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ATTI
DELLA
SOCIETÀ ITALIANA
DI SCIENZE NATURALI
E DEL
MUSEO CIVICO
DI STORIA NATURALE DI MILANO

VOLUME CVIII

I. B. A.
INTERNATIONAL BRYOZOOLOGY ASSOCIATION

PROCEEDINGS
of the
FIRST INTERNATIONAL CONFERENCE ON BRYOZOA

AGIP Direzione Mineraria Paleontological Laboratory S. Donato Milanese
August 12th-16th 1968

Edited by Enrico Annoscia, *Conference Chairman*

MILANO

31 Dicembre 1968

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Note: The discussion following each paper were not printed in these PROCEEDINGS owing to space and cost reasons. They will be duplicated separately. Anybody who is interested to have them is asked to request them to I.B.A. (c/o Dr. Enrico Annoscia, Via Mincio No. 3, 20139 Milan, Italy).

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Atti Soc. It. Sc. Nat. e Museo Civ. St. Nat. Milano - 108 : 4. 31-XII-1968

1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968

La Società Italiana di Scienze Naturali ed il Museo Civico di Storia Naturale di Milano sono lieti di poter ospitare nei loro Atti i Risultati di questo importante Congresso sui Briozoi, il primo a carattere internazionale dopo l' informale Incontro di Stoccolma del 1965 che dette origine alla costituzione dell' I.B.A. (International Bryozoology Association).

L' I.B.A., seppur così giovane, conta già quasi duecento aderenti, tutti specialisti di un gruppo di animali a torto per l'addietro trascurati, specie in Italia, da Paleontologi e da Zoologi, ma che già fanno sentire il loro peso negli studi stratigrafici ed ecologici.

Vogliamo qui ringraziare il Dr. Enrico Annoscia, organizzatore e Presidente del Congresso, che con particolare cortesia ci ha offerto l'opportunità di pubblicare un così grande numero di importanti lavori specializzati, permettendoci di offrire ai nostri Soci un quadro completo dei più moderni studi sui Briozoi, quale non è dato trovare sulle riviste scientifiche italiane.

The Italian Society of Natural Sciences and the Milan Civic Museum of Natural History are glad to give hospitality in their Review to the Proceedings of this important Conference on Bryozoa, the first international one after the informal Meeting of Stockholm in 1965, which gave birth to I.B.A. (International Bryozoology Association).

I.B.A., although so young, already enumerates two hundred members, all specialized on a group of animals blamely heretofore neglected, especially in Italy, by Paleontologists and Zoologists, but which are becoming more and more important in stratigraphical and ecological studies.

We wish to thank Dr. Enrico Annoscia, who organized and presided the Conference, for having most kindly offered us the opportunity to publish so many weight specialized papers, enabling us to offer to our Members a complete picture of the up-to-date studies on Bryozoa, which are not easily found in the Italian scientific reviews.

Giuseppe Nangeroni - Cesare Conci

Atti Soc. It. Sc. Nat. e Museo Civ. St. Nat. Milano - 108: 5-6, 31-XII-1968

1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968

ENRICO ANNOSCIA

CONFERENCE CHAIRMAN ADDRESS

Ladies and Gentlemen, old and new friends,

I am most glad to welcome you in San Donato Milanese, also on behalf of AGIP Paleontologists and Italian Bryozoologists.

This is the First International Conference organized by I. B. A. and the second on Bryozoa, after the first informal meeting held in Stockholm in 1965, when our Association was founded.

This Conference has been possible through the help of several bodies, which I want to thank, also on behalf of us all.

First of all I thank AGIP Direzione Mineraria-through the persons of General Manager Eng. E. Egidi and Vice-Manager Dr. D. Jaboli - which generously accepted to give hospitality our Conference, and the Mayor of S. Donato Milanese, Dr. G. Florio, who is a geologist and whose help was unvaluable for meeting organization expenses.

Particular thanks are due to AGIP Direzione Mineraria, to National Research Committee (C. N. R.), to « Camera di Commercio, Industria, Artigianato e Agricoltura », Milan, to « Amministrazione provinciale », Milan and to « Cassa di Risparmio delle Provincie Lombarde » Bank, which supplied us with funds for printing the Conference Proceedings Volume, and to Prof. C. Conci, Director of the Milan Civic Museum of Natural History and Vice-Chairman of the Italian Society of Natural Sciences, who generously accepted to print our Conference Proceedings in the review « Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano ».

I also thank the « E. Mattei » ENI Hydrocarbons Post-Graduate School, through the persons of Prof. M. Boldrini and Eng. E. Camatini, the ENI Public Relations Office, through the persons of Dr. Bellini delle Stelle, Mr. Salvadori and Mr. Foscari and the Mayor of Possagno, for the help and hospitality given to us.

Furthermore, I am deeply grateful to dr. Ascoli, who was very close to me in organizing this Conference, to dr. Cheetham, IBA Chairman, and to the pretty Secretary, Miss Cook.

Finally, I heartly thank you all for having come here and for having appointed me Chairman of this Conference. I wish this Conference might originate an important progress in the study of Bryozoa, so that this group of animals - wrongly forgotten since not long ago - might more and more be widely applied in the field of Stratigraphy and Ecology.

I have now a very sad news to give you: prof. Ernst Marcus, 75 years old, died on June 30th. This is a great lost for the Bryozoology. I would propose, in the Business Meeting, to dedicate this Conference to his Memory.

Atti Soc. It. Sc. Nat. e Museo Civ. St. Nat. Milano - 108: 7-12, 31-XII-1968

1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968

EVELINE DU BOIS REYMOND MARCUS (*)

ERNST MARCUS

8.VI.1893 - 30.VI.1968

ERNST MARCUS was born in Berlin in 1893. From his childhood he loved animals, especially seals and cats. As a school boy he collected beetles. In 1912 he entered the University of Berlin to study Zoology. He was beginning his Doctor's thesis in the Entomological Department of the Berlin Museum, when the 1914-1918 world war interrupted him. In 1919 he obtained his Doctor's Degree. Afterwards, the Director of the Museum gave him the collection of Bryozoa to study. He had no specialist to initiate him. He consequently had to make his own way with a rather old library and some material classified mainly by Kirchenpauer.

He was entrusted with collections from many expeditions. When he sent his first manuscript to Sweden, the Editor, THEODOR ODHNER, returned it and told him to translate it into German. The way it was, it seemed to be translated literally from Latin. Thus, ERNST MARCUS learned to take good care of his style. From his first publications Dr. O. NORDGAARD - TRONDHJEM recognized, that he did not know LEVINSEN's fundamental « Morphological Studies on the Cheilostomatous Bryozoa » (1909), and gave him the precious volume, too expensive for a student during the years of inflation.

In 1923 ERNST MARCUS obtained the « Privat-Dozent » and was appointed assistant of Professor Karl HEIDER at the Zoological Institute of the University of Berlin. In 1924 we married.

(*) Caixa Postal 6994, São Paulo, Brazil.

He had until then all illustrations for his papers done by a professional, but from then I took on all the drawings and we studied our Bryozoa together. For some of the technical details I was apter, and on such occasions he did the cooking. Till 1925 we only had preserved material, but that year we went to the station of Büsum and had our first experiences with living marine Bryozoa, published in 1926. In the same year we got our first living freshwater species in a lake near our house. These *Plumatella* were extremely rich and produced great numbers of larvae. One night he kept awake to observe the always nocturnal birth of the larva (1926. Verh. D. Z. G.). We succeeded to stain the nervous system in the living larva.

In 1929 Ernst Marcus was appointed Associate Professor.

Sidney F. Harmer in his Presidential Address to the Linnean Society London, 28th of May 1931, referred extensively to our work, which made us very proud.

During the years 1931 and 1932 we studied a population of *Lophopus crystallinus* and went to the pond where it was thriving every week (1934).

In 1935 Ernst Marcus was dismissed from the University due to the Nazi laws. By the Society for the Protection of Science and Learning Ltd. (Lord Beveridge) he was recommended for the Chair of Zoology at the University of São Paulo, Brazil, which he occupied from 1936 to 1963, when he had to retire at seventy years of age. In the collections of the Department we found lots of preserved Bryozoa and on the coast near Santos there were many opportunities to study the living animals and their larvae (1937-1939). Owing to the war it became impossible to continue our marine studies, so we began to work with freshwater material. Our most exciting discovery was the vestibular pore which frees the statoblasts from the living colony. For a long time we had suspected that statoblasts are freed, because so many of them swim on the surface over the colony, but we had thought that the chironomids feeding upon the polypids might also have opened the way for the statoblasts. By patient observation we succeeded to see the statoblast expelled like an airship from the hangar (1941, 1942).

From the freshwater Bryozoa our attention was then called to the accompanying fauna of Oligochaeta and Turbellaria, later

ERNST MARCUS

to terrestrial and marine Turbellaria, and only now and then we returned to the Bryozoa (1946, 1949, 1950, 1953, 1955, 1955, 1957, 1962, 1968).

From 1952 on we were chiefly occupied with Opisthobranch Gastropods. In the last years ERNST MARCUS' rhythm of work slowed down gradually, and in 1968 he weakened visibly, till he passed away on June 30, aged seventy-five.

We had a lively correspondence with THEODOR MORTENSEN - Copenhagen, whose collections from all the world contained many Bryozoa, during all the years until he died in 1953. We were always by letter in contact with the Bryozoologists S. F. HARMER, O. NORDGAARD, ANNA B. HASTINGS, R. S. BASSLER, RAYMOND C. OSBURN, MARY D. ROGICK, FRITZ WIEBACH, PATRICIA L. COOK, and others. In 1956 LIBBIE H. HYMAN came to see us to prepare the volume 5, Smaller Coelomate Groups, of her Treatise of the Invertebrates, in which she resumed many of our results.

ERNST MARCUS was correspondent member of 9 scientific Academies and Societies in Brazil, USA, Finland, Denmark, England, and Germany, and co-editor of the « Beiträge zur Neotropischen Fauna » (Fischer, Stuttgart) and the « Monitore Zoologico Italiano ».

PAPERS OF PROFESSOR ERNST MARCUS ON BRYOZOA

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22. 1930 - Bryozoa - In W. Junk, Tabulae Biologicae, v. 6 (= suppl. 2), pp. 311-327, 5 text-figs.
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25. 1936 a - Sôbre alguns phenómenos da vida dos Bryozoarios Marinhos - Arch. Inst. Biol. São Paulo, v. 7, pp. 203-208, 7 text-figs.
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43. 1950 a - Systematical remarks on the bryozoan fauna of Denmark - Vidensk. Medd. Dansk nat. For., v. 112, pp. 1-34, 5 text-figs.
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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968

Piero Ascoli (*) & Patricia L. Cook (**)

CONFERENCE REPORT

The First International Conference on Bryozoa of I.B.A. (International Bryozoology Association) was opened in the Conference Hall of E.N.I. (Italian Hydrocarbons National Company) First Skyscraper in S. Donato Milanese (Milan, Italy) at 8.30 a. m. on Monday, August 12 th, 1968.

Among the enrolled 72 I.B.A. members, 49 attended the Conference sessions. 45 papers were delivered. Owing to lack of time, the papers of the non attending members were considered read, since their abstracts were distributed to all present members in a folder containing many publications presented by various Institutions. Their complete texts will be published, together with the texts of the attending members' papers, in the Conference Proceedings.

The Conference Chairman, Dr. E. Annoscia, opened the Conference and welcomed the I.B.A. members on behalf of AGIP Paleontologists and Italian Bryozoologists.

The floor was taken by the I.B.A. Chairman, Dr. A. H. Cheetham, who thanked Dr. Annoscia for his great efforts and contribution in organizing the Conference, helped in this by Dr. P. Ascoli, Conference Secretary.

Dr. Cheetham opened the First Technical Session and gave the chair to Dr. R. Lagaaij, for presiding the Group 1: The Bryozoa in Oil Research. Three papers were delivered and discussed in this group.

At the end of papers of the Group 1st, Dr. Lagaaij gave the chair to Dr. I. Vigeland for presiding the 2nd Group: « Anatomy, Morphology and Skeletal Structure ». Fourteen papers were presented in this group.

The 1st Session was interrupted from 12.30 a. m. until 14.30 p. m. and ended at 17 p. m.

(*) Conference Secretary, AGIP Direzione Mineraria Paleontological Laboratory - S. Donato Milanese (Italy).

(**) IBA Secretary, British Museum (Natural History) - Zoology Department - London, U. K.

The members then visited the various AGIP Direz. Mineraria Laboratories (Muds-Cements Lab., Chemical Lab., Geochemical Lab., Petrological Lab. and Paleontological Lab.), stopping particularly in the latter and examining its equipment and collections of Bryozoa and other fossils. They then attended the cocktail party offered by the Mayor of S. Donato Milanese, which took place in the lobby near the 1st Skyscraper Conference Hall. At the beginning of the party, Eng. E. MERLINI welcomed the I.B.A. members on behalf of the AGIP Direz. Mineraria General Manager and wished them a most successful Conference.

AUGUST 13. The II Technical Session took place under the chairmanship of Dr. G. LARWOOD in the morning as well as in the afternoon, for the Group 3: Ecology and Paleoecology. Seven papers were presented and discussed.

Afterwards, the members attended the banquet offered by the AGIP Direzione Mineraria Management, at the Restaurant of the Motel Metanopoli. At the end of the banquet, Eng. E. MERLINI, on behalf of the Management, told he was most happy to give hospitality to the I.B.A. members and expressed to them his most sincere wishes for a very successful Conference. Answering Eng. MERLINI, the I.B.A. Chairman, Dr. A. H. CHEETHAM, expressed to him and to the AGIP Direzione Mineraria Management his warmest thanks for the hospitality given by AGIP and for all the facilities put at disposal of the members, which enabled them to carry on the Conference works in the best possible way.

AUGUST 14. The Technical Session III (Group 4: Evolutionary Patterns and Systematics) was held under the chairmanship of Mr. L. PITT, in the morning in the Conference Hall of the E.N.I. First Skyscraper, in the afternoon by the E. MATTEI Post-Graduate Hydrocarbons School Public Hall. Nine papers were presented and discussed in this group.

Around 5 p. m., the Conference members went to Milan, where they visited the Civic Museum of Natural History. They were welcomed by Prof. C. CONCI, Director of the Museum, who with the help of his assistants Drr. G. PINNA and C. LEONARDI, guided them through the exhibition halls of the various sections of the Museum. At the end of their visit, Prof. CONCI offered a cocktail party to the Conference members.

AUGUST 15. The whole day was taken by the field trip made to Possagno and Priabona to examine the Eocene-Miocene outcrops. There was a full itinerary in the morning and the party was entertained to lunch by the Mayor of Possagno. In the afternoon, visits were made to the Gallery of plaster casts and the Templum by Canova at Possagno, followed by further examinations of the outcrops at Priabona. On the return journey, a short stop was made at Marostica and at Sirmione on the Garda Lake, where the members enjoyed a picnic. All members were grateful to Dr. G. BRAGA, from the Padua Geological Department, who was in charge of the field-trip.

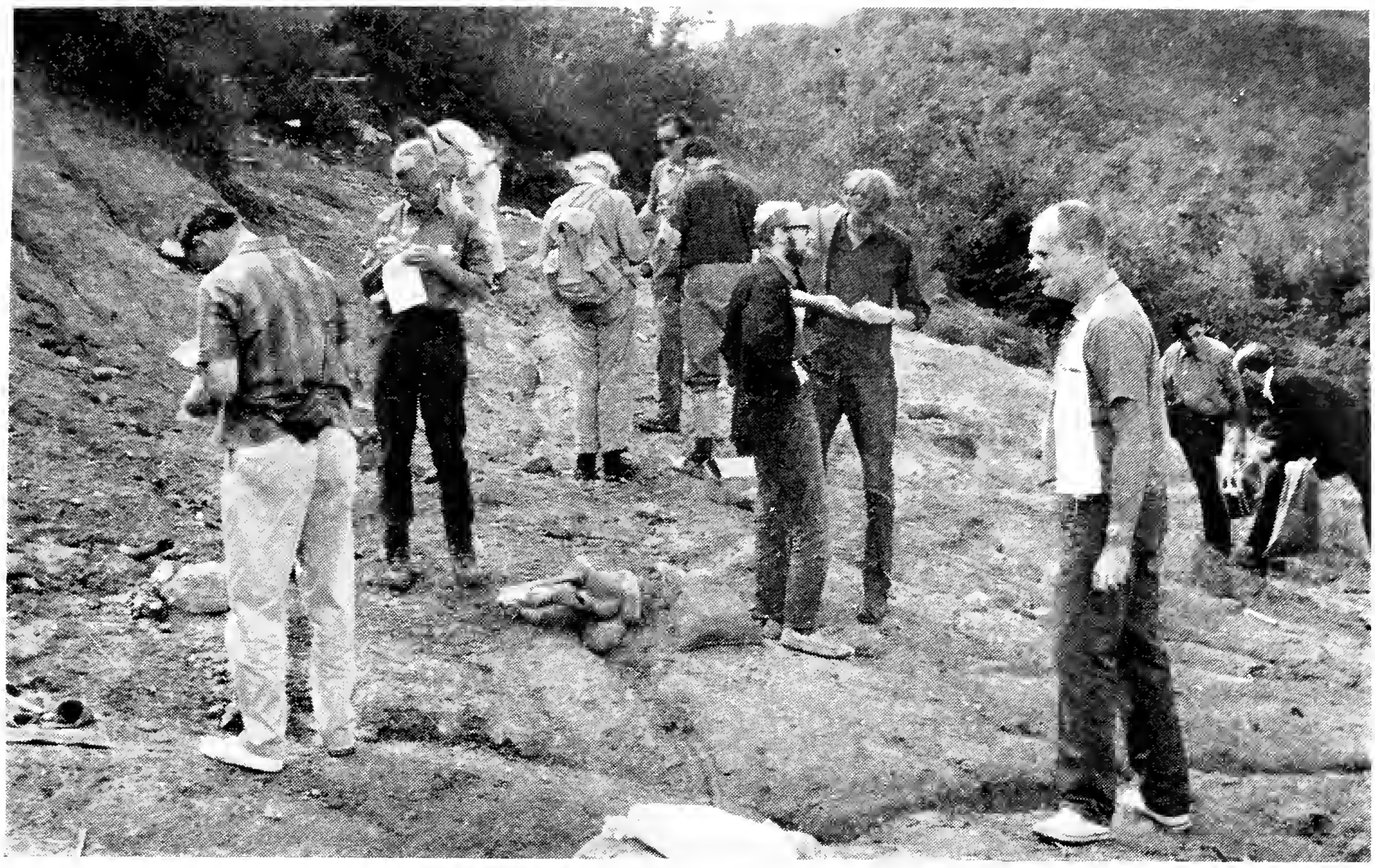


Fig. 1. — *Aug. 15, 1968.* A group of excursionists sampling the Eocene clays at Possagno (Treviso province, Venetia): Tavener-Smith, Lagaaij, Voigt, Braga, Lafrenz, Brood, Söderqvist, Rucker, Ghiurca and Schager are visible from left to right.

(Photo A. Debourle)

Fig. 2. — *Aug. 15, 1968.* A group of excursionists sampling the Eocene marls of Priabona (Vicenza province, Venetia): Lagaaij, Jebram, Labracherie, Prud'homme and Illies are visible from left to right.

(Photo A. Debourle)

AUGUST 16. This day was mostly dedicated to the « Business Meeting », divided into two sessions: « Old Business » in the morning and « New Business » in the afternoon. Both sessions were presided by the I.B.A. Chairman, Dr. A. H. CHEETHAM, while Miss P. COOK acted as Secretary and Prof. Y. V. GAUTIER as interpreter.

At 9.15 a. m. Dr. CHEETHAM opened the « Business Meeting », gave a synopsis of the agenda and then read the report of the Chairman and Secretary for the triennium 1965-1968.

The Association was founded at a meeting of 16 paleontologists and zoologists primarily associated with the fauna and stratigraphy of the North Sea area which took place at invitation of Prof. I. HESSLAND at Stockholm University in May, 1965. The University assisted in enabling the announcement of the founding of the Association and its objectives to be sent to 98 Bryozoologists. From the beginning, membership of the Association has been open to all workers on Bryozoa.

Thanks to the efforts of Dr. E. ANNOSCIA, Prof. T. PERRY, Prof. E. VOIGT and Miss E. C. POPE (of the Australian Museum), other potential members read published announcements and responded to the request for a list of names and adresses of interested workers.

By December 1965 the list of names totalled 154. It was duplicated with the help of the Smithsonian Institution and the Louisiana State University and sent to members with a request for information on research interests, location of type-specimens and comments on the feasibility of a conference in 1968.

The 1st International Conference on Bryozoa was made possible through the generosity of the AGIP Direzione Mineraria Management, who accepted to give hospitality to the Conference and placed their many facilities at the disposal of members, and of the Mayor of S. Donato Milanese, who supplied the sum to face the first organization expenses of the Conference.

At the end of the Conference the numbers of members had risen to 176, including the first Honorary Member, Dr. PIERO ASCOLI, who helped Dr. ANNOSCIA in organizing the entire Meeting and in making the Conference successful.

Dr. SCHAGER placed nominations for the Association Chairman, Prof. NILS SPJELDNAES, and Secretary, Miss PATRICIA L. COOK, on behalf of the Nominating Committee. There were no nominations from the floor.

Dr. CHEETHAM proposed that Prof. SPJELDNAES be Chairman for the next triennium of the I.B.A., seconded by Dr. G. LARWOOD. Prof. SPJELDNAES elected by acclamation. That the position of Secretary continue to be filled by Miss P. L. COOK, proposed by Dr. R. TAVENER SMITH, seconded by Dr. LARWOOD. Elected unanimously.

Dr. LARWOOD suggested that the Chairman of the Association be henceforth called the President, to avoid confusion with the Conference Chairman, particularly in correspondence. This was accepted by the Chair and by the members present.

Dr. ANNOSCIA proposed that the 1st Conference of I.B.A. should be dedicated to the memory of the late Prof. E. MARCUS. Accepted unanimously.

He gave also details of the history of the arrangements made for publishing the proceedings of the Conference. He asked that all papers for inclusion be submittd to him by September 15th and reported on the support given by the AGIP Direzione Mineraria Management and the Mayors of S. Donato Milanese and Possagno for the Conference.

Dr. CHEETHAM thanked Dr. ANNOSCIA for his work and announced that letters of thanks would be sent to those concerned on behalf of the Members of I.B.A.

Dr. RYLAND asked that a vote be taken on the proposal that a Committee be formed to study Terminology. Prof. SPJELDNAES suggested that proposals from members for the formation of such a Committee should be considered at the next Conference.

Dr. R. TAVENER SMITH asked Dr. R. BOARDMAN for a statement on the status of the Glossaries to be published in the revision of the Treatise on Invertebrate Paleontology. Dr. BOARDMAN stated that the Treatise revision is a research endeavour by individual Authors. Any glossary would therefore be one of individual opinion and primarily for terms as used in the Treatise. He further considered that we were generations away from enough understanding to produce a glossary that suggested, consciously or unconsciously, the fixing of terms. If the I.B.A. produced a Glossary it would certainly have authoritative connotations.

Dr. T. SCHOPF suggested that as the choice and acceptance of terms was an individual matter, there was no danger from an authoritative glossary. Dr. G. LARWOOD accepted the possibility of danger, but spoke of the value of a Committee considering the use of terms, particularly those common to both zoologists and paleontologists. He asked if Dr. RYLAND would be willing to form an informal investigation group which would report back to the I.B.A. Dr. RYLAND accepted the organization of such a group, and stressed his dependance upon the co-operation of members.

Dr. ANNOSCIA suggested that the Glossaries that he and Mrs. J. PRUD' HOMME had prepared be made available for any study group to consider and be made available for a study Committee. He also suggested that one member of any study group formed should be from the U.S.S.R.

After considerable further discussion, Prof. PERRY suggested that an informal Committee to discuss 50-100 disputed terms be established, which would report to the next Conference and give an estimate of the size and scope of a fuller study and the length of time it would take to produce it.

Dr. TAVENER SMITH proposed that a study group consisting of Dr. RYLAND and other members chosen by the Chairman institutes a pilot study on a small number of terms. Seconded by Dr. R. SCOLARO. Carried.

Dr. CHEETHAM gave the terms of an Advisory Council:

a) to advise the Chairman on the time and location of the next Conference and on any unforeseen problems, and

b) to provide continuity should any Officer of the Association stand down during 1968-1971.

The composition of the Advisory Council was discussed by Prof. PERRY, Dr. LARWOOD, and Dr. TAVENER SMITH. It was proposed and accepted to include Dr. CHEETHAM in the Council to ensure continuity and that the Council should be proportionally representative in the same manner as the Nominating Committee.

Dr. CHEETHAM suggested that the new Chairman submit a list of names after the closing of the Conference. This motion carried unanimously. Dr. CHEETHAM then asked that the meeting be closed. Proposed Dr. RUCKER, seconded Dr. SCOLARO. Carried.

The meeting closed at 11.23 a. m.

At 5.30 p. m., after the formal closing of the Conference, Prof. SPJELDNAES announced the names of the Advisory Council:

Dr. E. ANNOSCIA, Italy (Conference Chairman, 1968).
Prof. G. ASTROVA U.S.S.R.
Dr. R. BOARDMAN, U.S.A.
Dr. A. CHEETHAM, U.S.A. (Association Chairman, 1965-1968).
Dr. V. GHIURCA, Rumania.
Dr. R. LAGAAIJ, The Netherlands.
Dr. G. LARWOOD, U. K.
Mrs. J. PRUD'HOMME, France.
Dr. S. SAKAGAMI, Japan.
Dr. S. SCHAGER, Sweden.
Prof. E. VOIGT, W. Germany.

Additional Members could be chosen (i.e. Conference Chairman and Secretary) if and when necessary.

Prof. PERRY outlined the probable scope and feasibility of a news-letter for the Association. The University of Indiana would be able to provide secretarial facilities, but the question of postage had still to be investigated.

Prof. SPJELDNAES proposed that the feelings of the meeting on the desirability of a newsletter was indicated by a show of hands. The meeting approved a newsletter unanimously.

The Meeting closed at 5.45 p. m.

During the interval between the two sessions of the « Business Meeting », the IV Technical Session (Group 5: Biogeography and Biostratigraphy), under the chairmanship of Prof. N. SPJELDNAES, was held. Twelve papers were presented and discussed.

At 6 p. m. the Conference was officially closed after the past President Dr. CHEETHAM and the new President Dr. SPJELDNAES and the whole Assembly thanked Dr. ANNOSCIA and Dr. ASCOLI for having organized the Conference.

AUGUST 17. In the morning, about 10 Conference members went to the AGIP Direzione Mineraria Paleontological Laboratory, for informally examining some Bryozoological material at the microscope and exchanging ideas about it.

ATTENDING MEMBERS

1. - Dr. Enrico Annoscia - Specialized Paleontologist - AGIP Direzione Mineraria, Laboratorio Paleontologico, San Donato Milanese (Milan, Italy)
2. - Dr. Piero Ascoli - Specialized Paleontologist - AGIP Direzione Mineraria, Laboratorio Paleontologico, San Donato Milanese (Milan, Italy)
3. - Dr. Richard S. Boardman - Curator in Division of Invertebrate Paleontology - Smithsonian Institution, U. S. National Museum, Washington, D. C. 20560 (U.S.A.)
4. - Dr. Giampiero Braga - Assistant Professor of Paleontology - Istituto di Geologia e di Paleontologia dell'Università, Via Gotto, 20, Padova (Italy)
5. - Dr. Krister Brood - Assistant Professor - Geologiska Institutionen, Universitet i Stockholm, Kungstensgatan 45, Stockholm, Va (Sweden)
6. - Prof. John H. Bushnell - Associate Professor of Biology - Department of Biology, University of Colorado, Boulder, Colorado 80302 (U.S.A.)
7. - Dr. Alan H. Cheetham - Associate Curator in Division of Invertebrate Paleontology - Smithsonian Institution, U. S. National Museum, Washington, D. C. 20560 (U.S.A.)
8. - Miss Patricia L. Cook - Senior Experimental Officer in charge of Recent Bryozoa - British Museum (Natural History), Zoology Department, Cromwell Road, London, S.W. 7 (U.K.)
9. - Dr. André Debourle - Geologist - Société Nationale des Pétroles d'Aquitaine, 5, Rue Bonado, 64 Pau (France)
10. - Dr. Ferdinand D. Flor - Assistant - Geologisches Staatinstitut, Von-Melle-Park 11, 2000 Hamburg 13 (German Federal Republic)
11. - Prof. Yves V. Gautier - Professor of Cellular and Animal Biology - College Scientifique Universitaire d'Oran, Fac. des Sciences, Es Senia B.P. N° 16, Oran (Algeria)
12. - Dr. Virgil Ghiurca - Lecturer of Geology and Paleontology - Catedra de Geologie-Paleontologie, Universitatea « Babes Bolyai », str. Kogîlniceanu, 1, Cluj (Rumania)
13. - Dr. Reinmar Grimm - Assistant - Zoologisches Staatinstitut und Zoologisches Museum, Von-Melle-Park, 10, 2000 Hamburg 13 (German Federal Republic)
14. - Dr. Jean-Georges Harmelin - Oceanographer - Station Marine d'Endoume et Centre d'Oceanographie, Fac. des Sciences de Marseille, Rue de la Batterie-des-Lions, Marseille (7^{e}) (France)

15. - Mr. Peter J. Hayward - Student in Zoology at University of Reading - 8, Trinity Court, Trinity Road, London N. 22 (U.K.)

16. - Dr. Gero Hillmer - Assistant - Geologisches Staatinstitut, Von-Melle-Park, 11, 2000 Hamburg 13 (German Federal Republic)

17. - Mrs. Gisela Illies - Institut für Geologie der Universität - Kaiserstrasse, 12, 75 Karlsruhe (German Federal Republic)

18. - Mr. Diethardt Jebram - Cand. Rer. Nat. - Zoologisches Institut der Universität, Hegewischstrasse, 3, 23 Kiel (German Federal Republic)

19. - Dr. Olgert L. Karklins - Geologist - U. S. Geological Survey, E. 212 U. S. National Museum, Washington, D. C. 20242 (U.S.A.)

20. - Dr. Karl W. Kaufmann - Research Assistant - Marine Science Center, Lehigh University, Bethlehem, Pennsylvania 18015 (U.S.A.)

21. - Miss Monique Labracherie - Research Assistant C.N.R.S. - Laboratoire de Géologie, Fac. des Sciences de Bordeaux, 351, Cours de la Libération, 33 Talence (France)

22. - Dr. Hans R. Lafrenz - Geologist, Curator - Geologisches Staatinstitut, Von-Melle-Park, 11, 2000 Hamburg 13 (German Federal Republic)

23. - Dr. Robert Lagaaij - Paleontologist - Bataafse Internationale Petroleum Maatschappij N. V. (BIPM) Carel van Bylandtlaan, 30, 's-Gravenhage (The Netherlands)

24. - Dr. Gilbert Larwood - B. Sc., Ph. D., M. A., F. G. S. - Department of Geology, Science Laboratories, University of Durham, South Road, Durham (U.K.)

25. - Dr. Frank J. S. Maturo jr. - Associate Professor of Zoology - Department of Biological Sciences, University of Florida, Flint Hall, Gainesville, 32601 Florida (U.S.A.)

26. - Dr. Noël Mongereau - Assistant - Faculté des Sciences, Département des Sciences de la Terre, Université de Lyon, 86, Rue Pasteur, 69 Lyon (7e) (France)

27. - Mr. Osborne B. Nye - Pre-Doctoral Intern - Department of Paleobiology, Smithsonian Institution, U. S. National Museum, Washington, D. C. 20560 (U.S.A.)

28. - Prof. Thomas G. Perry - Professor of Geology - Indiana University, Department of Geology, Bloomington, Indiana 47405 (U.S.A.)

29. - Mr. Leslie J. Pitt - Amateur - I. Lancaster Road, North Harrow (Middlesex, U.K.)

30. - Miss Simone Pouyet - Research Assistant C.N.R.S. - Faculté des Sciences, Départment des Sciences de la Terre, Université de Lyon, 86, Rue Pasteur, 69 Lyon (7e) (France)

31. - Dr. Neil A. Powell - Curator of Invertebrate Zoology - National Museum of Canada, Natural History Branch, Ottawa 4 (Ontario, Canada)

32. - Mrs. Janine PRUD'HOMME - Technical Assistant of Higher Teaching Laboratoire de Géologie, Fac. des Sciences de Bordeaux, 351, Cours de la Libération, 33 TALENCE (France)

33. - Dr. Salvador REGUANT - Scientific Assistant C.S.I.C. - Instituto « Jaime Almera », Catedra de Paleontologia, Universidad de BARCELONA (Spain)

34. - Dr. James B. RUCKER - Oceanographer - Director of Laboratory Branch, U. S. Naval Oceanographic Office, WASHINGTON, D. C. 20390 (U.S.A.)

35. - Dr. John S. RYLAND - Lecturer in Zoology - Department of Zoology, University College of Swansea, Singleton Park, SWANSEA (Wales, U.K.)

36. - Dr. Sumio SAKAGAMI - Associate Professor, F.G.S.J., F.P.S.J., F.S.E.P.M. - Department of Geology, Hokkaido University of Education, Hachiman-cho, HAKODATE (Japan)

37. - Dr. Sten A. N. SCHAGER - Lecturer, Ph. D. - Geologiska Institutionen, Universitet i Stockholm, Kungstensgatan 45, STOCKHOLM Va (Sweden)

38. - Dr. Thomas J. M. SCHOPF - Assistant Professor - Department of Geological Sciences, Lehigh University BETHLEHEM, Pennsylvania 18015 (U.S.A.)

39. - Dr. Reginald J. SCOLARO - Department of Geology, University of Georgia, ATHENS, Georgia 30601 (U.S.A.)

40. - Miss Brigitte SIMMA-KRIEG - Ph. D. - Zoologisches Institut der Universität Wien, Dr. Karl Lueger Ring I, I, A 1010 WIEN (Austria)

41. - Mr. Thomas SÖDERQVIST - Geologiska Institutionen - Universitet i Stockholm, Kungstensgatan 45, STOCKHOLM Va (Sweden)

42. - Prof. Nils SPJELDNAES - Professor of Chronological Geology - Geologisk Institut, Aarhus Universitet, 8000, AARHUS (Denmark)

43. - Mr. A. R. D. STEBBING - Department of Zoology, University College of Swansea, Singleton Park, SWANSEA (Wales, U. K.)

44. - Dr. Ronald TAVERNER-SMITH - Lecturer in Geology - The Queen's University, Department of Geology, BELFAST, 7 (N. Ireland, U.K.)

45. - Dr. Antonio VIGANÒ - Assistant Professor - Istituto di Zoologia dell'Università, Via Elce di Sotto, PERUGIA (Italy)

46. - Prof. Immanuel VIGELAND - Research Associate Professor - Zoological Museum, University of Oslo, Sarsgt. 1, OSLO (Norway)

47. - Prof. Ehrhard VOIGT - Director of the Geological Institute, Prof., Dr., Dr. h. c., Geologisches Staatinstitut, Von-Melle-Park, 11, 2000, HAMBURG, 13 (German Federal Republic)

48. - Dr. Fritz WIEBACH - Ph. D., Private Naturalist - Schlossgebiet 15, 232 PLÖN (German Federal Republic)

49. - Dr. Bernard WALTER - Assistant - Faculté des Sciences, Département des Sciences de la Terre, Université de Lyon, 86, Rue Pasteur, 69 LYON (7^e) (France)

NON ATTENDING MEMBERS

50\. - Prof. Elena ANDROSOVA - Research worker - Zoologicheskii Institut Akademii Nauk S.S.S.R., LENINGRAD, B/164 (U.S.S.R.)

51\. - Prof. Galina G. ASTROVA - Chief of Laboratory - Paleontologicheskii Institut Akademii Nauk S.S.S.R. Leninskii Prospekt, 33, MOSKVA V/71 (U.S.S.R.)

52\. - Dr. William C. BANTA - University of Southern California, Department of Biology, University Park, LOS ANGELES, California 90007 (U.S.A.)

53\. - Miss Maria M. BARBOSA - Geologist Paleontologist - Museu Nacional, Quinta da Boa Vista, ZC/08, Guanabara, RIO DE JANEIRO (Brazil)

54\. - Prof. Louis DAVID - Chief of « Centre de Paléontologie Stratigraphique » - Université de Lyon, Fac. des Sciences, Département des Sciences de la Terre, 86, Rue Pasteur, 69, LYON 7^e (France)

55\. - Miss N. N. DUNAEVA - Geologicheskii Institut Ukrainskoi Akademii Nauk, Repina, 2, KIEV (U.S.S.R.)

56\. - Miss Annie FEY - Collège de France, Laboratoire de Biologie Marine, CONCARNEAU (Finistère) (France)

57\. - Dr. Jean Loup D'HONDT - Muséum National d'Histoire Naturelle, Laboratoire de Biologie des Invertébrés Marins, 57, Rue Cuvier, PARIS, 5^e (France)

58\. - Dr. HONNAPPA - M. Sc., F.P.T.C. (Vienna), Lecturer in Geology - Government Arts and Sciences College, 43, 1st Main Road, Maruthi Extension, Srirampuram, BANGALORE, 21 (India)

59\. - Prof. Tino LIPPARINI - Ph. D., F.G.S., Chief Geologist, Professor of Paleontology, Servizio Geologico d'Italia, Largo S. Susanna 13, ROMA (Italy) (until Nov. 1968) or Istituto di Paleontologia dell'Università, Via delle Cerchia, 5, SIENA (Italy)

60\. - Miss Geneviève LUTAUD - Research Assistant C.N.R.S. - Université de Paris, Fac. des Sciences, Laboratoire d'Anatomie et d'Histologie Comparées, 7, Quai St., Bernard, PARIS, 5^e (France)

61\. - Miss Alice MEDIONI - Assistant C.N.E.X.O. - Université de Paris, Biologie Marine, Laboratoire Arago, 66 BANYULS-SUR-MER (France)

62\. - Prof. Iraida P. MOROZOVA - Senior Scientist Worker - Paleontologicheskii Institut Akademii Nauk S.S.S.R., Leninskii Prospekt, 33, MOSKVA V/71 (U.S.S.R.)

63\. - Prof. Hugo I. MOYANO G. - Universidad de Concepcion - Instituto Central de Biologia, Casilla 1367, CONCEPCION (Chile)

64\. - Prof. Jean ROGER - Université de Paris, Fac. des Sciences, Laboratoire de Paléontologie, Bâtiment 504, 91, ORSAY (France)

65\. - Prof. June R. P. ROSS - Associate Professor in Biology - Western Washington State College, Dept. of Biology, BELLINGHAM, Washington 98225 (U.S.A.)

66\. - Mrs. Dorothy F. SOULE - Research Associate - Allan Hancock Foundation, University of Southern, California, LOS ANGELES, California 90007 (U.S.A.)

67\. - Prof. John D. SOULE - Professor of Histology - Allan Hancock Foundation, University of Southern California, LOS ANGELES, California 90007 (U.S.A.)

68\. - Dr. Dante TEDESCHI - Paleontologist - Pensione Bella, 17019 VARAZZE (Genova, Italy)

69\. - Miss Mady THOELEN - Universiteit te Leuven, Geologisch Instituut, Laboratorium voor Stratigraphische Paleontologie en Mikropaleontologie, St. Michielstraat, 6, LEUVEN (Belgium)

70\. - Dr. Tamara D. TROIZKAYA - Geologist - Moskva Gosudarstvennii Universitet, Geologicheskii Facultet, MOSKVA V.234 (U.S.S.R.)

71\. - Miss Lena A. VISKOVA - Junior Scientist Worker - Paleontologicheskii Institut Akademii Nauk S.S.S.R., Leninskii Prospekt, 33, MOSKVA, V/71 (U.S.S.R.)

72\. - Miss Ariadna M. YAROSHINSKAYA - Obi-Irtishkaya Ekspediziya, Per. Nakhanovicha, 8, G. TOMSK. 50 (U.S.S.R.)

LIST OF ATTENDING AND NON ATTENDING MEMBERS ACCORDING TO THE COUNTRIES

Algeria - Y. V. Gautier

Austria - B. Simma-Krieg

Belgium - M. Thoelen

Brazil - M. M. Barbosa

Canada - N. A. Powell

Chile - H. I. Moyano G.

Denmark - N. Spjeldnaes

France - L. David, A. Debourle, A. Fey, J. G. Harmelin, J. L. d'Hondt, M. Labracherie, G. Lutaud, A. Medioni, N. Mongereau, S. Pouyet, J. Prud'homme, J. Roger, B. Walter

Germany (West) - F. Flor, R. Grimm, G. Hillmer, G. Illies, D. Jebram, H. R. Lafrenz, E. Voigt, F. Wiebach

India - Honnappa

Italy - E. Annoscia, P. Ascoli, G. P. Braga, T. Lipparini, D. Tedeschi, A. Viganò

Japan - S. Sakagami

Netherlands - R. Lagaaij

Norway - I. Vigeland

Rumania - V. Ghiurca

Spain - S. Reguant

Sweden - K. Brood, S. A. N. Schager, T. Söderqvist

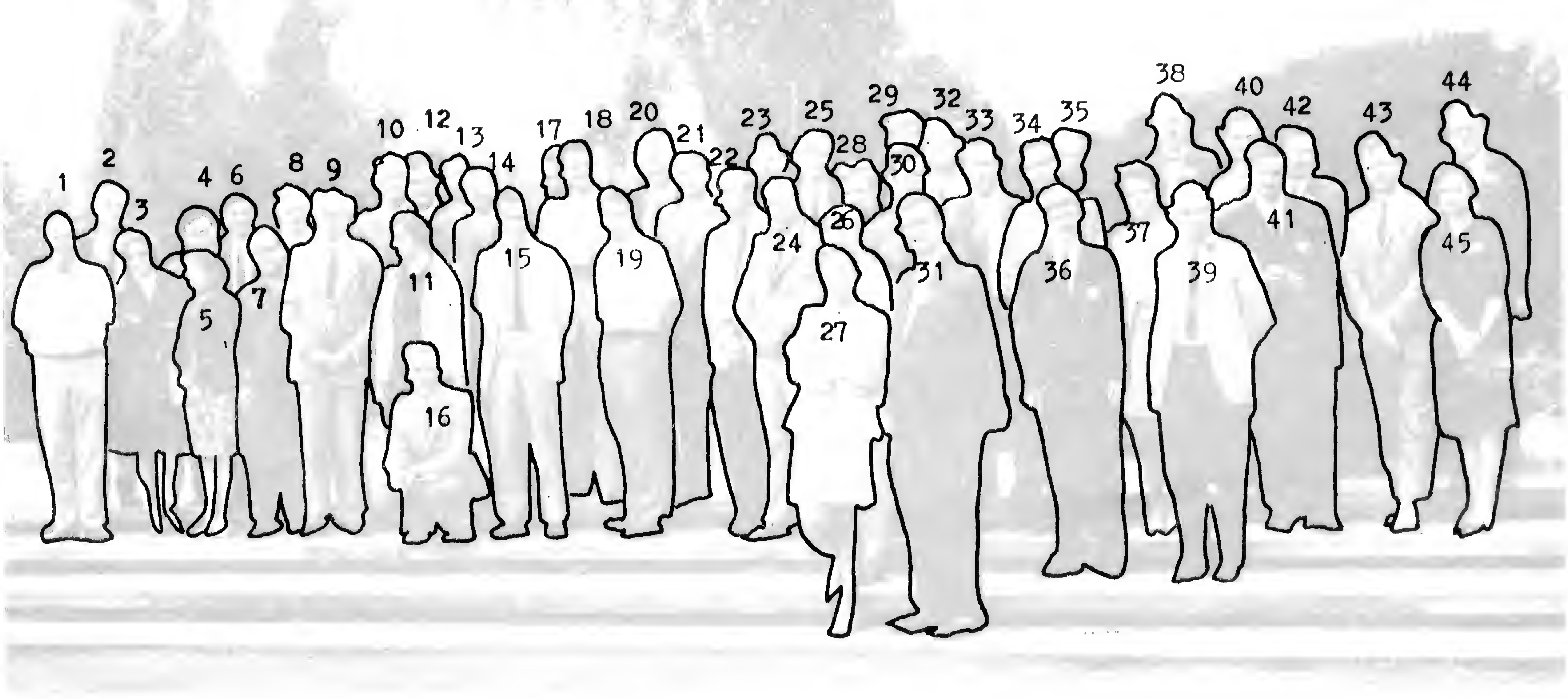
United Kingdom - P. L. Cook, P. J. Hayward, G. Larwood, L. J. Pitt, J. S. Ryland, A.R.D. Stebbing, R. Tavener Smith

U.S.A. - W. C. Banta, R. S. Boardman, J. H. Bushnell, A. H. Cheetham, O. L. Karklins, K. W. Kaufmann, F. J. S. Maturo jr, O. B. Nye, T. G. Perry, J. R. P. Ross, J. Rucker, T. J. M. Schopf, R. J. Scolaro, D. E. Soule, J. D. Soule

U.S.S.R. - E. Androsova, G. G. Astrova, N. N. Dunaeva, I. Morozova, T. D. Troizkaya, L. A. Viskova, A. M. Yaroshinskaya

Pl. I. — The Members attending the Conference grouped near the « E. Mattei » Monument in San Donato Milanese.
(Photogr. by « Studio 17, Milan »).

1, Rucker - 2, Bushnell - 3, Labracherie - **4, Sakagami - 5,** Prud'homme - 6, Ghiurca - 7, Reguant - 8, Debourle - 9, Voigt - 10, Lagaaij - 11, Illies - 12, Grimm - **13, Braga - 14,** Annoscia - 15, Larwood - 16, Viganò - 17, Lafrenz - 18, Gautier - 19, Nye - 20, Boardman - 21, Scolaro - **22, Tavener-Smith** - 23, Jebram - 24, Hillmer - **25, Karklins - 26,** Wiebach - 27, Cook - 28, Hayward - 29, Söderqvist - **30, Ryland - 31,** Cheetham - 32, Maturo - 33, Schopf - **34, Ascoli - 35,** Brood - 36, Kaufmann - 37, Pouyet - 38, Schager - 39, Perry - 40, Mongereau - 41, Harmelin - 42, Walter - 43, Powell - 44, Pitt - 45, Simma-Krieg.



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U.S.A. - W. C. Banta, R. S. Boardman, J. H. Bushnell, A. H. Cheetham, O. L. Karklins, K. W. Kaufmann, F. J. S. Maturo jr, O. B. Nye, T. G. Perry, J. R. P. Ross, J. Rucker, T. J. M. Schopf, R. J. Scolaro, D. E. Soule, J. D. Soule

U.S.S.R. - E. Androsova, G. G. Astrova, N. N. Dunaeva, I. Morozova, T. D. Troizkaya, L. A. Viskova, A. M. Yaroshinskaya

Pl. I. — The Members attending the Conference grouped near the « E. Mattei » Monument in San Donato Milanese.
(**Photogr.** by « **Studio 17, Milan** »).

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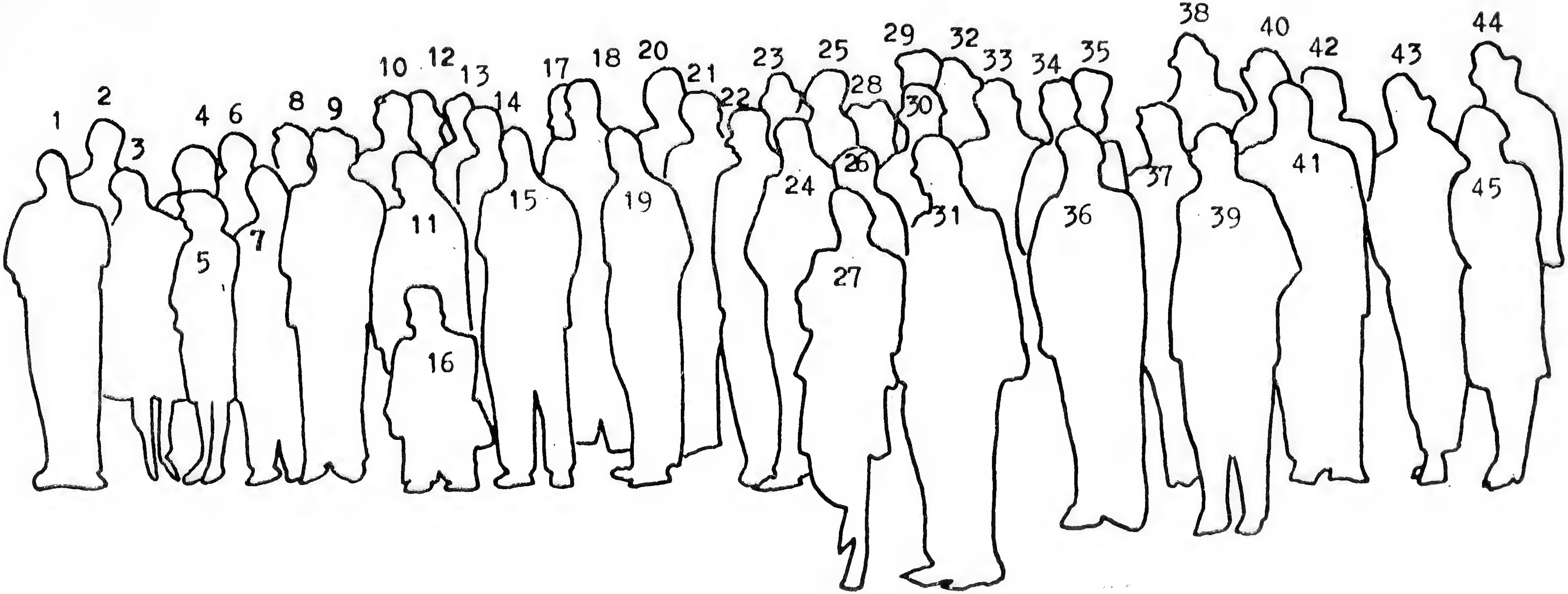

Atti Soc. It. Sc. Nat. e Museo Civ. St. Nat. Milano - 108: 25 27, 31-XII-1968

1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
1. Group 1: The *Bryozoa* in Oil Research.

ENRICO ANNOSCIA (*)

PALEONTOLOGICAL AND STRATIGRAPHICAL RESEARCH CARRIED OUT BY AGIP DIREZIONE MINERARIA PALEONTOLOGICAL LABORATORY

Riassunto. — L'A. espone brevemente l'attività svolta nel campo della Paleontologia e della Stratigrafia dal Laboratorio Paleontologico dell'AGIP Direzione Mineraria negli ultimi quindici anni.

Summary. — A. briefly gives some news about research carried out by AGIP Direzione Mineraria Paleontological Laboratory during the last fifteen years in the field of Paleontology and Stratigraphy.

This report, as announced in the first program sent to you, should have been presented to you by Dr. Tedeschi, who was in charge of the Paleontological Section up to last May. Since Dr. Tedeschi recently left AGIP, I was appointed to substitute him in this task.

I will briefly illustrate the activity of the Paleontological Section during the last 15 years, since the organization of the Section up to 1952 was exhaustively described by Dr. Jaboli in 1952, during the VII National Oil and Gas Congress held in Taormina.

The Paleontological Section comprises 18 paleontologists, 5 of which working at our Laboratories overseas (Persia, Egypt, Tunisia and Madagascar).

The activity of the Section has mostly been devoted to the Stratigraphical assistance to wells that AGIP and its associate

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(*) AGIP Direzione Mineraria, Servizio Geologico, Laboratorio Paleontologico San Donato Milanese, Milan, Italy.

companies were drilling in Italy and — mostly in the last years — abroad, with the help of Micropaleontology.

In this field the AGIP Paleontological Laboratory, already the most advanced of all in Italy as to the practical utilization of Foraminifera in Stratigraphy, published in 1957 an Atlas of Italian Foraminifera which soon got a world-wide reputation. This atlas was followed, two years later, by the atlas of Italian Microfacies, a copy of which is given by AGIP to all Conference members. This main activity was afterwards followed by a research activity devoted to groups of fossils different from Foraminifera which were commonly used in Italy in the paleontological and stratigraphical routine work.

Thus, the study of Ostracoda, Fusulinids and Paleozoic Megafossils, Mollusca, Brachiopoda, Coelenterata, Graptolithina, Bryozoa, and finally Algae, Spores, Pollens, Organic Microfossils, Nannoplankton and Problematica was began by five paleontologists.

To briefly summarize the work of such a team within 15 years of extensive work, it is not easy.

All these studies, even occasionally being peculiar to pure research, never forgot the main point of our Company which is the Oil research. Consequently, the research was devoted to the aim of using also groups of fossils different from traditional Foraminifera in the practical stratigraphical routine work. Therefore, with the help of Mollusca, Brachiopoda, Graptolithina, Bryozoa and organic Microfossils we were able to resolve some important problems of chronostratigraphy in North Africa.

Bryozoa were widely applied in the study of African Miocene (Libya, Egypt, Nigeria) and in resolving some stratigraphical problems of the Cretaceous from Persian Gulf. Furthermore, most of Central-Southern Italy shows a typical lithofacies of Bryozoa limestones belonging to Lower Miocene.

Ostracoda were extensively used in dating and correlating in Italy, North Africa and Iran, the Mesozoic, Tertiary and Quaternary deposits, particularly those scarce or lacking indicative Foraminifera.

Mollusca and Algae were many times used for the Mesozoic, Tertiary and Quaternary Stratigraphy in Italy, North Africa and Middle-East.

The RICHTER-BERNBURG method has been recently applied to a regional study of evaporitic cycles in the North Sea Zechstein.

The Section got a few months ago an electron microscope, which enabled us to improve the techniques on research of organic Microfossils and calcareous Nannofossils according to the up-to-date methods of paleontological investigation.

A study on the application of mathematical models for resolving some paleontological problems is now under way.

The amount of work carried out by the Paleontological Laboratory may be expressed by the following data:

from over 2150 wells drilled from 1953 up to day in Italy and from around 280 wells drilled abroad within the same period of time, 120.000 thin sections, 12.000 bottom and side well cores, over half a million cuttings, 800 slides and nearly 50 thin sections of Bryozoa from Paleozoic to Recent, were studied and kept in collection, beside ten thousand specimens of Foraminifera, Mollusca, Ostracoda, Spores, Pollens, Organic Microfossils and other fossil groups.

The Paleontological Section is equipped with a library of over 5.000 volumes and 10.000 reprints, among which some rare books by Soldani, Costa, Janus Plancus, and other classic Authors.

Nearly 80 scientific contributions were published withín the last 15 years.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
2. Group 1: The *Bryozoa* in Oil Research.

RICHARD S. BOARDMAN (*)

POTENTIAL USE OF PALEOZOIC *BRYOZOA* IN SUBSURFACE EXPLORATION

Riassunto. — Studi preliminari sugli strati produttivi ad olio del Simpson Group dell'Oklahoma (Ordoviciano medio) indicano che i Briozoi paleozoici possono essere facilmente identificati fino alla specie nei detriti di perforazione (cuttings) e che essi sono sufficientemente abbondanti da permettere un controllo stratigrafico dettagliato all' interno della formazione.

L'A. ritiene che risultati altrettanto buoni potrebbero essere ottenuti per tutto il Paleozoico dell'America settentrionale.

Summary. — Preliminary studies from the oil bearing Simpson Group (Middle Ordovician) of Oklahoma, indicate that Paleozoic Bryozoa can be identified readily to species from subsurface cuttings and that they are abundant enough to provide detailed stratigraphic control within the Group.

It is anticipated that comparable results would be obtainable generally throughout the Paleozoic of North America.

Use of Paleozoic Bryozoa in subsurface cores or cuttings is feasible because of their abundance generally in the stratigraphic column and the minute size of zooecia in colonies. To my knowledge, however, Bryozoa have not been used by industry in subsurface work for anything more than large scale ecologic interpretations or as horizon markers in a basin where a particular bed of Bryozoa happens to have distinctive characteristics. Apparently, advantage has not been taken of more detailed studies that would employ the classification or evolutionary trends of the phylum. Certainly this lack of detailed use is partly

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due to the scarcity of specialists and the resulting lack of modern faunal studies that would support detailed biostratigraphic application.

What is needed from bryozoologists before we can present a convincing inducement to industry is a substantial number of bryozoan papers that claim to solve stratigraphic problems. Preferably they would be based on careful collecting of thin, superimposed stratigraphic units and a population based taxonomy that attempted to deal with morphologic variation as a continuum through geologic time. Too many of our existing collections can not include the evolutionary intermediates that permit the well documented inferences of evolutionary trends and patterns that might be recognized and followed to advantage in biostratigraphic application.

One of the more easily solved problems in subsurface use of Paleozoic Bryozoa is that of preparation of specimens for study. Preparation from cores, of course, is comparable to techniques used in surface studies. Preparation from cuttings adds the problem of working with small fragments. In most Paleozoic Bryozoa, study from thin sections or peels is required and the present classification is based largely on internal morphology of individuals rather than growth habits or external appearance of the colony. To prepare sections of small fragments, the specimens can be embedded in a plug of polyester resin. The plug allows handling of the fragment so that oriented faces can be obtained by either grinding or cutting without breakage. Thin-bladed saws are available that use up a negligible thickness of the specimen in making a cut. A well oriented cut generally allows two oriented faces to be made into thin sections from even the smaller fragments. Acetate replicas or dry peels can be more quickly made and are quite adequate for identification at all taxonomic levels if the fauna is well known from thin section studies.

In Paleozoic Bryozoa, a fragment of several zooecia is generally all that is required to identify a specimen to genus. Most bifoliate and rhomboporoid cryptostome colonies have branches of such small widths that nearly all fragments recovered from cuttings can be considered potentially identifiable at the species level. In the larger stony Bryozoa such as the trepostomes and fistuliporoids, identification of a ramose or frondose form to the species level generally requires a longitudinal section that spans the width of the endozone and at least one side of the exozone.

In a short study of subsurface cuttings from the oil bearing Simpson group of lower Middle Ordovician age in Southern Oklahoma, 339 fragments of Bryozoa of all kinds were recovered from the 300 foot interval of the top formation. Thirty percent of these were too small or too poorly preserved to be identifiable. Of the remaining 70%, all were identified to genus, 1/3 of these were cryptostomes and potentially identifiable to species. The remaining 2/3 were stony Bryozoa and half of these were identifiable to species. Thus, 2/3 of Bryozoa identifiable at the generic level were identifiable at the species level and nearly half of all fragments recovered were considered identifiable at the species level.

Atti Soc. It. Sc. Nat. e Museo Civ. St. Nat. Milano - 108 : 31-36, 31-XII-1968

1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
3. Group 1: The *Bryozoa* in Oil Research.

YVES V. GAUTIER (*)

BRYOZOA AS MICROFOSSILS WHICH MAY BE USEFUL IN OIL RESEARCH

Riassunto. — L'A., richiamandosi ad uno scritto profetico di S. F. HARMER (1930) circa l'utilizzazione dei Briozoi nella ricerca geologica applicata, espone come tale utilizzazione potrebbe eventualmente essere inquadrata nella ricerca petrolifera.

L'A. si propone semplicemente di provocare una presa di coscienza collettiva dell'IBA dinanzi a questa possibilità di applicazione.

Summary. — The Author, referring to a prohetical paper by S. F. HARMER (1930) about the use of Bryozoa in economic geological research, explains how this use might be introduced in oil research.

The Author, simply proposes to originate a collective consciousness by IBA with regard to this possibility.

Résumé. — L'Auteur rappelle un écrit prophétique de S. F. HARMER (1930) concernant l'utilisation des Bryozoaires dans la recherche géologique appliquée et expose comment on pourrait envisager éventuellement cette utilisation dans le cadre de la recherche pétrolière. Il essaie simplement de provoquer une prise de conscience collective de l'IBA devant cette éventualité.

Dear colleagues and friends, ladies and gentlemen, I do not intend to tell you a long story since: firstly, we are about 50 who have to speak according to the newsletter of our Conference Chairman, Dott. ENRICO ANNOSCIA; secondly, if my paper is too long, it will tire you and a conference must not be tiring.

I intend only to try to awake a collective conscience among us and that is why the shortest is the best.

(*) Faculté des Sciences d'Oran - Oran, Algeria.

Thanks to our Association Chairman ALAN CHEETHAM I knew a title for my paper: « Aspects of paleoecology of Bryozoa » and thanks to my dear colleague and friend ROBERT LAGAAIJ I got two old texts of d'ORBIGNY & WATERS giving data on ecology of Bryozoa.

It seemed to me that there was no need to add more and more on this subject. Instead of that, I made up my mind to draw your attention to the fact that it would be good to try to see where we are going on and why, to have a synthetic view of our actual topics and try to elaborate a common or a « concerted action » instead of working each of us alone in his lab; that is to say that Bryozoa research may become tomorrow an applied research, although I know there is no difference between basic and applied research. There was, in this respect, a prophecy of the late Sir SYDNEY HARMER in 1930 already: « it is evident that many of the geological formations are well characterized by their Polyzoa. It is probable that with increasing knowledge, this phylum will become more important than at present as a means of correlating the age of strata, and that the assistance of students of the group will be more sought in connection with economic problems in Geology ». I raise the question why this prophecy did not until to day turn into realisation.

In November 1953, I attended a Congress in Banyuls sur mer and was told there by Prof. BOURCART, a marine geologist of the Sorbonne now retired, that a scientist of Bordeaux had worked on fossil Bryozoa for the applied research department of the Standard Oil Company; there is no doubt that what was done in the past by a man alone can be done to day by our Association; there are so many borings all over the world that everybody would have a lot to do, probably too much.

I was brought to this conclusion because every man, when he knows you work on Bryozoa, asks « what is their use? » The same question is raised by the committee which give grants or funds for research and thus you dont get enough money for

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Fig. 1. — This figure shows the way in which fragments of Bryozoa may be assembled in special CHAPMAN slides. Slides of this type are frequently used in routine-work on Foraminifera. (Fig. taken from LAGAAIJ & GAUTIER 1965).

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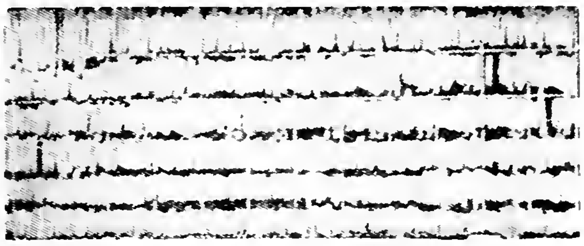

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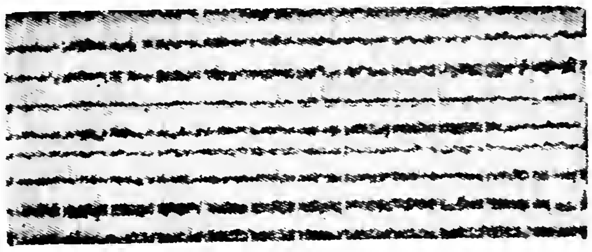

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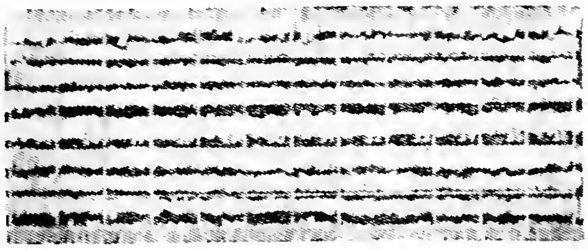

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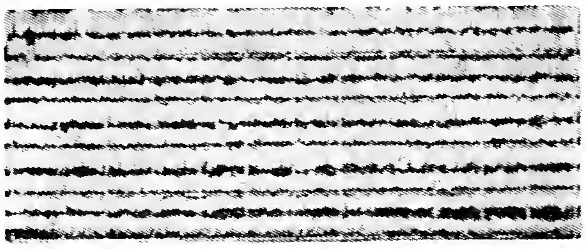

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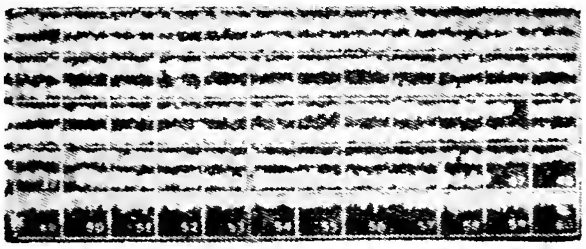

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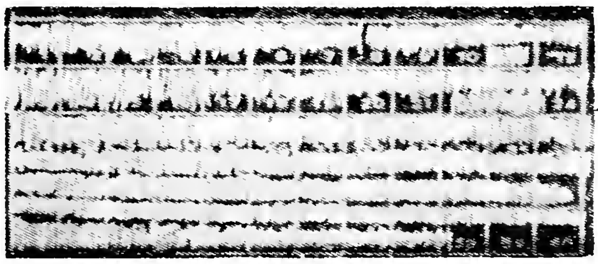

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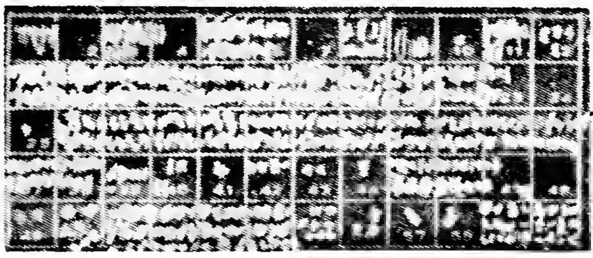

VII

your work. Instead of that, the atomic research for example is drawing much money and in this field you can work. We know of course that in our « brave new world » the atom is much more important that the « lovely group » (as said the late MARY D. ROGICK) but actually one is looking at us as to mild dreamers and that is not good for a scientist because if he is neither dangerous nor useful one does not take note of him.

Therefore I suggest that one of our main topics would be to draw the attention of the brain trusts of geological research and to tell them that a team does exist which is expert in Bryozoa, knowing that these invertebrates are abundant in many strata.

In this respect the best approach would be made by our colleagues who work already in the research departments of Oil societies, E. ANNOSCIA & R. LAGAAIJ, resp. of the AGIP and the Royal Dutch Shell. They may have the opportunity to show in the most appropriate place that Bryozoa will be, if we are helped, studied in the future as microfossils useful in oil research.

First of all, geologists have to record all the strata where Bryozoa are available and let it know to the I.B.A. Then, every specialist of a considered epoch would have to study the lot of Bryozoa with the usual check up, by a colleague specialised in the same epoch. By these means, age of strata may be confirmed when necessary. As one may see in the figure 2, Bryozoa may be as abundant as benthonic Foraminifera, Mollusca and Ostracoda and help then in the determination of the age of a strata and also in the knowledge of the ecological conditions in which the strata was deposited; as one knows, Bryozoa are very sensitive to even light changes of these conditions.

The fact that this meeting is held to day proves quite well that we are not only the « gallery of rogues » as said with humour ANNA B. HASTINGS of the British Museum but also that we may constitute an expert team in Bryozoa (we may be both of course).

Since the HARMER prophecy and in spite of the paper we wrote with R. LAGAAIJ in 1965 on the « Bryozoa assemblages of the Rhône delta area » (see figs. 1 & 2) it does not seem that

Bryozoa have been admitted really as useful microfossils; yet recent treatises of Paleontology are dealing with them (see BUGE & DUNCAN in the bibliography) but only as to a basic research group. That is why we have in the IBA to show that they may be used as well as Ostracoda and even, sometimes, as Foraminifera; what we have to do is to write a treatise analogous of ELLIS & MESSINA's treatise on Foraminifera: there is no doubt that this is our duty and there is good hope that it will be done in the next ten years. Thank you very much.

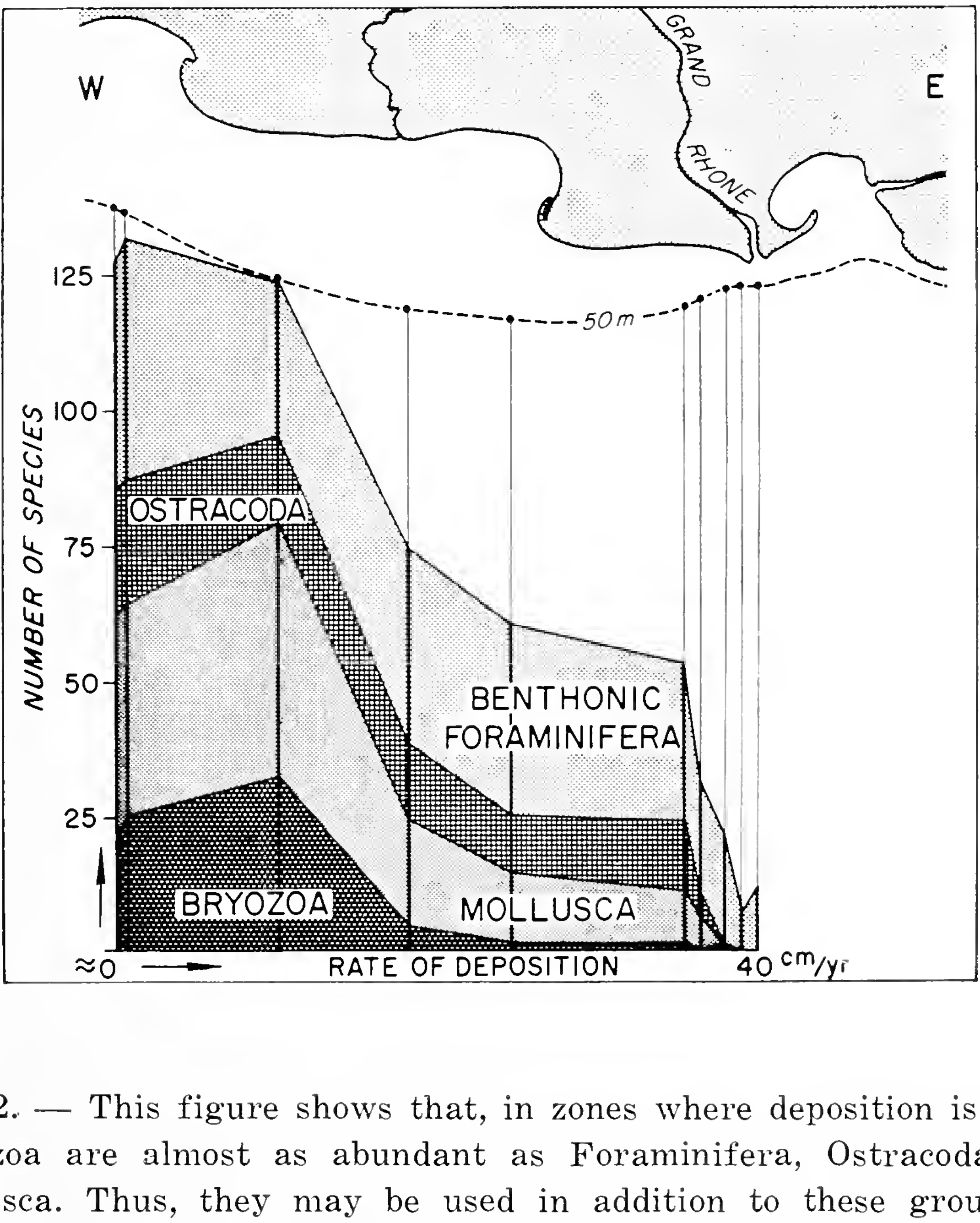

Fig. 2. — This figure shows that, in zones where deposition is slow, Bryozoa are almost as abundant as Foraminifera, Ostracoda and Mollusca. Thus, they may be used in addition to these groups to determine the age of undated strata or to correlate several strata. (Fig. taken from LAGAAIJ & GAUTIER 1965).

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
4. Group 2: Anatomy, Morphology and Skeletal Structure.

GERO HILLMER (*)

ARTIFICIAL MOULDS FOR STUDYING THE INTERNAL STRUCTURE OF PALEONTOLOGICAL OBJECTS

Riassunto. — La complicata struttura interna dei *Cheilostomata* e dei *Cyclostomata* e di altri oggetti paleontologici può essere studiata per mezzo della preparazione di impronte artificiali con poliesteri. Questo ancor poco conosciuto metodo è basato su un' impregnazione ed una polimerizzazione dei sedimenti a grana fine negli scheletri calcarei dei fossili. Gli scheletri vengono dissolti per mezzo dell'acido cloridrico e quindi l' interno dell'organismo rimane in ogni dettaglio come un' impronta tridimensionale artificiale con Poliestere.

Per mezzo di una buona preparazione è possibile fare un'esatta valutazione dei caratteri interni ed esterni ed avere una migliore conoscenza delle funzioni degli elementi scheletrici.

Summary. — The complicate interior of cheilostome and cyclostome Bryozoa and other paleontological objects can be studied by the preparation of artificial Polyester-moulds. This only little known study method is based on an impregnation and polymerization of the fine-grained sediments in calcareous skeletons of fossils. Then the skeleton will be dissolved by hydrochloric acid and thus the interior of the organism remains in every detail as a three-dimensional artificial Polyester-mould.

By a successfull preparation it is possible to make an exact valuation of the internal and external characters and a better knowledge about former functions can be obtained.

Résumé. — On peut étudier la structure interne, souvent compliquée, des Cheilostomes et des Cyclostomes en coulant des moules internes artificielles de polyester. Cette méthode peu connue consiste en une imprégnation et polymerisation des squelettes fossiles comblés de sédiments meubles suivies

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par un dissolution du squelette calcaire à l'acide chlorhydrique. On obtient de cette facon une image en relief des organes du fossile ainsi que d'autres éléments du squelette cachés à l'observation directe, comme par exemple les pseudo-pores, les septules etc. On peut y reconnaître aussi facilement le parcours des tunnels ramifiés des organismes perforants dans le squelette calcaire.

Le nombre des caractères diagnostiques peut être agrandi chez plusieurs fossiles à l'aide d'une étude des moules internes artificielles; la fonction de plusieurs éléments du squelette peut etre identifieé.

For a long time the various methods of preparation have been used to comprehend the complicate internal structure of bryozoa, foraminifers, ostracodes, and other fossils. Therefore in some institutes various modifications of study methods were developed, which I shall not take in consideration here.

To study colonies of bryozoa successfully it is necessary in most cases to have a *three-dimensional aspect of the interior of the colony* and their zooecia. This is a prime necessity in order to get an exact valuation of the internal and external characters. In literature many wrong determinations or oversimplified and erroneous interpretations show us that only those study methods can be used which are quantitatively and qualitatively exact and thus are the supposition for a satisfactory taxonomy. The hitherto used and known preparation methods to study the anatomy of bryozoa by means of oriented thin sections or serial sections resp. cellulose acetate technique are mostly time-consuming. But in many cases those methods are necessary especially for the study of Paleozoic stony and recrystallized Bryozoa — Trepostomata, Cryptostomata, etc.

If we find a more delicate material like most of the Mesozoic and Cenozoic *Bryozoa* of *Cyclostomata* and *Cheilostomata* then in most cases fossilization is more favourable for the preparation of artificial moulds. Here, however, all other study methods directed to the internal structure of these organisms have some of the following disadvantages:

a) The paleontological object will be destroyed by the grinding process. Later on nobody can examine the drawings of sections, because only the last polished section will remain as an evidence. To obtain this evidence we have to make dry peals or replicas, fotos and drawings of every oriented polished sections. And in spite of this effort we only get an incomplete three-dimensional picture.

b) Another disadvantage is, that the modification of study method for serial sections of brachiopods by SIEHL (1962) will take great financial and time-consuming pains. A grinding machine especially constructed for this purpose is necessary and much time will be required in the preparation of polished sections, replicas, fotos, and drawings.

In order to reduce time and material for study the interior of little paleontological objects, we only have to remember an about 100 years old method by BEISSEL (1860, 1865), who made artificial moulds of foraminifers and bryozoa. Later, VOIGT (1949, S. 9) points out the existence of natural silicified moulds from bryozoa in flint-boulders found in northern Germany. Stimulated by these facts WIESEMANN (1960) developed a more modern study method for the production of Polyester-moulds and this could be applied with great success. Thus he obtained many data for the description of internal structures of the genus *Beisselina* CANU 1913.

We will consider this technique further because only little is known in literature and beside that our own experience made an improvement of this technique possible. This study method can be applied to many other paleontological objects.

Preparation of the specimens.

The most important supposition for the preparation of satisfactory artificial moulds is, that skeletons of fossils are filled with fine-grained and colloidal sediments such as clay, marl, chalk etc. If we find carbonate skeletons and sediments in diagenetic lithification with cementation or recrystallization only the well-known preparation and handling of thin sections is practicable. To obtain artificial moulds we are using the following procedure:

1) The fossils may be obtained by carefully washing the sediments. We can clean the separated specimens very simply and

quickly by an Ultra-sonic apparatus. If we don't possess such an apparatus we can boil fossils for a short time in H_2O_2 solution.

2) Much experience with the various mixtures of Polyester have shown that the greatest problem is the difficulty to reach a complete impregnation and a slowly polymerization of the objects. This procedure is only possible by using a very watery Polyester-mixture and an exact dose. The following mixture conform to all requirements:

900 ml Vestopal H (Chemische Werke Hüls AG., Marl, Germany)
750 ml Styrol
4,0 ml Co-accelerator EWM, 1% metal.

For polymerization add to 100 ml of this diaphanous and very watery mixture 45 drops of Methyl-ethyl-keton-peroxyd (40% solution). Then the polymerization process will start. Before doing so the paleontological objects are placed in the oriented position wanted and covered with the mixture.

The following impregnation takes place in the vacuum of an exsiccator until the mixture is bubble-free. The impregnation time depends mainly on the sediments in the interior of the fossil objects. If it is a silty clay matrix the impregnation in vacuum will take nearly 4 hours. Immediately after this procedure the objects will be taken out and the polymerization will be finished in about 1 or 2 days. An acceleration of polymerization with too much catalyst and heat must be avoided.

3) After this, cut the hardened Polyester bloc with a diamond-mounted saw in such way, that the fossil lies in the middle of a few mm large bloc. Now you can cut the object as it is necessary for your study and put the sectional plane of the fossil in hydrochloric acid solution. The carbonate skeleton itself, very seldom impregnated by the Polyester mixture, can be dissolved partly or totally as you wish. Mostly it is very useful to start the dissolution of the calcareous specimens by dilute hydrochloric acid and to watch the procedure under the microscope. If important parts of the interior with certain peculiar structural features become visible one can stop the chemical action of the acid at once.

4) The interior of the organism remains in every detail as an artificial Polyester mould when the whole calcareous skeleton has been dissolved. Now the student has an excellent three-dimensional view of the interior for the most minute structural details become visible and can easily be observed. In addition to that there is a great advantage in always having an impression of the outside of an organism, which can be used as a control.

5) Beside this parts of the interior of their flexible unit can be separated by a fine needle under microscope. For example a bryozoa can be separated in all of their auto- and kenozooecia.

The above shown technique has been developed and methodically improved in dealing with bryozoa. But certainly it can be applied to foraminifers, ostracodes, brachiopods, ramifying tunnel systems of boring organism or other bore cavities in shells, etc.

In this manner WIESEMANN (1960) was able to observe on moulds of the genus *Beisselina* Canu 1913 form, size and position of the zooecia and their peristomia, ooecia, hetero- and kenozooecia, various pore channels etc. Extensive studies of our own specially on Lower Cretaceous Cyclostomata have enlarged the knowledge of the structure of the colony, too. Thus details e.g. can be made about the interzooecial pores, pseudopores, gonozooecia and the budding of the Cyclostomata.

It is possible to make an exact valuation of the internal and external character and a better knowledge about former functions can be obtained. Therefore the *preparation and study of artificial moulds is often necessary for a more natural systematic.*

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PLATE II.

Multizonopora arborea (Koch e Dunker, 1837).

Fig. 1. — Well preserved zoarium lies in a Polyester bloc. A tangential polished section was only made and in this peripheral region calcareous skeleton has been dissolved by hydrochloric acid. Auto-and kenozooecia connected by interzooecial pores can be seen as artificial moulds, × 17; Hauterivian of Schandelah, NW-Germany. Coll. H. BRANDES, Geol. Staatsinst. Hamburg.

Fig. 2. — Peripheral region of another zoarium shows auto- and kenozoecia with interzooecial pores. Obliquely frontal view; × 25; ibid. Coll. H. BRANDES, Geol. Staatsinst. Hamburg.

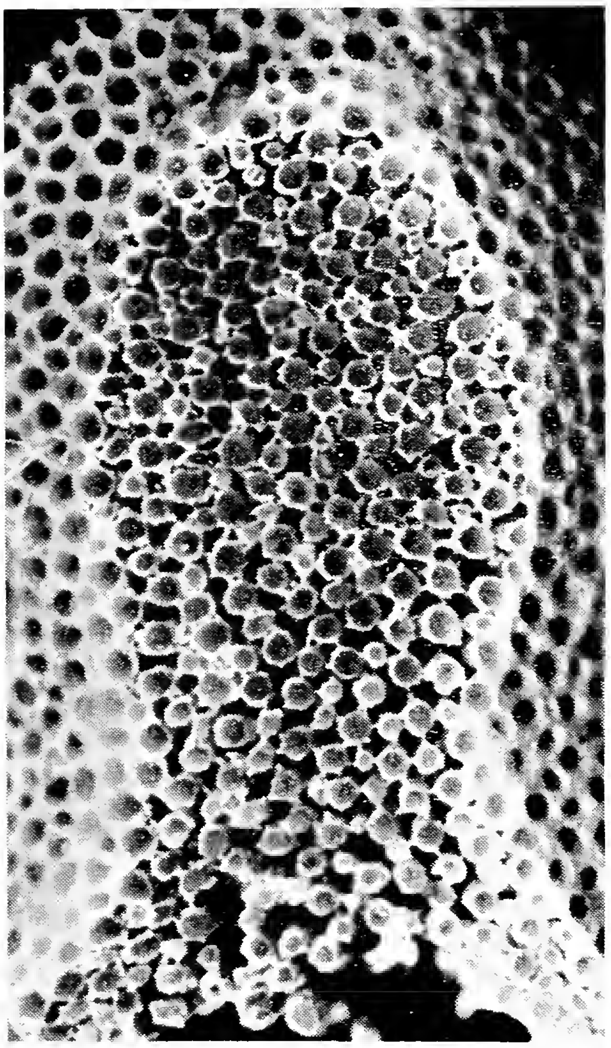
Fig. 3. — Lateral view from the same species, shows the central and peripheral region; × 25; ibid. Coll. H. BRANDES, Geol. Staatsinst. Hamburg.

Multicrescis tuberosa (Roemer, 1839).

Fig. 4. — Peripheral part of a multilamellar zoarium showing a subcolony (obliquely polished section) and budding; × 17; Hauterivian of Schöppenstedt, NW-Germany. Coll. H. BRANDES, Geol. Staatsinst. Hamburg.

Ceriopora spec.

Fig. 5. — Artificial moulds of autozooecia and the interzooecial pores among them. A central part of the zoarium was not impregnated by Polyester, therefore internal structure was partly destroyed by acid; × 12; Hauterivian of Schöppenstedt, NW-Germany. Coll. H. BRANDES, Geol. Staatsinst. Hamburg.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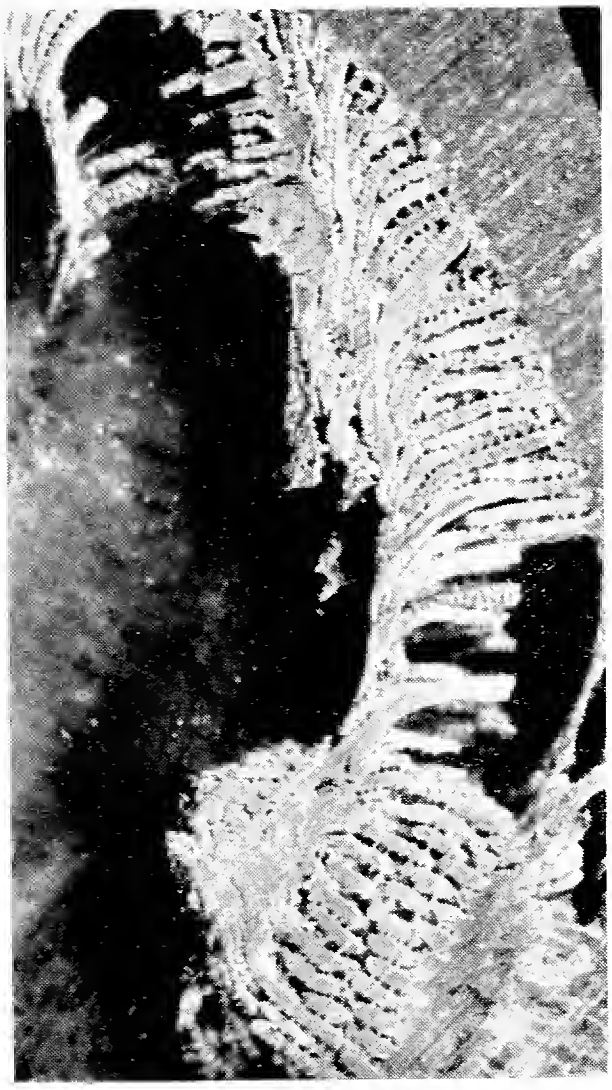
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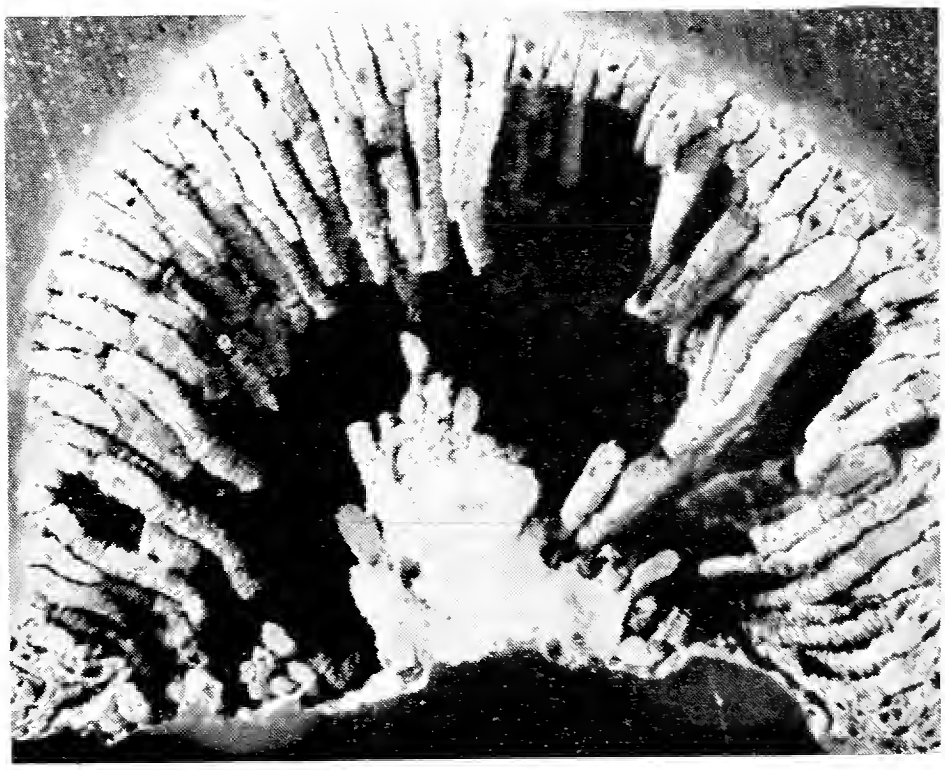
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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
5. Group 2: Anatomy, Morphology and Skeletal Structure.

EHRHARD VOIGT (*)

HOMOEOMORPHY IN CYCLOSTOMATOUS *BRYOZOA* AS DEMONSTRATED IN *SPIROPORA*

(Preliminary Report)

Riassunto. — Uno studio dettagliato del genere *Spiropora* Lamouroux, 1821 ha rivelato che molte differenti linee filetiche sono unite sotto lo stesso nome.

Per il gonozooide molto caratteristico di *Spiropora elegans* Lamouroux viene proposta la nuova famiglia *Spiroporidae.*

Le altre specie sono sistemate nelle famiglie *Entalophoridae* Reuss, 1869 insieme al nuovo genere *Spirentalophora* (specie tipo *Sp. bohemica* n. sp.) e *Coelospiropora* (specie tipo *C. hoelderi* n. sp.).

Questo è un tipico esempio di omeomorfia nei *Bryozoa Cyclostomata.*

Summary. — A detailed study of the genus *Spiropora* Lamouroux, 1821 revealed the fact that several different phylogenetic lineages are united under this name. Because of the very peculiar gonozooid of *Spiropora elegans* Lamouroux the new family *Spiroporidae* is erected.

Other species are placed in the Fam. *Entalophoridae* Reuss, 1869 with the new genera *Spirentalophora* (Type species *Sp. bohemica* n. sp.) and *Coelospiropora* (Type species *C. hoelderi* n. sp.). All this is an impressive example for homoeomorphy in cyclostomatous Bryozoa.

Zusammenfassung. — Eingehende Untersuchungen des Genus *Spiropora* Lamouroux, 1821 ergaben, dass unter diesem Namen Gattungen verschiedener phylogenetischer Herkunft zusammengefasst wurden. Auf Grund des sehr abweichenden Baues des Gonozoids von *Spiropora elegans* Lamouroux wird die neue Familie *Spiroporidae* errichtet. Andere Arten werden zu den neuen Gattungen *Spirentalophora* (Typspecies *Sp. bohemica* n. sp.) und *Coelospiropora* (Typspecies *C. hoelderi* n. sp.) gestellt.

Das behandelte Material bietet ein ausgzeichnetes Beispiel für eine homoeomorphe Entwicklung bei cyclostomen Bryozoen.

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One of the fundamental problems in taxonomy of Bryozoa is the discrimination of species in the Order *Cyclostomata* because of the existence of homoeomorphy. Many *Cyclostomata,* especially the suborder *Tubuliporina,* consisting of simple calcareous tubes with circular apertures, do not offer essential specific characters which allow a clear distinction of species in all cases. The only criteria which the student can use are the size and the diameter of the zooecia and the apertures as well as the mode of growth of the zoaria. It is difficult to distinguish species on these criteria alone, using conventional methods. Both criteria are not constant, that is they vary with ecologic conditions; thus, measurements from different portions of a single zoarium give variable results. Because of this many authors have defined species in a very large sense and therefore such « species » have a long stratigraphical range. For example *Entalophora proboscidea* (M. Edwards 1838) is assumed to range from the Jurassic to the present time. CANU & BASSLER (1922 p. 11) however already suggested that E. *proboscidea* may be in fact several species.

Another example is the well known «*Spiropora verticillata*» (Goldfuss 1826 p. 34 pl. 11 fig. 1) of the Cretaceous. This species was assumed by later authors to exist from the Neocomian to the Miocene and WATERS (1884 p. 686) thought that the ordovician *Mitoclema cinctosa* Ulrich (1882 p. 159 pl. 6 fig. 7, 7a), which is very similar to the cretaceous form, should belong to the same species. Recent studies of the present author have shown clearly that under this name « *Spiropora verticillata* » there had been united a number of very different species, p. ex. *Sp. neocomiensis* d'Orb., *cenomana* d'Orb., *ligeriensis* d'Orb., *laevigata* d'Orb. and some other forms which are regarded now to be distinct species or subspecies and belonging to different genera. Some of these species were listed by D'ORBIGNY (1850-1852) under different names in his prodrome, but they were united by him some years later in the « Paléontologie française » (1851-1854 p. 710) under the name « *Spiropora antiqua* » Defrance.

Indeed it is quite impossible to separate these forms on the basis of their morphological features. All offer in general the same morphological aspect, that is they appear as rod-like zoaria with apertures opening in whorls encircling the rod. They vary in the diameter of the stems, distance between whorls and the number and size of the peristomes, but these may vary considerably within the same zoarium and thus are undoubtly controlled by ecological factors as shall be shown in a thesis by F. FLOR (Hamburg). It must be emphasized that thousands of measurements made by FLOR have provided no satisfactory method for a separation of species because all data give mostly overlapping values. The possibility of recognizing that there must be represented several species as well as genera was the discovery of several different types of « ovicells » (gonozooids). By this it is evident that many different species have been lumped under the name of « *Sp. verticillata* », so grouped because of their external conformity.

The gonozooid of the cretaceous *Spiropora verticillata* (Goldfuss) (Fig. 1 A) agrees in general features with the gonozooid of the type species of the genus « *Spiropora* » which is *Spiropora elegans* Lamouroux (Fig. 1 D) from the Jurassic. Unfortunately the oeciostome of the latter species is not known and therefore it is incertain if it can be regarded as congeneric with *Spiropora verticillata.*

The gonozooid of that species is a long tube embracing the rods in several whorls, in contrast to the simple long baglike gonozooid of most other cretaceous *Spiropora,* which ressemble that of *Entalophora.* Because of the fundamental difference *Spiropora* must be regarded as representing a new family *Spiroporidae.*

The following results are founded upon more than 200 specimens with gonozooids and the oeciostome is constant enough in each species to be applied as a very trustworthy criterion to distinguish different species. This study follows CANU & BASSLER in emphasizing the importance of gonozooids in understanding the systematic relationships of *Cyclostomata* based upon a very rich collection of more than 5000 specimens.

The following families and genera are now discussed:

I. Family **Entalophoridae** Reuss 1869.

Genus **Spirentalophora** n. g.

Type species: *Spirentalophora bohemica* n. sp., Cenomanian Kank, CSSR.

Diagnosis: Zoarium like *Spiropora* but with gonozooids ressembling that of *Entalophora* which are well defined in their outlines. Oeciostome oval or elliptical, terminal. The gonozooid of this new genus was discussed and illustrated by CANU & BASSLER 1922 (*Mecynoecia* (?) *verticillata* Goldf. p. 13 pl. 1 figs 16-17). This was the first description of a gonozooid of a cretaceous « *Spiropora* ». Their belief that this was a specimen of *Sp. verticillata* was erroneous however because this specimen is *Sp. ligeriensis* d'Orbigny (1851-1854 pl. 615 figs. 13-15).

Stratigraphical range: Valanginian-Santonian.

Spirentalophora bohemica n. g. n. sp.

Fig. 1 C.

Holotype: Fig. 1 C, Cenomanian Kank, SE of Praha, CSSR. Cenomanian, Korycan-beds. U.S. Nat. Museum Washington.

Diagnosis: Slender cylindrical *Spirentalophora* with regular whorls built up by 8-14 peristomes. It differs from the very similar *Spirentalophora ligeriensis* (d'Orbigny) 1850 (D'ORBIGNY 1851-54 pl. 615 figs 13-15), erroneously included in the text in *Spiropora antiqua* (Defrance) by his convex gonozooid which covers the distance between 1-2 whorls. It is characterized by his huge oeciostome considerably exceeding the peristomes in diameter and which is transverse, salient and surrounded by a thick rim.

Measurements.

Diameter of zoaria	0,40 - 1,00 mm
Diameter of peristomes	0,15 - 0,25 mm
Diameter of zooecia	0,15 - 0,30 mm
Distance of whorls	0,80 - 1,70 mm
Length of gonozooids	1,70 - 2,50 mm
Width of gonozooids	0,40 - 0,55 mm

Stratigraphical Range: Cenomanian, CSSR.

Remarks: This species was probably included in the synonymy of « *Spiropora verticillata* » Goldfuss by the older authors. It is possible that the record of REUSS, NOWÁK and POČTA from Saxony and Bohemia represents this species.

Genus **Coelospiropora** n. g.

Type species: *Coelospiropora hoelderi* n.g. n.sp. Hauterivian Switzerland.

Diagnosis: Zoarium like *Spiropora* but with a hollow median axis showing transverse calcareous partitions (tabulae). Gonozooid ressembling *Spirentalophora* but with a very small inconspicuous terminal oeciostome.

Coelospiropora hoelderi n. g. n. sp.

Fig. 1 B.

Holotype: Fig. 1 B, Mus. Pal. Institut Tübingen.

Diagnosis: Same as the genus.

Measurements.

Diameter of zoaria	1,00 - 1,60 mm
Diameter of peristomes	0,15 - 0,25 mm
Diameter of zooecia	0,15 - 0,20 mm
Distance of whorls	0,90 - 1,60 mm
Length of gonozooids	4,00 - 5,00 mm
Width of gonozooids	1,00 - 1,60 mm

Description: The zoarium is bushy with branches about 1,5 mm thick. Whorls are regular and separated by about 1 mm. The axial canal is thin, about 1/5-1/6 of the diameter of the branches. The gonozooids are very long narrow sacks usually extending over 2-4 whorls and have a very small inconspicuous terminal oeciopore without protruding oeciostome.

Only one large branched zoarium collected by Prof. H. HÖLDER (Münster) is known at present.

Range and Distribution: Hauterivian, Landeron (Switzerland).

II. Family **Spiroporidae** n. fam.

Type genus: *Spiropora* Lamouroux 1821, Bathonian-Thanetian.

Diagnosis: Zoarium cylindrical, branched, solid, often club-shaped. Apertures arranged in whorls. The gonozooid is a long tube, which ascends parallel to the axis of the zoarium. At the apertural whorl the gonozooid mostly divides with two arms of the gonozooid extending around the zoarium thus embracing it, and with a third branch ascending distally to the next whorl, so that the gonozooid may extend over many whorls. One to several oeciostomes may be observed in a single gonozooid. They are small transverse eyelike slits without protruding rims located on the upper rim of the gonozooid.

Spiropora Lamouroux 1821.

Type species: *Spiropora elegans* Lamouroux, 1821, Bathonian, France.

Diagnosis: Same as family diagnosis.

Stratigraphic distribution: Bathonian-Thanetian.

Remarks: The first figures of gonozooids of that genus were given by Voigt (1964 p. 223 pl. 2 figs. 3-5) from the upper Cretaceous *Spiropora verticillata* (Goldfuss). Unfortunately the gonozooid of the type species *Spiropora elegans* (Fig. 1 D) is incompletely known and shows no oeciostome. Therefore the possibility cannot be excluded that the Cretaceous species of *Spiropora* with their very peculiar eyelike oeciostome may represent another genus than the type-species.

There is no family in which *Spiropora* could be placed because of its very unusual gonozooid. Therefore it is necessary to erect a new family for it. The description of some new forms and the discussion of the synonymy of *Spiropora verticillata* (Goldfuss) given by Gregory (1899 p. 256) must await a later

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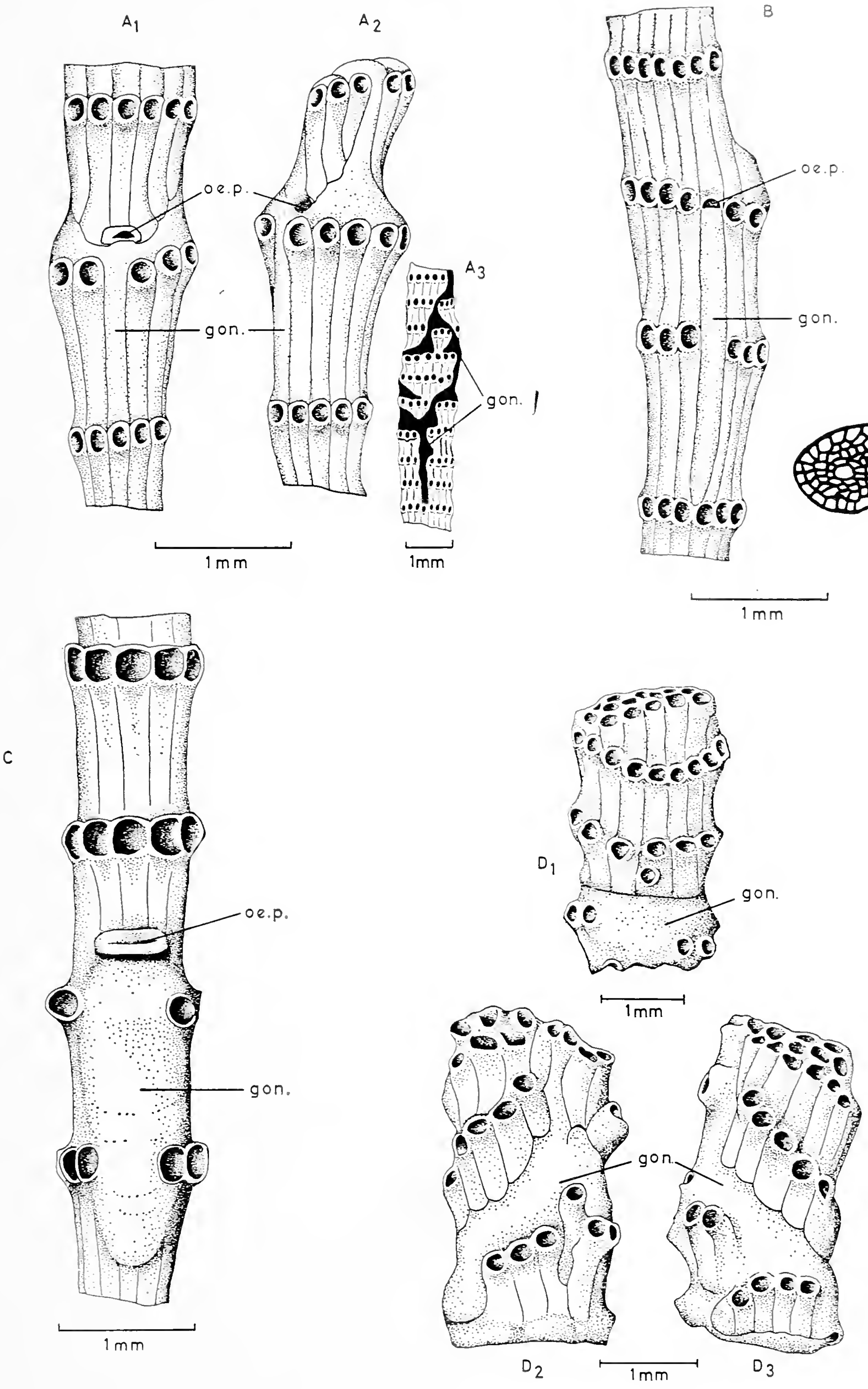
Fig. 1.
gon. = Gonozooid; oe. p. = Oeciopore.

A. *Spiropora verticillata* (Goldfuss).
A_1 Frontal view, A_2 Lateral view of the gonozooid; upper Santonian Hannover; Coll. E. Voigt Nr. 3633.
A_3 Sketch of a large gonozooid, Santonian, Vallstedt, Germany. Coll. E. Voigt Nr. 5345.

B. *Coelospiropora hoelderi* n. g. n. sp. with gonozooid and cross-section at right.
Hauterivian Landeron (Switzerland). Coll. Mus. Pal. Inst. Tübingen.

C. *Spirentalophora bohemica* n. g. n. sp., with gonozooid.
Cenomanian Kank, CSSR. Coll. U. S. Nat. Mus. Washington Nr. 651292.

D. *Spiropora elegans* Lamouroux with gonozooid. D_1-D_3 three different views of the same specimen Bathonian. Ranville, Calvados, France. Coll. E. Voigt.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publication. However it must be emphasized that GREGORY's synonymy including several different species, which has been followed by all subsequent authors, is incorrect. The main range of *Spiropora* is the late upper Cretaceous and Paleogene, although the first occurrence is proved in the Jurassic. Post Thanetian records of *Spirop. verticillata* must be still verified by the finding of gonozooids.

Measurements of *Spiropora verticillata* (Goldfuss),
(Fig. 1 A)

Diameter of zoaria	0,5 - 1,40 mm
Diameter of peristomes	0,50 - 0,20 mm
Diameter of zooecia	0,15 - 0,20 mm
Distance of whorls	0,70 - 1,60 mm
Length of gonozooids	may exceed the length of more than seven whorls.

Measurements of *Spiropora elegans* Lamouroux.
(Fig. 1 D)

Diameter of zoaria	1,10 - 2,00 mm
Diameter of peristomes	0,15 - 0,25 mm
Diameter of zooecia	0,20 - 0,35 mm
Distance of whorls	0,80 - 1,50 mm
Length of gonozooids	ca. 3,50 mm

Relation of « Spiropora » to « Entalophora ».

The question often discussed in the past, whether *Spiropora* could be included in *Entalophora* as one genus or separated into two genera is now irrelevant. The problem is not if « *Entalophora* » and « *Spiropora* » should be discerned, because very often the whorls in *Spiropora* become irregular and the distribution of the apertures offers the aspect of an « *Entalophora* ». The above evidence shows that a single morphologic type « *Spiropora* » or « *Entalophora* » is in fact the result of convergent evolution by several lineages. The problem is further complicated because the species « *Spiropora verticillata* » of authors consists of many different forms which must be regarded on the basis of gonozooids as several distinct taxa, not only at the species level but at the generic and family level as well. The task is now to discriminate all of these convergent and homoeomorphic forms by looking for their gonozooids and than to arrange them in a more natural system.

General Results.

These investigations have revealed that « *Spiropora* » is a zoarial growthform which arose at several times in different phylogenetic lineages. It is very instructive to see that the same « *Spiropora*-type » of growth was realized already in the Ordovician by the genus *Mitoclema* in the species *M. cinctosa* Ulrich (1882, p. 159, pl. 6, fig. 7 and 7 a). The figures of that species and those from cretaceous « *Spiropora* » are de facto indistinguishable and WATERS (1884, p. 681 and 686) thought *M. cinctosa* and *Spiropora verticillata* should be the same species. The single difference seems to be that the paleozoic forms have not yet produced gonozooids.

Homoeomorphy has made it difficult to differentiate taxa and to trace phylogenetic lineages in many groups of invertebrates (brachiopods, corals etc.). Very often internal structures as seen in sections have provided criteria with which to solve some of these problems. In the case of *Spiropora* the different kinds of gonozooids can be observed only in the fertile specimens. The specific or generic differences based upon the character of the gonozooid are by no means manifested either in the external or in the internal morphology of the specimens. This is one of the most impressive examples in Paleontology, illustrating the fact that an isolated specimen may not show all of the potential morphologic characters which should develop, even though these characters may be essential to the taxonomist's understanding of that group, much as the structure of a flower of a particular plant cannot be known only from observations of the leaves of that plant.

On the other hand it is quite depressing to admit that without the knowledge of the gonozooids *de facto* many specimens must be left indeterminable. There is no doubt that this same problem of homoeomorphy exists in many other groups of Bryozoa and it is a function of our present state of knowledge of the

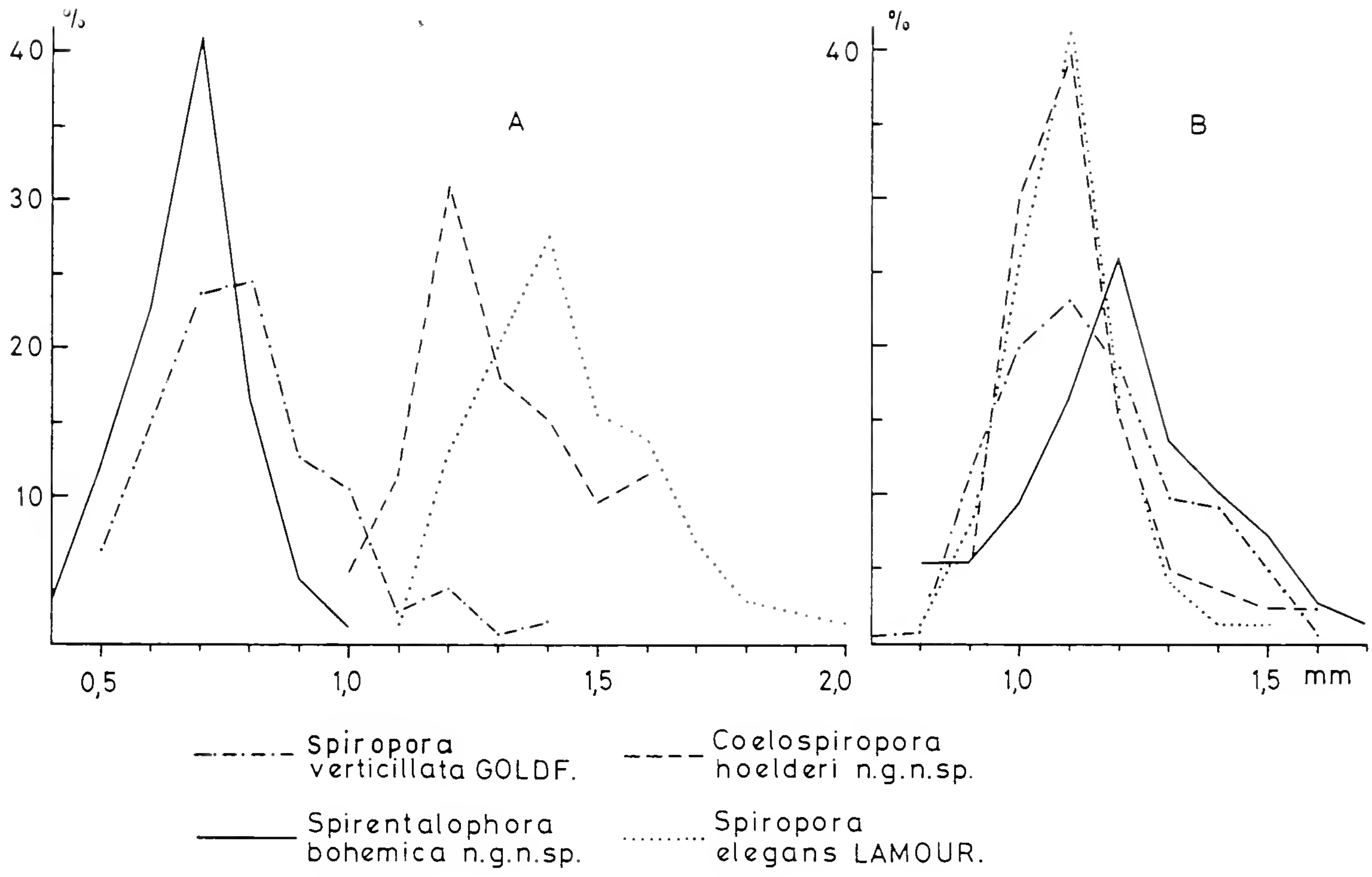

Fig. 2. — A) Diameter of the zoaria (stems) and B) Distance of the whorls.

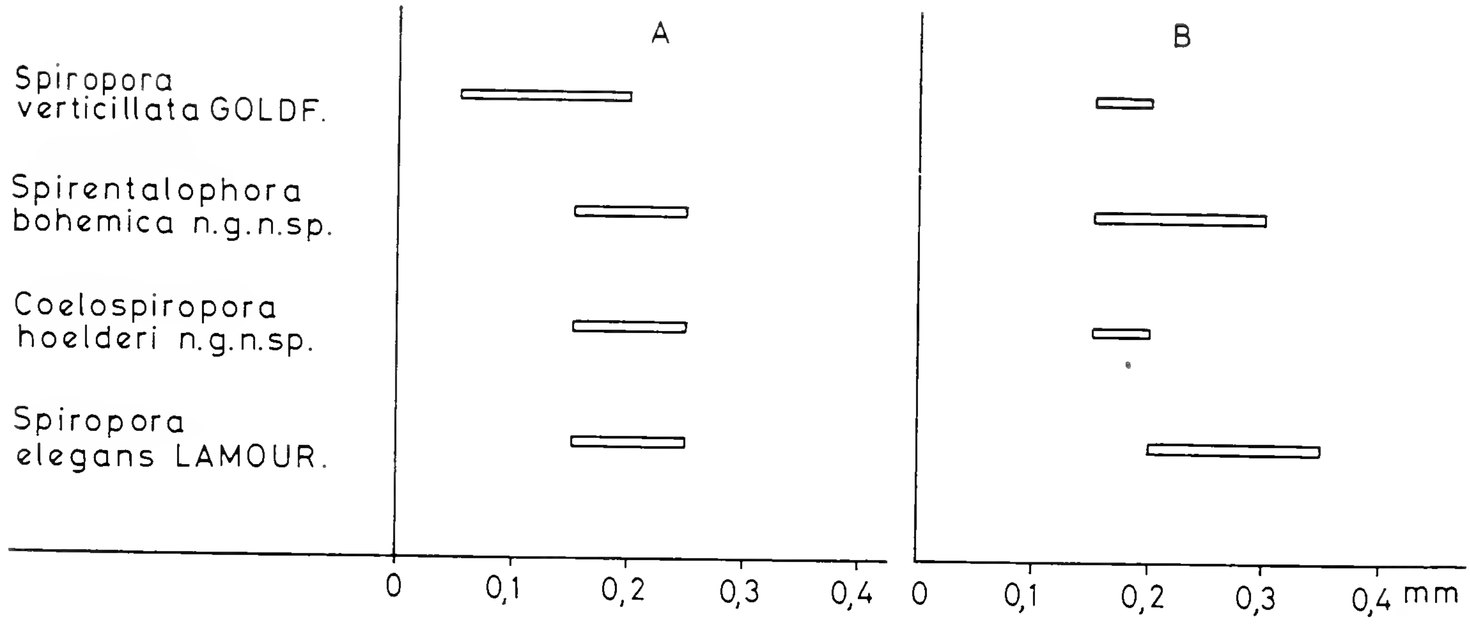

Fig. 3. — A) Variation of the peristome-diameter and B) Width of the zooecia of *Spiropora elegans* Lamour., *Spirentalophora bohemica* n. g. n. sp., *Coelospiropora hoelderi* n. g n. sp. and *Spiropora verticillata* (Goldf.).

group. Furthermore it would seem that observation of external characters and the statistical treatment of measurements are not always well adapted for the differentiation of natural species groups (Figs. 2-3).

The present author wishes to thank Mr. F. FLOR (Hamburg) for the drawings and measurements presented here. Mr. FLOR will collaborate with myself in preparing a more complete treatise on the same subject to be published soon. He wishes also to thank Mr. O. NYE, Smithsonian Institution (Washington) for reading over the manuscript.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
6. Group 2: Anatomy, Morphology and Skeletal Structure.

KARL W. KAUFMANN, Jr. (*)

THE BIOLOGICAL ROLE OF *BUGULA*-TYPE AVICULARIA (*BRYOZOA*)

(Preliminary Report)

Riassunto. — Il ruolo biologico primario degli avicularia di *Bugula simplex* e di *B. stolonifera* nell'area studiata è quella della difesa contro due specie di Anfipodi tubicoli - *Corophium insidiosum* e *Jassa falcata* - perchè:

a) gli avicularia sono costruiti per catturare questi Anfipodi meglio che altri organismi capaci di recare danno alla colonia;

b) gli Anfipodi arrecano un danno apprezzabile alla colonia, ma sembrano essere efficacemente controllati dagli avicularia.

Summary. — The primary biological role of the avicularia of *Bugula simplex* and *B. stolonifera* in the area studied is that of defense against two species of tube-building amphipod, *Corophium insidiosum* and *Jassa falcata* because:

a) The avicularia are better constructed for catching these amphipods than any other organism liable to harm the colony;

b) The amphipods do an appreciable amount of damage to the colony, but seem to be effectively controlled by the avicularia.

Introduction.

Since 1555, approximately 1000 papers have been written concerning the ecology of ectoprocts (SCHOPF, 1967), but none of these has dealt specifically with the biological role of avicularia. The most widely accepted theory is that the avicularia are used

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for defense (HINCKS, 1880, p. LXXIX; HARMER, 1909, p. 720; 1931, p. 135; MARCUS, 1926, p. C 58; HYMAN, 1959, p. 330). HARMER suggested that one of the biological roles of avicularia is that of defense against larve of encrusting species, particularly those of other ectoprocts, but this has not been examined experimentally. Other theories of the biological role of avicularia are equally lacking in evidence to support them. One of the oldest is that the avicularia are used to capture food. This theory has been discredited by HINCKS (1880, p. LXXVII) and others who noted, among other things, that the zooids cannot use the type of food that the avicularia catch, nor do they have any means of transferring it to their mouth. It has also been suggested that the avicularia aid in respiration, presumably by creating a current to remove the water that has passed through the lophophores (CANU and BASSLER, 1929, p. 360). CANU and BASSLER also suggested that the avicularia of certain *Reteporidae* distribute the prey among the colony through the creation of these same water currents.

The wide variety of different types of avicularia indicates that they are specialized to fulfill a variety of different biological roles which vary from species to species. There has yet to be presented sufficient evidence to prove conclusively that the avicularia of any one species fulfills any of the above biological roles. This paper provides support for the defense theory in the case of two species of *Bugula* through a structural analysis of their avicularia and an ecological study of the interaction of animals found on the colony with the avicularia.

Methods and Procedure.

The two species chosen for intensive study, *Bugula simplex*, and *Bugula stolonifera*, both grow in Eel Pond, Woods Hole, Massachusetts. Eel Pond is a circular, nearly enclosed bay approximately 300 meters in diameter, and is freely communicable with the ocean. There is no freshwater runoff into the bay, so the salinity is the same as that of the adjacent sea. All of the material used in the investigation was taken from two tires suspended from floating docks. In addition to observations of live material, extensive use was made of whole mounts in Lakeside cement for morphological studies.

Definitions.

I have adapted BOCK and VON WAHLERT'S (1965) definition of function and biological role to apply specifically to avicularia. A function of an avicularium is defined as a capability which the avicularium is mechanically and physiologically able to perform. A biological role of an avicularium is a role which the avicularium plays in acting on its environment. There may be more than one function, and some of these functions may aid it in fulfilling a number of biological roles. I shall define defense as follows: Avicularia can be said to fulfill a biological role of defense against an organism if (a) that organism is detrimental to the colony and if (b) the avicularia significantly reduce the danger which the animal poses to the colony.

Structural analysis.

To determine what functions the avicularia could best perform, a careful structural analysis of the avicularium was made. The mechanical advantage that the muscles have in closing the mandible was calculated for varying degrees of opening. The highest mechanical advantage is obtained when the mandible is completely closed (Fig. 1, Position A). This advantage rapidly diminishes to an almost negligible amount as the mandible opens to about 90° (Position C), and remains at this low value for the rest of the range of opening, about 180° (Position D). The maximum tension that may be developed in an isometric contraction of the adductor muscles at different extensions may vary considerably. However, the difference in mechanical advantage between positions completely closed and half-way open (Position C) means that the avicularium can hold objects of a small diameter (less than .1 mm) with a much firmer grasp than larger objects. The purpose of the spike on the end of the mandible is not to puncture, but during closing, to more rapidly reduce the gap between the mandible and the rostrum and thus prevent the escape of the prey.

The mean distance between adjacent avicularia on a single branch is .55 mm for *B. simplex* and .37 mm for *B. stolonifera.* An organism smaller than or even equal in length to these dimensions would not be caught nearly so often as an organism longer than 1 mm that could span several avicularia at the same time. The largest organism that was observed to be captured and held for a moderate length of time (three minutes) was a gam-

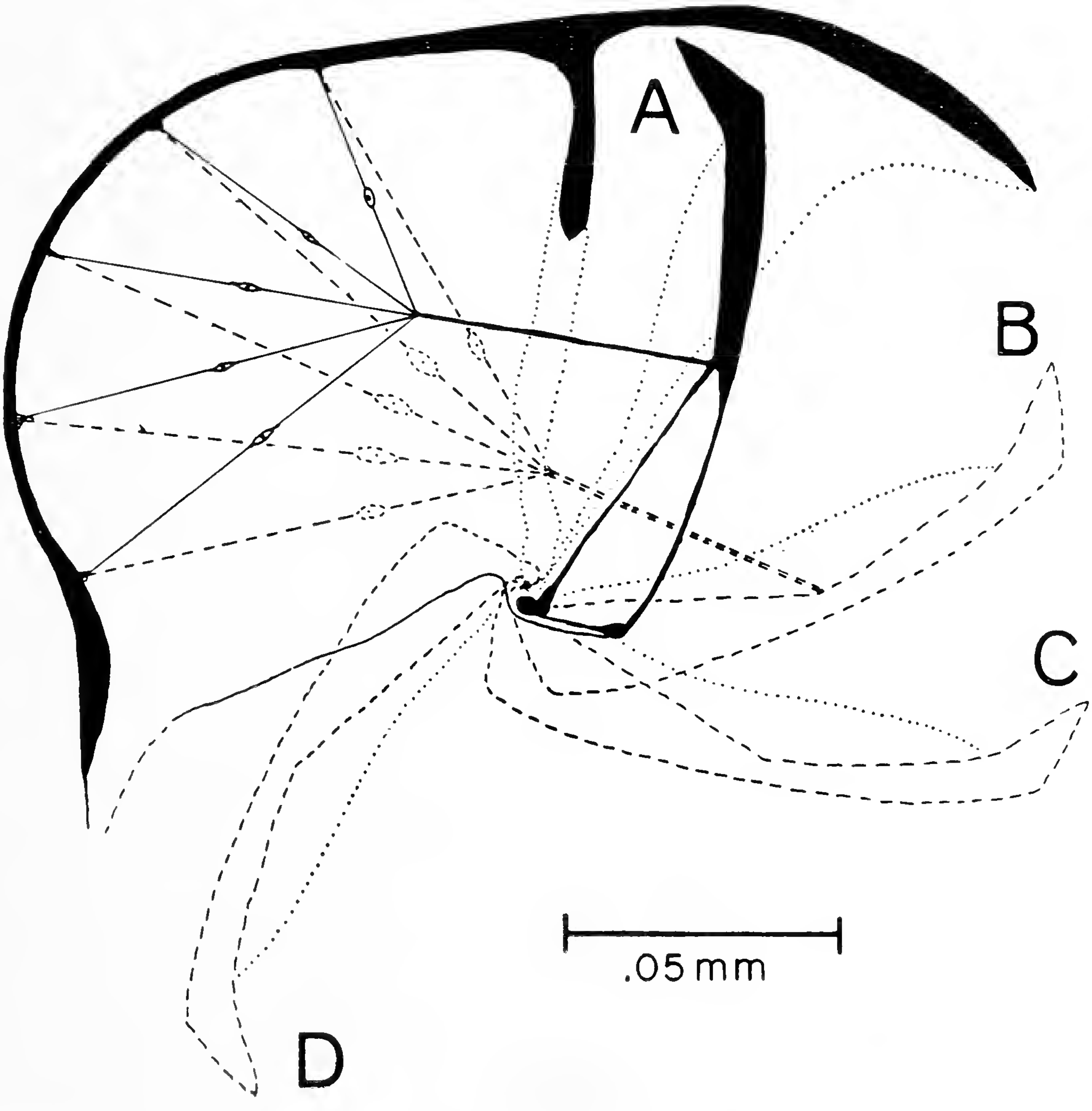

Fig. 1. — Sagittal section of avicularium of *Bugula simplex* with schematic representation of the adductor muscles and tendon. The mandible is shown in four different positions. At position B, the mechanical advantage is half that of position A. At positions C and D, the mechanical advantage is almost negligible.

marid amphipod 3 mm long, not including the long antennae. Animals with many appendages were observed to be caught far more often than those of similar size and abundance but with few appendages, such as nematodes. The many small hairy appendages increase the probability that part of the animal will come in contact with an avicularium and provide objects of a small enough diameter that the avicularia can hold with sufficient force. The avicularia are best able to catch and hold organisms from 1 to 3 mm long and with many appendages of small diameter.

Ecological observations.

There are two general classes of organisms that avicularia supposedly defend against predators and larvae: especially larvae of their own kind. No predators were found in Eel Pond that satisfied the definition of defense. HYMAN (1959, p. 432) and MARCUS (1926, n. C46) list a number of known predators, but most of them (fish, echinoids, holothurians, prosobranchs, nudibranchs) are too large to be effectively hindered by avicularia. Observations of smaller animals (amphipods, nematodes, copepods, flatworms) on the colonies under consideration yielded no evidence of any of them preying on Ectoprocts. Pycnogonids have been described as predators of Ectoprocts, but they were very rarely seen on the colonies and could not, therefore, be considered to do a significant amount of damage to the colonies in question. Thus, in this particular case, defense against predators cannot be said to be a biological role of the avicularia. Larvae of both *B. simplex* and *B. stolonifera* are .1 to .2 mm in diameter and have no appendages or long hairs. Similarly, the larvae of other animals found in Eel Pond are either smaller than the average distance between avicularia or have few easily grasped appendages or hairs. Thus, the avicularia studied are poorly suited for capturing larvae.

The animals that were found to best fit the terms of the definition of defense were the gammarid amphipods, *Corophium insidiosum* and *Jassa falcata*. Both of these amphipods were present in large numbers and built tubes of detritus and fecal pellets among the colonies. These tubes prevented nearby autozooids from feeding by clogging up the proximal parts of the colonies. The avicularia, however, effectively limited tube building by grabbing amphipods that wandered among the branches and holding them for varying amounts of time (minutes to hours). The size of the amphipods ranged from a minimum of .5 mm up to 5 mm. They had many small appendages, making it easy for the avicularia to grab and hold them. 51% were in the optimum size range of 1-3 mm.

Conclusion.

Because the two species of amphipods fit the terms of the definition both in being a threat to the colony and in being effectively controlled by the avicularia, and because the avicularia are better designed to capture them than any other organism on the colony, the primary biological role of the avicularia of *Bugula simplex* and *B. stolonifera* in Eel Pond is that of defense against *C. insidiosum* and *J. falcata*. The widespread distribution of both tube-building organisms and species with *Bugula*-type avicularia make it probable that this is not a unique relationship.

Acknowledgements.

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This extended abstract merely summarizes the results and line of reasoning of a paper now being prepared.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
7. Group 2: Anatomy, Morphology and Skeletal Structure.

NATALIE N. DUNAEVA (*)

ON THE MODE OF SEXUAL REPRODUCTION OF SOME TREPOSTOMATOUS *BRYOZOA*

(Preliminary Report)

Riassunto. — L'abbondanza di cisti negli zooecia di molte colonie di *Aisenvergia cylindrica* Dunaeva e di *Volnovachia distincta* Dunaeva, provenienti dal Carbonifero inferiore del Bacino del Donetz, viene considerata come una prima indicazione del modo di riproduzione sessuale nei *Trepostomata*.

Summary. — The abundance of cysts in the zooecia of many colonies of *Aisenvergia cylindrica* Dunaeva and *Volnovachia distincta* Dunaeva from the Lower Carboniferous of Donetz Basin is considered as a slight indication of the mode of sexual reproduction by *Trepostomata*.

In the strata of the Lower Carboniferous of Donetz basin occur some peculiar bryozoans — *Aisenvergia cylindrica* Dun., *Volnovachia distincta* Dun. —, referred to a new family *Aisenvergiidae* Dunaeva (DUNAEVA, 1964). The main feature of these bryozoans are the sygmoidally curving of zooecial walls and the close compression of the zooecial cavities in exozone which in the most exciting structure of g. *Aisenvergia* result in forming a cylindrical wall between endozone and exozone.

Apart from this unique inner structure the *Aisenvergiidae* from Donetz basin proved to be very interesting in some other ways.

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Many colonies of both genera possess small sphaerical to irregulary globular hollow bodies in zooecia. These bodies were observed more than in 160 thin-sections in different number — sometimes isolated, sometimes very numerous (fig. 1). In the last case they are often constricted. The bodies are about 30-80 μ in diameter and have definite walls consisting usually of two layers — the inner dark and thin, and the outer more thick, light and laminated. According to their position and size the sphaerical bodies look like eggs in the zooecia of some living Bryozoa (*Electra pilosa, Membranipora membranacea*).

Similar bodies, though never in such abundance, were mentioned in some Trepostomatous bryozoans by R. S. BASSLER (BASSLER, 1911) and R. S. BOARDMAN (BOARDMAN, 1960) as cysts.

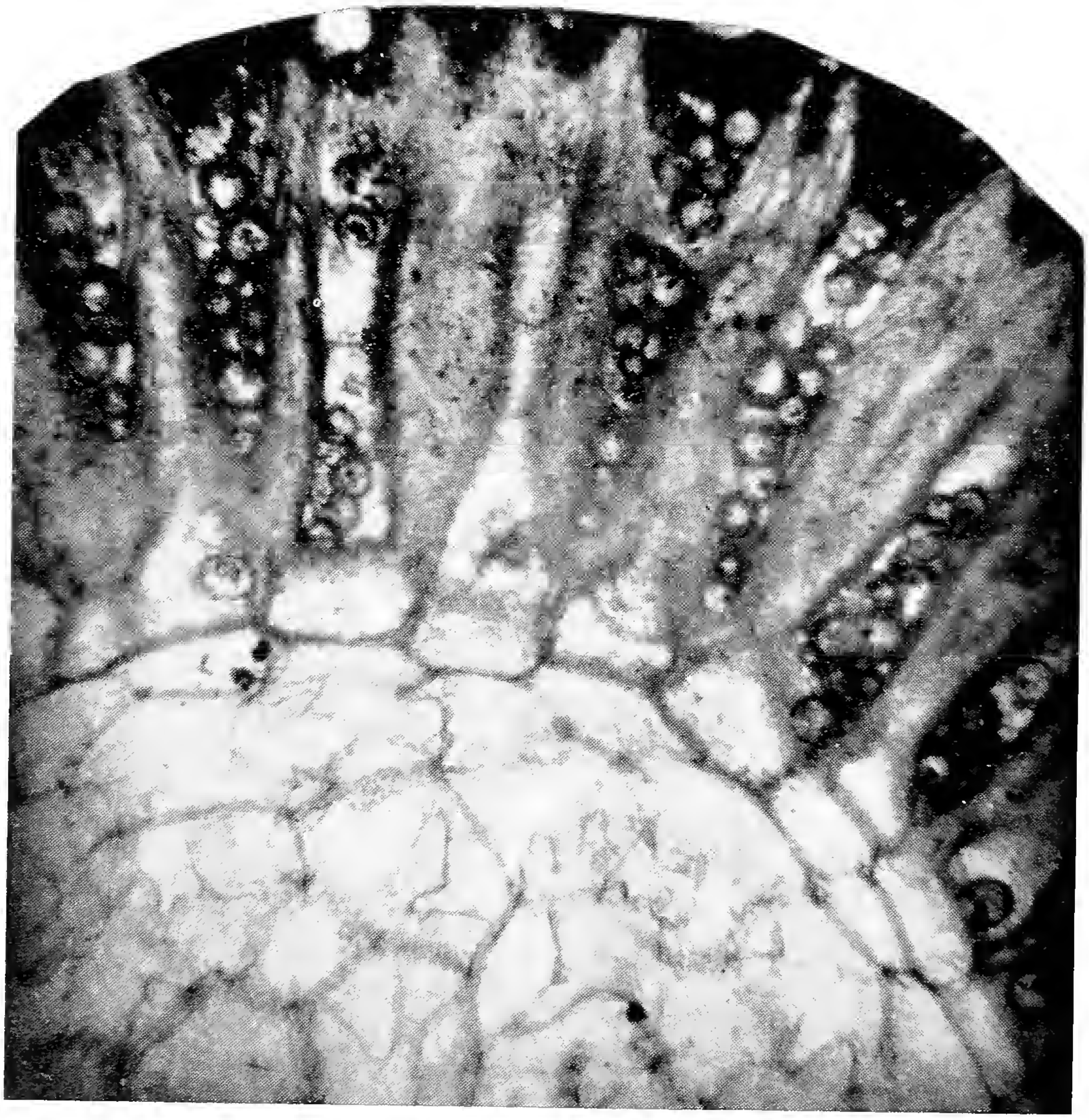

Fig. 1. — *Volnovachia distincta* Dunaeva. Transverse section showing many cysts in the zooecia. (× 60)
Donetz Basin, Lower Carboniferous, Zone C_1 at.

No definite explanation was given about the nature of these formations.

The unusual abundance and position of the cysts in the zooecia of *Aisenvergiidae* cause the assumption of their connection with the reproductive functions of colonies. This is confirmed by the fact that all the specimens of both species were collected in a small place (less than 20 m^2) in the same layer of limestone and most likely represent the colonies from the same population which grew simultaneously and were suddenly buried in the stage of sexual reproduction.

According to the investigations on recent Bryozoa (HARMER, BORG, SILÉN) the sexual reproduction of these animals may go on different ways. Two main types of sexual reproduction may be indicated by the recent Bryozoa of order *Cheilostomata, Ctenostomata* and *Cyclostomata*: 1) the ova develop in special brood-chambers (gonozooecia or ovicella); 2) the ova develop in the surrounding water where they are evacuated from the body cavity through the intertentacular organ or through the genital pore.

The ways of sexual reproduction of extinct Bryozoa (order *Trepostomata, Cystoporata* and *Cryptostomata*) are almost quite unknown. Some analogies with the brood-chambers were noticed in some genera of *Cryptostomata* (by genera *Polypora* and *Fenestella*). No evidence of ovicella are indicated up to day in *Trepostomata.*

The observations discussed above may serve as a slight indication of the mode of sexual reproduction of these extinct Bryozoa (at least of the group of them belonging to the family *Aisenvergiidae*).

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
8. Group 2: Anatomy, Morphology and Skeletal Structure.

GERO HILLMER (*)

ON THE VARIATION OF GONOZOOECIA OF ENCRUSTING « *BERENICEA* »-FORMS (LOWER CRETACEOUS) (*BRYOZOA*)

(Preliminary Report) (**)

Riassunto. — Vengono studiati su colonie incrostanti di forme del gruppo « *Berenicea* » (Hauteriviano della Germania settentrionale) la variazione e il valore tassonomico dei gonozooecia.

Il rapporto tra l'accrescimento dei gonozooecia e degli zooecia vicini è secondo CANU & BASSLER (1920, 1922) un criterio sistematico di primaria importanza per le famiglie *Diaperoeciidae* Canu, 1918, *Plagioeciidae* Canu, 1918 e *Oncousoeciidae* Canu, 1918.

Osservazioni morfologiche e sezioni lucide seriate praticate attraverso i gonozooecia hanno mostrato che questo rapporto negli accrescimenti non è un buon criterio sistematico per definire una famiglia.

Le famiglie *Diaperoecidae*, *Plagioeciidae* e *Oncousoeciidae* dovranno essere invalidate allorquando un nuovo concetto sistematico sarà elaborato.

Summary. — Variation and taxonomic value of gonozooecia of encrusting colonies of the « *Berenicea* »-form-group are studied. The classification of CANU (1918, 1919) and CANU & BASSLER (1920, 1922) are discussed. The investigations show, that these authors have depended too much on the character of gonozooecia. In encrusting « *Berenicea* » colonies the gonozooecia are not a distinguishing family character. We must reject the families *Diaperoeciidae* Canu, 1918, *Plagioeciidae* Canu, 1918 and *Oncousoeciidae* CANU, 1918, if we can establish a more natural systematic concept based on more exact defined taxonomic characters. We can realize this only by monographic investigations of exactly encircled smaller groups of forms.

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(**) The final paper will be published in the Review: « Paläontologische Zeitschrift ».

Résumé. — La variation et la valeur systematique des gonozoécies ont été étudiés sur des colonies encroûtantes de « *Berenicea* » (Hauteriviens de l'Allemagne du Nord). Le rapport entre la croissance des gonozoécies et des zoécies voisines est d'aprés CANU (1918) et CANU & BASSLER (1920, 1922) un critère systematique de premier ordre pour la famille des *Diaperoeciidae* CANU 1918, *Plagioeciidae* CANU 1918 et *Oncousoeciidae* CANU 1918.

Des observations morphologiques et des polissages en série à travers les gonozoécies ont montré que ce rapport de croissance n'est pas un bon critère systematique pour défínir une famille.

Les familles *Diaperoeciidae, Plagioecíidae* et *Oncousoeciidae* devront être rejetes dés qu'un nouveau concepte systématique sera élaboré.

During my studies of the Lower Cretaceous cyclostomatous Bryozoa from some classic localities of North Germany (Schandelah, Schöppenstedt, Berklingen, Gr. Vahlberg and Achim) — a complete revision of these Bryozoa is in preparation — I had occasion to study many different specimens with gonozooecia. In this report I only will discuss the variation and the systematic-taxonomic value of gonozooecia of encrusting colonies of the Berenicea form-group.

My effort aimed at testing the classification of CANU (1918, 1919) and CANU & BASSLER (1920, 1922) of this group and we will see, that the gonozooecium of some « *Berenicea* »-forms is not a very trust-worthy and constant character. These results are in contrary to the investigations of homoeomorph specimens of the « *Spiropora-group* » by E. VOIGT (1968), who demonstrated in this form-group, that we cannot separate these growth forms on the basis of their conventional morphological features but only on the different types of their gonozooecia. By means of voluminous fossil material VOIGT could demonstrate, that shape, size and developement of the gonozooecia and the ooeciostome referred to the ooeciopore is constant enough in each species to be applied as a very trustworthy criterion to distinguish different specimens. In this case he followed the systematic concept of CANU & BASSLER, which is mostly based on the character of the gonozooecium.

We know that the principles of classification following zoarial characters and gonozooecia are overlapping and that this is the main reason of the partly very unnatural systematics.

Canu & Bassler (1920) wrote, that a more natural systematics should mainly be based on the fact, « that the distinction between the families of *Cyclostomata*, like the other orders of Bryozoa, is or should be based on their larval forms, each family beeing characterized by a special larva. The larvae of the *Cyclostomata* are very similar to each other and difficult to discriminate, but fortunately they show their differences by the evolution of the embryos in ovicells of very different size, shape and position ».

According to this, only size, shape and position of the gonozooecia are the main characters for a separation of specimens. In spite of the zoological criticism of Borg (1936) many cyclostomatous families — like *Diaperoeciidae* Canu 1918, *Plagioeciidae* Canu 1918 and *Oncousoeciidae* Canu 1918, — are based only on this character.

There is no discussion, that quite generally in some cyclostomatous families the zoarial characters show much more variability as the gonozooecia or zoarial brood-chambers and their ooeciostomes, which are by fact the most constant characters. But in special groups the brood-chambers, however, vary so much, that it is impossible to establish a classification by using only this distinguishing character.

Canu & Bassler have discriminated and described a large number of different types of brood-chambers, which often differ only very slightly from one another as for example in some « *Berenicea* »-forms. Thus, for instance, the families *Diaperoeciidae*, *Plagioeciidae* and *Oncousoeciidae* are separated according to the shape and the position of the gonozooecium and the time relation between the growth of the gonozooecium and zooecial tubes. These are the most important characters for the diagnoses.

Species of « *Berenicea* » preserving gonozooecia are referred to several distinct genera and families. Some of them belong to the genus *Plagioecia* but others to *Diaperoecia* or *Oncousoecia*.

Colonies without brood-chambers belong futhermore to the genus *Berenicea* Lamouroux, 1821, because the type species *Berenicea prominens* has no gonozooecium.

Canu, 1918, gave the following family diagnosis, which are accepted in the Treatise (1953), of which I will briefely give the first-class character:

a. The globular or transverse sac-like gonozooecium of the family *Diaperoeciidae* is formed after the calcification of the distal tubes and therefore is placed among many tubes which project without disarrangement on the gonozooecium itself.

b. The gonozooecium of the family *Plagioeciidae* is formed before the calcification of the neighboring tubes, the formation of which it hinders. The longitudinal axis of the brood-chambers is perpendicular to the zooecial tubes.

c. The gonozooecium of the family *Oncousoeciidae* is parallel to that of the tubes and is developed at the same time as the adjacent zooecia, which are not disarranged in their respective position.

A great number of morphological very different colonies are united in these families. The reason is, that students quite generally believe that the morphology of the brood-chamber and the arrangement of the zooecia in relation to it shows the systematic relationships of these cyclostomatous species better than the very variable zoarial growth form. As we know it is quite right for some groups, but it is not a trustworthy criterion for others.

Thus, for instance, the seemingly well known ?*Diaperoecia polystoma* (ROEMER, 1839).

I had the occasion to study the type-species *Cellepora polystoma* ROEMER, 1839 and many conspecific colonies with gonozooecia.

CANU & BASSLER, 1922, referred these colonies with brood-chambers in the family *Diaperoeciidae*, because the gonozooecium is formed after the calcification of the surrounding tubes. Contrary to this meaning, my material of this species from the type-locality Schöppenstedt, NW-Germany, must increase the confusion, because some colonies show a gonozooecium of the *Plagioecia*-type, others of the *Diaperoecia*-type. In this relation a very grotesque example is, that we can recognize in one and the same encrusting colony two very different types of gonozooecia. This could give rise to the very unnatural separation of one part of this colony to the family *Diaperoeciidae* and the other part to the family *Plagioeciidae*.

Thus, my material generally shows, that size and shape of the gonozooecia varying considerably from an elliptical transversal sac to a heart-shaped extension. They are also more or less convex. The mostly terminal situated oeciostome is small and less than the zooecial diameter and adjacent to a zooecial aperture.

The oeciopore is mostly orbicular; only in two cases it is a little more elliptical. The time relation between the growth of the gonozooecium and the neighboring zooecia shows also great variation. At several gonozooecia we can recognize, that some tubes project through the central and peripheral region of the brood-chamber.

According to the systematic concept this finding shows, that the gonozooecia developed after the calcification of the tubes. In contrary to that, we can see, that other gonozooecia are not traversed by the tubes and therefore they must have developed before the calcification of the surrounding zooecia. Thus, just studying the morphology we can observe, that the gonozooecia of exactly conspecific specimens from the same locality with very similar ecologic conditions vary in size and form and developed not only before but also after the calcification of the surrounding tubes. Thus, we could arrange some colonies in the family *Plagioeciidae* and others in *Diaperoeciidae*. The colonies without gonozooecium we have to unite under the zoarial genus *Berenicea* Lamouroux.

We can examine the character of time relation between the growth of the brood-chamber and the surrounding zooecial tubes also by means of serial sections. The preparation of gonozooecia where no tubes traversed the roof of brood-chamber shows, that the development of gonozooecia and surrounding tubes occurred nearly at the same time and differences are mostly based on ecologic factors.

Results.

The results of my observations of encrusting colonies of the « *Berenicea* » form-group show us, that Canu and Bassler have depended too much on a single character. Gonozooecia surrounding peristomes or not, exist to a more or less extent in many other genera and it is not a distinguishing family character. The development of gonozooecia and surrounding zooecial tubes occurred nearly at the same time. Shape and size of the gonozooecium can show also great variation. Till now I was disappointed in my hope, that the gonozooecia show several types of oeciopores which may eventually result in the separation of these forms. All brood-chambers of encrusting « *Berenicea* » forms which I have seen, usually show, isolated terminal and ± median oeciostomes situated very near to a peristome in a directly continuation of the fertile zooecium. There exists only little variation in the shape of the oeciopore, which is mostly round and only sometimes a little elliptical. But we can hope, that more observations in fossil material will confirm the zoological statement of OSBURN (1953, S. 616), that the position and form of the oeciopores and their oeciostomes are fairly constant and usuable for exact determination.

These results demonstrate, that we must reject the families *Diaperoeciidae*, *Plagioeciidae* and *Oncousoeciidae*, if we can establish a more natural systematic concept based on more exact defined taxonomic characters. This finding exists for some other cyclostomatous families, too. In my opinion we have to work out a new systematics for the Order *Cyclostomata* mostly independent from the old one. We can realize this only by monographic investigations of exactly encircled smaller groups of forms.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
9. Group 2: Anatomy, Morphology and Skeletal Structure.

GISELA ILLIES (*)

ON THE GONOZOOECIUM OF *COLLAPORA STRAMINEA* (Phillips)

(*Bryozoa Cyclostomata*)

Riassunto. — *Collapora straminea* (Phill.), un *Cyclostomata* eretto, appare nel Bajociano medio della Regione dell'Alto Reno (strati a Briozoi). I suoi gonozooecia, sconosciuti finora, vengono qui descritti e illustrati.

Summary. — *Collapora straminea* (Phill.), an erect Cyclostome, appears in the Middle Bajocian of the Upper Rhine Region, forming so-called Bryozoa Beds. Its gonozooecium, which was unknown till now, shall be described.

Zusammenfassung. — *Collapora straminea* (Phill.), eine freiwachsende cyclostome Bryozoe, tritt im mittleren Bajocium des Oberrheingebietes gesteinsbildend auf. Das bisher unbekannte Gonozooecium dieser Art wird beschrieben.

In 1925 DEUSS described a Bryozoa Bed within the Bajocian strata of south western Germany. The layer is intercalated in marly succession containing the guide ammonite *Otoites sauzei* d'ORB. The form described here was collected on the « Galgenberg » (height 313,7 m) near Niederrimsingen W Freiburg i. Br.

According to DEUSS (1925, p. 13) the Bryozoa Bed consists of colonies of *Pustulopora quenstedti* Waagen, which is equalized (p. 66) with *Millepora straminea* Phill.

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Collapora straminea (Phillips, 1829)

(Pl. III, fig. 1-6)

Synonymy:

Millepora straminea Phillips 1829, 2nd. ed. 1835, pp. 115, 121, pl. IX, fig. 1.

Pustulopora quenstedti Waagen 1867, p. 641, pl. 32, fig. 10.

Cricopora acutimargo Waagen 1867, p. 641, pl. 33, fig. 7.

Collapora straminea (Phill.) Quenstedt 1881, pp. 223-225, pl. 151, figs. 49-56.

Haplooecia straminea (Phill.) Gregory 1896, pp. 159-161, text figs. 11-12.

Haplooecia straminea (Phill.) Canu & Bassler 1922, p. 97, text fig. 25, pl. 14, figs. 14-15.

Collapora straminea (Phill.) Walter 1967, p. 45, pl. 11, fig. 13.

The erect colonies contain numerous gonozooecia. The visible part of a gonozooecium is many times longer than the visible part of a zooecium and its width is still more than the double one of a zooecium (pl. III, figs. 1-5). The gonozooecium is narrowing towards the distal oeciopore, until its width is about the same of a normal peristome, and forms an oeciostome. The frontal plane of the gonozooecium is flattened or slightly arched. It is possible that the gonozooecia are budding like the zooecia as a very small and thin tube within the centre of the round stems.

The tube of the zooecium is widening in diameter the more it comes to the frontal layer (corresponding to the zooecial regions situated more or less along a radial line of the coneshaped growing zone at the end of the stem). Thereby the zooecial tube will be displaced by several younger generations of zooecia from the centre to the frontal plane. Therefore the length of the non-visible part of the tube is essentially longer than that of the visible part. The origin of a zooecium could not be ascertained precisely till now. The proximal part is very small.

Some observations lead to the assumption that the non-visible parts of gonozooecia and zooecia do not differ at all from each other. (1) There is no indication of a growing gonozooecium within a stem's cross section, situated proximal to its visible part.

(2) Injured gonozooecia show the equivalence of the inner tube of gonozooecia and zooecia at the transition from the inner to the outer region.

Within the frontal layer the gonozooecium is overgrowing the distal zooecia. Some of those overgrown zooecia will not be able any more to reach the frontal plane. The zooecia growing laterally beside the gonozooecium are mostly undisturbed. Small differently shaped frontal walls without peristomes will not often be observed.

Dimensions at the frontal plane. Gonozooecia: (a) Length 1.4-3.2 mm, (b) maximal width 0.45-0.85 mm, (c) depth (rectangular to (a) and (b)) 0.15-0.20 mm. Width of the ellipsoidal oeciopore 0.10-0.30 mm. Zooecia (situated beside the gonozooecia): (a) Length 0.40-0.70 mm, (b) width 0.20-0.30 mm. Peristome's width 0.14-0.20 mm.

The same or at least very similar stems of Bryozoa with equiformed gonozooecia were collected, too, from the Upper Aalenian and the Upper Bajocian of the same region.

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EXPLANATION OF PLATE III

Figs. 1-2. — *Collapora straminea* (Phill.) 1829. Gonozooecium with one oeciostome. Middle Bajocian, zone of *Otoites sauzei* d'ORB., Galgenberg near Niederrimsingen W Freiburg i. Br., Germany. Fig. 1 × 12, fig. 2, the same gonozooecium × 25. Collection G. Illies N° K1.

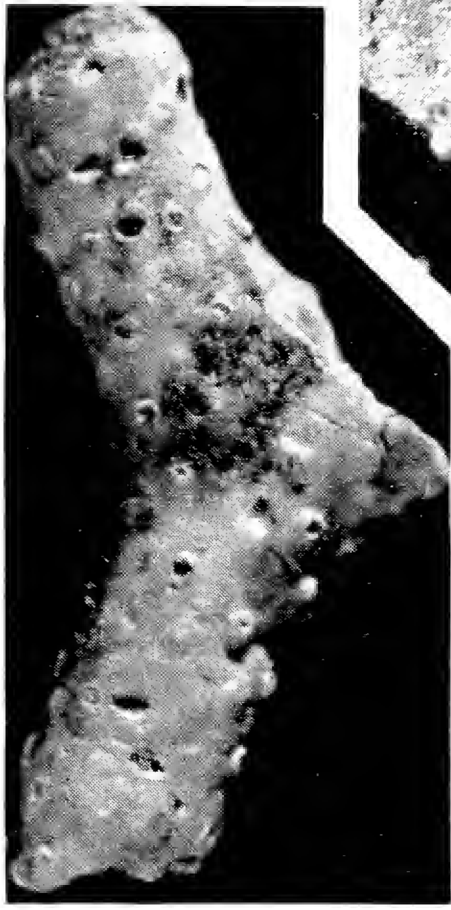
Fig. 3. — *Collapora straminea* (Phill.) 1829. Gonozooecium with one oeciostome. Middle Bajocian, zone of *Otoites sauzei* d'ORB., Galgenberg near Niederrimsingen W Freiburg i. Br., Germany. × 12.. Collection G. Illies N° K2.

Figs. 4-5. — *Collapora straminea* (Phill.) 1829. Type specimen of *Cricopora acutimargo* Waagen, 1867 (in BENECKE, 1868, I (III)), p. 641, pl. 33, fig. 7 a-b., Lower Bajocian, zone of *Sonninia sowerbyi* Mill., Gingen, Württemberg, Germany. Figs. 4, 5 each stem with one injured gonozooecium, about × 12. Bayer. Staatssammlung f. Paläontol. u. hist. Geol., München. N° AS XXII 26.

Fig. 6. — *Collapora straminea* (Phill.) 1829. Type specimen of *Pustulopora quenstedti* Waagen, 1867 (in BENECKE, 1868, I (III), p. 641, pl. 32, figs. 10 a-b., Lower Bajocian, zone of *Sonninia sowerbyi* Mill., Gingen, Württemberg, Germany, about × 12. Bayer. Staatssammlung f. Paläontol. u. hist. Geol., München. N° AS XXII 18.

5

6



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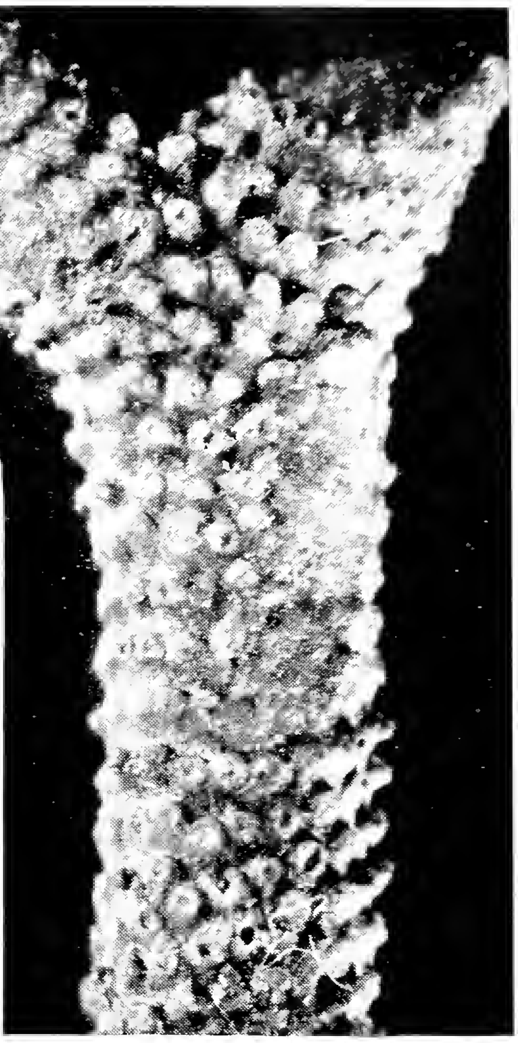

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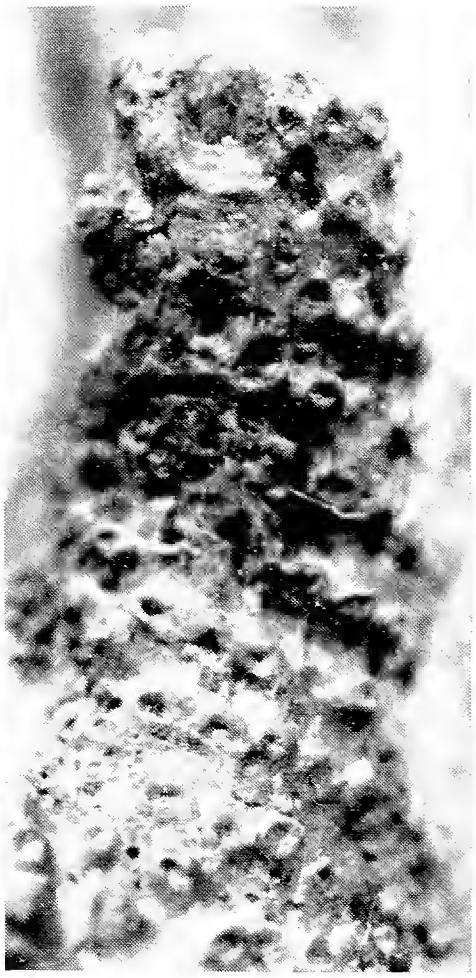

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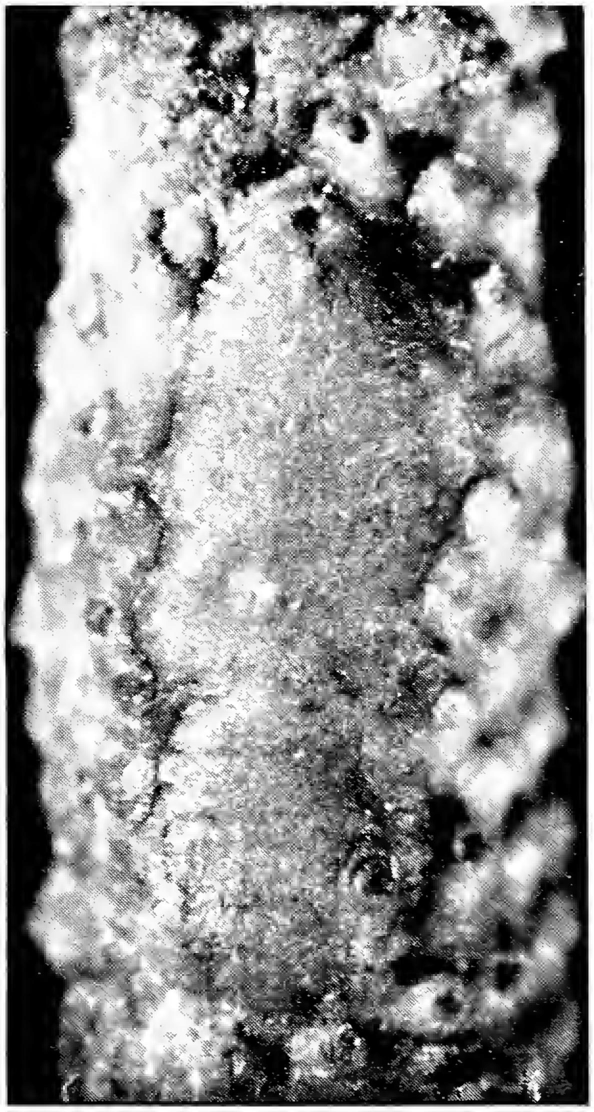

2

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
10. Group 2: Anatomy, Morphology and Skeletal Struct.

BRIGITTE SIMMA-KRIEG (*)

ON VARIATION AND SPECIAL REPRODUCTION HABITS OF *AETEA SICA* (Couch) (*BRYOZOA*)

(Preliminary Report) (**)

Riassunto. — L'A. ha presentato un rapporto preliminare del suo studio che è diviso in quattro parti: 1. habitus; 2. tipi di variazione; 3. modo di riproduzione; 4. conclusioni.

L'inusitata e grande capacità di variazione di *Aetea sica* (Couch) è stata divisa in quattro tipi, tre dei quali possono essere distinti l'uno dall'altro da speciali formazioni chiamate «sacculi» (prodotti della riproduzione asessuale).

Dopo aver riferito sulle possibili modificazioni di *Aetea sica*, l'A. affronta la questione della posizione degli *Inovicellata* nei *Gymnolaemata*.

Summary. — This study deals with four points. The habitus of *Aetea sica* (Couch), the types of variation, the reproduction habits, and a discussion of questions arising from these observations.

The habitus of *A. sica* was defined by the usual qualitative and quantitative criteria. Examination of numerous colonies showed that four types of variation occur.

Three of the types of zooidal varieties developed different asexual reproduction products, called *sacculi*, for the forms associated with zooidal types A and B, and apparently consisting of free autozooids for type C. The sacculi and the autozooids can be homologized, and their origin and development can be compared. The variation of the zooids appears to be related to the type of substratum.

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(**) The final paper will be published in: Cahiers de Biologie Marine.

Zusammenfassung. — Die vorliegende Arbeit behandelt vier Punkte. Den Habitus der *Aetea sica* (Couch), die Variationstypen, die Reproduktionsformen und eine Diskussion von Fragen, welche aus den vorangegangenen Beobachtungen resultieren.

Der Habitus der *Aetea sica* wurde durch die gebräuchlichen qualitativen und quantitativen Kriterien definiert. Eine Prüfung zahlreicher Kolonien zeigte, dass vier Variationstypen vorkommen.

Drei der vier Typen der zooidalen Varianten entwickelten verschiedene asexuelle Reproduktionsprodukte, welche für die Formen die mit den zooidalen Typen A und B korreliert sind, *Sacculi* genaannt werden und für den Typus C aus freien Autozooiden bestehen. Die Sacculi und die Autozoide des Typus C können homologisiert werden und ihr Ursprung und ihre Entwicklung kann verglichen werden. Die Variation der Zooide scheint mit dem Substratypus in Beziehung zu stehen.

The study presented deals with four points. I. The habitus, II. the types of variation, III. the reproduction habits of *Aetea sica* (Couch) and IV. a discussion.

As to I., the habitus of *Aetea sica* was defined by the so far usual criteria, which comprise qualitative and quantitative features. Concerning point II., it was found, after examination of numerous colonies of the species, that they show four types of variation, which coincide only partly with the known qualitative, but not with the quantitative features. Furthermore it was outlined that also within one colony, representing a special type, the rate of variation of the quantitative features was very high.

Point III. the reproduction habit, stated, that three of the four types of variation, develope different reproduction products, which can be homologized. For each of these formations, which were named « *sacculi* » for the type A and B and consist of an autozoid free, and not attached with its basal part, for type C, it was shown A. the habitus, B. the possible positions in relation to a colony and C. summarising, origin, development and maturity of a colony and its ways of reproduction by the sacculi A and B and the free autozooid, type C.

The hypothetical stages for the free type C correspond with veritable stages of the *sacculi* type A and B.

The discussion which follows as point IV., deals with, A. the assumption the sacculi constitute asexual reproduction products, B. the question after the species *Aetea sica* and possible site modifications as well a C. the position of the *Inovicellata* in the system of the *Gymnolaemata*.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
11. Group 2: Anatomy, Morphology and Skeletal Structure.

Olgerts L. Karklins (*)

ZOOECIAL BOUNDARY PATTERNS IN THE MIDDLE ORDOVICIAN GENERA OF THE FAMILIES *RHINIDICTYIDAE*, *STICTOPORELLIDAE* AND *PTILODICTYIDAE*

(*Bryozoa*)

Riassunto. — Un nuovo metodo viene usato nell' interpretazione delle strutture zoariali dei *Cryptostomata.* Esso mette in risalto le scure zone confinarie e la loro sistemazione in *Stictopora* Hall e in alcune specie di *Stictoporella* Ulrich e di *Pachydictya* Ulrich. *Stictopora* è caratterizzato dall'avere gli zoaria a disposizione lineare in cui gli zooecia adiacenti sono separati per mezzo di « range boundaries » lateralmente e per mezzo di « zooecial boundaries » longitudinalmente.

In *Stictoporella angularis* Ulrich gli « zooecial boundaries » sono poligonali in sezione tangenziale; gli zooecia non sono in file distinte e i « range boundaries » mancano. In *Pachydictya foliata* Ulrich gli « zooecial boundaries » descrivono una forma cilindrica nell'esozona e sono approssimativamente ovali in sezione tangenziale. Le pareti tra gli zooecia adiacenti nell'esozona contengono numerose zone scure, ma non vi sono « range boundaries ». *Pachydictya acuta* (Hall) è caratterizzata dall'avere « range partitions » nell'esozona che si estendono per tutto lo zoarium tra zooecia allineati longitudinalmente e sono quasi ad angolo retto con la superficie zoariale. Gli « zooecial boundaries » sono come quelli di *P. foliata* ma i « range boundaries », simili a quelli di *Stictopora*, sono sistemati lungo la mezzeria delle « range partitions ». La mancanza di « boundary pattern » nell'esozona è caratteristica in *Escharopora* Hall e *Graptodictya* Ulrich, che mostrano differenze nella configurazione delle laminae parietali zoeciali. (Translation into Italian from the Author's English summary by. E. Annoscia. Since the terms « zooecial boundary », « range boundary », and so on are new and have not yet equivalent terms in Italian, the translator preferred to use the original English terms in inverted commas).

(*) Publication authorized by the Director, U. S. Geological Survey - Washington D. C., USA.

Summary. A new approach is used in the interpretation of cryptostome zoarial structures that emphasizes the dark boundary zones and their spatial arrangement in *Stictopora* Hall and in some species of *Stictoporella* Ulrich and *Pachydictya* Ulrich. *Stictopora* is characterized by having zoaria with approximately linear ranges in which adjacent zooecia are separated by « range boundaries » laterally and by « zooecial boundaries » longitudinally. In *Stictoporella angularis* Ulrich the « zooecial boundaries » are polygonal in tangential views; zooecia are not in distinct alignment and the range boundaries are lacking. In *Pachydictya foliata* Ulrich the « zooecial boundaries » describe a cylindrical form in the exozone and are approximately oval in tangential views. The walls between adjacent zooecia in the exozone may contain numerous dark zones, but there are no « range boundaries ». *Pachydictya acuta* (Hall) is characterized by having « range partitions » in the exozone that extend throughout zoaria between longitudinally aligned zooecia and are about at right angle to zoarial surface. The « zooecial boundaries » are like those in *P. foliata* but the « range boundaries », similar to those in *Stictopora*, are located along the middle of the « range partitions ». Lack of « boundary pattern » in the exozone is distinctive in *Escharopora* Hall and *Graptodictya* Ulrich which show differences in the configuration of the zooecial wall laminae.

Zusammenfassung. — Ein neuer Einstellungsversuch ist angewendet für die Darstellung der allgemeinen Zoariumstrukturen der cryptostome Bryozoen. Diese Darstellung hebt die dunklen Grenzen und ihre räumliche Anordnung innerhalb der Gattung *Stictopora* Hall und bei manchen Arten der Gattung *Stictoporella* Ulrich und *Pachydictya* Ulrich hervor. Die Zooecien stehen bei *Stictopora* ungefähr in regelmässigen Längsreihen. Diese Zooecien sind seitlich durch die Grenzen der Längsreihen und der Länge nach durch die Grenzen der Zooecien abgetrennt. Bei *Stictoporella angularis* Ulrich sind die Grenzen der Zooecien vieleckig; die Zooecien befinden sich nicht in regelmässigen Reihen und es fehlen die Grenzen der Längsreihen. Bei *Pachydictya foliata* Ulrich werden die Grenzen der Zooecien in der verdickten Skeletzone röhrenförmig und ungefähr oval innerhalb des Tangentialschnittes. Die Wände zwischen den Zooecien in der verdickten Skeletzone können gelegentlich zahlreiche dunkle, unregelmässige, kurze grenzartige Züge erhalten, aber es fehlen die Grenzen der Längsreihen. Bei *Pachydictya acuta* (Hall) sind die Längsreihen der Zooecien in der verdickten Skeletzone des Zoarium durch Scheidewände abgetrennt. Diese Scheidewände erstrecken sich durch die Zoarien und sind ungefähr rechtwinklig zu dessen Oberfläche orientiert. Die Grenzen der Zooecien sind dieselben wie in *Pachydictya foliata*, und die Grenzen der Längsreihen sind ähnlich wie bei *Stictopora*, aber sie befinden sich in der Mitte, entlang der Scheidewand. Bei den Gattungen *Escharopora* Hall und *Graptodictya* Ulrich fehlt ein deutliches Muster der Grenzen in der verdickten Skeletzone. Diese Gattungen unterscheiden sich hinsichtlich der Gestaltung der Zooeciumlaminae in der verdickten Skeletzone.

A study of the Middle Ordovician genera of the families *Rhinidictyidae* Ulrich 1895, *Stictoporellidae* Nickles and Bassler 1900, and *Ptilodictyidae* Zittel 1880 indicates that there are several problems in the interpretation of the zoarial and zooecial wall structures. In order to solve these problems a new approach is used in which I have emphasized dark boundary zones and their spatial arrangement in zoaria as distinct morphological features in *Stictopora* Hall 1847, and in some species of *Pachydictya* Ulrich 1882 and *Stictoporella* Ulrich 1882 or lack of them in *Escharopora* Hall 1847, and *Graptodictya* Ulrich 1882.

The dark boundary zones are formed by abutting or adjoining zooecial laminae and, when present, they outline zooecia or other structural elements in zoaria. In thin sections the boundaries appear as dark lines representing the edge views of planar to curved boundary zones between zooecia that extend for different lengths throughout zoaria. These dark boundaries, when viewed in three dimensions, separate the laminate zoaria into well-defined segments. Some of the boundaries are associated with the individual zooecia but the others are zoarial features. These two kinds of boundaries taken together indicate a pattern of zoarial secretion which appears common to more than one genus in a family. Therefore I found that the boundary zones are useful in describing and regrouping the different genera.

Four distinct zooecial boundary patterns and two different configurations of laminae in the zooecial walls are described briefly. These structural features in zoaria together with other morphological features not discussed here are useful in grouping of genera and may result in revision of the concepts on which the definitions of the cryptostome families are based. The diverse boundary patterns appear to show evolutionary trends, for example in *Pachydictya*, and thus have a potential value in stratigraphic work.

In *Stictopora*, for example, *S. nicholsoni* (Ulrich) 1882 from the Tyrone Limestone, Kentucky, and *S. mutabilis* Ulrich 1886 from the Decorah Shale, Minnesota, U.S.A., and in related genera having zoaria with approximately linear zooecial ranges, the zoarial structure is characterized by two boundary zones. Both boundaries are similar in structure and begin at the mesotheca, but they differ in their relationships to the zooecia of a zoarium.

One of these boundaries is located between the longitudinally adjacent zooecia and it is here named the « zooecial boundary ». The other boundary separates the laterally adjacent zooecia and is continuous throughout the entire length of a zoarial branch. This boundary demarcates the zooecial ranges and therefore it is here named the « range boundary ». Both boundaries commonly carry short, rodlike structures which begin in the inner exozone. These structures are here described as the mural tubuli (oral communication, R. S. Boardman, 1966). The two sets of the boundaries form a distinct pattern that characterizes *Stictopora, Phyllodictya* Ulrich 1882, *Ptilotrypa* Ulrich 1890, and probably *Eurydictya* Ulrich 1890 and *Dicranopora* Ulrich 1882.

Another pattern of zooecial boundaries is shown in several *Stictoporella* species such as *S. angularis* Ulrich 1886 from the Decorah Shale, Minnesota, and *S. frondifera* Ulrich 1886 from the Decorah Shale, Minnesota, Iowa, and Wisconsin, U. S. A. In these species the dark zooecial boundaries are polygonal in tangental view and are readily discernible in longitudinal and transverse views showing the walls in the exozone.

In comparing the boundary zone pattern in *Stictoporella angularis* and in other related species with that in *Stictopora,* the following differences are noted. In *Stictoporella angularis* the zooecia are not aligned in distinct ranges as are those in *Stictopora* species. Consequently, there are no range boundaries in *S. angularis.* The zooecial boundaries divide the walls between adjacent cavities into two parts that are approximately equal in *Stictoporella angularis,* but not in *Stictopora* in which the zooecial boundaries are within the upper part of the walls between the longitudinally adjacent zooecia. Thus each zooid secretes on each side of itself about an equal quantity of calcite in *Stictoporella angularis.* In *Stictopora,* however, a larger amount of calcite is secreted distally and laterally than proximally. Furthermore, the zooecial boundaries appear to be approximately hexagonal or polygonal in *Stictoporella angularis* whereas in *Stictopora* the zooecial boundaries are crescent shaped, convex proximally. There are no mural tubuli in zooecial boundaries of *Stictoporella angularis* and the lack of the range boundaries was already noted. The species of these genera differ also in the general appearance of the zooecial wall laminae; in *Stictopora* the laminae are poorly defined whereas in *Stictoporella* they are distinct.

The zoaria of species discussed above show well-developed boundary zones separating the laminate structural segments. For purposes of comparison it might be appropriate to note here that in another large group of the cryptostome bifoliates the zooecial walls between adjacent cavities are constructed by apparently continuous and well-defined laminae. However, the boundary zones in the exozone zooecial walls have not been observed in this group of genera. In general, the pattern of the wall laminae and the lack of the boundaries seems to distinguish the genera of this broad group. The configuration of the wall laminae in section is generally sinuous. In *Escharopora subrecta* (Ulrich) 1886 from the Decorah Shale, Minnesota, U.S.A., the laminae of the walls are approximately M-shaped with broad crests as observed in transverse views. In *Graptodictya simplex* (Ulrich) 1886, also from the Decorah Shale in Minnesota, the curves of the laminae are more V-shaped and commonly form three pointed crests between adjacent cavities. On the zoarial surface these crests may appear as slightly raised flexuous ridges. The wall structures in *Escharopora* and *Graptodictya* have been redescribed by Ross (PHILLIPS, 1960, p. 17, 19; ROSS, 1960, p. 859; 1964, p. 941) in greater detail.

Several zooecial boundary patterns are observed among the many species that are currently assigned to *Pachydictya* Ulrich 1882. Two of these boundary patterns, both of which differ from that shown in the type of the genus, *Pachydictya robusta* Ulrich 1882 (PHILLIPS, 1960, p. 14) from the Middle Ordovician strata of Tennessee, U.S.A., are briefly discussed below.

In *Pachydictya foliata* Ulrich 1886, from the Decorah Shale of Minnesota, U.S.A., the zooecial boundaries are constructed similarly to those in *Stictopora* and *Stictoporella angularis,* but the zoarial arrangement is fundamentally different. Unlike *Stictopora,* the zooecial boundaries in *P. foliata* describe a cylindrical form in exozone and appear approximately oval in tangential view; they enclose the zooecial cavities and a part of the adjoining wall. There are no range boundaries in *P. foliata,* because the zooecia are not aligned in distinct ranges. The zooecial boundaries begin at the mesotheca and are characteristically indistinct in the endozone. At the base of the exozone the proximal segments of the boundaries curve and together with the distal part of the same boundary form a cylinder in the exozone. The part of the zooecial wall between the cavity and the boundary consists of indistinct, gently curving laminae. At the zooecial boundary these laminae abut or adjoin with those that form the part of the walls between the boundaries. The latter cannot be associated with any individual zooecium but appear to be secreted by the adjacent zooids of a zoarium. The laminae in the common tissue are broadly curved and are convex to the zoarial surface. The laminae between the boundaries contain dark, thin, intermittent zones that are approximately perpendicular to the zoarial surface and that trend in the general direction of the zoarial growth. Because of this trend the zones are most observable in the transverse views in which the plane of the thin section cut is approximately at right angles to them. The same zones generally are not observable in the longitudinal views because in these views the plane of the thin section is commonly parallel or slightly oblique to the zones but not in their plane. However, the zooecial boundaries are always visible in longitudinal views because of their cylindrical form, but they must not be confused with the intermittent dark zones in the same view. In the areas of maculae or monticules the dark zones are especially abundant.

Another zooecial boundary pattern is seen in *Pachydictya acuta* (Hall) 1847, *P. fimbriata* Ulrich 1895, *P. elegans* Ulrich 1895, all from the Decorah Shale, Minnesota, U.S.A., in *P. ambigua* Ross 1961 from the Ellis Bay Formation, Anticosti Island, Canada, and in related *Pachydictya* species from the Middle and Upper Ordovician strata of the U.S.A. The boundary zones in *Pachydictya acuta* are similar in construction to those in *P. foliata,* but the zoarial arrangement is modified.

The zooecial boundary encloses the zooecial cavity with the adjacent part of the zooecial wall like that in *Pachydictya foliata.* Unlike *P. foliata,* the zooecia are aligned in approximate ranges in the direction of the zoarial growth. These zooecial ranges are demarcated by range boundaries as in *Stictopora.* However, unlike *Stictopora,* the range boundaries are not shared in the exozone by the laterally adjacent zooecia but are formed along the middle of a wedge-shaped feature. This wedge-shaped feature is secreted in the exozone between the linear zooecial ranges, and it is here named the range partition.

The range partition begins at the base of the exozone and forms skeletal mass between the zooecial ranges. Externally this partition may appear as a slightly elevated and flexuous ridge. The range partition is demarcated on both sides by dark boundaries that appear as lines in transverse and tangential view. Along these boundaries the laminae of the range partition and those of zooecial walls adjoin or abut so that the apexes of these adjoining laminae point toward the endozone.

The structural relationships between the range partitions and the zooecial walls are seen best in the transverse thin sections. In these views of the exozone, five dark and distinct boundaries can be discerned. These are the edge views of the boundaries which are cut perpendicular to the thin section. These boundaries outline the zooecia, their ranges and the range partitions. The same boundaries can be recognized in tangential views if the transverse view is kept in mind. In longitudinal section the boundaries of the range partitions are not visible because in these views the plane of the thin section is approximately parallel to the boundaries. However, in an oblique cut they might be visible. The zooecial boundaries are observable in all three views because they have the cylindrical form in the exozone. Not uncommonly the boundaries are obscured by impurities in or between the lamine or by mural tubuli. However, by keeping in mind the three dimensional aspect of the boundaries these morphological features can be readily distinguished.

The boundary patterns in *Pachydictya foliata* and *P. acuta* are the only two of this genus which I have discussed in some detail. Further studies indicate that there are at least three other distinct patterns. These patterns can be observed in *P. robusta* from Tennessee, *P. bromidensis* Loeblich 1942 from the Bromide Formation, Oklahoma, and in *P. splendens* Ulrich 1890 from the Upper Ordovician of Illinois, U.S.A.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
12. Group 2: Anatomy, Morphology and Skeletal Structure.

RONALD TAVENER-SMITH (*)

SKELETAL STRUCTURE AND GROWTH IN THE *FENESTELLIDAE* (*BRYOZOA*)

(Preliminary Report) (**)

Riassunto. — Le pareti della branche dei Briozoi *Fenestellidae* hanno un piano di costruzione a tre foglietti: uno strato granulare mediano, fiancheggiato da tessuto laminato, sottile all' interno e denso all'esterno. Lo scheletro granulare si formava durante un unico continuo periodo di deposizione, mentre il tessuto laminato risultava da accrescimenti regolari successivi.

Bastoncini scheletrici si originavano dallo strato granulare e si irradiavano attraverso lo scheletro laminato. Questi bastoncini sono strutture solide e non c'è nessun indizio che siano state mai perforate.

Lo strato granulare si formava prima del tessuto laminato che lo fiancheggiava ed è quindi giustificabile l'uso dei termini « formazione primaria » e « formazione secondaria ». La zona di formazione primaria (granulare) e quella esterna di formazione secondaria erano secrete da un mantello esterno o coloniale, mentre il tessuto interno di formazione secondaria veniva deposto dall'ectoderma zooidale. E' quindi evidente che i *Fenestellidae* avevano una struttura parietale composta di due elementi, paragonabile a quella dei *Cyclostomata Horneridae* (BORG, 1926). Il mantello esterno era probabilmente originato come un'estroflessione ectodermale della regione vestibolare dell'ancestrula. Questo mantello era associato strettamente con lo sviluppo di tutte le strutture coloniali e formava un involucro completo esterno, perforato soltanto dalle aperture zoeciali. L'epithelium interno del mantello secerneva la maggior parte dello scheletro coloniale e, come nei Brachiopodi (WILLIAMS, 1968), è dimostrato che questo secerneva diversi prodotti nelle diverse fasi della crescita.

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(**) The talk on this subject to be given at the Milan Conference is based on a paper shortly to appear in « Palaeontology ». The following is a summary of the main points dealt with in that paper, and readers are referred to it for a fuller explanation and for illustrations.

La sistemazione delle pareti in nodi carenali, dissepimenti ed escrescenze spinose, è simile a quella delle branche, a parte il fatto che non c'è lo strato secondario interno. Queste strutture non avevano nessuna comunicazione interna con le cavità zoeciali e venivano deposte interamente dall'epithelium interno del mantello. Sostegni coloniali massicci, come quelli di *Lyropora* e di *Archimedes*, consistono interamente di tessuto secondario formato da una secrezione massiccia localizzata proveniente dal mantello esterno. La deposizione di calcite di questo tipo contribuiva efficacemente alla riparazione dei danni alla struttura retiforme.

Summary. — Branch walls of fenestellid bryozoans have a three-fold construction: a middle, granular layer, flanked by inner (thin) and outer (thick) laminated tissue. The granular skeleton was formed by a single, continuous depositional episode, while laminated tissue resulted from regular incremental additions. Skeletal rods originate from the granular layer and radiate through the laminated skeleton. These are solid structures, and there is no evidence that they were ever perforate.

The granular layer pre-dates the laminated tissue flanking it, and use of the terms *primary* and *secondary* is therefore justifiable. The primary (granular) and outer secondary (laminated) zones were secreted by an external (or colonial) mantle, while the inner secondary tissue was laid down by the zooidal ectoderm. It is therefore evident that fenestellid bryozoans had a « double » wall structure comparable to that in hornerid cyclostomes (Borg, 1926). The external mantle probably originated as an ectodermal evagination from the vestibular region of the ancestrula. It was closely associated with the growth of all colonial structures, and formed a complete external envelope pierced only by zooecial apertures. The inner mantle epithelium laid down most of the colonial skeleton and, as in brachiopods (Williams, 1968) there is evidence that this secreted different products at different stages of growth.

The wall arrangement in carinal nodes, dissepiments and spiny outgrowths is similar to that of branches, but the inner secondary layer is absent. These structures had no internal communication with zooecial chambers, and were laid down entirely by the inner mantle epithelium. Massive colonial supports, such as those of *Lyropora* and *Archimedes*, consist entirely of secondary tissue formed by massive, localised secretion from the external mantle. The formation of calcite deposits of this kind also played an effective part in the repair of structural damage to the meshwork.

1. Skeletal morphology.

Branch walls in fenestellid bryozoans are of three-fold construction: a middle granular layer is flanked by inner (thin) and outer (thick) laminated tissue. The middle layer has always been considered the fundamental wall component: it is invariably present as a continuous investment around zooecial chambers and extends above them as the core of the carina. Electron micrographs show that it has a distinctive granular texture without trace of lamination.

The outer laminated zone is generally well developed, especially on the reverse of branches. Each lamina is a sheet-like mosaic of calcite plates, and adjacent laminae are clearly defined. Laminae of this kind are known to form by incremental growth, and WILLIAMS (1968) suggested that in brachiopods a diurnal periodicity may be represented. If successive laminae were formed during equal time intervals, then width variations between them show that the rate of calcite secretion through time was not constant. Neither was it always constant from place to place even within the same time interval, for some laminae thicken locally into lenses. In these the platy structure of the mosaic is replaced by a granular one similar to that of the middle wall layer. If the presence of laminae is due to the addition of skeletal layers by increment, it is logical to suppose that their absence (i. e. granular texture) indicates continuous deposition. Also, the granular material appears to have formed at a relatively accelerated rate, as shown by lenses in the outer laminated skeleton. In spite of their distinctive textures, the granular and outer laminated wall zones show a perfect gradational contact, which must represent a transition from one mode of deposition to the other.

The inner wall element, lining zooecial chambers, is of similar appearance and structure to the outer laminated zone, though notably thinner. Development appears to have been checked when the chamber lining had achieved a certain thickness. The presence of this layer in chambers close to « young » branch tips shows that it is a true wall component and not merely a late-stage accretion characterising senility. The contact between inner laminated and granular wall zones is non-gradational.

The outer (but not the inner) laminated skeleton incorporates rod-like elements radiating from the granular layer. These are best seen in transverse sections of branches, but are also present in dissepiments and carinal nodes. Skeletal rods form minute prominences at the surface, and these are commonly arranged in rows along the crests of ridges (or « striae ») on the reverse side. Electron micrographs and other evidence show that the skeletal rods were always solid structures, contrary to the supposition of earlier authors. It is also certain that they are integral parts of the fenestellid skeleton, and not of algal origin as ELIAS & CONDRA (1957) suggested. The rods consist of granular skeletal tissue and must have resulted from continuing growth at an infinity of points on the outer surface of the granular layer. Their purpose is not obvious, but it may be significant that they are identical in structure and situation with the taleolae of strophomenide brachiopods (WILLIAMS 1968).

2. Reconstruction of secretory tissues.

Calcareous skeletal tissues are secreted by epithelial layers, and a hypothetical reconstruction of these facilitates understanding of the way in which colonies functioned and grew.

The gradational contact between the two outer wall zones of a fenestellid branch, their relative positions, and the fact that the skeletal rods grew outward from the granular layer through the laminated tissue *as this formed,* indicate the earlier age of the former. The structure of inter-zooecial walls shows equally clearly that the granular layer pre-dated the inner laminated chamber lining. Therefore the granular tissue was first formed (primary), and the inner and outer laminated skeleton was subsequently added (secondary). The presence of secondary tissue on either side of the granular layer indicates secretion from two epithelial layers: the inner being the zooidal ectoderm and the outer an external mantle which must have enveloped the entire colony. Other lines of evidence also point to the existence of an external mantle: laminae of the outer secondary skeleton must have been added from the exterior during growth; the sealing of zooecial apertures in the proximal parts of old colonies and formation of massive colonial holdfasts can only have been effected from the exterior. Also, the skeletal structure of carinal nodes and dissepiments can only be reasonably interpreted in terms of calcite deposition from an external membrane. Such an arrangement has already been reported (BORG, 1926) in the

Horneridae, and the writer has verified this and noted many similarities in the skeletal structure of hornerid and fenestellid colonies. As in *Hornera*, the fenestellid external mantle probably incorporated two secretory epithelia separated by a slit-like cavity (the « hypostegal coelom » of Borg). The outer mantle epithelium secreted an external periostracum, the inner one was the main calcite-secreting surface of the colony. The hypostegal coelomic space communicated with the body cavities of zooids beneath each zooidal aperture. Skeletal rods, supposed by SHULGA-NESTERENKO (1941) to be tubular ducts, possibly provided at their outer extremities (pustules) attachments for tendons maintaining the outer mantle epithelium in position.

Three epithelia therefore contributed to skeletal formation. The first was the zooidal ectoderm, which secreted the inner laminated wall. The second and third epithelia bounded the external mantle, a membraneous investment of the whole colony. The second (or inner mantle) epithelium secreted the primary, and later the outer secondary tissue and was therefore responsible for the major part of the colonial skeleton. The third (or outer mantle) epithelium produced an external cuticle only.

It is now known that before the commencement of calcareous deposition epithelia produce a proteinous layer upon which subsequent crystal seeding takes place. Where two secretory epithelia are in juxtaposition it is therefore expected that they will be separated by a cuticular layer, possibly doubled. This must have been the case in the fenestellid skeleton between the first and second epithelia, before formation of the calcareous wall commenced. It probably accounts for the non-gradational contact between the inner secondary and primary skeletal zones.

3. Skeletal formation and growth.

For a hypothetical growth pattern to be acceptable, it must be possible to trace the secretory tissues from their earliest appearance in the ancestrula. Derivation of the innermost (zooidal) epithelium is not in doubt, for it must have been a direct extension by budding from the ancestrular ectoderm. The origin of the external mantle is more obscure: it probably arose as a peripheral evagination of ectodermal epithelium from the vestibular region of the ancestrula. The « flap » so formed consisted of a doubled epithelial layer (second and third epithelia) with a slot-like extension of the body cavity between. It covered the ancestrular surface and extended into the adjacent substrate. As development proceeded the external mantle extended to form a continuous colonial investment pierced only by zooecial apertures.

In fenestellid colonies, as in modern fenestrate bryozoa, growth was mainly from the tips of branches, and in that situation the proliferation of epithelial cells and initial formation of cuticle took place. It is probable that the outer cover of zooidal buds at the branch tip was of cuticle, and that rigid calcareous walls only formed after the attainment of adult size and shape. At that stage a change of physiological activity in the second (inner mantle) epithelium led to the deposition beneath the cuticle of granular calcite. This primary wall was laid down in a clearly defined zone close behind the tip of a growing branch. As forward growth preceeded a further modification affected the same epithelial layer, and the deposition of calcite particles, previously continuous, became intermittent and particle shape changed from granular to platy. As a result, the transition from primary to outer (laminated) secondary skeleton took place. It seems that, by physiological adaptation, a single epithelial layer secreted different products at successive growth stages. A similar « conveyor belt » arrangement has been noted by WILLIAMS (1968) in the Brachiopoda.

4. Formation of other skeletal elements.

Dissepiments and carinal nodes show basically the same construction. Each has a primary core of granular tissue enveloped in laminated outer secondary material. The latter is penetrated by a system of skeletal rods radiating from the granular core and giving (in conjunction with the laminae) a « spiders web » pattern in transverse section. The inner secondary skeletal layer is not present in these structures, nor is there an axial canal to suggest the former presence of internal protoplasmic substance, or communication with zooecial chambers. However, an axial trail of dark granules (traceable to the junction between zooecial lining and primary skeleton in the adjacent branch) may record the earlier existence of a cuticular strand on which primary skeletal deposition took place.

Dissepiments were formed by the union of paired outgrowths from adjacent branches. It is probable that dissepimental buds were initiated at the growing tips of branches, for they were already developing vigorously while neighbouring zooidal walls were still in the cuticular stage: zooecia at the bases of dissepiments are commonly distorted in a way that would have been possible only if their walls were flexible.

Carinal nodes rise from the keel at more or less regular intervals. Their structure shows no indication of the former presence of internal soft parts, or of communication with zooecial chambers. There is no evidence that the nodes housed acanthopores, though there seems little doubt that they served a protective purpose. In some genera (e. g. *Hemitrypa*) the distal ends of carinal nodes branch, and the branches unite into a geometrically patterned superstructure screening zooecial apertures. The superstructure bars are of identical construction to carinal nodes and, like them, were undoubtedly secreted by an enveloping membrane.

Proximal parts of old colonies are commonly thickened and show an encrusting calcareous holdfast which attached the colony to its substrate. Formation of the holdfast was initiated by the secretion of primary tissue from the lower mantle surface where this extended over the substratum. Secondary tissue was subsequently added, resulting in a laminated texture and the attainment of massive proportions.

Colonial meshwork supports in such genera as *Lyropora*, *Anastomopora* and *Archimedes* resulted from sustained localised deposition of secondary calcareous substance from the inner mantle epithelium. In the first two genera the secretion of excessive laminated tissue on branches at the margins of a *Fenestella*-like meshwork caused the sealing of zooecial apertures, plugging of fenestrules and expansion of branches until these fused to form the V-shaped colonial support. In *Archimedes* a spiral mesh of the same basic type is supported by an axial screw of laminated secondary tissue. The colonial meshwork is continuous through the screw, and although the primary skeleton of branches shows no change, the laminated outer tissue thickens progressively towards the axis, with which it finally merges.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
13. Group 2: Anatomy, Morphology and Skeletal Structure.

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THE BODY WALL OF THE ENCRUSTING CHEILOSTOME *WATERSIPORA NIGRA* (Canu and Bassler)

(*Bryozoa*)

(Preliminary Report)

Riassunto. — Le sezioni con epon e metacrilato di *Watersipora nigra* e altri *Cheilostomata* incrostanti rivelano che:

1. - la calcificazione è inizialmente intracuticolare;
2. - le pareti laterali e gli organi di comunicazione sono più complessi di quanto non si conoscesse;
3. - gli organi laterali di comunicazione sono gemme di zooidi abortiti;
4. - la parete frontale è criptocistale.

Vengono poi discussi gli altri aspetti della morfologia e dell'evoluzione della cistide.

Summary. — Epon and methacrylate sections of *Watersipora nigra* and other encrusting cheilostomes reveal: (1) calcification is initially intracuticular; (2) lateral walls and communication organs are more complex than previously reported; (3) lateral communication organs represent aborted zooid buds; (4) the frontal wall is cryptocystal. Other aspects of the morphology and evolution on the body wall are discussed.

Resumen. — Las secciones de epon y methacrylate de *Watersipora nigra* y de otro *Cheilostomata* incrustante demuestran: (1) que al principio la calcificación es intracuticular; (2) que las paredes laterales y los órganos de comunicación son más complejos que los reportados anteriormente; (3) que los órganos de comunicación laterales son brotes de zoides abortados; (4) que la pared frontal es un cryptocysto. Otros aspectos de la morfología y evolución del cistidio son discutidos.

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This is a preliminary report of research in progress at the Allan Hancock Foundation, University of Southern California, Los Angeles. When completed, the results will comprise a dissertation, to be presented to the graduate faculty of the University of Southern California in partial fulfillment of the degree of Doctor of Philosophy. Most of the work has been prepared for publication as a series entitled « The body wall of cheilostome Bryozoa » (BANTA, in press).

Results are based primarily on gluteraldehyde-osmium fixed material embedded in epon or methacrylate and sectioned at one-half micron for viewing with the light microscope. Approximately twenty species have been examined in detail; I have especially emphasized *Watersipora nigra* (Canu and Bassler). The following is a list of the more important results.

1) SILÉN (1944: 436) was justified in distinguishing two categories of walls in cheilostome Bryozoa, « external walls » and « internal walls », but they must be redefined as follows: an external wall is a reinforced portion of the « ectocyst », an acellular secretion of epidermal cells produced by intussusceptive expansion of the cuticle of the ancestrula. An internal wall is a ledge-like partition which grows by apposition from the inner face of an external wall.

2) In *Watersipora*, external walls generally consist of the following: (a) an outer « cuticle », (b) a layer of calcium carbonate deposited on an organic matrix containing acid mucopolysaccharide, and (c) a previously undescribed structure, the « skeletal membrane », which develops as a differentiation of the organic matrix of the skeleton.

3) Lateral walls are external; they consist of the following: (a) a central cuticular layer, the «intercalary cuticle». This layer is continuous with frontal and basal cuticles and represents an invaginated portion of the ectocyst. (b) A pair of calcareous laminae, and (c) a pair of skeletal membranes. A distal (transverse) wall is an unpaired calcareous lamina surrounded by a pair of skeletal membranes, sometimes absent. This arrangement accounts for the observations of LEVINSEN (1909: 26) and SILÉN (1944: 435) that incinerated or KOCl-treated cheilostomes often tend to break up into longitudinal rows of zoecia. Failure to do so is sometimes due to calcification of the intercalary cuticle.

4) Matrices of wall layers overlap. Their relations with one another, particularly near an uncalcified window in the basal wall, indicate that calcium carbonate is an intracuticular deposit.

5) The annulus (pore ring) of a lateral communication organ is not continuous with a calcareous wall, but is actually a thickening of edge of a ruptured portion of the intercalary cuticle.

6) Rosette cells of both lateral and transverse communication organs possess a morphological polarity similar to that observed by BOBIN (1958) in *Bowerbankia* and other ctenostomes. « Special cells » plugging communication pores are borne on the side of the septula facing the more proximal of the two zooids sharing it. Polarity of lateral communication organs is also manifested by the position of the annulus.

7) Each communication pore is surrounded by a gasket-like ring of PAS-positive material with a central hole through which special cells protrude. This ring, the « pore cincture » may represent an intracellular accumulation within epidermal cells.

8) In some species of *Membranipora*, the annulus and pore plate of young specimens are modifications of the lateral wall, which is initially one-layered. Older, more heavily calcified specimens of the same species have a structure more comparable to that described for *Watersipora nigra*. This observation supports the theory that calcification is intracuticular and that many differences between species in the structure of septulae can be attributed to differences in the degree of calcification.

9) In the species studied by me, development of lateral septulae differs from the descriptions of SILÉN (1944: 456) and LUTAUD (1961: 211). Most important, the lateral wall of the septular area remains uncalcified until formation of the pore plate. The lateral wall is represented at this time by an unpaired, uncalcified ectocystal layer continuous with the intercalary cuticle. The ectocyst ruptures after the pore plate is established.

10) These findings are consistent with the view of SILÉN (1944: 475) that lateral septulae represent aborted zooid buds and that pore plates are homologous to transverse walls.

11) In some cheilostomes, lateral and transverse septulae play an important part in «reparative budding», a regeneration-like phenomenon described here for the first time. Reparative

buds are produced by zooids bordering dead regions of the colony. These buds, which may coalesce with similar buds from other zooids, produce new zooids within old zooecia. Since a complete new ectocyst is produced, this process may account for the so-called « regeneration » of whole zooids described by LEVINSEN (1907) and others.

12) The frontal wall of *Watersipora nigra* is an internal wall, which develops (by apposition) underneath the frontal ectocyst. The ascus develops as an invagination of the ectocyst proximal to the operculum. Parietal muscles differentiate and attach to the ascus in serial sequence from the distal to the proximal end.

13) The frontal wall is pierced by four multiporous pore plates, provided with special cells and pore cinctures.

14) In *Watersipora* the lining of the hypostega consists of a single layer of cells. It is probable, however, that the peritoneal lining has been secondarily lost and that the hypostega is a compartment of the coelom.

15) It is concluded that the frontal wall of *Watersipora* is a cryptocyst and that the affinities of the genus are with the *Cryptocystidea,* probably the *Coilostega.*

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
14. Group 2: Anatomy, Morphology and Skeletal Structure.

GILBERT P. LARWOOD (*)

FRONTAL WALL STRUCTURES OF CRETACEOUS AND RECENT *CRIBRIMORPHA* AND OTHER CHEILOSTOME *BRYOZOA*

(Preliminary Report)

Riassunto. — Le strutture delle pareti frontali di alcuni Briozoi *Cribrimorpha* cretacici sono comparate con quelle dei generi *Membraniporella* e *Cribrilaria* (*Cribrimorpha* recenti). Sono state prese in considerazione anche le strutture frontali dei generi *Hiantopora, Petalostegus* e *Canda.*

Summary. — The structures of the frontal walls of some Cretaceous cribrimorph bryozoans are compared with those of the Recent cribrimorph genera *Membraniporella* and *Cribrilaria.* The frontal structures of *Hiantopora, Petalostegus* and *Canda* are also considered.

Résumé. Les structures frontales de quelques bryozoaires cribrimorphes du Crétacé sont comparés avec ceux des genres cribrimorphes actuels *Membraniporella* et *Cribrilaria.* Les structures frontales des genres *Hiantopora, Petalostegus* et *Canda* sent aussi examineées.

In their evolution from membranimorph precursors in the early Cenomanian the cribrimorph Bryozoa evolved a number of distinctive structural patterns in the frontal wall. The frontal walls of Recent Cribrimorpha resemble those of many less heavily calcified Cretaceous forms. Both the less marked frontal calcification of some Recent non-cribrimorph cheilostomes and the ex-

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tensive tertiary frontal wall calcification of some later Cretaceous cribrimorphs may be interpreted as features relating to the whole zoarium.

Early Upper Cretaceous cheilostome bryozoans include genera with marginal spines which arched over the chitinous frontal membrane (the primary frontal wall) but which were not fused along the mid-line of the zooecia. *Anaptopora* and *Anotopora* from the Cenomanian are examples of such genera (LANG, 1916, 1921). Morphologically such genera demonstrate the derivation of cribrimorph costate secondary frontal walls from a membraniporid condition (LANG, 1921; LARWOOD, 1962).

Some Cenomanian cribrimorphs have divided intercostal spaces. *Polyceratopora euglypha* shows this condition but the precise nature of the lateral costal fusions is not clear. The Recent genus *Membraniporella* is most closely comparable to early Cretaceous cribrimorph genera of simple structure in which a few irregular lateral costal fusions are developed. *Membraniporella nitida* has these features but *M. marcusi* and *M. aragoi* demonstrate the formation of a costate secondary wall from marginal spines which branch distally in one plane. In Cretaceous cribrimorphs the secondary frontal wall appears always to be formed by unbranched spines.

Among post-Cenomanian Cretaceous cribrimorphs different species of *Pelmatopora* demonstrate the principal complications of the costate secondary frontal wall (LARWOOD, 1962).

An additional, though by no means invariably developed, feature of cribrimorph costae is the presence of pores on the upper surface. These lumen pores are visible in some Recent cribrimorphs as small uncalcified areas which are occupied in life by soft tissue. Similar pores in the costae of fossil cribrimorphs may be termed pelmata and pelmatidia (large and small lumen pores respectively). All the species of *Pelmatopora* display pelmata or pelmatidia in the upper walls of the costae. In species with no lateral costal fusions a single pelma is situated near the distal (inner) end of each costa. In species with a well developed series of lateral costal fusions a graded series of pelmata and pelmatidia occurs with the pelmata opposite each lateral costal fusion. In both fossil and Recent cribrimorphs pelmata and pelmatidia may be absent as in *Membraniporella nitida* and *Cribrilaria radiata*. In some fossil genera pelmata and pelmatidia occur in some species of a genus but not in others.

Among later Cretaceous cribrimorphs *Castanopora jurassica* exemplifies a marked development of pelmata, pelmatidia and lateral costal fusions (LARWOOD, 1962), and species of *Ubaghsia* such as *U. reticulata* and *U. ornata* demonstrate features developed by some heavily calcified forms in which there are very few pelmata on each costa and a small number of robust lateral costal fusions.

Although there are minor variations the basic pattern of this type of secondary frontal wall is the same in Cretaceous and in many Recent cribrimorphs, but the structure of the costae in some Recent cribrimorphs appears to be different. *Cribrilaria radiata* has a distinctive and different frontal wall structure not seen in other Recent genera and, with the possible exception of *Corbulipora*, not known fossil. In *Cribrilaria* the costae rise steeply from the margins of the frontal wall forming a peripheral ring of near-vertical hollow spines. At the level of the secondary frontal wall each of these spines branches inward to form costae which converge on a median-distal mucro . Lateral costal fusions join the costae which lack pelmata or pelmatidia.

Numerous genera of later Cretaceous cribrimorphs develop a tertiary frontal wall of abundant calcareous tissue above the secondary costate frontal wall. Tertiary frontal walls are well displayed by *Tricephalopora, Phractoporella, Polycephalopora, Coelopora, Steginopora, Disteginopora* and *Ubaghsia*. In such genera as *Ubaghsia* this extra calcification forms an irregular robust and raised lattice of calcareous tissue above the general level of the zooecial secondary frontal walls. The extensive development of such tertiary frontal walls has no close parallel in Recent cribrimorph genera. The scale of olocystal or tremocystal calcification in some ascophorans may be comparable with that of the tertiary frontal walls of some later Cretaceous cribrimorphs but its mode of formation is different.

Functionally, the significance of a well developed tertiary frontal wall would seem to relate to the colony as a whole rather than directly to individual zooecia. Its development affords protection for the more delicate subjacent costate frontal walls of zooecia and for their contained polypides. It acts as a coarse outer filter to the zoarium precluding penetration by larger organisms or by coarse detritus and it may even be effective in retaining a certain amount of graded detritus forming a further protection over the surface of the zoarium.

A similar interpretation could be made of frontal structures of some much less calcified *Cheilostomata*. Recent species of *Hiantopora* (*H. ferox* and *H. intermedia*) demonstrate the overgrowth of branched marginal spines in association with prominent avicularia combining to form a frontal shield over each zooecium. Since these shields are developed by adjacent zooecia they form a protective barrier for the whole colony and a filter in which the largest openings are located over the orifices of the zooecia.

The complex tertiary frontal walls developed in Cretaceous cribrimorphs are a specialised example of a zoarial filter and protective lattice.

An illustrated and extended account of the matters discussed in this paper will be published elsewhere.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
15. Group 2: Anatomy, Morphology and Skeletal Structure.

JAMES B. RUCKER (*)

SKELETAL MINERALOGY OF CHEILOSTOME *BRYOZOA*

Riassunto. — Un' indagine sulla costituzione mineralogica dello scheletro di 61 specie di *Cheilostomata* è stata condotta usando i raggi-X a diffrazione e particolari tecniche di colorazione.

La maggior parte delle 32 specie di *Anasca* si sono mostrate interamente calcitiche. Le specie con struttura mineralogica aragonitica o mista erano caratterizzate da colonie lunulitiformi liberamente viventi. Come la maggior parte degli *Anasca*, la sola specie di *Acanthostega* esaminata — *Cribrilaria radiata* — era interamente calcitica.

Gli *Ascophora* sono apparsi essere caratterizzati da uno scheletro carbonatico con costituzione mineralogica mista, sebbene siano state trovate specie monominerali sia con costituzione aragonitica che calcitica. Tra quelle specie con costituzione mineralogica mista, gli strati scheletrici primitivi formanti le pareti basali, laterali e distali e gli strati interni delle pareti frontali sono calcitici. La calcificazione aragonitca susseguente si ha tipicamente come un ulteriore ispessimento sulla superficie esterna della parete frontale.

La quantità di aragonite presente è apparentemente in relazione, in parte, con la maturità della colonia, che può essere, a sua volta, regolata entro certi limiti da parametri ambientali come la temperatura dell'acqua.

Summary. — A survey of the skeletal mineralogy of 61 species of *Cheilostomata* was conducted using X-ray diffraction and staining techniques. A majority of the 32 species of *Anasca* were wholly calcitic. Those species of aragonitic or mixed mineralogy were characterized by a free-living, lunulitiform colony. Like most *Anasca*, the single species of *Acanthostega* examined, *Cribrilaria radiata*, was entirely calcitic.

Ascophora appear to be typified by a skeletal carbonate of mixed mineralogy, although monomineralic species both of aragonitic and of calcitic composition were found. Among those species of mixed mineralogy, the primary skeletal layers forming the basal, lateral, and distal walls, and the inner layers of the frontal wall are calcitic. Subsequent aragonitic calcifi-

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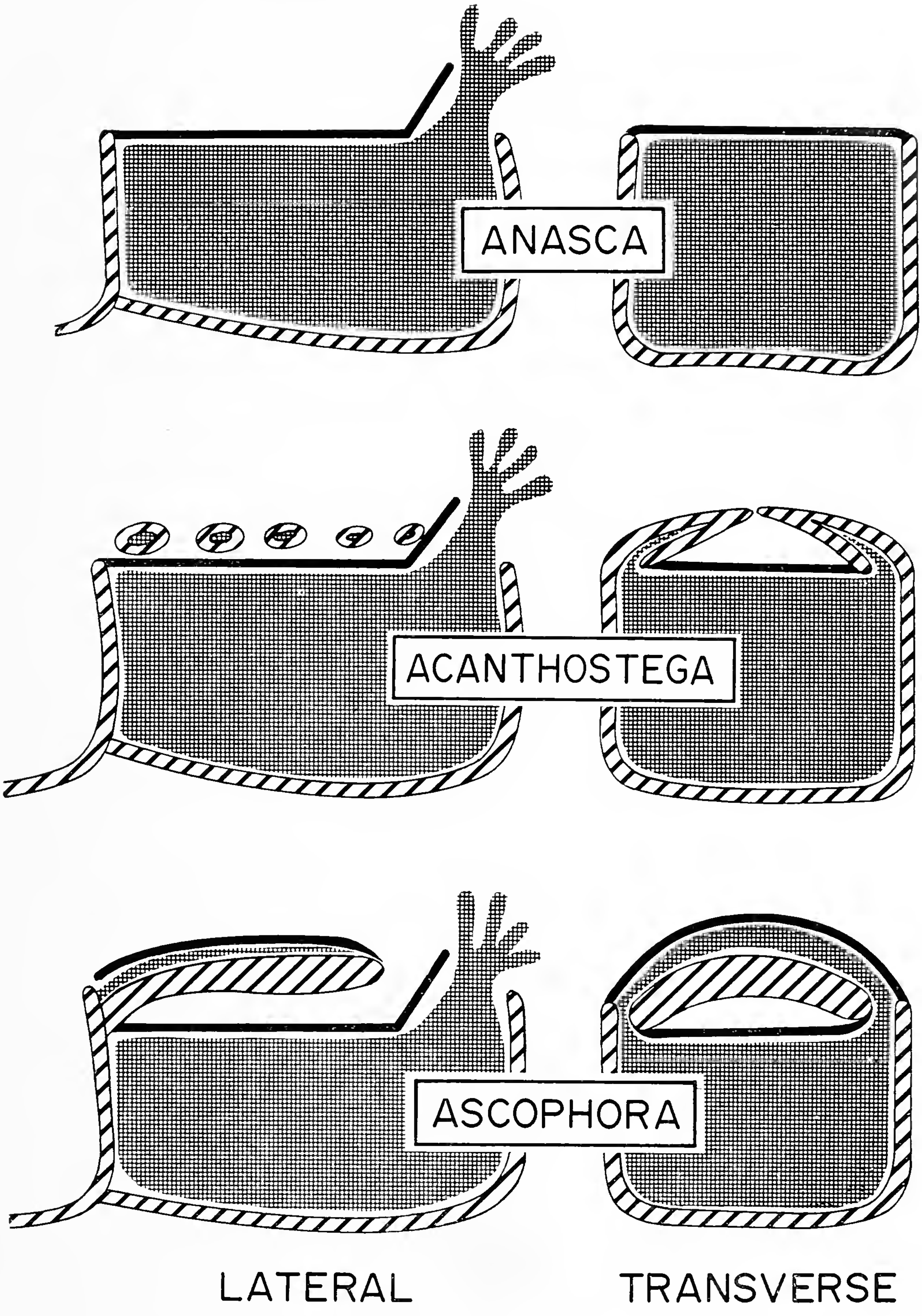
cation typically occurs as additional thickening on the outer surface of the frontal wall. The amount of aragonite present is apparently related, in part, to the maturity of the colony, which may be, in turn, regulated to some extent by environmental parameters such as water temperature.

Skeletal mineralogy of cheilostome Bryozoa.

Previous studies indicate that the carbonate exoskeletons of cheilostome Bryozoa ore composed either of calcite, of aragonite, or of a mixture of these two calcium carbonate minerals. No comprehensive survey of the taxa had previously been made, however, and little was known regarding the relationship between the carbonate mineralogy and the fundamental elements of skeletal morphology. SCHOPF and MANHEIM (1967) conducted an exhaustive search of the published data on the elemental chemical composition of Bryozoa, and determined the geochemical and mineralogic composition of several species. Still, most data reported on the minor-element chemistry of the skeletal carbonates, have not been accompanied by mineralogic studies (DODD, 1967).

In this study, the carbonate mineralogy of the calcareous exoskeletons of 61 species was determined using X-ray diffraction methods. Differential staining techniques were employed to determine the location of aragonite in bimineralic species, using Feigl's solution as the staining agent. A 45 minute exposure to the stain at 45°C. produced a fine-grained, black precipitate on the aragonite, and left the calcite unstained.

Fig. 1. — General configuration of the three suborders of *Cheilostomata*, showing lateral and transverse views. For simplicity, polypides, muscles, and various calcifying tissues are all shown by gray tone; non-calcifying, flexible, chitinous membranes are shown by heavy black lines; and calcareous zooecial walls are represented by a striped pattern. The *Anasca* have a calcifying epithelium in contact with the zooecial walls. The frontal surface is covered by tough, chitinous frontal membrane. The *Acanthostega* differ in having a costular shield composed of partially fused, hollow spines which arch over the elastic frontal membrane. The *Ascophora* have calcifying epithelial tissue in contact with the basal and lateral walls; it is possibly in contact also, at least in some *Ascophora*, with the basal primary laminae of the frontal wall during early stages of zooecial development. Subsequent calcification occurs on the outer surface of the frontal wall, secreted by epithelial cells beneath the epi-frontal membrane.


ANASCA
ACANTHOSTEGA
ASCOPHORA
LATERAL
TRANSVERSE

One hundred specimens representing 61 species belonging to the three suborders of *Cheilostomata* were studied: thirty two species of *Anasca*, one species of *Acanthostega*, and 28 species of *Ascophora*. The results of this survey are indicated in Table 1; several generalizations regarding the calcification within each suborder may be made.

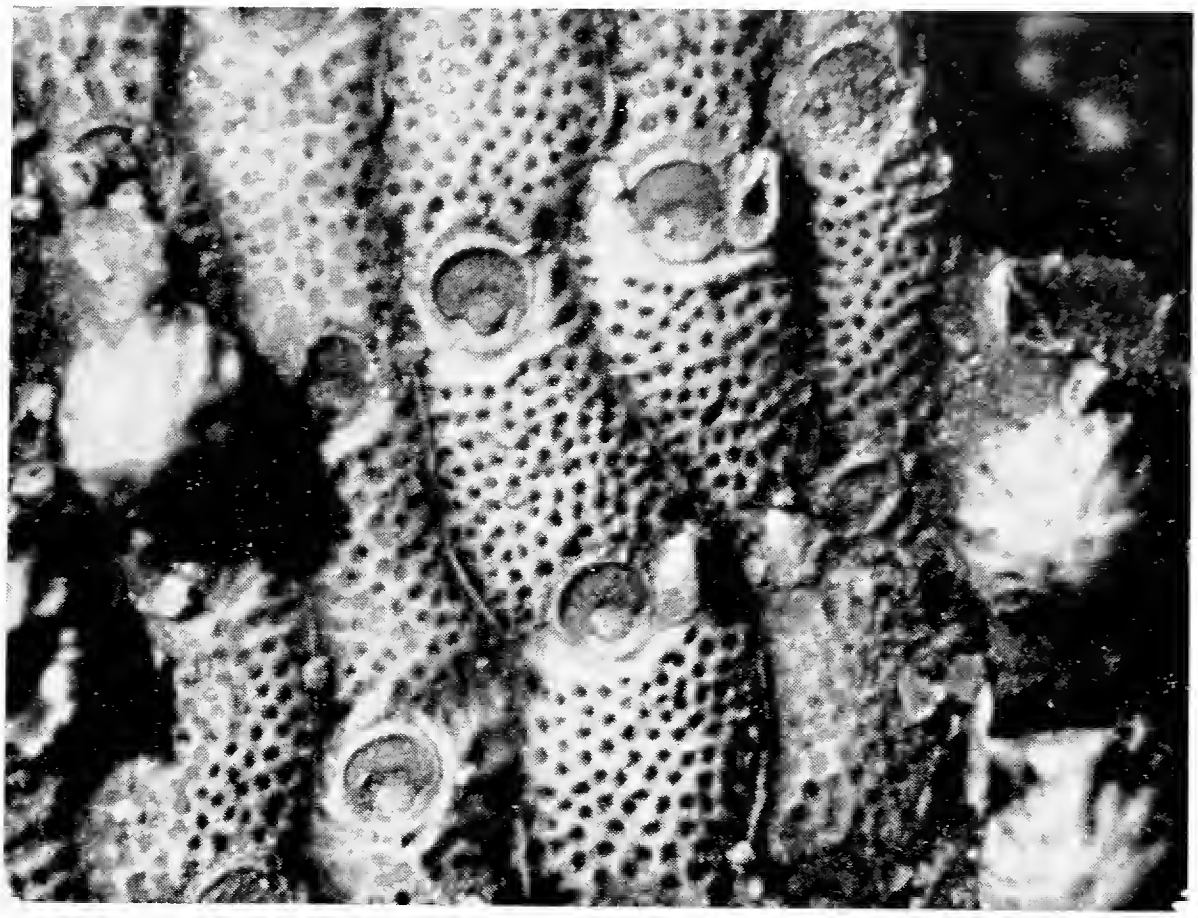
Anasca.

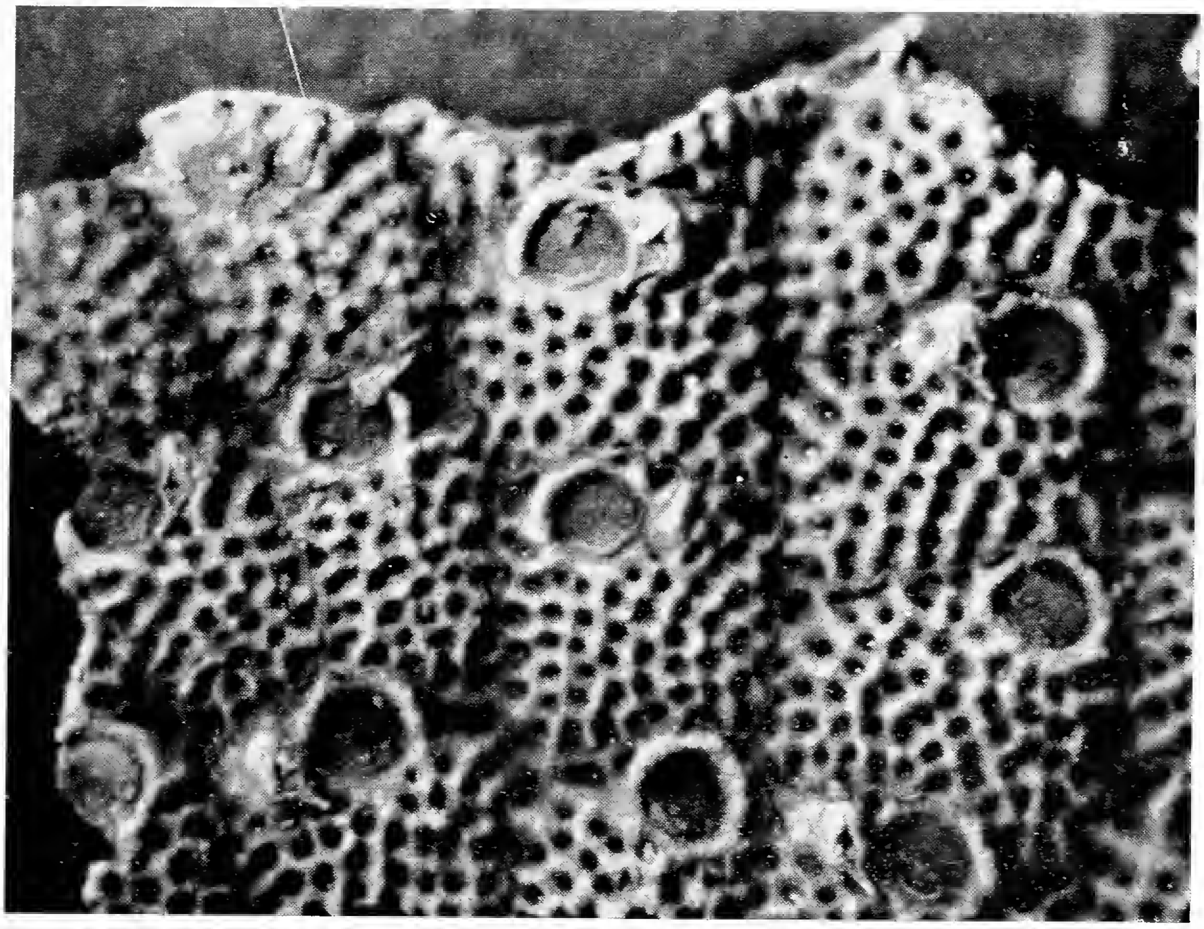
The fundamental anascan skeletal elements are shown in Figure 1. The *Anasca* are characterized by zooecia having carbonate basal, lateral and distal walls, but lacking a true frontal wall. Instead, they have a flexible frontal membrane. Of the 32 species studied, 25 were entirely calcitic. Six of the seven anascan species having mixed mineralogy belong to families which, for the most part, have a discoidal or freeliving zoarial form.

The similar aragonitic skeletal mineralogy of *Cupuladria* and *Discoporella* (both lunulitiform genera) tends to confirm the close relationship between them, which has been suggested by previous authors on the basis of morphologic similarities (Cook, 1965). Minor quantities of calcite, approximately five percent, were detected in *Discoporella*. Using staining techniques, it was determined that the tubercles on the basal zoarial surface were at least partially calcitic. Like the other lunulitiform species, *Setosellina goesi* was essentially aragonitic.

The lunulitiform genus *Lunulities* (both modern and Eocene species) was found to be of mixed calcite-aragonite mineralogy. The more soluble carbonate, aragonite, formed the thick basal wall, while the more insoluble carbonate, calcite, formed the lateral and distal walls.

Fig. 2. — Photographs of *Schizoporella unicornis* showing different degrees of calcification of the frontal wall, with the corresponding percent aragonite, up 33% aragonite, low 72% aragonite (determined by subsequent X-ray analysis of these same samples). The specimen having the lower aragonite content is characterized by a uniformly thin frontal wall, with numerous tremopores. With increasing aragonitic calcification on the outer surface, the frontal wall thickens and becomes more irregular, while the number of pores decreases.





The only other anascan found to be of mixed mineralogy was *Canda retriformis,* a species having an erect cellariiform habit. Insufficient material was available, however, to determine the site of aragonite deposition with staining tests, or to eliminate the possibility of sample contamination.

Acanthostega.

The suborder *Acanthostega* is somewhat more complex than *Anasca. Acanthostega* species are characterized by a frontal costular shield of partially fused spines, rising from the mural rim that arches over the frontal membrane (Figure 1). Discusson regarding this suborder must be postponed since, to date, only a single species has been analyzed.

Because of the basic similarities of most *Acanthostega* species to the membraniporiform *Anasca,* one would suspect that *Acanthostega* species might also have calcitic skeletal composition. The single species analyzed, *Cribrilaria radiata,* proved to be entirely calcitic; on this limited evidence, however, it would be premature to speculate that a calcitic skeletal composition is, in fact, characteristic of this suborder (Table 1).

Ascophora.

Ascophora is the most advanced suborder of the *Cheilostomata.* This suborder is characterized by species having a well-developed calcerous frontal wall (Figure 1), although it is recognized to develop in more than one way (Harmer, 1957). Twenty-eight species belonging to this group were analyzed; twelve species were found to be wholly calcitic, four species were aragonitic, and twelve were of mixed mineralogy (Table 1).

Species of mixed mineralogy were stained to determine the site of aragonite deposition. Invariably the aragonitie was restricted to the outer frontal wall.

Thirteen samples of a ubiquitous encrusting species, *Schizoporella unicornis* (sensu lato), from eight localities were studied. This species characteristically was of mixed skeletal mineralogy. The percent aragonite ranged from 25 to 72, and appeared to be directly related to the degree of frontal wall thickening (Figure 2). The degree of thickening of a frontal wall depends upon the age of the individual zooecia. The frontal walls of new zooecia at the growing edge of a colony are generally devoid of aragonite and are less heavily calcified than individuals in the central (older) portion of the same colony. The rate at which individuals thicken their frontal walls by aragonite deposition may be related to their growth rate, and may be controlled, in part, by various environmental parameters.

A temperature effect in the mineralogic skeletal composition of the bryozoan species, *Schizoporella unicornis,* from Bermuda was documented by LOWENSTAM (1954). He found that the amount of aragonite increased as the water temperature increased; similar results were noted in this study.

A plot of percent aragonite against the mean annual temperatures (taken from the Coast and Geodetic Surface Water Temperature and Salinity Summaries) at sample locations, indicated a positive relationship between temperature and aragonite content. No trend was noted between annual salinity and percent aragonite or percent $MgCO_3$.

Many of the monomineralic species reported are represented by a single analysis of a single specimen; it would be imprudent to discuss these taxa further, until more is known about their range of compositional variations.

Several specimens of two *Metrarabdotos* species were studied. One species, *M. tenue* was consistantly wholly calcitic. A closely related species, *M. unguiculatum* was of mixed mineralogy. The wall structures and mineralogy of these species were compared in detail by CHEETHAM et al. (In Press). It was found that the two species were quite similar in terms of both zooecial ontogeny and zooecial wall structure, in spite of the differences in mineralogy. Both species were composed of smooth, calcitic, primary skeletal layers forming the basal, lateral, and distal walls, and the inner layers of frontal wall of the zooecia. A superficial layer of deposited carbonate material was noted on the outer surface of the frontal wall; this layer was of a radiating, fibrous, aragonitic nature in *M. unguiculatum,* and of a wavy-lamellar, calcitic nature in *M. tenue.* This superficial material appears to be deposited from the epi-frontal tissue that characteristically covers the frontal wall of the Ascophora.

TABLE 1. - *Skeletal mineralogy.*

Species	Mineralogy		
	Calcite	Aragonite	Calcite & Aragonite
	ANASCA		
Eucratea loricata	X		
Membranipora aurita	X		
M. hastingsae	X		
M. unicornis	X		
M. tuberculata	X		
Biflustra savartii	X		
Electra anomala	X		
E. pilosa	X		
E. tenella	X		
Flustra foliacea	X		
Aplousina gigantea	X		
Chaperia condylata	X		
Steganoporella magnilabris	X		
Thalamoporella granulata	X		
T. distorta	X		
T. falcifera	X		
Setosellina goesi		X	
Cupuladria canariensis		X	
Discoporella doma		X*	
D. umbellata		X*	
Lunulites capulus			X
L. jacksonensis (Eocene)			X
Nellia tenella	X		
Bugula californica	X		
B. neritina	X		
B. simplex	X		
Dendrobeania murrayana	X		
Cellaria bassleri	X		
Canda retriformis			X**
Scrupocellaria regularis	X		
S. maderensis	X		
Caberea ellisi	X		
	ACANTHOSTEGA		
Cribrilaria radiata	X		

(*segue* TABLE 1)

Species	Mineralogy		
	Calcite	Aragonite	Calcite & Aragonite
ASCOPHORA			
Tremogasterina granulata			X
T. lanceolata			X
Gemelliporella prevailae		X	
Parasmittina spathulata			X
Smittoidea prolifica			X
Codonellina montferrandii	X		
Retoporellina marsupiata	X		
Cryptosula pallasiana	X		
Watersipora subovoidea	X		
Hippopodina feegeensis	X		
Hippoporina pertusa	X		
Harmerella dichotoma	X		
Mamillopora cupula		X	
Hippothoa hyalina	X		
Escharoides praestans	X		
Schizoporella unicornis (Sensu lato)			X
Stylopoma spongites		X	
Adeona cellulosa			X
Metrarabdotos tenue	X		
M. unguiculatum			X
Gemelliporina glabra			X
Microporella umbonata	X		
Celleporaria albirostris			X
C. vagans			X
C. granulosa		X	
C. aperta			X
Celleporina costazii	X		
Hippopetraliella marginata			X

* Minor quantities of calcite were detected on the tubercles of the basal surface.

** Twenty percent aragonite was detected on a single X-ray analysis of this species. However, insufficient material was available to do follow-up staining to determine the site of aragonite deposition, and to eliminate the possibility of contamination.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
16. Group 2: Anatomy, Morphology and Skeletal Structure.

Osborne B. Nye (*)

ASPECTS OF MICROSTRUCTURE IN POST-PALEOZOIC *CYCLOSTOMATA*

(*Bryozoa*)

Riassunto. — Nei *Cyclostomata* post-paleozoici è possibile identificare diaframmi basali, intermedi e terminali.

Questi diaframmi sono distinti per la loro posizione all' interno dello zooecium e per la direzione verso cui le laminae si flettono quando incontrano il rivestimento della parete zoeciale. La secrezione dei diaframmi è in relazione con la connessione del tessuto interzooidale attraverso i pori interzooidali. La circolazione così aumentata attraverso i pori interzooidali, non posseduta dalla maggior parte dei Briozoi paleozoici, costituisce un adattamento vantaggioso per i Briozoi post-paleozoici.

Summary. — Basal, intermediate and terminal diaphragms can be identified in post-Paleozoic cyclostomes. These diaphragms are distinguished on their position within the zooecium and the direction in which the laminae flex when joining the lining of the zooecial wall. The secretion of the diaphragms is related to the connection of interzooidal tissue through interzooidal pores. Increased circulation through interzooidal pores, not possessed by most Paleozoic Bryozoa may provide an adaptive advantage to most post-Paleozoic Bryozoa.

Résumé. — Parmi les *Cyclostomata* du Secondaire et Tertiaire on peut distinguer des diaphragmes basal, intermédiaire et terminal. Les diaphragmes sont determinés par leur position dans le zooécium et la direction d' inclinaison des laminae du diaphragme quand ils se jointent à la partie interieure de la paroi zoéciale. La mode sécrétoire des diaphragmes est liée à la jonction de l'épithelium interzoïdal à travers les pores interzoïdals.

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L'augmentation de circulation à travers les pores interzoïdal (la plupart des bryozoaires du Primaire ne demontré pas ce trait) a été un avantage pour l'adaptation des bryozoaires du Secondaire et Tertiaire.

Interzooidal pores are characteristic morphologic structures common in cyclostomes. Most Paleozoic bryozoans have nonporous walls with the exception of some Ordovician and Silurian ceramoporoids, but the mural pores of ceramoporoids do not appear to relate structurally to the interzooidal pores of post-Paleozoic cyclostomes. Most post-Paleozoic bryozoans characteristically develop porous walls; however Borg, 1926, and Silén, 1944 showed that interzooidal pores of cyclostomes are different anatomically from the communication pores of *Ctenostomata* and *Cheilostomata.*

Examination of the microstructure of the zooecial walls in cyclostomes shows that the laminae lining the wall generally parallel the zooecial cavity until they reach the locus of the pore. Here the laminae do not stop abruptly but deflect and contour the outline of the pore. Deflection of the laminae indicates that calcite was deposited by a secretory epithelium which lined the pore, therefore the pore is considered a primary structure.

The biologic role of interzooidal pores is suggested by microstructure of diaphragms of which three types, basal, intermediate and terminal, can be identified in post-Paleozoic cyclostomes.

Basal diaphragms lie within the zooecial cavity in an aboral position. They are usually thin and non-porous and have been observed in exozone and endozone portions of the zooecium. The laminae of this diaphragm curve orally as the diaphragm joins the zooecial wall and continue orally as a zooecial lining. The oral flexure of the laminae requires that the depositing epithelium was on the oral side of the diaphragm.

Terminal diaphragms (Borg, 1933, p. 290) are deposited at or close to the oral extremity of a single zooecium as a zooecial cover plate. This diaphragm is porous and relatively thick with laminae which flex aborally as the diaphragm joins the zooecial wall.

Intermediate diaphragms have a laminar configuration like that of the terminal diaphragms in that the laminae flex aborally to parallel the zooecial wall. The intermediate diaphragm is distinguished from the terminal diaphragm because it lacks pores, is usually thinner and is aboral in position.

The manner in which the laminae of the terminal and intermediate diaphragms join the zooecial lining requires that the soft tissues which deposited the laminae lay on the aboral side of the diaphragm. Soft tissues engaged in metabolic activities such as the deposition of calcareous tissue require a supply of nutritive and respiratory substances, and the means to eliminate toxic metabolic byproducts. This in turn requires either a storage facility or a direct communication with tissues able to supply these requirements. When the first laminae of the intermediate diaphragm is completed, a chamber is formed sealed off from the overlying zooecial cavity. This effect is essentially the same in the case of the porous terminal diaphragm because there is no zooid oral to the diaphragm. In all cases observed, however, the chamber is connected laterally to adjoining zooecial cavities by interzooidal pores. The evidence presented supports Borg's observations (1926, p. 201-202) that cell layers passed uninterrupted through the pores and his hypothesis that coelomic fluids carrying nutrients could be exchanged through interzooidal pores.

In most Paleozoic bryozoans the secretion of diaphragms within a zooecia formed a series of closed chambers. Living soft tissues were confined to a zone at the periphery of the zoarium, defined and underlain proximally by the last formed diaphragm. This skeleton would seem to have provided only a supporting function analogous to that of a coralline calyx with a relatively small protective potential. In post-Paleozoic cyclostomes, however, living tissues capable of metabolic activities could be supported throughout the zoarial framework, because of the communication system of interzooidal pores. This tissue may provide a temporary internal reservoir in time of stress when external conditions might be unfavorable to the existence of most feeding polypides. Under more favorable conditions, these underlying tissues might support the proliferation of new feeding polypides allowing the survival of the cyclostome colony. Thus post-Paleozoic bryozoans, provided with interzooidal communications, have a flexibility in reacting to environmental changes not possessed by most Paleozoic bryozoans.

Whether the development of interzooidal pores appeared in several lineages of *Bryozoa* which led to a polyphyletic group, or whether post-Paleozoic cyclostomes are monophyletic, can not be answered at present. However, it would seem that interzooidal pores provide one of the keys to an understanding of the extinction of most Paleozoic tubular Bryozoa and the successful adaption of post-Paleozoic *Cyclostomata* to their environment.

Many of the ideas expressed in this paper evolved from general discussions of the bryozoan seminar group at the U.S.N.M. Responsibility for application of these ideas to the *Cyclostomata* however is mine.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
17. Group 2: Anatomy, Morphology and Skeletal Structure.

S. THOMAS SÖDERQVIST (*)

OBSERVATIONS ON EXTRACELLULAR BODY WALL STRUCTURES IN *CRISIA EBURNEA* L.

(*Ectoprocta, Crisiidae*)

Riassunto. — *Crisia eburnea* (*Ectoprocta, Crisiidae*) quale briozoo *Cyclostomata* primitivo è stato studiato per mezzo del microscopio elettronico a scansione. La parete corporea extracellulare è risultata composta di una sottile cuticola organica, un sottile strato esterno ed un più spesso strato interno.

Lo strato esterno è composto da fasci di minuti prismi mentre lo strato interno ha una struttura lamellare, essendo composto da cristalli poligonali, tubulari, sovrapposti.

Viene discussa la struttura della parete corporea extracellulare e vengono date alcune definizioni corrette.

Summary. — *Crisia eburnea* (*Ectoprocta, Crisiidae*) as a « primitive » cyclostomatous bryozoan has been investigated by means of scanning electron microscopy. The extra-cellular body wall is composed of a thin organic cuticle, a thin outer and a thicker inner calcareous layer. The outer layer is composed of bundles of minute prisms while the inner layer has lamellar structure, being composed of polygonal, tabular, superimposed crystals. The structure of the extra-cellular body wall is discussed and some revised definitions are made.

Zusammenfassung. — *Crisia eburnea* (*Ectoprocta, Crisiidae*) als « primitiver » cyclostomate bryozoe ist mit Raster-Elektronen Mikroskopie untersucht worden. Das Aussenskelett ist aus einer dünnen äusseren und dickeren inneren Kalk-Schicht aufgebaut. Die äussere Schicht ist aus Bündeln kleiner Prisma zusammengesetzt, während die innere Schicht lamellare Struktur aufweist und ist aus polygonale, in Dachziegelschichtung angeordnete Kristallen, aufgebaut. Einige Definitionen der Aussenskeett sind diskutiert.

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Introduction.

Present knowledge of the structure of the body wall in cyclostomatous bryozoa (Ectoprocta; Cyclostomata) is based primarly on the works of BORG (1923, 1926) which are generally adopted by standard text-books (e. g. HYMAN, 1959). According to BORG the body wall is made up of four layers: cuticle, calcareous layer, ectoderm and mesoderm (see also CALVET, 1900).

In this report preliminary results of an investigation with a scanning electron microscope on the extra-cellular body wall in *Crisia eburnea* L. and some other cyclostomatous bryozoa are presented. In a forthcoming paper the results will be compared with biochemical and transmission electron microscopical data in order to reveal the ontogeny and morphology of the body wall.

Material and Methods.

Live colonies of *Crisia eburnea* L. were either fixed immediately or first trypsin digested in order to eliminate proteinaceous material from zooids, and then fixed. In order to obtain fresh wall structures the material was crushed and then immediately coated with carbon or gold and examined in a Cambridge « Stereoscan » scanning electron microscope. Micrographs were recorded in magnifications from 500 × to 20,000 ×.

Body wall in 'Crisia eburnea'.

The extra-cellular parts of the body wall were found to consist of three layers: 1) a thin cuticle, 2) a thin outer calcareous layer and 3) a thick inner calcareous layer.

1) The cuticle is preserved in non-digested preparations thereby indicating its proteinaceous nature. The cuticle shows no specific structures except for scattered, indistinct depressions and elevations, part of which might reflect the uneven, underlying crystal surface. The longitudinal, parallel folds (fig. 1) are artifacts caused by shrinkage of the cuticle in vacuum treatment. The cuticle is thinner (one tenth to one fifteenth of the wall) than that assumed by BORG (one fourth to one fifth; 1926).

2) The outer calcareous layer consists of bundles of crystals, each bundle comprising 20-50 crystals (fig. 1). At higher magnifications these crystals appear as prisms without any intracrystalline structure. BORG's (1926) observations that the body

wall is composed of « parallel, longitudinal strips/with/minute particles . . . parallel to the longitudinal axis of the bud » is correct only insofar as the outer surface is considered.

3) The inner calcareous layer consists of polygonal, tabular crystals (fig. 3), stacked like roofing-tiles. In transverse views (fig. 2) the same crystals are arranged as lamellae with approximately uniform thickness. Around the pores the crystals are deflected outwards indicating that the pore is a primary formation and has not been formed by the resorption of precipitated crystals.

The interzoidal wall, septum, dividing the common bud into two new zooids is constructed of lamellae of the same type. Seen in transverse view the septum has a lamellar structure with no « hyaline » middle zone (cf. *Diplosolen* below). This is probably due to the fact that the *Crisia* septum has a comparatively narrow growing front and crystals non-parallel to the growth direction are either entirely absent or too few crystals are present in this deflected region to be detectable under the technique used.

In four other recent species investigated, *Stomatopora sp.*, *Diplosolen intricarius* (SMITT), *Idmonea atlantica* JOHNSTON and *Heteropora pelliculata* WATERS, the inner part of the calcareous wall has the same architecture as in *Crisia*, i.e. superimposed, tabular, polygonal crystals. *Diplosolen* and *Heteropora* exhibits a broad « hyaline » zone of deflected crystal arrangement in the middle of the interzooidal wall. In *Heteropora* the « hyaline » zone is very thick and the lamellar zone is restricted to a few lamellae.

No indications of organic material were found in the calcareous layers.

Discussion.

The body wall is a functional unity consisting of those parts of the zooid involved in the protection and physical support of the zooids and colony. The cuticle and calcareuos layers are, by analogy to molluscs (WILBUR and SIMKISS, 1967) secreted by the epithelium of the zooid. During ontogeny the epithelium first secretes the cuticle as a terminal membrane and as a cuticle proper (cf. periostracum in molluscs). The cuticle is here defined as a nonmineralized, extra-cellular organic layer. Internal to the cuticle the outer and inner calcareous layers are then deposited. It is assumed that these two layers consist of calcium carbonate and small amounts of other minerals (SCHOPF and MANHEIM, 1967) in conjuntion with an organic matrix of probably heterogeneous nature. Both the mineral and organic matrices are secreted by the epithelium into a hypothetical narrow space between the cuticle and the epithelium, here termed the *extraepithelial fluid space* by analogy to molluscs. In this space one can assume that the crystals grow as polycrystalline aggregates, since carbon replicas of the inner surface of this layer in *Crisia* show this type of intracrystalline surface structure. Comb-like edges, as visible in fig. 3, might be indications of early stages of new crystals. BOARDMAN and TOWE, in an unpublished investigation, have found the same type of crystal intrastructure in *Heteropora pelliculata* by means of carbon replicas (personal communication).

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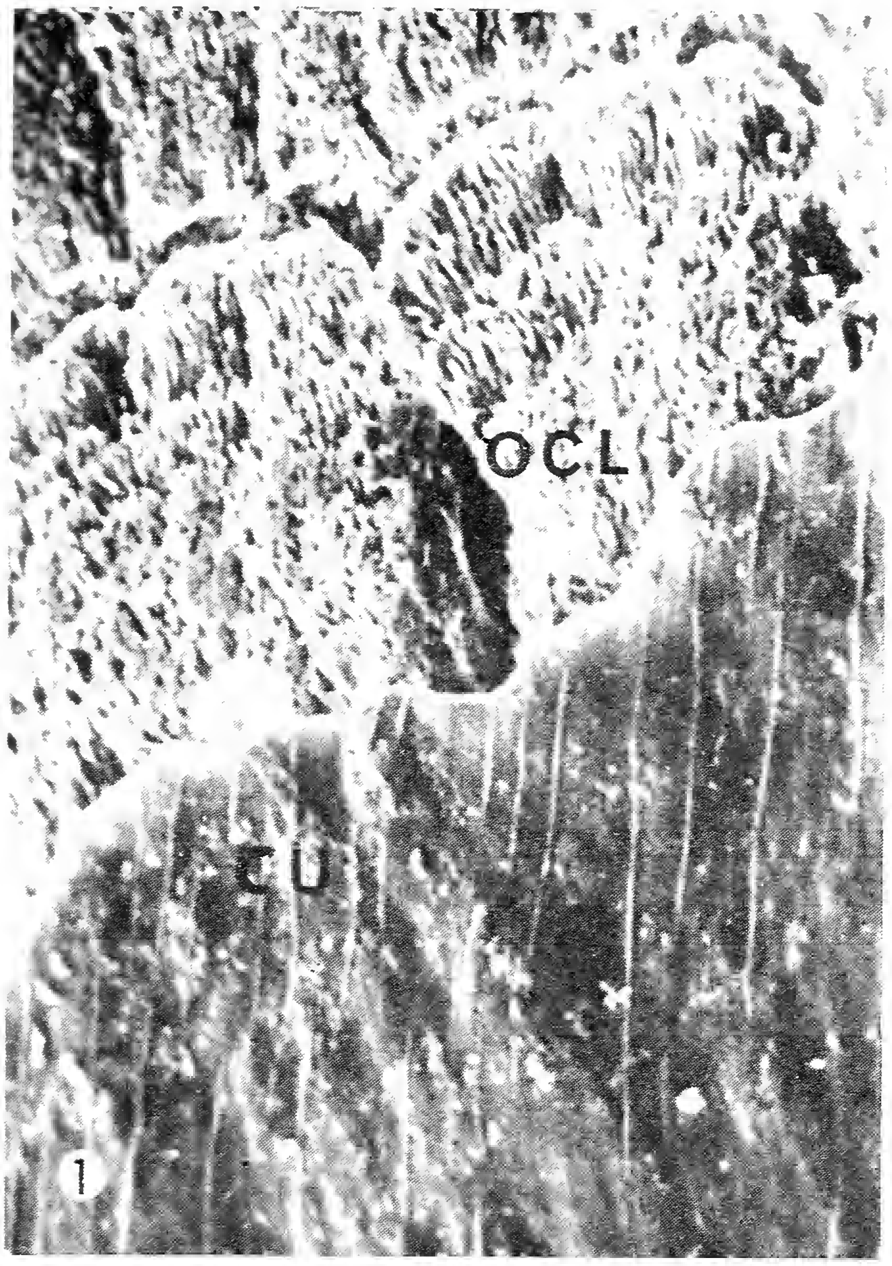
PLATE IV

Fig. 1. — *Crisia eburnea* autozooid. Outside view with outer calcareous layer (OCL) and cuticle (CU). Longitudinal folds in cuticle are artifacts caused by shrinkage in vacuum treatment. 1310 ×.

Fig. 2. — *Crisia eburnea* autozooid. Transverse view. Cuticle conceals outer calcareous layer. Note deflection of the lamellae of the inner calcareous layer (ICL) around the pore (P). 5290 ×.

Fig. 3. — *Crisia eburnea* gonozooid. Oblique inside view of tabular, polygonal crystals of inner calcareous layer. Note crystal deflection around the pore and comb-like edges on some crystals. 3260 ×.

Fig. 4. — *Stomatopora sp.* autozooid. Inside view of tabular, polygonal crystals of inner calcareous layer. Pulpy appearance in lower right corner is probably due to remaining cellular material. 1730 ×.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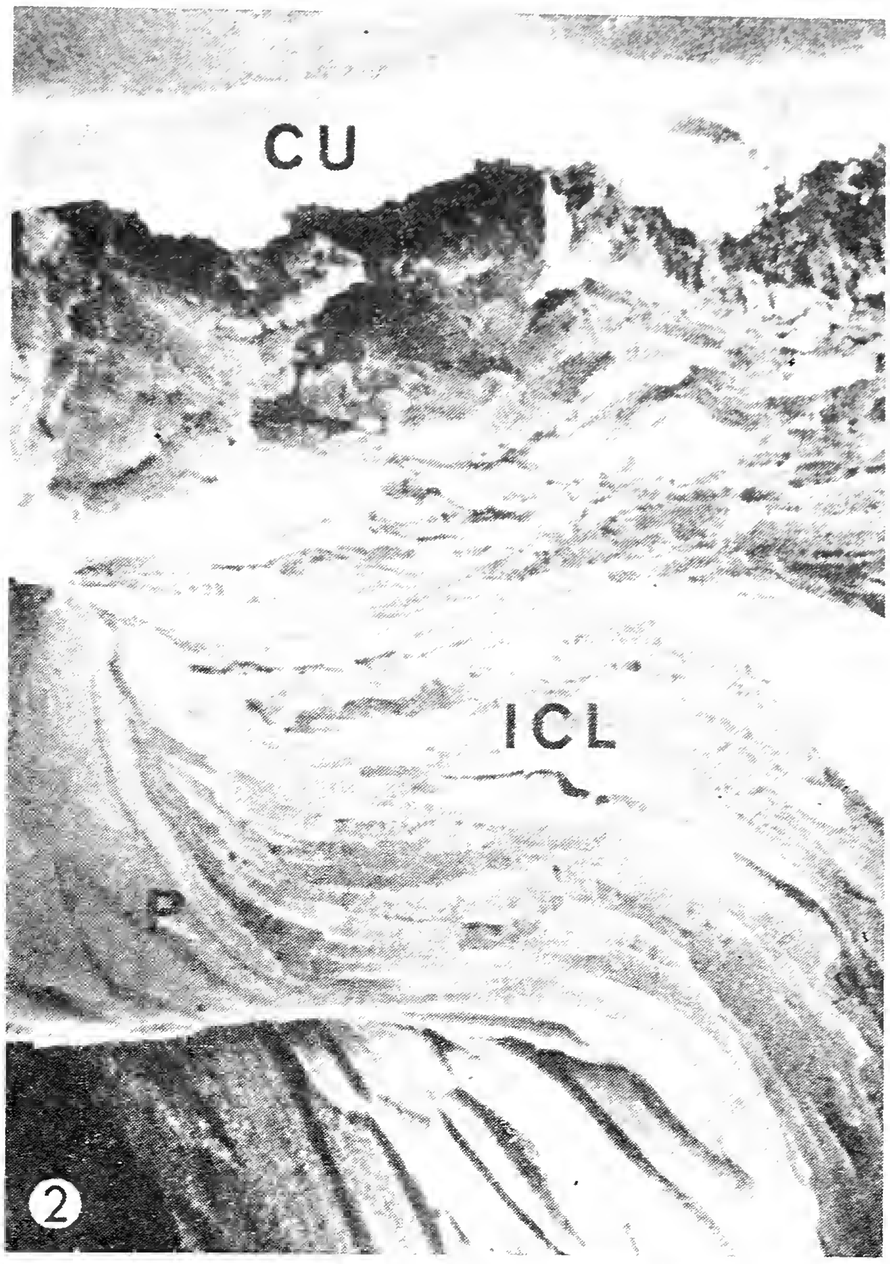
CU
1


CU
ICL
P
2


3


4

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
18. Group 3 : Ecology and Paleoecology.

DIETHARDT JEBRAM (*)

A CULTIVATION METHOD FOR SALTWATER *BRYOZOA* AND AN EXAMPLE FOR EXPERIMENTAL BIOLOGY

Riassunto. — Un metodo di coltivazione proposto da GRELL, SCHNEIDER, KAISSLING e da HAUENSCHILD e modificato, si applica molto bene ai Briozoi salmastri e di acque polialine. Per qualche specie assolutamente marina è necessaria una separazione del cibo dalla sua soluzione nutritiva. Come nutrimento per parecchie specie di Bryozoa si sono mostrate buone *Oxyrrhis marina* (Dinoflagellata) e *Cryptomonas* sp. (Cryptomonadina).

Per ottenere più colonie di specie incrostanti per mezzo della riproduzione asessuale, è stato sviluppato un nuovo metodo. I Briozoi sono lasciati crescere da un vetrino copri-oggetto all'altro. Questi vetrini copri-oggetto sono fissati ad un vetrino porta-oggetto per mezzo di sottili tubicini di polivinile.

Nelle condizioni di coltivazione usati, *Conopeum reticulum* (L.) sviluppa polipidi negli spazi triangolari interopesiali allargati. Dopo queste osservazioni, queste strutture furono riconosciute essere eterozooidi (« reticulozooidi »). Le pareti laterali dei vecchi zooidi crescono strato su strato verso l'alto. Per confronto con i reticulozooidi di *Conopeum*, le spine e i tubercula di *Membranipora* Blainville furono identificati come eterozooidi.

Summary. — A cultivation method, modified after GRELL, SCHNEIDER, KAISSLING and HAUENSCHILD proved effective for Bryozoans from brackish and polyhaline waters. For some typical marine species a separation of the food from its nutrient solution is necessary. As food for several Bryozoan species, *Oxyrrhis marina* (Dinoflagellata) and *Cryptomonas* sp. (Cryptomonadina) were effective. In order to obtain, by asexual means, more colonies of the incrusting species, a new method was developed, in which the Bryozoans were allowed to grow from one coverslip to another. These coverslips were held fast on glass slides by means of slit pieces of polyvinyl-tubing.

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Under the cultivation conditions used, *Conopeum reticulum* (L.) builds in enlarged « triangular, interopesial cavities » polypids. From these observations, these formed structures are recognized to be heterozooids (« reticulumzooids »). The lateral walls of old zooids grow layer by layer upwards. By comparison with the reticulumzooids of *Conopeum*, the spines and tubercula of the genus *Membranipora* Blainville are identified to be likewise heterozooids.

Résumé. — Une méthode de culture modifiée après Grell, Schneider, Kaissling et après Hauenschild s'applique bien aux Bryozoaires d'eau saumâtre et polyhaline. Pour quelques espèces strictement marines il est nécessaire de séparer les organismes servant de nourriture de leur bouillon eutrophié de culture. Comme nourriture pour plusieurs espèces de Bryozoaires *Oxyrrhis marina* (Dinoflagellata) et *Cryptomonas* sp. (Cryptomonadina) se sont montrés satisfaisants. Pour la propagation asexuelle d'espèces incrustantes une méthode nouvelle et simple à été trouvée. On laisse les Bryozoaires se répandre d'un couvre-objet à un autre. Les couvres-objet sont fixés sur les lames par des pièces de PVC-tuyau.

Sous les conditions de culture *Conopeum reticulum* (L.) développe des polypides dans des « espaces triangulaires, interopesiaux » agrandis ce qui nous rend à même de les identifiér comme hétérozooides (« reticulumzooides »). Les parois latérales de zooides vieillissants de *C. reticulum* s'accroissent, couche par couche, verticalement. Comparés avec les reticulumzooides de *Conopeum* aussi les épines et tubercules du genre *Membranipora* Blainville peuvent être identifiés comme hétérozooides.

Zusammenfassung. — Eine Kulturmethode, modifiziert nach Grell, Schneider, Kaissling und nach Hauenschild, eignet sich gut für Bryozoen aus dem Brackwasser und aus dem Polyhalinikum. Für einige vollmarine Arten ist eine Trennung des Futters von seinem eutrophierten Nährmedium notwendig. Als Futter für etliche Bryozoen-Arten haben sich *Oxyrrhis marina* (Dinoflagellata) und *Cryptomonas* sp. (Cryptomonadina) bewährt. - Für die ungeschlechtliche Vermehrung von flächig wachsenden Arten wurde eine neue, einfache Methode entwickelt: Die Bryozoen werden auf Deckgläsern wachsen gelassen, von einem Stück auf ein anderes, wobei die Deckgläser mit PVC-Schlauchstücken auf Objektträgern festgehalten werden.

Unter den Kulturbedingungen entwickeln sich bei *Conopeum reticulum* (L.) in vergrösserten « triangulären, interopesialen Räumen » Polypide, wodurch diese Gebilde als Heterozooide erkannt werden (« Reticulumzooide »). Die Lateralwände älter werdender Zooide wachsen bei *C. reticulum* schichtweise in die Höhe. - Durch Vergleich mit den Reticulumzooiden von *Conopeum* können die Dornen und Tubercula der Gattung *Membranipora* Blainville ebenfalls als Heterozooide identifiziert werden.

The first experimental researches on marine Bryozoa were done by MARCUS (1926) by simple rearing in natural seawater. SCHNEIDER (from 1955 on) and KAISSLING (1963) undertook their light-physiological experiments with *Bugula* using a cultivation method, which was developed by GRELL (1950, not published). My cultivation method for saltwater Bryozoa is also based on GRELL's methods (1).

Oxyrrhis marina (a heterotroph Dinoflagellata), which were fed by *Dunaliella* sp. (Phytomonadina), were used to feed the Bryozoans, as used by GRELL, as were also *Cryptomonas* sp. (Cryptomonadina), which is an organism recommended by HAUENSCHILD as food for marine animals. *Dunaliella* and *Cryptomonas* were cultivated in a nutrient solution, which is prepared according to a combined method of GRELL and HAUENSCHILD. The nutrient solution contains in 1000 cc seawater, 100 mg $NaNO_3$, 20 mg $Na_2HPO_4 \cdot 12\,H_2O$, and 10-20 ccm soil extract, and should be sterilized and filtered.

The seawater was obtained from the Kieler Förde (about 13-17‰ S). By dilution with tapwater I get 10‰ S. I produce 20-40‰ S by adding some concentrated, artificial seawater (about 153‰ S), which is prepared by making a solution of the 6 main marine salts (p.a.) (after the recept for the simple, artificial seawater of HAUENSCHILD, 1962).

The Bryozoa were reared, according to the different experimental conditions, in glass or plexiglass vessels of various sizes, usually at temperatures of 14-16°C, in dimlight, and aerated. Every 3-4 days the colonies were cleaned from faeces and bacteria by gentle brushing and provided with a new food suspension.

The admixtures of the nutrient solution for the autotrophic protists eutrophized the medium. This is tolerated by species from brackish and polyhaline waters, but some typical marine species do poorly in such an eutrophic medium. For these sensitive spe-

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(1) I am endebted to Prof. Dr. K. Grell for his kindness in introducing me to the cultivation methods in the protozoological laboratory of the Zoological Institute of the University of Tübingen, and for his providing me with the stock cultures of the foodorganisms.

I also thank very much Dr. J. P. Woodring, Dept. of Zoology, Louisiana State University, Baton Rouge, La. 70808, U.S.A., for his assistance in translating this manuscript into English.

cies the food must be separated from the nutrient medium and placed in normal, sterilized seawater, before it could be fed to the Bryozoa. This separation may be a problem. The cells pass through the pores of all paper filters and also through all fine fritted glass filters. Membrane filters provide a good separation, but are unpractical because they work too slowly. The cells may be separated from the medium by centrifugation. Because Bryozoa are very voracious, a large amount of food suspension is required, when one is rearing a larger number of Bryozoan colonies. Normal centrifugation is unpractical, because it separates at one time only a few cc. Therefore, a centrifuge is required that utilizes several larger vessels (containing 500 ccm, or more), and that has a high rotation speed. A continual passage centrifuge may better be used, in which in one tube the protistan suspension is led in, and out of an other tube the almost cell free medium comes out. The foodorganism cells can be washed out as a sediment from a trap mechanism, after some litres of protistan suspension have been run through the centrifuge (2). It should be noted, that by centrifuge separation a larger number of cells is lost.

The kind of food seems to be of great importance for the Bryozoa. Although several of the laboratory treated species fed well on both *Oxyrrhis* and *Cryptomonas*, and with both sorts of food grew and matured well, everytime the type of food was changed, all active polypids were reduced and replaced by a new one. The physiology of the polypids seem to be regulated by the food. A change of the kind of food requires a change in the physiology of digestion, which results in a change of the polypids. Probably some of the species, which grew poorly under my conditions, did so because of this phenomenon. Surely there are Bryozoan species, which require other kind of food than that used by me (3).

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(2) The continual passage centrifuge model available to me was old and intricate to handle, and so I used this method for only a few months. The results, however, were satisfactory with some marine species.

(3) Some days ago I received some reprints from J. S. Bullivant, New Zealand Oceanographic Institute, Department of Scientific and Industrial Research, Wellington, who reported good results in feeding *Zoobothryon verticillatum* and other Bryozoan species with *Phaeodactylum tricornutum, Monochrysis lutheri,* and other food species.

For laboratory rearing of Bryozoa the type of substrate is important. Plates of glass have prooved in many regards to be sufficient by many authors, for example for Hydrozoa and freshwater Bryozoa. I have used glass slides as a substrate for several saltwater Bryozoan species with good results. However, glass is not accepted by all species. Some species, above all stolonial and pseusostolonial forms, can not or only with difficulties adhere to the smooth surface. Moreover there are species, which seem to need special chemical conditions of the surface of the substrate. For example, penetrating *Ctenostomata* need lime or wood, and *Flustrellidra hispida* and *Membranipora membranacea* seem to need seaweeds such as *Laminaria* and *Fucus*. For such species special cultivation methods must be developed.

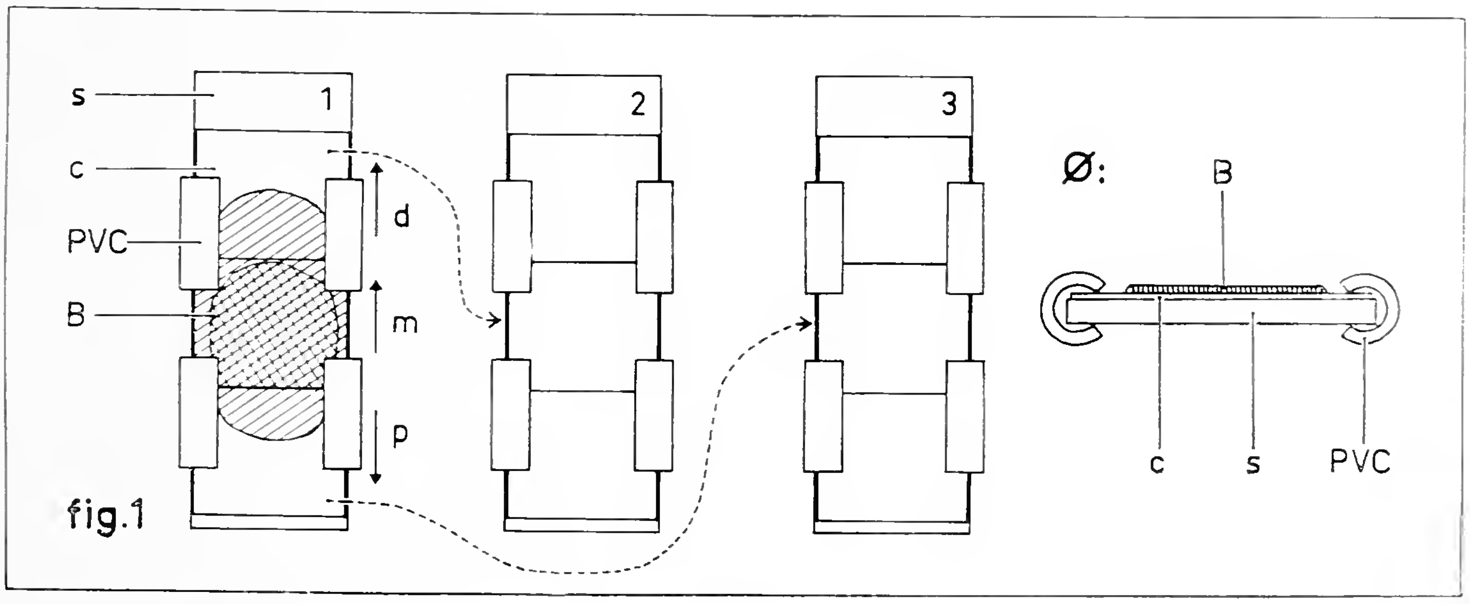

fig.1

Fig. 1. — Asexual multiplying of incrusting Bryozoa.

B = Bryozoan colony; c = coverslip; d = distal, m = middle, and p = proximal part of the growing colony; PVC = slit piece of polyvinyl tubing; s = glass slide.

Closely related to the substrate problem is the question of the asexual multiplication of incrusting colonies. Whilst bushy and stolonial forms are easily propagated by cutting off branches of the colonies, the incrusting species grow strongly adhering to the substrate and can only be subcultivated by separating a part of the substrate with a part of the adhering colony. I have developed a new, simple, but practical method for this: I allow the colonies, which are to be multiplied, to grow not on the slide itself but on coverslips, which are held fast on the slides by slit pieces of polyvinyl-tubing. The Bryozoa grow from one coverslip to the other. Afterwards, the colonies can be cut through along the border of the coverslips, and the separate pieces used for further subculturing (fig. 1). Since it is necessary for experimental research to use clone material of the animals to eliminate individual, genetic differences, this method is an important foundation for such experiments.

The following species I am currently rearing (or have reared) under the above mentioned conditions (some for over 3 years): (*Tubulipora* sp.), *Alcyonidium polyoum*, *A. hirsutum*, **Alcyonidium* sp., **Bowerbankia gracilis*, (*B. imbricata*), **Farella repens*, **Electra crustulenta*, **E. monostachys*, **E. pilosa*, (**E. posidoniae*), **Conopeum seurati*, **C. reticulum*, **Bugula stolonifera* (from the stock of GRELL), (**Cribrilina punctata*), (*Hippothoa hyalina*), (*Escharella immersa*), (*Microporella ciliata*), *Cryptosula pallasiana*.

* = well growing species, which became mature in the laboratory;
( ) = these species were reared only a short time, and/or grew poorly.

As an example for the importance of the work with cultivation methods, I will describe here the development of *Conopeum reticulum* (L.) in the laboratory. I have reared this species now about one year. It grows well and becomes mature under my cultivation conditions. After the colony was fed two months with *Cryptomonas*, I made the initial observation, which resulted in the determination of the following process: In the « triangular, interopesial cavities » on the proximal frontsides of the cystids of the autozooids, small redbrown bodies were to be seen, of nearly the same colour, as the gut of *Cryptomonas* fed autozooids. As the colony became older, some of the « triangular cavities » enlarged and were seen to contain polypids. Therefore, these structures are real zooids, and the name « reticulumzooid », used by several authors, is correct.

According to my observations in the laboratory the ontogeny of the zooids of *Conopeum reticulum* is to be devided into different stages (fig. 2):

STAGE I (about 1-2 weeks old) includes the growing border area of the colony (proceeding from the outer edge towards the middle): *a*) cystidbuds, containing young polypidbuds; *b*) « finished » cystids, including partially developed polypidbuds; in the proximal corners of the cryptocyst the lateral walls of the reticulumzooids start to grow, beginning under the frontal membrane of the autozooids; *c*) autozooids with evaginating polypids; in the meanwhile the calcification of the lateral walls of the reticulumzooids would be finished on the distal side, and now these walls reach over the frontal membrane of the autozooids; *d*) brown bodies appear in the autozooids by reduction of the first polypid generation; within the more developed reticulumzooids the first « feeding bodies » (see next stage) begin to grow.

fig. 2

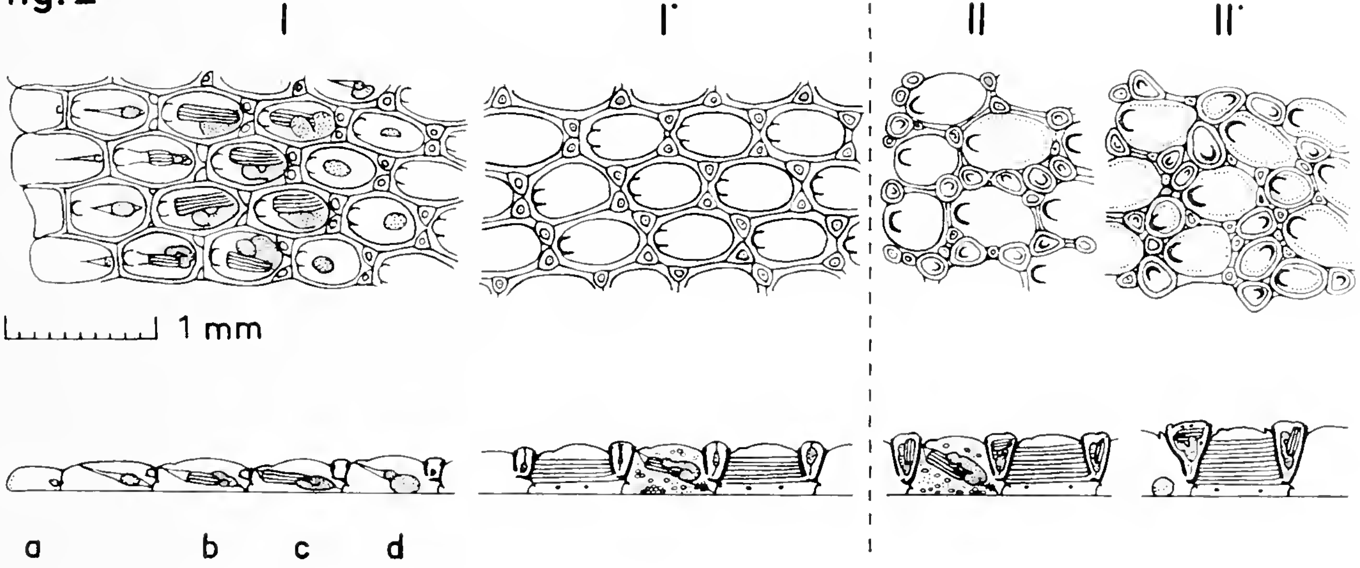

Fig. 2. — Developmental stages I-II′ of *Conopeum reticulum* (L.) in fontal view and sagittal section (schematic drawing). The dotted lines in the opesia of stage II′ show the wall building fold of the frontal membrane (see fmf in fig. 3 b) (not the cryptocyst). (Further explanation see text.).

STAGE I′ (about 2 weeks to 3 months old): Within the reticulumzooids the first generation of « feeding bodies » begins to take up food, which can be recognized by the red colour of *Cryptomonas* (some about the beginning of the 2.nd, most during the 6.th and the following polypid generations in the autozooids). The « feeding body » seems to consist of a very small excavation in a tissue layer; tentacles and a real gut are not to be seen; but the true nature of the « feeding body » until now is not certain. In the meantime the lateral walls of the autozooids are growing upwards, and with each polypid generation an additional layer is formed. Beginning in the 3.rd month the autozooids may become mature.

Stage II (beginning about the 4.th month): Some of the reticulumzooids have grown larger and contain a true, minute polypid with tentacles and an U-shaped alimentary canal. The cystidrooms of these reticulumzooids are enlarged, in that their lateral walls in growing layer by layer upwards have thereby also partly laterally expanded. In this way the cystids of the reticulumzooids take on a more or less conical form, whilst the aperture fields of the autozooids are gradually restricted. In this stage secondary reticulumzooids begin to grow. The autozooids in the meantime were or became mature. The lateral walls of the autozooids also grow upwards in layers, being apparently built up by cells under the lateral parts of the frontal membrane, a position where a fold appears in the older stages.

Stage II′ (beginning about the 5.th month): Whilst the cystids of some of the reticulumzooids continue enlarging themselves and partly expanding more to the sides, they build up generations of increasing larger polypids. Some of the polypids in the reticulumzooids attain the size of the polypids in the autozooids. Some reticulumzooids become mature. In contrast the autozooids of this age are not very active and many of them include for long periods of time a brown body; however, some also contain ovas.

In nature stage I and I′ are to be found. The « feeding bodies » seem to have been overlooked in the past, probably because they are so small. Until now the development of polypids in the « triangular cavities » was not observed in specimens from nature. Either the colonies did not reach the necessary age in nature, or unfavourable conditions in the natural habitats decisively reduced the vitality and growth rate. So this species possesses physiological potences for structure formations, which never or only seldom may achieve under natural conditions, but which can be realized under cultivation conditions.

The development of the reticulumzooids distinctly shows that the formation of a real polypid depends on a sufficiently enlarged volume of the cystid. The reticulumzooids are at first so small, that polypids with tentacles and a gut have unsufficient space. The formation of the « feeding bodies » in the first stage is an interesting morphological feature, which will later be described in detail in a separate, histological investigation.

The layer-type growth of the lateral walls seems to be a novelty within the *Cheilostomata.* The first impression is that this layered walls bear resemblances to those walls found in some *Cyclostomata,* but it is not yet clear, wether both structures can be directly compared.

The described observations allow a phylogenetic derivation of the spines of the genus *Membranipora* Blainville from zooids. A comparison of the first developmental stages shows without doubt, that the basis of the spines of *Membranipora membranacea* (L.)

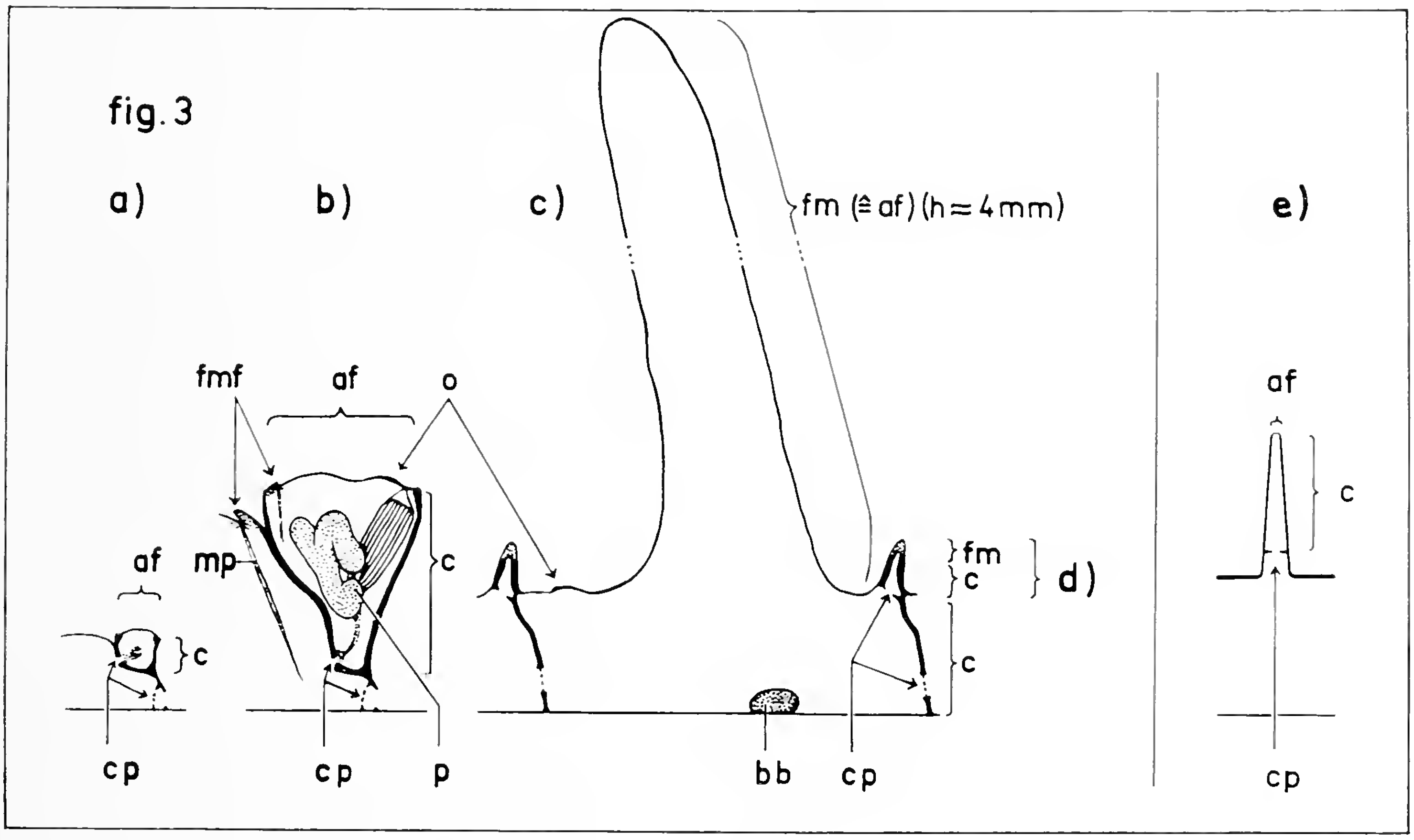

Fig. 3. — Schematic comparison of the reticulumzooids of *Conopeum* and the spines of *Membranipora.* a) starting stage, and b) old stage (II′) of a reticulumzooid of *Conopeum reticulum* (L.); c) towerzooid, and d) spine of *Membranipora membranacea* (L.); e) spine of the *Callopora*-type (schematic drawing). af = aperture field; bb = brown body; c = cystid (basal and lateral walls); cp = communication pores and rosette plates; fm = frontal membrane (≙ af); fmf = wall building fold of the fm; mp = parietal muscle; o = operculum; p = polypid.

are homologous to the cystidbuds of the reticulumzooids of *Conopeum reticulum* (L.). The building of the « towerzooids » from *Membranipora membranacea* may serve as a model for the spines. The towerzooids arise in that the frontal membrane grows like a tube upwards, after the polypids within these autozooids are reduced. In this case the autozooids themselves seem to come into a physiological condition that the bases of the spines have, when they start to build up the upper part of the spines. This upper part of the spines is homologous to the tube-like grown frontal membrane of the towerzooids. Thus, the spines of *Membranipora* represent much reduced towerzooids. (The « large spines » of *Membranipora villosa* Hincks illustrate an intermediate form.) - SILÉN (1942) derived the type of spines of *Callopora* Gray from zooids. The spines and tubercula of *Membranipora* are likewise heterozooids, perhaps they have developed in another phylogenetic way (analogous) (fig. 3).

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JOHN H. BUSHNELL (*)

ASPECTS OF ARCHITECTURE, ECOLOGY, AND ZOOGEOGRAPHY OF FRESHWATER *ECTOPROCTA*

(*Bryozoa*)

Riassunto. — Vengono esaminate otto specie di *Ectoprocta*: *Plumatella repens, Plumatella fruticosa, Plumatella casmiana, Plumatella fungosa, Cristatella mucedo, Hyalinella punctata,* trovate nella parte occidentale dell'America del Nord, *Fredericella sultana* proveniente dallo Stato del Colorado, negli Stati Uniti, e *Plumatella repens, Fredericella sultana,* e *Fredericella australiensis* dagli Stati di Chihuahua e Durango, nel Messico.

Le informazioni di carattere limnologico indicano che *P. fruticosa* è limitata agli ambienti aventi i più bassi valori e la più ristretta gamma di ceneri, di sostanze organiche, di CO_2 legato, e di pH, e che è la più vivacemente colorata di tutte le specie indigene del Colorado. Questa specie si trova soltanto nei laghi montani. *P. repens* cresce negli ambienti di più alto livello eutrofico, e *F. sultana* prevale nelle zone di terreno aperto. *P. casmiana* è l'unica specie incontrata in un ambiente prettamente alcalino dei Grandi Altopiani centrali, e *P. fungosa* è stata trovata soltanto nei laghi delle Montagne Rocciose occidentali. *F. australiensis* è stata notata in tre diverse località dell'arido altopiano centrale messicano.

Nelle colonie di *P. fruticosa* trovate nel Colorado, le minuscole aree di gemmazione si riscontrano di rado. Gli statoblasti di questa specie, in modo particolare quelle provenienti dagli stagni formati dalle morene glaciali, sono più grandi di quelle della maggior parte delle altre osservate. *P. casmiana* libera leptoblasti attraverso una cisti ialina e un poro vestibolare. Vengono pure descritti lo sviluppo zoariale di *P. fungosa*, e la insolita architettura zoariale di *F. australiensis*.

Si discute, inoltre, della classificazione di *F. australiensis*, e si fa notare quanto siano rari gli ambienti nel mondo dove si riscontra questa specie. Si accenna a certi aspetti della morfologia e dell'ecologia che possono costi-

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tuire argomenti validi contro la classificazione di *F. australiensis* e *F. sultana* sotto la medesima specie. Viene esaminata l'adattabilità di certe specie di *Ectoprocta*.

Summary. — Eight species of *Ectoprocta* from western North America are discussed: *Plumatella repens, Plumatella fruticosa, Plumatella casmiana, Plumatella fungosa, Cristatella mucedo, Hyalinella punctata,* and *Fredericella sultana* from the State of Colorado, U.S.A. and *Plumatella repens, Fredericella sultana,* and *Fredericella australiensis* from the States of Chihuahua, and Durango, Mexico.

Limnological information shows *P. fruticosa* restricted to habitats with the lowest values and narrowest range of ash, organic, bound CO_2, and pH, and the highest color of any Colorado species. This species is found only in montane lakes. *P. repens* is found in the more eutrophic habitats, and *F. sultana* has the most euryzonal distribution. *P. casmiana* was the only species associated with an alkali habitat on the central Great Plains, and *P. fungosa* only from montane lakes in the western Rocky Mountains. *F. australiensis* occurs at three sites in the high, arid central plateau of Mexico.

The diminutive budding zone of *P. fruticosa* is infrequent on Colorado colonies. Statoblats of this species, especially those from glacial moraine ponds are wider than most others reported. *P. casmiana* releases leptoblasts via a hyaline cyst and vestibular pore. Zoarial development is described for *P. fungosa.* Unusual zoarial architecture is described for *F. australiensis.* The species status of *F. australiensis* is considered, and attention is directed to the uniqueness of the world habitats of this species. Certain aspects of the morphology and ecology argue against the conspecificity of *F. australiensis* and *F. sultana.* The adaptive success of certain ectoproct species is considered.

Zusammenfassung. — Mann diskutiert acht Arten von *Ectoprocta* aus den westlichen Nord-Amerika: *Plumatella repens, Plumatella fruticosa, Plumatella casmiana, Plumatella fungosa, Cristatella mucedo, Hyalinella punctata* und *Fredericella sultana* aus Kolorado, Vereinigten Staaten, und *Plumatella repens, Fredericella sultana* und *Fredericella australiensis* aus den Staaten Chihuahua und Durango in Mexico.

Limnologische Informationen zeigen, dass *P. fruticosa* ist zu den Habitaten mit den niedrigsten Werten und den engsten Variationen der Asche, organisches, CO_2, pH, und höchster Farbe jeder Kolorado-Arten gehörig. Diese art ist nur in montanen Seen gefunden. *P. repens* ist in mehr eutrophischen Habitate gefunden, und *F. sultana* hat die meist allgemeine Verbreitung. *P. casmiana* ist die einzige Art, die mit einer Alkalischen Habitat auf der zentralen Prärie associiert ist, und *P. fungosa* kommt nur in den montanen Seen der westlichen Felsengebirgen vor *F. australiensis* ist von drei Lokalen der hohen, trockenen Zentral-Plateau Mexico bekannt.

Die winzige Knospenzone der *P. fruticosa* ist in Kolorado-Kolonien ausserordentlich. Die Statoblasten dieser Art, speziell aus glazialer Morän-

Dämme, sind breiter als von anderen Arten bekannt. *P. casmiana* löst Leptoblasten via eine hyaline Zyste und eine vestibulare Pore ab. Die zoariale Auswicklung ist für *P. fungosa* beschrieben. Eine ausser-ordentliche zoariale Struktur ist für *F. australiensis* beschrieben.

Die Art-Statur der *F. australiensis* is diskutiert, und Aufmerksamheit ist zu den Einzelheiten der Welt-Habitat dieser Art gewidmet. Speziellen Gesichtspunkte der Morphologie und der Oekologie sprechen wider jeder Auffassung, dass *F. australiensis* und *F. sultana* conspezifisch sind. Die adaptive Anpassung gewisser Ectoprocten ist diskutiert.

There are few studies or reports of Ectoprocta from western North America. The occurrence, form, and ecology of the freshwater *Ectoprocta* in the west are of particular interest, because the geology, soils, vegetation, lakes and streams are different from those in the midwestern and eastern regions of the continent. I shall, therefore, discuss certain aspects of my studies and observations on ectoprocts of western North America, especially as they relate to species of the genus *Plumatella* and the genus *Fredericella*. The organisms to be discussed are from the State of Colorado in the western U.S.A. and from the States of Chihuahua and Durango in Mexico.

Colorado has the highest mean elevation of any of the Rocky Mountain states, 2073 meters (PENNAK, 1963), and there is considerable intraregional variability in the geochemistry, topography, and climate of the Rocky Mountain region. There is great variation, biologically, chemically, and physically, in the lakes of the northern Colorado lake district, especially in the montane lakes (2500-3200 m.). PENNAK (1945) divided montane lakes limnologically into drainage and semi-drainage lakes. Most of the lakes fall into the first category and are situated in valleys where there is continuous inflow and outflow. Biologically, the most fertile lakes, supporting the greatest numbers of invertebrates and the most luxuriant growths of rooted aquatic plants, are the semi-drainage lakes without regular inflow and outflow. Lakes and ponds in the montane region are often closely encircled by spruce and pine, but on other occasions by willow and dwarf birch. On the western slopes of the Rocky Mountains in northern Colorado nearly pure stands of lodgepole pine surround some lakes while aspen may surround others. Many of these lakes are located on the nearly level surface of mesas where arid or semiarid conditions prevail.

The alpine lakes are far less variable and less productive. The exposed rocks of most of the Rocky Mountains are largely insoluble schists, gneisses, and granites low in nitrates, sulfates, phosphates, carbonates, and fluorides (PENNAK, 1963). There is little organic matter being washed into the majority of high lakes as water filters through a very thin soil cover. PENNAK has pointed out that many high lakes have a total ash content of less than 15 mg/l, 6 to 12 mg of this total being silicon compounds thereby leaving only 3-9 mg for all other inorganic ions. After silicon, calcium and bicarbonate ions are deducted, all other inorganic ions may contribute less than 1 mg/l to the total ash content of the water. The pH of the waters of the alpine and montane lakes in general are around neutrality or slightly below. PENNAK (1963) gives average figures of 28.52 and 10.41 mg/l respectively of ash and total organic matter in montane drainage lakes and 60.23 and 34.08 mg/l of the same in montane semidrainage lakes. Average figures for ash and organic matter for alpine lakes are, of course, lower. Calcium and phosphate-phosphorous are nearly the same for semidrainage and drainage montane lakes, while nitrate-nitrogen is considerably higher in the former, on the average 1.137 mg/l to 0.168 mg/l. That this nitrogen accumulator role of semidrainage lakes may be of fundamental importance in the biology of montane lakes has been strongly endorsed by PENNAK (1958).

There is a considerable increase in total residue in the plains lakes of Colorado as compared to the true mountain lakes. Plains lakes are those below 1700 meters in altitude. Considerable local variations in the geochemistry contribute to great variation in the plains, and lakes become more alkali the farther one travels east from the mountains. The greater distances the rivers flow out onto the plains the greater the accumulation of various chemicals. The nonalkali plains lakes average 202.96 mg/l ash and 24.96 mg/l of organic material, while comparable figures for alkali lakes are 1,729.78 and 237.20 mg/l (PENNAK, 1963). The only large bodies of water in the mountains of Colorado are the reservoirs, all formed in recent years. Of the natural lakes, mostly glacial in origin, almost none are as large as one square mile in size or much over 5 meters in depth. Nearly all the plains lakes in the Rocky Mountain region are artificial, formed by damming one or more shores, and connected via a network of irrigation canals. Some are flushed rather severely by regular inflow and outflow, or by irrigation needs; others have a more stable water level, thus encouraging the development of more stable biological communities.

In extremely thorough recent searches of Colorado plains, montane and alpine lakes, (a total of 44) seven species of *Ectoprocta* have been found in 31 lakes and 2 streams. All of the lakes in which ectoprocts were not found were either strongly alkali plains lakes, 25-150 miles east of the eastern foothills of the Rocky Mountains or certain of the very high alpine lakes, e.g., Summit Lake (3884 meters), at the base of rock and gravel strewn cirques. With respect to these two extremes of habitat, only one species, *Fredericella sultana*, has been found in Colorado in an alpine lake and only one species, in a single locale, in a shallow, central plains, alkali lake, *Plumatella casmiana.*

The two most common species in the Rocky Mountain region of western North America are *Plumatella repens* (12 sites) and *Plumatella fruticosa* (10 sites). Certain limnological data for all species are given in Table I. It is remarkable that *P. fruticosa* was discovered in ten of the 31 lakes in which ectoprocts were found. This equals the number of times this species was found in 123 ectoproct inhabited lakes in Michigan (BUSHNELL, 1965a). Prior to the Michigan report the species had been found in only two locations in the much more extensively explored eastern half of North America. This suggests that the species may be much more common in the western portions of the continent.

All specimens of *P. fruticosa* were taken from montane lakes and ponds both east and west of the Rocky Mountain Continental Divide. In the east the collections were taken largely from small glacial moraine ponds with the greatest abundance of colonies being taken from locations on top of the Arapahoe glacial moraine, a termino-lateral moraine. This moraine lies at the base of two valleys, both pointing into the Continental Divide. The ponds are all about 10,400′ in altitude, surrounded very closely by lodgepole pine and englemann spruce. In some cases the ponds are surrounded by a wide trembling sedge border (Fig. 1) while other ponds are overhung by dwarf birch and willows.

Collection sites to the west were small lakes largely encircled by lodgepole pine or aspen. All the montane ponds were from 0.3-1.5 meters in depth and frozen to the bottom in winter. In most of the ponds and lakes either *Nuphar polysepalum*, native to the Rocky Mountain region, or *Sparganium* sp. (or both) are present.

The lakes in which *P. repens* was found were mostly on the western edge of the Great Plains, adjacent to the foothills zone. Other collections were taken from montane, semidrainage lakes. In all cases they were taken from lakes with rich growths of rooted aquatics and floating algae, most commonly potomogetons, *Myriophyllum, Elodea canadensis* and *Ceratophyllum demersum*. The biological and chemical conditions most closely resembled those prevailing in large numbers of eutrophic waters in the lake districts of midwestern U.S.A.

Plumatella fungosa was found in four montane lakes west of the Continental Divide, all within a few miles distance from each of the other collection sites. Two of the locations are reservoirs; one a natural lake in the lodgepole pine surrounded by high rocky bluffs and traversed by a gentle inflow and outflow stream. The last location is a lake formed by beaver dams in a small drainage stream. The two small reservoirs in which the most luxuriant colonies appeared were partially surrounded by aspen, and otherwise by gentle slopes covered by sagebrush and other arid plateau vegetation. The thick encrustments of *P. fungosa* were found in small bays shaded by dense aspen groves. Dense growths of *Polygonum* and a remarkably rich plankton community were present.

None of the lakes in the high plateau district (North Park area) on the western slopes of the Rocky Mountains, where *P. fungosa* was found, are severely flushed by rapid inflow streams and snow melt in the spring and early summer. Because of this these lakes are not subject to the severe seasonal turbidity and loss of organic material, e.g., nitrates, characteristic of drainage lakes located in steeper terrain on the eastern slopes.

The two occurrences for *Plumatella casmiana*, previously identified in the western hemisphere only from material collected in Lake Erie or its environs, extends the range of this species considerably. The alkali reservoir from which it was collected in the treeless central Great Plains region of eastern Colorado has a maximum size of approximately 3696 acres. In this habitat the zooecia were attached to twigs of shrubs in a 6 ft. wide irrigation inlet and to a few pieces of deteriorated vegetation on a shallow wind-blown shore. The second collection was taken from a small gravel pit pond, 5 miles east of the foothill zone of the Rocky Mountains, near Boulder, Colorado. The basin of this 1/4 acre pond was a former gravel pit, one of several, in the vicinity. These gravel pits have been supplied almost entirely by ground water seepage from nearby Boulder Creek. While most of the associated gravel pit ponds or lakes (Sawhill lakes) lacked vegetation, the one in which *P. casmiana* was found was thickly overgrown from one shore to another by a rooted aquatic community of which *Ceratophyllum demersum* and *Elodea canadensis* were

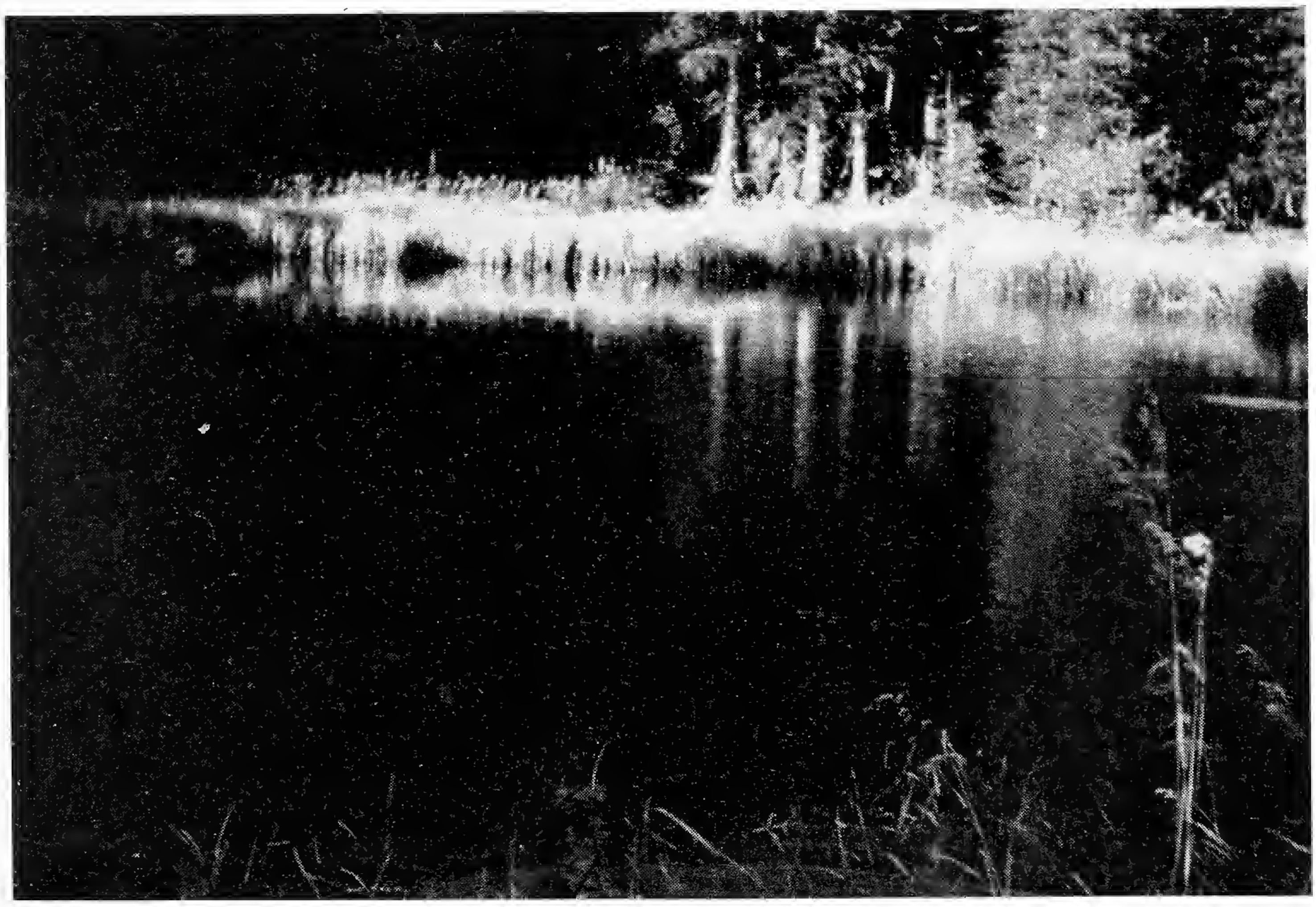

Fig. 1. — A moraine pond in the Rocky Mountains of Colorado. One of several montane ponds in which *Plumatella fruticosa* is found.

codominants. The ectoproct was covering every substrate in late June and early July of this year, i.e., logs, rocks, and densely entwined about the stems and leaves of the dominant rooted aquatic plants. By July 8 floating algal mats (*Rhizoclonium sp.*) occupied nearly all the open water among the rooted aquatic plants.

The single small colony of *Hyalinella punctata* was found in a semidrainage montane lake on the eastern slopes of the Continental Divide. A very thick and clear gelatinous zoarium had developed a small colony. No statoblasts had been produced, but the statoblast from which the colony had developed was present. It was the small type floatoblast, heretofore not reported for *Hyalinella punctata* in the western hemisphere.

The locations for *Cristatella mucedo* were Glacier Lake and Muskee Lake, both montane lakes. Small colonies of no more than 40-50 individuals were found in the early summer of 1967 and again in 1968. The temperature of the lake on July I, 1968, was 15°C. No large colonies were found in late summer and early autumn but numbers of statoblasts could be found along the rocky lake shores. This species was not unexpected as it has a holoarctic distribution in several colder north temperate lakes. The author has taken the species from two lakes 75 miles southwest of Hudson Bay in north central Canada.

The seven locations from which *Fredericella sultana* was taken establish the species as the most euryzonal and euryokous species in the Colorado collections. It occurs from lakes on the western Great Plains up to lakes in the alpine zone, in both eutrophic and oligotrophic situations and in both lotic and lentic waters. This wide range of habitat, evident for *F. sultana* in the Rocky Mountains region only reinforces the broad physical and chemical adaptability demonstrated and discussed for this species in an earlier study (BUSHNELL 1966).

The altitudinal range and certain standard limnological values for ectoproct habitats in Colorado are summarized in Table I. It is apparent that *F. sultana* inhabits waters with the lowest, or near the lowest, figures for all limnological measurements given. *Plumatella repens* shows somewhat higher figures for all categories. However, unpublished data for these same limnological categories from Michigan and Pennsylvania are generally consistent with Table I, except that *F. sultana* occurred in these states

TABLE I. - *Colorado Ectoprocta.*

Chemical information on littoral waters of collection sites. Single figures represent means for all sites (obtained from averages of three seasonal readings at each site). Minimum and maximum figures for each collection site in parentheses.

Species	No. of collection sites	Altitude (range meters)	ash mg/liter	organic mg/liter	Bound CO_2 ppm	pH	Color Platinum-cobalt
Plumatella repens	12	1559-2768	47.46 (21.37-491.13)	69.95 (21.66-180.51)	35.61 (10.00-71.40)	8.3 (7.4-9.3)	27.3 (4-55)
Plumatella fruticosa	10	2688-3200	9.90 (7.02-16.98)	18.05 (5.79-26.98)	6.53 (4.05-13.45)	7.1 (6.7-7.3)	48 (12-160)
Plumatella fungosa	4	2738-2860	82.14 (54.88-107.40)	58.06 (42.62-73.50)	57.22 (42.75-71.50)	8.7 (7.8-9.6)	41 (36-45)
Plumatella casmiana	2	1190-1573	771.96 (186.07-1357.84)	237.04 (91.80-382.26)	53.30 (49.35-57.25)	8.4 (8.2-8.6)	9 (7-11)
Hyalinella punctata	1	2617	40.71	59.22	19.65	7.4	49
Fredericella sultana	7	1555-3313	49.83 (7.71-210.47)	25.12 (5.55-88.62)	11.84 (3.65-33.16)	7.4 (6.9-8.3)	19 (7-47)
Cristatella mucedo	2	2768-3103	21.77 (21.56-21.97)	20.79 (19.23-22.34)	9.63 (7.95-11.30)	7.1 (6.9-7.3)	32 (17-47)

at sites with ash, organic, and pH readings nearly as high (in two cases higher) as *P. repens* in Colorado. *F. sultana* has a lower temperature tolerance, grows and begins development at lower temperatures, and demonstrates greater physical and chemical tolerances than other species in its ability to develop on wave washed shores, in rapid rivers and in locations near the bottom. There is increasing evidence that *F. sultana* will not tolerate the extreme high temperatures (e. g., 35°C. and over) endured by *P. repens,* or situations in which an extremely high pH prevails. While the low figures in Table I for *Plumatella fruticosa* are in close agreement with those for *F. sultana,* the ranges for this species are narrowest of all. This supports the contention (BUSHNELL 1966) that this species is more narrowly adapted to generally oligotrophic neutral or slightly acid, and often highly colored waters. Similar habitats, and associations with indicator organism of such habitats, *Tubella pennsylvanica* and *Batrachospermum ectocarpum* have been discussed for Michigan. The habitat data (Table I) for *Plumatella fungosa,* are consistent with those for *P. repens.* The measurements for species with fewer collection sites are important only as they may be combined with future limnological information.

The tabular information is not given to suggest that one or another factor is by itself restrictive or congenial for a particular species, but only to indicate that generally different environmental situations may be associated with different species. It suggests that other unmeasured factors, associated with these general limnological conditions, may govern the occurrence of freshwater ectoprocts.

A somewhat unexpected aspect of ectoproct distribution in Colorado is that only five co-occurrences of ectoprocts are recorded for the 33 extensively studied habitats in which these animals have been found. In none of these five lakes were more than two species found. Some of this is doubtless explained by the small size of the natural lakes in Colorado, from which a majority of the collections were made. The lakes of eastern North America, from which several species have been reported (BUSHNELL 1965a), have been much larger lakes. These larger lakes offer a considerably greater variety of intralake habitats, viz., bays with considerable plant growth, extreme wave washed shores, several different plant communities, and inlets where slowly moving rivers deposit considerable river borne organic material and detritus as they enter the lake. The fact that so many of the very small Colorado lakes are frozen to the bottom during the winter and that so few have even a temporary thermocline, and the enriching effects of a spring and autumn overturn, may be other factors. Certain barriers to easy distribution, e. g., mountain ranges, steep stream gradients, a vast semiarid region to the east, north and south (with predominantly strongly alkali ponds or reservoirs) and a prevailing westerly wind, may help to explain the paucity of species in any given habitat.

The five co-occurrences involved *F. sultana* and *P. fruticosa* on two occasions, in lakes no more than one mile distant and connected by a creek, *C. mucedo* and *P. repens, C. mucedo* and *F. sultana*, and *P. repens* and *H. punctata*. In no location were these co-occurring species found in close physical association.

Knowledge of the freshwater *Ectoprocta* of Mexico is limited essentially to a paper by RIOJA (1940) in which *P. fruticosa*, several phases of *P. repens, H. punctata* and *F. sultana* are all reported from Lake Xochimilco near Mexico City. The author has taken ectoprocts from the states of Durango and Chihuahua, with most collections coming from reservoirs or shallow irrigation lakes on the high plateau of central Mexico, in the Chihuahuan desert region of Chihuahua and northern Durango. A single small colony of *P. repens* was taken from a roadside pond (former excavation site) near the southern boundary of Chihuahua. The marshy habitat was largely overgrown with the tall *Typha domingensis*. A second collection was taken from a small lake in Durango province. Numerous colonies of *F. sultana* were found in a small stream high in the Sierra Madre Occidentale mountain range of west central Durango.

The most extensive and luxuriant specimens of *Ectoprocta*, *Fredericella australiensis*, were obtained from shallow reservoirs, or irrigation lakes, of the arid, largely treeless, somewhat rolling central plateau of Mexico (Fig. 2). The rare *F. australiensis* was taken from three sites of this region, one in Chihuahua and two in northern Durango. Rooted vegetation was not abundant in any of the lakes. One had patches of *Scirpus sp.* in the vicinity of the ectoproct growths, and a second very shallow irrigation reservoir had heavy bottom growths of *Ludwigia palustris.*

Colonies of *F. australiensis* were growing on almost all the plants and rocks sampled in these lakes. The near shore area of both lakes was covered with several inches of gyttja and the plants were often encrusted with a whitish detritus. Colonies found in the third lake were smaller. This lake was notably barren, with a bottom of large rocks and smaller rubble. All three lakes were created by the damming of small shallow desert streams or by irrigation canals from temporary streams. None of them was more than fifteen years old. All collections were made during August and the water temperature was 30°C-35°C during the day. A few insect larvae and oligochaetes were the

Fig. 2. — Big Boquilla Reservoir (Lake) in southern Chihuahua Desert, Mexico. Numerous colonies of *Fredericella australiensis* were taken here.

most obvious associated animals. However, the sponge *Asteromyenia plumosa* was closely associated with *F. australiensis* in one of the lakes.

Colony Form and Morphology.

Detailed measurements and descriptions of the eight species of *Ectoprocta* discussed in this paper will be contained in a separate publication now in preparation. However, certain aspects of the colony growth, measurements, and some speculative considerations are appropriate to the present discussion.

In general, all specimens of *P. repens*, *P. fruticosa*, and *P. casmiana* conform to previously published « typical » descriptions. Only one colony of *P. repens*, taken from a Colorado sandstone quarry, was somewhat unusual in that the zooecia protruded nearly vertically from the substrate for distances of 2.1 to nearly 3.0 mm. Several orifice areas were somewhat serrated. In all other characters these specimens and those from other locales conformed, e. g., lack of encrustation, statoblast morphology and measurements, tentacle number, shape of zooecia, amount of septation, and colony form, as summarized for this species by BUSHNELL (1965b; Table I).

Colonies of *P. fruticosa* are largely consistent with Michigan specimens (BUSHNELL, 1965c) in such characters as zooecial size, transparency, keeling, septation, tentacle number and growth pattern. Many colonies in the moraine ponds were only loosely attached to the substrate, sometimes hanging down from the undersurface of sticks for 3-6 centimeters. The linear series of small daughter zooecia produced by a mother zooecium were found in colonies from only two of the ten collection sites, in both cases from moraine ponds. This unique budding zone of *P. fruticosa* was found in colonies from only 4 of 10 collection sites in Michigan (BUSHNELL 1965c). It had not been mentioned previously for the western hemisphere (DAVENPORT, 1904, Lake Erie; ROGICK, 1935, Lake Erie; RIOJA, 1940, Mexico; MARCUS, 1942, Brazil). From the papers of JULLIEN (1885), WIEBACH (1954), and TORIUMI (1954) it is obvious that the linear budding zone of *P. fruticosa* frequently has a greater number of daughter buds in a series, and is more often observed, on european and eastern asiatic specimens, than on those from North America.

Statoblasts of *P. fruticosa* collected in western North America are not so narrow as those from Michigan or from the eastern hemisphere. The length to width ratio for floatoblasts from other collections is usually between 2.3 : 1 and 2.8 : 1 (e. g., BRAEM, 1890; PATEFF, 1924; TORIUMI, 1954; BUSHNELL, 1965c). Ratios for sessoblasts have been similar to those for floatoblasts. The length to width ratios of the statoblasts in Michigan collections is 2.45 : 1 for floatoblasts and 2.3 : 1 for sessoblasts. In the Colorado collections the length to width ratio for all but one collection site is 2.04 : 1 for floatoblasts and 2.31 : 1 for sessoblasts. Collections from lakes on the western slopes of the Rocky Mountains had the narrowest statoblasts, 2.21 : 1 for floatoblasts and 2.25 : 1 for sessoblasts. Brainard lake, a cold montane lake (10,000 ft. elev.) fed by two rushing streams emanating from tundra glaciers, has colonies of *P. fruticosa* with statoblasts consistently less elongate than most other reports (Fig. 3, 4). From measurements of more than 200 statoblasts in the past three years floatoblasts from Brainard lake have a length to width ratio of 1.60 : 1 and sessoblasts a ratio of 1.64 : 1.

Other reports of unusually wide statoblasts have been made for *P. fruticosa* (ANNANDALE, 1911, India; VORSTMAN, 1928, Java; MARCUS, 1942, Brazil). TORIUMI (1954) seriously questioned the validity of the VORSTMAN and ANNANDALE specimens, claiming, in effect, that they did not overlap the range of length to width rations of *P. fruticosa*. VORSTMAN gives a ratio of 1.6-2.0 : 1. MARCUS (1942) published the last description of unusually wide

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Fig. 3. — Wide floatoblast of *Plumatella fruticosa* from Brainard Lake, Colorado.

Fig. 4. — Wide sessoblast of *Plumatella fruticosa*.

Fig. 5. — Portion of a colony of *Plumatella fungosa* from Ninegar Reservoir, Colorado.

Fig. 6. — Densely entwined colony of *Fredericella australiensis* on stem of *Ludwigia palustris* from Big Boquilla Lake, State of Chihuahua, Mexico.

Fig. 7. — Statoblast of *Fredericella australiensis* from Big Boquilla Lake, State of Chihuahua, Mexico.

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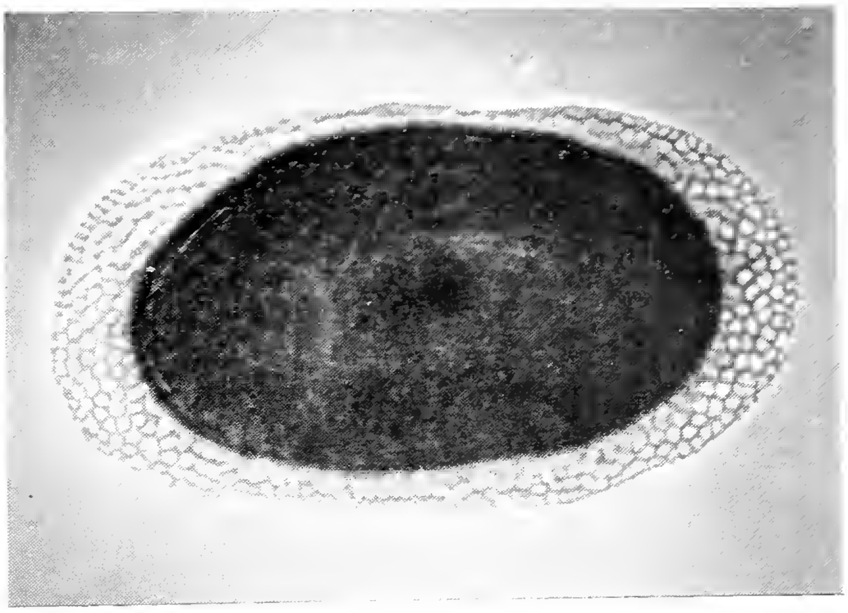

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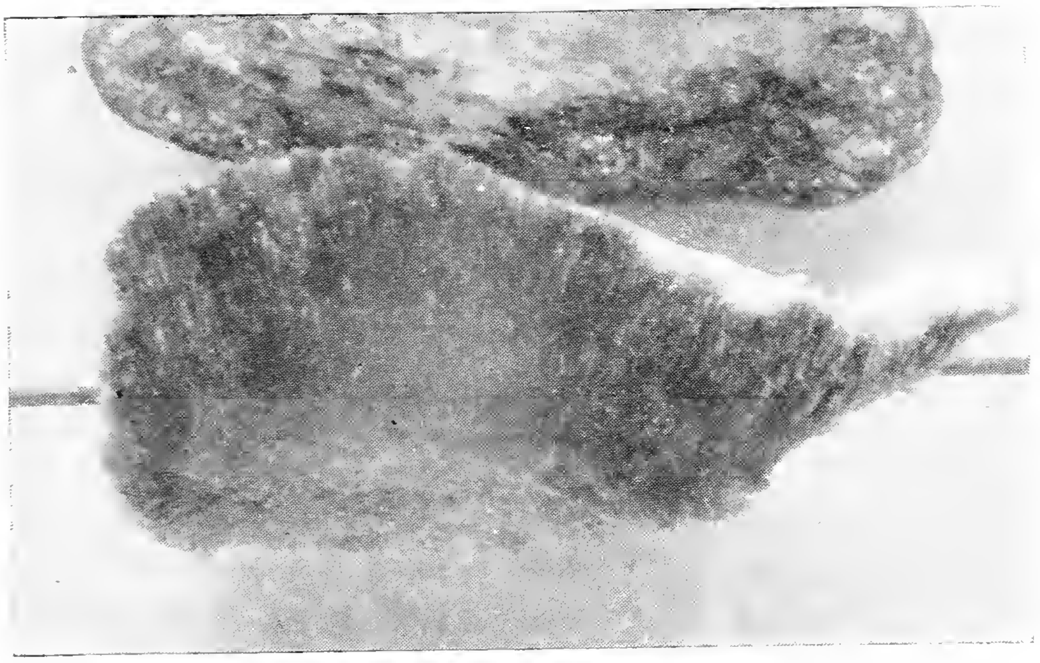

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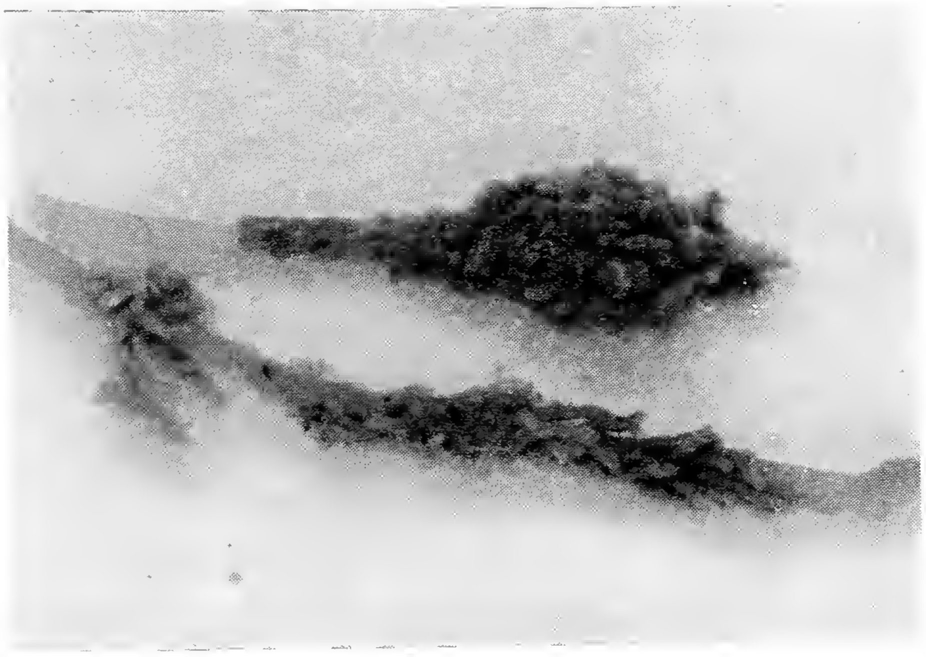

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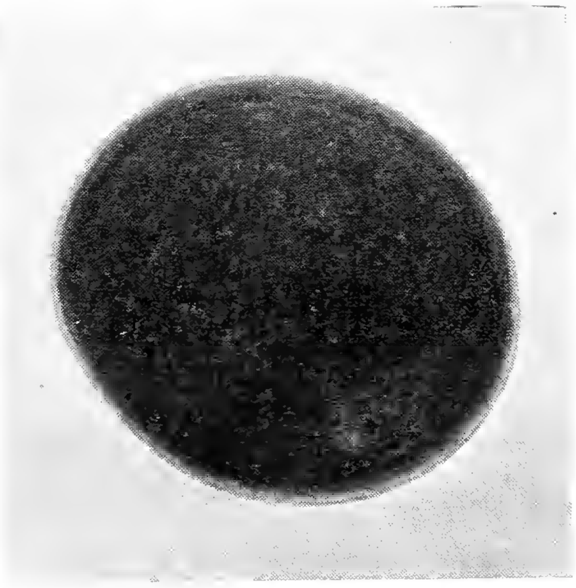

P. fruticosa statoblasts from colonies found in the southern portion of the State of São Paulo, Brazil. For these he gave an average ratio of 1.76:1 in the text, (1.66:1, in summary). This is close to the same as the figures for Brainard Lake, Colorado. His drawing, figure 2, showing a floatoblast of *P. fruticosa* is remarkably like figure 3, in this paper. Even though MARCUS was not completely satisfied with the identification of *P. fruticosa* in Brazil, and recent keys to the freshwater *Ectoprocta* continue to state that statoblasts of *P. fruticosa* are more than twice as long as broad, there is no doubt from the range of ratios for Colorado specimens that there is a continuum as regards shape. Once again the extreme variability of critical identification characters for freshwater ectoprocts is highlighted. A ratio of 1.6:1 is one extreme for statoblasts of *P. fruticosa*. The other extreme is a ratio of more than 3:1 for the commonly narrower european specimens (WIEBACH, 1954).

The lamella on the sessoblasts of *P. fruticosa* is characteristically wide and possesses the sharply defined reticulations, better developed by this species than by any other freshwater ectoproct. The tuberculations at the periphery of the capsule are not in general as abundant or elongate on Colorado samples as they are on so many of the Michigan specimens.

Specimens of *P. casmiana* from the western United States are in excellent agreement with descriptions by OKA (1907), ROGICK (1941), TORIUMI (1955a), SEBESTYEN (1961) and WIEBACH (1963). In fact, as one examines an increasing number of specimens of this species, there appears to be a refreshing consistency with respect to the architecture of the colony, the individual zooecia and polypides, and the statoblasts. The keel, encrustation, hyaline furrow, tentacle number (30-40 in Colorado specimens), and growth pattern are in close agreement for colonies collected from numerous regions of the world. There is a conformity with respect to float coverage on the pyknoblasts of all collections - similar in size to *P. repens*, but intermediate with respect to float coverage between *P. emarginata* and *P. repens*. The leptoblasts from many sites are likewise largely identical. Only leptoblasts were being produced by the hundreds of colonies found in Sawhill pond near Boulder, Colorado in June and early July, 1968. Most of the colonies from the alkaline Nee Noshe

Reservoir (July 1967) in the arid central Great Plains were producing leptoblasts, but a few had pyknoblasts. Some colonies at each location had developed from pyknoblasts, others from leptoblasts, and sessoblasts. In recent collections from Sawhill pond several leptoblasts were released through a vestibular pore. This phenomenon was first noted for species of *Stolella* and for *Hyalinella carvalhoi* by MARCUS (1941, 1942). WIEBACH (1952) described the release of floatoblasts from polypides of *P. fruticosa* through the agency of a protrusive hyaline cyst. A similar cyst was observed as the mechanism of release of leptoblasts in *P. casmiana*.

The author has continuing reservations about the species status of *Plumatella fungosa*. Certainly no characteristic argues more strongly for the species status of this form than the massive and physically tough zoarium produced by the vertical growth of parallel series of zooecia and by the unusually permanent adherence of all zooecia. A degree of zooecial adherence is known for other species, e. g., *P. emarginata*, but nowhere is it so important for colonial form as in *P. fungosa*. The zooecia will tear at any location before they will break at points of contact with other zooecia.

Certainly, as WESENBERG-LUND (1896) claimed, massive colonies of *P. fungosa* are formed by the simultaneous germination of numerous statoblasts on a substrate. Fungoid colonies of *P. repens* have been formed on a substrate over successive years (BUSHNELL 1965b), but the important colonial aspect (as stressed before) that must distinguish *P. fungosa* from other fungoid-type colonies is the vertical nature of the zooecia, and the denseness of the zoarium resulting from the total adherence of all zooecia. There is some question as to whether such a distinction is always made by biologists reporting fungoid masses as *P. fungosa*. Those colonies from Sardinia, pictured by CARRADA (1964), described by LACOURT (1949, reports *P. fungosa* as most common species in the Netherlands) may not be, in each case, the exact form portrayed by ALLMAN (1856).

The colonies in Colorado develop first as small intertwining colonies, germinated from sessoblasts in numerous parallel series on the substrate, and from large numbers of floatoblasts caught in detritus of the substrate. The remarkable stickiness of the newly germinated ancestrulae and subsequent zooecia insures that not only zooecia will adhere, but also ancestrulae will attach to any piece of sand or wood or detritus. This means that several zooecia, originally not contiguous, will eventually (with growth) be brought into physical contact by their strong adherence to small chunks of matter on which other zooecia are also adherent. BORG (1941) refers to the *P. repens*-type young colonies of *P. fungosa.* Small colonies in the early stages of growth are frequently encrusted. The base of a large zoarium is composed largely of horizontal zooecia richly intertwined. Later the zooecia of the total compound colonial mass is directed vertically (Fig. 5).

The statoblasts of *P. fungosa* in Colorado resemble those of *P. repens,* but they are larger (average 0,475 × 0,305 mm). Averages for Michigan floatoblasts for *P. repens* (BUSHNELL 1965b) were 0.35 × 0.26 mm. (Colorado floatoblast sizes are comparable). The largeness of the *P. fungosa* statoblasts is mentioned by ABRIKOSOV (1927a), BORG (1941), and LACOURT (1949). The latter describes a small and a large statoblast for colonies of *P. fungosa,* the large one not quite as large as the average for Colorado specimens.

The single small colony of *H. punctata* in a Colorado montane lake was colorless, linear, and with a zooecial diameter of more than 0.95 mm. There were no protruding zooecial tips, only a flat zoarial surface from which polypides could be extended. There were no statoblasts except the one from which the colony had originated. This floatoblast was a small floatoblast, only slightly larger than those described by LACOURT (1949). KRAEPELIN (1887) and TORIUMI (1955b) also refer to the small statoblasts sometimes associated with *H. punctata.*

The colonies of *F. australiensis* from Mexico were largely repent, not showing the long raised tips portrayed by ROGICK (1945) for Wyoming specimens. A keel was moderately developed on the repent portions, but largely absent on the somewhat raised tips. It was not nearly so well defined as on the repent zooecia of *F. sultana.* While the colonies were usually loosely encrusted the luxuriant colonies were different from previous descriptions in their growth form. They tended to intertwine forming compact nodular masses on the stems of plants (Fig. 6).

The colonies agree more closely in measurements, tentacle number, zooecial diameter, and zooecial shape (elliptical in cross section) with ROGICK's (1945) var. *browni* than with var. *transcaucasica* (ABRIKOSOV, 1927b) or *australiensis* (GODDARD, 1909). The statoblasts of the Mexican collections average 0.376 mm. by 0.292 mm. The zooecia while being as narrow as 0.235 mm., average 0.40 mm. (Fig. 7). There were often 3 to 4 statoblasts in each zooecium.

The species status of *F. australiensis* is in doubt. BORG's (1936) specimens from the central Sahara, as ROGICK (1945) suggested, appear to be *F. australiensis* rather than *F. sultana*. MARCUS (1946) described a variety from Brazil as *F. sultana crenulata*, seemingly intermediate between *F. sultana* and *F. australiensis*. MARCUS (1953) described *F. australiensis* for Lake Titicaca. ABRIKOSOV (1961) split *Fredericella* into several species, subspecies and varieties, feeling that differences in statoblast design and dimension are sufficient for increasing all subgeneric categories. Then BONETTO and CORDIVIOLA (1965), perhaps more reasonably, suggested that probably only one species of *Fredericella* should be recognized, *F. sultana*. They suggested this on the basis of collections in Argentina where statoblasts from a single locale show a continuum in shape, ranging from *F. sultana* through var. *crenulata* to *F. australiensis*. They also claim a direct relationship between narrowness and speed of water. Several freshwater ectoproctologists have doubtless considered that thinner zooecia, and a more pronounced keel (physical reinforcement), are likely to be associated with lotic situations. Indeed, it appears that this may be true for *Plumatella emarginata* which occurs more frequently in streams than does *P. repens*. Even though the author would like to accept the single species concept for *Fredericella* on the basis of such a contention, experience with United States collections of *F. sultana* will not support this. Numerous collections of extremely narrow statoblasts and narrow zooecia have come from lentic habitats. Nevertheless, if it is assumed that *F. australiensis* is, in fact, conspecific with *F. sultana*, then, presumably, environmental influences are of some importance in dictating the intraspecies differences between these two forms. All the major differences suggest this possibility. *F. australiensis* is consistently huskier than *F. sultana*, i.e., greater number of tentacles, noticeably wider zooecia, larger sessoblasts and a generally somewhat larger number of sessoblasts. If these are intraspecific differences, then it might be assumed further that the differences described are attributable to a more favorable environment, e.g., nutritional. It is generally true for animals that differences of magnitude of various body dimensions and number of parts, as a mark of intraspecies variation, is causally associated with nutrition or a generally more optimal environment. This suggests that the generally more robust *australiensis* form of *F. sultana* is found in the most favorable habitats. There is, unfortunately, no concrete evidence to support this. What scattered evidence does exist suggests, if anything, the opposite. The Mexican bodies of water are all new within the past 10-15 years. Except at Big Boquilla there was very little organic matter and no abundance of other organisms. The irrigation reservoir in Durango province was shallow. The water had a greyish turbidity following wind agitation of the water. The abundance of *F. australiensis* was greater here than at either of the other two Mexican sites.

Something besides nutrition may be assumed to be dictating intraspecies differences, but it can still be argued that if this is so the more robust *australiensis* must nevertheless enjoy the more optimal habitats. But then it is difficult to believe that there are so few optimal habitats for *F. sultana*, when the species is so much more common and cosmopolitan and frequently so luxuriant in its growth. It is possible that *F. australiensis* is an intraspecies variant with a peculiar genotype, for some reason especially successful at certain sites. Attention should be directed to the kinds of habitats in which *F. australiensis* has been found. Regrettably there is little quantitative limnological information on these locales, but there is a certain uniqueness about them. *F. australiensis* has never been found in any of the great temperate zone lake districts of the world where most of the collecting has taken place. In these regions, whether from lakes, ponds, or streams, only the typical *F. sultana* occurs. Instead, except for the intergrading statoblasts of the Argentine collections, reports of *F. australiensis* come from semiarid or arid desert regions, viz., inland New South Wales, the arid east Georgian region around Tiflis between the Caspian Sea and the Black Sea, a stream in the central Sahara, Lake Titicaca, an alkali pond in southwestern Wyoming, and from the arid Chihuahuan Desert and central plateau of Mexico. The range of soils found in such areas (BUNTING, 1965), e.g., chernozems, serozems, alkaline-calcareous rich in silt, grey-brown alluvium rich in calcium and magnesium carbonates, red calc-loams, gypseous clay, sand, will help dictate the water chemistry for such habitats. The mean water temperature at these locations may affect the aquatic life, as will the qualitatively and quantitatively different allochthonous material which is blown or leaches into the lakes and streams.

We are left with the somewhat tenuous supposition that these two forms, *F. sultana* and *F. australiensis*, are separate species and that any overlap in characteristics, reflects, again, the potential phenotypic plasticity of members of the *Phylactolaemata*. In this case the unique habitats frequented by *F. australiensis* suggest two species with a different ecology, with *F. sultana* being the more successful and euryokous form.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
20. Group 3: Ecology and Paleoecology.

THOMAS J. M. SCHOPF (*)

GENERALIZATIONS REGARDING THE PHYLUM *ECTOPROCTA* IN THE DEEP-SEA (200-6000 m)

Riassunto. — 1) La campionatura degli *Ectoprocta* di mare profondo proviene da collezioni dell'Atlantico settentrionale e da profondità di 200-1000 m. La natura della fauna è tale che 2) il numero delle specie decresce con la profondità; 3) le specie sono zonate secondo la profondità; 4) i primi colonizzatori appartengono a forme erette foliacee; 5) diverse stirpi (più di 5 famiglie) costituiscono la fauna così da suggerire più di un tempo di colonizzazione; 6) il contenuto dell' intestino (e quindi della dieta) include detriti; 7) gli avicularia e le ovicelle sono infine egualmente comuni sia nella fauna di mare profondo che in quella della piattaforma continentale.

Summary. — 1) Sampling of deep-sea ectoprocts is very biased towards collection from the North Atlantic and from depths of 200-1000 m. The nature of the fauna is such that 2) the number of species decreases with depth; 3) species are depth zoned; 4) the prime colonizers are erect, foliacous forms; 5) several lineages (more than 5 families) comprise the fauna thus suggesting more than one time of colonization; 6) the gut contents (and hence diet) includes detritus; 7) avicularia and ovicells are at least equally common in deep-sea forms as in continental shelf forms.

Samples. Conclusions from any type of biogeographic study are only as relevant as the distribution of data permit. Accordingly I have first been concerned with the restrictions imposed by the geographic and depth distribution of sampling programs.

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Fifty-five percent of the deep-sea stations with ectoprocts are in the North Atlantic, which has less than 20 percent of the World Ocean. Additionally, many stations of major expeditions in other oceans are associated with islands and their adjacent ridges. Institutions of the western coast of Europe and eastern coast of the United States have been responsible for a disproportionately large number of marine biological expeditions. Also, when away from port, ships use islands as home bases and tend to do a huge amount of their work near them. Reading the narrative of the Challenger expedition, for example, reveals how much more intensively the areas near islands were sampled compared with open ocean regions.

In terms of depth distribution, shallow areas are over represented in ectoprocts relative to deep areas. Of the 658 stations that have yielded deep-sea ectoprocts, 500 of them (75 percent) are from depths between 200 and 1000 meters. However, a consistent 20-30 percent of the stations in the depth intervals of 200-1000 m, 1000-2000 m, 2000-3000 m, 3000-4000 m, 4000-5000 m, and 5000-6000 m for the Challenger and Siboga expeditions, and Woods Hole Oceanographic Institution benthic ecology program, yielded ectoprocts. Thus the relatively small numbers of ectoproct collection in deep water is a sampling artifact.

Nature of the fauna. The following generalizations are offered regarding the nature of the deep-sea ectoproct fauna.

1) The number of species per station decreases with depth. Characteristically a maximum of 30-100 species exists per station on the continental shelf (0-200 m) and upper continental slope (200-600 m). This maximum number decreases to about 10 by 1000 m and to 5 by 2000 m and deeper. This decrease may be observed within specific expeditions and in a plot of species per station from all expeditions.

2) Species are depth zoned on transects from the continental shelf, over the continental slope and continental rise, and onto the abyssal plain. Currents run parallel to the contours and thus larvae are distributed along lines of approximately equal depth. A few exceptions to this general pattern are known but are not understood. These may represent sibling species.

3) The absence of hard substrates over most of the deep-sea insures that the prime colonizers are the erect forms that are capable of attaching to Foraminifera and to other solitary particles in the silt or clay matrix. Secondary colonizers are those that require a stable, flat surface and may exist on small pieces of shell, other ectoprocts, or hydroids that exist in the deep-sea.

4) Just as on the continental shelf, cheilostomes far outnumber cyclostomes and ctenostomes in deep-water. Several lineages, including both Anascans and Ascoporans, have invaded the deep-sea. The cheilostome families *Farciminaridae, Scrupocellaridae, Bicellariellidae, Cellaridae* and *Bifaxaridae* are commonly represented.

5) A shift in habitat off the continental shelf has meant a change in diet. Shelf ectoprocts flourish on filtering diatoms and coloured flagellates, neither of which occurs in abundance below the photic zone (about 100 m). The gut contents of the few specimens so far examined has revealed no recognizable organism. Only «detritus», including $CaCO_3$, could be recognized.

6) Lastly I would mention a few more aspects of morphology. Avicularia and ovicells are at least as common in deep-sea forms as in continental shelf forms. Thus the same selection pressures that cause these to evolve in shallow water exist in deep water, where the environment is nearly constant. Deep-sea soft-bottom species are typically not well calcified, but in this respect are not different from erect, bush-like forms of the continental shelf.

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21. Group 3: Ecology and Paleoecology.

PATRICIA LYNETTE COOK (*)

OBSERVATIONS ON LIVING *BRYOZOA*

Riassunto. — Vengono fatte le seguenti osservazioni su due specie viventi provenienti dal Ghana:

1. *Steganoporella buskii* - La parziale protrusione degli embrioni che si sviluppano dall'orificio della membrana sub-opercolare e la crescita dei primi zooidi nelle giovani colonie.

2. *Hippoporidra senegambiensis* - La forma dei polipidi negli autozooidi e negli zooidi corticali e l' insediamento larvale sulle conchiglie di *Turritella* abitate da paguri.

Summary. — The following observations were made on 2 living species from Ghana:

1. *Steganoporella buskii.* The partial protrusion of developing embryos from the orifice of the sub-opercular membrane, and the growth of the first zooids in young colonies.

2. *Hippoporidra senegambiensis.* The form of the polypides in the autozooids and the cortical zooids, and the larval settlement on *Turritella* shells inhabited by pagurid crabs.

Résumé. — Les observations suivantes ont fait sur deux espèces vivantes de Ghana:

1. *Steganoporella buskii.* La saillie partiale des embryons developpantes par l'orifice de la membrane suboperculaire, et l'accroissement des zooides primaires des colonies jeunes.

2. *Hippoporidra senegambiensis.* La forme des polypides des autozooides corticales, et la fixation des larves sur les coquilles de *Turritella* habitées par les écrevisses pagurides.

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Zusammenfassung. — An zwei lebenden Arten aus Ghana wurden folgende Beobachtungen gemacht:

1. *Steganoporella buskii.* Die teilweise Ausstülpung von sich entwickelnden Embryonen aus der Mundöffnung der suboperkularen Membran und das Wachstum der ersten Einzeltiere (Zooiden) in jungen Kolonien.

2. *Hippoporidra senegeambiensis.* Die Gestalt der Polypiden der Autozooiden, die Zooiden der « kortikalen » Zone und die Ansammlung von Larven an von Einsiedlerkrebsen bewohnten *Turritella* - Gehäusen.

Observations were made recently on more than 70 species of living Bryozoa from the coast of Ghana. Notes on 2 species are given here.

1. *Steganoporella buskii* Harmer. Large, encrusting and erect colonies were found from the littoral region, and from off-shore reefs (in 20 m) and the continental shelf (in 55 m).

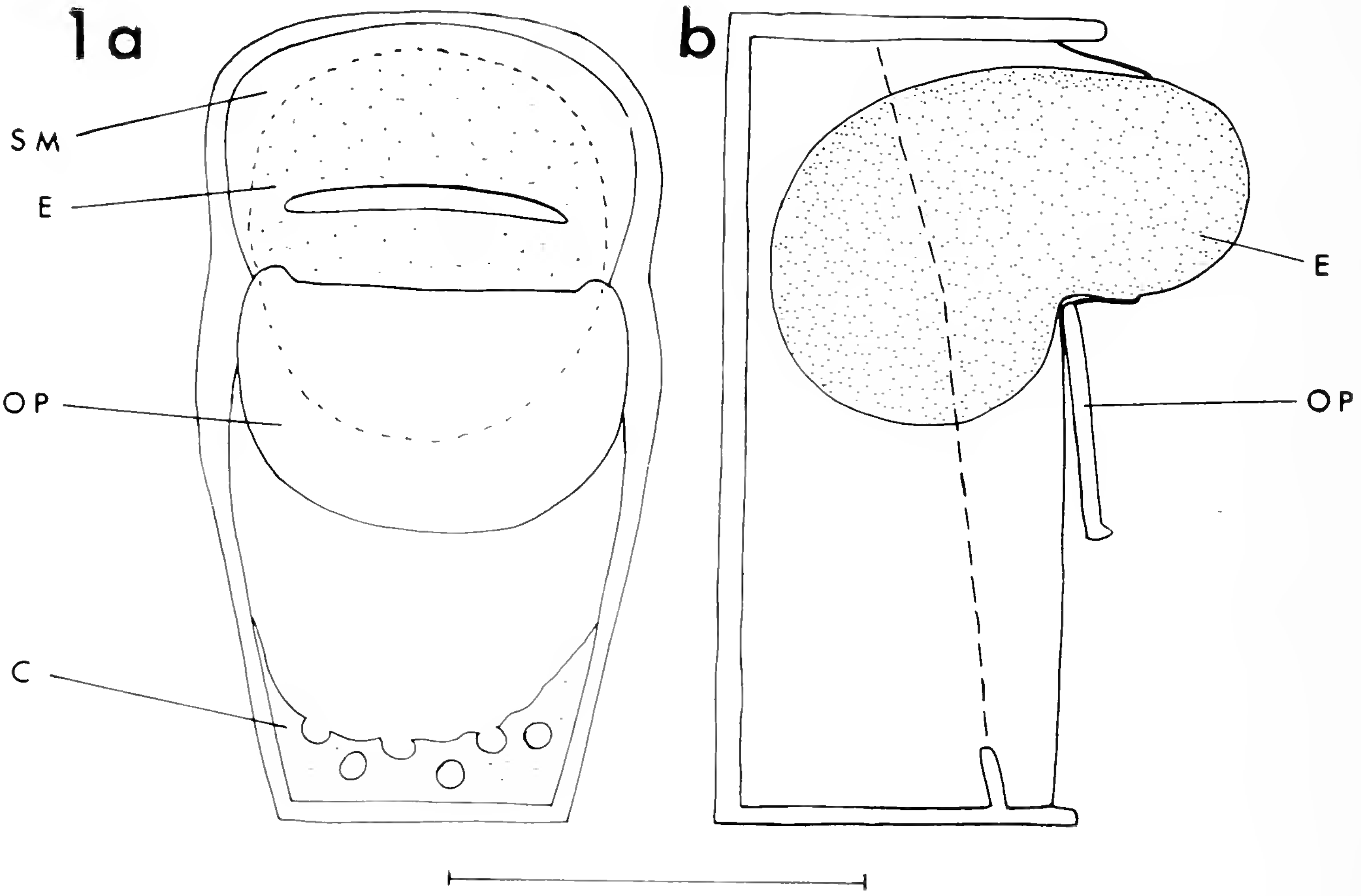

Fig. 1. — *Steganoporella buskii.* a. Frontal view of zooid with operculum open. b. Lateral view with embryo partially protruded. Operculum (*op.*), sub-opercular membrane (*sm*), embryo (*e*), degenerated cryptocyst (*c*). The broken line in b. indicates the position of the cryptocyst before degeneration. Scale = 0,5 mm.

Many zooids contained embryos, which are orange at first, becoming pink as the cilia become active. The polypide and cryptocyst degenerate as the embryo develops (see Cook, 1964 a: 50). The opercula of zooids with embryos open fully, exposing the subopercular membrane, which has a transverse, slit-like orifice. Developing embryos are partially protruded through this orifice, and remain in this position from 3-10 minutes. The operculum then closes. When their cilia are fully developed, the embryos are no longer protruded, and rotate within the distal part of the zooidal cavity for 2-5 days before release.

Coilostega with similar brooding arrangements, such as *Smittipora levinseni* (Canu & Bassler) and *Onychocella alula* Hastings, where the ovicells are vestigial and the large embryos are brooded in the distal part of the zooid, have not been seen to protrude

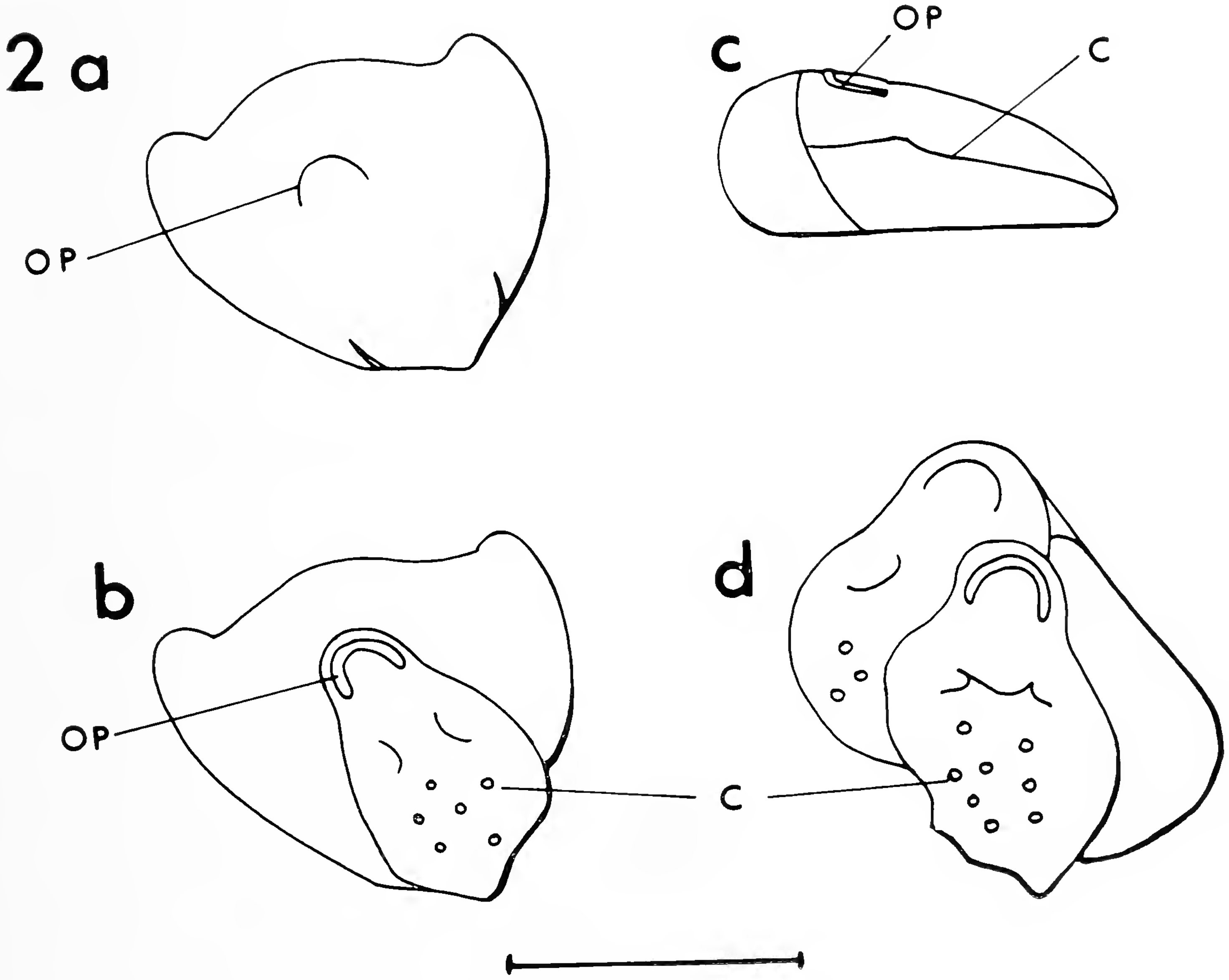

Fig. 2. — *S. buskii.* a. Primary sac. b. First zooid differentiated. c. Lateral view. d. Second zooid differentiated. Scale = 0,5 mm.

embryos. In these species the polypide is active during development of the embryo.

If the polypide is involved in the supply of oxygen to the embryo in species with internal brooding, it seems possible that the protrusion in *S. buskii* is necessitated by the absence of a polypide.

Larvae of *S. buskii* settled 33-48 hours after release. The primary individual on metamorphosis consists of a large, shield-shaped sac. The first zooid is differentiated from the central part of the sac, and is followed by 2 secondary zooids which are therefore not in fact budded from the primary zooid. Further observations must be made to see if this type of development is general in the *Coïlostega.*

2. *Hippoporidra senegambiensis* (Carter). Specimens were found in large numbers on muddy sea-bottoms from 30-40 m. The genus is exclusively associated with pagurid crabs inhabiting gastropod shells (see COOK, 1964 b: 22).

Two forms of zooid are known in *Hippoporidra.* The autozooid in *H. senegambiensis* has a polypide with 10-12 tentacles, the proximal 2 pairs are very short. Extrusion and retraction is rapid and frequent, and feeding occurs while the pagurid is moving. The cortical zooids are large and form the bases and centres of the protuberances and branches of the zoarium. They show no evidence of polypides in preserved material, and are filled with a yellow, granular substance. Living, young cortical zooids do possess a polypide. It has only 6 tentacles, which are without cilia. The distal pair is very long, the remaining pairs are reduced. Frequently the distal pair only is slowly extruded, and remains without movement for 2-3 minutes. The whole tentacular crown is then extended, but the tentacles are not expanded; they remain closely apposed, diverging slightly at the distal ends. The crown then makes 2-4 rapid lateral movements for from 3-6 seconds, is then retracted, and not extended again for from 10-30 minutes. The behaviour of these polypides is similar to that noted by SILÉN (1966), in zooids producing spermatozoa. Cortical zooids may thus have a dual function, but no spermatozoa have been seen in living or preserved specimens.

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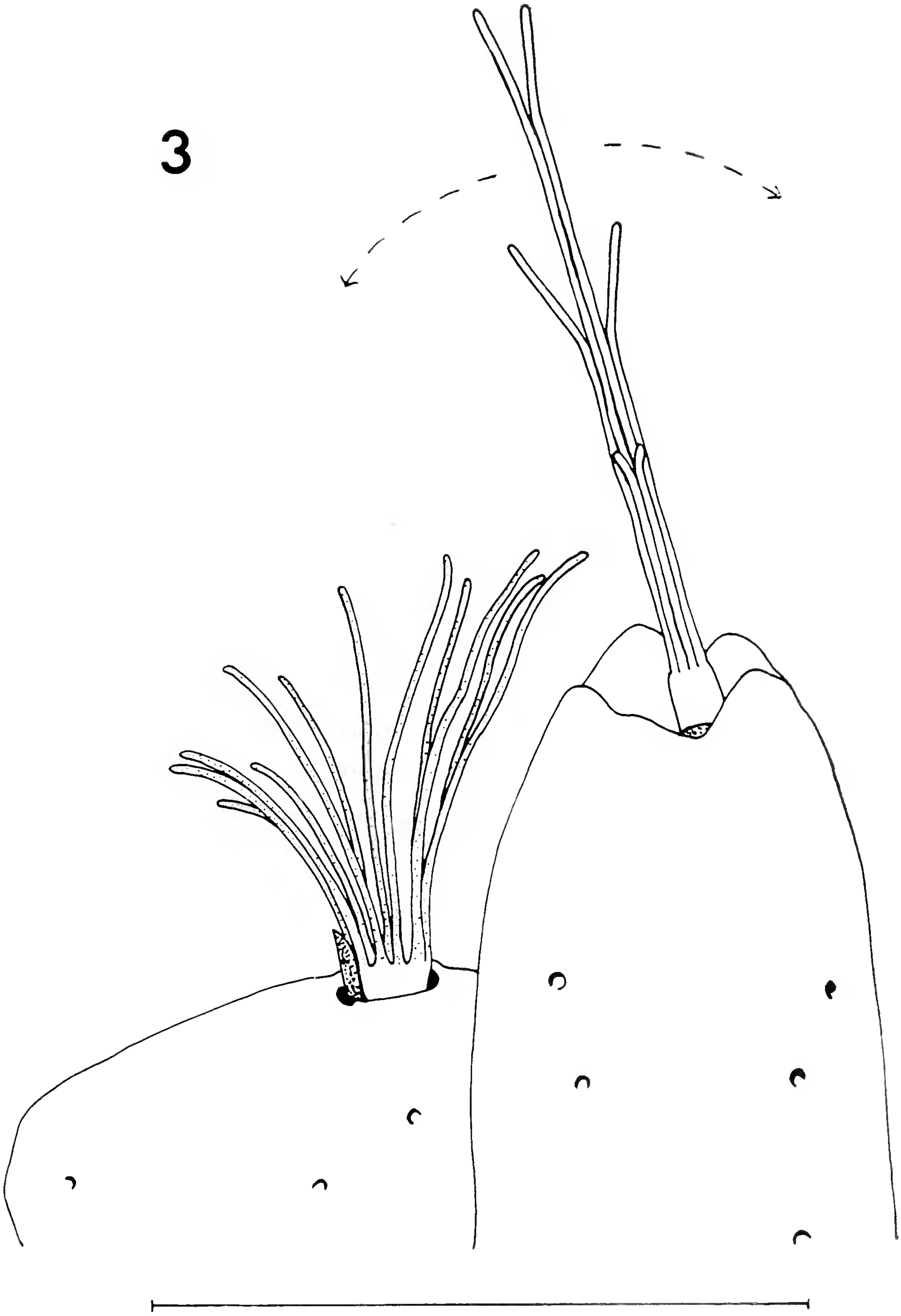

Fig. 3. — *Hippoporidra senegambiensis.* Autozooid (left) and cortical zooid (right), with tentacles extruded. Arrows indicate direction of lateral movements of tentacular crown of cortical zooid. Scale = 0,5 mm.

Breeding colonies were kept in dishes with different substrata provided for settlement of larvae. 10 ancestrulae were found on *Turritella* shells inhabited by pagurids. 8 were near the mouth of 2 shells, 2 half-way toward the apex of 2 other shells. No ancestrulae were found on shells inhabited by the gastropod, or colonised by other *Bryozoa*, nor on lamellibranch shells, shell fragments, or dead *Bryozoa*.

The indications are that most larvae settle near the mouth of *Turritella* shells inhabited by pagurids, and that the resulting colony is the most successful. Ancestrulae on other parts of shells are more liable to damage, but occasionally colonies develop in this way. Shells inhabited by the gastropod are unsuitable, probably due to the presence of the periostracum, and other substrata would normally be covered by mud in the areas where *H. senegambiensis* occurs.

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22. Group 3: Ecology and Paleoecology.

FERDINAND D. FLOR (*)

THE VARIATION OF *SPIROPORA VERTICILLATA* Goldfuss, 1827 FROM UPPER CRETACEOUS DEPOSITS

(*Bryozoa*)

Riassunto. — Viene esaminata la specie *Spiropora verticillata* Goldfuss, 1827 proveniente da depositi supra-cretacici dell'Europa settentrionale (Santoniano - Campaniano - Maastrichtiano e Daniano). Vi è una relazione tra le forme zoariali di crescita e la distanza dalla costa (? profondità, movimento dell'acqua). Questa specie può essere quindi usata come indicatore paleoecologico.

Summary. — It was investigated the species *Spiropora verticillata* Goldfuss, 1827 from Upper Cretaceous deposits (Santonian, Campanian, Maastrichtian, Danian) in Northern Europe. There is an interrelationship between the growth-form and coastal distance (? depth, water-movement). Thus this species can be used as paleoecological indicator.

Zusammenfassung. — Mit Hilfe variationsstatistischer Methoden wurde die Spezies *Spiropora verticillata* Goldfuss, 1827 aus dem Santonien, Campanien, Maastrichtien und Danien nordeuropäischer Fundorte bearbeitet. Dabei ergaben sich eindeutige Varianten der küstennahen und küstenfernen Fazies, die als bathymetrische Indikatoren verwendet werden können.

The fossil *Bryozoa* have proved to be important not only for stratigraphical but also for paleoecological research. Until now in literature synecological methods have been preferred to autecological methods. This report is based upon paleoautecological investigations of the species *Spiropora verticillata* Goldf. 1827 of different Upper Cretaceous deposits of Northern Europe. The gonozooecia of this species are characterized by a long and relatively

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thin tube. It begins between two zooecia in longitudinal-distal direction, continues transversally being closely attached to the following aperture-ring on the distal side. Then there follows again a longitudinal-distal part etc. This mode of growth may appear several times in a row.

The material used was taken from Santonian, Campanian, Maastrichtian and Danian and variation of this species in coastal areas were compared to off-coastal ones. A comparison of the total *Bryozoa*-fauna of these different biotopes already shows distinct differences. The free-growing forms of the Santonian coastal region in Northern Germany (Harzvorland) are normally larger and coarser than the corresponding *Bryozoa* in the off-coastal facies in Northern Germany and Denmark. The *Bryozoa Cyclostomata* are the most common ones there. Their characteristical structure is as follows: many lamina, bulbous, thick stems and thick lamina. But there are also some thin growth-forms, which had probably settled in the paleoecological caves of that region with strong water-movement. Comparable growth-forms of the coastal region have been found 500 km north of that region in the Campanian Cliff-facies of Sweden (Schonen).

In contrast to this biofacies the Campanian Chalk of Denmark and Northern Germany is characterized by *Bryozoa* of small and delicate growth-forms. In this off-coastal facies we don't find any specimens of the thick type.

The material used for research was made available by Prof. Dr. Dr. h. c. E. VOIGT, Geologisches Staatsinstitut, Hamburg, who kindly offered his private collection of Bryozoa for this purpose. I am very grateful to him.

Measurements: For variation-statistical comparison I measured the following criteria of the zoaria. 1. The diameter of the Bryozoa-stems (B in fig. 1 and table). It was measured in the middle section between two aperture-rings. That was done without specific orientation on unramified specimes. In a ramified section I measured vertically to the level of ramifying. 2. The height between the aperture-rings (H in fig. 1 and the table). In most cases the height was measured in longitudinal direction from the distal aperture-rim to distal rim of the following aperture-ring.

Localities: Nr. 1: Voldum, Jütland (Denmark), Danian. Nr. 2: Bastad, Schonen (Sweden), Campanian. Nr. 3: Hemmingslycke, Schonen (Sweden), Campanian. Nr. 4: Rügen (Eastern Germany), Lower Maastrichtian. Nr. 5: Faxe, Seeland (Denmark), Danian. Nr. 6: Lägerdorf near Hamburg (Western Germany), Lower Campanian. Nr. 7: Hemmoor near Bremen (Western Germany), Upper Maastrichtian. Nr. 8: Sudmerberg near Goslar (Western Germany), Santonian.

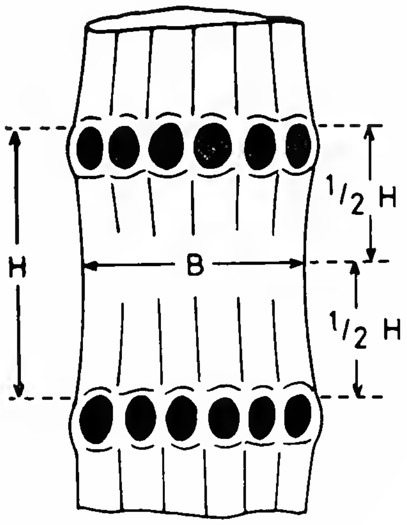

Fig. 1.

One of the results of the investigations in *Bryozoa* from 50 localities in Northern, Middle and Southern Europe is, that we find no change of the range in *Spiropora verticillata* between Santonian and Danian. Thus it is possible to compare the material with different stratigraphical value, too.

The range in mm (variation-statistical mean):

	B	H	Quantity of Measurements
Nr. 1 Voldum, Danian	0,8-1,8 (1,35)	1,2-2,0 (1,57)	76
» 2 Bastad, Campanian	1,3-2,3 (1,49)	0,6-1,9 (0,88)	56
» 3 Hemmingslycke, Camp.	1,0-2,7 (1,66)	0,7-1,7 (1,02)	177
» 4 Rügen, L. Maastr.	0,4-1,4 (0,63)	1,0-2,8 (1,61)	239
» 5 Faxe, Danian	0,4-1,0 (0,68)	1,1-2,1 (1,55)	231
» 6 Lägerdorf, L. Camp.	0,5-0,7 (0,60)	1,0-1,8 (1,28)	10
» 7 Hemmoor, U. Maastr.	0,6-1,4 (0,93)	1,0-2,1 (1,42)	88
» 8 Goslar, Santonian	0,7-1,6 (1,05)	0,4-1,2 (0,93)	22

It was shown by the measurements and the variation-statistical mean (M in mm), that the big variants are limited to the coastal deposits and the « dwarfed » variants are mostly found in off-coastal deposits. The comparison of the distance between the aperture-rings shows a contrary relation. The smallest distance between the aperture-rings is found at specimens from coastal facies. Specimens of *Spiropora verticillata* with the greatest distance we found in the facies of deeper water.

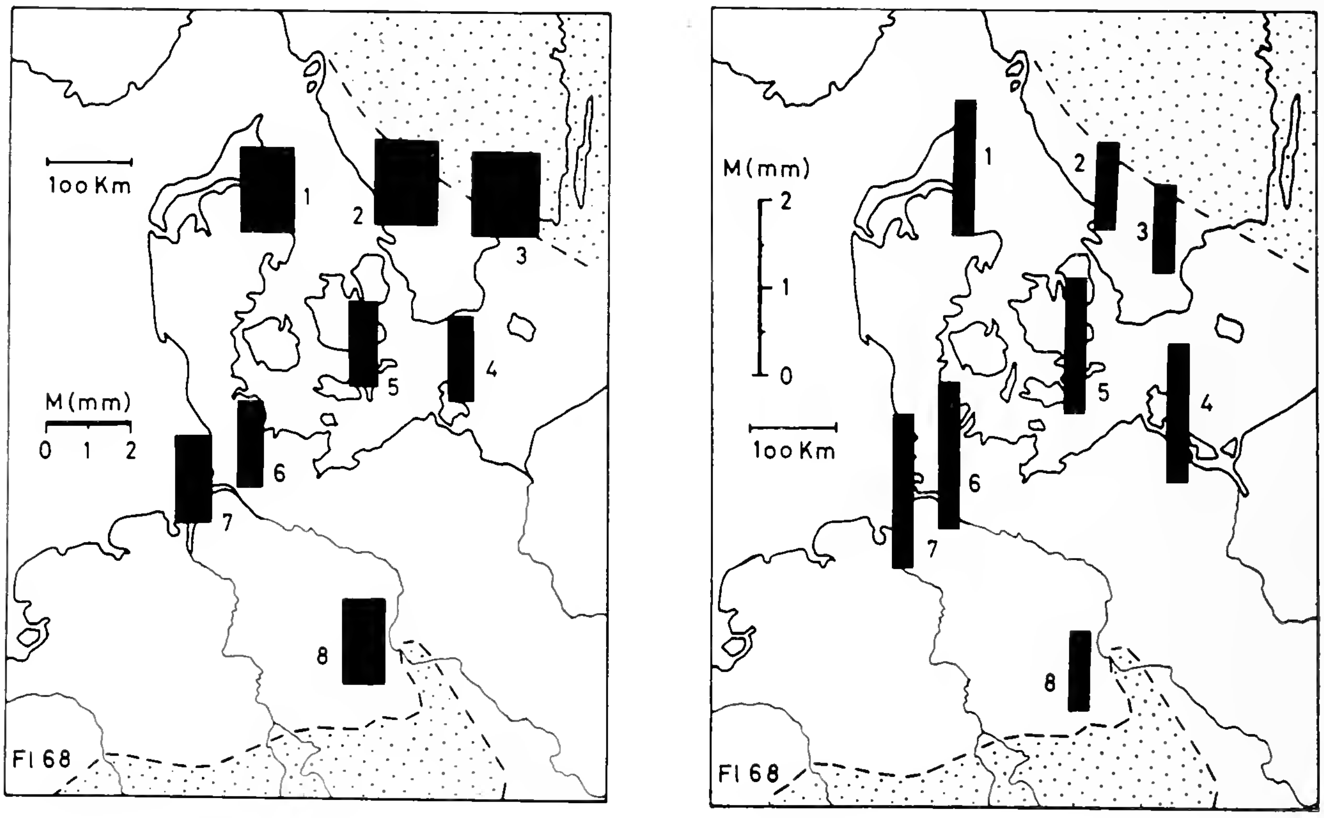

Fig. 2 (left). — Mean of the stem-diameter.
Fig. 3 (right). — Mean of the distance between the aperture-rings. The numerals indicate the localities. Paleogeographical (Upper Cretaceous) sketch: pointed = terrestric facies, unpointed = aquatic facies.

As a conclusion we can say, that the variants of the coastal facies are characterized by large diameter of the stems and relatively small distance between the aperture-rings; the specimens of the off-coastal regions are thin and have a relatively great distance between the aperture-rings. These relation may also be interpreted in a statical sense. There seems to be an interrelationship between growth-form and water-movement. Thus the *Bryozoa* of this species correspond in habitus to the total Bryozoa-fauna, as described in the beginning. So the species *Spiropora verticillata* can be used as bathymetrical indicator in Santonian, Campanian, Maastrichtian and Danian deposits of at least Northern Europe. A variation of the zooecia-diameter was not found in this geological period. Investigations about the thickness of the zooecia-wall are intended.

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VIRGIL GHIURCA (*)

LE BIOTOPE RÉCIFAL À BRYOZOAIRES DU MIOCÈNE DE LA ROUMANIE

Riassunto. — Nell'evoluzione del biotopo scopulare miocenico a Briozoi della Romania, vengono distinti due stadi principali, condizionati dalla variazione nella salinità delle acque:

1) Stadio stenoalino tortoniano, in cui si è sviluppata una ricca associazione scopulare a Briozoi.

2) Stadio salmastro sarmaziano, in cui la bassa salinità ha agito come un fattore selettivo sull'associazione scopulare a Briozoi, tale associazione risultando povera in generi e specie ma molto ricca in individui di grande taglia.

Summary. — In the development of the Miocene reefal biotope with *Bryozoa* from Roumania, two main stages are distinguished, particularly conditioned by the variation of the salinity, namely:

1) The Tortonian stenohalin stage in which there a rich reefal *Bryozoa* association developed.

2) The Sarmatian brackish water stage in which the low salinity acted as a selective factor upon the reefal Bryozoa association, resulting from these some associations poor in genera and species but very rich in individuals of high sizes.

En Roumanie a été signalée une faune riche en Bryozoaires dans le Triasique de Brasov (15), le Jurasique récifal de Dobroudja, l'Eocène supérieur du bassin de la Transylvanie (8, 14, 19, 21) et surtout dans la partie supérieure du Miocène qui affleure de nos jours presque dans toutes les régions du pays.

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Les faunes miocènnes a Bryozoaires ont attiré depuis longtemps l'attention des spécialistes comme A. E. REUSS (18), A. MANZONI (16, 17), qui ont décrit dans leurs ouvrages 54 espèces de Bryozoaires récoltées à Buituri et Lapugiul de Sus en Transylvanie. Parmi les formes décrites et decouvertes chez nous, 15 nouvelles espèces pour la littérature mondiale ont les holotypes décrits d'après les formes trouvées dans le deux localités.

La plupart des formes des Bryozoaires tortoniens décrites et trouvées à Lapugi et Buituri (7, 14), à Costei (11), Talmacel et Cisnadioara (13), en Transylvanie et les autres de Delinesti et Zorlentul Mare en Banat (12), ont été collectées des facies de plage formés de sable riche en coquilles de mollusques quelquefois roulées, semblable comme présentation au facies Pontilevien de l'Helvétien de France.

Une petite partie des formes signalées dans le Tortonien de Lapugi, Buituri et Costei provient des facies argileux plus profonds semblable au type des argiles de Baden en Autriche.

Dernièrement ont été mises en évidence des faunes riches en Bryozoaires récoltées des facies récifaux du Tortonien et du Sarmatien du bassins Baia-Mare (6), Simleu (9) et des autres points de la Transylvanie (10, 11, 13). Le facies récifal de la Roumanie a quelques affinités avec le facies sous-littoral Savignéen signalé par M. M. E. BUGE et P. CALAS de France (3). Leur caractère récifal chez nous est plus clair et mieux individualisé.

Le biotope récifal, le processus récifogénétique et l'étude complexe des récifs géologiques formés des biocénoses des Bryozoaires sont des domaines très interessants mais très peu étudiés.

Les formations récifales à Bryozoaires du Miocène supérieur de la Roumanie sont bien développées et c'est facile d'étudier en détail le biotope et leurs biocénoses. En peu des pages j'essayerai de tracer les principaux caractères du biotope récifal à Bryozoaires et d'établir surtout le composant et les traces essentielles des biocénoses récifaux, d'après mes propres recherches et utilisant les découvertes des autres chercheurs dans ce domaine.

Les récifs à Bryozoaires sont bien développés en Roumanie dans le cadre des dépôts tortoniens et sarmatiens, aussi dans les pays voisins (Autriche, Hongrie, Jugoslavie et l'Union Soviétique), pays appartenant à l'aire du bassin de la mer Paratethys.

Entre les deux types de dépôts récifaux à Bryozoaires d'âge tortonien et sarmatien il y a des différences essentielles, surtout en ce qui concerne le composant des biocénoses, différences conditionnées par la variation des facteurs physiques, chimiques et biologiques du biotope pendant les deux étapes données.

En Roumanie on peut très bien suivre l'évolution des faunes de Bryozoaires récifaux, depuis les associations stenohalines du Tortonien supérieur jusqu'à celles polihalines du Buglovien et puis chez les brahihalines du Sarmatien inférieur (Volhynien). On peut poursuivre plus loin l'évolution des faunes récifaux à Bryozoaires dans le Sarmatien moyen (Bessarabien) sur les aires de plat-formes Russe oú elles se dedevéloppent puis dans les conditions d'un milieu mesohalin, afin que, pendant le Sarmatien supérieur (Kersonien) l'adaptation au milieu oligohalin soit accomplie. Les formations récifales tortoniennes et sarmatiennes à Bryozoaires de l'Union Soviétique sont citées dans la littérature de spécialité sous les dénominations de Toltrys, Miodobores et Oncoïdes.

I - Ainsi pendant l'étape tortonienne, dans le cadre d'une mer douée d'une salinité normale le biotope récifal à Bryzoaires de la mer de Paratethys avait les suivantes caractéristique essentielles: la salinité autour de 35‰, la température entre 22°-28°C., une profondeur de 10 à 80 m., et maximum 150 m., le souslitée solide, rocheuse ou sabloneuse, pH 8,6-8,9, des eaux oxygénées, bien aérées dotées d'une nourriture abondante, des eaux sans une trop grande turbulence, la zone euphotyque bien éclairée étant la plus favorable.

Parm les biocénoses récifales développées dans de telles conditions on peut distinguer tout spécialement deux composants principaux entremêlés biologiquement l'un à l'autre de la manière suivante: des phytocenoses du type des prés sous-marins aux mélobesioidées, les plus abondantes étant les plantes du genre *Litothamnium*, *Archaeolitothamnium*, *Litophyllum*, *Mesophyllum*, *Jania*, *Melobesia* et les zoocénoses parmi lesquelles on trouve en prédominance les formes de Bryozoaires.

Parmi les faunes à Bryozoaires de type récifal ont été signalées en Roumanie (6, 9, 10, 11, 12) plus de 120 espèces. Les plus fréquentes et les plus importantes dans le processus récifogénetique ont été: *Sertella rubeschii* Rss., *S. cellulosa* Linné, *Cellaria fistu-*

losa Auct., *Crisia hörnesi* Rss., *Porella cervicornis* Pallas, *Tubucellaria ceroides* Ell. et Sol., *Scrupocellaria elliptica* Rss., *Ceriopora globulus* Rss., *Lichenopora deformis* Rss., *Calpensia cucullata* Rss., *Idmidronea atlantica* Johnst., *Cribrilaria radiata* Moll, *Ybselosoecia typica* Manz., *Cellaria farciminoides* Johnst., *Pleuronea pertusa* Rss., *Adeonella polystomella* Rss., *Hippopleurifera megalota* Rss., *Myriozoum truncatum* Pallas, *Hornera verrucosa* Rss., *Tervia vibicata* Manz., *Ceriopora cylindrica* Rss. et *Diaperoecia rugulosa* Manz.

Si nous analysons statistiquement la fréquence des epèces dans le cadre de l'association totale le résulat est le suivant: 64% d'espèces de Cheilostomes et 36% d'espèces de Cyclostomes. La fréquence statistique des individus dans le cadre de l'association récifale globale nous donne une proportion égale 50% Cheilostomates et 50% Cyclostomates.

Auprès de Bryozoaires et de Mélobesioidées il y a constament dans cette association récifale d'autres formes organiquement liées aux précédentes par exemple, parmi les Vers les genres *Serpula* et *Ditrupa*, les Brachiopodes avec les genres *Terebratula*, *Argiope* et *Mühlfelditia*, les Lamelibranchiates avec *Pecten*, *Pectunculus*, *Pycnodonta*, *Lithodomus* et puis les Echinides appartenant aux genres *Arbacina*, *Cidaris*, *Echinometra*, *Scutella*, *Echinolampas*, les Artropodes aussi représentès par des formes de Decapodes et les Foraminifères assez abondants surtout, les genres *Amphistegina* et *Heterostegina*.

Il semble que le rôle d'organisateur principal, dans le cadre des associations de ce type, revient aux algues calcaires, qui par le développement de leur thalles ont crée un milieu et une souslitée favorables pour le fixement et le développement des Bryozoaires et d'autres organismes bentonique, chose très bien remararquée par M. M. E. BUGE et P. CALAS (3) situation à laquelle s'ajoute bien etendu la constance durable des facteurs physiques et chimiques du biotope.

Par l'activité construtive commune de ces formes d'animaux ont pris naissance des formations récifales du type des biohermes et des biostromes classiquement développées dans le Tortonien du bassin Baia-Mare et dans le Buglovien de la plate-forme moldave. De telles formations sont également bien développées dans les bassins Simleu, Beius, Zarand, et Mures de la Transylvanie et Bahna-

Orsova de Banat et quelquefois dans les zones sous-carpathique oú les apports terrigènes étaient plus actifs. Une bonne partie de ces calcaires récifaux ont été décrits dans la littérature sous le nom de calcaires de Leitha.

Autour des biohermes se sont développés des facies réfciogénétiques composés de calcaires bioclastique et latéralement de calcaires oolitiques, de sables et limons calcaires qui s'encadrent dans la catégorie des roches sous-récifales. Les calcaires tortoniens sont en général campacts, blancs et composés de 30% Bryozoaires 30% Algues calcaires, 30% Foraminifères et 10% d'autre organismes de facies récifal. Dans la formations de ces calcaires on ne peut pas exclure quelques processus de précipitation directe du carbonate de calcium. Il faut souligner le fait que dans les associations composées de hexacoraillers les Bryozoaires et les algues sont absents en général.

II - Pendant l'étape sarmatienne après le changement des conditions paléogéographique qui a eu lieu sur la limite entre Tortonien et Sarmatien, la mer Paratethys perd son lien d'alimentation avec Tethys et se transforme dans un mer interne qui peu à peu s'adoucit et par fragmentation cette mer devient une série des bassins secondaires.

La salinité, l'un des facteurs esentiels du biotope est plus faible pendant le Buglovien 30%, et puis de 30% à 18% dans le Sarmatien inférieur, de 18% à 8% dans le Sarmatien moyen et de 8% à 0,5% durant le Sarmatien supérieur. Dans de tells conditions de milieu la formation et la composition des biocénoses récifaux à Bryozoaires sont déterminées évidement par la salinité qui a un rôle sélecteur en favorisant le développement de quelques espéces ou la disparition des autres. Les autres facteurs du biotope, la température, la profondeur, la souslitée, l'aération, la transparence le pH, restent en général les mêmes comme dans le Tortonien. Les phytocénoses d'algues marines sont elles aussi remplacées par de nouveaux types adaptés aux nouvelles conditions.

Dans les conditions du milieu brahihalin et puis mesohalin il ne reste plus de riches faunes de Bryozoaires tortoniens que peu d'espèces capables de s'adapter aux nouvelles conditions, en échange la taille des formes adaptées aux nouvelles conditions s'accroît et surtout la fréquence ahurissante du nombre d' individus dans le cadre de quelques espèces. La grande fréquence des individus et leur taille sont une sorte de compensation vis-à-vis de la pauvreté des genres et des espèces. Un cas presque similaire a été signalé par M. M. P. COTILLON et B. WALTER (4) dans le Crétacé inférieur des Basses Alpes et du Var.

Parmi les espèces de Bryozoaires tortoniens adaptées aux nouvelles conditions saumâtre et decouvertes en Roumanie il faut remarquer les espèces suivantes: *Schizoporella unicornis* Johnst., *S. tetragona* Rss., *Berenicea congesta* Rss., *Diastopora corrugata* Rss. et *Lepralia montifera* Ulr. et Bassler.

Dans les facies sarmatiens récifaux à Bryozoaires de la Roumanie, de l'Autriche (2) et de l'Union Soviétique (5,20) ont été signalées une serie de nouvelles espèces qui dérivent elles aussi par la sélection et l'adpatation des formes tortoniennes. Toute la faune récifale se compose des ces quelques forme citées et les suivantes: *Cryptosula terebrata* Sinz., *Schizoporella bessarabica* Nic., *S. semilunaris* Saulea Bocec, *S. tuberculata* S. Bocec, *S. variabilis* Rss., *S. terres* Eich., *S. spongitiformis* S. Bocec, *S. rhomboides* S. Bocec, *S. eichwaldi* Feof., *S. mariae* Feof., *S. biglobularis* Feof., *S. longiavis* Feof., *S. austriaca* Bobies, *Nitscheina lapidosa* Pallas, *N. leo* Feof., *N. kischenewensis* Feof., *Pyripora sarmatica* Bobies, *Enoplostomella wolfpassiegensis* Bobies.

Dans le Sarmatien inférieur (Volhynien) les associations sont prédominées presque exclusivement par les formes de *Cryptosula terrebrata* Sinzov, *Tubulipora cumulus* Sinzov, *Crisiella carnuntina* Bobies, et les quelques formes tortoniennes peu nombreuses adaptées aux nouvelles conditions déjà citées plus haut.

Durant le Sarmatien moyen (Bessarabien) de l'Union Soviétique la faune est plus reduite, on trouve en prédominance presque exclusive seulement les formes de *Nitscheina lapidosa* Pallas et *N. leo* Feofanova. Dans les biocénoses à Bryozoaires récifaux sarmatiens le pourcentage des formes Cheilostomates depasse 80% et celui de Cyclostomates baisse sous 20%. Dans les associations récifales il y a pas seulement des Bryozoaires, mais assez fréquemment des algues calcaires aussi, beaucoup de vers du genre *Serpula* et *Spirorbis,* parmi les Lamellibranchiates on trouve en prédomonance le genre *Cardium* et parmi les Foraminifères le genre *Nubecularia*.

En Roumanie les formations d'âge sarmatien inférieur et en partie moyen on les retrouve sous les mêmes formes de biohermes et biostromes dans le bassin de Baia-Mare, Simleu, Beius et Zarand et on cite de manière sporadique des facies à *Serpula* aussi dans la zone souscarpathique de la Muntenie et de l'Oltenie.

Il y a des cas, surtout dans le Sarmatien inférieur, qu'on trouve des récifs composés prèsque exclusivement des formes de *Cryptosula terebrata* Sinzov, par exemple le caz des formations récifaux du bassin de Baia-Mare et Simleu et surtout les restes d'un bioherme qui se trouve seulement sous forme de blocs à Berca dans les souscarpathes de la Muntenie. Les calcaires récifaux formés ont l'aspect des calcaires cavernaux mols, ou bien l'aspect des calcaires compacts, durs aux cavitées remplies de calcits, de calcédonie ou de quartz recristalisé.

Dans les régions de Podolie et de Moldavie en Union Soviétique les biohermes à Bryozoaires à *Serpula* et à *Nubecularia* sont très bien développés et forment trois alignement de récifs barrière. Des formations similaires sont signalées sur des aires moins restreintes en Autriche, Hongrie et Jugoslavie.

En conclusion, dans le développement du biotope récifal miocène à Bryozoaires de Roumanie et les pays limitrophes on distingue deux étapes principales conditionnées spécialement par les variations de la salinité, a savoir:

1) L'étape marine tortonienne caractérisée par une salinité normale, dans le cadre de laquelle s'est développée une riche association de Bryozoaires récifaux (plus de 120 espèces).

2) L'étape saumâtre sarmatienne pendant laquelle la salinité plus faible a actionné comme un facteur sélectif sur les associations de Bryozoaires récifaux en résultant des associations pauvres en genres et espèces, mais très riches en invidus qui sont de grandes tailles (25 espèces).

Les biohermes et les biostromes formés par l'activité constructrice des ces associations sont bien développés dans le Tortonien et dans le Sarmatien inférieur de Roumanie et pendant le Sarmatien moyen et supérier de l'Union Soviétique. En consequence sur ces aires on peut c'est à dire poursuivre l'évolution et l'adaptation par degrés des quelques faunes stenohalines à Bryozoaires de type récifal en passant d'un milieu marin à d'autre milieux polihalins, brahihalins, mesohalins et même oligohalins.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
24. Group 3: Ecology and Paleoecology.

REGINALD J. SCOLARO (*)

PALEOECOLOGIC INTERPRETATION OF SOME FLORIDA MIOCENE *BRYOZOA*

(Preliminary Report)

Riassunto. — La Formazione « Chipola » è nota per la sua ricca fauna tropicale: 52 specie di *Bryozoa* (24 delle quali si ritrovano nei mari attuali) sono state finora riconosciute. Delle specie tuttora viventi, il 42% ha distribuzione tropicale, il 46% è di acque temperate e il 12% è euritermo. Da ciò si può dedurre che i mari della Form. « Chipola » erano caldi con una salinità vicina al 35‰. Inoltre, persino nella relativamente piccola area in cui essa è esposta, la formazione può essere divisa in tre biofacies, ognuna delle quali è caratterizzata da una differente associazione briofaunistica. Queste differenze faunistiche includono un piccolo numero di specie guida, differenze nel numero delle specie e differenze morfologiche nell'ambito della specie. Esse sono in relazione principalmente con la diversità dei substrati.

Summary. — The Chipola Formation has long been known to contain a rich marine tropical fauna: fifty-two bryozoan species — twenty-four of which occur in Recent seas — have been found in it. Of the extant species, forty-two per cent are entirely tropical in distribution, forty-six per cent are warm temperate and twelve per cent are eurythermal, suggesting that the Chipola seas were warm, tropical waters with a salinity close to 35‰. Further, even in the relatively small area in which it is exposed, the formation can be divided into three biofacies, each characterized by a distinctive assemblage of bryozoans. These faunal differences include a few restrictive species, differences in species abundance and differences in morphology within species. They are related primarily to differences in substrate.

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The Chipola Formation has long been known to contain a rich marine tropical fauna. Yet Canu and Bassler in 1923 reported only five species of *Bryozoa* from the formation at the type locality on the Chipola River. Additional collecting from exposures in the vicinity of the type locality near Clarksville in northwestern Florida has yielded at least fifty-two bryozoan species, twenty-four of which occur in Recent seas. Of the extant species, forty-two percent are entirely tropical in distribution, forty-six percent are warm temperate, and twelve percent are eurythermal, suggesting that the Chipola seas were warm, tropical waters with a salinity close to 35‰. Further, even in the relatively small area in which it is exposed, the formation can be divided into three biofacies, each characterized by a distinctive assemblage of bryozoans. These faunal differences include a few restrictive species, differences in species abundance, and differences in morphology within species. They are related primarily to differences in substrate.

The Chipola Formation, middle Miocene in age, consists of blue-gray to yellow-brown, richly fossiliferous marls, generally bearing considerable amounts of quartz sands. Exposures of the formation are confined to the banks of Tenmile Creek, the Chipola River, and Farley Creek. Tenmile Creek flows from the west and Farley Creek from the east into the south flowing Chipola River. Elsewhere in the area, the formation is subsurface. As the geographic relief throughout Florida is small, the distribution of Chipola sediments is particularly fortuitous. The strike of the formation is approximately east-west and parallels the direction of Tenmile Creek and Farley Creek. The dip is southward and nearly parallels the direction of the Chipola River. Thus, as the slope of the river is less than the dip of the formation, the entire section can be collected by proceeding downstream. Although Tenmile Creek parallels the strike of the formation, a nearly complete section is represented here at one locality.

The incidence of three biofacies within the formation in the vicinity of the type locality near Clarksville, Florida is coincident with the geographic distribution of three lithofacies along Tenmile Creek, the Chipola River, and Farley Creek.

The dominant sedimentary type in the paleoenvironment exposed along Tenmile Creek probably was a mud with silt-sized clay particles and a low calcium carbonate content. The Recent records of *Membranipora tenuis* Desor, *Crassimarginatella leucocypha* Marcus, and living relatives of the fossil species *Metrarabdotos chipolanum* Cheetham indicate that the depth of water during Chipola time was generally greater than 18, but less than 31, meters. The greater abundance of these species in the Tenmile Creek biofacies than in the others is considered evidence of shallower water depth in the Tenmile Creek paleoenvironment. Extensive distribution of both the low and high salinity morphologic forms of *Hippoporella gorgonensis* Hastings supports the hypothesis of salinity variation and fluctuations down to 30‰ are thought to have occurred. Crosshatch impressions on the basal surface of *Diaperoecia* sp. and the occurrence of *Rhynchozoon edax* (Canu and Bassler), *Lichenopora* sp., and *Diaperoecia* sp. only as loose fragments in the sieve fractions indicates a soft, readily decomposable substrate, possibly fleshy algae or marine spermatophytes.

Specimens of these species were more common in the Tenmile Creek biofacies than in the other two, suggesting that plant organism were more common here. The large molluscan community is predominantly infaunal in habit. As minimal disruption of the original biotope has occurred, the mollusks probably did not provide a significant amount of substrate. Competition among sessile organism evidently was considerable and the number of bryozoan genera is smallest in the Tenmile Creek biofacies.

Marls of high calcium carbonate content with some quartz sands characterize the paleoenvironment exposed along the Chipola River. The bryozoan subassemblage is typified by substantial increases in the number of membraniporiform genera and by moderate increases in the number of cellariiform and vinculariiform genera. In addition, many species of all growth forms show significantly large increases in the frequency of occurrence, and some only noticeable increases, over those occurring in the Tenmile Creek paleoenvironment. An increase in the substrate availability in the form of a large epifaunal invertebrate assemblage of mollusks and coelenterates is a major cause for this change.

Sandy marls of high calcium carbonate content are typical in the paleoenvironment exposed along Farley Creek. All growth forms have their greatest representation in this biofacies both in the number of species and in the numerical abundance of each species. *Triporula stellata* (Smitt), *Hippaliosina rostrigera* (Smitt), *Celleporaria magnifica* (Osburn), and *Vibraculina* sp. are especially common. Particles of *C. magnifica* are so abundant that they constitute a small but significant part of the total bioclastic material. Maximum development of the bryozoan fauna is in part a response to substantial increases over the Chipola River biofacies in the substrate availability.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
25. Group 4: Evolutionary Patterns and Systematics.

RICHARD S. BOARDMAN (*)

COLONY DEVELOPMENT AND CONVERGENT EVOLUTION OF BUDDING PATTERN IN « RHOMBOTRYPID » *BRYOZOA*

Riassunto. — Studi tridimensionali dettagliati sui bizzarri tipi di gemmazione dei *Bryozoa* « rhombotrypidi » hanno dimostrato che questi tipi sono identici in tre generi largamente diffusi nel tempo e attualmente considerati come appartenenti a tre diverse famiglie. I tipi di gemmazione sono quindi considerati come un esempio di evoluzione convergente.

Summary. — Detailed three-dimensional studies of the bizarre budding pattern of « rhombotrypid » *Bryozoa* indicate that this pattern is identical in three genera widely spaced in time and presently considered to be in different family groupings. The budding pattern is therefore inferred to be an example of convergent evolution.

The post larval growth of a bryozoan colony has at least two major stages distinguished on morphology, budding habit, and position of zooids in the colony. The first stage, termed the stage of astogenetic change, is expressed by the colony founders which are restricted to the most proximal region of the colony, termed the zone of astogenetic change. Variation in morphology and budding pattern characterize these zooids.

As colony growth proceeds distally from the founder individuals, morphologically comparable zooids appear in one or more endlessly repeatable patterns of budding beginning the second major episode of colony growth, here termed the stage of asto-

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genetic repetition. This zone can contain considerable complexity producing more than one growth habit simultaneously, or cyclic developments of zooids of different morphologies and function along the same growth axis. Budding patterns, however, have the property of endless repetition of one to several kinds of zooids in characteristic arrangements.

In Paleozoic *Bryozoa,* the most detailed work to date on the earliest growth stages of bryozoan colonies was done by E. R. CUMINGS (1904, 1905, 1912). The stage of astogenetic change as here defined includes the *phylastic* and *nepiastic* stages of his earlier work (1904, p. 56). CUMINGS' *nepiastic* stage ends with « . . . the establishment of the definite budding habit of the colony ». The stage of astogenetic repetition corresponds to his *neanastic, ephebastic,* and *gerontastic* stages (CUMINGS, 1904, p. 59). « The *neanastic* stage begins with the assumption of the habit of budding that is to characterize the adult colony ». and, « . . . terminates with the development of an adult colony. The *ephebastic* and *gerontastic* stages refer, as in other organism, to fully adult and senile growths ».

CUMINGS was influenced by the theory of Recapitulation and his studies emphasized the first growth stages in bryozoan colonies. Further, he was impressed by morphologic irregularities caused by environmental factors in later growth of colonies. These influences led him to propose a challenging approach to bryozoan classification in which only the early *nepiastic* stage had phylogenetic significance or classificatory value above the generic level (CUMINGS, 1904, p. 76).

The present day philosophy of systematics contends that morphologic variation that is largely controlled genetically reflects phylogenetic relationships and potentially can have classificatory value at any hierarchial level. Obviously then, the approach to a phylogenetic classification is to distinguish genetic from extra-genetic variation in the bryozoan colony.

On the assumption that individuals in a colony are asexually produced and the same genetic makeup exists throughout a colony, morphologic variation within the colony can be considered extra-genetic in origin. Recognition of genetic variation within a single population and in populations distributed in time and space is then possible through comparison of zooids in similar extra-genetic circumstances of ontogeny, astogeny, polymorphism, and closely as determinable, microenvironment. Since CUMINGS' work, the taxonomy of Paleozoic *Bryozoa* at all categorical levels has been obtained almost entirely from characters in the zone of repetition. Certainly from this experience it has been demonstrated and is to be expected that features reflecting genetically controlled variation occur throughout a colony and that they are not modified beyond recognition by the environment. These genetically controlled variations then should be suitable for evaluation throughout the taxonomic hierarchy of the phylum.

Little has been published on the three dimensional morphology of zooecia and budding patterns of the zone of astogenetic repetition that compares with CUMINGS' work on the zone of astogenetic change. Budding patterns of hemispherical and discoidal zoaria of Ordovician age were discussed by MANNIL, 1961; fenestellate zoaria by TAVERNER-SMITH, 1965, and bifoliate and incrusting zoaria by BOARDMAN and UTGAARD, 1966. These papers serve to emphasize how little is known about zooecial form and budding and something of the potential for increased biological understanding and taxonomic use.

In most ramose *Bryozoa* lack of obvious pattern as seen in two-dimensional sections has made a three-dimensional understanding of zooecial shape and budding pattern appear difficult. In the Upper Ordovician genus *Rhombotrypa* ULRICH and BASSLER, 1904, p. 44, the exceptional regularity of the quadrate zooecia in the endozone and strong cyclic patterns in longitudinal section suggested that the genus might be a convenient starting point in the understanding of budding patterns in the ramose growth habit. The appearance of apparently similar quadrate zooecia and budding pattern in endozones in Middle Silurian (*Acanthotrypina* VINASSA DE REGNY, 1920, p. 221) and Upper Paleozoic (*Rhombotrypella* NIKIFOROVA, 1933, p. 9) genera of quite different morphologic characters in exozones further suggested the need for a detailed morphologic study before phylogenetic inferences could be made with any degree of reliability.

Each branch of a colony of *Rhombotrypa* is divided transversely into short segments defined by (1) zooecial orientation and (2) the appearance of new zooecia between those already established. Each segment can be thought of as a generation of growth. Boundaries between generations arch convexly in a distal direction across the endozone. Approximately half of the zooecia of a generation are terminated by curving outward to the exozone in a band around the branch, the inner half of the zooecia continue distally within the branch into later generations.

Within the endozone, aboral ends of new zooecia budded from all zooecial corners of the preceding zooecia to start the new generation. The new buds, quadrate like the older zooecia, are rotated 45° relative to zooecia in the preceding generation so that the buds grew by keeping their corners migrating along the sides of the earlier zooecia. Corners of the new zooecia came together at the midpoints of the earlier zooecial walls causing the earlier zooecia to be turned 45° with them and distributing the old and new zooecia in a checkerboard pattern.

The 45 degree rotation of zooecia and the initiation of budding from all zooecial corners of the preceding generation produced new zooecia with sides approximately 0.7 the length of sides of preceding zooecia at the generation boundary. In order for the budding pattern to be capable of endless repetition of comparable zooecia, an increase in cross sectional area was necessary for all zooecial tubes within any one generation of growth. A new generation began each time the zooecia attained the maximum cross sectional area established for that colony. Thus, zooecial cross sections remained comparable with each generation rather than getting progressively smaller.

No zooecia are terminated within the endozone. The equal expansion of zooecia within a generation was in effect growth from within the branch which forced all zooecia to curve outward to the exozone where they terminated. Approximately half of all zooecia in a generation terminate within the generation in a band around the branch, half of these were from earlier generations and half from the new generation in the checkerboard arrangement. The half of the generation remaining in the endozone continued on to later generations keeping the number of zooecia essentially constant along a branch enabling branch diameters to remain comparable.

Finally, the square zooecia were able to form a circular branch by virtue of zooecial expansion from within the branch forcing zooecia to curve outward until ultimately they intersected the zoarial surface at nearly right angles. The relatively close spacing of many small zooecia and progressive reductions in zooecial length as rows of zooecia approached the zoarial surface then combined to produce a smoothly curved zoarial exterior.

Detailed study of the three genera of different geologic ages indicates that their remarkable endozonal budding patterns are similar in all observable characters. Considering the taxonomic characters as they are now understood in the zone of astogenetic repetition, however, the exozones of the three genera are quite different and would be placed in different families by most workers.

Rhombotrypa, the Ordovician genus, has sharp zooecial boundaries, generally integrate walls, closely spaced planar and cystoidal diaphragms, and no acanthopores. *Acanthotrypina,* the Silurian genus, has poorly defined or no zooecial boundaries, amalgamate walls, few diaphragms in zooecia, pierced diaphragms in mesopores similar to those of *Trematopora,* and abundant large acanthopores. *Rhombotrypella,* the Upper Paleozoic genus, is a typical stenoporid with some development of moniliform zooecial walls, few perforated diaphragms in zooecia, and two sizes of acanthopores.

It is conceivable certainly that the Silurian and Upper Paleozoic genera are related. Intervening faunas are so poorly known, however, that no evidence is presently available. Using the characters of the entire zone of astogenetic repetition, the differences found in the exozone are inferred to place the genera in different families, and the budding pattern of the endozones, bizarre as it may be, apparently evolved independently and constitutes, an example of convergent evolution.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
26. Group 4: Evolutionary Patterns and Systematics.

ALAN H. CHEETHAM (*)

EVOLUTION OF ZOOECIAL ASYMMETRY AND ORIGIN OF PORICELLARIID CHEILOSTOMES

(*Bryozoa*)

Riassunto. — L'asimmetria zoeciale aumenta nelle popolazioni dei *Cheilostomata* « poricelariiformi » che si succedono dal Cretacico superiore all'Attuale.

La tendenza evolutiva è allometrica rispetto alle serie zoariali e produce un distinto dimorfismo zoeciale a partire dal Terziario medio. Quest'aumento della asimmetria è accompagnato dalla scomparsa delle ovicelle. Allo stesso tempo gli avicularia assumono un'orientazione asimmetrica e il tipo di gemmazione della colonia diventa più regolare.

Finora il genere *Nellia* è stato considerato come rappresentante di un altro gruppo, molto lontano dai *Poricellariidae*, ma l'estrapolazione di questa tendenza ci fa pensare che il genere *Nellia* sia in effetti il progenitore di quest'ultimo gruppo.

Nellia ha dato origine ad altri generi, compresi *Vincularia* e *Rimosocella* che sono convergenti con i *Poricellariidae* in uno o più caratteri della morfologia zoeciale o del tipo di gemmazione della colonia.

Summary. — Zooecial asymmetry increased in successive populations of poricellariid cheilostomes ranging from Late Cretaceous to Recent. The trend was allometric with respect to zoarial series and produced distinct zooecial dimorphism by mid-Tertiary time. Concomitantly with increasing asymmetry, ovicells were lost, avicularia assumed asymmetrical orientation, and the budding pattern of the colony became more regular.

Extrapolation of these trends suggests the genus *Nellia*, heretofore regarded as far removed from this group, to be ancestral to the poricellariids. *Nellia* appears also to have given rise to other genera, including *Vincularia* and *Rimosocella*, convergent with poricellariids in one or more features of zooecial morphology or budding pattern of the colony.

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Résumé. L'asymétrie zoéciale s'est accrût dans les populations successives des Cheilostomes poricellariides depuis le Crétacé supérieur jusqu'à l'Actuel. Cette tendance évolutionnaire était allométrique à l'égard des séries zoariales et a produit avant le Tertiaire moyen un dimorphisme zoécial distinct. Cette augmentation de l'asymétrie est accompagné par la disparition des ovicelles. Au même temps les aviculaires ont assumé une orientation asymétrique, et la modèle du bourgeonnement des colonies est devenu plus réglé.

Jusqu' ici le genre *Nellia* a été consideré comme le representatif d'un autre groupe, très eloigne des Poricellariides, mais la extrapolation de ces tendances suggère que le genre *Nellia* est en effet l'ancêtre de ce groupe. Aussi *Nellia* a probablement donné naissance a d'autres genres, y compris *Vincularia* et *Rimosocella*, qui sont convergents avec les Poricellariides dans un ou plusieurs des traits de la morphologie zoéciale ou du modèle du bourgeonnement des colonies.

Introduction.

Zooecia in cheilostome *Bryozoa* normally are bilaterally symmetrical and — in the absence of brood chambers, mandibles, or setae — monomorphic. Groups in which asymmetrical, polymorphic zooecia occur in regular positions in the budding pattern of a colony generally have been regarded as markedly divergent and taxonomically distinct from « normal » cheilostomes.

Poricellariids, which are widely distributed in sediments of Paleocene to Recent age (Lagaaij, 1968, fig. 4), are perhaps the most conspicuous and abundant of these groups. New occurrences in the Upper Cretaceous and Tertiary of the Gulf of Mexico-Caribbean region extend the known range and distribution of the group, and comparison of these populations with previously described poricellariids permits delineation of evolutionary trends in the morphology of their zooecia and the budding pattern of their colonies. Phylogenetic relationships of poricellariids to other cheilostomes may be inferred by extrapolation of these trends.

Zooecial morphology.

Zooecial asymmetry is deviation in shape and structure from the basic bilateral symmetry of cheilostome zooecia. As such, it is a fundamental property of the zooids of which the zooecia are part and, in this respect, is different from superficial asymmetry. The latter includes adventive asymmetry, i.e., asymmetrical distribution or orientation of spines, avicularia, and the like, and fortuitous asymmetry, such as results from crowding of zooids or bifurcation of series of zooids.

Zooecial polymorphism is discontinuous variation of the ordinary zooecia in a colony. Variation in the form of zooecia in the proximal zone of the zoarium, producing the record of astogenetic change, is a typical feature of cheilostome morphology and does not constitute polymorphism. Possession or lack of an ovicell or other brooding apparatus, constituting reproductive polymorphism, also is excluded here from zooecial polymorphism.

Poricellariid zooecia are segregated in distinct series in the zoarium on the basis of the direction of their asymmetry. All of the principal zooecial openings (opesiae) curve toward the midline of one side (frontal) of the zoarium and are completely hidden in the opposite view (dorsal). They are arranged in two sets of two series each, left and right frontal series lying in a frontal position, and left and right lateral series lying in a dorso-lateral position. The zooecia in the two series of a set, i.e., left and right frontals or left and right laterals, are mirror images. The amount of asymmetry of zooecia belonging to series of different sets may be the same or different. If different, the zooecia are dimorphic.

Zooecial asymmetry in poricellariids is expressed by zooecial shape and, structurally, by the unilateral opening (opesiule) in the cryptocyst for the parietal muscles, invariably lying toward the frontal side of the zoarium. In advanced poricellariids, adventive asymmetry, produced by the position and orientation of the avicularium lying on the proximal gymnocyst, is superimposed on and accentuates zooecial asymmetry.

In this study zooecial shape has been measured by three variates, zooecial length, zooecial width, and the angle (θ) between the zooecial axis and the bisectrix of the opesia. Avicularian orientation (the angle α between the avicularian axis and the zooecial axis) and avicularian length were used to measure adventive asymmetry. The asymmetrical distribution of the opesiule is invariable in the populations studied.

Evolutionary trends were determined from estimates of central values of the five variates in four successive poricellariid samples. Identification of trends in estimates is affected by variation, specifically by the relation between the amount of variation within a colony and the total variation in the colonies of a sample of a taxonomic population. All five measures are variable within and among colonies.

In three of the four samples analyzed, among-colony variation is not significantly different, on the average, from within-colony variation. For zooecial length and width, coefficients of variation range from 9 to 16 for samples and from 6 to 21 for specimens; 17 per cent or fewer of the specimens show significantly less variation (as determined by F-tests on variances) than the sample of which they are parts.

On the other hand, the fourth sample (Eocene) is heterogeneous with respect to zooecial width, as indicated by its high among-colony variation (21) compared to within-colony variation (8-12). A majority (62 per cent) of the included specimens display significantly less variation than the sample total. Division into two subsamples reduces the variation in each to a level (10 and 14) commensurate with specimen variation and with the variation shown by other samples. This sample, therefore, has been interpreted, in the following description of evolutionary trends, as representing two populations.

The variation within a poricellariid specimen thus serves to calibrate population variation and, for the majority of specimens, is not significantly different from that in a population sample. Therefore, relatively few specimens are needed to estimate population parameters, at least in the poricellariids studied.

Discontinuous variation in poricellariid characters, i.e., zooecial dimorphism, is indicated by a significant decrease, to a level below specimen variation, resulting from separation of the frontal and lateral sets of zooecia. Such decreases occur in zooecial width and the angle θ in Oligocene and Recent populations, and a decrease in the frontal series of one Eocene population suggests incomplete dimorphism in zooecial width. Zooecial length and avicularian characters appear not to be involved in dimorphism.

In general, the dimensional variates (zooecial length, zooecial width, and avicularian length) show no significant time-related changes in the amount of population variation. In accordance with previous studies, avicularian length has about twice the variation of zooecial dimensions. The orientational variates (the angles θ and α), on the other hand, trend distinctly from higher to lower values in younger populations.

Evolutionary trends in zooecial morphology of poricellariids may be characterized as follows.

1. Asymmetry increased gradually from Late Cretaceous to Recent, affecting both zooecial width and the angle θ, which became less variable as stable orientations were achieved. The amount of asymmetry in Recent populations (mean zooecial width, 24 dekamicrons; mean θ, 50°) is more than 50 per cent greater than that in Cretaceous populations (mean zooecial width, 14 dekamicrons; mean θ, 32°).

2. Lateral zooecia became more asymmetrical more rapidly than frontal ones. This allometric trend produced distinct zooecial dimorphism by Oligocene time, and in Recent populations, the lateral zooecia are about 50 per cent more asymmetrical in both zooecial width (26 dekamicrons) and the angle θ (64°) than frontal ones (21 dekamicrons; 36°). In Eocene time, some species diversification resulted from accelerated increase in zooecial width in at least one population.

3. Probably as a result of the rapidly increasing asymmetry of lateral zooecia, ovicells, which occur on lateral zooecia in Cretaceous poricellariids, were lost by Tertiary time. In Recent poricellariids, embryos develop within the zooecal cavities (WATERS, 1913, p. 492).

4. Through modification of distribution and orientation of avicularia, adventive asymmetry was superimposed on and accentuated zooecial asymmetry. In the Cretaceous, avicularia were generally paired and, with a great deal of variation (coefficient of variation, 81), directed proximally (mean angle α, 15°). By Eocene time, one avicularium had been lost, and the remaining one has rotated laterally to a nearly transverse position (mean angle α, 59°) in Recent poricellariids. Variation in orientation decreased (to a coefficient of 25-31) as a more stable position was reached. Concomitantly, avicularian length increased (from a mean of six dekamicrons in the Cretaceous to eight in Recent populations). Most of the change in avicularia took place between Eocene and Oligocene populations.

Avicularian evolution was more rapid in the lateral series, but, because of the inherently greater variation in avicularian characters, did not contribute significantly to dimorphism.

Budding pattern of the colony.

Evolutionary trends in zooecial form of poricellariids are correlated with a change in the budding pattern of the colony.

The colonies of living poricellariids are jointed, the calcified segments connected by uncalcified tubes in such a way that branching occurs at each joint. Most specimens, including all known fossils, consist of disarticulated segments whose connections are indicated by openings in both ends, three proximally and two groups of three each distally, in all material examined.

The arrangement of zooecia in a colony is regular not only in consisting of two frontal and two lateral series in each segment but also in having the budding alternate from series to series in a definite sequence. Each segment originates with three zooids, the proximal parts of which lie in the distal end of the next proximal segment and to which they are connected by one larger and two smaller tubes. Each of the three proximal zooids originates a series. Zooid 4, which begins the fourth series, arises by bifurcation from zooid 1 and does not participate in the joint. Zooids 1 to 4 increase progressively in length, width, and structural complexity and can be identified at the proximal end of each segment as a *primoserial zone of change*. (In modern poricellariids, a similar progression of zooecial changes occurs over the first few proximal segments of the colony, which thus form a zone of astogenetic change; WATERS, 1913, p. 490; HARMER, 1926, p. 315.) Beginning with zooid 4, zooecial morphology is approximately constant within each series. This portion of the segment, distal to the fourth zooid, is the *zone of repetitive budding* (and measurement of zooecial variates was restricted to this zone). The two sets of openings at the distal end of this zone correspond to the proximal ends of the first three zooids of the next segments. The larger opening of each group, representing zooid 1 of the next segment, develops by lineal addition to its series, whereas the two smaller ones, representing zooids 2 and 3, originate by bifurcation.

The first zooid of a segment may belong to any series. Segments originating with each of the four series (left and right lateral, left and right frontal) occur in about equal numbers in all of the samples studied. The sequence in which zooids belonging to the four series appear in the primoserial zone then serves as the template for budding and bifurcation in the zone of repetition. Two such templates occur in the poricellariids.

1. In all modern poricellariids zooid 4 of each segment belongs to the same set (frontal or lateral) as zooid 1. Zooids 2 and 3 belong to the two series of the other set. After a given number of zooids have budded, each series bifurcates in turn, in the same order in which its primoserial zooid appeared. The first and second bifurcate at the distal end of the segment, whereas the third and fourth bifurcate at the proximal ends (primoserial zones) of the next segments. Therefore, the first and second series have one more zooid each than the third and fourth. Moreover, the first zooids of the distal segments necessarily belong to different series than the first zooid of the proximal segment does. The whole budding pattern in the part of the colony distal to the zone of astogenetic change is thus deducible from a single segment. This strictly regular pattern occurs only in poricellariids having highly asymmetrical, distinctly dimorphic zooecia. It results from the lineal descent of zooids having the same relative positions in each segment, laterals giving rise to laterals and frontals to frontals throughout the distal part of the colony.

2. Cretaceous and early Tertiary poricellariids have a slightly less regular budding pattern in which lateral and frontal series apparently are not in continuous lineal arrangement throughout the distal part of the zoarium. The order in which the series bifurcate is the reverse of that in which they appear in the primoserial zone, and, as a consequence, each series has the same number of zooecia within a segment. The zooecial couplets 1-4 and 2-3 may each belong to the same set of series, frontal or lateral, as they do in advanced poricellariids, or they may belong to different sets. This pattern occurs only in those poricellariids having less asymmetrical, not distinctly dimorphic zooecia.

Evolution of the more regular budding pattern of modern poricellariids is thus a consequence of the development of dimorphic zooecia which in turn resulted from the allometric increase in zooecial asymmetry.

Inferred phylogenetic relationships.

The following inferences can be made about the ancestor of poricellariids by extrapolating these trends in the morphology of zooecia and the budding pattern of the colony: (1) The zooecia were monomorphic and probably symmetrical. (2) Ovicells of poricellariid structure (entozooecial) occurred on zooecia probably irrespective of zoarial series. (3) Avicularia of the same position and form as in poricellariids (adventive, gymnocystal; with pointed rostrum and pivotal bar) were paired and directed more or less proximally. (4) The budding pattern of the colony was like that of primitive poricellariids or slightly less regular.

The genus *Nellia*, regarded as far removed from poricellariids by HARMER (1926, p. 240), BASSLER (1953, p. 179), and CHEETHAM (1966, p. 48), fulfills these qualifications but differs conspicuously from poricellariids in having much less nearly complete cryptocysts. The budding of *Nellia tenella* follows the pattern of primitive poricellariids (HARMER, 1926, p. 243-244), though, because of its symmetrical zooecia, frontal and lateral series cannot be identified. Other species of *Nellia* have a simpler pattern (HARMER, 1926, p. 245; CHEETHAM, 1966, p. 52), in which only two proximal zooids participate in the joint, subequally. This pattern has also been described in the genus *Rimosocella* which has symmetrical zooecia and complete cryptocysts (CHEETHAM, 1960). The occurrence of *Nellia* having both types of budding together with primitive poricellariids in the Caribbean Upper Cretaceous, the oldest occurrence of both groups, makes their phylogenetic relationship more likely.

Through *Nellia*, the poricellariids are probably also related to the genus *Vincularia* in which the budding pattern is highly regular, but of a different form from that of the advanced poricellariids (CHEETHAM, 1966, p. 56-57). The zooecia are dimorphic, those identifiable as lateral series being slightly asymmetrical. The joints are tripartite, zooids 1 and 3 invariably belonging to the lateral series. The number of zooids is the same in each series, rather than binary as in advanced poricellariids. In some species of *Vincularia*, ovicells occur on lateral zooecia. Avicularia, where present, are single, but directed frontally, rather than laterally as in advanced poricellariids. Unlike poricellariids, *Vincularia* never developed extensive cryptocysts.

A great diversity of budding patterns has been described in the major cheilostome group generally called cellularines (HARMER, 1923). Many of the genera have jointed, biserial zoaria, and, though their zooecia are basically symmetrical, adventive asymmetry is common in the group. Of the budding types described by **HARMER**, type 8 appears first in the fossil record and may be regarded as the basic pattern in biserial forms. Though it is impossible to establish the homology of the two series of zooecia on morphological grounds, it is possible that the other two have been reduced to form the dorsal vibracula. Cellularines have gymnocystal spines, very little developed cryptocysts, and ovicells of a different structural type (hyperstomial) from *Nellia, Vincularia, Rimosocella,* and primitive poricellariids.

In summary, the following phylogenetic relationships are suggested on the basis of the stratigraphic distribution of these genera:

1. Poricellariids evolved from *Nellia* in Late Cretaceous time through inception of zooecial asymmetry, completion of the cryptocyst, and restriction of ovicells to lateral zooecia.

2. *Vincularia* evolved from *Nellia* in Paleocene time convergently with poricellariids through development of zooecial asymmetry and dimorphism, appearance of adventive avicularian asymmetry, restriction of ovicells to lateral zooecia, and modification of the budding pattern to greater regularity.

3. *Rimosocella* evolved from *Nellia* in Eocene time convergently with poricellariids through completion of the cryptocyst.

The cellularine cheilostomes also may have developed from *Nellia* in one or more lineages, going back to Eocene time, through structural changes in the ovicell and other features and thus may be related to the poricellariids.

If *Nellia, Vincularia, Rimosocella,* and the poricellariids are as closely related as the trends in their budding patterns and zooecial morphology suggest, their family assignments (HARMER, 1926; BASSLER, 1953; CHEETHAM, 1960, 1966) require revision. Whether they should be included with the cellularines in the superfamily *Scrupocellariacea* cannot be decided at this time.

Samples studied.

Upper Maestrichtian, Westmoreland Parish, Jamaica. Jerusalem Mountain Inlier; yellow calcareous shale between limestones with *Lopha arizpensis jamaicensis* (Trechman), about 70 feet below top of Cretaceous. Coll. J. E. Hazel.

Lutetian, Gourbesville (Manche), France. Sables de Fresville. Coll. D. Curry.

Rupelian, St. Stephens, Clarke County, Alabama. Chickasawhay Formation; Lone Star Cement Company quarry; buff calcareous sand with *Lepidocyclina undosa* Cushman. Coll. A. H. Cheetham.

Recent, Bombay, India. Beach sand, Juhu Beach, Salsette Island. Coll. Y. Nagappa.

Recent, Seria, Brunei. Beach sand, Panaga Beach. Coll. A. J. Key.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
27. Group 4: Evolutionary Patterns and Systematics.

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POSICIÓN SISTEMATICA DE LOS GENEROS *ROMANCHEINA, ESCHAROIDES, CELLARINELLA* Y *SYSTENOPORA*

(*Bryozoa, Cheilostomata, Ascophora*)

Riassunto. — E' stata studiata l'anatomia di *Romancheina martiali* Jullien, 1888; *Escharoides bubeccata* Rogick, 1955; *Escharoides tridens* (Calvet, 1909); *Cellarinella rossi* Rogick, 1956; *Cellarinella njegovannae* Rogick, 1956 e *Systenopora contracta* Waters, 1904, appartenenti alle famiglie *Exochellidae* e *Sclerodomidae.*

Il loro studio ha permesso di ottenere i seguenti risultati:

1. - Sotto la parete frontale calcarea vi è una grande cavità aperta distalmente.

2. - Il fondo di questa cavità è dato dalla membrana frontale interna che ha dei fascicoli muscolari nella parte inferiore dei suoi bordi laterali. Per conseguenza questa membrana è omologa di quella dei Briozoi *Anasca Malacostega.*

3. - Questa membrana ha una fessura distale, il cui bordo prossimale è un po' indurito e corrisponde agli opercoli dei generi *Bugula* o *Membranipora.*

4. - L'ancestrula di *Romancheina martiali* ha una parete frontale esterna molto calcificata che si sviluppa come una pericisti.

Di conseguenza si può dire che le specie studiate non appartengono agli *Ascophora vera* ma agli *Ascophora imperfecta* e si possono dunque ascrivere alle famiglie *Exochellidae* e *Sclerodomidae* nell'ultimo gruppo insieme alle famiglie *Umbonulidae, Celleporariidae, Chlidionopsidae, Petraliidae, Petraliellidae, Exechonellidae* e *Metrarabdotosidae.*

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Summary. — It has been made here an anatomical study of the following species: *Romancheina martiali* Jullien, 1888; *Escharoides tridens* (Calvet, 1909); *Escharoides bubeccata* Rogick, 1955; *Cellarinella rossi* Rogick, 1956; *Cellarinella njegovannae* Rogick, 1956 and *Systenopora contracta* Waters, 1904, which belong respectively to the families *Exochellidae* and *Sclerodomidae.*

Beneath the frontal calcareous external wall, there is a great cavity widely and distally open through the zoecial aperture. The floor of this subfrontal cavity is formed by the frontal internal membranous wall provided with lateral depressor muscles, and therefore it is homologous to the frontal wall of the *Bryozoa Cheilostomata Anasca Malacostega.* This membranous wall has a distally-placed slit to the outlet of the polipidian lophophore. The proximal rim of the slit is little hardened and correspond to the opercula such as those of the genera *Bugula* or *Membranipora.*

The ancestrula of *Romancheina martiali* has a very calcified frontal wall that is a pericyst according to its way of development.

Owing to the characteristics indicated above, these species do not belong to the *Ascophora Vera* but to the *Ascophora Imperfecta,* therefore the families *Sclerodomidae* and *Exochellidae* might be included in the latter group with *Umbonulidae, Celleporariidae, Chlidionopsidae, Petraliidae, Petraliellidae, Exechonellidae* and *Metrarabdotosidae.*

Résumé. — On a étudié anatomiquement les espèces suivantes: *Romancheina martiali* Jullien, 1888; *Escharoides bubeccata* Rogick, 1955; *Escharoides tridens* (Calvet, 1990); *Cellarinella rossi* Rogick, 1956; *Cellarinella njegovannae* Rogick, 1956 et *Systenopora contracta* Waters, 1904. Ces espèces appartiennent aux familles *Exochellidae* et *Sclerodomidae.*

Leur étude a permis d'obtenir les résultats suivants:

1. - Sous la parois frontale calcaire il y a une grande cavité ouverte distalement.

2. - Le sol de cette cavité est la membrane frontale interne laquelle a des fascicules musculaires dans la partie inférieure de ses bords lateraux. Et par conséquent cette membrane est homologue à celle des *Bryozoa Anasca Malacostega.*

3. - Cette membrane a une fente distale, dont le bord proximale est peu endurci, et celui-ci correspond aux opercules comme ceux des genres *Bugula* ou *Membranipora.*

4. - L'ancestrule de *Romancheina martiali* a une parois frontale externe très calcifiée qui se developpe comme un péricyste.

Par conséquent on peut dire:

Les espèces étudiées n'appartiennient pas aux *Ascophora Vera* sinon aux *Ascophora Imperfecta,* on peut donc placer les familles *Exochellidae* et *Sclerodomidae* dans le dernier groupe avec les familles *Umbonulidae, Celleporariidae, Chlidionopsidae, Petraliidae, Petraliellidae, Exechonellidae* et *Metrarabdotosidae.*

Introducción.

Tradicionalmente los *Cheilostomata* han sido divididos en los subórdenes *Anasca* y *Ascophora,* tomando en cuenta la ausencia o presencia de un saco de compensación respectivamente. En los *Anasca* se retiene la membrana frontal primitiva y, en general, el opérculo está poco diferenciado de ella, mientras que en la mayoría de los *Ascophora* existe un opérculo altamente diferenciado colocado sobre una abertura zoecial encuadrada en un marco calcáreo, ya que la pared frontal está fuertemente calcificada.

Sin embargo, al observar la gran variedad de géneros descritos dentro del orden *Cheilostomata* se puede fácilmente advertir que no existe una separación neta entre los dos subórdenes. Típicamente existe un grupo de transición entre ambos, los *Cribrimorpha,* en los que sobre la pared frontal primitiva se encuentra una capa calcárea o pericisto, formada por espinas soldadas entre si. Pero aparte de este grupo se advierte en muchos generos de *Anasca* la tendencia a formar un escudo protector sobre la pared frontal. Este es el caso, por ejemplo, de los géneros *Scrupocellaria, Aspidelectra, Tremopora, Arachnopusia,* etc. Este escudo está constituido por una espina que se modifica (*Scrupocellaria*), por espinas modificadas y extendidas sobre la membrana frontal o por varias espinas modificadas que coalescen entre si (*Tremopora* y *Arachnopusia* respectivamente). La presencia de estas espinas modificadas determina la aparición de una cavidad entre el escudo y la membrana frontal subyacente. Y esta cavidad viene a representar una especie de saco de compensación o asco, que no es homólogo al de los *Ascophora,* en los que el saco se origina de un grupo de células por detrás del opérculo (Harmer, 1957: 645).

La observación de que no exista un opérculo diferenciado o que sea difícilmente visible en algunos géneros colocados habitualmente en el suborden *Ascophora,* nos ha llevado pensar sobre su verdadera posición dentro del orden *Cheilostomata.* Esto es particularmente claro en el caso de los géneros *Cellarinella* y *Systenopora,* en los que la diagnosis genérica alude a la inexistencia de opérculo). Por otra parte en descripciones de especies del género *Escharoides*, como per ejemplo de *E. tridens* (Calvet), 1909, *E. barica* Rogick, 1955 y de otras, no se habla de opérculo o se dice que es muy tenue y difícil de ver (ROGICK, 1955: 447) Y finalmente en la diagnosis de *Romancheina martiali* Jullien, 1888, tampoco se hace alusión al opérculo.

Todas estas consideraciones nos han llevado a la realización de este trabajo con el fin de poner claro aunque sea someramente, la posición sistemática de estos cuatro géneros.

Materiales y metodos.

Los ejemplares de las especies en que se hace este estudio provienen del sur de Chile y de sus territorios antárticos. La procedencia exacta de ellos se indica en la Tabla I.

Las muestras fueron obtenidas principalmente por medio de rastra triangular, a excepción de las de *Romancheina martiali* que se obtuvieron con Draga Petersen de 0,1 m^2. Una vez obtenidas se fijaron en formol al 10% y luego fueron transferidas a alcohol de 70°.

TABLA I.

Areas de recolección de las especies estudiadas.

Localidades	Posición Geográfica	Expedición	Colectores	Fechas	Especies
Estrecho de Bransfield	63° 12′ S 58° 35′ W	XIX Exp. Ant. Chilena	H. Moyano	30-XII-64	*Cellarinella rossi y C. njegovannae*
Bahía Chile	62° 28′ S 59° 36′ W	XXII Exp. Ant. Chilena	A. Gallardo	13-I-68	*Escharoides bubeccata*
Bahía Chile	62° 29′ S 59° 39′ W	. . . .	N. González	-XI-51	*Escharoides tridens*
Bahía Margarita	67° 50′ S 68° 45′ W	XIX Exp. Ant. Chilena	H. Moyano	13-II-65	*Systenopora contracta*
Bahía Inútil	53° 30′ S 70° 11′ W	Expedición Centolla	A. Gallardo	3-V-62	*Romancheina martiali*

Para el estudio propiamente tal, se dibujaron vistas frontales y cortes longitudinales de las diferentes especies mediante cámara clara. Los cortes se obtuvieron puliendo un trozo zoarial sobre una piedra de asentar, luego se lavaron con agua corriente y por último se montaron bajo alcohol. Los dibujos de las partes blandas se obtuvieron de ejemplares que habían sido descalcificados con HCl diluido, después lavados y en último término montados en glicerina o gelatina-glicerina.

Sistemática.

El estudio se ha hecho sobre la base de tres especies de la familia *Exochellidae* y tres de la familia *Sclerodomidae* de acuerdo al sistema de BASSLER (1953). Ellas son respectivamente: *Romancheina martiali, Escharoides tridens, E. bubeccata, Cellarinella rossi, C. njegovannae* y *Systenopora contracta.*

POSICIÓN SISTEMÁTICA DE LAS ESPECIES ESTUDIADAS.

Phylum *Ectoprocta*
Clase *Gymnolaemata*
Orden *Cheilostomata* Busk, 1852
  Suborden *Ascophora* Levinsen, 1909

    Familia *Exochellidae* Bassler, 1935
      Género *Romancheina* Jullien, 1888
        R. martiali Jullien, 1888
      Género *Escharoides* Milne-Edwards, 1836
        E. tridens (Calvet), 1909
        E. bubeccata Rogick, 1955

    Familia *Sclerodomidae* Levinsen, 1909
      Género *Cellarinella* Waters, 1904
        C. njegovannae Rogick, 1956
        C. rossi Rogick, 1956
      Género *Systenopora* Waters, 1904
        S. contracta Waters, 1904.

Observaciones anatomicas.

Romancheina martiali Jullien, 1888

Figs. 1-13.

Se observaron seis colonias nuevas en las que pudo verse la ancéstrula. Lo más característico de ella es la presencia de 5 a 7 espinas gruesas que se originan lateral y proximalmente desde la parte media de la ancéstrula hasta el lado proximal vecino a su abertura. Las tres espinas proximales se juntan por sus extremos romos y dejan entre si orificios paralelos a sus longitudes. Las dos espinas laterales que esiguen a las anteriores también se sueldan a ellas pero quedan un poco aparte en sus extremos que se prolongan hacia adelante, de tal manera que queda un espacio entre los extremos de las espinas precedentes y los de éstas.

A medida que la colonia agranda por yemación de nuevas zoecias, se van depositando sales calcáreas sobre el frente ancéstrular, determinando la aparición de un área frontal distal con cavidades. Esta área se va cerrando progresivamente con la calcificación al igual que los orificios que quedaron entre las espinas proximales. En un estado más avanzado el área se cierra totalmente y la pared así formada, que equivale a un pericisto, se asemeja en cierto modo a la que se halla en las zoecias adultas. Lo que queda de este pericisto inicial en las ancéstrulas viejas es la presencia de orificios más o menos ocluídos entre las tres espinas proximales. Las dos espinas más distales nunca se fusionan a las cinco precedentes, quedan libres y se proyectan un poco lateralmente hacia adelante y arriba.

En las zoecias adultas (derivadas de la ancéstrula) no se observan estas espinas y, en cambio, la pared frontal aparece como un tremocisto en el que se destacan grandes poros perisféricos que delimitan costillas leves sobre el frontal. La parte anterior del frente zoecial se prolonga en dos puntas, a veces bastante largas, huecas y semejantes a las dos distolaterales de la ancéstrula. Las dos espinas más distales de la ancéstrula no aparecen en las zoecias postancestrulares, pero en cambio, en el lugar donde debieran aparecer se desarrollan las dos avicularias láterooorales.

Al hacer un corte longitudinal de las zoecias, se puede observar la existencia de una membrana frontal subyacente de color café, que lateralmente presenta varios manojos espaciados de fibras musculares. Esta membrana deja una hendidura transversal en su extremidad distal para la salida del polípido; sus bordes están apenas engrosados, y así, podríamos considerarla como el opérculo que está apenas diferenciado de la pared frontal. Muy por encima de esta membrana se halla la pared frontal calcárea externa, lo que hace que entre ambas exista una gran cavidad ampliamente abierta al exterior a través de la abertura zoecial. A ambos lados de la abertura zoecial externa se encuentra una avicularia, cuya función, a nuestro modo de ver, es impedir que otros seres vivos penetren a la cavidad subfrontal; sin embargo hemos podido constatar que en una zoecia se había fijado una ancéstrula de otra especie sobre el techo de esa cavidad.

La ovicela hiperestomial no es muy grande y está finamente perforada por poros bastante pequeños, escasos y ampliamente esparcidos.

Escharoïdes tridens (Calvet, 1909)

Figs. 14-16.

Esta especie que forma incrustaciones unilaminares sobre piedras, conchas, etc. presenta una pared frontal con areolas laterales que determinan la existencia, entre ellas, de costillas de poco desarrollo. La parte proximal de la abertura externa, como es común en todas las especies de este género, se levanta de tal manera que el plano apertural queda casi perpendicular al plano de la pared frontal. Y como en *Romancheina,* bajo ella existe una cavidad ampliamente abierta en sentido distal.

Lateralmente cada zoecia puede presentar dos avicularias de mandíbula redondeada. Por la posición que ocupan, hacia la parte media de los bordes zoeciales laterales, muchas veces enfrentan a la abertura de las zoecias vecinas. Sin embargo, de ninguna manera esto es totalmente regular, y por otra parte, su papel protector es menor que el que tenían en *Romancheina.*

Al destruir la pared frontal externa por descalcificación, aparece bajo ella una pared membranosa con músculos laterales que la deprimen al igual que en los *Malacostega*. La parte anterior de ella lleva una henditura más o menos semicircular que representa al opérculo apenas diferenciado. A ambos lados y por debajo de esta formación opercular aparecen dos manojos musculares más fuertes que corresponderían a los depresores del opérculo.

Las ovicelas son hiperestomiales y no perforadas, pero sí, rodeadas de areolas al igual que la pared frontal. En las muestras, desgraciadamente, no existían ancéstrulas que pudieran haberse estudiado.

Escharoides bubeccata Rogick, 1965

Figs. 17-18.

Los zoarios de esta especie se presentan como tallos más o menos aplastados que dan dos o más ramas al mismo tiempo por su extremidad distal. Al mismo tiempo los bordes zoariales son aserrados debido a la existencia de gigantescas avicularias frontales, y a que la parte distal de la pared frontal se eleva considerablemente.

Bajo la pared frontal calcárea existe otra pared membranosa que al igual que en *E. tridens* puede ser deprimida por los músculos laterales. En su parte anterior se abre dando lugar a un opérculo apenas insinuado. El área libre de esta membrana es mucho menor que en *E. tridens,* equivaliendo, más o menos, a un tercio de la longitud zoecial. A los lados de la abertura zoecial externa aparecen comunmente dos avicularias pequeñas cuya función sería la de proteger la entrada a la cavidad subfrontal. Además de éstas aparece, por lo general en las zoecias de los bordes, una gran avicularia implantada sobre la parte distal del frontal ya sea en posición mediana o lateral. Esta avicularia seguramente contribuye a la labor de las otras dos.

La ovicela es semejante a la de *E. tridens,* es decir, no perforada, con areolas e hiperestomial.

No existen ancéstrulas en nuestras muestras, pero sin embargo podemos hacer referencia a ellas a través de lo que señaló Rogick al describir la especie. Su ancéstrula (Rogick, 1955: 443 y 446), al igual que la de *R. martiali* presenta 7 espinas, que se curvan hacia el centro de la pared frontal pero sin soldarse entre si. De éstas las dos más distales son más gruesas y pueden ensancharse semejando a cuernos de alce. La diferencia con la de *Romancheina* estriba en que las espinas no se sueldan entre si y además la parte proximal de la ancéstrula de *E. bubeccata* no presenta el área acorozonada, rugosa y perforada que caracteriza a *R. martiali,* y en que las espinas que alcanzan mayor desarrollo son las dos más distales y no las immediatamente más anteriores como sucede en *Romancheina.*

Cellarinella rossi Rogick, 1956

Figs. 19-22.

Los zoarios que son muy calcificados, estrechos, ramificados y fijos al sustrato por rizoides quitinosos, presentan un aspecto erizado debido a los grandes umbos suborales. Externamente no se notan bordes zoeciales sino que sólo las aberturas de los zooides que en su parte distal presentan una saliente peristomial y en la proximal, una avicularia y un umbo puntiagudo. Entre todas esas estructuras no hay sino que poros infundibulares de distintos tamaños (tremóporos).

Al exterior no se hace presente la ovicela ni ningún otro accidente, pero al hacer un corte zoecial en sentido longitudinal se advierte un gran espacio entre el frontal tremocístico y la pared zoecial membranosa subyacente. Esta pared deja en su parte distal una abertura más o menos elíptica que está limitada por un labio proximal y otro distal, de tal manera que no se puede hablar de opérculo. Esta abertura se continúa en un tubo membranoso que rodea al lofóforo polipidiano. La pared membranosa posee además, músculos que la deprimen, siendo mayores los láterodistales.

Por dentro de la abertura externa existe otra avicularia, que desde fuera no se ve. Esta tendría por objeto proteger a las estructuras internas de cualquier animal que pudiera introducirse al espacio subtremocístico; su papel sería entonces como el de las avicularias orales de *Romancheina.* En suma, la presencia de la avicularia externa, de la interna y de la barra calcárea oral en el lado proximal de la abertura concurrirían a la protección del espacio interno.

Cellarinella njegovannae Rogick, 1956

Figs. 23-24.

De aspecto semejante al de la especie anterior, pero con tallos más anchos y superficie zoarial lisa por la ausencia de umbos frontales. Externamente sólo se notan las aberturas cuyo borde distal crece hacia abajo, y una avicularia pequeña a cada lado de ellas.

Bajo la pared frontal tremocística, aparece la interna membranosa y semejante a la de las especies precedentes. Aquí tampoco podemos hablar de opérculo y también podemos señalar que la cavidad subtremocística está ampliamente abierta por su parte distal. La protección de esa cavidad se logra por el estrechamiento de la abertura zoecial externa, por la presencia de las dos avicularias orales y por la existencia de la barra oral, tal como la que se señaló para *C. rossi.*

La estructura zoecial general y en especial lo que se refiere a la pared frontal interna provista de músculos depresores y enmascarada por la presencia de un tremocisto arqueado sobre ella, se mantiene para esta especie y para las otras del género.

Systenopora contracta Waters, 1904

Figs. 25-26.

El zoario en aspecto y constitución externa es semejante al de las dos especies precedentes. La diferencia más notable se refiere a la abertura zoecial externa que aparece como una hendidura longitudinal bordeada por varias avicularias. La pared frontal externa siempre es un tremocisto con poros infundibulares irregulares.

En un corte longitudinal se puede apreciar la misma cavidad interna que en las especies precedentes y la membrana frontal subyacente que presenta paquetes musculares laterales que la deprimen.

Por dentro de la abertura externa y lateralmente existe una avicularia interna proporcionalmente mayor que la que se halla en las especies de *Cellarinella* y su papel indudablemente será el de proteger la cavidad subfrontal.

Resumen y conclusiones.

De acuerdo al estudio realizado y vertido en las páginas anteriores podemos señalar:

A. - Las especies estudiadas de los géneros *Romancheina, Escharoides, Cellarinella* y *Systenopora,* presentan una pared externa calcárea que es un tremocisto o pleurocisto.

B. - Bajo la pared frontal externa existe una gran cavidad ampliamente abierta al exterior, a través de la abertura zoecial externa.

C. - Para impedir la entrada de partículas extrañas, larvas o parásitos a la cavidad subfrontal, existen avicularias externas cerca de la abertura zoecial (en todos los géneros estudiados), avicularias internas y barras orales por dentro de la abertura externa (*Cellarinella* y *Systenopora*).

D. - El piso de esta cavidad está formado por la pared membranosa frontal interna provista de músculos laterales depresores, y por lo tanto homóloga a la pared frontal de los *Bryozoa Cheilostomata Anasca Malacostega.*

E. - La pared membranosa presenta una hendidura de situación distal para la salida del polípido. El borde proximal de esta hendidura está poco endurecido y corresponde a opérculos tales como los de los géneros *Bugula* o *Membranipora.*

F. - La ancéstrula de *Romancheina martiali* tiene una pared frontal muy calcificada cuando se halla totalmente desarrollada. Esta pared se origina en su parte distal por la unión de cinco espinas lateromarginales, que dejan entre si hendiduras o fenestras que pueden llegar a cerrarse con la progresiva calcificación. De acuerdo al modo de desarrollo, esta pared es un pericisto.

Tomando en cuenta estas observaciones concluimos que:

1. - Los géneros estudiados no pertenecen a los *Ascophora Vera* sino que a los *Ascophora Imperfecta* (HARMER, 1957). Por lo tanto las familias *Sclerodomidae* y *Exochellidae* pueden ser

incluidas en el último grupo con *Umbonulidae, Celleporariidae, Chlidoniopsidae, Petraliidae, Petraliellidae, Exechonellidae* y *Metrarabdotosidae.*

2. - La pared frontal de la ancéstrula de *Romancheina martiali* JULLIEN, 1888, es un pericisto.

3. - Suponiendo que la estructura ancestrular tenga significado filogenético, la presencia de un pericisto en la ancéstrula de *Romancheina* indicaría que este género se ha originado de un *Cheilostomata Anasca.*

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EXPLICACIÓN DE LAS FIGURAS

Romancheina martiali Jullien, 1888

1. — Ancéstrula que muestra las tres espinas proximales y las dos próximolaterales, unidas por su extremidad sobre la línea media del frente ancestrular. Más allá de ellas se aprecia distalmente y al lado derecho una de las espinas anteriores que quedan libres.

2, 3, 4 y 5. — Ancéstrulas en las que se puede advertir el mayor crecimiento y ensanchamiento de las dos espinas laterodistales, que van formando un área distal que se proyecta por delante y arriba de la abertura ancestrular.

6. — En esta ancéstrula, la calcificación del área distal se ha completado habiendo desaparecido casi completamente las aberturas entre las espinas del pericisto. Las dos espinas distales libres sobresalen bastante más que los dos cuernos del área distal del pericisto.

7. — Colonia poco desarrollada en la que se nota la ancéstrula, cuya área distal no está totalmente calcificada. En cada zoecia aparecen areolas frontales que limitan costillas muy leves.

8. — Corte longitudinal de una zoecia adulta no ovicelada. La membrana frontal subyacente (*Mfc*) aparece cortada a lo largo por su línea media. Lateralmente y en el fondo se aprecian los músculos depresores de la membrana (*Md*). Entre la pared frontal externa (*Pfex*) y la membrana interna hay una gran cavidad (*Cav*) abierta ampliamente en sentido distal, y su salida está protegida por una avicularia lateral a cada lado (*Av*).

9. — Zoecia descalcificada con HCl. El lofóforo (*Lf*) es visible através de la pared frontal membranosa. En la parte distal de la membrana se halla la abertura para la salida del polípido (*Abi*) cuyos bordes apenas están diferenciados de la membrana frontal. El espacio ovicelar aparece en el extremo distal (*Ov*).

10. — Vista oral de tres zoecies. Las avicularias (*Av*) presentan un área cribada lateral (*Acr*). Por encima del área cribada se hallan las prolongaciones de la pared frontal calcárea (*Pra*). En la parte inferior de la abertura se ve el extremo distal de la membrana frontal (*Eamf*) y sobre ella la cavidad interna subfrontal (*Ci*). La ovicela (*Ov*) se abre hacia la abertura.

11. — Vista oral de una zoecia en que faltan las partes blandas. La ovicela (*Ov*), está perforada por pocos poros pequeños y ampliamente esparcidos. Entre estos poros hay tubérculos calcáreos romos.

12. — Corte longitudinal de zoecias. La pared frontal externa se alza por su parte distal (*Exaf*). Por sobre la ovicela hiperestomial (*Ov*), se halla la avicularia (*Av*). En la parte inferior de la pared lateral se pueden ver septulas multíporas (*Sep*) y en la parte superior de la misma las aberturas internas correspondientes a las areolas externas.

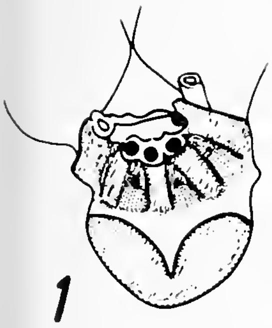
13. — Abertura zoecial mirada oblicuamente desde el lado distal. La ovicela en formación (*Ovf*) se demuestra como un repliegue ampliamente abierto que se va cerrando hacia arriba.

Escharoides tridens (Calvet, 1909)

14. — Varias zoecias en vista frontal. La abertura zoecial (*Abe*) ancha y ampliamente abierta lleva una espina a cada lado (*Op*). Entre las areolas del pleurocisto (*Pl*) hay algunas avicularias (*Av*), que a veces están apuntando hacia las aberturas zoeciales. La ovicela no perforada (*Ov*) se halla rodeada por areolas.

15. — Zoecia descalcificada mirada desde el lado frontal. La membrana frontal (*Mf*), está rodeada lateralmente y por su lado interno por manojos musculares (*Md*) que la deprimen. El polípido (*P*), cuyo lofóforo se aprecia por transparencia, puede salir al exterior a través de la abertura zoecial interna (*Abi*) cuyo borde proximal (opérculo) apenas está diferenciado de la membrana. En posición distal y en el lugar correspondiente a la ovicela se halla una gran célula huevo (*Ovul*).

16. — La misma zoecia anterior mirada desde el lado basal. En ella es posible apreciar en mejor forma el polípido y los músculos.



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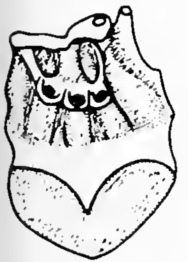

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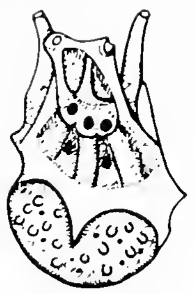

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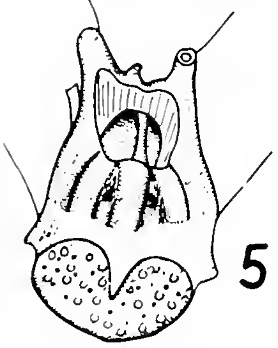

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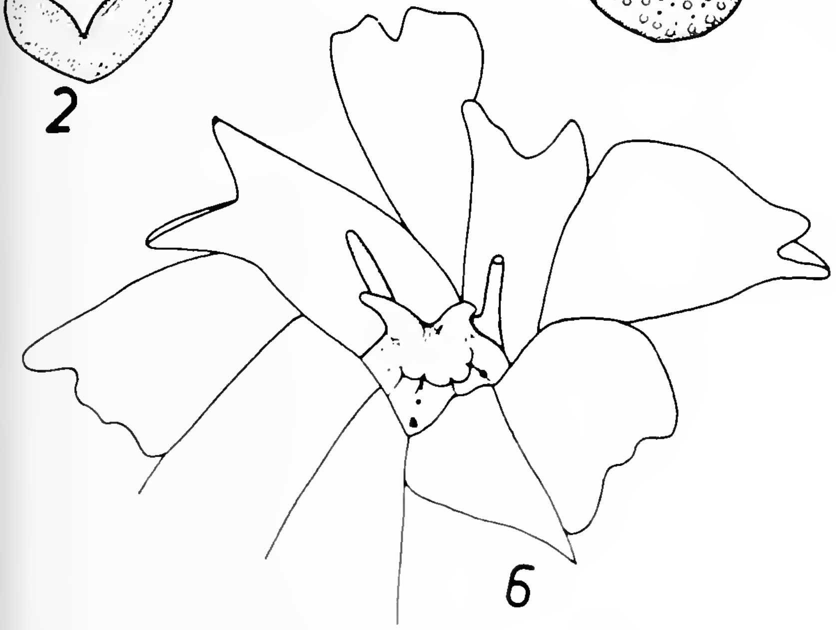

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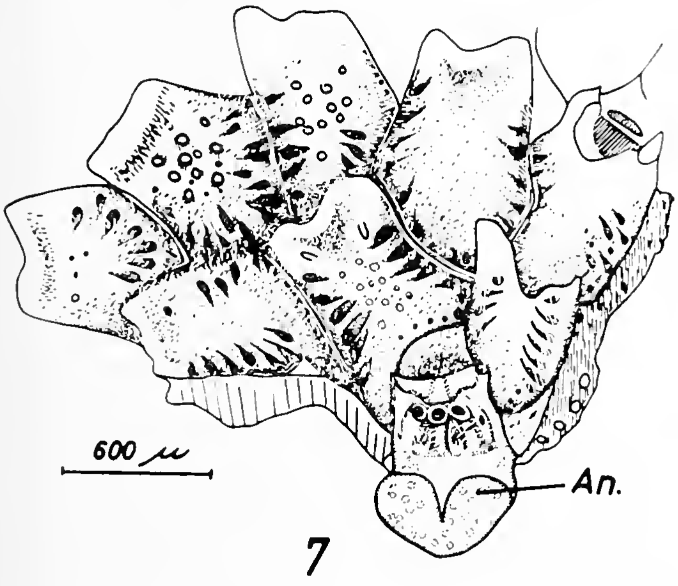

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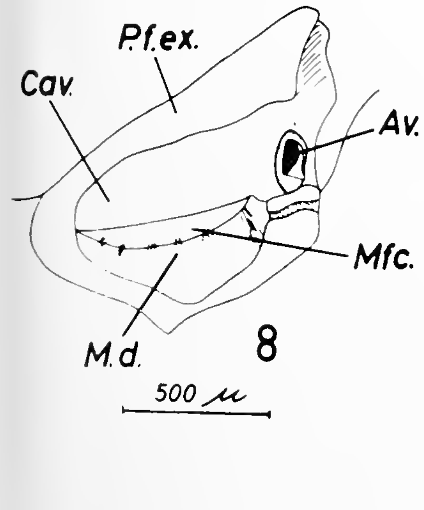

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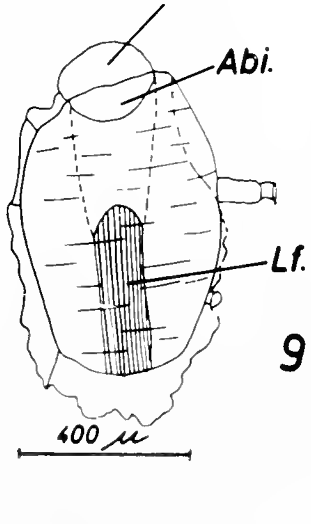

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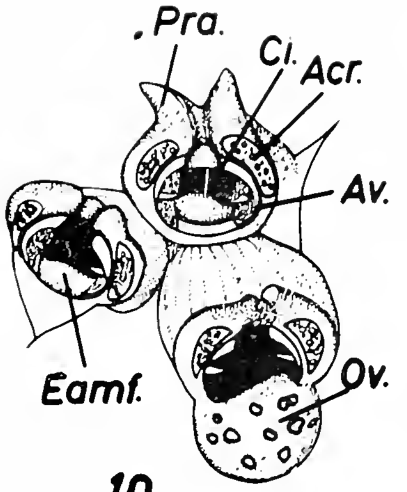

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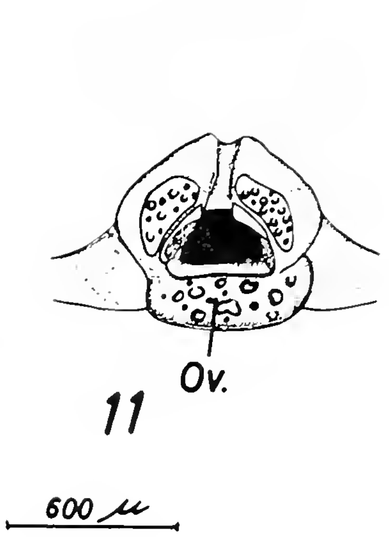

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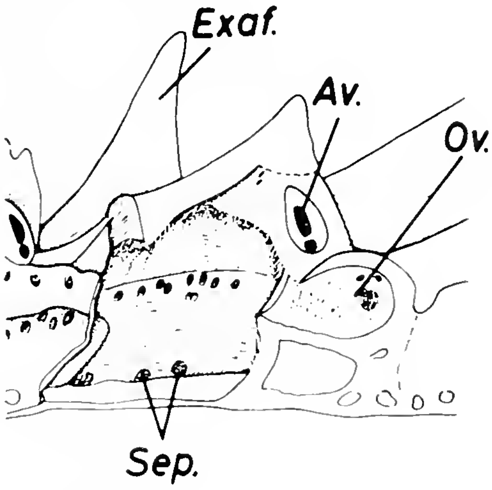

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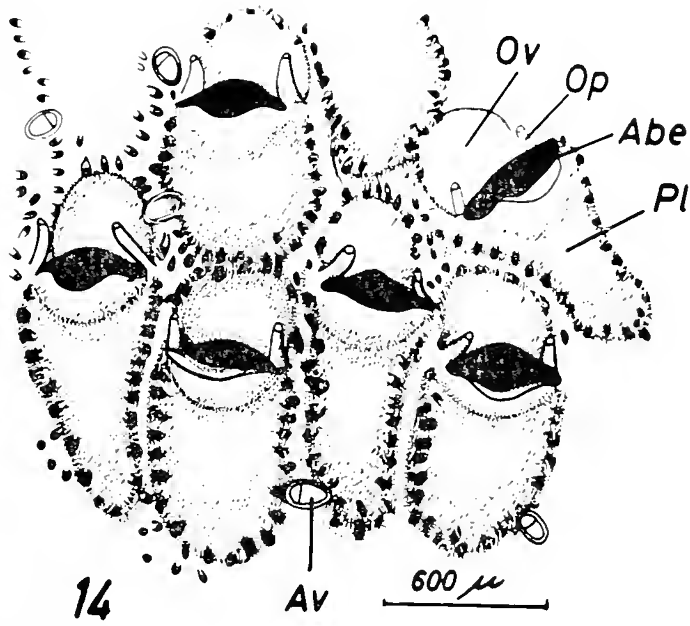

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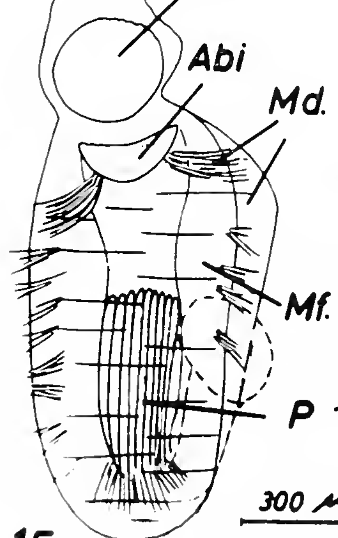

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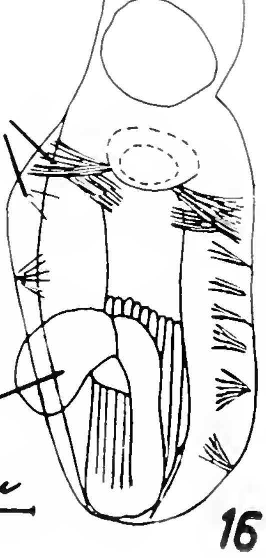

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Escharoides bubeccata Rogick, 1955

17. — Vista frontal de varias zoecias. La pared frontal pleurocística se eleva en dirección distal justo por delante de la abertura externa (*Abe*). En las zoecias marginales existe una gran avicularia frontal mediana o lateral (*Avf*). Y en la mayoría de las zoecias existe una pequeña avicularia a cada lado de la abertura (*Avo*).

18. — Corte longitudinal de una zoecia. Bajo la pared frontal (*Pl*) se halla la membrana frontal primitiva (*Mf*) y entre ambas una gran cavidad ampliamente abierta hacia adelante entre la abertura zoecial externa (*Abe*) y la abertura interna por la que sale el polípido (*Abi*). En la parte inferior de las paredes laterales se hallan varias séptulas multíporas (*Sep*).

Cellarinella rossi Rogick, 1956

19. — Zoecia descalcificada mirada lateralmente. La membrana frontal (*Mf*) deja una abertura en su parte distal (*Abi*), que aparece como una estructura casi bilabiada. El polípido (*P*) y los músculos depresores (*Md*) pueden verse lateralmente.

20. — Vista frontal de varias zoecias. La abertura externa (*Abe*) presenta por dentro de su lado proximal una elevación calcárea o barra oral (*Bo*). Bajo la parte proximal de la abertura existe una avicularia externa de mandíbula triangular (*Ave*) y junto a ella un umbo más o menos agudo (*U*). La ovicella hiperestomial no sobresale al exterior, pero, en cambio, los grandes orificios del tremocisto zoarial se disponen más o menos radialmente en la zona en que ella se desarrolla (*Zo*).

21. — Corte longitudinal de dos zoecias. Como ya se vio en las especies anteriores bajo el grueso frontal calcáreo se halla la membrana frontal primitiva (*Mf*), con opérculo prácticamente indiferenciado. La ovicela hiperestomial (*Ou*) se abre un poco por encima de la abertura externa hay un umbo (*U*), y en la parte anterior de la cavidad sufbrontal se halla la avicularia interna (*Avi*).

22. — Vista frontal de la misma zoecia de la figura 19.

Cellarinella njegovannae Rogick, 1956

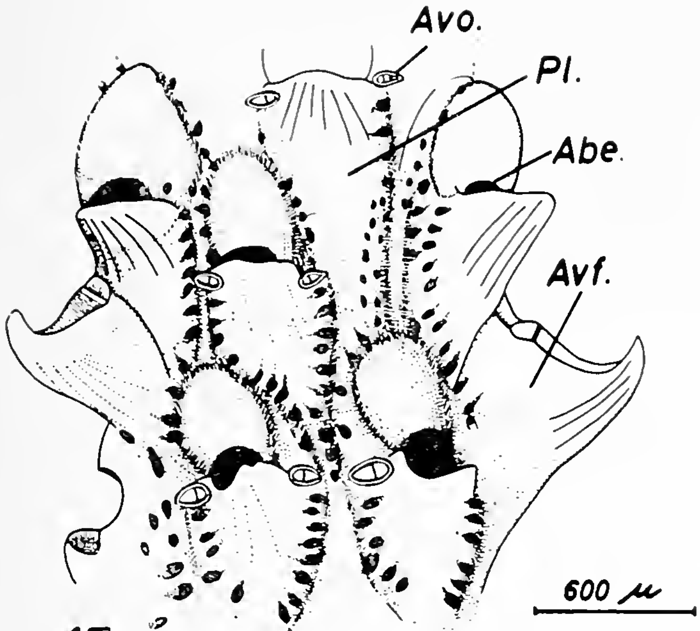
23. — Vista frontal de varias zoecias. La más característico de esta especie es el crecimiento en sentido proximal del borde distal de la abertura externa. Por dentro de ella se halla la barra oral (*Bo*) y a cada lado una avicularia pequeña (*Ave*) El tremocisto zoarial es característico por sus pequeños poros.

24. — Corte longitudinal de dos zoecias. La pared frontal tremocística está atravezada por canales correspondientes a los poros externos. Estos confluyen lateralmente abriéndose en el interior a los lados de la membrana frontal (*Mf*). La abertura interna (*Abi*) también tiene un aspecto bilabiado y está mucho más abajo que la abertura externa (*Abe*). La ovicela (*Ou*) es semejante a la de la especie precedente.

Systenopora contracta Waters, 1904

25. - Vista frontal de seis zoecias. La abertura externa a diferencia de *Cellarinella* es más largas que ancha. Junto a ellas hay una o varias avicularias externas pequeñas (*Ave*). Por dentro de la abertura by lateralmente hay una avicularia interna (*Avi*). La ovicela, aunque profundamente inmersa, se advierte al exterior.

26. — Corte longitudinal de una zoecia. Bajo el gruesto tremocisto frontal (*Tr*) hay una cavidad amplia cuyo piso es la membrana frontal (*Mf*). Esta membrana presenta una abertura apenas notoria en su parte anterior (*Abi*). Entre y por detrás de las aberturas externa e interna se abre ampliamente la cavidad ovicelar (*Ov*). La presencia de la avicularia interna (*Avi*) protege la cavidad interna de la entrada de seres extraños.



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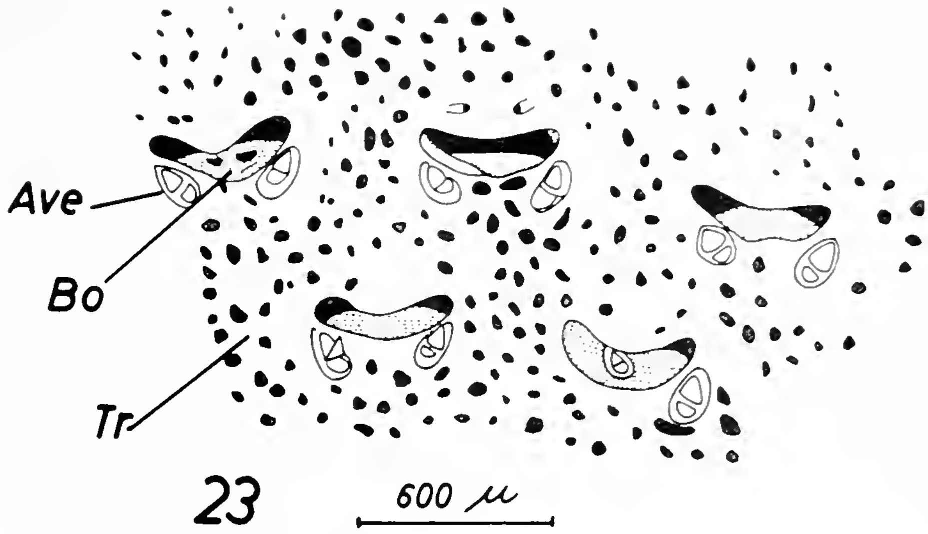

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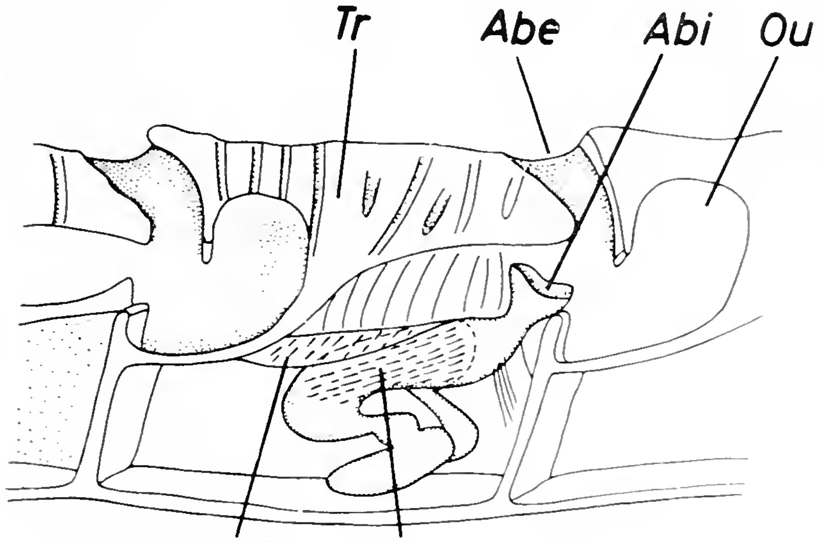

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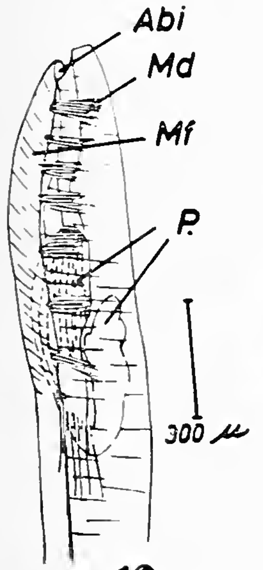

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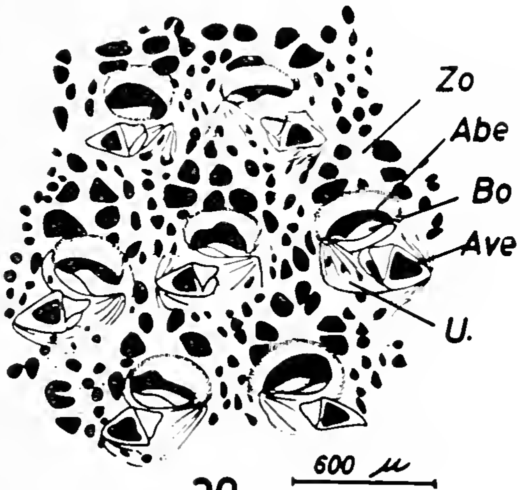

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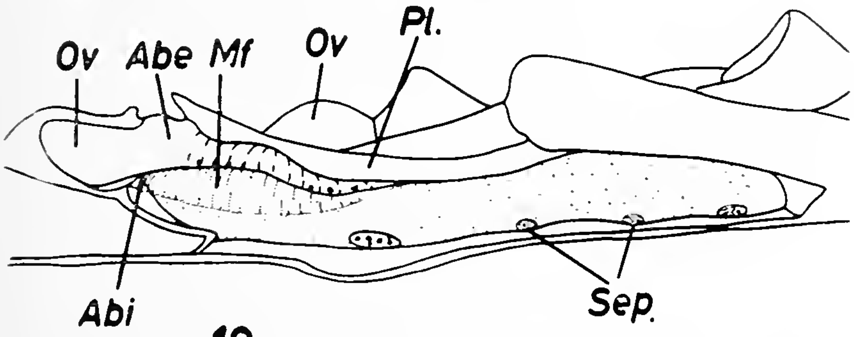

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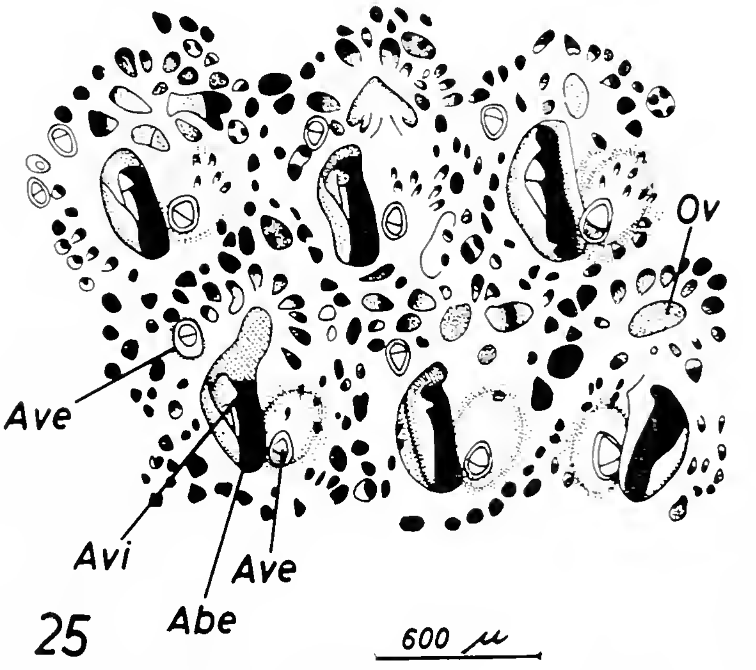

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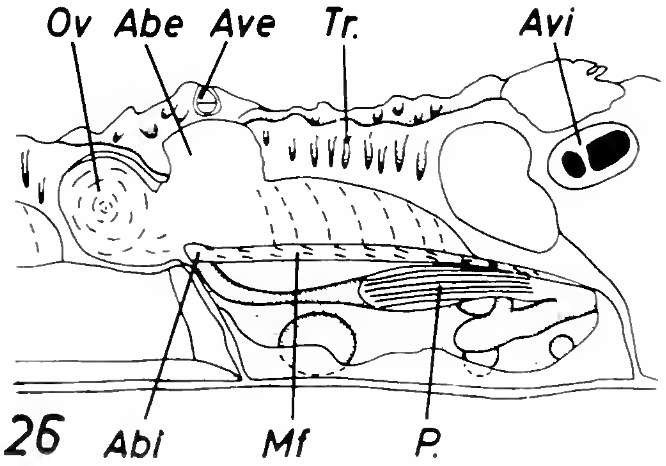

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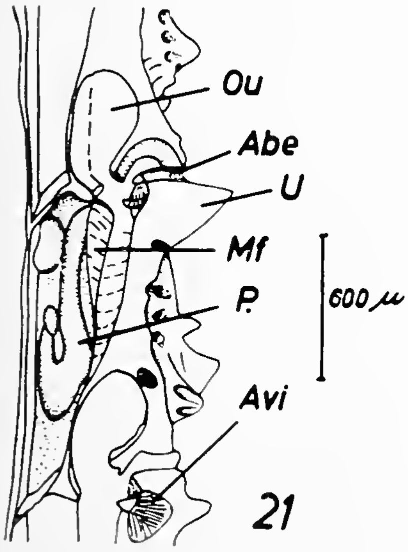

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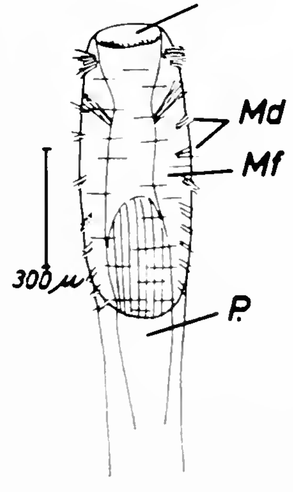

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Atti Soc. It. Sc. Nat. e Museo Civ. St. Nat. Milano - 108: 212-218, 31-XII-1968

1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
28. Group 4: Evolutionary Patterns and Systematics.

JANINE PRUD'HOMME (*)

RÉVISION DE QUELQUES TYPES DE LA COLLECTION D'ORBIGNY (CRÉTACÉ) CONSERVÉE AU MUSÉUM D'HISTORIE NATURELLE DE PARIS

(*Bryozoa*)

Riassunto. — Lo studio sistematico di varie specie di *Eschara* Lamouroux, 1801, descritte da D'ORBIGNY in Paléontologie Française, Terrains Crétacés, Tm. V, 1850-1851, permette di mettere in evidenza caratteri morfologici importanti quali la forma e la posizione dell'opesium, la natura delle ovicelle, la forma degli avicularia.

E' stata stabilita la posizione generica di ciascuna di tali specie ed è stato riportato un certo numero di sinonimi.

Summary. — Systematic studies of various species of the genus *Eschara* Lamouroux, 1801 described in D'ORBIGNY's Paléontologie Française, Terrains crétacés, Tome V, 1850-1851, have permitted us to point out important morphological characters such as shape and position of the opesia, nature of the ovicells, shape of the avicularia. Their generic position has been established and some synonyms were noted.

Résumé. — L'etude systématique des différentes espèces du genre *Eschara* Lamouroux, 1801, décrites par D'ORBIGNY dans la Paléontologie Française, Terrains Crétacés, Tome V, 1850-1851, nous ont permis de mettre en évidence les caractères morphologiques importants tels que la forme et la place de l'opésie, la nature des ovicelles, la forme des aviculaires. La position générique de chacune a été établie, et un certain nombre de synonymies ont été notées.

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Le genre *Eschara* Lamouroux, 1801 est représenté dans la collection D'ORBIGNY par une quantité considérable d' individus appartenant à de nombreuses espèces provenant surtout d'affleurements du Crétacé supérieur des Charentes, du Bassin de Paris et du Cotentin. L'examen de ces échantillons permet d'établir qu'ils correspondent en fait à de nombreux genres souvent difficiles à déterminer d'après les descriptions et les figures données par l'auteur. A cause du mélange très important existant parmi les spécimens et aussi à cause de la perte de certaines étiquettes indiquant la provenance du matériel, nous n'avons tenu compte dans ce travail que des types effectivement figurés par D'ORBIGNY.

En 1881 JULLIEN, travaillant sur cette collection, définit la famille des *Onychocellidae* et décrit les genres *Onychocella, Ogiva, Ogivalia, Dictuonia, Collura, Floridina* et *Smittipora.* Il prend comme critère générique la forme des opésies et celle des zoécies et il indique pour chaque nouveau genre les espèces qui le composent. En 1900 CANU reconnait déjà l' incohérence qui règne dans la collection et, reprennant les descriptions données par JULLIEN les discute, parfois les complète et y redistribue les différetes espèces. Dans aucune de ces publication n'est mentionnée la présence ni la nature des ovicelles qui sont actuellement considérés comme caractéristiques des genres et des familles. Aucun autre travail de synthèse n'a été fait depuis, et seules quelques espèces se retrouvent dans certaines publications de E. VOIGT sur le Crétacé supérieur d'Europe septentrionale. Notre but ici n'est pas de redonner une description complète de toutes les espèces d'*Eschara* non plus que de les figurer mais simplement en nous basant sur les principaux caractères morphologiques, de les intégrer dans les divers genres connus. Nous suivrons pour cela la classification donnée par R. S. BASSLER en 1953.

Famille des Onychocellidae Jullien, 1881.

— Genre *Onychocella* Jullien, 1881: un très petit nombre d'espèces peuvent être rattachées à ce genre avec certitude. *Eschara clito* (pl. 1, fig. 1) et *Eschara edusa* en présentent tous les caractères; par contre *Eschara nerei* a une opésie avec des indentations peu marquées, une dent proximale, et son attribution semble plus douteuse.

— Genre *Collura* Jullien, 1881: Le générotype, *Eschara athulia* (pl. 1, fig. 3) est représenté par un fragment de colonie sur lequel la forme particulière des cellules semble dûe à une altération identique à celle qui affecte souvent les colonies d'*Eschara royana* entre autres. La valeur de ce genre ainsi défini nous semble être douteuse.

— Genre *Ogiva* Jullien, 1881: Le générotype, *Eschara actaea* (pl. 1, fig. 4) est assez bien figuré par d'Orbigny en ce qui concerne l'allure des zoécies et des onychocellaires, mais les opésies sont en réalité beaucoup plus importantes. En général, les onychocellaires ont un rostre droit, saillant au-dessus du plan zoarial. On peut y ranger: *Eschara acasta, Eschara arethusa, Eschara cynthia.*
Trois autres espèces ont les caractéres essentiels identiques mais le rostre de l'onychocellaire est incurvé comme chez les *Onychocella.* Ce sont *Eschara cypraea* et *Eschara santonensis* que nous considérons comme synonymes, et *Eschara drya.*

— Genre *Ogivalia* Jullien, 1881: La seule différence existant avec le genre précédent réside dans la forme semi-circulaire de l'opésie. On peut y classer les espèces suivantes: *Eschara archosia* (pl. 1, fig. 8), *Eschara didymia* et *Eschara echo* dont la particularité est de posséder d'énormes aviculaires fuselés situés sur le marges des colonies.

— Genre *Onychocellaria* Voigt, 1957: Il est représenté par les espèces *Eschara arsinoe, Eschara calypso* et *Eschara camilla.*

— Genre *Rhebasia* Jullien, 1881: Dans le traité de R. S. Bassler il semble y avoir eu confusion entre le générotype cité: *Eschara dorilas* (pl. 1, fig. 5) et *Eschara doris* (pl. 1, fig. 2) qui paraît avoir été représenté à sa place. Les grands aviculaires à partie antérieure arrondie que l'on trouve chez *Eschara dorilas* feraient plutôt classer cette espèce parmi les *Thyracella* Voigt, 1930. Il semble qu'il soit difficile de conserver ce genre basé uniquement sur l'épaississement du bourrelet interzoécial.

— Genre *Smittipora* Jullien, 1881: La description originale complétée par CANU qui signale comme caractère commun à toutes les espéces crétacées « ... une facette plongeante qui se développe dans la partie supérieure de l'opésie ..., (et) porte l'ovicelle quand il existe ... » semble avoir été ignorée par R. S. BASSLER. Nous considérons ce genre dans le sens donné par CANU. Il renferme, en plus de nombreuses formes de « *Vincularia* », *Eschara calliope* (pl. 1, fig. 6) et *Eschara cornelia*. Il se pourrait qu'une partie des spécimens décrits sous le nom d'*Eschara claudia* (pl. 2, fig. 1) appartiennent à ce genre: ce sont ceux qui sont représentés sur la planche 675 du traité de D'ORBIGNY. Le type figuré sur la planche 671 n'a pas été retrouvé.

Famille des Microporidae Hincks, 1880.

— Genre *Aechmella* Canu et Bassler, 1917: Une seule espèce, *Eschara crithea* peut y être classée.

Famille des Aspidostomatidae Jullien, 1888.

— Genre *Euritina* Canu, 1900: En plus du générotype, *Eschara eurita* (pl. 2, fig. 2) et de l'*Eschara delia* que CANU avait lui-même attribués à ce genre, on peut y ranger *Eschara clytia* et peut-être aussi *Eschara egaea* bien que le seul spécimen de cette dernière soit en assez mauvais état.

— Genre *Rhagasostoma* Koschinsky, 1885: Ce genre d'un aspect très voisin de ceux de la famille des *Onychocellidae* s'en différencie essentiellement par des ovicelles hyperstomiaux et non endozoéciaux. De nombreuses espèces correspondent à sa description, mais parmi elles se trouvent beaucoup de synonymes. Ce sont: *Eschara acmon* (pl. 2, fig. 3), *Eschara aglaia* et *charonia*, la seconde n'étant qu'un fragment grêle de la première, *Eschara bellona* et *lamarcki* qui n'a rien de commun avec celle de VON HAGENOW, *Eschara cassiope* et *chloris*, *Eschara cepha, cressida, creona, cyane*, et enfin *Eschara cytherea*.

Trois autres espèces forment un groupe à part; ce sont: *Eschara aegle, Eschara aegon* (pl. 2, fig. 4) et *Eschara antiopa*.

Elles ont toutes des ovicelles hyperstomiaux, des opésies pourvues d' indentations opésiulaires nettes, des onychocellaires droits, longs. Leurs cellules sont nettement séparées les unes des autres, mais l'arrangement cellulaire donne cependant des lignées longitudinales. Ce même caractère se rencontre aussi chez *Eschara atalanta* et *Eschara cybele* (pl. 2, fig. 5), mais dont les aviculaires nombreux sont petits, droits avec un bec court. *Eschara andromeda* a les mêmes caractéristiques cellulaires et coloniales (pl. 2, fig. 6), mais possède des aviculaires droits à large bec spatulé. Il est possible que l'on soit amené à créer pour ce dernier groupe un genre différent.

Famille des Cellariidae Hincks, 1880.

— Genre *Dimorphocellaria* Voigt, 1930: Les trois espèces appartenant à ce genre: *Eschara amynthas, Eschara caecilia* et *Eschara callirhoe* (pl. 1, fig. 7) doivent être mises en synonymie.

Famille des Membranicellariidae Levinsen, 1909.

— Genre *Dictuonia* Jullien, 1881: Le générotype, *Eschara aceste* n'existant plus dans la collection, nous pensons pouvoir le remplacer par *Eschara danae* (pl. 2, fig. 7) qui semble identique. La seule différence par rapport à la figure donnée par R. S. Bassler est la taille plus importante de l'opésie. Nous y rangerons aussi *Eschara aegea, Eschara amata, Eschara elea, Eschara cleon* et son synonyme *Eschara echinata, Eschara cymodoce* qui n'est autre qu'*Eschara danae,* et *Eschara parisiensis.*

Deux espèces pourraient aussi être rapprochées de ce groupe: pour l'une d'elles, *Eschara achates,* (pl. 2, fig. 8) d'Orbigny avait créé le genre *Lateschara,* caractérisé par l'arrangement des zoécies qui, jointives latéralement, foment des lignées transverses et non longitudinales. Cette définition a été dernièrement reprise par E. Voigt en 1967 pour des spécimens d'URSS, d'Allemagne, du Danemark et d'Angleterre. Si ce genre *Lateschara* est conservé, sa place semble être proche de *Dictuonia.*

Famille des Coscinopleuridae Canu, 1913.

— Genre *Acoscinopleura* Voigt, 1956: Trois espèces y correspondent: *Eschara artemis, Eschara aspasia* et *Eschara clio.*

— Genre *Escharifora* d'Orbigny, 1852: *Eschara argyrias* et *Eschara bixa* en font partie.

En dehors de ces espèces qui appartiennent aux principales familles rencontrées lors d'une étude de la faune du Crétacé supérieur de France, un certain nombre d'autres, souvent existant dans la collection à l'état très fragmentaires, peuvent avoir aussi une attribution générique à peu près sûre. Ce sont *Eschara argia*: *Puncturiella*; *Eschara bonasia*: *Beisselina*; *Eschara diana*: *Taenioporina*; *Eschara clymene*: *Systenostoma*; alors que *Eschara dejanira* pourrait peut être, avec son aviculaire spatulé et son opésie denticulée, être une *Labioporella.*

Par ailleurs, les types d'*Eschara alimena, Eschara arcas, Eschara bolina, Eschara camaena, Eschara cydippe* et *Eschara electra* ayant disparu, ces dernières n'ont pas été redéterminées.

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PLANCHE V - G = 20.

Fig. 1. — *Onychocella clito* (d'Orbigny).
Meudon. Campanien. coll. D'ORBIGNY n° 7830. Type.

Fig. 2. — « *Rhebasia* » *doris* (d'Orbigny).
Vendôme. Santonien. coll. D'ORBIGNY n° 7853. Type.

Fig. 3. — « *Collura* » *athulia* (d'Orbigny).
Néhou. Sénonien. coll. D'ORBIGNY n° 7811. Type.

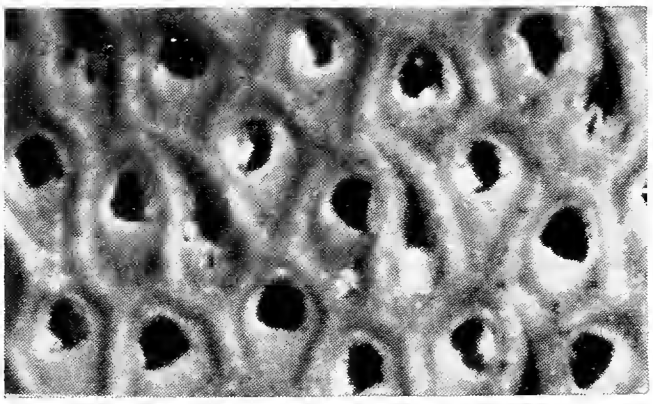
Fig. 4. — *Ogiva actaea* (d'Orbigny).
Fécamp. Coniacien. coll. D'ORBIGNY n° 7791. Type.

Fig. 5. — ? *Thyracella dorilas* (d'Orbigny).
Sans localité. coll. D'ORBIGNY n° 7854.

Fig. 6. — *Smittipora calliope* (d'Orbigny).
Meudon. Campanien. coll. D'ORBIGNY n° 7819. Type.

Fig. 7. — *Dimorphocellaria callirhoe* (d'Orbigny).
Royan. Maestrichtien. coll. D'ORBIGNY n° 7820. Type.

Fig. 8. — *Ogivalia archosia* (d'Orbigny).
Néhou. Sénonien. coll. D'ORBIGNY n° 7809.



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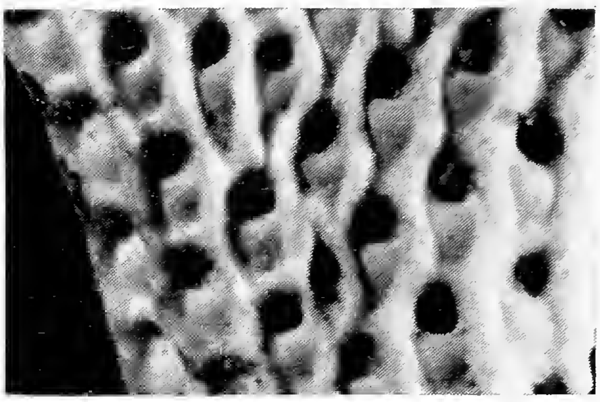

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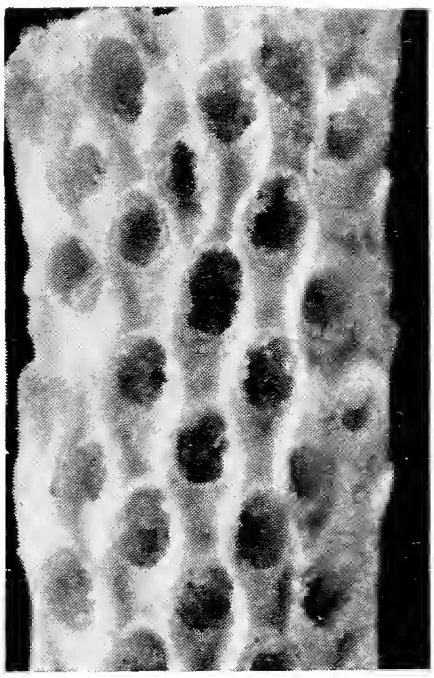

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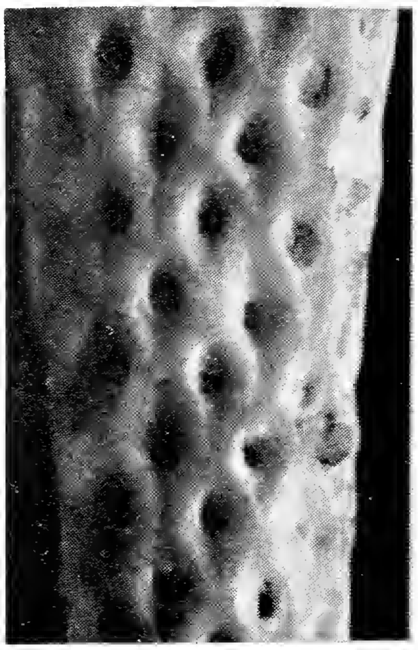

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PLANCHE VI - G = 20.

Fig. 1. — ? *Smittipora claudia* (d'Orbigny).
Sans localité. coll. D'ORBIGNY n° 7845. Type pl. 675.

Fig. 2. — *Euritina eurita* (d'Orbigny).
Sainte Maure. coll. D'ORBIGNY n° 7863. Type.

Fig. 3. — *Rhagasostoma acmon* (d'Orbigny).
Fécamp. Coniacien. coll. D'ORBIGNY n° 7790.

Fig. 4. — ? *Rhagasostoma aegon* (d'Orbigny).
Villedieu. coll. D'ORBIGNY n° 7797. Type.

Fig. 5. — ? *Rhagasostoma cybele* (d'Orbigny).
Tours. Coniacien. coll. D'ORBIGNY n° 7838.

Fig. 6. — ? *Rhagasostoma andromeda* (d'Orbigny).
La Flèche. Sénonien. coll. D'ORBIGNY n° 7794. Type.

Fig. 7. — *Dictuonia danae* (d'Orbigny).
Tours. coll. D'ORBIGNY n° 7845. Type.

Fig. 8. — « *Lateschara* » *achates* (d'Orbigny).
Fécamp. Coniacien. coll. D'ORBIGNY n° 7789. Type.


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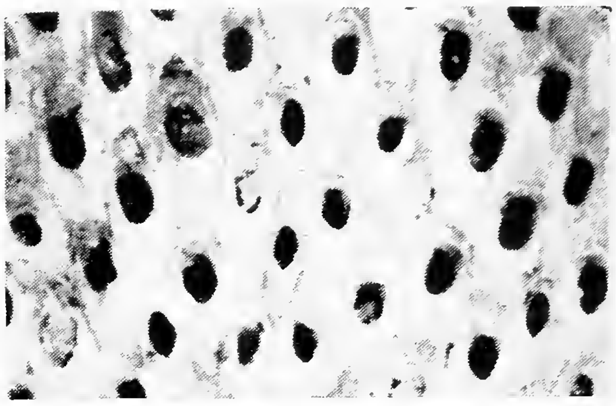
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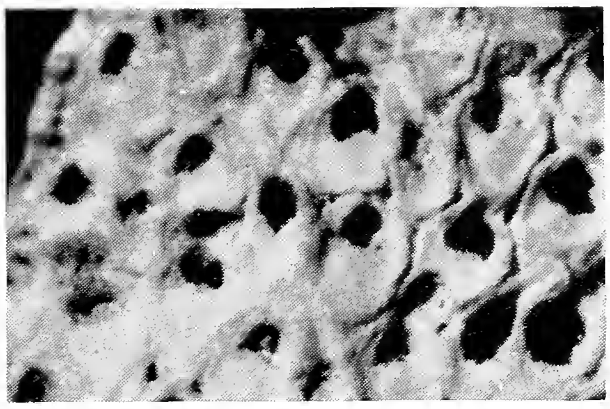
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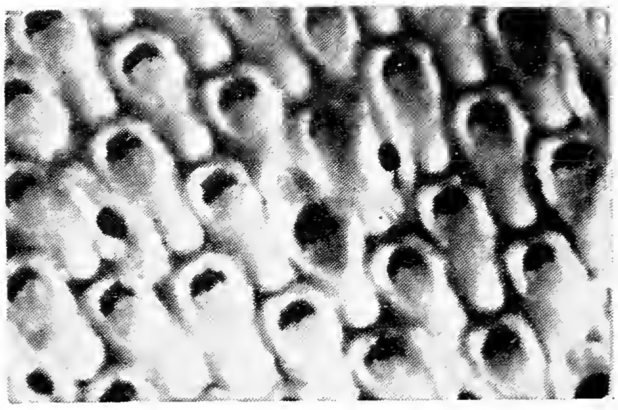
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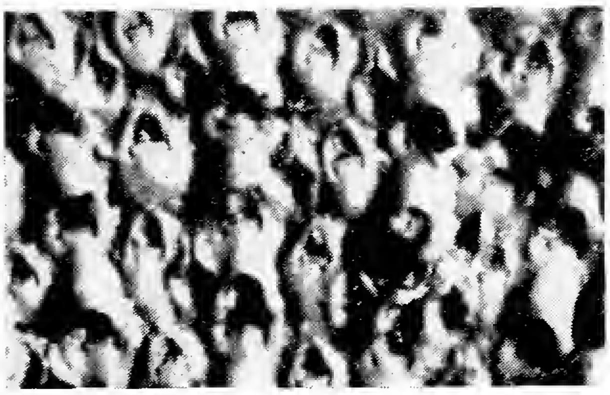
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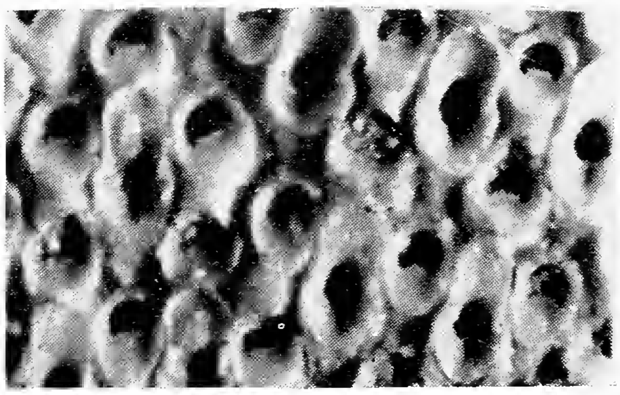
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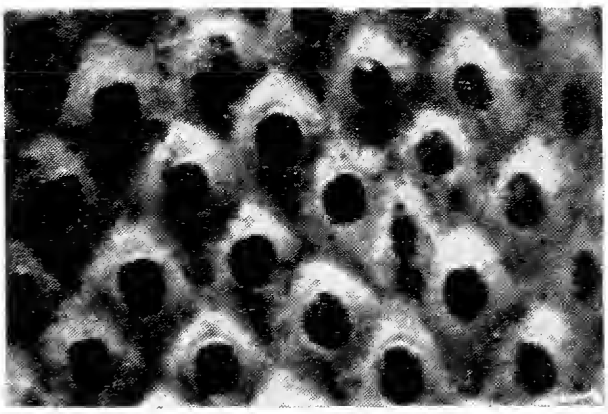
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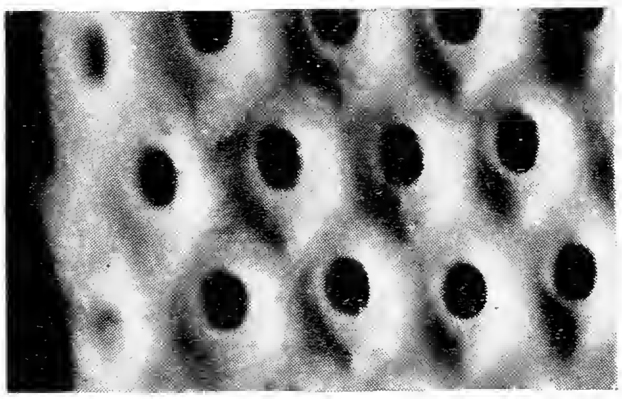
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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
29. Group 4: Evolutionary Patterns and Systematics.

STEN A. N. SCHAGER (*)

REMARKS ON THE GENUS *FLORIDINA* Jullien, 1881

(*Bryozoa*)

Riassunto. — Si è creduto nel passato che il genere *Floridina* avesse parecchie specie fossili nel Cretacico europeo e nel Terziario nord-americano. Uno studio sull'*avicularium* vicariante (*onychocellarium*) del genere considerato mostra come la maggior parte di queste specie appartenga ad altri generi e famiglie e come il genere *Floridina* si sia sviluppato nel Terziario superiore dell'America del Nord.

Summary. — The genus *Floridina* has been considered to have several fossil species in the European Cretaceous and N. American Tertiary. An investigation of the vicarious *avicularium*, the *onychocellarium*, of the genus indicates that most of these species must belong to other genera and families and that *Floridina* developed in the upper Tertiary of N. America.

Zusammenfassung. — Es ist bisher angenommen worden, dass die Gattung *Floridina* mehrere fossile Spezien in sowohl der europäischen Kreide als im Tertiär Nord Amerikas habe. Eine Untersuchung des vikariirendes Avikularium, das Onychocellarium, der Gattung zeigt dass die meisten Arten zu anderen Gattungen und Familien gehören müssen, und das *Floridina* in dem oberen Tertiär Nord Amerikas entstanden ist.

The family *Onychocellidae* Jullien, 1881 was originally given four genera based on modern species and several genera based on drawings by D'ORBIGNY on material from the upper Cretaceous of Europe. Additional genera have, by later authors, been based on both fossil and recent material.

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To-day are in general only three genera, with modern species, accepted: *Onychocella*, *Smittipora* and *Floridina*. Several genera, wholly fossil, are also accepted. *Floridina* is characterized by an autozooid with a cryptocyst that has an elliptic opesium with symmetric opesiulae. Its ovicell is endozooecial. It lacks spinae. Vicarious avicularia, of the type called onychocellarium, are present. No other type of avicularium may be observed. The onychocellarium has an elliptic opesium. The onychocellarium has straight borders the two distal ones being longer than the two proximal ones. The onychocellarium has a bimembraneous mandible. This description is compiled from JULLIEN 1881, LEVINSEN 1909, CANU and BASSLER 1920 and BASSLER 1953.

The oldest species that has been named *Floridina* appears in the Coniacian of Europe (VOIGT 1967 a). Higher up in the Cretaceous several species have been named *Floridina* not only in Europe (VOIGT 1923, 1930, BERTHELSEN 1962 and others) but also in Asia (VOIGT 1967 b). With the end of the Danian they have not been reported from Europe. On the other hand they have been described from the lower and middle Tertiary of E. and S. N. America (CANU and BASSLER 1917, 1919, 1920, 1923, 1927, 1933. CHEETHAM 1957, 1962, 1963 etc.) CANU and BASSLER have also introduced names like *Diplopholeos* and *Floridinella* for forms very similar to what has been called *Floridina*.

Many of these Cretaceous and Tertiary species are different from the *Floridina* - description as they have spines, lack avicularia etc.

Most authors have not considered JULLIEN's description of the onychocellarium, but have called all vicarious avicularia onychocellarium if they have been found in species that look similar to *Floridina*. The present author does not share this viewpoint. A study of the onychocellarium in recent material will show the following characteristics.

There is a pair of very strong closing muscles that runs from the proximal - lateral parts of the basal wall and via tendons is attatched to the distal - basal part of the mandible. An other pair of strong closing muscles runs from the distal - lateral part of the basal wall to the distal - basal part of the mandible. These four muscles (or tendons) need one or more openings in the cryptocyst. This opening or these openings must be of certain size and shape. One singe opening muscle is located in the central line proximal to the mandible. It runs from the basal wall to the ectocyst. When the ectocyst is depressed in its proximal part, the mandible will open. This opening muscle is smooth, the closing muscles have a striated pattern, which also appears more or less spiralized. The onychocellarian opesium can thus be either an oval opening which goes far enough in proximal direction to allow passage of the opening muscle and the tendons from the proximal closing muscles or it can be several small openings with one median proximal slit and several paired lateral-distal slits. The size, shape and position of such slits will give information on the size of the individual muscles and on the shape of the mandibular base. If the avicularian opesium does not correspond to these slits, the muscles are not developed in the correct way and the avicularium is not an onychocellarium.

Also the avicularian position in the zoarium is important. When a zooidrow divides there shall always be an onychocellarium as the first zooid in the distal-lateral row. The terminal row shall always have an autozooid as the next zooid. In the typegenus of the family, *Onychocella*, no other positions for onychocellaria have been observed. In the typespecies of *Floridina, F. antiqua* (Smitt, 1873), which is encrusting, one might also find onychocellaria where zooidrows become crowded owing to substratum factors. In this latter case a zooidrow disappears and its last zooid is an onychocellarium. Which type of zooid that will develop appears to depend on the distribution of the interzooidal communications. The normal autozooid has one proximal-terminal and on each side one proximal-lateral. Each of these pores is connected with distal parts of proximal zooids. Likewise three distal zooids are in their proximal parts connected with one autozooid by one distal-terminal pore and on each side of the latter one distal-lateral pore. When a zooidrow divides the distal-terminal pore goes to the terminal autozooid. One of the distal-lateral pores becomes a proximal-lateral pore in the lateral onychocellarium. This zooid does not have the proximal-terminal pore. Under these circumstances there does not develop a normal polypide, the zooid developes as an onychocellarium. The zoarial surface can sometimes give the impression that some autozooids are arranged in a circle around the onychocellarium (the « nuclear effect » of LAGAAIJ 1952).

A review of a number of species named *Floridina* from the Cretaceous and Tertiary shows that the majority of them, have avicularia in the wrong position, have avicularia with a different opesium or lack avicularia wholly. These species do not have onychocellaria, they cannot belong to the *Onychocellidae,* and they are thus not *Floridina*-species.

In the opinion of the present author there is only one, or possibly two, species that can be accepted as *Floridina.* The type-species *F. antiqua* (Smitt, 1873) is found living in the warm waters on both sides of the American continent and also on the W. African coast (COOK 1964). It has been reported fossil from the Eocene (CANU and BASSLER 1920, CHEETHAM 1957 and 1963). These fossil specimens do all refer to a species of an other genus. The present distribution indicates however that the species had developed before the closing of the Isthmus of Panama, and it could be expected fossil in the upper Tertiary of C. America. Dr. Scolaro, Georgia, USA has (personal communication, Aug. 1968) informed the present writer that he has collected the species in the Miocene of Florida.

The second species is *Floridina parvicella* (Canu and Bassler, 1923). It was first reported from the Pliocene of S. Carolina and has later been reported living in the Gulf of Mexico (LAGAAIJ, 1963). Dr. MATURO, Florida, USA has (personal communication, Aug. 1968) found it also off Florida. There may be doubts if this is a species or only a variety, it is characterized by tubercles in the interzooidal cornes. These tubercles were not observed by CANU and BASSLER but are present also in the fossil material (LAGAAIJ 1963, p. 178).

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30. Group 4: Evolutionary Patterns and Systematics.

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TERMINOLOGICAL PROBLEMS IN *BRYOZOA*

Riassunto. — Una terminologia precisa è essenziale per il progresso della Briozoologia. In questo lavoro, parole, la cui ortografia è sbagliata (olocyst) o che sono state formate male (cardelli) o che sono di origine oscura (opesia), sono state chiarificate etimologicamente mentre alcune altre parole, di significato confuso o ambiguo (anter, poster, porta, vanna, zooecium, ooecium, gonoecium, gonozooid) sono state discusse per arrivare a definizioni soddisfacenti. Indi, la classificazione di ovicelle dei *Cheilostomata* viene riconsiderata sulle basi di quattro attributi descrivibili: *a*) il metodo di formazione (indipendente o dipendente dallo zooide distale); *b*) la posizione relativa allo zooide distale (prominente, sub-immersa o immersa); *c*) la posizione dell'apertura ovicellare (iperstomiale o ipostomiale); *d*) il modo di chiusura (cleitrale o acleitrale). Finalmente l'A. suggerisce che questa Conferenza crei un Comitato per la Terminologia, comprendente due geologi e due zoologi, per preparare un glossario di termini usati in Briozoologia da sottomettere alla prossima Conferenza Internazionale.

Summary. — An unambiguous terminology is essential for the progress of bryozoology. In this paper some words mis-spelt (olocyst), wrongly formed (cardella) or of obscure origin (opesia) are clarified etymologically, while some others of confused or ambiguous meaning (anter, poster, porta, vanna, zooecium, ooecium, gonoecium, gonozooid) are discussed to arrive at satisfactory definitions. The classification of cheilostome ovicells is then reconsidered on the basis of four describable attributes, namely, (*a*) method of formation (independent of or dependent on the distal zooid), (*b*) position relative to the distal zooid (prominent, subimmersed or immersed), (*c*) situation of the ovicellar opening (hyperstomial or hypostomial), and (*d*) method of closure (cleithral or acleithral). Slight modifications to existing terminology are proposed. Finally it is suggested that this Conference should set up a Committee on Terminology, comprising two geologists and two zoologists, to prepare a draft glossary of terms used in bryozoology for submission to the next International Conference.

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The subject of terminology may sound unexciting, but its fundamental importance is obvious: an International Conference on Bryozoa would be impossible unless all the participants understood most at least of the special terms used to describe bryozoans. A clear, precise and economical terminology facilitates communication between teacher and student, and is essential for the easy exchange of information and ideas between research workers. The terminology used by bryozoologists at the moment, however, is frequently obscure in both application and derivation; it is even sometimes ambiguous. Thus HYMAN (1959: 285) observed: « The study of ectoprocts is burdened with a large and fantastic terminology, much of it dating from a period when the structure of the animals was not understood. Hence the terminology lacks relation to terms employed for other groups of animals. Frequently the ectoproctologists seem to get themselves entangled in their own terminology, using the same word (e.g., aperture) in several different senses ».

As generally understood, terminology is simply the system of terms belonging to any science or subject; but its etymological definition is the scientific study of terms. The two meanings are not so far divorced as might be supposed, for the inventor of new technical terms must pay due attention to etymology, particularly in the formation of diminutives and other compound words. It is appropriate here to draw attention to a most valuable book on the subject, *Composition of Scientific Words* (BROWN, 1956). Lack of care and/or knowledge leads to the introduction of misconstructed or wrongly spelt words, of which the following are some examples.

Cardellae. Introduced by JULLIEN (1888: 52) as a Latin plural, with French equivalent *cardelles*, for the processes inside the cheilostome orifice on which the operculum pivots. I am not aware that *cardelle* exists in vernacular French and, in the absence of any definite indication, assume that *cardella* must have been intended as a diminutive of Latin *cardo, -inis* (masc.), a hinge. The correct diminutive of *cardo*, however, would be *cardunculus* (pl. *carduncuIi*), which is admittedly rather ponderous. Fortunately, an alternative exists, for some authors refer to these structures as condyles (or *condyli*, the Latin plural derived from *κόνδυλος,* a prominence), which seems altogether much more satisfactory.

Olocyst. Introduced by Canu & Bassler (1920: 47), following Jullien (1888: 46), for the smooth, non-porous frontal wall of certain cheilostomes (e.g., *Hippothoa*). Olocyst is an example of incorrect transliteration, for it is derived from *ὅλος,* entire, together with *κύστις,* a sac or cell. Unfortunately Canu & Bassler, like Jullien, failed to realize that the aspirated vowel *(ὁ)* is always preceeded in transliteration by h, so that the correct rendering of *ὅλος* is *holos*, familiar in many compound words. Olocyst, therefore, is simply a misspelling of holocyst. Another example of confused spelling concerns zooid, but I have discussed this in an earlier paper (Ryland, 1967: 344).

Opesia. Introduced by Jullien (1888: 67) as a French word *opésie* for the central opening in the cryptocyst of many anascans. He gives the derivation from *ὀπῄσια,* buttonhole, a word which did not exist in classical Greek. Latinisation of this gives *opesia* (fem.), but Canu & Bassler, presumably inadvertently, rendered it as *opesium*. This incorrect spelling has persisted in the literature.

On the subject of muddles introduced by Canu & Bassler, I have earlier (Ryland, 1967: 346) pointed out their transposition of porta and vanna, which apply to the operculum, with anter and poster, which apply to the orifice. Subsequently, however, Hastings (*in litt.*) drew my attention to some additonal complications concerning these words. Jullien (1903: 16) gave the following definitions: « L' orifice . . . se divise en deux régions bien distinctes, à chacune desquelles est dévolue une fonction différente: la région antérieure . . . , c'est la région polypidienne qui est limitée en avant par la lèvre antérieure de l'orifice ou anter . . .; la lèvre operculaire qui ferme la région polypidienne s'appellera la porta . . .; la région postérieure de l'orifice sert uniquement à l'entrée à la sortie de l'eau ambiante dans cette poche à eau, que nous avons nommée compensatrix ou compensatrice, et se trouve limitée en arrière par la lèvre postérieure de l'orifice ou poster. . . . La lèvre de l'opercule qui ferme la compensatrice s'appellera la vanne ou vanna ». Thus anter and poster were introduced to describe the rim of the orifice, not the corresponding parts of its lumen.

Nevertheless, Brown (1952: 32) stated of the anter that it is: « Generally understood as that part of the orifice distal to the condyles in some Ascophora » (i.e., that anter and poster should be regarded as parts of the lumen, rather than of the rim). In the same year, however, Lagaaij (1952: 15) repeated exactly Jullien's definitions for anter and poster, but extended the meanings of porta and vanna to include the corresponding part of the orifice itself. Unless definitions for these terms can be agreed, a very confusing situation could arise. My own inclination is to follow the usage proposed by Brown. Two further examples of words redefined are heterozooid and gymnocyst (Levinsen, 1909: v and Borg, 1926: 188, 190 footnote).

Zooecium. Hyman (1959: 287) drew a distinction between the cystid and the zooecium, although broadly speaking both describe the body wall of the zooid. The history of the two words was reviewed by Ryland (1967: 344), who accepted Hyman's distinction between the complete body wall including its living layers (the cystid) and the durable calcareous element of the wall (the zooecium). Subsequent correspondence, however, suggests that many zoologists would be very happy to see the word zooecium disappear entirely from bryozoan terminology. Its derivation from *οἶκος* implies that it is a house inhabited by a separate entity, a « zooid », as a worm lives in a tube; whereas in reality the exoskeleton is just part of the zooid wall, and is often permeated by strands of living tissue. In a standard geological textbook it is stated that: « In the most familiar Bryozoa the autozooid lives in a chitinous or calcareous tube, the zooecium, which is in reality an external envelope, though commonly included by zoologists as an integral part of the wall of the zooid » (Shrock & Twenhofel, 1953: 200). So long as zooecium remains in use, I am afraid that this appalling misconception will continue.

Brood chambers. The terminology applied to the brood chambers in Bryozoa is complex and not entirely satisfactory. Where the complete structure is clearly a zooid morph, as in many cyclostomes, it is properly termed a gonozooid, from *γόνος*, offspring (Levinsen, 1909, as gonozooecium; Borg, 1926). The cheilostome equivalent of the gonozooid is the so-called gonoecium of the *Adeonidae* (Hincks, 1887: 152; Harmer, 1957: 788; Powell, 1967 a, 1906): but a gonoecium, literally, is a brood chamber of any description, irrespective of whether it is a zooid morph or not. Smitt (1867: 473) used *könhus*, which Borg (1926: 386), translated as gonoecium (cf. *djurhus* = zooecium), when discussing the idea that cyclostome brood-chambers might be diclinous.

Levinsen (1909: v, 282) more properly called the reproductive zooids of the *Adeonidae* gonozooecia (i.e., gonozooids). *Metrarabdotos* (Cheetham, 1968) presents a more difficult case, since the parent zooid is differentiated distally as an ovisac; but if these ovisacs are not homologous with ovicells, then the whole structure is again a gonozooid. The safest label here would be simply female or reproductive zooid. Where special female ovicellate zooids occur (e.g., in *Hippothoa*), it is misleading to use the term gonozooid (cf. Harmer, 1957: 641; Powell, 1967 a: 1906). If a distinctive name is really needed, gynaecozooid (*γυνή, γυναικός*, a female) might be appropriate, with androzooid (*ἀνήρ, ἀνδρός*, a male) available for any specialised male counterpart. It must be realized, however, that the situation found in *Hippothoa* is only an extreme instance of a widespread phenomenon. Ovicellate zooids by definition are distinguished by the possession of ovicells, and often also by an orifice of different size, shape and location (see p. 231): where should the line be drawn?

The special brood chamber characteristic of many cheilostomes is variously termed an ovicell or ooecium. I believe that some authors have refrained from using the latter word in the belief that it connotes a modified zooecium. Even if valid, this objection could not be maintained if the term zooecium were to be discarded; descriptively and etymologically ooecium is satisfactory if a latinized terminology is considered desirable.

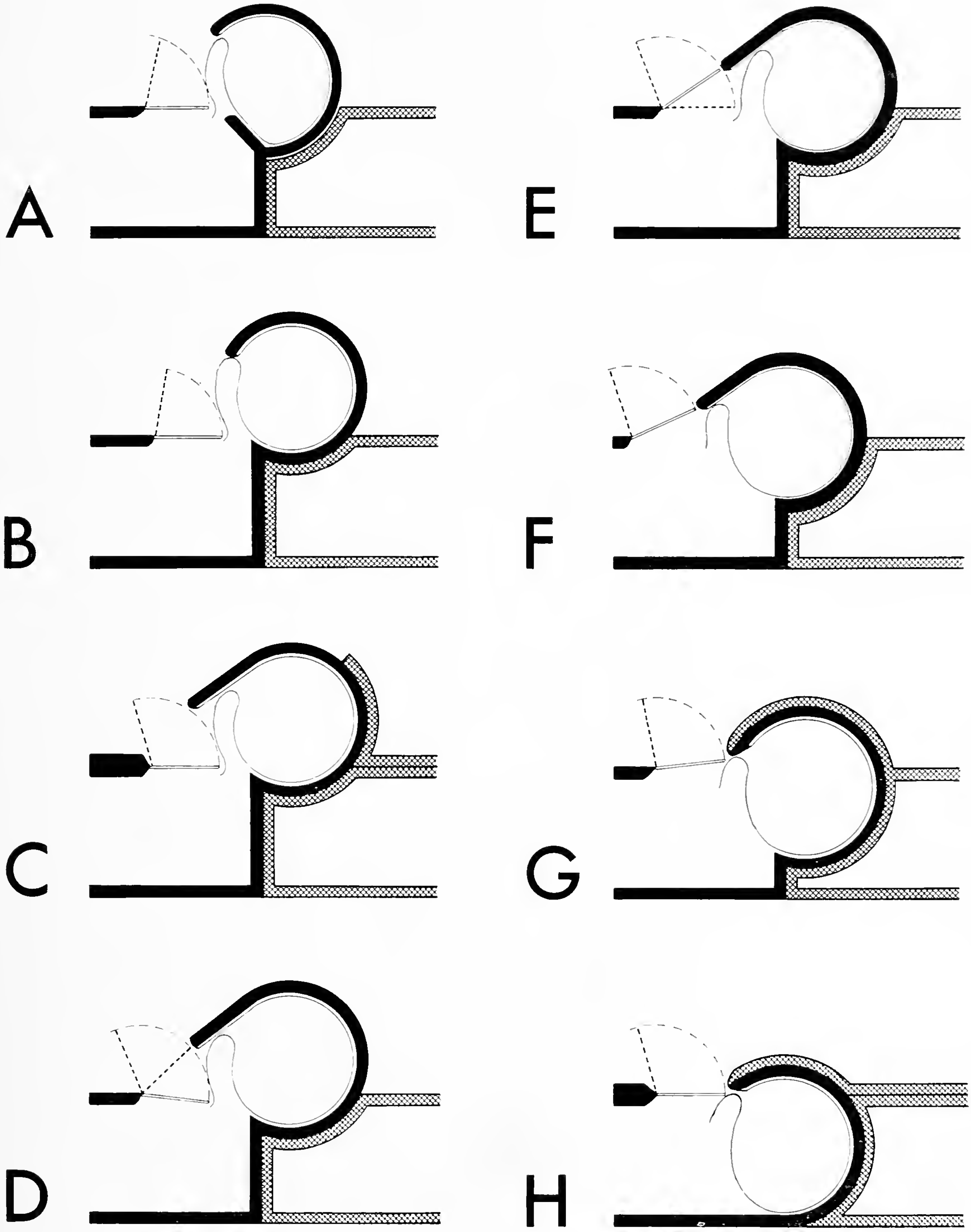
The term ooeciostome, which has been used to describe the opening of the cyclostome gonozooid, would obviously be far better employed as the name for the ooecial orifice in cheilostomes. For the opening of a gonozooid or other brood-chamber gonoeciostome might be appropriate.

Canu & Bassler (1920: 54) summarized a complicated and poorly explained terminology for describing ovicells. It seems clear, however, that their proposals, and the gratuitous alterations made to those of earlier authors, were based on inadequate analysis of the kind of feature they were trying to describe. Their mistake was to make unrelated attributes appear to be alternatives, and in consequence their classification is unsatisfactory and obscure.

There appear to be at least four independent attributes of ovicells that require characterization (see Fig. 1):

1) Method of formation. (*a*) In some genera, e.g., *Phylactella, Crepidacantha,* the ovicell develops on the distal wall of the parent zooid quite independently of the future distal zooid (Fig. 1 A), although in some instances the distal zooid may subsequently grow around the ovicell (Brown, 1954: 244, footnote 2). Ovicells of this type were termed independent by Levinsen (1909: 62), but Canu & Bassler substituted an extraordinarily inappropriate alternative, recumbent. (*b*) Other ovicells develop relatively later, and from their inception rest on the frontal wall of the distal zooid or its precursor (which is why it is so misleading to describe the independent ovicell as recumbent). Levinsen termed this second type of development dependent (Fig. 1 B-H).

Fig. 1. — Some types of ovicell found in the *Cheilostomata*, seen in optical section. The cystid is indicated by a thick line (black for the parent zooid, hatched for the distal zooid) which does not necessarily indicate the presence of calcification. Thus both the frontal and basal walls of the zooid may be entirely membranous; similarly, the distal/proximal wall has usually only a single shared calcified layer. The ovicellar structure demonstrated by Silén is assumed throughout, and the diagrams illustrate the various ways in which the basic ovicell can be related to the parent and distal zooids. The operculum is shown in the normal closed position, but open and alternative closed positions are indicated by heavy broken lines. Based on the published illustrations of Levinsen (1909), Canu & Bassler (1920), Silén (1944 b) and Powell (1967 b). A - independent, prominent, hyperstomial, acleithral; B - dependent, prominent, hyperstomial, acleithral; C - dependent, prominent, hyperstomial, pseudocleithral, with a partial cover from the distal zooid; D - dependent, prominent, hyperstomial, facultatively cleithral; E - dependent, subimmersed, hyperstomial, perfectly cleithral; F - dependent, subimmersed, hypostomial; G - dependent, separated endozooidal; H - dependent, endozooidal.


A
E
B
F
C
G
D
H

2) Position relative to the distal zooid. Irrespective of its mode of formation, an ovicell may be (*a*) prominent, i.e. resting superficially upon the distal zooid (Fig. 1 A-D), (*b*) partly embedded or subimmersed in it (Fig. 1 E-F), or (*c*) wholly immersed in it (Fig. 1 G-H) (HINCKS, 1880). The distal zooid is generally another autozooid, but may be a kenozooid, as in *Cribrilina* (LEVINSEN, 1909: 56), or an avicularium, as in *Spiralaria* (LEVINSEN, 1909: 125) in which the distal zooid may be an autozooid, an avicularium or a kenozooid (HASTINGS, *in litt.*). (*a*) and (*b*) together have generally been known as hyperstomial (LEVINSEN, 1902), but I suggest that the manner in which this term has been defined is slightly illogical. (*c*) is the endozooidal ovicell (endozooecial, LEVINSEN, 1902). It appears to be inherent in the definition of the endozooidal ovicell that it is overgrown by the frontal wall of the distal zooid (Fig. 1 G-H). It is not true, however, that prominent or subimmersed ovicells are never overgrown in this way. SILÉN (1944 b) has shown that there is no fundamental difference between the way in which hyperstomial and endozooidal ovicells develop.

3) Situation of the ovicellar opening. (*a*) Most commonly the ovicell opens superiorly to the orifice of the parent zooid (Fig. 1 A-E). This condition was described as superovicellate by JULLIEN (1888: 35). (*b*) The alternative situation, in which the ovicell opens below the orifice he called subovicellate (Fig. 1 F-H). When LEVINSEN (1902, 1909) proposed the terms hyperstomial and endozooidal (as endozooecial), he evidently overlooked JULLIEN's earlier categories of super- and subovicellate. JULLIEN's terminological definitions were the more precise, being based on the position of the ovicellar opening. LEVINSEN ought to have used the same criteria when defining his own terms, especially hyperstomial, but in fact used position of the ovicell relative to the distal zooid. In the interest of clarity, the definition of a hyperstomial ovicell should be *one that opens above the orifice*, though in practice it would continue to have its currently accepted connotation.

It is possible (at least in theory) for an ovicell to be only partially immersed in the distal zooid and yet open below the orifice (Fig. 1 F): it would be thus hypostomial (= subovicellate), but not endozooidal. JULLIEN placed the special female zooids of *Hippothoa* in this category.

4) Method of closure. (*a*) Many ovicells have no closing device other than the membranous inner vesicle which seals the opening (Fig. 1 A-B), although this may be somewhat chitinized (LEVINSEN, 1909: 57; SILÉN, 1944 a, fig. 19). This condition was described as aneucleithral (*ἄνευ*, without; *κλεῖθρον*, a bolt or means of closure) by JULLIEN (1888: 45) and CANU & BASSLER (1920: 54), but, since *aneu-* suggests derivation from *ἀ*- or *ἀν*- (without) plus *εὖ*- (well), a combination of suffixes which occurs in certain scientific words, it would be better to use the shorter and unambiguous acleithral. Acleithral hyperstomial ovicells may be recognized in fossil material, according to CANU & BASSLER, by the facts that the ovicell does not overlap the orifice and its opening is perpendicular to the orifice (Fig. 1 A-B). (*b*) In other hyperstomial ovicells, generally those exhibiting some degree of immersion in the distal zooid, the opening may be sealed by the slightly raised operculum of the parent zooid. JULLIEN described as cleithral this condition, which can be recognized in fossil material (CANU & BASSLER, 1920: 54) by the fact that the ovicell overlaps the orifice so that its opening obliquely faces the orifice (Fig. 1 C-F).

CANU & BASSLER appear correct in believing that grades of perfection within the cleithral system can be distinguished, but their terms are unacceptable. (i) The most primitive condition, really acleithral, but classified as cleithral by JULLIEN, is where the operculum in its traverse between closed and open momentarily seals off the ovicell (Fig. 1 C), but is never normally held in that position. This might be termed pseudocleithral (*ψευδής*, false), and is the situation found, e.g., in *Smittina*. (ii) In other genera the operculum can occupy one or other of two closed positions, the upper sealing off the ovicell, the lower closing the orifice only (Fig. 1 D). This occurs, e.g., in *Pentapora* (HASTINGS & RYLAND, 1968). CANU & BASSLER called this subcleithral, a compound word that is etymologically objectionable: facultatively or imperfectly (see iii) cleithral seems better. (iii) In what appears to be the most developed state, the normal position of the operculum in an ovicellate zooid is in the upper position. It thus permanently closes a common orifice and is perfectly cleithral. Whether the operculum is able to return to the lower position (Fig. 1 E), but usually does not, or whether it cannot (Fig. 1 F), or whether both situations occur, cannot be stated at present. In *Haplopoma* the calcified wall fabricates an « orifice », just like that of the non-ovicellate zooid, below the common orifice, but the operculum always appears to close the common orifice. Perhaps the rim of the latter functions as a stop. In anascans (e.g., in *Micropora*, examined for me by Dr. Anna B. HASTINGS) there is no calcified orifice as such, and it is perhaps to be expected that the operculum should close only the common orifice. Nevertheless, it would be unwise to assume that the condition illustrated in Fig. 1 E cannot exist. Here is a clear example of the need to study living material.

Further problems related to ovicells remain, even with respect to the types here discussed, and some special kinds of ovicell have not been mentioned at all. The terminology of the layers needs to be sorted out: SILÉN's (1944 b) alterations to established usage seem to me to be unacceptable. There are also several questions concerning the structure and degree of calcification of the ectocyst (sensu LEVINSEN); the extent of the contribution (if any) from the distal zooid; and the occurrence of ovicellar covers in which secondary calcification from the parent, distal or adjacent zooids spreads over the ovicell. These are morphological complications which SILÉN did not have to consider. His study clarified our understanding of ovicellar structure, but requires to be extended to more complex examples.

I wish to thank Dr. Anna B. HASTINGS for examining specimens, and for correspondence about the structure of ovicells.

Epilogue.

I have discussed briefly just a few technical terms which are etymologically or bryozoologically unsatisfactory. There are many more. This Conference would undoubtedly render a valuable service to science if it were to set up a committee to prepare a *Glossary of Terms relating to the Study of Bryozoa*. This committee should perhaps comprise four members: 1) a taxonomic or museum zoologist, 2) a zoologist from a teaching establishment, 3) a geologist interested in post-Palaeozoic Bryozoa, and 4) a specialist on the Palaeozoic. The terms of reference might be: to compile a list of descriptive terms applied to Bryozoa, giving for each 1) author and date of introduction; 2) etymological derivation; 3) the original definition; 4) a reworded or emended definition (if necessary) agreed by the Committee as being appropriate to the present time. If this proposal be accepted, the Committee might be asked to present its draft Glossary for the general consideration of members at the 2nd International Conference of the I.B.A.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
31. Group 4: Evolutionary Patterns and Systematics.

ENRICO ANNOSCIA (*)

PROBLEMS OF METHODOLOGY IN STUDYING AND DESCRIBING *BRYOZOA*

Riassunto. — Vengono presi in considerazione i metodi per la raccolta delle misure biometriche, le diagnosi e la terminologia briozoologica e vengono suggerite alcune soluzioni.

Summary. — The measurements methods, descriptions and terminology are taken into consideration and suggestions about these topics are given.

Résumé. — Les méthodes de mesuration biometrique, les diagnostiques et la terminologie bryozoologique sont pries en consideration et discutées, et quelques solutions sont suggérées.

The subject of my talk unintentionally follows the remarks of the colleague RYLAND. I was not able to read his text, but only a short abstract and I saw that generally speaking we all strongly require to clarify the terminology that we use in describing Bryozoa. « An unambiguous terminology is essential for the progress of Bryozoology » writes RYLAND in the abstract of his paper. I completely agree with him. As economic paleontologist working in an Oil Company, I felt all the load of an old, imprecise and blundering terminology which requested me an attention out of proportion with its real importance in my work. Every time specialists create a terminology, this is for a better understanding and not for uselessly complicating matters with equivo-

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cations which only splitting hairs philologists are able to understand. Yet, to split hairs does not mean Science.

This fact forced me to elaborate a first multilingual Glossary (in press) of Bryozoological terms which might be used as a basis for building up a finally simple and clear terminology. I so far gathered more than 1000 terms, as many as those comprised in the basic English!

Since the problem of terminology was investigated by dr. RYLAND, I don't want to spend many words on it, but I would like not to talk on terminology and semantics only: I would like to start when a Bryozoologist takes a sample in his hands until he describes its species.

Rather than a paper, my talk will be a series of proposals with some discreet suggestions.

We should all start from a fixed weight (for instance 100 gr.) of dry sample and we should give data on the percentage of dry residue after washing and the percentage of organic residue either referred to the total dry residue or to the whole dry sample, beside the percentage of Bryozoa referred to the total organic residue.

We will that way able to collect little by little a mass of uniform data which can be immediately compared one another without being manipulated or converted.

Statistical research on fossil as well as living populations are to-day more and more developing, being considerably helped by the use of Electron Computers. It is to-day unpossible to compare faunas studied by different Authors, because the necessary data lacks or are inadequate. Consequently, it would be advisable for all of us to give biometric measurements in the same way, even if in that case we do not intend to carry on a real statistical study. However, we will that way allow other people to do that easily.

To give to-day measurements as « Lz = 0,5 — 0,9 mm » does not make sense if also number of measured specimens, mean, standard deviation, observed range, etc. are not indicated. I think this is obvious to all and does not require any further explanation.

As to the symbols used for measurements, they are really too many. I enumerated 47 in my Glossary, but they are not all.

But the worst of it is that many Bryozoologists use the same symbols with a different meaning (fors instance « La » for area width as well as opening width; «Lo » for opesium width and orificium width, etc.). Shall we put also this field in order?

Let us now consider the diagnoses of new genera and species. Since Latin slowly became obsolete, no common scientific language exists any more. Everybody started writing diagnoses in his language either because he doesn't know other languages or for laziness or even nationalism. In conclusion, we need a real polyglot for interpreting the thousands and thousands of new diagnoses which are being given in so many language to-day. The new nations which are beginning to carry on scientific research did not yet begin to write diagnoses in Swahili, Arabic, Kurdish and so on. But don't worry: we will get them soon! Somebody may say that the important languages are few; well, I defy anybody to know them all!

My proposal to resume Latin might appear a selfish one because Italian is a neo-Latin language, but we cannot forget that an age-long scientific tradition supports the use of Latin. We might come to a compromise: diagnosis in the language according to which the text is written, accompanied by a Latin and/or English translation aside.

The paradigms of sistematic descriptions are mainly written in Latin to-day: *Derivatio nominis, Species-typus, Diagnosis, Locus typicus, Stratum typicum* and from here on the Latin mysteriously stops and everybody undaunted keeps paradigming in his language: Affinities, Variations and differences, Remarks, Measurements, Geologic Age, Occurrence, Call number and so on. Would it not be better to extend the use of Latin to all paradigms: *Collatio* for Affinities, variations and differences; *Notae* for Remarks; *Mensurae* for micrometric measurements; *Aetas* for Geologic age or Stratigraphical range; *Reperta* for Occurrence, Collected specimens or Observed material; *Locatio* for Call number; and so on?

Advantages are evident; whatever language be used in the text, we immediately know where to find the requested data, saving that way hours of translating work.

Latin terminology should be extended to the whole morphological nomenclature. We Bryozoologists, unlike other specialists, have the advantage of already commonly using Latin or Latin-like terms (*Opesium, Zoarium, Zooecium* and so on) (that they have or not a common meaning for everybody, this is another thing). It would be advisable not to loose this advantage, but on the contrary to extend the Latin nomenclature also to the body parts which do not have it yet (wall, axial region and so on). Once more the advantages are clear to everybody; whatever be the language used for the text, we know at least what we are talking about.

Many other things should be settled and I join with RYLAND's proposal to establish a Committee on Terminology to prepare a draft Glossary of terms used in Bryozoology for submission to the next International Conference. This Committee should also state the rules for the symbols to be used in giving biometric measurements, the way itself of taking them and the way to present them, too. The suggestions of this Committee of course do not constitute a law, but are only Recommendations which we all will freely have to follow.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
32. Group 4: Evolutionary Patterns and Systematics.

ROBERT L. ANSTEY - THOMAS G. PERRY (*)

BIOMETRIC PROCEDURES IN TAXONOMIC STUDIES OF PALEOZOIC *BRYOZOA*

(Preliminary Report)

Riassunto. — Poichè una specie paleontologica è definita da un insieme di caratteri tassonomici e poichè da un solo zoarium si possono ottenere molte misure di ciascun carattere tassonomico, i Briozoi si prestano in modo particolare alla descrizione quantitativa e all'analisi statistica.

L'analisi quantitativa fornisce criteri obiettivi per la descrizione e la differenziazione delle specie e permette inoltre una valutazione obiettiva delle variazioni morfologico-strutturali nell'ambito di un taxon. In tal modo la rigorosa definizione dei taxa per mezzo di studi quantitativi li rende più utili per la stratigrafia e per gli studi filogenetici e paleoecologici.

Com'è messo in evidenza dagli istogrammi di 17 specie di Briozoi paleozoici, la distribuzione dei caratteri tassonomici si avvicina per lo più ad una curva normale di frequenza o Gaussiana.

La normalità della distribuzione dei caratteri tassonomici è verificata statisticamente per mezzo del « Kolmogorov-Smirnov 1 - sample test ».

La normalità della distribuzione è un requisito richiesto per l'applicazione dei procedimenti statistici parametrici.

I procedimenti statistici analitici hanno la loro più valida applicazione nel differenziare gli zoaria di specie differenti e nello stabilire l'appartenenza di diversi zoaria alla stessa specie biologica.

E' necessario fare un programma per determinare il numero minimo di misure richieste per l'applicazione di questi « tests » statistici anche per ridurre al minimo i tempi ed il lavoro e per evitare l'utilizzazione di un numero superfluo di misure.

Il numero di esemplari può essere stimato statisticamente solo per quelle specie per le quali sono state date la media e la deviazione-standard dei caratteri tassonomici.

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In aggiunta alla normalità, i procedimenti statistici parametrici richiedono una selezione delle misure fatte a caso, l'omogeneità della varianza ed in generale un egual numero di misure.

Soddisfatti i requisiti richiesti, il « 2-sample t-test » può essere utilizzato per differenziare i valori medi dei caratteri tassonomici di due specie diverse. Similmente si può usare l'analisi parametrica della varianza, utilizzando l'« F-test », per determinare se gli zoaria in esame siano o no appartenenti alla stessa popolazione biologica.

Se i requisiti richiesti non sono soddisfatti, devono essere usati i procedimenti statistici non parametrici e della libera-distribuzione. Il corrispondente del « t-test » è il « Mann Whitney U-test » e il corrispondente dell'analisi parametrica della varianza è il « k-sample Kruskal-Wallis test ».

E' ovvio che i procedimenti statistici non devono essere considerati come la panacea di tutti i problemi tassonomici perchè si richiede il giudizio di tassonomi competenti per accertare quali caratteri sono di valore diagnostico sufficientemente alto da poter essere sottoposti ai procedimenti statistici e per stabilire il livello della sicurezza statistica desiderata.

Summary. — Data suggest that frequency distributions of numerical taxonomic characters of Paleozoic bryozoans commonly approximate normality, thereby permitting application of parametric statistical tests. Normality can be tested by calculating normal probabilities and using goodness-of-fit procedures. Sample randomness can be evaluated by means of the 1-sample runs test. The requisite number of measurements for taxonomic studies can only be determined statistically. The mean and standard deviation should be considered as absolutely necessary in any numerical taxonomic study. Ternary diagrams provide an effective means of showing concomitant variation in three taxonomic characters.

Résumé. — Les données suggèrent que les distributions de fréquence des caractères taxonomiques et numériques des bryozoaires paléozoïques approchent la plupart du temps la normalité, qui est une nécessité préalable à la réalisation des procédés statistiques paramétriques. La normalité peut être mise a l'épreuve par le calcul des probabilites normales, et l'emploi des procédés de « goodness-of-fit ». Le « randomness » de l'échantillon peut être évalué par le moyen du « 1-sample runs test ». Le nombre nécessaire de mesures pour les études taxonomiques ne peut être determiné que par la statistique. Le moyen et la deviation normale doivent être considérés comme absolument nécessaires pour les études taxonomiques et numériques. Les diagrammes ternaires pourvoient un moyen efficace de montrer la variation concomitante dans trois caractères taxonomiques.

Because a paleontologic species is an unique aggregation of taxonomic characters and because a single zoarium will commonly provide many measurements of each taxonomic character, bryozoans are particularly amenable to quantitative description and statistical analyses. Quantitative treatment furnishes objective criteria for the description and differentiation of species and further provides an objective evaluation of inherent morphologic -structural variation within a taxon. Thus, the rigorous definition of taxa by quantitative studies makes them more useful for stratigraphic, phyletic, and paleoecologic investigations.

In contrast to the philosophy that is strongly insinuated by the typological approach, quantitative studies have clearly revealed that considerable morphologic-structural variability characterizes most bryozoan taxa. As suggested by histograms for 17 Paleozoic bryozoan species, the distribution of taxonomic characters most commonly approximates a normal or Gaussian frequency curve. The normality of distribution of taxonomic characters has been verified statistically by means of the Kolmogorov-Smirnov l-sample test. Normality of distribution is a prerequisite for the application of parametric statistical procedures.

The most powerful means of presenting measurable taxonomic characters is through descriptive statistical procedures. Measures of central tendency, which include mean, median, and mode, indicate the typical development of each character in a species or a biological population. In contrast, measures of variability, which include range, standard deviation, coefficient of variability, and confidence intervals, demonstrate the limits of departure of each taxonomic character from its norm. Ternary diagrams are useful in displaying the concomitant variation of three taxonomic characters and are potentially of value in comparing species.

Analytical statistical procedures have their greatest use in differentiating zoaria of different species and in affirming that several zoaria belong to the same biological population. A sampling design is necessary to determine the minimum number of measurements that is required for the application of these statistical tests and also, in the interest of time and effort, to avoid utilization of a superfluously large number of measurements. Sample size can only be estimated statistically for those species for which the mean and standard deviation of taxonomic characters have been given. In addition to normality, parametric statistical procedures require random selection of measurements, homogeneity of variance, and generally equal numbers of measurements. Provided that the foregoing prerequisites are met, the 2-sample t-test can be utilized to differentiate the mean values of taxonomic characters of two different species.

Similarly, parametric analysis of variance utilizing the F-test can be employed to determine that several zoaria do or do not belong to the same biological population. If the preceding prerequisites are not satisfied, nonparametric or distribution-free statistical procedures must be employed; the analogue of the t-test is the Mann Whitney U-test, and the analogue of the parametric analysis of variance is the k-sample Kruskal-Wallis test.

Statistical treatment must not be regarded as the panacea of all taxonomic problems because the judgment of the competent taxonomist is required to ascertain which characters are of sufficiently high diagnostic value to receive statistical treatment and to establish the level of statistical confidence desired.

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33. Group 4: Evolutionary Patterns and Systematics.

FRITZ WIEBACH (*)

TAXONOMICAL AND OTHER REMARKS ON FRESHWATER *BRYOZOA*

(Preliminary Report)

Riassunto. — L'A. riferisce brevemente sui recenti tentativi per una migliore classificazione dei *Phylactolaemata*, su alcuni problemi da risolvere, su alcuni recenti ritrovamenti e sulla necessità di trovare altri esemplari di *Hislopia* e di *Afrindella tanganyikae*.

Summary. — A. deals with recent attempts for a more solid taxonomy of *Phylactolaemata*, some problems to be solved, some recent findings and the necessity to find samples of *Hislopia* and *Afrindella tanganyikae*.

This lecture mainly deals with the Phylactolaematous *Bryozoa*, and the division is the following one:

1. - recent attempts for a more solid taxonomy of Phylactolaematous genera
2. - some hints given to field and laboratory workers
3. - some problems to be solved
4. - some recent findings
5. - samples wanted in particular.

1. - A short survey is given on the systems of Phylactolaematous genera such as established by MARCUS (1942), TORIUMI (1956), ABRICOSSOV (1959) and LACOURT (1968). A number of twelve genera are considered as valid ones, viz. *Fredericella*,

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Plumatella, Hyalinella, Afrindella, Stolella, Stephanella, Gelatinella (so called tubular forms), *Lophopus, Lophopusella, Lophopodella, Pectinatella, Cristatella* (so called gelatinous forms), out of which *Afrindella* and perhaps also *Gelatinella* may want reconsideration.

2. - For a reliable classification all possible characteristics should be used, not only statoblasts, as is done by LACOURT in his recent « Monograph of the Freshwater Bryozoa Phylactolaemata » (1968). In addition to ROGICK's and BROWN's factors for classification are suggested median sections and diagrams of statoblasts and separation of statoblasts into halves and/or quarters by heating them in potash lye. Some objections are made to LACOURT's procedure of classification, and a respective example is given. A particular request is addressed to all field workers who may collect freshwater Bryozoa, viz. to keep a number of unfixed statoblasts in dry condition for later rearing purposes.

3. - Some problems to be solved: A) *Plumatella repens* and *Plumatella fungosa* are they valid species or only ecological variations of one and the same species? B) the problem of thin-walled floatoblasts (leptoblasts); C) the degree of alliance between *Plumatella emarginata* and *Plumatella casmiana;* D) the occurrence of piptoblasts in *Plumatella* samples; E) the problem of geminate colonies; F) are *Afrindella* and *Gelatinella* valid genera? G) is *Afrindella tanganyikae* a Tanganyika endemite or not? H) is *Urnatella gracilis* an immigrant in Europe?

4. - Some recent findings: A) *Bulbella abscondita* (*Gymnolaemata Ctenostomata*) in river Elbe; B) *Plumatella casmiana* in Italy; C) *Plumatella casmiana* and *Lophopodella carteri* in Bulgaria.

5. - More samples wanted of A) the species *Afrindella tanganyikae,* B) the genus *Hislopia,* especially from Africa (« missing link » between findings in South America and Asia).

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34. Group 5: Biogeography and Biostratigraphy.

ENRICO ANNOSCIA (*)

STATUS OF THE BRYOZOOLOGICAL STUDIES AND COLLECTIONS IN ITALY

Riassunto. — Viene dato un breve ragguaglio sullo stato degli studi briozoologici in Italia negli ultimi vent'anni.

Vengono inoltre presentati i risultati di un' inchiesta tesa ad accertare la consistenza e lo stato delle collezioni briozoologiche nei Musei italiani.

Un elenco delle più recenti contribuzioni sui Briozoi pubblicate in Italia chiude la breve nota.

Summary. — A brief excursus about research on fossil and living Bryozoa carried out in Italy in the last twenty years and the results of an inquiry on the Bryozoa collections status in Italian Museums are here reported.

A list of the latest papers on Bryozoa published in Italy is following at the end.

Introduction.

The studies of the Bryozoa in Italy did not meet with the favour of the students, although our outcrops from Palaeozoic to Pleistocene and seas are rich in Bryozoa.

Italian was the first great bryozoologist, F. IMPERATO (?1550-1631?); we had in Italy A. MANZONI, in the past century, A. NEVIANI e C. ZIRPOLO in this century; nevertheless, the Italian bryozoologists have been always numbered on one's fingers. For this reason the status of bryozoological studies in Italy is at the beginning: nearly all has still to be done.

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Many type localities are already recognized and published, but many others have to be searched and described, particularly the Palaeozoic and Mesozoic ones.

Only few bryofaunas are well described and illustrated; many of those described in the past should be revised.

Very few bryofaunas were compared with malacofaunas and microfaunas present in the same geologic section and in the adjacent sections, in order to establish exact local and regional stratigraphical ranges.

A large part of holotypes and paratypes of the Italian species established by ancient Authors are lost or their present location is unknown.

Only in the latter years the studies of the Bryozoa were resumed, either suggested by the need of oil research (ANNOSCIA in the AGIP Paleontological Laboratory of S. Donato Milanese) or suggested by scientific interests (ACCORDI, BRAGA, CARETTO, CERETTI, VIGANÒ in the Geologic or Zoological Institutes of various Universities, CARRADA, SACCHI, RANZOLI, RENZONI and RENZINI in the Zoological Stations).

A critical catalogue together with an Atlas of Italian fossil and living species (revised names of species with their description, stratigraphical and geographical ranges and good figures) and a revised list of the Italian type-localities would be welcome. On the other hand, many years of work of many workers will be necessary for this purpose.

A similar project together with a brief report on the status of byozoological studies and collections is to be suggested to all bryozoologists for their own countries. This might be the only way to achieve a satisfactory outline on the bryozoological studies status all over the world.

A card catalogue, like that by ELLIS & MESSINA for Foraminifera and Ostracoda, must be the final point of arrival of our young I.B.A.

The status of the collections of Bryozoa in Italian Museums is not better than the status of studies. Italian Museums, either the autonomous or the University ones, suffered more or less serious damages during the World War II. Most collections were destroyed and those which are still available are very badly arranged.

I sent, last december 1967, a questionary to about fourty Museums in order to make an inventory of bryozoological collections present in Italy. Only 12 compiled cards were returned to me!

In some Museum, no bryozoological collection is even present. Some other Museums could not establish the consistence of their collections since an inventory of them was lacking.

Bryozoological studies status.

The Italian bryozoologists are presently very few.

In the Universities are operating: Giampiero BRAGA at Padua Geological Institute on Tertiary Bryozoa; Enzo CERETTI at Bologna Geological Institute on Palaeozoic Bryozoa. Pier Giuseppe CARETTO (Turin Geological Institute) published only a paper on Tertiary Bryozoa and Bruno ACCORDI (Director of the Rome Geological Institute) published in the past some brief papers on *Conescharellina* from Tertiary of Venetia.

For living Bryozoa, Antonio VIGANÒ is working at the Zoological Institute of Perugia.

In the autonomous Institutions, only Gian Carlo CARRADA is presently working on living Bryozoa from fresh or brackish waters lakes at the Zoological Station of Naples. Finally, the writer is the sole bryozoologist working for the Industry.

Nevertheless, lists of Bryozoa are sometimes published together with studies of other fossils by several Authors, and some Zoologists (SACCHI, RANZOLI, RENZINI, ROSSI etc.) published in the past brief papers on Bryozoa.

I summarized the history of the bryozoological studies in Italy from IMPERATO (1599) until NEVIANI (1948) with a complete annoted bibliography in a work now in press. I think it is useless to repeat here what has been previously described. I rather like to inform about the studies published in the last twenty years. The bibliographic references, when not reported at the end of this paper, may be found in ANNOSCIA (1968) (2), since the whole bibliography is too long to be reported here.

Palaeozoic.

The sole Palaeozoic Bryozoa were described by CERETTI (1963-1967) from Carnia (Pontebba, Pramollo Pass and Auernig Mountain). The 55 described species belong to genera *Fenestella, Polypora, Penniretepora, Rhabdomeson, Rhombopora, Streblotrypa, Coeloconus, Rhombocladia* and *Sulcoretepora*. 29 species are new. The studied beds belong to Upper Carboniferous.

Nicosia & Del Bono (1956) reported some Bryozoa from Upper Ordovician of Iglesias Province (Sardinia).

Mesozoic.

Detailed studies on the Mesozoic Bryozoa were not published so far.

Sacchi Vialli (1964 a-b) reported *Ceriopora(?)* cf. *orbignyi* and *Neuropora* sp. from Upper Sinemurian of Saltrio (Varese, Lombardy). AGIP (1959) and Cita (1965) published two great Atlases of Italian Microfacies; in their plates some unnamed Mesozoic Bryozoa are illustrated.

Coenozoic.

Many studies were published on Italian Coenozoic Bryozoa. In the examined period of time, the first paper was published by Accordi (1947) on two new species of *Conescharellina* from Priabonian of Verona province (Venetia). He returned on the same topic in 1951 and 1965.

In 1949 Comaschi Caria published an important work on Sardinia flora and fauna. It is a list of all fossil species found there, with a list of type localities and a list of species arranged according to geochronology.

She published again on Sardinian fauna with lists of Bryozoa from Miocene of Cagliari environments (1959, 1960, 1963). The species are not described and illustrated.

Braga published four papers from 1963 to 1968 on the Eocene Oligocene and Miocene bryofauna from Berici and Lessini Mountains, Treviso environments and the Venetia type-localities studied by Reuss and Hoppenheimer in the last century.

The species are more than one hundred, well described and illustrated.

The writer, for oil research purposes, has carried out some studies on Bryozoa, publishing a big work on Biology, Systematics, Oil research, Bibliography and Nomenclature and several studies on Palaeozoic and Tertiary bryofaunas from Italy and Africa. Many of his research are unpublished and are summarized in another paper delivered in this same Conference.

Some Bryozoans, without description, were reported by MIRIGLIANO (1953) from Tirrenian of Gallipoli (Lecce province, southern Italy) and by FLORIDIA (1960) from Tortonian of Rosolini (Sicily).

CARETTO (1966) published a new classification of some Pliocene Bryozoa, previously described as Hydrozoa, from Piemont and Emilia.

Living Bryozoa.

Systematical studies on living Bryozoa were carried out by CARRADA, SACCHI and VIGANÒ.

CARRADA (1964) published his research on *Plumatella fungosa* and *Paludicella articulata* from brackish waters of Cabras lake (Sardinia) and, with the cooperation of SACCHI, published some research on *Victorella pavida* (1962, 1964) from Fusaro and Patria lakes (Naples).

SACCHI & RENZONI (1961, 1962) and SACCHI (1964) published their research on *Victorella pavida, Bowerbankia gracilis* and *Conopeum seurati* from the same lakes.

RANZOLI (1962, 1964) described *Zoobotryon verticillatum* and *Electra posidoniae* (studies on sexual behaviour and breeding in the Laboratory).

VIGANÒ (1964-1966) studied the biogeography, distribution and colonization of Bryozoa in Italian fresh waters lakes.

Some living Bryozoa are listed by RELINI (1966) in the « fouling » of Genua Harbour, by PARENZAN (1957, 1960, 1961, 1962) in the Gulf of Naples and Mar Grande of Taranto, and by ROSSI (1961) in a facies with Gorgonids from Mesco Point (Gulf of Genua).

Collections in Museums.

For the reader's convenience, I list here the Italian Museums according to the alphabetic order of towns.

BABI - University Geological and Palaeontological Institute (Ateneo Building, Nicolai street No. 2).

Collections: Bryozoa (*Cheilostomata* and *Cyclostomata*) from Uppermost Pliocene of Venusium (Potenza prov., Southern Italy) collected in 1953 by E. ANNOSCIA.

Doctorate Thesis: E. ANNOSCIA (1955).

Publications: E. ANNOSCIA (1963, 1968 (4)).

Bryozoologists: Missing.

BOLOGNA - University Geological and Palaeontological Institute (Zamboni str. No. 67).

Collections: Bryozoa from Upper Carboniferous of Auernig Mountain (Pontebba, Udine prov.).
121 slides and 71 thin sections.

Doctorate Thesis: Not indicated.

Publications: E. CERETTI (1963, 1964, 1967); E. CERETTI & A. POLUZZI (1968 (7)).

Bryozoologists: E. CERETTI (Palaeozoic Bryozoa) and A. POLUZZI.

Research under way: Probable stratigraphical meaning of *Cyclostomata* and *Cheilostomata* in the limestones with Bryozoa from Abruzzi.

CAGLIARI - University Geological and Palaeontological Institute - Museum « D. Lovisato » (Sa Duchessa, 1).

Collections: « Meneghini Coll. » - Ordovician from Fluminimaggiore. Ordovician from Portixeddu and Domusnovas (not published). Jurassic from Pozzo Monte d'Ussi (Nurra) (Bryozoa not determined and not published). Cretaceous from Punta Negra (Nurra) (Bryozoa not determined and not published, localities reported in COMASCHI CARIA (1949)). Eocene from Madonna del Rimedio (Orosei) (Bryozoa not determined, localities reported in COMASCHI CARIA (1949)). Miocene from Funtanazza (reported in DE ANGELIS & NEVIANI (1897), COMASCHI CARIA (1949) and ANNOSCIA (1968)), from Bosa Cagliari, Frasca Cap, Castelsardo, Dolianova, Donigala, Mandas, St. Andrea Frius, Seebra Point (Segariu), Mora Mountains (Torralba).

Doctorate Thesis: Subthesis in Palaeontology by A. PORCU (1965 (9)).

Publications: G. MENEGHINI (1857); C. F. PARONA (1887); E. MARIANI & C. F. PARONA (1887); G. DE ANGELIS D'OSSAT & A. NEVIANI (1897); D. LOVISATO (1901, 1902); G. DEGLI INNOCENTI (1929); I. COMASCHI CARIA (1949, 1959, 1960, 1963); E. ANNOSCIA (1968).

Not all Bryozoa listed in above reported Authors are kept in Museum « D. Lovisato ».

Bryozoologists: Missing.

CATANIA - University Geological Institute (Palazzo delle Scienze) and

FLORENCE - University Geological Institute (Lamarmora str. 4).

Collections, *Publications* and *Bryozoologists* are missing.

MILAN - University Palaeontological Institute (Piazzale Gorini, 5).

Collections: Bryozoa from Upper Devonian (Frasnian) of Chital, Pakistan (Shogram Fm.) and from Upper Permian (Murgabian) of central Elburg, Iran (Ruteh Fm.).

Doctorate Thesis: Not indicated.

Publications: N. FANTINI-SESTINI (1965 (8)).

Bryozoologists: Missing.

MILAN - Civic Museum of Natural Sciences (Corso Venezia).

The Museum had serious damages by bombs during the last World War II. The rich collections are mostly destroyed. It is not possible to establish now how many Bryozoans are still retained, since the inventory is under way.

Some living Bryozoa are exhibited in the windows.

MODENA - University Palaeontological Institute (University str. No. 4).

Collections: *Cheilostomata* and *Cyclostomata* from Pliocene of Castell'Arquato (Piacenza prov.), S. Venanzio, S. Valentino and Fossetta (Modena prov.). 39 slides.

Doctorate Thesis: Not indicated.

Publications: A. MANZONI (1875); I. NAMIAS (1890).

Bryozoologists: Missing.

NAPLES - Zoological Station (Villa Comunale).

Collections: Unknown consistence.

Publications: G. ZIRPOLO (1882, 1920, 1921, 1922, 1923, 1924, 1925, 1928, 1932, 1933); C. SACCHI (1964); C. SACCHI & A. RENZONI (1962); G. C. CARRADA & C. SACCHI (1962, 1964); G. C. CARRADA (1964).

Bryozoologists: G. C. CARRADA.

PADUA - University Geological and Palaeontological Institute (Giotto str., 20).

Collections: « Gottardi Coll. »: Eocene from Montecchio Maggiore (Vicenza prov., Venetia) - 105 slides.

« Fabiani Coll. »: Eocene from Berici Mountains - 41 slides.

« Braga Coll. »: Eocene, Oligocene and Miocene from Berici and Lessini Mountains and Treviso hills (Possagno) - 300 slides.

« Coppi-De Gregorio Coll. »: Pliocene from Modena Apennins - 21 slides.

Doctorate Thesis: M. TOMASI (1968 (10)).

Publications: The reported collections were published respectively by GOTTARDI (1885), FABIANI (1908), BRAGA (1963, 1965, 1968) (6).

The revision of the « Coppi-De Gregorio Coll. » is under way.

Bryozoologists: G. P. BRAGA (Tertiary).

Research under way: Revision of Upper Eocene Bryozoa Collection by Gottardi and Pliocene « De Gregorio Coll. » (Doctorate Thesis).

Statistical study of two Priabonian species: *Conescharellina perfecta* ACCORDI and *Conescharellina veronensis* ACCORDI (Doctorate Thesis).

PALERMO - University Geological and Palaeontological Institute (Corso Calatafimi, No. 260).

Collections: « Cipolla Coll. » from Pliocene of Altavilla (Palermo prov., Sicily).

Doctorate Thesis: Not indicated.

Publications: The collections were published by CIPOLLA (1920, 1921, 1924 and 1926/a).

Bryozoologists: Missing.

PERUGIA - University Zoological Institute (Elce di sotto Str.).

Collections: Not indicated.

Doctorate Thesis: Not indicated.
Publications: A. VIGANÒ (1964, 1965, 1968) (11, 12, 13).
Bryozoologists: A. VIGANÒ (living freshwater Bryozoa).

PISA - University Palaeontological Institute (S. Maria str., No. 53).
Collections: « Neviani Coll. »: Coenozoic Bryozoa from Tuscany.
« De Stefani and Neviani Coll. »: Neogene from Calabria - 100 slides.
« Gioli Coll. »: Neogene from Pianosa Island.
Bryozoa from Neogene of Apulia collected by G. TAVANI (1967-68).
Doctorate Thesis: Not indicated.
Publications: The reported collections were published respectively by NEVIANI (1900/d); DE STEFANI (1884) and NEVIANI (1901/f); GIOLI (1889) and NEVIANI (1902/e).
Bryozoologists: Missing.
Remark: The Museum of the Institute underwent serious damages during the last World War II; the material mostly was destroyed and what is still retained is not well ordered.

SAN DONATO MILANESE (Milan prov.) - AGIP Direzione Mineraria Paleontological Laboratory.
Collections: « Annoscia Coll. »: about 700 slides and 20 thin sections from Uppermost Devonian from Libyan CORI wells; Jurassic from Morocco; Cretaceous from Tunisian and Iranian AGIP wells; Eocene from Libyan CORI wells and Venetia outcrops; Oligocene from Liguria; Miocene from Libyan outcrops and CORI wells, from Tunisian and Nigerian AGIP wells and from Sardinian and Emilian outcrops; Pliocene from Emilian outcrops and from Lucania and Tuscany; Pleistocene from Sicily; Living Bryozoa from S. Remo, Sardinia and Adriatic sea.
Publications: The reported collections were in part published by ANNOSCIA & GRIGNANI (1968) and by ANNOSCIA (1963, 1965, 1966 and 1968) (3) (4) (5).
Research under way: Stratigraphy of Funtanazza (Sardinia): Oligocene-Miocene section.
Bryozoologists: E. ANNOSCIA.

TURIN - University Geological and Palaeontological Institut (Carignano Building, Accademia delle Scienze str., 5).

Collections: About 170 specimens of *Trepostomata, Cyclostomata, Cryptostomata* and *Cheilostomata* from Silurian, Devonian, Carboniferous, Permian, Jurassic, Cretaceous, Cenomanian, Senonian, Maastrichtian, and Tertiary from Europe and USA.

Doctorate Thesis: M. AJAZZI (1958 (1)).

Publications: P. G. CARETTO (1966).

Bryozoologists: No Bryozoologist is employed here. P. G. CARETTO sometimes works here.

VERONA - Civic Museum of Natural History (Lungadige Porta Vittoria, 9).

Collections « Zangheri Coll. »: Upper Pliocene from Capocolle (Forlì prov., Romagna) - 48 slides.

Publications: The « Zangheri Coll. » was studied by NEVIANI (1926) and CIPOLLA (1928) and revised by ANNOSCIA (1966/a).

Bryozoologists: Missing.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
35. Group 5: Biogeography and Biostratigraphy.

ELENA I. ANDROSOVA (*)

BRYOZOA CYCLOSTOMATA AND *CTENOSTOMATA* OF ANTARCTIC AND SUBANTARCTIC

(Preliminary Report)

Riassunto. — 18 specie di *Cyclostomata* e 2 di *Ctenostomata* sono state determinate nelle collezioni della Spedizione Sovietica Antartica negli anni 1956-1958 (vascello « Ob »). I Briozoi sono stati trovati in 35 stazioni, 29 delle quali antartiche e 6 subantartiche (Isole Herd, Kerguelen, Isole Principe Edoardo, Isole Falkland, Patagonia e Cile meridionale).

6 specie sono nuove per l'Antartico, tra cui 3 specie nuove.

Dai dati nuovi e dei precedenti osservatori, 121 specie di *Cyclostomata* e di *Ctenostomata* sono note ora per l'Antartico e il Subantartico. 13 però sono dubbie e non sono state prese in considerazione in questo studio.

Summary. — 18 species of *Cyclostomata* and 2 *Ctenostomata* were determined from the Collections of the Soviet Antarctic Expedition in the years 1956-1958 (Vessel « Ob »).

The Bryozoa were found on 35 stations, 29 of which belonging to Antarctic and 6 to Subantarctic (Herd isles, Kerguelen, Prince Edward isles, Falkland isles, Patagonia and South Chile).

6 species are new for Antarctic (3 are new species).

Using our data and data of previous investigators, 121 species of *Cyclostomata* and *Ctenostomata* are now known for Antarctic and Subantarctic. 13 of them are doubtful and are not taken into consideration in the analysis here given.

18 species of *Cyclostomata* and two of *Ctenostomata* had been determined from the collections of the Soviet Antarctic Expedition in the years 1956-1958 (vessel « Ob »): *Idmidronea ob-*

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tecta Borg; *I. magna*, sp. n.; *I. hula* Borg; *Idmonea atlantica* Forbes; *I. pulcherrima* Kirkpatrick; *Nevianipora milneana* (Orb.); *Entalophora buskii* Borg; *E. conferta* Ortmann; *E. rogickiana*, sp. n.; *Entalophora* sp.; *Fasciculipora ramosa* Orb.; *F. meandrina* Borg.; *Fasciculipora* sp., *Hornera falklandica* Borg; *H. smitti* Borg; *H. lasarevi*, sp. n., *Pseudidmonea fissurata* (Busk.); *P. gracilis* sp. n.; *Alcyonidium mytili* Dalyell; *A. flabelliforme* Kirkpatrick.

The Bryozoa had been found in 35 stations, 29 of which belong to Antarctic and 6 to Subantarctic (Herd isles, Kerguelen, Prince Edward isles, Falkland isles, Patagonia, South Chile).

11 from the 20 determined species had been gathered at the shoal of Antarctic, 7 species are from the Subantarctic region and two had been found both in Antarctic and Subantarctic.

Six species are new for Antarctic, three of them are described as species novae: they are *Entalophora rogickiana* (in honour of the late Dr. ROGICK), *Hornera lasarevi* and *Idmidronea magna*. We describe also *Fasciculipora* sp. and *Entalophora* sp.; there was no opportunity to determine them because of poor data. The last of the six is *Alcyonidium mytili*, which was found in Subantarctic by other investigators and is widely distributed in the north hemisphere.

The other seven species, which we determined from Antarctic, had been found in this region before. They are *Idmidronea obtecta, I. hula, Hornera smitti, Alcyonidium flabelliforme, Fasciculipora ramosa, Entalophora buskii, Idmonea atlantica.*

We give three species new for Subantarctic. One of them, *Pseudidmonea gracilis*, we describe as species nova. Two of them, *Idmonea pulcherrima* and *Entalophora conferta*, were already known from other parts of the world. 4 other species, *Nevianipora falklandica, Pseudidmonea fissurata, Fasciculipora meandrina* and *Hornera falklandica* were shown for this region by previous Authors.

Using our data and data of previous investigators, 121 species of *Cyclostomata* and *Ctenostomata* are now known for Antarctic and Subantarctic, 13 of which being doubtful. The last are not taken into consideration in the analysis we give.

There are altogether 59 species known from Antarctic. 22 of them (37,3%) are found in high latitudes only and can be considered as endemic of the region. 20 species (33,9%) are known both from Antarctic and Subantarctic and only 17 species (28,8%) are distributed in other parts of the World too.

In Subantarctic 49 species are known, which are not found in Antarctic, 24 (48,9%) of which are distributed in Subantarctic only, 25 had been found in other parts of the Ocean.

From the South America region 52 species are known; 13 of which, that is 25%, are limited to it and 39 (75%) are found outside the region also. From the region of Tristan da Cunha there are known 11 species, two of them being endemic. At the isles of Prince Edward 11 species are found, but all of them are known from other parts of the Ocean. At the shoal of the Kerguelen and Herd isles 25 species are described, 4 of them (16%) being endemic and others are characterized by broader destribution.

66 species of Bryozoa from both Antarctic and Subantarctic, that is 61,1% — more then a half known for these regions — are endemic.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
36. Group 5: Biogeography and Biostratigraphy.

FRANK J. S. MATURO, JR. (*)

THE DISTRIBUTIONAL PATTERN OF THE *BRYOZOA* OF THE EAST COAST OF THE UNITED STATES EXCLUSIVE OF NEW ENGLAND

Riassunto. — 241 specie di *Briozoi* e 5 specie di *Entoprocta* sono stati raccolti durante un'estensiva campionatura nella piattaforma continentale atlantica tra l'Hudson Canyon e Key West.

137 specie (56% del totale) rappresentano un ampliamento della zona di diffusione e circa 40 specie si pensa siano nuove.

Il modo di diffusione dei Briozoi mette chiaramente in luce l'importanza di Capo Hatteras come il maggiore punto di riferimento zoogeografico e la dipendenza diretta o indiretta di questa fauna dalla Corrente del Golfo. Soltanto il 12% delle specie (29) sono diffuse estesamente a Nord e a Sud del Capo. Le specie diffuse a N di Capo Hatteras comprendono l'8% del totale (19 sp.), povera cosa nella Provincia Virginiana che invece vede ben rappresentati i gruppi bentonici. Almeno il 67% delle specie (165) è diffuso a S di Capo Hatteras. Analisi preliminari dei dati della profondità e della temperatura di queste specie non sembrano incoraggiare l'opinione circa la divisione di quest'area in Provincia Caroliniana (piattaforma interna) e Provincia tropicale (piattaforma esterna).

Le tolleranze alla salinità e il substratum sembrano essere i fattori critici che controllano la diffusione. Relativamente poche sono le specie che si trovano negli ambienti di estuario o costieri soggetti ad abbassamenti della salinità.

La maggioranza è stata trovata essenzialmente nell'intera piattaforma continentale con convenienti disponibilità del substratum come principale fattore limitante.

La maggior parte delle specie sono limitate a plaghe isolate di depositi conchigliari, di brecciame e di affioramenti di vecchie scogliere. La maggior parte della piattaforma è un largo piano sabbioso dove si trovano praticamente solo 4 specie: *Cupuladria biporosa* (71 stazioni), *C. canariensis*

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(31 stazioni), *C. doma* (271 staz.) e *Discoporella umbellata depressa* (212 staz.).

L'attuale limite settentrionale di parte di questa fauna meridionale si estende fino a poche miglia a N di Capo Hatteras, ma soltanto al largo della costa nelle acque più profonde ai margini della Corrente del Golfo e della piattaforma.

18 specie (7%) sono diffuse in direzione Nord verso la Georgia e 15 specie (6%) non sono state raccolte più a Nord della Florida. Molte di queste sono rappresentate da singole raccolte indicanti che sono probabilmente molto rare e che la loro diffusione rimane imprecisata.

Questo studio è stato sostenuto dal NSF Grant G-24309 e dalla National Academy of Sciences - National Research Council Senior Research associate con la Smithsonian Institution.

Summary. — About 241 species of *Bryozoa* and 5 species of *Entoprocta* were collected. The major distributional patterns are clearly related to the barrier imposed by Cape Hatteras between the Virginian Coastal Current and the Florida Current. Approximately 12% of the species range extensively north and south of Cape Hatteras; 8% reach their southern limit and at least 67% reach their northern limit here. South of the Cape most of the shelf is a broad sandy plain where 4 lunulitiform species are the dominant bryozoans, the other species being limited to scattered patches of shell litter, ballast deposits, and ancient reef outcrops.

Résumé. — Environ 241 espèces de *Bryozoa* et 5 espèces d'*Entoprocta* furent ramassées. Les dessins principaux de la distribution sont clairement reliés à la barrière imposée par le cap Hatteras entre le courant de la côte de la Virginie et le courant floridien. Environ 12% des espèces se trouvent d'une façon extensive au nord et au sud du cap Hatteras; 8% y atteignent leur limite méridionale et au moins 67% y atteignent leur limite septentrionale ici. Au sud de ce cap la plus grande partie du banc continental est une large plaine de sable où 4 espèces lunulitiformes sont les bryozoaires dominants, les autres espèces étant limitées à des tâches éparpillées de débris d'écailles, de sédiments de lest, et d'anciens affleurements de récifs.

Introduction.

Studies on the bryozoan fauna of the east coast of the United States have, for the most part, been limited to collections in the shallow water areas immediately adjacent to the coast, including sounds, bays, and estuaries. South of Woods Hole, Massachusetts, these investigations have been quite limited. They include the reports by HUTCHINS (1945) on Long Island Sound; LEIDY (1855) on Rhode Island and New Jersey; OSBURN (1932, 1944) on Chesapeake Bay; VERRILL (1878), MCDOUGALL (1943), and PEARSE and WILLIAMS (1951) on North Carolina; MATURO (1957, 1959, 1966) on North Carolina, and Florida; DE POURTALES (1867), SMITT (1872, 1873), and OSBURN (1914) on the Florida Keys. The greater part of the continental shelf in this area has remained virtually unstudied for bryozoans except for a tantalizing glimpse of a tropical offshore fauna in the Beaufort, North Carolina, region given by OSBURN in scattered accounts (notably 1940) and by MATURO (1957, 1966).

In the summer of 1956, I received from Miss Maureen DOWNEY, now of the Smithsonian Institution, and Dr. I. E. GRAY, Duke Marine Laboratory, a piece of reef rock obtained from a Captain Fulcher of Morehead City, North Carolina. The rock had been collected from the « fishing banks », a series of extensive reefs about 21 miles offshore in depths of 26 to 30 m (13-15 fathoms) southwest of Cape Lookout, North Carolina. The main bank, as reported by RADCLIFFE (1914) from a survey conducted by the U. S. Fisheries Steamer *Fish Hawk,* lies in Lat. 34° 19′ N., Long. 76° 59′ W. and is the largest reef known on the coast. From the « Fulcher » rock, which measures about 37 cm on a side, were obtained an astonishing 77 species, only 8 of which were among the 66 species previously reported for the Carolina coast. These species were all common inhabitants of the Gulf of Mexico and the Caribbean Sea. This finding led to the hypothesis that the bryozoan fauna of the Gulf of Mexico and Caribbean Sea reaches its northern limit off the North Carolina coast, perhaps at Cape Hatteras. An investigation was started to test the hypothesis.

Sources of Materials.

Specimens for study were obtained from a number of sources:

Commercial shrimp boats were chartered for dredging and trawling operations on the continental shelf and slope off Cape Lookout and Cape Hatteras, and on coastal reefs off Fernandina Beach, Florida.

Several dredging trips off Sapelo Island, Georgia, were made using the facilities of the University of Georgia Marine Institute.

A SCUBA diving team was employed to collect reef fragments and parts of rocky outcrops south of Cape Lookout, Beaufort, New River Inlet, North Carolina, and off Fernandina Beach, Florida. This team provided the most successful means of collecting on rough bottom. Divers secured lines around large rocks which were then hauled aboard by winches.

Extensive collections of dredged material from shelf transects north and south of Cape Hatteras and Cape Lookout were obtained through the generosity of Dr. I. E. GRAY and Dr. Maximo CERAME-VIVAS. Some collecting trips were jointly sponsored with these colleagues.

About 500 lots (up to 25 or more species per lot) of bryozoan specimens from several hundred stations off Georgia and northern Florida were made available for study by Mr. Milton GRAY of the Sapelo Island Research Foundation. The station sites ranged from the coastal estuaries and marshes to shelf localities about 100 miles out.

Approximately 700 lots representing about 302 stations between the Hudson Canyon and Key West were received from the Bureau of Commercial Fisheries. This material was collected by the U. S. Geological Survey - Woods Hole Oceanographic Institution program of study of the Atlantic continental margin of the United States. The research vessel *Gosnold* occupied stations on a grid pattern of 10 nautical miles (18 km) throughout the length and width of the continental shelf and slope in this area. Biological samples were taken principally with a large (250 kg) Campbell grab which recovered about 0.2 cubic meter of sediments from an area of 0.6 square meter (EMORY and SCHLEE, 1963).

Resumé of the Physical Environment.

The continental shelf between Cape Cod, Massachusetts, and Key West, Florida, has been divided by zoogeographers into three marine provinces, namely, the Virginian, Carolinian, and Tropical (JOHNSON, 1934; HEDGPETH, 1953; CERAME-VIVAS and GRAY, 1966). As revised by the critical study of CERAME-VIVAS and GRAY, the Virginian Province extends from Cape Cod to Cape

Hatteras; the Carolinian Province covers the inner shelf from Cape Hatteras to Cape Kennedy, Florida, and the northern Gulf of Mexico; the Tropical Province is the outer shelf along the southeastern coast, extending as far north as the latitude of Oregon Inlet (north of Cape Hatteras). These provinces have different marine climates which are established by the circulation patterns of the coastal water masses and major geographical features such as prominent capes. Cape Hatteras is the focal point for these provinces, serving as a boundary between cooler northern waters and warmer southern waters. The boundary here results from several interdependent factors which have been succinctly summarized by CERAME-VIVAS and GRAY (p. 261) as follows:

«... 1) the Gulf Stream is closer to Cape Hatteras than to any point north of Cape Kennedy, Florida; the warm Florida Current follows the edge of the continental shelf northward from the Straits of Florida to well north of Diamond Shoals [Cape Hatteras] before swinging away from the coast and away from the shelf; 2) a cool Virginian Coastal Current flows southward from Cape Cod, routinely turns seaward off Cape Hatteras, eventually to be absorbed (FORD and MILLER, 1952); 3) the Carolinian Coastal Current, probably originating in part from run-off from the sounds and in part from a back eddy of the Florida Current, flows southwesterly from Cape Hatteras (GRAY and CERAME-VIVAS, 1963); 4) water masses south of Cape Hatteras lack persistent continuity with the water masses north of the Cape (BUMPUS, 1955); 5) the winter surface isotherms of this region are closely packed, reflecting a formidable temperature barrier during the cooler months of the year (PARR, 1933); 6) under certain meteorological conditions this barrier between water masses may be broken and the cooler waters of the Virginian Coastal Current then flow into Raleigh Bay [area between Cape Hatteras and Cape Lookout], augmenting the Carolinian Coastal Current (BUMPUS and PIERCE, 1955; GRAY and CERAME-VIVAS, 1963) ».

Distinctive temperature regimes are thus established in the three provinces, the differences being particularly accentuated in winter. In the vicinity of Cape Hatteras bottom temperatures in winter in the Virginian Province have been reported to reach as low as 4-4.5°C (Cerame-Vivas and Gray, 1966; Harrison, Norcross, Pore, and Stanley, 1967), while at the same latitude in the Tropical Province, bottom temperatures were 19.5°C (Cerame-Vivas and Gray). Winter surface temperature averages for the Carolinian and Tropical Provinces are 11-17°C and 17-23°C, respectively (based on data by Anderson, Moore, and Gordy, 1961). In summer the surface temperature differences between the Carolinian and Tropical Provinces disappear so that the water temperature over the whole southeastern shelf averages 26-29°C. Cerame-Vivas and Gray report that bottom temperatures are only a few degrees lower, even at 200 meters. Thermal stratification occurs in summer in the Virginian Province; bottom temperatures here are usually much colder than the surface temperatures, especially as depth increases (Harrison *et al.*, 1967). A new study by Walford and Wicklund (1968) compiles monthly surface and bottom temperature averages from many sources; the persistence of the thermal barrier at Cape Hatteras is strikingly illustrated.

Results.

Text figure 1 shows the stations from which bryozoans were collected during the *Gosnold* cruises. Blank spots in the orderly sampling pattern were also sampled but no bryozoans were recovered. The number of species identified from each station is also indicated. The other collecting sites were not plotted in the figure because they were sampled by non-standardized methods (trawl and dredge) and because they were too concentrated for the illustration scale employed. These stations cluster principally on either side of Cape Hatteras from Oregon Inlet to Cape Lookout, and in a broad band across the shelf off the coast of Georgia.

Fig. 1. — Map of the study area showing the locations of the *Gosnold* stations from which bryozoans and entoprocts were obtained. The number in each circle refers to the number of species found at that station. The 200 m and 2000 m depth contours are indicated; the edge of the continental shelf corresponds roughly with the 200 m line.

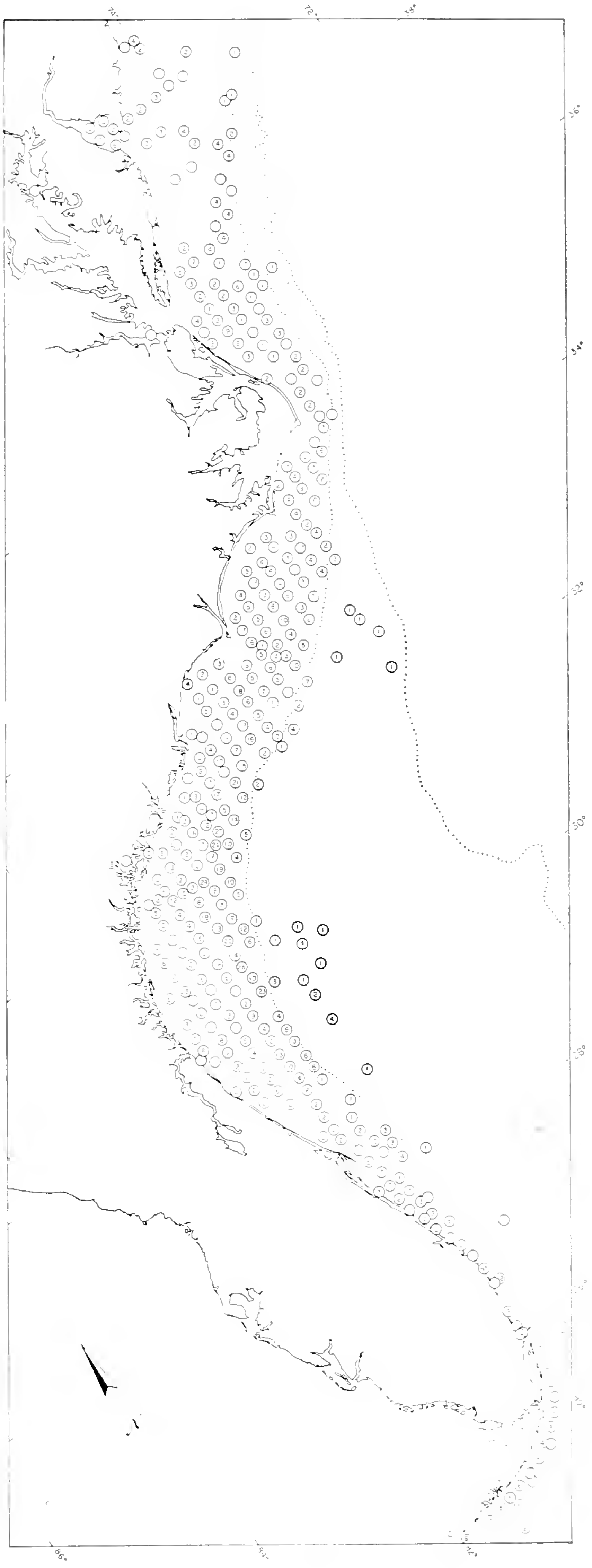

Fig. 1.

Two hundred forty-six species have been recognized in the material collected (Table 1). This number will change to some extent as final studies are completed; some species will doubtlessly be combined and others divided but the figure is reasonably final. For purposes of comparison, the number of species of bryozoans and entoprocts known from other Western Atlantic localities is:

Eastern Canada to Woods Hole:	about 120
Present Study Area:	246
Gulf of Mexico:	216
Brazil:	230

In spite of the large number of species recovered in the present study, a fair amount of bias in the sampling methods has selected against two groups of bryozoans: the chitinous ctenostomes and the oral-like species of the cheilostome family *Reteporidae*. The ctenostomes, being non-calcareous and frequently inconspicuous, all but disappear when removed with their substrate from the water which supports them. Under these circumstances even a well-trained eye will overlook them. The reteporids look so much like hydrozoan corals that most sorters will assign them as coelenterates, hence they only fortuitously fall into the hands of a bryozoologist. Another source of bias derives from the fact that relatively few of the station sites were in estuaries and bays, thereby missing a number of species which are typical of these environments. Finally, since it is impossible to keep everything in a sample haul, only « representative » aliquots of the sample could be retained for examination, plus any obvious specimens which were picked out at the time the haul was made. Hence uncommon species might have been missed.

Approximately 40 species have so far defied identification with known species and are probably new. Five of these have now been described (Maturo, 1966; Maturo and Schopf, 1968).

Of the 246 species found, 137 (56%) represent new range extensions (Table 1). These range extensions can be categorized as follows:

A. First records for the western North Atlantic Ocean:	21 species
B. First records for north of the Straits of Florida for species known from the Gulf of Mexico and the Caribbean Sea:	85 species
C. First records north of Cape Hatteras for species known from regions south:	38 species
D. First records for south of New England for species known from northern regions:	13 species
E. First records for south of Cape Hatteras for species known from northern regions:	2 species

Lest categories C and E be misleading some additional comment should be made. In the first instance, all of these « southern » species were recovered from the deeper water shelf areas well offshore which are still under the influence of the Gulf Stream. In the second case, the two « northern » species found south of Cape Hatteras, *Alcyonidium parasiticum* (Fleming) and *Cribrilina punctata* Hassall, should no longer be considered northern but rather as widespread eurythermal species.

Discussion.

The zoogeographical implications of the data are shown in the major groupings of Table 1 and are summarized in text figure 2.

Twenty-nine species (12%) range extensively north and south of Cape Hatteras. This agrees closely with the total estimated by Osburn (1912) to be widely distributed « cosmopolitan » species and in fact includes essentially the same species. Cerame-Vivas and Gray (1966) found 14% of the benthic macroinvertebrates of the Carolina coast to be widespread on both sides of Cape Hatteras.

Only 8% of the species (19) were found restricted to the Virginian Province in the Hatteras area. This finding corresponds well with a similar paucity of characteristic species in this province reported by CERAME-VIVAS and GRAY. They found a low 11.4% of the species in this category.

At least 67% of the species (165) range from the vicinity of Cape Hatteras southward. The total should be compared with the total of 27 species known to have this distribution prior to this report. The actual northern limit of part of this southern fauna extends a few miles north of the Cape, but only offshore in the deeper waters at the edge of the Gulf Stream and the shelf.

As pointed out earlier CERAME-VIVAS and GRAY divided the shelf in this region into a Carolinian and a Tropical Province. The boundary between these provinces was estimated by analysis of bottom temperatures and the affinities of the faunal assemblages from each collecting station. Likewise, each station was assigned to a particular province. The bryozoan material from sixteen of these stations both north and south of Cape Hatteras was examined by me and then each station was independently assigned to a province. Five were attributed to the Virginian Province and 11 to the Tropical Province. The designations agreed perfectly with assignments of these stations by CERAME-VIVAS and GRAY (personal communication). Preliminary analysis of the distribution of the species from the « Tropical Province » stations does not appear to show any of them limited to the outer shelf. Instead they seem to be widespread over the shelf wherever suitable substrates can be found. Since these species are known to occur in the Gulf of Mexico, Straits of Florida, and the Caribbean Sea, I am unable to recognize a Carolinian Province at the present time. Is is unfortunate that I could not examine material from stations whose other fauna led CERAME-VIVAS and GRAY to assign them to the Carolinian Province.

Nevertheless, another striking agreement does exist between the two studies. If one combines the percent of species in the present study which range from Cape Hatteras south with the percent of the remaining two categories (see below) adjusted for shelf species only, the result is that 76% of the total number of species most probably reach their northern limit at Cape Hatteras. The adjusted figure from CERAME-VIVAS and GRAY is 74.4% after combining the percent of species limited to the Tropical

Province (34.6%), the percent of species limited to the Carolinian Province (23.7%), and the percent common between them (16.1%).

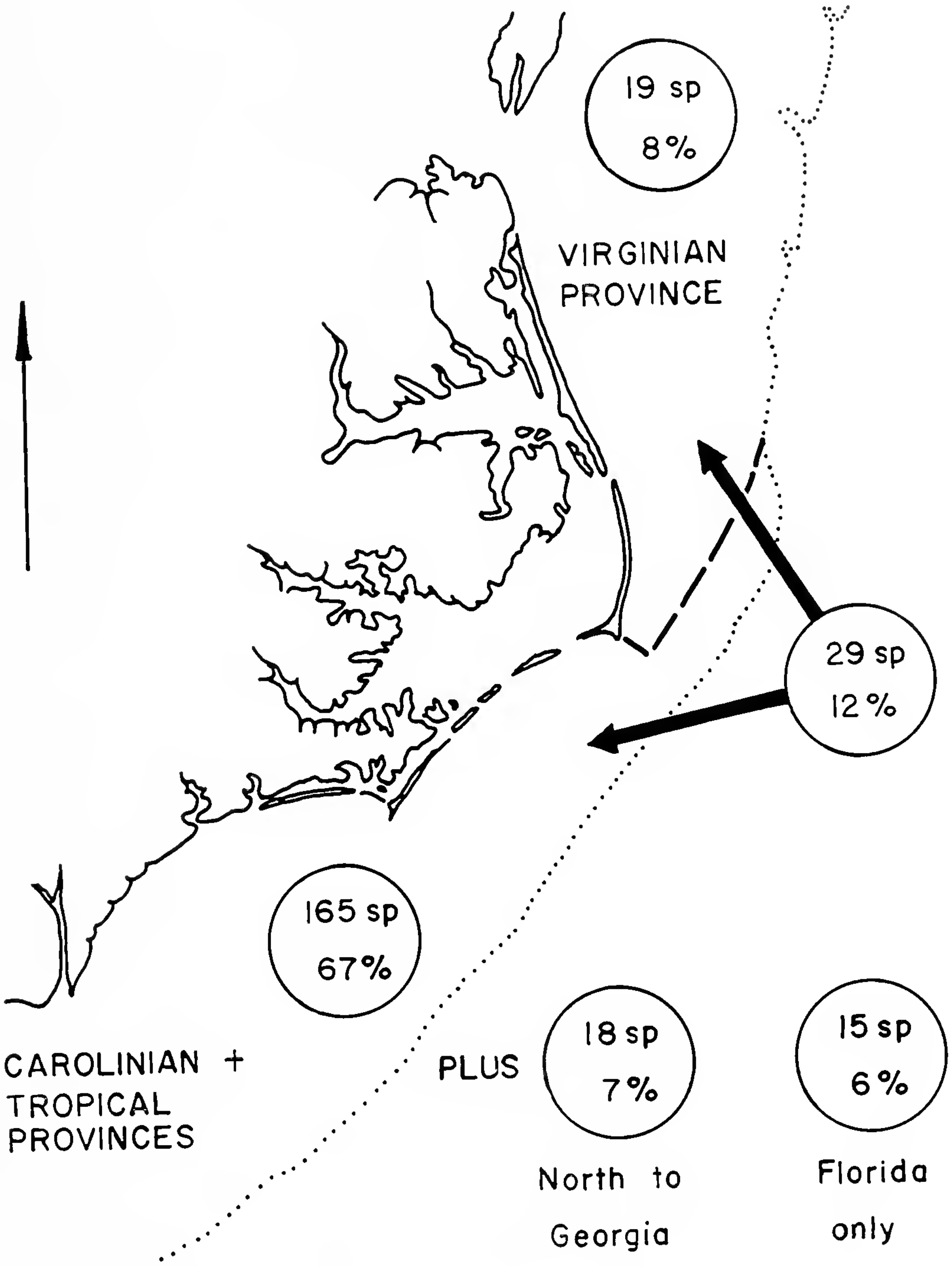

Fig. 2. — Distribution of bryozoan and entoproct species in the marine benthic provinces in the Cape Hatteras region. The distribution of species from other parts of the shelf is also summarized. Contour is 200 m.

Eighteen species (7%) were found no farther north than Georgia. Additional collecting would probably extend the records of nine species to the vicinity of Cape Hatteras. The remaining nine are not shelf species but were collected from the Blake Plateau.

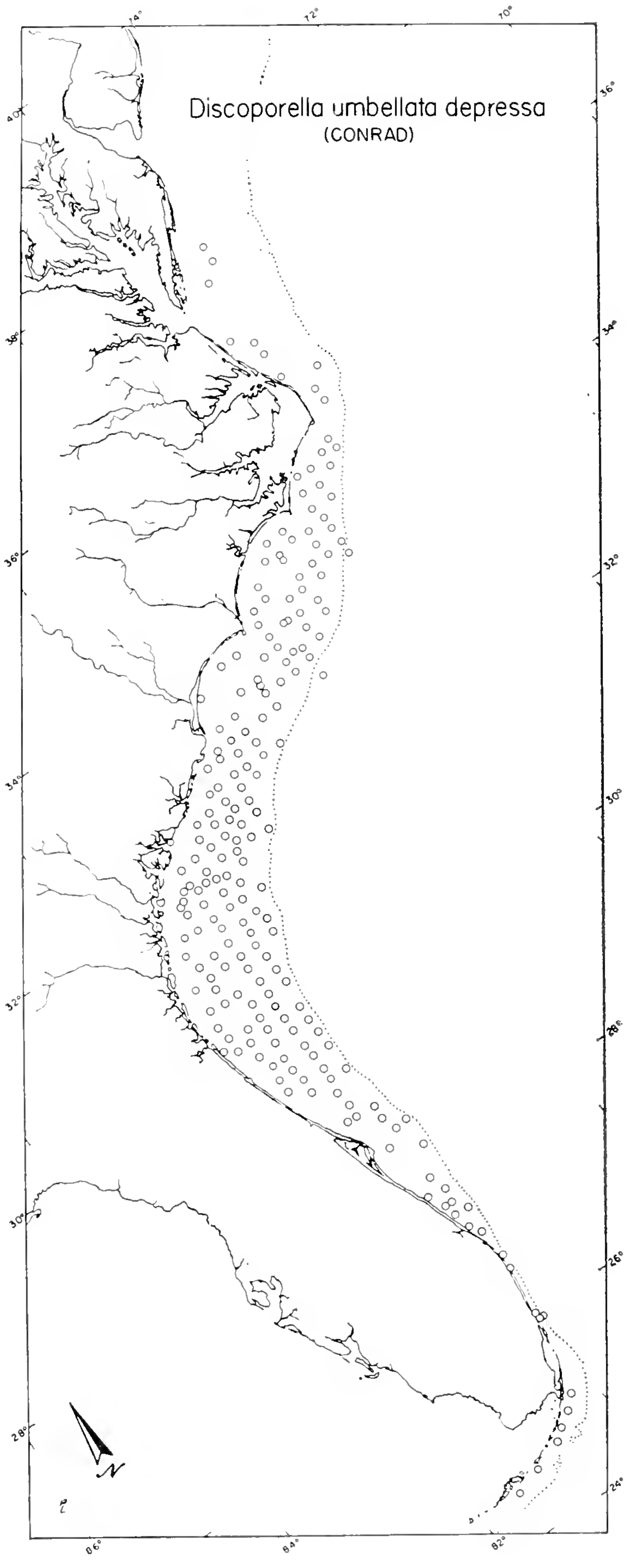

Fig. 3. — Distribution of *Gosnold* stations where *Discoporella umbellata depressa* (Conrad) was found. The 200 m contour is indicated.

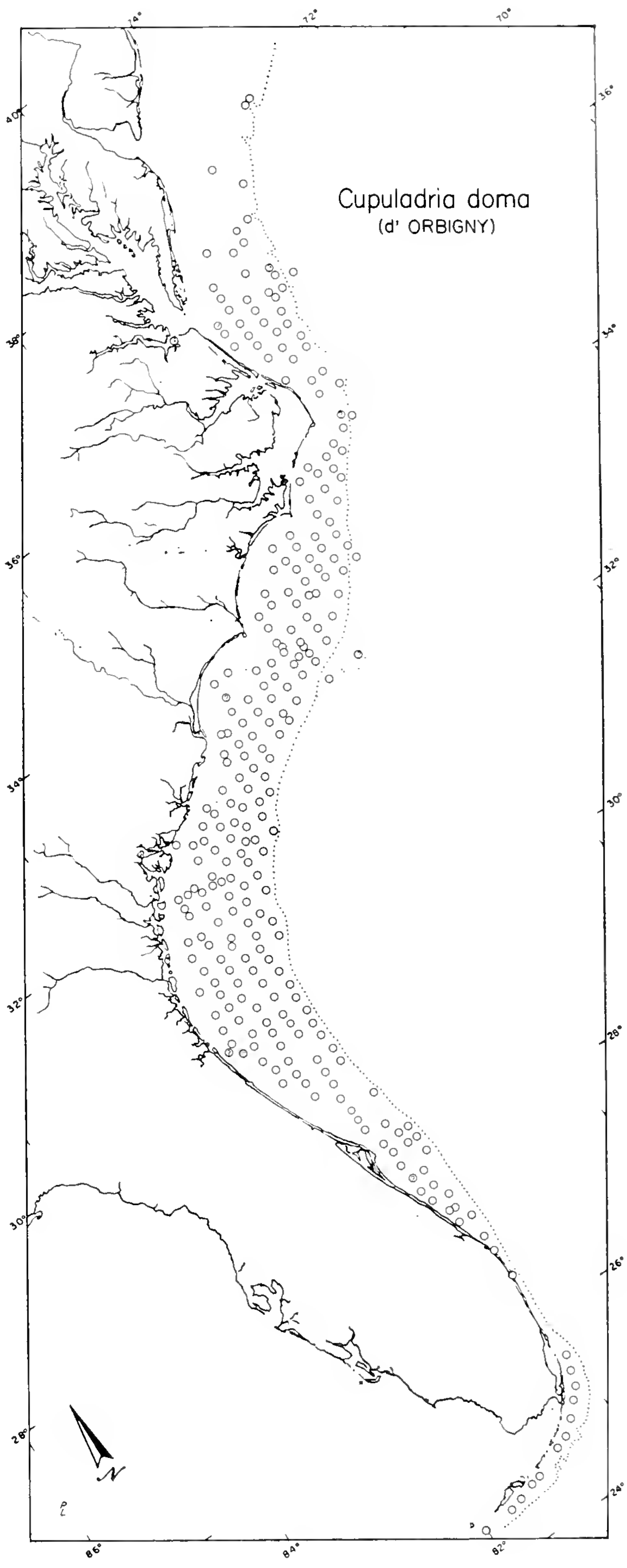

Fig. 4. — Distribution of *Gosnold* stations where *Cupuladria doma* (d'Orbigny) was found. The 200 m contour is indicated.

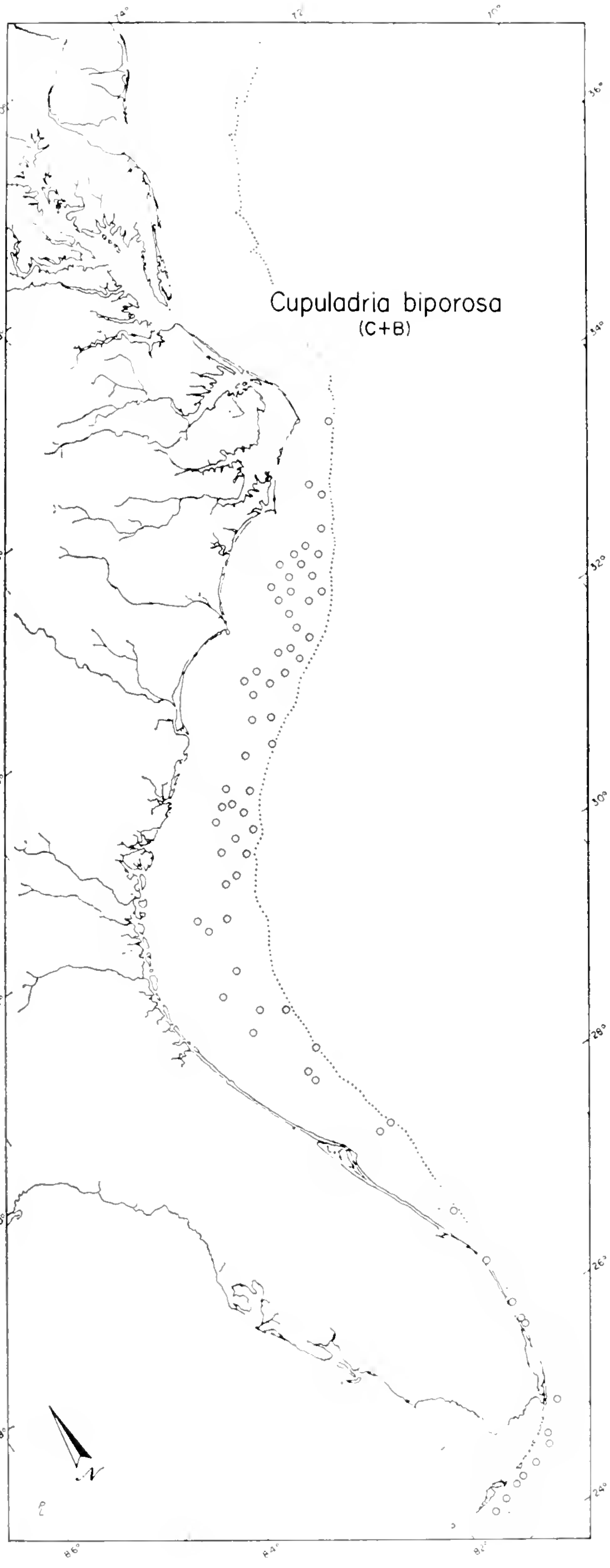

Fig. 5. — Distribution of *Gosnold* stations where *Cupuladria biporosa* Canu & Bassler was found. The 200 m contour is indicated.

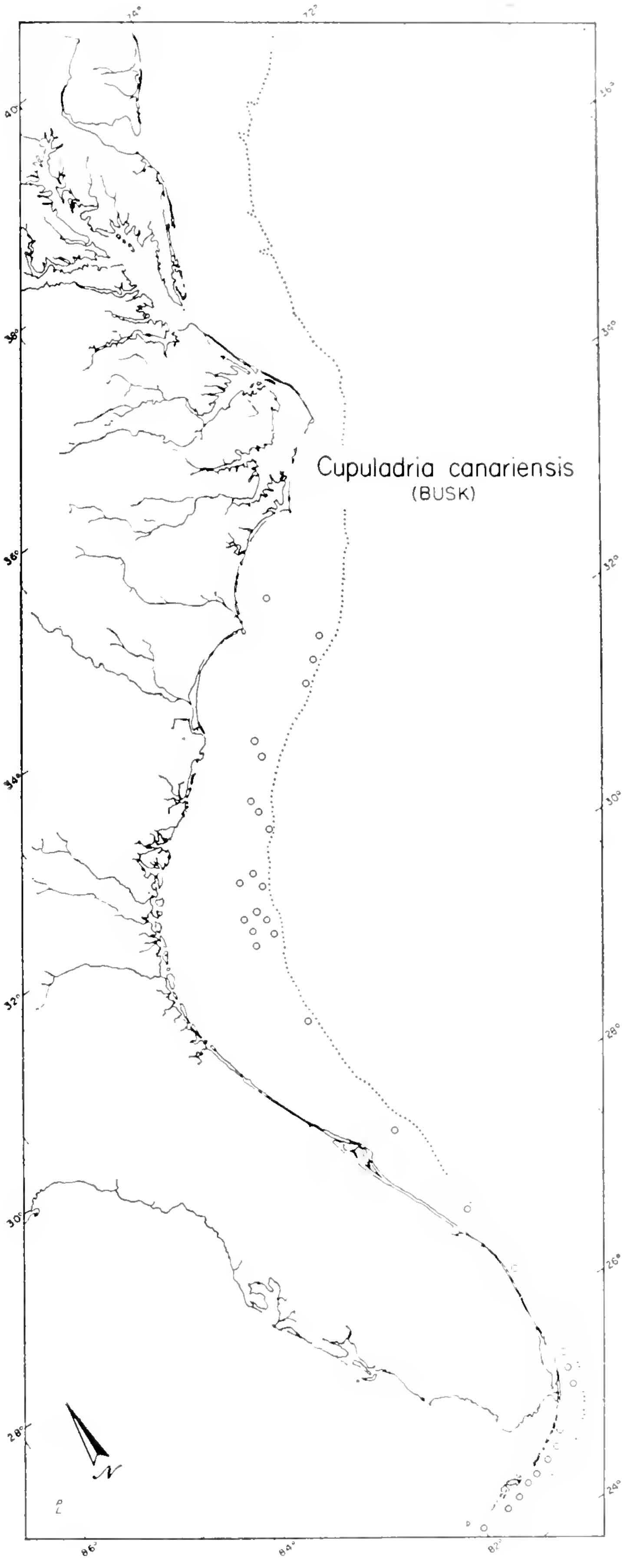

Fig. 6. — Distribution of *Gosnold* stations where *Cupuladria canariensis* (Busk) was found. The 200 m contour is indicated.

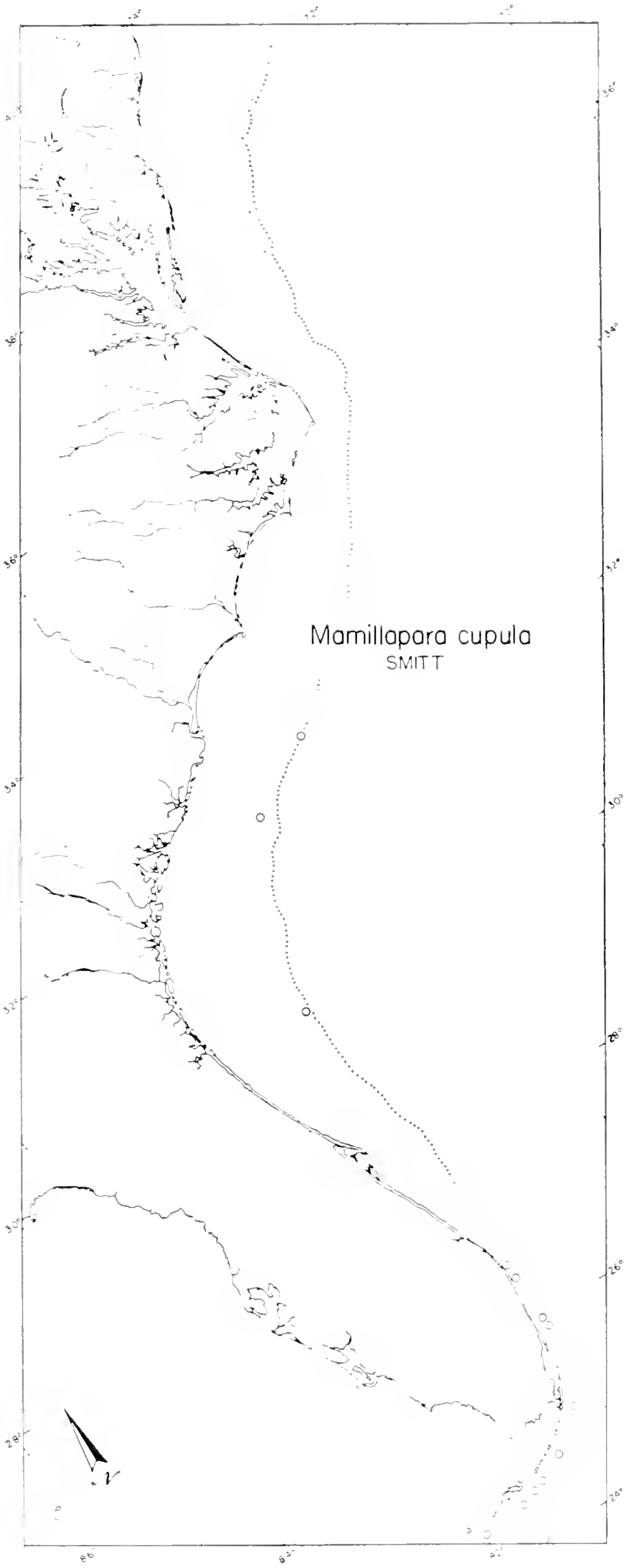

Fig. 7. — Distribution of *Gosnold* stations where *Mamillopora cupula* Smitt was found. The 200 m contour is indicated.

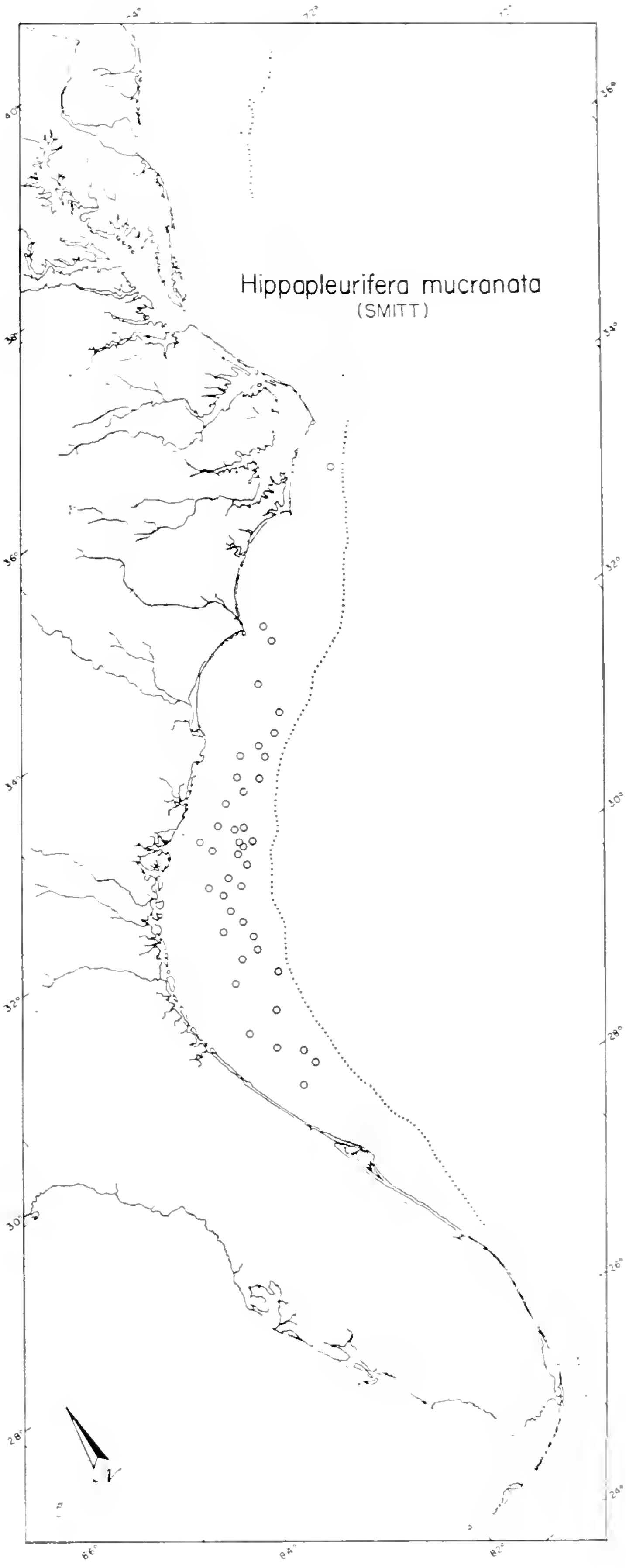

Fig. 8. — Distribution of *Gosnold* stations where *Hippopleurifera mucronata* (Smitt) was found. The 200 m contour is indicated.

Fifteen species (6%) were collected only off Florida. Many of these are represented by single collections, indicating that the species are probably very rare. Range limits are obviously difficult to determine under these circumstances.

The study clearly demonstrates the effectiveness of Cape Hatteras as a barrier to the dispersal of bryozoans and the dependence of a major portion of this fauna directly or indirectly on the Gulf Stream. The results, however, do not resolve the question of whether or not some species common to both the Beaufort area and the Gulf of Mexico have a disjunct distribution, i. e., are absent from the stenohaline (high salinity) area of peninsular Florida. Thorough investigations of the inlets and estuaries of that area are lacking but are being planned. One of the most often cited examples of disjunct distribution, *Hippoporina* (= *Hippodiplosia*) *americana* (Verrill), in fact does not occur south of Cape Hatteras, and the southern citations of what was thought to be this species confuse at least two species (MATURO and SCHOPF, 1968).

Salinity tolerances and substrate seem to be the critical factors affecting distribution. Relatively few species occur in estuarine or nearshore environments subject to lowered salinity. These are the 29 species with widespread distribution both north and south of Cape Hatteras. As noted from text figure 1, bryozoans were found at practically all *Gosnold* stations south of Cape Hatteras. The great variety of species found on the shelf in this area is by no means evenly distributed; the presence or absence of species clearly reflects the type of bottom (substrate) being sampled. Areas of ancient reef outcrops, ballast deposits, or shell litter are inhabited by a remarkable number of species, for example, the 77 species on the « Fulcher » rock or 28 species on a 10 cm pelecypod valve. However, most of the shelf here is a broad, sandy plain where virtually only four species occur: *Discoporella umbellata depressa* (Conrad) at 212 stations (fig. 3), *Cupuladria doma* (d'Orbigny) at 271 stations (fig. 4), *Cupuladria biporosa* Canu and Bassler at 71 stations (fig. 5), and *Cupuladria canariensis* (Busk) at 31 stations (fig. 6). These well-known lunulitiform species frequently occur in great numbers and are characteristic of stable sandy bottoms in various parts of the Atlan-

TABLE I.

Preliminary list of species collected. Species are arranged alphabetically by order groups under the geographical ranges. New range records are indicated by an asterisk (*) and the nearest previous report is given. The scientific names assigned are in some cases tentative working names subject to revision as current systematic studies proceed.

Species	Nearest Previous Report
Species ranging extensively north and south of Cape Hatteras:	
Aetea anguina (Linnaeus)	
*_Bugula fulva_ Ryland	Britain
*_Bugula stolonifera_ Ryland	Britain
Bugula turrita Desor	
*_Chorizopora brongniarti_ (Audouin)	Gulf of Mexico
Cleidochasma contractum (Waters)	
*_Conopeum reticulum_ (Linnaeus)	Beaufort, N. C.
*_Cribrilina punctata_ Hassall	Massachusetts
Electra hastingsae Marcus	
Hippoporidra sp.	
*_Hippoporina porosa_ (Verrill)	Massachusetts
Hippoporina verrilli Maturo & Schopf	
Hippoporina sp. « A »	
Membranipora tenuis Desor	
Microporella ciliata (Pallas)	
Parasmittina nitida (Verrill)	
Schizoporella cornuta Gabb & Horn	
Schizoporella « unicornis » auctt.	
Tessaradoma gracile (Sars)	
Turbicellepora dichotoma (Hincks)	
Aeverrillia armata (Verrill)	
Aeverrillia setigera (Hincks)	
*_Alcyonidium parasiticum_ (Fleming)	Massachusetts
Alcyonidium polyoum (Hassall)	
Amathia vidovici (Heller)	
Anguinella palmata van Beneden	
Bowerbankia gracilis Leidy	
Barentsia timida Verrill	
Barentsia laxa Kirkpatrick	
Pedicellina cernua (Pallas)	
Species ranging from Cape Hatteras north:	
*_Amphiblestrum flemingi_ (Busk)	Massachusetts
*_Amphiblestrum quadrata_ (Hincks)	Bay of Fundy
*_Amphiblestrum ?septentrionalis_ (Kluge)	Gulf of St. Lawrence
*_Callopora craticula_ (Alder)	Massachusetts
*_Callopora dumerilli_ (Audouin)	Maine
Callopora sp.	
*_Cellaria fistulosa_ auctt.	Massachusetts
Celleporella hyalina (Linnaeus)[1]	
Cryptosula pallasiana (Moll)[1]	
Electra hastingsae Marcus[1]	
*_Electra pilosa_ (Linnaeus)	Chesapeake Bay
*_Haplota clavata_ (Hincks)	Massachusetts
Hippoporina americana (Verrill)	

Species	Nearest Previous Report
**Scruparia ambigua* (d'Orbigny)	Massachusetts
**Tegella unicornis* (Fleming)	Massachusetts
Alcyonidium verrilli Osburn	
**Arachnidium fibrosum* Hincks	Britain
Triticella elongata (Osburn)[1]	
Crisia eburnea (Linnaeus)	

Species ranging from Cape Hatteras south:

Species	Nearest Previous Report
**Aetea ligulata* (Busk)[2]	Puerto Rico
**Aetea sica* (Couch)	Tortugas
**Aetea ?truncata* (Landsborough)[2]	Tortugas
Aimulosia sp. « B »	
**Alderina smitti* Osburn	Straits of Florida
Allantopora sp.	
**Antropora tincta* (Hastings)	Panama (Pacific coast)
**Aplousina gigantea* Canu & Bassler[2]	Beaufort, N. C.
**Arthropoma cecili* (Audouin)	Gulf of Mexico
**Arthropoma circinata* (MacGillivray)	Tristan de Cunha
**Beania hirtissima* (Heller)	Gulf of Mexico; Bermuda
Beania intermedia (Hincks)	
**Bellulopora bellula* (Osburn)	Gulf of Mexico
**Bracebridgia subsulcata* (Smitt)	Straits of Florida
Bugula marcusi Maturo	
**Bugula microoecia* Osburn	Tortugas
Bugula neritina (Linnaeus)	
**Caberea boryi* (Audouin)	Gulf of Mexico
?*Calyptotheca* sp. « A »	
**Caulibugula dendrograpta* (Waters)	Tortugas; Bermuda
Caulibugula pearsei Maturo	
*« *Cellepora* » *coronata* Smitt	Straits of Florida
**Celleporaria albirostris* (Smitt)	Straits of Florida
**Celleporaria ?aperta* (Hincks)	Indian Ocean
Celleporaria sp. « B »	
Celleporaria magnifica (Osburn)	
Celleporina hassalli (Johnston)	
Chaperia sp.	
**Cigclisula serrulata* (Smitt)	Gulf of Mexico
**Cigclisula turrita* (Smitt)	Straits of Florida
**Cleidochasma porcellanum* (Busk)[2]	Straits of Florida
*« *Coleopora* » *tubulosa* (Canu & Bassler)	Straits of Florida
**Copidozoum tenuirostre* (Hincks)	Straits of Florida
**Crassimarginatella leucocypha* Marcus[2]	Gulf of Mexico
**Crassimarginatella pyriformis* (Canu & Bassler)	Panama (Pacific coast)
**Crassimarginatella tuberosa* (Canu & Bassler)[2]	Straits of Florida
**Crepidacantha poissoni teres* Hincks[2]	Gulf of Mexico; Bermuda
**Crepidacantha setigera* (Smitt)[2]	Straits of Florida
**Cribrilaria radiata* (Moll)[2]	Beaufort, N. C.
**Cribrilina floridana* Smitt	Straits of Florida
**Cupuladria biporosa* Canu & Bassler	Gulf of Mexico
**Cupuladria canariensis* (Busk)	Florida
**Cupuladria doma* (d'Orbigny)[2]	Beaufort, N. C.
Cupuladria ?oweni (Gray)	
**Cycloperiella rubra* Canu & Bassler[2]	Caribbean Sea
**Discoporella umbellata depressa* (Conrad)[2]	Beaufort, N. C.
**Drepanophora tuberculata* (Osburn)	Tortugas
**Escharina pesanseris* (Smitt)[2]	Miami, Florida

Species	Nearest Previous Report
*_Escharina vulgaris_ (Moll)[2]	Gulf of Mexico
*_Exechonella antillea_ (Osburn)	Miami, Florida
*_Exochella longirostris_ Jullien	Gulf of Mexico
*_Fenestrulina malusi_ (Audouin)[2]	Gulf of Mexico; Bermuda
*_Floridina antiqua_ (Smitt)[2]	Miami, Florida
*_Floridina parvicella_ Canu & Bassler	Gulf of Mexico
*_Gemelliporella glabra_ (Smitt)	Miami, Florida
*_Hippaliosina rostrigera_ (Smitt)	New River Inlet, N. C.
*_Hippopleurifera mucronata_ (Smitt)	Florida
*_Hippopodina bernardi_ Lagaaij[2]	Gulf of Mexico
*_Hippoporella floridana_ Osburn	Gulf of Mexico
*_Hippoporella palliolata_ (Canu & Bassler)	Straits of Florida
Hippoporella uvulifera (Osburn)	
*_Hippoporidra calcarea_ (Smitt)[2]	Florida
*?_Hippoporina aculeata_ (Canu & Bassler)[2]	Miami, Florida
*_Hippothoa flagellum_ Manzoni[2]	Tortugas
*_Labioporella granulosa_ (Canu & Bassler)	Straits of Florida
*« _Lagenipora_ » _verrucosa_ Canu & Bassler[2]	Straits of Florida
« _Lagenipora_ » sp.	
*_Mamillopora cupula_ Smitt	Straits of Florida
*_Mastigophorella porosa_ (Smitt)[2]	Miami, Florida
*_Membranipora arborescens_ (Canu & Bassler)[2]	Beaufort, N. C.
Membranipora savarti (Audouin)	
Membranipora tuberculata (Bosc)[2]	
*_Membraniporella aragoi_ (Audouin)[2]	Brazil
*_Micropora coriacea_ (Johnston)[2]	Straits of Florida
Microporella sp. « G »	
*_Microporella marsupiata_ (Busk)[2]	Madeira
*_Microporella pontifica_ Osburn[2]	Gulf of Mexico
*_Microporella tractabilis_ Canu & Bassler[2]	Gulf of Mexico
*_Mollia patellaria_ Smitt	Florida
*_Monoporella divae_ Marcus	Gulf of Mexico
*« _Myriozoum_ » _ovum_ Smitt	Florida Keys
*_Nellia tenella_ (Lamarck)	Tortugas
*_Parasmittina crosslandi_ (Hastings)	Panama (Pacific coast)
*_Parasmittina fraseri_ Osburn	Mexico (Pacific coast)
*_Parasmittina numma_ (Marcus)[2]	Brazil
*_Parasmittina signata_ (Waters)	Gulf of Mexico
Parasmittina sp.	
*_Parasmittina spathulata_ (Smitt)[2]	Miami, Florida
Parasmittina sp. « X »	
Parasmittina sp. « Y »[2]	
*_Parellisina curvirostris_ (Hincks)[2]	Cuba
*_Parellisina latirostris_ Osburn	Gulf of Mexico
*_Petraliella bisinuata_ (Smitt)	Straits of Florida
*« _Phylactella_ » _aviculifera_ Osburn[2]	Tortugas
*_Reptadeonella violacea_ (Johnston)[2]	New River Inlet, N. C.
Retevirgula sp. « A »	
*_Retevirgula_ sp. « B » (_periporosa_ auctt)	Gulf of Mexico
*_Retevirgula caribbea_ (Osburn)	Gulf of Mexico
Rhynchozoon rostratum (Busk)	
*_Schizoporella canui_ Osburn[2]	Straits of Florida

Species	Nearest Previous Report
Schizoporella carvalhoi Marcus[2]	Brazil
Schizoporella floridana Osburn	
Schizoporella rugosa (Osburn)	Puerto Rico
Scrupocellaria bertholleti (Audouin)	Tortugas; Bermuda
Scrupocellaria harmeri Osburn	Gulf of Mexico
**Scrupocellaria regularis* Osburn	Straits of Florida; Bermuda
**Setosellina goësi* (Silen)	Straits of Florida
**Smittina smittiella* Osburn	Gulf of Mexico
**Smittipora levinseni* (Canu & Bassler)	Straits of Florida
**Smittoidea reticulata* (MacGillivray)	Gulf of Mexico
**Stephanosella* (*Buffonellaria*) *divergens* (Smitt)[2]	Straits of Florida; Bermuda
**Stylopoma informata* (Lonsdale)	Tortugas
Synnotum aegyptiacum (Audouin)	
Tetraplaria dichotoma (Osburn)	
Thalamoporella falcifera (Hincks)	
Thalamoporella gothica floridana Osburn	
**Tremogasterina granulata* Canu & Bassler	Straits of Florida
**Tremoschizodina lata* (Smitt)	Straits of Florida
**Triporula stellata* (Smitt)[2]	Tortugas
**Trypostega venusta* Norman[2]	Straits of Florida
?*Turbicellepora* sp. « A »	
Turbicellepora margaritacea (Pourtales)	
**Vittaticella contei* (Audouin)	Puerto Rico; Bermuda
Cribrilinidae A	
Hippoporinidae A	
?Hippoporinidae	
Schizoporellidae A[2]	
Schizoporellidae B	
Smittinidae A	
Smittinidae: *Porella* -like	
Alcyonidium sp. « A »	
Alcyonidium hauffi Marcus	
Alcyonidium mamillatum Alder	
Amathia alternata Lamouroux	
Amathia convoluta Lamouroux	
Amathia distans Busk	
Arachnidium sp.	
**Arachnoidea evalinae* Marcus	Brazil
Arachnoidea sp.	
**Buskia socialis* Hincks	Britain; Brazil
Nolella dilatata (Hincks)	
Nolella gigantea (Busk)	
Sundanella sibogae (Harmer)	
?*Terebripora* sp.	
Zoobotryon verticillatum (delle Chiaje)	
Crisia sp. « A »	
Crisia sp. « B »	
**Crisulipora occidentalis* Robertson	Brazil
Crisulipora ?orientalis Canu & Bassler	
Diaperoecia floridana Osburn	
**Diaperoecia rugosa* Osburn	Puerto Rico
**Entalophora delicatula* (Busk)	Straits of Florida
**Lichenopora buskiana* Canu & Bassler	Panama (Pacific coast)
**Lichenopora floridana* (Canu & Bassler)	Gulf of Mexico
Lichenopora sp.	
**Plagioecia dispar* Canu & Bassler[2]	Straits of Florida

Species	Nearest Previous Report	Species	Nearest Previous Report
* ?*Plagioecia floridana* (Canu & Bassler)	Straits of Florida	* *Tervia pourtalesi* (Smitt)	Straits of Florida
* *Platonea arcuata* (Canu & Bassler)	Straits of Florida	*Tubulipora* sp. « A »	
Proboscina sp. « A »		Cyclostomata B	
?*Stomatopora* sp.		* *Loxosomella illota* Nielsen	Miami, Florida

Species ranging northward to Georgia but not collected farther north; species found off Georgia only:

?*Alderina* sp.		* *Steganoporella magnilabris* (Busk)	Straits of Florida; Bermuda
* *Brettia cornigera* Busk[3]	British Virgin Islands	*« *Trematooecia* » *turrita* Osburn (not Smitt)	Puerto Rico
Bugula grayi Maturo		Celleporidae A[3]	
Bugula rylandi Maturo		Farciminariidae A[3]	
Caulibugula sp.		Flustridae: ?*Chartella*[3]	
* *Codonellina montferrandi* (Audouin)	Gulf of Mexico	*Alcyonidium* sp. « B »	
Porella sp. « A »[3]		?*Hornera* sp.[3]	
« *Schizellozoon* » *elongatum* Canu & Bassler[3]		*Loxocalyx* sp.	
* *Sertella marsupiata* (Smitt)[3]			
Smittoidea sp.[3]	Straits of Florida		

Species found off Florida only:

* *Calyptotheca tenuata* Harmer	Philippines	*Parellisina* sp.	
* *Coleopora americana* Osburn	Puerto Rico	* *Rhynchozoon solidum* Osburn	Tortugas
* *Columnella brasiliensis* (Busk)[4]	Puerto Rico	* *Tremogasterina malleolus* Canu & Bassler	Gulf of Mexico
Hippoporella pusilla (Smitt)		Flustridae A[3]	
Hippothoa «*eburnea*» (Smitt)		Schizoporellidae C	
?*Hippothoa* sp.		*Buskia* sp.	
Margaretta cereoides (Solander)		*Crisia elongata* Milne Edwards	
* *Microporella orientalis* Harmer	Panama (Pacific coast)		

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[1] Found south of Cape Hatteras to Beaufort, N. C., area in shallow waters immediately adjacent to the shore.

[2] Found north of Cape Hatteras in Tropical Province.

[3] From Blake Plateau; not a shelf species.

[4] Off shelf in Straits of Florida.

tic shelf (LAGAAIJ, 1963; MARCUS and MARCUS, 1962; COOK, 1963, 1965a, 1965b, 1965c). They have somehow escaped appropriate attention for a major component of the fauna of the southeast coast of the United States. Interestingly, these species must represent the only firm substrate larger than a sand grain in some areas and are themselves used as a substrate for other bryozoans and entoprocts. It was a fairly common occurence to find *Barentsia laxa* Kirkpatrick, or a small ctenostome or cheilostome growing on them.

Mamillopora cupula Smitt has a growth form similar to the cupuladrias and is found in the same habitat (fig. 7). It is not nearly as common as these and tends to be restricted more to the outer shelf.

Finally, after having examined such a large collection from essentially one region, the southeast coast, I was left with the distinct impression that shell litter from the shelf in this area had a characteristic appearance. This seemed to be the result of being incrusted with a common bryozoan assemblage, the most conspicuous species being *Hippopleurifera mucronata* (Smitt). This species has a bright red-brown to red orange color and forms characteristic patches on shell debris. It is much more common and widespread on the southeast shelf than is shown by its distribution in the *Gosnold* collections (fig. 8). Most shell samples in the M. Gray - Sapelo Collection from the broad shelf off Georgia contained this species.

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THE EARLY DEVONIAN AND EIFELIAN *BRYOZOA* FROM THE ALTAI

(Translated from Russian into English by S. R. Raskolenko)

Riassunto. — I depositi devonici dei Monti Altai, nella regione del sinclinorio « Anuiski-Chuiski », contengono una fauna varia ed abbondante, in gran parte rappresentata da Briozoi.

Uno studio paleontologico-stratigrafico dettagliato e la raccolta in serie di Briozoi in sezioni diverse per facies hanno permesso di precisare la loro distribuzione temporale ed areale.

I risultati dello studio sui Briozoi sono qui comparati con i dati degli studi sui Brachiopodi, sui Coralli, sugli Stromatoporoidei, sui Pesci e sulla Flora.

Questo studio ha permesso di effettuare una serie di sostanziali rettifiche nello schema del Devonico dell'Altai, confermato nel 1964 nella Conferenza sulla Stratigrafia della Siberia centrale.

Uno studio monografico sui Briozoi infradevonici ed eifeliani dei depositi del sinclinorio « Anuiski-Chuiski » ha permesso di stabilire quattro complessi a Briozoi in successione, dei quali tre appartengono ad un'età infradevonica ed il quarto mostra affinità con l' Eifeliano.

Vengono descritte alcune particolarità della forma della colonia, dello scheletro e della struttura parietale dei Briozoi devonici di questa regione e la loro stretta dipendenza con le condizioni di vita.

Si fanno considerazioni su una particolare diffusione geografica dei Briozoi in periodi diversi dell'esteso Devonico inferiore e medio.

Summary. — A various and abundant fauna, mostly composed by Bryozoa, is present in the area of the Anuiski-Chuiski Synclinorium (Altai Mountains).

A detailed paleontological and stratigraphical study and a collected succession of Bryozoa samples in sections with different facies permitted me the observation of their chronological and geographical ranges.

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The results of the study on *Bryozoa* are here compared with the results of the studies on *Brachiopoda*, Corals, *Stromatoporoidea*, Fishes and Flore. This study allowed me to essentially modificate the Devonian scheme of Altai, confirmed in 1964 during the Conference on the Middle Siberia Stratigraphy.

A monographical study on Early Devonian and Eifelian *Bryozoa* from the deposits of Anuiski-Chuiski Synclinorium enabled me to establish a succession of four *Bryozoa* units, three of which belonging to Early Devonian and the fourth showing Eifelian affinity.

Some peculiarities of asty, skeletal and wall structures of Devonian Bryozoa of this area and their close relationships with growth conditions are here reported.

Remarks on a peculiar geographical distribution of *Bryozoa* in different periods of the widespread Early and Middle Devonian are here made.

(Italian and English summaries were translated by E. Annoscia from the Russian Author's abstract).

The most complete and wide deposits of the lower Devon and Eifelian are represented in the North and Central Altai within the limits of Anuiski-Chuiski synclinorium. In the lower Devon of the Altai thick terrigenous series with bands and benches of limestones are widespread. Their abundant and variable fauna of Brachiopods, Pelecypods, Trilobites, Bryozoa, Rugosa Corals, Stromatoporoids and others is known. From the terrigenous deposits of the Ganin spring and the Peschanaya River the Brachiopods, Pelecypods and Trilobites were studied and described by L. L. Khalfin (L. L. Khalfin, 1948, 1967). On the evidence of this fauna L. L. Khalfin in the lower Devon of Anuiski-Chuiski synclinorium described three series and referred them to Siegenian stage (Ganin series), to lower Coblenzian (Kondratjev series) and to upper Coblenzian (Medvedevskaya series).

N. L. Bublichenko (1951) had contrary opinion. He referred all these series to Eifelian stage. Last time E. A. Elkin and R. T. Grazianova (1967) were of the same opinion. We collected, studied and described *Bryozoa* from the deposits studied by L. L. Khalfin (Ganin series) and by E. A. Elkin (deposits along the Ganin spring and the Kuvash River).

Four complexes of *Bryozoa* are given below:

1. from the deposits of the Ganin series (pseudotogatovyi and paramnigenievyi horizons of Siegenian age by L. L. Khalfin;

kireevsky and matveevsky horizons of Eifelian age by E. A. ELKIN);

2. from the lower Devonian limestones of the Ganin spring (Ganin horizon of the lower Devon by E. A. ELKIN);

3. from the Kuvash series (from the Kuvash River - Kuvash horizon of Eifelian by E. A. ELKIN);

4. from the middle Devonian limestones of the Ganin spring (Kuvash horizon of the Eifelian by E. A. ELKIN).

The complex of Bryozoa from the stratotype of the Ganin formation on the right bank of the Ganin spring is the oldest (table 1). There *Bryozoa* are developed in the terrigenous rocks which consist of green-grey limestone siltstones. Trepostomes are abundant. The following species are given:

Ganiella frequens Yaroshinskaya
Lioclema subramosum Ulrich et Bassler
Pseudobatostomella spinata Astrova
Leptotrypella semiramosa Astrova
Eridotrypa minuta Astrova
Eridotrypa vestira Yaroshinskaya
Ensipora tenuis (Hall).

Species *Lioclema subramosum* Ulr. et Bassler and *Ensipora tenuis* (Hall) are known from the lower Gelderberg of North America, from burubaiski horizon (Siegen) of Kazakhstan and from the Bolsheneverskaya formation of the lower Devon of upper Priamurjya.

Species *Eridotrypa minuta* Astr., *Pseudobatostomella spinata* Astr., *Leptotrypella semiramosa* Astr., are known from the borshovski horizon of Podolia. The deposits developed above the Ganin spring and referred by E. A. ELKIN to the matveevsky and kuvashsky horizons are analogous of the Ganin formation. Here, beside new species, abundant representatives of the species *Lioclema subramosum* Ulr. et Bassl., *Ensipora tenuis* (Hall) and also such species as *Paralioclema morosovae* Astr. and *Fistulipora orbiculata* Astr. are discovered. They are known from the barshovsky horizon of Podolia and from Ludlow of the Big Zelenez Island.

TABLE I.

Distribution of the lower Devonian and Eifelian bryozoan complexes of the Altai.

Names of the species	Lower Devon				Distribution and age
	Ganin strata	Ganin bands	Kuvash series	Middle Devonian deposits	
	I complex	II complex	III complex	IV complex	
Lioclema subramosum Ulr. et Bassl.	+				lower gelderberg, N. America
L. khalfini sp. nov.	+				
Pseudobatostomella spinata Astr.	+				borshovsky horizon, Podolia
Paralioclema morozovae Astr.	+				borshovsky horizon, Podolia
Anomalotoechus una sp. nov.	+				
Eridotrypa minuta Astr.	+				chortkovsky horizon, Podolia
E. vestira Yar.	+				
Leptotrypella pervulgata sp. nov.	+				
Leptotrypella semiramosum Astr.	+				chortkovsky horizon, Podolia
Ganiella frequens Yar.	+				
Ensipora tenuis (Hall.)	+				lower gelderberg, N. America
Semicoscinium parvulus sp. nov.	+				
Lioclema multiacantoporum Astr.		+			
Lioclema ganiense Astr.		+			
Pseudobatostomella celebrata Yar.		+	+		
Paralioclema magnum Astr.		+			losishensky bands Mining Altai
Reteporina ubensis Nekh.		+			
Reteporina nativa sp. nov.		+			
Fenestella sp.		+			
Semicoscinium sp.		+			
Ensipora altaica Astr.		+	+		
Lioclema kuvashensis sp. n.			+		
Pseudobatostomella spinatoformis sp. nov.			+		
Anomalotoechua bublitshenkoi Nekh.			+		losishensky bands Mining Altai
Eridotrypa nekhoroshevi Yar.			+		
E. ampla sp. nov.			+		
Fenestella perforata sp. nov.			+		
F. glarea sp. nov.			+		
F. kuvashensis sp. nov.			+		
Lioclema jakovlevi (Schoen.)				+	Eifel, Givet, Mounting Altai, Kusbasz.
Lioclema salairiense Moroz.				+	Eifel, Kusbasz.
Lioclema vulgatum sp. nov.				+	
Fistulipora devonica sp. nov.				+	

Thus, this complex of *Bryozoa* indicates the lower Devonian age of the Ganin formation, more exactly the lower part of the lower Devon. The second complex of *Bryozoa* is discovered in the lower Devonian limestones on the right bank of the Ganin spring, referred by E. A. ELKIN to the Ganin horizon. The *Bryozoa* were studied from the grey limestones and from the bands of platy clayey limestones.

They differ from the first complex with their specific and generic composition. Difference is in absence of common species (*Ganiella frequens* sp. n. is the only common species). *Cryptostomata* are rather numerous. The genera *Reteporina, Hemitrypa, Fenestella* appeared.

Beside the genus *Reteporina ubensis* Nekh. which is widespread in losishensky strata (¹) of the Altai, all species of *Cryptostomata* are new. Presence of new species of genera *Eridotrypa* and *Ensipora* indicates the Early Devonian age of this complex. The deposits of grey limestones developed near Khomichev ravine and on the left bank of the Solovjikha River are probably the analogues of the deposits of the Ganin horizon. Similar bryozoan species are — *Lioclema multiacanthoporum* Astr., *Paralioclema magnum* Astr.

The third bryozoan complex was studied from the Kuvash series, developed on the right bank of the Kuvash River. Here abundant *Bryozoa* with different composition are discovered in grey siltstones and clayey limestones. These deposits are younger than the Ganin formation and the lower Devonian limestones of the Ganin horizon. Abundant fenestellids indicate the young age of the Kuvash series. Such new species as *Fenestella glarea* sp. nov., *Fenestella perforata* sp. nov., *Semicoscinium amurenseformis* sp. nov. show great affinity with the middle Devonian species of the Mountain Altai and the Far East. Development of fenestellids and presence of the representatives of the genera *Eridotrypa* and *Ensipora* say about existence of this complex in the Early Devon. Presence in the deposits of the Ganin and Kuvash horizons of *Pseudobatostomella celebrata* sp. nov., *Ensipora altaica* sp. nov. gives possibility to propose that the latter

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(¹) Losishensky strata is mixed-lower-middle Devonian and it is required more detail study.

are of different age and partially correspond to the deposits of the Ganin horizon.

The fourth complex of Bryozoa is studied from grey limestones developed along the right bank of the Ganin spring. The Bryozoa here are abundant, but have monotypical composition. We know only two genera: *Lioclema* and *Fistulipora*. The representatives of the species *Lioclema jakovlevi* are abundant. This species is widespread in Givetian deposits of the Mountain Altai, Kusnez basin and Minusa kettle and rarely in Eifel of the Mining Altai. Species *Lioclema salairiense* Moroz. is developed in mamontovsky strata of Eifel of the Salaira. The representatives of new species of genera *Lioclema* and *Fistulipora* show affinity with the species from lebedyansky strata of Givetian formation of the Kusnez basin. This bryozoan complex is of the middle Devonian age. Stratigraphic evidence on *Bryozoa* from Devon are confirmed by the fauna of *Tabulata, Rugosa* corals, Stromatoporoids, fishes and flora (2).

Here the brief geological and facies characteristics of our bryozoan complexes are given.

In all three Early Devonian complexes local forms are dominant; species known from other regions and countries are rare, although some species, for example American *Lioclema subramosum*, is abundant. In the first complex among bryozoan species the *Trepostomata* are dominant. Besides particularly endemic species, there are 5 species identical with podolian ones (*Fistulipora orbiculata* Astr., *Eridotrypa minuta* Astr., *Pseudobatostomella spinata* Astr., *Pseudobatostomella morosovae* Astr., *Leptotrypella semiramosa* Astr).

The north American species are also widespread, especially *Lioclema subramosum* Ulr. et Bassl. and *Ensipora tenuis* (Hall). It is evident that the Devonian basin of the Mountain Altai at that time was connected with the European and north American basins. In the second complex of *Bryozoa*, Podolian and north American elements are absent. Fauna of basins of adjacent regions are present: some species appear, common with *Bryozoa* of the Kusnez, Minusa and Mining Altai basins. It is visible weak con-

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(2) Fauna was studied by the siberian workers - N. V. Mironova, V. K. Khalfina, S. K. Cherepnina, A. A. Sergienko, Flora -by S. A. Stepanov.

nection with the Kazakhstan Sea. In the third complex there are few species, elements of American and European fauna are absent and species morfological common or identical with species from the Mining Altai and East Siberia basins are very common: from ten known here species one is common and three ones are similar to the *Bryozoa* of the Mining Altai and East Siberia; the left species are particularly endemic. The fourth (Eifelian) complex is characterized by abundance of *Bryozoa* of the order *Trepostomata* with monotypic specific and generic composition. Geographical type of this *Bryozoa* was under the influence of fauna of the Kusnez and Minusa basins.

A remark should be made about the difference of the complexes of Early Devonian *Bryozoa* of the Mountain Altai and Middle Asia.

From all known Early Devonian *Bryozoa* of the Mountain Altai (63 species), only two new species (*Hemitrypa nativa* Yar., *Hemitrypa sandalicoformis* sp. nov.) have affinity with Early Devonian *Bryozoa* of Middle Asia where there are many fenestellids.

In deposits of the lower Devon and Eifel of the Mountain Altai the *Bryozoa* refer to the terrigenous and carbonate rocks.

Characteristic feature of *Bryozoa* of the first complex of the Ganin formation is abundance of *Trepostomata* and few *Cystoporata* and *Cryptostomata*. *Cystoporata* are in limestones and as a rule they are in biocoenosis with Tabulata and Stromatoporoids. They consist of large covered colonies, forming often small offsets (local genus *Ganiella*) and rarely thin covered laminate colonies as genus *Fistulipora*.

Abundant different *Trepostomata* are in the lower part of the Ganin formation in thin limestone-clay bands. Especially species *Lioclema subramosum* Ulr. et Bassl. is abundant with large branches, rarely with covered colonies and mature region. Branches of genera *Eridotrypa, Leptotrypella,* thin, net-like colony of genera *Semicoscinium* and *Fenestella* and banded-like colony of genus *Ensipora* are found. Whole colonies or large fragments are absent. The length of fragmental branches and nets of *Bryozoa* is not larger than 10 mm, rarely 3-5 mm. The fragments of colony are not rounded, mature region is well preserved. Probably, colonies of *Bryozoa* partly in their life-time, partly after their death were broken by swell and were buried near the inhabited place. Widespread thin branching bilateral symmetrical and thin net *Bryozoa*, lived probably in calm waters, where they can attach to the soft bottom. (ASTROVA, 1959). Here and there *Bryozoa* of this complex are in the terrigenous-clay rocks, and in the bright-grey clayey limestones.

On the clay bottom the *Bryozoa* are monotypical by the form of colonies (species of genera *Lioclema*, *Pseudobatostomella*, *Leptotrypella*). They had long branching colonies. Some branches were in width 0,03-0,07 mm and their length was 8-15 cm. Together with Bryozoa branches of Thamnoporids, shells of Brachiopods and fish remnants are seen. Development of branching colonies well preserved after death and absence of covered and sinter forms say about normal sea circumstances and about calm waters. In clay limestones we see abundant large well preserved thick branch colonies of *Trepostomata* (genera *Lioclema*, *Paralioclema*, *Leptotrypella*, *Pseudobatostomella*) and large fragments of wide banded with bilateral symmetrical colonies of genus *Ensipora*. Different *Tabulata* and *Rugosa* corals are here. In the upper part of the Ganin formation we can see depauperation of bryozoan fauna. There are only species *Lioclema subramosum* Ulr. et Bassl., *Ensipora tenuis* (Hall) and *Ganiella frequens* Yar. During the deposition of the upper part of the Ganin formation the *Bryozoa* lived in unfavourable conditions (probably shoaling and desalting). In the second complex we see two groups of *Bryozoa* according to the different types of sediments. The first group is in limestone-clay bands, among terrigenous rocks. It consists of the fragments of large-meshed colonies of *Cryptostomata* with thick bands (genera *Reteporina*, *Hemitrypa*, *Semicoscinium*, *Fenestella*).

The species of genus *Lioclema* with branching or small cone-like shape of colonies, covering pebble and also large branching colonies of genus *Paralioclema* with well mature region, thickened walls and abundant megacanthopores are represented in these sediments among *Trepostomata*. The character of colony and presence of genus *Hemitrypa* with secondary net indicate that the *Bryozoa* lived in near-shore part of basin, in condition of strong development of water. The second group of *Bryozoa* is represented by abundant, but exclusively monotypical *Cystoporata*. These *Bryozoa* are in bright-grey limestone and represented by genera *Ganiella* and *Fistulipora.*

Abundant *Ganiella* covered corals and develop large or laminate colonies with offsets of different length. Often we see the whole colonies and no fragments. Covered colonies of genus *Fistulipora* are rare and are represented by small fragments.

Beside *Cystoporata* there are *Tabulata, Rugosa* and Stromatoporoids. The representatives of genus *Ganiella* in the first and in the second complex are in limestones with terrigenous mixture and only together with *Tabulata* and Stromatoporoids. Probably the species of this genus can live only in clear water and belong to stenobiontic organism. The *Bryozoa* of the third complex are found in limestone-clay bands: they are abundant thin colonies of genera *Fenestella* and *Semicoscinium* of good preservation. Beside abundant *Fenestella* we find branches of genera *Lioclema, Eridotrypa, Pseudobatostomella.*

Almost all of them have thin branching colonies, small acanthopores and thin walls, thickened on the periphery. Covered and large colonies are found rarely. The *Bryozoa* of the third complex lived in calm shallow sea. Well preserved thin colonies of 10-18 mm of length indicate that the *Bryozoa* after death were not transported.

The *Bryozoa* of the fourth complex are developed in bright-grey limestones. They form crowded covered colonies. Large covered and branching colonies of genera *Lioclema* and *Fistulipora* are dominant. The width of the branches is 0,8-1,5 cm.

Bryozoa in these limestones are found sporadical and the other fauna is absent. In these sediments abundant *Tabulata,* Stromatoporoids and *Rugosa* are found. Abundance and difference of sea fauna in limestone indicate the good condition of life, light, aeration, salinity.

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1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
38. Group 5: Biogeography and Biostratigraphy.

SUMIO SAKAGAMI (*)

STUDY ON THE UPPER PALEOZOIC *BRYOZOA* OF JAPAN AND THE THAI-MALAYA DISTRICTS

(Preliminary Report)

Riassunto. — Attualmente sono conosciute in Giappone 181 specie di Briozoi e 87 sono note nel distretto maleo-tailandese.

Benchè vi siano soltanto tre specie in comune tra questi due distretti, le loro associazioni generiche sono intimamente in relazione l'una con l'altra.

Le nostre conoscenze dei Briozoi silurici e devonici dei distretti giapponese e maleo-tailandese sono molto limitate e si auspicano ulteriori studi su di essi.

Summary. — At present 181 species of Bryozoa are known from Japan and 87 species from the Thai-Malaya districts. Although there are only three species in common between these two districts, their generic assemblages are intimately related each other.

Our knowledge of the Silurian and Devonian Bryozoa from Japan and the Thai-Malaya districts are very limited and future study on them is desired.

At present 181 species of Bryozoa are known from Japan and 87 species from the Thai-Malaya districts. Although there are only three species in common between these two districts (*Fistulipora timorensis*, *Fenestella* cf. *retiformis* and *Fenestella* cf. *triserialis*), their generic assemblages are intimately related each other.

Among the interesting genera known from Japan and the Thai-Malaya districts, *Nipponostenopora* and *Hayasakapora* are

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established originally from Japan. *Nipponostenopora* is a Carboniferous genus and *Hayasakapora* is a Permian one. These two genera were recently recorded from strata of equivalent geological ages in the USSR.

The genus *Hexagonella* although not known from the Permian of Japan, has been recorded from the Permian of Thailand (3 spp.), the Salt Range (3 spp.), Australia (6), Timor (1) and the Ural region (1). Although it can be distinguished from *Meekopora* by the presence of hexagonal ridges, generic identification by only thin section is difficult, and for such reasons it is probable that *Hexagonella* occurs also in Japan.

The genus *Prismopora* which has been reported from the Devonian to Permian of the United States and the Permian of Australia, is also known from the Japanese Carboniferous and Permian strata. It is noted that the genus *Ascopora* which is common in European Russia is known only from the Permian of Thailand and not from elsewhere in southeast Asia, Australia and Japan.

Some species of *Streblascopora* which form the *Streblascopora marmionensis* group are widely distributed in the Circum-Pacific and the Russian regions.

Our knowledge of the Silurian and Devonian *Bryozoa* from Japan and the Thai-Malaya districts are very limited and future study on them is desired.

In general, the Japanese Carboniferous bryozoan fauna shows intimate relationship with those known from Turkestan, the Kuznetz and Donetz basins, and also has yielded species widely distributed in both the USSR. and USA., such as *Meekopora approximata* Ulrich, *Rhombopora exigua* Ulrich, *Fenestella triserialis* Ulrich and others. At present nothing is known of the Upper Carboniferous *Bryozoa* in Japan. In the Thai-Malaya district, in spite of the small faunas from the Lower Carboniferous, the bryozoan faunas contain both European and North American elements. The *Bryozoa* from EB-49 in Thailand are similar to the species described from the United States of America and are probably Lower Uralian in age.

The generic assemblages of the Japanese Permian *Bryozoa* resemble those of the Permian of Timor island, Australia and Vancouver island, and some genera are related to those of India, China and the USSR. The Thai-Malayan bryozoan fauna is closely related to those from the Permian of Timor island, Australia, Japan and Vancouver island, and bear characters common with those of European Russia, the Moscow basin, and the Ural mountains.

The research on these bryozoans are progressing and the results are expected to contribute to the biostratigraphy, correlation, taxonomy and other problems.

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39. Group 5: Biogeography and Biostratigraphy.

GISELA ILLIES (*)

ON SOME CYCLOSTOMATOUS *BRYOZOA* FROM THE MIDDLE JURASSIC OF SOUTHERN GERMANY

(Preliminary Report) (**)

Riassunto. — Vengono descritti i caratteri distintivi di *Proboscina alfredi* Haime, 1854, un briozoo *Cyclostomata* multiseriale con sezione trasversa arcuata, presente nel Bajociano superiore della Germania meridionale.

Summary. — Features of *Proboscina alfredi* Haime, 1854 with arched cross section, from Upper Bajocian of Southern Germany, are here investigated.

The features of *Proboscina alfredi* Haime, 1854, a multiserial cyclostome Bryozoan with arched cross-section, found in the Upper Bajocian of southern Germany will be investigated. The shape of the zooecia depends on their situation within a branch. A zooecium develops from the budding layer to the frontal plane. A zooecium consists of the endozone and the exozone. The endozone consists of the budding, rounding and interzooecial regions. The zooecia, being located along the medium line of a branch, differ from those situated at the lateral borders of the branch by unfinished growth of the latter ones. The development of the zooecia

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(**) The complete text of this paper will be published under the title: « Multiseriale Bryozoa Cyclostomata mit gewölbtem Zweigquerschnitt aus dem Dogger des Oberrheingebietes » in: Oberrheinische geologische Abhandlungen, 17 (2), pp. 217-249, pl. 1-5, Karlsruhe, October 1968.

originated from the growing zones forming the ends of the branches. The growing zone demonstrates the overlapping arrangement of the zooecia. The gonozooecium is an enlarged exozone of a tube lying within the frontal layer of the colony as flat as the zooecia. The bifurcations of the branches and the origin of the colonies will be treated.

All the attributes mentioned above are coincident within numerous varieties of the described species, in spite of the manifold figurations of the branches.

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40. Group 5: Biogeography and Biostratigraphy.

KRISTER BROOD (*)

STENOLAEMATOUS ECTOPROCTS FROM THE DANIAN DEPOSITS OF SWEDEN AND DENMARK

(*Bryozoa*)

(Preliminary Report)

Riassunto. — L'A. dà notizie preliminari su un suo ampio lavoro in cui vengono descritti gli *Ectoprocta Stenolaemata* provenienti dai depositi Daniani della Svezia meridionale e della Danimarca.

Si tratta di 75 specie (delle quali 24 nuove) appartenenti a 40 generi (dei quali 3 nuovi). Vengono istituite 3 nuove famiglie e 5 famiglie vengono invalidate.

Infine l'A. ripudia totalmente la tradizionale classificazione di CANU e di BASSLER e propone un nuovo sistema basato sulla classificazione preconizzata da BORG.

Summary. — A. gives a preliminary report about a big work in which he describes Stenolaematous Ectoprocts from Danian deposits of southern Sweden and Denmark.

In this work 75 species (24 new) belonging to 40 genera (3 new) and 3 new families are described.

The generally accepted classification by CANU and BASSLER is totally rejected and a system built on the classification founded by BORG for living species is suggested.

Zusammenfassung. — Stenolaemate Ectoprocten aus Dan-Ablagerungen in Süd-Schweden und Dänemark sind beschrieben worden.

75 Arten (24 neue Arten) aus 40 Gattungen (3 neue Gattungen) und 3 neue Familien beschrieben worden.

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Die allgmein angenommene Klassifizierung der CANU und BASSLER ist vollständig verworfen, und anstelle ein System, aufgebaut auf die von BORG entworfene Klassifizierung jetzlebenden Arten, vorgeschlagen worden.

Stenolaematous ectoprocts from the Danian deposits of Southern Sweden and Denmark are described. Three new families, *Filisparsidae* for *Filisparsa* and *Nevianipora*; *Borgellidae* for *Borgella*; *Tubigerinidae* for *Tubigera*; three new genera, *Pseudotervia,* referred to *Crisinidae; Borgella,* referred to *Borgellidae*; *Silenopora,* referred to *Heteroporidae*; and 24 new species are proposed. Totally 75 species belonging to 40 genera are described. The ovicells of 65 species are described and illustrated. One suborder, *Dactylethrata,* is rejected, and the weak arguments for accepting *Rectangulata* are discussed. The generally accepted classification of CANU and BASSLER is totally rejected, and a system built on the classification formed by BORG for modern species is suggested. Thus the families *Diaperoeciidae, Oncousoeciidae, Plagioceiidae, Tretocycloeciidae,* and *Leiosoeciidae,* are rejected. *Cytididae* is removed from *Cancellata* and placed in *Tubuliporina, Corymboporidae* is moved from *Cerioporina* to *Tubuliporina.*

Special interest has been devoted to the differences in zoarial growthform and variations in shape and size of the ovicells in species and genera. The studies show that *Berenicea, Reptomultisparsa, Cavaria, Pergensia, Plagioecia,* and *Mesenteripora* are synonyms of *Diastopora*; *Cryptoglena, Cavarinella, Parleiosoecia, Radiocavaria,* and *Reptomulticlausa* are synonyms; *Desmepora, Homeosolen,* and *Truncatulipora* do not differ from *Osculipora; Domopora, Stellihagenowia,* and *Tholopora* are synonyms of *Radiopora*; *Bimulticavea, Tecticavea* are complex colonies of *Radiocavea; Discocavea, Paricavea, Semimulticavea, Unicavea, Orosopora* and *Heteroporella* are all synonyms of *Disporella.* Variations in the shape of the ovicells that are possibly due to ecological conditions are commonly found in species of *Entalophora* and *Diastopora.* So are *Diaperoecia*- and *Plagioecia*-shaped ovicells found in the same species.

A short summary of the terms used for describing kenozooids and pores are given. Dactylethra, firmatopores, mesopores, and nematopores are kenozooids; Tergopores and vacuoles are pores. Cancelli is a term for extrazooidal cavities and should be restricted for *Lichenoporidae.*

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41. Group 5: Biogeography and Biostratigraphy.

GIAN PIERO BRAGA (*)

BRYOZOA FROM THE « MARNE ROSSE » OF SPILECCO

(LESSINI MOUNTAINS, VERONA)

Riassunto. — Dopo un accenno alla complicata situazione geologica dell'area da cui provengono i campioni esaminati, vengono fatte alcune considerazioni sulla interessante fauna a Briozoi delle « marne rosse » dello « Spilecciano » di Spilecco, mettendo in particolare risalto il valore del ritrovamento quale nuovo contributo alla migliore conoscenza dei Briozoi del Veneto.

Summary. — Following a hint on the complicated geology of the area from which the examined specimens come, some considerations on the interesting Bryozoan fauna of the « marne rosse » of « Spilecciano » of Spilecco are made, giving a particular stress to the value of the finding as a new contribution to a better knowledge of the *Bryozoa* in the Venetia region.

Résumé. — Après un coup d'oeil à la situation géologique compliquée de la zone d'où proviennent les échantillons examinés, on fait quelques considerations sur la faune intéressante à Bryozoaires dégagée des « marne rosse » du « Spilecciano » de Spilecco, soulignant son valeur pour une meilleure connaissance des Bryozoaires du Veneto.

Introduction.

The following brief notes are intended as some preliminary remarks on an interesting Bryozoan fauna originating from the « marne rosse » of the « Spilecciano » at Spilecco (Fig. 1). Even though its existence had already been pointed out by SCHWEIG-

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HAUSER (1952, p. 20), no one had taken the initiative of studying it. From a quick analysis this fauna turned out to be an almost new element in the overall knowledge existing on the Tertiary *Bryozoa* of the Venetia region (BRAGA, 1963-1966).

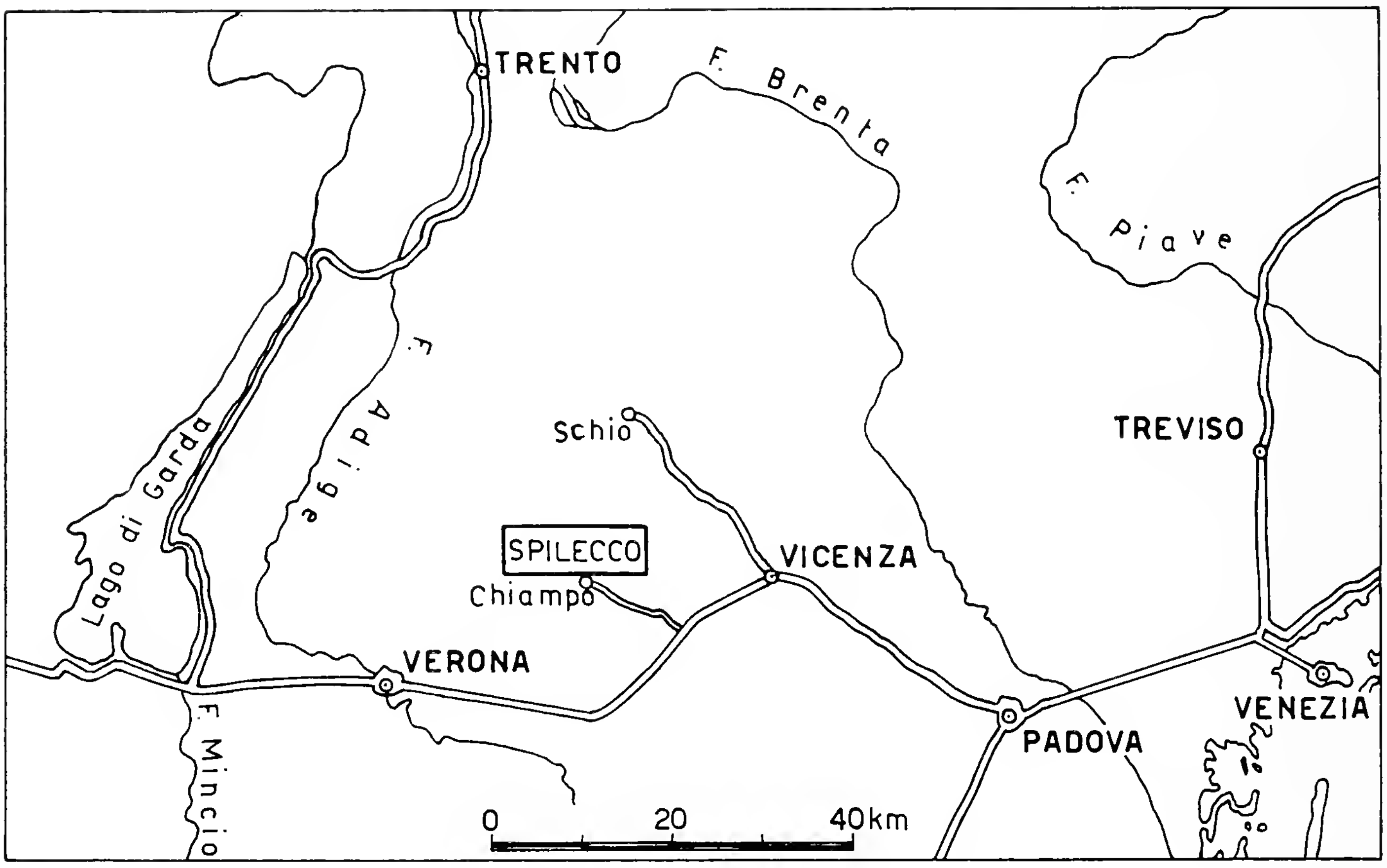

Fig. 1. — Map of Spilecco area.

I hope to enlarge upon this subject with a deeper paleontological study at a future date. I believe, however, that this simple indication has already a remarkable importance. As a matter of fact, to my knowledge, this is the first time that a Bryozoan fauna belonging to Paleocenic levels and very common in the Dano-Montian beds of North-West Europe is reported in Italy.

Short Geological Notes on the Spilecco Zone.

The reconstruction of a stratigraphical series in the surroundings of Spilecco is rather complicated because of the many faults, mainly vertical, that have greatly dislocated the Cretaceous-Eocenic series and due to the presence of volcanic rocks levels appearing as flow basalts, hyaloclastites, tuffs, layered volcanoclastic rocks and to the precariousness of the outcrops. This can be seen in the geological sketch map herewith enclosed and even better in the stratigraphic cross-section of pictures 1 and 2 (¹).

The most ancient formations of the series are represented by whitish, lightly clayey and thickly stratified limestones, that can be attributed to the Middle-Lower Cretaceous (Bian-

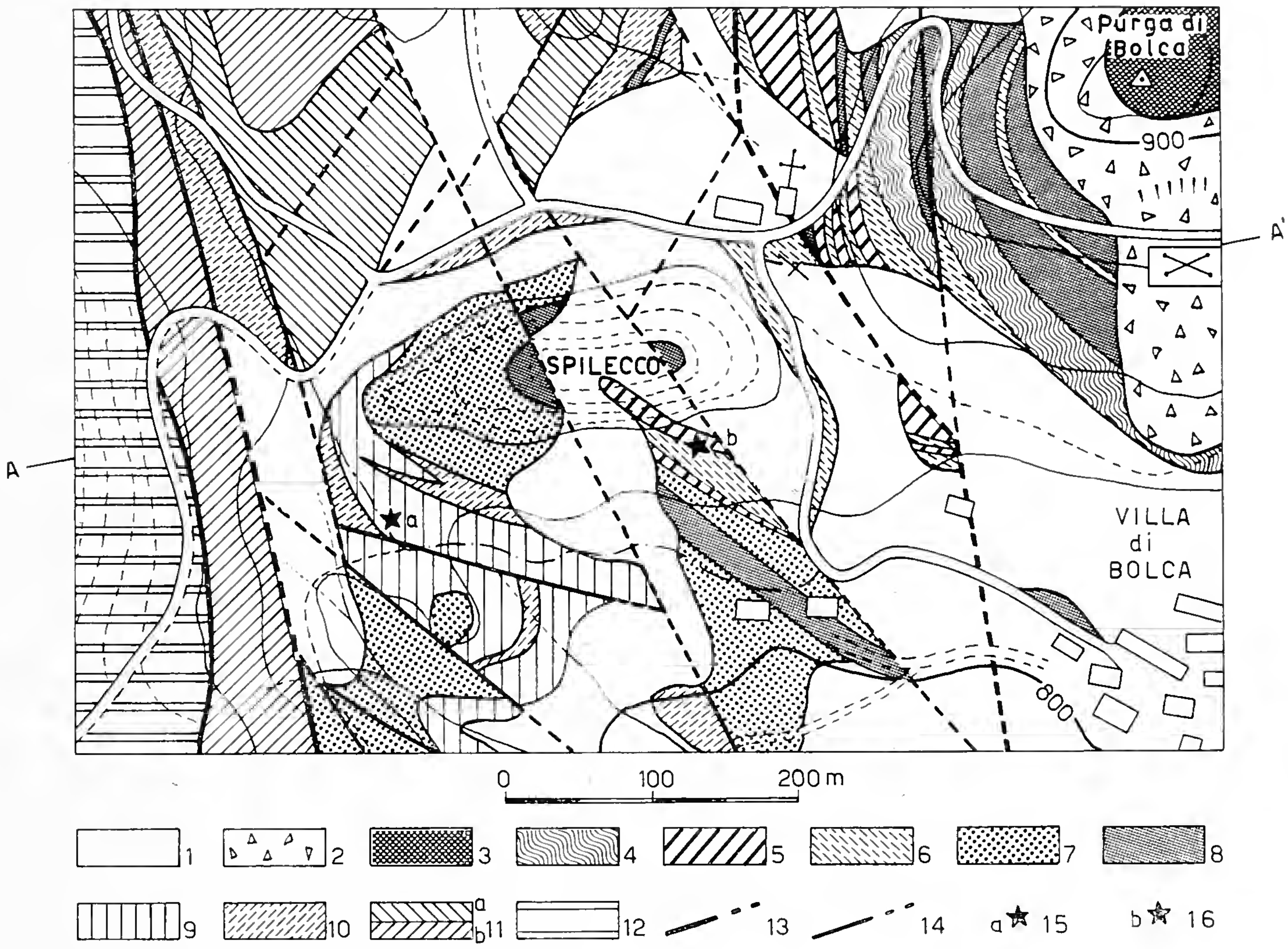

Fig. 2. — Geological sketch map of the Spilecco zone.

Simbols - 1: detrites; 2: slope slide detrites; 3: basaltic neck; 4: argillites with *Palmae*; 5. nummulitic limestones; 6: Eocenic layered volcanoclastic rocks; 7: hyaloclastites and pillow-breccias; 8: flow basalts; 9: Spilecco limestones; 10: Paleocenic layerd volcanoclastic rocks; 11: Scaglia rossa (a: Maastrichtian; b: Turonian-Santonian); 12: Biancone; 13: main faults; 14: minor faults; 15: points of collection of Paleocenic Bryozoa; 16: points of collection of Eocenic Bryozoa.

(¹) The geological sketch map and the cross-section are taken from a study done by G. Barbieri and F. Medizza published in the « Mem. Ist. Geol. e Min. Univ. Padova ».

cone) and by the thinly grained reddish marly limestones (Scaglia rossa) of the Upper Cretaceous. The boundary with the Paleocenic sediments is merely paleontologic (based on the *Discocyclinae*, *Nummulites* and planktonics *Foraminifera*) as the « Scaglia rossa » is found with the same facies in the Maastrichtian as well as in the Paleocene togheter with the interposition of a characteristic hard-ground.

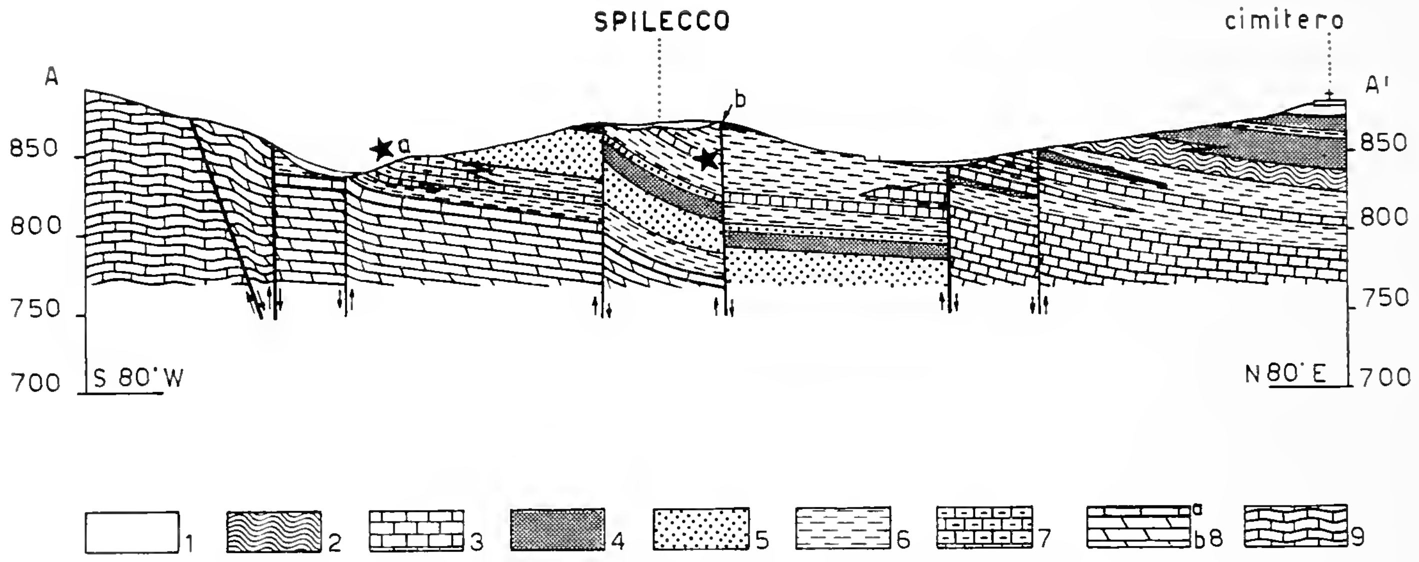

Fig. 3. — Geological cross-section A-A′ (Bolca-Spilecco).

Simbols - 1: Quaternary detrites; 2: argillites, siltites, lignites with *Palmae* and *Crocodilus vicetinus*; 3: nummulitic limestones; 4: flow basalts; 5: hyaloclastites and pillow-breccias; 6: layered volcanoclastic rocks; 7: Spilecco limestones; 8: Scaglia rossa (a: Maastrichtian; b: Turonian-Santonian); 9: Biancone.

Some reddish coarse-grained, hard richly fossiliferous limestones emerge on the Scaglia. Among the macrofossils we find many *Bryozoa*, Fish teeth, Echinoids fragments, Brachiopods and macroforaminifera. The benthonic and the planktonic, the latter in a lesser quantity, microforaminifera are well represented.

As previously said, basalt flows, hyaloclastites and tuff levels are inserted in the limestones.

This heterogeneous formation, a few meters thick, was called Spilecciano by Fabiani (1912 and 1915) and he identified it as representative of the Lower Eocene. Recalling here the history of the vicissitudes encountered by the Fabiani's Spilecciano is not befitting. It may be noted that the term Spilecciano, as Fa-

BIANI meant it, must be absolutely left out, as the limestones of Spilecco, because of the fauna they contain, are not Eocenic, but Paleocenic (CITA and BOLLI, 1961).

As the limestones and « marne rosse » of Spilecco contain *Bryozoa*, the subject of this study, they are of particular interest here (fig. 2, 15a). From the point of wiew of their fauna they belong to the *Globorotalia aequa* zone (according to LUTERBACHER, 1964) and therefore they should belong to the Upper Paleocene.

The series ends with some nummulitic limestones that can be seen on the bed of the Purga di Bolca, of the Cuisiano age, where rare *Bryozoa* (fig. 2, 16b) have been isolated into some marl levels, tuffs with Palmae and Molluscs, probably belonging to the Lower Eocene or to the low part of Middle Eocene.

Considerations on the Samples studied and on the Bryozoan Fauna.

The sample residue gathered in correspondence with the « marne rosse » (*Globorotalia aequa* zone) shows a very rich fauna with particularly abundant macroforaminifera (*Discocyclinae*, *Nummulites* and *Operculinae*), benthonic and planktonic microforaminifera, small Corals, plates and spines of Echinoids, stems of Crinoids and fragments of Molluscs (*Ostreidae*).

The inorganic residue is totally missing.

The *Bryozoa* are pretty well represented: among these, the *Cyclostomata* are far more numerous than the *Cheilostomata*. They appear in very soft, even if somewhat worn out (²), colonies, but they exclude the possibility of being reworked.

Thin *Quadricellaria* colonies, fine *Sertella* fragments and very numerous and fragile zoaria of *Entalophora*, *Filisparsa* and *Tervia* are exceptionally kept in the residue. The globose *Ceriopora* spheres are also frequent.

I am giving below here a list of the fauna that for the most part has been only determined by genus, as I could only find vague similarities in the numerous foreign publications related to the

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(²) The worning out is probably partly due to some difficulty in cleaning and washing the calcareous marl.

Bryozoan faunas of the Cretaceous and Paleocene and in the few ones on the Lower Eocene (³).

The affinity with eocenic fauna, particularly with the ones of the Venetia (BRAGA, 1963), is almost nil.

1. *Quadricellaria* sp., very abundant. It can be compared with *Q. elegans* d'Orb.
2. *Flustra* sp., very rare.
3. *Onychocella* sp., very rare. It has an affinity with *O. subpyriformis* d'ARCH., but the sizes, being slenderer, do not coincide.
4. *Vibracella* sp., rare. It seems similar to *V. rimosa* MARSSON
5. *Castanopora* sp., very rare. To some extent it can be compared to the *Cribrilina asperula* MARS.

6-7. *Sertella beaniana* KING, abundant. The zoaria are more or less slender, but they may be considered as variations of the species.

8. *Sertella tuberculata* (REUSS), rare.
9. *Sertella* sp., very rare. Very slender and with few apertures.
10. *Porina* sp., very rare. A sole specimen, badly kept.

11-14. *Entalophora* cf. *macrostoma* MILNE-EDWARDS, very abundant. We have very numerous specimens that can be subdivided into four groups according to their greater or lesser frequency of the apertures, that, however, may be included in the variability of the species.

15-19. *Filisparsa* sp., very abundant. In this grouping too there is a very great variability in the position and frequency of the apertures. The zoaria remind us of some species of MARSSON, like *F. gracilis, fragilis* and *pulchella.*

20. *Clavisparsa* sp., rare. There is some likeness to the *Entalophora turbinata* MARS.

21-22. *Idmonea* sp., abundant. Specimens very similar to *I. gracillima* REUSS, but much slenderer.

23. *Idmonea* sp., very rare. A sole very worn out specimen.
24. *Idmonea* sp., abundant. Zoaria with two little tubes on each side, one of which scarcely developed.

(³) I wish to thank Dr. Noël MONGEREAU for his courtesy in accepting to examine these interesting faunas himself.

25-28. *Tervia* sp., very abundant. The 25-26 specimens are like *Tervia bialternata* GREGORY; the others are very slenderer.
29. *Bicrisina* sp., rare. Very flat specimens with small and numerous apertures.
30. *Tubulipora* sp., rare.
31. *Ceriopora* sp., very abundant. Numerous spheroidal and mushroom-like specimens.

Beside these samples, there are in the residue other numerous specimens whose systematical position is not well established.

Another cleaned residue was picked up in an immediately higher level and it has appeared substantially similar to the previous one, even if less rich in its specimens.

Also the residues from marls intercalated with nummulitic limestones of Lower Eocene contain some *Bryozoa*, however, their number is very small. From a quick observation many species seem to have remained unchanged. This should not amaze us as the same can be observed in other zoological groups, like for instance, the benthonic Foraminifera, which perhaps are less sensitive to light variations and less influenced by the persistence of particular environmental factors.

Stratigraphic and Paleoecological deductions.

Very little can be said on the possibility of this fauna, as it has been determined, of being of any use for establishing the Paleocenic age of the « marne rosse ». This has already been shown through the macroforaminifera and planktonic Foraminifera by previous Authors (SCHWEIGHAUSER, 1953; CITA and BOLLI, 1961; MEDIZZA, 1965).

We can only stress the existence of a certain similarity of this faunal association with the *Bryozoa* of the Upper Cretaceous and the Paleocene of the Northern basins.

The pre-eocenic age of these *Bryozoa* is evidenced not only by the examination of the *Cyclostomata/Cheilostomata* very high ratio, but also by the total absence of still living species (BUGE and STARCH in PIVETEAU, 1952) and by the total lack of the species that are extensively found in the « marne a Briozoi » level of the Upper Eocene scattered all over the Venetia region (BRAGA, 1963).

Once a systematic and paleontological study has been finished, its main value lays in its contribution toward the knowledge of a new fauna and, perhaps, of numerous new species.

From the paleoecological point of view, we realize that we are here in the presence of essentially branched out and very fragile colonies, living therefore in very calm waters, associated with algal meadows, that supplied, beside a favourable environment for their living, the only suitable support for their settlement. The marno-argillaceous facies of Spilecco with its thin sediments, could not by itself provide a substratum for the building of the colonies.

The existence of this Bryozoan fauna and the wealth of macroforaminifera, such as *Nummulites* and *Discocyclinae*, confirms also the belief that at this point the sea had to be very shallow, i.e. about one hundred meters deep.

From the paleogeographic point of view this fact goes very well along the line of the regressive cycle that occurred in the Paleocene and linked to the early stages of the alpine orogenesis that caused the formation of shallow seas, or to emerged zones that are also the place of concomitant effusive manifestations with the formation of volcanic isles. This paleogeographic set-up was scattered all over the Trentino-Venetia area (PICCOLI, 1966).

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MONIQUE LABRACHERIE (*)

QUELQUES BRYOZOAIRES CHEILOSTOMES DE LA FALAISE DE HANDIA

(BIARRITZ, FRANCE)

Riassunto. — Dai sedimenti calcarei della Falesia di Handia (Biarritz, Francia) sono stati ottenuti vari esemplari di Briozoi.

Oggetto del presente studio è dare un elenco dei principali *Cheilostomata* rinvenuti, descrivere alcune nuove specie e completare lo studio delle forme che sono state descritte da d'ARCHIAC nel 1886 e da CANU nel 1910.

Summary. — Calcareous sediments of the « Falaise de Handia (Biarritz) » have yielded various specimens of *Bryozoa*.

The object of the present study is to make a list of the main *Cheilostomata* we found, to define some new species and also to complete the study of forms which have been described by d'ARCHIAC in 1886 and CANU in 1910.

Résumé. — Les sédiments calcaréo-marneux de la Falaise de Handia (Biarritz) ont livré une faune de Bryozoaires riche et variée.

L'objet de cette étude est de présenter les principaux Cheilostomes rencontrés, de définir les espèces nouvelles et surtout d'apporter des précisions sur les formes qui avaient été autrefois décrites par d'ARCHIAC en 1886 et CANU en 1910.

La faune recueillie dans les dépôts calcaréo-marneux de la falaise de Handia (Biarritz) est riche.

Les tris des divers résidus de lavage n'ont malheureusement pas fourni un matériel en parfait état de préservation. Du fait

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de la forte adhérence du sédiment nous avons dû procéder à un nettoyage plus poussé. Les échantillons libres furent alors traités par les ultrasons pendant une durée de 7 à 10 heures dans un bain d'eau naturelle; cette méthode sans donner des résultats spectaculaires a cependant facilité notre étude.

Les Cyclostomes sont numériquement importants mais peu variés tandis qu'une plus grande diversification existe chez les Cheilostomes.

Les Bryozoaires paléogènes du Sud de l'Aquitaine sont peu connus. Il faut toutefois mentionner les travaux de d'ARCHIAC (1) et ceux de CANU (6).

Au cours de ce travail nous nous sommes plus particulièrement attachés à apporter des précisions sur certaines espèces cheilostomes qui avaient été décrites par ces auteurs et que nous pensons avoir retrouvées. Il s'y ajoute de nombreuses autres formes qui n'ont jamais été citées dans la région, parmi celles-ci certaines apparaissent nouvelles, d'autres mieux connues ont une plus large distribution géographique. Parmi ces dernières il faut signaler :

Batopora multiradiata Reuss, *Batopora stoliczkai* Reuss, *Cellaria reussi* (d'Orbigny), *Chlidoniopsis vindobonensis* (Reuss), *Escharina procumbens* (Reuss), *Vincularia monstruosa* (Canu), *Vincularia polymorpha* (Canu), *Kionidella dactylus* (d'Orbigny), *Membraniporella radiata* (Reuss), *Nellia tenella* (Lamarck), *Onychocella subpyriformis* (d'Archiac), *Poricellaria alata* d'Orbigny, *Poricellaria complicata* (Reuss), *Scrupocellaria elliptica* (Reuss), *Scrupocellaria gracilis* Reuss, *Sparsiporina elegans* (Reuss), *Stenosipora protecta* (Koschinsky), *Stenosipora simplex* (Koschinsky), *Tubucellaria bipartita* (Reuss). De très nombreux spécimens appartenant au genre *Sertella* n'ont pu être déterminés spécifiquement.

Parmi les espèces qui paraissent nouvelles, quelques-unes n'ont pas, du fait de leur rareté, été décrites au cours de cette étude. Ces formes sont toutes présentes dans l' Eocène du Nord de l'Aquitaine; en raison de leur importance numérique dans cette région, leur diagnose complète sera donnée ultérieurement.

Famille CALLOPORIDAE Norman, 1903

Genre CRASSIMARGINATELLA Canu, 1900

Crassimarginatella macrostoma (Reuss)

Pl. VII - Figs. 1-6.

1847 *Cellaria macrostoma* Reuss, p. 64, pl. 8, figs. 5-6.
1869 *Biflustra macrostoma* (Reuss) Reuss, p. 274, pl. 33, figs. 12-13.
1877 *Flustrellaria macrostoma* (Reuss) Manzoni, p. 67, pl. 13, fig. 46.
1885 *Membranipora macrostoma* (Reuss) Koschinsky, p. 22.
1891 *Membranipora macrostoma* (Reuss) Waters, p. 11.
?1910 *Membranipora quadrifascialis* Canu, p. 842, pl. 16, fig. 1.
1949 *Crassimarginatella macrostoma* (Reuss) Buge, p. 264, fig. 1.
1963 *Acanthodesia macrostoma* (Reuss) Braga, p. 22, pl. 2, fig. 1.

Matériel. - Plus de 50 fragments.

Remarques. - Les variations zoariales sont moins importantes que celle signalées part Buge. La forme étalée est absente et les types pseudovinculariiforme et vinculariiforme sont les plus fréquents. Les aviculaires en tétha figurés par cet auteur n'ont pu être retrouvés malgré un matériel abondant. Cependant très rarement les zoécies qui se situent au départ de nouvelles rangées zoéciales peuvent présenter certaines modifications. Un léger étranglement s'observe dans la moitié supérieure délimitant une partie distale petite, semicirculaire et une grande région proximale elliptique. Les spécimens ne sont pas suffisamment préservés pour dire si l'on peut les considérer comme des aviculaires. Les ovicelles sont par contre très nombreux et typiques.

Les dimensions des zoécies sont très variables. Elles sont généralement plus faibles que celles que l'on peut relever sur les figures de Reuss.

Dimensions: Lz (10): 0,57 mm (0,42 - 0,75 mm)
lz (10): 0,28 mm (0,23 - 0,32 mm)
ho (10): 0,32 mm (0,23 - 0,37 mm)
lo (10): 0,15 mm (0,12 - 0,18 mm)

Distribution. - De l'Eocène supérieur au Miocène d'Europe.

Famille ONYCHOCELLIDAE Jullien, 1882

Genre SMITTIPORA Jullien, 1882

Smittipora? sp.

Pl. VII - Figs. 7-8.

Matériel. - 7 fragments.

Description. - Zoarium érigé, articulé, cylindrique, composé de 6 rangées longitudinales de zoécies séparées par un sillon à peine distinct.

Zoécies en forme de massue. Cadre périphérique étroit, légèrement surélevé.

Gymnocyste absent. Surface zoéciale concave profondément déprimée du côté opésial.

Opésie terminale oblongue, largement arrondie du côté distal.

Ovicelles et hétérozoécies non observés.

Dimensions: Lz (6): 0,56 mm (0,50 - 0,58 mm)
lz (6): 0,24 mm (0,23 - 0,25 mm)
ho (6): 0,23 mm
lo (6): 0,08 mm

Remarques. - Cette espèce est voisine de *Smittopora? sp.* Cheetham, 1966, elle présente le même nombre de rangées zoéciales cependant les zoécies sont plus élancées, le cryptocyste plus profond, l'opésie plus allongée et étroite.

Elle se rapproche également de *Smittipora midwayanica* Canu-Bassler, 1920, espèce à 8 rangées zoéciales et surtout de *Vincularia prismatica* (v. Hagenow) Berthelsen, 1962 par la forme de son opésie et ses mesures micrométriques. Cependant cette dernière possède un nombre de rangées zoéciales plus élevé.

Elle montre aussi de fortes affinités avec une espèce rencontrée dans les couches les plus inférieures de l' Eocène du Nord de l'Aquitaine, cependant dans ce dernier cas quelques spécimens ont permis l'observation d' hétérozoécies. Une description en sera donnée ultérieurement.

Famille PORINIDAE d'Orbigny, 1852

Genre PORINA d'Orbigny, 1852

Porina coronata (Reuss)

Pl. VIII - Figs. 17-19.

1847 *Cellaria coronata* REUSS, p. 62, pl. 8, fig. 3.
1869 *Acropora coronata* (Reuss) REUSS, p. 277, pl. 34, figs. 3-5.
1885 *Porina coronata* (Reuss) KOSCHINSKY, p. 42, pl. 4, figs. 7-9
1891 *Porina coronata* (Reuss) WATERS, p. 24, pl. 4, figs. 7-9.
1913 *Acropora coronata* (Reuss) CANU, p. 136, fig. 2.
1963 *Porina coronata* (Reuss) BRAGA, p. 30, pl. 3, figs. 14-15.

Matériel. - 50 fragments.

Remarques. - Les spécimens de la falaise de Handia ne se présentent jamais sous la forme cylindrique typique figurée par REUSS et la plupart des autres auteurs. WATERS en 1891 signale une grande variabilité de l'espèce spécialement dans la forme du zoarium, ceci n'a pu être vérifié, les rameaux sont toujours en frondes bilamellaires, comprimées avec des zoécies disposées en rangées régulières et alternes.

Le bombement péristomial n'est jamais observé.

Les aviculaires péristomiens sont généralement peu distincts à l'exception de celui dirigé distalement et situé immédiatement au-dessous de l'apertura. Les grands aviculaires à large mandibule signalés par WATERS sont plus rares mais existent sur tous nos spécimens. Ils occupent entièrement la surface zoéciale entre l'apertura et l'ascopore. Le rostre dirigé transversalement est fortement surélevé.

Les caractéristiques signalées ci-dessous sont très constantes et différencient cette forme de celle du Priabonien d' Italie identifiée par GP. BRAGA (3). Les différences observées justifieraient peut-être la création d'une variété ou d'une sous-espèce, nous hésitons cependant à le faire car une révision préalable des différentes formes de WATERS semble indispensable.

Dimensions: Lz (8): 0,61 mm (0,52 - 0,68 mm)
lz (8): 0,32 mm (0,31 - 0,37 mm)
ho (8): 0,15 mm (0,15 - 0,16 mm)

lo (8): 0,15 mm (0,13 - 0,17 mm)
L aviculaire: 0,35 mm
Ø ascopore: 0,07 mm, situé à 0,26 mm de l'orifice zoécial.

Distribution. - Eocène supérieur d'Europe.

Genre BEISSELINA Canu, 1913

Beisselina sp.

Pl. IX - Figs. 20-25.

Matériel. - Plus de 50 échantillons, souvent mal conservés.

Description. - Zoarium érigé, bilamellaire large de 1,5 à 2,5 mm avec des zoécies disposées alternativement et régulièrement en séries longitudinales qui deviennent transverses et obliques au niveau des bifurcations.

Limites zoéciales peu distinctes, soulignées parfois par la présence de petites pores. Péristomes importants raprochés sur les frondes calcifiées, plus petits et distants sur les branches moins épaisses.

Ascopore toujours assez volumineux occupe une position médiane entre les orifices zoéciaux voisins, se distingue très nettement en vue interne dans les spécimens brisés.

Petits pores de la frontale peu nombreux et souvent peu visibles ne peuvent généralement pas être identifiés avec certitude comme des aviculaires. Aviculaires frontaux multiples, polymorphes mais non observables régulièrement:

1. aviculaire au-dessus de l'orifice péristomial souvent immergé dans l'épaisseur de la frontale, plus rarement saillant;
2. aviculaires rares, petits, elliptiques dispersés sur la surface zoariale;
3. grands aviculaires accidentels.

Dimensions: Lz (5): 0,50 mm (0,47 - 0,52 mm)
lz (5): mesurée entre 2 ascopores: 0,25 mm
ho (5): 0,14 mm (0,13 - 0,15 mm)
Ø ascopore: 0,08 mm
Zoécies en vue interne:
Lz: 0,50 mm
lz: 0,26 mm

Remarques. - Nous ne pouvons pas identifier d'une façon certaine cette espèce comme *Eschara ampulla* d'Archiac, 1847. CANU l'a décrite et figurée à nouveau en 1910 en expliquant certaines variations. Il note en particulier la présence d'aviculaires qui n'ont pas été signalés par d'ARCHIAC. Plus spécialement il précise « il y a toujours un pore par zoécies » sous-entendant qu'il représente certainement un aviculaire. Il est probable que ce dernier corresponde à ce que nous appelons ascopore, cependant l'original? de d'ARCHIAC déposé à l'Ecole des Mines est loin d'être aussi bien conservé que le dit CANU et de ce fait aucun rapprochement valable n'est possible.

Nous sommes en présence d'une espèce très déconcertante par ses grandes variations ce qui est propre à toutes les *Beisselina*, cependant elle en diffère par sa pauvreté en aviculaires et par son gros ascopore toujours très distinctement visible.

Distribution. - Eocène de Biarritz.

Famille STOMACHETOSELLIDAE Canu & Bassler, 1917

Genre OCHETOSELLA Canu & Bassler, 1917

Ochetosella sp.

Pl. VIII - Figs. 15-16.

Matériel. - 10 fragments.

Description. - Zoarium libre cylindrique vraisemblablement bifurqué, formé de 6 ou 7 séries longitudinales de zoécies alternes.

Zoécies distinctes, séparées par un mince filet saillant, allongées, irrégulièrement hexagonales. Frontale légèrement convexe, modérément épaisse. Surface irrégulièrement mamelonnée, perforée de grosses aréoles pouvant former dans certains cas des costules périphériques proéminentes. Aréoles subcirculaires ou elliptiques.

Orifice invisible extérieurement profondément enfoncé dans le péristome épais, court, largement arrondi du côté distal, le bord proximal fortement saillant forme une sorte de large lèvre redressée légèrement sinueuse plus ou moins profondément entaillée. Aviculaire? oral arrondi sans pivot assez déjeté latéralement.

Ovicelle non observé.

Dimensions: Lz (8): 0,97 mm (0,88 - 1,12 mm)
lz (8): 0,48 mm (0,46 - 0,50 mm)
ho: difficilement mesurable
lo (8): 0,25 mm (0,22 - 0,28 mm)
Ø aviculaire: 0,10 mm

Remarques. - L'allure de la frontale avec ses épaississements interaréolaires peut faire penser que nous sommes en présence de branches assez âgées.

Cette espèce voisine de *O. jacksonica* Canu-Bassler, 1920 s'en différencie par des zoécies légèrement plus courtes. Comme dans cette dernière espèce le péristome est incomplet mais la lèvre inférieure apparaît plus large. D'autre part de très nombreuses zoécies sont pourvues d'un aviculaire voisin de celui rencontré chez *O. robusta* Canu-Bassler, 1920.

Famille TUBUCELLARIIDAE Busk, 1884

Genre TUBUCELLA Canu & Bassler, 1917

Tubucella canui n. sp.

Pl. X - Figs. 26-32.

?1846 *Pustulopora mamillata* D'ARCHIAC, p. 194, pl. 5, fig. 9.
?1862 *Porina confluens* ROEMER, p. 194, pl. 5, figs. 9a, b.
?1910 *Porina(?) mamillata* (d'Archiac) CANU, p. 847, pl. 17, figs. 7-9.
Origine du nom: en hommage au paléontologiste F. CANU.
Holotype: Coll. Br. N° 991 (Fac. des Sc. Bordeaux).
Paratypoïdes: 19 spécimens. Coll. Br. 992.
Localité-type: Biarritz: Falaise de Handia (échant. GA 18920).

Description. - Zoarium érigé, bilamellaire, cylindrique à aplati formé de branches dichotomes. Zoécies disposées plus ou moins régulièrement en rangées longitudinales et alternes avec un maximum de 6 rangées zoéciales sur chaque côté.

Zoécies allongées, indistinctes extérieurement. Suture péristomiale peu visible. Frontale modérément épaisse, plane ou faiblement convexe. Surface perforée de gros pores évasés. Ascopore légèrement plus gros que les autres pores frontaux, quelquefois légèrement saillant se confond le plus souvent avec eux.

Orifice petit, semi-circulaire, entièrement caché par le péristome. Péristome long, sessile sur la majorité de sa longueur, devient libre et saillant dans la portion distale. Surface péristomiale uniformément ponctuée de gros pores légèrement plus gros ou identiques à ceux de la frontale, parfois les pores marginaux deviennent très volumineux et la surface costulée. Orifice secondaire circulaire, petit.

Aviculaires frontaux ou marginaux multiples, polymorphes :

— 1 ou 2 aviculaires frontaux, arrondis ou triangulaires, plus rarement en forme de spatule et très grands, placés au niveau du péristome (indifféremment à droite ou à gauche lorsque l'aviculaire est unique, symétriquement lorsqu'ils sont doubles) en position presque interzoéciale ou très près de l'orifice zoécial. Rostre pointu ou largement arrondi dirigé transversalement vers l' intérieur, dans certains cas s'étend largement sur le péristome. Pivot transversal complet ou condyles visibles dans les aviculaires triangulaires, aucune structure apparente pour les aviculaires arrondis ;

— aviculaires marginaux sporadiques, très grands, placés sur la tranche des frondes, rostre pointu dirigé du côté proximal. Pivot transversal.

Ovicelle péristomial ; zoécie ovicellée à péristome très élargi, globuleux.

Dimensions : Zoécies.

Lz (8) : 0,96 mm (0,87 - 1,00 mm)
lz (8) : 0,28 mm (0,25 - 0,31 mm)
ho (8) : 0,12 mm (0,12 - 0,13 mm)
lo (8) : 0,12 mm (0,12 - 0,13 mm)

Aviculaires frontaux.

— En forme de spatule :

Laf (5) : 0,37 mm (0,35 - 0,40 mm)
laf (5) : 0,26 mm (0,25 - 0,27 mm)

— Triangulaires :

Laf (5) : 0,21 mm (0,18 - 0,27 mm)
laf (5) : 0,15 mm (0,12 - 0,18 mm)

— Arrondis :
Ø af (5) : 0,10 mm (0,09 - 0,11 mm)

Aviculaires marginaux.

Lam (3) : 0,58 mm (0,56 - 0,60 mm)
lam (5) : 0,30 mm (0,28 - 0,31 mm)

Remarques. - Cette espèce est très variable dans son aspect externe en particulier dans la disposition et l'allure des aviculaires, certaines zoécies peuvent en être totalement dépourvues. En vue interne les zoécies régulièrement alternes offrent une très grande régularité. La grosseur de l'ascopore le distingue parfaitement des autres pores frontaux, il se situe à environ 0,18 mm au-dessous de la ligne de suture péristomiale.

D'ARCHIAC en 1846 signale dans le Lutétien supérieur de la Goureppe une forme retrouvée plus tard par CANU en 1910 et classée sous le nom de *Porina(?) mamillata*. D'après les figurations de cet auteur il est vraisemblable que ce soit la même espèce que nous ayons à Handia. Malheureusement l'original de d'ARCHIAC a disparu et il n'a pas été possible de retrouver l'espèce dans la collection CANU. Il semble d'ailleurs qu'il y ait eu de la part de cet auteur confusion entre ascopore et aviculaire. Les grands aviculaires marginaux ne sont jamais signalés, mais CANU n'avait que peu d'échantillons. Il se peut également que ce soit la même forme signalée par ROEMER, mais sa description et figuration manquent de détails.

Deux autres *Tubucella* pourvues d'aviculaires mais très différentes ont été citées dans la littérature :

En 1991, WATERS sous le nom de *Porina(?) papillosa* (Reuss) décrit et figure une *Tubucella* avec aviculaires frontaux mais ces derniers se situent au-dessous de l'orifice zoécial.

Enfin, en 1929, CANU et BASSLER décrivent *Tubucella aviculifera*. Cette espèce du Lutétien belge, qui se retrouve dans l'Eocène moyen du Nord de l'Aquitaine est parfaitement bien caractérisée par ses aviculaires frontaux alternants.

Distribution. - Eocène de Biarritz.

Famille CHEILOPORINIDAE Bassler, 1936

Genre TETRAPLARIA Tenison-Woods, 1879

Tetraplaria sp.

Pl. VII - Figs. 9-12.

Matériel. - 6 fragments.

Description. - Zoarium cellariiforme. Internoeuds élancés toujours incomplets à section cruciforme, composés de 4 rangées zoéciales diamétralement opposées. Une double ouverture occupe l'extrémité proximale de l' internoeud, seule préservée dans les spécimens récoltés, constituée de la partie proximale très effilée des deux premières zoécies.

Zoécies adjacentes et alternes, en forme de massue, arrondies distalement, fortement rétrécies du côté proximal, bordées par un large filet.

Frontale très fortement convexe en forme de tête d'épingle. Surface perforée de nombreux pores subcirculaires, lisse dans la région située immédiatement au voisinage de l'orifice zoécial.

Orifice subcirculaire, plongeant vers l'axe du zoarium, semicirculaire du côté proximal largement arrondi distalement.

Ovicelle hyperstomial, globuleux légèrement allongé, également perforé.

Un seul exemplaire ovicellé.

Dimensions: Lz (4): 0,68 mm (0,62 - 0,75 mm)
lz (4): 0,26 mm (0,21 - 0,30 mm)
ho (4): 0,10 mm (0,08 - 0,11 mm)
lo (4): 0,12 mm
L ovicelle (1): 0,33 mm.

Remarques. - Cette espèce est très voisine de *T. petila* Cheetham, 1963. Cependant les deux petits tubercules oraux n'ont jamais été observés. La frontale est moins largement ponctuée et l'ovicelle apparaît plus allongé.

Une autre espèce très voisine est *Bigemellaria pedunculata* Mac Gillivray, 1895, l'auteur signale un sinus sur la lèvre inférieure qui apparaît beaucoup plus étroit.

Famille VITTATICELLIDAE Harmer, 1957

Genre DITAXIPORA Mac Gillivray, 1895

Ditaxipora labiata (Canu)

Pl. VII - Figs. 13-14.

1910 *Bactridium labiatum* CANU, p. 846, pl. 16, figs. 7-8.

Description. - Zoarium érigé, probablement articulé, composé d'internoeuds élancés, bisériés, formés au moins de 10 zoécies disposées alternativement; les orifices s'ouvrent sur une seule face. Ouverture unique circulaire à l'extrémité proximale. Extrémité distale non préservée.

Zoécies allongées, séparées par un sillon très distinct, bordées par un petit fil saillant, étroit du côté frontal, visible surtout sur les marges latérales et d'un large bourrelet du côté dorsal.

Frontale légèrement convexe, divisée en 2 compartiments légèrement déprimés par un système de crêtes saillantes un peu sinueuses en forme de T, la barre transversale est située immédiatement au-dessous de l'orifice.

Surface des dépressions latérales ponctuée. Pores frontaux circulaires souvent irrégulièrement distribués quoique dans certains cas ils peuvent s'aligner en 4 rangées longitudinales, 2 de part et d'autre de la crête médiane. Dorsale plane, surface perforée de 15 à 18 pores arrondis ou elliptiques irrégulièrement distribués.

Orifice presque terminal sur la frontale; le bord distal est très largement arrondi, le bord proximal souvent peu visible à peu près droit; une paire de petits condyles situés très bas généralement peu distincts.

Aviculaire frontal placé sur le bord externe des zoécies au niveau de l'orifice. Rostre court pointu dirigé distalement et légèrement vers l'extérieur. Pivot transversal.

Ovicelle non observé.

Dimensions: Lz (6): 0,44 mm (0,43 - 0,46 mm)
lz (6): 0,32 mm (0,31 - 0,33 mm)
ho (6): 0,09 mm (0,08 - 0,09 mm)
lo (6): 0,08 mm
L aviculaire (6): 0,12 mm (0,12 - 0,13 mm)

Remarques. - Les spécimens trouvés à Handia sont certainement identifiables à l'espèce *B. labiatum* Canu, 1910 bien que l'illustration donnée par cet auteur ne soit pas tout à fait suffisamment nette pour être très affirmatif.

Dans sa description, CANU ne signale pas en effet les crêtes frontales pourtant très visibles sur la majorité des échantillons récoltés, cependant, dans certains cas, la barre médiane longitudinale peut devenir presque invisible, seule persiste comme le signale d'ailleurs l'auteur une sorte de lèvre saillante immédiatement située au-dessous de l'orifice.

Les mesures qui ont été données coïncident avec celles que l'on peut relever sur la figuration de CANU.

Il est évident que cette espèce n'appartient pas au genre *Bactridium.* STACH en 1935 la classe dans le genre *Ditaxiporina* ainsi qu'une autre forme de l'Eocène du Bassin Aquitain, *Ditaxipora luteciana* Canu, 1913. Or ce genre est caractérisé par « the absence of median longitudinal band and by the fairly occurrence of avicularia on both sides of zooecia ».Ces 2 espèces semblent être mal placées dans ce genre. *Ditaxipora labiata* (Canu) présente de très grandes affinités avec l'espèce type *D. internodia* (Waters). Cette dernière possède des mesures micrométriques plus grandes quoique celles données plus tard par STACH soient plus faibles et très voisines de celles des spécimens de *B. labiatum* de Handia. Elle en diffère également par un compartimentage plus poussé et un nombre de pores frontaux et dorsaux moins grand.

Distribution. - Auversien de Biarritz.

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PLANCHE VII.

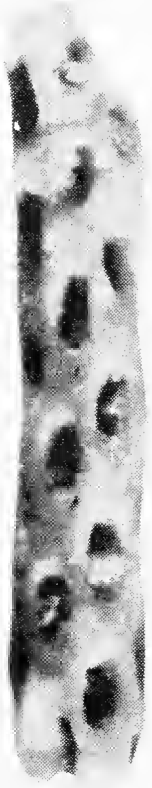
(Toutes les figures × 20)

Figs. 1-6. — *Crassimarginatella macrostoma* (Reuss). 1, échant. GA 18949, spécimen pseudovinculariiforme montrant un ovicelle. 2, échant. GA 18944, zoécies de régénération. 3, échant. 18949, vue frontale d'un spécimen avec ovicelles brisés. 4,5, échant. GA 18941, spécimens vinculariiformes. 6, échant. GA 18949, ? aviculaire.

Figs. 7-8. — *Smittipora? sp.* 7, échant. GA 7597, fragment assez mal conservé, chauffé et photographié sous une goutte d'eau. 8, échant GA 7591, spécimen montrant une zoécie bien conservée.

Figs. 9-12. — *Tetraplaria sp.* 9, 10, échant. GA 18919, extrémités proximales très effilées des internoeuds. 11, échant. GA 7597, zoécies normales montrant la surface zoéciale finement ponctuée. 12, échant. GA 7595, ovicelle sur un petit fragment.

Figs. 13-14. — *Ditaxipora labiata* (Canu). 13, échant. GA 18933, spécimen en vue frontale montrant les crêtes saillantes. 14, le même en vue dorsale.



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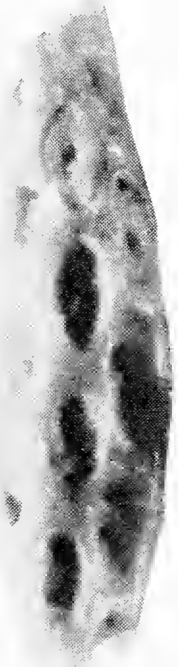

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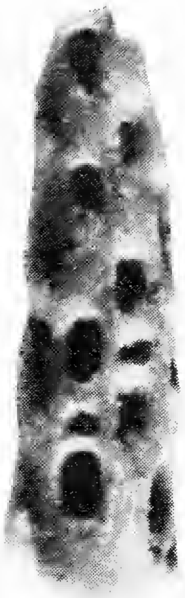

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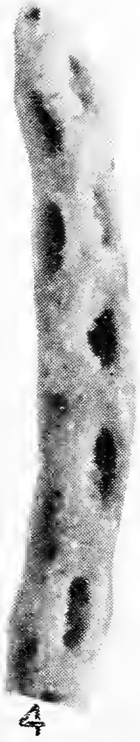

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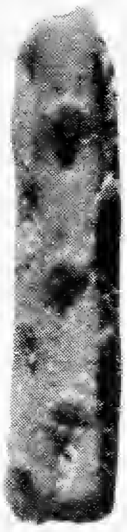

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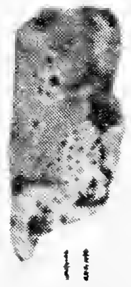

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PLANCHE VIII.

(Toutes les figures × 20)

Figs. 15-16. — *Ochetosella sp.* 15, échant. GA 18944, vue frontale d'un spécimen assez bien conservé montrant le gros aviculaire. 16, échant. GA 18938, spécimen montrant les costules périphériques saillantes.

Figs. 17-19. — *Porina coronata* (Reuss). 17, échant. GA 18920, extrémité distale. 18, échant. GA 18930, spécimen médiocrement préservé. 19, échant. GA 18936, vue frontale montrant les grands aviculaires à large mandibule et dans la région supérieure les aviculaires péristomiens.

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PLANCHE IX.

(Toutes les figures × 20)

Figs. 20-25. — *Beisselina sp.* 20, échant. GA 18921, surface zoariale montrant les petits aviculaires frontaux. 21, échant. GA 18949, spécimen montrant l'ascopore volumineux. 22, échant. GA 7597, aviculaire immergé au-dessus de l'orifice péristomial visible sur quelques zoécies. 23, échant. GA 18928, zoécies à péristomes petits et très saillants. 24, échant. GA 18924, fragment usé. 25, échant. GA 7597, vue interne de quelques zoécies montrant l'ascopore.


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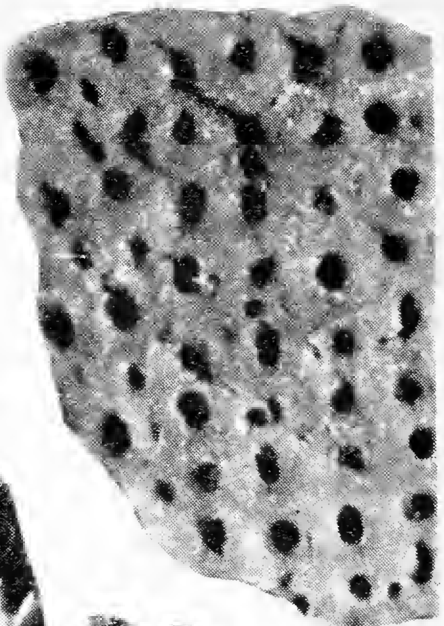
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PLANCHE X.

(Toutes les figures × 20)

Figs. 26-32. — *Tubucella canui n. sp.* 26, échant. GA 18920, spécimen à péristome peu saillant et à aviculaires frontaux arrondis. 27, échant. GA 18920, holotype. 28, échant. GA 7597, vue frontale montrant les grands aviculaires. 29, échant. GA 18942, spécimen montrant l'aviculaire marginal. 30, échant. GA 18920, holotype, aviculaire marginal. 31, échant. GA 18924, spécimen ovicellé. 32, échant. 18924, vue interne montrant l'ascopore.

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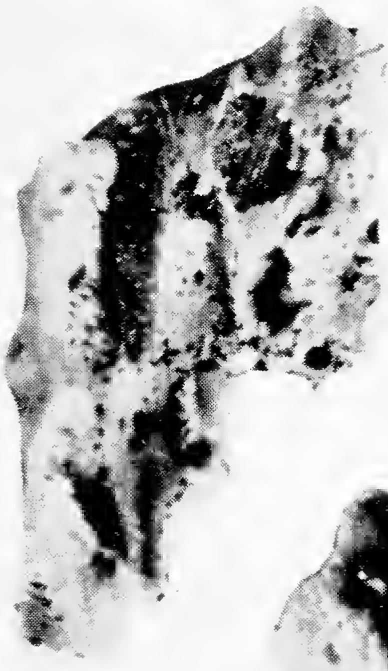

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Atti Soc. It. Sc. Nat. e Museo Civ. St. Nat. Milano - 108: 327-344, 31-XII-1968

1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
43. Group 5: Biogeography and Biostratigraphy.

LOUIS DAVID - NOËL MONGEREAU -
SIMONE POUYET (*) - S. RITZKOWSKI (**)

LES BRYOZOAIRES DU CHATTIEN DE LA REGION DE KASSEL

(HESSE - ALLEMAGNE)

Riassunto. — I Briozoi studiati provengono da 4 località situate nella regione di Kassel (Assia, Germania) e sono stati raccolti nella facies a sabbie marine di Kassel (« Kasseler Meeressand ») che rappresentano lo strato-tipo del Chattiano tedesco.

La parte sistematica comprende un elenco delle specie (7 *Cyclostomata* e 16 *Cheilostomata*), la loro diffusione in ogni località e la loro distribuzione stratigrafica.

Questa briofauna è presa a sostegno di alcune idee relative alla paleogeografia e alla paleoecologia del Golfo di Kassel.

Summary. — The studied *Bryozoa* are obtained from four localities situated in the area of Kassel (Hesse, Germany). They are been collected in the facies of « Kasseler Meeressand » representing the stratotype of the german Chattian.

The systematical part includes a list of species (seven *Cyclostomata* and sixteen *Cheilostomata*), their distribution in each locality as well as their stratigraphical distribution. This bryozoa's fauna shows some interesting ideas relating to the paleogeography and the paleoecology of the Kassel Gulf.

Zusammenfassung. — Die untersuchten Bryozoen stammen von 4 Lokalitäten der Umgebung von Kassel (Hessen, Deutschland). Sie wurden im

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« Kasseler Meeressand » aufgesammelt, der den Stratotyp des deutschen Chatts darstellt.

Der systematische Teil enthält eine Liste der Arten (7 *Cyclostomata*, 16 *Cheilostomata*), ihre Verteilung innerhalb jedes Vorkommens und ihre stratigraphische Verbreitung. Diese Bryozoen-Fauna liefert bemerkenswerte Anhaltspunkte für Paläogeographie und Palökologie des Kasseler Golfes.

I - Introduction.

Les assises ayant livré la faune de Bryozoaires ici étudiée sont celles du « Kasseler Meeressand » c'est à dire les assises-types du « Chattien » allemand (= Chattische Stufe) (W. HINSCH, 1958, p. 25). Il y a un intérêt stratigraphique certain à connaitre les associations de Bryozoaires rencontrés dans ces couches-types.

L'Oligocène supérieur du Nord de la Hesse a été révisé récemment du point de vue stratigraphique (S. RITZKOWSKI, 1965). Grâce en particulier à de nombreux sondages, les données classiques ont pu être complétées largement. Les Foraminifères et Ostracodes ont précisé la stratigraphie désormais établie sur des profils verticaux plus continus.

Les Bryozoaires recueillis par S. R. proviennent de quatre groupes de gisements, tous situés dans la région de Kassel (fig. 1):

1. - *Ahlberg*: sondage PREAG 2715, au SE d'Ahlberg (S. R., 1965, p. 96);
2. - *Ahnetal*: les assises du Kasseler Meeressand sont connues en affleurements et un sondage traverse le Rupélien sous-jacent (S. R., 1965, p. 100, fig. 22; 1967, p. 297, fig. 1);
3. - *Oberkaufungen*: sous ce nom sont rassemblés deux affleurements, l'un sur le versant ouest du Weinberg, l'autre sur le Gelber Berg près de Niederkaufungen (S. R., 1965, p. 112-114);
4. - *Glimmerode*: cette coupe intéresse les assises du Kasseler Meeressand sur 62 m d'épaisseur; les assises sont très riches en macro et microfossiles (S. R., 1965, p. 127, fig. 24; 1967, p. 319, fig. 10).

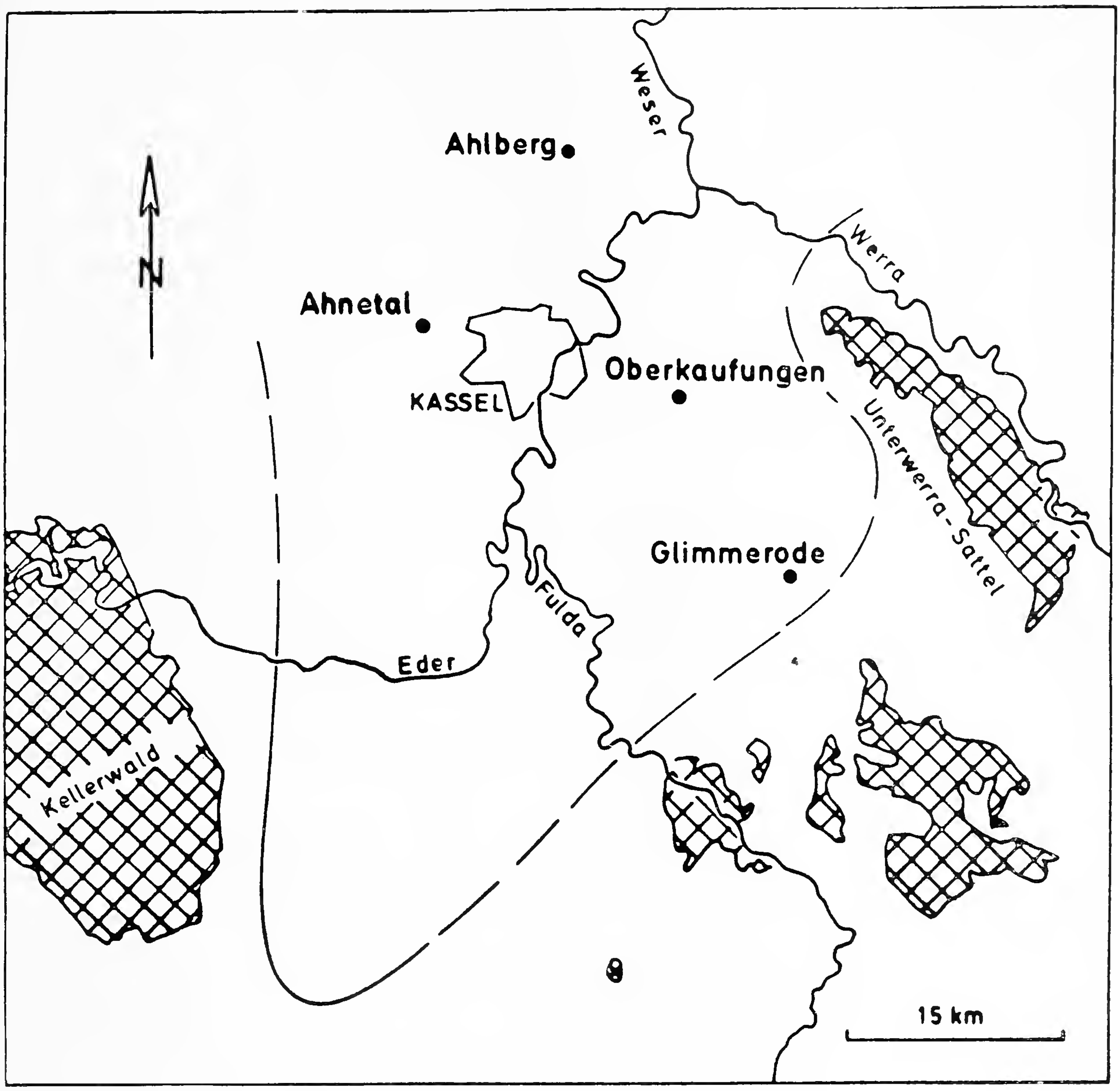

Fig. 1. — Situation des gisements étudiés avec indication approximative du rivage du golfe de Kassel.

On voudra bien se reporter à l'ouvrage de S. Ritzkowski, selon les références ci-dessus indiquées, pour avoir tous les détails nécessaires sur le plan de la stratigraphie et de la lithologie.

Les Bryozoaires oligocènes européens sont encore relativement mal connus. Les travaux les concernant sont pour la plupart anciens: ceux de R. A. Philippi, de A. E. Reuss, de F. A. Roemer et de F. Stoliczka datent de 1843 à 1867. Plus récentes sont les études de K. HUCKE et E. VOIGT (1929), de F. FRANKE (1939), E. DARTEVELLE (1952) et de G. BRAGA (1966).

Deux d'entre nous (L. D. et S. P., 1968) ont donné une étude paléontologique particulière de quelques Cheilostomes jusqu'à présent mal connus.

Les Bryozoaires déterminés dans le Kasseler Meeressand seront donc présentés ci-après sous la forme d'une simple liste systématique ne comprenant ni synonymie, ni description. Chaque espèce est présentée en suivant la classification de R. S. BASSLER (*in* Treatise of Invertebrate Paleontology, part G, 1953) avec indication du nombre d'échantillons triés et déterminés dans chaque prélèvement.

II - Liste systématique (*).

Ordre CYCLOSTOMATA Busk, 1852

A - Sous-ordre ARTICULATA Busk, 1859

Famille *Crisiidae* Johnston, 1847

Crisia sp.

Un seul échantillon indéterminable spécifiquement.

Localité :

Glimmerode :

— 57 à 58 m (FSL n° 19935)

B - Sous-ordre TUBULOPORINA Milne-Edwards, 1838

Famille *Tubuliporidae* Johnston, 1838

Bitubigera biseriata (Philippi, 1843)

Localités :

Ahlberg, sondage PREAG 2715 :

— 44 à 45 m (FSL n° 19902, 1 échantillon)

— 45 à 46 m (FSL n° 19903, 1 éch.)

(*) Les échantillons conservés à la Faculté des Sciences de Lyon sont désignés par FSL suivi du nombre de l'inventaire général des collections du Département des Sciences de la Terre. Le symbole GAU désigne les échantillons conservés au « Geologisch-Paleontologisches Institut der Georg-August-Universität » de Göttingen. (Orig. Nr. 632).

Ahnetal, affleurement 1:
(FSL n° 19901, 1 éch. et GAU n° 632-1, 1 éch.)

Glimmerode:
- 57 à 58 m (FSL n° 19898, 1 éch. et GAU n° 632-2, 1 éch.)
- 80,5 à 81 m (FSL n° 19899, 1 éch.)
- 81,5 à 82 m (FSL n° 19900, 1 éch.)

Famille *Entalophoridae* Reuss, 1869

Entalophora macrostoma (Milne-Edwards, 1838)

Localités:

Ahlberg, sondage PREAG 2715:
- 40 à 41 m (FSL n° 19932, 3 éch)
- 45 à 46 m (FSL n° 19933, 1 éch.)

Ahnetal, affleurement 4:
(FSL n° 19934, 1 éch.)

Glimmerode:
- 48 à 49 m (FSL n° 19924-19925-19926, 30 éch. et GAU n° 632-3, 10 éch.)
- 53 à 54 m (FSL n° 19927-19928, 2 éch.)
- 57 à 58 m (FSL n° 19929-19930, 9 éch.)
- 81,5 à 82 m (FSL n° 19931, 2 éch.)

C - Sous-ordre CANCELLATA Gregory, 1896

Famille *Horneridae* Gregory, 1899

Hornera biseriata Philippi, 1843

Localités:

Ahlberg, sondage PREAG 2715:
- 40 à 41 m (FSL n° 19910, 1 éch.)
- 44 à 45 m (FSL n° 19911, 1 éch.)
- 45 à 46 m (FSL n° 19912, 1 éch.)

Glimmerode:
- 48 à 49 m (FSL n° 19907, 1 éch.)
- 53 à 54 m (FSL n° 19908, 1 éch. et GAU n° 632-4, 1 éch.)
- 80,5 à 81 m (FSL n° 19909, 2 éch.)

Hornera concatenata Reuss, 1868

Localités :

Ahlberg, sondage PREAG 2715 :
— 30 à 31 m (FSL n° 19920, 1 éch.)
— 40 à 41 m (FSL n° 19921, 6 éch. et GAU n° 632-5, 3 éch.)
— 45 à 46 m (FSL n° 19923, 11 éch.)

Glimmerode :
— 33,5 à 34 m (FSL n° 19913, 3 éch.)
— 48 à 49 m (FSL n° 19914, 24 éch.)
— 49 à 50 m (FSL n° 19915, 25 éch.)
— 49 à 50 m (FSL n° 19915, 25 éch.)
— 53 à 54 m (FSL n° 19916, 19 éch.)
— 57 à 58 m (FSL n° 19917, 12 éch.)
— 80,5 à 81 m (FSL n° 19918, 4 éch.)
— 81,5 à 82 m (FSL n° 19919, 2 éch.)

Hornera tortuosa Roemer, 1863

Localités :

Ahlberg, sondage PREAG 2715 :
— 40 à 41 m (FSL n° 19896, 1 éch.)
— 45 à 46 m (FSL n° 19897, 1 éch.)

Glimmerode :
— 33,5 à 34 m (FSL n° 19891, 4 éch.)
— 48 à 49 m (FSL n° 19892, 2 éch.)
— 49 à 50 m (FSL n° 19893, 2 éch.)
— 53 à 54 m (FSL n° 19894, 4 éch.)
— 57 à 58 m (FSL n° 19895, 11 éch. et GAU n° 632-6, 4 éch.)
— 81,5 à 82 m (FSL n° 19904, 1 éch.)

Famille *Petaloporidae* Gregory, 1899

Reteporidea cancellata (Goldfuss, 1826)

Localités :

Ahlberg, sondage PREAG 2715 :
— 45 à 46 m (FSL n° 19906, 1 éch. et GAU n° 632-7, 2 éch.)

Glimmerode :
— 48 à 49 m (FSL n° 19905, 3 éch.)

Ordre CHEILOSTOMATA Busk, 1852

A - Sous-ordre ANASCA Levinsen, 1902

Division Malacostega Levinsen, 1902

Famille *Membraniporidae* Busk, 1854

Biflustra osnabrugensis Reuss, 1864

Localités :

Ahlberg, sondage PREAG 2715 :
- 44 à 45 m (FSL n° 130023, 2 éch.)

Glimmerode :
- 53 à 54 m (GAU n° 632-8, 1 éch.)
- 80,5 à 81 m (GAU n° 632-9, 1 éch.)
- 81,5 à 82 m (FSL n° 130024, 3 éch.)

Division Coilostega Levinsen, 1902

Famille *Lunulitidae* Lagaaij, 1952

Lunulites subplena Reuss, 1855

A part quelques rares spécimens entiers, nous avons trouvé de nombreux fragments à Ahlberg et Ahnetal où l'espèce constitue à elle seule la presque totalité des Bryozoaires récoltés.

Localités :

Ahlberg, sondage PREAG 2715 :
- 26 à 27 m (GAU n° 632-10)
- 30 à 31 m (GAU n° 632-11)
- 36 à 37 m (FSL n° 130030)
- 40 à 41 m (FSL n° 130031, 2 éch. et GAU n° 632-12)
- 44 à 45 m (GAU n° 632-13, 3 éch.)

Ahnetal, affleurement 1 (FSL n° 130025-130026 ; 130064)
affleurement 4 (FSL n° 130027-130028 et GAU n° 632-14)
sondage :
- 0,20 à 0,70 m (FSL n° 130029)
- 0,75 à 1,20 m (GAU n° 632-15)
- 1,10 à 1,50 m (GAU n° 632-16)

Oberkaufungen, Gelber Berg (GAU n° 632-17)
Weinberg (FSL n° 130032 et GAU n° 632-18)
(très nombreux échantillons dans tous les gisements).

Famille *Steginoporellidae* Bassler, 1952

Steginoporella elegans (Milne-Edwards, 1836)

Cette espèce n'existe pas dans les sondages, elle est très fragile et nous n'avons que 5 échantillons.

Localités :

Ahnetal, affleurement 4 (FSL n° 130033-130034, 3 éch. et GAU n° 632-19, 2 éch.)

Division Pseudostega Levinsen, 1909

Famille *Cellariidae* Hincks, 1880

Cellaria fistulosa Auct.

Localités :

Ahnetal, affleurement 4 (FSL n° 130035, 1 éch. et GAU n° 632-20, 1 éch.)

Glimmerode :

— 48 à 49 m (FSL n° 130036, 4 éch.)
— 53 à 54 m (GAU n° 632-21, 2 éch.)
— 80,5 à 81 m (FSL n° 130037, 1 éch. et GAU n° 632-22, 5 éch.)

B - Sous-ordre ASCOPHORA Levinsen, 1909

Famille *Hippoporinidae* Bassler, 1935

Hipposera formosa (Duvergier, 1923)

Localités :

Glimmerode :

— 48 à 49 m (GAU n° 632-23, 15 éch.)
— 49 à 50 m (FSL n° 130050-130051, 6 éch.)
— 80,5 à 81 m (FSL n° 130052, 1 éch.)

Famille *Mucronellidae* Levinsen, 1902

Smittina diplostoma (Philippi, 1843)

Localités :

Glimmerode :

— 49 à 50 m (FSL n° 130053-130069, 2 éch. et GAU n° 632-24, 2 éch.)

Smittina sp.

Une dizaine de frangments bilamellaires, difficiles à rattacher à une espèce connue.

Localités :

Glimmerode :

— 48 à 49 m (GAU n° 632-25, 1 éch.)
— 49 à 50 m (FSL n° 130054, 130066, 130067, 5 éch.)
— 53 à 54 m (FSL n° 130055, 1 éch.)
— 57 à 58 m (GAU n° 632-26, 2 éch.)

Reussia regularis (Reuss, 1866)

Localités :

Glimmerode :

— 48 à 49 m (FSL n° 130047, 130048, 130068, 10 éch.)
— 57 à 58 m (FSL n° 130049, 1 éch.)

Famille *Reteporidae* Smitt, 1867

Sertella sp.

Spécimens de petite taille indéterminables spécifiquement.

Localités :

Glimmerode :

— 53 à 54 m (GAU n° 632-27, 2 éch.)
— 57 à 58 m (GAU n° 632-28, 1 éch.)

Famille *Tubucellariidae* Busk, 1884

Tubucellaria sp.

Deux fragments de zoaria ne comprenant chacun que quelques zoécies. Il s'agit peut-être de *T. cereoides* (Ellis et Solander, 1786) mais il faudrait trouver d'autres spécimens pour pouvoir l'affirmer avec certitude.

Localité :

Glimmerode :

— 48 à 49 m (FSL n° 130056, 2 éch.)

Famille *Adeonidae* Jullien, 1903

Adeonellopsis subteres (Roemer, 1863)

Localités :

Glimmerode :

— 48 à 49 m (FSL n° 130043, 2 éch.)
— 49 à 50 m (FSL n° 130044, 5 éch.)

— 53 à 54 m (FSL nº 130045, 6 éch.)
— 57 à 58 m (GAU nº 632-29, 8 éch.)
— 80,5 à 81 m (FSL nº 130046, 1 éch., 130063, 1 éch.)
— 81,5 à 82 m (GAU nº 632-30, 5 éch.)

Bracebridgia polymorpha (Reuss, 1864)

Localités :

Ahlberg, sondage PREAG 2715 :
— 40 à 41 m (FSL nº 130038, 130065, 2 éch. et GAU nº 632-31, 1 éch.)
— 44 à 45 m (FSL nº 130039, 3 éch.)
Ahnetal, sondage :
— 0,75 à 1,20 m (GAU nº 632-32, 1 éch.)
Glimmerode :
— 49 à 50 m (FSL nº 130040, 4 éch.)
— 53 à 54 m (GAU nº 632-33, 2 éch.)
— 81,5 à 82 m (FSL nº 130041, 1 éch.)

Meniscopora brongniarti (Milne-Edwards, 1836)

Localités :

Glimmerode :
— 49 à 50 m (FSL nº 130042, 1 éch. et GAU nº 632-34, 1 éch.)
— 57 à 58 m (GAU nº 632-35, 2 éch.)

Famille *Myriozoidae* Smitt, 1867

Myriapora truncata (Pallas, 1766)

Localités :

Glimmerode :
— 48 à 49 m (GAU nº 632-36, 5 éch.)
— 49 à 50 m (FSL nº 130057, 3 éch.)
— 57 à 58 m (GAU nº 632-37, 1 éch.)

C - INCERTAE SEDIS

« *Eschara* » *fissimargo* Reuss, 1866

N'ayant trouvé qu'un seul spécimen avec sept cellules non ovicellées, il est impossible pour l' instant d' intégrer cette espèce dans un genre de Cheilostomes.

Localité :

Glimmerode :

— 81,5 à 82 m (FSL n° 130058, 1 éch.)

« *Eschara* » *wittei* Reuss, 1864

Nous avons de nombreux fragments de zoaria. Là encore, les ovicelles sont absentes d'où la difficulté de classer génériquement cette espèce.

Localités :

Glimmerode :

— 33,5 à 34 m (GAU n° 632-38, 2 éch.)
— 48 à 49 m (FSL n° 130059, 7 éch.)
— 49 à 50 m (GAU n° 632-39, 7 éch.)
— 53 à 54 m (GAU n° 632-40, 3 éch.)
— 57 à 58 m (FSL n° 130060, 3 éch.)
— 80,5 à 81 m (FSL n° 130061, 3 éch.)
— 81,5 à 82 m (FSL n° 130062, 1 éch. et GAU n° 632-41, 3 éch.)

III - Conclusions.

A - REPARTITION PAR GISEMENT

Nous donnerons d'abord les listes de répartition des espèces pour chaque gisement ici étudié.

AHLBERG :
Bitubigera biseriata
Entalophora macrostoma
Hornera biseriata
Hornera concatenata
Hornera tortuosa
Reteporidea cancellata
Biflustra osnabrugensis
Lunulites subplena
Bracebridgia polymorpha

AHNETAL :
Bitubigera biseriata
Entalophora macrostoma
Lunulites subplena

Steginoporella elegans
Cellaria fistulosa
Bracebridgia polymorpha

OBERKAUFUNGEN :
Weinberg : *Lunulites subplena*
Gelber Berg : *Lunulites subplena*

GLIMMERODE : *Crisia* sp.
Bitubigera biseriata
Entalophora macrostoma
Hornera biseriata
Hornera concatenata
Hornera tortuosa
Reteporidea cancellata
Biflustra osnabrugensis
Cellaria fistulosa
Hipposera formosa
Smittina diplostoma
Smittina sp.
Tubucellaria sp.
Adeonellopsis subteres
Bracebridgia polymorpha
Meniscopora brongniarti
Myriapora truncata
« *Eschara* » *fissimargo*
« *Eschara* » *wittei*

Nous constatons d'abord que *Lunulites subplena* est l'espèce la plus abondante dans les trois gisements proches de Kassel mais qu'elle manque totalement à Glimmerode. Ce fait pourrait être dû à la proximité du rivage pour cette dernière localité mais nous verrons que tous les Bryozoaires ont été entraînés par les courants avant fossilisation.

La présence de *Steginoporella elegans* en un seul point traduit simplement l'extrême fragilité des zoaria.

Le gisement de Glimmerode est donc le plus riche en espèces ; il n'y a pratiquement aucune différence significative avec Ahlberg ou avec Ahnetal qui sont plus pauvres. Il n'est pas possible de chercher un parallélisme des assises les unes avec les autres : la faune est hcmogène et il convient de la considérer dans son ensemble.

B - BIOSTRATIGRAPHIE

Le tableau ci-après donne la répartition stratigraphique connue des espèces déterminées :

	Liste des espèces	Eocène	Oligocène	Miocène	Pliocène	Quaternaire	Actuel
I	Cellaria fistulosa		▬	▬	▬	▬	▬
	Myriapora truncata	▬	▬	▬	▬	▬	▬
II	Hornera concatenata	▬	▬				
	Bracebridgia polymorpha	▬	▬				
	Meniscopora brongniarti	▬	▬				
	Adeonellopsis subteres	▬	▬				
	Steginoporella elegans	▬	▬	▬			
	Entalophora macrostoma	▬	▬	▬			
	Reteporidea cancellata	▬	▬	▬			
III	Reussia regularis		▬	▬			
	Hipposera formosa		▬	▬			
IV	Bitubigera biseriata		▬				
	Hornera biseriata		▬				
	Hornera tortuosa		▬				
	Biflustra osnabrugensis		▬				
	Lunulites subplena		▬				
	Smittina diplostoma		▬				
	« Eschara » fissimargo		▬				
	« Eschara » wittei		▬				

Fig. 2. — Tableau de répartition stratigraphique des espèces.

Les deux espèces du groupe I ont une large répartition stratigraphique et sont encore vivantes. Sur le plan stratigraphique, elles n'apportent rien mais seront utiles pour la paléoécologie.

Les quatre premières espèces du groupe II sont connues de l'Eocène.Oligocène de divers bassins d'Europe occidentale. Comptetenu de l' imprécision des connaissances sur les faunes de Bryozoaires, elles confirment l'âge oligocène. Les trois autres sont signalées jusqu'au Miocène supérieur mais leur répartition est centrée autour de l'Oligocène.

Dans le groupe III, les deux espèces sont connues de l'Oligocène et du Miocène d'Europe. L'une d'elles, *Hipposera formosa*, a été décrite dans l'Aquitanien d'Aquitaine et devient ainsi représentée dans l'Oligocène d'Allemagne. On peut considérer que la coexistence de ces espèces et de celles du groupe précédent est la plus sûre confirmation de l'âge oligocène.

Enfin, les huit espèces du groupe IV sont particulières à l'Oligocène d'Allemagne et n'ont pas encore été retrouvées ailleurs. Elles n'ont aucun intérêt stratigraphique immédiat. Ces formes propres au golfe de Kassel sont des espèces ou des sous-espèces géographiques dont on ne connait pas encore les relations réelles avec les espèces des autres domaines marins proches (atlantique aquitanien ou méditerranée par exemple). Il n'est cependant pas nécessaire de faire intervenir à leur propos un phénomène d'endémisme tant que l'évolution des faunes de Bryozoaires ne sera pas connue avec précision.

En résumé, les Bryozoaires du « Kasseler Meeressand » n'apportent pour l' instant aucune véritable précision stratigraphique sur les terrains qui les renferment. Par contre leur connaissance dans les assises-types du Chattien servira de base à des comparaisons ultérieures avec les faunes d'autres bassins oligocènes européens. A titre d'exemple, on a souvent admis que les couches chattiennes de Kassel étaient de même âge que les faluns de Labrède (Aquitanien inférieur) d'Aquitaine (cf. G. DENIZOT, 1957, p. 54, 97): les faunes de Bryozoaires sont nettement différentes ce qui exclut un âge identique ou bien traduit un long isolement géographique. Un tel problème serait à revoir à l'aide d'autres organismes et d'études plus détaillées.

C - PALEOECOLOGIE ET PALEOGEOGRAPHIE

L'ensemble des Bryozoaires recueillis se trouve dans des roches de faciès détritique relativement fin; leur fossilisation traduit une thanatocénose avec transport certain. Il ne faut donc rien attendre de la localisation des gisements fossilifères. Toutes les observations qui suivent sont valables pour le golfe de Kassel dans son ensemble sans qu'on puisse apporter des détails à l'intérieur.

Les premières déductions peuvent être tirées de l'étude des rares espèces encore vivantes:

Cellaria fistulosa est une espèce cosmopolite, sténobathe superficielle, vivant de préférence sur les fonds meubles de type sableux. Son optimum de fréquence se situe entre 30 et 80 m de profondeur.

Myriapora truncata est une espèce méditerranéenne, très abondante de 1 m à 130 m avec maximum sur les fonds coralligènes entre 30 et 60 m. Elle se rencontre aussi en Atlantique, à faible profondeur, près des côtes d'Espagne et du Maroc. Il est étonnant qu'une telle espèce se rencontre dans un golfe dépendant de l'Atlantique septentrional; il faut remarquer cependant qu'elle a déjà été citée dans le Pliocène des Pays-Bas ce qui conduirait à admettre une vaste répartition au Tertiaire suivie d'une régression (ou migration) durant le Quaternaire.

Rien ne laisse supposer la moindre dessalure de la mer: tous les groupes présents sont ceux qui, dans la nature actuelle, sont sténohalins.

Le classement des échantillons d'après les critères de forme zoariale mis au point finalement par M. LABRACHERIE et J. PRUD'HOMME (1966) montre que la quasi totalité de la faune est composée de *colonies dressées*, rigides ou flexibles, auxquelle s'ajoutent les seuls types lunulitiformes. L'absence de formes encroûtantes ou unilamellaires confirme l'existence prédominante de la biocénose coralligène. Il ne faut cependant pas oublier que la dispersion des gisements fossilifères et leur caractère de thanatocénose peut cacher une sélection mécanique *post-mortem* des Bryozoaires par les courants.

Sans éliminer la possibilité d'autres biotopes à Bryozoaires, on peut raisonnablement admettre la prédominance de la *biocénose coralligène* installée soit sur un substrat rocheux, soit plus probablement sur un fond meuble concrétionné.

En examinant la carte de répartition du substratum du « Kasseler Meeressand » (S. R. 1965, p. 77, fig. 19), on voit que le Trias a pu jouer le rôle de substrat rocheux au début de l' invasion marine. Par la suite, les fonds rocheux ayant peu à peu disparu, les zones sableuses avec coquilles et débris de coquilles ont été concrétionnés par les Algues, Bryozoaires ... et ont servi de support à la biocénose coralligène.

Sur les fonds détritiques côtiers vivaient sans doute les *Cellaria* qui se rencontrent aussi dans la biocénose coralligène; sur les fonds sableux, même instables, devaient vivre les *Lunulites* en grande abondance.

En résumé, le golfe de Kassel, durant le Chattien, devait être largement ouvert sur l'Océan Atlantique; sa profondeur ne devait guère excéder 100 m. En dehors de la zone littorale peu profonde, l'étage circalittoral comprenait des fonds meubles parfois biologiquement concrétionnées pour permettre l' installation de biocénoses coralligènes qui, ailleurs, étaient installées sur des fonds rocheux (ex. Trias). La profondeur de ces faciès à Bryozoaires devait être de 30 à 50 m environ, avec éclairement réduit (végétaux sciaphiles). La salinité devait être normale et les courants très faibles. De temps en temps, des courants plus violents mettaient fin à l'existence des biocénoses coralligènes, arrachant les colonies de Bryozoaires et les répartissant avec les particules détritiques dans les gisements qui sont les leurs aujourd'hui.

Ceci représente une vision synthétique, autrement dit « moyenne » de la paléoécologie et de la paléogéographie du golfe de Kassel. Ceci n'a donc aucune valeur absolue et seules de longues études détaillées pourraient permettre de mieux saisir le détail de la géographie du golfe à chaque moment de l' histoire du Chattien.

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FIRST FOSSIL FINDS OF SIX GENERA OF *BRYOZOA CHEILOSTOMATA*

Riassunto. — I generi *Cothurnicella, Crepis, Beania, Synnotum, Pasythea* e *Savignyella* (e le quattro famiglie corrispondenti *Cothurnicellidae, Beaniidae, Epistomiidae* e *Savignyellidae*) non erano stati finora descritti come fossili.

Le fotografie delle specie in questione, una tavola di distribuzione e carte della diffusione recente e fossile nel mondo di qualcuno di tali generi documentano queste scoperte e le loro implicazioni.

Appare da queste carte che la diffusione circumtropicale recente dei generi *Cothurnicella, Synnotum* e fors'anche di altre forme articolate di piccola taglia, non può essere spiegata come conseguenza di un trasporto a grande distanza da parte delle navi nei tempi storici, ma è il risultato di una diffusione così estesa osservabile già nel Miocene.

Summary. — The genera *Cothurnicella, Crepis, Beania, Synnotum, Pasythea* and *Savignyella* (and four of the corresponding families, viz. *Cothurnicellidae, Beaniidae, Epstomiidae* and *Savignyellidae*) have not previously been reported as fossils. Photographs of the fossil specimens concerned, a range chart, and maps of the Recent and fossil distribution of some of these genera on a global scale serve to document these new finds and their implication.

It appears from these maps that the circumtropical Recent distribution of the genera *Cothurnicella, Synnotum* and perhaps other small-sized jointed forms as well is not to be explained by long-distance transport on ships in historical times, as has sometimes been advanced, but has been inherited from an equally wide distribution in the Miocene.

(*) B.I.P.M. (Bataafse Internationale Petroleum Maatschappij N. V.) - 's-Gravenhage, The Netherlands.

Résumé. — Les genres *Cothurnicella, Crepis, Beania, Synnotum, Pasythea* et *Savignyella* (et quatre des familles correspondantes, viz. *Cothurnicellidae, Beaniidae, Epistomiidae* et *Savignyellidae*) n'ont pas été décrits comme fossiles auparavant. Des photographies des espèces en question, un tableau d'extension et des cartes de distribution récente et fossile de quelques uns de ces genres à l'échelle du globe, documentent ces nouvelles découvertes et leurs implications.

Il ressort de ces cartes, que la distribution circumtropicale récente des genres *Cothurnicella, Synnotum* et peut-être aussi d'autres formes articulées de petite taille, ne doit pas être expliquée, comme cela a parfois été le cas, par un transport à longue distance sur bateau durant les temps historiques, mais résulte d'une distribution tout aussi étendue observable au Miocène déjà.

Introduction.

The bryozoan fossils dealt with in this paper are all characterized by their small size. This is no mere coincidence. They all belong to forms which in the living state either formed articulated colonies, with internodes consisting of one to a few zooecia each connected by chitinous joints and with a radiculate or stolonate base (*Cothurnicella, Synnotum, Pasythea* and *Savignyella*), or formed a system of loosely incrusting single zooecia interconnected by tubular connections (*Crepis, Beania*). Both zoarial types are consistent with growth on perishable non-calcareous algal substrates or on higher marine plants, and the dead colonies are liable to fall apart into their individual components (internodes, triads, axial kenozooecia, disconnected autozooecia) before burial in the sediment. In the process of washing and sieving such sediment for microfaunal analysis, these small fossils are concentrated in the finer sieve fractions ($< 450\ \mu$).

Cothurnicella.

Cothurnicella was introduced in 1858 by Wyville Thompson for the highly characteristic delicate Recent species *Cellaria pyriformis* Bertoloni, 1810. No other species have been referred to *Cothurnicella*, which has thus remained a monotypical genus until the present day.

Three Lower Miocene records of *Cothurnicella pyriformis*, one from Aquitaine, France, the two others from East Java and

Madura, Indonesia, have recently been published elsewhere (LAGAAIJ, 1968). The map of the Recent and fossil distribution of this species issued on that occasion is reproduced here (fig. 1), with the addition of two new fossil records, viz.

a) From a dark-coloured clay underlying the yellow Point Addis Limestone on the W side of Point Addis, Victoria, Australia, i.e. from the basal part of the Oligocene Jan Juc Formation (Faunal Unit 4 of CARTER, 1964, pp. 42, 53). 1 specimen (Pl. XI, fig. 4). R. J. FOSTER ded.; and

b) from the Miocene Montserrat glauconitic Sandstone Member, Manzanilla Formation, San José River, Trinidad, W. I. Sample Du 21, collected by Mr. R. DUBEY. Numerous specimens.

However incomplete this map may be, it is evident that the wide Recent distribution of *C. pyriformis* in the tropical-warm temperate latitudes was already established in Mid-Tertiary times.

These records, however, do not constitute the oldest known occurrence of the genus, since a considerably older occurrence

Fig. 1. — World distribution of *Cothurnicella pyriformis* (BERTOLONI).

in the Upper Eocene of Cuba has come to my notice. The specimens concerned were found in a sample, B.322, from the Jabaco Formation, collected by Dr. P. J. BERMUDEZ 1 km S. of ingenio Saratoga, Matanzas Province, Cuba (see BERMUDEZ, 1950, p. 248).

The two available specimens (Pl. XI, figs. 7-10) are approximately twice the size of those of *C. pyriformis*. The differentiation in « head » and « tail » portions is less pronounced, and the point of attachment for the distal zooecium is situated slightly more proximally, but the general habit is entirely that of the genus. The zooecia are strongly compressed laterally, and the convex (dorsal) side has a sharp, almost keeled, edge, as in *C. pyriformis*. Of interest is the presence of three pairs of opesiules in this early form (Pl. XI, fig. 7).

The material in hand is too scanty to serve as the basis for the introduction of a new species, but it does establish the known range of the genus *Cothurnicella* and of the family *Cothurnicellidae* as Upper Eocene - Recent.

Crepis.

The genus *Crepis* was introduced by JULLIEN (1883, p. 523) for a uniserial deep-water species, *C. longipes*, incrusting on rock fragments dredged from 1068 and 2018 m off northern Portugal. Specimens identified as belonging to the same species were subsequently found in shallow water on hydroid and bryozoan substrates near New Guinea (29 m), Singapore (6-7 fms) and Port Darwin (HARMER, 1926, p. 318), and in the Malacca Straits (35 m) (SILÉN, 1941, p. 69). Two other Recent species, *C. verticillata* HARMER and *C. decussata* HARMER, are on record from east Indonesian and north Australian waters.

The fossil specimens of *Crepis* in my possession come from a hand-auger sample, h7 (5 m), from the Lower Miocene (Tertiary e_5) Tuban Formation, Prupuh, East Java, Indonesia (1).

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(1) For the stratigraphical position with respect to the planktonic foraminiferal zonation of this and other Indonesian samples referred to in the following pages reference is made to VAN DER VLERK & POSTUMA (1967, Table I).

Only single zooecia have been found (Pl. XII, figs. 1-2). They taper proximally and presumably were originally arranged in a linear series (lateral communication pores are lacking), the narrow tubular connecting parts having been broken off. They are being referred to *Crepis*, and not, for example, to *Pyripora*, on account of their well-developed proximal cryptocyst. Yet the fossils are not quite identical with the Recent type species. I have had an opportunity to compare them with a specimen of *Crepis longipes* from Singapore (29.9.13.82) in the British Museum (Natural History) and have noted that they are slightly larger and that the distal progression of their cryptocyst is distinctly less advanced, resulting in a larger opesia. They are therefore probably best referred to provisionally as *Crepis* aff. *longipes*. They are associated with an assemblage originating in shallow water.

This find establishes the known range of the genus as Lower Miocene - Recent.

Beania.

The genus *Beania* JOHNSTON, 1840, has not, to my knowledge, been previously reported as a fossil (see BASSLER, 1953, p. 182). Moreover, the *Beaniidae* rank among the 13 families of *Cheilostomata* of which no fossil representatives are known (LARWOOD, 1967, p. 390). A possible exception must be made for the record of *Stolonella* sp. from the Eocene of the Ludon well, given by LABRACHERIE (1961, p. 47, pl. II, fig. 8). At any rate, the following finds provide convincing evidence that *Beania* already existed in the Eocene of the Caribbean province.

Beania bermudezi sp. nov.

(Pl. XI - Figs. 11-14)

Holotype: The ovicelled specimen (single zooecium) figured on Pl. XI, figs. 13-14, from the Jabaco Formation (Upper Eocene), 1 km S. of ingenio Saratoga, Matanzas Province, Cuba. B.322. Dr. P. J. BERMUDEZ Coll. (see BERMUDEZ, 1950, p. 248). « Ingenio » is used in Cuba for sugar mill. U.S.N.M. Cat. No. 651153.

Paratypes: The seven remaining specimens (single zooecia) found in the above sample. U.S.N.M. Cat. Nos. 651154-651155.

Other material: One specimen (single zooecium) from the Loma Candela Formation (Middle Eocene), at Loma Candela, on the road from San Diego de los Baños to Paso Real, Pinar del Rio Province, Cuba. B.261. Dr. P. J. BERMUDEZ Coll. (see BERMUDEZ, 1950, p. 244).

Diagnosis: *Beania* with four tubular connections, 7-9 closely spaced spine(base)s on either side of the opesia, and a fairly large ovicell.

Description: *Zooecia* boat-shaped, heavily calcified for the genus, tubular part short and tapering proximally, expanded part wide and shallow. *Opesia* large, occupying the entire front of the expanded part of the zooecium, its sides straight and parallel and set with closely-spaced spine bases, 7-9 on either side. A lateral connecting tube was originally given off from the proximal half of the expanded part on either side. A dorsal connecting tube was originally given off from a prominent base on the dorsal face. *Ovicell* at the distal extremity of the zooecium, large and somewhat reclining, flanked by two short oblique spines.

Measurements:

Holotype (fertile) U.S.N.M. Cat. No. 651153

Lz = 1.08 mm.
lz = 0.33 mm.
ho = 0.60 mm.
lo = 0.20 mm.

Paratypes (sterile) U.S.N.M. Cat. Nos. 651154-651155

Lz	(3)	0.85	(0.041) mm.,	0.80 - 0.90	mm.
lz	(7)	0.31	(0.025) mm.,	0.26 - 0.35	mm.
ho	(3)	0.473	(0.021) mm.,	0.45 - 0.50	mm.
lo	(7)	0.156	(0.022) mm.,	0.13 - 0.175	mm.

Remarks: Among the various Recent species of *Beania*, *B. bermudezi* resembles *B. regularis* THORNELY and *B. mirabilis*

JOHNSTON in having four connecting tubes, but is at once distinguished from both by its large ovicell.

This ancient occurrence of *Beania* is interesting in the light of HARMER's ideas on the evolution within the genus. HARMER (1926, pp. 411, 420) regards *B. mirabilis* as the most highly modified representative of the genus, and in his view the reduction of the number of directly connected neighbour zooecia from six to four would constitute one of the advanced evolutionary features in this species, others being the loss of the ovicell and of the avicularia. Our finding of an Eocene representative of *Beania* with only four connecting tubes does not necessarily invalidate HARMER's views, but it does put such a development further back in geological time, viz. before the Middle Eocene.

The species is named after Dr. P. J. BERMUDEZ, Caracas, Venezuela, in recognition of his help and encouragement.

Distribution: Middle and Upper Eocene of Cuba.

Synnotum.

Synnotum is another of these small-sized genera which have not previously appeared in the fossil record. In addition to the type species, *Synnotum aegyptiacum* (AUDOUIN, 1826), there are two other Recent species known at present, which are confined to the tropical Indo-West Pacific (HARMER, 1926). *S. aegyptiacum*, on the other hand, has a typically circumtropical to warm-temperate Recent distribution (Fig. 2). A number of Recent occurrences shown on this map constitute new records and are among those listed in the Appendix. The fossil specimens in my possession are all Miocene, or Mio-Pliocene, in age and come from the following localities:

a) Sample Ct 5971, Lower Miocene (Tertiary $f_{1/2}$), Arnih, Madura Island, Indonesia, collected by Mr. M. R. Cleintuar. 1 specimen.

b) Sample from handauger hole 7 (5 m), Tuban Formation, Lower Miocene (Tertiary e_5), Tuban Formation, Prupuh, East Java, Indonesia. 1 specimen.

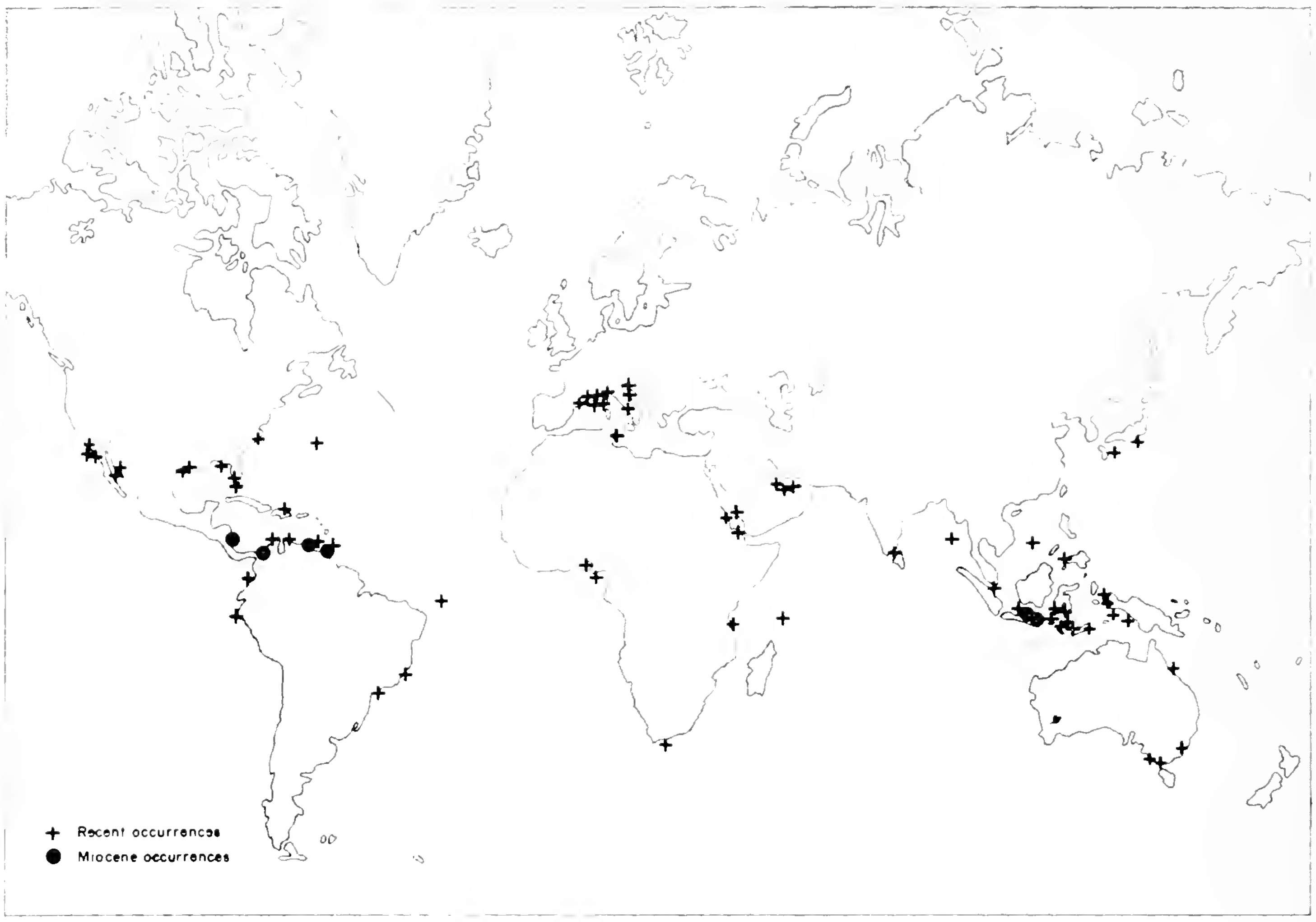

Fig. 2. — World distribution of *Synnotum aegyptiacum* (Audouin).

c) Sample Du 21, Montserrat Glauconitic Sandstone Member of Manzanilla Formation, Middle or Upper Miocene, San Jose River, Trinidad, W. I., collected by Mr. R. Dubey. 1 specimen.

d) Sample DB 345, Savaneta Member of Springvale Formation, Upper Miocene, Couva Main Road, gorge upstream of bridge B 1/6, collected by Dr. D. A. J. Batjes. 1 specimen.

e) Sample « Cubagua 8 », Cubagua Formation, Upper Miocene, La Caldera Canyon, Cubagua Island, Venezuela, collected by Dr. P. J. Bermudez. 1 specimen.

f) Sample vS 105, Tubará Formation, Mio-Pliocene, San Juan de Acosta, Departamento Atlantico, Colombia, S. A., collected by Dr. J. Van Soest. Several specimens (Pl. II, figs. 3-4).

g) Sample C 11^{A}, « Mio-Pliocene », Great Corn Island, Nicaragua, collected by Mr. H. Van Kuijk. 4 specimens.

These finds establish the known range of *Synnotum,* and that of the family *Epistomiidae* to which it belongs, as Lower Miocene - Recent.

Pasythea.

For several years I have been collecting data on the Recent and fossil distribution of this interesting genus and a sizeable dossier has been assembled. Several fossil species have been found, which together are distributed over five continents.

Within the scope of the present paper, however, only the oldest occurrence is of direct concern. This is the form (triads) figured on Pl. XII, figs. 5-6 from the Middle Eocene Loma Candela Formation, at Loma Candela, on the road from San Diego de los Baños to Paso Real, Pinar del Río Province, Cuba. Sample B. 261, collected by Dr. P. J. BERMUDEZ (see BERMUDEZ, 1950, p. 244). The distal tubular prolongation in the triads is considered a primitive character. Axial kenozooecia (Pl. XII, fig. 7) have also been found.

These observations establish the known time-stratigraphical range of *Pasythea* as Middle Eocene - Recent. It is obvious, therefore, that DAVIS's scheme of the phylogeny of the *Pasytheidae* (1934, p. 238) needs emendation. *Pasythea* now appears as in part contemporaneous with, and not just as a far descendant of, the Eocene-Oligocene genus *Dittosaria* BUSK, 1866. Their common ancestor, if any, is to be sought in beds of pre-Middle Eocene age.

Savignyella.

The ancient species *Eucratea lafontii* AUDOUIN, 1826, which is the type species of *Savignyella* LEVINSEN, 1909, is widely distributed in tropical - warm temperate latitudes (Fig. 3). On this map a number of Recent occurences of this species are shown which constitute new records. These are listed separately in the Appendix. A second Recent species, *S. otophora* (KIRKPATRICK, 1890), is found in the tropical Indo-West Pacific. Until recently no fossil representatives of the genus were known, but these have now turned up at the following Younger Tertiary localities in the Caribbean and in the Far East:

Fig. 3. — World distribution of *Savignyella lafontii* (AUDOUIN).

a) in a sample, « Cubagua 8 », from the Cubagua Formation (Upper Miocene), collected by Dr. P. J. BERMUDEZ from La Caldera Canyon, Cubagua Island, Venezuela. 2 specimens.

b) in a sample, C 11^A, from the « Mio-Pliocene » of Great Corn Island, Nicaragua, collected by Mr. H. VAN KUIJK. 16 specimens.

c) in a sample, Tu 823, from the Miocene Chipola Formation, collected by Dr. R. J. SCOLARO from Farley Creek, near Clarksville, Calhoun County, Florida. 2 specimens (Pl. XII, figs. 8-9) deposited in the collection of the United States National Museum. U.S.N.M. Cat. Nos. 651156 - 651157.

All three finds refer to *Savignyella lafontii* (AUDOUIN).

d) in a sample, Be 1421, from the Middle Miocene (Tertiary f_3) of Kali Ambunten, Madura Island, Indonesia, collected by Mr. E. TH. VAN DER BENT. 5 mediocre specimens (Pl. XII, figs. 10-11), which closely resemble *S. otophora* (KIRKPATRICK), the only notable difference being the absence in the fossils of the 3-5 larger lateral pores (rootlet foramina) which both KIRKPATRICK and HARMER (1957) observed in their Recent material.

The above finds extend the known stratigraphical range of the genus and of the family *Savignyellidae* into the Miocene.

Remarks on the time-stratigraphical and the geographical distribution.

The range chart (Fig. 4) summarizes our present knowledge of the time-stratigraphical distribution of the six genera discussed here, and which until now had been considered as Recent only. Fossil discoveries of this kind are interesting in two ways. They enable us to apply the Recent environmental requirements of these genera to the Tertiary samples in which they have now been found. They may also change our concepts of the evolution within families or higher taxonomic units (see remarks under *Pasythea*).

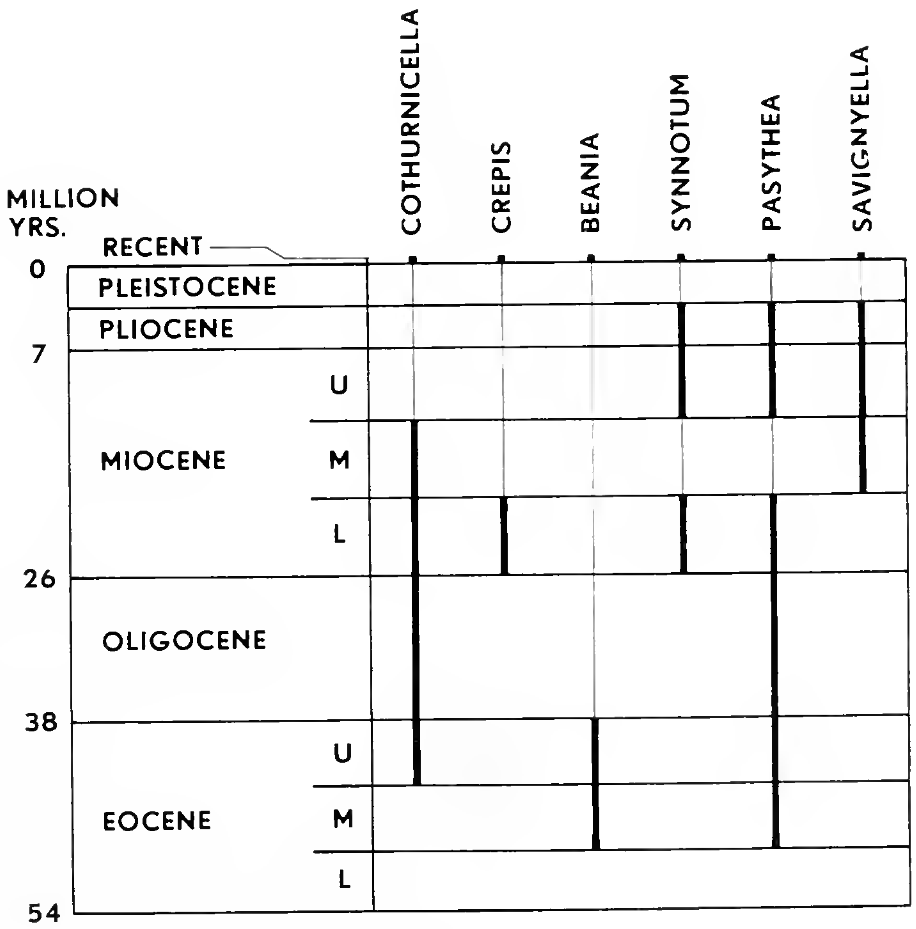

Fig. 4. — Time-stratigraphical range chart of the six genera discussed in this paper.

A few remarks are pertinent in connection with the maps of the Recent and fossil geographical distribution of some of the species concerned (Figs. 1-3). What *Cothurnicella pyriformis, Synnotum aegyptiacum,* and *Savignyella lafontii* have in common is their wide tropical - warm temperate Recent distribution. Initially it was a matter of surprise to me to find that their Miocene distribution - or what is known of it - turned out to be equally wide. On further consideration, however, this should not have been so surprising. The fact that a shallow-water marine benthonic species has a completely circumtropical Recent distribution has an important palaeontological implication, viz. that, as EKMAN (1953, p. 36) has implied, it must have lived in Miocene times. Moreover, it should already have attained a circumtropical distribution in the Miocene, because connections between the Gulf of Mexico and the Eastern Pacific have been severed after the Lower Pliocene (SCHUCHERT, 1935, pp. 29, 378) and those between the Mediterranean and the Indian Ocean ceased to exist in the Lower Miocene (RUGGIERI, 1967, p. 284). This theoretical consideration is to a greater or lesser extent proved by the maps of the Recent and fossil distribution of the three above-mentioned species.

Acknowledgements.

Collecting microfossils of the type dealt with in this paper is as often a matter of good neighbours as it is of good luck. Among the many friends and colleagues who kindly gave me access to sample material in their possession or contributed interesting specimens, I should like to thank in particular: Mr. R. WRIGHT BARKER, Dr. D. A. J. BATJES, Dr. P. J. BERMUDEZ, Mr. J. BROUWER, Mr. R. DUBEY, Dr. A. J. KEIJ, Dr. R. J. SCOLARO and Dr. I. M. VAN DER VLERK.

The photographs have been taken by Mr. W. GELUK.

Permission of Bataafse Internationale Petroleum Maatschappij N. V. to publish this paper is gratefully acknowledged.

Appendix.

Listed below are Recent occurrences of *Synnotum aegyptiacum* and *Savignyella lafontii* that constitute new records; some of these are shown on Figs. 2 and 3. The material is kept at the Koninklijke / Shell Exploratie en Produktie Laboratorium, Volmerlaan 6, Rijswijk, Netherlands.

a) *Synnotum aegyptiacum.*

T 1281 Persian Gulf. Lat. 25°45′—″ N, Long. 55°43′20″ E. 40 m. 18 specimens (internodes). Dr. A. J. Keij Coll.

T 950 Persian Gulf. Lat. 25°1′45″ N, Long. 54°23′40″ E. 25 m. 3 specimens (internodes). Dr. A. J. Keij Coll.

T 835 Persian Gulf. Lat. 25°55′35″ N, Long. 53°2′30″ E. 50 m. 1 specimen (internode). Dr. A. J. Keij Coll.

D 79 Nigeria. Lat. 4°14′41″ N, Long. 6°56′58″ E. 8 fms. 1 specimen (internode).

D 78 Nigeria. Lat. 4°14′05″ N, Long. 6°51′59″ E. 9 fms. 1 specimen (internode).

D 75 Nigeria. Lat. 4°12′58″ N, Long. 6°36′52″ E. 8 fms. 1 specimen (internode).

D 98 Nigeria. Lat. 4°09′20″ N, Long. 5°38′25″ E. 14 fms. 5 specimens (internodes).

D 213 Nigeria. Lat. 6°21′26″ N, Long. 4°09′52″ E. 7 fms. 1 specimen (internode).

D 155 Nigeria, off Lagos. Lat. 6°21′59″ N, Long. 3°24′02″ E. 6 fms. 1 specimen (internode).

H. Ms. « Owen » stn. 16. Nigeria. Lat. 4°03′ N, Long. 6°26′ E. 11 fms. 2 specimens (internodes).

Stn. 1197. W. of Tobago Island, W. I. Top of core. 41 fms. Several specimens (internodes). Orinoco Shelf Expedition Coll. See Koldewijn (1958).

Los Testigos, Venezuela. 50 m. 20 specimens (internodes). Dr. P. J. Bermudez ded.

1812 Tampa Bay, Florida. Lat. 27°38′09″ N, Long. 82°37′27″ W. 4½ fms. 2 specimens (branches). Dr. D. Moore Coll.

1815 Tampa Bay, Florida. Lat. 27°36′17″ N, Long. 82°43′18″ W. 7 fms. 2 specimens (branches). Dr. D. Moore Coll.

« Cavalier » 1956 Stn. 299. South of Calcasieu Pass, Louisiana. Lat. 28°59′15″ N, Long. 93°30′15″ W. 11 fms. 1 specimen (internode).

Matagorda Bay, Texas. 10 ft below present Colorado River Delta surface. 1 specimen (internode).

b) *Savignyella lafontii.*

T 1281 Persian Gulf. Lat. 28°54′—″ N, Long. 55°43′20″ E. 40 m. 1 specimen. Dr. A. J. KEIJ Coll.

T 923 Persian Gulf. Lat. 25°18′50″ N, Long. 54°15′20″ E. 36 m. 5 specimens. Dr. A. J. KEIJ Coll.

W 1223 Persian Gulf. Lat. 25°59′ N, Long. 51°40′ E. 21 m. 7 specimens. Dr. A. J. WELLS Coll.

D 99 Nigeria. Lat. 4°05′44″ N, Long. 5°35′37″ E. 17 fms. 1 specimen.

D 155 Nigeria, off Lagos. Lat. 6°21′59″ N, Long. 3°24′02″ E. 4 specimens.

Stn. 1197 W. of Tobago Island, W. I. Top of core. 41 fms. Several, mostly incomplete, specimens. Orinoco Shelf Expedition Coll. See KOLDEWIJN (1958).

Los Testigos, Venezuela. 50 m. 12 specimens. Dr. P. J. BERMUDEZ ded.

Bahia de la Habana, Cuba. 16 specimens. Dr. P. J. BERMUDEZ ded.
« Atlantis » 1951 Stn. 165. Lat. 28°43′30″ N, Long. 83°56′ W.

« Atlantis » 1951 Sten. 165. Lat. 28°43′30″ N, Long. 83°56′ W. 17 fms. 3 specimens.

« Atlantis » 1951 Stn. 164. Lat. 28°41′ N, Long. 84°02 W. 17 fms. 6 specimens.

« Cavalier » 1956 Stn. 21. Lat. 28°45′16″ N, Long. 95°15′24″ W. 10.5 fms. 1 specimen.

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PLATE XI.

1. *Cothurnicella pyriformis* (BERTOLONI). Frontal view.
   Lower Miocene (Tertiary e_5), Tuban Formation, Prupuh,
   East Java, Indonesia.
2. *Cothurnicella pyriformis* (BERTOLONI). Lateral view of fertile internode.
   Ibidem.
3. *Cothurnicella pyriformis* (BERTOLONI). Lateral view of sterile internode.
   Ibidem.
4. *Cothurnicella pyriformis* (BERTOLONI). Frontal view.
   Oligocene, Jan Juc Formation, W side of Point Addis,
   Victoria, Australia.
5. *Cothurnicella pyriformis* (BERTOLONI). Frontal view.
   Lower Miocene (« Upper Aquitanian »), Falun de Lariey,
   near Saucats (Gironde), France.
6. *Cothurnicella pyriformis* (BERTOLONI).Lateral view.
   Ibidem.
7. *Cothurnicella* sp. Frontal view.
   Upper Eocene, Jabaco Formation, Matanzas Province, Cuba.
8. *Cothurnicella* sp. Lateral view of same specimen.
9. *Cothurnicella* sp. Frontal view.
   Upper Eocene, Jabaco Formation, Matanzas Province, Cuba.
10. *Cothurnicella* sp. Lateral view of same specimen.
11. *Beania bermudezi* sp. nov. Frontal view of paratype. U.S.N.M. Cat. No. 651154.
    Upper Eocene, Jabaco Formation, Matanzas Province, Cuba.
12. *Beania bermudezi* sp. nov. Dorsal view of same specimen.
13. *Beania bermudezi* sp. nov. Frontal view of holotype. U.S.N.M. Cat. No. 651153.
    Upper Eocene, Jabaco Formation, Matanzas Province, Cuba.
14. *Beania bermudezi* sp. nov. Dorsal view of same specimen.

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PLATE I


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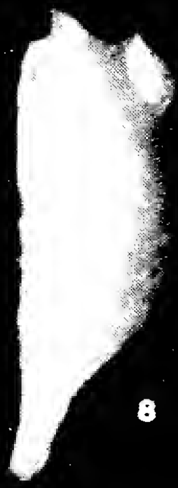
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PLATE XII.

1. *Crepis* aff. *longipes* JULLIEN.
   Lower Miocene (Tertiary e_5), Tuban Formation, Prupuh,
   East Java, Indonesia.
2. *Crepis* aff. *longipes* JULLIEN.
   Ibidem.
3. *Synnotum aegyptiacum* (AUDOUIN).
   Mio-Pliocene, Tubará Formation, San Juan de Acosta, Dpto.
   Atlantico, Colombia.
4. *Synnotum aegyptiacum* (AUDOUIN).
   Ibidem.
5. *Pasythea* sp. Triad.
   Middle Eocene, Loma Candela Formation, Loma Candela,
   Pinar del Rio Province, Cuba.
6. *Pasythea* sp. Triad.
   Ibidem.
7. *Pasythea* sp. Axial kenozooecium.
   Ibidem.
8. *Savignyella lafontii* (AUDOUIN). Lateral view. U.S.N.M. Cat. No. 651156.
   Miocene, Chipola Formation, near Clarksville, Calhoun
   County, Florida, U.S.A.
9. *Savignyella lafontii* (AUDOUIN). Frontal view of same specimen.
10. *Savignyella otophora* (KIRKPATRICK). Frontal view.
    Middle Miocene (Tertiary f_3), Kali Ambunten, Madura Island,
    Indonesia.
11. *Savignyella otophora* (KIRKPATRICK). Lateral view of same specimen.

all figures × 50.

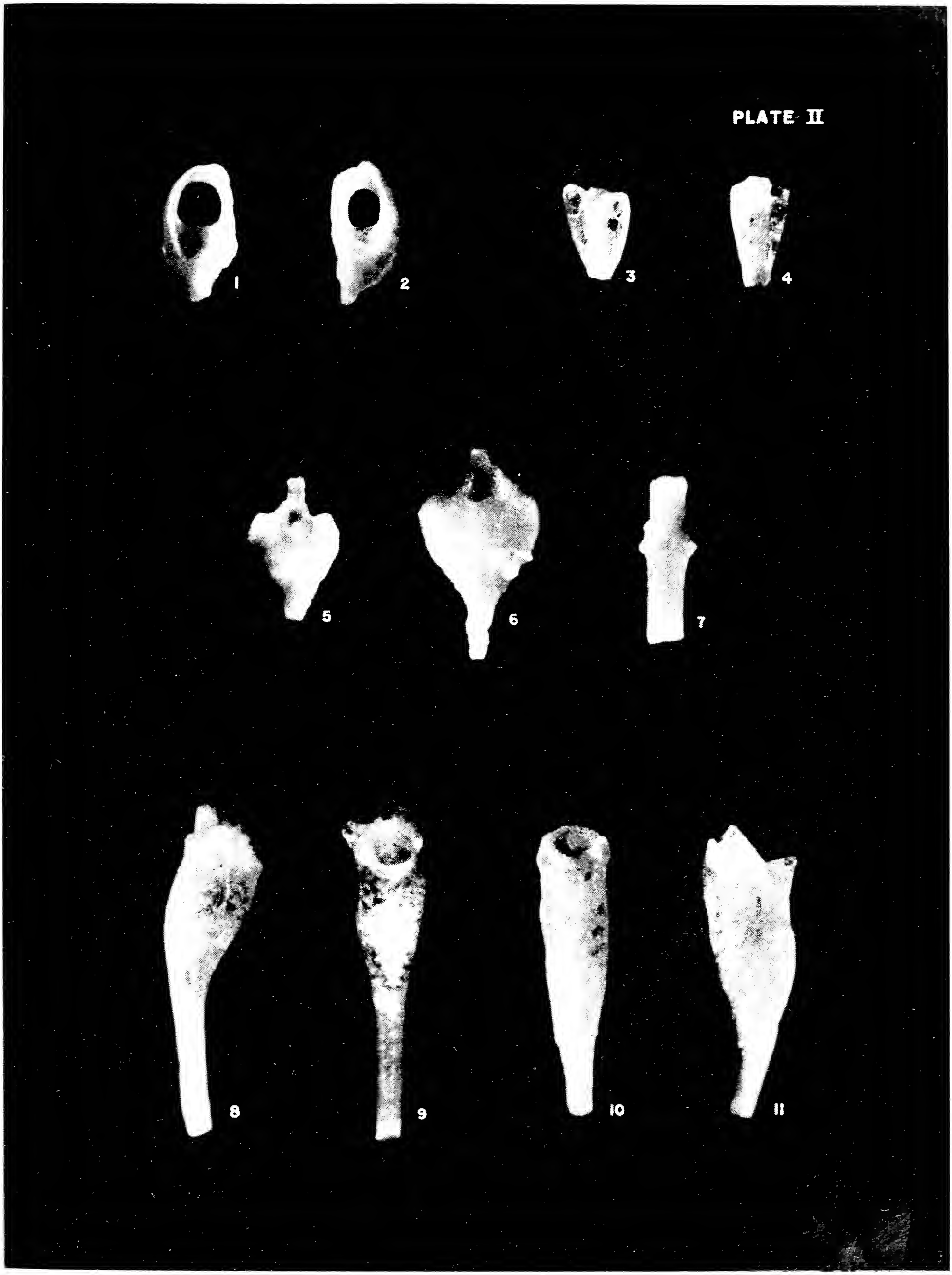

PLATE II

Atti Soc. It. Sc. Nat. e Museo Civ. St. Nat. Milano - 108: 361-368, 31-XII-1968

1st I.B.A. International Conference on Bryozoa, S. Donato Milanese, Aug. 12th-16th, 1968
45. Group 5: Biogeography and Biostratigraphy.

MADELEINE J. THOELEN (*)

THE *BRYOZOA* FAUNA FROM THE SANDS OF DEURNE, UPPER MIOCENE, AT DEURNE

(ANTWERPEN, BELGIUM)

Riassunto. — Le sabbie a *Terebratula perforata* Defrance (« Deurniano ») sono state osservate a Rivierenhof nelle immediate vicinanze di Deurne (Antwerpen, Belgio). Questi depositi sabbiosi glauconitici raggiungono uno spessore di m 1,50 nella sola serie studiata.

Viene riportata una tavola di distribuzione delle 56 specie rinvenute e vengono proposti un genere monospecifico *Obliquostoma* nov. gen. (Famiglia *Phylactellidae*) con la specie-tipo *O. dichotoma* nov. sp. ed una nuova specie *Cellaria unicella* nov. sp.

Dal punto di vista ecologico è da notare che questa tanatocenosi contiene diverse specie paleoartiche insieme a diverse specie con distribuzione subtropicale e tropicale.

Summary. — The Sands of Deurne with *Terebratula perforata* Defrance (« Deurnian ») were observed at Rivierenhof in the immediate neighbourhood of Deurne (Antwerpen, Belgium). These glauconitic sandy deposits reached a thickness of about 1,50 m in the only section studied.

A distribution table of the 56 species was made up.

One monospecific genus *Obliquostoma* nov. gen. (Family *Phylactellidae*) with type species *O. dichotoma* nov. sp. and one species *Cellaria unicella* nov. sp. are proposed herein.

From ecological point of view it is remarkable that this thanatocenosis contains several typical palearctic species and also several species with subtropical and tropical distribution.

Résumé. — Les Sables de Deurne à *Terebratula perforata* Defrance (« Deurnien ») ont été vus sur une épaisseur de 1,50 m au lieu-dit Rivierenhof près de Deurne.

Un tableau de répartition stratigraphique des 56 espèces trouvées à cet endroit a été établi.

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Un nouveau genre monospécifique *Obliquostoma dichtoma* nov. gen., nov. sp. (famille *Phylactellidae*) est proposé ainsi qu'une nouvelle espèce *Cellaria unicella* nov. sp.

Du point de vue écologique il est remarquable qu'il s'agit d'une thanatocénose comprenant plusieurs espèces paléarctiques ainsi que plusieurs espèces à répartition nettement tropicale et subtropicale.

Introduction.

During the E3 road-works in 1967 at Antwerpen it was possible to take several samples of the Sands of Deurne at Rivierenhof, Deurne, near the type locality. The outcrop shows glauconitic sands with a thickness of 1,50 m, especially rich in *Bryozoa*. The accompanying fauna is rather poor. One can find some molluscs, foraminifera, ostracods, corals, echinoderms, *Ditrupa* sp., the brachiopods *Mannia nysti* (Dewalque) and *Terebratula perforata* Defrance; the latter has been used in biostratigraphy for calling the Sands of Deurne « Sables à *Terebratula perforata* ».

These sands are situated between underlying Sands of Antwerpen (Miocene) and overlying Sands of Kattendijk (probably Pliocene).

Further details can be found in « Lexique stratigraphique international, vol. I, fasc. 4a, p. 62-63, 1957 », and in DE MEUTER, LAGA, RINGELE and ROOSE, 1967.

We thank Dr. L. VAN DE POEL as supervisor and Ir. W. P. VAN LECKWIJCK, head of the paleontological department.

Systematic description.

Phylum Bryozoa Ehrenberg, 1831

Familia *Phylactellidae* Canu and Bassler, 1917

Genus **Obliquostoma** nov. gen.

Type species: *Obliquostoma dichotoma* nov. sp., here designated.

Diagnosis: zoarium vincularian; primary orifice semi-circular, facing distally, not visible exteriorly. Secondary orifice subcircular; frontal wall bordered by areolae; ovicell hyperstomial, recumbent, with opening into the peristomie.

Discussion: the *Phylactellidae* is a very heterogeneous family, mostly recognized by the structure of the ovicell (hyperstomial, recumbent, with a large orifice). This new species cannot be referred to any known genus of the family, because of the constellation of following characters: cylindrical zoarium, dichotomously branching, oblique apertura, frontal areolae. The new genus looks like *Psilopsella* CANU and BASSLER, 1927; it is however always different from it by the vincularian mode of growth and the shape of the primary orifice.

Obliquostoma dichotoma nov. gen., nov. sp.

(Plate XIII, fig. 1 and 2)

Holotype: Slide B1026, deposited at the Laboratorium voor Paleozoölogie, Universiteit te Leuven.

Paratypes: 10 zoaria fragments: Slides B1027-B1036.

Locus typicus: Rivierenhof, Deurne near Antwerpen, Belgium.

Stratum typicum: Sands of Deurne (Upper Miocene).

Diagnosis: zoarium free, erect, cylindrical, dichotomously branching; zooecia oval, alternately arranged in six longitudinal rows around a central axis. Primary orifice semi-circular, facing distally, invisible exteriorly; peristomie arched, peristomice sub-circular, the proximal lip often straight; peristome generally poorly developed. Spines and avicularia absent; frontal wall flat, bordered by a single or a double row of areolae. Ovicell hyperstomial, deeply immersed; not conspicuous exteriorly, with opening into the peristomie.

Measurements (holotype): diameter of zoarium: 1,08-1,14 mm; length of the zooecium: 0,82-0,88 mm (without ovicell); breadth of the zooecium: 0,33 mm; length of the peristomice: 0,12-0,14 mm; breadth of the peristomice: 0,14-0,15 mm.

Familia *Cellariidae* Hincks, 1880

Cellaria ELLIS and SOLANDER, 1786

Cellaria unicella nov. sp.

(Plate XIII, figs. 3, 4, 5, 6)

1926 - *Cellaria sinuosa* (Hassall): CANU, p. 764 (fide LAGAAIJ, 1952, p. 49).

Etymology: *unicella* is referred to the autozooecia and the avicularia which have nearly the same width and shape.

TABLE 1.

Species	Eocene W. Europe	Oligocene W. Europe	Miocene Aquitaine	Miocene W. France	Vindobonian Vienna	Miocene Italy	Miocene Spain	Miocene N. Africa	Miocene Deurne	Redonian	Pliocene Belgium	Pliocene The Netherlands	Pliocene England	Pliocene Italy	Pliocene Spain	Pliocene N. Africa	Plio-Pleist. (Walton-Crag)	Pleistocene	Recent
Biflustra savartii (Savigny-Audouin, 1826)			+	+		+	+	+	+		+		+	+	+	+		+	+
Amphiblestrum trifolium (Wood, 1844)				?					+		+	+	+				+		
Ramphonotus intermedius Buge, 1957				+					+										
Cupuladria haidingeri (Reuss, 1847)					+	+	+		+	+	+	+	+	+	+	+			
Cupuladria canariensis (Busk, 1859)			+	+	+	+	+		+	+	+	+	+	+	+	+			+
Steraechmella buski Lagaaij, 1952					+				+				+						+
Cellaria mutabilis Canu, 1909			+	+					+							+			
Cellaria unicella nov. sp.									+										
Scrupocellaria elliptica (Reuss, 1847)			+	+	+			+	+					+		+			
Cribrilaria radiata (Moll, 1803)	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+
Hippothoa rugulosa (Reuss, 1873)			+	+	+	+		+	+					+				+	
Escharina milneana (Busk, 1859)									+			+	+						
Schizoporella sp.									+										
Schizomavella auriculata (Hassal, 1842)			+	+	+		+	+	+		+	+	+	+		+		+	+
Hippodiplosia perforata Canu and Lecointre, 1930				+					+		+	+					+	+	
Escharoides mamillata (Wood, 1844)									+			+	+				+	+	+
Hippopleurifera sedgwickii (Milne-Edwards, 1836)			+	+					+	+	+	+	+	+		+			
Porella cervicornis (Pallas, 1766)			+	+	+	+		+	+			+		+	+	+			+
Porella sinuosa (Busk, 1859)									+		+	+	+						
Porella pulchra Canu and Bassler, 1929	+								+			+							
Palmicellaria bicornis (Busk, 1859)									+		+	+	+						+
Vibraculina seguenziana Neviani, 1895									+					+					

Escharella immersa (Fleming, 1828)									+		+	+	+						+
Sertella beaniana (King, 1846)			+	+			+		+	+		+	+	+				+	+
Sertella cellulosa (Linnaeus, 1767)				+	+	+		+	+	+	+	+	+	+				+	+
Schizoretepora fungosa (Canu and Lecointre, 1930)				+					+	+									
Schizostomella neglecta (Manzoni, 1877)					+				+										
Trigonopora nysti (Houzeau) Lagaaij, 1952									+										
Adeonellopsis imbricata (Philippi, 1844)		+			+				+			+							
Cheiloporina articulata (Canu and Lecointre, 1930)				+					+										
« *Schismopora* » *coronopus* (Wood, 1844)				+	+		+	+	+		+	+	+	+		+		+	+
« *Schismopora* » *tubigera* (Busk, 1859)				+		+			+		+	+	+	+		+	+	+	+
Holoporella palmata (Michelin, 1847)				+					+	+	+	+	+						
Stichoporina reussi Stolicska, 1862	+	+							+										
Hemicyclopora cf. *H. polita* Norman, 1864									+										+
Obliquostoma dichtoma nov. gen., nov. sp.									+										
Crisia eburnea (Linnaeus, 1758)				+		+	+	+	+					+	+	+	+	+	+
Crisia strangulata Buge, 1956		+		+	+	+			+					+					
Entalophora clavata (Busk, 1859)									+		+		+						+
Mesenteripora meandrina (Wood, 1844)									+		+	+	+						
Berenicea patina (Lamarck, 1816)				+	+				+					+					+
Diaperoecia major (Johnston, 1847)			+	+	+	+			+			+		+		+		+	+
Ybsclosoecia subverticellata (Busk, 1859)				+					+	+		+	+						
Idmidronea atlantica [(Forbes) Johnston, 1847]			+	+		+		+	+							+			+
Idmonea notomale Busk, 1875									+					+					+
Idmonea disticha Goldfuss, 1847					+				+					+				+	
Tervia irregularis (Meneghini, 1847)				+	+	+			+	+		+		+				+	+
Hornera frondiculata Lamouroux, 1821			+	+	+	+			+	+	+	+	+	+					+
Hornera striata Milne-Edwards, 1838			+	+	+	+			+	+	+	+	+	+					
Hornera radians Defrance, 1821			+	+					+	+									
Hornera sp.									+										
Radiofascigera tabulifera (Reuss, 1865)		+							+										
Lichenopora hispida (Fleming, 1828)			+		+	+	+		+	+	+	+	+	+	+	+		+	+
Lichenopora venabulum (Jullien, 1888)									+	+	+	+							
Lichenopora proposita Canu and Lecointre, 1934				+					+										
Lichenopora mamillata Lagaaij, 1952									+			+							+

Holotype: fragment of a zoarium, Slide B1008, deposited at the Laboratorium voor Paleozoölogie, Universiteit te Leuven.

Paratypes: 10 fragments of zoaria, Slides B1009-B1018.

Locus typicus: Rivierenhof, Deurne near Antwerpen, Belgium.

Stratum typicum: Sands of Deurne (Upper Miocene).

Diagnosis: zoarium composed of long and slender cylindrical internodes, reaching a maximum diameter of 0,95 mm (average diameter of 20 specimens: 0,76 mm). Zooecia rhomboidal, arranged alternately in longitudinal rows, separated by their raised joint-margins, which are sometimes worn. Orifice situated in the distal half of the zooecium, transverse, trapezoidal with the proximal lip produced distally. The peristome is hardly raised. Both a proximal and a distal pair of minute oral denticles are present. Cryptocyst depressed, with a pair of conspicuous, parallel ridges laterally to the orifice. Avicularia rhombic, with straight, acuminate, distally directed rostrum and an immersed, relatively large, elliptical opesia. Ovicells entotoichal, with minute, circular orifice, sometimes partly occupied by a large denticle on the proximal lip.

Measurements (holotype): length of the zooecium: 0,41-0,48 mm; breadth of the zooecium: 0,22-0,25 mm; height of the orifice: 0,05-0,06 mm; breadth of the orifice: 0,10 mm; length of the avicularia: 0,40-0,50 mm; breadth of the avicularia: 0,22-0,25 mm; height of the avicularian orifice: 0,09-0,13 mm; breadth of the avicularian orifice: 0,07-0,09 mm.

Affinities: this species differs from the type species, *C. fistulosa*, in the shape of the avicularia, the constant presence of a distal pair of oral denticles and the shape of the opesia. From *C. mutabilis* and *C. sinuosa* it can immediately be separated by the rhombic avicularia. *C. neglecta* LAGAAIJ always lacks the oral denticles and has somewhat smaller opesia and avicularia.

Genus assignment: the present species is included in the genus *Cellaria* Ellis and Solander because of following characteristics: the cylindrical internodes of a typically jointed zoarium with rhomboidal zooecia; the reduced opesia with the proximal border formed by a small median process, at the sides of which are a pair of condyles; the vicarious avicularia with circular opesia; the entotoichal ovicells, inconspicuous in frontal view.

Distribution and ecology.

Table 1 shows the systematic list of the 56 species we found in the Sands of Deurne. Literature screening was done to find out how these species are stratigraphically distributed.

After BUGE (1964) we have made up a stratigraphical correlation table (table 2). We can draw the conclusion that 62% of our species are known from the Miocene and 75% from the Pliocene.

TABLE 2.

Sands of Deurne (Miocene)	100% (= 56 species)	Redonian	25%
Eocene W. Europe	5,3%	Pliocene Belgium	35%
Oligocene W. Europe	8%	Pliocene The Netherlands	51%
Miocene Aquitaine	28%	Pliocene England	42%
Miocene W. France	51%	Pliocene Italy	42%
Vindobonian Vienna	35%	Pliocene Spain	12%
Miocene Italy	28%	Pliocene N. Africa	26%
Miocene Spain	16%	Pleistocene	25%
Miocene N. Africa	17%	Recent	42%

The results obtained by LAGAAIJ (1955) for the Bryozoa of the Sands of Deurne are very similar: 62% Miocene species and 70% Pliocene species. These proportions of Miocene-Pliocene species are inverted when it concerns the Molluscs (GLIBERT and DE HEINZELIN, 1955):

Pelecypoda: 75% Miocene, 63% Pliocene.
Gastropoda: 67% Miocene, 45% Pliocene.

The thanatocenosis contains essentially eurytherm species but also typical palearctic species and species with a definite subtropical and tropical distribution.

Species occuring in warm to moderate waters are: *Biflustra savartii, Holoporella palmata, Cupuladria canariensis, Porella cervicornis, Tervia irregularis, Hornera frondiculata, Diaperoecia major* and *Trigonopora nysti.*

Species occuring in moderate to cold waters are: *Crisia eburnea, Berenicea patina, Idmonea notomale, Idmidronea atlantica, Sertella beaniana* and « *Schismopora* » sp.

Eurytherm species: *Cribrilaria radiata, Schizomavella auriculata* and *Lichenopora hispida.*

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PLATE XIII.

Fig. 1. — *Obliquostoma dichotoma* nov. gen., nov. sp., holotype, 10 ×.

Fig. 2. — *Obliquostoma dichotoma* nov. gen., nov. sp., holotype, 20 ×.

Fig. 3. — *Cellaria unicella* nov. sp., paratype, 20 ×.

Fig. 4. — *Cellaria unicella* nov. sp., paratype, 45 ×.

Fig. 5. — *Cellaria unicella* nov. sp., holotype, 45 ×.

Fig. 6. — *Cellaria unicella* nov. sp., holotype, 45 ×.

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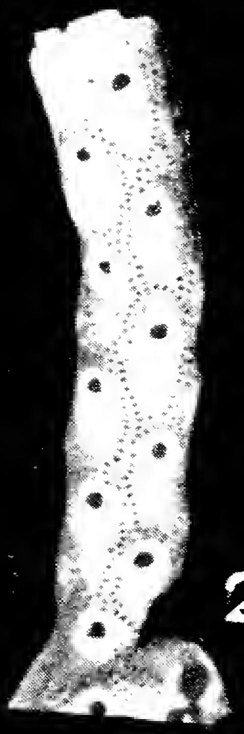

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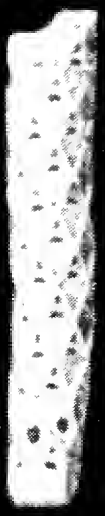

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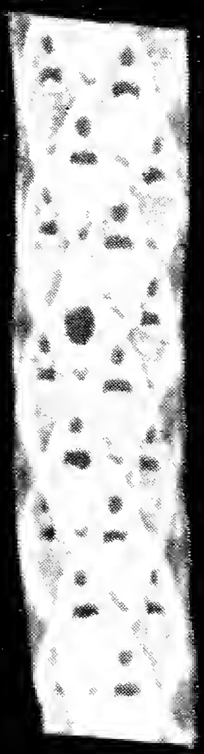

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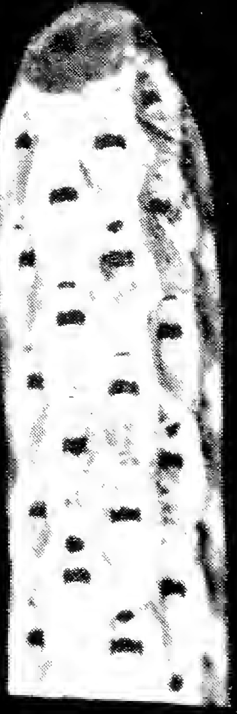

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