombre des phénomètes d'esterase dans le matériel de différents lacs

<table>
<thead>
<tr>
<th></th>
<th>Lake Rospuda</th>
<th>Lake Hancza</th>
<th>Lake Szelment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake Hancza</td>
<td>0.45</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake Szelment</td>
<td>0.73</td>
<td>0.54</td>
<td></td>
</tr>
<tr>
<td>Lake Serwy</td>
<td>0.67</td>
<td>0.62</td>
<td>0.45</td>
</tr>
</tbody>
</table>

Table 2 - Similarity of populations of Cytherissa lacustris from different lakes with respect to the composition of esterase phenotypes (Lakes Galadus omitted due to insufficient material).
Tabl. 2 - Similarité des populations de C. lacustris originaires de différents lacs par rapport à la composition des phénomètes d’esterase (Les données du lac Galadus ont été éliminées en raison d’un matériel insuffisant).

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IV - ECOLOGY & PALEOECOLOGY

IV - ECOLOGIE ET PALEOECOLOGIE
SPATIAL DISTRIBUTION OF CYTHERISSA LACUSTRIS LIVING IN MONDSEE.

DISTRIBUTION SPATIALE DE CYTHERISSA LACUSTRIS VIVANT DANS LE MONDSEE

by

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Key-Words: Cytherissa distribution, ostracods oxygen concentration, methods of mapping.
Mots-Cles: Distribution de Cytherissa, ostracodes, concentration en oxygène, méthodes de cartographie

Abstract

The spatial distribution of Cytherissa lacustris is viewed within three scale-dimensions i.e. the whole lake (on kilometer distances), the local area (on meter wide areas) and the organismic microdimension (on millimeter to centimeter scale). The population of C. lacustris form large patches in the sublittoral and upper-profundal zones of the lake. The global population is split in sub-populations mainly by areas with coarse sediment as in front of the stream discharges. C. lacustris occurs generally in well oxygenated zones (i.e. where the oxygen concentration is at least 4 mg l-1 and in fine, silty sediments. Within one local macro-patch in the central part of the lake (the site MO-7) C. lacustris builds a moderately dense and slightly aggregated sub-population. At the microscale level the spatial distribution is determined by the habitat heterogeneities and the oxygen concentration in the sediment. C. lacustris reacts actively i.e. moves out or avoids, sulfidic sediments. Other factors like the high concentration in carbon dioxide and hydrogen sulfide could constrain the recolonization of the fine sediment organically enriched during the sedimentation of dead plankton.

Résumé

La distribution spatiale de Cytherissa lacustris est examinée selon trois échelles, à savoir respectivement, l’ensemble du lac (distance d’un km.), le périmètre local (distance d’un m.) et microdimension de l’organisme (d’un mm. à un cm.). La population de C. lacustris constitue dans le lac de grandes taches dans les zones sublittorale et profonde superieure La population globale est divisée en sous-populations, principalement dans des zones à sédiment grossier comme en face de la décharge d’un affluent. C. lacustris se trouve généralement dans des zones bien oxygénées (c.a d. là où la concentration en oxygène est d’au moins 4 ml.l-1 et dans des sédiments fins et silteux. A l’intérieur d’une "macro tache"locale dans la partie centrale du lac (site MO 7), C. lacustris constitue une sous-population moyennement dense et faiblement agglutinée. A la plus petite échelle, la distribution spatiale est déterminée par l’hétérogénéité de l’habitat et par la concentration en oxygène dans le sédiment. C. lacustris réagit activement à des sédiments sulfidiques, c.a d. qu’elle se déplace ou fuit. D’autres facteurs comme la forte concentration en CO₂ et H₂S pourrait contraindre à la recolonisation d’un sédiment fin enrichi en matière organique lors de l’accumulation du plancton mort.
Fig. 1 - *Cytherissa lacustris*, femelle; A - left valve, external side; B - right valve, internal side; C - sieve plate; D - Carapace strongly covered with sediment. (SEM photographs produced by A. Loser, Univ. of Vienna, Dept. Marine Biology).

Fig. *Cytherissa lacustris*, femelle; A - valve gauche, côté externe; B - valve droite, vue interne; C - surface criblée; D - carapace abondamment couverte de sédiment (photographies effectuées au M.E.B. par A. Loser, Univ. de Vienne, Dept. Marine Biology).
INTRODUCTION

In the last fifty years, *Cytherissa lacustris* has ceased to occur in large areas of the Mondsee (Danielopol et al., 1985, 1988). It is interesting, however, to understand where *Cytherissa* still lives and from where in case of an improvement of the trophic situation of the lake the recolonization could occur (see blow section 3). Furthermore, Löffler (1972, 1975), Carbonel et al.(1988) repeatedly showed that the extinction of *Cytherissa lacustris* in various prealpine lakes is due to a combination of two factors: the sediment structure and the oxygen concentration at the sediment-water interface.Changes in the sediment structure, e.g. becoming poorly cohesive, occur during the eutrophication phases of a lake i.e. the sediment becomes enriched with organic rests, of phyto- and zooplankton (fig. 2) which sink to the bottom after their explosive development.*Cytherissa lacustris* with its strongly calcified valves (fig. 1) faces in this way difficulties to move in lighter organogenic sediments, (Powell, 1976). Löffler, (op.cit.) also noted that this situation starts before the installation of chronic hypoxic periods in the prealpine lakes.

In a previous paper Danielopol et al. (1988) suggested that the organogenic sediment which penetrated into the carapace space and/or stack on the carapace surface has a negative impact on the movement of *Cytherissa* limbs and valves. The carapaces which are ornamented with fossae, sieve pores and pseudochaetae (see fig. 1) accumulate easily organic sediment which makes it difficult for the ostracod to move. However, repeated observations on the frequency of individuals with sediment loaded carapaces show that this process can not fully explain the local extinction of this species. An alternative explanation for the disappearance of *C. lacustris* in Mondsee could be the negative impact of the low oxygen condition on the sediment at the sediment-water interface.

Geiger (1990) documented very well the importance of oxygen for the local extinction of this cytherid in Mondsee. We considered it important to continue looking not only at the extinction causes, but also at the survival aspects and their implication for further evolution of the *Cytherissa* population of Mondsee. Therefore, in this paper we present field observations on the *Cytherissa lacustris* related to the sedimentic structure and the oxygen situation of the lake investigated during 1983-1988, either by our study group or by our colleagues from the Universiety of Göttingen (Prof.J. Schneider, E. Horstemke, J. Helbig, B.Welzel and M.Hermann).

The distribution of the ostracods was mapped with a large whole lake grid in order to obtain a global view on the macroscale distribution and also within a local grid at a mesoscale level in order to obtain more details about the local population structure. We even continued the study at a lower level and investigated the microdistribution of *Cytherissa*. This was undertaken mainly by combining field data and laboratory experiments. Looking at the distribution of an ostracod species at three different scale-sizes i.e. a whole lake (dimension scale kilometers), the local one (dimension meter to kilometer distances) and the microscale one (dimension scale centimeter and millimeter), we expected to obtain a complex picture of the present-day distribution from which possible future consequences for the success of the recolonization could emerge.

This methodical approach was recently discussed by Powell (1989). Microevolutionary processes are visible at macro- and mesoscales as defined above (e.g. Thompson, 1985). Patch dynamics of local populations are at best perceived at over one meter distribution scales (Connell and Keough, 1985). Microscale distribution gives us the organismic dimension as perceived, hopefully, by the animal itself. At this level of description, the physiological aspects of the dispersal process (see for this approach Kitazato, 1984, Meyers et al, 1987 etc.) are easy to perceive.

Newrkla (1985) who studied the distribution of *C. lacustris* in an oligotrophic deep lake, the Attersee, noted that organic matter and oxygen concentrations are not the only constraints which limit the development of abundant populations of this species. Other factors could explain the low densities of *Cytherissa lacustris* in the deeper parts of Attersee.

In the present paper we explore alternative factors i.e. the possible negative impact of the hydrogen sulphide in the sediments and the high concentration of carbon dioxide concentrations at the sediment-water interface on the development of permanent and/or abundant local populations of *C. lacustris* in Mondsee.
Fig. 2 - Fine organogenic sediments from four sites of the Mooswinkl area, collected in Nov. 1986: A - MO-7/20 m deep; B - MO-7/70 m deep; C - MO-7/55 m deep; D - MO-7/67 m deep. (SEM photographs by Dr. P. Simonsberger, Univ. of Salzburg, Dept. Zoology).

Fig. 2 - Sédiments fins organogènes originaires de 4 sites de la zone de Mooswinkl, récoltés en Nov. 1986 : A - MO-7/20 m de profondeur ; B - MO-7/70 m ; C - MO-7/55 m ; D - MO-7/67 m (photographies au MEB par Dr. P. Simonsberger, Univ. de Salzburg, Dépt. de Zoologie).
2- SAMPLING SITES AND RESEARCH METHODS

Figure 3 shows the sites where samples for ostracod and oxygen measurements have been taken during 1985 and 1989. During a first sampling period we collected samples and measured the oxygen concentration in the deeper part of the lake i.e. below 20 m deep (fig 3). Fifty sites were investigated. In another sampling round we investigated the littoral and sublittoral zones i.e. we took samples at 3, 6, 12 m deep at 30 sites. We intensively investigated the bottom of the lake at three transects: MO-1, MO-7 and MO-9 (fig 3).

Figure 4 shows the position of the central part of the lake where two transects X and Y were sampled using the multiple corers Rinimuco and Mercedes-benthos (see description in Danielopol and Niederreiter, 1990a). Various combination patterns of sampling were used i.e. four replicate samples for one depth within 1 - 3 meters distance; this sampling design was repeated for two sites at 20 and 40 m deep on the transect MO-7; duplicate samples at one depth (40 m) within several hundreds of meters (see the position A, B, C in fig 4); finally, one sample at a single depth within a longitudinal depth transect (see dots and squares in fig 4). During September 1989 we took four series of samples at a 40 m deep on transect MO-7 using the Mercedes-benthos corer. One should remember that the Rinimuco sampler takes simultaneously 6 samples arranged in a circle with 50 cm diameter and the Mercedes-benthos device takes three samples. Because the position of the sampling units (SU) is not randomly chosen, the six or three SU have a pre-established position, i.e. a systematic sampling design, one could ask if this allows further statistical treatment of the Cytherissa lacustris distribution. A non-parametric test, Mann-Whitney, U-test, used on four series of samples showed no significant differences at a 5% level when we compared six samples on a fixed position with six samples.
(from a total of 24) randomly chosen. There is also no significant difference between the random samples and the fixed pattern of the Mercedes-benthos corer using the same non-parametric test.

Figure 5 shows a cross section of the Mondsee lake's bottom along transect MO-7. One notices that the slope on the northern side of the Mooswinkl bay (MOS) is less steep than on the Scharfling (SCH) side. Arrows indicate the sites intensively sampled using the Kajak-corer modified by R. Niederreiter (fig 6 A). The sublittoral zone of the Mooswinkl bay is a shelf on which coarse sediment is deposited directly on old glacial silty clays. The sampling programme of the whole lake was completed with the modified Kajak sampler. The area of the sampling tube is 19.6 cm which is smaller than the one of the multiple corer (i.e. 27.3 cm). The spatial distribution of the ostracods was checked for random or aggregated distribution using the Chi square test (variance to mean ratio) for agreement with a Poisson series (Elliott, 1977, Wimmer and Handl, 1990). The degree of the ostracod aggregation was also evaluated using the Green index which is independent of sample size (Ludwig and Reynolds, 1988).

Oxygen measurement in situ was obtained with an Orbisphere oxymeter, model 2607, with a sensor holder, model 2111, and a ministirrer (s in fig 6B). The electrode was operated from the boat and in order to avoid its sinking into the sediment the stirrer was fixed on a 50 cm diameter circular metal frame in such a way that the oxygen sensor remained located at 10 cm above the sediment surface (fig 6B). The exact position of the electrode on deep lake sediment was observed during 1989 at the site MO-1/40 m deep with a submersible videocamera "Sony" (Danielopol and Niederreiter, 1990a). For each site we measured the oxygen concentration at 0.1 m, 0.5 m, 1.0 m and 5 m above the sediment surface.

pH and sulphide were measured with Ingold electrodes, respectively the pH-type 406-M3 and H2S electrode type 245-85, at or in the sediment using cored sediment samples. For these parameters the cores were brought to the laboratory and the measurement proceeded in thermostatic rooms at 4 - 6°C. In order to check the oxygen values measured in the field at 10 cm above the sediment layer, we re-measured in the laboratory using the Orbisphere microflow-chamber system (through a slotted tube filled with silicon).

The oxygen at 0.1 m above the sediment layer (fig 11 A) shows good agreement between field and laboratory data. For the technique of the oxygen measurement using the microflow system, see Danielopol and Niederreiter, 1987, and here, fig 7.
Fig. 5 - Cross Section of Mondsee along the transect Mooswinkl - Scharfling-1 arrows indicate the sampling sites.
Fig. 5 - Coupe du Mondsee le long du transect Mooswinkl - Scharfling-1. Les flèches indiquent les sites d'échantillonnage.

Fig. 6 A - The Kajak corer mainly used for meiofauna sampling in Mondsee; B - The Orbisphere oxygen sensor (arrow) fixed in a stirrer (s) and with the circular frame
Fig. 6 - A - Le carotteur Kajak principalement utilisé pour l'échantillonnage de la meiofaune à Mondsee ; B - La sonde à oxygène Orbisphere (flèche) fixée à un aspirateur (s) avec un bâti circulaire.
Carbon dioxide concentrations at the sediment-water interface were calculated from alkalinity and pH values (fig 25). Small samples of water were extracted with a syringe using a J-shaped tube which prevented turbulences through the suction of the water near the sediment layer (fig. 7). For the sampling and the exact positioning of the electrodes into the core tubes we used a hand-operated micromanipulator.

The observation of the microdistribution of the ostracods within a reduced space was done using microaquaria (fig. 8) and an inverted stereomicroscope Wild. In a small plastic box (fig. 8 A) ostracods were settled using a rectangular grid. The ostracods were left to move within the whole box space, 4 x 8 cm, for various periods of time (24 - 72 hours). A rectangular framework was fixed at the end of the experiment into the sediment and each square was separately sampled and checked for Cytherissa specimens. In the miniaquarium (fig. 8 B) as well as in glass tubes with a 1.5 cm diameter we could observe the vertical movement of Cytherissa into the sediment (fig. 21 B).

The spatial microdistribution in natural field situations was quantified using the Plexiglas tubes of 27.3 cm surface. The first three centimeters were divided into four parts with a crossed plate and later on the sediment was frozen with liquid nitrogen. The 4 parts were then isolated, thawed and the ostracods extracted from the sieved residue.

Oxygen in the sediment was measured using microelectrodes from Micro-Sense Inc. (Clark-type) and from Sigma Instruments (cathode-type). Details about this technique are presented by Danielopol and Niedereiter (1990b).

The individual density of ostracods in various samples was graphically expressed as circled areas computed, following Danielopol, (1990). The data on the oxygen distribution in Mondsee were used by one of us (J.S.) to create contour maps using programme Surface 2 (Terra Sciences, Ltd.). About the techniques to represent the spatial variability using this programme see Sampson (1975) and Strobl (1988).

The limnological situation of the lake, considering the last ten years, was presented by Dokulil, 1984; Dokulil and Jagsch, 1989; Klee and Schmidt, 1987; Nauwerck, 1988; Schmidt, 1990; Welzel, 1988.

After the installation of the sewage treatment plant during 1973/74 which clears an important part of the used water of the Mondsee area, the ecological situation of the lake started to improve in 1980. One should remember that in the late sixties and during the seventies the lake became strongly eutrophied. During the summer stagnations massive plankton blooms occurred.

Fig. 8 - Mini-aquaria used for the observation of the active migration of Cytherissa lacustris; A - The minibox with the movable grid; B - the vertical aquarium.

Fig. 9 - Temperature (T) and oxygen (O2) dynamics in Mondsee, during 1984-1985, at three sites along the transect MO-1.

Fig. 9 Dynamiques de la température (T) et de l’oxygène (O2) dans le Mondsee, en 1984-1985, à trois sites le long du transect MO-1.
The lake bottom became anoxic in wide areas and the sediment was enriched with organic matter and phosphorus. During the last five years the oxygen situation improved as described by Geiger (1990).

Hypoxic areas, with less than 1 mg l⁻¹ oxygen, developed only during about three months at the end of the summer (see fig. 9), and only in restricted zones in the deeper part of the lake e.g. sites MO-1/45 m, MO-9/48m, MO-7/60 - 68 m and the surrounding zone (see figs. 3, 9, 10, 11, 13). The layer of hypoxic water was restricted to less than one meter (fig. 10). Other sites like MO-1/40 m which during the sixties experienced anoxic phases (at least from our paleolimnological information, see Danielopol et al., 1985) have now well oxygenated water, down to the bottom (fig. 9, 10). The distribution of oxygen in Mondsee (Sept. 1986) at 0.1 m, 0.5 m, 1.0 m and 5 m deep above the lake bottom is presented in four maps which can be obtained from Prof.G. Tichy, Institute of Geosciences, Univ. Salzburg.
Fig. 12 - Oxygen concentration in sediment, measured with the cathode-type electrode Sygma Instruments (Danielopol and Niederreiter, 1990b); star and triangle represent two successive measurements in a sample at several millimetres distance one from the other.

Fig. 12 - Concentration de l'oxygène mesurée dans le sédiment avec l'électrode de type-cathode de Sygma Instruments (Danielopol and Niederreiter, 1990b); l'étoile et le triangle représentent deux mesures successives prises à quelques millimètres de distance l'une de l'autre dans un échantillon de sédiment.

Fig. 13 - Oxygen distribution in September 1986 in Mondsee within the 20 m isobathymetric line and the sites where Cytherissa lacustris living (dots) or isolated valves (stars) have been found.

Fig. 13 - Répartition de l'oxygène en Septembre 1986 dans le Mondsee à l'intérieur de l'isobathe 20 m et dans les sites où Cytherissa lacustris a été trouvée vivante (points) ou sous forme de valves isolées (étoiles).
Fig. 14 - Quantitative distribution of the living specimens of *Cytherissa lacustris* at the site MO-7/20 m deep sampled with the multiple corer Rinimuco; the underlined number is the total sample cumulating the six sampling units; cross-no *Cytherissa* occurred in the sample (additional explanation see text).

Fig. 15 - Quantitative distribution of the living specimens of *Cytherissa lacustris* sampled with the Rinimuco multiple corer at the site MO-7/40 m deep and the sampling points A, B, C (see fig. 4) 1-2 replicate sampling series; percentages from the total number of individuals caught at the three sites (additional explanation see text).
The sedimentation of organic matter from zoo- and phytoplankton determines a fine organogenic sediment which covers most of the lake bottom and which is called by Welzel (1988, p.33) sediment type D. Figure 2 presents the structure of this organogenic sediment. Sandy sediments (with up to 40% sand) occur in front of the streams which discharge into the lake. High amounts of total phosphorus are stored in the sediments from the deeper part of the lake. The hypoxic zones correlate rather well with the areas containing more than 2000 ppm total P (see Welzel, 1988, p.40).
Fig. 18 - Quantitative distribution of the living specimens of *Cytherissa lacustris* sampled with the Rinimuco at the site MO-7/48 m deep. I-IV-replicated sampling series (additional explanation see text and fig. 14).

Fig. 18 - Distribution quantitative des individus vivants de *Cytherissa lacustris* le long du transect MO-7 par 48 m de profondeur. Échantillonnage effectué avec le multicarottier Rinimuco I-IV - séries successives d'échantillons (explications supplémentaires, voir dans le texte et fig. 14).

Fig. 19 - Quantitative distribution of the living specimens of *Limnocythere sancti-patricii* sampled with the Rinimuco multiple corer at the site MO-7/40 m deep and the sampling points A,B,C; 1,2 - replicated sampling series (additional explanation see text and figs 14, 15).

Fig. 19 - Distribution quantitative des individus vivants de *Limnocythere sancti-patricii* du site MO7 par 40 m de profondeur prélevés avec le multicarottier Rinimuco et les points d'échantillonnage : A,B,C; 1,2 - séries successives d'échantillons (explications supplémentaires, voir dans le texte et fig. 14, 15).
Spatial distribution of *Cytherissa*  

Fig. 20 - *Cytherissa lacustris* densities at various sampling sites and dates along the transect MO-7. Arithmetic mean (horizontal line) and 95% confidence limits (vertical lines). *n* on the abscissa - number of sampling units used for computation; *n* on the ordinate - number of *Cytherissa* individuals.

Fig. 20 - Densités de *Cytherissa lacustris* dans divers sites et périodes le long du transect MO-7. Moyenne arithmétique (ligne horizontale) et limites de confiance à 95% (lignes verticales). *n* en abscisse = nombre d'unités d'échantillonnage utilisés pour le calcul ; *n* en ordonnée = nombre d'individus de *Cytherissa*. 
Fig. 21 - Fine grained sediment bioturbated by *Cytherissa lacustris* individuals. A - surface of the sediment; B - lateral view with *Cytherissa* burrows; CL - *Cytherissa lacustris* in vertical position.

Fig. 21 - Sédiment à grain fin bioturbé par *Cytherissa lacustris*. A - surface du sédiment ; B - vue latérale avec les "terriers" de *Cytherissa* ; CL - *Cytherissa lacustris* en position verticale.
Spatial distribution of Cytherissa

Fig. 22 - Spatial distribution of Cytherissa lacustris in the miniaquaria. A - the exact distribution of various stages in each sampling site; B - the number of individuals in each sampling site; n - cumulated number of sampling units forming a block-quadrat unit; Id - Morisita index (with computed values) for each block-quadrat unit.

Fig. 23 - Active movement and choice experiments with Cytherissa lacustris; N - "normal" oxidized sediment from the site MO-7/40 m deep, < 60 µm grain size; B - "black" sulfidic and organogenic sediment from the site MO-9/48 m deep, < 60 µm grain size. A - experiments in Petri dishes of 3.5 cm diameter; B - experiment numbers indicate the individuals used for each experiment; a - live, d - dead in the horizontal miniaquarium; I - oxidized sediment on the whole surface; II - half area with oxidized sediment the rest covered with "sulfidic" sediment additional explanation, see text).

Fig. 23 - Mouvement actif et choix d'expérimentations avec Cytherissa lacustris; N - sédiment "normalement" oxydé du site MO-7 par 40 m de profondeur, grain moyen < 60 µm B - sédiment "noir" sulfidique et organogène du site MO-9 par 48 m de profondeur, grain moyen < 60µm. A - expériences dans des boîtes de Petri de 3.5 cm de diamètre; B - les numéros indiquent le nombre d'individus utilisés pour chaque expérience; a vivant, d - mort dans le microaquarium horizontal; I sédiment oxydé sur toute sa surface; II - demi-surface avec du sédiment oxydé, le reste étant recouvert par du sédiment sulfidique (explications complémentaires, voir le texte).
Fig. 24 - Oxygen measurements in Mondsee sediments and "choice experiments" with *Cytherissa lacustris*. A - Oxygen profile in the experimental set-up of B measured with the cathode-type electrode; B, C - experimental set-up on which *Cytherissa lacustris* has been exposed; arrows indicate the number (N) and the places where the ostracods were introduced; central numbers (N) indicate the number of the ostracod recovered; Percentages in each area calculated from the total number of ostracod recovered. D - oxygen profiles in the lake sediments measured with the cathode-type electrode Sygma Instruments; OF - surface of the sediment.

Fig. 25 - pH-alkalinity diagram from which the carbon dioxide concentration (as saturation value) can be read; pCO2(1x) - line, the dissolved CO2 in equilibrium with the atmospheric CO2.
**Table 1 - Densities of *Cytherissa lacustris* in the various samples with the Rinimuco sampler operated along transect MO-7; SU - numbers in sampling units. Mean - arithmetic mean; Sum - total number of living specimens in the sample; $s^2$ - variance of the sample; $\chi^2$ - value of the computed Chi-square test; Gi - value of the Green's index; n/m$^2$ - density of *C. lacustris* per square meter; C.L. - confidence limits 95% for the mean of those samples fitting a Poisson series; n-sampling units.**

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Table 1 - Densities of *Cytherissa lacustris* in the various samples with the Rinimuco sampler operated along transect MO-7; SU - numbers in sampling units. Mean - arithmetic mean; Sum - total number of living specimens in the sample; $s^2$ - variance of the sample; $\chi^2$ - value of the computed Chi-square test; Gi - value of the Green's index; n/m$^2$ - density of *C. lacustris* pro square meter; C.L. - confidence limits 95% for the mean of those samples fitting a Poisson series; n-sampling units.

Tableau 1 - Densités de *Cytherissa lacustris* de plusieurs échantillons prélevés le long du transect MO7 avec le carottier Rinimuco; SU - nombre d'unités d'échantillonnage. Mean - moyenne arithmétique ; Sum - nombre total d'individus vivants dans l'échantillon ; $s^2$ - variance de l'échantillon ; $\chi^2$ - valeur du test $\chi^2$ calculée ; Gi - valeur de l'indice de Green ; n/m$^2$ - densité de *C. lacustris* par mètre carré ; C.L. - Intervalles de confiance à 95 % pour la moyenne des échantillons qui suivent une distribution de type Poisson.
4 - SPATIAL PATTERNS OF CYTHERISSA LACUSTRIS

4 - 1. Distribution in the whole lake

Figure 13 shows the sites where C. lacustris was found living during our sampling survey. We added also several places where only valves occurred, but where we suspected that this ostracod species still lived. One can see that the northern side of the lake is better inhabited by C. lacustris. The southern side, especially the central part of the lake, is devoid of Cytherissa. This could be due to the steep slope of the basin (e.g. fig. 5). All the places where C. lacustris occurs are located in areas where the oxygen concentration above the sediment is at least 4 mg l\(^{-1}\) (fig. 13). This confirms both Delorme's (1983) observations, in that this species lives in lakes with at least 3 mg l\(^{-1}\) dissolved oxygen, and also Geiger's data (1990). However, it is interesting to mention that not all the well oxygenated areas in fig. 13 are occupied by C. lacustris thereby supporting Newkla's (1985) observation that other factors could constrain the distribution of this species in prealpine lakes.

If the distribution of this species is to be considered with regards the sediment characteristics, one notices that some areas rich in sandy sediments, up to 38% sand, like the south-eastern part of the lake down to 10-12 m deep (Horsthemke, 1986) are inhabited by Cytherissa lacustris. However, in the littoral shallow habitats (3-6 m deep) Cytherissa occurs only seldom with few specimens. Permanent and abundant populations have been always found at a 12-20 m deep. This confirms the data of Powell (1976) in that C. lacustris prefers silty sediments to coarse sandy substrates. The distribution of Cytherissa lacustris along the Mondsee shores is always interrupted by the coarse clastic sediment in front of streams like the Wangauer Ache, Fuschler Ache etc. It is also suspected that water currents prevent the implantation of permanent populations in these areas. Looking at fig. 13 one can see that the spatial distribution of this species is markedly interrupted. Sywula and Geiger (1990) showed that the population around the site Mooswinkl (the transect MO-7) differs genetically and phenotypically from those located in the south-eastern part of the lake around the site See. In conclusion, the potential recolonization of the deeper part of the lake could start at various areas around the northern side of the lake. However, the recolonization would involve most probably genetically differentiated local populations.

4 - 2. The local distribution

We investigated intensively the spatial patterns of Cytherissa lacustris at various depths of the transect MO-7 (fig. 4). We were interested to know, if within distances of several meters, the individuals of this ostracod species distribute in strong aggregation or evenly. Figure 14 and Table 1 show that for samples taken at 20 m deep the aggregation pattern is very low, no important clumps forms, and Green's index have very low values (under 0.3). Remember that this index scales from 0 a random pattern to one for a maximal aggregation (Ludwig and Reynolds, 1988).

The same situation is visible (fig. 15) when one compares samples taken at wider distances (about 200 meters spaced one from the other, series A - C in fig. 3). Once again no strong aggregation occurs. A Man-
Spatial distribution of *Cytherissa*

Whitney U-test shows no significant at 5% level of significance between these samples. Within transect MO-7 we took samples at 12 m, 20 m and 40 m deep (fig. 16). Once again no significant differences occurred between the sites (see location on fig. 4, transect), but one can discern optically areas of strong aggregation which encompass 2-4 sampling units, interspaced by areas with low abundances. Samples taken with the Mercedes-benthos multiple corer at 40 m deep at MO-7 site (fig. 17 and Table 2) showed a similar pattern i.e. the local populations are more or less evenly distributed with rare increases into aggregation.

A completely different picture emerges for *Cytherissa lacustris* at 48 m deep during 1985. From a continuous distribution at 40 m deep one sees in fig. 18 at 48 m deep a completely reduced population where small clumps are interspaced within a large uninhabited area.

A similar picture presents the distribution of *Limnocythere sancti-patricii* at 40 m deep (fig. 19). We believe that the constraining factor which determines this patchy distribution is the low oxygen concentration in the sediments as discussed by Geiger (1990). Evidences for this assertion are for instance the observation that at 50-55 m deep the oxygen concentration was lower than at the upper depths (fig. 11 A). Also the distance of the oxygen penetration in our sample MO-7/50 m is lower than that of shallower depth MO-7/20m (cf. fig. 24 D). Interesting enough the 12 m deep site at MO-7 and the 20 m deep site at MO-9 have lower oxygen concentrations near the bottom than the deeper sites (cf. fig. 11 A, 11 B, 24 D). This is due to the oxygen solubility at the higher water temperature of the 12 m deep site as compared to those of the deeper ones.

Figure 20 shows the mean values for the samples taken with the multiple corer Rinimuco. 95% confidence limits have been calculated for those series of samples where agreement with Poisson series was established by the Chi-square test (Elliott, 1977). For the samples which show an aggregated pattern only the arithmetic mean is given. One sees from these data that the mean values for *C. lacustris* found in sampling units within an area of 27.3 cm is between 5 and 40. Extrapolated to one square meter it represents between 1000 and 15.000 individuals (Table 1).

Similar data are obtained for the sampling series taken with the Mercedes-benthos corer (Table 2). Lower values and larger confidence limits are displayed by the sample series taken at MO-7/48 m deep (fig. 20, Table 1). As compared to the data already published (Danielopol et al.,1988, Geiger, 1990) the *C. lacustris* abundances presented here are lower because we considered in this sampling programme only the adults and the last three juvenile instars.

Fig. 26 Concentration of hydrogen sulphide in the first cm. of sediments (A) and within the experimental flask containing *C. lacustris* exposed 17 h. to two different concentration of Na-sulphid. A-Various samples from MO-7 and MO-9 transects. Note the variability of replicate sample for the sites MO-9/48 m and 30 m deep. Fig. 26 Concentration en hydrogène sulfure dans le premier cm. du sédiment (A) et à l’intérieur du récipient expérimental contenant *C. lacustris* exposé pendant 17 h. à deux concentrations différentes de sulfure de Na. A-Échantillons variés des transects MO-7 et MO-9. Noter la variabilité des échantillons répliqués des sites MO-9/48 m et 30 m de profondeur.
An intensive sampling programme undertaken by Geiger and Yu Yin during 1988 along the transect MO-7 with sample sites at 9, 12, 15, 18, 21, 30, 40, 55 60 and 63 m deep (data in Yu Yin, 1988, Hermann et al., in prep.) show that Cytherissa lacustris has a continuous distribution within the zone 12-40 m deep.

During repeated sampling at depths greater than 55 m along the transect MO-7 (between Mooswinkl and Scharfling) over the years as well as the intensive sampling programme along the transect Y (fig. 4) using the Rinimuco multible corer living Cytherissa lacustris were not caught. Only fossil specimens were found in the deeper sediment layers. Therefore, one can conclude that in the Mooswinkl bay area a macropatch of Cytherissa lacustris exists down to 40 m deep. From this area one could expect a recolonization of the surrounding zone of the deeper part of the lake. At the same time one should expect a redevelopment of the remnant patch of C. lacustris existing in MO-7/50-55 m deep.

4 - 3 Spatial microdistribution

Three questions were asked considering the microdistribution of Cytherissa lacustris:

a. Does it aggregate within small areas (less than 10 cm distance) as a result of environmental heterogeneities or behavioral reactions? Such cases have been described for deep sea harpacticoids by Eckman and Thistle (1988) and for ostracods like Cyprideis torosa by Heip (1976) and for Keijella bisanensis by Abe (1983).

b. How important are the vertical movements of C. lacustris within the sediment? There is an important amount of literature showing that meiofauna lives permanently or penetrates ephemerally into the deeper layers of fine sediment where little or no oxygen occurs (e.g. Meyers et al., 1987, Dye, 1983, Powell, 1989). Considering Cytherissa lacustris, Newrka and Wijegoonawardana (1987) showed that this species penetrates the Mondsee sediments down to more than 2 cm deep and Yu Yin (1988) mentions isolated specimens which were found at a 6 cm deep in the sediment.

c. Do ostracods perceive the environmental microheterogeneities? That the superficial layers of sediment present a strong heterogeneity considering the spatial distribution of the organic matter or the oxygen concentration is a well known fact (e.g. Silverberg et al, 1987, Gee and Warwick, 1985, here fig. 12). Surface dwelling ostracods like Heterocypris incongruens are known to react positively to well oxygenated microhabitats (Benzie, 1984). Here we present experimental evidence that C. lacustris can discriminate between oxidized and better aerated sediments and reduced (sulphidic) sediments with a lower oxygen content.

In order to answer the first question we took five samples with the Rinimuco corer at the site MO-7/20 m deep. Each sample was divided in 4 equal parts and Cytherissa lacustris was extracted from the first 3 cm of sediment (see also section 2). The distribution of the ostracods in each sampling core was checked for random distribution using the variance to mean ratio test (Elliott, 1977). All five samples show agreement with the Poisson series, therefore no aggregation could be detected on the microscale area of several square centimeters.

In the microaquarium described in fig. 8 A we placed at fixed spaces at 32 sites 160 specimens of Cytherissa lacustris (i.e. two adults and three juveniles stage 7 and 8 pro site). After 48 hours we extracted from each square the ostracods. Figure 22 shows the distribution of C. lacustris at the end of the experiment. No significant aggregations of neither females nor juveniles are visible (fig. 22 A) as described by Heip or Abe (op. cit.).

The plot of the Morisita Index (see description in Ludwig and Reynolds, 1988) over various block sizes (fig. 22 B) shows no sharp peak. A break in the Morisita Index occurs at the n-16 combination which one could interpret as the building of two aggregates within an area of 16 square centimeters.

Cytherissa lacustris can theoretically at very high densities bioturbate the surface of the lake sediment. In a series of experiments we exposed on small areas (1,76 cm^2) 30 to 80 specimens (1) on finely grained

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(1) This is equivalent to about (175.000 to 450.000 C. lacustris individuals pro square meter, densities that we never observed in Mondsee (see also Geiger 1990)
Spatial distribution of *Cytherissa* (less than 60 μm) sediment either from MO-7/40 m deep (a sediment well oxidized) or from the site MO-9/48 m deep (an organogenic sediment rich in sulphides and having a black colour). Figure 21 A shows the surface of the sediment from MO-7/40 m deep. One can see in fig. 21 B that *C. lacustris* digs holes deep into the sediment and the burrows remain open for longer periods of time (days). The main bioturbation activity occurs in the upper 3 mm layer. In poorly oxygenated sediments *Cytherissa lacustris* remains in vertical position close to the external opening of the burrow. Sediments exposed at 1-2 mg l⁻¹ oxygen and 4°C temperature for up to one month show marked differences between those containing *C. lacustris* and those without ostracods. *Cytherissa lacustris* in an 8 mm deep sulphidic sediment from MO-9/48 m penetrates in the first 6 mm which are oxidized. Burrows of *Cytherissa* are visible down to the bottom. In a parallel tube without *Cytherissa* only 3 mm of sediment are oxidized, the rest being black in colour.

The small size juveniles of the 6th stage penetrate down to 4 mm deep. Only the individuals in the last stages 7, 8 and the adult penetrate deeper. The oxygen penetration in the sample with *Cytherissa* is about 3.5 mm and in the barren sediment 2.5 mm.

In experiments with *Cytherissa* exposed on oxidized sediment from MO-7/40 m deep, 1-2 mg l⁻¹ oxygen and 4°C temperature, we found *Cytherissa* specimens down to 13 mm deep (one juvenile 8th stage). The lower boundary of the oxygen penetration lays between 4-5 mm deep. Burrows of *Cytherissa* are visible down to the bottom of the aquarium. We consider that through the large tubes (more than 150 μm diameter) oxygen can penetrate into the anoxic or hypoxic sediments and allows *Cytherissa* to live in the deeper layers. The field data of Yu Yin (1988) of Mondsee confirm our laboratory observations i.e. in the deeper layers of sediments only adult and last juvenile stages penetrate successfully. Figure 12 shows our sediment choice experiments. In a first series we used oxidized sediment (N) and a sulphidic one (B) from the sites MO-7/40 m and MO-9/48 m deep. We exposed in 3.4 cm diameter Petri dishes series of 10 and 40 *Cytherissa lacustris* (females and 8th stage juveniles). Figure 23 A shows that the ostracods prefer the oxidized sediment. They explore the sulphidic one, too, but in the end select the oxidized one. In another type of experiment (fig. 23 B) we exposed ostracods at fixed sites in half of the aquarium. On oxidized sediment (fig. 23 B, I) *Cytherissa* spread within 48 hours into the inhabited zone while in the experiment having the empty area covered with sulphidic sediments (fig. 23 B, II) ostracods did not colonize. Finally, in another experiment where we could measure also the oxygen of the sediment (fig. 24, A-C), we divided the microaquarium space (27.3 cm) in four sub-areas, two covered with oxidized sediment and two with sulphidic sediment. One can see that at the end of the experiment after 24 or 48 hours the relative frequency of *C. lacustris* was higher in the oxidized areas (fig. 24, B, C). Oxygen measured in the two types of sediments after 24 hours shows (fig. 24 A) a significant difference between the sulphidic and the oxidized one.

From these data one can assume that the recolonisation of organogenic and sulphidic sediments of Mondsee will occur slowly because *C. lacustris* can recognize either the negative microenvironment and actively avoid it or can move preferentially in the oxidized zones.

### 5 - H₂S AND CO₂ AS POSSIBLE CONSTRAINING FACTORS FOR THE RECOLONIZATION OF MONDSEE SEDIMENTS

Accumulation of putrefactive hydrogen sulphide and production of carbon dioxide from sediment respiration in eutrophic lakes can have important toxic effects on the oxybiontic benthos fauna (e.g. Theede et al, 1969). Concerning *Cytherissa lacustris* in Mondsee we considered the possibility that this species does not resettle in the deeper layers of the lake e.g. the area of MO-1 and MO-9, 30-40 m deep, or MO-7/60 m deep, because of accumulation of hydrogen sulphide in the sediment and carbon dioxide at the water-sediment interface. Exploration of the lake's bottom with the submersible videocamera shows that large areas at these three sites are covered with white coloured sulphur bacteria interspaced by uncovered sediments.

The hydrogen sulphide concentration as measured by one of us (B.R.) with the sulphide electrode in the first centimeters (see methods) shows concentrations of 4.10⁻⁹ at the sites MO-7/63 and 68 m deep to 1.17.10⁻⁷ at the sites MO-9/48 m deep (fig. 26 A).
Lower values occur at the site MO-7/40 m deep as compared to those at the sites MO-9/30 and 40 m deep (cf. fig. 26 A). In order to test the toxicity of the H2S on *Cytherissa lacustris* we exposed series of 50 to 60 specimens in Natrium sulphide (Na2S.3H2O) which developed H2S concentrations of 1.08.10^-5 mol l^-1, respectively in another experiment 2.15.10^-6 mol l^-1 (fig. 26 B). At these hydrogen sulphide concentrations a mortality of 12.5% after 17 hours occurred in the former case, and 9.3% in the latter one. These data suggest that hydrogen sulphide concentrations in the sediment even if they are not so high as under the experimental conditions mentioned above, still could have a long-term toxic effect. This could explain too why this species does not reoccupy the deeper part of the lake where the oxygen in the water is higher than 1 mg l^-1 (cf. fig. 9, 10, 13).

Carbon dioxide at the sediment-water interface at both transects MO-7 and MO-9 showed during September 1988 high concentrations. Figure 25 shows that at the deeper lake-sites at 60-63 m deep the values are highest. Tölderer-Farmer (1985) noted that *Limnocythere sancti-patricii* at those sites with signs of eutrophication had very poorly calcified carapaces. It is possible that high concentrations of carbon dioxide in water could have a negative effect on the calcification of the ostracod carapaces (see also discussion in Danielopol and Casale, 1990). Therefore, new field and experimental investigations are needed on the effect of the hydrogen sulphide and the carbon dioxide as potential constraints on the recolonization of the profundal zone of Mondsee by *Cytherissa lacustris*.

6 - CONCLUSIONS

1. *Cytherissa lacustris* lives in well oxygenated areas (i.e. at least 4 mg l^-1 oxygen in the water overlying the sediments) and prefers fine (silty) sediments which are oxidized.

2. A widely spread population of *C. lacustris* still exists in Mondsee located especially in the sub-littoral and the upper-profundal of the lake.

3. Sub-populations of this species are spatially separated mainly by areas with coarse sediments. A recolonization of the depauperated profundal zone is expected to be achieved by these sub-populations.

4. Within a mesoscale area, MO-7 (12 - 40 m deep) *Cytherissa lacustris* develops moderately dense and little aggregated sub-populations.

5. A sharp decrease in density occurs at site MO-7/50 m deep. Here the continuous local population found in the surrounding upper area (MO7/40 m) reduces to a few remaining patches.

6. At a microscale level, one can see that *Cytherissa lacustris* can penetrate into the deeper layers of the sediment which are normally hypoxic or anoxic.

7. *Cytherissa lacustris* seems to perceive the heterogeneities of the microhabitat. One can experimentally see that the species moves out or avoids sulphidic and poorly oxygenated sediments.

8. High concentrations of hydrogen sulphide in the sediment and carbon dioxide in the water could constrain the recolonization of the profundal habitats with *Cytherissa lacustris*.

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THE ROLE OF OXYGEN IN THE DISTURBANCE AND RECOVERY OF THE CYTHERISSA LACUSTRIS POPULATION OF MONDSEE (Austria)

LE ROLE DE L'OXYGENE DANS LES PERTURBATIONS ET LES RETABLISSEMENTS DES POPULATIONS DE CYTHERISSA LACUSTRIS DE MONDSEE (AUTRICHE).

by

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Mots-Clés: Eutrophisation, oxygène, microélectrodes, sédiment, ostracodes

Abstract

Lake eutrophication during the sixties and early seventies caused major changes in the profundal ostracod assemblages of Mondsee.

The population structure of the cold stenothermic, infaunal species Cytherissa lacustris was the most severely disturbed and it disappeared from sediments deeper than 40m. It is herein demonstrated that declining oxygen conditions play a major role in the local extinction of Cytherissa lacustris.

The comparison of oxygen data from the lake bottom with those obtained at a corresponding depth in the open water has been used to reconstruct the bottom oxygen concentrations which occurred during the onset of eutrophication and to show the influence of restoration measures.

Microelectrode and redox potential measurements were used to determine the oxygen penetration depth in the sediments. Maximum penetration depth was 5-8mm, depending on the oxygen concentration in the overlaying water, porosity and the reductive capacity of the sediments.

Due to its low activity and low standard metabolism, Cytherissa lacustris is less sensitive to low oxygen concentrations than littoral ostracod species (LD50 = 10 days versus LD50 ~ 1 day at 0.1mg.l-1 O2, 11°C).

Therefore additional factors such as the long development time, the endobenthic lifestyle and low active migration potential are proposed in order to explain the disappearance of Cytherissa lacustris from a large proportion of the lake.

Recolonization as a consequence of improved oxygenation of the sediments occurred at a very low rate (10m/3 years) when compared with other meiofauna species.

Résumé

L'eutrophisation du lac durant les années 60 et le début des années 70 a été la cause de changements majeurs dans les assemblages fauniques des ostracodes profonds.

La structure de la population de l'espèce sténotherme froide et endobenthique Cytherissa lacustris a été particulièrement perturbée à tel point qu'elle a disparu des zones plus profondes que 40 m. Il est montré ici que les conséquences de la dépétition de l'oxygène jouent un rôle majeur dans des extinctions locales de Cytherissa lacustris.

La comparaison entre les données de l'oxygène au fond du lac et celles obtenues à des profondeurs équivalentes en eau libre a été utilisée pour retrouver les concentrations en oxygène qui régnaient au fond au cours du début de l'eutrophisation et pour montrer l'incidence des mesures de restitution.

Une microélectrode et des mesures du potentiel redox ont été utilisées pour déterminer la profondeur de pénétration de l'oxygène dans les sédiments. La pénétration maximum mesurée est de 5-8mm, dépendant de la concentration en oxygène à l'interface, de la porosité et de la capacité réductrice du sédiment.

En raison de sa faible mobilité et de son métabolisme bas, Cytherissa lacustris est moins sensible à de faibles concentrations en oxygène que des ostracodes littoraux. (LD50 = 10 jours par rapport à LD50 ≤ 1 jour à 0,1mg.l-1 O2, 11°C).
Par conséquent, d'autres facteurs comme un long temps de développement, un mode de vie endobenthique, une faible potentialité de migration active sont proposés dans cet ordre pour expliquer la disparition de *Cytherissa lacustris* d'une grande partie du lac.

La recolonisation est une conséquence d'une amélioration de l'oxygénation des sédiments qui s'est produite pour un très faible taux de sédimentation (10m/3 ans), si l'on compare avec d'autres composants de la meiofaune.

1. INTRODUCTION

The study of disturbances of ecosystems resulting from human activity has become a wide and important field of research for both applied and theoretical ecologists during the last decades (Sousa, 1984; Gray 1989; Underwood, 1989).

Many lake ecosystems underwent dramatic changes due to increased nutrient input (e.g. phosphorus compounds originating mainly from sewage).

The higher eutrophication level of a lake is expressed not only in the pelagic zone but also in dramatic changes of benthic habitat characteristics such as organic carbon content, phosphorus content, oxygenation and accumulation of toxic compounds (e.g. H₂S) (Hakanson and Jansson, 1983; Gollerman, 1977).

The response of the meiofaunal community to the effects of eutrophication (nutrient enrichment, oxygen depletion) is well documented in the marine literature (Josefson and Widbom 1988; Elmgren 1975; Widbom and Elmgren 1988; Nichols 1976). A decrease in diversity and a shift in dominance to opportunistic species is generally observed (Gray 1989; Underwood 1989). Similar trends can be assumed for limnic habitats even though data are comparatively scarce (Särkäa 1989; Kansanen 1981).

Particular importance is attached to oxygen as a factor in disturbance processes (Jonasson 1972). The sensitivity of meiofauna to declining oxygen conditions is species characteristic and depends on their respiratory physiology (Lasserre, 1976; Lasserre and Renaud-Momant, 1973; Wieser et al., 1974) life history, reproductive potential and migratory behaviour (Josefson and Widbom, 1988).

The use of ostracods, and their fossil and subfossil remains, in disturbance studies is well established in paleoecology. Many of these studies have concentrated on natural, catastrophic events (Van Harten 1987; Jarvis et al., 1988), e.g. sea level rising or oceanic anoxia.

In studies on the impact of human activities on aquatic systems however, ostracods are often neglected, even though the few works available clearly demonstrate their potential indicative value (Elmgren 1975; Widbom and Elmgren 1988; Josefson and Widbom, 1988; Delling, 1981). This neglect may be due to a general lack of data on the autecology of ostracods, for freshwater species in particular.

Löffler (1972, 1975, 1983) showed that the freshwater ostracod, *Cytherissa lacustris*, a parthenogenetic, cold-stenothermic species, disappeared from eutrophied pre-alpine lakes already before eutrophication became apparent from sedimentological parameters. Delorme (1978) determined the critical lower oxygen level for this species as 3 mg.l⁻¹. In order better to understand the ecological requirements of *Cytherissa lacustris*, an intensive study on the subfossil and recent ostracod population was carried out in Mondsee (see also related papers in this volume).

Mondsee, an oligo-mesotrophic lake in the pre-alpine region of northern Austria, received high amounts of domestic sewage as a result of highly developing tourism during the sixties and seventies. Blooms of *Oscillatoria rubescens* were frequently observed (Dokulil and Jagsch, 1989) and oxygen depletion occurred in the deeper parts of the hypolimnion during summer stagnation (Jagsch and Megay, 1982). The construction of a sewage treatment plant in 1973/74 improved the water quality of the lake considerably (Dokulil and Jagsch, 1989) but profound sediments remain eutrophic to this day (Helbig, 1986; Herman in prep.).

As an immediate consequence, the ostracod assemblage from Mondsee underwent profound changes leading to the disappearance of *Cytherissa lacustris*, the most sensitive species (Danielopol et al., 1988), from large parts of the lake.

The present paper has the following objectives:
1. To assess methods which allow open water oxygen data to be extrapolated to the situation on, and in, the sediments.
2. To describe the disturbance-recolonization process of *C. lacustris* as mediated by the dynamics of the oxygen regime.
3. To discuss the species-specific characteristics which cause the vulnerability of *Cytherissa lacustris* to low oxygen conditions.
2. STUDY AREA

Mondsee (fig.1) is a mesotrophic lake in northern Austria (47°49' N, 13°25' E; altitude 488m) with a surface area of 14.21 km², a maximum depth of 68.3m (mean depth 36.0m) and a volume of 510 million m³. The theoretical water renewal time is 1.7 years and the catchment area of 247 km² largely comprises agricultural land and forests (Dokulil and Jäger, 1985).

Mondsee is the warmest of the deep Salzkammergut lakes with 20-24°C surface water temperature in summer and summer bottom temperatures of 12-18°C in the littoral and 4-6°C in the profundal.

The lake was monomictic during the investigation period although dimictic periods are reported by Jagsch and Megay, (1982) and stratified from July until November. During summer stagnation oxygenation of the lake is poor and oxygen depletion occurs frequently (see also results).

The lake basin was preformed by tectonic disturbances along the line of overthrust of the Northern Calcareous Alps to the Flysch, and shaped and deepened by glacial activity. Two major basins of different depth (45m and 68.3m) can be distinguished.

Despite similar limnological characteristics in the open water, the two basins differ considerably in their sediment properties. This difference was most probably established before eutrophication has started, as demonstrated by differences in the faunal assemblages (Danielopol et al., this volume; Liepolt, 1935) and sediment characteristics (Helbig, 1986).

The sampling transect MO-7 includes the sheltered bay of Mooswinkl (9m, 12m, 15m littoral-infralittoral), a rather steep slope (20m, 30m, 40m - upper profundal) and the flat lower profundal region (50m, 60m, 68m). Sediment properties of the sampling transect are given in Table 1.
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Table 1: Sediment characteristics of station MO-7. Data from different authors
Tableau 1: Caractéristiques du sédiment de la station MO-7. Données de différents auteurs
1) Hermann. in prep. (May 1988)
2) this study (August 1988)/Cette étude (Août 1988)
3) Conde (unpubl.) (August 1989)

The infra-littoral (10m-20m) and the upper profundal zones (20m-40m) are less affected by the consequences of eutrophication due to the morphology of the site and continue to exhibit dense populations of Cytherissa lacustris. The deeper profundal sediments (50m-67m) show increased accumulation of organic matter and low oxygen concentration during summer stagnation. At the beginning of the study period in 1983, no specimens of Cytherissa lacustris could be found in areas deeper than 40m.

3. METHODS

3.1. SAMPLING

For subfossil analysis 3 replicate cores were taken with a modified Kajak-Corer in depths of 40m, 50m and 60m. The sediment columns were cut in 2 cm slices (39.3 cm³) and washed through a sieve with 200μm mesh-size. The number of valves was determined for the last 5 stages under a stereomicroscope (Wild, 12x); whole carpaces were counted as two valves. Mean and standard error were calculated using a log(x+1) transformation (Elliott, 1977).

Station MO-7 was sampled in summer 1983, 1985 and 1988 for the collection of living specimens of Cytherissa lacustris. In 1983 and 1985 6 replicate cores were taken along a profile at 6m, 12m, 20m, 30m, 40m, 50m and 60m. In 1988, more sampling stations with 3 replicate cores were included (9m, 12m, 15m, 18m, 20m, 30m, 40m, 50m, 55m, 60m, 65m and 67m).

The uppermost 3 cm of the sediment column were washed and sieved through a net with 100μm mesh size in 1983 and 1985 and 200μm in 1988. Ostracods were counted alive and the last 5 stages determined. Mean values and 95% confidence limits were calculated using log transformed values (Elliott, 1977). The data are presented as Ind/20 cm² to allow easy comparison with literature values.

3.2. OXYGEN MEASUREMENTS

In 1984/1985, oxygen measurements in the lake were carried out monthly. During periods of rapid change (i.e. at the beginning and the end of summer stagnation) weekly intervals were chosen. The polarographic oxygen sensor (Orbisphere, model 2603) was fixed on a metal ring to allow exact determination of the distance of the electrode from the sediment surface (+0.1 m, +0.5 m, +1m and +5m). As the electrode showed low drift, calibration was done in the laboratory. Oxygen data for 1976, 1983 and 1988 are derived from transformed values measured by the Institute of Fishery Research, Scharfling, Austria, using the Winkler method.

The percentage of lake bottom area with less than 3 mgO₂/l was calculated by planimetry of a depth contour map of the lake using a digitizing tablet (VACOM, resolution 0.1mm).
Oxygen microprofiles were measured in the sediment in order to assess the oxygen diffusion and penetration depth in different types of sediment. Two kinds of experiments were designed:

Core samples from the transect MO-7 (see above) were taken along a depth profile (12m, 15m, 18m, 20m, 30m, 40m, 50m, 60m, 65m and 67m). For the first three centimeter of the sediment column, average water content and organic matter (loss on ignition at 450 °C for two hours) were determined and the redox potential was recorded. Porosity was calculated from the water content assuming a bulk density of the sediment of 2.6 (Hakanson and Jansson, 1983; Berner, 1982).

Parallel cores were gently pushed into incubation tubes (height = 60mm, diameter = 50mm) in such a way that samples remained undisturbed (Danielopol and Niederreiter, this volume). The incubation tubes were submerged in a temperature controlled water bath (6 °C) and flushed with dry room air for 24 hours to achieve air saturation of the sediments. A peristaltic pump provided continuous mixing of the overlaying water to avoid any oxygen gradient above the sediment surface.

In a second experimental run, a core from 40m depth, treated in the same way as described above, was exposed to different oxygen concentrations (0.6 mg.l⁻¹, 1.0 mg.l⁻¹, 1.4 mg.l⁻¹, 1.6 mg.l⁻¹, 1.8 mg.l⁻¹, 1.9 mg.l⁻¹, 5.2 mg.l⁻¹, 9.4 mg.l⁻¹ and 10.3mg.l⁻¹). Low oxygen levels were maintained using a high precision gas mixing pump (DIGAMIX, SA 2713, Wösthoff), delivering a constant mixture of nitrogen and room air to the water bath (Gnaiger and Forstner, 1985). Within a period of 12 hours after changing the oxygen concentration the new equilibrium was established.

Microelectrodes:

Clark-type microelectrodes as described by Revsbech and Jorgensen (1986) were used to determine the oxygen concentration in and above the sediment. Cathode and anode are placed in a single glass capillary filled with the electrolyte solution to ensure independence from the conductivity of the surrounding medium (freshwater). The tip diameter of 100 μm was chosen as a compromise between satisfactory resolution, response time and mechanical resistance. The electrodes were of a commercially available type (Micro-Sense, Israel) and only those were used which showed high reproducibility over a wide range of oxygen concentrations (1 - 100% air saturation).

The electrodes were mounted on a manually operated micro-manipulator allowing accurate steps of 50 μm, connected via shielded cables to a supplier-converter (Technical University of Vienna, polarization voltage -0.75V) and placed in a Faraday cage to reduce electrical noise. Calibration was carried out between each measurement. The oxygen concentration in the overlaying water, measured with a polarographic oxygen sensor (Orbisphere 2603) served as the 100 % calibration point. Zero oxygen depth was reached when further downward probing of the electrode no longer altered the electrode signal. The value obtained was taken as the zero calibration point. Between these two points the signal was tested for linearity. Electrodes with non-linear response or with considerable drift were rejected. Measurements were carried out in 100 μm steps starting from the sediment surface. The exact positioning of the electrode at the sediment surface was controlled under a stereo - microscope (Wild, 12x).

3.3 REDOX - POTENTIAL

Redox potentials were recorded during August 1988 in sediment columns along the MO7-transect. A platinum electrode and a calomel reference electrode were calibrated in a solution of Fe+++ and Fe++-ions (Metrohm) with a potential of +250 mV.

Measurements were carried out at room temperature immediately after sampling by pushing the platinum electrode through a silicon slit in the perspex tube, the reference electrode remaining in contact with the overlaying water.

3.4. OXYGEN TOLERANCE EXPERIMENTS

Due to the variable abundance of the ostracod species in the lake, the number of specimens used in the experiments varies considerably (Table 4). The animals were sorted under a stereo-microscope (Wild, 12x), the instars determined and transferred to the experimental vessels (fig.2).

For each control date separate vessels were incubated to avoid recovering of the experimental animals during the control procedure. Animals were exposed to different temperatures and oxygen concentrations (4°-0.1mg.l⁻¹, 4°-1.0mg.l⁻¹, 11°-0.1mg.l⁻¹, 18°-1.0mg.l⁻¹). The vessels were incubated at full oxygen saturation to allow adaptation to experimental temperatures. After 12 hours the oxygen content was slowly reduced to the desired level by means of a gas mixing pump (description see above). Data from culture experiments run at 100 % oxygen saturation (Geiger, this volume) served as a control.

Animals were checked after three days to assess the mortality due to adaptation problems. Subsequent controls were carried out weekly. Mortality was determined after a period of 12 hours of recovery at full oxygen saturation. An animal was considered as being dead, if no visible movement of the limbs occurred within five minutes.
Fig. 2 - Experimental setup for oxygen tolerance experiments.

*Fig. 2 - Protocole d'expérimentation pour la tolérance à l'oxygène.*

**A**: Aquarium for incubation of the experimental vessels/Aquarium pour l'incubation des récipients à expériences

- O2E: Polarographic oxygen sensor
- Sa: Plate filled with experimental vessels
- Si: Sieve preventing the formation of air bubbles
- Pu: Peristaltic pump for continuously mixed water flow (Direction of water flow indicated by arrows)

**B**: Experimental vessel/récipients à expériences

- Si: Lateral sieve (100 μm)
- 1, 2, 3: Upper and lower lid with sieves (100 μm)
- The vessels are filled with sediment up to level of the lateral sieve

The LD50 was determined graphically. The statistical significance of the differences between the obtained survival curves was calculated using Peto and Peto's Logrank test (Pyke and Thompson, 1986)

### 4. RESULTS

#### 4.1. THE DISTURBANCE PROCESS

To document the disturbance process of *Cytherissa lacustris* sediment cores from 40m, 50m and 60m lake depth (station MO-7) were analyzed in 1984 for subfossil material. In fig.3, the number of subfossil shells is plotted against the depth of the sediment layer.

At 60m lake depth, a sharp decrease in numbers between 10-12 cm and 14-16 cm can be observed, leading to complete disappearance in the 6-8 cm layer. The occurrence of a few shells of juveniles in the uppermost layer may be due to drift from shallower areas (post-mortem or specimens which did not complete their development). No living *Cytherissa* were found in these samples.

At 50m, the decrease in number of shells is slower but disappearance occurs at the same time as in 60m. Some shells of juveniles most probably carried by drift were found in the 0-2 cm layer.
The number of shells at the 40m site is generally higher than at lower lake depths (76 valves/40 cm³) and starts to decrease in the same layer (10-12 cm) as in 50m and 60m but they never disappear completely.

Subsequent recovery is fast and population size increases in the uppermost layers to numbers similar to those found in populations from 12m or 20m.

As an immediate consequence of the reduction in numbers, the population structure is heavily disturbed (The data from fig.4 are derived from a single core). In the undisturbed populations of the deeper sediment layers (12-14 cm for 40m and 14-16 cm for 60m), the youngest juveniles (< Vth instar) account for 30 to 40% of the total population. All stages are present and none of them is dominant. The same pattern is displayed by living populations (Danielopol et al., 1988).

When the number of individuals decreases, development is incomplete and some stages become under-represented whereas others increase in proportion. No stage specific sensitivity could be observed.

4.2. OXYGEN DYNAMICS

Concurrent measurements of oxygen concentrations were made above the site MO-7-67m in the open water and at the corresponding depth at the sediment surface with a polarographic oxygen sensor in the years 1985 and 1986. The linear least square regression fitted to the data was highly significant ($y = 1.01x - 8.43, r^2 = 0.966, N = 22$, where $y$ refers to the oxygen concentration at the sediment surface (μmol.dm⁻³) and $x$ to the oxygen concentration in the open water (μmol.dm⁻³), (fig.5).

This relationship was used to compare the oxygen data from 1976, 1983 and 1988, (measured by the Institute of Fishery research, Scharfling, using the Winkler method and samples from approximately 1m
Fig. 4: Percentage distribution of subfossil instars and adults of *Cytherissa lacustris*.

*Fig. 4: Distribution du pourcentage de stades juvéniles et adultes subfossiles de *Cytherissa lacustris*.

A: MO-7, 60 m, B: MO-7, 40 m*
above the sediment) with data from 1985 (measurements were done at the sediment surface with a polaro-
graphic oxygen sensor)
The development of oxygen and temperature in 1985 at the transect MO-7 is shown in fig. 6. At 12m the oxygen content is clearly a function of the bottom temperature whereas oxygen at the intermediate depths (20m and 40m) decreases slightly during the summer stagnation period. Oxygen depletion occurs at the deepest site (67m) and hypoxic conditions (<1mg.l⁻¹ or 31.2 μmol.dm⁻³) last for four months (September-December)

When samples between the years 1976 to 1988 are compared (fig. 7A and 7B) considerable changes of the oxygen situation of the lake are observed. The effects of eutrophication are most strongly expressed in 1976, when oxygen concentrations at the 67m site are below the Imgl-1 threshold from June until December, whereas in 1988 this hypoxic period is reduced to two months. A similar trend can be seen at the 50m site: In 1976, extremely low values occur from September until November (<50 μmol.dm⁻³). In 1988, concentration declines for two months (Nov., Dec.) below 100 μmol.dm⁻³ (3mg.l⁻¹) - a crucial value for the occurrence of Cytherissa lacustris (Delorme, 1978). In 1988, the oxygen content at 50m was never less than 125 μmol.dm⁻³ (4mg.l⁻¹).

The continuous amelioration of the oxygen situation at the sediment surface starting in 1983 is reflected by a shortening of the conditions of low oxygen content (<3mg.l⁻¹) in time and space (Table 2).

<table>
<thead>
<tr>
<th>Year</th>
<th>% lake bottom area with &lt; 3 mg O₂ l⁻¹ for at least one month</th>
<th>Period of less than 3 mg O₂ l⁻¹ (months)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>68m</td>
</tr>
<tr>
<td>1976*</td>
<td>62.9</td>
<td>7</td>
</tr>
<tr>
<td>1983*</td>
<td>50.9</td>
<td>6</td>
</tr>
<tr>
<td>1985</td>
<td>33.2</td>
<td>6</td>
</tr>
<tr>
<td>1988*</td>
<td>16.8</td>
<td>4</td>
</tr>
</tbody>
</table>

Table 2: Development of hypoxic conditions in Mondsee from 1976 -1988 (*based on data from the Institute of Fishery Research, Scharfling, transformed using equation $y = 1.01x - 8.43$ from fig. 5).

Measurements of redox potential in sediment cores differing in porosity and organic matter content (see table 1) were made in August 1988 (fig.8). Simultaneously the oxygen concentration at the sediment surface was recorded. An empirical second order linear regression between Eh (mV) at 0.5-1.0 cm sediment depth - the
Fig. 6: Temperature and oxygen at various sampling depth at 10 cm above the sediment (1984-1985).

Fig. 6 : Température et oxygène mesurés en divers endroits à 10 cm au-dessus du sédiment (1984-1985).
Fig. 7: Development of lake bottom oxygen concentrations before (1976) and after (1983, 1985, 1988) restoration measures. 3 mg l\(^{-1}\) 1 mg l\(^{-1}\) \(A: 50 \text{ m} \); \(B: 67 \text{ m}\). The data from 1976, 1983 and 1988 are from the Institute of Fishery Research, Scharfling, transformed using the equation \(y = 1.01x - 8.43\) (see also fig. 5).
depth of main occurrence of *Cytherissa lacustris* and O2-content (µmol dm⁻³) in the overlaying water measured in the lake was fitted to the data (fig.9) \( y = 0.00541x^2 + 2.41x + 3.26, r^2 = 0.96, N = 10 \).

The zero oxygen depth as determined with redox-potential measurements (200 mV - threshold) decreases with increasing lake depth (4cm in 12m and 20m, 0.5cm in 67m lake depth) (fig.8). If measured in the sediment layer, where *Cytherissa Lacustris* is most abundant (0.5cm-1.0cm), the 200mV value corresponds to \( \approx 100 \) µmol.dm⁻³ (3 mg.l⁻¹) oxygen at the lake bottom (fig. 9). Below an oxygen concentration of 3 mg.l⁻¹ in the water overlaying the sediment, oxygenation of the sediments is not sufficient for the occurrence of *Cytherissa lacustris*.

Oxygen penetration depth in the sediment, measured with O₂-microelectrodes, depends mainly on porosity, if the effect of reductive processes is eliminated by aerating the sediments for 24 hours. It increases with increasing lake depth because of increasing porosity (Tab.3).

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>15</th>
<th>18</th>
<th>21</th>
<th>40</th>
<th>50</th>
<th>55</th>
<th>60</th>
<th>63.5</th>
<th>68</th>
</tr>
</thead>
<tbody>
<tr>
<td>Penetr. depth (mm)</td>
<td>2.0</td>
<td>2.5</td>
<td>3.0</td>
<td>3.1</td>
<td>4.0</td>
<td>4.0</td>
<td>4.5</td>
<td>4.5</td>
<td>5.7</td>
</tr>
<tr>
<td>Porosity (0-3cm)</td>
<td>0.8750</td>
<td>0.896</td>
<td>0.896</td>
<td>0.910</td>
<td>0.911</td>
<td>0.914</td>
<td>0.917</td>
<td>0.912</td>
<td>0.921</td>
</tr>
<tr>
<td>Porosity* (0-1cm)</td>
<td>0.8660</td>
<td>0.864</td>
<td>0.866</td>
<td>0.926</td>
<td>0.937</td>
<td>0.947</td>
<td>0.941</td>
<td>0.940</td>
<td>——</td>
</tr>
</tbody>
</table>

Table 3: Oxygen penetration depths, measured by microelectrodes, and porosity (August 1988).

*Data from June, 1989 (Hupfer, unpubl.)

*Tableau 3 : Profondeur de pénétration de l'oxygène mesurées avec une microélectrode et porosité (Août 1988)

*Données de Juin 1989 (Hupfer, non publié).*

Two typical oxygen profiles, one from 20m and one from 63m are shown in fig.10. Within core variability was low (± 0.5mm) and may be partly explained by the roughness of the sediment surface thus making it difficult to determine the exact position of the electrode tip at the sediment.
The experiments using a single type of sediment (M07-40m, porosity = 0.8863) demonstrate the dependence of the oxygen penetration depth from the oxygen content of the overlying water (fig.11) \( y = 0.0000541x^2 + 0.0364x + 0.868, r^2 = 0.97, N = 10 \). To summarize the field and laboratory data, the declining oxygen conditions in the lake led to a reduction of the inhabitable substrate in both the horizontal and the vertical directions. The restoration measures are visible from 1983 onwards as a shortening of the hypoxic period in time and space which provides potential areas for recolonization by the benthic fauna.

4.3.- OXYGEN TOLERANCE

The oxygen tolerance of selected ostracod species was determined in the laboratory at a single oxygen concentration (0.1 mg.l\(^{-1}\), 11°C). The \( LD_{50} \)-values for the six species are listed in table 4.

![Graph showing relationship between redox potential and oxygen](image)

**Fig. 9:** Relationship between redox potential at 0.5-1.0 cm sediment depth (main occurrence of *Cytherissa lacustris*) and oxygen at the lake bottom. Data are from August 1988. Broken line: 200 mV corresponding to \( \sim 3 \text{mg} \text{O}_2 \text{l}^{-1} \). (relative electron activity) \( = \frac{E_h (\text{mV})}{59.1} \) at 25°C.

**Fig. 10:** Oxygen microelectrode profiles in sediments differing in porosity and organic matter content.

![Graph showing oxygen microelectrode profiles](image)

**Fig. 10:** Profils d'oxygène mesuré à la microélectrode dans des sédiments différents par leur porosité et leur teneur en matière organique.
Isocypris beauchampi and Limnocythere inopinata are the most sensitive species with a LD50 value of ≤ 1 day. The next most sensitive species are Cypridopsis vidua (< 7 days) and Potamocypris sp. (6-7 days). Adult specimens of Cytherissa lacustris appear to be less vulnerable (LD50 = 10 days). Highest survival was shown by Cypria ophthalica and Cyclocypris ovum (LD50 = 20-30 days), which are both swimming forms, occurring mainly above the sediment surface. Using reducing sediment as substrate, the LD50 for Cypria ophthalica falls to half the value for well oxygenated sediments.

The LD50 value of the later instars of Cytherissa lacustris at different temperatures and oxygen concentrations are listed in (Table 5). Applying Peto and Peto's Logrank test to the survival data statistically significant differences are obtained between all stages except stages VI and V. At oxygen concentrations of 0.1 mg.l\(^{-1}\), these two stages showed lowest survival (12-14 days at 4°C and < 5 days at 11°C).

### Table 4: LD50 (0.1 mg.l\(^{-1}\) O\(_2\), 11°C) for selected ostracod species of Mondsee.

<table>
<thead>
<tr>
<th>Species</th>
<th>LD50 (d)</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Isocypris beauchampi</em></td>
<td>0.5</td>
<td>20</td>
</tr>
<tr>
<td><em>Limnocythere inopinata</em></td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td><em>Cypridopsis vidua</em></td>
<td>&lt;7</td>
<td>11</td>
</tr>
<tr>
<td><em>Potamocypris sp.</em></td>
<td>6-7</td>
<td>10</td>
</tr>
<tr>
<td><em>Cytherissa lacustris (Ad.)</em></td>
<td>10</td>
<td>36</td>
</tr>
<tr>
<td><em>Cypria ophthalica</em></td>
<td>28-29</td>
<td>61</td>
</tr>
<tr>
<td><em>C. ophthalica</em> (eutroph. Sed.)</td>
<td>13-14</td>
<td>65</td>
</tr>
<tr>
<td><em>Cyclocypris ovum</em></td>
<td>21</td>
<td>27</td>
</tr>
</tbody>
</table>

Tableau 4 : LD \(_{50}\) (0.1 mg.l\(^{-1}\) O\(_2\), 11°C) pour des espèces sélectionnées d’ostracodes du Mondsee.

Fig. 11 : Relationship between oxygen penetration depth as determined with microelectrodes and oxygen concentrations in the overlaying water (sediment from MO-7-40m).
Oxygen and Cytherissa

LD₅₀ (days) Cytherissa lacustris

<table>
<thead>
<tr>
<th>O₂ mg/l</th>
<th>0.1</th>
<th>1.0</th>
<th>0.1</th>
<th>1.0</th>
<th>100 %</th>
<th>100 %</th>
<th>100 %</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LD₅₀ N</td>
<td>LD₅₀ N</td>
<td>LD₅₀ N</td>
<td>LD₅₀ N</td>
<td>LD₅₀ N</td>
<td>LD₅₀ N</td>
<td>LD₅₀ N</td>
</tr>
<tr>
<td>Ad</td>
<td>&lt;8</td>
<td>8</td>
<td>23</td>
<td>20</td>
<td>100</td>
<td>7</td>
<td>20</td>
</tr>
<tr>
<td>VII</td>
<td>20</td>
<td>25</td>
<td>20</td>
<td>20</td>
<td>100</td>
<td>30</td>
<td>35</td>
</tr>
<tr>
<td>VI</td>
<td>14</td>
<td>15</td>
<td>&gt;30</td>
<td>20</td>
<td>100</td>
<td>160</td>
<td>55</td>
</tr>
<tr>
<td>V</td>
<td>12</td>
<td>10</td>
<td>&gt;30</td>
<td>20</td>
<td>100</td>
<td>&gt;140</td>
<td>55</td>
</tr>
</tbody>
</table>

Table 5: LD₅₀ values (days) for juvenile and adult Cytherissa lacustris at several oxygen and temperature levels.

All stages are extremely sensitive when high temperatures (18°C) and low oxygen concentrations are combined. In this case LD₅₀ values are a third of the values found at 4°C.

Mortality due to laboratory stress was low and individuals could be kept at 100% air saturation for more than 240 days (For a detailed analysis of the influence of temperature on survival see also Geiger, this volume).

4.4 - RECOLONIZATION

The distribution of Cytherissa lacustris with depth at the site MO-7 in the years 1983, 1985 and 1988 is shown in fig. 12.

In 1983, highest numbers were recorded in the sublittoral and upper profundal. The high mean value for the 40m site is misleading, as all individuals were found in a single core, indicating an extremely patchy distribution. Cytherissa did not occur at depths below 40m.
In 1985, *Cytherissa* was present in high numbers (up to 110,000 Ind.m$^{-2}$) in the infralittoral and upper profundal down to 40m. Lower confidence limits than in 1983 indicate reduced patchiness and the establishment of a permanent population. A few specimens were present at the 50m site.

Sampling in 1988 included 11 depths (3 parallel cores). The use of a net with 200μm mesh size resulted in lower numbers (I-IV instars were lost). If they had been included 30-40 % more animals would have been found. The abundance of *Cytherissa lacustris* was similar at all depths down to 50m with a slight peak in the sublittoral. The 1988 samples were the first where the sediments in 50 and 55m were permanently populated. *Cytherissa* did not occur in the upper littoral (0-8m) or below 55m in any of the three years (1983, 1985 and 1988).

The vertical distribution of *Cytherissa* in the sediments is determined by the redox conditions (fig. 13). Most of the individuals are concentrated in the uppermost sediment layer (0-1cm) with high redox potential (>275mV). Only adults and VIII-instar juveniles can be found in deeper layers (Danielopol et al., 1988; Hermann et al., in prep) if redox conditions are favorable.

5. DISCUSSION

The disappearance of *Cytherissa lacustris* from large parts of the profundal zone of lakes as a consequence of eutrophication is well documented in the literature (Löffler, 1972; 1975; Delorme, 1978). The results presented here show that the *Cytherissa* population of Mondsee is drastically reduced in numbers already before the onset of anoxic conditions in the hypolimnion. This is similar to the data of Löffler (1972, 1975) who argued that changes in the sediment structure through enhanced sedimentation of fine material together with declining oxygen conditions might be responsible for the local extinction of this species. As *Cytherissa lacustris* in Mondsee disappeared only from areas deeper than 40m, and a sedimentation of small sized phytoplankton must have affected the entire lake bottom, this hypothesis cannot be applied to the particular situation of this lake. Eutrophication in Mondsee has favoured larger sized algae (Findenegg, 1969; Dokulil et al., 1990) and an increase in the silt fraction of the profundal sediments through high biogenic calcite precipitation in the epilimnion has been observed (Horsthemke, 1986). The formation of the flocculent reduced sediments is a result of both enhanced sedimentation and low oxygen concentrations (low remineralization under reduced conditions (Berner, 1982). In the present study, the role of oxygen is, therefore, considered to be of greater importance than changes in the sediment structure.

As estimated by sediment accumulation rates measured with the $^{137}$Cs-technique of 5mm/year (Irlweck, 1990), *Cytherissa lacustris* starts to disappear at the site MO-7-60m between 1965 and 1970. The few existing oxygen data from this period (Findenegg, 1969) indicate, that anoxic conditions, if present, were restricted to the deepest station (68m).

Assuming a sediment accumulation rate of 3.5mm/year for the MO-7-50m site (Irlweck, 1990), disappearance of *Cytherissa* must have occurred in the early seventies. At 40m, this phenomenon is less clear and perhaps occurred later here than at greater depths (no $^{137}$Cs-data are available for 40m). At this depth, oxygen values below 3 mg.l$^{-1}$ were first observed in the water column in November 1976 but never for longer than one month (Jagsch and Megay, 1982).
Considering the high tolerance of low oxygen concentrations of this species, low oxygen content at the sediment surface for less than one month may reduce the population in numbers as observed in the sub-fossil record, but will not lead to complete disappearance.

The extrapolation of the open water oxygen data to the situation above and in the sediments, allows the reconstruction of the oxygen conditions during the disturbance and recolonization period. Transformation of the open water values was necessary as a considerable oxygen gradient was found above the sediment. Largest differences were found at the onset of oxygen depletion (Geiger unpubl.). The existence of similar gradients within a few decimeters is known from studies of the marine environment (Jorgensen, 1980; Rosenberg and Loo, 1988).

The penetration of oxygen into the sediment depends on porosity, reductive capacity of the sediment, and the oxygen concentration in the overlying water. In Mondsee, sediment penetration through molecular diffusion alone is limited to the first 5-8 mm. This corresponds to the thickness of the brownish-oxidized layer. Values for marine sediments (Revsbech, 1979; Reimers et al., 1986) and other lakes (Sweerts, 1988) are also within this range.

If the zero oxygen depth is determined using the 200mV redox potential, values of 1-3 cm are obtained. These differences by an order of magnitude can be explained by the burrowing activity of macrofauna (in our case tubificids and chironomids) creating localized oxic zones within a generally anoxic environment (see also Revsbech, 1979, Jorgensen, 1980, 1989). Similar to the penetration depth as determined with microelectrodes, the redox potential zero depth is dependent on the oxygen concentration in the overlying water, but Eh based values showed better correlation with the depth distribution of oxybiontic meiofauna (Herman et al, in prep.) and may therefore provide a better estimate of the oxygen availability. The 200 mV threshold for Mondsee sediments at 0.5-1.0 cm sediment depth - the depth of most abundant occurrence of *Cytherissa la­cu­stris* - corresponds to oxygen concentrations of 2.5 - 3 mg.l⁻¹ in the overlying water.¹ The same value of 3 mg.l⁻¹ in the open water was found by Delorme (1978) to be the critical oxygen concentration for *Cytherissa lacustris* in Canadian lakes. Oxygen values below 3 mg.l⁻¹ in the open water lead to a reduction of the inhabitable substrate in the vertical for endobenthic species such as *Cytherissa lacustris*. With further reduction of the O₂-concentrations, bioturbation by macrozoobenthos may be reduced (Jorgensen, 1980; Rhoads, 1974) and sediments become less aerated (Fukuhara, 1987). A decrease in bioturbation activity during eutrophication in Mondsee can be assumed by the existence of laminated sediments, which are preserved only if macrofaunal burrowing is lacking (see also Davis, 1974). Ostracods and meiofauna are less efficient in bioturbation and only adults and the last larval stages (VIIIth stage) of *Cytherissa lacustris* penetrate actively in the deeper sediment layers (1-3cm) (Danielopol et al., 1988; Hermann et al., in prep.). As a result they are more dependent on the surrounding sediment oxygen conditions than macrofauna.

Survival experiments can provide useful information about the potential limits of occurrence of a given species (Wieser et al, 1974; Stickle et al., 1989). The control of more sensitive life history parameters such as fecundity and growth can only be carried out if the species of interest is readily cultured. As culturing of *Cytherissa lacustris* under low oxygen concentrations was not successful, survival data were used to define the oxygen requirements of different ostracod species.

The younger stages (Vth and VIth instar) showed significantly lower survival at all oxygen levels than the older ones. These findings are in agreement with observations on the number of sieve pores (Danielopol, this volume), which are fewer in young juveniles than in adults and last instar larvae. The accumulation of mitochondria near the sieve pores (Keyser, 1983) indicates that they probably serve as areas of additional oxygen transport. This may also explain the restriction of the young larval stages to the well oxygenated uppermost sediment layer (0-1 cm).

The profundal or sublittoral species (*Cytherissa lacustris*, *Cypria ophthalmitica*) show higher oxygen tolerance than the littoral, epibenthic species (*Isocypris beau­champi, Limno­cythere inopinata, Cypridopsis vida­ua*). These findings are in agreement with those for other benthic organisms such as chironomids and oligochaetes (Jonasson, 1972) or marine macrofauna (Pearson and Rosenberg, 1978; Seliger et al., 1985).

Respiration rates of *Cytherissa lacustris* at 100 % air saturation are low (1.02 ml O₂.10µg⁻¹.h⁻¹ at 15°C, Newrkla, 1985) if compared to other ostracod species (Hagerman, 1969; Herman and Heip, 1982; Peper, 1986) indicating low standard metabolism.

The generally low activity together with the observed closing of the shells and most probably further reduction of the metabolism may account for the relatively high oxygen tolerance. The sensitive reaction of *Cytherissa lacustris* is therefore not an immediate consequence of its oxygen requirements. It can be better understood by considering additional information about its life cycle, reproductive potential, migratory behaviour and mode of benthic life.

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¹ This empirical relationship was found during the summer stagnation period 1988 and still has to be checked for a wider range of sediment and lake types for different seasons.
Occurrence of a species in a given environment can be seen as a balanced state of mortality and permanent renewal of the population through reproduction and immigration. If, due to some environmental stress, mortality increases faster than renewal occurs, the particular species will disappear.

Due to its slow development and the long duration of its life cycle (Geiger, 1990), *Cytherissa lacustris* cannot avoid hypoxic periods. Continuous low reproduction (Geiger, 1990), low active migration over long distances and the endobenthic type of life are further handicaps when rapid changes in the environment occur.

Recolonization does take place if environmental conditions (i.e. oxygen) improve, even if at a very low rate compared to other meio- and macrofauna (Fleeger and Chandler, 1983; Wahl, 1985; Coull, 1969; Josefson and Widbom, 1988).

In the case of Mondsee, refuge areas for this species are limited due to unfavorable substrate or too high temperatures in the littoral. This may further reduce the speed of recolonization.

Further improvement of the sediment oxygen conditions including a decrease in reductive substances are needed before stable populations can become re-established in the formerly depopulated areas of the lake.

The data presented in this paper confirm the potential value of *Cytherissa lacustris* as a bio- and paleobiological indicator for oxygen as suggested by Löffler (1972, 1975 and 1983). More strictly this applies to the oxygen availability in sediments of deep, temperate lakes (e.g. the pre-alpine lakes of Austria). The analysis of changes in abundance and population structure of this species provides information on the process of disturbance as well as on recolonization. Furthermore, negative long-term effects are visible already before this can be detected with sedimentological and/or physico-chemical methods.

The analysis of the subfossil assemblages allows the reconstruction of sediment oxygen conditions in the past but additional sedimentological and paleolimnological information is required to strengthen the inference.

The existence of a permanent and stable population before the onset of disturbance has to be documented (population structure, replicate samples). It should be considered that changes in the abundance of subfossil *Cytherissa* might be due also to local events such as the input of allochthonous material (Danielopol et al., 1985) or caused by other factors than oxygen (e.g. lake level rising or climatic changes (Handl, 1989). Genetically distinct clones as observed even in a single lake (Sywula and Geiger, this volume) may exhibit differential responses to low oxygen conditions similar to those found in *Daphnia*-populations (Weider and Lamper, 1985). The possibility of ecophysiological adaptations to low oxygen as demonstrated by Geiger (this volume) for temperature, cannot be excluded. Further information can be obtained from the analysis of other ostracod species and subfossil remains (Löffler, in Carbonel et al., 1988).

The most promising and efficient way to use *Cytherissa lacustris* as a bio- and paleobiological indicator is the integration of sedimentological and ecological data within an interdisciplinary framework.

6. CONCLUSIONS

1) The oxygen situation in the open water of Mondsee only partly reflects the situation in the sediments.

2) Oxygen availability in the sediment for meiofauna is reduced even if open water values remain still high (3mg.l⁻¹).

3) Ostracods, like other meiofaunal groups suffer higher disturbance than macrobenthic species which are more independent of the surrounding medium because of bioturbation activity.

4) Due to its long life cycle, the endobenthic lifestyle and low active migration capacity *Cytherissa lacustris* is highly vulnerable despite of a relatively high tolerance to low oxygen conditions.

5) Long periods of low stress seem to affect *Cytherissa lacustris* more severely than does short term intensive stress.

6) The rate of recolonization depends on the life history, reproductive potential, and mobility of the animal as well as the size of the refuge areas.

7) *Cytherissa lacustris* is proposed as a bio-indicator for sediment oxygen availability.
ACKNOWLEDGEMENTS

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FIELD AND LABORATORY STUDIES ON THE LIFE CYCLE
OF CYTHERISSA LACUSTRIS (SARS) (CRUSTACEA,
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ETUDES DU CYCLE DE VIE DE CYTHERISSA LACUSTRIS
(SARS) (CRUSTACEA, OSTRACODA) SUR LE TERRAIN ET
IN VITRO. MISE EN RELIEF DU ROLE DE LA TEMPERATURE

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Key-Words: Life cycle, Cytherissa lacustris, temperature, ostracods.

Mots-CleS: Cycle de vie, Cytherissa lacustris, température, ostracodes.

Abstract:
Life cycle characteristics of the parthenogenetic, freshwater ostracod species Cytherissa lacustris from Mondsee (Austria) were studied for 3.5 years both in the field and in the laboratory at two depth stations differing in their temperature regime (12m and 20m).

Highest abundances were recorded in 20m with maximum numbers of 107000 ind./m². At this depth, Cytherissa lacustris was the dominant ostracod species. The method described by Rigler and Cooley (1974) was used to determine the development time of all instars from field data. Laboratory development times are included in the calculations. Overall development time (1st- VIIIth instar) is 1.9 years in 12m and 2.2 years in 20m. The high instar specific mortality of instar V and VI (53% and 23.5%) explains the low numbers of adults (< 20%) at both depths.

Animals from 12m are better adapted to higher temperatures than animals from 20m which live in a thermically stable environment (4-6°C throughout the year). Cytherissa lacustris from Mondsee appears to be adapted to the stable environmental conditions of the profundal zone of the lake with low fecundity and an extremely long life cycle compared to other meiofauna species. Together with other factors (see related papers in this volume), the life history characteristics of this species are responsible for its high vulnerability towards environmental disturbances.

Résumé:
Les caractéristiques du cycle de vie de l'ostracode parthénogénétique d'eau douce Cytherissa lacustris du Mondsee ont été étudiées pendant 3 ans et demi tant in situ qu'au laboratoire à deux stations différant par leur profondeur (12 et 20 m) et leur régime thermique.

Les plus grandes abondances ont été observées à la station de 20 m avec un maximum de 107 000 individus par m². A cette profondeur, Cytherissa lacustris était l'espèce d'ostracodes dominante. La méthode mise au point par Rigler et Colley (1974) pour mesurer le temps de développement de chaque stade en milieu naturel a été utilisée. Le temps de développement in vitro sont inclus dans les calculs. Dans tous les cas, le temps de développement (stades I à VIII) est de 1,9 jours à 12 m et de 2,2 jours à 20 m. Un taux élevé de mortalité aux stades V et VI (53% et 23,5% respectivement) explique la faible proportion d'adultes (<20%) aux deux profondeurs.

Les animaux de 12 m sont mieux adaptés à une élévation de la température que ceux de 20 m qui vivent dans un milieu thermiquement stabilisé (4-6°C au cours de l'année). Cytherissa lacustris du Mondsee apparaît comme bien adaptée aux conditions de stabilité du milieu des zones profondes du lac avec une faible fécondité et un cycle de vie très long par rapport à celui de l'ensemble du reste de la méiofaune. En connexion avec d'autres facteurs du milieu (cf. autres articles de ce volume), les caractéristiques du cycle de vie de cette espèce sont responsables de la grande vulnérabilité de celle-ci aux perturbations du milieu de vie.
1. INTRODUCTION

Most of the quantitative studies on the population dynamics of meiobenthic organisms were carried out to investigate the role of meiofauna in the trophic foodweb and to determine the amount of energy passing through it (Gerlach, 1971). Therefore only organisms with high abundances and biomass values similar to macrofauna were considered extensively in freshwater ecology (Heip, 1976; Herman et al., 1983) with special attention given to harpacticoid copepods (Sarvala, 1979; Kovarc, 1990).

The role of meiofauna as potential bioindicators is well described in the marine literature (Elmgren, 1975; Gray, 1989) where rare species often have a high indicative value if environmental disturbances are to be detected (Coull and Palmer, 1984).

Freshwater ostracods have proved to be excellent tools in both limnology and paleolimnology to assess long- and short-term changes of the environmental conditions as their calcareous shells are deposited in the sediments so that changes in the populations over time can be easily traced (Löffler, 1975). Despite this, quantitative data on the life cycle characteristics of freshwater ostracods are scarce. Most of the data which is available relates to fast developing species (McGregor, 1969; McLay, 1978a,b; Danielopol 1980; Martens et al, 1985) and/or brackish water species (Theisen, 1966; Delling, 1981, Heip, 1976).

The parthenogenetic freshwater ostracod Cytherissa lacustris was studied over a period of 3.5 years within the framework of an interdisciplinary project. This project was initiated in order to explain the disappearance of the species from most of the prealpine lakes of Austria as a consequence of increased eutrophication (Löffler, 1975; Danielopol, 1988 and related papers in this volume).

The life cycle characteristics of Cytherissa were thought to be, among other factors, responsible for its sensitivity compared to other ostracod species (Delorme, 1978; Danielopol et al., 1988). Löffler (1971) and Kitchell and Clark (1979) considered this species to be long-lived, with a life cycle well above one year similar to that of Cypria ophtalmica (Thaler, 1977) and Cyprideis torosa (Heip, 1976).

Literature data suggest that Cytherissa lacustris is cold stenothermic as it is generally found in the profundal zone of large, deep lakes. Its occurrence in the littoral of small, high alpine lakes (Schmassmann, 1924) is explained by the low temperatures found at these altitudes (Löffler, 1975). Nevertheless, this species is also found in small water bodies of Northern Germany (Delling, 1981) with high summer temperatures and in shallow lakes of southern Sweden (Scharf, pers. comm.), experiencing large fluctuations of bottom temperatures.

Fig. 1 - Study area with station MO-7-12 m and MO-7-20 m.
Fig. 1 - Zone étudiée avec les stations MO-7-12 m et MO-7-20 m.

The main objectives of the present paper are:

1) To describe the abundance pattern of Cytherissa lacustris over a period of 3.5 years at two lake depths (12m and 20m) with differing temperature regimes.
To determine the development time of this species from field and laboratory data and to discuss the suitability of methods developed for other crustacean groups.

3) To specify the temperature requirements of this species and to explain its biogeographic distribution pattern. Using survival experiments at high temperatures.

2. STUDY AREA

Mondsee (fig. 1) is the warmest of a series of lakes in the Salzkammergut-lake area (Northern Austria) with surface water temperatures in summer of up to 26°C. During summer the thermocline is well expressed (10m-20m) and the lake is thermally stratified from June until November, depending on weather conditions and wind action.

At the sampling transect MO-7 (fig. 1) a large population of Cytherissa lacustris still exists although this species has disappeared from other parts of the lake (see related paper in this volume). Due to its geomorphology, the shallow areas (0-30m) in this part of the lake were less affected by the consequences of heavy eutrophication of the lake during the sixties and seventies and could therefore serve as a reference point for undisturbed habitat conditions.

The sampling stations are located at 12m and 20m deep and differ in their temperature regimes (fig. 2). Bottom temperatures at 12m vary between 4°C and 16°C whereas at 20m constant temperatures are observed (4°C-6°C). Sediment characteristics are similar at the two stations (Geiger, 1990) and are therefore not considered in the present paper. The 12m station is at the upper limit of occurrence of Cytherissa lacustris in Mondsee. Abundant populations are restricted to the sublittoral and upper profundal (20m-40m) with a maximum at 20m-30m depth (Danielopol et al., 1988).

For a more detailed description of the study area and the sampling transect MO-7 see also related paper in this volume and Danielopol et al., 1988.

3. MATERIAL AND METHODS

3.1. SAMPLING

Starting in September 1984, seasonal samples were taken at two stations (MO-7-12m and MO-7-20m) with a modified Kajak-corer (6 replicates). After January 1986, the sampling interval was reduced to one month in order to detect possible short term fluctuations. Due to the ice cover of the lake from February to April and technical problems, sampling is not complete over the whole investigation period (September 1984-March 1988).

The seasonal samples from 1984-1985 were washed through 100 µm mesh-size and all stages including the smallest juveniles, were counted under a stereomicroscope (Wild, 12x and 50x). The size range of the different stages is given in table 1.

The monthly samples were sieved through a net with 200 µm mesh size and only the number of the last four juvenile stages (in the present paper referred to as Vth-VIIIth instar) and the adults could be assessed. As the species reproduces parthenogenetically, only females were observed.

All data are given as Ind./Core (19.63 cm²). Log x+1 transformed values were used to calculate the 95% confidence limits. Confidence limits derived from log x+1 transformed values should be used, if the distribution of the animals is contagious (Krebs, 1989).
Fig. 3 - Developmental stages of the ovaries of Cytherissa lacustris.

**Fig. 3** - *Stades de développement des ovaires de Cytherissa lacustris.*

- **A**: Only ovocytes present/ovocytes seulement présents
- **B**: Few (1-2) developed eggs in the ovaries/1-2 oeufs développés dans les ovaires
- **C**: 6-10 developed eggs/6-10 oeufs développés.
3.2. EGG NUMBERS

To estimate the fertility and main period of reproduction, mean egg numbers were counted and the state of the ovaries observed under a microscope (Reichart, 200x). Females were collected monthly, dissected under the stereomicroscope the valves removed and stained with an alcoholic solution of 5% fast green (Sigma). Subsequent disstaining in 96% ethanol and embedding in glycerine was necessary to detect the presence or absence of ripe eggs in the ovaries. Figure 3 shows the three developmental stages of the ovaries which could be distinguished.

For the determination of the main reproductive period, stages B and C were pooled. Egg number was determined as exactly as possible but specimens where all eggs were clearly visible were too few to allow firm conclusions.

3.3. CULTURES

Two series of experiments were carried out at three different temperatures (6°C, 12°C and 18°C) to determine the development time of the last four instar larvae. In the first series, the animals were caught in winter (December, 1984) at 12m and 20m depth (60 animals/instar). To determine whether seasonal adaptations towards temperature occur in this species, a similar set of animals were collected in summer (June, 1985).

The following procedure was used for all experiments: The animals were picked out under a stereomicroscope, staged and transferred to experimental vessels (30 per vessel; 60 in total for each stage) and allowed to adapt to experimental temperatures. The vessels - open perspex tubes of two cm diameter and two cm height, closed at the bottom with a net with 100 μm mesh size - were fixed on a heavy plate and submerged in a temperature controlled, aerated water bath. Sediment of <100μm grain size was added in surplus. For the weekly controls, the plate was taken out of the water bath, the sieves were washed with tap water and the number of animals alive, molted or dead was recorded. Only specimens which passed one entire stage under laboratory conditions were considered for the calculation of development time.

3.4. SURVIVAL AT 30°C

A total of 224 specimens (44 adults and 60 for juvenile stages VIth-VIIIth) of Cytherissa were exposed to 30°C for 24 days. The experimental methodology was the same as described by Geiger (1990) for the oxygen tolerance experiments. Every two days, the number of dead animals was recorded. The LD50 was calculated and the survival curves of the different stages tested for significance using Peto and Peto's Logrank Test (Pike and Thompson, 1986).

4. CALCULATION OF DEVELOPMENT TIME FROM LABORATORY AND FIELD DATA

The method described by Rigler and Cooley (1974) was used to estimate the instar development times from the abundance curves. This method was first applied to multivoltine copepod populations with widely overlapping generations where single cohorts cannot be easily distinguished but peaks in the abundance curve are visible.

The difference between the mean pulse time (Mi) is equal to half of the sum of two consecutive stages. The mean pulse time, or centre of gravity, of the abundance peak is calculated as the sum of the products of the number of animals x days divided by the summed number of animals,

\[
M_i = \frac{\sum (\text{days} \times \text{animals})}{\sum \text{animals}}
\]  

where the index i denotes the respective stage. The most distinct peaks were chosen arbitrary from the abundance curves and the differences \(M_{i+1} - M_i\) were calculated. Distinct peaks were only visible in the VIth, VIIth and VIIth in 20m depth and the VIth and VIIth stage in 12m depth. With k instars there are k unknown development times, but only k-1 equations of the type thus

\[
M_{i+1} - M_i = (T_i + T_{i+1})
\]
being not directly soluble. Rigler and Cooley (1974) suggest an iterative approach minimizing negative mortalities or the determination of the development time of a single stage in the laboratory. As our data yielded only two equations, the iterative method could not be applied.

Knowing the ratio between the development times of the VIth and VIIIth and the VIIth and VIIIth stages from culture experiments at 18°C (Table 2) all the equations could be solved.

\[ M_{VII} - M_{VI} = \frac{1}{2} (T_{VII} + T_{VI}) = (T_{VII} + 0.66T_{VII}) \]  

(Eq. 3)

assuming, the ratio of the development times of two consecutive stages is approximately constant over the whole range of temperatures.

For stages I - IV, where no field data were available, an exponential regression line was fitted to the data from the older stages and the correspondent values were calculated.

The areas under the peaks were calculated using the trapezoidal rule:

\[ A_i = \frac{1}{2} \sum (a + b) * h \]  

(Eq. 4)

where a and b are the numbers of individuals at time \( t_i \) and \( t_{i+1} \) and \( h = (t_{i+1} - t_i) \).

Dividing these areas by the corresponding development times gives the number of animals entering a given stage (Southwood, 1978) and from the difference between two consecutive stages, stage specific mortality can be calculated.

\[ N_i = \frac{A_i}{d_i} \]  

(Eq. 5)

5. RESULTS

5.1. TEMPORAL CHANGES IN THE ABUNDANCE PATTERN

The Cytherissa lacustris population from the transect MO-7 was investigated over a period of 3 1/2 years at two depths (12 and 20m). In figure 4, the total number of individuals (Vth..Adult) is plotted against time for each of the two depths., the error bars representing 95% confidence limits from log x+1 transformed values.

![Fig. 4 - Abundance of total Cytherissa lacustris (Vth..Adult) Data are given as Ind/Core (20 cm²).](image)

In 12m, the highest densities were recorded in December 1985 (28370 Ind/m²) and in September 1987 (19300 Ind/m²). The peak in December 1986 is most probably due to sampling errors because it occurs at a period with generally decreasing numbers. Figures 5 and 6 show the mean values (geometric means) for all stages and the numbers of each stage expressed as a percentage of the stages from the total. The high numbers in winter are due to individuals in stage V which comprise more than 40% of the total population. This
suggests that the main reproductive period is in autumn. The youngest juveniles (II\textsuperscript{th}-III\textsuperscript{th} instar) were investigated in 1984-1985. Including these in the total would double the numbers for total Cytherissa. Parthenogenetic females never account for more than 20% of the total population indicating high juvenile mortality. Distinct peaks occur only in the younger stages (V\textsuperscript{th} and VI\textsuperscript{th}). Confidence limits are high (40-50% of the mean) and the population pattern is aggregated for all sampling dates and stages. The rough estimate of the overall development time, calculated from the time interval between the two major peaks, is 1.88 years.

At 20m depth (fig. 4), maximum abundance of total Cytherissa was recorded in July 1985 (107600 Ind/m\textsuperscript{2}). A sharp decrease in numbers occurs in January 1986. Numbers of individuals fluctuate markedly around a mean value of 15000 Ind/m\textsuperscript{2}, a tenth of the value observed in the year 1985. Due to the morphology of the site, erosion of sediments is likely at the 20m station (Hermann, 1990) and the fall in numbers could be a result of the loss of a large part of the population through erosion. The percentage of V\textsuperscript{th} stage juveniles decreased from 35% to 18% during this period (fig. 7 and 8). After this disturbance, adults were very rare (0.5-2% of the total) but at the end of the investigative period, the population seems to recover. High numbers of VI\textsuperscript{th} and VII\textsuperscript{th} instar larvae accounted for 80% of the total (fig. 7 and 8).

High numbers observed in May and July 1985 are due to a dramatic increase in VI\textsuperscript{th} stage juveniles. This indicates that the main reproductive period is later than at the 12m station. Peaks in the abundance curve are more clearly expressed than at 12m (fig. 7 and 8) and can be followed through the younger stages (V\textsuperscript{th}, VI\textsuperscript{th} and VII\textsuperscript{th}) at least. These peaks were used for the estimation of instar development times. Confidence limits are significantly smaller and the distribution is less aggregated than at 12m. The overall development time, estimated in the same way as for 12m, using the small peak after the sharp decrease, is 2.2 years.

At both depths, the percentage of adults is low (fig. 9) again indicating high juvenile mortality.

5.2. REPRODUCTION

The percentage of egg carrying adults in the total adult population is shown in fig. 10. The numbers were obtained by inspection of the ovaries of fixed and stained females under the microscope. The appearance of developed eggs (90-100\(\mu\)m in diameter) in the ovaries was used to distinguish the egg carrying females. Maximum values occurred in both depths in autumn and spring. Reproductive activity was considerably reduced during summer. Eggs were most probably laid at distinct time intervals. Egg laying in the laboratory did not take place but up to 10 eggs (mean value = 4) of similar developmental stage were found in the ovaries (fig. 3).

5.3. DETERMINATION OF INSTAR DEVELOPMENT TIME

The development time of the last juvenile stages, from 12 and 20m, was determined in the laboratory at three different temperatures.

Animals could be kept living for more than 200 days with low mortality (fig. 11) but the animals only moulted at higher temperatures. At temperatures which the animals experience in the field (6°C in 20m), no animals were found to develop through an entire instar period. Table 3 shows the development time of instars determined in the laboratory:

Hatching success (for the second moult) was generally low. 10.0 - 16.7% (12°C) and 7.8 - 11% (18°C) for animals from 12m and 2% (12°C) and 2.8% (18°C) for animals from 20m. V\textsuperscript{th} instar larvae from 12m could be kept up to the VII\textsuperscript{th} stage at 18°C.

5.4. DEVELOPMENT TIME AND MORTALITY FROM FIELD DATA

The distinct peaks of the smoothed abundance curves of stage V, VI and VII from 20m were used to calculate development times, numbers of individuals entering and leaving the stages and hence stage specific mortality following the method described by Rigler and Cooley, 1974 (for a description of the most important calculations see also paragraph 4). Development times for stages I-IV are derived from the fitted exponential regression curves (For 12m: \(y = e^{0.442x + 7.535}, r^2=0.92, n=4\); for 20m: \(y = e^{0.4421x + 8.802}, r^2 = 0.92, n=4\)).

The results are shown in table 4 (12m) and 5 (20m):

Heavy mortality of the V\textsuperscript{th} and VII\textsuperscript{th} stage juveniles appears to be a natural phenomenon. The same can be supposed for the older larval stages. This would explain the low number reaching the adult stage. The overall calculated development time is in good agreement with the estimates from the abundance curve of total Cytherissa.
Fig. 5 - Abundance of juvenile stages V-VIII and adults between September 1984 and March 1988 in 12 m depth.

Fig. 6 - Percentage of juvenile stages V-VIII and adults from total in 12 m depth (N is taken from total abundance curve).
### Life cycle of Cytherissa lacustris

#### Table 1: Size ranges of adult and juvenile Cytherissa lacustris determined under the stereomicroscope (12x, 25x)

<table>
<thead>
<tr>
<th>STAGE</th>
<th>SIZE RANGE (µM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADULTS</td>
<td>840-960</td>
</tr>
<tr>
<td>VIII</td>
<td>700-800</td>
</tr>
<tr>
<td>VII</td>
<td>540-600</td>
</tr>
<tr>
<td>VI</td>
<td>440-480</td>
</tr>
<tr>
<td>V</td>
<td>340-380</td>
</tr>
<tr>
<td>IV</td>
<td>280-300</td>
</tr>
<tr>
<td>III</td>
<td>220</td>
</tr>
<tr>
<td>II</td>
<td>180</td>
</tr>
</tbody>
</table>

#### Table 2: Ratio between development times of late instars of Cytherissa lacustris at different temperatures $R_d = d_{t_{i+1}}/d_t$

<table>
<thead>
<tr>
<th>STAGE</th>
<th>$18^\circ C$</th>
<th>$12^\circ C$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_{dVI-dVII}$</td>
<td>0.66</td>
<td>0.71</td>
</tr>
<tr>
<td>$R_{dVII-dVIII}$</td>
<td>0.85</td>
<td>0.94</td>
</tr>
</tbody>
</table>

#### Table 3: Development times of juvenile instars of Cytherissa lacustris from laboratory experiments.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Duration of peaks (Days)</th>
<th>Dev. Time (Days)</th>
<th>$N^0/m^2$ entering the stage</th>
<th>Mortality (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>VIII</td>
<td>224</td>
<td>189</td>
<td>125</td>
<td></td>
</tr>
<tr>
<td>VII</td>
<td>662</td>
<td>136</td>
<td>59</td>
<td></td>
</tr>
<tr>
<td>VI</td>
<td>484</td>
<td>115</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>V</td>
<td>69</td>
<td>113</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>IV</td>
<td>45</td>
<td>111</td>
<td>27</td>
<td></td>
</tr>
<tr>
<td>III</td>
<td>15</td>
<td>113</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>II</td>
<td>10</td>
<td>113</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>10</td>
<td>25941</td>
<td>47</td>
<td></td>
</tr>
</tbody>
</table>

#### Table 4: Field data derived development times using Eq 1-5 and the fitted exponential regression line $y = e^{0.442x} + 7.535$ for the 12m station

<table>
<thead>
<tr>
<th>Stage</th>
<th>Duration of peaks (Days)</th>
<th>Dev. Time (Days)</th>
<th>$N^0/m^2$ entering the stage</th>
<th>Mortality (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>VIII</td>
<td>550</td>
<td>261</td>
<td>8755</td>
<td>23.5</td>
</tr>
<tr>
<td>VII</td>
<td>850</td>
<td>221</td>
<td>37157</td>
<td>53</td>
</tr>
<tr>
<td>VI</td>
<td>490</td>
<td>145</td>
<td>69580</td>
<td></td>
</tr>
<tr>
<td>V</td>
<td>490</td>
<td>69</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>IV</td>
<td>30</td>
<td>50</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td>III</td>
<td>20</td>
<td>30</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>II</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>2.2</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

#### Table 5: Field data derived development times using Eq 1-5 and the fitted exponential regression line $y = e^{0.442x} + 7.535$ for the 20m station

<table>
<thead>
<tr>
<th>Stage</th>
<th>Duration of peaks (Days)</th>
<th>Dev. Time (Days)</th>
<th>$N^0/m^2$ entering the stage</th>
<th>Mortality (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>VIII</td>
<td>550</td>
<td>261</td>
<td>8755</td>
<td>23.5</td>
</tr>
<tr>
<td>VII</td>
<td>850</td>
<td>221</td>
<td>37157</td>
<td>53</td>
</tr>
<tr>
<td>VI</td>
<td>490</td>
<td>145</td>
<td>69580</td>
<td></td>
</tr>
<tr>
<td>V</td>
<td>490</td>
<td>69</td>
<td>50</td>
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</tr>
<tr>
<td>IV</td>
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<td>III</td>
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<td></td>
</tr>
<tr>
<td>II</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>2.2</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Fig. 7 - Abundance of juvenile stages V-VIII and adults between September 1984 and March 1988 in 20 m depth.

Fig. 7 - Abondance des juvéniles stades V-VIII et des adultes entre Septembre 1984 et Mars 1988 par 20 m de profondeur.

Fig. 8 - Percentage of juvenile stages V-VIII and adults from total in 20 m depth (N is taken from total abundance curve).

Fig. 8 - Pourcentage de juvéniles stades V-VIII et d'adultes par 20 m de profondeur (N est donné de la courbe d'abondance totale).
Life cycle of Cytherissa lacustris

Fig. 9 - Adults and juveniles of Cytherissa lacustris from 12 m and 20 m depth.

Fig. 10 - Percentage of egg carrying adults from total adults (pooled data from 1986 and 1987).

Fig. 10 - Pourcentage d'adultes portant des œufs par rapport au total des adultes (données de 1986 et 1987).
Fig. 11 - Survival curves for all instars of *Cytherissa lacustris* at three different temperatures (6, 12, and 18°C).

Fig. 11 - Courbes de survie de tous les stades de *Cytherissa lacustris* à 3 températures différentes (6, 12 et 18°C).
5.5. TEMPERATURE AND SURVIVAL

The survival curves at three different temperatures are shown in figure 12. Peto and Peto's Logrank-test between the survival curves for the Vth and VIth stages from 12m and 20m at 12°C and 18°C gave statistically significant differences. The animals from 20m have lower survival at high temperatures (12°C and 18°C) than the animals from 12m (fig. 11). Cytherissa lacustris from 20m has a narrower optimum temperature range than individuals experiencing fluctuating temperatures (i.e. from 12m) even though juvenile mortality in the field is similar (see above).

In order to test the hypothesis, that the tolerance of Cytherissa lacustris towards high temperatures allows for passive dispersal through birds, an additional set of experiments was carried out at 30°C. The results are presented in figure 12. Stage VI and VII showed lowest survival (LD₅₀ = 6 days), followed by the adults (LD₅₀ = 8.6 days) and stage VIII (LD₅₀ = 10.4 days). Some specimens survived for 30 days.

6. DISCUSSION

6.1. ABUNDANCE PATTERN

The abundance pattern at the two stations (12m and 20m) reflects the situation at the upper limit of occurrence of Cytherissa lacustris. This is particularly true for the 12m station as no specimens could be found above 9m lake depth (for a detailed description of the depth distribution see Geiger, 1990 and Danielopol et al., 1988). In Attersee, a lake with similar limnological characteristics but lower trophic level, Cytherissa lacustris occurs down to a depth of 100m, with highest numbers at 20m depth (Newrkla, 1985).

Maximum numbers recorded are of the same order of magnitude as found for other profundal ostracod species (Thaler, 1977) but considerably lower than for brackish water and littoral species (Heip, 1976; Ranta, 1979).

The restriction of this species to the sublittoral and profundal is thought to be due to its temperature requirements (Löffler, 1971; Delorme, 1978). In the light of the data presented above, temperature alone can explain its absence from the shallower parts of the lake but not from the zone between 5m and 10m. Therefore additional factors have to be considered.

6.2. METHODS OF CALCULATING DEVELOPMENT TIME AND STAGE SPECIFIC SURVIVORSHIP

The method used to get an estimate of development time and survival from field data was developed by Rigler and Cooley (1974) for populations where generations rather than cohorts can be followed or where cohorts are widely overlapping. This method was subjected to criticism because the authors considered stage specific survival as being constant. Hairston and Twombly (1985) included some knowledge of survivorship in their calculations and stated that both development time and stage specific survival cannot be derived simultaneously from a single data set. However, Saunders and Lewis (1987) were able to demonstrate, that within certain limits, the error of the estimate is less than 10% when survivorship data are not included. Both development time and survivorship can be estimated with satisfactory accuracy over a wide range of \( \frac{t_{i+1}}{t_i} \) ratios, if survival \( s_{i+1} \) is greater than \( s_i \). In the present study development time was found to increase exponentially with age but the ratios \( \frac{t_{i+1}}{t_i} \) lay well between the above mentioned range. Survival of the later instars is higher than that of the younger and this method can therefore be applied.
6.3. LIFE CYCLE

The life cycle of Cytherissa lacustris as determined by the methods described above appears to be extremely long for a freshwater ostracod species. Species of similarly slow development are found in cyclopoid and harpacticoid copepods (Herzig, 1983; O’Doherty, 1985) and ostracods of the families Cytheridae and Cypridiidae (Cohen and Morris, 1990). The life cycle of Cypria opthalmica was determined by Thaler (1977) as lasting 8 months at 13.5 °C and 1 1/2 months at 9°C. Therefore it can be assumed that long-lived meio-benthic species are more common that hitherto believed and their rarity is mainly due to lack of knowledge.

Gerlach (1971) and Heip (1976) even consider low numbers of generations as typical for the meio-benthos. A long development time can generally be seen as an adaptation to low food levels (detritus) to minimize the energy demands.

In some ways, Cytherissa lacustris reveals adaptations to the comparatively stable conditions of the profundal:

The lack of true seasonality in the abundance pattern. Highest abundances are found in both winter (12m) and summer (20m) (see also Cohen and Morin, 1990).

Highest numbers of egg carrying females can be observed during the colder periods. No temperature tolerance experiments could be carried out for eggs and instars I-IV, but the youngest juveniles investigated (Vth and VIIth stage) always showed lowest tolerance towards stress factors such as high temperature and low oxygen (Geiger, 1990).

Low fecundity and continuous reproduction occur mainly in species which live in a predictable environment (Heip, 1976) where the low intrinsic rate of increase per day is outnumbered by an elongated reproductive timespan. Reduction in numbers of offspring and continuous reproduction is also observed in species which suffer high juvenile mortality (O’Doherty, 1985). In this case the enhanced risk for the juveniles is compensated by a slow but continuous release of eggs. An alternative strategy would be a variable timing of life history events such as the splitting of cohorts in fast and slow growing individuals. This strategy is typical for littoral species like Leuroleberis zealandica (Fenwick, 1984) and Cyprideis torosa (Heip, 1976). Cytherissa lacustris seems to adopt the former of the two alternatives. This strategy is of considerable use if predation pressure is low as it is in the profundal zone which is dominated by detritus feeders like oligochaetes, Chironomus thummi and Chironomus anthracinus (Herman et al., in prep.). The high juvenile mortality observed in Cytherissa lacustris in the sublittoral may be due to invertebrate predators such as Procladius sp., turbellerians, cyclopoid copepods which occur in high numbers (Geiger, unpubl.). Nevertheless this must remain unproven until the predator-prey interactions of benthic organisms are studied in detail.

The relationship between development time and temperature in Cytherissa lacustris is somewhat obscured by the fact that food conditions play a major role if postembryonal stages are compared with regard to their development. A typically cold stenothermic species should show normal development even at low temperatures and a retardation phase at the higher end of the temperature scale (Herzig, 1983; Sarvala, 1979). In the laboratory experiments, however, Cytherissa performed best at the higher temperatures. If mortality is included, optimal development was at 12°C. At 6°C, the temperature at which maximum numbers are recorded in the field, no development could be observed. This is most probably due to unfavorable food conditions in the experimental vessels. Unsufficient food levels can considerably retard development (Sarvala, 1979). At higher temperatures, enhanced bacterial growth could have enriched the food thus providing better conditions than at 6°C. Mortality in the 6°C experiments over the whole investigation period of 240 days was not higher than at the higher temperatures. Juvenile stages are thus capable of enduring unfavourable conditions by retarding their development.

In the field, food conditions are better in the profundal (high amounts of organic carbon, high bacterial biomass (Hupfer, in prep.) and food is more readily utilizable. Higher population densities could be expected in the profundal. In Mondsee, the low oxygen concentrations during summer stagnation hinder the occurrence of Cytherissa lacustris at depths greater than 40m but abundant numbers can be found in the subfossil record (see related papers in this volume).

The observed small differences in the duration of the life cycle between 12m and 20m (1.9 years versus 2.2 years) can be assumed to be the result of the higher temperatures at 12m. Physiological adaptation capabilities within the limits of tolerance (temperature never exceeds 18°C) are greater than reported in the literature (Löffler, 1975; Delorme, 1978). The fact that the "cold adapted" individuals from 20m showed lower survival at higher temperatures provides additional evidence for this explanation. Between 12°C and 15°C-18°C, Cytherissa lacustris can regulate its respiration rate (Newrkla 1985) and the low metabolic rate can be maintained over this range of temperatures.

Genetic differentiation of life history characteristics with regard to temperature as reported for Daphnia (Korpelainen, 1986) and Mesocyclop edax (Wyngaard, 1986) was not found (Sywula and Geiger, 1990) but cannot be excluded for larger, geo-graphically distinct areas or even for separated areas within a lake.
Individuals of *Cytherissa lacustris* found in Northern Germany may react differently towards temperature than those from Mondsee.

7. CONCLUSIONS

1. The life cycle of *Cytherissa lacustris* depends, if differences in food supply can be neglected, mainly on temperature and takes 1.9 years at 12m depth and 2.2 years at 20m. No information can be given for the life-span of the adults but it is assumed that they are long-lived.

2. The low reproductive potential is outweighed by continuous egg laying over a long period of time.

3. The temperature range over which successful moulting can be observed in the laboratory is high (up to 18°C). Slow development at 6°C is explained as a consequence of food shortage.

4. The reaction norm of *Cytherissa lacustris* towards temperature in the laboratory depends on the temperature regime experienced in the field. Animals from 12m (temperature amplitude 12-14°C) perform better at higher temperatures than animals from 20m (Temperature amplitude 2°C).

5. High mortality of the youngest juveniles is most likely due to invertebrate predation by *Procladius*, turbellarians and cyclopoid copepods but this must be confirmed by further studies.

6. Its restricted occurrence in the sublittoral and profundal is found to depend not only on temperature. Poor food quality and low oxygen concentration play a greater role than considered up to now.

7. Tolerance of high temperatures (30°C) is sufficient to allow *Cytherissa lacustris* to survive longer periods (1 week). This may be important for a potential passive dispersal by birds and hence help to elucidate the biogeographic distribution pattern of this species.

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LONG-AND SHORT-TERM PERTURBATIONS OF THE CYTHERISSA LACUSTRIS POPULATION IN MONDSEE: A PALEOLIMNOLOGICAL PERSPECTIVE.

PERTURBATIONS A LONG ET COURT TERME SUR LES POPULATIONS DE CYTHERISSA LACUSTRIS DANS LE MONDSEE: UNE PERSPECTIVE PALEOLIMNOLOGIQUE

by

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Abstract

Paleolimnological investigations on short cores of the Mondsee show that changes in the ostracod assemblages and/or in the abundances of selected species like Cytherissa lacustris reflect long- and short-term environmental disturbances which occurred in the lake in the last 30-40 years. Experimental studies combined with field observations on the survival of Cytherissa lacustris under low oxygen conditions suggest that this parameter is a driving force in the local extinction of this species especially when the sediments have a low porosity or high organic content. The recolonization of the defaunated places of the profundal zone of Mondsee, by Cytherissa lacustris is ongoing. The rapidity of the reinvansion of perturbed benthic habitats depends on the distance from the ostracod source to the defaunated area as well as on the ecological capacities of various species to reinvade and reajust to the new habitat conditions. The marginal zone of the lake especially the infralittoral and the upper profundal should be protected against further environmental deteriorations because these areas contain populations of ostracods from which the recolonization of the profundal zone can restart.

Résumé

Les recherches paleolimnologiques sur des carottes courtes de Mondsee montrent que les variations dans les associations d'ostracodes et/ou dans l'abondance de certaines espèces telles que Cytherissa lacustris sont le reflet à long et court terme des perturbations qui se sont produites dans le lac dans les derniers 30-40 ans. Des études expérimentales combinées à des observations in situ sur la survie de Cytherissa lacustris sous des conditions de faible oxygénation suggèrent que ce paramètre est un facteur causal dans l'extinction locale de cette espèce, notamment lorsque le sédiment a une faible porosité ou une forte teneur en matière organique. La recolonisation des endroits défaunés de la zone profonde du Mondsee par Cytherissa lacustris est en cours. La vitesse de recolonisation des habitats benthiques dépend de la distance de la source des ostracodes de la zone défaunée ainsi que des capacités écologiques des espèces à reconquérir et à se réadapter aux nouvelles conditions du milieu. Les marges, particulièrement les zones infralittorale et profonde supérieure devraient être protégées de futures détériorations du milieu du fait que ces domaines contiennent des populations d'ostracodes à partir desquelles la recolonisation des zones profondes peut redémarrer.

1. INTRODUCTION

Mondsee is a prealpine lake moderately deep, mean depth 36 m, maximum depth 68 m). The bottom of the lake experiences many short-term disturbances. For instance allochthonous sediment influxes during rainy periods or induced by human activities, or sediment displacement at the bottom due to unusual water currents or due to fish activities, determine changes in the sediment structure and composition and induce perturbation of the distribution of organisms living on/in the sediments. Such disturbances occur during periods of hours, days or months.
Long-term disturbances of the lake bottom imply processes which act on a time-scale of years. For instance the slow change of the trophic state of the lake from a meso-oligotrophic to an eutrophic one during the last 30-40 years induced also drastic changes in the ostracod fauna especially those living in the deeper part of the lake. Löffler (1972), Danielopol et al. (1985, 1988), Geiger (1990), Handl (1989) described some of the changes of the ostracod fauna of this lake e.g. *Cytherissa lacustris* disappeared in the last years from wide areas of the profundal zone, the local populations of several other species like *Leucocythere mirabilis*, *Limnocythere sancti-patricii* and *Fabaeformiscandona caudata* are also strongly decimated (for a description of the spatial distribution pattern of the former species see Danielopol et al., 1990).

In this contribution we address the following questions:

1) How can we identify the origin of the perturbations in the ostracod assemblages and/or local populations of unique species? We try to differentiate between perturbations caused by long-term disturbances (e.g. the eutrophication event of Mondsee in the last 40 years) from short-term environmental disruptions. Our null hypothesis is that a slow change of the fauna due to the steady increase of the production of phyto- and zooplankton will enhance during successive years an increase of oxygen depletion within the sediment and therefore some of the ostracod fauna will be affected. Because of the wide distribution and the general bathimetry of the lake (fig. 1) large spatial effects in the ostracod fauna could be expected. Similar faunal perturbations should be visible in cores taken at wide distances one from the others.

To test this hypothesis we shall compare the vertical distribution of the subfossil ostracods from short cores (about 30 cm length) taken at the deepest sites of the north-western basin (the site MO-9/47 m deep and the site MO-8/67 m deep in central basin (fig. 1). The both sites are located at a distance of 2.5 km one from the other. For short term disturbances we shall analyse cores taken along the transect MO-7 and also informations obtained from our samples got at the site MO-9/47 m deep (fig. 1).

![Fig. 1: Sampling sites (dots) in Mondsee; MO-9/47 m with the sampling sites from the present study and Danielopol et al., 1985 La-Loibichl, Ba Baggersee; MO-3 the sampling site from Danielopol et al., 1985. MOS Mooswinkl, SCH-Scharfling.](image-url)
2) How can one explain the low population densities in the fossil record? This could be due either to biological causes e.g. an organismic stress or to an unsufficient sampling intensity. When the living population is very sparse, the chance of the organisms to remain represented in the fossil record is low. Therefore one can not decide if the absence of ostracod remains always means the local extinction of a species or is just due to a random sampling effect. We shall discuss this problem by comparing replicate samples from the same site. In paleolimnological studies of Ostracoda one usually compares the densities of fossil valves in a fixed volume of sediment, generally between 5 and 40 cm$^3$ (Löffler, 1986). If during some periods the rate of sedimentation is very high, and the ostracods continue to live in this type of environment one could see by comparing with samples deposited during periods with lower sedimentation rates, a decrease in total valve densities (a dilution effect). Such cases are well known to palynologists too. Therefore it is interesting to investigate this problem in Mondsee where the sediments deposited in the last 30-40 years have been radiochemically dated (Irlweck and Danielopol, 1985; Irlweck, 1990).

3) How can we see with paleolimnological methods the recolonization of the Mondsee profundal zone by ostracods? This problem was addressed by Geiger (1990) too and ecological data are also presented by Danielopol et al. (1990). Here we bring supplementary data which can be used for other paleontological situations without present-day continuity as well as for the future environmental protection policy of the Mondsee.

The interest of looking to environmental disturbances and to organismic perturbations within both short- and long-time scales for ecological studies has been stressed out by Frost et al. (1988) inter alia. For an exact definition of such concepts like disturbance, stress and perturbation we followed Rykiel (1985) and for the concept of local extinction we followed the definition of Park (1980, p. 117): "local extinctions are said to have occurred when all individuals of a given species within a specified area (generally of stated size) have been removed either by death of by enforced or induced permanent migration elsewhere." The special interest of our investigations for paleolimnological studies is the unique chance to work in a lake for which the evolution of the main parameters are known for the last 30-40 years. The history of the eutrophication of Mondsee is well documented, see inter alia informations in Findenegg (1969), Schwarz (1979), Jagsch and Megay (1982), Dokulil (1984), Klee and Schmidt (1987), Schmidt (1990). Helbig (1987) and Welzel (1988) presented synoptically not only the main events which produced the trophic-change of Mondsee but included also informations on short term disturbances which left sedimentological traces in the lake i.e. the discharges of course ligneous material (bark and wooden fragments) of the Scharfling area during the end of 50th in the central basin of the lake (see below) or the influx of gravel and sandy sediment during the beginning of the 60th in the north-western basin, when the nearby highway was constructed.

2. SAMPLING SITES AND METHODS

Fig.2 Cross section of the Mondsee between Loibichl (Lo) and Baggersee (Ba), the transect MO-9. Oxygen profiles near the bottom measured during 1986 and data from Müller (1982) for the oxygen concentrations measured during 1975, 1976.

*Fig. 2 - Radiale MO-9 dans le Mondsee entre Loibichl (Lo) et Baggersee (Ba). Profils d'oxygène près du fond mesurés en 1986 et données de concentrations en oxygène mesurées en 1975-1976 (Müller 1982).*
The sampling sites are located along two main transects (see fig. 1), the MO-9-transect (Loibichl-Baggersee) and the MO-7-transect (Mooswinkl bay - Scharfling). Cross sections of the basins along these transects are presented in the Figures 2 and 11. For comparative purposes the position of the site MO-3 too, where Danielopol et al. (1985) described the changes of the ostracod fauna within the last 50 years is given in fig. 1.

Considering the transect MO-9 (fig. 2) one can see that the slope of the both sides Loibichl (LO) and Baggersee (BA) are very steep down to about 35 meter, followed on one side by an irregular bottom on the Loibichl side and a flat and more uniform bottom on the opposite side. During the summer stagnation the oxygen situation in the profundal zone at 47 m becomes critical, values below 1 mg l⁻¹ or less are registered during several months (Danielopol et al. 1990). Figure 2 shows the oxygen situation at various depths during 1986. The data are compared with those presented by Muller (1982) for the years 1975 and 1976. One can see that low oxygen concentrations (less than 1 mg l⁻¹) occurred at deep deeper than 40 m during the seventies. During 1960-1962 gravel and sand have been discharged in the lake along the transect MO-9. This happened especially during stormy weather when boats transporting material for the construction of the highway Vienna-Salzburg were obliged to through parts of their load in the lake (R. Niederreiter pers. comm. to D.L.D.).

This record is visible in the sediment cores from the site MO-9, 47 m deep (Danielopol et al. 1986). The Scharfling side of the transect MO-7 (fig. 1, 11) has a very steep slope.

At the Mooswinkl side a higher number of sampling depths has been successfully investigated for os-tracods. During the end of the fifties an influx of coarse ligneous material was introduced into the lake (Helbig, 1987; Welzel, 1988) on the Scharfling side. This is visible in the sediments from 50 m, 60 m and 67 m deep, (see fig. 1), but not on the Mooswinkl side at equivalent depths. Comparing the oxygen situation for 1986 (fig. 11) with those registered during 1969 and 1976 (unpubl. data A. Jagsch). During 1969, 2 mg l⁻¹ oxygen were recorded in the deepest zone. The worst situation occurred in 1976, when the less than 1 mg l⁻¹ oxygen layer at the deepest part of the lake extended from the bottom up to 50 m deep, while in 1986 only 3-5 meters above the deepest site where hypoxic. This oxygen poor layer develops especially at the end of summer and during autumn (fig. 3). Comparing the oxygen values along the transect MO-7 at the sediment surface with those registered in the water column above the deepest site (MO-7/67-68 m deep) (fig. 12) significant differences for the 60 m deep but closer values for the 40 and 50 m depths (see also data in Geiger, 1990) can be seen.
Fig. 4 - The core sample taken during July 1985 at the site MO-9.47 m deep.

Fig. 4 - Échantillons carottés prélevés en juillet 1985 sur le site MO-947 m.
Fig. 5 - A. Changes in the total abundances of ostracod valves in the core sample MO-9/47 m; B. Changes of the ostracod assemblage in the same core sample.

Fig. 5 - A. Variations de l'abondance totale des valves d'ostracodes dans l'échantillon carotté MO-P/47 m. B. Variations de l'association d'ostracodes dans le même échantillon.
Therefore we used the data presented in Figure 11, which show the oxygen situation during 1969 and 1976 in the water column for inferring the oxygen situation at the sediment surface. This would imply that during 1976 on both sides of the MO-7 transect at 50 m deep hypoxic conditions existed at the bottom. The first sign of eutrophication have been recorded by Findenegg (1969). This author noted an increase in diatoms (e.g., *Fragilaria crotonensis* bloom during the winter 1958). During 1960-1962 with the influx of important quantities of sediment, algal development slowed down due to the high turbidity of the lake. A reincrease of the algal biomass was noticed in 1965 (Findenegg op. cit.) and massive algal blooms with Oscillatoria rubescens occurred during 1968 (Jagsch & Megay, 1982). Since 1974 a sewage treatment plant collects the sewage water from a part of the catchment area of Mondsee. The quantities of total phosphorus have been reduced and since the beginning of 1981 a trend towards reoligoitrophication can be observed (Dokulil, 1984; Klee and Schmidt, 1986; Schmidt, 1990).

Sediment cores were obtained with a modified Kajak corer with special tubes, as described by Danielopol and Niederreiter (1990). Samples of 20, 25 and 50 cm$^3$ were sieved wet through a 100 μm sieve and the residue was examined for ostracods. For the sites MO-7, 50 m deep, both on Mooswinkl and Scharfling sides 3 replicate cores were taken. The ostracod data are expressed as number of valves (a carapace was counted, as two valves).

Living ostracods have been sampled at 20 m and 30 m deep at the site MO-9, Loibichl in September 1985 and 1988 (6 sampling units per site). The first two centimeters of sediment were sieved through a 100 μm sieve and the ostracods picked out. We looked especially living specimens of *Cytherissa lacustris*. The survival time of *Cytherissa lacustris* exposed to low oxygen concentrations (0.6 mg l$^{-1}$) and to fine grained sediments (less than 60 μm) differing in porosity and total organic carbon was investigated in microaquaria immersed in a through flow aquarium of the Innsbruck type (see description of the set-up in Geiger, 1990 and Danielopol and Niederreiter, 1990). Diversity of fossil and recent ostracod assemblages was expressed as K-dominance curves (for a description see Danielopol et al. 1985). Oxygen concentrations were measured as described in Danielopol et al., 1990).

3. RESULTS

3.1. THE CORE MO-9, 47 M AND ITS OSTRACOD FAUNA

The core sample was taken in July 1985 (see position fig. 1). Sedimentological aspects can be seen in fig. 4. A detailed description is provided also by Danielopol et al. (1986). The lower part of the sediment column (29 - 16 cm) consists of silty-gray sediment without distinct laminations. Between 16 and 9 centimeters, the sediment is grey coloured; between 11.5 and 14 cm it contains up to 40 % fine gravel (data in Danielopol et al., 1986, fig. 9B). This gravel layer represents the influx of the refuse during the period of the highway construction. The upper part of the sediment column from 8 cm to the top, is strongly laminated, with alternating dark and light coloured layers. This section represents the period between 1968 to 1985, when the lake experienced repeated algal blooms (review in Schmidt et al., 1985).
Figure 5A shows the total densities of the ostracod valves and the abundances for each species (fig. 5B) in each of the 2 cm layers (wet sediment volume per sampling layer, 25 cm$^3$). From 28 cm to 20 cm deep the total ostracod abundance and the species richness remained more or less constant.

A decrease in total abundance occurs in layer 10; it is due to the drastic diminution of the *Cytherissa lacustris* paleopopulation. A even more dramatic change occurs in layer 9 with the disappearance of *Limnocythere - Leucocythere* species and a reduction in abundances of the other species. The layers 7 and 8 are dominated by coarse sediment and contain only one species (*Candona neglecta*). In the 6th layer a decrease in the abundance of this latter species and the reappearance of *Cypria lacustris* and *Fabaeformiscandona protzi* are visible. *Candona candida*, a species which prefers coarse littoral sediments (Danielopol et al., 1985) occurs in this layer for the first time. In the 5th and 4th layer between 10 and 6 cm deep which has been deposited after 1962, a tremendous increase in total ostracod abundance, the species richness and abundance of *Cypria lacustris*, *C. neglecta*, *C. candida* and *F. protzi* can be seen. These latter species seem to find better living conditions than in the previous layers. After this event a sharp decrease in ostracod numbers and species richness can be observed in layer 3. The first four centimeters contain only 2 valves of *Cypria lacustris* and a valve of *Limnocythere*. Fig. 6 shows the evolution of the ostracod assemblage at the site MO-7/47 m deep expressed as K-dominance curves and computed as described in Danielopol et al. (1985). Four different phases can be distinguished. An increase in dominance from the lowest layer to the 10th one, a sharp increase in dominance in the 9th layer, a recrease of the dominance in the upper layers and finally a dramatic drop in diversity and abundances in the top three layers.
3.2. THE OSTRACOD FAUNA IN THE CORE MO-8/67 M

This core has been taken (for the sampling site see fig. 1) in October 1984. Figure 7 shows the ostracod distribution in the core (total length of the sediment column, 34 cm). The total ostracod fauna was quantified down to 16 centimeters deep. The rest of the core was examined only for Cytherissa lacustris.

The lower section between 35 and 24 cm deep consists of gray-silty sediment with low organic content. The section between 24 and 14 cm contains a high amount of coarse, wooden detritus especially in the layers 11 to 9 (fig. 7). Between 20 and 17 cm deep a diffuse light-dark layering is visible. The uppermost 12 centimeters show distinct dark/light laminae.

Between the 17th and the 13th layer, abundances of Cytherissa lacustris are high (more than 100 valves per layer). They start to decrease sharply in the 12th and 11th layer and Cytherissa lacustris occurs for the last time in the 10th layer. In the 8th layer ostracod abundances for most of the species are very low. At the same deep, Klee and Schmid (1987) found high numbers of diatoms which corresponds to the record of Findenegg (1969, p. 140) who wrote: "In den Jahren 1958-1960 fallen besonders in der kühlen Jahreszeit beachtliche Algenmengen unter einem Quadratmeter der Seefläche auf, besonders stark daran sind Diatomeen, vor allem Fragilaria beteiligt. Dies gilt auch noch für die April-Serie 1961". The 7th layer displays an increase in ostracod abundances especially of C. neglecta, F. protzi and Cypridina lacustris. This layer corresponds most probably to the period between 1962-1964, with reduced algal productivity (Findenegg, 1969). Species abundance decreases once again in the 6th layer where Leucocythere mirabilis disappears. The last five layers, which represent the sediments of the last 15 years with high organic content have reduced numbers of species with insignificant abundances. Figure 8 shows the relative frequencies of the various postembryonal stages of Cytherissa lacustris. The lower layers have a normal population structure where all the stages are represented. The population structure is heavily disturbed (i.e. some of the instars disappeared), only in the 10th layer.

3.3. DISTRIBUTION OF THE CYTHERISSA LACUSTRIS AND LIMNOCYHERE SANCTI PATRICII IN CORE SAMPLES FROM 50 M DEPTH OF THE TRANSECT MO-7 (FIG. 1)

The two sampling sites called also MO 7/50 m MOS (Mooswinkl) and MO 7/50 m SCH (Scharfling) are separated by a distance of about 850 m. There replicate sediment samples of 20 cm length persite have been studied. Sampling units of 40 cm³ for each core were sieved through 100 μm, Cytherissa and Limnocythere valves extracted and the juvenile stages identified (fig. 9, 10). The core samples from the Scharfling side contain in the deeper horizon, between 12 and 20 cm deep (with a maximum in the layers 8 and 9 in fig. 9D) a large accumulation of coarse, wooden detritus. This allochthonous material was already noticed in the core MO-8/67 m and is not visible in the 60 m and 50 m deep samples from the Mooswinkl side. This layer corresponds to the wood clearing on the Scharfling side during the end of the fifties (Weltzel, 1987; Klee and Schmidt, 1987). In the samples from MO-7/50 m, MOS (fig. 9A) a significant decrease in numbers of Cytherissa lacustris occurs only in the 4th layer with total disappearance in the 2nd layer and a reappearance in the 1st layer.
In contrast to *C. lacustris*, *L. sancti-patricii* (fig. 9C) never disappeared from the samples. Interesting enough we did not find living specimens at this site during 1984 and 1985. One could suspect a very sparse population with only few individuals which were not caught during our sampling programme. The variation in numbers of *Cytherissa lacustris* within the three samples from the Scharfling side (fig. 9, B) is due to spatial micro-scale heterogeneities. While one of the samples (I in fig. 9 B) show a gradual reduction of abundances through the 10th to 8th layers, the two others react in the opposite way, with increasing densities in the 9th and 8th layers. *Cytherissa lacustris* and *Limnocythere sancti-patricii* disappear completely in the 6th layer and none of them reoccur in the upper part of the cores (fig. 9 B, C).

At the Scharfling side *C. lacustris* disappeared earlier than at the Mooswinkl side as a consequence of the major influx of organic detritus. The sedimentation rate measured in 1986 by Irlweck (1990) for MO-7/50 m MOS is 3±0.3 mm per year. This suggests that the major dismantling event of the *C. lacustris* subpopulation occurred during 1970 at the Mooswinkl side. Low oxygen concentrations have been recorded at this depth during 1976 (fig. 4). The earlier disappearance of *Cytherissa* and *Limnocythere* at the site MO 7/50 m SCH is due to local sediment perturbations. The high influx of organic matter during the end of the fifties enhanced at the beginning an increase in ostracod numbers. Later increased sediment respiration lead to local oxygen depletion thus creating a stressful situation expressed as a rapid decrease in abundance.

Figure 10 shows the frequencies of the various stages in the MO 7/50 m SCH sampling units. One can see that at low densities the different growth stages are randomly represented and only by pooling for each layer the three sampling units one can get a complete sery of stages. In order to interpret the data correctly for samples with low abundances of fossils, it is necessary to increase the sampling units. This point is not always realized by many paleoecologists who neglect more or less the quantitative approach to their work. In order to verify if *Limnocythere sancti-patricii* still exists as a living populations at the site MO-7/50 m MOS or if the valves are just drifted their from other sites we investigated intensively this area during 1986 (Danielopol et al., 1990) and 1988. Yu Yin (1988) found this species represented by few specimens at 48 m
Fig. 10 - Relative frequency of the post-embryonal growth stages of *Cytherissa lacustris* in various sediment layers of the core samples (I-III) from the site MO- m Scharfling (SCH).

Fig. 10 - Fréquence relative des stades de croissance post-embryonnaire de *Cytherissa lacustris* dans divers niveaux de sédiments des échantillons (I-III) de la carotte MO- m Scharfling (Sch).
Fig. 11 - Cross-section of the Mondsee between Mooswinkl and Scharfling. Arrow indicate sampling sites location during the period 1983-1986. Oxygen profiles measured during November 1986 (our data) and data from 1969 and 1976 (Dr. Jagsch, unpubl.)

Fig. 12 - Oxygen profiles near the bottom and in the water column measured during 1986 at the MO-7/50 m deep sites, MOS-Mooswinkl side, SCH-Scharfling, t-temperature.
Those specimens (fig. 14 A-D) showed poorly calcified valves with fine organogenic sediment in the internal carapace space similar to that found in *Cytherissa lacustris* (Danielopol et al., 1988).

This suggests that *L. sancti-patricii* lives in sub-optimal conditions and could explain the low densities at this site.

3.4. ACTUOPALEONTOLOGICAL DATA: SHORT-TERM SURVIVAL EXPERIMENTS OF *CYTHERISSA LACUSTRIS* EXPOSED TO LOW OXYGEN CONTENT AND VARIOUS SEDIMENT SUBSTRATES

<table>
<thead>
<tr>
<th>SEDIMENT LOCATION</th>
<th>g S (µm)</th>
<th>% H2O</th>
<th>% TOC</th>
<th>O2 mg/l</th>
<th>t °C</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>MO-7/20 m</td>
<td>&lt; 60</td>
<td>84</td>
<td>6,5</td>
<td>0,6</td>
<td>4</td>
<td>76</td>
</tr>
<tr>
<td>MO-7/45 m</td>
<td>&lt; 60</td>
<td>84</td>
<td>0,5</td>
<td>0,6</td>
<td>4</td>
<td>95</td>
</tr>
<tr>
<td>MO-8/67 m</td>
<td>&lt; 60</td>
<td>85</td>
<td>6,3</td>
<td>0,6</td>
<td>4</td>
<td>60</td>
</tr>
<tr>
<td>MO-9/48 m</td>
<td>&lt; 60</td>
<td>83</td>
<td>7,2</td>
<td>0,6</td>
<td>4</td>
<td>24</td>
</tr>
<tr>
<td>MO-7/PG12 m</td>
<td>&lt; 60</td>
<td>60</td>
<td>2</td>
<td>0,6</td>
<td>4</td>
<td>49</td>
</tr>
<tr>
<td>MO-1/12 m</td>
<td>&lt; 60</td>
<td>74</td>
<td>7,7</td>
<td>0,6</td>
<td>4</td>
<td>86</td>
</tr>
<tr>
<td>MO-1/12 m</td>
<td>&lt; 60</td>
<td>60</td>
<td>5,7</td>
<td>0,6</td>
<td>4</td>
<td>24</td>
</tr>
<tr>
<td>Sand</td>
<td>90-200</td>
<td>-</td>
<td>0,6</td>
<td>4</td>
<td>36</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 13 - Survival rates of *Cytherissa lacustris* exposed on various sediment at a low oxygen concentration. n-number of individuals at the beginning of the experiment, t-temperature, O2-oxygen in mg l-1, TOC-total organic carbon, H2O-water content of the sediments, Gs-grain size fraction, LT50-median of the survival values, L-mortality, T-time in days (D). Data plotted as cumulative percentage curves.

Figure 13 shows the survival rates of *C. lacustris* exposed at 0.6 mg/l oxygen on various sediments (fine gravel sediment below 60 µm size) differing in organic content and porosities. For comparative analysis we exposed ostracods on coarse sediments (fine sand), in which *C. lacustris* can not dig, and substrates with high organic matter and low oxygen content. This experiment was run for 50 days. The highest mortality was observed in hypoxic water and organic rich sediments from the sites MO-9/48 m deep and MO-7/67 m deep (LT50 ~ 20 days). The lowest mortality is in pure sand and low oxygen concentration. *C. lacustris* exposed on fine glacial sediments, which is very cohesive, and low in organic content showed also low survival. Intermediary reactions are those of ostracods exposed on the sediments from the sites MO-7/20 m and 45 m deep. This experiment in which we took only the 8th juvenile stage and adults, shows us that low oxygen content is a driving force in the extinction of the *C. lacustris* especially in conjunction with other factors like high organic content of the sediment, low porosity and sediment structure. Between the sediments of the site MO-1/12 m and the sites MO-9/48 m and MO-7/67 m with high organic content there is an important difference. In the former sediment accumulated much allochthonous organic matter more or less
refractory to decomposition while the latter is composed mainly of organic matter derived from autochthonous lake plankton which is easier to degrade. This implies that in this latter the sediment respiration should be higher than in the littoral sediment type and for an endosediment dwelling organism like \textit{C. lacustris} the oxygen constraints are stronger.

3.5. DISCUSSION: THE POSSIBILTY OF THE RECONSTRUCTION OF LONG VERSUS SHORT-TERM ENVIRONMENTAL DISTURBANCES IN MONDSEE WITH OSTRACOD DATA

We consider that the slow increase of algal production during the fifties culminating in the blooms recorded by Findenegg (op.cit), during 1958 and 1960 represents a long-term disturbance. We saw that the density of \textit{Cytherissa lacustris} decreases slowly in samples from various deep lake sites like MO-7/47 m, MO-8/67 m which correlate well with our previous data (see Danielopol et al., 1985) for the sites MO-3/44 m and MO-9/47 m depths.

This reflect the gradual increase (over years) in the eutrophication of the lake, with the subsequent oxygen depletion within the sediment. Only an even distribution of sedimentation of phyto- and zooplankton over large areas of the lake can explain this large-scale perturbation of \textit{Cytherissa lacustris} which culminated in its local extinction in the profundal zone of the northern and central basin. The slow changes in the ostracod diversity as expressed by the K-dominance curves in figure 6A between the 14th to the 10th layer expresses very well the changes of the trophic state of the lake and the subsequent oxygen depletion in the surficial sediment layers. A well dated short-term disturbance is the discharge of gravel-sandy sediments at the site MO-7/47 m. These are instantaneous disturbances that covered small areas of the lake bottom. The ostracod fauna was practically burried by the high amount of inorganic material. In the core sample, MO-9/47 m, discussed above we noticed that in the layers 8 and 7 only one species, \textit{Candona neglecta}, survived. Four other species, represented in the previous layers, disappeared. The persitence of \textit{C. neglecta} in the gravel layer is due to the fact that this species can live also in interstitial habitats e.g. in alluvial sediments of various streams.

One can ask if such ostracod perturbations occurred commonly during the history of the Mondsee. Handl (1989) examined the ostracod changes at the site MO-9/49 m deep in a 7 m long sediment core which encompass the last 6000 years. Handl (op.cit.) showed that the ostracod assemblage remained more or less stable for the whole period, \textit{Cytherissa lacustris} occur through most of the core. Compared to the thousand of years of persistance the disappearance of \textit{Cytherissa} within several years due to eutrophication of the lake is an extremely impressive example of an environmental catastrophe.

3.6. THE RECOLONIZATION OF SELECTED PROFUNDAL HABITATS IN MONDSEE BY THE OSTRACOD FAUNA

How fast the resilience of the ostracod assemblage proceeds and how selected species reinvade defaunated areas is a problem of much interest for Mondsee. One should remember that important funds have been invested in order to reduce the trophic level of the lake (Jagusch and Megay, 1982). The eutrofication is already visible in a decrease in phytoplankton production (Dokulil, 1984; Schmidt, 1990). The ostracod recolonization can be seen as an example of what happens to the benthic fauna after a given environmental disturbance. It is of interest to know, beside the dynamics of the recolonization, where the relictual areas are from where the fauna can redeploy.

A knowledge of these areas and if possible a knowledge on the rules and chances of recolonization from such areas is important for the development of sound environmental protection policies. Some of the species like \textit{Cytherissa lacustris} and \textit{Leucocythere mirabilis} are representatives of a late Quaternary psychrophilic fauna represented in our present days by very disjunct geographical distributions (Danielopol et al., 1990). The reconstruction of their history and evolution has a cultural interest. For instance \textit{Leucocythere mirabilis} disappeared from large parts of Europe before we could study its morphology and ecology. The few specimens found in Mondsee constitute the basis for a monographic redescription of this species (Danielopol et al., 1990). The study of our core samples as well as previous studies (Danielopol et al., 1985, 1988) show that the long-term disturbance produced local extinctions of \textit{Cytherissa lacustris} on a wide spatial-scale i.e. it affected the profundal zone of the lake at deeper depths. In the northern basin the \textit{C. lacustris} subpopulation, within the isobathimetric line of 30 to 40 m deep or in the central basin within the 50 to 60 m deep isoline, was destructed. This process happened during the 1950ies for the sites MO-9/47 m or MO-8/67 m. After more than 25 years no recolonization of these areas occurred even if for the transect MO-9 an important local population of \textit{Cytherissa lacustris} exists (fig. 1) on the Loibichl side at 20 m deep. Intensive sampling at greater depths during 1985 (i.e. six samples taken at 30 m deep) did not yield any specimen of \textit{C. lacustris} at that time. However, a new sampling campaigne in 1988 demonstrated the reoccurrence of this species at 30 m. The same observations for the transect MO-7 on the Mooswinkl side have been made by Geiger (1990) and Figure 9 A shows that after the short interruption of the \textit{Cytherissa} records in the sediment horizon deposited during the seventies the species reoccurs in the uppermost layer. In 1985 living specimens were found at this site. Samples from 1988 studied by Yu Yin (op. cit.) show that \textit{C. lacustris} occurs also at 55 m
Fig. 14 - *Limnocythere sancti patricii* from the site MO-7-48 m deep (leg. Yu Yin, 1988). A - carapace; B - limbs, general view; C - poorly calcified valve, detail from A; D - organogenic sediment accumulated into the carapace space, detail from B.

Fig. 14 - *Limnocythere sancti-patricii* du site MO-7-48 m (leg. Yu Yin, 1988). A - carapace; B - appendices, vue générale; C - valve mal calciifiée, détail de A; D - sédiment organogène accumulé à l'intérieur de la carapace, détail de B.
depths. Note that during 1982-1983 this species was found only down to 40 m deep, Danielopol et al., 1985; Geiger, 1990).

Some of the deeper sites like MO-9/47 m deep or the central basin on the Scharfling side at depths between 50 m and 68 m seems to be difficult to reinvade not only because of recurrent periods of hypoxia as described here and in Danielopol et al. (1990) but also because no refuge area exists from where recolonization could take place (see Danielopol et al., 1985, 1988, Danielopol et al., 1990). This is in agreement with classic ideas of island biogeography, as described by Mac Arthur and Wilson (1967) and with more recent ideas of Rickfels (1987).

When disturbances affect restricted areas for short periods of time and when they are located closely to a faunal source area, recolonisation proceeds rapidly. This is the case of the recolonisation of the site MO-9/47 m after the sediment influx disturbance discussed above or the recolonisation of the site MO-7/50 m MOS (see also data in Danielopol et al., 1990). The restoration of the ostracod assemblage at the site MO-9/47 m is dependent on the ecological capacities of the various species. In the new microhabitat of the layers 5 and 4, with a mixture of coarse and fine grained sediments, *Cypria lacustris*, *F. protzi*, *C. neglecta* and the new invader *C. candida* found better life condition than in earlier stages. Figure 6 A show that the recolonization of the site MO-9/47 as expressed here by the fossil record in the 5th layer resulted in a higher diversity than those existing in the 9th horizon immediately before the "gravel disturbance". Comparing the present day ostracod assemblages of the sites MO-9/30 m and 20 m (fig. 6B) it can be showed that their diversity expressed by the K-dominance curves, are in between the fossil data from layer 6 and 5. This suggests that the environmental conditions at which the present day ostracods live at Loibichl sites could have some analogies with the past conditions which existed at the site MO-9/47 m during the 60ties. Recolonization of the profundal zones started from the infralittoral and upper profundal areas. It is therefore of high interest to protect the marginal area of the lake against further environmental deterioration.

4. CONCLUSIONS

Changes in ostracod assemblages or in abundance of selected species reflect long and/or short term disturbances in the lacustrine environment.

Under experimental conditions, with low oxygen concentrations superposed on high organic content or low porosity of the sediments induced a low survival rates of *Cytherissa lacustris* showed lowest survival. Similar situation could have occurred under natural condition in Mondsee during the increase of the trophic state of the lake.

The recolonization of the profundal zone of the Mondsee by *Cytherissa lacustris* in the last years is an ongoing process.

The recolonization process of the Mondsee depends on the magnitude of the disturbance evaluated on both space and temporal scales.

Slowest recolonization is experienced by those sites located at remote distances from the faunal sources.

The source areas from where the recolonization of the perturbated benthic ostracod fauna of the profundal zone will start are the sublittoral and the upper profundal zone especially on the north eastern side of the lake. These areas have to be protected against further environmental deteriorations.

Paleolimnological evidence on the distribution of other species than *Cytherissa lacustris* suggests that further ecological research needed in order better to understand their substrate requirements. Given this information they could be used for further paleological reconstructions.

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TO SEE AND NOT TO BE SEEN: THE EVOLUTIONARY PROBLEMS OF OSTRACODA.

VOIR ET NE PAS ETRE VU: LES PROBLEMES EVOLUTIFS CHEZ LES OSTRACODES

by

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Keys-Words: ostracods, carapace pigmentation, Cytherissa ecology, cryptic coloration, fish predation.

Mots-Clés: ostracodes, pigmentation de la carapace, écologie de Cytherissa, coloration de camouflage, prédation par les poissons

Abstract

The first systematic investigation on the coloration of limnic ostracods is presented. The coloration of sixteen species were studied. The most common colors are green, brown, black and white. No warning colors like red are present in limnic ostracods. There are two major patterns of carapace pigmentation: fully or patchily coloured. In the latter case patches of pigment cover an unpigmented background, or the reverse, with unpigmented patches on a fully pigmented area.

The cryptic value of the carapace coloration is discussed. The coloration pattern of free swimming species which live in shallow water habitats, shows shadow camouflage patterns i.e. patch pigmented carapaces (e.g. Cypria ophthalmica, Cypridopsis vidua, Chlamydotheca unispinosa, C. colombiensis etc.) disruptive colouration, coloured stripes on the valves in the case of C. vidua and countershading (e.g. Notodromas persica). The color pattern of Cytherissa lacustris, which is completely brown in colour, combined with the endosediment living style makes the species less vulnerable to fish predation. The coloration of this species has a low adaptive value.

Résumé

Nous présentons ici les résultats des premières recherches systématiques sur la coloration chez les ostracodes limniques. La coloration de 16 espèces a été étudiée. Les couleurs les plus fréquentes sont le vert, le brun, le noir et le blanc. Aucune coloration de type intimidation, dans les rouges, n’existe chez les ostracodes limniques. La coloration se manifeste principalement de deux manières : coloration intégrale ou par taches. Dans ce dernier cas, les taches pigmentées couvrent un fond non pigmenté ou inversement, des taches dépigmentées parsèment un fond coloré.

La valeur de camouflage de la coloration des carapaces est discutée ici. La coloration d'espèces nageuses vivant dans des habitats d'eaux peu profondes montre des traces de camouflage en ombre, c'est à dire une pigmentation par taches discontinuées (comme par exemple chez Cypria ophthalmica, Cypridopsis vidua, Chlamydotheca unispinosa, C. colombiensis, etc...), par bandes colorées sur les valves (Cypridopsis vidua), ou par contour ombré (Notodromas persica). Les traces de couleur chez Cytherissa lacustris qui est complètement brune en relation avec la présence dans le sédiment montrent un mode de vie d'une espèce moins vulnérable à la prédation des poissons. La coloration de cette espèce a une faible valeur adaptative.
Fig. 1 - Pigmented ostracod carapaces.
A, B - Chlamydotheca unispinosa, female; A - left side. B - right side. C-F - Chlamydotheca colombiensis, female; 
C, F - left side. D - right side; E - dorsal side; G-H - Cypris pubera female; G - left side; H - dorsal side; I - 
Prionocypris zenkeri, right valve; J, K - Notrodromas persica, male; J - dorsal side; K - left side and ventral area up. 
(a1, a2 = 1st and 2nd antennae; md = mandible; wl = walking leg; ov = ovary; pd = postero-dorsal area; hg = 
hepatic gland; am = adductor muscle scars; dm = dorsal muscle scars; oa = ocular area.)
1. INTRODUCTION

Most of the ostracods have well developed eye structures. In several groups ostracod evolved lens structures also on the valves (Kontrovitz and Myers, 1984; Kontrovitz, 1987) which improve vision. Mbahinzireki et al. (1990) demonstrated that ostracods have the capacity to behave as subjects who actively perceive their environment, but at the same time can be the object of predation for other animals like fishes.

During the study of the carapace morphology of various marine Xestoleberididae, Bonaduce and Danielopol (1988) noted that some of the *Xestoleberis* species which live on algae have not only well developed eyes and diverse carapace lenses, but also variously pigmented valves. It was hypothesized that the ostracod colouration has an adaptive value and an investigation of this problem was planned. That was the first part of this research project. Unfortunately due to logistic difficulties, we could not complete this study using the marine Xestoleberididae, but we found that limnic ostracods present the same type of problem. Therefore, we concentrated on this latter group and here present some of our results. That is the second part of this research project.

In the following, we present a review on the colour types and pigmentation patterns of several limnic ostracods and we examine the cryptic value of their colour patterns. This contribution is organised in a way which enables to better evaluate the potential reduction of the *Cytherissa lacustris* abundances by fish predation. Should the answer be positive, ecological and evolutionary implications will emerge. For instance, some of the patchy distributions or the local extinctions of populations of this species could be explained by this biotic process. Such a possibility was presented by Löffler (in Carbonel et al. 1988). This author wrote (p.428): "Increasing predation by fish could be responsible for major changes in benthic ostracod fauna, if it comprises large species". But the importance of fish predation on *Cytherissa* can be at best evaluated in a comparative study. This is the strategy we used in our project and for which Mbahinzireki et al. (1990) presented one part of the research, while the other ones are offered here.

Fish predation on ostracods can also have evolutionary consequences. Kornicker and Sohn (1971) demonstrated experimentally, using limnic ostracods, that fishes can passively disperse some of the preyed ostracods. The same could be possible with *Cytherissa lacustris*, a parthenogenetic species with robust limbs and carapace which could resist to the fish digestion. By passive transport, new habitats could be colonized by this species.

Important literature on the origin and evolution of coloration of animals exists (e.g. Endler, 1978; 1988; Lythgoe, 1979 ; Saidel, 1988) ; the type of colour and the colour patterns have an adaptive value; their origin and further maintenance can be related to prey-predator interactions.

Considering this topic applied to ostracods, only casual information exists. Hartmann (1975) complained about this situation and suggested to start a systematic study on the ostracod coloration. Our project was partly inspired by this suggestion.

2. MATERIAL ET METHODS

The following ostracod species, adult and juvenile living specimens, have been used for this study:

1. *Cytherissa lacustris*
2. *Limnocythere sancti-patricii*
3. *Limnocythere inopinata*
4. *Cypridopsis vidua*
5. *Cypria opthalmica*
6. *Candonia neglecta*
7. *Herpetocypris repians*
8. *Cypris pubera*
9. *Prionocypris zenkeri*
10. *Notodromas persica*
11. *Chlamydotheca colombiensis*
12. *Darwinula stevensoni*.
Fig. 2 - Ostracod carapaces and valves.

A-C - *Cypria ophthalmica*; A - female from Mondsee littoral zone, carapace right side; B, C - male specimens from Mondsee profundal zone; B - slightly pigmented specimen, right side; C - unpigmented specimen, left side; D-F - *Cypridopsis vidua*, female; D, E - lateral view, right side; F - dorsal side.

(E - naupliar eye, te testes; w - white pigmented patch; 1-5 - pigmented stripes and/or patches.

Fig. 2 - Carapaces et valves d’ostracodes.

A-C - *Cypria ophthalmica* ; A - femelle de la zone littorale du Mondsee, carapace, valve droite ; B, C - mâles de la zone profonde du Mondsee ; B - valve droite d’un individu faiblement pigmenté ; C - valve gauche d’un individu non pigmenté ; D-F - *Cypridopsis vidua*, femelle ; D, E - valve droite, vue latérale ; F - vue dorsale.

(E - œil nauplien, testicule ; w = tache pigmentée blanche ; 1-5 - bande pigmentée et/ou taches).
The first six species commonly occur in Mondsee (Danielopol et al., 1985). *H. reptans* was found in a small stream in Scharfling (Mondsee area); *Prionocypris zenkeri* was collected in a limnocren spring at Limanu on the Black Sea coast in Romania; the *Notodromas persica* material studied here originates from the Caldarusani lake near Bukarest; *Cypris pubera* has been found in a fish pond near Braila (Romania); the origin of *C. colombiensis* is unknown. Living material of this species was given to us by Dr. M.Dokulil from an aquarium hold in Mondsee which contains tropical fishes. Roesler (1985) described this species from a temporary well located in the valley of the Rio Cauca in Columbia.

Besides these ostracods, we examined fixed material of *Chlamydotheca unispinosa* from Lake Titicaca (leg. P. Carbonel), *Pseudocandona inaequivavis* from Lake Baikal (leg. H. Löffler). *Cypria cavernae* from caves around Trieste (leg. F. Gasparo), *Cypria ophthalmica* from Neusiedlersee (leg. M. Cruz-Mendez), from Lunz-Mittersee (leg. D.L.D.) and from Halleswiessee (leg. M. Handl).

Living and fixed ostracods have been observed under the stereomicroscope, the light and the scanning electron microscope. Their movements and cryptic colouration has also been recorded using a video camera fixed on a stereomicroscope Wild-2. For the prey-predator experiments fishes *Vimba elongata*, have been used. These experiments as well as the experimental setup are presented in Mbahinzireki et al. (1990). Here we shall reproduce only the major conclusions of their paper.

3. RESULTS

3.1. TYPES OF COLORATION IN FRESHWATER OSTRACODA.

Many ostracods have only the carapace colored due to accumulation of granular pigments in the epidermal cells which lie under the calcite wall of the valves (Hartmann, 1966).

Other ostracods have no epidermal pigments and the carapace being thick and ornate shows a grey colour (e.g. *Limnocythere sancti-patricii* and *L. inopinata*). The unpigmented carapace of *Candona* (e.g. *Candona neglecta*) shows a white-yellow colour. Some ostracods are colored by the pigmented food ingested. Such is the case with *Pseudocandona inaequivavis* from Lake Baikal where both the epidermic cells of the carapace and the soft body are of red-brown color (Danielopol, 1978).

The most common colours of freshwater Ostracoda are: a) brown with different intensities, e.g. *Cytherissa lacustris*, *Cyclocypris ovum*, *Cypria ophthalmica*; b) black, e.g. *Cypridopsis vidua*, *Notodromas persica*; *Darwinula stevensoni* presents a black pigment on the dorsal side which is located within the soft body; c) green, e.g. *Cypris pubera*, *Prionocypris zenkeri*, *Herpetocypris reptans*, *C. vidua*; *Darwinula stevensoni*; d) yellow-greyish to brown, e.g. *Heterocypris incongruens*; e) white, e.g. *Notodromas persica*, *Darwinula stevensoni*, *C. vidua*.

One can recognize several alternative colouration types i.e. monochrome, di- and trichromatic. Examples of the former are *Cytherissa lacustris* and *Cypris pubera* (fig. 1, G-H) where the carapace is brown and respectively green in colour. Areas not pigmented are the muscle scars in the central and dorsal part of the carapace. The dichromatic pattern can be of two types. One due to two different pigments, e.g. in *Notodromas persica* (fig. 1, J-K) where most of the carapace is black and the dorsal part is white in colour. An alternative dichromatic pattern originates from the combination of large pigmented surfaces of the carapace interspersed with unpigmented patches. *Prionocypris zenkeri* (fig. 1, I) is of green colour and only the central part and the area around the ovaries which is less or unpigmented appear in white colour. The trichromatic patterns are due to the fact that one of the pigments has different intensities. The adult of *Cypridopsis vidua* (fig. 2, D) is such an example. It has a lateral patch of white pigments surrounded by stripes of light-brown to dark-brown. Some of the stripes can be completely dark-brown (e.g. the stripes 1 and 2); others remain light-brown or reddish (e.g. the stripes 3-5). This is due to the fact that after the molting and the calcification of the carapace during several days the pigment slowly accumulates and it changes its colour due to quantitative accumulation in the epidermal cells (when more chromogranules accumulate in the cells the colouration appears dark) and also due to chemical changes (oxidation process?). Such pigmentary differences can also be seen in *Chlamydotheca unispinosa* (fig. 1, A - B) and *Chlamydotheca colombiensis* (fig. 1, C-F). Here the trichromatic pattern is due to background pigmentation which is green in combination with areas where the colouration appears dark-green to black (e.g. around the hepatopancreatic gland in fig. 1, A - B; or around the dorsal part of the carapace and the ovary in fig. 1, D
Fig. 3 - Videocamera microphotographs of living ostracods against their substrate background; *Cytherissa lacustris* adult specimens on sediments from the littoral, A - respectively profundal; B - zone of Mondsee; C-D - *Cypridopsis vidua* within a phytal habitat (arrows indicate the ostracod individuals and their cryptic colour patterns).

Fig. 3 - Microphotographies à la caméra vidéo d'ostracodes vivants sur leur substrat; spécimens adultes de *Cytherissa lacustris* de sédiments des zones littorale (A) et profonde (B) du Mondsee. C-D - *Cypridopsis vidua* dans un habitat phytal (les flèches indiquent les individus et leur couleur de camouflage).
and F). The third colour is white due to the lack of epidermal pigments and the transmission of the soft body colour through the transparent carapace.

One has to note that the colouration changes immediately after the molting process. The chromogranules start to accumulate after the calcification of the valves. Once the synthesis of the chromogranules stops the colouration pattern remains fixed. There is no adjustable homochromy as in other Crustacea (Pasteur, 1982).

There are no informations on the chemical composition of the various pigments. Considering the knowledge on crustacean pigments (Ghidalia, 1985) one could speculate that the brown and black granules of pigments are melanins and/or ommochromes, and the white pigments pterins. Yellow-brown pigments on the soft body and the carapace of the ostracods could be due to the ingestion of carotenoids.

It is important to note that freshwater ostracods, unlike marine ones, do not display red and blue colous (Müller, 1894). It may be important to emphasize that in the case of the limnic water mites the red coloration is a warning signal for predators (Kerfoot, 1982).

3.2. PATTERNS OF CARAPACE PIGMENTATION.

One can classify the colored carapaces in two groups, i.e. fully coloured and patchy coloured. One can distinguish several patterns:

1) patches of pigments disposed on a pigmented background, e.g. *Notodromas persica* (fig.1, J and K) is an example; it has a white patch on a black background.

2) Pigmented patch-areas on an unpigmented background. *Chlamydotheca colombiensis* (fig. 1, C-F), *Cypria ophthalmica* (fig. 2, A and B), *Cypridopsis vidua* (fig. 2, D, F) are such examples. *C. ophthalmica*, for instance, develops anterior, dorsal and posterior pigmented patches. In some specimens the size varies and the coloured areas fuse (fig. 2, A), while in others they remain quite isolated (fig. 2, B). *Cypridopsis vidua* develops coloured stripes (fig. 2, D-F). Their position is fixed and can be easily identified (we numbered them 1 to 5, fig. 2). Their shape is quite variable depending on their developmental stage. Compare fig. 2 E where the dorsal stripe (3), is partly developed, with fig. 2 D showing an older specimen where the stripe is fully developed and coalesced with the lateral stripes (1 and 2).

Experiments with adults of *C. vidua*, maintained at 20 °C and in full light in the laboratory, show that specimens after the molting develop first the stripes 1 and 2 followed by the stripes 4 and 5. Stripe 3 develops gradually. Once developed, they can extend covering also the ventral side of the carapace. During this time the pigments, as mentioned above, change in colour intensity from light-green to dark-green up to black or from light-brown (reddish) to dark-brown up to black. The colour changes in the lateral stripes progressively from the dorsal side to the ventral one.

Within natural populations of *C. vidua* one is impressed by the wide range of colour pattern variability of this species due to the differences of physiological state and developmental stages of the various individuals.

3) Unpigmented patch areas within a pigmented background. This is the case with *Chlamydotheca* species. *Chlamydotheca unispinosa* has completely coloured adult females as well as specimens in which some areas are unpigmented (fig. 1, A and B). Especially unpigmented (and therefore appearing white in colour) are the zones which are in contact with mobile limbs like the antennae (a1, a2 in fig. 1, A and B). In the case of *Chlamydotheca colombiensis* (fig. 1, C-F) the unpigmented areas are also in those parts where mobile inner limbs come in contact with the epidermal tissue of the carapace, i.e. the antennae (a1, a2), the mandibles (md), the walking legs (wl) and the ovary (ov). It is remarkable that this pigmentation patterns seem to be very stable, genetically fixed.

Our specimens from Mondsee have the same pigmented/depigmented patterns as those figured by Roesler (1985) in the original description. One can ask, how these pattern arose? It reminds of Cuenot's example of camel callosities where an ereditary assimilation of mechanically induced morphological changes are seen (Cuenot, 1951).

In many strongly pigmented ostracods the carapace area located in front or around the eyes is unpigmented (fig. 1, J and H) as a necessity for better vision (for marine examples see Bonaduce and Danielopol, 1988).
Fig. 4 - A-E - Stems of *Chara fragilis*; A - general view of two stems examined (x and xx); B, D, E - details of the stem xx (note in D the accumulation of diatoms and in E the network of filamentous bacteria; C - smooth area of the stem x without "Aufwuchs"; F - *Vimba limbata* faeces containing *Cypridopsis vidua*; (note the high number of crushed carapaces).

Fig. 4 - A-E - Tiges de *Chara fragilis*; A - vue générale des deux tiges examinées (* et **) ; B - détails de la tige ** (noter en D l'accumulation de Diatomées et en E la trame de Bactéries filamentueuses) ; C - surface lisse de la tige * sans "Aufwuchs" ; F - Excréments de *Vimba limbata* contenant *Cypridopsis vidua* (remarquer le grand nombre de carapaces broyées).
3.3. THE CRYPTIC VALUE OF THE CARAPACE COLORATION.

Danielopol (in Carbonel et al. 1988) reviewed some of the literature pertaining to fish predation on limnic ostracods. Especially ostracod species which live in shallow water habitats are exposed to fish predation. Uiblein and Winkler (1988) showed that in Mondsee the young fishes (stages +3) of the fish *Vimba elongata* feed intensively on ostracods. This is the common meiofaunal crustacean group found in the fish stomachs. The authors suggest that the young fishes learn to eat on shell preys starting first with ostracods; later on they switch to larger Bivalvia preys.

The carapace colourations help the animals to be cryptic in several ways, i.e. substrate homochromy, shadow camouflage, disruptive colouration and countershading.

It is interesting to note that most of the coloured ostracods live in the photic zone of limnic habitats (of course, this applies also to marine ostracods). One can ask, how protective the colour pattern they display, is against fish predation. This is a problem which was investigated by Mbahinzireki et al. (1990) and here will be summarized only for several case studies. We shall also add our data to their observations.

*Cytherissa lacustris* - This is a benthic species which creeps slowly on the substrate and penetrates deeply into it (Danielopol et al. 1988). Immediately after the molt the individuals have a light- to dark-brown colour. This is a substrate homochromy as most of the lake sediments which are oxidized display such colour. The colour of the aged individuals is masked by the sediment which sticks to the valves (fig. 3, A, B). The animals, therefore, should be only distinguished with difficulty by those fishes which forage by vision.

It is interesting that the colour of *Cytherissa lacustris* does not change with depth, i.e. in both shallow and deep lake habitats this species displays the same colour. *Cytherissa lacustris* exposed on the sediment was little eaten (only 5% of the total number of specimens) by *Vimba elongata* in Mbahinzireki’s experiments (op.cit.). Without sediment and within one hour exposure about 90% of the *Cytherissa* specimens were eaten by this fish. The lower predation risk of *Cytherissa lacustris* because of its endosediment life style is similar to the one described by Hershey (1987) for chironomids.

*Cypria ophthalmica* - This species which swims closely to the bottom or stays between macrophytes has a pigmented pattern which was discussed by Danielopol (in Carbonel et al., 1988). Table 1 shows that in shallow habitats like the littoral zone of Mondsee and in the shallow lakes Halleswiessee, Lunzer Mittersee, Neusiedlersee and the Myerwies pond most of the speciemns are pigmented. Those populations living in habitats poorly illuminated, like the profundal zone of Mondsee and an open well in Greece, have a higher percentage of unpigmented specimens.

<table>
<thead>
<tr>
<th>Site</th>
<th>Habitat</th>
<th>N</th>
<th>% Pigm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mondsee</td>
<td>littoral z.</td>
<td>112</td>
<td>99</td>
</tr>
<tr>
<td>Mondsee</td>
<td>profundal z.</td>
<td>130</td>
<td>45</td>
</tr>
<tr>
<td>Halleswiessee</td>
<td>littoral z.</td>
<td>278</td>
<td>100</td>
</tr>
<tr>
<td>Lunz-Mittersee</td>
<td>littoral z.</td>
<td>360</td>
<td>98</td>
</tr>
<tr>
<td>Neusiedlersee</td>
<td>littoral z.</td>
<td>146</td>
<td>100</td>
</tr>
<tr>
<td>Mayerwies f</td>
<td>fish pond</td>
<td>106</td>
<td>100</td>
</tr>
<tr>
<td>Aghios Georghios</td>
<td>open well</td>
<td>347</td>
<td>84</td>
</tr>
</tbody>
</table>

Table 1 - Relative frequency of pigmented individuals of *Cypria ophthalmica* in various limnic habitats (N - number of adult individuals examined; % P - relative frequency of pigmented individuals in the sample).

The extreme depigmentation is presented by *Cypria cavernae* (Wagenleitener,1990) from caves around Trieste. This latter species is a blind exclusively troglobite dwelling animal. Danielopol (in Carbonel et al. 1988) speculated that the anterior, posterior and dorsal colour patches on *C. ophthalmica* can make the swimming animal invisible for fish predators. It is not clear, why the pigment disappears in the case of animals living in aphotic habitats. Is this due to a physiological blockage of the pigment synthesis or to a genetic process? Is this character state eliminated by the relaxation of the selective pressure of fish predation and the occurrence of a genetic drift mechanism? Such cases have been discussed by Wilkens (1988) for cave dwelling fishes.
Cypridopsis vidua - This species lives mainly in shallow water habitats; being a good swimmer it Elects also the macrophyte stems. Mbahinzireki et al. (1990) showed that C. vidua, when alternative Substrates are offered, likes shadowed and strongly illuminated substrates and smooth versus biological complex macrophyte stems, it actively elects macrophytes with a rich "Aufwuchs", while preferring the shadowed areas. The complex macrophyte stems are Chara fragilis with its calcareous tubes. Fig. 4 shows that the smooth stretch (C) has fewer algae and bacteria as compared with the calcareous one (B, D, E). The colouring of the C. vidua carapace represents in our opinion a disruptive colour pattern. Fig. 3, C and D, show that the stripes disrupt the general carapace shape on both well and poorly illuminated substrates.

The experiments of Mbahinzireki et al. (op.cit.) with Vimba elongata demonstrate that this fish catches C. vidua less successfully on black substrates than on white and green ones. The poorest foraging success is during complete darkness. The faeces of the fishes show a high percentage of ostracods which are ingested and further crushed (fig. 4, F).

The large variability of the colour pattern mentioned earlier could have an adaptive value, too. Endler (1988, p. 506) noted: "Animal colour patterns and backgrounds may be regarded as mosaics of patches which vary in size, colour, reflectance and shape. Therefore, to be cryptic, a colour pattern must resemble a random sample of the background colour pattern perceived by predators at the ages, times, visual conditions and microhabitats in which the prey are most vulnerable to predation." (for supplementary discussions see also Endler, 1978, 1984).

Chlamydotheca unispinosa and C. colombiensis (fig. 1, A - F) display in our opinion a shadow camouflage pattern, if this species lives in well illuminated habitats between macrophytes.

Notodromas persica presents a typical countershading pattern. This species lives in shallow water bodies and is a neustonic animal, i.e. it stays fixed on the inner side of the water surface using the enlarged ventral carapace structures. The dorsal part of the ostracod which is pigmented white lies downwards and a predator, looking upwards, will not see the ostracod shape. The intense black colour of the ventral and anterior or posterior side could play a protective role against the intense light existing at the air-water interface (Lythgoe, 1979, Wicksten, 1989).

The green colour with a white patch of Prionocypris zenkeri could be non-adaptive and those of Cypris pubera green coloured is not well known how protective it is. Such non-adaptive or slightly adaptive coloration patterns are discussed by Goodhart (1987) in a paper on various snails.

CONCLUSIONS

1. The color pattern of Cytherissa lacustris combined with the ostracod behaviour of living mainly into the sediment makes the species less vulnerable to fish predation. The possible reduction in abundances or local extinction of this ostracod species is not plausible to be due to fish predation.

2. The color pattern of Cytherissa lacustris has a lower adaptive value than that of other ostracods like e.g. Cypridopsis vidua.

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THE CARAPACE PRESERVATION OF CYTHERISSA LACUSTRIS: ITS POSSIBLE USE FOR PALEOENVIRONMENTAL RECONSTRUCTIONS.

PRESERVATION DE LA CARAPACE DE CYTHERISSA LACUSTRIS : POSSIBILITES D'UTILISATION POUR DES RECONSTITUTIONS DE PALEOENVIRONNEMENTS

by

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Key-Words: Cyttherissa lacustris, ostracoda, carapace, paleoecology
Mots-Cles : Cyttherissa lacustris, ostracode, carapace, paleoécologie

Abstract

The frequency of valves which are either broken, opaque or black coloured as well as the proportion of intact carapaces (articulated valves) has been investigated at two sublittoral (12 m deep) sites in Mondsee which are rich in coarse sediment and organic detritus. One of them has turbulent water conditions, the other one being less affected by the running water discharge of a nearby stream has stagnant water conditions. Differences exist in the degree of preservation of the Cyttherissa lacustris valves. At the high energy site the frequency of broken valves and disarticulated carapaces is higher than at the more stable site. At this latter one the black coloured valves are more abundant. No significant differences exist between the opaque (milky) valves of the two sites. The paleoecological implications are discussed.

Résumé

La fréquence des valves cassées, opaques ou colorées en noir ainsi que la proportion des carapaces entières (valves articulées) ont été examinées dans deux sites sublittoraux (12 m de profondeur) du Mondsee riches en sédiment grossier et en détritus organiques. L'un d'entre eux connaît des conditions hydrodynamiques élevées, l'autre, qui semble moins affecté par la turbulence d'un courant proche, a des conditions d'eau stagnante. Il existe des différences dans le degré de préservation des valves de Cyttherissa lacustris: dans le site soumis à une haute énergie, la fréquence des valves brisées et des carapaces désarticulées est plus grande que dans le site plus stable. Dans celui-ci, les valves colorées en noir sont plus abondantes. Il n'existe pas de différences significatives entre les valves opaques des deux sites. Les implications paleoécologiques sont discutées.

1 - INTRODUCTION

In a stimulating paper Oertli (1971) demonstrated that the aspects of the ostracod carapace preservation can help the micropaleontologist to better locate propitious sedimentary facies in which hydrocarbon and gas accumulate. Oertli (op.cit) noted that sites with a high rate of sedimentation and high organic content harbour also a larger proportion of ostracod carapaces, the valves are well preserved (with few signs of corrosion and fracture) and many are black coloured or pyritized. Howe (1971) showed that"torose" Cytherideids in the Gulf of Mexico were very common in the deltaic facies (sandy sediments deposited close to the coast line) in which petroleum reservoirs developed.
With the help of nodated Cytherideis Howe (op. cit.) was able to reconstruct the paleocoast lines during the Tertiary helping the oil companies to locate their productive fields.

Cytherissa lacustris is a cytherideid which can nodate and which has a very wide ecological and geographical distribution in Europe (Löffler and Danielopol 1978). This species prefers lacustrine habitats with cold water. It occurs in various depths, from 1 m to 200 m (Löffler 1969, Powell 1976, Danielopol, in Carbonel et al. 1988). The possible reconstruction of paleoenvironmental situations using the aspect of the carapace of Cytherissa lacustris preservation in a similar way as discussed by Oertli (1971) and Howe (1971) is extremely attractive.

As this ostracod species occurs in many Late-Glacial and Holocene lacustrine deposits in Europe and North America and is easy to identify, the aspect of the carapace preservation could be an effective and helpful way for paleolimnological descriptions.

Here we present our preliminary investigations with the intention to verify the applicability of Oertli's and Howe's methods (which work well with marine fossils) to Cytherissa lacustris from Recent sediments of Mondsee where the environmental conditions are well understood. If this test is positive, further usage of this method could be undertaken using fossil material of Cytherissa.

2 - TYPES OF OSTRACOD CARAPACE PRESERVATION.

Danielopol et al. (1986) reviewed the way in which the ostracod carapace decomposes by biological and physico-chemical processes. Ostracods build a double-walled carapace, the latter consisting of two valves fixed with a hinge. The external wall is formed by calcite crystals enclosed in an organic matrix. The outer layer, the epicuticle, of the carapace is also formed by an organic film. Because the crystals are tightly packed the thin wall of the valves appear translucid (fig.1 A, B). After the death of the animal the carapace can disarticulate, especially in high-energy environments with a low sedimentation rate or in shallow turbulent water habitats. Through the activity of micro-organisms microborings occur on and within the hard wall of the valves. The organic matrix is damaged either through the activity of the microborers or through the physical abrasion due to the turbulence or instability of the environment in which the valves were deposited. The chemical activity of the water causes further alterations, i.e. the dissolution of the calcite crystals, and micro-spaces or holes may occur internally within the calcitic wall which determine the opaque or milky aspect of the valve (fig. 1, C, D). In other cases, water rich in dissolved iron-sulphide may cause a dark aspect of the valve (fig. 1 F). In a high-energy environment, valves or carapaces which have already weakened wall structures can break easily. Experimental research on this subject is presented by Handl (1989).

Fig. 1 - The preservation state of the valves and the limbs of C. lacustris obtained under experimental conditions. A, B - transparent valves from Mondsee before exposure to the experimental conditions; C, D - opaque-milky valves obtained after a week's exposure period in organogenic sediment and water, pH 6.5; E, F - carapace with limbs and valve black coloured, obtained after 7 weeks exposure period in organogenic sediment and water, pH 6.75 and temperature 18°C (enlargement X 32).
With the help of nodated *Cytherideis* Howe (op. cit.) was able to reconstruct the paleocoast lines during the Tertiary helping the oil companies to locate their productive fields.

*Cytherissa lacustris* is a cytherideid which can nodate and which has a very wide ecological and geographical distribution in Europe (Löffler and Danielopol 1978). This species prefers lacustrine habitats with cold water. It occurs in various depths, from 1 m to 200 m (Löffler 1969, Powell 1976, Danielopol, in Carbonel et al. 1988). The possible reconstruction of paleoenvironmental situations using the aspect of the carapace of *Cytherissa lacustris* preservation in a similar way as discussed by Oertli (1971) and Howe (1971) is extremely attractive.

As this ostracod species occurs in many Late-Glacial and Holocene lacustrine deposits in Europe and North America and is easy to identify, the aspect of the carapace preservation could be an effective and helpful way for paleolimnological descriptions.

Here we present our preliminary investigations with the intention to verify the applicability of Oertli’s and Howe’s methods (which work well with marine fossils) to *Cytherissa lacustris* from Recent sediments of Mondsee where the environmental conditions are well understood. If this test is positive, further usage of this method could be undertaken using fossil material of *Cytherissa*.

2 - TYPES OF OSTRACOD CARAPACE PRESERVATION.

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3 - SAMPLING SITE, MATERIAL, METHODS.

During 1987 we investigated the spatial distribution of nodated, respectively unnodated, *Cytherissa lacustris* in the central and eastern basins of Mondsee (fig. 2). Geologically, the northern side of the lake belongs to the flysch zone (e.g. between Seehof and See), while the southern side (e.g. between Scharfling and See on fig. 2) is formed by carbonate rocks. Horsthemke (1986) differentiated a central basin of conical shape with the deepest depth (69 m) and a shallow small basin formed at the end of the lake which could be approximately delineated by a straight line between Marienau and Kreuzstein and around the locality of See (fig. 2). This latter basin is very shallow and is characterized by a high detrital sedimentation due to the discharge of several mountain streams. One of those is the Ortlerbach which, especially, during the rainy periods discharges high amounts of water and sediment which flow in the direction of the Seeache (fig. 2 see arrow), the effluent stream of Mondsee. The sediments in the shallow depths down to 20 m below the Ortlerbach mouth are formed by sand and silty material. The sand fraction which is rich in quartz amounts up to 38 percent of the total sediment volume (Horsthemke 1986).

The sites where valves and carapaces of *Cytherissa lacustris* were collected are presented in fig. 2. The samples around the mouth of the Ortlerbach are located 100 m west (W) and 100 m east (E), respectively, from this stream at 12 m deep. The bottom sediments are sandy and rich in organic allochthonous (plant) detritus. There are fewer turbulences and there is less sediment transport at site W than at site E during rainy and high water discharge periods.

The site See at 6 and 12 m deep contains a predominantly coarse sandy sediment and much allochthonous organic detritus. The site MO-7 at 12 and 20 m deep contains silty sediments with fine organic detritus. At all these sites living specimens of *Cytherissa lacustris* occur with dead carapaces and valves in the upper three centimeters of the sediment layer. At the site Pi (Pichlauhot) and Scharfling no living *Cytherissa* or carapaces occur in the upper layer. The data plotted on fig. 2 come from cores taken from 40 m and 60 m deep, respectively. Here valves of *Cytherissa* were extracted from 20 to 30 cm deep into the sediment. Besides *C. lacustris* we identified also the accompanying species in our ostracod samples in order to define littoral and/or profundal assemblages.

To test the differences of the degree of carapace preservation between the subfossil populations of *Cytherissa* occurring at the sites W and E in the Ortlerach area we used a χ²-test on a two by two contingency table (Elliott 1977). We distinguished between nodated and unnodated *Cytherissa* phenotypes. In this case we only examined the postero-ventral node, the most persistent one, and only adult and last instar carapaces and valves (the carapaces were counted as two valves).

4 - RESULTS

*Cytherissa lacustris* in Mondsee around the Ortlerbach mouth as well as close to the See locality (fig. 2) occur in the littoral and sublittoral samples in association with *Candona candida*, *Candona neglecta*, *Fabaeformiscandona protzi*, *Cypria ophthalmica*, *Cyclocypris ovum*, *Cypriodopsis vidua*, *Herpetocypris reptans*, *Limnocythere sancti-patricii*, *L. inopinata*, *Darwinula stevensoni* and *Leucocythere mirabilis*. At site E, *Psychrodromus fontinalis* and *Pseudocandona albicans* occur also. These are species which live commonly in slowly flowing water and, here, are maybe transported passively by the Ortlerbach. They do not occur at site W in more stagnant waters.

The deep lake sites have ostracod assemblages which contain, besides *C. lacustris*, the species *Limnocythere sancti-patricii*, *Leucocythere mirabilis*, *Candona neglecta*, *Fabaeformiscandona caudata*, *F. protzi*.

The frequency of nodated valves of *Cytherissa lacustris* sampled around the Ortlerbach and in See is higher than at the other sites (fig. 2). We do not know, if this is environmentally or genetically cued and if it is related to the sedimentary peculiarities of this area (see further discussions on this subject in Sywula & Geiger, 1990 and Carbonel et al., 1990). Here, we just want to emphasize the analogy with the Howe (1971) data, i.e. an abundance of nodated Cytherideidae in deltaic sandy facies near the shore line.
Fig. 2 - Mondsee with sampling sites where the relative frequency of nodation and the state of the carapace preservation of *C. lacustris* was investigated. Columns indicate relative frequency in percentage of the non-nodated valves from the total count in the sample (number located close to the column). For the site SEE the mean value of the percentage of non-nodated valves and standard deviation is given. *n* - sampling units, MO-7 Mooswinkel bay, Pi - Pichlauhof, Ma-Kr the transect Marienau-Kreuzstein. W and E sampling sites for carapace preservation used in this paper. Arrows indicate the direction of the water flow in Mondsee.

**Fig. 2** - Carte du Mondsee avec les sites d'échantillonnage où ont été étudiées la fréquence relative de la nodation et les états de conservation des carapaces de *C. lacustris*. Les colonnes indiquent les fréquences relatives en pourcentage des valves non-nodees par rapport au nombre total dans l'échantillon (nombre indiqué à côté de la colonne). Pour le site SEE, la valeur moyenne des pourcentages de non-nodeés et la déviation-standard sont notées. *n* = unités d'échantillonnage. MO7: baie de Mooswinkel, Pi: Pichlauhof, Ma-Kr: transect entre Marienau et Kreuzstein; W et E sont les sites d'échantillonnage pour l'étude du présent papier. Les flèches indiquent la direction de l'apport de l'eau dans le Mondsee.
Table 1 shows the distribution of completely preserved and broken valves of *C. lacustris* at the two sites W and E around the Ortlerbach mouth. There is a statistically significantly higher density of broken valves downwards the Ortlerbach (in E) where the water regime is more turbulent and the sediment transport more active than at site W.

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>B</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>W</td>
<td>122</td>
<td>21</td>
<td>143</td>
</tr>
<tr>
<td>E</td>
<td>132</td>
<td>55</td>
<td>187</td>
</tr>
</tbody>
</table>

Chi-square value / Valeur du $\chi^2$: 9.9

Significant difference / Différence significative: $P < 0.05$

Table 2 shows that the frequency of disarticulated carapaces is higher at site E (25%) as at site W (17%). Still, the difference is not significant at a 5 percentage level.

<table>
<thead>
<tr>
<th></th>
<th>V</th>
<th>C</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>W</td>
<td>85</td>
<td>29</td>
<td>114</td>
</tr>
<tr>
<td>E</td>
<td>133</td>
<td>27</td>
<td>186</td>
</tr>
</tbody>
</table>

Chi-square value / Valeur du $\chi^2$: 2.39

No significant difference / Différence non-significative: $P > 0.05$

Table 3 shows that in the clastic sediments of site W, rich in organic allochtonous material and with more or less stagnant water, the frequency of black coloured valves is high (23 %), while at site E no such valves occurred in our samples.

<table>
<thead>
<tr>
<th></th>
<th>B</th>
<th>U</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>W</td>
<td>33</td>
<td>110</td>
<td>143</td>
</tr>
<tr>
<td>E</td>
<td>0</td>
<td>187</td>
<td>187</td>
</tr>
</tbody>
</table>

Table 3 - Comparative distribution of black-coloured (B) versus uncoloured (U) valves of *C. lacustris* in samples from Mondsee (Ortlerbach area) at the sites W and E. N = total number of valves.

Tableau 1: *Tableau de contingence 2 à 2 pour un test $\chi^2$ de la signification des différences entre valves de *C. lacustris* complètement préservées (C) et brisées (B) dans des échantillons du Mondsee (zone de l'Ortlerbach) sur les sites W et E. N = nombre total de valves.*

Tableau 2: *Tableau de contingence 2 à 2 pour un test $\chi^2$ de la signification des différences entre valves (V) et carapaces (C) de *C. lacustris* dans des échantillons du Mondsee (zone de l'Ortlerbach) sur les sites W et E. N = nombre total de valves.*

Tableau 3: *Distribution comparée des valves de *C. lacustris* colorées en noir (B) et incolores (U) dans les échantillons du Mondsee (zone de l'Ortlerbach) sur les sites W et E. N = nombre total de valves*
Table 4, finally, shows that there are no significant differences between the opaque valves of *C. lacustris* occurring around the Ortlerbach mouth. As the milky (or chalky) aspect occurs mainly because of the chemical dissolution of the carbonate crystals (Danielopol et al., 1986), it appears that the phenomenon exists in both stagnant and slowly flowing environments alike.

<table>
<thead>
<tr>
<th></th>
<th>O</th>
<th>T</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>W</td>
<td>70</td>
<td>19</td>
<td>89</td>
</tr>
<tr>
<td>E</td>
<td>112</td>
<td>20</td>
<td>132</td>
</tr>
</tbody>
</table>

Chi-square value / Valeur du $\chi^2$ = 1.01

no significant difference / Différence non-significative: $P > 0.05$

Table 4 - A two by two contingency table for Chi-square test of significance of differences between opaque-milky (O) and transparent (T) valves of *C. lacustris* in samples from Mondsee (Ortlerbach area) at the sites W and E.

<table>
<thead>
<tr>
<th></th>
<th>O</th>
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<td>E</td>
<td>112</td>
<td>20</td>
<td>132</td>
</tr>
</tbody>
</table>

5 - CONCLUSIONS

1. The data presented here using a limnetic ostracod species, *C. lacustris*, follow the model proposed by Oertli (1971) and Howe (1971).

2. In habitats closely located to the shore line and in areas under to deltaic conditions, one finds an abundant fauna of nodated Cytherideids. For the moment, we do not know, if this reflects a real ecological pattern or if it represents just an exceptional analogy to the marine situation described by Howe (op.cit.).

3. High energy habitats with stronger sediment transport and water turbulence contain a higher proportion of broken valves and disarticulated carapaces.

4. Littoral habitats with more stagnant water conditions and rich in allochtonous organic matter harbour a significant fraction of black coloured carapaces and valves.

5. A definition of a littoral or a profundal habitat in which *C. lacustris* occurs can be made using the informations offered by the ostracod assemblages. The littoral assemblage is more species-rich and contains species which do not occur at depth exceeding 15 m (e.g. *C. vidua*, *H. reptans*, *D. stevensoni*, *L. inopinata*).

6. The present study is an actuopaelontological exercise. Now, one should try to apply Oertli's model using *C. lacustris* from lake sediments deposited during remote Late-Glacial or Holocene times, in order to identify limnic deltaic facies, high energy versus stagnant water environments etc.

7. The statistical distribution of nodated valves of *C. lacustris* related to various types of habitats should be further investigated.

ACKNOWLEDGMENTS

The technical help received from our colleagues in Mondsee, R. Niederreiter and K. Maier, during the sampling programme and M. Kaiser for counting the nodated *Cytherissa* in the laboratory is greatly appreciated. One of us (D.L.D.) is much indebted to H.J. Oertli (Pau) for the initial impetus to develop this project. We thank colleagues for their helpful discussions and informations: E. Horsthemke and J. Schneider (Göttingen), P. Carbonel (Talence), J.P. Colin (Begles), H.J. Oertli (Pau), W. Geiger (Mondsee). Financial support was received from the Fonds zur Förderung der wissenschaftlichen Forschung, Project P. 5614 granted to D.L.D.
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THE MORPHOLOGICAL VARIABILITY OF THE CARAPACE OF CYTHERISSA LACUSTRIS ECOPHENOTYPIC ASPECTS

LA VARIABILITE MORPHOLOGIQUE DES CARAPACES DE CYTHERISSA LACUSTRIS. ASPECTS ECOPHENOTYPIQUES

by

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Key-Words: ostracods, polymorphism, organic matter, terrigenous, carbonates, Holocene.
Mots-CleS: ostracodes, polymorphisme,matière organique,terrigènes,carbonates,Holocène.

Abstract

The carapace ornamentation of many ostracod species often varies and may be more or less developed. For Cytherissa lacustris, the most common ornamentation features are reticulation and nodation. The study of 4 stations and transects in Mondsee and stations in Attersee and in Mittersee show that the variability can be related to events occurring at the water-sediment interfaces:

- reticulation relates to the carbonate saturation levels;
- nodation is developed mainly in the littoral area receiving supplies from the surroundings with allochtonous organic matter complexing with silica.

These observations are tested for periods of different climatic characteristics: at the Late Glacial (13000 years BP) and at the Atlantic period (5500-7000 years BP).

Résumé

L'ornementation de la carapace de nombreuses espèces d'ostracodes est souvent variable et peut être plus ou moins développée. Chez Cytherissa lacustris, les types d'ornements les plus fréquemment observés sont la réticulation et la nodation. L'étude de 4 stations et transects dans le Mondsee et de stations dans l'Attersee et le Mittersee montre que la variabilité peut être reliée aux phénomènes qui ont lieu à l'interface eau-sédiment selon deux manières:

- la réticulation est reliée au niveau de saturation des carbonates;
- la nodation est principalement développée dans la zone litorale où affluent les apports du bassin versant avec de la matière organique allochtone complexée avec de la silice.

Ces observations ont été testées dans des périodes à caractéristiques climatiques différentes: au Tardiglaciaire (13000 ans BP) et à l'Atlantique (5500-7000 ans BP).

1 - INTRODUCTION

Our aim here is to determine the link between the observed morphological variability and environmental factors and to test the results under limnic, especially extinct paleoenvironmental conditions. Furthermore, we present a system using all parameters which can be obtained through examination of phenotypes taken in polymorphic populations of Cytherissa lacustris and sometimes of Limnocythere sanctipatricii.
2 - ORNAMENTATION: GENERALITIES AND PROBLEMS

As in the brackish environments, two main types of ostracod shell ornamentation can be observed in the limnic environments, particularly for *Cytherissa lacustris*: reticulation and nodation. Reticulation consists of a network of polygonal meshes with more or less thick walls which cover the entire valve. Reticulation reflects directly the network of epidermal cells (Okada, 1981). Nodation consists of hollow tubercles which are developed in areas whose placings are genetically controlled (Kilenyi, 1972). The presence or number of tubercles can vary between left or right valves, and also between individuals within one and the same population. Such intraspecific variations appear as the effect of the "environmental cued polymorphism" defined by Clark, 1976 (Peyrouquet et al., 1988). It is therefore very important to know the controlling parameters:

- regarding to reticulation, the role of carbonate saturation levels at the water-sediment interface has been shown. In the marine environment, equilibrium is controlled by organic matter and its precocious degradation (Peyrouquet et al. 1988, Carbonel and Hoibian 1988, Tölderer-Farmer, 1985).

- regarding nodation, however, a synthesis of numerous ecophenotypical hypotheses so far proposed converge towards a causing factor, complexing organic matter, and a limiting factor: salinity (Vesper, 1972; Peyrouquet, 1977, Tölderer-Farmer, 1985, Carbonel and Tölderer-Farmer 1988). In fact, it is probable that nodation is due simultaneously to action of genetic mechanisms and environmental changes, as showed in works on living populations of *Cyprideis torosa* (Kilenyi, 1972) or more recently, *Cytherissa lacustris* in Mondsee and Attersee, using electrophoretic techniques (Sywula and Geiger, 1990).

The following questions are raised here:

1-are the parameters which induct reticulation in the marine or brackish environments applicable to the limnic system?

2-can we continue characterizing the type of dissolved organic matter responsible for nodation?

The material studied here originates from prealpine lakes (Mondsee, Attersee, Lunz-Mittersee) whose environmental conditions (in particular, dissolved oxygen in water column and at the bottom, trophic level, qualitative and quantitative variations in organic matter, hydrodynamical and sedimentological data) and recent evolution are well known. The ostracods which live in the lakes nowadays are mainly represented by Cyprididae and a few Cytheridae. *Cytherissa lacustris* from the latter group, display ornamentation polymorphism. We will study this populations, and sometimes this of *Limnocythere sancti-patricii*. Two types of ornamentation were recognized: reticulation and nodation.

*C. lacustris*: the reticulation consists of polygonal cells with thick, often poorly visible and rarely varied walls (pl.1, B). Nodation consists of 7 nodes per valve and generally with more nodes on the right valve than on the left. Variation is noticeable from the seventh moult, important at moult 8 and it reaches a maximum at the adult stage. However, juveniles are always more noded. Therefore, this nodation type can be classified as follows (pl.1, A-F):

- weak nodation: 7 or less nodes poorly visible in juveniles, none in adults (only bumpy surface),
- medium nodation: 7 strong nodes in juveniles, 1 in adults,
- strong nodation: 7 very obvious nodes in juveniles and 7 in adults

In this paper, we consider only the adult stages and presence or absence of nodes.

*L. sancti-patricii*: reticulation is formed by more or less thick polygonal cells (Tölderer-Farmer, 1985). Their interval wall can be subdivided into many sub-cells. The architectural variation is a function of the degree of calcification ranging from smooth and thin forms to those with a double and much thicker reticulation (pl.2, A-E). Nodation is shown by a single tubercle which is developed more or less at the level of the postero-dorsal expansion (pl.2, F-I). In this species, nodation is symmetrical and more frequent in juveniles and in females rather than in males. It is less frequent than with *Cytherissa*. 

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3 - DISTRIBUTION OF PHENOTYPES IN THE PRESENT-DAY ENVIRONMENT

Understanding this distribution should allow us to determine the parameters controlling polymorphism.

3-1 THE PRESENT-DAY ENVIRONMENTS.

The environmental conditions vary in the lake:
- the morphology at the bottom, with e.g. a maximum depth in the southern part of the Mondsee (67m) and steep slope or weak slope at the lake's termination (site MO-4).
- the morphology of the shore with grasses or forest;
- the type of substratum, triassic calcareous or dolomitic formations (southern shore of Mondsee and Attersee) or cretaceous flysch with marls and sandstones (north and eastern shore of Mondsee, southeastern and eastern shore of Attersee);
- the hydrodynamism (circulation and seasonal mixing or stratification of the waters);
- at the trophic point of view, between the eutrophic zone in the north and the oligomesotrophic one in the south;

Six stations in the lake have been studied in Mondsee (fig. 1):

![Diagram of Mondsee with stations and valve counts]

Figure 1: Mondsee, position of stations and number of *Cytherissa lacustris.*

Dotted surfaces: percentage of noded individuals

*Figure 1: Mondsee, position des stations et nombre de Cytherissa lacustris*
*Surfaces pointillée: pourcentage d'individus nodés*
- MO-4/P3 station in the SE end of the lake in an oligotrophic zone with two sites respectively at 6m and 12m deep;
- MO-7, near Mooswinkl, station located in a bay on the east coast in a mesotrophic zone, with three sites at 12, 20 and 40 m deep;
- MO-6, near Scharfling, on the southern coast with two sites at 40 and 60m deep (deeper part of the lake) in a eutrophic zone;
- Near Pichi at 20 and 40m deep;
- 100m upstream (Oberhalb) and downstream (Unterhalb) of the mound of Ortlerbach, at 12m deep, for studying the possible influence of a little river;
- Cross-section in Mondsee, KM (fig. 1), between Kreutzstein (southern coast with a dolomitic karst) and Marienbad (northern coast with flysch). 9 sites have been sampled, respectively from SSW to NNE at 10, 15, 20, 25, 30, 33, 30, 25 and 20m deep.

3-2 RESULTS

At station MO-7 (Mooswinkl), Limnocythere are poorly calcified and poorly reticulated and smooth. Cytherissa are better calcified and weakly noded. The ratio of noded Cytherissa is (fig. 1):

<table>
<thead>
<tr>
<th>MOOSWINKL</th>
<th>MO-7 / 12 m</th>
<th>MO-7 / 20 m</th>
<th>MO-7 / 40 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>left valve: % noded (tot nb)</td>
<td>62 (116)</td>
<td>64 (111)</td>
<td>67 (106)</td>
</tr>
<tr>
<td>right valve: % noded (tot nb)</td>
<td>72 (118)</td>
<td>94 (125)</td>
<td>85 (99)</td>
</tr>
<tr>
<td>Σ: % noded (tot nb)</td>
<td>68 (234)</td>
<td>79 (238)</td>
<td>76 (205)</td>
</tr>
</tbody>
</table>

At station MO-4, the 2 species are better calcified and reticulated; Limnocythere sometimes have a weak nodation, and noding of Cytherissa is stronger than in MO-7. The ratio of noded Cytherissa is (fig. 1):

<table>
<thead>
<tr>
<th>MO-4</th>
<th>MO-4 / P3 6m</th>
<th>MO-4 / P3 12m</th>
</tr>
</thead>
<tbody>
<tr>
<td>left valve: % noded (tot nb)</td>
<td>-</td>
<td>81 (74)</td>
</tr>
<tr>
<td>right valve: % noded (tot nb)</td>
<td>-</td>
<td>89 (75)</td>
</tr>
<tr>
<td>Σ: % noded (tot nb)</td>
<td>98 (98)</td>
<td>85 (149)</td>
</tr>
</tbody>
</table>

At the station MO6, the 2 species are poorly calcified, faintly reticulated; nodes are weak in Cytherissa, and absent in Limnocythere. The proportion of noded Cytherissa is 64% (118 individuals) at 40m deep, and 66% (116 individuals) at 60m deep.

At the station Pichi (fig. 1), the noded Cytherissa are more abundant: 100% (11 individuals) at 20 m, and 77% (236 individuals at 40 m: 60% left valves for 109 ind., 91% right valves for 125 ind.).

At the station "Ortlerbach", Cytherissa are noded in majority without great differences between the two stations (fig. 1):

<table>
<thead>
<tr>
<th>ORTLERBACH</th>
<th>Ortlerb.: 100m Upstream / 12m</th>
<th>Ortlerb.: 100m Downstream / 12m</th>
</tr>
</thead>
<tbody>
<tr>
<td>left valve: % noded (tot nb)</td>
<td>80 (54)</td>
<td>85 (75)</td>
</tr>
<tr>
<td>right valve: % noded (tot nb)</td>
<td>89 (53)</td>
<td>91 (78)</td>
</tr>
<tr>
<td>Σ: % noded (tot nb)</td>
<td>85 (107)</td>
<td>88 (153)</td>
</tr>
</tbody>
</table>
In the cross-section KR-MA, the contrast between the two sides of the lake is clearly showed (fig.2):

On the southern side, the global ratio of noded *Cytherissa* is always less than 65%, on the other side, this ratio is more than 75%. The number of noded individuals decreases weekly from 10 to 30 m. The change of ratio between noded and unnoded individuals is particularly spectacular for the strongest nodes (see table below). The contrast is less marked in right valves than in left ones: the right valves are always more noded than the left ones.

<table>
<thead>
<tr>
<th>CrossSection</th>
<th>% strong nodes.</th>
<th>% strong nodes.</th>
<th>% without nodes</th>
<th>% without nodes</th>
<th>Σ % noded. (tot nb of valves)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mar.-Kreuzs.</td>
<td>R.V.</td>
<td>L.V.</td>
<td>R.V.</td>
<td>L.V.</td>
<td></td>
</tr>
<tr>
<td>10m M</td>
<td>67</td>
<td>39</td>
<td>14</td>
<td>18</td>
<td>84</td>
</tr>
<tr>
<td>15m M</td>
<td>59</td>
<td>34</td>
<td>14</td>
<td>36</td>
<td>75</td>
</tr>
<tr>
<td>20m M</td>
<td>75</td>
<td>33</td>
<td>7</td>
<td>23</td>
<td>85</td>
</tr>
<tr>
<td>25m M</td>
<td>67</td>
<td>28</td>
<td>0</td>
<td>18</td>
<td>91</td>
</tr>
<tr>
<td>30m M</td>
<td>53</td>
<td>34</td>
<td>16</td>
<td>25</td>
<td>80</td>
</tr>
<tr>
<td>33m</td>
<td>52</td>
<td>33</td>
<td>19</td>
<td>36</td>
<td>72</td>
</tr>
<tr>
<td>30m K</td>
<td>25</td>
<td>11</td>
<td>38</td>
<td>67</td>
<td>47</td>
</tr>
<tr>
<td>25m K</td>
<td>41</td>
<td>8</td>
<td>23</td>
<td>50</td>
<td>63</td>
</tr>
<tr>
<td>20m K</td>
<td>43</td>
<td>16</td>
<td>30</td>
<td>47</td>
<td>61</td>
</tr>
</tbody>
</table>
From these observations, one can conclude that:

1. The two species show a similar tendency in regard to variation in ornamentation.

2. Reticulation increases with a decrease in saturation of organic matter, and decrease with depth. This feature is in complete agreement with what occurs in the marine realm with organic matter degradation by bacteria with a lowering of oxygen and increase in pCO2, decrease in pH and increase in carbonate solubility. Ostracods encounter difficulties to bio-precipitate their calcitic shell and therefore build a shell "with austerity" that is with minimum ornamentation (Peypouquet et al., 1988; Carbonel and Hoibian, 1988).

3. Nodation is more evident in oligotrophic sampling stations and in the areas closest to the shore. However, it is in these areas that a maximum supply from the surroundings of the basin occurs. This supply consists of organic matter which is more or less mineralized during the transport to the lake. The origin of such an allochthonous organic matter is due to the draining of grasses and formation of humic components, the passage through the detritic substrate and enrichment in dissolved silica.

   In addition, nodation decreases with depth. Nevertheless, the proposition that nodation is caused by chelated dissolved organic matter (Peypouquet, 1979) is partly confirmed here. However, this idea deserves a better definition: if it was just any type of organic matter all the sampling stations and more particularly the eutrophic ones, would favour the production of noded valves; yet, the contrary occurs. It is at the stations closest to the shore, which are oligotrophic, that nodation is the strongest, and where local productivity is the poorest and surprisingly, where supply from the surroundings is the most important.

   The type and origin of the organic matter appear to be important here. In fact, the occurrence of nodation is linked to the allochthonous organic matter. More particularly, this matter consists of humic and fulvic acids which possess strong complexing power towards elements like Fe, Si, Al (Erhardt, 1973). The fact that nodation is a common phenomenon for numerous species and environments (Carbonel and al., 1983), implies complexing of very common elements by organic matter. The preponderance of nodation at stations where water which drains the flysch rich in terrigenous elements (in particular Si and Al) ends up, seems to point out to organosilicates or organosilicoaluminates complexes. Chemical analyses of the valves show also a particularly important concentration of Si at the level of nodes (Carbonel and Tölderer-Farmer, 1988, Carbonel and Farmer, 1990).

   This hypothesis is confirmed by two examples: in the Attersee, valves of Limnocythere sancti-patricii sampled at 6m deep are noded and reticulated (more than 30%), whereas those taken around 50 m are not: allochthonous organic matter is concentrated in the littoral zone (Behbehani et al., 1986; Behbehani, 1987). In the Lunz-Mittersee lake, which has a dolomitic terrain surrounding the basin, the valves are smooth at the station sampled down to 2 m (less than 5%). It is possible therefore to link a medium rich in allochthonous organic matter complexing chemical elements, derived from silicate rich terrains, with Si in the carapace.

   Two conclusions can be drawn from the above:
   - the two phenomena of reticulation and nodation are not inter-related: all possible situations can occur: intense reticulation and strong nodation or absence of nodation as well as weak reticulation and presence or absence of nodation
   - the relationship between reticulation and carbonate equilibrium is as equally present in the limnic environment as it is in the marine environment. The intensity of the reticulation is more marked in the littoral or sub-littoral stations, not directly because of depth, but in relation with seasonal stratification of the lake: bottom of profundal zone is less reoxygenated than in the littoral area. This intensity is also inversally proportional to autochthonous organic matter productivity (e.g. eutrophy, depth).

   - Nodation is associated with a number of factors of the following characteristics:
     + preponderance in the littoral zone,
     + terrigenous sedimentation, complexing allochthonous organic matter,
     + nature of surrounding basin, with detritic sediments or carbonated sediments
     + time variations (mixing of seasonal phenotypes).

4 - PALEOENVIRONMENTS OF PREALPINE LAKES

The causes affecting shell ornamentation in populations of Cytherissa lacustris and Limnocythere sancti-patricii in modern day lakes being known, we aim at testing these interpretations on the same species from the same localities, but for older sequences which were deposited under different climatic conditions. This should further confirm and refine our ideas. Two periods, particularly well-documented in regard to climate, will be studied here: the late-glacial (13000 y BP) and the Atlantic period (5500-7000 y BP) from cores taken in Mondsee lake.
At the Late-Glacial (core st. MO-7, fig. 1), *Cytherissa lacustris* and *Limnocythere sancti-patricii* were very rare, poorly ornamented, poorly calcified and very rarely noded.

The Atlantic period appears to be a period during which conditions were best for the development of ornamentation for both species: at stations MO-2 (in Mondsee, on the northern shore, near the Limnological Institute) and MO-4 (in Mondsee in the southeastern termination), valves are strongly calcified and nodes well developed. These two stations represent a littoral environment and receive detritic supplies of sediment rich in vegetal debris. Those stations were situated close to two small streams. The core at station MO-4 shows that: for 2 levels, there is maximum nodation, between 45 and 55 cm and later, at the top; the first one was developed before the erosive phase associated with the recent Atlantic period (Schmidt, 1981). This nodation can be related to episodes of strong detritic supplies at the same time as an increase in humidity (presence of pine and silver birch in the pollen spectra (Schmidt, 1981). Nodation becomes very strong at the top with also an increase in temperature, humidity and detritic supplies. Nodation during this period is maximum and it is linked to an increase in rainfall and therefore to the washing of soils with maximum terrigenous supplies. This period is characterized by an increase in temperature, therefore the alteration of soils and a resulting enrichment in allochthonous organic matter complexing with a series of elements reaching the littoral zone.

During the Upper Holocene, in core MO4 (8m), the same phenomenon yet less intense than during the Atlantic episode is found for the two ostracods *Cytherissa lacustris* and *Limnocythere sancti-patricii*. The nodation is more developed during phases of increase in detritic supplies (fig. 3) because an intense rainfall and high energy level.

**Figure 3: Core MO-4 / 8m, upper Holocene**

*Figure 3: Carotte MO-4 / 8m, Holocène supérieur*
5 - CONCLUSIONS

Present-day examples, tested under periods of different climatic characteristics, show that the polymorphism of ostracods relates to events occurring at the water-sediment interfaces:

-regarding the carapace bioprecipitation, the valves are more or less well-calcified. The reticulation is connected with carbonate equilibrium at water-sediment interface: in littoral zones, there exist conditions of oversaturation (temperature, oxygen of photosynthesis, often, high energy level) while in profundal zone, exist conditions of undersaturation (decreasing of oxygen because water stratification and eutrophication at the bottom).

-regarding the appearance of nodes (which is a genetically controlled phenomenon yet to be determined): in the littoral zone receiving supplies from the surroundings, they are developed when there is also a supply of allochthonous organic matter complexing with ions originating from the draining through silicate-rich soils.

These two phenomena are independent of each another, but are influenced by prevailing climatic conditions: during a cold and poorly rainy period, these phenomena are slowed down, but are more pronounced during a warm and moist climate.

Our work shows that ostracods provide accurate information on events affecting the formation and evolution of limnic systems today and in the past. However, as indicated by works on present-day environments and Cytherissa or other ostracods, (Danielopol et al., 1990; Geiger, 1990 a-b; Martens, 1990; Sywula and Geiger, 1990), the relationships between fauna and environmental parameters are more complex and data obtained from living faunas are not always recorded in fossilizable parts of ostracods.

ACKNOWLEDGEMENTS

This work was carried out during cooperation between IGBA, Bordeaux and the Limnologisches Institut der O.A.W. We wish to thank Professor H. Löffler for allowing us to use the facilities at the Mondsee laboratory, and also all those who collaborated on this project, and more particularly Dr. Dz. Dan Danielopol, co-leader of this cooperation. We are much indebted to Alliance Française, which has given subventions for French students in Mondsee.

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**PLATE 1 / PLANCHE 1**

*Cytherissa lacustris* x120

- **A**: R.V., strong nodation / V.D. *nodation forte* - MO-4 / 8m
- **B**: Carapace, dorsal view, strong nodation / Carapace, vue dorsale, *nodation forte* - MO-4 / 8m
- **C**: R.V., medium nodation / V.D., *nodation moyenne* - MO-4 / 8m
- **D**: Carapace, dorsal view, weak nodation / Carapace, vue dorsale, *nodation faible* - MO-4 / 8m
- **E**: R.V., weak nodation / V.D., *nodation faible* - MO-7 / 18m
- **F**: L.V., without nodation / V.G. *non nodée* - MO-6 / 67m
- **G**: Detail of nodation and reticulation / Détail de la réticulation et de la nodation - MO-4 / 8m x400
Cytherissa, ecophenotypical aspects

A

B

C

D

E

F

G
PLATE 2 / PLANCHE 2

A-E. *Limnocythere sancti-patricii* MO-4 K.7 x120
A: L.V. juvenile, very strong node / V.G. juvénile, node très fort
B: R.V. female, strong node / V.D. femelle node fort
C: L.V. female, medium node / V.G. femelle, node moyen
D: R.V. male, weak node / V.D. mâle, node faible
E: L.V. male, unnoded / V.G. Mâle, non nodé

F-I. *Limnocythere sancti-patricii* MO-4 K 7 details of the postero-ventral area / détails de la zone postéro-ventrale x300
F: Strong node, double reticulation / node fort, double réticulation
G: Medium node, double reticulation / node moyen, double réticulation
H: Weak node, double reticulation / node faible, double réticulation
I: No node, double reticulation / pas de node, double réticulation
Cytherissa, ecophenotypical aspects

A

B

C

D

E

F

G

H

I
THE CHEMICAL COMPOSITION OF THE CARAPACE OF CYTHERISSA

COMPOSITION CHIMIQUE DE LA CARAPACE DE CYTHERISSA

by

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Key-Words: Carapace, chemical analysis, S.E.M., trophic level, ornamentation

Mots-Clés: Carapace, Analyse chimique, M.S.E., niveau trophique, ornementation

Abstract

The quantitative microprobe analysis (SEM) of the chemical elements contained in the Cytherissa carapaces showed that:
- the increase of elements linked to organic matter such as P, Mn, Fe in the individuals molted in mesotrophic environments in opposition with the individuals molted in oligotrophic environments;
- the concentration of Si and Al on the nodes or on the genetically predetermined sites where the nodes are situated.

1-INTRODUCTION

As it has been already demonstrated, ostracods can build a variably ornamented carapace under the pressure of some factors controlling the environment at the water-sediment interface. This is observed mainly for the phenomena of reticulation (agradation and degradation sensu Peypourquet et al., 1980) controlled by the carbonate equilibrium, and of nodation (occurrence of hollow phenotypic tubercles on the surface of the valves). The relationships between ostracod ornamentation and physico-chemical parameters were discussed with analysis of convergences and some ecological arguments. The first valuable arguments were forwarded by Okada (1981) However, it is necessary to known whether these hypotheses are credible and whether they correspond to a quantifiable reality. It is for this reason that we use the SEM-analysis methodology.

We try to answer here two sets of questions:
1-are the morphological variations of the ostracod valves reflected in a change of the chemical composition?
2-are these chemical changes significant in regard to environmental changes?
2-METHODODOLOGY

Valves were cross-sectioned in as much as possible according to the antero-posterior axe and perpendicularly to the axe itself so as to measure the global as well as punctual (in particular sites of the ornamentation) chemical composition of the carapace.

Valves analyzed belong to adult and juvenile stage 8 Cytherissa.

Points analyzed cover inner and outer part of the carapaces. Each section consists of at least a dozen points and each sample of 2 to 3 sections (about 30 points per sample). Once polished and metallized with carbon, sections were analyzed with a CAMECA (Camebax micro) electronic microprobe having 3 spectrometers. Twelve elements were measured, according to their frequency in water and in carbonates constituting the valves. Sr with inutilizable results were not considered; and Ca, main constituent of the carbonate of the valves (always more than 48%) is examined separately. Only ten elements were considered together: Na, Mg, S, Cl, Fe, Si, P, Mn, Al and Ba in decreasing order.

Analyses were run under the following conditions: voltage, 15kV; current consumed, 0,42x10⁻⁹A; analysis field, 2,5x2,5μm. The limits of the electron probe detection are of about 10⁻³%, depending on the element and matrix considered. Results are given in atomic concentration percentages.

For global analyses, we have mixed all the values measured in the valves (minimum 30 points for each valve). For punctual analyses, we have measured 3 areas with a minimum of 5 points / site: node area, internode area and node site, when the node is not materialized. (external and internal points in the 3 cases).

The analyses were performed on Cytherissa from 3 stations in Mondsee (fig. 1): MO-4 See (8m) in an oligotrophic zone, MO-7 Mooswinkl (12m) in a mesotrophic zone, MO-3 (30m), in an infralittoral eutrophic zone).

Fig.1: Location map of the sampling sites / Carte de localisation des sites d'échantillonnage
3-RESULTS

Two sets of results are given: the data of global composition and the location of some elements within the ornamentation.

3-1 GLOBAL COMPOSITION

The global composition of the *Cytherissa* valves shows some differences between the 3 stations (fig.2, tab. 1): in station MO-4, valves contain small amounts of P and Fe, a great deal of Na, Mg, and S (0,1 to 0,3%), Fe, P and Si vary between 0,1 and 0,04%; Mn, Al and Ba do not exceed 0,04%. In station MO-7/12m, Mg, Na, S and Cl show values between 0,3 and 0,15%, Fe, P and Si, vary between 0,06 and 0,11%, Mn have a value of 0,04, Ba and Al , less than 0,03%. In the "profundal" station, the values show a radical change: P and Fe increase, Mg and Cl decrease: Fe, Mg, S, Na, P vary between 0,15 and 0,25%, Si, Cl, Mn, between 0,1 and 0,07%, Ba and Al, always less than 0,01%.

![Graph showing composition of Cytherissa valves](image)

**Fig.2: Average value of each element in *Cytherissa* carapace in the 3 studied stations**

**Table 1: Values formulated in atom percentage x 10^3**

<table>
<thead>
<tr>
<th></th>
<th>Mg</th>
<th>Na</th>
<th>S</th>
<th>Cl</th>
<th>Fe</th>
<th>P</th>
<th>Si</th>
<th>Mn</th>
<th>Al</th>
<th>Ba</th>
</tr>
</thead>
<tbody>
<tr>
<td>MO-4</td>
<td>205</td>
<td>210</td>
<td>190</td>
<td>110</td>
<td>60</td>
<td>50</td>
<td>40</td>
<td>12</td>
<td>11</td>
<td>8</td>
</tr>
<tr>
<td>MO-7</td>
<td>290</td>
<td>185</td>
<td>160</td>
<td>230</td>
<td>62</td>
<td>120</td>
<td>85</td>
<td>41</td>
<td>21</td>
<td>8</td>
</tr>
<tr>
<td>MO-3</td>
<td>185</td>
<td>170</td>
<td>180</td>
<td>80</td>
<td>235</td>
<td>140</td>
<td>92</td>
<td>70</td>
<td>27</td>
<td>8</td>
</tr>
</tbody>
</table>

In summary, we observe that obtained information can characterize each trophic level: in oligotrophic station, the values of Ba, Al, Mn, Si, P are minimal; these elements show maximal values in meso- and eutrophic stations. Fe is maximal in eutrophic station. S have the same values in the three stations. Ca is less concentrated in the valves from the "profundal", eutrophic station (40,5 x 10^3 ppm) than in littoral, oligo to mesotrophic stations (49 x 10^3 ppm).
3-2 CHEMICAL ELEMENTS IN THE ORNAMENTATION

The main morphological characteristic of *Cytherissa* is its capacity to build hollow tubercles on the carapace (Danielopol et al., 1990; Carbonel et al., 1990). At station MO-4/See, nodes have maximum development. At station MO-7/12m, they are abundant to in moderate number; in station MO-3/30m, they are less numerous to rare. We use only the measures made on the adult valves. The distribution of the values of the ten elements measured are the following (fig.3, tab.2):

![Graphs showing the distribution of elements](image)

These values show that:
- between internal and external parts of the valve, S is more abundant in the inner part than in the outer (about 23% in regard to average) like Mg (3%). Si, P, Cl, Fe, Al and Mn, are more abundant in the outer part, Na is variable, Ca is practically unvariable;

Table 2: Mean values of 11 elements in some sites of ornamentation in the valves of *Cytherissa*

<table>
<thead>
<tr>
<th>Site</th>
<th>Posit.</th>
<th>Ca %</th>
<th>Na ppm</th>
<th>Mg ppm</th>
<th>Si ppm</th>
<th>Cl ppm</th>
<th>Fe ppm</th>
<th>P ppm</th>
<th>Si ppm</th>
<th>Mn ppm</th>
<th>Al ppm</th>
<th>Ba ppm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Node</td>
<td>Intern</td>
<td>49,24</td>
<td>216</td>
<td>181</td>
<td>212</td>
<td>128</td>
<td>121</td>
<td>47</td>
<td>33</td>
<td>25</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Extern</td>
<td>49,15</td>
<td>308</td>
<td>158</td>
<td>123</td>
<td>160</td>
<td>140</td>
<td>54</td>
<td>131</td>
<td>27</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Intern</td>
<td>49,31</td>
<td>254</td>
<td>203</td>
<td>173</td>
<td>103</td>
<td>88</td>
<td>32</td>
<td>7</td>
<td>22</td>
<td>0</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Extern</td>
<td>49,31</td>
<td>230</td>
<td>190</td>
<td>112</td>
<td>126</td>
<td>106</td>
<td>39</td>
<td>15</td>
<td>28</td>
<td>8</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Site of</td>
<td>Intern</td>
<td>49,38</td>
<td>233</td>
<td>151</td>
<td>186</td>
<td>96</td>
<td>81</td>
<td>31</td>
<td>12</td>
<td>19</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>node</td>
<td>Extern</td>
<td>49,04</td>
<td>227</td>
<td>168</td>
<td>121</td>
<td>115</td>
<td>94</td>
<td>79</td>
<td>139</td>
<td>21</td>
<td>23</td>
<td>7</td>
</tr>
</tbody>
</table>
- in ornamentation (nodation in this case), the differences between nodes and internode areas appear as weak, except for Si which shows a variation more than 100% (tabl.2). The difference is stronger in valves without nodes in the normal place of the nodes. This observation confirm the genetical predetermination of the place of the nodes.

4-CONCLUSIONS

This study has confirmed both results already obtained, and provided new information on the following points:

Mg is preferentially distributed in the inner part of the valves and appears to be influenced by the temperature (cf. Cadot et al., 1975, Chivas et al., 1986)

Si, Na, Al concentrate on the outer part of the nodes, while Ba, S and Cl concentrate on the inner part at the contact of epidermal cells.

The occurrence and the abundance of P, Fe and Mn appear to be systematically associated with the trophic level of the environment.

These two last results are very important, because they indicate a direct relationship between chemical composition of the carapace and environment.

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V - THE ANCILLARY ASPECTS OF THE "CYTHERISSA PROJECT"

V - LES ASPECTS ANNEXES DU "PROJET CYTHERISSA"
THE NEGATIVE BINOMIAL DISTRIBUTION AND ITS INTEREST FOR THE PALEOECOLOGICAL RESEARCH ON LIMNIC OSTRACODA

LA DISTRIBUTION BINOMIALE NEGATIVE ET SON INTERET POUR LA RECHERCHE PALEOECOLOGIQUE DES OSTRACODES LIMNIQUES

by

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Key-Words: statistical distributions, ostracods, paleoecology
Mots-Cles: distributions statistiques, ostracodes, paleoécologie

Abstract:
A short description of the negative binomial distribution (NB \( \mu, k \)), its relation to the Poisson distribution and associated statistical aspects are presented. Furthermore some evidence that the NB \( \mu, k \) can be successfully fitted to ostracod data of living and fossil material is given. In this context two examples are discussed. One example is in connection with a subsampling strategy for fossil ostracods used by Danielopol and Casale (1988). The other describes a sample of living \textit{Cytherissa lacustris}. In addition to the performance of the \( \chi^2 \)-test of goodness of fit and the estimation of the parameters of the NB \( \mu, k \) a comparison of histograms of observed and expected frequencies is presented.

Résumé:
Une brève description de la distribution binomiale négative (NB \( \mu, k \)), ses relations avec la distribution de Poisson et les aspects statistiques corollaires sont présentés ici. De plus, il est mis en évidence que le NB \( \mu, k \) peut être appliqué avec succès aux données fournies par les ostracodes sur du matériel aussi bien vivant que fossile. Deux exemples sont discutés dans cette optique. L’un d’entre eux est en relation avec la méthodologie de sous-échantillonnage utilisée par Danielopol et Casale (1988). Le second décrit un échantillon de \textit{Cytherissa lacustris} vivantes. En plus du résultat du test de fiabilité \( \chi^2 \) et de l’estimation des paramètres du NB \( \mu, k \), il est présenté une comparaison des histogrammes des fréquences observées et prévues.

1. INTRODUCTION

Suppose we are mainly interested in the mean value \( \mu \) of the abundance of an ostracod population in an area of given size and shape (square, circle, etc.). In order to gather information about \( \mu \) we take a sample of size \( n \) and estimate \( \mu \) by the sample mean (arithmetic mean) \( \bar{x}_n \) of the counts \( x_1, \ldots, x_n \).

However in order to construct confidence limits for \( \mu \) it is necessary to find a mathematical model, which can be fitted reasonably well to the given data. In the present paper we will investigate two of the most commonly used mathematical models in animal ecology relating to this subject: the Poisson series \( P \mu \) with parameter \( \mu > 0 \) and the negative binomial series NB \( \mu, k \) with the parameters \( \mu > 0 \) and \( k > 0 \).
Actually ostracods, living or fossil, can be spatially dispersed randomly or can form aggregated pattern of individuals. Here "randomly" means that a Poisson distribution can be fitted well to the given spatial dispersion. Despite the NB $\mu, k$ is a natural extension of the $P_{\mu}$ (see below) there are more probability distributions specifying "aggregated pattern" like Thomas' distribution, Neyman's Type A, B and C distributions and Polya-Aeppli distribution, see Southwood (1966). Hence rejection of the $P_{\mu}$ does not necessarily mean the acceptance of the negative binominal model.

If the data are in accordance with a $P_{\mu}$ the construction of the confidence intervals for $\mu$ is straightforward, cf. e.g. Krebs (1989). However, if the data are well described by a NB $\mu, k$ this matter is much more complicated. The reason for this is the presence of the so-called nuisance parameter $k$.

(First of all the estimation of the parameter $k$ is awkward. This can be seen from the definition of the maximum likelihood estimate $\hat{k}_n$ below. However, the crucial problem is to overcome the difficulty of the stochastic dependance of the estimators $\hat{x}_n$ and $\hat{k}_n$. This problem has been solved by Anscombe (1950). He gave a detailed discussion with this respect on which the algorithm of the construction of the confidence interval, e.g. given in Krebs (1989), is based.

But the parameter $k$ of the NB $\mu, k$ is not always a nuisance parameter since it can be interpreted as an index of aggregation (the smaller the $k$, the greater the clumping and conversely the larger the $k$ the less the clumping).

The application of the NB $\mu, k$ in the biological sciences seem to have started around 1950, cf. e.g. Anscombe (1949) and Bliss and Fisher (1953). One of the few applications of the NB $\mu, k$ on ostracods is due to McLay (1978), who studied the behavior of two limnic ostracod species, living in small water bodies in Canada. Chalupsky and Leps (1985) studied the spatial distribution of various Oligochaeta worms. When comparing the goodness of fit of their data with both the NB $\mu, k$ and the Neyman type A distribution, they found that the NB $\mu, k$ fitted their data better.

In the present contribution we present a short description of the NB $\mu, k$ and its relation to the $P_{\mu}$. Furthermore we give some evidence that the NB $\mu, k$ can be successfully fitted to ostracod data of both living and fossil material. We also discuss the validity of the sample size for the subsampling strategy used by Danielopol and Casale (1988) when working with fossil ostracods and the construction of a confidence interval for the mean value $\mu$.

### 2. THE NEGATIVE BINOMIAL DISTRIBUTION NB $\mu, k$ AND ITS RELATION TO THE POISSON DISTRIBUTION $P_{\mu}$

A random variable $X$ is said to have a negative binomial distribution NB $\mu, k$ with parameters $\mu>0$ and $k>0$, if its probabilities are given by

$$P \left( X = x \right) = \binom{k + x - 1}{x} \left( 1 + \frac{\mu}{k} \right)^{-k} \left( \frac{\mu}{\mu + k} \right)^x, \quad x = 0, 1, 2, 3, \ldots \quad (1)$$

The probabilities of the NB $\mu, k$ may also be calculated from the recursion formula

$$P \left( X = x + 1 \right) = P \left( X = x \right) \cdot \frac{k + x}{x + 1} \frac{\mu}{\mu + k}, \quad x = 0, 1, 2, 3, \ldots \quad (2)$$

and the initial value

$$P \left( X = 0 \right) = \left( 1 + \frac{\mu}{k} \right)^{-k}.$$
The parameter $\mu$ is the mean value of this distribution. The parameter $k$ describes the degree of "clumping", see Elliott (1977). Observing that the variance of the NB $\mu,k$ is $\mu(1+\mu/k)$, the variance to mean ratio:

$$\frac{\text{V}}{\mu} = 1 + \frac{\mu}{k}$$

is often considered as a measure for aggregation.

Whereas $\mu$ is a location parameter of the NB $\mu,k$ which does not reflect its aggregation pattern, there is another which does: the mode. The mode of the NB $\mu,k$ is a value $m\in\{0,1,2,...\}$ with maximum probability; that is

$$P(X=m)=\max\{P(X=x):x\in\{0,1,2,...\}\}$$

From the recursion formula it can be seen that $m$ lies in the interval

$$\left[\mu - \left(1 + \frac{\mu}{k}\right), \mu - \left(1 + \frac{\mu}{k}\right) + 1\right].$$

(Furthermore, if the boundaries of this interval are integers, the NB $\mu,k$ is bimodal. Otherwise it is unimodal. See Elliott, 1977).

If for fixed mean value $\mu$ the parameter $k$ approaches infinity, then the NB $\mu,k$ approaches the Poisson distribution $P\mu$ with parameter $\mu$; that is

$$\lim_{k\to\infty,\mu/\text{fixed}} \left(1 + \frac{\mu}{k}\right)^{-k} \left(\frac{\mu}{\mu + k}\right)^x = e^{-\mu} \frac{\mu^x}{x!}, \quad x = 0, 1, 2, 3, \ldots$$

This limiting relation is reflected in that of the variance to mean ratio

$$\lim_{k\to\infty,\mu/\text{fixed}} 1 + \frac{\mu}{k} = 1$$

and hence in the limiting relation of the intervals containing the modes:

$$\lim_{k\to\infty,\mu/\text{fixed}} \left[\mu - \left(1 + \frac{\mu}{k}\right), \mu - \left(1 + \frac{\mu}{k}\right) + 1\right] = [\mu - 1, \mu].$$

In the case of a $P\mu$ the ratio $V/\mu$ equals 1, in that of a NB $\mu,k$ this ratio is always greater than 1. Therefore the estimate $s^2_{\text{n}/x_n}$ of the ratio $V/\mu$ serves as a criterion for a decision in favour or against $P\mu$.

Roughly speaking, $P\mu$ may be seen as the special case of a NB $\mu,k$ for "$k = \infty". This fact is illustrated in fig.1.

Fig.1: Illustration of the connection of negative binomial and Poisson distribution.

*Fig.1: Illustration de la connection entre distribution binomiale negative et distribution de Poisson.*
Goodness of fit test and estimation of parameters for a NB $\mu, k$

Our decision in favour or against the acceptance of a negative binomial model is based on a $\chi^2$-statistic of the form

$$\chi^2 = \sum_{i=1}^{j} \frac{(O_i - n \cdot P_{\mu,k}(C_i))^2}{n \cdot P_{\mu,k}(C_i)}$$

where $O_i$ and $P_{\mu,k}(C_i)$ are the observed and expected frequencies of suitable classes $C_i \in \{1, 2, \ldots, j\}$ which form a partition of the set $\{0, 1, 2, 3, \ldots\}$ of possible values of the counts $x_1, \ldots, x_n$.

For the evaluation of the expected frequences, however, the parameters $\mu$ and $k$ of the NB$\mu,k$ have to be estimated. As already mentioned, the sample mean $\bar{x}_n$ serves as an estimate for $\mu$. For the estimation of the parameter $k$ we use the following three different methods.

The **moment-estimate** is defined by

$$\hat{k}_n = \frac{\bar{x}_n^2}{\bar{x}_n^2 - \bar{x}_n}.$$

If positive-valued it may serve as an entry for the Newton iteration in order to determine the maximum-likelihood-estimate. A negative value of $\hat{k}_n$ rather indicates to apply a $\chi^2$-test of goodness of fit to a Poisson or even to a logarithmic series distribution (cf. Bliss and Fisher, 1953).

The **maximum-likelihood-estimate** $\hat{k}_{n\mu}$ is the zero of the function

$$f(k) = \sum_{x \geq 0} \left( \frac{A(x)}{k + x} \right) - n \log \left( 1 + \frac{\bar{x}_n}{k} \right),$$

where $A(x)$ is the number of observations exceeding each $x$ (cf. Bliss and Fisher, 1953).

The **minimum-$\chi^2$-estimate** $\hat{k}_n$ is defined as the value $k$ which minimizes the $\chi^2$ statistic above for $\mu = \bar{x}_n$. However, since this estimate may heavily depend on the used classes $C_i$, caution is recommended (cf. Kotz and Johnson, 1985, volume 5).

### 3. RESULTS

In this part two specific data sets of ostracods are described. The first one (Example 1, Fig.2) being a set of fossil material and the second one (Example 2, Fig.5) originates from a living population.

In both cases the data are fitted to a NB$\mu,k$ (Example 1, Fig.3 and Example 2, Fig.6). For the estimation of the parameters the described methods are used. The $\chi^2$-statistic of the goodness of fit test is based on a partition of the following type: two boundary classes with expected frequences $\geq 2$ and a certain number of classes of equal length in between. The total number of classes is approximately $\sqrt{n}$ (the square root of the sample size $n$). For the comparison of the histograms (Example 1, Fig.4 and Example 2, Fig.6) of observed and expected frequences the boundary classes (of unequal length) are excluded.

**Example 1: Fossil ostracod material**

The fossil ostracods used for this study are from Holocene sediments of Mondsee respectively from a core taken at 4.5m depth in the south-eastern part of the lake near the locality See (for the exact location see MON,K1 in Behbehani et al. 1985). The sediments investigated were deposited in a littoral facies during the
Atlanticum about (7000-5000 B.P.). A detailed description is presented in Handl (1989). Samples of 10cc extracted from 85cm and 95cm depth in the core were prepared with H$_2$O$_2$ / H$_2$O 1:3 solution in order to set out the ostracod fossils. The disaggregated sediment was wet sieved through a 200 μm sieve. The residue was deposited in a micropaleontological Fema tray of 9x5cm$^2$. Large detritus particles were eliminated before starting to look for ostracods. The sediment residue was evenly distributed under water with a brush in such a way to cover evenly within a thin layer all the bottom surface, i.e. the 45 quadrats. This procedure was developed by Danielopol and Casale (1988). The ostracods were picked up under a stereo microscope Wild-2 with a pipette and the counts tabulated for each of the 45 quadrats.

The same operation was repeated for samples taken from a core extracted at the site MO-7 (Mooswinkl) at 40m deep in Mondsee (for exact location of this site see Danielopol et al. 1985). The sediments examined were deposited in a deep lake facies and the age should be probably more or less equivalent with those of the previous samples, i.e. Atlanticum.

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Fig.2: The observed numbers of ostracod shells in the cells of a Fema tray.

Fig.2: Nombre de valves d’ostracodes comptées dans les cellules d’un plateau de l’re FEMA

![Graph](image-url)

Fig.3: Comparison of the histograms of the observed (dotted) and expected frequencies for the data from Fig.2.

Fig.3: Comparaison entre les histogrammes des fréquences comptées (pointillés) et des fréquences prévues sur les données de la fig.2.
Parameter estimation and $\chi^2$-goodness of fit test:

Estimate for $\mu$:
Sample mean $\bar{x}_n = 15.889$

Estimates for $k$:
1. Moment estimate
\[ \hat{k}_n = 7.254 \]
2. Maximum-Likelihood estimate
\[ \hat{k}_n = 7.792 \]
3. Minimum-$\chi^2$ estimate
\[ \hat{k}_n = 7.400 \]

Sample variance $s_n^2 = 50.692$

Sample variance to sample mean ratio $s_n^2 / \bar{x}_n = 3.190$

Observed $\chi^2$-value = 0.608 (degrees of freedom = 3)

Example 2: Living Cytherissa lacustris

Living Cytherissa lacustris were collected from Mondsee at the site MO-7 (see Danielopol et al. 1985 for exact location) at 20m and 40m deep, using a multicorer Rinimuco, (Danielopol and Niederreiter, 1990). Six sampling tubes (units) fixed equidistantly on a circle with 60cm diameter collect simultaneously sediment and benthic organisms. The multicorer sampling was replicated four times at slightly different located sites within an area of 1-2m$^2$ of the lake bottom. The sites have been chosen randomly. The 24 sampling units from Fig.5 have been collected from one depth in October 1985. The upper layer of sediment (the first two centimeters) have been extruded and sieved through a 200μm sieve. The residue was examined for ostracods. From each sampling unit we counted the living Cytherissa lacustris specimens.
Statistical distribution of ostracoda

12 19 12 10
7 7 8 0
17 16 8 5
21 17 8 7
5 10 3 4
1 15 2 13

Fig. 5: Data from 4 samples using a multicorer Rinimuco: every column represents the counts of living Cytherissa lacustris specimens in the six tubes of the multicorer.

Figure 5: Données de 4 échantillons prélévés avec le multicarottier Rinimuco: chaque colonne représente le comptage d'individus vivants de Cytherissa lacustris dans les 6 tubes du multicarottier.

Fig. 6: Comparison of the histograms of the observed (dotted) and expected frequencies for the data from Fig. 5.

Fig. 6: Comparaison entre les histogrammes des fréquences observées (pointillés) et des fréquences prévues pour les données de la figure 5.

Fig. 7: Comparison of the histograms of the observed (dotted) and expected frequencies for the classes of equal length used for the for $\chi^2$-test goodness of fit.

Figure 7: Comparaison entre les histogrammes des fréquences observées (pointillés) et des fréquences prévues pour des classes de même taille utilisées pour le test $\chi^2$ de fiabilité.
Parameter estimation and $\chi^2$-goodness of fit test:

Estimate for $\mu$:
Sample mean $\bar{x}_n = 9.875$

Estimates for $k$:

1. Moment estimate
   \[ \hat{k}_n = 4.082 \]

2. Maximum-Likelihood estimate
   \[ \hat{k}_n = 3.029 \]

3. Minimum-$\chi^2$ estimate
   \[ \hat{k}_n = 3.05 \]

Sample variance $s_n^2 = 33.766$

Sample variance to sample mean ratio $\frac{s_n^2}{\bar{x}_n} = 3.419$

Observed $\chi^2$-value = 2.929 (degrees of freedom = 2; observed level of significance = 0.2312)

4. DISCUSSION

Goodness of fit with respect to a Gamma distribution

The continuous analogue of the negative binomial distribution is the Gamma distribution. Hence we may (for sufficiently large $\mu$) try to fit our data also to a Gamma distribution. Although the following example indicates that it may be reasonable to do so, we did not investigate this in detail so far.

![Histogram and Gamma distribution](image.png)

Fig.8: Comparison of a histogram for the data from Example 1, Fig.2 with the density of the fitted Gamma distribution.

Figure 8: Comparaison entre les histogrammes pour les données de l'exemple 1, fig.2 avec la densité de la distribution Gamma.
The Gamma distribution with mean value $\mu>0$ and exponent $k>0$ is defined by the density function

$$f(x) = \frac{k^k}{\mu^k \Gamma(k)} x^{k-1} e^{-\frac{x}{\mu}}, \quad x > 0,$$

where $\Gamma(k)$ is the Gamma function, e.g. Kotz and Johnson (1985, volume 3).

**Determination of the sample size for the subsampling strategy**

An important practical request for the analysis of ostracod data is to keep the sample size sufficiently small. In the case of the fossil ostracods, for instance, the effort of time and work is to high to count out all 45 cells of a Fema tray. Hence it is desirable to take a sample of size smaller than 45. Danielopol and Casale (1988) used a stratified sample of size 15 with 8 peripheral cells and 7 central cells. For a subsampling strategy in connection with Example 1, the specific problem is to give both an estimate and a confidence interval for the total number of ostracod shells in the Fema tray on the basis of a subsample of an appropriate sample size. Our considerations and computer simulations suggest that a sample size of about 15 seems to be necessary to meet the assumptions for the construction of such an interval. In addition, however, the sample size must be determined with respect to the required precision, that is the relative length and the level of the confidence interval, cf. Krebs (1989). For a detailed description of the construction of confidence interval for $\mu$ both for $P_\mu$ and $NB_\mu,k$ we refer to Krebs (1989).

**Final remarks**

The senior author is preparing a computer program written in Turbo Pascal for the negative binomial model. It will be sent at request to those colleagues who are interested in estimating the parameter $k$ and in using the $\chi^2$-goodness of fit test. Similar programs written in Fortran (Krebs, 1989) and Basic (Ludwig and Reynolds, 1989) already exist.

In conclusion we hope that the present contribution and the available computer programs will encourage more ostracodologists to use the presented mathematical model in their research.

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NEW SAMPLING EQUIPMENT AND EXTRACTION METHODS FOR MEIOBENTHIC ORGANISMS.

NOUVEL EQUIPEMENT DE PRELEVEMENT ET METHODES D'EXTRACTION DES ORGANISMES MEIOBENTHIQUES

by

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Key-Words: Sampling equipment, meiofauna, benthic organisms, ecology, micropaleontology.
Mots-Cles: Equipement d'échantillonnage, meiofaune, organismes benthiques, écologie, micropaléontologie

Abstract:
Two types of multiple corers for the sampling of the benthic fauna are described. Their way of operation and efficiency are reviewed. Laboratory methods for the extraction of the sediment from the corer and the ostracods from the sample are presented.

Résumé:
Deux types de multicarottiers destinés à l'échantillonnage de la faune benthique sont décrits. Leur mode d'action et leur efficacité ont été améliorés. Les protocoles de laboratoire pour l'extraction du sédiment du carottier et des ostracodes du sédiment sont présentés.

1-INTRODUCTION

Our knowledge of the ecology of benthic organisms living in lakes is less advanced than of planktonic ones. McIntosh (1985) identified three difficulties which impeded the advancement of the ecology of limnic organismic communities i.e. difficulties dealing with sampling methodology, with the taxonomical identifications of the organisms and with accurate sampling programmes which could encompass the tremendous environmental variability. When we started in 1982 the study of the benthic ostracods of Mondsee, we were confronted immediately with these problems. One of us (D.L.D.) invested part of his research time in taxonomical identification of Mondsee ostracods and in effective ways to sample these microcrustaceans. We discovered that the Ekman grab and the Kajak corers were the only sampling devices existing for the benthic fauna at the laboratory in Mondsee at that time and were inefficient for intensive quantitative sampling programmes. Both sampler types did not always penetrate into the sediment, did not retain the sediments when lifted to the boat and the processing time of the positive samples was too long. Another persistent problem when sampling benthic fauna was the fact that we did not know the exact position of the device on the bottom of the lake. Especially for replicate sampling from a fixed position one would return to areas already disturbed by previous actions. To encompass these difficulties one of us (R.N.) constructed in a first stage a modified Kajak corer, much similar to the one described by Newrkla (1983) (see figure in Danielopol et al., 1990), and later on developed two new types of multiple corers based on this model.

The aim of this paper is to briefly describe the multiple corer devices we used in Mondsee, their way of operation and their advantages as compared to other similar sampling equipment. Here we also present a
Fig. 1 - The Rinimuco corer, general view. A - before sampling. B - extraction of the loaded tubes.

Fig. 1 - Carottier Rinimuco, vue d'ensemble. A - avant échantillonnage. B - extraction du tube rempli.
simple device we use for the extraction of the sediment from the sampling tube and some comments on the techniques to extract ostracods, especially *Cytherissa lacustris*, from the cored material.

It is maybe necessary to emphasize that in the last fifty years research groups working on the ecology of the benthic organisms split depending on the sampling and processing methods they use. Benthic fauna can be divided into three groups: the macrofauna - animals retained by a sieve with 1 mm mesh aperture; the meiofauna - small animals which are collected on fine sieves between 100 and 40 μm mesh and the microfauna - animals which being very small pass through the 40 μm sieves.

It is interesting to note that for the meiofauna research which is dealt with mainly by zoologists and ecologists micropaleontology is the closest equivalent branch within the earth sciences activities. Strong parallels exist in the way the two research directions developed, namely their strong dependence on sampling and processing methods for small organisms, living or fossil.

### 2. THE MULTIPLE CORER RINIMUCO (fig. 1 and 2).

#### 2.1. PRINCIPLE

This is a gravity sampler with six modified Kajak corers fixed on a metal circular framework. The closing system of the core tubes can be simultaneously operated for the six samplers. For the principle of construction and functioning of our modified Kajak corer one can see Newrkla (1983).

#### 2.2. DESCRIPTION

Figure 2 shows a cross section through the Rinimuco corer. One notices that, as compared to the Newrka modified Kajak corer, one of us (R.N.) developed new solutions for the closing system of the sampling tubes (see blow). The metal framework of the corer is formed by a 50 cm diameter ring on which are equidistantly fixed six modified Kajak corers (mK). Between them are fixed six metal weights (20) which help to stabilize the multiple corer on the lake bottom. The metal ring is connected by horizontal and oblique branches (4) to the vertical cocking system (1-10). This latter is formed by a tube (5) which moves in a guided shaft (3) which latter is connected to the mK corers by two external rods (7) fixed on the upper side with a ring (8). The lower part forms the locking mechanism (6, 9, 10), in open position, for the six mK corers. The rod 9 is fixed to the ridge 6; when this is

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*Fig. 2 - Diagram of the Rinimuco corer in cross section (additional explanations in text).*

*Fig. 2 - Schéma du carottier Rinimuco en coupe (explications complémentaires dans le texte).*
Fig. 3 - The Mercedes-Benthos corer. A - general view of the sampler and the operation platform. B & D - the sampler and the videocamera. C, E, F - the sampler operating at 40 m depth in Mondsee (arrow points out the location of a previous sampling site, additional explanations in text).

Fig. 3 - Carottir Benthus-Mercedes. A - vue d'ensemble du carottir et plate-forme de travail. B & D - carottir équipé avec une videocamera. C, E, F - carottir opérant par 40 m de profondeur dans le Mondsee (le flèche indique l'endroit d'un site d'échantillonnage précédent ; (explications complémentaires dans le texte).
lowered the spring 10 releases the conical valve (11) of the corer. On the upper part of the vertical tube 5 a mobile weight messenger (2) and a handle (1) are positioned.

The modified Kajak corer (mK version Niederreiter (11-19)) is formed by an upper conical valve with a rod (11) which moves through a guide plate (16). On the valve the pin 12 holds extended the ball valve 17 by a rope (13). The sampler tube 19 is tightened to the head collar 14 through the rubber ring 15. The conical valve 11 fits in the funnel-shape collar (14). The mK closing mechanism, the collar and the guide ring 18 (this latter being a metal weight which stabilizes the corer) are connected to each other by four rods (7). The total weight of the corer is about 60 kg and it has a height of 180 cm. The six sampling Plexiglas tubes are 50 cm long and 6 cm in diameter. The sampling area of a tube is 27.3 cm² and the whole area for six sampling units is 0.28 m².

2.3. OPERATION

The corer is lowered to the bottom of the lake from a boat platform. For cocking the system and handling the core tubes we built a support on which the corer is held in a fixed position (fig 1 AS). The support has six mobile plates which can be lowered and the core tubes are fixed to the collar from below (fig 1 B). The Rinimuco device once loaded with the tubes and cocked i.e. the upper valve 12 and the ball catch are in open position, is lowered slowly to the bottom of the lake with the help of a solid cord. A controlled slow descent will reduce the potential bow wave once the corer penetrates into the sediment. When the core Plexiglas tubes are in the sediment (in our case the penetration depth into deep lake muddy sediments is about 30 cm) the messenger 2 is released and kicked onto ring 8; this latter releases rod 9 which frees the conical valve 11 which closes tightly the upper part of the core tube. Pin 12 being lowered cord 13 and ball 17 become free too. By lifting out the corer the tube 5 connected to the handle 1 moves up into the guide tube 3 and brings simultaneously the six balls into the closing position (fig 1 B) which hinders the cored sediment to escape outside during the uplift journey of the device. The efficiency of this corer concerning the sampling of *Cyllherissa lacustris* from the Mondsee sediments is presented by Danielopol et al. (1990).

2.4 THE ADVANTAGES OF THE RINIMUCO CORER

Simultaneous sampling is achieved and the area sampled is exactly known (i.e. within one square meter scale). As compared to the original Kajak-one tube device (see description in Kajak, 1971, and discussion in Brinkhurst, 1974) the multiple corer is much more stable having the gravity center much lower. This allows to take samples where the Kajak, Kajak-Brinkhurst or Kajak-Newrkla samplers do not effectively work i.e. in areas with steep underwater slopes (this is the case in Mondsee e.g. the site Mo-7 between 20 - 50 m depth, see Danielopol et al., 1990) or in areas with very strong water currents e.g. the large streams like the Danube in Austria (Herzig, pers.comm. to D.L.D.) For this latter situation the Rinimuco device performed very well (Herzig, 1990). The ball catcher works effectively not only in shallow water areas like in Fenchel’s model (details in Fleeger et al. 1988) but in deep lake environment (like the Mondsee between 40 and 65 m depth), too.

The Scottish Marine Biological Laboratory corer which cores well in deep sea sediments (McIntyre and Warwick, 1984) has the disadvantage of being very heavy and it needs the gear-handling facilities of a large vessel (Fleeger et al., 1988). Similar difficulties had Newrka and Dudjiski with a multiple corer developed at the Limnological Institute in Vienna and which could not effectively be operated from a boat (Dudjinski, pers.comm.). The tom-tom corer (Chandler et al., 1988) uses shorter core tubes (15 to 25 cm length) and has a complicated stabilizing (trigger) plate which has to be regulated depending on the bottom sediment characteristics. It has no external core catcher. Due to these characteristics it seems that this corer will perform less well at deeper depths like our sampling sites in Mondsee (between 12 and 65 m depth).

Finally, one should note that our modified Kajak multiple corer has a much simpler mechanism which can be operated from remote distances as compared to the Jenkin surface-mud sampler, in use for about 50 years at the Freshwater Biological Association in Windermere (Ohnstad and Jones, 1982).
3. THE MERCEDES BENTHOS MULTIPLE CORER (figs. 3, 4)

3.1. PRINCIPLE

This is a corer with the possibility of being used between 3 and 12 modified-Kajak (mK) corers simultaneously. The position of the tubular sampler is changeable. The new modified-Kajak corer type allows to use Plexiglas tubes with different diameters and lengths. The corer is equipped with a submersible videocamera and two electric lamps powered by a battery unit. With this videocamera the operator can from above choose the sampling site and monitor the sampling operation.

3.2. DESCRIPTION

Figure 3 A shows a general view of the Mercedes-benthos corer (Mb) with the line going to the tripod's winch (Tw). The corer (fig 3 B) is formed by a horizontal triform framework on which are fixed the mK corer units and a vertical stem on which are located the videocamera (V), the battery unit (B) and the electric lamps (L). The position of the videocamera and the electric lamps is changeable (e.g. see their position in Figs. 3 B and D). The same applies for the Kajak corer units (e.g. compare their position in Figs. 3 B and C).

Figure 4 shows diagrammatically the main details of the new modified Kajak corer and of the vertical stem (6) of the metal framework. The mK unit is fixed with a collar (18) to the horizontal branch (5) through the mobile rod (7) and the screw of the lever (4). The length of the branch (5) is 60 cm which can be extended. The mK corer has an upper cap unit in plastic (17) in which stays the core tube (8) and a free metal valve (14). This latter one can move in the cap chamber allowing the water to penetrate through the windows (15) and to circulate through the open tube (8) when the Mb corer is lowered into the water. In closed position the valve (14) tightly seals the upper part of the cap's chamber due to a rubber ring (13). The Plexiglas tube of the corer (we used tubes with 6 cm diameter and 50 cm length) can be tightly fitted to the cap's corer through an o rubber ring and the interchangeable adapter collar (29). The fixation of the tube to the collar is done through the lever (4).

The adapter collar (20) can be changed and one can use other collars to be fitted with tubes with smaller diameters (e.g. 5 cm diameter). The position of the core tube is also fixed through a short guide tube and two lateral rods (19). The lengths of these latter can be modified by screwing on additional (or deleting) segments depending on the length of In the open position the ball catcher (11) is fixed to the pin (12) by two cords (9, 10), one being elastic (9), and an interchangeable line (3) to the hook (2). This latter moves through the guide ring (16). The messenger (1) lowers the hook (2) and frees the line (3) when the outside rope is no stretched anymore by the winch.

The Mercedes-benthos corer with three core tubes, the videocamera and the electric components weighs about 40 kg.

We used a videocamera Sony (type AVC-D5CE) enclosed in a metal box with Plexiglas windows. The camera can be teleoperated from outside with a cable of 80 m length, the image is received on a TV-monitor and a videorecorder.
3.3 OPERATION

The corer is operated from a boat platform (fig 3 A). It is lowered slowly with a manual winch and its position above the bottom is controlled with the videocamera. The images are received by a TV-monitor placed in the dark space of the hut (see fig 3 A). The images received were recorded on a videorecorder also placed in the hut. The electric supply for the videorecorder and the TV-monitor is produced by a motor-electro-aggregate. Once the sampling site is located (fig 3 E) the multiple corer is slowly penetrating into the sediment minimizing the sediment bow wave (fig 3 F). By removing the corer from the sediment the elastic cord (9) (fig 4) retracts the ball and automatically closes the tube from below (Figs. 3 B, C). The valve (14) (fig 4) during the lowering of the corer is pressed upwards by the water flowing through the core tube from below. Once the corer tube penetrates into the sediment the valve returns to its closed position and will remain tightly fixed on the o ring (13), pressed by the water column during the uplift movement of the sampler.

With the help of the videorecorder we can reconstruct the spatial position of the various sampling sites and therefore describe accurately the origin of the spatial distribution of the organisms collected.

The incorporated battery allows 4 hours to illuminate the underwater sites with the two lamps. The light can be operated from above.

3.4. COMPARATIVE DATA OF THE MERCEDES-BENTHOS CORER AND THE RINIMUCO SAMPLER

The main innovation of the former multiple corer lies in the incorporation of the submersible videocamera and the electric system to illuminate the sampling area. Due to this innovation we discovered an unexpected diverse lake bottom and we could choose the places relevant to our sampling programme. The second innovation as compared to the previous multiple corer is the new design of the metal framework and of the Kajak units. The corer is very flexible allowing the utilization of different types of tubes depending on the lake topography and sediment texture or research requirements. The closing system of the new modified Kajak sampler is simpler, easier to handle and increases the chances of getting undisturbed sediments from deep lake sites. Finally, one should note that the new benthos sampler which incorporates a videocamera is as successful in sampling benthos from deep lake sites as the more expensive and complicated devices deployed from manned submersibles. For such an example see Boyer and Hedrick (198) and their reports on their Lake Superior Dive Project.

The advantage of the Mercedes-benthos multiple corer as compared to the sampling and photographing the sediments by divers is due to its possibility to have access to deeper sites where the divers have difficulties to go or for which they need special and expensive diving equipment.

4. LABORATORY METHODS FOR THE EXTRACTION OF THE MEIOFAUNA.

4.1. PRINCIPLE

One of the difficulties of quantitative ecology of meiobenthos is the efficient extraction of the fauna from the cored sediment. Because of its small size one is confronted with a tedious effort to process large sediment samples as those collected by box grabs or large tubular corers. Another problem is the sieving of fine grained sediments because of clogging of the sieves, finally large numbers of animals require much time.
to be picked out from the sample residue. Here we present several solutions: a) in order to reduce the sediment volume to relevant layers we used a sample extruder device with a horizontal sectioning plate. For paleolimnological purposes we used presectioned (halved) smaller tubes which can be opened in the laboratory and the sediment easily cut out making it possible to isolate thin sediment layers with round plates; b) a double side washing system of the sediment sample in the sieve (in a closed vessel from inside and simultaneously the sieve from outside through the net) avoids the clogging of the sieve; c) living ostracods like *Cytherissa lacustris* are first killed in diluted alcohol an then sorted through combined ellutriation and decantation methods.

The method works well because most of the animals die having the valves open and they float on the surface of the diluted alcohol solution. The small juveniles are better removed by ellutriation while the adults and the last juvenile stages, being heavier, can be better extracted by decantation and by picking out under the stereomicroscope from the heavy sediment fraction.

### 4.2. Description

a) The collection of the surficial layer. Figure 5 A shows a funnel (Fu) which can be fixed on the upper part of the sampler tube (Tu). The funnel is tightened to the Plexiglas tube with an o ring. The sediment is extruded from inside with a piston (Pi). The required sediment layer is sliced horizontally with a thin plastic plate which is introduced laterally through a slotted area. The plate when traversing the funnel cuts the sediment and closes the bottom of the funnel. The sediment then is transported to the sieve to be washed.

For paleolimnological researches presectioned (halved) core tubes (Tu) are fixed (fig 5 B) with an adhesive tape (At). An upper ring (Ad) remains uncut to maintain the rigidity when the tube is fixed to the nK sampler. The upper ring (Ad) is tightened to the halved core tubes also with adhesive tape. In the laboratory the water overlaying the sediment sample is removed, the tape is cut and the upper ring (Ad) removed. Then it is sliced in two halves which can easily be separated. With thin round plastic plates one can isolate laminae of small volume which can be easily transported to the sieve.

b) The double side washing system of the sample - A normal sieve with 20 cm diameter and 20 cm height is closed with a cover through which penetrates a rotatory sprinkling tube which moves horizontally through the out-coming water alternatively on the two opposite halves. From below the sieve the sediment sample is washed, too.

c) The extraction of ostracods, especially *Cytherissa lacustris*, from the sediment residue - Because living *Cytherissa lacustris* have a high specific gravity (see Löffler, 1990) animals behave hydrodynamically like coarse sand grains. The extraction of ostracods from high amounts of sediment residues can be facilitated, if one adds a diluted solution of alcohol. Ostracods, especially *Cytherissa lacustris*, are killed slowly and die with the valves open. By ellutriation the juveniles with a smaller weight and with a larger
Sampling and extraction of meio-benthos

surface/volume ratio float and can be recuperated with the supernatant liquid after stirring the sample. The heavier ostracods e.g. the adult and last instars of *Cytherissa lacustris*, remain with the coarse sediment residue and will be picked up under a stereomicroscope. The Rose Bengal staining method (see e.g. in Pfankuche and Thiel, 1988) can help effectively in the separation of the freshly killed ostracods from the coarse sediment grains. Note that the ellutriation-decantation method described here does not work with fossil ostracod material.

4.3. ADVANTAGES OF OUR LABORATORY METHODS

Rutledge and Fleeger (1988) showed that subsampling in tubular cored sediment produces significant biases, therefore, they suggest to use small volumes of sediment which are extracted form the whole surface of the tubular sampler. The two methods to isolate thin slices of sediment represent a simple solution to avoid the biases noted by Rutledge and Fleeger (op.cit.).

The double washing system through rotatory sprinkling has as compared to the classical simple wash side system the advantage to speed the sieving process and to avoid too strong water flows on the sediment which normally destroys the minute and delicate organisms.

The flotation system in diluted alcohol solution was tried first by Prof., H.Löffler (pers.comm. to DLD). The combination of the ellutriation with the decantation method gives for ostracods with high specific gravities better results than the simple ellutriation as used with the Boisseau method (see for this latter method Pfankuche and Thiel, 1988). We found that for *Cavernocypris subterranea* from coarse sandy residues the efficiency of the extraction was poor because the ostracods tend to close the valves when the water turbulence in the Boisseau vessel is increased and they are not eliminated selectively from the sand grains. *Cytherissa lacustris*, especially the last instars and the adults, behaves more or less like *C. subterranea*. For that reason they are not satisfactorily eliminated by simple flotation or ellutriation methods (Geiger, pers.comm. to DLD).

5. CONCLUSIONS

The equipment and the techniques described here represent a substantial progress as compared to those we used at the beginning of our work at the benthos laboratory in Mondsee. They allowed the development of successful sampling programmes (see Danielopol et al., 1990).

We consider the Mercedes-benthos multiple corer one of the most performant samplers actually available for benthos research. Its attractiveness comes from its high flexibility and from the possibilities to further improve it with the addition of electrodes which could simultaneously measure in situ various sediment parameters.

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Laboratory studies on core sampling with application to subtidal meiobenthos collection.
THE MEASUREMENT OF DISSOLVED OXYGEN IN LACUSTRINE SEDIMENTS. LABORATORY SET-UP AND TECHNIQUES

MESURE DE L'OXYGÈNE DISSOUS DANS LES SEDIMENTS LACUSTRES. PROTOCOLES ET TECHNIQUES DE LABORATOIRE.

by

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Abstract

The equipment and the technique of measuring dissolved oxygen in lacustrine sediments with a cathode-type microelectrode, Sigma Instruments Berlin, is described in detail. The performance of this electrode is compared with that of a Clark-type microelectrode produced by Micro-Sense Inc.

The micro-heterogeneity of the oxygen distribution in the sediment is presented for three types of sediments. Suggestions concerning further experiments of the cathode-type electrode for lacustrine sediments are presented (e.g. the need for the improvement of the calibration in the zero-oxygen zone).

Résumé

L'équipement et la technique de mesure de l'oxygène dissous dans les sédiments lacustres à l'aide d'une microélectrode de type-cathode fabriquée par Sigma Instruments, Berlin sont décrits en détail. Les performances de cette électrode sont comparées à celles de la microélectrode de type Clark fabriquée par Micro-Sense Inc.

La micro-hétérogénéité dans la distribution de l'oxygène dans les sédiments est étudiée sur trois types de sédiments. Des propositions concernant des expériences futures avec la microélectrode de type-cathode sont présentées (p.ex. la nécessité d'améliorer la calibration dans la zone anoxique).

1. INTRODUCTION

The description of the spatial distribution of the dissolved oxygen of interstitial water from fine grained sediments is of paramount interest to both biologists and geochemists. The former are interested in understanding the sediment environment in which many organisms commonly live or lived in the past. This is also the case with us when studying the ecology of Cytherissa lacustris. The geochemists are interested in describing the dynamics of chemical processes occurring in the sediments which in most cases depend on the oxygen situation of the microenvironment.

The measurement of dissolved oxygen in undisturbed finely grained sediments poses a number of difficulties. For instance, it is complicated to either extract enough interstitial water from the sediment in order to measure the oxygen concentration with the classical Winkler method or it is impossible to measure with the standard polarographic oxygen sensors (POS) in undisturbed sediments. The most common oxygen electrode type used in aquatic ecology is the Clark-type. The measurement of dissolved oxygen with the POS is based on the diffusion of the gas through a membrane to a reducing cathode electrode. In most of the commercially available POS the size of the electrode is very large (from several millimeters to one centimeter diameter) and permanent stirring of the water is necessary.
Fig. 1: Equipment for measuring dissolved oxygen with microelectrodes. A - Gas-mixing pump. B - Aquarium with constant oxygen supply and permanent water circulation (The Innsbruck model). C - The laboratory set up for measuring oxygen in sediments: 1 - thermostatic aquarium with constant oxygen supply, 2 - oxygen microelectrode (cathode-type), 3 - reference electrode, 4 - oxygen polarographic electrode (Clark-type), 5 - micromanipulator, 6 - millivoltmeter and supplier-converter, 7 - sediment core into the "Niederreiter chamber", 8 - Faraday cage.

Fig. 1 : Equipement pour mesurer l'oxygène dissous avec des microélectrodes. A - Pompe pour le mélange des gaz. B - Aquarium avec approvisionnement constant en oxygène et circulation permanente d'eau (Innsbruck model). C - Equipement de laboratoire pour mesurer l'oxygène dans le sédiment: 1 - aquarium thermostatisé avec approvisionnement constant d'oxygène, 2 - microélectrode à oxygène (type-cathode), 3 - électrode de référence, 4 - électrode à oxygène polarographique (Clark-type), 5 - micromanipulateur, 6 - millivoltmètre et convertisseur-alimenteur, 7 - carotte de sédiment dans la "chambre Niederreiter", 8 - cage de Faraday.
Measurement of oxygen in sediment

Due to this situation one can not get punctual measurements in situ within the sediment without completely disturbing the sediment texture.

Revsbech (1983), Baumgärtl and Lübbers (1983) described polarographic oxygen microelectrodes which having a microscopic membrane and very thin cathode tips do not need stirring. Therefore, they are ideal for measuring the dissolved oxygen occurring in the interstitial water of the finely grained sediments. The equipment and the set-up for measuring oxygen with this cathode-type microelectrode will be here presented. The interest of this presentation is two-fold.

First, the commercial equipment being very expensive, we present here simple and cheaper solutions. Secondly, we present data on the functioning of the cathode-type microelectrode and on the difficulties we discovered during the work with these sensors, especially when working in lacustrine sediments. This is especially important, because up to now the oxygen sensitive microelectrodes have been used mainly in marine ecology (review Revsbech and Jørgensen, 1986). One of the difficulties with the cathode-type microelectrode noted by Revsbech (1983) is that water rich in Mg- and Ca-ions and low in Na- and K-ions produces less stable signals in this type of electrode. There is little experience with the usage of the oxygen microelectrodes in lacustrine sediments (Sweerts and Cappenberg, 1988; Sweerts et al., 1989; Geiger 1990) and our work can be of help to those interested in using this new and promising technology.

In the following we present the set-up we used in the laboratory during the "Cytherissa project". There are two main components: a) the electrodes and the measurement instrumentation, and b) the aquarium and its accessories. Further, we shall present the way we prepared the sediment samples for oxygen measurements and the technique of the calibration of the microelectrodes and subsequent oxygen measurements.

2. THE ELECTRODES AND THE MEASUREMENT INSTRUMENTATION

For the present set-up we used both oxygen cathode-type microelectrodes with a reference calomel electrode (the latter from Ingold Inc.) as well as combined (Clark) oxygen microelectrodes. In the former case, we tried the following products: oxygen microelectrodes from a) Diamond Electro-Tech Inc., Ann Arbor, Michigan; the glass type 723 and the metal needle type 760; b) from Sigma Instruments, Berlin, i.e. a metal needle electrode with a diameter of 0.35 mm and teflon-membrane. The gold cathode has a diameter of 0.012 mm and it is fixed obliquely. As compared to the Diamond electrodes the Sigma one gave better results in our experiments and we used it extensively. c) from Micro-Sense, Ramat Gan, Israel i.e. a combined glass (Clark-type) microelectrode with a distal tip of 0.1 mm diameter. In this microsensor the cathode is bathed in an electrolyte solution in which a reference electrode Ag/AgCl is immersed (Revsbech and Jørgensen, 1986). The combined oxygen microelectrode could be used only for a short period of time, because of the fragility of the glass structure. We found that the Sigma needle electrode is much more robust and has the advantage that the membrane can be replaced by the supplier. The disadvantages of this electrode-type will be discussed in the next sections.

The electrical signals of the microelectrodes were converted in pO2 (mass concentration of oxygen, mg/l) by calibration against an oxygen Clark-type electrode with a stirrer from Orbisphere, Geneva (model 2112 with the sensor type nr. 2120). This is one of the most precise oxygen electrodes commercially available with a minimal drift of less than 1% per month.

The cathode-type microelectrode is polarized at about 0.75 V versus the calomel reference electrode and the current originating from the reduction of the oxygen at the gold surface is proportional to the oxygen partial pressure in the surrounding medium (Revsbech & Jørgensen, 1986). The very low current on Pico A can be measured with a Keithley Picoammeter which is expensive or can be transformed in millivolts with a supplier converter device and measured with a normal millivoltmeter. We used a converter constructed by Dr.F. Kohl (Technical University, Department of Electrotechnic, Vienna) which is much cheaper than the
Keithley digital multimeter instrument. Supplier converters are offered with a normal pH-meter also by Micro-Sense (Ramat Aviv, Israel). The electric current to the cathode is supplied by a 9 V battery inserted in the converter. The Orbisphere electrode was used with an Orbisphere instrument model 2607.

Because of the very low electric signals produced by the electrodes one has to protect the measuring circuits from surrounding electric noises of the laboratory with a Faraday cage. For a general view of the electrodes and their accessories see fig. 1 C and 2.

3. AQUARIUM AND ACCESSORIES

Because dissolved oxygen concentration is dependent on the water temperature and because the measurements of a sediment core takes several minutes one has to use a thermostatic water bath when working in the laboratory. The commercially available ones are expensive and have the disadvantage of being of metal. From the lateral side one cannot observe well when the point of the microelectrode arrives closely at the sediment surface. Therefore, one of us (R.N.) developed a glass-aquarium in which one can maintain the water at constant temperatures and stable oxygen concentrations for long periods of time. The principle of the aquarium is based on a model developed at the university of Innsbruck by Dr. E. Gnaiger and his associates. This latter (fig. 1 B) has an aquarium pump which permanently circulates the water and allows the maintenance of constant oxygen concentrations provided by a gas-mixing-pump (fig. 1 A).

Our aquarium (fig. 1 C, 2 and 3 A - D) has two compartments: a lower one in which water from a cooling water system is steadily circulated (with a pump) and maintains the constant temperature in an upper compartment (the thermostatic aquarium) where water has constant dissolved oxygen concentrations, too. The thermostatic aquarium has about 4 l volume, the dimensions are 10 (h) x 26 (l) x 16 (b) cm for the thermostatic (upper) compartment and 4 x 26 x 16 cm for the cooling (lower) compartment. The cooling compartment in the aquarium has the shape of a labyrinth (fig. 3 C, D). The thermostatic compartment of the aquarium is covered with a plate in which enough space is allowed for the movement of the oxygen cathode microelectrode (see number 4 in fig. 3 B) as well as places for the fixation of the other electrodes and gas tubes (fig. 3 B, C). The cooling water is produced by a cooling aggregate in a large aquarium (50 l) provided with a thermoregulator (number 5 in fig. 2). The transmission of the water in the upper aquarium is done with a small pump (fig. 2). Two other important accessories to the thermostatic aquarium are the gas mixing pump and the micromanipulator. We are using a W. östhof SA 27/3 gas mixing pump (fig. 1 A) than can mix in several combinations nitrogen and air an/or oxygen. The prepared gas mixture is further distributed into the aquarium (fig. 2, 3 A). The micromanipulator is hand-driven and was built by one of us (R.N.), in
Mondsee (fig. 1C). It has a depth resolution of 0.01 mm and can be moved on both vertical and horizontal axes.

In front of the aquarium we fixed a stereo-microscope Wild with which we can observe the position of the oxygen cathode-microelectrode and the sediment peculiarities in the "Niederreiter chamber" (see below). The general circuits of our set-up of measuring dissolved oxygen in sediments is presented synthetically in figure 2. A strip-chart recorder was used either for registering the microelectrode signals (see Geiger 1990) or to register the long-term stability of the oxygen and the temperature measured with the Orbisphere POS.

4. THE PREPARATION OF THE SEDIMENT SAMPLE

The interest of measuring dissolved oxygen in sediments with microelectrodes stems from the observation that steep gradients exist in the upper few millimeters of the sediment exactly in the layer where most of the biological activities occur. The prerequisite for an oxygen measurement in such sediments is to have samples with undisturbed sedimentological structures. There are two possibilities to achieve that. The easiest is to collect samples from shallow water sediments and transport them to a nearby laboratory (e.g. Revbech et al., 1980, 1981; Sweerts et al., 1989). It is more difficult to obtain undisturbed sediments from deep water sediments, because the possibility of changes of the sediment texture increases during sampling, recovery and the further transport to the laboratory. Therefore, there are only few studies of such sediments (e.g. Jørgensen and Revsbech, 1989). An alternative for these difficulties is that of Reimers et al. (1984) who developed a set-up for measuring oxygen of deep sea sediments in situ.

In our case we were interested in measuring the oxygen concentration of the sediment especially from the profundal zones of the Mondsee where during the summer stagnation low oxygen concentrations develop in the overlying water (see Danielopol et al., 1990 and Geiger, 1990).
The samples were collected with a Kajak corer modified by Niederreiter (details in Danielopol and Niederreiter, 1990). The perspex tubes have a 5 cm diameter and 50 cm length. Sediment cores of about 30 cm length were brought in a stative and (in some of the cases) in a thermostatic box from the lake to the laboratory in order to avoid sediment disturbance and strong temperature changes. The sediment is extruded from the tube with a piston (fig. 4 B). The first 5-7 cm are pushed in the short tube of 10 cm length which at the upper side has a removable cover and a valve. This is the so-called "Niederreiter chamber". The surficial layer of sediments is gently transferred to the "Niederreiter chamber" and the overlaying water is eliminated through the open valve. In this way the surface of the sediment remains, in most cases, undisturbed. Once this operation is finished a thin round plate cuts the sediment between the initial tube and the chamber. The bottom cover is applied on the plate. The upper valve is then closed and the sediment completely enclosed in the chamber is transported to the thermostatic aquarium.

Before the installation of the chamber in the aquarium one has to open the valve and to remove the upper cover. The sediment located in the "Niederreiter chamber" is left in the aquarium several hours in order to equilibrate the oxygen concentration and the temperature to the surrounding medium.

5. CALIBRATION OF THE CATHODE-TYPE MICROELECTRODE, OXYGEN MEASUREMENTS, COMPARATIVE DATA

The success of the usage of the oxygen microelectrodes depends on how well we can calibrate them as well as on their response time and stability during the measurements.

In our case the calibration curve being linear we took as upper calibration point the value of the oxygen concentration of the thermostatic aquarium and a zero oxygen value that we obtained in a closed circuit of a miniaquarium (fig. 4 A). Into this latter one we bubbled pure nitrogen and due to the gas pressure the water circulated across a perforated wall. The Orbisphere electrode as well as the reference and the cathode electrode were fixed through the upper cover into the miniaquarium. The transfer from the thermostatic aquarium to this zero calibration chamber is done easily with the micromanipulator (fig. 3 B).
Figure 5 shows that the cathode-type microelectrode Sigma is very stable and the drift is about 1% per minute when calibrated in oxygenated water against the Orbisphere sensor. The zero value of the electrode is obtained in the calibration chamber after a surprising long period of time between (15 and 30 minutes). This is why we adopted the Revsbech (1983) solution i.e. to take as zero value the minimal electrical signal which remains constant in the deeper sediment layers. Figures 6 - 8 show such data. The response time of this electrode (i.e. the return from the deep sediment layer with zero value to the stable - standard oxygen value in the overlaying water of the aquarium) is variable and longer than that recorded for other oxygen microelectrodes. Figures 6-8 show response times which vary between 1 and 7 minutes. For the Clark-type microelectrode of Micro-Sense Inc. the response time is 1-2 seconds (e.g. Geiger, 1990) which is similar to the data of the literature (e.g. Reimers et al., 1984). The return signal in the overlaying water was in most cases 90-99%, close to the initial signal (see fig. 6 - 8).

The response time of the Diamond needle electrode membrane with DePe X - resin is less than 1.5 minutes (Helder and Bakker, 1985).
For the oxygen measurement we stepwise, with the micromanipulator, pushed the cathode microelectrode into the sediment at intervals of 1.0 mm and we recorded the signal after 1 minute. Reimers (1987) used intervals of 50 seconds. The stabilization time of the Sigma electrode is much longer than of the Clark microelectrodes (e.g. the Micro Sense electrodes used by us and Geiger react within 1-2 seconds).

Figures 6 - 8 show different types of micro-heterogeneities of the oxygen concentration in various types of sediment from Mondsee. (For the location of the sampling sites and ecological description see Danielopol et al., 1988). The sediment of the site MO-7 at 20 m deep (fig. 6).

An important difference is visible in the first millimeters below the surface area, if the space between the two measurement-points were within 1-2 millimeters. For the sample MO-1, 6 m deep (fig. 7) the heterogeneity is visible on both vertical and horizontal axes within an area of 2-4 millimeters. Finally, the measurement of the sample MO-1, 40 m deep, shows little difference of the oxygen concentrations between the two runs, but a significant one at the sediment water interface (Fig. 8).

The microscale oxygen heterogeneities noted here are similar to those discussed by Reimers et al. (1984) and Meyers et al. (1987), Geiger (1990). The heterogeneities are not due to the ambiguity in localizing the sediment interface as Reimers et al. (op. cit.) suggested for their data, because we could in all the cases, with the help of the stereomicroscope, follow the position of the electrode point and fix it exactly at the sediment-interface with the micromanipulator. Most probably these microscale heterogeneities are biologically or chemically induced. Differences in signals could be also due to local poisoning of the microelectrode as.
discussed by Revsbech (1983). We have for the moment no information on the reaction of the Sigma electrode to various poisoning chemical sources, especially hydrogen sulphide. We conditioned the electrode previously to the routine measures following Reimers et al. (1984) i.e. by inserting it the first time into the sediment and leaving it for equilibration in the overlying water for 20 minutes.

6. CONCLUSIONS

a. The set-up for measuring dissolved oxygen in lacustrine sediments is much cheaper and very effective as compared to the available commercially accessories.

b. The cathode-type electrode Sigma is successfully used for measurements of oxygen in lacustrine sediments.

c. One has to note that its main disadvantage is its sluggish reaction as compared to the Clark-type microelectrode (e.g. the Micro Sense one tested also successfully by us and by Geiger, 1990).

d. One needs further investigations in order to improve the reaction time of the electrode and the zero calibration i.e. one could increase artificially the conductivity of the water adding NaCl or one could improve the zero oxygen calibration using stronger reducing chemicals like NaSO3 with CoCl2 as a catalyst (Gnaiger, 1983).

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W. Geiger (Mondsee) tested various electrode types and provided informations on the Micro Sense electrodes. Mr. Elizer Traub (Micro Sense Inc., Ramat Aviv) and Dr. G. Safe (Sigma Instruments, Berlin) offered useful informations on their products.

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Oxygen concentration and exchange in sediment cores with circulated overlying water. 
VI - CONCLUSIONS

VI - CONCLUSIONS
Abstract

This contribution synthesizes the main achievements of the "Cytherissa project" and explores the various possibilities to use further these data for evolutionary biological topics and applied (paleo)ecology. We present retrospectively the epistemological framework within the project we carried out, the sociological organization of our working group and our cultural motivations. In this way, we demonstrate that the title chosen for our project - Cytherissa, the Drosophila of paleolimnology - is not a loosely metaphor, but reflects the structure of the project; it gives a concrete coherence to an abstract idea that we could materialize through a pluridisciplinary approach.

Résumé

Cette contribution synthétise les principaux résultats du "projet Cytherissa" et prospecte les diverses possibilités d'utilisation future des données dans des contextes de biologie évolutive et de (paleo)écologie appliquée. Nous présentons après coup l'ossature épistémologique autour de laquelle le projet s'est articulé, l'organisation sociologique de notre groupe de travail et nos motivations culturelles. Dans cette optique, nous montrons que le titre choisi pour notre projet - Cytherissa, la Drosophile de la paleolimnologie - n'est pas une vague métaphore, mais qu'elle est l'image de la structure du projet; elle fournit un support concret à une idée abstraite que nous pouvons matérialiser à travers une approche pluridisciplinaire.

1-THE OBJECTIVES OF THE PROJECT

The interest to study the ostracod Cytherissa grew independently in several laboratories:

In Austria, at the Limnological Institute of the Austrian Academy of Science, we were mainly involved with the elucidation of the causes which determine the local extinction of C. lacustris. Therefore, one of the main objectives of the "Cytherissa project" was to understand the evolutionary pathways of Cytherissa species and the causes which determined partly or fully the extinction of some of them.

In France, at the Department of Geology and Oceanography of the University of Bordeaux 1, we were interested to explore how extensive can we use the information provided by the carapace morphology of Cytherideidae for the reconstruction of paleoenvironments.

During the completion of our work we added to the project several other objectives like the elucidation of the phylogenetical relationships between the Cytherissa and other Cyprideididae groups. Therefore we associated other colleagues to our initial research group dealing with systematics and morphology of the Cytherideidae.
For the ecology and paleoecological studies, we produced new devices, we experimented new research methods and techniques. All these activities had one objective. The improvement of current ecological and paleolimnological methods.

2-RETROSPECTIVE VIEW ON THE ACHIEVEMENT OF THE PROJECT

We consider useful to present the synthesis of our main data and to point out how one can further build on this monographic research. Most of the scientific publications are presented as perfect constructs. We found useful to describe how we worked and what were our motivations during the completion of the project. Normally, this is the domain of the historian of science. We consider that we can do the job by introspection. We hope that our colleagues will in this way better understand our work and that we tried to integrate the "Cytherissa project" within a broader scientific and cultural framework.

2-1. EPISTEMOLOGICAL FRAMEWORK

The "Cytherissa project" was conceived as a cooperative work between neontologists and paleontologists. One of the most common approach to study past events is to use the actualism, where the study of the present-day situation helps to understand or to better interpret the past history. For our two topics of research, we used a slightly different approach that we shall call "historical pluralism". Each of us remained the expert of the ecological and evolutionary studies done on ostracods which lived during a given time period. Some of us as zoologists got inspiration for ecological studies from the study of fossil ostracods and the reverse was true for the paleontologists looking at the neontological results. There was no unidirectional approach of study as in the actualism but bi/an/multidirections of inspiration. We succeeded through this approach to stimulate what Wilson (1989 p.242) called: "the search for parallel and analogous phenomena in broader groups of organisms". It is through this activity that first we tested our hypothesis and further we explored the degree of generality of our conceptual and/or empirical models. After a long period of ecological research dominated by the search for integrative parameters and quantitative data, all having in a long-term the aim to construct abstract models which should portrait natural situation (we have in mind the Odum's ecological approach looking for the general characteristics of ecosystems traversed by energy flows and transfer of matter) one has the feeling that a return to the old values so cherished to the natural history is inevitable. Bradbury et al. (1986) noted that many biological processes are essentially qualitative in nature. Wilson (op.cit. p.242) points out that one sees "...the return of the expert naturalist to a position of leadership (due to) the increased esteem and growth of studies of particular groups of organisms for their own sake." Botkin et al. (1979) suggest that an ecosystem theory can be constructed in an easily understood and economical way, from a series of descriptors which are represented by the species list one find in a given environment and reduced state vectors which are the key-parameters which explain the presence of the species within the chosen environments.

Studying paradigmatic animals in detail is a modern approach in biology. Recent progress in developmental biology was done by an intensive study of such animals like Drosophila fly and the nematode Caenorhabditis. Hodgkin (1990) noted that when one compares the pathways of such biological patterns as sex-determination between these two animal groups one sees an overall organization but differences in the ways of realization. Also, the reverse can be true dissimilar structures which can converge in what they real-ize. Therefore, studying one ostracod in a detailed way is a modern approach from which we can get by comparative and analogic methods new insights in related groups.

Another modern approach to ecological studies are to produce long-term observations in order to see cyclical or recurrent patterns (Gray and Christie, 1983). Such studies as those analyzed by Gray and Christie (op.cit.) are very unfrequent because of the research policies which favor short term studies which are financially and administratively easier to control. Paleoecological reconstructions can overcome all these difficulties and provide in some case valuable observations, therefore this approach was proposed by Watson and Clark (1985) to be more frequently used by both ecologists and paleontologists. Our project reflects well this point of view. Platt (1964) emphasized that certain methods of scientific thinking may produce more rapid progress than others. Platt (op.cit.) proposed the method of "strong inference" which includes the following operations that we used extensively during the whole research period:

1 = One should device an alternative hypothesis (this is the old method proposed by Chamberlin, a geologist, in 1987),
2 = One should carry very well chosen (or crucial) experiments with alternative possible outcomes,
3 = One should modify (recycle) the procedures and repeat the observations in order to verify the hypothesis or to device new subhypotheses.
If one looks through this volume one notices that several topics presented in the "Cytherissa project" were repeated by different students working with slightly different methods, concepts and finalities. Sometimes, the conclusions converged in other cases there are divergence of conclusions and opinions. This procedure represents a pluralism of thinking which allows and/or stimulates to look for new experiments and supplementary explanations.

Salt (1983), quoting Polyá noted that a scientist seeking to solve a problem has two tasks before him: "a solution to find" and "a solution to prove". In our project, some of us proposed functional explanations for the empirical observations (e.g. Carbonel et al., 1990 when they interpret the polymorphism of Cytherissa lacustris carapace in Mondsee). It remains that other students should continue our work and try to prove or disprove our hypothetical solutions.

**THE INTEGRATIVE APPROACH AND ITS DOMAIN OF RELEVANCE**

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Fig. 1: The integrative approach and its domain of relevance

Fig. 1: L’approche intégrante et ses domaines d’application

Fig. 1 is a flow chart depicting our integrative approach of working and its domain of relevance. We started from the two general topics, the biological extinction problem and the usage of the ostracod carapace as environmental markers; we documented the general interest of these topics before we started with field observations. The preliminary field work consisted especially in looking in a lake which could simulate in a miniaturized way processes which are difficult to observe in large aquatic systems like a sea or the oceanic bottom. From the preliminary observations we devised our working hypothesis on the local extinction and alternative pathways which could produce the carapace polymorphism of Cytherissa. We developed a set-up to carry laboratory experiments pertaining to the key parameter, the oxygen concentration, which could explain the local disappearance of Cytherissa ostracods from their habitats. We continued to compare laboratory data with the field situation which could give us also alternative explanations (Danielopol et al., 1990c, who looked to the concentration of CO₂ and H₂S as alternative parameters which could explain the disappearance of C. lacustris in particular areas of Mondsee).

Finally, we approached these problems at a higher level of generality when we interpreted the situation of the whole lake and we produced a general model for the local disturbance and the possible recolonization of Cytherissa ostracods in Mondsee (Geiger, 1990a in particular, but also Danielopol et al. 1990c).

With such data in hand we shall try below to use the model to explain complex field situations as they occur in oceans or old limnic environments. Note that we achieved this programme of research by combining field observations in space and time (which are a product of natural experiments), with laboratory manipulations. The former permit together data that would be not possible to produce experimentally, the latter allow to control and/or precise field situation. This powerful research method was advocated by Diamond (1983).
2-2. HUMANISTIC CONSIDERATIONS

We are in many occasions asked to develop our research project within a multidisciplinary framework, and with a large group of researchers. Having such an intellectual infrastructure, it is believed that one can solve easier complex biological problems. The project that we presented here looks like a multidisciplinary project but only a posteriori. It started as an interdisciplinary activity through the communication and collaboration of two paleontologists from Bordeaux and zoologists from Mondsee and Vienna, each specialist having their own interest and respecting the personality and preoccupations of the other partners. It is through a horizontal and a vertical communication system that we attracted a quite large number of people to work with us, and it is a pleasure to present here the results of their research.

The horizontal communication means those which developed between students who have already experienced closely related topics or ostracod groups and who accepted to work on some of the problems posed by our two topics and hypotheses. We think for instance of the specialists working with genetics and mathematics who joined us either to help to clarify the evolutionary problems of *Cytherissa* or helped to advance our quantitative ecological methods.

The vertical communication was that which arose between established researchers and our university students who joined us and worked on some of the subtopics. We gave them the material, instructions, ideas to solve problems. It was a pleasure to see that some of these students found creative solutions or new ways of presenting the data. A strange feeling of happiness united us all every time when one of us got a positive result within his subtopic. The "Cytherissa project" became "Our project" and this is why it is important to publish it as whole volume and not as scattered papers in widely dispersed journals.

The cooperation between the various researchers started, not from the idea that we have to achieve a multidisciplinary project in order to get "big science" results, but it started on a friendly basis and mutual understanding between students. We were always ready to accept people to work with us and we were always ready to speak about our project, ideas and results. It is this openness and antiauthoritarian system, remembering the Paul Feyerabend suggestions to treat science, that we achieved this work with the cooperation of colleagues from seven laboratories based in Austria, France and Germany, that a dozen students from various countries completed PhD or Master theses in our laboratories or just worked for various periods of time with us.

We tried to produce basic research with a possible usage for the applied scientific domain: hence the cooperation between such laboratories as those of the Austrian Academy of Sciences with those of the University of Bordeaux and Esso-REP at Bègles for instance.

The cultural aspect of the project is reflected also by the fact that some of our methods of research and even scientific ideas have analogies with those used by students working within other disciplines, remember the analogy that we found between the engineering and architecture solutions of Perronet and the Ecole des Ponts et Chaussées in Paris (Heinrich, 1983) and the functionnal morphological solutions of the ostracod carapace we stressed out. Some of our methods can be used in other situations too e.g. the sampling devices like the Rinimuco developed for and by the *Cytherissa* project was one of the successes in a research programme on the Ecology of the Benthos on the Danube near Vienna.

Finally, we believe that through working with the *Cytherissa* project, we achieved two goals: we continued to explore the unknown and we attained during this research period a kind of intellectual enrichment (see Wilson, 1989).

2-3. THE CONTRIBUTION OF THE "CYTHERISSA PROJECT" TO THE SPECIES EXTINCTION PROBLEM.

2-3-1 General questions

Within the evolutionary trajectory of a species, extinction marks the last step (fig.2).
Extinction therefore is a natural part of evolution (Myers, 1989). We assisted in the last years to an intense activity on the study of species extinctions. The ways a species slowly or abruptly disappears are diverse and various models were proposed. Beside normal or "background" extinctions most of the research concentrated on catastrophic extinction (see Raup, 1984), which recurred during the earth history as the mass extinction events or those occurring under our eyes due to human environmental disruptions. Flessa (1983) entitled his report at a meeting on extinction process: "Extinction is here to stay" and Lewin (1982) wrote: "Extinction leaves its marks in ecology" (Science). In evolutionary biology we are dealing with the problems of the origin of the species, we follow the successes of the species, or its insufficiencies materialized by the local (or partial) extinction and/or total disappearance (fig.2). One can study one of these three aspects from various points of view summarized in fig.2. As with all the aspects pertaining to the basic mechanisms of life, the extinction of species is difficult to study and/or to reduce to several principles or a general model. Several students noted their uncomfortable position when dealing with extinction problems. Raup (1988) pointed out that we need more empirical data on the species extinctions which occurred during the last part of the history of the earth (the last thousand, hundred years, this is the shallow time) in order to understand better and interpret the massive extinction events which happened in the deep time. Most probably, the species extinction concept has to be viewed as a central tendency of the patterns of its members (this way to represent a concept is used by cognitive psychologists and applied to organismic biology by Sokal (1985). Figure.2 shows the various directions within which we studied Cytherissa. In fact one can use our data for the elucidation of the extinction of various species, mainly of C. lacustris that we studied in an intensive way.

Quinn and Signor (1989) reviewed some of the major future research directions which could explain the phenomenon of "mass extinction". They noted that one needs more information on the life history traits, on the trophic specializations, on the habitats and geographic distributions of the disappearing species. The present volume concentrated at least on one species, Cytherissa lacustris, which locally disappeared from whole lakes or partly from definite areas of some lakes. There are few such case histories for other ostracods species studied up to date. The second question, Quinn and Signor (op.cit.) posed is how much from the information on species extinctions in Recent time can be extrapolated to those which disappeared in the deep time. Considering Cytherissa lacustris, we investigated mainly one key factor, the oxygen low concentration. Hypoxic environments existed recurrently during the long earth's history and as we shall show below (see sections 2-3 and 2-4), there are strong analogies between our present-day observations and paleoecological information.

There is also a need to understand better what are the possible taphonomic biases when one studies the extinction of a species through the observation of fossil material. Considering the subfossil Cytherissa lacu-
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Mondsee, Danielopol et al. (1990c) showed that the disappearance of the species could be recorded at an earlier phase as its real disappearance from an habitat because the fossil rests in the sediment are so diffusely dispersed that we cannot efficiently sample them. In the last years, ecologists made an effort to build general models which could portray in a precise way the risk of extinction (Pimm et al., 1988) or the mechanism of selective extinction (Fowler and McMahon, 1982). Fig. 3 combines in a flow-chart aspect of several extinction models. These aspects apply in our opinion also to several *Cytherissa* species especially to *Cytherissa lacustris*.

![Flow-chart showing the main pathways which lead to extinction of species](image)

Fig. 3: Flow-chart showing the main pathways which lead to extinction of species

There are two classes of causes which induce extinctions, i.e. the environmental and the organismic ones. Hsu (1989, p.4) noted that: "environmental stresses rather than biotic interactions have been the most decisive factors influencing the course of biological evolution". The position is certainly iconoclastic, but fits well with one aspect of the biological evolution of many species, i.e. with their extinction. Once again our data on *Cytherissa lacustris* obtained at Mondsee corroborate this view.

Pimm et al. (1988) pointed out to demographic stochasticity as well as to the minimum viable population concept. These properties depend on the life history strategy of a given species and on the frequency and amplitude of environmental disturbances. Considering *Cytherissa* species, it is interesting to note that the amphigonic species are more prone to extinction than the parthenogenetic ones. This latter type of reproduction offers the advantage to start a population and to persist with only one propagule. One needs several specimens for amphigonic species and at low densities, it could be difficult for isolated individuals to encounter during the reproduction phase.

Fowler and Mc.Mahon (1982) formalized the concept of selective extinction. They proposed a model in which a suit of morphological traits of an organism can explain why some species are more prone to extinction than others. One of these traits is the long generation time. In the case of *Cytherissa lacustris*, we know that this species develops very slowly (Geiger, 1990b). One should expect that this species should be more vulnerable to extinction than others. Effectively, this is the case, however this explains only local extinction situations. At the level of the whole species, one could adopt the view of Fowler and Mc Mahon (op.cit.) who consider that those species with some evolutionary plasticity are less vulnerable to extinction. We noted in various chapters that *Cytherissa lacustris* displays some morphological and ecological flexibility and one can see local differences between populations of this species within the very wide geographic distribution.

Raup (1981) defined two types of environmental crises which produce species extinction, i.e. point and threshold crises. The former includes disasters in the classic sense, they are short-term and their occurrence is completely stochastic. The threshold crises are typically deterministic and occur within longer periods of time. The local extinction of *Cytherissa lacustris* can be cued by both types of crises, as we showed in this volume. The reaction of *C. lacustris* to threshold crises should be stressed out because it has an application in paleoenvironmental reconstructions, i.e. this species disappears through the early stages of the environmental deterioration of the benthic habitats (Danielopol et al., 1983).

Finally, one could ask what is the scientific interest of the study of the extinction of some of *Cytherissa* species or of populations of *Cytherissa lacustris*. Fig. 3 summarizes this. One should note the interest for the general topic, the organic diversity of the earth. This is a special sensitive problem when one assists to the fast decaying rate of a high number of species all over the world (Ehrlich, 1988). In an applied
research perspective, the precise knowledge on the causes of extinction of a species is interesting because one could from this fact, reconstruct the environmental context in others words we can use the disappearance of a species as a (paleo)ecological marker. There is also the economical value of various species. Their destruction produces invaluable economical damage. This is not the case for Cytherissa species. In this latter case, one could replace the economical value by the cultural one and one shall find as we shall argument below, a loss of valuable item, useful for our intellectual life.

2-3-2 Evolutionary pathways within the Cytherideidae

The study of the morphological diversification of the Cytherissa group points out to a series of evolutionary trends that were realized parallely within various groups of Cytherideidae. They are: -the carapace will evolve through paedomorphosis,

- the carapace displays a polymorphism of nodation and reticulation,
- the trends one can see within the Cytherissa group and within the Cytherideidae, e.g. compare the realisation of paedomorphic carapaces within the group of Cyprideis, Cytheridea, Cytherissa, Vernonella etc.,
- the limbs, especially the thoracic legs P1 and P2 for the male changed by paedomorphosis in asymmetric organs. This has been independently realized within the Cyprideis, Cytheridea and Cytherissa. Several groups within the Cytherideidae have a wide tolerance to live in low-saline waters. There are several biological traits which are much similar in the case of Cyprideis, Cytheridea and Cytherissa: the post-embryonal developmental time is very long, one year or longer in the case of Cyprideis (Heip, 1976) and approximately two years for Cytherissa (Geiger, 1990b). A very low oxygen consumption was noticed for Paracyprideis fennica and Eucytheridea bairdii (Peper; 1986) and for Cytherissa lacustris (Newrkla, 1985). Peper (op.cit.) noted that the oxygen consumption rate was correlated with the type of movement of these species. Both the Cytherideinæ species, and Cytherissa lacustris move very slowly and live within the sediment. Higher oxygen consumption rates were noticed by fast moving species which live at the surface of the sediment like, Leptocythere pellucida (Peper, 1986). One assists at least when we compare the Cyprideis with Cytherissa groups to the realisation of various evolutionary innovations. Within the Cyprideis group, one assist to the development of an extremely complicated hinge, a complex hemipenis and a large dorsal brood pouch (at the female). No such structures exist at Cytherissa. The sieve pores areas become very large in the case of Cytherissa as compared to Cyprideis. Cytherissa lacustris is a parthenogenetic species one should note that this species does not seem to be less successful in the colonization of large geographical areas as compared to amphigonic species like Cyprideis torosa. This confirms the idea of Lynch (1984) that parthenogenesis is not a "cul de sac" in the evolution of a taxon as Maynard-Smith (1971) suggested. The success of Cytherissa lacustris to colonize the Holarctic is due probably to its biological peculiarities i.e. a generalist species, with rather wide tolerance limits for temperature and salinity variations, with a slow metabolism and a long development, with no fixed period of ovogenetic activity. Electrorethic and morphologic studies point out to genotypic and phenotypic diversity. This complex of traits helps the animal to live in harsh environments; they belong to what Greenslade (1983) called the adversity selected traits and the strategy of acquiring or maintaining such traits is called A-selection. This is another life strategy different from the ~ and K-strategies of McArthur and Wilson. So even if in some lakes in Europe or North-America Cytherissa could be a glacial relic it does not mean that this species is less well adapted than other faunistical elements to their environmental conditions (see also Newrkla, 1985). The morphological and genetical data presented by Sywula and Geiger (1990) point out the possibility of microevolutionary processes which could specialize various populations of Cytherissa to local conditions. A similar situation was recently described by Rossi and Menozzi (1990). When studying the comparative morphology of Cytherissa species, we noted (Danielopol and, Tetart, 1990; Danielopol, 1990) that several carapace and limb traits have characteristics which are far from being optimally designed or having an adaptive role. These are for instance the paedomorphic shape of the carapace, the assymetric structure of the paedomorphic legs of the males in both Cytherissa and Cyprideis. The functional role of the pseudochaetae on the carapace surface and the development of nodes through the deformation of the carapace wall is also questionable. The production of such traits is a good illustration of the possibilities of Cyprididae to evolve redundant structures or to develop poorly designed carapace forms beside the production of highly integrated and functional structures like the carapace hinge complex discussed by Danielopol et al. (1990a) in the case of Cytherissa sernovi and Cyprideis (remember that the static solution resemble those used by the engineers who construct bridges).

Finally, the penetration of Cytherissa in inland waters and the colonization of wide geographic areas, mainly freshwater habitats, is absolutely unexpected. It is also unexpected why within other Cytherideidae groups like Cyprideis and Cytheridea only few species live now in freshwater habitats some of them being endemic to old lakes like Tanganyika. May be this is a new argument for what Riepel (1984, p.84) expressed
very well: "Evolution appears as an intrinsically stochastic process... (it) is controlled by the environment, evolutionary novelties must function with respect to the inner and outer context of the organism, but the process as a whole is not predictable".

2-3-3 Living Cytherissa ostracods, symbolic objects in the nature protection battle.

There is a real problem to chose a coherent strategy for the protection of the organismic diversity. Many pragmatic conservatimists argue that normal "background" extinctions occurred always during the earth's history. Why should we bother about the disappearance of several minute species of ostracods from Mondsee will argue lay people from Upper Austria? Ostracods like *Cytherissa lacustris* have no economical value for men, they do not contribute to the fish food in no way, they are not key-stone species within the benthic ecosystem of this lake.

However, the paleolimnological research of Handl (1989) showed that in Mondsee at site MO-9/47m deep where the sediment and the ostracod assemblages were stored in an uninterrupted sequence since about 6000 years (from the Atlanticum to present-day), one can observe an important environmental change. The sediment-core studied by Handl (op.cit.) is about 7m.long, sampled at short intervals 5 to 20 cm.distance. One can see from the deeper part to the upper one strong fluctuations in ostracod abundances. However *Cytherissa lacustris* occur through most of the sediment column, only in the upper layers which belong to the 1950-ies period does *Cytherissa lacustris* start to decrease and disappears before 1960-1962 when a natural marker the sandy gravel sediment accumulated on the bottom of the lake during the nearby highway construction (Danielopol et al.,1985). The water quality of the Mondsee deteriorated rapidly due to an increase in the anthropic pollution around the lake. It is impressive to see the permanency of a species during 6000 years to disappear within several years. Therefore, the local disappearance of *Cytherissa lacustris* is a suggestive example of the meaning of an environmental catastrophe in its classical connotation, significant event that causes sudden changes in the configuration or composition of parts of the earth (Raup, 1984). This author asked what could be a sudden change. How can we make the environmental catastrophe definition precise and operational ? Here we suggest that if we have a record of about 6000 years for *Cytherissa lacustris*, the local disappearance of the species within less than 60 years means an event which occurred instantaneously for a geologist i.e. in less than 1% from the total time record. But *Cytherissa lacustris* which still exists in the sublittoral and the upper profundal of the Mondsee (see Danielopol et al,1990c) restarted to colonize profundal lake areas. It is this sluggish process of recolonization in the case of destroyed sublacustrine zones due to the eutrophication that gives us another insight on the environmental catastrophes i.e. the difficulties to restore the previous ecological system. In this way *Cytherissa lacustris* tells us the chronique of the lake in a suggestive way better than one could read from the study of chemical an/or sedimentological parameters.

Finally, why should we protect this species? Because it has a cultural value, we shall argue. It helps us to realize inter alia, the magnitude of our non-sensical activities. But, as we demonstrated throughout this whole series of papers, *Cytherissa lacustris* helps us to access to a series of exciting intellectual problems related to the organismic evolution. These problems by the challenges they exerted on our minds brought a sense of cultural beauty. Why not leave to the next generation of scientists discover similar cultural experiences regarding living *Cytherissa* populations?

2-4 HOW TO USE CYTHERISSA AS ECOLOGICAL MARKERS - A PROSPECTIVE SKETCH.

2-4-1 *Cytherissa lacustris* as an ecological indicator for oxygen depletion in the lacustrine environment. Needs for future researches.

The suitability of using meiofauna for monitoring low oxygen concentration in aquatic habitats was excellently summarized by Elmgren (1975). This author noticed that in those areas were oxygen concentrations fluctuated markedly one would need frequently to measure this parameter. It is easier to observe organisms who integrate this parameter over longer periods of time (day, months). The problem in this case rely on the understanding the limits of the ecological tolerance of the meiofauna to this factor. Elmgren (op.cit.) noted that for those areas with extended low oxygen concentrations, the ostracods are a very suitable group to mark this ecological situation. To a similar conclusion one can arrive when reading the contribution of Geiger (1990a) and Danielopol et al. (1990c). A further improvement of our knowledge in the way one can use *Cytherissa lacustris* as an oxygen monitoring tool is motivated also by the need to extrapolate such data to other ostracod groups which have no living representatives but which seem to behave like *Cytherissa*.
Cytnerissa, Conclusions

From their study one could expect to better differentiate between anoxic and hypoxic events and to better reconstruct the dynamics of anoxia during various geological periods of time. For instance, the analogy between the paleoenvironment reconstruction of the Early Holocene in the Mediterranean by van Harten (1987) is suggestive. When discussing the anoxic event in the Eastern Mediterranean, this author noted (p.268) that the ostracods seem to indicate that the acme of the anoxic event did not come unannounced. The available evidence suggests that "the content of oxygen reduced before actual sapropel began to form". This is exactly the analogous situation we described during the Cytnerissa project in Mondsee (Geiger,1990a; Daniellopol et al.1990c). Similar situation has shown by Grosdidier and Bignoumba (1984) in the lacustrine Lower Cretaceous from West-Africa. On the basis of the ostracod faunas, the presence of polyutrophic to mero-mictic lakes characterized by sporadic oligospecific and pyritized assemblages indicating well stratified waters with strongly reducing bottom condition and high algal productivity. When organic content dropped, (oligotrophic lakes), the ostracodes became more numerous and diversified. This change is interpreted as climatically-controlled from humid without distinct seasons to increase in aridity and marked seasonality which enhanced circulation and therefore oxygenated the bottom of the lake. We suggest here that Cytnerissa lacustris should be further studied in respect to its short-and long-term reactions to low oxygen concentrations. It would be interesting to know the oxygen consumption and surviving rates for various larval stages under hypoxic conditions and low and high temperatures. Sywula and Geiger (1990) noticed genetic and morphological differences between local populations. One should check for local differences in respect to the reaction of these ostracods to low oxygen concentrations. Preliminary observations (Daniellopol et al.,1990c) showed that CO₂ and H₂S can be additional factors which produce the local extinction of Cytnerissa lacustris. Therefore, the impact of these parameters should be investigated in connection to the oxygen requirements. Especially interesting would be to investigate on possible morphological differences in the carapace shape and structure between Cytnerissa individuals which develop either under hypoxic or normoxic conditions. Commonly low oxygen conditions at the sediment-water interface are correlated with sediment rich in organic matter and high CO₂ concentration. One could expect in these cases to see poorly calcified or strangely ornated Cytnerissa individuals. It is necessary to continue to measure the oxygen concentration in the sediments respectively in the microhabitats where Cytnerissa lives. We never achieved to measure comparatively the oxygen concentration in the Cytnerissa sediment burrows or in tubes dug by other organisms and where Cytnerissa can live. Also how Cytnerissa behaves in such labyrinth systems remain to be explored. Especially it would be interesting to know if Cytnerissa can adopt a facultative anaerobic way of life as Wieser et al (1974) described for various marine interstitial meioorganisms.

Finally, one should explore the dynamics of anoxia and hypoxia at sediment-water interface. Especially, the relationships between low oxygen concentration in water (the so-called 3mg l⁻¹ oxygen, critical value) and the oxygen depletion rate in the sediment. As Southam et al.(1982) showed inter alia the dynamics of anoxia depends on many factors, the most important being the mineralization of the organic matter, the bacterial activity in the sediment, the production of CO₂ and H₂S which further bind oxygen and increase the anoxic or hypoxic layers. Such a phenomenon can be observed throughout the geological times, both in marine and non-marine environments. For example, during the various Global Anoxic Events, the extinction of the benthic fauna, especially, the ostracods, occurs at the paroxysmal phase of the event. A good illustration can be found at the Cenomanian-Turonian Oceanic Anoxic Event (Jarvis et al., 1988).

2-4-2 Morphological variability and paleoecological interpretations

Throughout the evolution of the Vernoniella-Cytnerissa lineage, we have demonstrated that for each change in the paleoenvironment, corresponds an important variation in the carapace morphology. Two examples are particularly demonstrative: one in the Jurassic-Cretaceous with the genus Vernoniella, the other during the Quaternary with Cytnerissa.

Vernoniella in the Berriasian

The first occurrence of the genus Vernoniella is in shallow-marine deposits of the Middle Jurassic (Colin et al., 1990). The carapace of these forms is smooth and strictly monomorphic. Later, during the Upper Jurassic (Oxfordian, Lower Kimmeridgian), in coastal environments, appear forms with reticulate carapaces but without nodes. At the Jurassic-Cretaceous boundary, and with the simultaneous development of "Purbeckian facies" corresponding to brackish and freshwater lagoonal environments, the genus Vernoniella shows very strong morphological variability especially marked by the development of a strong nodation. In the same levels, Vernoniella is associated with other genera such as Darwinula, Theriosynoecum, Fabanella and Cypridea. When the marine environment is without major chemical changes, the morphology of
Vernoniella is relatively stable: the reticulation appears, related to carbonate equilibria at the water-sediment interface (see Peypouquet et al., 1988). On the other hand, when the environment becomes very unstable with strong changes, particularly affecting the salinity, appears a strong morphological variability of the nodation. This nodation, seems to be more developed in the less saline episodes of the "Purbeckian facies". Similar trends have been observed in closely related groups such as Neocyprideis and Cyprideis (Colin et al., op.cit.)

-Cytherissa in the Quaternary

In the subalpine lakes, important populations of Cytherissa lacustris developed during the interglacial periods (Handl, 1989). These populations are more or less polymorphic. However, during some periods they display an important polymorphism. For example, during the Atlanticum period, the Cytherissa lacustris population is strongly nodded. At the same time, other ostracods such as Limnocythere sancti-patricii, present, in the association are also nodded (Carbonel et al., 1990). In the present-day, Cytherissa lacustris and Limnocythere sancti-patricii are weakly nodded or unnoded. This observation can be related to a climatic change between Atlanticum and the present time: During the Atlanticum, very strong and frequent rainfalls bring into the lakes an important amount of clastic sediments and humic matters. At the present-day, rainfalls are less frequent, less important and more seasonally controlled (Carbonel et al. op.cit.).

- In conclusion, the example of the development of the nodation in the Vernoniella-Cytherissa lineage shows that it is always linked to major changes in the environment. The apparition of the nodation in Vernoniella at the Jurassic-Cretaceous boundary is related to the apparition of brackish-to freshwater environments succeeding to marine environments. At the same time, the climate changes with the development of seasonal cycles characterized by an alternance of humid and arid periods. During the arid phases, evaporites are often deposited (Carbonel et al., 1998). In the case of Cytherissa lacustris in the subalpine lakes, it has been observed a stronger nodation during a humid period. Both cases show that morphological variability of the ostracod carapaces can be used for detailed paleoecological interpretations.

2-4-3 Carapace geochemistry and paleoenvironments

The chemical analysis of Cytherissa carapaces showed two important facts:
- the amount of elements linked to the organic matter such as P, S or Mn have higher values in individuals coming from mesotrophic or eutrophic zones than in oligotrophic zones (Carbonel and Farmer, 1990).
- on the other hand, the more noded carapaces, found in zones with important inflows of organo-clastics, mainly silico-organic complexes show higher values of Si et Al especially in the nodes than in specimens living in areas without this type of inflow (Carbonel et al., 1990; Carbonel and Farmer, 1990).

These observations demonstrate that the amount of certain chemical elements in the carapaces reflects the water composition and the chemical equilibrium at the water-sediment interface.

3 - EPILOGUE

The finality of our project is heuristic; it means that we tried to increase the knowledge on particular subjects where we are convinced that they have a general interest. However in a period when one speaks of good science in terms of prediction value we shall disappoint our readers and evaluators when we shall say that we have been inspired during our research by what A.de Saint-Exupery in Citadelle wrote: "Je ne saurai prévoir mais je saurai fonder. Car l'avenir on le bâtit." We tried to show during this project that one can approach complex biological problems through a detailed study of one animal group. We built here the basis for future research and we pointed from time to time out possible new directions of investigation. Unfortunately, to our project lacks the predicative power so cherished by those involved in environmental policies. Our greatest satisfaction would be to see other people taking over the project and trying to adapt to their special needs some of our results and ideas.

A first reaction in this sense is as noted by one of us (Danielopol, 1990), the development of similar studies by U.Grafenstein and his associates at the Technical University in München.

We are informed that some of our colleagues will explore the ostracods of lake Bâikal and they consider to restudy some of the endemic Cytherissa species.
There is not only a need to permanently verify our results but also if one finds them interesting to try to build new hypotheses on them. In this way, we hope that we were persuasive enough for those readers who looked rather sceptically to the metaphoric title: "Cytherissa, the Drosophila of Paleolimnology". We hope that we convinced them that it is not only a nice title but also an intellectually exciting story.

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