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**catinus** (*Velutinellus*), MARINESCU 1970, p 317  
**codapavonis** (*Velutinopsis*), MARINESCU 1970, p 315  
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ERRATA, Vol. 7, 2-3

Volume 7, No. 2-3 was unavoidably delayed by the printer; 13 October 1969 is the publication date rather than 31 July 1969 as given on p ii.

*Oncomelania hupensis chiu* [= *Tricula chiu* HABE & MIYAZAKI 1962] is a new name combination, but not a new name as listed on p vii.



CONTENTS OF VOL. 9

ADEGOKE, O. S., DESSAUVAGIE, T. F. J. & YOLOYE, V. L. A. Biology and population dynamics of two sympatric species of <i>Neritina</i> from Southern Nigeria . . . . .	47
ALVAREZ, J. Über die Verbreitung der Land— und Süßwasserschnecken in Mittel— spanien in Bezug auf die verschiedenen Böden und Gewässer. . . . .	53
ANT, H. Zur wärm-glazialen Überdauerung europäischer Landgastropoden in Eisrandnähe. . . . .	249
AZEVEDO, J. F. de, XAVIER, M. d. L., PEQUITO, M. M. & SIMOES, M. Contribution to the morphological and biochemical identification of some strains of the <i>Bulinus truncatus</i> group. . . . .	25
BACKHUYS, W. The elevation—effect in <i>Cylindrus obtusus</i> (Drap. 1805) . . . . .	251
BAYNE, C. J. Survival of the embryos of the grey field slug <i>Agriolimax reticulatus</i> following desiccation of the egg . . . . .	391
BEBBINGTON, A. & THOMPSON, T. E. Reproduction in <i>Aplysia</i> (Gastropoda: Opisthobranchia) . . . . .	253
BERRIE, A. D. Factors affecting growth and reproduction of freshwater Planorbidae in East Africa . . . . .	35
BINDER, E. Cephalic accessory sexual organ of <i>Gymnarion</i> : speciation and phylogeny (Pulmonata: Helicarionidae). . . . .	59
BOSS, K. J. Systematics of the Vesicomylidae (Mollusca: Bivalvia). . . . .	254
BOVARD, P., FOULQUIER, L. & GRAUBY, A. Etude de la cinétique et de la répartition du Radiocésium chez un bivalve d'eau douce ( <i>Unio requieni</i> Mich.). . . . .	65
BROWN, S. C. The structure and function of the digestive system of the mud snail <i>Nassarius obsoletus</i> (Say) . . . . .	447
BRUGGEN, A. C. van Notes on the distribution of terrestrial molluscs in Southern Africa. . . . .	256
BURCH, J. B. & LINDSAY, G. K. An immuno—cytological study of the African subgenus <i>Bulinus</i> s.s. . . . .	37

BURCH, J. B. & PATTERSON, C. M.	
The systematic position of the Athoracophoridae (Gastropoda: Euthyneura) . . . . .	259
BUTOT, L. J. M. & KIAUTA, B.	
Cytotaxonomic observations in the stylommatophoran family Helicidae, with considerations on the affinities within the family . . .	261
CHEVALLIER, H.	
Taxonomie et biologie des grands <i>Arion</i> de France (Pulmonata: Arionidae) . . . . .	73
CLARKE, A. H.	
Some aspects of adaptive radiation in recent freshwater molluscs. . .	263
COOMANS, H. E.	
Biological aspects of mangrove molluscs in the West Indies . . . . .	79
D'ASARO, C. N.	
The comparative embryogenesis and early organogenesis of <i>Bursa corrugata</i> Perry and <i>Distorsio clathrata</i> Lamarck (Gastropoda: Prosobranchia). . . . .	349
DUNDEE, D. S.	
Introduced molluscs of the United States . . . . .	264
EEDEN, J. A. van & COMBRINCK, C.	
The influence of the substratum on population increase and habitat selection by <i>Lymnaea natalensis</i> Krs. and <i>Bulinus (B.) tropicus</i> Krs. (Mollusca: Basommatophora) . . . . .	39
ETGES, F. J. & MALDONADO, J. F.	
The present status of bilharziasis in the Dominican Republic . . . . .	40
FOURNIE, J. & CHETAIL, M.	
Physiologie de l'organe de perforation de <i>Purpura (Thais) lapillus</i> . Role de l'anhydrase carbonique . . . . .	265
GIROD, A.	
Distribution and ecology of Helicodontinae in Northern Italy. . . . .	267
GITTENBERGER, E.	
Die Gattung <i>Trissexodon</i> Pilsbry . . . . .	267
GIUSTI, F.	
A malacological survey of the small Tuscan Islands . . . . .	85
HADL, G.	
Beiträge zur Ökologie und Biologie der Pisiden des Lunzer Untersee . .	268
HAEFELFINGER, H. R.	
Zur Systematik der Glossodoridier des Mittelmeeres . . . . .	93

HOHORST, W.	Die Biotope der Leberegelschnecke ( <i>Galba truncatula</i> ) und ihre Bedeutung. . . . .	42
MEAD, A. R.	<i>Aeromonas liquefaciens</i> in the leucodermia syndrome of <i>Achatina fulica</i> . . . . .	43
MEULEMAN, E. A.	The ultrastructure of the digestive—gland cells of <i>Biomphalaria pfeifferi</i> Krs., an intermediate host of <i>Schistosoma mansoni</i> Sambon. . . . .	43
JOOSSE, J. & REITZ, D.	Functional anatomical aspects of the ovotestis of <i>Lymnaea stagnalis</i> (L.). . . . .	101
KIAUTA, B. & BUTOT, L. J.	Contribution to the knowledge of the cytotaxonomic conditions in the stylommatophoran superfamily Zonitacea. . . . .	269
KNUDSEN, J.	Remarks on the biology of abyssal bivalves. . . . .	271
KRAEMER, L. R.	Flapping behavior in the Lampsilinae (Pelecypoda: Unionidae): Some aspects of its neurobiology. . . . .	272
KROLOPP, E.	Faunengeschichtliche Untersuchungen im Karpatenbecken . . . . .	111
LARYEA, A. A.	The arterial gland of <i>Agriolimax reticulatus</i> (Pulmonata: Limacidae). . . . .	273
LLOYD, D. C.	Studies on the odour of <i>Oxychilus alliarius</i> (Pulmonata: Zonitidae). . . . .	274
LUCAS, A.	Remarques sur l'hermaphroditisme juvenile de quelques Veneridae (Bivalvia). . . . .	275
MARAZANOF, F.	Contribution a l'etude ecologique des mollusques des eaux douces et saumatres de Camargue. . . . .	277
MARINESCU, F.	<i>Velutinellus</i> , nouveau genre fossile de la famille des Lymnaeidae, et ses relations avec <i>Velutinopsis</i> et <i>Valenciennius</i> . . . . .	313
MEIER-BROOK, C.	Substrate relations in some <i>Pisidium</i> species (Eulamellibranchiata: Sphaeriidae). . . . .	121

MORPHY, M. J., ROSS, J. G. & TAYLOR, S. M.	
Problems of <i>Lymnaea truncatula</i> ecology in investigations of fascioliasis. . . . .	127
MORRISON, J. P. E.	
Zoogeography of hydrobiid cave snails . . . . .	278
NATARAJAN, R.	
Cytological studies of Indian molluscs (Archaeogastropoda: Neritidae). . . . .	279
NAWRATIL, O.	
Probleme der Massenvermehrung von <i>Helix pomatia</i> L. (Weinbergschnecken). . . . .	135
OBERZELLER, E.	
Die Verwandtschaftsbeziehungen der <i>Rhodope veranii</i> Köll. zu den Oncidiiden, Vaginuliden und Rathouisiiden in Bezug auf das Nervensystem . . . . .	282
ØKLAND, J.	
Distribution and ecology of the freshwater snails (Gastropoda) of Norway. . . . .	143
PAGET, O. E.	
Presidential address (Third European Malacological Congress). . . .	9
PETITJEAN, M.	
Le Strontium dans la coquille des Muricidés (No Abstract received) .	
POSTMA, N.	
Seven reproducible characteristics of mechanical behaviour in the snail's foot musculature ( <i>Helix pomatia</i> L.) . . . . .	153
PURCHON, R. D. & BROWN, D.	
Phylogenetic interrelationships among families of bivalve molluscs. .	163
RADOMAN, P.	
On the taxonomy and biogeography of Hydrobiidae . . . . .	173
RAVERA, O.	
Population characteristics of <i>Viviparus ater</i> Christofori and Jan (Gastropoda: Prosobranchia) from two habitats of Lago Maggiore (Northern Italy) . . . . .	284
RENZONI, A.	
Observations on the tentacles of <i>Vaginulus borellianus</i> Colosi . . . .	284
RICHARDS, C. S.	
Genetic studies on <i>Biomphalaria glabrata</i> : tentacle and eye variations . .	327
RICHARDS, C. S.	
Genetic studies on <i>Biomphalaria glabrata</i> : mantle pigmentation . . .	339

RUNHAM, N.W.	
The use of the scanning electron microscope in the study of the gastropod radula: The radulae of <i>Agriolimax reticulatus</i> and <i>Nucella lapillus</i> . . . . .	179
SALEUDDIN, A. M. S.	
Isoenzymes of alkaline phosphatase of <i>Anodonta grandis</i> Say (Bivalvia) during shell regeneration . . . . .	501
SALVAT, B.	
Dominance biologique de quelques mollusques dans les atolls fermes (Tuamotu, Polynesie). . . . .	187
SALVINI-PLAWEN, L. v.	
Solenogastres und Caudofoveata (Mollusca: Aculifera): Organisation une phylogenetische Bedeutung . . . . .	191
SCHALIE, H. van der	
American mussel resources in relation to the Japanese pearl industry . . . . .	285
SCHALIE, H. van der	
The control of schistosome dermatitis in the Great Lakes region (U.S.A.) . . . . .	44
SESHAIYA, R. V.	
Some observations on the life-histories of South Indian freshwater mussels . . . . .	286
SIEBER, R.	
Lebensformen fossiler Bivalven. . . . .	288
SOLEM, A.	
Phylogenetic position of the Succineidae. . . . .	289
STARMÜHLNER, F.	
Zur Molluskenfauna des Felsitoral von Rovinj (Istrien). . . . .	217
STOHLER, R.	
Growth studies on <i>Olivella biplicata</i> (Sow. 1825). . . . .	290
STRAUCH, F.	
The influence of climate on the adult size of recent and fossil <i>Hiatella arctica</i> (L.) and its importance for determination of palaeotemperature . . . . .	291
STRUHSAKER, J. W. & COSTLOW, J. D., Jr.	
Some environmental effects on the larval development of <i>Littorina picta</i> (Mesogastropoda), reared in the laboratory . . . . .	403
TRUEMAN, E. R.	
The fluid dynamics of molluscan locomotion . . . . .	243

VOVELLE, J.	Elaboration de la matière operculaire chez <i>Tricolia pullus</i> (L.) (Gasteropode: Prosobranche) . . . . .	293
Waidhofer, C.	Anatomische Untersuchungen des Zentralnervensystems von <i>Fimbria fimbria</i> (Boh.) und <i>Melibe leonina</i> (Gould) (Gastropoda: Opisthobranchia) . . . . .	295
WALDEN, H.	Recent advances in land mollusc research in Sweden . . . . .	297
WARWICK, T.	Systematics of the genus <i>Potamopyrgus</i> (Hydrobiidae) in Europe, and the causation of the keel in this snail. . . . .	301
WONDRAK, G.	Die Ultrastruktur der Sohlendrüsenzellen von <i>Arion rufus</i> L. . . . .	303
YOUNG, D. K.	The functional morphology of the feeding apparatus of some Indo-West-Pacific dorid nudibranchs . . . . .	421
ZILCH, A.	Report on the General Assembly of Unitas Malaologica Europae . . .	17

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PROCEEDINGS of the THIRD

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HARVARD  
UNIVERSITY.

PROCEEDINGS

of the

Symposium on MOLLUSCS AS PARASITES OR THEIR TRANSMITTERS

and the

THIRD EUROPEAN MALACOLOGICAL CONGRESS

(Vienna, 2-6 September 1968)

*Edited by Oliver E. PAGET*

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## PREFACE

Since the Third European Malacological Congress was to be held in Vienna, Austria, exceptional possibilities existed to unite malacologists from Western and Eastern Europe in a neutral country for scientific lectures and discussions. Although the advance registration allowed hopes for a great success in this respect, adverse political circumstances at the very last minute blasted these expectations. This is especially regrettable because Vienna offers special suppositions for such an international meeting.

In continuation of the attempt carried out so successfully in Copenhagen, a two-days' -Symposium preceded the Congress which was dedicated to the topic "Molluscs as parasites or their transmitters."

I want to express my warmest thanks to the members of the Organizing Committee who were of great support in preparing the Congress. The same goes for all those who have contributed to the success of the arrangements in one way or another. The willingness of the session Chairmen, who were invited by me to chair the various sessions, was greatly appreciated. The excursions were excellently guided by the following scientists (in alphabetical order): Prof. Dr. F. Bachmayer, W. Backhuys, L. Butot, E. Gittenberger, G. Hadl, W. Klemm, Dr. H. Kollmann and Prof. Dr. W. Kühnelt.

It is a pleasure for me to thank the Austrian Ministry of Education, the UNITAS MALACOLOGICA EUROPAEA, and the Society of Friends of the Natural History Museum for their financial support, which was willingly given to support the Congress. Especially I want to thank the Director of the Natural History Museum, Prof. Dr. K. H. Rechinger, who generously offered to me all the help the Museum could give. Also, I wish to thank Director Dr. E. Becker-Donner (Museum of Ethnology) and the I.W.K. (Institute for Science and Art) who put their lecture halls at my disposal.

Sincerest thanks and appreciation are due also to Dr. J. B. Burch and the editors of MALACOLOGIA, who declared their readiness to publish the Proceedings of the Congress under most generous conditions as a special volume of MALACOLOGIA. In doing this, they have taken a very heavy burden off of the Organizing Committee and have given a most valuable contribution to the final success of the Congress.

O. E. PAGET  
(President)



CONTENTS

SYMPOSIUM ON MOLLUSCS AS PARASITES OR THEIR TRANSMITTERS  
and THIRD EUROPEAN MALACOLOGICAL CONGRESS

	Page
Preface . . . . .	iii
Introduction . . . . .	1
Program . . . . .	3
Excursions . . . . .	7
Presidential Address . . . . .	9
Report on the General Assembly of UNITAS MALACOLOGICA EUROPAEA . . . .	17
<u>Symposium on Molluscs as Parasites or their Transmitters</u>	
AZEVEDO, J. F. de, XAVIER, M. d. L., PEQUITO, M. M. & SIMÕES, M.: Contribution to the morphological and biochemical identification of some strains of the <i>Bulinus truncatus</i> group . . . . .	25
BERRIE, A. D.: Factors affecting growth and reproduction of freshwater Planorbidae in East Africa . . . . .	35
BURCH, J. B. & LINDSAY, G. K.: An immuno-cytological study of the African subgenus <i>Bulinus</i> s.s. . . . .	37
EEDEN, J. A. van & COMBRINCK, C.: The influence of the substratum on population increase and habitat selection by <i>Lymnaea natalensis</i> Krs. and <i>Bulinus</i> ( <i>B.</i> ) <i>tropicus</i> Krs. (Mollusca, Basommatophora). . . . .	39
ETGES, F. J. & MALDONADO, J. F.: The present status of Bilharziasis in the Dominican Republic. . . . .	40
HOHORST, W.: Die Biotope der Leberegelschnecke ( <i>Galba truncatula</i> ) und ihre Bedeutung. . . . .	42
MEAD, A. R.: <i>Aeromonas liquefaciens</i> in the leucodermia syndrome of <i>Achatina fulica</i> . . . . .	43
MEULEMAN, E. A.: The ultrastructure of the digestive-gland cells of <i>Biomphalaria pfeifferi</i> Krs., an intermediate host of <i>Schistosoma</i> <i>mansoni</i> Sambon. . . . .	43
SCHALIE, H. van der: The control of schistosome dermatitis in the Great Lakes region (U.S.A.). . . . .	44
<u>Third European Malacological Congress</u>	
ADEGOKE, O. S., DESSAUVAGIE, T. F. J. & YOLOYE, V. L. A.: Biology and population dynamics of two sympatric species of <i>Neritina</i> from Southern Nigeria. . . . .	47
ALVAREZ, J.: Über die Verbreitung der Land- und Süßwasserschnecken in Mittelspanien in bezug auf die verschiedenen Böden und Gewässer. . . . .	53
ANT, H.: Zur würm-glazialen Überdauerung europäischer Landgastropoden in Eisrandnähe. . . . .	249
BACKHUYS, W.: The elevation-effect in <i>Cylindrus obtusus</i> (Drap. 1805). . . . .	251
BEBBINGTON, A. & THOMPSON, T. E.: Reproduction in <i>Aplysia</i> (Gastropoda, Opisthobranchia). . . . .	253
BINDER, E.: Cephalic accessory sexual organ of <i>Gymnavion</i> : speciation and phylogeny (Pulmonata, Helicarionidae). . . . .	59
BOSS, K. J.: Systematics of the Vesicomylidae (Mollusca, Bivalvia). . . . .	254
BOVARD, P., FOULQUIER, L. & GRAUBY, A.: Etude de la cinetique et de la repartition du Radiocesium chez un bivalve d'eau douce ( <i>Unio requieni</i> Mich.). . . . .	65
BRUGGEN, A. C. van: Notes on the distribution of terrestrial molluscs in Southern Africa. . . . .	256

CONTENTS (Continued)

BURCH, J. B. & PATTERSON, C. M.: The systematic position of the Athoracophoridae (Gastropoda, Euthyneura). . . . .	259
BUTOT, L. J. M. & KIAUTA, B.: Cytotaxonomic observations in the stylommatophoran family Helicidae, with considerations on the affinities within the family. . . . .	261
CHEVALLIER, H.: Taxonomie et biologie des grands <i>Arion</i> de France (Pulmonata, Arionidae). . . . .	73
CLARKE, A. H.: Some aspects of adaptive radiation in recent freshwater molluscs. . . . .	263
COOMANS, H. E.: Biological aspects of mangrove molluscs in the West Indies. . . . .	79
DUNDEE, D. S.: Introduced molluscs of the United States. . . . .	264
FOURNIE J. & CHETAIL, M.: Physiologie de l'organe de perforation de <i>Purpura (Thais) lapillus</i> : role de l'anhydrase carbonique . . . . .	265
GIROD, A.: Distribution and ecology of Helicodontinae in Northern Italy. . . . .	267
GITTENBERGER, E.: Die Gattung <i>Trissexodon</i> Pilsbry. . . . .	267
GIUSTI, F.: A malacological survey of the small Tuscan Islands. . . . .	85
HADL, G.: Beiträge zur Ökologie und Biologie der Pisidien des Lunzer Untersee. . . . .	268
HAEFELFINGER, HR.: Zur Systematik der Glossodoridinae des Mittelmeeres. . . . .	93
JOOSSE, J. & REITZ, D.: Functional anatomical aspects of the ovotestis of <i>Lymnaea stagnalis</i> (L.). . . . .	101
KIAUTA, B. & BUTOT, L. J.: Contribution to the knowledge of the cytotaxonomic conditions in the stylommatophoran superfamily Zonitacea . . . . .	269
KNUDSEN, J.: Remarks on the biology of abyssal bivalves. . . . .	271
KRAEMER, L. R.: Flapping behavior in the Lampsilinae (Pelecypoda, Unionidae): Some aspects of its neurobiology. . . . .	272
KROLOPP, E.: Faunengeschichtliche Untersuchungen im Karpatenbecken. . . . .	111
LARYEA, A. A.: The arterial gland of <i>Agriolimax reticulatus</i> (Pulmonata, Limacidae). . . . .	273
LLOYD, D. C.: Studies on the odour of <i>Oxychilus alliarius</i> (Pulmonata, Zonitidae). . . . .	274
LUCAS, A.: Remarques sur l'hermaphroditisme juvenile de quelques Veneridae (Bivalvia). . . . .	275
MARAZANOF, F.: Contribution a l'etude ecologique des mollusques des eaux douces et saumâtres de Camargue. . . . .	277
MEIER-BROOK, C.: Substrate relations in some <i>Pisidium</i> species (Eulamellibranchiata, Sphaeriidae). . . . .	121
MORPHY, M. J., ROSS, J. G. & TAYLOR, S. M.: Problems of <i>Lymnaea truncatula</i> ecology in investigations of fascioliasis. . . . .	127
MORRISON, J. P. E.: Zoogeography of hydrobiid cave snails. . . . .	278
NATARAJAN, R.: Cytological studies of Indian molluscs (Archaeogastropoda, Neritidae). . . . .	279
NAWRATIL, O.: Probleme der Massenvermehrung von <i>Helix pomatia</i> L. (Weinbergschnecken). . . . .	135
OBERZELLER, E.: Die Verwandtschaftsbeziehungen der <i>Rhodope veranii</i> Köll. zu den Oncidiidae, Vaginulidae und Rathouisiidae in bezug auf das Nervensystem. . . . .	282

CONTENTS (Continued)

ÖKLAND, J.: Distribution and ecology of the freshwater snails (Gastropoda) of Norway. . . . .	143
PETITJEAN, M.: Le Strontium dans la coquille des Muricidés [no abstract received] . . . . .	..
POSTMA, N.: Seven reproducible characteristics of mechanical behaviour in the snail's foot musculature ( <i>Helix pomatia</i> L.). . . . .	153
PURCHON, R. D. & BROWN, D.: Phylogenetic interrelationships among families of bivalve molluscs. . . . .	163
RADOMAN, P.: On the taxonomy and biogeography of Hydrobiidae. . . . .	173
RAVERA, O.: Population characteristics of <i>Viviparus ater</i> Christofori & Jan (Gastropoda, Prosobranchia) from two habitats of Lago Maggiore (Northern Italy). . . . .	284
RENZONI, A.: Observations on the tentacles of <i>Vaginulus borellianus</i> Colosi. . . . .	284
RUNHAM, N. W.: The use of the scanning electron microscope in the study of the gastropod radula: The radulae of <i>Agriolimax reticulatus</i> and <i>Nuccella lapillus</i> . . . . .	179
SALVAT, B.: Dominance biologique de quelques mollusques dans les atolls fermes (Tuamotu, Polynesie). . . . .	187
SALVINI-PLAWEN, L. v.: Solenogastres und Caudofoveata (Mollusca, Aculifera): Organisation und phylogenetische Bedeutung. . . . .	191
SCHALIE, H. van der: American mussel resources in relation to the Japanese pearl industry. . . . .	285
SESHAIYA, R. V.: Some observations on the life-histories of South Indian freshwater mussels. . . . .	286
SIEBER, R.: Lebensformen fossiler Bivalven. . . . .	288
SOLEM, A.: Phylogenetic position of the Succineidae. . . . .	289
STARMÜHLNER, F.: Zur Molluskenfauna des Felslitorals von Rovinj (Istrien). . . . .	217
STOHLER, R.: Growth studies on <i>Olivella biplicata</i> (Sow. 1825). . . . .	290
STRAUCH, F.: The influence of climate on the adult size of recent and fossil <i>Hiatella arctica</i> (L.) and its importance for determination of palaeotemperature. . . . .	291
TRUEMAN, E. R.: The fluid dynamics of molluscan locomotion. . . . .	243
VOVELLE, J.: Elaboration de la matière operculaire chez <i>Tricolia</i> <i>pullus</i> (L.) (Gastropoda, Prosobranchia). . . . .	293
WADHOFER, Ch.: Anatomische Untersuchungen des Zentralnerven- systems von <i>Fimbria fimbria</i> (Boh.) und <i>Melibe leonina</i> (Gould) (Gastropoda, Opisthobranchia). . . . .	295
WALDEN, H.: Recent advances in land mollusc research in Sweden. . . . .	297
WARWICK, T.: Systematics of the genus <i>Potamopyrgus</i> (Hydrobiidae) in Europe, and the causation of the keel in this snail. . . . .	301
WONDRAK, G.: Die Ultrastruktur der Sohlendrüsenzellen von <i>Arion rufus</i> L. . . . .	303
List of participants . . . . .	307
Index . . . . .	313





## INTRODUCTION

The Third European Malacological Congress took place in Vienna, Austria, at the Museum of Natural History, from September 4th to 6th, 1969. The Congress was preceded by a Symposium on September 2nd to 3rd with the topic: "Molluscs as parasites or their transmitters."

The General Assembly of UNITAS MALACOLOGICA EUROPAEA was held on September 6th at the Natural History Museum.

The Symposium was welcomed by Dr. Oliver E. Paget, President of the Congress and of UNITAS MALACOLOGICA EUROPAEA. At the opening session, Dr. Paget had the pleasure to welcome not only 155 participants from 27 countries (9 of which are outside Europe), but also as guests of honour his excellency, the Minister of Education, Dr. Th. Piffel-Percevic, and the Director of the Natural History Museum, Prof. Dr. K. H. Rechinger, both of whom also gave addresses of welcome. The Minister expressed the special interest both he and the Ministry had in the Congress and its results. He assured the Congress that the further development of the Department of Molluscs of the Natural History Museum would be taken into sympathetic consideration and support. After the opening of the Congress, the Minister, the Director and the participants visited the new exhibition on Molluscs at the Museum.

During the Congress, four excursions were undertaken to Rax, Bad Fischau and Bad Vöslau, Vösendorf, and to Mödling.

On the first day, September 4th, all the participants of the Congress were invited by Bruno Marek, Lord Mayor, to the Vienna Town Hall. Next day there was a reception at the Natural History Museum, given by the Organizing Committee, the Directory of the Natural History Museum, and the Society of Friends of the Natural History Museum. At both occasions the members of the Congress used the opportunity to renew old friendships and connections, and to make new ones.



PROGRAM

SYMPOSIUM ON MOLLUSCS AS PARASITES OR THEIR TRANSMITTERS

September 2nd Chairman: H. Hohorst

Morning Session

BURCH, J. B.: An immuno-cytological study of the African subgenus *Bulinus* s.s.

ETGES, F. J.: The present status of bilharziasis in the Dominican Republic.

MEULEMAN, F. A.: The ultrastructure of the digestive gland-cells of *Biomphalaria pfeifferi*, an intermediate host of *Schistosoma mansoni*.

September 2nd Chairman: J. B. Burch

Afternoon Session

SCHALIE, v. d.: The control of *schistosoma* dermatitis in the Great Lakes Region (U. S. A.).

AZEVEDO, J. Fraga de: Classification of *Trematoda* vector snails by biochemical methods and its importance.

MEAD, A.: *Aeromonas liquefaciens* in the leucodermia syndrome of *Achatina fulica*.

September 3rd Chairman: J. A. v. Eeden

Morning Session

HOHORST, W.: Biotope der Leberegelschnecke *Galba truncatula* und ihre Besiedlung.

BERRIE, A. D.: Factors effecting growth and reproduction of freshwater Planorbidae in East Africa.

EEDEN, J. B. v.: Aspects of the substratum as a factor in the biology of *Lymnaea natalensis* Krauss and *Bulinus tropicalis* Krauss.

THIRD EUROPEAN MALACOLOGICAL CONGRESS

Sections A + B: Systematics, Faunistics, Physiology, Genetics

Sections C + D: Ecology, Zoogeography, Anatomy, Biogeny

September 4th Chairman: H. Lemche Section A + B

Afternoon Session

SALVINI-PLAWEN, L. v.: Solenogastres und Caudofoveata- ihre Organisation und phylogenetische Bedeutung.

PURCHON, R. D.: Phylogenetic interrelationships among families of bivalve molluscs.

RADOMAN, P.: Taxonomie der Hydrobiidae.

ALVAREZ, J.: Eine neue Methode zur Präparation von Süßwasser-conchylien.

STARMÜHLNER, F.: Neu-Kaledonien (invited lecture).

## PROGRAM (Continued)

September 4th      Chairman: H. Janus      Section C + D

Afternoon Session

- ALVAREZ, J.: Über die Verbreitung von Land- und Süßwasserschnecken in Mittelspanien in bezug auf Böden und Gewässer.  
 ANT, H.: Zur würm-glazialen Überdauerung europäischer Landgastropoden in Eisrandnähe.  
 ÖKLAND, J.: Distribution and ecology of the freshwater snails of Norway.  
 CLARKE, A.: Adaptive radiation in North American freshwater molluscs.

September 5th      Chairman: F. Star m ü h l n e r      Section A + B

Morning Session

- BOSS, K.: Deep-sea bivalves, the genus *Vesicomya* and its relatives.  
 SOLEM, A.: Phylogenetic position of the Succinaeidae.  
 GIUSTI, F.: A malacological survey of the Tuscan Little Islands.  
 GITTENBERGER, E.: Die Gattung *Trissexodon*.

September 5th      Chairman: F r a g a d e A z e v e d o      Section A + B

Morning Session

- BACKHUYS, W.: Der Elevationseffekt bei *Cylindrus obtusus* Drap.  
 BUTOT, L.: Cytotaxonomic observations in the stylommatophoran family Helicidae.  
 KROLOPP, E.: Faunengenetische Untersuchungen im Karpatenbecken.  
 STRAUCH, F.: Klimaabhängiges Größenwachstum bei *Hiatella arctica*.  
 BEBBINGTON, A.: Reproduction in *Aplysia*.

September 5th      Chairman: B. Salvat      Section C + D

Morning Session

- BINDER, E.: Cephalic accessory sexualorgan of *Gymnarrion*-speciation and phylogeny.  
 GIUSTI, F.: The fine structure of the alimentary canal in *Mytilus gallo-provincialis* Lam.  
 RENZONI, A.: Observations on the tentacles of gastropods.  
 JOOSSE, J.: Anatomy and function of the reproductive system of *Lymnaea stagnalis*.  
 KIAUTA, B. (read by Butot): Contribution to the knowledge of the cytological conditions in the stylommatophoran family Vitrinidae.  
 LARYEA, A.: The arterial gland of *Agriolimax reticulatus*.  
 LUCAS, A.: Remarques sur l'hermaphrodisme juvenile de quelques Veneridae (Bivalves).

September 5th      Chairman: O. E. Paget      Section A + B

Afternoon Session

- POSTMA, N.: Über das mechanische Verhalten der Muskulatur des Schneckenfusses.  
 LLOYD, D.: The odour of *Oxychilus alliarius*.

## PROGRAM (Continued)

FOULQUIER, L.: Etude de la cinétique et de la repartition du radiocésium chez un bivalve d'eau douce.

KRAEMER, L. R.: Flapping behavior in the Lampsilinae (Pelecypoda, Unionidae): some aspects of its neurobiology.

PEAKE, J.: Solomon- Islands (invited lecture).

September 5th Chairman: R. Schlickum Section C + D

## Afternoon Session

KNUDSEN, J.: Remarks on the biology of abyssal bivalves.

MEIER-BROOK, C.: Substrate relations in some *Pisidium*-species.

SIEBER, R.: Ökologie und Lebensformen fossiler Bivalven.

September 5th Chairman: F. Starmühlner Section C + D

## Afternoon Session

OBERZELLER, E.: Verwandtschaftsbeziehungen der *Rhodope veranyi* zu den Soleolifera in bezug auf das Nervensystem.

WADHOFER, Chr.: Vergleichende Untersuchungen über das Nervensystem von *Fimbria fimbria* und *Melibe leonina* (Opisthobranchia).

VOVELLE, J.: Elaboration des matériaux operculaire chez Prosobranches.

WONDRAK, G.: Das elektronenoptische Bild des Sekretionsablaufes in Söhlendrüsenzellen von *Arion rufus*.

HADL, G.: Anatomische Merkmale bei einigen *Pisidium*-Arten und der Einfluss des Parasitismus.

RUNHAM, N.: Scanning electron microscope studies on the mollusc radula.

September 6th Chairman: L. Salvini-Plawen Section A + B

## Morning Session

PETITJEAN, M.: Le strontium dans la coquille des Muricidae.

TRUEMAN, E.: The fluid dynamics of molluscs.

FOURNIE, J. & CHETAÏL, M.: Role de l'anhydrase carbonique dans l'organe de perforation de *Purpura (Thais) lapillus*.

RAVERA, O.: Population characteristics of *Viviparus ater* settled in two habitats of a subalpine lake- Lago Maggiore.

STARMÜHLNER, F.: Die Molluskenfauna des Felslitorals der Nordadria.

HAEFELFINGER, HR.: Die Glossodoridier des Mittelmeers.

September 6th Chairman: N. Postma Section C + D

## Morning Session

BRUGGEN, A.: On the distribution of terrestrial molluscs in Southern Africa.

CHEVALLIER, H.: Biologie des Limaciens du genre *Arion* en France.

DUNDEE, D.: Introduced molluscs of the United States.

GIROD, A.: La distribution du genre *Helicodonta* dans le Nord de l'Italie.

NAWRATIL, O.: Biologie und Zucht der Weinbergschnecke *Helix pomatia* L.

MORPHY, M. J.: Problems of *Lymnaea truncatula* ecology in investigations of fascioliasis.

## PROGRAM (Continued)

STOHLER, R.: Growth studies on *Olivella biplicata*.

September 6th      Chairman: F. Toffoletto      Section A + B

Afternoon Session

WARWICK, T.: Systematics and shell ornamentation in the prosobranch  
*Potamopyrgus* in Europe.

COOMANS, H.: Biological aspects of mangroove molluscs in the West Indies.

BURCH, J. B.: The systematic position of the Athoracophoridae.

ANGELETTI, S.: My new book on shells.

September 6th      Chairman: S. P. Dance      Section C + D

Afternoon Session

SALVAT, B.: Dominance biologique de quelques especes de mollusques dans  
les atolls fermes (Archipel des Tuamotu, Polynesia).

SCHALIE, H. v. d.: American mussel resources in relation to the Japanese  
pearl industry.

MARAZANOFF, F.: Contribution à l'étude écologique des mollusques des  
eaux douces et saumatres de Camargue.

MORRISON, J.: Zoogeography of hydrobiid cave-snails.

WALDÉN, H.: Recent advances in landmollusc-research in Scandinavia.

EXCURSIONS

The Rax-alp (September 3rd)

Two groups, guided by E. Gittenberger and W. Backhuys.

Vienna woods, Klosterneuburg - Ladies' program (September 4th)

A whole-day excursion toured the monastery and famous Altar of Verdun.

Mödling (September 5th)

Two groups guided by W. Klemm and L. Butot.

City tour - Ladies' program (September 5th)

Fischau (September 6th)

Two groups guided by W. Kühnelt and G. Hadl.

Leopoldsdorf (September 6th)

A paleontological excursion guided by F. Bachmayer and H. Kollmann.

Porcelain manufacture - Ladies' program (September 6th)

Museum of Fine Arts, Imperial Treasure, "Heurigen" (September 7th)

Tour of Austria, 4 days (departed September 8th)





PRESIDENTIAL ADDRESS

Ladies and gentlemen!

I am fully aware of the fact that English, without doubt, is the language understood by most of all attending this Congress. Nevertheless, I ask for your understanding when giving my Presidential Address in German. German is the language of this country, and German is also one of the official languages of the European Malacological Congresses. Therefore, I hope you will understand my choosing German for this Address. Thank you!

Meine sehr geehrten Damen und Herren!

Ich glaube, diese kleine Einleitung jenen Kollegen schuldig gewesen zu sein, die die deutsche Sprache nicht vollständig beherrschen.

Auf diesem Kongress wird so viel und so ausführlich in den einzelnen Sektionen über malakologische Fragen gesprochen, dass ich mich entschlossen habe, insoferne aus dem Rahmen zu fallen, als ich kein fachliches Thema gewählt habe, sondern einige Probleme behandeln möchte, die sich mir im Zusammenhang mit diesem Kongress und vor allem in bezug auf das Aufgabengebiet der UNITAS und ihre internationale Zusammenarbeit aufgedrängt haben. Die UNITAS MALACOLOGICA EUROPAEA ist eine sehr junge Organisation und daher noch manchmal mit einigen Kinderkrankheiten behaftet. Viele und wichtige Aufgaben sind für diese Organisation vorgesehen. In erster Linie ist es die internationale jedoch auf Europa beschränkte Zusammenarbeit. Leider habe ich den Eindruck, dass sie bisher nur im Rahmen der üblichen und ausgezeichnet funktionierenden kollegialen Kontakte geblieben ist. Vielleicht werden Sie sich wundern, dass ich als derzeitiger Präsident der UNITAS an dieser eigenen Organisation Kritik übe. Ich möchte aber sagen, dass mir gerade deshalb ihr Gedeihen und ihre Zukunft und darüber hinaus ihre Schwächen besonders am Herzen liegen. Die Zeit meiner Präsidentschaft für diesen Kongress ist nur mehr auf wenige Tage beschränkt. Das gleiche gilt für die Präsidentschaft bei der UNITAS. Ich möchte daher diese Gelegenheit nicht vorübergehen lassen, ohne an Sie den Appell zu richten, durch Ihren Beitritt zu dieser Organisation jene Ziele zu unterstützen, die sie sich gestellt hat.

Ziele, die zweifellos im Interesse eines jeden einzelnen liegen und die nur erreicht werden können, wenn wir wirklich alle zusammenarbeiten. Hauptziel der UNITAS ist es, den europäischen Malakologen eine Dachorganisation zu geben, unter deren Auspizien die regelmässige Abhaltung von Kongressen gewährleistet wird. Während der übrigen 3 Jahre wird sie aber den Erwartungen nicht immer gerecht, die wir in sie gesetzt haben. Durch den regelmässigen Wechsel in der Präsidentschaft werden alle jene Projekte, die der jeweilige Präsident im Auge hat, die ihm besonders am Herzen liegen, nur kurz angeschnitten und fallen spätestens nach 3 Jahren wieder der Vergessenheit anheim. Meine Pläne lassen sich daher kurz in dem Satz zusammenfassen: Aktivierung der UNITAS durch Eigeninitiative, durch die Schaffung permanenter Komitees und die Koordinierung bestimmter Arbeiten. Unter Aktivierung der UNITAS verstehe ich nicht nur eine gewisse Reorganisation

in ihren Aufgaben, sondern diese Aktivierung muss in erster Linie von ihren Mitgliedern ausgehen. Um Ihnen deutlicher zu machen, was ich darunter verstehe, möchte ich nur eine einzige Tatsache anführen: Sowohl für diesen Kongress, als auch für den kommenden im Jahr 1971 mussten die Vorschläge für den Tagungsort wie auch für das Komitee und den Präsidenten vom Vorstand der UNITAS ausgehen, um den Anforderungen der Satzungen zu entsprechen. Von keiner anderen Seite und von keiner Gruppe von Einzelmitgliedern wurden Vorschläge eingereicht, die den Satzungen entsprachen. Ich weiss nun nicht, ob man diese Inaktivität einer gewissen Gleichgültigkeit der Mitglieder anlasten soll, oder nur dem übergrossen Vertrauen, das man in die Beschlüsse des Vorstandes setzt, dem man derartige Entscheidungen zur Gänze überlässt. So schmeichelhaft das einerseits wäre, so glaube ich doch, dass es sehr zu begrüessen ist, wenn durch ein regeres Interesse der Mitglieder jeweils mehrere Vorschläge zur Wahl des nächsten Präsidententeams als auch zur Wahl des neuen Tagungsortes vorliegen würden. Nicht nur die Auswahlmöglichkeiten wären grösser, sondern das Wesentliche daran ist, dass wir uns alle (und ich möchte mich dabei durchaus nicht ausschliessen), verantwortlich fühlen für das Geschick dieser von uns selbst geschaffenen Organisation, an der wir entweder als Mitglieder beteiligt oder in anderer Weise interessiert sind.

Ich möchte Ihnen aber darüber hinaus nun einige Vorschläge unterbreiten, die dieser Aktivität auch in anderer Richtung dienen sollen und möchte damit meinen Beitrag dazu leisten, die UNITAS zu einer lebendigen und aktiven Organisation zu gestalten.

Jeder, der einmal mit den Vorbereitungsarbeiten für Kongresse oder eine Tagung zu tun hatte, weiss, wieviel Arbeit dahintersteckt, die mit dem Ende des Kongresses meist nutzlos geworden ist. Die erste Hauptarbeit bei der Vorbereitung dieses Kongresses war es, alle in Frage kommenden Malakologen zu erfassen. Das Adressenmaterial, das ich im Laufe meiner Vorarbeiten für diesen Kongress zusammengetragen habe, umfasst annähernd 2.000 Adressen. In dieser Zahl sind alle Malakologen enthalten, deren ich habhaft werden konnte. Zweifellos fehlt noch ein beträchtlicher Teil. Aber es ist immerhin eine gute Ausgangsbasis und eine so grosse Zahl von Malakologen mit Adresse und Arbeitsgebiet zur Verfügung zu haben, wäre sicherlich für jeden von uns interessant, ist aber in den wenigsten Fällen wirklich zugänglich. Die Auswahl der erfassten Malakologen erfolgte nach den Mitgliederlisten der diversen malakologischen Gesellschaften, nach den Teilnehmerlisten der bisherigen Kongresse, sowie nach den Autoren malakologischer Arbeiten der letzten 10 Jahre in sämtlichen mir zur Verfügung stehenden malakologischen Zeitschriften. Diese Adressen werden natürlich fortlaufend ergänzt und dadurch die Liste erweitert. Nach der restlosen oder fast restlosen Erfassung aller Malakologen wäre es daran gelegen, die einzelnen Arbeitsgebiete durch die publizierten Arbeiten näher zu umreissen. Das würde zwar für jeden von Ihnen und für jeden, der dabei erfasst wird, zweifellos eine gewisse Arbeitsbelastung bedeuten. Ich bin aber davon überzeugt, dass sich jeder gerne dieser Aufgabe unterziehen wird im Hinblick auf den grossen Vorteil, den er dann daraus ziehen kann. Ich möchte nun in diesem Zusammenhang nicht den Eindruck erwecken, dass ich lediglich mit guten Ratschlägen vorangehe, deren Durchführung ich dann anderen überlasse. Es geht nämlich nicht so sehr um das Finden neuer Probleme (davon gibt es zweifellos genug), sondern in erster Linie um deren Durchführung. Ich möchte daher vor diesem Forum eine Feststellung treffen, die meinen

Vorschlägen einen realen Hintergrund gibt. Ich stelle die Ergebnisse meiner bisherigen Vorbereitungsarbeiten zur Erfassung aller Malakologen vollständig zur Verfügung. Ich bin darüber hinaus bereit, diese Arbeit fortzusetzen und damit allen Kollegen zugänglich zu machen. Es ist selbstverständlich, dass ich diese Arbeit nur mit Ihrer Mithilfe und der der übrigen Malakologen durchführen kann. Wesentlich wäre jedoch, dass mir die Generalversammlung der UNITAS diese Aufgabe offiziell überträgt.

Die Museen stellen zweifellos die Zentralstellen der allgemeinen Zusammenarbeit und die Keimzellen der malakologischen Forschung dar und damit zusammenhängend kann die Rolle der Museumskustoden gar nicht hoch genug eingeschätzt werden. Sie verwalten ausserordentlich wertvolle, umfangreiche und häufig auch historisch unschätzbare Sammlungen, die die Grundlagen der meisten Arbeiten darstellen oder aber für die Durchführung einer Arbeit durch die Fülle des vorhandenen Vergleichsmaterials von grösster Bedeutung sind. Ich möchte daher den Vorschlag machen, bei allen künftigen Kongressen jeweils einen Tag im Anschluss an die übrigen Beratungen für Besprechungen der Museumskustoden vorzusehen und für Fragen, die ausschliesslich die Museumsarbeiten betreffen. Leider war es für diesen Kongress noch nicht möglich, diesen Plan durchzuführen, ich wäre jedoch glücklich, wenn diese Anregung für die Zukunft aufgenommen würde.

Eine weitere Frage, die mir sehr am Herzen liegt und sicherlich auch manchem anderen, ist die Erfassung der jeweils neuesten Literatur. Das Studium der einschlägigen Literatur ist oft ausserordentlich zeitraubend und vielen Wissenschaftlern ist sie nicht immer in ausreichendem Mass zugänglich. Wenngleich an den meisten grossen Museen die entsprechende Literatur aufliegt, so gibt es doch zahlreiche kleinere Aufsätze, die nicht in malakologischen Zeitschriften publiziert werden und damit oft der Aufmerksamkeit entgehen. Die derzeitigen Zusammenfassungen erscheinen meist erst sehr spät und sind vor allem nicht jedem zugänglich. Im allgemeinen verfügen auch nur Museen und manche Institute darüber. Ich halte es daher für zweckmässig, eine Zentralstelle zu schaffen, die die Titel der gesamten publizierten malakologischen Literatur eines Jahres aus Europa sammelt und am Ende des jeweiligen Jahres hektographiert an die Interessenten versendet. Die Hauptfrage ist auch hier, wer sich dieser Aufgabe unterziehen soll. Auch in diesem Fall bin ich bereit, mich dieser sicherlich nicht kleinen Aufgabe zu widmen. Voraussetzung dafür wäre allerdings Ihre Mitarbeit und die Zusage jeweils eines Separatums an die Molluskensammlung des Naturhistorischen Museums in Wien. Sie werden nun vielleicht mit Recht der Ansicht sein, dass es sich dabei um eine sehr geschickte Methode handelt, meine Sammlungsbibliothek aufzuwerten und zu vergrössern. Das ist zweifellos richtig. Ich glaube aber, dass es trotzdem nur ein bescheidener Ausgleich wäre für die damit verbundene und sicherlich nicht geringe Arbeit. Vor allem aber ist es eine *conditio sine qua non*, denn ohne Ihre Mitarbeit ist dieser Plan von vornherein zum Scheitern verurteilt. Ausserdem wird diese Liste der eingelaufenen Separata jährlich an die Interessenten versendet, sodass nicht nur die "Bereicherung" der Sammlungsbibliothek im Vordergrund steht, sondern die Tatsache der besseren und schnelleren Information der Kollegen. Wenn auch einige der hier vorgebrachten und angeschnittenen Ideen bereits bei anderen Anlässen angedeutet oder angeregt wurden, so kann ich mich des Eindrucks nicht erwehren, dass es in fast allen bisherigen Fällen eben nur bei den Vorschlägen geblieben ist, weil die Durchführung der Arbeiten von niemandem übernommen werden wollte.

Die Tatsache jedoch, dass ich mich bereit erkläre, diese Aufgaben selbst zu übernehmen, enthebt Sie, meine Damen und Herren, der unangenehmen Belastung, ein Opfer dafür ausfindig zu machen. Ich möchte aber auch in diesem Fall vorschlagen, diese meine Anregungen in der Generalversammlung kurz zu diskutieren und durch Ihre Zustimmung ihr den Charakter einer offiziellen Beauftragung zu geben. Es würde mir damit sicherlich leichter gemacht werden, für diese Aufgabe nicht nur die Unterstützung der UNITAS, sondern auch die der offiziellen Stellen des österreichischen Unterrichtsministeriums zu erreichen. Wie Sie gehört haben, hat der Herr Bundesminister für Unterricht heute vormittag recht weitgehende Zusicherungen und Versprechungen gemacht, die mich hoffen lassen, dass in Zukunft die Belange der Mollusken-Sammlung des Naturhistorischen Museums in Wien von offizieller Stelle aus grössere Beachtung und Unterstützung finden werden.

Eine weitere, meiner Meinung nach sehr wesentliche Frage ist jene der Erfassung der wissenschaftlichen Sammlungen, seien sie nun Museums-, Instituts- oder Privatsammlungen. Mr. Dance hat in seinem Buch "Shell Collecting" in dieser Richtung einen ganz wesentlichen Beitrag geleistet, indem er die historisch wichtigen Sammlungen zusammengefasst hat. Es liegen bekanntlich auch von einigen Museen und Institutionen Publikationen vor, die eine Zusammenfassung der in ihnen enthaltenen Sammlungen bringen. Die Erfassung der historischen Sammlungen ist zweifellos von grossem Wert im Zusammenhang mit jenen Arbeiten, deren Grundlage sie darstellen. Ich bin aber der Ansicht, dass eine solche Zusammenfassung sich nicht nur auf jenes Material stützen sollte, das ein Mindestalter von 100 Jahren aufweisen muss, um in die Reihe dieser Auserwählten aufgenommen zu werden. Durch die Erfassung auch jüngerer Sammlungen und die möglichst genaue Beschreibung ihres Inhalts würde zahlreichen Kollegen die Möglichkeit gegeben werden, das für ihre Arbeiten notwendige Material ungeheuer zu erweitern und damit ihre Ergebnisse auf eine wesentlich breitere Basis stellen zu können. Bei der Abfassung von Monographien, bei vergleichenden Untersuchungen und Ähnlichem, kann das untersuchte Material nicht umfangreich genug sein. Und selbst in den Museen steht es nicht immer in ausreichendem Ausmass zur Verfügung. Durch eine möglichst umfangreiche und lückenlose Erfassung auch kleinerer Sammlungen bietet sich jedoch die Möglichkeit, über ein ungleich grösseres Reservoir zu verfügen. Material, das infolge seines relativ geringen Ausmasses niemals Grundlage für eine umfassende Arbeit sein könnte und damit brachläge, könnte damit der Vergessenheit und der Unbedeutendheit entrissen werden und als kleines Steinchen eines Mosaiks wertvolle Dienste leisten können. Und wenn wir alle, wie ich hoffe, uns zum Grundsatz der gemeinsamen Zusammenarbeit bekennen (und das tun wir sicherlich, sonst hätten wir uns nicht zu diesem Kongress zusammengefunden), dann darf es dabei keine Bedenken selbststüchtiger oder kleinlicher Art geben, die ein solches Vorhaben verhindern könnten. Mein Versuch, auch kleinere Sammlungen zu erfassen, hat recht gute Ergebnisse gebracht. Ich möchte auch an dieser Stelle all jenen danken, die der Aufforderung, an dieser Liste mitzuarbeiten, Folge geleistet haben. Diese Liste ist das Ergebnis meiner ersten versuchsweisen Umfrage und ich hoffe, dass eine Vervollständigung und ein weiterer Ausbau auch fernerhin Ihre Unterstützung finden wird, um nach und nach eine wirklich wertvolle Arbeitsunterlage damit zu erreichen.

Eine besondere Schwierigkeit stellen die Faunenlisten der einzelnen Länder dar. Wenngleich gute Ansätze vorliegen und für eine Reihe von Ländern bereits derartiges vorhanden ist, so bleibt noch sehr viel zu tun übrig, um

eine Fauna Malacologica Europaea zu erreichen. Es wäre äusserst verdienstvoll, wenn sich in jedem europäischen Land ein Museumskustos oder interessierter Malakologe fände, der diese zwar ausserordentlich zeitraubende und mühsame, aber ungemein verdienstvolle Arbeit übernähme. Lange Literatursuchen nach den Erstbeschreibungen würden in Zukunft erspart bleiben, zahllose Synonymiefragen könnten ein für allemal geklärt werden und damit den Malakologen Europas ein einmalig wertvolles Instrument in die Hand gegeben werden. Ich hoffe allerdings, dass Sie nicht annehmen, dass ich mich auch dieser Aufgabe unterziehen werde, denn das ginge wirklich über meine Kräfte.

Das Aufgabengebiet der UNITAS MALACOLOGICA EUROPAEA ist natürlich primär auf das europäische Gebiet beschränkt. Ich halte es aber für ausserordentlich wichtig, auch die Zusammenarbeit mit aussereuropäischen Vereinigungen zu fördern, ich erwähne nur die AMERICAN MALACOLOGICAL UNION, die AUSTRALIAN MALACOLOGICAL SOCIETY und andere. Hier in Europa stellt ja die UNITAS die Dachorganisation aller europäischen malakologischen Gesellschaften dar und bewahrt auf diese Weise den Zusammenhang. Wesentlich ist jedoch auch meiner Ansicht nach die Zusammenarbeit der kontinentalen Organisationen, in denen ja die kleineren Verbände zusammengeschlossen sind. Ich stelle mir die Zusammenarbeit in erster Linie so vor, dass durch Austausch der jeweiligen Publikationen oder Proceedings der wissenschaftliche Kontakt gegeben ist und damit eine Zusammenarbeit der Mitglieder derartiger Vereinigungen ermöglicht und erleichtert wird.

Es wäre Aufgabe der jeweiligen Präsidenten dieser Vereinigungen, miteinander Kontakt aufzunehmen und vielleicht sogar darüber hinaus eine gewisse Koordination der Themen von Symposien zu erreichen. Da nicht alle europäischen Malakologen Zugang zu aussereuropäischen Publikationen haben, sollte die UNITAS hier vermittelnd eingreifen und diese Verbindung zustandebringen.

Ich bitte, mich gerade in diesem Punkt nicht misszuverstehen. Ich bin ein glühender Verfechter der Separierung der europäischen Malakologen in einer eigenen Vereinigung, mit eigenen Kongressen. Ich bin strikt gegen eine internationale Vereinigung der Malakologen, die es in Hinkunft einem Grossteil der europäischen Malakologen unmöglich machen würde, die regelmässigen Kongresse zu besuchen. Und damit allein wäre schon eine der wesentlichsten Funktionen der UNITAS zunichte gemacht. Solange die Kongresse ausschliesslich in Europa abgehalten werden, ist es für die meisten von uns doch irgendwie im Bereich der Möglichkeiten, daran teilzunehmen. Was ich aber anregen möchte, ist eine lockere Verbindung der einzelnen grossen malakologischen Vereinigungen der Welt.

Bewahren wir uns unsere Unabhängigkeit, stellen wir das grosse Aufgabengebiet Europa in den Mittelpunkt unserer Betrachtungen, streben wir aber jene Verbindungen mit aussereuropäischen Vereinigungen an, die unsere Arbeiten erst sinnvoll machen durch das gemeinsame Ziel der malakologischen Forschung. Und wenn sich die UNITAS MALACOLOGICA EUROPAEA dieser Vermittler- und Verbindungsrolle besinnt, wenn sie diese einmalige Chance ergreift, die sie im weltweiten Rahmen einnehmen könnte, dann würde sie in Zukunft jene Bedeutung gewinnen, die ich ihr als scheidender Präsident von ganzem Herzen wünsche!

## RÉSUMÉ

## Presidential Address by Dr. PAGET

By the following suggestions the activity of UNITAS, up to now mostly limited to the organisation of Congresses, shall be activated.

- 1) Invitation to all members to prove their interest in the UNITAS by active cooperation with suggestions for the committees and places for coming congresses.
  - 2) Comprehension of all malacologists together with their field of work. x)
  - 3) Appreciation of the importance of museum-collections and their curators by including in coming congresses an extra day for discussion of their problems.
  - 4) Comprehension of the newest malacological literature of a current year by sending the published papers to Dr. Paget. Annually a list will be sent to all participants. x)
  - 5) Continuing comprehension of private-museum and institute-collections to complete the started list. x)
  - 6) Fauna lists of all European countries, according to the newest system with the final aim of a Fauna Europaea.
  - 7) Cooperation of the large continental malacological organisations by exchange of the "Proceedings," and making them available to all members at the different congresses.
  - 8) Creation of a permanent UNITAS-Committee, the members of which are willing to work on these tasks without termination and independently of the congresses.
- x) For all projects, mentioned under 2), 4) and 5), Dr. Paget is willing to work on them when authorized by the UNITAS.

Voici quelques propositions par lesquelles l'activité de l'UNITAS, qui, jusqu'à maintenant s'est bornée à l'organisation des congrès réguliers, devrait être intensifiée:

- 1) Les participants devraient faire preuve de leur intérêt vis-à-vis de cette organisation en faisant des propositions concernant les lieux de congrès et les comités.
- 2) Le recensement de tous les malacologues en indiquant l'orientation de leurs recherches. x)
- 3) La mise en valeur de l'importance des collections de musées et de leurs directeurs de section responsables en consacrant une journée entière à leurs problèmes au cours des congrès.
- 4) Le recensement des travaux récents dans le domaine de la malacologie pour un an en Europe en envoyant à M. Paget les travaux en question. Tous les ans, une liste sera envoyée à tous les participants. x)
- 5) Le recensement intensifié des collections privées et des collections appartenant à des instituts différents et la continuation de la liste actuelle. x)
- 6) La création d'un ensemble de listes sur la faune des pays européens d'après le système de plus moderne en vue d'une faune européenne.
- 7) La collaboration des grandes organisations des malacologues par l'échange

des publications respectives. Aux différents congrès les participants devraient avoir accès à ces travaux.

- 8) La création d'un comité permanent de l'UNITAS, dont les membres se chargeront de l'exécution de ces travaux sans limite temporelle.
- x) M. Paget se déclare prêt d'effectuer les travaux cités sous 2), 4) et 5) si l'UNITAS les lui confère.





REPORT ON THE GENERAL ASSEMBLY OF  
UNITAS MALACOLOGICA EUROPAEA

by the Secretary, Dr. A. ZILCH

The 1968 meeting of the General Assembly of UNITAS MALACOLOGICA EUROPAEA took place at the Vienna Natural History Museum on Friday, September 6, at 6:00 p.m. Sixty-five members were present. We again thank Mr. G. I. Crawford for being the Chairman.

The assembly followed the order of the agenda which had been mailed to all members on 31 May 1968 (dated 4 June), in accordance with paragraph 8 of the Rules of UNITAS.

1. Confirmation of new members

The new members of UNITAS as shown in an appendix to the agenda were confirmed.

2. Report by the President on UNITAS' work

Dr. Paget, the President, gave a short review on the work of UNITAS during the last 3 years, especially the different letter actions of the Secretary. It is to be noted that the amended version of the Rules containing the alterations as approved by the last General Assembly in Copenhagen in 1965 was published and mailed to all members in June 1966. On 3 May 1967, a meeting of the Council took place in Basle.

Twenty-five new members had joined UNITAS since the last General Assembly in August 1965. Three members died (Dr. L. R. Cox in 1965, Dr. H. E. Quick in 1967, and Dr. W. J. Rees in 1967); 2 members resigned. Thus, the number of members increased from 120 in August 1965 to 140 in September 1968. The 140 members consisted of:

Ordinary members (personal 108, collective 9) . . . . .	117
Corresponding members (all personal) . . . . .	23

The 140 members came from 31 countries.

a) Ordinary members in 20 countries:

Algeria (1), Austria (2), Belgium (1), Denmark (7), Egypt (1), France (16), Germany (13), Great Britain (21), Hungary (2), Israel (2), Italy (13), Netherlands (18), Norway (2), Poland (1), Portugal (1), Rumania (2), Sweden (4), Switzerland (7), Turkey (1), Yugoslavia (2).

b) Corresponding members in 11 countries:

Australia (1), Brazil (1), Canada (1), Ethiopia (1), Ghana (1), Hawaii (1), Japan (1), New Zealand (1), Nigeria (2), South Africa (1), U.S.A. (12).

3. Presentation of statement of accounts by the Treasurer

Dr. Forcart, the Treasurer, presented the following statement of accounts (in Swiss Francs) for the period from July 1, 1965, to August 8, 1968. The statement had been approved by the auditors Mr. Dance and Mr. Kuiper.

	S. Fr.
Income . . . . .	4,408.40
Expenditure . . . . .	<u>1,319.31</u>
Excess of Income . . . . .	3,089.09

Assets Schweizerischer Bankverein Basel (E.H. 941085) . . . . .	5,315.74
Balance 1.7.1965 . . . . .	2,226.65
Balance 8.8.1968 . . . . .	5,315.74
Excess . . . . .	3,089.09

#### 4. Approval of acts of councillors

The acts of the councillors for the period from 1965 to 1968 were approved.

#### 5. Postal ballot on new councillors for the period 1968-1971

In February 1968 all ordinary personal members of UNITAS were invited to nominate members for the new Council for the period from 1968 to 1971, in accordance with paragraph 11 of the Rules. To his regret the Secretary has received only one proposal which was signed by 6 ordinary members on May 25, 1968, and, therefore, corresponded with the Rules. The Council of UNITAS agreed to this proposal. According to paragraph 11 of the Rules, the proposal was mailed as a ballot to all 105 ordinary personal members on July 10, 1968. At the General Assembly the Secretary announced the following result of the voting in which 60 members had participated:

	yes	no	abstention
President:			
Dr. E. Binder, Switzerland	59	-	1
Vice President:			
Dr. F. E. Loosjes, Netherlands	57	-	3
Secretary:			
Dr. A. Zilch, Germany	60	-	-
Treasurer:			
Dr. L. Forcart, Switzerland	60	-	-
Member of Council:			
Mr. G. I. Crawford, England	59	-	1

Thus the above office holders were elected members of Council.

#### 6. Election of auditors for the period 1968-1971

The following members were appointed auditors: Mr. S. P. Dance, England, and Avv. Dott. F. Toffoletto, Italy.

#### 7. Subscription for the period 1968-1971

The annual subscription rates of 10.00 Swiss Francs for ordinary members and 5.00 Swiss Francs for corresponding members were not altered.

#### 8. Fixing of year and place of the next Congress

The President-Elect, Dr. Binder, invited the members of UNITAS to the next Congress in Geneva in 1971. The invitation was accepted.

#### 9. Any other business

Lengthy discussions arose about the suggestions of Dr. Paget as indicated in his Presidential Address (see above). Finally the General Assembly authorized Dr. Paget to carry out the proposals numbers 2, 4 and 5; the remaining subjects were postponed to the next General Assembly which will take place in Geneva in 1971. By this assignment of Dr. Paget, the members of UNITAS are at the same time requested to give him any assistance possible in accomplishing his task.

## RAPPORT SUR L'ASSEMBLÉE GÉNÉRALE DE L'UNITAS MALACOLOGICA EUROPAEA

L'assemblée générale de l'UNITAS MALACOLOGICA EUROPAEA s'est tenue le vendredi, 6 septembre 1968, à 18 h au Musée d'Histoire Naturelle de Vienne. 65 membres y étaient présents. Nous remercions Monsieur G. I. Crawford d'avoir une fois de plus accepté de présider les débats.

L'assemblée s'est tenue à l'ordre du jour qui fut envoyé le 31 mai 1968 (daté du 4 juin). conformément au § 8 des statuts à tous les membres.

### 1. Confirmation des nouveaux membres

Les nouveaux membres de l'UNITAS ont été confirmés.

### 2. Rapport du président sur sa gestion

Le président, Docteur Paget, a donné un bref résumé sur l'activité de l'UNITAS au cours des trois dernières années. Le texte des nouveaux statuts, où les modifications décidées lors de l'assemblée générale de 1965 à Copenhague ont été apportées, a été envoyé en juin 1966 à tous les membres. Le 3 mai 1967 a eu lieu une séance du comité à Bâle.

25 nouveaux membres sont entrés dans l'UNITAS depuis la dernière assemblée générale en août 1965. 3 membres sont décédés (Dr. L. R. Cox 1965, Dr. H. E. Quick 1967 et Dr. W. J. Rees 1967), 2 membres ont démissionné, ce qui fait que le nombre est jusqu'en septembre 1968, monté à 140 (voir tableau synoptique dans le texte anglais).

### 3. Présentation des comptes par le trésorier

Le trésorier, Dr. Forcart, a donné un aperçu de l'état financier de l'UNITAS pour le temps du 1<sup>er</sup> juillet 1965 jusqu'au 8 août 1968. La comptabilité a été contrôlée par les Messieurs Dance et Kuiper (voir tableau synoptique dans le texte anglais).

### 4. Décharge du comité

L'assemblée a donné au comité 1965-1968 décharge pour sa gestion.

### 5. Election du nouveau comité pour 1968-1971

En février 1968 tous les membres individuels ordinaires de l'UNITAS ont été invités à envoyer des propositions pour l'élection du nouveau comité pour 1968-1971, conformément au § 11 des statuts. Malheureusement le secrétaire n'a reçu qu'une proposition conforme aux statuts et signée de six membres ordinaires. Le comité de l'UNITAS a adopté cette proposition. Selon le § 11 des statuts cette proposition a été envoyée le 10 juillet 1968 à tous les 105 membres ordinaires individuels pour vote. A l'occasion de l'assemblée générale le secrétaire a publié le résultat de l'élection, à laquelle 60 membres ont participé (voir tableau synoptique dans le texte anglais). Les membres proposés à l'élection ont été ainsi élus dans le nouveau comité.

### 6. Election des réviseurs des comptes pour 1968-1971

Mr. S. P. Dance, Angleterre et Avv. Dott. F. Toffoletto, Italie, ont été élus réviseurs des comptes.

### 7. Fixation de la cotisation pour 1968-1971

La cotisation annuelle de SF 10.00 pour membres ordinaires, et SF 5.00 pour membres correspondants n'a subi aucun changement.

### 8. Choix de l'année et du lieu du prochain congrès

Le président élu, Dr. Binder, a invité les membres de l'UNITAS pour le prochain congrès en 1971 à Genève. Cette invitation fut acceptée.

### 9. Divers

Les propositions du Dr. Paget dans sa "Presidential Address" (prière de s'y référer) ont donné lieu à des discussions animées. L'assemblée générale a chargé finalement Dr. Paget de réaliser les propositions 2, 4 et 5, les autres points ont été ajournés jusqu'à la prochaine assemblée générale à Genève en 1971. Cette mission donnée au Dr. Paget constitue en même temps une invitation aux membres mêmes de l'UNITAS de l'aider dans sa tâche dans toute la mesure du possible.

## BERICHT ÜBER DIE GENERALVERSAMMLUNG DER UNITAS MALACOLOGICA EUROPAEA

Die Generalversammlung der UNITAS MALACOLOGICA EUROPAEA fand am Freitag, dem 6. September 1968, um 18 Uhr im Naturhistorischen Museum in Wien statt. Es waren 65 Mitglieder anwesend. Wir danken Herrn G. I. Crawford, dass er wieder das Amt des Chairman übernommen hat.

Die Versammlung folgte der Tagesordnung, die am 31. Mai 1968 (Datum vom 4. Juni) gemäss § 8 der Satzung an alle Mitglieder verschickt worden ist.

### 1. Bestätigung neuer Mitglieder

Die neuen Mitglieder der UNITAS wurden bestätigt.

### 2. Tätigkeitsbericht des Präsidenten

Der Präsident, Dr. Paget, gab eine kurze Übersicht über die Tätigkeit der UNITAS während der letzten drei Jahre. Die Neufassung der Satzung, unter Berücksichtigung der auf der Generalversammlung in Kopenhagen 1965 beschlossenen Abänderungen, ist im Juni 1966 an alle Mitglieder verschickt worden. Am 3. Mai 1967 hat eine Vorstandssitzung in Basel stattgefunden.

Seit der letzten Generalversammlung im August 1965 sind 25 neue Mitglieder der UNITAS beigetreten. Drei Mitglieder sind verstorben (Dr. L. R. Cox 1965, Dr. H. E. Quick 1967, Dr. W. J. Rees 1967), zwei Mitglieder haben ihren Austritt erklärt. Dadurch ist die Mitgliederzahl bis September 1968 auf 140 angestiegen. (Vgl. die Zusammenstellung in der englischen Fassung).

### 3. Vorlage des Rechnungsabschlusses durch den Schatzmeister

Der Schatzmeister, Dr. Forcart, gab eine Übersicht über die finanziellen Verhältnisse der UNITAS für die Zeit vom 1. Juli 1965 bis 8. August 1968. Die Rechnungsführung ist von den Herren Dance und Kuiper geprüft worden. (Vgl. die Zusammenstellung in der englischen Fassung.)

### 4. Entlastung des Vorstandes

Der Vorstand (1965-1968) wurde entlastet.

### 5. Wahl des neuen Vorstandes für 1968-1971

Im Februar 1968 wurden alle persönlichen ordentlichen Mitglieder der UNITAS aufgefordert, Vorschläge für die Wahl des neuen Vorstandes für

1968-1971, entsprechend § 11 der Satzung, einzureichen. Der Sekretär hat leider nur einen Vorschlag erhalten, der der Satzung entsprach und von sechs ordentlichen Mitgliedern unterzeichnet war. Der Vorstand der UNITAS hat sich diesem Vorschlag angeschlossen. Gemäss § 11 der Satzung ist dieser Vorschlag am 10. Juli 1968 an alle 105 persönlichen ordentlichen Mitglieder zur Wahl abgeschickt worden. Auf der Generalversammlung gab der Sekretär den Ausgang der Wahl bekannt, an der sich 60 Mitglieder beteiligt haben (vgl. die Zusammenstellung in der englischen Fassung). Die zur Wahl vorgeschlagenen Mitglieder wurden damit in den neuen Vorstand gewählt.

#### 6. Wahl der Rechnungsprüfer für 1968-1971

Zu Rechnungsprüfern wurden ernannt: Mr. S. P. Dance, England, und Avv. Dott. F. Toffoletto, Italien.

#### 7. Festsetzung des Beitrages für 1968-1971

Der Jahresbeitrag von 10.00 S. Fr. für ordentliche Mitglieder und 5.00 S. Fr. für korrespondierende Mitglieder wurde nicht geändert.

#### 8. Bestimmung des Jahres und Ortes des nächsten Kongresses

Der gewählte Präsident, Dr. Binder, hat die Mitglieder der UNITAS für den nächsten Kongress 1971 nach Genf eingeladen. Diese Einladung wurde angenommen.

#### 9. Verschiedenes

Über die von Dr. Paget in seiner "Presidential Address" (siehe dort) gemachten Vorschläge gab es längere Debatten. Die Generalversammlung beauftragte schliesslich Dr. Paget, die Vorschläge 2, 4 und 5 durchzuführen; die übrigen Punkte wurden bis zur nächsten Generalversammlung 1971 in Genf vertagt. Dieser Auftrag an Dr. Paget stellt aber gleichzeitig auch einen Auftrag an die Mitglieder der UNITAS selbst dar, ihn bei der Durchführung seines Vorhabens weitestgehend zu unterstützen.



PROCEEDINGS

of the

Symposium on MOLLUSCS AS PARASITES OR THEIR TRANSMITTERS

(Vienna, 2-3 September 1968)





## PROC. SYMP. MOLL. AS PARASITES OR THEIR TRANSMITTERS

CONTRIBUTION TO THE MORPHOLOGICAL AND BIOCHEMICAL  
IDENTIFICATION OF SOME STRAINS OF  
THE *BULINUS TRUNCATUS* GROUP

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## INTRODUCTION

When a plan is organized to fight against *Schistosoma* in a certain geographical area, the first objective is to evaluate the local presence, distribution and prevalence of the vector snails. For that purpose it is fundamental to do a careful survey in the locality concerned in order to determine important aspects of the problem, beginning with a detailed investigation of the existing water bodies in order to collect the snails for study of their morphology, taxonomy and systematics. Simultaneously, their ecology, biology and action as parasite vectors must be considered.

The majority of vector snails usually present many difficulties in classification, either by external or internal anatomy. On the other hand, it is well known that the same species of snail can present remarkable differences in its susceptibility for the same species of *Schistosoma*, as happens, for instance, with *Biomphalaria glabrata* of Recife, Brasil. The latter can be experimentally infected with local *S. mansoni* at the rate of 83.9%, while the same snail species from Bahia, Brasil can be infected with the same strain of *Schistosoma* only at the rate of 1.7% (BARBOSA & BARRETO, 1960). Also, some years ago (AZEVEDO, et al., 1954) it was possible for us to infect *Planorbarius metidjensis* from Algarve, Portugal with *S. haematobium* from Portuguese Guinea, but later, with the same geographical strains of both snail and parasite it was not possible to obtain an infection, even after several experiments. Additionally, some years ago we could infect *P. metidjensis* with the Portuguese strain of *S. haematobium* (AZEVEDO, et al., 1948) at the rate of 80.9%.

The above mentioned alterations may be the result of genetic changes occurring in the snail populations, which result in the appearance of strains with different characteristics and behaviour as intermediate hosts of trematode parasites. Paralleling the occurrence of genetic changes in the snail populations may be variations in the chemical constitution of the snails, as was shown by WRIGHT (1964) by the chromatographic characteristics of the mucus which showed differences between individuals of the same population, which can vary with the snail's ages.

As a contribution to the knowledge of this problem, we have studied and compared the morphology and some aspects of the biochemical constitution of certain geographical strains of the *Bulinus truncatus* group with susceptibility to *Schistosoma haematobium* from Portuguese Guinea and from Angola. These results will be presented in the following sections. But first, we wish to discuss briefly the *B. truncatus* snail group and the *S. haematobium* parasite complex.

The *Bulinus truncatus* group

Until now 12 strains have been described in the *Bulinus truncatus* group (MANDAHL-BARTH, 1965). Concerning the representation in Portugal of that group, Mandahl-Barth thinks that the different morphology of the mesocones of lateral teeth of the radula is

enough to consider it as a species particular to Portugal, giving it the designation of *Bulinus (B.) contortus*.

Meanwhile prior observations made by Medeiros (1962), and later one by CRISTO (1968) about the Portuguese *Bulinus* of Coimbra (center of the country) in comparison with the *B. truncatus* from Teheran and Bagdad, confirmed the observations of MANDAHL-BARTH about the morphology and size of the mesocones of the lateral teeth, but the authors thought that such small differences did not justify the specific differentiation proposed by MANDAHL-BARTH.

In order to clarify the classification on the Portuguese *Bulinus* we have made some biomorphological studies on 2 populations: the northern one (Coimbra) belonged to the strain studied by MANDAHL-BARTH, whereas the strain from southern Portugal (Algarve) (Fig. 1) has now been studied for the first time. As the ecological conditions of Algarve are very different from those of the north, we thought that it would be convenient to consider representatives of the two areas. Indeed the southern territory of Portugal is much warmer than the northern, and presents other particularities due to the chain of high mountains that limits its north boundary.

At the same time we studied representatives of *Bulinus truncatus* from Tchad, Liban and Egypt, the only ones at our disposal.

#### The *Schistosoma haematobium* complex

The morphological characteristics fundamental to this complex concern the shape and size of the eggs and adults. The common biological characteristics are: mammals as definitive hosts; *Bulininae* snails as vectors; and special localizations in the reservoirs. Concerning the vectors, it is necessary to mention one exception: *S. haematobium* of southern Portugal, which has a Planorbinae, *Planorbarius metidjensis*, as intermediate host.

In view of the special ecological, morphological and biological characteristics of the formerly Portuguese *S. haematobium* (\*) we propose that it be designated *S. haematobium europeense*, having in consideration particularly its intermediate host.

#### COMPARATIVE STUDY OF THE DIFFERENT COMPONENTS OF THE *BULINUS TRUNCATUS* GROUP

We wished to study the greatest possible number of representatives of the *Bulinus truncatus* group, but unfortunately we have been able till now to obtain only the Portuguese strains from north and south and the mentioned representative of *Bulinus truncatus*. We present now the results obtained from the comparative studies of these strains, con-

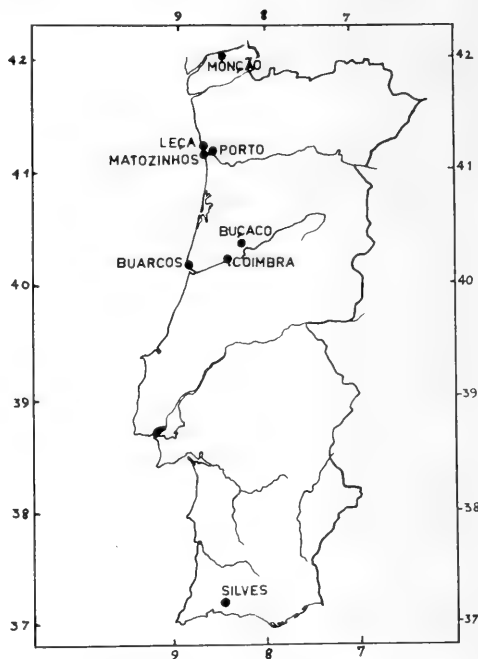


FIG. 1. Localities in Portugal from which snail specimens of the current study originated.

\*A survey made in Algarve in May 1966 did not reveal any case of vesical bilharziasis (Azevedo, et al., 1966).

sidering their morphology, chromatography of the mucus, electrophoresis of the blood and the susceptibility "in vivo" and "in vitro" to infection by two geographically different strains of *S. haematobium*, one from Portuguese Guinea and the other from Angola.

### Morphology

We must consider here as main characteristics the shell, the radula and the genitalia.

Shell. There are not great differences between the shells of the strains concerned, with the exception of the Tchad specimens which had shorter spires and more obtuse apices. Also the shell from the Portuguese *Bulinus* is darker and it seems that the shell of the northern strain is smaller than the shell of those from Algarve. This difference may occur because the northern region is colder, thus not allowing as good a development as in the south. From measurements of 6 specimens (Table 1), it seems that the northern specimens are smaller than the southern ones. The ratio of total height of the shell to height of the aperture (Table 2) is bigger in the *Bulinus* from southern Portugal than in the specimens from the north, and bigger than those from Egypt, Liban and Tchad.

TABLE 1. Different sizes of the snails studied, in mm.

Strains		Height	Height of the aperture	Biggest diameter
Portugal	North	6.7	4.2	4.6
	South	9.0	5.2	5.5
Tchad		8.1	5.9	5.8
Egypt		8.5	5.5	5.5
Liban		8.1	5.7	5.4

TABLE 2. Relation between the total height of the shell and the height of the aperture

Portugal	North	1.6
	South	1.73
Tchad		1.38
Egypt		1.54
Liban		1.42

Genitalia. As remarkable differences in the species studied, we observed that all the strains from Portugal and Tchad were aphaallic, but those from Liban and Egypt presented a well developed penial complex. This complex was similar in the 2 strains except that the preputium of the Liban specimens was narrower and longer than that of the Egyptian specimens, and each of them had a vergic sheath longer and narrower than the preputium. The prostate was always round and smaller in the aphaallic speci-

mens, with a bladder-shaped defferent canal which, in the Portuguese specimens, is narrower and longer than in those of Tchad.

**Radula.** There are some differences in the morphology of the mesocones of the lateral teeth; in *Bulinus* from Coimbra and Liban they are pointed, while the more typical arrow-head shape is seen in the specimens from Tchad and Algarve, and though not so distinct, in those from Egypt. In fact, in each geographical strain studied the central, lateral, intermediate and marginal teeth had their own different and peculiar morphology.

#### Chromatography of the mucus

MICHEJDA (1958) and MICHEJDA and cols. (1958) observed that the fluorescence pattern obtained with the surface mucus of the snail was characteristic of the species. The method was further applied to *Lymnaea* (WRIGHT, 1964), who concluded that by using chromatography it is possible to determine the genetic characteristics of the populations.

In order to clarify the systematics of the mentioned *Bulinus truncatus* group, we studied the chromatography of the mucus of the strains at our disposal. Although more observations are needed, the first interesting results obtained justify their presentation here.

**Methods.** We used at first the circular technique of Wright (1964), but the chromatograms so obtained were not satisfactory, perhaps because we could obtain a very small quantity of mucus. Meanwhile we tried ascending and descending paper chromatography, employing as the solvent butanol, acetic acid and water in the proportions of 4:1:5. We obtained the best results with the ascending technique. After chromatography, the sheets were exposed to ammonia vapour, and then viewed under u.v. light (350 $\mu$ , Camag universal u.v. lamp).

**Results.** The results presented in Table 3 were not the same for each strains. Thus, for the snails from Tchad we observed 4 spots and only 3 for the others. In all of them appeared 1 white spot with a low Rf value, followed by another smaller spot with a nearly circular perimeter of bright blue, which was more intensive in the snails from Egypt and Liban than in those from Portugal.

The substance with the highest Rf value appears in snails from Tchad, as a bright yellowish spot; it is light yellow in the *Bulinus* from Portugal and lilac blue in the snails from Egypt and Liban. A fourth fluorescent spot was seen in the snails from Tchad - a yellowish spot lighter than the former.

TABLE 3. Rf values and chromatographic spots in the different strains of *Bulinus*

Rf. (*)	0. 20	0. 25 - 0. 40	0. 40 - 0. 60	0. 60 - 0. 80
Portugal	Whitish	Blue	Pale yellowish	-
Tchad	"	Strong blue	Strong yellowish	Yellow
Egypt	"	Strong blue	Lilac blue	-
Liban	"	Strong blue	Lilac blue	-

$$(*) \text{ Rf} = \frac{\text{distance travelled by substance}}{\text{distance travelled by solvent front}}$$

Electrophoresis of the blood

Studies conducted by TARGETT (1963) on *Bulinus (B.) truncatus* showed that fractionation of blood proteins occurred. Snail sizes were 4.5 x 2.5 mm and 9.0 x 5.0 mm (height and diameter). The best results were obtained with alkaline buffer of high pH. In applying this method, we used snails of several ages and we tried several buffers and different voltages, but we had difficulties obtaining good fractionations; this was mainly dependent of the buffer pH, which must reach 11.8.

Our results show that 3 fractions are present in *Bulinus* from Portugal and Egypt and 2 fractions in the snails from Tchad and Liban, in addition to the biggest spot which corresponds to hemoglobin (Table 4).

Meanwhile the size of the snails, related to their age, surely has an influence on the results, and this we intend to study; it is possible with our technique to take blood several times from the heart of a snail without killing it.

TABLE 4. Showing comparative separations of blood proteins from *Bulinus* of Portugal, Tchad, Egypt and Liban

Strains		Sizes (mm)	Separations obtained	Migration from application point
Portugal	North	H - 6	Hemoglobin +	Hemoglobin 2 cm
		D - 4.5	three fractions	The others $\left\{ \begin{array}{l} 1 \text{ cm} \\ 1.5 \text{ cm} \\ 1.7 \text{ cm} \end{array} \right.$
	South	H - 5.2	Hemoglobin +	Hemoglobin 2 cm
		D - 3.6	three fractions	The others $\left\{ \begin{array}{l} 1 \text{ cm} \\ 1.5 \text{ cm} \\ 1.7 \text{ cm} \end{array} \right.$
Tchad	H - 5.2	Hemoglobin +	Hemoglobin 1.9 cm	
	D - 3.2	two fractions	The others $\left\{ \begin{array}{l} - \\ 1.4 \text{ cm} \\ 1.6 \text{ cm} \end{array} \right.$	
Egypt	H - 5.6	Hemoglobin +	Hemoglobin 2 cm	
	D - 4	three fractions	The others $\left\{ \begin{array}{l} 1 \text{ cm} \\ 1.6 \text{ cm} \\ 1.8 \text{ cm} \end{array} \right.$	
Liban	H - 5.2	Hemoglobin +	Hemoglobin 2.1 cm	
	D - 3.6	two fractions	The others $\left\{ \begin{array}{l} 1.1 \text{ cm} \\ 1.6 \text{ cm} \\ - \end{array} \right.$	

Susceptibility of the snails to *Schistosoma haematobium*

In order to evaluate susceptibility we can study the subject in the field, determining the natural rate of infection of the snails by cercariae, but it is always desirable that these observations be confirmed by experimental study in the laboratory. For this

purpose we can use the classical method of infection of the snails "in vivo" or we can try "in vitro" infection. We have applied these 2 methods to evaluate the susceptibility of the snails concerned to the geographical strains of *S. haematobium* studied, one from Portuguese Guinea and the other from Angola.

Study "in vivo" of the susceptibility of the snails to *S. haematobium* from Portuguese Guinea and from Angola.

Each snail was exposed to 3 miracidia of human origin and the susceptibility to infection, and its degree was evaluated by the rate of infection of the snails, number of cercariae eliminated, precocious mortality, longevity and degeneration or normal development of the miracidia as seen in sections of the snail organs. To accomplish this study we evaluated also the virulence of the cercariae eliminated, as proof of the efficiency of the vector; this was done by determining the relation between the number of cercariae utilized to infect the experimental animal, and the number of worms obtained, as well as the relative proportion of animals that eliminated viable eggs.

As definitive host we used the hamster *Cricetus auratus*. Each animal was exposed to 500-600 cercariae and sacrificed at the end of 4 weeks. The eggs were obtained from the liver and bowel, and the miracidia used to infect new snails. We collected the adult worms by section and pression of the liver.

The results obtained are presented in Table 5. Concerning the strains from Portuguese Guinea, we have verified that there is greater affinity between the 2 Portuguese populations and the strain from Tchad, than between the Portuguese populations and those from Liban and Egypt; the rates of infection were respectively 27.6, 21.4 and 49.2%. The *Bulinus* from Liban was refractory and the *Bulinus* from Egypt was infected only at the rate of 4.5%.

The number of eliminated cercariae was much higher in the snails of the Tchad population than in the Portuguese ones; i.e., the former 25 snails eliminated 10,880 cercariae, while the 240 snails from Algarve eliminated 8,043, and 501 specimens from Coimbra eliminated only 6,575.

The proportion of infected animals that produced viable eggs was highest in the Portuguese population from Coimbra; this was followed by the strain from Tchad and finally that from Algarve. On the basis of these results it is not clear if the snails from Tchad are more susceptible than the Portuguese ones, because a greater number of the former snails were submitted to the infection; this might explain the differences observed. Nevertheless, we can conclude that there are some differences between them and those from Egypt and Liban, a conclusion which is not in accordance with the results obtained by the chromatographic method.

Concerning the strain of *S. haematobium* from Angola, we have tried only a small number of snails (this strain is very recent in our laboratory) and we cannot consider the negative results and the snail control as conclusive. With the snail control, *Bulinus* (*Ph.*) *africanus*, only three became infected; but up to now, 48 days after the infection, they have eliminated a great number of cercariae, which we have utilized to infect hamsters. Meanwhile, the fact that the control snails were infected proves that the experimental conditions were good. The low rate of infection observed is also perhaps the consequence of the great mortality which occurred between the 3rd and the 12th days after infection; only 3 surviving till the 30th day, when they were then placed in a stove at 37° C in order to verify the elimination of cercariae.

Study of the susceptibility of the snails "in vitro".

As an alternative to the classic method of evaluating the susceptibility of the snails, BENEX (1965) had the idea of evaluating susceptibility by submitting only the tentacles,

TABLE 5. Susceptibility of different strains of the *Bulinus truncatus* group to *Schistosoma haematobium* from Portuguese Guinea and Angola

	"In vivo"							"In vitro"		
	Snail populations	No. of snails exposed to infection	No. of positive snails	Total of cercariae	Rate of infection	No. of infected hamsters	% of hamsters that produce viable eggs	Positives	Negatives	
Portuguese Guinea strain of <i>S. haematobium</i>	Portugal	Coimbra (Center of the Country)	531	147	6,575	27.6%	12	50 %	-	-
		Algarve (South of the Country)	240	50	8,043	21.4%	15	20 %	-	-
	Tchad	25	13	10,880	49.2%	19	36.8%	-	-	
	Egypt	22	1	96	4.5%	-	-	-	-	
	Liban	25	0	-	-	-	-	-	-	
Angola strain of <i>S. haematobium</i>	Portugal Continental	Coimbra (Center of the Country)	13	0	-	-	-	-	-	100%
		Algarve (South of the Country)	39	0	-	-	-	-	-	-
	Ultramar	Angola	52	2	500	3.8%	1	0.0	-	-
	Tchad	10	0	-	-	-	-	-	0	100%
	Liban	-	-	-	-	-	-	-	0	100%
S. mansoni Brazil	Egypt	-	-	-	-	-	-	-	0	100%
	Control ( <i>A. glabratus</i> Brazil)	-	-	-	-	-	-	-	10 (30 snails)	90%

taken off the snails and maintained "in vitro" in a special nutritive medium, to the miracidia. We also have used this method, with the same very rich nutritive culture medium, having verified that the tentacles could survive for 26 days, retaining a normal appearance and good vitality, although this reduced gradually with time, as was evident from a reduction of their movements. With time they became round, and lost the ability to move at the end of 5-6 days, with the exception of the cilia. At the same time there were signs of degeneration of the nucleus and nervous cells, and loss of mucus cells.

Until now it has only been possible to attempt infection of *Bulinus* from Coimbra, Tchad, Liban and Egypt with a strain of *S. haematobium* from Angola. Sixty miracidia were used with each tentacle on the first day of its maintenance in the medium, and sections were made at different intervals (24 - 72 hours) in order to follow the infection; however, we have obtained no infection. As a control, however, we submitted the tentacles of *Biomphalaria glabrata* to infection with miracidia of *S. mansoni* from Brasil. We obtained a rate of infection of 10% as proof of the good experimental conditions; this is confirmed by the normal aspect of the evolution of the miracidia in the tentacle.

From the results obtained from the "in vivo" and "in vitro" studies of susceptibility of the snails concerned to the *Schistosoma haematobium* of Angola, it seems that they are unsusceptible to it. Meanwhile other researches are in progress in order to arrive at definitive conclusions, and particularly to see if these results are the first proof that *S. haematobium* from Portuguese Guinea and Angola are biologically different.

#### INTERPRETATIONS AND CONCLUSIONS

In this study several morphological, biological and chemical factors were considered in order to establish the relationship that exists between some *B. truncatus* strains and two geographical strains of African *S. haematobium*. It is, nevertheless, difficult to define these relationships, and more and detailed studies are necessary to arrive at definitive conclusions.

On the basis of the results obtained, we can arrive at the following conclusions:

- a) morphology; there are some differences between the shell, the radula and genital organs of the strains examined.
- b) chromatograms of the mucus show a close similarity between the *Bulinus* from Egypt and Liban and a very distinct difference between the latter and the *Bulinus* from Tchad and Portugal (between these 2 there is little similarity). All show the first spots with the same colour, although with differences of intensity, but the Tchad *Bulinus* shows a fourth spot.
- c) electrophoresis shows also some differences in the strains studied, particularly between those of Tchad and Liban on the one hand and those of Portugal and Egypt on the other.
- d) there were some differences in the degree of susceptibility "in vivo" and "in vitro" of the snails studied to the *S. haematobium* from Portuguese Guinea and none was susceptible to *S. haematobium* from Angola; this seems to prove that the *S. haematobium* from Portuguese Guinea is biologically different from the same species of *Schistosoma* from Angola.
- e) the differences observed in the susceptibility "in vivo" between the strains from Liban and Egypt are in accordance with the differences also observed in the respective chromatograms.
- f) the electrophoregrams of snail blood also show some differences between them which are in accordance with the differences in the respective chromatograms.



## PROSPECTS TO BE CONSIDERED

With our paper we hope to have given an idea of the difficulties encountered while investigating the relationship between *Schistosoma* and its snail vectors, and which justify new and more intensive studies. We think that the main reasons for our incomplete information are a consequence of the limited knowledge that we have about the biology, physiology and genetics of the snails and of the schistosomes themselves. It is therefore desirable to increase research in these fields, and we think that an important contribution can be made by the electronic microscope and by developing methods for the chemical and genetic studies. The subjects mentioned are only examples of what we need to do; much other research is necessary in order to clarify the important problem of differences existing between the geographical strains of *Schistosoma haematobium* and the corresponding *Bulinus truncatus* vectors, and the methods to use for their specific classification.

## SUMMARY

In order to study the differences between the components of *Bulinus truncatus* group, as vectors of the strains of *Schistosoma haematobium* complex, studies were made of 1) the morphology of some geographic strains; 2) the chromatography of their mucus; and 3) the electrophoresis of the blood. These were compared with the susceptibility of those snails to 2 geographical strains of *S. haematobium*, one from Portuguese Guinea and the other from Angola.

From the results obtained, it seems that the snails present remarkable differences between them, particularly concerning their biological behaviour; it seems also that the strain of *S. haematobium* from Portuguese Guinea is different from the Angola one.

## BIBLIOGRAPHY

- AZEVEDO, J. F. de, FARO, M. M. & GOMES, F. A. C., 1954, Susceptibility of *Planorbis metidjensis* to *Schistosoma haematobium* of Portuguese Guinea and to *S. mansoni* of Mozambique. *Anais Inst. Med. Trop.*, Lisbon, 11: 251-260.
- AZEVEDO, J. F. de, SILVA, J. B., COITO, A. M., COELHO, M. F. & COLAÇO, A. T. F., 1948, O foco português de Schistosomíase. *Anais Inst. Med. Trop.*, 5: 175-223.
- AZEVEDO, J. F. de, XAVIER, M. L., FERNANDEZ, A. R., PINHÃO, R., JANZ, G. J., QUEIROZ, J. S., CORREIA, M. & NEVES, S., 1966, Situação do foco de bilharziose do Algarve em 1966. Em publicação.
- BARBOSA, F. S. & BARRETO, A. C., 1960, Differences in susceptibility of Brazilian strains of *Australorbis glabratus* to *Schistosoma mansoni*. *Exp. Parasitol.*, 9: 137-140.
- BENEX, J., 1965, Recherches sur l'infection expérimentale de tentacules de planorbes en survie, par des miracidiums de *Schistosoma mansoni*. Thèse, Paris.
- CRISTO, M. I., 1968, Considerações sobre a posição sistemática de *Bulinus (B.) contortus* (Michaud) de Portugal. - Em publicação. Carcia de Orta, Junta de Investigações de Ultramar.
- MANDAHL-BARTH, G., 1965, The species of the genus *Bulinus*, intermediate hosts of *Schistosoma*. *Bull. Org. Mond. Santé*, 33: 33-44.
- MEDEIROS, L. C. M. de, 1962, A proposito do morfologia do *Bulinus (B.) contortus* de Portugal. - Apresentado ao Cong. Luso-Espanhol para o Progresso das Ciências, Porto, Junho, 22-26, 1962.
- MICHEJDA, J., 1958, Biochemical bases for the taxonomy of snails. I. Chromatographic analysis of some fresh-water snails. *Bull. Soc. Amis Sci. Lett.*, Poznań, B 14 341-344.

- MICHEJDA, J. & TURBAŃSKA, A., 1958, Biochemical bases for the taxonomy of snails. III. Differences in chromatographic patterns of various organs and tissues. *Bull. Soc. Amis Sci. Lett.*, Poznań, B 14: 362-365.
- MICHEJDA, J. & URBAŃSKI, J., 1958, Biochemical bases for the taxonomy of snails. II. An attempt at a chromatographic analysis of some species of snails. *Bull. Soc. Amis Sci. Lett.*, Poznań, B 14: 346-347.
- TARGETT, G. A. T., 1963, Electrophoresis of blood from intermediate and non-intermediate snail hosts of schistosomes. *Exp. Parasitol.*, 14: 143-151.
- WRIGHT, C. A., 1962, The significance of infra-specific taxonomy in bilharziasis. *Bilharziasis*, Ciba Foundation Symposia, 103-112.
- WRIGHT, C. A., 1964, Biochemical variation in *Lymnaea peregra* (Mollusca, Basommatophora) *Proc. zool. Soc. Lond.*, 142: 371-378.

FACTORS AFFECTING GROWTH AND REPRODUCTION OF  
FRESHWATER PLANORBIDAE IN EAST AFRICA

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## ABSTRACT

Information about the life cycles of freshwater pulmonate snails is not very extensive. Most studies have been in the northern temperate zone where the snails tend to have simple annual cycles, but small species may have more than one generation per year and large species may require more than a year for a single generation (HUNTER, 1961; BERRIE, 1965). Growth proceeds rapidly under favourable conditions of temperature and food supply and variation in these conditions and in endogenous factors causes differences in the growth rates of populations in different habitats or of the same population in different years. Some aspects of the maturation of the reproductive system are related to the size of the snails while other aspects are associated with the time of year, and oviposition takes place when the snails are large enough and the environmental conditions are favourable (BERRIE, 1966).

The planorbid snails which act as intermediate hosts of schistosomes in Africa are medium sized and, in most parts of the continent, they are seldom subjected to low water temperatures. In these circumstances the snails might be expected to breed continuously maintaining the populations at a level determined by the environmental resistance. Such a situation has never been reported presumably because some environmental factors undergo changes which affect the growth and reproduction of the snails.

Some of these factors have been investigated under laboratory conditions. The growth rates of *Bulinus globosus* and *Biomphalaria pfeifferi* increase with rise in temperature but at temperatures of 30° C or over there is a decline in survival and fecundity (SHIFF, 1964; STURROCK, R. F., 1966; SHIFF & GARNETT, 1967). The intrinsic rate of natural increase is greatest at about 25° C and both species are capable of rapid population expansion at this temperature. Most laboratory studies have been carried out at constant temperatures and experiments involving diurnal fluctuations comparable to those experienced in natural habitats would be very useful. Infection with schistosomes affects the growth and fecundity of snails although there is some variation in the effects which have been reported on growth. Infection of *B. pfeifferi* causes a temporary increase in the growth rate which is proportional to the intensity of the infection but survival and fecundity are reduced (STURROCK, B. M., 1966). When snails are maintained at high densities in aquaria, their growth and fecundity are both reduced in proportion to the degree of crowding. This has been demonstrated in several African planorbids but the causal mechanisms have not been identified.

In temporary pools in East Africa, populations of *Bulinus nasutus* and *B. globosus* build up very rapidly under favourable conditions with high rates of growth and fecundity which can result in short life cycles at such times (WEBBE, 1962; BERRIE, unpubl.). However, the great increase in population size combined with the gradual decrease in the size of the habitats causes conditions to deteriorate. Populations of *Bulinus ugandae* and *Biomphalaria sudanica tanganyicensis* in ditches in Uganda appear to have a simple annual life cycle with a period of reproductive activity associated with the first rains (BERRIE, 1964). At first the young snails grow quite rapidly, but the growth rate soon slows down until eventually growth practically ceases for a considerable time prior to the next reproductive period. During most of the year the populations consist mainly of snails which are large enough to become sexually mature, and the absence of reproductive activity must be attributed to adverse environmental conditions which change with the start of the rains. There are a number of ways in which the rains could affect the snails, and the factors which trigger the reproductive period cannot yet be identified. We know surprisingly little about the food requirements of snail populations which may be one important factor.

A population of *Biomphalaria sudanica tanganyicensis* in a small pool in Uganda showed inhibition of growth during five months when the population density was high (BERRIE, 1968). The density was drastically reduced by collecting, and the water volume was simultaneously increased by rain. The remaining snails immediately resumed rapid growth and a period of reproductive activity followed. Water taken from the pool during the period of growth inhibition was found to contain a soluble toxin capable of causing such inhibition (BERRIE & VISSER, 1963).

The growth and reproduction of African planorbids often seem to vary and may be responding to a variety of intrinsic and extrinsic factors. If these natural population regulators can be identified it should be possible to reach a fuller understanding of the dynamics of natural populations, and it may be possible to consider new methods of controlling snail populations.

## REFERENCES

- BERRIE, A. D., 1964. Observations on the life-cycle of *Bulinus (Physopsis) ugandae* Mandahl-Barth, its ecological relation to *Biomphalaria sudanica tanganyicensis* (Smith), and its role as an intermediate host of *Schistosoma*. *Ann. trop. Med. Parasitol.*, 58, 457-466.
- BERRIE, A. D., 1965. On the life cycle of *Lymnaea stagnalis* (L.) in the West of Scotland. *Proc. malacol. Soc. London*, 36, 283-295.
- BERRIE, A. D., 1966. Growth and seasonal changes in the reproductive organs of *Lymnaea stagnalis* (L.). *Proc. malacol. Soc. London*, 37, 83-92.
- BERRIE, A. D., 1968. Prolonged inhibition of growth in a natural population of the freshwater snail *Biomphalaria sudanica tanganyicensis* (Smith) in Uganda. *Ann. trop. Med. Parasitol.*, 62, 45-51.
- BERRIE, A. D. & VISSER, S. A., 1963. Investigations of a growth-inhibiting substance affecting a natural population of freshwater snails. *Physiol. Zool.*, 36, 167-173.
- HUNTER, W. R., 1961. Life cycles of four freshwater snails in limited populations in Loch Lomond, with a discussion of infraspecific variation. *Proc. zool. Soc. London*, 137, 135-171.
- SHIFF, C. J., 1964. Studies on *Bulinus (Physopsis) globosus* in Rhodesia. I. The influence of temperature on the intrinsic rate of natural increase. *Ann. trop. Med. Parasitol.*, 58, 94-105.
- SHIFF, C. J. & GARNETT, B., 1967. The influence of temperature on the intrinsic rate of natural increase of the freshwater snail *Biomphalaria pfeifferi* (Krauss) (Pulmonata: Planorbidae). *Arch. Hydrobiol.*, 62, 429-438.
- STURROCK, B. M., 1966. The influence of infection with *Schistosoma mansoni* on the growth rate and reproduction of *Biomphalaria pfeifferi*. *Ann. trop. Med. Parasitol.*, 60, 187-197.
- STURROCK, R. F., 1966. The influence of temperature on the biology of *Biomphalaria pfeifferi* (Krauss), an intermediate host of *Schistosoma mansoni*. *Ann. trop. Med. Parasitol.*, 60, 100-105.
- WEBBE, G., 1962. The transmission of *Schistosoma haematobium* in an area of Lake Province, Tanganyika. *Bull. Wild. Hlth. Org.*, 27, 59-85.

AN IMMUNO-CYTOLOGICAL STUDY OF THE AFRICAN SUBGENUS *BULINUS* s.s.<sup>1</sup>J. B. Burch<sup>2</sup> and G. K. Lindsay*Museum of Zoology, University of Michigan, Ann Arbor, Michigan, U. S. A.*

## ABSTRACT

The planorbid genus *Bulinus* is found over most of the African continent where habitats are suitable for freshwater pulmonate snails. The genus is also found on the East African islands and selectively in many Mediterranean and Middle Eastern countries. The medical importance of the genus lies in the fact that certain of its species are the intermediate hosts of human urinary bilharziasis.

The various bulinine species traditionally have been grouped into 3 taxa (lately referred to as subgenera, formerly as genera): *Bulinus* s.s., *Physopsis* and *Pyrgophysa*. It is the subgenus *Bulinus* s.s., comprising the *tropicus* and *truncatus* species groups of MANDAHL-BARTH (1957, *Bull. Wld. Hlth. Org.*, 16: 1103-1163), that is of special concern in the present study, because few of the taxa that have been established within these 2 species groups currently can be defined with any precision in terms of the limits of morphological variation and geographical distribution. Also, the validity of the 2 groups themselves has been questioned. Yet, on both parasitological and cytological grounds, there do seem indeed to be 2 distinct groups, that can be defined with some precision. The more northern *truncatus* group is polyploid and, as far as known, is susceptible to infection with *Schistosoma haematobium*, either under natural or experimental conditions. The more southern group is diploid and generally is not considered to be susceptible to human schistosome infection.

Assigning species to the 2 groups has proven difficult for malacologists. For example, species that were first placed with one group by Mandahl-Barth only to be shifted by him later to the other group are: *Bulinus guernei*, *B. natalensis* and *B. sericinus*. Characters that are currently being used to assign species to one or the other of the 2 species groups in question are the shape of the mesocones of the first lateral teeth of the radula, the degree of presence or absence of a male copulatory organ, and the shape of the shell.

Recently, it has been reported that the *truncatus* group, previously thought not to occur south of the great African lakes, occurs as far south as South-West Africa and the Transvaal (MANDAHL-BARTH, 1965, *Bull. Wld. Hlth. Org.*, 33: 33-44; SCHUTTE, 1965, *Ann Mag. nat. Hist.*, 8: 409-419; 1966, *Ann. trop. Med. Parasit.*, 60: 106-113). This information is based on the occurrence of *Bulinus natalensis* and *B. depressus* in those regions and the fact that these 2 species apparently have "arrow-head shaped" mesocones on the first lateral teeth of the radula, thought to be characteristic of the *truncatus* species group (in contrast to the "triangular shaped" mesocones thought to be characteristic of the *tropicus* species group). However, *B. natalensis* has 18 pairs of chromosomes, a characteristic of the *tropicus* group (some *B. natalensis* populations have one to several extra chromosomes), and, as shown by the present study, this species also shows immunological affinities with the *tropicus* species group rather than the *truncatus* group.

In the present investigation the use of an immunological method employing the specific absorption technique enabled the observation of "identity" or "non-identity" between various of the 37 populations tested against the 3 species for which there were antisera. The results (Table 1) show that there is good correlation between serological tests and the chromosomal ploidy of the populations, and a lack of complete correlation with characters of the radular mesocones, the single feature currently given the most importance for species group identification.

It is concluded from these results that (1) the subgenus *Bulinus* s.s. does indeed comprise more than one species group, each of which can be identified cytologically, parasitologically and immunologically; (2) little reliance can be placed on those morphological characters now being used to place a species into its species group; and (3) in face of the intensive but unrewarding morphological research already devoted to the genus, perhaps simple biochemical tests should be employed instead of morphological characters by field workers attempting to ascertain the potential of natural populations for transmitting urinary bilharziasis.

A more detailed account of these studies will be published in *Malacological Review*.

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TABLE 1. "Non-identity" reactions, observed in the micro-Ouchterlony immunodiffusion test, between antigens and antisera of various populations of *Bulinus* s. s.

Popu- lation no.	Species of <i>Bulinus</i> furnishing antigen	Country	Haploid chromosome number (n)	Occurrence of "non-identity" <sup>++</sup> reaction		
				n=18 antiserum	n=36 antiserum	n=72 antiserum
1	<i>B. sp.</i>	Senegal	18	o <sup>‡</sup>	-	2
2	<i>B. sp.</i>	Senegal	18	o	-	-
3	<i>B. sp.</i>	Ethiopia	18	-	-	3 + 1
4	<i>B. sp.</i>	Ethiopia	18	o	-	-
5	<i>B. sp.</i>	Ethiopia	18	o	2	-
6	<i>B. sp.</i>	Ethiopia	18	o	1 + 2	3 + 1
7	<i>B. sp.</i> <sup>+</sup>	Ethiopia	18	2 + 2	3 + 1	2 + 1
8	<i>B. tropicus alluaudi</i>	Kenya	18	o	3	3
9	<i>B. tropicus tropicus</i>	Rhodesia	18	o	3 + 2	2 + 1
10	<i>B. tropicus tropicus</i>	Rhodesia	18	o	2 + 1	2
11	<i>B. tropicus tropicus</i>	Rhodesia	18	o	3	-
12	<i>B. tropicus tropicus</i>	Rhodesia	18	o	2 + 2	-
13	<i>B. tropicus tropicus</i>	Rhodesia	18	o	3 + 1	2 + 1
14	<i>B. tropicus tropicus</i>	Rhodesia	18	o	2 + 1	2
15	<i>B. tropicus tropicus</i>	Rhodesia	18	o	3 + 2	-
16	<i>B. tropicus tropicus</i>	S. Africa	18	o	3 + 2	2
17	<i>B. natalensis</i>	Rhodesia	18	o	3	-
18	<i>B. natalensis</i>	Rhodesia	18	o	2	2
19	<i>B. truncatus</i> ssp.	Corsica	36	3 + 1	o	2
20	<i>B. truncatus truncatus</i>	Iran	36	2 + 1	o	2
21	<i>B. truncatus truncatus</i>	Iran	36	2 + 1	o	2
22	<i>B. truncatus truncatus</i>	Egypt	36	3 + 2	o	-
23	<i>B. truncatus truncatus</i>	Egypt	36	3 + 2	o	2
24	<i>B. truncatus truncatus</i>	Sudan	36	2 + 2	o	2
25	<i>B. truncatus</i> ssp.	W. Aden	36	2	o	-
26	<i>B. truncatus rohlfsi</i>	Mauritania	36	1 + 2	o	-
27	<i>B. truncatus rohlfsi</i>	Ghana	36	1 + 1	o	2
28	<i>B. guernei</i>	Gambia	36	2 + 1	o	-
29	<i>B. coulboisi</i>	Tanzania	36	3 + 2	o	3 + 1
30	<i>B. coulboisi</i>	Tanzania	36	1 + 2	o	-
31	<i>B. coulboisi</i>	Tanzania	36	3 + 1	o	-
32	<i>B. sp.</i>	Ethiopia	54	2 + 2	-	2 + 2
33	<i>B. sp.</i>	Ethiopia	72	1 + 1	-	-
34	<i>B. sp.</i>	Ethiopia	72	2 + 1	-	-
35	<i>B. sp.</i>	Ethiopia	72	1 + 1	2	o
36	<i>B. sp.</i>	Ethiopia	72	1 + 1	2 + 2	o
37	<i>B. sp.</i>	Ethiopia	72	1 + 1	2 + 1	o

<sup>++</sup> In terms of number and intensity of "non-identity" precipitation bands: 1 = weak; 2 = medium; 3 = strong (3 + 2 = two bands occurred, one strong and one medium in intensity).

<sup>‡</sup> o = no "non-identity" reaction occurred

THE INFLUENCE OF THE SUBSTRATUM ON POPULATION INCREASE AND HABITAT SELECTION BY *LYMNAEA NATALENSIS* KRS. AND *BULINUS (B.) TROPICUS* KRS. (MOLLUSCA, BASOMMATOPHORA)

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ABSTRACT

In the course of an extensive survey of the freshwater snails in the Republic of South Africa it was noticed that the most commonly occurring species were, in the majority of cases, found to be associated with habitats containing a muddy substratum. This posed the question whether the substratum, as such, was in any way of critical importance in the selection and suitability of the habitat for the snails in question. Two species viz. *Bulinus (Bulinus) tropicus* Krs. and *Lymnaea natalensis* (Krs.) and 5 different substratum types were selected. Observations on these were made in an outdoor river model and in both out- and indoor aquaria.

The criteria chosen for testing the suitability of the substratum were: (1) certain population statistics such as survivorship ( $1_x$ ), reproduction rate ( $m_x$ ), proportional egg curve ( $V_x$ ) and nett reproduction rate ( $R_c$ ), from which the capacity for increase ( $r_c$ ) were calculated; (2) growth rate as reflected by weight increase; (3) the ability of the snails to select a particular substratum type from a randomly distributed series.

On the basis of the performance of the snails on each or the relative number of snails which visited each substratum type under the conditions created the substratum types were, in each case, arranged in a so-called success sequence. Some of the sequences arrived at are given in Table 1.

The behaviour studies revealed no definite active selection of any specific substratum type and the  $r_c$  sequences arrived at is correlated with the abundance of microflora rather than with increasing or decreasing particle size of the substratum type. Under the conditions prevailing in our experimental setup our results therefore seem to have been determined by the availability of suitable food rather than by a direct affect of the substratum.

TABLE 1. Performance of *Lymnaea natalensis* and *Bulinus tropicus* on five different substratum types where M = mud, K = stones, S = sand, G = gravel and Fs = fine sand

Species	Item	Success sequence				
		1	2	3	4	5
<i>L. natalensis</i>	$r_c$	M >	K >	S >	G =	Fs
	Growth rate	M >	K >	S ≥	G >	Fs
<i>B. tropicus</i>	$r_c$	K =	Fs =	M >	S >	G
	Growth rate	M ≥	K >	S >	Fs >	G
<i>L. natalensis</i> and <i>B. tropicus</i>	Microflora	M >	K >	S >	G >	Fs

## THE PRESENT STATUS OF BILHARZIASIS IN THE DOMINICAN REPUBLIC

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## ABSTRACT

Relatively few reports have been published concerning prevalence and distribution of *Schistosoma mansoni* and its molluscan vectors in the Dominican Republic. The parasite was first reported in this country by PONCE PINEDO (1945), who also identified the town of Hato Mayor as the endemic focus (1947). OLIVIER, VAUGHN & HENDRICKS (1952) confirmed that Hato Mayor was the primary focus of transmission, and reported an incidence of 21.4% in children, with approximately equal frequency in boys and girls. Following chemical treatment of the stream Paña Paña and several tributaries, VAUGHN et al. (1954) reported successful elimination of snails from the area; no snails were found in the 6 month period immediately after a single application of sodium pentachlorophenate at 15 ppm. While it is uncertain when the population of *Biomphalaria glabrata* recovered from this treatment, one of us (FJE) noted a very large population in Paña Paña stream in July, 1959. MALDONADO (1962) reported an overall positivity to the Bilharzia Skin Test of 30% in school children in Hato Mayor, with boys showing the highest rate (46%).

On the basis of evidence gathered in 6 surveys made during 1963-68, it is apparent that *Biomphalaria glabrata* is far more widely distributed in the Dominican Republic than previously reported. Five well-established populations are located as follows: the Rio Maguá drainage system, including Paña Paña stream, around Hato Mayor; the swamps and stream in the town of Miches; irrigation canals of the Rio Cuarón near the town of Nisibón, east of Miches; extensive rice-fields and irrigation canals surrounding the town of Cotufí in the central valley; and a large swamp 9 km. from the northern town of Nagua. These foci are separated by distances of up to 240 km., and establish a range of approximately 1/6 the total area of the Dominican Republic. *Tropicorbis riisei*, another planorbid species, is far more widely dispersed, from the Haitian border to the east end of the island and from the north to the south coast. Unlike *B. glabrata*, *T. riisei* is practically continuously distributed in all fresh-water habitats.

Surveys for human cases of *Schistosoma mansoni* infection, using the standard adult antigen intradermal test and direct fecal examination, have confirmed the continuing high rate of transmission in Hato Mayor. In other localities where *Biomphalaria glabrata* was found, our findings were essentially negative. One equivocal finding of 22% positive intradermal reaction among a group of school-age boys was contradicted by negative fecal examinations. It is suggested that this group may have shown false-positive skin test reactions by cross-reaction to avian-mammalian cercarial exposure, a phenomenon recently demonstrated by MOORE, et al (1968).

In 1963, Paña Paña stream and collateral bodies of water in the area of Hato Mayor were seeded with about 1750 specimens of *Marisa cornuarietis*; this snail has been suggested as an effective biological control agent in Puerto Rico by RADKE, RITCHIE & FERGUSON (1961). In the ensuing 5 years, periodic surveillance has shown that the snails were washed downstream for several kilometers, but have returned to Hato Mayor and established a very dense population in the Rio Maguá since July 1967. This stream, into which Paña Paña drains, was only partially inhabited by the upstream-migrating *M. cornuarietis* population; consequently one portion of the stream has an undisturbed *Biomphalaria glabrata* population, another portion of about 1.5 km. length has numerous *M. cornuarietis* and practically no *B. glabrata*, and a third zone of about 500 m contains both species overlapping. Presumably the latter zone represents the level to which *M. cornuarietis* has migrated, and where time and numbers have not been sufficient to inhibit the existing *B. glabrata* population, as has apparently happened further down-stream.

The recent finding (1968) of an apparently newly introduced population of the Oriental snail, *Tarebia granifera*, in the vicinity of Nisibón has introduced yet another complicating factor into the problem of Dominican snail population interactions. *T. granifera*, most probably introduced from Puerto Rico, is believed to inhibit natural populations of *Biomphalaria glabrata* there, but the mechanism of inhibition is uncertain. The manner of introduction even into Puerto Rico is unknown, but it appears to have been a natural event in the Dominican Republic, judging from the extremely remote area in which it has been first found.

Because of the generally uncontrolled situation in the Dominican Republic, with respect to Bilharziasis, continued surveillance of known populations of *Biomphalaria glabrata*, *Marisa cornuarietis*, and *Tarebia granifera* and extended surveys for snails and Bilharziasis are contemplated. As pointed out by OLIVIER, VAUGHN & HENDRICKS (1952), the Dominican Republic was (and remains) a favorable situation for such studies. In addition to the potential threat of spreading in this country, Bilharziasis in this area is of biological and epidemiological interest as the northwestern-most extent of the range of neotropical *Schistosoma mansoni* and its molluscan vector, *B. glabrata*.



## REFERENCES

- MALDONADO, J. F., 1962. Encuesta sobre esquistosomiasis en la poblacion de Hato Mayor, a base de la intradermoreaccion. Unpublished report to Ministry of Health, Dominican Republic.
- MOORE, G. T., KAISER, R. L., LAWRENCE, R. S., PUTNAM, S. M., & KAGAN, I. G., 1968. Intradermal and serologic reactions to antigens from *Schistosoma mansoni* in schistosome dermatitis. *Amer. J. trop. Med. & Hyg.*, 17: 86-91.
- OLIVIER, L., VAUGHN, C. M. & HENDRICKS, J. R., 1952. Schistosomiasis in an endemic area in the Dominican Republic. *Amer. J. trop. Med. & Hyg.*, 1: 680-687.
- PONCE PINEDO, A. M., 1945. Seis casos autoctonos de esquistosomiasis de Manson. Congr. Med. Dominicano del Centenario (1944): 382-390.
- PONCE PINEDO, A. M., 1947. Esquistosomiasis de Manson en Santo Domingo. *Puerto Rico J. pub. Hlth. & Trop. Med.*, 22: 316-324.
- RADKE, M. G., RITCHIE, L. S. & FERGUSON, F. F., 1961. Demonstrated control of *Australorbis glabratus* by *Marisa cornuarietis* under field conditions in Puerto Rico. *Amer. J. trop. Med. & Hyg.*, 10: 370-373.
- VAUGHN, C. M., OLIVIER, L., HENDRICKS, J. R. & MACKIE, T. T., 1954. Mollusciciding operations in an endemic area of schistosomiasis in the Dominican Republic. *Amer. J. trop. Med. & Hyg.*, 3: 518-528.

DIE BIOTOPE DER LEBEREGELSCHNECKE (*GALBA TRUNCATULA*)  
UND IHRE BESIEDLUNG

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## ZUSAMMENFASSUNG

Im Entwicklungskreislauf des "Grossen Leberegels" (*Fasciola hepatica*) übernehmen Süßwasserschnecken aus der Familie Lymnaeidae (Schlamm- und Schnecken) die Rolle des Zwischenwirtes. Obwohl sich aber viele einheimische Schlamm- und Schnecken-Arten experimentell infizieren lassen, ist *Galba truncatula* der einzige natürliche Zwischenwirt in Europa. Der Hauptgrund für diese Tatsache ist nicht zuletzt den besonderen Lebensgewohnheiten dieser Schnecke zuzuschreiben.

*Galba truncatula* ist amphibisch lebend und findet noch in den kleinsten Wasseransammlungen ausreichende Lebensbedingungen, wodurch sie mit Weidetieren (Rinder, Schafe), den hauptsächlichsten Endwirten des Leberegels, in besonders engen Kontakt kommt. Aber auf welche Weise erfolgt die Besiedlung dieser oft völlig isolierten Biotope? Untersuchungen zur Verbreitung von *Galba truncatula* in der Umgebung von Frankfurt am Main, die seit 1932 durchgeführt werden, geben Gelegenheit, auch diese Frage zu untersuchen.

In der Umgebung von Frankfurt am Main ist *Galba truncatula* allgemein verbreitet. Man findet sie aber fast ausschliesslich nur im offenen Gelände, und ihre bevorzugten Lebensräume sind Entwässerungsgräben von Wiesen oder Weiden, sowie Strassengräben und Quelltümpel. Meist handelt es sich um kleine und kleinste Wasseransammlungen, deren Wasserstand sehr starken jahreszeitlichen Schwankungen, in Abhängigkeit von den anfallenden Niederschlagsmengen, ausgesetzt ist. Diese Fundplätze trocknen gelegentlich völlig aus, und die Siedlungsdichte ihrer Populationen wechselt daher ständig. Manchmal erlöschen solche Fundplätze vollkommen, können aber unter Umständen eines Tages wieder neu besiedelt werden. Grössere Gewässer wie Bäche oder Tümpel werden von *Galba truncatula* nur in den äussersten Randzonen besiedelt. Solche Fundplätze sind sehr anfällig gegen Hochwasser und daher gewöhnlich nur von kurzer Lebensdauer.

Von anderen Schlamm- und Schneckenarten, die mit *Galba truncatula* am gleichen Fundort vergesellschaftet sind, findet sich nördlich des Main-Flusses nur *Radix peregra*. Südlich des Mains findet man dagegen *Radix peregra* und *Galba palustris*, gelegentlich auch *Galba glabra* und *Lymnaea stagnalis*. Eine sichere Unterscheidung mancher dieser Arten nach der Gehäuseform ist, besonders bei kleineren Exemplaren, häufig sehr schwierig, liess sich aber nach dem Bau der Geschlechtsorgane stets eindeutig durchführen. Bei *Galba palustris* zeigten sich Übereinstimmungen mit den von Jackiewicz (1959) für "*Galba corvus*" beschriebenen Verhältnissen.

Die Untersuchungen über die Besiedlung der Fundplätze durch *Galba truncatula* für die Verhältnisse der Umgebung von Frankfurt am Main haben zu folgenden Ergebnissen geführt. Bei den meisten Fundplätzen erfolgt die Besiedlung durch Verschwemmung von lebenden Schnecken aus dem Oberlauf der Gewässer, besonders bei Hochwasser. Bei anderen Fundplätzen, insbesondere bei solchen, die an der äussersten Peripherie, d.h. in den Quellbezirken von Bachsystemen gelegen sind oder die völlig vom Wasserzulauf isoliert sind, ist eine solche Art der Besiedlung nicht möglich. Hier könnte man an die Möglichkeit einer Besiedlung durch Verschleppung von Schnecken durch Vögel denken, worauf in der Literatur schon mehrfach hingewiesen worden ist. An einem Fundort besonderer Art, es handelt sich um die gemauerten Wasserbecken eines Friedhofs, aus denen die Besucher das Wasser zum Blumengiessen schöpfen, konnte nachgewiesen werden, dass *Galba truncatula* durch Wasserkäfer verschleppt werden kann.

Die Untersuchungen über die Besiedlung von natürlichen Fundplätzen bei *Galba truncatula* wurden durch Beobachtungen an einem künstlichen Grabensystem in einem Versuchsgarten unseres Institutes ergänzt. Hierbei konnte nachgewiesen werden, dass *Galba truncatula* rheotaktische Bewegungen ausführt. Markierte Schnecken krochen in dem Grabensystem gegen die Strömungsrichtung des Wassers und überwandten hierbei mühelos sogar mehrere vom Wasser nur schwach überrieselte Steinstrufen. Innerhalb von 24 Stunden wurden Strecken von 4 Meter und mehr zurückgelegt. Da *Galba truncatula* an vielen natürlichen Fundorten ständig einer Verschwemmung durch das fließende Wasser ausgesetzt ist, kommt den rheotaktischen Bewegungen eine hohe ökologische Bedeutung zu. Auf diese Weise kann die Wiederbesiedlung der Fundplätze auch gegen die Strömungsrichtung erfolgen und *Galba truncatula* kann aus eigener Kraft bis in die äussersten peripheren Bezirke von fließenden Wassersystemen vordringen, wo sich ihre bevorzugten Biotope befinden.

AEROMONAS LIQUEFACIENS IN THE LEUKODERMIA  
SYNDROME OF *ACHATINA FULICA*

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ABSTRACT

Populations of the giant African snail, *Achatina fulica*, in the Indo-Pacific region manifest a frank, enzootic disease syndrome. Coincident with the development of the disease in the older populations, there appears a predictable, statistically significant progressive population decline that may ultimately result in localized extinction. A Gram-negative rod bacterium repeatedly has been isolated at a statistically significant level from the leucodermic lesions and from the abundant terrestrial isopod *Metoponorchus pruinosus*, which is frequently found in close association with the giant snails. Through methods of determinative bacteriology and techniques of serology, immunochemistry and fluorescein isothiocyanate conjugates, this bacterium has been identified as *Aeromonas liquefaciens* (Family Pseudomonadaceae), heretofore found only in aquatic vertebrates. The bacteria apparently do not act alone in producing the observed enzootics, but act in concert or seriatim with other extrinsic and intrinsic stress factors. An endotoxin, lethal both to snails and mice, has been demonstrated in this bacterium. Possible coincident or precursory viral parasitemia may exist as a complicating factor; however, introducing tissue homogenates from infected snails into established tissue cultures of *A. fulica* on specially modified basic media have so far proven inconclusive. It is believed that when molluscan pathology is more fully comprehended, there will emerge more convincing explanations of natural fluctuations of snail populations and more effective population control of harmful species. (This research was supported by grant AI-01245 from the National Institute of Allergy and Infectious Diseases, U. S. Public Health Service, and grant GB-2463 from the National Science Foundation, Washington, D. C., U. S. A.)

THE ULTRASTRUCTURE OF THE DIGESTIVE GLAND CELLS OF  
*BIOMPHALARIA PFEIFFERI* KRAUSS, AN INTERMEDIATE HOST  
OF *SCHISTOSOMA MANSONI* SAMBON

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ABSTRACT

Mature daughter sporocysts of *Schistosoma* species are living mainly in the interstitium of the digestive gland of the host snail.

Obviously, the function of the digestive gland and the mid-intestine determines this predilection-site. It seemed interesting to investigate with the electron-microscope, together with other histological and histochemical methods, the organs and tissues in the area concerned of normal, starved and parasitized snails. As an experimental animal *Biomphalaria pfeifferi* (Pulmonata, Planorbidae) was chosen. In the present paper the fine structure of the digestive gland of adult, unparasitized snails is described and the function of the different cell types is discussed. The observations indicate that the main functions of the digestive gland epithelium of *Biomphalaria pfeifferi* are: intracellular digestion, production and secretion of enzyme granules and excretion of waste products.

Presumably the gland is not important as a storage-organ for reserve-material. At the ultrastructural level the amount of glycogen in the gland epithelium is very small when compared to that in certain other cells of the body. Therefore, very probably, the preference of the daughter sporocysts to live in the interstitium is not related to a supposed storage function of the digestive gland, but rather to the fact that in this area intracellular digestion and absorption take place, rendering the blood very rich in soluble food materials.

THE CONTROL OF SCHISTOSOME DERMATITIS IN THE GREAT LAKES REGION (U. S. A.)

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ABSTRACT

Dr. W. W. Cort (1928) first demonstrated that "swimmers' itch" or schistosome dermatitis was caused by the penetration of non-human schistosome cercariae into the bodies of persons who waded or swam in certain freshwater lakes. In recent years this human nuisance has increased considerably, so that for each of the past 2 years at least 100 lakes in Michigan were reported to have had outbreaks of swimmers' itch.

For many years the Water Resources Commission in Michigan each summer has employed high school teachers to work as "itch crews" - teams of men to assist resort and cottage owners in eradicating infected snails found on their beaches. Although copper sulphate is still used extensively, better and more sophisticated methods are being developed, such as the application of Bayluscide sprayed over lakes by airplane.

It has long been recognized that reasonably good control methods will be impossible without methods for eradicating snail intermediate hosts. These problems are very involved since there are known to be at least a dozen itch-producing non-human schistosomes in the Great Lakes region. The snails (2 Lymnaeids and 1 *Physa*) at present incriminated and responsible for most of the schistosome dermatitis in Michigan were studied some 30 years ago by Drs. Donald McMullen and Paul Beaver. Recent studies indicate that conditions have changed and a new appraisal is necessary to determine which snails are at present involved, their ecology in relation to schistosome dermatitis infestation, and what methods should be recommended for their control.

PROCEEDINGS

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BIOLOGY AND POPULATION DYNAMICS OF TWO SYMPATRIC SPECIES  
OF *NERITINA* FROM SOUTHERN NIGERIA<sup>1</sup>

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INTRODUCTION

Two polymorphic, partially sympatric species of *Neritina* inhabit the shallow marginal lagoons and estuaries of southwestern Nigeria (Fig. 1). The commonest, *Neritina glabrata* Sowerby, 1849, has a small (1-7 mm) shell, beautifully and variously banded, lined and spotted with white, black and red against a yellow background (Fig. 2). The other, *Neritina* n. sp. is larger (about 12 mm), higher spired, and similarly banded, lined and spotted, but in a drab combination of dark grey and brown colours (Fig. 3).

In the present study, specimens of both species were collected from seven stations in the western Nigeria lagoon between Epe in the east and Badagri in the west.

THE WESTERN NIGERIAN LAGOON

The ecological setting of the coastal lagoons of southern Nigeria has been the subject of several detailed studies (Webb, 1958; Olaniyan, 1961; Sandison, 1966, 1966a; Sandison and Hill, 1966; Hill, 1967; Hill and Webb, 1958). The salient features are summarized below.

The Western Nigerian lagoon is the largest of the lagoon systems of the Guinea Coast. It stretches for about 160 miles from Cotonou to the western edge of the Niger Delta (Webb, 1958, p. 310). Several large rivers drain into the lagoon in the area studied, the most important being the Yewa, Ogun, Ona and Oshun rivers. Besides, the lagoon makes contact with the sea at Lagos and Cotonou. These factors make this stretch of the lagoon sites of ecological interest because of the major fluctuations in salinity observed. These diurnal and seasonal fluctuations are the result of the interplay of tidal effects and the influx of large volumes of fresh water during the rainy months.

The data published by Hill and Webb (1958) for Ikoyi jetty are shown in Fig. 4. The salinity of the lagoon is highest between December and May, and from August to September. These correspond to the dry months. The excessive rains between March and June, September and November, are primarily responsible for the low lagoon salinity between June and July, October and November.

REPRODUCTION

The breeding cycle of both species is closely linked with the seasonal fluctuations in the lagoon salinity. Eggs are laid primarily between February and March at the peak of the high salinity season. Fertilization is internal and eggs are enclosed in an agglutinated egg capsule (Fig. 5).

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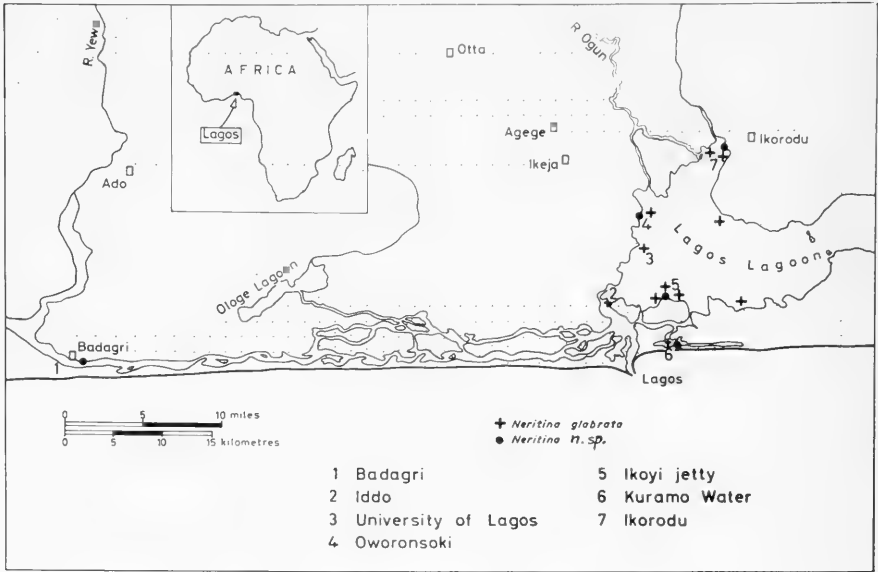


FIG. 1. Map of southwestern Nigeria showing sampled localities and the distribution of *Neritina glabrata* and *Neritina n. sp.*



FIG. 2. A few of the colour variations seen in *Neritina glabrata*.



FIG. 3. *Neritina n. sp.* showing range in coloration of shell.



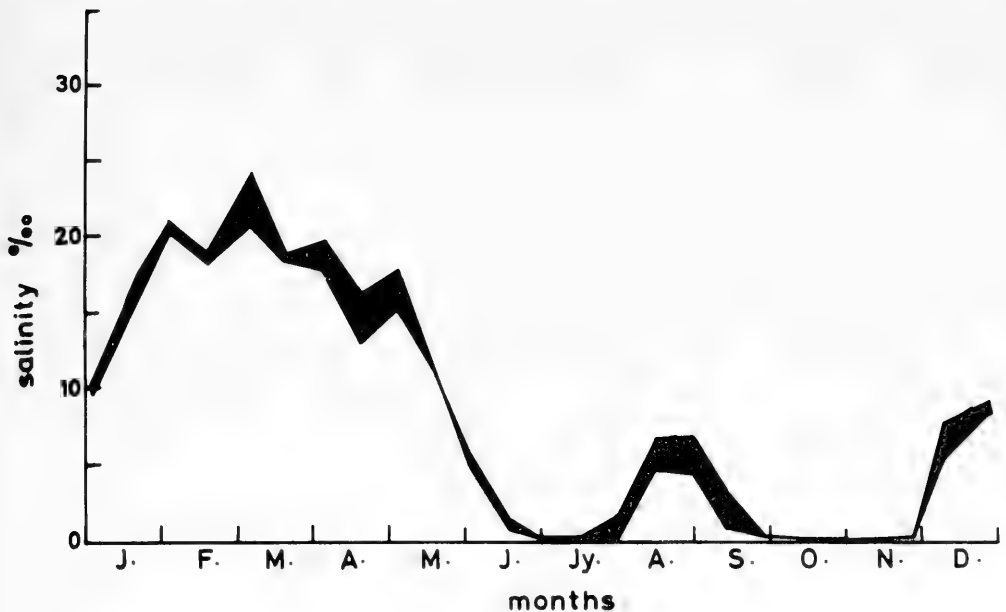


FIG. 4. Typical annual fluctuation in lagoon salinity at high and low tides (after Hill & Webb, 1958).

Each egg capsule is uniformly hemispherical with an ovate outline. Average diameter is between 0.5 and 1.5 mm. The capsule wall is composed of quartz grains with occasional amphibolite embedded in a matrix of chitin which also lines the floor of the capsule. The basal wall of the capsule lacks agglutinating material and is composed primarily of dense chitin. Collapse of the capsule occurs above this dense chitinous base during hatching. The two species show preference for sand grains of a particular size grade. Capsules of *Neritina glabrata*, though smaller, bear larger sand particles (Fig. 5). The new species, however, utilizes grains that are barely perceptible at a magnification of over 80 times. As many as 6 to 17 eggs may be present in each capsule of *Neritina glabrata*. *Neritina* new species sometimes has over 30 eggs in one capsule. The eggs develop during the low salinity months between April and December. The veliger stage is passed in the capsule.

The pediveligers are mechanically released from the capsules in January at the high salinity season. The capsules break above the basal chitinous rim. Released pediveligers are about 0.13 mm high.

#### LARVAL BEHAVIOUR

Larval activity and substrate selection were observed by artificially hatching mature capsules of *Neritina glabrata* with a scalpel in a watchglass under a binocular microscope.

Newly released larvae remain quiescent (except for slow ciliary action) for periods varying between one and five minutes. Contact with saline water is a prerequisite for the initiation of active swimming movements. There is a sudden burst of activity as the cilia of the two velar lobes begin to beat vigorously. Soon the larvae

swim off, round and round, one after the other. As they swim (aperture upwards) they perform clockwise gyratory movements punctuated at short intervals by passive drops

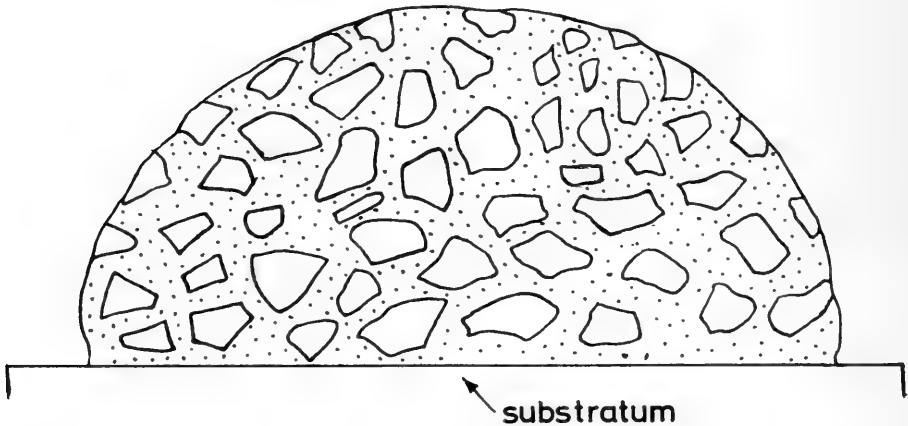


FIG. 5. Egg capsule of *Neritina glabrata*. Actual specimen is about 1 mm long.

to the bottom. The rapidity of "take-off" is enhanced by highly saline waters. It is slower in diluted brine. Larvae hatched and immersed for considerable periods in distilled water are physiologically retarded and fail to recover fully when transferred into more saline water. Such larvae were incapable of active swimming.

The pediveligers settle in the protected niches afforded by closely packed sand grains or in hollows and depressions on wood. When a site is selected, the gyratory movement ceases and the larva feeds actively. When dislodged from a selected site, the gyratory (sampling) movements are resumed until another suitable site is found. The examined larvae retained the ability to swim actively when disturbed for about 2-3 days at the end of which a thin golden shell has been secreted (veliconch).

#### ECOLOGY AND POPULATION STUDIES

*Neritina glabrata* and *Neritina* new species are partially sympatric. The former lives primarily in the lagoon bottom sand but may also creep on concrete walls and metallic supports of jetties. The species shows a preference for clean coarse sand with little or no organic decay. It was rare in the stiff, fine silty sand of Lighthouse and Badagri Creeks. Specimens of the new species on the other hand are found attached to mangrove roots, walls and water plants but never in the bottom sand. Thus, at all sympatric locations the two species are ecologically differentiated; interspecific competition thus seems to be absent.

Both species are abundant at a number of locations. *Neritina glabrata* is commonest at Ikoyi and part of Kuramo Water. Its average population density at Ikoyi during the

breeding season is about 20 per square foot. The density decreases appreciably during the low salinity months. Highest density and maximum size of *Neritina* new species was at the west end of Kuramo Water and at Badagri. Where both species live sympatrically, (e.g., Ikoyi, Oworonsoki, Ikorodu and part of Kuramo Water) *Neritina glabrata* outnumbers the new species and both rarely attain maximum adult size.

## REFERENCES

- HILL, M. B., 1967. The Life Cycles and salinity tolerance of the serpulids *Mercierella enigmatica* Fauvel and *Hydroides uncinata* (Philippi) at Lagos, Nigeria. *Jour. Anim. Ecol.*, 36, pp. 303-321, 8 figs.
- HILL, M. B. & WEBB, J. E., 1958. The ecology of Lagos Lagoon. II. The topography and physical features of Lagos Harbour and Lagos Lagoon. *Phil. Trans. Roy. Soc., London*, ser. B, no. 683, 241, pp. 319-333, pl. 14, 6 figs.
- OLANIYAN, C. I. O., 1961. Observations on the salinity and stratification of tidal currents in Lagos Harbour, Nigeria. *J. West Afr. Sci. Assoc.*, 7, pp. 49-58.
- SANDISON, EYVOR E., 1966. The effect of salinity fluctuations on the life cycle of *Balanus pallidus stutsburi* Darwin in Lagos Harbour, Nigeria. *J. Anim. Ecol.*, 35 pp. 363-378, 8 figs.
- SANDISON, EYVOR E., 1966a. The effect of salinity fluctuations on the life cycle of *Gryphaea gasar* (Adanson Dautzenberg) in Lagos Harbour, Nigeria. *Jour. Anim. Ecol.*, 35, pp. 379-389, 5 figs.
- SANDISON, EYVOR E. & HILL, M. B., 1966. The distribution of *Balanus pallidus stutsburi* Darwin, *Gryphaea gasar* (Adanson) Dautzenberg, *Mercierella enigmatica* Fauvel and *Hydroides uncinata* (Philippi) in relation to salinity in Lagos Harbour adjacent creek. *Jour. Anim. Ecol.*, 35, pp. 235-250.
- SOWERBY, G. B., 1849. *Thes. Conch.* II. no. 10, p. 535.
- WEBB, J. E., 1958. The ecology of Lagos Lagoon I. The Lagoons of the Guinea Coast. *Phil. Trans. Roy. Soc. Lond.*, ser. B. no. 683, 241, pp. 307-318, pls. 11-13, 3 figs.



ÜBER DIE VERBREITUNG DER LAND- UND SÜSSWASSERSCHNECKEN  
IN MITTELSPANIEN IN BEZUG AUF DIE VERSCHIEDENEN BÖDEN  
UND GEWÄSSER

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ZUSAMMENFASSUNG

Obwohl diese Mitteilung im allgemeinen nicht auf Grund von Analysen, sondern nur durch empirische Beobachtungen erarbeitet wurde, ist sie ganz übereinstimmend mit den Angaben einer anderen Arbeit. Die Analysen dieser Arbeit zeigen uns ohne Zweifel, dass im allgemeinen doch ein grosser Einfluss der Böden und Gewässer mit einem hohen Kalzium-Gehalt auf die Verbreitung der Schnecken besteht. Dieser Einfluss ist aber nicht bei jeder Art von gleicher Bedeutung. Manche Wasserschnecken können (experimentellerweise oder in der Natur) ohne Kalzium leben. Die von FRÖMMING (1956) erwähnten Beispiele auf S. 34 seines Buches, dass der Härtegrad (oder Kalkgehalt) eines Wohngewässers für die Schnecken keine Rolle spielt, gibt uns auch Anlass zu glauben, dass die verschiedenen Arten nicht immer gleich in bezug auf den Kalkgehalt des Milieus reagieren; der Einfluss anderer Faktoren kann die Physiologie verändern und andererseits kann es auch möglich sein, dass bei Wasserschnecken vor allem unter bestimmten Umständen das Kalzium nicht aus dem Wasser direkt entnommen wird, sondern nur auf indirekte Weise mit der Nahrung (Pflanzen) aus dem Boden.

VORWORT

Der Anteil an Schneckenarten in bezug auf die ganze Molluskenfauna ist in Mittelspanien sehr gering. Im Vergleich mit anderen Regionen, wo man nicht nur grosse Massen von Schnecken finden kann, sondern auch viele verschiedene Arten, ist die Umgebung der Stadt (etwa 60 km um Madrid) von diesen Tieren fast unbewohnt. Wenn man nun auf den Gedanken kommt, dass in jedem Bezirk Spaniens, wo der Boden kalkig ist, viele Schnecken vorkommen, wenn man dabei noch weiss, dass diese Tiere grosse Mengen von Kalziumkarbonat benötigen um ihre Gehäuse zu entwickeln, kann man leicht daraus folgern, dass diese Mollusken direkt vom Boden das Kalzium entnehmen können, und daher ein Mangel oder Fehlen dieses Stoffes im Boden die Seltenheit oder das Verschwinden der Schnecken bedingt.

So kamen wir zu dem Schluss, die Beziehungen zwischen Böden (oder Gewässer) und Schnecken in Mittelspanien näher zu studieren.

KURZE GEOLOGISCH-EDAFISCHE BESCHREIBUNG  
DER BÖDEN IN MITTELSPANIEN

Die Böden der Umgebung von Madrid bestehen hauptsächlich aus Sedimenten des Tertiärs (Miozän). Die Verteilung derselben ist innerhalb 60 km um die Stadt so, dass man insgesamt von 5 Stufen reden muss, die sich von NO nach SW erstrecken und von verschiedener Breite sind. Der Verlauf ist fast parallel zum benachbarten Gebirge. Die 1. Stufe besteht aus Granit oder Gneis und steigt bis auf Höhen von 2.400 m. Das echte Bergland fängt schon mit 1.100 m. H. an. Es ist teilweise mit Kiefernwald bedeckt.

Die 2. Stufe ist eng und unterbrochen; sie besteht aus 4 Flecken von Kalkstein der Kreidezeit. Die Pflanzenwelt ist sehr spärlich und besteht hauptsächlich aus *Thymus*-Arten.

Die nächste Stufe (1. aus Flöz) ist aus einer Mischung von grobem Quarzsand und Kalk-Tonerde entstanden; sie erstreckt sich am Fusse des Gebirges in Höhen zwischen 1.100 und 900 m. Die Flora dieses Geländes besteht vorwiegend aus Gebüsch von Wacholder und *Cistus*-Arten. An feuchten Stellen sind aber andere Pflanzen zu finden wie Pappeln, Eschen, Wildrosen usw.

Die 4. Stufe besteht aus Kieselsand und Tonerde; sie ist breiter als die vorhergehende und dehnt sich über ein Gelände in ungefähr 700 m. Höhe aus, in dem die Stadt Madrid liegt. Der Pflanzenbewuchs ist sehr verschieden; an Flüssen und anderen Gewässern sind Binsen, Schilfrohr und Rohrkolbenarten sehr häufig sowie Eschen, Pappeln und Weiden. An trockenen Hügeln findet man Winterreiche und *Retama sphaerocarpa* (Lam.) (Ginsterart). Stellenweise sind auch Kulturpflanzen zu finden.

Die 5. Stufe liegt am tiefsten; sie besteht aus Tonerde und erstreckt sich besonders die Flusstäler entlang. An manchen Stellen, südöstlich der Stadt, erscheinen Flecken einer dicken Schicht von Gipsgesteinen, die ein ödes, steppenartiges Gelände verursachen, das sich in einer Höhe zwischen 600 und 400 m. und in einem Areal von ungefähr 40 qkm erstreckt.

### ÖKOLOGISCHE ÜBERSICHT DER GEWÄSSER

Die fliessenden und stehenden Gewässer des untersuchten Bezirkes müssen, in bezug auf die Ökologie der betreffenden Mollusken, in folgende Gruppen eingeteilt werden: (1) Bergland, fliessende oder stehende Gewässer auf Granitboden, über 1.200 m. (2) Dieselben unter 1.200 m bis auf 900 m Höhe. Dieselben wie letztere aber auf Kalksteinboden. (3) Stehende oder fliessende Gewässer der Ebene (oder Hügelland) von 900 bis 500 m Höhe. (a) Auf Tonerde mit Sand und Kalk; (b) Auf Tonerde mit sehr wenig Sand; (c) Auf echter Tonerde; und (d) Auf salzigen oder gipsigen Böden.

Grosse oder kleine Wasserflächen der verschiedenen Typen, die nicht beständig sind, kommen im allgemeinen für Mollusken nicht in Frage. Die Gewässer über 1.200 m oder vielmehr über 1.500 m, haben immer wenige oder keine Pulmonaten. Die unter 1.200 m liegenden haben immer dieselben Arten, *R. peregra* (Müll.) *Physa acuta* Drap. und *Ancylus costulatus* Küst., letztere fast nur in Bächen mit einer starken Strömung. Man kann gut beobachten wie die Gewässer, je tiefer ihre Lage ist, reicher an Individuen der erwähnten Arten werden und dabei auch andere Arten vorkommen, aber nur da wo Gehalt an Kalziumkarbonat reicher ist. Diejenigen, die sich auf Kalkstein befinden, haben bei einer Höhe von 900 m. grosse Mengen von Individuen der erwähnten *Physa* und *Lymnaea* Arten und weitere 5 Arten. Gewässer unter 900 m haben immer Gastropoden. Die Pulmonata sind dabei reich vertreten. Bei salzigen oder gipshaltigen Gewässern sind *R. auricularia* (L.) und vielfach auch *Ph. acuta* Drap. zu finden, jedoch nur, wenn das Wasser kein Kochsalz enthält. Die Planorbidae sind nur in reinen, kalten und fliessenden Gewässern auf Sand mit Kalk heimisch.

Die 8 Arten, die in Mittelspanien zu finden sind, kommen viel zahlreicher in der Ebene als im Gebirge vor. Einige sind aber doch nur Bewohner von Gebirgsbächen und Quellen des Hügellandes.

### WICHTIGE, NICHT EDAFISCHE, IN DER VERBREITUNG NEGATIV WIRKENDE FAKTOREN

Man kann sagen, dass die Trockenheit der wichtigste dieser Faktoren ist, und zwar nicht nur diejenige des Bodens, sondern auch die der Luft. Diese hängt von jener ab.

In Mittelspanien sind zwei wichtige Regenperioden: im Frühling und im Herbst, und dazwischen eine lange Trockenheitsetappe, die 2 bis 3 Monate dauert. Diese Trockenheit ist so gross, dass die Schnecken immer einen Sommerschlaf (Estivation) halten müssen. Diese Unterbrechung der Lebensaktivität ist bei hygrophilen Arten nicht möglich, daher kommen diese in der untersuchten Fauna nicht vor. Wenn doch einige zu finden sind, treten sie nur spärlich am Ufer von Gewässern oder an ganz speziellen Biotopen mit mikroklimatischer Feuchtigkeit auf.

Der zweite Faktor in dieser Hinsicht ist die Temperatur, und zwar diejenige des Winters mit sehr vielen Frosttagen, sowie die hohen Temperaturen des Sommers; beide wirken sich in bezug auf Feuchtigkeitsmengen sehr ungünstig auf die Mollusken aus. Es sind aber die grossen Schwankungen des typischen Kontinentalklimas Mittelspaniens, die eine wirklich negative Wirkung auf die Schneckenwelt haben. Man kann daher nur wenige thermophile Arten finden.

#### DER MENSCHLICHE EINFLUSS AUF DIE VERBREITUNG DER SCHNECKEN

Dieser Einfluss wird im Laufe der Zeit leider immer grösser, vor allem bei den Süsswasserarten. Es handelt sich aber nicht nur um die Bekämpfung von Zwischenwirten gefährlicher Viehschmarotzer, sondern im allgemeinen um alle Arten, die im Wasser oder auf dem Land leben. Unter dem "menschlichen Einfluss" meine ich vor allem das ständige und immer schnellere Wachsen der Städte, die so alle guten Orte mit den interessanten Arten der Lokalfauna ganz zerstören und verschwinden lassen. In der Umgebung der Stadt Madrid sind viele grosse Teiche, bewaldete Orte mit Bächen usw. ganz verschwunden, denen vor 60 Jahren viele Arten noch sehr häufig waren, die jetzt ausserordentlich selten oder nicht mehr zu finden sind. In den Sammlungen des National Museums in Madrid werden die Schalendieser Arten aufbewahrt. Grossen negativen Einfluss haben auch alle Abfallstoffe der Stadt und der Industrie, sowie die Insektenvertilgungsmittel, die in die Gewässer gelangen. Viele kleine Nebenbäche des Manzanares, die vor 30 Jahren dicht mit *Planorbarius metidjensis* (Forb.) besetzt waren, beherbergen zur Zeit kein einziges Exemplar mehr.

Der menschliche Einfluss ist aber nicht immer negativ. Bei manchen Arten ist er sogar so günstig, dass in einigen Jahren nur diese übrig bleiben werden, und zwar immer in der Nachbarschaft des Menschen. Das ist der Fall z.B. mit *H. (Cryptomphalus) aspersa* Müll., obwohl sie, als Leckerbissen geschätzt, wie auch andere Arten, in grossen Mengen verzehrt wird.

#### Die in Mittelspanien noch lebenden Arten.

- |  |   |
|--|---|
| 1. <i>Oxychilus lucidus</i> Drap.              | 13. <i>Jamnia quadridens</i> (Müll.)      |
| 2. <i>Euparypha pisana</i> (Müll.)             | 14. <i>Vallonia costata</i> (Müll.)       |
| 3. <i>H. (Cryptomphalus) aspersa</i> Müll.     | 15. <i>Granopupa granum</i> (Drap.)       |
| 4. <i>Eobania vermiculata</i> (Müll.)          | 16. <i>Truncatellina rivieriana</i> Bens. |
| 5. <i>Cepaea nemoralis</i> (L.)                | 17. <i>Succinea stagnalis</i> Gass.       |
| 6. <i>Leucochroa (Xeromagna) arigo</i> Ross.   | 18. <i>Radix auricularia</i> (L.)         |
| 7. <i>H. (Xerotricha) conspurcata</i><br>Drap. | 19. <i>Radix pereger</i> (Müll.)          |
| 8. <i>Cermea virgata</i> da Costa              | 20. <i>Galba truncatula</i> (Müll.)       |
| 9. <i>Iphigena ventricosa</i> (Drap.)          | 21. <i>Physa acuta</i> Drap.              |
| 10. <i>Cochlicella conoidea</i> Drap.          | 22. <i>Planorbarius metidjensis</i> Forb. |
| 11. <i>Monacha cartusiana</i> (Müll.)          | 23. <i>Anisus spirorbis</i> (L.)          |
| 12. <i>Rumina decollata</i> (L.)               | 24. <i>Ancylus costulatus</i> (Küst.)     |
|  | 25. <i>Ancylus fluviatilis</i> Müll.      |

Arten, die während der letzten 40 Jahren verschwunden sind.

Arten	Fundorte
1. <i>Oxychylus pazi</i> Bgt.	Toledo
2. <i>Ena obscura</i> (MÜLL.)	Escorial (Castañar) VI-1917
3. <i>Pupa gratiosa</i> West.	S. Fernando (Jarama) VII-1897
4. <i>Lauria cylindracea</i> Da Costa	Escorial (Herreria) V-1920
5. <i>Armiger crista</i> (L.)	Soto de Migascalientes (Madrid)
6. <i>Hippeutis complanatus</i> (L.)	Soto de Migascalientes (Madrid)
7. <i>Anisus perezi</i> Gräells.	Soto de Migascalientes, Rio Manzanares und Casa de Campo (Madrid) VII-98.
8. <i>Gyraulus albus limophilus</i> (West.)	Lozoya (Madrid)
9. <i>Gyraulus albus</i> (Müll.)	El Pardo, Estanque d.l. Florida und Escorial (Batán) (Madrid) V-1910.

## SCHRIFTTUM

- AHO, J., 1966, Ecological basis of the distribution of the littoral freshwater moll. *Ann. Zool. Fen.* 3, p 287-322 Helsinki.
- FRÖMMING, E., 1954, Biologie der mitteleuropäischen Landgastropoden, Berlin.
- FRÖMMING, 1956, Biologie der mitteleuropäischen Süßwasserschnecken, Berlin, (Dunk. Humb.)
- GERMAIN, L., 1930, Mollusques terrestres et fluviatiles, *FAUNE de FRANCE* 21-22, Paris, Lechevalier.
- HAAS, F., 1929, Fauna malacológica terrestre y de agua dulce de Cataluña. *Trab. Mus. Cien. Nat.* 13, Barcelona.
- HUBENDICK, B., 1951, Recent Lymnaeidae, *Kungl. Sv. Vetensk. Hand.* 3, Stockholm.
- JANUS, H., 1962, Unsere Schnecken und Muscheln. *Kosmos*, Stuttgart.
- ÖKLAND, J., 1964, The eutrophic lake Borrevann (Norway) - an ecological. . . *Folia Lim. Scandinavica* 13, Oslo.
- MANIGAULT, P., 1960, La coquille des Mollusques: structure et formation. in GRASSE *Traité de Zool.* 5 f.2, Paris.
- NEUMANN, D., 1961, Ernährungsbiologie einer rhipidoglossen Kiemenschnecke. *Hidrobiologia, Acta Hyd. Hydrograph. et Prot.* 17, 1-2, Den Haag.

## ABSTRACT

In this paper, the author points out the importance of the different soils and their contents on chalk carbonate in the distribution of the pulmonata snails in the center of Spain. He gives a description of each soil, its composition and its geological origin in the surroundings of Madrid. It is given also an indication on the preference of determinated soils or respectly waters for the 25 species found in the studied country. He points out the most important climate factors, such as temperature and wetness or dryness, and their influence on the snails. At last he studied also the influence of men on the regression of the dispersion of some species.





## Landschnecken Arten

- △ *O. lucidus* Drap.
- ▲ *Eup. pisana* Müll.
- ★ *Eob. vermiculata* Müll.
- ★ *Cep. nemoralis* L.
- *H. (Cript.) aspersa* Müll.
- *H. (Xerom.) arigoi* Ross.
- *H. (Xerct.) conspurcata* Drap.
- *H. (Cer.) variabilis* Drap.
- + *Coch. ventricosa* Drap.
- x *Coch. conoidea* Drap.
- \* *Th. carthusiana* Müll.
- \* *R. decollata* L.
- ⊕ *Ch. quadridens* Müll.
- ⊗ *V. costata* Müll.
- ⊙ *Cr. granum* Drap.
- ⊕ *Tr. rivieriana* Bens.
- ⊕ *S. stagnalis* Gass.

## Bodenarten

- |                     |                  |
|---------------------|------------------|
| ■ GYPS              | ▨ MERGEL         |
| □ TONERDE           | ▨ KALKSTEIN      |
| ▨ SAND-KALK TONERDE | ▨ GRANIT         |
| ▨ GYPS TONERDE      | ▨ KIESEL TONERDE |

## Süsswasserschnecken Arten

- ⊕ *Ancylastrum fluviatile* L.
- ⊕ *Physa acuta* Drap.
- ⊕ *Coretus metijtensis* Farb.
- ⊕ *Spiralina spirorbis* L.
- ⊕ *Galba truncatula* Müll.
- ⊕ *Radix pereger* (Müll.)
- ⊕ *Radix auricularia* L.

Die Verbreitung der Land- und Süßwasserschnecken in der Umgebung von Madrid in bezug auf die Bodenarten und Gewässer.

Bemerkung: Die verschiedenen Zeichen können auf den schwarzen Flächen weiss erscheinen, sind aber dieselben.

Für die häufigen Arten sind nur einige extreme Fundorte angegeben.



CEPHALIC ACCESSORY SEXUAL ORGAN OF *GYMNNARION*: SPECIATION  
AND PHYLOGENY (PULMONATA, HELICARIONIDAE)

Eugène Binder

*Muséum d'Histoire Naturelle, Genève, Switzerland*

Several species of the African genus *Gymnarrion* (PILSBRY, 1919) carry on their head a peculiar organ (BINDER, 1964, 1965) that exists in no other genus and which has been provisionally called the frontal organ. This organ is used in courtship, when the snails remain for long periods head to head before copulating. Its complete development is in correlation with that of the genital system, although there exists no anatomical connection between both: it is complete only in adult individuals during the mating season; accidental castration resulting in atrophy of the genital tract, also leads to the atrophy of the frontal organ. This organ is situated above the snail's mouth, between the 4 tentacles and usually rather nearer the dorsal pair. It is retractile and stays normally hidden inside the head while the animal is alive, but it can be pushed out by the inner pressure of the body, in the same way as the tentacles. This is possible because the organ is essentially a hollow expansion of the body-wall. It is pulled back by retractor muscles which join dorsally the body wall's muscular layer. The surface is usually covered with numerous papillae, much smaller than the warts on the rest of the body. In those species that were studied histologically, the epithelium on this part is devoid of mucus cells. In some species there are lobes of erectile tissue each carrying a calcified hook (BINDER, 1965).

Since the discovery of the frontal organ in a few species from the Ivory Coast and Sierra Leone, I have had the opportunity to examine numerous specimens from various parts of Africa<sup>1</sup>, among which another 15 species possess a frontal organ. These show a remarkable diversity of shapes; most of them can be arranged in series in an attempt to reconstruct their phylogenetical relationships.

The simplest form of frontal organ seen so far consists of a slight swelling of the forehead (Mus. Tervuren, without origin). This could hardly be distinguished as a frontal organ if it were not covered with many small papillae, which show it to be a specialised area of the body surface (Fig. 1). Other simple forms appear as more pronounced expansions, in the shape of a bag (Mus. Tervuren 218 271 - Elisabethville I), and their surface has much the same appearance as that of the rest of the head (Fig. 2). One species from Upemba National Park (IRSNB 2227) has a frontal organ in the shape of a tongue, flattened and bent downward, covered with polygonal papillae separated by deep furrows (Fig. 4). In one species of Nigeria (Tervuren 793 957) and one from Chirinda Forest, South Africa, it has a conical shape and, in the latter species, it has lost its warts and has a smooth surface (Fig. 3). Other variations derived from the simple bag are the small narrow cylinder (IRSNB, Upemba 1882) (Fig. 5), or the strong

<sup>1</sup>Appreciation is expressed to the following for the loan of material for study: Dr. W. Adam, Institut royal des Sciences naturelles de Belgique, Brussels; A. Houben, Institut des Parcs nationaux, Brussels; Dr. P. L. G. Benoit, Musée royal de l'Afrique centrale, Tervuren; Prof. E. Fischer, Muséum national d'Histoire naturelle, Paris; Dr. R. Kilius, Naturhistorisches Museum der Humboldt-Universität, Berlin; Dr. A. C. van Bruggen, Rijksmuseum van Natuurlijke Historie, Leiden; Dr. A. Holm, Zoologiska Institutionen, Universitet, Uppsala; Dr. R. Oleröd, Naturhistoriska Riksmuseet, Stockholm.

column found in Elisabethville II (Tervuren 794 831). In this species, the surface of the frontal organ is without warts or papillae, but conspicuously wrinkled lengthwise. The end is flattened dorso-ventrally and divided in two rounded lobes which do not carry hooks (Fig. 6).

*Gymnarion* with frontal organs carrying hooks seem to follow a separate line of descent from the start. They were found up to now only in the western part of Africa, from Sierra Leone to Angola. Those from the Loma Mountains (Sierra Leone) and from Mount Nimba (Ivory Coast) have already been described (BINDER, 1964). Several species from Ghana (Tervuren 608 884) and Cameroons (Stockholm 425), seem to differ only in the number of hooks, where the frontal organ is concerned. A species from Angola (Berlin 39423) is very peculiar in that it has 12 to 15 pairs of hooks, each retracting separately in the middle of a circular pad (Fig. 7); the central pairs are largest and the more lateral ones are smaller; on the edges of the frontal organ the pads around the smallest pairs are scarcely bigger than the warts on the rest of the animal. It looks as if there were a gradual change from face-wart to hook-and-pad. This form seems to be rather primitive among the hooked frontal organs, being less differentiated from the plain surface of the head. In the form from Misahöhe, Togo (Berlin 47201), the 5 pairs of hooks can also be retracted individually, but the whole frontal organ is encircled with a sphincter and a circular bulge, and is usually retracted or pushed out as a whole (Fig. 8). This device is intermediate between the former and the species of Mt. Nimba with their hooks arranged in a crown and encircled with a single sphincter. In those species, the number of hooks is somewhat variable: each hook-carrying lobe can be split in two, or pairs of lobes can be replaced by single lobes. The passage from one formula to another with more or fewer hooks is thus very easy. Only the knowledge of their distribution can give an indication as to which way the change has taken place; for instance, the 40-hooked *G. duplex*<sup>2</sup>, which is very localised, is probably evolved from the more widely distributed *G. coronatus*<sup>3</sup> with 12 hooks.

*G. columna*<sup>4</sup> from Mt. Loma shows a further step in evolution by raising its crown of hooks on a strong cylindrical column (Fig. 9). *G. anchora*<sup>5</sup>, also from Mt. Loma, has the most elaborate form of frontal organ known so far, with its hooks reduced in number to a single pair, but very large, inserted on the summit of a strong column and with two tufts of finger-like papillae localised near the ventral edge (Fig. 10). In these two last species, the lobes appear first during development, become retractible later, and the column develops last. The hooks are only differentiated from the edge of the lobes when the animals are adults.

Some species are difficult to relate to any other. For instance, one single specimen

<sup>2</sup>Description in the press. Called "forme B" in BINDER 1964.

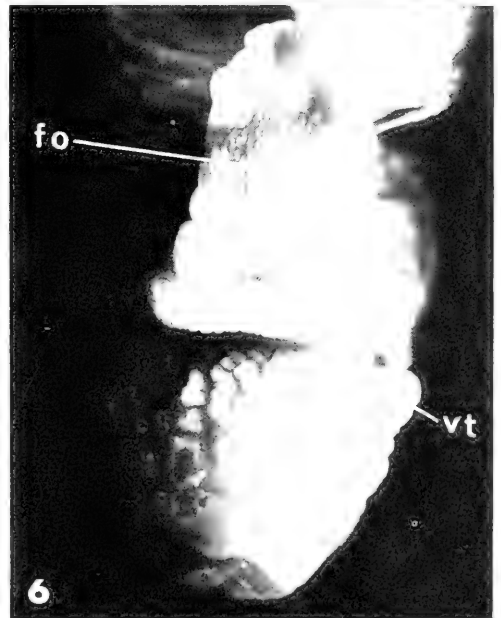
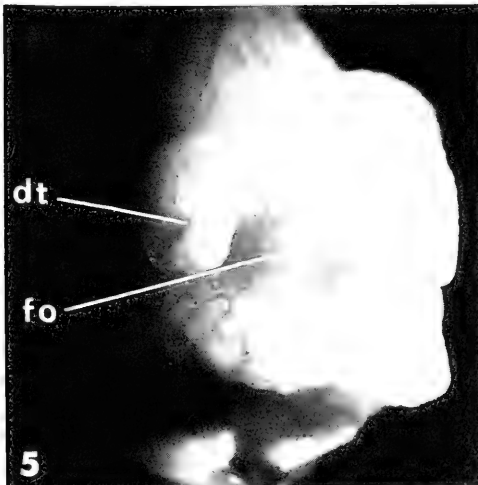
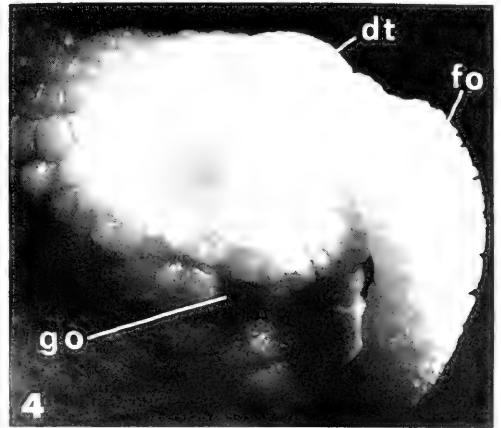
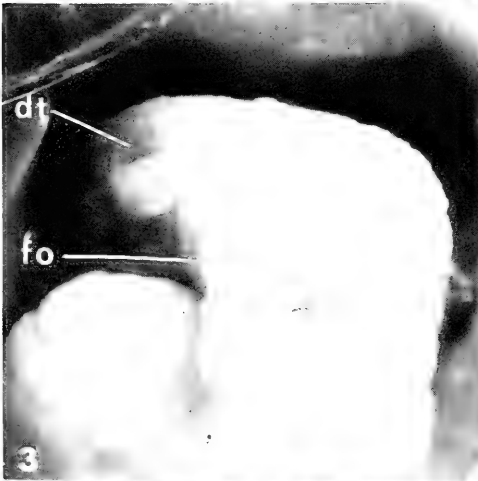
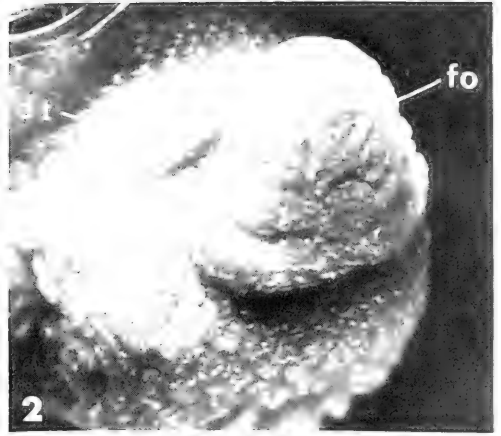
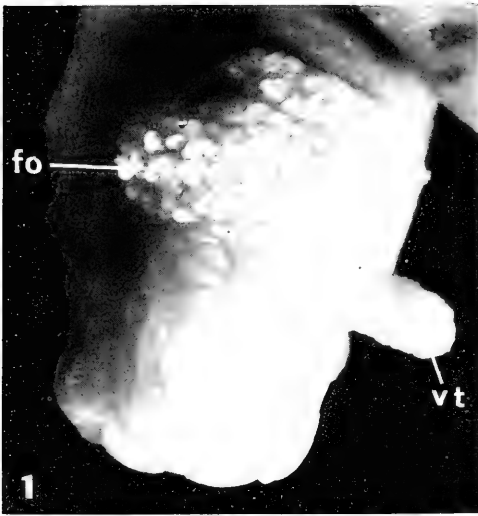
<sup>3</sup>id., "forme A".

<sup>4</sup>Description in the press. Called "forme C" in BINDER 1964.

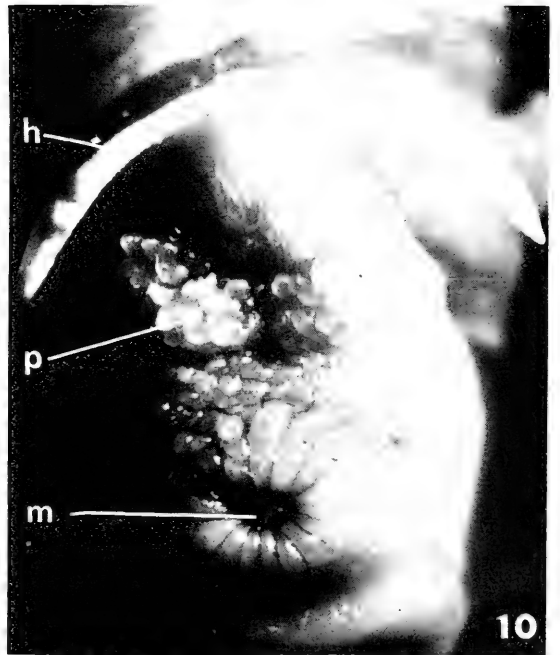
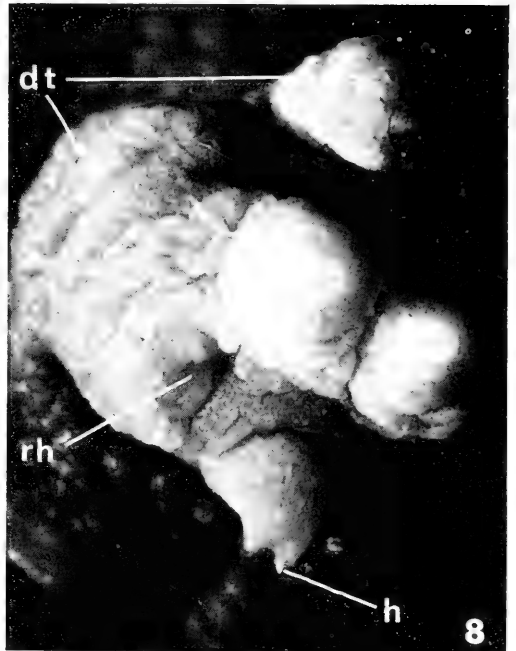
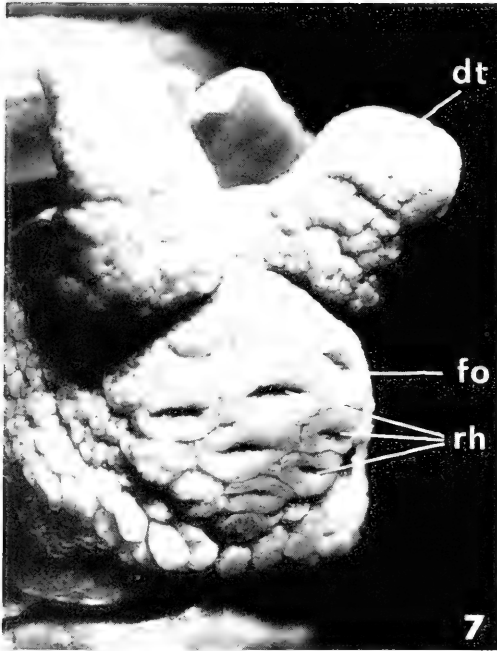
<sup>5</sup>id., "forme D".

#### ABBREVIATIONS TO FIGURES

dt, dorsal tentacle; fo, frontal organ; go, genital opening; h, hooks (broken in Fig. 8); m, mouth; p, papillae; rh, retracted pairs of hooks; s, scale-like modified warts; vt, ventral tentacle.



FIGS. 1-6. Various shapes of frontal organ without hooks. (See text.)



FIGS. 7-10. Various shapes of frontal organ with hooks. (See text.)



FIG. 11. Frontal organ plus modified warts on the right side of the head. (See text.)

from Tshela, Congo (Tervuren 249 530) carries 3 straight horizontal strakes across its front; it is uncertain whether these may at times differentiate hooks. This frontal organ is supplemented by a curious differentiation of the body surface on the right side, where the usual warts take on a rounded flattened shape and cover each other, somewhat like scales (Fig. 11).

Summing up, there seem to be two main trends: one toward a lengthening of a simple expansion of the body-wall and its modification into various shapes, the other toward the development of hooks and their arrangement into diverse patterns, with eventually the secondary formation of a carrying column.

As to the geographical aspect of this evolution, among the species known to this day, those without hooks on their frontal organ are those from Central and South-East Africa: Katanga, Zambia, S. Rhodesia, Tanganyika. The hooked species have all been found on the Western side of Africa: Sierra Leone, Guinea, Ivory Coast, Ghana, Togo, Nigeria, Cameroon, Lower Congo, Angola. Among these, the primitive forms occur in Angola and the most evolved ones in Sierra Leone. If Vavilov's principle applies here, it would indicate that the frontal organ-carrying group of *Gymnarion* originated in extreme West Africa.

The shape of the frontal organ, when present, is a very good taxonomical character, and the first reliable one. The genus *Gymnarion* is remarkably uniform; until now "species" were based on very unconvincing distinctions between shell forms, sizes and proportions. Identifications, even by the best malacologists, were completely random. Now it appears that there are many more species than it was ever suspected, each clearly distinct from the others. These species are restricted to the rather particular habitat of altitude savannas or low, sparse mountain forest: they seem to need a certain amount of light, but also of humidity, and they feed on dicotyledonous plants, not on grass. This sort of habitat is broken up into many separate areas rising like islands out of the almost continuous dense lowland forest of tropical Africa, and each mountain range has its own species - or group of species - of *Gymnarion* with a frontal organ. Thus there is at least a geographic cause to the subdivision of that group into many species.

Being a means of recognition during courtship, and capable of a certain amount of variability, the frontal organ might be in itself a factor of speciation, differences that arise in this respect between populations acting as reproductive barriers. One would be tempted to accept this as an explanation of the great number of species with frontal organs, if it could be proved that the other species of *Gymnarion* are less numerous. To investigate this, I have searched for other taxonomically useful characters in species already clearly distinguishable by their frontal organ. I have found that the details of the folds of the coating of the penis, which at first sight look rather accidental, differ in fact between species and show a perfect coincidence with the frontal organ. The use of this new anatomical character, and perhaps others still to be discovered, now makes a proper revision of the genus *Gymnarion* possible. The work done until now has shown me already that there are also quite a number of species, heretofore undistinguishable, among the *Gymnarion* without a frontal organ, and that consequently a considerable amount of speciation has taken place in the absence of that organ.

To ascertain the possible role of the frontal organ in speciation, it would be necessary to study in the field the relations between recent or incipient species, where they occur, like *G. coronatus* and *G. duplex* on Mt. Nimba. Failing this, it is not possible to come to a conclusion on this point yet. The remarkable diversification of shape of the frontal organ does not correspond to any adaptation to diverse environments or modes of life. Rather, like many features used at mating-time, it tends to assume an exaggerated size and degree of elaborateness. This is perhaps because, before being a means of species-recognition, such features are primarily a means of recognition between individuals who are in the proper physiological state for reproduction, and extreme types can be favoured by selection if they elicit an overoptimal mating response in other individuals.

Ethological observations are needed to reveal the exact functioning of the frontal organ during courtship. Its existence implies a very particular mating behavior, probably as diverse in detail among species as the organ itself; until now, it is only known that, in *G. coronatus*, the partners approach each other from the front with their organs retracted, press tightly front against front and remain a long time in that position without moving; their frontal organ cannot be seen from the outside during that phase.

#### REFERENCES

- BINDER, E., 1964, Existence d'un organe de fixation sur la tête de certains Heli-carionidae (Mollusques Gastéropodes). *Arch. Sci.*, Genève, 18: 89-92.  
BINDER, E., 1965, Structure de l'organe sexuel frontal des *Gymnarion* des Monts Nimba. *Rev. suisse Zool.* 72: 584-593.

#### SUMMARY

Many species of the genus *Gymnarion* Pilsbry exhibit between their tentacles a retractile organ which exists in no other group of Molluscs. It plays a role in courtship and its development is in correlation with that of the sexual organs, it is thus an external indicator of a Mollusc's endocrinological state.

This organ is distinctly different from species to species and provides a very good taxonomic character. A tentative phylogeny of the known forms shows two main trends in its evolution, but the causality of that evolution is not clear; it is not adaptive.

As a means of recognition between individuals of a same group, the presence of the frontal organ may have an incidence on the mode of speciation by facilitating the establishment of reproductive isolation between populations.



ETUDE DE LA CINÉTIQUE ET DE LA RÉPARTITION DU RADIOCESIUM  
CHEZ UN BIVALVE D'EAU DOUCE (*UNIO REQUIENI* MICHAUD)

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INTRODUCTION

Les besoins croissants en énergie conduisent à un développement rapide des centrales nucléaires. Cette industrie naissante pose un nouveau problème hydrobiologique puisqu'elle contribue à augmenter la teneur de certains éléments dans le milieu ou même à en introduire d'autres. La radioécologie doit contribuer à sa solution; PEREDEL'SKY en donne la définition suivante: "La signification particulière de la radioécologie réside dans la possibilité de bien comprendre les chemins de la transmission des radioisotopes, leurs concentrations et leurs dispersions . . . ainsi que l'augmentation du danger pour l'homme due à la chaîne écologique des organismes du milieu ou de la culture" [1]. Sur des bases écologiques et physiologiques un problème de radioprotection est posé [2], "c'est ainsi que telle algue ou tel mollusque quoique n'ayant qu'une place insignifiante dans la chaîne alimentaire pourra être choisi comme terme sensible à cause de son caractère révélateur de l'état de la pollution." [3] En eau douce, vu la variabilité des milieux, les études partent toujours d'une situation locale.

Dans cette optique nous nous proposons d'étudier la cinétique du radiocésium chez *Unio requieni* (Michaud). Les échantillons ont été récoltés dans la partie Nord du delta du Rhône où ils sont assez répandus. Le 137-césium est un produit de fission à vie longue que l'on retrouve dans les "retombées" à la suite des explosions nucléaires ou dans les effluents issus du traitement du combustible irradié produits dans les réacteurs nucléaires [4].

CONDITIONS EXPERIMENTALES

Les bivalves, par leur biogéographie, leur mode de vie et leur métabolisme constituent des témoins biologiques intéressants. [5] [6] [7] [8] [9] *Unio requieni* a porté successivement des noms différents; de nombreuses variétés ont été décrites. GERMAIN ne signale qu'*Unio requieni* (Michaud) [10], il en donne une équivalence avec *Unio pictorum* (Draparnaud, 1805). MARAZANOFF cite *Unio requieni* (Michaud) [11] PERRIER [12], ADAM [13], ELLIS [14] n'indiquent que *Unio pictorum* (Linnaeus, 1758). *Unio requieni* (Michaud) est répandue dans toute la France, dans les rivières, les canaux et les étangs, en particulier dans l'Ouest et dans le Bassin Rhodanien. Récemment, elle a été citée en Camargue par MARAZANOFF [11] [15]. Depuis, dans cette région, nous l'avons retrouvée en d'assez nombreux endroits.

La distinction chez les bivalves entre la coquille et les "parties molles" a un intérêt pratique immédiat. La coquille, à métabolisme lent, pourra en quelque sorte représenter l'historique de la radiocontamination; (par exemple pour le radiostrontium suivant le métabolisme du calcium [6]). Les parties molles dont le métabolisme est beaucoup plus rapide répondront de manière directe aux fluctuations de la radioactivité du milieu, (en particulier pour le radiocésium et le radiocérium). Mais leur principale caractéristique réside dans leur grande capacité de filtration de l'eau. Grâce à l'action des cils vibratils l'eau rentre par le siphon inhalent, est filtrée à

travers le réseau branchial et ressort par le siphon exhalent. Le transit de cette eau permet une absorption directe des sels par diffusion à travers les membranes et une incorporation par l'intermédiaire de la nourriture [16] [17]. (La question restant ouverte d'ailleurs quant à la qualité exacte de cette nourriture et au mode actif ou passif d'alimentation . . .).

Les *Unio*, et ceci est important pour notre propos, sont donc en contact permanent avec les deux éléments du milieu les plus susceptibles d'être contaminés; à savoir: l'eau et les particules organiques ou minérales en suspension. Les bivalves ont toujours été récoltés dans des zones dont le courant est faible ou nul. Les eaux sont calcaires, dures, à pH légèrement basique. Le sédiment est de type vaseux riche en argiles.

Les animaux de tailles comparables sont placés au laboratoire dans des aquariums en résine polyester contenant environ 20 litres d'eau et 7 Kg de sédiment. On place une quarantaine d'échantillons par aquarium. (Graphiques 1 et 2). On contamine l'eau de l'aquarium en une seule fois en assurant la meilleure homogénéisation possible. ( $2\mu$  Ci/litre de 137-cesium). La solution utilisée est composée de  $11\mu$  g/g de  $\text{CO}_3 \text{Cs}_2$  à  $26,9\mu$  Ci/g  $\pm$  3% de 137-cesium.

L'eau est prélevée par pipettage dans des capsules et comptée après évaporation. (Chaque point représente la moyenne de cinq prélèvements). Les animaux sont disséqués; (trois lors de chaque prélèvement); les organes sont pesés frais, placés à l'étuve pendant 30 heures à  $110^\circ\text{C}$  et pesés secs (les parties molles sont placées telles quelles dans les capsules de comptage; les coquilles sont broyées). On effectue les comptages sur un sélecteur d'amplitude monocanal dont la sonde est constituée d'un scintibloc  $\text{SC}_3 \text{N}^5\text{O}1$  "3/4 2." On suit pendant 70 jours l'évolution de la contamination de l'animal; à ce stade on replace les bivalves dans de l'eau inactive et l'on étudie pendant 230 jours le processus de décontamination.

## RESULTATS

### *Etude de la contamination par le 137-cesium*

#### a) Evolution de l'activité de l'eau et du sédiment

On observe une décroissance très rapide et très importante de l'activité de l'eau. On obtient, entre 15 et 20 jours, un "état d'équilibre" où l'activité de l'eau ne représente plus que 0,5% à 1% de l'activité initiale. (Courbes 1) La majeure partie du radio-cesium est passée dans le sédiment (98% environ). En effet il se produit une adsorption et une absorption du radiocesium entre les feuillets alumino-silicatés des argiles. Des liaisons rigides s'établissent qui provoquent une fixation irréversible du 137-cesium. Ce phénomène constitue une loi générale de la migration du 137-cesium dans les cours d'eau à fonds sablo-limoneux et vaseux [18]. En conséquence, dans des conditions particulièrement avantageuses du point de vue de la biomasse, les *Unio* ne retiennent au maximum qu'1% de l'activité introduite dans l'aquarium. Ce 1% représente en quelque sorte une limite maximum de contamination puisque nos conditions expérimentales correspondent à des conditions particulièrement défavorables et qui ne peuvent pratiquement pas se présenter dans la nature.

#### b) Evolution de l'activité des animaux

Nous considérons en premier lieu l'animal pris dans son ensemble en séparant seulement la coquille, les parties molles et les liquides internes. Les Courbes 1 permettent de tirer un ensemble de données générales. A début de l'expérience les animaux vivent dans une eau dont l'activité est élevée; pendant cette période d'une dizaine de jours ils fixent une quantité relativement importante de 137-cesium. Il se

produit corrélativement un processus de décontamination qui aboutit à un "état d'équilibre" vers le 30ème jour (pour des gastéropodes d'eau douce TIMOFEYEVA RESOVSKAYA donne 3 semaines) [19]. Avec un décalage dans le temps que nous tenterons d'expliquer plus loin, l'évolution de l'activité des animaux suit en quelque sorte l'évolution de l'activité de l'eau. La donnée principale réside dans la très grande différence que l'on observe entre l'activité spécifique de la coquille et des parties molles. La coquille ne retient le 137-césium que par des phénomènes d'adsorption. Le brossage et le lavage éliminent la majeure partie de la radioactivité due aux particules de vase ou aux microorganismes [20] [9]. Le bord externe de la coquille a toujours l'activité spécifique la plus élevée.

TABLEAU 1

Temps (jours)	Activités spécifiques (Des/min/g sec)	
	Coquille totale	Bord externe
17	1 700	35 000
30	450	25 900
48	670	11 900
69	320	3 600

Il subsiste cependant des liaisons rigides que l'on ne peut enlever. On est autorisé à penser que la fixation du 137-Cs par la coquille des bivalves est essentiellement fonction de la surface mise en contact avec l'eau. Les parties molles ont une activité spécifique beaucoup plus élevée (Ce résultat est assez général et se retrouve pour d'autres radioéléments et d'autres espèces) [21]. Ici en effet ce sont de véritables phénomènes métaboliques qui interviennent. Il peut se produire soit des échanges ioniques directs entre l'eau et l'animal, soit une incorporation du radiocésium par la nourriture. En ce qui nous concerne l'aquarium était placé à l'obscurité dans une eau contenant peu de microorganismes. Ce problème a été abordé [8], mais des études plus poussées devraient permettre d'établir quelle est l'importance respective de chacun de ces processus physiologiques.

L'activité des liquides internes est très faible mais cependant toujours supérieure à celle de l'eau. Le liquide palléal est en "équilibre" avec l'eau; ce sont donc surtout le liquide extra-palléal et le sang qui ont une activité supérieure à celle de l'eau. Des études à ce sujet sont en cours et démontrent essentiellement la rapidité des échanges.

Si l'on considère la répartition de l'activité on constate que les parties molles représentent 69% de l'activité de l'animal total (Graphique 2). Les chiffres sont comparables à ceux que nous avons obtenus sur *Margaritana margaritifera* (Linnaeus) [9] GETSOVA, et al. sur *Anodonta cellensis* retrouvent 40% du 137-Cs dans la coquille et le reste dans les parties molles (22). Pour aller plus loin dans l'analyse il faut considérer uniquement l'activité des organes internes (Tableau 2). On peut constater que, à l'"équilibre," les écarts entre les activités spécifiques des différents organes sont peu importants. C'est la masse musculaire qui présente les valeurs les plus élevées (en particulier les muscles adducteurs). Il y a là une relation certaine avec le fait que le muscle contient le plus fort pourcentage de potassium stable; vu sa parenté chimique avec le césium on peut considérer que ce dernier suit le métabolisme du potassium. Cette relation a déjà été trouvée plusieurs fois et démontrée,

en particulier par les travaux de BRYAN [23].

Le manteau vient ensuite. Son bord a toujours une activité nettement supérieure à celle de la partie interne (c'est peut-être en rapport direct avec l'activité élevée du pourtour de la coquille). L'activité spécifique des siphons est peut-être due en partie à de fines particules retenues par les cils vibratiles. La masse viscérale et les branchies ont des activités spécifiques comparables (la valeur atteinte par les branchies internes est toujours supérieure à celle des branchies externes). Tout ceci joue plutôt en faveur de mécanismes d'échanges directs du radiocesium.

Si l'on ne prend en compte que l'ensemble des parties molles, on constate qu'il existe une "constante de distribution" du 137-cesium; les moyennes obtenues sont exprimées dans le Graphique 4. Ces moyennes sont comparables à celles obtenues par GETSOVA su *Anodonta cellensis* [22].

De ces données expérimentales nous pouvons tenter de dégager un certain nombre de lois générales:

L'intensité des échanges du radiocesium est maximum entre l'eau et le sédiment. L'activité de l'eau baisse très rapidement au profit de la pellicule supérieure de la vase. La quantité de radioélément retenue par les bivalves est faible par rapport à l'activité introduite.

La coquille ne retient du 137-cesium que par des phénomènes d'adsorption; pour les parties molles, au contraire, il s'agit de processus métaboliques.

L'activité spécifique des parties molles est toujours nettement supérieure à celle de la coquille. Les activités spécifiques des différents organes sont comparables avec cependant des valeurs plus élevées pour les muscles<sup>1</sup>.

Cette capacité de fixation est fonction du métabolisme et des échanges osmotiques qui s'établissent entre l'eau extérieure et l'animal. Ces échanges s'effectuent en particulier entre les ions  $Cs^+$  et  $K^+$ . A l'appui de cette thèse on peut faire remarquer que la capacité de fixation du 137-Cs est beaucoup plus faible pour les organismes marins que dulcicoles [23] [21].

Les différences en sels de l'eau influent sur la rapidité des échanges ioniques. C'est pourquoi nous avons voulu étudier la dynamique de la décontamination lorsque des "*Unio*" contenant une quantité connue de radiocesium sont replacées dans un courant d'eau inactive.

#### *Etude de la décontamination*

La Courbe 2 montre que les parties molles sont essentiellement responsables du mécanisme régulier de la décontamination. La coquille, malgré un processus de décontamination visible, donne des résultats relativement anarchiques. Il s'agit bien d'un phénomène physique; les coquilles selon les circonstances, (degré d'enfouissement par exemple) ont adsorbé du radiocesium de manière plus ou moins intense. L'activité des liquides internes n'est pratiquement plus détectable. Si l'on représente

<sup>1</sup> En radioprotection on exprime cette capacité de fixer les radioéléments par le "facteur de concentration." Il se définit comme étant le rapport, à l'"équilibre," entre l'activité spécifique de l'animal (ou de l'organe) et l'activité spécifique de l'eau exprimée avec la même unité. Nous avons obtenu les résultats suivants:

Animal total	FC = 43	Masse musculaire	FC = 347
Parties molles	FC = 312	Masse viscérale	FC = 308
Coquille	FC = 10	Manteau	FC = 314
Liquides internes	FC = 3	Branchies	FC = 308

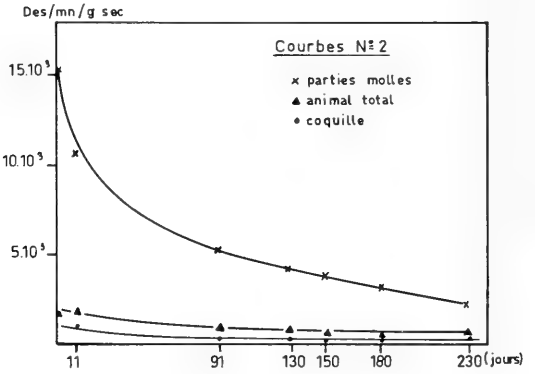
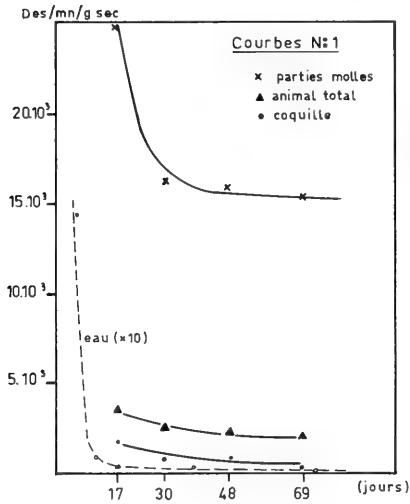
TABLEAU 2

Organes	Activités spécifiques (Des/min/g sec)			
	17 jours	30 jours	48 jours	69 jours
Masse musculaire	21 800	19 300	17 800	16 000
Muscle du pied	19 600	18 400	16 000	15 200
Muscles adducteurs	23 400	20 000	19 500	17 400
Manteau total	23 600	17 700	14 300	15 100
Bord du manteau	24 600	18 500	16 200	16 700
Reste du manteau	18 000	16 200	11 000	13 400
Siphons	33 300	18 500	17 000	15 000
Masse viscérale totale	28 200	14 900	14 400	17 000
Branchies totales	30 600	14 800	14 400	17 000
Branchies internes	31 800	17 700	19 500	17 900
Branchies externes	29 900	13 100	11 000	16 200
Palpes	22 300	13 300	19 600	25 200

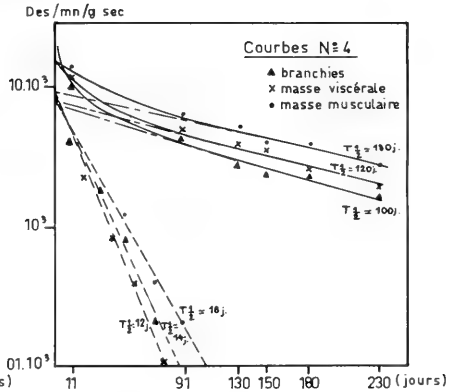
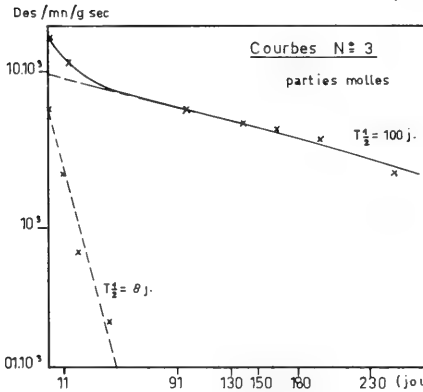
TABLEAU 3

Organes	Moyenne activité spécifique. (Des/min/g sec)						
	Fin période de contamination	11 jours	91 jours	130 jours	150 jours	180 jours	230 jours
Masse musculaire totale	16 000	13 500	5900	4800	3900	3800	2800
Muscle du pied	15 200	11 600	4600	2600	2900	3700	2400
Muscles adducteurs	17 400	15 000	7200	7400	5100	3900	3500
Masse viscérale totale	17 000	10 900	4900	4300	3700	2600	2000
Branchies totales	17 000	10 700	4300	2700	2300	2300	1600
Branchies internes	17 900	11 500	2100	2900	2900	1700	1200
Branchies externes	16 200	10 000	6300	1900	2600	-	2300
Manteau total	15 100	10 900	6200	4900	4400	4200	3500
Bord du manteau	16 700	11 700	5900	6600	5500	4800	4700
Reste du manteau	13 400	10 100	6400	4200	3600	4000	2900
Siphons	15 000	11 300	5000	5400	3000	4800	2300
Palpes	25 000	5 300	3000	-	4100	-	4200

**CONTAMINATION**  
(Évolution de l'activité spécifique)

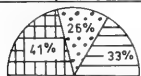


**DECONTAMINATION**  
(Dynamique)



**GRAPHIQUES de DISTRIBUTION de L'ACTIVITÉ**

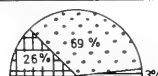
Pourcentage des poids



41% 26% 33%

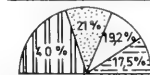
- Coquille
- Parties molles
- Liquides internes

Répartition de l'activité



26% 69% 3%

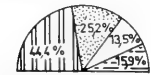
Pourcentage des poids



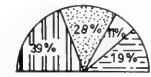
21% 192% 17,5%

- Masse viscérale totale
- Masse musculaire
- Branchies
- Manteau

Répartition de l'activité



25,2% 13,5% 15,9%



39% 28% 11% 19%

avec une échelle semi-logarithmique la décroissance de l'activité des parties molles (Courbe 3) on constate qu'elle ne représente pas une fonction simple; une période de décontamination rapide ( $T\ 1/2 = 8$  jours) est suivie par une période de décontamination lente ( $T\ 1/2 = 100$  jours). (Ce type de courbe a déjà été trouvé sur des bivalves) [8] [20].

Ce type de processus de décontamination se retrouve pour chaque organe (Tableau 3) mais les vitesses diffèrent (Courbes 4). Ceci est bien visible pour les périodes longues où l'on constate 30 jours d'écart entre les branchies et la masse musculaire. Le muscle est bien l'organe préférentiel de stockage du 137-césium. Par conséquent, après 230 jours de décontamination, la masse musculaire représente, par rapport à l'activité totale des parties molles, un pourcentage plus important (Graphique 5); il en est de même pour le manteau. Par contre les valeurs de la masse viscérale et des branchies ont baissé. Ces résultats ont surtout une importance pratique, puisqu'ils permettent de définir le temps nécessaire pour qu'un animal (ou un organe) perde la majeure partie du radioélément incorporé à la suite d'une radio-contamination aiguë.

### CONCLUSION

Nous retiendrons quelques données essentielles: la quantité de radiocésium fixée par les bivalves est faible par rapport à l'activité introduite. Le véritable métabolisme du radioélément se situe au niveau des parties molles. La capacité de fixation du 137-Cs est différente pour chaque organe, le "facteur de concentration" est maximum pour ceux ayant une forte teneur en potassium stable, comme les muscles. Les phénomènes de diffusion à travers les membranes et de transfert actif des sels sont responsables de la majeure partie de l'absorption du 137-Cs. On rejoint ainsi les travaux de FLORKIN sur l'osmorégulation [24]. Si l'on considère que l'ion  $Cs^+$  suit les mêmes voies que l'ion  $K^+$ , il est normal que dans un milieu où la quantité de potassium est faible la dose de césium fixé soit proportionnellement forte. Le même raisonnement s'applique à la décontamination puisque les bivalves rejettent une urine hypoosmotique. La période biologique est donc relativement longue. Ces données, d'ordres écologique et biologique, définissent sur le plan de la protection les conditions locales les plus favorables à une contamination des "Unio" par le 137-Cs. Ces conditions sont remplies dans des zones peu éloignées du point de rejet, à fonds sablo-vaseux, peu profondes et à courant lent. Dans de tels sites l'utilisation de ces bivalves comme "dosimètres biologiques" dans le cas d'une pollution par le 137-césium paraît valable. Ce type d'étude qui nécessite de nombreux approfondissements permet cependant de mettre en relief la nécessité de lier les problèmes appliqués à ceux de la recherche fondamentale.

### BIBLIOGRAPHIE

- [1] PEREDEL'SKY, A. A., 1957, Fondements et problèmes de la radioécologie. *Zh. Obshch. biol. SSSR.*, 18-1: 17-30.
- [2] BOCQUET, H., 1965, Radioécologie et pollution radioactive du milieu. *Produits et problèmes pharmaceutiques*, 20(2): 3-8.
- [3] BOVARD, P., 1966, La Radioécologie. *B. I. S. T.*, 106: 37-38.
- [4] FONTAINE, Y., 1960, La contamination radioactive des milieux et des organismes aquatiques. *Rapport C. E. A.*, 1588 (France): 15-37.
- [5] CARTER MELVIN, W., 1961 Biological uptake of radioactive nuclides by clams. *University of Florida LC. Card. No. Mic. 60-6662.*
- [6] NELSON, D. J., 1962, Clams as indicators of strontium-90. *Science*, 137(3523): 38-39.

- [7] RAVERA O., ET AL., 1962, A research program for the study of radioactivity in mollusks as a possible index to the contamination of a lake. *N. S. A.*, 16(17): 22428.
- [8] CANCIO, D., FOULQUIER, L. & GRAUBY, A., 1968, Modalités de la contamination d'un bivalve d'eau douce par le radiostrontium et de sa décontamination: *Anodonta cygnea* (L.). *Rapport C.E.A.*, R-3421. Documentation Française, Paris, 34 p.
- [9] FOULQUIER, L., BOVARD, P. & GRAUBY, A., 1966, Contamination expérimentale de *Margaritana margaritifera* (L.) par le 137-césium. *Rapport C.E.A.*, R-3054. Documentation Française, Paris, 34 p.
- [10] GERMAIN, L., 1931, *In*: Faune de France. XII-T1, Mollusques. *Ed.*, Lechevalier, Paris, p 715-774.
- [11] MARAZANOFF, F., 1964, Introduction à l'étude écologique des mollusques des eaux douces et saumâtres de Camargue. *La Terre et la Vie*, 3: 359-374.
- [12] PERRIER, R., 1930, *In*: Faune de la France illustrée. T IX Mollusques. *Ed.*, Delagrave Paris, p 118-119.
- [13] ADAM, W., 1960, *In*: Mollusques terrestres et dulcicoles. T.I. *Inst. Roy. Sci. natur. Belg.*, Bruxelles, p 325-330.
- [14] ELLIS, A. E., 1962, *In*: British freshwater bivalve molluscs. *Ed.*, Burlington House, Piccadilly, London, p 10-16.
- [15] MARAZANOFF, F., 1964, Complément à l'inventaire de la faune invertébrée camarguaise. *La Terre et la Vie*, 3: 375-379.
- [16] ROBERTSON, J. D., 1964, Osmotic and ionic regulation. *In: Physiology of Mollusca*. T.I. Eds., K. M. Wilbur & C. M. Yonge, Acad. Press, New York and London, p 283-331.
- [17] OWEN, G., 1966, Feeding. *In: Physiology of mollusca*. T II. Eds., K. M. Wilbur & C. M. Yonge., Acad. Press, New York and London, p 29-42.
- [18] CLANTON, H., 1963, Sorption and release of radionuclides by sediments. *T.I.D.*, 17664: 113-125.
- [19] TIMOFEYEVA-RESOVSKAYA, Ye. A., 1963, Distribution of radioisotopes in the main components of freshwater bodies. (Monograph.) (J.P.R.S. 21-816). *Tr. inst. Biol. Akad. Nauk. SSSR.*, Ural'skiy filial (30): 1-78.
- [20] LEANDRI, M. & CHARREL, J., 1963, Essais de décontamination expérimentale des coquillages méditerranéens pollués par des eaux rendues radioactives. *Rev. Hyg. et Méd. Soc.* T. 2(5): 411-416.
- [21] POLIKARPOV, G. G. 1966, Concentration of radionuclides of the first group of elements in the periodic system. *In: Radioecology of aquatic organisms*. North-Holland Publ. Co., Amsterdam; Reinhold Book Div., New York, p 61-80.
- [22] GETSOVA, A. B., LYAPUNOVA, N. A., POLIKARPOV, G. G. & TIMOFEYEVA-RESOVSKAYA, Ye. A., 1964, Concentration of chemical elements from aqueous solutions by freshwater organisms. Commun. 6. Accumulation of the radioisotopes of eight different elements in the tissues of *Anodonta cellensis*. *Nauchn. Dokl. Vyssh. Shkoly* (Biol.), 4: 82-88.
- [23] BRYAN, G. W., 1963, The accumulation of cesium-137 by brackish water invertebrates and its relation to the regulation of potassium and sodium. *J. Mar. biol. Ass. U. K.*, 43(2): 541-565.
- [24] FLORKIN, M. & DUCHATEAU, G., 1948, Sur l'osmorégulation de l'*Anodonta cygnea*. *Physiol. Comp. et Oecol.*, 1:29-45.



TAXONOMIE ET BIOLOGIE DES GRANDS *ARION* DE FRANCE  
(PULMONATA: ARIONIDAE)

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1. Systématique

Trois grandes espèces du genre *Arion* ont été identifiées en France: *Arion rufus* (L.) (= *A. ater rufus* Quick), *Arion lusitanicus* Mabilley et *Arion subfuscus* Draparnaud. On a l'habitude de classer *Arion rufus* dans le sous-genre *Arion* s.s. (= *Lochea*) et *A. subfuscus* dans le sous-genre *Mesarion*. L'espèce *A. lusitanicus*, encore peu étudiée, appartient au groupe de *A. rufus* par ses caractères externes et généraux mais son appareil génital se rapproche morphologiquement de celui des *Mesarion* (Fig. 1).

L'étude du polymorphisme de ces trois espèces et des étapes de leur croissance permet de placer dans la synonymie probablement tous les autres grands *Arion* cités en France par la littérature. En particulier *Arion ater* Germain, *A. aggericola* Mab., *A. hibernus* Mab., *A. brevierei* Poll., *A. rubiginosus* Baudon, *A. flavus* Nilss., *A. tenellus* = *virescens* Millet se rapportent très vraisemblablement à des variétés ou à des formes juvéniles ou séniles de *A. rufus*, *A. lusitanicus* et *A. subfuscus*.

2. Répartition géographique

*Arion lusitanicus* est répandu en France principalement au sud de la Loire: Vendée, Charente maritime, Gironde, vallée de la Garonne, Massif Central, Gard, Pyrénées centrales et orientales. On le retrouve près de Paris et à Reims où il a sans doute été introduit (Fig. 2).

*Arion rufus* occupe le Nord et l'Est de la France, la région parisienne, la Normandie, la Bretagne, la vallée de la Loire, la Dordogne et les Pyrénées occidentales.

*Arion subfuscus* paraît répandu dans presque toute la France mais il semble manquer dans les parties hautes des Pyrénées.

3. Variations et Taxonomie

Il existe une variation chromique de *A. lusitanicus* et *A. rufus* en relation avec l'altitude. Nous avons constaté ce phénomène dans le Massif Central, pour *A. lusitanicus*, et dans les Pyrénées, pour *A. lusitanicus* et *A. rufus*. A partir de 500 m d'altitude, ces deux espèces présentent des variétés mélaniques parfois similaires: formes noires ou brun foncé. Ces variétés sombres d'altitude de *A. lusitanicus* et *A. rufus* correspondent, dans l'ensemble, à l'"*Arion ater*" (non *Arion ater ater* Quick) cité par la plupart des anciens auteurs français comme "un grand *Arion* noir vivant dans les montagnes."

Plus précisément la variété noire de *A. lusitanicus* (var. *nigrescens* Collinge) correspond à l'*Arion nobrei* Pollonera. La variété noire de *A. rufus* (var. *atra* (L.)), elle, offre dans les Pyrénées les variantes suivantes: la variété *atra aterrima* Dumont et Mortillet est toute noire; la variété *atra marginella* (Schranck) présente la marge du pied jaune ou orangée; enfin nous avons trouvé une forme *atra sulcata* Morelet

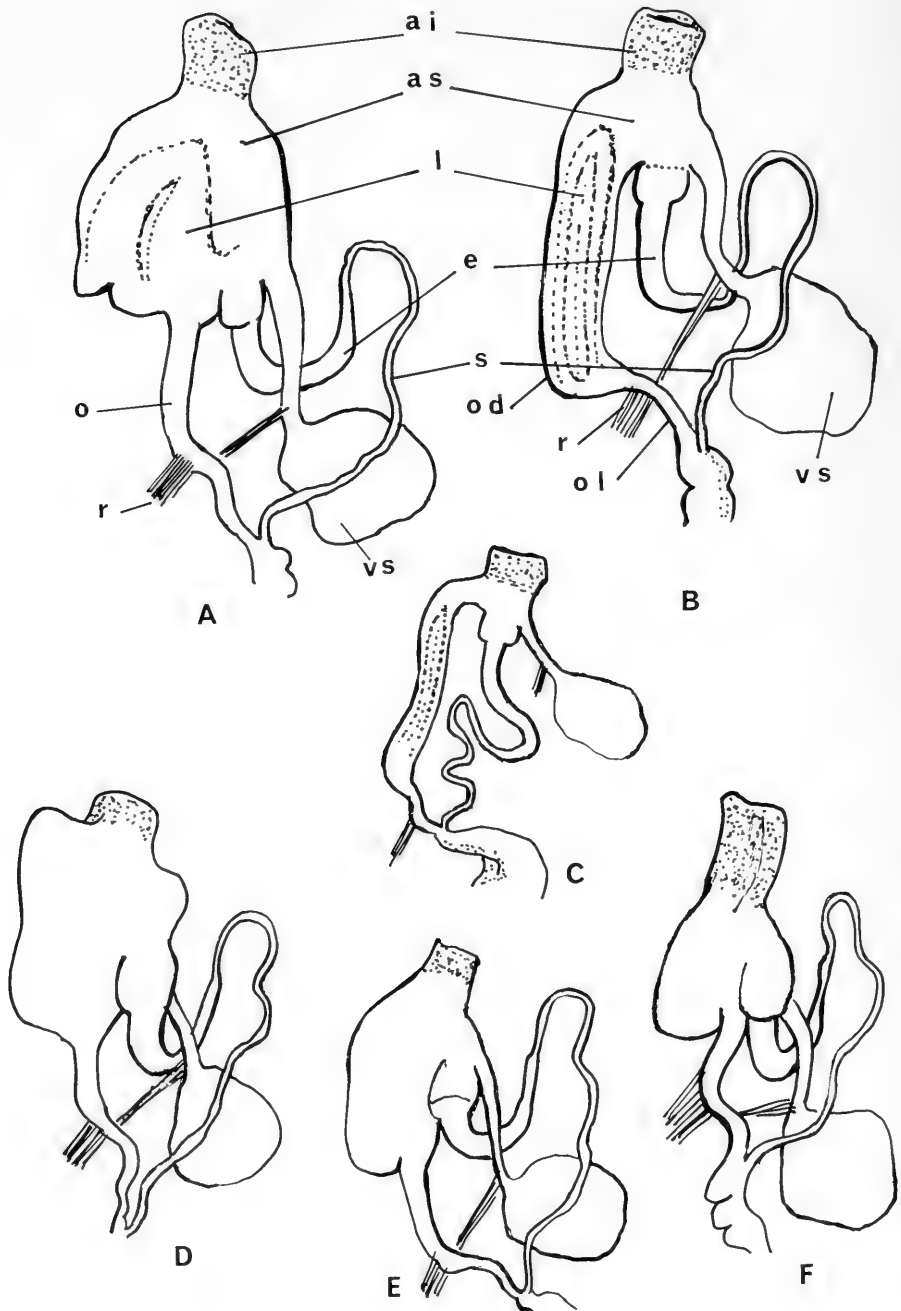


FIG. 1. Parties supérieures de l'appareil génital de grands Arionidae de France (x 3, 5 à 5). A. *Arion rufus* (L.), Seine maritime. B. *Arion lusitanicus* Mab., Livry-Gargan près de Paris. C. *Arion subfuscus* Drap., forêt de Compiègne. D, E, F. *Arion rufus* (L.) des Pyrénées occidentales françaises. D: exemplaire de Bidarray; E: ex. de Ferrières, val de l'Ouzon, alt. 555 m (var. *atra sulcata*); F: ex. du col d'Aubisque, alt. 1710 m (var. *atra marginella*).

ai atrium inférieur  
 as atrium supérieur  
 e épiphallus  
 l ligula  
 o oviducte

od oviducte partie distale  
 ol oviducte libre  
 r muscles rétracteurs  
 s spermiducte  
 vs vésicule séminale

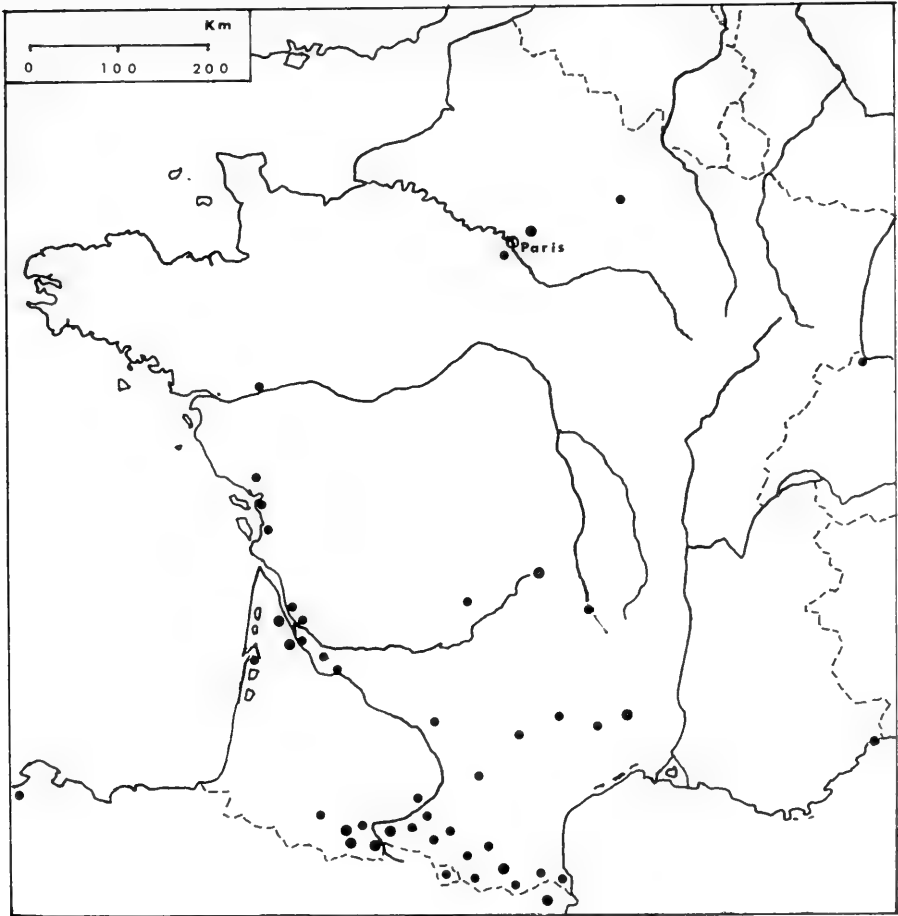


FIG. 2. Répartition en France de *Arion lusitanicus* Mabille.

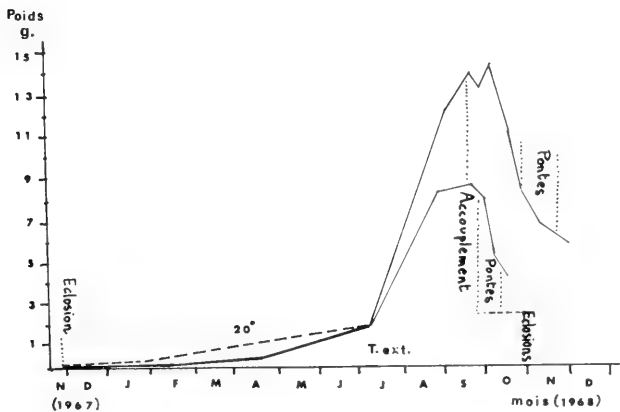


FIG. 3. Croissance pondérale de *Arion lusitanicus*, à Paris (Le trait épais correspond à la croissance moyenne d'individus placés à température externe; le trait interrompu à celle d'individus, provenant de la même éclosion, élevés à 17-20°C. Les courbes en traits fins correspondent à la croissance estivale et aux phases adultes et séniles de deux individus placés ensemble à température externe).

correspondant bien à l'*Arion sulcatus* décrit et figuré par Morelet (1845, p. 28, pl. 1): gros *Arion* assez amorphe, noir ou brun très foncé, à tubercules vermiculés et très saillants et à marge du pied brune ou de la couleur du corps. L'appareil génital de ces formes pyrénéennes ne nous a pas semblé offrir de différences très nettes avec celui des *Arion rufus* du Nord de la France (Fig. 1). Nous rangeons donc, pour le moment, les *Arion* s.s. des Pyrénées occidentales françaises dans l'espèce *Arion rufus* (L.).

#### 4. Cycle biologique et croissance

*A. rufus*, *A. lusitanicus* et *A. subfuscus* présentent un cycle normalement annuel: croissance juvénile au printemps, stade adulte et reproduction en été, ponte le plus souvent en octobre et mort du géniteur en général peu de temps après la ponte (phase sénile). Ceci concorde avec les histogrammes en valeurs pondérales et en stades de maturité génitale donnés par B. J. Smith (1966) pour une population naturelle d'*Arion ater* (*A. ater ater* Quick) en Grande Bretagne et aux courbes de croissance établies par Abeloos (1942, 1944) pour *A. rufus* et *A. subfuscus* placés en élevage à 20° C.

Abeloos distinguait trois phases de croissance: la phase infantile, la phase juvénile et la phase adulte s'achevant par la sénilité. Ces trois phases correspondent aux stades de gamétogenèse découverts par Lüsüs (1961) pour *A. rufus* et par B. J. Smith (*supr. cit.*) pour *A. ater*: stade mâle, stade hermaphrodite et stade femelle.

Sur le plan biométrique la phase juvénile se décompose en deux périodes: une période pré-estivale à taux de croissance modéré, variant principalement sous l'effet des conditions climatiques (température), et une période de croissance estivale à taux très fort qui amène l'animal au stade adulte (Fig. 3).

#### 5. Facteurs modifiant la croissance

Des expériences, inspirées par celles d'Abeloos, concernant la modification de la vitesse de croissance sous l'effet de facteurs défavorables (jeûne ou sous-alimentation, basse température, surpopulation) ont été effectuées. Ces expériences mettent en évidence la plasticité de la croissance durant la phase infantile et la phase juvénile pré-estivale. Par plasticité nous entendons un processus de croissance qui permet à l'animal très jeune d'atteindre la taille et le stade génital précédant la phase de croissance estivale quels que soient les facteurs externes entrant en jeu durant la période pré-estivale. Expérimentalement ceci signifie que des *Arion* infantiles ou très jeunes soumis à un facteur défavorable voient leur taux de croissance devenir faible, nul ou négatif pendant le temps où le facteur inhibiteur se fait sentir, mais que, dès que celui-ci est supprimé, les jeunes *Arion* prennent un taux de croissance leur permettant de retrouver les valeurs pondérales normales. L'expérience de la Fig. 3 montre, ainsi, que des *Arion* nés en laboratoire en novembre et élevés à 17-20° C présentent un taux de croissance juvénile pré-estivale constant. Des individus issus de la même éclosion et élevés à la température extérieure ont, eux, un taux de croissance faible pendant les froids de l'hiver mais le taux va augmenter au printemps, avec l'adoucissement de la température, si bien que ces individus ayant subi le froid atteindront le même stade pondéral et génital que leurs congénères élevés à la température du laboratoire.

L'expérience portant sur l'effet d'un jeûne durant la période pré-estivale conduit à un résultat similaire: de très jeunes *Arion* soumis à un jeûne d'une vingtaine de jours regagnent, au bout de quatre mois, la valeur pondérale pré-estivale des individus témoins (loi d'Abeloos).

Par contre les facteurs défavorables altèrent, plus ou moins profondément, le terme de la croissance s'ils surviennent au seuil de la croissance estivale ou durant celle-ci.

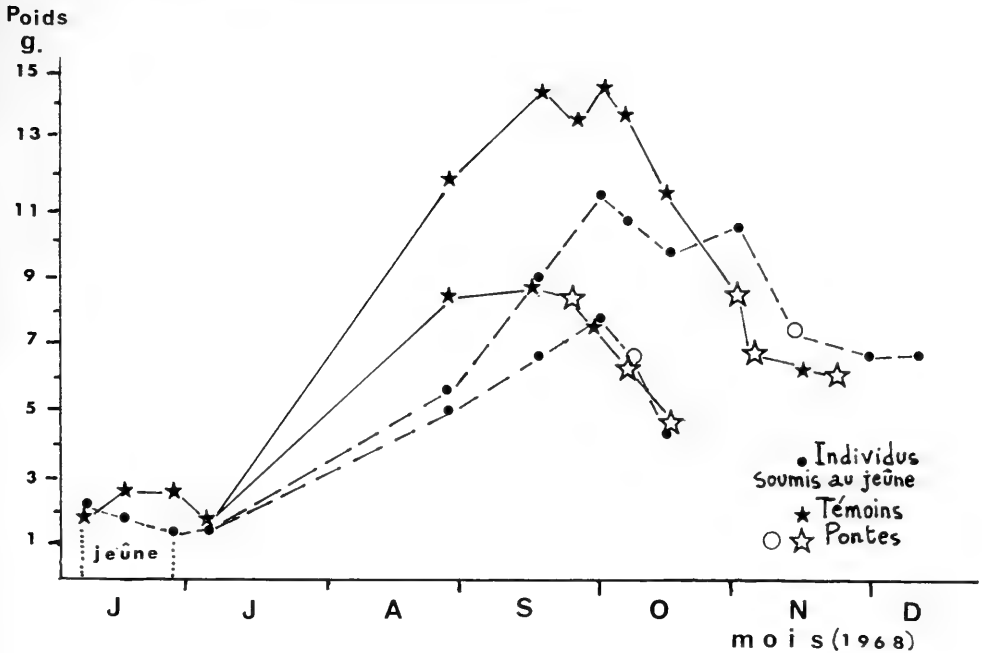


FIG. 4. Effet de dénutrition (jeûne de 21 jours) sur la croissance terminale de *Arion lusitanicus* à la fin de la période pré-estivale (stade pondéral de 2 g). Elevages mis à température externe, à Paris.

Prenons, par exemple, l'effet d'un jeûne sur des *A. lusitanicus* terminant leur croissance juvénile pré-estivale (Fig. 4). Les individus ayant subi le jeûne parviendront au stade adulte mais un peu plus tard que les individus témoins et avec des valeurs pondérales plus faibles. Leurs pontes seront également tardives: celles des individus témoins vont éclore, après une incubation de 30 jours, avant les froids; les oeufs des individus retardés ne pourront éclore qu'après l'hiver, c'est à dire vers le mois de mars.

Si les facteurs défavorables surviennent durant la croissance estivale, celle-ci sera le plus souvent stoppée. Au lieu d'être adulte, l'*Arion* demeurera, en automne, à un stade génital juvénile. Expérimentalement nous avons constaté que de tels individus à croissance arrêtée survivent avec une valeur pondérale et un stade génital stationnaires et qu'ils reprennent parfois leur croissance au printemps de l'année suivante.

## 6. Conséquences écologiques

Tous ces phénomènes expliquent la physionomie particulière à chaque station des populations naturelles d'*Arion*: cycles écologiques différents, tailles adultes inégales, etc. Les facteurs caractéristiques de chaque biotope (latitude, microclimat, végétation, éléments nutritifs, densité de la population, espèces concurrentes . . .) jouent un rôle d'accélérateur ou de ralentisseur de la croissance de la population ou d'une partie de la population. Les facteurs défavorables sont particulièrement inhibiteurs, nous l'avons vu, au moment de la croissance estivale: ils retardent le stade adulte et, de ce fait, les pontes, ils abaissent la taille et le poids des individus adultes et, dans certains cas, ils peuvent arrêter totalement la croissance pondérale et génitale.

Le cycle écologique des grandes espèces du genre *Arion* est donc de un an dans beaucoup de cas; mais les individus n'ayant pas atteint le stade adulte en automne, soit parce que nés trop tardivement, soit parce qu'ayant eu leur croissance estivale perturbée, sont susceptibles de parvenir au stade adulte durant l'été de l'année suivante, après avoir subi un repos de croissance de plusieurs mois.

#### LITTÉRATURE CITÉE

- ABELOOS, M., 1942, Les étapes de la croissance chez la Limace rouge (*Arion rufus* L.). Evolution des caractéristiques de croissance chez les Mollusques Arionidés, *C. R. Acad. Sc. Paris*, 215: 38 et 96.
- ABELOOS, M., 1944, Recherches expérimentales sur la croissance. La croissance des Mollusques Arionidés, *Bull. biol. France & Belg.*, 78: 215-256.
- LÛSIS, O., 1961, Postembryonic changes in the reproductive system of the slug *Arion ater rufus* L., *Proc. Zool. Soc. London*, 137: 433-468.
- MORELET, A., 1845, Description des Mollusques terrestres et fluviatiles du Portugal, Paris.
- SMITH, B. J., 1966, Maturation of the reproductive tract of *Arion ater* (Pulmonata: Arionidae), *Malacologia*, 4(2): 325-349.

## BIOLOGICAL ASPECTS OF MANGROVE MOLLUSKS IN THE WEST INDIES

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## INTRODUCTION

Mangroves form a very special tropical shore habitat. Mangrove trees are found in shallow salt or brackish water, with a mud or sand bottom. The water needs to be calm, therefore lagoons, bays and estuaries are preferable. Most mangroves are found between 25° (to 30°) north and south latitude. According to McGill (1958) mangroves dominate about 75% of the tropical coastlines.

There are two mangrove floras in the world, an oriental or Indopacific (East Africa, Indian Ocean and West Pacific), and an occidental mangrove flora (tropical America and West Africa). Compared to the Indopacific, the occidental flora is very poor in species of mangrove trees. According to Van Steenis (1962, p. 166) the Indopacific has 43 species of mangroves, while in tropical America and West Africa only 10 species occur. However, other authors (Abel, 1926) recognize 23 species in the Indopacific, and 4 mangrove species in America and West Africa. In the West Indies are present: the red mangrove, *Rhizophora mangle* L. (fam. Rhizophoraceae); the black mangrove, *Avicennia nitida* Jacq. (Verbenaceae); the white mangrove, *Laguncularia racemosa* Gärtn. (Combretaceae); and the grey mangrove, *Conocarpus erectus* L. (Combretaceae). Mangroves do not form one systematical unit, they belong to different families of Dicotilous plants. They are unusual for the fact that they are higher plants living in seawater.

Every species has its special place in the mangrove wood: *Rhizophora* is growing close to and in the water, *Avicennia*, *Laguncularia* and *Conocarpus* are usually found farther inland. The four species do not always grow together, the community often consists of only one or two species. *Rhizophora mangle* is mostly present.

To live in their special habitat, mangroves are furnished with aerial and prop roots. The reproduction is peculiar because mangroves are viviparous: the seeds on the tree are growing out into seedlings, and the seedlings can be transported via the sea to new lands or islands far away. Therefore, mangroves are excellent pioneer plants (Stephens, 1962).

Compared to the rich tropical flora, the mangrove habitat is very poor in number of species. This is also true for the fauna: the number of species is small, however the number of specimens is often very large. The distribution of animals in a mangrove swamp is more complex than the zonation of a rocky shore (Berry, 1963); physical conditions vary in the mangrove area.

The mollusks of the West Indian mangroves are the subject of this study. The author has studied mangrove mollusks on the Netherlands Antilles and in Puerto Rico, and he has visited several mangrove areas in Florida.

## MOLLUSKS OF THE CARIBBEAN MANGROVES

For the malacologist only the red mangrove, *Rhizophora mangle*, is important, as shells have only been found on this tree in the West Indies. The prop roots of *Rhizophora* are an excellent substratum for many animals to live on, not only mollusks, and algae are also found on the roots. The relation of mollusk to mangrove is different for many species. We are, therefore, able to make a division.

### 1. Exclusive mangrove mollusks

Only three species are always and only found on the prop roots: one gastropod, the periwinkle *Littorina angulifera* (Lamarck), and two pelecypods, *Crassostrea rhizophorae* (Guilding) and *Isognomon alata* (Gmelin).

*Littorina angulifera* is very common and lives on the roots above the water. We found 1 to 3 specimens at one branch, never crowded together. Sometimes the animal climbs as high as the leaves, but mostly it stays near the water. This peculiar marine snail is more a land than a water animal. Our experiments showed that when a number of specimens were kept submerged in seawater, 50% of the animals died within two days (Coomans, 1962). *Littorina angulifera* reacts on the water level; in areas with tides or wave action, the animals are found higher on the roots than in areas without tides or waves. This species is the first mollusk that appears on new mangroves, as was found by us on newly formed mangrove islands in Puerto Rico. With its host plant *Rhizophora mangle*, *Littorina angulifera* is found on both sides of the Atlantic Ocean (Rosewater, 1963). This periwinkle was extensively studied by Lenderking (1954) and Marcus & Marcus (1963).

*Crassostrea rhizophorae*, the mangrove oyster, is the second mollusk to be a true mangrove species, found only on *Rhizophora*, after which it is named. The oyster prefers the mangroves in lagoons, and is not often found in open sea, where it never reaches the maximum size. The shell grows fast, 5 cm in half a year. The maximum size is 10 cm. The oysters are crowded together on the prop roots, fixed with one valve to the mangrove. This species is edible and commercially used, but the oysters can only be collected with the substratum. These mollusks are responsible for the story of the seamen from centuries ago that in the tropics the oysters grow on trees! Mattox (1949) has studied *Crassostrea rhizophorae* in Puerto Rico.

The species is not found on the mangroves in Florida; the mangrove oyster there is *Crassostrea virginica* (Gmelin). The distribution of *C. virginica* is from Florida north to the Gulf of St. Lawrence.

*Isognomon alata* (Gmelin), the flat oyster, lives in clusters on the mangrove roots, attached with a byssus. This species is more common in the Netherlands Antilles than in Puerto Rico.

### 2. Sessil pelecypods often found on mangroves

Many bivalves are fixed to a substratum with one of the valves or with a byssus, and these species can also be found on mangroves. *Brachidontes exustus* (Linné) is common under water from top to bottom on the prop roots. This small mussel also lives on stones outside the mangrove lagoon. A larger mussel species, *Br. recurvus* (Rafinesque), is also found on mangroves, but it is not so common. The third Caribbean species, *Br. citrinus* (Röding), is not recorded from mangroves. More Mytilidae are mentioned in the literature to be found on the roots of *Rhizophora*: *Modiolus americanus* (Leach) from Margarita Island (Rodriguez, 1959, p. 277), and *Mytella guyanensis* (Lamarck) from Brazil (Gerlach, 1958, p. 668).

Both West Indian pearl oysters, *Pteria colymbus* (Röding) and *Pinctada radiata* (Leach) can be found on mangroves; also several Chamidae are recorded, i.e., *Chama macerophylla* Gmelin and *C. congregata* Conrad. *Ostrea frons* Linné, commonly attached with one valve to sea fans (*Gorgonaria*), is occasionally found on mangroves. The list can be closed with *Anadara notabilis* (Röding), *Isognomon radiata* (Anton), and *Pododesmus rudis* (Broderip).

### 3. Predators of mangrove oysters

Since the prop roots of *Rhizophora* are often loaded with oysters, these animals are attracting predating gastropods. The carnivorous *Murex brevifrons* Lamarck is a



common predator on the oysters. On the islands Aruba and Bonaire we found *Melongena melongena* (Linné) associated with mangrove areas; in Florida it is *Melongena corona* (Gmelin). The South American *Pugilina morio* (Linné) is reported from mangroves on Martinique (Usticke, 1960); this is probably the most northern distribution of the species.

#### 4. Sessile mollusks on mangrove oysters

A number of small gastropods use the shells of the mangrove oysters to live on, although they are also found elsewhere. Other sessile animals are living, too, on the oysters: *Balanus* spec. and tube worms. Several limpets were collected by us from the mangrove oysters: *Diodora cayenensis* (Lamarck), *Lucapina sowerbii* (Sowerby), *Emarginula pumila* (A. Adams), *Hemitoma octoradiata* (Gmelin), several *Acmaea*'s, and the pulmonate *Siphonaria*. Two slipper shells, *Crepidula aculeata* (Gmelin) and *C. convexa* Say are *Rhizophora* bound. On the very crowded roots the oysters are growing one on another, and the mytilid *Brachidontes exustus* (Linné) often lives in great quantities on the mangrove oysters.

#### 5. Boring pelecypods in mangrove roots

The wood borer *Teredo* is found in either living or dead mangrove wood, and it is surprising that the stone boring *Lithophaga bisulcata* (d'Orbigny) is mentioned from mangroves in Curaçao.

#### 6. Mollusks living in or on other organisms at the mangrove roots

The prop roots of *Rhizophora* in the West Indies are often crowded with organisms. In addition to oysters, one finds Crustacea (*Balanus*, hermit crabs, shrimps), Tunicata (*Ascidia nigra*, *Bothryllus*), Bryozoa, Vermes, Echinodermata (brittle stars), Coelenterata, Porifera, and algae.

A number of mollusks are living in or on these organisms: *Ostrea permollis* Sowerby and the tube shell *Vermicularia knorri* (Deshayes) live in sponges. A small mytilid, *Musculus lateralis* (Say) finds a host in *Bothryllus*, many mussels live together in the mantle of this tunicate.

Many species of green, red and brown algae are found on the prop roots, and they serve as hosts for small gastropods. Robertson (1960) found seven species of gastropods on the red alga *Bostrychia* in the Bahamas. Warmke & Almodovar (1963) mentioned some 80 tiny species of gastropods and 12 pelecypods collected from 25 species of algae in Puerto Rico. A number of these algae were found on mangroves.

The first Caribbean bivalved gastropod, *Berthelinia caribbea* Edmunds, was found on the alga *Caulerpa* from mangrove beds at Jamaica (Edmunds, 1962, 1963). The species was also collected on mangrove algae in Puerto Rico (Warmke, 1966).

#### 7. Mollusks of the mud flats

Mangroves always are growing on sand or mud to hold the roots. In this substratum burrowing pelecypods are living; they belong to the mangrove fauna, although they are never found on the mangrove trees. Some of the bivalves often found burrowed in the sandy or muddy bottom of the lagoon are *Asaphis deflorata* (Linné) and *Trachycardium muricatum* (Linné), several Lucinidae, and the Veneridae *Anomalocardia brasiliiana* (Gmelin) and *Chione cancellata* (Linné).

Gastropods are crawling on the mud flats, and since they are able to move around these gastropods are regularly found on the mangrove trees. Some of them are present in very large numbers: *Batillaria minima* (Gmelin), *Cerithidea costata* (Da Costa), *Neritina virginea* (Linné), *Cerithium variabile* C. B. Adams, *Bulla* species, and some Ellobiidae: *Melampus coffeus* (Linné) and *M. bidentatus* Say, *Detracia*

*bullaoides* (Montagu) and *Tralia ovula* (Bruguère) (cf. Morrison, 1958). *Melampus coffeus* was studied by Golley (1960) and by Marcus & Marcus (1965, p. 20-42). Not all the gastropod shells climbing on mangrove roots do contain mollusks, some of them are inhabited by hermit crabs.

#### 8. Gastropods of the mangrove lagoon

Mollusks from the mangrove lagoon, living on stones or other organisms, can occasionally be found on the mangroves. To mention some of them: *Cerithium litteratum* Born and *C. eburneum* Bruguère, *Columbella mercatoria* (Linné), *Fasciolaria tulipa* (Linné), *Modulus modulus* (Linné), *Purpura patula* (Linné). Edmunds (1964) collected thirteen species of eolid nudibranches from mangrove roots in Jamaica.

*Cypraea zebra* Linné is living in Florida on mangroves; however, on the West Indian islands this species does not belong to the mangrove fauna.

#### 9. Mollusks from outside the mangrove area

Accidentally, some intertidal mollusks from the seashore may enter the mangrove lagoon and try to reach their intertidal habitat by climbing the mangrove trees. Several Neritidae and Littorinidae are thus living on the prop roots of *Rhizophora mangle*. They maintain the zonation as in their natural habitat on the rocks: *Nerita tessellata* Gmelin and *Littorina nebulosa* (Lamarck) are close to the water, *Nerita versicolor* Gmelin and *N. peloronta* Linné more upward, while *Tectarius muricatus* (Linné), when found on *Rhizophora*, is far from the water.

When the mangroves are in open sea, close to the rocky shore, the intertidal gastropods from the rocks are found more often on the prop roots.

### DISCUSSION

Comparing the Caribbean mangrove mollusks with those from the Indopacific mangroves (cf. Lim, 1963), it is striking that many of the mangrove mollusks in both faunas belong to identical families, and often to the same genus, which is shown in the list below. Since Lim's study is not an inventarisation of the oriental mangrove mollusks, the species mentioned from the West Indies are also selected.

	West Indies	East Indies
Gastropoda		
Neritidae	<i>Neritina virginea</i> (L.)	<i>Nerita birmanica</i> Phil.
Littorinidae	<i>Littorina angulifera</i> (Lam.)	<i>Littorina melanostoma</i> (Gray)
Cerithiidae	<i>Cerithium litteratum</i> (Born)	<i>Cerithium patulum</i> Sow.
Potamididae	<i>Cerithidea costata</i> (Da C.) <i>Batillaria minima</i> (Gmel.)	<i>Cerithidea obtusa</i> Lam. <i>Terebralia sulcata</i> (Born) <i>Telescopium telescopium</i> L.
Muricidae	<i>Murex brevifrons</i> Lam.	<i>Murex martineanus</i> Reeve
Melongenidae	<i>Melongena melongena</i> (L.)	<i>Melongena pugilina</i> Born
Ellobiidae	<i>Melampus coffeus</i> (L.) <i>Melampus bidentatus</i> Say <i>Tralia ovula</i> (Brug.) <i>Detracia bullaoides</i> (Mont.)	<i>Ellobium aurismidae</i> L. <i>Ellobium aurisjudae</i> L. <i>Cassidula spec.</i>

Pelecypoda		
Arcidae	<i>Anadara notabilis</i> (Röd.)	<i>Anadara granosa</i> (L.)
Isognomonidae	<i>Isognomon alata</i> (Gmel.)	<i>Isognomon isognomon</i> (L.)
Ostreidae	<i>Crassostrea rhizophorae</i> (Guil.)	<i>Crassostrea parasitica</i> (Gmel.)
Anomiidae	<i>Pododesmus rudis</i> (Brod.)	<i>Aenigma rosea</i> Gray
Mytilidae	<i>Brachidontes exustus</i> (L.)	
	<i>Modiolus americanus</i> (Leach)	<i>Modiolus</i> spec.
Veneridae	<i>Anomalocardia brasiliiana</i> (Gm.)	<i>Paphia luzonica</i> Sow.
	<i>Chione cancellata</i> (L.)	<i>Meretrix meretrix</i> (L.)
Asaphidae	<i>Asaphis deflorata</i> (L.)	<i>Gari togata</i> (Desh.)
Teredinidae	<i>Teredo</i> spec.	<i>Teredo manii</i> (Wright)

Two families have a number of species in the mangrove area, both in the oriental and in the occidental fauna, and they can more or less be considered as typical mangrove mollusks: they are the Potamididae and the Ellobiidae.

## LITERATURE

- ABEL, O., 1926, Fossile Mangrovestümpfe. *Palaeont. Zeitschr.*, 8: 130-139.
- BERRY, A. J., 1963, Faunal zonation in mangrove swamps. *Bull. Nat. Mus. Singapore*, 32: 90-98.
- COOMANS, H. E., 1962, "Brainwash" experiments with mollusks. *Ann. Rep. 1962 Amer. Malacol. Un.*, 10-11.
- EDMUNDS, M., 1962, Bivalved gastropod from Jamaica. *Nature*, 195(4839): 402.
- EDMUNDS, M., 1963, *Berthelinia caribbea* n. sp., a bivalved gastropod from the West Atlantic. *J. Linn. Soc. London, Zool.*, 44: 731-739, pl. 1.
- EDMUNDS, M., 1964, Eolid Mollusca from Jamaica, with descriptions of two new genera and three new species. *Bull. Mar. Sci. Gulf Caribb.*, 14: 1-32.
- GERLACH, S. A., 1958, Die Mangroveregion tropischer Küsten als Lebensraum. *Z. Morph. und Ökol. Tiere*, 46: 636-730.
- GOLLEY, F. B., 1960, Ecologic notes on Puerto Rican Mollusca. *Nautilus*, 73: 152-155.
- LENDERKING, R. E., 1954, Some recent observations on the biology of *Littorina angulifera* Lam. of Biscayne and Virginia Keys, Florida. *Bull. Mar. Sci. Gulf Caribb.*, 3: 273-296.
- LIM, C. F., 1963, A preliminary illustrated account of mangrove molluscs from Singapore and South-West Malaya. *Malayan Nat. J.*, 17: 235-239, pl. 39-42.
- MARCUS, E. & MARCUS, E. 1963, Mesogastropoden von der Küste São Paulos. *Abh. Akad. Wiss. Lit., Math. Naturw. Kl.*, 1963: 1-105.
- MARCUS, E. & MARCUS, E., 1965, On Brazilian supratidal and estuarine snails. *Zoologia*, 25: 19-82.
- MATTOX, N. T., 1949, Studies on the biology of the edible oyster, *Ostrea rhizophorae* Guilding, in Puerto Rico. *Ecol. Monogr.*, 19: 339-356.
- McGILL, J. T., 1958, Coastal landforms of the world. Map suppl. in R. J. RUSSELL, 1959, Second coastal geography conf. Coastal Stud. Inst., Louisiana State Univ.
- MORRISON, J. P. E., 1958, Ellobiid and other ecology in Florida. *Nautilus*, 71: 118-124.

- ROBERTSON, R., 1960, The mollusk fauna of Bahamian mangroves. *Amer. Malacol. Un.*, 26: 22-23.
- RODRIGUEZ, G., 1959, The marine communities of Margarita Island, Venezuela. *Bull. Mar. Sci. Gulf Caribb.*, 9: 237-280.
- ROSEWATER, J., 1963, Problems of species analogues in world Littorinidae. *Ann. Rep. 1963 Amer. Malacol. Un.*, 5-6.
- STEPHENS, W. M., 1962, Tree that makes land. *Sea Frontiers*, 8: 219-230.
- USTICKE, G., 1960, Shelling in Martinique. *N. Y. Shell Club Notes*, 62: 5-6.
- VAN STEENIS, C. G. G. J., 1962, The distribution of mangrove plant genera and its significance for palaeogeography. *Proc. Kon. Ned. Akad. Wet.*, ser. C, 65: 164-169.
- WARMKE, G. L., 1966, Two species of the bivalve gastropod *Berthelinia* found in Puerto Rico. *Nautilus*, 79: 139-141.
- WARMKE, G. L. & ALMODÓVAR, L. R., 1963, Some associations of marine mollusks and algae in Puerto Rico. *Malacologia*, 1: 163-177.

## A MALACOLOGICAL SURVEY OF THE SMALL TUSCAN ISLANDS

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## INTRODUCTION

That the Tuscan Archipelago is particularly interesting can be seen from the number of malacological studies already done on it, including those of Issel (1866, 1872), Gentiluomo (1868), Paulucci (1866), Pollonera (1905, 1909), Caziot (1916), Razzauti (1917, 1936), Colosi (1920), Buttner (1926), Bisacchi (1929), Pfeiffer (1932) and Sacchi (1957b). These studies were mostly done on malacological materials collected by other researchers such as the explorer Giacomo Doria, the botanist Bicknell, the paleontologist Major and the entomologist Cavanna. Although excellent, not being specialists, it is probable that many infrequent species escaped their notice. Moreover, the main taxonomic characteristic to be considered till now has been the shell, which often shows great variability in a harsh environment like that of small islands.

The neglect of anatomical study has led, on one hand, to unjustified subdivisions of forms with identical anatomical characteristics as in the case of *Cerņuella* (s.str.) *profuga* (Schmidt), of *Marmorana* (*Ambigua*) *argentarolae* (Paulucci) and of *Helicigona* (*Chilostoma*) *planospira occultata* (Paulucci); and on the other hand, it has precluded the identification of numerous species distinguishable only on an anatomical level. Thus these islands require a more careful and detailed examination. The present research is an effort to complete the prospect of the malacological peopling of each island of the Archipelago, to correct the systematic position of each species and to ascertain their origin and, where possible, to make biogeographic comparisons with nearby Corsica and Sardinia, Tuscany, the Appennines and the promontory of Argentario.

From many aspects, the promontory of Argentario can be considered as an island, faunistically corrupted by its direct connection with the Tuscan coast and by a consequent high anthropization. Even though my exploration covered only four of the six islands of the Archipelago: Capraia, Gorgona, Giglio and Montecristo, it is possible to reach some preliminary conclusions.

## FAUNISTIC OBSERVATIONS

Among the most interesting faunistic data resulting from my research is the finding of 15 species previously unknown on the Tuscan Archipelago. They are: the brackish water species *Truncatella subcylindrica* (Linnaeus) found on the rocks of the coast of Gorgona, the fresh water species *Armiger crista* (Linnaeus) in the pools of "Vado del Porto" at Capraia, the humus species *Hypnophila dohrni* (Paulucci) under the calcareous stones in Giglio, the rock-clinging *Pyramidula rupestris* (Draparnaud) under a group of stones near the village of Capraia, the calciophile species *Granopupa* (s.str.) *granum* (Draparnaud) and *Granopupa* (*Rupestrella*) *philippi* (Cantaine) at the base or on the surface of the rocks of the calcareous part of Giglio, the calciophile and hygrophile *Acanthinula aculeata* (Müller) under the dead leaves of a group of *Ailanthus* near "Cala Maestra" at Montecristo, *Jamīnia quadridens* (Müller) under the calcareous stones near the hill "Franco" on Giglio, *Vitreā* (s.str.) *contracta* (Westerlund) and *crystallina* (Müller) the former on Montecristo and the latter on

Giglio, a new species of *Lehmannia* I named *Lehmannia caprai* Giusti on Capraia and Gorgona, *Deroceras* (s.str.) *caruanae* (Pollonera) and *Hohenwartiana moitessieri* (Bourguignat) near "Cala Scirocco" at Gorgona, *Testacella scutulum* Sowerby ubiquitous in Capraia, Montecristo and near the harbour of Giglio and lastly *Trochoidea* (s.str.) *pyramidata* (Draparnaud) on Gorgona and Giglio (Giusti, 1968).

There are also many species not yet recorded for the individual islands studied. In Capraia there are ten of them, bringing the total up to twenty; eight species on Montecristo bring its total to thirteen; twelve species on tiny Gorgona bring its total to twenty species and, to conclude, thirteen species on Giglio make its total thirty-eight, including *Helix* (*Cryptomphalus*) *aspersa* Müller, which can be found even as a quaternary fossil in the arenous deposits (Giusti, 1968).

Undoubtedly the most interesting result was obtained from the systematic examination of the different groups of *Oxychilus*. These results, though incomplete since I have not yet had the possibility of studying the *Oxychilus* of Pianosa and Giannutri, revealed that there is a different species of this group of *Zonitidae* on each island. I was able to distinguish the species of Gorgona, Capraia and Giglio by a study of the genital apparatus and I named them *Oxychilus* (s.str.) *gorgonianus* Giusti, *Oxychilus* (s.str.) *pilula* (Westerlund) and *Oxychilus* (s.str.) *igilicus* Giusti, respectively (Giusti, 1968).

It was previously thought that the species of Gorgona and Giglio were very close either to *Hyalinia guidonii* De Stefani or to *Hyalinia scotophila* De Stefani var. *notha* Paulucci from the Tuscan Appennines (Paulucci, 1886; Bisacchi, 1929), and that the species of Capraia was very close to *Hyalinia lucida* Draparnaud (Razzauti, 1917). However, the most interesting result was the finding of many adult samples of the *Zonitidae* living at Montecristo. Probably the study of young samples was what led it to be referred either to *Oxychilus* (s.str.) *oppressus* (Shuttleworth) (Forcart, 1967), or to *Oxychilus* (s.str.) *obscuratus* (Porro) (Bisacchi, 1929). Instead, the shell clearly reveals that we are in the presence of a new and distinct entity, as does the structure of the genital and radular apparatuses.

I think that the peculiar structure of the shell, flattened, strongly crenated, wrinkled, opaque and with a rhomboid buccal opening, very similar to that of certain species of *Aegopsis* and of some *Trochomorpha* and, therefore, quite different from that of any other *Oxychilus*, as well as the particular radular formula  $\left(\frac{11-14}{1} + \frac{4}{3} + \frac{C}{3} + \frac{4}{3} + \frac{11-14}{1}\right)$ , makes the creation of a new supraspecific entity at a subgeneric level necessary. So I named it *Oxychilus* (*Alzonula*) *oglasticola* Giusti (Giusti, 1968).

Lastly, I found specimens of another species of *Oxychilus* on the promontory of Argentario and on Giglio and studied the anatomy of several samples from the first spot (near Porto Ercole). This *Oxychilus* revealed itself very different from any other, and particularly from *Oxychilus* (s.str.) *oppressus* (Shuttleworth) (= *Hyalinia lybisonis* Paulucci) which Paulucci (1866) considered synonymous with it. So I named it *Oxychilus* (s.str.) *argentarius* Giusti (Giusti, 1968).

#### BIOGEOGRAPHICAL OBSERVATIONS

Many elements with completely different origins belong to the malacological fauna of the Tuscan Archipelago. According to their present geonomy, they may be divided into the following groups.

A) *More or less differentiated endemic forms related to other European forms.*

1) Strongly differentiated endemisms belonging to very fragmented European groups with a wide Mediterranean geonomy.

I consider *Oxychilus* (*Alzonula*) *oglasticola* Giusti of Montecristo as belonging to

this group. This species can be considered a relict, with a high degree of differentiation. I also place the other species of *Oxychilus* present on the other islands in this group. The above mentioned considerations and the European geonemy, which the genus as a whole now shows, lead us to the supposition that originally the Tyrrhenis was populated by a strain that first became differentiated from the continental one. Subsequently, factors of isolation, cacuminal at first and then insular, further fragmented it *in loco*.

2) Slightly differentiated endemisms belonging to European groups with a very reduced mediterranean geonemy.

*Helicigona (Chilostoma) planospira occultata* (Paulucci), which is common on the Argentario and Giglio, belongs to this group.

B) *Species with a European or Euromediterranean geonemy.*

Among these I mention the following species: *Pomatias elegans* (Müller), *Helix (Cryptomphalus) aspersa* (Müller), *Limax (Limacus) flavus* Linnaeus, *Milax (s.str.) nigricans* (Schultz), *Milax (s.str.) sowerby* (Férussac), *Devoceras (s.str.) caruanae* (Pollonera), *Vitrea (s.str.) contracta* (Westerlund), *Vitrea (s.str.) crystallina* (Müller), *Vitrea (s.str.) diaphana* (Studer), the fresh water species *Armiger crista* Linnaeus and one brackish water species *Truncatella subcylindrica* Linnaeus. The presence of fossil shells of *Helix (Cryptomphalus) aspersa* Müller in arenous deposits, probably dating back to the quaternary, is particularly interesting.

This confirms the ancient settling of the species on this island, a factor which is often difficult to determine because of the introduction of the larger snails by man, especially for his own alimentation.

C) *Mediterranean forms.*

Most of the molluscs of the Tuscan Archipelago may undoubtedly be included in this class, which may be further subdivided into:

1) Endemic species of Tyrrhenic origin.

Undoubtedly the well known *Tacheocampylaea (s.str.) tacheoides* (Pollonera), ubiquitous on Capraia, and also the *Tacheocampylaea (s.str.) elata* Simonelli, quaternary fossil on the island of Pianosa, belong to this group. These two species, which I prefer to keep distinguished even though they are often considered synonymous (La Greca & Sacchi, 1957; Razzauti, 1936), show a strong affinity with the other species of the genus *Tacheocampylaea* that we can find in Sardinia and Corsica. The above mentioned observations and the presence in the Southern France, more precisely in the department of Drome, of some fossil miocenic shells of *Tacheocampylaea (Mesodontopsis) chaixii* (Michaud), further confirm the hypothesis of the presence of a Tyrrhenis. Besides, they support the hypothesis of a very old, probably premiocenic, origin of a part of the malacological fauna of Corsica, Sardinia, Pianosa and Capraia.

Also, the *Cochlodina* of Gorgona seems to me very interesting, even though till now completely disregarded. This last species was first referred by Bisacchi (1929) to *Cochlodina porroi* (Pfeiffer) after the examination of a couple of dead samples. I could find it commonly enough on the walls near "Torre Vecchia" and on the bark of several oak trees in the valley near the churchyard. An examination of these materials and a comparison of them with the samples of the Paulucci collection, shows that the species of Gorgona can be considered very near to *Cochlodina klusteri* (Rossmässler). In fact, the species differs from *Cochlodina porroi* (Pfeiffer) which is synonymous with *Cochlodina meisneriana* (Shuttleworth) in the striations of its shells, which appear less marked and more dense. The genital apparatus, very uniform in the genus *Cochlodina*, does not give us enough characteristics to distinguish *Cochlodina klusteri* (Rossmässler) from *Cochlodina meisneriana* (Shuttleworth).

I think that we are in the presence of a group of forms, including *Cochlodina klüsteri* (Rossmässler, 1836) with its three varieties that are *sarda* (Villa, 1836), *sancta* (Paulucci, 1882), *sophiae* (Paulucci, 1882) and the *Cochlodina meisneriana* (Shuttleworth, 1843) with its variety *porroi* (Pfeiffer, 1848), all of them referable to a single entity. This is supported by the fact that, as Paulucci (1882) and Boettger (1878) stated, the Sardinian species, *Cochlodina klüsteri* (Rossmässler), is present in Corsica, and that the Corsican species, *Cochlodina meisneriana* (Shuttleworth), is present even in Sardinia. Aside from the systematical problem, we have another important proof of an ancient connection between Corsica, Sardinia and the northern part of the Tuscan Archipelago.

## 2) Forms with a central-Mediterranean geonemy.

Many species belong to this group, including *Helix* (*Cantareus*) *aperta* Born, *Granopupa* (*Rupestrella*) *philipii* (Cantraine), the fresh water species *Gyraulus agraulus* (Bourguignat) and *Hypnophila dohrni* (Paulucci). I want to draw attention to this last species more than to the others, on which there is a rich bibliography (Sacchi, 1952, 54, 55; La Greca & Sacchi, 1957). *Hypnophila dohrni* (Paulucci) is a Sardinian species inhabiting the calcareous areas near Sassari. I referred the *Hypnophila* I gathered on the calcareous hill of Giglio to it rather than to the *Hypnophila etrusca* (Paulucci), which inhabits the promontory of Argentario and the island of Elba where I was able to find it recently. In fact, the species of Giglio has a more conic and less oval shape and a weaker tooth near the exterior side of the buccal opening. These characteristics are the same as those of the Sardinian species *Hypnophila dohrni* (Paulucci). However, I think that these characteristics are not sufficient to maintain the distinction between *Hypnophila dohrni* (Paulucci) and *Hypnophila etrusca* (Paulucci); rather, we can consider them to be forms of the same entity.

In addition to the close relationship between the Tuscan Archipelago and Sardinia that this situation shows, we must also keep in mind that the genus *Hypnophila* is also diffused in North Africa, Sicily, the Egadi Archipelago, the Lipari island, Greece and Dalmatia, but is lacking on the mainland of Italy. Unless we explain this geonemy with the shaky hypothesis of a relatively recent Sicilian bridge (Jeannel, 1942; Sacchi, 1955), it can only be justified by the well known tertiary connections between Maghreb, Sicily, Sardinia and Tuscan Archipelago, all belonging to Tyrrhenis. The presence of forms of *Hypnophila* in Greece, Albany and Dalmatia also implies a vast tertiary diffusion that later broke up. The present geonemy is only a residue of this.

A similar but more continuous distribution is shown by *Granopupa* (*Rupestrella*) *philipii* (Cantraine), which I found on the island of Giglio. In fact, this last species is very common in Maghreb, Sicily and Sardinia, where it was found by Paulucci (1882), in the Balkan peninsula, in Dalmatia and in many localities of southern Italy.

The finding of *Marmorana* (*Ambigua*) *argentarolae forsythi* (Paulucci) on the western side of Giglio, on the small calcareous hill named "Franco," is also noteworthy. The subgenus *Ambigua* is known to inhabit the Appennines; the species itself was only known to live on the Argentario promontory and the islet of Argentarola. Its presence on Giglio repeats the situation of other species that also show a close relationship between Giglio and Argentario. It seems very likely that Giglio and Argentario were connected over a long period during the quaternary.

## 3) Forms with a western-Mediterranean geonemy.

Many species belong to this group. *Helicella* (*Xerotricha*) *conspurcata* (Draparnaud), *Helicella* (*Xerotricha*) *apicina* (Lamarck), *Trochoidea* (s.str.) *trochoides* (Poiret), *Cochlicella acuta* (Müller), *Caracollina lenticula* (Michaud), *Papillifera* (s.str.) *papillaris* (Müller), *Jaminia* (s.str.) *quadridens* (Müller) and lastly genus *Pleuropunctum*



Germain (1929) are among the most important. But the last two are particularly significant because they are not easily importable and are more closely bound to a particular kind of environment.

The presence of the central and southern European species *Jaminia* (s.str.) *quadridens* (Müller) on Giglio, once again shows the close connection of Sardinia and Corsica with the southern part of the Tuscan Archipelago and provides another link in the distribution of this species from the southwestern regions of Europe to the southern Apennines (Bacci, 1953). The distribution of the genus *Pleuropunctum* is also extremely interesting. I have found one species of this genus, *Pleuropunctum micropleuros* (Paget), previously known to inhabit only Sardinia and Giglio, on the island of Montecristo and on the central-southern Apennines (Giusti, 1968). Other species are found in Algeria, Spain and southern France. It seems possible that the settlement of *Jaminia quadridens* (Müller) and of *Pleuropunctum micropleuros* (Paget) on the Tuscan islands was very ancient, dating back to the tertiary.

#### 4) Forms with a north-Mediterranean geonomy and a prevalently Italian distribution.

Among the few forms that belong to this group, there are *Hygromia* (s.str.) *cinctella* (Draparnaud), *Limax* (s.str.) *corsicus* Moquin Tandon, *Papillifera* (s.str.) *solida* (Draparnaud) and *Hohenwartiana moitessieri* (Bourguignat). The most interesting of these is the small humus species *Hohenwartiana moitessieri* (Bourguignat), that I collected on Gorgona and that closely relates the fauna of the northern part of the Tuscan Archipelago with that of Corsica, southern France and Piedmont Alps, and gives us another example of Tyrrhenic distribution.

#### 5) Forms with a circum-Mediterranean geonomy.

*Granopupa* (s.str.) *gramum* (Draparnaud) present throughout the Mediterranean and in Portugal, Transcaucasus and Persia, *Theba pisana* (Müller) and *Cochlicella barbara* (Linnaeus) can be listed among these.

#### D) Species with a very extensive geonomy.

Such forms are very rare, as for example the palearctic *Lymnaea (Radix) peregra* Müller and the oloarctic *Lymnaea (Galba) truncatula* (Müller), which are not significant because of their probable introduction by birds. Lastly, there is *Lauria* (s.str.) *cylindracea* (Da Costa) common throughout the Mediterranean area, in Portugal, France, Belgium, Norway, Crimea and Transcaucasus.

### CONCLUSIONS

*Oxychilus*, which is represented by a distinct species on each island and is present even as a fossil in quaternary arenous deposits at Giglio, seems to suggest the hypothesis of a single peopling of the small islands of the Tuscan Archipelago. Therefore, it seems possible that successive cacuminal and insular geographic isolations led to differentiation by genetic drift.

It is much more difficult to coordinate the data on the other molluscs of the Tuscan Archipelago and draw conclusions. In fact, given the notable geological differences in the islands of the Archipelago (some calcareous, some volcanic), ecological factors must have played a very important role in the malacological peopling of these islands, which, as is known, is greatly influenced by the chemical composition of the environment. Therefore, it is practically impossible to say whether the calciophile forms that inhabit Giglio, Giannutri and the Argentario promontory, where calcium abounds, also reached the volcanic part of the Tuscan Archipelago and were subsequently eliminated or avoided it entirely. Thus an overall view of the peopling of the Tuscan Archipelago is very problematical.

Nevertheless, the permanence *in loco* of a certain number of species that seem quite significant to me, suggests the following conclusions. The process of settling must have taken place in several periods. The most ancient one, probably dating back to the tertiary, was characterized by the presence of many forms over a wide area corresponding to Tyrrhenis. Some are strictly tyrrhenic (*Tacheocampylaea*, *Oxychilus*, *Cochlodina* and *Hohenwartiana*); others have a wider prevalently central-Mediterranean geonemy (*Hypnophila*, *Granopupa*, *Trochoidea*, *Caracollina*, *Vitrea*, *Hygromia*, *Papillifera* and *Pomatias*) and remained on these islands after the breaking up of Tyrrhenis. During the quaternary, forms like *Limax*, *Milax*, *Helix*, *Deroceras* and *Marmorana* must have arrived over the Corsican-Tuscan bridge. Lastly, other more common forms may have arrived later in the quaternary, as well as by subsequent importation by man, as in the case of *Ferrussacia (Pegea) carnea* (Risso) on the island of Pianosa.

A careful study of the Appennine malacofauna and especially that of Sardinia, which has not been re-examined for a long time, is called for. Since the southern part of the Tuscan Archipelago is closely related to these areas, it would be absurd and risky to draw more detailed conclusions using only our present data on molluscs.

#### BIBLIOGRAPHY

- ALZONA, C. & BISACCHI, J., 1969, Malacofauna Italica. (In press).
- BISACCHI, J., 1929, Molluschi terrestri e fluviatili raccolti dal Marchese Giacomo Doria nell'Arcipelago toscano (1875-1901). *Ann. Mus. Civ. St. Nat. Genova*, 53: 164-186.
- BÜTTNER, K., 1926, Beiträge zur Kenntnis der Land- und Süßwasserfauna Korsikas. 5. Mollusca (ausschliesslich der Nacktschnecken). *Mitt. Zool. Mus. Berlin*, 12(2): 235-240.
- CAZIOT, E., 1916, Note sur les Campylaea de la Sardaigne et des îles de Capraia, de Pianosa et de Corse. *Bull. Soc. zool. France*, 41: 65-76.
- COLOSI, G., 1920, Limacidi e Arionidi conservati nel R. Museo Zoologico di Firenze. *Monit. Zool. Ital.*, 31: 61-73.
- DE STEFANI, C., 1875, Molluschi viventi nella valle del Serchio superiore. *Bull. Soc. Malacol. Ital.*, 1: 35-67.
- DE STEFANI, C., 1879, Nuovi molluschi viventi nell'Italia centrale. *Bull. Soc. Malacol. Ital.*, 5: 38-48.
- DE STEFANI, C., 1883, Molluschi viventi nelle Alpi Apuane, nel Monte Pisano e nell'Appennino adiacente. *Bull. Soc. Malacol. Ital.*, 9: 11-253, 1 tab.
- FORCART, L., 1965, Rezente Land- und Süßwassermollusken der süditalienischen Landschaften Apulien, Basilicata und Calabrien. *Verh. naturf. Ges. Basel*, 76(1): 59-194.
- FORCART, L., 1967, Die systematische Stellung toskanischer *Oxychilus*-Arten und Neubeschreibung von *Oxychilus (Ortizius) lanzai* n. sp. *Arch. Molluskenk.*, 96(3/6): 113-123.
- GERMAIN, L., 1930, Mollusques terrestres et fluviatiles. *Faune de France*, 21: 1-477, tabs. 1-13.
- GENTILUOMO, C., 1868, Catalogo dei molluschi terrestri e fluviatili della Toscana. *Boll. Malacol. Ital.*, 1: 67-100.
- GIUSTI, F., 1968, Notulae Malacologicae II. Il genere *Oxychilus* nell'Arcipelago toscano, con descrizione di un nuovo sottogenere e di quattro nuove specie: *Oxychilus (Alzonula) oglasicola* n. subgen., n. sp., *Oxychilus (s.str.) gorgonianus* n. sp., *Oxychilus (s.str.) igilicus* n. sp., ed *Oxychilus (s.str.) argentaricus* n. sp. *Atti Soc. Tosc. Sci. Nat.* 75, serie B: 218-235.
- GIUSTI, F., 1969, Notulae Malacologicae III. Sulla sistematica e distribuzione del *Pleuropunctum micropleuros* (Paget) nell'Italia appenninica. *Boll. Zool.* 36(1): 87-100.

- GIUSTI, F., 1968, Notulae Malacologicae IV. L'isola di Montecristo e lo Scoglio d'Africa. *Atti Soc. Tosc. Sc. Nat.*, 75, serie B: 239-254.
- GIUSTI, F., 1968, Notulae Malacologicae V. Le isole di Capraia, Gorgona e Giglio. *Atti Soc. Tosc. Sc. Nat.*, 75, serie B: 265-324.
- HESSE, P., 1932, Zur genaueren Kenntnis einiger italienischer Heliciden. *Arch. Molluskenk.*, 64: 189-197, tab. 14, figs. 1-3.
- HOFFMANN, H., 1926, Beiträge zur Kenntnis der Land- und Süßwasserfauna Korzikas. 6. Die Nacktschnecken. *Mitt. aus dem Zool. Mus. Berlin*, 12(2): 241-262.
- ISSEL, A., 1866, Dei molluschi raccolti nella provincia di Pisa. *Mem. Soc. Ital. Sci. Nat. Milano*, 2(1): 1-38.
- ISSEL, A., 1872, Appendice al catalogo dei molluschi raccolti nella provincia di Pisa. *Atti Soc. Ital. Sci. Nat. Milano*, 25: 58-76.
- ISSEL, A., (1873), Di alcuni molluschi raccolti nell'isola di Sardegna dal Dott. Gestro. *Ann. Mus. Civ. St. Nat. Genova*, 4: 275-281, 2 figs.
- JEANNEL, R., 1942, La genese des faunes terrestres. Paris, 337 pp.
- KOBELT, W., 1898, Studien zur Zoogeographie. II. Die Fauna der meridionalen Sub-Region. Wiesbaden, 368 pp.
- LA GRECA, M. & SACCHI, C. F., 1957, Problemi del popolamento animale nelle piccole isole mediterranee. *Ann. Inst. e Mus. Zool. Univ. Napoli*, 9: 1-189, 20 figs., 7 tabs..
- PAULUCCI, M., 1878, Matériaux pour servir à l'étude de la faune malacologique terrestre et fluviatile de l'Italie et de ses îles. Paris, 54 pp.
- PAULUCCI, M., 1882, Note malacologiche sulla fauna terrestre e fluviatile dell'isola di Sardegna. *Bull. Soc. Malacol. Ital.*, 8: 139-381, 9 tabs.
- PAULUCCI, M., 1886, Conchiglie terrestri e d'acqua dolce del Monte Argentario e delle isole circostanti. *Bull. Soc. Malacol. Ital.*, 12: 6-62, 2 tabs.
- PFEIFFER, K., 1932, Die Murellen, Helicigonon und Tacheocampylaeen des Toskanischen Archipels und des Monte Argentario. *Arch. Molluskenk.*, 64: 173-189, 13 tabs.
- POLLONERA, C., 1905, Molluschi terrestri e fluviatili dell'Isola d'Elba e Pianosa. *Boll. Mus. Zool. e Anat. Compt. Torino*, 20(517): 3-9, 1 tab.
- POLLONERA, C., 1909, Tacheocampylaea dell'isola di Capraia. *Boll. Mus. Zool. e Anat. Compt. Torino*, 24(608): 15-17, 1 tab.
- RAZZAUTI, C., 1917, Contributi alla conoscenza faunistica delle isole toscane. *Atti Soc. Tosc. Sci. Nat.*, 31: 196-224.
- RAZZAUTI, C., 1936, Contributi alla conoscenza faunistica delle isole toscane. 4. Le Tacheocampylaea di Pionosa e di Capraia. *Atti Soc. Tosc. Sci. Nat.*, 45(3): 1-4.
- SACCHI, C. F., 1954, Contributo alla conoscenza dei popolamenti delle piccole isole mediterranee. II. Cenni biogeografici sulla malacofauna di Iviza (Pitiuse). *Boll. Zool.*, 21(1): 1-40, 8 tabs., 6 figs.
- SACCHI, C. F., 1955, Il contributo dei molluschi alle ipotesi del "ponte siciliano." Elementi tirrenici ed orientali nella malacofauna del Maghreb. *Arch. Zool. Ital.*, 40: 49-181.
- SACCHI, C. F., 1956, Sulla malacofauna terrestre di Pantelleria. *Atti Soc. Ital. Sci. Nat.*, 95: 33-44.
- SACCHI, C. F., 1957b, Relazioni tra superficie insulare e mole corporea in Eobania vermiculata (Müll.) dell'Arcipelago toscano. *Boll. Zool.*, 24: 1-8.
- SIMONELLI, V., 1889, Terreni fossili dell'isola di Pianosa nel Mar Tirreno. *Boll. R. Comitato geol. d'Ital.*, 10(7/8): 193-237, 5 tabs.



ZUR SYSTEMATIK DER GLOSSODORIDINAE DES MITTELMEERES<sup>1</sup>

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EINLEITUNG

Im Rahmen einer Revision der Gattung *Glossodoris* Ehrenberg hat Pruvot-Fol 1951, sowie später in der Faune de France 1954 "Opisthobranches" die Glossodoridinae des Mittelmeeres bearbeitet.

Die seit gut einem Jahrzehnt an verschiedenen biologischen Stationen des Mittelmeeres (Banyuls, Villefranche, Neapel) durchgeführten Studien an Opisthobranchia, und die damit verbundenen regelmässigen Fänge, erlauben uns erneut auf das Problem der Systematik der Glossodoridinae im Mittelmeer zurückzukommen. Heute steht dem Malakologen wesentlich mehr Vergleichsmaterial zur Verfügung; Farbphotographie und Kinematographie bieten Dokumente, welche nicht von subjektiven Eindrücken und von den zeichnerischen Fähigkeiten des Beobachters abhängig sind. Färbung und Musterbildung sind bei Glossodoridinae ebenso wichtige Bestimmungsmerkmale wie Radula und Genitaltrakt. Neben dem fixierten Material sollten auch Notizen über das Verhalten, über Zeichnung und Körperfärbung vorliegen. Für diese Arbeit wurden die Originalveröffentlichungen der Diagnosen konsultiert.

Dank schulde ich Fräulein Dr. L. Schmekel (Neapel), G. Niçaise (Villefranche/Lyon) und vielen anderen, welche mir Material und Unterlagen für diese Arbeit überlassen haben.

ALLGEMEINE BEMERKUNGEN

Schon vor einigen Jahren habe ich (Haefelfinger, 1959) die Ontogenese des Zeichnungsmusters einiger Glossodoridinae (*G. gracilis*, *krohni*, *luteorosea* und *tricolor*) beschrieben. Die seit diesem Zeitpunkt gefundenen Exemplare dieser Arten haben die damals publizierten Resultate bestätigt. Im Katalog der Opisthobranchia der Bucht von Villefranche (Haefelfinger, 1960) wurden zwei weitere Glossodoridinae als unbestimmte Arten erwähnt. Von der einen Art konnte das einzige Exemplar als *Glossodoris valenciennesi* bestimmt werden, bei der zweiten Art, welche in mehreren Exemplaren in Villefranche und später auch in Banyuls gefunden wurde, handelt es sich um *Glossodoris messinensis*.

LISTE UND SYNONYMIE DER MITTELMEER-GLOSSODORIDINAE

1. *Glossodoris elegantula* (Schultz-Philippi) 1844 (Doris)

Synonyme: *Chromodoris elegantula* Vayssière 1913

Bemerkungen: Diese Art soll angeblich von Pruvot-Fol in Villefranche wieder gefunden worden sein. Es ist allerdings sehr fraglich, ob es sich um eine *Glossodoris* handelt. Wahrscheinlich ist es *Diaphorodoris luteocincta papillata* Portmann 1959.

<sup>1</sup>Vorläufige Mitteilung.

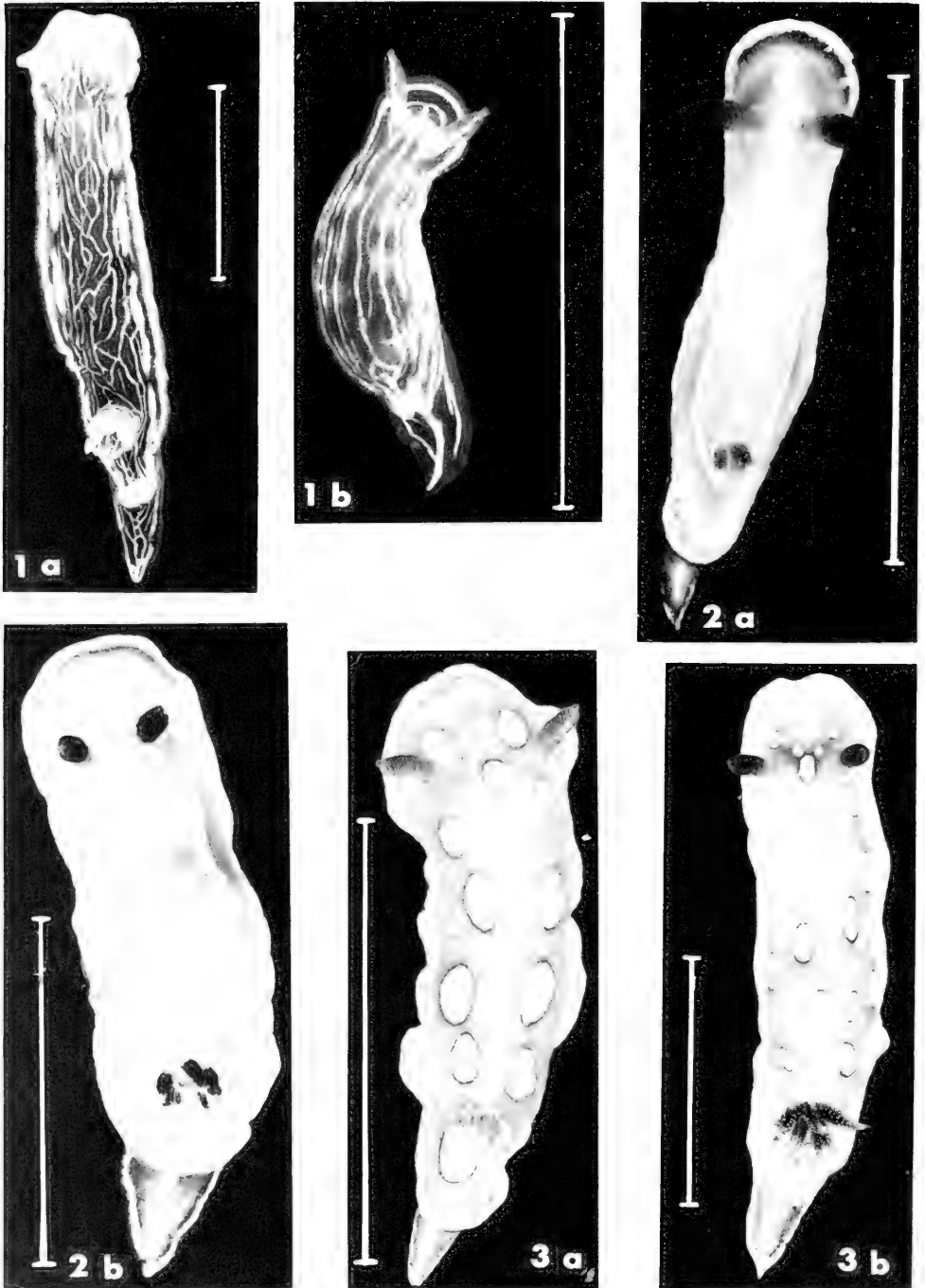


ABB. 1. *Glossodoris gracilis*. a, adult; b, juvenil.

ABB. 2. *Glossodoris krohni*. a, juvenil; b, adult.

ABB. 3. *Glossodoris luteorosea*. a, juvenil; b, adult.

Der weisse Strich auf den Abbildungen entspricht einem Zentimeter Länge.

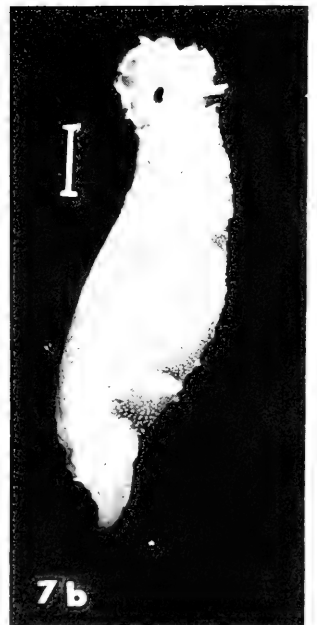
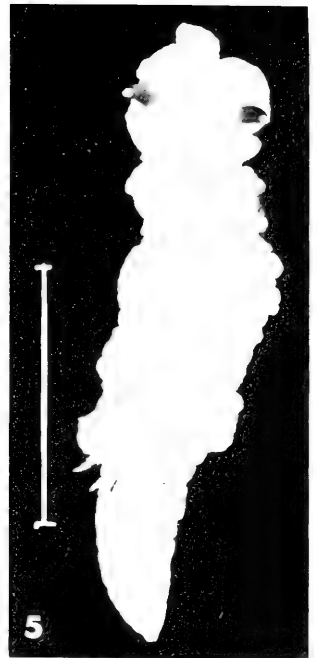


ABB. 4. *Glossodoris messinensis*. a, juvenil; b, adult.

ABB. 5. *Glossodoris purpurea* adult, die juvenile Form unterscheidet sich nur durch die Grösse.

ABB. 6. *Glossodoris tricolor* adult, die juvenile Form unterscheidet sich nur durch die Grösse.

ABB. 7. *Glossodoris valenciennesi*. a, juvenil; b, adult.

2. *Glossodoris gracilis* (Rapp) 1827 (Doris)  
 Synonyme: *Doris gracilis* Delle Chiaje 1841; *Doris orsinii* Vérany 1846; *Doris pasinii* Vérany 1846; *Doris pulcherrima* Cantraine 1835/40; *Doris tenera* Costa 1840; *Doris villae* Vérany 1846; *Doris villafranca* Risso 1818; *Chromodoris villafranca* Vayssièr 1913.  
 Bemerkungen: *Glossodoris gracilis* ist in Färbung und Musterbildung sehr variabel. Stadien von 5-10 mm Länge können bei oberflächlicher Beobachtung mit *Glossodoris tricolor* und *messinensis* unter Umständen verwechselt werden.  
 Depot: Nat. Hist. Mus. Basel, Gastropoda Nr. 7192.
3. *Glossodoris krohni* (Vérany) 1846 (Doris)  
 Synonyme: *Doris pallens* Rapp 1827 (adultes Exemplar); *Chromodoris trilineata* von Ihering; ?; *Doris lutescens* Delle Chiaje 1841?.  
 Bemerkungen: Da sich das Zeichnungsmuster im Verlaufe der Entwicklung verändert (Liniensystem wird in längliche Inseln aufgelöst) ist der Zusammenhang zwischen den beiden Formen erst in den vergangenen Jahren zutage getreten. Mit einiger Sicherheit kann daher auch *Doris lutescens* als Synonym betrachtet werden.  
 Depot: Nat. Hist. Mus. Basel, Gastropoda Nr. 7193
4. *Glossodoris luteorosea* (Rapp) 1827 (Doris)  
 Synonyme: *Chromodoris iheringi* Bergh 1879; *Chromodoris luteorosea* Vayssièr 1901/1913/1919; *Doris parthenopeia* Delle Chiaje 1841.  
 Bemerkungen: Diese Art hat ein sehr spezifisches Färbungsmuster, das kaum mit einer anderen Art verwechselt werden kann.  
 Depot: Nat. Hist. Mus. Basel, Gastropoda Nr. 7194
5. *Glossodoris messinensis* (von Ihering) 1880 (Chromodoris)  
 Synonyme: *Glossodoris fauntandraui* Pruvot-Fol 1951.  
 Bemerkungen: Lange Zeit blieb diese durch von Ihering beschriebene Form verschollen, respektive wurde mit *gracilis* verwechselt. (Variante des Zeichnungsmusters). Die von Pruvot angefertigten Farbskizzen von *Glossodoris fauntandraui* sind sehr ungenau. In groben Zügen stimmen sie jedoch mit *messinensis* überein. Eigene Erfahrungen und Angaben von G. Niçaise haben gezeigt, dass auch bei dieser Art ziemliche Abweichungen in Färbung und Musterbildung auftreten können. Die Radula von *fauntandraui* und *messinensis* stimmen ebenfalls sehr genau überein.  
 Depot: Nat. Hist. Mus. Basel, Gastropoda Nr. 1102
6. *Glossodoris purpurea* (Laurillard) 1831 (Doris)  
 Synonyme: *Doris albescens* Schultz-Philippi 1836/44; *Doris pirainii* Vérany 1846; *Doris venulosa* Leuckart 1828.  
 Bemerkungen: *Glossodoris purpurea* ist die einzige Glossodoridier-Art des Mittelmeeres, welche kein Zeichnungsmuster aufweist, sie ist daher sehr leicht zu identifizieren.  
 Depot: Nat. Hist. Mus. Basel, Gastropoda Nr. 7196
7. *Glossodoris tricolor* (Cantraine) 1836/41 (Doris)  
 Synonyme: *Goniodoris coelestis* Deshayes 1866; *Glossodoris coelestis* Mangold-Wyss 1958; *Glossodoris coelestis* Pruvot-Fol 1951/54.  
 Bemerkungen: Beobachtungen haben gezeigt, dass die für *Glossodoris coelestis* typischen Tuberkel auf der Rückenfläche nicht immer gleich stark in Erscheinung treten, das heisst je nach Kontraktionszustand der Schnecke sind sie mehr oder weniger ausgeprägt. Es ist daher mit Sicherheit anzunehmen, dass die Arten *tricolor* und *coelestis* identisch sind, da keine weiteren Unterscheidungsmerkmale vorliegen.  
 Depot: Nat. Hist. Mus. Basel, Gastropoda Nr. 7195
8. *Glossodoris valenciennesi* (Cantraine) 1835 (Doris)  
 Synonyme: *Doris elegans* Cantraine 1835; *Chromodoris cantrainii* Bergh 1892/99; *Doris calcava* Vérany 1846; *Doris nardii* Vérany 1846; *Doris picta* Schultz-



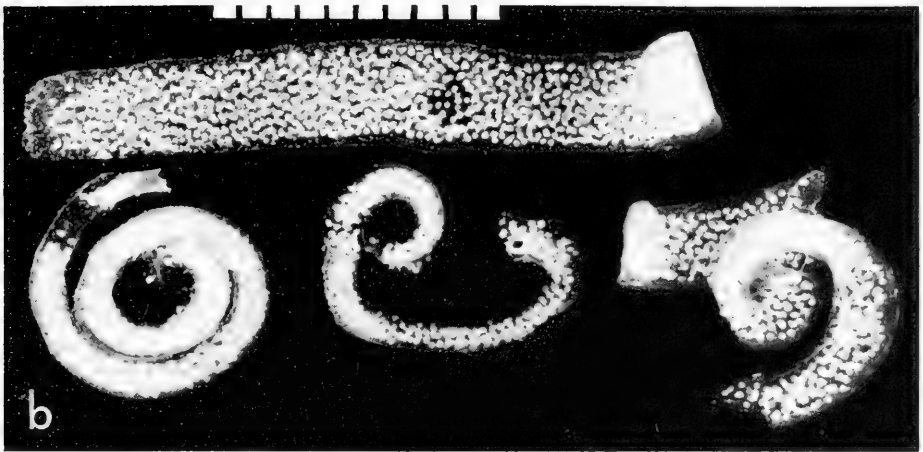
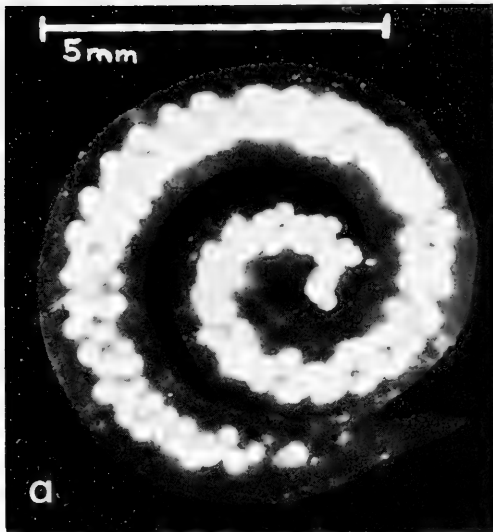


ABB. 8. a, Gelege von *Glossodoris gracilis*; b, Verschiedene Gelege von *Glossodoris messinensis*.

Philippi 1836/44; *Doris scacchiana* Delle Chiaje 1830/41; *Doris schultzi* Delle Chiaje 1841.

Bemerkungen: Diese grösste Glossodoridierart des Mittelmeeres zeigt auch die stärksten Variationen in Färbung und Musterbildung. Es ist daher nicht erstaunlich, dass so viele Synonyme auftreten. *Valenciennesi* unterscheidet sich jedoch in charakteristischer Weise von den übrigen Formen des Mittelmeeres.

Depot: Nat. Hist. Mus. Basel, Gastropoda Nr. 7197.

#### DISKUSSION

Die meisten der von verschiedenen Autoren beschriebenen Glossodoridinae konnten eindeutig identifiziert werden, da ein umfangreiches Vergleichsmaterial vorlag. Einzig bei *Doris lutescens* Delle Chiaje bestehen noch geringe Zweifel.

Problematisch bleibt, wie schon erwähnt, *Glossodoris elegantula* Schultz-Philippi. Das vorhandene Aquarell zeigt uns eindeutig eine *Diaphorodoris luteocincta papillata* Portmann 1959. Es ist immerhin erstaunlich, dass die von Schultz-Philippi erwähnte Art, mit Ausnahme eines zweifelhaften Wiederfundes durch Pruvot-Fol, bis heute nicht mehr gesichtet wurde.

Einige Schwierigkeiten bietet die Abgrenzung und Identifizierung der blauen Glossodoridinae des Mittelmeeres.

Typisches Merkmal für *Glossodoris coelestis* sollen Tuberkel auf dem Notum sein. Die Beobachtung vieler Dutzende von lebenden Tieren haben deutlich gezeigt, dass die Grösse der Tuberkel eng mit dem Kontraktionszustand der Schnecke zusammenhängt. Es ist durchaus möglich, dass einem Beobachter dieses Merkmal entgeht. Vergleichen wir die Diagnose von *tricolor* Cantraine mit der Abbildung von *coelestis* Deshayes, welche durch keine schriftliche Diagnose ergänzt wird, so stellt man eine grosse Uebereinstimmung fest. Im übrigen genügt die Veröffentlichung einer Abbildung den Nomenklaturregeln gemäss nicht für die Gültigkeit einer Art.

Mit Ausnahme der Erscheinungsform können keine weiteren Merkmale verglichen werden, da die zitierten Autoren keine anatomischen Merkmale (Radula, Genitaltrakt) beschrieben haben. Man geht aber nicht fehl, wenn man die beiden Namen als Synonyme betrachtet und aus den oben erwähnten Gründen die Art mit *tricolor* bezeichnet. Etwas schwieriger sind die Verhältnisse bei *gracilis* und *messinensis*, da beide Arten sehr starke Variationen der Färbung und Musterbildung zeigen. Das gefangene Material kann aber in frischem Zustand nach folgenden Merkmalen geschieden werden: *messinensis* zeigt immer einen breiten weissen Mittelstreifen, gelegentlich etwas gelb getönt, der als breites Band die Kiemen umfasst und zwischen den Rhinophoren nach vorne auf der Stirn eine Art Anker bildet. Auch auf den Flanken findet man neben feineren Linien ein breites weisses Band. Selbst juvenile Exemplare zeigen dieses Merkmal, nur etwas weniger deutlich, da auch junge *gracilis* eine weisse Mittellinie aufweisen und sich das arttypische dorsale Liniensystem erst im Verlaufe des Wachstums bildet (Haefelfinger 1959).

Der wesentlichste Unterschied besteht sicher in bezug auf Gelege und Larvalentwicklung. *Glossodoris messinensis* produziert ein Laichband mit vielen, relativ kleinen Eiern, aus denen immer Veliger schlüpfen, welche im Pelagial eine Metamorphose durchlaufen. *Glossodoris gracilis* hingegen legt einen Laich mit wenigen, grossen Eiern ab, der Veliger durchläuft die Metamorphosestadien im Ei drin und es schlüpft eine winzige Schnecke von kaum Millimeterlänge. Die von Pruvot-Fol 1941/54 gegebene Synonymie von *gracilis* bedarf also einiger Korrekturen. *Gracilis* und *messinensis* sind zwei verschiedene Arten, *tricolor* und *coelestis* sind Synonyme und bilden eine dritte Art von blauen Glossodoridiern.

Die vierte blaue Glossodoridier-Art, *Glossodoris valenciennesi*, zeigt sicher die grössten Variationen der optischen Gestaltung. Der Farbton des Körpers schwankt zwischen blau und grün bis zur intensiven satten Farbe. Die Farbe des sehr variablen Zeichnungsmusters variiert von weiss bis gelb. Junge Exemplare können jedoch am breiten weissen Notumrand, die adulten am welligen Notumrand gut erkannt werden. Dieser Variabilität wegen ist es begreiflich, dass *valenciennesi* Anlass zu vielen Artschöpfungen gab.

#### LITERATUR

- BERGH, R., 1877, Kritische Untersuchungen der Ehrenberg'schen Doriden. *Jb. dt. Malakozool. Ges.*, 4: 45-76.  
 BERGH, R., 1879, Neue Chromodoriden. *Malakozool. Bl. N. F.*, 1: 87-116.  
 BERGH, R., 1892, Die cryptobranchiaten Dorididen. *Zool. JB.* 6: 103-144.

- BERGH, R., 1899, Nudibranches et Mersenia provenant des Campagnes de la Princesse-Alice. *Rés. Camp. Sc. Monaco*, 14.
- CANTRAINE, F., 1835, Diagnose de quelques espèces nouvelles de Mollusques. *Bull. Acad. Sc. Bruxelles*, 2: 383-386.
- CANTRAINE, F., 1841, Malacologie méditerranéenne et littorale I. *Now. Mém. Acad. R. Sci. Bruxelles*, 13: 46-94.
- CHIAJE, ST. DELLE, 1823, Memoria su la storia e notomia degli animali senza vertebri. I (Taf.), II (Text).
- CHIAJE, ST. DELLE, 1841, Descrizione e notomia degli animali invertebrati della Sicilia citeriore, Napoli.
- COSTA, A., 1840, Statistica fisica e economica dell'isola di Capri II, Neapel.
- DESHAYES, A., 1866, Tafel in Fré dol: *Le Monde de la Mer*, Pl. XVII.
- FORBES, E., 1844, Report on the Mollusca and Radiata of the Aegean Sea, and on their distribution. XII. *Report Brit. Assoc. Adv. Sci.*
- HAEFELFINGER, HR., 1959, Remarques sur le développement du dessin de quelques Glossodoridiens. *Rev. Suisse Zool.*, 66: 309-315.
- HAEFELFINGER, HR., 1960, Catalogue des Opisthobranches de la Rade de Villefranche-sur-Mer et ses environs (A.M.). *Rev. Suisse Zool.*, 67: 323-351.
- IHERING, H. von, 1880, Beiträge zur Kenntnis der Nudibranchier des Mittelmeeres I. *Malakozool. Bl. N. F.*, 2: 57-112.
- LEUCKART, F. S., 1828, Breves animalium quorundam maxima ex parte marinorum descriptiones. Heidelberg.
- PHILIPPI, R. A., 1836, In Schultz-Philippi. *Enumeratio molluscorum Siciliae I.* Berlin.
- PHILIPPI, R. A., 1844, In Schultz-Philippi. *Enumeratio molluscorum Siciliae II.* Berlin.
- PRUVOT-FOL, A., 1951, Etudes des Nudibranches de la Méditerranée. *Arch. Zool. Exp. et gén.*, 88: 1-80.
- PRUVOT-FOL, A., 1951a, Révision du genre *Glossodoris* Ehrenberg. *J. Conch.*, Paris, 41: 76-164.
- PRUVOT-FOL, A., 1953, Etude de quelques Opisthobranches de la côte atlantique du Maroc et du Sénégal. *Trav. Inst. Sc. Chérif.*, 5: 1-93.
- PRUVOT-FOL, A., 1954, Opisthobranches. Faune de France, 58. Paris.
- RAPP, W., 1827, Ueber das Molluskengeschlecht *Doris* und Beschreibung einiger neuer Arten desselben. *Nov. Acta Acad. Lep. Carol. Nat. Cur.*, 13: 515-522.
- RISSO, A., 1826, Histoire naturelle de l'Europe méridionale, 4. Paris.
- SCHMEKEL, L., 1968, Ascoglossa, Notaspidea und Nudibranchia im Litoral des Golfes von Neapel. *Rev. Suisse Zool.*, 75: 103-155.
- VAYSSIÈRE, A., 1902, Recherches zoologiques et anatomiques sur les Opisthobranches du Golfe de Marseille. III. Nudibranches. *Ann. Mus. Hist. Nat. Marseille*, 6.
- VAYSSIÈRE, A., 1903, Id. Supplément. *Ann. Mus. Hist. Nat. Marseille*, 8.
- VAYSSIÈRE, A., 1909, Note sur une anomalie tentaculaire chez un *Chromodoris elegans* Cantraine. *Ann. Sci. Nat. Zool.*, 10: 109-110.
- VAYSSIÈRE, A., 1913, Mollusques de la France. Enc. Scientifiques Paris.
- VERANY, J. B., 1846, Catalogo degli animali invertebrati del Golfo di Genova e Nizza. Genova.



FUNCTIONAL ANATOMICAL ASPECTS OF THE  
OVOTESTIS OF *LYMNAEA STAGNALIS*

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ABSTRACT

During investigations on the endocrine aspects of reproduction in the freshwater pulmonate snail *Lymnaea stagnalis* (Linnaeus), the ovotestis of this species was studied. In order to determine the general structure of the ovotestis a plastic model was prepared from the gonad of an adult specimen. The number of acini appeared to be 21. Their shape and size showed a great variability. The number of yolk containing oocytes varied from 16-91 per acinus. The total number of oocytes in this specimen was about 1000.

The structure of the acini was studied by the light- and phase-contrast microscope. The germinal epithelium of the acini consists of ciliated cells, and cells with microvilli and lipid droplets. Most probably both the sex and the nurse cells arise from the germinal epithelial ring. This is a narrow rim of cells, which borders the germinal epithelium against the area of developing sex cells.

The female cells remain in close contact with the basal lamina of the acinus wall. A motile phase is followed by a sessile vitellogenic phase, during which the oocyte is surrounded by a number of follicle cells.

The male sex cells are continuously in contact with the Sertoli cells. The Sertoli cells form an epithelial layer, which divides the lumen of the acinus in a female and a male compartment.

Spermiation begins with the enlargement of the Sertoli cell. Then the cytoplasmic remainders of the spermatids are absorbed by the Sertoli cell. At the same time the spermia start their free life. After spermiation the Sertoli cells do not die. They remain at their position in the epithelial layer. Most probably they have now a phagocytotic function, as they show cytoplasmic stalks projecting into the lumen of the acinus. In these stalks groups of granules with a lysosomal structure are found.

The plastic model of the ovotestis and a similar model of a single acinus were used to investigate the location and arrangement of the developing sex cells in the acini. The sessile oocytes appeared to be present in a region called the vitellogenic area. This area of the acinus wall is apposed to the digestive gland. Around this area the spermatogenic zone is present, in which the male cells are found. This zone is bordered by the germinal epithelial ring.

With regard to the arrangement of the sex cells in the acini of *Lymnaea stagnalis*, a hypothesis is put forward. In this hypothesis a primary role is attributed to the digestive gland.

INTRODUCTION

In the literature several times attention has been paid to the gonad of the hermaphrodite freshwater snail *Lymnaea stagnalis* (Linnaeus) (Gastropoda, Pulmonata, Basommatophora) (ARCHIE, 1941; BRETSCHNEIDER, 1948a,b; BRETSCHNEIDER & RAVEN, 1951; AUBRY, 1962; JOOSSE, 1964). Among these papers the thorough description of the histology of the ovotestis of *L. stagnalis lillianae* given by ARCHIE, is of special interest. Data regarding the electron microscopy and histochemistry of oogenesis has been presented by RECOURT (1961) and UBBELS (1968).

During our investigations on the endocrine aspects of reproduction, the anatomy of the ovotestis under different experimental conditions has been studied (JOOSSE, 1963, 1964, 1967; JOOSSE, et al., 1968). Our interest is primarily focused on problems like: the site of origin of the sex cells, the role of the nurse cells and the mechanism of ovulation and spermiation. Some of the results obtained from these investigations are presented in this paper.

### MATERIALS AND METHODS

Adult snails (shell height 27-34 mm) bred in the laboratory or collected in the field, were dissected after decapitation.

For light microscopy the entire ovotestis surrounded by the digestive gland was fixed in Stieve's sublimate, upgraded in ethanol and amyacetate and embedded in paraffin wax (m.p. 58° C). Serial sections (thickness 5 or 15 $\mu$ ) were cut, and stained with Gomori's chrome-hematoxylin-phloxin method.

For phase-contrast and electron microscopy glutaraldehyde and OsO<sub>4</sub> fixed, and Epon 812-embedded material (PEASE, 1964) was used. The thickness of the sections for phase-contrast microscopy was 2 $\mu$ .

For preparing a model of the ovotestis serial sections (thickness 15 $\mu$ ) were cut from the ovotestis of an adult specimen (shell height 28 mm). Every second section was photographed (magn. 66x). The acini and the efferent ducts of the ovotestis were outlined on transparent sheets of PVC-plastic of appropriate thickness (2 mm). The areas concerned were cut out and joined together with a suitable adhesive. In a similar way a second model was prepared of a single acinus using 2 $\mu$  thick Epon-sections at a magnification of 118x.

### GENERAL STRUCTURE OF THE OVOTESTIS

The ovotestis of *Lymnaea stagnalis* is situated in the top of the shell. It is surrounded by the digestive gland, except at the central columellar side. From the study of the model of the ovotestis (Fig. 1) it appeared that its shape is highly irregular.

The ovotestis consists of a number of blind sacs called acini. As is shown in Figs. 1, 2 and 3 their shape is also irregular, due to folds of the wall. The folds divide the acinus in several compartments, which often have been considered as single acini. Thus, ARCHIE (1941) estimated the number of acini in *Lymnaea stagnalis lillianae* at about 100. However, when an acinus is defined as an irregular blind sac, having a secondary vas efferens (Fig. 3), then the reconstructed ovotestis appears to consist of only 21 acini.

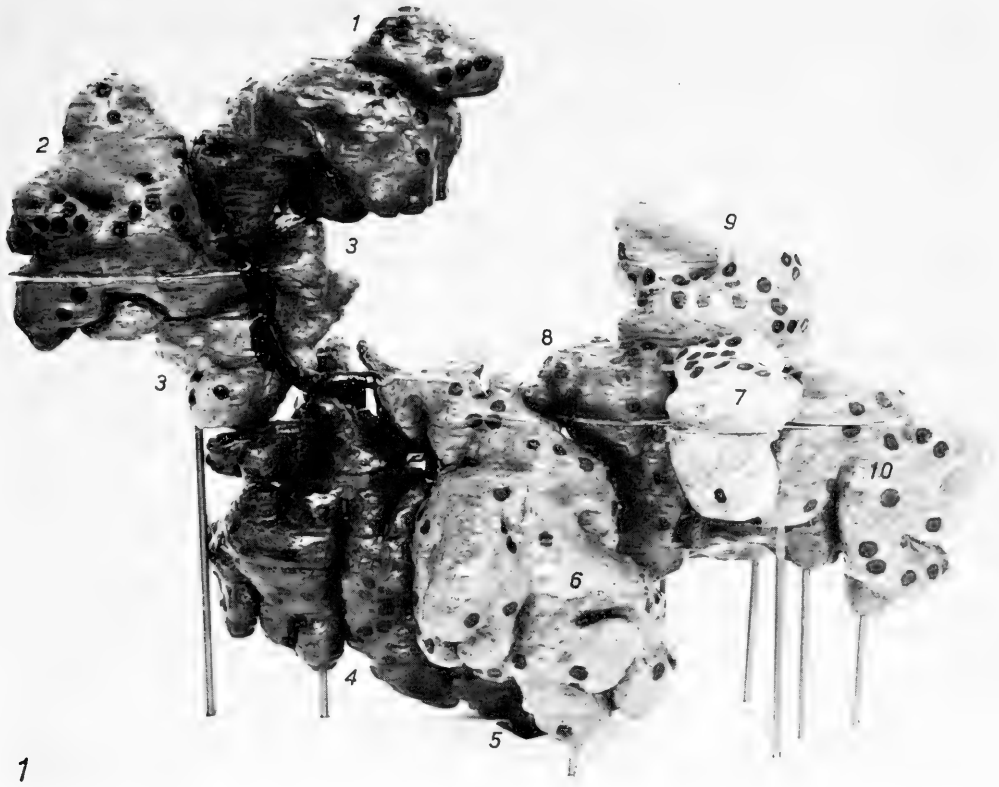
The acini are divided into 2 groups. The secondary vasa efferentia of each group fuse to a primary vas efferens, which join to form the spermoviduct.

The acini show a great variability of size. Apparently the number of gametes produced by them is also different. In the reconstructed specimen the number of yolk

FIG. 1. This is a photograph of a part of the plastic model of an ovotestis. 10 acini can be seen. On acinus 3 a primary vas efferens is visible. The location of oocytes is indicated by black dots. Note the difference in size of acinus 6 and 7. (Magnification 30x)

FIG. 2. This is a photograph of the plastic model of a single acinus. White: vitellogenic area. Black: spermatogenic zone. Dotted area: vas efferens. This side of the acinus is apposed to the digestive gland. (x45)

FIG. 3. The same plastic model photographed from the side which is apposed to another acinus (cf. Fig. 2). Black: spermatogenic zone. Dotted area: germinal epithelium, except the secondary vas efferens at the upper right side. Below: two cut surfaces. (x45)



1



2

3

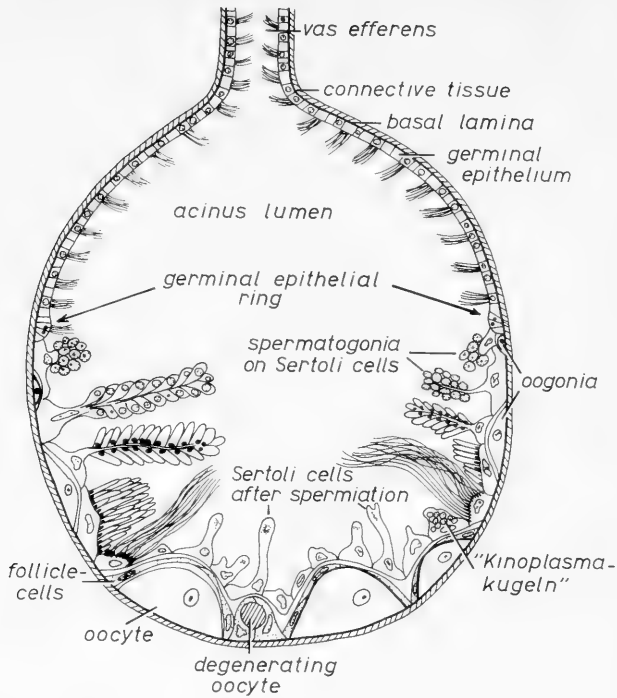


FIG. 4. Scheme of a longitudinal section through an acinus.

containing oocytes varied from 16-91 per acinus. The total number of oocytes in this ovotestis was about 1000.

### THE GERMINAL EPITHELIAL RING

In Fig. 4 a scheme of a longitudinal section through an acinus is presented. The epithelium of the (secondary) efferent duct is continuous with the epithelium lining a large part of the lumen of the acinus. In literature this layer of cells is called the germinal epithelium. In this epithelium two cell types can be distinguished: ciliated cells and cells with microvilli. The latter contain lipid droplets. The epithelium is separated from the underlying connective tissue by a basal lamina, which extends outside the region of the germinal epithelium around the entire acinus.

The germinal epithelium is bordered against the area of developing sex cells by a narrow rim of epithelial cells. This closed rim has an irregular course around the wall of the acinus. It is proposed to call this rim the germinal epithelial ring (Figs. 4 and 6). From this structure apparently all cells involved in gametogenesis originate (cf., BARTH & JANSEN, 1960, 1962). These cells are the spermatogonia, oogonia and their nurse cells. To avoid misunderstanding the nurse cells of the female sex cells are called follicle cells and those of the male sex cells Sertoli cells.

### MOTILITY OF THE DEVELOPING SEX CELLS

BARTH & JANSEN (1962) described the origin of oogonia and follicle cells from the germinal epithelium in *Australorbis glabratus*. Each oogonium accompanied by one follicle cell moves to a more distal position on the acinus wall. There the oogonia



become sessile, and the follicle cell gives rise to a follicle, consisting of a fixed number of cells around an oocyte (RAVEN, 1963). Then vitellogenesis starts.

In *Lymnaea* similar phenomena are described by BRETSCHNEIDER & RAVEN (1951). The origin of the follicle cells in this species, however, has not been studied in detail.

As soon as the female sex cells have arisen from the germinal epithelial ring, they are always in close contact with the nurse cell and the basal lamina of the acinus wall, but they do not contact each other (Fig. 4).

The male sex cells are continuously in contact with the Sertoli cells. In *Lymnaea stagnalis* the Sertoli cells are in contact with the basal lamina only at those places where no female cells are present. However, they keep always contact with each other, thus forming an epithelial layer of male nurse cells. This layer divides the lumen of the acinus in a male and a female compartment (Figs. 4 and 5).

As the new Sertoli cells arise from the germinal epithelial ring, the cells with later stages of the male sex cells are always more distally located in the epithelium (Fig. 4).

### SPERMATION

MERTON (1924, 1926, 1930) suggested that in gastropods the sperm cells become motile and lose their contact with the Sertoli cells after the passage of cytoplasmic globules originating from the Sertoli cells ("Kinoplasma-kugeln") along the tails of the spermatids. However, BARTH & JANSEN (1960) described the reverse in *Australorbis glabratus*: the cytoplasmic globules in the Sertoli cells represent the remainders of the cytoplasm of the spermatids.

Similar phenomena were observed in sections of the ovotestis of *Lymnaea stagnalis*. At the end of the spermiogenesis, spermiation begins with the enlargement of the Sertoli cells. The heads of the spermia get scattered. Each sperm head is connected with a cytoplasmic globule. These globules are absorbed by the Sertoli cells and the sperm cells start their free life (Figs. 7 and 8).

### THE ROLE OF THE SERTOLI CELLS AFTER SPERMATION

ARCHIE (1941) described in the ovotestis of *Lymnaea stagnalis* cells filled with cytoplasmic globules which she called gland cells. She attributed to them a secretory function. Apparently these cells are Sertoli cells just after spermiation, the globules representing the cytoplasmic remainders of the spermatids (Fig. 8). Gradually the cytoplasmic globules are replaced by a group of small and dense granules (Figs. 9 and 10). These granules become situated in a bulbshaped cytoplasmic stalk of the Sertoli cell which extends into the lumen of the acinus. From a preliminary electron microscope study the granules appeared to have a lysosomal structure. In light microscope sections the presence of vacuoles containing different kinds of material in the cytoplasmic stalk was established. Thus, probably the Sertoli cells in this phase get a specialized phagocytotic function.

The spermiated Sertoli cells do not die, but keep their position in the epithelium (Fig. 5). The survival of the Sertoli cells is easily demonstrated in the old snails fixed during winter, in which a great number of Sertoli cells covers the "bottom" of the acini.

### THE VITELLOGENETIC AREA AND THE SPERMATOGENETIC ZONE

In literature (e.g., ARCHIE, 1941; AUBRY, 1962; BARTH & JANSEN, 1962) it is generally accepted that in pulmonates the sex cells in order to ripen, move to the "bottom" of the acinus. Since it appeared from our model that the acini have a highly

irregular shape, it seemed worthwhile to investigate in more detail the location and arrangement of the developing sex cells in the acini of *Lymnaea stagnalis*.

To this end the position of those oocytes having a size above  $90\mu$ , was indicated on the surface of the plastic reconstruction of the ovotestis (Fig. 1). These oocytes represent the greater part of the yolk-containing oocytes. Remarkably, the oocytes appeared to be located only on those parts of the wall of the acini which are apposed to the lobes of the digestive gland. They were completely absent on parts of the acini which border other acini or the columella.

Furthermore, on the model of the single acinus the location of the (sessile) female cells, the male cells and the germinal epithelium were indicated in detail (Figs. 2 and 3). Again from this model it became apparent that the position of the sessile oocytes is restricted to those parts of the acinus wall apposed to the digestive gland. Moreover, it appeared that this region is not occupied by oogonia or male sex cells. Therefore it is proposed to call this area the vitellogenetic area.

The male sex cells appeared to be present in a spermatogenetic zone which surrounds the area of the sessile oocytes (Figs. 2, 3 and 4). In contrast to the vitellogenetic area the spermatogenetic zone has a rather constant width ( $+ 220\mu$ ). In cross sections it is usually represented by 5 Sertoli cells: 3 with spermatogonia or spermatocytes, and 2 with spermatids. Spermiation occurs at the border of the vitellogenetic area. The spermatogenetic area is bordered by the germinal epithelial ring.

From these results the following hypothesis is put forward. The arrangement of the sex cells in an acinus of *Lymnaea stagnalis* is determined primarily by the digestive gland. The size of the surface area of an acinus which is apposed to the lobes of the digestive gland determines the shape and size of the vitellogenetic area. The mode of action of the digestive gland in this respect is unknown, but a nutritive role seems plausible.

The location of the spermatogenetic zone is determined by the vitellogenetic area, as it follows closely the outline of this area.

The spermatogenetic zone in its turn determines the outline of the germinal epithelial ring. The remaining part of the acinus wall consists of inactive germinal epithelium.

FIG. 5. Section through an acinus, in which the epithelial layer of Sertoli cells after spermiation is cut. Moreover the vitellogenetic area apposed to the digestive gland can be seen. cs: cytoplasmic stalks of Sertoli cells after spermiation; dg: digestive gland; f: follicle cell; oc: oocyte; og: oogonium. (x180)

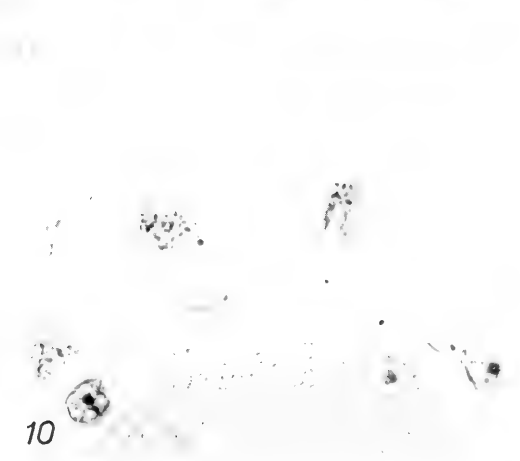
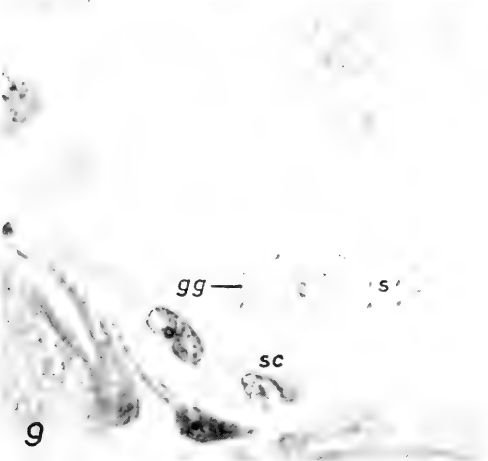
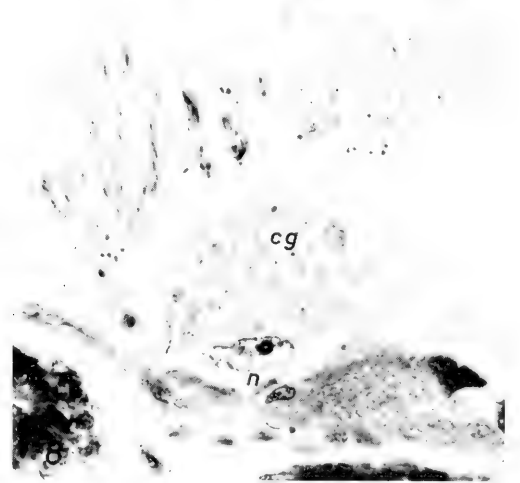
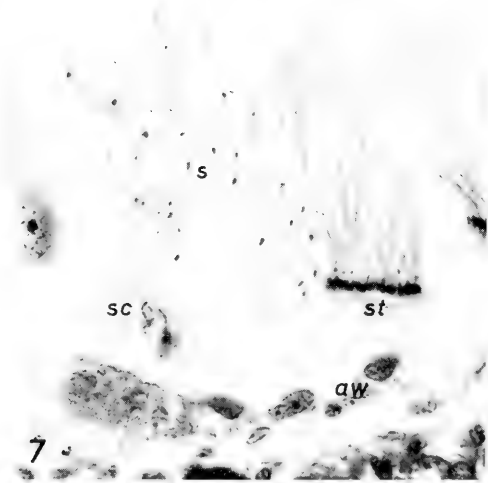
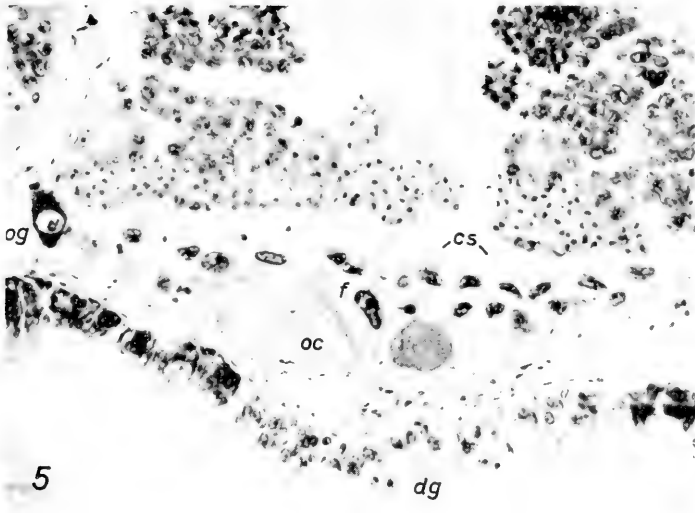
FIG. 6. Cross section through the germinal epithelial ring. ge: germinal epithelium; ger: germinal epithelial ring. (x420)

FIG. 7. Section through a Sertoli cell with spermatids, and a spermiating Sertoli cell. aw: acinus wall; s: spermia with cytoplasmic globules; sc: spermiating Sertoli cell; st: Sertoli cell with spermatids. (x480)

FIG. 8. Sertoli cell just after spermiation. The cytoplasm is filled up with a great number of cytoplasmic globules ("Kinoplasmakugeln"). cg: cytoplasmic globules; n: nucleus of Sertoli cell. (x480)

FIG. 9. Section through a group of spermiating sperm cells, and a Sertoli cell after spermiation, in which a group of granules can be seen, situated in a long cytoplasmic stalk. gg: group of granules; s: spermiating sperm cells; sc: Sertoli cell after spermiation. (x480)

FIG. 10. Section through an oocyte covered by the epithelial layer of Sertoli cells. Three cytoplasmic stalks each with a group of granules, and one nucleus of a Sertoli cell can be seen. (x480)



On the basis of this hypotheses it is evident that the oogonia have to move from their site of origin to an area of the acinus wall which is apposed to the digestive gland.

In many species of pulmonates the gonad is surrounded by the digestive gland. To support the hypothesis of the relation between gonad and digestive gland, further studies are needed to demonstrate the location of the vitellogenetic areas in other pulmonates. In planorbid snails the ovotestis is located caudally to the digestive gland. Nevertheless these species have clear vitellogenetic areas (BARTH & JANSEN, 1962). Perhaps here a favoured blood supply of these areas is the primary factor.

#### ACKNOWLEDGEMENTS

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#### LITERATURE CITED

- ARCHIE, V. E., 1941, The histology and developmental history of the ovotestis of *Lymnaea stagnalis lillianae*. Thesis Univ. Wisconsin.
- AUBRY, R., 1962, Étude de l'hermaphrodisme et de l'action pharmacodynamique des hormones de Vertébrés chez les Gastéropodes Pulmonés. *Archs. Anat. microsc. Morph. Exp.* (Suppl.) 50: 521-602.
- BARTH, R. & JANSEN, G., 1960, Ueber den Begriff "Kinoplasma" in der Spermio-genese von *Australorbis glabratus olivaceus* (Mollusca, Pulmonata, Planorbidae). *Mem. Inst. Oswaldo Cruz*, 58: 209-228.
- BARTH, R. & JANSEN, G., 1962, Beobachtungen über die Entwicklung und Ernährung der Eizellen von *Australorbis glabratus olivaceus* (Gastropoda, Pulmonata, Planorbidae). *Ann. Acad. Brasil. Ciencias*, 34: 381-389.
- BRETSCHNEIDER, L. H., 1948, Insemination in *Limnaea stagnalis*. *Proc. K. ned. Akad. Wet.* (C), 51: 358-362.
- BRETSCHNEIDER, L. H., 1948b, The mechanism of oviposition in *Limnaea stagnalis*. *Proc. K. ned. Akad. Wet.* (C) 51: 616-626.
- BRETSCHNEIDER, L. H. & RAVEN, C. P., 1951, Structural and topochemical changes in the egg cells of *Limnaea stagnalis* L. during oogenesis. *Archs. néerl. Zool.*, 10: 1-31.
- JOOSSE, J., 1963, The dorsal bodies and neurosecretory cells of the cerebral ganglia of *Lymnaea stagnalis* L. (a preliminary note). *Gen. Comp. Endocrinol.*, 3: 709.
- JOOSSE, J., 1964, Dorsal bodies and dorsal neurosecretory cells of the cerebral ganglia of *Lymnaea stagnalis* L. *Archs. néerl. Zool.* 16: 1-103.
- JOOSSE, J., 1967, Gametogenesis and oviposition in *Lymnaea stagnalis* L. during starvation and irradiation treatments. *Gen. Comp. Endocrinol.*, 9: 511.
- JOOSSE, J., BOER, M. H. & CORNELISSE, C. J., 1968, Gametogenesis and oviposition in *Lymnaea stagnalis* as influenced by  $\gamma$ -irradiation and hunger. *Symp. zool. Soc. Lond.*, no. 22: 213-235.
- MERTON, H., 1924, Lebenduntersuchungen an den Zwitterdrüsen der Lungenschnecken. Ein Beitrag zur Plasma- und Spermienbewegung. *Z. Zellen-Gewebelehre*, 1: 671-687.
- MERTON, H., 1926, Die verschiedenartige Herkunft des Kinoplasmas der Samenzellen. Eine Parallele zur Nährstoffversorgung des wachsenden Eis. *Biol. Zbl.*, 46: 650-678.
- MERTON, H., 1930, Die Wanderungen der Geschlechtszellen in der Zwitterdrüse

von *Planorbis*. *Z. Zellforsch. Mikr. Anat.*, 10: 527-551.

PEASE, D. C., 1964, *Histological techniques for electron microscopy*, 2nd ed. New York: Academic Press.

RAVEN, C. P., 1963, The nature and origin of the cortical morphogenetic field in *Limnaea*. *Devl. Biol.*, 7: 130-143.

RECOURT, A., 1961, Electronenmicroscopisch onderzoek naar de oogenese bij *Limnaea stagnalis* L. Thesis, Utrecht.

UBBELS, G. A., 1968, A cytochemical study of oogenesis in the pond snail *Limnaea stagnalis*. Thesis, Utrecht.



## FAUNENGESCHICHTLICHE UNTERSUCHUNGEN IM KARPATENBECKEN

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Bezüglich der faunengeschichtlichen Untersuchungen eines Gebietes spielt die Molluskenfauna eine wichtige Rolle. Die kalkhaltigen Schalen der Mollusken werden leicht fossilisiert, dementsprechend kommen ihre Reste in den Sedimenten gewöhnlich in grossen Mengen allgemein verbreitet vor. Deshalb können wir den Ursprung und die Entfaltung einer Molluskenfauna eines gegebenen Gebietes nicht nur theoretisch, sondern auch auf Grund konkreter Tatsachen verfolgen. Ähnliche Möglichkeiten finden wir - soweit es Festlandfaunen anbelangt - nur noch bei Wirbeltieren.

Im Hinblick auf das Verfolgen der einzelnen Phasen der Faunengeschichte und das Entstehen der heutigen Fauna ist dem Pleistozän besonderes Gewicht beizumessen. Besondere Bedeutung für die Faunengeschichte besitzen die klimatischen Änderungen dieser Zeit, die das Faunenbild umgestalteten. Daraus folgt, dass wir die meisten Angaben in bezug auf die Ausbildung der Molluskenfauna eben aus der Untersuchung der pleistozänen Fauna erhalten werden.

Infolge seiner zentralen Lage ist Ungarn faunengeographisch ein Gebiet von ausschlaggebender Bedeutung im Karpatenbecken. Deshalb sind die faunengeschichtlichen und faunistischen Ergebnisse der Untersuchungen auch ausserhalb der Landesgrenzen gültig. Faunengeschichtliche Angaben sind überhaupt jene, die wir auf das ganze Gebiet des Beckens als gültig betrachten können wenn man die Gebiete des höheren Berglandes am Beckenrande ausser acht lässt.

Die Angaben hinsichtlich der Ausbildung und der Entfaltung unserer Molluskenfaunen hat L. Soós, der Nestor der ungarischer Malakologen zusammengefasst (Soós, 1926). In diesem Werk beschäftigte sich der Verfasser vornehmlich mit den tertiären Wurzeln unserer Fauna. Der Meinung der damaligen Monoglacialisten entsprechend hat er die älteren pleistozänen Faunen als "präglacial" bezeichnet und nur die Würm-Periode als Pleistozän registriert.

Bis zum II. Weltkrieg wurden unsere Kenntnisse hauptsächlich durch die Untersuchungen von M. Rotarides mit vielen Angaben über die pleistozäne Fauna bereichert (Rotarides, 1931, 1936). Diese Angaben beziehen sich aber überwiegend auf die Lössfauna des Würm.

Nach dem II. Weltkrieg, hauptsächlich in den Jahren nach 1950, nahmen die malakologischen Untersuchungen wieder einen Aufschwung. Die allgemeine Verbreitung der feinstratigraphischen und der Schlammungs-Methoden haben auf dem Gebiet der Paläontologie grosse Mengen auch für die quantitative Auswertung geeignetes pliozänes und pleistozänes Mollusken-Material geliefert. Dies ermöglichte eine quantitative Betrachtungsweise der Faunen-Untersuchungen. Besonders die altpleistozäne Fauna lieferte viele neue Angaben. Soós kannte nämlich nur drei "präglaziale," also Vor-Würm-Faunen. Auf Grund der vom Verfasser untersuchten altpleistozänen und jüngeren interglazialen Faunen hat sich die Zahl der aus Ungarn bekannt gewordenen pleistozänen Arten auf 32 erhöht, und erreicht gegenwärtig 171. Diese Zahl ist auch im Vergleich zu der rezenten Molluskenfauna mit 213 Arten genug hoch.

Wichtigere faunengeschichtliche Angaben über das Karpatenbecken ausserhalb Ungarns kennen wir nur aus der Südslowakei, durch die Arbeiten von V. Ložek; diese beziehen sich jedoch auf Molluskenfaunen der höheren Gebirge des Beckenrandes (Ložek, 1964b).

Selbstverständlich wäre es noch voreilig, über die Ausbildung und Entfaltung der Molluskenfauna des Karpatenbeckens eine eingehende und endgültige Zusammenfassung zu geben. Für die vorliegende Arbeit hat sich der Verfasser bloss das Zitieren teilweise noch nicht publizierter neuer Angaben der letzten 20 Jahre zum Ziel gesetzt.

Den Grundstock unserer Fauna bildet der im zweiten Teil des Tertiärs in ganz Zentral-Europa verbreitete südliche Faunen-Typus, in dem schon einige der heutigen Arten auftreten. In dieser Beziehung ist das Karpatenbecken ein recht ungünstiges Gebiet; während wir z.B. aus Deutschland die klassischen Vorkommen dieser Fauna kennen, sind bei uns marine Sedimente vorherrschend und die terrestrische Fauna fehlt beinahe ganz.

Im Pliozän war das Karpatenbecken vom brakischen Pannon-See bedeckt, aus dem nur die höheren Gebirge emporragten. Wir kennen dagegen viele Fundstellen mit Süßwasser- und Landschnecken-Fauna des Mittel-Pliozän, vom Ende des Ober-Pannon, in dem sich die Auffüllung des Pannon-Sees und dessen Aufteilung vollzog. Feinstratigraphische Untersuchungen dieser Funde durch F. Bartha vermehrten die Zahl der kleinwüchsigen Arten, die wir in unserem Lande bis zum Tertiär verfolgen können (Bartha, 1954, 1955). Derzeit kennen wir 41 solche Arten, doch wird die Zahl dieser Formen noch höher, wenn wir die vorher als ausgestorben bezeichneten, aber von den rezenten Vertretern nicht grundlegend abweichenden Arten (wie *Vertigo callosa*, *Vallonia subpulchella*) an Hand uns zur Verfügung stehenden quantitativen Materials revidieren. Ich glaube, eine Revision würde zeigen, dass viele als tertiär beschriebene Arten mit rezenten ident sein werden.

Eine merkwürdige Eigenschaft der oberpannonischen Faunen ist, dass sie relativ viele charakteristische Arten des offenen, trockenen Gebietes führten (z.B. *Abida frumentum*, *Truncatellina cylindrica*, *Vallonia costata*). Das Karpatenbecken zeigte damals einen ausgeprägteren kontinentalen Charakter als die Umgebung.

Vom oberen Abschnitt des Pliozäns haben wir recht wenig Angaben. In dem Gebiet des Flusssystemes, das sich an Stelle des Pannonischen Sees bildete, kommen aus Tiefbohrungen einige ornamentierte *Unio*-Funde, *Viviparus*- und *Valvata*-Gehäuse vor, die mit den levantinen Arten von Slawonien Verwandtschaft zeigen. Neben ihnen finden wir auch Arten, die noch heute leben. Die Landschnecken-Fauna ist noch kaum bekannt, am interessantesten ist eine noch nicht genau bestimmte *Cochlostoma*.

Sehr wenige Angaben stehen uns vom Anfang des Pleistozäns zur Verfügung. In der fluviatilen Fauna des Günz tritt der aus den Tiefbohrungen der Grossen Tiefebene bekannte und im Mittleren Pleistozän ausgestorbene *Viviparus böckhi* zuerst auf. Die Süßwasser-Fauna zeigt ausser dem erwähnten endemischen *Viviparus*, sowie *Hydrobia longaeva*, *Corbicula fluminalis*, modernes Gepräge. Unter den Landschnecken finden wir wieder Steppen-Arten; hier erscheint auch die Art *Helicella hungarica*. Die taxonomischen Beziehungen dieser bei uns auch jetzt lebenden Art zu *H. striata* müssen noch geklärt werden.

Die nächste Periode ist der Zeitabschnitt, dessen Molluskenfauna uns infolge meiner Untersuchungen der letzten Jahre ausreichend bekannt ist. Im Gebiet der Hauptbruchlinie längs der Donau und hauptsächlich in der Umgebung von Budapest brechen laue und heisse Quellen auf. Einige von diesen waren schon während des Pleistozäns tätig, was zur Bildung umfangreicher Travertin- und Kalkschlamm-Lager geführt hat. Es war an vielen Fundstellen in den Kalkschlammschichten möglich, denen früher keine besondere Aufmerksamkeit gewidmet wurde, eine reiche Wirbeltier- und Molluskenfauna zu sammeln. Die paläontologischen Angaben beweisen, dass sich diese Sedimente grösstenteils im Günz-Mindel-Interglazial und Mindel-Glazial abgelagert haben. Aus dieser Zeitspanne konnten wir im ganzen 90 Arten nachweisen (Krolopp, 1961).

Nachdem es sich um Sedimente handelt die in Thermen abgelagert wurden, besteht



die Wasserschnecken-Fauna infolge des speziellen Milieus meistens aus thermophilen Formen, die von den Stammformen einigermaßen verschiedene und dem Warmwasser angepasste Formen der Kaltwasser-Arten darstellen. Man kann als solche folgende erwähnen: *Theodoxus prevostianus*, *Fagotia acicularis audebartii*, *Bithynia tentaculata thermalis*. Dazu kommen noch einige eurytherme Arten. Ein merkwürdiges Vorkommen stellt *Melania tuberculata* dar, die heute in der Umgebung des Mittelmeeres lebt.

Die Landschnecken-Fauna des Zeitabschnittes kennen wir schon besser. Im Günz-Mindel-Interglazial zeigt sich ein interessanter Gegensatz. Zum Teil besteht die Fauna aus Arten, die auch heute noch in dieser Umgebung leben. Andererseits kommen einige schon ausgestorbene Arten vor. Diese sind: *Gastrocopta serotina* und *Zonitoides sepultus*. Ložek betrachtet die beiden Arten als Leitfossilien des mitteleuropäischen Altpleistozäns, die mit jüngeren Faunen nicht näher verbunden sind (Ložek, 1964a).

Die Interglazial-Fauna wurde unter dem Einfluss der Mindel-Vereisung von einer bedeutend abweichenden Fauna abgelöst. Unseren heutigen Kenntnissen gemäss erschienen im Gebiet des ungarischen Mittelgebirges zur selber Zeit zum erstenmal diejenigen alpinen, alpin-karpatischen und nördlichen Arten, die heutzutage hier nicht mehr leben oder nur als Relikte vorkommen, dagegen charakteristische Arten der jüngeren pleistozänen Lössfaunen waren. Folgende Arten können wir als solche erwähnen: *Vallonia tenuilabris*, *Clausilia cruciata*, *Perforatella bidentata*, *Trichia striolata*. Im Mindel-Interstadial kehrt die Fauna des Günz-Mindel-Interglacials wieder zurück, aber ohne die erwähnten ausgestorbenen Arten.

Die quantitative Auswertung feinstratigraphischer Methoden an den gesammelten Probenserien beweist, dass sich inzwischen nicht nur das Faunabild, sondern auch die Dominanz-Werte der Arten veränderten. Zum Nachweis der kleineren klimatischen Oszillationen - wo sich die Artzusammensetzung nicht oder wenigstens nicht wesentlich ändert - wird die Änderung der Dominanz-Werte angewendet.

Zur Demonstration dieser Methode führe ich diejenigen Diagramme vor, welche die Änderungen der Dominanz-Werte der wichtigeren Faunenglieder der aus einem 2,5 m mächtigen Kalkschlammkomplex stammenden Probenserie (Fundstelle am Péterhegy) zeigen (Abb. 1). Die Dominanzkurven einiger Arten - ihren abweichenden ökologischen Ansprüchen entsprechend - ändern sich entgegengesetzt, bei anderen Arten zeigen sie identischen Ablauf, bei wieder anderen sind komplizierte Zusammenhänge zu vermerken.

Die erwähnten Beobachtungen, sowie die quantitativen Untersuchungen von M. Kretzoi an pleistozänen Kleinsäuger-Faunen (Kretzoi, 1956) haben mich dazu veranlasst, bei der ökologischen Gruppierung eine andere, von derjenigen meiner Kollegen abweichende Methode zu verwenden.

Es muss angenommen werden, dass bei den altpleistozänen Arten die Möglichkeit einer Änderung der ökologischen Anforderungen im Laufe der Zeit nicht ausgeschlossen werden kann. Zum Beispiel sei hier *Pupilla muscorum* erwähnt, die im Günz-Mindel-Interglazial nicht vorkam oder bei einer Dominanz unter 4% blieb, im kühleren Mindel<sub>1</sub> aber auf über 13% anstieg. In den Würm-altrigen Löss-Schichten dagegen ist es gerade umgekehrt: im Fall hoher Dominanz von Arten, die ein feuchtkaltes Klima beweisen (im Glazial) tritt die Form in kleiner Individuenzahl auf, steigt aber auch mit der steigenden Dominanz der auf ein milderes Klima verweisenden Arten (in einem Fall 29,7%, beziehungsweise 59,8%) (Krolopp, 1966). Eine andere Art, *Vertigo pygmaea*, meldet sich im Mindel mit kälteindizierenden Formen an, im Würm aber in milderen Zeitabschnitten.

Ein weiterer Gesichtspunkt ist der, dass die Ökologie einiger heute seltener, im Pleistozän dagegen häufiger Arten sehr oft nicht genügend bekannt ist. In einigen Fällen ist die Frage berechtigt, ob die auf Grund von Schalen oder Schalenresten identifizierten Schneckenfunde tatsächlich mit den heute lebenden Arten ident sind

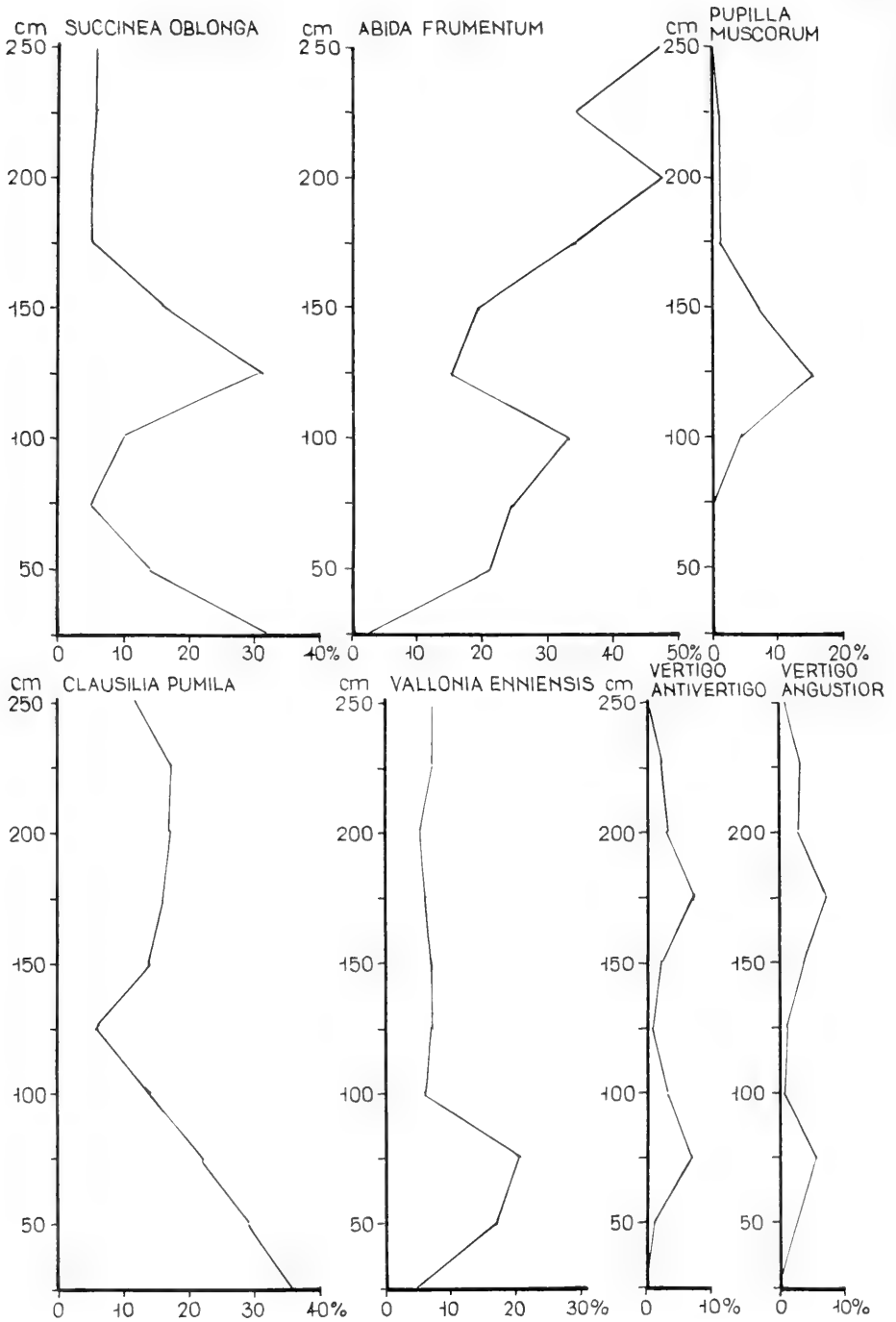


ABB. 1. Die Änderungen der Dominanz-Werte der wichtigeren Faunenglieder auf dem Profil am Péterhegy.

oder nicht. Endlich muss gelegentlich mit einem solchen Zusammenspiel der ökologischen Faktoren gerechnet werden, die eine Zusammensetzung der Fauna verursachen, die in unserem gegebenen Gebiet ja sogar überhaupt nicht vertreten ist (zum Beispiel die mitteleuropäischen Lössfaunen).

Deshalb hat der Verfasser bei der ökologischen Gruppierung der Arten die Dominanzkurven stets berücksichtigt, beziehungsweise zur Grundlage erhoben. Es muss nämlich als selbstverständlich angenommen werden, dass Arten, die an Hand vieler Profile konsequent parallel verlaufende Dominanz-Kurven aufweisen, wohl auch auf äussere Faktoren auf gleiche Weise antworteten, demnach also auch dieselben oder wenigstens ähnliche ökologische Ansprüche stellen. Nachdem aber unter den Umweltfaktoren eben die Änderungen des Mikroklimas die bedeutendsten sind, welche letztere in Widerspiegelung der Änderungen in der Pflanzendecke auf das Makroklima umgedeutet werden können, ist den einzelnen Kurventypen eine klimaandeutende Rolle anzuerkennen. Natürlich ist es kein Zufall, dass wir die Mehrzahl der an Hand parallelen Ablaufes ihrer Klimakurve als zusammengehörig gefundene Arten auch bis jetzt für solche gleicher oder wenigstens ähnlicher Ökologie halten dürfen. Dabei kann der ökologische Charakter diesbezüglich mangelhaft bekannter, beziehungsweise nur als fossil bekannter Arten auf Grund ihrer Dominanz-Kurve in eine entsprechende Gruppe eingeteilt und zufolge ihre ökologischen Eigenschaften ermittelt werden. In bezug auf die bereits erwähnte *Gastrocopta serotina* ist soviel schon jetzt festzustellen, dass sie eine wärmeliebende, trockenheitvertragende Art gewesen sein musste; sie kommt in grösserer Zahl dort vor, wo die Dominanz xerothermer Elemente auffallend hoch ist (in einem Beispiel 78%) (Krolopp, 1961).

Auf Grund obiger Überlegungen kann die Landschnecken-Fauna in folgende 6 - durch Dominanz-Kurve bestätigte - ökologische Typen aufgeteilt werden:

1. Wärmeliebende, trockenheitduldende (xerotherme) Arten (z.B. *Abida frumentum*, *Truncatellina claustralis*, *T. cylindrica*, *Helicella hungarica*).

2. Wärmeliebende, feuchtigkeitsbedürftige Arten (z.B. *Vertigo moulinsiana*, *V. antivertigo*, *Vallonia enniensis*).

3. Feuchtigkeitsbedürftige Arten (z.B. *Carychium minimum*, *Zonitidae*, *Limacidae*).

4. Feuchtigkeitsbedürftige, kälteduldende Arten (z.B. *Succinea oblonga*, *Nesovitrea hammonis*, *Perforatella bidentata*).

5. Trockenheit- und kälteduldende Arten (z.B. *Pupilla muscorum*, *P. sterri*, *Vallonia tenuilabris*, *V. costata*).

6. Weitere, in keiner obigen Gruppen unterbrachte Arten (z.B. fossile Arten, *Acanthinula aculeata*).

Wenn wir die Prozentzahl der einzelnen Gruppen durch Raumdiagramme wiedergeben, erhalten wir vom obenerwähnten Profil der Fundstelle am Péterhegy folgendes Bild (Abb. 2).

Es ist klar zu entnehmen, dass in der Mitte und am Ende der Schichtenfolge eine beträchtliche Klima-Verschlechterung angedeutet ist. An Hand wirbeltierpaläontologischer Beweise vertritt das Profil die Zeitspanne, die aus dem Günz-Mindel-Interglazial ins Mindel-Glazial überführte.

Die vorgeführte Methode ist geeignet, die Schichtenfolge, bzw. Einzelschichten an Hand quantitativ-faunistischer Untersuchungen zu vergleichen, identifizieren und so auch chronologisch einzustufen. Es ist mir gelungen, die Kalkschlamm-Schichten der Lokalitäten aus der Umgebung von Budapest folgenderweise zu chronologisieren (Abb. 3).

Die drei ersten Kolonnen geben Faunen eines Günz-Mindel-Alters wieder. Die 4. und 5. zeigen Übergangsfauen, während die 6. und 7. zwei verschiedene Mindel-Faunen vertreten. Die zwei letzten Kolonnen illustrieren die Fauna der zwei oberen Schichten des letzten Fundortes, die eine zwischen-Mindel-altrige Klima-

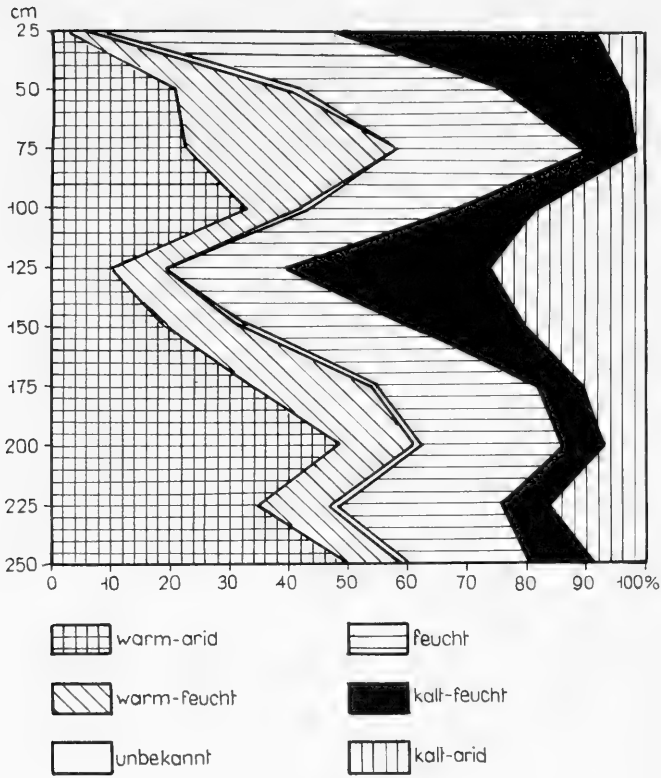


ABB. 2. Die Änderungen der Prozentzahl der ökologischen Gruppen im Profil am Péterhegy.

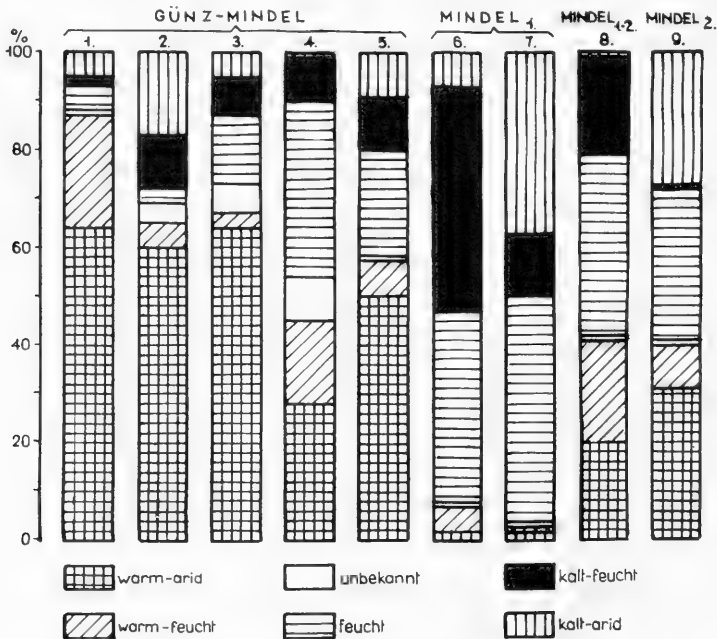


ABB. 3. Ökologisches Bild der Molluskenfaunen in Kalkschlammsschichten der Budapester Lokalitäten.

Verbesserung (wohl das Mindel<sub>1-2</sub> Interstadial), bzw. die darauffolgende Klimaverschlechterung (Mindel<sub>2</sub> Glazial?) andeuten. Das geologische Alter dieser Fundstelle ist auch durch wirbeltierpaläontologische Belege bewiesen (Jánossy, 1962).

Aus der Zeitspanne zwischen Mindel-Riss-Interglazial und Riss-Würm-Interglazial stehen uns sehr wenig Belege zur Verfügung, allein aus dem nördlichen Teil des ungarischen Mittelgebirges, aus dem Bükk-Gebirge, sind in letzter Zeit einige Faunen bekannt geworden. Von hier und aus diesem Zeitabschnitt sind folgende für unser Pleistozän neue Arten zum Vorschein gekommen: *Acicula polita*, *Oxychilus depressus*, *Vitrina bielzi*, *Phenacolimax annularis* (Krolopp, 1969).

Das letzte Interglazial (Riss-Würm) ist durch eine für ganz Mitteleuropa bezeichnende Fauna, die "Banatica-Fauna," gekennzeichnet. Diese Fauna ist auch von unserem Gebiet bekannt, mit den Charakterformen *Pomatias elegans*, *Mastus bielzi*, *Aegopis verticillus*, *Soósia diodonta* und einer endemischen Süßwasserform, *Belgrandia tataënsis* (Krolopp, 1964a). Die wohl schon im Pleistozän ausgeprägte Kontinentalität unseres Beckens trägt dafür wahrscheinlich die Schuld, dass eben die namengebende Art der Fauna, *Helicigona banatica*, allein aus dem nördlichsten Glied des Mittelgebirges, aus der Riss-Würm-Fauna des Bükk-Gebirges, nachzuweisen war und zwar in Begleitung anderer, nur hier angetroffener montaner Formen (z.B. *Isognomostoma isognomostoma*, *Perforatella dibothryon*) (Krolopp, 1964b).

Aus dem Zeitabschnitt nach dem Riss-Würm-Klimaoptimum und aus dem Frühwürm kennen wir Faunen mit Übergangscharakter, in denen die Formen, die ein wärmeres, niederschlagreicheres Klima beanspruchen (z.B. *Carychium minimum*, *Vertigo anti-vertigo*, *Vallonia enniensis*, *Clausilia pumila*) noch vorkommen (Krolopp, 1965). Diese Formen verschwinden wohl mit dem Kältemaximum des Würm<sub>3</sub> und erscheinen erst im Postglazial wieder. In milderen Abschnitten des Würm - wohl wieder dem mehr kontinentalen Charakter des Karpatenbeckens entsprechend - zeigen xerotherme Arten das wärmere Klima an (z.B. *Abida frumentum*, *Chondrula tridens*, *Helicella hungarica*).

Obwohl wir in bezug auf die ungarische Lössfauna über sehr viele alte Angaben verfügen, sind in letzter Zeit doch einige für das ungarische Pleistozän neue Arten aus unserem Löss bekannt geworden: *Catinella arenaria*, *Vertigo pseudosubstriata*, *Semilimax kotulae*.

Feinstratigraphische Schlamm-Aufsammlungen wurden nur in den letzten Jahren durchgeführt. Für grössere Gebiete gültige Feststellungen konnten aber nur in bezug auf Süd-Transdanubien getroffen werden. Hier ist der jüngere, würmaltrige Löss durch zwei Boden-Niveaus dreigeteilt. Für den unteren Löss sind bei einer *Succinea oblonga*-Dominanz Formen weiter ökologischer Valenz bezeichnend (z.B. *Pupilla muscorum*, *Vallonia costata*, *Trichia hispida*). Die mittleren Löss-Schichten führen eine Fauna, die wärmeres, trockeneres Klima andeutet (z.B. *Pupilla triplicata*, *Helicella hungarica*, *Vallonia costata*). *Succinea oblonga* fehlt hier. In oberen Lösslagen ist wieder *Succinea oblonga* vorherrschend, neben ihr sind *Pupilla sterri*, *Columella columella*, *Vallonia tenuilabris* die charakteristischen Formen (Krolopp, 1966).

Aus dem Postglazial stehen uns nur sehr wenig Angaben zur Verfügung. Das stufenweise Verschwinden einiger am Ende des Pleistozäns noch häufigen Formen können wir zwar nachprüfen, wie z.B. bei *Valvata pulchella*, wohl aber nicht solche Entwicklungsphasen der Fauna, die Ložek in der karpatischen Fauna Südslowakiens nachweisen konnte (Ložek, 1964b). Die Ursache dieser Umstände ist einerseits im Mangel entsprechenden Datenmaterials, andererseits aber in der bereits erwähnten Kontinentalität des Beckenlandes zu suchen. Eine richtige Montanfauna hat sich im ungarischen Mittelgebirge nicht ausgebildet - die holozänen Klimaänderungen haben bloss Dominanzschwankungen verursacht.

Endlich sei hier ein Beispiel zur Darstellung der Beziehungen zwischen Faunengeschichte und Tiergeographie vorgelegt. Das Nordglied unseres Mittelgebirges,

das in seiner Hauptmasse um 800 m hohe Bükk-Gebirge, wird seitens unserer Zoologen auf Grund der vielen karpatischen Elemente meist zum Karpathicum gerechnet. Meine Untersuchungen haben nachweisen können, dass das Bükk-Gebirge schon vom Mittleren Pleistozän an eine eigenartige Mollusken-Fauna führte, die sich derjenigen der Karpaten anschloss, wonach eben die paläontologische Dokumentation die Berechtigung obiger Annahme gut unterstützen - ja beweisen - konnte.

## LITERATUR

- BARTHA, F., 1954, Die pliozäne Molluskenfauna von Öcs. *M. Áll. Földt. Int. Évk.*, 42(3): 167-205.
- BARTHA, F., 1955, Untersuchungen zur Biostratigraphie der pliozänen Molluskenfauna von Várpalota. *M. Áll. Földt. Int. Évk.*, 43(2): 275-359.
- JÁNOSSY, D., 1962, Der erste Nachweis von *Hippopotamus antiquus* Desmarest, 1822 im ungarischen Altpleistozän (Budapest). *Állattani Közl.*, 49(1-4): 63-74.
- KRETZOI, M., 1956, Die altpleistozänen Wirbeltierfaunen des Villányer Gebirges. *Geologica Hung. Ser. Pal.*, 27: 125-256.
- KROLOPP, E., 1961, Die zoogeographische und ökologische Untersuchung der Molluskenfauna des altpleistozänen Kalkschlammes der Umgebung von Buda. (Dissertation). p 1-141. (Maschinenschrift, ungarisch).
- KROLOPP, E., 1964a, Die Molluskenfauna. In: Vértes, etc.: Tata, eine mittelpaläolithische Travertin-Siedlung in Ungarn. *Arch. Hung.*, 43: 87-103.
- KROLOPP, E., 1964b, Das erste pleistozäne Vorkommen von *Helicigona banatica* Rm. (Gastropoda) in Ungarn und dessen zoogeographische Bedeutung. *Ann. Hist.-Nat. Mus. Nat. Hung.*, 56: 185-188.
- KROLOPP, E., 1965, Biostratigraphische Untersuchung der Pleistozänbildungen des Dörög-Esztergomer Beckens. *M. Áll. Földt. Int. Évi Jel.* 1963 évről, p 133-147.
- KROLOPP, E., 1966, Biostratigraphische Untersuchung der Lössbildungen in der Umgebung des Mecsekgebirges. *M. Áll. Földt. Int. Évi Jel.* 1964 évről, p 173-191.
- KROLOPP, E., 1969, Die Molluskenfauna der Felsnische bei Uppony. Eiszeitalt. u. Gegenw., 19: 37-41.
- LOŽEK, V., 1964a, Neue Mollusken aus dem Altpleistozän Mitteleuropas. *Arch. Molluskenk.* 93(5-6).
- LOŽEK, V., 1964b, Quartärmollusken der Tschechoslowakei. *Rozp. U.u.g.*, 31: 1-374.
- ROTARIDES, M., 1931, Die Schneckenfauna des ungarischen Lösses und die ungarische rezente Schneckenfauna, mit besonderer Berücksichtigung der Lösses von Szeged. *A Szegedi Alföldkut. Biz. Könyvt.* 6(A/8): 1-180.
- ROTARIDES, M., 1936, Untersuchungen über die Molluskenfauna der ungarischen Lössablagerungen. *Festschr. Embrik Strand*, 2: 1-52.
- SOÓS, L., 1926, The Past of the Hungarian Mollusc Fauna. *Ann. Mus. Nat. Hung.*, 24: 392-421.

## AUSZUG

Infolge ihrer guten Fossilisationsfähigkeit und der im allgemeinen massenhaften und ziemlich gleichmässigen Verbreitung in den geologischen Formationen kommt den Mollusken bei den faunengeschichtlichen Untersuchungen eine sehr wichtige Rolle zu.

Die Angaben über Entfaltung der bereits lebenden Molluskenfauna des Karpatenbeckens sind 1926 durch L. Soós zusammengefasst worden. Seit dieser Zeit sind sehr viele paläontologische Daten zusammengebracht worden, die einerseits das Erscheinen einiger Gattungen bzw. Arten klären oder in ein anderes Licht setzen, andererseits aber über die Molluskenfauna mehrerer geologischer Zeitabschnitte ein besseres

Gesamtbild abgeben. Die nach Einführung der Schlämm-Methode durchgeführten Massenuntersuchungen ergaben vor allem eine Vermehrung der kleinen Formen. So wuchs besonders die Zahl derjenigen Arten an, die bereits im Pliozän dem Karpatenbecken angehört haben. Dabei sind 32 (etwa 20%) der um 170 Arten zählenden pleistozänen Molluskenfauna des Karpatenbeckens im Laufe der letzten 25 Jahre bekannt geworden.

An Hand der Bearbeitung der quantitativen Verhältnisse der fossilen Faunen gelang es nicht nur in bezug auf das Faunenbild der einzelnen Abschnitte des Pleistozäns, sondern auch über das zahlenmässige Verhältnis der einzelnen Arten zueinander grundlegende Angaben zu gewinnen. Eine Änderung in diesen Verhältniszahlen gibt uns eine neue Möglichkeit biostratigraphischer Feingliederung.





SUBSTRATE RELATIONS IN SOME *PISIDIUM* SPECIES  
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The species of the sphaeriid genus *Pisidium* are mostly mud dwelling clams living in freshwaters in all parts of the world. In temperate zones, waters are generally inhabited by several species of the genus. For example, in Lake Titisee in High Black Forest (Germany), one sample taken with an Ekman-Birge-grab may consist of up to 7 *Pisidium* species. This joint occurrence is in contrast to our experiences on snail genera, and it seems to be not in accordance with "Gause's principle." A view upon the different surfaces of the shells, however, appear to reflect differences in ecological enrichment. A dense growth of blue-green algae commonly occurring on the shells of *Pisidium hibernicum* Wstl. in Lake Titisee led me to study the more abundant species of that lake with regard to their substrate relations.

Certain grain size preferences which mean horizontal substrate relations could be found in the following experiments. Two fractions of muddy original Titisee sediment, free of minerals, one of which having grain sizes of more than 0.8 mm, the other of less than 0.5 mm, were put side by side in a Petri dish as shown in Fig. 1. The layer was about 1 cm thick and was covered with lake water. In each experiment 50 to 86 (average 60) individuals of 3 species were alternately arranged on the limit between the 2 fractions. Ten experiments using day light and exposure times of 75 hours on the average yielded grain size preferences as follows (Fig. 2). *Pisidium lilljeborgii* Cl. clearly preferred ( $67 \pm 14\%$ ) the fine-grained fraction, whereas *P. hibernicum* ( $40 \pm 15\%$ ) and, particularly, *P. nitidum* Jen. ( $31 \pm 13\%$ ) tended to avoid it and to migrate into the coarse sediment. The interspecific differences in behaviour were statistically significant on the 0.1%-level (Chi-square method). These findings are in agreement with own observations on the distribution of the 3 species in Lake Titisee. Down to a depth of 2 m the bottom is formed by gravel, here and there having troughs which are filled up with fine detritus. From 2 to 4 m there is a zone of dense vegetation formed by *Isoetes lacustris*, *Litovella uniflora*, *Myriophyllum* sp., and *Nitella* sp. This belt is catching coarse materials such as leaves, small branches, pine cones, wood debris, etc. Below it the sediment again consists of fine mud. In the coarse sediment of the *Isoetes*-zone, *P. hibernicum* constitutes the by far greatest part of the *Pisidium*-fauna, whilst in the fine grained sediment both above and below this vegetation zone, *P. lilljeborgii* is the predominant species. *P. nitidum* has its greatest abundance in the *Isoetes*-zone too; below it, however, its abundance so rapidly decreases that I believe it is on other than substrate reasons.

Besides the horizontal substrate relations, there was some evidence of vertical substrate relations. As was obvious from the green colour of *Pisidium hibernicum*, this species must exert an at least temporary epipelagic mode of life, otherwise photosynthesis of the blue-green algae would not be guaranteed. In the laboratory, too, *P. hibernicum* would prefer to creep upon the mud surface rather more than other

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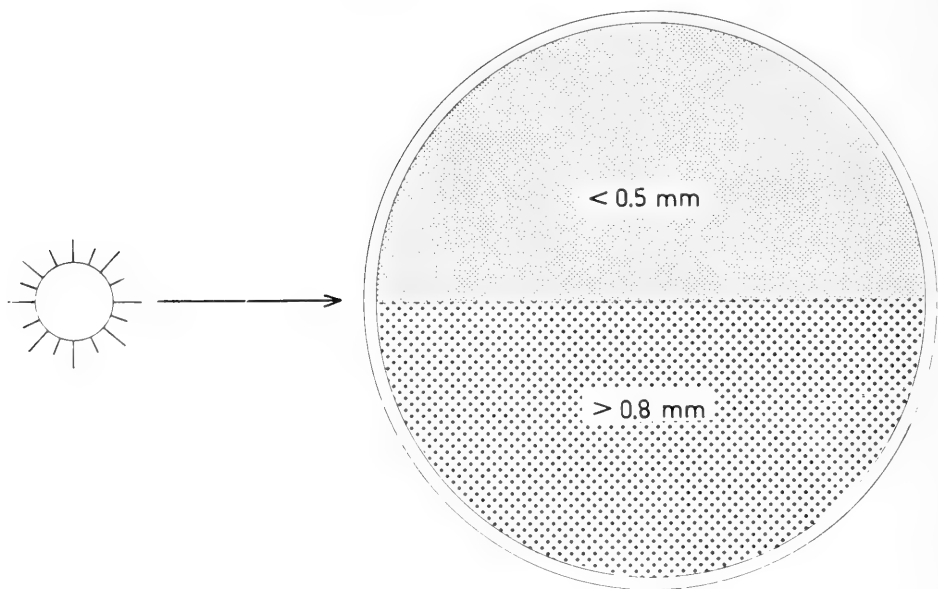


FIG. 1. Petri dish used for substrate choice experiments. The arrow indicates that light fell in the direction of the limit between the sediment fractions. For further details see text.

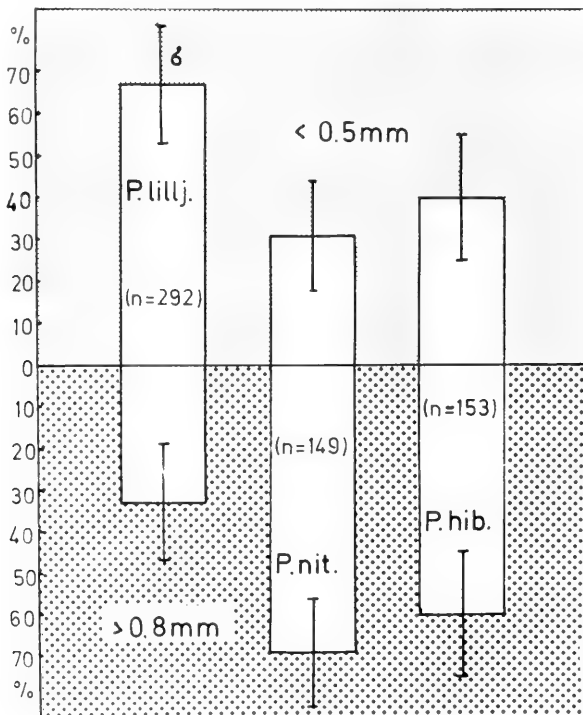


FIG. 2. Horizontal substrate relations in *Pisidium lilljeborgii*, *P. nitidum*, and *P. hibernicum* from Lake Titisee. The figure shows the percentages of individuals preferring sediment fractions of different grain sizes after experiments in Petri dishes as shown in Fig. 1.

species do. Bright sunshine, of course, induced even *P. hibernicum* to burrow totally into the sediment. The differences in behaviour between *P. hibernicum* and the other pisidia could merely be due to gradual differences in phototactic or light induced positive geotactic reaction. A series of 10 experiments showed that this at least cannot be the only explanation.

A mixed community of specimens of 3 or 4 species was put on mud in Petri dishes and covered with a second mud layer approximately 1 cm in height. One dish was exposed to diffuse daylight, while the other one was kept in total darkness just beside it. Every midday and evening at the following days, all individuals visible from the surface were collected and identified. After each reading the animals were put back below the sediment surface. In the first 6 experiments a total of 134 individuals of *Pisidium lilljeborgii*, *P. nitidum* and *P. hibernicum* were used. The other 4 experiments were done with 160 individuals of 4 species including the profundal species, *P. conventus* Cl. The percentages of animals which have left the interior of the sediment at the reading times are given in Fig. 3, which combines the results of both series of experiments. As expected, the proportion of individuals exhibiting an epipellic mode of life was much greater in darkness than in light. Nevertheless, the differences between *P. hibernicum* and the other species examined were still existent, being statistically significant on the 0.1%- resp. on the 1%-level in the 2 series. The cause of the interspecific differences is not yet known; the only statement which can be derived from the light experiments and from occasional observations is that *P. hibernicum* is induced to enter below the sediment surface at higher light intensities than the other species.

Summarizing the results referred to above, the substrate relations of the 3 species common in the litoral zone of Lake Titisee can be described as follows: *Pisidium lilljeborgii* prefers an endopellic mode of life in fine grained organic sediment. *P. nitidum* is strongly restricted to biotopes below the sediment surface, too, but prefers coarse organic sediment with large-pored interstitial spaces which enable the animal to provide itself with water sufficiently rich in oxygen. *P. hibernicum* frequently would creep on the sediment surface, preferring coarse organic substrate which prevents the animals from sinking in.

It has to be regarded that the behaviour patterns demonstrated here are not necessarily representative of all species named. But at least *Pisidium hibernicum* seems to prefer an epipellic mode of life elsewhere, too, as the shells may bear green or blue-green algae also in other lakes.

Finally, I may be allowed to present some details of the endopellic mode of life, which appeared to be principally similar in the 4 species m.a. Fig. 4 is summing up the findings of a lot of cuvette observations which were confirmed by flashlight photographs of dark experiments. In the beginning of a burrowing act the clam bores itself steeply into the sediment, the angle between sediment surface and boring hole being about 70°. Some mm below the surface the clam abruptly changes its digging direction and forms a canal several mm in length and approaching a line parallel to the surface (bc in Fig. 4). Then the animal takes in a resting position with its beaks kept down. The pedal aperture, which hence lies upwards, is opened and the anal siphon is stretched out in direction of the burrowing canal. The way taken by the nutrient and respiration water remained obscure until a suspension of carmine grains was used. Soon after the carmine had been added, the sediment particles in a funnel-like region above the foot slit (marked by arrows in Fig. 4) carried red caps demonstrating that the water takes its way through the interstitial pores of the sediment.

The ingestion of the water exclusively takes place through the pedal aperture, like in Erycinacean bivalves (Ponder, 1967). The branchial opening is either absent, as in *Pisidium conventus* and other neotenic pisidia, or kept closed, as in all European

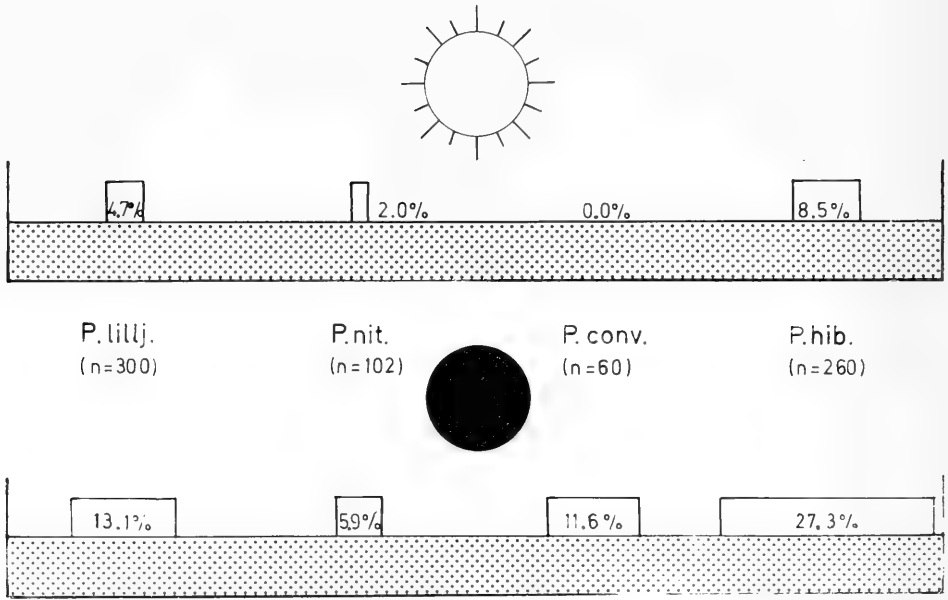


FIG. 3. Vertical substrate relations in *Pisidium lilljeborgii*, *P. nitidum*, *P. conventus*, and *P. hibernicum* from Lake Titisee. The percentages of individuals migrating to the sediment surface in light (above) and dark experiments (below) are indicated. Before each experiment the animals were exposed below the sediment surface.

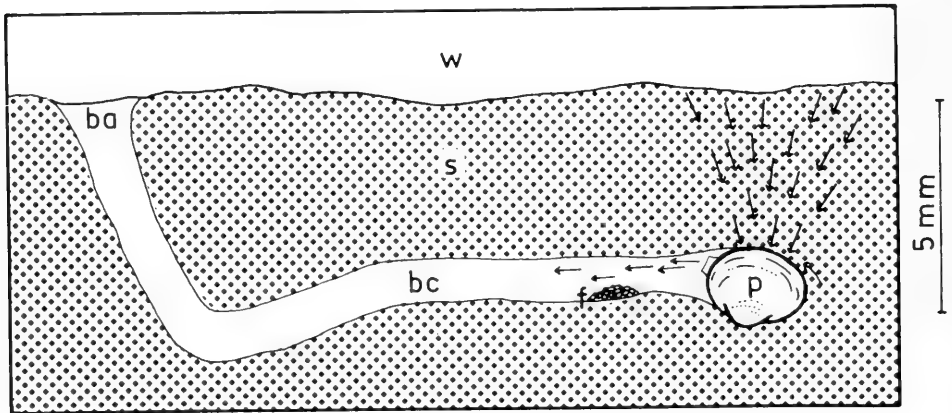


FIG. 4. Endopelic position of a *Pisidium* animal after cuvette studies on *Pisidium lilljeborgii*, *P. nitidum*, *P. conventus*, and *P. hibernicum* from Lake Titisee. Key to lettering: bc, burrowing canal; f, accumulation of feces; p, *Pisidium* animal; s, sediment; w, water.

species of the subgenus *Rivulina* which I could examine till now.

The assertion can often be found in literature that in *Pisidium* the water is ingested through the branchial opening. In my opinion, this error is due either to a conclusion from analogy from the related genus *Sphaerium*, or to the fact that the branchial opening is indeed opened in disordered (e.g., by a relaxing agent) or in dead animals. A branchial aperture which is kept open, however, really serves as an ingestion opening besides the foot slit in living clams.

The water and the feces leaving the clam through the anal siphon are pressed into the burrowing canal where the feces (f) are accumulated in a considerable distance from the animal. As far as is known to me, no investigator of endopelic animals has till now come across a mode of life like that in *Pisidium*, which is completely lacking a boring hole for the ingestion of water. Only Pratt & Campbell (1956) reported on observations on *Venus mercenaria*, which sometimes is unable to keep its burrowing aperture open and thus is forced to inhale water through the pores of the sediment.

#### REFERENCES

- PONDER, W. F., 1967, Observations on the living animal and mode of life of some New Zealand Erycinacean bivalves. *Trans. Roy. Soc. New Zealand, Zoology*, 10(3): 21-32.
- PRATT, D. M. & CAMPBELL, D. A., 1956, Environmental factors affecting growth in *Venus mercenaria*. *Limnol. Oceanogr.*, 1: 2-17.



PROBLEMS OF *LYMNAEA TRUNCATULA* ECOLOGY  
IN INVESTIGATIONS OF FASCIOLIASIS

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*Fasciola hepatica* is a parasite responsible for serious disease problems in sheep and cattle in many parts of the world. It is of particular importance in Ireland. Estimates of economic loss due to this disease in Northern Ireland suggest that it may amount to over £3,000,000 per year. Investigations have been undertaken at the Veterinary Research Laboratories at Stormont, Belfast, over the past 6 years, and studies have been made into the effects of infection in sheep, cattle and pigs (Annual Report, 1967). Initially, studies concentrated on the clinical pathology and immunology of the disease in sheep and cattle, but during the past 2-3 years more attention has been paid to the epidemiology, and to the inter-relationship between climatic conditions and infection levels in farm livestock. Predictions of the incidence of fascioliasis have been made over several years using climatic data, and on these predictions, warnings have been used to alert farmers to initiate prophylactic measures. Studies have followed the build up of metacercariae on pasture and consequent infections in tracer animals (Ross, 1967a, 1967b, 1968). These studies linked with abattoir surveys of infection (Ross, 1966), preliminary studies of snail habitats and increase in snail populations, have produced a picture of the epidemiology and seasonal trends of the disease (Ross & O'Hagan, 1968). During these studies it became clear that much of the data required to relate infections in livestock to numerical variations in snail populations and their infection levels were not present, and that techniques and literature required to obtain this information were not available. Further studies have now been initiated to investigate the epidemiology of *Fasciola hepatica* infections in sheep and cattle, and to correlate the findings with detailed studies on the ecology of *Lymnaea truncatula*. A team has been formed and is now working on the problem at this laboratory.

The incidence of fascioliasis in Northern Ireland is particularly high and in some areas, especially in the western region, where there is a high rainfall, a 50% mortality occurs in sheep, if dosing with anthelmintics is not practiced at 3-week intervals. In eastern areas where the annual rainfall is lower, the incidence is not quite so high, and less frequent dosing is often employed with success. The overall incidence of fascioliasis has been estimated from abattoir surveys performed over a number of years by Gracey (1959). Data from this survey are presented in Table 1. The number of cattle slaughtered at different abattoirs in Northern Ireland is shown, and the percentage of these in which, because of heavy fluke infection, the liver was unfit for human consumption and therefore condemned. It should be emphasised that these figures must not be confused with incidence of clinical cases of the disease. A survey of this kind can at best give only an indication of the geographical incidence of fascioliasis. As most of the cattle may have experienced at least 2 fluke seasons and may have been sold on more than one occasion prior to being brought for slaughter, the data cannot indicate details of the year or source of infection. Despite inadequacies, these statistics can provide a useful picture of the distribution and incidence of disease, when figures from abattoir surveys are plotted on a rainfall map of the Province (Fig. 1). There is apparently a fairly good correlation between areas with a high

incidence of disease and areas of high rainfall, a relationship which has been established in England by Ollerenshaw (1966). The average incidence of heavy infections in cattle is around 67% in Northern Ireland, and in problem areas is over 90%. More particular surveys have shown that the absolute incidence of infection in both sheep and cattle is between 95 and 100%.

More detailed abattoir surveys have also provided data on the seasonal incidence of fascioliasis. Fig. 2 shows the results of a survey carried out at Belfast Abattoir during the 1964/65 season (Ross, 1966). The immature flukes show a peak infection in the liver during the September–November period. In the spring, lower infections are observed either due to winter carry-over of metacercariae on the pasture, or to retardation of immature flukes in secondary infections (Ross, 1967c). The mature flukes show a peak that follows that of the immatures after a delay of about 2 months. This is the period spent by the immature flukes wandering through the liver, and at the end of this time they migrate to the bile duct and reach maturity. Comparing the levels of immatures in October 1965 and October 1964, the higher level in the former year may have been partly due to a greater incidence of the disease in Northern Ireland.

In Fig. 3, which shows the average monthly temperatures for Northern Ireland (Meteorological Office, 1968), a horizontal line has been positioned at 10° C and it can be seen that temperatures above this, at which maturation of fluke eggs and propagation of *Lymnaea truncatula* proceed, are present in Northern Ireland only from mid-May to mid-October. The build up of sufficient numbers of snails to support and produce a significant infection on the pasture, must therefore occur within these months. A water surplus giving rise to waterlogged conditions favours development of both the snail and the fluke eggs. It has been shown by Ollerenshaw & Rowlands (1959) that measurement of variations in the amount and distribution of rainfall and in transpiration during these months, offers a method of estimating the possible build up of snail populations and their infection levels and the resultant levels of infection in livestock. These factors have been used to produce the formula which gives the value known as the Meteorological Value (Mt.) for each month from May–October, indicating the degree of wetness of habitats. Summation of meteorological values for each month from May–October provides an estimate for the incidence of infection within any year. Table 2 presents meteorological values for Northern Ireland for the past 4 years and for one year, 1958, in which a disastrous fluke infection occurred. The predicted incidence, based on meteorological values for each year, is also shown. The values and predictions are compared with actual incidence, based on figures obtained from post-mortem material and from epidemiological studies carried out during these years. The correlation between observed and calculated incidence of disease is seen to be fairly good, except for one year, 1967, when an over-estimate of incidence occurred. It is suggested that the lower incidence in that year was due to an abnormally dry June. From this it is clear that while this method of estimating snail propagation is useful, it needs modification, and that more detailed studies of the dynamics of snail populations in relation to variations in climatic conditions are required.

Earlier epidemiological studies at the Veterinary Research Laboratories, Belfast, have related climatic conditions, snail density, incidence of infection in snails and the pattern of metacercariae infection on the pasture, to infections in sheep and cattle, and have compared these over a number of years (Ross, 1967a, 1967b, 1968). Fig. 4 shows some of the results of studies carried out on a site in the east of Ulster. It can be seen that there is a peak in the percentage of infected snails during the period June–October, for the 1966/67 season. This peak is followed by a rapid decline in the percentage of infected snails, coincident with the period during which the mature cercariae emerge from the snail and pass on to the grass, where they encyst to form



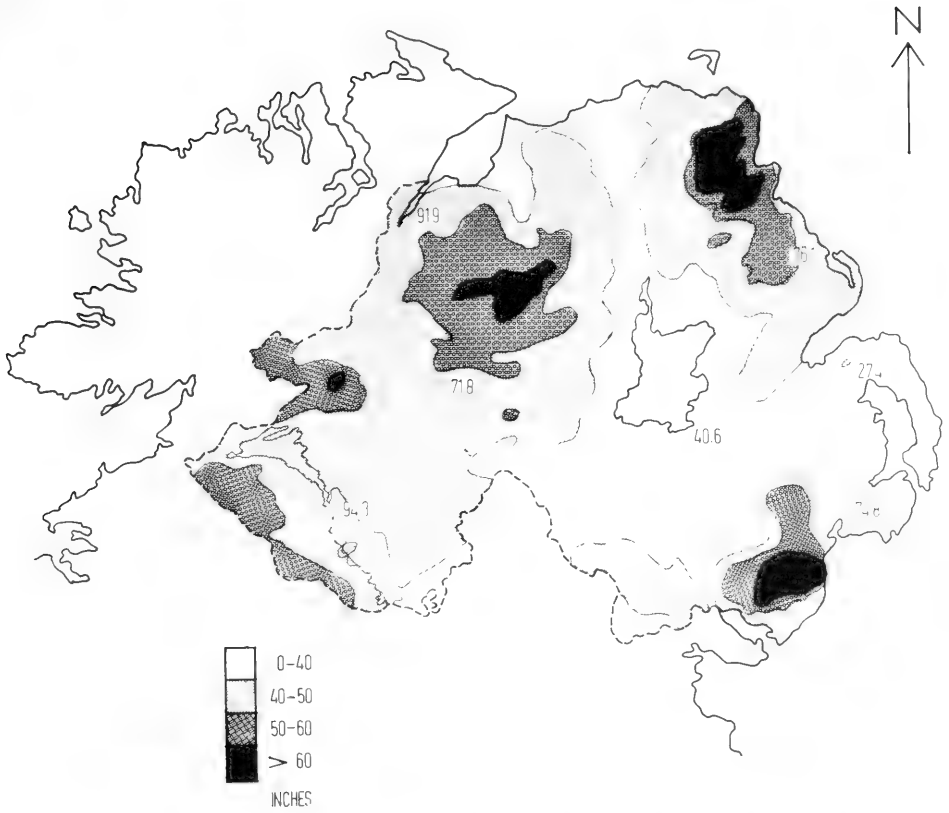


FIG. 1. Map of Northern Ireland, showing percentage condemnation rates of bovine livers together with details of the distribution and annual average amount of rainfall, (Met. Office, 1967, 1968).

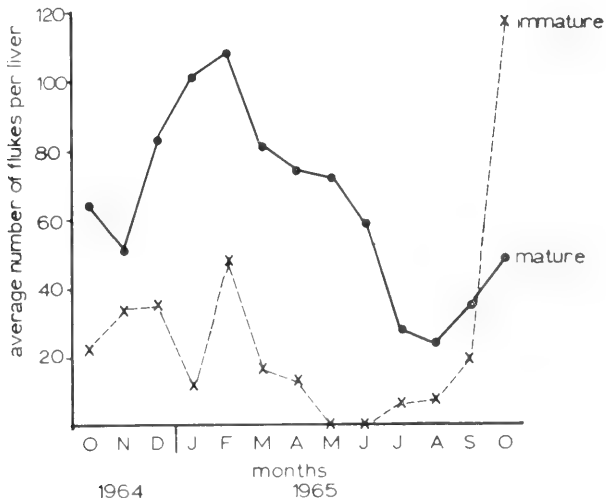


FIG. 2. Seasonal incidence of fascioliasis in Northern Ireland.

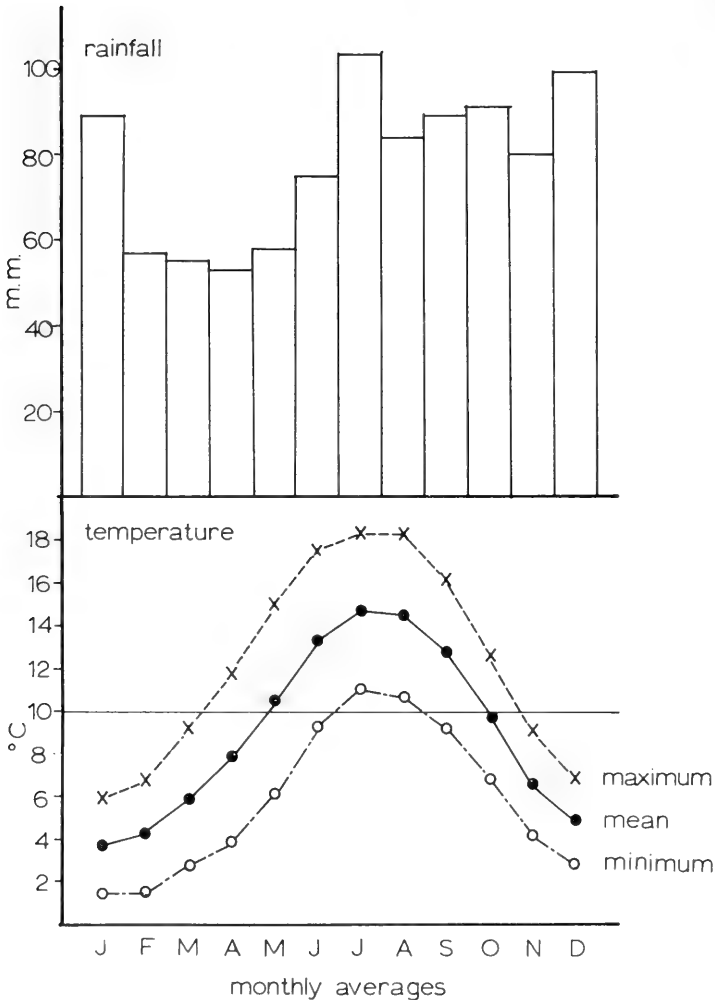


FIG. 3. Monthly average temperature and rainfall for Aldergrove Met. Station, (Met. Office, 1967, 1968).

metacercariae. This is indicated in the lower graph in Fig. 4. A spectacular peak in metacercariae infection during October, is followed by a decrease during the early part of the winter, with little carry-over of infection on the pasture over the winter period. The percentage of infected snails for the 1964/65 season, is also shown, and it is suggested that the very low incidence of infection during the July-September period was probably an anomaly arising from problems involved in sampling. However, this data has been included, as it demonstrates - together with that for the 1966/67 season and field observations over a number of years - that carry-over of infection in the snail does not appear to be of significance in Northern Ireland. This leads us to suggest that any late infection of livestock, during the spring and early summer, is more likely to be due to carry-over of metacercariae infection on the pasture, rather than to carry-over of infection in the snail. A carry-over infection in the snail has been suggested in England by Ollerenshaw & Rowlands (1959). It is clear that further

TABLE 1. Incidence of bovine fascioliasis in Northern Ireland

Abattoir	Total bovine kill	Percentage of animals affected with fascioliasis
Enniskillen	2,724	94.3
Londonderry	8,326	91.9
Larne	3,770	76.1
Downpatrick	2,163	74.8
Lurgan	8,288	40.6
Newtownards	2,930	27.4

TABLE 2. Comparison of meteorological predictions and actual incidence of disease, for the east of the Province

Year	Aggregate of monthly "Mt." values	Predicted incidence of fascioliasis	Actual incidence of fascioliasis
1958	500	Disastrous	Disastrous
1964	412	Average	Average
1965	453	Above average	Above average
1966	431	Average	Average
1967	429	Average	Below average

TABLE 3. Survey of snail populations on fluke sites, following outbreaks of fascioliasis

County of site	Date of disease outbreak	Type of disease	Date of snail sampling	Snails per lb. of soil	Percentage of snails infected	Site size
Armagh	Oct.	Acute	Nov.	136	50	Extensive
Down	Nov.	Acute	Nov.	52	25	Extensive
Antrim	Oct.	Subacute	Oct.	6.7	75	Extensive
Down	Sept.	Subacute	Sept.	1.9	100	Moderate
Down	Nov.	Chronic	Oct.	0.6	10	Moderate
Fermanagh	Jan.	Chronic	Oct.	23	10	Small
Antrim	Dec.	Chronic	Sept.	2.5	30	Moderate

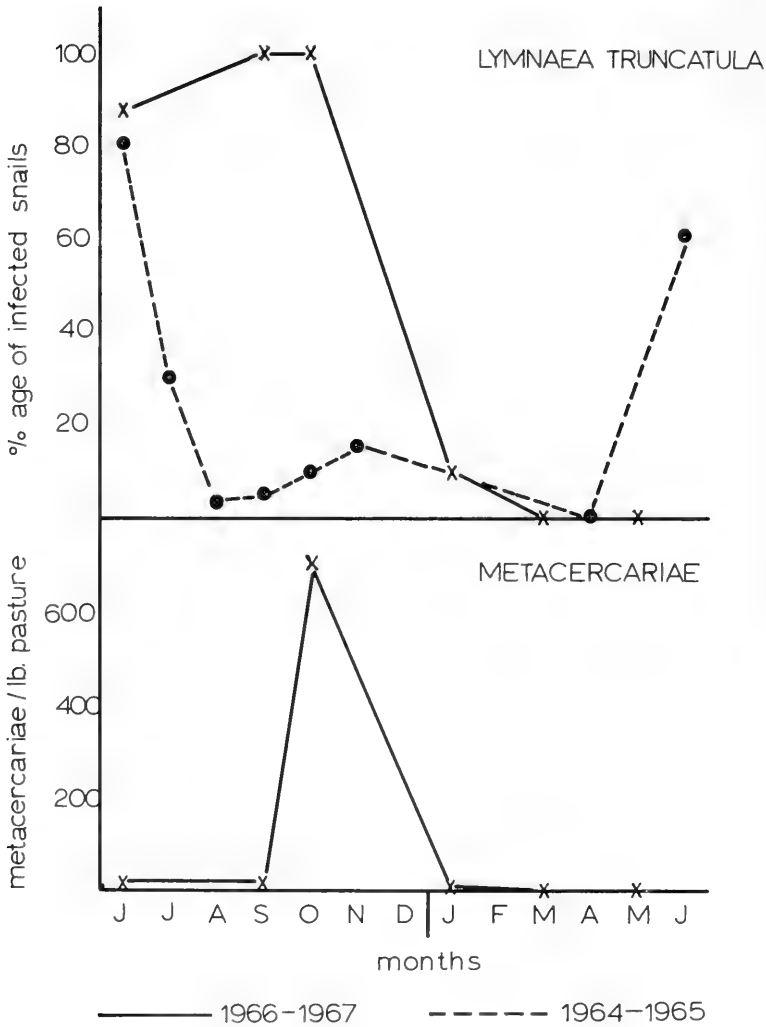


FIG. 4. Fluctuations in levels of snail and pasture infection.

studies are required to determine the nature, extent and importance of carry-over infection in and between different regions.

More recent investigations (Ross & O'Hagan, 1968) with sheep on a site in the east of the Province, suggest that there is a minimum level of snail population and percentage of snails infected, necessary to produce a significant disease, but this relationship does not appear to be a simple one. Table 3 indicates that acute outbreaks of fascioliasis occurred from October to November on extensive sites, where there were high densities of snails of which a considerable percentage were infected. Sub-acute outbreaks occurred during September and October on moderate to extensive sites, having lower densities of snails, but a higher incidence of infection within the populations. Chronic cases of the disease occurred later in the winter from November-January, on small to moderate sites, where there were very low densities of snails, of which only a small percentage were infected.

Whilst these studies have enlarged our knowledge of fascioliasis, there are still

many factors in the ecology of the snail which are unknown and require investigation. Of the problems needing attention, one of the most important is the need for design of techniques and methods which will allow accurate assessment of the dynamics and density of snail populations and the distribution of animals within their habitat. This is particularly relevant with the advent of renewed interest in control of fluke disease by application of molluscicides. The snail *Lymnaea truncatula* has a great reproductive potential; Kendall (1953) has found that under optimum conditions in the laboratory, snails may reach maturity in 21 days, and that an individual snail is capable of giving rise to 25,000 in 12 weeks. Field observations on the rate of population increase under natural conditions suggest an 8-10 fold seasonal increase, which is perhaps more realistic (Sosipatrov & Shumakovich, 1966). Partial destruction of snail populations by molluscicides may be a feasible control measure, but until ecological studies have established such details as rates of population increase and repopulation, molluscicidal control schemes will remain uncertain in their efficiency. Any form of molluscicidal control must aim either at complete annihilation of populations on specific sites or decimation of populations of infected snails prior to the emergence of cercariae. An accurate site assessment is extremely important, as observations suggest that a residual population of snails left on the pasture after molluscicidal treatment can effect a rapid recovery resulting in an increase of the population towards its former high level.

Visual count methods, either for a standard period of time or over a unit area of habitat, are not sufficiently accurate either as a basis for ecological study or when attempting to assess the extent of a flukey site prior to implementing some form of control. These subjective methods are at a considerable disadvantage in that they depend to a very large extent on the visual acuity and diligence of the searcher, and furthermore they suffer from being biased. When one considers that a newly hatched snail is little more than  $1/2$  mm in height, the limitations of such methods are obviously apparent. Work at present in progress at Belfast suggests that snails are frequently found in moist areas of pasture where there is a thick green sward and these areas are often not suspected of harbouring the snail, and yet it has been found to be present in substantial numbers. Conversely, it is not uncommon for the experienced worker to find that searches for snails on sites, which had previously shown large concentrations of snails, often prove fruitless when examined after an interval of only a week or so. In these circumstances then, the visual searching method is not to be recommended.

A rigorous sampling technique is an absolute essential, in that it will be instrumental in providing some of the basic ecological data required firstly, as a basis for developing systems of forecasting and disease control, and secondly, in implementing such control measures, whether they involve anthelmintic treatment, molluscicidal application or pasture management. At the present state of our knowledge, it would appear that a combination of these methods is required in most circumstances and that future selection of the most effective method or combination of methods, will be dependent to a very large extent on the conditions prevailing in the problem area, of which details of the snail populations will perhaps be cardinal.

Information on the dynamics of snail populations, mortalities over winter periods, and reproductive potential of different sized populations at the beginning of the breeding season are just some of the required details, which would be of great use to the pesticide expert as he would be in a more informed position to give advice as to when in the year treatment should be applied. Information on the influences of different environmental factors such as climate, different kinds of pasture management, water conditions, to mention but a few, on the behaviour of the snails and their distribution and population dynamics, will provide some of the basic knowledge required

for designing molluscicidal control programmes and in formulating more effective systems of disease forecasting.

The requisite basic techniques to provide much of this information are now established at the Stormont laboratory, and investigations are proceeding which - in conjunction with epidemiological studies of the disease in farm animals - should answer many of these important questions. A vast quantity of data on individual facets of fascioliasis has been collected in the past, but has suffered from lack of complementary studies on snail populations. The recent renewed interest in molluscicidal control has, however, highlighted this deficiency, and it is hoped that it will stimulate more detailed investigations of this disease complex.

#### REFERENCES

- GRACEY, J. F., 1959, A study of disease incidence and wastage in livestock in Northern Ireland. Ph.D. Thesis, Queen's University, Belfast.
- KENDALL, S. B., 1953, The life history of *Lymnaea truncatula* under laboratory conditions. *J. Helminth.*, 27: 17-28.
- Meteorological Office, Belfast, 1967, Monthly and annual averages of rainfall for Northern Ireland; WMO period 1931-1960. Hydrological memorandum, No. 35.
- Meteorological Office, Belfast, 1968, Averages of air temperature, 1931-1960. Memorandum.
- OLLERENSHAW, C. B., 1966, The approach to forecasting the incidence of fascioliasis over England and Wales 1958-1962. *Agr. Meteorol.*, 3: 35-53.
- OLLERENSHAW, C. B. & ROWLANDS, W. T., 1959, A method of forecasting the incidence of fascioliasis in Anglesey. *Vet. Rec.*, 71: 591-598.
- ROSS, J. G., 1966, An abattoir survey of cattle liver infections with *Fasciola hepatica*. *Brit. Vet. J.*, 122: 489-494.
- ROSS, J. G., 1967a, An epidemiological study of fascioliasis in sheep. *Vet. Rec.*, 80: 214-217.
- ROSS, J. G., 1967b, A further season of epidemiological studies of *Fasciola hepatica* infections in sheep. *Vet. Rec.*, 80: 368-371.
- ROSS, J. G., 1967c, Experimental infections of cattle with *Fasciola hepatica*: high level single infections in calves. *J. Helminth.*, 41: 217-222.
- ROSS, J. G., 1968, Epidemiological studies of fascioliasis. *Vet. Rec.*, 81: 695-699.
- ROSS, J. G. & O'HAGAN, J., 1968, *Lymnaea truncatula* population studies: the use of a soil sampling technique in studies of fascioliasis. *Brit. Vet. J.*, 124: 266-269.
- SOSIPATROV, G. V. & SHUMAKOVICH, E. E., 1966, [Population dynamics and density of the mollusc *Galba truncatula* and its infestation with larvae of *Fasciola hepatica* in Moscow province conditions.] *Mater. konf. obshch. hel'mint.*, 1: 253-256.
- VAN DEN BRUEL, W. E. & MOENS, R., 1964, Des possibilites d'utilisation de la cyanamide calcique pour la lutte contre la distomatose bovine par la destruction de *Limnaea truncatula* Müller, hôte intermediaire de *Fasciola hepatica* L. *Parasitica*, 20(2): 41-70.
- Veterinary Research Laboratories, 1967, Annual report on research and technical work. Ministry of Agriculture, Northern Ireland. p 95-109.

PROBLEME DER MASSENVERMEHRUNG VON  
*HELIX POMATIA* L. (WEINBERGSCHNECKEN)

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EINLEITUNG

Pressemeldungen zufolge beträgt der jährliche Bedarf Frankreichs - wo die Weinbergschnecke seit altersher ein Volksnahrungsmittel ist - 90.000 Tonnen. Während in Frankreich selbst die Weinbergschnecke so gut wie ausgestorben ist, kann das Sammeln von Wildschnecken in den klassischen Weinbergschneckenländern: Deutschland, Österreich, Polen, Tschechoslowakei, Teile Jugoslawiens, Italiens und der Schweiz, nur einen Teil dieser benötigten Menge erbringen. Frankreich ist deshalb auf den Import von qualitativ nicht gleichwertigen Schnecken wie z.B. *Helix aspersa*, *Helix rumelica*, aus Ostländern angewiesen. Importeure und Konservenerzeuger in Frankreich betonen immer wieder, dass sie die echte Weinbergschnecke aus mehrfachen Gründen vorziehen und einige Fabrikanten sind bereits dazu übergegangen, ihre Ware auf der Etiketle durch den Aufdruck "*Helix pomatia*" zu kennzeichnen, was in diesem Fall als Gütesymbol zu werten ist.

Zu dieser bereits jetzt grossen Menge für Speisezwecke benötigter Schnecken wird in naher Zukunft ein Bedarf der pharmazeutischen Industrie dazukommen; dies ist aufgrund der laufenden Forschungen unbedingt zu erwarten. Es seien in diesem Zusammenhang bloss die bereits erzielten Erfolge bei der Pertussisbehandlung mit einem Präparat erwähnt, dessen wirksame Substanz auf einem Sekret der *Helix pomatia* beruht (Pantlen, 1953; Mainil, 1950; Quevauviller, et al., 1953), ferner sei der Arbeiten Prokop's und Mitarbeiter gedacht, nach welchen die Bestimmung menschlicher Blutgruppen mit dem Anti-A<sub>HP</sub> und die Feststellung von Aszitesumorzellen möglich ist (Prokop et al., 1965; Rackwitz et al., 1965; Kim et al., 1966; Dietz, 1966; Uhlenbruck & Prokop, 1966; Uhlenbruck et al., 1966; Prokop, 1967; Prokop et al., 1967; Prokop et al., 1968) und schliesslich könnte die Weinbergschnecke in der Behandlung des Diabetes mellitus (Präparat "Diabetex" von Dr. A. Roswadowski in Tailfingen, W. Germany) oder zumindest für die Diät eine Bedeutung erlangen.

Zu einer weiteren Bedarfserhöhung führte letztlich der Umstand, dass in den mitteleuropäischen Ländern das Schneckenessen aus der Vergessenheit wieder in die Mode rückte; Österreich blieb davon nicht ausgenommen.

Diesem enormen Bedarf, der nicht einmal mehr annäherungsweise gedeckt werden kann und in der Zukunft eine weitere Erhöhung erfahren wird, steht auf der anderen Seite der Rückgang des Naturvorkommens in den klassischen Weinbergschneckenländern gegenüber: durch die Methoden der modernen Landwirtschaft gelangen chemische Dünge- und Pflanzenschutzmittel immer mehr in die Randgebiete der eigentlichen Anbauzonen, Wegränder, Bachufer, Windschutzstreifen etc., und damit in den Lebensbereich der Weinbergschnecken. Aus den Weingärten ist die "Weinberg"-schnecke dieserart längst vollständig verschwunden. Zieht man wirtschaftliche Aspekte in Erwägung, so ergibt sich die Notwendigkeit, die Weinbergschnecken in Zucht-kulturen zu vermehren, eigentlich von selbst. Der jährliche Deviseneingang für Österreich betrug allein aus dem Export der gesammelten Wildschnecken an die drei Millionen Schilling, wobei diese Summe nur die vorhandene Menge Schnecken, nicht aber die Nachfrage limitierte; zweifelsohne hätte eine weit grössere Menge ohne

Schwierigkeiten abgesetzt werden können. Es steht somit fest, dass die Weinbergschnecke ein Faktor ist, dessen volkswirtschaftliche Bedeutung nicht übersehen werden darf. Darüber hinaus könnte die Züchtung von Weinbergschnecken vielen Kleinlandwirten, Gebirgsbauern, Rentnern etc., eine Nebeneinnahme erbringen, die eine echte Krisenfestigung darstellen würde.

## ZÜCHTUNG

Obwohl die Weinbergschnecke in jedem Anfängerpraktikum der meisten Universitäten seziert wird, ist über ihre Biologie und Populationsdynamik beinahe nichts bekannt. Die genaue Kenntnis gerade dieser ist aber unbedingt notwendige Voraussetzung, wenn ein Naturgesetz durchbrochen werden soll; dies ist immer der Fall, wenn Massenvermehrung einer bestimmten Art angestrebt wird.

Da eine Weinbergschnecke im Laufe ihres Lebens mehr als zweihundert Eier ablegen kann, kommt es in der Natur immer wieder zu Massensterben von Jungtieren und auch adulten Tieren, da schliesslich, soll die Bestandesdichte der Art erhalten bleiben, nur aus einem einzigen Ei eine geschlechtsreife Schnecke werden darf. Zu ähnlichen Massensterben ist es früher oftmals auch in den "Schneckengärten" gekommen und auch heute noch können solche Vorkommnisse nicht völlig ausgeschlossen werden.

### 1. Historischer Überblick

Die erste Notiz über eine Züchtung von Weinbergschnecken findet sich bei Marquart (Marquart, 1909), wonach der Gesamtwert der im Donautal gezüchteten Schnecken 1909 sechs Millionen Mark betragen haben soll. Andere Angaben beziehen sich meistens auf die Mast der Tiere: Weinbergschnecken wurden im Frühjahr und im Sommer in freier Wildbahn gesammelt, gefüttert und im Herbst als Deckelschnecken verkauft. Gehege zu solcher Schneckenmästerei besaßen bereits die alten Römer, später im Mittelalter besonders die Klöster, da die Schnecken von der Mönchen als Fastenspeise sehr geschätzt wurden.

Der wissenschaftliche Nachweis der Züchtungsmöglichkeit von *Helix pomatia* wurde erstmals von der Dipl. Biologin G. Hein erbracht (Hein, 1952). Dr. G. Nietzsche (Nietzke, 1963) und Dr. K. Königer (Königer, 1965, 1966, 1967) bestätigen eine gewinnbringende Züchtungsmöglichkeit unter bestimmten Voraussetzungen. Seither haben sich viele Züchter auf diesem neuen Gebiet der landwirtschaftlichen Sonderkulturen mit wechselndem Erfolg versucht. Die hervorstechendsten Erfolge hat wohl F. J. Jungwirth auf seinen zwei Hektar grossen Anlagen auf der Schwäbischen Alb erzielt (Jungwirth, 1967), aber auch aus Österreich werden erste Erfolge gemeldet (Nawratil, 1963, 1964, 1965, 1966, 1967, 1968; Fröschl, 1968; Juza, 1968). In den Oststaaten sind mit grosser Wahrscheinlichkeit mehrere staatliche Versuchsanlagen mit der Verbesserung der Züchtungsmöglichkeiten von *Helix pomatia* beschäftigt. Das Interesse an diesem kleinen Tier, das grosse Devisen bringen kann, ist allerorts vorhanden.

### 2. Biologie

Die Tiere überwintern in einer selbstgegrabenen Erdhöhle im Freien. Ab etwa Ende Februar besteht eine Bereitschaft zum Erwachen aus dem Winterschlaf. Das auslösende Moment ist mit grosser Wahrscheinlichkeit eine Resultante aus der Kombination der beiden Faktoren: Temperatur und Luftfeuchtigkeit, bezw. Bodenfeuchte. Versuche, welche die Tageslänge für das Erwachen aus der Winterruhe verantwortlich machen wollen, sind im Gange, jedoch halte ich diese für weniger aussichtsreich. In unseren Breiten erwachen die Schnecken in der Regel im April/Mai. Bald nach der ersten Nahrungsaufnahme, noch im Mai-Juni, erfolgt die Copulation, welche mit wechselseitiger Befruchtung abschliessen kann. Im Juli werden die Eier in eine





selbstgegrabene Eihöhle in den Boden gelegt (maximale Beobachtungsziffer einer einzigen Eiablage: 105 Stück), im Durchschnitt 50 bis 70 Stück. Nach etwa drei Wochen schlüpfen die Jungtiere, verbleiben meistens noch einige Wochen in der Eihöhle, wo die Eihäute aufgezehrt und Erde gefressen wird. Frühestens Mitte August kommen die Jungschnecken in einer feucht-warmen Nacht erstmals an die Oberfläche. Im ersten Jahr lassen sie sich bei Tageslicht kaum blicken; unter den Amphibien, Reptilien, Vögeln und Säugern gibt es viele, die das zarte Fleisch von Jungschnecken zu schätzen wissen. Bei Tagesanbruch suchen diese daher gut geschützte Schlupfwinkel auf oder sie gehen überhaupt wieder in den Boden hinein. Mit drei Jahren werden sie geschlechtsreif. Die Verkaufsgrösse erlangt ein Teil der Tiere bereits mit zwei, der Rest mit drei Jahren. In

freier Wildbahn sterben die meisten vor Erreichung der Geschlechtsreife ab. In Farmgehegen muss den Faktoren, welche diese Sterblichkeit verursachen, entgegengewirkt werden.

### 3. Mortalität

#### a) Bakteriologische, virologische und histologische Untersuchungsergebnisse

Untersuchungen am Hygiene-Institut der Universität Wien (Nawratil & Loew, 1968) ergaben, dass die untersuchten Krankheitserscheinungen von *Helix pomatia*, welche mit einer Muskelstarre beginnen und schliesslich den Tod der Tiere herbeiführen, nicht bakteriell verursacht werden. Eine wie immer geartete bakterielle Infektion liegt nicht vor.

Die virologischen Untersuchungen ergaben eindeutig, dass keine auf Warmblütler übertragbare Vireninfektion vorliegt. Wenn die Anwesenheit eines gastropoden- oder vielleicht sogar artspezifischen Virus auch nicht mit völliger Sicherheit ausgeschlossen werden konnte, weisen die erzielten Ergebnisse in Zusammenhang mit vielen Beobachtungen der Tiere und des Krankheitsverlaufes im Biotop doch mehr auf eine Toxinbildung in den erkrankten Tieren hin, die dann eine Sekundärerkrankung darstellte. Bei Überimpfung von Pressafthomogenaten erkrankter Tiere auf gesunde lösen diese Toxine u.U. die gleichen Krankheitssymptome aus. Diese Hypothese wird bis zu einem gewissen Grad auch durch die histologischen Untersuchungen gestützt, welche keinerlei Differenzierungen oder pathologische Veränderungen des Gewebes erkrankter Tiere, wie solche durch Virenbefall in der Regel bewirkt werden, gegenüber demjenigen gesunder erkennen liessen.

#### b) Klimatische Faktoren

Es ist daher mit grösster Wahrscheinlichkeit anzunehmen, dass die Ursache der Erkrankungen im Einwirken ungünstiger klimatischer Faktoren auf die Tiere zu finden ist. Die diesbezüglichen Untersuchungen sind noch im Gange. Es wird vermutet, dass die Resistenz der Tiere eng mit der Bildung der bakteriostatischen Substanz

(Loew & Nawratil) in der Eiweissdrüse zusammenhängt, welche während Ruheperioden (sommerliche Trockenstarre und Winterruhe) entsteht. Es könnte sich dabei um dieselbe Substanz handeln, welche als "Anti-A<sub>HP</sub>" bezeichnet wurde (Prokop, 1967, 1968) und mittels welcher menschliches Blut gewisser A-Gruppen und Bakterienstämme, welche endständig nichtreduzierend gebundenes N-Acetyl-D-Galaktosamin in der Zellwand tragen, agglutiniert wird. Es liegt nahe, dass eine Substanz vorhanden sein muss, welche die Entwicklung von Darmbakterien und Gärungserregern - bes. während der sommerlichen Trockenstarren bei relativ hohen Temperaturen - verhindern kann. Würde diese Substanz jedoch nur während oder besonders am Beginn von derartigen Ruheperioden gebildet, dann müsste während und nach einer Witterungsperiode welche keine Ruhepause induziert (z.B. lang anhaltende Regenfälle), eine grössere Mortalität auftreten. Ebenso dürfte die Möglichkeit der Bildung dieser Substanz zeitlich und quantitativ beschränkt sein, so dass nach Ablauf einer gewissen Periode eine neuerliche Aktivitätsentfaltung mit Nahrungsaufnahme erfolgen muss, um den Stoff neu bilden zu können. Währt eine Trockenpause also zu lange, so tritt ebenso wie bei fortdauernder nasser Periode eine grössere Sterblichkeit auf. Da durch höhere Temperaturen der Gesamtstoffwechsel eine erhebliche Steigerung erfährt, können Trocken- und Hungerperioden in der Regel im Sommer nicht in der gleichen Länge überdauert werden als im Winter.

Tatsächlich konnte in den Jahren 1961-1968 unter den beschriebenen Umständen sowohl in den Freigehegen der Versuchsanlagen wie auch unter markierten Tieren in der freien Wildbahn ein Ansteigen der Mortalitätsrate - 20-80% des oft in die Tausende gehenden Untersuchungsmaterials - beobachtet werden.

#### NOTWENDIGE MASSNAHMEN - AUSBLICK

Der Einfluss klimatischer Einwirkungen - Dauer und Stärke - besonders von Temperatur und Luftfeuchtigkeit auf die Bildung der bakteriostatischen Substanz (vermutlich das Anti-A<sub>HP</sub> oder eine eng damit verwandte Substanz) muss an einem statistisch repräsentativen Material von *Helix pomatia* untersucht werden. Dies ist, sollen die Ergebnisse nicht durch Zufall und Glück allein begünstigt werden, nur in einem Institutsbetrieb möglich. Zur Beschleunigung der Beobachtungen sind Klimakammern, bezw. Räume, in welchen Temperatur und Luftfeuchtigkeit regulierbar sind, notwendig. Die Arbeitsgrundlage eines solchen Institutes müsste für mindestens zehn Jahre gesichert sein, da *Helix pomatia* mit drei Jahren Geschlechtsreife erlangt und die Nachkommenschaft bis zur F<sub>3</sub> verfolgt werden sollte. Durch eine Regulierung des Kleinklimas nach den gewonnenen Erkenntnissen wird eine wirtschaftlich interessante Auswertung mit viel grösserer Sicherheit als heute möglich sein, ähnlich, wie dies bei der Fisch- und Austernzucht bereits jetzt der Fall ist.

#### SUMMARY

Among other central European countries Austria is exporting snails (*Helix pomatia*) to France. The yearly income for Austria resulting from this snail export business is about 3 million Austrian shillings and is limited only by the amount of available snails, not by a lack of buyers. Breeding of these animals would be interesting for both the breeder and the Austrian State. The scientific proof of the breeding possibility was done first by G. Hein in 1952. Since then a lot of people tried their luck breeding snails economically. However, because of a disease that sometimes caused a high mortality rate amongst the animals, the breeding results were not always the expected ones. As it was not known whether this disease was caused by bacterial infection or not, investigations had been carried out.

## Results

1. No bacteria-infection could be traced either with sick or with healthy animals. On the contrary, a substance bacteriostatical or even bacteriolitical to certain groups of bacteria (such as containing N-Acetyl-D-Galactosamine) could be noticed.
2. It was proved that there is no infection of a virus transmittable to mammals. A virus transmittable from sick to sound snails could not be proved. Histological investigations did not show any difference in the tissues of sick and sound snails. Although the possibility of a virus specific to gastropods or even to *Helix pomatia* causing the mortality was not fully discarded, the results of the virological investigations together with observations of the ecological and environmental nature pleaded for a toxical poisoning of sick snails.
3. The primary cause of the sickness most probably is to be found in climatic factors (temperature and moisture) such as not enough change in dry and humid periods.
4. Most probably the resistance of the animals depends on the bacteriostatic substance which is built in the beginning of inactive periods (dry weather periods during the summertime, and hibernation). It is suggested that this substance in the protein gland is the same or at least a very similar one than being described by Prokop as Anti-A<sub>HPP</sub>.
5. A 10-year research program, to be carried out in an adequate institute, is proposed to clear all open questions and make the breeding of *Helix pomatia* a prosperous business.

## LITERATUR

- DIETZ, G., 1966, Über das Verhalten von Anti-A<sub>hel</sub> in verschiedenen Milieus. *Ztschr. f. Immunitätsforschung, Allergie u. klinische Immunologie*, 131: 475-479.
- FRÖSCHL, K., 1968, Erfahrungen der Schneckenfarm Schlag, Königswiesen. tip, Nürnberg, 6: 463-464.
- HAFERLAND, W., KIM, Z., UHLENBRUCK, G., & NELSON, D. S., 1967, Zur Frage der Einheitlichkeit des Agglutinins Anti-A<sub>hel</sub>. *Ztschr. f. Immunitätsforschung, Allergie u. klinische Immunologie*, 132: 93-102.
- HEIN, G., 1952, Die Weinbergschnecke. Lebensweise, Verbrauch, Handel u. Zucht. *Ztschr. f. hygien. Zoologie*, Berlin, 40: (Heft 8/9).
- JUNGWIRTH, F. J., 1967, Die Zucht der Weinbergschnecke, *Helix pomatia*. Ein im Entstehen begriffener Erwerbszweig. Vlg. Jungwirth, Hausen/Kill. W. Germany.
- KIM, Z., UHLENBRUCK, G., PROKOP, O., & SCHLESINGER, D., 1966, Über die B-Substanz und das Anti-A<sub>hel</sub> von *Helix pomatia*. *Ztschr. f. Immunitätsforschung, Allergie und klinische Immunologie*, 130: 290-295.
- KOENIGER, K., 1965, Die Zucht der Weinbergschnecke in einem nicht typischen Schneckengebiet. Tip, Nürnberg, 11: 823-824 und tip, 12: 910-912.
- KOENIGER, K., 1966, Die Zucht der Weinbergschnecke in einem nicht typischen Schneckengebiet. tip, 1: 23-25.
- KOENIGER, K., 1967, Weinbergschnecken fühlen sich pudelwohl. tip, 10: 749-751.
- MAINIL, M. J., 1950, Inhibition d'Hemophilus pertussis "in vitro" et lyse des substances mucoides qu'il sécrète, au moyen d'un extrait de sécrétions de Gastéropodes. *Ann. pharm. franc.*, 8: 734-736.
- MARQUART, R., 1909, Die Schnecken, *Zoolog. Beobachter*, Ludwigsburg, 50: 112-114.
- MEISENHEIMER, J., 1912, Die Weinbergschnecke. Vlg. Klinkhardt, Leipzig.
- NAWRATIL, O. J., 1963, Berichte aus dem ADKPZ in Österreich. tip, Nürnberg, 6: 406-408.
- NAWRATIL, O. J., 1963, Trockenresistenz von *Helix pomatia*. tip, 7: 437-440.
- NAWRATIL, O. J., 1963, Zucht und Züchtung, tip, 8: 510-513.

- NAWRATIL, O. J., 1963, Züchtung einer neuen Rasse aus einer Wildform. tip, 9: 622-624.
- NAWRATIL, O. J., 1964, Verwertung von Schnecken in aller Welt. tip, 4: 274-276.
- NAWRATIL, O. J., 1964, Neue Wege in der Zucht von Speiseschnecken. tip, 5: 352-354.
- NAWRATIL, O. J., 1964, Wichtiges zur Ernährungsfrage der Weinbergsschnecken nach der Winterruhe. tip, 6: 407-409.
- NAWRATIL, O. J., 1964, Futterbedarf der Weinbergsschnecken in Gehegen. tip, 7: 496-498.
- NAWRATIL, O. J., 1965, Erste Ergebnisse der Mitarbeiter in Österreich. tip, 4: 295-296.
- NAWRATIL, O. J., 1966, Neue Forschungsvorhaben des ADKPZ für die kommende Weinbergsschneckensaison 1966. tip, 3: 179-181.
- NAWRATIL, O. J., 1966, Schneckenparadies in der Südsee. tip, 9: 676-678.
- NAWRATIL, O. J., 1966, Unterstützung geplanter Forschungsvorhaben auf dem Gebiet der Weinbergsschneckenzucht durch österreichische Förderungsgesellschaften. tip, 10: 745-748.
- NAWRATIL, O. J., 1966, Praktische Erfahrungen über den Einfluss des Bodens und des Bewuchses in Schnecken-Zuchtgehegen. tip, 11: 834-836.
- NAWRATIL, O. J., 1967, Zur Frage der Ursache von Verlusten in Weinbergsschnecken-gehegen. tip, 8: 633-635.
- NAWRATIL, O. J., 1967, Haltungsfragen und Wachstumsleistungen in Terrarien gezüchteter Achatinen und Placostylen. *Sitzungsberichte d. Österr. Akad. d. Wiss., Mathem.-nat. wiss. Kl., Abt. I*, 176: 5-20.
- NAWRATIL, O. J., 1968, Ausfälle in der Weinbergsschneckenzucht durch dauernde Beschattung. tip, 7: 542-545.
- NAWRATIL, O. J., 1968, Zur Fütterungsfrage in den Weinbergsschnecken-gehegen. tip, 8: 633-635.
- NAWRATIL, O. J., & LOEW, J., 1969, Zur Frage einer bakteriellen oder Vireninfektion von *Helix pomatia* in Farmgehegen. *Ztschr. f. Bakt., Mikrobiol. u. Hygiene*, in Druck.
- NAWRATIL, O. J., & LOEW, J., 1969, Über die bakteriostatische Substanz in *Helix pomatia* und deren Entstehungsbedingungen. In Vorbereitung.
- NIETZKE, G., 1963, Die Weinbergsschnecke. Vlg. Eug. Ulmer, Stuttgart.
- PANTLEN, H., 1953, Ein neuer Weg der Pertussisbehandlung. *Med. Klinik*, 34: 1223-1224.
- PROKOP, O., SCHLESINGER, D., & RACKWITZ, A., 1965, Über eine thermostabile "antibody-like substance" (Anti-A<sub>hel</sub>) bei *Helix pomatia* und deren Herkunft. *Ztschr. f. Immunitäts- u. Allergieforschung*, 129: 402-412.
- PROKOP, O., RACKWITZ, A. & SCHLESINGER, D., 1965, A "New" Human Blood Group Receptor A<sub>hel</sub>. *Journ. forensic Med.*, 12: 108-110.
- PROKOP, O., 1967, Die Helixagglutinine. *Allergie u. Asthma*, 13: 96-98.
- PROKOP, O., SCHLESINGER, D. & GESERICK, G., 1967, Thermostabiles B-Agglutinin aus Konserven von Lachskaviar. *Ztschr. f. Immunitätsforschung, Allergie u. klin. Immunologie*, 132: 491-494.
- PROKOP, O., GRAFFI, A. & SCHNITZLER, ST., 1968, "Immunochemical Endgrouping" mit *Helix*-Agglutininen an Aszitestumorzellen. Vergleich mit den Blutzellen der Tiere. *Acta biol. germ.*, 20: K9-15.
- PROKOP, O., UHLENBRUCK, G. & KÖHLER, W., 1968, A new source of antibody-like substances having anti-blood group specificity. *Vox Sanguinis*, 14: 321-333.
- PROKOP, O., UHLENBRUCK, G. & KÖHLER, W., 1968, Protectine, eine neue Klasse antikörperähnlicher Verbindungen. *D. Deutsche Gesundheitswesen*, 23: 318-320.
- QUEVAUVILLER, A., MAINIL, J. & GARCET, S., 1953, Le mucus d'*Helix pomatia*. *Rev. de Pathologie générale et comparée*, 1953: 1514-1539.

- RACKWITZ, A., SCHLESINGER, D. & PROKOP, O., 1965, Über ein Blutgruppenprinzip B (Anti-A) bei *Helix hortensis*. Ein neuer menschlicher A-Rezeptor A<sub>hel</sub>. *Acta biol. med. germ.*, 15: K187-189.
- UHLENBRUCK, G., PROKOP, O. & HAFERLAND, W., 1966, Agglutination von *E. coli* durch ein Agglutinin aus *Helix pomatia*. *Zentrbl. Bakt., Parasit., Infektionskrkh. u. Hygiene*, 1 Orig. 199: 271-272.
- UHLENBRUCK, G., SCHMID, D. O. & PROKOP, O., 1966, Über die Natur des A-hel Rezeptors an menschlichen und tierischen Blutkörperchen. *Acta biol. med. germ.*, 16/1: 9-12.



DISTRIBUTION AND ECOLOGY OF THE FRESH-WATER SNAILS  
(GASTROPODA) OF NORWAY

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ABSTRACT

The article is a preliminary report of some of the results arrived at in a study comprising the distribution, ecology and morphology of the fresh-water snails of Norway, including aspects of regional limnology. When finished, the study is expected to be printed in *Folia Limnologica Scandinavica*.

Fresh-water snails and data on environmental factors have been collected in about 1,350 lakes, rivers, ponds and other topographical types of water bodies. The distribution patterns of the various species are discussed in relation to: (1) possibilities for immigration following the last glaciation, and (2) present-day environmental factors (topographical type of habitat, altitude above sea level, geology, vegetation in the surroundings, macrovegetation in the water, substratum, wave exposure and physical and chemical factors in the water (pH, content of calcium, etc.)).

This is a preliminary report of some of the results arrived at in a study comprising the distribution, ecology and morphology of the fresh-water snails of Norway, including aspects of regional limnology (Ökland, in preparation).

Many data have not yet been fully evaluated and maps and diagrams are still incomplete. In this report a certain emphasis will be put on the background for the investigation, and on some of the methods and principles employed.

For the planning of the study two papers were of special importance, those of Boycott (1936), dealing with the habitats of fresh-water Mollusca in Britain, and of Hubendick (1947), considering the distribution and ecology of the fresh-water gastropods in South Sweden. These two studies had shown that the distribution of fresh-water gastropods could be correlated with certain factors of environment. The importance of the various factors seemed nevertheless to be different in the two areas. It was also evident that neither Britain nor South Sweden presented such a wide variety of habitats within a small geographical area as that which occurs in southeastern Norway. Here the gradient from lowland districts to high mountain areas, up to more than 2,000 metres above sea level, is of great ecological significance. Also, - and I consider this still more important - in the lowland part of southeastern Norway we find the region which geologically is called the Oslo Region. This fairly small geographical area has an unusually wide variety of bed rock and Quaternary deposits which greatly influence hydrochemical and biological factors in its numerous water bodies. In the present study this southeastern part of Norway has been especially closely studied.

The material was mainly collected during field studies carried out in 1953-57 and 1960-62 (the years 1958-59 were devoted to studies in a single lake and its environs, cf. Ökland, 1964). Of the about 1,350 habitats investigated, some 850 were sited in lakes, the remaining ones being sited in (or consisting of) ponds, ditches, mires, puddles, and slow-flowing and rapid flowing rivers. In all habitats investigated several factors of environment were measured. About 60,000 specimens of gastropods were collected and brought to the laboratory for closer examination.

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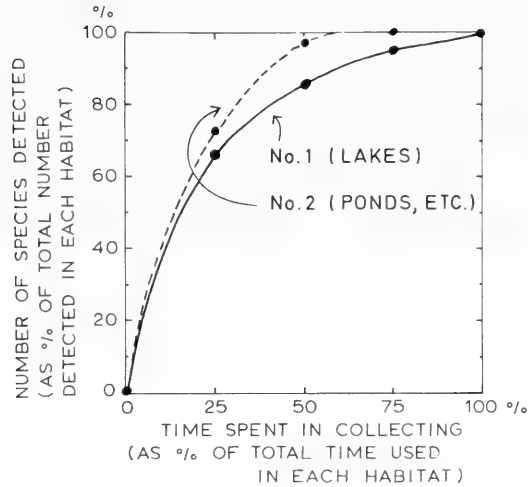


FIG. 1. Evaluation of the collecting efficiency in 1956, showing how the number of species detected in a given type of habitat increases with the time spent in collecting. The curves represent average values for, respectively, (1) 81 lakes, and (2) 49 ponds, puddles, ditches and mires.

The collecting of gastropods was restricted to shallow water, down to a depth of about 1.5 m. The major collecting device among vegetation and on soft bottom was a sieve mounted on a rod, about 1.8 m in length.

The habitat was the smallest unit investigated in the field. In each lake or river usually only one habitat was investigated. The habitat may be defined as a place where gastropods were sought and certain ecological factors measured and classified. In lakes and rivers the habitat consists of a certain stretch of shore - usually about 200 m - defined by special ecological characteristics. The average investigation time per habitat in lakes and rivers was 1 hour. For the smaller water bodies like ponds and puddles, the entire water body was investigated and considered as one habitat.

Experience soon showed for how long each habitat had to be investigated in order to obtain a satisfactory idea of the number of species present. Fig. 1 indicates how the number of species detected in a given type of habitat increases with the time spent in collecting. It also represents an evaluation of the collecting efficiency. The diagram refers only to habitats investigated in a special year. For the smaller water bodies, 97% of the total number of species found was encountered during the first half period of collecting, and not a single new species was found during the last 25% of the total collecting time. For the lakes, however, we note that the time interval covering the last 25% of total collecting time yielded a 5% increase in new species. Table 1 indicates the name of the 27 species of fresh-water gastropods present in Norway, and summarizes their main geographical distribution. A survey of my material as regards number of specimens collected and number of habitats where a given species was found is included.

There are two major factors determining the distribution patterns of the fresh-water gastropods: (1) dispersal abilities connected to the immigration following the last glaciation, and (2) present-day environmental factors in the fresh-water habitats.

The distribution patterns of species listed in column C (Table 1) seem to be related to barriers of dispersal. These species are present in the south of Norway and in the north of Norway, but they are lacking in areas in between, and also lacking in most parts of the western coastal areas. Among the fresh-water plants and the fresh-



TABLE 1. The fresh-water snails of Norway, with major geographical distribution ranges. Sources: The author's material, literature records, and museum collections (the latter still under revision).

	Type of distribution in Norway <sup>3</sup>							The Author's Material (Preliminary figures)	
	A	B	C	D	E	F	G	Number of specimens collected	Number of habitats with the species
Family: Lymnaeidae									
<i>Lymnaea stagnalis</i> (L.)	-	-	C	-	-	-	-	1,450	93
<i>L. palustris</i> (Müll.)	-	-	C	-	-	-	-	1,050	45
<i>L. truncatula</i> (Müll.)	A	-	-	-	-	-	-	3,200	405
<i>L. glabra</i> (Müll.)	-	-	-	D	-	-	-	1,750	71
<i>L. peregra</i> (Müll.)	A	-	-	-	-	-	-	15,550	788
<i>L. auricularia</i> (L.) s. str.	-	-	C	-	-	-	-	485	3
<i>L. glutinosa</i> (Müll.)	-	-	-	-	E	-	-	50	3
Family: Physidae									
<i>Physa fontinalis</i> (L.)	-	-	-	-	E	-	-	1,550	64
<i>Aplexa hypnorum</i> (L.)	-	-	-	-	E	-	-	500	24
Family: Planorbidae									
<i>Planorbarius corneus</i> (L.) <sup>1</sup>	-	-	-	-	E	-	-	200	6
<i>Planorbis planorbis</i> (L.)	-	-	-	-	E	-	-	35	2
<i>P. carinatus</i> Müll.	-	-	-	-	E	-	-	65	2
<i>Anisus spirorbis</i> (L.)	-	-	-	-	E	-	-	900	16
<i>Bathyomphalus contortus</i> (L.)	-	B	-	-	-	-	-	6,050	370
<i>Gyraulus acronicus</i> (Férussac)	-	B	-	-	-	-	-	19,300	782
<i>G. albus</i> (Müll.)	-	-	-	-	E	-	-	170	10
<i>G. laevis</i> (Alder)	-	-	-	-	-	-	G	-	-
<i>G. crista</i> (L.)	-	B	-	-	-	-	-	2,450	112
<i>Hippeutis complanatus</i> (L.)	-	-	-	-	E	-	-	1,100	73
<i>Segmentina nitida</i> (Müll.)	-	-	-	-	E	-	-	150	1
Family: Ancyliidae									
<i>Ancylus fluviatilis</i> Müll.	-	-	-	-	E	-	-	450	26
<i>Acroloxus lacustris</i> (L.)	-	-	-	-	E	-	-	1,000	88
Family: Viviparidae									
<i>Viviparus viviparus</i> (L.) <sup>1</sup>	-	-	-	-	E	-	-	200	8
Family: Valvatidae									
<i>Valvata cristata</i> Müll.	-	-	-	D	-	-	-	2,230	86
<i>V. piscinalis</i> (Müll.)	-	B	-	-	-	-	-	2,350	99
<i>V. sibirica</i> Middendorff	-	-	-	-	-	F	-	225	7
Family: Hydrobiidae									
<i>Potamopyrgus jenkinsi</i> (Smith) <sup>2</sup>	-	-	-	-	E	-	-	4,000	21

<sup>1</sup>Introduced c. 1890.

<sup>2</sup>A recent immigrant.

<sup>3</sup>A. Distributed in total Norway; B. Distributed in most parts of Norway; C. Distributed in the south and in the north, but lacking in areas in between and in most of the western coastal areas; D. Distributed only in parts of South Norway (including Trøndelag); E. Distributed only in parts of South Norway (lacking in Trøndelag); F. Distributed only in the northern parts of Norway; G. Distributed only in the western (Atlantic) parts of Norway.

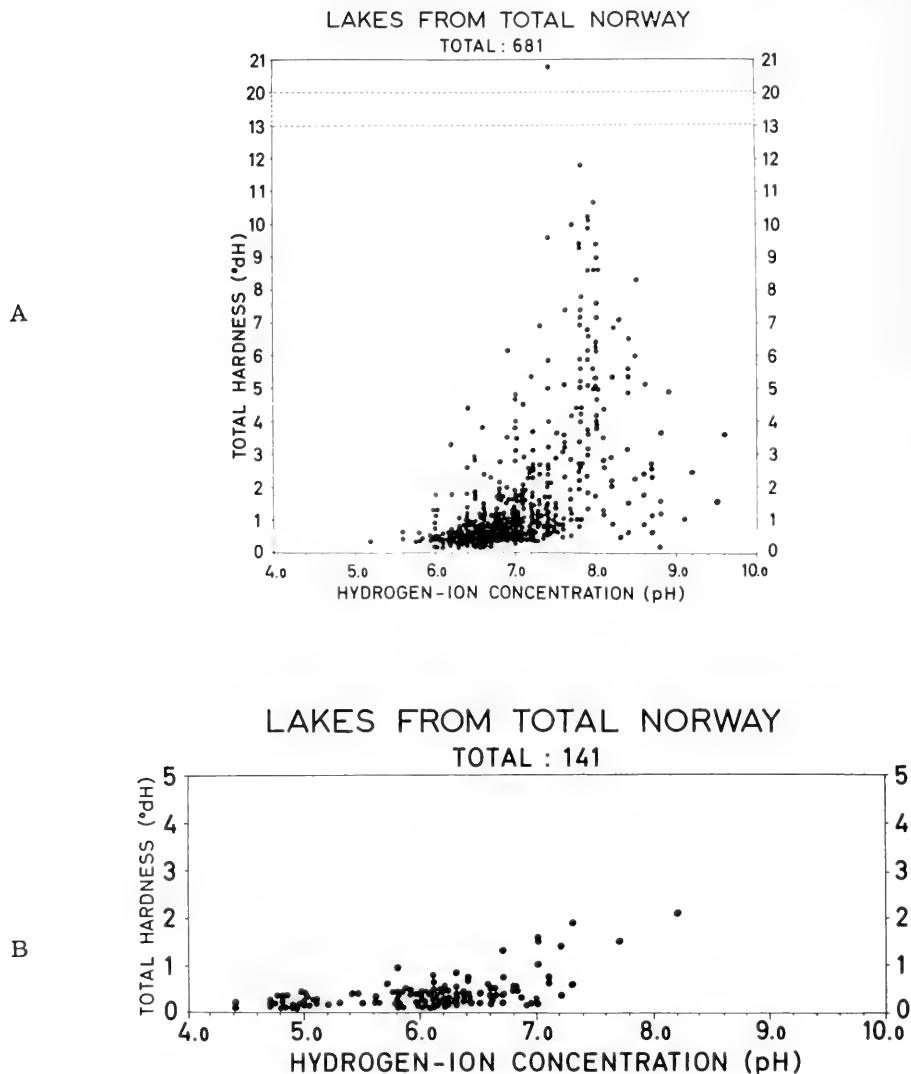


FIG. 2. Values for total hardness and hydrogen-ion concentration in 832 Norwegian lakes. Each lake is represented by one dot, based on a single surface water sample. The values for total hardness are given as °dH (1 °dH = 10 mg 'CaO'/l. Method: EDTA). A: Lakes with gastropods. B: Lakes where gastropods were not detected.

water fishes similar patterns of distribution are also found. Such species are mainly distributed in areas with slow-flowing water connections between Norway and the Baltic basin, from which a major part of the fresh-water organisms of Norway probably came in late- and post-glacial time.

Although dispersal abilities at least to some extent may influence the distribution patterns of gastropods, most fresh-water snails seem to be rather easily and freely dispersed, mostly in a passive way. The major agent for the dispersal is probably ducks and other water fowl. The main reason for presence or absence of certain

FREQUENCY DEVIATIONS IN RELATION TO TOPOGRAPHICAL WATER TYPE

ZERO: EXPECTED VALUE IN RANDOM DISTRIBUTION  
 ■ INCREASED FREQUENCY    ▨ DECREASED FREQUENCY

- A: LAKES
- B: PONDS
- C: DITCHES
- D: MIRES
- E: PUDDLES
- F: SLOW-FLOWING RIVERS
- G: RAPID

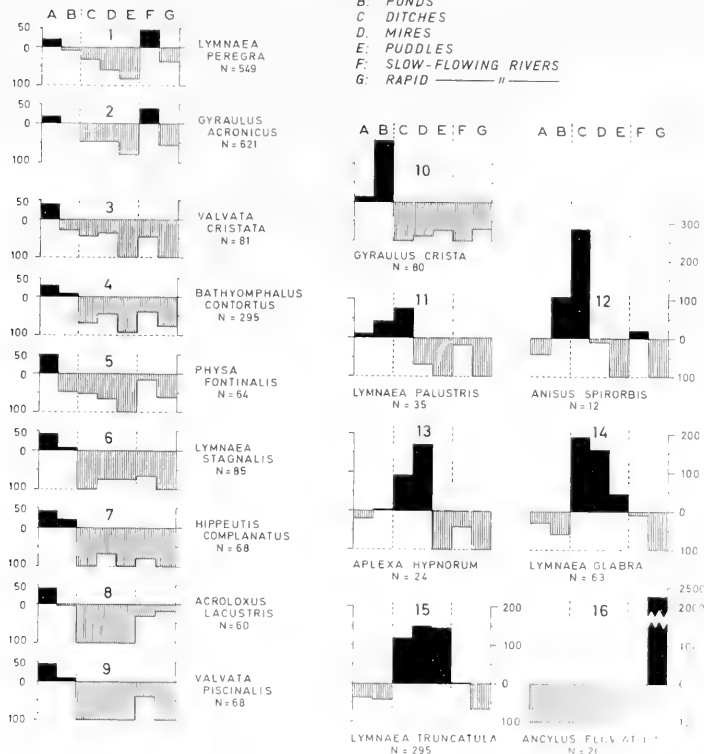


FIG. 3.

species of fresh-water gastropods is therefore connected with environmental factors in the fresh-water habitats.

Of the many environmental factors affecting the distribution we may shortly mention the total hardness of the water and the hydrogen-ion concentration. Fig. 2 shows values for total hardness and pH in 832 Norwegian lakes. (On average the calcium content of the water represents about 75% of the hardness values, the remaining part mainly being due to magnesium.) We note that lakes in which gastropods were not found in general are poor in lime and many of them are rather acid, with low pH-values.

Considering the fairly restricted geographical area of southeastern Norway, we may suppose that the distribution patterns here are mainly regulated by the different environmental conditions. The remaining part of this very preliminary report pertains to this southeastern part of Norway, roughly corresponding to the Norwegian concept of "Östlandet."

We shall first consider Figs. 3-5 dealing with "frequency deviations" and constructed on the assumption that within the small geographical area of southeastern Norway the presence or absence of certain species of gastropods are due to the different environmental conditions.

Fig. 3 pertains to 955 habitats investigated in southeastern Norway, split up into the different topographical categories A-G: Lakes, ponds, ditches, mires, puddles, slow-flowing and rapid-flowing rivers. Only the 16 species which I have found in at

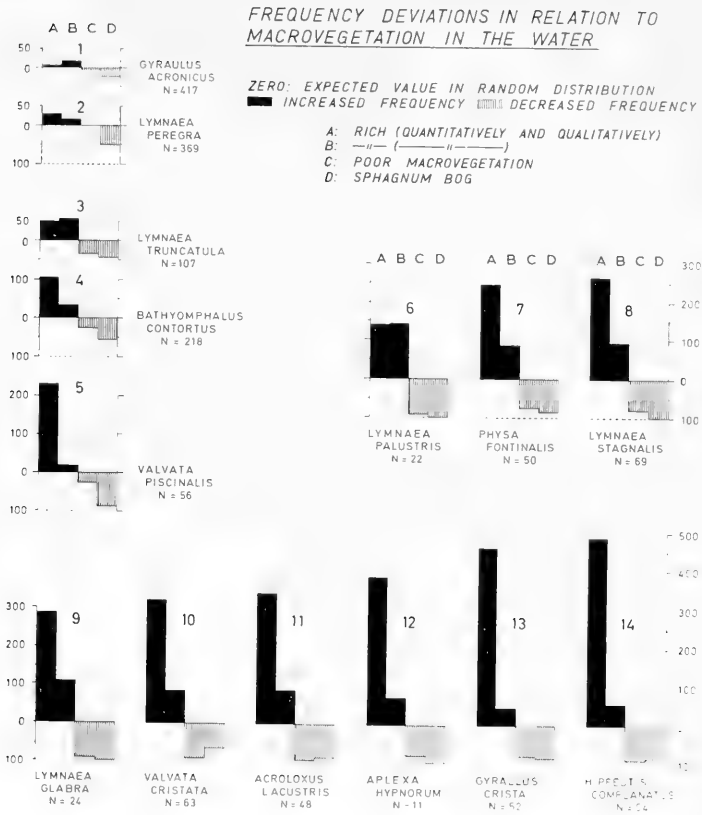


FIG. 4.

least 10 habitats are included. For each species black columns represent increased frequency, shaded columns decreased frequency, and the zero level represents expected frequency in random distribution. A decreased frequency of -100 represents complete absence in the category in question. We note, for instance, that *Lymnaea truncatula* (species No. 15) shows an increased frequency in the most shallow water bodies like ditches, mires, and puddles, a decreased frequency in lakes, ponds, and rapid-flowing rivers, and the frequency in slow-flowing rivers is very near that expected in random distribution. The calculation of this expected value may be illustrated by an example: Of the about 1,000 habitats investigated about 500 are lakes. Now, since *Lymnaea truncatula* has been found in about 300 habitats in all, we might expect that in a random distribution about one-half of these finds - that is about 150 records - would be from lakes, since the lakes constitute one-half of the habitats investigated. Instead, *Lymnaea truncatula* has only been collected in about 100 lake habitats, this representing a decreased frequency in relation to the expected value of 150. This decreased - or in other cases increased - frequency has been standardized in the diagrams in proportion to the different number of habitats investigated in each category, thus enabling a comparison of frequencies between different categories. Fig. 3 also indicates that *Ancylus fluviatilis* (species No. 16) has a tremendously increased frequency in rapid-flowing rivers, decreased frequency in slow-flowing rivers, and complete absence in stagnant waters (in Norway, this species does not occur in lakes as it does in other countries). In Fig. 3 we also note that a great many species show a tendency to a slightly increased frequency in lakes.

FREQUENCY DEVIATIONS IN RELATION TO TOTAL HARDNESS IN THE WATER

ZERO: EXPECTED VALUE IN RANDOM DISTRIBUTION  
 ■ INCREASED FREQUENCY □ DECREASED FREQUENCY

1°dH = 10 mg CaO/l

A: 0-1°dH  
 B: 1-2-||-  
 C: 2-5-||-  
 D: 5-21-||-

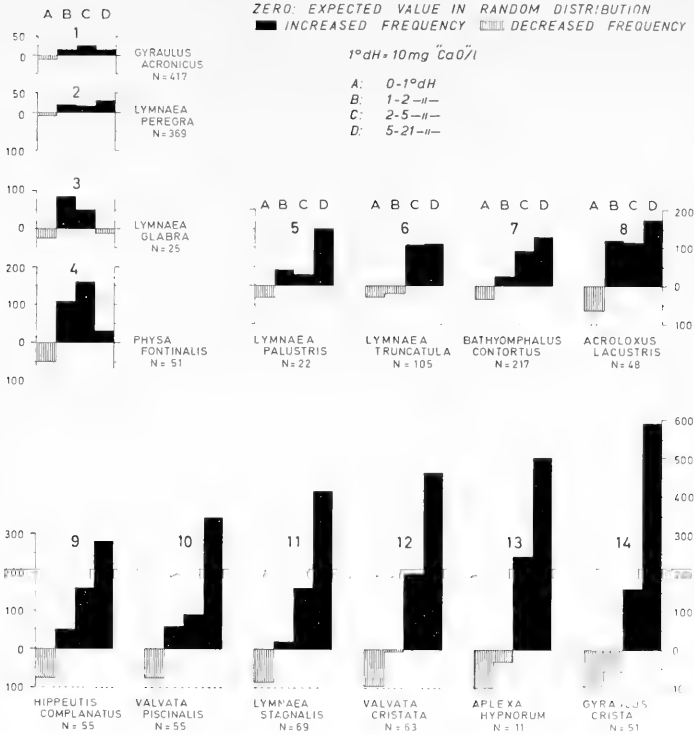


FIG. 5.

Fig. 4 pertains only to lakes and indicates frequency deviations in relation to macrovegetation in the water. The lake habitats are grouped into 4 categories according to how the macrovegetation in the water is developed: (A) rich macrovegetation, both quantitatively (much plant material) and qualitatively (many plant species); (B) rich macrovegetation, but only quantitatively (much plant material, but few species); (C) poor macrovegetation, and (D) *Sphagnum* bog.

We note that all species of gastropods show decreased frequency in habitats dominated by *Sphagnum* bogs, and most species also present decreased frequency in habitats with poor vegetation (category C). Where the macrovegetation is rich both quantitatively and qualitatively (as found in most eutrophic lakes), we note that the frequency of most of the species tends to be greatly increased.

Fig. 5 also pertains to lakes only. It indicates frequency deviations in relation to total hardness in the water. The lake habitats are grouped into 4 categories (A-D) according to the value for total hardness. We note that most species are favoured by a high content of lime salts in the water. Two species, *Gyraulus acronicus* (No. 1) and *Lymnaea peregra* (No. 2), however, are not particularly affected.

If we consider the relation between gastropods and environment in general, we find that although each species has its own way of reacting to the medium which surrounds it, there are general trends common to many species. This implies that we can study the importance of certain factors of environment in relation to the gastropod fauna as a whole (cf. also Hubendick, 1947).

TABLE 2. Lakes in southeastern Norway and occurrence of gastropods. The environment is treated from 9 different points of view (elevation above sea level, geology, etc., listed to the left). Each of these 9 categories is split up into groups, the elevation above sea level, for instance, into 5 groups (0-99 m, 100-199 m, etc.). For each group are indicated: (1) Total number of lakes investigated, (2) Mean frequency deviation for the gastropods (a measure explained in the text, positive figures indicating that the frequency is greater than expected in random distribution, negative figures indicating a decreased frequency), (3) Mean number of species per lake, and (4) Number of lakes with a given number of species.

LAKE ENVIRONMENT			TOTAL NUMBER OF LAKES INVESTIGATED	FREQUENCY DEVIATIONS MEAN VALUE FOR 14 SPECIES	MEAN NUMBER OF SPECIES PER LAKE	NUMBER OF LAKES WITH GIVEN NUMBER OF SPECIES					
						0-2 SPECIES		3-4 SPECIES		5-12 SPECIES	
						N	%	N	%	N	%
1	ELEVATION ABOVE SEA LEVEL	0 - 99 m	100	+ 81.0	4.0	28	28	36	36	36	36
		100 - 199 m	128	+ 20.6	3.2	62	48	35	27	31	24
		200 - 499 m	177	- 7.3	2.8	88	50	54	31	35	20
		500 - 999 m	121	- 67.8	2.0	79	65	42	35	0	0
		1000 <	16	- 78.1	1.9	14	88	2	13	0	0
		TOTAL	542			271		169		102	
2	GEOLOGY	UNALTERED CAMBRO-SILURIAN ROCKS	61	+ 193.1	6.2	3	5	14	23	44	72
		MARINE CLAY	109	+ 103.1	4.1	28	26	39	36	42	39
		ALTERED CAMBRO-SILURIAN ROCKS, ETC.	108	- 54.5	2.6	56	52	49	45	3	3
		PRE-EOCAMBRIAN ROCKS, ETC.	244	- 69.9	1.7	184	75	59	24	1	0
		TOTAL	522			271		161		90	
3	VEGETATION IN THE SUBURROUNDS	CULTIVATED FIELDS (A)	70	+ 155.5	5.2	15	21	15	21	40	57
		PASTURE LANDS	14	+ 41.8	4.0	5	36	4	29	5	36
		BOTH (A) AND (B)	143	+ 40.9	3.7	48	34	52	36	43	30
		CONIFEROUS FOREST (B)	259	- 50.3	2.1	157	61	88	34	14	5
		SUBALPINE BIRCH FOREST	30	- 72.2	1.8	23	77	7	23	0	0
		REGIO ALPINA	26	- 81.4	1.5	23	89	3	12	0	0
		TOTAL	542			271		169		102	
4	MARINO-VEGETATION ALONG THE SHORE	RICH VEG. (QUANT. AND QUAL.)	41	+ 238.0	6.5	1	2	8	20	32	78
		RICH VEG. (QUANTITATIVELY)	173	+ 65.6	4.1	52	30	60	34	61	35
		POOR MACROVEGETATION	255	- 61.4	2.0	159	62	90	35	6	2
		SPHAGNUM BOG	72	- 75.9	1.4	59	82	11	15	2	2
		TOTAL	541			271		169		101	
5	SUBSTRATUM	GYTTJA	10	+ 238.9	7.2	0	0	2	20	8	80
		DY-GYTTJA	132	+ 102.4	4.6	29	22	45	34	58	44
		CLAY	30	+ 9.3	3.2	13	43	10	33	7	23
		STONES	251	- 37.5	2.4	139	55	91	36	21	8
		DY	118	- 57.6	1.7	90	76	21	18	7	6
		TOTAL	541			271		169		101	
6	WAVE EXPOSURE	BOTH SMALL (A) AND MEDIUM (B)	62	+ 73.6	3.9	17	27	22	36	23	37
		SMALL WAVE ACTION (A)	216	+ 42.8	3.6	96	44	55	26	65	30
		MEDIUM WAVE ACTION (B)	227	- 51.4	2.1	137	60	78	34	12	5
		HEAVY WAVE ACTION	37	- 59.1	2.2	21	57	14	38	2	5
		TOTAL	542			271		169		102	
7	HYDROGEN-ION CONCENTRATION	pH = 4.4 - 6.6	214	- 57.7	1.7	161	75	43	20	10	5
		pH = 6.8 - 7.2	222	- 9.8	3.0	96	43	93	42	33	15
		pH = 7.4 - 7.8	58	+ 144.9	5.4	6	10	18	31	34	59
		pH = 8.0 - 8.8	40	+ 153.1	5.7	5	13	11	28	24	60
		TOTAL	534			268		165		101	
8	TOTAL HARDNESS	°dH = 0 - 1	363	- 55.2	2.0	243	67	103	28	17	5
		°dH = 1 - 2	71	+ 30.9	3.6	19	27	35	49	17	24
		°dH = 2 - 5	57	+ 115.1	5.0	7	12	23	40	27	47
		°dH = 5 - 21	49	+ 229.7	6.7	1	2	8	16	40	82
		TOTAL	540			270		169		101	
		9	WATER COLOUR AND TURBIDITY	TURBID WATER	43	+ 72.2	3.7	18	42	12	28
CLEAR, COLOURLESS WATER	261			- 4.7	3.1	117	45	92	35	52	20
SLIGHTLY BROWNISH-YELLOWISH WATER	150			+ 2.2	3.0	76	51	46	31	28	19
STRONGLY BROWNISH WATER	87			- 25.2	2.0	59	68	19	22	9	10
TOTAL	541					270		169		102	

In Table 2 such an aspect is presented. It refers to an investigation of 542 lakes in southeastern Norway. The lake environment is considered from 9 different points of view, as shown to the left. Each of these 9 major viewpoints is split up into different categories, and for each category are indicated number of lakes investigated, mean frequency deviation based on gastropods which have at least 10 occurrences in lake habitats, mean number of species per lake, and number of lakes with 0-2 species, 3-4 species, and 5-12 species (absolute number and percent).

If, for instance, we consider the elevation above sea level, we note that the frequency of gastropods decreases from lowland districts to areas of higher elevation. The mean number of species per lake also decreases (from 4.0 to 1.9). In the two last altitudinal groups comprising lakes located more than 500 m above sea level, none of the lakes investigated contained more than 4 species of gastropods, the majority having from 0 to 2 species.

Accordingly, Table 2 enables us to point out some general trends in the correlation between major factors of environment and the occurrence of fresh-water gastropods in southeastern Norway. It does not, of course, deal with the rather complicated problem of interaction between different factors.

#### LITERATURE CITED

- BOYCOTT, A. E., 1936, The habitats of fresh-water Mollusca in Britain. *J. Anim. Ecol.*, 5: 116-186.
- HUBENDICK, B., 1947, Die Verbreitungsverhältnisse der limnischen Gastropoden in Südschweden. *Zool. Bidr. Uppsala*, 24: 419-559.
- ÖKLAND, J., 1964, The eutrophic lake Borrevann (Norway) - an ecological study on shore and bottom fauna with special reference to gastropods, including a hydrographic survey. *Folia limnol. scand.*, 13: 1-337.
- ÖKLAND, J. (In preparation). Fresh-water snails (Gastropoda) of Norway. Their distribution, ecology and morphology, including aspects of regional limnology. (Provisional title). *Folia limnol. scand.*





SEVEN REPRODUCIBLE CHARACTERISTICS OF MECHANICAL BEHAVIOUR  
IN THE SNAIL'S FOOT MUSCULATURE (*HELIX POMATIA* L.)

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## INTRODUCTION

At the First European Malacological Congress in London (Postma, 1962) we gave a survey of the myogenic mechanisms that are responsible for a peculiar postural function of certain molluscan muscles, as recorded by an extension-time kymogram: tetanical activity as well as catch (Sperrung), respectively maintaining tension and shortening, or yielding with a given resistance to a stretching load.

Our object was the *Helix* foot musculature whose functioning is governed by the neurones of the cerebral and pedal ganglia and the intramuscular nerve net as well as by a few synapses in the pedal nerves, described by Schlote (1955). For the preparation of the foot muscle and mounting it in the lengthening device we refer to Postma (1962). We would like to introduce the three reasons which led Jordan to distinguish two mechanisms: a. the specific functional division of labor existing between cerebral and pedal ganglia: the former governing contractile (tetanical) activity (primarily via inhibition), the latter catch (autonomic controlled loosening) (Postma, 1962); b. contraction exhibits an optimal temperature, i.e., heat reduces resistance-like viscosity (Postma, 1962, appendix item 9; Jordan & Kipp, 1939); c. contractions superpose themselves on the extension time-curve.

In addition, we observed an interaction between both mechanisms: on the one hand the resistance may hinder movability (slackening as well as shortening), and on the other hand a certain degree of catch will ensure an optimal support of the contractile effect (Postma, 1962, appendix item 4). The distension which often introduces a contraction was interpreted as a loosening\* of catch in favour of shortening (Postma, 1962, appendix item 17). Jordan's argumentation was weak in two respects: that the kymogram reveals summatively part of both mechanisms in the resistance registered, and the role of the nerve net is unknown (Nieuwenhoven & Postma, 1969).

More convincing are results obtained from the ABRM\* of *Mytilus edulis* L.: nerve cells are absent (Deane & Twarog, 1957)<sup>1</sup>, C.A.\* and catch are functions of different groups of proteins, actin and myosin or these two together with paramyosin as the third one (Rüegg, 1960). These functions are abolished by specific substances: catch by 5-HT\* (Leenders, 1967b) and contraction by acto-myosin interaction inhibitors, such as salyrgan (Portzehl, 1952) and thiourea (Rüegg, 1963). Catch and C.A. may be measured separately, i.e., by the tension or shortening remnant\* (Jordan & Kipp, 1939) and by peak tension\* respectively. Moreover the ABRM lends itself to treatment by modern technics (Leenders, 1967), such as glycerine-extraction (fiber model) and quick release-recovery\*.

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\*For explanation please see p 160, 161.

<sup>1</sup>Recently Dr. H. H. J. Jaspar (lab. of neurophysiol.) did not succeed in making nerve fibers visible.

### CORRECTION AND COMPLETION OF THE MODEL OF CONTRACTILE AND CATCH MECHANISMS

According to Johnson et al., (1959) who reported catch by crystallization of paramyosin when pH decreased for 0.1 unit (thread model) and as well C. A. producing tension but not shortening, we proposed (Postma, 1962) a model including paramyosin linkages ("bolt pins") responsible for catch and linkages between actin and myosin ("wheels"), which would be active during production of tension or shortening (sliding filament hypothesis, Huxley, 1956). However, Leenders (1966) not only showed that the peak tension but also the tension remnant increase with ATPase\* activity. Since the mechanisms are not independent, Leenders (1967a, b) was led to propose his actomyosin-paramyosin hypothesis: one can better imagine an induction by paramyosin which prevents the contractile active actomyosin linkages from detaching. Moreover, Leenders successfully estimated an interaction similar to that which we observed in the *Helix* foot musculature. His contention is, therefore, in agreement with our functional interpretation of the pre-contractile slackening (Leenders, 1967). Thus we incorporate it into the sequence of activity stages which constitute a contraction. Moreover, we have inserted details obtained by proteolytic (Szent-Györgyi, 1953), structure-protein combining (Huxley, 1965) as well as electron-optical (Hanson & Lowy, 1964; Huxley, 1964) methods into the diagram shown in Fig. 1. Since smooth muscle exhibits "dense bodies" instead of Z-membranes, we limited our diagram to a detail lifted from a striated muscle sarcomere (a-b-c-d, between stage 2 and 3; Postma, 1962, p 154, fig. 1E) and represented it in stages 1-6 as explained in the fine type which follows:

#### Explanation to the model in FIG. 1

Stages of contraction (Proc. 1st Europ. Malac. Congr. p 162, fig. 11 sub. e-f-p, p-q, q-r and r-s): st(age 1. "resting length" (= r.l.). Stimulation between st. 1 and 2, followed by activation; a. break of linkages ( $\rightarrow \leftarrow$ ) allowing distension for 5% r.l.; b. myosin heads hook onto actine sites again (st. 3); c. contractile activation ( $\uparrow$ , st. 4), causing filament sliding and shortening (st. 5). Stimulation is stopped and relaxation follows (st. 6), unless catch ( $-o-$ ) makes it impossible (st. 5-p'). Afterwards lysis ( $\downarrow$ ) of catch is needed (st. 5-p"). Table between st. 3 and 4: four columns, st. 1 to 6, L(linkages) (in percent of available head and site pairs), A(ctivated) and C(atch).

#### THE REPRODUCIBLE CHARACTERISTICS

The kymogram of mechanical behaviour of the *Helix* foot is the summative expression of tetanic activity or its inhibition and of catch or its lysis (Nieuwenhoven & Postma, 1969). This behaviour may be modified considerably by extension, which necessarily implies the existence of a pronounced physiological change, whose site in the neuromuscular system, however, is unknown; perhaps these changes would involve sensory sources, synapses, neuromuscular junctions or pure myogenic sites (Büllbring, 1955; Rüegg & Tregar, 1966) As yet the snail's foot musculature is too complex for further analysis. More is to be expected from a study on the *Mytilus* ABRM, but little is known about reactions to stretch by molluscan retractor and adductor muscles. Thus the best data on stretch resistance are described in the following characteristic behaviour of the *Helix* foot:

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\*For explanation please see p 161.

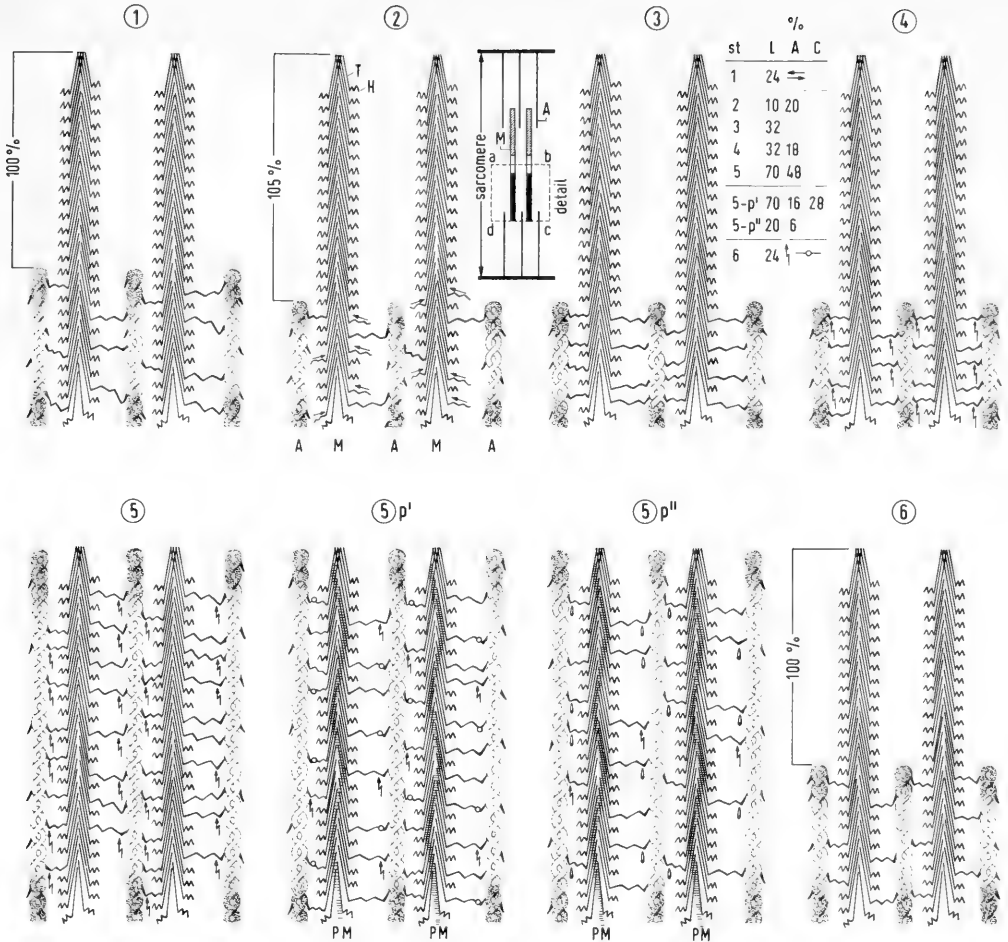


FIG. 1. Sequence of activity stages of a detail ( $\frac{ab}{dc}$ ) in a sarcomere in longitudinal section. M = Myosin molecules aggregated to filaments by the 'tails' (T).  $\text{w}$  = terminal 'heads' (H) (Huxley, 1964). A = Actin filaments: 2 strings twisted around each other, alongside active sites (J) to which the 'heads' may attach themselves, forming cross-bridges, which together constitute a structural network; the heads have capacity to split ATP, too.  $\equiv$  PM = Paramyosin: situation of molecules unknown; capacity to induce catch of bridges, causing fixation of structuration.

### 1. Specific role of the pedal ganglia<sup>2</sup>

The functional division of labor between cerebral and pedal ganglia, with respect to contraction and catch respectively, has been discussed previously (Postma, 1962). However, it may be mentioned that the *Helix* foot as P-preparation\* shows initially a low resistance to deformation. Lengthening is quickly followed by a synchronized catch: elongation starts nearly free, but ceases suddenly and at a certain niveau\* is maintained (Fig. 3-C heavy line parts).

<sup>2</sup>For *Mytilus* ABRM is only reported that the pedal ganglia cause autonomically a low catch level (Twarog, 1960, 1967).

\*For explanation please see p 160, 161.

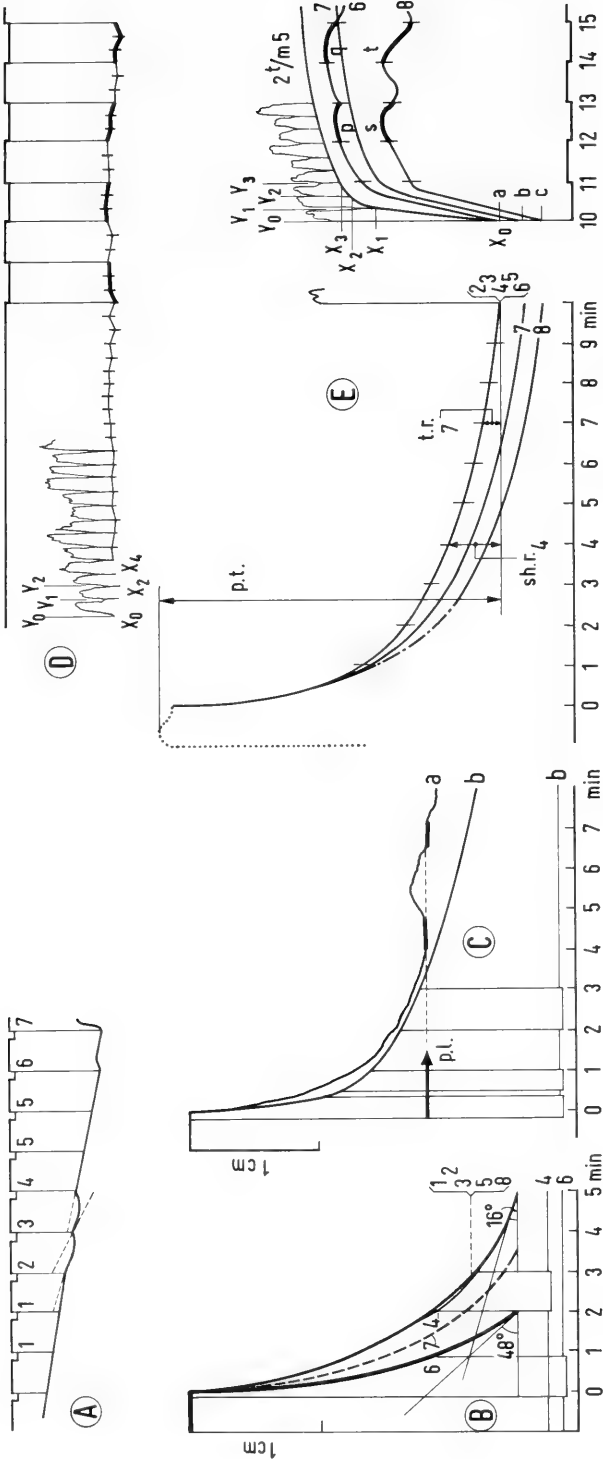


FIG. 2. Lengthening kymograms of *Helix* feet, N(et)-preparations\*. Abcissa: time in minutes; ordinates: elongation (in cm), measured from abscissa at the top, and caused by loading (10 g) the muscle; recording lever (Postma, 1933). -- Fig. 2A. Estimation of thresholds for evoking slackening and shortening. The numbers at the top indicate increasing strengths of stimuli: 1: subliminal; 2, 3 and 4: slackening, increasing effects; 5: indifference; 6 and 7: stronger stimuli cause contraction. -- Fig. 2B. Effect of lytic stimulation on pedal nerves. Curves 1, 2, 3, 5 and 8: without stimulation; during the 3rd min of the 4th extension stimulation with little or no effect. In the 6th curve, stimulation began 10 sec before the load was applied: the decrease of resistance is considerable; the periods of stimulation are indicated in the lower abscissa. -- Fig. 2C. The establishment of equilibrium between load and tension (heavy line parts) at plate length (p.l.) and the development of some shortening, shown in curve a are prohibited by stimulation in kymogram b. -- Fig. 2D. Testing of lytic stimulation on the resting foot. The recording lever is drawn up (time  $y_0$ ) for 20 sec, after which muscle and thread between foot and lever are stretched with the aid of 2 g load, till the lever stops (point  $x_1$ ). Every 20 sec that lifting and stretching are repeated and afterwards the line  $x_0$ - $x_2$ - $x_4$  etc., is drawn. Left half: stretching without; right side: with stimulation; every effect absent. -- Fig. 2E. Application of lytic stimulation during recovery\*. Left side: resistance free shortenings to 'peak tension' (p.t.), followed by slackening with remnants of shortening (tension) e.g., at 4 and 7 min lengthening (sh. r. 4, t. r. 7), 2-6 normal lengthening curves. Right side: recoveries. Curves 2-5 normal ones. After the 6th and 8th extension the pedal nerves are stimulated with lytic strength.

\*For explanation see p 160, 161.

### 2. External resistance during shortening<sup>3</sup>

The influence of external resistance was likewise discussed previously (Postma, 1962). It suppresses restoration of the C.A./catch ratio present before shortening was evoked (Postma, 1963, p 241).

### 3. The foot's reaction to lengthening

That extension itself changes the resistance to stretch was demonstrated via stimulation of sufficient strength to abolish the resistance (Fig. 2). Our observation (Postma & Mertens, 1966), that lytic stimulation - needed for completely counteracting resistance - is lower than that for contraction, has been confirmed (Fig. 2A). The effect is not pronounced and, therefore, understandably overlooked by Jordan at the start of his experiments (Postma, 1942; Lowy & Millman, 1959a, b). The same is shown in Fig. 2B curve 4 (3rd min). However, we had the impression that lengthening itself generates catch, which may oppose the effect of lytic stimulation. Therefore, we repeated the experiment (6th curve) switching-on excitation (1 min) 20 sec before the load was applied. The elongation that normally is reached in 5 min takes now 2 min, and the angle made with the abscissa is 3 times that without stimulation (48 i.st.o. 16°; cf. also Fig. 2C). Next we investigated the effect of lytic stimulation of the pedal nerves on the foot in resting condition (Fig. 2D). In order to do this, we first verified the behaviour of the muscle without stimulation by placing it under a small stretching load, insufficient to produce elongation; every reaction failed. Obviously detectable activity is obtained only if the foot is lengthened, or shortly after. In the resting muscle the linkages were stable.<sup>4</sup>

### 4. After-effects

Two such effects have been observed: one during recovery\* (extending load removed), and the other after lytic stimulation. Fig. 2E shows the initial fast recovery phase subsequent to unloading, followed by a slower after-recovery (curves 2-5 on right side). By lytic stimulation the quick recovery is retardable only; the second phase of recovery shows undermining (p, q) tending to reversal (s, t). Interruption of stimulation initiates resumption of recovery. Our conclusion is, therefore: the lengthening diagram as well as the recovery graphs reveal an active component. According to Leenders (1966), catch is produced simultaneously with C.A. That is, activity may continue after removal of the load and contribute to recovery.

The after-effect of lytic stimulation is shown in the Figs. 2B and 2E. After the effective stimulation (2B, curve 6) two resistance free contractions have been evoked, each followed by registration of a lengthening kymogram (7th and 8th). The latter repeats the course of the consecutive curves 1-6 preceding lytic stimulation: the resistance level\* is restored, in contradiction with curve 7. In Fig. 2E, the lengthening diagrams 7 and 8 show stimulation outlasting loss of resistance. The same holds for the 7th recovery; its level did not return to that of the recoveries produced by unstimulated musculature. The after-effects might suggest the activity of centra that produce these effects or the presence of certain substances (one which maintains catch, another which causes lysis).

<sup>3</sup>The condition of absence of external resistance was reported earlier with respect to *Pecten* adductor muscle (Bozler, 1930).

<sup>4</sup>Jordan (1930, 1935) distinguished stable and unstable catch as 'old' and 'young' viscosity.

\*For explanation please see p 161.

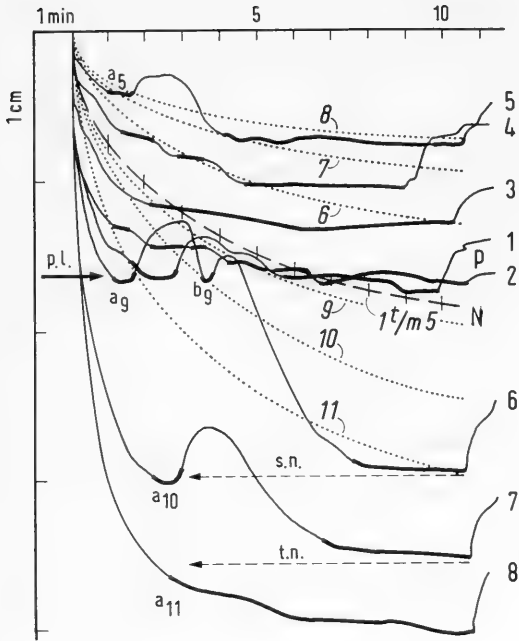


FIG. 3. Two series of lengthening diagrams obtained with 2 different *Helix* feet: 1 P-preparation (curves 1-8), the other an N-preparation (1-5 and dotted lines 6-11). Both series begin with curves characteristic for a "moderate" extending load: No. 2 as well as 2-5 (—, with spread I) repeat the type and course of the first ones. The 3 next lengthening reactions are obtained with half the 'moderate' load: the asynchronous catch (dotted curves 6-8) develops a proceeding increase of resistance (level). In the P-preparation, the niveaux of synchronized catch (heavy line-parts) shown by curves 1 and 2 (p.l.) rise stepwise in Nos. 3-5, with transient shortening at still higher niveau (a<sub>5</sub>). Afterwards lengthening is repeated with double 'moderate' load, which causes an opposite progression: gradual decrease of level (dotted graphs 9-11), stepwise descendance of niveaux, often preceded by a combination of catch and transient shortening (a<sub>9</sub> and b<sub>9</sub> at p.l., a<sub>10</sub> 2d niveau s.n.) at the length reached by the extension that preceded (according to adaptation? Cf. also Fig. 5, 14th-18th min); in curve 11 without contraction (a<sub>11</sub>, 3d niveau t.n.).

## 5. Reactions to the extending load

The weight of the load also plays an important role with respect to alteration in the ratio between the number of linkages active in catch and C.A. (Fig. 3). A small load emphasises catch development, a large one excess of lysis. As a result, only lengthening with moderate loads ensures restoration of the original ratio C.A./catch by shortening, with the provision that it can take place independently of external friction and that excitation is accomplished with the aid of 'indifferent' stimulus strength. The latter and the moderate load must be estimated at the beginning of each experiment if one is to obtain a series of repeating curves under otherwise unaltered conditions.<sup>5</sup>

## 6. Interaction between catch and C.A.

Since we had the impression that a high resistance to lengthening may either limit the speed as well as amplitude of contraction, or extremely low level causes impotence, we attempted to mimic that interaction by alteration of extending loads. Such an experiment is shown in Fig. 4. Indeed, there must be an optimal number of linkages guaranteeing sufficient 'internal support' (Postma, 1967) to develop resistance and shortening; fewer cause failure and too many would prevent normal movability.

## 7. Time, elongation and velocity

It struck us that critical situations - reactive interruption of lengthening, if it is induced by maintenance of length, or only in combination with collapse or shortening - often occur subsequent to certain time intervals, e.g., after start of extension or its continuation and at predisposed lengths. Two examples are given in Figs. 5 and 6. It ordinarily happens that interruption of resistance to lengthening which is preconditioned by stretch is finally overcome by lytic activity, i.e., caused by stimulation of the cerebral ganglia (in Fig. 5 before 18th min), as well as by autonomic activity of the pedal ganglia (Fig. 6, 4th min).

<sup>5</sup>Jordan (1905a, b) had reported earlier the promotion of shortening induced by small loads and lysis by large ones. He therefore distinguished between 'myogenic' and 'neurogenic' catch.

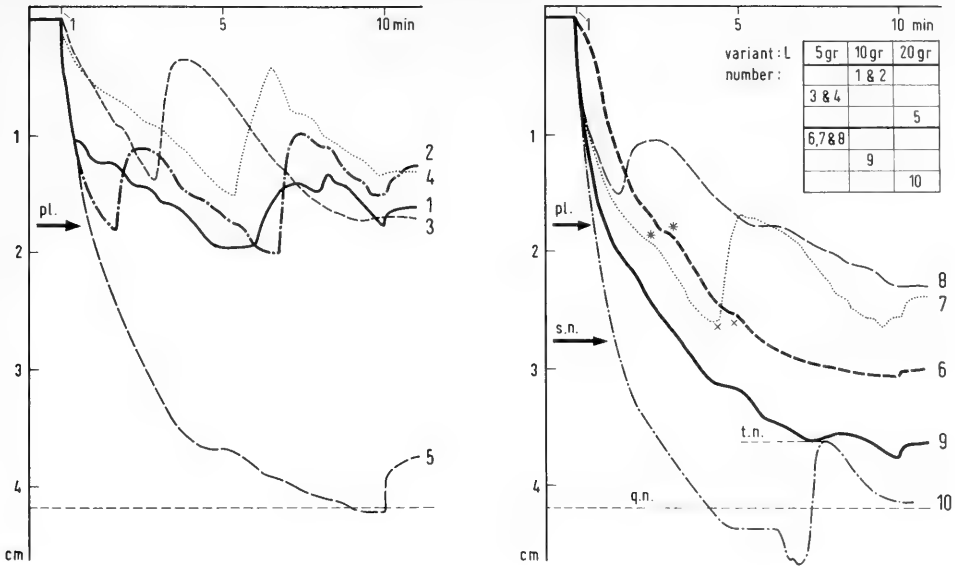


FIG. 4. Curves from a P-preparation. Table in the right corner gives numbers of successive extension curves and the loads (L) used: 10 g is nearly the indifferent load, 1 and 2 show critical reactions at p.l.; 3 and 4 respond at higher niveau, without progression. 20 g load causes break through of p.l.; not earlier than after 4 min and nearly 4 cm lengthening catch is manifest again (curve 5). Curves 6-8 with 5 g load show restoration of power to offer resistance and to develop contraction: No. 6 with 2 failures to stop lengthening (respectively at p.l., and at 2d niveau s.n.) and an after-effect of lysis (5th extension with 20 g load); No. 7 a failure at (\*), contraction at (x); No. 8 with restored power to lift 5 g and a transient niveau at p.l. Curve 9 with 10 g load: the course of Nos. 1 and 2 is not repeated, the restoration is not yet stabilized; thus after-effects present.

SUMMARY AND DISCUSSION

We described the great variability of mechanical behaviour of the *Helix* foot musculature. Its reproducibility (plate length, restoration of C.A./catch ratio) and the variability being experimentally inducible (depending on weight of load and stimulation strength), permits a hypothetical union of the behaviour and its scope under the 2 antagonistic effects mentioned earlier and its interaction. Extension of the foot activates both C.A. and catch; if the load is small, development of resistance is strengthened; a large load and weak stimulation promote lysis. An equilibrium between both antagonistic effects ensures a certain resistance level. The duration and velocity of lengthening will also be decisive for the mechanical behaviour (time-factor). Fast lengthening promotes quick generation of catch and increase of resistance until elongation is blocked. This effect occurs when the resistance is initially low, accruing from the presence of pedal ganglia, warmth or certain seasonal conditions (e.g., hibernation). An important question is how much the natural ratio bound/free actin sites ('structural condition') at the beginning of the loading, differs from that required to stop lengthening. The same holds for the critical-value of collapse. Pertinent in this connection is whether specific substances (Postma, 1962, appendix item 10b) in *Helix* foot are responsible for C.A. and make and break of linkages (depolarizers like acetylcholine and 5-HT, ions like Ca<sup>++</sup>), and what are the sensitive sites might turn out to be. With respect to the myogenic basis in *Mytilus* ABRM Leenders has

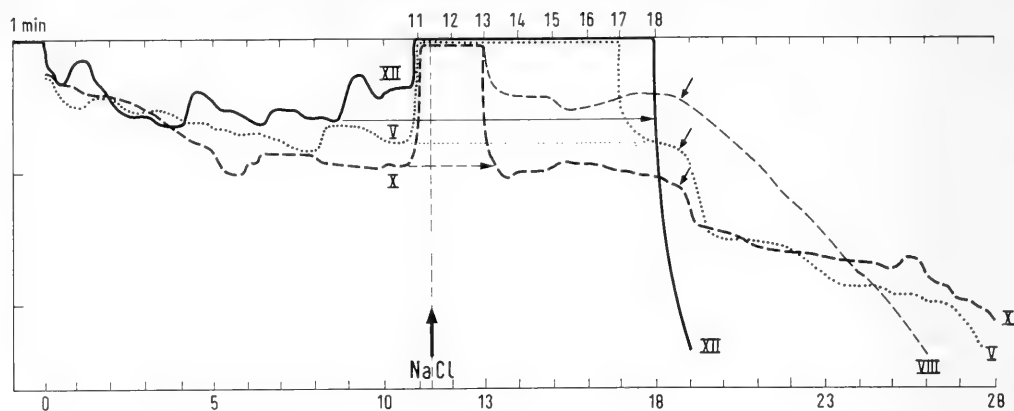


FIG. 5. Pairs of consecutive kymograms, each pair obtained from another *Helix* foot (V, VIII, X and XII) C-preparation. Ordinates and abscissa as in Fig. 2. Left half: curves which show tendency to prohibit that p.l. is surpassed. Right side: after restoration of the original condition by resistance-free contraction, chemical stimulation is applied (11th min) to the cerebral ganglion. Just 6-7 min later occurs abandonment of p.l. (✓), no matter whether at the end of the 13th (VIII and X), 17th (V) or 18th min is re-loaded (XII). Thus destruction of catch requires a certain time; the effect is, however, considerable only when during 6-7 min 'latency' the foot remained unloaded: catch generating lengthening was absent.

successfully observed a variability in mechanical response as a function of  $Ca^{++}$  liberated by different classes of stimulus<sup>6</sup>, C.A./catch interaction included (Leenders, 1967a, fig. 5 p 133, with optimal support by catch).

#### ABBREVIATIONS AND TERMS

ABRM = anterior byssal retractor muscle.

C.A. = contractile activity.

5-HT = 5-hydroxytryptamine = serotonin. The mechanical behaviour of the snail's foot muscle is the result of C.A. and catch of the actin-myosin linkages. Slackening requires linkage break via catch release (= lysis) or loosening. A lytic phenomenon reveals lysis e.g., caused by stimulation or accompanying contraction. Under isotonic conditions C.A. produces shortening, isometric registration delivers tension. In smooth musculature its maximum is characteristic for the response to a very definite excitation, known as 'peak tension' (Fig. 2E). Slackening is measured as tension decay via the 'tension remnant' at certain intervals after peak tension. Or it is recorded under isometric conditions via an extending load as lengthening-time curve. Its course is dependent on the presence of nervous centra. We distinguish:

C-preparations = with intact collar ring;

P-preparations = after removal of the cerebral ganglia under control of pedal ganglia;

N-preparation = under influence of nerve net only. The latter produce an extension kymogram typically different from those developed by P- and C-preparations (Figs. 3 and 5): the resistance to stretch is measurable via the slope of the curves (angle with abscissa), according to asynchronous C.A and catch, which show a

<sup>6</sup>Cf. also: BULLARD, Belinda, 1967, The nervous control of ABRM of *Mytilus edulis*. Comp. Biochem., 23: 749-759.



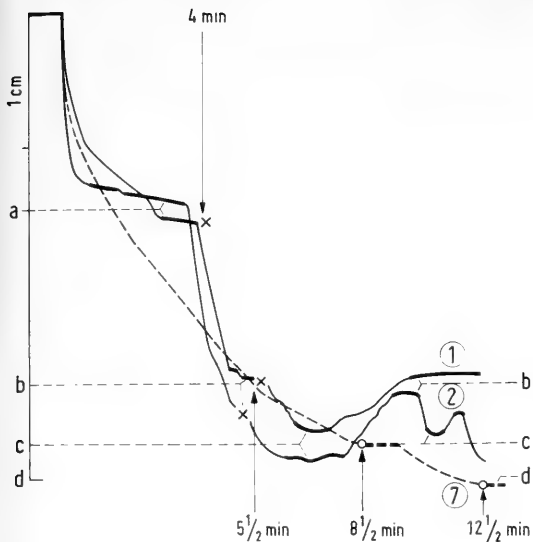


FIG. 6. Consecutive extension curves obtained from one *Helix* foot: Nos. 1 and 2 as P-preparation, No. 7 after extirpation of pedal ganglia. Critical elongations at the niveaux a-d at characteristic times. Collapse 4 min after loading and blocked lengthening in Nos. 1 and 2; successful catch in No. 1 and failure (x) in No. 2 at 5 1/2 min.

Both followed by once more interruption (niv. c) and return to niv. b. The N-preparation tries to interrupt extension at niv. c, known from the P-preparation after 8 1/2; and once more at niv. d after 12 min lengthening.

- DEANE, H. W. & TWAROG, B. M., 1957, Histology of an invertebrate smooth muscle. *Anat. Rec.*, 128: 538-539.
- HANSON, J. & LOWY, J., 1964, The structure of actin filaments etc., of vertebrate striated muscle. *Proc. R. Soc. B.*, 160: 449-459.
- HUXLEY, H. E., 1956, Muscular contraction. *Endeavour* 15: 177-188.
- HUXLEY, H. E., 1964, Structural arrangements and the contraction mechanism in striated muscle. *Proc. R. Soc., B.* 160: 442-448.
- HUXLEY, H. E., 1965, The mechanism of muscular contraction. *Sci. Am.*, 213: 18-27.
- JOHNSON, W. H., KAHN, J. S. & SZENT-GYÖRGYI, A. G., 1959, Paramyosin and contraction of 'catch muscles'. *Science*, 130: 160-161.
- JORDAN, H. J., 1905a, Untersuchungen zur Physiologie des Nervensystems bei Pulmonaten. *Pflüg. Arch. ges. Physiol.*, 106: 189-228.
- JORDAN, H. J., 1905b, Untersuchungen zur Physiologie des Nervensystems bei Pulmonaten. *Pflüg. Arch. ges. Physiol.*, 110: 533-597.
- JORDAN, H. J., 1930, Der Tonus glatter Muskeln als Funktion der Muskelfluidität u.s.w. *Proc. R. Acad. Sci.*, Amsterdam, 33: 788-791.
- JORDAN, H. J., 1935, Tonische Verkürzung und tonisches Festhalten der Verkürzung bei den Muskeln von *Aplysia limacina* unter Einfluss wechselnder Temperaturen. *Proc. R. Acad. Sci.*, Amsterdam, 38: 358-364.

gradual and prolonged increase in resistance. It is distinguished as 'level' from 'niveau' or length secured by synchronized catch, characteristic for P- and C-preparations. That niveau is conditioned by the length to which the foot permitted stretching taut and was pinned out on the wax plate before and during dissection (cf. p(ate) l(ength)). After removal of the extending load, the *Helix* foot partly reshortens (= 'recovery') because of the tension present. The same occurs when under isometric conditions the muscle is allowed to distend suddenly ('quick release'), assumed that C. A. has not yet stopped (= 'q.r.-recovery').

ATP = Adenosine Tri-Phosphoric acid; the energy rich P-bonds can be split by the enzymatic capacity of actomyosin-ATPase, under placing the energy at the disposal of the filament-sliding mechanism (C. A.).

#### REFERENCES

- BOZLER, E., 1930, Untersuchungen zur Physiologie der Tonusmuskeln. *Z. vergl. Physiol.* 12: 579-602.
- BÜLBRING, E., 1955, Correlation between membrane potential, spike discharge and tension in smooth muscle. *J. Physiol.* 128: 200-221.

- JORDAN, H. J. & KIPP, P. J., 1939, Die Leistungen und feine Struktur der glatten Hohlmuskeln bei *Metridium senile* L. *Proc. R. Acad. Sci.*, Amsterdam, 42: 849-858.
- LEENDERS, H. J., 1966, Kontraktion und Spannungsrückstand an glycerinextrahierten Muskelfasern (ABRM) von *Mytilus edulis*. *Naturwiss.*, 53: 617.
- LEENDERS, H. J., 1967a, Der Einfluss der Sperrung auf die Kontraktion. Untersuchungen am ABRM von *Mytilus edulis* L. *Pflüg. Arch.*, 295: 127-135.
- LEENDERS, H. J., 1967b, Ca-coupling in the anterior byssus retractor muscle of *Mytilus edulis* L. *J. Physiol.*, 192: 681-693.
- LOWY, J. & MILLMAN, B. M., 1959a, Contraction and relaxation in smooth muscles of lamellibranch molluscs. *Nature*, Lond., 183: 1730-1731.
- LOWY, J. & MILLMAN, B. M., 1959b, Tonic and phasic responses in the anterior byssus retractor muscle (ABRM) of *Mytilus*. *J. Physiol.*, 149: 68P-69P.
- NIEUWENHOVEN, S. J., L. M. v. & POSTMA, N., 1969, Le comportement mécanique de la musculatur du pied de l'Aplysie ponctuée (*Aplysia punctata* Cuv.) et sa base nerveuse. *Neth. J. Zool.* 19: 140-143.
- PORTZEHL, H., 1952, Der Arbeitszyklus geordneter Aktomyosinsysteme (Muskel und Muskelmodelle). *Z.f. Naturforsch.* 7b, 1-10.
- POSTMA, N., 1933, Recherches sur l'allongement du pied de l'escargot (*Helix pomatia* L.) etc. *Proc. R. Acad. Sci.*, Amsterdam, 36: 360-371.
- POSTMA, N., 1942, Active changes in the (viscosoid) tonus of smooth muscles extended by means of a weight. *Arch. neerl. Physiol.*, 26: 426-434.
- POSTMA, N., 1962, Some features of gastropod musculature and the control mechanism of its activity. *Proc. First Europ. Malac. Congr.*, 153-167.
- POSTMA, N., 1963, The contribution to smooth muscle physiology in general by the study of postural function in molluscs. *Proc. malac. Soc. Lond.*, 35: 225-245.
- POSTMA, N., 1967, Zwei Beispiele von "innerer Unterstützung" der Verkürzungsaktivität des Fusses der Weinbergschnecke. *Pflüg. Arch.*, 294: 49.
- POSTMA, N. & MERTENS, J., 1966, Ueber Reizschwellen für Tonuslösung beim *Mytilus*-ABRM und *Helix*-Fuss. *Pflüg. Arch.*, 289: S. R 40.
- RÜEGG, J. C., 1960, Tropomyosin and tonus in lamellibranch adductor muscles. *Biochem. bio-phys. Acta*, 35: 278-279.
- RÜEGG, J. C., 1963, Actomyosin inactivation by thiourea and the nature of viscous tone in a molluscan smooth muscle. *Proc. R. Soc., B.* 158: 177-195.
- RÜEGG, J. C. & TREGAR, R. T., 1966, Mechanical factors affecting the ATPase activity of glycerol-extracted insect fibrillar flight muscle. *J. Physiol.*, 165: 497-512.
- SCHLOTE, F. W., 1955, Die Erregungsleitung im Gastropodennerven und ihr histologisches Substrat. *Z. vergl. Physiol.*, 37: 373-415.
- SZENT-GYÖRGYI, A. G., 1953, Meromyosins, the sub-units of myosin. *Arch. Bioch. & Biophys.*, 42: 305-320.
- TWAROG, B. M., 1960, Innervation and activity of a molluscan smooth muscle. *J. Physiol.*, 152: 220-235.
- TWAROG, B. M., 1967, The regulation of catch in molluscan muscle. *J. gen. Physiol.*, 50: 157-169.

#### ZUSAMMENFASSUNG

Einige Reaktionen der isolierten und in Verbindung mit höheren Nervenzentren stehenden Fussmuskulatur der Weinbergschnecke auf a. Dehnung, b. Grösse der Dehnungslast und c. Unterbrechung der Dehnung, werden beschrieben. Hierbei fallen Gesetzmässigkeiten bei bestimmten Längen und Zeiten auf. Dieses mechanische Verhalten der *Helix*-Fussmuskulatur wird unter Berücksichtigung der Befunde LEENDERS am ABRM der Miesmuschel diskutiert.

PHYLOGENETIC INTERRELATIONSHIPS AMONG FAMILIES  
OF BIVALVE MOLLUSCS

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INTRODUCTION

One of us (R.D.P.) has been responsible for the zoological aspects of the investigations reported in this paper, including accumulation of data, drafting the questionnaire and interpretation of the information supplied by the computer program. The remainder of the work, including the drafting of computer programs, the encoding of the raw data, and the handling of the computer, has been the responsibility of the other (D.B.).

We would like to express our thanks to Dr. M. E. Solari, of the Department of Mathematics, Chelsea College of Science and Technology, for her very helpful advice on methods adopted in the investigation.

THE TRADITIONAL, INTUITIVE APPROACH

Cox (1960), reviewing attempts to classify the Bivalvia during the last 200 years, observed that zoologists are still divided in their opinions even as to the name of the class! The terms "Lamellibranchiata" and "Pelecypoda" are not strictly applicable to all members of the class, and the older, Linnean term "Bivalvia" is more appropriate from a descriptive point of view. We follow Cox in using the Linnean term "Bivalvia," and pray that other names for the class be abandoned.

Two centuries after Linnaeus' *Systema Naturae*, and one century after *The Origin of Species*, we seem to have made little progress in our attempts to produce a natural classification of the Bivalvia. Most of the classificatory systems reviewed by Cox (1960) are little more than clerical systems based on only one or two organ systems such as the shell, the ligament, hinge teeth, pallial line, mantle fusion, siphons, ctenidial structure, ctenidial frontal ciliation, stomach structure, etc. These various classificatory systems agree or conflict with each other to greater or lesser extent according to the taxobases employed. Cox concluded from his review that "The history of bivalve taxonomy ... has been one of continual disagreement as to which characters are of real taxonomic value; that is, which give the most reliable clue to phylogenetic affinities."

We propose to comment briefly on only a few of the more interesting classificatory systems, as follows: The system of Thiele (1935) is unsatisfactory in three respects. The Nuculacea and Arcacea are not closely related and should not be associated in the order Taxodonta; the Protobranchia, in fact, should be assigned to a separate subclass (Owen, 1959; Purchon, 1959; Yonge, 1959). The term "Anisomyaria" is unsuitable for an assemblage which includes the Dimyidae and does not include all anisomyarian bivalves. Finally, *Trigonia* is a filibranch, and should not be included in an order named the Eulamellibranchia.

The systems of Pelseneer (1891, 1906, 1911) are based on gross ctenidial structure. The ctenidia, as organs of feeding, are liable to exhibit adaptive changes and are accordingly ill-suited as markers of phylogenetic relationship. Ridewood (1903) showed that union of adjacent ctenidial filaments could be arranged in five stages, i.e., by inter-locking ciliated discs (two stages) and by organic unions (three stages). In

four families, the Arcidae, Anomiidae, Aviculidae and Spondylidae, some species had advanced in this respect one stage beyond the remainder of the family. This is strong evidence of parallel evolution by a number of phylogenies through a series of "functional strata" (Figure 1) (Ridewood, 1903; Purchon, 1960a). The distinction between Filibranchia and Eulamellibranchia is a gross over-simplification.

Atkins (1938) distinguished two categories of bivalves, according to the types of cilia found on the frontal surfaces of ctenidial filaments. It is difficult to accept Atkins' judgement that the latero-frontal cilia of the Ostreidae are "anomalous" on the basis of the evidence published, and it appears that this conclusion was reached on other grounds with a view to placing the Ostreidae where on *a priori* grounds Atkins thought suitable.

Classification of the Bivalvia by sub-division into progressively smaller units has not been very successful. An archaic feature may have been lost independently in many different phylogenies, and an advanced feature may have evolved independently in more than one phylogeny. Sub-division of the class according to the occurrence of such organs could produce very different results according to the relative importance assigned to each variable. It follows that little may be achieved by attempting to collate the available classificatory systems, each of which is based on subjective appraisals of a restricted range of anatomical variables.

An alternative approach to classification is to cluster genera into families, families into sub-orders, etc., according to the available evidence. This depends on a subjective appraisal of the reliability of the evidence; what is the statistical probability of a given organ, or complex of organs, evolving independently in two unrelated phylogenies? If this probability is sufficiently low it can safely be disregarded. One of us (R.D.P.) has been taken to task on the validity of this line of reasoning (Ghiselin *et al.*, 1967), but remains unrepentant. The families Tellinidae, Psammobiidae, Donacidae, Semelidae and Solecurtidae possess a cruciform muscle and partly on the basis of this information the first four of these families are clustered together in the order Tellinacea (Graham, 1934, 1934a). The Solecurtidae are doubtless derived from the same origins. The presence of a shell apophysis, and the insertion of the pedal muscles on to this apophysis, in the families Pholadidae and Teredinidae offer good grounds for grouping these two families in the order Adesmacea. The proposition that the common possession of such features is evidence of descent from a common ancestry, carries sufficiently high probability for acceptance.

When we turn to the occurrence of a postero-dorsal stomach caecum, appendix, or wood-storing caecum, on the other hand, we are on more difficult ground. These organs are judged to be homologous (Purchon, 1941, 1960) and this indicates that their possessors are related by descent from a common ancestor. This does not necessarily indicate close relationship between the orders Tellinacea and Adesmacea, for a homologous stomach caecum has also been found in certain species of *Mytilus*, *Ostrea*, and *Lima* (Reid, 1965; Dinamani, 1967). This suggests that the stomach appendix (=caecum) may be an extremely archaic structure which may have been possessed by all, or very many, bivalves in the remote past, but which has been independently lost in the majority of lineages.

To summarise, these contrasted and complementary methods of elaborating a phylogenetic classification of the Bivalvia do not seem to have taken us very far towards our objective. The most that has been achieved by attempts to sub-divide the class into smaller categories has been the isolation of the Protobranchia in a distinct subclass. Some success has been achieved in the clustering of families into orders (we have not attempted to review the whole of this field of endeavour), but much remains to be done.

In drafting a classificatory system it is sound scientific procedure to use one's

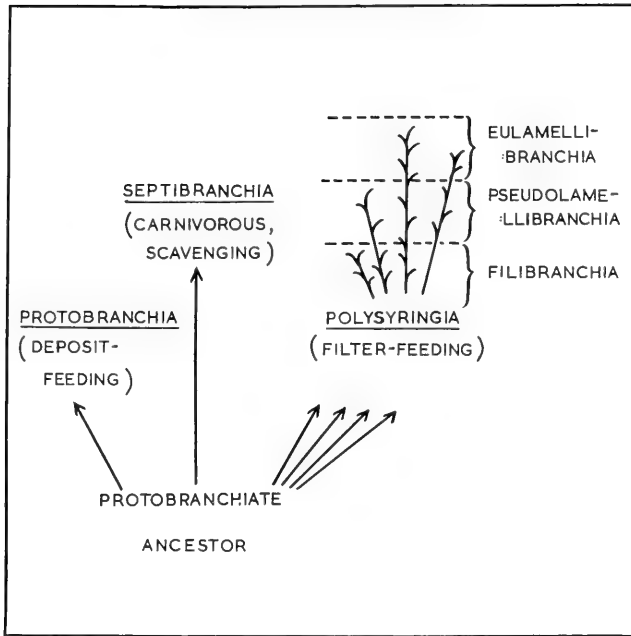


FIG. 1. Diagrammatic representation of the probable course of the early stages of adaptive radiation of bivalve molluscs, on the basis of the feeding mechanisms adopted. The terms "Filibranchia", "Pseudolamellibranchia" and "Eulamellibranchia" represent a sequence of functional strata through which many lineages of filter-feeding bivalves may be evolving independently.

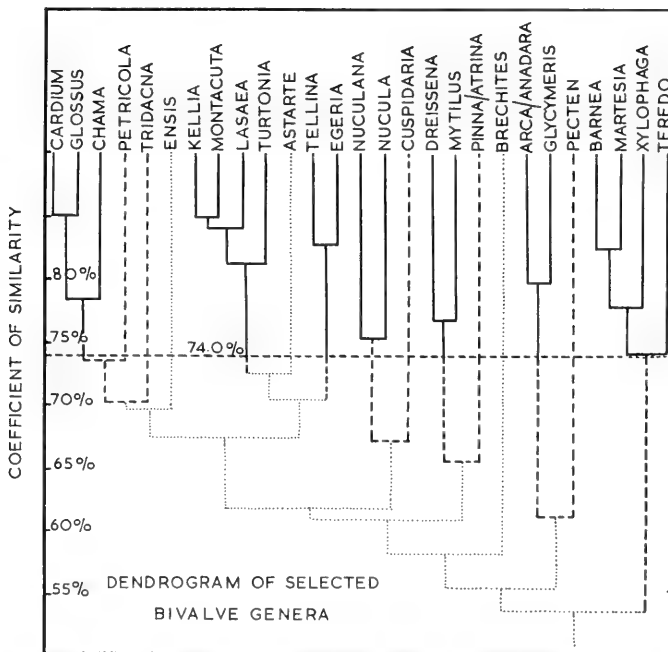


FIG. 2. Due to inadequacy of data from any one source it was necessary to combine information from *Arca similis* and from *Anadara granosa* to form the lineage "Arca/Anadara." *Anadara* is a sub-genus of *Arca*, and the two species are comparable in being members of the superficial in-fauna and in lacking byssal attachment in the adult state. It was similarly necessary to combine data from different sources to form the lineage "Pinna/Atrina."

intuition and thereby avoid unnecessary expenditure of time and energy in the laborious accumulation of data which may ultimately prove useless. Our previous remarks, therefore, should not be regarded as being unappreciative of the efforts of our predecessors. As regards the phylogenetic classification of the Bivalvia, however, such intuitive selection of evidence has not been generally successful. It is possible that the emergence of the highly efficient filter-feeding habit led to an immediate, explosive radiation with the simultaneous production of many independent lineages, few of which underwent subsequent major sub-division. If this had been the case there would be few examples of close phyletic relationship between pairs, or among groups, of families, and all attempts to detect phylogenetic groupings of families would be doomed to failure. This is by no means impossible.

Alternatively, perhaps, there may be phyletic groupings of families evidence of which lies in subtle combinations of characters rather than in the crude presence or absence of only one or two characters. If so, such phyletic relationships could only be revealed by the detailed analyses of large numbers of characters which can now be made with the aid of computers. Before pursuing this further we must refer to an observation by Ridewood (1903). Although Ridewood drew up a system of classification on the evidence supplied by his very extensive review of the structure of the ctenidia of bivalves, he regarded this as being no more than one contribution towards a solution of the problem. After many other reviews had been made of other organ systems, Ridewood envisaged the results of all these reviews being compared, a definitive classificatory system being produced from all the evidence. Ridewood doubtless had not considered the vast scope of such an exercise, the extent to which evidence from different organ systems would be in conflict rather than in harmony, or the great aid which would eventually become available through the use of computers. Undoubtedly, however, his view was right. Now, perhaps, we are beginning to approach the time when an attempt can be made to review the whole evidence, and this paper is a preliminary report on current work at Chelsea College of Science and Technology on this subject. The chief purpose of this paper is to ascertain whether the procedures adopted are capable of producing meaningful results and, if so, what level of credibility can be applied to the results of the comparisons by computer. If, beyond these objectives, the analysis throws any new light on probable phylogenetic relationships above the level of families, then the exercise will be extended with a view to increasing the level of acceptability of results.

#### INVESTIGATION WITH THE AID OF COMPUTER PROGRAMS

The first step in the present exercise was to study the methods of numerical taxonomy as expounded by Sokal & Sneath (1963). Difficulties were encountered regarding the methods of dealing with multi-state characters; generally speaking, where there were three or more answers to any one question it was not possible to arrange the answers in a linear series and assign a hierarchical series of values to the various alternative answers. Even where this would have been possible, much important information would have been lost by the subsequent process of determining the mean of all the answers to a given question and grouping all those answers below the mean on the one hand, and all those answers above the mean on the other hand. Even if this procedure had been desirable on analytical grounds, which it was not, it would have been quite impracticable for the present exercise; it would have necessitated re-calculating means for all questions whenever a few more genera were added to the survey before the coefficients of similarity of these genera could be assessed. The procedure adopted for multi-state characters was to treat each answer to a given question as being distinct from all other possible answers to that question. When comparing any two genera with a view to assessing the coefficient of similarity, for each question posed

the animals are either identical or they are different. By the adoption of this procedure no information is lost, and no preliminary assumptions (e.g., as to affinities between filibranchs and pseudolamellibranchs, between pseudolamellibranchs and eulamellibranchs,) are made.

In the present exercise all criteria are held to be equally relevant, and none is weighted. The only limit to the questions employed has been availability of information. The questions have not been confined to comparative anatomy, but have ranged over geographic distribution, ecological preferences, behaviour, physiology, etc. It is appreciated that excessive attention to one organ system might bias the results, but it is thought better to use all the available information rather than to omit some information (necessarily on subjective grounds) in order to balance the information obtained from contrasted sources. The purpose of the exercise is to obtain the largest possible random sample of information relating to the genetical constitution of each genus investigated. As many different answers were drafted as were required to record objectively the different conditions observed. It follows that as the investigation extends to cover more genera, the number of possible answers to any one question will gradually increase. Since each answer is regarded as distinct from all other possible answers, no difficulty is encountered with regard to those genera which have already been processed. At the present time 27 genera have been subjected to scrutiny, and the questionnaire includes 96 questions. 49 of these questions have 2 alternative answers, 20 have 3 alternative answers, 5 have 4 alternative answers, 11 have 5 alternative answers, 7 have 6 alternative answers, while 1 each have 7, 8, 9 and 11 alternative answers. In all there was a total of 310 possible answers to the 96 questions posed.

For each genus certain questions were logically barred, and these were not used; thus for septibranchs it was not possible to answer questions concerning the structure and ciliation of the ctenidial lamellae. For each genus a few questions could not be answered due to lack of available information. This paper is confined to consideration of 27 genera for which a very high proportion of answers was obtained. When comparing any two genera two statistics were available: 1) the total number of questions for which answers were obtained for both genera, 2) the number of questions for which the same answer was obtained for both genera. The latter was expressed as the percentage of the former, this figure providing a measure of the coefficient of similarity of the two genera. Thus *Barnea* and *Martesia*, both members of the family Pholadidae showed a coefficient of similarity of 82.4%, while *Tellina* and *Egeria* which are members of different families in the order Tellinacea showed a coefficient of similarity of 82.7%.

The organisation of the computer program was as follows: The data, comprising the coded answers to the questionnaire, were read for each genus under investigation and stored internally. Each genus was then compared with every other genus under investigation and the two statistics, 1 and 2 defined above, were calculated and stored. The second phase was the production of the results in such a way that a dendrogram could easily be constructed. At each step one genus was combined with a second genus, or with a group of genera, the choice being made so that the coefficient of similarity was the highest of all the possible pairings, whereupon the identifying codes for the cluster of genera were output together with the calculated coefficient. One of the pair was deleted from further consideration, and its two statistics added to the corresponding quantities for the second group, the group thus newly formed being identified by the higher of the code numbers of its two constituents. In this way the total number of groups was reduced by one, and the process was repeated until only one group remained. The dendrogram so produced is shown in Figure 2.

Inspection of Fig. 2 shows that analysis of data by computer corresponds closely

at many points with the traditional views on the phylogenetic groupings of genera. This is in spite of the random nature of the information used, and the inclusion of many data hitherto regarded as irrelevant to any discussion on phylogeny; e.g., the grouping of the erycinaceans, *Kellia*, *Montacuta* and *Lasaea*; e.g., the grouping of the tellinaceans, *Tellina* and *Egeria*; e.g., the grouping of the protobranchs *Nucula* and *Nuculana*; e.g., the grouping of *Arca similis* and *Anadara granosa* with *Glycymeris*. The most striking cluster, however, is that of the rock- and wood-boring pholads, *Barnea* and *Martesia* with *Xylophaga* and with the shipworm, *Teredo*.

It is clear that if the exercise were extended to cover many more genera, there would be substantial changes in the lowermost part of the dendrogram; we should not take too seriously the suggested groupings for *Ensis*, *Astarte* and *Brechites* (dotted lines), or for *Petricola*, *Tridacna*, *Cuspidaria*, *Pinna* and *Pecten* (broken lines). It seems necessary, therefore, to adopt a "level of credibility" for such a dendrogram, below which the associations suggested should not be regarded as trustworthy. In this case the highly orthodox results for the rock- and wood-boring genera in the Pholadidae and Teredinidae suggest that the "level of credibility" of the dendrogram should be set at 74.0%.

It is hoped that extension of the survey to cover many more genera will provide good grounds for setting the level of credibility at a considerably lower level, and that the procedure will accordingly become capable of throwing light on successively higher taxonomic groupings. For the present, however, it is safest to confine our attention to clusterings above the 74% level.

Sokal & Sneath (1963) emphasise that numerical taxonomy is incapable of establishing phylogenetic relationships, but only coefficients of similarity; close phylogenetic relationship may be obscured by strongly divergent evolution, while convergent evolution may suggest a closer phyletic relationship than is true. At the same time, however, Sokal & Sneath agree that convergent evolution will seldom completely obscure the fundamental differences between only distantly related lineages. It seems probable, therefore, that a high coefficient of similarity will generally truthfully indicate a close phyletic affinity. On these grounds it seems possible to consider the clusters above the 74% level in Fig. 1 as being indicative of possible phylogenetic relationship. This view is firmly upheld by the details of clustering of the genera *Barnea*, *Martesia*, *Xylophaga* and *Teredo*, of the genera *Tellina* and *Egeria*, of the genera *Nuculana* and *Nucula*, of the genera *Arca*, *Anadara* and *Glycymeris*, and of the genera *Kellia*, *Montacuta*, *Lasaea* and *Turtonia*. The systematic position of *Turtonia* has been discussed by Oldfield (1955) and by Ockelmann (1964); *Turtonia* is considered to be a neotenous veneracean by Ockelmann, and it is unfortunate that, having been unable to include any member of the Veneridae in the investigation, it has not been possible to put Ockelmann's views to the test.

The clustering of *Cardium*, *Glossus*, and *Chama* is interesting, and more detailed investigations of possible affinity between these genera is desirable; *Cardium* and *Glossus* are both rather tumid members of the superficial in-fauna of sedimentary deposits, while *Chama* is attached by cementation to the surface of rocks. The most striking feature of the exercise is the clustering of *Dreissena* and *Mytilus*, at a coefficient of similarity of 76.8%. The generally accepted view, which has recently been re-stated by Yonge & Campbell (1968) is that the eulamellibranch *Dreissena* is unrelated to the filibranch *Mytilus*, and that resemblance between these two genera is due to the adoption of a similar mode of life, and to convergence. The present exercise reveals that the similarities between *Dreissena* and *Mytilus* far outweigh the differences numerically. Should the features of dissimilarity be so heavily weighted that convergent evolution is deemed to be more probable than descent from a common ancestor? If convergence has occurred between these two genera, what is the statistical probability of the achievement of so high a coefficient of similarity?



We revert once more to the work of Ridewood (1903) who showed that in four families one or two species had advanced beyond the remainder in ctenidial structure. Is it not probable that *Dreissena* is another such example, which evolved from the fili-branch to the eulamellibranch state? *Dreissena* has advanced in other respects, notably in the fusion of left and right mantle lobes with the production of inhalant and exhalant siphons. There can be no doubt that *Dreissena* is not a mytilid, but if we do not allow ourselves to be over-impressed with its eulamellibranch status, we might eventually concede that *Dreissena* may have evolved directly from a mytilid ancestry, and may exhibit closer phyletic relationship with the Mytilidae than with any family in the Eulamellibranchia.

#### DISCUSSION

We have first to consider to what errors the adopted procedure may be susceptible. Firstly, it is probable that the results of the investigation will be influenced to some extent by the proportions in which information is contributed from different organ systems, etc. Thus a great increase in knowledge of the physiology of digestion, for example, would be expected to cause some changes in the coefficients of similarity and in the dendrogram. Ideally, therefore, the quantities of data from contrasted sources should be well balanced, and the data as a whole should provide a random sample of information on the gene complexes of the genera studied. We cannot claim that the questionnaire used in this exercise is ideally balanced, but this cannot be rectified by subjective suppression of information on our part. The information utilised is certainly random, in that it has not been selected, and it is hoped that the results of the exercise will, at least, supply some useful indications.

A second likely source of error in a simple system such as that employed here, is the possible occurrence of instability, i.e., of obtaining different results if the data are presented to the computer in a different order. To obviate this risk one of us (D.B.) ran the program with the whole of the 27 sets of data presented in about 55 different orders, identical results being obtained in each case.

Extension of the survey to include many more genera would introduce many more primary clusters, and this would probably change the lowermost parts of the dendrogram. To meet this undeniable criticism the dendrogram has been drafted appropriately, and only those clusters set in continuous lines merit serious consideration at the present time; broken lines indicate possible associations, the details of which are subject to adjustment after consideration of many more genera; the dotted lines have little or no significance, and should be disregarded.

After these precautionary remarks, the first and most important question to be answered is whether the information provided by computer analysis of this large body of data is meaningful in terms of phylogenetic relationships at and above the level of families? If so, what is the lower limit of credibility for the results (dendrogram in Fig. 2)? It is encouraging to find that to a considerable extent the results of the investigation endorse the wisdom of earlier malacologists who did not have the advantage of such extensive biological information, or the opportunity to analyse extensive data by computer. The coefficients of similarity reported for *Barnea*, *Martesia*, *Xylophaga* and *Teredo* are highly orthodox in their implications on the affinities of these genera; this suggests that a level of credibility might well be set as low as 74% in Fig. 2, and that all clusterings above this level are worthy of serious consideration. Most of these clusters are, in fact, generally acceptable, and do not call for further discussion. Further consideration should be given to the cluster: *Cardium* / *Glossus* / *Chama*, and to the cluster: *Dreissena* / *Mytilus*. It is not our present intention, however, to pursue such matters of detail; our purpose is to determine whether the

procedure adopted is capable of supplying meaningful indications of phyletic relationship, and it appears to us that the results of the exercise are very encouraging.

As the clustering process advances there is a steady decrease in the number of questions which receive identical answers from all genera in the cluster; conversely there is a steady increase in the number of questions the answers to which vary from one genus to another within the cluster. It has been contended that this increase may interfere with the efficiency of the clustering process. We do not think that this is a serious issue, but it would be possible to test the question by interrupting the course of the program at, say 5% intervals, and deleting such questions as have ceased to provide consistent answers within the individual clusters. It has been conventional to disregard, for phyletic considerations, any character which shows variability within the genus or within the family, e.g., hermaphroditism, which occurs sporadically in many lineages. Such characters are clearly useless as major criteria for sub-division of the class, yet they may be of considerable importance in an exercise in numerical taxonomy. Thus hermaphroditism, though sporadic in many lineages, seems to be characteristic of the Anatinacea. Accordingly, it is doubtful whether it would be desirable to exclude such variable characters from the program in an attempt to make the later stages of clustering more accurate. Apart from any question of progressive amendments of the data in order to delete questions and answers which have no relevance to later parts of the clustering process, it would be highly desirable to analyse the data for a different purpose; namely to ascertain which questions and answers are of prime importance for systematic purposes. It would be of the greatest value to obtain by such objective methods an acceptable decision as to "which characters are of real taxonomic value ..." (Cox, 1960)!

A further point of importance which may emerge from the analysis of extensive data by computer programs concerns the coefficients of similarity which generally indicate differences between phylogenies at generic, at familial, or at ordinal level. The information at present available is inadequate for this purpose; thus *Barnea* and *Martesia*, both members of the family Pholadidae, have a coefficient of similarity of 82.4%, while an almost identical coefficient (82.7%) is shown by *Tellina* (family Tellinidae) and *Egeria* (family Donacidae) which are both members of the order Tellinacea. The levels at which taxonomic terms such as genus, family, order, etc., can best be applied will naturally vary somewhat from one phylogeny to another - partly, perhaps, according to the number of genera in each phylogeny and partly according to the degree of structural adaptation to habitat and to mode of life. One would not wish to impose any strict regularity in the use of such terms, but the existence of a more extensive dendrogram than that presented here (Fig. 2) would probably assist by indicating the occasional need for intermediate terms such as super-family or sub-order.

#### REFERENCES

- ATKINS, D., 1938, On the ciliary mechanisms and inter-relationships of lamelli-branches. VII, Latero-frontal cilia of the gill filaments and their phylogenetic value. *Quart. J. micr. Sci.*, 80: 346-436.
- COX, L. R., 1960, Thoughts on the classification of the Bivalvia. *Proc. malac. Soc. Lond.*, 34: 60-88.
- DINAMANI, P., 1967, Variation in the stomach structure of the Bivalvia. *Malacologia*, 5: 225-268.
- GHISELIN, M. T., DEGENS, E. T., SPENCER, D. W. & PARKER, R. H., 1967, A phylogenetic survey of molluscan shell matrix proteins. *Breviora*, 262: 1-35.
- GRAHAM, A., 1934, The cruciform muscle of lamelli-branches. *Proc. roy. Soc. Edinb.*, 54: 17-30.

- GRAHAM, A., 1934a, The structure and relationships of lamellibranchs possessing a cruciform muscle. *Proc. roy. Soc. Edinb.*, 54: 158-187.
- OCKELMANN, K. W., 1964, *Turtonia minuta* (Fabricius), a neotenous veneracean bivalve. *Ophelia*, 1: 121-146.
- OLDFIELD, E., 1955, Observations on the anatomy and mode of life of *Lasaea rubra* (Montagu) and *Turtonia minuta* (Fabricius). *Proc. malac. Soc. Lond.*, 31: 226-249.
- OWEN, G., 1959, The ligament and digestive system in the taxodont bivalves. *Proc. malac. Soc. Lond.*, 33: 215-223.
- PELSENEER, P., 1891, Contribution à l'étude des lamellibranches. *Arch. de Biol.*, 11: 147-312.
- PELSENEER, P., 1906, *A Treatise on Zoology*, ed. E. R. Lankester, V, The Mollusca. A. & C. Black, London.
- PELSENEER, P., 1911, Les lamellibranches de l'expédition du Siboga, Partie anatomique. *Siboga Expédition. Monogr.* No. 53a.
- PURCHON, R. D., 1941, On the biology and relationships of the lamellibranch *Xylophaga dorsalis* (Turton). *Journ. mar. biol. Assn. U.K.*, 25: 1-39.
- PURCHON, R. D., 1959, Phylogenetic classification of the Lamellibranchia, with special reference to the Protobranchia. *Proc. malac. Soc. Lond.*, 33: 224-230.
- PURCHON, R. D., 1960, The stomach in the Eulamellibranchia; stomach types IV and V. *Proc. zool. Soc. Lond.*, 135: 431-489.
- PURCHON, R. D., 1960a, Phylogeny in the Lamellibranchia. *Proc. Cent. & Bicent. Congr. Biol. Singapore*, 1958, 69-82.
- REID, R. G. B., 1965, The structure and function of the stomach in bivalve molluscs. *Journ. Zool.*, 147: 156-184.
- RIDEWOOD, W. G., 1903, On the structure of the gills of lamellibranchs. *Phil. Trans. B*, 194: 147-284.
- SOKAL, R. R. & SNEATH, P. H. A., 1963, *Principles of Numerical Taxonomy*. Freeman, London.
- THIELE, J., 1935, *Handbuch der systematischen Weichtierkunde*. 3 Teil. Fischer, era.
- YONGE, C. M., 1959, The status of the Protobranchia in the bivalve Mollusca. *Proc. malac. Soc. Lond.*, 33: 210-214.
- YONGE, C. M. & CAMPBELL, J. I., 1968, On the heteromyarian condition in the Bivalvia with special reference to *Dreissena polymorpha* and certain Mytilacea. *Trans. roy. Soc. Edinb.*, 68: 21-43.



## ON THE TAXONOMY AND BIOGEOGRAPHY OF HYDROBIIIDAE

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In examining the gastropod family Hydrobiidae, in particular its representatives from Lake Ohrid and from waters of Dinaric karst (Yugoslavia), I noticed many errors in taxonomy, which is based mainly on the shell. For that reason I did not consider their present taxonomy to be reliable.

Two groups of errors are to be found here. On the one hand, the anatomically different species are included in the same genus because of their similar shells; in some cases species from different families, even from different subclasses, are included in the same genus. On the other hand, the anatomically similar species are separated into different genera (in some cases in different subfamilies) owing to their conchological differences.

Some examples of these errors follow: *Bythinella robiči* Clessin (1887) anatomically is a *Sadleriana* (Radoman, 1965) (Fig. 1), *Sadleriana virescens* Küster (1852) is a *Pseudamnicola*, *Sadleriana macedonica* Kusčer (1936) is a *Horatia* (Radoman, 1966a), *Pseudamnicola consociella* Wagner (1927) is a *Hydrobia* (Radoman, 1966a) (Fig. 2), *Lithoglyphus notatus* Frfld (1865) is a *Pseudamnicola* (Radoman, 1966a), *Lithoglyphus pygmaeus* Frfld (1863) is a *Sadleriana* (Radoman, 1966b), *Valvata ohridana* Polinski (1929, 1932), later determined as a *Horatia* (Komarek, 1953) in fact is a *Pseudohoratia* (Radoman, 1967b), *Gocea ohridana* Hadžišče (1956) determined as a representative of Hydrobiidae, is a species of Valvatidae (Radoman, 1962), and, finally, a non-hydrobiid example, *Gyraulus relictus* Polinski (1929) (Pulmonata) is a *Valvata* (Radoman, 1955).

Some examples of the second group of errors are: *Hydrobia prespensis* Urbanski (1939) (syn. *Micromelania prespensis* Hadžišče, 1953), *Hydrobia grochmalickii* Polinski (1929) (syn. *Pyrgohydrobia grochmalickii* Radoman, 1955) and *Diana thiesseana* (Godet) Kobelt (1878) all belong to the same genus, *Diana* (Fig. 3); anatomically they are quite similar. *Pyrgula sturanyi* and *Neofossarulus stankoviči* (from Lake Ohrid) both are representatives of the genus *Chilopyrgula* (Radoman, 1955). The Lake Ohrid species *ornata* I determined to be a *Pseudamnicola* on the basis of its anatomy (Radoman, 1956); but on the basis of its shell it was determined by Hadžišče (1956) as a new genus, *Ohrigocea*.

On the basis of shell similarities 5 species were erroneously included in the genus *Pseudamnicola* (Radoman, 1966a), 5 in *Horatia* (Radoman, 1966a) and 9 in *Lithoglyphus* (Radoman, 1966b).

These and several other examples of taxonomic errors should not be considered exclusively subjective ones, but they are often conditioned by the objective unsuitability of the shell as an exclusive taxonomic character.

The taxonomic importance of the radula (especially when regarding genus determination) is not greater than that of the shell. For instance, radulae in Pyrgulinae and Micromelaniinae are similar in spite of different anatomies of these 2 groups. The nervous system, if considered independently from other characters, also cannot always show relationships of the genera. For example, the nervous systems are quite similar in *Hydrobia* and *Pyrgula*, genera of 2 different subfamilies.

The examples mentioned above, and many others, show that systematics based on one single character can cause numerous errors. Nevertheless, it is possible to find

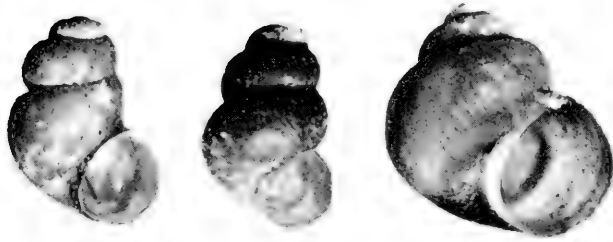


FIG. 1. *Bythinella*, *Sadleriana robiči*, *Sadleriana fluminensis*



FIG. 2. *Hydrobia consociella*, *Pseudamnicola curta*, *Hydrobia ventrosa*, *Hydrobia gagathinella*.

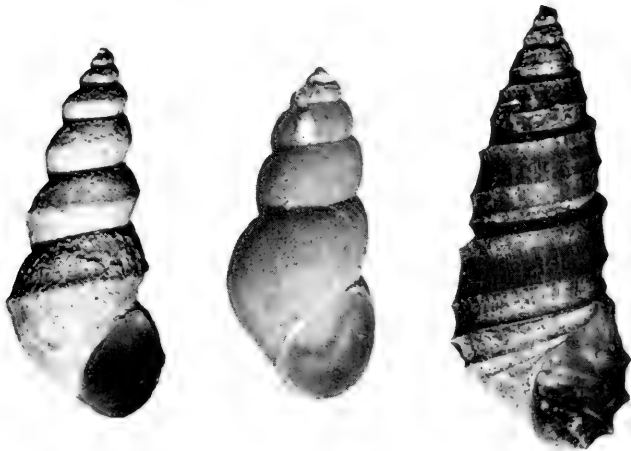


FIG. 3. *Diana prespensis*, *D. grochmalickii*, *D. thiesseana*.

a single character that is suitable for classifying species, genera and other taxa, but such a character should be used only in conjunction with other characters. According to my experience with the family Hydrobiidae, such a character is the genital systems, especially that of the female.

The following examples show, however, that in different genera the anatomy of some systems of organs cannot always be similarly correlated. According to an analysis of the constitution of female reproductive organs and of the nervous systems, the genera *Emmericia* and *Lithoglyphus* are so similar that they cannot be distinguished. However, the differences between the 2 in the anatomy of accessory parts of the male reproductive organs are quite obvious, making it possible to distinguish these 2 genera (Radoman, 1966b, 1967a). On the other hand, the anatomical characters of the nervous systems and of the male reproductive organs would not enable one to distinguish the genera *Hydrobia* and *Pyrgula*, which, however, are clearly distinctive according to the reproductive apparatus of their females (Radoman, 1955a, 1955b). Many further examples can be cited which show that phylogenetic relationships can be determined only after considering a number of different anatomical characteristics. This does not mean that shell-morphology has no importance in taxonomical determinations: it must be taken in account when distinguishing different species of the same genus which have basically the same anatomical characteristics. In the taxonomic determination of higher groups, beginning with the genus, shell morphology should be used only in a correlation with anatomical characteristics. Otherwise, the errors mentioned above are unavoidable.

I consider that correct generic diagnoses are of cardinal importance for a reliable assessment of phylogenetic and taxonomic relationships in a family as well as between several families and other groups. Only by complex anatomical analyses was it possible to detect with certainty the differences among the Baicaliinae, Micromelaniinae and Pyrgulinae, and to determine their genera and species (Koshov, 1951, Radoman, in manuscript). However, the taxonomy of the Hydrobiinae is not yet clear (e.g., it seems obvious that the genera *Emmericia* and *Lithoglyphus* should not be grouped with the genus *Hydrobia*, or this genus allied to *Pseudamnicola* and *Sadleriana*).

In my anatomical examinations of Hydrobiidae I was able to see that the taxonomic characters of genera are predominantly internal. This stimulated me to try to form conchylio-anatomical diagnoses of several hydrobiid genera, i.e., diagnoses containing both conchological and anatomical records. I have now succeeded in diagnosing about 20 genera.

All this forces one to conclude that it is indispensable to give a conchylio-anatomical diagnoses on the type species, quoting its exact type locality, before introducing a new genus name. Additionally, in my opinion, good figures are more important, especially for the main characters, than a verbal description, however extensive it might be. If we omit to do so, further descriptions and classification of new species on the basis of purely conchological genera diagnoses inevitably leads to the accumulation of new errors, in addition to the numerous old ones, and to their unjustified "modernization."

As it is well known, a correct taxonomy, as a reflection of phylogenetic relations, is of great importance for the establishment of biogeographical relationships between small or large territories, and are important for explanations of speciation processes. There are examples which illustrate a disharmony between at least a part of present taxonomy and the geographical distribution of Hydrobiidae, and we can see to what extent a correction of taxonomical errors "purges" the erroneously conceived biogeographical picture.

To mention again the Baicaliinae, Micromelaniinae and Pyrgulinae, Thiele (1929) placed several species from the United States, Japan, China, South Africa and Australia, together with the north Italian *Pyrgula annulata*, in the hydrobiid subfamily

Truncatellinae. On the other hand, he included *Diana* from Greece and other pyrgulid forms from Lake Ohrid (Macedonia) in a separate family, Micromelaniidae. Polinski (1929, 1932) included 2 species from Lake Ohrid (*Micromelania filocincta* and *Stankovicia baicaliiformis*) in genera identical or related to those from the Caspian Sea (the first species) or to those from Baical Lake (the latter), and pointed at the biogeographical relations of these water basins. Using the shell, sometimes the radula, Thiele (1929) included the genera *Baicalia* and *Micromelania* in the same subfamily, while Kozhov (1951), considering their anatomies, placed these 2 genera into 2 families, the first of which is confined to Baical and the second to Ponto-Caspian basin.

According to my anatomical examinations, there are no representatives of the Baical and Caspian hydrobiid fauna in Lake Ohrid, the Ohrid hydrobiid fauna being related to the endemic fauna of the Dinaric karst, or, more extensively, to that of Adriatic and Aegean drainage areas. The representatives of the group Pyrgulinae are spread from Lake Garda in Italy, through the Adriatic (Dalmatic) littoral zone (*Pyrgula annulata* in Garda, Zrmanja River, Lake Bačina, in some tributaries of Neretva, and in Lake Scutari), in Lake Ohrid (endemic genera: *Chilopyrgula*, *Ochridopyrgula*, *Micropyrgula*, *Stankovicia*, *Trachyochridia*, *Ginaia*), in Lake Prespa (*Diana prespensis*) and in 2 Greek lakes: Lake Trichonia (*Diana thiesseana*) and Lake Amvrakia (*D. schlikumi*). From the malacological literature, some representatives of the Pyrgulinae are also reported for Turkey and Israel, but it is necessary to prove this distribution from anatomical inspection of the species.<sup>1</sup>

An anatomical examination is also necessary in the case of some alleged representatives of this subfamily in southern France, e.g., *P. pyrenaica* Bourg. and *P. darieuxi* Fol. & Beril. The Pyrgulinae is mainly an Adriatic-Aegean group, which is taxonomically and biogeographically different from the subfamilies Baicaliinae and Micromelaniinae.

#### LITERATURE CITED

- CLESSIN, S., 1887, Molluskenfauna Österreich-Ungarns. Nürnberg, Bauer & Raspe, 860 p.
- HADŽIŠČE, S., 1953, Prilog poznavanju gastropoda Prespanskog i Ohridskog jezera. *Glasnik biološke sekcije*, Zagreb, Ser. II/B, T. 7: 174-177.
- HADŽIŠČE, S., 1956, Beitrag zur Kenntnis der Gastropodenfauna des Ohridsees. III. *Recueil des travaux*, Ohrid, IV, 1(14): 57-107.
- KOBELT, E., 1878, Diagnosen neuer Arten. *Jahrb. dtsh. Mal. Ges.*, B.V: 319-321.
- KOMAREK, J., 1953, Herkunft der Süßwasser-Endemiten der dinarischen Gebirge... *Arch. f. Hydrobiologie*, Stuttgart, 48, 3: 269-349.
- KOSHOV, M. M., 1951, K morfologii i istorii Bajkalskih endemičnyh molljuskov sem. Baicaliidae. *AN SSSR Trudy Bajkalskoj limnologičeskoj stancii*, XIII: 93-119.
- KÜSTER, H. C., 1852, Die Gattungen *Paludina*, *Hydrocaena* und *Valvata*. In: Martini & Chemnitz, *Syst. Conch. Cab.*, I, 21: 1-96, Nürnberg (Bauer & Raspe).
- KUŠČER, I. J., 1936, Zur Kenntnis der Molluskenfauna von Südserbien und Montenegro. *Bull. Soc. sci. Skopje*, 17(5): 101-104.
- POLINSKI, V., 1932, Die relikttäre Gastropodenfauna des Ochrida-Sees. *Zool. Jb. Syst.*, 62: 611-666.
- RADOMAN, P., 1955a, Morfološko-sistematska istraživanja ohridskih hidrobida. *Srpsko biološko društvo*. Pos. izd. 1, 106 p, Beograd.

<sup>1</sup> Meanwhile, from Hartwig Schütt I received specimens of *Chilopyrgula zilchi* (Schütt, 1964, *Arch. f. Mollk.* 93, 5/6), and established that this form, conchologically similar to *Pyrgula*, anatomically could not be included in the Pyrgulinae. The results of this examination will be published soon.



- RADOMAN, P., 1955b, Prilog poznavanju gastropoda ohridskog basena. *Recueil des Travaux*, Ohrid, III, 2(12): 23-39.
- RADOMAN, P., 1956, Nove ohridske hidrobide. *Arh. bioloških nauka*, Beograd, VIII(1/2): 87-92.
- RADOMAN, P., 1962, Nove ohridske hidrobide (II). *Arh. bioloških nauka*, Beograd, XIV(1/2): 69-93.
- RADOMAN, P., 1965, Das Genus *Sadleriana*. *Glasnik Privodnjačkog Muzeja*, Beograd, B20: 121-126.
- RADOMAN, P., 1966a, Die Gattungen *Pseudamnicola* and *Horatia*. *Arch. Moll.*, Frankfurt, 95(5/6): 243-253.
- RADOMAN, P., 1966b, The zoogeographical and phylogenetic interrelations of the genera *Lithoglyphus* and *Emmericia*. *Glasnik Privodnjačkog Muzeja*, Beograd, B21: 43-49.
- RADOMAN, P., 1967a, Speciation of the genus *Emmericia* (Gastropoda) on the Adriatic area. *Basteria*, 31(1/3): 27-43.
- RADOMAN, P., 1967b, Revision der Systematik einiger Hydrobiidenarten aus dem Ohrid See. *Arch. Moll.*, Frankfurt, 96(3/6): 149-154.
- RADOMAN, P., Pyrgulinae, eine Unterfamilie der Hydrobiidae. Im Manuskript.
- THIELE, J., 1929/31. Handbuch der systematischen Weichtierkunde. I. Gustav Fischer, Jena, 778 p.
- URBANSKI, J., 1939, Über drei neue Schneckenarten aus dem südlichen Teile Jugoslaviens. *Zool. Pol.*, 3: 260-266.
- WAGNER, A., 1927, Studien zur Molluskenfauna der Balkanhalbinsel . . . *Ann. Zool. Mus. Polen. Hist. nat.*, 6(4): 263-301.



THE USE OF THE SCANNING ELECTRON MICROSCOPE IN  
THE STUDY OF THE GASTROPOD RADULA: THE RADULAE  
OF *AGRIOLIMAX RETICULATUS* AND *NUCELLA LAPILLUS*

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## INTRODUCTION

Recent studies have shown that the scanning electron microscope with its very great depth of focus even at high magnifications allows us for the first time to examine the detailed three dimensional morphology of the smaller radular teeth (Runham & Thornton, 1967; Thompson & Hinton, 1968). The patterns of wear seen on the teeth also make it possible to deduce the orientation of the teeth during feeding (Runham & Thornton, 1967). For these morphological studies the radula was removed from the animal, cleaned, laid flat on a brass stub, and then air-dried. In life the radula covers the odontophore cartilages which usually have the form of a U-shaped gutter. Therefore, in order to obtain detailed information on how the teeth are used during feeding it is essential to examine the radula while it is still covering the underlying cartilage. Studies of this kind have been made on the grey field slug *Agriolimax reticulatus* and on the dog-whelk *Nucella lapillus* and are reported here.

## MATERIALS AND METHODS

*Agriolimax reticulatus* and *Nucella lapillus* were collected locally. The animals were allowed to crawl and then beheaded with a sharp scalpel. The dorsal skin of the head was completely removed so as to expose the buccal mass. Removal of the dorsal wall of the buccal mass exposed the odontophore (consisting of the radula, odontophore cartilages and associated muscles) in the buccal cavity. The exposed part of the radula which covers the anterior surface of the odontophore was then washed repeatedly with saline to remove mucus and any food particles. The lateral and ventral walls of the head were then dissected away very carefully so as to cause as little disturbance as possible to the musculature of the buccal mass. The isolated buccal mass was laid on a weak gelatin gel which coated the surface of a brass stub; it was rapidly frozen by plunging into liquid nitrogen, and then freeze dried at  $-60^{\circ}$  C in a Speedivac-Pearse Tissue Drier (Edwards High Vacuum Ltd.). When dry the stub was removed and placed in a vacuum coating unit where the buccal mass was coated with an approximately 400 Å thick layer of gold which was applied in two stages, firstly from above and then from the side while the stub was slowly rotated in both cases. This procedure was essential in order to get the specimen evenly coated. The buccal mass was examined in a Cambridge Stereoscan scanning electron microscope.

THE RADULA OF *AGRIOLIMAX RETICULATUS*

The morphology of the teeth has been described in detail elsewhere (Runham & Thornton, 1967) and so will not be given in detail here. Each transverse row of the radula consists of a symmetrical central tooth and on each side of this are a number of lateral teeth (approximately 20) and these are flanked by the marginal teeth (approximately 20). The distinction between these teeth can clearly be seen in Fig. 1.

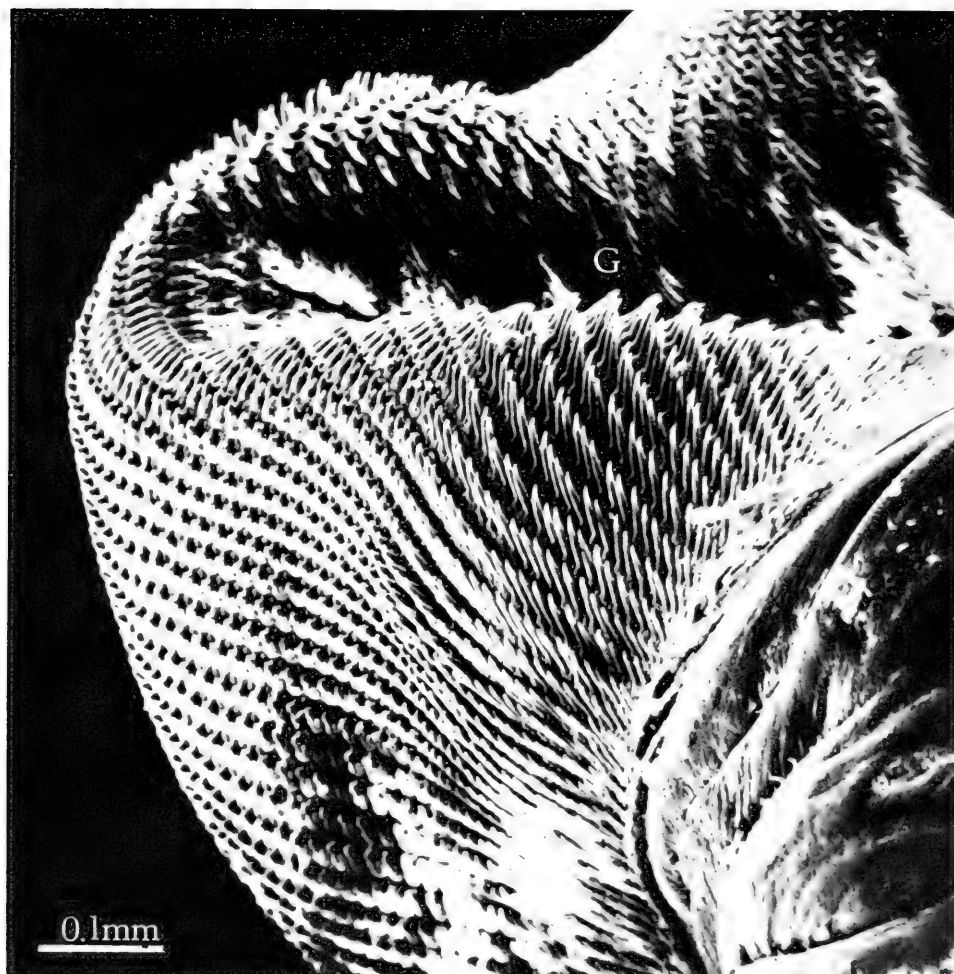


FIG. 1. *Agriolimax reticulatus*. Lateral view of the odontophore tip. Note the dorsal groove (G).

The radula is secreted by the radular gland which lies in the gutter formed by the cartilages and projects from its posterior end. New teeth are added to the radula at its posterior end and at 20°C they move forwards at a rate of 5 rows a day (Isarankura & Runham, 1968). Within the gland the radula is curled up at its lateral edges so that in transverse section the radula forms an almost complete ring with the central teeth occupying the mid-ventral position and the outermost marginal teeth from the two sides almost touching dorsally. Within the radular gland all the teeth point inwards. Towards the anterior end of the radula the secretory epithelium above the teeth breaks down and is succeeded by an epithelium having a thick cuticle, the collostyle hood (Runham, 1963). As the radula moves forward out of the radular gland (Fig. 4) the teeth are exposed. This newly emerged radula still lies in the u-shaped gutter formed by the odontophore cartilages, the radula lining the walls of the gutter and the teeth projecting into it. The collostyle hood forms a vertical wall marking the posterior limit of the dorsal groove in the odontophore (Fig. 4). There is a pattern of markings

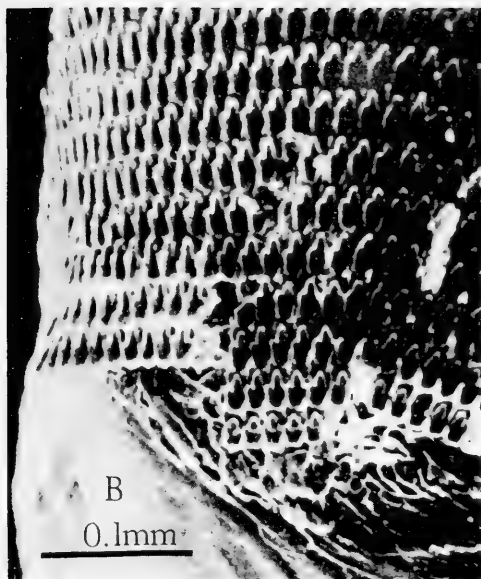


FIG. 2. *A. reticulatus*. Anterior edge of the radula and the buccal cuticle (B). Note the blocks of worn teeth detaching at the edge.



FIG. 3. *A. reticulatus*. The surface of the buccal cuticle next to the anterior edge of the radula.

on the surface of the collostyle hood cuticle of approximately the same width as the teeth. It is not known if these markings arise during formation of the cuticle or during use of the radula.

At their anterior end the odontophore cartilages taper to form a conical tip with a dorsal groove. The anterior end of the radula is reflected over the edges of the groove and backwards over the conical tip of the cartilages (Fig. 1). At the extreme anterior edge of the radula worn teeth drop off and are usually swallowed (Isarankura & Runham, 1968). The detachment of blocks of these teeth can be seen in Fig. 2. As this detachment is only seen along this anterior edge of the radula and not along the lateral edges it is unlikely that it is an artefact due to drying. The buccal cuticle near to this detachment area has characteristic markings which may represent scars of the old teeth.

During feeding the mouth is opened and the odontophore is brought forward and downward to meet the substrate. When first applied to the substrate the tip of the odontophore is at its most posterior position. The cartilage is then rotated so that the tip moves rapidly forward to its most anterior position when it is withdrawn into the buccal cavity. The odontophore carries out a series of these "licking" movements. It has been shown very clearly in many other molluscs, from an analysis of feeding tracks (Markel, 1958, 1967), that while the odontophore is moving in this way so the radula is also moving over the cartilages. The speed at which the teeth rasp the substrate is the sum of the speed of the feeding stroke of the odontophore plus the speed of movement of the radula over the cartilage. When the odontophore is in its most posterior position at the start of the feeding stroke the radula is pulled out of the groove in the cartilages to its greatest extent, and when it has reached its most anterior position the radula has been pulled back into the groove to its greatest extent. As the radula moves out of the gutter over the edge of the cartilage and on to the surface of the cartilage and vice versa so the orientation of the teeth changes.



FIG. 4. *A. reticulatus*. Latero-dorsal view of the groove in the odontophore. Note the collostyle hood (C) and the newly emerged teeth (T).

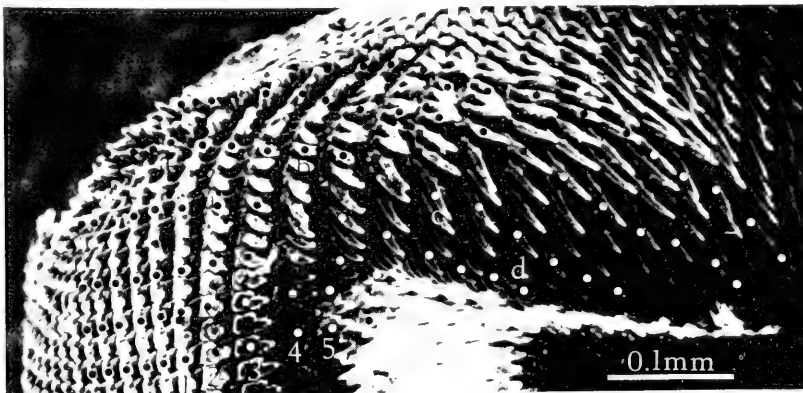


FIG. 5. *A. reticulatus*. Dorsal view of the odontophore shown in Figure 1. 2 longitudinal rows of lateral teeth and 5 rows of marginal teeth are marked. The numbers and letters are explained in the text.

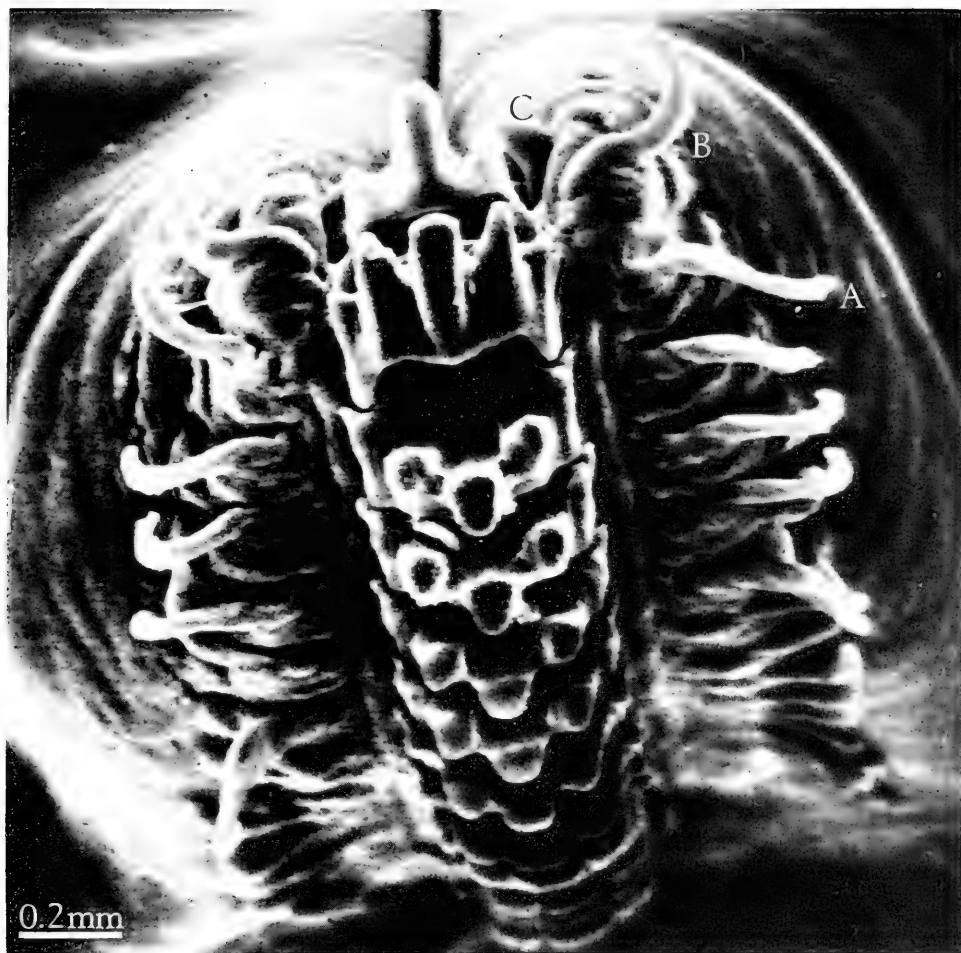


FIG. 6. *Nucella lapillus*. Anterior view of the odontophore tip. The letters are explained in the text.

The orientation of the teeth depends upon their position on the cartilage and this depends in turn on the particular stage of the radula movement cycle. From an examination of the tip of the odontophore at any stage of the cycle and a study of the orientation of the teeth in successive rows the change in orientation of any one tooth during the cycle can be deduced.

An analysis of the orientation of lateral teeth using photographs taken at several magnifications and from several angles (e.g., Fig. 5), shows that as they move over the edge of the cartilage the teeth rotate through approximately  $125^\circ$ . With reference to Fig. 5, tooth 1 is moving forwards to the edge of the cartilage with its cusps well exposed since the tooth in position 2 has rotated upwards. Taking tooth 1 as a base line, tooth 2 has rotated through  $35^\circ$ , 3 has rotated through  $75^\circ$ , 4 through  $110^\circ$ , and 5 through  $125^\circ$ . Thus if the teeth cusps at position 1 penetrate food material it will be lifted up and then dragged towards the groove. This type of movement may result in the tearing off of chunks of food, in contrast to the removal of small pieces by the rasping of teeth on the outside of the odontophore. Examination of the crop

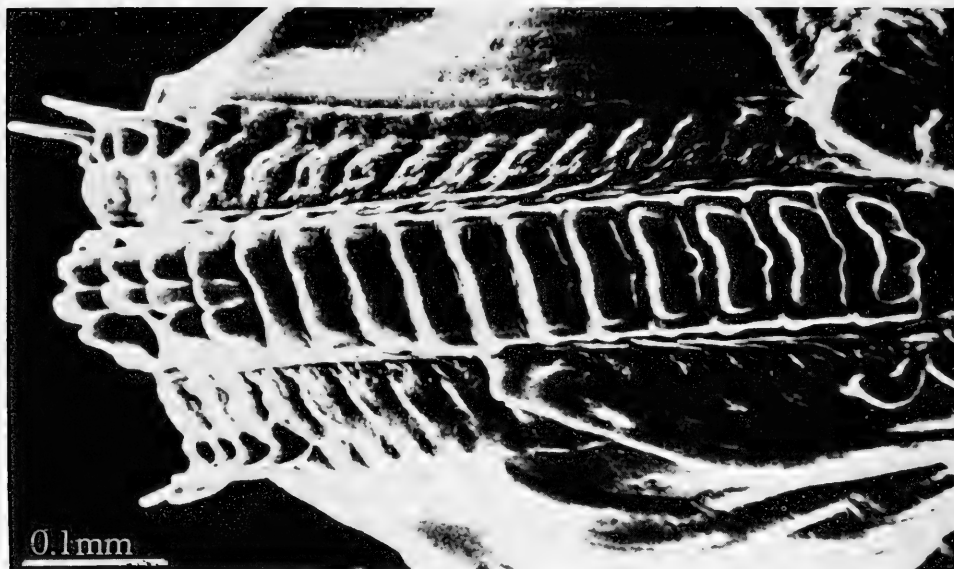


FIG. 7. *N. lapillus*. Ventral view of the odontophore shown in Figure 6. Note that the teeth are extremely worn.

following a meal reveals a mixture of large and small pieces (Walker personal communication). The marginal teeth on the outside of the odontophore have the narrow cusp erect (Fig. 5A) but as the teeth pass back over the lateral walls of the groove they swing downwards into the groove (Fig. 5 BCD). It is unlikely that such tall cusps would be used for rasping, but the downward movement of the cusps would hold material against the lateral teeth and assist in the tearing off of large pieces and their transport.

#### THE RADULA OF *NUCELLA LAPILLUS*

Although the buccal mass of *Nucella lapillus* is at the end of a long proboscis it is anatomically similar to that of *Agriolimax*. The cartilage and radula are however very narrow and each transverse row of teeth consists of only a central tooth and a single lateral tooth on each side. The detailed morphology of the teeth will be described elsewhere, but it should be noted that the central teeth have three large heavy cusps and the laterals have an inwardly curved very narrow cusp on the outer side of the tooth. As shown in Fig. 7, the central teeth are worn while the lateral teeth in the same row are less worn. *Nucella* feeds on bivalves and barnacles (Largen, 1967) using the radula together with the accessory boring organ (Fretter & Graham, 1962) to bore a hole through the shell, and then it consumes the tissues. It is likely from the shape and wear of the central tooth that this tooth is used for boring. There is extensive rotation of the central teeth as they pass over the tip of the cartilages (Fig. 6). The lateral teeth on the convex outer surface of the odontophore have the cusps directed away from the central teeth. As these teeth pass backwards over the odontophore tip, however, the hook-shaped cusp rotates inwards and downwards between the backward pointing central teeth (Fig. 6 ABC). The movement and shape of these lateral teeth must result in the radula gaining a very efficient hold on soft tissue and in conjunction with the retraction of the buccal mass will result in the tearing off of pieces



of tissue. A rasping mode of feeding would presumably not be very effective for the removal of soft tissue.

### CONCLUSIONS

The scanning electron microscope in conjunction with freeze drying thus enables us to examine the gastropod radula while it is in a similar position to that taken up during feeding and can give us a better understanding of the functions of the teeth.

### ACKNOWLEDGEMENTS

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### REFERENCES

- FRETTER, V., & GRAHAM, A., 1962, British Prosobranch Molluscs. Ray Society, London.
- ISARANKURA, K. & RUNHAM, N. W., 1968, Studies on the replacement of the Gastropod radula. *Malacologia*, 7(1): 71-91.
- LARGEN, M. J., 1967, The diet of the dog-whelk, *Nucella lapillus*. *J. Zool., Lond.*, 151: 123-127.
- MARKEL, K., 1958, Bau und Funktion der Pulmonaten-Radula. *Z. wiss. Zool.*, 160: 213-289.
- MARKEL, K., 1967, Über funktionelle Radulatyphen bei Gastropoden unter besonderer Berücksichtigung der Rhipidoglossa. *Vie et Milieu*, 17: 1121-1138.
- RUNHAM, N. W., 1963, A study of the replacement mechanism of the pulmonate radula. *Q. Jl. microsc. Sci.*, 104: 271-277.
- RUNHAM, N. W. & THORNTON, P. R., 1967, Mechanical wear of the gastropod radula: a scanning electron microscope study. *J. Zool., Lond.*, 153: 445-452.
- THOMPSON, T. E. & HINTON, H. E., 1968, Stereoscan electron microscope observations on opisthobranch radulae and shell structure. *Bijdragen Tot de Dierkunde*, 38: 91-96.



DOMINANCE BIOLOGIQUE DE QUELQUES MOLLUSQUES  
DANS LES ATOLLS FERMES (TUAMOTU, POLYNÉSIE);  
Phénomène récent - Conséquences actuelles

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Il y a maintenant 5 600 ans, les actuels atolls des Tuamotu étaient des formations récifales au raz de l'eau, sans parties émergées. Cette situation resta inchangée pendant deux millénaires et demi, malgré une montée du niveau de la mer, car les coraux se maintenaient à la surface par leur croissance en hauteur. Il y a 3 000 ans, le niveau de la mer commença à baisser; la différence de niveau entre le début d'émer-sion et l'actuel niveau est de trois mètres.<sup>1</sup>

Il y a ainsi quelques trois millénaires (1 000 ans avant J.C.), l'émer-sion de la couronne récifale de chacune de ces formations provoquait un isolement plus ou moins complet des eaux contenues dans un lagon, en fonction de la continuité de cette couronne récifale émergée, qui donnait sa physionomie à ce qu'est actuellement un atoll. Tous les intermédiaires étaient créés entre un atoll ouvert, avec une ou plusieurs passes assurant de larges échanges hydrologiques entre les eaux de l'océan et celles du lagon, et un atoll fermé aux eaux intérieures confinées.

Cinq missions en Polynésie française de 1965 à 1968<sup>2</sup> nous ont permis d'étudier onze atolls de type différent du sud et de l'est de l'Archipel des Tuamotu (Mururoa, Fangataufa, Réao, Turéia, Maturei Vavao, Marutea Sud, Pukarua, Pukapuka, Hao, Vahitahi, Nukutavake).<sup>3</sup> L'étude de la faune malacologique de chaque lagon permet d'avancer les conclusions suivantes.

Chaque atoll fermé n'est caractérisé que par deux ou trois espèces malacologiques. A la très grande pauvreté en nombre d'espèces s'oppose une extrême richesse en nombre d'individus des espèces propres au lagon. Il est important de noter que chacun d'eux possède sa "carte d'identité" malacologique, car aucun n'est semblable à un autre; celle-ci se définit spécifiquement et par l'importance numérique relative des espèces entre elles.

Dans chaque atoll ouvert, la faune malacologique est riche en espèces, mais leurs densités de peuplement sont extrêmement faibles. Toutes les espèces, qui peuvent être récoltées dans tous les atolls fermés, se retrouvent sans exception dans un seul atoll ouvert.

Cette opposition des richesses spécifiques d'une part et en densité de peuplement d'autre part, de la faune malacologique, entre les atolls ouverts et les atolls fermés, s'exprime également dans le cadre de l'ensemble des peuplements animaux de ces lagons. Dans les atolls ouverts, les Mollusques n'occupent qu'une place tout à fait négligeable dans le bios; les madréporaires sont largement prédominants. En revanche, dans les atolls fermés, les Mollusques, par leurs incroyables densités de peuplement, sont prépondérants, autant sinon plus que les coraux. On assiste à une importance

<sup>1</sup>LALOU (C.), LABEYRIE (Y.) et DELIBRIAS (G.). *C. R. Acad. Sci. Paris*, 263, série D, 1966, p. 1946.

<sup>2</sup>Conventions Muséum National d'Histoire Naturelle - Direction des Centres d'Expérimentations Nucléaires - Service Mixte de Contrôle Biologique.

<sup>3</sup>Importance de la faune malacologique dans les atolls polynésiens. *Cahiers du Pacifique*, n° 11, p 7-49, 12 photographies, 7 figures.

croissante de la faune malacologique, en rapport avec l'isolement hydrodynamique du lagon.

Les espèces, qui jouent ce rôle déterminant dans les atolls fermés, sont au nombre de quatre: *Tridacna maxima*, *Pinctada maculata*, *Chama imbricata* et *Arca ventricosa*. Pour *Tridacna maxima*, la concentration maximale observée (100% du substrat; Pukarua, Vahitahi, Réao, Turéia) est de 63 individus au mètre carré, soit une biomasse en poids frais (valves exclues) de 4,9 kg. A Vahitahi, par exemple, dans un périmètre du lagon d'une largeur de 2 mètres (rivage) et d'une longueur de 39 mètres (perpendiculaire à la ligne de rivage), allant jusqu' à la profondeur de 4 mètres (faciès à Acropora, avec alternance de substrats meuble et dur), le nombre de bénitiers recensés est de 696, soit 90 000 à l'hectare (biomasse en poids frais - valves exclues - égale à 7 tonnes). Il est à noter que l'espèce est consommée par les habitants. Pour *Pinctada maculata*, la concentration maximale (100% du substrat; Fangataufa) peut atteindre 350 à 400 individus au mètre carré, soit une biomasse approximative en poids frais de 1200 à 1400 g - valves exclues - mais la répartition des individus en paquets isolés les uns des autres ne donne généralement qu'une densité de l'ordre de 100 à 150 individus au mètre carré.

L'abondance des bénitiers dans les atolls fermés doit être soulignée, car ceux-ci contribuent dans une très large mesure au comblement du lagon. Reprenant les données de l'exemple pré-cité, la densité des bénitiers correspond à 37 tonnes de valves à l'hectare. Leurs valves, en s'accumulant, constituent des cordons lagunaires de plusieurs mètres d'épaisseur et de centaines de mètres carrés de surface qui réduisent la superficie du lagon, où la sédimentation est par ailleurs très importante. La faune malacologique accélère ainsi les processus de comblement des lagons des atolls fermés.

Nous avons tout lieu de penser qu'il y a 5 500 ans, alors que les atolls étaient totalement immergés, la faune malacologique n'était guère plus abondante que dans les atolls actuellement très ouverts. Il y a 3 000 ans, l'abaissement du niveau de la mer a entraîné l'émersion des couronnes récifales créant des atolls ouverts ou fermés. Le confinement des eaux des lagons a permis, dans les atolls fermés, la multiplication, l'épanouissement et la prépondérance de quelques Mollusques, pour d'évidentes raisons, entre autres, de moindre dispersion larvaire. C'est cette explosion malacologique que nous observons aujourd'hui, 3 000 ans après sa naissance, dans ces atolls fermés, où les Mollusques contribuent inexorablement à leur perte même, par comblement du lagon jusqu'à sa disparition finale.

\* \* \* \* \*

Three thousand years ago the present Tuamotu atolls were fully submerged reefs. Their present exposure results from a lowering of approximately three meters of the ocean level. This accounts for the shape of present closed or open atolls as well as intermediate forms, the morphology of such formations depending on the fact that exchange between outer sea water and lagoon water does occur or not.

In open atolls the Mollusks display a great specific diversity together with a small number of individuals (Mururoa, Hao). On the contrary in closed atolls a few species are to be found along with a high number of individuals. (Réao, Turéia, Pukarua, Vahitahi . . .). In open atolls Mollusks are of little importance in comparison with the whole faunal community, while on the other hand they are a major feature of closed atolls community (they may be as important as corals and even more important).

Every closed lagoon could be identified through its molluscan specific fauna as well as its relative abundance of species. Sessile Mollusks which can thrive in closed atolls are few in species: *Tridacna maxima*, *Pinctada maculata*, *Chama imbricata*

and *Arca ventricosa*. *Tridacna maxima* may occur with heavy densities such as 63 individuals per square meter which means a biomass of 4,9 kg live weight. Over a lagoon side 2 m. wide and 39 m. long transect extending from the shore line down to 4 m. deep, an important population of *Tridacna* reached 696 individuals and was evaluated as 7 tons of soft parts and 37 tons of shells per hectare.

Being heavily concentrated these Mollusks play an active part in the filling up of lagoons. The important deposits of *Tridacna* shells are able to build up large lagunal bar rubbles; these can attain several meters thickness and spread over several hundred square meters.

Thus it can be concluded that three thousand years ago when the emergence of reef formations took place, an extraordinary outburst of molluscan fauna occurred in lagoons of closed reefs. At the present time Mollusks are the prominent group of the whole fauna and play an important part in the land-building in the lagoons of these atolls.



SOLENOGASTRES UND CAUDOFOVEATA (MOLLUSCA, ACULIFERA):  
ORGANISATION UND PHYLOGENETISCHE BEDEUTUNG

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## INHALT

Kurzfassung . . . . .	191
1. Systematik und Organisation . . . . .	193
2. Phylogenetische Bedeutung einzelner Organe (Muskulatur, Darmtrakt, Ernährung und Lokomotion [Coelomfrage], Ctenidien, Larven) . . . . .	199
3. Discussion . . . . .	211
Zusammenfassung/Summary . . . . .	214
Literaturverzeichnis . . . . .	214

## KURZFASSUNG

The organization of the aplacophoran molluscs has been greatly neglected in the last 50 years, and the revision of these groups according to recent systematic principles requires the separation of the Chaetodermatidae from the Solenogastres as an independent class Caudofoveata. The term 'Aplacophora' - which expresses only an equal level of organization in both groups (in not yet having developed shell-like structures) - therefore has to be dropped. Both classes, the Solenogastres (*sensu nomine*) and the Caudofoveata, show significant phylogenetic relations in various characteristics:

The existence of numerous serially-arranged pairs of dorsoventral muscular bundles in Solenogastres and Caudofoveata represent the starting-point of a continuous sequence of increasing concentration, which extends further over the Placophora (16 pairs of bundles) and the Tryblidiacea (10-2 pairs) to the remaining Conchifera (8-0 pairs). A comparison of these conditions with the situations of musculature and digestive tract within the turbellarians consequently also demands a diverticulate intestine for the original molluscs.

The testcell-larva of Solenogastres and Bivalvia-Protobranchia (partly as well as these of Scaphopoda) must be placed at the very root of the molluscan stem and can phylogenetically be considered a strongly fundamented type, for, due to its various further relationships, the Trochophorae can easily be derived from the testcell-larva (comp. DREW, CHANLEY). Supporting facts for these correlations include the lack of protonephridia, the relatively late rectal anlage, and the caudal directed growth of the nerve-cords out of the cerebral centre; while the development of protonephridia and the local sinking of ganglionic layers phylogenetically have taken place convergently in more highly differentiated groups.

The adult nervous system, however, does not permit the use of the term 'Amphineura', for neither Solenogastres nor Caudofoveata actually possess two separate pairs of medullary cords, which is true on the other hand of the conchiferous Tryblidiacea.

Therefore, the Solenogastres and the Caudofoveata as well as the Placophora, are consequently to be placed under the concept ACULIFERA (HATSCHEK, 1891), in contrast to the Conchifera. The organization of the Solenogastres and Caudofoveata demands in summary greater notice and more intensive consideration.

In Betrachtung der Formenfülle der Mollusken ziehen auf Grund ihrer Quantität zweifellos die Conchiferen das grössere Augenmerk auf sich (sodass vielfach nur sie als Mollusca schlechthin betrachtet werden), doch vermögen kleine Splittergruppen oft ein Gleiches an Qualität zu offenbaren. So stellen die in der Weichtierkunde seit langem vernachlässigten aplacophoren Mollusken zwar eine nur geringe Formenzahl, doch

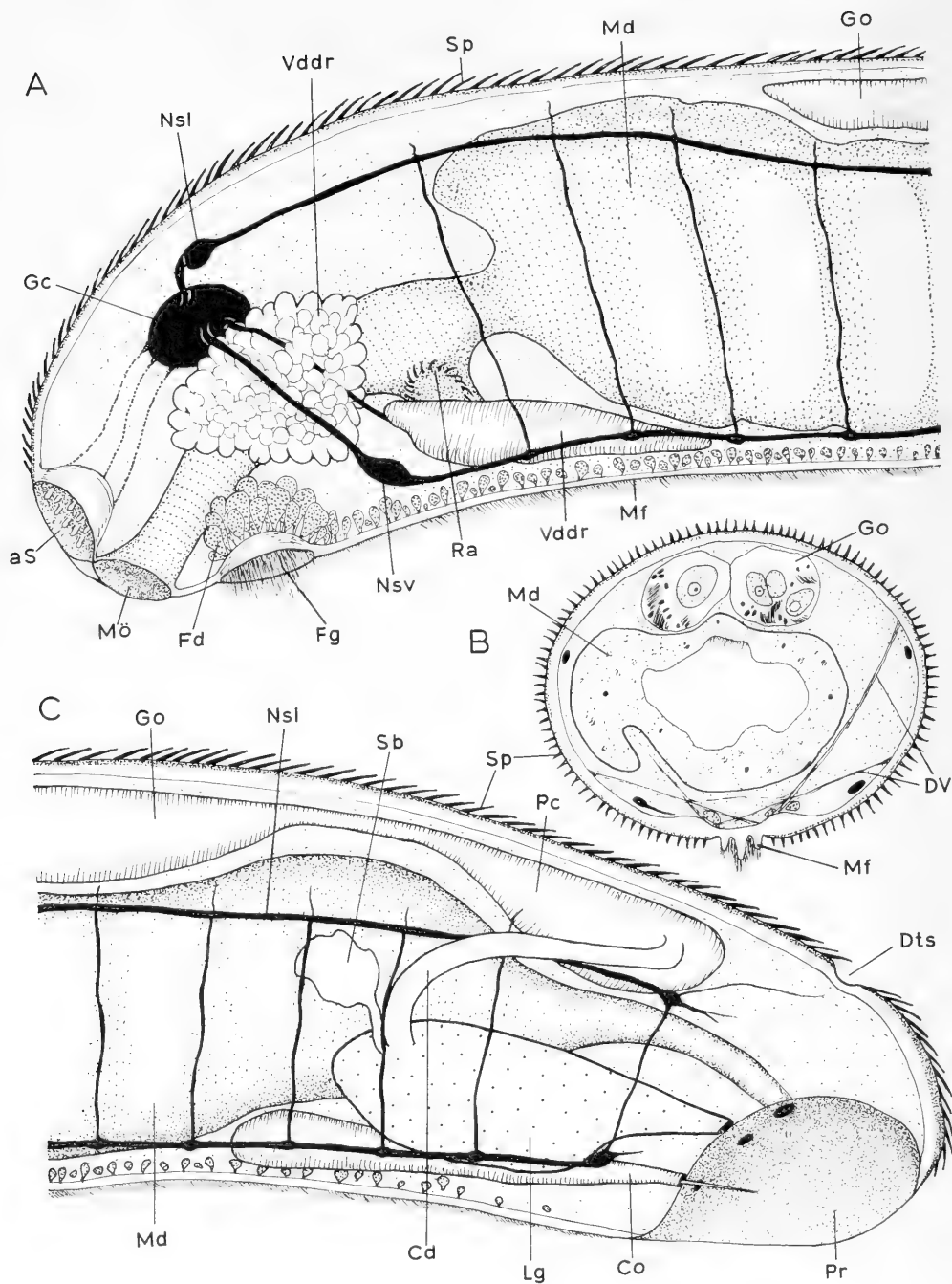


ABB. 1. Organisationsschema der Solenogastres. **A.** Vorderende, linke Körperwand abgetragen; **B.** Querschnitt in der Körpermitte; **C.** Hinterende, linke Körperwand abgetragen. (aS, atriales Sinnesorgan; Cd, Coelomduct; Co, Copulationsstacheln mit Scheide; Dts, dorsoterminales Sinnesorgan; DV, Dorso-ventral-Muskeln; Fd, Fussdrüsen; Fg, Flimmergrube; Gc, Cerebralganglion; Go, Gonade; Lg, Laichgang; Md, Mitteldarm; Mf, Fussfurche mit Falten; MÖ, Mundöffnung; NSl, laterales und NSv, ventrales Nervensystem; Pc, Pericard; Pr, Pallialraum; Ra, Radula-Apparat; Sb, Samenblase (Recept. sem.); Sp, Spicula; Vddr, Vorderdarmdrüsen).



geben sie aber durch ihre Organisation begründeten Anlass mehr als bisher beachtet zu werden.

## 1. SYSTEMATIK UND ORGANISATION

Im Anschluss an die Studien von WIREN (1892), ODHNER (1919), S. HOFFMAN (1949) und BOETTGER (1955, 1959) müssen die aplacophoren Mollusken auf Grund ihrer Organisation als zwei unabhängige Klassen von Solenogastres (*sensu stricto* = *sensu nomine*) und von Caudofoveata (welche aus den alten 'Aplacophora', oder fälschlich auch Solenogastres allgemein genannt, herauszulösen sind; vgl. Bryozoa - Kamptozoa) aufgefasst werden (vgl. p. 196); als zwei convergente Entwicklungslinien würden sie daher in einem gemeinsamen Begriff 'Aplacophora' nur eine künstliche Stadiengruppe, nicht aber eine natürliche systematische Einheit darstellen.<sup>1</sup> Zusammen mit den Placophora bilden Caudofoveata und Solenogastres so die drei Klassen des Mollusken-Unterstammes Aculifera (früher Amphineura),<sup>2</sup> --- im Gegensatz zu den fünf Klassen des zweiten Subphylum Conchifera.

Die SOLENOGASTRES oder Furchenfüsser (Abb. 1; früher Aplacophora-Neomeniida) stellen 1,5 mm bis 30 cm grosse Aculifera mit seitlich abgerundetem Körper dar, deren Mantel vollkommen mit Cuticula und Kalkspicula bedeckt ist; der Fuss ist allein durch die medioventrale, meist mit mehreren Falten versehene Längsfurche vertreten. Der Pallialraum zeigt sich durch die seitliche Verschmälerung der Körpers auf eine subterminale Höhle beschränkt, zusätzlich aber als drüsige Laichgänge in das Körperinnere verlagert (S. HOFFMAN); Ctenidien fehlen, doch bildet die caudale, respiratorische Pallialraum-Wand verschiedentlich sekundäre Atem-Anhänge aus. Der Verdauungstrakt mit Vorderdarmdrüsen und Radula weist am Mitteldarm serielle Ausbuchtungen oder Divertikel auf, alternierend mit zahlreichen paarigen Strängen der Dorsoventral-Muskulatur. Das Nervensystem bildet neben Cerebral-, Ventral-, Lateral- und Buccalganglien auch an den vier Längsstämmen Concentrationen der Nervenzellen zu mehr oder minder regelmässig aufgereihten Ganglien aus, an welchen querverbindende Commissuren und Connective entspringen; an besonderen Sinnesorganen treten das praeorale Atrium und die dorsoternale Sinnesgrube auf. Die

<sup>1</sup>Wenn auch der Name 'Aplacophora' (v. IHERING, 1876) als erste Bezeichnung vor 'Solenogastres' (GEGENBAUR, 1878) gegeben wurde, so verliert ersterer durch die Aufteilung der Gruppe in zwei selbständige Klassen sowohl an Wert wie an Sinn; eine Gegenüberstellung von 'Aplacophora' (für die Vertreter mit Ventralfurche) zu den Caudofoveata (Vertreter mit Ctenidien und Fuss-Schild) wäre jedoch ebenso irreführend (da die Caudofoveata auch noch aplacophor sind), wie das Belassen einer den Chitonen gleichwertigen einzigen Klasse von 'Aplacophora' mit Solenogastres (oder 'Ventreprolicida') und Caudofoveata als Unterklassen (vgl. BOETTGER, 1955). Wir werden den stammesgeschichtlichen Beziehungen nur dann einigermaßen gerecht, wenn wir drei unabhängige Entwicklungslinien auch systematisch als drei gleichwertige Kategorien führen (hier als Klassen). Dass GEGENBAUR aus Unkenntnis auch *Chaetoderma* in die Bezeichnung Solenogastres (= "Bauchfurcher", also Furchenfüsser) mit einbezog, wurde schon von SIMROTH (1894: 131) und ODHNER (1919: 78) beanstandet. Da für höhere Systemkategorien jedoch keine (oft ja unsinnige) nomenklatorische Festlegung besteht, wird vorgeschlagen, jene Vertreter mit einer ventralen Fussfurche endgültig als die Klasse Solenogastres (*sensu nomine*; Furchenfüsser) zu bezeichnen, --- die mit einem postoralen Fuss-Schild und mit echten Ctenidien versehenen Arten jedoch als eigene Klasse Caudofoveata (Schildfüsser) herauszuziehen. Caudofoveata, Solenogastres und Placophora bilden daher drei gleichwertige Klassen der Aculifera (SALVINI-PLAWEN, 1967b, 1969).

<sup>2</sup>Auch die Bezeichnung 'Amphineura' ist irreführend und daher sinnlos; ein tatsächlich amphineures Nervensystem (zwei Paar getrennte Markstränge) besitzen nämlich nur die Placophora und die Tryblidiacea (*Neopilina*)! Da weder den Solenogastres, noch den Caudofoveata im strengeren Sinn eine Amphineurie zukommt, und da die Tryblidiacea den Conchifera zugeordnet sind, verliert die Bezeichnung 'Amphineura' als Zusammenfassung von Solenogastres, Caudofoveata und Placophora vollkommen an Wert und namengebende Bedeutung. Der Name ACULIFERA (HATSCHKE, 1891) fasst hingegen diese drei Klassen (den CONCHIFERA gegenüberstehend) mit einem gleichen Merkmalskomplex zusammen, dem Mollusken-Mantel, und ist daher sowohl vergleichend-anatomisch wie auch rein nomenklatorisch als vollwertig vorzuziehen. Aculifera (Stachel-Weichtiere) und Conchifera (Schalen-Weichtiere) bilden daher eine sinnvolle Gruppierung der acht Molluskenklassen in zwei Unterstämme.

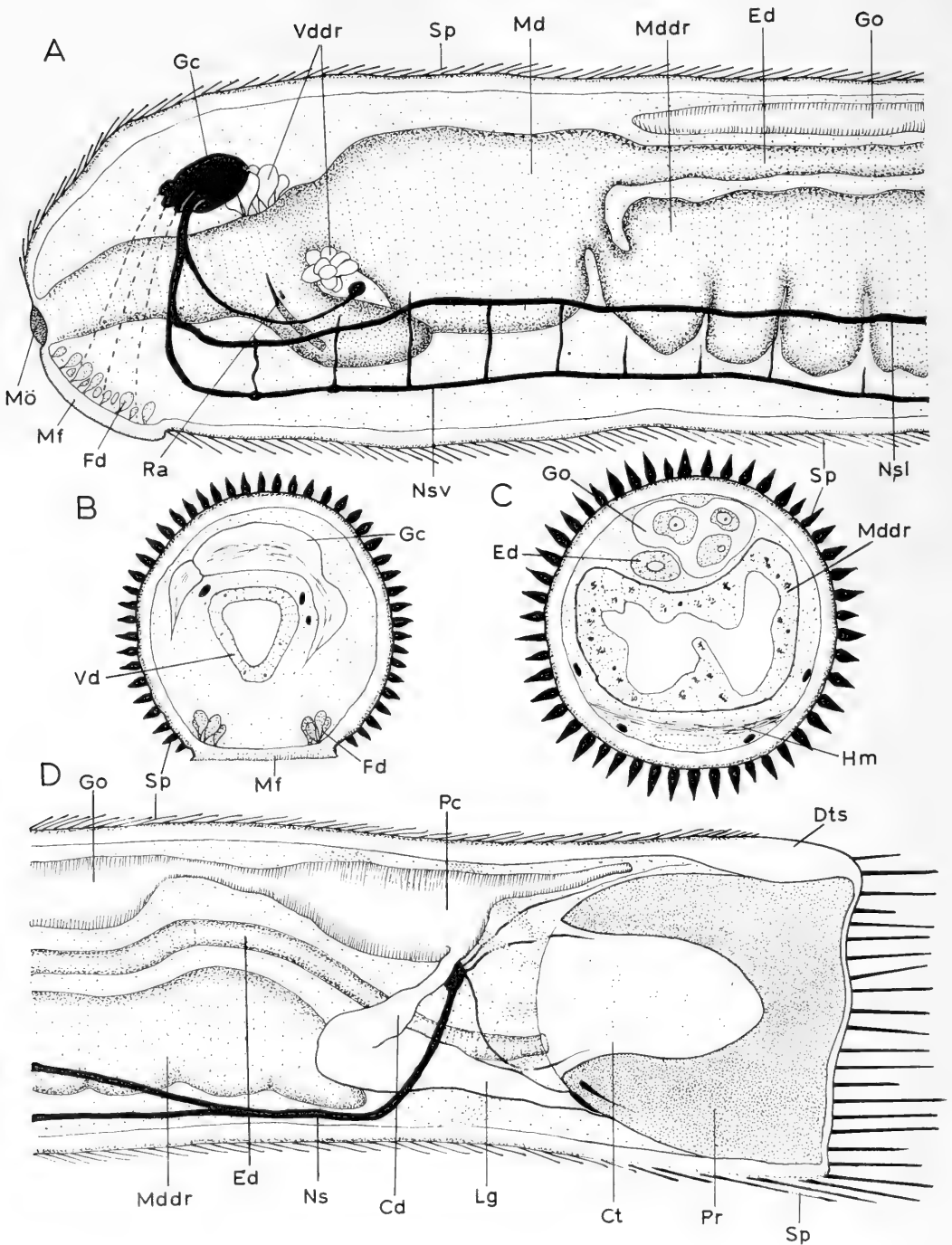


ABB. 2. Organisationsschema der Caudofoveata. **A.** Vorderende, linke Körperwand abgetragen. **B.** schräger Querschnitt durch das Vorderende mit Fuss-Schild. **C.** Querschnitt in der Körpermitte. **D.** Hinterende, linke Körperwand abgetragen. (Cd, Coelomoduct; Ct, Ctenidien; Dts, dorsoterminals Sinnesorgan; Ed, Enddarm; Fd, Fussdrüsen; Gc, Cerebralganglion; Go, Gonade; Hm, Horizontalmuskel, Lg, Laichgang; Md, Mitteldarm; Mddr, unpaarer Mitteldarmsack; Mf, Fuss-Schild; MÖ, Mundöffnung; Ns (Nsl, Nsv), Nervensystem (lateral, ventral); Pc, Pericard; Pr, Pallialraum; Ra, Radulaapparat; Sp, Spicula; Vd, Vorderdarm; Vddr, Vorderdarmdrüsen).

paarigen Keimdrüsen sind hermaphroditisch und die Geschlechtsprodukte werden, da die eigentlichen Gonoducte rückgebildet sind, über Pericard, Coelomoducte und Laichgänge ausgeleitet; die innere Befruchtung wird durch Samenblasen und häufig auch durch eine Genitalpapille (Penis) oder gar durch Copulationsstacheln ('Liebespfeile') ergänzt. Die Entwicklung erfolgt über eine Hüllglocken-, seltener über eine Trochophora-ähnliche Larve. Die rein marinen Solenogastres mit 110 Arten in 51 Genera leben freibeweglich auf der Sediment-Oberfläche, oder epizoisch meist auf Cnidaria.

Die *CAUDOFOVEATA* oder Schildfüsser (Abb. 2; früher Aplacophora-Chaetodermatida) sind als 3 mm bis 14 cm grosse Aculifera mit gestrecktem, wurmförmigen Habitus charakterisiert, deren Körper vollkommen vom Mantel mit Cuticula und Kalkschuppen eingehüllt ist und lediglich eine einheitliche oder geteilte, postorale Grab- und Sinnesplatte freilässt, den Fuss-Schild. Der terminale, glockenförmige Pallialraum weist ein Paar echter Ctenidien auf und zeigt sich weiterhin auch als paarige Rinne (oder als paariger Gang) in das Körperinnere verlagert. Der Verdauungstrakt mit Vorderdarmdrüsen und einer teilweise stark umgeformten Radula bildet einen unpaaren, ventralen Mitteldarmsack aus; regelmässige Ausbuchtungen und serielle Dorsoventral-Muskulatur sind nur mehr ausnahmsweise, und hier auf den vorderen Darmabschnitt beschränkt, ausgebildet. Das Nervensystem mit zentralem Cerebralkomplex weist allein Buccal- und Ventral-Ganglien auf, doch vereinen sich die lateralen Nervenstränge mit der jeweiligen ventralen Bahn, sodass auch die querverbindenden Commissuren und Connective auf den vorderen Körperabschnitt eingeschränkt sind; an der Pallialraum-Glocke befindet sich eine dorsale, längliche und grosse Sinnesgrube. Die meist verschmolzenen Keimdrüsen sind getrenntgeschlechtlich und die Genitalprodukte werden, da die eigentlichen Gonoducte (convergent zu den Solenogastres) rückgebildet sind, über Pericard, Coelomoducte und Laichgänge ausgeleitet. Die Befruchtung findet frei im Meerwasser statt und es treten dementsprechend keine Genital-Hilfsorgane auf; die larvale Entwicklung ist noch unbekannt. Die rein marinen Caudofoveata mit 55 Arten in 6 Genera (3 Familien) sind Grab-Formen im Sediment.

Diese skizzierten Organisationsmerkmale von Solenogastres und Caudofoveata lassen ihre deutliche Unabhängigkeit voneinander, wie auch von den Placophora erkennen (vgl. BOETTGER 1955, 1959). Das genaue vergleichend-anatomische Studium dieser drei Aculifera-Klassen lässt manche der Organisationszüge von Caudofoveata und Solenogastres bei detaillierter Auflösung als bedeutend ursprünglicher wie bei den Chitonen erkennen, wobei sich insgesamt die Caudofoveata in der Stammesgeschichte der Weichtiere am frühesten abgespalten haben müssen (Abb. 4). Es liegt bei ihnen eine Organisation vor, welche vom gemeinsamen Ausgangspunkt allein durch regressive Umbildungen differenziert erscheint: Alle nicht auch ebenso entweder bei Solenogastres oder bei Placophora anzutreffenden, also als ursprünglich anzusprechenden Merkmale müssen nämlich auf die mit der Lebensweise correlative Abrundung des Körpers zurückgeführt werden; allein der gerade Darmkanal mit dem unpaaren Verdauungssack ist als eine gruppeneigene Neubildung zu werten. Von einem turbellariomorphen, flachen und gleitend-kriechenden 'Urmollusken' ausgehend (Abb. 3), dürfte sich der Caudofoveata-Zweig zur grabenden Lebensweise spezialisiert haben, wobei der Körper zur Wurmform abgerundet wurde. Das tastende und suchende Graben mit dem Vorderende bewirkte naturgemäss eine Schrägstellung des gesamten Körpers, wodurch das Hinterende mit den Kiemen aus dem Sediment ragte. Hier begann auch die (entgegen BOETTGER 1955: 243) von hinten nach vorne fortschreitende Rückbildung des Fusses, welcher erst mit der lokomotorischen Anpassung an die neue Gestalt (Schwellkörper-graben) auch am Vorderende verschwand; die postorale Grab- und Sinnesplatte, der Fuss-Schild, stellt jedoch noch diesen letzten Fussrest dar (vgl. p. 196 und HOFFMAN 1949: 376-384). Die zum Atmen der nunmehrigen Sedimentbewohner lebensnotwendigen Ctenidien blieben daher erhalten, rückten aber mit dem Pallialraum nach terminal.

Der postorale Fuss-Schild zeigt durch seine Histologie und durch die lateralen Drüsenbildungen eine detaillierte Gleichheit mit dem Molluskenfuss der Solenogastres (S. HOFFMAN 1949: 352-362, 372-385). Die cerebrale Innervierung des Fuss-Schildes erzwingt jedoch seine Homologie allein mit dem vorderen, cerebral innervierten Abschnitt des Fusses bei jenem gemeinsamen Vorfahren (Urmollusk, Abb. 3) mit noch der gesamten Ventralfläche als lokomotorisches Gleitorgan. Die Unterteilung dieser Ventralfläche in einen rein lokomotorisch-pedalen (ventral innervierten) Fuss und in einen praepedal-oralen (cerebral innervierten) "Kopf"-Abschnitt erfolgte daher erst nach Abspaltung der Caudofoveata, was durch die erst danach entwickelte, kompakte und ventral innervierte Fussdrüse (Solenogastres, Placophora; Conchifera) belegt wird. Der Fuss-Schild der Caudofoveata stellt somit sowohl einen (Ur-)Molluskenfuss-Rest dar, wie er zudem die deutlich basal abgezweigte Stellung der Caudofoveata innerhalb der Aculifera belegt.

Die Stufung bei der Spicula-Bildung innerhalb der Aculifera in 1. eine intrazelluläre Anlage, welche den Kontakt zum Epithel verliert (Caudofoveata, Solenogastres, Placophora), in 2. eine intrazelluläre Anlage mit Zellschlauch und basalem Cuticula-Becher (Solenogastres, Placophora), sowie in 3. eine Bildung aus mehreren Zellen (nur bei Placophora) zeigt eine deutliche Differenzierungs-Abfolge. Sie ist zusammen mit der Spikeltypen-Zahl bei Caudofoveata (1), bei Solenogastres (1+2) und bei Placophora (1+4 mit zahlreichen Abwandlungen) als ein weiterer Beleg für die basale Abzweigung der Caudofoveata innerhalb der Mollusken-Phylogenie zu werten.

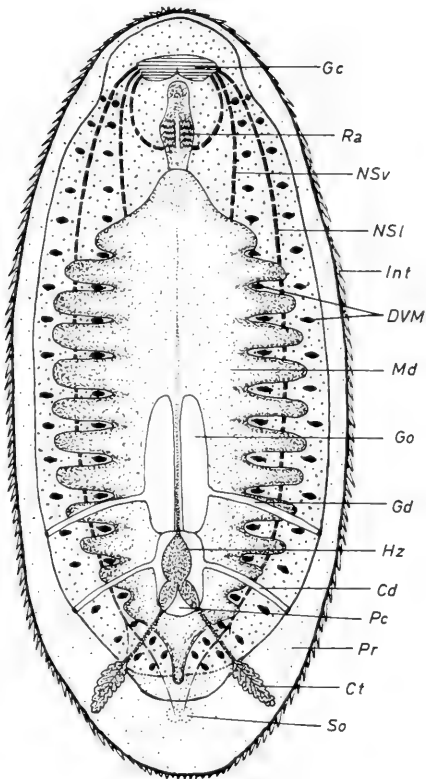


ABB. 3. Rekonstruierte Stammform der Mollusken ('Ur-Mollusk') von dorsal. Cd, Coelomoduct; Ct, Ctenidium; DVM, Dorsoventral-Muskulatur; Gc, Cerebralganglion; Gd, Gonoduct; Go, Gonade; Hz, Herz; Int, Spicula-tragendes Integument (Stachel-Cuticula); Md, Mitteldarm; NSl, laterales und NSv ventrales Nervensystem; Pc, Pericard; Pr, Pallialraum; Ra, Radula; So, Sinnesorgan).

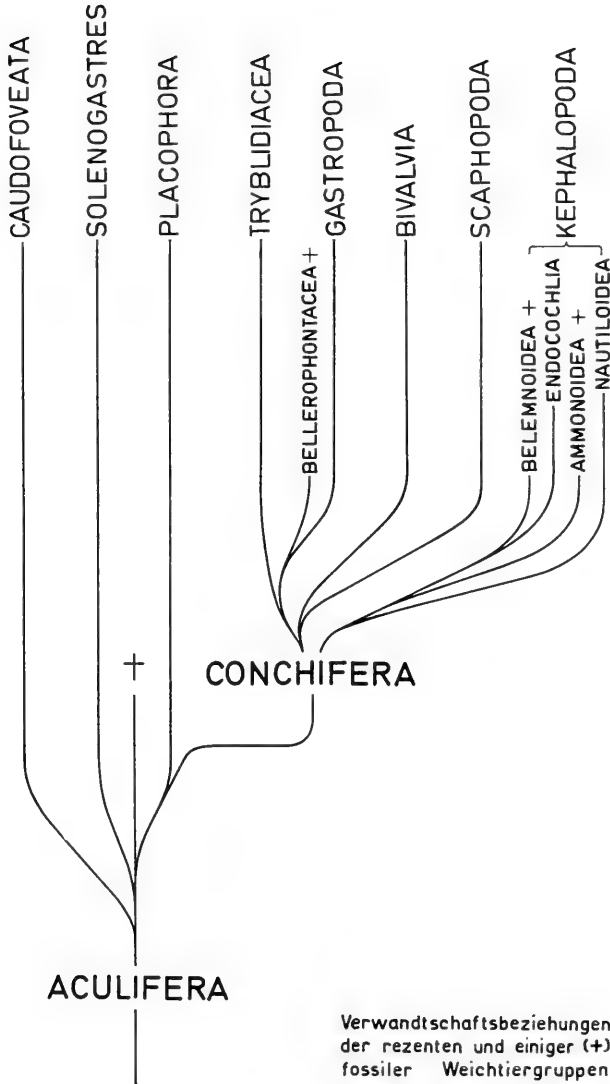


ABB. 4. Phylogenie der Mollusca: Verwandschaftsbeziehungen der rezenten und einiger fossiler Weichtiergruppen.

Die Solenogastres dürften sich hingegen ganz gegenteilig umgebildet haben, da sie sich trotz des schmalen Fusses (Fussfurche) allein mit dessen Hilfe auf Cilien fortbewegen (SALVINI-PLAWEN 1968 b). Die stammesgeschichtliche Umbildung von dem turbellariomorphen, flachen und gleitend-kriechenden 'Urmollusken' (Abb. 3) muss daher derart vermutet werden, dass nicht eine Änderung in der Bewegungsart eingetreten ist (wie es BOETTGER, 1955: 237 ff, annehmen möchte), sondern dass die Lebensweise geändert wurde; sie verlangte in zunehmendem Masse eine grössere Beweglichkeit, d.h. dass hier durch eine mehr schließende oder windende Lokomotion eine Körperverschmälerung begünstigt wurde. Die vollständige Rückbildung der Ctenidien kann ebenfalls daraus erklärt werden, da die Solenogastres als Bewohner

der Sediment-Oberfläche auf Grund ihres steten Kontaktes mit dem freien Wasser genügend Gasaustausch durch die Körperhaut bestimmter Regionen erhielten (was bei einer grabenden Fortbewegung, vgl. BOETTGER, nicht vorstellbar wäre) und dadurch die Kiemen ohne grosse Einbusse der Atmung verschwanden. --- Die Solenogastres zeigen aber durch detaillierte Übereinstimmungen mit den Placophora im Fuss mit Fussdrüse und im spiculatragenden Integument (vgl. p. 196), dass ihre Stammesgeschichte zumindest bezüglich dieser Merkmale eine Zeitlang mit den Käferschnecken gemeinsam verlief; in ihrer eigenständigen Phylogenie nach der Abspaltung haben sie sich jedoch trotz der habituellen Umformung (mit Verlust der Gonoducte und Ctenidien) in etlichen Merkmalen progressiv differenziert (vgl. Geschlechtsapparat).

Die Placophora wiederum haben offensichtlich die ursprüngliche Körperform der turbellariomorphen, flachen und gleitend-kriechenden Stammform (Abb. 3) gross-teils beibehalten (vgl. auch Nervensystem), wenn auch etliche Merkmale eigenständig spezialisiert sind (Mehrfachbildung der Ctenidien, Verdauungstrakt, Schalenplatten); sie erscheinen aber vor allem durch die Ausbildung der acht dorsalen Kalkplatten samt der davon abhängig concentrirten Dorsoventral-Muskulatur in Richtung auf die späteren Conchifera höher differenziert.

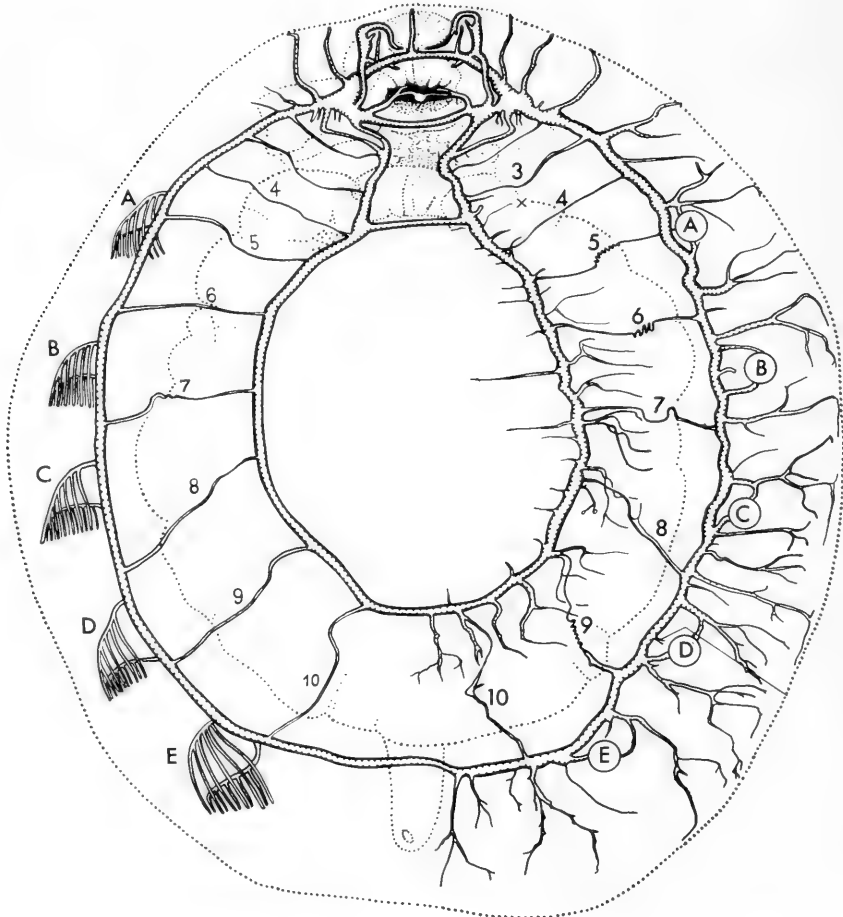


ABB. 5. Das Nervensystem von *Neopilina* (aus LEMCHE & WINGSTRAND, 1959). 3-10, 3. bis 10. Lateropedal-Connectiv; A-E, Ctenidien.

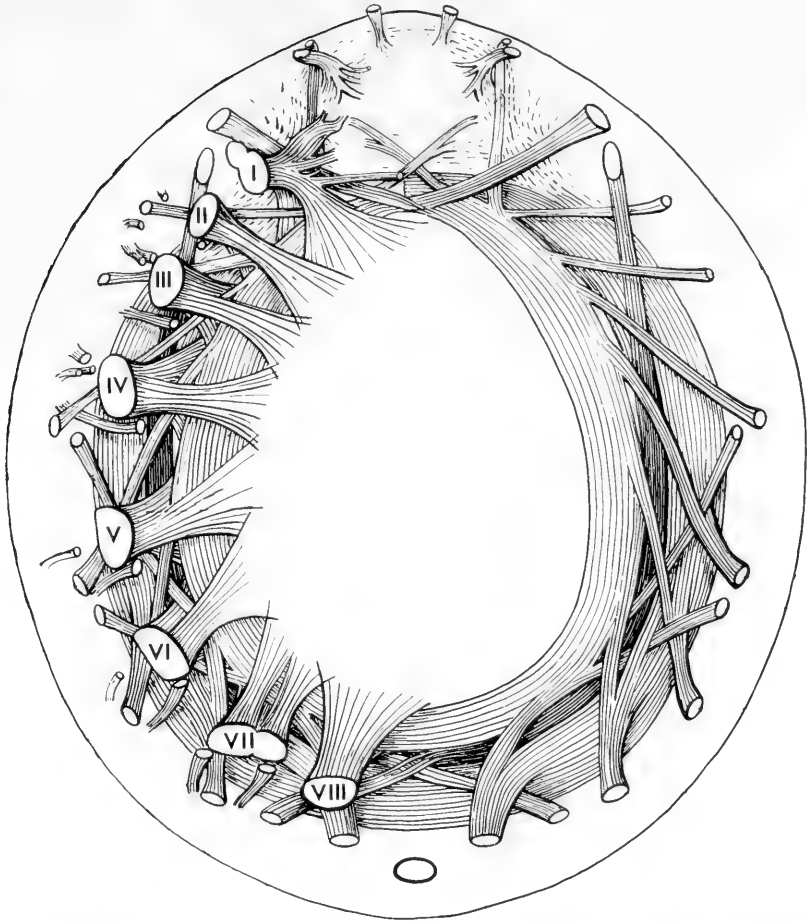


ABB. 6. Das Muskelsystem von *Neopilina* (aus LEMCHE & WINGSTRAND, 1959). I-VIII Dorsoventral-Muskelstränge.

Diesen umrissenen Grundzügen zufolge erkennen wir also die Entwicklung von drei unabhängigen Gruppen Caudofoveata, Solenogastres und Placophora aus einer gemeinsamen Stammform ('Urmollusk'), welche gemäss den systematischen Prinzipien auch mit der gleichwertigen System-Kategorie eingeordnet werden müssen. Es braucht nach den obigen Ausführungen wohl nicht mehr besonders betont werden, dass eine Ableitung der Solenogastres und Caudofoveata von Placophora --- quasi von Cryptochitoniden durch Dorsalplatten-Verlust (wie noch häufig, besonders in der Paläontologie, vertreten wird) --- ebenso unhaltbar ist, wie die Proklamation von *Neopilina* als eine dem Ursprung der Mollusken nahestehende Form; die Stammform der Weichtiere hatte zweifellos eine aculifere Organisation (vgl. BEEDHAM & TRUEMAN, 1968: 448-450).

## 2. PHYLOGENETISCHE BEDEUTUNG EINZELNER ORGANE

Im Anschluss an den Organisations-Abriss von Solenogastres und Caudofoveata sollen einige charakteristische Bauplan-Merkmale herausgegriffen werden, welche die jeweiligen morphologischen Beziehungen der Vertreter der beiden Klassen deutlich hervorheben und die phylogenetische Bedeutung darlegen.

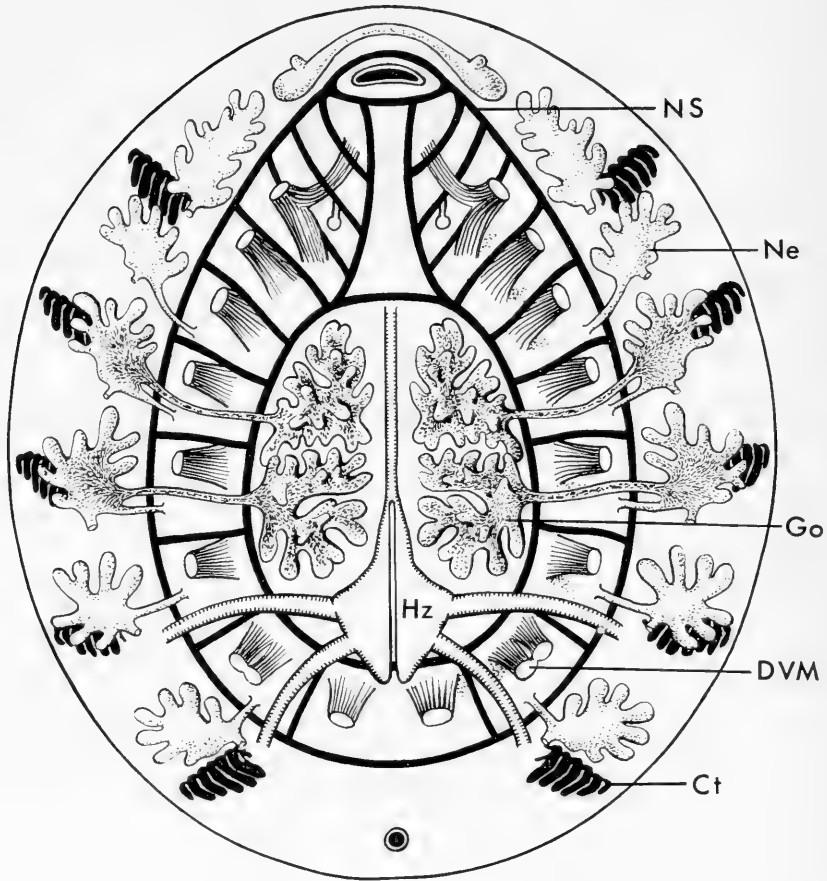


ABB. 7. Organisationschema von *Neopilina*, (aus LEMCHE & WINGSTRAND) nach Abb. 5 & 6 korrigiert! (Ct, Ctenidien; DVM, Dorsoventral-Muskelbündel; Go, Gonaden; Ne, Nephridien; NS, Hauptnervensystem).

#### a) Muskulatur

Abgesehen vom vollständig erhaltenen, dreischichtig ausgebildeten Hautmuskelschlauch bei Solenogastres und Caudofoveata, zeigt sich, dass ihnen auch die bei allen Weichtieren zwischen Mantel und Fuss verlaufenden, charakteristischen Dorsoventral-Stränge zu eigen sind. Durch die jüngsten Funde recenter Tryblidiacea hat sich zudem eine klaffende Merkmalslücke bedeutungsvoll geschlossen, denn entgegen dem verfälschten *Neopilina*-Organisations Schema (welches so oft abgebildet wird) zeigen sich nämlich die Muskelbündel, das Nervensystem, die Ctenidien und die Nephridien bei *Neopilina* lagemässig keineswegs übereinstimmend correlliert (wie die anatomischen Darstellungen von WINGSTRAND einwandfrei belegen: Abb. 5, Ctenidium A müsste bei dem 6. Connectiv liegen!); darüberhinaus sind die Muskelstränge I und VII noch deutlich zweiteilig (Abb. 6)! Damit schliesst sich aber das allgemeine Bild zu einer lückenlosen Concentrationsreihe (Abb. 8):

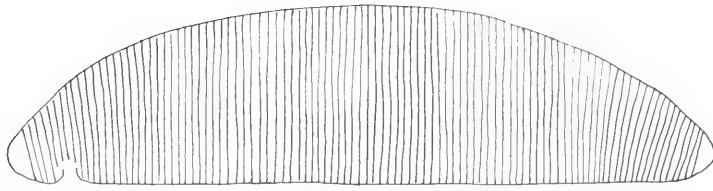
Die Solenogastres weisen einheitlich eine durchgehende Serie von paarigen, sich am Fuss überkreuzenden Dorsoventral-Strängen auf (entgegen der Behauptung von LEMCHE 1959: 431), und selbst für die weitgehend rückgebildeten Caudofoveata konnte bei einer



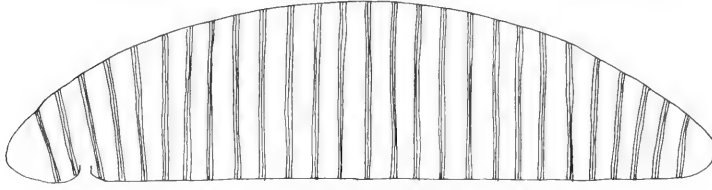
jüngst entdeckten, relativ ursprünglichen Art (*Scutopus ventrolineatus*) im Vorderkörper eine gleichartige Anordnung der Muskulatur aufgefunden werden. Eine derartige Strangreihe hat mit der Anlage von mehreren dorsalen Kalkplatten verständlicherweise eine daraufhinführende Concentration erfahren, sodass die acht beweglichen Schalenstücke der Käferschnecken daher mit je zwei Paar Dorsoventral-Bündel, zusammen also mit 16 hintereinanderliegenden Strangpaaren gegen den Fuss hin verankert sind. Die stammesgeschichtliche Verschmelzung jener dorsalen Kalkplatten zu einer einheitlichen Concha (vgl. BOETTGER; 1955: 250; 1959: 388) findet in der weiteren Concentration der Dorsoventral-Muskulatur ihr Äquivalent, was innerhalb der Tryblidiacea festzustellen ist; die in vielen anderen Merkmalen weitgehend spezialisierte *Neopilina* (Abb. 7) gibt uns mit ihren 8 bzw. 10 Strangpaaren ein recentes Beispiel dieser Übergangsformen (Verschmelzung von je zwei Käferschnecken-Strängen zu einem Bündel). Die weitere Verdichtung und Concentration der nun als Schalen- oder Fuss-Muskel bezeichneten Dorsoventral-Stränge innerhalb der Conchifera ermöglichte Hand in Hand damit eine zunehmende Beweglichkeit des Tieres in der Schale und (bei Gastropoda, Scaphopoda und Kephelopoda) das Absetzen eines distincten Kopfabschnittes, wodurch der Mantel mit Concha auf den Eingeweidessack beschränkt wurde. So lassen sich die Gastropoden über Zustände ableiten, wie sie die fossilen Gattungen der Tryblidiacea *Drahomira* PERNER (7 Muskelpaare), *Tryblidium* LINDSTRÖM, *Pilina* KOKEN, etc. (6 Muskelpaare), *Cyrtonella* HALL (3-2 Muskelpaare) und *Sinuitopsis* PERNER (3 Muskelpaare) zeigen, und wie die Bellerophontacea (1 Muskelpaar) überleiten. Dass die mit Sinus oder Schlitzband versehene Concha der Bellerophontacea noch exogastrisch gewunden war, belegen die Verhältnisse bei der genannten *Sinuitopsis acutilira* (HALL), welche trotz der noch drei-paarigen Muskeln schon (wie auch *Cyrtolites ornatus* CONRAD?) einen Sinus zeigt (ROLLINS & BATTEN, 1968); die absolute Symmetrie des einzigen Muskelpaares der Bellerophontacea (vgl. KNIGHT, 1947) spricht zudem gegen eine schon eingetretene Torsion. Die erst danach erfolgte mutative Torsion des Eingeweidessackes um  $180^{\circ}$  --- der bereits vorhandene Sinus (bzw. das Schlitzband) begünstigte hierbei das Überleben der tortierten Formen (Ableitung der Faeces nach oben) --- bedingte bei den echten Gastropoda daher die Rückbildung des primär rechten Muskels und die Drehung der Schalenschnecke nach hinten: endogastrische Concha (Schlitzband und Pallialraum vorne: Prosobranchia), welche mit einem unpaaren (ursprünglich linken, nun) rechten Spindelmuskel verstrebt ist; Reste des Gegenmuskels sind bei wenigen Arten erhalten.

Für die Bivalvia wird die zunehmende Concentration der Dorsoventral-Muskulatur in einer median geknickten (zweiklappigen) Tryblidiaceen-Schale (Diplacophora) einerseits durch die actinodonte *Babinka* BARRANDE (8 Muskelpaare; vgl. McALESTER, 1965) fossil, recent (atavistisch?) durch Formen wie *Modiolus* (7 Paare), *Mesodesma* (5 Paare) u.a.m. belegt, und andererseits durch die ctenodonten Protobranchia (*Nucula*, *Yoldia*, *Nuculana*, mit 6-3 Muskelpaaren; vgl. YONGE 1953). Ähnliche Muskel-Concentrationen lassen sich schliesslich auch für die Scaphopoda und Kephelopoda annehmen.

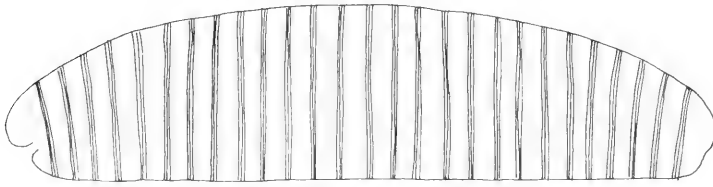
Der besonders in der Paläontologie vertretenen Ansicht, dass die Käferschnecken sich (völlig unverständlich) durch "Zerfall" der Concha in acht Schalenplatten differenziert hätten (YONGE, 1939: 133; FRETTER & GRAHAM, 1962: 8), stehen die eindeutigen Verhältnisse bei Solenogastres und Caudofoveata markant gegenüber. Zudem ist die Gelenkigkeit der 8 Platten nur auf eine primäre Einrollfähigkeit der (aculiferen) Tiere zurückzuführen, nicht jedoch von einem conchiferen Zustand her! Auch scheint die Tatsache noch nicht aufgefallen zu sein, dass an Muskeleindrücken bisher stets nur acht Paar oder weniger, nicht aber mehr aufgefunden wurden (vgl. McALESTER, 1965: 236), obwohl sie allerdings auch (als geteilt) in 16-Zahl auftreten könnten: Alle Mollusken vor dem phylogenetischen Erscheinen der Tryblidiacea bzw. Placophora waren zwar mit mehr als 8 bzw. 16 Strangpaaren versehen, besaßen aber



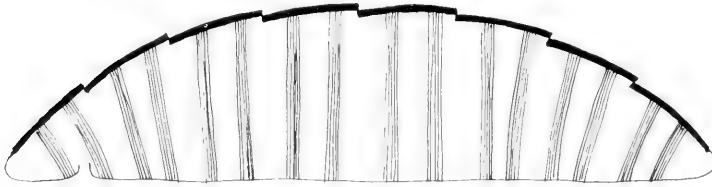
**Turbellaria**  
ohne  
Darmdivertikel



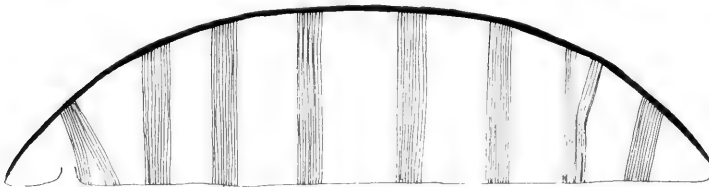
**Turbellaria**  
(und Nemertini)  
mit Divertikel



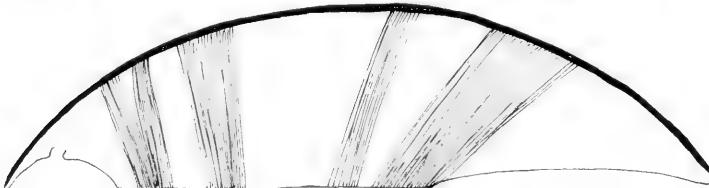
**Solenogastres**  
(mit Divertikel)



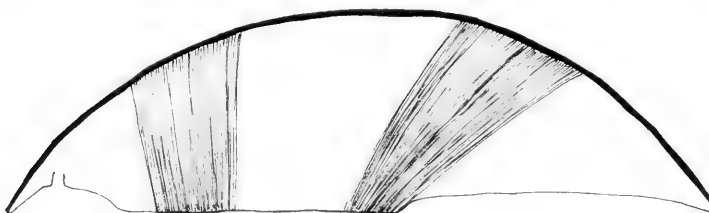
**Placophora**  
(mit 8 Schalenplatten)



**Tryblidiacea**  
(Neopilina)



**Bivalvia I**  
(Nuculacea)



**Bivalvia II**  
(als Vertreter der  
weiteren Conchifera)

**ABB. 8.** Schematische Darstellung der zunehmenden Verdichtung in der Dorsoventral-Muskulatur zur Demonstration der phylogenetischen Konzentrationsreihe.

noch keine Schalen, --- können (!) daher auch nicht beschalt aufgefunden werden. Zudem begünstigt eine konisch gewölbte Schale allein eine Concentration, wodurch auch secundär vermehrte Muskelstränge unwahrscheinlich sind (vgl. auch BOETTGER, 1955); die Eindrücke bei den Verwandten der fossilen Gattung *Stenothecoides* RESSER sind hingegen nicht als Dorsoventral-Muskeln zu werten, und zudem stellt die Gruppe der teils asymmetrischen Arten (Stenothecoida) durch die Zweiklappigkeit (YOCHELSON, 1969) wenn überhaupt Conchifera, so einen Seitenzweig der Muscheln dar.

Es ergibt sich zusammenfassend somit eine lückenlose Concentrationsreihe der zahlreichen Strangpaare vom Solenogastren-Zustand über das Placophoren- und Tryblidiaceen-Stadium bis zu den Gegebenheiten bei Gastropoda, Bivalvia, Scaphopoda und Kephelopoda (Abb. 8). Der phylogenetische Ausgangspunkt für die Molluskenwurzel ist also in einer Anordnung zu suchen, wie sie die Dorsoventral-Muskulatur heute noch bei Solenogastren zeigt (vgl. Abb. 1, 3).

#### b) Darmtrakt

Ein solcher stammesgeschichtlicher Anschluss von den Weichtieren zurück lässt sich leicht in den Muskulatur-Verhältnissen verschiedener Plathelminthen-Gruppen erkennen (Abb. 8). So sind z.B. bei Turbellarien ohne Divertikel-Darm die dorsoventralen Muskelfasern ungeordnet und netzartig verknüpft (bei jenen Formen der, nach KARLING 1967, Archoophora, Prolecithophora, Proseriata, Rhabdocoela und Lecithoepitheliata, deren Darmrohr nicht dem Hautmuskelschlauch anliegt); die vorwiegend grösseren Vertreter weisen hingegen durch einen Divertikel-Darm als Verteiler-System bereits eine correlative Gruppierung der Muskelfasern zu serialen Strängen auf (Polycladida, Tricladida). Dieses zweite Bild findet sich nun in völliger Gleichheit auch bei den Solenogastres: ein mit serialen Aussackungen versehener Mitteldarm, in dessen Aussparungen die Muskelstränge verlaufen. Da die derartige Muskulatur-Anordnung bei den Plathelminthes und bei den Mollusken (wie auch Nemeritinen) --- wie die vergleichende Anatomie ergibt --- durch die ventrale Sohlenbewegung nicht im Zusammenhang mit speziellen Lokomotionsorganen (Peristaltik, Borsten, Beine) entstanden sein kann, ist allein die, durch die mit der habituellen Vergrößerung bedingte Anlage von Darmaussackungen als Ursache für die Fasern-Aufteilung zu sehen. Da nun weiterhin selbst jene Solenogastres-Arten ohne Divertikeldarm die serialen Muskelstränge besitzen (es sind fast durchwegs kleine Vertreter), ist ein solches Fehlen von Aussackungen als secundär zu betrachten (Zwergformen, tierische Nahrung). Wir sind somit mit gutem Grund berechtigt anzunehmen, der ursprünglichsten Ausgangsform der Weichtiere, dem 'Urmollusk' (Abb. 3), einen Divertikeldarm zuzusprechen, --- so wie er bei den recenten Solenogastres (und teils auch Caudofoveata) noch vorliegt.

#### c) Ernährung und Lokomotion (Coelomfrage)

Die Frage nach der ursprünglichsten Form der Radula wird allgemein zugunsten des zweiteiligen Typus erörtert (vgl. BOETTGER 1955, 1959), womit nicht nur durch die Anwesenheit der Radula allein, sondern besonders durch diese ursprüngliche Zweiteiligkeit (vgl. die häufige Endgabelung der Gastropoden-Radulascheide) auf eine carnivore Ernährung der Mollusken-Vorfahren geschlossen werden kann. Die sowohl bei Solenogastres (Abb. 9) wie auch bei Caudofoveata (Abb. 10) primär ausgebildete distiche Räder-Radula stellt eine zusätzliche Bestätigung dar. Da jene Coelomata, welche sich als errante Formen Substrat-gebunden repräsentieren, generell im Zusammenhang mit der Coelomanlage zu Microphagen oder Detritusfressern geworden sind (grabende Lebensweise ! vgl. Echiurida, Sipunculida, Annelida, Branchiotremata), liegt hierin ein deutliches Indiz, dass die Mollusken als carnivore Formen (vgl. besonders die ursprünglicheren Solenogastres) ihre ursprüngliche Lebensweise bei-

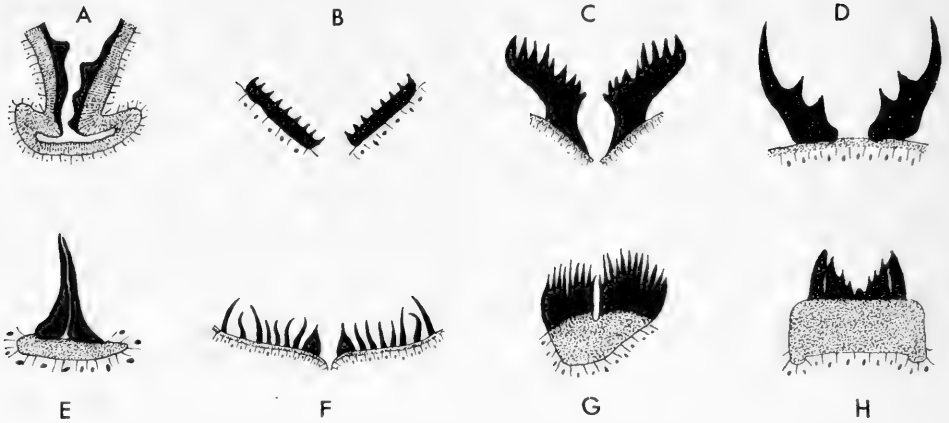


ABB. 9. Verschiedene Radula-Typen (je eine Querreihe) bei Solenogastres. **A.** *Cyclomenia holoserica*. **B.** *Kruppomenia minima*. **C.** *Epimenia verrucosa*. **D.** *Genitoconia atriolonga*. **E.** *Dondersia californica*. **F.** *Dorymenia weberi*. **G.** *Anamenia amboinensis*. **H.** *Alexandromenia crassa* (schwarz = Radula-Zähne, punktiert = cuticulare Basis; nach verschiedenen Autoren zusammengestellt).

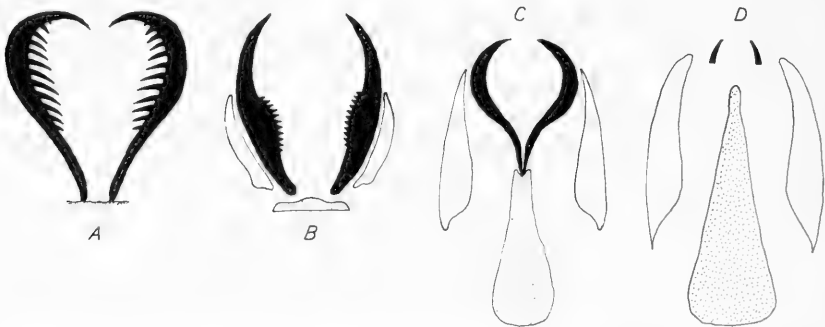


ABB. 10. Reduktionsreihe der Radula (je eine Querreihe) bei den Caudofoveata. **A.** *Scutopus*. **B.** *Prochaetoderma*. **C.** *Falcidens*. **D.** *Chaetoderma* (schwarz = Radula-Zähne, punktiert = cuticulare Basis; Original, leicht schematisiert).

behalten und damit auch keine durchgreifende Bauplanänderungen wie die Anlage eines Körper-Coeloms erfahren haben.

Im Gegensatz zu den Solenogastres sind die Caudofoveata jedoch grabende Formen. Diese Lebensweise kann aber mit Bestimmtheit als sekundär bezeichnet werden, denn einerseits ist bei den ursprünglicheren Limifossoridae (die Genera *Limifossor*, *Scutopus*, *Metachaetoderma*) eine mehrreihige, distiche Greif-Radula ausgebildet (Abb. 10A), diese zeigt aber andererseits bei den Chaetodermatidae (*Falcidens*, *Chaetoderma*) durch die Ernährung der Tiere als Partikelfresser im Substrat derart radikale Rückbildungen (Abb. 10C, D), dass hier kaum mehr von einer Radula im engeren Sinne gesprochen werden kann! Die Lokomotion der Caudofoveata erfolgt hingegen auf Grund ihres durch die Lebensweise reduzierten Fusses mit Muskulatur und Körperlympe als Schwellkörper-System, so wie es TRUEMAN (1968) für zahlreiche weitere Grabformen angibt (vgl. *Bivalvia*, *Scaphopoda*, *Gastropoda-Naticidae* und *-Kephalaspidea*; *Enteropneusta*, etc.). Die grabende Fortbewegung der Caudofoveata ist so z.B. direkt

mit den Sipunculida vergleichbar, welche allerdings mit einem Körper-Coelom versehen zum Graben praedestiniert sind. Die wenig vollkommene Lokomotion der Caudofoveata (SALVINI-PLAWEN, 1968a) erfolgt mit Hilfe des Haemocoels des Vorderkörpers (vgl. Nemertini; bei Bivalvia und Scaphopoda dagegen mit dem Fuss-Haemocoel) und wäre daher mit Hilfe eines Körper-Coeloms ungleich besser (vgl. Sipunculida, Entero-neusta). Da die funktionelle Ursache ansich also gegeben ist, warum ist ein derartiges hydrostatisches Lokomotions-Skelett, das Körper-Coelom, bei Weichtieren nicht ausgebildet? --- und zwar atavistisch, wenn es schon stammesgeschichtlich vorhanden gewesen sein soll (vgl. Echiurida: *Bonellia*-Weibchen ohne Coelom, Zwergmännchen aber mit Coelom!). Auch hiermit ergibt sich also der zwingende Schluss, dass die Mollusca kein Körper-Coelom besessen haben.

In einer eigenen Studie war schon auf die ursprüngliche Bedeutung und auf die zu folgernde Entstehung des Gonopericardial-Coeloms der Mollusken ausführlich eingegangen worden (SALVINI-PLAWEN, 1968c), womit nur resumierend festgehalten zu werden braucht, dass sich im Weichtierstamm eine gruppeneigene, coelomatische Bildung *sui generis* differenziert hat, welche primär als schützende Herzblase (zur Sicherung des Gleitraumes der Herzpumpe) angelegt und durch Einlagerung der Keimzellen schliesslich funktionell-bedingt in Gonocoel und Pericard unterteilt wurde. Da das mit den Turbellarien und Nemertinen übereinstimmende amere Bauprinzip (acoelomate Organisation) den Beleg dafür gibt, dass dem Molluskenstamm die ciliare Sohlenlokomotion typisch zu eigen war (und teils noch ist), kann schon daraus (entgegen GUTMANN, 1966) nicht angenommen werden, dass sich die Mollusken-Ahnen auf andere Weise fortbewegt hätten. Zudem sehen wir, dass z.B. bei den Hirudinea (welche gegenüber den Solenogastren oder Placophoren zweifellos als höher differenziert betrachtet werden müssen) zwar kaum mehr eine echte Spiralfurchung auftritt, doch aber eine deutliche Anlage von metameren Coelomsäcken; wie viel klarer wäre daher erst recht bei den ursprünglicheren Mollusken eine zumindest vorübergehende Körpercoelombildung zu erwarten, wenn die Spiralfurchung sogar als typisch vorliegt. Noch einschneidender werden die Verhältnisse im Vergleich zu den stark abgeleiteten Arthropoden oder den parasitischen Pentastomiden, bei welchen Gruppen trotz dem Mangel jeglicher Anhalte bei der Furchung doch aber die (metameren) Coelomsäcke zur Ausbildung kommen; --- und ausgerechnet die weniger differenzierten, freilebenden Weichtiere (bes. Aculifera) sollten bei einem ehemals angeblich vorhanden gewesenen Körpercoelom keine Anklänge in der Ontogenie (oder weiteren Morphologie) zeigen, obwohl für die atavistische Coelombildung ja ausgesprochen praedestinierte Grabformen auftreten (Caudofoveata, Bivalvia, Scaphopoda)? So ist also die gleitend-kriechende Sohlenbewegung der Mollusken als ursprünglich zu betrachten. Diese vererbte Fortbewegung auf der ventralen Körperseite mit Cilien erübrigt ja ein lokomotorisches Coelom, denn eine flüssigkeitserfüllte sekundäre Leibeshöhle wird erst bei einer Bewegungsform notwendig, welche einen geschlossenen Hautmuskelschlauch wirken lassen soll, etwa wie bei grabender oder peristaltischer Fortbewegung (vgl. CLARK, 1964), --- ein Hydroskelett erübrigt sich daher bei allen Formen mit ciliarer Fortbewegung oder ventraler Sohlen-Lokomotion!

Diese auch von REMANE (1967: 614) vertretene Ansicht enthält den Schlüssel zur funktionell-bedingten Coelom-Bildung schlechthin, denn es wird klar, dass erst eine aus verschiedenen Gründen induzierte Einbusse der ciliaren Lokomotion bei nicht-sessilen Organismen die Herausbildung eines hydrostatischen Körper-Coeloms begünstigte.

REMANE widerspricht sich allerdings selbst hinsichtlich seines postulierten 'Urcoelomaten', welchen er an die Wurzel von Protostomia und Deuterostomia stellt, also an die Wurzel der Eilateria (1967: 606):

- a) Das Hydroskelett (Körpercoelom oder sekundäre Leibeshöhle) ist für die Wirkung des Hautmuskelschlauches, der es umgibt, erforderlich (REMANE, 1967: 614);
- b) Bei schlängelnder oder peristaltischer Bewegung ist ein geschlossener Hautmuskelschlauch notwendig (*loc. cit.*);

c) Ciliare Lokomotion oder Fortbewegung auf ventralem Fuss macht ein Körpercoelom überflüssig, bzw. ein vorhandenes Coelom wird dadurch bedeutungslos und kann eingeengt oder aufgelöst werden (*loc. cit.*);

d) Die Fortbewegung durch Wimpern ist ursprünglich (primitiv) (*loc. cit.*).

Daraus folgt: ein ursprüngliches Tier mit Wimpern-Lokomotion benötigte kein hydrostatisches Coelom.

Wieso hat aber dann REMANE's Urcoelomat (1967: 604-605, Abb. 6) Cilien (-Bewegung) und ein (funktionall ja überflüssiges) dreiteiliges Coelom???

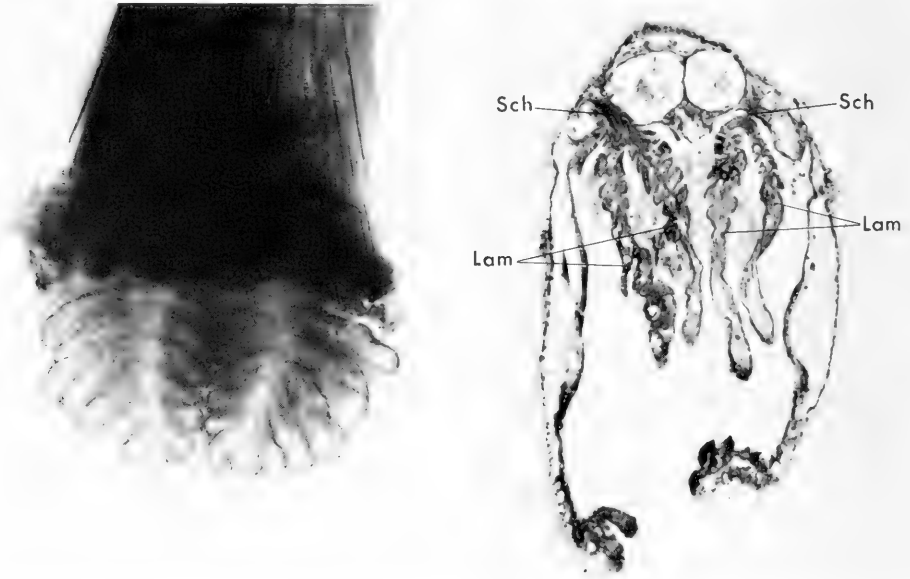


ABB. 11. Körperende von *Falcidens crossotus* (Caudofoveata) mit exponierten Ctenidien (Lebendphoto).

ABB. 12. Schräger Schnitt durch den Pallialraum von *Prochaetoderma californicum* (Caudofoveata). (Lam, Kiemenlamelle; Sch, Ctenidium-Schaft).

#### d) Ctenidien

Ein Blick auf die Verhältnisse des Pallialraumes ist ebenfalls einer genaueren, auflösenden Betrachtung wert. Die Discussion um die ursprüngliche Zahl der Ctenidien findet einerseits in der Theorie Ausdruck, wonach es sich bei den höheren Conchifera um eine Reduktion der Kiemen zur Zweizahl handelt, ausgehend von einigen Paaren wie bei *Neopilina* (vgl. FRETTER & GRAHAM, 1962), --- andererseits wird hingegen die höhere Ctenidienzahl bei Placophoren, bei *Neopilina* und *Nautilus* als Mehrfachbildung eines einzigen Paares angesehen (YONGE, 1947; BOETTGER, 1955, 1959). Letztere Ableitung gewinnt eine ungleich höhere Wahrscheinlichkeit angesichts der zwei Ctenidien bei den ja früh abgespaltenen Caudofoveata (Abb. 11). Dieses einzige Kiemenpaar könnte man allerdings ebenfalls wiederum als ein Reduktionsprodukt erklären (wie man alles, was sich nicht in eine vorgefasste Theorie einfügt, mit Reduktions-Postulaten übergehen kann), und tatsächlich wurden auch bei *Prochaetoderma californicum* "two pairs of gills of a rather primitive structure" gemeldet (SCHWABL, 1963: 267). Eine Überprüfung ergab jedoch, dass es sich in Wahrheit nicht um zwei Paar ursprüngliche, sondern um ein einziges, hochdifferenziertes Ctenidien-Paar handelt (Abb. 12), welches --- analog zu den Bivalvia --- je zwei stark vergrößerte Kiemenblätter pro Schaft ausbildet. Da aber damit nicht der Platzmangel für die Ctenidienzahl bestimmend sein kann (vier Kiemenblätter haben ja Raum), und da sich bei Vergrößerung der Respirationsfläche in dieser ursprünglicheren Gruppe wohl eher

atavistisch die Anlage eines zweiten Kiemenpaares gebildet haben würde (wenn es schon einmal vorhanden gewesen wäre) als eine komplizierte Umgestaltung des phylogenetisch Fixierten, --- daraus darf man somit dem einzigen Ctenidienpaar der Caudofoveata mit gutem Grund phylogenetische Bedeutung beimessen. Schliesslich weist ja das Vorhandensein von nur zwei Herz-Atrien (auch der polybranchiaten Placophora) deutlich darauf hin (bei Caudofoveata ist das doppelte Atrium verschmolzen-unpaar und meist nur durch die beiden Atrioventricular-Öffnungen ersichtlich), dass ihnen zugeordnet (!) nur zwei Ctenidien als ursprünglich anzunehmen sind (vgl. H. HOFFMANN, 1951: 181).

Nach neueren Befunden scheint auch keineswegs mehr so sicher, dass auch den Vorfahren des tetrabranchiaten *Nautilus* zwei Ctenidienpaare zukamen. Da nun belegt werden konnte, dass sowohl die Baktriten als Ausgangsgruppe für die Ammonoidea und Endocochlia (= Dibranchiata), wie auch die Goniatiten der Ammoniten selbst nur wenig (10? --- keinesfalls aber 80-90) Fangarme besessen haben (KOLB, 1961; ZEISS, 1968), einen Tintenbeutel aufwiesen (LEHMANN, 1967b) und zudem eine nur sieben-zählige Radula zeigten (LEHMANN, 1967a), ist auch den exogastrischen Ammoniten eine annähernd dibranchiate Organisation beizulegen. Wenn auch die Kiemenzahl der fossilen Formen wohl nicht festzustellen sein wird, so ist doch die Ursprünglichkeit der *Nautilus*-Organisation äusserst zweifelhaft geworden. Zwar erweist sich die Zehnarmigkeit der Baktriten und Goniatiten insofern als unbefriedigend, als die 6-10 zipfelige, mit Saugnäpfen bewehrte Buccalmembran der recenten Decabrachia als Fangarm-Rudimente aufgefasst werden müssen, --- doch ist eine daraus resultierende 16-20 Armigkeit als ursprünglicher Zustand wohl vertretbar.

#### e) Larven

In einer Gegenüberstellung von Larven-Merkmalen ist innerhalb der Aculifera der Vergleich auf die Verhältnisse bei Solenogastres und Placophora beschränkt, da die Entwicklung der Caudofoveata noch nicht erforscht ist.

Der für die Anneliden-Verwandtschaft der Mollusken stets hervorgehobene Vergleich der jeweiligen Ontogenie hat bei genauer Betrachtung etliche 'Schönheitsfehler' von weittragender Bedeutung: Zunächst besteht bekanntlich der tiefgreifende Unterschied in den sog. 'Kreuz-Bildungen' innerhalb der Spiralfurchung, welcher nur über so neutrale nicht-determinierte Zustände wie bei den Turbellaria erklärbar ist. Die nach PRUVOT (1890) und BABA (1940, 1951) auch bei Solenogastres auftretende Kreuzbildung fügt sich in das Bild der Mollusken ein (*Nematomenia banyulensis* mit *Dentalium*-ähnlicher, *Epimonia verrucosa* mit *Patella*- oder *Ischnochiton*-ähnlicher Ausbildung); trotz dieser bei Mollusken und Anneliden so durchgreifenden Unterschiede werden die jeweiligen Larven oft allzu gewollt gleichgesetzt. Eine weitere, folgeschwere Abweichung zeigt sich nämlich auch in den Larven selbst (Abb. 13), als bei Bivalvia-Protobranchia und bei Solenogastres eine sogenannte Hüllglocken-Larve ausgebildet wird, --- ein Typus, welcher auch noch bei den Scaphopoda anklingt und bei welchem der eigentliche Embryo (Imaginalkörper) von einer Hülle grosser Deckzellen umgeben ist. Diese Hüllglockenlarve (engl. Testcell-larva) muss durch ihre Übereinstimmung bei systematisch so weit entfernten Gruppen, zudem bei so ursprünglichen Vertretern wie Solenogastres und Bivalvia-Protobranchia (teils auch Scaphopoda), als Stamm-eigen betrachtet und also an die Wurzel der Mollusken gestellt werden, --- so wie verschiedentlich schon betont worden ist (DREW, 1901; YONGE, 1939; THOMPSON, 1960). Die leicht denkbare Abwandlung der Hüllglockenlarve zum Trochophora-Typus (Hüllglocke = Prototroch-Abschnitt = Velum) und weiter zur Veliger-Larve einerseits (vgl. DREW, 1901: 338; CHANLEY, 1968), und die starken Ähnlichkeiten dieser Hüllglocken-Ontogenie mit den Larven von Turbellarien und Nemertinen, von *Sipunculus nudus* und der Anneliden-Endolarve (*Serosa* = ectoderme Larvaire = Hüllglocke, Amnionhöhle = Peri-Imaginalraum; vgl. HATSCHKE, 1884 und DAWYDOFF, 1959) wie *Mitraria* andererseits (Abb. 14), --- diese Beziehungen lassen nicht nur auf die Ursprünglichkeit des Hüllglocken-Typus innerhalb der Weichtiere schliessen, sondern sie deuten auf eine tief in den stammesgeschichtlichen Entwick-

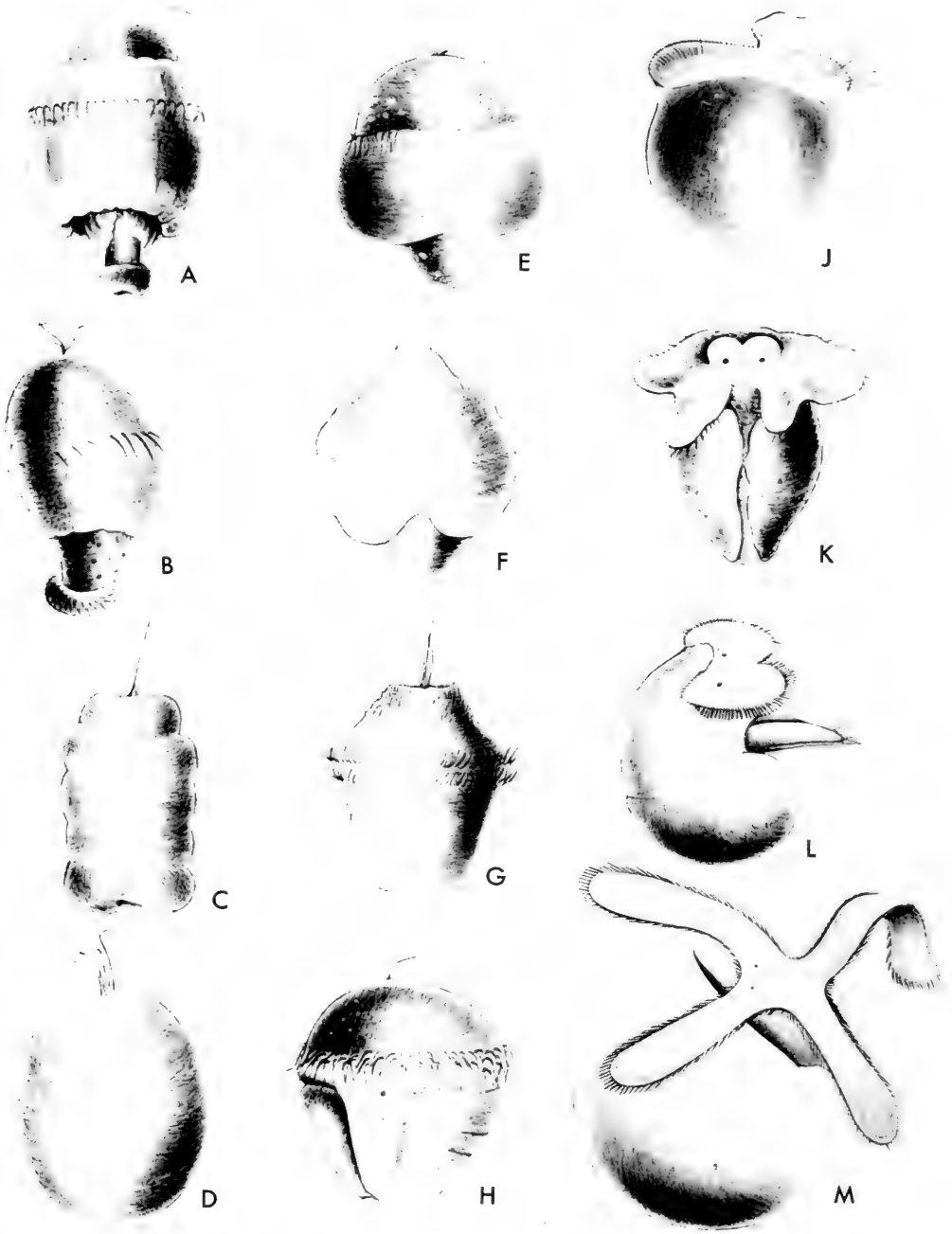


ABB. 13. Mollusken-Larven. A-D. Hüllglocken-Typus. E-F. Übergangs-Typus. G-H. Trochophora-Typus. I-M. Veliger-Typus. A. *Nematomenia banyulensis* und B. *Neomenia carinata* (Solenogastres). C. *Yoldia limatula* und D. *Nucula proxima* (Bivalvia-Protobranchia). E. *Epimения verrucosa* (Solenog.). F. *Dentalium dentale* (Scaphop.). G. *Patella* sp. (Gastropoda). H. *Ischnochiton magdalenensis* (Placophora). J. *Dreissena polymorpha* (Bivalvia). K. *Gasteropteron rubrum*. L. *Nassa* sp. M. *Murex ramosus* (Gastropoda); (nach verschiedenen Autoren, wenig verändert).



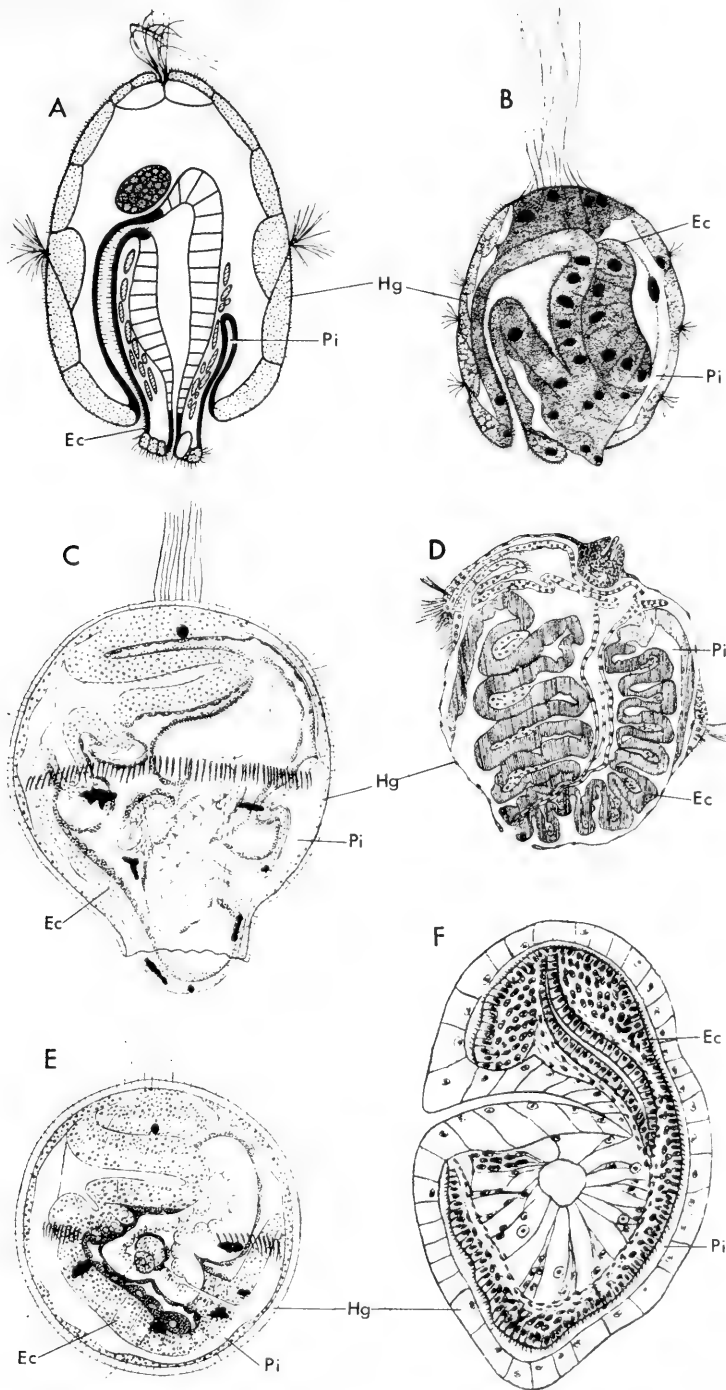


ABB. 14. Längsschnitte durch Larven vom Hüllglocken-Typus. **A.** *Neomenia carinata* (Solenogastres). **B.** *Nucula proxima* (Bivalvia-Protobranchia). **C.** *Sipunculus nudus* (Sipunculida). **D.** *Polygordius* sp. (Archiannelida). **E.** *Sipunculus nudus*. **F.** *Lineus ruber* (Nemertini). (Ec, imaginales Ectoderm; Hg, Hüllglocke; Pi, Periimaginalraum) (nach verschiedenen Autoren).

lunGS-Vorgängen verwurzelte Larve, als deren Differenzierung erst mannigfaltig der Trochophora-Typus convergent fixiert worden ist. Dementsprechend finden wir nicht nur bei den Bivalvia diese Schritte repräsentiert (Abb. 13C, D-J; vgl. CHANLEY, 1968), sondern auch innerhalb der Solenogastres (Abb. 13A, B-E) tritt der fortgeschrittenere, Trochophora-ähnliche Übergangstypus bei *Epimения* auf; nur mehr die Andeutung einer Hüllglocke und eines Imaginalzapfens zeigt sich gleicherweise auch bei *Dentalium*. Ein ähnlicher Differenzierungs-Weg ergibt sich auch bei den Sipunculiden (*Sipunculus* --- übrige Vertreter) und bei den Anneliden (Endolarve, Mitraria --- Trochophora).

Ein nächstes Kriterium ergibt sich aus der Tatsache, dass bei allen ursprünglicheren Mollusken (Solenogastres, Placophora, Scaphopoda, Bivalvia-Protobranchia und fast allen marinen Gastropoda) keine Protonephridien in den Larven zur Ausbildung kommen (vgl. H. HOFFMANN, 1951: 181); die Protonephridien fehlen aber bezeichnenderweise auch den Larven der Plathelminthes, Nemertini, Sipunculida, Brachiopoda, Bryozoa und Deuterostomia! Die dazu im starken Gegensatz hervortretende Ausbildung larvaler Excretionsorgane bei Annelida, bei nicht-marinen Gastropoda, bei den meisten Bivalvia und bei einigen anderen Gruppen kann mit REMANE (1967: 604) als unabhängig entstanden beurteilt und muss als Convergenz erklärt werden.

Besondere Erwähnung verdient weiterhin, dass den meisten dieser ursprünglichen Larven (*Epimения*, *Halomenia*, *Acanthochiton*, *Chiton*, *Patella*, *Dentalium*, *Nucula*, *Yoldia*) ein Enddarm fehlt, und erst während der Metamorphose verbindet sich das Rectum mittels Durchbruch mit dem bestehenden Mitteldarm. Diese späte Anlage bei Mollusca ebenso wie bei Nemertini (!) lasst im Sinne der 'Biogenetischen Regel' auf afterlose Ahnen ähnlich den Turbellarien schliessen, --- wogegen bei den der gemeinsamen Wurzel morphologisch nicht mehr so nahestehenden Annelida sowie den weiteren Mollusca der Enddarm bereits genetisch stärker fixiert ist und daher in der Anlage auch ontogenetisch vorgezogen wird.

Schliesslich ergeben sich durch den Bildungsmodus des Nervensystems phylogenetische Hinweise. Bisher nur für die Chitonen gewürdigt (vgl. HANSTRÖM, 1928; KORSCHULT, 1936), werden bei Solenogastren-Larven die beiden paarigen Längsbahnen ebenfalls als caudale Auswüchse des cerebralen Zentrums angelegt. Dieser mit den Placophora übereinstimmende Bildungsmodus gewinnt bei einem Blick auf die Verhältnisse bei Turbellarien und Nemertinen besondere Bedeutung: Auch bei diesen Gruppen werden die Längsnervenstränge durch caudales Auswachsen ohne direkte Beziehungen zum Ectoderm angelegt, --- nicht aber durch lokale Einwucherung wie bei Annelida und Conchifera. Daraus lasst sich zumindest ablesen, dass die morphologische Entfernung der Aculifera zu den Turbellaria/Nemertini bedeutend geringer ist, als diejenige der Conchifera und Annelida (dass die Aculifera sich also bezüglich des Nervensystems direkt von turbellariomorphen Ahnen ableiten lassen). Angesichts der Tatsache, dass auch bei einem hochentwickelten Solenogaster (*Neomenia carinata*) die beiden ventralen (nicht aber lateralen) Nervenbahnen schon durch Einwucherung gebildet werden, muss für diesen abgeleiteteren Modus eine dreifache (!) Convergenz festgestellt werden. Diese Parallelbildungen lassen sich jedoch mit HAMMERSTEN & RUNNSTRÖM (1925: 312, 1926: 50) zwanglos derart erklären, "dass zunächst eine Konzentration von Nervenzellen in den Marksträngen zu Ganglien stattgefunden hat, wonach diese auf verkürzte Weise durch lokale Wucherungen ihre Entwicklung genommen haben."

Im adulten Zustand lasst sich jedoch innerhalb der Aculifera für das Nervensystem weniger Übereinstimmung erkennen, besonders was die irreführende Bezeichnung 'Amphineura' betrifft, denn weder Solenogastres noch Caudofoveata zeigen eine typische Amphineurie als zwei getrennte Paare von Marksträngen; wohl aber sind solche Ver-

hältnisse innerhalb der Conchifera bei Trybliidae, Pedalmarkstränge auch bei vielen Gastropoda-Diotocardia ausgebildet. Dementsprechend grenzt der morphologisch gut fundamentierte Begriff *Aculifera* die drei Klassen Solenogastres, Caudofoveata und Placophora deutlich gegenüberstellend von den Conchifera ab.

#### DISCUSSION

Die Verwandtschaftsbeziehungen der Caudofoveata und Solenogastres sind hiermit grossteils aufgedeckt, und nach der Organisation im Rahmen der funktionellen Morphologie ergeben sich sowohl für die Caudofoveata und Solenogastres innerhalb der Weichtiere (Abb. 4) eindeutige phylogenetische Rückschlüsse, wie sich auch die Mollusken insgesamt in das stammesgeschichtliche Bild (Abb. 15) einfügen.

Die in Abb. 15 skizzierten Verhältnisse lassen sich in einigen unsicher erscheinenden Punkten durch folgende Beziehungen untermauern:

- a) Die Ableitung der Metazoa aus den Protozoa erfolgt im Anschluss an IVANOV (1968); '*Phagocytella*' (oder '*Parenchymella*') stellt hierbei ein hypothetisches Zwischenstadium dar (vgl. auch METSCHNIKOFF, 1886: 145-159).
- b) Die Ableitung der Hydrozoa aus der Scyphozoen-Wurzel, und diese wiederum aus den Anthozoen-Ahnen wird durch die Ursprünglichkeit der Anthozoa eindeutig unterstützt: Die Radiär-Symmetrie muss sekundär sein, da sich die Bilaterie der Anthozoen nur von einer freibeweglichen (kriechenden) Ausgangsform verstehen lässt; die Polypen-Form stellt gegenüber der Meduse den ursprünglicheren Typus dar, da einerseits die Anthozoen keinen Hinweis auf Medusen geben, und andererseits die Entwicklungsvorgänge auch verschiedentlich darauf hinweisen (vgl. z.B. WERNER, 1966: 346); der Differenzierungsgrad der Nesselkapsel-Typen nimmt (von gruppenspezifischen Sonderbildungen abgesehen) deutlich von Anthozoa zu Scyphozoa und Hydrozoa zu (vgl. BOUILLON & LEVI, 1967; 454-455); die Mittelschicht (Stützlamele, Mesogloea) kann zwanglos als zusehends vereinfachtes Mesenchym (Ecto-Mesoderm) aufgefasst werden, welches bei den Anthozoa noch am deutlichsten zur Ausbildung kommt.
- c) Die acoelomaten Kamptozoa (Entoprocta) zeigen in den Larven der ursprünglicheren Loxosomatidae (JÄGERSTEN, 1964; FRANZEN, 1967) homoiologe Verhältnisse zu den Weichtieren, wodurch die Gruppe näher an die Mollusken gebunden wird: die funktionelle und morphologische Ähnlichkeit dieser Kamptozoen-Larven durch die medioventrale, bewimperte Kriechsohle (Fuss) mit Schleimdrüsen, durch die Peripedal-Furche und durch den 'Mantel' mit Falte lässt auf einen gemeinsamen turbellariomorphen Ausgangspunkt der Gruppe mit den Mollusken schliessen, welcher bei den Kamptozoen nur sekundär durch den Übergang zur Sessilität differenziert wurde.
- d) Die coelomaten Echiurida zeigen durch die starken Übereinstimmungen in der Entwicklung mit den Anneliden einerseits (Spiralfurchung, Borstenbildung), durch das interkalare Wachstum des imaginalen Rumpfabchnittes (einheitliches Coelom, ohne Teloblastie!) andererseits, dass sie kurz vor der Articulaten-Differenzierung abgezweigte 'Protanneliden' darstellen (vgl. KORN, 1960). Die atavistischen Verhältnisse der Mesoderm-Ausbildung beim *Bonellia*-Weibchen (ohne Coelom, nur Muskulatur und Mesenchym) entsprechen hierbei in etwa noch den Zuständen vor der phylogenetischen Coelom-Differenzierung (vgl. Mollusca).
- e) Die coelomaten Sipunculida zeigen durch Furchung, Bildung des Nervensystems und andere ontogenetische Merkmale deutliche Beziehungen zum Anneliden-Zweig, unterscheiden sich aber einschneidend durch das Fehlen von Coelom-Metamerie (keine Teloblastie!). Die schizocoele Coelombildung und die Larven-Entwicklung wiederholen hingegen noch Zustände vor der phylogenetischen Coelom-Differenzierung (vgl. HATSCHKE, 1884; HYMAN, 1959; AKESSON, 1958; JÄGERSTEN, 1963). Das allgemeine Fehlen von Protonephridien und die Hüllglocke ('Serosa'-Zellen) der *Sipunculus*-Larve einerseits, wie die (stark verkürzte) Kriechsohle mit Drüse ('lip-gland') der *Pelagosphaera*-Larven andererseits, belegen zudem die gemeinsame turbellariomorphe Wurzel mit den Mollusken-Vorfahren.
- f) Die schon früher vorgenommenen Versuche, die Tentaculata an die Sipunculida zu nähern (Coelom-Anordnung, etc.) haben durch das Auftreten der Spiralfurchung bei Phoronidea (RATTENBURY, 1954) einen eindeutigen Beleg erfahren, wodurch der Anschluss an die coelomaten Spiralia gegeben ist (vgl. auch SIEWING, 1967: 141, 165).
- g) Die Chaetognatha stellen im Hinblick auf ihr Nervensystem einwandfrei Gastro-

neuralia mit Zygoneurie dar, auch wenn die larvale Urmund-Region zum Körperende der heranwachsenden Tiere wird (vgl. aber unten). Die eindeutigen, ontogenetischen Beziehungen zu den Tentaculata-Brachiopoda (zweiteiliges Coelom, etc.) bekräftigen zudem die weitere Verwandtschaft mit dieser Gruppe und machen eine Stellung der Chaetognatha innerhalb der Deuterostomia unhaltbar!

- h) Der Anschluss der Deuterostomia oder Notoneuralia selbst an Gastroneuralia oder Protostomia hat primär in den Coelom-Verhältnissen zu den Tentaculata eine deutlichere Beziehung (als sog. "Archicoelomata", vgl. SIEWING, 1967); das Fehlen von Protonephridien in den Larven weist auf die Spiralia-Wurzel hin (vgl. p 210). Doch lassen sich die durch die zeitliche Entwicklungsdistanz verwischten Übergänge von Spiraliern zu Deuterostomiern unschwer ablesen: Die Deuterostomie stellt an sich kein abtrennendes Merkmal dar, sind doch auch die 'protostomen' Nematomorpha und andere Formen wie *Viviparus* (Gastropoda), u.a.m. deuterostom (vgl. auch SIEWING, 1967: 145)! Die enterocoel Coelombildung lässt sich zwanglos als ein zeitliches Vorziehen der Coelom-Formierung aus dem äquivalenten Zellmaterial in der Spiralia-Larven verstehen (vgl. KORSCHOLT, 1936: 113); diese Formierung erscheint daher gegenüber der Schizocoelie lediglich stark verkürzt und auf das Wesentliche beschränkt ('rationalisiert'), zudem natürlich auch modifiziert (zeitliche Spanne und morphologischer Abstand). Vermittelnde Verhältnisse zeigen sich ja bei den Tentaculata (vgl. RATTENBURY, 1954: 326-331; HARTMAN, 1963).

Das dorsale Nervensystem (Notoneurie), mit einem Nervengeflecht schon bei den protostomen Phoronidea entwickelt, zeigt sich ja nur bei den hochentwickelten Chordonia in tatsächlich allein notoneuraler Ausbildung; sowohl die Enteropneusta, wie die Pterobranchia weisen ein Übergangsstadium in Form von Strangverdichtungen sowohl in der Dorsomediane wie in der Ventromediane auf! Die mit den Tentakeln als dorsal orientierten Pogonophora (Herz = dorsal) lassen ebenfalls ein ventrales Nervensystem feststellen. So erscheint also die Notoneurie als solche allein bei den Chordonia fixiert, wogegen die noch mehr basal stehenden Gruppen der Pentacoela (Enteropneusta, Pterobranchia und Pogonophora mit fünf Coelomhöhlen) jede Anschlussmöglichkeit offen lassen.

Letztlich bleiben also die Coelom-Bildungsverhältnisse für die Ableitungs-Beziehungen am deutlichsten bestimmend; durch den (mit dem Übergang zur Sessilität) rückgebildeten Kopf-Abschnitt der Tentaculata kann allein deren phylogenetische Wurzel auch als Ausgangsbasis für die Deuterostomier-Entwicklung angenommen werden.

Als Modell für die Phylogenie der Deuterostomier selbst mag die Abbildung 21 bei REMANE (1967: 644) die Beziehungen verdeutlichen, wobei die Pogonophora im Sinne JÄGERSTEN's mit dorsalen Tentakelkrone angenommen und als echte Pentacoela aufgefasst werden.

Die gewonnenen Erkenntnisse und Correlationen lassen nun zusammenfassend im Überblick feststellen, dass den meist stark vernachlässigten Solenogastres und Caudofoveata jeweils eine Organisation zukommt, welche im Rahmen der Mollusca allgemein verschiedene Fragen und Probleme in ein neues Licht rücken. Besonders an den herausgegriffenen Organsystemen der Muskulatur, des Darmtraktes, des Coeloms und der Ontogenie wird deutlich, dass speziell der stammesgeschichtliche Fragenkreis aufschlussreich aufgeheilt wird. Umso nachteiliger wirkt es sich aus und umso bedauerlicher ist die Tatsache, dass das jahrzehntelange Desinteresse an diesen Gruppen eine unbearbeitete Materialfülle hat anhäufen lassen, welche mit der Wiederaufnahme der Studien nur schrittweise bearbeitet und ausgewertet werden kann.

Als Folge der Ausführungen braucht wohl nicht mehr im Detail betont zu werden, dass jegliche morphologisch-phylogenetische Discussion über Mollusken ohne eine Berücksichtigung von Solenogastres und von Caudofoveata falsche Voraussetzungen bringt; die angebliche Metamerie der Trybliacea gibt ein deutliches Beispiel hierfür. Aber auch in der vergleichenden Anatomie der Weichtiere erweisen sich die Vertreter der beiden Klassen als aufschlussreich, und widerlegen die häufige Sinngebung, dass Mollusca und Conchifera identisch wären (Conchifera als "true molluscs" bei FRETTER & GRAHAM, 1962: 9), --- denn nicht die Artenzahl, nicht die Häufigkeit und nicht die Popularität legen hier die wissenschaftliche Bedeutung einer Tiergruppe dar, sondern allein die Organisation und der morphologische Aufbau!

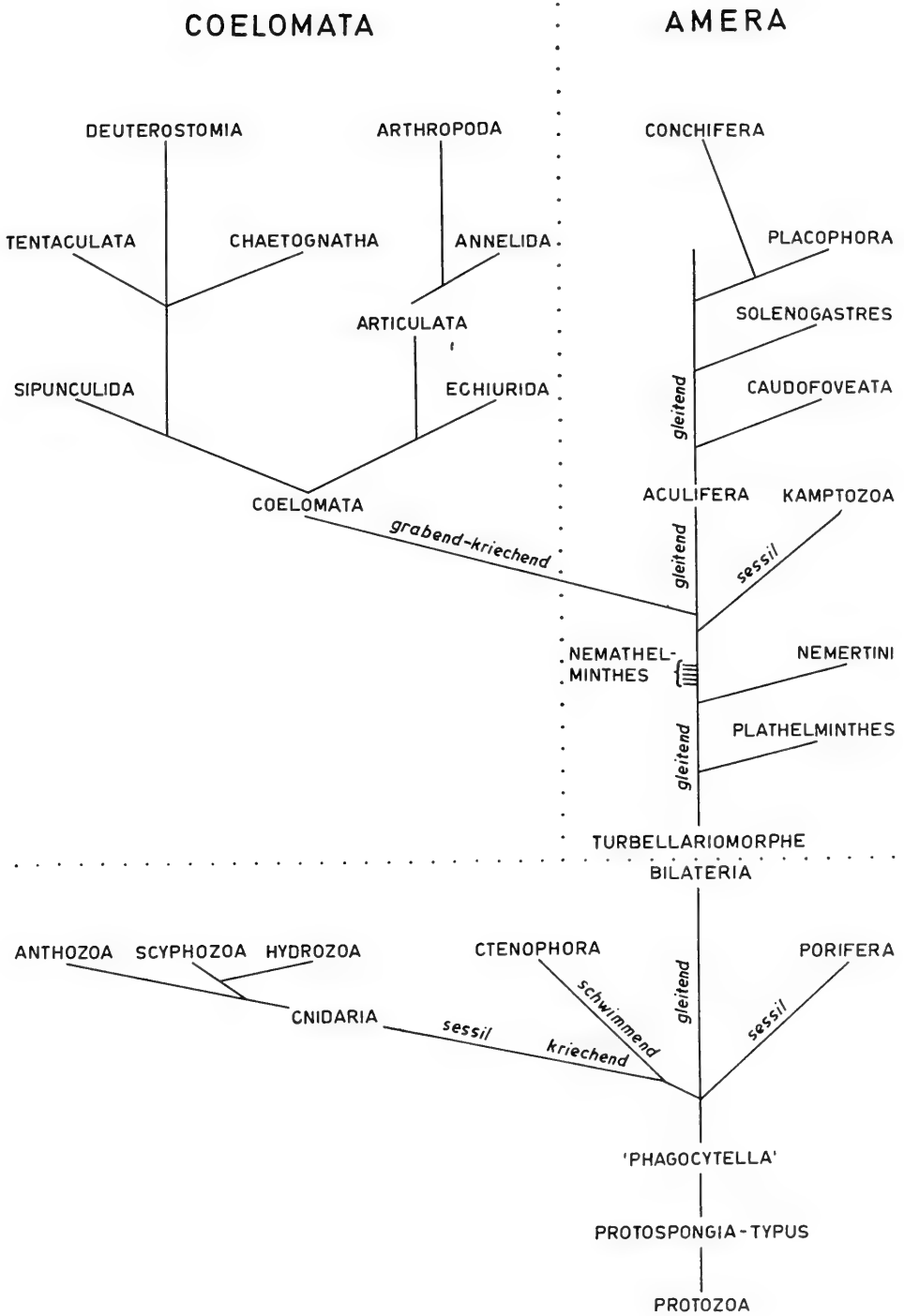


ABB. 15. Stammesgeschichtliche Entwicklungs-Beziehungen der recenten Tiergruppen (Die Längen der Ableitungsstriche sind raumbedingt und sollen nicht morphologische Entfernungen ausdrücken.).

## ZUSAMMENFASSUNG

Anhand eines Organisations-Abrisses für die beiden Klassen Solenogastres und Caudofoveata werden einige phylogenetisch bedeutungsvolle Merkmalskomplexe herausgegriffen und dargelegt:

1. Die serial angeordnete **Dorsoventral-Muskulatur** bildet einerseits den **Ausgangspunkt** einer sich zunehmend verdichtenden Concentration der Stränge über Placophora- und Tryblidiacea- bis zu den weiteren Conchifera-Verhältnissen, und lasst **andererseits**, leicht den stammesgeschichtlichen Anschluss an turbellariomorphe Ahnen erkennen.
2. Der Divertikeldarm bei Solenogastres ist als für die Mollusken ursprünglich aufzufassen und lasst sich ebenfalls aus einer turbellariomorphen Wurzel ableiten.
3. Lebensweise und Radula-Bau geben im Zusammenhang mit der Lokomotionsfrage deutliche Belege für die von den Ahnen **ererbte** aceolomate Organisation des Molluskenstammes.
4. Die Annahme von der ursprünglichen Zweizahl der Ctenidien bei Mollusken wird durch die Verhältnisse bei Caudofoveata gestützt.
5. Die Hüllglocken-Larve der Solenogastres und Bivalvia-Protobranchia muss als **ein** tief in den stammesgeschichtlichen Entwicklungsvorgängen verwurzelter Typus aufgefasst werden: das Fehlen von Protonephridien bei Aculifera (und weiteren Gruppen), die späte Enddarm-Anlage und der Modus der Bildung des Nervensystems unterstützen in eindeutiger Weise diese Annahme.
6. Der morphologische Wert der Vertreter beider Klassen sollte nicht durch deren geringe Artenzahl übersehen werden.

## SUMMARY

The phylogenetical importance of both classes, the Solenogastres as well as the Caudofoveata, is pointed out by means of several characteristics of their organization:

1. The former term 'Aplacophora' states only the same level of organization and cannot be upheld further: the Caudofoveata have to be separated from the Solenogastres and placed (besides the Placophora) as a third class within the Mollusca-Aculifera.
2. The numerous serially-arranged dorsoventral muscles as in the recent Solenogastres represent the starting point of an increasing concentration within the molluscs which extends as a continuous sequence over the Placophora and Tryblidiacea to the remaining Conchifera.
3. The relationship of musculature and diverticular digestive tract between Platyhelminthes and Solenogastres leads to a turbellariomorphic ancestor for the molluscs.
4. The manner of living compared with the anatomy of the radular apparatus shows in connection with the problem of locomotion that the mollusc stem originated from an aceolomate organization.
5. The original number of two ctenidia within the mollusc stem is supported by the conditions in the Caudofoveata.
6. The Testcell-larva of Solenogastres and Bivalvia-Protobranchia (and partly as well as those of Scaphopoda) has to be considered phylogenetically as a strongly fundamented type which belongs at the very root of the Spiralia. This statement is supported by the lack of protonephridia within the primitive representatives (Turbellaria, Nemertini, Aculifera, Sipunculida), by the retarded anlage of the rectum within most of these larvae, and by the manner of the development of the larval nervous system within Aculifera as well as Turbellaria and Nemertini.
7. The adult situation of the nervous system within Solenogastres and **Caudofoveata** does not correspond with the term 'Amphineura', which therefore has to be replaced by **ACULIFERA** (HATSCHEK, 1891). The amphineury within the conchiferous tryblidiacea (*Neopilina*) supports this conception.
8. The enormous morphological value of the representatives of both classes, Solenogastres as well as Caudofoveata, should not be neglected simply because of the relatively low number of species.

## LITERATURVERZEICHNIS

- ÅKESSON, B., 1958, A study of the nervous system of the Sipunculoideae. *Unders. Öresund*, 38: 1-249.
- BABA, K., 1940, The early development of a solenogastre, *Epimenia verrucosa* (NIERSTR.). *Annot. Zool. Jap.*, 19(2): 107-113.
- BABA, K., 1951, General sketch of the development in a Solenogastre *Epimenia verrucosa* (NIERSTR.). *Misc. Rep. Res. Inst. Nat. Resources Jap.*, 19-21: 38-46.
- BEEHDAM, G. & TRUEMAN, E., 1868, The cuticle of the Aplacophora and its evolutionary significance in the Mollusca. *J. Zool.*, London, 154: 443-451.
- BOETTGER, C., 1955, Beiträge zur Systematik der Urmollusken (Amphineura). *Zool Anz.*, Suppl., 19: 223-256.
- BOETTGER, C., 1959, Discussionsbeitrag, in: Protostomian interrelationships in the light of *Neopilina*, by H. LEMCHE. *Proc. XVth Intern. Congr. Zool.*, London, Sect. 4: 386-389.

- BOUILLON, J. & LEVI, C., 1967, Ultrastructure du cnidocil, de l'appareil cnidociliare, de l'appareil péri-nématocystique et du cnidopode des nématocystes d'hydroides. *Ann. Sci. Nat., Zool. Biol. Anim.* (Paris), Sér. 12, 9(3): 425-456.
- CHANLEY, P., 1968, Larval development in the class Bivalvia. *Symp. Moll., Mar. Biol. Ass. India*, Abstr. (43): 34-35.
- CLARK, R., 1964, *Dynamics in metazoan evolution: The origin of the coelom and segments*. Clarendon Press, Oxford, 313 p.
- DREW, G., The life-history of *Nucula delphinodonta*. *Quart. J. Micr. Sci.*, 44: 313-391.
- FRANZEN, Å., 1967, A new loxosomatid from the Pacific (Gilbert Islands) with a note on internal budding in Entoprocta. *Ark. f. Zool.*, Ser. 2, 19(20): 381-390.
- FRETTER, V. & GRAHAM, A., 1962, *British prosobranch molluscs*. Ray Society, London, 144: 1-755.
- GUTMANN, W., 1966, Funktionsmorphologische Beiträge zur 'Gastrea-Coelomtheorie.' *Senck. Biol.*, Frankfurt, 47(3): 225-250.
- HAMMARSTEN, O. & RUNNSTRÖM, J., 1925, Zur Embryologie von *Acanthochiton discrepans* BROWN. *Zool. Jahrb. Anat.*, 47(2): 261-318.
- HAMMARSTEN, O. & RUNNSTRÖM, J., 1926, Ein Beitrag zur Diskussion über die Verwandtschaftsbeziehungen der Mollusken. *Acta Zool.*, Stockholm, 7: 1-67.
- HANSTRÖM, B., 1928, *Vergleichende Anatomie des Nervensystems der wirbellosen Tiere unter Berücksichtigung seiner Funktion*. Springer-Verl., Berlin, 628 p.
- HARTMAN, W., 1963, A critique of the enterocoele theory. The lower Metazoa, Univ. Calif. Press, No. 63-22707: 55-77.
- HATSCHKE, B., 1884, Über die Entwicklung von *Sipunculus nudus*. *Arb. Zool. Inst. Wien*, 5: 61-140.
- HOFFMANN, H., 1951, Mollusca. *Handb. Biol.*, von L. v. BERTALANFFY, 6(6): 161-208.
- HOFFMAN, S., 1949, Studien über das Integument der Solenogastres. *Zool. Bidr.*, Uppsala, 27: 293-427.
- HYMAN, L., 1959, *The Invertebrates: Volume V. Smaller coelomate groups*. McGraw-Hill Book Co., New York, N. Y., U.S.A. 783 p.
- IVANOV, A., 1968, Der Ursprung der vielzelligen Tiere --- ein phylogenetischer Entwurf (in russ.). *Nauk-Verl.*, Leningrad, 287 p.
- JÄGERSTEN, G., 1963, On the morphology and behavior of *Pelagosphaera* larvae (Sipunculoidea). *Zool. Bidr.*, Uppsala, 36(1): 27-35.
- JÄGERSTEN, G., 1964, On the morphology and reproduction of entoproct larvae. *Zool. Bidr.*, Uppsala, 36(3): 295-314.
- KARLING, T., 1967, Zur Frage von dem systematischen Wert der Kategorien Archophora und Neophora (Turbellaria). *Comment. Biol. Soc. Sci. Fenn.*, 30(3): 1-11.
- KNIGHT, J., 1947, Bellerophon muscle scars. *J. Paleontol.*, 21(3): 264-267.
- KOLB, A., 1961, Die Ammoniten als Dibranchiaten. *Geol. Bl. NO-Bayern*, 11(1): 1-26.
- KORN, H., 1960, Ergänzende Beobachtungen zur Struktur der Larve von *Echiurus abyssalis* SKOR. *Zeitschr. wiss. Zool.*, 164(3-4): 199-237.
- KORSCHULT, E., 1936, *Vergleichende Entwicklungsgeschichte der Tiere*. Fischer-Verl., Jena, xx & 1314 p.
- LEHMANN, U., 1967a, Ammoniten mit Kieferapparat und Radula aus Lias-Geschieben. *Paläontol. Zeitschr.*, 41(1/2): 38-45.
- LEHMANN, U., 1967b, Ammoniten mit Tintenbeutel. *Paläontol. Zeitschr.*, 41(3/4): 132-136.
- LEMICHE, H., 1959, *Neopilina* (Un molusco actual, con caracteres de tipo fósil, y su significado). *Rev. Univ. Madrid*, 8(29-31): 411-442.
- LEMICHE, H. & WINGSTRAND, K., 1959, The anatomy of *Neopilina galathea* LEMICHE, 1957 (Mollusca Tryblidiacea). *Galathea Report*, 3: 9-72.
- McALESTER, A., 1965, Systematics, affinities, and life habits of *Babinka*, a transitional Ordovician lucinoid bivalve. *Paleontology*, London, 8(2): 231-246.

- METSCHNIKOFF, E., 1886, *Embryologische Studien an Medusen*. A. Hölder, Wien, VI & 159 p.
- ODHNER, N., 1919, Norwegian Solenogastres. *Bergens Mus. Aarb.* 1918/19, 3: 1-86.
- PRUVOT, G., 1890, Sur le développement d'un Solénogastre. *C. R. Acad. Sci., Paris*, 111(2): 689-692.
- RATTENBURY, J., 1954, The embryology of *Phoronis viridis*. *Journ. Morph.* Washington, 95(2): 289-350.
- REMANE, A., 1967, Die Geschichte der Tiere. In: *Die Evolution der Organismen*, von G. HEBERER; Fischer-Verl., Stuttgart, 1: 589-677.
- ROLLINS, H. & BATTEN, R., 1968, A sinus-bearing monoplacophoran and its role in the classification of primitive molluscs. *Paleontology*, London, 11: 132-140.
- SALVINI-PLAWEN, L. v., 1967a, Kritische Bemerkungen zum System der Solenogastres (Mollusca, Aculifera). *Zeitschr. zool. Syst. Evolut.-Forsch.*, 5(4): 398-444.
- SALVINI-PLAWEN, L. v., 1967b, Contributions to the systematics of the lower molluscs. *Adv. Abstr. Contr. Fish. Aquat. Sci. India*, 1(3): 43-45.
- SALVINI-PLAWEN, L. v., 1968a, Über Lebendbeobachtungen an Caudofoveata (Mollusca, Aculifera), nebst Bemerkungen zum System der Klasse. *Sarsia*, 31: 105-126.
- SALVINI-PLAWEN, L. v., 1968b, Über einige Beobachtungen an Solenogastres (Mollusca, Aculifera). *Sarsia*, 31: 131-142.
- SALVINI-PLAWEN, L. v., 1968c, Die 'Funktions-Coelomtheorie' in der Evolution der Mollusken. *Syst. Zool.*, 17(2): 192-208.
- SALVINI-PLAWEN, L. v., 1969, Beiträge zur Systematik der niederen Mollusken. *Proc. Symp. Moll., Mar. Biol. Ass. India*, Symp. Ser. 3, Part 1: 248-256.
- SCHWABL, M., 1963, Solenogaster mollusks from Southern California. *Pacific Sci.*, 17(3): 261-281.
- SIEWING, R., 1967, Diskussionsbeitrag zur Phylogenie der Coelomaten. *Zool. Anz.*, 179(1/2): 132-176.
- SIMROTH, H., 1894, Amphineura. In: BRONN's *Klassen und Ordnungen des Tierreiches*, 3(1): 128-355.
- THOMPSON, T., 1960, The development of *Neomenia carinata* TULLBERG. *Proc. Roy. Soc. London*, 153B(951): 263-278.
- TRUEMAN, E., 1968, Burrowing habit and the early evolution of body cavities. *Nature*, 218(5136): 96-98.
- VAGVOLGYI, J., 1967, On the origin of molluscs, the coelom, and coelomatic segmentation. *Syst. Zool.*, 16(2): 153-168.
- WERNER, B., 1966, *Stephanoscyphus* (Scyphozoa, Coronatae) und seine direkte Abstammung von den fossilen Conulata. *Helgoländer wiss. Meeresunters.*, 13(4): 317-347.
- YOCHELSON, E., 1969, Stenothecoida, a proposed new class of Cambrian Mollusca. *Lethaia*, 2(1): 49-62.
- YONGE, C., 1939, The protobranchiate molluscs, a functional interpretation of their structure and evolution. *Philos. Transact. Roy. Soc. London*, Ser. B, 230: 79-147.
- YONGE, C., 1947, The pallial organs of the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Philos. Trans. Roy. Soc. London*, Ser. B, 232: 443-518.
- YONGE, C., 1953, The monomyarian condition in the Lamellibranchia. *Roy. Soc. Edinburgh*, 62(11/12): 443-478.
- ZEISS, A., 1968, Fossile Cephalopoden mit Weichteilen. *Natur & Museum*, 98(10): 418-424.



## ZUR MOLLUSKENFAUNA DES FELSLITORALS BEI ROVINJ (ISTRIEN)

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## EINLEITUNG

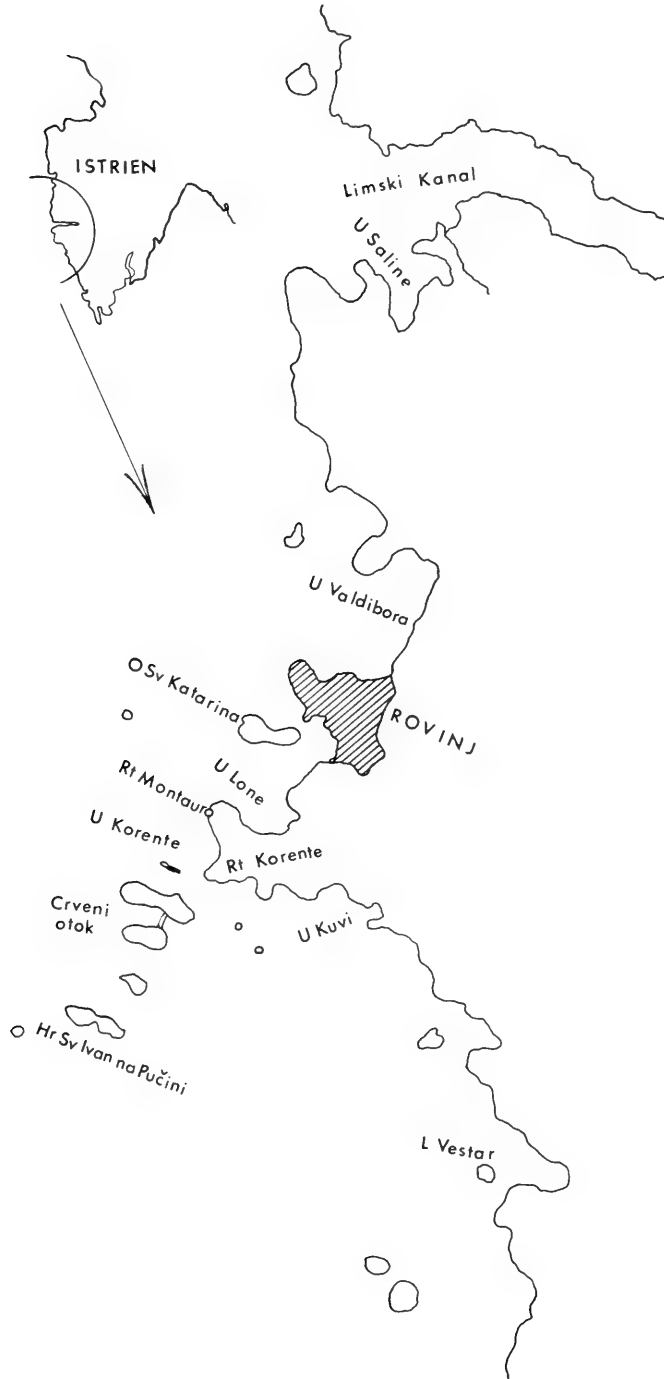
Angaben über das Vorkommen und die Verteilung von Mollusken der Adria, bzw. der Nord-Adria wurden in der älteren Literatur ausschliesslich von Konchyliologen gemacht, u.a. von STOSSICH (1865), WEINKAUFF (1866/67), CARUS (1889/93) und BRUSINA (1896). Die ersten ökologischen und biologischen Angaben über Adria-Tiere (darunter auch von Mollusken) stammen von LORENZ (1863), weiters von WIMMER (1883), der vor allem Notizen über das Tiefenvorkommen adriatischer Konchylien machte. ZIMMERMANN (1907) beschrieb im Adria-Führer die Lebensräume der häufigsten Küstenmollusken.

Eine Zusammenstellung aller im Golf von Triest (Nord-Adria) gefundenen Mollusken, mit kurzen Angaben über ihr Vorkommen gab GRAEFFE (1903), einen weiteren Beitrag zur Kenntnis der nordadriatischen Küsten-Molluskenfauna leistete ODHNER (1914) mit zahlreichen biologischen und ökologischen Bemerkungen aus dem Raum von Rovinj. Aus dem Gebiet von Rovinj stammen auch die ausführlichen Bodenuntersuchungen von VATOVA (1928). Neben anderen Meerestieren wurden in diesen langjährig durchgeführten Aufsammlungen auch die Mollusken berücksichtigt, deren Verteilung, Häufigkeit und Vergesellschaftung nach Dredschnetz-Proben ermittelt wurde. KÜHNELT (1930, 1933, 1938, 1942 und 1950) führte eingehende Studien über die Bohrmuscheln des felsigen Küstenlitorals von Rovinj durch. Eine umfassende Liste von 913 in der Adria gefundenen Molluskenarten (bzw. Unterarten) verfasste COEN (1937). Von den genannten Arten (bzw. Unterarten) entfallen 10 auf die Placophora, 560 auf die Gastropoda (davon 450 Prosobranchia, 100 Opisthobranchia und 10 Pulmonata), 320 auf die Bivalvia und 23 auf die Cephalopoda.

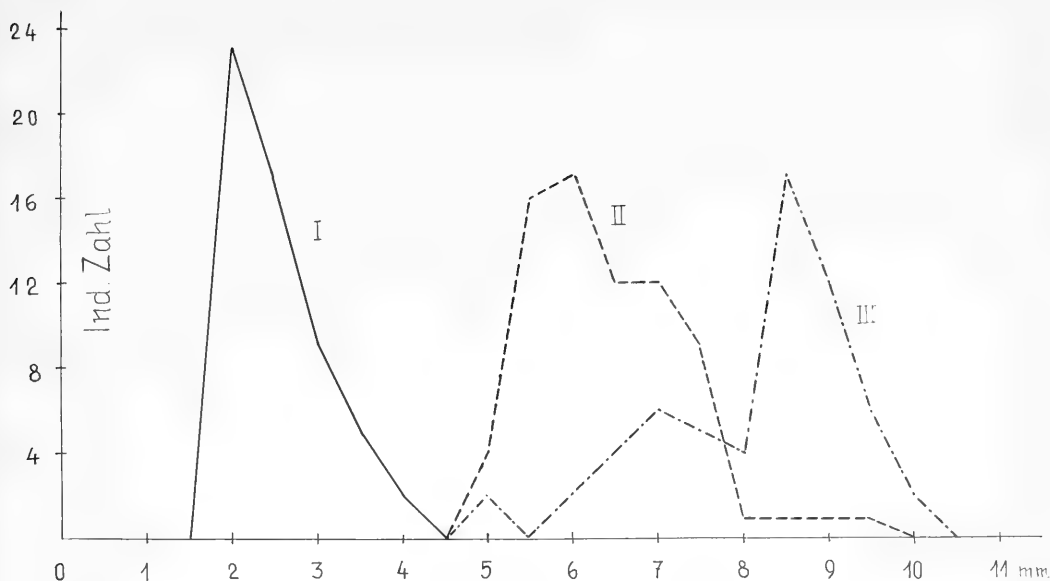
LELOUP & VOLZ (1938) veröffentlichten eine umfassende Monographie der Placophora der Adria. Sie enthält umfassende systematische, anatomische, biologische und ökologische Angaben über diese Tiergruppe. Ein Verzeichnis der häufigsten Mollusken-Arten des adriatischen Litorals (mit besonderer Berücksichtigung von Aufsammlungen aus dem Gebiet von Rovinj), kurze Notizen über Vorkommen und Biologie finden sich in der von RIEDL (1963) herausgegebenen FAUNA UND FLORA DER ADRIA in der Bearbeitung der Mollusca von STARMÜHLNER.

## MATERIAL UND SAMMELMETHODE

Das in dieser Studie dargestellte Material von Mollusken aus dem Felslitoral bei Rovinj (Tafel 1) stammt von Aufsammlungen, die während der Exkursionen des 1. Zoologischen Institutes der Universität Wien an das Institut za Biologiju Mora während der Jahre 1953 bis 1967, also innerhalb von 14 Jahren in den Sommermonaten durchgeführt wurden. Als Aufsammler betätigten sich neben dem Autor noch die Mitarbeiter des 1. Zoologischen Institutes, vor allem die Herren Dr. Heinz SPLECHTNA, Univ. Prof. Dr. Rupert RIEDL, Dr. Eduard PIFFL, weiters Frau Univ. Prof. Dr. Anneliese STRENGER, sowie die Teilnehmer der Meeresbiologischen Kurse der Universität Wien. Letztere waren in Arbeitsteams eingeteilt, die unter der Leitung der



TAFEL 1. Die istriatische Küste bei Rovinj sowie die umliegenden Inseln und Buchten.



TAFEL 2. Verteilung der einzelnen Grössenklassen von *Littorina neritoides* im Supralitoral: I = Gezeitenmittelniveau (GM) - 56 Ind., dchschn. H.: 2'6 mm; II = 100 cm oberhalb GM - 56 Ind., dchschn. H.: 6'4 mm; III = 200 cm oberhalb GM - 54 Ind., dchschn. H.: 8'15 mm.

genannten Damen und Herren die einzelnen litoralen Lebensräume besammelten.

Die Aufsammlungen wurden zum Grossteil mit der freischwimmenden Tauchmethode (siehe RIEDL 1953, 1954, 1966; STARMÜHLNER 1955a, b, 1968), d.h. mit Flossen, Tauchglas und Schnorchel durchgeführt. Nur tiefere Proben unter 10-15 m wurden vom Schiff aus mit Bodenschleppnetzen, Dredschen oder bei Weichböden mit Bodengreifern entnommen. Bei quantitativen Aufsammlungen wurden in der Regel Proben von einem oder mehreren gleichförmigen Probenquadraten von  $1/16\text{ m}^2$  Fläche (25 cm Seitenlänge) entnommen. Bei diesen Proben-Entnahmen arbeiteten mindestens 2, meist aber 3 oder 4 Taucher zusammen. Ein Taucher bestimmte mit dem Probenquadrat die zu besammelnde Fläche, die nach Bestimmung der Lage, Tiefe, Exposition, Höhe und Zusammensetzung des Pflanzenbewuchses (oder Bewuchses durch sessile Tierformen, wie Spongiaria, Hydrozoa, Anthozoa, Bivalvia, Ascidia u. dgl.) abgesammelt wurde.

Der abgetragene Aufwuchs mit der aufsitzenden oder dazwischen lebenden Mikro- und Mesofauna (zu letzterer zählt die überwiegende Mehrzahl der Mollusken!) wurde von einem zweiten Taucher in einen knapp daruntergehaltenen Plastiksack gefüllt, wobei geachtet wurde, dass keine grösseren Stücke abgetragenen Materials weggeschwemmt wurden. Um auch die Bewohner des in Kalkfelsen reich entwickelten Endolithions in die Probenaufsammlung zu bekommen, wurde mit Hammer und Meissel auch das Felsgestein bis etwa 5-10 cm Tiefe abgetragen, soweit als Bohrgänge von Muscheln und Bohrschwämmen feststellbar waren.

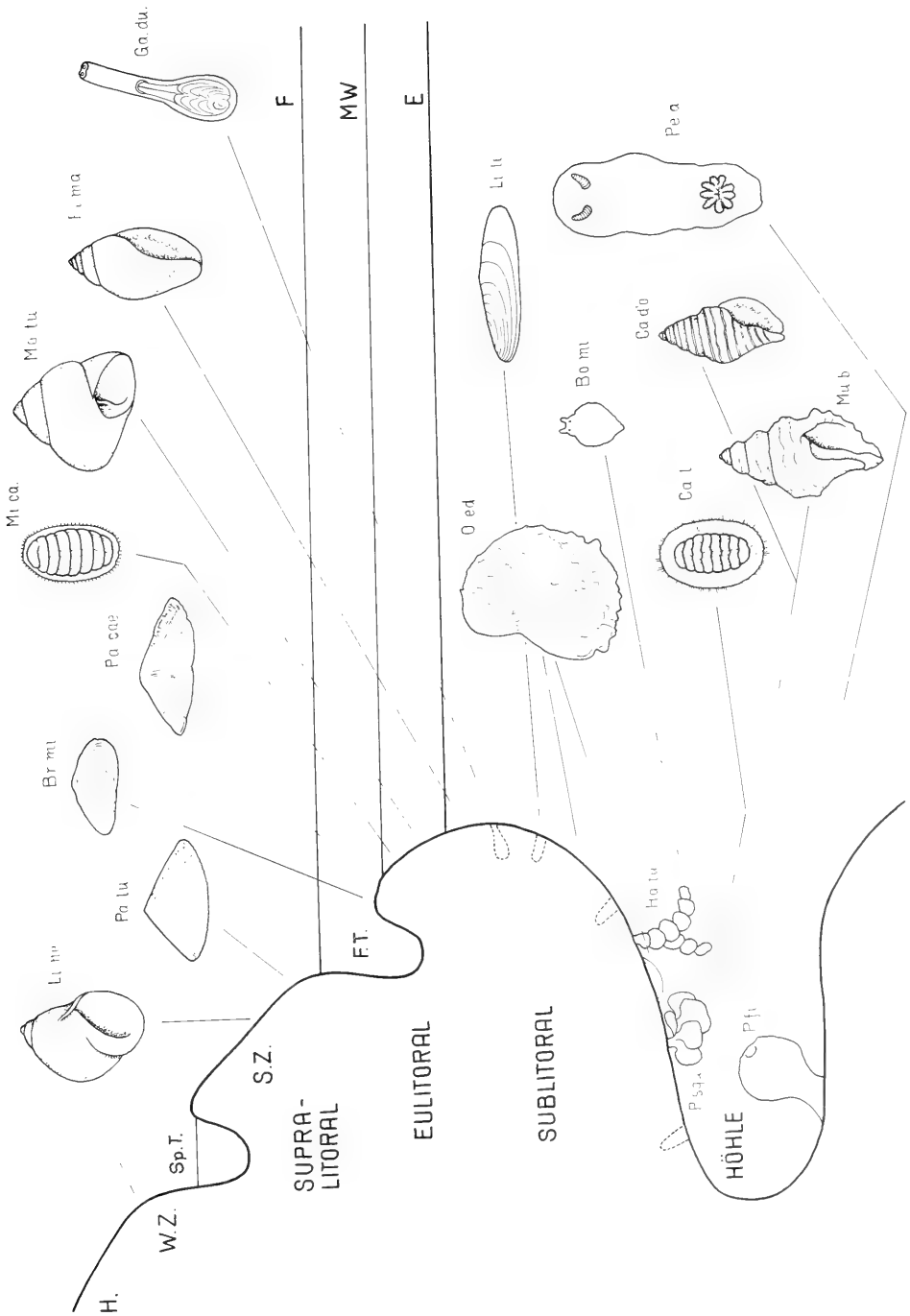
Die derart aufgesammelten Proben wurden anschliessend im Labor des Institut za Biologiju Mora aufgearbeitet. In der Regel wurde zuerst die Methode der Klimaverschlechterung angewendet, d.h. die Probe kam in ein grosses Glasaquarium, wurde vollkommen mit Wasser bedeckt und so aufgestellt, dass eine Ecke dem Tageslicht ausgesetzt war. Die baldige Verschlechterung des Wasserklimas ( $\text{O}_2$ -Mangel)

## TAFEL 3

Molluskenleitformen des Supra-, Eu- und Sublitorals (inklusive Höhlen) primärer Hartböden.

Allgem. Abkürzungen: W.Z. = Weisse Zone; H. = Halophytenzone; S.Z. = Schwarze Zone; F.T. = Fluttümpel; Sp.T.: Spritzwassertümpel; F. = Flutniveau; MW = Mittelwasserniveau der Gezeiten; E. = Ebbeniveau.

Pflanzen- und Tiernamenabkürzungen: Li.ne. = *Littorina neritoides*; Pa.lu.: *Patella lusitanica*; Br.mi. = *Brachyodontes minimus*; Pa.coe.: *Patella coerulea*; Mi.ca. = *Middendorfia caprearum*; Mo.tu. = *Monodonta turbinata*; Pi.ma.: *Pisania maculosa*; Ga.du. = *Gastrochaena dubia*; O.ed.: *Ostrea edulis*; Li.li. = *Lithophaga lithophaga*; Bo.mi.: *Bosellia mimetica*; Ca.l. = *Callochiton laevis*; Mu.b.: *Murex blainvillei*; Ca.d'o. = *Cantharus d'orbigny*; Pe.a. = *Pellodoris atromaculata*; P.fi. = *Petrosia ficiiformis*; P.sq.: *Peyssonnelia squamaria*; Ha.tu. = *Halimeda tuna*.



zwingt vagile Tiere, darunter vor allem Kleingastropoden (Rissoidea, *Bittium*, Trochidae, Buccinidae u.a., viele Opisthobranchia) und manche kleine vagile Bivalvia (wie *Musculus*) an die Oberfläche zur Lichtseite, wo sie leicht mit Pinzette oder Pipette abgesammelt werden können. Später wurde der Rest des Materials unter dem Binokular nach lebenden Mollusken ausgesucht. Nach der Fixierung des Materials mit Seewasser-Formol erfolgte in der Regel nach Ausschütteln der Probe ein zweites Aussuchen, um eventuell übersehene Kleinstschalen zu bekommen.

#### DIE MOLLUSKENGESSELLSCHAFTEN DER EINZELNEN KÜSTENZONEN

Die Aufsammlungen im Küstenlitoral erstreckten sich auf folgende Küstenzonen (Tafel 3):

- 1) Supralitoral: Küstenstreifen über der Flutlinie des Eulitorals, soweit der Einfluss des Meeres durch Wellenschlag noch jenen des Landes deutlich überwiegt. Die Höhererstreckung schwankt je nach dem Expositionsgrad zwischen 25 cm und über 10 m (RIEDL 1963):
  - a) Primärer Hartboden
  - b) Sand, -Kiesküste
- 2) Eulitoral: Küstenstreifen zwischen der Ebbe- und Flutlinie, die Gezeitenzone (intertidal), deren Breite in der Nord-Adria ca. 50 cm erreicht und nur bei sehr flachem Küstenwinkel wesentlich breiter werden kann (RIEDL 1963):
  - a) Primärer Hartboden (Epi- und Endolithion).
- 3) Sublitoral: Schliesst unter der Ebbelinie dem Eulitoral an und stellt im Bereich der seichten Nord-Adria den ständig untergetauchten Abschnitt der Küstenabböschung dar (RIEDL 1963):
  - a) Primärer Hartboden
    - a' ) Epilithion
    - a'' ) Endolithion
  - b) Höhlen mit Epi- und Endolithion
  - c) Rollblöcke (Felsgeröll und -blöcke im Bereich des Küstenlitorals, die je nach Grösse von den Wasserströmungen häufiger oder seltener umgelagert (gerollt) werden (RIEDL 1966).
  - d) Phytalbewuchs auf primären Hartböden:
    - d' ) *Cystoseira*-Bestände
  - e) Anschüttungsböden auf primären Hartböden:
    - e' ) Mischböden mit vorherrschendem Porifera (meist *Geodia*) -Bewuchs  
Ascidia-Bewuchs  
*Vidalia volubilis*-Bewuchs
    - e'' ) Sekundäre Hartböden: Bryozoa-Bestände (vorherrschend *Hippodiplosia*-, *Myriozoom*-, *Retepora*- und *Flustra*-Arten) auf Schellmaterial (mit leeren Schalen von Pectinacea, Veneracea, Limidae, Cardiacea u.a. Bivalvia) sowie flächiger Kalkalgen (meist *Lithothamnium*-Arten).
  - f) Reine Sedimentböden:
    - f' ) Sandböden
    - f'' ) *Posidonia*-, *Zostera*-Bestände auf Sandböden
    - f''' ) Phytallose Schlamm- und Tonböden

#### 1) Supralitoral (Tafel 3)

Die Grenzen des Supralitorals werden durch die Küstenneigung und Exposition bestimmt. Die Wirkung des Wellenschlages reicht von wenigen Zentimetern (z.B. an

geschützten Stellen im Limski-Kanal) bis zu maximal 10 m über dem Gezeitenmittelwasser (=GM) auf pelagischen Inseln (z.B. an der dem Schirokko-Wind nach SSW exponierten Küste der Insel Banjole). Bei sehr flachen Küstenabschnitten können die Wellen auslaufen oder sie kippen über. Bei steiler Küstenneigung geht die Orbitalbewegung der Wasserteilchen allmählich in eine Pendelbewegung über, wobei das Maximum der Höhenwirkung bei einer Neigung von etwa 30° eintritt. Der Einfluss von Spritz- und Sprühwasser reicht bei starkem Wellenschlag wesentlich höher als der der fließenden Woge. Von grosser Bedeutung für die Ausbreitung des Supralitorals ist ausserdem die Neigung zum Sonneneinfall, da starke Erhitzung an Südhängen zur Austrocknung der für das Supralitoral kennzeichnenden Blaualgen führt.

#### a) Primärer Hartboden

Von der Flutlinie lassen sich gegen die Halophytenzone zu im Supralitoral der Felsküste der Nord-Adria zwei Zonen unterscheiden:

**Die Schwarze oder Lithophyten-Zone:** Charakterisiert durch endolithische Blaualgen, wie *Mastigocoleus testarum*, *Hyella caespitosa*, *Entophysalis granulosa* u.a., sowie die braunschwarze Flechte *Lichina confinis*. Der genannte Bewuchs bewirkt die dunkle, "schwarze" Färbung des Kalkgesteines. An exponierten Stellen mit starker Besiedlung durch die Seepocken *Chthamalus stellatus stellatus* und *Ch. st. depressus*.

**Die Weisse Zone:** Starke Abnahme der Blaualgen, dadurch Hervortreten des hellen Kalkgesteines, auf dem die gelborange Flechte *Caloplaca aurantia* siedelt.

Am Unterrand der Schwarzen Zone, deren Breite bis 2 m über dem GM betragen kann, finden sich zahlreiche Fluttümpel ausgewaschen, während in der "Weissen Zone," deren Ausdehnung bis 5 m über der Schwarzen Zone, bzw. 2 bis 6 m über dem GM betragen kann, Spritzwassertümpel auftreten.

Die Charakterart des Supralitorals ist unter den Mollusken *Littorina neritoides* (L.), deren Verbreitung von der Gezeitenmittellinie bis zur oberen Grenze der "Weissen Zone" reicht, um die sich die Halophytenzone anschliesst. Auf SSW exponierten Abhängen (z.B. auf der Insel Banjole) mit einer Neigung von ca. 30° reicht die Art von der Gezeitenmittellinie bis ca. 3 m-5 m oberhalb in die "Weisse Zone." An der Grenze zwischen Eu- und Supralitoral (Gezeitenmittelwasser bis Flutlinie) finden sich ausschliesslich juvenile, dunkel pigmentierte Individuen, während gegen die Spalten des Supralitorals (Übergang zwischen "Schwarzer" und "Weisser" Zone) die Individuenzahlen pro Flächeneinheit allmählich ab-, die Grössen der Individuen dagegen zunehmen. Die Schalen nehmen eine kalkweisse Färbung an, was auf den allmählichen Verlust des schützenden, dunklen Periostrakums der älteren Individuen zurückzuführen ist. Folgende Tabelle gibt eine Zusammenstellung von Auszählungen pro 1/16 m<sup>2</sup> an der SSW-Küste der Insel Banjole (15. Juli 1967):

25 cm	oberhalb des GM	135	Ind./1/16m <sup>2</sup>	(z. T. in leeren Balaniden-Gehäusen)
50 cm	oberhalb des GM	50	Ind./1/16m <sup>2</sup>	(in Löchern und Spalten)
100 cm	oberhalb des GM	9	Ind./1/16m <sup>2</sup>	(in flachen Vertiefungen)
100 cm	oberhalb des GM	75	Ind./1/16m <sup>2</sup>	(in tiefer Rinne)
200 cm	oberhalb des GM	vereinz.	Ind./1/16m <sup>2</sup>	(in Spalten u. dgl.)
300 cm	oberhalb des GM	die letzten Tiere		(in Spalten u. dgl.)

Die Tabelle zeigt, dass die Tiere in der "trockenen" sog. "Weissen Zone" tagsüber, während der starken Einstrahlung, truppweise in Spalten, Löchern zusammengeballt sind (Tafel 6, Abb. 1), während sie auf den freien Flächen fehlen. Sie wandern mit zunehmendem Alter vom Gezeitenniveau, wo sich die Larven festsetzen, gegen die "Schwarze" und "Weisse" Zone. Tafel 2 zeigt eine graphische Darstellung der Verteilung der einzelnen Grössenklassen von *Littorina neritoides* (Tafel 6, Abb. 2) aus

dem Gezeitenmittelniveau (I), 100 cm oberhalb des GM (II) und 200 cm oberhalb des GM (III).

An der unteren Grenze des Supralitorals überschneidet sich das Vorkommen von *L. neritoides* mit der Obergrenze des Vorkommens von *Patella lusitanica* GMELIN.

Die Fluttümpel an der Grenze zwischen Eu- und Supralitoral werden im Gezeitenwechsel ständig mit frischem Seewasser erneuert. Daher sind sie von den gleichen Tieren besiedelt, die in dieser Zone auftreten, abgesehen von grösseren, freischwimmenden Organismen. An Algen werden - z.B. in den Fluttümpeln der Insel Banjole - *Lyngbya confervoides*, *Chaetomorpha aerea* und *Cladophora pellucida*, sowie *Fosliella* sp. und *Lithophyllum* sp. als krustenförmige Überzüge festgestellt. Vereinzelt treten auch *Ulva lactuca*, *Polysiphonia sertularioides*, *Acetabularia mediterranea* und verkümmerte *Cystoseira* sp. -Büschel auf.

Die Fluttümpelränder sind von *Littorina neritoides* besetzt, daneben *Patella lusitanica* in höher, *Patella coerulea* L. in tiefer gelegenen Tümpeln. Von den typischen Eulitoralbewohnern gelangen die Placophoren *Middendorfia caprearum* (SCACCHI) und *Chiton olivaceus* SPENGLER in die Fluttümpel, wo sie vor allem flache Vertiefungen besiedeln. Von den Gastropoda tritt gelegentlich *Monodonta turbinata* (BORN) auf, während die Bivalvia durch *Brachyodontes minimus* (POLI), *Mytilus galloprovincialis* LAM., *Ostrea edulis* L. im Epilithion und *Gastrochaena dubia* (PENNANT) (Tafel 8, Abb. 2) im Endolithion vertreten sind.

In die Spritzwassertümpel im Bereich der "Weissen Zone" gelangt Meerwasser nur durch auslaufende Wellen und einfallende Gischt. Mit wachsendem Abstand vom Meer werden die Bedingungen extremer. Vor allem wirkt sich die starke Einstrahlung und die dadurch bedingte hohe Temperatur sowie das Ansteigen des Salzgehaltes durch Verdunstung und Eindickung begrenzend für die Besiedlung von Meeresorganismen aus. Trotzdem findet man pflanzliche Besiedlung von Blau- und Grünalgen, Flagellaten und Diatomeen. Von den Mollusken findet sich nur *Littorina neritoides* an den Tümpelrändern, vereinzelt auch knapp unter der Wasseroberfläche.

#### b) Sand- und Kiesküste

Diese Formation ist bei Rovinj nur in wenigen Buchten, so bei der sog. Saline am Eingang des Limski-Kanal ausgebildet. In den Lückenräumen tritt in durchfeuchteten Abschnitten *Truncatella subcylindrica* (L.), seltener *Alexia myosotis* (DRAPARNAUD) auf.

### 2) Eulitoral (Tafel 3)

#### a) Primärer Hartboden

Das GM zwischen Ebbe- und Flutlinie wird in der Nord-Adria, wie im gesamten Mittelmeer, durch die Pferdeaktinie *Actinia equina* (L.) gekennzeichnet, die hier ihr Hauptvorkommen zeigt. Die für die Fluttümpel genannten Algen treten im ganzen Eulitoral auf. Weiters finden sich im stark bewegten Wasser an häufigeren Arten: *Nemalion helminthoides*, *Laurencia obtusa*, *Enteromorpha*-Arten, *Padina pavonia*, *Corallina mediterranea* und *Jania rubens*. Im unteren Bereich des Eulitorals schliessen bereits die Braunalgenbestände des hochwüchsigen Phytal mit *Cystoseira mediterranea*, *C. barbata* und *Sargassum*-Arten an. Seltener sind bei Rovinj (z.B. auf der Leuchtturm-Insel Sv. Ivan na Pučini) Kalkalgenbänke, sog. Trottoir's, ausgebildet. Sie werden vor allem von *Lithothamnium*- und *Corallina*-Arten aufgebaut.

Unter den Mollusken treten die in den Fluttümpeln erwähnten Arten im Eulitoral besonders auffällig in Erscheinung. Unter der Placophora finden sich *Middendorfia caprearum* und *Chiton olivaceus* regelmässig, während unter den Gastropoda *Patella lusitanica* mit der höheren Schale im Bereich zwischen GM und Flutgrenze, die flachere



*Patella coerulea* dagegen zwischen GM und Ebbelinie sitzt. Typische Bewohner sind weiters *Monodonta turbinata*, *Pisania maculosa* (LAM.) - letztere vor allem bei Auftreten von *Ulva*-Beständen - *Columbella rustica* (L.) und vereinzelt *Conus ventricosus* GMELIN. Während die erstgenannte Art Algenschaber ist, zählen *Pisania* und *Columbella* zu den saprophagen Formen und *Conus* jagt nach Nereiden.

Unter den Bivalvia finden sich in kleinen Spalträumen *Brachyodontes minimus* und unter der Ebbelinie *Mytilus galloprovincialis*. *Ostrea edulis* besiedelt exponierte, stark umspülte Felspartien, wo sich auch vereinzelt *Chama gryphoides* (L.) und *Ch. gryphina* (LAM.) finden. Im Endolithion des Eulitorals ist vor allem *Gastrochaena dubia* (Tafel 8, Abb. 2) an stark exponierten und umspülten Flächen in grosser Dichte anzutreffen, wobei die verkalkten Siphonen ihre Lage anzeigen. Daneben finden sich *Petricola lithophaga* RETZIUS, sowie die Löcher von *Lithophaga lithophaga* (L.), deren Hauptverbreitung im unteren Eulitoral liegt und vom Algenaufwuchs der Felsen abhängig ist. In *Corallina mediterranea*-Beständen ist die Muschel *Musculus marmoratus* (FORBES) gelegentlich anzutreffen.

Abschliessend lässt sich sagen, dass für das Eulitoral der nordadriatischen Felsküste folgende Molluskenvergesellschaftungen typisch sind (Tafel 3):

Placophora: *Middendorfia caprearum* - *Chiton olivaceus* - Assoz.

Gastropoda: *Patella lusitanica* - *P. coerulea* - *Monodonta turbinata* - *Pisania maculosa* - Assoz. mit *Columbella rustica* und *Conus ventricosus*.

Bivalvia: *Brachyodontes minimus* - *Mytilus galloprovincialis* - *Ostrea edulis* - *Chama gryphoides* - Assoz. im Epilithion und mit einer *Gastrochaena dubia* - *Lithophaga lithophaga* - Assoz. im Endolithion, vereinzelt *Petricola lithophaga*.

### 3) Sublitoral

#### a) Primärer Hartboden

An exponierten Steil- und Überhängen, besonders an N-exponierten Küstenab-  
böschungen, tritt der höherwüchsige Algenbewuchs, das eigentliche Phytal, der sonst in der Regel an die untere Eulitoralgrenze anschliesst, etwas zurück. Neben krusten-  
bildenden Kalkalgen, wie *Lithophyllum incrustans*, *L. racemus* und *Pseudolithophyllum  
expansum* treten auffälliger höchstens *Cladophora* sp.-Bestände, *Corallina mediterranea*  
und *Codium bursa* auf. Daneben wird die Felsoberfläche hauptsächlich von Schwämmen,  
wie *Cacospongia scalaris*, *Halichondria panicea*, *Dynamena cavolinii* ua. Arten,  
von Hydrozoen, wie *Aglaophenia pluma* und Bryozoen, wie *Schizoporella sanguinea*  
überzogen.

Unter den Mollusken treten von den eulitoralen Formen unter den Gastropoda die  
*Patella*-Arten und *Monodonta turbinata* allmählich zurück. *Columbella rustica*,  
*Pisania maculosa*, gelegentlich *Cerithium rupestre* RISSO in grösserer Zahl und  
vereinzelt *Diodora graeca* (L.) sind neben kleinen Muriciden, *Cantharus d'orbigny*  
(Tafel 6, Abb. 4), die stets, aber meist vereinzelt auftreten, für das obere, bebrandete  
Sublitoral typisch. Wesentlich individuenreicher sind an exponierten Felsen sessile  
Bivalvia, wobei vor allem *Mytilus galloprovincialis* und *Ostrea edulis* in Nestern  
auftreten. Im Endolithion erreicht an derartigen Standorten *Lithophaga lithophaga*,  
mit 10-20 Ind./1/16m<sup>2</sup> hohe Individuendichten, während *Gastrochaena dubia* (Tafel 8,  
Abb. 2) und *Petricola lithophaga* etwas zurücktreten.

Die primären Hartböden des Sublitorals sind an Standorten mit niederwüchsiger  
Schattentalgen-Vegetation und Bewuchs sessiler Tierarten durch folgende Mollusken-  
Vergesellschaftungen charakterisiert:

Epilithion:

Gastropoda: *Columbella rustica* - *Pisania maculosa* - *Cerithium rupestre* -

Assoz. mit *Diodora graeca*, *Cantharus d'orbigny* u. selteneren Arten.

Bivalvia:

*Mytilus galloprovincialis* - *Ostrea edulis* - Assoz.

Endolithion:

Bivalvia:

*Lithophaga lithophaga* - Assoz. mit vereinzelt *Gastrochaena dubia* und *Petricolà lithophaga*.

b) Höhlen (Tafel 3)

Einen besonderen Lebensraum stellen die Brandungshöhlen im Bereich des felsigen Küstenlitorals dar. RIEDL (1966) definiert eine Meereshöhle topographisch als "ganz oder teilweise unter der Wasserlinie gelegene und von genügend beständigen Teilen des Felslitorals grossteils umschlossene Räume ab einem Volumen von 1 m<sup>3</sup>, deren Eingangsweite die Innenweite gewöhnlich nicht übertrifft, dennoch aber eine zureichende Kommunikation mit dem offenen Meer bietet" (S. 108). Derartige Höhlen sind an der Felsküste von Rovinj z.B. am sog. Stadtfelsen unterhalb des Leuchtturmes der Stadt und - als Grotte - auf der Insel Banjole ausgebildet. Gegen die schattigen bis lichtlosen Teile der Höhle nimmt der Algenbewuchs des primären Hartboden allmählich ab und geht in einen Bewuchs sessiler Tierarten über (Porifera, Cnidaria, Balanidae, Bivalvia, Ascidia, sessile Polychaeten u.a.) über. Die Höhleneingänge sind je nach Belichtungsverhältnissen von Schattenalgen, wie *Halimeda tuna*, *Peyssonnelia squamaria* und gegen die inneren Flächen zu mit krustigen Kalkalgen wie *Pseudolithophyllum expansum* u.a. Arten bewachsen. Die grünen, flachen Thalli von *Halimeda* sind häufig von *Bosellia mimetica* (Tafel 7, Abb. 1) einer Sacoglossa besiedelt, die in Färbung und Körperform einen Thallus von *Halimeda* imitiert. Auf den roten, polsterförmigen *Peyssonnelia*- und den krustenförmigen *Pseudolithophyllum*-Beständen sind dagegen die ebenfalls rot gefärbten Placophora *Callochiton laevis* (MONTAGU) und *Chiton corallinus* RISSO anzutreffen. Im Innern der Höhlen dominieren sehr häufig Schwämme als Bestandbildner, darunter *Chondrosia reniformis*, *Hemimycale* sp., *Mycale massa*, *Anchinoe* sp., *Cacospongia scalaris*, *Ircinia*-Arten, *Petrosia ficiformis* u.a. Arten, weiters Hydrozoen-Kolonien von *Plumularia* sp., *Aglaophenia* sp., Anthozoen-"Wiesen" mit *Epizoanthus* sp. oder *Parazoanthus axinellae*.

Auch von den sessilen Bivalvia treten an den Höhlenwänden an gut bespülten Wänden im Epilithion einige Arten als Bestandbildner auf, vor allem *Ostrea edulis* und *Arca lactea*. Im Endolithion dominiert wieder *Lithophaga lithophaga*, seltener *Gastrochaena dubia* (Tafel 8, Abb. 2) und *Petricolà lithophaga*. In kleinen Hohlräumen sitzt häufig *Beguinea calyculata* (L.). Unter den Gastropoda finden sich in den Höhlenbeständen, bedingt durch das Fehlen der Algen, nur mehr saprophage, karnivore Arten, darunter einige Spezialisten. So sind vor allem die Muricidae vertreten, mit Arten wie *Muricidea blainvillei* (PAYRAUDEAU), *Tritonalia edwardsi* (PAYRAUDEAU) und *Tritonalia aciculata* (LAM.), seltener findet sich *Murex trunculus* L. Von den Buccinidae ist vor allem *Cantharus d'orbigny* (Tafel 6, Abb. 4), von den Nassidae *Nassa reticulata* und von den Toxoglossa *Conus ventricosus* anzutreffen. An den Höhlenwänden sitzen ausserdem stets die Gehäuse von *Vermetus*-Arten. Unter den Spezialisten sei vor allem *Peltdoris atromaculata* BERGH (Tafel 7, Abb. 2) erwähnt, die sich ausschliesslich auf dem Schwamm *Petrosia ficiformis* findet, der die Nahrung dieser Dorididae bildet.

Die Mollusken- Vergesellschaftungen in den Meereshöhlen bei Rovinj sind durch folgende Arten zu charakterisieren (Tafel 3):

Epilithion:

1) Nordexponierte Überhänge, Höhleneingänge:

a) auf *Halimeda tuna*; *Bosellia mimetica*

b) auf *Peyssonnelia squamaria* und Kalkalgen:

*Callochiton laevis* - *Chiton corallinus* - Assoz.

## 2) Höhlenwände im licht- und phytalfreien Bereich:

Gastropoda: *Muricidea blainvillei* - *Tritonalia edwardsi* -  
*Cantharus d'orbigny* -Assoz. mit *Vermetus*-Arten.

Bivalvia: *Ostrea edulis* - *Arca lactea* -Assoz.

3) Auf Drusen des Schwammes *Petrosia ficiformis*:

*Peltodoris atromaculata*

Endolithion:

Von den Eingängen bis zu den inneren Höhlenwänden:

*Lithophaga lithophaga* - *Gastrochaena dubia* -Assoz.  
mit *Petricola lithophaga*, *Beguinea calyculata*.

## c) Rollblöcke

An den Grenzen des Felslitorals zu den Anschüttungsböden treten bei Rovinj häufig Geröll- und Blockfelder auf. RIEDL (1966) gibt auf S. 56 in der Tabelle 2 eine Übersicht über die Grössenordnungen von Rollblöcken in Beziehung mit ihrer mittleren Liegezeit und den geschätzten Umrollungen pro Jahr (mobiles Substrat). So liegen nach seinen Berechnungen grosse Felsblöcke von 5 bis 10 m Durchmesser wahrscheinlich 10-15 Jahre bis sie einmal vollständig oder teilweise umgerollt werden. Sie zeigen an ihrer Oberfläche die typischen Phytalbestände des besonnten, primären Felslitorals, an ihren Seitenwänden Phytal-Schattenalgen und an hohl liegenden Unterseiten typische Höhlenbestände. Auch ihre Molluskenfauna setzt sich aus den gleichen Arten wie im einheitlichen Felslitoral zusammen.

Blöcke unter 2 m Durchmesser haben dagegen in der Regel nur mehr eine Liegezeit unter einem Jahr und werden z.B. bei einem Dchm. von 1 m ca. einmal pro Jahr umgerollt. Geröll mit 10 cm Durchmesser wird dagegen durchschnittlich bis 24 mal im Jahr gewendet! Die Besiedlung dieser Rollblöcke kann daher nur durch raschwüchsige und kurzlebige sessile Arten erfolgen, wie z.B. durch die Algen *Lyngbya* sp., *Acetabularia mediterranea* und *Melobesia* sp., die Bryozoe *Lichenopora radiata* und den Anneliden *Spirorbis pagenstecheri*. Unter den Mollusken, welche vor allem die Unterflächen von Rollblöcken besiedeln, sind von den Placophora *Chiton olivaceus*, *Acanthochiton communis* (RISSO), *A. fascicularis* (L.), sowie *Lepidopleurus cajetanus* (POLI) typisch, während unter den Gastropoda *Haliotis lamellosa* LAM. dominiert. Seltener, aber stets anzutreffen sind *Diodora gibberula* (LAM.) und *D. graeca* (L.), *Emarginula*-Arten, kleine Muricidae, Buccinidae, sowie, festsitzend, *Capulus hungaricus* (L.). Von den Bivalvia finden sich neben *Chama*-Arten und *Anomia ephippium* im Epi-, *Lithophaga lithophaga*, *Gastrochaena dubia* (Tafel 8, Abb. 2) und *Petricola lithophaga* im Endolithion.

Epilithion:

Placophora: *Chiton olivaceus* - *Acanthochiton* - *Lepidopleurus cajetanus* -Assoz.

Gastropoda: *Haliotis lamellosa* - *Diodora* - *Emarginula* -Assoz.  
mit *Capulus hungaricus* u.a. Arten.

Bivalvia: *Anomia ephippium* - *Chama* - Assoz.

Endolithion:

Bivalvia: *Lithophaga lithophaga* - *Gastrochaena dubia* -Assoz.  
mit *Petricola lithophaga*.

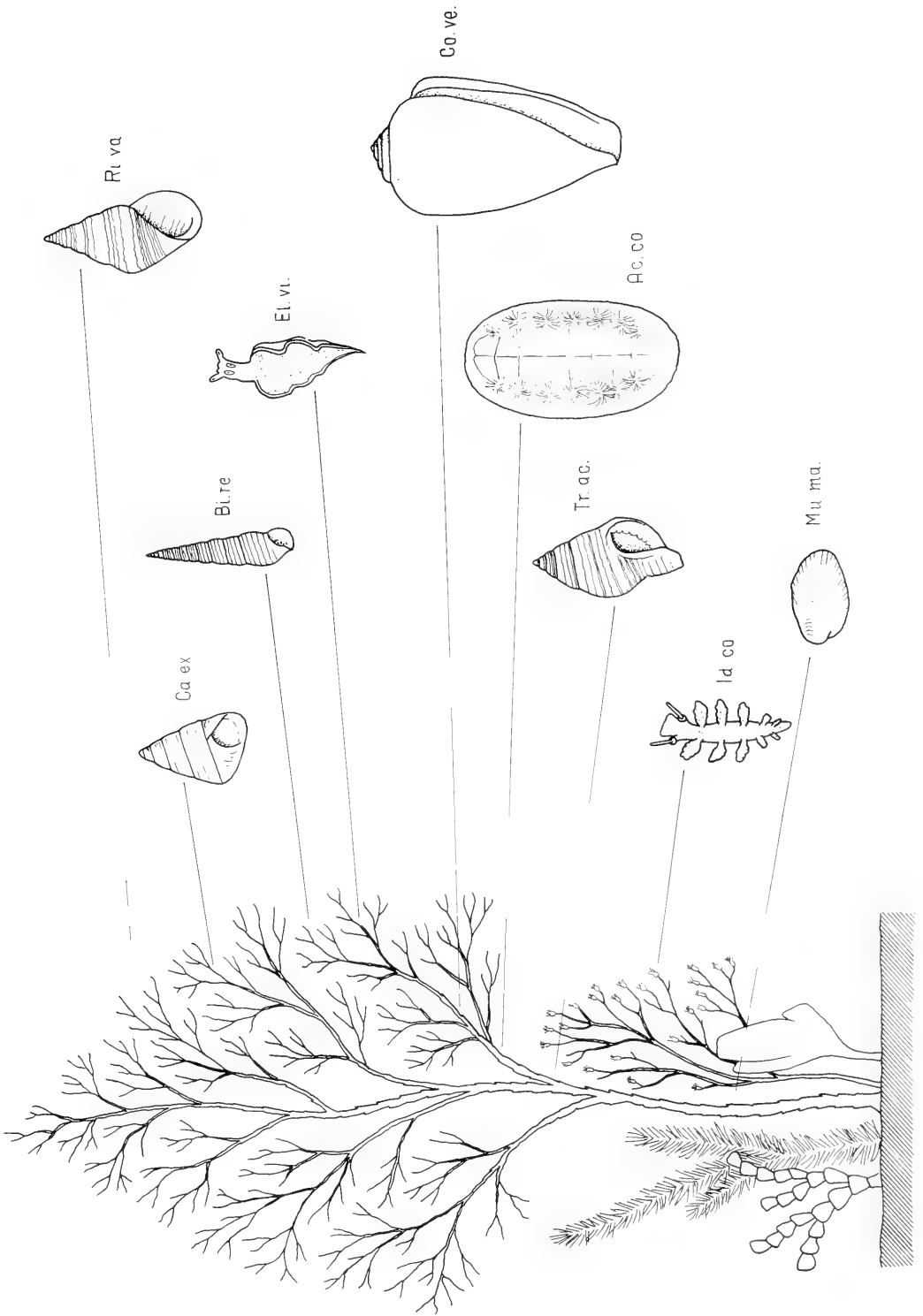
## d) Phytalbewuchs auf primären Hartböden (Tafel 4)

Das hochwüchsige Phytal im besonnten freien Sublitoral der primären Hartböden wird bei Rovinj fast ausschliesslich von *Cystoseira*-Arten bestimmt. Es treten dabei u.a. *Cystoseira spicata*, *C. adriatica*, *C. abrotanifolia*, *C. crinita* und *C. corniculata* auf, und zwar reinwüchsige und gemischte Bestände. Je nach Lage des Standortes wirken sich die Schwingungen des Brandungshorizontes mehr oder weniger stark auf die Sedimentationsverhältnisse in den Beständen aus. Bei starker Wasserbewegung,

## TAFEL 4

Molluskenleitformen des Phytalbewuchses auf primären Hartböden (*Cystoseira* sp.-Bestand mit *Halimeda tuna*, *Digenea simplex*, *Udotea petiolata* (als Beispiel neben anderen Arten) und Hydrozoenstöckchen im Unter- und Zwischenwuchs.

Tiernamenabkürzungen: **Ca.ex.** = *Cantharidus exasperatus*; **Ri.va.** = *Rissoa variabilis*; **Bi.re.** = *Bittium reticulatum*; **El.vi.** = *Elysia viridis*; **Co.ve.** = *Conus ventricosus*; **Ac.co.** = *Acanthochiton communis*; **Tr.ac.** = *Tritonalia aciculata*; **Id.co.:** *Idulia coronata*; **Mu.ma.** = *Musculus marmoratus*.



wie z.B. in reinen *C. spicata*-Beständen, finden sich nur größere Schellpartikel, dagegen findet keine Schlamm- oder Detritusabsetzung statt, Epiphyten- und Epizoen-Aufwuchs ist gering oder fehlend, die Fauna auffallend artenarm.

Bei schwacher Wasserbewegung - wie z.B. in *Cystoseira abrotanifolia* - *C. crinita* - Mischbeständen - wirken die Büschel der Braunalgen als Sediment- und Detritusfänger. Es kommt zum schichtenförmigen oder unregelmässigen Ablagern von Sedimentmaterial, sowie zu starkem Epiphyten- und Epizoen-Auf- und Zwischenwuchs. Ein engverzweigtes Lückenraumsystem ermöglicht das Vorkommen einer artenreichen, vagilen Kleinfaua. Unter den Gastropoda finden sich spezielle Ernährungstypen: Aufwuchsäser (Diatomeenfresser), wie Rissoacea, kleine Trochidae, *Bittium reticulatum* DA COSTA; Algensauger, wie die Sacoglossa *Elysia viridis* (MONTAGU) und *Thuridilla splendida* (Tafel 7, Abb. 4); Saprophage, wie *Columbella rustica*, *Pisania maculosa*; Räuber, wie *Conus ventricosus*.

Unter den Epiphyten der *Cystoseira*-Büscheln treten u.a. folgende Arten besonders in Erscheinung: *Botryocladia botryoides*, *Laurencia* sp., *Jania rubens*, *Ceramium* sp. in den distalen Verzweigungen, Kalkalgen, wie *Fosliella* sp. als Krusten auf den Stämmchen und *Acetabularia* sp., *Dictyota* sp., *Halimeda tuna*, *Peyssonelia squamaria* und *Sargassum* sp. in den schattigen Bodenpartien. Zwischen den *Cystoseira*-Beständen siedeln häufig mehrjährige *Padina pavonia*-Büschel. Dazu kommt ein dichter Diatomeen-Aufwuchs auf den verzweigten Algenfäden.

Im Tieraufwuchs, vor allem an den Stämmchen in Bodennähe, finden sich Porifera, Bryozoa, wie *Amanthia*-, *Membranipora*-, und *Scrupocellaria*-Arten, sowie Stöckchen von Hydrozoen. Sind letztere reichlich ausgebildet, so sind stets auch Aeolidiacea, die sich von ihnen ernähren, anzutreffen. Gelegentlich wurden dabei folgende Arten festgestellt: *Idulia coronata* (GMELIN), *Flabellina affinis* (GMELIN) (Tafel 7, Abb. 5), *Calmella cavolini* (VERANY), *Coryphella lineata* (LOVEN), *Trinchesia foliata* (FORBES & GOODSIR), *Favorinus branchialis* (RATHKE), *Facelina drummondii* (THOMSON), *Hervia peregrina* (GMELIN) und *Spurilla neapolitana* (DELLE CHIAJE).

Am Kalkalgenaufwuchs der Stämmchen (*Fosliella* sp.) sitzen vereinzelt Placophora, wie *Chiton olivaceus* und *Acanthochiton communis*; von den Gastropoda kann vereinzelt *Haliotis tuberculata* in juvenilen Exemplaren vorhanden sein. Massenvorkommen zeigen in den Cystoseiren die aufwuchsäsenden Prosobranchia. Unter ihnen dominiert *Rissoa variabilis* (v. MÜHLFELD) (Tafel 6, Abb. 3), *Alvania cimex* (L.), *Bittium reticulatum* DA COSTA, *Cantharidus exasperatus* (PENNANT), *C. striatus* (L.), *Calliostoma laugierii* (PAYRAUDEAU) und *Gibbula varia* (L.). Vereinzelt finden sich *Tricolia pulla* (L.) und *T. speciosa* (v. MÜHLFELD). Unter den sparophagen, gelegentlich auch karnivoren Arten sind *Columbella rustica*, *Pisania maculosa*, *Cantharus d'orbigny* (Tafel 6, Abb. 4), *Tritonalia aciculata*, *Muricidea blainvillei* und *Tritonalia edwardsi* vereinzelt anzutreffen. Zu den seltenen Formen zählen *Fusus*- und *Mitra*-Arten, *Pusia tricolor* (GMELIN), sowie *Murex trunculus* L.; *Conus ventricosus* ist stets vertreten.

In einem, mit Epiphyten stark durchwachsenen *Cystoseira*-Mischbestand fanden sich nach quantitativen Aufsammlungen durchschnittlich 7-8 Ind. von *Bittium reticulatum*, 3-5 Ind. von *Rissoa variabilis* (Tafel 6, Abb. 3), 2-3 Ind. von *Alvania cimex*, 1-2 Ind. von *Cantharidus*-Arten, 1-2 Ind. von *Columbella rustica*, 1-2 Ind. von *Conus ventricosus* und 1 Ind. von *Tritonalia aciculata* auf je 1/16 m<sup>2</sup> besammelter Fläche. Die übrigen, vorher genannten Arten traten nur sporadisch und nicht in jeder Probe auf. Die durchschnittliche Individuendichte betrug für Mollusken 25-26 Ind./1/16 m<sup>2</sup> *Cystoseira*-Büschel, davon ca. 23-24 Prosobranchia, der Rest Bivalvia, Placophora oder Opisthobranchia.

Die Bivalvia sind im hochwüchsigen Phytal spärlich vertreten. Der dichte Zwischenwuchs ermöglicht den Filtrierern nur kümmerliche Entwicklung. Nur kleine Arten,

die Spalträume ausnützen können, treten auf, wie *Musculus marmoratus* (FORBES) (Tafel 8, Abb. 3) und an Standorten in der Nähe des Eulitorals gelegentlich auch *Brachyodontes minimus* und in Spalten zwischen Kalkalgen und Epizoen *Beguinia calyculata*.

Die *Cystoseira*-Bestände des Phytals lassen sich nach Dominanz und Frequenz der gefundenen Mollusken wie folgt charakterisieren (Tafel 4):

Placophora: *Chiton olivaceus* - *Acanthochiton communis* -Assoz. auf dem krustigen Kalkalgenwuchs der Stämmchen.

Gastropoda: *Bittium reticulatum* - *Rissoa variabilis* - *Alvania cimex* -Assoz. mit *Cantharidus*-Arten, *Columbella rustica*, *Conus ventricosus*, *Tritonalia aciculata*, *Elysia viridis*, *Thuridilla splendida* u.a. Arten. Bei Hydrozoen-Zwischenwuchs mit Aeolidiacea, wie *Idulia coronata*, *Flabellina affinis*, *Calmella cavolini*, *Coryphella lineata*, *Trinchesia foliata*, *Favorinus branchialis*, *Facelina drummondi*, *Hervia peregrina* und *Spurilla neapolitana*.

Bivalvia: *Musculus marmoratus*-*Brachyodontes minimus*-Assoz. mit *Beguinia calyculata*.

#### e) Anschüttungsböden (Tafel 5)

Auf den Anschüttungsböden, welche die primären Hartböden überlagern, lassen sich in der Nord-Adria bei Rovinj einerseits Mischböden, andererseits Sekundäre Hartböden unterscheiden.

Die Mischböden, die sich aus Schell, verschlammten Sand mit dazwischen aufwachsenden Sedentariern und Krustenalgen zusammensetzen, werden häufig durch das Überwiegen bestimmter Auf- und Zwischenwuchs-Sedentariern gekennzeichnet. Bei Rovinj finden sich - in Tiefen zwischen 20 und 30 m - Mischböden mit vorherrschendem Porifera-Bewuchs (vor allem *Geodia cydonium*, mit einem Dchm. bis 80 cm) und vorherrschendem Ascidia-Bewuchs (*Phallusia mamillata*, *Ascidia virginea*, *A. mentula*, *Aplidium conicum*, *Distoma adriaticum* u.a. Arten). Auf bestimmten Mischböden dominiert die Rotalge *Vidalia volubilis* in dichten Beständen. Selbstverständlich finden sich auch alle Übergänge zwischen den genannten Typen der Mischböden.

Auf den Geodia-Mischböden, z.B. NO der Insel Banjole in ca. 33 m Tiefe, bewirkt die rückläufige Küstenkonvektions-Strömung einen feinen Detritusstrom zum Meeresboden und begünstigt die Entwicklung sessiler Strudler und Filtrierer.

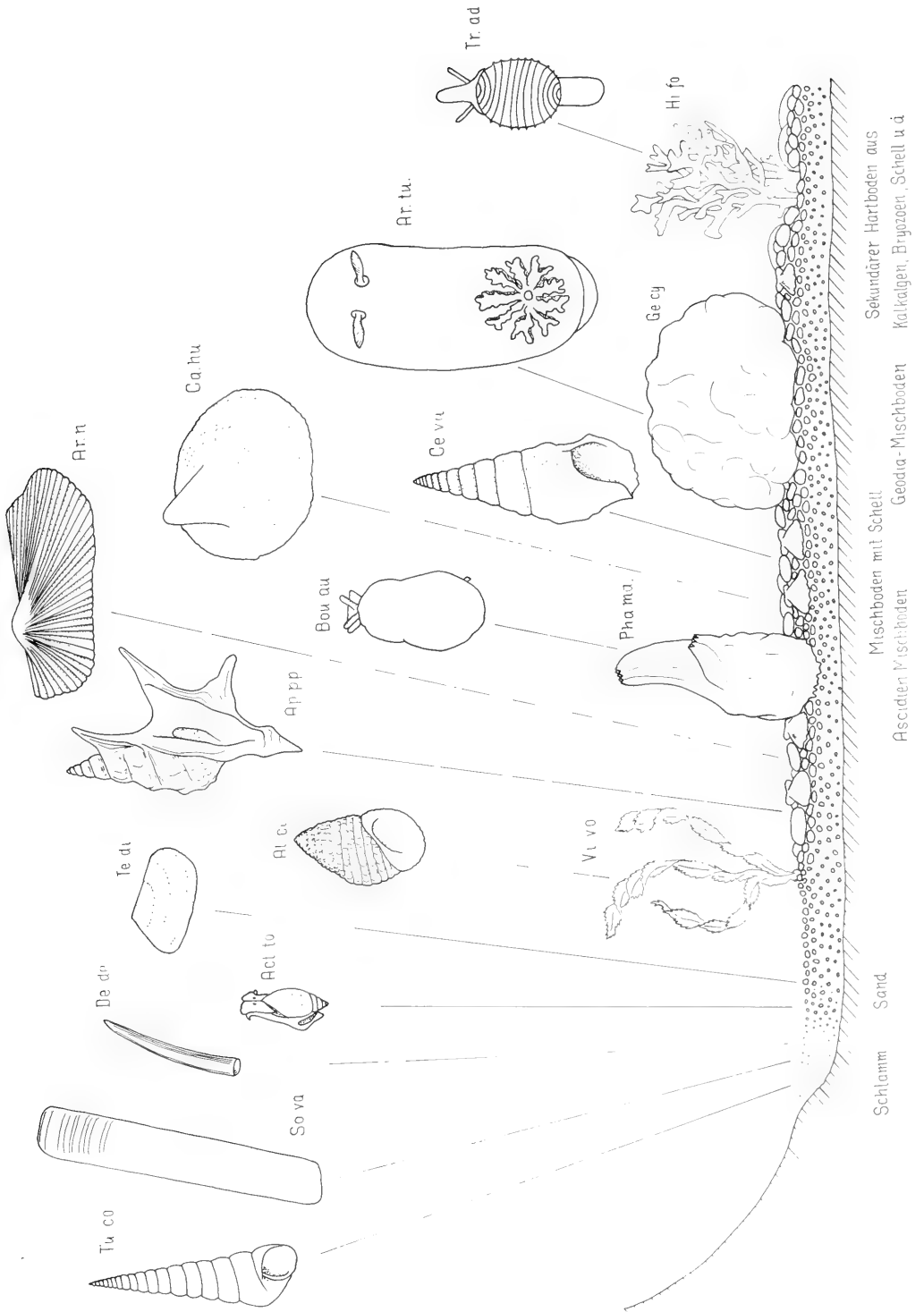
Die Aszidien-Mischböden finden sich dagegen mehr auf den leicht geneigten Anschüttungsflächen mit verschlammtem Sand, bei schwacher Strömung, z.B. N der Figarole-Inseln in ca. 25 m Tiefe. Beide Mischböden zeigen in Dredsnetz-Proben viel Schellmaterial, hauptsächlich von Muscheln aus Sedimentböden. Ihre Schale dient vielen Sedentariern als Anheftungsfläche. Zu den häufigsten Arten des Schells zählen *Pecten jacobaeus* L., *Chlamys*- und *Lima*-Arten, *Pitaria chione* (L.), *Venus verrucosa* (L.) und andere Veneridae, sowie Cardiacea. Gelegentlich treten die genannten Arten in den Fängen auch in lebenden Exemplaren auf. Im Sediment ist lebend stets *Cardium exiguum* GMELIN und *Nucula nucleus* (L.) vertreten. Unter den Gastropoden tritt hier von den grösseren Arten vor allem *Aporrhais pes pelecani* (L.) (Tafel 6, Abb. 5), sowie *Cerithium vulgatum* BRUGUIERE, seltener *Cassidaria echinophora* (L.) in Erscheinung. Die letztgenannten Arten finden sich auch auf grossen, mit Algen und Schwämmen bewachsenen Schellteilen, daneben *Murex trunculus* L., *Diodora italica* (DEFRANCE), *Astraea rugosa* (L.), *Calliostoma conulus* (L.) und *C. zizyphinus* (L.). Unter den sessilen Prosobranchia sind *Vermetus*-Arten, *Capulus hungaricus*, *Calyptrea sinensis* (L.), sowie *Crepidula*-Arten (Tafel 8, Abb. 1) stets auf Schell und

## TAFEL 5

Molluskenleitformen der Abschüttungsböden auf primären Hartböden (Schlamm-, Sand-, Misch- und Sekundäre Hartböden).

Pflanzen-, und Tiernamenabkürzungen: Tu.co. = *Turritella communis*; So.va. = *Solen vagina*; De.de. = *Dentalium dentale*; Act.to. = *Actaeon tornatilis*; Te.di. = *Tellina distorta*; Vi.vo. = *Vidalia volubilis*; Al.c. = *Alvania cimex*; Ap.p.p. = *Aporrhais pes pelecani*; Ar.n. = *Arca noae*; Bou.au. = *Bowieria aurantiaca*; Pha.ma. = *Phallusia mamillata*; Ca.hu. = *Capulus hungaricus*; Ar.tu. = *Archidoris tuberculata*; Ge.cy. = *Geodia cydonium*; Tr.ad. = *Trivia adriatica*; Hi.fo. = *Hippodiplosia foliacea*.





Kalkalgenkrusten zu finden. Auch Placophora treten hier regelmässig auf. Unter den Opisthobranchia treten die Doridaceae vor allem auf Schwammböden auf, am auffälligsten sind dabei *Archidoris tuberculata* CUVIER (Tafel 7, Abb. 3) und *Dendrodoris limbata* (CUVIER), während die Pleurobranchidae mehr Aszidiengründe bevorzugen, als die auffällig orangerote *Bowwiera aurantiaca* (RISSO).

Von den sessilen Bivalvia sind auf den Mischböden die *Arca*-Arten mit *Arca noae* L., *A. barbata* L. und *Arca lactea* (Tafel 8, Abb. 1) sowie *Modiolus barbatus* (L.) besonders häufig. Lebend treten aber auch, wie bereits erwähnt, die frei schwimmenden *Chlamys*- und *Lima*-Arten (Tafel 8, Abb. 4) auf.

Bei Überwiegen des Bewuchses durch die Rotalge *Vidalia volubilis*, z.B. im Val di Lone (S der Katharinen-Insel) in 14 m Tiefe, treten wie im Phytal des Felslitorals, aufwuchsäsende Arten in Erscheinung wie *Alvania cimex* und *Bittium reticulatum*, daneben finden sich wieder *Cerithium vulgatum* und *C. rupestre* sowie vereinzelt *Murex trunculus*. Von den Opisthobranchia tritt *Polycera quadrilineata* (MÜLLER) und *Glossodoris gracilis* (RAPP) auf, während im Sediment neben *Philine aperta* (L.) die sandbewohnenden Muscheln *Cardium exiguum* und *Nucula nucleus* stets in grösserer Individuenzahl gefunden werden. Auf dem Schell siedeln zwischen *Vidalia*-Büscheln *Arca noae*, *A. lactea* und *Modiolus barbatus*.

Zur Charakterisierung der Mischböden bei Rovinj lassen sich folgende Leitformen anführen (Tafel 5):

Geodia-, Ascidia-, Vidalia-Mischböden:

Placophora: Auf Kalkalgen (*Lithothamnium* u.a.):

*Chiton corallinus* - *Callochiton laevis* -Assoz.

Gastropoda: *Cerithium vulgatum* - *Aporrhais pes pelecani* - Assoz. mit *Murex trunculus*, *Diodora italica*, *Astraea rugosa*, *Vermetus*-Arten, *Calyptraea sinensis*, *Capulus hungaricus*, *Archidoris tuberculata*, *Dendrodoris limbata*, *Bowwiera aurantiaca* u.a. selteneren Arten.

Bivalvia: Im Schell leere Schalen von *Pecten jacobaeus*, *Chlamys*-, *Lima*-, *Cardium*-Arten, *Pitaria chione*, *Venus verrucosa* u.a. Veneridae.  
Im Sediment: *Cardium exiguum* - *Nucula nucleus*  
Assoz.

Auf Schell, Kalkalgen, Asziden u.dgl.:

*Arca noae* - *Modiolus barbatus* -Assoz.

Auf Vidalia volubilis:

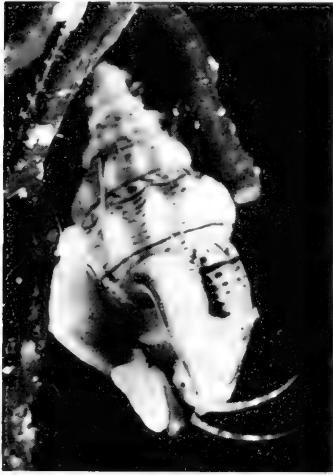
Gastropoda: *Alvania cimex* - *Bittium reticulatum* -Assoz. mit *Cerithium rupestre*, *C. vulgatum*, *Murex trunculus*, *Polycera quadrilineata*, *Glossodoris gracilis* u.a. selteneren Arten.

Die Sekundären Hartböden bilden sich auf Mischböden aus Schellmaterial, das durch Kalkalgen, Schwämme und aufwachsende, stückchenbildende, verkalkte Bryozoen, wie *Hippodiplosia*-, *Myriozoom*-, *Retepora*-, *Flustra*-u.a. Arten verbunden wird. Die Kalkalgen sind vorwiegend durch *Lithothamnium*-Arten repräsentiert, während sich der Schell hauptsächlich aus den leeren Schalen der bereits bei den Mischböden aufgezählten Muscheln zusammensetzt. Auch die Vergesellschaftungen der Mollusken zeigen eine ähnliche Zusammensetzung wie auf den Mischböden, wobei allerdings sessile Formen dominieren:

Gastropoda: *Capulus hungaricus* - *Calyptraea sinensis* - Assoz. mit *Murex trunculus*, *Diodora italica*, *Astraea rugosa*, *Cerithium vulgatum*, *Trivia*



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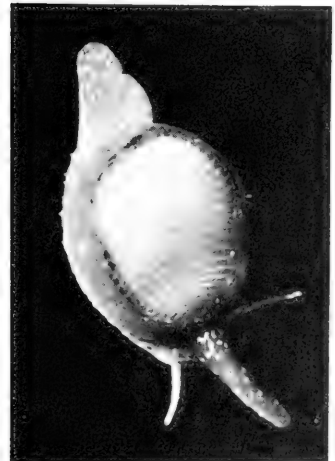
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## TAFEL 6

- ABB. 1. *Littorina neritoides* in Felsspalten des Supralitorals (Foto: M. Wimmer-Mizzaro).  
 ABB. 2. Verschiedene Grössenstufen von *Littorina neritoides* (Foto: M. Wimmer-Mizzaro).  
 ABB. 3. *Rissoa variabilis* (Foto: M. Wimmer-Mizzaro).  
 ABB. 4. *Cantharus d'orbigny* (Foto: H. Splechtna).  
 ABB. 5. *Aporrhais pes pelecani* (Foto: H. Splechtna).  
 ABB. 6. *Trivia adriatica* (Foto: M. Wimmer-Mizzaro).

*adriatica* (MONTEROSATO) (Tafel 6, Abb. 6),  
*Calliostoma*-Arten und *Archidoris tuberculata*.

Placophora und Bivalvia sind mit den gleichen Arten wie auf den Mischböden vertreten.

f) Reine Sedimentböden (Tafel 5)

Bei Rovinj finden sich reine Sedimentböden nur an wenigen Küstenflächen. Es handelt sich dabei um Seeböden, die durch Anschüttung entstanden sind. Man kann sie nach Zusammensetzung und Korngrößen der beteiligten Sedimente in Geröll-Schotter-Schell-Sand-Schlamm-Tonböden ordnen. Die oberen Schichten werden je nach ihrer Exposition und Korngröße durch die Wasserbewegungen mehr oder weniger umgeschichtet. Die Mollusken der Gerölle und Schotter (Rollblockfelder), sowie der Schellböden (Mischböden) wurden bereits besprochen. Die feineren Sedimentböden können bei Rovinj in Sand- und phytallose Schlamm- und Tonböden unterteilt werden.

Sandböden finden sich bei Rovinj zwischen dem Punta Corrente und der Roten Insel (Isola Rossa oder Crveni Otok), sowie NO der Konverzada-Insel in der Bucht von Kuvi. Diese Böden sind zum Teil von Seegrass-Beständen aus *Zostera marina* oder *Posidonia oceanica* bewachsen.

SALVINI-PLAWEN (1968) untersuchte die interstitielle Kleinfafauna der groben und mittelfeinen Sande bei Rovinj und fand in den Proben folgende Mollusken, deren Nachweis zum Grossteil neu für die Nord-Adria war:

Grobsande:

Placophora: *Lepidopleurus cancellatus* (SOWERBY),  
*L. intermedius* SALVINI-PLAWEN.

Gastropoda: Prosobranchia: *Caecum glabrum* (MONTAGU)  
Opisthobranchia: *Microhedyle milaschewitchii*  
(KOWALEVSKY), *M. glandulifera* (KOWALEVSKY),  
*Pseudovermis papillifera* KOWALEVSKY, *P. schulzi*  
MARCUS & MARCUS, *Hedylopsis spiculifera*  
(KOWALEVSKY), *Philinoglossa helgolandica*  
HERTLING, *Tergipes despectus* (JOHNSTON),  
*Embletonia pulchra* (ALDER & HANCOCK).

Mittelfeine Sande:

Gastropoda: Opisthobranchia: *Microhedyle glandulifera* (KOWALEVSKY),  
*M. lactea* (HERTLING).

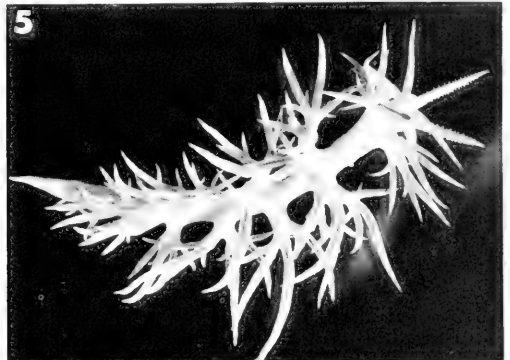
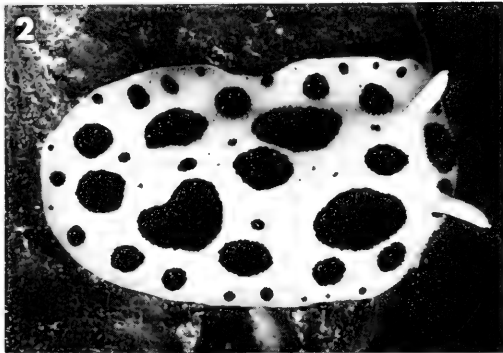
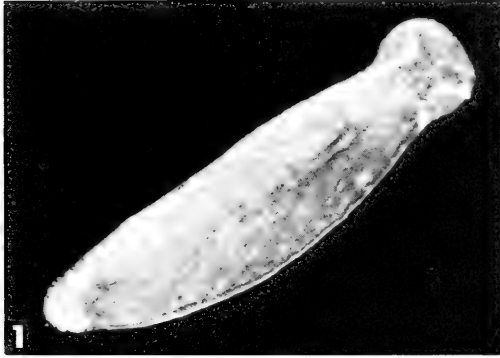
In der makroskopischen Molluskenfauna der Sandböden dominieren die sandbohrenden Bivalvia, Scaphopoda, sowie sandgrabenden Prosobranchia, wie räuberische *Natica*- und saprophage *Nassa*-Arten, sowie grabende Cephalaspidea unter den Opisthobranchia (Tafel 5):

Gastropoda: Prosobranchia: *Natica millepunctata* LAM. -  
*Nassa mutabilis* (L.) -Assoz. mit *Polynices guillemini* (PAYRAUDEAU), *Nassa neritea* (L.).  
u. selteneren Arten.

Opisthobranchia: *Actaeon tornatilis* (L.) -  
*Bulla striata*- Assoz. mit *Philine aperta*,  
*Haminea hydatis* (L.), *Retusa*-Arten, *Scaphander lignarius* (L.), *Aglaja depicta* RENIER u.a.  
Cephalaspidea.

Scaphopoda: *Dentalium dentale* L. - *Dentalium vulgare*  
DA COSTA -Assoz.

Bivalvia: *Tellina distorta* (POLI) (Tafel 8, Abb. 5) -  
*Divaricella divaricata* (L.) -Assoz. mit *Solen*



## TAFEL 7

- ABB. 1. *Bosellia mimetica* (Foto: M. Wimmer-Mizzaro).  
 ABB. 2. *Peltodoris atromaculata* (Foto: M. Wimmer-Mizzaro).  
 ABB. 3. *Archidoris tuberculata* (Foto: M. Wimmer-Mizzaro).  
 ABB. 4. *Thuridilla hopei* (Foto: M. Wimmer-Mizzaro).  
 ABB. 5. *Flabellina affinis* (Foto: M. Wimmer-Mizzaro).

*vagina* L., *Pinna nobilis* L. (meist zwischen Seegräs-Beständen!), *Chlamys*-, *Cardium*-Arten (darunter *Cardium exiguum*, *C. tuberculatum*), *Venus gallina* L., *Pitaria*-, *Venerupis*-Arten, *Maetra stultorum* (L.), *Donax trunculus* L., *Psammobia depressa* (PENNANT), *Solenocurtus strigillatus* (L.), *Arcopagia balaustina* (L.), *Gastrana fragilis* (L.), *Macoma tenuis* (DA COSTA), *Angulus planatus* (L.), *A. incarnatus* (L.), *Pharus legumen* (L.), *Ensis ensis* (L.) und *E. siliqua* (L.).

Auf den Seegräsern dominieren unter den Mollusken wieder die aufwuchsäsenden Formen der Prosobranchia, wie Rissoacea, kleine Trochidae und *Bittium reticulatum*. In der Wurzelregion treten auch grössere Arten, wie *Cerithium rupestre*, *Columbella rustica* und *Conus mediterraneus* auf. Unter den Opisthobranchia ist auf den Seegräsblättern die winzige, flachgedrückte *Runcina coronata* (QUATREFAGES) sowie *Elysia viridis* anzutreffen. Bivalvia sind nur durch kleine, sessile Arten am und zwischen dem Kalkalgen- und flächigen Bryozoenaufwuchs der Wurzelregion vertreten, wie *Arca lactea* (Tafel 8, Abb. 1), *Modiolus barbatus*, *Brachyodontes minimus* und - eingeböhrt - *Gastrochaena dubia*.

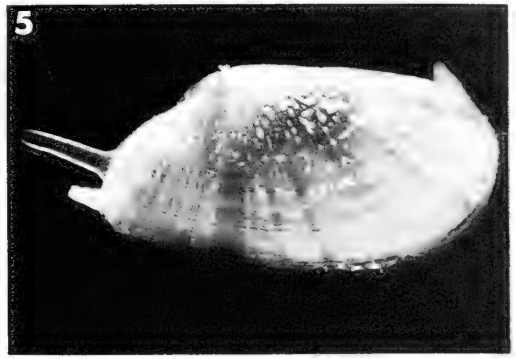
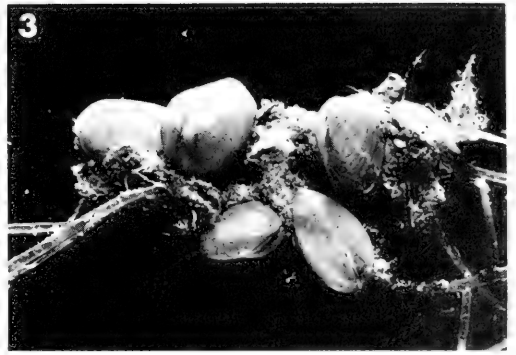
Gastropoda: *Alvania cimex* - *Bittium reticulatum* -Assoz. mit *Gibbula varia*, *Cantharidus striatus*, versch. Rissoacea, *Cerithium rupestre*, *Columbella rustica*, *Conus ventricosus*, *Runcina coronata*, *Elysia viridis*.

Bivalvia: *Arca lactea* - *Modiolus barbatus* -Assoz. mit vereinzelt *Brachyodontes minimus*, *Gastrochaena dubia*.

Phytallose Schlamm- und Tonböden sind bei Rovinj in der Bucht des Val di Bora, N des Institut za Biologiju Mora, sowie im Limski-Kanal ausgebildet. Während die erstgenannte Bucht eine Tiefe von ca. 18 m erreicht, beträgt sie im Limski-Kanal bei Sotto Castello bis 32 m. Unter den Prosobranchia dominieren schlammbohrende Arten, wie *Turritella communis* RISSO und *Turritella triplicata* (BROCCHI), *Natica*- und *Polynices*-Arten, *Aporrhais pes pelecani* (Tafel 6, Abb. 5) und *Nassa*-Arten. Opisthobranchia wurden bisher sehr selten gefunden und zwar ausschliesslich leere Schalen von Cephalaspidea. Die Scaphopoda zeigen mit *Dentalium*-Arten einen hohen Anteil in den Proben, ebenso die in Weichböden eingegrabenen Bivalvia, wie *Tellina*-Arten (Tafel 8, Abb. 5), *Venus casina* L., *Cardium paucicostatum* SOWERBY, *Aloidis gibba* (OLIVI), sowie die Protobranchia-Gattungen *Nucula* und *Leda*. Placophora fehlen den feinen Sedimentböden (Tafel 5):

Gastropoda: *Turritella* - *Aporrhais pes pelecani* -Assoz. mit *Natica*- und *Polynices*- und *Cythara*-Arten, *Strombiformis subulata* (DONOVAN), *Melanelia arcuata* (LEACH), *Chrysallida interstincta* (MONTAGU), *Eulimella acicula* (PHILIPPI), *Turbonilla lactea* (L.) und *Murex brandaris* L.

Scaphopoda: *Dentalium dentalium* - *D. panormitanum* -Assoz.  
Bivalvia: *Solen vagina* - *Cardium paucicostatum* - *Aloidis gibba* -Assoz. mit *Nucula nucleus*, *Leda fragilis* (CHEMNITZ), *Venus casina*, *Tellina*-Arten, *Abra alba* (WOOD), u.a. selteneren Arten.



## TAFEL 8

ABB. 1. *Arca lactea* mit *Crepidula* sp. aufsitzend (Foto: M. Wimmer-Mizzaro).

ABB. 2. *Gastrochaena dubia* im aufgeschlagenen Felsgestein des Eulitorals (Foto: M. Wimmer-Mizzaro)

ABB. 3. Gruppe von *Musculus marmoratus* an Algen sitzend (Foto: M. Wimmer-Mizzaro).

ABB. 4. *Lima inflata* (Foto: M. Wimmer-Mizzaro).

ABB. 5. *Tellina distorta* mit ausgestreckten Siphonen (Foto: M. Wimmer-Mizzaro).

## ZUSAMMENFASSUNG

Im Bereich des Felslitorals, sowie küstennaher Anschüttungsböden der istrianischen Westküste bei Rovinj wurden durch mehrere Jahre (1953-1967) qualitative und quantitative Aufsammlungen von Mollusken durchgeführt.

## 1. Supralitoral:

- a. Primärer Hartboden: *Littorina neritoides*-*Patella lusitanica*-Assoz.  
 b. Sand-Kiesboden: *Truncatella subcylindrica*-*Alexia myosotis*-Assoz.

## 2. Eulitoral:

## a. Primärer Hartboden:

Placophora: *Middendorfia caprearum*-*Chiton olivaceus*-Assoz.

Gastropoda: *Patella (lusitanica, coerulea)*-*Monodonta turbinata*-*Pisania maculosa*-Assoz. mit *Columbella rustica* und *Conus ventricosus*.

Bivalvia: *Brachyodontes minimus*-*Mytilus galloprovincialis*-*Ostrea edulis*-*Chama (gryphoides, gryphina)*-Assoz. im Epilithion und *Gastrochaena dubia*-*Lithophaga lithophaga*-Assoz. im Endolithion, vereinzelt *Petricola lithophaga*.

## 3. Sublitoral:

## a. Primärer Hartboden (Felslitoral):

## Epilithion:

Gastropoda: *Columbella rustica*-*Pisania maculosa*-*Cerithium rupestre*-Assoz. mit vereinzelt *Diodora graeca*, *Cantharus d'orbigny*, u.a. selteneren Arten.

Bivalvia: *Mytilus galloprovincialis*-*Ostrea edulis*-Assoz., mit *Chama*-Arten.

## Endolithion:

Bivalvia: *Lithophaga lithophaga*-*Gastrochaena dubia*-Assoz. mit *Petricola lithophaga*.

## b. Höhlen:

Höhleingänge, Nordexponierte Überhänge: Auf *Halimeda tuna*: *Bosellia mimetica*; Auf *Peyssonnelia squamaria* und krustenförmigen Kalkalgen (z.B. *Pseudolithophyllum* sp.): *Callochiton laevis*-*Chiton corallinus*-Assoz.

Höhlenwände im phytallosen Bereich:

## Epilithion:

Gastropoda: *Muricidea blainvillei*-*Tritonalia edwardsi*-*Cantharus d'orbigny*-Assoz. mit *Vermetus*-Arten.

Bivalvia: *Ostrea edulis*-*Arca lactea*-Assoz.

Auf Drusen des Schwammes *Petrosia ficiformis*:

Gastropoda: *Peltodoris atromaculata*

## Endolithion:

Bivalvia: *Lithophaga lithophaga*-*Gastrochaena dubia*-Assoz. mit *Petricola lithophaga*, *Begünea calyculata*.

## c. Rollblöcke:

## Epilithion:

Placophora: *Chiton olivaceus* - *Acanthochiton (communis, fascicularis)* - *Lepidopleurus cajetanus*-Assoz.

Gastropoda: *Haliotis lamellosa*-*Diodora*-*Emarginula*-Assoz. mit *Capulus hungaricus*, u. kleineren vagilen Arten (kleine Trochidae, Muricidae).

Bivalvia: *Anomia ephippium*-*Chama (gryphoides, gryphina)*-Assoz.

Endolithion: Wie im freien Felslitoral.

d. Phytalbewuchs (Strauchalgen der Gattung *Cystoseira*):

Placophora: Am krustigen Kalkalgenaufwuchs der Stämmchen (z.B. *Fosliella* sp.): *Chiton olivaceus*-*Acanthochiton*-Assoz.

Gastropoda: *Bittium reticulatum*-*Rissoa variabilis*-*Alvania cimex*-Assoz. mit *Cantharidus*-, *Gibbula*-Arten, Rissoidae, *Columbella rustica*, *Conus ventricosus*, *Tritonalia aciculata*, *Elysia viridis*, *Thuridilla splendida*, und bei starkem Hydrozoenzwischenwuchs mit versch. Aeolidiacea.

Bivalvia: *Musculus marmoratus*-*Brachyodontes minimus*-Assoz. mit vereinzelt *Begünea calyculata*.

## e. Anschüttungsböden:

*Geodia*-, *Ascidia*-, *Vidalia volubilis*-Mischböden:

Placophora: Auf Schell und Kalkalgen (*Lithothamnium*): *Chiton corallinus*-*Callochiton laevis*-Assoz.

Gastropoda: *Cerithium vulgatum*-*Aporrhais pes pelecani*-Assoz. mit *Murex trunculus*, *Diodora italica*, *Astraea rugosa*, *Vermetus*-Arten, *Calyptrea sinensis*, *Capulus hungaricus*, *Archidoris tuberculata*, *Dendrodoris limbata*, *Bowieria aurantiaca* u.a. Arten.

Bivalvia: Schellmaterial: Leere Schalen von *Pecten jacobaeus*, *Chlamys*-, *Lima*-, *Cardium*-, *Veneriden*-Arten, *Pitaria chione*, *Venus verrucosa*.



Im Sediment: *Cardium exiguum*-*Nucula nucleus*-Assoz.

Auf den Büscheln von *Vidalia volubilis*:

Gastropoda: *Alvania cimex*-*Cerithium vulgatum*-Assoz. mit *Cerithium rupestre*, *Murex trunculus*, *Polycera quadrilineata*, *Glossodoris gracilis* u. selteneren Arten.

Sekundäre Hartböden:

Placophora und Bivalvia: Auf Kalkalgen, Schell, sowie im Sediment die gleichen Arten wie auf den Mischböden.

Gastropoda: *Capulus hungaricus*-*Calyptrea sinensis*-Assoz. mit *Murex trunculus*, *Astraea rugosa*, *Cerithium vulgatum*, *Trivia adriatica*, *Calliostoma*-Arten, *Archidoris tuberculata* u. a. Arten.

f. Reine Sedimentböden:

Sandböden:

Mikrofauna der Grobsande:

Placophora: *Lepidopleurus cancellatus*-*L. intermedius*-Assoz.

Gastropoda: Prosobranchia: *Caecum glabrum*

Opisthobranchia: *Microhedyle* (mit *M. milaschewitchii*, *M. glandulifera*)-*Pseudovermis* (mit *P. papillifera*, *P. schulzi*)-*Hedylopsis spiculifera*-*Philinoglossa helgolandica*-Assoz. mit *Tergipes despectus*, *Embletonia pulchra*.

Mikrofauna der mittelfeinen Sande:

Opisthobranchia: *Microhedyle glandulifera*-*Microhedyle lactea*-Assoz.

Makrofauna der Sandböden:

Gastropoda: Prosobranchia: *Natica millepunctata*-*Nassa mutabilis*-Assoz. mit *Polynices*-Arten.

Opisthobranchia: *Actaeon tomatis*-*Bullaria striata*-Assoz. mit *Philine aperta* und mehreren selteneren Cephalaspidea.

Scaphopoda: *Dentalium dentale*-*D. vulgare*-Assoz.

Bivalvia: *Tellina distorta*-*Divaricella divaricata*-Assoz. mit *Solen vagina*, *Pinna nobilis*, *Chlamys*-, *Cardium*-, *Venus*-, *Macra-Donax*-, *Angulus*-, *Tellina*-Arten.

Seegräser (*Posidonia*, *Zostera*):

Gastropoda: *Alvania cimex*-*Bittium reticulatum*-Assoz. mit *Gibbula varia*, *Cantharidus striatus*, *Cerithium*-Arten, versch. Rissoidae, *Columbella rustica*, *Conus ventricosus*, *Runcina coronata*, *Elysia viridis* u. a. Arten.

Bivalvia: *Arca lactea*-*Modiolus barbatus*-Assoz.

Phytallose Schlamm- und Tonböden:

Gastropoden: *Turritella* (mit *T. triplicata*, *T. communis*)-*Aporrhais pes pelecani*-Assoz. mit *Natica millepunctata*, *Polynices*-, *Cythara*-, *Melanella*-, *Chrysallida*-, *Eulimella*-, und *Turbonilla*-Arten, *Murex brandaris*.

Scaphopoda: *Dentalium dentale*-*D. panormitanum*-Assoz.

Bivalvia: *Solen vagina*-*Cardium paucicostatum*-*Alويدis gibba*-Assoz. mit *Nucula*-, *Leda*-, *Tellina*-Arten, *Venus casina*, *Abra alba* u. a. Arten.

## LITERATURVERZEICHNIS

- BRUSINA, S., 1896, Faunistisches von der Adriaexkursion der Yacht "Margita." *Compt. Rend. Seances 3. Congr. Int. d. Zool. Leyden*.
- CARUS, V., 1889/93, *Prodromus Faunae Mediterranea*. Stuttgart, 2: 61-459.
- COEN, G., 1937, Nuovo saggio di una sylloge molluscorum Adriaticorum. *R. Com. Talassogr. Ital. Mem.*, 290.
- GRAEFFE, E., 1903, Übersicht über die Fauna des Golfes von Triest, nebst Notizen über Vorkommen, Lebensweise, Erscheinungs- und Laichzeiten der einzelnen Arten. *Arb. Zool. Inst. Wien-Triest*, 14: 88-136.
- KÜHNELT, W., 1930, Bohrmuschelstudien I, *Palaeobiologica*, 3: 53-91.
- KÜHNELT, W., 1933, Bohrmuschelstudien II, *Palaeobiologica*, 5: 371-407.
- KÜHNELT, W., 1938, Beziehungen zwischen Kalkstoffwechsel und Atmung bei Mollusken der Meeresküste. *Zool. Anz.*, 124: 182-190.
- KÜHNELT, W., 1947, Bohrmuschelstudien III, *Palaeobiologica*, 7: 428-447.
- KÜHNELT, W., 1950, Contributions à la connaissance de l'endofauna des sols marins durs. *Coll. Int. Centre Nat. Rech. Scient. Ecol. Paris. Ann. Biol.*, 27: 281-291.
- LELOUP, E. & VOLZ, P., 1938, Die Chitonen der Adria. *Thalassia*, Rovigno, 2.

- LORENZ, J., 1863, *Physikalische Verhältnisse und Verteilung der Organismen im Quarnerischen Golfe*. Wien, 379 p.
- ODHNER, N. H., 1914, Beiträge zur Kenntnis der marinen Molluskenfauna von Rovigno in Istrien. *Zool. Anz.*, 44: 156-170.
- RIEDL, R., 1953, Quantitative ökologische Methoden mariner Turbellarienforschung. *Österr. Zool. Ztschr.*, 4: 108-145.
- RIEDL, R., 1954, Unterwasserforschung im Mittelmeer. Österreichische Tyrrhenia-Expedition 1952. *Naturw. Rundschau*, Heft 2: 65-71.
- RIEDL, R., 1963, *Fauna und Flora der Adria*. Hamburg/Berlin, 640 p.
- RIEDL, R., 1966, *Biologie der Meereshöhlen*. Hamburg/Berlin, 636 p.
- SALVINI-PLAWEN, L., 1968, Neue Formen im marinen Mesopsammon: Kamptozoa und Aculifera (nebst der für die Adria neuen Sandformen). *Ann. Naturhist. Mus. Wien*, 72: 231-272.
- STARMÜHLNER, F., 1955a, Zur Molluskenfauna des Felslitorals und submariner Höhlen am Capo di Sorrento (1. Teil). *Ergebnisse der Österreichischen Tyrrhenia-Expedition 1952, Teil IV. Österr. Zool. Ztschr.*, 6: 147-249.
- STARMÜHLNER, F., 1955b, Zur Molluskenfauna des Felslitorals und submariner Höhlen am Capo di Sorrento (2. Teil). *Ergebnisse der Österreichischen Tyrrhenia-Expedition 1952, Teil IV. Österr. Zool. Ztschr.*, 6: 631-713.
- STARMÜHLNER, F., 1968, Investigations about the Mollusc-fauna in submarine caves. *Symp. Moll. Cochín (India) Part I*: 137-163.
- STOSSICH, A., 1865, *Enumerazione dei molluschi del Golfo di Trieste*. Triest.
- VATOVA, A., 1928, Compendio della flora e fauna del mare Adriatico presso Rovigno con la distribuzione geogr. delle specie bentoniche. *R. Com. Talass. Ital. Mem.*, 143.
- WEINKAUFF, M. C., 1867/68, *Konchylien des Mittelmeeres, ihre geographische und geologische Verbreitung*. Kassel, 2 Bde., 512 u. 301 p.
- WIMMER, A., 1883, Fundorte und Tiefenvorkommen einiger adriatischer Conchylien. *Verh. d. k. k. Zool. - Bot. Ges.*, 32: 255-264.
- ZIMMERMANN, H., 1907, Tierwelt am Strande der blauen Adria. *Ztschr. Naturw. Halle.*, 79.

THE FLUID DYNAMICS OF MOLLUSCAN LOCOMOTION

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ABSTRACT

The importance of hydraulic mechanisms in molluscan locomotion is discussed in terms of examples from the three major Classes, namely *Patella*, *Ensis* and *Sepia*. In both the gastropods and the bivalves a double fluid-muscle system of internal (blood) and external (water) fluids is utilised while in jet propulsion the cephalopods use only the external fluid. Experiments with *Patella* have shown that the blood in the haemocoelic spaces near the sole of the foot and water, together with mucus, beneath the sole are both concerned with the progression of retrograde pedal locomotory waves. The passage of the latter correspond to negative pressures or suction beneath the foot. In *Ensis* high pressure pulses (120 cm of water) are generated equally and simultaneously in the pedal haemocoel and mantle cavity during burrowing by means of adduction of the valves, the blood causing dilation of the foot and the water from the mantle cavity a jet which facilitates movement into the sand. In the cephalopods high pressure (200 cm in *Sepia*) is developed in the mantle cavity for the purpose of swimming. The possibility of a corresponding pressure pulse within the body, as in bivalves, and a consequent surge of blood passing to the head is envisaged as being incompatible with the high neural organization of this group. It is suggested that the extensive coelom in cephalopods may in part diminish this effect.

INTRODUCTION

Until relatively recently little was known about the hydraulic mechanisms of molluscs. Studies using manometers and the traditional techniques of functional anatomy by Trueman (1954) on *Mya* and by Chapman and Newell (1956) on the latter and *Scrobicularia* demonstrated the relationship between fluid pressures and siphonal movements. More modern techniques of continuously recording pressure changes and body movements by means of transducers coupled to multichannel pen recorders (Hoggarth & Trueman, 1967) have further elucidated fluid-muscle systems in the three major molluscan groups.

Many soft-bodied animals have developed a capacious fluid skeleton which acts as a hydraulic organ. It is well known, e.g. Chapman, 1958, that a fluid-muscle system must operate with a constant volume of relatively incompressible, non-viscous fluid and generally has two sets of muscles, for example, longitudinal and circular muscles, acting in mutual antagonism. The clam, *Mya*, is one of the best examples in the Mollusca for with the siphonal and pedal apertures closed the mantle cavity is virtually watertight and the water enclosed acts together with the blood in the haemocoel as the fluid of an antagonistic muscle system. Through the agency of these fluids, from which pressure pulses may be recorded (Trueman, 1966), adduction causes siphonal extension and conversely siphonal retraction produces an increase in gape of the valves.

This paper will be restricted to a discussion of aspects of locomotion in Gastropoda, Bivalvia and Cephalopoda, one example being taken from each group. Previous work has conveniently been summarised in all Classes by Morton (1964), by Gray (1968) in respect of gastropods and by Trueman (1968b) concerning the burrowing activity of bivalves.

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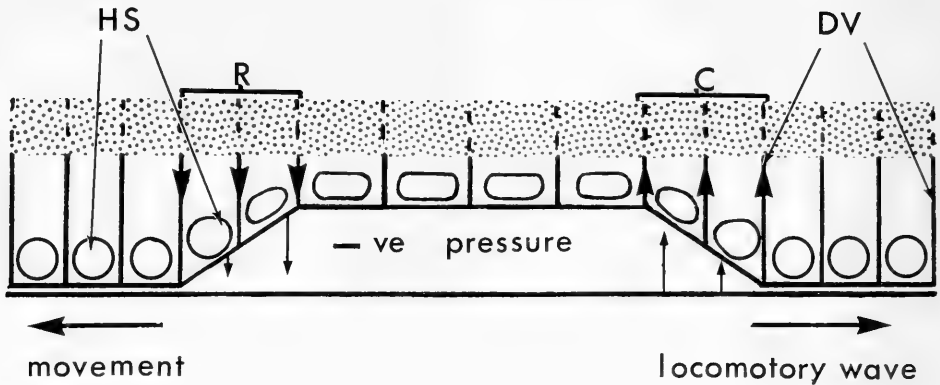


FIG. 1. Diagram of a parasagittal section of the foot of *Patella* indicating the factors involved in the progression of a retrograde locomotory wave (locomotory wave, arrow) and the forward movement of the foot (movement, arrow). Haemocoelic spaces (HS) are distorted and a negative pressure is exerted beneath the foot by the contraction (C) of the dorso-ventral muscles (DV). This suction draws the epithelial sole of the foot down when these muscles relax (R). The stippled dorsal region represents a thick layer of muscle fibres, many of which lie transversely across the foot, immediately above the haemocoelic spaces.

#### THE DYNAMICS OF LOCOMOTION

##### (a) *Patella vulgata* L.

*Patella* is adapted for life on a hard substratum having a foot which serves both for locomotion and adhesion. In this genus separate locomotory waves pass down each lateral half of the sole of the foot from the anterior margin. Such locomotory waves are described as being ditaxic and retrograde.

The anatomical features of the foot concerned with locomotion are the superficial epithelium, the haemocoelic spaces and the musculature. The latter principally consists of dorso-ventral or shell muscles, passing from the sole of the foot to the shell and the transverse muscles (Fig. 1). According to Jones (1968) there is no longitudinal muscle near the sole of the foot although some fibres lie in the dorsal pedal region, running through the transverse fibres. Blood occupies numerous spherical cavities (of about  $10 \mu$  in diameter) of the diffuse pedal haemocoel which is situated ventrally in close proximity to the epithelium of the sole (Fig. 1). The passage of each locomotory wave involves the contraction (C) of the dorso-ventral muscles so as to lift the sole off the substrate. The epithelium is stretched, partially by the tension of these muscles, as is indicated by the increased interval between the dorso-ventral muscle fibres in Fig. 1. The sole shortens to its original length as it is lowered at the end of the step (R). This process results in forward movement as the raised region of the sole passes across the foot as a retrograde locomotory wave. Analysis of cine film in which the sole of the foot was marked by shallow transverse incisions has allowed these movements to be demonstrated (Jones, 1968). This lengthening of the part of the foot not attached to the ground is exactly paralleled by the mechanism employed by the earthworm in retrograde locomotion (Gray, 1968), for in worms the segments form anchorages or *points d'appui* at their shortest length and are moved forwards at segmental elongation.

It was not possible to record pressures from the pedal haemocoel, because of the small size of the blood spaces, but it is reasonable to assume that as the foot is raised each part is somewhat compressed against the musculature above, so becoming deformed (Fig. 1). Increase in the lateral dimensions of the foot is prevented by the transverse musculature and the deformation of the haemocoel results in elongation

of the epithelial surface. A colleague, Dr. H. D. Jones, has been able to show negative pressures of as much as 15 cm of water beneath each pedal wave caused by the contraction of the dorso-ventral muscles raising the epithelium so as to produce a suction-like effect on the water and mucus beneath the foot. These muscles contract at the leading edge of the pedal wave (Fig. 1, C) and, by means of the negative pressure produced, antagonise the muscles at the lagging edge so that as these relax (R), the sole is drawn down into the substrate. The progression of the pedal wave in *Patella* is thus brought about by the antagonism of muscles using both internal and external hydraulic systems and the presence of longitudinal muscle fibres adjacent to the sole is not required for locomotion except possibly at the trailing edge of the foot.

(b) *Ensis arcuatus* (Jeffreys)

The locomotory activity of burrowing bivalves follows a common pattern throughout the group (Trueman, 1968b) and, although much modified in form, the rapidly burrowing *Ensis* is a good example. The burrowing process consists of cyclically repeated movements involving two principal stages: a, probing movements of the foot with the shell held in position by the valves pressing against the sand (penetration or shell anchor); and b, adduction of the valves followed immediately by pedal retraction, the foot being dilated and held in the sand by the terminal or pedal anchor (Trueman, 1967; 1968a). The fluid-muscle system is a double system consisting of two separate fluid filled chambers, the mantle cavity and the haemocoel. During pedal extension and probing, however, only the latter participates, the shape of the foot being changed by antagonism between the retractor muscles and the transverse and protractor muscles. The blood is the fluid of this system in which relatively low pressures, rising to a maximum of 10 cm of water in *Ensis*, are involved. Keber's valve prevents the outflow of blood and ensures that the foot operates at a nearly constant volume.

Adduction of the valves affects both internal and external fluids simultaneously and equally, pressure pulses of up to 120 cm of water and 0.5 sec. duration being recorded (Fig. 2a). In the haemocoel this pressure causes pedal dilation which ensures a secure anchorage of the foot so that at pedal retraction the closed shell is drawn down. The pressure in the mantle cavity produces powerful jets of water which assist movement of the shell by loosening the adjacent sand. The hinged shell thus acts as the basis of a hydraulic system by means of which the strength of adduction may be used in digging.

During adduction the valves of *Ensis* pass through  $20^\circ$ , a relatively wide angle compared with other burrowing bivalves, e.g. *Mactra corallina*,  $8^\circ$ , and represents a reduction in the volume enclosed between the valves of about 20%. Of this 1/3 rd may be accounted for by the passage of blood distally so as to dilate the foot, and 2/3 rds as water ejected from the mantle cavity. In consequence of extensive mantle fusion (Owen, 1959) and closure of the siphons the water is restricted into powerful jets emerging through the pedal and fourth pallial apertures.

(c) *Sepia officinalis* (L.)

It has long been recognised that contraction of the mantle muscles of a squid or cuttlefish produces a high pressure in the mantle cavity, a jet of water from the funnel and movement of the animal in the opposite direction (Morton, 1964). Recordings from the mantle cavity of *Sepia* (200-250 g. wet weight) showed a regular fluctuation of pressure associated with respiration of about 44/min. with an amplitude of less than 1 cm of water (Fig. 2c). This rhythm is broken by high pressure pulses produced during jet swimming. Visual observations made during the respiratory rhythm indicated that the funnel was closed by a valvular flap as the pressure rose and that this opened as the pressure fell allowing water to flow out. At the same time the inhalent

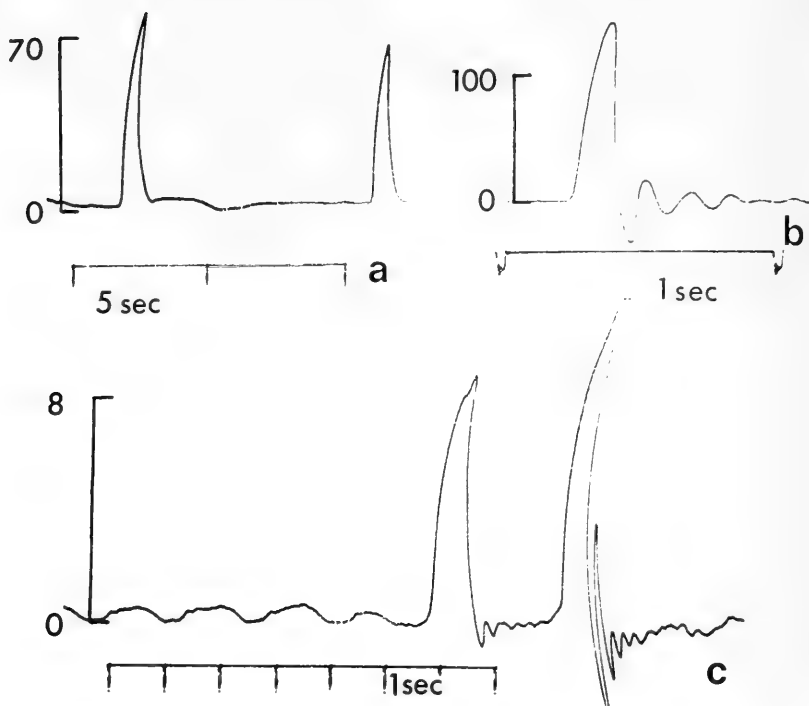


FIG. 2. Pressure recordings (cm of water) obtained from a, the pedal haemocoel of *Ensis arcuatus* during burrowing; b & c, the mantle cavity of *Sepia officinalis*. a, pressure pulse generated by adduction of the valves; b, pulse produced by mantle contraction during jet swimming; c, respiratory pressure fluctuations followed by two swimming pulses of increasing amplitude and decreasing pulse width which interrupt the respiratory rhythm. Oscillations occurring after the pressure pulses in b & c are due to the effect of sudden reduction of pressure on the recording instrument.

channel is effectively blocked by the outer collar of the funnel locking into the cartilaginous sockets of the mantle. This mechanism ensures that water passes out through the funnel and is particularly effective at the higher pressures produced during swimming. Recordings of the pressure generated in the mantle cavity of *Sepia* during jetting showed pulses of up to 200 cm of water with a duration of 150 msec. at 3/4 amplitude (Fig. 2b). Such a maximal pressure pulse has a steep leading edge and is brought about by a giant fibre response. Pulses of smaller amplitude show a slower rise in pressure and longer duration (Fig. 2c), possibly due to the contraction of the mantle under the control of small diameter nerve fibres as Young (1938) suggested in respect of contractions of the mantle of *Loligo*.

Data derived from recordings has allowed some assessment of the motor performance of *Sepia*, *Loligo*, *Eledone* and *Octopus* and a discussion of the dynamics of their propulsion (Trueman & Packard, 1968). The momentum (mass x velocity) of an animal during jet propulsion is shown to be dependent on the volume and velocity of the jet (Packard, 1966). Thus maximum swimming velocities depend on the expulsion of as large a volume of water as possible from the mantle cavity. High velocity is attained by the restriction of the exhalent current to a narrow funnel and by pulses of high pressure but of short duration. Jetting cannot be a continuous process in the cephalopods because of the need to refill the mantle cavity. This occurs between pulses by the expansion of the mantle brought about by contraction of the radial muscles (Wilson, 1960).

## DISCUSSION

Hydraulic systems have been developed in the three principal groups of molluscs for locomotory purposes. Extension of the foot in gastropods and bivalves is brought about by relatively low internal pressures and apart from jet propulsion in the cephalopods high pressures only occur in the body cavities of animals that burrow. Similarly shaped pressure pulses with rapid rise time are produced in the bodies of both bivalves and cephalopods but greater amplitude and shorter duration is characteristic of the latter group.

The extent of the haemocoel in the foot is at its maximum in those molluscs that burrow in which it functions as a hydraulic organ for the transference of the force of muscular contraction from one part of the body to another. Thus the pedal haemocoel of bivalves shows a larger cavity in *Ensis*, a genus notable for powerful digging movements, than in more sedentary bivalves, e.g. *Anodonta*. Similarly the foot of the burrowing gastropod *Natica* is greatly expanded by fluid-filled cavities in comparison to that of *Patella* (Trueman, 1968c).

In all the molluscs discussed here the external fluid is exploited as an integral part of the hydraulic mechanism of locomotion in addition to the body fluid in the haemocoel. Both the Cephalopoda and the Bivalvia utilise the water contained within the mantle cavity for locomotory purposes the pressure being generated by the pallial muscles or, in the latter, their derivative, the adductor muscles (Yonge, 1957), the jet produced in the Pectinidae by the flapping of the valves being used in swimming. In both Classes advantage is to be gained by increased mantle capacity, for example, by the relatively wide gape of the valves in *Ensis* and *Chlamys*, and by the restriction in the size of the mantle openings so as to produce a more intense jet, as in the funnel of *Sepia*.

In burrowing bivalves the flow of blood into the foot at adduction serves a locomotory function; but in the cephalopods the production of a jet must cause a surge of blood into the large haemocoelic channels in the head, possibly affecting the focussing of the eyes (Boycott & Young, 1956), which is scarcely compatible with the high neural organisation of this group. Normal respiratory pressures in *Sepia* can have little effect on blood flow but Johansen & Martin (1962) demonstrated that in the large *Octopus dofleini* such pressures affect the circulatory system. The principal disadvantage of jet propulsion would thus appear to be the flow of blood to the head caused by the pressure pulses. The extensive development of the coelom adjacent to the mantle cavity may well function to restrict the surge of blood to the vena cava, effectively buffering the arterial circulation from the effect of high pressure.

## ACKNOWLEDGMENTS

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## REFERENCES

- BOYCOTT, B. B. & YOUNG, J. Z., 1956, The subpedunculate body and nerve and other organs associated with the optic tract of cephalopods. *In*: Bertil Hanström: zoological papers in honour of his sixty-fifth birthday, p. 76-105. Wingstrand, K. G. (Ed.). Lund, Zoological Inst.
- CHAPMAN, G., 1958, The hydrostatic skeleton in the invertebrates. *Biol. Rev.*, 33: 338-371.

- CHAPMAN, G. & NEWELL, G. E., 1956, The role of the body fluid in relation to movement in soft bodied invertebrates. II. The extension of siphons of *Mya arenaria* L. and *Scrobicularia plana* (da Costa). *Proc. roy. Soc. B*, 145: 564-580.
- GRAY, J., 1968, Animal locomotion. London, Weidenfeld & Nicolson.
- HOGGARTH, K. R. & TRUEMAN, E. R., 1967, Techniques for recording the activity of aquatic invertebrates. *Nature*, Lond., 213: 1050-1051.
- JOHANSEN, K. & MARTIN, A. W., 1962, Circulation in the cephalopod, *Octopus dofleini*. *Comp. Biochem. Physiol.*, 5: 161-176.
- JONES, H. D., 1968, Aspects of the physiology of *Patella vulgata* L. Ph.D. thesis, University of Hull.
- MORTON, J. E., 1964, Locomotion. In: Physiology of the Mollusca, Vol. I, p. 383-423. Wilbur, K. M. & Yonge, C. M. (Eds.). New York, Academic Press.
- OWEN, G., 1959, Observations on the Solenacea with reasons for excluding the family Glaucomyidae. *Phil. Trans. B*, 242: 59-97.
- PACKARD, A., 1966, Operational convergence between cephalopods and fish: an exercise in functional anatomy. *Archo. zool. Ital.*, 51: 523-542.
- TRUEMAN, E. R., 1954, The mechanism of the opening of the valves of burrowing lamellibranch, *Mya arenaria*. *J. exp. Biol.* 31: 291-305.
- TRUEMAN, E. R., 1966, Fluid dynamics of the bivalve molluscs *Mya* and *Margaritifera*. *J. exp. Biol.*, 45: 369-382.
- TRUEMAN, E. R., 1967, The dynamics of burrowing in *Ensis* (Bivalvia). *Proc. roy. Soc. B*, 166: 459-476.
- TRUEMAN, E. R., 1968a, Burrowing habit and the early evolution of body cavities. *Nature*, Lond., 218: 96-98.
- TRUEMAN, E. R., 1968b, The burrowing activities of bivalves. *Symp. zool. Soc. Lond.*, 22: 167-186.
- TRUEMAN, E. R., 1968c, The mechanism of burrowing of some naticid gastropods in comparison with that of other molluscs. *J. exp. Biol.*, 48: 663-678.
- TRUEMAN, E. R. & PACKARD, A., 1968, Motor performances of some cephalopods. *J. exp. Biol.*, 49: 495-507.
- WILSON, D. M., 1960, Nervous control of movement in cephalopods. *J. exp. Biol.*, 37: 57-72.
- YONGE, C. M., 1957, Mantle fusion in the Lamellibranchia. *Publ. Staz. zool. Napoli*, 29: 151-171.
- YOUNG, J. Z., 1938, The functioning of the giant nerve fibres of the squid. *J. exp. Biol.*, 15: 170-185.



ZUR WÜRM-GLAZIALEN ÜBERDAUERUNG EUROPÄISCHER  
LANDGASTROPODEN IN EISRANDNÄHE

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## ZUSAMMENFASSUNG

Im letzten Interglazial (Eem, Riss/Würm) war die mitteleuropäische Landgastropodenfauna optimal entwickelt. Die Lebensbedingungen waren äusserst günstig und vielseitig. Als gegen Ende der Eem-Warmzeit die Temperaturen zurückgingen (75 000 vor heute), setzte auch eine langsame Abnahme der Zahl der Land- und Süsswassermollusken-Arten ein. Im Würm-Glazial erreichte die Verarmung der Molluskenfauna ihren Höhepunkt. Es ist verständlich, dass die Verarmung in Eisrandnähe am grössten war. Die Ausdehnung der Gletschermassen war im Würm - im Vergleich zu anderen Glazialen - relativ gering. Während des Maximums des Würms (20 000 bis 18 000 vor heute) betrug die Absenkung der Jahresmitteltemperaturen: Südengland -12°, Pariser Becken -13°, Zentral-Ungarn -13°, Nordukraine -9°, Mittellauf der Wolga -8°, West-Sibirien -3°. Die Absenkung der Juli-Temperaturen betrug: Südfrankreich -10°, Wiener Pforte -9°, NO-Mitteuropa -7° bis -8°, Südural und Nordjakutien -5°. Für Landgastropoden ist neben der Temperatur der Wasserhaushalt von ausschlaggebender Bedeutung. Im Würmglazial war es nicht nur kälter, sondern auch trockener. Die Niederschläge sanken durchschnittlich um 40-60%. Ein weiterer wichtiger Faktor für die Existenz von Landgastropoden ist die Vegetation. Der Wald fehlte in Mitteleuropa in Eisrandnähe völlig. An seine Stelle war die Lössteppe getreten. In der nächsten Umgebung der Alpen und in Nordeurasien herrschten *Artemisia*-Steppen, die südliche Ukraine und der Süden West-Sibiriens wurden durch *Chenopodiaceae* gekennzeichnet. In Mitteleuropa fanden sich niedrigwüchsige Pflanzengesellschaften mit *Potentilla*, *Plantago*, Cruciferen, Compositen, Papilionaceen und Gramineen. Im Osten Europas sind die Böden damals sicherlich stark salzhaltig gewesen. Ein relativ stabiles Klima wird für Mittel- und Ost-Sibirien angegeben. Dort sind zum Teil Waldsteppen nachgewiesen. Während anfangs in Mitteleuropa Grassteppen herrschten, wurden sie später durch Kräutersteppen ersetzt. Die Böden waren in Dauerfrostgebieten Brodelböden, die immer wieder frisches Material aus der Tiefe nach oben brachten. Die Auslaugung bzw. Auskalkung war also gering. Begünstigt wurde dieser Umstand durch die geringen Niederschläge. In Eisrandnähe Nordwest-Deutschlands sind folgende Landgastropoden nachgewiesen: *Succinea oblonga*, *Trichia hispida*, *Pupilla muscorum*, *Columella columella*, *Vertigo parcedentata*, *Cochlicopa lubrica*, *Truncatellina cylindrica*, *Vertigo antivertigo*, *Vertigo pygmaea*, *Vertigo substriata*, *Vallonia pulchella*, *Vallonia costata*, *Vallonia tenuilabris*, *Succinea putris*, *Succinea antiqua*, *Punctum pygmaeum*, *Discus rotundatus*, *Arion* sp., *Eucobresia diaphana*, *Nesovitrea hammonis*, *Nesovitrea petronella*, *Limax* sp., *Deroceras* sp., *Euconulus fulvus*, *Clausilia pumila*, *Helicigona lapicida*, *Arianta arbutorum*. Das sind 24% der rezenten Fauna im gleichen Gebiet. Insgesamt gesehen waren also die Lebensbedingungen für Landgastropoden während des Würmglazials zur Zeit seines Maximums in Eisrandnähe Nordwestdeutschlands relativ günstig, so dass Arten des holopaläarktischen und europäischen Verbreitungstyps mit grosser ökologischer Valenz die Eiszeit am Ort zu überdauern vermochten. In Süddeutschland liegen besondere Verhältnisse vor, die in der Bodenmorphologie begründet sind. Dort gab es viele ökologische Nischen, deren Lokalklima ein besseres Ausharren ermöglichte. Ausserdem war die Wirkung der alpinen Eiskappe nicht so stark wie die der nordischen.

Neben diesen mitteleuropäischen Eisrand-Refugien gab es in Europa noch andere Gebiete, an denen Landgastropoden unter besonderen Bedingungen die Würm-Eiszeit überdauern konnten. In Nordwest-Skandinavien blieben einige Gebiete an der Küste infolge des Golfstromes eisfrei. Hier überdauerten z.B. etwa 29% der Carabiden die Eiszeit. Durch zahlreiche endemische Pflanzenarten (z.B. *Papaver relictum*, *Taraxacum dourense*) ist diese Annahme ziemlich gesichert, obwohl sie von einigen Geologen abgelehnt wird. Auch im Inland gab es eisfreie Stellen (Nunatak). Ähnliche Verhältnisse finden wir in den Alpen. Hier ist eine reiche Kleinfaua nachgewiesen, die inneralpin die Eiszeit überdauert hat. Unter den Mollusken gehören verschiedene Vitriniden und *Cylindrus obtusus* hierher. Dass viele Arten in unmittelbarer Nähe des Eises zu leben vermögen, zeigen neuere Untersuchungen in Island. In wenigen hundert Metern vom Eisrand entfernt leben dort z.B.: *Arion ater*, *A. subfuscus*, *A. intermedius*, *Cochlicopa lubrica*, *Columella aspera*, *Euconulus fulvus*, *Nesovitrea hammonis*, *Vitrina pellucida* u.a.; Arten mit etwas höheren Ansprüchen an die Temperatur lebten in Süd-England: *Acme inchoata*, *Truncatellina britannica*, *Geomalacus maculosus*, *Zonitoides excavatus* und *Ashfordia granulata*.

Die Lebensbedingungen in Eisrandnähe waren also keineswegs so ungünstig, wie es vielfach angenommen wird. Keineswegs ist aber die Annahme berechtigt, dass es im Sinne einer Tabula-rasa-Theorie zur völligen Auslöschung gekommen ist. Von den rezenten Arten lebten in Mitteleuropa 25-30% auch während des Maximums des Würmglazials an den gleichen Stellen wie heute.

## LITERATUR

- ANT, H., 1963, Die würmperiglaziale Molluskenfauna des Lippe- und Ahse-Tales bei Hamm. *Neues Jahrb. Geol. Paläont. Mon.-H.*, 1963, 77-86.
- ANT, H., 1963, Faunistische, ökologische und tiergeographische Untersuchungen zur Verbreitung der Landschnecken in Nordwestdeutschland. *Abh. Landesmus. Naturk. Münster*, 25: 1-125.
- ANT, H., 1965, Der boreo-alpine Verbreitungstypus bei europäischen Landgastropoden. *Zool. Anz. Suppl.*, 28: 326-335.
- ANT, H., 1966, Die Bedeutung der Eiszeiten für die rezente Verbreitung der europäischen Landgastropoden. *Malacologia*, 5: 61-62.
- ANT, H., 1967, Die Geschichte der westfälischen Landschneckenfauna. *Veröff. Naturwiss. Vereinig. Lüdenscheid*, 7: 35-47.
- FRENZEL, B., 1960, Die Vegetations- und Landschaftszonen Nord-Eurasiens während der letzten Eiszeit und während der postglazialen Wärmezeit. II. *Akad. Wiss. Lit. Mainz, Abh. Math.-naturwiss. Kl.*, 1960, 287-453.
- FRENZEL, B., 1967, Die Klimaschwankungen des Eiszeitalters. Braunschweig (Vieweg).
- HOLDHAUS, K., 1954, Die Spuren der Eiszeit in der Tierwelt Europas. *Abh. Zool. Bot. Ges. Wien*, 18: 1-493.
- LINDROTH, C. H., 1949, Die fennoskandischen Carabidae. III. Allgemeiner Teil. *K. Vet. Vitterh. Samh. Handl. F. 6. Ser. B*, 4: 1-911
- LINDROTH, C. H., 1965, Skaftafell, Iceland, a living glacial refugium. *Oikos, Suppl.*, 6: 1-142.
- LÖVE, A. & D. (edit.), 1963, North Atlantic Biota and their History. Oxford (Pergamon).
- MANI, M. S., 1967, Ecology and Biogeography of high altitude Insects. Den Haag (Junk).
- STEUSLOFF, U., 1938, Neue Beiträge zur Molluskenfauna und Ökologie periglazialer und altalluvialer Ablagerungen im Emscher-Lippe-Raum. *Arch. Moll.*, 70: 161-193.
- STEUSLOFF, U., 1943, Der Lebensraum der Lössschnecken. *Z. Geschiebeforsch. Flachlandsgeol.*, 19: 18-26.
- STEUSLOFF, U., 1951, Neue Beobachtungen und Erkenntnisse über Flora, Fauna und Klimageschichte des Würmperiglazials in der Niederterrasse der Emscher und der Lippe. *Abh. Landesmus. Naturk. Münster*, 14: 1-45.
- THIEL, E., 1951, Die Eiszeit in Sibirien. *Erdkunde*, 5: 16-35.
- THIENEMANN, A., 1950, Verbreitungsgeschichte der Süßwassertierwelt Europas. Stuttgart (Schweizerbart).
- WOLDSTEDT, P., 1955, Norddeutschland und angrenzende Gebiete im Eiszeitalter. Stuttgart (Koehler).
- WOLDSTEDT, P., 1954, 1958, Das Eiszeitalter. I. II. Stuttgart (Enke).

THE ELEVATION EFFECT IN *CYLINDRUS OBTUSUS* (DRAPARNAUD 1805)

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## ABSTRACT

The elevation effect may be defined as the phenomenon, that certain mountain plants or animals occur only on mountains or mountain ranges exceeding a certain minimum altitude; it also includes the fact that, on these mountains, the organisms in question may descend to comparatively low altitudes. These organisms are absent on mountains or mountain ranges which are lower than the required minimum altitude. The elevation effect may be expressed in figures as the difference between the minimum required altitude of the mountains and that of the lowest known locality. If, for example, a plant occurs from 1500 m onwards, but only on mountains exceeding 2200 m, the elevation effect amounts to 2200-1500=700 m. So far this effect has been demonstrated to occur in mountain plants on Java, New Zealand and in Switzerland (van Steenis, 1933, 1934; Backhuys, 1968).

The explanation is that each mountain plant occupies a zone of permanent establishment, on both sides bordered by a zone of temporary localities, the critical altitude being the lower contour of the zone of permanent establishment. In other words, mountain plants can only descend to their lowest localities on mountains of which the summits are within or above the zone of permanent establishment, ensuring a constant source for descending diaspores. The lowest localities are entirely dependent on a continuous supply of diaspores from the permanent, higher situated populations.

The elevation effect is influenced by various ecological factors, the most important of which are: temperature, soil, physiognomy of the vegetation, autecology, dispersal biology and man. It appears that the lowest localities always occur on sites which in one way or another differ from the surrounding habitat e.g., by lower temperature, more open vegetation, etc. Such "enclaves" show most of the characters of higher situated zones; these are for example borders of streams, glaciers, deep ravines, waterfalls, etc.

Since the animal world is often closely connected with the vegetation, the question arose whether this phenomenon could also be found in montane animals. As an example we took *Cylindrus obtusus* (Draparnaud, 1805), a land snail endemic to Austria. The distribution of this species is well-known and all localities have been enumerated and numbered by Adensamer (1937) and by Klemm (1961).

It appears that all localities of *Cylindrus obtusus* are situated on mountains or mountain ranges exceeding 1600 m. The lowest known locality of *Cylindrus obtusus*, however, is at an altitude of 1100 m. Thus the elevation effect of *Cylindrus obtusus* amounts to 500 m.

In connection with what we have found about the lowest known records of mountain plants, it is not surprising to find that the lowest localities of *Cylindrus obtusus* are situated in "enclaves" in the vegetation, showing most of the characters of higher situated zones.

## ZUSAMMENFASSUNG

Unter dem Elevations-Effekt versteht man die Erscheinung, dass z.B. Bergpflanzen nur auf Bergen oder Bergkomplexen vorkommen, die eine bestimmte minimale Gipfelhöhe besitzen, und dass die betreffenden Pflanzen auf diesen Bergen und Bergkomplexen tief hinabsteigen können. Auf Bergen und Bergkomplexen, die niedriger als diese minimale Gipfelhöhe aber höher als der niedrigste Fundort sind, kommen diese Pflanzen nicht vor. Der Elevations-Effekt kann zahlenmässig ausgedrückt werden als der Unterschied zwischen dieser minimalen Gipfelhöhe und dem niedrigsten Fundort. Wenn eine Pflanze z.B. vorkommt ab 1500 m, aber nur auf Bergen, die höher als 2200 m sind, beträgt der Elevations-Effekt also 2200 - 1500 = 700 m.

Bisher ist dieser Effekt bei Bergpflanzen auf Java, auf Neu-Seeland und in der Schweiz gefunden worden (v. Steenis, 1933, 1934, Backhuys, 1968). Die Erklärung dieses Effekts ist, dass wir im Verbreitungsgebiet einer Bergpflanze eine Zone der Dauer-Ansiedlung, die nach oben wie nach unten durch je eine Zone von zeitweilig möglichen Standorten begrenzt wird, unterscheiden können; die minimale Gipfelhöhe stimmt mit der untersten Grenze der Zone der Dauer-Ansiedlung überein. Für die Instandhaltung der Populationen auf niedrigen Standorten ist eine stetige Diasporenzufuhr von oben herab notwendig. Auf hohen Bergen kann die Art bis auf grosse Tiefe vorkommen, weil die Diasporenzufuhr aus der höheren Zone ununterbrochen stattfindet.

Der Elevations-Effekt wird von verschiedenen ökologischen Faktoren beeinflusst, wovon die wichtigsten sind: die Temperatur, der Boden, die Physiognomie der Vegetation, die Autökologie, die Verbreitungs-

biologie und der Mensch. Es zeigt sich, dass die niedrigsten Fundorten sich auf Stellen befinden, die auf irgendeine Weise von der Umgebung abweichen z.B. durch eine niedrigere Temperatur, offenere Vegetation usw. Solche Enklaven, z.B. Fluss-Alluvionen, Gletscher, tiefe Schluchten, Wasserfälle usw., zeigen die Eigenschaften höher gelegener Zonen.

Da die Tierwelt oft eng mit der Vegetation zusammenhängt, haben wir uns gefragt, ob dieser Effekt auch bei Tieren gefunden werden könnte. Als Beispiel haben wir *Cylindrus obtusus* (Draparnaud, 1805) gewählt, eine in Österreich endemische Landschnecke. Die Verbreitung dieser Art ist sehr gut bekannt und alle Fundorte sind von Adensamer (1937) und von Klemm (1961) beschrieben und numeriert worden. Es zeigt sich, dass alle Fundorte von *Cylindrus obtusus* auf Bergen, die höher als 1600 m sind, liegen. Der niedrigste Fundort von *Cylindrus obtusus* liegt aber auf einer Höhe von 1100 m. Der Elevations-Effekt von *Cylindrus obtusus* beträgt also etwa 500 m.

In Zusammenhang mit dem, was wir in bezug auf die niedrigsten Fundorte von Pflanzen gefunden haben, ist es nicht verwunderlich, dass die niedrigen Fundorte von *Cylindrus obtusus* in Enklaven in der Vegetation liegen, die die Eigenschaften höher gelegener Zonen zeigen.

#### REFERENCES

- ADENSAMER, W., 1937, *Cylindrus obtusus* (Draparnaud, 1805), seine relikhafte Verbreitung und geringe Variabilität, sowie zoogeographisch-phylogenetische Betrachtungen über alpine Mollusken überhaupt. *Arch. Moll.*, 69(3): 66-116.
- BACKHUYS, W., 1968, Der Elevations-Effekt bei einigen Alpenpflanzen der Schweiz. *Blumea*, 16(2): 273-320.
- KLEMM, W., 1961, Fortführung der Numerierung der Fundorte von *Cylindrus obtusus* (Draparnaud). *Arch. Moll.*, 90(1/3): 43-49.
- STEENIS, C. G. G. J. van, 1933, Report of a botanical trip to the Ranau Region, South Sumatra. *Bull. Jard. Bot. Btzg.*, 3(13): 1-56 (esp. chapt. 7: Occurrence of mountain plants at low altitudes, p 37-56).
- STEENIS, C. G. G. J. van, 1934, On the origin of the Malaysian mountain flora. Part 2. Altitudinal zones, general considerations, and renewed statement of the problem. *Bull. Jard. Bot. Btzg.*, 3(13): 289-518 (esp. 292-302).

REPRODUCTION IN *APLYSIA* (GASTROPODA, OPISTHOBRANCHIA)

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## ABSTRACT

*Aplysia*, like other Euthyneura, is hermaphrodite. The present work has been concerned with 3 northeast Atlantic species: *A. depilans* (Gmelin 1791), *A. fasciata* Poiret 1789 and *A. punctata* Cuvier 1803. A number of authors have described the anatomy of the aplysiid reproductive system and these are listed by Thompson & Bebbington (1969). The hermaphrodite tracts of *Aplysia* show incomplete separation of the efferent channels for the male and female gametes. The system functions so as to translocate oocytes (by ciliary action) during oviposition, to expel autosperms (by ciliary and muscular action), and to receive allosperms transferred during chain-copulation.

Study of the ultrastructure of the aplysiid spermatozoon shows that previous authors (Retzius 1906, Tuzet 1940 and Franzén 1955) have misinterpreted the various components of this unique type of gamete. The nucleus is shown to have a helical structure which extends to the anterior tip of the head; no acrosome could be detected. The flagellum originates anteriorly close to the anterior tip of the gamete and has a pair of mitochondrial strands helically disposed along its length.

The efferent passage of female gametes during oviposition and the build-up of the spawn-mass were followed in serial sections of ovipositing specimens. Artificial fertilizations are reported for the first time for an internally fertilizing gastropod.

Maturation and fertilization of the ova are complete a few hours after spawning and two polar bodies are extruded. Two cells are formed, one of which (AB) is larger than the other (CD). The second division is also unequal. During divisions the cells tend to meet over only a relatively small area but later become closely associated and their shape modified. The spiral nature of cleavage is most obvious after the third division. Cleavage continues in a series of alternate dextrotropic and laeotropic divisions to form a stereoblastula. The sterroblastula gastrulates by epiboly. The larval shell darkens 2-3 days after it is formed. By the time the veliger is ready for hatching the egg string is fragile and easily broken.

After hatching the larvae swim upwards and may become trapped in the surface film of the water. During swimming the velar lobes are held uppermost, the shell down. Locomotion is effected by the beat of the long velar cilia which impart a forward motion to the larva. Swimming activity is interrupted at intervals, the larva partially retracting into the shell and sinking slowly. Veliger larvae have been maintained in the laboratory for up to a fortnight after hatching.

Many problems about reproduction in *Aplysia* remain. The search for a food-plant or substance which will induce progressive development and settlement of the larvae must go on. Without this information the details of metamorphosis remain a mystery. The method by which the allosperms are activated in the receptaculum seminis has not been shown. Nothing is known about the endocrine control of reproduction; Vicente (1966) and Kupferman (1967) have claimed to have solved this problem, but their results have proved impossible to verify. Finally, by what means do stray male and female gametes get into the gametolytic gland and are the spermatozoa allosperms or autosperms or both?

## REFERENCES

- FRANZÉN, A., 1955, Comparative morphological investigations into the spermiogenesis among Mollusca. *Zool. Bid.*, Uppsala, 30: 399-456, pls. 1 and 2.
- KUPFERMANN, I., 1967, Stimulation of egg laying: possible neuroendocrine function of bag cells of abdominal ganglion of *Aplysia californica*. *Nature*, Lond., 216: 814-815.
- RETZIUS, G., 1906, Die Spermien der Gastropoden. *Biol. Unters.*, 13: 1-36, taf. I-XII.
- THOMPSON, T. E. & BEBBINGTON, A., 1969, Structure and function of the reproductive organs of three species of *Aplysia* (Gastropoda, Opisthobranchia). *Malacologia*, 7(2/3): 347-380.
- TUZET, O., 1940, La spermiogénèse d'*Aplysia depilans* Linné. *Arch. Zool. exp. gén.*, 81(notes et rev.): 130-138.
- VICENTE, N., 1966, Sur les phénomènes neurosécrétoires chez les Gastéropodes Opisthobranches. *C. R. Acad. Sci.*, Paris, 263: 382-385.

## SYSTEMATICS OF THE VESICOMYIDAE (MOLLUSCA; BIVALVIA)

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## ABSTRACT

Benthic, shelled mollusks which live in the deepsea from the edge of the continental shelf to the abyssal plain are usually small in size with delicate sculpturing and a thin, pearly shell substance enveloped externally by a drably colored periostracum. The archibenthic zone between 200 and 1,000 meters may be described as aphotic or dysphotic since little if any light penetrates beyond these depths. The substrate may be a fine mud or silt and occasionally considerable organic material occurs in the water immediately above the substrate since in certain archibenthic habitats, unusually large, filter feeding bivalves are found which have been referred to the family Vesicomysiidae.

This family was established by Dall & Simpson (1901) for a group of predominantly archibenthic, infaunal mollusks characterized by a peculiar, but heterodont, dental configuration, dehiscent periostracum and often heavy, chalky shells. Numerous species have been described from material collected by the major oceanographic expeditions, and certain of them have been listed and reviewed (Lamy, 1920; Odhner, 1960; Boss, 1968).

The affinities of the group have been questioned: representative species have been considered in the Isocardiidae, Kelliellidae, Veneridae, Carditidae and Arcticidae. Anatomical material and new species recently obtained from the Caribbean Sea near Panama offer new data which clarify the systematic position of the group. Anatomically, both the vesicomysid genera *Calyptogena* and *Callogonia* are typified by a large, laterally compressed and anteriorly pointed foot with a concomitant extensive ventral pedal gape. Posteriorly there are small incurrent and excurrent siphonal openings associated with posterior thickenings of the mantle muscles which function as siphonal retractors and may or may not leave a vague pallial sinus impressed on the shell. Apparently homorhabdic and nonplicate, the gills consist of a large, ventrally directed inner demibranch and a dorsal, smaller outer demibranch. Both have descending and reflected lamellae. The thick and tumid gills are also large and extensive with the dorsal portion of the outer demibranch extending into the umbonal cavity. The labial palps are significantly reduced to extremely small folds or lips which border the mouth. The combination of these anatomical traits with the conchological ones involving the periostracum, ligament, dentition, shell substance, and configuration of the pallial line serve to circumscribe the limits of the Vesicomysiidae.

Nevertheless, various and diverse members of this group show conchological features in common with the Kelliellidae and, possibly, the Veneridae. The Vesicomysiidae are anatomically and conchologically distinct from the Isocardiidae, Carditidae, Arcticidae and Astartidae. The morphology of *Kelliella* was discussed by Clausen (1958) while the great anatomical diversity of the Veneridae was the subject of Ansell's research (1961). *Kelliella*, at about 3 mm in maximum length, and the vesicomysids, *Calyptogena* and *Callogonia* at over 100 mm, differ greatly in size but anatomically they are quite similar. *Kelliella*, however, has a cylindrical foot, only a single posterior siphon and an anterior incurrent water flow, which is probably a primitive feature in the Heterodonta (Allen, 1958; 1968). The vesicomysids have both posterior siphons developed but their pallial currents have not been studied.

With a discontinuous but cosmopolitan distribution, the species of the Vesicomysiidae form into distinct *Artenkreise* in which the most closely related or analogous species are geographically isolated from each other. Five generic assemblages may be distinguished: 1) *Vesicomys* which may be further subdivided into smaller shelled forms with 7 species and larger shelled forms with 6 species; 2) *Callogonia* (+ *Archivesica*) with 9 species; 3) *Calyptogena* with 7; 4) *Ectenagena* with 2; and 5) *Kelliella*-like forms with 9 species.

The smallest of the vesicomysids are all included in the fifth assemblage mentioned above. Among them is the type-species of *Vesicomys*, *Callocardia atlantica* Smith 1885, which may prove to be a *Kelliella*, in which case some nomenclatorial changes will have to be made. Nonetheless, the systematic relationships of the Vesicomysiidae seem to be with the venerid clams, for their dentition is virtually identical with that of *Venerupis*, they have incurrent and excurrent siphons developed posteriorly and possess an extensive anteroventral pedal gape. Further, if *Vesicomys* and *Kelliella* prove to be synonymous, and if *Calyptogena*, *Callogonia* and *Ectenagena* confamilial, then it is quite possible that the smallest individuals in this group are neotenous venerids, similar in that respect to the neotenous venerid *Turtonia* (Ockleemann, 1964).

## LITERATURE CITED

- ALLEN, J. A., 1958, On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). *Phil. Trans. R. Soc. (B)*, 241: 421-484, 53 figs.
- ALLEN, J. A., 1968, The functional morphology of *Crassinella mactracea* (Linsley) (Bivalvia; Astartacea). *Proc. malac. Soc. London*, 38(1): 27-40.
- ANSELL, A. D., 1961, The functional morphology of the British species of Veneracea (Eulamellibranchia). *J. mar. biol. Ass. U. K.*, 41: 489-515.
- BOSS, K. J., 1968, New species of Vesicomysidae from the Gulf of Darien, Caribbean Sea (Bivalvia; Mollusca). *Bull. Mar. Sci.*, 18(3): 731-748, 28 figs.
- CLAUSEN, C., 1958, On the anatomy and histology of the eulamellibranch *Kelliella miliaris* (Philippi) with observations on the ciliary mechanisms in the mantle cavity. *Nytt Mag. Zool.*, 6: 144-175.
- DALL, W. H. & SIMPSON, C. T., 1901, The Mollusca of Puerto Rico. *U.S. Fish. Comm. Bull.*, 20(1): 351-524, pls. 53-58.
- LAMY, E., 1920, Révision des Cypricardiacea et de Isocardiacea vivantes. *Jour. de Conch.*, 64: 259-307.
- OCKELMANN, K. W., 1964, *Turtonia minuta* (Fabricius), a neotenous Veneracean bivalve. *Ophelia*. 1(1): 121-146.
- ODHNER, H. H., 1960, Mollusca. *Rept. Swed. Deep-sea Exped.*, 2(Zool. 22): 365-400, 2 pls., 12 text-figs.

## NOTES ON THE DISTRIBUTION OF TERRESTRIAL MOLLUSCS IN SOUTHERN AFRICA

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## ABSTRACT

Southern Africa, the subcontinent south of the Cunene and Zambezi Rivers, represents an immense stretch of country with a varied geography and climate. Rainfall is of prime importance to the land molluscs and in many cases appears to be the limiting factor (e.g., in the genus *Xerocerastus*); the greatest number and diversity of species is found to the east of the main watershed formed by the Drakensberg range.

Southern Africa is inhabited by about 640<sup>1</sup> indigenous species of terrestrial molluscs, representing 73 genera and 27 families. This works out at approximately 49 species per 100,000 square miles; this high figure is about equalled by the ex-Belgian Congo, but is much lower in Europe (>40) and North America (9). This may be caused by the diversity of habitat from tropical rain forest to desert, the location of Southern Africa at subtropical and tropical latitudes, and the chequered geological history ('Gondwanaland', etc.).

In the overall picture the dominant families are the Streptaxidae (>135 species), Endodontidae (>110 species), Subulinidae (about 80 species) and Urocyclidae (about 70 species). Achatinidae and Enidae are also very well represented. These six families between them account for almost 75% of the known species of the area. Of the above families the Streptaxidae and Subulinidae are circumtropical and the Enidae an Old World family; the Achatinidae and Urocyclidae are African families (Achatinidae with one genus endemic to Madagascar). The Endodontidae belong to the Southern Relict Fauna (cf. Solem, 1959).

A marked endemism at various levels characterizes this assemblage of species: endemic families (one: Aperiidae), subfamilies (one: Oopeltinae, Arionidae), tribes (one) and genera (16: *Chondrocyclus*, *Afriboy-sidia*, *Afrodonta*, *Oopelta*, *Sheldonia*, *Xerocerastus*, *Coeliaxis*, *Metachatina*, *Trigonephrus*, *Tulbaghinia*, *Dorcasia*, *Prestonella*, *Nata*, *Natalina*, *Apera*, *Sculptaria*). *Fauxulus* and *Trachycystis* may be considered near-endemics or subendemics, i.e., genera of which the bulk of the subgenera and species are endemic to Southern Africa. Of the endemic genera eight belong to families not otherwise represented in Subsaharan Africa, viz., Arionidae, Acavidae, Amphibulimidae, Rhytididae and Corillidae. The endemic genera belong to three groups of families, viz., families belonging to the Ethiopian Region (Urocyclidae and Achatinidae), those belonging to the Southern Relict Fauna (Endodontidae, Acavidae, Rhytididae and Aperiidae) and those belonging to more widely distributed families (Cyclophoridae, Chondrinidae, Arionidae and Subulinidae). The families Amphibulimidae and Corillidae, represented by the genera *Prestonella* and *Sculptaria* respectively, are probably also Southern Relict elements.

Endem centres of great importance are South West Africa, where a specialized fauna with peculiar Subulinidae, Achatinidae, Acavidae, Corillidae, etc., has developed, and the Southwest Cape Province with endemic Endodontidae, Arionidae, Acavidae and Rhytididae. Minor centres are particularly found in the interrupted parts of the Drakensberg range (N. Transvaal, E. Rhodesia); endemism here is on a specific rather than generic level.

Twenty-one families (78% of the total) and 57 genera (also 78% of the total) testify to connections with Central and East Africa, from which areas much of the fauna must have been derived. However, only about 70 species (11% of the total), mainly belonging to four families, are known also to occur north of the Zambezi.

The tropical element is strongly represented among the terrestrial molluscs of Southern Africa. It is mainly confined to southeast Africa in a rapidly narrowing belt along the coast east of the main watershed. In some groups the extension is two-pronged, penetration in a westward direction having been accompanied by adaptation to the semi-desert conditions of the central and western parts of Southern Africa (e.g., Achatinidae). From north to south there is a rapid decrease in the number of taxa of tropical families as witnessed by the number of genera in the Subulinidae:

south of the Zambezi River	11	roughly at 17° Lat. S.
south of the Limpopo River	9	roughly at 22° Lat. S.
south of the Tugela River	7	roughly at 29° Lat. S.
south of the Great Fish River	6	roughly at 33° 30' Lat. S.
south of the Gouritz River	1	roughly at 34° 30' Lat. S.

<sup>1</sup>All figures are approximate.



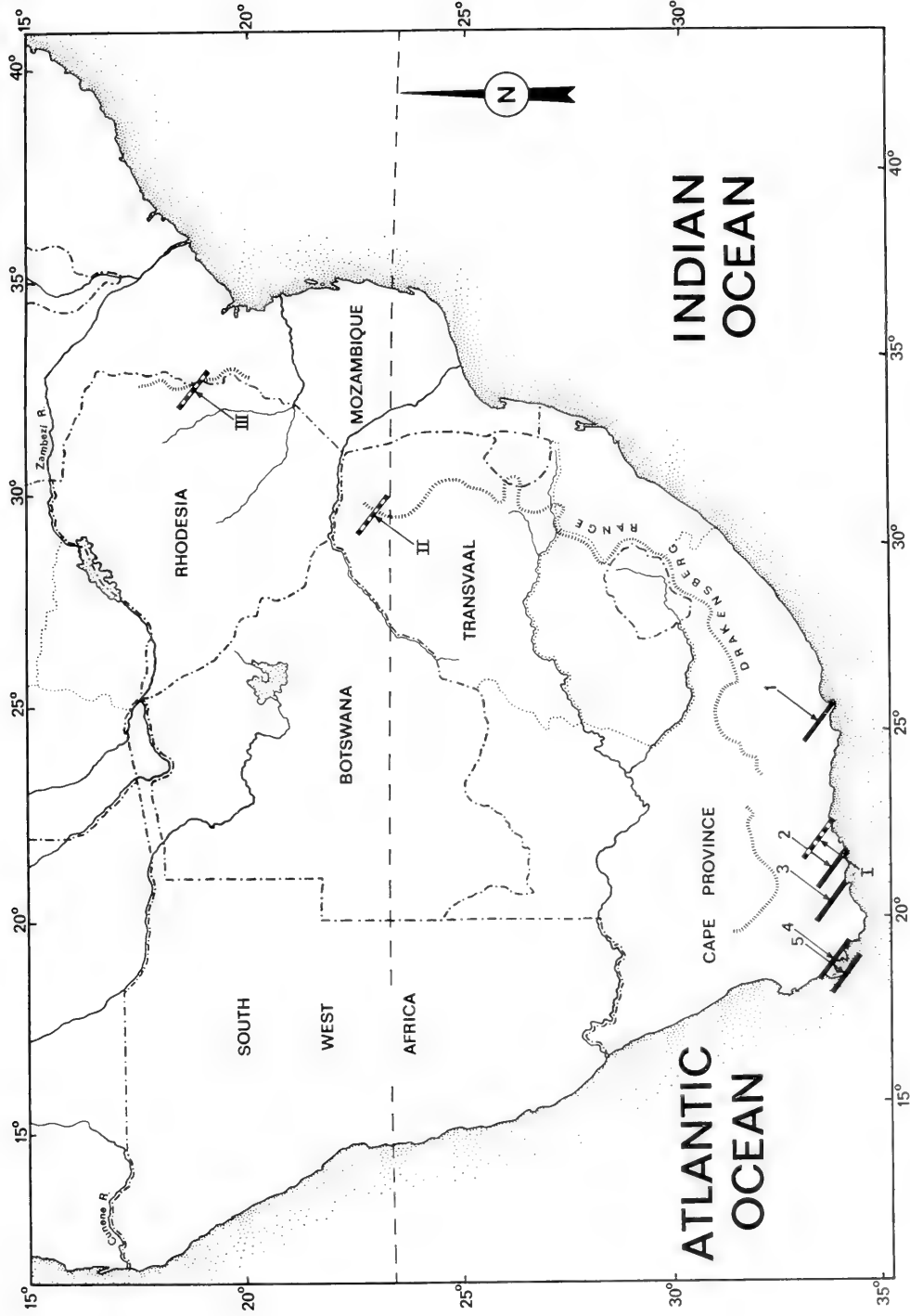


FIG. 1. Distributional limits of some temperate (Southern Relict) and tropical families in southeastern Africa. Temperate families: I = Acavidae, II = Rhytididae, III = Aperiidae; tropical families: 1 = Veronicellidae, 2 = Streptaxidae, 3 = Achatinidae, 4 = Subulinidae, 5 = Urocycychidae. H. Heijn del.

The distribution pattern of the temperate elements is the reverse of the above. Southern Relict elements such as the Endodontidae, Acavidae, Aperidae and Rhytididae show a marked decrease in number of species north of the Great Fish River, which trend is continued north of the Limpopo and Zambezi Rivers. Fig. 1 shows the southern limits of some tropical and northern limits of some temperate families in the area under discussion.

This illustrates the essential bipolarity in the distribution of the Southern African land molluscs: from north to south the typically African character of the terrestrial molluscs gradually changes into that of a Southern Relict Fauna. The tropical elements must have originated in Central and East Africa, while the Southern Relict elements must have had their origin in the south. Darlington (1965) has summarized data on the southern continents and has concluded that at one time these have been much closer than today, although probably not forming a closed and continuous continent ('Gondwanaland'). Absence of relevant fossils on the Northern Hemisphere leads to the preliminary conclusion that the Southern Relict mollusc families may indeed have originated on this "continent."

Detailed distributions have been greatly influenced by the climate in the past and present, particularly in and after the Pleistocene. A few elements must have come from the north at a time when much of Africa enjoyed a considerably cooler and wetter climate; these palaeogenic elements are found e.g., in the families Arionidae (genus *Oopelta*) and Clausiliidae (*Macroptychia africana*).

The distribution of the land molluscs of Southern Africa has been more extensively dealt with in the present author's recent paper (Van Bruggen, 1969).

#### REFERENCES

- BRUGGEN, A. C. van, 1969, Studies on the molluscs of Zululand with notes on the distribution of land molluscs in Southern Africa. *Zool. Verhand.*, Leiden, 103: 1-116.
- DARLINGTON, P. J., 1965, Biogeography of the southern end of the world. *Harvard University Press*, Cambridge, Mass.
- SOLEM, A., 1959, Zoogeography of the land and freshwater Mollusca of the New Hebrides. *Field. (Zool.)*, 43: 239-359.

THE SYSTEMATIC POSITION OF THE ATHORACOPHORIDAE  
(GASTROPODA: EUTHYNEURA)<sup>1</sup>J. B. Burch<sup>2</sup> and C. M. Patterson*Museum of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A.*  
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Burch (1968, *J. malacol. Soc. Austr.*, 11: 62-67) has shown that tentacular structure and mode of tentacle retraction in the Athoracophoridae are different from that described in other Stylommatophora, indicating that these slugs may be quite distinct. However, we recently studied in detail the tentacle retraction of Succineidae (*Catinella*, *Omalonyx*, *Oxyloma*, *Quickia* and *Succinea*), and the unexpected results of these studies caused us to re-examine living animals of as many different land snail groups as were immediately available to us (Fig. 1). This led to a reappraisal of previous views on the systematic position and affinities of the Athoracophoridae and their relation to the Succineidae.

In the Stylommatophora, the extended eye-bearing tentacle is an elongate hollow structure with an eye at its tip. The tentacle is functionally highly contractile and retractile. In regard to retraction type, it is invertible (introvertible, i.e., the eye of the extended tentacle can be withdrawn by a direct and initial pulling-back of the eye, producing a progressive inversion of the tubular tentacle beginning at the distal end and proceeding proximally, or in the words of Hyman (1967, *The Invertebrates*, McGraw-Hill, N. Y., 6: 551), "turning the outside in"). In addition to inverting, the tentacles of non-athoracophorid species can be partially withdrawn by contraction (in some species a contraction up to 3/4 the maximum length of the extended tentacle before the eye has to be inverted for continued withdrawal), but in none of the species we examined could complete withdrawal of the tentacle be accomplished without inversion. In all non-athoracophoran species inversion could be initiated at any stage during contraction. The tentacles of some species are thickened as contraction continues, but in others there is little or no noticeable thickening of the tentacle. Additionally, in all non-athoracophorid and non-succineid species the tentacles are covered with a rugose dermis which is a continuation of the skin-pattern of the dorsal head-foot. This rugose pattern extends distally to the base of the bulbous tip bearing the eye.

Tentacle retraction in the Succineidae, although similar to that described above, and on superficial inspection appearing identical, on closer observation can be seen to have some noteworthy differences from the other Stylommatophora, and to have certain similarities to the athoracophorid *Aneitea*. The rugose dermis of the head-foot region of the Succineidae extends onto the eye-bearing tentacles, but for only about 1/2 the length of the tentacle. There the rugose pattern abruptly stops and the remaining 1/2 of the tentacle is smooth. The proximal tentacle tapers noticeably to the junction between the proximal rugose half and the distal smooth half. At this point the distal half continues in an untapered rod-like fashion to the terminal optical bulb. The tentacles can be contracted as in the other non-athoracophorid Stylommatophora, i.e., on direct stimulation, the tip of the distal half of the tentacle can be inverted at any position. But, during non-invertible withdrawal, most of the initial contraction is accomplished by the tapering rugose basal half. On continued non-invertible retraction the distal smooth rod-like portion seems to partially slide into the proximal part, reminiscent of *Aneitea*, although the terminal half of the tentacle cannot quite completely retract into the basal half before it is necessary to invert.

Therefore, the tentacle characteristics of the Succineidae seem to be intermediate between the tracheopulmonate slugs on the one hand and to the remaining Stylommatophora on the other, and hence, in this respect, the Succineidae would seem to be an ideal ancestral type to both groups (Fig. 1, 1). Such a relationship would seem to apply to various other anatomical characters as well (e.g., body surface pattern, pedal grooves, male genitalia). Certain specialized structures in the tracheopulmonate slugs and the other Stylommatophora could have been derived from less specialized ones in the Succineidae. Accordingly, we conclude that the Athoracophoridae are related to the Succineidae, and perhaps should be included with them in the same stylommatophoran suborder (Heterurethra). Other workers have reached the same conclusions from a study of different characters (Mörch, 1865, *J. Conchyl.*, 13: 275, 391; Baker, 1955, *Nautilus*, 68(4): 109-112; Van Mol, 1967, *Mem. Acad. roy. Belg.*, 37(5): 1-168).

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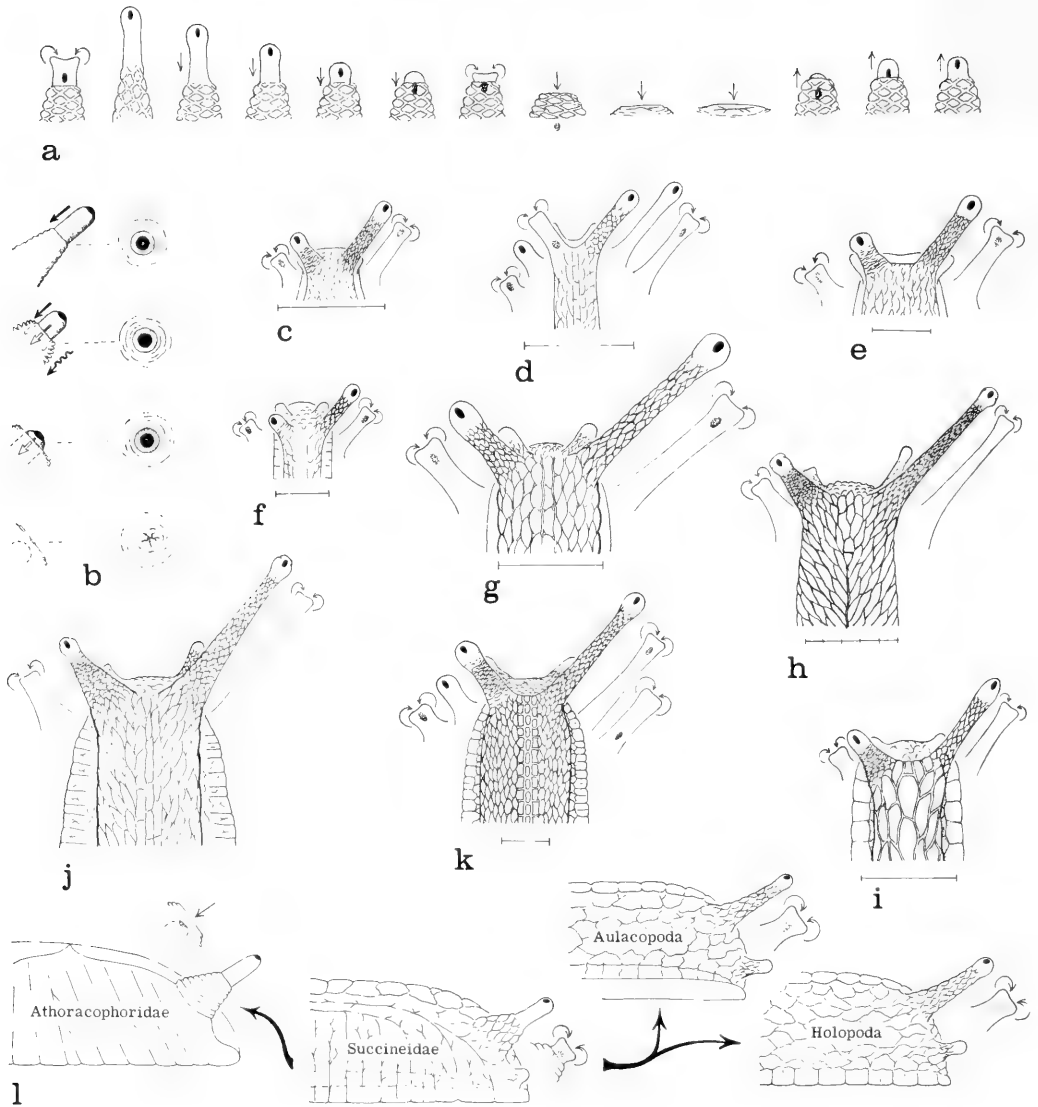


FIG. 1. Tentacle retraction in Stylommatophora. (a) Successive stages of withdrawal and reversion of a tentacle of *Catinella vermeta* (Heterurethra; Succineacea) [Michigan, U.S.A.]; (b) Successive stages of tentacle retraction in *Aneitea* sp. (Heterurethra; Athoracophoracea) [New Hebrides]; (c) *Leptachatina* sp. (Orthurethra; Cionellacea) [Kauai, Hawaii]; (d) *Vallonia pulchella* (Orthurethra; Pupillacea) [Michigan, U.S.A.]; (e) *Auriculella auricula* (Orthurethra; Achatinellacea) [Oahu, Hawaii]; (f) *Zonitoides nitidus* (Sigmurethra; Aulacopoda; Zonitacea) [Michigan, U.S.A.]; (g) *Discus cronkhitei catskillensis* (Sigmurethra; Aulacopoda; Endodontacea) [Michigan, U.S.A.]; (h) *Cryptozona bistrialis* (Sigmurethra; Aulacopoda; Ariophantacea) [Madras State, India]; (i) *Opeas* sp. (Sigmurethra; Holopodopes; Achatinacea) [Madras State, India]; (j) *Planispira fallaciosa* (Sigmurethra; Holopoda; Helicacea) [Madras State, India]; (k) *Stenotrema leai* (Sigmurethra; Holopoda; Polygyracea) [Michigan, U.S.A.]; [The tentacle on the left side of each animal in b-k above illustrates maximum contraction of the tentacle before the eye must be inverted for continued withdrawal.]; (l) Possible phylogenetic relationships of Athoracophoridae, Succineidae, Aulacopoda and Holopoda, based on method of tentacle retraction, dermal surface pattern, and pedal grooves. Scale lines in mm.

CYTOTAXONOMIC OBSERVATIONS IN THE STYLOMMATOPHORAN FAMILY HELICIDAE,  
WITH CONSIDERATIONS ON THE AFFINITIES WITHIN THE FAMILY<sup>1</sup>

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## ABSTRACT

Up until now 55 species and subspecies of Helicidae belonging to 5 subfamilies have been studied cytologically. We have reexamined 20 species and subspecies. In the course of the present study 10 varieties are dealt with for the first time. Their main cytological data are given in Table 1.

TABLE 1. New chromosome numbers in the family Helicidae

Subfamily and species	n	Origin
<b>Helicellinae</b>		
<i>Candidula</i>		
<i>gigaxi</i> (Pfeiffer, 1848)	27	Netherlands, Belgium
<i>intersecta</i> (Poiret, 1801)	26	Netherlands
<b>Hygromiinae</b>		
<i>Zenobiella</i>		
<i>umbrosa</i> (Pfeiffer, 1828)	23	W. Germany, Austria
<i>Trichia</i>		
<i>hispida</i> (Linnaeus, 1758)	23	Netherlands, Belgium
<i>striolata montana</i> (Studer, 1820)	23	W. Germany, Denmark
<i>striolata danubialis</i> (Clessin, 1874)	23	W. Germany
<b>Campylaeinae</b>		
<i>Chilostoma</i>		
<i>cingulatum baldensis</i> (Rssm., 1839)	30	W. Germany
<i>achates achates</i> (Rssm., 1835)	30	Austria
<i>planospira illyrica</i> (Stabile, 1864)	30	W. Germany, Italy
<i>intermedium</i> (Férussac, 1821)	30	Italy

We could confirm the chromosome numbers given by previous authors. In *Theba pisana* (Müller, 1774) and *Cepaea hortensis* (Müller, 1774) there was a controversy between the chromosome numbers given by elder workers and those published recently by RAINER (1967). In both cases we could confirm the original counts.

The true and/or pseudovariation in the chromosome numbers of Helicidae is due to the following phenomena:

- I. Supernumerary chromosomes. These are found so far only in *Helix pomatia* Linnaeus, 1758, and are characterized by the following features:
  - a. Their occurrence is not characteristic for populations. They are present in some specimens of the same population and not in others. If they occur, they occur in different numbers, even within one and the same individual. We have found them in one and the same specimen in the following combinations:  $2n + 1$  supernumerary univalent ( $n + 1$  sup. univ.),  $n + 3$  sup. univ.,  $n + 1$  sup. bivalent,  $n + 1$  sup. biv. +  $1$  sup. univ.,  $n + 1$  sup. trivalent, and  $n + 1$  sup. triv. +  $1$  sup. univ.
  - b. Supernumerary chromosomes are the smallest of the chromosome set.
  - c. They are not heteropycnotic at pachytene but they are positively heterochromatic at early diakinesis.
  - d. At metaphase they are usually not situated in the equatorial plane.

<sup>1</sup>RIN-communication No. 3

- e. They have a delayed anaphase I.  
 f. They do not divide at anaphase II but follow the other chromosomes to one of the two poles.
- II. Delayed pairing. In *Candidula gigaxi* one pair of chromosomes has a delayed pairing at diakinesis. In many figures of early metaphase I it occurs in univalent stage. The chromosome number being in this way 26 bivalents and 2 univalents. At late metaphase the univalents are also paired and 27 bivalents occur in the picture. The haploid chromosome number is the number of bivalents of homologous autosomes. Therefore the delayed paired univalents cannot be counted separately.
- III. Numeric variation, not due to supernumeraries or delayed pairing, has been observed only in *Trichia striolata montana*. In an individual of this species ( $n = 23$ ) we found one early metaphase figure with 26 elements, but in most of the figures studied 22 bivalents occurred. For the time being we are unable to explain the nature and mechanisms causing this situation.
- The haploid chromosome numbers in the family vary from 21 to 30. The distribution of the chromosome numbers within the family and subfamilies is given in Table 2.

TABLE 2. Distribution of chromosome numbers in the subfamilies of Helicidae

Subfamily	Number of species examined	Number of species with chromosome number (n)									
		21	22	23	24	25	26	27	28	29	30
Helicellinae	13			4	1		6	2			
Hygromiinae	10	1		8	1						
Helicodontinae	1							1			
Campylaeinae	11									3	8
Helicinae	20		3			3	4	8			2
Totals of family	55	1	3	12	2	3	10	11		3	10

It is apparent from Table 2 that there is no family type number *sensu* WHITE (1954) in the Helicidae. The type numbers on the other hand can be identified for the subfamilies Helicellinae (26), Hygromiinae (23), Campylaeinae (30) and Helicinae (27). The distribution of the chromosome numbers within the family and subfamilies is in favour of the suggestion that the family represents an unnatural group.

As far as chromosome numbers are concerned, Helicinae, Campylaeinae, and Helicellinae combined with Hygromiinae form three cytologically well defined groups.

An evolutionary trend in the direction from 27 to 22 is apparent in the Helicinae. The total chromosome length remains in all species approximately the same, regardless of the actual chromosome number. From the cytological point of view the Bradybaenidae fill up the gap between Helicinae and Campylaeinae.

As to the group combination Helicellinae-Hygromiinae it is apparent that, if Rainer's idea (1967) is accepted and *Cochlicella* is brought into the tribe Monacheae, and the tribe is moved to the subfamily Hygromiinae, the original subfamilies form, from a cytological point of view, a closed up natural unit. If, on the other hand, there are other grounds to stick to the present organisation of the subfamilies, the two subfamilies together form a closed up natural system, which is not allied to any other helicid subfamily (cf. Table 2).

In our opinion Helicinae and Campylaeinae should be given family rank, whereas the combination Helicellinae-Hygromiinae should be regarded a single independent family.

## LITERATURE CITED

- GRIETHUYSEN, G. A. van, 1968, Waarnemingen over de variatie van het karyotype en het gedrag in de meiose bij de wijngaardslak *Helix pomatia* Linnaeus, 1758 (Gastropoda, Stylommatophora: Helicidae). *Genen en Phaenen*, 12(2): 44-45.
- RAINER, M., 1967, Chromosomenuntersuchungen an Gastropoden (Stylommatophoren). *Malacologia*, 5(3): 341-373 (with bibliography).
- WHITE, M. J. D., 1954, Animal cytology and evolution, *Cambridge Univ. Press*, 2nd ed. 454 p.

## SOME ASPECTS OF ADAPTIVE RADIATION IN RECENT FRESHWATER MOLLUSCS

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## SUMMARY

Adaptive radiation is the evolutionary sequence of events leading to the differentiation and proliferation of new taxa from a common ancestor. These events are (1) acquisition of new adaptive characters, (2) immigration into previously unoccupied geographical areas and (3) speciation in these new areas. Total results are usually observable only by study of successive fossil assemblages but study of living faunas may shed important light on the detailed nature of individual events.

In eastern North America the Lymnaeidae, Planorbidae and Sphaeriidae (here called Group 1) are primarily subarctic, and the Viviparidae, Pilidae, Pleuroceridae and Unionidae (Group 2) are primarily warm-temperate. Other families show less complete correlations with climatic zones. Important adaptive biological characteristics of the families in Group 1 and Group 2, attained through prior completion of Event 1 (acquisition), correlate remarkably well with aspects of their environment and justify the formulation of the following generalizations.

(a) Adaptive characters in Group 1 include the ability to be passively transported and the capability for facultative self-fertilization. These are interdependent features which especially fit Group 1 to complete Event 2 (immigration) in the north.

(B) Adaptive characters in Group 2 include brood protection, the dioecious habit, ecological specificity, heavy shells and (in Unionidae) parasitism on fishes. These features fit Group 2 to withstand the more intense selective predator pressures which operate in the warm-temperate region and also to complete Event 2.

Eight subspecies of boreal freshwater gastropods appear to have evolved in eastern North America since the Pleistocene, *i.e.*, *Valvata sincera ontariensis* Baker, *Helisoma anceps royalense* Walker, *H. campanulatum collinsi* Baker, *Helisoma corpulentum vermilionense* Baker, *Helisoma corpulentum whiteavesi* Baker, *Lymnaea stagnalis sanctaemariae* Walker, *L. calascopium nasoni* Baker, and *L. c. preblei* Dall. All of these subspecies, except *L. c. preblei*, occur only in Lake Superior and in nearby adjacent portions of the Lake Superior and Hudson Bay watersheds. The Lake Superior region, therefore, appears to be the most active recent site for freshwater gastropod evolution in boreal eastern North America. Similar isolative and adaptive factors associated with the unique ecology of Lake Superior may have contributed to the partial completion of Event 3 (speciation) in all seven instances.

## PROC. THIRD EUROP. MALAC. CONGR.

## INTRODUCED MOLLUSCS OF THE UNITED STATES

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## ABSTRACT

Up to the present we have knowledge of 204 species of foreign molluscs which have been reported as being present in the continental United States. We will doubtlessly find other records as we proceed with preparing for publication the "Introduced Molluscs of Eastern North America." A similar work, "Introduced Molluscs of Western North America," was published in 1966 by G. Dallas Hanna of the California Academy of Sciences. The dividing line between east and west is, of course, a natural barrier, the Rocky Mountains.

These molluscan invaders are not limited to land. Both freshwater and marine forms occur also. Over the years various ones of these molluscs have managed to become established at least well enough so that they have been reported as being present by various malacologists. The introduced land molluscs live in cultivated areas or places modified greatly by human activities. Parks, nurseries, flower gardens, vegetable gardens, orchards, etc., are the types of places where they are most likely found. Only a minority penetrate into natural habitats. Not every species which manages to get into the country is able to become established. Most of those which do become established do not cause much visible upset of other populations; on occasion, however, they do become serious pests.

These molluscs come from all over the world and arrive in various ways: on plants being imported, in cargoes of fruits, household goods of our military personnel, military equipment, with shipments of tropical fishes, in luggage of tourists or as stowaways. In the words of Elton (1953), "one of the primary reasons for the spread and establishment of species has been quite simply the movement around the world by man of plants, especially those intentionally brought for crops or garden ornament or forestry." It is also likely that a few arrive through means of their own such as flying, drifting, or gradually spreading from adjacent areas.

Two examples of species which have been introduced in recent years and which have been spreading rapidly are an Asiatic clam and a veronicellid slug.

The clam, *Corbicula fluminea*, was first discovered in the United States in the Columbia River system in the northwest in 1939. From there it spread first through California, and by 1956 it was in our desert southwest region in irrigation canals. By 1961 it had appeared in the Tennessee and Cumberland drainages; in 1962 it was found in the Ohio River system; in 1963 it was in the streams in southern Louisiana; in 1964 it was taken at Vicksburg on the Mississippi River; since then it has been reported in numerous localities in Florida. In areas where it is found it occurs in great numbers, and in many of these areas it is a serious pest for companies using sand from the rivers.

Another mollusc on which there are good data is a veronicellid slug which seems to be related to *V. aberrans* or *V. angustipes* from Rio Grande del Sur in Brasil, but which we have yet been unable to positively identify.\* It was found in the U. S. for the first time in Mobile, Alabama and New Orleans, Louisiana in 1960. Since then it has been spreading throughout the southeastern U.S., and it is now found in great numbers in Louisiana, Mississippi, Alabama, Florida and is still spreading. I have had the opportunity of being on hand and watching the performance of this mollusc since its introduction. I have been able to carefully follow its spread and have had the opportunity of studying its ecological requirements and its morphology. This is one of the few cases where we know the date and points of entry and have been able to follow the course of events since its introduction.

The goal is now to complete the listing of the introduced species, to determine, where possible, the present existence of these, and then to summarize the results. My feeling is that, if all of these aliens are registered now, and if we keep records as to their whereabouts and study some of them in detail as I and others have already done, then we will be able to combat any uprising by them which might occur in the future.

Generally most of these introduced forms seem to manage to find a place for themselves without causing much visible upset of other populations; on occasion their entry has many repercussions.

\*In the meantime the slugs could be identified to be *Vermicella ameghini* Gambetta.

## REFERENCE

ELTON, C., 1953, *The Ecology of Animals*. Methuen & Co., Ltd., London.



PHYSIOLOGIE DE L'ORGANE DE PERFORATION DE *PURPURA* (THAÏS) *LAPILLUS*:  
 ROLE DE L'ANHYDRASE CARBONIQUE

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RÉSUMÉ

L'étude histoenzymologique de l'organe de perforation de la Pourpre par la méthode de Häusler (Chétail et Binot, 1967) montre que cette formation recèle de l'anhydrase carbonique, enzyme dont la présence est également confirmée par la méthode biochimique de Meldrum et Roughton (Chétail et Fournié, 1968). Si l'anhydrase carbonique est vraiment responsable du percement des valves calcaires des proies de *Purpura*, en utilisant le "diamox," inhibiteur spécifique de l'enzyme, on pouvait s'attendre à un ralentissement ou à une suppression du processus de perforation; au contraire, l'activation de l'anhydrase carbonique par le CO<sub>2</sub> qui est l'un des substrats de cette enzyme permettait d'espérer une accélération du phénomène de percement (Rosenberg, Chétail et Fournié; Chétail et Rosenberg). Pour vérifier cette hypothèse, une étude physiologique a été entreprise en ajoutant dans l'eau d'élevage des animaux, soit du "diamox" à diverses concentrations pour les expériences d'inhibition "in vivo," soit du CO<sub>2</sub> pur ou deux mélanges différents de CO<sub>2</sub> + O<sub>2</sub> pour les essais d'activation. Pour interpréter les résultats expérimentaux, nous nous sommes constamment référés aux observations effectuées sur des animaux témoins élevés en eau de mer normale; dans ces conditions, les tentatives de perforation aboutissent toujours à un résultat positif, soit: 50% de trous complets, 33% de trous incomplets et 17% d'empreintes.

**Expériences d'inhibition "in vivo":** pour les faibles concentrations en "diamox" (10<sup>-3</sup>M et 3.10<sup>-3</sup>M), on observe une diminution du nombre des trous complets dans le premier cas et leur disparition totale dans le second; par contre pour ces deux concentrations, on note une élévation du nombre des empreintes que l'on peut interpréter ainsi: par suite de l'inhibition de la majeure partie de l'enzyme au niveau de l'organe de perforation, les Pourpres qui normalement auraient dû effectuer un trou complet ne peuvent plus réaliser qu'une empreinte. Pour les concentrations plus fortes en "diamox" (5.10<sup>-3</sup>M et 7.10<sup>-3</sup>M), on obtient une même inhibition totale de l'enzyme, toutes les tentatives de perforation restant sans résultat, pour un temps de fixation pourtant beaucoup plus élevé que celui noté chez les témoins. Si l'on remplace les animaux "diamoxés" en eau de mer normale et que l'on observe leur comportement, on constate que l'inhibition de l'anhydrase carbonique est réversible et que ce sont les Pourpres soumises aux doses de "diamox" les obligeant à un jeûne absolu, qui n'ontrent le plus d'activité lors de leur remise dans leur milieu normal.

**Expériences d'activation "in vivo":** L'activation de l'anhydrase carbonique par le CO<sub>2</sub> pur se traduit par une augmentation du nombre des trous complets (égal en fait à la somme de trous complets et incomplets dénombrés chez les témoins), une diminution du nombre des trous incomplets (égal au nombre des empreintes chez les témoins) et la disparition des empreintes; on peut interpréter ainsi ces résultats: par suite de l'activation de l'anhydrase carbonique au niveau de l'organe de perforation, les Pourpres qui normalement n'auraient effectué qu'un trou incomplet ou une empreinte ont pu réaliser à la place, soit un trou complet dans le premier cas, soit un trou incomplet dans le second. Par contre, le temps moyen de fixation nécessaire pour obtenir un trou complet ou incomplet est supérieur à celui observé chez les témoins, par suite de l'effet anesthésique de ce gaz. Pour éliminer cet effet, nous avons utilisé deux mélanges gazeux contenant des proportions différentes de gaz carbonique et d'oxygène; les résultats obtenus montrent que l'activation de l'anhydrase carbonique est proportionnelle à la quantité de CO<sub>2</sub> dissoute dans l'eau de mer des élevages: C'est ainsi qu'avec le mélange 5% CO<sub>2</sub> + 95% O<sub>2</sub> on obtient deux fois plus de trous complets que chez les témoins en un temps légèrement plus court, tandis qu'avec le mélange 95% CO<sub>2</sub> + 5% O<sub>2</sub> on en compte jusqu'à trois fois plus, et ceci en un temps nettement plus bref: le CO<sub>2</sub> facilite donc considérablement le percement. L'anhydrase carbonique catalyse la réaction réversible: CO<sub>2</sub> + H<sub>2</sub>O ⇌ H<sub>2</sub>CO<sub>3</sub> ⇌ H<sup>+</sup> + HCO<sub>3</sub><sup>-</sup>; l'action du gaz carbonique peut alors s'expliquer ainsi: en présence d'une teneur en CO<sub>2</sub>, accrue par rapport aux conditions normales, la réaction catalysée par l'anhydrase carbonique dans le sens de l'hydratation du CO<sub>2</sub> est favorisée; il en résulte une production supplémentaire d'ions H<sup>+</sup> responsable de la dissolution plus rapide du carbonate de calcium des valves de Lamellibranches par les Pourpres élevées en eau de mer enrichie en CO<sub>2</sub>.

En résumé, ces expériences d'inhibition et d'activation "in vivo" prouvent que l'anhydrase carbonique décelée dans l'organe de perforation est l'agent impliqué lors du percement des valves calcaires des proies de *Purpura* (Thaïs) *lapillus*; en outre, les résultats obtenus par l'action du CO<sub>2</sub> apportent des précisions sur le mécanisme chimique de la réaction en cause. Il est probable que les ions H<sup>+</sup> émis sous l'action de l'anhydrase carbonique sont échangés contre des ions Ca<sup>++</sup> dont la concentration est très élevée

pendant l'activité de l'organe de perforation, comme nous l'avions mentionné auparavant (Chétail et Binot 1967), mais ce point de vue n'a pu encore être confirmé; cependant, il n'est pas impossible qu'un cation autre que  $\text{Ca}^{++}$  soit aussi impliqué dans ces échanges.

En résumé, nos résultats montrent clairement que l'acidité produite au niveau de l'organe de perforation, sous l'influence de l'anhydrase carbonique, est responsable de la dissolution du  $\text{CaCO}_3$  des valves des Lamellibranches par la Pourpre et que cette activité anhydrique s'accompagne d'échanges ioniques complexes dont la nature reste à préciser.

## REFERENCES

- CHÉTAIL, M. & BINOT, D., 1967, Présence et rôle de l'anhydrase carbonique dans l'organe accessoire de perforation de *Purpura lapillus* L. *C. R. Acad. Sci.*, 264(7): 946-949.
- CHÉTAIL, M., BINOT, D. & BENSALÉM, M., 1968, Organe de perforation de *Purpura lapillus* L. (Muricidé): histochimie et histoenzymologie. *Cah. Biol. Mar.*, 9: 13-22.
- ROSENBERG, A. J., CHÉTAIL, M. & FOURNIE, J., 1968, Intervention de l'anhydrase carbonique dans le mécanisme de perforation des valves de Lamellibranches par *Purpura (Thaïs) lapillus* L. (Gastéropode Prosobranchie Muricidé). *C. R. Acad. Sci.*, 266: 944-947.
- CHÉTAIL, M. & ROSENBERG, A. J., 1968, Carbonic anhydrase and shell boring mechanism by *Purpura (Thaïs) lapillus* L. *Am. Zool.*, 8: 802.
- CHÉTAIL, M. & FOURNIE, J., 1968, Shell boring mechanism in the gastropod, *Purpura (Thaïs) lapillus*: a physiological demonstration of the role of carbonic anhydrase in the dissolution of  $\text{CaCO}_3$ . *Am. Zool.*, 9(3): 232-237.

## DISTRIBUTION AND ECOLOGY OF HELICODONTINAE IN NORTHERN ITALY

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## ABSTRACT

The wood-inhabiting Mollusca and other species with similar microenvironmental exigencies, are not so well fit as the calcareous rock-inhabiting species for a biogeographic detailed study of a region. However, an attempt is carried out in this work with some species of the subfamily *Helicodontinae*. In Northern Italy *Drepanostoma nautiliforme* PORRO is distributed only in Piedmont and the western side of Lombardy. This small snail with a merely woodland ecology seems to have a residual distribution, for in the Pleistocene it lived in the Northern Alps, too, as we can see from the Quaternary fossils. Also, *Helicodonta obvoluta* (Müller) is a typical form of the woodland communities and in connection with the progressive reduction of the deciduous wood tends to leave those parts of Lombardy that were occupied immediately after the Würm post-glacial period. Therefore, it is more frequent in rather undisturbed zones at the head of the Prealps valleys and at the top of the mountains. This fact causes a general rarefaction of the area occupied by the species which, in many cases, presents clearly disjointed distribution. *Helicodonta angigyra* (Ziegler) having a higher ecological valence can profit alone by environmental conditions arisen in the historical times, connected with wood degradation, human trade, and consequently a new vegetable and morphologic aspect of so many Lombard zones.

DIE GATTUNG *TRISSEXODON* PILSBRY<sup>1</sup>

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## ZUSAMMENFASSUNG

In der Gattung *Trissexodon* (Gastropoda, Pulmonata, Helicodontinae) werden zwei rezente und zwei fossile Arten untergebracht. Von den beiden rezenten Arten, *T. constrictus* (Boubée), dem Genotypus aus den westlichen Pyrenäen und *T. quadrasi* (Hidalgo), aus Ost-Spanien, konnten einige Tiere anatomisch untersucht werden.

Es stellte sich heraus, dass die beiden rezenten Arten durchaus nicht nahe verwandt sind und in zwei verschiedene Gattungen gehören. Die von Ortiz de Zarate (1943: 82) gegebene Abbildung der Genitalorgane von *T. constrictus* erwies sich als unrichtig.

Für *Helix quadrasi* wird eine neue Gattung aufgestellt. (Siehe E. Gittenberger, 1968).

Ausserdem wird auf vier unbenannte Arten aus Jugoslawien hingewiesen, die im Gehäuse *T. constrictus* etwas ähnlich sehen und in einigen Sammlungen unter *Trissexodon* eingeordnet wurden. Die Anatomie ist unbekannt. Es handelt sich hier um Spelaediscinae. Für die vier neuen Arten wird eine neue Gattung mit zwei Untergattungen aufgestellt. (Siehe E. Gittenberger, 1969).

Von den beiden fossilen Arten wird eine, *Polygyra plioauriculata* Sacco, in *Protodrepanostoma* Germain zurückverwiesen. Die andere, *Helix subconstrictus* Souverbie, kann in der Gattung *Trissexodon* bleiben.

## LITERATUR

- GITTENBERGER, E., 1968, Zur Systematik der in die Gattung *Trissexodon* Pilsbry (Helicidae, Helicodontinae) gerechneten Arten. *Zool. Meded. Rijksmus. Nat. Hist. Leiden*, 43(13): 165-172.
- GITTENBERGER, E., 1969, Beiträge zur Kenntnis der Pupillacea; Die Spelaediscinae. *Zool. Meded. Rijksmus. Nat. Hist. Leiden*, 43(22): 287-306.
- ORTIZ DE ZARATE, A., 1943, Observaciones anatómicas y posición sistemática de varios Helícidos españoles, 1. *Bol. Real Soc. Esp. Hist. Nat.*, 41(1/2): 61-83.

<sup>1</sup>In extenso as thesis.

## BEITRÄGE ZUR ÖKOLOGIE UND BIOLOGIE DER PISIDIEN IM LUNZER UNTERSEE

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## ZUSAMMENFASSUNG

Die häufigsten, aber dabei am wenigsten bekannten Süßwassermuscheln sind die Sphaeriidae. Sie fehlen in fast keinem Biotop, weder in grossen Gewässern noch in kleinen Wasseransammlungen. Die Verbreitung ist grossteils nicht geographisch gebunden und Wasserscheiden sowie Meerengen bilden keinerlei Hindernis für die Ausbreitung, die hauptsächlich endo- und ektozoologisch durch Wassergefügel, Fische, Insekten u.a. erfolgt. Für das Vorkommen sind lediglich klimatische und ökologische Faktoren ausschlaggebend.

Obwohl der Lunzer Untersee (Seehöhe 608 m, max. Tiefe 33 m), ein Voralpensee, faunistisch als sehr gut erforscht gelten kann, finden wir Angaben über die Weichtierfauna sehr selten. Über Pisidien ist meines Wissens überhaupt nichts bekannt.

Es ist nun sowohl die räumliche Verteilung der verschiedenen Arten im See, als auch die jahreszeitlichen Unterschiede in der Besiedlung von Interesse.

An Hand der Besiedlungsverhältnisse lassen sich drei Zonen unterscheiden. Das Litoral von 0-8 m als Litoral I, die Zone zwischen 8 und 12 m als Litoral II, und darunter das Profundal. Die Tiefenverteilung der verschiedenen Arten dürfte hauptsächlich von der Temperatur und vom Substrat abhängig sein. Die Substratverhältnisse lassen sich relativ einfach charakterisieren. Zwischen 0 und 8 m, dem Litoral I, finden wir sehr kalkreichen Schlamm und Seekreide mit grossen Mengen von Molluskenresten. Diese Zone weist einen geringen Makrophytenbewuchs auf. Von 0-2 m überwiegt *Phragmites*, daran schliessen sich einige *Potamogeton*-Arten an. Vor allem diese Potamogetonzone wirkt infolge einer ziemlich starken biogenen Kalkausscheidung sehr limitierend auf die Pisidienfauna. Diese Kalkausfällung verursacht einen ziemlich starken Regen, der die Tiere durch Verschüttung in ihren Lebensgewohnheiten empfindlich stören dürfte. Wir finden hier in quantitativen Proben eine sehr geringe Individuendichte. An diese Zone schliesst sich das Litoral II zwischen 8 und 12 m an, wo wir schon Feinschlamm mit Eisenaussfällungen antreffen, die sich dann bis in die tiefsten Stellen des Sees erstrecken. An Makrophytenbewuchs tritt nur noch *Fontinalis* auf. Die Profundalregion besteht aus ziemlich einheitlichen Feinschlamm-sedimenten.

Die sieben Pisidiumarten verteilen sich nun wie folgt: *Pisidium nitidum*, *P. milium*, *P. liljeborgi* und *P. subtruncatum* im Litoral I, *P. conventus* und *P. personatum* (im den oberen Teilen) im Profundal. Im Litoral II findet sich mit *P. nitidum*, *P. casertanum*, *P. liljeborgi* und *P. conventus* die artenreichste Fauna. Dieses Gebiet ist zum Teil als Misch- und Überschneidungsgebiet aufzufassen. Von diesen 7 Arten überwiegen nun zwei in zum Teil beträchtlichem Masse. *P. conventus* als charakteristische Profundalform bildet grossteils eine einartige Population und wird nur in den oberen Teilen von *P. personatum* begleitet, welches in anderen Seen manchmal noch weit tiefer als *P. conventus* geht und dieses verdrängt, was aber hier nicht der Fall ist. *P. conventus* ist eine typische Kaltwasserart, die in unseren Breiten auf das Profundal von Seen beschränkt bleibt und nur in höheren geographischen Breiten bis ins seichte Litoral reicht. Zu dieser Kaltstenothermie dürfte sich noch eine Rheophobie gesellen, die es den Tieren nicht gestattet, sich auch in kalten Fließgewässern anzusiedeln, sowie gewisse Ansprüche an das Substrat. Die Temperatur im Biotop erreicht und überschreitet selten 12° Celsius. Im Litoral I überwiegt bei weitem *P. nitidum*. Die anderen Arten treten zahlenmässig stark zurück.

Die zeitlichen Änderungen der Besiedlungsdichte sind hauptsächlich von den Lebenszyklen der einzelnen Arten, wann und wie oft Nachkommen herangebildet werden, abhängig. Bei *Pisidium nitidum* werden die meisten Jungtiere im Juli und August frei. Zu dieser Zeit erreicht die Temperatur im Biotop ihr Maximum. In den tieferen Zonen, die von *P. conventus* bewohnt werden, sind die Temperaturverhältnisse relativ ausgeglichen. Man findet bei *P. conventus* sowohl in 10 als auch in 20 m Tiefe das ganze Jahr hindurch trüchtige Tiere. Die Brutperioden sind bei dieser Art nicht zeitlich korreliert, sondern erfolgen das ganze Jahr hindurch nach Erreichen einer bestimmten Körpergrösse. Neben diesen Populationszunahmen, die sich mehr oder minder durch die Brutperioden erfassen lassen, treten nun noch Abnahmen auf. Diese können sowohl durch Parasiten als auch durch Räuber verursacht werden. Darüber ist allerdings noch zu wenig bekannt, um sichere Aussagen zu machen.

## PROC. THIRD EUROP. MALAC. CONGR.

CONTRIBUTION TO THE KNOWLEDGE OF THE CYTOTAXONOMIC CONDITIONS  
IN THE STYLOMMATOPHORAN SUPERFAMILY ZONITACEA<sup>1</sup>

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## ABSTRACT

PERROT (1938), HUSTED & BURCH (1946), BEESON (1960), LAWS (1966) and RAINER (1967) have published on the cytology of 16 species of the families Zonitidae, Milacidae and Limacidae. In the course of the present study 7 species of the families Vitrinidae and Zonitidae were examined. None of them have been previously studied cytologically. The haploid chromosome number  $n = 31$  was found in all Vitrinidae. The same haploid number occurs in the zonitid *Aegopinella nitidula*, whereas *Oxychilus cellarius* and *O. draparnaudi* have 24 bivalents ( $2n = 48$  in the latter species). Their main cytological data are given in Table 1.

TABLE 1. New chromosome numbers in the superfamily Zonitacea

Family and species	n	2n	Origin
Vitrinidae			
<i>Vitrina pellucida</i> (Müller, 1774)	31		Netherlands, W. Germany
<i>Vitrinobrachium breve</i> (Ferussac, 1821)	31		Netherlands, W. Germany
<i>Eucobresia diaphana</i> (Draparnaud, 1805)	31		Netherlands
<i>Phenacolimax major</i> (Ferussac, 1807)	31		Netherlands
Zonitidae			
<i>Aegopinella nitidula</i> (Draparnaud, 1805)	31		Netherlands
<i>Oxychilus cellarius</i> (Müller, 1774)	24		Netherlands
<i>Oxychilus draparnaudi</i> (Beck, 1837)		48	Netherlands

The family numeric pattern is clear in the Vitrinidae only ( $n = 31$ ). In the Zonitidae the chromosome numbers vary greatly:  $n = 20$  in 1 species of Vitreinae;  $n = 24$  in 2 species, 30 in 2 species and 31 in 2 other species of Zonitinae; in the Gastrodontinae  $n = 30$  or about 30 in *Zonitoides nitidus* (Müller, 1774) and *Z. excavatus* (Alder, 1830) according to our photographs, which, however, do not permit a final decision.

In the Milacidae the family type number is probably 33. In the Limacidae 2 species have  $n = 24$ , 4 species  $n = 30$  and 3 species have 31 bivalents.

As to the trend of the karyotypic evolution within the superfamily, it is probably of importance that in the high- $n$  complements (30-31) the chromosomes are of gradually decreasing magnitude, whereas the low- $n$  karyotypes show two exceptionally long pairs. This situation seems to suggest several centric fusions resulting in a reduced chromosome number and exceptional relative length of some pairs of chromosomes. It is particularly clear in the species *Aegopinella* - *Oxychilus* and probably also in *Limax* - *Malacolimax*, *Lehmannia*.

The direction of the evolution from the high to the low chromosome number is also apparent in the stylommatophoran family Helicidae. Apart of the variation in chromosome number, the morphology of the karyotype is extremely uniform within single zonitacean families. This applies to the relative length of the elements, chiasma frequency, chiasma morphology, and the number of notably bigger and smallest elements. Nevertheless, as far as our material is concerned, minute, but clear and constant karyotypic differences enable cytotaxonomic separation of *Vitrina pellucida*, *Vitrinobrachium breve*, *Eucobresia diaphana* and *Phenacolimax major*.

<sup>1</sup>RIN-communication No. 4

## LITERATURE CITED

- BEESON, G. E., 1960, Chromosome numbers of slugs. *Nature*, London, 186: 257-258.
- HUSTED, L. & BURCH, P. R., 1946, The chromosomes of polygyrid snails. *Amer. Nat.*, 80: 410-429.
- LAWS, H. M., 1966, The cytology and anatomy of *Oxychilus alliarius* (Miller) (Mollusca, Zonitidae) a new introduction to South Australia. *Rec. S. Austr. Mus.*, 15: 257-260.
- PERROT, M., 1938, Etude de cytologie comparée chez les gasteropodes pulmonés. *Rev. Suisse Zool.*, 45: 487-566.
- RAINER, M., 1967, Chromosomenuntersuchungen an Gastropoden (Stylommatophora). *Malacologia*, 5(3): 341-373.

## REMARKS ON THE BIOLOGY OF ABYSSAL BIVALVES

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## ABSTRACT

The study is based mainly on the collection of bivalves obtained by the "Galathea" deep-sea expedition (1950-52) at depths greater than 2000 m, 127 samples from 50 stations, a total of 1500 specimens. The collection comprises 76 species, of which 36 (besides 11 from the hadal zone, below 6000 m) are described as new. Three species are represented by valves only, no less than 27 of the 76 species are represented by a single specimen, and only 19 species are represented by 10 or more specimens. Besides the "Galathea" collection a smaller number of samples from other sources have been included, so that altogether 159 samples with some 1700 specimens, distributed over 91 taxa, have been studied in some detail.

During the study numerous samples from the earlier deep-sea expeditions have been examined, partly to solve taxonomic problems, but also in an attempt to determine whether a given species is known from specimens alive at capture or from empty valves only, as this is frequently not mentioned in the literature.

Altogether I have examined about 75% of the existing samples of abyssal bivalves, in addition to several hundred samples of bathyal bivalves. Taxonomic revision of a number of species and the exclusion of numerous records of shallow-water bivalves only represented by empty valves has considerably reduced the number of species of bivalves known from depths greater than 2000 m. Including the 36 new species obtained by the "Galathea" expedition, altogether about 230 species are known from depths between 2000 and 6000 m. Thirty-eight are bathyal species which penetrate into the abyssal zone (mostly upper part), leaving about 192 species as an "endemic" abyssal bivalve fauna. It should be emphasized, however, that the upper limit of the abyssal zone is not sharp, and varies in different parts of the World Ocean, although it appears that the upper limit of a number of comparatively well-known species is located between 2000 and 2500 m depth.

Our knowledge of the abyssal bivalves is still very deficient. This is, for instance, shown by the fact that 122 of the 192 species have only been recorded once, and only 11 species have been recorded 10 times or more. It should also be noted that only about 270 samples of abyssal bivalves have been obtained, and only 80 samples with bivalves have been obtained below 4000 m (the average depth of the World Ocean).

The horizontal distribution of some species has been worked out: *Malletia cuneata* (Jeffreys) is known from the Arctic Ocean (at great depths only), and the World Ocean including the Antarctic and the E. Pacific. It appears to be the only species common to the Arctic Ocean and the abyssal depths of the World Ocean. *Arca orbiculata* Dall is found throughout the World Ocean, including the E. Pacific, and a similar distribution is found in *Acar asperula* (Dall), although no records are at hand from the easternmost part of the E. Pacific (Panama region). *Abra profundorum* (Smith) is known from the Atlantic, Indian Ocean and W. Pacific, while no records are available from the E. Pacific. In one case it has been found that one subspecies, *Limopsis pelagica pelagica* Smith, is widely distributed in the Atlantic and Indian Oceans (but apparently absent from the W. Pacific). In the E. Pacific it is replaced by *L. pelagica dalli* Lamy. A similar type of distribution has been found in *Poromya tornata* (Jeffreys) (Atlantic and Indian Oceans), which is replaced in the E. Pacific by *P. perla* Dall. *Propeamussium meridionale* (Smith) is known only from the Pacific (including the E. Pacific) and the Indian Oceans, but appears to be absent from the Atlantic, while *Cyclopecten undatus* (Verrill & Smith) is known mainly from the Atlantic (with one record from the Indian Ocean). Finally, *Myonera undata* (Verrill) is found in both the Atlantic and Indian Oceans, but not in the Pacific. Nearly all the species referred to above are known from between 10 and 40 records and most of them are known from a depth below 4000 m.

In the distribution of the bivalves outlined above, there is no indication of either an Atlantic subregion versus an Indo-pac-Pacific region as has been suggested by Ekman (1953) or an Atlantic-Indian subregion versus a Pacific subregion (Madsen, 1961), although a corresponding distribution has been found in a few individual species.

In a few species the size of the samples made a closer study of the intraspecific variation possible. This is particularly the case in the following species: *Malletia cuneata*, *Acar asperula*, *Limopsis pelagica* (both subspecies) *Arca orbiculata*, *Propeamussium meridionale* and *Abra profundorum*. In the three last-mentioned species only a very small range of variation was observed, but the three first-mentioned species varied widely in many characters (shape of the shell, dentition of hinge, etc.). However, no geographical variation could be observed, nor was there any variation which could be correlated with the depth. It appeared that whenever larger samples were present, the species' whole range of variation would generally be found within the sample.

In several groups (Isopoda, Amphipoda) a very limited distribution has been found in many abyssal

species. Apparently many species are confined to a single basin ("basin endemism"). Clarke (1962) advocated the generally restricted distribution of abyssal non-cephalopod molluscs, stating that the known mean geographical spread for most species is 2.0 ocean basin. The present survey has established a very wide distribution for many species. The alleged "basin endemism" is probably only due to the fact that most species (in case of the bivalves 64%) have only been recorded once. Additional records may considerably extend the known distribution of numerous species.

The composition of the abyssal bivalve fauna differs from that of other areas by the high proportion of Protobranchia (49%) and Septibranchia (25%), while all other families (with the exception of the Pectinidae, 7%) are very poorly represented. The number of abyssal bivalve species appears to be roughly twice the number of species of the arctic fauna and the antarctic fauna, living under the same temperature conditions. However, it seems most likely that numerous abyssal species of bivalves still remain undiscovered.

A detailed account is in print.

#### LITERATURE CITED

KNUDSEN, J. (In press). The systematics and biology of abyssal and hadal bivalvia. *Galathea Report* vol. 11.

MALACOLOGIA, 1969, 9(1): 272

#### PROC. THIRD EUROP. MALAC. CONGR.

#### FLAPPING BEHAVIOR IN THE LAMPSILINAE (PELECYPODA: UNIONIDAE): SOME ASPECTS OF ITS NEUROBIOLOGY

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#### ABSTRACT

Though apparently peculiar to the Lampsilinae, flapping behavior nonetheless involves portions of the behavior repertoire found in many bivalves. Coordinated functions of the foot, marsupium, valves, and siphons during flapping behavior greatly alter the supposed normal relationships between the body and shell. Most striking feature is the rhythmical movement of the mantle flaps. The mantle flaps, which have eyespots and "tails," are remarkably fishlike in appearance, and constitute a permanent anatomical feature of the mature female, as an extension of the inner lobe of the mantle edge, just anteroventrad to the branchial siphons.

In the present paper: (1) Flapping behavior and evidence (from field and aquarium studies, as well as anatomical investigations) for its role as a spawning mechanism were described briefly.

(2) The gross and microscopic neuroanatomy of siphonal and flap regions of *Lampsilis ventricosa*, *L. fasciola*, and *L. siliquoidea* were compared. An unusual, small but conspicuous mantle ganglion was found to be consistently present in both male and female specimens of these three species. This mantle ganglion is located inside the mantle edge, nearly in line with the posterior pallial nerve, and at the point where the pulsing movements of the mantle flaps are initiated during flapping behavior. Further, the connections which this ganglion makes with nerves which extend to the visceral ganglion, to the posterior pallial nerve and distally into the mantle flap, suggest that the mantle ganglion may be a significant neuro-anatomical entity in mantle flap movements.

(3) Experimental evidence was presented to show that certain changes in light intensity can account for diurnal changes in flapping behavior which have been monitored in *Lampsilis ventricosa*.

(4) An hypothesis was offered concerning one possible role of the flap movements *per se* in the spawning process, *i.e.*, that the bellows-like movement of the mantle flaps over the gravid ovisacs of the marsupia aids in the suspension of the recently shed glochidia in the water, and thus helps to effect their necessary contact with the fish host.

A detailed account of some of the work on which the foregoing findings are based, is to be published in a regular issue of *Malacologia*.



THE ARTERIAL GLAND OF *AGRIOLIMAX RETICULATUS* (PULMONATA: LIMACIDAE)

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ABSTRACT

The arterial gland of *Agriolimax reticulatus* consists of irregularly shaped masses of opaque whitish tissue situated discontinuously along the distal portion of the cephalic artery and along its branches, especially the posterior pedal artery. The tissue is divided into lobules with thick bundles of collagen fibres between. Each lobule is composed of irregular cells and intercellular channels, in some cases leading directly to the edge of the gland. Intracellular ducts connect with the intercellular channels.

Granules occur within the cells and these appear to be of two main types. Each **A** type granule has an amorphous, moderately homogenous, electron dense content which normally completely fills its limiting membrane. These granules stain deeply with Toluidine blue. **B** type granules are less electron dense, their contents have a flocculent appearance and they stain only lightly or moderately with Toluidine blue. These granules contain a variable number of irregular spaces.

The granules release their contents into the intercellular channels directly or into the intracellular ducts.

Histochemical tests for carbohydrates, certain hydroxysteroid dehydrogenases, calcium, copper and acid phosphatase were all negative. Tests for lipid were only faintly positive. The secretory granules, however, stained intensely with Bromophenol blue and gave positive reactions to tests for tyrosine and aspartic and glutamic acids. Tests for SS and SH groups were only weakly positive.

Chromatographic analysis for steroids gave negative results.

Microprobe analysis revealed an accumulation of copper within the arterial gland tissue but it was not possible to localise its position within the cells.

As copper and protein were both present within this gland it was decided to test the arterial gland tissue for haemocyanin. Rabbit antiserum to *Helix aspersa* haemocyanin was prepared and found to cross react with *Agriolimax reticulatus* haemocyanin. Immunoelectrophoresis performed using this antiserum and homogenised arterial glands from *Agriolimax reticulatus* gave negative results.

The arterial gland in *Agriolimax reticulatus* contains secretion at all stages of reproductive development. The size of the gland is extremely variable between individuals but neither size nor histology could be related to reproductive development.

Of a number of gastropod species examined for the presence of the gland, tissue with a similar appearance to the arterial gland of *Agriolimax reticulatus*, when stained with Azan, was found in 4: *A. caruanae*, *Limax flavus*, *Oxychilus alliarius*, *O. cellarius*.

STUDIES ON THE ODOUR OF *OXYCHILUS ALLIARIUS* (PULMONATA, ZONITIDAE)

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ABSTRACT

*Oxychilus alliarius* produces an odour indistinguishable from that of garlic. The general opinion of naturalists is that it is a defensive adaptation produced on irritation.

Experiments at isolating portions of the body showed the odour to originate from the right side of the mantle near to the pneumostome. It is liberated on stimulation in a characteristic brown viscous mucus. Analysis of this mucus showed it to be a single entity, a protein/carbohydrate complex, especially rich in protein. Inorganic material constituted eight percent of the dry weight and is probably mainly calcium carbonate, and this may be responsible for the marked viscosity of the mucus.

A gas liquid chromatographic analysis of the volatiles produced on irritation of *Oxychilus alliarius* showed one very large peak and a few minor ones. The main peak was identified as propyl mercaptan.

The cells responsible for the odour are grouped into a small cluster and react very positively to histochemical tests for disulphide and sulphhydryl groups. A 3-dimensional picture produced from serial sections of the region showed that the odour gland cells discharge into a groove which is part of the pneumostome channel although somewhat separate from the main lumen. Ultrastructurally the odour gland cells have a large central vacuole in which accumulates the secretion. The cytoplasm is peripheral and characterised by many golgi bodies and their associated vesicles. The cells are invested with muscle fibres for discharge of the secretion.

Sulphur-35 in the diet was demonstrated autoradiographically to be incorporated into the odour gland. There was a considerable time lag in the appearance of the label in animals which had not been previously stimulated and therefore had undepleted odour reserves.

Experiments to determine the function of the odour showed that it was not a sex attractant, nor did it have antibiotic properties. Time-lapse ciné photographic experiments using hedgehogs as predators showed a statistically significant rejection of *Oxychilus alliarius* in favour of other non-garlic *Oxychilus spp.* Therefore the odour seems to have a defensive function against small mammals, certainly at least against hedgehogs.

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REMARQUES SUR L'HERMAPHRODISME JUVÉNILE  
DE QUELQUES VENERIDAE (BIVALVIA)

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Sur de jeunes exemplaires de Bivalves, on découvre, avant que la glande génitale ne soit fonctionnelle, une structure particulière des éléments germinaux, où l'on peut déceler quelques cellules sexuées. Cette manifestation précoce de la sexualité est extrêmement fugace, ce qui explique qu'elle soit restée longtemps ignorée. Le présent travail rend compte des résultats que j'ai obtenus sur un certain nombre de Veneridae: *Dosinia exoleta* et *Venus verrucosa*, originaires de Locmariaquer (Bretagne, France), *Venus striatula* originaires de Morgat (Bretagne), *Mercenaria mercenaria* originaires de Milford (U.S.A.), *Venerupis decussata* originaires de Plestin (Bretagne), *Venerupis pullastra*, *V. aurea* et *V. rhomboïdes* originaires de Brest (Bretagne).

## TECHNIQUES ET MÉTHODES

Pour chaque exemplaire des coupes histologiques sont effectuées dans la région intéressante, c'est-à-dire entre la région péricardique et la base du pied. On y trouve des tubules qui pénètrent à travers le conjonctif en longeant l'anse intestinale et en contournant les faisceaux musculaires de la base du pied. Or dans ces tubules, qui sont des éléments transitoires, il existe une manifestation sexuelle qui se traduit par le développement d'un nombre limité de gamètes.

## RÉSULTATS

Les résultats obtenus sont résumés dans le tableau suivant.

Espèces	Date	Taille en mm	Sexe indéterminé	♂	♀	♂♀	Total
<i>Dosinia exoleta</i>	mars	8-12	3	1	5	2	11
<i>Venus verrucosa</i>	mars	6-21	3	4	2	1	10
<i>Venus striatula</i>	toute l'année	3-12	5	4	1	12	22
<i>Mercenaria mercenaria</i>	mai	5-10	13	9	3	2	27
<i>Venerupis decussata</i>	février	12-21	5	9	9	3	26
<i>Venerupis decussata</i>	septem.	10-20	0	5	2	8	15
<i>Venerupis pullastra</i>	mars	7-20	3	4	0	0	7
<i>Venerupis aurea</i>	mars	9-20	6	12	2	0	20
<i>Venerupis rhomboïdes</i>	mars	10-19	12	9	3	0	24

On doit considérer ces résultats comme un sondage préliminaire, car le nombre d'exemplaires examinés est relativement faible, notamment pour *Venerupis pullastra* (7), *Venus verrucosa* (10), *Dosinia exoleta* (11). Enfin pour *Venerupis decussata* où 41 exemplaires ont été étudiés, il apparaît une différence notable entre septembre et février pour un même biotope: Plestin. Ceci pose le problème des variations possibles au cours du cycle annuel. Remarquons à ce propos que la sexualité juvénile semble se manifester toute l'année, même chez les espèces où le cycle de reproduction des adultes est limité dans le temps.

## MODALITÉS DE L'HERMAPHRODISME JUVÉNILE

Les cas d'hermaphrodisme juvénile que j'ai décelés chez les Veneridae sont de trois types:

- 1) Ovocytes prévitellogéniques et spermatoocytes (et parfois, spermatides). C'est le cas le plus fréquent

chez *Venerupis decussata*, *Venus verrucosa*, *Dosinia exoleta*.

2) Ovocytes prévitellogéniques et présence de spermatozoïdes (ce qui n'exclut pas l'existence de spermatozoïdes et de spermatides) rare chez *Venerupis decussata*, fréquent chez *Venus striatula*.

3) Ovocytes à vitellus (accompagnés ou non d'ovocytes prévitellogéniques) et présence de spermatozoïdes. Vu chez *Venus striatula* et *Mercenaria mercenaria*.

En outre, j'ai observé chez *V. decussata* en particulier, des ovocytes plus ou moins désagrégés à côté de spermatozoïdes intacts. Toutefois, ces structures étant mal caractérisées, je ne les ai pas comptées au nombre des hermaphroditismes. Enfin, il faut noter la présence très fréquente d'amœbocytes parmi les éléments sexués. Ceci est en relation avec le caractère fugace et abortif de la sexualité juvénile.

#### CONCLUSION

La sexualité juvénile existe chez toutes les espèces étudiées. L'hermaphroditisme juvénile existe mais semble faible pour *Dosinia exoleta*, *Mercenaria mercenaria*, *Venus verrucosa*. Par contre, il est bien marqué pour *Venus striatula* et *Venerupis decussata*.

L'hermaphroditisme juvénile a déjà été signalé chez *Mercenaria mercenaria* (Loosanoff, 1937), *Venerupis decussata* (Lucas, 1968) et *Venus striatula* (Lucas, 1965, 1966). Chez cette dernière espèce Ansell (1961) avait en outre observé de l'hermaphroditisme postlarvaire. A notre connaissance, les autres espèces n'ont fait l'objet d'aucune étude sur la sexualité juvénile.

#### BIBLIOGRAPHIE

- ANSELL, A. D., 1961, The development of the primary gonad in *Venus striatula* (Da Costa). *Proc. Malacol. Soc. London*, 34: 243-247.
- LOOSANOFF, W. R., 1937, Development of the primary gonad and sexual phase in *Venus mercenaria* L. *Biol. Bull.*, 72: 389-405.
- LUCAS, A., 1965, Recherche sur la sexualité des Mollusques Bivalves. *Bull. Biol. Fr. Belg.*, 99: 115-247.
- LUCAS, A., 1966, Manifestation précoce de la sexualité chez quelques Mollusques bivalves. *Lav. Soc. Malacol. Ital.*, 3: 153-158.
- LUCAS, A., 1968, Mise en évidence de l'hermaphroditisme juvénile de *Venerupis decussata* (L.) (Bivalvia, Veneridae). *C. R. Acad. Sc. Paris*, tome 267, série D: 2332-2333 pl. 1.

CONTRIBUTION À L'ÉTUDE ÉCOLOGIQUE DES MOLLUSQUES  
DES EAUX DOUCES ET SAUMÂTRES DE CAMARGUE<sup>1</sup>

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RÉSUMÉ

Parmi les 43 espèces mentionnées, la plupart sont caractéristiques des eaux douces ou faiblement oligo-saumâtres. Les espèces d'eaux saumâtres sont réduites. Deux espèces marines: *Cardium glaucum* et *Abra ovata* sont capables de s'adapter aux milieux mixohalins et hyperhalins.

11 espèces appartiennent aux Gastéropodes prosobranches, 20 aux pulmonés basommatophores, 12 aux Lamellibranches.

A noter l'importance qualitative des espèces limniques, localisées dans les eaux homoihalines ou faiblement oligohalines. Cette abondance serait liée, depuis l'extension de la riziculture en Camargue, à une augmentation des biotopes d'eau douce.

Dans les eaux oligohalines et faiblement mésohalines cohabitent souvent des formes dulçaquicoles très résistantes et des formes mieux adaptées aux variations plus importantes des salinités (*Potamopyrgus jenkinsi*, *Pseudamnicola anatina*, *Pseudamnicola compacta*, *Bithynia tentaculata*, *Physa acuta*, *Lymnaea palustris*, *L. peregra*, *Ancylus fluviatilis*).

Dans le domaine des eaux méso-poly et hyperhalines des étangs de moyenne et basse Camargue, l'instabilité des facteurs physico-chimiques s'accroît, la salinité varie considérablement. Les alternances d'inondations et d'assèchements, la faible profondeur des marais, déterminent un tri des espèces; les Mollusques sténohalins sont éliminés au profit d'espèces eurithermes et euryhalines. On assiste à une réduction du nombre des espèces et à une pullulation des individus de chaque espèce. Ne persistent au maximum que 4 espèces: *Cardium glaucum*, *Abra ovata*, *Hydrobia acuta*, *Hydrobia ventrosa*.

Lorsque la salinité dépassait 60 à 70 ‰, nous n'avons jamais rencontré de Mollusques dans les milieux aquatiques du delta du Rhône.

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<sup>1</sup>In extenso in: *Annales de Limnologie*, Toulouse, 1969 (in press).

## PROC. THIRD EUROP. MALAC. CONGR.

## ZOOGEOGRAPHY OF HYDROBIID CAVE SNAILS

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## ABSTRACT

Functional ducts of the male organs and opercular differences have been used since 1948 to clearly separate the 4 subfamilies Hydrobiinae, Amnicolinae, Bythiniinae and Emmericiinae, of the small freshwater prosobranch snail family Hydrobiidae.

The Hydrobiinae possess only 1 functional duct (the vas deferens) in the verge. North American Hydrobiine cave snails include only 1 species of *Lartetia* from a cave in Virginia, and 1 of *Antroselates*, a blind relative of *Lithoglyphus*, from the Mammoth Cave region of Kentucky.

There are no members of the Amnicolinae (also called the Bythinellinae; with the vas deferens and a "flagellum" structure in the verge) known to live in North American caves. Nor are any Bythiniinae (with vas deferens and "flagellum," and a calcareous operculum) recorded from caves in North America.

*Fontigens* and 4 other North American genera possess the triple-ducted male organ of *Emmericia*, and so belong to the subfamily Emmericiinae. *Fontigens* and 1 other group with eyes are widespread in Appalachian and Ozarkian springs. Some few of these *Fontigens* species now living in caves have greatly reduced eyes. At least 3 other generic groups known from the Appalachian and Ozark regions have been living subterraneously so long they do not now show any eye structures whatsoever. In several North American (Appalachian) caves, 2 species (1 blind and 1 not blind) are known to be living together, thus indicating 2 waves of invasion into underground headwaters in 2 different geological eras.

The European genera such as *Avenionia* and *Paladhilia*, and the Japanese genera such as *Akiyoshia*, *Moria* and *Saganoa*, cannot be correctly and finally placed in the appropriate subfamily until the gross male anatomy of each of the pertinent type species is described and figured. In all cases type locality material of the species and genus should be studied because similarities of such small shells, of so few different shapes, may mask radically different anatomical features.

Until the hydrobiids from the Dalmatian and East Asiatic caves are classified to the correct subfamily, the relict zoogeographic stories of these cave snails will remain seriously incomplete.

## SELECTED BIBLIOGRAPHY

- ALTENA, C. O. van Regteren, 1946, Faunistische aanteekeningen I. *Avenionia bourguignati* (Locard) in Nederland. *Basteria*, 10(3/4): 45-46.
- HUBRICHT, L., 1940, The Ozark amnicolas. *Nautilus*, 53(4): 118-122.
- HUBRICHT, L., 1963, New species of Hydrobiidae. *Nautilus*, 76(4): 138-140.
- KURODA, T. & HABE, T., 1957, Troglobiontic aquatic snails from Japan. *Venus*, 19: 183-196, figs. 1-18.
- MORRISON, J. P. E., 1949, The Cave Snails of Eastern North America. *Amer. malac. Union, News Bull. and annual Rep. for 1948*: 13-15.
- SIEBOLD, W., 1904, Anatomie von *Vitrella quenstedtii* (Wiedershein) Clessin. *Jahresh. Verein. f. Vaterl. Naturk. Württemberg*, 60: 198-226; pls. 6 and 7.

CYTOLOGICAL STUDIES OF INDIAN MOLLUSKS (ARCHAEOGASTROPODA: NERITIDAE)<sup>1</sup>

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There is a scarcity of information on the chromosomes of Indian snails, and the few references available come only from this laboratory (Seshaiya, 1938, *Proc. silver Jub. Session Indian Sci. Congr.*, 3: 170; Jacob, 1954, *Nature*, 174: 1061-1062; 1957, *Trans. roy. Soc. Edin.*, 63: 341- ; 1958, *Ibid.*, 63: 433- ; 1959, *J. zool. Soc. India*, 11(1): 17-25; 1959, *Cytologia*, 24: 487-497; Ramamoorthi, 1958, *J. zool. Soc. India*, 10(1): 33-38; Natarajan, 1958, *Curr. Sci.*, 27: 311-312; 1958, *J. zool. Soc. India*, 10(2): 103-107; 1959, *Ibid.*, 11: 30-33; 1960, *Ibid.*, 12(1): 69-79). Patterson (1967, *Malacologia*, 5(2): 111-125), in a recent review, has indicated a similar lack of information for nearly all the Streptoneura. The purpose of the present study of the chromosomes of 10 neritid species from the Indian region is to document these chromosome numbers, thereby increasing our knowledge of cytology of the Archaeogastropoda, and of its world-wide, highly diverse family Neritidae.

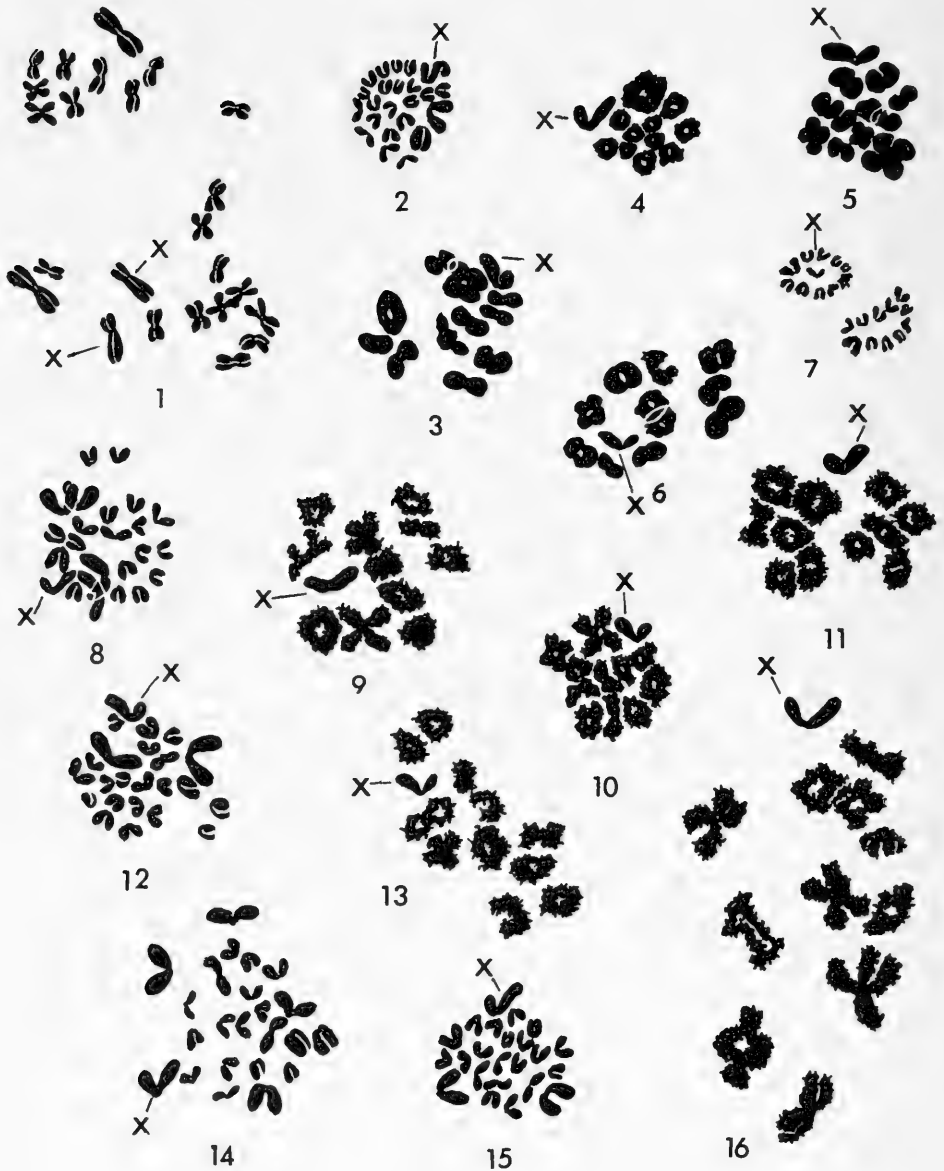
The family Neritidae in India is represented chiefly by 3 genera: *Nerita*, *Neritina* and *Septaria*. *Nerita* occurs mainly in the sea, *Neritina* lives in brackish waters, and *Septaria* is confined to freshwater. The present account deals with the chromosomes of 4 species of *Nerita* and 1 species of *Neritina* from the Andaman Islands, and 4 species of *Neritina* and 2 species of *Septaria* from peninsular India. *Neritina ovalansiensis* was studied from both places.

The results obtained are summarized in Table I. The chromosome numbers of *Septaria tessellata* is  $2n = 22 + X$  in the male, and  $2n = 22 + XX$  in the female. The haploid number is  $n = 11 + X$  in both. The karyotype of the male consists of one pair of large metacentric chromosomes with median centromeres, one large metacentric element (X) with a submedian centromere, and 10 pairs of small metacentric chromosomes with median centromeres. The female karyotype is similar but contains 2 large metacentric elements (2X) with submedian centromeres. Therefore, it is clear that the male is heterogametic. The X-chromosome can be spotted easily during male meiosis because it occurs as a univalent. In other neritid species in the present study, only male cells were studied. The chromosome number of each was  $2n = 22 + X$  and/or  $n = 11 + X$ . The X-chromosomes of these species were always present as univalents, and in each species this univalent had a submedianly placed centromere.

There are 3 previous reports of chromosome numbers of the Neritidae. Alexenko (1928, *Z. Zellforsch. mikroskop. Anat.*, 8: 80-124) reported *Theodoxus fluviatilis* to have 10 chromosomes during the first division of meiosis, and 19 and 20 chromosomes in spermatogonial and oögonial cells respectively, with a X-0 sex-determining mechanism in males. Tuzet (1930, *Arch. Zool. exp. gen.*, 70: 95-229) reported 9 chromosomes during meiosis and 18 in spermatogonial cells of this same species, with a X-Y sex-determining mechanism in males. Nishikawa (1962, *J. Shimonoseki College Fisheries*, 11(3): 149-186) reported  $n = 11$ ,  $2n = 22$  in males of *Puperita (Heminerita) japonica*, and could find no evidence for sex chromosomes. Patterson (1967, *Venus, Jap. J. Malacol.*, 25(2): 69-72) found *Clithon retropictus* to have 12 chromosomal elements present during male meiosis, and *Neritina (Dostia) violacea* to have 14 elements. This latter species has the highest chromosome numbers yet found in the Neritacea. Both species studied by Patterson had a heterochromatic bivalent which she suggested may be associated with sex determination.

There are a number of records of the occurrence of sex chromosomes in mollusks, but most of these were published before 1931 and reported observations from techniques that would be considered inadequate today (Patterson, 1967, *Malacologia*, 5(2): 111-125). More recent reports of sex chromosomes (all in the Mesogastropoda) are those of Jacob (1959, *Cytologia*, 24(4): 487-497), Jacob (1959, *J. zool. Soc. India*, 11(1): 17-25), Burch (1960, *Amer. malacol. Union ann. Repts.*, 1959, 20: 15), Patterson (1963, *Ibid.*, 30: 13-14) and Patterson (1965, *Malacologia*, 2(2): 259-265). The present report of a chromosomal sex-determining mechanism in the Neritidae is the only recent record so far in the Archaeogastropoda. It would be of considerable interest to know if sex chromosomes actually occur in other Archeogastropoda, since the Neritacea are considered to be an annectant group bridging the morphological gap between the archeogastropods and mesogastropods, and because it has been speculated that the ancestral mollusk was hermaphroditic (Fretter & Graham, 1962, *British prosobranch molluscs*, Ray Soc., London, p 385).

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FIGURES 1 - 16. Chromosomes of Indian mollusks. FIG. 1. *Septaria tessellata*, female,  $2n = 22 + x + x$ , oogonial late metaphase. FIG. 2. *S. tessellata*, male spermatogonial metaphase,  $2n = 22 + x$ . FIG. 3. *S. tessellata*, female I metaphase,  $n = 11 + x$ . FIG. 4. *S. tessellata*, male I metaphase,  $n = 11 + x$ . FIG. 5. *S. compressa*, male I metaphase,  $n = 11 + x$ . FIG. 6. *Neritina retifera*, male I metaphase,  $n = 11 + x$ . FIG. 7. *N. retifera*, male II metaphase,  $n = 11$  and  $n = 11 + x$ . FIG. 8. *N. ovalaniensis*, male spermatogonial metaphase,  $2n = 22 + x$ . FIG. 9. *N. ovalaniensis*, male diakinesis,  $n = 11 + x$ . FIG. 10. *Dostia crepidularia*, male diakinesis,  $n = 11 + x$ . FIG. 11. *Nerita chamaeleon*, male diakinesis,  $n = 11 + x$ . FIG. 12. *N. dombeyi*, male spermatogonial metaphase,  $2n = 22 + x$ . FIG. 13. *N. layardi*, male diakinesis,  $n = 11 + x$ . FIG. 14. *N. plicata*, male spermatogonial metaphase,  $2n = 22 + x$ . FIG. 15. *N. rumphii*, male spermatogonial metaphase,  $2n = 22 + x$ . FIG. 16. *N. plicata*, male diakinesis,  $n = 11 + x$ . Magnification ca. 4100.



TABLE 1. Chromosome numbers in Indian Neritidae

Species	Chromosome number	Locality
<i>Nerita</i>		
<i>N. chamaeleon</i> Linnaeus	$n = 11 + x$ ♂	Andaman Islands
<i>N. plicata</i> Linnaeus	$n = 11 + x$ ♂ $2n = 22 + x$ ♂	Andaman Islands
<i>N. dombeyi</i> Récluz	$n = 11 + x$ ♂	Andaman Islands
<i>N. rumphii</i> Récluz	$n = 11 + x$ ♂	Andaman Islands
<i>Neritina</i>		
<i>N. oualaniensis</i> Lesson	$2n = 22 + x$ ♂ $n = 11 + x$ ♂	Andaman Islands
<i>N. oualaniensis</i> Lesson	$2n + 22 + x$ ♂ $n = 11 + x$ ♂	South India
<i>N. retifera</i> Benson	$2n = 22 + x$ ♂ $n = 11 + x$ ♂	South India
<i>N. layardi</i> Lesson	$n = 11 + x$ ♂	South India
<i>N. (Dostia) crepidularia</i> Lamarck	$2n = 22 + x$ ♂ $n = 11 + x$ ♂	South India
<i>Septaria</i>		
<i>S. tessellata</i> (Lamarck)	$2n = 22 + x$ ♂ $n = 11 + x$ ♂ $2n = 22 + xx$ ♀ $n = 11 + x$ ♀	South India
<i>S. compressa</i> (Benson)	$n = 11 + x$ ♂	South India

DIE VERWANDTSCHAFTSBEZIEHUNGEN DER *RHODOPE VERANII*  
KÖLLIKER ZU DEN ONCIDIIDAE, VAGINULIDAE  
UND RATHOUIIIDAE IN BEZUG AUF DAS NERVENSYSTEM

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ZUSAMMENFASSUNG

*Rhodope* wurde 1847 von Kölliker entdeckt und als Nudibranchia beschrieben. Doch von jeher war ihre systematische Stellung problematisch. Bereits 1854 beschrieb Schultze *Rhodope* als ein Turbellar mit dem Namen *Sidonia elegans*. Schmidt (1858) und Diesing (1862) folgten der Annahme. Bronn (1866) reihte sie unter die Opisthobranchia. Ihering (1877) will in ihr sogar eine Zwischenform von Turbellarien und Mollusken sehen. Graff (1883) erkannte, dass *Sidonia* synonym zu *Rhodope* ist, stellt sie aber auch als Zwischenform auf. Böhmig (1893) bringt die erste grosse Arbeit über den Feinbau heraus, stellt die Lage der Körperöffnungen und eine äussere Anatomie des Nervensystems klar. Obwohl ihn die Vergleiche zu den Gastropoda, sogar zu den Stylommatophora leiten, stellt er eine neue Klasse der Scolecida auf. Thiele (1926) und Hoffmann (1931) reihen *Rhodope* hinter die Doridacea und Eolidiacea, und Boettger (1955) schliesst sie mit einem gewissen Vorbehalt den Doridacea an. Erst die genaue Untersuchung der Ontogenie von *Rhodope* durch Riedl (1960) zeigt, dass es sich um einen "Pulmonaten" handelt. Die Furchung geht nach dem Typus der Spiraler mit der Kreuzbildung, wie es für die Gastropoda charakteristisch ist. Die Entwicklung ist eine direkte, es wird kein Larvenorgan voll ausgebildet und wieder reduziert. Es tritt auch keine Veligerlarve auf.

Die Bildung des Nervensystems ist durchwegs eine ektodermale. Gleichzeitig mit der Bildung der Augen entstehen die Cerebropleuralganglien in paarigen, weit voneinander entfernten Keimbezirken, wachsen aber bald zusammen. Ein Sulcus deutet dann kurz die Trennung zwischen cerebralen und pleuralen Ganglien an. Die Ganglien rücken sehr eng aneinander, um den Oesophagus gruppiert. Kommissuren und Konnektive treten durch die Bindegewebsmembran hindurch. Die Buccalganglien bilden nur einen Plexus, sie zerfallen, sobald die Visceralerkette abgeschlossen ist. Nach dem 12. Entwicklungstag sieht man nur mehr einen Ganglienkomplex, nachdem die Bindegewebshüllen der einzelnen Ganglien zurückgetreten und die Ganglien aneinandergerückt sind.

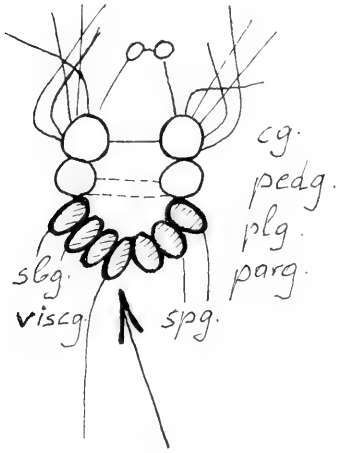
Das Wesentliche aber ist die Verlagerung des Subintestinalganglions und Abdominalganglions nach links. Endgültig besteht die linke Oberschlundgruppe aus Cerebropleural- und Parietalganglien, die rechte aus Cerebropleural-, Parietal- und Supraintestinalganglion. Die Unterschlundgruppe besteht aus Subintestinal- und Abdominalganglion. Nur die Pedalganglien stellen kein Verschmelzungsprodukt dar.

Auch bei den sogenannten Pulmonata liegt ein einheitlicher Zug in der Verlagerung der Ganglien bei Verkürzung der Visceralschlinge. Zu dieser Tendenz gehört das Einbeziehen der Parietalganglien mit den Cerebropleuralganglien, die Verschmelzung von Subintestinal- und Abdominalganglien und die Verlagerung nach links. Besonders bei den urtümlichen Stylommatophora lässt sich die Tendenz deutlich erkennen, die ganz den Verhältnissen bei *Rhodope* entspricht.

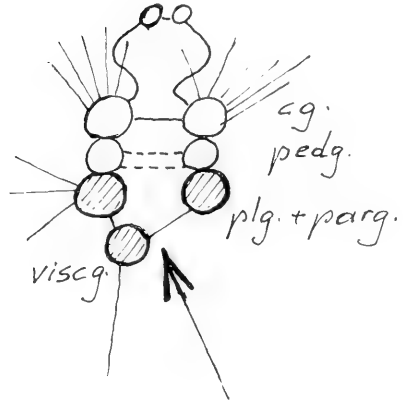
Die amphibisch lebend, marinen Oncidiidae sind zwar ihrer äusseren Morphologie nach den Doridacea sehr ähnlich, sie zeigen aber im inneren Bau viel mehr Übereinstimmung mit den primitiven Stylommatophoren. Das Nervensystem ist sehr konzentriert und zeigt ebenfalls eine deutliche Linksverlagerung der Visceralganglien. Die landlebende Gruppe der Vaginulidae zeigt ebenfalls ein sehr konzentriertes Nervensystem. Die Cerebralganglien sind unter den Oesophagus gerückt, alle Kommissuren und Konnektive sind bis zum Verschwinden verkürzt. Eine Trennung der einzelnen Ganglien ist kaum möglich. Auch die Rathouisiidae mit dem Vertreter *Atopos* sind hierbei zu nennen. Es ist wohl das am meisten konzentrierte Nervensystem, von Kommissuren und Konnektiven ist nichts zu sehen.

Die sehr ähnlichen Verhältnisse der Konzentrierung, Verkürzung und Linksverlagerung der Visceralganglien all dieser gezeigten Gruppen (Oncidiidae, Vaginulidae, Rathouisiidae und der *Rhodope*) weisen auf eine enge Verwandtschaft hin. Sie sind nach dem euthyneuren System in die aus den Cephalaspidea sich entwickelnden *Soleolifera* einzuordnen, die die einzige Ordnung der Euthyneura ist, die keinerlei Gehäuse ausbildet. Nun zeigen die Untersuchungen des Zentralnervensystems eine deutliche Zusammengehörigkeit dieser Gruppen. Denn wie all diese Gruppen weist auch *Rhodope veranii* in bezug auf das Nervensystem eine hohe Zentralisierung, starke Verkürzung von Schlundring und Visceralschlinge bei freien und nach links gerückten Visceralganglien auf.

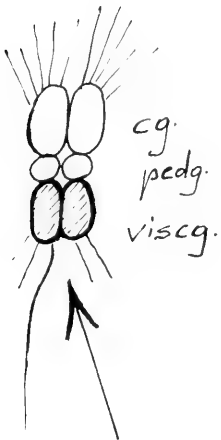
Vaginulidae



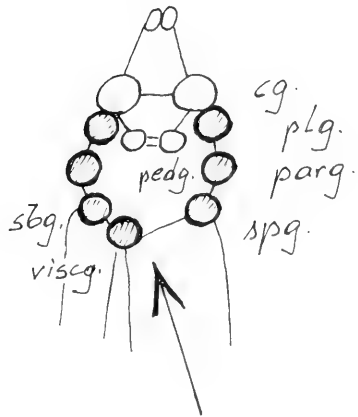
Oncidiidae



Rathousiidae



Rhodopidae



Schemat. Darstellung d. Zentralnervensyst.

- |       |                 |        |                      |
|-------|-----------------|--------|----------------------|
| cg.   | -- Cerebralggl. | parg.  | -- Parietalggl.      |
| pedg. | -- Pedalggl.    | sbg.   | -- Supraintest. ggl. |
| plg.  | -- Pleuralggl.  | viscg. | -- Visceralggl.      |
|       |                 |        |                      |
|       |                 |        |                      |
|       |                 |        |                      |

PROC. THIRD EUROP. MALAC. CONGR.

POPULATION CHARACTERISTICS OF *VIVIPARUS ATER*, CRISTOFORI AND JAN  
(GASTROPODA, PROSOBRANCHIA) FROM TWO HABITATS OF LAGO MAGGIORE  
(NORTHERN ITALY)

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ABSTRACT

A study on two populations of *Viviparus ater* settled in two stations of Lago Maggiore was carried out from 1962 to 1965 on several hundred of specimens. The two stations (Lavorascio and La Rotta) were small bays ecologically very similar but rather distant one from the other, which consented an almost perfect genetical isolation.

The material was collected by a sledge with a nylon net, but to measure the population density all the specimens settled on a square meter were collected by hand.

The population density decreased with depth and the highest concentration of young Molluscs and females was found in very shallow water. The higher mean value was observed at 0.5 m depth (10.45 individuals/sqm) and the lower one at 10 m (1 individual/sqm). The mean number of individuals per hectare was 50750 representing a biomass of 293 kg (wet weight); 117 kg due to the shells and 176 to the soft tissues.

For both stations the mean size of the females was greater than that of the males, but the bigger individuals were collected at La Rotta. About the individual growth for an increase of the height of the shell of 1 cm, the wet weight of the soft tissues increased of about 3.3 grams for the male and female without embryos, and 3.8 grams for the female with embryos; for the same increase of the shell height its wet weight increased about 1 gram.

In both stations the fertility seems more strongly connected with the number of embryos per female than with the sex-ratio. An increase of specific fertility with the size of the mother was observed, that is, for the same population, with the age of the female. The percentage of females bearing embryos varied with the station and the season, but throughout the year females with embryos were found.

To evaluate the metabolism of *Viviparus* its oxygen consumption was measured in the laboratory as well as in the field. From the results obtained the following conclusions may be drawn: 1) at temperatures lower than 15 °C the metabolic rate was very low and the temperature coefficient (Q) was far lower than 2; 2) at temperatures higher than 15 °C the youngest animals had a Q equal to 3; this coefficient decreased with increasing animal size until it became lower than 2 for the biggest Molluscs; 3) the difference in oxygen uptake by individuals of different size increased with temperature. During the season at which the population attained its highest metabolic and reproductive activity the oxygen uptake by the specimens settled on an hectare was about 16 g/hr.

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<sup>1</sup>This paper will be published "in extenso" in another journal.

PROC. THIRD EUROP. MALAC. CONGR.

OBSERVATIONS ON THE TENTACLES OF *VAGINULUS BORELLIANUS* COLOSI<sup>1</sup>

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ABSTRACT

The author has conducted several experiments with the amputation of the tentacles of *Vaginulus borellianus* (Gastropoda, Soleolifera) with the following purpose in mind:

a) to see whether regeneration occurs in this species and, if so, to analyse the phases and manner of this process as well as the structure and ultrastructure of the regenerated organ;

b) to investigate the possible relationship between the tentacle components (more precisely, their glandular and neuroglandular components) on one hand and the development of the gonads on the other.

The following results have been obtained:

- 1) The process of regeneration of amputated tentacles (optic and lower) in *Vaginulus* is substantially the same as that described in the numerous studies of other pulmonates.
- 2) The weights of the body and ovotestis and the number of eggs in the ovotestis of experimental animals show no significant variations either in comparison with each other or with the control animals.
- 3) Regarding both structure and ultrastructure, whereas the sensory cells in tentacles that have regenerated after a single amputation do not differ appreciably from the controls, those in tentacles that have regenerated after repeated amputations of regenerative blastema are considerably altered, especially at their apical end.
- 4) The eye consistently did not regenerate in any of the experimental animals (whether the tentacles were cut off once or the blastema was cut off repeatedly).

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<sup>1</sup>Will be published later *in extenso* in another publication.

MALACOLOGIA, 1969, 9(1): 285

PROC. THIRD EUROP. MALAC. CONGR.

AMERICAN MUSSEL RESOURCES IN RELATION TO THE JAPANESE PEARL INDUSTRY

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ABSTRACT

Harvesting of fresh-water mussels from streams in the Interior Basin of the United States has in recent years assumed a position of importance equal to that reached at the turn of this century in the heyday of the Pearl Button Industry. The new market created by the cultured pearl industry in Japan is extensive. Exploitation of several rivers, such as the Tennessee, the Wabash and the Muskingum has become a matter of concern both to malacologists and governmental agencies responsible for regulating and protecting that resource.

Two surveys were conducted during the past several years aimed at obtaining a better understanding of the effect of intensive commercial harvesting on the mussel fauna. One extended over a period of three years in "Kentucky Lake," an impoundment which the Tennessee Valley Authority created by means of a dam in the lower Tennessee River at Paducah, Kentucky. The other - a current program - involves a more normal river situation in the Muskingum River (a tributary to the Ohio) in Ohio. Both sites are interesting in their own unique way: the one in Tennessee has impounded water piled up to a hundred feet in depth above the mussel beds; the Muskingum is a less disturbed and more typical stream presenting a different set of problems.

The study of the Muskingum is designed to determine: (1) the location of the beds in the lower 85 miles of river; (2) population levels maintained by both the commercial and non-commercial species; and (3) the effect of gear used in harvesting the mussels (among other factors). Hopefully, with this information it will be possible to find methods for maintaining maximum yields for the expanding industry. Some assessment of natural and human influences is necessary to protect the interests of all parties concerned.

## PROC. THIRD EUROP. MALAC. CONGR.

SOME OBSERVATIONS ON THE LIFE-HISTORIES OF SOUTH INDIAN  
FRESHWATER MUSSELS

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## ABSTRACT

We have a wealth of information on the biology of European and North American freshwater mussels, but we know little regarding the Indian species. The more common species occurring in South India are *Lamellidens marginalis* (Lamarck), *L. consobrinus* (Lea), *L. corrianus* (Lea), *Parreysia corrugata* (Müller), *P. rugosa* (Gmelin). I have made a more or less complete study of the development of *Lamellidens corrianus* and the life-histories of all these species. The development of *Lamellidens* is very similar to that of *Anodonta*, which was studied by Lillie (1895) and Herbers (1913). The present note reports the chief features of the parasitic stage of the glochidium in the life-history of these mussels.

The mussels were periodically obtained from ponds and streams, and maintained alive in aquaria in the laboratory for the collection of glochidia. Healthy glochidia were available chiefly during July and August and again during December. The glochidia were transferred to petri dishes and small glass troughs for effecting infection on suitable hosts. Glochidial infection was successfully carried out on a dozen species of freshwater fish and also on the tadpoles of the frogs, *Rana hexadactyla* and *Rhacophorus maculatus*. Among the fish, the murrel, *Ophiocephalus* was particularly well suited as a host for the glochidia, as it could be easily handled, and as it could also stand heavy glochidial infection. Three species of the murrel, *Ophiocephalus punctatus*, *O. gachua* and *O. striatus* are of common occurrence locally, and these were all equally suitable hosts for the glochidia. Of the frog tadpoles, those of *Rhacophorus* have little pigmentation and proved suitable for glochidial infection. Heavily pigmented tadpoles, such as those of the toad *Bufo melanostictus* were unsuitable, as the glochidia after encystment failed to metamorphose.

The glochidia of the mussels studied are of the hooked variety, i.e., with hooks on the glochidial shell, and attach themselves to the fins of the host. After attachment on the fin, the encystment is completed within half an hour by the growth of the surrounding tissue.

The noteworthy feature in the life-history is the very short duration of the parasitic or encysted stage, i.e., the duration for metamorphosis of the glochidium. Glochidia collected in July and August metamorphosed in three days, whereas glochidia obtained in December took six to eight days to metamorphose.

According to Harms (1907), the time for metamorphosis of the glochidium of the European mussel *Anodonta cygnaea* (L.) varies from 12 days to 80 days depending on temperature, as shown below:

Water temperature from 8 to 10° C	80 days
Water temperature from 16 to 18° C	22 days
Water temperature from 20° C	12 days

Lefevre and Curtis (1912) studied the duration of the parasitic stage of the glochidia of different mussel species of North America, and found a general relationship between temperature and duration of the parasitic stage. For *Symptonata* the findings were as follows:

Temperature	Duration of parasitic stage
16.0° C	14 - 16 days
16.3° C	15 - 18 days
17.3° C	11 - 14 days
17.8° C	9 - 13 days

Thus the glochidia of the South Indian mussels, it will be seen, metamorphose much more rapidly than the European and North American species. During the warm months with a temperature of 29° to 30° C in the medium, the metamorphosis took only three days. In the cold season with a temperature of about 24° to 25°, the metamorphosis took 6 to 8 days.

The speeding up of the organogenesis is also interesting. During the warm months the encysted glochidia show all the definitive structures of the juvenile mussel.

In the case of the glochidia encysted on the fins of tadpoles, the repair of the breached fin-tissue, after the metamorphosed glochidium drops down, is very rapid and the movement of cells to bridge the gap can

be observed under the microscope.

The abbreviation of the life-history is an adaptation to environmental conditions and is also observed in several other tropical organisms. For example the frogs, *Cacopus systoma* and *Rhacophorus maculatus*, often breed in shallow pools of rainwater during the warm months, and metamorphosis is much shortened as compared to that in the cold months.

Another feature of interest is with regard to the number of successive glochidial infections which a fish could stand. It was observed that a single specimen of *Ophiocephalus* could successfully serve as a host for six or seven infections. But further infections were unsuccessful and the glochidia dropped off without metamorphosis.

An attempt was made to determine the approximate time taken by the juvenile mussel to attain maturity by collection of shells of various sized groups, and observing the lines of growth on the shell and noting the periods of retardation of growth. From the observations made so far, it is inferred that the juvenile mussel takes about two years to attain maturity. In the European mussel sexual maturity is not attained till the fifth year.

#### REFERENCES

- LILLIE, F. R., 1895, The Embryology of the Unionidae. *Journ. Morph.* 10: S. 1-100.
- HARMS, W., 1907, Über die postembryonale Entwicklung von *Anodonta piscinalis*. *Zool. Anz.* 31: S. 801-814, 7 Abb.
- LEFEVRE, G. U. & CURTIS, W. C., 1912, Studies on the Reproduction and Artificial Propagation of Freshwater Mussels. *Bull. Bur. Fish. Washington*, 30: (Document Nr. 756) S. 105-201. Taf. 6-17, 4 Abb.
- HERBERS, K., 1913, Entwicklungsgeschichte von *Anodonta cellensis* Schröt. *Zeitschr. f. wiss. Zool.*, 108, S. 1-174. 104 Abb.

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## ZUSAMMENFASSUNG

Unter den fossilen Bivalvia ist eine grosse Zahl kennzeichnender Lebensformen zu beobachten. Sie stimmen entweder mit solchen rezenter Muscheln überein oder stellen mehr oder weniger eigene Typen dar. Bei der Ermittlung der letzteren müssen nicht bloss biologische Merkmale, wie etwa einseitige morphologische Spezialisierung, Vergesellschaftung, Bewuchs u.ä., verwendet werden, sondern auch geologische, wie etwa Vorkommen in Lebensstellung und faziologisches Auftreten sowie paläogeographische und regional-tektonische Verbreitung. Dadurch lassen sich fast alle fossilen Bivalvia hinsichtlich ihrer Lebensformen und Lebensweisen erfassen. Nur einige können noch nicht befriedigend gedeutet werden, so rostroconchide Conocardien, bei welchen es noch einer eingehenderen paläoökologischen Analyse bedarf.

Von den Lebensformen, die mit solchen rezenter Muscheln weitgehend übereinstimmen, seien beispielsweise grabende und bohrende Vertreter von *Solen*, *Pinna* und *Lithophaga* angeführt, die schon im Paläozoikum durch verwandte oder konvergente Typen verfolgbar sind, wie *Palaeosolen* und "*Sulcatopinna*." Ferner sind zu nennen Kugel- oder globöse Formen des Bewegungswassers, wie *Linga columbella*, *Cardita partschi* und *Glycymeris pilosa*; halbkugelförmig gewölbte Formen finden sich bei *Pecten*, *Gryphaea* u.a. Mytiliform sind neben Mytiliden *Myoconcha*. Auch Linsen- und Scheibentypen des Flachwassers kommen vor (*Codokia*; *Placuna*, *Carolia*).

Die als überwiegend fossil zu bezeichnenden Lebensformen treten etwa bei einzelnen Arten der hier in einem z.T. weiterem systematischen Sinne gebrauchten Gattungen *Trigonia*, *Megalodus*, *Congerina*, *Hippurites*, *Eumorphotis*, *Inoceramus* und *Dicerata* auf. Sie sind als benthonisch zu betrachten und bildeten Angehörige der Epi- und Endofauna. Als nicht benthonische, aber bewegte Formen dürfen *Posidonia*, *Monotis* und *Daonella* angesehen werden.

Trigonien gehörten überwiegend dem Seichtwasserbereich an. Ihrer grossen Area und ihrer starken Skulptur kann unter Hinweis auf die Lebensweise des rezenten *Corculum cardissa* die funktionelle Bedeutung der Einebnung und Verankerung in das Bodensediment zugesprochen werden. Ähnliche Verhältnisse liegen bei *Myophoria* und *Roudairea* vor; auch einige Arten der paläozoischen Gattung *Grammysia* (*G. undata* u. *G. nodocostata*) und *Mecynodon* (*M. carinatus*) weisen in gleiche Richtung. Die meist im dem Rifffern nahen Kalkschlick vorkommenden Megalodontidae stellen wenig tief eingegrabene Triasmuscheln dar. Der Hippuriten-Typus ist ein nicht litoraler Seichtwasservertreter und scheint ausser bei den Rudisten auch bei Spondyliidae (*Sp. olsenae* u.a. Arten) auf. Liegeformen des wenig weichen Bodens weisen *Congerina* (*C. subglobosa*), *Linga* (*L. lineata*) und die devonische *Congeriomorpha* auf, welche eine vordere Liegefläche und eine schwache Byssusfestheftung gehabt haben. Bei den flach mützenförmigen Bivalven, wie *Eumorphotis aurita*, *E. telleri*, *Claraia clarae*, *Anomia patelliformis* und wohl auch der der rezenten *Enigmonia aenigmatica* sehr ähnlichen paläozoischen *Hercynella bohemia*, die durch Byssus oder Cicatrix festgeheftet waren, handelt es sich um Formen der mehr oder weniger bewegten Flachsee. Unter den *Inoceramen* sind meist Seichtseeformen zu finden; nur der radialgerippte *Inoceramus sulcatus* des Albiens und die gryphaeaartige Art *I. involutus* deuten auf stärkeres Bewegungswasser hin. Charakteristische Rollformen des Bewegungswassers kommen neben *Lucinidae* (*Linga*) bei *Diceraten* vor, deren mit stark eingerollten Wirbelteilen versehene Vertreter die Hänge der Tithonriffe besiedelten. Eine nicht benthonische Lebensweise meist des tieferen Stillwassers ist aus Fossilisation, Bauform und Vergesellschaftung für die meist dünnchaligen *Posidonien*, *Daonellen* und *Monotidae* zu erschliessen.

Bei den verschiedenen Lebensformen lassen sich zahlreiche kennzeichnende Spezialisierungsmerkmale feststellen, in welchen meist eine möglichst funktionsgerechte Ausbildung der Typen zum Ausdruck kommt, wobei einzelne fossile Fälle besonders aufschlussreich erscheinen. So tritt Schalenabplattung in lateraler oder antero-posteriorer Richtung auf, ferner Kugel- und Kelchbildung. Die Flügel- und Ohrenbildung, etwa der *Pectinidae*, ermöglicht eine sichere Klappenbewegung; die gegen ihren Schlossrand stark abgewinkelten Schalen bei *Bakevelliidae* (*Gervillia*) u.a. gewährleisten eine nicht zu grosse und vor allem gleich weite Öffnung der Klappen. Abgeflachte hintere Schalentile bewirken eine Abschwächung mechanischer Einwirkung bei starker Wasserbewegung (*Trigonia*, *Grammysia*, *Mecynodon*).

Zu zahlreichen Lebensformen fossiler Bivalvia können konvergente Beispiele anderer Schalentiere; besonders der *Brachiopoda*, aufgezählt werden. So entsprechen *Mucrospirifer reidfordi* und einzelne *Productacea* in Form und Lebensstellung *Tridacnidae*; *Meekella* und *Richtiofenia* sind Hippuritentypen. Darin kommt hiemit eine allgemeinere biologische Gestaltung zum Ausdruck.

Die stratigraphische Uebersicht der Lebensformen fossiler Bivalvia weist auf charakteristische und unterscheidende Eigenschaften erdgeschichtlicher Formationen hin.

Die hier verwendete Literatur wird in einer eigenen der Paläoökologie der fossilen Bivalvia gewidmeten Uebersichtsdarstellung angeführt.



PROC. THIRD EUROP. MALAC. CONGR.

PHYLOGENETIC POSITION OF THE SUCCINEIDAE

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ABSTRACT

Traditionally the Succineidae have been considered to be primitive Stylommatophora, either ancestral to the more advanced Sigmurethra or a side branch of pulmonate evolution. Recent suggestions that they are opisthobranchs or a distinct, primitive order were thought to be bolstered by the discovery of low chromosome counts in various Catinellinae.

Studies on aulacopod sigmurethrans with reduced visceral humps and dissection of several succineids suggest a revision of their phylogenetic position. Rather than being primitive land snails occupying a habitat transitional between water and land, the succineids are a phylogenetically advanced group that has made a partial reversion to a near aquatic habitat. They are secondarily derived from the arionid-limacoid group in the Sigmurethra and thus much more advanced than the Orthurethra or Mesurethra. Previously cited "primitive" features in the Succineidae can be shown to be either secondary modifications correlated with the reduction in visceral hump and altered shell form, or consistent with alternative explanations.

The transverse kidney and pallial configuration in the Succineidae is duplicated in the endodontoid subfamily Charopininae, since shortening and broadening of the kidney is one method of compensating for pallial cavity compression. Possession of a closed and complete secondary ureter is phylogenetically much more important and indicates that the Succineidae is advanced, rather than primitive. Features in the reproductive system of the Succineidae cited by Rigby and Quick as differentiating them from the most advanced Helicidae and Zonitidae are duplicated in the more generalized aulacopod lines. For example, a bifurcated talon is characteristic of the Discinae; completely separated prostate and uterine oviducal tubes are in the Endodontinae and many other taxa; and the trend to separation of the penial region into penis proper and epiphallus is duplicated in several arionid subfamilies.

Odhner's suggestion that the subfamily Catinellinae is a natural assemblage occupying a more primitive position is not supported by dissections. *Catinella*, *Quickella* and *Mediappendix* appear to be relatively advanced genera that are independently derived from "*Succinea*"-type ancestors. Their low chromosome numbers can be interpreted as resulting from a drastic reduction series. These genera inhabit marginal, temporary, pioneer habitats where it is advantageous for a species to build up a population quickly with minimal variation. Reduction in chromosome numbers lowers the possibility of variation. Under these circumstances, a reduction series produces a selective advantage.

Morphological structures of the Succineidae are consistent with their being considered as slightly aberrant members of the more generalized aulacopod Sigmurethra and thus they are among the phylogenetically more advanced land snails; the subfamily Catinellinae is polyphyletic and its genera derived from the Succineinae; and low chromosome numbers in the Catinellinae probably result from aneuploid changes.

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GROWTH STUDIES ON *OLIVELLA BIPPLICATA* (SOWERBY, 1825)<sup>1</sup>

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ABSTRACT

Based on field observations it was assumed that *Olivella biplicata* had a life span of possibly 3 or 4 years. To ascertain the actual life span under natural conditions (as contrasted to laboratory experiments) a method of marking shells without causing interference with the natural life processes of the animals was devised; groups of marked animals were then released in a particularly favorable spot where the species occurs naturally yet is, at the same time, kept from emigrating. This makes periodic recapture of the marked animals possible; after re-measuring they are released in the same place.

Early results indicated that the life span is considerably longer than was assumed; estimates of from 8 to 15 years appear now more than reasonable. Growth spurts have been observed, but in general annual increments seem to vary between 1 and 3 millimeters.

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<sup>1</sup>In extenso in *Veliger*, vol. 11, p 259-267.

THE INFLUENCE OF CLIMATE ON THE ADULT SIZE OF RECENT AND FOSSIL  
*HIATELLA ARCTICA* (LINNÉ) AND ITS IMPORTANCE FOR DETERMINATION  
OF PALAEOTEMPERATURE

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## ABSTRACT

*Hiatella arctica* (Linne) has had a world wide distribution from the early Tertiary through to the present. Study of recent *Hiatella* has shown that features such as numerical distribution, shell form, and growth are temperature-controlled. Studies on fossil *Hiatella* reveal a similar pattern. In particular:

1. Numbers of *H. arctica* individuals in given faunal assemblages increase polewards, in both absolute and comparative terms as the number of other lamellibranchs present decrease. This feature results both from the direct influence of temperature on a species thriving best in arctic conditions and from the indirect influence of temperature in decreasing the number of species in competition with *Hiatella* in the same zone.
2. Adult shell size varies in length between 6 and 45 mm, the larger being found near the poles, the smaller near the equator. This result appears even more closely controlled by temperature than the preceding case, although the lack of competition in the Arctic no doubt plays an important role in encouraging unrestricted growth.
3. The rugosa-type developed by boreal and arctic *Hiatella* is not a function of environmental adaptation but of the average of absolute size.

By using the results based on feature 2 above, it has proved possible to demonstrate an analogous temperature related control of adult shell size for fossil populations of *Hiatella arctica*. Measurements on accurately placed and dated fossil populations show a clear increase in shell size between Eocene and late Glacial times.

This size/age relationship can be used to derive quantitative temperature data from size measurements of adult fossil populations. Temperature curves representing yearly temperature minima and maxima for different *Hiatella* shell lengths were derived from a series of recent samples reaching from the tropics to the Arctic. These curves were superimposed with the shell length of fossil *Hiatella* populations. Minimum and maximum temperature values as well as the mean can be read from the graph directly:

M. Europe:	winter - summer	yearly average temperature
M. Eocene	26,0 <sup>0</sup> to 28,0 <sup>0</sup> C	27,0 <sup>0</sup> C
O. Oligocene	20,5 <sup>0</sup> to 27,0 <sup>0</sup> C	23,5 <sup>0</sup> C
Miocene	ca. 17,0 <sup>0</sup> to 27,0 <sup>0</sup> C	22,0 <sup>0</sup> C
Pliocene	13,5 <sup>0</sup> to 22,0 <sup>0</sup> C	17,5 <sup>0</sup> C
Waltonian	12,0 <sup>0</sup> to 21,0 <sup>0</sup> C	16,5 <sup>0</sup> C
Newbournian	8,0 <sup>0</sup> to 19,0 <sup>0</sup> C	13,5 <sup>0</sup> C
Butleyan	5,0 <sup>0</sup> to 17,5 <sup>0</sup> C	11,0 <sup>0</sup> C
Eem-Interglacial	ca. 10,0 <sup>0</sup> to 20,0 <sup>0</sup> C	15,0 <sup>0</sup> C
Late Würm	-1,0 <sup>0</sup> to 11,0 <sup>0</sup> C	5,0 <sup>0</sup> C
(Recent, Dogger Bank	6,0 <sup>0</sup> to 16,0 <sup>0</sup> C	11,0 <sup>0</sup> C)

These values can clearly only be taken as working approximations, for one has but to consider the variations present in such a narrowly defined area as the present day North Sea to realise the almost certainly equal complexity of its forerunners. Nevertheless, the method allows a significant advance to be made on the hitherto published temperature data for the marine Cenozoic. This is particularly true of the area of Middle and Northwest Europe from which the bulk of the measurements was made.

LITERATURE CITED

STRAUCH, F., 1968, Determination of cenozoic sea-temperatures using *Hiatella arctica* (LINNÉ). *Palaeogeogr., Palaeoclimat., Palaeoecolog.*, 5: 213-233.

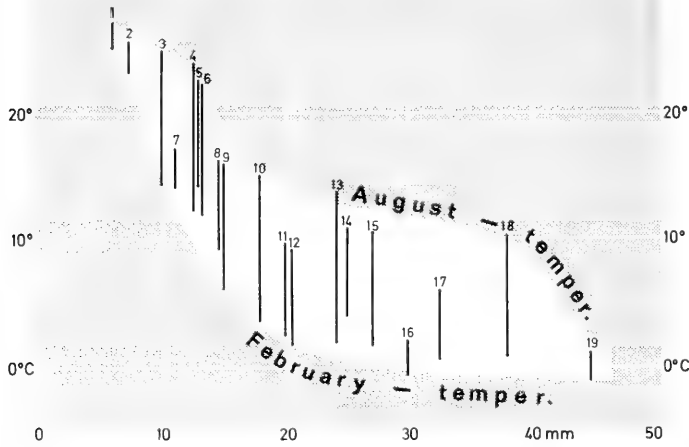


FIG. 1. Average length of adult specimens of recent *Hiatella arctica* of different localities in relation to temperature internals. (STRAUCH 1958). 1 = Barbados, 2 = Hawaii, 3 = Algiers, 4 = Pisa, 5 = Naples, 6 = Zadar, 7 = St. Barbara, Calif., 8 = S. Bretagne, 9 = Dogger Bank, North Sea, 10 = Oslo Fjord, 11 = Varanger Fjord, 12 = Tjørnes, N. Iceland, 13 = Hardanger Fjord, 14 = Lofoten, 15 = Unalaska Is., 16 = Spitsbergen, 17 = Jan Mayen, 18 = Bering Is., 19 = East Greenland).

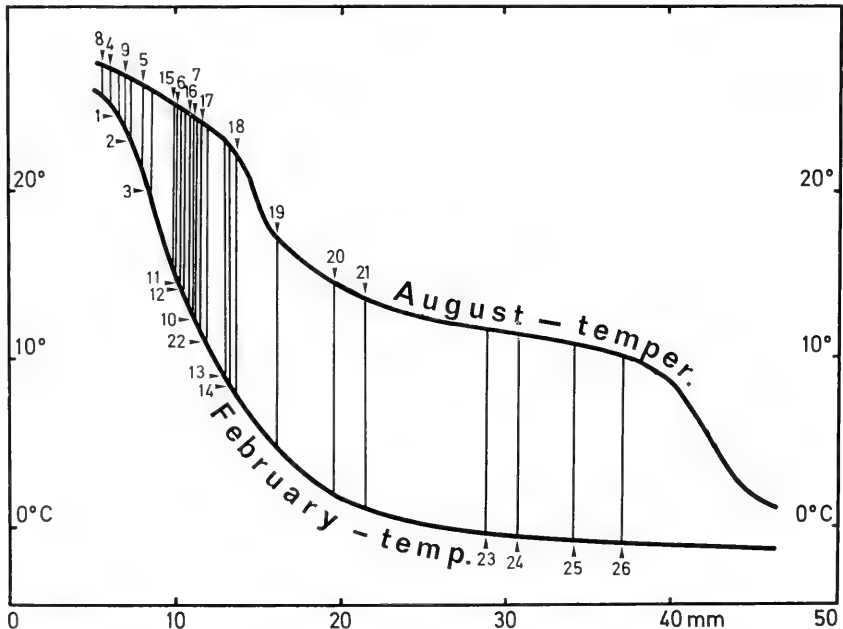


FIG. 2. Standards of temperature curves with fossil data of *Hiatella arctica* indicated. (Only samples of the southern Cenozoic North Sea were used: 1-3 = Oligocene, 4-9 = Miocene, 10-14, Pliocene, 15-21 = Early Pleistocene, 22 = Eem, 23-26 = Late Würm.) (STRAUCH 1968)

ELABORATION DE LA MATIÈRE OPERCULAIRE CHEZ *TRICOLIA PULLUS* (L.),  
GASTROPODA, PROSOBRANCHIA

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## RÉSUMÉ

Des recherches antérieures, non intégralement publiées, portent sur quelques Prosobranchia (*Gibbula magus*, *Thaïs lapillus*, *Viviparus viviparus*), et nous assurent que l'opercule de ces espèces est une lame homogène de protéine durcie par "tannage quinonique," excluant la participation de toute trace de chitine, même à l'état de trame que la matière sclérifiée imprégnerait. Chez *Tricolia pullus*, calcification et durcissement de matière protéique coexistent: les deux disques, calcaire et organique, qui peuvent se dissocier chez les *Turbinidae* pris au sens large, matérialisent topographiquement cette superposition. Les seules études voisines de notre propos concernent *Turbo* ou *Astravium*, abordés d'une façon descriptive; grâce à HOUSSAY, SAHM, KESSEL, HUBENDICK, on connaît le rôle d'un bourrelet operculaire indépendant du bourrelet palléal, à l'origine des zones de croissance de l'opercule, à propos duquel KESSEL a judicieusement corrigé les vues de HOUSSAY en situant à sa face inférieure la composante organique qu'il interprète comme "conchine" et non plus comme "revêtement chitineux."

Nous avons précisé par des voies surtout histochimiques, à partir d'une étude d'anatomie microscopique détaillée, non seulement la nature des divers composants de l'opercule complexe de *Tricolia*, mais aussi la situation et l'apparence cytologique des tissus sécréteurs correspondants. Cet opercule oligogyre spiral apparaît comme un ménisque blanc, elliptique, marqué d'une spirale interne en relief. Il est serti par le repli operculaire, enveloppe tégumentaire pigmentée, en croissant lobulé sur les côtés qui, sur le vivant, le recouvre aux deux-tiers et se révèle indépendant du bourrelet palléal postérieur dont la fixation le rapproche. Toute décalcification découvre une lame organique inférieure discrète, ambrée, adhérent au disque operculaire par une zone en fer à cheval élargie aux extrémités et complétée caudalement par un repli plissé.

Sur coupes sagittales de la région pédieuse, on situe les tissus intéressants à partir du repère d'une "gouttière operculaire." Cette incision est délimitée crânialement par le repli operculaire, dont l'arête lobée présente de hautes cellules sécrétoires. Au rebord caudal, l'opercule organique succède immédiatement à un sillon qui s'extroverse à son contact sur le vivant, grâce à un système d'éléments vacuolaires qui permet à des cellules glandulaires d'assurer la croissance de la spirale organique. Celle-ci, même sans présenter la "lamelle hyaline" réfléchie caractéristique de *Gibbula* ou *Thaïs*, prend donc à l'origine un aspect cuticulaire. Suit un épithélium cubique à tonofibrilles qui représente la zone d'adhérence du disque operculaire à la musculature sous-jacente. Dans le deuxième tiers de la surface du disque, l'opercule repose sur le repli plissé riche en mucocytes. Histologie et observation sur le vivant imposent de rechercher dans les catégories cellulaires antérieures du repli et de la gouttière les éléments sécréteurs de l'opercule.

On a pratiqué les tests histochimiques en gardant l'opercule en place. Sa fraction minérale est assez fragile pour être solubilisée non seulement par les fixateurs picriques, mais aussi par les fixateurs bichromatés postchromés; elle disparaît en tous cas par traitement au Complexon. La fraction organique de l'opercule révèle alors trois strates:

- Une lame interne, d'épaisseur constante, correspondant seule à une scléroprotéine tannée. Rouge à l'Azan, réfractaire aux tests de Mucopolysaccharides, elle s'affirme comme une protéine à radicaux aromatiques par des tests signalétiques (Vert Malachite), ou spécifiques des groupements réducteurs (R. argentaffine) ou des polyphénols (R. chromaffine), la Dopa-réaction donnant à son niveau une condensation mélanique.

- Une pellicule intermédiaire "adhésive" mucopolysaccharidique. Bleue à l'Azan, réagissant au Bleu Alcian et, métachromatiquement, au Bleu de Toluidine, elle comporte surtout des mucopolysaccharides acides, même si l'A.P.S. suggère une discrète composante "mucoïde."

- Une matrice organique calcaire topographiquement indépendante. Ses réponses aux tests des mucopolysaccharides, son affinité pour les laques nucléaires (notamment l'Hémalum viré par une solution picriquée) en proposent la nature mucoprotidique.

A la stratification de l'opercule correspondent, depuis le repli operculaire jusqu'au rebord caudal de la gouttière, des bandes de cellules sécrétoires différentes:

- Les sécrétions à l'origine de la protéine "tannée" ont été révélées notamment par la réaction argentaffine pour les radicaux aromatiques, et par la Dopa-réaction pour le phénolase associée. Située juste à la limite inférieure du sillon, une mince bande de cellules à sécrétion apicale argentaffine poussiéreuse

doit jouer le rôle principal, mais les cellules hautes à cytoplasme basophile qui précèdent juste la zone d'adhérence peuvent aussi intervenir, de même que les cryptes glandulaires de la paroi opposée de la gouttière, dont on connaît l'homologue chez *Thafs* ou *Gibbula*.

- L'épithélium du fond de la gouttière présente des cellules calciformes riches en mucopolysaccharides acides qui les impliquent dans l'élaboration de la pellicule intermédiaire.

- La crête du repli operculaire définit un lobe sécrétoire dont les hautes cellules sont soit vacuolaires soit chargées de granules. Signalée par une légère coloration vitale à l'Alizarine, la détection du calcaire à leur niveau a été pratiquée par les méthodes aux métaux lourds. La méthode de Lillie, variante "in toto" du Kossa avec décalcification simultanée, est apparue plus positive encore que celle de Stoelzner au niveau des sécrétions granuleuses. La sécrétion mucoprotidique doit être associée à l'élément minéral. Pour confirmer ces images d'élaboration calcique (quasi inconnues au niveau de l'épithélium palléal des Mollusques), on a recouru à un procédé indirect. Le rôle intermédiaire des phosphatases alcalines est suffisamment établi à propos de la coquille pour qu'on puisse les considérer comme des indicateurs valables: on les a détectées par diverses techniques, dont celle de Pearse qui écarte toute ambiguïté et qui révèle l'enzyme sur un liseré apical de la région intéressée exclusivement.

En conclusion, histologie et histochimie concourent pour rattacher à des tissus sécrétoires différents et éloignés les divers éléments constitutifs de l'opercule composite de *Tricolia*. Il est facile de reconnaître dans le disque organique inférieur une lame homogène de protéine durcie par tannage quinonique, qui en fait l'homologue de l'opercule tout entier, tel qu'il apparaît chez les autres Prosobranchia déjà étudiés. Isolé par la couche intermédiaire "adhésive" de mucopolysaccharides, le disque calcaire superficiel tient aussi son indépendance de son lieu d'élaboration, et sa matrice calcaïfne mucoprotidique est différente des deux strates organiques auxquelles elle se superpose sans transition. On pourrait évoquer à son propos, en disposition inversée, les situations respectives de la coquille calcaire et du periostracum (dont divers travaux portant sur les Lamellibranchiata indiquent qu'il s'agit d'une protéine tannée), n'était la frontière très tranchée qui individualise les composants "organique" et "minéral" de l'opercule de *Tricolia*.

#### BIBLIOGRAPHIE

- HOUSAY, F., 1884, Recherches sur l'opercule et les glandes du pied des Gastéropodes. *Arch. Zool. exp. gén.*, 2: 271-288.
- HUBENDICK, B., 1948, Über den Bau und das Wachstum des konzentrischen Operculartypus bei Gastropoden. *Ark. for Zoologi*, 40: 1-28.
- KESSEL, E., 1942, Über Bau und Bildung des Prosobranchier-Deckels. *Z. Morph. u. Ökol. Tiere*, 38: 197-250.
- SAHM, W. (in FLEISCHMANN, A.), 1932, Vergleichende Betrachtungen über das Schalenwachstum der Weichtiere. *Z. Morph. u. Ökol. Tiere*, 25: 555-590.
- VOVELLE, J., 1967, Sur l'opercule de *Gibbula magus* (L.), Gastéropode Prosobranch: édification, nature protéique et durcissement par tannage quinonique. *C. R. Acad. Sc., Paris*, 264: 141-144.

ANATOMISCHE UNTERSUCHUNGEN DES ZENTRALNERVENSYSTEMS VON  
*FIMBRIA FIMBRIA* UND *MELIBE LEONINA*

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## ZUSAMMENFASSUNG

Die Opisthobranchia *Fimbria fimbria* und *Melibe leonina* sind Arten der Familie Tethymelibidae, die den Aeolidiaceae zugeordnet ist. Das Zentralnervensystem dieser beiden Formen, besonders von *Fimbria fimbria*, ist in der Literatur oft erwähnt, aber noch nie genau untersucht worden. Die spärlichen Abbildungen sind unexakt und zum Teil auch falsch.

Die Opisthobranchia weisen in ihren verschiedenen Organen bestimmte Entwicklungstendenzen auf. Die Hauptlinie dieser Evolution reicht von einer asymmetrischen Körperform mit Schale und nicht konzentriertem Nervensystem zu einer symmetrischen Form, die schalenlos und durch eine Konzentration der Ganglien charakterisiert ist. Von Ihering 1922 hat eine dieser Theorie entgegengesetzte Ansicht geäußert. Für ihn gilt das konzentrierte Nervensystem gewisser Nudibranchia, z.B. *Fimbria fimbria*, als "Protoganglienmasse" und somit als ursprünglicher Ausgangspunkt, während sich die Formen mit getrennten Ganglien sekundär davon ableiten sollen. Hanström 1929 hat darauf hingewiesen, dass die Konzentration des diffusen Nervensystems in ein zentrales und die Verschmelzung von ursprünglich getrennten Ganglien zu höheren, fest vereinten Einheiten einen im ganzen Tierreich gemeinsamen Prozess darstelle, und dass Iherings Theorie dazu in schroffem Gegensatz stehe und abgelehnt werden müsse.

Nach den neueren Untersuchungen charakterisiert Wirz 1952 den Entwicklungsprozess zur Konzentration des Nervensystems durch drei Vorgänge, die aber nicht immer gekoppelt sein müssen.

1. Cephalisation: so wird der Vorgang der Ganglienwanderung zum Vorderpol genannt.
2. Cerebralisation: unter diesem Prozess versteht man die Verschmelzung der nach vorne gewanderten Ganglien. Die Verschmelzung erfolgt nach ganz bestimmten Regeln. Das Nervensystem wird dadurch zu einer zentralisierten Bildung, einem "Gehirn."

3. Telencephalisation: dieser Vorgang besteht zunächst in der Bildung von Spezialzellen in den höchsten Zentren, den Cerebralganglien, dann in deren Zunahme an Masse, und schliesslich werden Funktionen, deren Sitz sich bei den ursprünglichen Formen in den rückwärtigen Ganglien befindet, in die Cerebralganglien verlagert. Diese Bildung von Integrationszentren wird Telencephalisation genannt.

Das Zentralnervensystem von *Fimbria fimbria* (Abb. 1), das in eine kompakte, milchig- durchsichtige Bindegewebshülle eingeschlossen ist, weist eine sehr starke Konzentration an der Schlundoberseite auf. Bei oberflächlicher Untersuchung scheinen sich alle Hauptganglien in eine einzige elliptische Masse zu vereinigen. Entfernt man die Bindegewebshülle, so kann man deutlich die einzelnen Ganglienzellen sehen, die bis 1 mm Durchmesser erreichen können. Diese extrem grossen Nervenzellen treten nur in bestimmten Regionen des cerebralen, pleuralen und pedalen Bereiches auf und sind mehr oder weniger stark gestielt. Sie bilden dadurch ein ganz lockeres Gefüge, wodurch die Gangliengrenzen verwischt werden. Hebt man die Ganglienzellen mit einer Pinzette ab, so wird die Form des zentralen Nervenfaserteils sichtbar. Die Cerebral- und Pleuralmassen sind miteinander verschmolzen, die Pedalganglien sind aber dem Cerebropleuralkomplex nur genähert. Die getrennten Cerebropedal- und Pleuropedalkonnective sind deutlich zu erkennen. Auf der rechten Ventralseite des Zentralnervensystems (Abb. 2) ist das Abdominalganglion deutlich sichtbar, und es ist nicht mit dem Pleuralkomplex verschmolzen, sondern diesem nur angelagert. Es hat spindelförmige Gestalt und ist in seiner Grösse reduziert. Beim durchscheinenden Licht sind am Faserkomplex deutlich dunkle und helle Stellen zu unterscheiden. In den dunklen Regionen sind die Nervenfasern besonders dicht gelagert und sie stellen die Ganglienzentren dar, während zwischen diesen die Nervenfasern wesentlich seichter verlaufen. Von einer Verschmelzung der Hauptganglien zu einer einheitlichen Masse kann man eigentlich nicht sprechen. An der Ventralseite des Zentralnervensystems kann man im Gegensatz zur Dorsalseite auch schon nach der Zellgrösse die Ganglienregionen feststellen. Riesenzellen treten hier nicht auf. Seitlich am Schlund (Abb. 3) liegen die Buccalganglien, die aus wenigen, verschiedenen grossen Zellen bestehen.

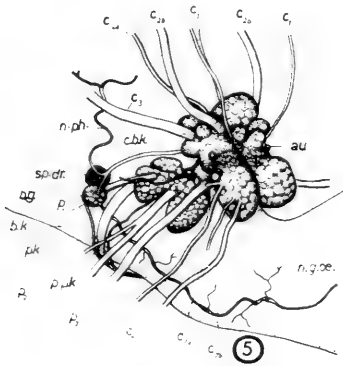
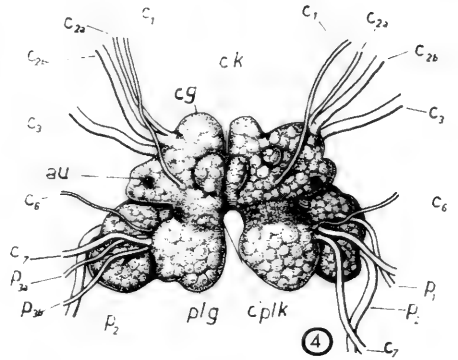
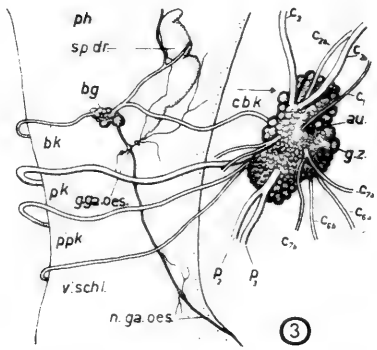
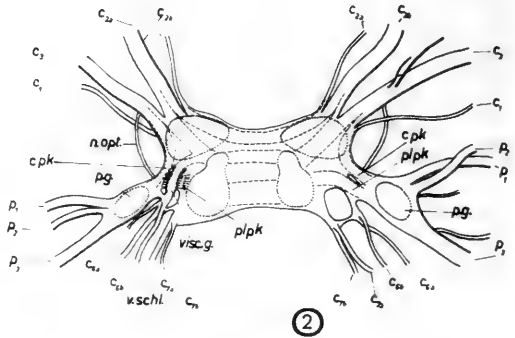
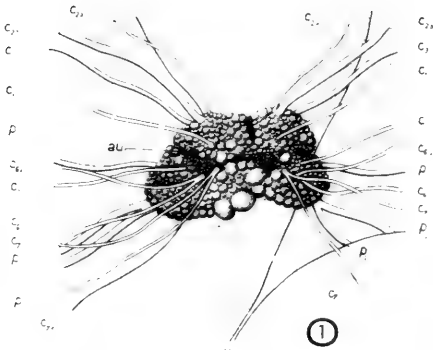
Beim Zentralnervensystem von *Melibe leonina* sind die Hauptganglien ohne nähere Untersuchung schon deutlich zu unterscheiden. Alle Ganglien bzw. Ganglienkomplexe haben eine unregelmässige und asymmetrische Form. Besonders der cerebrale Anteil ist stark zerklüftet. Die Nervenzellen der Ganglien (Abb. 4) sind in ihrer Grösse nicht so extrem verschieden wie bei *Fimbria fimbria*. Sie sind nicht gestielt und dem Faseranteil locker aufsitzend, sondern durch eine enge Bindegewebshülle zu einer festen Form zusammengepackt. Auch an der Ventralseite ist die Zerklüftung der Ganglien deutlich sichtbar. Die Cerebropedal- und Pleuropedalkonnective (Abb. 5) bilden im Gegensatz zu *Fimbria fimbria* einen einheitlichen Strang. Die Buccalganglien sind bei *Melibe leonina* von kugeligiger Gestalt und bestehen aus zahl-

reichen Nervenzellen.

Zwischen dem Zentralnervensystem von *Fimbria fimbria* und *Melibe leonina* gibt es zahlreiche morphologische Unterschiede, die jedoch im Hinblick auf ihre systematische Stellung nicht von Bedeutung sein dürften, da die beiden Arten in Bau und Funktion der übrigen Organsysteme und in ihrer Lebensweise übereinstimmen. Wie weit histologische Unterschiede im Zentralnervensystem vorhanden sind, wird noch zu untersuchen sein.

BIBLIOGRAPHIE

IHERING, H. von, 1922, Phylogenie und System der Mollusken. Arch. Moll. 1: Heft 1.  
 HANSTRÖM, B., 1929, Zur vergleichenden Anatomie des Zentralnervensystems der Opisthobranchier. Z. f. Morph. u. Ökol. Tiere 16. Bd 1: 2. Heft.  
 WIRZ, K., 1952, Remarques sur l'évolution du système nerveux des Opisthobranches. Arch. zool. exp. gen. 88: Notes et Revue 161-177.





## RECENT ADVANCES IN LAND MOLLUSC RESEARCH IN SWEDEN

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## ABSTRACT

An extensive, faunistic-ecological survey of the land molluscs (and some further terrestrial groups) in central and southern Sweden, is being carried out by the Göteborg Natural History Museum. It was started in 1921 by the late Dr. Hans Lohmander. The survey was presented by the present author at the First Europ. Malac. Congress, 1962. Since that time the survey has advanced considerably, and a brief report about the most important advances is justified.

Concerning the scope, principles and methods reference should be made to the Congress Report (Waldén, 1965). Fig. 1 shows how far the survey has advanced up to 1968. The black areas are surveyed in detail, from the dotted areas only scattered literature or museum records exist, and the white areas are entirely unknown. Besides the coherently surveyed area in southern and central Sweden, certain river valleys in northern Sweden have been investigated, in connection with their exploitation for hydroelectricity, which makes it necessary to collect documentary evidence of the destroyed areas for the future.

Since 1962 more than 2,600 collecting sites have been investigated, of which about 2,250 are situated in southern Sweden and more than 350 in the northern river valleys. In all more than 18,000 localities have been investigated in Sweden since the survey started. Parallel with the field work, the large amount of material left behind by Dr. Lohmander is being gradually worked out.

Besides the Swedish survey the Museum carries out surveys of a more extensive character in neighbouring countries. Thus a revision of the Norwegian collections of land molluscs has been undertaken and supplementary work has started, in cooperation with the Zoological Museums in Norway. Already the present work has rather profoundly modified the picture of distribution of the species of *Carychium*, *Succinea*, *Columella*, *Cochlicopa*, *Vitrea*, *Nesovitrea* and *Euconulus*, of certain species of *Vertigo*, *Vallonia*, *Arion* and *Deroceras*, and of *Acanthinula aculeata*. Two species, viz. *Clausilia dubia* and *pumila*, should evidently be eliminated from the list of Norwegian species, whereas others should be added, as *Vertigo genesii* and *geyeri*, *Limax valentianus* and *Zonitoides arboreus*. Obviously the results from Norway are of great importance when the conditions in Sweden are interpreted.

In connection with his survey in southern Sweden Dr. Lohmander did extensive collecting work in Denmark during 1930-39 and 1954-58. In all he investigated some 1,500 localities. Owing to the decease of Dr. Lohmander this survey also was not finished by him. However, an agreement has been made to undertake supplementary collecting work in cooperation with the Aarhus Natural History Museum in Denmark, so the remaining gaps in the survey will be covered.

## TAXONOMIC REVISION

The genera *Nesovitrea* and *Columella* have been revised. In the genus *Nesovitrea* (Waldén, 1966b) the specific distinction between *hammonis* (Ström) and *petronella* (L. Pfeiffer) has been definitely proved. The nearctic species, *electrina* (Gould) and *binneyana* (Morse), are clearly distinguished from the European species, without any intermediates.

In the genus *Columella* a new species, *C. aspera* Waldén (1966a, p 53) has been recognized. It is definitely clear that *C. columella* (Martens) also is a distinct species. The survey has also made clear that the nearctic so-called *C. edentula*, described as *C. simplex* by Gould, is remarkably distinct both from the European *edentula* (Drap.) and *aspera*. It may possibly be a distinct species, but this needs further work to be proved. On the other hand *C. alticola* (Ingersoll) without any doubt is conspecific with *C. columella*.

Until now very little has been published about *C. aspera*, but it appears to be the prevalent species of the genus in NW Europe. Fig. 2 shows its distribution in the province of Halland in SW Sweden. It is almost ubiquitous here, being particularly prevalent in oligotrophic areas. *C. edentula* (Fig. 3) proved to be rare and local, mainly confined to luxuriant woods and fens, especially on calcareous soil.

For a number of further aggregate groups conclusive evidence has been obtained that they are composed of distinct species, though the results have not yet been published. These are *Vertigo arctica* and *ronnebyensis* (the relation to the nearctic *V. modesta* is disregarded in the present connection), *V. genesii* and *geyeri*, *Arion circumscriptus*, *silvaticus* and *fasciatus*. In addition to this the relation between *Deroceras laeve* and *sturanyi*, which Simroth and his followers considered to represent stages of a sex-change cycle, has been definitely disentangled.

On the other hand, the complex of *Cochlicopa* species must still be regarded as far from solution.



Fig. 1

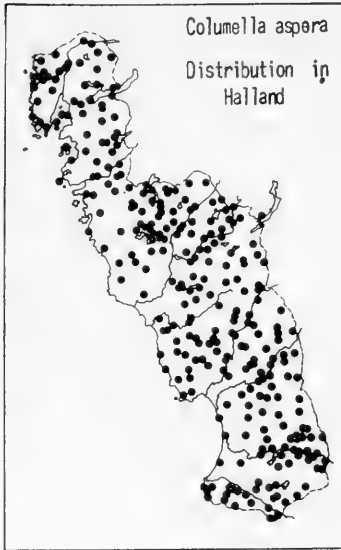


Fig. 2

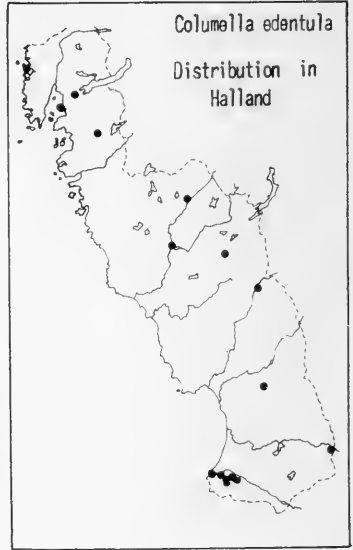


Fig. 3



Fig. 4



Fig. 5

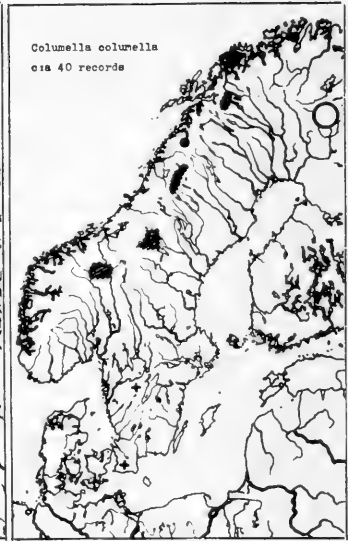


Fig. 6

## FAUNISTIC RESULTS

Some examples of a wider zoogeographical interest will be considered. The three species regarded below are of particular interest, because they were characteristic of the coldest phases of the Pleistocene in central Europe and in the British Isles. Today they are, outside Scandinavia, limited to the highest alpine areas of Europe.

The subfossil Mollusca are included in the survey. When the distribution is considered both recent and fossil evidence are included. Subfossil records from localities, where the species are now extinct, have been indicated on the maps by crosses.

*Vertigo arctica* (Wallenberg) (Fig. 4). This species has proved to be regularly distributed along the high mountain ridge, and on lower levels in northernmost Scandinavia. Besides, it has a seemingly isolated occurrence in the mountain gorge Skärälid in southernmost Sweden. *V. arctica* appeared very early after the ice age. Later it seems to have become extinct, except in the mountains and at Skärälid. Evidence from several sites indicate that it must have survived the Post Glacial Warm Period (Atlanticum) here. The recent occurrence in the south is reasonably regarded as relict.

*Vertigo genesii* Greder (Fig. 5) also occurs over a large stretch in the Scandinavian mountains, though it is decidedly rarer than *V. arctica*. In southern Sweden it still lives in cold spring bogs on the calcareous mountains of Västergötland. Fossil evidence is known from this area, from Jämtland in northern Sweden and from southernmost Sweden. In the last area it is now extinct. The recent distribution is quite consistent with the fossil history. The occurrence in Västergötland has a clearly relict character.

*Columella columella* (Martens) (Fig. 6) has a similar distribution to *V. genesii*, though it is decidedly more northern. It occurs on low levels in northernmost Scandinavia. It is evidently absent in southern Sweden. There it is known only from the oldest strata, and disappears when the Warm Period begins.

Above it has been pointed out that the typical alpine and Glacial Period species *V. arctica* and *genesii* were able to survive the Post Glacial Warm optimum in southernmost Sweden. The mollusc fauna here of this period has a remarkably heterogeneous character. On the one hand it comprises typical central European species, such as *Laciniaria biplicata*, *Iphigena ventricosa* and *Monachoides incarnatus*, which are today much rarer. Together with those species (though, of course, in different habitats) there lived the above mentioned alpine species and, in addition, the boreal species *Nesovitrea petronella* and *Discus ruderatus*, which are today decidedly much rarer in this part of Sweden.

The co-occurrence of these very different faunal groups stands in contrast to the hitherto known botanical evidence. Reasonably it must modify the conception of the climate during the Post Glacial Warm Period.

## REFERENCES

- WALDÉN, H. W., 1965, Terrestrial faunistic studies in Sweden. *Proc. First Malac. Congress*, 95-109.  
 WALDÉN, H. W., 1966a, Einige Bemerkungen zum Ergänzungsband zu EHRMANN's "Mollusca" in "Die Tierwelt Mitteleuropas." *Arch. Moll.*, 95: 49-68.  
 WALDÉN, H. W., 1966b, Zur Frage der Taxonomie, Nomenklatur und Ökologie von *Nesovitrea hammonis* (Ström) und *petronella* (L. Pfeiffer). *Ibid.*, 95: 161-195.



SYSTEMATICS OF THE GENUS *POTAMOPYRGUS* (HYDROBIIIDAE) IN EUROPE,  
AND THE CAUSATION OF THE KEEL IN THIS SNAIL

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## ABSTRACT

The snail *Potamopyrgus jenkinsi* (Smith), was first described as *Hydrobia jenkinsi* by Smith (1889), from Thames estuary specimens. Thiele (1928) transferred the snail to the genus *Potamopyrgus*. Warwick (1952) reported differences between material collected at localities well inland and that found in brackish waters near the coast. These coastal specimens were identical with early Thames estuary specimens in the British Museum (Natural History). They are therefore considered to be *P. jenkinsi* sensu stricto. The shell whorls are convex with a marked suture. The whorls increase rapidly in size growing a stout shell and the mantle is deeply pigmented. There is a dense patch of pigment near the eye. *P. jenkinsi* s.s. is usually limited in Western Europe to brackish water and freshwaters of the coastal zone. Rarely it has been found in inland localities. The species ranges from Finland to the Mediterranean coast of France. Though somewhat slender and stout forms both occur there is little variation in shell shape and the species is not polymorphic. An ornamented variety (var. *carinata*) with a keeled shell occurs. Populations with well marked keels are rare. Usually all specimens in a population are smooth or the keel is present only as a line in a low proportion. *P. jenkinsi* s.s. bears a distinct resemblance in shell shape to species of this genus found in southeastern Australia, Tasmania and New Zealand. However, it differs from these Australasian snails in various characters.

The *Potamopyrgus* found in inland localities belongs to a type provisionally called Strain A, Warwick (1952). This has a very distinctive shell and pigmentation of the soft parts. The shell is slenderer and more elongate than in *P. jenkinsi* s.s. The suture is shallower and the whorls are distinctly less convex, being somewhat flat. In clean shelled specimens the mantle colouration is seen to be much paler. This is true too of the pigment patch near the eye. The remarks about ornamentation in *P. jenkinsi* s.s. apply also to Strain A. This strain is the commonest and most widespread form of *Potamopyrgus* in Europe. It is found in coastal waters even if they are strongly brackish (19% seawater). Usually it is the only form found well inland in Europe. In 1950 specimens of *Potamopyrgus* from coastal streams in Wales were collected, their shells had the black deposit usual in this genus. When bred in the laboratory the pigmentation was studied through the clean shell. Though like *P. jenkinsi* s.s. there was a black pigment patch near the eye in other respects pigmentation was different. The ground colour of the mantle seen through the body wall is pale. It has, however, numerous irregular patches of darker pigment. Shell shape is much as in *P. jenkinsi* s.s. with slender and stout forms occurring. This strain has been provisionally called "C", Warwick (1952). Strain C differs from strain A and *P. jenkinsi* s.s. in the facility with which it grows a keel. The keel is often well developed as tufts of spines. This strain is common on the Welsh and Irish coasts. In England it occurs in Kent and East Anglia and inland in Derbyshire. On the Continent it has been found at two localities near Biarritz, France. The type of distribution is like that of *P. jenkinsi* s.s. It is proposed elsewhere to re-describe *P. jenkinsi* s.s. and to describe strains A & C as species of the genus *Potamopyrgus*. It is appreciated that the splitting up of somewhat similar populations of completely parthenogenetic animals presents taxonomic problems. How such a matter should be treated must, according to Mayr (1963), be decided for each case. There seems to be valid grounds in this case. Here we have 3 forms showing differences in shell shape, pigmentation, ornamentation and distribution. Todd (1964) showed that at least one physiological difference occurs as well. Two and more rarely three of these strains may sometimes occur side by side. When they do so strain A can be separated by shell shape and pigmentation. It is more difficult to separate *P. jenkinsi* s.s. and Strain C as their shell shape is similar. However, well-keeled specimens may belong to C and this strain often has nearly colourless tentacles. If clean shelled material is available, the patchy mantle pigmentation of C is diagnostic.

The causation of the keel has attracted interest and attention. Robson (1925) bred keeled snails but obtained only smooth offspring. Boycott (1929), breeding aculeate snails, obtained a low percentage of keeled forms. Boettger (1949) also produced some keeled snails in the laboratory. The conditions under which these keeled snails occurred were inconclusive. The above work suggests that the keel is partly due to environmental characters. Warwick (1952) suggested that keel formation was partly genetical, partly environmental. It has been substantiated that different populations have different threshold values for keel formation. However, Warwick's suggestion that algal metabolites are responsible for keel formation has not been confirmed by later work. Since 1952, work has been continued on this problem, and reproducible results have been obtained. Strong keels have been grown from smooth parents of *P. jenkinsi* and strain A. These experiments will be fully described elsewhere. The keel develops in the presence of an adequate

quantity of humic materials in the water or food. In nature, amongst other sources of such material, one may mention dead leaves of deciduous trees and dead stems and leaves of sedges (*Carex* spp.).

## REFERENCES

- BOETTGER, C. R., 1949, Hinweise zur Frage der Kielbildung auf der Schale der Wasserschnecke *Potamopyrgus crystallinus jenkinsi* (E. A. Smith). *Arch. Moll.*, 77: 63-72.
- BOYCOTT, A. C., 1929, The inheritance of ornamentation in *var. aculeata* of *Hydrobia jenkinsi* Smith. *Proc. malac. Soc. Lond.*, 18: 230-234.
- MAYR, E., 1963, Animal Species and Evolution. Oxford Univ. Press, London, 797 p.
- ROBSON, G. C., 1926, Parthenogenesis in the mollusc *Paludetrina jenkinsi*. Part II - The Genetical Behaviour Distribution, etc., of the Keeled Form ("var. carinata"). *J. exp. Biol.*, 3: 149-160.
- SMITH, E. A., 1889, Notes on British *Hydrobiae*, with description of a supposed new species. *J. Conch., Lond.*, 6: 142-145.
- THIELE, J., 1928, Revision des Systems der Hydrobiiden und Melaniiden. *Zool. Jahrb. Jena. Syst.*, 55: 351-402.
- TODD, M. E., 1964, Osmotic balance in *Hydrobia ulvae*, and *Potamopyrgus jenkinsi* (Gastropoda: Hydrobiidae). *J. Exp. Biol.*, 41: 665-677.
- WARWICK, T., 1952, Strains in the mollusc *Potamopyrgus jenkinsi* (Smith). *Nature, Lond.*, 169: 551-552.

DIE ULTRASTRUKTUR DER SOHLENDRÜSENZELLEN VON *ARION RUFUS* L.

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## ZUSAMMENFASSUNG

Die Sohlendrüsenzelle ist gekennzeichnet durch einen Drüsenbauch und einen mehr oder weniger von diesem abgesetzten, gewundenen Drüsenhals. Im apikalen Bereich ist sie durch eine Zonula adhaerens, eine Zwischenzone und eine Zonula septata (WONDRAK, 1968) mit den Epithelzellen verbunden. Die freie Oberfläche des Drüsenhalses ist eingebuchtet und an ihrem Rand stehen Mikrovilli, die bei Extrusion des Sekretes verschwinden. Im Hals findet man, neben Zwischen- und Endprodukten der Schleimsynthese, Mitochondrien und Ausläufer des Ergastoplasmas.

Im Drüsenbauch fällt vor allem das hochorganisierte Ergastoplasma auf (WONDRAK, 1967; Abb. 4, 7), dessen Membranabstand, ausgenommen an den Verzweigungsstellen, sehr konstant ist (ca. 0,15 - 0,2  $\mu$ ). Ins Innere ragen kleinste, senkrecht zu den Membranen stehende Tubuli von ca. 0,02  $\mu$  Durchmesser (Abb. 2, 3). Wo der perinukleäre Spalt erweitert ist, beinhaltet er die gleichen Tubuli (Abb. 1). Die gleiche Differenzierung des Ergastoplasmas weisen die Zymozyten der Speicheldrüse von *Helix aspersa* (QUATTRINI, 1967), die "metachromatic cell" von *Helicella obvia* (RÖHLICH & BIERBAUER, 1966), welche sicher eine Sohlendrüsenzelle darstellt, sowie die Pedaldrüsenzellen von *Arion rufus* und die Sohlendrüsenzellen von *Helix pomatia* (WONDRAK, 1969) auf. Die Mitochondrien stehen mit dem Ergastoplasma in engem Kontakt. Der Golgi-Apparat zeigt je nach Funktionsstadium verschieden weite Bläschen mit unterschiedlich elektronendichtem Inhalt. An den Zellbauch treten vegetative Nervenendigungen heran (Abb. 5).

An manchen Zellen sieht man stark zerklüftete Drüsenbäuche, die von der Oberfläche Bläschen einschütren, welche man immer extrazisternal zwischen den Membranen des Ergastoplasmas beobachtet, das sich hier bis in die Spitzen der Vorwölbungen erstreckt. Während der verschiedenen Stadien der Sekretsynthese, soweit sie als solche elektronenoptisch erkennbar sind, konnten keine strukturellen Veränderungen des Ergastoplasmas beobachtet werden. Der Golgi-Apparat zeigt in seinen Vesikeln häufig elektronendichtes Material (Abb. 6). An anderen Stellen erscheint sein Inhalt "herausgelöst" und seine Lamellen sehr stark erweitert (Abb. 4). Im Zytoplasma liegen membranbegrenzte, elektronendichte, schwammartig strukturierte Granula von ca. 0,5 - 0,8  $\mu$  Durchmesser. Sie scheinen aus häufig zu sehenden, weniger elektronendichten und nicht membranbegrenzten Gebilden von unregelmässiger Gestalt zu entstehen. An anderen Stellen liegen extrazisternal sehr grosse Vakuolen, die von stark erweiterten Golgi-Membransystemen stammen und deren Inhalt "herausgelöst" erscheint (Abb. 4). Die dunklen Granula findet man bis in den apikalen Teil des Drüsenhalses, doch konnte niemals ihre Extrusion beobachtet werden. Auch trägt die freie Oberfläche in diesem Stadium immer Mikrovilli. Dagegen sieht man oft Zellen, die ihren homogenen, wenig dichten Inhalt durch den weit offenen Drüsenhals abgeben.

## LITERATURVERZEICHNIS

- QUATTRINI, D., 1967, Osservazioni sulla ultrastruttura dei dotti escretori delle ghiandole salivari di *Helix aspersa* Müller (Mollusca, gastropoda, pulmonata). *Caryologia*, 20: 191-206.
- RÖHLICH, P. & BIERBAUER, J., 1966, Electron microscopic observation on the special cells of the optic tentacle of *Helicella obvia* (Pulmonata). *Acta Biol. Hung.*, 17: 359-373.
- WONDRAK, G., 1967, Die exoepithelialen Schleimdrüsenzellen von *Arion empiricorum* (Fér.). *Z. Zellforsch.* 76: 287-294.
- WONDRAK, G., 1968, Elektronenoptische Untersuchungen der Körperdecke von *Arion rufus* L. (Pulmonata). *Protoplasma*, 66: 151-171.
- WONDRAK, 1969, Elektronenoptische Untersuchungen der Drüsen- und Pigmentzellen aus der Körperdecke von *Arion rufus* L. (Pulmonata). *Z. mikr. anat. Forsch.* 80: 17-40.

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ABB. 1. Perinukleärer Spalt. Fixierung: Glutaraldehyd. Kontrastierung: Bleizitrat. Vergrößerung: 48000: 1.

ABB. 2. Querschnitt durch Tubuli des Ergastoplasmas. Fixierung: Glutaraldehyd - Osmiumsäure. Kontrastierung: Phosphorwolframsäure. Vergrößerung: 88000: 1.

ABB. 3. Längsschnitt durch Tubuli des Ergastoplasmas. Fixierung: Glutaraldehyd - Osmiumsäure. Kontrastierung: Phosphorwolframsäure. Vergrößerung: 88000: 1.

ABB. 4. Drüsenbauch. Fixierung: Glutaraldehyd. Kontrastierung: Bleizitrat. Vergrößerung: 20800: 1.

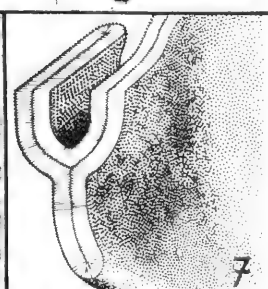
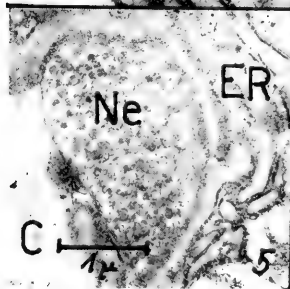
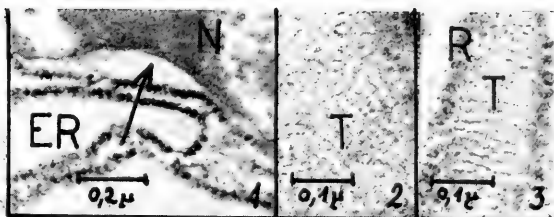
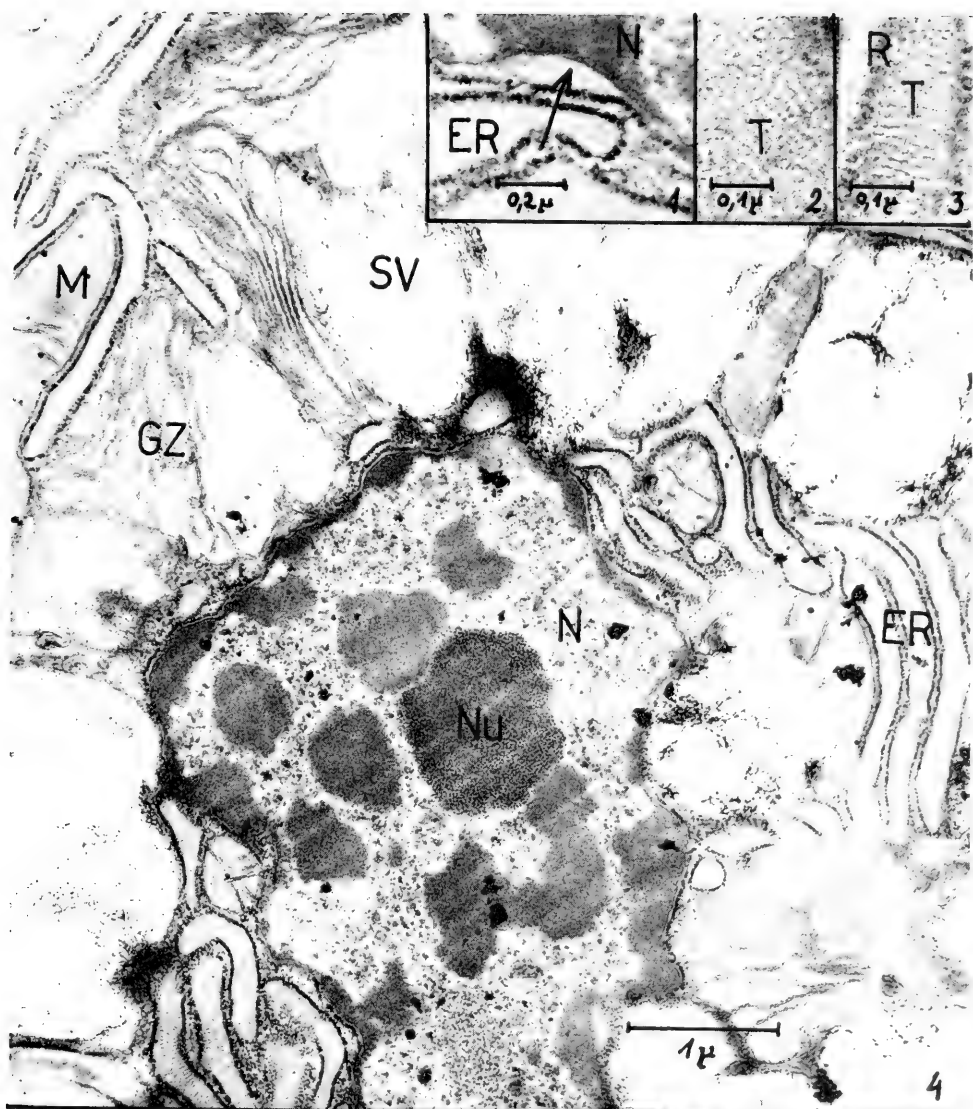
ABB. 5. Synapse. Fixierung: Glutaraldehyd. Kontrastierung: Bleizitrat. Vergrößerung: 128000: 1.

ABB. 6. Golgi-Zone. Fixierung: Glutaraldehyd - Osmiumsäure. Kontrastierung: Bleizitrat. Vergrößerung: 19200: 1.

ABB. 7. Schema des Ergastoplasmas.

C, Kollagenfibrillen; ER, Ergastoplasma; GZ, Golgi-Zone; M, Mitochondrium; N, Zellkern; Ne, Nerv; Nu, Nukleolus; R, Ribosomen; S, Sekretgranulum; SV, Sekretvakuole; T, Tubuli; —> weist auf erweiterten perinukleären Spalt mit tubulären Innenstrukturen. Alle Schnitte stammen von in Epon eingebettetem Material.







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By an unfortunate oversight the name of Dr. B. C. Dazo was omitted completely in the Proceedings of the Second Malacological Congress in Copenhagen. Therefore it should be mentioned that Dr. Dazo, who is member of the *Unitas Malacologica Europaea*, was a participant of the Second Congress and presented a paper there on "Determining sites of bilharzial transmission."



INDEX TO SCIENTIFIC NAMES

- aberrans*, *Veronicella*, 264  
*Abida*, 112, 115, 117  
     *frumentum*, 112, 115, 117  
*Abra*, 238, 241, 271, 277  
     *alba*, 238, 241  
     *ovata*, 277  
     *profundorum*, 271  
*abrotanifolia*, *Cystoseira*, 277, 230  
*Acanthinula*, 85, 115, 297  
     *aculeata*, 85, 115, 297  
*Acanthochiton*, 210, 227, 228, 230, 231, 240  
     *communis*, 227, 228, 230, 231, 240  
     *fascicularis*, 227, 240  
*Acar*, 271  
     *asperula*, 271  
*Acavidae*, 256-258  
*Acetabularia*, 224, 227, 230  
     *mediterranea*, 224, 227  
*achates*, *Chilostoma achates*, 261  
*achates achates*, *Chilostoma*, 261  
*Achatina*, 43  
     *fulica*, 43  
*Achatinacea*, 260  
*Achatinellacea*, 260  
*Achatinidae*, 256, 257  
*Acicula*, 117  
     *polita*, 117  
*acicula*, *Eulimella*, 238  
*acicularis audebartii*, *Fagotia*, 113  
*aciculata*, *Tritonalia*, 226, 228, 230, 231, 240  
*Acmaea*, 81  
*Acme*, 249  
     *inchoata*, 249  
*Acroloxus*, 145  
     *lacustris*, 145  
*acronicus*, *Gyraulus*, 145, 149  
*Acteon*, 232, 236, 241  
     *tornatilis*, 232, 236, 241  
*Actinia*, 224  
     *equina*, 224  
*aculeata*, *Acanthinula*, 85, 115, 297  
*aculeata*, *Crepidula*, 81  
*Aculifera*, 191, 193, 195, 205, 209, 210, 212, 214  
*acutilira*, *Simulopsis*, 201  
*acuta*, *Cochlicella*, 88  
*acuta*, *Hydrobia*, 277  
*acuta*, *Physa*, 54, 55, 277  
*Adesmacea*, 164  
*adriatica*, *Cystoseira*, 227  
     *adriatica*, *Trivia*, 232, 235, 236, 241  
     *adriatica*, *Distoma*, 231  
*Aegopinella*, 269  
     *nitidula*, 269  
*Aegopis*, 86, 117  
     *verticillus*, 117  
*Aenigma*, 83  
     *rosea*, 83  
*aenigmatica*, *Enigmonia*, 288  
*Aeolidiacea*, 230, 231, 282, 295  
*aerea*, *Chaetomorpha*, 224  
*Aeromonas*, 43  
     *liquefaciens*, 43  
*affinis*, *Flabellina*, 230, 231, 237  
*Afriboysidia*, 256  
*africana*, *Macroptychia*, 258  
*africanus*, *Bulinus*, 30  
*Afrodonta*, 256  
*aggericola*, *Arion*, 73  
*Aglaophenia*, 225, 226  
     *pluma*, 225  
*agraulus*, *Gyraulus*, 88  
*Agriolimax*, 179-182, 184, 273  
     *caruanae*, 273  
     *reticulatus*, 179-182, 273  
*Ailanthus*, 85  
*Akiyoshia*, 278  
*alata*, *Isognomum*, 80, 83  
*alba*, *Abra*, 238, 241  
*albescens*, *Doris*, 96  
*albus*, *Gyraulus*, 56, 145  
*albus*, *limophilus*, *Gyraulus*, 56  
*Alexandromenia*, 204  
     *crassa*, 204  
*Alexia*, 224, 240  
     *myosotis*, 224, 240  
*alliaris*, *Oxychilus*, 273, 274  
*alhuaudi*, *Bulinus tropicus*, 38  
*Alloidis*, 238, 241  
     *gibba*, 238, 241  
*alticola*, *Columella*, 297  
*Alvania*, 230-232, 234, 238, 240, 241, 243  
     *cimex*, 230-232, 234, 238, 240, 241  
*Alzonula*, 86  
     *oglasticola*, 86  
*Amanthia*, 230  
*Ambigua*, 85, 88  
     *argentarolae forsythi*, 88  
     *forsythi*, *argentarolae*, 88  
*amboinensis*, *Anamenia*, 204  
*ameghini*, *Veronicella*, 264  
*americanus*, *Modiolus*, 80, 83

- Ammonoidea, 209  
 Amnicolinae, 278  
 Amphibulimidae, 256  
 Amphineura, 191, 193, 210, 214  
 Amphipoda, 271  
*Anadara*, 80, 83, 165, 168  
   *granosa*, 83, 165, 168  
   *notabilis*, 80, 83  
*Anamenia*, 204  
   *amboinensis*, 204  
   *anatina*, *Pseudamnicola*, 277  
 Anatinacaea, 170  
*anceps royalense*, *Helisoma*, 263  
*Anchinoe*, 226  
*anchora*, *Gymnarion*, 60  
 Ancyliidae, 145  
*Ancylus*, 54, 55, 145, 148, 277  
   *costulatus*, 54, 55  
   *fluviatilis*, 55, 145, 148, 277  
*Aneitea*, 259, 260  
*angigyra*, *Helicodonta*, 267  
*anguistipes*, *Veronicella*, 264  
*angulifera*, *Littorina*, 80, 82  
*Angulus*, 238, 241  
   *incarnatus*, 238  
   *planatus*, 238  
 Anisomyaria, 163  
*Anisus*, 55, 56, 145  
   *perezi*, 56  
   *spirorbis*, 55, 145  
 Annelida, 203, 210  
*annularis*, *Phenacolimax*, 117  
*annulata*, *Pyrgula*, 175, 176  
*Anodonta*, 67, 68, 247, 286  
   *cellensis*, 67, 68  
   *cygnaea*, 286  
*Anomalocardia*, 81, 83  
   *brasiliiana*, 81, 83  
*Anomia*, 227, 240, 288  
   *ephippium*, 227, 240  
   *patelliformis*, 288  
 Anomiidae, 83, 164  
 Anthozoa, 212, 219  
*antiqua*, *Succinea*, 249  
*antivertigo*, *Vertigo*, 115, 117, 249  
*Antroselates*, 278  
*Apera*, 256  
 Aperiidae, 256-258  
*aperta*, *Cantareus*, 88  
*aperta*, *Helix*, 88  
*aperta*, *Philine*, 234, 236, 241  
*apicina*, *Helicella*, 88  
*apicina*, *Xerotruchia*, 88  
 Aplacophora, 191, 193, 195, 214  
*Aplexa*, 145  
   *hypnorum*, 145  
*Aplidium*, 231  
   *conicum*, 231  
*Aplysia*, 253  
   *depilans*, 253  
   *fasciata*, 253  
   *punctata*, 253  
*Aporrhais*, 231, 232, 234, 235, 238, 240, 241  
   *pes pelecani*, 231, 232, 234, 235, 238, 240, 241  
*arboreus*, *Zonitoides*, 297  
*arbustorum*, *Arianta*, 249  
*Arca*, 165, 168, 188, 189, 226, 227, 232, 234, 238-241, 271  
   *barbata*, 234  
   *lactea*, 226, 227, 234, 238-241  
   *noae*, 232, 234  
   *orbiculata*, 271  
   *similis*, 165, 168  
   *ventricosa*, 188, 189  
 Arcaea, 163  
 Archaegastropoda, 279  
 Archiannelida, 208  
 Archicoelomata, 213  
*Archidoris*, 232, 234, 236, 237, 240, 241  
   *tuberculata*, 232, 234, 236, 237, 240, 241  
*Archivesica*, 254  
 Archoophora, 203  
 Arcidae, 83, 164  
*Arcopagia*, 238  
   *balaustina*, 238  
*arctica*, *Hiatella*, 291, 292  
*arctica*, *Vertigo*, 297, 299  
*arcuata*, *Melanella*, 238  
*arcuatus*, *Ensis*, 245, 246  
*avenaria*, *Catinella*, 117  
*argentaricus*, *Oxychilus*, 86  
*argentarolae forsythi*, *Ambigua*, 88  
*argentarolae forsythi*, *Marmorana*, 88  
*Arianta*, 249  
   *arbustorum*, 249  
*arigo*, *Leucochroa*, 55  
*arigo*, *Xeromagna*, 55  
*Arion*, 73-78, 249, 297, 303  
   *aggericola*, 73  
   *ater*, 73, 76, 249  
   *ater ater*, 73, 76

- ater rufus*, 73  
*aterrima, rufus atra*, 73  
*atra, rufus*, 73  
*atra aterrima, rufus*, 73  
*atra marginella, rufus*, 73, 74  
*atra sulcata, rufus*, 73, 74  
*brevieri*, 73  
*circumscriptus*, 297  
*fasciatus*, 297  
*flavus*, 73  
*hibernus*, 73  
*intermedius*, 249  
*lusitanicus*, 73-77  
*lusitanicus nigrescens*, 73  
*marginella, rufus atra*, 73, 74  
*nigrescens, lusitanicus*, 73  
*nobrei*, 73  
*rubiginosus*, 73  
*rufus*, 73, 74, 76, 303  
*rufus, ater*, 73  
*rufus atra*, 73  
*rufus atra aterrima*, 73  
*rufus atra marginella*, 73, 74  
*rufus atra sulcata*, 73, 74  
*silvaticus*, 297  
*subfuscus*, 73, 74, 76, 249  
*sulcata, rufus atra*, 73, 74  
*sulcatus*, 76  
*tenellus*, 73  
*virescens*, 73  
 Arionidae, 73, 256, 258  
 Ariophantacea, 260  
*Armiger*, 56, 85, 87  
   *crista*, 56, 85, 87  
*Artemisia*, 249  
 Articipidae, 254  
 Asaphidae, 83  
*Asaphis*, 81, 83  
   *deflorata*, 81, 83  
 Ascidia, 81, 219, 222, 226, 231, 234, 240  
   *mentula*, 231  
   *nigra*, 81  
   *virginea*, 231  
*Ashfordia*, 249  
   *granulata*, 249  
*aspera, Cohumella*, 249, 297  
*aspersa, Cryptomphalus*, 55, 86, 87  
*aspersa, Helix*, 55, 86, 87, 135, 273, 303  
*asperula, Acar*, 271  
*Astarte*, 168  
 Astartidae, 254  
*Astraea*, 231, 234, 240, 241  
   *rugosa*, 231, 234, 240, 241  
*Astraliium*, 293  
*ater, Arion*, 73, 76, 249  
*ater, Arion ater*, 73  
*ater, Viviparus*, 284  
*ater ater, Arion*, 73, 76  
*ater rufus, Arion*, 73  
*aterrima, Arion rufus atra*, 73  
 Athoracophoracea, 260  
 Athoracophoridae, 259, 260  
*Athopos*, 282  
*atlantica, Callocardia*, 254  
*atra, Arion rufus*, 73  
*atra aterrima, Arion rufus*, 73  
*atra marginella, Arion rufus*, 73, 74  
*atra sulcata, Arion rufus*, 73, 74  
*Atrina*, 165  
*atriolonga, Genitoconia*, 204  
*atromaculata, Peltodoris*, 220, 226, 227,  
   237, 240  
*audebartii, Fagotia acicularis*, 113  
 Aulacopoda, 260  
*aurantia, Caloplaca*, 223  
*aurantiaca, Bowwiera*, 232, 234, 240  
*auratus, Cricetus*, 30  
*aurea, Venerupis*, 275  
*auricula, Auriculella*, 260  
*auricularia, Lymnaea*, 145  
*Auricularia, Radix*, 54, 55  
*Auriculella*, 260  
   *auricula*, 260  
*auris judae, Ellobium*, 82  
*auris midae, Ellobium*, 82  
*aurita, Eumorphotis*, 288  
*Australorbis*, 31, 104, 105  
   *glabratus*, 31, 104, 105  
*Avenionia*, 278  
*Avicennia*, 79  
   *nitida*, 79  
 Aviculidae, 164  
*axinellae, Parazoanthus*, 226  
  
*Babinka*, 201  
*Baicalia*, 176  
*baicaliiformis, Stankovicia*, 176  
 Baicaliinae, 175, 176  
 Bakevilliidae, 288  
 Balanidae, 226  
*Balanus*, 81  
*baldensis, Chilostoma cinculatum*, 261  
*balustina, Acropagia*, 238  
*banatica, Helicigona*, 117  
*banyulensis, Nematomenia*, 207, 209  
*barbara, Cochlicella*, 89

- barbata*, *Arca*, 234  
*barbata*, *Cystoseira*, 224  
*barbatus*, *Modiolus*, 234, 238, 241  
*Barnea*, 167-170  
*Basommatophora*, 39, 101  
*Bathyomphalus*, 145  
   *contortus*, 145  
*Batillaria*, 81, 82  
   *minima*, 81, 82  
*Beguinea*, 226, 227, 231, 240  
   *calyculata*, 226, 227, 231, 240  
*Belgrandia*, 117  
   *tataënsis*, 117  
*Bellerophonacea*, 201  
*Berthelinia*, 81  
   *caribbea*, 81  
*bidentata*, *Perforatella*, 113, 115  
*bidentatus*, *Melampus*, 81, 82  
*bielzi*, *Mastus*, 117  
*bielzi*, *Vitrina*, 117  
*Bilateria*, 205  
*binneyana*, *Nesovitreia*, 297  
*Biomphalaria*, 25, 32, 35, 40, 43  
   *glabrata*, 25, 32, 40  
   *pfeifferi*, 35, 43  
   *sudanica tanganyicensis*, 35  
   *tanganyicensis, sudanica*, 35  
*biplicata*, *Laciniaria*, 299  
*biplicata*, *Olivella*, 290  
*birmanica*, *Nerita*, 82  
*bistrialis*, *Cryptozona*, 260  
*bisulcata*, *Lithophaga*, 81  
*Bithynia*, 113, 277  
   *tentaculata*, 277  
   *tentaculata thermalis*, 113  
   *thermalis, tentaculata*, 113  
*Bittium*, 220, 228, 230, 231, 234, 238, 240, 241  
   *reticulatum*, 228, 230, 231, 234, 238, 240, 241  
*Bivalvia*, 163, 164, 166, 191, 201, 203-210, 214, 217, 219, 222, 225-227, 230, 231, 234, 236, 238, 240, 241, 243, 247, 254, 275, 288  
*blainvillei*, *Murex*, 220  
*blainvillei*, *Muricidea*, 226, 227, 230, 240  
*böcklii*, *Viviparus*, 112  
*bohemica*, *Hercynella*, 288  
*Bonellia*, 205, 212  
*borellianus*, *Vaginulus*, 284  
*Bosellia*, 220, 226, 237, 240  
   *mimetica*, 220, 226, 237, 240  
*Bostrychia*, 81  
*Bothryllus*, 81  
*Botryocladia*, 230  
   *botryoides*, 230  
*botryoides*, *Botryocladia*, 230  
*Bouvieria*, 232, 234, 240  
   *aurantiaca*, 232, 234, 240  
*Brachidontes*, 80, 81, 83  
   *citrinus*, 80  
   *exustus*, 80, 81, 83  
   *recurvus*, 80  
*Brachiopoda*, 210, 213, 288  
*Brachyodontes*, 220, 224, 225, 231, 238, 240  
   *minimus*, 220, 224, 225, 231, 238, 240  
*Bradybaenidae*, 262  
*branchialis*, *Favorinus*, 230, 231  
*brandaris*, *Murex*, 238, 241  
*brasiliansa*, *Anomalocardia*, 81, 83  
*Brechites*, 168  
*breve*, *Vitrinobrachium*, 269  
*brevierei*, *Arion*, 73  
*brevifrons*, *Murex*, 80, 82  
*britannica*, *Truncatellina*, 249  
*Bryozoa*, 193, 210, 222, 230  
*Buccinidae*, 222, 226, 227  
*Bufo*, 286  
   *melanostictus*, 286  
*Bulininae*, 26  
*Bulinus*, 25-33, 35, 37-39  
   *africanus*, 30  
   *alluaudi, tropicus*, 38  
   *contortus*, 26  
   *coulboisi*, 38  
   *depressus*, 37  
   *globosus*, 35  
   *guernei*, 37, 38  
   *nasutus*, 35  
   *natalensis*, 37, 38  
   *rohlfsi, truncatus*, 38  
   *sericinus*, 37  
   *tropicus*, 37-39  
   *tropicus alluaudi*, 38  
   *tropicus tropicus*, 38  
   *truncatus*, 25, 26, 28, 29, 31-33, 37, 38  
   *truncatus rohlfsi*, 38  
   *truncatus truncatus*, 38  
   *ugandae*, 35  
*Bulla*, 81  
*bullaoides*, *Detraci*, 82

- Bullaria*, 236, 241  
   *striata*, 236, 241  
*bursa*, *Codium*, 225  
*Bythinella*, 173, 174  
   *robiči*, 173  
 Bythinellinae, 278  
 Bythiniinae, 278  
  
*Cacopus*, 287  
   *systema*, 287  
*Cacospongia*, 225, 226  
   *scalaris*, 225, 226  
*Caecum*, 236, 241  
   *glabrum*, 236, 241  
*caespitosa*, *Hyella*, 223  
*cajetanus*, *Lepidopleurus*, 227, 240, 241  
*calcara*, *Doris*, 96  
*californica*, *Dondersia*, 204  
*californicum*, *Prochaetoderma*, 206  
*Calliostoma*, 230, 231, 236, 241  
   *conulus*, 231  
   *laugieri*, 230  
   *zizyphinus*, 231  
*Callocardia*, 254  
   *atlantica*, 254  
*Callochiton*, 220, 226, 234, 240  
   *laevis*, 220, 226, 234, 240  
*Callogonia*, 254  
*callosa*, *Vertigo*, 112  
*Calmella*, 230, 231  
   *cavolini*, 230, 231  
*Caloplaca*, 223  
   *aurantia*, 223  
*calyculata*, *Beguinia*, 226, 227, 231, 240  
*Calyptogena*, 254  
*Calyptraea*, 231, 234, 240, 241  
   *sinensis*, 231, 234, 240, 241  
*campanulatum*, *collinsi*, *Helisoma*, 263  
 Campylaeinae, 261, 262  
*cancellata*, *Chione*, 81, 83  
*cancellatus*, *Lepidopleurus*, 236  
*Candidula*, 261, 262  
   *gigaxi*, 261, 262  
   *intersecta*, 261  
*Cantareus*, 88  
   *aperta*, 88  
*Cantharidus*, 228, 230, 231, 238, 240, 241  
   *exasperatus*, 228, 230  
   *striatus*, 230, 238, 241  
*Cantharus*, 220, 225-227, 230, 235, 240  
   *d'orbigny*, 220, 225-227, 230, 235, 240  
   *cantrainii*, *Chromodoris*, 96  
  
*caprai*, *Lehmannia*, 86  
*caprearum*, *Middendorfia*, 220, 224, 225, 240  
*Capulus*, 227, 231, 232, 234, 240, 241  
   *hungaricus*, 227, 231, 232, 234, 240, 241  
*Caracollina*, 88, 90  
   *lenticula*, 88  
*Cardiacea*, 222, 231  
*cardissa*, *Corculum*, 288  
*Cardita*, 288  
   *partschi*, 288  
*Carditidae*, 254  
*Cardium*, 168, 169, 231, 234, 238, 240, 241, 277  
   *exiguum*, 231, 234, 238, 241  
   *glaucum*, 277  
   *paucicostatum*, 238, 241  
   *tuberculatum*, 238  
*Carex*, 302  
*caribbea*, *Berthelinia*, 81  
*carinata*, *Neomenia*, 207, 208, 210  
*carinata*, *Potamorpyrgus jenkinsi*, 301  
*carinatus*, *Mecynodon*, 288  
*carinatus*, *Planorbis*, 145  
*carnea*, *Ferrussacia*, 90  
*carnea*, *Pegea*, 90  
*Carolia*, 288  
*cartusiana*, *Monacha*, 55  
*caruanae*, *Agriolimax*, 273  
*caruanae*, *Deroceras*, 86, 87  
*Carychium*, 115, 117, 297  
   *minimum*, 115, 117  
*casertanum*, *Pisidium*, 268  
*casina*, *Venus*, 238, 241  
*Cassidaria*, 231  
   *echinophora*, 231  
*Cassidula*, 280  
*catascopium nasoni*, *Lymnaea*, 263  
*catascopium preblei*, *Lymnaea*, 263  
*Catinella*, 117, 259, 260, 289  
   *arenaria*, 117  
   *vermeta*, 260  
 Catinellinae, 289  
*catskillensis*, *Discus cronkhitei*, 260  
 Caudofoveata, 191, 193-195, 199-201, 203-206, 209, 212-214  
*Caulerpa*, 81  
*cavolini*, *Calmella*, 230, 231  
*cavolinii*, *Dynamena*, 225  
*cayenensis*, *Diodora*, 81  
*cellarius*, *Oxychilus*, 269, 273

- cellensis*, *Anodonta*, 67, 68  
*Cepaea*, 55, 261  
   *nemoralis*, 55  
   *hortensis*, 261  
 Cephalaspidea, 204, 236, 238, 241, 282  
 Cephalopoda, 201, 203, 217, 243, 247  
*Ceramium*, 230  
*Cerithidea*, 81, 82  
   *costata*, 81, 82  
   *obtusa*, 82  
 Cerithiidae, 82  
*Cerithium*, 81, 82, 225, 231, 234, 238,  
   240, 241  
   *eburneum*, 82  
   *litteratum*, 82  
   *patulum*, 82  
   *rupestre*, 225, 234, 238, 240, 241  
   *variabile*, 81  
   *vulgatum*, 231, 234, 240, 241  
*Cernuella*, 55, 85  
   *profuga*, 85  
   *virgata*, 55  
 Chaetoderma, 193, 204  
 Chaetodermatida, 195  
 Chaetodermatidae, 191, 195, 204  
 Chaetognatha, 212, 213  
*Chaetomorpha*, 224  
   *aerea*, 224  
*chaixii*, *Mesodontopsis*, 87  
*chaixii*, *Tacheocampylaea*, 87  
*Chama*, 80, 168, 169, 188, 225, 227, 240  
   *congregata*, 80  
   *gryphina*, 225, 240  
   *gryphoides*, 225, 240  
   *imbricata*, 188  
   *macerophylla*, 80  
*chamaeleon*, *Nerita*, 280, 281  
 Charopinae, 289  
 Chaenopodiaceae, 249  
*Chilopyrgula*, 173, 176  
   *zilchi*, 176  
*Chilostoma*, 85, 87, 261  
   *achates achates*, 261  
   *baldensis*, *cingulatum*, 261  
   *cingulatum baldensis*, 261  
   *intermedium*, 261  
   *illyrica*, *planospira*, 261  
   *occultata*, *planospira*, 85, 87  
   *planospira illyrica*, 261  
   *planospira occultata*, 85, 87  
*Chione*, 81, 83  
   *cancellata*, 81, 83  
*chione*, *Pitaria*, 231, 234, 240  
*Chiton*, 210, 224-227, 230, 231, 234, 240  
   *corallinus*, 226, 234, 240  
   *olivaceus*, 224, 225, 227, 230, 231, 240  
*Chlamys*, 231, 234, 238, 240, 241, 247  
 Chondrinidae, 256  
*Chondrocyclus*, 256  
*Chondrosia*, 226  
   *reniformis*, 226  
*Chondrula*, 117  
   *tridens*, 117  
*Chordonia*, 213  
*Chromodoris*, 93, 96  
   *cantrainii*, 96  
   *elegantula*, 93  
   *iheringi*, 96  
   *luteorosea*, 96  
   *trilineata*, 96  
   *villafranca*, 96  
*Chrysallida*, 238, 241  
   *interstincta*, 238  
*Chthamalus*, 223  
   *depressus*, *stellatus*, 223  
   *stellatus*, 223  
   *stellatus depressus*, 223  
   *stellatus stellatus*, 223  
*cimex*, *Alvania*, 230-232, 234, 238, 240,  
   241  
 Cionellacea, 260  
*cingulatum baldensis*, *Chilostoma*, 261  
*cinctella*, *Hygromia*, 89  
*circumscriptus*, *Arion*, 297  
*Cistus*, 54  
*citrinus*, *Brachidontes*, 80  
*Cladophora*, 224, 225  
   *pellucida*, 224  
*clarai*, *Claraia*, 288  
*Claraia*, 288  
   *clarai*, 288  
*Clausilia*, 113, 117, 249, 297  
   *cruciata*, 113  
   *dubia*, 297  
   *pumila*, 117, 249, 297  
 Clausiliidae, 258  
*claustralis*, *Truncatellina*, 115  
*Clithon*, 279  
   *retropictus*, 279  
 Cnidaria, 195, 226  
*Cochlicella*, 55, 88, 89, 262  
   *acuta*, 88  
   *barbara*, 89  
   *conoidea*, 55  
*Cochlicopa*, 249, 297  
   *lubrica*, 249

- Cochlodina*, 87, 88, 90  
*kilsteri*, 87, 88  
*meisneriana*, 87, 88  
*porroi*, 87, 88  
*sancta*, 88  
*sarda*, 88  
*sophiae*, 88  
*Cochlostoma*, 112  
*Codium*, 225  
*bursa*, 225  
*Codokia*, 288  
*Coelioxys*, 256  
*coelestis*, *Glossodoris*, 96, 98  
*coelestis*, *Goniodoris*, 96  
*Coelomata*, 203  
*coerulea*, *Patella*, 220, 224, 225, 240  
*coffeus*, *Melampus*, 81, 82  
*collinsi*, *Helisoma campanulatum*, 263  
*Columbella*, 82, 225, 230, 231, 238, 240, 241  
*mercatoria*, 82  
*rustica*, 225, 230, 231, 238, 240, 241  
*columbella*, *Linga*, 288  
*Columella*, 117, 249, 297, 299  
*alticola*, 297  
*aspera*, 249, 297  
*columella*, 117, 249, 297, 299  
*edentula*, 297  
*simplex*, 297  
*columella*, *Columella*, 117, 249, 297, 299  
*columna*, *Gymnarion*, 60  
*colymbus*, *Pteria*, 80  
*communis*, *Acanthochiton*, 227, 228, 230, 231, 240  
*communis*, *Turritella*, 232, 238, 241  
*compacta*, *Pseudamnicola*, 277  
*complanatus*, *Hippeutis*, 56, 145  
*compressa*, *Septaria*, 280, 281  
*Conchifera*, 191, 193, 199, 201, 203, 206, 210, 212, 214  
*confervoides*, *Lyngbyia*, 224  
*confinis*, *Lichina*, 223  
*Congerina*, 288  
*subglobosa*, 288  
*Congeriomorpha*, 288  
*congregata*, *Chama*, 80  
*conicum*, *Aplidium*, 231  
*Conocarpus*, 79  
*erectus*, 79  
*conoidea*, *Cochlicella*, 55  
*consobrinus*, *Lamellidens*, 286  
*consociella*, *Hydrobia*, 174  
*consociella*, *Pseudamnicola*, 173  
*conspurcata*, *Helicella*, 55, 88  
*conspurcata*, *Xerotricha*, 55, 88  
*constrictus*, *Trissexodon*, 267  
*contortus*, *Bathyomphalus*, 145  
*contortus*, *Bulinus*, 26  
*contracta*, *Vitreia*, 85, 87  
*conulus*, *Calliostoma*, 231  
*Conus*, 225, 226, 228, 230, 231, 238, 240, 241  
*ventricosus*, 225, 226, 228, 230, 231, 238, 240, 241  
*conventus*, *Pisidium*, 123, 124, 268  
*convexa*, *Crepidula*, 81  
*Corallina*, 224, 225  
*mediterranea*, 224, 225  
*corallina*, *Mactra*, 245  
*corallinus*, *Chiton*, 226, 234, 240  
*Corbicula*, 112, 264  
*fluminalis*, 112  
*fluminea*, 264  
*Corculum*, 288  
*cardissa*, 288  
*Corillidae*, 256  
*corneus*, *Planorbarius*, 145  
*corniculata*, *Cystoseira*, 227  
*cornuarietis*, *Marisa*, 40  
*corona*, *Melongena*, 81  
*coronata*, *Idulia*, 228, 230, 231  
*coronata*, *Runcina*, 238, 241  
*coronatus*, *Gymnarion*, 60, 64  
*corpulentum vermilionense*, *Helisoma*, 263  
*corpulentum whiteavesi*, *Helisoma*, 263  
*corrianus*, *Lamellidens*, 286  
*corrugata*, *Parveysia*, 286  
*corsicus*, *Limax*, 89  
*corvus*, *Galba*, 42  
*Coryphella*, 230, 231  
*lineata*, 230, 231  
*costata*, *Cerithidea*, 81, 82  
*costata*, *Vallonia*, 55, 112, 115, 117, 249  
*costulatus*, *Ancylus*, 54, 55  
*coulboisi*, *Bulinus*, 38  
*crassa*, *Alexandromenia*, 204  
*Crassostrea*, 80, 83  
*parasitica*, 83  
*rhizophorae*, 80, 83  
*virginica*, 80  
*Crepidula*, 81, 231, 239  
*aculeata*, 81  
*convexa*, 81  
*crepidularia*, *Dostia*, 280, 281  
*crepidularia*, *Neritina*, 281

- Cricetus*, 30  
   *auratus*, 30  
*crinita*, *Cystoseira*, 227, 230  
*crista*, *Armiger*, 56, 85, 87  
*crista*, *Gyraulus*, 145  
*cristata*, *Valvata*, 145  
*cronkhitei*, *Discus*, 260  
*crossotus*, *Falcidens*, 206  
*cruciata*, *Clausilia*, 113  
*Cryptomphalus*, 55, 86, 87  
   *aspersa*, 55, 86, 87  
*Cryptozona*, 260  
   *bistrialis*, 260  
*crystallina*, *Vitrea*, 85, 87  
*cuneata*, *Malletia*, 271  
*curta*, *Pseudamnicola*, 174  
*Cuspidaria*, 168  
*Cyclomenia*, 204  
   *holoserica*, 204  
*Cyclopecten*, 271  
   *undatus*, 271  
Cyclophoridae, 256  
*cydonium*, *Geodia*, 231, 232  
*cygnaea*, *Anodonta*, 286  
*cylindracea*, *Lauria*, 56, 89  
*cylindrica*, *Truncatellina*, 112, 115, 249  
*Cylindrus*, 249, 251  
   *obtusus*, 249, 251  
*Cypraea*, 82  
   *zebra*, 82  
*Cyrtollites*, 201  
   *ornatus*, 201  
*Cyrtionella*, 201  
*Cystoseira*, 222, 224, 227, 228, 230, 231, 240  
   *abrotanifolia*, 227, 230  
   *adriatica*, 227  
   *barbata*, 224  
   *corniculata*, 227  
   *crinita*, 227, 230  
   *mediterranea*, 224  
   *spicata*, 227, 230  
*Cythara*, 238, 241  
  
*dalli*, *Limopsis pelagica*, 271  
*danubialis*, *Trichia striolata*, 261  
*Daonella*, 288  
*darieuxi*, *Pyrgula*, 176  
*Decabrachia*, 209  
*decollata*, *Rumina*, 55  
*decussata*, *Venerupis*, 275, 276  
*deflorata*, *Asaphis*, 81, 83  
  
*Dendrodoris*, 232, 234, 240  
   *limbata*, 232, 234, 240  
*dentale*, *Dentalium*, 207, 232, 236, 241  
*Dentalium*, 207, 209, 210, 232, 236, 238, 241  
   *dentale*, 207, 232, 236, 241  
   *panormitanum*, 238, 241  
   *vulgare*, 236, 241  
*depilans*, *Aplysia*, 253  
*depressa*, *Psammobia*, 238  
*depressus*, *Bulinus*, 37  
*depressus*, *Chthamalus stellatus*, 223  
*depressus*, *Oxychilus*, 117  
*Deroceras*, 86, 87, 90, 249, 297  
   *caruanae*, 86, 87  
   *laeve*, 297  
   *sturanyi*, 297  
*despectus*, *Tergipes*, 236, 241  
*Detracia*, 81, 82  
   *bullaoides*, 82  
*Deuterostomia*, 205, 210, 213  
*Diana*, 173, 174, 176  
   *grochmalickii*, 174  
   *prespensis*, 174, 176  
   *schlikumi*, 176  
   *thiesseana*, 173, 174, 176  
*diaphana*, *Eucobresia*, 249, 269  
*diaphana*, *Vitrea*, 87  
*Diaphorodoris*, 93, 98  
   *luteocincta papillata*, 93, 98  
   *papillata*, *luteocincta*, 93, 98  
*dibothryon*, *Perforatella*, 117  
*Dibranchiata*, 209  
*Diceras*, 288  
*Dictyota*, 230  
*Digena*, 228  
   *simplex*, 228  
Dimyidae, 163  
*diodonta*, *Soósia*, 117  
*Diodora*, 81, 225-227, 231, 234, 240  
   *cayenensis*, 81  
   *gibberula*, 227  
   *graeca*, 225-227, 240  
   *italica*, 231, 234, 240  
*Diotocardia*, 212  
*Diplacophora*, 201  
*Discinae*, 289  
*Discus*, 249, 260, 299  
   *catskillensis*, *cronkhitei*, 260  
   *cronkhitei catskillensis*, 260  
   *rotundatus*, 249  
   *ruderatus*, 299  
*Distoma*, 231



- adriaticum*, 231  
*distorta*, *Tellina*, 232, 236, 239, 241  
*divaricata*, *Divaricella*, 236, 241  
*Divaricella*, 236, 241  
*divaricata*, 236, 241  
*dofleini*, *Octopus*, 247  
*dohrni*, *Hypnophila*, 85, 88  
*dombeyi*, *Nerita*, 280, 281  
Donacidae, 164, 170  
*Donax*, 238, 241  
*trunculus*, 238  
*Dondersia*, 204  
*californica*, 204  
*d'orbigny*, *Cantharus*, 220, 225-227, 235, 240  
*Dorcasia*, 256  
Doridacea, 234, 282  
Dorididae, 226  
*Doris*, 96, 97  
*albescens*, 96  
*calcara*, 96  
*elegans*, 96  
*gracilis*, 96  
*lutescens*, 96, 97  
*nardii*, 96  
*orsinii*, 96  
*pallens*, 96  
*parthenopeia*, 96  
*pasinii*, 96  
*picta*, 96  
*pirainii*, 96  
*pulcherima*, 96  
*scacchiana*, 97  
*schultzi*, 97  
*tenera*, 96  
*venulosa*, 96  
*villae*, 96  
*villafranca*, 96  
*Dorymenia*, 204  
*weberi*, 204  
*Dosinia*, 275, 276  
*exoleta*, 275, 276  
*Dostia*, 279-281  
*crepidularia*, 280, 281  
*violacea*, 279  
*dovrense*, *Taraxacum*, 249  
*Drahomira*, 201  
*draparnaudi*, *Oxychilus*, 269  
*Dreissena*, 168, 169, 207  
*polymorpha*, 207  
*Drepanostoma*, 267  
*nautiliforme*, 267  
*drummondi*, *Facelina*, 230, 231  
*dubia*, *Clausilia*, 297  
*dubia*, *Gastrochaena*, 220, 224-227, 238-240  
*duplex*, *Gymnarion*, 60, 64  
*Dynamena*, 225  
*cavolinii*, 225  
*eburneum*, *Cerithium*, 82  
*echinophora*, *Cassidaria*, 231  
Echiurida, 203, 205, 212  
*edentula*, *Columella*, 297  
*califis*, *Ostrea*, 220, 224-227, 240  
*edwardsi*, *Tritonalia*, 226, 227, 230, 240  
*Egeria*, 167, 168, 170  
*elata*, *Tacheocampylaea*, 87  
*electrina*, *Nesovitrea*, 297  
*Eledone*, 246  
*elegans*, *Doris*, 96  
*elegans*, *Pomatias*, 87, 117  
*elegans*, *Sidonia*, 282  
*elegantula*, *Chromodoris*, 93  
*elegantula*, *Glossodoris*, 93, 98  
Ellobiidae, 81-83  
*Ellobium*, 82  
*auris judae*, 82  
*auris midae*, 82  
*Elysia*, 228, 230, 231, 238, 240, 241  
*viridis*, 228, 230, 231, 238, 240, 241  
*Emarginula*, 81, 227, 240  
*pumila*, 81  
*Embletonia*, 236, 241  
*pulchra*, 236, 241  
*Emmericia*, 175, 278  
Emmericiinae, 278  
*Ena*, 56  
*obscura*, 56  
*Endocochlia*, 209  
Endodontacea, 260  
Endodontidae, 256, 258  
Endodontinae, 289  
Enidae, 256  
*Enigmonia*, 288  
*aenigmatica*, 288  
*enniensis*, *Vallonia*, 115, 117  
*Ensis*, 168, 238, 245-247  
*arcuatus*, 245, 246  
*ensis*, 238  
*siliqua*, 238  
*ensis*, *Ensis*, 238  
*Enteromorpha*, 224  
Enteropneusta, 204, 205, 213  
*Entophysalis*, 223

- granulosa*, 223  
 Entoprocta, 212  
*Eobania*, 55  
     *vermiculata*, 55  
*ephippium*, *Anomia*, 227, 240  
*Epimenia*, 204, 207, 209, 210  
     *verrucosa*, 204, 207, 209  
*Epizoanthus*, 226  
*equina*, *Actinia*, 224  
*erectus*, *Conocarpus*, 79  
*etrusca*, *Hypnophila*, 88  
*Eucobresia*, 249, 269  
     *diaphana*, 249, 269  
*Euconulus*, 249, 297  
     *fulvus*, 249  
 Eulamellibranchia, 163-165  
 Eulamellibranchiata, 121  
*Eulimella*, 238, 241  
     *acicula*, 238  
*Eumorphotis*, 288  
     *aurita*, 288  
     *telleri*, 288  
*Euparypha*, 55  
     *pisana*, 55  
*europeense*, *Schistosoma haematobium*,  
     26  
*Euthyneura*, 253, 259, 282  
*exasperatus*, *Cantharidus*, 228, 230  
*excavatus*, *Zonitoides*, 249, 269  
*exiguum*, *Cardium*, 231, 234, 238, 241  
*exoleta*, *Dosinia*, 275, 276  
*expansum*, *Pseudolithophyllum*, 225, 226  
*exustus*, *Brachidontes*, 80, 81, 83  
  
*Facelina*, 230, 231  
     *drummondi*, 230, 231  
*Fagotia*, 113  
     *acicularis audebartii*, 113  
     *audebartii, acicularis*, 113  
*Falcidens*, 204, 206  
     *crossotus*, 206  
*fallaciosa*, *Planispira*, 260  
*fasciata*, *Aplysia*, 253  
*fasciatus*, *Arion*, 297  
*fascicularis*, *Acanthochiton*, 227, 240  
*Fasciola*, 42, 127  
     *hepatica*, 42, 127  
*fasciola*, *Lampsilis*, 272  
*Fasciolaria*, 82  
     *tulipa*, 82  
*fauntandraui*, *Glossodoris*, 96  
*Fauxulus*, 256  
  
*Favorinus*, 230, 231  
     *branchialis*, 230, 231  
*Ferrussacia*, 90  
     *carnea*, 90  
*ficiformis*, *Petrosia*, 220, 226, 227, 240  
*Filibranchia*, 164, 165  
*filocincta*, *Micromelania*, 176  
*Fimbria*, 295, 296  
     *fimbria*, 295, 296  
*fimbria*, *Fimbria*, 295, 296  
*Flabellina*, 230, 231, 237  
     *affinis*, 230, 231, 237  
*flavus*, *Arion*, 73  
*flavus*, *Limax*, 87, 273  
*fluminalis*, *Corbicula*, 112  
*fluminea*, *Corbicula*, 264  
*fluminensis*, *Sadleriana*, 174  
*Flustra*, 222, 234  
*fluviatilis*, *Ancylus*, 55, 145, 148, 227  
*fluviatilis*, *Theodoxus*, 279  
*foliacea*, *Hippodiplosia*, 232  
*foliata*, *Trinchesia*, 230, 231  
*Fontigens*, 278  
*Fontinalis*, 268  
*fontinalis*, *Physa*, 145  
*forsythi*, *Ambigua argentarolae*, 88  
*forsythi*, *Marmorana argentarolae*, 88  
*Fosliella*, 224, 230, 240  
*fragilis*, *Gastrana*, 238  
*fragilis*, *Leda*, 238  
*frons*, *Ostrea*, 80  
*frumentum*, *Abida*, 112, 115, 117  
*fulica*, *Achatina*, 43  
*fulvus*, *Euconulus*, 249  
*Fusus*, 230  
  
*gachua*, *Ophiocephalus*, 286  
*gagathinella*, *Hydrobia*, 174  
*Galba*, 42, 55, 89  
     *corvus*, 42  
     *glabra*, 42  
     *paustris*, 42  
     *truncatula*, 42, 55, 89  
*gallina*, *Venus*, 238  
*galloprovincialis*, *Mytilus*, 224-226, 240  
*Gari*, 83  
     *togata*, 83  
*Gasteropteron*, 207  
     *rumbrum*, 207  
*Gastrana*, 238  
     *fragilis*, 238  
*Gastrochaena*, 220, 224-227, 238-240

- dubia*, 220, 224-227, 238-240  
*Gastrocopta*, 113, 115  
   *serotina*, 113, 115  
*Gastrodentinae*, 269  
*Gastroneuralia*, 212, 213  
*Gastropoda*, 101, 143, 201, 203, 204, 207,  
   210, 212, 213, 217, 224-227, 230,  
   231, 234, 236, 240, 241, 243, 253,  
   259, 267, 282, 284, 293  
*genesii*, *Vertigo*, 297, 299  
*Genitoconia*, 204  
   *atriolonga*, 204  
*Geodia*, 222, 231, 232, 234, 240  
   *cydonium*, 231, 232  
*Geomalacus*, 249  
   *maculosus*, 249  
*Gervillia*, 288  
*geyeri*, *Vertigo*, 297  
*gibba*, *Aloidis*, 238, 241  
*gibberula*, *Diodora*, 227  
*Gibbula*, 230, 238, 240, 241, 293, 294  
   *magnus*, 293  
   *varia*, 230, 238, 241  
*gigaxi*, *Candidula*, 261, 262  
*Ginaia*, 176  
*glabra*, *Galba*, 42  
*glabra*, *Lymnaea*, 145  
*glabrata*, *Biomphalaria*, 25, 32, 40  
*glabrata*, *Neritina*, 47-51  
*glabratus*, *Australorbis*, 31, 104, 105  
*glabrum*, *Caecum*, 236, 241  
*glandulifera*, *Microhedyle*, 236, 241  
*glaucum*, *Cardium*, 277  
*globosus*, *Bulinus*, 35  
*Glossodoridinae*, 93, 97, 98  
*Glossodoris*, 93-98, 234, 241  
   *coelestis*, 96, 98  
   *elegantula*, 93, 98  
   *fauntandraui*, 96  
   *gracilis*, 93, 94, 96, 98, 234, 241  
   *krohni*, 93, 94, 96  
   *luteorosea*, 93, 94, 96  
   *messinensis*, 93, 95, 96, 98  
   *purpurea*, 95, 96  
   *tricolor*, 93, 95, 96, 98  
   *valenciennesi*, 93, 95-98  
*Glossus*, 168, 169  
*glutinosa*, *Lymnaea*, 145  
*Glycymeris*, 168, 288  
   *pilosa*, 288  
*Gocea*, 173  
   *ohridana*, 173  
*Goniodoris*, 96  
   *coelestis*, 96  
*Gorgonaria*, 80  
*gorgonianus*, *Oxychilus*, 86  
*gracilis*, *Doris*, 96  
*gracilis*, *Glossodoris*, 93, 94, 96, 98,  
   234, 241  
*graeca*, *Diodora*, 225-227, 240  
*Grammysia*, 288  
   *nodocostata*, 288  
   *undata*, 288  
*granifera*, *Tarebia*, 40  
*Granopupa*, 55, 85, 88-90  
   *granum*, 55, 85, 89  
   *philippi*, 85, 88  
*granosa*, *Anadara*, 83, 165, 168  
*granulata*, *Ashfordia*, 249  
*granulosa*, *Entophysalis*, 223  
*granum*, *Granopupa*, 55, 85, 89  
*gratiosa*, *Pupa*, 56  
*grochmalickii*, *Diana*, 174  
*grochmalickii*, *Hydrobia*, 173  
*grochmalickii*, *Pyrgohydrobia*, 173  
*Gryphaea*, 288  
*gryphina*, *Chama*, 225, 240  
*gryphoides*, *Chama*, 225, 240  
*guernei*, *Bulinus*, 37, 38  
*guidonii*, *Hyalinia*, 86  
*guillemini*, *Polynices*, 236  
*guyannensis*, *Mytella*, 80  
*Gymnarion*, 59, 60, 63, 64  
   *anchora*, 60  
   *columna*, 60  
   *coronatus*, 60, 64  
   *duplex*, 60, 64  
*Gyraulus*, 56, 88, 145, 149, 173  
   *acronicus*, 145, 149  
   *agraulus*, 88  
   *albus*, 56, 145  
   *albus limophilus*, 56  
   *crista*, 145  
   *laevis*, 145  
   *limophilus, albus*, 56  
   *relictus*, 173  
*haematobium*, *Schistosoma*, 25-27, 29-33,  
   37  
*haematobium europeense*, *Schistosoma*,  
   26  
*Halichondria*, 225  
   *panicea*, 225  
*Halimeda*, 220, 226, 228, 230, 240

- tuna*, 220, 226, 228, 230, 240  
*Haliotis*, 227, 230, 240  
   *lamellosa*, 227, 240  
   *tuberculata*, 230  
*Halomenia*, 210  
*Haminea*, 236  
   *hydatis*, 236  
*hammonis*, *Nesovitrea*, 115, 249, 297  
*Hedylopsis*, 236, 241  
   *spiculifera*, 236, 241  
*helgolandica*, *Philinoglossa*, 236, 241  
Helicacea, 260  
*Helicella*, 55, 88, 112, 115, 117, 303  
   *apicina*, 88  
   *conspurcata*, 55, 88  
   *hungarica*, 112, 115, 117  
   *obvia*, 303  
   *striata*, 112  
Helicellinae, 261, 262  
Helicidae, 261, 262, 269, 289  
*Helicigona*, 85, 87, 117, 249  
   *banatica*, 117  
   *lapicida*, 249  
   *occultata*, *planospira*, 85, 87  
   *planospira occultata*, 85, 87  
Helicinae, 262  
*Helicodonta*, 267  
   *angigyra*, 267  
   *obvoluta*, 267  
Helicodontinae, 262, 267  
*Helisoma*, 263  
   *anceps royalense*, 263  
   *campanulatum collinsi*, 263  
   *collinsi*, *campanulatum*, 263  
   *corpulentum vermilionense*, 263  
   *corpulentum whiteavesi*, 263  
   *royalense*, *anceps*, 262  
   *vermilionense*, *corpulentum*, 263  
   *whiteavesi*, *corpulentum*, 263  
*Helix*, 55, 86-88, 90, 135-139, 153,  
   156, 158-162, 261, 267, 273,  
   303  
   *aperta*, 88  
   *aspersa*, 55, 86, 87, 135, 273, 303  
   *pomatia*, 135, 139, 153, 261, 303  
   *quadrasi*, 267  
   *rumelica*, 135  
   *subconstrictus*, 267  
*helminthoides*, *Nemalion*, 224  
Hemichordata, 203  
Hemimycale, 226  
*Hemitoma*, 81  
   *octoradiata*, 81  
*Heminerita*, 279  
   *japonica*, 279  
*hepatica*, *Fasciola*, 42, 127  
*Hercynella*, 288  
   *bohemica*, 288  
*Hervia*, 230, 231  
   *peregrina*, 230, 231  
Heterurethra, 259, 260  
*hexadactyla*, *Rana*, 286  
*Hiatella*, 291, 292  
   *arctica*, 291, 292  
*hibernicum*, *Pisidium*, 121-124  
*hibernus*, *Arion*, 73  
*Hippeutis*, 56, 145  
   *complanatus*, 56, 145  
*Hippodiplosia*, 222, 232, 234  
   *foliacea*, 232  
*Hippurites*, 288  
Hirudinea, 205  
*hispida*, *Trichia*, 117, 249, 261  
*Hohenwartiana*, 86, 89, 90  
   *moitessieri*, 86, 89  
Holopoda, 260  
Holopodopes, 260  
*holoserica*, *Cyclomenia*, 204  
*hopei*, *Thuridilla*, 237  
*Horatia*, 173  
*hortensis*, *Cepaea*, 261  
*hungarica*, *Helicella*, 112, 115, 117  
*hungaricus*, *Capulus*, 227, 231, 232, 234,  
   240, 241  
*Hyalinia*, 86  
   *guidonii*, 86  
   *lybisonis*, 86  
   *lucida*, 86  
   *notha*, *scotophila*, 86  
   *scotophila nota*, 86  
*hydatis*, *Haminea*, 236  
*Hydrobia*, 112, 173-175, 277, 301  
   *acuta*, 277  
   *consociella*, 174  
   *gagathinella*, 174  
   *grochmalickii*, 173  
   *jenkinsi*, 301  
   *longaeva*, 112  
   *respensis*, 173  
   *ventrosa*, 174, 277  
Hydrobiidae, 145, 173, 175, 278, 301  
Hydrobiinae, 175, 278  
Hydrozoa, 212, 219  
*Hyella*, 223  
   *caespitosa*, 223  
*Hygromia*, 89, 90

- cinctella*, 89  
 Hygromiinae, 261, 262  
*Hypnophila*, 85, 88, 90  
   *dohrni*, 85, 88  
   *etrusca*, 88  
*hypnorum*, *Aplexa*, 145  
  
*Idulia*, 228, 230, 231  
   *coronata*, 228, 230, 231  
*igilicus*, *Oxychilus*, 86  
*iheringi*, *Chromodoris*, 96  
*illyrica*, *Chilostoma planospira*, 261  
*imbricata*, *Chama*, 188  
*incarnatus*, *Angulus*, 238  
*incarnatus*, *Monachoides*, 299  
*inchoata*, *Acme*, 249  
*incrustans*, *Lithophyllum*, 225  
*inflata*, *Lima*, 239  
*Inoceramus*, 288  
   *involutus*, 288  
   *sulcatus*, 288  
*intermedium*, *Chilostoma*, 261  
*intermedius*, *Arion*, 249  
*intermedius*, *Lepidopleurus*, 236, 241  
*intersecta*, *Candidula*, 261  
*interstincta*, *Chrysallida*, 238  
*involutus*, *Inoceramus*, 288  
*Iphigena*, 55, 299  
   *ventricosa*, 55, 299  
*Ircinia*, 226  
*Ischnochiton*, 207, 209  
   *magdalenensis*, 207  
 Isocardiidae, 254  
*Isoetes*, 121  
   *lacustris*, 121  
*Isognomon*, 80, 83  
   *alata*, 80, 83  
   *isognomon*, 83  
   *radiata*, 80  
*isognomon*, *Isognomon*, 83  
 Isognomonidae, 83  
*Isognomostoma*, 117  
   *isognomostoma*, 117  
*isognomostoma*, *Isognomostoma*, 117  
 Isopoda, 271  
*italica*, *Diodora*, 231, 234, 240  
  
*jacobaeus*, *Pecten*, 231, 234, 240  
*Jaminia*, 55, 85, 88, 89  
   *quadridens*, 55, 85, 88, 89  
*Jania*, 224, 230  
   *rubens*, 224, 230  
  
*japonica*, *Heminerita*, 279  
*japonica*, *Puuperita*, 279  
*jenkinsi*, *Hydrobia*, 301  
*jenkinsi*, *Potamopyrgus*, 145, 277, 301  
*jenkinsi carinata*, *Potamopyrgus*, 301  
  
 Kamptozoa, 193, 212  
*Kellia*, 168  
*Kelliella*, 249  
 Kelliellidae, 254  
*kimatula*, *Yoldia*, 207  
*knorri*, *Vermicularia*, 81  
*kotulae*, *Semilimax*, 117  
*krohni*, *Glossodoris*, 93, 94, 96  
*Kruppomenia*, 204  
   *minima*, 204  
*küsteri*, *Cochlodina*, 87, 88  
  
*Laciniaria*, 299  
   *biplicata*, 299  
*lactea*, *Arca*, 226, 227, 234, 238-241  
*lactea*, *Microhedyle*, 236, 241  
*lactea*, *Turbonilla*, 238  
*lactuca*, *Ulva*, 224  
*lacustris*, *Acroloxus*, 145  
*lacustris*, *Isoetes*, 121  
*laeve*, *Deroceras*, 297  
*laevis*, *Callochiton*, 220, 226, 234, 240  
*laevis*, *Gyraulus*, 145  
*Laguncularia*, 79  
   *racemosa*, 79  
 Lamellibranchiata, 163, 294  
*Lamellidens*, 286  
   *consobrinus*, 286  
   *corrianus*, 286  
   *marginalis*, 286  
*lamellosa*, *Haliotis*, 227, 240  
 Lampsilinae, 272  
*Lampsilis*, 272  
   *fasciola*, 272  
   *siliquoidaea*, 272  
   *ventricosa*, 272  
*lapicida*, *Helicigona*, 249  
*lapillus*, *Nucella*, 179, 183, 184  
*lapillus*, *Purpura*, 265  
*lapillus*, *Thais*, 265, 293  
*Lartetia*, 278  
*Lasaea*, 168  
*lateralis*, *Musculus*, 81  
*laugieri*, *Calliostoma*, 230  
*Laurencia*, 224, 230  
   *obtusa*, 224

- Lauria*, 56, 89  
   *cylindracea*, 56, 89  
*layardi*, *Nerita*, 280, 281  
*leai*, *Stenotrema*, 260  
*Lecithoepitheliata*, 203  
*Leda*, 238, 241  
   *fragilis*, 238  
*legumen*, *Pharus*, 238  
*Lehmannia*, 86, 269  
   *caprai*, 86  
*lenticula*, *Caracollina*, 88  
*leonina*, *Melibe*, 295, 296  
*Lepidopleurus*, 227, 236, 240, 241  
   *cajetanus*, 227, 240, 241  
   *cancellatus*, 236  
   *intermedius*, 236, 241  
*Leptachatina*, 260  
*Leucochroa*, 55  
   *arigo*, 55  
*Lichenopora*, 227  
   *radiata*, 227  
*Lichina*, 223  
   *confinis*, 223  
*lignarius*, *Scaphander*, 236  
*lillianae*, *Lymnaea stagnalis*, 101, 102  
*lilljeborgii*, *Pisidium*, 121-124, 268  
*Lima*, 164, 231, 234, 239, 240, 288  
   *inflata*, 239  
   *lineata*, 288  
*Limacidae*, 115, 269, 273  
*Limax*, 87, 89, 90, 249, 269, 273, 297  
   *corsicus*, 89  
   *flavus*, 87, 273  
   *valentianus*, 297  
*limbata*, *Dendrodoris*, 232, 234, 240  
*Limidae*, 222  
*Limifossor*, 204  
*Limifossoridae*, 204  
*limophilus*, *Gyraulus albus*, 56  
*Limopsis*, 271  
   *dalli*, *pelagica*, 271  
   *pelagica*, 271  
   *pelagica dalli*, 271  
   *pelagica pelagica*, 271  
*lineata*, *Coryphella*, 230, 231  
*lineata*, *Lima*, 288  
*Lineus*, 208  
   *ruber*, 208  
*Linga*, 288  
   *columbella*, 288  
*liquefaciens*, *Aeromonas*, 43  
*Lithoglyphus*, 173, 175, 278  
   *notatus*, 173  
*Lithophaga*, 81, 220, 225-227, 240, 288  
   *bisulcata*, 81  
   *lithophaga*, 220, 225-227, 240  
*lithophaga*, *Lithophaga*, 220, 225-227, 240  
*lithophaga*, *Petricola*, 225-227, 240  
*Lithophyllum*, 224, 225  
   *incrustans*, 225  
   *racemus*, 225  
*Lithothamnium*, 222, 224, 234, 240  
*Litorella*, 121  
   *uniflora*, 121  
*litteratum*, *Cerithium*, 82  
*Littorina*, 80, 82, 219, 220, 223, 224,  
   235, 240  
   *angulifera*, 80, 82  
   *melanostoma*, 82  
   *nebulosa*, 82  
   *neritoides*, 219, 220, 223, 224, 235,  
   240  
*Littorinidae*, 82  
*Lochea*, 73  
*Loligo*, 246  
*longaeva*, *Hydrobia*, 112  
*Loxosomatidae*, 212  
*lubrica*, *Cochlicopa*, 249  
*Lucapina*, 81  
   *sowerbii*, 81  
*lucida*, *Hyalinia*, 86  
*lucidus*, *Oxychilus*, 55  
*Lucinidae*, 81, 288  
*lusitanica*, *Patella*, 220, 224, 225, 240  
*lusitanicus*, *Arion*, 73-77  
*lusitanicus nigrescens*, *Arion*, 73  
*luteocincta papillata*, *Diaphorodoris*, 93, 98  
*luteorosea*, *Chromodoris*, 96  
*luteorosea*, *Glossodoris*, 93, 94, 96  
*lutescens*, *Doris*, 96, 97  
*luzonica*, *Paphia*, 83  
*lybisonis*, *Hyalinia*, 86  
*Lymnaea*, 28, 39, 42, 54, 89, 101, 102,  
   105, 106, 127, 128, 133, 145, 148,  
   149, 263, 277  
   *auricularia*, 145  
   *catascopium nasoni*, 263  
   *catascopium preblei*, 263  
   *glabra*, 145  
   *glutinosa*, 145  
   *lillianae*, *stagnalis*, 101, 102  
   *nasoni*, *catascopium*, 263

- natalensis*, 39  
*palustris*, 145, 227  
*peregra*, 54, 89, 145, 149, 277  
*preblei*, *catascopium*, 263  
*sanctaemariae*, *stagnalis*, 263  
*stagnalis*, 42, 101, 102, 105, 106, 145  
*stagnalis lillianae*, 101, 102  
*stagnalis sanctaemariae*, 263  
*truncatula*, 89, 127, 128, 133, 145, 148  
Lymnaeidae, 42, 145, 263  
*Lyngbyia*, 224, 227  
*confervoides*, 224
- macedonica*, *Sadleriana*, 173  
*macerophylla*, *Chama*, 80  
*Macoma*, 238  
*tenuis*, 238  
*Macroptychia*, 258  
*africana*, 258  
*Mactra*, 238, 241, 245  
*corallina*, 245  
*stultorum*, 238  
*maculata*, *Pinctada*, 188  
*maculatus*, *Rhacophorus*, 286, 287  
*maculosa*, *Pisania*, 220, 225, 230, 240  
*maculosus*, *Geomalacus*, 249  
*magdalenensis*, *Ischnochiton*, 207  
*magnus*, *Gibbula*, 293  
*major*, *Phenacolimax*, 269  
*Malacolimax*, 269  
*Malletia*, 271  
*cuneata*, 271  
*mamillata*, *Phallusia*, 231, 232  
*mangle*, *Rhizophora*, 79, 80, 82  
*manii*, *Teredo*, 83  
*mansonii*, *Schistosoma*, 25, 31, 32, 40, 43  
*Margaritana*, 67  
*margaritifera*, 67  
*margaritifera*, *Margaritana*, 67  
*marginalis*, *Lamellidens*, 286  
*marginella*, *Arion rufus atra*, 73, 74  
*marina*, *Zostera*, 236  
*Marisa*, 40  
*cornuarietis*, 40  
*Marmorana*, 85, 88, 90  
*argentarolae forsythi*, 88  
*forsythi*, *argentarolae*, 88  
*marmoratus*, *Musculus*, 225, 228, 231,  
239, 240  
*Martesia*, 167-170  
*martineanus*, *Murex*, 82  
*massa*, *Mycale*, 226
- Mastigocleus*, 223  
*testarum*, 223  
*Mastus*, 117  
*bielzi*, 117  
*maxima*, *Tridacna*, 188, 189  
*Mecynodon*, 288  
*carinatus*, 288  
*Mediappendix*, 289  
*mediterranea*, *Acetabularia*, 224, 227  
*mediterranea*, *Corallina*, 224, 225  
*mediterranea*, *Cystoseira*, 224  
*Meekella*, 288  
Megalodontidae, 288  
*Megalodus*, 288  
*meisneriana*, *Cochlodina*, 87, 88  
*Melampus*, 81, 82  
*bidentatus*, 81, 82  
*coffeus*, 81, 82  
*Melanella*, 238, 241  
*arcuata*, 238  
*Melania*, 113  
*tuberculata*, 113  
*melanostictus*, *Bufo*, 286  
*melanostoma*, *Littorina*, 82  
*Melibe*, 295, 296  
*leonina*, 295, 296  
*Melobesia*, 227  
*Melongena*, 81, 82  
*corona*, 81  
*melongena*, 81, 82  
*pugilina*, 82  
*melongena*, *Melongena*, 81, 82  
Melongenidae, 82  
*Membranipora*, 230  
*mentula*, *Ascidia*, 231  
*mercatoria*, *Columbella*, 82  
*Mercenaria*, 275, 276  
*mercenaria*, 275, 276  
*mercenaria*, *Mercenaria*, 275, 276  
*mercenaria*, *Venus*, 125  
*Meretrix*, 83  
*meretrix*, 83  
*meretrix*, *Meretrix*, 83  
*meridionale*, *Propeamussum*, 271  
*Mesarion*, 73  
*Mesodesma*, 201  
*Mesodontopsis*, 87  
*chaixii*, 87  
Mesogastropoda, 279  
*messinensis*, *Glossodoris*, 93, 95, 96, 98  
*Mesurethra*, 289  
*Metachaetoderma*, 204

- Metachatina*, 256  
*metidjensis*, *Planorbarius*, 25, 26, 55  
*Metorponothus*, 43  
   *pruinusosus*, 43  
*Microhedyle*, 236, 241  
   *glandulifera*, 236, 241  
   *lactea*, 236, 241  
   *milaschewitchii*, 236, 241  
*Micromelania*, 173, 176  
   *filocincta*, 176  
   *prespensis*, 173  
*Micromelaniidae*, 176  
*Micromelaniinae*, 173, 175, 176  
*micropleuros*, *Pleuropunctum*, 89  
*Micropyrgula*, 176  
*Middendorfia*, 220, 224, 225, 240  
   *caprearum*, 220, 224, 225, 240  
*Milacidae*, 269  
*milaschewitchii*, *Microhedyle*, 236, 241  
*Milax*, 87, 90  
   *nigricans*, 87  
   *sowerby*, 87  
*milium*, *Pisidium*, 268  
*millepunctata*, *Natica*, 236, 241  
*mimetica*, *Bosellia*, 220, 226, 237, 240  
*minima*, *Batillaria*, 81, 82  
*minima*, *Kruppomenia*, 204  
*minimum*, *Carychium*, 115, 117  
*minimus*, *Brachydontes*, 220, 224, 225, 231, 238, 240  
*Mitra*, 230  
*Mitraria*, 209, 210  
*modesta*, *Vertigo*, 297  
*Modiolus*, 80, 83, 201, 234, 238, 241  
   *americanus*, 80, 83  
   *barbatus*, 234, 238, 241  
*Modulus*, 82  
   *modulus*, 82  
*modulus*, *Modulus*, 82  
*moitessieri*, *Hohenwartiana*, 86, 89  
*Monacha*, 55  
   *cartusiana*, 55  
*Monacheae*, 262  
*Monachoides*, 299  
   *incarnatus*, 299  
*Monodonta*, 220, 224, 225, 240  
   *turbinata*, 220, 224, 225, 240  
*Monotidae*, 288  
*Monotis*, 288  
*Montacuta*, 168  
*montana*, *Trichia striolata*, 261, 262  
*Moria*, 278  
*morio*, *Pugilina*, 81  
*moulinsiana*, *Vertigo*, 115  
*Mucrospirifer*, 288  
   *reidfordi*, 288  
*Murex*, 80, 82, 207, 220, 226, 230, 231, 234, 238, 240, 241  
   *blainvillei*, 220  
   *brandaris*, 238, 241  
   *brevifrons*, 80, 82  
   *martineanus*, 82  
   *ramosus*, 207  
   *trunculus*, 226, 230, 231, 234, 240, 241  
*muricatum*, *Trachycardium*, 81  
*muricatus*, *Tectarius*, 82  
*Muricidae*, 82, 226, 227, 240  
*Muricidea*, 226, 227, 230, 240  
   *blainvillei*, 226, 227, 230, 240  
*muscorum*, *Pupilla*, 113, 115, 117, 249  
*Musculus*, 81, 222, 225, 228, 231, 239, 240  
   *lateralis*, 81  
   *marmoratus*, 225, 228, 231, 239, 240  
*mutabilis*, *Nassa*, 236, 241  
*Mya*, 243  
*Mycale*, 226  
   *massa*, 226  
*Myoconcha*, 288  
*Myonera*, 271  
   *undata*, 271  
*Myophoria*, 288  
*myosotis*, *Alexia*, 224, 240  
*Myriophyllum*, 121  
*Myriozoom*, 222, 234  
*Mytella*, 80  
   *guyannensis*, 80  
*Mytilidae*, 154, 169  
*Mytilus*, 154, 155, 159, 164, 168, 169, 224-226, 240  
   *galloprovincialis*, 224-226, 240  
*nardii*, *Doris*, 96  
*nasoni*, *Lymnaea catascopium*, 263  
*Nassa*, 207, 226, 236, 238, 241  
   *mutabilis*, 236, 241  
   *neritea*, 236  
   *reticulata*, 226  
*Nassidae*, 226  
*nasutus*, *Bulinus*, 35  
*Nata*, 256  
*natalensis*, *Bulinus*, 37, 38  
*natalensis*, *Lymnaea*, 39  
*Natalina*, 256



- Natica*, 236, 238, 241, 247  
     *millepunctata*, 236, 241  
 Naticidae, 204  
*nautiliforme*, *Drepanostoma*, 267  
*Nautilus*, 206, 209  
*neapolitana*, *Spurilla*, 230, 231  
*nebulosa*, *Littorina*, 82  
*Nemalion*, 224  
     *helminthoides*, 224  
*Nematomenia*, 207, 209  
     *banyulensis*, 207, 209  
*Nematomorpha*, 213  
*Nemertini*, 205, 208, 210, 214  
*nemoralis*, *Cepaea*, 55  
*Neofossarulus*, 173  
     *stankovici*, 173  
*Neomenia*, 207, 208, 210  
     *carinata*, 207, 208, 210  
 Neomeniida, 193  
*Neopilina*, 193, 198-201, 206, 214  
*Nerita*, 82, 279-281  
     *birmanica*, 82  
     *chamaeleon*, 280, 281  
     *dombeyi*, 280, 281  
     *layardi*, 280, 281  
     *peloronta*, 82  
     *plicata*, 280, 281  
     *rumphii*, 280, 281  
     *tessellata*, 82  
     *versicolor*, 82  
 Neritacea, 279  
*neritea*, *Nassa*, 236  
 Neritidae, 82, 279  
*Neritina*, 47-51, 81, 82, 279, 281  
     *crepidularia*, 281  
     *glabrata*, 47-51  
     *oualaniensis*, 279-281  
     *retifera*, 280, 281  
     *violacea*, 279  
     *virginea*, 81, 82  
*neritoides*, *Littorina*, 219, 220, 223, 224,  
     235, 240  
*Nesovitrea*, 115, 249, 297, 299  
     *binneyana*, 297  
     *electrina*, 297  
     *hammonis*, 115, 249, 297  
     *petronella*, 249, 297, 299  
*nigra*, *Ascidia*, 81  
*nigrescens*, *Arion lusitanicus*, 73  
*nigricans*, *Milax*, 87  
*Nitella*, 121  
*nitida*, *Avicennia*, 79  
*nitidula*, *Aegopinella*, 269  
*nitidum*, *Pisidium*, 122, 124, 268  
*nitidus*, *Zonitoides*, 260, 269  
*noae*, *Arca*, 232, 234  
*nobilis*, *Pinna*, 238, 241  
*nobrei*, *Arion*, 73  
*nodocostata*, *Grammysia*, 288  
*notabilis*, *Anadara*, 80, 83  
*notatus*, *Lithoglyphus*, 173  
*notha*, *Hyalinia scotophila*, 86  
 Notoneuralia, 213  
*Nucella*, 179, 183, 184  
     *lapillus*, 179, 183, 184  
*nucleus*, *Nucula*, 231, 234, 238, 240  
*Nucula*, 168, 201, 207, 208, 210, 231,  
     234, 238, 240, 241  
     *nucleus*, 231, 234, 238, 240  
     *proxima*, 207, 208  
 Nuculacea, 193  
*Nuculana*, 168, 201  
 Nudibranchia, 282, 295  
*nudus*, *Sipunculus*, 208, 209  
  
*oblonga*, *Succinea*, 115, 117, 249  
*obscura*, *Ena*, 56  
*obscuratus*, *Oxychilus*, 86  
*obtusa*, *Cerithidea*, 82  
*obtusa*, *Laurencia*, 224  
*obtusus*, *Cylindrus*, 249, 251  
*obvia*, *Helicella*, 303  
*obvolvata*, *Helicodonta*, 267  
*occultata*, *Chilostoma planospira*, 85, 87  
*occultata*, *Helicogona planospira*, 85, 87  
*oceanica*, *Posidonia*, 236  
*ochridana*, *Valvata*, 173  
*Ochridopyrgula*, 176  
*Octopus*, 246, 247  
     *dofleini*, 247  
*octoradiata*, *Hemitoma*, 81  
*officinalis*, *Sepia*, 245, 246  
*oglasticola*, *Alzomula*, 86  
*oglasticola*, *Oxychilus*, 86  
*ohridana*, *Gocea*, 173  
*Ohrigocea*, 173  
*olivaceus*, *Chiton*, 224, 225, 227, 230,  
     231, 240  
*Olivella*, 290  
     *biplicata*, 290  
*olsenae*, *Spondylus*, 288  
*Omalyonyx*, 259  
 Oncidiidae, 282  
*onzariensis*, *Valvata sincera*, 263

- Oopelta*, 256, 258  
*Oopeltinae*, 256  
*Opeas*, 260  
*Ophiocephalus*, 286, 287  
   *gachua*, 286  
   *punctatus*, 286  
   *striatus*, 286  
*Opisthobranchia*, 93, 217, 222, 230, 236,  
   238, 241, 253, 282, 295  
*oppressus*, *Oxychilus*, 86  
*orbiculata*, *Arca*, 271  
*ornatus*, *Cyrtolites*, 201  
*orsinii*, *Doris*, 96  
*Orthurethra*, 260, 289  
*Ostrea*, 80, 81, 164, 220, 224-227, 240  
   *edulis*, 220, 224-227, 240  
   *frons*, 80  
   *permollis*, 81  
*Ostreidae*, 83, 164  
*oualaniensis*, *Neritina*, 279-281  
*ovata*, *Abra*, 277  
*ovula*, *Tralia*, 82  
*Oxychilus*, 55, 56, 86, 87, 89, 90, 117,  
   269, 273, 274  
   *alliaris*, 273, 274  
   *argentarius*, 86  
   *cellarius*, 269, 273  
   *depressus*, 117  
   *draparnaudi*, 269  
   *gorgonianus*, 86  
   *igilicus*, 86  
   *lucidus*, 55  
   *obscuratus*, 86  
   *oglasticola*, 86  
   *oppressus*, 86  
   *pazi*, 56  
   *pilula*, 86  
*Oxyloma*, 259  
  
*Padina*, 224, 230  
   *pavonia*, 224, 230  
*pagenstechevi*, *Spirorbis*, 227  
*Paladilhia*, 278  
*Palaeosolen*, 288  
*pallens*, *Doris*, 96  
*palustris*, *Galba*, 42  
*palustris*, *Lymnaea*, 145, 277  
*panicea*, *Halichondria*, 225  
*panormitanus*, *Dentalium*, 238, 241  
*Papaver*, 249  
   *relictum*, 249  
*Paphia*, 83  
   *luzonica*, 83  
  
*papillaris*, *Papillifera*, 88  
*papillata*, *Diaphorodoris luteocincta*, 93  
   98  
*Papillifera*, 88-90  
   *papillaris*, 88  
   *solida*, 89  
*papillifera*, *Pseudovermis*, 236, 241  
*parasitica*, *Crassostrea*, 83  
*Parazoanthus*, 226  
   *axinellae*, 226  
*parcedentata*, *Vertigo*, 249  
*Parenchymella*, 212  
*Parreysia*, 286  
   *corrugata*, 286  
   *rugosa*, 286  
*parthenopeia*, *Doris*, 96  
*partschi*, *Cardita*, 288  
*pasinii*, *Doris*, 96  
*Patella*, 207, 209, 210, 220, 224, 225, 240,  
   244, 245, 247  
   *coerulea*, 220, 224, 225, 240  
   *lusitanica*, 220, 224, 225, 240  
   *vulgata*, 244  
*patelliformis*, *Anomia*, 288  
*patula*, *Purpura*, 82  
*patulum*, *Cerithium*, 82  
*paucicostatum*, *Cardium*, 238, 241  
*pavonia*, *Padina*, 224, 230  
*pazi*, *Oxychilus*, 56  
*Pecten*, 157, 168, 231, 234, 240, 288  
   *jacobaesus*, 231, 234, 240  
*Pectinacea*, 222  
*Pectinidae*, 247, 272, 288  
*Pegea*, 90  
   *carnea*, 90  
*pelagica*, *Limopsis*, 271  
*pelagica*, *Limopsis pelagica*, 271  
*pelagica dalli*, *Limopsis*, 271  
*pelagica pelagica*, *Limopsis*, 271  
*Pelagosphaera*, 212  
*Pelecypoda*, 83, 163, 272  
*pellucida*, *Cladophora*, 274  
*pellucida*, *Vitrina*, 249, 269  
*peloronta*, *Nerita*, 82  
*Peltodoris*, 220, 226, 227, 237, 240  
   *atromaculata*, 220, 226, 227, 237, 240  
*Pentacoela*, 213  
*peregra*, *Lymnaea*, 54, 89, 145, 149, 277  
*peregra*, *Radix*, 42, 54, 55, 89  
*peregrina*, *Hervia*, 230, 231  
*perezi*, *Anisus*, 56  
*Perforatella*, 113, 115, 117  
   *bidentata*, 113, 115

- dibothryon*, 117  
*perla*, *Poromya*, 271  
*permollis*, *Ostrea*, 81  
*personatum*, *Pisidium*, 268  
*pes pelecani*, *Aporrhais*, 231, 232, 234, 235, 238, 240, 241  
*petiolata*, *Udotea*, 228  
*Petricola*, 168, 225-227, 240  
*lithophaga*, 225-227, 240  
*petronella*, *Nesovitrea*, 249, 297, 299  
*Petrosia*, 220, 226, 227, 240  
*ficiformis*, 220, 226, 227, 240  
*Peyssonnelia*, 220, 226, 230, 240  
*squamaria*, 220, 226, 230, 240  
*pfeifferi*, *Biomphalaria*, 35, 43  
*Phagocytella*, 212  
*Phallusia*, 231, 232  
*mamillata*, 231, 232  
*Pharus*, 238  
*legumen*, 238  
*Phenacolimax*, 117, 269  
*annularis*, 117  
*major*, 269  
*Philine*, 234, 236, 241  
*aperta*, 234, 236, 241  
*Philinoglossa*, 236, 241  
*helgolandica*, 236, 241  
*philippi*, *Granopupa*, 85, 88  
*philippi*, *Pupestrella*, 85, 88  
*Pholadidae*, 164, 167, 168, 170  
*Phoronidea*, 212, 213  
*Phragmites*, 268  
*Physa*, 44, 54, 55, 145, 277  
*acuta*, 54, 55, 277  
*fontinalis*, 145  
*Physidae*, 145  
*Physopsis*, 37  
*picta*, *Doris*, 96  
*pictorum*, *Unio*, 65  
*Pilidae*, 263  
*Pilina*, 201  
*pilosa*, *Glycymeris*, 288  
*pilula*, *Oxychilus*, 86  
*Pinctada*, 80, 188  
*maculata*, 188  
*radiata*, 80  
*Pinna*, 165, 168, 238, 241, 288  
*nobilis*, 238, 241  
*pirainii*, *Doris*, 96  
*pisana*, *Euparypha*, 55  
*pisana*, *Theba*, 89, 261  
*Pisania*, 220, 225, 230, 240  
*maculosa*, 220, 225, 230, 240  
*piscinalis*, *Valvata*, 145  
*Pisidium*, 121-125, 268  
*casertanum*, 268  
*conventus*, 123, 124, 268  
*hibernicum*, 121-124  
*lilljeborgii*, 121-124, 268  
*milium*, 268  
*nitidum*, 122-124, 268  
*personatum*, 268  
*subtruncatum*, 268  
*Pitaria*, 231, 234, 238, 240  
*chione*, 231, 234, 240  
*Placophora*, 191, 193, 195, 198, 199, 201, 207, 209, 210, 212, 214, 217, 224-227, 230, 231, 234, 236, 238, 240, 241  
*Placuna*, 288  
*planatus*, *Angulus*, 238  
*Planispira*, 260  
*fallaciosa*, 260  
*Planorbarius*, 25, 26, 55, 145  
*corneus*, 145  
*metidjensis*, 25, 26, 55  
*Planorbidae*, 35, 43, 54, 145, 263  
*Planorbinae*, 26  
*Planorbis*, 145  
*carinatus*, 145  
*planorbis*, 145  
*planorbis*, *Planorbis*, 145  
*planospira illyrica*, *Chilostoma*, 261  
*planospira occultata*, *Chilostoma*, 85, 87  
*planospira occultata*, *Helicigona*, 85, 87  
*Plantago*, 249  
*Plathelminthes*, 203, 210, 214  
*Pleurobranchidae*, 234  
*Pleuroceridae*, 263  
*Pleuropunctum*, 88, 89  
*micropleuros*, 89  
*plicata*, *Nerita*, 280, 281  
*plioauriculata*, *Polygyra*, 267  
*pluma*, *Aglaphenia*, 225  
*Plumularia*, 226  
*Pododesmus*, 80, 83  
*rudis*, 80, 83  
*Pogonophora*, 213  
*polita*, *Acicula*, 117  
*Polycera*, 234, 241  
*quadrilineata*, 234, 241  
*Polycladida*, 203  
*Polygordius*, 208  
*Polygyra*, 267  
*plioauriculata*, 267  
*Polygyracea*, 260

- polymorpha*, *Dreissena*, 207  
*Polynices*, 236, 238, 241  
   *guillemini*, 236  
*Polysiphonia*, 224  
   *sertularoides*, 224  
*pomatia*, *Helix*, 135-139, 153, 261, 303  
*Pomatias*, 87, 90, 117  
   *elegans*, 87, 117  
*Porifera*, 222, 230, 231  
*Poromya*, 271  
   *perla*, 271  
   *tornata*, 271  
*porroi*, *Cochlodina*, 87, 88  
*Posidonia*, 222, 236, 241, 288  
   *oceanica*, 236  
*Potamididae*, 82, 83  
*Potamogeton*, 268  
*Potamopyrgus*, 145, 277, 301  
   *carinata*, *jenkinsi*, 301  
   *jenkinsi*, 145, 277, 301  
   *jenkinsi carinata*, 301  
*Potentilla*, 249  
*preblei*, *Lymnaea catascopium*, 263  
*prespensis*, *Diana*, 174, 176  
*prespensis*, *Hydrobia*, 173  
*prespensis*, *Micromelania*, 173  
*Prestonella*, 256  
*prevostianus*, *Theodoxus*, 113  
*Prochaetoderma*, 204, 206  
   *californicum*, 206  
*Productacea*, 288  
*profuga*, *Cerņuella*, 85  
*profundorum*, *Abra*, 271  
*Prolecithophora*, 203  
*Propeamussium*, 271  
   *meridionale*, 271  
*Proseriata*, 203  
*Prosobranchia*, 201, 217, 230, 231, 236,  
   238, 241, 284, 293, 294  
*Protobranchia*, 163, 164, 191, 201, 207-  
   210, 214, 238, 272  
*Protodrepanostoma*, 267  
*Protostomia*, 205, 213  
*proxima*, *Nucula*, 207, 208  
*pruinosis*, *Metopornothus*, 43  
*Psammobia*, 238  
   *depressa*, 238  
*Psammobiidae*, 164  
*Pseudamnicola*, 173-175, 277  
   *anatina*, 277  
   *compacta*, 277  
   *consociella*, 173  
   *curta*, 174  
*Pseudolithophyllum*, 225, 226, 240  
   *expansum*, 225, 226  
*Pseudohoratia*, 173  
*Pseudolamellibranchia*, 165  
*Pseudomonadaceae*, 43  
*pseudosubstriata*, *Vertigo*, 117  
*Pseudovermis*, 236, 241  
   *papillifera*, 236, 241  
   *schulzi*, 236, 241  
*Pteria*, 80  
   *colymbus*, 80  
*Pterobranchia*, 213  
*Pugilina*, 81  
   *morio*, 81  
*pugilina*, *Melongena*, 82  
*pulchella*, *Vallonia*, 249, 260  
*pulchella*, *Valvata*, 117  
*pulcherrima*, *Doris*, 96  
*pulchra*, *Embletonia*, 236, 241  
*pulla*, *Tricolia*, 230, 293  
*pullastra*, *Venerupis*, 275  
*Pulmonata*, 43, 54, 73, 101, 217, 262,  
   273, 274, 282  
*pumila*, *Clausilia*, 117, 249, 297  
*pumila*, *Emarginula*, 81  
*punctata*, *Aplysia*, 253  
*punctatus*, *Ophiocephalus*, 286  
*Punctum*, 249  
   *pygmaeum*, 249  
*Pupa*, 56  
   *gratiosa*, 56  
*Puuperita*, 279  
   *japonica*, 279  
*Pupilla*, 113, 115, 117, 249  
   *muscorum*, 113, 115, 117, 249  
   *sterri*, 115, 117  
   *triplicata*, 117  
*Pupillacea*, 260  
*Purpura*, 82, 265  
   *lapillus*, 265  
   *patula*, 82  
*purpurea*, *Glossodoris*, 95, 96  
*Pusia*, 230  
   *tricolor*, 230  
*putris*, *Succinea*, 249  
*pygmaea*, *Vertigo*, 113, 249  
*pygmaeum*, *Punctum*, 249  
*pyramidata*, *Trochoidea*, 86  
*Pyramidula*, 83  
   *rupestris*, 85  
*pyrenaica*, *Pyrgula*, 176

- Pyrgohydrobia*, 173  
   *grochmalickii*, 173  
*Pyrgophysa*, 37  
*Pyrgula*, 173, 175, 176  
   *annulata*, 175, 176  
   *dariewxi*, 176  
   *pyrenaica*, 176  
   *sturanyi*, 173  
 Pyrgulinae, 173, 175, 176  
  
*quadrasi*, *Helix*, 267  
*quadrasi*, *Trissexodon*, 267  
*quadridens*, *Jamina*, 55, 85, 88, 89  
*quadrilineata*, *Polycera*, 234, 241  
*Quickella*, 289  
*Quickia*, 259  
  
*racemosa*, *Laguncularia*, 79  
*racemus*, *Lithophyllum*, 225  
*radiata*, *Isognomon*, 80  
*radiata*, *Lichenopora*, 227  
*radiata*, *Pinctada*, 80  
*Radix*, 42, 54, 55, 89  
   *auricularia*, 54, 55  
   *peregra*, 42, 54, 55, 89  
*ramosus*, *Murex*, 207  
*Rana*, 286  
   *hexadactyla*, 286  
 Rathousiidae, 282  
*recurvus*, *Brachidontes*, 80  
*reidfordi*, *Mucrospirifer*, 288  
*relictum*, *Papaver*, 249  
*relictus*, *Gyraulus*, 173  
*reniformis*, *Chondrosia*, 226  
*requieni*, *Unio*, 65  
*Retama*, 54  
   *sphaerocarpa*, 54  
*Retepora*, 222, 234  
*reticulata*, *Nassa*, 226  
*reticulatum*, *Bittium*, 228, 230, 231, 234,  
   238, 240, 241  
*reticulatus*, *Agriolimax*, 179-182, 273  
*retifera*, *Neritina*, 280, 281  
*retropictus*, *Clithon*, 279  
*Retusa*, 236  
 Rhabdoceola, 203  
*Rhacophorus*, 286, 287  
   *maculatus*, 286, 287  
*rhizophorae*, *Crassostrea*, 80, 83  
*Rhizophora*, 79-82  
   *mangle*, 79, 80, 82  
  
*Rhodope*, 282  
   *veranii*, 282  
*rhomboides*, *Venerupis*, 275  
 Rhytididae, 256-258  
*Richthofenia*, 288  
*riisei*, *Tropicorbis*, 40  
*Rissoa*, 228, 230, 231, 235, 240  
   *variabilis*, 228, 230, 231, 235, 240  
 Rissoacea, 230, 238  
 Rissoidae, 222, 241  
*rivieriana*, *Truncatellina*, 55  
*Rivulina*, 125  
*robiči*, *Bythinella*, 173  
*robiči*, *Sadleriana*, 174  
*rohlfsi*, *Bulinus truncatus*, 38  
*ronnebyensis*, *Vertigo*, 297  
*rosea*, *Aenigma*, 83  
*rotundatus*, *Discus*, 249  
 Roudairea, 288  
*royalense*, *Helisoma anceps*, 262  
*rubens*, *Jania*, 224, 230  
*ruber*, *Lineus*, 208  
*rubiginosus*, *Arion*, 73  
*rubrum*, *Gasteropteron*, 207  
*runderatus*, *Discus*, 299  
*rudis*, *Pododesmus*, 80, 83  
*rufus*, *Arion*, 73, 74, 76, 303  
*rufus*, *Arion ater*, 73  
*rufus atra*, *Arion*, 73  
*rufus atra aterrima*, *Arion*, 73  
*rufus atra marginella*, *Arion*, 73, 74  
*rufus atra sulcata*, *Arion*, 73, 74  
*rugosa*, *Astraea*, 231, 234, 240, 241  
*rugosa*, *Parveysia*, 286  
*rumelica*, *Helix*, 135  
 Rumina, 55  
   *decollata*, 55  
*rumphii*, *Nerita*, 280, 281  
 Runcina, 238, 241  
   *coronata*, 238, 241  
*rupestre*, *Cerithium*, 225, 234, 238, 240,  
   241  
*Rupestrella*, 85, 88  
   *philippi*, 85, 88  
*rupestris*, *Pyramidula*, 85  
*rustica*, *Columbella*, 225, 230, 231, 238,  
   240, 241  
  
 Sacoglossa, 226  
*Sadleriana*, 173-175  
   *fluminensis*, 174  
   *macedonica*, 173

- robiči*, 174  
*virescens*, 173  
*Saganoa*, 278  
*sancta*, *Cochlodina*, 88  
*sanctaemariae*, *Lymnaea stagnalis*, 263  
*sanguinea*, *Schizoporella*, 225  
*sarda*, *Cochlodina*, 88  
*Sargassum*, 224, 230  
*scacchiana*, *Doris*, 97  
*scalaris*, *Cacospongia*, 225, 226  
*Scaphander*, 236  
*lignarius*, 236  
*Scaphopoda*, 191, 201, 203-205, 207, 209,  
210, 214, 236, 238, 241  
*Schistosoma*, 25-27, 29-33, 37, 40, 43  
*europense*, *haematobium*, 26  
*haematobium*, 25-27, 29-33, 37  
*haematobium europense*, 26  
*mansoni*, 25, 31, 32, 40, 43  
*Schizoporella*, 225  
*sanguinea*, 225  
*schlikumi*, *Diana*, 176  
*schultzei*, *Doris*, 97  
*schulzi*, *Pseudovermis*, 236, 241  
*Scolecida*, 282  
*scotophila notha*, *Hyalinia*, 86  
*Scrobicularia*, 243  
*Scrupodellaria*, 230  
*Sculptaria*, 256  
*Scutopus*, 201, 204  
*ventrolineatus*, 201  
*scutulum*, *Testacella*, 86  
*Scyphozoa*, 212  
*Segmentina*, 145  
*Semelidae*, 164  
*Semilimax*, 117  
*kotulae*, 117  
*Sepia*, 245, 246  
*officinalis*, 245, 246  
*Septaria*, 279-281  
*compressa*, 280, 281  
*tessellata*, 279-281  
*Septibranchia*, 272  
*sepultus*, *Zonitoides*, 113  
*sericinus*, *Bulinus*, 37  
*serotina*, *Gastrocopta*, 113, 115  
*sertularoides*, *Polysiphonia*, 224  
*Sheldonia*, 256  
*sibirica*, *Valvata*, 145  
*Sidonia*, 282  
*elegans*, 282  
*Sigmurethra*, 260, 289  
*siliqua*, *Ensis*, 238  
*siliquoidea*, *Lamprosilis*, 272  
*silvaticus*, *Arion*, 297  
*sincera ontariensis*, *Valvata*, 263  
*sinensis*, *Calyptraea*, 231, 234, 240, 241  
*Sinuitopsis*, 201  
*acutilira*, 201  
*similis*, *Arca*, 165, 168  
*simplex*, *Columella*, 297  
*simplex*, *Digenea*, 228  
*Siphonaria*, 81  
*Sipunculida*, 203, 205, 208, 210, 212, 214  
*Sipunculus*, 208-210, 212  
*nudus*, 208, 209  
*Solecurtidae*, 164  
*Solen*, 232, 236, 238, 241, 288  
*vagina*, 232, 238, 241  
*Solenocurtus*, 238  
*strigillatus*, 238  
*Solenogastres*, 191-193, 195, 196, 198-  
200, 203, 204, 207-210, 212, 214  
*Soleolifera*, 282, 284  
*solida*, *Papillifera*, 89  
*Soösia*, 117  
*diodonta*, 117  
*sophiae*, *Cochlodina*, 88  
*sowerbii*, *Lucapina*, 81  
*sowerbyi*, *Milax*, 87  
*Spelaeodiscinae*, 267  
*speciosa*, *Tricolia*, 230  
*Sphaeriidae*, 121, 263, 268  
*Sphaerium*, 125  
*sphaerocarpa*, *Retama*, 54  
*Sphagnum*, 149  
*spicata*, *Cystoseira*, 227, 230  
*spiculifera*, *Hedylopsis*, 236, 241  
*spirorbis*, *Anisus*, 55, 145  
*Spirorbis*, 227  
*pagenstecheri*, 227  
*splendida*, *Thuridella*, 230, 231, 240  
*Spondylidae*, 164, 288  
*Spondylus*, 288  
*olsenae*, 288  
*Spongiaria*, 219  
*Spurilla*, 230, 231  
*neapolitana*, 230, 231  
*squamaria*, *Peyssonnelia*, 220, 226, 230  
240  
*stagnalis lillianae*, *Lymnaea*, 101, 102  
*stagnalis*, *Lymnaea*, 42, 101, 102, 105,  
106, 145  
*stagnalis sanctaemariae*, *Lymnaea*, 263

- stagnalis*, *Succinea*, 55  
*stankovići*, *Neofossarulus*, 173  
*Stankovicia*, 176  
     *baicaliiiformis*, 176  
*stellatus*, *Chthamalus*, 223  
*stellatus*, *Chthamalus stellatus*, 223  
*Stenothecoida*, 203  
*Stenothecoides*, 203  
*Stenotrema*, 260  
     *lei*, 260  
*sterri*, *Pupilla*, 115, 117  
*Streptaxidae*, 256, 257  
*Streptoneura*, 279  
*striata*, *Bullaria*, 236, 241  
*striata*, *Helicella*, 112  
*striatula*, *Venus*, 275, 276  
*striatus*, *Cantharidus*, 230, 238, 241  
*striatus*, *Ophiocephalus*, 286  
*strigillatus*, *Solenocurtus*, 238  
*striolata*, *Trichia*, 113  
*striolata danubialis*, *Trichia*, 261  
*striolata montana*, *Trichia*, 261, 262  
*Strombiformis*, 238  
     *subulata*, 238  
*stultorum*, *Mactra*, 238  
*sturanyi*, *Deroceras*, 297  
*sturanyi*, *Pyrgula*, 173  
*Stylommatophora*, 259, 260, 282, 289  
*subconstrictus*, *Helix*, 267  
*subcylindrica*, *Truncatella*, 85, 87, 224, 240  
*subfuscus*, *Arion*, 73, 74, 76, 249  
*subglobosa*, *Congerina*, 288  
*subpulchella*, *Vallonia*, 112  
*substriata*, *Vertigo*, 249  
*subtruncatum*, *Pisidium*, 268  
*subulata*, *Strombiformis*, 238  
*Subulinidae*, 256, 257  
*Succinea*, 55, 115, 117, 249, 259, 289, 297  
     *antiqua*, 249  
     *oblonga*, 115, 117, 249  
     *putris*, 249  
     *stagnalis*, 55  
*Succineacea*, 260  
*Succineidae*, 259, 260, 289  
*Succineinae*, 289  
*sudanica tanganyicensis*, *Biomphalaria*, 35  
*sulcata*, *Arion rufus atra*, 73, 74  
*sulcata*, *Terebralia*, 82  
*Sulcatopinna*, 288  
*sulcatus*, *Arion*, 76  
*sulcatus*, *Inoceramus*, 288  
*Symptonata*, 286  
*systema*, *Cacopus*, 287  
*Tacheocampylaea*, 87, 90  
     *chaixii*, 87  
     *elata*, 87  
     *tacheoides*, 87  
*tacheoides*, *Tacheocampylaea*, 87  
*tanganyicensis*, *Biomphalaria sudanica*, 35  
*Taraxacum*, 249  
     *dovreense*, 249  
*Tarebia*, 40  
     *granifera*, 40  
*tataënsis*, *Belgrandia*, 117  
*Taxodonta*, 163  
*Tectarius*, 82  
     *muricatus*, 82  
*Telescopium*, 82  
     *telescopium*, 82  
*telescopium*, *Telescopium*, 82  
*telleri*, *Eumorphotis*, 288  
*Tellina*, 167, 168, 170, 232, 236, 238, 239, 241  
     *distorta*, 232, 236, 239, 241  
*Tellinacea*, 164, 167, 170  
*Tellinidae*, 164, 170  
*tenellus*, *Arion*, 73  
*tenera*, *Doris*, 96  
*Tentaculata*, 213  
*tentaculata*, *Bithynia*, 277  
*tentaculata thermalis*, *Bithynia*, 113  
*tenuilabris*, *Vallonia*, 113, 115, 117, 249  
*tenuis*, *Macoma*, 238  
*Terebralia*, 82  
     *sulcata*, 82  
*Teredinidae*, 83, 164, 168  
*Teredo*, 81, 83, 168, 169  
     *manii*, 83  
*Tergipes*, 236, 241  
     *despectus*, 236, 241  
*tesselata*, *Septaria*, 279-281  
*tesselata*, *Nerita*, 82  
*Testacella*, 86  
     *scutulum*, 86  
*testarum*, *Mastigocleus*, 223  
*Tethymelibidae*, 295  
*Thais*, 265, 293, 294  
     *lapillus*, 265, 293  
*Theba*, 89, 261  
     *pisana*, 89, 261

- Theodoxus*, 113, 279  
   *fluviatilis*, 279  
   *prevostianus*, 113  
*thermalis*, *Bithynia tentaculata*, 113  
*thiesseana*, *Diana*, 173, 174, 176  
*Thuridilla*, 230, 231, 237, 240  
   *hopei*, 237  
   *splendida*, 230, 231, 240  
*Thymus*, 54  
*togata*, *Gari*, 83  
*tornata*, *Poromya*, 271  
*tornatilis*, *Acteon*, 232, 236, 241  
*Toxoglossa*, 226  
*Trachycardium*, 81  
   *muricatum*, 81  
*Trachycystis*, 256  
*Trachyochridia*, 176  
*Tralia*, 82  
   *ovula*, 82  
*Trichia*, 113, 117, 249, 261, 262  
   *danubialis*, *striolata*, 261  
   *hispidia*, 117, 249, 261  
   *montana*, *striolata*, 261, 262  
   *striolata*, 113  
   *striolata danubialis*, 261  
   *striolata montana*, 261, 262  
*Tricladida*, 203  
*Tricolia*, 230, 293, 294  
   *pulla*, 230, 293  
   *speciosa*, 230  
*tricolor*, *Glossodoris*, 93, 95, 96, 98  
*tricolor*, *Pusia*, 230  
*Tridacna*, 168, 188, 189  
   *maxima*, 188, 189  
*Tridacnidae*, 288  
*tridens*, *Chondrula*, 117  
*Trigonephrus*, 256  
*Trigonia*, 163, 288  
*trilineata*, *Chromodoris*, 96  
*Trinchesia*, 230, 231  
   *foliata*, 230, 231  
*triplicata*, *Pupilla*, 117  
*triplicata*, *Turritella*, 238, 241  
*Trissexodon*, 267  
   *constrictus*, 267  
   *quadrasi*, 267  
*Tritonalia*, 226-228, 230, 231, 240  
   *aciculata*, 226, 228, 230, 231, 240  
   *edwardsi*, 226, 227, 230, 240  
*Trivia*, 232, 234-236, 241  
   *adriatica*, 232, 235, 236, 241  
*Trochidae*, 222, 230, 238, 240  
*Trochoidea*, 86, 88, 90  
   *pyramidata*, 86  
   *trochoides*, 88  
*trochoides*, *Trochoidea*, 88  
*Trochomorpha*, 86  
*Tropicorbis*, 40  
   *riisei*, 40  
*tropicus*, *Bulinus*, 37-39  
*tropicus*, *Bulinus tropicus*, 38  
*tropicus alluaudi*, *Bulinus*, 38  
*tropicus tropicus*, *Bulinus*, 38  
*Truncatella*, 85, 87, 224, 240  
   *subcylindrica*, 85, 87, 224, 240  
*Truncatellina*, 55, 112, 115, 249  
   *britannica*, 249  
   *claustralis*, 115  
   *cylindrica*, 112, 115, 249  
   *rivieriana*, 55  
*Truncatellinae*, 176  
*truncatula*, *Galba*, 42, 55, 89  
*truncatula*, *Lymnaea*, 89, 127, 128, 133, 145, 148  
*truncatus*, *Bulinus*, 25, 26, 28, 29, 31-33, 37, 38  
*truncatus*, *Bulinus truncatus*, 38  
*truncatus rohlfsi*, *Bulinus*, 38  
*truncatus truncatus*, *Bulinus*, 38  
*trunculus*, *Donax*, 238  
*trunculus*, *Murex*, 226, 230, 231, 234, 240, 241  
*Tryblidiacea*, 191, 193, 200, 201, 212-214  
*Tryblidium*, 201  
*tuberculata*, *Archidoris*, 232, 234, 236, 237, 240, 241  
*tuberculata*, *Haliotis*, 230  
*tuberculata*, *Melania*, 113  
*tuberculatum*, *Cardium*, 238  
*Tulbaghinia*, 256  
*tulipa*, *Fasciolaria*, 82  
*tuna*, *Halimeda*, 220, 226, 228, 230, 240  
*Turbellaria*, 209, 210, 214  
*turbinata*, *Monodonta*, 220, 224, 225, 240  
*Turbinidae*, 293  
*Turbo*, 293  
*Turbonilla*, 238, 241  
   *lactea*, 238  
*Turritella*, 232, 238, 241  
   *communis*, 232, 238, 241  
   *triplicata*, 238, 241  
*Turtonia*, 168, 254  
*Udotea*, 228



- petiolata*, 228  
*ugandae*, *Bulinus*, 35  
*Ulva*, 224, 225  
*lactuca*, 224  
*umbrosa*, *Zenobiella*, 261  
*undata*, *Grammysia*, 288  
*undata*, *Myonera*, 271  
*undatus*, *Cyclopecten*, 271  
*uniflora*, *Litorella*, 121  
*Unio*, 65, 66, 68, 71, 112  
*pictorum*, 65  
*requieni*, 65  
Unionidae, 263, 272  
Urocyclidae, 256, 257  
  
*vagina*, *Solen*, 232, 238, 241  
Vaginulidae, 282  
*Vaginulus*, 284, 285  
*borellianus*, 284  
*valenciennesi*, *Glossodoris*, 93, 95-98  
*valentianus*, *Limax*, 297  
*Vallonia*, 55, 112, 113, 115, 117, 249,  
260, 297  
*costata*, 55, 112, 115, 117, 249  
*enniensis*, 115, 117  
*pulchella*, 249, 260  
*subpulchella*, 112  
*tenuilabris*, 113, 115, 117, 249  
*Valvata*, 112, 117, 145, 173, 263  
*cristata*, 145  
*ochridana*, 173  
*ontariensis*, *sincera*, 263  
*piscinalis*, 145  
*pulchella*, 117  
*sibirica*, 145  
*sincera ontariensis*, 263  
Valvatidae, 145  
*varia*, *Gibbula*, 230, 238, 241  
*variabile*, *Cerithium*, 81  
*variabilis*, *Rissoa*, 228, 230, 231, 235,  
240  
Veneracea, 222  
Veneridae, 81, 83, 168, 231, 234, 254,  
275  
*Venerupis*, 238, 254, 275, 276  
*aurea*, 275  
*decussata*, 275, 276  
*pullastra*, 275  
*rhomboides*, 275  
*ventricosa*, *Iphigena*, 55, 299  
*ventricosa*, *Arca*, 188, 189  
*ventricosa*, *Lampsilis*, 272  
*ventricosus*, *Comus*, 225, 226, 228, 230,  
231, 238, 240, 241  
Ventriculicida, 193  
*ventrolineatus*, *Scutopus*, 201  
*ventrosa*, *Hydrobia*, 174, 277  
*venulosa*, *Doris*, 96  
*Venus*, 125, 231, 234, 238, 240, 241, 275,  
276  
*casina*, 238, 241  
*gallina*, 238  
*mercenaria*, 125  
*striatula*, 275, 276  
*verrucosa*, 231, 234, 240, 275, 276  
*veranii*, *Rhodope*, 282  
*vermeta*, *Catinella*, 260  
*Vermetus*, 226, 227, 231, 234, 240  
*Vermicularia*, 81  
*knorri*, 81  
*vermiculata*, *Eobania*, 55  
*vermillionense*, *Helisoma corpulentum*,  
263  
*Veronicella*, 264  
*aberrans*, 264  
*ameghini*, 264  
*angustipes*, 264  
Veronicellidae, 257  
*verrucosa*, *Epimonia*, 204, 207, 209  
*verrucosa*, *Venus*, 231, 234, 240, 275,  
276  
*versicolor*, *Nerita*, 82  
*verticillus*, *Aegopis*, 117  
*Vertigo*, 112, 113, 115, 117, 249, 297,  
299  
*antivertigo*, 115, 117, 249  
*artica*, 297, 299  
*callosa*, 112  
*genesii*, 297, 299  
*geyeri*, 297  
*modesta*, 297  
*moulinsiana*, 115  
*parcedentata*, 249  
*pseudosubstriata*, 117  
*pygmaea*, 113, 249  
*ronnebyensis*, 297  
*substriata*, 249  
*Vesicomya*, 254  
Vesicomyiidae, 254  
*Vidalia*, 222, 231, 232, 234, 240, 241  
*volubilis*, 222, 231, 232, 234, 240, 241  
*villae*, *Doris*, 96  
*villafranca*, *Doris*, 96  
*villafranca*, *Chromodoris*, 96

- violacea, Dostia*, 279  
*violacea, Neritina*, 279  
*virescens, Arion*, 73  
*virescens, Sadleriana*, 173  
*virgata, Cernuella*, 55  
*virginea, Ascidia*, 231  
*virginea, Neritina*, 81, 82  
*virginica, Crassostrea*, 80  
*viridis, Elysia*, 228, 230, 231, 238, 240, 241  
*Vitre*a, 85, 87, 90, 297  
   *contracta*, 85, 87  
   *crystallina*, 85, 87  
   *diaphana*, 87  
*Vitreinae*, 269  
*Vitrina*, 117, 249, 269  
   *bielzi*, 117  
   *pellucida*, 249, 269  
*Vitrinidae*, 269  
*Vitrinobrachium*, 269  
   *breve*, 269  
*Viviparidae*, 145, 263  
*Viviparus*, 112, 145, 213, 284, 293  
   *ater*, 284  
   *böckhi*, 112  
   *viviparus*, 145, 293  
*viviparus, Viviparus*, 145, 293  
*volubilis, Vidalia*, 222, 231, 232, 234, 240, 241  
*vulgare, Dentalium*, 236, 241  
*vulgata, Patella*, 244  
*vulgatum, Cerithium*, 231, 234, 240, 241  
*weberi, Dorymenia*, 204  
*whiteavesi, Helisoma corpulentum*, 263  
*Xerocerastus*, 256  
*Xeromagna*, 55  
   *arigo*, 55  
*Xerotricha*, 55, 88  
   *apicina*, 88  
   *conspurcata*, 55, 88  
*Xylophaga*, 168, 169  
*Yoldia*, 201, 207, 210  
   *kimatula*, 207  
*zebra, Cypraea*, 82  
*Zenobiella*, 261  
   *umbrosa*, 261  
*zilchi, Chilopyrgula*, 176  
*zizyphinus, Calliostoma*, 231  
*Zonitacea*, 260, 269  
*Zonitidae*, 86, 115, 269, 274, 289  
*Zonitinae*, 269  
*Zonitoides*, 113, 249, 260, 269, 297  
   *arboreus*, 297  
   *excavatus*, 249, 269  
   *nitidus*, 260, 269  
   *sepultus*, 113  
*Zostera*, 222, 236, 241  
   *marina*, 236

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# MALACOLOGIA

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VELUTINELLUS, NOUVEAU GENRE FOSSILE DE LA FAMILLE  
DES LYMNAEIDAE, ET SES RELATIONS AVEC VELUTINOPSIS  
ET VALENCIENNIUS

Florian Marinescu

*Institute Géologique du Comité Géologique, Bucarest, Roumanie*

RESUME

Cette note comprend la description de 4 Lymneides provenant de gisements situés sur le versant oriental des Carpates Meridionales (Bassin Dacique), en Olténie, Roumanie. Ces espèces sont: *Velutinopsis velutina* Deshayes, espèce peu connue en Roumanie, provenant du Méotien inférieur, *Velutinopsis codapavonis* sp. n., du Pontien inférieur, et 2 espèces appartenant au genre nouveau *Velutinellus*: *Velutinellus catinus* sp. n. (catinus = encensoir romain) et *V. pileus* sp. n. (pileus = bonnet distinctif des nobles daces), aussi du Méotien inférieur.

Le genre *Velutinellus* est caractérisé par la grande expansion du péristome, qui débordé largement la spire très réduite. Les formes décrites antérieurement sous les noms de "*Lymnaea*" *amplecta* Gorjanovic-Kramberger, *Velutinopsis rugosa* Gorjanovic-Kramberger et *V. transiens* Moos sont, elles aussi, attribuées à *Velutinellus*.

Le développement ontogénétique des coquilles de *Velutinellus* suggère que ce genre dérive de *Velutinopsis velutina* et qu'il se relie à *Valenciennius* par l'intermédiaire de *Provalenciennesia*. La ligne philétique présumée, appelée ici "ligne évolutive valencienne des Lymnéides," serait la suivante:

*Radix* → *Velutinopsis* → *Velutinellus* → *Provalenciennesia* → *Valenciennius*  
↙ *Undulotheca*

L'auteur suppose que les espèces pannoniques *Velutinellus rugosus* et *V. transiens* proviennent des formes décrites du Bassin Dacique, qui auraient émigré dans le Bassin Pannonique à cause d'une augmentation de la salinité dans le Bassin Dacique lors de la sédimentation des couches à *Dosinia*. La forme plate des coquilles, caractéristique des genres *Undulotheca*, *Provalenciennesia* et *Valenciennius* représente une adaptation aux conditions spéciales de vie dans un bassin dont le fond est constitué de vase imbibée d'eau.

La position systématique du genre *Valenciennius* Rousseau, 1842, connu du Pliocène supérieur (Pontien), est encore sujet à discussion: certains auteurs en font une famille indépendante, alors que d'autres s'opposent à ce qu'on le sépare de la famille des Lymnaeidae. Malgré ces divergences, tous sont d'accord pour reconnaître sa descendance d'une forme de *Radix*, par l'intermédiaire de *Velutinopsis* Sandberger, 1875, et de *Provalenciennesia* Gorjanovic-Kramberger, 1923, et pour placer son évolution dans le secteur sud-est du Bassin Pannonique.

Les seuls représentants de cette filiation connus jusqu'à présent dans le Bassin Dacique ont été *Radix*, *Velutinopsis* et

*Valenciennius*. Les formes de *Radix* sont signalées dès le Sarmatien; celles de *Velutinopsis* et *Valenciennius* sont connues du Pontien. Dernièrement, *Velutinopsis* a été mentionnée dans le Méotien supérieur aussi.

Le très riche matériel paléontologique du Néogène supérieur du Bassin Dacique (surtout de l'ouest de l'Olténie-Roumanie) a fourni quelques formes de cette famille, qui n'ont pas encore été décrites et dont deux représentants forment un nouveau genre: *Velutinellus*. Certaines formes de *Velutinopsis*, déjà décrites, telles que *Velutinopsis rugosa* Gorjanovic-Kramberger, *V. transiens* Moos ainsi que "*Lymnaea*" *amplecta* Gorjanovic-

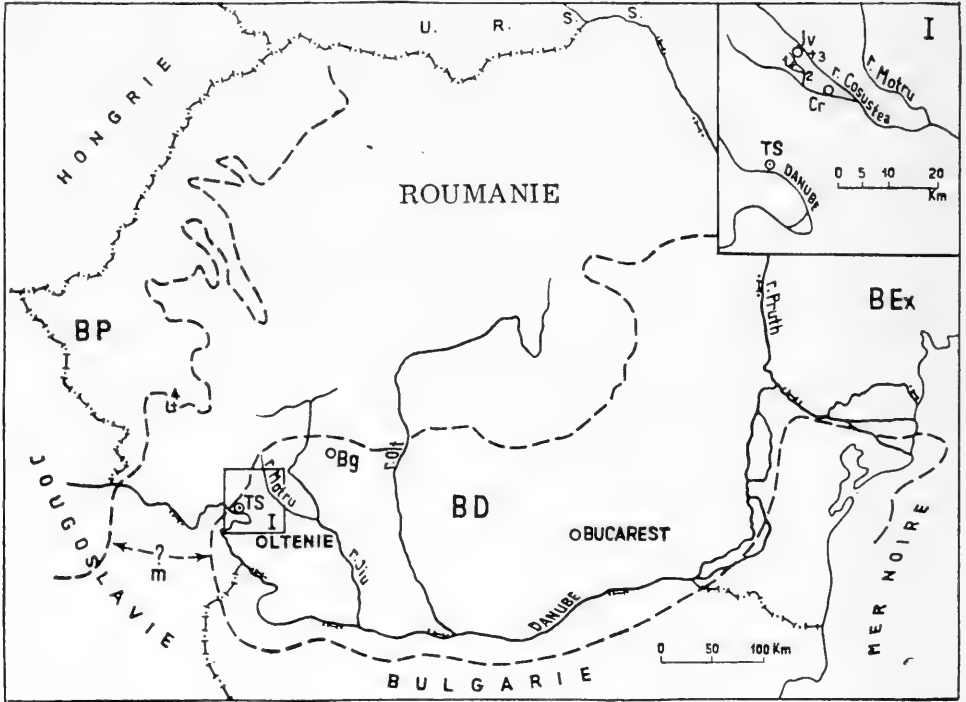


FIG. 1. Carte montrant l'emplacement des gisements mentionnés (+) en Roumanie, particulièrement en Olténie (I), ainsi que les bassins où se sont développés les Lymnaeides du groupe *Valenciennius*. TS Tarnu Severin; Cr, Crăgești; Iv, Ilovăț; Bg, Bengești; 1, gisement du vallon Fintinele; 2, vallée Iazoștea; 3, gisement d'Ilovăț; 4, Soceni. BP, Bassin Pannonique; BD, Bassin Dacique; BEx, Bassin Euxinique; m, voie présumée de migration à travers les Carpates méridionales.

Kramberger, sont aussi placées dans ce genre.

Les observations sur le développement

ontogénétique des coquilles de *Velutinellus* ont suggéré leur position intermédiaire entre *Velutinopsis* et *Valenciennius*.

Genre *Velutinopsis* Sandberger, 1875  
 Espèce type *Lymnaea velutina* Deshayes  
*Velutinopsis velutina* (Deshayes, 1838)  
 Pl. I, Fig. 4-5

- 1838 *Lymnaea velutina* Deshayes, Mém. Soc. Géol. Fr. sér. 1, t. III, 1, p. 64, pl. V, figs. 12-14.  
 1923 *Velutinopsis velutina* (Deshayes); Wenz, Fossilium Catalogus, pars 21, p. 1326 (avec synonymie).  
 1942 *Radix (Velutinopsis)* cf. *velutina* (Deshayes); Wenz, Senckenbergiana, Bd. 24, p. 68, pl. 24, fig. 380.  
 1944 *Velutinopsis velutina* Deshayes; Moos, Vestnik drz. geol. Zavoda II/III, p. 345, pl. XXI, figs. 3-5.

Jusqu'à présent cette espèce a été rencontrée surtout dans le Pontien (Pliocène) par I. Motaș (de l'Institut de Géologie et Géographie de l'Académie

Roumaine), à Bengesti (Olténie septentrionale, Roumanie), mais les exemplaires mentionnés ne sont pas précisément typiques: ils ont la coquille plus épaisse



et l'apex un peu plus élevé. Les deux exemplaires plus anciens que nous possédons, provenant du Méotien inférieur, ont une coquille presque lisse et ornée seulement de stries d'accroissement, dont quelques-unes sont mieux marquées. La spire est très petite, représentée seulement par deux tours; l'apex ne dépasse pas en hauteur le niveau de la spire. Le dernier tour, large et bien développé, s'achève par une ouverture ovale, très évasée. Le bord columellaire du péristome est faiblement soudé à la coquille.

Le gisement se trouve dans le vallon Fintînele [Fig. 1 (1), texte] affluent droit de la vallée Iazoştea, à l'ouest de Crăguşti, Olténie.

Age: Méotien inférieur. L'un des exemplaires a été trouvé dans l'horizon basai, à gravières, avec plusieurs exemplaires de *Theodoxus (Ninia) geticus* Marinescu, *Unio subrecurvus* Teisseyre et quelques espèces de *Teisseyreomya* et *Congeria*. Le deuxième provient du même gisement, mais à 2 m au-dessus, du niveau à *Dosinia maeotica* Andrusov.

### *Velutinopsis codapavonis* sp. n.

Pl. I, Figs. 1-3; Fig. 2 texte

Coquille mince, très fine, peu bombée, en forme de casquette. La spire très petite, basse, à deux tours; l'apex ne dépasse pas le niveau de la spire. Le dernier tour, extrêmement développé, a les bords très évasés, en éventail, ou en queue de paon (d'où le nom). La partie ventrale de la coquille n'est pas visible, mais le bord columellaire du péristome ne paraît pas être soudé à la spire.

Dimensions de 3 exemplaires, en millimètres:

	holo- type	paratypes	
hauteur de la spire:	1,2	2,0	1,0

longueur de la coquille:	5,3	6,6	4,0
largeur du péris- tome:	3,0	5,5	3,3
hauteur du péri- stome:	6,8	7,0	5,6

La coquille étant très fine, les exemplaires n'ont pu être détachés de la roche. Cette espèce est nettement différente de toutes les espèces de *Velutinopsis* connues. Le développement exagéré du dernier tour en est très caractéristique. Il entraîne le développement de la largeur du péristome, qui représente plus de quatre fois la hauteur de la spire. Le bord postérieur de l'ouverture ne dépasse pas la spire. On remarque que cette partie postérieure est bordée par une nervure très fine, qui lui donne plus de résistance. Les exemplaires ont été trouvés dans le versant gauche de la vallée Coşuştea, à Ilovăţ, Olténie [Fig. 1 (3), texte], en amont du pont Borceaşti, dans les argiles marneuses bleu cendré, conchoïdes, à plusieurs Ostracodes, *Radix* et à quelques petits exemplaires de *Valenciennius*. Au-dessus se trouvent des argiles marneuses à *Congeria digitifera* Andrusov, *Paradacna*, *Didacna otiophora* Brusina, recouvertes par des argiles marneuses à *Limnocardium zagrabiense* Brusina et nombreux exemplaires de *Valenciennius* (zone  $\beta$ , Marinescu, 1964).

Le niveau type se trouve à 2,5 m environ au-dessus de la limite Méotien-Pontien, à la partie supérieure d'une intercalation de 20 cm d'argiles sableuses, d'âge Pontien inférieur.

### Genre *Velutinellus* g. n.

Coquille en casquette ou capuchon, ordinairement lisse, couverte seulement de stries d'accroissement, plus rarement à plis plus ou moins accusés. La spire est très petite, réduite à 1-2 tours, aplatie. Le dernier tour a un accroissement très rapide, le diamètre presque égal à la

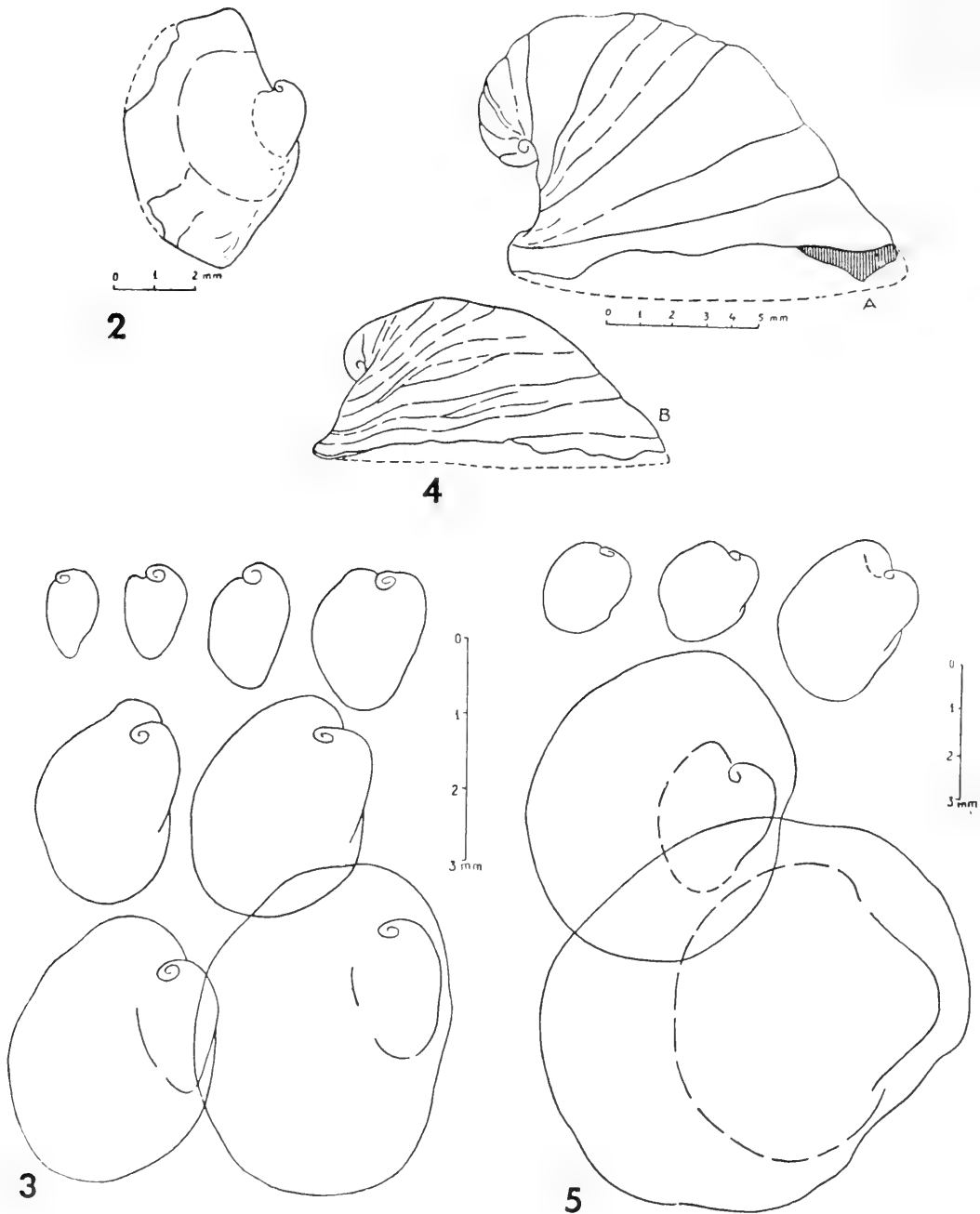


FIG. 2. *Velutinopsis codapavonis* sp. n. (holotype).

FIG. 3. *Velutinellus catinus* gen. n., sp. n. Stades de développement dans une même coquille (holotype).

FIG. 4. A. Profil de *Velutinellus pilleus* et B. de *Velutinellus catinus* (holotypes).

FIG. 5. *Velutinellus pilleus* gen. n., sp. n. Stades de développement dans une même coquille (holotype).

hauteur. Son ouverture, circulaire ou elliptique, est très large et se développe en dépassant la spire par son bord postérieur, qui est libre (non soudé à la coquille).

Par ses caractères, *Velutinellus* est nettement différent de tous les autres genres des Lymnaeidae. Il est vrai que, pendant les premiers stades de développement, les coquilles de *Velutinellus* présentent des ressemblances avec les exemplaires adultes de *Velutinopsis*, mais au cours de leur évolution ultérieure elles prennent une direction différente; c'est pourquoi *Velutinellus* a été considéré comme un genre indépendant. Le nom dérive de *Velutinopsis velutina*, ancêtre présumé des formes que nous allons décrire.

Les données connues nous permettent d'assimiler à *Velutinellus* l'espèce "*Lymnaea*" *amplecta* de Gorjanović-Kramberger (1901: 136, pl. X, figs. 13-14). Bien que les exemplaires figurés soient incomplets, les traits du dernier tour sont très proches de ceux de *Velutinellus*. L'exemplaire figuré par Moos (1944: pl. XXI, fig. 6) comme *Velutinopsis rugosa* présente, lui-aussi, certains caractères génériques de *Velutinellus*. Cet exemplaire se distingue de celui figuré, en dessin, par Gorjanović-Kramberger (1901: pl. X, fig. 16) comme type de l'espèce et qui appartient plutôt au genre *Velutinopsis*. Quant à *Velutinopsis transiens* Moos (1944: pl. XXII, fig. 10), dont l'ouverture dépasse la spire, cette espèce appartient elle-aussi au genre *Velutinellus*.

***Velutinellus catinus* g. n., sp. n.**

(espèce type)

Pl. I, Figs. 9-12, Figs. 3, 4B, texte.

Coquille de petites dimensions, en casquette ou en assiette, recouverte de fines stries d'accroissement et de rides irrégulières, peu marqués. La spire, très petite, basse, se réduit à un seul tour.

Le dernier tour, pas très haut, s'élargit rapidement. L'ouverture, ovoïde ou subcirculaire, a les bords étendus: le bord postérieur dépasse la spire.

Dimensions (mm): holo- paratypes  
type

hauteur de la spire:	1,2	1,0	1,1
hauteur de la coquille:	5,0	2,2	2,0
largeur du péristome:	11,0	4,8	4,6
hauteur du péristome:	10,5	7,2	5,2

Le nom reflète sa ressemblance avec les encensoirs (cassolettes) des romains, nommés *catinus* ou *catinum*. Pendant le développement de *Velutinellus catinus* (Fig. 5, texte) les stades jeunes sont semblables à *Velutinopsis velutina*. Ensuite, le dernier tour se développe très rapidement, sans qu'il y ait, toutefois, une différence trop grande entre la rapidité de croissance de la partie antérieure et celle de la partie postérieure; par conséquent, les stries d'accroissement les plus accusées forment entre elles des angles faibles (8°-15°). La coquille est ornée de plis peu marqués, plus évidents dans la région antérieure, recouverts à leur tour de fines stries d'accroissement (préfiguration des anneaux de *Valenciennius*?) Dans la région latéro-postérieure de la coquille, il y a un sillon siphonal à peine visible, situé exactement dans une petite courbure de l'ouverture, à l'endroit où, chez les *Radix* actuelles, il y a le pneumostome.

Gisement: Les graviers du Méotien inférieur vu vallon Fîntînele, à l'ouest de Crăgusești, Olténie (Fig. 1, texte), à 1, 5m au-dessous du niveau à *Dosinia maeotica*, à côté de *Congeria ramphophora* Brusina, *Unio subrecurvus*, *Teisseyreomya subatava* (Teisseyre) etc. C'est encore de cet endroit que provient un des exemplaires décrits de *Velutinopsis velutina* et les exemplaires de *Velutinellus pilleus* sp. n.



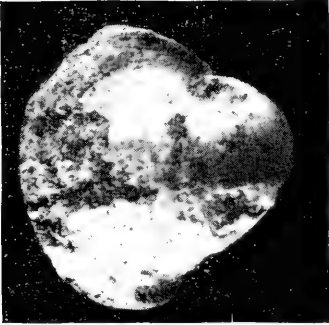
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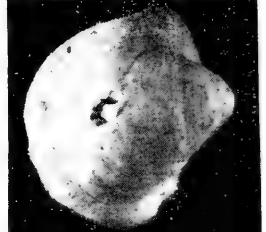


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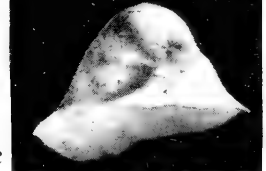
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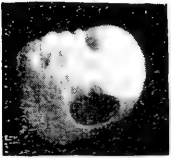
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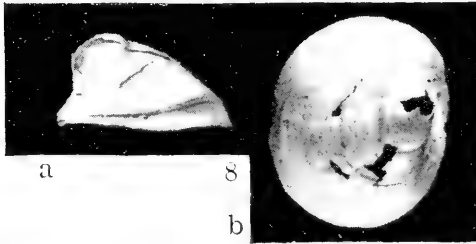
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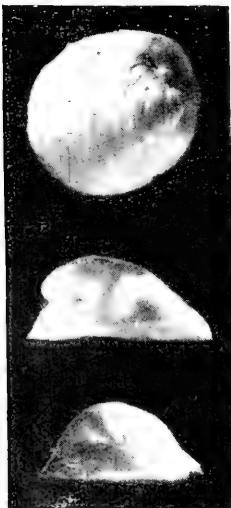


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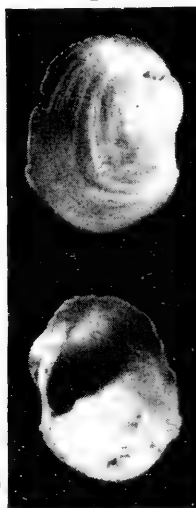
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a

b

11



a

b



a

b

12

**Velutinellus pilleus** g. n., sp. n.

Pl. I, Figs. 6-8. 4A, 5, texte

Coquille de dimensions réduites, assez haute, fine, très fragile, presque lisse, recouverte seulement de stries d'accroissement, dont quelques-unes mieux marquées. La spire est petite, représentée par un seul tour; l'apex est au niveau de la spire, la protoconque est bien visible. Le dernier tour se développe très rapidement en largeur et aussi en hauteur, comme un entonnoir. L'ouverture, irrégulièrement elliptique, dépasse la spire de son bord postérieur.

Dimensions (mm):	holo- type	paratype
hauteur de la spire:	1,5	..
hauteur de la coquille:	8,0	5,5
largeur du péristome:	13,0	11,2
hauteur du péristome:	15,3	13,2

La morphologie externe de cette forme rappelle le bonnet distinctif des nobles daces, nommé pilleum ou pilleus.

L'espèce décrite diffère de "*Lymnaea*" *amplecta* Gorjanović-Kramberger (1901: 136, pl. X, figs. 13-14), dont on ne connaît pas la spire, par les dimensions plus réduites par la hauteur proportionnelle-

ment plus petite, par l'ouverture allongée transversalement (dans le sens de la largeur).

Quant au développement de la coquille on remarque une première étape, de jeunesse, qui suit la protoconque, pendant laquelle l'aspect général est semblable à celui de *Velutinopsis velutina* et aussi à celui de *Velutinellus catinus*. Ce n'est qu'après cette étape que le bord postérieur du péristome commence à se développer plus rapidement, en dépassant la spire, dont les dimensions restent très réduites (Fig. 3, texte). Ainsi les stades adultes des deux espèces deviennent nettement différents, le dernier tour de *Velutinellus catinus* se développant moins rapidement en hauteur que celui de *V. pilleus*. La partie antérieure de la coquille se développe à une allure considérablement plus grande que la partie postérieure: les stries de croissance qui sont rapprochées se rejoignent en un même point dans la partie postérieure, au-dessous de la spire. Toutefois, à des distances presque égales il y a des plis mieux marqués; les plis rapprochés forment entre eux des angles de 25°-30° (Fig. 4A, texte). Dans la région latérale et postérieure on peut observer un sillon à peine visible, comme chez l'espèce précédente.

Gisement: Gravieres fossilifères du Méotien basal, dans le même niveau que

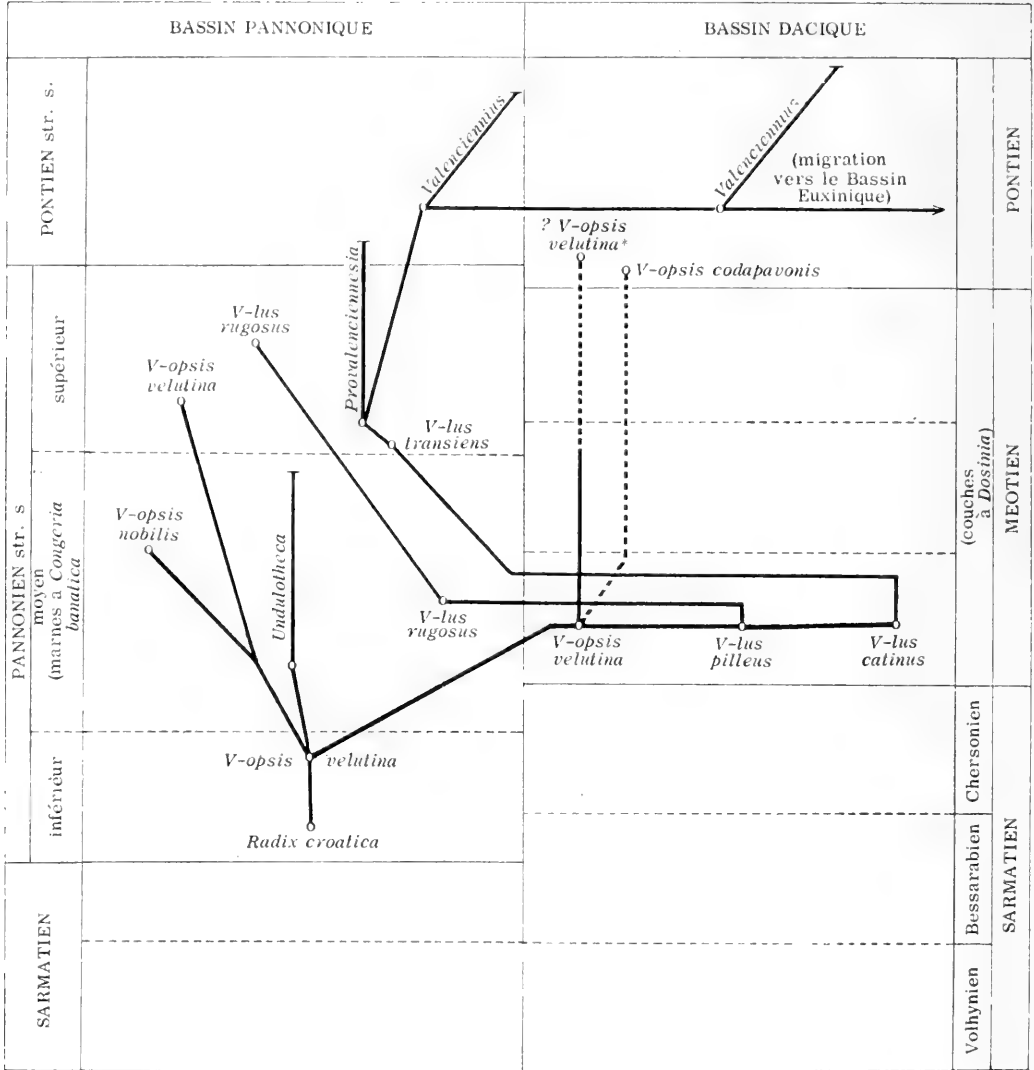
FIGS. 1-3. *Velutinopsis codapavonis* sp. n. Pontien inférieur, argiles marneuses; rive gauche de la vallée Coșuștea, a Ilovăț, au nord de Turnu Severin, Olténie [Fig. 1(2), Texte] (5x). FIG. 1. Holotype.

FIGS. 2-3. Paratypes.

FIGS. 4-5. *Velutinopsis velutina* Deshayes. Le vallon Fintinele, à Huent de la vallée Iazouștea; Crăgulești, au nord de Turnu Severin; Olténie [Fig. 1(1), texte] (2x). FIG. 4. Méotien inférieur, horizon a *Dosinia*: sables. FIG. 5. Méotien inférieur, horizon inférieur, a *Congeris* et *Teisseyreomya*; a, vue apicale; b, vue dorsale.

FIGS. 6-8. *Velutinellus pilleus* gen. n., sp. n. Méotien inférieur, horizon inférieur, a *Teisseyreomya* et *Congeris*. Le vallon Fintinele. FIG. 6. Holotype; a, vue dorsale; b, vue apicale; c, vue postérieure (2x). FIG. 7. Exemple jeune (10x). FIG. 8. Paratype; a, vue apicale; b, vue dorsale (2x).

FIGS. 9-12. *Velutinellus catinus* gen. n., sp. n. Même horizon, même gisement, FIG. 9. Holotype; a, vue dorsale; b, vue apicale; c, vue postérieure (2x). FIGS. 10-11. Paratypes; a, vue dorsale; b, vue ventrale (4x). FIG. 12. Exemple jeune; a, vue apicale; b, vue dorsale (5x).



\* Cette forme pourrait être une variété ou même une sous-espèce.

TABLEAU 1. Les relations phylogéniques problem de *Velutinellus* avec *Velutinopsis* et *Valenciennius*

*Velutinellus catinus* sp. n., à 1,5 m au-dessous du niveau a *Dosinia*. dans le vallon Fintinele, à l'ouest du village Crăgesti (Olténie).

DISCUSSION SUR LES RELATIONS PHYLOGENIQUES DE *VELUTINELLUS*

Mis a part les caractères morphologi-

ques qui caractérisent les différentes espèces, l'évolution des Lymnaeides est marquée, a partir de *Radix*, par la réduction de la spire et l'accroissement considérable du dernier tour, entraînant le développement du péristome qui s'évase. Nous avons nommé cette orthogenèse, qui conduit à *Valenciennius*, "évolution valencienne des Lymnaeïdes". *Radix kobelti* Brusina est un des nomæreux

exemples qui indiquent cette tendance, sans dépasser pour autant le cadre admis pour le genre.

A partir, probablement, de *Radix croatica* Gorjanovic-Kramberger (Moos, 1944) c'est un nouveau genre qui se détache, *Velutinopsis* (Tableau 1), dont l'unique représentant repéré jusqu'à présent dans le Bassin Dacique, *Velutinopsis velutina*, apparaît au Méotien inférieur, dans l'horizon antérieur à l'horizon à *Dosinia maeotica* (c'est à dire dans le "Susswasser Bank" des "Dosinien-Abteilungen" de Krejci Graf, 1926).

Du genre *Velutinopsis* se détache, dans le Bassin Pannonique, comme branche collatérale, *Undulotheca* Gorjanovic-Kramberger, 1923, dont le convergent est *Velutinopsis nobilis* Reuss. Cette branche ne continue pas l'évolution valencienne. Les formes d'*Undulotheca* atteignent rapidement des grandes dimensions, sans donner une trop grande variété morphologique; elles sont douées d'une ornementation de type *Valenciennius*, mais présentent une morphologie semblable à *Velutinopsis*. Cette branche s'éteint vite, vers la fin du Pannonien str. s., avant d'avoir pu traverser la barrière carpatique.

Le genre *Velutinellus* se détache de *Velutinopsis*, presque en même temps que *Undulotheca*, en suivant la ligne d'évolution valencienne des Lymnéides. Chez *Velutinellus*, le dernier tour, se développe encore plus; le bord postérieur du péristome débordé la spire, qui garde des dimensions insignifiantes par rapport au reste de la coquille. Les deux espèces daciques de ce genre (*V. pilleus* et *V. catinus*) ont été signalées toujours au Méotien inférieur, dans le même gisement que *Velutinopsis velutina*; elles sont les seules connues jusqu'à présent dans le Bassin Dacique. Dans le Bassin Pannonique on peut encore rapporter à ce genre quelques formes décrites antérieurement: "*Lymnaea*" *amplecta*, "*Velutinopsis*" *rugosa* et "*Velutinopsis*" *transiens*. De

celles-ci *Velutinellus rugosus* est presque contemporaine des espèces daciques, mais présente une morphologie un peu plus évoluée. Chez les formes extracarpatiques—*Velutinellus pilleus* et *V. catinus*—on observe aussi un très vague pli de la coquille, placé précisément là où, chez les formes actuelles de *Radix*, se trouve le pneumostome. Avec *Provalenciennisia* ce pli va s'accuser graduellement, jusqu'à des exagérations telles qu'on les trouve chez *Valenciennius*.

L'évolution ontogénique de *Velutinellus pilleus* prouve sa descendance directe de *Velutinopsis velutina*; dès ses premiers représentants, dont les caractères sont encore instables, se détache *Velutinellus catinus*, forme quelque peu plus évoluée. Il reste encore à élucider les relations philogéniques existant entre les formes daciques de *Velutinellus* et leurs vicariantes pannoniques. Il en est de même pour les rapports des formes pannoniques de *Velutinellus* avec *Provalenciennisia*, vu que tant *Velutinellus rugosus*, que *Velutinopsis nobilis*, qui ont été considérées comme étant sur la ligne directe d'évolution (Moos, 1944; Taktakischvili, 1967), ne semblent être que des formes extrêmes, qui ne sauraient aboutir au genre *Provalenciennisia*. Pourtant les données que nous possédons à ce sujet n'excluent pas la possibilité que *Provalenciennisia* soit dérivée des exemplaires daciques de *Velutinellus*, dont les caractères sont encore variables et qui auraient migré de l'est vers l'ouest.

Pour le moment, dans le Bassin Dacique reste à combler un hiatus entre les formes de *Velutinellus* du Méotien inférieur et celles de *Valenciennius* connues au Pontien inférieur. L'interruption est due, en premier lieu, à la barrière que constitue l'augmentation de la salinité durant la partie supérieure du Méotien inférieur, pour l'évolution de ces formes. C'est pourquoi les formes de transition doivent être recherchées dans le Bassin Pannonique,

où les conditions de salinité restent à peu près les mêmes. Les autres conditions de milieu diffèrent cependant, puisque le milieu sableux du Méotien dacique est remplacé par celui, vaseux, du Pannonien.

Nous ferons remarquer que, d'une manière générale, toutes les grandes formes de Lymnaeidae: *Undulotheca*, *Provalenciennesia*, *Valenciennius*, se rencontrent dans des dépôts argilo-marneux largement répandus dans la région sud-est du Bassin Pannonique durant le Pannonien et le Pontien et dans tout le Bassin Dacique, durant le Pontien. Ceci laisse supposer que ces mollusques se soient adaptés à ces conditions spéciales, i.e., à un bassin au fond recouvert de vase fine, imprégné d'eau, en développant un pied, dont la surface devait être assez large pour empêcher l'animal de s'envaser. La coquille, très mince et aplatie, mais de grandes dimensions, commence à s'onduler en devenant de la sorte plus résistante. Ainsi la zone sud-est du Bassin Pannonique, qui offre les conditions les plus propices au développement des grandes formes de Lymnéides, a joué pour elles le rôle de niche évolutive.

Grâce à l'évolution rapide de ces formes on a pu séparer plusieurs horizons dans les dépôts pannoniens et pontiens du secteur croate du Bassin Pannonique (Moos, 1944). On connaît déjà, dans le Bassin Pannonique, la corrélation existant entre les marnes à *Undulotheca* et *Congeria banatica* R. Hoernes, qui représentent le faciès de large (Beckenfacies) du Pannonien moyen, et les dépôts comportant la faune de Soceni (Fig. 1 (4), Texte), indiquant le faciès littoral (Randfacies). D'autre part certains éléments de la faune de Soceni, surtout des Congeries—*C. ramphophora*, *C. soceni* Jekelius, *C. politioanei* Jekelius (Kojumdieva, 1961, et données inédites de l'auteur)—sont connus dans le Méotien inférieur du Bassin Dacique, d'où la correspondance entre le Meotien inférieur et une partie

du Pannonien moyen (Tableau 1). On peut donc déduire que pendant que le genre *Undulotheca* se développait dans le Bassin Pannonique, comme branche collatérale, dans le Bassin Dacique apparaissaient les formes de *Velutinellus*. Celles-ci, dérivant de *Velutinopsis velutina* (immigrant pannonique dans le Bassin Dacique, tout comme les Congeries mentionnées), émigrent, en revenant vers l'ouest, où elles trouvent des conditions meilleures d'épanouissement, vu que l'augmentation de la salinité qui se produit au niveau de la faune à *Dosinia* empêche leur évolution sur place. Ces migrations ont été favorisées par le très riche échange de faunes, qui existaient dans cette région, entre les deux bassins, à une époque qui correspond à la plus grande expansion des dépôts pannoniens et méotiens. C'est de formes daciques de *Velutinellus* que dérive probablement *Velutinellus transiens* qui semble être à l'origine du genre *Provalenciennesia*.

L'apparition du genre *Valenciennius* dans le Pontien semble suivre de très près celle du genre *Provalenciennesia*, ayant dérivé des formes primitives de celui-ci. Cette question devra être analysée en détail, parallèlement aux études sur les représentants daciques de ce groupe.

## BIBLIOGRAPHIE

- DESHAYES, G. P., 1838, Description des coquilles fossiles recueillies en Crimée par M. de Verneuil et observations générales à leur sujet. *Mem. Soc. geol. Fr.*, ser. 1, 3: 37-69.
- GORJANOVIC-KRAMBERGER, K., 1901, Ueber die Gattung *Valenciennesia* und einige unterpontische Lymnaeen. Ein Beitrag zur Entwicklungsgeschichte der Gattung *Valenciennesia* und ihr Verhältnis zur Gattung *Lymnaea*. *Beitr. z. Pal. Oesterr.-Ung. u. des Orients*, 13: 121-140.
- GORJANOVIC-KRAMBERGER, K., 1923, Die Valenciennesiiden und einige andere Lymnaeiden der pontischen Stufe des Unteren Pliozans in ihrer stratigraphischen und genetischen Bedeutung. *Glasnik. hrv. prirod. Društva*, Zagreb, 35: 87-114.



- KOJUMDGIEVA, E., 1961, Etude paléontologique et biostratigraphique du Méotien inférieur de la Bulgarie du nord-ouest. *An. Dir. Gen. rech. geol.*, Sofia, **11** (1960): 139-155.
- KREJCI GRAF, K. & WENZ, W., 1926, Jungtertiäre Landschnecken aus Sudrumanien. *N. Jahrb. f. Miner. u. Geol.*, **55**(B): 53-65.
- MARINESCU, FL., 1964, Propuneri cu privire la orizontarea Pontianului din partea occidentala a Basinelui Getic (Propositions sur les zones du Pontien de la partie occidentale du Bassin Getique). *Acad. R. P. Rom., Stud. Cerc. Geol.*, **9**(1): 73-80. Bucarest.
- MARINESCU, FL., 1967, Observations sur le Pannonien de Caransebes. *Acad. R. P. Rom., Stud. Cerc. Geol.*, **12**(2): 465-469. Bucarest.
- MOOS, A., 1944, Neue Funde von Lymnaeiden, insbesondere von Valenciennesiiden im Pannon Kroatiens. *Vestnik drž. geol. Zavoda*, Agram, **B.** (2/3): 341-350.
- TAKTAKISCHVILI, I. G., 1967, *Historische Entwicklung der Familie Valenciennesiidae*. Tbilisi (Ed. Mitzinereba).
- WENZ, W., 1923, Gastropoda extramarina tertiaria. *Fossilium Catalogus I Animalia*, **21**: 1323-1337. Berlin.
- WENZ, W., 1942, Die Mollusken des Pliozans der rumanischen Erdöl-Gebiete als Leitversteinerungen für die Aufschluss-Arbeiten. *Senckenbergiana*, **24**: 1-293. Frankfurt.
- WENZ, W., 1959, Gastropoda. Teil 2, Euthy-neura, Lief. 1, (In: O. Schindewolf, *Handbuch der Paläozoologie*, Bd. 6), p 94-96. Berlin (Gebr. Borntraeger).

## ABSTRACT

*VELUTINELLUS*, A NEW FOSSIL GENUS, AND ITS RELATION TO  
*VELUTINOPSIS* AND *VALENCIENNIUS* (LYMNAEIDAE)

F. Marinescu

This note comprises the description of 4 fossil lymnaeids from beds on the eastern slopes of the southern Carpathians (Dacic Basin) in Oltenia, Roumania. These species are: *Velutinopsis velutina* Deshayes from the lower Meotian, a species not well known in Roumania, *Velutinopsis codapavonis* sp. n. from the lower Pontian, and 2 species of *Velutinellus* g. n., i.e., *V. catinus*, sp. n. (catinus=roman incenser) and *V. pilleus*, sp. n. (pilleus=distinctive cap of dacian nobles), also from the lower Meotian.

Characteristic for the genus *Velutinellus* is the great expansion of the peristome, which widely projects beyond the much reduced spire. The forms previously described under the names of "*Lymnaea*" *amplecta* Gorjanovic-Kramberger, *Velutinopsis rugosa* Gorjanovic-Kramberger and *V. transiens* Moos are here also assigned to *Velutinellus*.

The ontogenetic development of the shell of *Velutinellus* suggests that this genus derives from *Velutinopsis velutina* and that it is related to *Valenciennius* through *Provalenciennesia*. The presumed phyletic line, here designated as the "valencian evolutive line of the lymnaeids," is given as follows:

Radix → *Velutinopsis* → *Velutinellus* → *Provalenciennesia* → *Valenciennius*  
    ↘ *Undulotheca*

The author assumes that the panonic species *Velutinellus rugosus* and *V. transiens* originate from the forms described from the Dacic Basin. These have presumably emigrated into the Pannonic Basin on account of an increase in salinity in the Dacic Basin at the time of sedimentation of the layers containing *Dosinia*. The flat shape of the shell, characteristic for the genera *Undulotheca*, *Provalenciennesia* and *Valenciennius* is thought to represent an adaptation to the special conditions in a basin whose substrate consists of soft waterlogged mud.







## GENETIC STUDIES ON *BIOMPHALARIA GLABRATA*: TENTACLE AND EYE VARIATIONS

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### ABSTRACT

(With the technical assistance of James W. Merritt)

Selection, isolations, and self-fertilization through 7 generations of albino *Biomphalaria glabrata* (Basommatophora: Planorbidae) resulted in progressive increase to a relatively stable 60% frequency of progeny with tentacle variations indicating multifactor inheritance. At this frequency level progeny of snails with or without tentacle variations showed the same frequency of the character suggesting incomplete penetrance. Mating a tentacle variation albino with a normal strain black-eye and later with a normal strain wild type *B. glabrata* resulted in post-cross  $F_1$  progeny of the albino including tentacle variations. The post-cross  $F_1$  progeny of the black-eye and wild type mates all appeared normal, but when these were selfed, more than half produced offspring with tentacle variations. These results demonstrated genetic transmission of the character and suggested a maternal effect. The crosses revealed that the eyes were involved as well as the tentacles and that the character showed variable expressivity: double, branched, short, absent, or sack-like tentacles; double, absent, or displaced eyes.

The control of freshwater mollusks which serve as intermediate hosts of parasites such as the schistosomes involves many factors, one of the least understood being molluscan genetics. Newton (1953) demonstrated that susceptibility of *Biomphalaria* (= *Australorbis*) *glabrata* (Say) to infection with *Schistosoma mansoni* involves multifactor inheritance. Involvement of genetics in the tendency of *B. glabrata* to climb out of water and estivate, thus surviving drought and avoiding chemical molluscicides, was reported by Richards (1968). Occurrence of genetic resistance to chemicals in insect vectors of disease suggests the possibility of genetic resistance in mollusks also. Planning of experimental studies on mollusks and interpretation of results should take into account the possible influence of genetic factors.

Sturtevant (1923) and Boycott & Diver (1923) showed that sinistral coiling in *Lymnaea peregra* is a single-factor recessive

character with maternal inheritance. Crabb (1927) studied several morphological variations in freshwater snails, concluding from his results that the characters studied were not genetically determined. Newton (1954) demonstrated that albinism in *Biomphalaria glabrata* is genetically determined by a single recessive factor showing Mendelian inheritance. Richards (1967) has described a third pigmentation allele, "black-eye", dominant over albino but recessive to wild type pigmentation.

One of the characters studied by Crabb (1927) was forked tentacle in *Physa gyrina* and *Lymnaea stagnalis appressa*. Davis, Moose & Williams (1965) described a specimen of a hybrid *Oncomelania* with abnormalities of tentacles and eyes. Tentacle abnormalities are not uncommon in most freshwater snails, being generally attributed to disease, mechanical or chemical damage or irritation. Wong & Wagner (1956) observed tentacular branch-

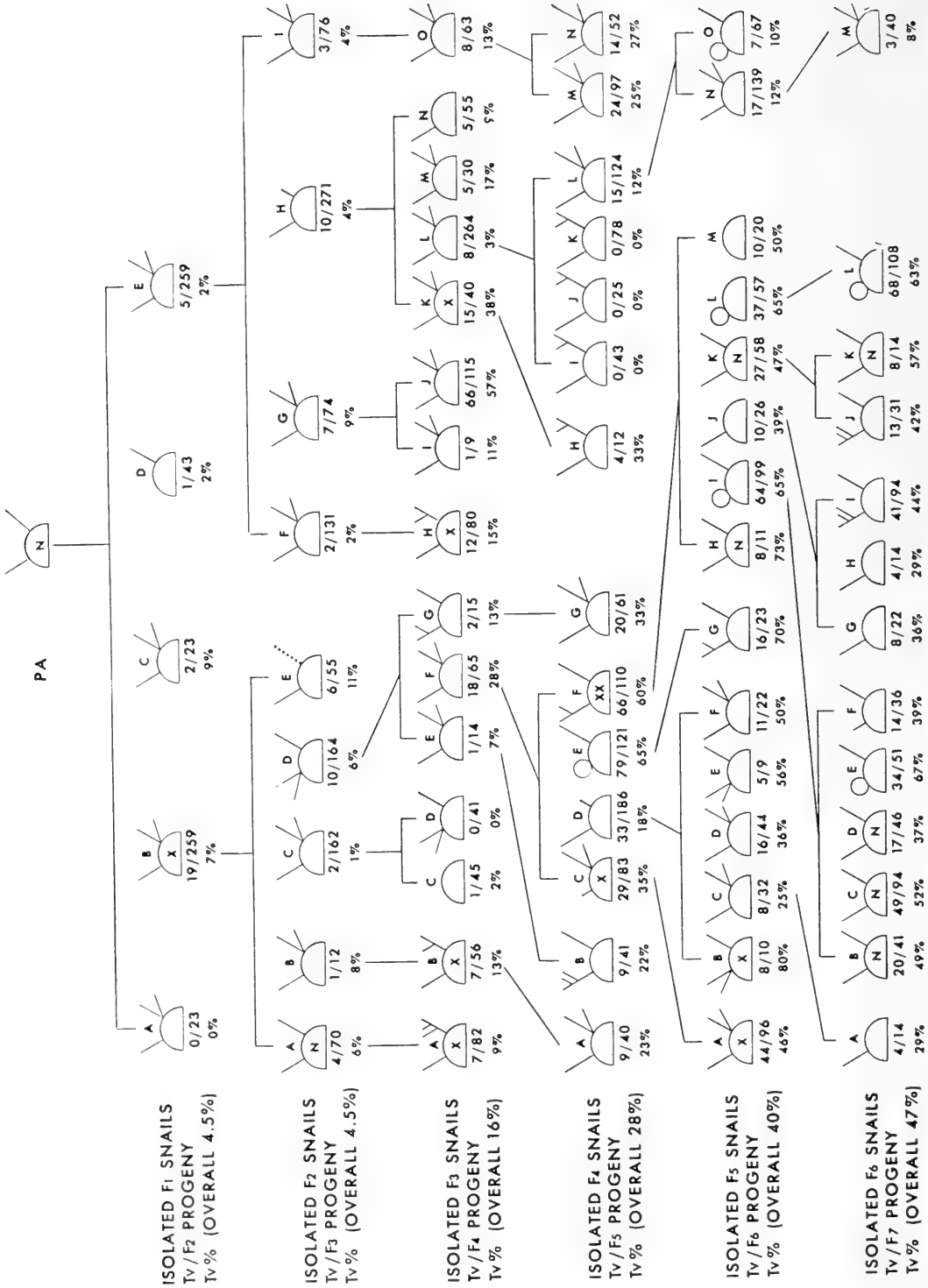


TABLE 1. Comparison of tentacle variation production; for all snail isolations for all progeny deriving from F<sub>4</sub>-f, and for a succession of isolations from F<sub>4</sub>-f of snails with normal phenotypes.

Generation (Fig. 1)	Average Of all isolations	Progeny deriving from F <sub>4</sub> -f	
		Average of all progeny	Succession of normal phenotypes
F <sub>4</sub>	16% Tv	F <sub>4</sub> -f	
F <sub>5</sub>	28% Tv	60% Tv	40% Tn (F <sub>5</sub> -k)
F <sub>6</sub>	40% Tv	58% Tv	47% Tv   53% Tn (F <sub>6</sub> -k)
F <sub>7</sub>	47% Tv	50% Tv	57% Tv   43% Tn (ave. F <sub>7</sub> -d, F <sub>7</sub> -e)
F <sub>8</sub>	50% Tv	50% Tv	53% Tv   47% Tn (ave. F <sub>8</sub> -a, F <sub>8</sub> -b)
F <sub>9</sub>	i *	i *	57% Tv   43% Tn

\* Insufficient isolations for comparisons.

ing in 4 specimens of *Oncomelania* in several thousand, and demonstrated it could be induced by ultraviolet light. The appearance of several young *Biomphalaria glabrata* with either double right or left tentacles among the offspring of an albino snail suggested inheritance might be involved and led to the studies reported here.

MATERIALS AND METHODS

Albino and wild type pigmented *Biom-*

*phalaria glabrata* descended from a cross between Brazilian albino and Puerto Rican wild type snails (Newton, 1955) and the "black-eye" mutant (Richards, 1967) were used in these studies. Snails were reared in 400 ml beakers with Petri dish covers, in aerated tap water, and fed Romaine lettuce.

Albino snails were reared in isolation and progeny were obtained by self-fertilization. Young snails with tentacle variations (Tv) and normal appearing

FIG. 1. Selections for tentacle variation production in albino *Biomphalaria glabrata* through 7 generations by isolation and self-fertilization. PA was the parent albino. Diagrams represent head and tentacles. "N" within the diagram indicates a normal appearing snail. "X" within the diagram indicates a snail mated after it had produced progeny by self-fertilization.





controls (Tn) were selected for isolation and rearing. Selection, isolated rearing, and self-fertilization were followed through 7 generations in appreciable numbers, a few snails being followed for several additional generations.

Albinos showing tentacle variations, following self-fertilization, were mated with either black-eye or wild type snails from normal strains. One of the  $F_1$  generation albinos was mated twice following self-fertilization, first to a black-eye, and later to a wild type snail. Snails were mated for one week, after which they were reisolated and their subsequent progeny followed. In the following, "A" indicates albino, "B" black-eye, and "C" wild type pigmentation.

## RESULTS

### Successive selections with isolations and self-fertilization

Results of selection, isolations, and self-fertilization through 7 generations are shown in Fig. 1. Tentacle variations occurred on either right, left, or both sides (Fig. 3A), including: double tentacles, branched tentacle, short tentacle, tentacle absent, or enlarged contractile sac. (It was not discovered that eye variations were also involved until later when matings with snails with pigmented eyes were performed). Tentacle variations were observed in 0% to 9% (avg. 4.5%) of the progeny of 5  $F_1$  snails; 1% to 11% (avg. 4.5%) of the progeny of 9  $F_2$  snails; 0% to 57% (avg. 16%) of the progeny of 15  $F_3$  snails; 0% to 65% (avg. 28%) of the progeny of 14  $F_4$  snails; 10% to 80% (avg. 40%) of the progeny of 15  $F_5$  snails; and 8 to 67% (avg. 47%) of the progeny

of 13  $F_6$  snails. The progressive and persistent increase in Tv frequency associated with selection suggested inheritance.

### Tentacle variations in progeny of normal appearing snails

Production of 6%  $F_3$  Tv progeny by  $F_2$ -a (Fig. 1), which appeared normal, was attributed to overlooking some slight abnormality in  $F_2$ -a. When normal  $F_5$ -h and  $F_5$ -K produced 73% and 47% Tv progeny, however, more "normal" snails were included in subsequent selections. The average Tv frequency in progeny of the 13 isolated  $F_6$  generation snails was 47%. Of the 13 snails the 4  $F_6$  Tn snails averaged 48% Tv progeny; the 9  $F_6$  Tv snails 46%. Beginning with  $F_5$ -K, data were obtained on 4 successive generations of "normal" isolated snails. The Tv progeny frequencies of these Tn snails are compared in Table 1 with the overall Tv frequencies of progeny of  $F_1$ -f, and with averages of Tv frequencies of all snails in each generation. Not shown in Fig. 1,  $F_7$ -d and  $F_7$ -e (13 Tv/27 and 22 Tv/39) and  $F_8$ -a and  $F_8$ -b (10 Tv/20 and 7 Tv/10) were averaged because of the small numbers.

### Matings to determine if transmission is genetic

Albino  $F_1$ -b with a double right tentacle, which produced by self-fertilization 7% Tv progeny, was mated with a Tn wild type hybrid (P-Ca-1). The post-cross  $F_1$  progeny of P-CA-1 (in C : A ratio 1 : 1) were all normal. Ten pigmented and 10 albino  $F_1$  offspring were isolated and reared. The pigmented snails produced, by self-fertilization, all Tn  $F_2$  progeny in 3 : 1 (total observed 579C : 201A) ratio.

FIG. 2. Diagram showing the results of mating an albino *Biomphalaria glabrata* ( $F_1$ -F in Fig. 1) with tentacle variation, first with a normal black-eye *B. glabrata*, and 6 weeks later with a normal wild type *B. glabrata*. Diagrams with fine lines and without eyes indicated represent albinos, diagrams with heavy lines and showing eyes represent black-eyes, and diagrams with shading and eyes represent wild type snails.

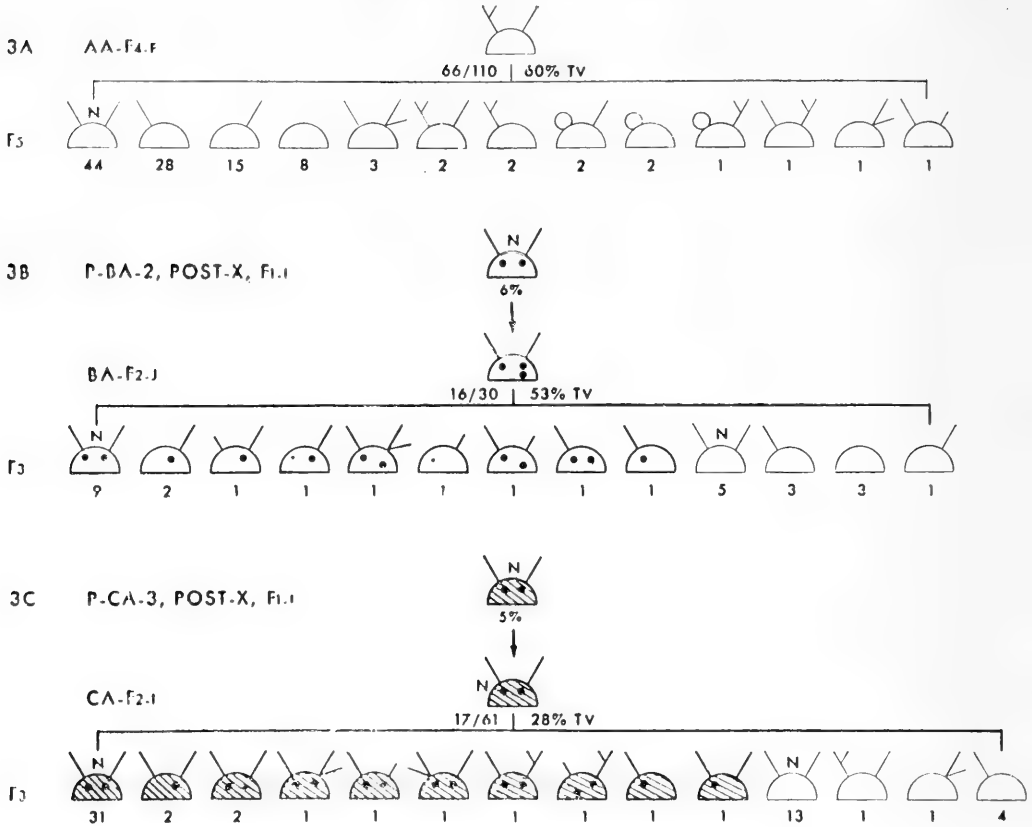


FIG. 3. Examples of the range of expressivity of tentacle and eye variations among progeny of 3 individual isolated *Biomphalaria glabrata* reproducing by self-fertilization. Albinos, black-eyes, and wild type snails are represented as in Fig. 2. 3A shows the offspring by self-fertilization of albino F<sub>4</sub>-f (Fig. 1). 3B shows the offspring of black-eye F<sub>2</sub>-j from the first cross in Fig. 2. 3C shows the offspring of wild type F<sub>2</sub>-i from the second cross in Fig. 2 (F<sub>3</sub>-i, and F<sub>3</sub>-l in Fig. 2 were snails produced by F<sub>2</sub>-i after the tabulation summarized in Fig. 3C had been made).

The isolated albinos produced 607 observed progeny, all Tn albinos.

The above cross, involving an albino with low Tv frequency in its offspring, failed to demonstrate transmission of the character in cross-fertilization. Subsequently albino F<sub>3</sub>-f, with branched left tentacle and with 60% Tv frequency in its progeny by self-fertilization, was mated twice (Fig. 2). The first mating was with a black-eye hybrid (P-BA-2) which had produced all Tn black-eye (17B) and albino (6A) progeny in 3 : 1 ratio by self-fertilization. The albino and black-

eye parents both produced F<sub>1</sub> progeny in 1 : 1 ratio (B : A) after mating, indicating reciprocal cross-fertilization.

Albino F<sub>4</sub>-f produced 103A:97B post-cross F<sub>1</sub> progeny with 29 (14%) showing tentacle variations. Eye abnormalities were also observed in black-eye F<sub>1</sub> snails. These were usually associated with tentacle variations, both apparently being manifestations of the same genetic factors influencing development. Eye abnormalities, on either or both sides (Figs. 2, 3B, and 3C), included: double eyes, eye absent, eye enlarged or reduced,

TABLE 2. Frequency of tentacle variations in progeny of abnormal snails before and after mating with normal snails.

Normal mate			Albino with tentacle variation			
Genotype	Pre-cross progeny; Tv frequency	Snail No. (Fig. 1)	Tentacle variations in pre-cross progeny by self-fertilization		Tentacle variations in post-cross progeny by cross-fertilization	
			Tv/total progeny	Tv %	Tv/total progeny	Tv %
CA	0% ×	F <sub>3</sub> -a	7/82	9%	5/56	9%
CB	0% ×	F <sub>3</sub> -b	7/56	13%	13/153	9%
CB	0% ×	F <sub>3</sub> -h	12/80	15%	7/78	9%
BA	0% ×	F <sub>3</sub> -k	15/40	38%	1/90	1%
BA	0% ×	F <sub>4</sub> -c	29/83	35%	11/88	13%
BA	0% ×	F <sub>4</sub> -f	66/110	60%	29/200	14%
CB	0% ×	F <sub>5</sub> -a	44/96	46%	7/97	7%
CB	0% ×	F <sub>5</sub> -b	8/10	80%	19/114	17%
Totals		8	188/557	34%	92/876	11%

eye displaced forward or backward. A series of post-cross F<sub>1</sub> offspring were isolated, those that produced F<sub>2</sub> progeny by self-fertilization being shown in Fig. 2. Two of 6 F<sub>1</sub> Tv snails produced F<sub>2</sub> Tv progeny (14% and 3%); 2 of 9 F<sub>1</sub> Tn snails produced F<sub>2</sub> Tv progeny (1% and 4%).

All the post-cross F<sub>1</sub> progeny (68B:62A) of P-BA-2 appeared normal. Nine of 17 isolated F<sub>1</sub> Tn snails which produced F<sub>2</sub> progeny by self-fertilization produced F<sub>2</sub> Tv snails in frequencies ranging from 2% to 14%. This indicated the tentacle and eye variations were genetically controlled and had been transmitted from F<sub>4</sub>-f by cross-fertilization.

Six weeks after the first cross F<sub>4</sub>-f was mated with a Tn hybrid wild type pigmented snail P-CA-3. P-CA-3 has produced 55C:6A F<sub>1</sub> progeny by self-fertilization. With the numbers involved, the departure from the expected 3 : 1 ratio is not unusual and still demonstrated the dominance of the gene for pigmentation. One of these F<sub>1</sub> snails had an abnormal tentacle. Whether this was genetic or due to mech-

anical or other cause could not be determined, since it failed to produce viable offspring. Both F<sub>4</sub>-f and P-CA-3 produced F<sub>1</sub> progeny in 1 : 1 (C : A) ratio after mating, indicating reciprocal cross-fertilization.

Albino F<sub>4</sub>-f produced 39A:33C post-cross F<sub>1</sub> progeny, 36 (50%) with tentacle (or eye) variations. Five of 9 F<sub>1</sub> Tv snails isolated produced F<sub>2</sub> Tv progeny in frequencies ranging from 2% to 11%; 2 of 8 F<sub>1</sub> Tn snails produced F<sub>2</sub> Tv progeny 2% to 4%.

All the post-cross F<sub>1</sub> progeny (26C:23A) of P-CA-3 appeared normal. Fourteen of 19 F<sub>1</sub> Tn snails isolated produced F<sub>2</sub> Tv progeny by self-fertilization in frequencies ranging from 2% to 24%.

A limited number of snails from both crosses were followed, by isolation and self-fertilization, through additional generations. Although Tv frequencies varied there was a general increase. Twenty-one of 37 F<sub>9</sub> snails followed produced F<sub>3</sub> Tv progeny in frequencies ranging from 0% to 53%; and 19 of 23 F<sub>3</sub> snails

TABLE 3. Comparison of tentacle variations in progeny before and after mating of snails all with high Tv production.

Parent pigment genotype	Pre-cross F <sub>1</sub> progeny by self-fertilization		Post-cross F <sub>1</sub> progeny by cross-fertilization		
	Tv/total	Tv %	Pigment ratio	Tv/total	Tv %
<i>Cross 1</i>					
BA	16/30	53%	3B:3A	5/6	83%
AA	16/37	43%	16B:18A	18/34	53%
Totals	32/67	48%		23/40	58%
<i>Cross 2</i>					
CC	*	41%	died		
AA	10/20	50%	all C	27/44	62%

\*Numbers not available.

produced F<sub>1</sub> Tv progeny in frequencies ranging from 0% to 68%.

#### Effect of mating on tentacle variations production

Albino F<sub>1</sub>-f produced 60% Tv progeny by self-fertilization; only 14% after mating with P-BA-2 (0% Tv progeny by self-fertilization). Comparable results were obtained in 7 other matings as shown in Table 2. The albino parents involved in crosses are indicated by "x"s in Fig. 1. Tv frequencies in their pre-cross progeny ranged from 9% to 80% (avg. 34% based on snail numbers). All produced mixed phenotype post-cross F<sub>1</sub> progeny in 1:1 ratios indicating cross-fertilization, with Tv frequencies ranging from 1% to 17% (avg. 11%).

Two crosses were made in each of which both mates had produced high % Tv progeny by self-fertilization. The results are shown in Table 3. In the first cross a BA hybrid producing 53% Tv progeny by self-fertilization was mated with an albino producing 43%. Post-cross pigmentation ratios indicated reciprocal cross-fertilization. Post-cross %

Tv progeny increased for both snails. The second cross was between a CC and an AA with pre-cross Tv progeny 41% and 50% respectively by self-fertilization. The wild type snail died after mating without laying any eggs. The albino produced all pigmented post-cross progeny with 62% Tv offspring.

#### DISCUSSION

The progressive increases in frequency of Tv progeny with successive generations of selection and self-fertilization (Fig. 1) indicate inheritance of the characters. Increase by steps through several generations suggests multifactor inheritance. In the more successful series such as that leading to F<sub>4</sub>-f, the major steps appear to be approximately 3X increases. Matings with normal snails producing 0% Tv in their pre-cross progeny resulted in an average decrease in the post-cross Tv progeny of the Tv parents to 1/3 the pre-cross frequency (Table 2). These results suggest a genetic mechanism rather than cytoplasmic inheritance or infection (viral or bacterial).



FIG. 4. Snail with double right tentacle.



FIG. 5. Snail with double right tentacle and right eye displaced backward.

Although some of the series shown in Fig. 1 continued to produce variable and low Tv frequencies as long as followed, the progeny derived from  $F_3$ -f (28%) never dropped below 18% Tv production. This series appeared to reach a relatively stable plateau of Tv frequency production of about 50-60%. The few selections followed for several generations beyond those included in Fig. 1 average 50-60%. Three high frequencies ( $F_5$ -b, 80%;  $F_5$ -g, 70%; and  $F_5$ -h, 73%) are based on small numbers and are not significant. None of the snails was observed to produce 100% Tv progeny. Frequencies shown are conservative, however, since minor tentacle variations might be overlooked and eye variations were not included in the albino series.

Two crosses between snails with pre-cross Tv progeny near 50% resulted in post-cross Tv progeny production as high or higher than before mating (Table 3).

Whatever the gene combination involved consists of, it apparently exerts its influence in embryonic development and results in a variable "expressivity" as illustrated in Figs. 3A, 3B, and 3C. Selections of a

single variation, such as double right tentacle, through a series of generations resulted in increasing Tv frequencies but the expression of tentacle abnormalities continued to be variable. The frequent occurrence of an enlarged contractile sac in place of a tentacle (usually on the left side) was an interesting expression of the Tv character. Circulation of hemolymph in the extension of the hemocoel into a normal tentacle may be observed to be aided by peristaltic contractions of the tentacle. The contractile sac appeared to be a shortened and expanded tentacle with rhythmic contractions forcing the hemolymph, red in the case of *Biomphalaria glabrata*, in and out of the sac.

As shown in Table 1, the progeny derived from snail  $F_3$ -f (60% Tv production) through 3 succeeding generations continued to average 50% or more Tv production. Selections of normal appearing snails for 4 succeeding generations from  $F_4$ -f continued to produce Tv frequencies comparable to, or slightly higher than, the Tv snails in the same generations. This suggests that these Tn snails might be carrying the same

genetic composition as  $F_1$ -f and its Tv progeny, and this genetic composition might represent a homozygous condition with incomplete (50-60%) penetrance of the phenotypic expressions.

In both of the matings with  $F_1$ -f, the post-cross  $F_1$  progeny of P-BA-2 and P-CA-3 all appeared normal while some of the post-cross progeny of  $F_1$ -f in each case showed tentacle and eye variations suggesting a maternal effect. As many (actually more) of the isolated post-cross  $F_1$  snails of P-BA-2 and P-CA-3 produced Tv progeny as the post-cross  $F_1$  snails from  $F_1$ -f. This supports the suggestion that maternal inheritance may be involved in this character, as in reverse coiling in snails (Sturtevant, 1923; Boycott & Diver, 1923).

In his attempts to demonstrate inheritance of characters in snails, Crabb (1927) concluded: "The only instance in all the cultures which suggested inheritance of any of the distinguishing characters was that of an  $F_1$  *Physa gyrina* which had a prong on the medial side of its right tentacle near the tip, as had its mother, but it also had a prong on the medial side of the left tentacle near the base, which did not occur in the mother." If the 3 suggested phenomena in tentacle variation inheritance (variable expressivity, incomplete penetrance, and maternal inheritance) occur in other genetic characters in mollusks, failure to recognize these complications could lead to erroneous conclusions.

The location of abnormalities in the head region, progressive response to selection, variable penetrance and expressivity, abnormalities in progeny of normal appearing parents, and suggestion of maternal effect are strikingly parallel to the tumorous head condition in *Drosophila melanogaster* (Gardner & Ratty, 1952; Gardner & Woolf, 1949).

The phenomena observed in tentacle variation inheritance in *Biomphalaria*

*glabrata*, and the fact that the inheritance apparently has a multifactor basis, complicate the use of the character as a genetic marker. The information provided by this inheritance, however, may be helpful in studies on other characters in mollusks, such as infectivity for various parasites and resistance to chemical molluscicides. Some of the snails with one tentacle missing showed a tendency to circle in the direction of the missing tentacle. In physiological studies it might be useful to compare reactions to light, chemicals, etc., of normal snails and snails with one tentacle or one eye missing.

#### LITERATURE CITED

- BOYCOTT, A. E. & DIVER, C., 1923, On the inheritance of sinistrality in *Limnaea peregra*. *Proc. Roy. Soc. Lond. B*, 95: 207-213.
- CRABB, E. D., 1927, Genetic experiments with pond snails *Lymnaea* and *Physa*. *Amer. Naturalist*, 61: 54-67.
- DAVIS, G. M., MOOSE, J. W. & WILLIAMS, J. E., 1965, Abnormal development in a hybrid *Oncomelania* (Gastropoda; Hydrobiidae). *Malacologia*, 2: 209-217.
- GARDNER, E. J. & RATTY, F. J., 1952, Penetrance and expressivity of tumorous head in *Drosophila melanogaster* and relative viability of flies carrying tumorous head genes. *Genetics*, 37: 49-61.
- GARDNER, E. J. & WOOLF, C. M., 1949, Maternal effect involved in the inheritance of abnormal growths in the head region of *Drosophila melanogaster*. *Genetics*, 34: 573-85.
- NEWTON, W. L., 1953, The inheritance of susceptibility to infection with *Schistosoma mansoni* in *Australorbis glabratus*. *Exp. Parasit.*, 2: 242-257.
- NEWTON, W. L., 1954, Albinism in *Australorbis glabratus*. *Proc. helminth. Soc. Wash.*, 21: 72-74.
- NEWTON, W. L., 1955, The establishment of a strain of *Australorbis glabratus* which combines albinism and high susceptibility to infection with *Schistosoma mansoni*. *J. Parasit.* 41: 526-528.
- RICHARDS, C. S., 1967, Genetic studies on *Biomphalaria glabrata* (Basommatophora: Planorbidae), a third pigmentation allele. *Malacologia*, 5: 335-340.
- RICHARDS, C. S., 1968, Aestivation of *Biomphalaria glabrata* (Basommatophora: Planor-

bidæ): Genetic studies. *Malacologia*, 7: 109-116.

STURTEVANT, A. H., 1923, Inheritance of direction of coiling in *Limnaea*. *Science*, 58: 269-270.

WONG, L. W. & WAGNER, E. D., 1956, Some effects of ultra-violet radiation on *Oncomelania nosophora* and *O. quadrasii*, snail intermediate hosts of *Schistosoma japonicum*. *Trans. Amer. micro. Soc.*, 75: 204-210.

## RESUME

### GENETIQUE DE *BIOMPHALARIA GLABRATA*: VARIATIONS DES TENTACULES ET DES YEUX

C. S. Richards

La sélection, l'isolement et l'autofécondation pendant 7 générations de *Biomphalaria glabrata* albinos, aboutit à l'augmentation progressive, jusqu'à une fréquence relativement stable de 60% de descendants qui ont des variations du tentacule, ce qui indique une hérédité multifactorielle. A ce niveau de fréquence les descendants de ces mollusques, avec ou sans variations du tentacule, montrent la même fréquence du caractère, ce qui suggère une expressivité partielle. En croisant un albinos à variation tentaculaire avec des individus normaux à yeux noirs et, plus tard, avec des individus normaux du type sauvage de *B. glabrata*, on obtient des descendants post-F<sub>1</sub> d'albinos, comportant des variations tentaculaires. Les descendants post-F<sub>1</sub> des hybrides d'yeux noirs et de types sauvages sont tous normaux, mais lorsque ceux-ci sont autofécondés, plus de la moitié donne naissance à des variations du tentacule. Ces résultats prouvent la transmission génétique du caractère et suggèrent une influence maternelle. Les croisements révèlent que les yeux sont impliqués aussi bien que les tentacules et que le caractère montre de multiples aspects: doubles, branchus, courts, absents ou en saccule pour les tentacules; doubles, absents ou déplacés pour les yeux.

## RESUMEN

### GENETICA DE *BIOMPHALARIA GLABRATA*: VARIACION EN OJOS Y TENTACULOS

C. S. Richards

Selección, aislamiento y autofertilización a través de 7 generaciones de ejemplares albinos de *Biomphalaria glabrata*, resultaron en un aumento progresivo hacia una progenie estable, con frecuencia relativa de 60% con variaciones de tentáculos, indicando factores hereditarios múltiples. A este nivel de frecuencia, la progenie de los caracoles con o sin variación de tentáculo, mostraron la misma frecuencia del carácter, sugiriendo penetración incompleta. Apareando un ejemplar albino de *B. glabrata* de tentáculo variable, con uno de cepa normal de ojos negros, y más tarde con otra normal de tipo silvestre, el resultado fué de F<sub>1</sub> caracoles albinos que incluían variaciones tentaculares. La progenie F<sub>1</sub> de la cruce de tipos de ojos negros con los de tipo silvestre pareció normal, pero cuando estos individuos se autofertilizaron, más de la mitad produjeron descendientes con variaciones en los tentáculos, y en ambas variaciones de ambas maneras: tentáculos dobles, ramificados, cortos, ausentes o saculares; ojos dobles, ausentes, o desplazados.

## АБСТРАКТ

ГЕНЕТИКА *BIOMPHALARIA GLABRATA*: ИЗМЕНЧИВОСТЬ  
ЩУПАЛЕЦ И ГЛАЗ

Ч. С. РИЧАРДС

Селекция, изоляция и самооплодотворение в течение 7 поколений альбиносов *Biomphalaria glabrata* проявились в постепенном увеличении (вплоть до относительной стабильности около 60% частоты встречаемости) поколений с изменчивостью щупалец. Это указывает на наличие полифакториальной наследственности. При такой частоте встречаемости количество потомства и моллюсков, обладающих или не обладающих изменчивостью щупалец, имели одинаковую частоту встречаемости, что заставляет предполагать неполное проникновение. Скрещивание штаммов альбиносов, имеющих изменчивость щупалец с нормальными черноглазыми популяциями, а потом с нормальными дикими популяциями *B. glabrata*, давали в последующем поколении  $F_1$  альбиносов, имевших изменчивость щупалец. Последующее скрещивание из поколения  $F_1$  черноглазых с дикими формами дало нормальных с виду моллюсков, но когда эти последние были смешаны, то более половины из них дали потомство с изменчивостью щупалец.

Эти результаты показали на генетическую передачу характера и предполагают наличие скрещивания. В результате последнего оказалось, что глаза моллюсков, также как и щупальца, охвачены изменчивостью, характер которой выражается весьма различно: щупальца были двойные, разветвленные, короткие, мешковидные или вовсе отсутствовали; глаза-двойные, смещенные или, их не было.



## GENETIC STUDIES ON *BIOMPHALARIA GLABRATA*: MANTLE PIGMENTATION

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### ABSTRACT

Black mantle pigmentation in *Biomphalaria glabrata* was studied microscopically and genetically. Self-fertilization of isolated snails through several generations was employed to select for pigment variations. The basic pigment types (wildtype, blackeye and albino) were used as markers in crossing experiments.

Black mantle pigment granules occur in *Biomphalaria glabrata* in 2 general types of distribution; diffuse, and in localized groups of cells forming discrete spots. Selection resulted in true breeding spotted and unspotted stocks.

Crosses between spotted and unspotted stock snails produced spotted F<sub>1</sub>s. Although albinos could not produce black pigment, they transmitted the character for spotted or unspotted mantle.

*Biomphalaria glabrata* in collections from various field localities shows a considerable range of variation in patterns of mantle pigmentation (Richards & Ferguson, 1965). Little is known of the roles of environmental conditions, genetics, or both in this pigment variation. Newton (1954) and Paraense (1956) suggested that the pigment variation was probably influenced by multifactorial genetics. Mantle pigment patterns have been used as characters in descriptions of many planorbid snail species. It is pertinent from a systematic standpoint to know to what extent these patterns are stable or to what extent they vary within a species such as *B. glabrata*.

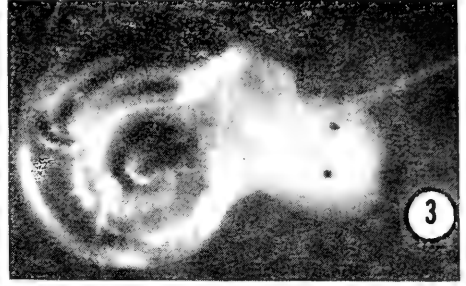
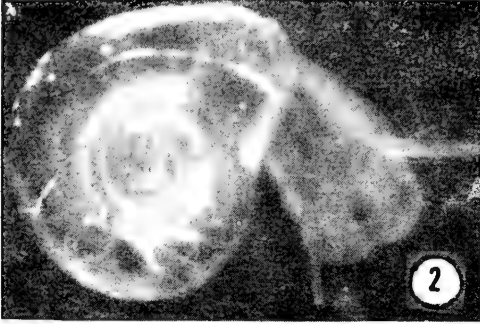
The relative transparency of albino *Biomphalaria glabrata* makes possible observations *in vivo* of migration and development of parasites, normal organ development in the snail host, and pathology in infected hosts. In experimental studies where it is desired to compare host-parasite relations in albino and pigmented snails, it would be useful to

employ "pigmented" strains in which the mantle pigment was so restricted as to permit *in vivo* observations. Such strains would be of particular value in species in which albinos are not available.

If mantle pigment pattern variation is genetically determined, such visible variation may be linked with physiological factors such as susceptibility to parasite infection, resistance to molluscicides, etc. Observations of pigment variations in the course of studies on estivation in *Biomphalaria glabrata* (Richards, 1968) led to the following studies.

### METHODS

The albino (A) strain of *Biomphalaria glabrata* developed by Newton (1955), the blackeye (B) mutant of that albino strain (Richards, 1967), and a wild type strain (C) of the same origin as the albino strain were used. Snails were reared in 400 ml and 250 ml beakers with Petri dish covers, and fed Romaine lettuce. Selected young snails were isolat-



**A** = ALBINO



**BU** = UNSPOTTED BLACKEYE



**BS** = SPOTTED BLACKEYE

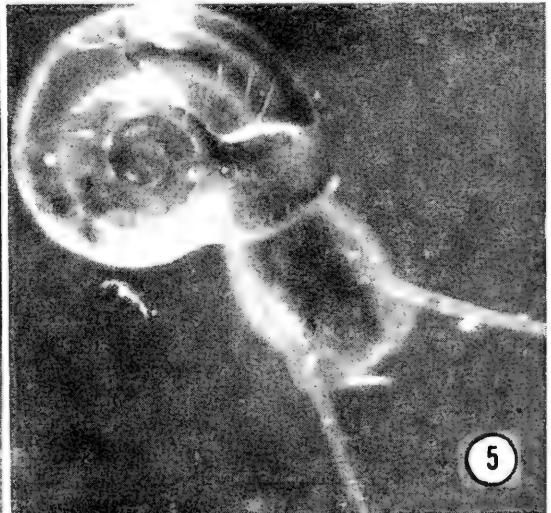


**CU** = UNSPOTTED WILD TYPE



**CS** = SPOTTED WILD TYPE

①



ed and reared to obtain progeny by self-fertilization. Mature snails were mated for one week and re-isolated to obtain progeny by cross-fertilization.

## RESULTS

### Descriptions of black pigmentation

Pigment types of *Biomphalaria glabrata* are shown diagrammatically in Fig. 1. Albino *B. glabrata* lack black pigment (Fig. 2); black eye snails (Figs. 3, 4) have variable black mantle pigmentation and pigmented eyes but are deficient in a black pigmentation typical of wild type strains in head and foot and mantle collar; and wild type snails (Figs. 5, 6) have black eyes, black pigmentation in head and foot and mantle collar (Fig. 7, 8) and variable black mantle pigmentation. Black mantle pigmentation in black eye and wild type snails is of 2 types; diffuse, background pigmentation (Fig. 9); and discrete spots of varying size, shape, and distribution (Figs. 10, 11). Diffuse pigmentation is generally distributed throughout the mantle in some snails, restricted to limited areas in some, and absent in others. Pigment spots vary from black to pale gray and are numerous and distributed throughout the mantle in some snails, range through decreasing degrees of distribution to the condition of a few spots over the kidney, and in some snails are lacking.

Diffuse pigmented areas in *Biomphalaria glabrata* show scattered, small, spherical, black granules in epithelial cells (Fig. 9). Similar-appearing black granules are concentrated in groups of epithelial cells to form pigment spots in the mantle (Figs. 10, 11). Spots vary in shape: round, irregularly shaped, elongate trans-

verse stripes, or coalescence of spots to form large irregular pigmented areas (Harry & Hubendick, 1964). In completely spotted snails, the spots are typically evenly spaced but not in regular rows. When spotting is incomplete: absence of spots is first evident in the mantle area to the left of the kidney, then on the inner right side, the most consistent areas to have spots being over the kidney and on the mantle collar.

In the head and body and collar of wild type snails the cells with concentrated pigment granules are primarily in the connective tissue area beneath the epithelium (Fig. 8), and may be rather evenly distributed among cells with few or no pigment granules giving a peppered appearance (Fig. 7).

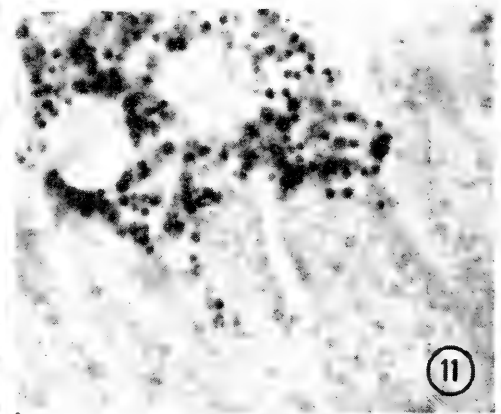
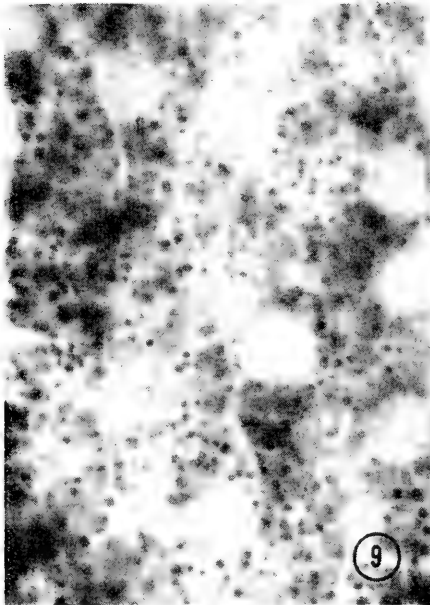
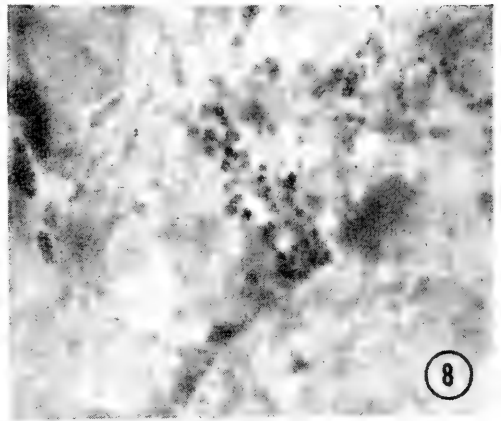
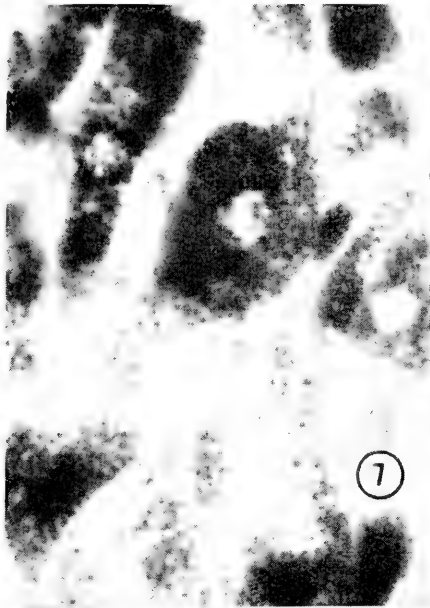
### Selection for diffuse black mantle pigmentation

Selection failed to produce true breeding strains for diffuse pigmentation. Strains were obtained predominantly with and predominantly lacking diffuse pigment. These differences were not constant, however, apparently being influenced by other factors in addition to genetics. Some snails developed diffuse mantle pigment soon after hatching. In other snails diffuse pigment was not evident in juveniles but developed as they grew older. In some snail clones from a single parent by self-fertilization, individuals isolated while young and reared singly remained free of diffuse pigmentation while the crowded snails not isolated developed diffuse pigmentation.

### Selection for spotted and unspotted mantle strains by isolation and self-fertilization

Isolations of selected wild type snails

FIG. 1. Diagram of 5 pigment types in *Biomphalaria glabrata*. Figs. 2-6. Photographs of 5 pigment types taken at 12x. Fig. 2, albino; Fig. 3, unspotted blackeye; Fig. 4, blackeye with spotted mantle but deficient in black pigment in collar and body; Fig. 5, wild type with black pigment in collar and body but lacking mantle spots; Fig. 6, spotted wild type.



FIGS. 7-11. Photomicrographs of *B. glabrata* taken at 1000 $\times$  magnification. Fig. 7, Black pigment granules in cells of head of wild type *B. glabrata* showing discontinuous distribution of pigment, giving stippled or "peppered" appearance; Fig. 8, Black granules in pigment cell in the sub-epithelial connective tissues of the mantle collar of a wild type snail; rod-shaped bodies are golden-brown pigment granules occurring in all 5 pigment types; Fig. 9, Diffuse mantle pigmentation, showing scattered black granules, occurring in some wild type and blackeye snails; white circular areas are nuclei of epithelial cells; Fig. 10, Mantle spot in wild type snail, consisting of 4 epithelial cells with concentrated black pigment granules; Fig. 11, two cells of mantle spot in blackeye snail, showing concentrated black granules and clear nuclei.

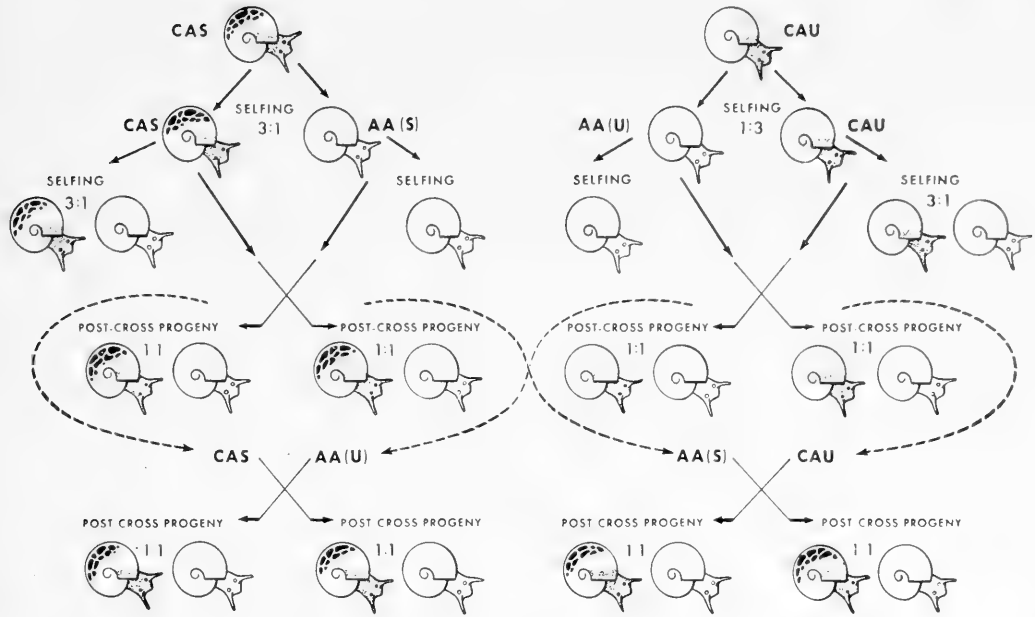


FIG. 12. Composite diagram of crosses illustrating transmission of mantle pigment pattern.

through several generations resulted in 2 strains; one breeding true for extensive spotting (S) (Fig. 6), the other unspotted (U) (Fig. 5). The unspotted strain provided snails with almost as clear visibility through the mantle as albinos. Occasionally an individual in this strain developed a few pale spots over the kidney. Two similar blackeye strains (Figs. 3, 4) were derived by selection.

Transmission of spotted mantle pigmentation by crossing (Fig. 12)

In selecting for spotted (S) and unspotted (U) strains enough isolations were followed in each generation to insure inclusion of heterozygotes (CA) so that albinos would be available.

Wild type snails from the S strain were reared in isolation and allowed to reproduce by self-fertilization. CAS represents several such snails, producing progeny in 3:1 phenotypic ratio (CS:A-), the C offspring being spotted. CAS was then mated with AA(S), an albino from an

S strain colony. After re-isolation both CAS and AA(S) produced progeny in 1:1 phenotypic ratio (CS:A-), demonstrating reciprocal cross-fertilization and with the C offspring from both parents spotted.

Wild type snails from the U strain were reared in isolation and allowed to reproduce by self-fertilization. CAU represents several such snails, producing progeny in 3:1 phenotypic ratio (CU:A-), the C offspring being unspotted. CAU was then mated with AA(U), an albino from a U strain colony. After re-isolation both CAU and AA(U) produced progeny in 1:1 phenotypic ratio (CU:A-), demonstrating reciprocal cross-fertilization and with the C offspring from both parents unspotted. Totals counted from 5 such crosses were as follows: AA(U) progeny 35CAU: 42AA, CAU progeny 50CAU: 45AA.

When a CAS was mated with an AA(U), both CAS and AA(U) produced post-cross progeny in 1:1 phenotypic ratio

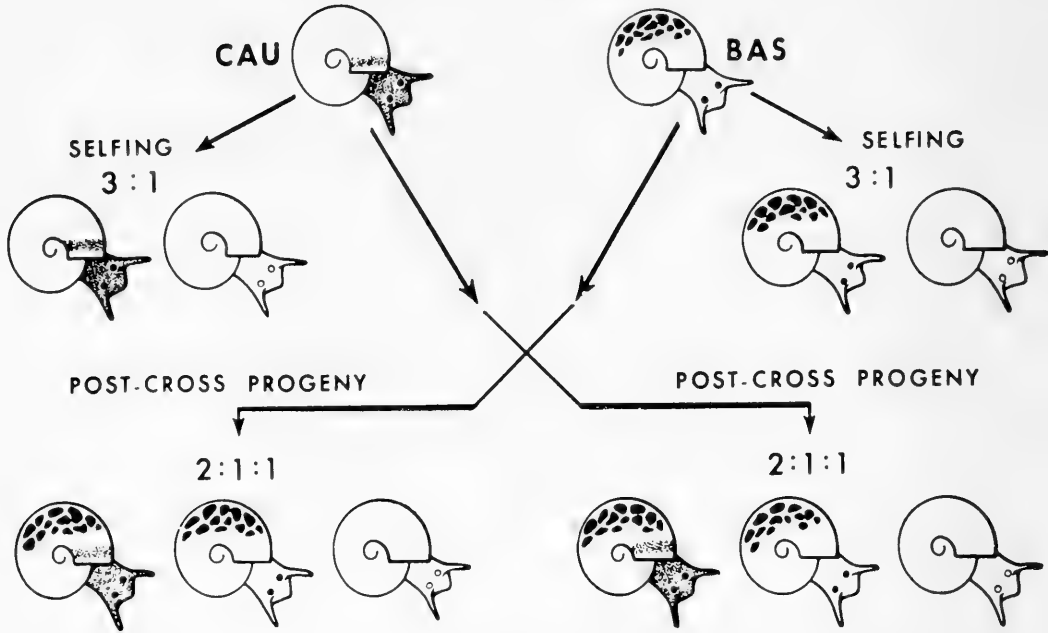


FIG. 13. Diagram of cross between unspotted wild type and spotted black-eye *B. glabrata*.

(CS:A-), the C offspring being spotted. In some of such matings the AA(U) was first mated with a CAU; one AA(U), for example, producing post-cross progeny 16 CAU: 11 AA. After 6 weeks the same AA(U) was mated with a CAS; the AA(U) then producing post-cross progeny 26 CAS: 28AA.

When a CAU was mated with an AA(S) both CAU and AA(S) produced post-cross progeny in 1:1 phenotypic ratio (CS:A-), the C offspring being spotted. Totals counted from three such matings were as follows: AA(S) progeny 39 CAS; 40 AA, CAU progeny 23 CAS: 17 AA. In some of these matings, the CAU was first mated with an AA(U), both parents producing post-cross progeny 1:1 with the C offspring unspotted. When the same CAU was subsequently mated with an AA(S), both parents produced post-cross progeny 1:1 with the C offspring spotted. One CAU produced no eggs by self-fertilization, produced 14 CAU:14AA after mating with an AA(U), and produced

20 CAS: 13 AA after a subsequent mating with an AA(S).

Inheritance of mantle spotting in black-eye snails was similar to that in wild type. When a CAU snail was mated with BAS (a spotted black-eye hybrid, Fig. 13), both parents produced post-cross progeny in 2:1:1 phenotypic ratios (2 CS: 1 BS: 1 A-), the C and B offspring being spotted. For example a CAU which produced 15 CAU: 5 AA by selfing was mated with a BAS which produced 17 BAS: 3 AA by selfing. After reisolation the CAU produced 14 CS: 6 BS: 8 AA; the BAS produced 14 CS: 8 BS: 5AA.

#### Segregation of mantle pigment types following mixed crosses

When spotted progeny resulting from a cross between S and U parents were isolated they typically produced by self-fertilization progeny in mixtures including spotted (S), intermediate incompletely spotted (I), and unspotted (U).

## DISCUSSION

Apparently age and environmental conditions in addition to inheritance are factors influencing development of diffuse pigmentation.

Production of wild type and blackeye strains either with or without spotted mantle pigment by selection and inbreeding (isolation and self-fertilization) suggested inheritance of this character. This is pertinent to the use of mantle pigment patterns in taxonomic descriptions. Since several generations of selection were required to establish such strains, apparently inheritance involved multiple factors.  $F_1$  hybrids from a mixed cross commonly produced progeny varying from spotted to unspotted with variable intermediate stages. Analysis of tabulations of the variable pigment patterns in such progeny did not readily reveal information as to number of factors involved and their interactions. It is considered beyond the scope of the current exploratory genetic studies to pursue the statistical analysis of such variable progeny.

Crosses demonstrated that the spotted condition is dominant over unspotted. When an unspotted hybrid wild type (CAU) was mated with a spotted hybrid blackeye (BAS), each snail produced spotted post-cross progeny. The resulting 2:1:1 ratios, with occurrence of B snails in post-cross progeny of the CAU parent and C snails in post-cross progeny of the BAS parent, demonstrated reciprocal cross-fertilization. Production of post-cross spotted C and B offspring by the unspotted CAU parent demonstrated genetic transmission of the pigment pattern character.

Production of post-cross unspotted CAU progeny by AA(U) mated to CAU and production of post-cross spotted CAS progeny by the same AA(U) after a subsequent mating with a CAS, again

demonstrated genetic transmission of the pigment pattern character. Of particular interest were the matings of either CAU or BAU with AA(S) snails, resulting in spotted post-cross CAS or BAS offspring respectively by the unspotted parents. This demonstrated that albino AA(S), derived from heterozygous spotted strain parents, carried and transmitted factors for the spotted pigment pattern, while lacking the ability to form black pigment themselves.

Albino snails have proved of great value in research. Albinism has served as a genetic marker in systematic and other studies. The transparency of albinos has enabled *in vivo* observations of normal organ development, pathology, and development and migration of parasites. Mantle pigment in species other than *Biomphalaria glabrata* probably has a similar genetic basis. In species in which albino strains are not available it might be possible by selection to develop wild type strains sufficiently deficient in pigment to permit better *in vivo* observations of internal phenomena. Lack of spotting, even though having a multi-factor basis, might also serve as a genetic marker at least for one generation in experimental studies.

The matings  $C \times BB$  or  $C \times BA$  can provide qualitative as well as quantitative evidence of reciprocal cross-fertilization. Reciprocal cross-fertilization is indicated quantitatively but one-sided cross-fertilization only qualitatively by progeny in the following matings:  $CB \times BB$ ,  $CB \times BA$ ,  $CB \times AA$ ,  $C \times AA$ , or  $BA \times AA$ . Only one-sided cross-fertilization is demonstrated by the progeny in the following crosses:  $CC \times BB$ ,  $CC \times BA$ ,  $CC \times AA$ , or  $BB \times AA$ . Mantle pigment spotting provides qualitative indicators for reciprocal cross-fertilization in all the above matings if the first mate listed is from an unspotted strain and the second from a spotted strain.

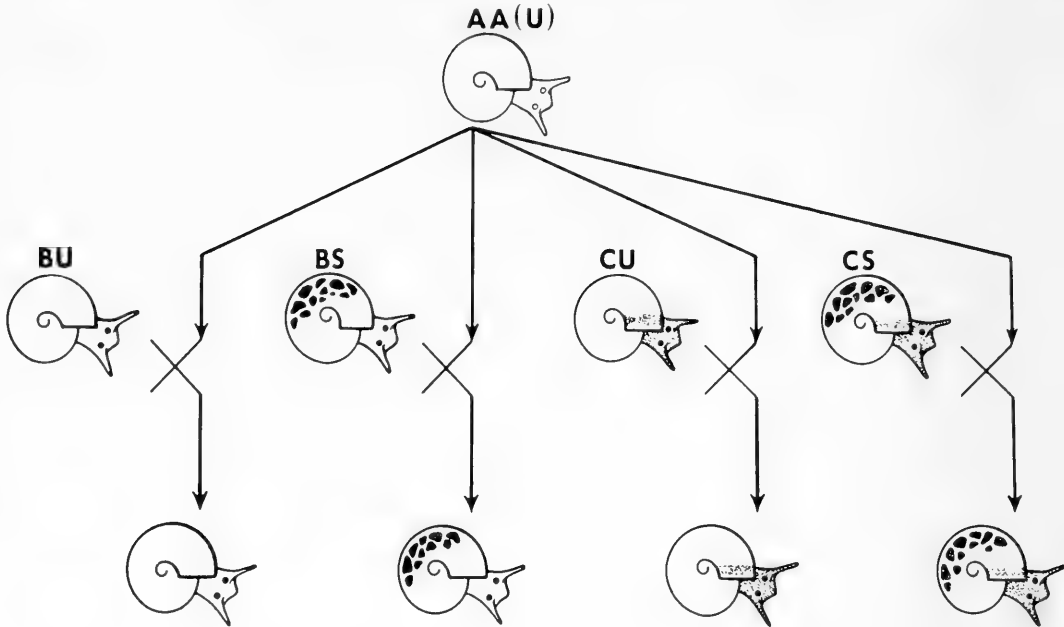


FIG. 14. Diagram illustrating use of pigmentation as marker in experimental multiple matings.

The value of *Biomphalaria glabrata* as a molluscan genetic model was suggested in a previous paper (Richards, 1967). Variability, capacity for reproduction by self-fertilization through a consecutive series of generations facilitating selection for a particular character, dominance of cross-fertilization when two snails are associated together, return to self-fertilization usually about 6 weeks after re-isolation, and occurrence of 3 basic pigment alleles (albino, blackeye, wild type) were summarized. In experimental studies it was possible to self an albino and mate it as many as 4 times in sequence, alternating blackeye and wild type mates, and distinguishing the albino's progeny as to male parent. Incorporating mantle spotting, an albino from an unspotted strain can be mated in series as follows: unspotted blackeye, unspotted wild type, spotted blackeye, and spotted wild type with reasonable assurance that progeny from each mating can be distinguished accurately. Furthermore, placing the albino in association with 4 such mates

concurrently (Fig. 14) should provide information on reproductive dynamics in natural populations.

#### LITERATURE CITED

- HARRY, H. W. & HUBENDICK, B., 1964, The freshwater pulmonate Mollusca of Puerto Rico. *Meddelawden Göteborgs Musei Zool, Ardelning*, 136: 1-77.
- NEWTON, W. L., 1954, Albinism in *Australorbis glabratus*. *Proc. Helminth. Soc. Wash.*, 21: 72-74.
- NEWTON, W. L., 1955, The establishment of a strain of *Australorbis glabratus* which combines albinism and high susceptibility to infection with *Schistosoma mansoni*. *J. Parasit.*, 41: 526-528.
- PARAENSE, W. L., 1956, A genetic approach to the systematics of planorbid molluscs. *Evolution*, 10: 403-407.
- RICHARDS, C. S., 1967, Genetic studies on *Biomphalaria glabrata* (Basommatophora: Planorbidae), a third pigmentation allele. *Malacologia*, 5: 335-340.
- RICHARDS, C. S., 1968, Aestivation of *Biomphalaria glabrata* (Basommatophora: Planorbidae): Genetic studies. *Malacologia*, 7: 109-116.
- RICHARDS, C. S. & FERGUSON, F. F., 1965, Variability in *Australorbis glabratus* (Say). *Trans. Amer. microsc. Soc.*, 84: 580-587.



## RESUME

ETUDES GENETIQUES SUR *BIOMPHALARIA GLABRATA*:  
PIGMENTATION DU MANTEAU

C. S. Richards

La pigmentation noire du manteau chez *Biomphalaria glabrata* a été étudiée en microscopie et en génétique. On a utilisé l'autofécondation d'individus isolés pendant plusieurs générations, comme méthode de sélection pour les variations pigmentaires. Les types pigmentaires de base (type sauvage, yeux noirs et albinos) ont été utilisés comme références dans les expériences de croisements.

Les granules pigmentaires noirs du manteau existent chez *Biomphalaria glabrata* sous deux formes de distribution; diffus et localisés par groupes de cellules formant de discrètes ponctuations. La sélection aboutit à des lignées pures ponctuées et non ponctuées.

Les croisements entre lignées ponctuées et non ponctuées produit des générations  $F_1$  ponctuées. Bien que les albinos ne puissent pas produire du pigment noir, ils transmettent le caractère de manteau ponctué ou non-ponctué.

## RESUMEN

ESTUDIOS GENETICOS EN *BIOMPHALARIA GLABRATA*:  
PIGMENTACION DEL MANTO

C. S. Richards

Se estudio, microscópica y genéticamente, la pigmentación negra del manto de *Biomphalaria glabrata*. Para variaciones de pigmento se seleccionaron individuos—aislados por varias generaciones—, por autofertilización. Tipos básicos de pigmento, (silvestre, ojo negro, albino), se usaron como testigos en los experimentos de cruzamientos.

Gránulos de pigmento paleal negro aparecen en *Biomphalaria glabrata* en dos tipos de distribución general: difusos, y en grópos de células localizadas formando discretas manchas. La selección resultó en linajes con y sin manchas.

Cruza entre esos linajes, manchados y no manchados, produjeron  $F_1$  manchados. Aunque los albinos no pueden producir pigmento negro, transmitieron el caracter de mantos manchados y no manchados.

## АБСТРАКТ

ГЕНЕТИЧЕСКИЕ ИССЛЕДОВАНИЯ *BIOMPHALARIA GLABRATA*:  
ПИГМЕНТАЦИЯ МАНТИИ.

Ч. С. Ричардс

Черная пигментация мантии у *Biomphalaria glabrata* изучалась микроскопически и генетически. Для отбора пигментных вариаций использовалось самооплодотворение в течение нескольких поколений у изолированных моллюсков. Основные типы пигментированных особей (дикие, черноглазые и альбиносы) использовались как обладатели сигнальных генов в опытах по перекрестному оплодотворению. Гранулы черного мантийного пигмента встречаются у *B. glabrata* среди особей двух главных типов распространения; диффузные и локализованные группы клеток могут образовывать дискретные пятна. В результате селекции у гомозиготных форм получены пятнистые и неокрашенные популяции.

Скращивание пятнистых и неокрашенных форм дают пятнистых  $F_1$ . Хотя альбиносы и не могут образовывать черный пигмент, они передают основу для форм пятнистой и неокрашенной мантий.

THE COMPARATIVE EMBRYOGENESIS AND EARLY  
ORGANOGENESIS OF *BURSA CORRUGATA* PERRY AND  
*DISTORSIO CLATHRATA* LAMARCK (GASTROPODA:  
PROSOBRANCHIA)<sup>1</sup>

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ABSTRACT

Due to their close relationship at the familial level, a comparative study of development in *Bursa corrugata* and *Distorsio clathrata* can demonstrate certain dissimilarities in ontogeny which are indicative of adaptability at the larval level. To achieve this goal, the following data are presented. Breeding, spawning and the structure of the egg capsules are described. Embryogenesis, including development to the 1st torsional stage, is outlined. Organogenesis is traced from the torsional pause through the end of the 1st planktotrophic veliger stage which coincides with diverticulation of the left digestive gland.

In summary, the taxonomic characters of the 1st veliger stage are outlined and the gradual change of larval characters with time is noted. Trends in the development of the long-term planktotrophic species leading to natatorial independence are discussed in relation to the organ systems involved. Ontogenetic variations which are examined include the formation of polar lobes, some aspects of torsion, the methods of larval nutrition and the sculpture of the protoconch.

CONTENTS

	PAGE	PAGE
I. INTRODUCTION . . . . .	350	2. Embryogenesis . . . . . 370
II. METHODS . . . . .	351	3. Organogenesis . . . . . 374
III. <i>BURSA CORRUGATA</i> . . . . .	351	V. DISCUSSION . . . . . 382
1. Breeding habits, spawning and egg capsule morphology . . . . .	351	1. Taxonomic characters of the first veliger stage . . . . . 382
2. Embryogenesis . . . . .	355	2. Development of natatorial independence . . . . . 383
3. Organogenesis . . . . .	361	3. Ontogenetic variations and their significance . . . . . 384
IV. <i>DISTORSIO CLATHRATA</i> . . . . .	368	ACKNOWLEDGMENTS . . . . . 386
1. Breeding habits, spawning and egg capsule morphology . . . . .	368	LITERATURE CITED . . . . . 386

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## I. INTRODUCTION

The Prosobranchia comprises the largest subclass of the Gastropoda and contains some of the most successful marine animals in terms of ability to exploit diverse habitats. Of nearly 40,000 extant species of marine gastropods (Abbott, 1954), approximately 25,000 are prosobranchs (Schilder, 1947). Considering the size, availability and significance of the group, it is unfortunate that the developmental history (or any part of it) is known for less than 1% of the species. As pointed out by Anderson (1960), most observations have been limited to temperate North American and European species. If one examines this body of work, it becomes evident that the bulk of descriptive investigation is concentrated in 4 principal areas, mentioned briefly below. Studies of reproductive habits and egg capsules with cursory examination of the embryos are most common. Even in an intensively studied region like the British Isles, the basic data on reproduction are unknown for almost half of the species listed in Fretter & Graham (1962). The 2nd area of investigation, which is concerned with cleavage and cell lineage, is the result of monumental works by Patten (1886), Conklin (1897) and others. Unfortunately, most of this work is limited to primitive species. The 3rd segment includes moderately detailed observations on capsulated and some free-living stages. Pelseneer (1911) and Fioroni (1966a) provided the best examples of this work because they compared several different species. Lebour's work (especially 1937 and 1945) and Thorson's (1946) are examples of general developmental studies which point out the important stages. The 4th area, which includes the most complete work on the development of prosobranchs, is usually limited to studies of the primitive archeogastropods and species with direct development. As

pointed out by Fretter & Graham (1962) for the British species, the later developmental stages have been followed in adequate detail only in *Patella*, *Haliotis*, *Viviparus* and *Pomatias*. On a world-wide basis some species of *Littorina*, *Crepidula*, *Thais* and *Nassa* can be included in this group.

Developmental information on tropical species is extremely sparse. Most papers are concerned with describing egg capsules and include only cursory embryological observations. Typical examples are Thorson's (1940) studies on the egg masses and larval development of gastropods from the Iranian Gulf, Knudsen's (1950) review of spawning and development in marine prosobranchs from tropical West Africa, Ostergaard's (1950) observations on the egg capsules of Hawaiian marine gastropods and Kohn's (1961) account of spawning behavior, egg masses and larval development in *Comus* from the Indian Ocean. A complete description of embryogenesis and organogenesis has not been compiled for a single tropical marine prosobranch.

After considering the past approach to studies of prosobranch development, it is necessary to outline the aims of this research in light of the introductory remarks. First, south temperate and tropical species have been selected to provide regional data. Second, as in the earlier work, detailed studies of undescribed egg masses have been made. Third, basic outlines of major embryogenetic and organogenetic changes have been completed for comparative purposes. Fourth, some taxonomic characters of the veliger stages have been described to aid the planktonologist. In contrast to much of the previous work, developmental data have been based on serial sections and illustrated by detailed drawings. Finally, the major divergences between the 2 ontogenies have been examined.

The 1st species described here is *Bursa corrugata* Perry (= *caelata* Borderip). Most contributions to the knowledge of bursid life histories are limited to descriptions of egg capsules with short notes on the enclosed embryos. Petit & Risbec (1929) and Risbec (1931) published figures of egg capsules from *Ranella* (= *Bursa*) *gyrina* and *Ranella* (= *Bursa*) *granifera* with some comments on the contents. Data on *B. spinosa*, including figures of the egg mass, egg capsules and an embryo during the early stages of larval kidney formation, were provided by Thorson (1940). Abbott (1954) included a photograph of the egg mass of *B. californica*. Fioroni (1966 a, b) reviewed some aspects of the development of an unidentified bursid with nutrient eggs. The egg mass of *B. granularis*, as described and illustrated by Cernohorsky (1967), differs radically from other known egg masses of this genus in having the capsules completely embedded in a gelatinous matrix.

The 2nd species described in this study is *Distorsio clathrata*, about which little was previously known. The reproductive habits, egg capsules and larval stages of *D. clathrata* have not been previously described.

## II. METHODS

The histological methods employed follow those used by D'Asaro (1965, 1966). Somewhat better results are obtained by sectioning at 8 microns.

Rearing methods for the larval stages are relatively simple and also follow the methods suggested by D'Asaro (*op. cit.*). Although both Florida Current water and water collected daily at high tide from Bear Cut (near Miami, Florida) were used in culture, the former was most suitable for both species. Algal foods came from 2 sources, the partially filtered water and added supplementary food. *Platymonas* sp., *Dunaliella tertiolecta* and *Chlorella*

sp. (alone and in combinations) at concentrations less than 8,000 cells/ml were used as supplementary foods for both *Bursa corrugata* and *Distorsio clathrata*, with only partially successful results. *Bursa* remained active for 20 days and *Distorsio* for 16 days.

Illustrations were prepared by comparing tracings of photo-micrographs with freehand drawings of the same individual. Most figures, especially those of later stages, were drawn as semi-transparent objects with some organs outlined as they appear in optical section.

## III. BURSA CORRUGATA

### 1. Breeding Habits, Spawning and Egg Capsule Morphology

*Bursa corrugata* is a relatively rare species on the southeast coast of Florida and in the Caribbean Sea; however, it becomes more common on the Pacific coast between Lower California and Ecuador (Abbott, 1954). All egg capsules were obtained from captive individuals collected in the Pacific region. These collections were made by Dr. F. M. Bayer of the Institute of Marine Science, University of Miami, from Perico Island in the Gulf of Panama at varying intervals from 1963 through 1965.

Populations of mixed sexes were kept in aquaria with running sea water and fed the bivalves, *Chione cancellata*, *Codakia orbicularis* and *Cardita floridana*. An abundance of food after several weeks of starvation usually produced spawning. Oviposition under these conditions occurs only between October and May. Certain individuals maintained this pattern for three consecutive breeding seasons. A female may spawn several times each season.

Copulation occurs from several hours to a week before oviposition. Egg capsules were deposited only in corners of the aquaria on slate or glass. No attempt was

Cade to test substrate preferences. communal spawning was not observed and the presence of egg capsules did not appear to induce oviposition. Each female broods her egg mass until hatching begins.

After oviposition, the egg mass undergoes a series of color variations caused by embryonic development and not by changes in the transparent and colorless capsular membranes. Freshly laid, white capsules gradually become yellowish-white in 4 days. Those capsules which remain white contain either sterile or decaying eggs. Between the 8th and 9th day a granular, brown color appears and increases in intensity until hatching occurs. This pigment is produced by the shell gland and isolated in the protoconch. Color changes are uneven, beginning with older capsules and gradually spreading over the whole mass.

A typical egg mass is roughly oval, slightly concave and matches the outline of the female's aperture. The capsules incline toward the center (Fig. 1A). A cross section at the capsular base above the stalk has roughly the shape of an obtuse triangle with the obtuse angle facing the periphery of the mass (Fig. 3A). Opposite this angle, the wall is convex, while the walls forming the sides of the angle are either straight or slightly concave. This configuration allows each capsule to fit tightly against those in the preceding row. There is some evidence that a female can control the shape of a capsule. During oviposition, aberrations in the normal pattern are corrected by changing the gross outline of several capsules thus re-establishing the positional relationship. The basal membrane, which cements the egg mass to the substrate, is composed of uneven segments. Each basal segment is attached by its central margin to the convex side of an egg capsule (Figs. 1B-1C). Lateral ribs originate at both ends of the basal connecting segment and radiate toward the apex.

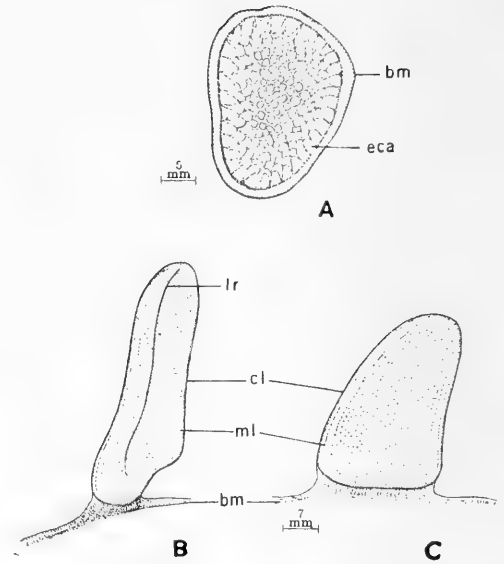


FIG. 1. Egg capsules of *Bursa corrugata* A, a typical egg mass (apical view); B, central egg capsule (lateral view); C, peripheral egg capsule (view of the peripheral side).

Capsular walls have a typical three-layered construction which Amio (1963) has shown to be characteristic of highly evolved mesogastropods. The outer layer is rugose at the apex, especially in the vicinity of the escape aperture, and smooth over the remainder of the capsule and the basal segment. The middle layer is spongy and fibrous. Distinctively, the inner layer does not extend into the stalk or basal segment. It is similar in appearance to the middle layer; however, it takes a darker stain. No preformed, escape-aperture plug is present. In place of the plug there is a flaw in the fibrous texture of the membranes associated with an external lengthwise fold.

The number of capsules per mass from a sample of 5 ranged from 110 to 150. Quantitative variations are due to the size of the body whorl because each female produces only as many capsules as she can cover with the aperture during brooding. In the breeding population under exami-

nation, the width of the aperture between the medial lip and the columella ranged from 16 to 25 mm. Egg masses produced

by these individuals had corresponding diameters between 14 and 25 mm. The total number of capsules may increase

## KEY TO ABBREVIATIONS

a	archenteron	lr	longitudinal ridge
ab	albumen	m	myoblast
ac	albumen cell	ma	mantle anlage
ad	anal duct	mc	mantle cavity
ah	adult heart	mg	metapodial ganglion
ak	adult kidney	mi	micromeres
al	anlage of the left digestive gland	ml	membranous layer
anc	anal cell	mn	metapodial node
ap	apical plate	mo	mouth
apo	animal pole	mp	mesopodial lobe
asr	apical sensory region	msl	metapodial sensory lobe
b	blastopore	o	operculum
bl	beak line	og	osphradial ganglion
bm	basement membrane	oi	osphradial invagination
c	columella	ov	optic vesicle
ca	carina		
cc	cerebral commissure	p	proctodeum
ccs	concave side	pa	pedal anlage
cg	cerebral ganglion	pal	pallial lobe
ch	chamber	pas	pallial sinus
cl	coriaceous layer	pc	protoconch
cm	columellar muscle	pes	peripheral side
cr	cephalic region	pg	pedal ganglion
cs	cephalic sinus	pl	polar lobe
evs	convex side	plg	pleural ganglion
cym	central yolk mass	pls	pallial secretory cells
d	deutoplasm	po	posterior ciliary band
da	digestive anlage	pp	propodium
di	diverticulum	pr	preoral ciliary band
dml	dorsal mantle lip	prs	protostyle
ds	dorsal extension of the pretorsional shell gland	ps	pedal sinus
e	esophagus	pse	peripheral storage cells
ea	escape aperture	pt	prototroch
ec	ectodermal cells	ra	renopericardial anlage
eca	egg capsule	rdg	right digestive gland
eg	excretory granule	rt	right tentacle
em	embryo	s	stomodeum
fg	food groove	sb	site of the blastopore
fl	fibrous layer	sc	segmentation cavity
fr	food-storage region	seg	supra-esophageal ganglion
g	growth line	sg	shell gland
gc	glandular cells	sp	stomodeal plug
gl	gastric lumen	ss	style-sac stomach
gs	gastric shield	sta	statocyst
hg	hypobranchial gland	sto	stomach
i	intestine	t	typhlosole
ldd	left digestive duct	v	vacuole
ldg	left digestive gland	vc	vacuolated cell
lf	luminal fissure	vg	visceral ganglion
lh	larval heart	vl	velar lobe
lk	larval kidney	vls	velar sinus
		vs	visceral sinus

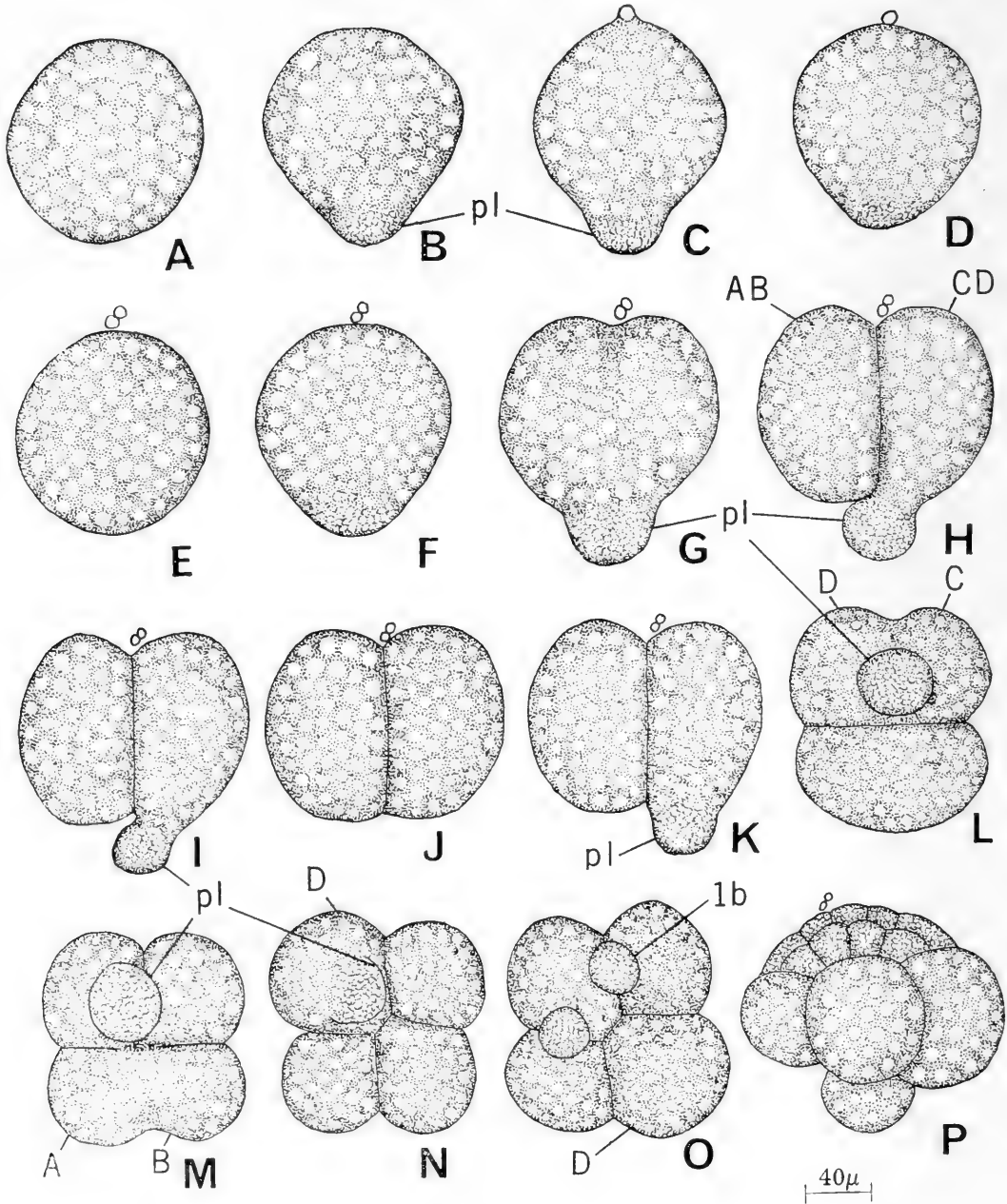


FIG. 2. Development of *Bursa corrugata*: A, an egg at oviposition; B, extrusion of the 1st polar lobe; C, 1st polar body with the polar lobe at apogee; D, retraction of the 1st polar lobe; E, 2nd polar body; F, extrusion of the 2nd polar lobe; G, onset of the 1st cleavage; H, completion of the 1st cleavage plane; I, retraction of the 2nd polar lobe; J, complete 2-cell stage; K, extrusion of the 3rd polar lobe; L, vegetal view of the 3rd polar lobe at the onset of CD cleavage; M, vegetal view of early AB cleavage; N, retraction of the 3rd polar lobe by D; O, 3rd cleavage; P, late cleavage stage with a prominent vegetal blastomere.



when oviposition occurs in a crevice because the egg mass is molded to conform with the irregularities of the substrate.

The dimensions of a capsule vary with its position in the egg mass. This relationship was also shown in *Bursa spinosa* (Thorson, 1940). The central capsules are taller and narrower at the base than the peripheral ones (Figs. 1B-1C). Both types are roughly pyramidal in outline with rounded edges. In egg masses which have been produced on flat substrates, differentiation between the 2 types is reduced. The average dimensions from a sample of 10 central capsules are: length-5.5 mm, width at the base-2.3. For 10 peripheral capsules the average measurements are: length-3.4 mm, width at the base-3.0 mm.

Positional variations in capsular size are reflected by their contents. The average number of embryos in the previously measured central capsules was 900. Peripheral capsules contained an average of 600. Since approximately a 4 to 1 ratio exists between the number of central and peripheral capsules, an estimate of the total number of embryos per mass can be made. The smallest examined contained approximately 92,000 and the largest 115,000.

## 2. Embryogenesis

*Bursa corrugata* is a dioecious species with internal fertilization. The exact site of fertilization was not determined, but as demonstrated in the Gastropoda by Yonge (1960), it is probably in the medial oviduct close to the albumen gland.

Maturation is characterized by well defined polar lobes similar to those found in the scaphopods, pelecypods and gastropods listed by Raven (1958). The first external evidence of plasmic reorganization is present 1 hour after oviposition. In 2 hours, the primary polar lobe reaches its apogee concurrently with production of

the first polar body (Figs. 2A-2C). A steady reabsorption of the lobe occurs during the second stage of maturation culminating in production of the second polar body concurrently with total absorption of the primary lobe (Figs. 2D-2E). This process is completed in about 3 hours at 24°C. All polar lobes contain granular cytoplasm and have few or no yolk granules, a condition similar to another tonnagean, *Argobuccinum oregonense* (Phillpott, 1922).

Formation of the secondary polar lobe which reaches its maximum size when the first longitudinal cleavage plane appears, marks the onset of cleavage (Figs. 2F-2G). A distinct "trefoil" stage develops when the cleavage plane separates AB from CD leaving the polar lobe associated with the CD blastomere. The secondary polar lobe is then absorbed by CD forming the 2 celled stage (Figs. 2H-2J). Further cleavage is irregular and differs somewhat from the so-called normal pattern of spiral cleavage. Prior to formation of the 4 cell stage, a tertiary polar lobe develops vegetally on the CD blastomere. When this lobe reaches its greatest magnitude, a longitudinal cleavage plane begins to divide CD. The polar lobe is retained on the D blastomere (Figs. 2K-2M). Both C and D blastomeres are completed before the cleavage of AB begins. When A and B are distinct the tertiary polar lobe is reabsorbed producing a D blastomere slightly larger than the other blastomeres (Fig. 2N).

Cleavage rates affecting the 8 cell stage are unequal. Dextral formation of 1a-1b is completed before 1c-1d (Fig. 2 O). Similar inequalities are common in succeeding stages. Since cleavage is not followed in detail beyond this point, it is not possible to identify the prominent blastomere located at the vegetal pole in later stages (Fig. 2P). A typical stereoblastula is present prior to gastrulation (Fig. 3B).

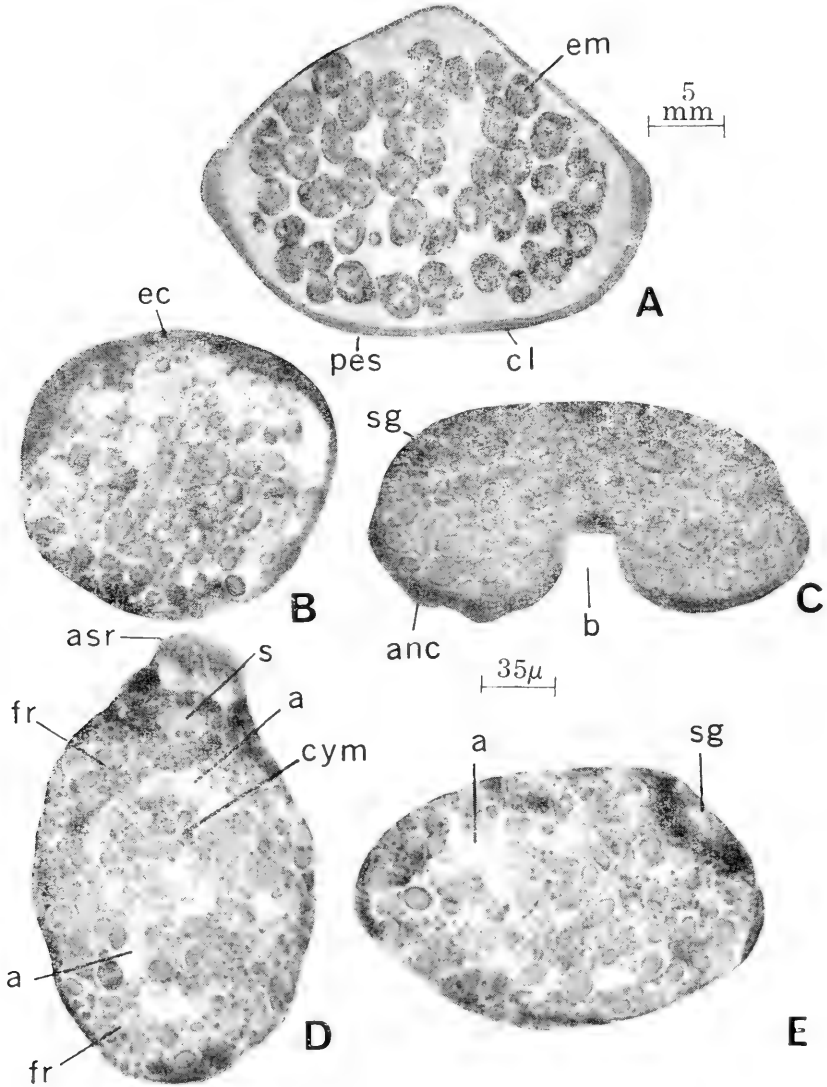


FIG. 3. Development of *Bursa corrugata*: A, cross-section of an egg capsule; B, cross-section of a stereogastrula (4 days); C, parasagittal section through the stomodeum (5 days); D, frontal section through the archenteron (8 days); E, parasagittal section through the invagination of the shell gland (8 days).

*Four Days.*—Gastrulation, beginning shortly after completion of the 64-cell stage, produces an early stereogastrula similar to that of *Crepidula fornicata* (Conklin, 1897). Epibolic growth continues to extend the cap of micromeres around the macromeres toward the vegetal pole. Extremely rapid proliferation by the descendants of 2d forms a recognizable

shell gland anlage.

*Five Days.*—The major part of epibolic gastrulation is completed during the early fifth day when the macromeres are completely enclosed by micromeres. A prominent shell gland with an expanded margin around the macromeres toward the vegetal pole is present (Figs. 3C & 4A). The posterior region associated with the shell gland is characteristically flattened.

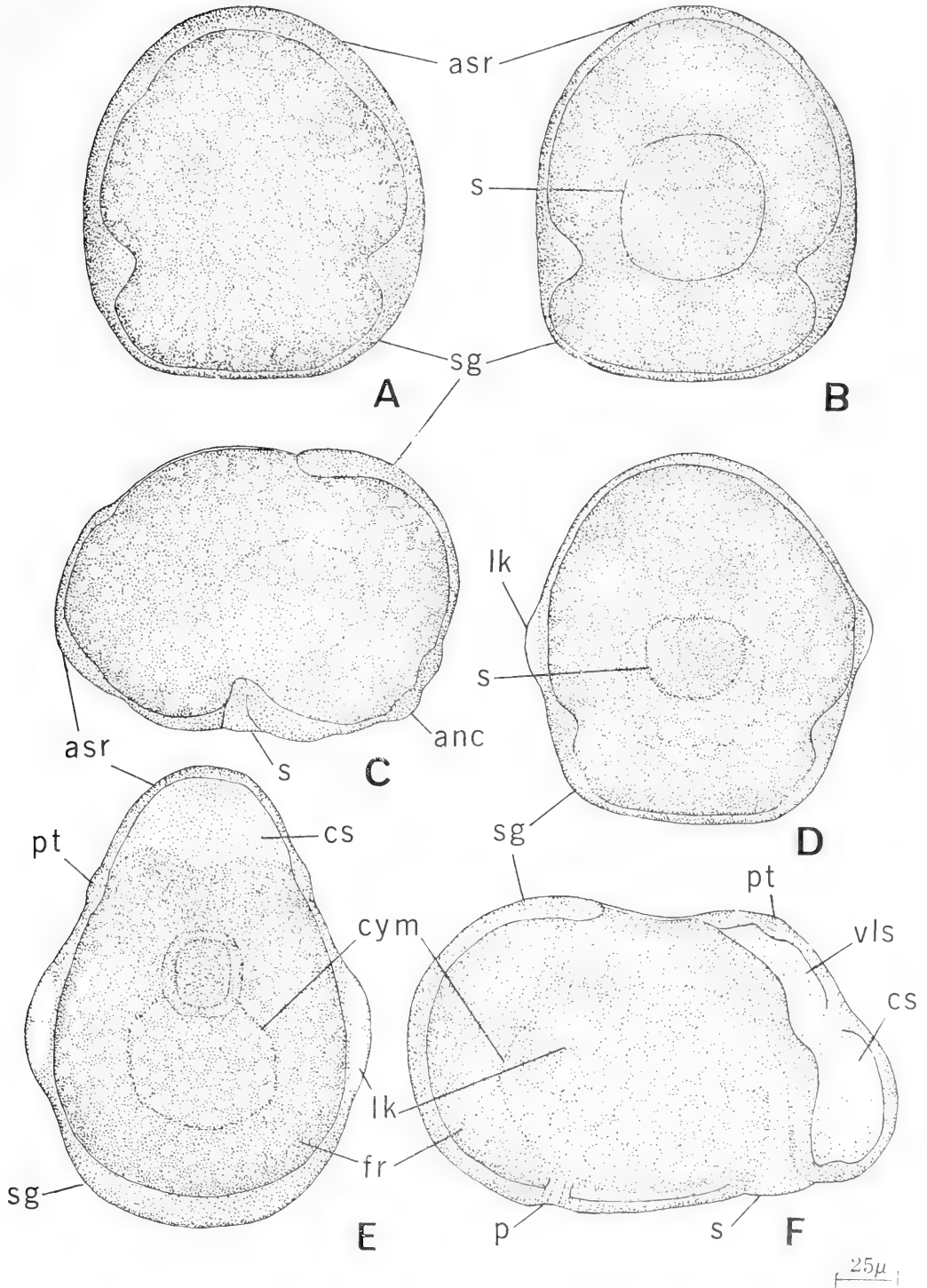


FIG. 4. Development of *Bursa corrugata*: A, dorsal view of the primordial shell gland stage (5 days); B, ventral view of the stomodeal invagination (5 days); C, left side during the stomodeal invagination (5 days); D, ventral view during the early stages of larval kidney formation (6 days); E, ventral view during formation of the prototroch (7 days); F, right side during formation of the proctodeum (7 days).

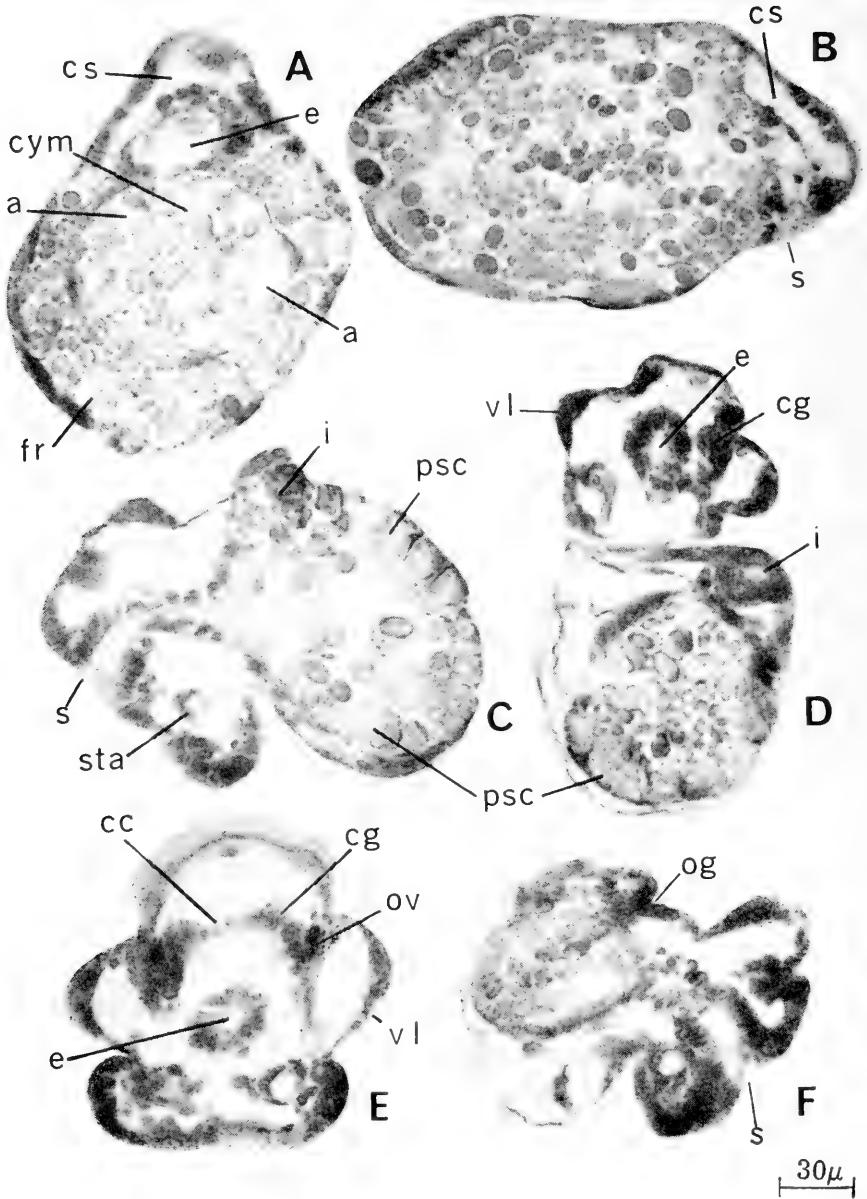


FIG. 5. Development of *Bursa corrugata*: A, frontal section through the stomodeum and archenteron (8 days); B, parasagittal section through the cephalic sinus (8 days); C, sagittal section through the esophagus and digestive anlage (9 days); D, frontal section through the digestive anlage (9 days); E, oblique section through cephalic and pedal regions in the plane of the major ganglia (10 days); F, parasagittal section through the osphradial invagination (11 days).

Apical sensory development is limited to an undifferentiated cap of cells. Near the end of the fifth day, an invaginatory

process at the site of the blastopore produces an unusually wide stomodeum surrounded by a lip of transparent ectoder-

mal cells (Fig. 4B). A pedal anlage forms posterior the stomodeum. Two anal cells mark the future site of the proctodeum (Fig. 4C). Mesodermal rudiments can be identified at this time.

*Six Days.*—The appearance of extensive ciliation and resulting motility are characteristic of this period. Conspicuous cilia line the dorsal and ventral lips of the shell gland, the whole pretrochal region and the stomodeum. The trochoblasts remain unciliated.

Blastocoelic and archenteric cavities are absent during early embryogenesis. In later stages, certain blood sinuses appear which are homologous with the blastocoel of other species. The archenteric region is gradually outlined by a layer of smaller deutoplasmic macromeres, which make up the walls of the digestive anlage, surrounding the larger deutoplasmic macromeres of the central yolk mass. The diameter of the stomodeum is reduced concurrently with the formation of the archenteric wall. The anlagen of the larval kidneys develop laterally just anterior to the lip of the shell gland (Fig. 4D).

Two major sets of growth vectors begin to change the shape of the embryo. The first, which shifts the anal cells ventrally and the larval kidneys anteriorly, is a process of ventral flexion induced by expansion of the trunk region. A 2nd set of growth vectors, associated with flexion, lengthens the embryo, especially in the pretrochal and pleural regions (Fig. 4E). This process continues until protoconch formation and torsion begin.

*Seven Days.*—Major components of several organ systems appear following the beginning of differential growth. Yolk material is separated into 2 distinct areas; the gastric food-storage region, which is diffused through the walls of the digestive anlage, and the central yolk mass (Figs. 3D & 5A). Between the pedal anlage and the lip of the shell gland,

there is a narrow, proctodeal invagination touching the archenteric wall (Fig. 4F). The stomodeum continues to decrease in diameter and becomes roughly rectangular in outline. Its junction with the archenteron is still closed.

In the pretrochal region, 3 sinuses, which are homologous with a blastocoel, appear. The cephalic sinus develops under the apical cap anterior to the stomodeum, while the velar sinuses expand dorsal and lateral to the stomodeum (Figs. 4F & 5B). Formation of the sinuses is the result of anteriorly directed growth processes and delamination. Shortly after the appearance of the cephalic sinus, cerebral ganglia proliferate from the cephalic plates. Ciliation is now specialized. The apical sensory region has short, stout cilia which extend ventrally in a wide band to the stomodeal lip. The velar region has very fine cilia and a row of enlarged, dorsal trochoblasts. Prototrochal ciliation appears first on these cells. Specialized stomodeal and pedal ciliation associated with the feeding mechanism is present.

*Eight Days.*—Pretrochal developments are coupled with further expansion of the velar and cephalic sinuses. A cerebral commissure, which is later invaded by nerve fibers, develops by proliferation of ectodermal cells between the ganglia (Fig. 6A). There is a non-ciliated area separating the prototroch and apical sensory region.

Posttrochally, a conspicuous expansion and thickening in the trunk region marks the beginning of the major phase of shell gland development. Only a slight invagination precedes growth (Fig. 3E). The principal growth vectors are dorsally oriented. Further expansion of the larval kidneys surpasses and obscures the support cells. Fioroni (1966a, b) presented detailed drawings of larval kidneys in a bursid which are equivalent to those of *Bursa corrugata* at the 8th day. Expansion of

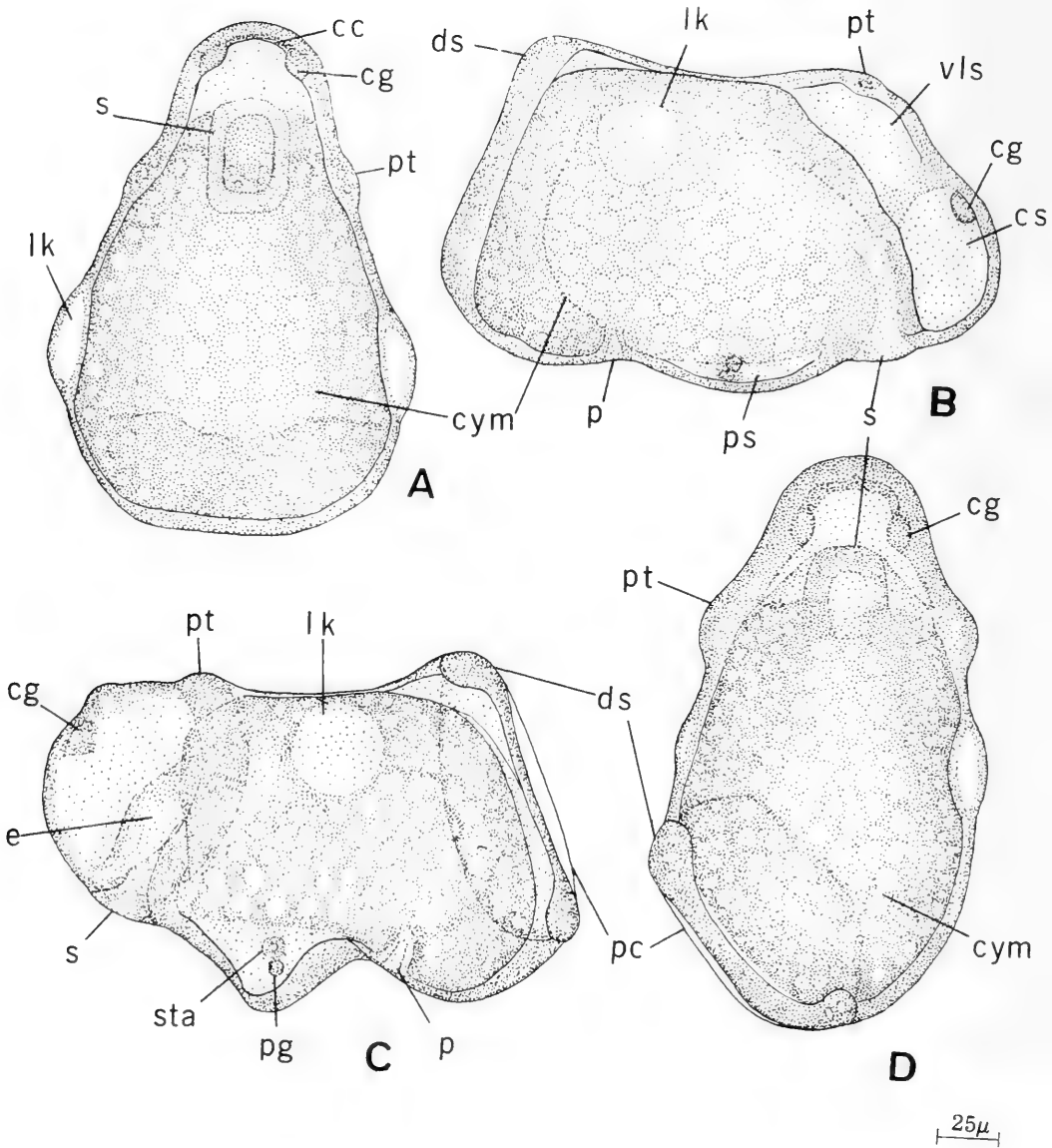


FIG. 6. Development of *Bursa corrugata*: A, ventral view at the beginning of formation of ganglia (8 days); B, right side during expansion of the shell gland (8 days); C, left side of a pretorsional veliger (9 days); D, dorsal view at the beginning of the 1st stage of torsion (9 days).

the pedal and visceral sinuses begins (Fig. 6B).

*Nine Days.*—This period can be divided into 2 parts; (a) the completion of pretorsional growth; and (b) the first stage of torsion. Prior to torsion, the combined

effect of the major growth vectors already mentioned produces a typical early veliger (Figs. 5C-5D & 6C). The head-foot region is now distinct due to expansion of the various sinuses and ectodermal differentiation. Lateral, pedal invaginations

produce the statocysts. Statolith formation begins shortly after invagination. In the visceral region, the prominent dorsal process of the shell gland is enlarged by expansion of the visceral sinus. Mesodermal elements consolidating in this sinus produce the columellar muscle. Prior to torsion, its origin is located in the dorsal process of the rudimentary protoconch. Insertions are primarily on the left ventral side with a major subesophageal branch to the right side. Other mesodermal elements consolidate into the renopericardial anlage. Secretion of a conchiolinous matrix, which began during the 8th day, produces a pustulate, reddish-brown protoconch. Considerable expansion of the pretorsional, dorsal mantle lip takes place.

The first stage of torsion shifts the dorsal process of the shell gland 90 degrees to the left (Figs. 6D & 8A). This shift involves an elapsed time in excess of 24 hours. The probable, but not confirmed, first stage effector is a right larval retractor. Following the first stage there is a pause, the interval of which varies with the culture method and temperature. It may be as short as 1 day or as long as 5 days. The final stage of torsion is completed somewhat faster than the first. During the second stage, the columellar muscle is prominent (Figs. 7A-7B). If differential growth, associated with the formation of the columellar muscle, is the primary cause of the second stage of torsion, it can be only partially applied to the process in *Bursa corrugata* because a well developed columellar muscle is present before the second stage begins. Total torsional movement is slightly less than 180 degrees.

### 3. Organogenesis

*Ten Days.*—Prior to this stage embryogenesis has been limited to specific, isolated structures. During the torsional

pause the veliger becomes increasingly systematized. In the nervous system, the pleural ganglia, which are the 3rd major pair, arise from lateral, ectodermal proliferations in the pleural grooves. The ganglia of the visceral loop are not identifiable, but some type of anlage must be present in each case at this time. Connective formation is the result of fibrous, interconnecting outgrowths of the respective ganglia. Cerebropleural connectives develop first. Both the cerebral and pedal commissures are narrow bands of cells closely associated with the ectoderm. The tentacular nerves extending from the cephalic ganglia to the tentacular anlagen function as accessory connectives. Other sensory structures include the optic vesicles, which appear as invaginations on the cerebral plate lateral to the cerebral ganglia (Figs. 5E & 8A), and the tentacular anlagen bordering the apical sensory region. The vesicles remain open until the end of torsion. Prior to closing, black retinal pigment develops in each vesicle.

In the digestive system, the anterior portion of the gastric stomach is well defined. A gastric lumen is present. During the torsional pause, the unmodified intestine is located on the ventral right side. The anlage of the left digestive gland appears as a swelling on the visceral mass.

Initially, circulation and blood pressure are maintained by myoblasts found in all body sinuses (Figs. 7A-7B & 7D) and circular muscles below the ectodermal layers. Contraction by these muscles shifts fluids back and forth between the sinuses providing rudimentary circulation before the larval heart develops. The increase in body size is mainly a product of sinusoidal expansion, a process which involves transport of fluids from the surrounding medium into the rudimentary circulatory system and ectodermal expansion. This process, which began much

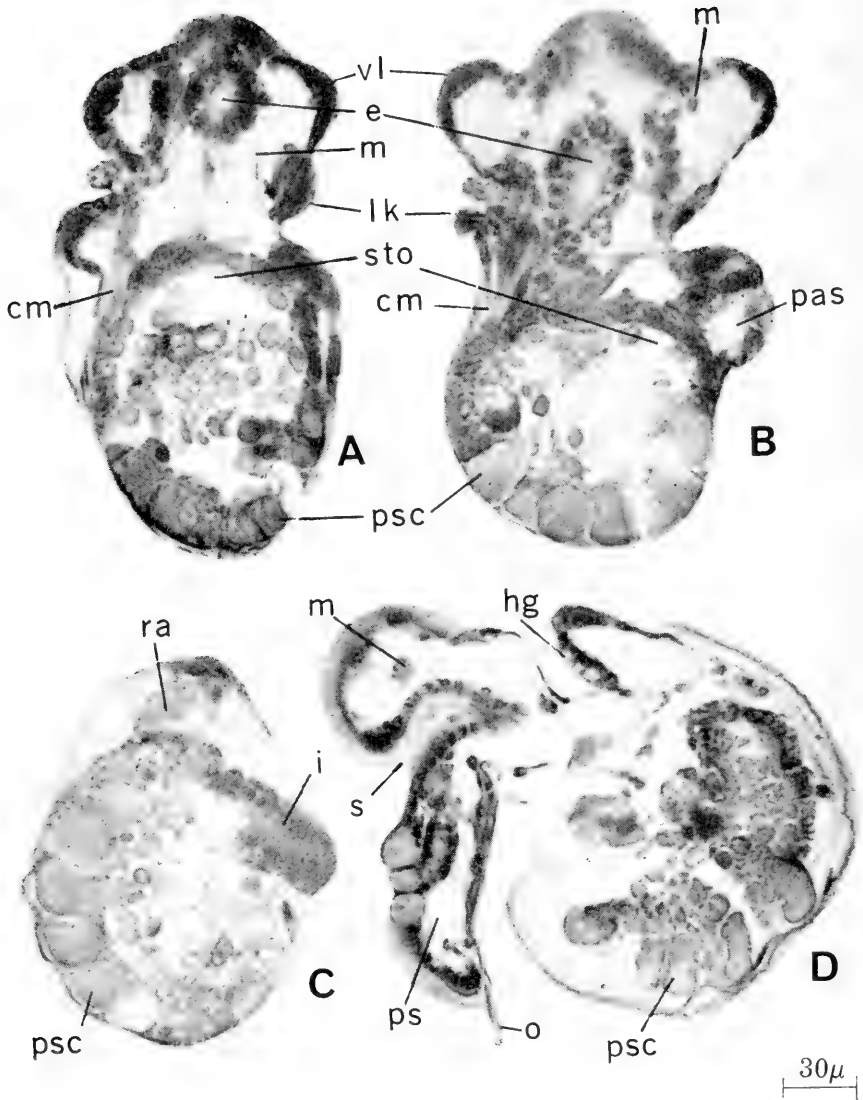


FIG. 7. Development of *Bursa corrugata*: A, frontal section through the columellar muscle (10 days); B, frontal section through the anlage of the digestive gland (11 days); C, oblique section through the intestine and the anlage of the digestive gland (12 days); D, parasagittal section through the foot and visceral mass (13 days).

earlier, enters its most active stage during expansion of the velar lobes (Fig. 8B). Certain myoblasts also function as accessory retractors for specific organs.

The torsional pause marks the point of greatest expansion by the larval kidneys (Figs. 8A-8C). These organs are now

more granular in appearance and contain large vacuolated regions. Subsequent development produces a gradual decrease in size and finally complete absorption in the post-hatching stages.

Pretrochally, the velar lobes begin to expand while a concomitant increase in



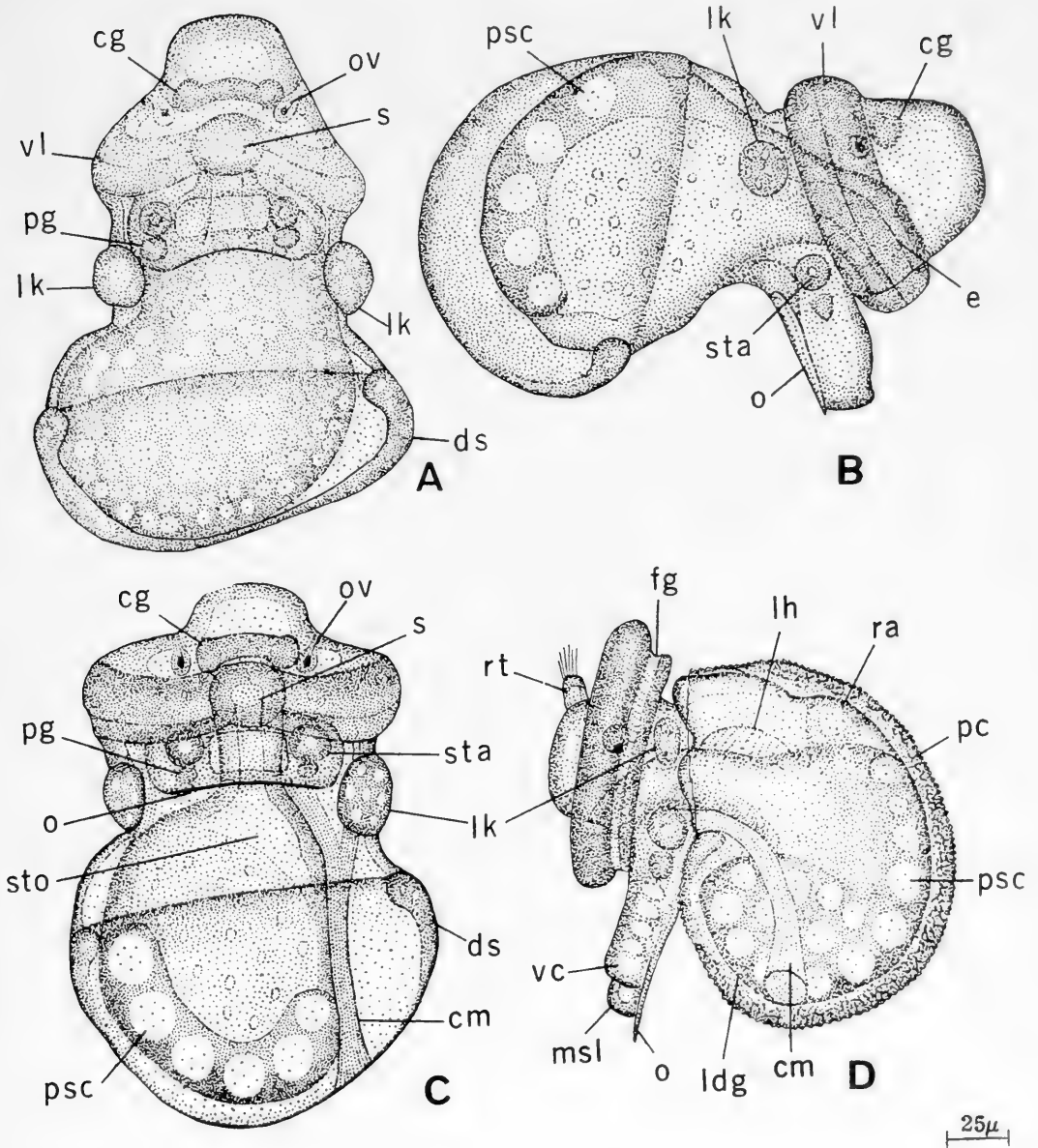


FIG. 8. Development of *Bursa corrugata*: A, ventral view during the torsional pause (10 days); B, right side during the torsional pause (10 days); C, ventral view at the beginning of the 2nd stage of torsion (11 days); D, left side of an early post-torsional veliger (12 days).

velar ciliation, producing the rudimentary food grooves, takes place. In the pedal region the posterior ectoderm of the foot differentiates into an opercular gland, which immediately secretes a thin, mem-

branous operculum. In the visceral region, the cap-like shell gland expands at a uniform rate surrounding the digestive anlage. Before the enveloping process is completed, there is a change in the

sculpture of the protoconch. Plate-like structures appear, especially in the region close to the mantle lip, concurrently with an increase in the intensity of pigmentation. Similar structures have been reported from other tonnacans (Amio, 1963, Thorson, 1940).

*Eleven Days.*—The 11th day is marked by the beginning of 2 important processes: (1), the absorption of nutrient material by specialized peripheral cells in the anlage of the left digestive gland and (2), the ascension of the dorsal, mantle lip with the concomitant appearance of the mantle cavity. Prior to the onset of the second torsional stage, there is a sudden increase in the size of certain peripheral cells. These cells become very prominent and sharply outlined in the living veliger (Figs. 8B-8D). Anderson (1959) and Fioroni (1966a, b) found similar cells in other tonnacans. Cell expansion begins shortly before the esophagus is complete and functional. Initially, there is a gradual disintegration of archenteric yolk from the macromeres followed by absorption and possible phagocytic ingestion of the fragments by the peripheral cells. These cells appear in the left digestive anlage and spread laterally to the edge of the stomach anlagen. Lateral expansion continues until the posterior wall of the visceral mass is tightly packed with a single layer of these extremely large cells (Figs. 5C-5D, 7A-7D). Before the process of absorption is complete the esophagus opens allowing the veliger to swallow capsular fluids. Although these fluids are somewhat viscous there is no evidence proving ingestion. However, the peripheral cells are in the same position as albumen ingesting cells in other species, have a similar origin, function and ultimate fate and, therefore, are homologous.

Formation of the mantle skirt also begins prior to the second stage of torsion. The process is quite similar to velar

expansion. When the mantle lip elongates it develops interconnected sinuses. As the ectodermal layers surrounding each sinus expand, haemocoelic fluid-pressure maintains the shape of the structure. During the formative stages these sinuses are very large (Fig. 7B). The actively expanding dorsal lip produces the mantle cavity by folding anteriorly over the pleural groove. The folding process resembles *Crepidula* (Moritz, 1939) and does not involve an invagination like that of *Pila* (Ranjah, 1942). As torsion and mantle cavity formation proceed, there is a small invagination on the left side in the pleural region which forms the osphradial ganglion (Fig. 5 F). During the folding process, this ganglion is shifted into the roof of the mantle cavity.

*Twelve Days.*—In agitated sea water at 24°C, the final stage of torsion begins gradually and is completed before the end of the 12th day. After torsion, the mantle is no longer adherent to the protoconch and at times extends beyond the lip of the shell. Rapid anterior growth produces the primary body whorl and rudiments of an apertural beak. The protoconch is composed of scale-like plates with raised edges which present a serrated outline when seen in a side view (Fig. 8D). Increased pigmentation and the scaly structure of the protoconch greatly reduce transparency and make observations of internal developments difficult.

Cephalic modifications affect the sensory and feeding apparatus. Growth of the right tentacle provides a primary sensory organ. Separation of the preoral and postoral ciliary bands sharply outlines the food grooves and indicates the close proximity of hatching. Pedal modifications include a marked reduction of the sinuses, formation of the propodial anlage and development of a metapodial sensory node.

In the digestive system, the diameter of peripheral cells has increased 5 fold due

to the rapid assimilation of archenteric yolk. Concurrently, there is further evidence of disintegration in the archenteric region including collapsed and displaced cells and large intercellular spaces. The result of this reorganization is the formation of the lumen of the left digestive gland and isolation of peripheral cells in this gland (Fig. 7C). Both the gastric stomach and the anlage of the style-sac stomach have well defined, anterior walls free of yolk granules. The intestine extends from the right side of the style-sac stomach to the right median edge of the mantle skirt (Fig. 7C).

The larval heart and the renopericardial complex begin to develop during the last stage of torsion (Figs. 7C & 8D). As in other prosobranchs, the larval heart is located in the torsional plane, dorsal and to the right of the esophagus. It begins to beat shortly after formation. The presence of this systemic pump is usually associated with the appearance of food grooves and the final expansion of the velar lobes. The renopericardial complex is located posterior and to the left of the mantle cavity. Expansion of the complex begins at about the same time as the appearance of the larval heart. The dorsal, balloon-like part of the complex is the anlage of the adult kidney. Both larval kidneys are greatly reduced in size.

*Thirteen Days.*—Organogenesis has reached the final phase of the prehatching stage in which the basic, functional organs needed by a planktonic veliger are formed. The digestive system has a complete food gathering apparatus which lacks only the final expansion of the velar lobes. The mouth and esophageal cilia are functional. A gastric-shield primordium is present, but only the anterior walls of the gastric stomach are free of yolky material. Deutoplasmic reserves remain in the posterior walls of the gastric stomach, the left digestive gland and as scattered remnants

of the archenteric yolk. Dorsal to the left digestive gland on the right side of the gastric stomach, an unmodified, right digestive gland evaginates. The style-sac stomach has the short, fused cilia which are so characteristic of this organ. Intestinal ciliation is complete and apparently functional.

As indicated by the veliger's reaction to its environment, all basic nervous and sensory units are functional. The cerebral commissure separates from the ectodermal layer. In addition to the cerebral nerves already mentioned, there is a pair of apical nerves which terminate in the sensory region (Fig. 9A), and a pair of statocyst nerves, which terminate in the cerebral ganglia. A positive phototaxis is indicative of functional optic vesicles. The major ganglia are arranged in a typical streptoneurous pattern of cerebrals, pleurals, pedals, esophageals and visceralis. A large, prominent osphradial ganglion is situated on the left side of the mantle cavity (Fig. 10A). In the living veliger, the supra-esophageal osphradial connective is conspicuous.

The columellar muscle is the major body retractor. From its origin on the left side, this muscle passes ventral to the esophagus and divides into 2 major branches (Fig. 9B). Each branch divides again with segments entering the cephalic, velar and pedal sinuses. Velar insertion is on both faces of the lobes while pedal insertion is directly on the operculum and the ventral ectoderm (Figs. 10A-10B).

Externally, the veliger is modified by reduction of the apical sensory region and lateral expansion of the foot. Pedal expansion accompanies the formation of large, vacuolated border cells, which give the ventral pedal region a reticulated appearance (Fig. 9C). The operculum extends well beyond the metapodium. Development of the hypobranchial gland matches the expansion of the mantle cavity (Fig. 7D).

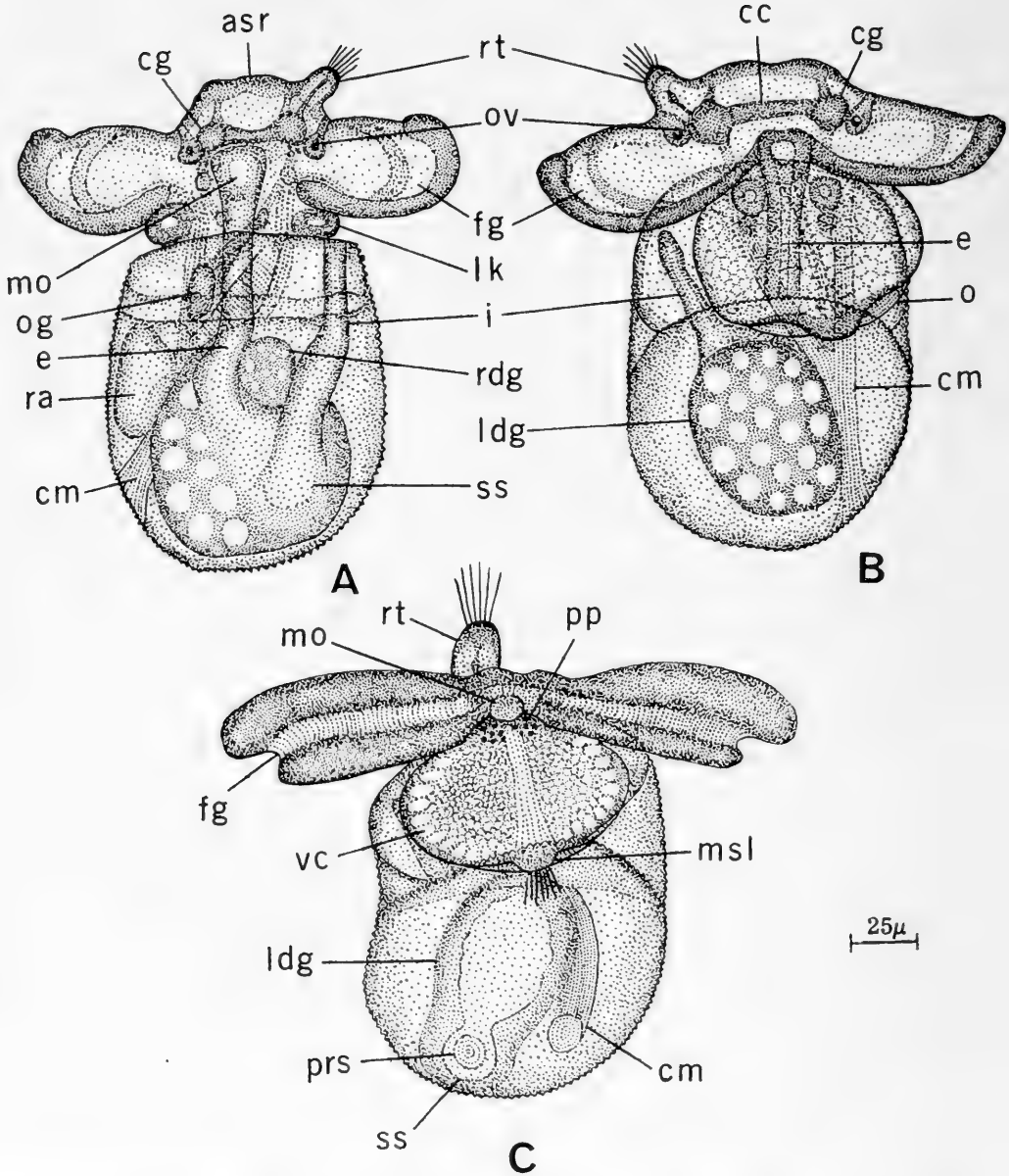


FIG. 9. Development of *Bursa corrugata*: A, dorsal view of a veliger 24 hours prior to hatching (13 days); B, ventral view of a veliger during hatching (14 days); C, ventral view of a 15 day veliger.

*Fourteen Days.*—Hatching through a split at the capsular apex begins during the early part of the 14th day. The point of release occurs at a definite stage in ontogeny when the organs necessary for planktonic existence are fully formed. All

basic organs in the digestive system are functional and feeding begins almost immediately. The velar food grooves are typically wide. A prominent gastric shield is present in the gastric stomach. Consolidation of the paired digestive

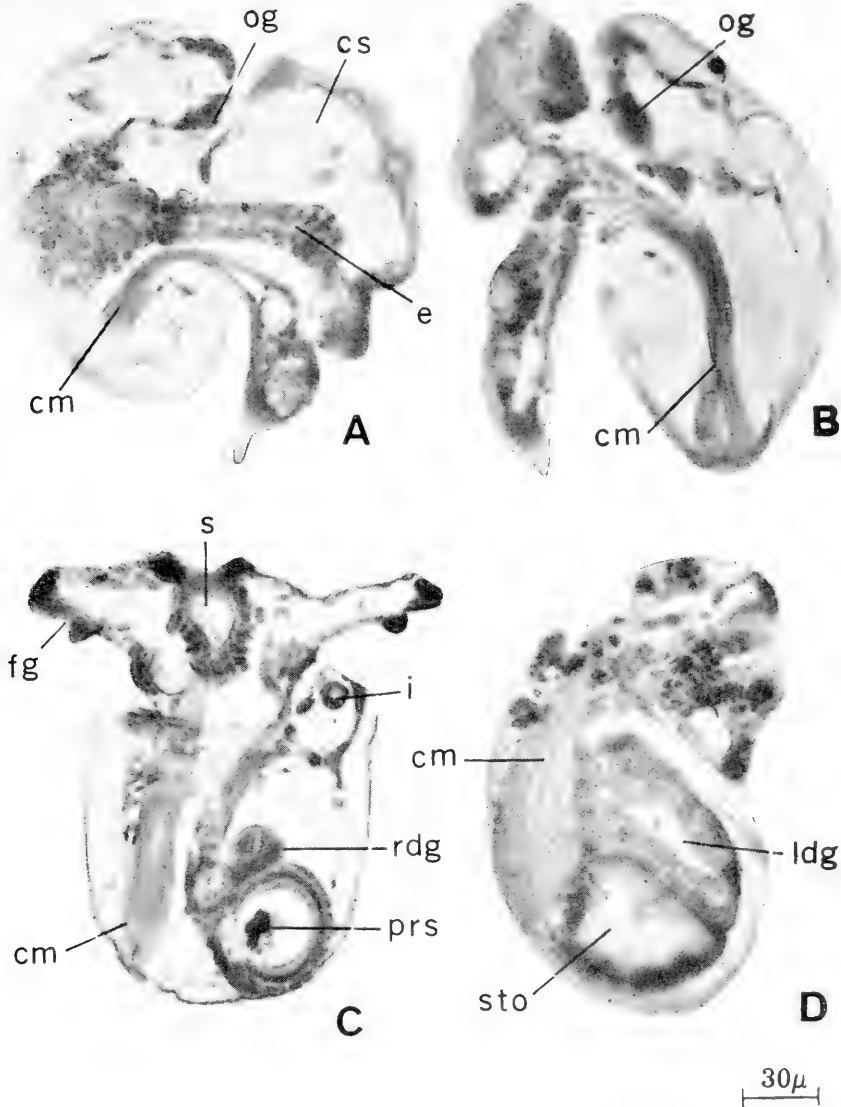


FIG. 10. Development of *Bursa corrugata*: A, oblique section through the osphradial ganglion (13 days); B, parasagittal section through the columellar muscle (13 days); C, frontal section through the style-sac stomach and the right digestive gland (14 days); D, beginning of diverticulation in the digestive gland (17 days).

glands is nearly complete. The lumen of the left digestive gland is unobstructed by yolk, and there is a drastic reduction in the number and size of the peripheral storage-cells. Small digestive ducts appear in the right digestive gland. The style-sac stomach contains both major and minor typhlosoles bordering an

intestinal groove which leads across the floor of the stomach into the intestine. At this stage, both typhlosoles are approximately equal in size.

The protoconch is now composed primarily of the plate-like structures mentioned earlier. The plates are circular and adjacent in regions produced

by the primary shell gland. On the body whorl, which was formed by the mantle, each plate is overlapped by the preceding one. Continued shell growth produces the columella and deepens the mantle cavity. The apertural lip has only the slightest trace of a beak.

Sensory structures are greatly expanded at hatching. The right tentacle and the metapodial sensory node are covered with stiff bristles, contain nervous tissue and are elongated. Both optic vesicles are partially closed over the crystalline lenses.

*Fifteen Days.*—A variety of foods are found in the stomach of the early planktotrophic veliger of *Bursa corrugata* including *Platymonas*, *Dunaliella* and assorted unidentified flagellates. The walls of the gastric stomach contain black pigment granules which appear at the onset of feeding. A second structure associated with the onset of feeding is the protostyle (Figs. 9C & 10C). Peripheral storage cells are no longer present, consequently there is a reduction in the diameter of the left digestive gland and the formation of luminal fissures (Fig. 10D). The insertions of both digestive glands function as valves controlling the passage of food particles.

Thirty-six hours after hatching the veliger develops purplish-black pigment granules on the propodial rudiment (Fig. 9C). The last vestiges of the larval kidneys are absorbed. Expansion of the renopericardial anlage produces a functional adult kidney and a rudimentary heart. The latter is located near the left, ventral side of the kidney to which it is connected by a renopericardial duct.

*Eighteen Days.*—The veligers examined from this and succeeding stages had atrophied digestive glands with no diverticulation, a sign of starvation. Even with selected phytoplankton from the partially filtered water, growth was greatly reduced and the daily mortality was high. The probable cause of

mortality was the lack of a specific food organism.

Even though the veligers are in a weakened and morphologically atypical stage, it is possible to make a few assumptions based on present developmental trends which will give a picture of the next veliger stage. The protoconch is completely covered by the previously mentioned plates and the beak is reduced. Three types of pigment are present. The shell is reddish-brown, obscuring the viscera. Purplish-black pigment granules are spread through parts of the digestive tract, the ciliary bands and portions of the foot. On the foot, a border of large vacuolated cells with a greenish tint is present (Fig. 9C). A velar lengthening process is indicative of the future appearance of 2 pairs of velar lobes.

#### IV. *DISTORSIO CLATHRATA*

##### 1. Breeding Habits, Spawning and Egg Capsule Morphology

Egg masses were produced in the laboratory by individuals collected in the Florida Straits on 14 September, 1965. Collections were made with a 10-foot try net (otter type) from the R/V "Gerda" (Stations: G755-756, 24°49'5"N/80°37'W) at depths of 22 to 26 fathoms. Specimens were maintained on board ship in plastic boxes at ambient temperatures and transferred to a water table in the shore based laboratory.

Oviposition began within 24 hours after collection and continued intermittently for 5 days. Copulation was not observed. Although a variety of substrates were available, all egg masses were deposited on polyethylene refrigerator boxes. Communal spawning was not observed. The egg masses of 3 individuals were selected for examination.

Capsule production in this species is rapid. Approximately 1,500 were produced in a period of 24 hours or about

one every 2 minutes. Fortunately, the transparent substrate permitted observations of the spawning process. Pustulate capsules are released from the oviduct and passed through the mantle cavity to the right side of the propodium, where they enter a lateral fold running across the ventral surface. After passing to the midline of the foot, each capsule is agitated slightly, surrounded by mucus and then held firmly on the substrate for a few seconds. The pedal gland does not envelop each egg case. When the animal is undisturbed the process is continuous with a capsule being held on the right of the fold as the preceding one is attached to the substrate. Spawning females do not deposit all available ova in a single mass. This accounts for the wide range in the total number of capsules per mass (250 to 1,500).

The position of each capsule clearly shows the movements of the female during oviposition (Fig. 11A). As each pustulate structure is cemented to the substrate, the propodium moves in a short, lateral arc. When the 1st arc is completed, the animal moves over the freshly deposited material and begins an arc in the opposite direction.

Like so many other prosobranchs, the egg capsules of *Distorsio clathrata* undergo a series of color changes related to the acquisition of embryonic pigment. Initially, the capsules are white or grayish-white. After ingestion of albumen on the 5th day, the capsules appear granular. On the 12th day, a pinkish-brown tint appears. Gradually this color changes to heliotrope at hatching on the 15th day. Capsules with dead embryos remain white.

Capsular size is relatively uniform within the main body of the egg mass. Variations occur at the beginning and end of oviposition or wherever the spawning animal made a sharp change in direction. The average diameter of 10 capsules from

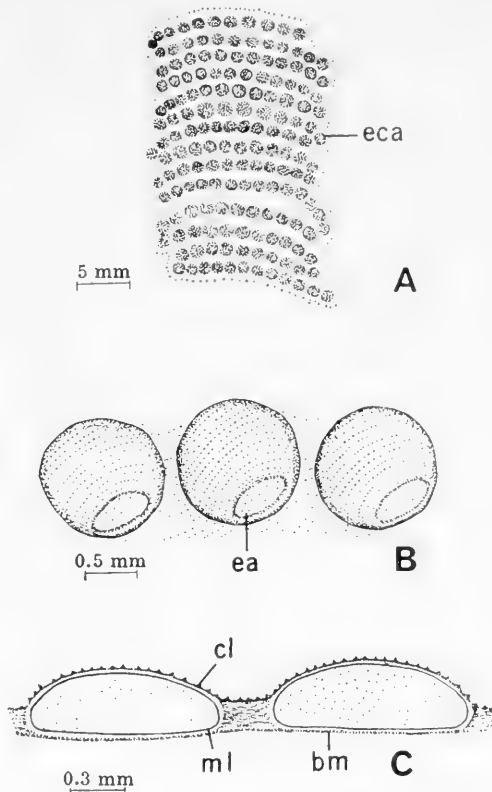


FIG. 11. Egg capsules of *Distorsio clathrata*; A, segment of a typical egg mass (dorsal view); B, 3 egg capsules showing the escape-aperture (dorsal view); C, a cross-section of 2 egg capsules.

the median portion of a mass was 1.1 mm. The average height of the same capsules was 0.5 mm.

The upper surface of each pustulate structure is covered by a coriaceous layer sculptured by curved striations, while an inner membranous layer forms most of the walls (Figs. 11B-11C). A basement membrane attaches the capsules to each other and to the substrate. At hatching, a large oval escape-aperture appears on one side (Fig. 11B).

The number of embryos contained in each capsule ranged from 20 to 40 with an average of 35. Since the total number of capsules per mass varied from 250 to

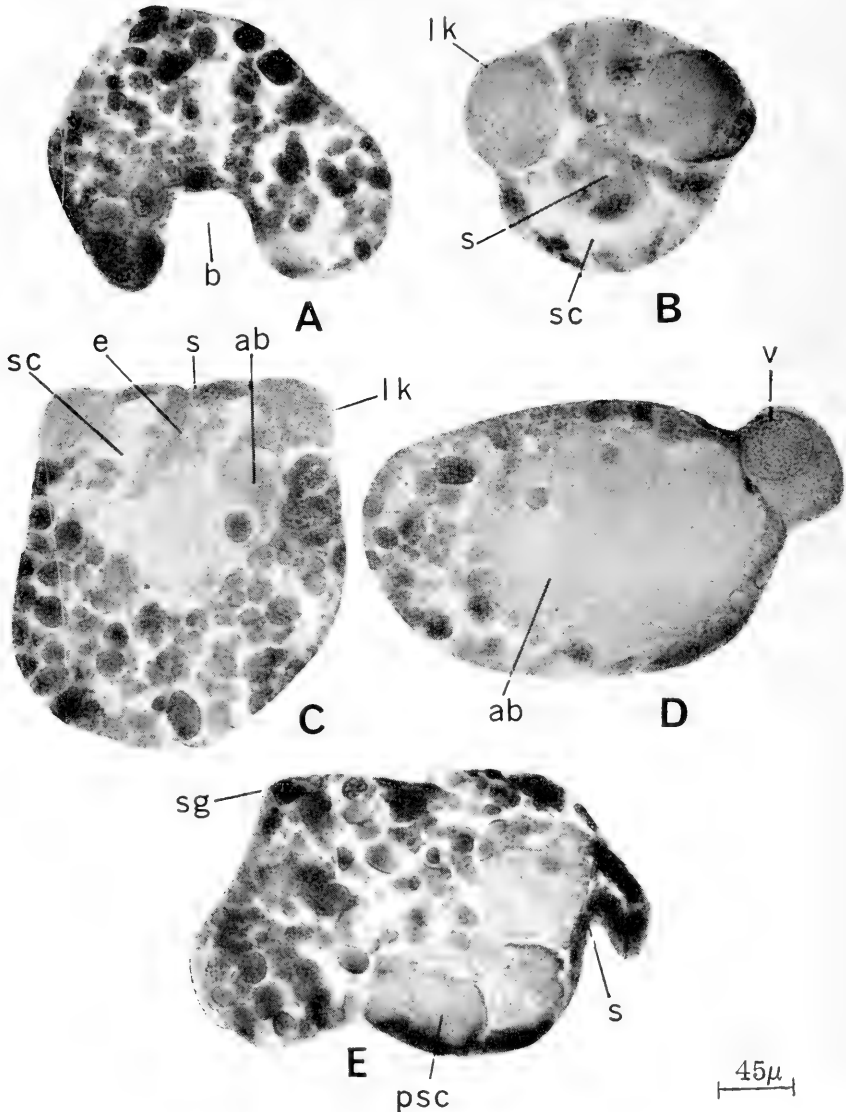


FIG. 12. Development of *Distorsio clathrata*: A, cross-section of the stereogastrula; B, cross-section through the stomodeal region; C, frontal section through the esophagus; D, parasagittal section through the archenteron (5 days); E, oblique section through the stomodeum and the peripheral storage-cell (5 days).

1,500, the material examined contained from 9,000 to 53,000 embryos.

## 2. Embryogenesis

The data on early cleavage are incomplete because *Distorsio clathrata* is rarely observed spawning, and only a single

series was available for examination. A second difficulty is introduced by the presence of a granular, albuminous fluid in each capsule which obstructs observation. Removal of the embryos from the capsules results in a high percentage of atypical development.



Cleavage proceeds to the 4 cell stage in 8 hours. The formation of primary blastomeres is highly irregular. Like most of the higher prosobranchs studied by Bobretzky (1877) and Pelseener (1911) the CD and D blastomeres are consistently larger. This disparity in size can be followed in the successors of D though the later stages of gastrulation. Typically, D protrudes laterally and ventrally from the vegetal region. After 24 hours, a stereoblastula appears.

Epibolic gastrulation begins at 30 hours. Expansion of the successors of 2d produces the initial stages of flexion as early as 35 hours. Ectomeres surround the embryo by the end of the 3rd day. The 2nd phase of gastrulation forms an open blastopore and archenteron by invagination (Fig. 12A). Shortly thereafter, the blastopore partially closes. Deutoplasmic storage, for the most part, is in the successors of the macromeres, which are incorporated into the walls of the archenteron. Two large ectodermal cells, lateral to the stomodeum, are the anlagen of the larval kidneys. Generation of entomesoderm begins during this stage.

*Four Days.*—Partial closure of the blastopore results in the formation of the stomodeum (Fig. 12B). The cells making up the stomodeal lip and esophagus increase in diameter and become ciliated. No organized ciliation is present in the archenteron. Rapid, early completion of the anterior digestive tract is the prelude to ingestion of the granular albumen (Fig. 12C). All traces of albumen are removed from the capsules before the 5th day. Expansion of the larval kidneys coincides with the intake of albumen. These kidneys are located dorsal and lateral to the stomodeum and extend sharply away from the ectoderm. Each renal cell is surrounded basally by support cells and is in contact with the rudimentary blastocoel and the entoderm (Fig. 12C). The kidneys are filled with a

granular fluid and contain colorless vacuoles (Fig. 12D). A shell gland anlage develops posterior to the larval kidneys. Cilia are concentrated on the lips of the anlage and on the lateral trochoblasts. Growth of the apical sensory region begins near the end of the 4th day.

*Five Days.*—The most obvious change during the 5th and 6th days is the far reaching growth process which slowly shifts the position of major structures. Part of this flexional process is due to expansion of the shell gland. During the 5th day, the embryo is somewhat spherical with protruding, dorsal larval kidneys (Fig. 13A). The shifting process moves the kidneys away from the stomodeum (Fig. 13B). At the same time there is a lengthening of the whole embryo along an axis from the apical sensory region through the site of the shell gland. A period of rapid, aimless rotation ensues with propulsion being provided by the cilia of the secondary trochoblasts, stomodeum and sensory region.

*Six Days.*—The removal of albumen from the archenteron is due to the activity of specialized, peripheral storage-cells (Fig. 12E). These cells, which are almost entirely vacuolated, become arranged into a 1 cell thick layer in parts of the anterior digestive anlage. Cellular intake of nutritional fluid is probably by phagocytic activity. The process is aided by the early appearance of 2 types of cilia, the slender gastric type and the fused cilia of the rudimentary style-sac stomach. Rotation of the stomach contents moves albumen into the vicinity of the peripheral cells. Removal of albumen from the primitive stomach gradually produces a centrally located transparent region in the living veliger (Fig. 13B). Expansion of the pedal anlage adds another set of growth vectors which modify the earlier reorganization (Fig. 13C). Vacuoles take up most of the volume of the larval kidneys.

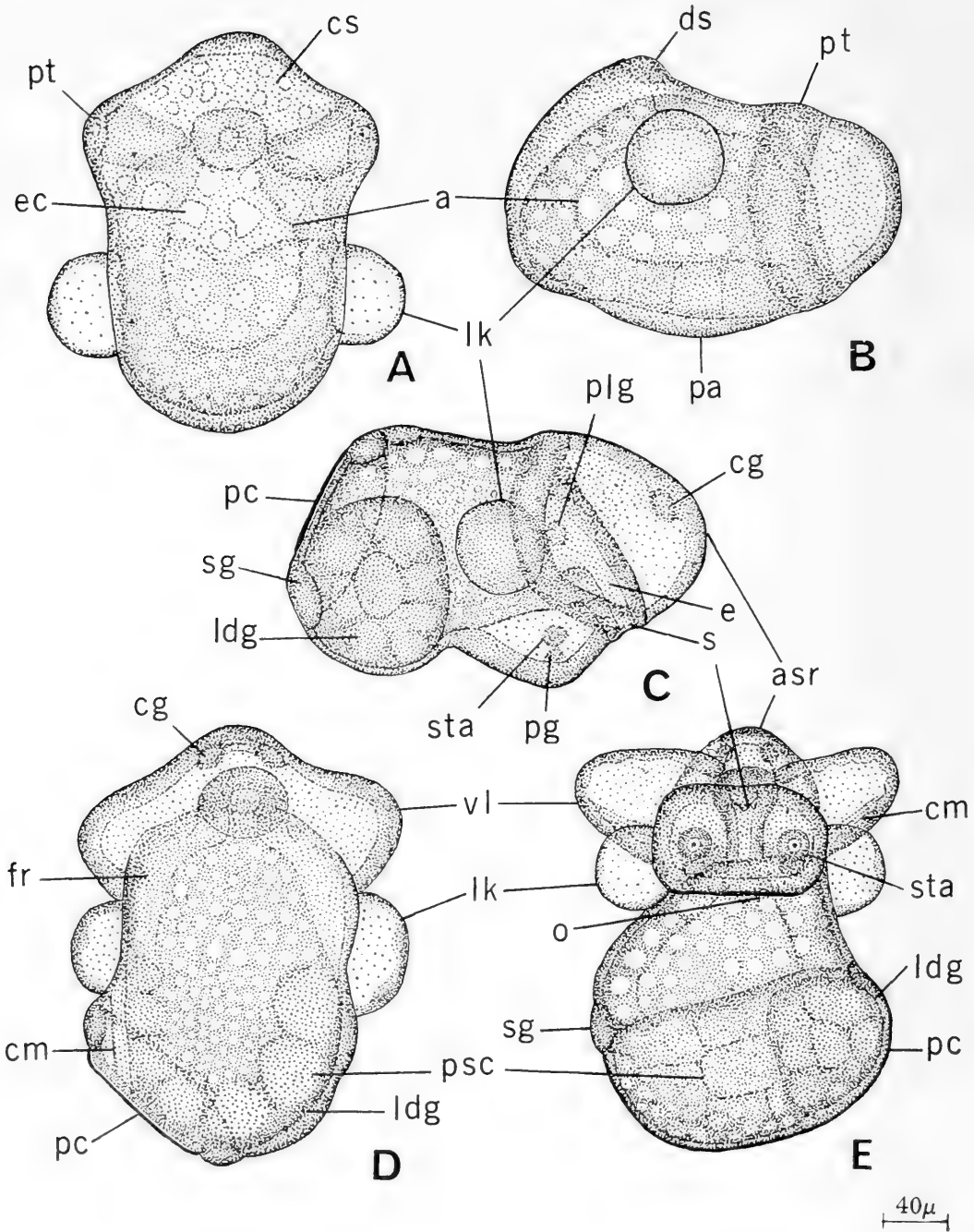


FIG. 14. Development of *Distorsio clathrata*: **A**, ventral view during expansion of the velar sinuses (8 days); **B**, formation of the dorsal process of the shell gland (8 days); **C**, formation of ganglia on the right side (9 days); **D**, localization of peripheral cells in the left digestive gland during the torsional pause seen in dorsal view (9 days); **E**, beginning of the last stage of torsion seen in ventral view (10 days).

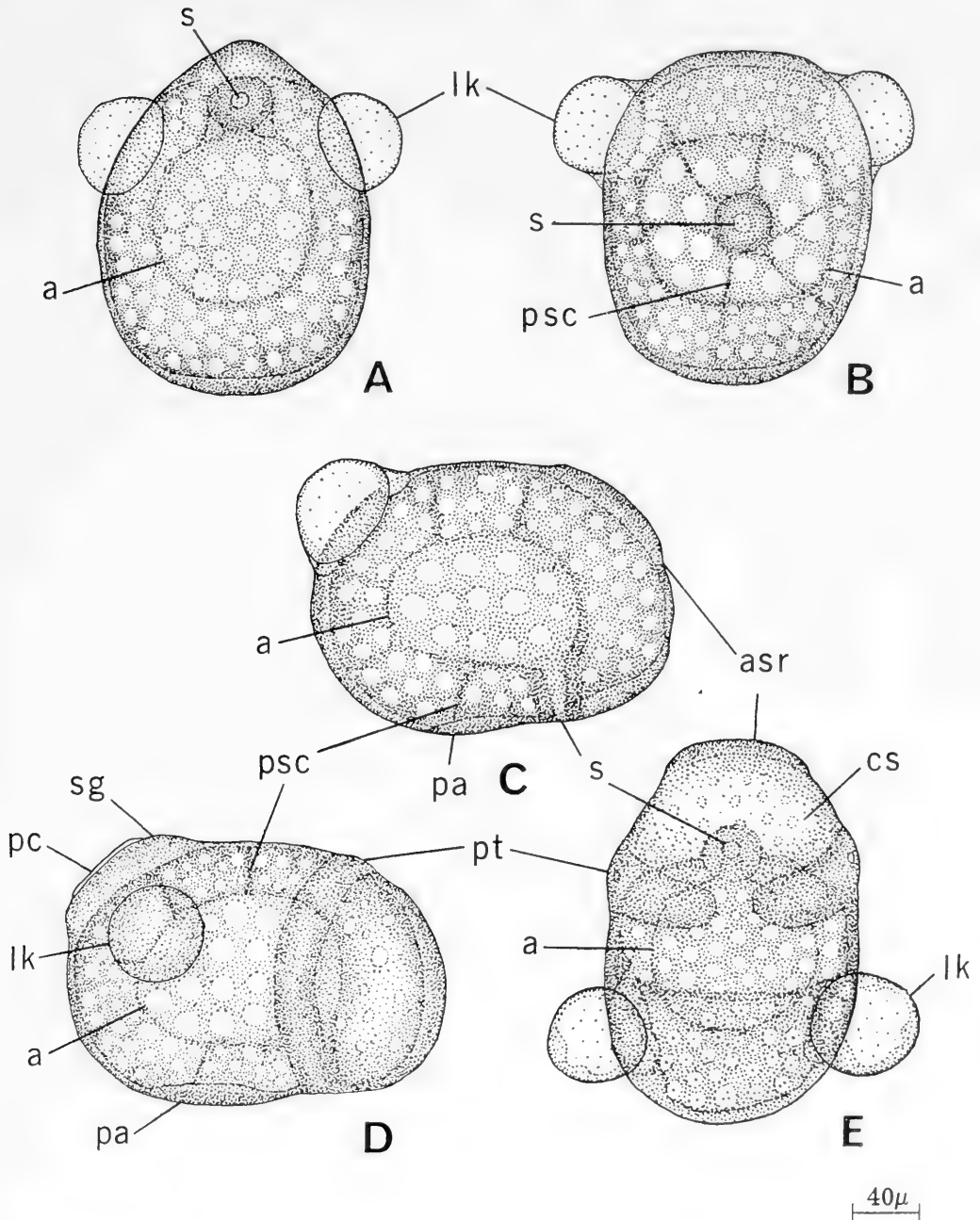


FIG. 13. Development of *Distorsio clathrata*: A, ventral view during ingestion of albumen (5 days); B, flexion (6 days); C, peripheral cells and the pedal anlage seen from the right side (6 days); D, evagination of the shell gland (7 days); E, formation of the sinuses and protoconch in ventral view (7 days).

Seven Days.—Evagination of the shell gland is followed by the immediate secretion of a conchiolinous protoconch

(Fig. 13D). The major growth vector of the shell gland is dorsally oriented. Both the dorsal and ventral lips of the

gland contain medial, ciliary bands which expand laterally. As the shell gland becomes cap-shaped, the growing edge contributes to a process which shifts the larval kidneys anteriorly.

A marked increase in size and the production of definitive velar ciliation indicate the beginning of the major stage of prototrochal development (Figs. 13D-13E). Definitive ciliation stops the aimless rotation and produces a forward movement. The apical sensory region develops the short, fused cilia typical of this structure. A prominent cephalic sinus is present.

*Eight Days.*—Pretrochally, velar expansion begins (Fig. 14A). Growth of the lobes constricts the wide apical region and shifts the plate to its definitive position. The cephalic plates are covered with delicate cilia unlike the sensory type. Posterior to the sensory area, the dorsal ectoderm is marked by large, irregular epidermal cells.

Posttrochally, the shifting larval kidneys reach their definitive position in the pleural region (Fig. 14A). The shell gland has a dorsal process (Fig. 14B). Pedal expansion begins, but no sinus is present. The majority of the peripheral storage-cells lie in the pleural and pedal regions (Fig. 12E). An obscure proctodeal invagination appears posterior to the rudimentary foot (Fig. 15A).

### 3. Organogenesis

*Nine Days.*—After the dorsal process of the shell gland is fully expanded, the first stage of torsion begins. The primary effector of this stage is probably the right larval retractor; however, the origins and insertions of this muscle could not be accurately traced. After approximately 90 degrees of rotation occurs, there is a 24 to 36 hour pause.

Three pairs of major ganglia are formed from the ectoderm during early torsion (Fig. 14C). The cerebral ganglia

arise as invaginations at the edges of the cephalic plates. Small, lateral proliferations into the ventral sinus produce the pedal ganglia. Dorsal to these proliferations, lateral invaginations form the statocysts. In the pleural groove, a delaminatory process close to the larval kidneys produces the pleural ganglia. Development of commissures occurs almost immediately between the components of the cerebral and pleural pairs. In both cases, the connecting structure arises as a delaminated, ectodermal band penetrated by fibrillar outgrowths. All connectives appear as fibrillar outgrowths interspersed with ectodermal cells.

Prior to torsion, there is considerable evidence of utilization of albumen and degeneration of the remaining macromeres. Fragments of yolk are scattered through the archenteron (Figs. 15A-15B). The expanding cephalopedal complex begins to separate itself from the food-storage regions of the digestive anlage. This trend in growth ultimately shifts the remaining peripheral storage-cells posteriorly in the visceral region. In addition, new storage-cells appear in the anlage of the left digestive gland, which absorb remnants of yolk from the macromeres (Fig. 14D). The gastric region, surrounding the esophageal insertion, contains non-yolky cells. As torsion progresses, the stomach complex divides into gastric and style sac components which are contractile and contain specialized cilia. The intestine is formed when the proctodeum opens on the anterior face of the style sac.

At this point, the larval kidneys reach the stage of maximum expansion. Each kidney is typically spherical, contains a central vacuole and borders on the posterior velar sinus (Fig. 15C). On the right side, mesodermal elements consolidate into the renopericardial anlage.

Pretrochally, the cephalic and velar sinuses are well defined. Ciliary con-

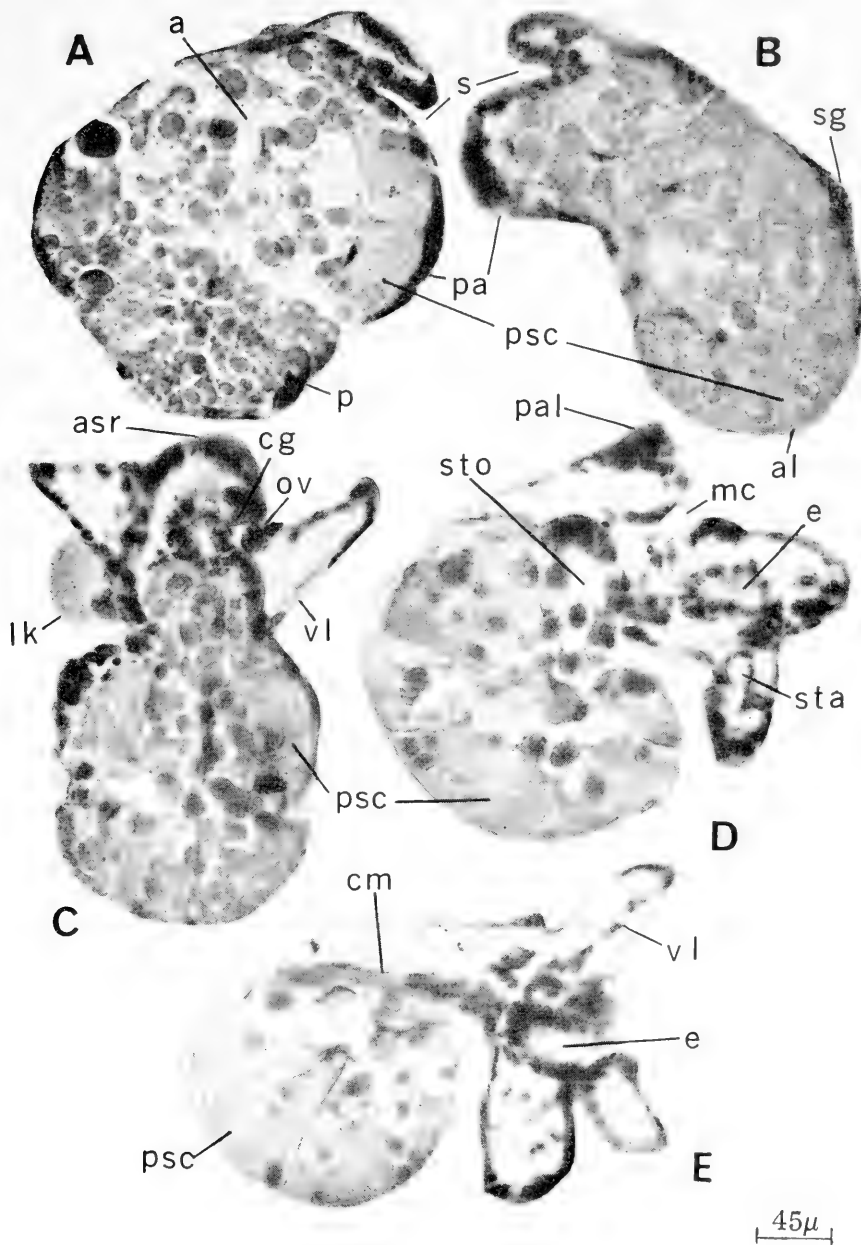


FIG. 15. Development of *Distorsio clathrata*: A, parasagittal section through the proctodeal plate (8 days); B, parasagittal section through the digestive anlage (8 days); C, oblique section through an optic vesicle (10 days); D, sagittal section through the digestive anlage and pallial lobe (11 days); E, parasagittal section through the left digestive gland (12 days).

nections from the velar lobes to the stomodeum are complete, but the protoch is unmodified. Poststrochally, the

membranous protoconch covers one third of the visceral mass (Figs. 14C-14D). Mesodermal cells consolidate on the left

side near the protoconch in what was the pretorsional dorsal process. This band of cells is the anlage of the columellar muscle. Except for the opercular gland, the pedal region is covered with unspecialized cilia.

*Ten Days.*—Most of this period is taken up by the torsional pause and a decrease in length due to consolidation in each system. A prominent columellar muscle appears prior to the last stage of torsion. Branches of the muscle insert on the walls of the velar and pedal sinuses. The early protoconch covers  $\frac{3}{4}$  of the visceral mass (Fig. 14E). Secretion of the operculum is complete.

The left digestive gland arises from the posterior remnant of the digestive anlage. The remaining peripheral storage-cells are isolated in this area. At first, the lumen of the gland is narrow, but rapid growth causes expansion as the contents of the peripheral cells are utilized. Ciliation of the digestive tract is entire.

Developments in the nervous system are basically consolidations, including shortening of connectives with a concomitant decrease in total length and compaction of the ganglionic cells into ovate structures. Optic vesicles invaginate at the border of the apical and cephalic plates, slightly dorsal to the cerebral ganglia (Fig. 15C). Each vesicle is connected to the cerebral ganglia by outward expanding nerve fibres. Statoliths appear in the statocysts.

*Eleven Days.*—Torsion is completed during the early part of the 11th day. The end of rotation coincides with completion of the initial protoconch and formation of the elevated pallial lobe and early mantle cavity (Fig. 15D). When the unsculptured and unpigmented protoconch is in its definitive position, the dorsal mantle lip begins a process of ascension similar to that found in *Crepidula adunca* (Moritz, 1939) and *Bursa corrugata*. The lateral fold created by

growth of the shell gland over the pleural region produces the mantle cavity, but the folding process is not completed. Instead, the lip continues to expand dorsally forming a pallial lobe (Fig. 16A). Dorsal expansion is followed by the appearance of atypically long cilia on the lobe and a heliotrope pigment in the ectodermal cells of the cavity. At first, most of the pigment is centralized in the mantle skirt. Later, it gradually spreads over the whole cavity.

All major ganglia, except the buccals and viscerals have developed. The cerebral commissure separates its ganglia with a nodal expansion that later disappears. No obvious nerves connecting the cerebrals to the apical sensory region are present. Red, retinal pigment is produced in the optic vesicles. Secretion of a crystalline lens begins after pigment formation. The esophageal ganglia are not distinguishable until torsion is complete. The supraesophageal-osphradial connective becomes prominent and obscures part of the visceral loop.

*Twelve Days.*—The continued dorsal expansion of the pallial lobe has a concomitant effect on the shape of the protoconch. Since the trend of growth in the mantle lip is toward the right side, the aperture lip is distorted in the same direction (Fig. 16B). There is a slight disparity in size between the velar lobes with the right lobe being larger. Formation of the right tentacle begins at this time. A connective extends from the tentacle to the right cerebral ganglion. There is no sensory structure associated with the pedal region prior to hatching. The ciliated margin of the foot extends to the lip of the round operculum.

Circulation of fluids, which had been controlled by sinusoidal contraction, now becomes systematized. The renopericardial anlage, located on the dorsal left side near the mantle cavity, has a schizocoel. This structure will become the

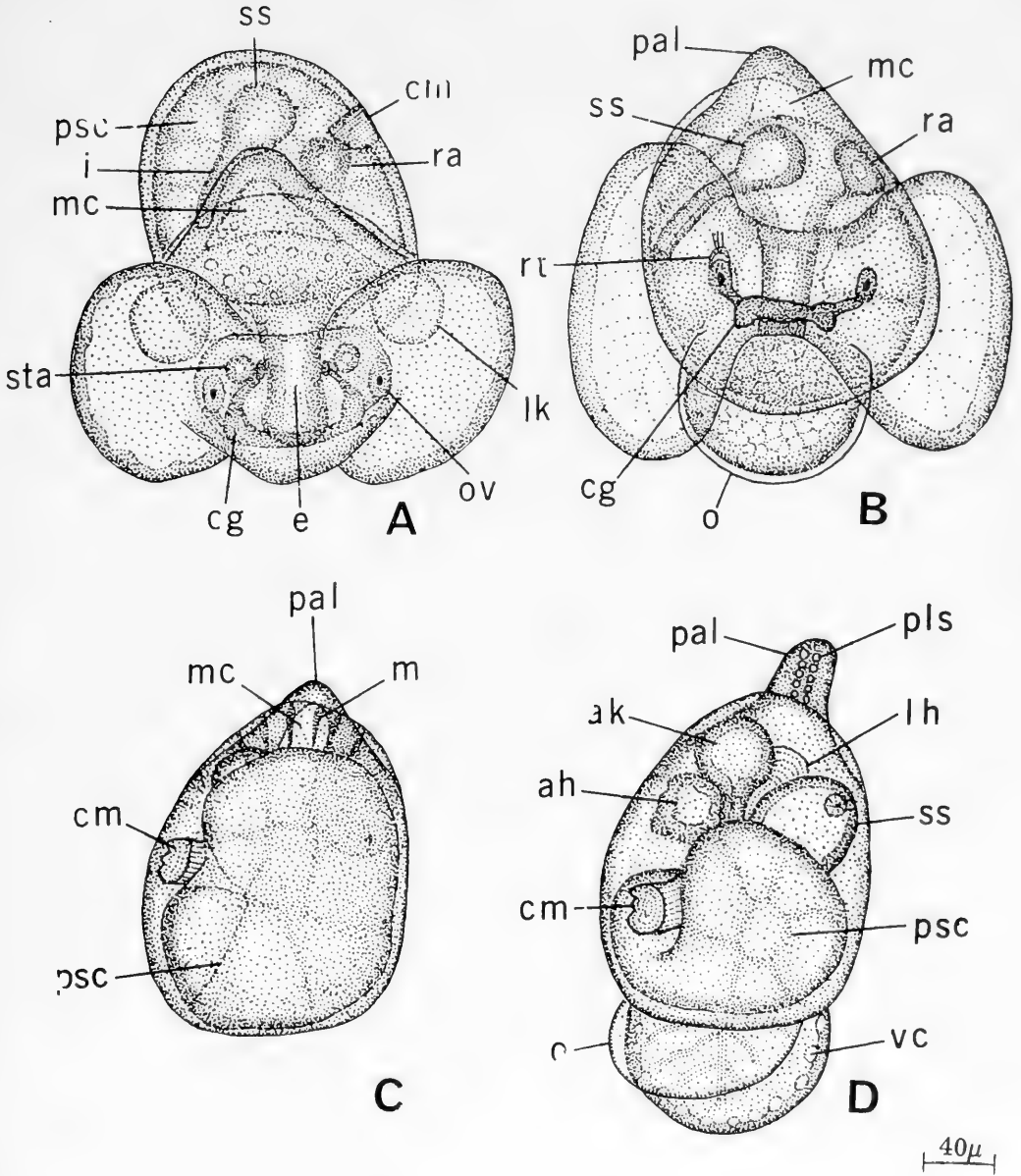


FIG. 16. Development of *Distorsio clathrata*: **A**, formation of the pallial lobe in velar view (11 days); **B**, formation of the pallial lobe (12 days); **C**, dorsal view of the visceral region only (13 days); **D**, dorsal view of the visceral region and the foot (14 days).

adult kidney after evaginations produce the adult heart and possibly the gonadal anlagen. Interconnecting sinuses on the floor of the mantle cavity in the torsional plane produce rudiments of the larval

heart and the anterior aorta. The larval kidneys are reduced to a quarter of their original size.

*Thirteen Days.*—Numerous myoblasts are connected to the dorsal mantle lip

where they function as pallial retractors. Other large clusters of similar cells occur just posterior to the renopericardial anlage where they act as accessory visceral retractors. Myoblasts unrelated to those of the columellar muscle form radial pedal retractors and connect the ectodermal layers of the foot. The major retractor or columellar muscle has its origin on the left side of the protoconch and passes anteriorly through a fold in the visceral mass (Figs. 15E & 16C). After passing ventral to the esophagus the insertions are in the cephalic and pedal regions.

Final absorption of the larval kidneys takes place over a 24-hour period. Remnants of the kidneys are reduced to a cluster of granular, yellowish cells. No excretory bodies were observed being released.

The anlage of the definitive right digestive gland is the last of the major digestive organs to develop. It appears just dorsal to the junction of the left gland and the gastric stomach. Yolk filled cells still give the complex stomach a rounded appearance (Fig. 16C).

Externally, the veliger is only slightly modified. Pedal ciliation is complete. On the metapodium there is a sensory node with bristles projecting beyond the edge of the operculum. The pallial lobe is carried folded over the dorsal aperture-lip.

*Fourteen Days.*—Hatching through an oval escape-aperture (Fig. 11B) begins at the end of the 14th day. Apparently enzymes secreted by the embryo dissolve the borders of the aperture plug as suggested by Pelseener (1935) and Davis (1967). Constant incidental collisions by the rapidly swimming veligers gradually tear away the oval region. Once the capsule is open, all normal veligers escape within minutes. Hatching is uneven and does not always begin with the oldest capsules. It is important to note that at the moment of escape each veliger,

regardless of age, has reached the same ontogenetic stage.

All major ganglia and sensory organs required by a planktotrophic veliger are present. The visceral ganglia, which are difficult to identify, appear as simple proliferations on the floor of the mantle cavity. The left tentacular anlage is nodular and undeveloped, but it has a nerve trunk from the left cerebral ganglion. A similar nerve extends to a ganglion at the distal end of the right tentacle. Sensory organs cover the right tentacle. In the left posterior mantle cavity, a swelling marks the initial development of the osphradium.

Including the food grooves, the veliger has a completely functional digestive system. Feeding begins immediately after hatching. The walls of the style-sac stomach contain yolk-free cells (Fig. 16D), although some remnants of embryonic food are localized in the gastric food-storage region. An evagination into the anlage of the right digestive gland occurs before it becomes functional. At this stage, the intestine extends directly from the anterior style-sac stomach to the right side of the mantle skirt (Fig. 17A). The heliotrope pigment, which was first localized in the mantle cavity, spreads to the esophagus, gastric stomach, renopericardial anlage, larval heart and the anterior aorta.

Both hearts are active at 14 days. Contraction by the larval heart is much more rapid than that of the definitive heart which rarely contracts. The adult structure is located ventral and to the left of the definitive kidney (Fig. 16D). A renopericardial duct connects these organs. Anlagen of the ductus arteriosus and posterior aorta are present as narrow sinuses. Except for the anterior aorta, the functional circulation is maintained through interconnecting sinuses. A renal valve opening into the mantle cavity could not be detected, but the kidney contracts rapidly.



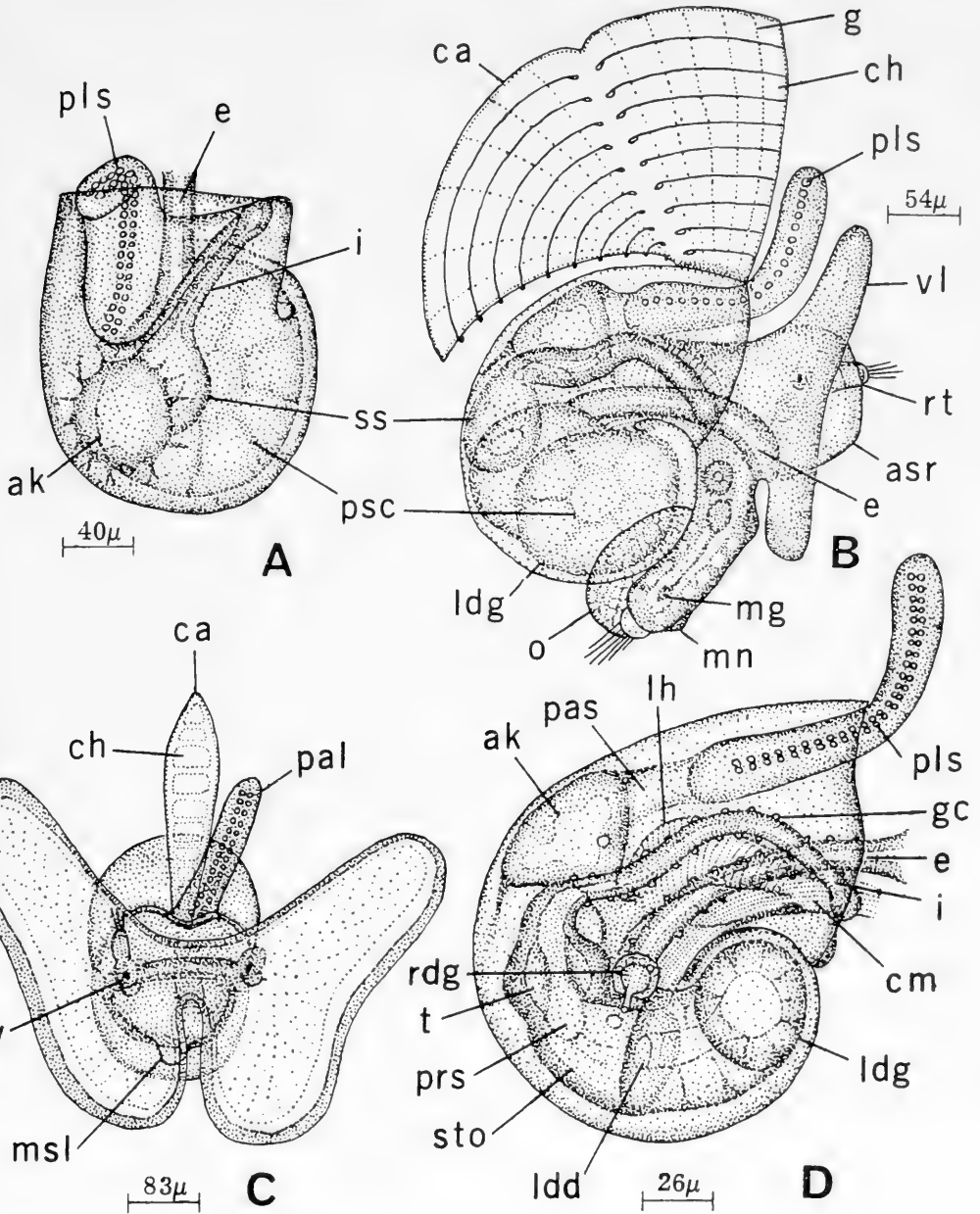


FIG. 17. Development of *Distorsio clathrata*: **A**, dorsal view of the visceral region only (14 days); **B**, right side of a carinate veliger (15 days); **C**, velar view of a carinate veliger (16 days); **D**, right side of the visceral mass only (16 days).

Conspicuous lines of cells appear in the mantle skirt and on the edge of the foot (Figs. 16D & 17A). These pallial cells are associated with formation of a carina

on the protoconch at a later stage. They are organized into a band, two cells wide, which extends from the posterior mantle cavity near the osphradium to the dorsal

edge of the pallial lobe. Each cell appears to have a secretory nature and is closely associated with the pallial ectoderm in contact with the protoconch. On the foot, large vacuolated cells develop on the mesopodial and metapodial border (Fig. 16D) and gradually spread into the ventral ectoderm.

*Fifteen Days.*—The appearance of a complex carinate structure attached to the dorsal aperture-lip spectacularly marks the first day of planktotrophic growth (Figs. 17B-17C). Production of the conchiolinous keel by the pallial lobe begins shortly after hatching. The lobe is extended posteriorly over the protoconch and executes an anteriorly directed arc as secretion progresses. After the initial arc, all further carinal growth proceeds concomitant with the formation of the protoconch. The carina is attached only on the apertural beak at the beginning of the arc; however, further growth lengthens the point of attachment. Seen laterally, there are numerous growth lines parallel to the dorsal lobe (Fig. 17B). Perpendicular to the lobe there are 8-11 bands of conchiolin. When seen in cross section it is immediately apparent that the bands of conchiolin actually delimit chambers (Fig. 18A). The third chamber from the top is usually the largest with the sides tapering rapidly to a sharp, dorsal edge. A more gradual tapering occurs between the third chamber and the basal attachment. Occasionally, a pause in the secretory process produces a break in the bands (Fig. 17B). The height of the carina averages  $177\mu$  with the longest dimension of the veliger including the carina averaging  $460\mu$ . Clench & Turner (1957) examined the protoconch on the adult shells of *Distorsio clathrata* but they found no sculpture of any type. Apparently the carina is a characteristic of the early larval stages that is covered over by later whorls or lost. Concurrent with keel production,

a light brown pigment is evenly distributed through the protoconch and the operculum becomes reticulated. A rudimentary columella is present.

Modifications in the digestive system are concerned with feeding and handling increasing quantities of algal food. All embryonic food stored in the walls of the complex stomach has been used. Remnants of the peripheral storage-cells are still present in the left digestive gland. The typhlosoles of the style-sac stomach produce a protostyle when feeding begins (Figs. 18B-18D). Heliotrope pigment is distributed through the whole digestive system except for the digestive glands. Sites of greater concentration are located in the walls of the style-sac where the pigmented cells are arranged in a linear pattern. The intestine bends sharply to the right, just posterior to the kidney, and extends to the right side of the mantle cavity. Then it curves dorsally to the middle of the cavity and turns ventrally again near the edge of the mantle (Fig. 18E). Occasionally, the swollen and ciliated anal region extends beyond the pallial lip.

*Sixteen Days.*—Further expansion of the carina is balanced by dorso-ventral elongation of the velum, which, with lateral folding, gradually produces 2 pairs of velar lobes (Fig. 17C). When fully expanded the narrow dorsal lobes extend to the upper edge of the carina. Normally, they are held at a 45 degree angle to the keel. The ventral lobes are shorter and wider than the dorsal pair. All velar food grooves are narrow.

A rudimentary hypobranchial gland occupies the mantle skirt between the intestine and the pallial lobe. The parallel rows of cells in the lobe extend posteriorly to a large pallial sinus which separates them from the edge of the definitive kidney (Fig. 18F).

Transparent cells of undetermined function are scattered over the esophagus and intestine (Fig. 17D). Insertions of

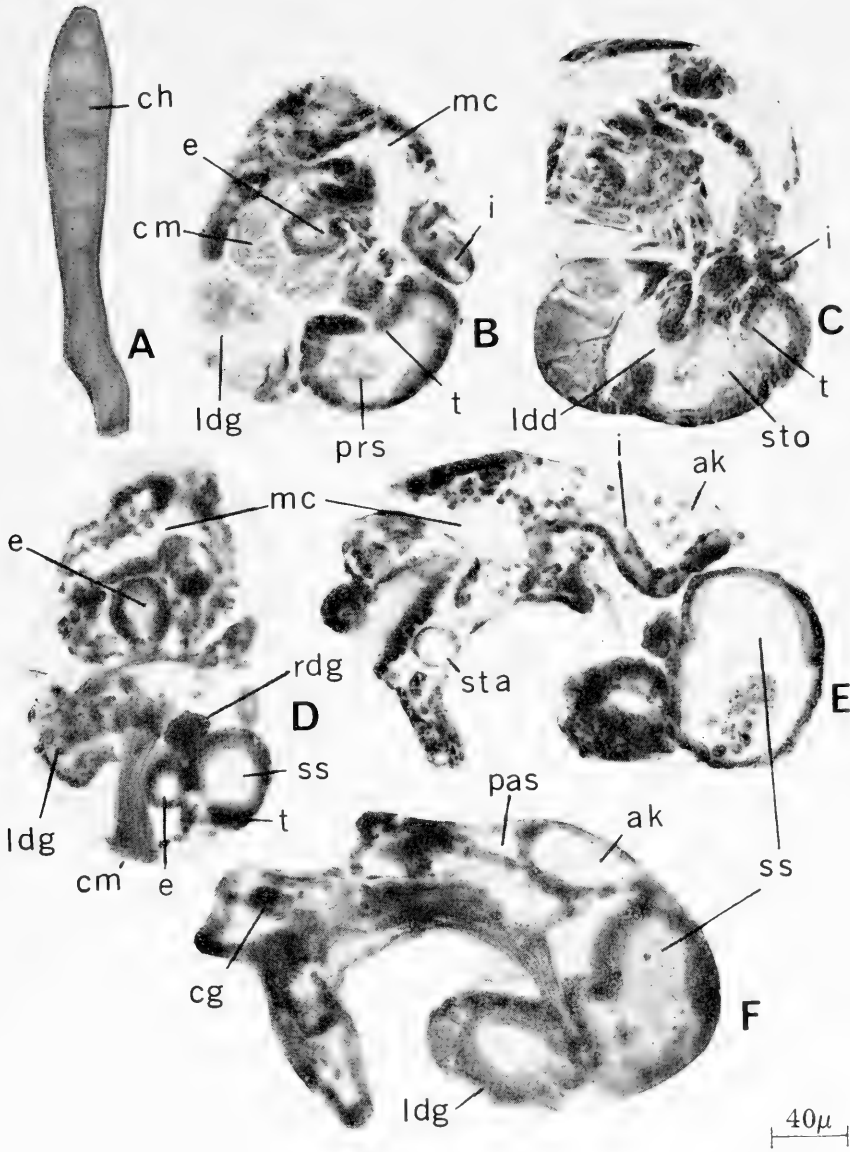


FIG. 18. Development of *Distorsio clathrata*: A, cross-section of the carina (15 days); B, cross-section of the body at hatching (15 days); C, oblique section through the stomach (15 days); D, cross-section through the body (16 days); E, parasagittal section on the right side (18 days); F, parasagittal section through the kidney (18 days).

ducts in the gastric stomach are easy to identify at this stage. The esophagus opens on the right ventral side at the edge of the style sac. Of the digestive ducts, the left one is the largest and opens on the posterior left side (Fig. 18C). A

portion of the left gland extends from its point of insertion under the stomach to a definitive position in contact with the right gland. The right digestive duct opens dorsal to the esophageal insertion. All insertions function as valves. There is

no caecal region in the gastric stomach.

Three contractile organs are present, the larval and adult hearts and the adult kidney. A large renal duct, which responds to each contraction, opens into the posterior mantle cavity (Fig. 17D). Pallial sinuses already are arranged in a tentidial pattern.

*Eighteen Days.*—Pedal modifications begin with the formation of the propodial anlage and the metapodial node. A terminal metapodial lobe is found in most planktotrophic veligers, but the medial node is uncommon (Fig. 17B). Large, transparent cells, similar to the border cells, lie in parallel lines in the mid-vental foot. The reticulated operculum is approximately circular. Within the foot, the nerve pattern is modified by a folding of the pedal commissure and the formation of a metapodial nerve and ganglion (Fig. 17B). Four distinct branches of the columella muscle insert in the foot.

The mouth becomes triangular in shape and mobile concomitant with the appearance of the propodial anlage. Purplish-black pigment outlines the mouth and typhlosoles. Both digestive glands are elongated with the left being twisted. Prominent granulations develop in the anterior lobe of the left gland and in the whole right gland. The first stages of digestive diverticulation are marked by the appearance of swollen areas on the left side of the major gland.

The eighteen-day stage was the last to be examined in this series because the gradual decrease in thickness of the digestive glands without corresponding growth was indicative of slow starvation and atypical development.

## V. DISCUSSION

### 1. Taxonomic Characters of the First Veliger Stages

From hatching to the beginning of

digestive diverticulation the veligers of the species examined have a number of general characters common to other prosobranch veligers as well as a number of more specific characters. Prosobranch characters include a dextral protoconch with a single whorl, bilobed velum, right cephalic tentacle, metapodial sensory structures and a complex gastric system including a style-sac stomach, protostyle and gastric shield. An apertural beak on the protoconch with some type of linear sculpturing is characteristic of most long-term, prosobranch veligers. A prominent osphradial ganglion and the supra-esophageal osphradial connective mark the higher prosobranchs. To prevent confusion with similar opisthobranch veligers, when coiling of the shell is not pronounced, the absence of a secondary kidney located near the anus should be noted.

*Bursa corrugata* has a relatively undistinguished first veliger stage. The typical apertural beak is reduced in size until it is difficult, on this character alone, to distinguish between this species and an opisthobranch such as *Coryphella* (Hurst 1967). However, the dextral shell and the lengthening of the velar lobes into 2 pairs are characteristic of planktotrophic prosobranchs. Characters indicative of the superfamilial relationships of *B. corrugata* can be based with some degree of certainty on the sculpture of the protoconch (for the 1st veliger stage only). The reticulated sculpture formed by fused plates, which have raised edges, has been described for tonnids and now bursids, both of which are in the same superfamily, Tonnacea. Amio (1963) listed the types of protoconch sculpture found in a number of families and he included the tonnids along with the cypraeids, cerithiids and littorinids in a group with so-called "beaten" shells. Thorson (1940) also used the terms "beaten" in his description of the veligers of *Dolium*

(=*Tonna*). Examination of the literature and fresh material from the groups in Amio's category has shown that 2 or more structural types are included. The "beaten" or reticulated type formed by fused plates is more typical of tonnids and bursids while the other groups have a sculptured network without plates.

The 1st veliger stage of *Distorsio clathrata* has the same general prosobranch characters as *Bursa corrugata* with one exception. The velar lobes change rapidly from one equal pair to 2 unequal pairs during the first 24 hours after hatching. The color of the soft parts and the unusual structure of the protoconch offer characters of value on a generic level. Usually color is considered an unimportant character, but Fretter & Graham (1962) have pointed out its usefulness in identifying prosobranch veligers. Although pigment granules of several types are scattered through the soft parts of *D. clathrata*, the heliotrope pigment, which colors the organs of the mantle cavity and the whole digestive system except for the digestive glands, is distinctive. In the veligers of other species, black or shades of purple are common, but typically the pigment is located in specific glands or ectodermal chromatophores. The 2nd generic character is the carinate protoconch. The complexity of the carina rivals that of the echinospira group, since the keel is made up of a number of chambers attached to the shell. No other known veliger has a similar carinate protoconch.

There is one condition which hinders the use of the previously mentioned characters in identification. Long-term planktotrophic veligers do not have instars in development. The early veliger stage is of relatively short duration, transcending into another stage in which both general and specific characters change in relation to definitive developments. Because of this gradual change, identifi-

cation is difficult when only part of the ontogeny is known.

## 2. Development of Natatorial Independence

A study of early organogenesis in the species examined points out the immediate problem of the long-term veliger, the development of natatorial independence. This ontogenetic process is in contrast to that occurring in prosobranch groups with direct development in which the natatory apparatus is suppressed, or in groups with short-term veligers in which there is an early appearance of structures with great post-metamorphic significance, such as the radular sac.

The velar apparatus should be examined first because of its direct relationship to swimming and feeding. After completion of torsion, the cells associated with the rudimentary protoconch separate into 2 distinct ciliary bands. These remain in close association until a few hours before hatching when a shift in position results from the formation of ciliated food-grooves. The ciliary apparatus of the mouth and the median pedal regions is completed at this time. As a result, the veliger is equipped at hatching for swimming and feeding.

In the digestive system, most modifications necessary for assimilation are completed prior to hatching. Embryonic foods from the gastric storage region and the remaining storage cells of the left digestive gland provide reserve energy to sustain the early veligers in their first planktotrophic stage. In atypical situations, the food reserves can maintain *Bursa corrugata* 9 to 10 days and *Distorsio clathrata* up to 14 days. If laboratory culture is successful the embryonic foods are used much faster. In *Thais haemastoma*, when reserves are coupled with an acceptable algal food, most stored food is absorbed in 4 or 5 days (D'Asaro, 1966). Fluctuations in the external food supply

modify the absorption rate in all storage areas. With an increase in acceptable phytoplankton, there is an increase in growth and rapid decrease in stored nutrients. This is indicative of a mechanism to delay growth when external food supplies are minimal. Larval structures associated with the utilization of phytoplankton, which are lost or modified after metamorphosis, include the style-sac stomach, protostyle and gastric shield.

All major ganglia except those concerned with the buccal apparatus are differentiated prior to hatching. Of these, in *Bursa corrugata* and *Distorsio clathrata*, the cerebrals and pedals are larger, while in certain advanced groups, for example *Thais haemastoma* (D'Asaro, 1966), the osphradial ganglion is most prominent. At hatching, each species exhibits a positive phototaxis which is indicative of functional photoreceptors, while responses such as contraction upon stimulation suggest the development of functional tactile organs.

The transition from an embryonic stage to a free-living stage is most obvious in the excretory systems. As the larval kidneys cease functioning and are absorbed concurrent development of the renal anlage produces a functional excretory organ. Only *Bursa corrugata* retains the larval kidneys for the first 2 or 3 days of the free-living stage.

Expansion of the velar lobes and other sinusoid regions is influenced by fluid pressure which is maintained by the larval heart. This commences before the final development of the first pair of velar lobes. At hatching, the larval heart is contracting rhythmically. The definitive heart becomes functional at or slightly after hatching and slowly takes over the functions of the larval pump.

Hatching in each case occurs when the combined development of all organ systems has reached a point at which the

planktotrophic veliger can make use of the primary food supply in the ocean. As mentioned earlier, opening of the egg capsules is probably the result of enzymatic action controlled by the embryo. If veligers are released artificially from their capsules before reaching this stage, mortality during rearing is abnormally high.

### 3. Ontogenetic Variations and Their Significance.

Variations in the general ontogenetic pattern in prosobranchs, which are sometimes quite marked even in members of the same genus, can be placed in several categories: those which are significant in the organization of the embryo, those

An example of organizational variation between the species examined concerns the presence of polar lobes in *Bursa corrugata* and the absence of lobes in *Distorsio clathrata*. These polar structures are also found in certain polychaetes, scaphopods, pelecypods and other prosobranchs. In several tonnacans which have been examined to date, at least two different patterns of lobe movement can be mentioned. A good example of a rhythmic type of polar lobe movement is found in *B. corrugata*. In this case, a plasmic shift, expanding and retracting a lobe containing granular, nonyolky protoplasm, takes place at each maturation and cleavage stage through the second cleavage. *Argobuccinum oregonese* (Phillpott, 1925) has a nonrhythmic, granular lobe present up to the second cleavage. Anderson (1959) looked at the early cleavage stages of *Cymatilesta spengleri*, but no mention of polar lobes was made.

The Neogastropoda typically have lobe formation. In the Muricacea, *Purpura lapillus* (Pelseneer, 1911), *Ocenebra aciculata* (Franc, 1940) and *Thais haemastoma* (D'Asaro, 1966) all have polar lobes, but differ from the tonnacans in having nonrhythmic, deutoplasmic

types. In the Buccinacea, a rhythmic pattern similar to that in *Bursa corrugata* appears again. *Ilyanassa* (Morgan, 1935) has a rapid sequence of production with a yolky lobe extruded at each stage. Not all buccinaceans have a rhythmic pattern. *Fulgur* (Conklin, 1907) has no lobe formation up to the first cleavage, when a granular, non-deutoplasmic lobe appears.

Several points can be made from the examples. First, except for some members of the same genus, there is no case in which the sequence, quantity and quality of the polar lobes exactly matches that of another group. Second and more important, in groups where the greatest similarities occur, such as the bursids and the nassariids, the homologies are exceptions to the typical type of development in that family. The function of the polar lobe in embryonic organization was partially explained by Clement (1952); consequently, it is probable that the extreme variation in size, content and sequence of formation reflect the solution of organizational problems at the embryonic level. As noted by DeBeer (1958), polar lobes may not have been possessed by a common ancestor, but instead the prerequisite conditions for their development have been inherited. Therefore, although lobe formation is an obvious point in ontogeny it offers no reliable clues for phylogeny within the Prosobranchia.

Perhaps the best example of divergence between the 2 species in a major ontogenetic process which affects the larval stages, can be found in the early development of the digestive system. In *Bursa corrugata*, the archenteric wall arises from the digestion of the large yolky blastomeres. There is no evidence of albumen ingestion; instead, the macromeres disintegrate and are absorbed or phagocytized by peripheral storage-cells, producing an open archenteron. *Distorio clathrata* also has peripheral storage-

cells but the process is different. In this case, the archenteron is open at the end of gastrulation, since it is formed partially by invagination. As soon as the blastopore (stomodeum) becomes ciliated, the viscous albumen is ingested, filling the archenteron. Then the albumen is phagocytized by peripheral cells in the archenteric wall.

Several important points should be mentioned. First, the processes creating the archenteric cavities are entirely different. Second, the major functional difference between the 2 species with peripheral cells is that one stores ovarian yolk in peripheral cells, while the other stores initially oviducal albumen. Third, the peripheral storage-cells in *D. clathrata* are somewhat different in structure and are more widely distributed through the digestive anlage than those of *B. corrugata*. Aside from these differences, both species hatch between the 14th and 15th day and have a long-term plantotrophic veliger with a digestive system typical of that stage. Ontogenetic deviations in the Prosobranchia due to the various types of early larval nutrition were examined by Fioroni (1966a, 1967) and correctly termed examples of caeogenesis.

Although an explanation of the torsional process is not a purpose of this paper, it is desirable to point out a major difference between torsion in the Archeogastropoda and that in the higher prosobranchs, since the process directly affects larval and adult stages. Crofts (1955) suggested that differential growth associated with development and migration of the columellar muscle brings about the 2nd stage of torsion, at least in the Archeogastropoda. The ontogenetic evidence from the species examined does not completely support this claim for the higher groups for the following reasons. In each species the organization of columellar myoblasts begins before the onset of the second stage of torsion and is completed before or near

the end of this stage. There is no evidence of migration by the insertion of the columellar muscle during torsion; and finally, there is no columella present until several days after torsion.

An alternative cause for the 2nd torsional stage in the higher prosobranchs can be considered. It could be a complex of differential growth vectors (which may include those of the columellar muscle evolved from the mechanism demonstrated by Crofts in more primitive groups. Naef (1913) thought the whole torsional process in higher prosobranchs was derived from a secondary modification based on differential growth. Some evidence exists to support part of this claim. Fretter & Graham (1962) listed 5 species in which torsion is said to be induced only by differential growth. It can also be stated that a certain amount of growth must occur just to compensate for the shearing stress which takes place in the affected tissues. This factor is especially important in the larger yolky embryos possessed by many mesogastropods and nearly all neogastropods.

The final example of divergence between the species examined concerns the protoconch and appears to be significant at the larval level. It was stated earlier that the reticulated sculpture formed by fused plates is characteristic of most tonnids and is also found in bursids, both of which are tonnaceans. *Distorsio clathrata*, which was included in the Cymatiidae by Clench & Turner (1957), is also a tonnacean; however, the protoconch of the 1st larval stage is unsculptured except for growth striae and a dorsal carina. The carina is reminiscent of the linear formations of dorsal spines or knobs present in the tonnids examined by Simroth (1911) or the unidentified veliger of *Cymatium* type figured by Lebour (1945), yet its greater complexity should not be overlooked. The chambered character of the keel is a result of the secretion of perio-

stracum (conchiolin) by the pallial lobe. Unusual larval structures resulting from a modification of this process are not unknown. A classical example is the echinospira larva of the Lamillariidae, Eratoidea and Capulidae. There is no question that the echinospira is a larval adaptation of significance only to the larva. This appears to be true for *D. clathrata* also, since Clench & Turner (1957) did not find a keel on the protoconch of postlarval shells of this species and showed that the distorted shell is the result of overgrown denticles and plicae.

In summation, the following hypotheses can be made: (1) the early veliger stages of prosobranchs have specific morphological characters which may allow grouping or identification when the larval stages of all members of a taxa have been studied; (2) the immediate problem of long-term planktotrophic veligers is to develop natatorial independence, in contrast to the delayed development and modified digestive systems in species without free-living larvae; and (3) most of the ontogenetic variations between the species examined are of significance only in the larval stages.

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#### LITERATURE CITED

- ABBOTT, R. T., 1954, *American seashells*. Van Nostrand, New York, N.Y., 541 p.
- AMIO, M., 1963, A comparative embryology of marine gastropods, with ecological considerations. *J. Shimonoseki Coll. Fish.*, 12: 229-353.
- ANDERSON, D. T., 1959, The reproduction and early life history of the gastropod *Cymatilesta spengleri*, *Proc. Linn. Soc. N.S.W.*, 84: 232-237.



- ANDERSON, D. T., 1960, The life histories of marine prosobranch gastropods. *J. malacol. Soc. Aust.*, 4: 16-30.
- BOBRETZKY, N., 1877, Studien über die embryonale Entwicklung der Gastropoden. *Arch. mikr. Anat.*, 13: 75-169.
- CERNOHORSKY, W. O., 1967, The Bursidae, Cymatiidae and Colubrariidae of Fiji (Mollusca: Gastropoda). *Veliger*, 9(3): 310-329.
- CLEMENT, A. C., 1952, Experimental studies on germinal localization in *Ilyanassa*. I. The role of the polar lobe in determination of the cleavage pattern and its influence in later development. *J. exp. Zool.*, 121: 593-626.
- CLENCH, W. J. & TURNER, R. D., 1957, The family Cymatiidae in the Western Atlantic. *Johnsonia*, 3(36): 189-244.
- CONKLIN, E. G., 1897, The embryology of *Crepidula*. A contribution to the cell lineage and early development of some marine gastropods. *J. Morph.*, 13(1): 1-226.
- CONKLIN, E. G., 1907, The embryology of *Fulgur*. A study of the influence of yolk on development. *Proc. Acad. nat. Sci. Philad.*, 1907: 320-359.
- CROFTS, D. R., 1955, Muscle morphogenesis in primitive gastropods and its relation to torsion. *Proc. zool. Soc. Lond.*, 125: 711-750.
- D'ASARO, C. N., 1965, Organogenesis, development and metamorphosis in the queen conch, *Strombus gigas*, with notes on the breeding habits. *Bull. Mar. Sci.*, 15(2): 359-416.
- D'ASARO, C. N., 1966, The egg capsules, embryogenesis, and early organogenesis of a common oyster predator, *Thais haemastoma floridana* (Gastropoda: Prosobranchia). *Bull. Mar. Sci.*, 16(4): 884-914.
- DAVIS, C. C., 1967, Emergence of veliger larvae from eggs in gelatinous masses laid by some Jamaican marine gastropods. *Malacologia*, 5(2): 299-309.
- DE BEER, G. R., 1958, *Embryos and ancestors*. Clarendon Press, Oxford, 159 p.
- FIORONI, P., 1966a, Zur Morphologie und Embryogenese des Darmtraktes und der transitorischen Organe bei Prosobranchiern (Mollusca, Gastropoda). *Rev. suisse Zool.*, 73(4): 621-876.
- FIORONI, P., 1966b, Un nouveau cas de rotation des oeufs nutritifs chez un gasteropode prosobranchie marin. *Vie Milieu*, 27(1-A): 109-120.
- FIORONI, P., 1967, Quelques aspects de l'embryogenèse des Prosobranches (Mollusca, Gastropoda). *Vie Milieu*, 18: 153-174.
- FRANC, A., 1940, Recherches sur le développement d'*Ocenebra aciculata*, Lamarck (Mollusque gastéropode). *Bull. biol. France Belg.*, 74(3): 327-345.
- FRETTER, V. & GRAHAM, A., 1962, *British prosobranch molluscs: their functional anatomy and ecology*. Ray Society, London. 755 p.
- HURST, A., 1967, The egg masses and veligers of thirty northeast Pacific opisthobranchs. *Veliger*, 9(3): 255-288.
- KNUDSEN, J., 1950, Egg capsules and development of some marine prosobranchs from tropical West Africa. *Atlantide Rep.*, 1: 85-130.
- KOHN, A. J., 1961, Studies in spawning behavior, egg masses, and larval development in the gastropod genus *Conus*, Part I. Observations on nine species in Hawaii. *Pacific Sci.*, 15(2): 163-180.
- LEBOUR, M. V., 1937, The echinospira larvae of the British prosobranchs with special reference to those living in the plankton. *J. mar. biol. Ass. U.K.*, 22: 105-166.
- LEBOUR, M. V., 1945, The eggs and larvae of some prosobranchs from Bermuda. *Proc. zool. Soc. Lond.*, 114: 462-489.
- MORGAN, T. H., 1935, Centrifuging the eggs of *Ilyanassa* in reverse. *Biol. Bull.*, 68: 268-279.
- MORITZ, C. E., 1939, Organogenesis in the gastropod *Crepidula adunca* Sowerby. *Univ. Calif. Publ. Zool.*, 43(11): 217-248.
- NAEF, A., 1913, Studien zur generellen Morphologie der Mollusken. I. Teil: Über torsion und asymmetrie der Gastropoden. *Ergebn. Zool.*, 3: 73-164.
- OSTERGAARD, J. M., 1950, Spawning and development of some Hawaiian marine gastropods. *Pacific Sci.*, 4: 75-115.
- PATTEN, W., 1886, The embryology of *Patella*. *Arb. zool. Inst. Univ. Wien*, 6: 149-174.
- PELSENEER, P., 1911, Recherches sur embryologie des Gastropodes. *Mém. Acad. r. Belg. Cl. Sci.*, 3: 1-167.
- PELSENEER, P., 1935, Essai d'ethologie d'après l'étude mollusques. Acad. Roy. Belg., *Publ. Found. Agathon Potter*, 1: 1-662.
- PETIT, G. & RISBEC, J., 1929, Sur la ponte de quelques Gastéropodes Prosobranches. *Bull. Soc. Zool. France*, 54: 564-570.
- PHILLPOTT, C. H., 1925, Observations on the early development of *Argobuccinum oregonense*. *Publ. Puget Sound mar. biol. Stn.*, 3(74): 369-380.
- RANJAH, A. R., 1942, The embryology of the Indian apple-snail, *Pila globosa* (Swainson)--Mollusca, Gastropoda. *Rec. Indian Mus.*, 44(3): 217-322.
- RAVEN, C. P., 1958, *Morphogenesis: The analysis of molluscan development*. Pergamon Press, New York, 309 p.

- RISBEC, J., 1931, Note sur la reproduction de quelques Prosobranches neocaledoniens. *Ann. Inst. oceanogr. Monaco*, 10: 23-33.
- SCHILDER, F. A., 1947, Die Zahl der Prosobranchier in Vergangenheit und Gegenwart. *Arch. Molluskenk.*, 76: 37-44.
- SIMROTH, H., 1911, Die Gastropoden des nordischen Planktons. *Nord. Plankt.*, 5: 1-36.
- THORSON, G., 1940, Studies on the egg masses and larval development of the gastropods from the Iranian Gulf. *Danish Scientific Investigations in Iran*, Part 2. Ejnar Munksgaard, Copenhagen, p. 159-238.
- THORSON, G., 1946, Reproduction and larval development of Danish marine bottom invertebrates. *Medd. Kommn. Danm. Fisk.-og. Havunders.*, 4: 1-523.
- YONGE, C. M., 1960, General characters of Mollusca. *Treatise on Invertebrate Paleontology*, Univ. Kansas Press, Lawrence, 1: 1-36.
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## RESUME

EMBRYOLOGIE COMPAREE DU DEBUT DE L'ORGANOGENESE  
DE *BURSA CORRUGATA* PERRY ET *DISTORSIO CLATHRATA*  
LAMARCK (GASTROPODA: PROSOBRANCHIA)

C. N. D'Asaro

Par suite de la proche parenté de *Bursa corrugata* et *Distorsio clathrata* au niveau de la famille, une étude comparative de leur développement peut mettre en évidence certaines différences ontogéniques qui indiquent une adaptabilité au niveau larvaire. Dans ce but, les données suivantes sont présentées. La reproduction, l'émission des gamètes et la structure des capsules des oeufs sont décrites. L'embryologie, y compris le premier stade de torsion, est esquissée. L'organogenèse est suivie depuis la pause suivant la torsion jusqu'à la fin du premier stade veliger planctotrophique, ce qui coïncide avec l'apparition de diverticules dans la glande digestive gauche.

En résumé, les caractères taxonomiques du premier stade veliger sont esquissés et les changements progressifs des caractères larvaires sont notés. Les tendances du développement d'espèces à longue période planctotrophique conduisant à la natation libre sont discutées, compte tenu de la différenciation des organes. Les variations ontogéniques qui sont examinées comprennent la formation de lobes polaires, certains aspects de la torsion, les modes de nutrition des larves et la sculpture de la protoconque.

## RESUMEN

EMBRIOGENESIS COMPARADA Y ORGANOGENESIS TEMPRANA  
DE *BURSA CORRUGATA* PERRY Y *DISTORTIO CLATHRATA*  
LAMARCK (GASTROPODA: PROSOBRANCHIA)

C. N. d'Asaro

Por sus estrechas relaciones en el nivel familiar, un estudio comparado de *Bursa corrugata* y *Distortio clathrata* puede demostrar ciertas disimilaridades en ontogenia indicadoras de adaptación en el estado larval. Con tal propósito se presentan los datos siguientes sobre puesta y estructura de las cápsulas ovígeras, crianza. Embriogenesis, incluyendo desarrollo del primer proceso de torsión, se sumariza. La organogénesis fué seguida desde la pausa torsional hasta el final del estado veligero planctotrófico, el cual coincide con la diverticulación de la glándula digestiva izquierda.

En resumen, los caracteres taxonómicos del primer estado veligero son delineados, y se nota el cambio gradual de los caracteres larvales. Se discute la tendencia, en el desarrollo de las especies con largos periodos planctotróficos, a la independencia natatoria, en relación al sistema de órganos envueltos. Entre las variaciones ontogénicas examinadas se incluyen: formación de lóbulos polares, algunos aspectos de la torsión, métodos de nutrición larval, y escultura de la protoconcha.

## АБСТРАКТ

О СРАВНИТЕЛЬНОМ ЭМБРИОГЕНЕЗЕ РАННЕМ ОРГАНОГЕНЕЗЕ У  
*BURSA CORRUGATA* PERRY И *DISTORSIO CLATHRATA* LAMARCK  
(GASTROPODA: PROSOBRANCHIA)

Ч. Н. Д'АЗАРО

При сравнительном изучении развития у близко-родственных (на уровне семейства) форм *Bursa corrugata* и *Distorsio clathrata*, можно заметить некоторое несходство в их онтогении, что может служить показателем адаптации их личинок к условиям среды. Для получения этих выводов были прослежены и описаны их размножение, откладка яиц и структура яйцевой капсулы, а также эмбриогенез, включая развитие зародыша, вплоть до первой стадии торсии. Органогенез был прослежен, начиная от торсионной паузы вплоть до первой планктотрофной стадии велигера, которая совпадает с образованием дивертикулы левой пищеварительной железы.

В итоге определены: таксономический характер первой стадии велигера и постепенное изменение во времени общего характера личинки. Рассматривается тенденция в развитии планктотрофных видов с долго-плавающей личинкой, приводящая к независимому образу жизни, в связи с системой расположения внутренних органов. Рассматриваются также онтогенетические изменения, включая образование полярных лопастей, некоторые вопросы, связанные с торсией, способы питания личинок и скульптура протокоиха.



SURVIVAL OF THE EMBRYOS OF THE  
GREY FIELD SLUG *AGRIOLIMAX RETICULATUS*,  
FOLLOWING DESICCATION OF THE EGG

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ABSTRACT

Embryos of *Agriolimax reticulatus* were found to survive a weight loss (by dehydration) of 60–80% from the eggs. Advanced embryos were more tolerant of drying than very young embryos. Newly laid eggs were less susceptible when drying occurred more rapidly; *i.e.*, at 50% relative humidity as compared to 90% relative humidity. Drying appeared to have no delayed effect upon the viability of the embryos.

Eggs of both ages lost weight at the same rate, but grouping caused a significant slowing of the rate compared to that of eggs dried singly, the outer eggs of a group drying more rapidly.

INTRODUCTION

The eggs of the terrestrial slug *Agriolimax (Deroceras) reticulatus* appear to have no structural provision for resistance to desiccation, and studies have shown that these eggs have a very poor water retaining capacity (Bayne, 1968). It has been recorded (Carrick, 1939, 1942; Arias & Crowell, 1963) that turgidity of the eggs is dependant upon the maintenance of permanent contact with a moist surface. Since development of the embryos may take several months in the surface layers of the soil (Carrick, 1942), the eggs may from time to time be exposed to drying conditions (South, 1965), and there is the possibility that the embryos might be specifically equipped to survive such exposures.

This paper reports on experiments which measured the effect of desiccation upon the embryos of *A. reticulatus*.

MATERIALS AND METHODS

Newly laid eggs and eggs with advanced embryos (stage V, Carrick, 1939) of *Agriolimax reticulatus* were used. Newly laid eggs were obtained from slugs in laboratory culture as described previously (Bayne, 1966). Stage V (Fig. 1) is reached after about 2/3 of the developmental period, and is easily determined by examination of the transparent eggs under a dissecting microscope. Eggs containing such advanced embryos were obtained by keeping newly laid eggs in moist conditions at 17-20°C for 1-2 weeks. Each egg was examined prior to the experiment and those appearing to be abnormal, unhealthy, dead, infertile, or in any way damaged, were rejected.

The desiccation apparatus, consisting of a glass fibre balance in a constant environment chamber, has been described previously (Bayne, 1968).

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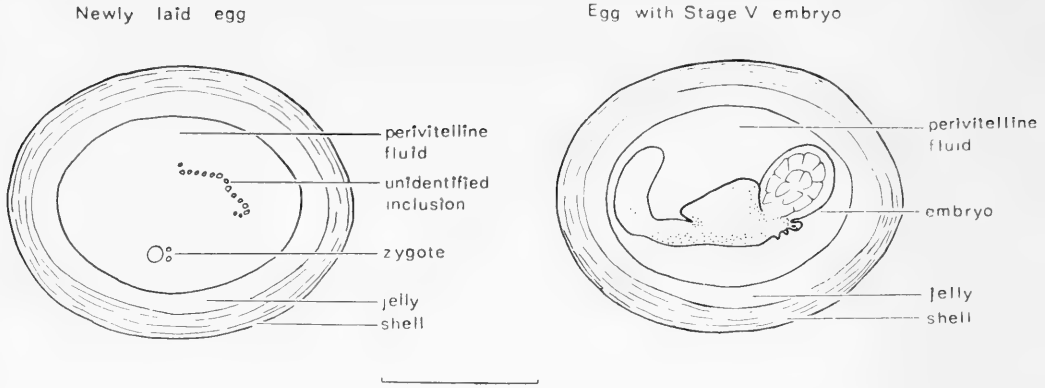


FIG. 1. *Agriolimax reticulatus* eggs, newly laid (left) and containing a stage V embryo (right). The fate of the unidentified inclusion is uncertain, and it may be ingested, together with the perivitelline fluid, by the embryo. Measurement line 1 mm.

In order to determine the ability of the embryos to survive drying of the eggs, groups of 10 eggs were desiccated to different degrees, and another 5 were kept as controls for each group. The amount of desiccation undergone by the individual eggs of a group varied slightly due to their position on the pan, the outermost drying more rapidly. More critical experiments were, therefore, carried out using single eggs: in this way the exact amount of drying undergone by each egg could be controlled, permitting a more accurate determination of the 'upper lethal limit'. With these latter experiments another 2 eggs were cultured as controls for each experimental egg.

Prior to each experiment the fully hydrated eggs were rolled on filter paper to remove excess water. When groups of 10 eggs were dried to 90, 80, 70, 60 or 50% of their original weight, the eggs were spread in a single layer, with neighbouring eggs in contact. For experiments involving a greater degree of desiccation, the eggs were spaced out on the pan to ensure greater uniformity of individual desiccation rates.

Experiments at 90% and at 50% relative humidity (R.H.) were carried out once with the fan on and once with it off.

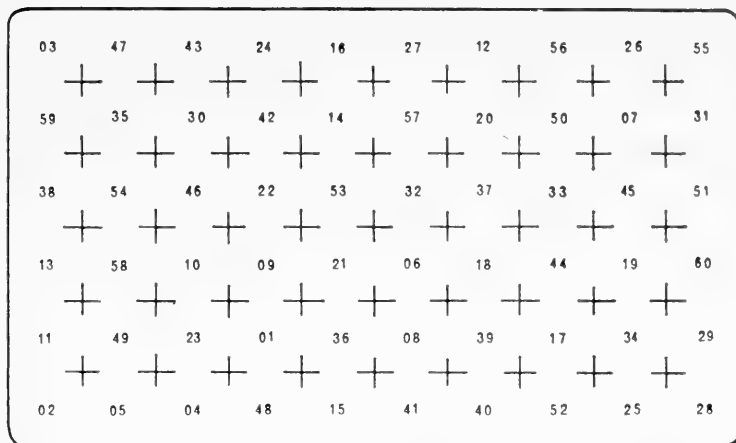
The temperature was kept at  $20 \pm 0.5^\circ\text{C}$ . At the higher humidity the time taken to lose a weight of water was 4-5 times as long as at the lower humidity, so that exposure of the embryo to reduced hydration was more prolonged at 90% R.H.

As soon as the eggs had been dried the requisite amount, they were transferred to the culture vessel (Fig. 2) where they were kept on saturated filter paper, in contact with free water. The culture vessel was kept in the dark in a room at  $19 \pm 2^\circ\text{C}$ . These conditions have been shown to be conducive to healthy development (Cardot, 1924; Carrick, 1942), and hatching occurs in 2-3 weeks.

The eggs were examined at weekly intervals, and the numbers living and hatched were noted. Newly laid eggs were considered to have survived desiccation (i.e., to be viable) if development continued after the experiment, and stage V embryos if the caudal and cephalic vesicles (Carrick, 1939) were pumping after rehydration. Hatchability was assessed simply as the numbers hatching within 3 or 4 weeks.

The results presented below represent experimental data weighted by control values.

A



B

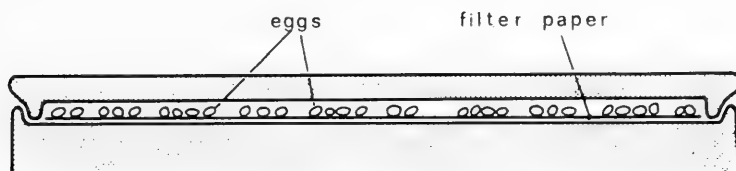


FIG. 2. The culture chamber to which eggs were transferred directly after desiccation. A. Plan of the lid. The numerical order of the culture sites was randomised by use of a table of random numbers. Eggs from successive experiments were placed on the correspondingly numbered sites. Crosses delineate culture sites. B. Sectional front elevation. The filter paper was kept saturated with distilled water.

Viability ( $V$ ) was calculated as follows:

$$V = vd \left( \frac{200 - vc}{100} \right)$$

where  $vd$  = percentage viability of desiccated eggs.

$vc$  = percentage viability of control eggs. By this means any decrease in viability in the controls was used to give a compensatory factor which then increased the viability value of the experimental eggs.

The hatchability value ( $H$ ) is the number hatching expressed as a percentage of those

surviving  $\left( \frac{hd \times 100}{vd} \right)$ . The control

data were then used to weight this value as above. Thus:

$$H = \left( \frac{hd \times 100}{vd} \right) \left( \frac{200 - hc}{100} \right) \\ = \frac{hd(200 - hc)}{vd}$$

where  $hc$  and  $hd$  are the percentage values for control and desiccated eggs.

Dry weight determinations were made of newly laid eggs and of eggs containing stage V embryos. For each of the 2 age classes 3 separate determinations were made. Groups of 20 clean eggs were weighed, then dried to constant weight in an oven at  $107 \pm 1^\circ\text{C}$ .

TABLE 1. Viability and hatchability values for eggs of *Agrilolimax reticulatus* after weighting by control values, from desiccation experiments with groups of 10 eggs each.

% Relative Humidity	Egg Stage	% Weight Loss	Fan On			Fan Off			
			Hours*	Viability %	Hatchability %	Hours*	Viability %	Hatchability %	
90	Newly laid	10	2.25	90	73	2.0	100	100	
		20	(5.30)**	33	87	4.25	77	100	
		30	7.0	0 (31%)*	0	7.0	12	100	
		40	7.5	0	0	8.6	0	0	
		60	—	—	—	13.6	0	0	
	V	10	2.0	100	94	?	99	100	
		20	5.75	95	86	6.0	100	88	
		30	(6.5)	100 (33%)	95	7.0	100 (31%)	100	
		40	—	—	—	9.0	100	100	
		50	11.5	100	88	12.0	100	100	
		60	6.2	90	88	7.1	80 (63%)	88	
		77	—	—	—	—	50	100	
	50	Newly laid	10	0.33	100	100	0.6	100	88
			20	0.85	77	100	1.0	100	100
30			1.3	100	100	1.2	84	0	
40			2.0	100	100	1.8	100 (43%)	100	
50			2.4	72 (54%)	100	2.25	78	31	
60			(1.9)	100	100	2.0	88	0	
70			3.25	66	63	2.0	55	38	
V		10	0.4	100	100	0.4	100	100	
		20	0.7	100	88	0.75	100	88	
		30	1.3	100	44	1.3	95	93	
		40	(1.6)	100 (41%)	100	1.75	100	96	
		50	—	—	—	2.1	90	100	
		60	2.15	100	75	(>2.0)	88	96	
		70	2.25	80	100	2.7	80	100	
80	2.3	44	96	2.9	44	100			

\* Hours, expressed in the decimal system, refer to the time taken to reach the requisite weight.

\*\* = Time taken is in doubt.

\*\*\* = weight loss not exactly coinciding with the desired loss.

When viability of the control was 100%, viability of the desiccated eggs was taken as valid.

When hatchability of the desiccated eggs was the same as the viability of the desiccated eggs, the hatchability of the desiccated eggs was taken as 100%. Some experiments were duplicated and in those cases the mean values have been taken. In occasional cases of doubt as to viability and hatchability the value given is the mean of the 2 doubtful limits.

## RESULTS

The results are presented in Table I, and discussed below.

### 1. Rate of weight loss

The rate at which the eggs lost weight (considered to be due to loss of water) was calculated from the experimental data.



TABLE 2. Summary of 3 statistical tests comparing the influences of different factors (paired) on the rates of weight loss (mg/hour).

Variables Compared	Variance ratio		Students t		Fisher-Behrens		Significance
	F	p	't'	p	d	p	
Fan on/fan off	1.100	>0.05	0.2110	>0.8	—	—	none
Newly laid eggs/stage V eggs—at 90% R.H.	1.713	>0.05	2.261	>0.05	—	—	none
Newly laid eggs/stage V eggs—at 50% R.H.	6.353	<0.05 >0.01	—	—	0.0274	>0.7	none
Newly laid eggs/stage V eggs—all experiments	1.034	>0.05	0.1698	>0.8	—	—	none
50% R.H./90% R.H.	17.66	<0.01	—	—	8.5859	<0.001	very high
* Eggs grouped/eggs dried singly	3.065	>0.05 <0.1	8.200	<0.001	2.746	<0.02	high

\* For this comparison the rates were calculated as mg/egg/hour. It was necessary to use experiments in which more than 50% of the weight was lost; however only experiments common to both 'grouped' and 'single' conditions were used.

Earlier experiments (Bayne, 1967) had shown that the rate of drying of *A. reticulatus* eggs was almost constant to 50% of the weight loss. For comparison of drying rates, therefore, data were taken only from experiments which involved loss of from 10 to 50% of the weight. Any experiments which were not repeated identically with 'fan on' and 'still' conditions were excluded. The effects of various factors on the drying rates were then examined statistically (Table 2) using the procedures detailed by Bailey (1959).

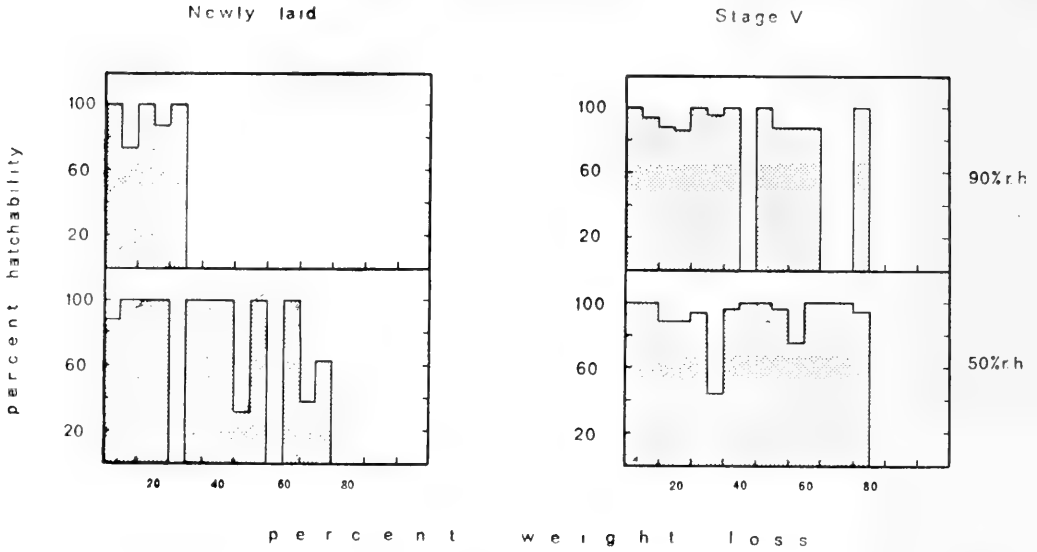
It is seen that air movements caused by the fan were insufficient to cause a significant increase in the desiccation rate, at least with groups of 10 eggs. Also, unlike many insect eggs (Browning, 1953), the rate of drying was the same in *Agriolimax* for both newly laid eggs and eggs containing well developed embryos. But rate differences due to age would probably

not have been detectable with the present experimental procedure (Bayne, 1968). The relative humidity of the surrounding air however has a very significant effect upon desiccation rate. Finally it is clear that the habit of laying eggs in clusters rather than singly must have a marked effect on the drying rates of eggs in the middle of the bunch if the relative humidity falls to less than 100%. In these experiments grouping of eggs on the balance pan significantly retarded the desiccation rates.

## 2. Survival

Figure 3 has been constructed from the hatchability data in Table 1. Although not all the eggs surviving a desiccation experiment hatched, there appeared to be no additional (delayed) effect acting to depress hatchability. If there had been such an effect, it would have been mani-

HATCHABILITY



VIA B I L I T Y

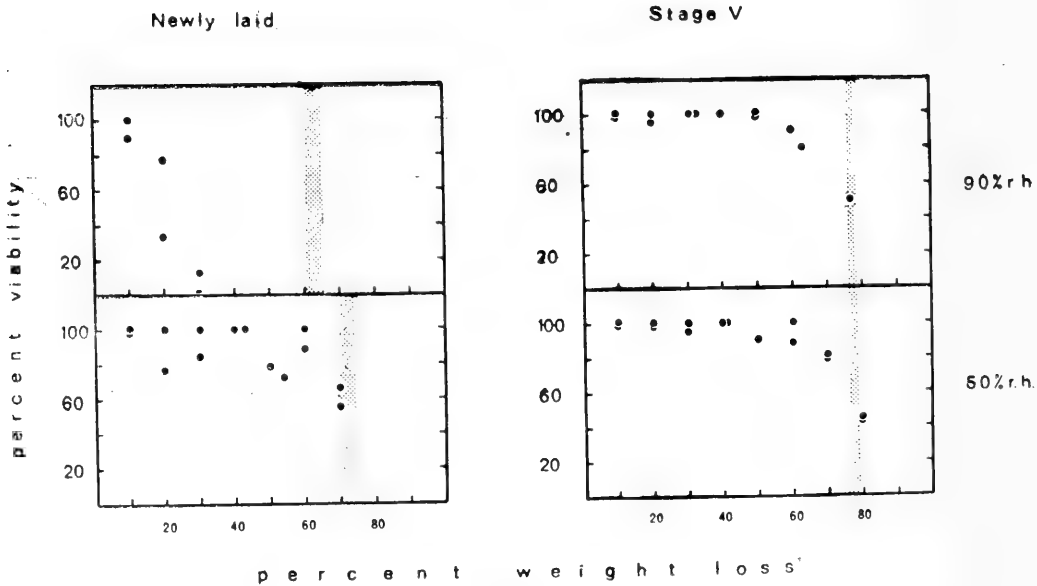


FIG. 3. Hatchability of newly laid and stage V eggs after desiccation at 90% and 50% relative humidity (from data in Table 1). The method for calculation of the plotted values is given on page

FIG. 4. Viability of newly laid and stage V eggs after desiccation at 90% and 50% relative humidity. The dots represent results from experiments with 10 eggs (Table 1), and the vertical bars represent the upper lethal limits estimated from experiments with single eggs (Table 3).

TABLE 3. Viability of *Agriolimax reticulatus* eggs desiccated singly.

% Relative Humidity	Egg Stage	% Weight loss	Fan On			Fan Off			Estimated upper lethal limit (% wt loss)
			Hrs*	viability des.	con.	Hrs*	viability des.	con.	
90	Newly laid	40	2.6	+	+	2.7	+	+	60-65
		50	3.1	+	+	2.9	+	+	
		50	3.0	+	+				
		60	3.5	+	+	3.25	?	+	
		60				3.5	o	+	
		70	4.25	o	+	5.0	o	+	
		70				3.8	o	+	
	V	70	4.2		+				76-79
		70	4.2		+				
		76	6.5		o				
		79	5.2		o	4.8	+	+	
		80	4.4		o				
		80	6.0		o				
	50	Newly laid	70	1.2	o	+	1.0	+	+
70			1.0		+				
80			1.5		o	1.4	o	+	
80			1.4		o				
V		70	0.9		+	1.25	+	?	76-79
		70	1.0		+				
		75	1.25		+	1.3	+	+	
		80	1.7		o	1.4	o	+	
		80	2.5		o				
		84							

\* Hours, expressed in the decimal system, refer to the time taken to reach the percentage weight loss indicated.

des. = desiccated

+ = viable

con. = control

o = dead

festes most clearly near the upper lethal limit.

For this reason viability data only are presented in Table 3, for experiments involving the drying of individual eggs.

These data permit an estimate of the upper lethal limit to within a few percent. Since the proportions of the shell and jelly layers vary somewhat between eggs, this upper limit (a percentage drying value) is subject to individual variation of a few per cent. Such variation would be in addition to physiological variation between embryos. The estimates of upper lethal

limit are thus probably as nearly accurate as they can be.

In Figure 4, the ranges of weight loss over which death of individual (single) eggs occurred (vertical bars, taken from Table 3) are superimposed upon the viability data for groups of 10 plotted from Table 1. The discrepancy between the upper lethal limits for newly laid eggs at 90% R. H. (30% vs. 60-65% weight loss) arrived at by the 2 procedures is unresolved; it is hoped that further work will clarify the reasons for the difference. Since the experiments involving 1 egg

were of a more critical nature than those involving 10, the indicated limit of 60-65% is probably valid. In the other 3 classes (i.e., newly laid eggs at 50% and stage V eggs at 50% and 90% R.H.) the values obtained in both series of experiments agree more closely.

#### Effect of humidity

The newly laid eggs are able to survive more drying at 50% R.H. than at 90%, whereas no difference was found with the older eggs. In these experiments eggs were transferred to moist conditions as soon as the required weight loss had occurred. Drying was more rapid at the lower humidity, so that exposure of the embryo to the dry conditions was for a shorter duration, and this may have been responsible for the greater survival at 50% R.H. It is also possible that at this rate of drying the degree of hydration in the outer and inner regions of the egg are further from equilibrium at any one time than at the slower rate. Thus the embryo, located towards the centre of the egg, may be exposed to less dehydration at the lower humidity.

#### Effect of age

At both relative humidities the advanced embryos were more tolerant of dehydration than the newly laid embryos. Determinations of the dry weights of eggs from both age groups gave very similar values. Newly laid eggs had an average dry weight of 10.2% and stage V eggs of 9.6%. This difference is not significant ('t' test  $p > 0.1$ ). Since stage V embryos occupy a considerable volume of the egg (Fig. 1), it is clear that the dehydration experienced in these experiments must have resulted in the loss of some water from the embryos.

### DISCUSSION

Weight cycles due to variations in the

degree of hydration were shown to be normal phenomena in terrestrial snails and slugs as early as 1934 (Howes & Wells). A high degree of tolerance to desiccation has been reported for several adult gastropods; a highly hydrated *Limax tenellus* has been reported to survive 80% weight loss (Kunkel, 1916), *Australorbis glabratus* a 70% loss (von Brand, McMahon & Nolan, 1957), and *Helix* a 58% loss (Kunkel, 1916). Brown (1961), Kensler (1965) and Emerson (1965) considered desiccation tolerance in relation to vertical distribution on the sea shore. The latter author reported 50% survival of *Littorina scutulata* at about 65% water loss. However, a value as low as 14% water loss was sufficient to cause 50% mortality in *Calliostoma ligatum* (Emerson, 1965). The pulmonate *Ovatella myosotis* was one of the most susceptible species of intertidal invertebrate studied by Kensler (1965). There is thus a considerable degree of variation in resistance to desiccation in gastropods. Few papers mention desiccation survival of adult slugs. However, Getz (1959) and South (1965) both found that *Agriolimax (Deroceras) reticulatus* survived dry conditions better than various *Arion* species despite the very much thinner body wall of *Agriolimax*.

The ability of capsule-bound embryos of gastropods to survive considerable water loss now seems well established. Reports in the early literature (e.g., Binney, 1878) of successful development of oven-dried eggs when transferred to moist conditions was unacceptable to Carrick (1942) and to Arias & Crowell (1963), and in the light of results presented by Carmichael & Rivers (1932), Karlin & Bacon (1961), and by the present author (this paper), those early reports seem to be clearly disproven. Recently Wolda (1965) talking of *Cepaea nemoralis* reported that 'draught kills eggs rather rapidly.' Gugler (1963) claimed that various snail eggs,

after drying out, continued to develop when remoistened, but Karlin & Bacon (1961) showed that *Limax maximus* eggs did not; in neither of these 2 cases was the amount of drying specified.

The striking feature of the present results is the great amount of water loss which was tolerated. This tolerance contrasts with that shown by the egg of the cricket *Gryllulus commodus*, which is killed by 20-30% loss of weight (Browning, 1953).

Carmichael & Rivers (1932), working with the slug *Limax flavus*, reported a survival of 85% weight loss by some eggs, a value higher than any reported in the present paper. If percentage dry weight values of *Limax* are similar to those found in *Agriolimax*, as they are likely to be, the reported value would mean that only about 5% of the water was left in the egg when desiccation was ended. These authors further found that, when the eggs had lost 65% of their original weight just prior to hatching, the embryos had lost 35-40% of their weight. It may be significant that a large part of the volume of the stage V embryo consists of perivitelline fluid in the digestive canal and hepatic lobe (Carrick, 1939). Von Brand et. al., (1957) and Emerson (1965) report that, in dehydrating snails, the percentage of water lost from the tissues (excluding blood) is considerably less than that lost from the whole animal. A similar ability to keep the tissues hydrated may occur in advanced embryos of slugs. It would have been very interesting to know what percentage of weight loss was due to extra-embryonic material, and what percentage to dehydration of the embryo in *Agriolimax reticulatus*, but the small size of these eggs made such an assessment impossible.

Carmichael & Rivers (1932) found a greater tolerance by the younger *Limax* eggs; whereas I found the younger eggs of *A. reticulatus* to be more susceptible.

Walton (1918) and McCraw (1961) report that embryos of *Lymnaea* become more susceptible to drying as hatching is approached. However the increased tolerance of the later developmental stages which was found in the present work was paralleled by the results of Arias & Crowell (1963), also working with *Agriolimax*, in which a greater tolerance to high and low temperatures was observed in more advanced embryos. Similarly, Chrosic chowski (1962) noted a greater desiccation tolerance in more developed eggs of *Biomphalaria*.

Carmichael & Rivers (1932), in contrast to the present results, reported that the age of the *Limax* embryo affected the rate of desiccation. Their experiments did not involve control of physical conditions, and moreover would not be expected to detect rate variations due to the characteristics of the eggs (Bayne, 1968).

Further information would be of interest. Keeping eggs partially dehydrated for varying periods before returning them to moist conditions could be used to investigate whether or not the embryos can become acclimated to water loss (Segal, 1961). In view of reports by Walton and McCraw (see McCraw, 1961) that partial drying of egg masses of *Lymnaea* prolonged the hatching process, such an effect should be investigated in terrestrial species. The view of the present author is that hatching is neither delayed nor prolonged by drying in *Agriolimax*. It would also be of interest to obtain desiccation survival values for an aquatic species. Bretschneider (1948) mentions Neumann's finding that "*Limnaea*" egg masses could survive 95 minutes of exposure to the air, but the work was unfortunately not quantitative.

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### LITERATURE CITED

- ARIAS, R. O. & CROWELL H. H., 1963, A contribution to the biology of the grey garden slug. *Bull. S. Calif. Acad. Sci.*, 62: 83-97.
- BAILEY, N. T. J., 1959, *Statistical Methods in Biology*. The English Universities Press Ltd., London.
- BAYNE, C. J., 1966, Observations on the composition of the layers of the egg of *Agriolimax reticulatus*, the grey field slug. *Comp. Biochem. Physiol.*, 19: 317-338.
- 1968, A study of the desiccation of egg capsules of eight gastropod species. *J. Zool., Lond.*, 155: 401-411.
- BINNEY, W. G., 1878, The terrestrial air-breathing mollusks. *Bull. Mus. comp. Zool.*, Harvard, 4: 1.
- BRETSCHNEIDER, L. H., 1948, The mechanism of oviposition in *Limnaea stagnalis* L. *Proc. K. ned. Akad. Wet.*, 51: 616-626.
- BROWN, A. C., 1961, Desiccation as a factor influencing the vertical distribution of some South African gastropods from intertidal rocky shores. *Port. Acta. biol.* 7B(1-3): 11-23.
- BROWNING, T. O., 1953, The influence of temperature and moisture on the uptake and loss of water in the eggs of *Gryllulus commodus* Walker (Orthoptera: Dryllidae). *J. exp. Biol.*, 30: 104-115.
- CARDOT, H., 1924, Observations physiologiques sur les embryons des gastéropodes pulmonés. *J. Physiol. Path. gen.*, 22: 575-586.
- CARMICHAEL, E. B. & RIVERS, T. D., 1932, The effect of dehydration upon the hatchability of *Limax flavus* eggs. *Ecology*, 13: 375-380.
- CARRICK R., 1939, The life history and development of *Agriolimax agrestis* L., the grey field slug. *Trans. R. Soc. Edinb.*, 59: 563-597.
- 1942, The grey field slug, *Agriolimax agrestis* L., and its environment. *Ann. appl. Biol.*, 29: 43-55.
- CHROSCIECHOWSKI, P., 1962, Observaciones en el laboratorio y en el campo raso sobre la resistencia al desecamiento de algunos gasteropodos Venezolanos, especialmente del huesped intermediario de la *Esquistosomiasis mansoni*. *Revta Venez. Sanid. Asist. Soc.*, 27: 159-178.
- EMERSON, D. N., 1965, Tissue hydration during desiccation of three species of intertidal prosobranch snails. *Rep. Am. malac. Un.*: 52-53.
- FISHER, R. A. & YATES, F., 1953, *Statistical tables for biological, agricultural and medical research*. Oliver & Boyd, London.
- GETZ, L. L., 1959, Notes on the ecology of slugs: *Arion circumscriptus*, *Deroceras reticulatum*, and *D. laeve*. *Am. Midl. Nat.*, 61: 485-598.
- GUGLER, C. W., 1963, The eggs and egg-laying habits of some mid-western land snails. *Trans. Kans. Acad. Sci.*, 66: 195-201.
- HOWES, N. H. & WELLS, G. P., 1934, The water relations of snails and slugs. II. Weight rhythms in *Arion ater* L. and *Limax flavus* L. *J. exp. Biol.*, 11: 344-351.
- KARLIN, E. J. & BACON, C., 1961, Courtship; mating, and egg laying behaviour in the Limacidae (Mollusca). *Trans. Amer. microsc. Soc.*, 80: 399-406.
- KENSLER, C. B., 1965, *Ecological studies of intertidal crevice fauna*. Ph. D. thesis, University of Wales.
- KUNKEL, K., 1916, *Zur Biologie der Lungensnecken*. Winter, Heidelberg.
- McCRAW, B. M., 1961, Life history and growth of the snail *Lymnaea humilis* Say. *Trans. Amer. microsc. Soc.*, 80: 16-27.
- SEGAL, E., 1961, Acclimation in molluscs. *Amer. Zoologist*, 1: 235-244.
- SOUTH, A., 1965, Biology and ecology of *Agriolimax reticulatus* (Mull.) and other slugs: spatial distribution. *J. Anim. Ecol.*, 34: 403-417.
- VON BRAND, T., McMAHON, P. & NOLAN, M. O., 1957, Physiological observations on starvation and desiccation of the snail *Australorbis glabratus*. *Biol. Bull.*, Woods Hole, 113: 89-102.
- WALTON, 1918, In: McCraw, B. M. (1961).
- WOLDA, H., 1965, The effect of drought on egg production in *Cepaea nemoralis* (L.). *Archs. néerl. Zool.*, 16: 387-399.

## RESUME

LA SURVIE D'EMBRYONS D'*AGRIOLIMAX RETICULATUS*,  
SUIVANT LA DESSICATION DES OEUFS

C. J. Bayne

Des embryons d'*Agriolimax reticulatus* peuvent survivre à une perte de poids de 60 à 80% à partir des oeufs. Les embryons âgés sont moins tolérants à la dessiccation que les jeunes. Les oeufs fraîchement pondus sont moins sensibles quand la dessiccation intervient plus rapidement, c.a.d. quand ils sont exposés à une humidité relative de 50% au lieu de 90%. La dessiccation ne semble pas avoir d'effets ultérieurs sur la viabilité des embryons.

Les oeufs d'âges différents perdent du poids au même taux, mais leur groupement provoque une diminution significative du taux par rapport à celui des oeufs desséchés isolément; les oeufs de l'extérieur se déshydratent plus rapidement que ceux du centre.

## RESUMEN

SUPERVIVENCIA DE EMBRIONES DE LA BABOSA GRIS DE  
CAMPO *AGRIOLIMAX RETICULATUS*, DESPUES DE LA  
DESECACION DEL HUEVO

C. J. Bayne

Embriones de *Agriolimax reticulatus* sobrevivieron una pérdida de peso de 60 a 80% por deshidratación de los huevos. Embriones avanzados fueron más tolerantes que los embriones muy jóvenes. Huevos recién puestos fueron menos susceptibles cuando la desecación ocurrió rápidamente, por ejemplo a 50% de humedad relativa comparada con 90%. La desecación pareció no tener efecto en el desarrollo de los embriones. Huevos depositados temprano, y los recién puestos perdieron peso a la misma velocidad pero, cuando estaban agrupados en proceso fue más lento que en los aislados: los de la periferia del grupo se deshidrataron más rápido que los del centro.

## АБСТРАКТ

ВЫЖИВАНИЕ ЭМБРИОНА СЕРОЙ ПОЛЕВОЙ УЛИТКИ  
*AGRIOLIMAX RETICULATUS* ПРИ ВЫСЫХАНИИ ЯЙЦА

К. Ж. БЭЙН

Было обнаружено, что эмбрионы *Agriolimax reticulatus* выживают при потере веса яйца (благодаря дегидрации) на 60-80%. Более развитые эмбрионы более выносливы к высыханию, чем очень молодые. Вновь отложенные яйца более выносливы к более быстрому высыханию при 50% относительной влажности, по сравнению с 90%. По-видимому, высушивание не оказывает замедляющего действия на выживаемость эмбрионов.

Яйца обоих возрастов теряли вес с одинаковой скоростью, но при собирании их в группы наблюдалось значительное замедление этой скорости, по сравнению с яйцами, высушиваемыми по отдельности. Яйца, находящиеся снаружи группы, высыхали быстрее, чем бывшие в середине.





SOME ENVIRONMENTAL EFFECTS ON THE LARVAL  
DEVELOPMENT OF *LITTORINA PICTA* (MESOGASTROPODA),  
REARED IN THE LABORATORY

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ABSTRACT

The results described are from a general study of population ecology and intraspecific shell variation of Hawaiian *Littorina picta*. Larvae from snails of two extreme types of shell sculpture populations and an intermediate shell sculpture population were reared under constant laboratory conditions and their differences in shell morphology, growth, and mortality assessed. These differences are assumed to reflect genotypic variation.

The laboratory conditions for rearing larvae are outlined and several experiments leading to the determination of these conditions are discussed. The major environmental factors studied were the effects of antibiotics, food, salinity, temperature, and substrate on larval growth and mortality. In general, rearing conditions for all sculpture types are similar. The highest growth and survival are obtained when larvae are reared in sea water within a salinity range of 35-40 o/oo and temperature range of 24-25°C, treated with 20-25 ppm of Polymixin B sulfate and fed *Phaeodactylum tricorutum*. The mortality of laboratory-reared larvae was in general very high. The maximum survival to settlement obtained was approximately 50%; through metamorphosis, 10%. The average survival through metamorphosis, however, was only about 1%. The laboratory conditions, therefore, may not provide the most optimal environment for the larvae.

There are variations in the growth and mortality of different sculpture types at the salinity-temperature extremes. These are correlated with the distribution of sculpture types in the natural environment. Heavily-sculptured shell forms occurring on drier, low wave action substrata have larvae which are more resistant to high salinity and less resistant to low temperature than the larvae of smooth shell forms which occur on wet substrata with strong horizontal wave force. All types of larvae settle on a surface covered with an algal film. Another major stimulus to settlement is probably the intermittent removal of water from the bowl after approximately 3 weeks of development. The above environmental factors are discussed in relation to their importance in mortality of larvae and post-veligers in the natural environment.

INTRODUCTION

Only a few planktotrophic gastropod larvae have been reared through metamorphosis in the laboratory. They include the neogastropod larvae of *Nassarius obsoletus* and *N. vibex* (Scheltema 1961, 1962a, 1962b) and *Strombus gigas* (D'Asaro, 1965). Recently, a number of

gastropod larvae have been reared by Fretter & Montgomery (1968). At present, little is known of the environmental factors affecting the development of planktotrophic larvae. Some of the more important studies are those of Scheltema (1961, 1962b, 1965, 1967) and Paulson & Scheltema (1968) on the effect of substratum, salinity, temperature and

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food on development of *Nassarius* larvae. Fretter & Montgomery (1968) have studied the food and feeding of many other marine prosobranchs. Most prosobranch larvae successfully reared through metamorphosis have been those with shorter planktotrophic larval stages (e.g., *Crepidula*; Conklin, 1897). Many mesogastropod larvae, such as *Littorina* are often more difficult to rear because of their relatively long planktotrophic lives (several weeks) and consequently, little is known of their ecology.

In contrast to the few studies on rearing planktotrophic gastropod larvae, there have been a large number on rearing of marine bivalve larvae. Most of these are summarized and discussed by Loosanoff & Davis (1963) and Walne (1964), whose work has been of particular value. Ecological studies of marine larvae are, in general, rare, especially quantitative studies of the effect of environmental factors on morphology and physiology of larvae. Among the few such investigations are those of Costlow, Bookhout & Monroe (e.g., 1960, 1962) on the effect of salinity and temperature on development, growth and mortality of various species of crab larvae.

The following results are part of a general study being made of intraspecific variation and population ecology of Hawaiian *Littorina*. The relationship of larval development studies to the basic problem of the origin of shell variation and details of the morphology and behaviour of larvae are discussed elsewhere (Struhsaker, 1968; Struhsaker & Costlow, 1968). Shell sculpture variation in *L. picta* is apparently related to physiological variation in resistance to desiccation and extreme salinity. Smaller, smooth-shell forms (with less resistance to desiccation and high salinity) inhabit supratidal areas with heavy horizontal wave force and wet conditions. The larger, heavily sculptured forms (with

higher resistance to desiccation and high salinity) occur in supratidal areas with slight horizontal wave force (mostly spray) and drier conditions. Intermediate shell forms occur in intermediate habitats. The total sampled Oahu population shows a bimodal distribution of shell type with most of the total population either smooth forms or heavily sculptured forms; there are fewer intermediate forms. The bimodal distribution and other evidence suggests that *L. picta* may exhibit an example of adaptive polymorphism, the variation in shell sculpture being associated with varying topography and wave action on different substrata. The 2 polymorphic population extremes may have originated from disruptive selection by various wave forces and moisture conditions within the heterogeneous supratidal habitat of the Hawaiian Islands (Struhsaker, 1968).

In larval studies, the larvae from parents of extreme types of shell sculpture were reared under constant laboratory conditions. The significant and consistent morphological and physiological variations of larvae reared under these conditions were assumed to indicate genotypic variation between the shell forms (Struhsaker, 1968). In the following study, the rearing conditions and the experiments leading to their definition are described. The environmental factors found most important to larval development and thus of primary interest were: previous history of parental snails, disease (bacteria and fungi), food type, food concentration, larval concentration, salinity, temperature, and substratum at metamorphosis.

## MATERIALS AND METHODS

Copulating pairs of *Littorina picta* were collected at full moon periods during flood or ebb of the tide. The copulating male and female were separated and

placed into labeled plastic bags (no water). The best results in larval rearing experiments were obtained by placing females in individual spawning dishes within 2 days after collection. Methods for analyzing and describing spawning, spawning periodicity and fecundity were described previously (Struhsaker, 1966).

The rearing conditions are as follows:

1. Rearing containers: Straight-sided stacking dishes (4 inch and 10 inch diameters). Larger containers can be used, but larvae are more difficult to locate and tally.

2. Volume of sea water: With larvae and food at appropriate concentrations, 1.40 liters in 10 inch stacking dishes and 0.25 liters in 4 inch stacking dishes. In general, larger volumes give best survival.

3. Filtration: Cuno Filter (Aqua-pure water filter with cartridge No. P110, Cuno Engineering Corporation, Meriden, Connecticut). The Cuno filter removes most particles above 10 microns in diameters. It is composed of non-toxic cellulose fibers and filters water rapidly (approximately 5 gallons/5 minutes, with gravity flow). Filter cartridges, if reused, should be washed immediately after use and dried in the sun. Ideally, new cartridges should be used for each filtration because fungus may accumulate in cartridges. If allowed to age in the dark (for 2-4 weeks), filtered sea water does not need the treatments Nos. 4 or 9 below and gives very satisfactory results.

4. Sterilization of sea water: Ultra-violet light (apparatus designed after Loosanoff & Davis, 1963). Water must be filtered before running through the UV light unit and antibiotics not added until after the treatment (see p 13).

5. Sterilization of apparatus: Soak in 50 ppm of Combistrep (Charles A. Pfizer & Co., Inc., New York, N.Y.) in distilled water for 12 hours. After treatment, all

apparatus should be carefully washed with a pressure nozzle.

6. Salinity: 35 to 40 ppt.

7. Temperature: 25°C.

8. Light: Approximately 12 hours light, 12 hours dark.

"Examolights," MacBeth Daylighting Corporation; approximately 100 foot-candles at surface. This approximates  $X10^{-1}$  of the intensity of light over the surface of the ocean. Higher light intensities should be avoided because they promote high rate of algal growth which is harmful to larvae.

9. Antibiotics: Polymixin B, 20 to 25 mg/liter sea water (20 to 25 ppm). This treatment results in good survival and does not affect growth rate significantly. Combistrep, 0.2 cc (50 mg/liter sea water = 50 ppm) reduces mortality greatly if larvae are transferred to treated water only after larval shell is developed and the larvae have hatched from the capsule. Larvae should then be treated only at critical moments, as Combistrep may affect the growth rate.

10. Larval concentration: 250 larvae/1.40 liters; 50 larvae/0.25 liters. Concentrations over 0.5 larvae/ml reduce growth rate significantly.

11. Food type: *Phaeodactylum tri-cornutum*, a diatom. Algae are most conveniently cultured in Erlenmeyer culture flasks (2.8 liters) filled with Cuno-filtered sea water. Add 1 cc each of Nutrient A and Nutrient B per liter of sea water (see Loosanoff & Davis, 1963 for ingredients) plus 0.56 cc Combistrep/2.8 liters sea water (50/liter=50 ppm). Air is continually bubbled into the flasks which are maintained at 19-20°C in constant temperature cabinets. Lights used are the same as above (8). New cultures are started every 2 days.

12. Food concentration: Approximately  $10^4$  algal cells/ml. Concentration of algal cells is determined by hemocytometer counts or a Coulter counter. New

algae are added to appropriate concentration after every water change. It is very important not to overfeed the larvae.

13. Water change: Daily for first 7 days, then every 2 days; when large number of larvae, through sieve; when small number, by hand pipetting. Changes are made with a stainless steel sieve, using 0.44 mm of the U.S. Standard Sieve Series, Newark Wire Cloth Co., Newark, N.J.

14. Settlement Substratum: From approximately day 21, larvae are introduced to 1.40 liter stacking dishes which are covered with a thin layer of alga or detritus. This film of food must be present for metamorphosis to occur. To grow algal film, pieces of appropriate alga, 1.0 liter of filtered sea water, and 1 cc/liter of Nutrient A and 1 cc/liter of Nutrient B (see 11) are introduced into stacking dishes. Bowls are then placed in constant temperature cabinets with same conditions used to grow *Phaeodactylum tricorutum* (11). The addition of small rocks from natural substratum (must also be covered with algae or detritus) may also promote settlement. All other possibly competing organisms must be carefully removed. For *Littorina*, tilting the finger bowls on a rack so that half the bowl is submerged and half above the water seems to stimulate settlement.

Photomicrographs and larval counts during larval development were taken at 3 or 7 day intervals. Measurements were made from negatives.

Most experiments were done using the eggs from a single female of intermediate population shell type, except for the salinity-temperature experiments where the 2 extreme types were contrasted (Struhsaker, 1968).

Factorial and multiple regression analyses were performed with the aid of an IBM 7040 computer.

## RESULTS

### Previous history of parents

There is considerable variation among larvae of *Littorina picta* prior to hatching from the capsule. This variation occurs among the larvae of an individual female and larvae of females from a single population (or sculpture type). There are diverse sizes of spawns, larval sizes at hatching, percentages of abnormal larvae spawned and viabilities of larvae. Determining which of these variations are attributable to the previous environmental history of parents and which to inherent genetic variability is still an unsolved problem.

An individual female may spawn several successive days (Struhsaker, 1966). The number of eggs per spawn will differ greatly between the days (from approximately 10-1,000 eggs). The reason for this variation is unknown. The number of abnormal larvae may be greater on one day than another. For example, the 1st day's spawn often contains a higher percentage of abnormalities than do later spawns. This could be induced by some environmental factor (e.g. extremes of temperature or desiccation) affecting the eggs while they are still in the female genital tract and in the first polar stage of Metaphase I. Viability of larvae from a single spawn may also vary; some larvae seem never to feed and to die within a few days after hatching, while others feed normally and survive to metamorphosis. Because the larvae were treated alike and given abundant food, the differences may indicate genetic variation in viability. Females of a single population also show the variations described above but the range of variation is greater.

The results of experiments in which several morphological, physiological and behavioral traits of different shell sculpture populations were contrasted are summarized elsewhere (Struhsaker, 1968). There



FIG. 1. Normal and abnormal larvae at hatching (3 days); A, normal protoconch (without larva); B, abnormal larva (without protoconch). Only a small cap of shell present (arrow). Empty capsule at left.

are significant differences, probably genetic, between larvae of extreme sculptured and extreme smooth shell populations. These differences include larval size, growth rate, shell sculpture and viability.

#### Abnormalities

Abnormal larvae were often observed during the larval experiments. The most common type is a larva with an abnormally incomplete protoconch at hatching. Normal larvae have fully-developed protoconchs at this time (Fig. 1-A). In several experiments most of the larvae hatched with only a small piece of shell on the visceral hump (Fig. 1-B). Protoconch development varied from this extreme of a small cap of shell to a

protoconch nearly normal in size, enclosing most of the larva. Several environmental factors produce this shell abnormality; overcrowding (more than 300 larvae/0.25 liters), fungal contaminations and application of certain antibiotics (particularly Combi-strep) during the first 3 days of early development before hatching. The mechanism by which this abnormal shell development is induced is unknown. Larvae with incompletely developed protoconchs usually die within 4 to 5 days after hatching.

Another type of abnormal larva has an incompletely developed body with a large space between the larva and protoconch, while normal larvae always fill the protoconch. This abnormality has not

TABLE 1. Factorial analysis of variance. The effect of time, antibiotic and antibiotic concentration on mortality of larvae. Three weeks  $\times$  4 antibiotics  $\times$  2 concentrations per antibiotic  $\times$  2 replications. Only significant main effects and interactions shown. Each treatment combination consists of 2 replicates (r) or 2 bowls of larvae (65 larvae/bowl).

Source	<i>Ss</i>	<i>Df</i>	Mean square	<i>F</i> ratio	<i>Df</i>	Probability
Week (w)	11,515.55	1	11,515.55	4,515.90	1, 3	$\Gamma < 0.01$
Antibiotic (a)	5,435.56	3	1,811.85	710.53	3, 3	$\Gamma < 0.01$
Concentration (c)	382.95	1	382.95	150.18	1, 3	$\Gamma < 0.01$
Week-Antibiotic (wa)	1,270.14	3	423.38	166.03	1, 3	$\Gamma < 0.05$
Week-Concentration (wc)	125.37	1	125.37	49.16	3, 3	$\Gamma < 0.01$
Antibiotic-Conc. (ac)	708.57	3	236.19	92.62	1, 3	$\Gamma < 0.05$
wac	1,394.36	3	464.79	182.27	3, 3	$\Gamma < 0.01$
Error (wacr)	7.66	3	2.55			

been definitely correlated with any environmental factor. It appears more common in day 1 spawns than in later spawns from the same female. It may also be induced by extremes of environment while the eggs are in the early stages in the female genital tract.

Occasionally, unusual early developmental stages and capsules are observed. The embryos are smaller than normal and fail to differentiate beyond a late cleavage stage or do not differentiate at all. The outer capsules are often aberrantly-shaped and contain more than one of these embryos. This abnormality occurs in spawns of females exposed to long periods of desiccation (more than a month). In most cases, abnormal early stages are rare. Females, although desiccated for long periods, usually still spawn normally.

Some larvae, otherwise appearing normal, do not feed, and die within a few days from hatching. This may result from incomplete development of the intestinal tract.

#### Diseases

Both marine bacteria and fungi have deleterious effects on larval development, the degree depending upon the larval stage and the concentration of the disease organisms. Ordinarily, at low concentrations, neither bacteria nor fungus will

kill larvae, particularly when the larval protoconch is fully formed and the water changed daily. Earlier stages are more susceptible to disease. Another generalization is that the bacteria and fungi are more deleterious in smaller volumes of sea water. This may be due to the proportionately greater surface area suitable for bacterial growth (Zobell, 1946). Diseases are of considerable importance to the success of rearing larval littorines in small laboratory containers, but their importance as a mortality factor in the natural planktonic environment is uncertain.

In most experiments no identifications of bacteria or fungi were made and no studies made of the mechanism by which they affect the larvae. However, several types and concentrations of antibiotics were tested. Many of these increase survival of larvae, particularly when the treatment is applied after the protoconch is formed. Antibiotic treatment before hatching may result in larvae with abnormal shells. Some of the antibiotic treatments dramatically decrease growth rate; most do not. Still other antibiotics seem to produce an accumulative toxic effect.

The results of a factorial experiment with continual antibiotic treatment are summarized in Table 1. All factors were

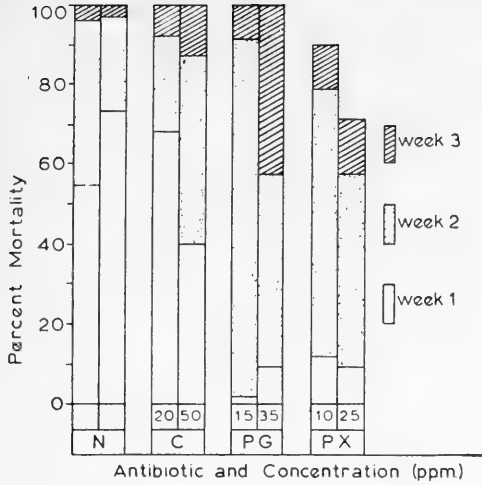


FIG. 2. Percent mortality of *Littorina picta* larvae at one week intervals, throughout development to metamorphosis, under different antibiotic treatments. N=no antibiotic; C=Combistrep (20 and 50 ppm); PG=Penicillin G (15 and 35 ppm); PX=polymixin (10 and 25 ppm).

kept constant under optimal conditions with the exception that antibiotics were added. The antibiotics used were Polymixin B, Penicillin G and Combistrep (containing streptomycin sulfate). The antibiotics and concentrations selected were based on results from preliminary experiments. The effect on the mortalities is shown in Fig. 2. A significant difference between mortalities of larvae treated with different antibiotics and concentrations was obtained ( $P < 0.01$ ). Polymixin gives better survival than other antibiotics and there is a significant interaction between the antibiotic and concentration; a concentration of Polymixin at 25 ppm results in significantly higher survival than at 10 ppm ( $P < 0.01$ ). There is also a significant interaction between the week of development, and type and concentration of antibiotic indicating that the effect of treatment varies between weeks. Only larvae treated with Polymixin B survived to settlement after 3 weeks of development.

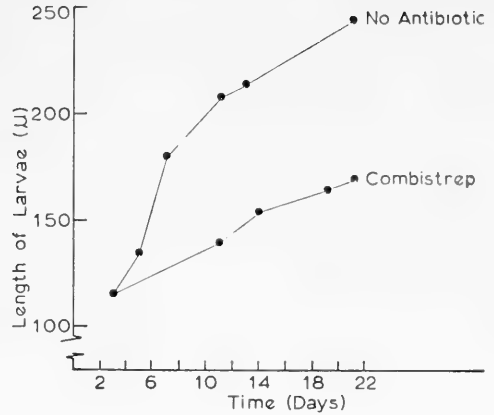


FIG. 3. Growth rate of *Littorina picta* larvae reared with no antibiotic compared to growth rate of larvae reared in water with 50 ppm Combistrep applied continually throughout development. Each point represents the mean maximum dimension of 10 larvae.

Penicillin G at 35 ppm decreased mortality in the beginning, but all larvae died by about day 16. Those larvae subjected to no antibiotic or Combistrep suffered highest mortality. The difference in mortality between replicates of untreated larvae (Fig. 2, N) after the 1st week was probably due to faster growth of bacteria and higher rate of larval mortality in the bowl where larvae first began to die. By the end of the 2nd week, mortality was approximately the same and very high in both bowls.

Periodic dosage with antibiotics seems preferable to continual treatment. The optimal times for treating larvae are immediately after hatching, at about 1 week intervals, or at any time mortality increased. When Combistrep (50 ppm) is applied to larvae in this way, the mortality is significantly decreased (to around 20% at time of settlement as opposed to 80-90% untreated), and the growth rate is not significantly decreased. Continual treatment of larvae with Combistrep, as in the above experiment, results in a significantly decreased growth rate (Fig. 3). Of the

TABLE 2. Factorial analysis of variance. The effect of time and food treatment on mortality of larvae. Three weeks  $\times$  4 food treatments  $\times$  4 replications. Only significant main effects and interactions shown. Each treatment combination consists of 2 replicates (r) or 2 bowls of larvae (65 larvae/bowl).

Source	Ss	Df	Mean square	F ratio	Df	Probability
Week (w)	3,724.93	2	1,862.47	15.9	2, 6	P < 0.01
Food (f)	3,093.89	3	1,031.29	8.8	3, 6	P < 0.05
Error (wf)*	704.45	6	117.41			

\* Not a significant interaction between week and food treatment (wf) as tested by the week-food-replication (wfr) mean square.

3 antibiotics, Polymixin B is most suitable for continuous treatment of larvae since it not only significantly lowers the mortality, but it also does not affect the growth rate when used in the indicated concentrations. Higher concentrations of Polymixin B than those used above are usually lethal.

Ultraviolet light was also used to sterilize water in some experiments. For any water contaminated with fungus, UV light was the only treatment found effective. Water was run slowly through a unit containing ultraviolet light bulbs (Loosanoff & Davis, 1963). Several problems were encountered, however. Water had to be filtered carefully before running through the UV unit because the ultraviolet light often induced chemical changes in suspended particles producing highly toxic end-products. This was noticeable, for example, when water was first treated with Penicillin G. When this water was subsequently treated with ultraviolet it acquired a very acrid smell and was highly toxic to larvae.

Experiments on the isolation, identification and treatment of the pathogenic bacteria inducing death of larvae are now in progress. Preliminary results indicate that the bacterium responsible for most mortality is a yellow-pigment producing, gram-negative motile bacillus. When cultures of veligers are inoculated with

only small amounts of this bacterium, the larvae die within 1 hour. When pieces of the yellow material produced by the bacteria are taken in by the larvae, they contract into the protoconch and ciliary action ceases within 5 minutes.

According to Zobell (1946) most marine bacteria (85% or more) are gram-negative. This may explain the higher effectiveness of Polymixin B and Combistrep (with streptomycin) in reducing mortality of larvae since they are specific against gram-negative bacteria. Penicillin G, on the other hand, is specific against gram-positive bacteria.

#### Food

Some experiments were conducted in which larvae were fed different species of unicellular algae, but none with varying concentrations of algae. The initial concentration used was approximately  $2.0 \times 10^4$  cells/larva (or  $4.0 \times 10^4$  cells/ml sea water). This concentration was frequently adjusted, however, depending upon temperature, light conditions and the number of larvae remaining alive. The feeding rates of the larvae and the length of time between water changes also affects the concentration. Overfeeding is usually toxic to larvae, for 2 possible reasons: larvae are caught and entangled in clumps of algae and cannot feed



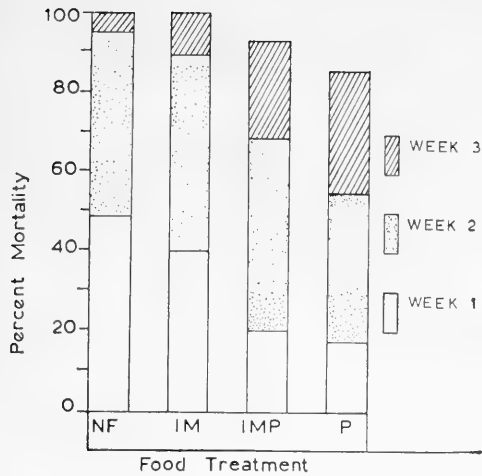


FIG. 4. Percent mortality of *Littorina picta* larvae at one week intervals, throughout development to metamorphosis, under different food treatments. NF=No food; IM=*Isochrysis* + *Monochrysis*; IMP=*Isochrysis* + *Monochrysis* + *Phaeodactylum*; P=*Phaeodactylum*.

normally, and/or some toxic metabolite is released by the algae in a lethal concentration.

Three species of algae were fed to veligers: the green flagellates *Isochrysis galbana* and *Monochrysis lutheri*, and a diatom, *Phaeodactylum tricornerutum*. These were selected on the basis of their suitability for feeding oyster and clam larvae (Loosanoff & Davis, 1963) and *Nassarius* larvae (Scheltema, 1962a). Also, their isolation and culture have been outlined previously in detail (Droop, 1954; Guillard & Ryther, 1962; Levin, 1959; Provasoli & Pitner, 1953).

The results of a factorial experiment varying food type are summarized in Table 2. All factors were kept constant at optimal conditions except food, and no antibiotics were used in food experiments because they sometimes depress growth rates. All larvae were collected from intermediate parents. Preliminary results indicated that neither *Isochrysis galbana* nor *Monochrysis lutheri* alone were suffi-

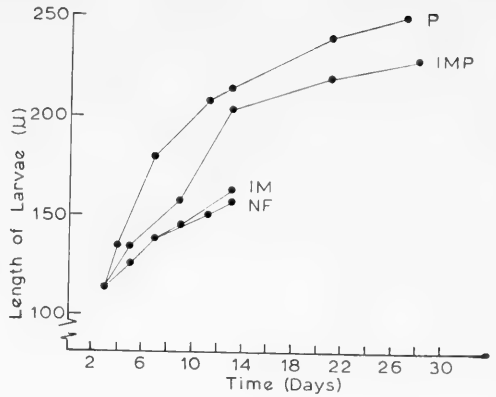


FIG. 5. Growth rate of *Littorina picta* larvae to metamorphosis under different food treatments. NF=No food; IM=*Isochrysis* + *Monochrysis*; IMP=*Isochrysis* + *Monochrysis* + *Phaeodactylum*; P=*Phaeodactylum*. Each point represents the mean maximum dimension of 10 larvae.

cient to sustain growth of *Littorina picta*. *Phaeodactylum tricornerutum*, however, gave good growth and survival. For this reason, the algae were tested in combinations only, as shown in Fig. 4 and 5.

Table 2 shows that there is a significant difference between the mortalities of larvae given different foods ( $P < 0.05$ ).

Those fed *Phaeodactylum tricornerutum* either alone or in combination (as shown in Fig. 4 and 5) survived significantly better than those given the combination of *Isochrysis galbana* and *Monochrysis lutheri* and those given no food at all. Only larvae fed some *Phaeodactylum tricornerutum* survived to metamorphosis.

The absolute growth rates of larvae fed the different foods are shown in Fig. 5. Those fed *Phaeodactylum tricornerutum* alone grew fastest, followed by those fed 1/3 *P. tricornerutum*. The slight growth of those fed *Isochrysis galbana* plus *Monochrysis lutheri* and those given no food is probably due to contamination with a few cells of *P. tricornerutum* from pipettes used in changing larvae.

On the basis of these data and because *Phaeodactylum tricornerutum* is easiest to

TABLE 3. Factorial analysis of variance. The effect of time, shell sculpture, salinity, and temperature on mortality of larvae. Three weeks  $\times$  2 sculpture types  $\times$  3 salinities  $\times$  3 temperatures  $\times$  2 replications. Only significant main effects and interactions shown. Each treatment combination consists of 2 replicates (r) or 2 bowls of larvae (65 larvae/bowl).

Source	Sum of square	Df	Mean square	F ratio	Df	Probability
Weeks (w)	6,3916.94	2	31,958.47	192.02	2, 8	P < 0.01
Temperature (t)	20,333.17	2	10,166.59	61.08	2, 8	P < 0.01
Salinity (s)	6,751.65	2	3,375.83	20.28	2, 8	P < 0.01
Week-Sculpture (wp)	1,517.34	2	758.67	4.56	2, 8	P < 0.05
Week-Temp. (wt)	3,672.74	4	918.18	5.52	4, 8	P < 0.05
Sculpture-Temp. (pt)	1,809.25	2	904.62	5.44	2, 8	P < 0.05
Error (Wtspr)	1,331.48	8	166.44			

culture, this diatom seems the best larval food at present. Experiments using similar species of unicellular algae occurring in Hawaii must still be performed. Preliminary results indicate that larvae grow slightly faster (with about the same survival) in cultures in which *P. tricor-nutum* is supplemented with some local unidentified nannoplankton (10-20 microns).

#### Temperature and Salinity

Several experiments on the effect of various salinities and temperatures on larval development were conducted. In the experiment described here, the growth and mortality of larvae from 2 extreme sculpture populations (heavily sculptured vs. smooth; see Introduction, and Struhsaker, 1968 for differences between shell types) were contrasted under 9 different combinations of temperature and salinity, with 2 replications per combination. A factorial analysis was performed and the percent mortalities under different treatment combinations assessed. This analysis is presented in Table 3. The percent mortalities are shown in Fig. 6 and the growth rates in Figs. 7 and 8.

The results are summarized as follows:

1. The larval shells resemble those of adults in parental populations (Struhsaker, 1968).

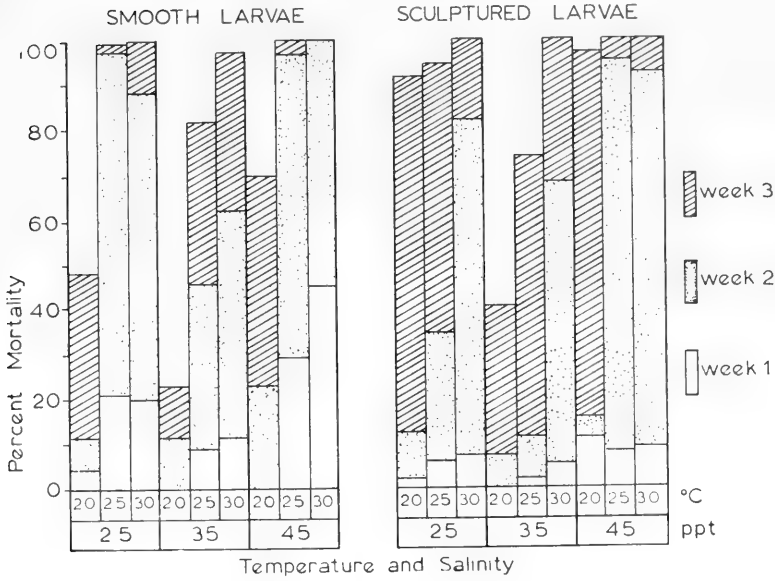
saker, 1968).

2. There is a significant interaction between time (week) of development and sculpture ( $P < 0.05$ ); with time, the mortality of smooth larvae increases more rapidly than the mortality of sculptured larvae.

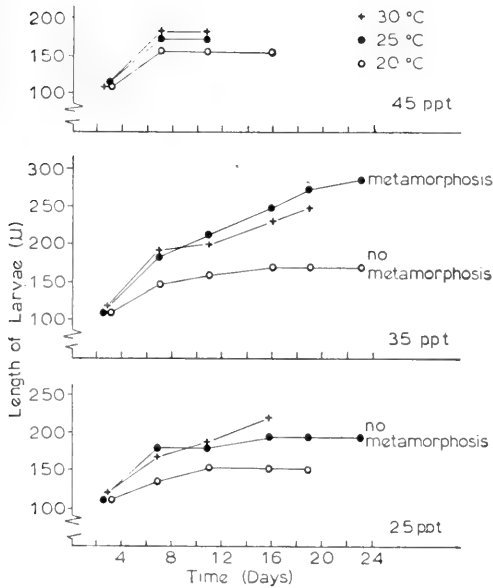
3. There is a significant interaction between time (week) and temperature, ( $P < 0.05$ ); with time, the mortality at different temperatures varies, the mortality being higher at higher temperatures, lower at lower temperatures and becoming proportionately greater each week.

4. There is a significant difference in mortality between salinities ( $P < 0.01$ ). The mortality rate at mean salinity (35 o/oo) is significantly lower than at extreme salinities (25 o/oo or 45 o/oo). There is an indication that sculptured forms survive better than smooth forms at higher salinity, particularly at a higher temperature.

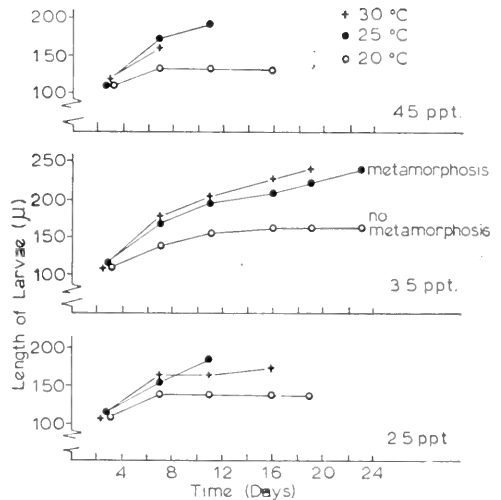
The variations in mortality between extreme sculpture types appear to be associated with the supratidal environment in which each is found (Struhsaker, 1968). The smooth form, in areas with greater water renewal and cooler temperatures, is more tolerant to low temperature, less tolerant to high temperature, and high salinity.



6



7



8

FIG. 6. Percent mortality of *Littorina picta* larvae (smooth and sculptured populations), at one week intervals throughout development; different combinations of salinity—temperature.

FIG. 7. Growth rate of *Littorina picta* sculptured larvae under different salinity-temperature combinations. Each point represents the mean maximum dimension of 10 larvae.

FIG. 8. Growth rate of *Littorina picta* smooth larvae under different salinity-temperature combinations. Each point represents the mean maximum dimension of 10 larvae.

Data are insufficient for significant regression analyses and prediction of optimal salinity-temperature combinations (as in Costlow, et. al., 1960, 1962). However, the information available shows that the optimal salinity range is approximately 35 o/oo to 40 o/oo. Larval mortalities increase sharply either below or above that range in both sculpture types. As development proceeds, larvae appear more tolerant of salinity variation.

The optimal temperature range is from approximately 24°C to 28°C. Below 24°C, larval survival may be high (probably in part because of decreased bacterial growth), but the growth rate is considerably slowed because larvae do not swim or feed normally. Above 28°C, larvae grow normally or slower than normal (bacterial contamination may suppress the growth of larvae) and the mortality is high. Because of the possible effect of bacterial contamination, the isolated effect of temperature on larval growth and mortality is difficult to interpret.

The absolute growth curves of larvae are shown in Figs. 7 and 8; sculpture forms of *Littorina picta* are shown in Fig. 7, smooth forms in Fig. 8. The growth rates of the sculptured forms are, in general, highest. The depression of growth at higher and lower salinities and higher and lower temperatures can be seen in both sculpture types.

In a few preliminary experiments, it was found that when larvae were removed (after 1 week's exposure) from high and low salinities (25 ppt and 45 ppt) and high and low temperatures (20°C and 30°C), they were able to recover and survive to metamorphosis when placed in a salinity of 35 ppt at 25°C.

#### Substrate

Only a few experiments were performed to test various substrates. Larvae were usually placed in bowls containing attached pieces of rock from the natural substrate

about 1 week prior to the time metamorphosis usually occurs (3-4 weeks; 3-4 whorls). Four pieces of rock, approximately 1-5 cm<sup>3</sup> were attached to the bottom of the bowls with aquarium cement. The rocks used were palagonite tuff, reef limestone, basalt and white quartz. Quartz does not occur in the natural environment, but was included for color contrast. Some larvae metamorphosed on all the rocks, but others also attached on the bottom of the glass bowl. Settlement appeared to depend more on the presence of an algal film on the bottom of the bowl and the rocks. The post-veligers were obviously feeding on this film. Removing portions of the film from the surface resulted in snails accumulating only in areas where algae were still present. After snails are older, however, they tend to aggregate in holes on the surface of the rocks, moving out over the surface of the glass bowl only at night when feeding activity is greater.

If appropriate food is not present on the substrate, larvae will continue to swim and feed on *Phaeodactylum tricorutum* for as long as 5-6 weeks and until their shells have attained the juvenile number of whorls (5-6). After approximately 3 weeks, the larvae metamorphose at any time if there is suitable algae or detritus on the surface of the bowl.

#### DISCUSSION AND CONCLUSIONS

Thorson (1950) discusses the factors affecting the mortality of marine larvae. Food, salinity, temperature, currents, predation, and availability of substratum are the major environmental factors suggested as being significant. Most estimates of mortality in planktotrophic larvae are extremely high (about 99%). Thorson believes the greatest mortality is probably due to predation.

Several environmental factors will significantly affect the survival and growth of

*Littorina picta* larvae in laboratory cultures. All of these may not be significant in the mortality of larvae in the natural environment because of new factors introduced by culture conditions and also because the larvae are able to survive within the extremes encountered in the open sea. Survival of larvae in the laboratory may be less than in the natural environment. The maximum survival of larvae in laboratory cultures up until time of settling was approximately 50%; through metamorphosis survival was about 10%. The mean survival through metamorphosis, however, was only about 1%. It is likely that larval survival in the field will approximate this, but the periods of greatest mortality may differ and originate from different factors (Struhsaker, 1969).

In general, the requirements of the larvae of Hawaiian *Littorina picta* are specific, although the larvae are highly flexible with respect to their tolerance to certain factors (i.e. salinity, temperature). They do not develop normally when overcrowded, without the appropriate type and amount of food, outside of a certain salinity-temperature range, or in water with heavy bacterial or fungal contaminations. Many of the results reflect the requirements of larvae in the natural environment, but others, such as overcrowding and disease, may be applicable only to the laboratory environment. The difficulty in rearing the larvae suggests that their requirements are specific during the planktotrophic stage. Also, the physical marine environment of Hawaii is relatively stable and a wide range of tolerances would not be expected in the marine larvae.

Bacterial contaminations may be critical factors in the mortality of larvae only in laboratory conditions. How important this factor is in the mortality of marine larvae in the natural environment is still uncertain. Marine bacteria and fungi

tend to accumulate on egg capsules and larval shells. In some fish eggs, for example, the bacteria reduce the buoyancy of the eggs, causing them to sink (Oppenheimer, 1955). The concentration of bacteria in the sea water, however, is relatively small (Zobell, 1946), and thus may not be a significant factor in the mortality of eggs or larvae in most instances.

Similarly, abnormal larvae are produced in the laboratory by overcrowding and antibiotics, which are not important factors in the natural environment. The variation in appearance and viability of the larvae may not be affected entirely by environmental factors, however; some abnormalities may result from incomplete and incompatible genetic combinations. Loosanoff & Davis (1963) believe that this is rare in clam and oyster larvae and that most of the abnormalities they encounter in cultures are due to lack of food, overcrowding, etc. The types of abnormal larvae which they describe are similar to those of *Littornia picta*, as for example, the incomplete shell development.

Guillard (1959) also found that bacterial toxins would kill oyster larvae or retard their growth. He stated that high temperatures favor growth of bacteria and sometimes inhibit growth of larvae. Loosanoff & Davis (1963) determined that Combistrep (50 ppm) inhibited growth of bacteria and reduced mortality, but at certain concentrations it also inhibited growth of larvae. These results are consistent with experiments with *Littorina picta*.

Scheltema (1962a) used *Phaeodactylum tricornutum* successfully to feed *Nassarius* larvae. D'Asaro (1965) used natural phytoplankton supplemented with *Platymonas* to feed *Strombus gigas* larvae. Most workers agree that food is a critical factor in successfully rearing larvae through metamorphosis. However, *Littornia picta* larvae have the ability to live

without food for several days after hatching, and it seems doubtful that in the natural plankton they would starve, although they may grow more slowly.

Salinity and temperature also affect growth and mortality of larvae in laboratory cultures. Costlow, Bookhout & Monroe (1960, 1962) found that the optimal salinity ranges for development differed among different larval stages of some crabs, and that salinity was the chief limiting factor in the distribution of these larvae. Unlike *Littorina picta* larvae, they are subject to a wide range of salinity associated with their migration from oceanic waters into estuaries. *L. picta* larvae do not encounter a wide range of salinities until they reach the supratidal region, at which time salinity may be an important mortality factor in the larvae and post-veligers. The temperature range of *L. picta* larvae is also much narrower than crabs, which may be a major factor limiting this endemic species to the Hawaiian Islands. The effect of temperature is difficult to separate from effect of bacteria; the latter may alter the growth and mortality of larvae in experiments without antibiotics.

Scheltema (1965) found a lower and wider range of salinity tolerance in *Nassarius* larvae (>15 ppt-17 ppt), at least at the lower range, than occurs in *Littorina picta* (>30 ppt). *Littorina picta* larvae will survive in salinities as low as 20 ppt, but they do not metamorphose and they eventually die.

As with salinity, *Nassarius obsoletus* larvae have a lower and a wider temperature tolerance range than *Littorina picta* larvae (Scheltema, 1967). In *N. obsoletus*, larvae completed development at 16-17°C while *L. picta* larvae did not complete normal development at 20°C. The lower limit (approximately 23°C) for normal development of *L. picta* is in accordance with the narrow environmental tempera-

ture range occurring in the Hawaiian Islands.

Similar to *Nassarius*, *Littorina picta* has some flexibility when replaced in optimal conditions after a period of exposure to extreme salinities or temperatures. Further, *L. picta* can also delay metamorphosis for some time (up to at least 8 weeks) when no appropriate substratum is provided.

At present, little is known of predation on larval *Littorina*. The laboratory results and field experiments done with other mortality factors, indicate that predation on settling larvae is only a minor mortality factor for this species. The most important factors affecting mortality of *L. picta* are the extremes of salinity, oxygen, temperature, wave action and oxygen which settling larvae and post-veligers encounter at time of settlement in the supratidal region (Struhsaker, 1968).

#### ACKNOWLEDGMENTS

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#### LITERATURE CITED

- CONKLIN, E. G., 1897, The embryology of *Crepidula*. *J. Morph.*, 13: 1-226.
- COSTLOW, J. D., JR., BOOKHOUT, C. G. & MONROE, R., 1960, The effect of salinity and temperature on larval development of *Sesarma cinereum* (Bosc) reared in the laboratory. *Biol. Bull.*, 118: 183-202.
- COSTLOW, J. D., JR., BOOKHOUT, C. G., & MONROE, R., 1962, Salinity-temperature effects on the larval development of the crab, *Panopeus herbstii* Milne-Edwards, reared in the laboratory. *Physiol. Zool.*, 35: 79-93.
- D'ASARO, C., 1965, Organogenesis, development and metamorphosis in the Queen Conch,

- Strombus gigas*, with notes on breeding habits. *Bull. mar. Sci.*, 15: 359-416.
- DROOP, M. R., 1954, A note on the isolation of small marine algae and flagellates for pure culture. *J. Mar. biol. Assn. U.K.*, 33: 511-541.
- FRETTER, V. & MONTGOMERY, M. C., 1968, The treatment of food by prosobranch veligers. *J. Mar. biol. Assn. U.K.*, 48: 499-519.
- GUILLARD, R. R. L., 1959, Further evidence of the destruction of bivalve larvae by bacteria. *Biol. Bull.*, 117: 358-266.
- GUILLARD, R. R. L. & RYTHER, J. H., 1962, Studies of marine planktonic diatoms. I. *Cyclotella nana* Husted and *Detonula confervacea* (Cleve) Gran. *Can. J. Microbiol.*, 8: 229-239.
- LEWIN, R. A., 1959, The isolation of algae. *Rev. Algol.*, 3: 181-197.
- LOOSANOFF, V. & DAVIS, H. C., 1963, Rearing of Bivalve Mollusks. In: *Advances in Marine Biology*, Vol. I, Academic Press, N.Y. 136 p.
- OPPENHEIMER, C. H., 1955, The effect of marine bacteria on the development and hatching of pelagic fish eggs, and the control of such bacteria by antibiotics. *Copeia*, 1: 43-49.
- PAULSON, T. C. & SCHELTEMA, R. S., 1968, Selective feeding on algal cells by the veliger larvae of *Nassarius obsoletus* (Gastropoda; Prosobranchia). *Biol. Bull.*, 134: 481-489.
- PROVASOLI, L., PINTNER, I. J., 1953, Ecological implications of *in vitro* nutritional requirements of algal flagellates. *Ann. N. Y. Acad. Sci.*, 56: 839-851.
- SCHELTEMA, R. S., 1961, Metamorphosis of the veliger larvae of *Nassarius obsoletus* (Gastropoda) in response to bottom sediment. *Biol. Bull.*, 120: 92-109.
- SCHELTEMA, R. S., 1962a, Pelagic larvae of New England intertidal gastropods. I. *Nassarius obsoletus* Say and *Nassarius vibex* Say. *Trans. Amer. microsc. Soc.*, 81: 1-11.
- SCHELTEMA, R. S., 1962b, Environmental factors affecting the length of pelagic development in the gastropod, *Nassarius obsoletus*. *Amer. Zoologist*, 2: 445.
- SCHELTEMA, R. S., 1965, The relationship of salinity to larval survival and development in *Nassarius obsoletus* (Gastropoda). *Biol. Bull.*, 129: 340-354.
- SCHELTEMA, R. S., 1967, The relationship of temperature to the larval development of *Nassarius obsoletus* (Gastropoda). *Biol. Bull.*, 132: 253-265.
- STRUHSAKER, J. W., 1966, Breeding, spawning, spawning periodicity and early development in the Hawaiian *Littorina*: *L. pintado* (Wood), *L. picta* Philippi and *L. scabra* (Linnaeus). *Proc. malac. Soc. Lond.*, 37: 137-166.
- STRUHSAKER, J. W., 1968, Selection mechanisms associated with intraspecific shell variation in *Littorina picta* (Prosobranchia: Mesogastropoda). *Evolution*, 22: 459-480.
- STRUHSAKER, J. W., 1969, Population ecology of the Hawaiian *Littorina*. (In prep.).
- STRUHSAKER, J. W. & COSTLOW, J. D., JR., 1968, Larval development of *Littorina picta* Philippi (Prosobranchia: Mesogastropoda), reared in the laboratory. *Proc. malac. Soc. Lond.*, 38: 153-160.
- THORSON, G., 1950, Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, 25: 1-45.
- WALNE, P. R., 1964, The culture of marine bivalve larvae. In: *Physiology of Mollusca*, p 197-210, Vol. I, Ed., K. M. Wilbur & C. M. Yonge. Academic Press, N.Y.
- ZOBELL, C., 1946, *Marine microbiology*. Chronica Botanica Co., Waltham, Mass. 240 p.

## RÉSUMÉ

QUELQUES EFFETS D'ENVIRONNEMENT SUR LE DEVELOPPAMENT  
LARVAIRE DE *LITTORINA PICTA* (MESOGASTROPODA), ÉLEVÉ  
EN LABORATOIRE

J. W. Struhsaker et J. D. Costlow

Les données suivantes proviennent d'une étude sur l'écologie des populations et sur la variation intraspécifique du test de *Littorina picta*, de Hawaï. Les larves d'individus provenant de populations appartenant aux 2 types extrêmes de sculpture du test et au type intermédiaire, ont été élevées dans les conditions constantes du laboratoire. Leur mortalité, leur croissance et leurs différences dans la morphologie du test ont été évaluées. Ces différences doivent rendre compte de la variation génotypique.

Les conditions du laboratoire pour l'élevage des larves sont décrites et plusieurs expériences, qui ont conduit à déterminer ces conditions, sont discutées. Les principaux facteurs externes étudiés ont les effets des antibiotiques, de la nourriture, de la salinité, de la température et du substrat sur la mortalité et la croissance des larves. En général, les conditions d'élevage pour tous les types de sculpture sont similaires. La meilleure croissance et la plus faible mortalité sont obtenues quand les larves sont nourries avec *Phaeodactylum tricorutum* et élevées dans de l'eau de mer dont la salinité est entre 35-40‰, la température entre 24-25°C et qui a été traitée par 20-25 ppm de sulfate de Polymixine B. La mortalité des larves élevées en laboratoire a généralement été très élevée. Le maximum de survivants obtenus jusqu'à la fixation a été d'environ 50%; et après métamorphose de 10%. La moyenne de survivants après la métamorphose, seulement d'environ 1%. Ainsi donc, les conditions de laboratoire ne doivent pas fournir les conditions optimales d'environnement pour les larves.

Il y a eu des variations dans la croissance et la mortalité des différents types de sculpture du test pour les extrêmes de température-salinité. Celles-ci sont en corrélation avec la distribution des types de sculpture du test dans la nature. Les formes fortement sculptées, qui se rencontrent sur les substrats desséchés où l'action des vagues est faible, ont des larves qui sont plus résistantes aux fortes salinités et moins résistantes aux basses températures que les larves des formes à coquilles lisses, qui se rencontrent sur les substrats humides où la force horizontale des vagues est forte. Tous les types de larves se fixent sur une surface recouverte d'un film d'algues. Un autre important stimulus de fixation est probablement le fait d'enlever l'eau du récipient par intermittence, après approximativement 3 semaines de développement. Les facteurs d'environnement cités ci-dessus, sont discutés en relation avec leur importance dans la mortalité des larves et des postvéligères dans l'environnement naturel.

A. L.

## RESUMEN

### EFFECTOS AMBIENTALES SOBRE LA LARVA DE *LITTORINA PICTA* (MESOGASTROPODA) CRIADA EN LABORATORIO

Struhsaker y Costlow

Los resultados descriptos forman parte de un estudio general de la ecología y variación intraespecífica de *Littorina picta* de Hawaii. Bajo condiciones constantes se criaron en el laboratorio larvas de dos tipos con diferencia extrema en escultura y otra con escultura intermedia, para determinar sus diferencias en la morfología conchológica, desarrollo y mortalidad. Se asume que esas diferencias representan variaciones genotípicas.

Se indican las condiciones en laboratorio y los experimentos conducentes a la determinación de esas condiciones. Los factores ambientales principales fueron el efecto de antibióticos, alimento, salinidad, temperatura y substrato, sobre el desarrollo y mortalidad de las larvas. En general, condiciones para todos los tipos de escultura son similares. El mayor desarrollo y supervivencia se obtuvieron en larvas criadas en agua de mar con una salinidad de 35/40 ‰ y temperaturas de 24/25°C, tratados con 20-25 ppm sulfato de Polimixina B y alimentadas con *Phaeodactylum tricorutum*. La mortalidad fue en general elevada y la supervivencia máxima aproximadamente de un 50%, y 10% experimentaron metamorfosis. El término medio de supervivencia después de metamorfosis fue, sin embargo, sólo de 10% más o menos. En consecuencia, las condiciones de laboratorio no proveen el ambiente óptimo para las larvas.

Hay variación en el desarrollo y mortalidad de diferentes tipos de escultura a salinidad y temperaturas extremas, que se correlacionan con la distribución de los tipos esculturales en el ambiente natural. Conchas con escultura fuerte aparecen en substrato seco de bajo oleaje y tienen larvas que son más resistentes a alta salinidad y menos resistentes a baja temperatura que las larvas de concha lisa las cuales viven en substratos siempre húmedos de oleaje horizontal más fuerte. Todos los tipos de larvas se asentaron sobre



superficies cubiertas con película de algas. Otro estímulo importante para el asentamiento es probablemente la remoción intermitente de agua del recipiente, después de un periodo de desarrollo aproximado de 3 semanas. Los factores indicados se discuten en relación a su importancia en la mortalidad de las larvas e individuos post-veligeros en el ambiente natural.

J. J. P.

### АБСТРАКТ

#### НЕКОТОРЫЕ ВОЗДЕЙСТВИЯ ВНЕШНЕЙ СРЕДЫ НА ЛИЧИНОЧНОЕ РАЗВИТИЕ *LITTORINA PICTA* (MESOGASTROPODA), ВЫРАЩЕННЫХ В ЛАБОРАТОРИИ

Ж. В. ШТРУХЗАКЕР И ДЖ. Д. КОСТЛОУ

Описываемые результаты получены при общем изучении популяционной экологии и внутривидовой изменчивости раковины у гавайской *Littorina picta*. Личинки моллюсков из популяций двух крайних популяций по типу скульптуры раковины и из промежуточной были выращены при постоянных лабораторных условиях: наблюдались их различия в морфологии раковины, в росте и смертности. Предполагается, что эти различия отражают генетическую изменчивость.

Описываются лабораторные условия для выращивания личинок и обсуждаются некоторые эксперименты, приводящие к определению этих условий. Большинство изученных факторов внешней среды были: влияние антибиотиков, пищи, солености, температуры и субстрата на рост личинок и их смертность. В общем, условия выращивания для всех типов по скульптуре раковины были одинаковы. Сымый большой рост и высокая выживаемость были получены, когда личинки выращивались в морской воде при солености 35-40‰ и при температуре 24-25°C, обрабатывались 20-25 ppm Polymixim B-сульфатом, при кормлении *Phaedactylum tricornutum*. Смертность личинок, выращенных в лаборатории, была в общем очень велика. Максимум личинок, доживших до оседания, был приблизительно 50%, а до метаморфоза-10%. Средняя выживаемость от начала до конца метаморфоза, однако, была лишь около 1%. Лабораторные условия, таким образом, не могут обеспечить самые оптимальные условия для выживания личинок.

Имеются колебания роста и смертности у личинок с различным типом скульптуры раковины при крайних значениях солености и температуры. Они скоррелированы с распространением моллюсков с различным типом скульптуры раковины в естественных условиях. Формы сильно скульптурированной раковины встречаются на более сухих субстратах; места со слабым влиянием волнения имеют личинку, которая более устойчива к высокой солености и менее устойчива к низкой температуре, чем личинки форм с гладкой раковинной, которые встречаются на влажном субстрате, подвергающемся сильным горизонтальным воздействиям волн. Все типы личинок оседают на субстрат, покрытый пленкой водорослей. Другим видным стимулом для оседания является возможно перемежающаяся смена воды в резервуаре после приблизительно 3-х недель развития личинок.

Выше рассмотрены факторы внешней среды в соответствии с их значимостью для отмирания личинок и в стадии пост-велигер в естественных условиях.



# THE FUNCTIONAL MORPHOLOGY OF THE FEEDING APPARATUS OF SOME INDO-WEST-PACIFIC DORID NUDIBRANCHS

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## ABSTRACT

Forty-eight species of Indo-West-Pacific dorids (Nudibranchia, Doridacea) are grouped into general feeding types, each with characteristic morphological adaptations of the buccal apparatus associated with specialized feeding. The functional morphology of the buccal apparatus of 4 feeding types is discussed: (1) rasping sponge-feeders, (2) sucking sponge-feeders, (3) engulfing opisthobranch-feeders, and (4) boring polychaete-feeders.

Extensive adaptive radiation among the dorids is especially evident in their various foods and modes of feeding. Conspicuous morphological adaptations to food are shown in the structure of the buccal apparatus. Members of each family group of dorids exhibit similar structure of the buccal apparatus and similar feeding habits. Because the buccal parts of dorids are used by taxonomists as major characters, it is not surprising that the dorids are grouped into rather discrete feeding types which parallel the taxonomic groups.

The sponge feeders, which comprise 7/8 of the dorids studied, are represented by the rasping sponge-feeding Dorididae and Hexabanchidae and by the sucking sponge-feeding Dendrodorididae. The engulfing opisthobranch-feeders are represented by 5 species of the Gymnodoridinae (family Polyceridae) and the boring polychaete-feeders by a single species of the Vayssiéridae.

The buccal apparatus of the dorids has undergone adaptive evolution in association with specialized feeding habits. Differences in feeding among the 4 types are explained by differing structure (or loss) of radular teeth and modifications of musculature involved in the operation of the buccal mass and the radula. Similarities are given between the feeding mechanism of each feeding type and that found in other opisthobranch, prosobranch and pulmonate gastropods.

## INTRODUCTION

The only comprehensive accounts available on the functional morphology of the feeding apparatus, commonly termed the "buccal apparatus," in an opisthobranch mollusc are Lemche's (1956) work on

*Cylichna* and Hurst's (1965) study of *Philine*, *Scaphander*, *Acteon*, *Cylichna* and *Retusa*. These animals are members of the order Cephalaspidea, presumably the most primitive order in the subclass Opisthobranchia. No complete account of the morphology and operation of the

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buccal apparatus in members of the order Nudibranchia has yet been given.

Descriptions are available of the anatomy, histology and functioning of the digestive systems of 4 aeolids, *Aeolidia papillosa*, *Cratena glotensis*, *Eoliina alderidi* and *Facelina drummondi* (Graham, 1938), and 1 dorid, *Jorunna tomentosa* (Millott, 1937), but the musculature and functioning of the buccal apparatus are largely ignored. Forrest (1953) describes the functioning of the digestive system and the feeding habits of 13 species of dorids from the British Isles but gives only a general account of the functioning of the buccal apparatus possessed by 2 feeding types: the sponge-eating dorids and the ascidian-and bryozoan-eating dorids.

Studies undertaken in the British Isles and the Netherlands on the food of nudibranchs suggest that North Atlantic dorids of the same family groups are restricted to similar types of food: one subfamily of the Polyceridae (Polycerinae) to bryozoans; the Onchidorididae to bryozoans and barnacles; the Goniodorididae (=Okeniidae) to ascidians; and the Dorididae to sponges (reviewed by Thompson, 1964). There are no comparable studies of dorids in the Indo-West-Pacific faunal region. This region contains not only more species of dorids than the North Atlantic, but it also has an almost entirely different species composition.

Four general feeding types are distinguished on the basis of morphological study of the buccal apparatus of 48 species of Indo-West-Pacific dorids, and on food studies of 18 of these (Young, 1965). These feeding types are: (1) rasping sponge-feeders, (2) sucking sponge-feeders, (3) engulfing opisthobranch-feeders, and (4) boring polychaete-feeders.

The present study deals with the gross morphology and the function of the buccal apparatus of each of the 4 feeding types represented by 48 species of Indo-West-

Pacific dorids. It is beyond the scope of this paper to completely identify all muscles of the buccal apparatus in any one species and, as such, this account differs from the comprehensive studies of *Cylichna* by Lemche (1956) and of *Philine* by Hurst (1965). Emphasis is given to those components of the apparatus that appear to be functionally important.

## METHODS AND MATERIALS

Forty-three species were examined from collections from Oahu and Kauai in the Hawaiian Islands between 1962 and 1966 (Kay & Young, 1969). Four additional species were collected from Eniwetok Atoll during 1965 and one further species was obtained from Palmyra Atoll during 1962 (Young, 1967).

Collections were made primarily from the intertidal zone to a depth of 5 meters, and several were taken in depths up to 100 meters by dredging.

The dorids were relaxed by refrigeration, fixed in 5% formalin and preserved in 70% ethyl alcohol.

Dissections were made under a dissecting microscope using fine needles, forceps and razors. The buccal apparatus was stained with aqueous methylene blue. The radular teeth and buccal armature were permanently mounted with Euparal on microscope slides.

Observations of feeding behaviour made from dorids held in aquaria were supplemented by observations in the field and analyses of feces and stomach contents. The results from these food studies will be discussed by the author in detail elsewhere.

## RESULTS

### 1. Rasping sponge-feeders

#### 1. Alimentary tract

In the rasping sponge-feeding dorids

TABLE 1. Thirty-nine rasping sponge-feeding dorids studied here, and their taxonomic positions.

## FAMILY DORIDIDAE

## Subfamily Doridinae

- Doriopsis granulosa* Pease 1860
- Doriopsis pecten* (Collingwood 1881)
- Doriopsis viridis* Pease 1861
- Doriorbis nucleola* (Pease 1860)

## Subfamily Archidoridinae

- Archidoris hawaiiensis* Kay & Young 1969
- Archidoris nubilosa* (Pease 1871)

## Subfamily Platydoridinae

- Platydoris formosa* (Alder & Hancock 1866)
- Platydoris* sp.

## Subfamily Discodoridinae

- Discodoris fragilis* (Alder & Hancock 1866)
- Carminodoris grandiflora* (Pease 1860)
- Carminodoris nodulosa* (Angas 1864)

## Subfamily Halgerdinae

- Halgerda rubra* (Bergh 1905)
- Halgerda graphica* Basedow & Hedley 1905
- Halgerda apiculata* (Alder & Hancock 1866)

## Subfamily Trippiinae

- Trippa osseosa* (Kelaart 1859)
- Trippa echinata* (Pease 1860)
- Trippa scabriuscula* (Pease 1860)

## Subfamily Kentrodoridinae

- Jorunna tomentosa* (Cuvier 1804)
- Asternotus cespitosus* (van Hasselt 1824)

## Subfamily Diaululinae

- Thordisa hilaris* Bergh 1905
- Thordisa setosa* (Pease 1860)
- Peltdoris fellowsi* Kay & Young 1969

## Subfamily Chromodoridinae

- Hypselodoris vibrata* (Pease 1860)
- Hypselodoris peasei* (Bergh 1880)
- Hypselodoris lineata* (Eydoux & Souleyet 1852)
- Hypselodoris kayae* Young 1967
- Hypselodoris tryoni* (Garrett 1873)
- Hypselodoris daniellae* Kay & Young 1969
- Chromodoris geometrica* (Risbec 1928)
- Chromodoris trimarginata* (Winckworth 1946)
- Chromodoris albopustulosa* (Pease 1860)
- Chromodoris imperialis* (Pease 1860)
- Chromodoris lilacina* (Gould 1852)
- Chromodoris decora* (Pease 1860)
- Chromodoris petchialis* (Gould 1852)
- Chromodoris youngbleuthi* Kay & Young 1969

## FAMILY HEXABRANCHIDAE

- Hexabranchnus marginatus* (Quoy & Gaimard 1832)
- Hexabranchnus aureomarginatus* Ostergaard 1955
- Hexabranchnus pulchellus* (Pease 1860)

that were dissected (Table 1), the mouth is ventral to the most anterior portion of the mantle, anterior to the foot and between 2 ventrolateral oral tentacles. Posterior to the mouth is a muscular buccal apparatus which opens posterodorsally into a greatly distensible esophagus (Figs. 1-4, es).

Among these 39 species of dorids, salivary glands are absent only in *Jorunna tomentosa* (Millot, 1937). In all others, a pair of free-ending, elongate salivary glands (Figs. 1-4, sg) enter at each side of the esophageal junction with the buccal mass and open into the lumen of the buccal mass. The nerve ring encircles the esophagus immediately posterior to the buccal apparatus. A pair of buccal ganglia (Figs. 2, 3, 5, 6, bg) lie ventral to the esophagus at the buccal-esophageal junction.

The esophagus extends posteriorly and opens posteroventrally into a thinwalled midgut (Figs. 1-4, mg). The midgut opens into the digestive diverticula of the massive digestive gland (dg). The caecum (ca) appears as a blind sac on the left side or to the rear of the midgut. The intestine (in) runs forward from the midgut, bends to the right (thereby forming the characteristic "dorid loop" of the Doridacea), and passes posteriorly on the dorsolateral right surface of the digestive gland to the anus. The anus is in a median posterodorsal position and is usually surrounded by secondary branchiae.

## 2. Buccal Apparatus

*Morphology* The generalized buccal apparatus of rasping sponge-feeding dorids may be divided into 3 distinct regions: an

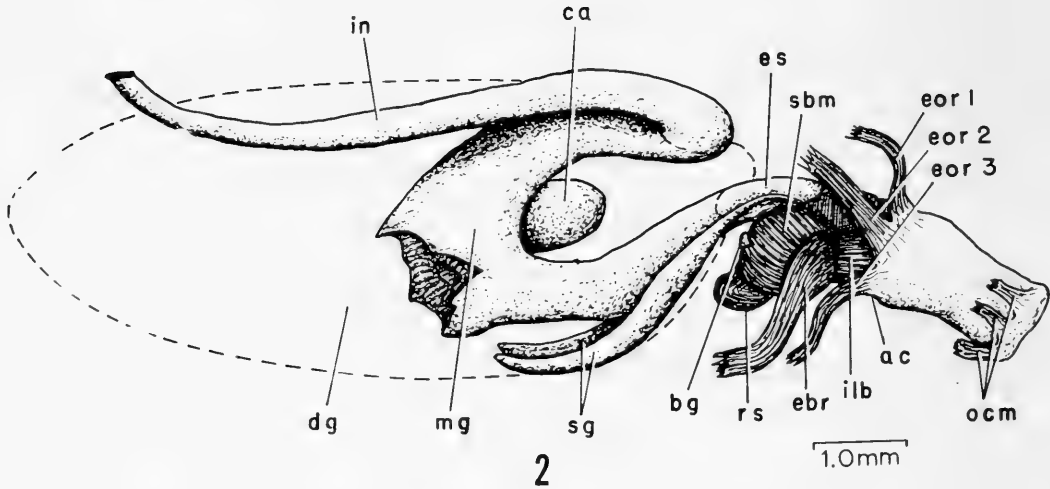
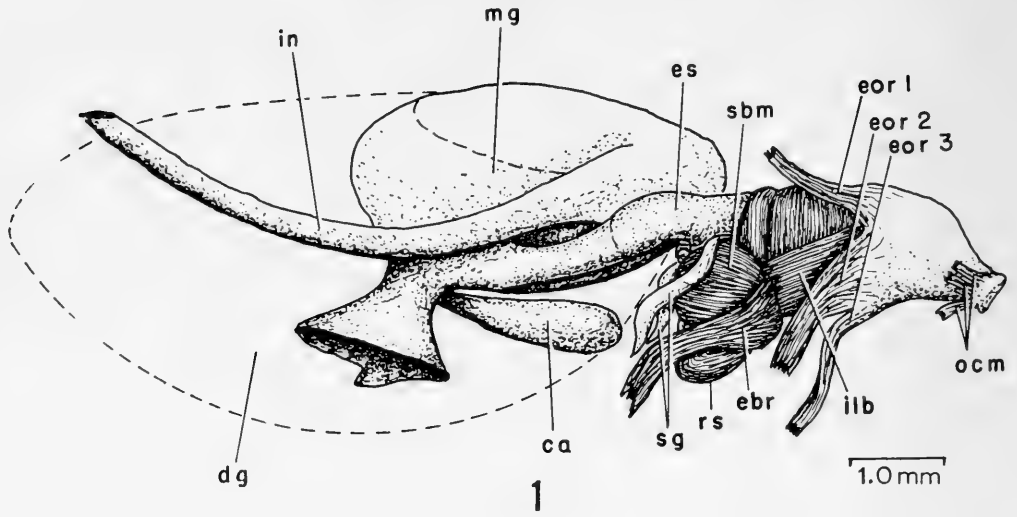


FIG. 1. *Doriopsis granulosa*. Lateral view of the alimentary tract (anterior at right).

FIG. 2. *Chromodoris decora*. Lateral view of the alimentary tract (anterior at right).

ac	anterior constriction	ebr	extrinsic buccal retractor muscle
arp	anterior radular protractor muscle	ebr 1, 2	extrinsic buccal retractor muscles 1, 2
ato	anterior transverse odontophoral musculature	eor 1-3	extrinsic oral retractor muscles 1-3
bb	buccal bulb	erm	esophageal retractor muscle
bg	buccal ganglion	es	esophagus
bl	buccal lip	ibr	intrinsic buccal retractor muscles
bm	buccal mass	il	inner lip
bs	buccal sheath	ilb	intrinsic longitudinal buccal musculature
bv	buccal vestibule	in	intestine
ca	caecum	ioj	intrinsic oblique buccal musculature
ct	connective tissue	j	jaw
dg	digestive gland	lbr	lateral buccal retractor muscles
		lc	lateral cartilage

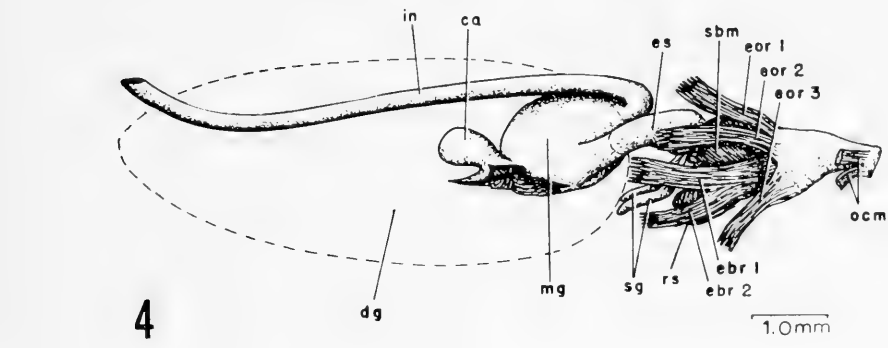
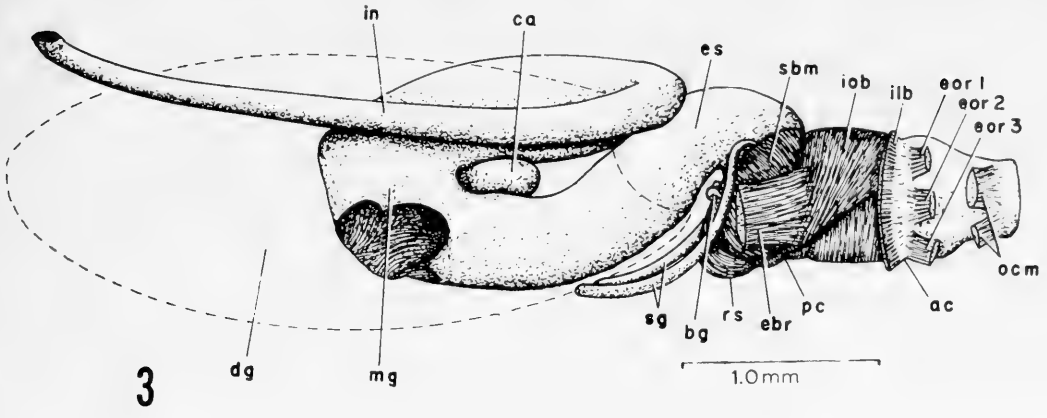


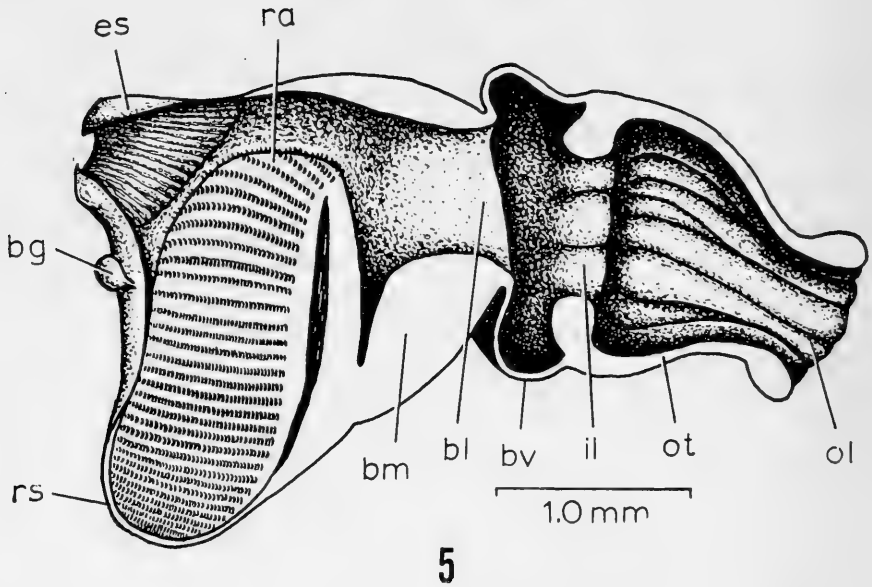
FIG. 3. *Hexabranchus marginatus*. Lateral view of the alimentary tract with the intrinsic buccal longitudinal musculature cut away and with the extrinsic buccal retractor muscle, the extrinsic oral muscles 1-3 and the oral branches of the columellar muscle severed for illustrative purposes (anterior at right).

FIG. 4. *Halgerda graphica*. Lateral view of the alimentary tract (anterior at right).

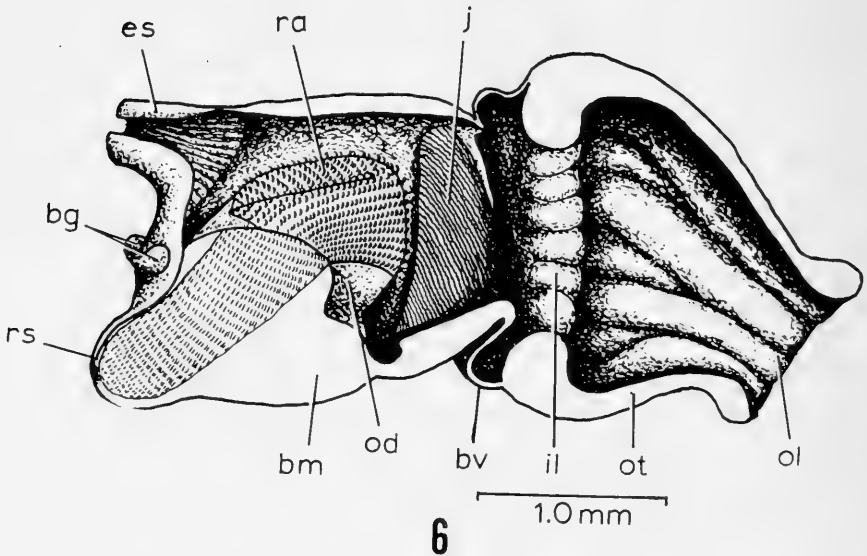
anterior, an intermediate and a posterior buccal region. These regions are visibly separated by 3 constrictions of the buccal wall, the "lips" (Alder & Hancock, 1855).

The anterior buccal region commence at the outer lip (Figs. 5, 6, ol) at the mouth, passes back through a plicated oral tube (ot) and terminates posteriorly at the inner lip (il). Both the outer and

mar	marginal radular protractor muscle	ph	pharynx
mbr	medial buccal retractor muscles	poc	posterior odontophoral compressor muscle
med	medial radular retractor muscle		
mg	midgut	pto	posterior transverse odontophoral musculature
ocm	oral branches of the columellar muscle	ra	radula
od	odontophore	rm	radular membrane
ol	outer lip	rs	radular sac
ot	oral tube	rt	radular teeth
pc	posterior constriction	sbm	superficial buccal musculature
pd	duct of ptyaline gland	sg	salivary glands
pg	ptyaline gland		



5



6

FIG. 5. *Doriopsis granulosa*. Right sagittal section of the buccal apparatus (anterior at right).

FIG. 6. *Chromodoris decora*. Right sagittal section of the buccal apparatus (anterior at right).

inner lips are ring-like thickenings of connective tissue encircled by sphincter muscles. The wall of the oral tube is composed of loose connective tissue which is interspersed with muscle fibers and glands, as in *Philine* (Sterner, 1912;

Hurst, 1965). Longitudinal muscle fibers extend along the length of the oral tube. Oral branches of the columellar muscle (Figs. 1-4, ocm) pass from insertions in the oral tube at the level of the outer lip and intermesh with the medial and lateral



branches of the columellar muscle which lie along the length of the body wall enclosing the haemocoel. Three pairs of muscles, the *extrinsic oral retractor muscles* (Figs. 1-4, eor 1, 2, 3), insert posteriorly in the oral tube and pass posterolaterally to origins in the adjacent body wall.

The intermediate buccal region lies immediately posterior to the inner lip of the oral tube. This region is similar to that in pulmonates termed the "buccal vestibule" (Figs. 5, 6, bv) by Amaudrut (1898). The wall of the buccal vestibule is thin, membranous and highly pliable. The cuticular lining of the posterior buccal region usually ends at the buccal vestibule, but in the Hexabanchidae it also lines the buccal vestibule. While few intrinsic muscles are on this structure itself, the wall of the buccal vestibule serves as an area for attachment of longitudinal musculature from the posterior buccal region.

The heavily muscled, posterior buccal region, or the "buccal mass" (Alder & Hancock, 1855), is bounded anteriorly by a broad, ring-like thickening of circular musculature at the buccal lip (Fig. 5, bl) and posteriorly by the esophageal orifice. The buccal mass encloses the ventrally positioned odontophore (Fig. 6, od) which bears the radula (Figs. 5, 6, ra).

The lumen of the buccal mass is lined with a thin cuticular layer (Fig. 7A). The histology of this layer has been described in *Jorunna tomentosa* by Millott (1937). In some rasping sponge-feeders the cuticular layer is thickened at the buccal lip as a jaw. The jaw has a characteristic shape appearing, for example, as a horseshoe with the free ends directed dorsally (Fig. 7B) or 2 plicated lateral plates (Fig. 7C). Imbedded in the jaws are densely set, singly hooked or bifid, chitinous elements or buccal armature.

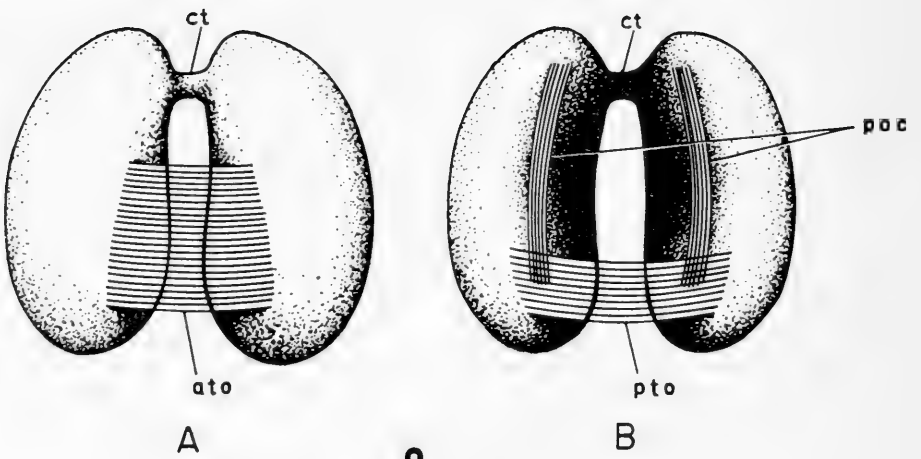
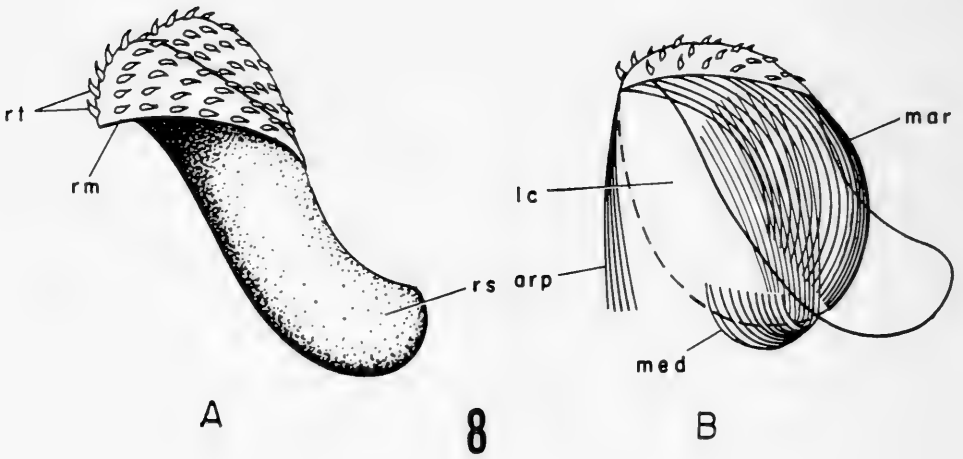
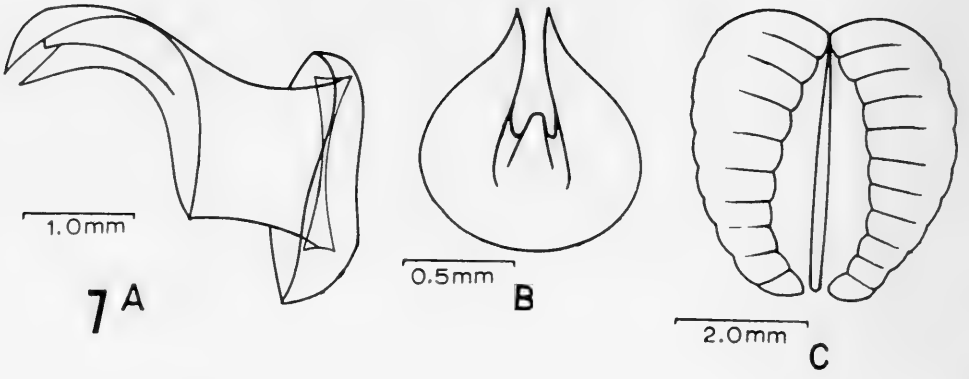
From the posteroventral portion of the buccal mass, a rounded radular sac (Figs.

1-6, 8A, rs) protrudes between 2 lateral thickenings. Passing obliquely in an anteroventral direction from a postero-medial origin dorsal to the radular sac and ventral to the esophagus, a thin sheet of superficial buccal musculature (Figs. 1-4, sbm) spreads over each lateral thickening and inserts at a dorsoventral furrow marking the anterior boundary of the lateral thickening. The dorsoventral furrow or posterior constriction (Fig. 3, pc) extends ventrally from the esophageal junction with the buccal mass and passes mid-ventrally into the buccal mass immediately anterior to the radular sac.

When the layers of intrinsic buccal musculature are removed, it is seen that the lateral thickenings of the buccal mass are protrusions of the superficial buccal musculature caused by the underlying odontophore. The odontophore is bounded on each side by a thick layer of musculature which passes posterodorsally from lateral origins with the odontophoral cartilages to insertions along the lateral edge of the radular membrane (Fig. 8A, rm) borne upon the odontophore. Because of its presumed function, this layer of musculature will be termed the *marginal radular protractor muscle* (Fig. 8B, mar).

The radular membrane is composed of 2 directly opposable, elongate semicircles of tissue upon which are borne regular transverse rows of posteriorly recurved radular teeth (Fig. 8A, rt). The halves of the radular membrane are joined ventrally and posteriorly so that the posterior portion forms the pouch-like radular sac. The dorsal portion of each half is stretched laterally across the odontophore by the marginal radular protractor muscle.

The rows of radular teeth in each half of the radular membrane are positioned so that an individual tooth in a given row has its mirror image directly opposite in the corresponding row of the opposite half of the radular membrane. The teeth are



all laterals with hook-shaped tips and medial, wing-like projections or flanges. The outer edges of the teeth are smooth, denticulate or pectinate.

On both sides of the radula are ovoid, laterally compressed masses of connective tissue termed the odontophoral cartilages or "lateral cartilages" (Prashad, 1925) (Figs. 8B, 1c; 9 A, B). These cartilages are composed of large, vacuolated, connective tissue cells which are reported to be interspersed with muscle fibres and deposits of calcium salts and glycogen in cephalaspidean opisthobranchs (Gabe & Prenant, 1952). The lateral cartilages form the support of the radula and are sites of origin for muscles that operate the radula and odontophore.

A thin strip of muscle, which is here termed the *posterior odontophoral compressor muscle* (Fig. 9B, poc), is attached to the posteroventral and posterodorsal edges of each lateral cartilage. With the exception of the posterior odontophoral compressor muscle, the surfaces of the lateral cartilages are devoid of any conspicuous intrinsic musculature.

The lateral cartilages are united antero-dorsally by a thin strip of connective tissue (Fig. 9AB, ct). Ventral to this connection, they are joined by transverse muscle fibres, the *anterior transverse odontophoral muscles* (Fig. 9A, ato). These muscles are overlaid by a pair of dorsoventrally directed muscles, termed the "anterior radular protractor muscles" in *Cylichna* by Hurst (1965) (Fig. 8B, arp), connecting the cuticular lining and the ventral portion of the buccal wall to the anterior edge of

the radular membrane and forming the anterior portion of the odontophore. Posteroventrally the lateral cartilages are connected by a muscle band, the *posterior transverse odontophoral muscle* (Fig. 9B, pto), forming the posterior portion of the odontophore. The radula is thereby encompassed laterally by the lateral cartilages, anteriorly by the anterior transverse odontophoral muscle and posteriorly by the posterior transverse odontophoral muscle.

Paired muscles, which are similar to the "medial radular retractor muscles" in *Cylichna* (=Musculus retractor radulae medialis, Lemche, 1956), each connect the ventrolateral portion of a lateral cartilage to the dorsomedial-inner surface of the radular membrane (Fig. 8B, med). The radula thereby stands upright between the paired medial radular retractor muscles and the lateral cartilages.

Several layers of muscle fibres, the *intrinsic longitudinal buccal musculature* (Figs. 1-3, ilb), originate at the posterior constriction on each side of the buccal mass. The thicker outer layer of musculature passes anteriorly to lateral insertions in the posterior-most edge of the oral tube, whereas the thinner inner layer has insertions in the wall of the buccal vestibule. In the Hexabranthidae, an additional layer of musculature, the *intrinsic oblique buccal musculature* (Fig. 3, iob), passes obliquely in an anterodorsal direction around each side of the buccal mass from origins in the posterior constriction and inserts mid-dorsally along the buccal wall.

FIG. 7. A. *Thordisa hilaris*. Lateral view of the cuticular lining of the buccal mass. B. *Hypselodoris vibrata*. Anterior view of the horseshoe-shaped jaw. C. *Hexabranthus marginatus*. Anterior view of the lateral plate-like jaws.

FIG. 8. A. Lateral view of a radula of a rasping sponge-feeding dorid. B. Lateral view of a radula, a lateral cartilage (area within dotted line), and radular musculature of a rasping sponge-feeding dorid.

FIG. 9. A. Anterior view of the lateral cartilages and odontophoral musculature of a rasping sponge-feeding dorid. B. Posterior view of the lateral cartilages and odontophoral musculature of a rasping sponge-feeding dorid.

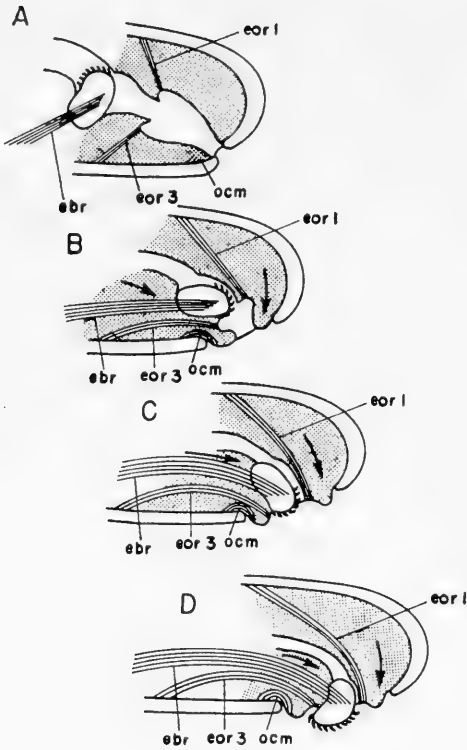


FIG. 10. Protraction of the odontophore in a rasping sponge-feeding dorid (diagrammatic). Arrows depict increase in blood pressure in the cephalic haemocoel. **A.** Retracted position of the odontophore. **B.** Opening of the outer and inner lips and foreshortening of the buccal mass. **C.** Opening of the buccal lip and protrusion of the odontophore. **D.** Protracted position of the odontophore; radula in position for the upward and forward rasping stroke.

The posterior constriction is a common area of muscle attachment and because of the great amount of intertwining of muscle fibres it is often difficult to ascertain the exact connections of muscles converging in this area. It is apparent, however, that the superficial buccal musculature forms insertions with the circular muscles of the buccal wall and the intrinsic longitudinal buccal musculature.

The only muscles connecting the buccal mass to the body wall are the *extrinsic buccal retractor muscles* (Figs. 1-3, ebr).

The paired extrinsic buccal retractor muscles are undivided in the majority of the rasping sponge-feeding dorids, but in some dorids (e.g., *Halgerda graphica*; Fig. 4, ebr 1, 2) each muscle is divided distally into 2 parts. These muscles have insertions in the posterior constriction of the buccal mass and ventrolateral origins in the medial branches of the columellar muscle. Muscle fibres from the extrinsic buccal retractor muscles insert along the ventrolateral anterior edge of the lateral cartilages as well as in the superficial and intrinsic buccal musculature.

*Function.* Observations of rasping sponge-feeding dorids in the process of feeding indicate that the sequence of events described by Millott (1937) in *Jourunna tomentosa* may generally apply throughout the entire group. These feeding movements are summarized as follows: (1) expansion of the outer and inner lips; (2) exposure of the buccal lip; (3) expansion of the buccal lip; (4) protrusion of the odontophore through the parted lips; (5) upward and forward movement of the radula over the odontophore; (6) simultaneous retraction of the odontophore and the radula; and (7) contraction of the buccal lip.

Protrusion of the odontophore and foreshortening of the buccal apparatus (Fig. 10, A-D) is initiated by contraction of the intrinsic longitudinal buccal musculature. The absence of any extrinsic buccal muscles that could act as protractors suggests that increased blood pressure in the cephalic haemocoel probably plays an important role in the protrusion process as shown in *Philine* by Hurst (1965). Posterolateral support of the odontophore is given by the superficial buccal musculature.

The buccal lip and the jaw (if present) are expanded by relaxation of the circular musculature of the buccal wall during the protraction phase of the odontophore.

The shape of the jaw is largely determined by the state of contraction or relaxation of the muscles of the buccal wall. The jaw probably assists in directing the odontophore as it passes in and out between the buccal lip. The jaws in those dorids having recurved buccal armature may also function in grasping portions of sponge which are then rasped away by the radular teeth.

The odontophore is the complex, largely self-contained unit of connective tissue, cartilage and muscles that provides support for the radula and aids its operation. The operation of the radula depends on the production of a firm "bending plane" (Ankel, 1937) and on the stretching of the radular membrane over it so that the functional teeth are erected and exposed to the feeding surface. The bending plane is produced by the support given to the radular membrane by underlying lateral cartilages which, in turn, can be flexed posteriorly by contraction of the posterior odontophoral contractor muscles. The hooked tip of each radular tooth (aided by denticles, if present) acts in rasping away small pieces of sponge and the concave surface produced by the flange acts as a scoop in conveying the particles to the esophagus.

As the odontophore is protruded through the widespread buccal lip, the radular membrane is pulled anteriorly and laterally over the lateral cushions by contraction of the anterior radular protractor muscles and the marginal radular protractor muscles. The lateral pull of the marginal radular protractor muscles expands the radular membrane and exposes and erects the functional radular teeth. Contraction of the anterior transverse odontophoral muscle and relaxation of the posterior transverse odontophoral muscle act in spreading the lateral cartilages and increasing the area of the radular rasping surface.

The upward and forward movement of

the radula occurs when the radular membrane is brought up and over the tips of the lateral cushions by the contraction of the paired medial radular retractor muscles. This movement, which immediately follows relaxation of the opposable protractor muscles (the marginal radular protractor muscles and the anterior radular protractor muscles), acts in directing the erected teeth against the feeding surface so that pieces of sponge are rasped away.

Retraction of the odontophore into the buccal mass is brought about by contraction of the paired extrinsic buccal retractor muscle. The oral tube is retracted by contraction of the oral branches of the columellar muscle and the extrinsic oral retractor muscles.

According to Millot (1937), when the odontophore is completely retracted and thrust into the esophageal opening, sponge particles are taken up by the posteriorly beating cilia which line the esophageal lumen. Mucus secreted by the glandular cells of the buccal apparatus and the esophagus coats the sponge particles while enzymes secreted by the salivary glands initiate digestion (Forrest, 1953).

### 3. Discussion

Although a comprehensive functional morphological study of the buccal apparatus of rasping sponge-feeding dorids is lacking in the literature, it is apparent from the terminology used by early workers that generalized functions of the more conspicuous external musculature had been determined at an early date. For example, in 1855 Alder & Hancock used the terms, "retractor muscles of the channel of the mouth," "retractor muscles of the buccal mass" and "protractor muscles" respectively for the "extrinsic oral retractor muscles", "extrinsic buccal retractor muscles" and "intrinsic longitudinal buccal musculature."

TABLE 2. Homologous buccal musculature of *Cylichna*, *Philine* and the rasping sponge-feeding dorids.

<i>Cylichna</i> (Lemche, 1956)	<i>Philine</i> (Hurst, 1965)	<i>Dorids</i> (Young, present study)
M. constrictor pharyngis anterior	Sphincter muscles	Circular musculature at buccal lip
M. pharyngis posterior	Superficial buccal musculature	Superficial buccal musculature
M. retractor radulae medialis	Radular occlusor muscles	Medial radular retractor muscles
M. retractor radulae marginalis	?	Marginal radular protractor muscles
M. rotellae dorsoventralis	Outer oblique muscles	Anterior radular protractor muscles
? M. rotellae circularis	Anterior transverse muscle	Anterior transverse odontophoral muscle
? M. rotellae circularis	Posterior transverse muscle	Posterior transverse odontophoral muscle
M. columellaris dorsolateralis lateralis ventrolateralis	Outer branch of columellar muscle Inner branch of columellar muscle	Oral branches of the columellar muscle
M. pharyngis longitudinalis ventralis	Ventral tensor muscles	Intrinsic longitudinal buccal musculature
M. retractor pharyngis	Extrinsic muscle pairs IV and V	Extrinsic buccal retractor muscles

The musculature of the buccal apparatus of rasping sponge-feeding dorids exhibits few obvious homologies (Table 2) to that described in *Cylichna* (Lemche, 1956) and *Philine* (Hurst, 1965). Homologies are masked, in part, because of their radically different modes of feeding. The radula of these cephalaspidean opisthobranchs has a "grabbing" function (Hurst, 1965), whereas the radula of rasping sponge-feeding dorids has a rasping action.

Among the prosobranch gastropods, several members of the Fissurellidae graze upon sponges (Morton, 1958), but their mode of feeding is distinctly different from the feeding of rasping sponge-feeding dorids. The Fissurellidae have rhipidoglossan radulae. The function of this

type of radula involves a complex interaction of buccal muscles with 2 pairs of cartilages producing a sweeping or brushing action of the radula (Fretter & Graham, 1962).

The prosobranch gastropods possessing taenioglossan radulae have a feeding mechanism basically similar to that of the rasping sponge-feeding dorids. Although the food, radular teeth and buccal musculature are dissimilar, the operation of the radula of *Viviparus* (which feeds on algae), as described by Eigenbrodt (1941), resembles that of these dorids. In both, the radular membrane spreads and passes over the bending plane produced by a single pair of supporting cartilages and the teeth are erected against the feeding

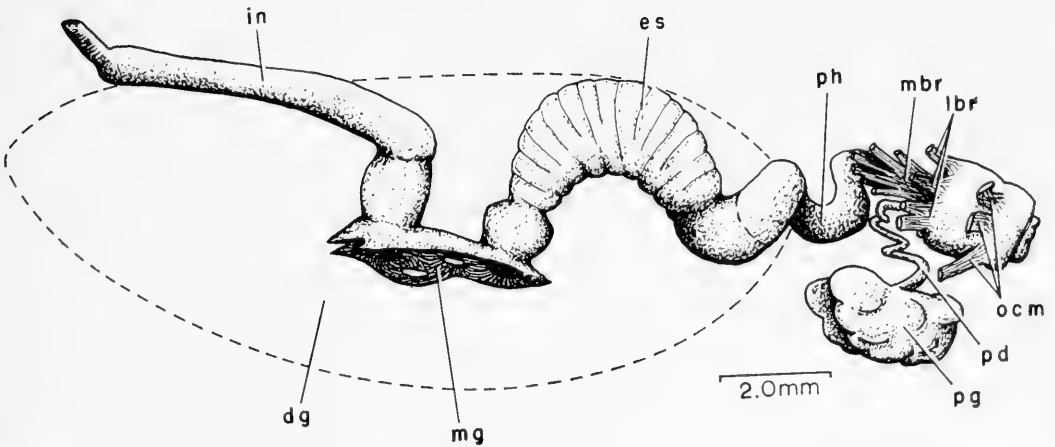
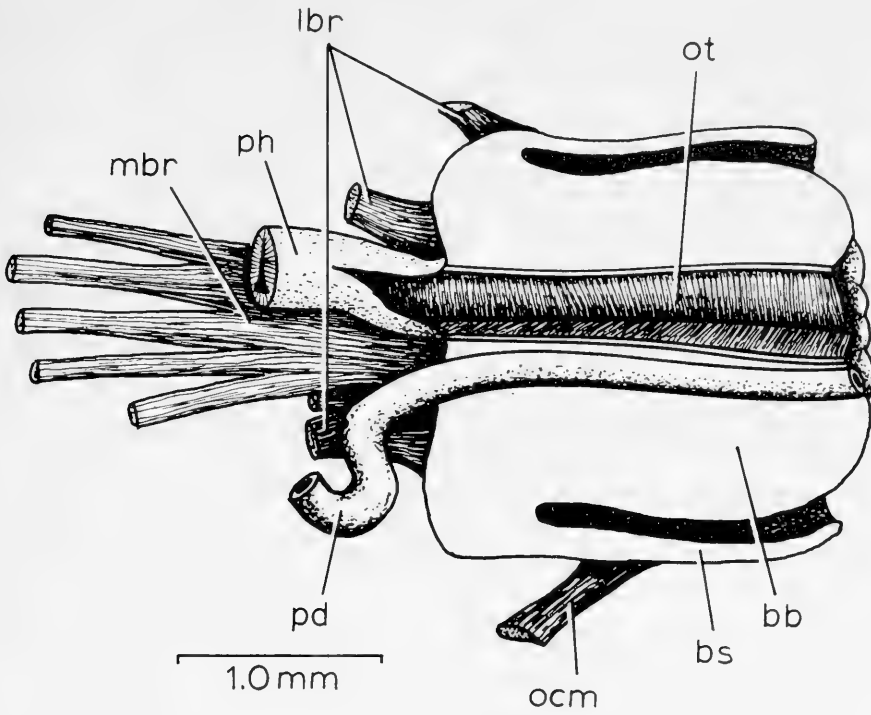


FIG. 11. *Dendrodoris nigra*. Right sagittal section of the anterior portion of the buccal apparatus (anterior at right).

FIG. 12. *Dendrodoris nigra*. Lateral view of the alimentary tract with the extrinsic muscles of the buccal apparatus severed for illustrative purposes (anterior at right).

surface. When the radular membrane is retracted, the recurved radular teeth rasp against the food and tear away pieces which are then passed back into the esophagus.

## II. Sucking sponge feeders

### 1. Alimentary tract

The sucking sponge-feeding dorids, represented in this study by *Dendrodoris nigra* (Stimpson, 1855), *D. tuberculosa* (Quoy & Gaimard, 1832) and *Dendrodoris coronata* Kay & Young, 1969 of the family Dendrodorididae, have a mouth that is situated anterior to the foot, ventral to the anterior portion of the mantle and between 2 small oral tentacles. The oral tube (Fig. 11, ot) with a triangular shaped bore extends posteriorly from the mouth, through the muscular buccal bulb (bb) and into the elongate, coiled pharynx (Figs. 11, 12, ph).

A large bilobed gland, the "ptyaline gland" (Bergh, 1884) (Fig. 12, pg), lies underneath the buccal bulb and gives rise to a duct (Figs. 11, 12, pd) which enters the posteroventral portion of the buccal bulb immediately ventral to the oral tube. The duct extends along the entire length of the buccal bulb and opens ventrally at the mouth opening.

Two small salivary glands are located at the junction of the pharynx with the esophagus, as described and figured by Eliot (1906, Pl. 57, figs. 4,7) in *Doridopsis* (= *Dendrodoris*) *nigra*, and 2 buccal ganglia each have a connective leading anteriorly to the nerve ring immediately posterior to the buccal bulb.

The esophagus (Fig. 12, es), which is enclosed by a large digestive gland (dg), extends posteriorly from the pharynx into an extremely thin-walled midgut (mg). The midgut is so perforated by digestive diverticulae of the digestive gland that its shape cannot be determined by gross dissection. The intestine (in) emerges

from the posterior portion of the midgut and extends posteriorly to a terminal, mid-dorsal anus. There is no indication of the so-called "dorid loop" in the intestine.

### 2. Buccal apparatus

*Morphology.* The buccal apparatus of the dendrodorids is quite unlike any others in the Doridacea. The structure is so highly modified in association with specialized feeding that the odontophore and radula are absent. It is reasonable to suppose, as suggested by Hancock (1865) and Eliot (1906), that the buccal ganglia and salivary glands mark the commencement of the esophagus and the termination of that portion of the alimentary tract homologous with the buccal apparatus of other dorids.

The anterior portion of the buccal apparatus is partially enclosed by a sheath of connective tissue, termed the "buccal sheath" (Fig. 11, bs) by Hancock (1865). The buccal sheath is open anteriorly to the exterior and connected posteriorly to an underlying mass of intrinsic musculature, the buccal bulb. The buccal bulb is largely comprised of longitudinal and transverse muscle fibres as shown by Hancock (1865). The triangular lumen of the oral tube is lined with cuticle from which bundles of radial muscles radiate out to circular musculature surrounding the tube similar to that described by Brown (1934) in the oral tube of *Philine* and by Maas (1965) in the first buccal pump of some pyramidellids.

Oral branches of the columellar muscle (Figs. 11, 12, ocm) insert in the ventrolateral anterior portion of the sheath and extend posteriorly to the medial branches of the columellar muscle along the foot. Several pairs of muscles, which will be termed the *extrinsic lateral buccal retractor muscles* (lbr), insert posterolaterally in the buccal bulb and pass laterally to origins in the adjacent body wall. The



number of extrinsic lateral buccal retractor muscles varies within and between species (e.g., 3-4 pairs in *Dendrodoris nigra*). A pair of broad muscles, the *extrinsic medial buccal retractor muscles* (mbr), originate posteriorly in the columellar muscle of the foot, pass anteriorly and insert along each side of the oral tube and the surrounding circular musculature of the buccal bulb.

**Function.** The food of the dendrodorids has long been a source of speculation but the only account verified by both field observations and gut examinations is that of Ghiselin (1964) who reports that *Doriopsilla albopunctata* feeds on "a variety of sponges." Food studies demonstrate that *Dendrodoris nigra* feeds on the sponge *Halichondria dura* in Hawaii. Several specimens of *D. nigra* held in aquaria were observed during the process of feeding to each thrust an everted proboscis through an osculum of *H. dura*. Spicules of *H. dura* were recovered from the feces and alimentary tracts of specimens of *D. nigra* collected from the field.

Protraction of the buccal bulb (Fig. 13, A-C) is brought about by increased blood pressure in the cephalic haemocoel as suggested by Hancock (1865). An absence of any muscles that could act as protractors precludes protraction of the buccal bulb by muscular action. Feeding occurs while the buccal bulb is in the protracted position.

The term "suctorial" was used to describe the buccal apparatus of the dendrodorids by Alder & Hancock (1866), and although later workers retain this function of the buccal apparatus as descriptive for the group, no attempt has been made to describe the way in which the supposed suction is achieved. It is possible that closure of the triangular lumen of the oral tube in the dendrodorids, as in the 1st buccal pump of the pyramidelids (Maas, 1965), is produced by the

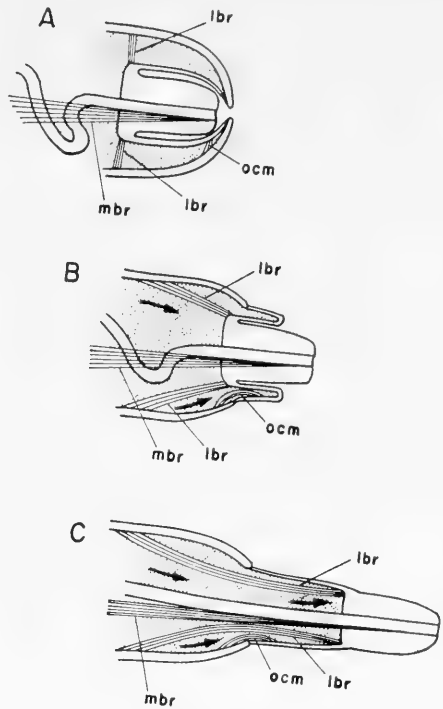


FIG. 13. Protraction of the buccal bulb in a sucking sponge feeding dorid (diagrammatic). A. Retracted position of the buccal bulb. B. Increased blood pressure in the cephalic haemocoel (depicted by arrows) and opening of the buccal sheath. C. Protracted position of the buccal bulb; buccal bulb in position for feeding.

antagonistic activity of circular musculature surrounding the tube to radial muscles connecting the lumen with the outer wall of the tube. The lumen is tripartite and constricted when the radial muscles are relaxed, whereas the lumen is triangular and open when the radial muscles are contracted. The antagonistic action of the circular muscles to the radial muscles accentuates the contractions and dilatations of the lumen of the oral tube. Negative pressure or suction within the tube is produced by differential contractions along the oral tube resulting in peristaltic activity moving food particles in an anterior to posterior direction.

Contractions of the extrinsic lateral buccal retractor muscles and the extrinsic medial buccal retractor muscles cause retraction of the buccal bulb after feeding is accomplished, as suggested by Hancock (1865). The retraction of the buccal sheath is aided by contraction of the oral branches of the columellar muscle. These muscles can produce a very rapid retraction of the buccal bulb and the buccal sheath when the animal is disturbed while it is feeding.

Studies by Krukenberg (1881) on the ptyaline gland or "acidogenous drusen" (acidogenic gland) of *Doriopsis* (= *Dendrodoris*) *limbata* suggested that the tissue and the secretion of the gland are slightly acidic as determined by litmus paper. In the present investigation extracts of the ptyaline gland of *Dendrodoris nigra* had pH values ranging from 6.0 to 6.5 as determined by pH indicator papers. Krukenberg also found that extracts of the ptyaline gland were free of peptic, tryptic and diastatic enzymes, in contrast with extracts of the digestive gland which contained all 3 enzymes in abundance. The active substance of the ptyaline gland was not characterized.

As previously discussed, the duct of the ptyaline gland is morphologically peculiar in that it does not empty into the oral tube but to the exterior through the mouth. This feature suggests that the substance secreted by the ptyaline gland affects the food material before it is drawn into the oral tube by suctorial action. Hancock (1865, p 191) suggested that the secretion of the ptyaline gland either dissolves food matter or is toxic to prey because, "The feeble structure of the buccal organ seems to suggest the requirements of some such aid, as, in these animals, there is neither cutting nor prehensile organs of any kind."

The absence of a ptyaline gland in the genus *Doriopsis*, whose members have a similar sucking buccal apparatus as

*Dendrodoris* (Eliot, 1906) and at least one species of which feeds on sponges (Ghiselin, 1964), suggests that the secretion of the ptyaline gland may not be essential to this type of feeding. If this is true; however, it is questionable how the spongin fibres are broken down in order that the mesenchymal cells and spicules may be ingested by the suctorial action of the buccal apparatus.

### 3. Discussion

Homologies of the buccal apparatus of the sucking sponge-feeders with that of the rasping sponge-feeders are difficult to determine. Both feeding types ingest similar food but by radically different methods: one uses a mechanical rasping action and the other, possibly a chemical action, followed by mechanical suction. The odontophore and radula have been lost in the sucking sponge-feeders through adaptive evolutionary processes.

Hancock (1865) suggested that the retractors of the buccal sheath (the extrinsic lateral buccal retractor muscles) of the sucking sponge-feeders are homologous with the retractors of the oral tube (the extrinsic oral retractor muscles) of the rasping sponge-feeders. If the oral tube of a typical rasping sponge-feeder is drawn over the buccal mass, and the odontophore (with all intrinsic musculature involved in its operation) is removed, the resultant appears like the buccal apparatus of a sucking sponge-feeder (Fig. 14, A-C). The extrinsic medial buccal retractor muscles of the dendrodorids appear to be homologous with the extrinsic buccal retractor muscles of the rasping sponge-feeding dorids.

Eliot (1906, p 664) suggested that the suctorial tube of the dendrodorids has apparently replaced the odontophore and through evolutionary processes the oral tube has "...been pulled backwards through the nerve-collar, and the buccal ganglia have moved with it...". The

salivary glands of the dendrodorids, though greatly reduced in size, have retained their position at the esophageal-buccal junction as in other dorids. Because a triangular shape of lumen connected with the passage of food has arisen in the pyramidellids (Maas, 1965) and in *Philine* (Brown, 1934), as well as in the dendrodorids, it appears that this shape is mechanically efficient. It is likely that a maximal change in volume of lumen is achieved with this shape (Hurst, pers. comm.).

The absence of a homologue of the ptyaline gland in the rasping sponge-feeding dorids suggests an early divergence of the dendrodorids from the lineage giving rise to those dorids with a rasping type of buccal apparatus. A pair of glands similar to the ptyaline gland is found in the muricid prosobranchs. These glands, which are termed the "accessory salivary glands," have a common duct that passes forward to empty lubricating secretions into the ventral region of the mouth (Carriker, 1943).

The buccal apparatus of the sucking sponge-feeders is placed within the anterior haemocoel similarly to the pleurembolic proboscis of the prosobranchs; whereas the buccal apparatus of the rasping sponge-feeders is comparable in placement to the acrembolic prosobranch proboscis. According to Fretter & Graham (1962), the pleurembolic type of proboscis in the prosobranchs is more advanced and more efficient mechanically than the acrembolic type.

Two prosobranchs, *Cerithiopsis tubercularis* and *Triphora perversa*, each have a long acrembolic proboscis which is passed through an osculum to the softer inner tissues of the sponge (Fretter, 1951), in much the same manner as the buccal bulb of *Dendrodoris nigra*. In contrast to the dendrodorids, however, these prosobranchs have a pair of jaws that break up

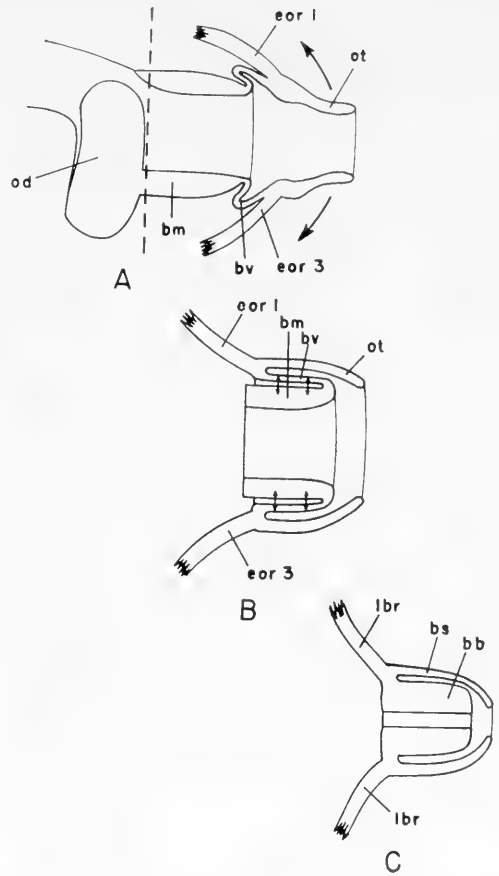


FIG. 14. Hypothetical sequence in the derivation of a sucking sponge feeding type of buccal apparatus from a rasping sponge-feeding type of buccal apparatus (diagrammatic). A. Prostomium is displaced posteriorly over the buccal mass of a rasping sponge feeding buccal apparatus and the portion of the buccal mass posterior to the dotted line is removed. B. Wall of the buccal vestibule fuses with that of the buccal mass. C. Lumen of the buccal mass constricts: buccal apparatus now imparts an outward appearance of a sucking sponge-feeding type.

the sponge tissue before it is moved to the buccal cavity by radular teeth.

Although quite different in morphology, an example is found in the cephalaspidean opisthobranch *Retusa* of a buccal apparatus which is devoid of an odontophore and a radula (Hurst, 1965). The lateral muscles and the buccal retractor

muscles of *Retusa* are similar in function to the extrinsic medial retractor muscles of *Dendrodoris*. Although Hurst states that *Retusa* probably employs suction as a means of obtaining food, no protrusion of the buccal apparatus is reported to occur.

### III. Engulfing opisthobranch-feeders

#### 1. Alimentary tract

The engulfing opisthobranch-feeding dorids are represented by *Gymnodoris okinawae* Baba, 1936; *G. bicolor* (Alder & Hancock, 1866); *G. alba* (Bergh, 1877); *G. plebeia* (Bergh, 1877) and *G. citrina* (Bergh, 1877) of the subfamily Gymnodoridinae (family Polyceridae). The mouth is anteroventral, lying anterior to the foot, ventral to the cephalic hood and between 2 ventrolateral oral tentacles. Posterior to the mouth is the large muscular buccal apparatus which opens posterodorsally into the greatly expansible esophagus (Figs. 15, 16, es).

Free-ending, lobulate salivary glands (Fig. 15, sg) enter at each side of the esophageal-buccal junction and open into the lumen of the buccal mass. The salivary glands, in contrast to those of the rasping sponge-feeding dorids, closely adhere to the buccal apparatus. Connectives from the cerebral ganglia overlying the buccal mass extend ventrally to the pair of medially connected buccal ganglia (Figs. 15, 16 bg) ventral to the esophagus.

The esophagus opens into the anterior end of the thin-walled midgut (Fig. 15, mg) which is perforated with large openings leading into the digestive diverticula of the digestive gland (dg). The midgut is larger and the digestive gland is smaller than those in the rasping sponge-feeding dorids. The midgut opens dorsally into the intestine (in) which is often so short that there is only an indication of the characteristic "dorid loop" of the Doridacea (in the extremely short

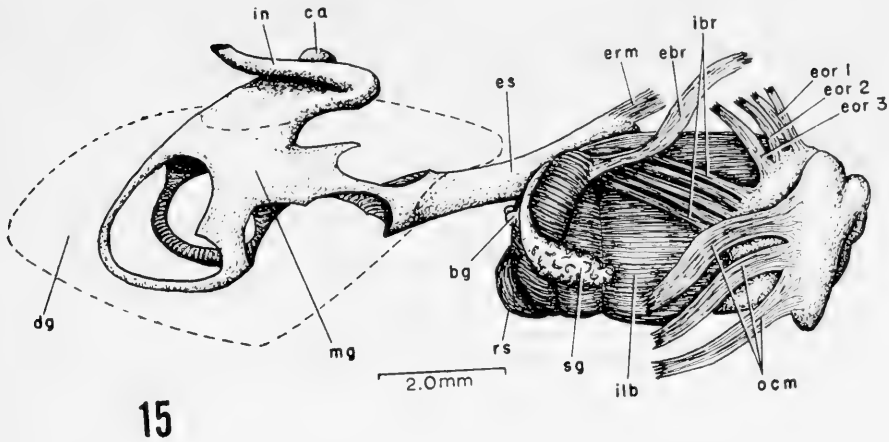
intestine of *Gymnodoris bicolor* no dorid loop is formed). A small caecum (ca) opens into the left side of the intestine at the midgut-intestine junction. The intestine terminates at the mid-dorsal anus.

#### 2. Buccal apparatus

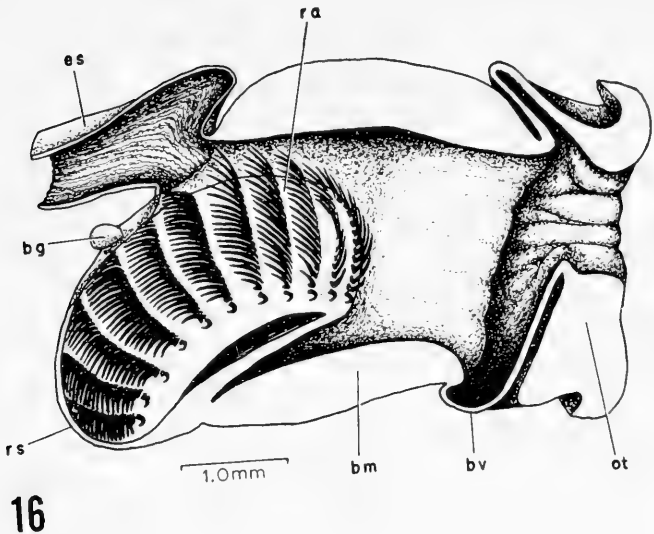
*Morphology.* The buccal apparatus of engulfing opisthobranch-feeding dorids may be differentiated into a short, anterior oral tube (Fig. 16, ot), a dilated, intermediate buccal vestibule (bv) and a muscular, posterior buccal mass (bm).

The oral tube is comprised of connective tissue interspersed with muscle fibres and glands. Sphincter muscles encircle the oral tube, but unlike the rasping sponge-feeding dorids, an outer and an inner lip cannot be distinguished. Oral branches of the columellar muscle (Fig. 16, ocm) insert anteriorly in the oral tube and connect posteriorly to the medial and lateral branches of the columellar muscle which in turn extend along the lateral and ventral body wall to posterior terminations. Three pairs of muscles, the *extrinsic oral retractor muscles* (Fig. 15, eor 1, 2, 3), insert dorsolaterally in the posterior edge of the oral tube and extend posterolaterally to origins in the adjacent body wall.

The *intrinsic buccal retractor muscles*, (Fig. 15, ibr) pass from dorsolateral origins in each side of the posterior portion of the buccal mass and insert laterally in the wall of the oral tube immediately ventral to the insertions of the extrinsic oral retractor muscles. A thin layer of intrinsic buccal longitudinal musculature (ilb) overlies the buccal wall and extends from the anterior edge of the superficial buccal musculature to the anterior margin of the buccal mass. Circular musculature forms the main bulk of the buccal wall. The inner surface of the buccal wall is lined with a thin layer of extremely flexible cuticle. No jaws are present, but a pair



15



16

FIG. 15. *Gymnodoris okinawae*. Lateral view of the alimentary tract (anterior at right).

FIG. 16. *Gymnodoris okinawae*. Left sagittal section of the buccal apparatus (anterior at right).

of cuticular plate-like thickenings are found on both sides of the anterior buccal wall in *Gymnodoris citrina*.

The superficial buccal musculature forms the lateral thickenings of the buccal mass which provide posterolateral support for the odontophore. The radular sac (Figs. 15, 16 rs) projects posteroventrally from between the lateral thickenings and forms a slight bulge to the rear of the buccal mass. As in the rasping sponge-

feeders, the superficial buccal musculature passes anteroventrally from a postero-medial origin at the rear of the buccal mass and inserts at a dorsoventral furrow marking the anterior edge of the lateral thickenings.

The only extrinsic muscles of the buccal mass, the *extrinsic buccal retractor muscles* (Fig. 15, ebr), insert in the anterodorsal portion of the superficial buccal musculature on each side of the buccal mass.

Their origin is anterodorsal to the buccal mass in the anterior body wall. The *esophageal retractor muscle* (erm), inserts in the dorsal esophageal wall posterior to the esophageal-buccal junction and passes anteriorly to origins in the body wall immediately dorsal to the origin of the extrinsic buccal retractor muscles.

As in the rasping sponge-feeding dorids, the odontophore is comprised of the radula and the lateral cartilages with their complex of odontophoral musculature. The more pronounced differences between the components of the odontophore of the engulfing opisthobranch-feeders and those of the rasping sponge-feeders are: (1) the radular membrane is shorter and broader; (2) the lateral cartilages are thinner and unconnected; (3) the medial radular retractor muscles are inserted more posteriorly along the inner surface of the radular membrane; and (4) the radular teeth are narrow and more elongate.

*Function.* The feeding movements of the buccal apparatus are described from observations of *Gymnodoris okinawae* and *G. bicolor* in the process of devouring their prey. *Gymnodoris okinawae* feeds on members of the saccoglossan family Elysiidae, whereas *G. bicolor* feeds on members of its own genus, *Gymnodoris*. Eversion of the entire buccal apparatus results in the odontophore projecting anteroventrally in relation to the dorsally situated esophageal orifice. The odontophore is spread and the radular teeth are erected. The prey is grasped by the radular teeth following closure of the odontophore. The odontophore is retracted and the prey is drawn into the esophagus. If the prey is large, these movements may continue until the entire animal is passed progressively into the esophagus by rhythmical in and out movements of the odontophore.

Versatility in the feeding movements of this type of buccal apparatus was indi-

cated by observations of *Gymnodoris bicolor* feeding on the egg masses of its prey *Gymnodoris okinawae*. The sequential feeding movements in this process are: (1) the oral tube parts; (2) the buccal wall is exposed as a narrow vertical slit; (3) the buccal lumen expands; (4) the odontophore protrudes; (5) the radula is spread and the teeth are erected; (6) the odontophore narrows and the radular teeth grasp the egg mass; (7) the odontophore retracts and a portion of the egg mass is torn away; and (8) the lumen of the buccal mass is reduced to a slit-like aperture. The entire sequence occurs in 5 second intervals at 26°C.

The buccal mass is protruded to a varying extent according to whether the animal is feeding on motile prey or egg masses. While feeding on egg masses, the buccal mass moves in a sequence similar to that of the buccal mass of rasping sponge-feeding dorids; the main difference is in the operation of the odontophore. Because of this similarity in the sequence of feeding movements, only the functional morphology of the buccal apparatus involved in the prey-engulfing sequence will be discussed.

Protrusion of the buccal apparatus is brought about by increased blood pressure in the cephalic haemocoel (Fig. 17 A-C). In contrast with the same process in rasping sponge-feeding dorids, the buccal mass in the gymnodorids is protruded outwardly from the prostomium and entirely everted. Although the longitudinal intrinsic buccal muscles are involved in protraction of the odontophore and foreshortening of the buccal mass, the extrinsic muscles of the buccal apparatus are involved only in the retraction process. Because the extrinsic buccal muscles have anterior origins, greater protraction of the buccal mass is possible than in the rasping sponge-feeders which have extrinsic buccal muscles with posterior origins.

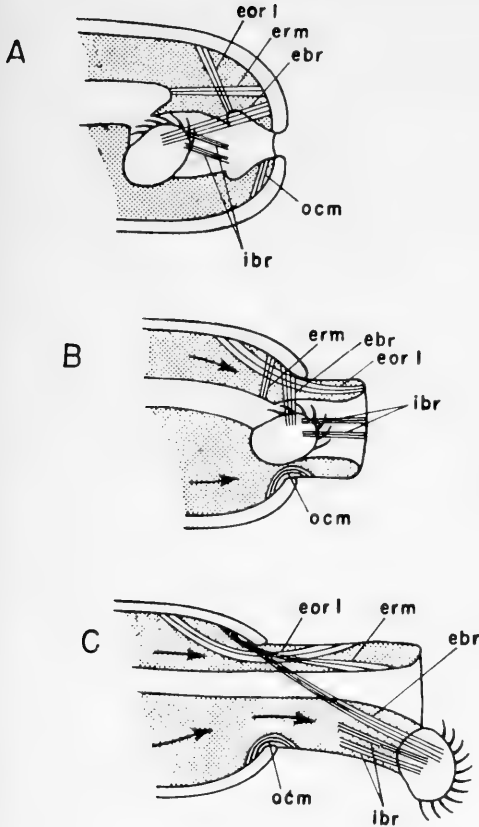


FIG. 17. Protraction of the odontophore in an engulfing opisthobranch-feeding dorid (diagrammatic). **A.** Retracted position of the odontophore. **B.** Increased blood pressure in the cephalic haemocoel (depicted by arrows) and opening of the lumen of the oral tube and the buccal mass. **C.** Protracted position of the odontophore with the entire buccal apparatus everted; radula open and in position to grasp prey.

The functional differences in the operation of the odontophore of engulfing opisthobranch-feeders and of rasping sponge-feeders may be explained, in part, by 2 major factors. Firstly, the odontophore in the gymnodorids may be widely spread because the lateral cartilages have no connections of connective tissue. Secondly, the radula may be spread wider than in the rasping sponge-feeders because the medial radular retractor muscles are

inserted more posteriorly on each side of the radular membrane.

The radular membrane is pulled over each lateral cartilage by contraction of the marginal radular protractor muscles. The lateral tension upon the radular membrane erects the elongate radular teeth. Simultaneously, contraction of the anterior radular protractor muscles protracts the radula and exposes all the functional radular teeth.

The odontophore is closed by contraction of the medial radular retractor muscles which also retracts the radula and directs the radular teeth inward and backward. The elongate radular teeth pierce the epidermis of the prey, thereby exerting a firm grip while the prey is drawn into the esophagus.

Retraction begins with the withdrawal of the esophagus by the contraction of the esophageal retractor muscle. This process is accompanied by a decrease in blood pressure in the cephalic haemocoel.

Retraction of the odontophore and the everted buccal mass is accomplished by contraction of the extrinsic and intrinsic buccal retractor muscles. Finally, the oral tube is retracted by contraction of the extrinsic oral retractor muscles and the oral branches of the columellar muscle. The shape of the buccal mass is maintained throughout the entire process by support given by the superficial buccal musculature and muscles of the buccal wall.

### 3. Discussion

The buccal apparatus of the engulfing opisthobranch-feeders exhibits several interesting differences from that of the rasping sponge-feeders. The main morphological differences enabling the gymnodorids to devour large prey are: (1) the mouth and buccal apparatus are anteriorly directed; (2) the salivary glands adhere only to the buccal mass; (3) the oral region is short; (4) the extrinsic oral retractor muscles insert dorsolaterally in

the oral tube; (5) the extrinsic buccal retractor muscles have anterior origins; (6) the lateral cartilages are unconnected; (7) the medial radular retractor muscles have posterior insertions along the radular membrane; (8) the radular teeth are narrow and elongate; and (9) the esophagus is connected anteriorly to the body wall by the esophageal retractor muscle.

The buccal apparatus of the cephalopidean opisthobranch *Philine* (Hurst, 1965), which has a similar engulfing type of feeding, exhibits several interesting homologies with that of the engulfing opisthobranch-feeders. The most pronounced of these is the apparent homology between the extrinsic buccal retractor muscles of *Gymnodoris* and the extrinsic retractor pair II of *Philine*. These muscles apparently serve as retractors of the buccal mass in both animals, although Hurst (1965) suggested that extrinsic retractor muscle pair II in *Philine* aids initially in protraction of the buccal mass. In contrast with the retraction of the buccal apparatus in *Philine*, where the esophagus is withdrawn lastly and with difficulty (Hurst, 1965), the retraction of the esophagus in *Gymnodoris* is brought about as a preliminary step in the retraction process by contraction of the esophageal retractor muscle, a muscle not present in *Philine*.

Similar engulfing processes are accomplished by gastropods other than *Philine* and *Gymnodoris*. Examples of a buccal apparatus which functions by protraction of the odontophore, gripping of prey by fang-like radular teeth and drawing the prey into the esophagus by retraction of the odontophore is found in the prosobranch *Ianthina* (Graham, 1965) and in the pulmonate *Testacella* (Lacaze-Duthiers, 1887; Webb, 1893). Graham (1965) has pointed out that the feeding mechanism of *Philine*, *Ianthina* and *Testacella* differs mainly in the extent of

protraction of the odontophore and eversion of the buccal mass.

#### IV. Boring polychaete-feeders

##### 1. Alimentary tract

The boring polychaete-feeders are solely represented by *Okadaia elegans* of the family Vayssiereidae. This minute dorid is rarely longer than 4 mm as an adult. In comprehensive morphological treatments of *Okadaia elegans*, Baba (1931, 1937) reports that the alimentary tract commences at a ventral mouth and passes progressively through a stomodaeum lined with ciliated cells and mucous gland cells; a large, jawless buccal mass lined anteriorly with chitin; an elongate esophagus lined with ciliated cells and internal folds; a thin-walled, U-shaped stomach perforated with openings from a 3-4 lobed liver; and an anteriorly directed intestine that describes a typical dorid loop and opens at a mid-dorsal anus. Although the liver is divided into 3 or 4 lobes, Baba (1931, p 76) reports that it is unramified and that it should be considered as the holohepatic type.

##### 2. Buccal apparatus

*Morphology.* The pear-shaped buccal apparatus of *Okadaia elegans*, as figured in sagittal section by Baba (1937, Fig. 9), encloses an odontophore and radula. No salivary glands are present. Muscle fibers, which arise from the base of the odontophore, surround the radula sheath and terminate at the tip of the odontophore and "...control the protraction and retraction of the odontophore" (Baba, 1937, p 160). The radula bears teeth with the formula, 35-44 × 3.0.3. They are differentiated as follows: the 1st lateral is hamate, tipped with 3 spiny denticles; the 2nd lateral is simply hamate; and the 3rd lateral is plate-like (Baba, 1937, p 159).

A pair of "pharyngeal valves" is reported by Baba (1937, p 160-161) to



project downward from the posterodorsal wall of the buccal mass. These structures, which bear ciliated cells and cuticle, are devoid of gland cells and are sensory in function according to Baba.

*Function.* Observations of specimens of *Okadaia elegans* in the process of feeding on spirorbid polychaetes indicate that there are 2 distinct phases of feeding: the boring phase and the engulfing phase. Although Baba (1937) states that *Okadaia elegans* feeds on *Spirorbis*, he fails to describe the mechanism for feeding upon such prey enclosed in calcareous tubes. The purpose of this discussion, therefore, is to report the peculiar feeding habit of *Okadaia elegans*.

During the boring phase, each individual exhibits an up and down movement of the head while the rest of the animal remains in a fixed position. A round hole, 57 to 88 $\mu$  in diameter, is bored near the posterior portion of the calcareous tube. No tube of a spirorbid polychaete has been observed with more than one bored hole. After the hole is bored, the dorid extends its odontophore through the hole and grasps the polychaete with its erected radular teeth. Thereafter, the feeding mechanism is very much like that of the engulfing opisthobranch-feeders; the polychaete is drawn progressively into the esophagus by in and out movements of the odontophore and swallowed whole. Depending on the size of the predator and prey, the boring phase takes from 35 minutes to 6 hours and the engulfing phase from 15 to 30 minutes for completion.

The radular teeth of *Okadaia elegans* serve at least 2 different functions. The serrated 1st lateral tooth is probably utilized as a boring tool, whereas the more elongate, hooked 2nd lateral tooth serves in grasping the prey.

### 3. Discussion

Whereas the swallowing phase of the boring polychaete-feeding dorids is much like that of the engulfing opisthobranch-feeding dorids, the boring phase is unique among the Opisthobranchia. Members of the Prosobranchia in the families Muricidae and Naticidae also feed on animals enclosed by a hard calcareous outer covering. Mechanical boring of the shells of molluscan prey by muricean borers has been demonstrated by such workers as Pelseneer (1925), Graham (1941) and Jensen (1951); but Carriker (1959) has more recently shown that the boring mechanism in these animals is aided by chemical activity.

It is not known if chemical action assists the boring process in *Okadaia elegans*. The histological sections of Baba (1937), however, demonstrate no glandular structures in *Okadaia elegans* which might assist boring as does the accessory boring organ in *Urosalpinx cinerea* and *Eupleura caudata* (Carriker, 1959)<sup>3</sup>.

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Grateful acknowledgment is due Dr. E. Alison Kay (University of Hawaii, Honolulu, U.S.A.) for her interest and aid in all aspects of this study. The author appreciates the comments and criticisms of the manuscript by Dr. Melbourne R. Carriker (Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Mass. U.S.A.), Dr. Anne Hurst (University of Reading, Reading, U.K.) and Dr. Michael Ghiselin (University of California, Berkeley, Calif., U.S.A.). This study was supported by a Marine Science Graduate Research Fellowship from the Bureau of Commercial Fisheries, and the final aspects of the work and preparation of the manuscript were done in the Systematics-Ecology Program under support of Grant GB-4509 from the National Science Foundation, Washington, D.C., to the Systematics-Ecology Program.

<sup>3</sup> Research subsequent to that reported in this paper indicates that tube-boring by *O. elegans* is aided by secretions from a gland within the stomodaeum (See Young, 1969).

## REFERENCES

- ALDER, J. & HANCOCK, A., 1855, *A monograph of the British nudibranchiate Mollusca*. Ray Soc., Lond., 438 p.
- ALDER, J. & HANCOCK, A., 1866, Notice of a collection of nudibranchiate Mollusca made in India by Walter Eliot Esq., with descriptions of several new genera and species. *Trans. zool. Soc. Lond.*, 5: 113-145.
- AMAUDRUT, A., 1898, La partie antérieure du tube digestif et la torsion chez les mollusques gastéropodes. *Amer. Sci. Nat. Zool.*, 7: 1-291.
- ANKEL, W. E., 1937, Wie frisst *Littorina*? 1. Radula-Bewegung und Fressspuren. *Senckenbergiana*, 19: 317-333.
- BABA, K., 1931, A noteworthy gill-less holohepatic nudibranch *Okadaia elegans* Baba, with reference to its internal anatomy. *Annot. Zool. Japon.*, 13: 63-83.
- BABA, K., 1937, Contribution to the knowledge of a nudibranch, *Okadaia elegans* Baba. *Jap. J. Zool.*, 7: 147-190.
- BERGH, R., 1884, Report on the Nudibranchiata. *Rep. Sci. Res. Challenger, Zoology*, 10: 1-154.
- BROWN, H. H., 1934, A study of a tectibranch gasteropod mollusc, *Philine aperta* (L.). *Trans. Roy. Soc. Edinb.*, 58: 179-210.
- CARRIKER, M. R., 1943, On the structure and function of the proboscis in the common oyster drill *Urosalpinx cinerea* Say. *J. Morph.*, 73: 441-506.
- CARRIKER, M. R., 1959, Comparative functional morphology of drilling mechanism in *Urosalpinx* and *Eupleura* (muricid gastropods). *Proc. XV Int. Cong. Zool.*, Lond., p 373-376.
- EIGENBRODT, H., 1941, Untersuchungen über die Function der Radula einiger Schnecken. *Z. Morph. Okol. Tiere*, 37: 735-791.
- ELIOT, C., 1906, On the nudibranchs of the southern India and Ceylon, with special reference to the drawings by Kelaart and the collections belonging to Alder and Hancock preserved in the Hancock Museum at Newcastle-on-Tyne. *Proc. Zool. Soc. Lond.*, 2: 636-691.
- FORREST, J. E., 1953, On the feeding habits and the morphology and mode of functioning of the alimentary canal in some littoral dorid nudibranchiate Mollusca. *Proc. Linn. Soc. Lond.*, 164: 225-235.
- FRETTER, V., 1951, Observations on the life history and functional morphology of *Cerithiopsis tubercularis* (Montagu) and *Triphora perversa* (L.). *J. Mar. biol. Ass. U.K.*, 29: 567-586.
- FRETTER, V. & A. GRAHAM, 1962, *British prosobranch molluscs*. Ray Soc. Lond., 755 p.
- GABE, M. & M. PRENANT, 1952, II. Recherches sur la gaine radulaire des mollusques. 5. L'appareil radulaire de quelques opisthobranches cephalaspidés. *Bull. Lab. marit. Dinard*, 37: 13-17.
- GHISELIN, M. T., 1964, Feeding *Dendrodoris (Doriopsis) albopunctata*, an opisthobranch gastropod. *Ann. Rep. Amer. malacol. Union*, 1964, 31: 45-46.
- GRAHAM, A., 1938, The structure and function of the alimentary canal of aeolid molluscs, with a discussion on their nematocysts. *Trans. Roy. Soc. Edinb.*, 59: 267-307.
- GRAHAM, A., 1941, The oesophagus of the stenoglossan prosobranchs. *Proc. Roy. Soc. Edinb.*, B, 61: 1-23.
- GRAHAM, A., 1965, The buccal mass of ianthinid prosobranchs. *Proc. malacol. Soc. Lond.*, 36: 323-338.
- HANCOCK, A., 1865, On the anatomy of *Doriopsis*, a genus of the nudibranchiate Mollusca. *Trans. Linn. Soc.*, 25: 189-207.
- HURST, A., 1965, Studies on the structure and function of the feeding apparatus of *Philine aperta* with a comparative consideration of some other opisthobranchs. *Malacologia*, 2: 281-347.
- JENSEN, A. S., 1951, Do the Naticidae (Gastropoda Prosobranchia) drill by chemical or mechanical means? *Vidensk. Medd. dansk. naturh. For naturh. Foren. Kbh.*, 113: 251-261.
- KAY, E. A. & YOUNG, D. K., 1969, The Doridacea (Opisthobranchia: Mollusca) of the Hawaiian Islands. *Pacific Sci.*, 23(2): 172-231.
- KRUKENBERG, C. F. W., 1881, Nachträge zu meinen vergleichend physiologischen untersuchungen über die Verdauungsvorgänge. *Vergl. Physiol. Studien*, 5: 58-71.
- LACAZE-DUTHIERS, H. de, 1887, Histoire de la *Testacella*. *Arch. Zool. exp. gén.*, 5: 459-596.
- LEMICHE, H., 1956, The anatomy and histology of *Cylichna* (Gastropoda, Tectibranchia). *Skr. Zool. Mus. Copenhagen*, 16: 1-278.
- MAAS, D., 1965, Anatomische und histologische untersuchungen am mundapparat der Pyramidelliden. *Z. Morph. Okol. Tiere*, 54: 566-642.
- MILLOTT, N., 1937, On the morphology of the alimentary canal, process of feeding, and physiology of digestion of the nudibranchiate mollusc *Jorunna tomentosa* (Cuvier). *Phil. Trans. Roy. Soc. Lond.*, (B), 228: 173-217.
- MORTON, J. E., 1958, *Molluscs*. Hutchinson and Co., Lond., 232 p.
- PELSENEER, P., 1925, Gastropodes marins carnivores *Natica* et *Purpura*, *Ann. Soc. zool. Belg.*, 55: 37-39.

- PRASHAD, B., 1925, Anatomy of the common Indian apple-snail, *Pila globosa*. *Mem. Ind. Mus.*, 8: 91-151.
- STERNER, R., 1912, Die Hautdrüsen bei den Cephalaspidea. *Bull. Intern. Acad. Sci. Cracovie. Cl. Sci. Math. nat.*, B: 1001-1042.
- THOMPSON, T. E., 1962, Studies on the ontogeny of *Tritonia hombergi* Cuvier (Gastropoda Opisthobranchia). *Phil. Trans. Roy. Soc. Lond.*, (B) 245: 171-218.
- THOMPSON, T. E., 1964, Grazing and the life cycles of British Nudibranchs. In: Crisp, D. J. (ed.), *Grazing in terrestrial and marine environments*. Blackwell Sci. Publ. Ltd., Lond. p 275-297.
- WEBB, W. M., 1893, On the manner of feeding in *Testacella scutulium*. *Zoologist*, 17: 281-289.
- YOUNG, D. K., 1965, Biological implications of the food habits of some Indo-West-Pacific Doridacea (Nudibranchia, Mollusca). *Amer. Zool. Abstr.*, 5: 638-639.
- YOUNG, D. K., 1967, New records of Nudibranchia (Gastropoda: Opisthobranchia) from the Central and West-Central Pacific with a description of a new species. *Veliger*, 10: 159-173.
- YOUNG, D. K., 1969, *Okudaia elegans*, a tube-boring nudibranch mollusc from the Central and West Pacific. *Amer. Zool.*, 9: 903-907.

## RESUME

LA MORPHOLOGIE FONCTIONNELLE DE L'APPAREIL  
DIGESTIF DE QUELQUES NUDIBRANCHES DORIDIENS DE  
L'INDO-PACIFIQUE OUEST

D. K. Young

Quarante-huit espèces de doridiens de l'Indo-Pacifique Ouest ont été groupées en types nutritionnels généraux, chaque type étant caractérisé par les adaptations morphologiques de l'appareil buccal, en relation avec une nourriture spécialisée. La discussion porte sur la morphologie fonctionnelle de l'appareil buccal de 4 types nutritionnels: (1) racleurs d'éponges, (2) suceurs d'éponges, (3) avaleurs d'opisthobranches, (4) perceurs de polychètes.

L'extension de la radiation adaptative chez les Doridiens est particulièrement évidente, en ce qui concerne la nourriture et le mode de nutrition. D'évidentes adaptations morphologiques à la nutrition ont été montrées par l'étude de la structure de l'appareil buccal. Les représentants de chaque famille de doridiens montrent une structure similaire de l'appareil buccal et des modes de nutrition semblables. Du fait que les éléments de l'appareil buccal des doridiens sont utilisés par les taxonomistes comme caractères prépondérants, il n'est pas étonnant que les doridiens soient groupés dans des sortes de types nutritionnels qui se superposent aux groupes taxonomiques.

Les mangeurs d'éponges, qui comptent 7-8 représentants parmi les doridiens étudiés, sont représentés par les Dorididae et les Hexabranchidae racleurs d'éponges et par les Dendrodorididae suceurs d'éponges. Les avaleurs d'opisthobranches sont représentés par les 5 espèces de Gymnoridinae (famille des Polyceridae) et les perceurs de polychètes par une seule espèce de Vayssiéridae.

## RESUMEN

MORFOLOGIA FUNCIONAL DEL APARATO ALIMENTICIO  
DE ALGUNOS NUDIBRANQUIOS DEL INDO-PACIFICO  
OCCIDENTAL

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Cuarenta y ocho especies de dóridos del Indo-Pacífico occidental se agruparon según los tipos de su alimentación general, cada tipo con adaptaciones morfológicas características del aparato bucal asociado con alimentación especializada. Se discute la morfología funcional de 4 tipos así separados: (1) raspadores de esponjas, (2) succionadores de esponjas, (3) sumidores de opisthobranchios, y (4) perforadores de poliquetos.

Extensa radiación adaptiva se evidencia en los dóridos, especialmente en los varios tipos de alimento y manera de alimentarse. El aparato bucal presenta adaptaciones morfológicas conspicuas. Miembros de cada familia de los Doridacea exhiben estructura similar del aparato bucal y hábitos alimenticios similares. Parte del aparato bucal se han aplicado a la taxonomía como caracteres principales, y así no es extraño que los dóridos se puedan separar en tipos alimenticios paralelos a los taxonómicos.

Los que se alimentan de esponjas—comprendiendo 7/8 de los dóridos estudiados—, están representados por los raspadores Doridiidae y Hexabbranchidae, y por los chupadores Dendrodoridiidae. Los sumidores, o engullidores, de opistobranquios están representados por 5 especies de Gymnodoridiinae (family Polyceridae) y los perforadores de poliquetos por una sola especie de Vayssiereidae.

El aparato bucal de los dóridos ha experimentado evolución adaptiva asociada con hábitos alimenticios especiales. Diferencias en alimentación de los 4 tipos se explican por diferencias (o pérdida) estructurales de dientes radulares y modificaciones de la musculatura que opera en la masa bucal y en la rádula. Se dan las similitudes entre los mecanismos de alimentación en cada tipo, y aquellos encontradas en otros opistobranquios, prosobranquios y gastrópodos pulmonados.

#### АБСТРАКТ

#### ФУНКЦИОНАЛЬНАЯ МОРФОЛОГИЯ АППАРАТА ДЛЯ ЗАХВАТА ПИЩИ У НЕКОТОРЫХ ИНДО-ЗАПАДНО-ТИХООКЕАНСКИХ ГОЛОЖАБЕРНЫХ МОЛЛЮСКОВ ДИРИДИД

Д.К. ЯНГ

Сорок четыре вида Индо-западно-тихоокеанских Доридид были сгруппированы в соответствии с общим характером типа их питания, каждый из которых характеризуется морфологическими адаптациями их ротового аппарата. Рассматриваются 4 типа их питания: 1) скребушие губкоеды, 2) сосущие губкоеды, 3) заглатывающие задне-жаберных моллюсков и 4) сверлящие формы, питающиеся полихетами.

Экстенсивная адаптивная радиация среди Доридид особенно заметна по разнообразию их пищи и различным способам питания. Хорошо заметные морфологические адаптации к пище наблюдаются в строении ротового (буккального) аппарата. Моллюски из каждой группы семейства Доридид имеют сходство в устройстве ротового аппарата и в способе питания. Ввиду того, что части ротового аппарата Доридид служат главными систематическими признаками, не удивительно, что они группируются в довольно дискретные группы по типам питания, параллельным и таксономическим группам. Губкоеды (7-8 форм из изученных Доридид) представлены скоблящими, питающимися губками *Dorididae* и *Hexabbranchidae*, а также сосущими губкоедами из *Dendrodoridae*. Формы заглатывающие *Ophistobranchia* представлены пятью видами из *Gymnodoridinae* (семейство *Polyceridae*) и сверлящими полихетофагами (единичные виды из *Vayssiereidae*).

Буккальный аппарат Дириид претерпел адаптивную эволюцию в связи со специализацией образа их питания. Различия в питании среди 4 указанных типов объясняется различной структурой (или утерей) радулярного зуба и модификацией мускулатуры, принимающей участие в работе буккального комплекса радулы.

Рассматривается сходство между механизмом захвата пищи к каждому типу питания и тем, который наблюдается у других моллюсков-*Opisthobranchia*, *Prosobranchia* и *Pulmonata Gastropoda*.

THE STRUCTURE AND FUNCTION OF THE DIGESTIVE  
SYSTEM OF THE MUD SNAIL  
*NASSARIUS OBSOLETUS* (SAY)<sup>1</sup>

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ABSTRACT

The American Atlantic coast mud snail, *Nassarius obsoletus* (Say) is a member of the typically carnivorous rachioglossan Gastropoda. In nature, however, *N. obsoletus* is a non-selective deposit-feeder subsisting almost entirely on ingested sand and mud. The present study was undertaken to clarify the mechanism of functioning of the digestive system of this animal.

Anatomical and histological studies indicate that *Nassarius obsoletus* has all of the structural modifications associated with assumption of a carnivorous mode of existence. These modifications include: an elongate protrusible proboscis; rachioglossan radular dentition; an elongate, movable siphon and bipectinate osphradium; well-developed valve of Leiblein, gland of Leiblein, and salivary glands; a simplified stomach possessing a very reduced gastric shield; no efficient ciliary sorting areas; and well-developed muscular layers surrounding the alimentary canal. In contrast to these clearly carnivorous characteristics, *N. obsoletus* possesses a mucoprotein crystalline style within its stomach—a feature associated with structural adaptation for handling a herbivorous diet. Histochemical studies indicate that the midgut gland contains enzymes capable of splitting esters and glucuronides and thus for metabolizing some of the principal constituents of algae. Feeding experiments using finely divided particulate material and histochemical localization of phosphatase activity both indicate that phagocytosis and intracellular digestion do not occur. *In vitro* enzyme analyses of tissue homogenates of the various digestive organs reveal the presence of esterase, lipase,  $\alpha$ -amylase, protease, and several disaccharases. Analyses of stomach fluid and crystalline styles similarly reveal the presence of the hydrolytic enzymes extracellularly within the lumen of the stomach. A review of the feeding habits and behavior is presented along with physiological evidence that the crystalline style aids in the digestive process and is therefore truly functional, rather than being merely a remnant of the mucous fecal string.

It is concluded from the data presented that *Nassarius obsoletus*, although structurally possessing all the features of a typical carnivorous rachioglossan nevertheless is able to subsist almost entirely on a diet of algal detritus; that it possesses the hydrolytic enzymes necessary to breakdown the principal constituents of algae; that the initial breakdown occurs extracellularly; that phagocytosis and intracellular digestion do not occur; and that absorption of soluble digestion products occurs most probably in the midgut gland or epithelium lining the stomach-intestine.

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## CONTENTS

I. 1. INTRODUCTION . . . . .	448
II. ANATOMY AND HISTOLOGY . . . . .	448
1. Materials and methods . . . . .	448
2. Organ and tissue structure . . . . .	449
3. Evaluation of data . . . . .	468
III. ENZYME HISTOCHEMISTRY . . . . .	472
1. Materials and methods . . . . .	472
2. Results . . . . .	473
3. Evaluation of data . . . . .	474
IV. <i>IN VITRO</i> ENZYME ANALYSES . . . . .	477
1. Materials and methods . . . . .	477
2. Results . . . . .	479
3. Evaluation of data . . . . .	481
V. ASPECTS OF DIGESTIVE PHYSIOLOGY AND BEHAVIOR . . . . .	484
VI. GENERAL DISCUSSION . . . . .	489
ACKNOWLEDGMENTS . . . . .	494
LITERATURE CITED . . . . .	494

## I. INTRODUCTION

The gastropod genus *Nassarius* (Prosobranchia, Neogastropoda) is world-wide in distribution. A representative of this genus, *Nassarius (Ilyanassa) obsoletus* (Say), is one of the most abundant animals of the intertidal mud flats along the Atlantic Coast of North America.

Although much of the basic biology of *Nassarius obsoletus* has not been studied in detail, the animal has, nevertheless, been the subject of many experimental and descriptive studies. These have been in the areas of: experimental embryology (Crampton, 1896; Morgan, 1933; Dan & Dan, 1942; Clement, 1952, 1956, 1960 and 1962; Clement & Lehmann, 1956a and 1956b; Berg & Kato, 1959; Cather, 1959, 1963 and 1967; Collier, 1960 and 1961; Clement & Tyler, 1967); larval development (Scheltema, 1956, 1961, 1962a, 1962b and 1965; Paulson & Scheltema, 1967); behavior and physiological ecology (Dimon, 1905; Batchelder, 1915; Stephens, *et al.*, 1953; Jenner & Chamberlain, 1955; Jenner, 1956a, 1956b, 1957 and 1958; Baylor, 1958; Brown, *et al.*, 1959 and 1960; Scheltema, 1964; Nagabhushanam & Sarojini, 1965; Carr, 1967a

and 1967b); and parasitology (Martin, 1938 and 1939; Stunkard, 1938a, 1938b and 1961; Rankin, 1940; Stunkard & Hinchliffe, 1952; Sindermann, 1960; Printz, 1962).

The results of several of these studies point to the fact that the feeding habits and digestive system of *Nassarius obsoletus* show features which are quite unusual for a member of the Neogastropoda. Although neogastropods are regarded as primarily carnivorous (Fretter & Graham, 1962; Hyman, 1967) and all other species of *Nassarius* which have been studied are classified as carnivores (Yonge, 1954; Martoja 1964), *Nassarius obsoletus* has been reported (Jenner, 1956b) to possess a crystalline style, a structure considered to be a definitive characteristic of purely herbivorous molluscs (Yonge, 1930). Scheltema (1956 and 1961) has presented evidence strongly suggesting that the feeding habits and perhaps even nutritional requirements of adult *N. obsoletus* are of prime importance in determining the time and place of settling and metamorphosis of their planktonic veliger larvae.

The present study was undertaken to elucidate the mechanism by which the digestive system of this animal functions. The results are presented in four parts: tissue and organ structure; enzyme histochemistry; *in vitro* enzyme analyses; and digestive physiology and behavior. A brief evaluation is presented at the end of each part, dealing with that section. The general discussion at the end attempts a synthesis of the data into a coherent picture of structure and function.

## II. ANATOMY AND HISTOLOGY

## 1. Materials and methods

All descriptions are based on fresh and preserved specimens collected from the vicinities of Woods Hole and Barnstable Harbor, Massachusetts. In some cases,

animals were maintained at the University of Michigan in sea-water aquaria on a diet of frozen shrimp prior to fixation or examination. Dissections were carried out on living animals and also on those previously hardened in ten percent formalin.

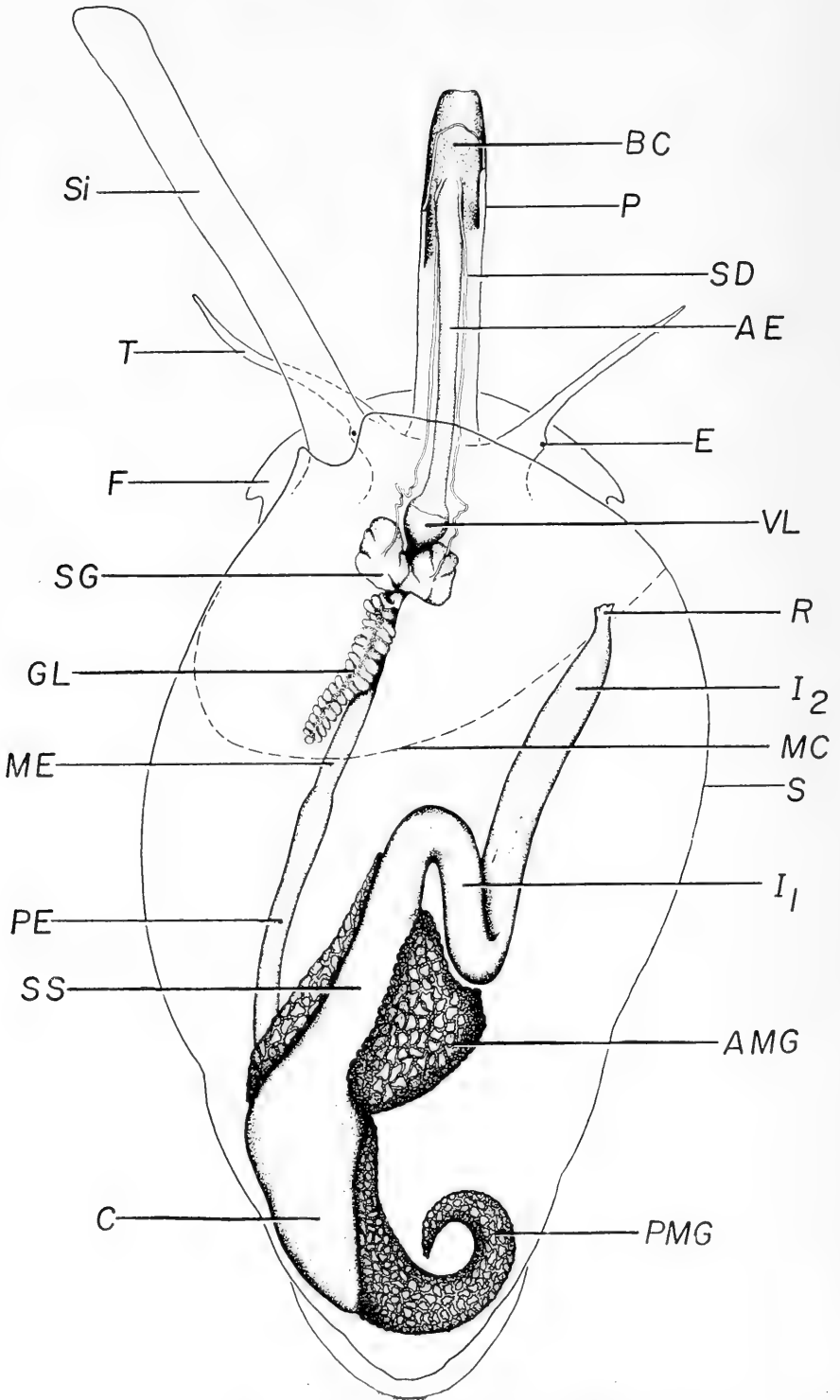
For most general histological work Carnoy's, Bouin's, Zenker's, Helly's and Atkins' fixatives were used, with the first two giving the best nuclear detail while the last three yielded the clearest overall histological results. Materials so fixed were paraffin embedded, sectioned at 4-10 microns, and stained with Heidenhain's iron hematoxylin, Weigert's iron hematoxylin with Orange G, Heidenhain's azan, Mayer's mucicarmine, and Bismarck brown with methyl green. In addition, some salivary gland and midgut gland material was fixed in acrolein or glutaraldehyde and embedded in Epon according to the method of Luft (1961). This Epon-embedded material was then sectioned at one-half to 2 microns on a Porter-Blum ultramicrotome with a glass knife and subsequently stained with Azure B bromide at pH 8.0, Weigert's iron hematoxylin with Alcian blue, or Toluidine blue in 2.5% sodium carbonate.

Special techniques employed for the detection of tissue components and for the characterization of mucins included: the coupled tetrazonium reaction for proteins, using Fast blue B salt as coupler (Burstone, 1955); the DMAB-Nitrite method for tryptophan on formalin-fixed tissues (Adams, 1957); the Periodic acid-Schiff (PAS) technique for vicinal hydroxyl groups using Lillie's "cold Schiff" reagent (Lillie, 1965); the PAS reaction preceded by digestion in 1/1000 malt diastase for one hour; the standard toluidine blue method for metachromatic substances (Pearse, 1960); toluidine blue preceded by digestion for up to 24 hours in bovine testicular hyaluronidase; the Alcian blue method for acid mucopoly-

saccharides carried out at a pH below 2 (Steedman, 1950; Mowry, 1963); the combined Alcian blue-PAS technique according to Mowry (1963); the dialysed iron method for acid mucopolysaccharides (Hale, 1946; Mowry, 1963); and the methylene blue extinction technique according to Dempsey & Singer (1946). In addition, formalin-fixed tissue was stained for calcium with Nuclear fast red according to the method of McGee-Russell (1958) and endogenous iron was detected by the Prussian blue reaction on formalin-fixed, paraffin embedded material.

## 2. Organ and tissue structure

The digestive tract of *Nassarius obsoletus* (Fig. 1) is similar to those of the European species, *N. reticulatus*, and *N. incrassatus*, figured by Fretter & Graham (1962) and Martoja (1964). At the apex of the long pleurembolic proboscis lies the buccal cavity. A pair of salivary ducts open into the dorsal posterior aspect of this cavity just anterior to the level where the esophagus originates. The long esophagus can be divided, following Graham's (1939 and 1941) terminology, into the following regions: the anterior esophagus, extending dorsal to the radular mass from the buccal cavity to the valve of Leiblein; the midesophagus, commencing with the valve of Leiblein, proceeding through the nerve ring—salivary gland complex, and terminating posterior to the gland of Leiblein and its opening; and the postesophagus, continuing posteriorly and ending at its stomach opening which lies at a level between the posterior caecum and the anteriorly-directed style sac. The posterior and anterior midgut glands almost completely envelop the caecum and style sac, respectively. Anteriorly from the style sac, the intestine makes a sharp S-curve at the level of the heart and kidney and then arches forward dorsally within the mantle. A rectal





papilla protrudes from the roof of the mantle cavity on the right side.

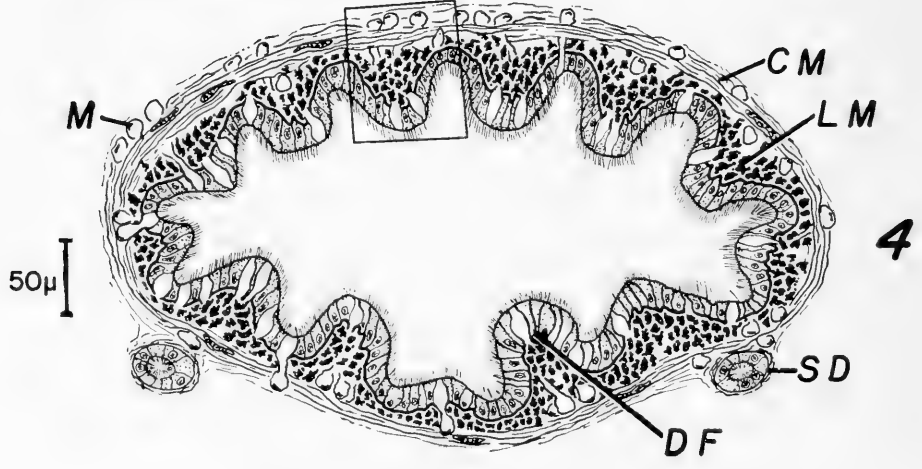
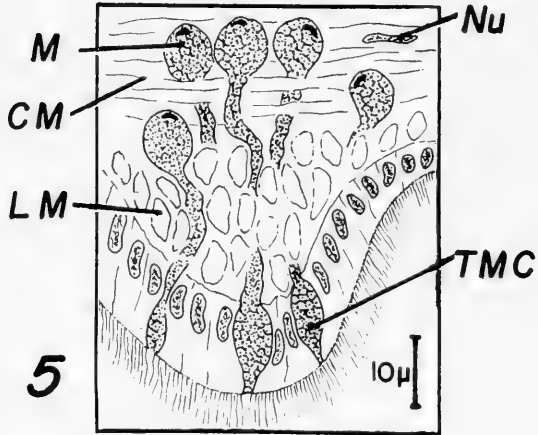
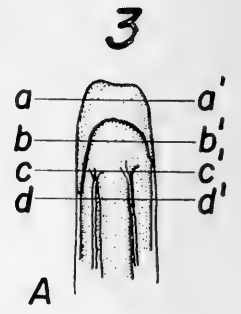
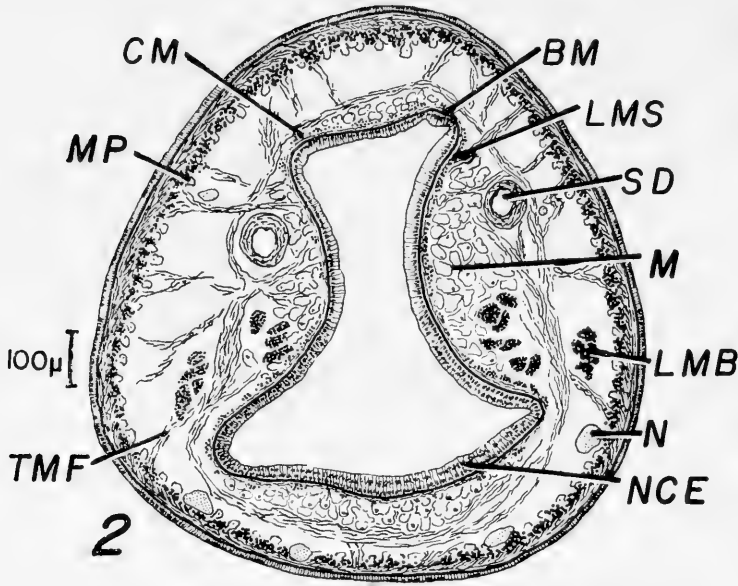
*Buccal region:* The ventrally-directed triangular mouth delimits the anterior border of the buccal cavity. The cavity itself (Figs. 2 and 3) is roughly triangular in cross section. As it extends posteriorly, a horizontal partition divides it into a

dorsal chamber which soon leads into the anterior esophagus and a ventral chamber (Fig. 3, C-E) which encloses the odontophore and radular apparatus (not shown).

The buccal cavity is lined with a smooth layer of simple columnar epithelium (Fig. 2, NCE) the cells of which have basally located oval nuclei. The cells

FIG. 1. The digestive system of *Nassarius obsoletus*, viewed dorsally. The apex of the visceral mass has been uncoiled slightly for illustrative purposes. For interpretation of the lettering on this and following figures, see Key to Abbreviations below:

AE	Anterior esophagus	MG	Midgut glands
AMG	Anterior midgut gland	MGC	Mucous goblet cell
BC	Buccal cavity	MGD	Duct of midgut gland
BM	Basement membrane	MiT	Minor typhlosole
BV	Blood vessel	Mo	Mouth
C	Caecum	MO	Midgut gland openings
CC <sub>1</sub> , CC <sub>2</sub>	Columnar cells, types 1 and 2, of midgut gland	MP	Mucous cells of proboscis outer epithelium
CCC	Ciliated columnar cell	MS	Mucus string adherent to style
CE	Ciliated epithelium	Mu	Mucin in salivary duct
CF	Ciliated folds	N	Nerve
Cil	Cilia	NCE	Non-ciliated columnar epithelium
CM	Circular muscle	Nu	Nucleus
CP	Conical papilla	OPE	Opening from posterior esophagus
CS	Outline of crystalline style	P	Proboscis
CT	Connective tissue	PE	Posterior esophagus
Cut	Cuticle	PG	Pigment Granules
DC	Dorsal chamber	PMG	Posterior midgut gland
DF	Remnants of primitive dorsal fold	PsE	Pseudostratified epithelium
E	Eye	R	Rectum
EMC	Epithelium of mantle cavity	RCC	Ring of ciliated cells
F	Foot	RI	Refractile inclusions
G	Granules in lumen of salivary duct	RP	Reaction product
GC	Epithelial granule cell	S	Shell outline
GC <sub>1</sub> , GC <sub>2</sub>	Granule cells, types 1 and 2, of salivary gland	SD	Salivary duct
GCF	Granule cell fragments	SG	Salivary gland
GL	Gland of Leiblein	Si	Siphon
GS	Gastric shield	Sp	Septum
H	Haemocyte	SR	Stomach region
I <sub>1</sub> , I <sub>2</sub>	Regions 1 and 2 of intestine	SS	Style sac
IG	Intestinal groove	SSA	Saddle-shaped area of stomach
L	Lumen of gland or duct	StH	Style head
LM	Longitudinal muscle	StS	Style shaft
LMB	Longitudinal muscle bundles	T	Tentacle
LMS	Longitudinal muscle sheath	TC	Triangular cell
LS	Lateral sulcus	TMC	Expanded tip of mucous cell
M	Mucous cells	TME	Thickened wall of midesophagus
MaT	Major typhlosole	TMF	Transverse muscle fibers
MC	Mantle cavity outline	Ty	Typhlosole
ME	Midesophagus	VC	Ventral chamber
		VG	Ventral groove
		VL	Valve of Leiblein



are non-ciliated but often contain very fine black pigment granules scattered in the apical 1/3 of the cells. Underlying the epithelial layer is a prominent basement membrane which stains very strongly with Schiff's reagent or with aniline in preparations stained with Heidenhain's Azan. Immediately beneath this basement membrane lies a thin irregular layer of longitudinally directed muscle fibers interspersed with a rather loose connective tissue. Along the walls of the buccal cavity and beneath the muscle layer lie 4 large concentrations of mucous gland cells (Fig. 2, M, and Fig. 29). These large gland cells have dense basally located semilunar nuclei and are of the unicellular type, each communicating with the lumen of the buccal cavity by a conspicuous neck which can be traced through the muscle layer and basement membrane and emerging between the cells of the lining epithelium. The gland cells contain a PAS-positive acid mucopolysaccharide as shown by the PAS reaction, toluidine blue metachromasia, the Hale and Alcian blue techniques, and by a methylene blue extinction point of less than 2.

Underlying these elements is a large haemocoelic cavity traversed by three sets of muscles directed as follows: a thin continuous band of circular muscles (Fig. 2, CM) loosely enveloping the buccal complex; 4 sets of longitudinal muscle bundles (LMB) lying in the ventral half of the proboscis; and an irregular complement of transverse muscle fibers (TMF) inserting in the connective tissue underly-

ing the proboscis epithelium. As stated above, the salivary ducts empty dorso-laterally into the rear of the buccal cavity. In cross sections taken at the posterior levels of the cavity, the terminal portions of the salivary ducts can be seen lateral to the mucous gland cells and just beneath the circular muscle layer (SD). The salivary ducts at this level are composed of a very thin endothelium surrounded by a relatively thick coat of circularly directed smooth muscle.

*Anterior esophagus:* The anterior esophagus, like the rest of the esophagus, is characterized by the presence of conspicuous longitudinally folded walls (Fig. 4). These folds, in the anterior esophagus, are of similar size with the exception of the 2 folds which occupy the mid-ventral position (DF). These two folds are somewhat larger than the rest and the furrow between them is noticeably larger. As Graham has shown (1939), these folds are the remnants of the primitive dorsal folds which have migrated ventrally and have thus expanded the originally dorsal food channel to include virtually the entire area of the esophagus with the exception of the present mid-ventral furrow.

The epithelium lining the anterior esophagus is of the simple columnar type having oval subcentral nuclei (Fig. 5). These epithelial cells, in contrast to those of the buccal cavity, possess long cilia. These ciliated cells are strongly acidophilic at their bases, but exhibit increasing basophilia at their apices. A prominent basement membrane underlies the epithe-

FIG. 2. Cross-section of the proboscis at the posterior end of the buccal cavity. Heidenhain's Azan.

FIG. 3. Relationship of buccal cavity to proboscis, diagrammatic. A. Anterior of proboscis, viewed dorsally, epidermis partially cut away. B.-E. Sections through levels a-a' to d-d', respectively.

FIG. 4. Cross-section of anterior esophagus in the region of the middle of the proboscis. Heidenhain's Azan.

FIG. 5. Detail of wall of anterior esophagus, in cross-section. Weigert's iron haematoxylin-Alcian blue.

lial layer. Immediately below this membrane is located a heavy continuous layer of longitudinally directed muscle bundles (Fig. 4, LM) interlaced at irregular intervals with connective tissue. A continuous circular layer of muscle (CM) surrounds the longitudinal muscle fibers.

A distinctive feature of the anterior esophagus is the presence of mucous gland cells lying beneath the longitudinal muscle layer (Figs. 4 and 5, M). Most of these mucous cells lie outside the circular muscle coat, but a few of the cell bodies may be found between the 2 muscle layers. These submucosal gland cells are similar in structure to those underlying the buccal cavity, having similar dimensions and dense semilunar nuclei disposed towards the base of the cells. The mucin within these cells, a PAS-positive acid mucopolysaccharide, is histochemically identical to that of the buccal cavity gland cells (see Table 1 for a comparison of staining properties). The necks of the mucous cells pass through the muscle layers and basement membrane and often dilate at the level of the epithelium to become two to three times as wide as the adjacent ciliated columnar cells (Fig. 5). There are no goblet mucous cells among the ciliated columnar cells lining the lumen of the anterior esophagus.

The salivary ducts accompany the anterior esophagus along the ventrolateral margins, being loosely attached to the circular muscle layer by strands of connective tissue (Fig. 4, SD). The ducts at this level, in contrast to their appearance in the region of the buccal cavity, are composed of a ciliated cuboidal epithelium a single layer thick surrounded by a very thin coat of connective tissue. The lightly-staining nuclei are round and located in the center of the cells. The cytoplasm is uniformly acidophilic with no trace of basophilia. In some preparations the salivary ducts at the level of the anterior esophagus contain granules

which stain intensely with acid dyes, Heidenhain's hematoxylin, and several histochemical reagents (Fig. 16 G). Granules of the same size with identical staining characteristics have been observed in the salivary glands and will be more completely described below.

*Valve of Leiblein:* The anterior esophagus terminates posteriorly near the base of the proboscis at a pear-shaped organ (Figs. 1, 6, and 7) known as the valve of Leiblein (Fretter & Graham, 1962). This organ consists of a posteriorly directed cone-shaped protuberance (Fig. 6, CP) that is enclosed in a chamber formed by the expanded walls of the anterior portion of the midesophagus (Figs. 6 and 7). The inner surface of the valve of Leiblein shows longitudinal folds similar to those of the anterior esophagus, with the exception that no trace of the primitive dorsal folds or midventral furrow can be found.

Histologically, the inner cone-shaped papilla is lined with a continuation of the ciliated simple columnar epithelium found in the anterior esophagus. There are no muscle layers directly underlying this epithelium. Confluent with this papilla lies a ring of tall ciliated columnar epithelial cells so disposed as to give the appearance of a triangle in longitudinal section (Fig. 7 and 15, RCC). These cells have lightly-staining oval nuclei located centrally. The cytoplasmic staining properties of these cells are distinctive. The usual acid and basic counterstains fail entirely to color the cytoplasm, and the PAS reaction is also negative. In contrast, the cells exhibit strong metachromasia with toluidine blue, are colored by the dialysed iron method for acid mucopolysaccharides, and are heavily colored, metachromatically, with methylene blue, below pH 2. The Alcian blue method for acid mucopolysaccharides is completely ineffective in staining the cells, however.

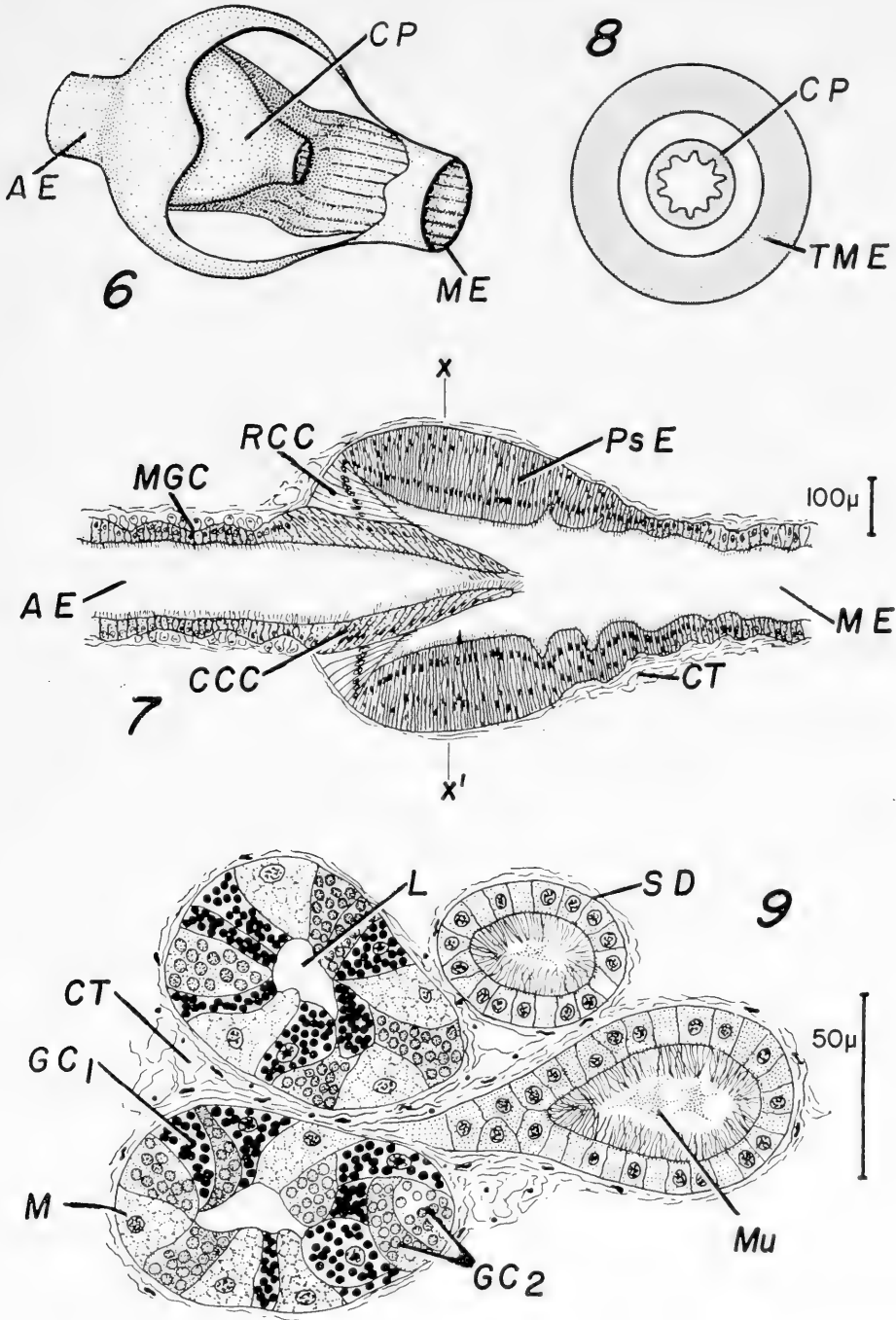
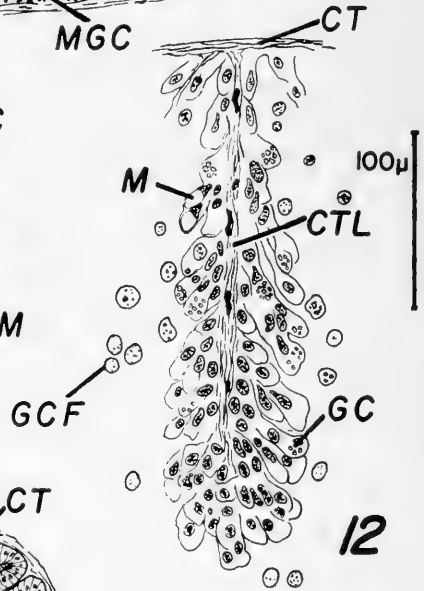
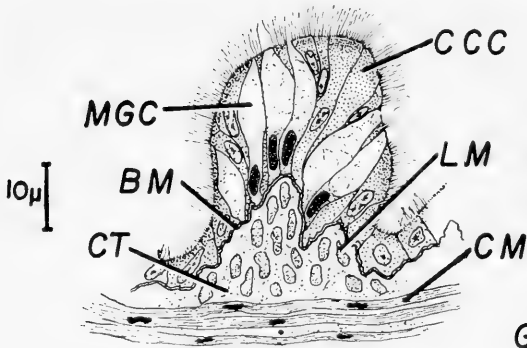
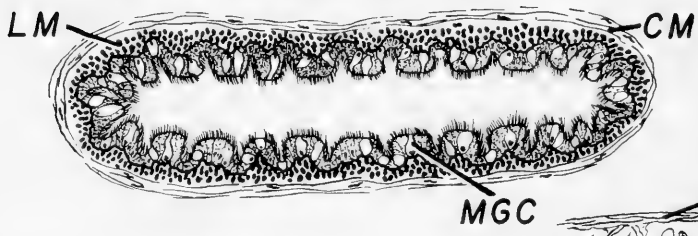
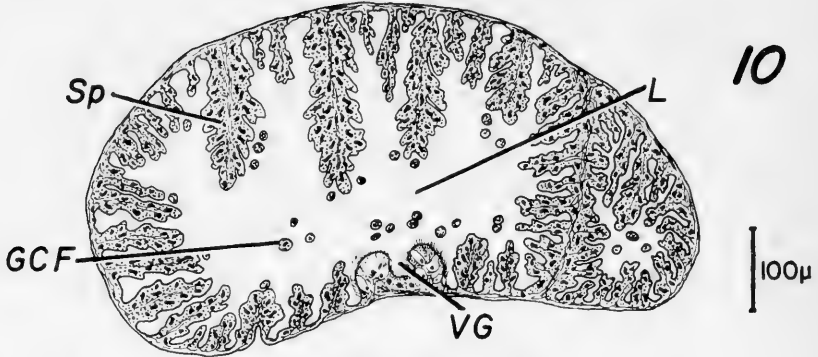


FIG. 6. Stereogram cut-away view of the valve of *Leiblein*.

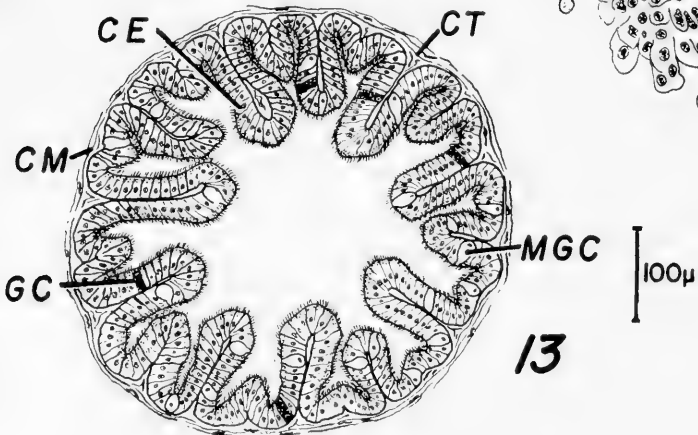
FIG. 7. Sagittal section of valve of *Leiblein*. Heidenhain's Azan.

FIG. 8. Diagrammatic cross-section through valve of *Leiblein* at level x-x' of figure 7.

FIG. 9. Cross-section through portion of the salivary gland tissue showing ducts and secretory ductules. Heidenhain's haematoxylin-Alcian blue.



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The adjacent thickened part of the valve of Leiblein is composed of a pseudostratified columnar epithelium which bears cilia at its luminal border (Fig. 7). The cells making up this part are of 2 morphological types. The first type extends from basement membrane to lumen, bears cilia, and has dense small nuclei which are very uniformly located 1/5 of the distance from the apical tip. The other type extends from the basement membrane to approximately 2/3 the height of the tissue layer but does not reach the lumen. The nuclei of the cells are scattered in the basal 1/3 of the cytoplasm. The cytoplasmic staining properties of these cells are identical, but, like those described above, differ from the typical pattern. These cells orthochromatically bind methylene blue below pH 2, and are strongly stained by Alcian blue and the dialysed iron reagent, indicative of acid mucopolysaccharides. Contrary to the above, however, these cells remain unstained after treatment with toluidine blue. The pseudostratified layer gradually diminishes in height and merges into the simple columnar epithelium lining the midesophagus.

The outer surface of the valve of Leiblein is covered with a thin coat of connective tissue. There are only a few muscle fibers found in the connective tissue sheath and none arranged in an orderly enough fashion to be termed a true muscle layer.

*Midesophagus:* The midesophagus continues posteriorly from the valve of Leiblein and passes through the ring of tissue formed by the ganglionic mass and

salivary glands. About half way along its length, the midesophagus receives along its mid-dorsal surface the duct from the gland of Leiblein and then continues rearward to the level to the columellar muscle where an externally visible expansion in tube diameter marks the beginning of the postesophagus (Fig. 1). The wall of the midesophagus shows an increase in the number of folds over that of the anterior esophagus, but there is no trace of either dorsal folds or a specialised channel leading into the gland of Leiblein (Fig. 10).

The epithelium lining the midesophagus is of a simple columnar type consisting of three distinct cell types. The most prevalent are ciliated columnar cells with subcentral, oval nuclei (Fig. 11, CCC). These cells are similar to those found in the anterior esophagus and, like them, show an acidophilic character at their bases yielding to basophilia at their apices. These cells make up about 85% of the cell population. The next most numerous type are mucous cells. These cells have the typical goblet shape, being narrow basally and expanding distally (MGC). The nuclei of these cells are dense and elongate and are located basally. The cytoplasm immediately surrounding the nuclei is acidophilic while the mucin at the expanded tip of the cells is a PAS-positive acid mucopolysaccharide (for histochemical characterization, see Table 1). The cells present in the fewest numbers (ca. 1%) are similar in size and shape to the simple columnar cells but differ from them in possessing no cilia and in containing scattered

FIG. 10. Cross-section through the gland of Leiblein (above) and midesophagus (below). Heidenhain's Azan.

FIG. 11. Detail of wall of midesophagus, in cross-section. Heidenhain's Azan.

FIG. 12. Detail of septum of gland of Leiblein, in cross-section. Heidenhain's haematexylin.

FIG. 13. Cross-section of post-esophagus. Heidenhain's Azan.

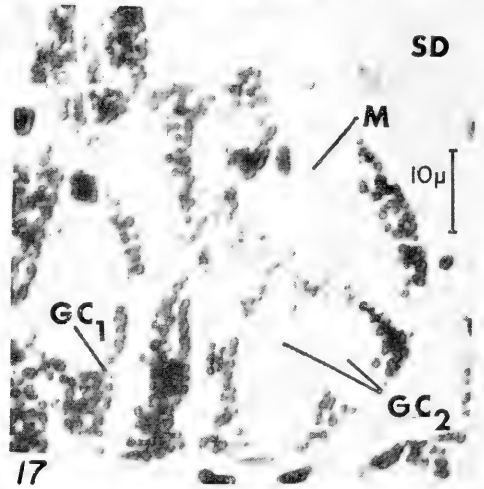
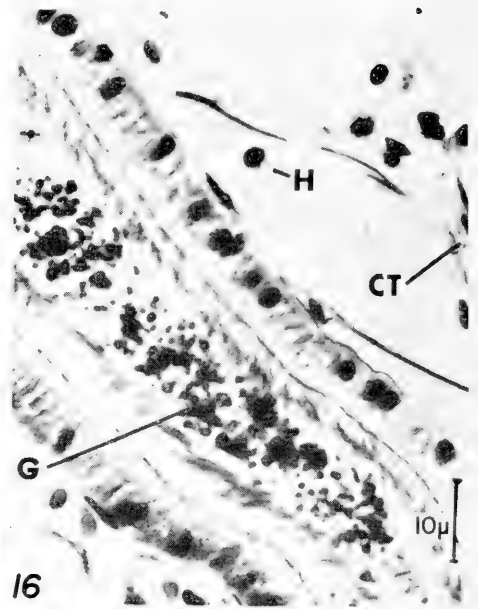
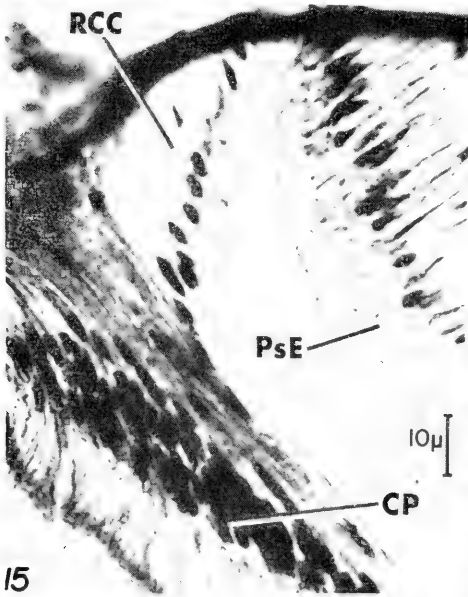
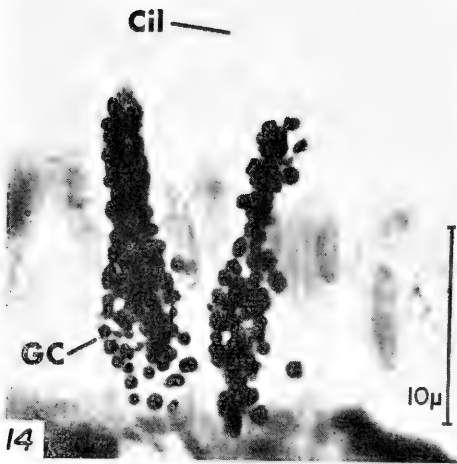


FIG. 14. Epithelium lining the midesophagus, showing cells containing mucoprotein granules. Heidenhain's haematoxylin.

FIG. 15. Sagittal section through the valve of Leiblein in the area of the ring of ciliated cells. Weigert's iron haematoxylin-Orange G.

FIG. 16. Salivary duct at the level of the valve of Leiblein. Heidenhain's haematoxylin.

FIG. 17. Secretory ductule of the salivary gland. Heidenhain's haematoxylin.

throughout their cytoplasm small granules (Fig. 14, GC) which stain intensely with acid dyes and Heidenhain's hematoxylin. The glycoprotein nature of these granules

is shown, histochemically, by the facts that they are PAS-positive, are strongly stained by the coupled tetrazonium reaction for proteins, and that they have a



methylene blue extinction point in excess of 6.

The heavy inner layer of longitudinal muscle fibers surrounded by an outer circular muscle coat (Figs. 10 and 11) is identical with that of the anterior esophagus. There are, however, no submucosal gland cells present in the midesophagus.

*Salivary glands:* The pair of salivary glands which superficially appear to be a single entity form a horse-shoe-shaped structure partially surrounding the dorsal and lateral aspects of the midesophagus, posterior to the valve of Leiblein and in contact with the anterior surface of the ganglionic ring (Fig. 1, SG). After careful removal of the connective tissue surrounding the glands, however, one can observe that the white lobular tissue is divided into two discrete organs, each with its own duct leading from the approximate center of its anterior surface, past the valve of Leiblein, and into the proboscis lateral to the anterior esophagus.

The glands themselves are of the acinar type with small ductules ramifying through the mass of tissue. Lining the ductules is a layer of nonciliated columnar epithelium usually only a single cell in depth and composed of 3 morphologically distinct types of cells present in approximately equal numbers (Fig. 9). The first type of cell (Fig. 9, M) generally has a triangular shape with the base being equal to the height of the cell. These cells have round, lightly-staining nuclei located subcentrally and are filled with a mucin as indicated by the avidity with which they take up mucicarmine and Bismark brown. Histochemical procedures further indicate that this mucin is a PAS-negative acid mucopolysaccharide (see Table 1). The 2nd type of cell (Figs. 9 and 17 GC<sub>1</sub>) is usually of a more typically columnar shape, although the apical end is often expanded. These cells have a round central nucleus with a single prominent nucleolus and are filled with

large granules which stain very intensely with azocarmine B and Heidenhain's hematoxylin. These granules are also very intensely stained by the coupled tetrazonium procedure for proteins, the DMAB-nitrite reaction for tryptophan, and the PAS technique, all indicative of a glycoprotein composition. These granules are identical in size and staining characteristics with the granules found in the salivary ducts. The cytoplasmic ground substance of these cells fails to take up either acid or basic dyes. The third type of cell (Figs. 9 and 17, GC<sub>2</sub>) is structurally similar to the preceding but differs markedly in its staining properties. This cell type shows more variation in the intensity with which the structures are stained than the previous type, but, in general, the granules show less to much less affinity towards hematoxylin and azocarmine while the ground cytoplasm exhibits strong to weak affinities for these dyes. The same variation in intensity is to be seen with the histochemical stains, the spherules being especially conspicuous in never being colored as intensely as those of type 2 cells. Within this variation, a consistent pattern can be observed with regard to the relative staining intensity of ground substance and granules. In the majority of cases the 2 show an equal affinity for the dyes, while the remaining cells of this type can be arranged in a scale of decreasingly stained cytoplasm with a corresponding increase in the intensity with which the granules are colored (Fig. 9, GC<sub>2</sub>). Very probably the variation observed in these cell types is correlated with a differentiation of the granules culminating in the definitive cell type described as type 2.

Ciliated salivary ducts with a structure identical to that described above are found throughout the salivary glands. These ducts often contain the intensely staining granules and/or an amorphous material with acid mucopolysaccharide

staining characteristics (Mu). The glandular tissue of the salivary glands is held together by a thin matrix of connective tissue. There are very few smooth muscle fibers present.

*Gland of Leiblein:* The gland of Leiblein is a single, elongate organ which lies immediately behind the salivary gland /ganglion complex on the dorsal surface of the midesophagus (Fig. 1, GL). This tan to brown organ is connected at its anterior end by a short duct to the mid-dorsal surface of the midesophagus. The gland tapers gradually at its free posterior end and slight lateral indentations are observable along its length. Internally the gland is of the monopodial branching type and septa just inward laterally at placible corresponding to the externally visible indentations. The spacious lumen (Fig. 10) is partially divided by these septa while a conspicuous midventral groove (Fig. 10, VG) bounded by a pair of folds runs down the axis of the gland and into the duct, eventually merging with one of the grooves of the dorsal wall of the midesophagus.

Histologically the septa are made of thin connective tissue lamellae covered with a pseudostratified columnar epithelium so arranged that in cross section they have a feather-like appearance (Fig. 10, Sp). Two types of cells can be seen lining the septal walls: granular and mucous. The granular cells are of the columnar type with basal oval nuclei (Fig. 12, GC). The cytoplasm of these cells is acidophilic at the base but has little affinity for acid dyes at the cell apex. The colorless tips of the cells are usually expanded where they reach the lumen and are filled with granules and vacuolus of various sizes and shapes. Next to the septa and indeed throughout the lumen of the gland can be found what are presumably nipped-off tips of these cells (Figs. 10 and 12, GCF) containing granules resulting from an apocrine type

of secretion of the granular septal cells. Histochemical procedures indicate that the granular contents of both the free cell fragments and the tips of the septal cells are principally mucoprotein (see Table 1). The mucous cells (Fig. 12, M) are of the typical goblet type, containing a PAS-positive acid mucopolysaccharide, and are scattered sparsely throughout the septal walls.

The ventral folds are composed of a ciliated simple columnar epithelium which is reduced to a ciliated cuboidal epithelium in the furrow of the ventral groove (Fig. 10, VG). Interspersed with the columnar cells are typical mucous goblet cells containing a PAS-positive acid mucopolysaccharide. Covering the entire gland of Leiblein is a thin sheet of connective tissue which is confluent with the lamellar cores of the septa. Little if any muscle is present.

*Postesophagus:* The beginning of the postesophagus is marked by an expansion in the diameter of the tube. Accompanying this, internally, the folds have made a marked increase in depth, although the number of folds remains approximately the same (Fig. 13).

Histologically the epithelium lining the lumen is identical to that of the midesophagus. Here, again, ciliated columnar cells predominate. Also present in small numbers are goblet cells containing PAS-positive acid mucopolysaccharide and non-ciliated columnar cells containing glycoprotein granules. A conspicuous difference is found, however, in the sub-epithelial structure. In contrast to the heavy inner longitudinal and outer circular muscle layers found encasing the midesophagus, only an extremely thin layer of circular muscle fibers is found surrounding the postesophagus (Fig. 13, CM). In addition, only a small amount of connective tissue is to be found beneath the basement membrane underlying the epithelium and the muscle layer.

*Stomach:* Viewed from the dorsal aspect, the stomach has the shape of an elongate tubular sac which assumes the form of a semicircle as it spirals apically with the rest of the visceral mass (Fig. 1). The stomach is widest in girth at its middle, where the postesophagus enters ventrally, and then gradually tapers to a bluntly rounded tip at the apical end. The midgut glands closely envelop the stomach except at the left dorso-lateral surface (Fig. 1, AMG and PMG). The expanded midpart of the stomach approximately corresponds with its internal division into caecum (posterior) and style sac (anterior). The caecum (Figs. 1, and 18, C) is a cone-shaped bag at the anterior edge of which the postesophagus empties midventrally. The walls of the caecum are thrown into numerous low folds running longitudinally. Towards the left side, just anterior to the opening of the esophagus, lies an area of ciliated folds converging on a smooth saddle-shaped prominence (Fig. 18, SSA). To the right of the esophageal opening lies a low, longitudinally directed ridge, at either end of which are located the openings to the midgut glands (MO). Immediately to the right of the low ridge lies a large area of smooth epithelium along whose most median edge there often lies a delicate sheet of transparent cuticle, the gastric shield (GS). This last-named structure, when present, can easily be lifted in its entirety from the underlying epithelium and viewed separately. The gastric shield of *N. obsoletus* is unusual in that it is not found in all specimens. Those animals recently collected from the field almost always have the shield present, but they are absent from the majority of animals maintained for any extensive length of time in the laboratory on a diet of frozen shrimp.

Just anterior to the above-mentioned areas lies a deep transverse sulcus (LS) which is in open communication with the

midventral longitudinally directed intestinal groove (IG). Bounding this groove on either side lie 2 large ciliated ridges, the major and minor typhlosoles (MaT and MiT). The minor typhlosole forms the left border of the intestinal groove and terminates anteriorly at the end of the style sac where the first region of the intestine makes an abrupt curve to the right. Along the right side of the intestinal groove runs the major typhlosole. It is somewhat wider than the minor typhlosole and instead of terminating at the end of the style sac it continues into the intestine, accompanying it through the sigmoid curve before gently blending into the intestinal wall.

In most animals recently collected from the field, the style sac will be filled by a gelatinous rod whose core may be filled to a varying degree with sand particles and algal detritus. This rod is the crystalline style (CS). The style of *Nassarius* (Fig. 24), when present, usually extends the entire length of the style sac. Anteriorly it tapers to a fine point, while the other end, which extends rearward as far as the gastric shield, is blunt or mushroom-shaped and often has debris or aropy mucous string adherent to it. Like the gastric shield, the crystalline style is almost always present in those animals examined in the field, but it is absent from the majority of animals maintained for any extensive length of time in the laboratory on a diet of frozen shrimp. Laboratory animals which are not fed shrimp but have access to algal scum almost always possess both shield and style.

Histologically, the lining of the caecum contains mucous goblet cells (Fig. 21, MGC) and granule-filled nonciliated columnar cells (NCE) structurally and histochemically identical with their counterparts in the mid- and postesophagus (see also Table 1). The predominant cell type is of the simple columnar variety,

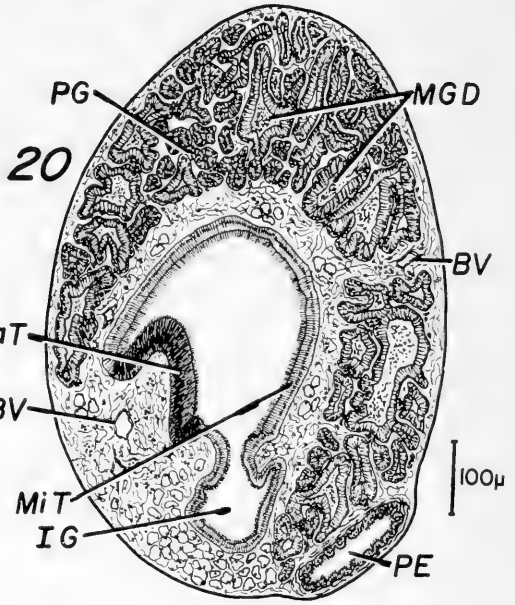
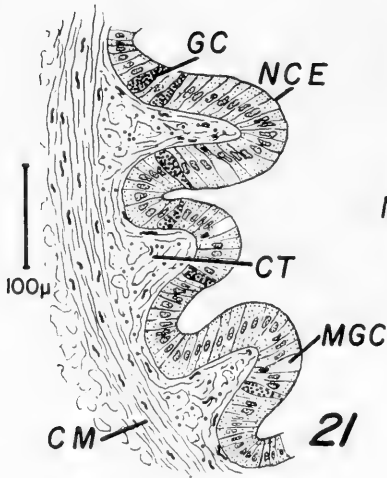
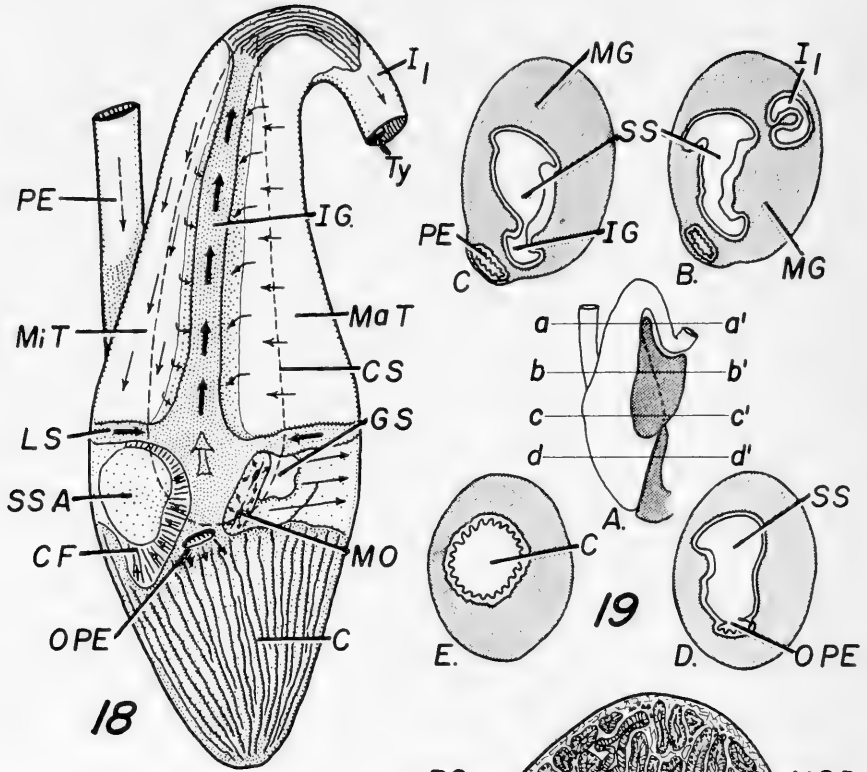


FIG. 18. Interior view of stomach (caecum and style sac), opened by a dorsal longitudinal incision and laid back slightly. Arrows indicate ciliary currents discussed in text.

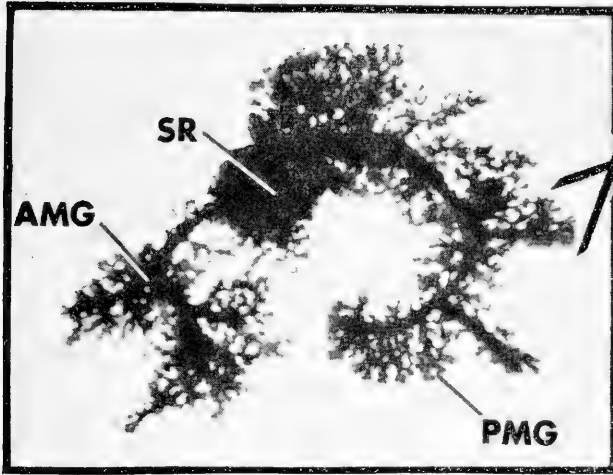
FIG. 19. Relationship of stomach to visceral mass, diagrammatic. A. Stomach and midgut glands, viewed dorsally. B.-E. Sections through levels a-a' to d-d', respectively.

FIG. 20. Cross-section through visceral mass at the mid-region of the style sac. Heidenhain's Azan.

FIG. 21. Detail of wall of caecum, in cross-section. Heidenhain's haematoxylin.

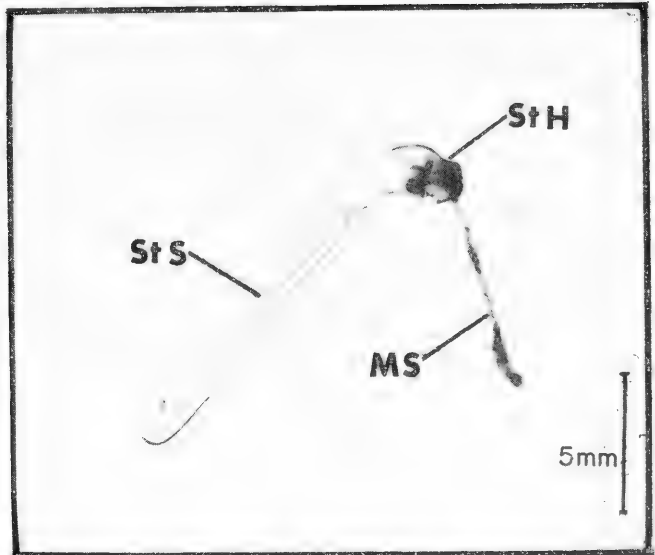
FIG. 22. Vinyl acetate injection showing a side view of the branching ductwork of the midgut glands. Most of the stomach region has been cut away for clarity.

FIG. 23. Vinyl acetate injection showing in more detail a top view of the secondary duct system indicated in Fig. 22.



23

22



24

FIG. 24. A crystalline style removed from the style sac of *Nassarius obsoletus*.

TABLE 1. Histochemical affinities of various components of the digestive system.

	Coupled Tetra- zanium	DMAB- Nitrite	PAS	Dias- tase	Tolui- dine Blue $\gamma$ -meta- chro- masia	Hyalu- roni- dase	Methy- lene Blue Extinc- tion point	Alcian Blue	Dia- lysed Iron
<i>Buccal cavity</i>									
subepith. mucous cells	-	-	-	fast	+	fast	<2	+	+
<i>Ant. esophagus</i>									
subepith. mucous cells	-	-	-	fast	+	fast	<2	+	+
<i>Midesophagus</i>									
epithelial mucous cells	-	-	-	fast	+	fast	<2	+	+
granular cells	-	-	-	fast	+		>6	-	-
<i>Postesophagus</i>									
epithelial mucous cells	-	-	-	fast	+	fast	<2	+	+
granular cells	-	-	-	fast	-		>6	-	-
<i>Salivary glands</i>									
Type 1 granular cells	-	-	-	fast	-		>6	-	-
Type 2 granular cells	-	+	+	fast	-		>6	-	-
Mucous cells	-	-	-		+	fast	<2	+	-
<i>Valve of Leiblein</i>									
"Ring" cells	-	-	-		+	fast	<2	-	+
Pseudostratified layer	-	-	-		-		<2	+	+
<i>Gland of Leiblein</i>									
Granular septal cells	-	-	+	fast	-		>6	-	-
Free granular cell fragments	-	-	+	fast	-		>6	-	-
Septal mucous cells	-	-	-	fast	-	fast	<2	+	+
Mucous cells of ventr. groove	-	-	-	fast	+	fast	<2	+	+
<i>Midgut gland</i>									
Triangular cells	-	-	-		-			-	-
Mucous cells	-	-	+	fast	+	fast	<2	+	+
<i>Caecum</i>									
Epithelial mucous cells	-	-	+	fast	+	fast	<2	+	-
Granular cells	-	-	+	fast	-		>6	-	-
<i>Style sac</i>									
Major typhlosole	-	-	+	fast	-		2-3.5	-	-
Minor typhlosole	-	-	-		-			-	-
Epithelial mucous cells	-	-	+	fast	+	fast	<2	+	+

TABLE 1.—(contd.)

	Goupled Tetra- zonium	DAMB- Nitrite	PAS	Dias- tase	Tolui- dine Blue $\gamma$ -meta- chromasia	Hyalu- roni- dase	Methy- lene Blue Extinc- tion point	Alcian Blue	Dia- lysed Iron
Crystalline style	+	+	+	fast	+	fast	2-3.5	-	+
Gastric shield	+	-	+	fast	-		2-3.5	-	-
<i>Intestine (1)</i>									
Epithelial mucous cells	-	-	-		+	fast	<2		+
<i>Intestine (2)</i>									
Epithelial mucous cells	-	-	-		+	fast	<2	+	+
<i>Rectum</i>									
Epithelial mucous cells	-	-	-		+	fast	<2	+	+

lacking the conspicuous granules. This type of cell in the caecum differs from those in the esophagus, however, in being devoid of cilia. The subepithelial tissue structure more closely resembles that of the postesophagus than that of the mid-esophagus. Underlying the basement membrane immediately below the epithelium is an area composed of connective tissue with a small amount of irregularly oriented muscle fibers (CT). In this area also are to be found numerous hemocytes. These blood cells have never been observed in the lumen of the caecum or between the cells of the lining epithelium. Beneath the layer of connective tissue a very heavy layer of circular muscle fibers (CM) envelops the entire caecum. No longitudinal muscle layer is present.

The lining of the style sac region of the stomach stands in sharp contrast to that of the caecum. The minor typhlosole (Fig. 20, MiT) and roof of the stomach are composed of a layer of ciliated simple columnar epithelium. The oval nuclei are uniformly located 1/3 of the distance from the base of the cells, and the cyto-

plasm exhibits a moderate uniform acidophilia. The epithelium of the intestinal groove (IG) consists mainly of a similar ciliated columnar epithelium which on the floor of the groove shortens to an almost cuboidal shape. In addition, goblet cells containing a PAS-positive acid mucopolysaccharide are scattered throughout the sides and floor of the groove. The epithelium of the major typhlosole (MaT) is conspicuous, being entirely made up of much taller, exceedingly thin ciliated cells. These cells also differ in having elongate very dense nuclei and, perhaps most noteworthy, a cytoplasm exhibiting pronounced basophilia. Histochemical tests indicate that the cytoplasm of these cells contains copious amounts of glycoprotein. This glycoprotein is more or less evenly distributed throughout the cells and is not confined to discrete granules.

Underlying the lining epithelium of the style sac is a thick layer of loose connective tissue containing numerous hemocytes, a few irregularly arranged muscle fibers, and blood vessels (Fig. 20). Also lying in this loose connective tissue be-

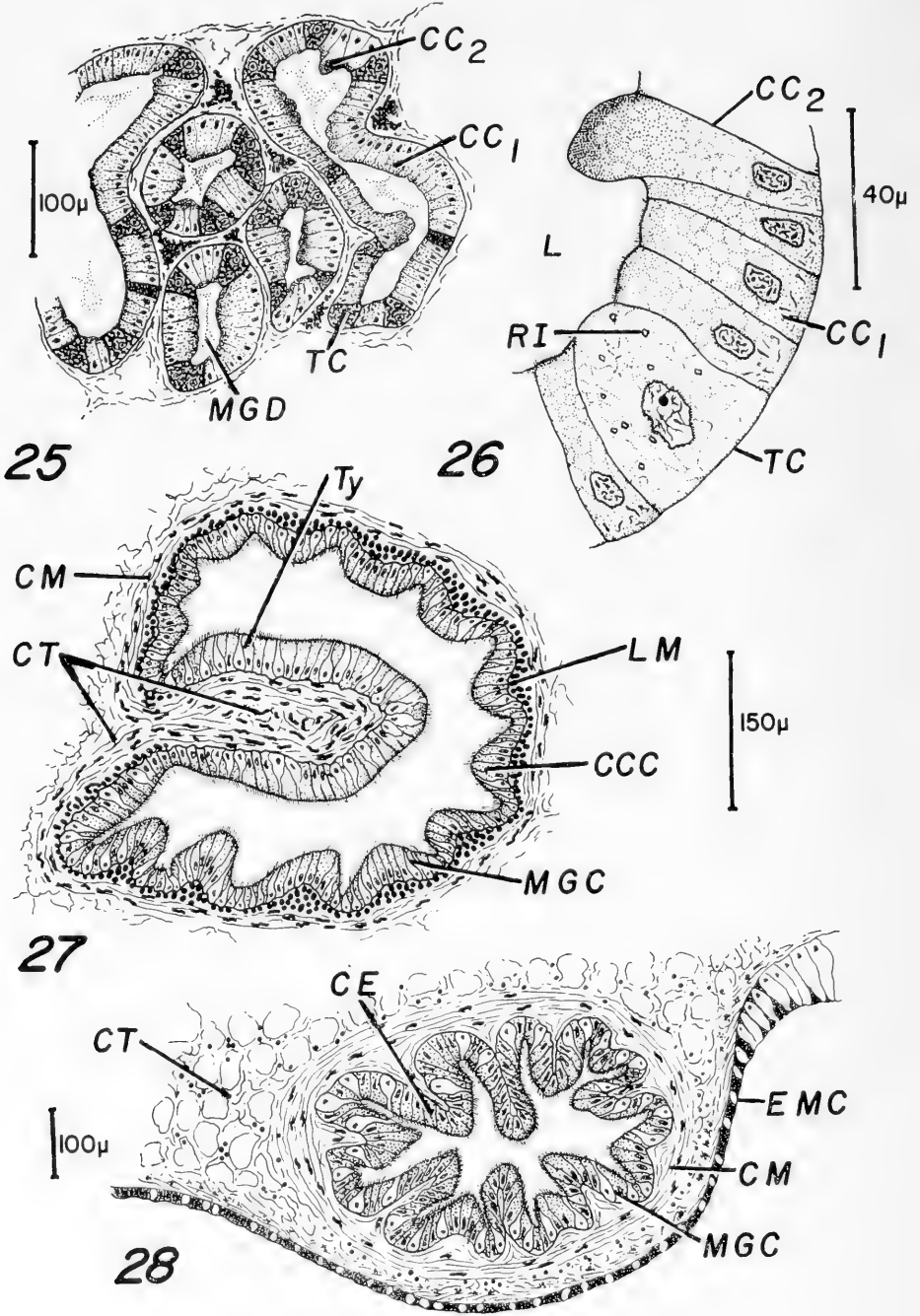


FIG. 25. Section through portion of midgut gland tissue. Heidenhain's Azan.

FIG. 26. Detail of midgut gland tubule. Epon, Azure B bromide.

FIG. 27. Cross-section through proximal region of intestine. Heidenhain's Azan.

FIG. 28. Cross-section through the distal region of the intestine. Heidenhain's Azan.



tween style sac and midgut gland are two aggregations of large cells with basal nuclei which contain large amounts of calcium within them. Indeed, these are the only sites in the visceral mass of the snail which contain calcium in sufficient amounts to be avidly stained by Nuclear fast red.

*Midgut glands:* The 2 midgut glands constitute the greatest bulk of the visceral mass (Fig. 1, AMG, PMG). The anterior gland forms a cradle ventral and lateral to the style sac, starting approximately at the level of the anterior duct into the stomach and proceeding anteriorly to the region of the sigmoid curve of the intestine. The posterior gland begins at its duct into the stomach anteriorly, accompanies the caecum on its right ventrolateral border, and continues spiraling toward the apex of the shell along with the gonad. The midgut glands have an acinar structure and are permeated by a tree-like network of ducts (Figs. 22 and 23).

In cross sections of the visceral mass, the tubules of the midgut glands are cut in both cross and longitudinal sections. There are 4 types of cells distinguishable in the midgut gland tubules. First, there are mucous cells, containing a PAS-positive acid mucopolysaccharide, present in very small numbers (less than 1%) scattered at random within the tubules. A 2nd type of cell is present at the angles of the tubules. These cells are usually of a triangular shape with a large subcentral nucleus containing a prominent nucleolus (Figs. 25 and 26, TC). The cytoplasm is highly vacuolated and slightly, but uniformly, acidophilic. This cell type, in addition, becomes stained throughout the cytoplasm by the DMAB-nitrite technique for tryptophan. Scattered within the apical 3/4 of the cytoplasm are small yellow refractile inclusions (RI) which do not take up the usual cytoplasmic dyes. The apical cytoplasm normally bulges

slightly into the lumen of the tubule.

The cell type most prevalent (approximately 85%) is a simple columnar cell with an oval nucleus located uniformly 1/3 of the distance from the base of the cells (Figs. 25 and 26, CC<sub>1</sub>). This cell type has a frothy appearance subapically, the cytoplasm being acidophilic throughout most of the cell but becoming lightly basophilic at the luminal edge. The prussian blue staining technique indicates the presence of iron scattered throughout the cytoplasm. The apex of the cell is covered with short microvilli which were clearly visible only in Epon sections. The fourth cell class is very similar to the preceding, except that the apex of the cell dilates into the lumen of the tubule and is devoid of microvilli (CC<sub>2</sub>). Nearly the entire apical expansion is strongly basophilic. The latter 2 cell types in all probability represent activity stages of a single class of cells. Nothing resembling food vacuoles could be found in these cells, either in animals which had just been taken from the field or in animals which had been maintained on any of the experimental diets.

Between the ramifying tubules of the midgut gland loose connective tissue, blood vessels, numerous hemocytes, and aggregations of dark brown to black pigment granules are present (Figs. 20 and 25).

*Intestine:* Proceeding anteriorly from the style sac, the intestine goes but a short way before taking a sharp right-hand bend which signals the beginning of the transverse sigmoid curve (Fig. 1). This curving portion of the intestine crosses the visceral mass just posterior to the kidney and forms the forward boundary of the anterior midgut gland. After completing the sigmoid curve, the intestine arches dorsally within the right side of the mantle tissue.

The intestine can be divided, histologically, into two distinct parts which

roughly correspond to the sigmoid portion and to the dorsally arching segment. The first part of the intestine (Fig. 27) has its walls thrown into longitudinal folds similar to the esophagus. Unlike the esophagus, however, the first part of the intestine possesses a large shelf-like typhlosole along its right wall (Fig. 27, Ty). This typhlosole is a continuation of the major typhlosole found in the style sac but is histologically very distinct from the latter. The epithelium lining the lumen of the intestine is of a simple columnar type consisting of 2 classes of cells: ciliated columnar cells (CCC) and mucous goblet cells (MGC). The ciliated cells are identical to their counterparts in the esophagus. The mucous cells contain a PAS-negative acid mucopolysaccharide with a methylene blue extinction point far below any other mucin observed. The mucous goblet cells show a great increase in number over those found in the esophageal regions, comprising approximately 35% of the cells lining the lumen of the intestine. The mucous cells of the intestinal region also show a distribution different from that found in the esophagus. In the esophagus and along the typhlosole of the first part of the intestine the mucous cells are distributed essentially at random. Along the folded walls of the intestine, in contrast, the mucous goblet cells are conspicuously confined to the regions of the furrows and are not to be found along the projecting folds. Underlying the basement membrane beneath the epithelium, a heavy layer of longitudinal muscle fibers surrounds the first part of the intestine (Fig. 27, LM). These longitudinal muscles are confined to the areas of folded epithelium and are not present in the typhlosole. Outside this layer of longitudinal fibers is a layer of circular muscle fibers which encases the entire intestinal tube and penetrates the typhlosolar fold, ultimately coming to lie directly beneath the basement mem-

brane in this region (CM).

The longitudinal folds are continued in the second portion of the intestine; the typhlosole, however, is not present. The types and distribution of cells lining the lumen are identical with the preceding part of the intestine. The subepithelial structure of this part of the intestine differs markedly from the first part in that there is no longitudinal muscle layer underneath the lining epithelium, although a strongly developed circular muscle layer is present (Fig. 28, CM).

*Rectum:* The intestine terminates in a short papilla which projects freely into the pallial cavity from the right side of the mantle roof. Histologically the rectum is identical with the latter portion of the intestine.

### 3. Evaluation of Data

Among the described species of *Nassarius*, the general anatomical and histological features of the digestive systems are similar (see Fretter & Graham, 1962, for *N. reticulatus*; Martoja, 1964, for *N. reticulatus*, *N. corniculum*, and *N. incrasatus*; Dimon, 1905; and this study for *N. obsoletus*). The following discussion summarizes some of the salient anatomical and histological characteristics of the digestive system of *Nassarius obsoletus* in particular, and of the Nassariidae in general.

One of the striking, easily observable, features of *N. obsoletus* is the extreme length of the extended proboscis (Figs. 1 and 36). This highly-developed proboscis is characteristic of all the rachiglossan Neogastropoda (Pelseneer, 1906) and is correlated with their usually carnivorous habit (Blegvad, quoted in Yonge, 1954; Fretter & Graham, 1962; and Martoja, 1964). Although not previously considered in the present study, the radular dentition of *N. obsoletus* (figured by Dimon, 1905, p 50) shows the typical rachiglossan pattern of 1+R+1 which

is well-adapted for the tearing and rasping of soft material such as flesh.

The solid cuticular thickenings (=“jaws” or “mandibles”) found at the anterior end of the buccal cavity of toxoglossan and some rachiglossan neogastropods (Pelseneer, 1906; Hyman, 1967) are absent in *N. obsoletus* and apparently the other species of *Nassarius* studied. The buccal cavity of *N. obsoletus* also differs from the condition found in most other gastropods (Fretter & Graham, 1962) in possessing as the only mucous cells of the lining of this cavity, large flask-shaped gland cells located *beneath* the longitudinal muscle layer, rather than having the more typical goblet-type cells confined entirely to the epithelial layer.

These subepithelial mucous cells continue the length of the anterior esophagus and, as in the buccal cavity, they are the only type of secretory cell found in the lining tissue. The rest of the esophageal tube is characterized by the presence of goblet-type mucous cells in the lining epithelium. The anterior esophagus further differs from the rest of the esophagus by the absence of cells containing glycoprotein granules. In addition, as mentioned above, the only remnants of the primitive dorsal folds and food channel (Graham, 1939) to be found in *N. obsoletus* are in the anterior esophagus. A further notable feature of the anterior esophagus (and indeed of the esophagus in general) is that though it bears cilia along the entire lining surface, it possesses a very well-developed subepithelial muscle coat. This fact is in accord with observations made in the present study (see part 4) and earlier by Jenner (1956b) that peristalsis plays an important part in moving food along the alimentary canal.

Correlated with the extensive development of the rachiglossan proboscis is the presence of the valve of Leiblein.

As Graham has emphasized (1941), it performs the extremely important function of preventing food from returning to the anterior esophagus in animals which continuously elongate and contract the anterior end of their alimentary canal during feeding. Fretter & Graham (1962, p 217) state that among the rachiglossan gastropods, “. . . in the Buccinacea the valve of Leiblein is reduced or even absent (*Galeodes*, *Semifusus*, *Busycon*)”. The Nassariidae, apparently, form a consistent exception to this, for in *N. obsoletus* and all the other species of *Nassarius* illustrated, a well-developed valve of Leiblein is present (Fretter & Graham, 1962; Martoja, 1964).

The salivary glands and ducts also show the effects of the elaboration of the proboscis. In the Nassariidae, as in the rest of the Stenoglossa, the differential growth of the anterior part of the gut has “pulled” the salivary glands and ducts “through” the nerve ring, the salivary glands thereby assuming a position in front of the cerebral commissure and the salivary ducts thus becoming free of any restraint imposed by the nerve ring (Fretter & Graham, 1962). The cell composition of the salivary gland tubules appears identical in the three species of *Nassarius* which have been studied in this respect (Fretter & Graham, 1962; Martoja, 1964). The mucous secretion presumably aids in lubrication of the radular apparatus during feeding; the function of the glycoprotein granules is not clear. Basic protein secretory products are of widespread occurrence in the saliva of snails (Fretter & Graham, 1962), and in several species the presence of enzymatic activity associated with the salivary glands has been shown (proteases in *Murex* by Hirsch, 1915, and by Mansour-Bek, 1934; amylase in *Littorina* by Jenkins, cited in Fretter & Graham, 1962; and disaccharases in *Nassarius obsoletus*, this study, part 3). Whether

the proteinaceous granules are the source of the enzymatic activity remains to be shown. From the histological structure of the salivary glands and ducts it would appear that secretory pressure is responsible for moving the granules and mucus from the glandular tubules into the salivary ducts, at which point ciliary action conveys the secretory products distally to the buccal cavity. The circular muscles at the terminal ends of the salivary ducts presumably act as sphincters in helping to regulate the flow into the buccal cavity.

As shown by Graham (1941) and reviewed by Fretter & Graham (1962), the elongation of the proboscis in the *Rachiglossa* has been further accompanied by a "stripping off" of the glandular area associated with the midesophagus, resulting in the formation of a discrete organ, the gland of Leiblein, whose only contact with the parent midesophagus is by the duct emptying into it. Presumably, therefore, this duct from the gland of Leiblein marks the most posterior extent of the "pre-stripped" midesophagus (Graham, 1941). From the histological evidence, however, this appears not to be the case in *N. obsoletus*. As described above, a well-defined structural change occurs in the esophageal region some distance posterior to the duct from the gland of Leiblein, at the level of the columellar muscle.

That functional activity has been retained by the gland of Leiblein regardless of anatomical shifting is attested to by the conspicuous apocrine secretions reported for these glands in rachiglossans in general and in *N. reticulatus* (Martoja, 1964) and *N. obsoletus* (this study) in particular. Further evidence for a functional role for the gland of Leiblein is given by the repeated demonstration of digestive enzyme activity in its secretion (Hirsch, 1915; Mansour-Bek, 1934; Brock, 1936; this paper part 3).

The stomach of *N. obsoletus* is comparable with those of other rachiglossans in the assumption of a sac-like shape, in showing a migration of the esophageal opening posteriorly, and in the reduction of ciliary sorting fields to a minimum (for illustrations of other rachiglossan stomachs, see Graham, 1949, Morton, 1958b; Fretter & Graham, 1962; Martoja, 1964; and Wu, 1965). The caecum of *N. obsoletus* is apparently unique among the Nassariidae in lacking ciliation. The deep longitudinal folding undoubtedly serves the mechanical function of allowing a great deal of expansion when the snail has ingested food, thereby permitting the caecum to serve as a temporary storage organ for this material. The underlying heavy circular musculature is then responsible for moving the food mass anteriorly into the style sac region of the stomach.

The possession of a gastric shield, regarded as a primitive character in the Gastropoda, has been confirmed for all the species of *Nassarius* studied in detail (Graham, 1949; Martoja, 1964; and the present study), and for a related species, *Cyclope neritea* (Morton, 1958b). The production of a crystalline style in the "carnivorous" *Stenoglossa* is incompatible with the principal that "a crystalline style and the carnivorous habit cannot normally co-exist" (Yonge, 1930). Although neither Martoja (1964) nor Graham (1949) report the presence of styles in the Nassariidae studied by them, styles are definitely present in *Cyclope neritea* and *Nassarius obsoletus*. Whether or not these styles are truly functional (*i.e.*, as repositories of enzymes) or merely neomorphic protostyles derived from food string aggregations, is not known for *Cyclope*, but it has been shown (this study, part 3) that styles of *N. obsoletus* do indeed exhibit enzymatic activity.

With regard to the cellular composition

of the midgut glands, it is apparent that the histology of the midgut gland varies considerably from animal to animal amongst the prosobranchs (Fretter & Graham, 1962). The types and structure of midgut gland cells herein described for *N. obsoletus* are in good agreement with those described by Martoja (1964) for the European species of *Nassarius*. Little attempt will be made here to relate the cell types found in *N. obsoletus* with those found in the rest of the Gastropoda. The difficulties and pitfalls of synonymy for even a single genus are well illustrated in Sumner's thorough review (1965) of the midgut gland cells of *Helix*. Nevertheless, the triangular cells of *N. obsoletus* agree well with the "cellules coniques" of Martoja (and, in general, with the "secretory cells" of Fretter & Graham) and the columnar cells (types, or phases, 1 and 2) with Martoja's "cellules cylindriques" (and Fretter & Graham's "digestive cells").

The intestine, as previously shown, is characterized by a regional differentiation due to the presence or absence of a typhlosole and to differences in the subepithelial muscle coat. A great increase in the number of mucous cells in the intestine as compared with the esophagus is also a conspicuous feature. The latter 2 characteristics, in particular, are undoubtedly correlated with consolidation of the feces and movement of material through the intestinal lumen (see further discussion of this below, in part IV and general discussion).

In view of Martoja's conclusion (1964) that the amoebocytes of the European species of *Nassarius* play a very important role in the digestion of food, it is noteworthy that in *N. obsoletus* no histological evidence could be observed that the amoebocytes (hemocytes) were ever present within the lumen of the gut or even between the epithelial cells lining the

various regions of the alimentary canal.

Finally, the digestive tract of *N. obsoletus*, like those of all gastropods, is characterized by the abundance of mucus-secreting cells. The functional correlates of this are well-known and understood (Morton, 1958; Fretter & Graham, 1962; for reviews and extensive bibliographies). Investigations (principally histochemical) on the diversity of mucin types in molluscs are still in their infancy. Those studies which have been made (for example by Martoja, 1964, on the digestive systems of certain of the Nassariidae, and by Smith, 1965, on the reproductive tract of the slug *Arion ater*) indicate that great diversity and regional differentiation of mucin types is the rule, even within a single organ system. The following histochemically-detected classes of mucins are conspicuously present in the digestive system of *Nassarius obsoletus*: (1) PAS-positive acid mucopolysaccharides of epithelial goblet cells: in midesophagus, postesophagus, ventral groove of gland of Leiblein, septal cells of gland of Leiblein, caecum, midgut gland, and ventral groove of style sac; (2) PAS-positive acid mucopolysaccharides of subepithelial unicellular gland cells: in buccal cavity and anterior esophagus; (3) PAS-negative acid mucopolysaccharides of epithelial goblet cells: in 1st and 2nd part of the intestine and rectum; (4) PAS-negative acid mucopolysaccharides in gland cells of salivary tubules; (5) DMAB-nitrite positive glycoproteins in gland cells of salivary tubules; (6) DMAB-nitrite negative glycoproteins in epithelial columnar cells: in midesophagus, postesophagus, and caecum; (7) Histochemically problematical mucins in valve of Leiblein; and (8) glycoprotein/acid mucopolysaccharide material of the crystalline style. Thus, the present histochemical study adds further evidence for the preponderance of mucin heterogeneity in gastropod organ systems.

### III. ENZYME HISTOCHEMISTRY

#### 1. Materials and methods

All animals used in this part of the study had been maintained at the University of Michigan in sea-water aquaria prior to fixation. Tissues were quick-frozen by quenching in isopentane cooled by liquid nitrogen and then sectioned at 8–12 microns on an International model CT cryostat equipped with a razor blade holder. Fixation, either before or after sectioning, was carried out in Lillie's buffered neutral formalin at 4°C for 1 hour.

**Acid phosphatase:** Two methods were employed for the detection of this enzyme. The first was Gomori's lead nitrate method (Gomori, 1950) on post-fixed material with sodium  $\beta$ -glycerophosphate as substrate. The other was the simultaneous azo dye method (Barka & Anderson, 1963) on prefixed material. In this method, sodium  $\alpha$ -naphthyl acid phosphate was the substrate and freshly diazotized pararosanilin was used as coupler. The reaction was carried out at room temperature in barbiturate buffer (pH 6.0). Results from both Gomori and simultaneous coupling techniques were in complete agreement.

**Alkaline phosphatase:** As in the preceding case, 2 different methods were employed. These were the Gomori (1952) calcium-cobalt method and the simultaneous coupling technique as given in Barka & Anderson (1963). In the former, sodium- $\beta$ -glycerophosphate was used as substrate on post-fixed tissue. Sodium  $\alpha$ -naphthyl acid phosphate was employed as substrate in the latter, with Fast red TR as diazo coupler. This reaction was carried out on prefixed material at pH 9.2 in barbiturate buffer. As before, results obtained from the Gomori and simultaneous coupling methods were in agreement.

**Esterase:** The indoxyl acetate method

for nonspecific esterases was employed, according to the method of Holt & Withers (1952) and Holt (1958). Prefixed tissue sections were incubated at 37°C. in O-acetyl-5-bromindoxyl. The incubating medium was maintained at pH 6.5 with tris (hydroxymethyl) aminomethane buffer, and the enzyme activity was rendered visible by the formation of insoluble indigo with ferricyanide-ferrocyanide as the redox pair.

**Cathepsin C:** This method, developed by Hess & Pearse (1958), utilizes indoxyl acetates as substrate (O-acetyl-5-bromindoxyl was used in the present study). The indoxyl liberated by enzymatic hydrolysis is converted, as in the previous method, to indigo by ferricyanide-ferrocyanide oxidation. The specificity for cathepsin C is achieved by preincubation of all sections in E-600 (diethyl-p-nitrophenyl phosphate) which inactivates all B-type esterases present in the tissue. Sections subsequently incubated in activator ( $1 \times 10^{-3}$ M cysteine) and inhibitor ( $1 \times 10^{-3}$ M lead nitrate) are compared with control sections, and any cell, containing indigo in the control section, which contains more indigo after incubation with the activator and less after the use of the inhibitor, is considered to exhibit esterase activity of the type associated with cathepsin C.

**Leucine Amino Peptidase:** The simultaneous coupling method of Nachlas, *et al.* (1957) using L-leucyl- $\beta$ -naphthyl amide as substrate was employed. The coupler used was Fast blue B salt and the reaction was carried out in acetate buffer (pH 6.5) at 37°C.

**Beta-glucuronidase:** This enzyme was detected by the post-coupling method of Seligman, *et al.* (1954). The synthetic substrate used was 6-bromo-2-naphthyl- $\beta$ -D-glucuronide. Sections were incubated in phosphate-citrate buffer (pH 4.9) at 37°C. and Fast blue B salt was used as the diazo coupler.

Gomori's Tween method for lipase (Pearse, 1960), using Tween 80 (polyoxyethylene sorbitan monooleate) as substrate, was performed on the various tissues, but was eventually abandoned because only patchily-distributed non-specific staining could be obtained. Post-coupling techniques for  $\beta$ -glucosidase and  $\beta$ -galactosidase (Rutenberg, *et al.*, 1958) using 6-bromo-2-naphthyl glycosides were likewise abandoned because of failure to achieve consistent results.

Sections incubated in medium lacking substrate and pre-incubation of sections in water at 95°C for 5 minutes were used as controls for all staining procedures.

## 2. Results

*Buccal cavity:* The only enzyme demonstrable in the buccal cavity was a non-specific esterase. Enzyme activity was present in the entire lining epithelial layer, although it was not localized identically in every cell. All cells exhibited enzyme activity at their apical regions, while more basal activity varied among the cells from none at all to complete and even distribution throughout the entire cytoplasm.

*Anterior esophagus:* Enzymes demonstrable in the anterior esophagus included acid phosphatase, esterase, and leucine amino peptidase. The acid phosphatase activity was confined to the apices of the cells lining the lumen of this region. The non-particulate homogeneous reaction product formed a distinct continuous band immediately beneath the cilia. No particulate reaction sites in the cytoplasm of these cells were observed. Esterase activity was scattered along the epithelium, rather than exhibiting the continuity observable in the buccal cavity epithelium. The cellular distribution, however, was similar to that found in the buccal cavity epithelial cells—being present apically in all the cells exhibiting activity, but varying to the extent to

which it extended into the basal cytoplasm. Leucine amino peptidase activity was found in all cells in the epithelial lining. Activity was confined to the distal 2/3 of the cells and the reaction product was present as a homogeneous precipitate throughout this area.

*Midesophagus:* Enzymes demonstrable in the midesophagus include acid phosphatase, alkaline phosphatase, esterase, and leucine amino peptidase. The reaction product of acid phosphatase activity was confined to a thin homogeneous layer at the luminal border of the epithelium, as in the anterior esophagus. Alkaline phosphatase activity was similarly localized along the margin of the lining epithelial cell layer. In both, no activity was observed deeper within the cell cytoplasm. Esterase activity was again scattered throughout the epithelial lining and intracellular localization was varied, as before. Leucine amino peptidase activity was present homogeneously throughout the apical 2/3 of the cells lining the midesophagus.

*Postesophagus:* Enzymes present in the postesophageal epithelium included acid phosphatase, alkaline phosphatase, and esterase. The distribution of these enzymes in the lining epithelial cells was identical to that described above.

*Valve of Leiblein:* The only enzyme demonstrable in the valve of Leiblein was acid phosphatase. The sites of localization were in the ciliated columnar epithelial cells which are directly continuous with the lining epithelia of the anterior and midesophagus, and in the cells which make up the "ring" surrounding the cone-shaped papilla. Activity in the ciliated cells was confined, as before, to the luminal border. In the cells of the "ring", however, the reaction product was deposited homogeneously throughout the entire cytoplasm. No enzyme activity was observed in the pseudostratified portion of the valve of Leiblein.

*Gland of Leiblein:* Enzymatic activity in the gland of Leiblein was demonstrable for alkaline phosphatase, acid phosphatase, and leucine amino peptidase. Acid and alkaline phosphatase activity was present in some, but not all, of the septal cells. In those cells in which activity was found, the reaction product was confined to the apical borders of the cells. Very strong leucine amino peptidase activity was present in all the septal cells. The reaction product was deposited homogeneously throughout the cytoplasm of these cells and not restricted to a particular portion of them.

*Salivary glands:* No enzymatic activity could be demonstrated by any of the histochemical techniques employed.

*Caecum:* Enzymes detectable in the epithelium lining the caecum included acid phosphatase, alkaline phosphatase, and esterase. Localization of these enzymes was identical to that of the post-esophagus.

*Style sac:* Alkaline phosphatase, acid phosphatase, and esterase were demonstrable in the epithelium lining the style sac. The distribution of phosphatase activity was as follows: a very thin homogeneous band of activity appeared at the luminal border along the roof of the style sac; contrasting sharply with this at the regions of the minor typhlosole and ventral groove was a thick band of much greater activity which extended below the apices of the cells into the cytoplasm. The reaction product deposited in this thick band of enzyme activity was also homogeneous. No activity could be detected in the basal cytoplasm of these cells. In the cells covering the major typhlosole, no phosphatase activity whatsoever could be demonstrated. Esterase activity was confined to the regions of the roof of the style sac, the minor typhlosole, and the ventral groove.

*Midgut gland:* Enzymes demonstrable in the midgut gland included alkaline phos-

phatase, acid phosphatase, esterase, cathepsin C, and  $\beta$ -glucuronidase. Leucine amino peptidase activity could not be detected. Phosphatase activity, as in the previous tissues, was confined to a thin band on the luminal border of the midgut gland tubules (Figs. 30 and 31). Not all cells gave the reaction, but apparently there was no strict correlation with cell type, as both the triangular cells and the columnar cells exhibited activity. Strong esterase activity was shown by the cells of the midgut gland tubules. This activity was spread throughout the cytoplasm (Fig. 32). Beta-glucuronidase activity was found throughout the cells of the midgut gland tubules. Cathepsin C activity was found scattered throughout the epithelial lining of the tubules. This enzyme was apparently confined to the columnar cells, being most noticeable in type 2 cells which bulge into the lumina of the ducts. The intracellular localization was homogeneous throughout the cytoplasm of the cells.

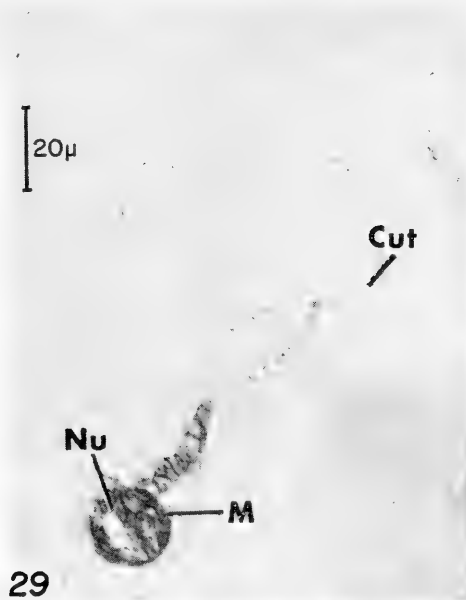
*Intestine:* In both regions of the intestine, acid phosphatase, alkaline phosphatase, and esterase could be demonstrated. The activity and distribution of these enzymes was essentially identical to that found in the caecum and esophagus. Additionally, in the second part of the intestine, leucine amino peptidase could be detected in the epithelial lining. Activity of this enzyme was spread throughout the apical 2/3 of the cells.

*Rectum:* In the rectum, no enzymatic activity could be detected by any of the techniques employed.

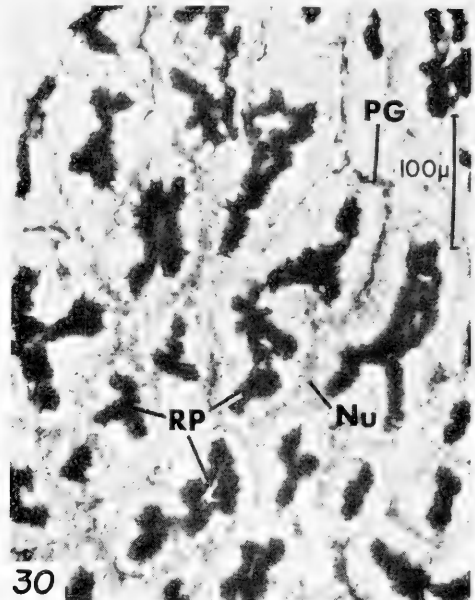
### 3. Evaluation of data

Although a large literature has accumulated on the histochemical localization of hydrolytic enzymes (principally in vertebrate tissues), the biological significance (or functional role) correlated with the observed enzymatic distribution is in most cases not well known. Few specific

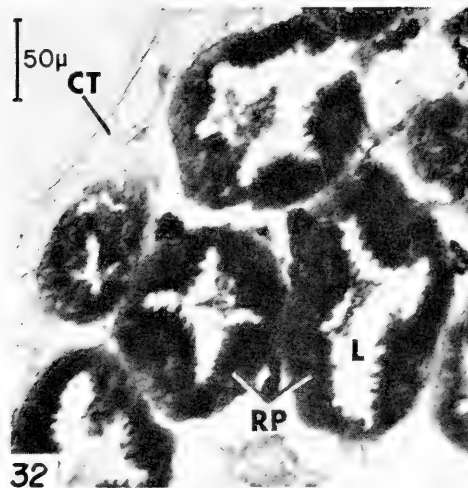




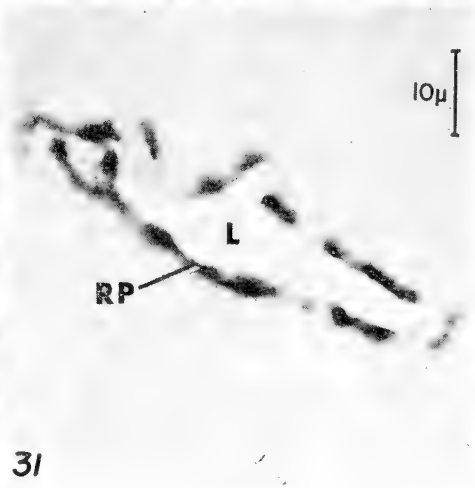
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32



31

FIG. 29. Subepithelial mucous gland cell within wall of buccal cavity. PAS technique.

FIG. 30. Midgut gland tubules showing a heavy deposit of acid phosphatase reaction product along the luminal borders. Gomori lead nitrate method with Mayer's haemalum counterstain.

FIG. 31. Cross-section of single midgut gland tubule showing acid phosphatase localization confined to cell apices. Simultaneous coupling method, no counterstain.

FIG. 32. Midgut gland tubules showing strong esterase activity throughout the cells. Indoxyl acetate method.

conclusions, therefore, can be drawn concerning the histochemical data just presented (see Table 2 for tabulated results).

The presence of alkaline phosphatase along the free cell borders of the epithelia in *Nassarius obsoletus* is consistent with

TABLE 2. Enzyme histochemistry of various components of the digestive system.

	Acid phosphatase	Alkaline phosphatase	Esterase	Cathepsin C	$\beta$ -Glucu- ronidase	Leucine amino peptidase
<i>Buccal cavity</i>						
Epithelial cells						
<i>Ant. esophagus</i>						
Epithelial cells	+	-	-	-	-	-
<i>Midesophagus</i>						
Epithelial cells	-	-	-	-	-	-
<i>Postesophagus</i>						
Epithelial cells						
<i>Salivary glands</i>						
Granule cells	-	-	-	-	-	-
<i>Valve of Leiblein</i>						
"Ring" cells	..	-	-	-	-	-
Epithelial cells	..	..	-	-	-	-
<i>Gland of Leiblein</i>						
Septal cells			-			
<i>Midgut gland</i>						
Columnar cells		..	-		-	-
Haemocytes	-	-		-	-	-
<i>Caecum</i>						
Epithelial cells						
<i>Style sac</i>						
Roof epithelium			-	..		-
Major typhlosole	-	..	-		-	+
Minor typhlosole	..	..	-			-
Ventral groove	-	..				-
<i>Intestine (1)</i>						
Epithelial cells					-	-
<i>Intestine (2)</i>						
Epithelial cells						+
<i>Rectum</i>						
Epithelial cells	-	-				

the localization found in many vertebrate tissues. Although clear-cut evidence of a specific functional role is lacking for alkaline phosphatase, the nearly universal

association of this enzyme with especially active cell surfaces (such as those possessing microvilli) is taken to indicate that it participates in the movement of mole-

cules across the cell membrane (Rothstein, *et al.*, 1953).

The membrane-associated acid phosphatase and non-specific esterase likewise are thought to act in the transport of material into the cell (Richardson, *et al.*, 1955). Acid phosphatase, an enzyme which has been clearly shown to be associated with lysosomes (deDuve, 1959), was not found in the subapical cytoplasm of the midgut gland cells of *Nassarius obsoletus*. This finding is of special interest in view of the current concept of the mechanism of intracellular digestion in which lysosomes play a central role (deDuve & Wattiaux, 1966). This apparent lack of a significant lysosomal component correlates well with the histological picture using conventional procedures in which no evidence of food-vacuole formation could be observed.

The presence of especially strong esterase activity throughout the midgut gland cells may well reflect a metabolic role rather than a purely digestive one, for it is well established that, in addition to hydrolytic activity, esterases are capable of participating in synthetic reactions as well as mediating replacement of ester components, the latter process being known as transesterification (Hofstee, 1960).

Esterase activity of the type associated with cathepsin C was found in the columnar cells of the midgut glands. As stressed by Tallan, *et al.*, (1952), intracellular catheptic activity results from a whole family of enzymes rather than a single proteinase. Cathepsin C has been shown to be an organophosphate-resistant member of this family which is hom-specific with chymotrypsin with regard to substrate specificity. Again, the physiological role of this enzyme is not clear; it is believed, however, that catheptic activity plays a role in the biosynthesis of the peptide bonds of proteins and of

naturally occurring peptides (Fruton & Simmonds, 1958).

Especially strong leucine amino peptidase activity was found in the gland of Leiblein septal cells and in the epithelial cells lining the second part of the intestine. Its presence in the gland of Leiblein may well be correlated with the secretory activity of that organ, but its presence in, and restriction to, the posterior region of the intestine is of unknown significance.

Beta-glucuronidase activity was found to be present in the midgut gland of *N. obsoletus*. This enzyme is one of the hydrolytic enzymes also known to be often linked with lysosomal particles (deDuve, 1959; deDuve & Wattiaux, 1966) although in the midgut gland cells of *N. obsoletus*, the enzymatic activity was distributed throughout the entire cytoplasm. The presence of  $\beta$ -glucuronidase has been histochemically rendered visible in gastropod tissue previously (Billet & McGee-Russell, 1955, in *Helix*), and in a survey study, Dodgson, *et al.*, (1953) have biochemically demonstrated its presence in a number of marine gastropods including the rachioglossans *Nucella lapillus* and *Buccinum undatum*. These latter investigators concluded that, on the basis of the variety of gastropods which possessed  $\beta$ -glucuronidase activity, there was apparently no strict correlation with habitat or feeding preferences. They did point out, however, that it was possible that the enzyme plays a digestive role, inasmuch as many of the marine algae on which some of these snails feed contain polysaccharide material rich in uronic acid residues. This type of functional role appears very probable for the  $\beta$ -glucuronidase of *Nassarius obsoletus*.

#### IV. *IN VITRO* ENZYME ANALYSES.

##### 1. Materials and methods

*Preparation of tissues:* All tissues used were from recently collected snails which

were maintained in running seawater aquaria at the Marine Biological Laboratory, Woods Hole, Massachusetts. The shells of the snails were gently cracked using a "C"-clamp and the soft parts removed *in toto* by grasping the columellar muscle with a pair of watchmaker's forceps. The tissues investigated were carefully dissected out under a stereomicroscope. Only posterior midgut glands were used, as these could be freed most cleanly from adjacent tissues (stomach caecum and gonad). The gland of Leiblein and salivary glands could be cleanly separated from their adjacent organs, the esophagus and cerebral ganglia respectively. The excised tissue was then quickly rinsed in cold distilled water and placed in cold (0°C) molluscan Ringer's solution without buffer (Cavanaugh, 1956). The cold tissues were subsequently homogenized at low speed in a glass tissue grinder with a teflon pestle and the resulting homogenate was allowed to stand in the cold for 1 hour with intermittent agitation. The preparation was then centrifuged for 10 minutes at *ca.* 3000 rpm to remove the larger unsuspended particles. The supernatant was decanted and assayed for enzymatic activity.

Crystalline styles were removed from animals, quickly rinsed in cold distilled water and only those portions of the styles containing no obvious debris allowed to dissolve in cold molluscan Ringer's. Stomach fluid was obtained by making a slit in the caecum where it lies adjacent to the surface of the visceral mass and inserting a fine-tipped Pasteur pipette into the lumen. Special care was taken to insure that no midgut gland material was inadvertently picked up. The stomach fluid was immediately put into cold Ringer's solution. In an effort to eliminate bacterial contamination, both the crystalline style and stomach fluid preparations were then filtered through a 0.22 micron Millipore filter held by a

Swinnex filter apparatus (both from Millipore Filter Corp., Bedford, Mass.). The resulting solutions were assayed for enzymatic activity.

*Determination of enzymatic activity:* Disaccharase, amylase, and cellulase activities were estimated by measuring the liberation of glucose from the various substrates. The reaction mixture for the disaccharase determinations contained 1.0 ml enzyme preparation, 10 micromoles of sugar (maltose, cellobiose, sucrose, melibiose, or lactose) and 100 micromoles of buffer, made up to a final volume of 2.0 ml. The reaction mixture for the amylase determinations contained 1.0 ml enzyme preparation, 0.1 mg starch or glycogen and 100 micromoles buffer, made up to a final volume of 3.0 ml. The reaction mixture for cellulase determinations was identical to those for amylase determinations with sodium carboxymethyl cellulose as substratum. Phosphate buffer was employed in the experiments, at pH 6.0 for the disaccharases, and at pH 7.0 for the amylases and cellulases. All reactions were run at 20°C from 2 to 24 hours. Toluene was added to the reaction mixtures to inhibit bacterial activity on all runs over 3 hours. Reactions were stopped by the addition of equimolar amounts of Ba(OH)<sub>2</sub> and ZnSO<sub>4</sub> according to the method of Weichselbaum & Somogyi (1941). Glucose in the protein-free supernatant was determined with the "Glucostat" reagent, with the exception that the reagent was dissolved in 0.25 M tris (hydroxymethyl)—aminomethane—HCl buffer instead of phosphate. This modification has been introduced (Dahlqvist, 1961) to inhibit maltase present in commercial preparations of glucose oxidase. Control tubes containing only tissue preparations, or only substrate, in buffer, were run simultaneously with all experimental mixtures, and enzymatic activity was taken as the difference in the amount of glucose in the

experimental tube and the amount of glucose in the control tubes. One ml samples of the enzyme preparations were precipitated with trichloroacetic acid (TCA) at a final concentration of 5% and set aside for tissue protein determinations. Colorimetric determinations on all experiments were made with a Coleman Jr. spectrophotometer.

Esterase and lipase activity were estimated by the method of Seligman & Nachlas (1963) in which 2-naphthol liberated from 2-naphthyl laurate is coupled with tetrazotized 0-dianisidine to give a purple azo dye which is then extracted with ethyl acetate and determined colorimetrically. The reaction mixture consisted of 1.0 ml enzyme preparation, 500 micromoles buffer, 10 micrograms substrate, with or without 1.0 ml  $8 \times 10^{-2}$  M sodium taurocholate, made up to a final volume of 7.0 ml. The buffers used were phthalate-NaOH at pH 5.5 and 6.0; phosphate at pH 5.5, 6.0, 6.5, 7.0, 7.25, 7.5, 7.75, and 8.0; barbiturate-HCl at pH 8.0, 8.25, 8.5 and 9.0; and glycine-NaOH at pH 9.0, 9.5 and 10.0. All reactions were run at 20°C for 2 hours and stopped by the addition of TCA to give a final concentration of 5%. One ml samples of the enzyme preparations were precipitated with TCA and set aside for tissue protein determinations. Control tubes containing only tissue preparations, or only substrate, in buffer, were run simultaneously with all experimental mixtures and esterase activity was taken as the difference in the amount of 2-naphthol in the experimental tubes lacking taurocholate and the amounts of 2-naphthol in the control tubes. Similarly, lipase activity was taken as the amount of 2-naphthol liberated in the presence of taurocholate in excess of the total amount in the tubes lacking taurocholate and the control mixtures.

Protease activity was estimated by measuring the liberation of TCA-soluble

protein from TCA-insoluble protein (casein and bovine serum albumen). The reaction mixture consisted of 1.0 ml enzyme preparation, 0.1 mg substrate, and 100 micromoles of phosphate buffer (pH 6.0 and 8.0), made up to a final volume of 3.0 ml. Control tubes containing only tissue preparations, or only substrate, in buffer, were run simultaneously with all experimental mixtures. Protein in this assay as well as the protein in all preceding assays was measured by the method of Lowry, *et al.* (1951).

## 2. Results

### *Enzymatic cleavage of disaccharides:*

Table 3 shows the distribution of disaccharase activity in the organs examined. It can be seen that maltose and cellulose were hydrolyzed by all the tissues tested, with highest activity recorded for the crystalline style, stomach fluid, and gland of Leiblein. Midgut gland preparations were able to hydrolyze the  $\alpha$ - and  $\beta$ -galactosides in low amounts and the stomach fluid also had trace amounts of activity. The gland of Leiblein, in contrast, shows considerable hydrolytic activity with lactose as substrate. Invertase (sucrase) activity did not parallel maltase activity at all, rather it was found only in the midgut gland with traces of activity in the stomach fluid.

### *Enzymatic cleavage of polysaccharides:*

Hydrolysis of starch, glycogen, and sodium carboxymethylcellulose is shown in Table 4. Highest activities were found in extracts of the crystalline style and in stomach fluid with starch and glycogen as substrates. Midgut gland preparations also showed some activity with these substrates. Midgut gland preparations showed moderate activity, and stomach fluid low activity, with carboxymethylcellulose as substrate.

*Esterase—lipase activity in midgut gland homogenates:* The histochemical investigations reported above (part 2) had shown

TABLE 3. Disaccharase activity in *Nassarius obsoletus*. (Activity expressed as micromoles substrate hydrolyzed/gram tissue protein/hour. All experiments run at pH 6.0 at 20° C.)

Organ	Maltose	Cellobiose	Sucrose	Melibiose	Lactose
Salivary glands	230	58.8	nil	nil	nil
Gland of Leiblein	420	1860	nil	nil	563
Crystalline style	3800	36.0	nil	nil	nil
Stomach fluid	1710	59.0	trace	trace	trace
Midgut gland	287	66.5	278	6.94	34.7

TABLE 4. Amylase and cellulase activity in *Nassarius obsoletus*. (Activity expressed as micromoles glucose liberated/gram of tissue protein/hour. All experiments run at pH 7.0 at 20° C.)

Organ	Glycogen	Starch	Sodium carboxymethyl-cellulose
Salivary glands	nil	trace	nil
Gland of Leiblein	trace	trace	trace
Crystalline style	2650	2790	trace
Stomach fluid	1090	1170	27.0
Midgut gland	415	439	196

TABLE 5. Protease activity in *Nassarius obsoletus*. (Activity expressed as micrograms protein rendered soluble/gram of tissue protein/hour. All experiments run at pH 6.0 at 20° C.)

	Salivary glands	Gland of Leiblein	Midgut gland	Stomach kuid
TCA-soluble protein	nil	2380	260	7220

the presence of strong non-specific esterase activity in the midgut gland; the technique for demonstration of lipase by means of the Gomori Tween method,

however, gave equivocal results. The method of Seligman & Nachlas (1963) was used to determine whether any differences could be detected *in vitro*

between esterase activity and lipase activity. With the technique employed it appears that there is indeed a lipase present. Maximum activities for the tissue homogenate are similar for both enzymes (803 micromoles/gram protein/hour for the esterase and 850 micromoles/gram protein/hour for the lipase). However, as the pH dependency curves show (Fig. 33), the shape of the curves and the pH optima for the enzymes are clearly different. The lipase optimum appears to be about 7.5, while that for the esterase is 8.25.

**Proteolytic activity:** Enzymatic hydrolysis of protein is shown in Table 5. The values given are for the maximum activity measured with casein as substrate at pH 6.0. Lower but significant activity was observed at pH 8.0 with casein as substrate, but only traces of activity were observed with bovine serum albumen as substrate, either at pH 6.0 or 8.0.

### 3. Evaluation of results

From the results on hydrolytic activity reported above, one can draw some reasonable, if not highly specific, conclusions about the enzymatic complement of the digestive system of *Nassarius obsoletus*.

Disaccharide and polysaccharide substrates were chosen so as to give the presumably complete set of glycosidic linkages which are thought to be of paramount importance in determining glycosidase specificity (Veibel, 1950). Thus, for maltose to be hydrolyzed, an  $\alpha$ -glucosidase must be present; similarly for cellobiose, a  $\beta$ -glucosidase; for sucrose, an invertase ( $\alpha$ -glucosidase or  $\beta$ -fructosidase); for melibiose, an  $\alpha$ -galactosidase; for lactose, a  $\beta$ -galactosidase; for glycogen and starch, an amylo-1, 4-glucosidase; and for cellulose, a  $\beta$ -1, 4-glucosidase (cellulase). Since most enzyme characterizations have been done with yeast and bacteria as source materials,

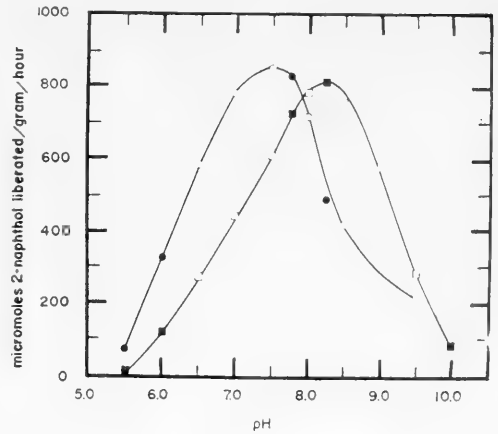


FIG. 33. Lipase-esterase pH curves from midgut gland homogenates. Circles=lipase; squares=esterase. Closed figures=single determination; open figures=mean of 3 determinations.

only general comparisons can be drawn.

Two classes of enzymes are known to act on the disaccharide sucrose, namely  $\alpha$ -glucosidases (glucosido-invertases) and  $\beta$ -fructofuranosidases (Neuberg & Mandl, 1950). The animal invertases that have been sufficiently characterized, however, are all of the glucosido-invertase type (Myrback, 1960). There has been controversy over whether or not maltase and invertase (sucrase) activity results from two types of enzyme or from a single  $\alpha$ -glucosidase with low specificity with regard to the aglucon moiety. The evidence is somewhat conflicting, but data on metazoan enzymes indicate that animal maltase is incapable of acting on sucrose (Gottschalk, 1950). From the distribution of maltase activity shown in Table 3, it appears that since tissue preparations, run simultaneously, showed maltase activity but had no hydrolytic effect with sucrose as substrate, there is a true maltase present in at least the salivary glands, gland of Leiblein, crystalline style, and stomach fluid. The finding of both maltase and sucrase action in the midgut gland (and their near equality

in activity) may indicate that there is a single relatively unspecific  $\alpha$ -glucosidase present whose lower activity is perhaps an indication of a metabolic role rather than a purely digestive one. The site of origin of the high maltase activity in the stomach fluid and style is not clear. The organs which are known to release products into the digestive tube (salivary glands, gland of Leiblein, and midgut gland; Fretter & Graham, 1962; Hyman, 1967) appear to have too little maltase to contribute significantly to the extremely high activity found in the style. The substance of the style (principally mucoprotein) is thought to be secreted by the typhlosoles of the style sac and perhaps these structures are also responsible for secretion of enzymes which are absorbed on to the style, the activity in the stomach fluid resulting from the dissolution of the style and concomitant release of enzymes (Morton, 1958a).

Cellobiase ( $\beta$ -glucosidase) activity was observed in all the organs examined, but was especially high in the gland of Leiblein, an organ whose apocrine secretion has been referred to before. The problem again arises as to whether a true cellobiase is responsible or whether a rather broad range  $\beta$ -glucosidase is acting. In a review of the subject, Pigman (1941) concludes that the evidence does not favor the concept of one enzyme responsible for the hydrolysis of all  $\beta$ -glucosides. He proposed that " $\beta$ -glucosidase" is not a single enzyme, strictly speaking, but rather a class of closely related enzymes, which all show an ability to hydrolyze  $\beta$ -glucoside linkages. However, Fisher (1964), working with a partially-purified  $\beta$ -glucosidase from the roach, *Blaberus craniifer*, found that this presumably single enzyme was able to hydrolyze six  $\beta$ -glucosides including cellobiose, phenyl- $\beta$ -D-glucoside, p-nitrophenyl-p-D-glucoside, salicin, arbutin, and gentiobiose.

The foregoing does not take into

account enzymes which are active on long chain  $\beta$ -glucoside polymers such as cellulose and its derivatives. Evidence on this score is much more satisfactory as it has been repeatedly shown that cellulases from widely different sources attack only the polysaccharide; that cellobiose is the smallest product formed; and that cellulase and cellobiase can be separated into distinct entities, chiefly by chromatography (Pigman, 1950). From the data presented in Tables 3 and 4 it would appear safe to say that a cellobiase (or a  $\beta$ -glucosidase with a marked specificity for cellobiose) is present in the gland of Leiblein and that the activity observed in the stomach fluid and crystalline style has as its site of origin the apocrine secretion of the gland of Leiblein. The activity in the midgut gland is presumably endogenous and may or may not be correlated with the cellulase activity reported below.

A small amount of  $\alpha$ -galactosidase activity was detected in the midgut gland using melibiose as substrate. Studies on yeast glycosidases indicate that  $\alpha$ -galactosidase is a true entity, being separable from other glycosidases (Veibel, 1950). The low activity detected in the midgut gland perhaps indicates a metabolic function rather than a truly digestive one.

The  $\beta$ -galactosidase activity found in the gland of Leiblein and midgut gland may be due to a relatively unspecific  $\beta$ -glucosidase found in the organs. It is known that practically all  $\beta$ -glucosidase preparations are able to hydrolyze  $\beta$ -galactosides, although there exist  $\beta$ -galactosidases which can be freed of  $\beta$ -glucosidase activity (Veibel, 1950). Beta-glucosidase and  $\beta$ -galactosidase activities in *Nassarius obsoletus* can readily be interpreted as resulting from enzymes solely of the  $\beta$ -glucosidase type showing  $\frac{1}{2}$  to  $\frac{1}{3}$  the activity with a  $\beta$ -galactoside as substrate. Unlike the evidence suggesting the existence of a specific cellobiase, there have been no studies reported in



which a lactase has been separable from  $\beta$ -galactosidase activity.

Alpha-amylase of metazoan origin is known to catalyze the hydrolysis of  $\alpha$ -1, 4-glucosidic linkages of polysaccharides such as starch, glycogen and their derivatives. It has been further characterized as being distinct from  $\alpha$ -glucosidases which act on smaller molecules; as having no hydrolytic activity on the  $\alpha$ -1, 6-glucoside branch points in complex polysaccharides; and as having as its primary products larger oligosaccharides (dextrins) which are later broken down to yield maltose, isomaltose, and branched-chain products of low molecular weight (Baumann & Pigman, 1957). The amylase values shown in Table 4 are derived from somewhat indirect evidence, namely the formation of glucose. Since all preparations with presumed amylase activity also have high maltase activity, there seems no reason to doubt that an  $\alpha$ -amylase is present which converts the starch and glycogen into disaccharides, which in turn are broken down by endogenous maltase liberating glucose.

Cellulases act on the  $\beta$ -glucoside linkages of complex homopolymers such as cellulose and its derivatives. It is the consensus that, as for the  $\alpha$ -amylases, the cellulases have distinct enough properties to warrant separation from  $\alpha$ -glucosidases (Pigman, 1950). Little significance, however, can be attached to the cellulase activity shown in Table 4, for although the first unequivocal preparation of a cellulase was derived from a gastropod mollusc (the pulmonate, *Helix*), further studies have shown that many of the reported cellulases of presumed animal origin were, in fact, due to microbial contamination (Florkin & Lozet, 1949; Stone & Morton, 1959). Although both filtration and toluene were used to remove possible bacterial activity in the tissue preparations, the resulting cellulase activity must be viewed cautiously since it is

known that microbial cellulases are of the soluble extracellular type which would not be removed by filtration or added toluene. Isolation and cultivation of bacteria present in the tissues and gut of *Nassarius obsoletus* appears to be the only way to resolve the source of the enzyme.

Definitions of the terms lipase and esterase have usually been based on the chain length of the carboxylic acid. Thus, "lipase" has referred to esterases capable of attacking fatty acid esters with a long carbon chain, especially, fats, and "esterases" (or "alioesterases") to enzymes attacking short-chain aliphatic esters. More recent classification divides fatty acid esterases into esterases acting on substrates in solution (esterases proper) and esterases (lipase-type esterases) which act predominantly on undissolved substrates (Hofstee, 1960). In the method employed in this study, a suspension of 2-naphthyl laurate was used as substrate. The principal of the determination is that lipase and esterase hydrolyze 2-naphthyl laurate to 2-naphthol and lauric acid. In the absence of a surface-active agent (taurocholate) most of the hydrolysis is due to esterase, while in the presence of taurocholate the hydrolysis is due to lipase and esterase. The difference presumably corresponds to lipase activity. As Fig. 33 indicates, there is considerable hydrolytic activity (*ca.* 800 micromoles/gram/hour) shown towards the substrate. Addition of a surface-active agent more than doubles the rate at which the substrate is hydrolyzed by the preparation, and this activation, when plotted relative to pH, indicates that most probably an esterase of the lipase-type is present along with their esterases.

Proteases are usually classified as exopeptidases or endopeptidases according to whether they act on terminal (amino or carboxy) amino acids or internal peptide linkages. From the protease activities presented in Table 5, and from the

TABLE 6. Summary of hydrolytic enzymes detectable in the digestive system of *Nassarius obsoletus* by *in vitro* methods. Preparations of high activity are italicized.

Source	Enzymatic activity	Substrate
Salivary glands	$\alpha$ -glucosidase <i><math>\beta</math>-glucosidase</i>	maltose cellobiose
Gland of Leiblein	$\alpha$ -glucosidase <i><math>\beta</math>-glucosidase</i> <i>protease</i>	maltose cellobiose casein
Crystalline style	<i><math>\alpha</math>-glucosidase</i> <i><math>\beta</math>-glucosidase</i> <i><math>\alpha</math>-amylase</i>	maltose cellobiose starch, glycogen
Stomach fluid	<i><math>\alpha</math>-glucosidase</i> <i><math>\beta</math>-glucosidase</i> <i><math>\alpha</math>-amylase</i> (cellulase?) <i>protease</i>	maltose cellobiose starch, glycogen carboxymethyl-cellulose casein
Midgut glands	$\alpha$ -glucosidase <i><math>\beta</math>-glucosidase</i> $\alpha$ -galactosidase <i><math>\beta</math>-galactosidase</i> glucosido-invertase $\alpha$ -amylase (cellulase?) <i>esterase</i> <i>lipase</i> <i>protease</i>	maltose cellobiose melibiose lactose sucrose starch, glycogen carboxymethyl-cellulose 2-naphthyl laurate 2-naphthyl laurate casein

method of determining protein (namely by coloration of aromatic amino acids), it would appear that the only type of protease capable of rendering soluble enough aromatic amino acid residues to give such high readings would be of the endopeptidase category. The resulting soluble protein is most probably a mixture of relatively short-chained peptides rather than a solution of amino acids. From the fact that greater activity was observed at pH 6.0 than was seen at pH 8.0, it may be tentatively assumed that the enzyme is of the trypsin type.

Table 6 summarizes the enzyme complement of the digestive organs of *Nassa-*

*rius obsoletus* as revealed by this *in vitro* study.

## V. ASPECTS OF DIGESTIVE PHYSIOLOGY AND BEHAVIOR

Much of the general behavior of *Nassarius obsoletus* has been discussed by Dimon (1905), Copeland (1918), Jenner (1956a, 1957 and 1958), Scheltema (1964), and Carr (1967). The following is a brief synthesis of the knowledge relating to distribution and feeding activities, drawn from the above-mentioned studies and confirmed and (in places) amplified by the present investigator.

1. *Nassarius obsoletus* is found on mud/

sand flats from a few inches above the average low tide level to approximately 10 or 12 feet below it.

2. The tidal flats on which *N. obsoletus* occurs are characteristically rich in organic material.

3. On these tidal flats, *N. obsoletus* is the numerically dominant gastropod species.

4. The distribution of these snails is not random; the snails showing, instead, a marked tendency for forming (and apparently, shifting and reforming) extensive aggregations.

5. In these aggregations, *N. obsoletus* is present in enormous numbers. Data from the Invertebrate Zoology class at the Marine Biological Laboratory at Woods Hole gave peak densities of 5860 snails per meter<sup>2</sup> for aggregations of adult snails at North Falmouth, Massachusetts (F.M. Fisher, personal communication). The biomass of living snail tissue at this density (at 0.5 gm living tissue/snail) equals approximately 3 kilograms/meter<sup>2</sup>. Scheltema (1961) reports densities of 23,000/meter<sup>2</sup> for newly-settled larvae.

6. On the mud-sand flats, *Nassarius* is usually found moving very slowly along the surface, scooping up quantities of the substratum with its proboscis only partially extended (Fig. 35).

7. *Nassarius* will feed only when completely covered by water, or at least when there is enough water present to cover its shell aperture.

8. *N. obsoletus* in nature is primarily a deposit-feeder. The stomach contents of snails examined in the field uniformly consisted of great quantities of sand, mud, and organic detritus.

9. *Nassarius* in nature has been observed to feed actively on the larger algae (such as *Ulva*) and in the laboratory it will graze on algal scum covering the walls of aquaria.

10. In nature and in the laboratory, snails show a marked preference for the

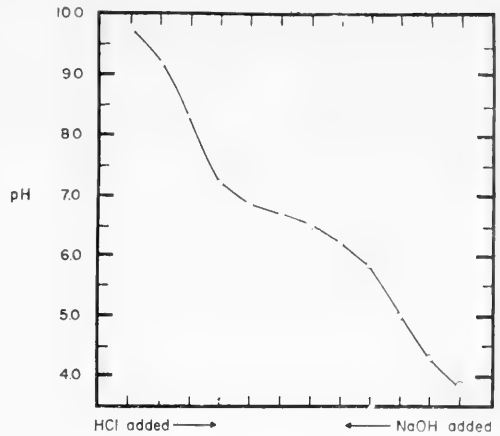


FIG. 34. Titration curve of crystalline styles in solution.

flesh of dead animals. *Nassarius* has been observed to eat the following (dead) animals: *Mya*, *Mytilus*, *Modiolus*, *Nassarius*, *Littorina*, *Nereis*, *Squilla*, hermit crabs, and frozen shrimp (*Penaeus*). In addition, Dimon (1905) reports observing a living nereid being devoured by a cluster of *Nassarius* in the field, but this was apparently an exceptional instance.

11. *N. obsoletus* exhibits a distinct behavioral response to the presence of decaying meat. In order of occurrence, the following events take place: (a) Initial detection of soluble diffusing substances from the meat leads to an overall increased activity. Animals which are partially or completely buried extend their siphons and, after a short interval, come rapidly to the surface of the substratum. (b) This increase in activity is immediately followed by relatively rapid forward locomotion accompanied by a constant sweeping of the siphon from side to side in approximately 120° arc in front of the snails. (c) After a brief period of randomly-directed forward locomotion, the snails orient themselves against the direction of the current flow (rheotaxis) and move upstream. (d) The snails continue

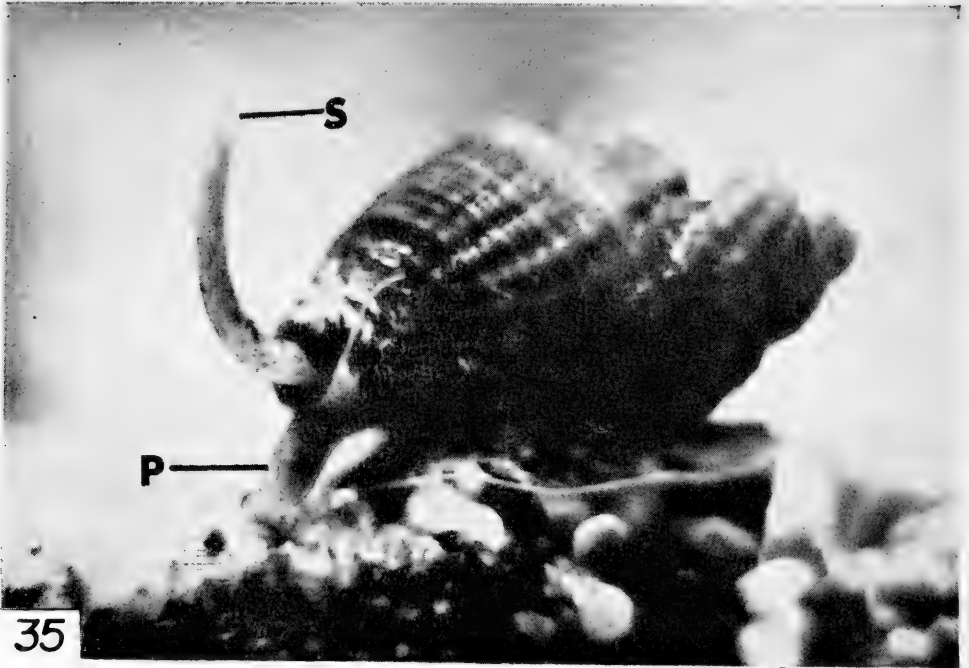


FIG. 35. *Nassarius obsoletus* with proboscis extended as far as the substratum. This is its normal position when the animal is feeding on surface detritus.

movement upstream with "searching" movements of their siphon and, as the meat is neared, the proboscis is extended and radular action begins (Fig. 36). (e) Upon reaching the meat, the proboscis is applied to the surface and, by radular action, the proboscis literally bores a hole deep into the food mass (see also Carr, 1967a and 1967b).

12. That the initial response to meat is chemical rather than visual is easily shown by the following facts: (a) In nature, animals which are close by, but upstream from, a decaying piece of meat do not become characteristically active or exhibit any of the behavioral traits associated with the detection of meat (as in 11, above). On the other hand, animals which are much farther away, but downstream, from the same piece of meat do become active and go through the searching movements, eventually reaching and

eating the meat. (b) In the laboratory, a single drop of meat juice introduced into the aquarium is sufficient to elicit the easily-observed responsive activities discussed under 11 (a-b), above.

13. Clear evidence for a rheotaxis is provided by the behavior of animals in nature preparatory to feeding [as in 11 (c), above] and by the following observations of animals under laboratory conditions: (a) If a drop of meat juice is added to a battery jar containing snails and the water stirred so as to give a unidirectional current (clockwise, for example), the animals become active and, after a few moments of randomly-directed locomotion, move with searching movements against the direction of the current (counterclockwise in this case). By reversing the direction of the current, the animals will turn 180° in their path and more as before against the current. (b) If

a piece of meat is dropped into the middle of an aquarium in which the water has been allowed to become still, the snails become active, but mill about with no uniform directional heading. Those that do perchance contact the meat stop and begin feeding, and thereby many snails eventually find the food, but by the mechanism of klinokinesis (Fraenkel & Gunn, 1940) rather than by a directed taxis.

The time of retention of food in the digestive tract has been used as an indication of the efficiency of the digestive process (Prosser & Brown, 1961). In *N. obsoletus* just taken from its natural habitat and isolated in aquaria, the gut is completely emptied of sand and mud in approximately 12 hours. Observations on previously-starved animals fed on frozen shrimp indicate that the passage of this type of food is completed more rapidly, often in as short a period as 4 hours. Whether or not the observed feeding times can be directly correlated with the "efficiency of the digestive process" remains an unanswered question. Nevertheless, it would not be too surprising if the digestion of organic material within a matrix of sand and mud particles would be less efficient than digestion of a concentrated "pure" food form such as animal tissues. What physiological mechanisms may be involved in regulating the speed of food flow through the gut can only be guessed.

As Jenner (1956b) has pointed out, the mechanism of primary importance in propulsion of material through the digestive tract is one of peristaltic contraction of the walls of the alimentary canal. As has been shown (part 1, above), the musculature surrounding the various portions of the gut is well-developed, and thus the anatomical basis for such peristaltic movements is clearly established.

The formation of fecal material, its consolidation and elimination, are thought

to have been at least partially responsible for many of the evolutionary specializations found in the Gastropoda (for example: the extensive elaboration of mucous glands in the intestine; the formation of food/fecal strings; the shift of the anus to the right side of the pallial cavity; the great reliance on, and success of, the pectinibranch ctenidium; the shift in pallial water currents from ventro-dorsal to lateral; and so on). In light of such theoretically important considerations, it is of interest to note the conditions which obtain in *Nassarius obsoletus*. Although mucous goblet cells abound in the intestinal region, no discrete consolidated fecal pellets, such as are known from microphagous herbivores, are formed by *N. obsoletus*. If animals are taken from the field and placed in clean seawater-filled finger bowls, defecation can be observed and fecal products examined. The great bulk of expelled material consists of sand particles which have mucus adhering to them. The mucus has insufficient binding capability, however, to hold the heavy sand grains together in a fused mass. Presumably the size and weight of the particles cause them to settle rapidly out of the mantle cavity and thus prevent them from interfering with the ctenidium and the respiratory currents. Lighter and more finely divided material is held together somewhat better than the sand grains, but the compactness of consolidation does not approach that found in forms subsisting solely on a diet of minutely-divided particulate material.

Characteristic of the molluscan stomach is the presence of numerous ciliated folds and ridge systems which act as particle "sorting fields". These are particularly well-developed in the lamellibranch Bivalvia and in those Archaeogastropoda and Mesogastropoda which are of the continuously-grazing microherbivore type. The food strings and crystalline styles of lamellibranchs and style-bearing proso-

branches are likewise propelled by extensively ciliated surfaces. In *N. obsoletus*, the entire alimentary canal with the exception of the caecum is lined by ciliated epithelium as shown in part I. The stomach, however, is simplified with regard to sorting fields in comparison to most of the lower gastropods. It does, however, retain vestiges of organized ciliated fields which are often absent in the more specialized Neogastropoda. The following ciliary currents were determined by the use of finely divided particulate material such as carmine and carborundum.

Issuing from the esophageal opening (Fig. 18, OPE), a relatively weak current proceeds posteriorly for a very short distance and then terminates abruptly at the anterior edge of the caecal folds. No ciliary activity could be observed along the folded walls of the caecum itself. To the left of the esophageal opening a series of currents run along the small transverse folds converging on to the smooth saddle-shaped area (SSA). Although this region of transverse folds most closely resembles a sorting field of the type found in lamelli-branches and lower gastropods, there is no sign of the characteristic separation of particles by size or of the presence of two currents perpendicular to each other to effect such a separation.

To the right of the esophageal opening are found currents issuing from the openings of the mjdut glands and a current directed away from the ventral midline across the large area of smooth epithelium adjacent to the gastric shield. Within the sulcus forming the posterior boundary of the typhlosoles are found strong currents directed medially towards the ventral intestinal groove. A strong current continues along the floor of this groove carrying particles entrapped in mucus anteriorly toward the intestine. Strong ciliary activity is found on both typhlosoles: a posteriorly-directed current along

the face of the minor typhlosole (MiT) presumably forces the crystalline style backward against the gastric shield, while ciliary activity directed medially along the surface of the major typhlosole (MaT) causes the style to rotate in a clockwise direction when viewed from the rear. Currents on the sides of the typhlosoles are directed ventrally and serve to carry particles into the anteriorly flowing currents of the intestinal groove.

In *Nassarius obsoletus*, therefore, there is no evidence that the stomach accomplishes any particle separation through the mechanism of ciliary sorting fields.

Perhaps the most notable feature of the stomach of *Nassarius obsoletus* is the presence of a crystalline style. Functionally, the crystalline styles of lamelli-branches and lower gastropods are thought to act as: (1) repositories for digestive enzymes; (2) "capstans" which aid in drawing mucus food strings into the stomach; and (3) buffer sources to maintain the pH of the stomach fluid (Morton, 1952 and 1960). It is of interest to note how the style of *N. obsoletus* compares with styles found elsewhere in the Mollusca with regard to these functions.

It has been clearly demonstrated that the style of *Nassarius obsoletus* does contain hydrolytic enzymes (part III, above). It is unlikely, however, that the style of these animals in nature acts as a capstan to any significant extent, since, as has been discussed above, the bulk of ingested material is sand and coarse mud (coated, but not tightly bound, by mucus) which is passed along the alimentary canal by muscular peristalsis.

In an effort to determine whether or not the style of *Nassarius obsoletus* has any buffering capability, 10 styles were allowed to dissolve in 10.0 ml of glass-distilled water. The resulting solution was titrated with 0.01 N HCl and 0.01 N NaOH and the pH determined with a Sargent model PB pH meter. The titra-

tion curve is given in Fig. 34. It shows buffering action between pH 5·8 and 7·2, the midpoint being at pH 6·5. This agrees well with values for the stomach fluid of pH 6·0–6·5 obtained by the use of indicators (bromthymol blue and bromocresol purple).

The style of *Nassarius obsoletus*, therefore, apparently does have a buffering function in addition to the enzymatic one discussed above.

## VI. GENERAL DISCUSSION

Studies on the functional morphology of molluscs by Atkins, Fretter, Graham, Morton, and Yonge, among others (reviewed by Morton, 1958a; Fretter & Graham, 1962; Wilbur & Yonge, 1964; Owen, 1966; and Hyman, 1967), offer convincing evidence that the first molluscs most probably all fed on small particles. These particles were non-selectively scraped up from the substratum by the radula, bound by mucous secretions into a "food string", transported along the alimentary canal by ciliary activity, and eventually subjected to phagocytosis and intracellular digestion within the blind tubules of the midgut gland. Such dependence on the intracellular mode of digestion imposed the requirement that the food particles presented to the digestive cells be within certain size limits to allow for phagocytosis. Among the earliest evolutionary features to appear in molluscs, therefore, were mechanisms designed to grade and sort particles according to size and to transport the sorted particles to their proper destinations within the digestive tract. The extensive use of mucous secretions to bind the particulate food material together for transport through the alimentary canal led to the production, within the stomach, of a mucoprotein rod, the forerunner of the crystalline style, or protostyle. This rod gained increased

functional significance as it assumed the mechanical burden of drawing the mucus food-string into the stomach, as it became a repository for extracellular amylases, and as it added a buffering effect to maintain the pH of the stomach.

The lamellibranch bivalves adopted the habit of feeding on particles suspended in the surrounding water and thus avoided the larger particulate material which made up the bulk of the ingested matter of deposit feeders. Further refinement of food selection was achieved by the use of ciliary sorting fields on the labial palps and within the stomach itself. Digestion in this group has *presumably* remained for the most part intracellular, although a partial breakdown does occur extracellularly of material, such as polysaccharide, the digestion of which is comparatively difficult.

The gastropods, with notable exceptions, retained use of the radular apparatus to scrape up food material from the substratum in a non-selective manner. Early dietary specialization led some gastropods to become microphagous herbivores, feeding primarily on algal fragments rasped from rocks and other hard surfaces. Sorting by size of particle was accomplished almost solely by means of ciliary sorting fields within the stomach—these functioning similarly to those found in the Bivalvia.

Among living prosobranchs, some of the Archaeogastropoda and Mesogastropoda retain the habit of microphagous herbivory although the evolutionary trend has been for gastropods to adopt macroherbivorous or carnivorous habits. The mesogastropod microherbivores retain possession of ciliary sorting fields within the stomach, and certain entire superfamilies (Rissoacea, Cerithiacea, and Calyptraeacea) are characterized by the possession of a crystalline style. Here, as in the lamellibranchs, the primary mode of digestion is intracellular, with

partial extracellular digestion taking place by means of crystalline style enzymes.

The rachiglossan Neogastropoda (including the superfamilies Buccinacea, Muricea, and Volutacea) are characteristically carnivorous. The modifications which have occurred to equip such snails for a diet of animal flesh include: (1) development of the rachiglossan radula, possessing three sharp-cusped teeth per row, which is extremely well-suited for tearing bits of flesh from solid animal tissue; (2) size increase and elaboration of the proboscis which allows penetration of the feeding apparatus deep into animal tissues and into relatively inaccessible places such as between bivalve shells and into tunicate tests; (3) extension of the mantle tissue into a long movable canal (the siphon) which allows delicately-controlled intake of the surrounding water which is then directed over (4) a well-developed bipectinate osphradium which is employed as a chemosensory organ for the detection of food; (5) development of a valvular device in the esophagus (the valve of Leiblein) which allows protrusion and elongation of the proboscis without regurgitation of food material; (6) essentially complete conversion to extracellular digestion; (7) specialization of glands (such as the salivary glands, gland of Leiblein, and midgut gland) to produce extracellular enzymes; (8) simplification of the stomach into a bag where enzymes and food are mixed and digestion occurs, and from which soluble material passes into the ducts of the midgut gland for absorption; (9) great reduction or complete loss of ciliary sorting fields, since there is no longer the requirement for separation of particles from one another according to size; (10) loss of a crystalline style, since the proteinaceous style presumably would be digested by the extracellular proteases of strictly carnivorous forms; and (11) great reduction

or more often complete loss of the gastric shield, since with the crystalline style absent, there no longer is abrasion between a style head and the lining epithelium.

The Buccinacea amongst the Neogastropoda are known to be the least specialized of the carnivorous Rachiglossa. Within the Buccinacea, members of the family Buccinidae frequently eat living flesh, while the family Nassariidae characteristically feed on dead or decaying animal matter.

The anatomy of the *Nassarius* species studied agrees in almost every detail with the characteristics listed above associated with assumption of a carnivorous existence. Thus, the presence of the rachiglossan radula, the extremely long and protrusible proboscis, the long siphon and bipectinate osphradium, the well-developed valve of Leiblein, salivary glands, and gland of Leiblein, the simplification of stomach structure, the absence of efficient sorting ciliate regions, and the reduced gastric shield—all bespeak the typical carnivorous rachiglossan structure.

Likewise, almost all of the species of *Nassarius* are described as being carnivorous, subsisting on a diet of dead and decaying animal flesh (Blegvad, quoted in Yonge, 1954; Graham, 1955; Morton, 1958a; Fretter & Graham, 1962; and Martoja, 1964).

In addition to exhibiting the anatomical characteristics listed above, however, *Nassarius obsoletus* also possesses a crystalline style, and in apparent contrast to the other *Nassarius* species, *N. obsoletus* is clearly a deposit feeder. There can be very little doubt that in its natural habitat *N. obsoletus* receives almost all of its nutrition from the organic debris found within the mud and silt of the intertidal flats. This organic debris to the greatest extent consists of living unicellular algae, algal degradation products, and attendant micro-organisms.



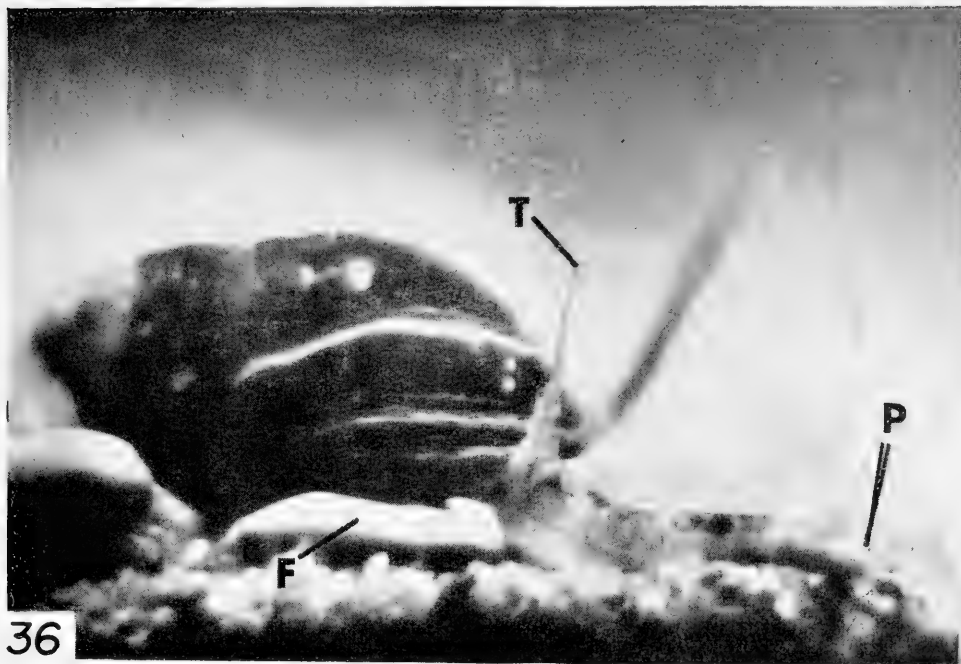


FIG. 36. *Nassarius obsoletus* with its proboscis greatly (but not completely) extended. This animal was preparing to feed on a piece of dead meat (out of camera range).

From Newell's (1964) study, it is apparent that certain deposit-feeding molluscs actually digest only the protein derived from the microbial coating on the silt and organic debris. In the two species of deposit-feeders studied (*Hydrobia ulvae* and *Macoma balthica*), the amount of ingested organic carbon (presumably derived from living unicellular algae and algal degradation products) was almost totally recoverable in the feces, while the organic nitrogen ingested (derived mainly from bacterial synthesis) was retained (and presumably metabolized) by the molluscs. Although experiments to determine carbon and nitrogen ingestion/egestion ratios have not yet been done for *N. obsoletus*, the author concurs with Scheltema (1964) that most probably the main nutritional component of the ingested material is the microfloral carbohydrate and not the bacterial pro-

tein. The presence of crystalline styles and concomitant absence of extracellular proteases within the stomachs of *N. obsoletus* on the mud flats argues strongly for this conclusion.

From the data presented in this study, we may attempt to describe *Nassa riu obsoletus*, although anatomically a carnivore, is able to handle a herbivorous (or more strictly an omnivorous) diet.

The present findings all point to the fact that intracellular digestion, either by migrating amoebocytes, or by cells of the midgut gland, does not occur to any significant extent. The evidence bearing on this point includes the observations that: (1) *Nassarius obsoletus* clearly lacks any efficient mechanism (ciliary or otherwise) to sort and separate particles according to size. Such a mechanism is obviously a prime requisite in view of the extreme variation in size range of the

ingested material. (2) There is no uptake by the midgut gland cells or amoebocytes of finely particulate material such as carmine or carborundum, nor is there any histological evidence of food vacuole formation in the midgut gland cells. (3) Acid phosphatase activity in the midgut gland cells is confined to the luminal border rather than having particulate localization in the more basal cytoplasm (which would be expected if phagocytosis, and hence lysosomal activity, occurred). (4) No histological evidence was observed of amoebocytes being within the lumen of the digestive tract or between the cells of the lining epithelium, nor did amoebocytes within the midgut gland haemocoel show a positive reaction in any of the histochemical procedures employed for the demonstration of hydrolytic enzymes.

On the other hand, data from the *in vitro* enzyme determinations reveal the presence of a variety of enzymes within the stomach lumen and in extracts of the crystalline style, thus strongly suggesting that extracellular digestion does indeed take place. The crystalline style itself contains several carbohydrate-splitting enzymes including  $\alpha$ -glucosidase,  $\beta$ -glucosidase, and polysaccharases capable of hydrolyzing starch and glycogen. The stomach fluid likewise contains enzymes like those of the crystalline style (and most probably derived from it) and, in addition, it has definite traces of glucosido-invertase,  $\alpha$ -galactosidase,  $\beta$ -galactosidase, and cellulase activity. These findings (along with the histochemical and/or *in vitro* demonstration of esterase, lipase, and  $\beta$ -glucuronidase activity within the midgut gland) offer strong evidence that the digestive system of *Nassarius obsoletus* has sufficient hydrolytic enzymes to digest and ultimately metabolize the algal constituents (such as structural polysaccharides and various esters and polymers of galactose and uronic acids) which form

the greatest proportion of its ingested food material (Fox, 1950; Black, 1954).

Extracellular protease activity (Table 5) was found in the stomach fluid of certain animals just taken from the field, the styles being absent from these animals. This fact, and the observation that snails which were maintained in the laboratory exclusively on a diet of meat invariably lacked styles and gastric shields, can best be explained following Yonge's (1930) reasoning that a proteinaceous crystalline style cannot co-exist with extracellular proteolytic enzymes without itself being subject to dissolution by enzymatic action. The presence of a style in a snail can be taken as clear evidence for the absence of extracellular proteases. Animals feeding on mudflats unquestionably ingest some animal tissues and micro-organisms as a matter of course; the presence of a style indicates, however, that they cannot be digesting these materials extracellularly. The ingestion of large quantities of animal flesh, such as occurs regularly during laboratory maintenance, or sporadically in nature, apparently elicits release of extracellular proteases which digest meat (as well as style) protein. The intriguing questions which arise here involve: (1) the apparent reciprocal relationship between the presence of a style versus the presence of extracellular proteases in the lumen of the stomach; and (2) the influence (control?) exercised over these by the type of food ingested.

The site of secretion of the enzymes found in the stomach fluid and crystalline style is not known with certainty. It seems probable, however, that the gland of Leiblein, midgut gland, and perhaps salivary gland are chiefly responsible for such enzyme production. In particular, the high tissue activities of protease,  $\alpha$ -glucosidase, and  $\beta$ -galactosidase found in the gland of Leiblein suggest that these enzymes are derived primarily from this source. Similarly, it seems not improb-

able that the midgut gland is the primary source of glucosido-invertase,  $\alpha$ -galactosidase, and the polysaccharases which act on starch and glycogen. As stated before, the origin of the cellulase activity is very much in doubt—a microbial origin, however, seems not unlikely.

The site of uptake of the digested food awaits final clarification from further studies. The presence in *Nassarius obsoletus* of microvilli along the luminal border of the columnar cells in the midgut gland agrees with the findings of Sumner (1966) who, by electron microscopy, demonstrated the presence of microvillar brush borders in the midgut gland cells of the pulmonate *Helix*. Sumner also showed the presence of pinocytotic vesicles and channels extending into the cytoplasm of the midgut gland cells. Terrestrial pulmonates such as *Helix* are macroherbivores in which extracellular digestion occurs in a thin-walled stomach and absorption of the soluble food material occurs in the midgut gland. It is not unlikely, therefore, that the midgut gland of *N. obsoletus* has a similar absorptive function.

The presence of phosphatases along the luminal borders of the midgut gland cells, as has been mentioned previously, is also indicative of metabolically active cell surfaces. There has been little evidence until recently that uptake of soluble digestive products in non-cephalopod molluscs occurs elsewhere than in the midgut gland tubules. Recent studies by Greer & Lawrence (1966) and Lawrence & Lawrence (1966) have shown, however, that isolated intestinal segments of the polyplacophoran *Cryptochiton stelleri* are able to actively transport basic and neutral amino acids and the monosaccharides D-glucose, 3-O-methyl glucose, and D-galactose. The results of these studies suggests that, for *C. stelleri* at least, the gut is of greater importance than the midgut gland in the uptake of soluble

digestive products. This may well prove to be true for many other molluscs, including *Nassarius obsoletus*.

Following conventional descriptions of dietary preference and digestive capability, one must classify *Nassarius obsoletus* as an omnivore. The omnivory practiced by *N. obsoletus*, however, is significantly different from that found in most other animals. Although it is capable of feeding on, and utilizing, both plant and animal materials, *N. obsoletus* apparently "commits" itself to one or the other, rather than feeding on and digesting both simultaneously. The "commitment" is to some degree forced upon it by circumstance. The presence of a style in typical mud flat snails indicates that no proteases are normally present in the lumen of the gut and hence even though some animal material is undoubtedly taken in, there are no extracellular enzymes present to digest it. Such an animal is functionally a total herbivore. On the other hand, when a piece of carrion is present on the mud flats, the snail shows a strong preference for this and will attack it to the exclusion of its normal fare. At such times both proteases and carbohydrases are present in the stomach, but due to the strong behavioral response, the snail has ensured that it will eat a meal of essentially pure meat. During this time the animal is functioning solely as a carnivore. It seems more accurate, therefore, to classify the snail as a *facultative herbivore/carnivore* rather than as an omnivore.

The adaptive value of such a digestive mechanism in a mud flat snail seems reasonably clear-cut. It permits utilization of the algal debris deposited at each receding tide and yet allows for the utilization of the occasional bit of carrion washed up on the flats. The origin of such a habit is more obscure. Presumably the ancestral stock could not compete in other regions with the more

efficient mesogastropod microherbivorous grazers such as *Littorina* or with the more specialized stenoglossan carnivores such as the whelks and drills. Its unique digestive mechanism has permitted evolutionary success in the mud flat habitat.

In conclusion, the data show that *Nassarius obsoletus*, although possessing the many structural modifications associated with a carnivorous mode of feeding and digestion, nevertheless has been able to utilize a primarily herbivorous diet. From the anatomical evidence alone, this appears to be a secondary adaptation derived from a principally carnivorous ancestry. There is nothing in the structure of *N. obsoletus* to suggest that it is an intermediate form of a basically herbivorous line which is in the process of "becoming" carnivorous. Physiologically, the presence of secreted hydrolytic enzymes and a functional crystalline style permits extracellular digestion of algal components—a situation necessitated by the absence of mechanisms for sorting particles according to size (a prerequisite for any significant amount of phagocytosis and intracellular digestion). The crystalline style of *Nassarius obsoletus*, apparently absent in the other *Nassarius* species, is likely a neomorphic addition. There is no evidence that any of the Buccinacea have evolved directly from any of the style-bearing mesogastropod groups, and furthermore it is thought not unlikely that styles have been evolved several times within the Mollusca (Robson, 1922; Yonge, 1932; and Morton, 1960).

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#### LITERATURE CITED

- ADAMS, C. W. M., 1957, A p-dimethylamino-benzaldehyde nitrite method for the histochemical demonstration of tryptophane and related compounds. *J. clin. Path.*, 10: 56–62.
- BARKA, T. & ANDERSON, P. J., 1963, *Histochemistry. Theory, Practice and Bibliography*. Harper & Row, New York, 660 p.
- BATCHELDER, C. H., 1915, Migration of *Ilyanassa obsoleta*, *Littorina litorea*, and *Littorina rudis*. *Nautilus*, 29: 43–46.
- BAUMANN, H. & PIGMAN, W. W., 1957, Naturally occurring glycosides and glycosidases. In: *The Carbohydrates*, (W. Pigman, ed.) Academic Press, New York, p 536–600.
- BAYLOR, E. R., 1958, The responses of snails to polarized light. *J. exp. Biol.*, 36: 369–376.
- BERG, W. E. & KATO, Y., 1959, Localization of polynucleotides in the egg of *Ilyanassa*. *Acta. Embr. Morph. Exp.*, 2: 227–233.
- BILLETT, F. & MCGEE-RUSSELL, S. M., 1955, The histochemical localization of  $\beta$ -glucuronidase in the digestive gland of the Roman Snail (*Helix pomatia*). *Quart. J. micros. Sci.*, 96: 35–48.
- BLACK, W. A. P., 1954, Constituents of the marine algae. *Ann. Rep. Chem. Soc., (Biochem.)*, 50: 322–335.
- BROCK, F., 1936, Suche, Aufnahme und enzymatische Spaltung der Nahrung durch die Wellhornschncke *Buccinum undatum*. *Zoologica*, 34: 1–136.
- BROWN, F. A., WEBB, H. M. & BRETT, W. J., 1959, Exogenous timing of solar and lunar periodism in metabolism of the mud snail *Ilyanassa (Nassarius) obsoletus* in the laboratory. *Gamma J. Med. Sci.*, 8: 233–242.
- BROWN, F. A., BENNETT, M. F. & WEBB,

- H. M., 1960, A magnetic compass response of an organism. *Biol. Bull.*, 119: 65-74.
- BURSTONE, M. S., 1955, An evaluation of histochemical methods for protein groups. *J. Histochem. Cytochem.*, 3: 32-49.
- CARR, W. E. S., 1967a, Chemoreception in the mud snail, *Nassarius obsoletus*. I. Properties of stimulatory substances extracted from shrimp. *Biol. Bull.*, 133: 90-105.
- CARR, W. E. S., 1967b, Chemoreception in the mud snail, *Nassarius obsoletus*. II. Identification of stimulatory substances. *Biol. Bull.*, 133: 106-127.
- CATHER, J. N., 1959, The effects of x-radiation on the early cleavage stages of the snail, *Ilyanassa obsoleta*. *Rad. Res.*, 11: 720-731.
- CATHER, J. N., 1963, A time schedule of the meiotic and early mitotic stages of *Ilyanassa*. *Caryologia*, 16: 663-670.
- CATHER, J. N., 1967, Cellular interactions in the development of the shell gland of the gastropod, *Ilyanassa*. *J. exp. Zool.*, 166: 205-224.
- CAVANAUGH, G. M., 1956, *Formulae and Methods*. IV ed., Marine Biol. Lab. Publ., Woods Hole.
- CLEMENT, A. C., 1952, Experimental studies on the germinal localization in *Ilyanassa*. I. The role of the polar lobe in the determination of the cleavage pattern and its influence on later development. *J. exp. Zool.*, 121: 593-626.
- CLEMENT, A. C., 1956, Experimental studies on the germinal localization in *Ilyanassa*. II. The development of isolated blastomeres. *J. exp. Zool.*, 132: 427-446.
- CLEMENT, A. C., 1960, Development of the *Ilyanassa* embryo after removal of the mesentoblast cell. *Biol. Bull.*, 119: 310.
- CLEMENT, A. C., 1962, Development of *Ilyanassa* following removal of the D macromere at successive cleavage stages. *J. exp. Zool.*, 149: 193-216.
- CLEMENT, A. C. & LEHMANN, F. E., 1956a, Über das Verteilungsmuster von Mitochondrien und Lipoidtropfen während der Furchung des Eies von *Ilyanassa obsoleta*. *Die Naturwiss.*, 20: 478-479.
- CLEMENTS, A. C. & LEHMANN, F. E., 1956b, The distribution of mitochondria and lipid droplets during early cleavage in *Ilyanassa obsoleta*. *Biol. Bull.*, 111: 300.
- CLEMENT, A. C. & TYLER, A., 1967, Protein-synthesizing activity of the anucleate polar lobe of the mud snail *Ilyanassa obsoleta*. *Sci.*, 158: 1457-1458.
- COLLIER, J. R., 1960, The localization of some phosphorus compounds in the egg of *Ilyanassa obsoleta*. *Exp. Cell Res.*, 21: 548-555.
- COLLIER, J. R., 1961, The effect of removing the polar lobe on the protein synthesis of the embryo of *Ilyanassa obsoleta*. *Acta Embr. Morph. Exp.*, 4: 70-76.
- COPELAND, M., 1918, The olfactory reactions and organs of the marine snails *Alectrion obsoleta* and *Busycon canaliculatum*. *J. exp. Zool.*, 25: 177-228.
- CRAMPTON, H. E., 1896, Experimental studies on gastropod development. *Arch. Entw. mech.*, 3: 1-19.
- DAHLQVIST, A., 1961, Determination of maltase and isomaltase activities with a glucose-oxidase reagent. *Biochem. J.*, 80: 547-551.
- DAN, K. & DAN, J. C., 1942, Behavior of the cell surface during cleavage. IV. Polar lobe formation and cleavage of the eggs of *Ilyanassa obsoleta* Say. *Cytologia*, 12: 246-261.
- de DUVE, C., 1959, Lysosomes, a new group of cytoplasmic particles. In: "Subcellular Particles," *Am. physiol. Soc.*, Wash., D.C. (T. Hayaishi, ed.) p 128-159.
- de DUVE, C. & WATTIAUX, R., 1966, Functions of lysosomes. *Ann. Rev. Physiol.*, 28: 435-492.
- DEMPSEY, E. W. & SINGER, M., 1946, Observations on the chemical cytology of the thyroid gland at different functional stages. *Endocrinology*, 38: 270-295.
- DIMON, A. C., 1905, The mud snail: *Nassa obsoleta*. *Cold Spring Harbor Monogr.*, 5: 1-48.
- DODGSON, K., LEWIS, J., & SPENCER, B., 1953, Studies on sulphatases. 3. The arylsulphatase and  $\beta$ -glucuronidase of marine molluscs. *Biochem. J.*, 55: 253-259.
- FISHER, F. M., 1964, The properties and specificity of a  $\beta$ -glucosidase from *Blaberus craniifer*. *Biol. Bull.*, 126: 220-234.
- FLORKIN, M. & LOZET, F., 1949, Origine bacterienne de la cellulase du contenu intestinal de l'Escargot. *Arch. Int. Physiol.*, 57: 201-207.
- FOX, D. L., 1950, Comparative metabolism of organic detritus by inshore animals. *Ecology*, 31: 100-108.
- FRAENKEL, G. S. & GUNN, D. L., 1940, *The Orientation of Animals*. Oxford Univ. Press, London 376 p.
- FRETTER, V. & GRAHAM, A., 1962, *British Prosobranch Molluscs*. The Ray Society, London, 755 p.
- FRUTON, J. S. & SIMMONDS, S., 1958, *General Biochemistry*. 2nd ed. John Wiley, New York, 1077 p.
- GOMORI, G., 1950, An improved histochemical technic for acid phosphatase. *Stain Tech.*, 25: 81-85.

- GOMORI, G., 1952, *Microscopic Histochemistry*. Univ. of Chicago Press, Chicago, 273 p.
- GOTTSCHALK, A., 1950,  $\alpha$ -D-Glucosidases. In: *The Enzymes*, 1st ed. (J. B. Sumner & K. Myrback, eds.) Academic Press, New York, p 551-582.
- GRAHAM, A., 1939, On the structure of the alimentary canal of style-bearing prosobranchs. *Proc. zool. Soc. Lond.*, 109: 75-112.
- GRAHAM, A., 1941, The oesophagus of stenoglossan prosobranchs. *Proc. Roy. Soc. Edin.*, 61: 1-23.
- GRAHAM, A., 1949, The molluscan stomach. *Trans. Roy. Soc. Edin.*, 61: 737-778.
- GRAHAM, A., 1955, Molluscan diets, *Proc. malac. Soc. Lond.*, 31: 144-159.
- GREER, M. L. & LAWRENCE, A. L., 1966, Active transport of amino acids by a marine invertebrate. *Amer. Zool.*, 6: 318-319.
- HALE, C. W., 1946, Histochemical demonstration of acid mucopolysaccharides in animal tissues. *Nature, Lond.*, 157: 802.
- HESS, R. & PEARSE, A. G. E., 1958, The histochemistry of indoxylesterase of rat kidney with special reference to its cathepsin-like activity. *British J. exp. Path.*, 39: 292-299.
- HIRSCH, G. C., 1915, Ernährungsbiologie fleischfressender Gastropoden (*Murex, Natica, Pterotrachea, Pleurobranchaea, Tritonium*). I Teil. Makroskopischer Bau, Nahrungsaufnahme, Verdauung, Sekretion. *Zool. Jb.*, (Abt. Physiol.), 35: 357-504.
- HOFSTEE, B. H. J., 1960, Fatty acid esterases of low eserin sensitivity and related enzymes. In: *The Enzymes*, 2nd ed. (P. Boyer, H. Lardy and K. Myrback, eds.) Academic Press, N.Y., p 485-498.
- HOLT, S. J., 1958, Indigogenic staining methods for esterases. In: *General Cytochemical Method*, Vol. 1 (J. F. Danielli, ed.) Academic Press, N.Y. p 375-398.
- HOLT, S. J. & WITHERS, R. F. J., 1952, Cytochemical localization of esterases using indoxyl derivatives. *Nature, Lond.*, 170: 1012-1014.
- HYMAN, L. H., 1967, *The invertebrates*, Vol. VI, McGraw Hill, New York, 792 p.
- JENNER, C. E., 1956a, A striking behavioral change leading to the formation of extensive aggregations in a population of *Nassarius obsoletus*. *Biol. Bull.*, 111: 291.
- JENNER, C. E., 1956b, The occurrence of the crystalline style in the mud snail *Nassarius obsoletus*. *Biol. Bull.*, 111: 304.
- JENNER, C. E., 1957, Schooling behavior in mud snails in Barnstable Harbor leading to the formation of massive aggregations at the completion of sexual reproduction. *Biol. Bull.*, 113: 328-329.
- JENNER, C. E., 1958, An attempted analysis of schooling behavior in the marine snail, *Nassarius obsoletus*. *Biol. Bull.*, 115: 337-338.
- JENNER, C. E. & CHAMBERLAIN, N. A., 1955, Seasonal resorption and restoration of the copulatory organ in the mud snail *Nassa obsoleta*. *Biol. Bull.*, 109: 347.
- LAWRENCE, A. L. & LAWRENCE, D. C., 1966, Active transport of monosaccharides by the intestine of the chiton, *Cryptochiton stelleri*. *Amer. Zool.*, 6: 319.
- LILLIE, R. D., 1965, *Histopathologic technic and practical histochemistry*. 3rd ed. The Blakiston Co., Inc., New York, 715 p.
- LOWRY, O. H., ROSEBROUGH, N. J., FARR, A. L. & RANDALL, R. J., 1951, Protein measurement with the folin phenol reagent. *J. biol. Chem.*, 193: 265-275.
- LUFT, J. H., 1961, Improvement in epoxy resin embedding methods. *J. Biophys. Biochem. Cytol.*, 9: 409-414.
- MANSOUR-BEK, J. J., 1934, Über die Proteolytischen Enzyme von *Murex anguliferus* Lam. *Z. Vergl. Physiol.*, 20: 343-369.
- MARTIN, W. E., 1938, Studies on trematodes of Woods Hole: I. The life cycle of *Lepocreadium setiferoides* (Miller and Northup), Allocreadiidae, and the description of *Cercaria cumin-giae*. *Biol. Bull.*, 75: 463-474.
- MARTIN, W. E., 1939, Studies on the trematodes of Woods Hole: II. The life cycle of *Stephanostomum tenue*. *Biol. Bull.*, 77: 65-73.
- MARTOJA, M., 1964, Contribution à l'étude de l'appareil digestif et de la digestion chez les gasteropodes carnivores de la famille des Nassarides. *Cellule*, 64: 237-334.
- McGEE-RUSSELL, S. M., 1958, Histochemical methods for calcium. *J. Histochem.*, 6: 22-42.
- MORGAN, T. H., 1933, The formation of the antipolar lobe in *Ilyanassa*. *J. exp. Zool.*, 64: 443-467.
- MORTON, J. E., 1952, The role of the crystalline style. *Proc. malacol. Soc. Lond.*, 29: 85-92.
- MORTON, J. E., 1958a, *Molluscs*. Hutchinson, London, 232 p.
- MORTON, J. E., 1958b, The habits of *Cycloper neritea*, a stylebearing stenoglossan gastropod. *Proc. malac. Soc. Lond.*, 34: 96-106.
- MORTON, J. E., 1960, Gut functions in ciliary feeders, *Biol. Revs.*, 35: 92-140.
- MOWRY, R. W., 1963, The special value of methods that color both acidic and vicinal hydroxyl groups in the histochemical study of mucins, with revised directions for the colloidal iron stain, the use of Alcian Blue 8GX and their combinations with the periodic acid

- Schiff reaction. *Ann. N.Y. Acad. Sci.*, 106: 402-423.
- MYRBACK, K., 1960, Invertases. In: *The Enzymes*, 2nd ed. (P. Boyer, H. Lardy & K. Myrback, eds.) Academic Press, New York, p 379-395.
- NACHLAS, M. M., CRAWFORD, D. T. & SELIGMAN, A. M., 1957, The histochemical demonstration of leucine aminopeptidase. *J. Histochem. Cytochem.*, 5: 264-278.
- NAGABHUSHANAM, R. & SAROJINI, R., 1965, Note on the effects of experimental desiccation on three molluscs from Virginia, *Nassarius obsoletus*, *Branchidontes recurvus*, *Mya arenaria*. *Sci. Cult.*, 31(5): 257.
- NEUBERG, C. & MANDL, I., 1950, Invertase In: *The Enzymes*, 1st ed. (J. B. Sumner & K. Myrback, eds.) Academic Press, New York p 527-550.
- NEWELL, R., 1965, The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. *Proc. zool. Soc. Lond.*, 144: 25-45.
- OWEN, G., 1966, Digestion. In: *Physiology of Mollusca*, Vol. II. (K. Wilbur & C. M. Yonge, eds.) Academic Press, New York, p 53-96.
- PAULSON, T. & SCHELTEMA, R., 1967, Selective feeding on algal cells by the veliger larvae of the gastropod *Nassarius obsoletus* (Say), *Amer. Zool.*, 7(4): 770-771.
- PEARSE, A. G. E., 1960, *Histochemistry, Theoretical and Applied*. 2nd ed., Little, Brown & Co., Boston, 998 p.
- PELSENEER, P., 1906, Mollusca. Part V. In: *A Treatise on Zoology*. (E. R. Lankester, ed.). Adam and Chas. Black, London, 355 p.
- PIGMAN, W. W., 1941, Action of almond emulsin on the phenyl glycosides of synthetic sugars and on  $\beta$ -thiophenyl-D-glucoside. *J. Res. Natl. Bur. Stds.*, 26: 197-204.
- PIGMAN, W. W., 1950, Cellulases, hemicellulases, and related enzymes. In: *The Enzymes*, 1st ed. (P. B. Sumner & K. Myrback, eds.) Academic Press, New York, p 725-739.
- PRINTZ, D. W., 1962, Effects of parasitism on certain tissues of *Nassarius obsoletus*. *J. Elisha Mitchell sci. Soc.*, 78: 90.
- PROSSER, C. L. & BROWN, F. A., 1961, *Comparative Animal Physiology*. 2nd ed. Saunders, Philadelphia, 688 p.
- RANKIN, J. S., 1940, Studies on the trematode family Microphallidae Travassos, 1921. IV. The life cycle and ecology of *Gynaecotyla nassicola*. *Biol. Bull.*, 79: 439-451.
- RICHARDSON, D., BERKOWITZ, S., & MOOG, F., 1955, The functional differentiation of the small intestine. V. The accumulation of non-specific esterase in the duodenum of chick embryos and hatched chicks. *J. exp. Zool.*, 130: 57-69.
- ROBSON, G. C., 1922, On the connection between the style sac and intestine in Gastropoda and Lamellibranchia. *Proc. malac. Soc. Lond.*, 15: 41-46.
- ROTHSTEIN, A., MEIER, R. & SCHAERF, T., 1953, The relationship of the cell surface to metabolism. IX. The digestion of phosphorylated compounds by enzymes located on the surface of the intestinal cell. *Am. J. Physiol.*, 173: 41-46.
- RUTENBURG, A. M., RUTENBURG, S. H., MONIS, B., TEAGUE, R., & SELIGMAN, A. M., 1958, Histochemical demonstration of  $\beta$ -D-galactosidase in the rat. *J. Histochem. Cytochem.*, 6: 122-129.
- SCHELTEMA, R. S., 1956, The effect of substrate on the length of planktonic existence in *Nassarius obsoletus*. *Biol. Bull.*, 111: 312.
- SCHELTEMA, R. S., 1961, Metamorphosis of the veliger larvae of *Nassarius obsoletus* in response to bottom sediment. *Biol. Bull.*, 120: 92-109.
- SCHELTEMA, R. S., 1962a, Pelagic larvae of New England intertidal gastropods, I. *Nassarius obsoletus* Say and *Nassarius vibex* Say. *Trans. Amer. microsc. Soc.*, 81: 1-11.
- SCHELTEMA, R. S., 1962b, Environmental factors affecting length of pelagic development in the gastropod *Nassarius obsoletus*. *Amer. Zool.*, 2: 445.
- SCHELTEMA, R. S., 1964, Feeding and growth in the mud snail, *Nassarius obsoletus*. *Chesapeake Sci.*, 5: 161-166.
- SCHELTEMA, R. S., 1965, Relationship of salinity to larval survival and development in *Nassarius obsoletus*. *Biol. Bull.*, 129: 340-353.
- SELIGMAN, A. M., TSOU, K-C., RUTENBURG, S. H., & COHEN, R. B., 1954, Histochemical demonstration of  $\beta$ -D-glucuronidase with a synthetic substrate. *J. Histochem. Cytochem.*, 2: 209-229.
- SELIGMAN, A. M. & NACHLAS, M. N., 1963, Lipase. In: *Methods of Enzymatic Analysis*. (H. Bergmeyer, ed.) Academic Press, New York, p 776-778.
- SINDERMANN, C. J., 1960, Ecological studies of marine dermatitis-producing schistosome larvae in northern New England. *Ecology*, 41: 678-684.
- SMITH, B. J., 1965, The secretions of the reproductive tract of the garden slug *Arion ater*. *Ann. N.Y. Acad. Sci.*, 118: 997-1014.

- STEEDMAN, H. F., 1950, Alcian Blue 8GS. A new stain for mucin. *Quart. J. microsc. Sci.*, 91: 477-479.
- STEPHENS, G. C., SANDEEN, M. I. & WEBB, H. M., 1953, A persistent tidal rhythm of activity in the mud snail *Nassa obsoleta*. *Anat. Rec.*, 117: 635.
- STONE, B. A. & MORTON, J. E., 1959, The distribution of cellulases and related enzymes in the Mollusca. *Proc. malac. Soc. Lond.*, 33: 127-141.
- STUNKARD, H. W., 1938a, The morphology and life cycle of the trematode *Himastha quissetensis*. *Biol. Bull.*, 75: 145-164.
- STUNKARD, H. W., 1938b, *Distomum lasium* Leidy, 1891 (Syn. *Cercariaeum lintoni* Miller and Northup, 1926), the larval stage of *Zoogonus rubellus* (Olsson, 1898). *Biol. Bull.*, 75: 308-334.
- STUNKARD, H. W., 1961, *Cercaria dipteroerca* Miller and Northup, 1926 and *Stephanostomum dentatum* (Linton, 1900) Manter, 1931. *Biol. Bull.*, 120: 221-237.
- STUNKARD, H. W. & HINCHLIFFE, H. B., 1952, The morphology and life history of *Microbilharzia variglandis* (Miller and Northup, 1926). *J. Parasitol.*, 38: 248-265.
- SUMNER, A. T., 1965, The cytology and histochemistry of the digestive gland cells of *Helix*. *Quart. J. microsc. Soc.*, 106: 173-191.
- SUMNER, A. T., 1966, The fine structure of digestive gland cells of *Helix*, *Succinea*, and *Testacella*. *J. Roy. microsc. Soc.*, 85: 181-192.
- TALLAN, H., JONES, M. & FRUTON, J. S., 1952, On the proteolytic enzymes of animal tissues. X. Beef spleen Cathepsin C. *J. biol. Chem.*, 194: 793-805.
- VEIBEL, S., 1950,  $\beta$ -Glucosidase. In: *The Enzymes*, 1st. ed. (P. B. Sumner & K. Myrback, eds.) Academic Press, New York, p 584-618.
- WEICHELBAUM, T. E. & SOMOGYI, M., 1941, A method for the determination of small amounts of ketone bodies. *J. biol. Chem.*, 140: 5-20.
- WILBUR, K. & YONGE, C. M., 1964, *Physiology of Mollusca*, Vol. I, Academic Press, New York, 473 p.
- WU, S. K., 1965, Comparative functional studies of the digestive system of the muricid gastropods *Drupa ricina* and *Morula granulata*. *Malacologia*, 3: 211-234.
- YONGE, C. M., 1930, The crystalline style of the Mollusca and a carnivorous habit cannot normally coexist. *Nature*, Lond., 125: 444-445.
- YONGE, C. M., 1932, Notes on feeding and digestion in *Pterocera* and *Vermetus*, with a discussion on the occurrence of the crystalline style in the Gastropoda. *Sci. Rep. Gt. Barrier Reef Exped.*, 1: 259-281.
- YONGE, C. M., 1954, Physiological anatomy of the alimentary canal in invertebrates. *Tabul. biol.*, Hague, 21(20): 1-24.

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## RESUME

### LA STRUCTURE ET LE FONCTIONNEMENT DE L'APPAREIL DIGESTIF DE LA NASSE, *NASSARIUS OBSOLETUS* (SAY)

S. C. Brown

La nasse des côtes américaines atlantiques, *Nassarius obsoletus* (Say) est un représentant des Gastropodes rachiglosses, typiquement carnivores. Dans la nature, cependant, *N. obsoletus* est un mangeur de détritus non sélectif, se nourrissant presque exclusivement par ingestion de sable et de boue. La présente étude a été entreprise pour clarifier le mécanisme du fonctionnement de l'appareil digestif de l'animal.

Des études anatomiques et histologiques indiquent que *Nassarius obsoletus* a toutes les modifications structurales associées à l'acquisition d'un mode de vie carnivore. Ces modifications comprennent: un proboscis allongé et extensible; une dentition radulaire rachidienne, un long siphon mobile et une osphradie bipectinée; un pharynx de Leiblein, une glande de Leiblein et des glandes salivaires bien développées; un estomac simple possédant un bouclier gastrique très réduit; pas d'airs de triage ciliés réellement efficaces; et des couches musculaires entourant le tube digestif fortement développées. En contraste avec ces caractéristiques clairement carnivores *N. obsoletus* possède un stylet cristallin mucoprotéique dans son estomac: c'est là un fait en relation avec une adaptation structurale à un régime herbivore. Des études histochimiques montrent que la glande digestive contient des enzymes capables de fractionner les esters et les glucuronides et donc de métaboliser quelques uns des principaux constituants des algues. Des



expériences de nutrition portant sur l'utilisation de matériel finement divisé en particules et sur la localisation de l'activité des phosphatases, montrent conjointement qu'il n'existe ni phagocytose, ni digestion intracellulaire. *In vitro* les analyses enzymatiques de tissus provenant des divers organes digestifs, révèlent la présence d'estérase lipase,  $\alpha$ -amylase, protéase et de plusieurs disaccharases. Des analyses du suc gastrique et du stylet cristallin révèlent, de façon similaire, la présence d'enzymes extracellulaires à l'intérieur de la lumière de l'estomac. Au cours d'examen des modes de nutrition et du comportement, il est apparu avec évidence que, physiologiquement, le stylet cristallin aide la digestion et qu'on doit par conséquent le considérer comme vraiment fonctionnel plutôt que comme un simple reste du cordon fécal muqueux.

Selon les données présentées, on en conclut que *Nassarius obsoletus*, bien que possédant structurellement toutes les caractéristiques d'un carnivore rachidien typique, est cependant capable de subsister presque entièrement avec un régime de détritus d'algues; qu'il possède les enzymes hydrolysantes nécessaires pour attaquer les principaux constituants des algues; que le début de l'hydrolyse est extra-cellulaire; que la phagocytose et la digestion intra-cellulaire n'ont pas lieu et que l'absorption des produits solubles de digestion a probablement lieu dans la glande digestive ou au niveau de l'épithélium qui sépare l'estomac de l'intestin.

A. L.

## RESUMEN

### ESTRUCTURA Y FUNCION DEL SISTEMA DIGESTIVO EN EL CARACOL DEL BARRO, *NASSARIUS OBSOLETUS* (SAY)

S. C. Brown

El caracol que habita los barros de la costa del Atlántico de Estados Unidos, *Nassarius obsoletus* (Say), pertenece al grupo de los gastrópodos raquiglosos típicamente carnívoros; sin embargo, no selecciona su alimento y subsiste enteramente ingiriendo arena y barro. Este estudio aclara el mecanismo, y función, del sistema digestivo.

Estudios anatómicos e histológicos indican que *Nassarius obsoletus* tiene todas las modificaciones estructurales asociadas con una existencia carnívora. Estas modificaciones incluyen: proboscis alargada; rádula raquiglosa; sifón alargado y móvil y un osfradio pectinado; válvula de Leiblein bien desarrollada y glándulas salivares; estómago simplificado con un escudo gástrico reducido; áreas de selección ciliar no eficientes y tejido muscular bien desarrollado alrededor del canal alimenticio. En contraste con estas características tan claramente carnívoras, posee en el estómago un estilete cristalino mucoproteico—asociado con la adaptación estructural para una dieta herbívora. Estudios histoquímicos indican que el intestino medio contiene enzimas capaces de desdoblar esterasa y glucoronidos, para metabolizar algunos de los constituyentes principales de las algas. Experimentos en nutrición, usando materiales finamente divididos y localización histoquímica de fosfatasa, indicaron que tanto la fagocitosis como la digestión intracelular no tienen lugar. Enzimas *in vitro* de tejidos de los diferentes órganos digestivos revelan la presencia de esterasa, lipasa, amilasa, proteasa y varios disacáridos. Análisis del fluido estomacal y estilete cristalino, ambos revelaron la presencia de enzimas hidrolíticas extracelularmente dentro del lumen del estómago. La revisión de los hábitos alimenticios se presenta junto con la evidencia fisiológica de que el estilete cristalino ayuda en el proceso digestivo y es verdaderamente funcional, en vez de ser un remanente de la mucosa fecal.

En conclusión, aunque *Nassarius obsoletus* posee todas las condiciones típicas de un carnívoro es, sin embargo, capaz de subsistir casi completamente de una dieta de detritos de algas; produce enzimas hidrolíticas para desdoblar los principales constituyentes de las algas; el desdoblamiento inicial se produce extracelularmente; no hay caso de fagocitosis o digestión intracelular, y la absorción de los productos solubles de digestión ocurre probablemente en la glándula del intestino medio o en el revestimiento del estómago-intestino.

J. J. P.

## АБСТРАКТ

СТРУКТУРА И ФУНКЦИЯ ПИЩЕВАРИТЕЛЬНОЙ СИСТЕМЫ ИЛОВОГО  
МОЛЛЮСКА *NASSARIUS OBSOLETUS* (SAY)

С. С. БРОУН

Иловая улитка американского атлантического побережья *Nassarius obsoletus* (Say) является представителем типичных хищных моллюсков из рахиглосных *Gastropoda*. В природе, однако, *N. obsoletus* является безвыборочно-заглатывающим донные осадки: ил и песок. Настоящее исследование было предпринято для выяснения механизма работы пищеварительной системы этого моллюска.

Анатомическое и гистологическое исследование показывают, что *N. obsoletus* имеет все структурные модификации, связанные с предположительно хищным образом жизни, это: удлинённый вытягивающийся хобот, радула с рахиглосными зубчиками, удлинённый подвижный сифон и двугребенчатый осфорадум; хорошо развитый клапан и железа Лебейна и слюнные железы; просто устроенный желудок с сильно редуцированным гастрическим щитком; отсутствие хорошо развитой ресничной области; хорошо развитые мускульные слои, окружающие пищеварительный тракт.

В противоположность этим признакам хищного образа питания, *N. obsoletus* обладает в желудке мукопротеиновым кристаллическим стебельком, т.е. органом, связанным с адаптацией к растительноядному типу питания. Гистохимическое изучение показывает, что железа средней кишки содержит энзимы, способные расщеплять эстеры, глюкорониды и таким образом усваивать основные компоненты водорослей. Опыты по питанию, когда употреблялись тонко растёртые частицы пищи, а также гистохимическая локализация активности фосфатазы показали, что фагоцитоз и внутриклеточное переваривание не имеет места.

Энзимовый анализ гомогената тканей *in vitro*, взятых из различных пищеварительных органов, указывает на наличие эстеразы,  $\alpha$ -амилазы, протеазы и некоторых дисахараз. Анализ желудочного сока и кристаллического стебелька сходным образом показал наличие экстрацеллюлярных гидролитических энзимов внутри желудка. Образ питания и поведения моллюсков, наряду с физиологическими данными, указывает, что кристаллический стебелек помогает процессу пищеварения и является истинно функциональным, а не остатком слизистого фекального тяжа.

Из полученных данных видно, что *Nassarius obsoletus*, хотя и обладает всеми структурными признаками типичного хищника из рахидоглосных гастропод, тем не менее может существовать почти целиком на водорослевом детрите. Он обладает гидролитическими энзимами, необходимыми для расщепления основных компонентов водорослей. Первичное расщепление происходит внеклеточно. Фагоцитоз и внутриклеточное переваривание не наблюдаются. Всасывание растворённых пищевых веществ может встречаться наиболее вероятно в средней кишке или в эпителии, выстилающем внутренность желудка.

ISOENZYMES OF ALKALINE PHOSPHATASE IN *ANODONTA GRANDIS* (BIVALVIA: UNIONIDAE) DURING SHELL REGENERATION<sup>1</sup>

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ABSTRACT

The isoenzymes of alkaline phosphatase of the freshwater mussel *Anodonta grandis* Say have been separated electrophoretically on cellulose acetate strips. In normal specimens 3 isoenzymes were detected in the mantle, the digestive diverticula and the kidney each. In specimens part of whose shells had been removed an additional band appeared in the mantle.

The total enzyme activity was estimated in all 3 tissues of normal specimens and was greatest in the kidney. During shell regeneration increase of the enzyme in the mantle was twofold whereas that in the digestive diverticula was only slight. From histological evidence, the digestive diverticula and the stomach seem the probable sources of enzyme increase in the mantle, though the kidney should not be excluded.

INTRODUCTION

The diverse sites of alkaline phosphatase activity in vertebrate and invertebrate tissues indicate that this enzyme may be important in several different functions. The enzyme has been implicated in the secretion of protein fibres, synthesis of mucoproteins, ossification and cellular differentiation. Alkaline phosphatase is among the many enzymes which occur in multimolecular forms, *i.e.*, as isoenzymes. The number has been varyingly reported as 3 (Keiding, 1959), 4 (Chiandussi, Green & Sherlock, 1962), 8 (Taswell & Jeffers, 1963) and 16 (Boyer, 1961).

Information about the isoenzymes of alkaline phosphatase in molluscs is very scanty. Norris & Morrill (1964) electrophoretically separated 4 isoenzymes from the digestive diverticula (liver) and 2 from the mantle of *Lymnaea palustris*.

In the developing embryo of *Ilyanassa obsoleta*, Morrill & Norris (1965) found 1 band which appeared on the 7th day.

Alkaline phosphatase has been associated directly or indirectly with molluscan shell formation. Increase of enzyme activity has been recorded during shell regeneration in *Helix* (Manigault, 1939; Wagge, 1951). After removal of a piece of shell, I found a great increase of this enzyme in the mantle of *Anodonta* in the vicinity only of the shell injury (Saleuddin, 1967). However, no quantitative estimation of the amount present in the tissues of either normal or injured specimens were then made. In the present investigation an attempt has been made to quantitatively determine enzyme activity in the digestive diverticula and in the mantle with and without shell injuries: enzymic assay with kidney tissue was done using only normal specimens. Isoenzymes of alkaline phosphatase have

<sup>1</sup> This work was carried out during the tenure of a post-doctorate fellowship from the National Research Council of Canada.

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been separated electrophoretically on cellulose acetate membranes and the changes brought about by shell injuries in the number and relative concentration of isoenzymes have been recorded.

### MATERIALS AND METHODS

Specimens of *Anodonta grandis* were collected from Lake Wabamun, 45 miles west of Edmonton, Alberta, Canada, and maintained in running water at 15°C. Shell regeneration was induced by removing about 25 sq. mm of shell from the ventral edge of the left valve with an electric saw. Care was taken so as not to injure the underlying mantle. Tissues were removed 1, 4 and 8 days after shell injury. Tissue homogenates of the mantle, digestive diverticula and kidney were prepared in the following manner. Fresh tissues were frozen quickly in an acetone-dry ice mixture. They were then removed and pulverized while frozen, suspended in 0.6M sucrose solution (1 ml of sucrose solution per 600 mg of tissue) and homogenized. In order to activate the release of bound enzyme, n-butanol was added to the homogenate in the proportion of 1:10 by volume. The mixture was stirred for 10 minutes and then centrifuged at 13,000 X g for 10 minutes. The butanol was removed from the top of the supernatant by suction and the rest of the supernatant was stored at -20°C until needed. During this entire process the temperature was not allowed to rise above 4°C.

Electrophoresis was carried out on cellulose acetate strips using a Beckman Microzone Model R-101 apparatus. Barbitol buffer of pH 8.6 and ionic strength 0.05 was used. Samples of 0.5  $\mu$ l of homogenate were applied to the middle of the membrane and run for 1 1/2 hr at 250 volts at an ambient temperature of 4°C. The strip was then fixed in absolute ethanol for 1-2 minutes. Excess

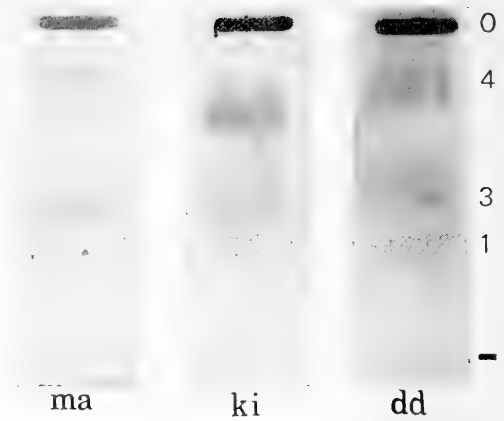
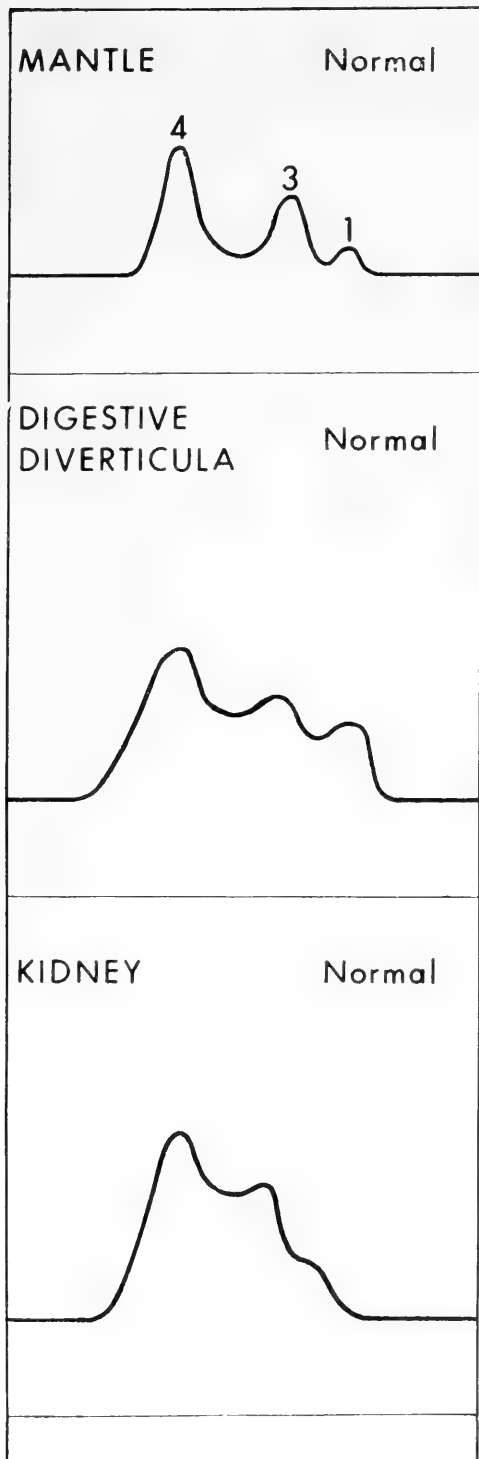


FIG. 1. Electrophoretic separation of isoenzymes of alkaline phosphatase from tissue extracts of uninjured *Anodonta grandis* on cellulose acetate strips. ma, mantle; ki, kidney; dd, digestive diverticula, o=origin, —=cathode, 1, 3, 4, =stained isoenzymes.

ethanol was removed by draining, and the strip was stained for alkaline phosphatase for 1 hour, following the staining procedure of Burstone (1958). The staining solution was prepared by first mixing thoroughly 1 ml N-N-dimethylformamide and 20 mg naphthol phosphate AS-TR. To this mixture 100 ml of tris buffer, pH 8.3, and 50 mg of Fast Red TR (5-chloro-o-toluidine) were added. The solution was filtered and 2 or 3 crystals of  $MgCl_2$  were added to the filtrate. After staining and drying, the optical density of the strip was scanned with a densitometer (model 525 of Photovolt Corporation, New York).

The method of Klein, Read & Babson (1960) was followed for the quantitative assay of alkaline phosphatase. This method has been elaborated by Warner-Chilcott Laboratories, Morris Plains, N.J. A volume of 0.2 ml homogenate was incubated for 30 minutes at 37°C with sodium phenolphthalein phosphate in tris buffer of pH 9.6. Micrograms of phenolphthalein liberated were read at 550  $m\mu$  with a Bausch and Lomb Spectronic



20 colorimeter, and were converted into King-Armstrong units by using a conversion table (Bulletin of Warner-Chilcott for colorimetric assay of alkaline phosphatase).

## RESULTS

In normal specimens of *Anodonta grandis* 3 isoenzymes of alkaline phosphatase represented by 3 distinct bands (1, 3, 4, Figs. 1, 2) were present in the mantle, digestive diverticula and kidney each. All migrated toward the cathode. In all 3 tissues, band 4 was the most prominent but showed a slight difference in electrophoretic mobility. Bands 1 and 3, however, showed similar migration in all tissue extracts (Figs. 1 and 2).

The total enzyme activity in the mantle, digestive diverticula and kidney of normal mussels are 13, 28 and 33 King-Armstrong units respectively (Table 1).

In regenerating specimens the change in enzyme has been followed in the mantle and digestive diverticula only. The isoenzyme patterns, during regeneration are shown in Fig. 2. After 24 hours, bands 1 and 4 of the mantle increase in prominence while 3 remains unchanged. Band 2 which appeared close to band 1 became indistinguishable at 4 days for reasons unknown, only to reappear on the 8th day of regeneration. The isoenzymes of the digestive diverticula showed only a slight increase in intensity during shell regeneration.

In regenerating mussels the total enzyme activity in the mantle tissue increased more than twofold at 24 hours, showed further increase at 4 days, and had returned toward normal at 8 days. In the digestive diverticula enzyme activity did not change markedly (Table 1).

FIG. 2. Densitometric tracings of electrophoretic pattern shown in Fig. 1. Peaks of curves correspond to bands.

TABLE 1. Total alkaline phosphatase found in 3 organs of *Anodonta grandis* with and without shell injuries, expressed in King-Armstrong units. The figures represent average values followed by standard deviations.

TISSUES	Normal	After injury		
		24 hrs.	4 days	8 days
Mantle	13±0·669	32±1·53	35±1·417	17±0·816
Digestive diverticula	28±0·816	34±1·635	30±1·532	28±1·052
Kidney	33±0·823	—	—	—

—Not measured.

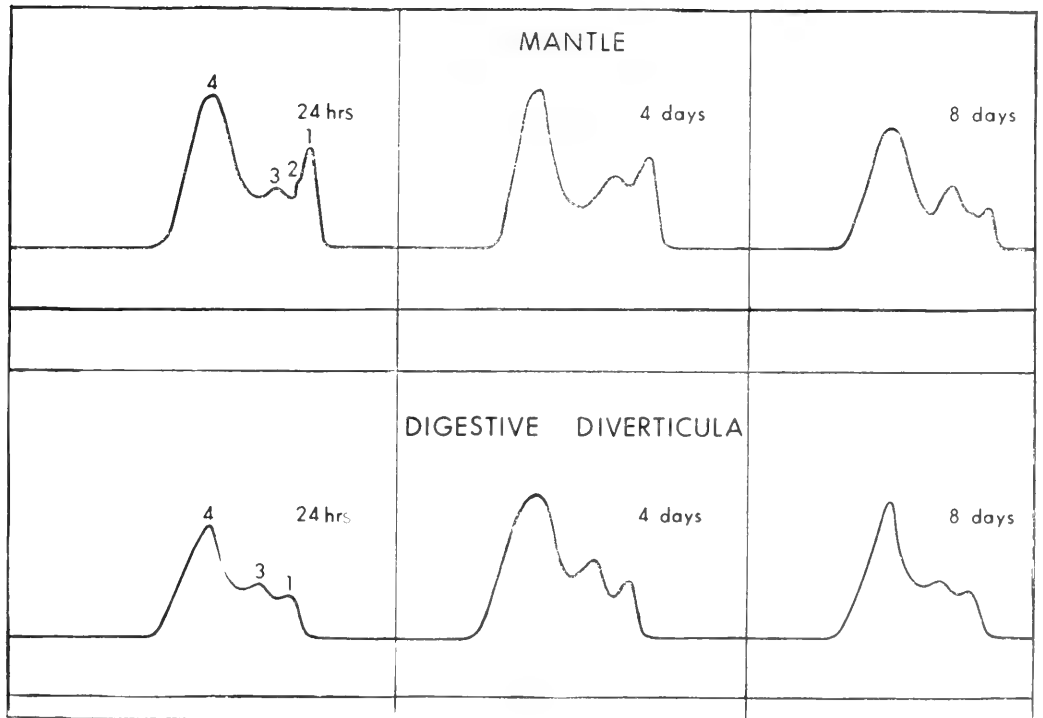
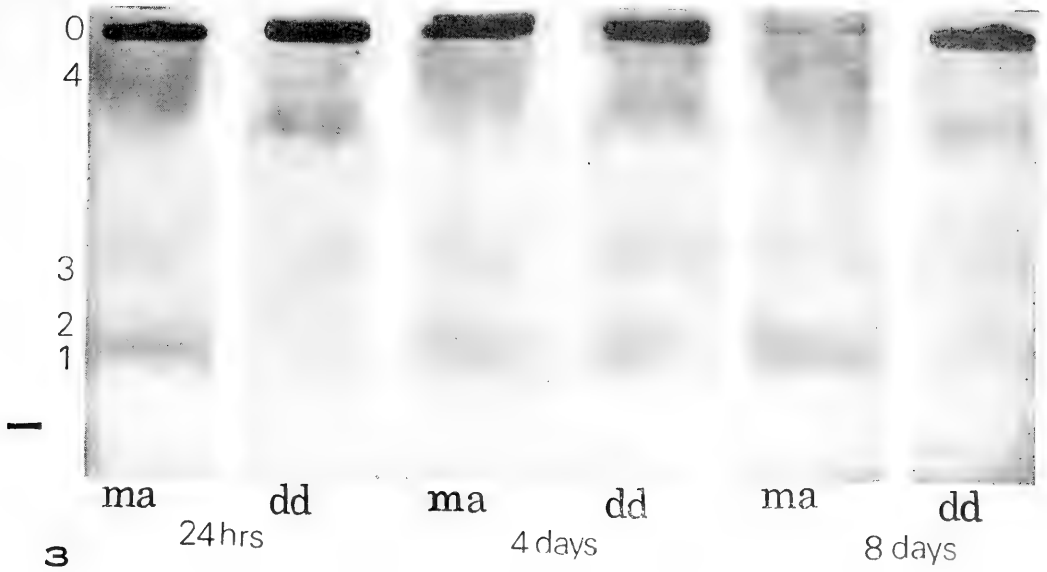
### DISCUSSION

The isoenzymes of alkaline phosphatase in the mantle, digestive diverticula and kidney of *Anodonta grandis* moved toward the cathode. However the direction of the movement can be changed by changing buffer pH and ionic strength or by changing placement of the sample on the strip. Latner & Raine (1962) reported that the positions of the isoenzymes of human serum alkaline phosphatase in relation to major serum proteins can be altered by using a discontinuous buffer system.

The number of isoenzymes in all 3 tissues of *Anodonta* was 3, whereas Norris & Morrill (1964), using *Lymnaea palustris*, found 4 in the digestive diverticula (liver) and 2 in the mantle. In the embryo of *Ilyanassa obsoleta*, Morrill & Norris (1965) found 1 band; they did not mention adult tissues. During the shell regeneration of *Anodonta*, an additional band appeared in the mantle within 24 hours. Haije & de Jong (referred to by Wilkinson, 1966) found that an additional alkaline phosphatase isoenzyme appeared in human serum when the intestine was damaged by radiation.

When a piece of shell is removed from *Anodonta*, the regenerating area is covered

by a thin organic layer within 24 hours, but calcification is not observed until 8 days after shell injury (Saleuddin, 1967). Alkaline phosphatase has been reported in tissues such as mantle and bone, involved in calcification. Neuman, Distefeno & Mulryan (1951) proposed the theory that this enzyme may aid calcification by removing the crystal poisons or inhibitors which would otherwise interrupt the growth of crystals. In reviewing this theory, Simkiss (1964) was unable to draw definite conclusions in that alkaline phosphatase does remove crystal poisons by hydrolysis but some products of hydrolysis, such as orthophosphate, inhibit calcification. In *A. grandis* the increase of enzyme in the mantle of injured specimens does not correspond to the period of calcification, but to the elaboration of the organic layer when calcium deposition is not yet taking place. The enzyme increase in the mantle is much greater than that observed in the digestive diverticula (Table 1). The sources of this increase are probably the main ducts of the digestive diverticula and the stomach. Both histological and histochemical evidence seem to support this view: there is an increase of the enzyme activity in the brush border area of the main ducts of the digestive diverticula 24 hours after



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FIG. 3. Electrophoretic separation of isoenzymes of alkaline phosphatase from tissue extracts of *Anodonta grandis* at various times during shell regeneration. ma, mantle; dd, digestive diverticula; o, origin; — =cathode. Note the appearance of band 2 in mantle only.

FIG. 4. Densitometric tracings of electrophoretic patterns shown in Fig. 3.

shell injury. This increase is accompanied by aggregation of blood cells staining positively for alkaline phosphatase in the blood spaces of the digestive diverticula. A similar situation is also observed in the vicinity of the stomach. These blood cells are presumably taking active part in transporting the enzyme to the mantle, since a marked increase in the number of such positively staining blood cells has also been observed in the mantle. If we accept the digestive diverticula as the main source for the increase of enzyme in the mantle during regeneration one would expect identical electrophoretic migration of the isoenzymes in these 2 tissues; but this is not the case (Figs. 3 & 4). It might be that the enzyme is altered when released for the digestive diverticula and during the transportation to the mantle. Examples of such alterations are known. Keiding (1964) mentions that the transformation of human  $\beta_2$  lymph phosphatase into  $\alpha_1$  bile phosphatase is probable. Butterworth, *et al.* (1965), while working on urine phosphatase, found that the enzyme fraction from urine moved faster than that from the kidney and suggested that the enzyme is altered in urine after release from the kidney. Nevertheless, the kidney and intestine of *Anodonta* should not be excluded as possible sources for the increase of enzyme in the mantle during shell regeneration.

#### LITERATURE CITED

- BOYER, S. H., 1961, Alkaline phosphatase in human sera and placentae. *Science*, **134**: 1002-1004.
- BURSTONE, M. S., 1958, Histochemical comparison of naphthol-AS-phosphates for the demonstration of phosphatases. *J. Natl. Cancer Inst.*, **20**: 601-616.
- BUTTERWORTH, P. J., MOSS, D. W., PITKANEN, E. & PRINGLE, A., 1965, Some characteristics of alkaline phosphatase in human urine. *Clin. Chim. Acta*, **11**: 220-226.
- CHIANDUSSI, L., GREEN, S. F. & SHERLOCK, S., 1962, Serum alkaline phosphatase fractions in hepato-biliary and bone diseases. *Clin. Sci.*, **22**: 425-434.
- HODSON, A. W., LATNER, A. L. & RAINE, L., 1962, Isoenzymes of alkaline phosphatase. *Clin. Chim. Acta*, **7**: 255-261.
- KEIDING, N. R., 1959, Differentiation into three fractions of the serum alkaline phosphatase and the behaviour of the fractions in diseases of bone and liver. *Scand. J. clin. Lab. Invest.*, **11**: 106-112.
- 1964, The alkaline phosphatase fractions of human lymph. *Clin. Sci.*, **26**: 291-297.
- KLEIN, B., READ, P. A. & BABSON, A. L., 1960, Rapid method for the quantitative determination of serum alkaline phosphatase. *Clin. Chem.*, **6**: 269-275.
- MANIGAULT, P., 1939, Recherches sur le calcaire chez les mollusques. Phosphatase et précipitation calcique. *Histochimie du calcium. Ann. Inst. oceanogr.*, **18**: 331-426.
- MORRIL, J. B. & NORRIS, E., 1965, Electrophoretic analysis of the hydrolytic enzymes in the *Ilyanassa* embryo. *Acta Embryol. Morphol. exp.*, **8**: 232-238.
- NEUMAN, W. F., DISTEFANO, V. & MULRYAN, B. J., 1951, The surface chemistry of bone. III. Observations on the role of phosphatase. *J. biol. Chem.*, **193**: 227-235.
- NORRIS, E. & MORRIL, J. B., 1964, An electrophoretic analysis of hydrolytic enzymes in adult organs and developing embryo of *Limnaea palustris*. *Acta Embryol. Morphol. exp.*, **7**: 29-41.
- SALEUDDIN, A. S. M., 1967, The histochemistry of the mantle during the early stage of the repair of the shell. *Proc. malac. Soc. Lond.*, **37**: 371-380.
- SIMKISS, K., 1964, Phosphates as crystal poisons of calcification. *Biol. Rev.*, **39**: 487-505.
- TASWELL, H. F. & JEFFERS, M. T., 1963, Isoenzymes of serum alkaline phosphatase in hepatobiliary and skeletal diseases. *Amer. J. Clin. Path.*, **40**: 349-356.
- WAGGE, L. E., 1951, The activity of amoebocytes and of alkaline phosphatases during the regeneration of the shell in the snail *Helix aspersa*. *Quart. J. micr. Sci.*, **92**: 307-321.
- WILKINSON, J. H., 1966, *Isoenzymes*. J. P. Lippincott, Philadelphia.



## RESUME

ISOENZYMES DE LA PHOSPHATASE ALCALINE CHEZ *ANODONTA GRANDIS* (BIVALVIA: UNIONIDAE)

A. S. M. Saleuddin

Les isoenzymes de la phosphatase alcaline du bivalve d'eau douce *Anodonta grandis* Say ont été séparées par électrophorèse sur bandes d'acétate de cellulose. Chez les exemplaires normaux, 3 isoenzymes ont été détectées dans le manteau, les diverticules digestifs et le rein. Chez les exemplaires dont les coquilles avaient été enlevées, une bande supplémentaire est apparue pour le manteau.

L'activité enzymatique totale a été testée pour les trois tissus sur des individus normaux et s'est montrée plus importante dans le rein. Pendant la régénération de la coquille, l'augmentation d'enzyme dans le manteau a été double, tandis que dans les diverticules digestifs l'augmentation a été faible. Si l'on s'en réfère à l'histologie, les diverticules digestifs et l'estomac semblent être les sources probables de l'augmentation d'enzyme dans le manteau, bien que le rein ne doive pas être exclu.

A. L.

## RESUMEN

ISOENZIMAS DE FOSFATASA ALCALINA EN *ANODONTA GRANDIS* (BIVALVIA: UNIONIDAE) DURANTE LA REGENERACION DE LA CONCHA

A. S. M. Saleuddin

Las isoenzimas del epígrafe en la almeja de agua dulce *Anodonta grandis* fueron separadas electroforéticamente en tiras de acetato de celulosa. En ejemplares normales se detectaron 3 isoenzimas en el manto, divertículos digestivos y riñones; en otros, parte de cuyas conchillas fueron quitadas, una banda adicional apareció en el manto.

La actividad enzimática total se calculó en los tres tejidos de ejemplares normales y fué mayor en los riñones. Durante regeneración de la concha, la cantidad de enzima en el manto fué doble, mientras que en los divertículos digestivos aumentó poco. Hay evidencia histológica de que esos divertículos, y el estómago, puedan ser las fuentes principales de aumento enzimático en el manto, aunque el riñón no debe excluirse de esta consideración.

J. J. P.

## АБСТРАКТ

ИЗОЭНЗИМЫ ЩЕЛОЧНОЙ ФОСФАТАЗЫ У *ANODONTA GRANDIS*  
(*BIVALVIA: UNIONIDAE*) ВО ВРЕМЯ РЕГЕНЕРАЦИИ РАКОВИНЫ

А. С. САЛЕУДДИН

Изоэнзимы щелочной фосфатазы у пресноводного моллюска *Anodonta grandis* Say были выделены электрофоретически на целлюлозную ацетатную ленту. У обычных экземпляров моллюсков были обнаружены 3 изоэнзима: в мантии, в пищеварительной дивертикуле и в почке. У тех экземпляров, у которых раковина была удалена, в мантии были обнаружены они добавочно.

Общая активность энзимов была определена во всех трех тканях нормальных экземпляров моллюсков и наиболее высокой была в почке. Во время регенерации раковины количество энзимов в мантии возрастало в 2 раза, в то время, как в пищеварительной дивертикуле оно увеличивалось лишь слабо.

Судя по гистологическим данным, пищеварительная дивертикула, желудок, а возможно, и почка, являются вероятным источником увеличения энзимов в мантии.

## INDEX TO SCIENTIFIC NAMES

- aciculata*, *Ocenebra*, 384  
*Acteon*, 421  
*adunca*, *Crepidula*, 376  
*Aeolidia*, 422  
     *papillosa*, 422  
*Agriolimax*, 391, 92, 94, 95, 97-99  
     *reticulatus*, 391, 92, 94, 95, 97-99  
*alba*, *Gymnodoris*, 438  
*albopunctata*, *Doriopsilla*, 435  
*albopustulosa*, *Chronodoris*, 423  
*alderi*, *Eolidina*, 422  
*amplecta*, *Lymnaea*, 313, 17, 19, 21  
*Anodonta*, 501-06  
     *grandis*, 501-05  
*apiculata*, *Halgerda*, 423  
*appressa*, *Lymnaea stagnalis*, 327  
Archidordinae, 423  
*Archidoris*, 423  
     *hawaiiensis*, 423  
     *nubilosa*, 423  
*Argobuccinum*, 355, 84  
     *oregonense*, 355, 84  
*Arion*, 398, 471  
     *ater*, 471  
*Asternotus*, 425  
     *cespitosus*, 423  
*ater*, *Arion*, 471  
*aureomarginatus*, *Hexabranhus*, 423  
*Australorbis*, 327, 98  
     *glabratus*, 398  
*balthica*, *Macomo*, 491  
*banatica*, *Congerina*, 322  
*bicolor*, *Gymnodoris*, 438, 40  
*Biomphalaria*, 327, 29, 31, 32, 36, 39, 41, 42, 45, 46, 99  
     *glabrata*, 327, 29, 31, 32, 36, 39, 41, 42, 45, 46  
*Blaberus*, *cranifer*, 482  
*Buccinum*, *undatum*, 477  
*Bursa*, 349, 51, 52, 54-63, 66-68, 76, 82-85  
     *caelata*, 351  
     *californica*, 351  
     *corrugata*, 349, 51, 52, 54-63, 66-68, 76, 82-85  
     *granifera*, 351  
     *granularis*, 351  
     *gyrina*, 351  
     *spinosa*, 355  
*Busycon*, 469  
*caelata*, *Bursa*, 351  
*californica*, *Bursa*, 351  
*Calliostoma*, 398  
     *ligatum*, 398  
*cancellata*, *Chione*, 351  
*Cardita*, 351  
     *floridana*, 351  
*Carminodoris*, 423  
     *grandiflora*, 423  
     *nodulosa*, 423  
*catinus*, *Velutinellus*, 313, 16, 17, 19-21  
*caudata*, *Eupleura*, 443  
*Cepaea*, 398  
     *nemoralis*, 398  
*Cerithiopsis*, 437  
     *tubercularis*, 437  
*cespitosus*, *Asternotus*, 423  
*Chione*, 351  
     *cancellata*, 351  
*Chlorella*, 351  
Chromodoridinae, 423  
*Chromodoris*, 423, 24, 26  
     *albopustulosa*, 423  
     *decora*, 423, 24, 26  
     *geometrica*, 423  
     *imperialis*, 423  
     *lilacina*, 423  
     *petechialis*, 423  
     *trimarginata*, 423  
     *youngbleuthi*, 423  
*cinerea*, *Urosalpinx*, 443  
*citrina*, *Gymnodoris*, 438, 39  
*clathrata*, *Distorsio*, 349, 51, 68-70, 72, 73, 75, 77, 79, 81, 83-86  
*Codakia*, 351  
     *orbicularis*, 351  
*codapavonis*, *Velutinopsis*, 313, 15, 16, 19  
*Congerina*, 315, 17, 22  
     *banatica*, 322  
     *digitifera*, 315  
     *politioanae*, 322  
     *ramphophora*, 317, 22  
     *soceni*, 322  
*corniculum*, *Nassarius*, 468  
*corrugata*, *Bursa*, 349, 51, 52, 54-63, 66-68, 76, 82-85  
*Coryphella*, 382  
*cranifer*, *Blaberus*, 482  
*Cratena*, 422  
     *glotensis*, 422  
*Crepidula*, 350, 56, 64, 74, 404  
     *adunca*, 376  
     *fornicata*, 356  
*croatica*, *Radix*, 320, 21  
*Cyclope*, 470  
     *neritea*, 470  
*Cyllichna*, 421, 22, 29, 32  
*Cymatilesta*, 384  
     *spengleri*, 384  
*Cymatium*, 386  
     *daniellae*, *Hypselodoris*, 423  
     *decora*, *Chromodoris*, 423, 24, 26  
Dendrodorididae, 421  
*Deroceras*, 391, 98

## INDEX TO SCIENTIFIC NAMES

- reticulatus*, 391, 98  
*Dendrodoris*, 433-38  
     *nigra*, 433-37  
     *limbata*, 436  
 Diaululinae, 423  
*Didacna*, 315  
     *otiophora*, 315  
*digitifera*, *Congerina*, 315  
 Discodoridinae, 423  
*Discodoris*, 423  
     *fragilis*, 423  
*Distorsio*, 349, 51, 68-70, 72, 73, 75, 77, 79-81, 83-86  
     *clathrata*, 349, 51, 68-70, 72, 73, 75, 77, 79-81, 83-86  
*Dolium*, 382  
 Doridacea, 434, 38  
 Dorididae, 423  
 Doridinae, 423  
*Doridopsis*, 434, 36  
     *nigra*, 434  
     *limbata*, 436  
*Doriopsilla*, 435, 436  
     *albopunctata*, 435  
*Doriopsis*, 423, 24, 26  
     *granulosa*, 423, 24, 26  
     *nucleola*, 423  
     *pecten*, 423  
     *viridis*, 423  
*Dosinia*, 313, 15, 17, 20, 21  
     *maeotica*, 315, 17, 21  
*Drosophilia*, 336  
     *melanogaster*, 336  
*drummondi*, *Facelina*, 422  
*dura*, *Halichondria*, 435  
*Dunaliella*, 351, 68  
     *tertiolecta*, 351  
*echinata*, *Trippa*, 423  
*elegans*, *Okadaia*, 442, 43  
*Eolidina*, 422  
     *alderi*, 422  
*Eupleura*, 443  
     *caudata*, 443  
*Facelina*, 422  
     *drummondi*, 422  
*fellowsi*, *Peltodoris*, 423  
 Fissurellidae, 432  
*flavus*, *Limax*, 399  
*floridana*, *Cardita*, 351  
*formosa*, *Platydorid*, 423  
*fornicata*, *Crepidula*, 356  
*fragilis*, *Discodoris*, 423  
*Fulgur*, 385  
*galbana*, *Isochrysis*, 411  
 Gastropoda, 349, 50, 55, 447, 87  
*geometrica*, *Chromodoris*, 423  
*geticus*, *Ninia*, 315  
     *geticus*, *Theodoxus*, 315  
*gigas*, *Strombus*, 403, 15  
*glabrata*, *Biomphalaria*, 327, 29, 31, 32, 36, 39, 41, 42, 45, 46  
*glabratus*, *Australorbis*, 398  
*glotensis*, *Cratena*, 422  
 Goniodorididae, 422  
*grandiflora*, *Carminodoris*, 423  
*grandis*, *Anodonta*, 501, 02-05  
*granifera*, *Bursa*, 351  
*granifera*, *Ranella*, 351  
*granularis*, *Bursa*, 351  
*granulosa*, *Doriopsis*, 423, 24, 26  
*graphica*, *Halgerda*, 423, 25, 30  
 Gymnodoridinae, 438  
*Gymnodoris*, 438-40, 42  
     *alba*, 438  
     *bicolor*, 438, 40  
     *citrina*, 438, 39  
     *okinawae*, 438-40  
     *plebeia*, 438  
*Cryptochiton*, *stelleri*, 493  
*gyrina*, *Bursa*, 351  
*gyrina*, *Physa*, 327, 36  
*gyrina*, *Ranella*, 351  
*haemastoma*, *Thais*, 383  
*Halgerda*, 423, 25, 30  
     *apiculata*, 423  
     *graphica*, 423, 25, 30  
     *rubra*, 423  
 Halgerdinae, 423  
*Halichondria*, 435  
     *dura*, 435  
*Haliotis*, 350  
*hawaiiensis*, *Archidoris*, 423  
*Helix*, 471, 77, 83, 93, 501  
 Hexabranchidae, 423  
*Hexabranchus*, 423, 29  
     *aureomarginatus*, 423  
     *marginatus*, 423, 25, 29  
     *pulchellus*, 423  
*hilaris*, *Thordisa*, 423, 29  
*Hydrobia*, 491  
     *ulvae*, 491  
*Hypselodoris*, 423, 29  
     *daniellae*, 473  
     *kayae*, 423  
     *lineata*, 423  
     *peasei*, 423  
     *vibrata*, 423, 29  
*Ianthina*, 442  
*Ilyanassa*, 385, 448, 501  
     *obsoleta*, 501  
*imperialis*, *Chromodoris*, 423  
*incrassatus*, *Nassarius*, 468  
*Isochrysis*, 411  
     *galbana*, 411

# INDEX TO SCIENTIFIC NAMES

- Jorunna*, 422, 23, 27, 30  
     *tomentosa* 422, 23, 27, 30  
*kayae*, *Hypselodoris*, 423  
 Kentrodoridinae, 423  
*lapillus*, *Nucella*, 477  
*lapillus*, *Purpura*, 384  
*ligatum*, *Calliostoma*, 398  
*lilacina*, *Chromodoris*, 423  
*Limax*, 398, 99  
     *flavus*, 399  
     *maximus*, 399  
     *tenellus*, 398  
*limbata*, *Dendrodoris*, 436  
*limbata*, *Doridopsis*, 436  
*Limnocardium*, 315  
     *zagrabiense*, 315  
*lineata*, *Hypselodoris*, 423  
*Littorina*, 350, 98, 403, 04, 06, 09, 11, 13-16, 69,  
     85, 94  
     *picta*, 403, 04, 06, 09, 11, 13-16  
     *scutulata*, 398  
*lutheri*, *Monochrysis*, 411  
*Lymnaea*, 313, 17, 19, 21, 27, 99, 501, 04  
     *amplecta*, 313, 17, 19, 21  
     *palustris*, 501, 04  
     *peregra*, 327  
     *stagnalis appressa*, 327  
     *velutina*, 314  
 Lymnaeidae, 313  
*Macoma*, 491  
     *balthica*, 491  
*maeotica*, *Dosinia*, 315, 17, 21  
*masoni*, *Schistosoma*, 327  
*marginatus*, *Hexabranchus*, 423, 25, 29  
*maximus*, *Limax*, 399  
*melanogaster*, *Drosophila*, 336  
 Mesogastropoda, 489  
*Modiolus*, 485  
*Monochrysis*, 411  
     *lutheri*, 411  
*Murex*, 469  
 Muricidae, 443  
*Mya*, 485  
*myosotis*, *Ovatella*, 398  
*Mytilus*, 485  
*Nassa*, 350  
*Nassarius*, 403, 04, 11, 15, 16, 47-49, 51, 61, 63,  
     68-71, 75, 77, 80-94  
     *corniculum*, 468  
     *incrassatus*, 468  
     *obsoletus*, 403, 16, 47-49, 51, 63, 69-71, 75, 77,  
     80-94  
     *reticulatus*, 449, 61, 62, 70  
     *vibex*, 403  
 Naticidae, 443  
*nemoralis*, *Cepaea*, 398  
*Nereis*, 485  
     *neritea*, *Cyclope*, 470  
     *nigra*, *Dendrodoris*, 433-37  
     *nigra*, *Doridopsis*, 434  
     *Ninia*, 315  
         *geticus*, 315  
     *nobilis*, *Velutinopsis*, 321  
     *nodulosa*, *Carminodoris*, 423  
     *nubilosa*, *Archidoris*, 423  
     *Nucella*, 477  
         *lapillus*, 477  
     *nucleola*, *Doriopsis*, 423  
     *Nudibranchia*, 421, 22  
     *obsoleta*, *Ilyanassa*, 501  
     *obsoletus*, *Nassarius*, 403, 16, 47-49, 51, 63, 69-71  
         75, 77, 80-94  
     *Ocenebra*, 384  
         *aciculata*, 384  
     *Okadaia*, 442, 43  
         *elegens*, 442, 43  
 Okeniidae, 422  
*okinawae*, *Gymnodoris*, 438, 39, 40  
 Onchidorididae, 422  
*Oncomelania*, 327, 29  
*orbicularis*, *Codakia*, 351  
*oregonense*, *Argobuccinum*, 355, 84  
*osseosa*, *Trippa*, 423  
*otiophora*, *Didacna*, 315  
*Ovatella*, 398  
     *myosotis*, 398  
     *palustris*, *Lymnaea* 501, 04  
     *papillosa*, *Aeolidia*, 422  
     *Paradacna*, 315  
     *Patella*, 350  
     *peasei*, *Hypselodoris*, 423  
     *pecten*, *Doriopsis*, 423  
     *Peltodoris*, 423  
         *fellowsi*, 423  
     *Penaeus*, 485  
     *peregra*, *Lymnaea*, 327  
     *perversa*, *Triphora*, 437  
     *petechialis*, *Chromodoris*, 423  
     *Phaeodactylum*, 403, 06, 11, 14, 15  
         *tricornutum*, 403, 06, 11, 14, 15  
     *Philine*, 421, 22, 26, 30, 32, 34, 37, 42  
     *Physa*, 327, 36  
         *gyrina*, 327, 36  
     *picta*, *Littorina*, 403, 04, 06, 09, 11, 13-16  
     *Pila*, 364  
     *pilleus*, *Velutinellus*, 313, 16, 17, 20, 21  
 Platydoridinae, 423  
*Platydoris*, 423  
     *formosa*, 423  
*Platymonas*, 351, 68, 415  
*plebeia*, *Gymnodoris*, 438  
*politioanei*, *Congeria*, 322  
 Polyceridae, 421, 22, 38  
 Polycerinae, 422

# INDEX TO SCIENTIFIC NAMES

- Pomatias*, 350  
*Prosobranchia*., 448  
*Proralenciennesia*, 313, 21, 22  
*pulchellus*, *Hexabranchnus*, 423  
*Purpura*, 384  
     *lapillus*, 384  
*Radix*, 313, 14, 15, 17, 20, 21  
     *croatica*, 320, 21  
     *kobelti*, 320  
     *velutina*, 314  
*ramphophora*, *Congerina*, 317, 22  
*Ranella*, 351  
     *granifera*, 351  
     *gyrina*, 351  
*reticulatus*, *Agriolimax*, 391, 92, 94, 95, 97-99  
*reticulatus*, *Deroceras*, 391, 98  
*reticulatus*, *Nassarius*, 449, 61, 68, 70  
*Retusa*, 421, 37, 38  
*rubra*, *Halgerda*, 423  
*rugosa*, *Velutinopsis*, 313, 17, 21  
*Scaphander*, 421  
*scabriuscula*, *Trippa*, 423  
*Schistosoma*, 327  
     *masoni*, 327  
*scutulata*, *Littorina*, 398  
*Semifusus*, 469  
*setosa*, *Thordisa*, 423  
*soceni*, *Congerina*, 322  
*spengleri*, *Cymatillesta*, 384  
*spinosa*, *Bursa*, 355  
*Squilla*, 485  
*stagnalis appressa*, *Lymnaea*, 327  
*stelleri*, *Cryptochiton*, 493  
*Strombus*, 403, 15  
     *gigas*, 403, 15  
*subatava*, *Teisseyreomya*, 317  
*subrecurvus*, *Unio*, 315, 71  
*Teisseyreomya*, 315, 17, 19  
     *subatava*, 317  
*tenellus*, *Limax*, 398  
*tertiolecta*, *Dunaliella*, 351  
*Testacella*, 442  
*Thais*, 350, 83, 84  
     *haemastoma*, 383, 84  
*Theodoxus*, 315  
     *geticus*, 315  
     *Thordisa*, 423, 29  
         *hilaris*, 423, 29  
         *setosa*, 423  
*tomentosa*, *Jorunna*, 422, 22, 23, 27, 30  
*Tonna*, 383  
*transiens*, *Velutinopsis*, 313, 17, 21  
*tricornutum*, *Phaeodactylum*, 403, 06, 11, 14, 15  
*irtmarginata*, *Chromodoris*, 423  
*Triphora*, 437  
     *perversa*, 437  
*Trippa*, 423  
     *echinata*, 423  
     *osseosa*, 423  
     *scabriuscula*, 423  
*Trippiinae*, 423  
*tubercularis*, *Cerithiopsis*, 437  
*Ulva*, 485  
*ulvae*, *Hydrobia*, 491  
*undatum*, *Buccinum*, 477  
*Undulotheca*, 313, 20, 22  
*Unio*, 315, 17  
     *subrecurvus*, 315, 17  
*Unionidae*, 501  
*Urosalpinx*, 443  
     *cinerea*, 443  
*Valenciennius*, 313-15, 17, 20-22  
*Vayssiereidae*, 442  
*velutina*, *Lymnaea*, 314  
*velutina*, *Radix*, 314  
*velutina*, *Velutinopsis*, 313, 14, 17, 19, 21  
*Velutinellus*, 313, 14, 16, 17, 19-22  
     *catinus*, 313, 16, 17, 19-21  
     *pilleus*, 313, 16 17, 19-21  
     *rugosus*, 313, 20, 21  
*Velutinopsis*, 313-17, 19-22  
     *codapavonis*, 313, 15, 16, 19, 20  
     *nobilis*, 321  
     *rugosa*, 313, 17, 21  
     *transiens*, 313, 17, 21  
     *velutina*, 313, 14, 17, 19-22  
*vibex*, *Nassarius*, 403  
*vibrata*, *Hypselodoris*, 423, 29  
*viridis*, *Doriopsis*, 423  
*Viviparus*, 350, 432  
*youngbleuthi*, *Chromodoris*, 423  
*zagabiense*, *Limnocardium*, 315

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Contributors in the English language are advised to follow the recommendations of the *Style Manual for Biological Journals* obtainable from the American Institute of Biological Sciences, 2000 P Street N.W., Washington, D.C. 20036, U.S.A. In particular, simplified practices, such as the following are favored: numbers should not be written out except at the beginning of a sentence; percentages following a number are expressed as %; abbreviations of measures (after a number): mm, ml, kg, etc. have no period nor an s in the plural.

*Illustrations* must be carefully executed and so planned that they may be printed as figures of a size appropriate to either one column or the full width of a page of the journal. The maximum size of a printed figure is 13.5 × 20 cm. Large illustrations must be accompanied by a smaller photograph for the editors. Drawings and lettering must be in black India ink or carbon black printing on white, blue tracing, or blue-lined paper. Charts should be drawn large enough to stand a reduction of one half to one third. This should be taken into consideration especially in relation to the lettering. Letters and numbers must not be less than 1 mm in height preferably larger, after reduction. A number of drawings or photographs may often be conveniently grouped together to fit a page.

*Bibliography.* See current number of MALACOLOGIA for desired form of citing. In particular, it should be noted that the journal uses the ampersand (&) for "and"; "et al." may be used in the text, but not in the list of references at the end: in addition to the volume number, complete page numbers of articles and books must be cited: for books, the publisher and city also must be cited.

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*Correspondence.* All manuscripts and figures, as well as inquiries, should be sent directly to the Managing Editor, C. J. Bayne, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A.

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*Bibliographie.* Die gewünschte Form des Zitierens ist aus Argendeinem der jüngeren Hefte ersichtlich. Zu merken ist in dieser Hinsicht insbesondere der Gebrauch des &-Zeichens bei Angabe der Autoren. Der Ausdruck "et al." (bzw. "und Mitarbeiter") darf zwar in Text gebraucht werden, nicht aber im Literaturverzeichnis am Ende der Arbeit, wo alle Autoren namentlich angeführt werden müssen. Ausser Angabe des Jahrganges (Nummer des Bandes) werden auch die Seitenzahlen, bei Zeitschriften wie bei Büchern, verlangt; bei letzteren auch Herausgeber (Verlag) und Verlagsort.

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*Korrespondenz.* Beiträge, Bestellungen, Zahlungen oder Anfragen sind zu richten an: C. J. Bayne Managing Editor, MALACOLOGIA, Museum of Zoology, The University of Michigan, Michigan 48104, U.S.A.



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MALACOLOGIA accepte de publier des travaux originaux, soit descriptifs soit expérimentaux, consacrés principalement ou exclusivement à l'étude des Mollusques. Les contributions peuvent être de longues monographies ou des mises-au-point synthétiques ainsi que de courts articles de recherches, mais les notes brèves ne sont pas acceptées. MALACOLOGIA a pour but d'être l'organe d'expression commun pour divers sujets malacologiques tels que l'anatomie, l'écologie, la malacologie médicale, la paléontologie, la physiologie et la taxonomie. Le journal s'attache tout particulièrement à maintenir un certain niveau d'érudition. Tous les manuscrits sont revus par au moins deux éditeurs.

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