

ALEXANDER LIEBAU

HOMOLOGOUS  
SCULPTURE PATTERNS  
IN TRACHYLEBERIDIDAE  
AND RELATED  
OSTRACODS

HOMOLOGE SKULPTURMUSTER  
BEI TRACHYLEBERIDIDEN  
UND VERWANDTEN OSTRAKODEN

*Translated from German*

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Dissertation approved by the Faculty for the Conferring of Academic Degree of Doctor of Natural Science, Department for Mining and Geological Science, University School of Engineering, Berlin

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LAZAR STANOJEVIĆ

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PAUL PIGNON

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## PREFACE TO THE ENGLISH EDITION

In its original version, this paper was a dissertation; the inordinately long introduction and the detailed division and numbering of articles are reminiscent of this.

Since publication of the German text, the ornament studies outlined in this paper have been expanded and now encompass several hundred species more. Each new example has confirmed the value of homologizing elements and patterns of ornamentation. No major correction of the original argumentation, therefore, has been necessary. Thus, together with the related papers by POKORNÝ and BENSON, this book may form a base for a new understanding for the ostracod sculpture, and through it, the relationship within the group as a whole.

Alexander Liebau

Geologisch-Paläontologisches  
Institut der Universität  
Tübingen  
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**Rapporteurs: Professor Dr J.-G. Helmcke**  
**Professor Dr A. v. Hillebrandt**

## CONTENTS

Foreword .....	7
Explanatory Notes .....	8
1. Introduction .....	9
1.1. <i>Cytheracea</i> and <i>Trachyleberide</i> Group of Families .....	9
1.2. Morphology and Variability of the Shell Sculpture in <i>Trachyleberide</i> Ostracods .....	10
1. Morphology of the Shell .....	10
1.1. Brief Introduction to the Morphology of Shell .....	10
1.2. Supplement: Definition of Sculptural Elements Usings Descriptive vs. Morphogenetic Criteria .....	12
2. Discontinuous Variability (Polymorphisms) .....	13
2.1. Molting Stages .....	13
2.2. Sexual Dimorphism .....	14
2.3. Further Polymorphisms s. l. ....	14
3. Continued Variability .....	14
3.1. Variability of Fine Sculpture .....	14
3.2. Paleocological Influences on Sculpture .....	17
1.3. Sculpture Characters and Taxonomy .....	18
1. Systematics .....	18
2. Conventional Standards for Characters .....	20
3. Zoological Significance of Sculpture Characters .....	22
4. Principles of Identification and Evaluation of Taxonomic Characters .....	22
5. Evolution of Variability .....	24
6. Systems of Characters Having Approximately Numerically Constant Elements .....	24
7. Previously Established Homologies of Fine Sculptures .....	26
2. <i>Limburgina</i> -Type Reticulation .....	28
2.1. Overview .....	28
2.2. Naming of Reticulation Meshes .....	29
2.3. Intraspecific Variability of Reticulation in <i>Limburgina ornata</i> ..	30
2.4. Homologous Reticulation Meshes in <i>Limburgina ornata</i> .....	33
2.5. Intrageneric Variability of Lateral Reticulation in <i>Limburgina</i> ..	33
2.6. Replacement of the Median Rib by N. Neshes .....	36

3.	<i>Limburgina</i> -Type Conation .....	37
3.1.	Survey .....	37
3.2.	Macroconation in <i>Oerthiella horridula</i> .....	38
3.3.	Conation in <i>Limburgina ornata</i> .....	40
4.	Pore Systems and Fine Sculpture .....	41
4.1.	Mesh Pores .....	41
4.2.	Cone Pores .....	42
4.3.	Sensory Bristles .....	46
4.4.	Conclusion .....	46
5.	Climo and Ortho-Pleural Coarse Sculpture .....	49
6.	Taxonomic Distribution of <i>Limburgina-Type Fine Sculpture</i> ....	53
6.1.	Introduction .....	53
6.2.	<i>Limburgina</i> -Type Fine Sculpture in Ostracods with Ortho-Pleural Coarse Sculpture .....	53
1.	<i>Limburgina</i> aff. <i>depressa</i> .....	53
2.	<i>Mauritsina</i> .....	54
3.	<i>Cythereis</i> .....	56
4.	<i>Kingmaina</i> .....	56
5.	<i>Echinocythereis</i> .....	59
6.	" <i>Quadracythere</i> " <i>prava</i> .....	59
7.	" <i>Quadracythere</i> " <i>sp.</i> .....	60
6.3.	<i>Limburgina</i> -Type Fine Sculpture in Ostracods with Clinopleural Coarse Sculpture .....	63
1.	<i>Leguminocythereis</i> s. l. ....	63
2.	<i>Spinicythereis</i> .....	71
3.	<i>Dumontina</i> .....	71
4.	aff. <i>Falunia</i> .....	71
5.	<i>Mosaeleberis</i> .....	73
6.	<i>Cytheretta</i> and cf. <i>Cytheretta</i> .....	74
6.4.	Results .....	75
7.	Phylogenetic and Taxonomic Conclusions .....	77
7.1.	Limitations .....	77
7.2.	Taxonomically Significant Affiliations .....	77
7.3.	Appendix: Foreseeable Changes in the Framework of Families and Subfamilies .....	80
8.	Summary .....	82
9.	Taxonomic Register .....	86
10.	References .....	90
11.	Additional Notes .....	93

## FOREWORD

“What significance does the sculpturing of a shell have? I am rather puzzled by this question, and hardly anybody would hope that we shall ever clarify this particular significance of the enormously varied sculpturings.”

G. W. MÜLLER, 1934, p. 89

- “Among the different forms of ostracod shells, the surface sculpture is a complex of indicators which can be considered causally or phylogenetically only with greatest difficulty.”

G. HARTMANN, 1963, p. 91.

It has been shown that the shell ornaments of many ostracods coincide so much that it seems both possible and rewarding to make a homologizing comparison of their network patterns. Analogies can be drawn with insects, for example, whose wing veins have long been investigated by this method. Unlike the insect studies, the following investigations in ostracods were made from fossil material which covers thousands of species and innumerable individuals, allowing the phylogenetic review of the smallest steps. Besides this, the ostracods have very many characters of negligible variability, and, assuming that sculpture patterns can be homologized, they could become nearly ideal objects for phylogenetic, biostratigraphic and constructive morphologic investigations. The main body of this Dissertation presents evidence for the possibility of homologizing individual elements of the fine sculpture beyond the borderlines of species and genera.

The Introduction includes an outline of attitudes toward the general topics which have been contested in the discussions on sculpture ornaments. The greater part of the scope of understanding of ostracod

paleontology with regard to species, genera and families, has not been taken into consideration.

My cordial thanks for assistance are due to Mrs. Dr B. Moos and Mrs. Professor Dr J.—G. Helmcke, Professor Dr A. v. Hillebrandt, Professor Dr H. Hiltermann, Dr H. J. Oertli, and Professor Dr B. Ziegler. My special thanks are due to Professor Helmcke (Biology, T. U. Berlin), whose willingness to intercede has made this Dissertation possible. I am indebted to his associates, above all Mr. R. Rau for making photographs with a raster electron microscope (Stereoscan). Dr Oertli (Practical Ostracod Paleontology; SNPA Pau, France) has reviewed the dissertation from the taxonomic point of view and I am indebted to him. He also helped with further Stereoscan photographs, including those represented in Figs. 11—13.

The raster electron microscope used to investigate an appreciable part of the ostracod material was donated by the Volkswagenwerk Foundation.

The *Studienstiftung des deutschen Volkes* (Student Grant Foundation of the German People) assisted me until 1970 with a doctoral scholarship. Then I received a scholarship from the *Senat der Stadt Berlin* (Senate of Berlin City) (West).

## EXPLANATORY NOTES

Unless otherwise noted, all statements on the valves or shells refer to adult specimens of fossil or Recent ostracods.

Indicators for the details of ostracod shells are explained or defined on the basis of Figs. 1—3, 7, 8 and 10, and their captions.

The following abbreviations are used in captions: L (left valve), A (adult individual), A-1 (ultimate juvenile stage) and A-2 (penultimate juvenile stage).

Except for two photographs reproduced, all drawings are based on photos obtained by raster electron microscope.

The *Bundesanstalt für Bodenforschung* (Federal Institute of Soil Science) lent specimens of the Maastrichtian calcareous tufa. The ostracods from this material are duly marked in the figures. Otherwise the author's own ostracod material is presented.

# 1. INTRODUCTION

## 1.1. CYTHERACEA AND TRACHYLEBERIDE GROUP OF FAMILIES

Cytheracea are minute to medium-sized ostracods, whose carapaces are commonly 0.5—1.00 mm long. Their shells are as a rule heavily calcified, with pronounced sculpturing, and are equipped with strong hinges. These animals live principally in shallow seas, crawling about and feeding on plants, detritus or virtually anything. In the littoral and sublittoral zones they make up by far the largest part of the ostracod fauna as regards numbers of species and individuals. Only a few representatives appear in brackish or fresh waters. Cytheracea can be traced back to the Lower Paleozoic, but it is only toward the beginning of the Jurassic that its members appear increasingly often and in a broad variety of forms.

Among the Cytheracea the "Trachyleberide family group" has many lavishly sculptured representatives (see p. 19). This group covers Trachyleberidae, Hemicytheridae and Cytherettidae (s. 1), and probably more families which, however, are not included in this paper. Ostracod shells classified among the three said families are often found in Cretaceous and Recent sediments of the upper shelf. Since these animals live a distinctly benthonic life confined to shallow waters, and since the transport of larvae is obviously negligible, they regularly form faunal provinces whose distribution can be treated paleontologically as well. The Cytheracea can be compared, for example, with the Neogastropoda, in terms of their occurrence, phylogenetic radiation since the Cretaceous, and by the wealth of bizarre shell forms.

## 1.2. MORPHOLOGY AND VARIABILITY OF THE SHELL SCULPTURE IN TRACHYLEBERIDE OSTRACODS

### 1.2.1. Morphology of the Shell

#### 1.2.1.1. *Brief Introduction to the Morphology of the Shell*

The ostracod shell (carapace) develops from a skin fold divided into two flaps and calcified. These flaps form the shell. The valves are hinged along the middle line of the back by a flexible chitinous ligament, whose action opposes that of the adductor muscle. The inner leaf (inner lamella of the shell) of the skin fold is usually only calcified at its periphery. This calcified part of the inner lamina is visible as a duplication of the margin on the inside of the valve. The insertions of the adductor muscles and the muscles leading to the antennae make up the central muscular field. Other muscular parts

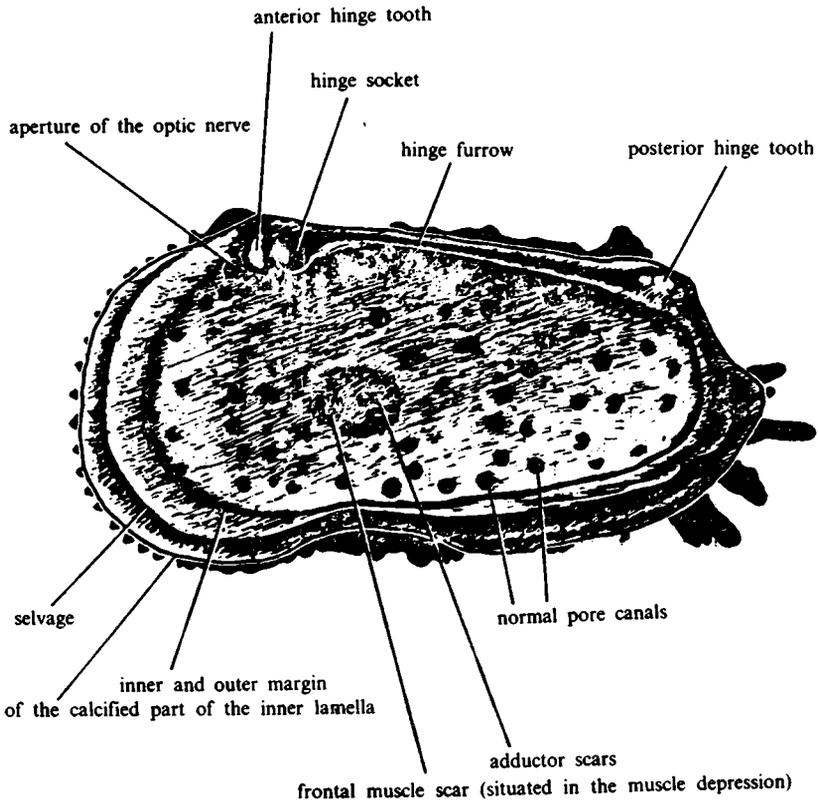


Fig. 1. Inner view of the right valve of an adult trachyleberid ostracod. Length of the valve 0.9 mm.

belong to the mandible and antennule. The carapace is perforated by numerous pore canals. In live animals these usually lead to the sensory bristles situated on the outside of the shell. The "marginal" pore canals are easily visible under strong light (see Fig. 2). The aperture for the optic nerve also resembles a pore opening.

After the removal of noncalcified parts the details as shown in Figs. 1 and 2 can be seen on the inside of the valve.

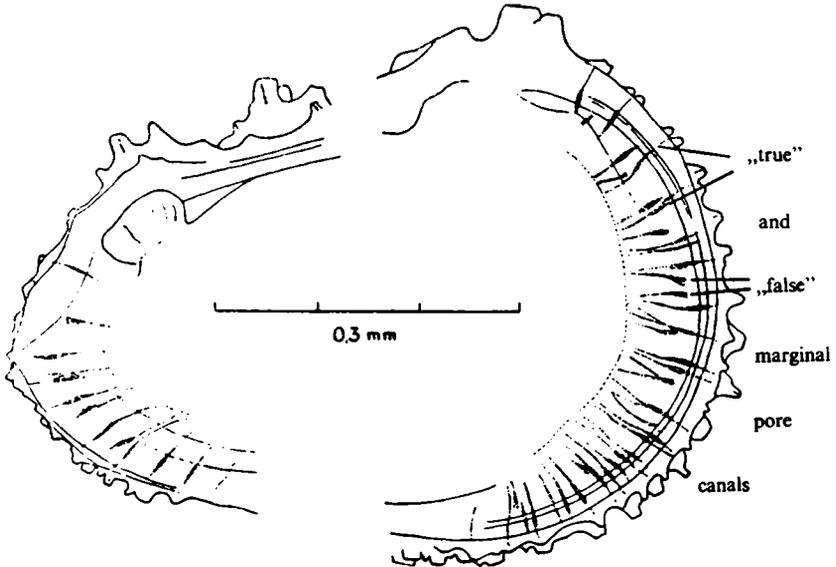


Fig. 2. The inner face of the anterior and posterior marginal zones of the left valve with translucent marginal pore canals. (*Cythereis ornatissima*) REUSS, (1846) from the Bohemian Coniac. From POKORNY, 1963.

The outside of the valve of a primitive, richly sculptured Trachyleberide ostracod (Fig. 3) commonly presents the following coarse sculpture:

eye node,

muscle node,

marginal ribs (anterior and posterior ribs are strongest) and longitudinal ribs (dorsal, median and ventral). (Elevated crests and swollen ridges and furrows may also be included here.)

Coarse sculpture is usually covered with fine sculpture (see also Fig. 12, 1), which can be made up of the following components:

tuberculation (spine and tubercle systems)

reticulation (meshwork),

punctation (pitting) and (inconspicuous) ridges,

swellings and furrows.

Tuberculation, reticulation and punctation are components of fine sculpture, and are themselves composed of more or less numerous elements, including:

- tubercles<sup>1)</sup> (spines, nodes),
- reticulation meshes
- pits (puncta).

Some of the inner shell characters can be observed on the outside, where they are represented by the corresponding forms, such as:

- pore openings
- muscle scars
- (see also ocular projections)

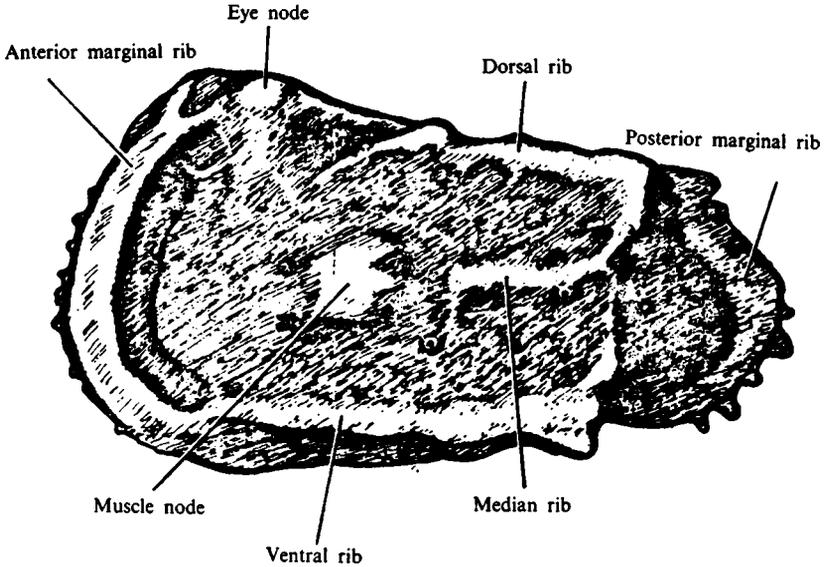


Fig. 3. Gross sculpture on the left valve of a Trachyleberide ostracod (further data on p. 50).

#### 1.2.1.2. *Supplement: Definition of Sculptural Elements Usings Descriptive vs. Morphogenetic Criteria.*

The above listed terms of the morphology of sculpture can be understood either purely in terms of form or in terms of origin and development. There follow two examples of the problems related to these two conceptions:

<sup>1)</sup> Originally, "Tuberkel" (tubercle) was used as a semidescriptive term covering both "spine" and "tubercle" as defined later by SYLVESTER-BRADLEY & BENSON (1971), including all types of pore cones but without specifically relating to the presence of pores. A general term for all of these types is important since corresponding elements in the ornament of different specimens within one population may show all transitions from spine to tubercle shape. Now the term "cone" (derived from "pore cone", not referring to a cone-shape) is used in this paper in this sense.

Even among congeneric species, some forms may have a low, inconspicuous ridge in place of the typical strongly-defined median rib.

Observed purely morphologically, such a low ridge should be classified as fine sculpture. But if it is homologized with the strong median ribs of the earlier sculptured forms, then it is difficult to avoid concluding that it is a less-developed, perhaps relic median rib; consequently, it is an element of coarse sculpture.

The "pits" (contrasted with reticulation meshes) may be defined thus: small circular depressions on the shell which are separated at least by the equivalent of their diameter. Following this interpretation, *Kingmania hagenowi* (BOSQUET, 1854) from the West European Upper Cretaceous manifests different gradations between true reticulation and typical pitting. Whether they are classified as pits or meshes, certain elements in this species (and in other species: see main body of the paper) have constant positions; the pits of one individual are homologous with the meshes of the other. Distinguishing between pits and meshes would seem to be arbitrary in this case. (It is on still another basis that the micro and macroreticulations are distinguished; see Section 2.1.)

Thus the purely form-dependent definition of sculpture elements often results in artificial partitioning of types. The heritage-related definition, on the other hand, is speculative and presumes a breadth of observations and conclusions, yet does not separate those features closely related by origin. Both methods are indispensable. However, the two forms of definition should always be distinguished so as to avoid basic misunderstandings.

The above listed terms are usually understood as purely form-related. Terms applied to sculpture that are introduced in the main body of this study are most often defined with regard to origin and development.

## 1.2.2. Discontinuous Variability (Polymorphisms)

### 1.2.2.1. Molting Stages

At the time the nauplius leaves the egg it is already equipped with a shell. This is the larval stage designated A-8 (adult stage minus 8 moltings). The 8th molting (maturation molting) is the last; (in rare cases claims for one additional adult molt have been made however).

During shell morphogeny, the maturation molting is associated with a far greater change than are the preceding moltings. The juvenile valves, even molts of the ultimate larval stage, have thinner shells than those of adults, and their sculpture is mostly less pronounced. Juvenile shells have relatively higher anterior ends; the dorsal and ventral edges converge sharply toward the posterior end.

The internal lamina appears only as a narrow ledge on the inside of the free margin of the valve. Sexual dimorphism in this form of the shell as a rule is not yet developed.

### 1.2.2.2. *Sexual Dimorphism*

Sexual dimorphism is not normally observable until the adult stage. The males almost always have a more elongated carapace than the females and they are less numerous. Differences in proportions can vary appreciably within the limits of one genus but it is probably characteristic for the species. Except for elongation, the sculpture of males mostly corresponds to that of females. Among the exceptions are males from the genera *Occultocythereis*, *Carinocythereis* and "*Hermanites*" (gr. *paijenborchianus* KEIJ, 1957). These males have been found to have a conspicuously shortened ventral rib on the right valve (compare TRIEBEL, 1961, MOOS, 1963 and 1965, and VAN MORKHOVEN 1962/63). One sex-linked character relating to the median rib and dorsal rib was described by OERTLI (1966) for *Protocythere emslandensis* BARTENSTEIN & BURRI, 1955. Different configurations of meshes are present in *Limburgina ornata* (BOSQUET, 1847) and in one undescribed *Oertliella* s. l. in connexion with sexual dimorphism: this is manifested as variation in position of a certain reticulation mesh (K8, see Section 2.3.).

### 1.2.2.3. *Further Polymorphisms s. l.*

Other discontinuously varying characters are not often observed on ostracods. VAN MORKHOVEN (1962, Vol. I, p. 81) reported a *Buntonia* species from the West African Paleocene, saying that certain individuals showed inversion of hinge structure and valve size; that is, he found specimens with characters "reversing" those of normal individuals. (In normal ostracods, the left valve is larger than the right, and the right valve bears the anterior hinge tooth.) Discontinuous variation was observed by the author also in the reticulation ornament of an Upper Cretaceous *Hermanites*-like taxon. In some valves a certain reticulation mesh was absent, whereas it was present on all other valves. Gradations between these two forms were not found. Both types belong to the same species; this is indicated by the presence, among other things, of the characters on right and left valves, respectively, of the same individual.

## 1.2.3. *Continuous Variability*

### 1.2.3.1. *Variability of Fine Sculpture*

The author was able to observe five types of variation that could be determined genetically:

(1) Numerical Variation: the number of elements (e.g. tubercles) in one component of the fine sculpture (tuberculation) changes from one specimen to the next.

At times one can distinguish "true" and "apparent" numerical variation. The apparent numerical variation is a special form, a consequence of the variation of expression of characters, (see Point 4).

The true numerical variability is inevitably associated with the variability of arrangement (see Point 2). Observations show that the large spines and large reticulation meshes in Trachyleberide ostracods are numerically constant or only slightly variable. There is a transition between very slight numerical variability and numerical conformity. Some degree of numerical conformity (constancy) is necessary for reidentification of fine sculpture elements on different specimens through homologizing.

(2) Variation in Position: elements (e.g. reticulation meshes) of a component of the fine sculpture (reticulation) take different positions in different specimens. The mutual spatial relationships (configuration) of these elements are changed. This is definitely the case with the true numerical variation, but even with the numerical constancy there may be certain shifts in individual elements.

(3) Variation of Form: the shape of certain elements in one component of the fine sculpture may vary (either in one valve or from one individual to another).

This component of variability can be established only with difficulty if it is masked by weak ornament expression.

(4) Variation of the Strength of Expression: one component (e.g. tuberculation) of the fine sculpture or only some of its elements (tubercles) may be strongly developed in one specimen and only weakly expressed in another.

In an extreme cases such elements are not developed at all (most often this effects groups of elements or major parts of the ornament field, but not single elements). If the elements which remain (tubercles) are invariable in position, then the positions of missing elements remain unoccupied and gaps in the pattern appear. The number of elements which are still recognizable then decreases, but this numerical deviation ("apparent numerical variation") is of an entirely different nature than that of the true numerical variation (under Point 1 above). In the case of true numerical variation there are no gaps, that is, they cannot be established with certainty. The "remaining" elements do not have invariable positions. It is possible to test this with elements of fine sculpture which are connected with pore canals: even when the definite tubercle or reticulation mesh is entirely lost, its pore opening remains in its proper place.

(5) Size variation (see Fig. 4).

The first two types of variation appear to be obviously correlated with one another. Independent of these is the 4th type of variation (strength of expression). At least in one group of cases this seems to be associated with the incomplete calcification of the middle layer of the shell (HERRIG, 1966, p. 821). Strength of expression is characteristic for the species, and thus genetically conditioned, in some *Cythereis* s. l. and *Mauritsina* s. l. According to

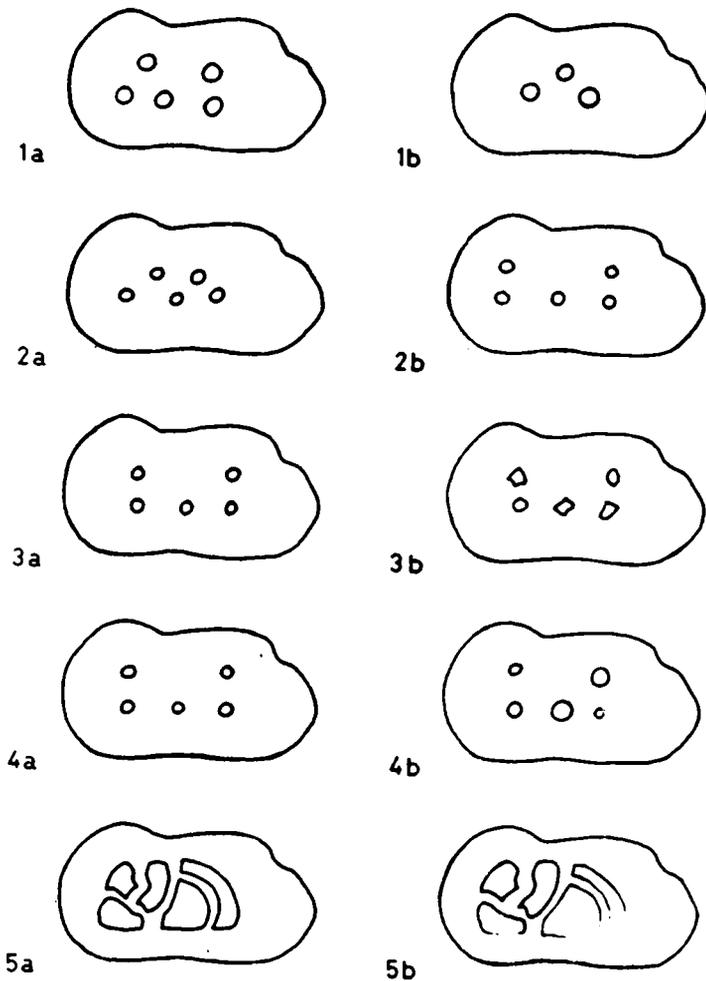


Fig. 4. Components of a complex variability of sculpture: (1) numerical variation always related to variability of position, (2) variation of position, (3) variation of form, (4) variation of size, (5) variation of strength of expression.

arguments put forward by HERRIG (1966), the strength of expression can vary according to environment, so that "phenocopies" (apparent copies) occur. (Endogenous (see below) and exogenous variability here obviously leads to the same result):

There the following variability patterns are distinguished:

- (1) Exogenous (conditioned by environment) variability and
- (2) Endogenous (genetically conditioned) total variability including:
  - (a) Endogenous variability of the number
  - (b) Endogenous variability of the position

- (c) Endogenous variability of form
- (d) Endogenous variability of the strength of expression
- (e) Endogenous variability of size

For a reasonable taxonomic evaluation of fine sculpture, it is of basic importance to estimate the range and composition of its variability.

### 1.2.3.2. *Paleoecological Influences on Sculpture*

HERRIG (1966, p. 821) notes several relationships which, according to him, exist among paleoecological influences, the formation of the median calcareous layer of the shell, and the kinds of fine sculpture. *Mauritsina varia* (HERRIG, 1965) from the Rügen Upper Cretaceous is unusual in that the macroreticulation is replaced by a system of minute pits ("microreticulation", see Section 2.1), or by entirely smooth surfaces. As evidence for the effect of environment, HERRIG explains that these changes appear in definite horizons in representatives of several genera simultaneously.

CARBONNEL (1969) describes an uncommon intraspecific variation in *Elofsonella amberii* CARBONNEL 1969, from the Miocene of Southern French. One group of these specimens is characterized by an elongate median rib, while in others there are two short ribs side by side in its place. Most adult specimens are reticulate; about 15 percent are without fine sculpture. In juveniles, too, differences appear in sculpture. The material originates from a facies dominated by *Crassostrea crassissima* (LAM). The cause of this variation, CARBONNEL assumes, is the inflow of fresh water.

The species aff. *Hermanites* sp., originating from the lagoonal Maastrichtian of the Tremp basin (cf. LIEBAU, 1971), shows in one population the reduction of the dorsal rib in many specimens. The adjacent reticulation can be changed simultaneously. In other populations the dorsal and ventral ribs are poorly developed. The fauna accompanying these populations with strong ribs indicates euhaline salinity; the fauna of other populations indicates somewhat reduced salt content (polyhaline).

Specimens of *Oertliella horridula* (BOSQUET, 1854), also from the Maastrichtian of the Southern Pyrenees, can sometimes show partially reduced tuberculation. In this context there occur certain reticulation meshes which are otherwise known only in the predecessors of this species and in the larval stage of the species group. The impoverished fauna accompanying such populations corresponds to a biofacies of the euhaline or polyhaline lagoonal type.

These two examples show that association between abnormal sculpture and impoverished accompanying fauna can be related to environmental influence. The faunas with a few species or with more species, associated with respectively abnormal or normal sculpture, alternate several times within the stratigraphic section. This rules out the existence in these cases of sculpture evolution. The presence of populations with intermediate sculpture types shows that there are not two separate ecological races or species alternating in occurrence, but a single species changing with its environment.

### 1.3. Sculpture Characters and Taxonomy

#### 1.3.1 Systematics

Table I presents the suprageneric distribution of the investigated species (main body of this paper). Many of the higher taxa are provisionally formulated. The uncertainty expressed here is evident in the literature, too. Continual classification or reclassification of taxa by different authors demonstrates that vigorous debates have been going on in this portion of systematics in recent years. It is only exceptionally that all authors would agree upon which genus should be classified under which family or subfamily. Despite the scarcity of review works, two to four different taxonomic associations have been proposed for most genera. The following suprageneric taxa from the literature encompass the species and genera dealt with in this study:

Brachycytheridae/inae PURI, 1954; Campylocytherinae PURI, 1960; Cythereidinae BEROUSEK, 1952; Cytherettidae/inae TRIEBEL, 1952; Cytheridae/inae BAIRD, 1850; Echinocythereidinae HAZEL, 1967; Hemicytheridae/inae PURI, 1953; Leguminocythereididae/inae HOWE, 1961; Mauritsininae DEROO, 1962; Pterygocytheridae PURI, 1957; Pterygocythereidini MANDELSTAM, 1960; Protocytherinae LJUBIMOVA, 1955; Thaerocytherinae HAZEL, 1967; Trachyleberididae/inae/ini SYLLVESTER-BRADLEY, 1948.

Table I  
Investigated Species and Their Suprageneric Distribution<sup>2)</sup>

"Quadracythere" prava	Hemicytheridae s. l.
"Quadracythere" sp.	
Limburgina aff. depressa	
Limburgina pseudosemicancellata	
Limburgina ornata	
Oertliella horridula	
Oertliella sp. 1	
Oertliella sp. 2	
"Spongicythere" koninckiana	
Kingmaina cristata	
Echinocythereis scabra	Hemicyth./Trachyl.? — Echino- cytherideinae
Mauritsina latebrosa	Trachyleberididae — Mauritsininae

<sup>2)</sup> List of species revised according to 1975 data (arrangement as in table I):

*Pokornyella (Tenedocythere) prava*  
*Quadracythere (s. l.) sp.*  
*Limburgina aff. depressa*  
*Limburgina? pseudosemicancellata*  
*Limburgina ornata*  
*Oertliella (Horrificiella) horridula*  
*Oertliella (Horrificiella) sp. 1*  
*Oertliella (Horrificiella) sp. 2*  
*Histocythere koninckiana*  
*Kingmaina cristata*  
*Echinocythereis aff. scabra*  
*Mauritsina latebrosa*

Table I (continued)

Mauritsina sp.	Trachyleberididae — Mauritsininae
Cythereis longaeva longaeva	Trachyleberididae — "Cythereidinae s. n."
Spinicythereis geinitzi	Trachyleberididae-Faluniinae s. l.?
Dumontina sp.	Dumontina sp.
aff. Falunia sp.	aff. Falunia sp.
Mosaeleberis sp. 1	Mosaeleberis sp. 1
Mosaeleberis sp. 2	Mosaeleberis sp. 2
"Leguminocythereis" angulatopora	"Leguminocythereis" angulatopora
"Leguminocythereis" bosquetiana	"Leguminocythereis" bosquetiana
"Leguminocythereis" aff. bosquetiana	"Leguminocythereis" aff. bosquetiana
"Leguminocythereis" striatopunctata	"Leguminocythereis" striatopunctata
cf. Cytheretta sp.	Cytherettidae
Cytheretta haimeana	Cytherettidae
Leguminocythereis scarabaeus	Leguminocythereididae
(Authors and years given in Taxonomic Register)	(All families belong to Ostracoda-Podocopida-Podocopina-Cytheracea)

The studies consulted for this purpose (given in chronological order) are:

OERTLI, 1956; KEIJ, 1957; POKORNY, 1957 and 58; MANDLSTAM et al., 1960; H. V. HOWE et al., 1961; VAN MORKHOVEN, 1962/63; REYMENT, 1963; HARTMANN, 1963 and 64; SZCZECZURA, 1965; DEROO, 1966; HAZEL, 1967; und PIETRZENIUK, 1969.

The differences in opinion primarily pertain to the nomenclatural rank of taxa. Zoologists, like some paleontologists, emphasize the insignificant number of differences in the structure of extremities, and observe these forms as representatives of two or at most three subfamilies. The other paleontologists primarily consider morphological differences in shells and the multitude of species, and also the high degree of phyletic differentiation made possible by an abundance of characters (HAZEL, 1969, correspondence). Thus they give priority to higher categories.

The present author supports the latter standpoint, since his investigations lead to an increased number of characters and, consequently, the improved possibility of taxonomic differentiation.

*Mauritsina* sp.  
*Cythereis longaeva longaeva*  
*Trachyleberididae (Spinicythereis) geinitzi*  
*Paracaudites* sp.  
 "Triginglymus" gr. *grignonensis*  
*Mosaeleberis* sp. 1  
*Mosaeleberis* sp. 2  
 "Triginglymus" *angulatoporus*  
*Forbesicythere?* *bosquetiana*  
*Alteratrachyleberis?* cf. *bullata*  
*Alteratrachyleberis?* *striatopunctata*  
 cf. *Cytheretta* sp.  
*Cytheretta haimeana*  
*Leguminocythereis scarabaeus*  
 For generic interpretations see LIEBAU, 1975a.

Hence the present work deals with the *families* Trachyleberididae, Hemicytheridae and Cytherettidae.

The Trachyleberididae and Hemicytheridae are particularly closely affiliated, according to OERTLI, 1956, MANDELSTAM, 1960, POKORNY, 1964f, VAN MORKHOVEN, 1962/63, HARTMANN, 1964, and HAZEL, 1967. The last three authors indicate the close relationship of Trachyleberididae and Cytherettidae. Since the results of the present study mainly confirm this conception, the author attempts to cover these families with a provisional higher taxon; for this purpose the term trachyleberide family group<sup>3)</sup> is applied. The word "trachyleberide" in this context is used formally to mean "with rough shell". The corresponding term is the "trachyleberid ostracods". It is not inconceivable that this group of families will be enlarged to include other families or subfamilies, most probably the Jurassic predecessors of trachyleberidides and cytherettides.

### 1.3.2. Conventional Standards for Characters

For decades there a relatively rigid ranking has been in use for taxonomic evaluation of the shell characters. The bases for these standards are contained in the major works by TRIEBEL (1941, etc.), POKORNY (1958), VAN MORKHOVEN (1962/63), HARTMANN (1966f) and HAZEL (1967), among others. Practical application of this system of evaluation can be observed in any number of morphological, taxonomic and biostratigraphic publications. In this system the following criteria are valid:

(1) Structure of the hinge: details of the hinge (e.g. the form of the anterior hinge tooth on the right valve) are generally decisive for the classification into genera or families.

(2) Configuration of the muscular field: distribution, outline and in certain cases the degree of separation of the adductor and antennal scars are in the same way characteristic of genera and families. The borderline between *Trachyleberididae* and *Hemicytheridae* is drawn by some authors, for example, predominantly on the basis of the limits of the antennal scar (cf. HAZEL, 1967).

(3) The form of the calcified part of the inner lamella is considered to be diagnostic for genus and sometimes family.

(4) The number, form and distribution of the marginal pore canals can be found in every complete diagnosis of a genus.

(5) The form of the carapace and outline of the valve are taken by many authors to represent generic, and occasionally familial, characters. This is to some extent the case in earlier conceptions of the Brachycytheridae, Hemicytheridae and Leguminocythereididae.

(6) Of the elements of coarse sculpture the muscle node is considered particularly significant for delimiting species and genera. The absence (or nonoccurrence) of eye nodes (if these are to be included in sculpture) can at times decide generic classification. A few

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<sup>3)</sup> "Trachyleberide family group" = Trachyleberididae s. l. in LIEBAU, 1975a.

years ago the occurrence and form of the longitudinal and marginal ribs began to become substantial components of diagnostic work (this new appraisal is partly associated with the trend toward conceiving genera as narrower categories than before).

(7) Only sketchy use is made of fine sculpture in the diagnosis of genera, if it is mentioned at all. "In *Trachyleberis* the spines on the posterior half of the valve are distributed on the surface, unlike *Actinocythereis* where they are grouped into three longitudinal rows" (this is how it is understood by VAN MORKHOVEN, 1962/63, etc.). This is one example of a relatively detailed interpretation of the fine sculpture in the diagnosis of genera. The fine sculpture has by far greater significance for the description of species, especially for the delimitation of very similar ones. Here again, however, the ornaments are outlined in but a few words or sentences. In other cases certain conspicuous elements of fine sculpture are singled out for emphasis.

As a rule, what remains disregarded taxonomically is the morphology of the shell in the preadult stages, the distribution of pore canals on the surface, the distribution of distal openings of pore canals situated on the margin, sex differences in the proportions of the shell, almost all details of fine sculpture and the paleoecological tolerances.

Deviations from this scheme are mostly insignificant; some authors emphasize this or that group of characters more than others. The author who pioneered the work of investigating the muscular field, hinge and pore canals was TRIEBEL. He considered sculpture, and fine sculpture in particular, less important for the taxonomy of species or genera. In his *Treatise* (1961, p. 88), SCOTT also stresses the significance of the hinge and muscular field. In like manner, the diagnoses of the genera within Cytheracea in the *Treatise* (HOWE, REYMENT, SYLVESTER-BRADLEY and VAN DEN BOLD) contains data on the "internal" characters, but with only a few references to the sculpture. VAN MORKHOVEN (1962/63) emphasizes, among other things, the significance of "primary ornamentation" at the generic level (criticisms of this approach were made by HARTMANN, 1966f, p. 63). POKORNY (1957) and DEROO (1966) investigated the origin and structure of the hinge in *Podocopida* and *Cytheracea*, respectively. POKORNY found indications of parallel developments in the hinge structure and in the evolution of the muscular field (POKORNY, 1964, 1968). Thus he opposes formal and rigid adherence to criteria of character weighting. HARTMANN (1963) takes into consideration especially the form of the free margin of the valve and compares the data of shell morphology with those of the morphology of the extremities of the recent representatives. These are also considered by HAZEL, 1967, who, in addition, ranks the muscular field configuration particularly highly.

The criticism of the rigid adherence to this scheme of evaluation becomes most obvious when obviously heterogeneous groups of forms are combined to form genera or families. Thus objections can be raised to the classification of *Leguminocythereididae* HOWE, 1961, and *Brachycytheridae* PURI, 1954 (compare POKORNY, 1957 and

1964, and HARTMANN, 1963 and 1964) based mainly on carapace shape. HARTMANN is able to support part of his criticism by invoking the morphology of the extremities of live representatives. PO-KORNY contrasts the "diagnostic" viewpoint with one based on phyletic relationship.

A general change in criteria has so far occurred only in level of application and in the reevaluation of the notions of genus and family. Thus, for example, the characters which in 1940 constituted a genus (*Isocythereis* TRIEBEL) were considered in 1962 to be adequate for a new subfamily (Mauritsiniinae DEROO), while today (HAZEL, 1969, written communication) they are already recognized as separating families. This has not affected ranking of characters.

### 1.3.3. Zoological Significance of Sculptural Characters

In the past the zoologist took little notice of shell characters in ostracods; HARTMANN, however, deals extensively with paleontologically important characters as well. In a study on ostracods (1966f), in "Bronn's Classes and Orders", he deals with the hard parts of the ostracod morphology. A separate section is dedicated to the taxonomic value of the sculpture. HARTMANN (1966, p. 64) says:

"The significance of sculpture for systematics can be included in the following three points:

(1) Surface sculpture is a valid character only for species differentiation; genera, families and higher units based on the surface sculpture indicators (wings, beaks, ribs) are mostly artificial units.

(2) Surface sculpture should not be taken as a single character but as character complex dependent on widely different endogenous and exogenous factors.

(3) For the phylogenetic observations the surface sculpture is only a very limited means, especially when the functional significance of the character is still unknown.

In support of this, I have been kindly allowed to quote from HARTMANN's letter (September 1969):

"...There are very closely affiliated species with sculpture of genetically common origin. Such coincidence can not be used for the establishment of genera, although they may be adequate for subgenera, unless we want to create a system dependent on but one character, which is unnatural. These principles follow from a comparative study of the soft body and the shell".<sup>4)</sup>

### 1.3.4. Principles of Identification and Evaluation of Taxonomic Characters

The evaluation of taxonomic characters of ostracods is based, so far as the author visualizes this set of problems, on a predominantly deductive argumentation which has been or can be tested with

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<sup>4)</sup> In spite of his contrary opinion on this matter, Prof. Hartmann gave the author the opportunity to continue the ornament studies in Hamburg during 1972 and 1973.

empirical results. The present study is also an attempt to improve the premises upon which these deductive standards are based. The assertion that the "fine sculpture as an external character is appropriate for the delimitation of species alone", is contrasted here with a different statement founded on exact observations. The question arises as to the possibility of establishing methods by which appropriate standards for the evaluation of characters could be established.

In determining the taxonomic value of one group of characters the author attempts to proceed by the following steps:

(a) objective survey of the morphological details ("raw material" of morphological characters)

(b) understanding their intraspecific or interspecific distribution from which

(c) endogenous variabilities (in number, position, form, size, and strength of expression) and exogenous variability can be derived.

It is from this total variability in its broadest sense that the taxonomic value of one group of characters follows.

Thus the present author opposes the apparently plausible (hinted at, e.g., by GOCHT and GOERLICH, 1957) that the zoologist alone can discover the standards for characters leading to natural systematics. Samples rich in individuals and species with numerous characters (if possible from several horizons) are often available to the ostracod paleontologist; from these it is usually possible to carry out a species-level delimitation corresponding to genetic relationships. It is on this basis then that the variability, and hence the taxonomic value of individual groups of characters, can be reevaluated.

In this way it is possible to deduce the taxonomic value of the *Limburgina*-type reticulation (main body of this study) from its distribution pattern or from variability (in the broadest meaning) within the fossil material. The relationship of this fine sculpture to a system of sensory organs (Section 4), and hence soft parts (at this point a deductive argumentation is possible), are not of substantial importance within this context.<sup>5)</sup>

This argumentation is confirmed by the investigations of reticulation and tuberculation patterns of Paleozoic ostracods. Here, for example, in *Nodibeyrichia* and *Clavofabella* (both being Silurian Beyrichiida) one can also identify tuberculation or reticulation patterns which are, as in the trachyleberid group of families, associated with systems of pores. Nevertheless, in Paleozoic forms patterns of fine sculpture with an entirely different variability appear: the number of elements varies within one species significantly (in *Clavofabella*, from one valve to the other in the complete carapaces). In keeping with this, another, much lower taxonomic value must be attributed to the ornaments of fine sculpture in such cases.

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<sup>5)</sup> See paper on left-right variation, LIEBAU 1975b.

### 1.3.5. Evolution of Variability

The preceding section discussed the relationships between variability and taxonomic utility in single characters. Strict adherence to a standard of evaluation presumes that variation remains the same. This presumption is not correct or is correct only when confined to closely related taxonomic groups.

The Beyrichiida, used in the preceding section for comparison, confirm that one and the same suite of characters within the ostracods can have very different variability. Also, for example, the muscular fields in Cypridinacea, Bairdiacea, Cypridacea and Cytheracea differ not only in ornamentation but also in the kind and degree of variability. These differences can be explained only by the fact that the variability of this field of characters has changed in some or in all groups. Evidently, variability has evolved.

For this reason the author does not attempt to reorganize the rigid, conventional ranking of taxonomic characters (example: the *Limburgina*-type reticulation pattern should be given greater attention than the muscular field in all cases from now on.) Instead, an attempt is being made to work with "flexible standards" i.e. in each individual case to examine the variability and to gauge the meaning of observed characters.

### 1.3.6. Systems of Characters Having Approximately Numerically Constant Elements

A reticulation pattern with "about 70" reticulation meshes offers two taxonomically useful characters:

- (1) reticulation is present.
- (2) mesh size "intermediate" (e.g.).

A reticulation pattern with *exactly* 70 reticulation meshes and whose elements have constant positions that are individually mapped, contains at *least* 71 taxonomically useful criteria:

- (1) a reticulation is present
- (2) the occurrence and distribution of each of the 70 elements can be significant.

In this case the elements (meshes) are genetically defined with regards to their number and position.<sup>6)</sup> Thus each mesh is the potential bearer of the character. The difference in utility is considerable. Investigations along this line seem to be rewarding.

*Full numerical constancy* in one system of morphological elements, however, signifies a decided decrease in its taxonomic value, since no changes take place. Thus the number of valves (two) *within* the class Ostracoda is a morphological trait without taxonomic value, and this is not a character at all; it cannot be used for the definition of individual species, genera, families or orders.

An ideal situation of taxonomic utility, on the other hand, is as follows: in a system with as many elements as possible having

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<sup>6)</sup> Correction: there is a class of small cones ("mesocones") which do not evolve as individual elements, although they have constant positions.

approximate numerical constancy of elements, occasional changes take place. The frequency of these changes is great enough to be helpful in distinguishing races. The changes within this suite of characters can be located with precision, since each of the elements has its particular position and form; that is to say, it is individualized. Thus in a given instance one can establish the absence of an element, since the elements surrounding it can be discerned individually.

Figure 5 illustrates the different evaluation potentials of patterns with approximate constancy of elements:

(1) is an example of nearly indeterminable elements. If a change in number occurs (1b), it cannot be localized (e.g. the extra element). The utility here is little higher than with broad numerical variation.

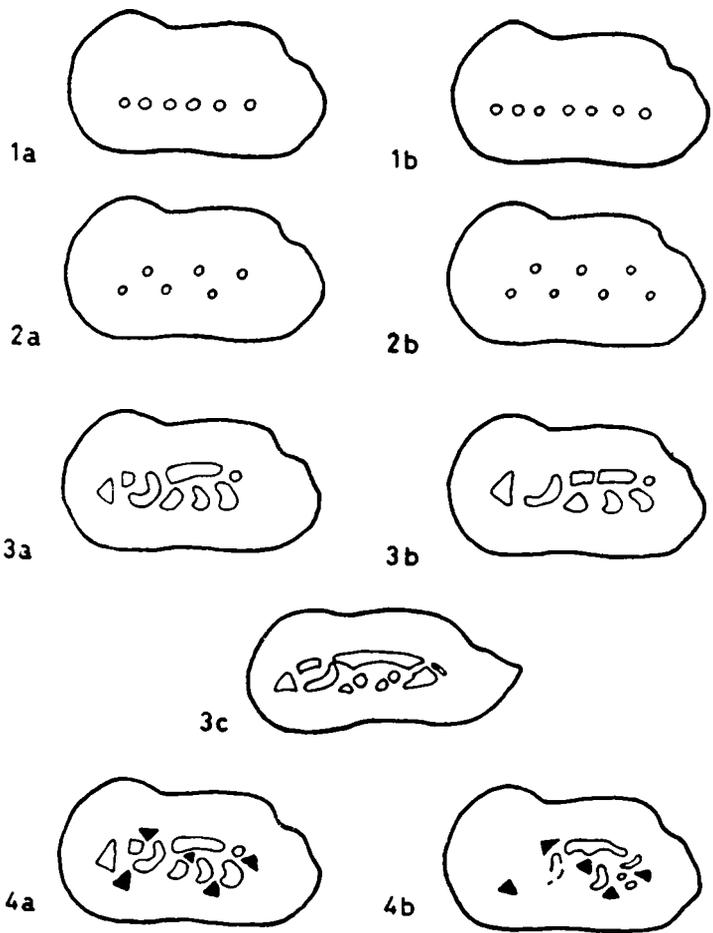


Fig. 5. Ornaments with different degrees of complexity: (1) and (2) pattern of "point" elements, (3) and (4) network pattern, the latter showing overlapping patterns, in principle corresponding to the Limburgina-type fine sculpture (see main body).

(2) although the elements are uniform in this case, the complication in their distribution means a marked increase in taxonomic value. A new additional element (2b) can be determined with a high degree of probability.

(3) the complex configuration is augmented by special features of the outlines of elements. Even if the number of elements changes (3b) or if they become deformed (3c), the possibility of identification is very high.

(4) the first system of characters overlaps another (black triangles); both show approximate constancy in the number and distribution of elements. (In trachyleberid ostracods the macroreticulation corresponds to one of these fields of characters and a cone or pore pattern to the other.) The complexity of the combined patterns, and hence the possibility of identifying the elements is extremely high. With great changes, too (4b), it is possible to show relationships, even when the comparison involves large phyletic distances.

Figure 5 shows that approximate numerical constancy can be fully utilized only if the position of a change can be precisely located. Most favorable is a high degree of complexity, e.g. mutual overlapping and interweaving of several complex systems of characters. A certain arrangement of this complexity is important for mnemonic reasons. The figure also shows that the network patterns can be much better evaluated than point or line patterns. They can, presuming constant locations of elements, also be used as a system of coordinates for the identification of elements in other systems of characters (spines, ribs) which overlap or border on the network.

Examples of network patterns with approximate constancy of elements are: configuration of skull bones in vertebrates, the design of horny plates on the turtle shell, the distribution of scales on the snake head and the innervation patterns of insect wings. The author regards the reticulation of the trachyleberid ostracods of the *Limburgina*-type as a further example.

### 1.3.7. Previously Established Homologies of Fine Sculpture

So far the elements of fine sculpture of one ostracod species have been homologized with corresponding elements of another only in relatively few cases.

As early as 1940 TRIEBEL observed the large pore cones of *Cythereis* ornamentation and established that at least one cone regularly recurs in the same position. He termed it the "Lücken stündiger Porenkegel", (pore cone situated in a gap; = "pore conulus" in POKORNY, 1963 and 1966; "subcentral pore cone" in HERRIG, 1966; compare "T17" in this study, p. 39). It is to be regretted that TRIEBEL did not pay attention to this pore cone when he examined other genera, for example *Isocythereis* or *Paracytheretta*.

In revising *Cythereis ornaticissima* (REUSS, 1846), POKORNY (1963) compared the details of fine sculpture in the area around the eyenode in several *Cythereis* species from the Czechoslovakian Upper Cretaceous. The tubercules were named individually.

In his monograph on the genus *Cyprideis* (Cytheracea, Cytherideidae), SANDBERG (1964) indicated that in this genus the arrangement of nodes is genetically fixed and that it can be used to delimit one species from another.

(Nearly a hundred years of investigating *Cyprideis* shows that almost without exception no distinction has been made between the genetically fixed arrangement of nodes and the ecologically controlled strength of expression. The Pattern of nodes, which can be traced back to the Upper Cretaceous, was interpreted by some authors as the product of ecological conditioning alone. Those who have commented on this finding include: HIRSCHMANN, 1909, SARS, 1922/28, TRIEBEL, 1941, WAGNER, 1957, VAN MORKHOVEN, 1962/63, SANDBERG, 1966f, and MALZ & TRIEBEL, 1970.)

From examining the *Protocythere* species (trachyleberid group of families) from the Lowermost Cretaceous, OERTLI (1966) noticed that three tubercles occupied constant positions.

The largest step forward so far is POKORNY's work (1966); he homologized, the larger lateral spines of *Cythereis* with those of *Pterygocythereis* (group of *Pterygocythereis spinigera* POKORNY, 1966). This was a comparison between two subfamilies (within Trachyleberididae s.l.).

Two recent species of *Normanicythere* (Hemicytheridae), which replace one another vicariously, were investigated by NEALE and SCHMIDT (1967). With the help of comprehensive identification of reticulation meshes and pits the authors were able to reconsider the separation of the species.

In Cypridea (Cypridacea, Cyprideidae) nodes appear which are similar to those of *Cyprideis*. ANDERSON (1967) showed that they have constant positions and named them individually. The results of these observations were applied in descriptions.

The reticulation patterns in the different species of *Radimella* (Trachyleberididae s.l. or Hemicytheridae) were associated by POKORNY (1968 and 1969), who homologized comparable meshes and groups of meshes in the different species. In this way he could distinguish the otherwise very similar species and could show a species radiation in the littoral zone of the Galapagos Islands.

## 2. LIMBURGINA-TYPE RETICULATION

### 2.1. OVERVIEW

Examination of ornamentation in several genera has indicated that there is approximate constancy of elements in several components of fine sculpture within the trachyleberid family group.

Reticulation of the lateral side appeared to be particularly appropriate for introductory research. The lateral reticulation of *Limburgina ornata* (BOSQUET, 1847), was chosen both as a starting point and as a system of reference. Reticulation patterns in other genera and species are compared with *Limburgina ornata* through mesh-by-mesh homologizing, so this pattern will be called the "limburgina-type".

There are several reasons that *Limburgina ornata* was chosen for this purpose. Its lateral reticulation is very clearly ordered: In the number and distribution of meshes its ornamentation links primitive Trachyleberididae and Hemicytheridae (see Section 7). Since it is a type-species, this form has a relatively certain nomenclatural position. Unfortunately, in this species, as in most other *Limburgina*, the pore conation is rather poorly developed. However, it is possible to rely on the fine sculpture of an affiliated genus, *Oertliella*, for this purpose. (Section 3).

Relationships between the *Limburgina*-type reticulation and a system of normal pore canals are discussed in Section 4.

Occasionally the *Limburgina*-type reticulation is overlain by another reticulation system. The latter consists of smaller elements which show considerable numerical variability. Obviously they are not connected with pores. Within the scope of this study, however, detailed investigations of the mentioned "microreticulation" are not undertaken. Where both forms of reticulation appear together, the *Limburgina*-type reticulation is called "macroreticulation" as opposed to "microreticulation".<sup>7)</sup>

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<sup>7)</sup> Complete definition of microreticulation is as follows: Elements smaller than neighbouring ones of the macroreticulation. No relation to a pore sys-

## 2.2. NAMING OF RETICULATION MESHES

For the naming of individual elements of lateral reticulation the fact that the meshes are arranged in series (Fig. 6) is convenient for mnemonic reasons. In Fig. 7, 70 "normal" meshes (equipped with pores) of *Limburgina ornata* are individually lettered and numbered. (The relationship between meshes and pores is dealt with in Section 4.) Four additional meshes were named from another *Limburgina* species (N-meshes, see p. 36). Mesh P5, which appears posteroventrally from P4, is shown on *Mauritsina latebrosa* (see p. 54).

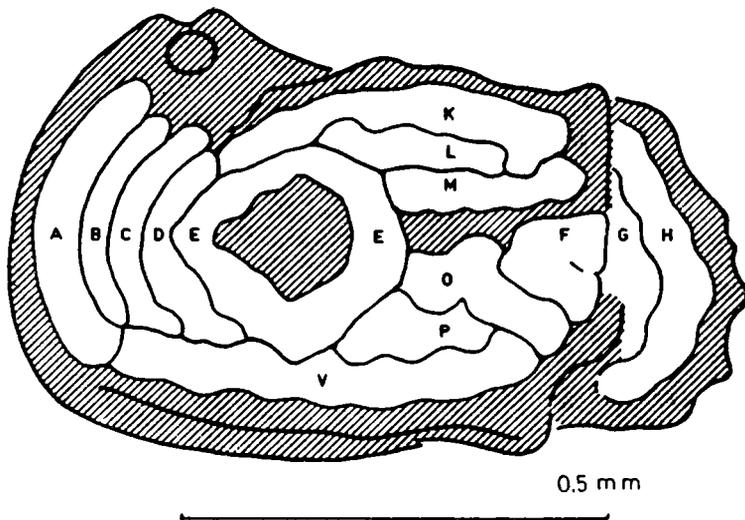


Fig. 6. Mesh rows of lateral reticulation of *Limburgina ornata* (BOSQUET, 1847) (much simplified).

G-meshes have not been thoroughly investigated as yet. On the basis of their position they only very seldom be comprehended. At least 3 other meshes of the normal construction and connected with pore canals can appear within the E-ring on the muscle node (MH-meshes). These have not been closely investigated either. The same holds true for the "secondary meshes", or meshlike depressions in front and beyond the ocular projection, (here they are designated "PR and SO") and on the ribs (with *Spinicythereis* and *Dumnontina*,

tem. Numerical variation; no constant positions of elements. Microreticulation pits may cover the sola of macroreticulation meshes or replace the whole macroreticulation, but do not occur on macroreticulation muri (in contrast to foveolation). With very few exceptions the occurrence of microreticulation excludes that of microconation. Often related to calcification strength (tendency to weak calcification: microreticulation predominantly in cold- or brackish-water facies or e. g. in larval stages). Microreticulation concept: see also LIEBAU, 1975b: 78 (Delaware symposium); descriptive terms see SYLVESTER-BRADLEY & BENSON, 1971.

for example).<sup>9)</sup> According to observations so far, they do not have direct contact with pore canals and differ in this respect substantially from the other meshes of the *Limburgina*-type reticulation.

In addition to reticulation meshes, pore cones were also noted (Fig. 7, e.g. "T25"). They are discussed in Section 3.

### 2.3. INTRASPECIFIC VARIABILITY OF RETICULATION IN LIMBURGINA ORNATA

Reticulation patterns on 55 valves of adult ♂♂ and ♀♀ *Limburgina ornata* from the Tuffaceous Chalk of Maastricht have been compared with one another. As a reference system, the scheme presented in Fig. 7 was used. The author tried to find out whether and to what extent the 70 meshes of the anterior and central reticulation systems could be recognized on individual specimens.

Correspondence: excluding reduction of mesh walls (see below) and individual positional shifts; in the following cases, reticulation ornaments were found to coincide in the respects explained above:

17 out of 20 left valves ♀♀

25 out of 30 right valves ♀♀

0 out of 2 left valves ♂♂

3 out of 3 right valves ♂♂

i.e. a total 45 (82%) out of 55 valves

Absent or doubled meshes: variations in the number of meshes can be observed or inferred in the following specimens:

(a) with one additional mesh:

L ♀ : approximately at P4

R ♀: appr. at C3

L ♀ : appr. at M2

R ♀: appr. at B2

L ♀ : ? appr. at P4

(b) absent meshes:

L ♀ : without M2

R ♀: without B3

L ♀ : without B3

R ♀: without B5, D1

? without C1

? without E3, E9, E6

R ♀: ? without P2

R ♀: ? without B4

(L designates the left and R right valve). Three valves are listed under both (a) and (b).

Doubled or missing meshes of the given pattern of reticulation. Only in isolated cases can one safely say which mesh in a group is

<sup>9)</sup> These meshes are named in LIEBAU, 1975a: Fig. 1.

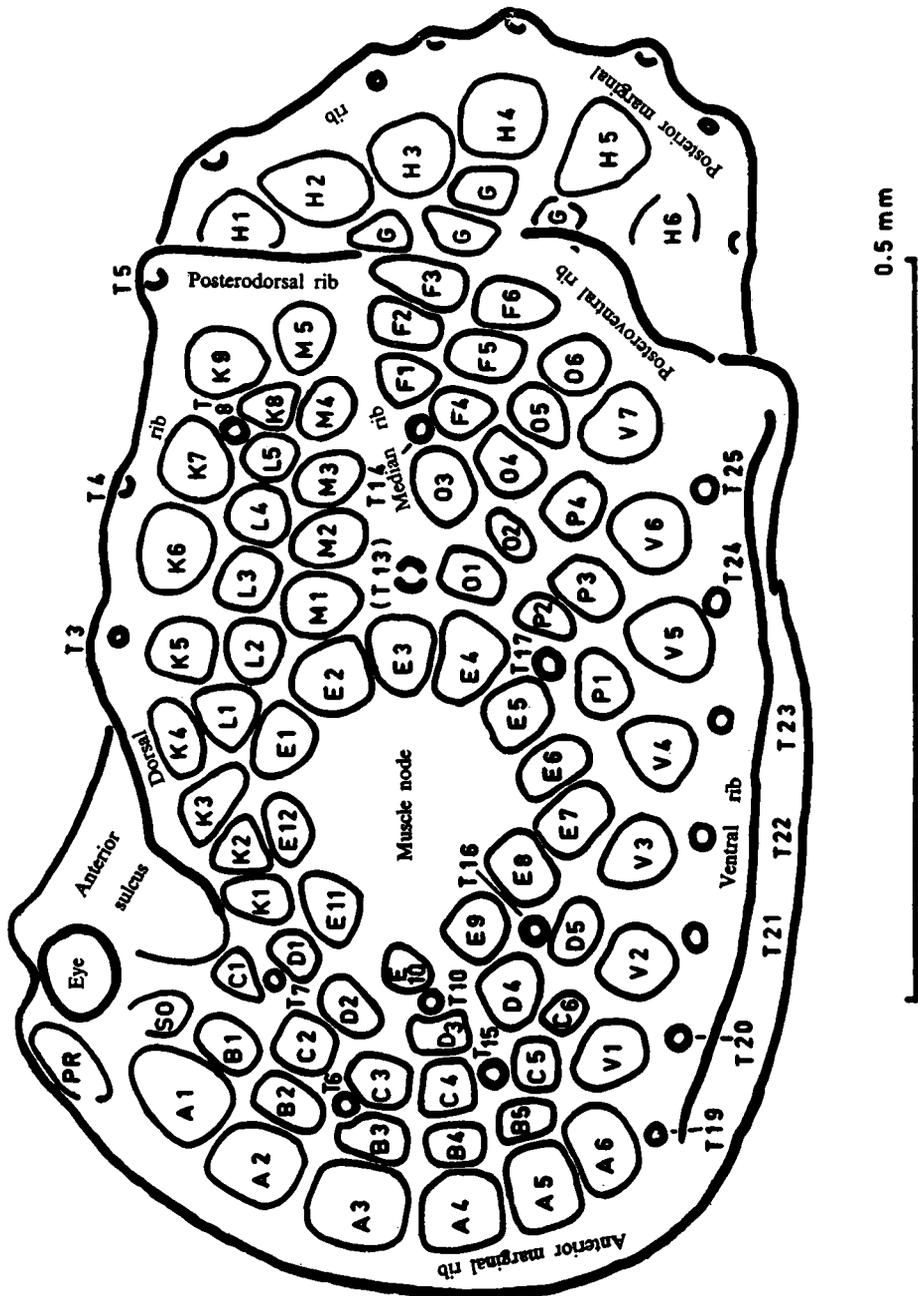


Fig. 7. *Limburgina ornata* (BOSQUET, 1847). Meshes of the lateral reticulation are individually named. This reticulation is the reference system for comparing *Limburgina*-type patterns of fine sculpture. In designating cones ("T3, T4", etc.), the conclusion from Section 33 have been used. The figure is a composite drawn from several female left valves. Upper Maastrichtian, Tuffitic chalk of Maastricht. Taken from LIEBAU, 1969.

absent or duplicated. Several interpretations are often possible. The doubling of an adjacent mesh (e.g. the extra "P5" from P4) or the intrusion of a mesh (e.g. from the section behind) has similar consequences; the gaps can be taken as resulting from unification of meshes or reductions of mesh walls. Out of about 3850 meshes investigated, the doubling rate in 55 valves was 0—0.15% and the rate of reduction about 0.1—0.3%.

Reduction of mesh walls: the most frequent alterations result from the unification of neighboring meshes. Here the walls separating adjacent meshes are poorly developed or missing altogether (reduction of mesh walls), so that instead of two (or several) meshes there is only one, noticeably larger mesh. Here the pattern of adjacent meshes is not disturbed. Only infrequently is there a completely homogeneous "aggregate mesh", whose origin can be established by the number of pores (see Section 4): also, a faint ridge is often observed at the solum of such a mesh. (Of course, even minute amounts of adhering sediment can make clear evaluation impossible.) In certain reticulated areas, mesh fusion (of different degree) is frequent: the mesh walls between the A and B series (always between A1 and B1, A2 and B2, etc.) are more or less reduced in 28 valves (51%). In 6 specimens K8, K9 and sometimes L5 are fused in the same manner and in 3 (or 4) cases the wall between P2 and P3 is missing. Further areas with reduced mesh walls were found, apparently irregularly scattered, in 14 out of 16 individuals (these could also be interpreted as loss of meshes; see above). Two specimens showed 3 and 5 deviations of this kind, respectively.

On a total of 17 valves (31%) not one deviation was registered. Four valves had 4—6 deviations each. The lateral reticulations of the right and left valves in *Limburgina ornata* are bilaterally symmetrical since no deviations could be found to occur significantly on either valve.

All the 5 valves of ♂♂ show this peculiarity: mesh K8 lies in a row between K7 and K9. With the valves of ♀♀, mesh K8 is invariably moved ventrally to intrude into the L row of meshes.

Valves of juvenile specimens were not available.

In terms of carapace size and proportions and above all the form of reticulation, this species shows a higher variation than is usual for *Trachyleberididae* and *Hemicysteridae*. This probably pertains also to the above data on deviations in reticulation. In the expression of reticulation two forms may be differentiated: in one the walls of meshes are strongly thickened distally, so that the openings of meshes look like minute pinpricks, while in others the mesh walls are lower and narrowed at their distal ends, resulting in a reticulation with markedly broad meshes. In the latter type there also appears a somewhat more pronounced pore conation. Intermediate forms are much more frequent than these two extreme types. In some samples one type is more represented than the other, which may suggest ecological influence. These differences in the expression of reticulation do not pertain to the number and distribution of meshes.

## 2.4. HOMOLOGOUS RETICULATION MESHES IN *LIMBURGINA ORNATA*

From the above comparison of 55 valves of *Limburgina ornata* it can be seen that: the same mesh pattern appears in all the investigated valves, not counting isolated deviations. The lateral reticulation in *Limburgina ornata* is approximately constant in the number and arrangement of meshes. This reticulation pattern is much too complex to recur in exactly the same form by chance alone or conditioned by function (convergently) in very many individuals. Thus the detailed coincidence has to be genetically conditioned. Reticulation patterns in different individuals are homologous mesh for mesh.

## 2.5. INTRAGENERIC VARIABILITY OF LATERAL RETICULATION IN *LIMBURGINA*

In addition to *Limburgina ornata*, 19 other *Limburgina* species were investigated for lateral reticulation. These come from West and Central European Turonian to Eocene localities.

Additional meshes, related to the lateral reticulation in *Limburgina ornata*, appear only in the form of "N-meshes" in the median rib area region (they are discussed in the following section). The only mesh that is often absent is E10. Its reduction is as a rule associated with the development of a ridge on the anterior face of the muscle node. Meshes very often merge; this applies most of all to A1+B1, A2+B2, etc., E1+L1, and the link between K1 and the meshes on the anterior sulcus. The posterior K-meshes are often connected with one another and with L5; the central K-meshes (K5—K7) sometimes combine with the L-meshes below them. Other combinations are: M1+M2, M3+M4, O1+O2 and O5+O6. The N-meshes (see below) set up only these bonds: N1 + N2 and N3 + N4. (It is difficult to distinguish between the merging of meshes and the absence of one mesh. If the meshes concerned are arranged longitudinally one beside another, for example O1 + O2 and perhaps M1 + M2, then these are the elongated males, in which the otherwise connected meshes sometimes still appear as separate entities.) The only mesh which substantially changes its position is K8. In this genus it was impossible to attribute the position of K8 to sexual dimorphism except in *Limburgina ornata*. Three species, including *Limburgina semicancellata* (BOSQUET, 1847) and *Limburgina longiporacea* DE-ROO, 1966, have obviously flattened reticulation and the mesh series merged into shallow furrows. Two *Limburgina* species with relatively clear lateral reticulation are shown in Figs. 8 and 9.

In discussing the data on intrageneric variability it was presumed that the mesh names defined for *Limburgina ornata* would be easily applied to the other *Limburgina* species. Actually it proved that the meshes of lateral reticulation in *Limburgina pseudosemican-*

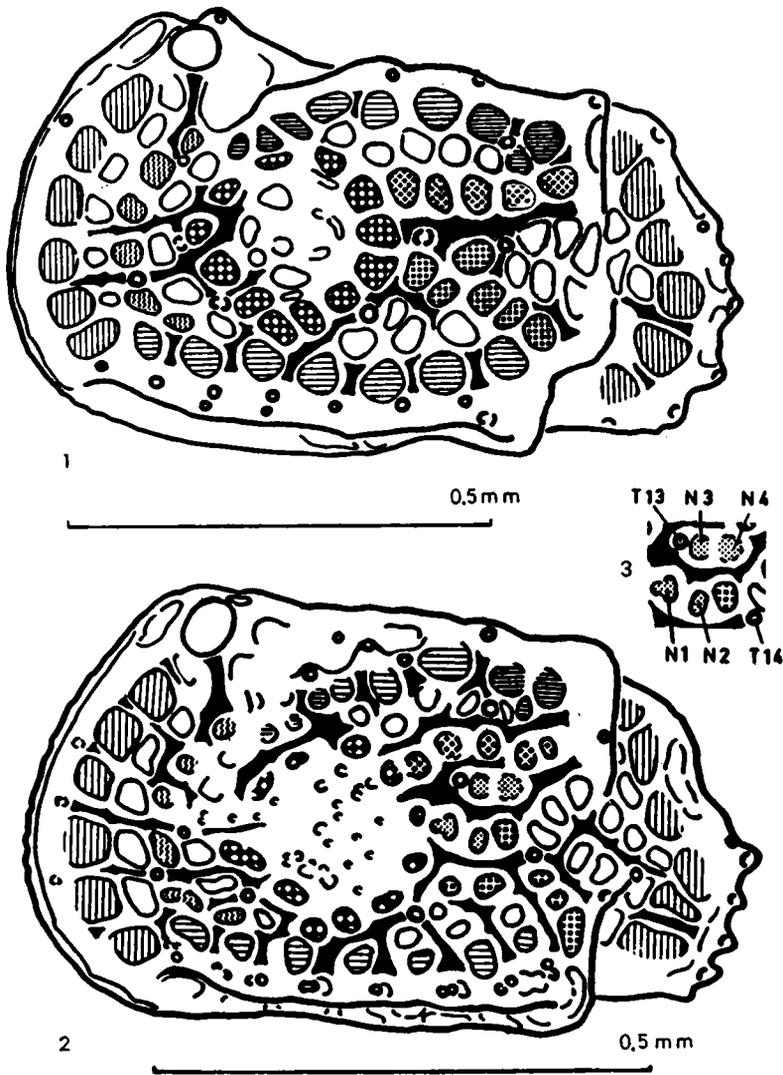


Fig. 8.

(1) *Limburgina ornata* (BOSQUET, 1847). Instead of letters & numbers, shading is used to mark components of reticulation. For key see (7). The median rib and the ridge-like reinforced walls of meshes within reticulation are blackened. Basic drawing as under (7).

(2) *Limburgina aff. depressa* DEROO, 1966. The median rib is reduced to a system of low-lying ridges; in its place 4 additional meshes appear ("N-meshes", see Fig. 3. Two cones ("T13" and "T14"), which can be seen in *Limburgina ornata* as protuberant or elevated parts of the median rib, are in this case more or less isolated between the meshes. The front part of the dorsal rib is broken up into a series of cones. Left valve of a female. Lower Maastrichtian from Mas de Guillen on Montsech (southern Pyrenees), horizon bearing *Praeradiolites pulchellus*.

(3) Meshes and cones in the region of the median rib in *Limburgina aff. depressa*. Detail from Fig. 2 with mesh designations. Magn. the same as under Fig. 2.

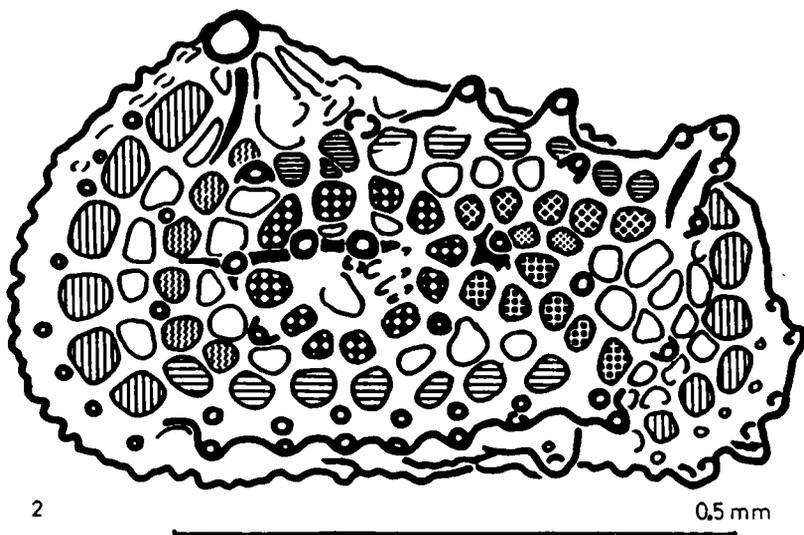
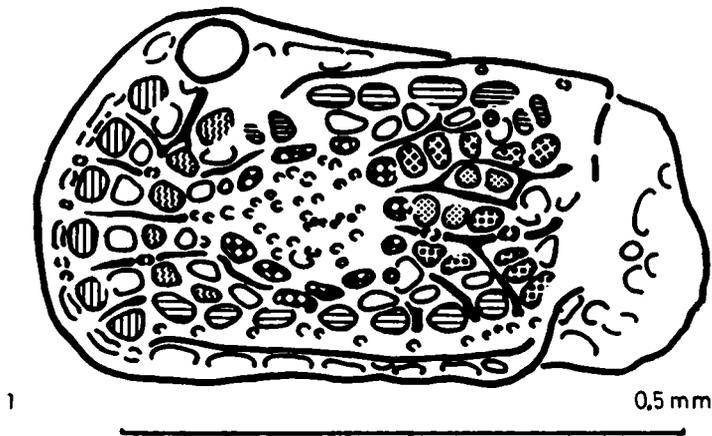


Fig. 9.

(1) *Limburgina pseudosemicancellata* (VAN VEEN, 1936). Another example of a *Limburgina*-type reticulated species with reduced median rib. Mesh K3 and a portion of the reticulation on the posterior part were not observable on this specimen, due to incomplete preservation. Left valve of a female. Upper Maastrichtian tuffitic chalk of Maastricht (Sample 12649 of the Federal Institute for Geosciences, Hannover).

(2) *Oertliella harridula* (BOSQUET, 1854). In combination with Fig. 8. this is an example of intergeneric comparison of the *Limburgina*-type reticulation ornament: on this valve of an *Oertliella* species, as compared with the above *Limburgina* species, meshes F4, L5 and P2 are missing. There are only two N meshes. In other respects all meshes of lateral reticulation can be individually recognized (further data on this specimen in Fig. 10).

*callata* (VAN VEEN 1936), except for the N-series meshes, are individually homologous to those of the *ornata* reticulation (Fig. 7). This augmentation corresponds exactly to that used for the intraspecific comparisons with *Limburgina ornata*.

## 2.6. REPLACEMENT OF THE MEDIAN RIB BY N. MESHES

In most of the investigated *Limburgina* species (c.f., preceding section), the median rib is more or less reduced. In its place there are most often 2—4 additional meshes that are not observed in the *Limburgina ornata* reticulation. These meshes are referred to as "N1", "N2", "N3" and "N4". (For definition see Fig. 8, 3).

As a rule the following relationship exists: if the median rib is broad and high, it can contain at most several minute pits; the more flattened it is the larger these depressions will be. If the rib is absent altogether, there are in its place four normal-sized reticulation meshes. As is known from intermediate morphological stages, meshes N1 and N2 come out from the median rib on its anteroventral side, corresponding with N3 and N4 on the postdorsal side. The remainder of the median rib, reduced to a thin ridge, often appears as a relic between the pairs of N-meshes.

Fig. 8, 2 and Fig. 9, 1 show two *Limburgina* species in which the median rib is transformed into a system of ridges of low relief through the development of N-meshes.

In several *Limburgina* species the median rib seems to be in the process of disappearing. It is likely that this signifies the substitution of the median rib by N-meshes, the process always recurring in the same way.

At times two tubercles are also seen which may remain after reduction of the median rib (T13 and T14, see p. 38).

### 3. LIMBURGINA-TYPE CONATION

#### 3.1. SURVEY

The valves of *Cythereis* and *Oertliella* can be covered with 500 to 800 tubercles and spines. The larger pore cones are here called "macrocones". They occur beside and between the meshes of lateral reticulation and occupy, like these, more or less constant positions. Hence they can be a valuable supplement and check for the system of characters of lateral reticulation (as markers with constant positions, cf. p. 24). For this reason it is important that the cones be distinguished from other kinds of tubercles and spines and that they should be named individually. On the basis of size, variability, alignment and distribution the author has grouped the tubercles and spines into 4 classes:

(1) "Microcones"<sup>9)</sup> minute tubercles showing appreciable numerical variability in most cases. Typically they extend from the crests of reticulation mesh walls. They protrude inwards at an acute angle to the surface of the valve or are parallel with it in the space above the reticulation mesh (this is the case in *Cythereis*, *Oertliella*, *Trachyleberidae*). Often this results in the formation of "spongy" reticulation. Microcones can also be directed distally, in which case they lie on the walls of meshes like strings of beads (*Echinocythereis*). In some cases every microcone shows a depression at its tip, which can be considered a pore opening.

(2) Mesocones are usually slightly larger than microcones and are always distally directed. In the typical case they are either on almost every intersection of the reticulation (*Cythereis*) or midway between such points on the mesh walls (*Oertliella*).<sup>10)</sup> Thus mesocones

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<sup>9)</sup> Microconation and microreticulation (footnote 8) are both grouped together as "microornament", characterized by small elements varying in number and without clear relationship to pore systems.

<sup>10)</sup> According to SYLVESTER-BRADLEY & BENSON, 1971, conjunctive and disjunctive spines, respectively. Genetics: mutations do not affect single mesocones, but the whole mesoconation or unexactly defined parts of it.

have firmly fixed locations. They also occur in species which are weakly or not at all reticulate. Each cone seems to contain a pore opening.

(3) Marginal cones<sup>11)</sup> are arranged in 1—3 rows parallel to the free margin of the valve. Their size varies. In the cases investigated here (Cythereis, Oertliella, Mauritsina) they show approximate constancy in number and distribution. Leading to them are the marginal pore canals. (Also belonging in this category are cones referred to by other authors as anterior marginal denticles and posterior spination.)

(4) Macrocones occur infrequently, and are found in specific locations in the reticulation of the *Limburgina*-type. They are distinctly larger than neighbouring mesocones. A pore canal (simple macrocones) or several canals (complex macrocones) run through them. As far as can be observed, the pore canals are long and thin (see also POKORNY, 1963). If the macrocones are missing, their pore openings often still mark the appropriate positions. They always lie between or beside reticulation meshes, never within them.

Among the four types of cones certain gradations are possible. In LIEBAU, 1969 the micro and mesoconation is designated as the "secondary tuberculation". (Fig. 4, 1 of that paper shows the meso and macrocones. Data on absence of pore openings must now be revised and supplemented.)

The author believes that there are also cone-like structures on the shell which are not associated with pore canals and which could have originated in rather different ways.

The present work describes only the macrocones of the lateral side. An extensive description of the other groups of cones will appear in a later publication.

### 3.2. MACROCONATION IN OERTLIELLA HORRIDULA

*Oertliella horridula* (BOSQUET, 1854) (Fig. 10) is strongly reticulate and at the same time richly conate. Nearly every mesh in the lateral reticulation can be correlated with a mesh in the reticulation pattern of *Limburgina ornata*. Only N3 and N4 are not present on *Limburgina ornata*, but these are found on *Limburgina depressa* (see Section 2.6.). Five meshes are almost always missing in the lateral reticulation of adult specimens of *O. horridula*: E10, F4, L5 and P2 (and, in comparison with *Limburgina* sff. *depressa*: N1 and N2). Two of these meshes (F4 and L5), however, can occasionally be demonstrated on specimens with short spines (expression of conation is again obviously influenced by paleoecological factors; see Section 1.2.3.2.). All the listed meshes have been found by the author on other *Oertliella* species. Juvenile stages (A-1) of this group of species

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<sup>11)</sup> The system of marginal pore cones (= "periconation", reserved term) is composed of meso- and macrocones (see LIEBAU, 1975a, 354).

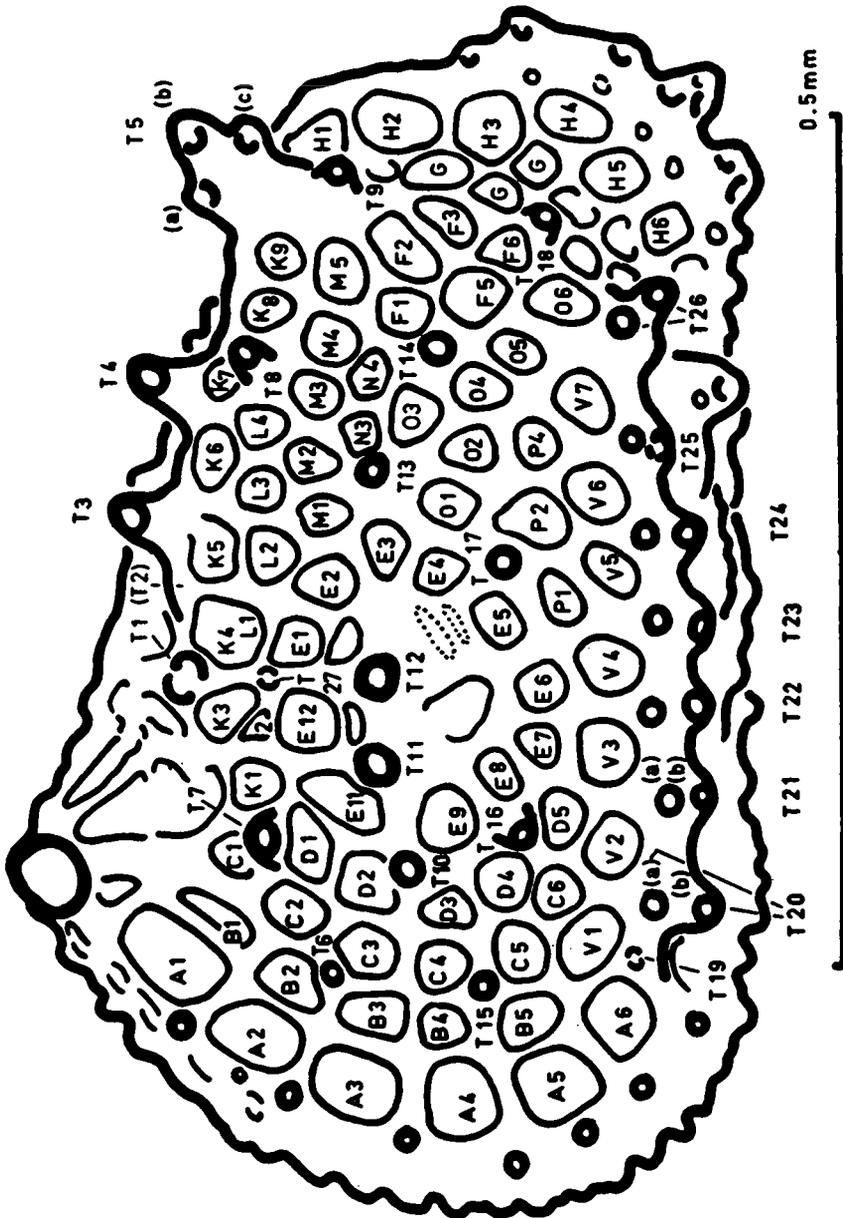


Fig. 10. Lateral reticulation and conation of *Oertliella horridula* (BOSQUET, 1854). The conation is more complete than that in *Limburgina ornata* and serves as an additional reference pattern for the definition of conation. Stippled outlines indicate minute pits in the region of the lower adductor muscle scars. The drawing is made from the left valve of a female. Upper Maastrichtian tuffaceous chalk of Maastricht (sample 12649 of the Federal Institute for Geosciences, Hannover). Revised from LIEBAU, 1969, Fig. 1 (2).

show E10, N1 and N2. K2 and K3, and K4 and L1 are often fused. To summarize, it is possible to contend that intergeneric variability of lateral reticulation in *Limburgina* vs. *Oertliella* is hardly greater than the intrageneric variability within *Limburgina*. (Both genera differ in the muscle area and often also in the fine and course sculpture: *Limburgina* usually has the median rib, *Oertliella* never has one, and the conation of *Limburgina* is much reduced).

Such great coincidence of reticulation patterns allows the macroconation pattern, the second major component of fine sculpture of the *Limburgina*-type, to be defined in a species of *Oertliella*. Fig. 10 shows the position and names of 27 macrocones within and on the edges of the lateral reticulation.

(Fig. 10 in many respects corresponds to Fig. 1, 2, in LIEBAU, 1969, but it had to be corrected with respect to T19, T27 and within the 0-series. New results from a thorough investigation of the horridula-aculeata phylogeny have made these corrections important.)

### 3.3. CONATION IN LIMBURGINA ORNATA

Low macrocones are also found in the reticulation on *Limburgina ornata* (BOSQUET, 1847). In investigating the 55 valves (p. 29) from the Tuffaceous Chalk of Maastricht, the following cones were observed:

Macrocones	Position between reticulation meshes	Frequency of occurrence
T6	B3/C3 or B2/C2/C3	3 out of 55 valves
T7	C1/D1	2 out of 55 valves
T8	K7/L4/L5	3 out of 55 valves
T10	D3/E10	4 out of 55 valves
T14	F1/03/04	2 out of 55 valves
T15	C4/C5	9 out of 55 valves
T16	D5/E9/E8	20 out of 55 valves
T17	E5/E4/P1/P2	46 out of 55 valves

Here again, if the cones are visible at all they have stable positions within the reticulation. Variability thus applies to the size, but not to the distribution of cones. ("Apparent numerical variability", cf. p. 15, is not taken into consideration here). The strength of conation is correlated with the formation of mesh walls. In the valves with "spongy" reticulation (mesh walls broadened distally, see p. 33) only a few cones are observable, and even these are only manifested as low-lying nodes or ridges.

## 4. PORE SYSTEMS AND FINE SCULPTURE

### 4.1. MESH PORES

At the sola of the reticulation meshes in some *Oertliella* species one can observe slightly convex lattices or sieves: These are approximately circular in outline and their size is equivalent to one-fourth to one-half of the mesh diameter. In *Oertliella* sp. 2 from the Lower Eocene of Gan (Southern France) the diameter of these sieve dates is about 20—25  $\mu$  (Fig. 13, 3). Sieve openings are partly irregular and partly ordered in rows; their number is about 100 to 200 per sieve. On the inside of the valves wide-mouthed normal pore canals lead in to the sieve. Hence the lattices or sieves are "sieve-like pore canals".

With photographs obtained by SEM (scanning electron microscope) (magn. 750x) the lateral sides of several *Oertliella* species were searched for such sieve pore canals. Adult valves of *Oertliella aculeata* cf. *aculeata* (BOSQUET, 1852) and four affiliated species, and *Oertliella lichenophora* (BOSQUET, 1852) were examined. These came from the Lower Tertiary of the southern Pyrenees, Aquitania and the Paris basin. A convex sieve can be observed at the sola of the following meshes:

A1 — A6, B3, B5, C3, C5, D1, D2, D4, D5, E2 — E5, E7, E9, E11, E12, F2, F5, F6, 2 G-meshes, H2, H3, K5, K6, K8, K9, L1, L3, M2 — M5, N4, O2 — O4, O6, P1, P4, V3 — V7.

In the majority of remaining meshes it is also likely that sieve pores will be found; in the few specimens the author examined, the corresponding mesh sola were covered with sediment or hidden by uncommonly high mesh walls. Some meshes do indeed seem to lack pores, or least the large sieve pores. Thus, for example, sieve pores were found at the sola of meshes O4 and O6 in 3 out of every 7 investigated valves, whereas mesh O5, situated between these, showed a smooth sola in 5 out of 7 such cases. The three anterior K-meshes (K1—K3) do not seem to have any sieve pores, either. It is remarkable that, in contrast with almost all other mesh walls, those between O4 and O5 and between K2 and K3 never have micro or mesocones (see P. 37).

In the *Limburgina* species, also, at a certain stage of calcification and preservation of the shell, pores on the sola of reticulation meshes are visible. In these species they appear as minute cones at the tip of which the mouth of a crater-like pore canal is observable. Although the proximal openings (on the inside of the valves) are never as large as they are in *Oertliella*, they are still relatively easy to observe. Corresponding observations have been made on the Upper Cretaceous "Spongicythere" and "*Hermanites*" species and on *Pokornyella ventricosa* (BOSQET, 1852) from the Lower Tertiary.

#### 4.2. CONE PORES

The relationship between cones and pore canals has long been known. Such cones with pore openings were termed "*Porenkegel*" (pore cones) by TRIEBEL (1940). In Cythereis and Pretygocythereis (1963, p. 6 and 1966, p. 308) POKORNY distinguishes the large "pore conulus" (T17) from smaller "pore spines" (principally mesocones, but also macro and pericones). Light-transmission observations (see also POKORNY 1963) show that these pore canals are long and thin. The distal aperture of such a pore canal forms either only a small depression at the tip of a cone or it is an enlarged, funnel-like structure so that the cone resembles an open tube (Fig. 11). Proximal openings are relatively small and only seldom observable. In contrast with reticulation meshes, there are cones with 2 or more pore-anlagen. Thus one can differentiate simple and complex pore cones. The complex pore cones can break up to from several simple ones, and vice-versa.

The same Lower Tertiary *Oertliella* specimens checked for mesh pores (see above) showed pore openings in the following macrocones:

One opening is detectable on each of the following: T1—T4, T6—T10, T13—T18 and T27. There are least two pores on T11, three pores are visible on T5, and there are at least three on T12 and T26.

It is very likely that the cones of the ventral rib T20—T25 have two or three pore cones each. (On the two valves of an *Oertliella* sp. six similar, bifurcated cones were noticed in this region. Because of their location their tips were usually damaged. It was only in one case that an obviously complete T25 cone was found: each of the branches had at its end a deep depression, while between the two branches an inconspicuous, third opening appeared. This opening was also present on T21—T25. The apertures of the pore of the upper branch appear in T21a—T23a; the mouth of the lower branch was observable on one T24b.)

No pore opening was visible in T19 on the investigated specimens, probably because of poor preservation.

In an *Oertliella* species with particularly long spines (Figs. 11 and 12) pore canals are visible on cross sections of the broken cones. Whereas the completely preserved cones or cone branches have one deep funnel-like opening with a maximum diameter of about 10  $\mu$  (at 770—820  $\mu$  length of valve and 40—80  $\mu$  length of spine), the cross section reveals a canal of 1—3  $\mu$  in diameter about midway along

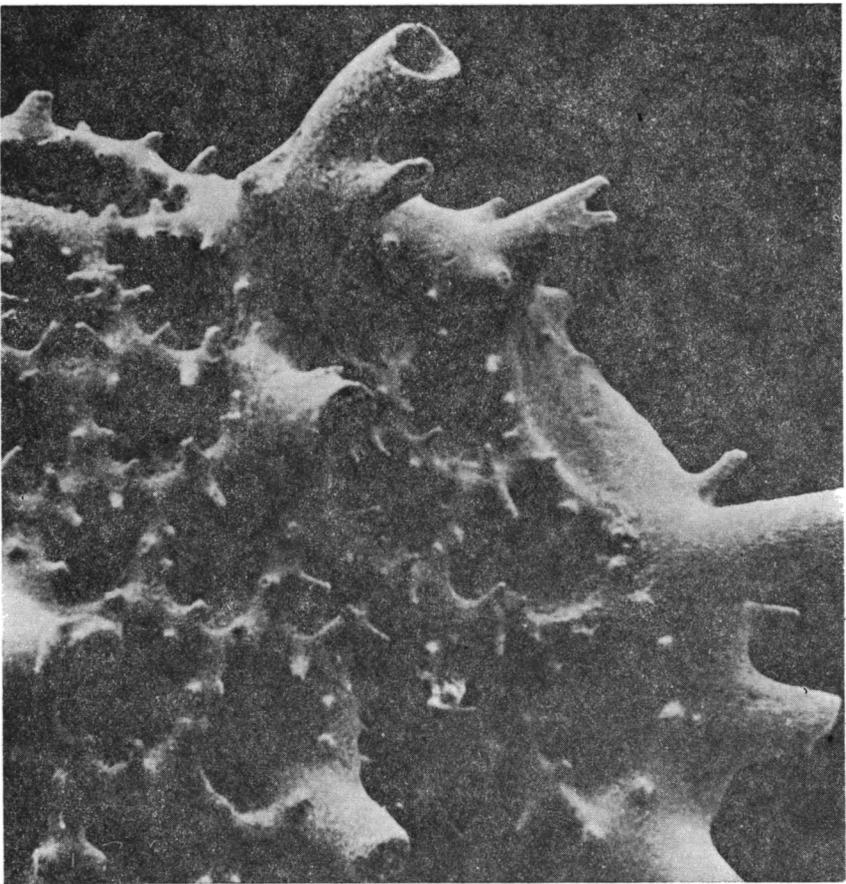


Fig. 11. *Oertliella* sp. 1. The postero-dorsal part of the left valve of a female. Above is the conspicuous main branch (T5b) of cone T5. It is not damaged and there is a deep funnel-like opening observable within. The left branch (T5a) is broken. T9 and T18 (above and below the center of the photograph, respectively) are preserved as stumps. At the left margin of the photograph T14 is situated (cf. Fig. 12). Lower Eocene (Cuisian with *Alveolina oblonga* and *Assilina placentula*), Tuilerie de Gan near Pau (southern France). Scale: width of the picture corresponds to 0.25 mm.

the spine length. These observations were carried out on cones and branches T9, T12 (main branch) and T14 and T22a.

The following conclusions are drawn:

(1) Mesh pores: short, broadly open, often with a funnel-like proximal opening, terminating distally at the base of a mesh, sometimes in the form of a sieve? observable from the outside.

(2) Cone pores: long, thin pore canals whose aperutres lie at the tips of cones.

The number and arrangement are approximately constant for both types of pore in the investigated trachyleberid ostracods.

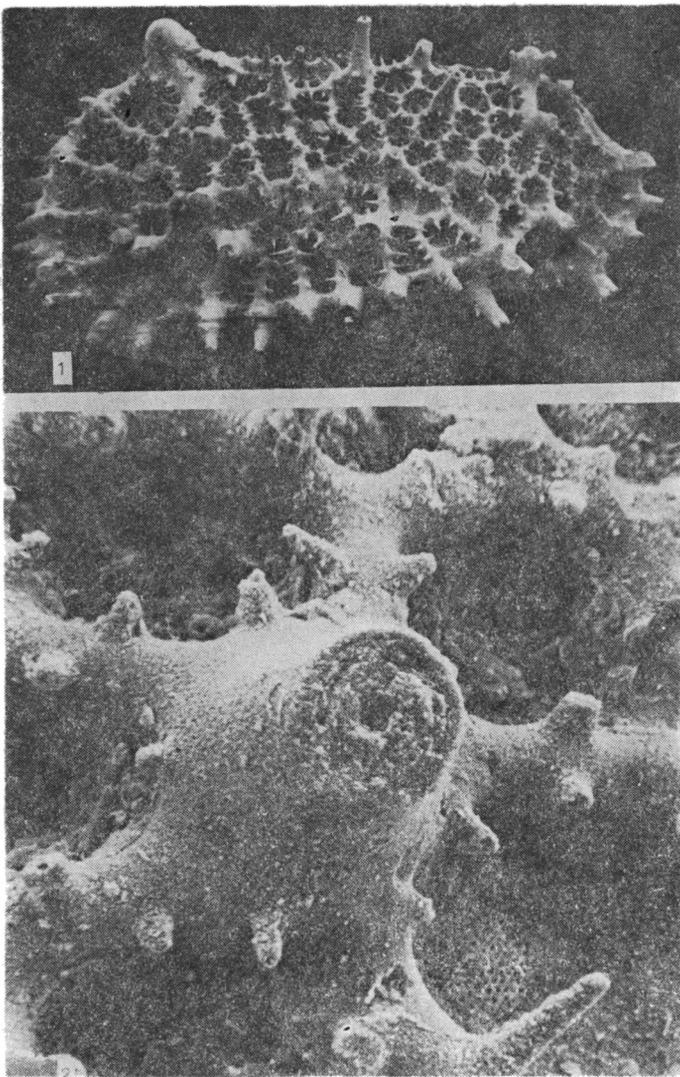


Fig. 12.

(1) *Oertliella* sp. 1. Lateral view of the left valve. Long macro and microcones are characteristic for this population, or subspecies. Characteristic for the species is the formation of large aggregate meshes in lateral reticulation, particularly near the ribs. Two aggregate meshes (01—02 and 04—05), postero-ventrally from the middle of the valve, still show very faint transverse ridges; these are mesh wall relics, and do not have microcones. Same species and sample as in Fig. 11. width of picture corresponds to 1.0 mm.

(2) *Oertliella* sp. 1. A detail of a left valve: cone T14 and its vicinity. Only the stump of the cone is preserved. In the center of the plane of breakage the position of the pore canal is marked by a depression. To the right below the cone there is a well-preserved sieve pore on the solum of mesh F4. The same species and sample as the preceding. Width of picture corresponds to 0.1 mm.

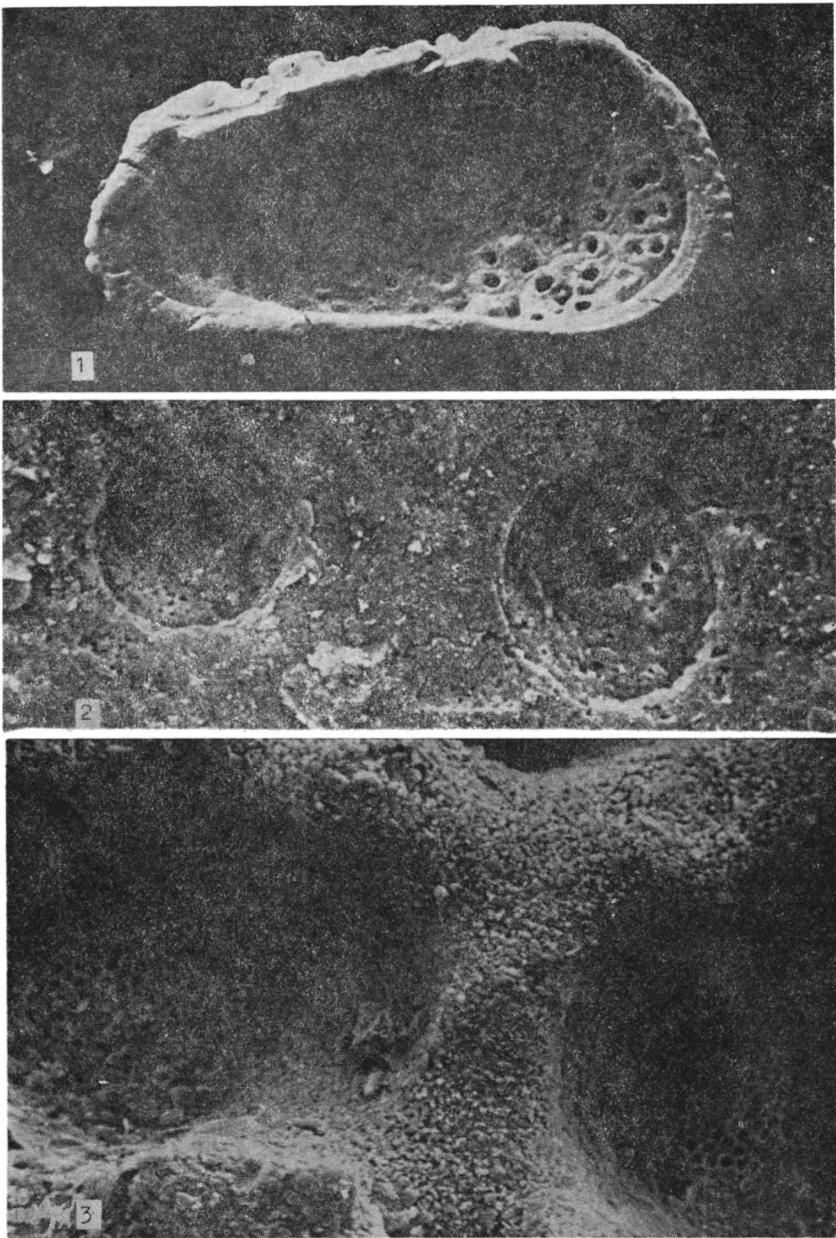


Fig. 13.

- (1) *Oertliella* sp. 2. The left valve of an adult female (inside). The valve is incompletely calcified, and it is similar in appearance to a larval stage. There are conspicuous pore canals with wide openings. Lower Eocene of southern France; the same sample as in Figs. 11 and 12. Width of picture corresponds to 1.15 mm.
- (2) Two sieve pores from within (segment from the above valve). The same species and sample as above. Width of picture corresponds to 0.1 mm.
- (3) Two sieve pores seen externally. Part of the lateral reticulation of the left valve. Sieves lie on the sola of meshes 02 (left) and 04 (right). The same species, sample and scale as under (2) above.

bably serve as tactile sensory organs; the sieves of mesh pores are likely to be related to sensory organs for light. Thus, reticulation of the Limburgina-type on one hand, and the macroconation on the other belong to different, although similar, systems of sensory organs.

Since each mesh (not including the exceptions mentioned on p. 41) has its own pore, it is possible to homologize not only the meshes but also individual pores in species and genera having Limburgina-type reticulation. Accordingly, it is possible to compare, for example, the pores of meshes A5 or M3 in *Cythereis*, *Mauritsina*, *Oertliella* and *Limburgina*. The large sieve pores of *Oertliella* are, for example, homologous with the differently shaped mesh pores in "*Spongicythere*" *koninckiana* (see Fig. 14, 1; compare with Fig. 13, 2). Also in certain circumstances, a given pore can be traced through its ontogeny.

Thus, while following phylogenetic development of the Limburgina-type reticulation it is possible to follow the evolution of a system of sensory organs as well.

## 5. CLINO AND ORTHO-PLEURAL COARSE SCULPTURE<sup>15)</sup>

In this section a brief description is given of the two coarse sculpture ornaments appearing on the Limburgina-type species. Comprehending and tracing these types of coarse sculpture should yield data on phylogenetic relationships and an appropriate classification.

Elements of coarse sculpture considered within a network of systematically defined fine sculpture can be exactly defined with regard to position and relative dimensions. Hence transformations, reductions and redevelopments of ribs or nodes (these are the coarse sculpture elements) can be detected consistently when compared with the Limburgina-type ornament. Good examples are provided by several analyses of sculptures, e.g. those made on *Limburgina* aff. *depressa* (p. 53), *Kingmaina cristata* (p. 56), "*Quadracythere*" (both species, pp. 59 and 60) and "*Leguminocythereis*" aff. *bosquetiana* (p. 63).

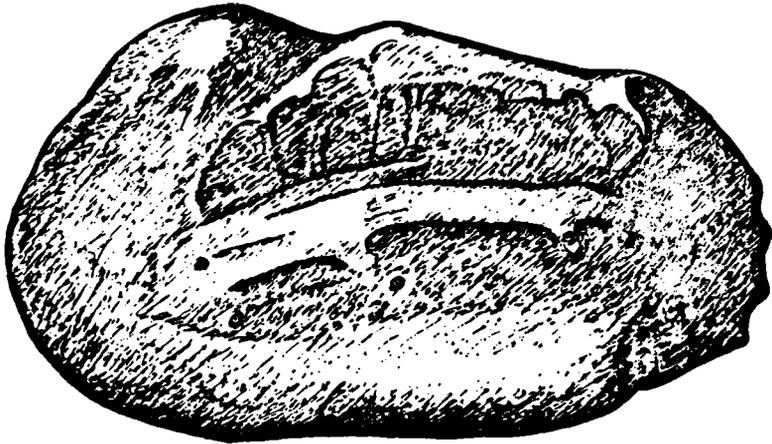
Both of the following patterns of coarse sculpture apparently have particular significance for the history of the sculpture of trachyleberide ostracods:

*Clinopleural Coarse Sculpture*: the median rib passes from the anteroventral into the posterodorsal part of the valve. The muscle node is suggested by a flattened elevation and enlargement on the anterior part of the rib; often it is crossed by a series of meshes or ridges parallel to the median rib. The anterior marginal rib is clearly formed only in some species. The ventral rib is in most cases broad, swollen or reduced. Very often the shells are strongly asymmetric

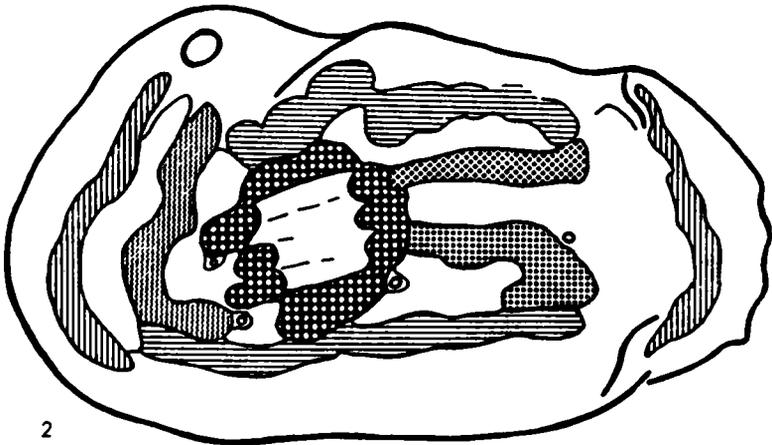
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<sup>15)</sup> The differentiation between the "clinopleural sculpture" and the "orthopleural" one was partly a mistake, as convergent forms were included in the "clinopleural" group. There is now evidence that *Mosaeleberis*, the reference form for the "clinopleural" sculpture, is derived from either *Rehacythereis* or a similar good "orthopleural" genus.

and then the right valve is considerably lower. Typical examples are found in the genera *Mosaeleberis* (cf. Figs. 15 and 31), *Protocythere*, *Veenia*, *Paracytheretta*, and partly in *Cytheretta* (s.l.).



1



2

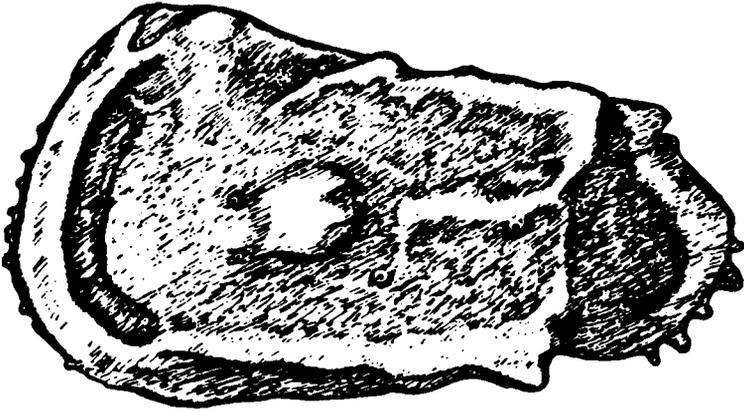
0,5 mm

Fig. 15.

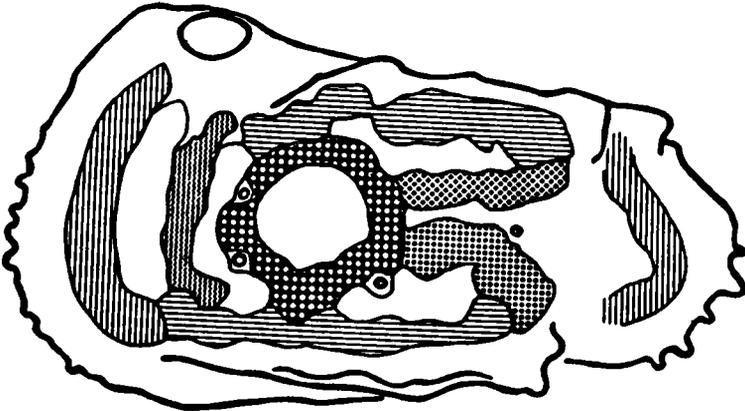
(1) The pattern illustrates clinopleural coarse sculpture. As points of reference, cones T10, T16, T17 and T18 are drawn in, but the rest of the fine sculpture is mostly left out. The drawing is based on the left valve of the *Mosaeleberis* sp. 1 shown in Fig. 31 under (1).

(2) Patterns of mesh rows in clinopleural sculpture. Reference points are the same cones as in (1) above. Drawing patterned after those above.

*Orthopleural Coarse Sculpture*: the median rib is short and originates behind the muscle node, clearly separate from it, and ends shortly behind T14. The muscle node lies within an almost circular ring of E-meshes and is not reticulated or only poorly reticulated in the primitive representatives.



1



2

0,5 mm

Fig. 16.

(1) The pattern represents orthopleural coarse sculpture. The reference points are the same cones as in Fig. 15; otherwise, the fine sculpture is mostly left out. The drawing is based on the *Mauritsina latebrosa* (SZCZECURA, 1965) presented in Fig. 17 (1) (see also Fig. 3).

(2) Pattern of mesh rows in orthopleural sculpture. The reference points are the same cones as in the three preceding figures. Drawing patterned after those above.

In the strong anterior marginal rib there are concentrated pores from three rows of pericones. The ventral rib is also pronounced. The ventral side is flattened and the shells are fairly symmetrical. In its typical form, this pattern is found in species of the genera *Mauritsina*, *Cythereis s.l.* (with many exceptions; cf. Section 7), *Curfsina* and *Limburgina*.

The other kinds of coarse sculpture in trachyleberid ostracods have probably originated from these two types.

## 6. TAXONOMIC DISTRIBUTION OF LIMBURGINA-TYPE FINE SCULPTURE

### 6.1. INTRODUCTION

So far the Limburgina-type ornament has been identified by the author on around 250 species.<sup>16)</sup> Most of these are "Cythereis" and "Hermanites" or "Quadracythere" — like ostracods from the Upper Cretaceous and the Lower Tertiary in Western Europe. They belong to the early Trachyleberididae s.l. and Hemicytheridae s.l. The examples presented below were chosen because they represent a spectrum including widely differing forms. The intention is to outline the distribution of the *Limburgina*-type ornament among the Upper Cretaceous and more recent ostracods. Doing so, in some cases, e.g. with aff. *Falunia* and *Cytheratte*, has stretched interpretation to the limits of what is currently possible.

An analysis of the sculpture of Lower Cretaceous and Jurassic ostracods is not presented.

### 6.2. LIMBURGINA-TYPE FINE SCULPTURE IN OSTRACODS WITH ORTHO-PLEURAL COARSE SCULPTURE

#### 6.2.1. *Limburgina* aff. *depressa* (Fig. 8, 2)

Among the latest Cretaceous species of *Limburgina* in the Tremp basin, *Limburgina* (s.l.) aff. *depressa* DEROO, 1966, stands out in its similarity with the Tertiary species of *Hornibrookella*. This is partly due to absence of the median rib, (already discussed on p. 36), but even more to the shape of the dorsal rib: The primary dorsal rib is interrupted about halfway along its length. The posterior end of the true dorsal rib is connected directly to the rib-like, reinforced ante-

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<sup>16)</sup> The *Limburgina*-type ornament in a larger sense is used as a character of the Trachyleberididae s. l. in LIEBAU 1975a.

rior part of the dorsal marginal rib by a mesh wall of the dorsal reticulation that joins it just above K6. The result is a homogeneous-looking dorsal rib-structure which in dorsal view runs in a shallow arc from the eye node to the posterior end of the (true) dorsal rib. The anterior part of the primary dorsal rib (above K3, K4 and K5) is much reduced: only a series of cones T1, T2 and T3, often connected by relatively high "mesh walls" (i.e. rib relics), still separates the dorsal from the lateral reticulation. In the phylogenetically older Trachyleberididae from the Lower Cretaceous, the dorsal rib develops in the same manner as in *Limburgina ornata*. Hence their rib structure must have evolved earlier than that of *Limburgina aff. depressa*.

A similar or identical transformation of the dorsal rib is observable in certain "Quadracythere" species of the European Tertiary like *Hermanites? demeriacensis* KEIJ, 1958, and *Hornibrookella macropora* (BOSQUET, 1852). This rib structure can also be observed on recent representatives; POKORNY (1968) described *Radimella dictyon* from the Southeast Pacific, which clearly shows this structure (POKORNY, 1968, p. 361, Fig. 1: "AS" and "LD" represent the anterior and posterior ends of the primary dorsal marginal rib. "AD" is the pronounced rib-like anterior region of the dorsal margin which coalesces with "LD" into a secondary dorsal rib.). A further example of this configuration of ribs is shown by "*Quadracythere*" sp. (Fig. 21).

### 6.2.2. *Mauritsina* (Fig. 17)

*Mauritsinae* DEROO, 1962, are characterized by the complex form of their muscular field. DEROO (1966) understands them as an independent unit, equivalent to Trachyleberidinae, Cytherettinae, Schizocytherinae and others.

*Mauritsina latebrosa* (SZCZETCHURA, 1965) (Fig. 17, 1) from the Upper Cretaceous of the southern region of the Baltic Sea is strongly macroreticulated. Its mesh ornament coincides with that of *Limburgina* uncommonly well. There is only one deviation visible: it has an additional "P5" mesh, situated between P4 and V7. In some specimens it is connected with P4 into a double mesh. The A and H series of meshes are deeply incised furrows traversed only by low-lying cross-pieces (relic mesh walls).

So far the *Mauritsina latebrosa* and the similar *Mauritsina baria* (HERRIG, 1965) have been interpreted as *Cythereis* species, but the muscle areas have been unknown. On a third and closely affiliated species, "*Cythereis latebrosa confinis*", SZCZETCHURA, 1965 the author could observe the muscle scars, which are identical to those of the type-species of *Mauritsina*.

On *Mauritsina varia*, HERRIG (1966) defined the relationship between the shell structure and the degree of expression of fine sculpture.

*Mauritsina* (s.l.) sp. (Fig. 17, 2) represents a numerous group of species, which is present in the upper sublittoral campanian of the Maastrichtian of the southern Pyrenees. Whereas microreticulation

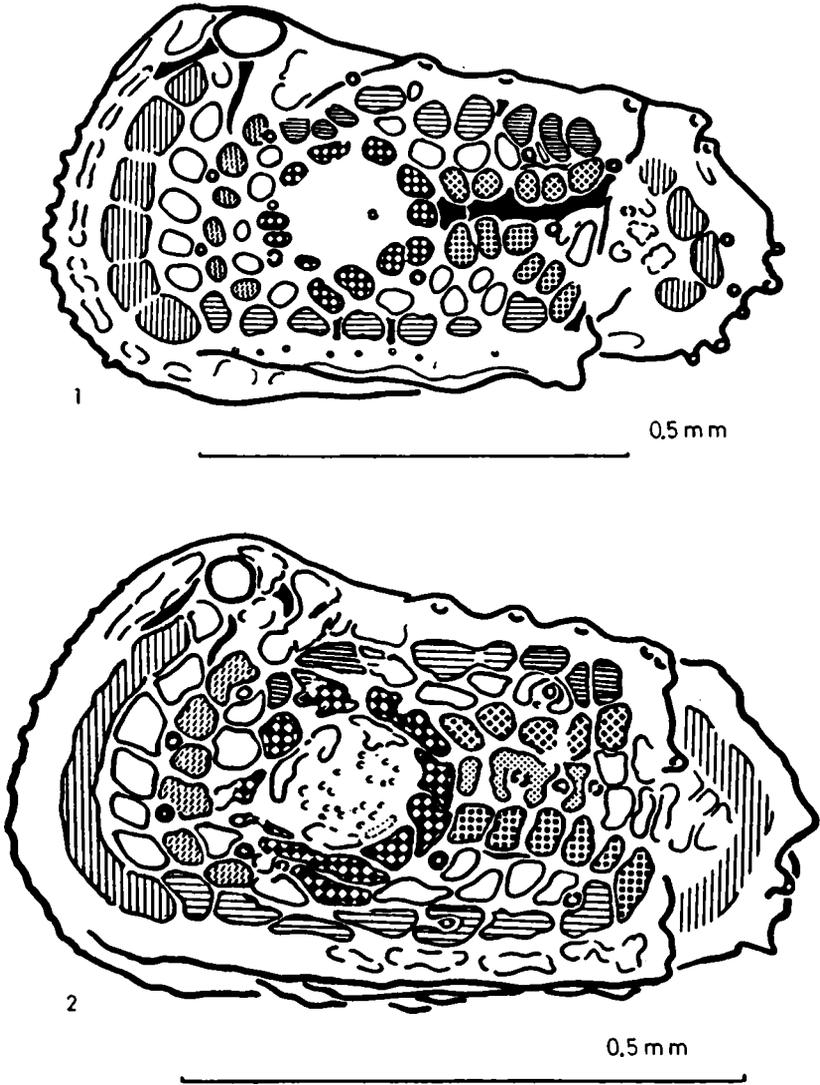


Fig. 17.

- (1) *Mauritsina* (s. l.) *latebrosa* (SZCZETCHURA, 1965). Left valve of a male. Ervatic boulder, Berlin-Spandau, origin northeastern Germany to southern Baltic; Upper Campanian glauconitic facies. The median rib and several ridges within the reticulation are solid black. Presentation as in Fig. 8 (1).
- (2) *Mauritsina* (s. l.) sp. left valve of a female. Lower Maastrichtian, SE Montesquiú, northern edge of the Tresp basin (Southern Pyrenees). The strong microreticulation is not figured. Presentation as in Fig. 8 (1).

is strong, the macroreticulation, if present in this species, has low-lying, inconspicuous mesh walls deformed in a pattern resembling that of a stretched hairnet. In spite of this, the number and distribution of meshes is almost the same as in the above-mentioned *Mauritsina* species. Mesh P5 is present. Four depressions on the low median rib can be related to the N-meshes in the figured specimen (the two central depressions are partly connected). The N-meshes are in a row. The A and H rows of meshes, like those of other *Mauritsina* species, develop as furrows. At times it is noticeable that on the posterior of the A-furrow both A and B pores are incorporated into a single row.

Also on a Lower Cretaceous *Cythereis* s. l. species a double row of pores was observable at the posterior edge of an A furrow. Apparently, the anterior mesh pores are concentrated thereby a special bundle of sensory organs. Two other genera with A and H furrows are *Spinoleberis* and *Curfsina*.

Each of the two figured *Mauritsina* s.l. species represents a separate group of species. In external appearance they fully conform to "Cythereis" S-1.

#### 6.2.3. *Cythereis* (Fig. 18, 1)

Specimens of *Cythereis longaeva* POKORNY, 1963, figured by POKORNY (1963) demonstrate a reticulated pattern of the Limburgina-type, which is like that of *Mauritsina* s.l. At least their A series of meshes is formed in the same way, i.e. as a shallow furrow. The greatest differences show up in the posterodorsal part and are related to the specific form of the dorsal rib and median rib.

The genus *Cythereis* is of particular significance, for it was classified as early as 1849 by JONES and thus is the earliest valid genus of the trachyleberid group of families. For some time nearly all the species of Trachyleberididae and Hemicytheridae were classified as *Cythereis*. It was only after 1920 that this taxonomic complex was rearranged. The revision of *Cythereis* type-species was undertaken by POKORNY in 1963.

#### 6.2.4. *Kingmaina* (Fig. 18, 2)

The genus *Kingmaina* KEIJ, 1957 was classified amongst Brachytheridae in the Treatise (1961) and by SZCZECURA, 1965. *Kingmaina cristata* (BOSQUET, 1954), from the Tuffaceous Chalk of Maastricht is a rather primitively sculptured representative still showing several macrocones and a portion of the dorsal rib. The antero-ventral region of the lateral reticulation was only incompletely observable on the specimen shown in the figure. Specimens of other species, e.g. *Kingmaina* cf. *opima* SZCZECURA, 1965, from the Lower Eocene of South France, also has the usual grouping of meshes in this section. Taken as a whole, this genus, in spite of its very different shell form, almost entirely coincides with *Limburgina* s.l. in respect of lateral reticulation.

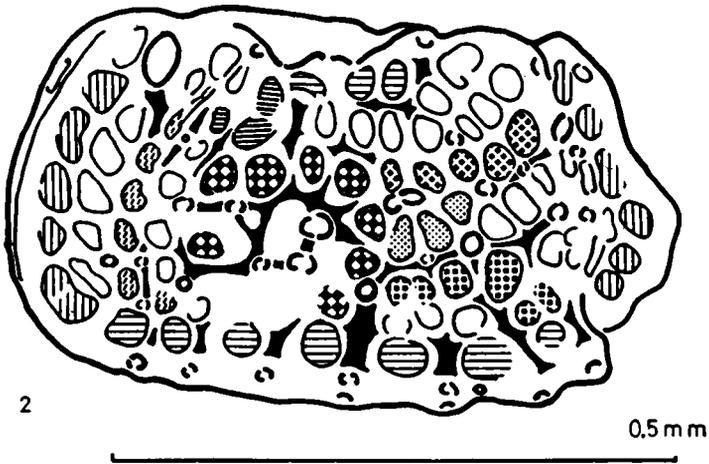
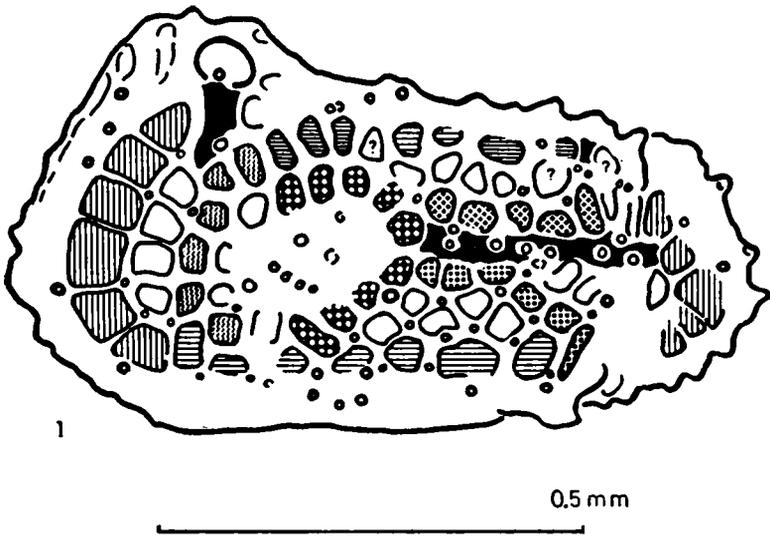
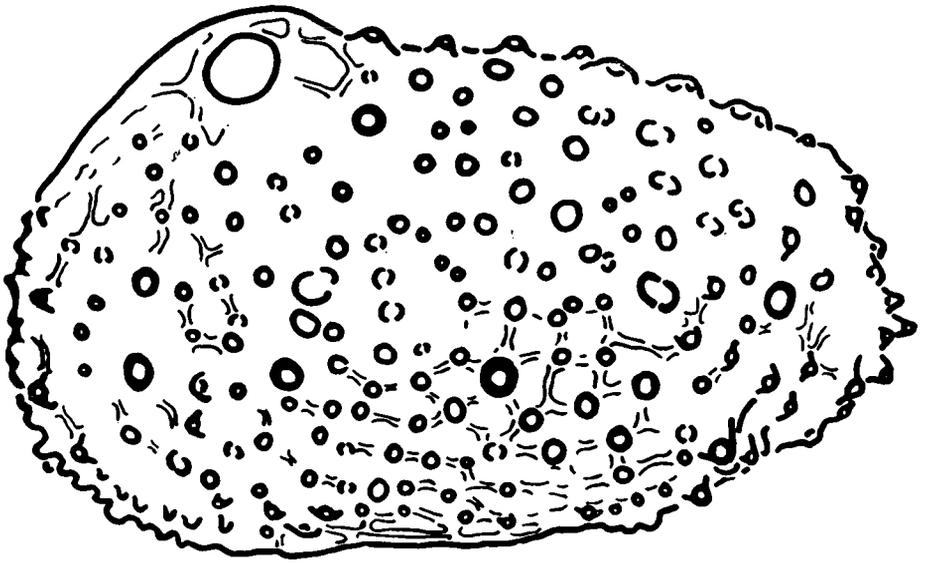


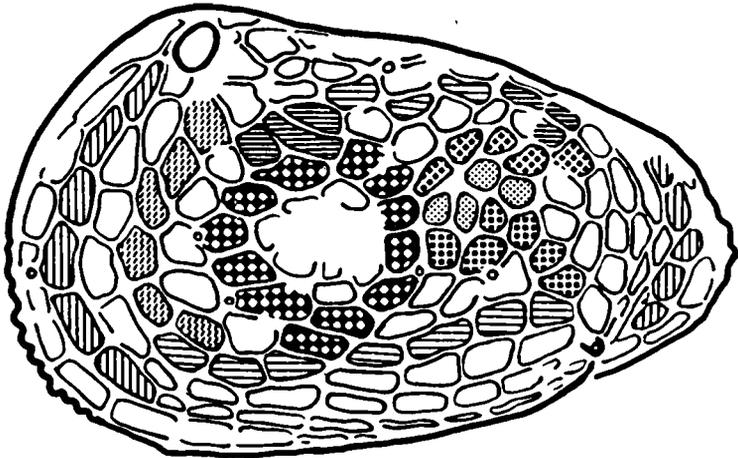
Fig. 18.

(1) *Cythereis* (s. str.) *longaeva longaeva* POKORNY 1963. Left valve of a female. The drawing is based on a figure in Pokorny, 1963 (plate II, Fig. 2). Upper Turonian of Kostice, Bohemia. The median rib and some ridges within the reticulation are in black. Presentation as in Fig. 8 (2).

(2) *Kingmaina cristata* (BOSQUET, 1854.) Left valve of a female. Tuffaceous Chalk, of Maastricht (sample 12650 of the Federal Institute for Geosciences, Hannover). Presentation as above.



1



2

0.5 mm



Fig. 19.

(1) *Echinocythereis scabra* (VON MÜNSTER, 1830). Left valve of a female. The Lower Marine Sand Fm. of the Mainz Basin (Rupelian), Welschberg at Waldböckelheim. The faint reticulation is not shaded. Scale as under (2).

(2) The same species from the same sample as under (1). Left valve of the ultimate juvenile stage (A-1). The digram mainly shows a network of microcone rows, which look like strings of beads. Sometimes larger cones also occur.

The network designs and some macrocones are also shown.

### 6.2.5. *Echinocythereis* (Fig. 19)

The adult stage of the genus *Echinocythereis* PURI, 1953, the type-genus of Echinocythereidinae HAZEL, 1967, shows fine sculpture made up of many cones of different sizes. Mesh walls appear only in a few species and then are weakly expressed, low bridges connecting larger cones.

*Echinocythereis scabra* (VON MÜNSTER, 1830) is a characteristic representative of this genus.<sup>17</sup> At least the last two larval stages show, unlike the adult stage, a clearly reticulated pattern which is obviously of the *Limburgina*-type.

The posterior quarter of the lateral side (Fig. 19, 2) can be interpreted in different ways. Figure 19, 2, shows an attempt to explain this portion of mesh pattern on the basis of reticulation in certain *Oertliella* species.

The reticulation pattern of the *scabra* larvae is phylogenetically older than the cone ornament of the adults. For this reason, Echinocythereis species with adult stage reticulation should be interpreted as examples of neoteny or, more generally, as rejuvenation of a partially-reduced former ornament. Particularly instructive in this respect is the sculpture development of the *isabenana-aragonensis* of the South Pyrenean Upper Paleocene, described by OERTLI (1962).

### 6.2.6. "Quadracythere" *prava* (Fig. 20)<sup>18</sup>

Adult specimens of the Recent *Quadracythere prava* (BAIRD, 1850) have a system of strong ridges between which subordinate reticulation meshes are observable. The meshes can be identified only by comparison with the next younger molting stage, in which the ridges are easily visible and the reticulation is more uniform and clear. Correlation with the *Limburgina* reticulation is uncertain only in the region of the anterior L series, because two extra meshes are present here. Otherwise the reticulation is obviously of the *Limburgina*-type. Recognizable cones are: T7, T13, T16 and T17.

A precise comparison of juvenile and adult sculptures reveals substantial coincidences as well as differences. It is in the region of the ventral rib that the two stages resemble each other most closely. Thus, it is now possible to document what was assumed in the above discussion: the two stages in fact belong to the same species. (ROME, 1942, described the juvenile stage as "*Cythereis polygonata*").

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<sup>17</sup> The typical *Echinocythereis scabra* was redescribed by MOOS, 1973: 29. The investigated species is not conspecific with *E. scabra*.

<sup>18</sup> "*Quadracythere*" *prava* (BAIRD) is the type species of *Tenedocythere* SISSINGH, 1972, established as a subgenus of *Quadracythere*, but connected by transitional forms with *Pokorniyella*. "*Cythereis polygonata*" was figured among the characteristic ostracodes of the "abyssal" in PURI et al., 1969, while the conspecific adult was regarded as a member of the upper shelf fauna. For the transport of littoral ostracode larvae into the deep sea compare YASSINI, 1969: pl. XIII.

6.2.7 "Quadracythere" sp. (Figs. 21 and 22)

In this recent species from the littoral of the Portuguese coast the adult individuals have strong ribs and ridges with only suggestions of reticulation between them. Even so, its relationship with

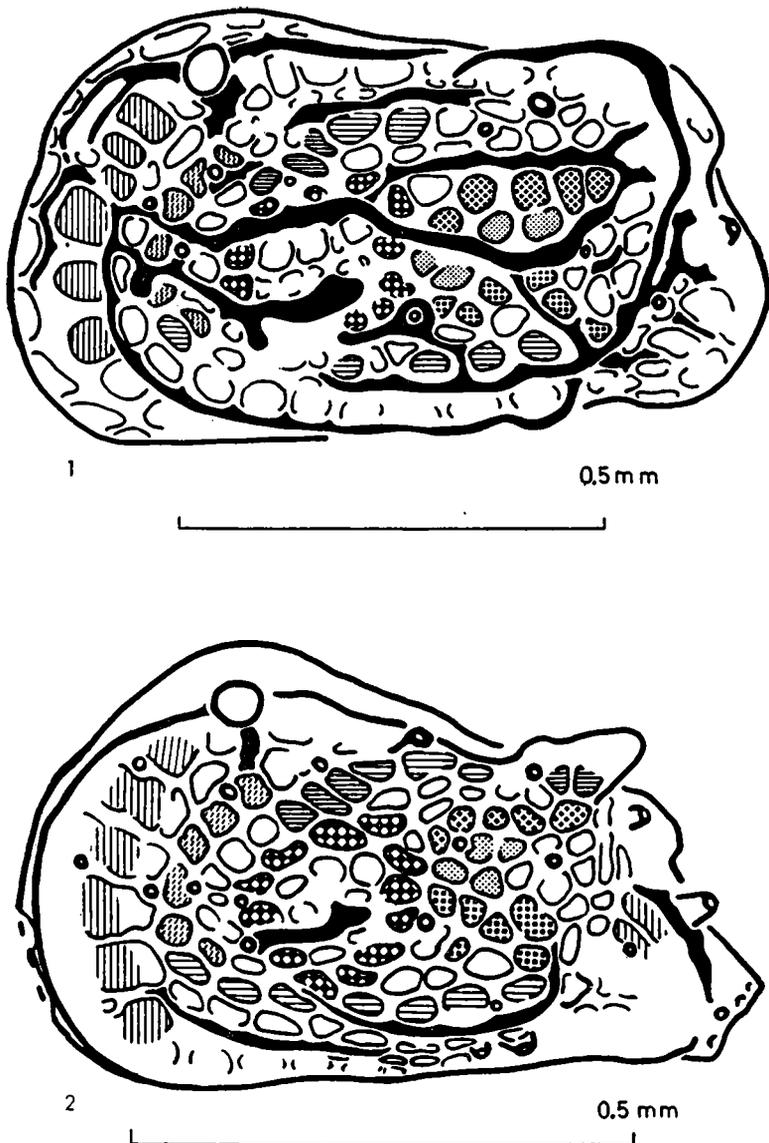
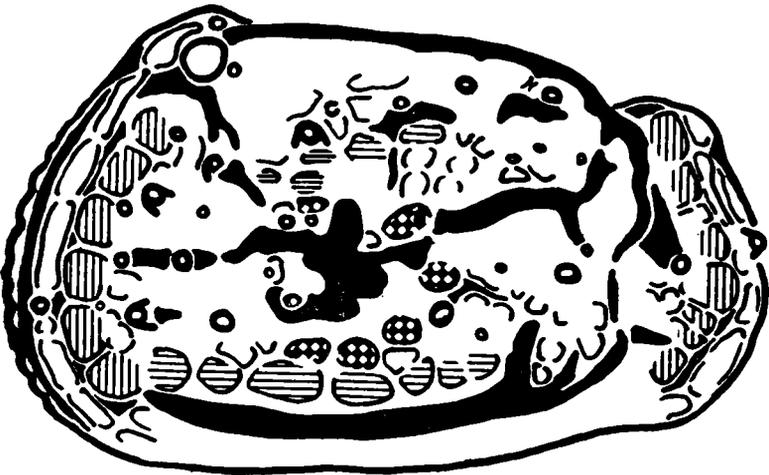


Fig. 20.

- (1) "*Quadracythere*" *prava* (BAIRD, 1850). Left valve of a recent species of the Mediterranean, about 80 km east of Tripoli, Libya. Presentation method partly as in Fig. 8 (1), but all the ribs and ridges are blackened.  
(2) Left valve of the ultimate juvenile stage (A-1); otherwise as above.



1



2

0.5mm

Fig. 21.

- (1) "*Quadracythere*" sp. Left valve of a male. Recent, Portuguese coast near S. Martinho do Porto. Presentation method as above. Scale as under (2).  
 (2) Left valve of a female. As above.

*Limburgina* reticulation can be demonstrated because ornamentation of juvenile specimens is intermediate between the two patterns of sculpturing.

In juveniles the ridges are negligible, but thus serve to emphasise macroreticulation and macroconation. Comparison of these patterns is hampered by intensive fragmentation of meshes which particularly affects the posterior parts of meshes which particularly

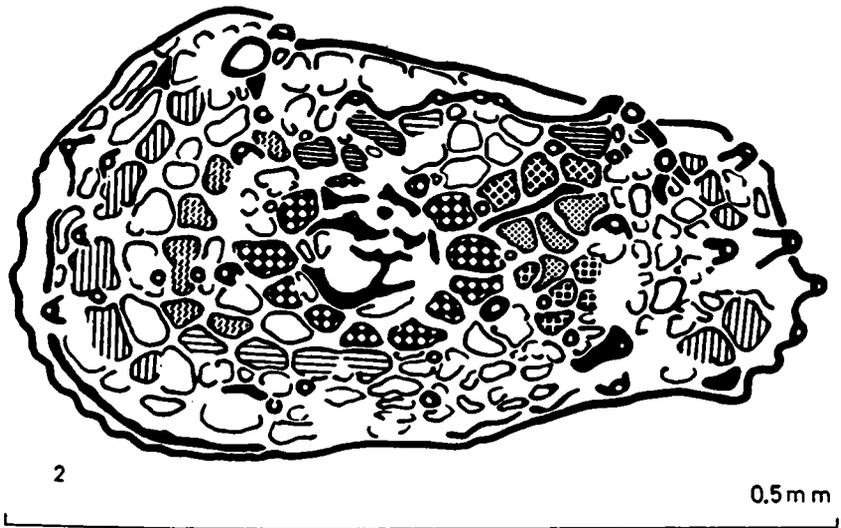
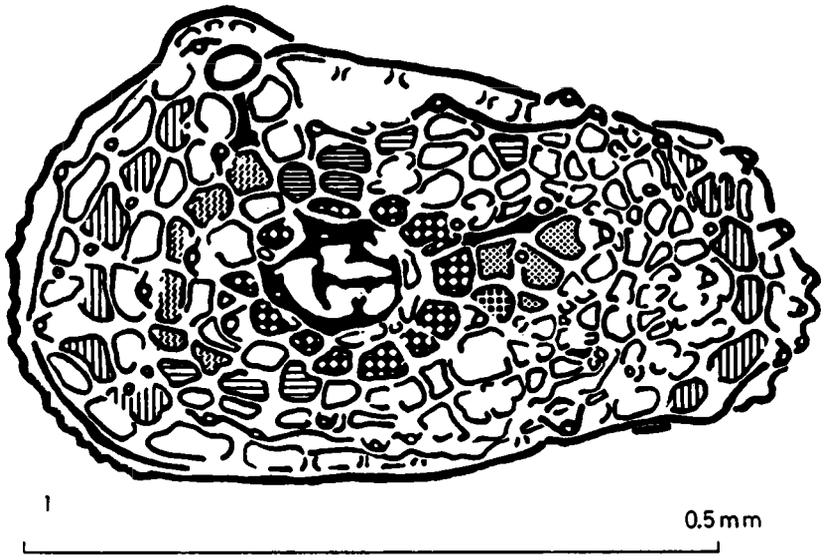


Fig. 22.

(1) Left valve of the ultimate juvenile stage (A-2); otherwise as above.

affects the posterior parts of the reticulation. Furthermore, in stage A-2 (Fig. 22, 2) the dorsal rib is approximated posteriorly by the median rib at an acute angle (the same allometry is shown by the juvenile stages of "Leguminocythereis", Figs. 25 and 26). The anterior series of meshes can be well identified, as can the meshes

which border on the muscle node and cones T7, T16 and T17. Their characteristic pattern shows that this is *Limburgina*-type reticulation.

The apparently "homogeneous" dorsal rib of the adult stage, when compared with the juvenile sculpture, turns out to be a secondary structure composed of one anterior dorsal marginal rib and one posterior rib relic (compare *Limburgina* affl. *depressa*, p. 67). The median rib is probably another secondary structure, since it passes above the N-meshes. The ventral rib, however, corresponds to that of *Limburgina*.

### 6.3. LIMBURGINA-TYPE FINE SCULPTURE IN OSTRACODS WITH CLINOPLEURAL COARSE SCULPTURE

#### 6.3.1. *Leguminocythereis* s.l. (Figs. 23—29)<sup>19)</sup>

The genus *Leguminocythereis* HOWE, 1936, together with *Tringglymus* BLAKE, 1950 and other genera, makes up *Leguminocythereididae* HOWE, 1961. HAZEL (1967) and others treat this family as a younger subjective synonym of *Campylocytherinae* PURI, 1960. The type-species of *Leguminocythereis* comes from the Louisiana Oligocene, but most of the species classified under this genus are from the European Tertiary. Such classification of the European group of species (around "*Cytherina*" *striato-punctata* ROEMER, 1938, and *Leguminocythereis sorneana* OERTLI, 1956) has been questioned by VAN MORKHOVEN (1962/63, Vol. II, p. 175) and HOWE, Sen. (correspondence, 1969).

"*Leguminocythereis*" aff. *bosquetiana* (JONES & SHERBORN, 1889) from the Lower Eocene of Southern France. In its adult stage (Fig. 23) this species is very swollen ventrolaterally. Ribs are not present, but the reticulation ornament is nevertheless partly comparable with that of *Limburgina*. The pore openings, which correspond to specific macrocones (T16, T17, T18) constitute important fixed points. This interpretation is confirmed and supported by ontogenic sculptural changes. Juvenile stages (see Figs. 23 and 24, 1) clearly show a muscle node and traces of three longitudinal ribs (Fig. 24, 1). It is particularly the third of the five juvenile valves (Fig. 25, 1) that shows a reticulation ornament comparable with that of *Limburgina*.

In valves of younger stages the ribs are more strongly expressed, but there is a singular irregularity: the posterior end of the median rib, along with the neighboring fine sculpture, is moved toward the posterodorsal corner. This allometry is also seen in other juvenile trachyleberid ostracods (Fig. 22, 2).

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<sup>19)</sup> "*Leguminocythereis*": The European species group belongs perhaps to *Alteratrachyleberis* LI, 1964.

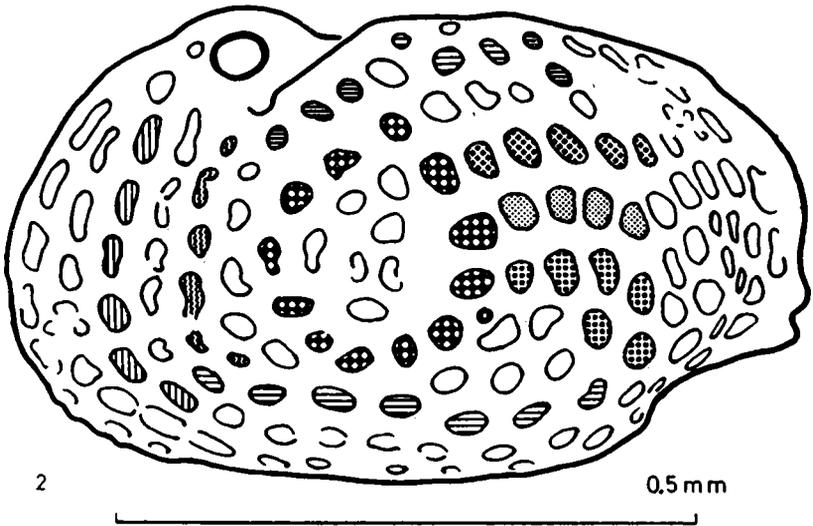
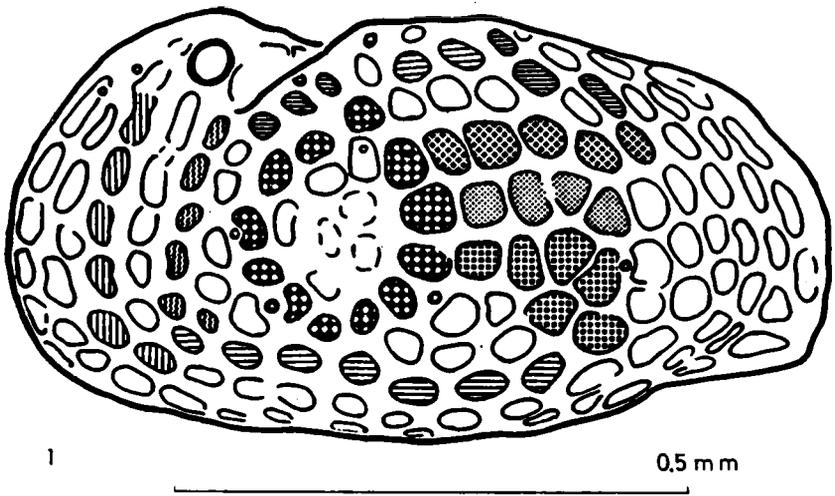


Fig. 23.

- (1) "*Leguminocythereis*" aff. *bosquetiana* (JONES & SHERBORN, 1889). Left valve of a male (Cuisian) with *Assilina placentula* and *Alveolina oblonga*, Tuilerie de Gan near Pau, Southern France. Presentation as above.  
 (2) Left valve of a female; otherwise as above.

It is to be regretted that not enough material of the figured pre-adult valves was available, to confidently assign them to the proper molting-stages.

"*Leguminocythereis*" *striatopunctata* (Figs. 27—28).

"*Leguminocythereis striatopunctata* (ROEMER, 1838) deviated particularly strongly from the typical sculpture and shell pattern of *Trachyleberididae* s.l. Its carapace is very swollen ventrolaterally. The sculpture is composed of a system of approximately concentric costulae which are united by low-lying transverse ridges. The figured specimens come from the Middle Eocene of the Paris Basin.

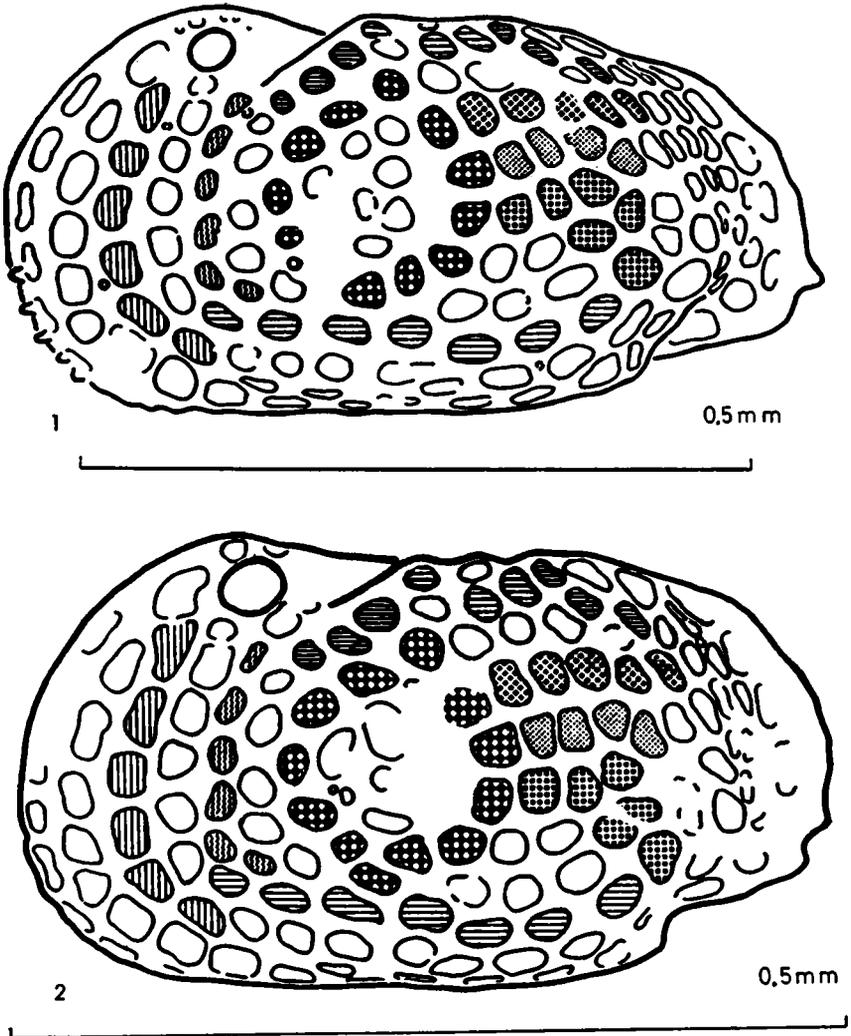


Fig. 24.

- (1) The left valve of the ultimate juvenile stage, perhaps of a male (♂ A-1?).  
Otherwise as above.
- (2) The left valve of the ultimate (?) juvenile stage, perhaps of a female (♀ A-1 ?); otherwise as above.

At first glance, an attempt to find correlations between this sculpture and the network ornament of the prismatic *Limburgina ornata* seems to promise little success. Yet there is a sufficient number of the intermediate morphological forms available: juvenile sta-

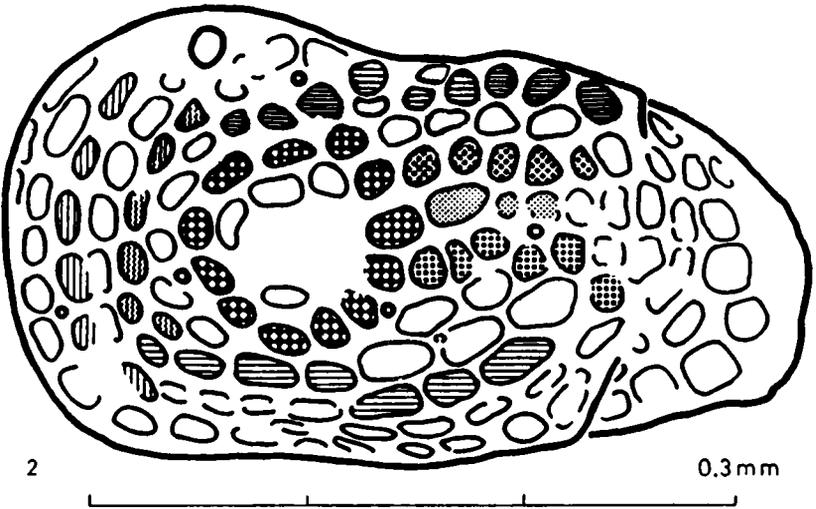
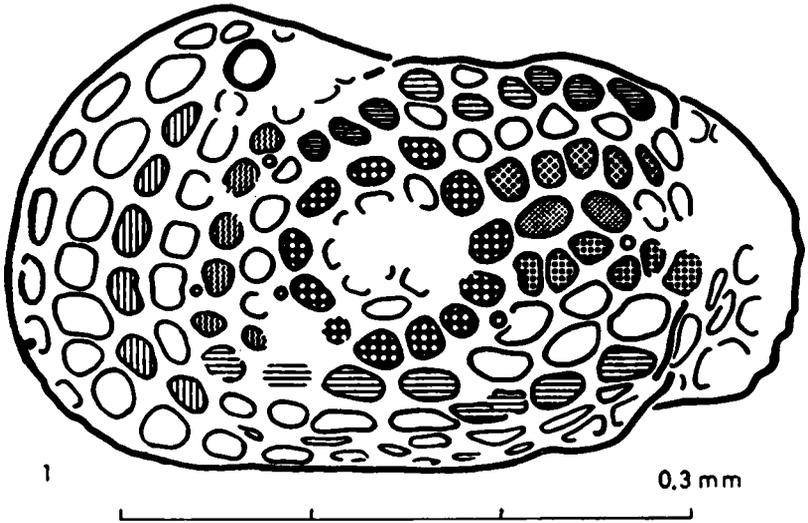


Fig. 25.

- (1) The left valve of the penultimate (?) juvenile stage (A-2 ?); otherwise as above.
- (2) The right valve of a late juvenile stage (penultimate, A-2 ?) represented as a left valve. The valve is bent in its anterodorsal quarter; outlines and pattern are thus somewhat deformed. Otherwise as above.

ges represented in Fig. 26 (the same species?)<sup>20</sup> permit comparison of the *striatopunctata* sculpture with that of adult male "*Leguminocythereis*" aff. *bosquetiana*. It is through this form and its ontogeny that comparison with the *Limburgina* reticulation becomes possible (see above). In this lengthy chain of reasoning, the possibility of ma-

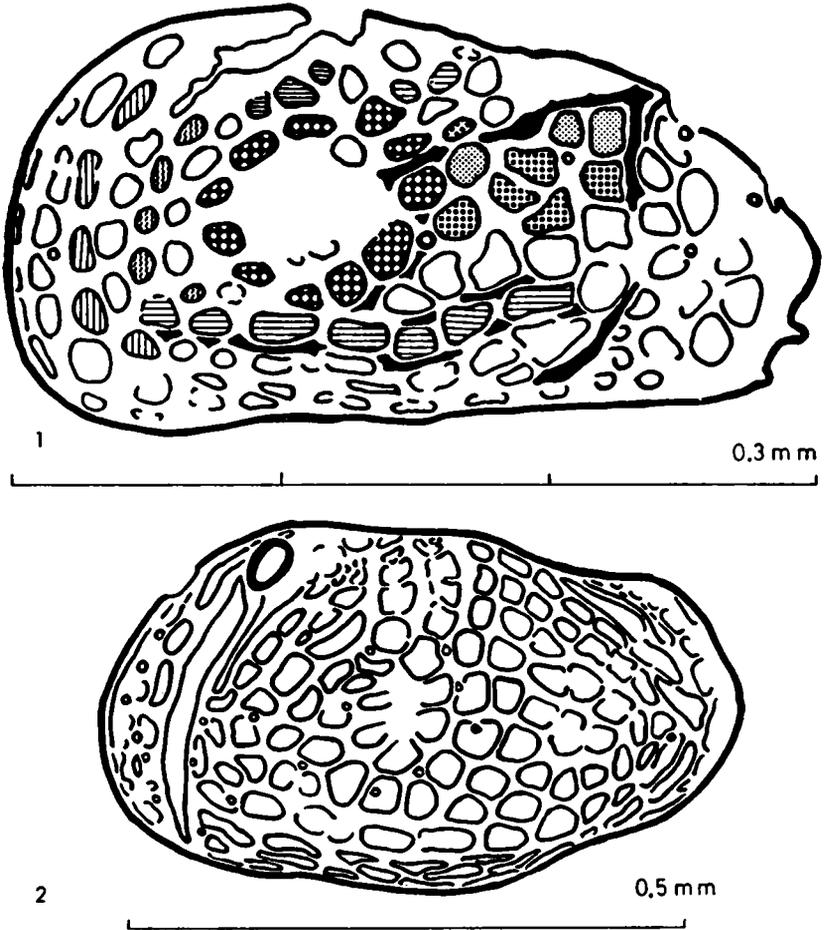
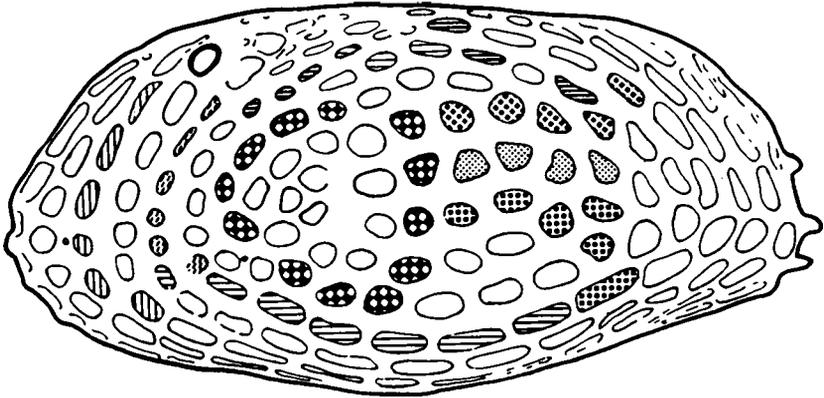


Fig. 26.

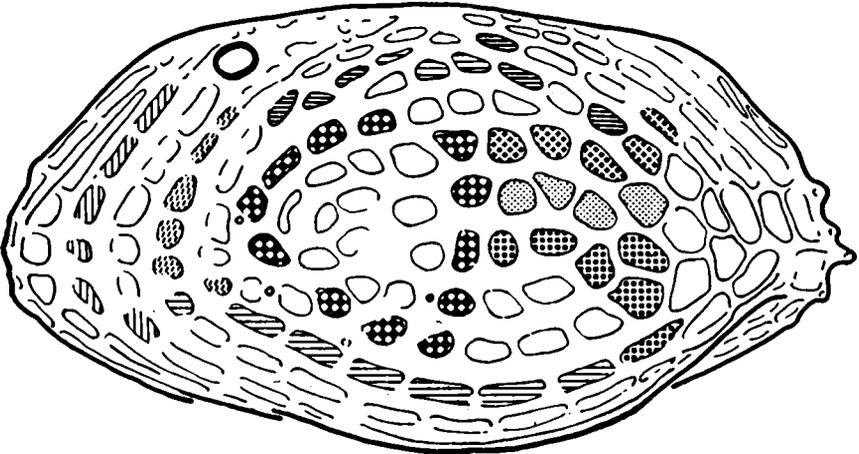
- (1) The right valve of third (?) stage prior to the end of juvenile phase (A-3?), represented as a left valve. Several ribs and ridges are blackened. The valve is cracked dorsally. Otherwise as above.
- (2) *Leguminocythereis* (s. str.) *scarabeus* HOWE & LAW, 1936. The left valve, topotype of the type-species, leg. et ded. H. V. HOWE, *Catahoula parish*, Louisiana Oligocene.

<sup>20</sup> The figured larval stages belong to an undescribed species of the same group. Its adult specimens now have been obtained from a larger sample of the Grignon Lutetian.

king errors is large. In spite of this the characteristic outlines of certain meshes (K1—K3, C5—C6, E-meshes), the occurrence of pore openings in larger cones (T16, T17 and others) and some peculiarities in the arrangement of rows, provide persuasive evidence for *Limburgina-type* reticulation in "*Leguminocythereis*" *striatopunctata*.



0,5 mm



0,5mm

Fig. 27.

(1) "*Leguminocythereis*" *striatopunctata* (ROEMER, 1838). The left valve of a male. Parisian "calcaire Grossier", Grignon Lutetian with *Orbitolites complanatus*. Presentation method fully complies with that in Fig. 8 (1), but the ribs or ridges are not blackened.

(2) The left valve of a female; otherwise as above.

*“Leguminocythereis” angulatopora* and *bosquetiana* (Fig. 29).

Two more species from the Paris Eocene, *“Leguminocythereis” angulatopora* (REUSS, 1850) and *“Leguminocythereis” bosquetiana* (JONES & SHERBORN, 1889) have reticulation that can be associated with *“Leguminocythereis” aff. bosquetiana* and hence *Limburgina* as well (Fig. 29). The former was assigned to the genus *Triginglymus* by KEIJ, (1957), the latter to *Bradleya* by KEIJ (1957) and PIETRZENIUK (1969).

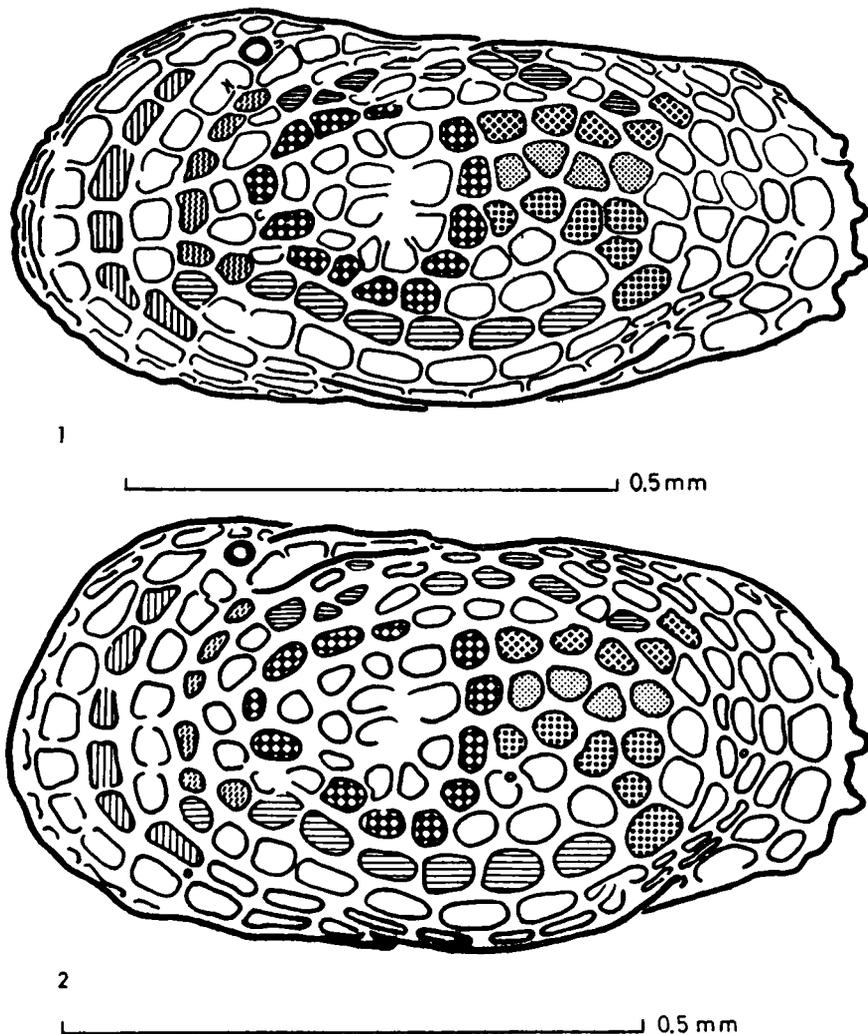


Fig. 28.

- (1) The late juvenile stage of *“Leguminocythereis” striatopunctata* (see Fig. 25) or of some similar species. Sample and presentation method as in Fig. 25.  
(2) The stage closest to the juvenile stage of the form shown under (1) above.  
Left valve; otherwise as above.

*Leguminocythereis* s. str. (Fig. 26, 1)

After investigating four European species an attempt can be made to compare them with the type-species *Leguminocythereis*. Figure 24, 1 shows a specimen of *Leguminocythereis scarabaeus* (HOWE & LAW, 1936) from the type locality. So far the author has

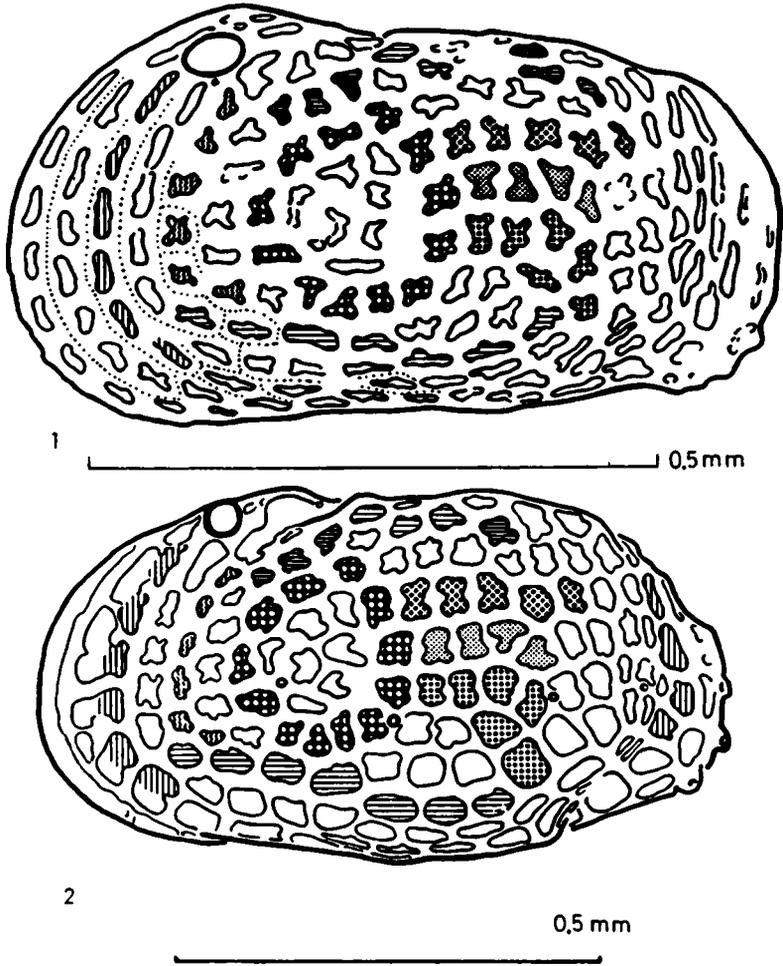


Fig. 29.

(1) "*Leguminocythereis*" *angulatopora* (REUSS, 1850). Left valve of a female. Parisian "calcaire grossier", Grignon Lutetian. The walls of meshes are expanded at their distal ends by the lateral extensions of the crests of mesh walls ("spongy" reticulation). The course of the central portions of meshes is in some places indicated by faint ridges which are shown here as stippled lines. The drawing is similar to the preceding one in the method of presentation.

(2) "*Leguminocythereis*" *bosquetiana* (JONES & SHERBORN, 1889). Right valve of a female, represented as a left valve. Same sample as under (1), presentation method as above.

failed to clearly relate this reticulation pattern to that of the European "*Leguminocythereis*" species or with that of the other genera. Apparently the European species constitute a genus of their own.

### 6.3.2. *Spinicythereis* (Fig. 30, 1)

The laterally flattened shell of *Spinicythereis*, in this case of *Spinicythereis geinitzi* (REUSS, 1874), is covered with many meshes of various sizes. The eye node and cones T10, T14 and T17 are helpful for orientation while the A, H and V meshes, and above all the anterior K meshes, can be recognized by their outline. Parts of lateral reticulation situated between them can be identified subsequently in the same manner.

On the anterior marginal and ventral ribs, in the dorsal region and on the posterior edge there appear smaller meshes (auxiliary meshes), that apparently do not contain any pore openings.

The eye node is shifted far back. The magnitude of this shift affects the adjacent network of meshes, which is accordingly deformed.

### 6.3.3. *Dumontina* (Fig. 30, 2)<sup>21)</sup>

In substantial portions of its ornamentation the genus *Dumontina* DEROO, 1966, coincides with *Spinicythereis*. The shift of the eye node is also present. The dorsal and median ribs can be recognized. The ventral rib is present only as a blunt border. The auxiliary meshes of the dorsal and ventral ribs are expressed in a way similar to that of normal meshes. Those on the anterior marginal rib are partly fused into a furrow.

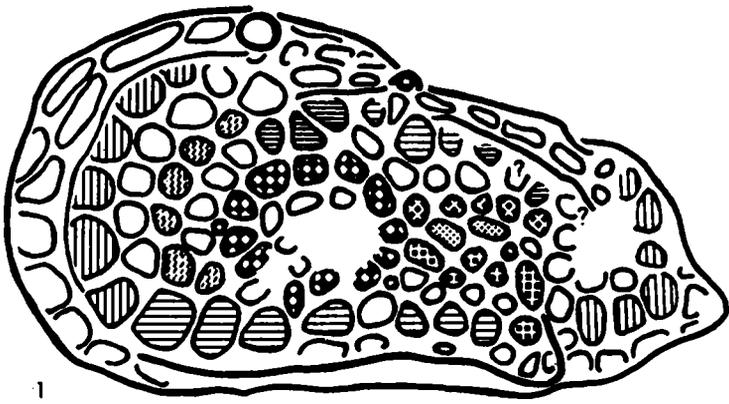
In the reticulation pattern, and particularly in the arrangement of mesh rows, this ornament is intermediate between the group of genera including *Mosaeleberis*, *Falunia* and "*Leguminocythereis*" gr. *striatopunctata* on one hand and forms like *Mauritsina* and *Limburgina* on the other (clinopleural and orthopleural sculpture patterns; see Section 5).

### 6.3.4. aff. *Falunia* (Fig. 30, 3)<sup>22)</sup>

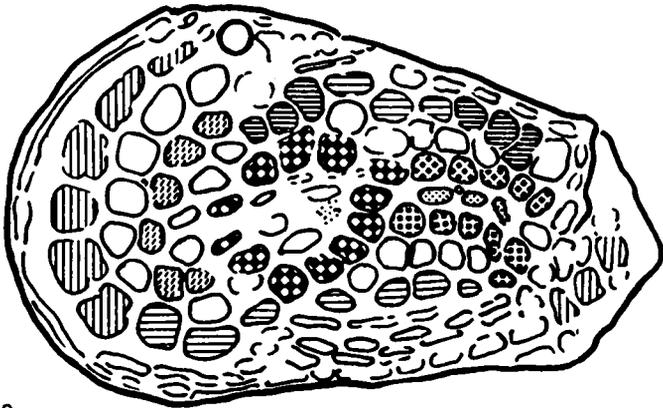
*Falunia*, *Protocytheretta*, *Loculocytheretta*, and some species of *Costa* s.l. are distinguished by a group of mesh rows and often also ridges, which, parallel with the long median rib, traverse the muscle node. The species shown in the figure, from the Paris Basin Eocene, suggests how such an ornament can be related to the ornament of *Limburgina*. Interpreted in this way, the cone pores designated under T8, T10, T16, and T17 are located between the same meshes as in *Limburgina*.

<sup>21)</sup> *Dumontina* DERRO, 1966, is now regarded as a junior subjective synonym of *Paracaudites* DELTEL, 1962.

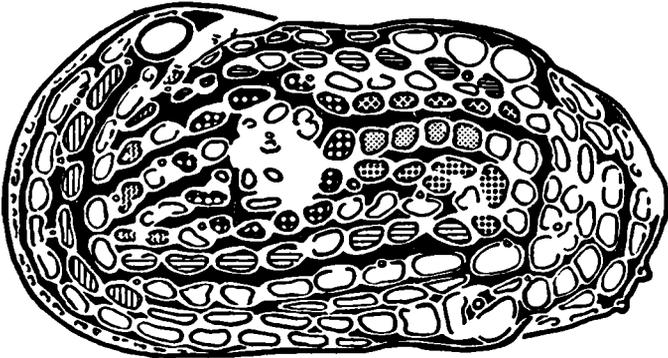
<sup>22)</sup> *Falunia*, *Faluniinae*: The type species of *Falunia* is interpreted as a larval of a *Cytheretta* species (*Cytherettinae*) in LIEBAU, 1975a: 360. The investigated "aff. *Falunia* sp." belongs to the "*Triginglymus*" *grignonensis* group, which is close to *Hammatocythere* KEEN, 1972.



1



2



3

0.5 mm

Fig. 30.

(1) *Spincythereis geinitzi* (REUSS, 1874). The left valve. Coniacian of Bohemia. Drawing according to the type-species *Spincythereis* illustrated in POKORNY, 1964. The inside edges of the anterior marginal and dorsal ribs are lined; in other respects the drawing corresponds to the preceding.

(2) *Dumontina* sp. The left valve of a female. Basal Maastrichtian of the northern edge of the Tremp Basin southeast of Montesquiú (northern Spain). The reticulation pattern is supplemented by a right valve from another female. The strong microconation is not shown. Otherwise the presentation is as above.

(3) aff. *Falunia* sp. Left valve. Parisian "calcaire grossier" Fm., Grignon Lutetian. Ridges and ribs are blackened; otherwise as above.

### 6.3.5. *Mosaeleberis* (Fig. 13)

The group of species including "*Cypridina*" *interrupta* BOSQUET, 1847, is apparently intermediate between *Cythereis* s.l., *Veenia* s.l., *Paracytheretta* and *Leguminocythereis* s.l. with regard to

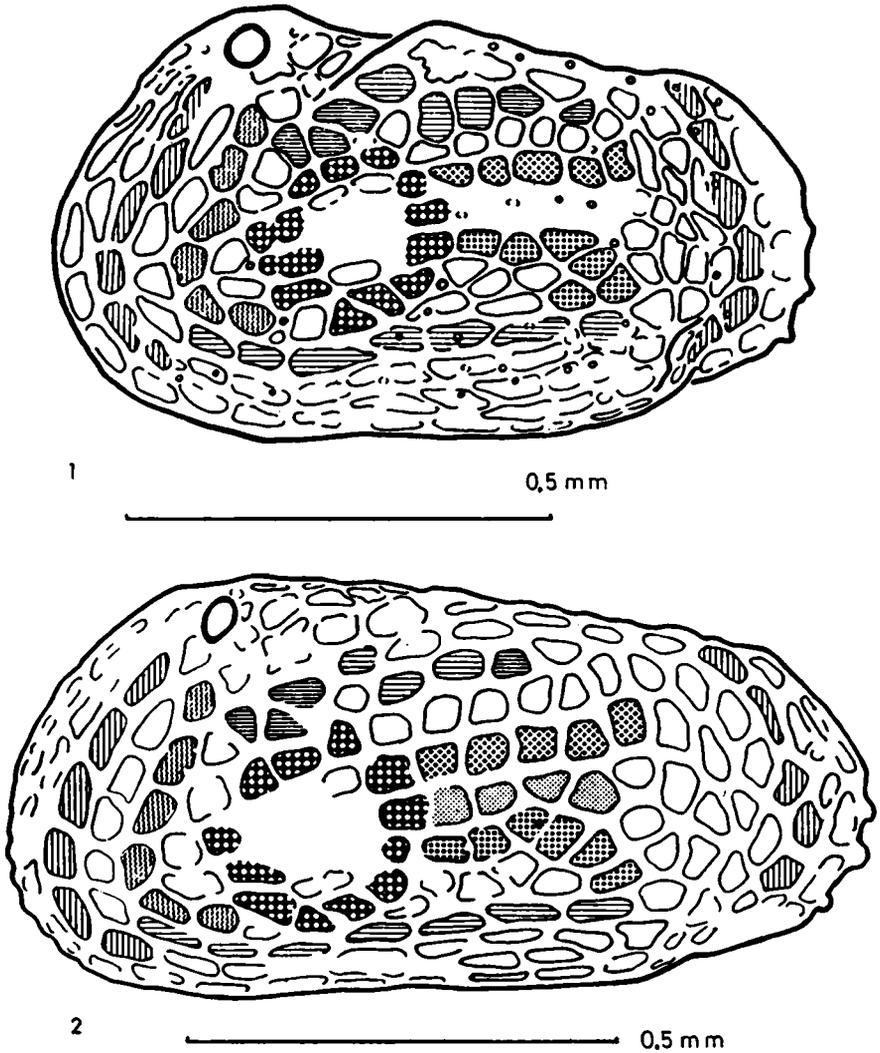


Fig. 31.

(1) *Mosaeleberis* sp. 1. Left valve of a female. Upper Middle Santonian in bryozoan detritus facies of Gehrden near Hannover. The drawing of the pattern is composite. The strong microreticulation is not shown. Otherwise the presentation is as above.

(2) *Mosaeleberis* sp. 2. Left valve. Outline and pattern are somewhat deformed because in the stereoscan photo of the specimen used to make the drawing the postdorsal portion of the valve was somewhat elevated. The sample and presentation method as above.

the form of the shell, rib pattern and fine sculpture. This explains their various inclusion in Trachyleberididae as *Cythereis* (in HOWE & LAURENCICH, 1958), in *Cytherettidae* as *Protocytheretta* (in SZCZUCHURA, 1965) and in *Protocytherinae* as the independent genus *Mosaeleberis* DEROO, 1966.

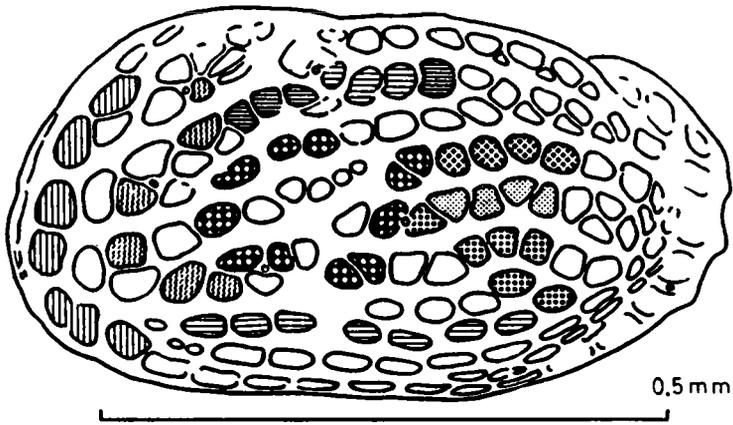
The macroreticulation has low-walled meshes and is usually covered with strong microreticulation formed in a manner peculiar to this genus. The macroreticulation pattern is *Limburgina*-type, although certain details are difficult to interpret.

#### 6.3.6. *Cytheretta* and cf. *Cytheretta* (Fig. 32)

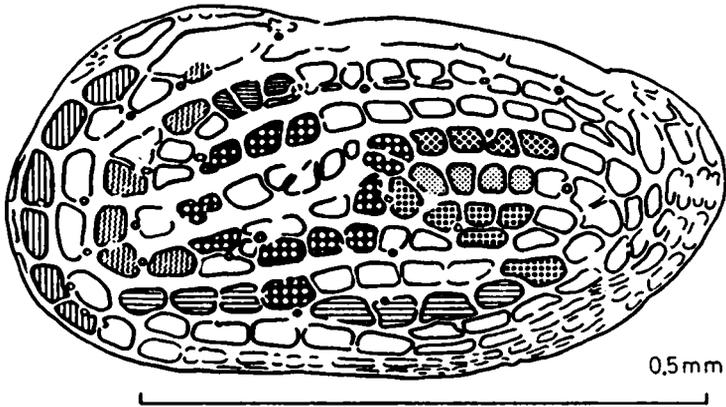
Whereas most species *Cytheretta* are either smooth or have only ridge-sculpture, *Cytheretta haimeana* (BOSQUET, 1852) has connected its ridges into a reticulated pattern connected with crossed bridges interreticulation by means of cross-bridges. In the 5 investigated valves the meshes are approximately constant in number and arrangement.

In the attempt to relate the *Cytheretta* reticulation with that of *Limburgina* the starting point was the pattern in *Mosaeleberis* (Fig. 31). In addition, comparison with cf. *Cytheretta* *wsp.* was useful (Fig. 32, 2). This species seems very similar to *Cytheretta haimeana*, but it has different valve outline, and it lacks the broadened inner lamella typical of *Cytheretta*. Both species are from the same locality in the Paris Basin Middle Eocene.

These elements were recognizable on *Cytheretta haimeana* and c.f., with some reservations: the anterior K meshes, the N series, parts of the E ring, and pores of cones T16 and T17. Relative to the other meshes these drawings represent only an initial attempt at interpretation. The uncertainty lies in the chain of reasoning from *Limburgina* via *Mosaeleberis* to *Cytheretta*. A comparison between *Cytheretta haimeana* and cf. *Cytheretta*, however, yields many coincidences. Some of the common properties, like the conspicuously-formed pair of meshes behind the E ring, indicate very close affiliation. But c.f. *Cytheretta* *sp.* does not show the very characteristic broadening of the inner lamella of *Cytheretta*. Thus it either provides a model for a predecessor of *Cytheretta* that has retained the primitive form of the inner lamella (in this case *Paracytheretta* could not be ancestral to *Cytheretta*) or is a descendant of *Cytheretta*, in which the cytheretid inner lamella is underdeveloped. In any case, this example can be incorporated into discussions on the value of diagnoses of genera and families (see also TRIEBEL and MALZ, 1969, and GRUNDEL, 1969).



1



2

**Fig. 32.**

(1) cf. *Cytheretta* sp. Left valve. Parisian "calcaire grossier" Fm. Lutetian with *Orbitolites complanatus*, Grignon. Presentation method as above. The interpretation of the pattern is tentative.

(2) *Cytheretta haimeana* (BOSQUET, 1852). The left valve of a female. Presentation method as above. Interpretation of the pattern is tentative.

## 6.4. RESULTS

The *Limburgina*-type ornament, including examples from preceding sections, has been detected in 25 figured species from at least 14 genera. The examples demonstrate that the homologous patterns of fine sculpture in ostracods can appear together with various carapace shapes, coarse sculpture patterns, configurations of the muscle scars, and types of hinge structure.

Depending on the preferred system, either two sub-families or several families can serve to taxonomically encompass the forms having *Limburgina*-type ornamentation.

(1) After HARTMANN (1964):

Cytheridae — Trachyleberidinae and  
„ — Cytherettinae.

(2) According to the systematics in the *Treatise* (1961):

Brachycytheridae  
Cytherettidae  
Leguminocythereididae  
Trachyleberididae.

(3) After HAZEL (1967):

Trachyleberididae — Trachyleberidinae  
— Mauritsininae  
— Echinocythereidinae  
— Pterygocytherinae  
— Cytherettinae  
Hemicytheridae — Thaerocytherinae.

Relationships following from the authors investigations are shown in Table I (p. 18); arguments for this classification are given in Section 7 below.

Up until now, the ornament of the type species of *Leguminocythereis* could not be homologized with that *Limburgina*.

Jurassic and Lower Cretaceous ostracods, as noted before, were not taken into consideration here.

## 7. PHYLOGENETIC AND TAXONOMIC CONCLUSIONS

### 7.1. LIMITATIONS

Conclusions as to phyletic relationship and correct systematic position are fairly easily inferred for the majority of examples investigated. Nevertheless, such consideration is mostly left aside here for the following reasons:

(1) Other systems of characters, such as ventral reticulation and marginal conation have not been investigated sufficiently.<sup>23)</sup>

(2) A substantial component of the history of sculpture is the evolution of ribs. These must be defined with greater precision with the aid of macrocones (as fixed points) and reticulation.

(3) Many species whose morphology may be expected to supply much information have not yet been studied.

(4) In standard phylogenetic and taxonomic argumentation there is commonly no room for assuming reversed development. However, examples of this can be found in the evolution of the sculpture of trachyleberid ostracods. They can be explained partly by neoteny and partly by the removal of a genetic block in the formation of ornamentation (see also *Echinocythereis*, p. 76) These are apparently only the reversal of very small mutation steps, which is tolerated within DOLLO'S Law. Nonetheless, the finding of phyletic relationships is hampered to a great extent by this factor.

### 7.2. TAXONOMICALLY SIGNIFICANT AFFILIATIONS

In the following paragraphs, hints of phyletic relationships are included insofar as they are important for taxonomic arrangement in this paper.<sup>24)</sup>

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<sup>23)</sup> For new data see LIEBAU, 1975a, figs. 1—3.

<sup>24)</sup> A more recent interpretation of this matter is outlined in LIEBAU, 1975a.

*Cythereis* assigned by the author to the ostracods with orthopleural sculpture, but *Cythereis* s. str. shows certain similarities to the clinopleural forms in the structure of posterior parts of the dorsal rib and median rib. Since two cones from the posterior part of the median rib enter into the adjacent vertical branch of the dorsal rib of *Cythereis*, s.l., the true orthopleural pattern of the ribs, like that of *Mauritsina latebrosa*, is formed. These orthopleural representatives, together with genera such as *Curfsina* and *Spinoleberis* (neither discussed here), evidently make up one phylogenetically homogeneous group. Of the suprageneric taxa discussed in the present study, the subfamily Cythereidinae BEROUSEK, 1952, is the oldest by nomenclature. The two other subfamilies could be subordinated to it as the following tribes:

Cythereidini BEROUSEK	}	Cythereidinae BEROUSEK
Mauritsinini DEROO		
Spinoleberidini POKORNY		

The *Oertliella* group,<sup>25)</sup> i.e. *Oertliella* and "*Spongicythere*" gr. *koninckiana*, also has similar *Limburgina*-type sculpture and orthopleural sculpture much like that of *Mauritsina latebrosa*, but the median rib and mesh 25 are missing. The muscular field is formed as in *Cythereis*, and thus is more primitive than that of *Mauritsina*; but the hinge is more evolved than in either.

Important characters are to be found in the ventral sculpture and the area around the ventral rib. Looked at in this way, *Cythereis* and *Mauritsina* are closely related (ridges parallel to the margin on the ventral side are characteristic) whereas *Oertliella* and "*Spongicythere*" gr. *koninckiana* belong to a clearly different group (on the ventral side series of meshes radiate from the postventral corner of the shell toward the ventral ribs).

*Limburgina* resembles *Oertliella* in many characters, but, on one hand several species have an additional median rib, and on the other the loss of the antennal scar from the muscle field characteristic of later *Hemicytherede* has already begun. One species, *Limburgina* aff. *depressa*, assumes the characters of sculpture of the highly evolved species "*Quadracythere*", *Radimella* and *Mutilus*. Accordingly, *Limburgina* should be considered an early *Quadracythera*-like *Hemicytheride*, for which HAZEL (1967) established the subfamily *Thaerocytherinae*. The *Oertliella* group is somewhat more primitive, but only with regard to its muscle scar, and it can hardly be excluded here.

*Kingmaina* has the internal characters of *Oertliella*, but the dorsal rib is reduced at least in the region of the median sulcus, while the ventral part of the shell is drawn backward in a winglike manner

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<sup>25)</sup> In 1972, one year after the original publication of this paper, BENSON described the appendage morphology of a recent descendent of *Oertliella*: in most characters it represents a primitive *Trachyleberidine* stage, its "knee apparatus", however, is of the true *Hemicytherine* type (BENSON, 1972: 60).

on both sides. HAZEL (1967) wanted to include *Kingmaina* in Pterygocytherinae, which have the same carapace shape. The argument against this is that the reticulation in *Kingmaina* is positioned in a specific way to support the winglike extensions of the shell (the region of the ventral rib is reinforced from within as with columns). In the nonreticulated *Pterygocythereis* there are no such reinforcements, so that the similarity in the shell form seems to be a result of functional convergence.

Homologous relationships between *Pterygocythereis* and *Cythereis* in cone pattern were demonstrated by POKORNY as early as 1966, and for this reason Pterygocytherinae should also be included among the ostracods with Limburgina-type ornament. It is particularly the early representatives that can be very well compared with *Oertliella* with regard to the ventral marginal sculpture and the formation of the ventral rib. Also, other relatives of *Oertliella* include a number of (still undescribed) species with the habitus of *Pterygocythereis* and with a tendency toward reduced reticulation.

In the morphology of appendages *Pterygocythereis* resembles *Trachyleberis* to a considerable extent (see NEALE, 1959), but the coincidence seems to be in primitive characters, whereas Hemicytheride (introduced already with the Echinocythereidinae) stand out in some advanced properties (cf. POKORNY, 1964, concerning *Trachyleberidinae* and *Hemicytherinae*). In the absence of clues to the direct affiliation relationship between *Pterygocythereis* and *Trachyleberis*, it seems that the similar construction of appendages reflects the structure of some earlier common ancestor, perhaps that of *Cythereis* s.l. Here it appears possible to establish the exact relationship of Cythereidinae to Trachyleberididae s. str.

Echinocythereidinae, with regard to appendages lies between Trachyleberididae and Hemicytheriade (see VAN MORKHOVEN, 1962/63, and HAZEL, 1967). The development of the reticulation pattern agrees with this.

Only little can be said about the systematics of the clinopleural representatives. Already in the Upper Jurassic and Lower Cretaceous Protocytherinae one meets with the clinopleural gross sculpture. Protocythere should be thought of as the ancestor of the younger subfamilies of the trachyleberid family group but with considerable reservations: first, the eye nodes are reduced (at least in the cases known to the author they are not innervated) and, secondly, the hinge is very differently structured. At best the Pseudoprotocythere hinge resembles that of Trachyleberididae. It is also uncertain whether the "blind" Buntohiinae (clinopleural?) and Cytherettidae (clinopleural) should be included here (see also VAN MORKHOVEN, 1962/63).

The clinopleurally sculptured genera and groups of species with eye nodes are *Mosaeleberis*, "*Leguminocythereis*" *striato-punctata* group and aff. *Falunia* (these three are investigated in this study), as well as other *Falunia* s. str. and *Veenia*. Sculptural intermediates for the orthopleural group of Trachyleberididae are *Isocythereis*, "*Cythereis*" *acuticostata*, the here investigated *Dumontina* and *Spinicythe-*

reis (and perhaps *Trachyleberidea*). Faluminae can serve as a superior taxon for these ostracods, if the peculiarities of the *Falunia*-hinge are considered a phenomenon of reduction without suprageneric meaning (cf. VAN MORKHOVEN, 1962/63, concerning *Urocythereis* sp. and *Campylocythere*, and POKORNY, 1964, about *Neireina*).

*Trachyleberis* s. str. could not be investigated by the author. It remains a problem what should be understood under *Trachyleberidinae* s. str. and how the other subfamilies should be organized. Two species of *Acanthocythereis* (this genus is at least in external appearance close to *Trachyleberis*) possess reticulation and cone patterns which are clearly different from those in the investigated *Cythereidinae* and *Hemicytheridae*.

### 7.3. APPENDIX: FORESEEABLE CHANGES IN THE FRAMEWORK OF FAMILIES AND SUBFAMILIES

Cythereidinae and Faluniinae sensu novo would have an essentially different content from that of their original conception. However, the author was not able to collect enough material to provide well-founded new diagnoses of these taxa. Hence they are used in this study only provisionally, and not as well-defined groupings.

By enlarging *Hemicytheridae* to include the *Oertliella* group a change in the diagnosis of the family becomes necessary; the result of this new diagnosis is that *Hemicytheridae* can no longer be formally distinguished from the standard version of *Trachyleberididae*. The decisive step toward the disqualification of static systematics, however, was already made by POKORNY (1968, see also 1957 and 1964), in forming *Spinoleberidinae*. (*Spinoleberidinae*, according to the configuration of the muscular field, should be formally classified under *Hemicytheridae*, but other characters confirm that it is closer to *Cythereis*, and hence to *Trachyleberididae*. The similarity in the scar patterns with *Hemicytheridae* is the result of convergence. Thus there is no shell character that definitively separates *Hemicytheridae* and *Trachyleberididae*.)

Some of the investigated ostracods were temporarily included in the "families" *Brachyocytheridae* and *Leguminocythereididae*. Among the *Leguminocythereididae*, *Leguminocythereis scarabeus* is for the time being apparently the only certain representative of this family (HAZEL, 1967). Since ancestors, possible closely-related species and even the muscle scars of the type species are unknown, the position of this genus is isolated mainly due to the absence of data. (However, the taxa *Leguminocythereis* and *Leguminocythereididae* were of great practical value because in these the secondarily ribless, as their name suggests "bean-shaped", the *Trachyleberididae* could be combined into a (single) form-group.) As for *Brachycythere* (and, accordingly *Brachyocytheridae*), probably not even the type spe-

cies is well known.<sup>26)</sup> REUSS (1854) described it (from the Austrian Upper Cretaceous) but only inadequately; however, the diagnoses of genus and family were based on specimens from the Texan Upper Cretaceous, which were considered by ALEXANDER (1933) to be conspecific with the species described by REUSS. The appropriateness of that association is open to doubt. Moreover, a large part of the Brachytheridae could already have been distributed into other taxa (Progonoxytheridae, or Macrodentini, Trachyleberididae s. l., or Pterygocytherinae and Hemicytheridae s. l.), so that this "family" consists of only a handful of forms of dubious affinity. The Brachytheridae, as a group defined by form only, was also discussed by HARTMANN (1963 and 1964), who considered it to be an artificial group (see also POKORNY 1957, 1958 and 1964).

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<sup>26)</sup> The type species of *Brachythere* is now being studied by the author. It differs in muscle scar characters from the Texas material.

## 8. SUMMARY

The correlation between genetically conditioned variability and the taxonomic significance of characters has been pointed out in the Introduction. The taxonomic value of morphological peculiarities of hard parts can thus be methodically dealt with. Patterns whose elements show approximate constancy in occurrence are particularly useful taxonomically. In such patterns, each element is genetically fixed<sup>27)</sup> and thus it is a potential character. Network patterns can more easily be used than the line or point patterns.

The sculpture of the lateral side of some reticulate ostracods from the superfamily Cytheracea was investigated. The compared species belong to Trachyleberididae, Hemicytheridae and Cytherettidae (all s. l.). The results are as follows:

(1) The network patterns of the investigated species of Trachyleberididae, Hemicytheridae and Cytherettidae show approximate constancy in the number and position of meshes.

(2) Network patterns of these species are genetically related with each other. They are homologous with each other and hence mesh could be traced back to a general "primitive ornament".

(3) The reference-object for comparison was the reticulation of the lateral side of *Limburgina ornata* (BOSQUET, 1847), a simply ornamented species from the uppermost Cretaceous of Holland. Its reticulation meshes have been individually named. Reticulation ornaments with the *Limburgina ornata* pattern are called "Limburgina-type".

(4) Apart from the mentioned true reticulation, which is also called here "macroreticulation", there is often present another system of minute pits, which, however, are highly variable in number. This second system of pits is designated "microreticulation"<sup>27)</sup>.

(5) In the listed ostracods four classes of cones can be distinguished. The differences pertain to size, position, alignment and variability.

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<sup>27)</sup> Microreticulation was not studied in this paper.

(6) Closer investigations were made of the spines or tubercles referred to as "macrocones". They are situated on the longitudinal ribs, muscle node and walls of the reticulation meshes. Since the adjacent reticulation meshes are individually defined it can be shown that the macrocones also occupy invariable positions. Like the reticulation meshes, they (macrocones) are approximately constant in arrangement and number. As in the case of macroreticulation, the pattern of macroconation can be traced from one species to another by homologizing.

(7) On *Oertliella horridula* (BOSQUET, 1854) the macrocones are named individually.

(8) At the solae of all or almost all reticulation meshes the distal end of a pore canal with a wide lumen is found. In *Oertliella* (which is very close to *Limburgina*) these pore canals are proximally widened and are distally covered by a convex sieve. Thus these are sieve pore canals; they are described mostly from recent forms.

The macroreticulation can include individual meshes without any pores.<sup>13)</sup>

(9) Macrocones, often called "pore cones", contain long and thin pore canals. Some ("simple") macrocones always show only one pore opening, while others (complex macrocones) commonly have two or more pore canals.

When the macrocones are morphologically absent, their pores are still observable in the proper places.

(10) Mesh pores and cone pores, like the meshes or cones to which they belong, can be homologized from one species to another. (Thus the large sieve pore canals of *Oertliella* are homologous to the differently structured pores of the meshes in "*Spongicythere*" *koninckiana*.)

(11) Relationships exist between the *Limburgina*-type fine sculpture and two systems of sensory bristles:

In recent ostracods relationships are known between two types of pores and sensory bristles of different sizes. Mesh pores and cone pores can be homologized with each type, respectively. Thus they belong to two different, although mutually similar, systems of sensory organs.

*Limburgina*-type reticulation and macroconation are, consequently, two components of fine sculpture whose elements usually represent the distal enclosures of the units of certain sensory organs.<sup>13)</sup>

(12) *Limburgina*-type patterns of meshes and cones, and thus the corresponding elements of sensory organs, can be found in the families Trachyleberididae, Hemicytheridae and Cytherettidae (all s. l.) also the genera and groups of species which in the *Treatise* are included under *Brachyocytheridae* or *Leguminocythereididae*.

(13) The major components of coarse sculpture are the ribs. By reference to adjacent and overlying elements of fine sculpture, if these have constant positions, the relative proportions of the ribs can be defined.

Thus it is possible to establish that the investigated group of ostracods can have differently structured dorsal ribs, median ribs and ventral ribs, respectively. Phylogenetically younger rib components can be distinguished from older ones.

(14) Two different but related structural types of coarse sculpture or rib pattern are separately named: "clinopleural" and "orthopleural". Each of the two coarse sculptures corresponds to a particular *Limburgina*-type fine sculpture.<sup>15)</sup>

Since several characters combined with one another occur in both types of structure, it seems that homogeneous related groups are involved.

Belonging to the clinopleural group are Cytherettide, the European species of "Leguminocythereis", and, for example, *Mosaeleberis*.<sup>15)</sup> The orthopleural are: Cythereis, *Mauritsina* and their close relatives; they represent part of Trachyleberidae.

In a broad sense, the orthopleural group should include also the hemicytheriform ostracods, which can possess specific structure of the dorsal rib.

(15) From these analyses and comparisons of sculptures, new evidence is obtained for the close relationship of Trachyleberididae, Hemicytheridae, and other groups of genera, which are for this reason classified by the author under the provisional term "trachyleberid family group". At the same time it has become clear (as is demonstrated above all by the rib patterns) that these suprageneric taxa must be reorganized. If this is done, *Mauritsininae* and *Spinoleberinae* are likely to be subordinated to *Cythereidinae*. Hemicytheridae should probably be enlarged to include the *Oertliella* group.<sup>28)</sup> The author is unable to give a complete revision of these taxa at present, however.

(16) Investigations of the preadult stages are most useful for the study of the sculpture history of several genera.

Although the sculpture of larval stages is subject to certain allometries it nevertheless often shows primitive characters which are lost in the adult specimens. These observations hence comply with the Biogenetic Law.

(17) Each of the investigated elements of fine sculpture with approximately constant occurrence, which can partly be traced from the Cretaceous to the Recent, obviously is genetically determined. They can mutate individually and hence they are potential carriers of characters. Each has its own history. This holds true also for the *Limburgina*-type fine sculpture as a whole. Part of this history can be distinguished in the ontogeny of the single taxon. Polymorphism due to molting does not present a taxonomic complication, but an increase in the number of characters.

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<sup>28)</sup> *Oertliella* group = Oertliellini LIEBAU, 1975.

Distinguishing among and making use of different variabilities, in which particular attention was paid to numerical constancy, has systematically led to the finding of many elements of sculpture which can be homologized.

The homologizing comparison of sculpture patterns has resulted in a multiplicity of taxonomic characters in trachyleberid ostracods.

## 9. TAXONOMIC REGISTER

Unless otherwise specified all genera belong to Trachyleberididae s. l., or Hemicytheridae s. l., and hence Ostracoda-Podocopida-Podocopina-Cytheracea. Individual higher taxonomic categories (like "ostracods", "trachyleberidide" etc.) are not listed or are listed only with incomplete reference to the text. For some genera "s. l." is differentiated from "s. str." (Page numbers marked with\* refer to figures.)

- Acanthocythereis HOWE, 1963 80
- Actinocythereis PURI, 1953 20
- Bairdiacea SARS, 1888 (Podocopida-Podocopina) 23
- Beyrichiida POKORNY 1953. (=Palaecopida HENNINGSMOEN, 1953) 23
- Brachycythere ALEXANDER, 1933 80
- Brachycytheridae PRI, 1954 (Cytheracea) 20, 21, 56, 76, 80, 81, 83
- Bradleya HORNIBROOK, 1952 69
- Buntonia HOWE, 1935 14
- Buntoniinae APOSTOLESCU, 1961 80
- Campylocythere EDWARDS, 1944 80
- Campylocytherinae PURI, 1960 20, 63
- Carincythereis RUGGIERI, 1956 14
- Clavofabela MARTINSSON, 1955 (Beyrichiida-Primitiopsacea Primitiopsidae) 23
- Costa NEVIANI, 1928 71
- Curfsina DEROO, 1966 52, 56, 78
- Cypridacea BAIRD, 1845 23
- Cypridea BOSQUET, 1852 (Podocopina-Cypridacea-Cyprideidae) 27
- Cyprideis JONES, 1857 (Cytheracea-Cytherideidae) 26
- Cypridina interrupta BOSQUET, 1847 73
- Cypridinacea BAIRD, 1850 (Myodocopida-Myodocopina) 23
- Cytheracea BAIRD, 1850 9, 18, 21, 23, 82.
- Cythereidinae BEROUSEK, 1952 18, 78, 80, 84
- Cythereidini BEROUSEK, 1952 78
- Cythereis JONES, 1849 26, 37, 38, 42, 48, 54, 56, 74, 78, 80, 84.
- C. acuticostata TRIEBEL, 1940 80.
- C. latebrosa confinis SZCZECURA, 1965 54
- C. ornatissima (REUSS, 1846) 11,\* 26

- C. polygonata ROME, 1942 59
- C. s. l. = "Cythereis" 15, 46, 48, 56, 73, 77, 80
- C. s. str. 77  
Cytheretta MÜLLER, 1894 (Cytheracea) 50, 53, 74, 76.
- C. haimeana (BOSQUET, 1852) 18, 95,\* 96, 76
- cf. C. sp. 18, 75, 74, 76, 75, 74  
Cytherettidae TRIEBEL, 1952 9, 21, 18, 19, 74, 76, 80, 82, 107  
Cytherettinae TRIEBEL, 1952 54, 76, 76  
Cytheridae BAIRD, 1850 76  
Cytherina striato-punctata ROMER, 1838 63  
Dumontina DEROO, 1966 29, 71 80
- D. sp. 18, 72  
Echinocythereidinae HAZEL, 1967 18, 59, 76, 79, 80  
Echinocythereis PURI, 1954 37, 59, 59, 77
- e.-isabenana-aragonensis group (both species: OERTLY, 1960) 59
- E. scabra (VON MÜNSTER, 1830) 18, 59, 59\*.  
Elofsonella amberii CARBONNEL, 1969 17  
Falunia GREKOFF et MOYES, 1955 73, 80
- aff. F. 53, 73, 80
- aff. F. sp. 18, 79  
Faluniinae MANDELSTAM, 1960 18, 19, 20, 77, 81, 82, 83, 84, 85.  
Femicytherinae PURI, 1953 79.  
Hermanites PURI, 1955
- H.? dameriensis KEIJ, 1958 54
- "H." gr. pajenborchianus KEIJ, 1957 14
- H. s. l. = "Hermanites" 42, 53
- aff. H. sp. 16, 17  
Hornibrookella MOOS, 1965 53
- H. macropora (BOSQUET, 1852) 54  
Isocythereis TRIEBEL, 1940 21, 26, 79.  
Kingmaina KEIJ, 1957 47, 79
- K. cf. opima SZCSECHURA, 1965 56
- K. cristata (BOSQUET, 1854) 18, 49, 56, 57
- K. hagenowi (BOSQUET, 1854) 13  
Leguminocythereididae HOWE, 1961 (Cytheracea) 18, 20, 21, 63, 76, 80 83  
Leguminocythereis HOWE, 1936 (Leguminocythereididae-Cytheracea) 63,  
76, 80
- "Leguminocythereis" 73, 84
- "L." angulatopora (REUSS, 1850) 18, 70\*.
- "L." aff. bosquetiana (JONES et SHERBORN, 1889) 18, 49 63, 64\*, 65\*, 66,  
67\* 70
- "L." bosquetiana (JONES et SHERBORN, 1889) 18, 60, 70\*
- L. scarabaeus HOWE et LAW, 1936 18, 67\* 70, 80
- L. sorneana OERTLI, 1956 63
- "L." striatopunctata (ROMER, 1838) 18, 68\*, 69\*, 71
- "L." — striatopunctata group 71, 79  
Limbargina DEROO, 1966 28, 29, 33, 33, 36, 40, 41, 48, 52, 56, 59, 63, 67,

- 68, 69, 71, 74, 75, 76, 78, 79.
- L. aff. depressa* DEROO, 1966 18, 33, 34\*, 38, 49, 83, 54, 63, 78
- L. longiporacea* DEROO, 1966 33
- L. ornata* (BOSQUET, 1847) 14, 18, 28, 29, 30\*, 31\*, 32, 33\*, 34, 36, 38, 40, 54, 66, 82
- L. pseudosemicancellata* (VAN VEEN, 1936) 18, 33\*, 35
- L. semicancellata* (BOSQUET, 1854) 33
- Loculicytheretta* RUGGIERI, 1954 71
- Macrodentinini MANDELSTAM, 1960 Lex: [Macrodentinae] (Cytheracea-  
-Progonocytheridae?) 81
- Mauritsina* DEROO, 1962 38, 48, 52, 54, 55, 71, 78, 84
- M. latebrosa* (SZCZECHURA, 1965) n. comb. 18, 29, 51, 54, 55
- M. s. l.* 15, 56
- Mauritsina* sp. 18, 55
- M. varia* (HERRIG, 1965) n. comb. 17, 54
- Mauritsininae DEROO, 1962 18, 21, 76, 84.
- Mauritsinini DEROO, 1962 78.
- Mosaeleberis* DEROO, 1966 50, 71, 74, 79, 84
- M. sp. 1.* 18, 50, 73
- M. sp. 2.* 18, 73
- Mutilus* NEVIANI, 1928 78
- Nereina* MANDELSTAM, 1957 [recte *Finmarchinella* SWAIN, 1963] 80
- Nobideyrichia* HENNINGSMOEN, 1954 23
- Normaniccythere* NEALE, 1959 27
- Occultocythereis* HOWE, 1951 14
- Oertliella* POKORNY, 1964 28, 37, 38, 40, 41, 42, 43, 44, 45, 47, 48, 59, 78, 83
- Oe. aculeata* cf. *aculeata* (BOSQUET, 1852) 41
- Oe. group* 78, 80, 84
- Oe. horridula* (BOSQUET, 1854) 17, 18, 34, 38, 39\*, 83.
- Oe. lichenophora* (BOSQUET, 1852) 41
- Oe. s. l.* 14
- Oe. sp. 1* 18, 43, 44
- Oe. sp. 2.* 18, 41, 45
- Ostracoda* LATREILLE, 1806 18
- Paracytherette* TRIEBEL, 1941 26, 50, 73, 74
- Podocopida* MÜLLER, 1894 18, 21.
- Podocopina* SARS, 1866 18
- Pokornyella ventricosa* (BOSQUET, 1852) 42
- Progonocytheridae SYLVESTER-BRADLEY, 1948 81
- Protocythere* TRIEBEL, 1938 27, 50, 79
- P. emslandensis* BARTENSTEIN & BURRI, 1955 14
- Protocytheretta* PURI, 1958 71, 74
- Protocytherinae LJUBIMOVA, 1955 74, 79
- Pseudoprotocythere OERTLI, 1966 79
- Pterygocythereidini MANDELSTMAN, 1960 (ex: Pterygocytherides; based  
on Pterygocythereis)
- Pterygocythereis BLAKE, 1933 27, 42, 79

- P. spinigera* POKORNY, 1966 27  
 Pterygocytherinae PURI, 1957 76, 79, 81  
 Quadracythere HORNIBROOK, 1952
- "Qu." prava (BAIRD, 1850) 18, 56, 60  
 "Qu." prava group 59  
 „Qu. producta (BRADY, 1866) 46  
 "Qu." s.l. = "Quadracythere" 49, 53, 54, 78  
 "Qu." sp. 18, 54, 60, 61, 62  
 Radimella POKORNY, 1968 27, 78
- R. dictyon* POKORNY, 1968 54  
 Schizocytherinae HOWE, 1961 54  
 Spinicythereis POKORNY, 1964 29, 71, 79
- S. geinitzi* (REUSS, 1874) 18, 71, 72  
 Spinoleberidinae POKORNY, 1968 80, 84  
 Spinoleberidini POKORNY, 1968 78  
 Spinoleberis DEROO, 1966 56, 78  
 Spongicythere HOWE, 1951 42
- "S." koninckiana (BOSQUET, 1847) 18, 47\*, 48, 83  
 "S." konickiana group 78  
 Thaerocytherinae HAZEL, 1967 76, 78  
 Trachyleberidea BOWEN, 1953 37, 80  
 Trachyleberide group of families 9, 19, 27, 28, 56, 80, 84  
 Trachyleberide ostracods 10, 12, 15, 19, 26, 49, 52, 63, 78  
 Trachyleberididae SYLVESTER-BRADLEY, 1948 9, 18, 19, 20, 27, 74, 76,  
 81, 82 83, 84  
 Trachyleberididae SYLVESTER-BRADLEY, 1948 54, 76, 79, 80  
 Trachyleberidini SYLVESTER-BRADLEY, 1948 18  
 Trachyleberis BRADY, 1898 20, 79, 80  
 Tringlymus BLAKE, 1950 63, 69  
 Urocythereis RUGGIERI, 1950
- U. sp.* 80  
 Venia BUTLER & JONES, 1957 50, 73, 79

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## 11. ADDITIONAL NOTES

p. 11. The last sentence in the caption to Fig. 2 should read: From POKORNY, 1963 (marks added).

pp. 18, 49 and 63 "*Leguminocythereis* aff. *bosquetiana* (JONES & SHERBORN, 1889) could be determined with somewhat greater precision as: "*Leguminocythereis*" cf. *bullata* HASKINS, 1970.

pp. 41—48. Two new studies on sieve and other pores were not taken into consideration: Omatsola, M. E. (1970). "On Structure and Morphologic Variation of Normal Pore System in Recent Cytherid Ostracoda (Crustacea) — *Acta Zool. (Sweden)* 51: 115—124 (1 Fig., 3 Plates), 1970.

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