VOL. 14 NO. 1-2 1973

MALACOLOGIA

PROCEEDINGS of the FOURTH EUROPEAN MALACOLOGICAL CONGRESS

Geneva 1971

PROCEEDINGS

of the

FOURTH EUROPEAN MALACOLOGICAL CONGRESS

(Geneva, 7-11 September 1971)

Edited by Eugène E. BINDER

Published by the Department of Invertebrates,
Museum of Natural History, Geneva, Switzerland,
and the Institute of Malacology,
Ann Arbor, Michigan, U.S.A.

Geneva, 1973

(Price, US$ 25 or S Fr. 80)

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PREFACE

The present number is assigned to the Proceedings of the 4th European Malacological Congress, held in Geneva from September 7-11, 1971 under the sponsorship of UNITAS MALACOLOGICA EUROPAEA. Besides the papers delivered, it contains the report of the General Assembly of U.M.E. and also gives an account of some of the meetings the Congress has either sponsored or been host to, and which wished to see their decisions published. Discussion sessions on topics treated in the papers were well attended and stimulating, but the Congress's means did not permit a recording of the lively exchange of ideas, which will thus remain the sole benefit of the participants.

The Congress Committee tender their thanks to all authors for their valuable contribution, to those members who acted as chairmen of communication or discussion sessions, and to all those whose personal intervention contributed to the success of the undertaking. A special acknowledgement should be made to the memory of Professor A. Jayet, deceased shortly after Congress, who led the paleontological part of the excursion to the Jura.

We are thankful to the Town authorities of Geneva and to the director of the Natural History Museum for placing the Museum's rooms and its personnel at our disposal for the duration of Congress.

The Congress is indebted to the State and to the Town of Geneva for the financial support of its meeting. The Swiss National Fund for Scientific Research* and the firm Hoffmann La Roche & Co. in Basle have generously contributed to the general expenses, and particularly to the publication costs of these proceedings. We also acknowledge the kind gestures made by the Société Française de Malacologie and by Dr. E. Loosjes in Wageningen.

Even with the aforementioned financial help, the publication of these proceedings would not have been possible had it not been for the generous offer by Dr. J. B. Burch and the Institute of Malacology to have the proceedings published in their international review *"Malacologia"*, thus earning once again the gratitude of all the members and organizers of the Congress.

E. BINDER
(President)

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*Grant no. 3,444.70

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INTRODUCTION

The 4th European Malacological Congress, sponsored by UNITAS MALACOLOGICA EUROPAEA (U.M.E.), took place in Geneva at the Museum of Natural History from September 7 to 11, 1971, hosted by Dr. E. Binder, president of the UNITAS. One hundred and sixty-seven malacologists participated, coming from 26 countries, including 10 outside Europe.

The Congress proper was preceded by a 1-day meeting of museum curators in charge of mollusc collections. The Congress was also host to working conferences of council members of malacological societies, and of directors of malacological reviews. The European Invertebrate Survey and the Commission Faunistique Continentale de la Société Française de Malacologie held a joint meeting to set up a common program of work and to unify their methods of mapping. A discussion meeting was held on the possible role of malacologists in the protection of molluscs, which brought forth a draft resolution submitted to U.M.E. The General Assembly of U.M.E. closed the working part of the Congress, as usual.

The opening session of the Congress was honoured by the presence of representatives of the State and of the City of Geneva: Monsieur le Conseiller d'Etat André Chavanne, chargé du Département de l'Instruction Publique, and Madame le Conseiller Administratif Lise Girardin, Délégué aux Beaux-Arts et à la Culture. Conseiller Chavanne welcomed the Congress on behalf of both State and City authorities. The President, Dr. E. Binder, after delivering his address, and representing the Museum Director, Dr. W. Aellen, expressed his pleasure at receiving the Congress in the new Museum building and his wishes for a fruitful and agreeable session.

During the Congress, a special room was reserved for exhibits of material or figures and photographs by Congress members. Two invited lectures were given, one by Dr. K. J. Boss, on the number of mollusc species, the other by Dr. W. Streiff on molluscan endocrinology. A half-day boat tour was organized on Lake Geneva, and a whole day excursion led the participants to a variety of paleontological and ecological stations ranging from the foot of the Jura to the Col du Marchairuz and to Lac de Joux.

All those taking part in the Congress were invited to a cocktail party at the Hotel Métropole on the first day by the authorities of the State and City of Geneva. At the end of the Congress, a closing dinner was given at the Airport Restaurant; these occasions were welcome opportunities for renewed personal contact.

ALLOCUTION PRESIDENTIELLE

Mesdames et Messieurs,

Pour la quatrième fois, les malacologues d'Europe et d'ailleurs se réunissent sous les auspices de l'UNITAS MALACOLOGICA EUROPAEA. Au nom de l'UNITAS, je vous souhaite la bienvenue à ce Congrès. Je suis heureux de constater que vous êtes venus nombreux, ce qui témoigne du développement et du rayonnement de l'UNITAS. Je tiens à saluer particulièrement ceux d'entre vous qui sont venus de loin et qui ont dû entreprendre un déplacement important et parfois de longues formalités pour se joindre à nous pendant ces quelques jours.

La composition du congrès est harmonieusement équilibrée cette année par un important contingent de malacologues français. Ceci n'est pas dû uniquement à la proximité de la France mais surtout à la fondation, depuis le dernier congrès, de la Société Française de Malacologie qui est en rapport étroit avec l'UNITAS et qui était d'ailleurs en gestation lors du congrès de Vienne en 1968. Son président, son secrétaire, son trésorier et plusieurs membres du conseil sont membres de l'UNITAS et se trouvent parmi nous aujourd'hui. Cette jeune société comptait déjà au bout d'un an plus d'une centaine de membres et elle a déjà tenu son premier congrès à Caen, il y a exactement une année. Elle publie le périodique "Haliotis". Un autre événement heureux du même ordre est la fondation de la Société Malacologique Israélienne, animée par notre collègue Mienis. Cette société, elle aussi, a déjà organisé un colloque et elle a sa publication, intitulée "Argamon". A l'opposé de ces sociétés nouvelles, la Deutsche Malakozoologische Gesellschaft a fêté son centième anniversaire, ce dont nous avons déjà eu le plaisir de la féliciter.

Nouvelles sociétés malacologiques, anciennes sociétés malacologiques toujours jeunes et vivaces, c'est ainsi que se manifeste la vitalité de la recherche dans notre domaine. Si l'UNITAS peut se flatter d'avoir influencé dans une certaine mesure la vie des sociétés nationales, cette influence a été réciproque: La Société Française de Malacologie a collaboré de façon très positive en apportant une aide financière à ce congrès, où elle s'est fait officiellement représenter, et en prenant l'initiative d'un essai de coordination des comités des sociétés malacologiques. La Société Malacologique Italienne a proposé un candidat à la présidence de l'Unitas, ainsi que le lieu du prochain congrès. Les sociétés néerlandaise, française et allemande ont présenté des candidats au poste de vice-président. Il est d'ailleurs souhaitable d'améliorer la coordination entre les diverses sociétés malacologiques, et l'UNITAS devrait pouvoir jouer un rôle central. Une réunion des membres des conseils de sociétés malacologiques et de l'UNITAS aura lieu dans ce but au cours de ce congrès.

Beaucoup d'aspects du présent congrès sont les résultats de décisions prises, de voeux exprimés lors du dernier congrès ou d'influences, de tendances manifestées depuis lors. Ainsi nous avons réalisé une des suggestions faites par notre prédécesseur, de réunir en marge du congrès les conservateurs de musées chargés des collections de Mollusques. Cette réunion a eu lieu hier, elle a compté une quarantaine de participants et je crois pouvoir dire qu'elle fut à la fois longue, fertile et agréable. Quant au congrès lui-même, sa forme répond à un désir généralement exprimé de ne pas comprendre plusieurs sections parallèles, afin de permettre à chaque congressiste d'entendre toutes les communications qui l'intéressent. Cela implique évidemment un temps de parole fort court et nécessitera une certaine discipline de la part des orateurs - et sans doute aussi une certaine fermeté de la part des présidents de séances - mais cette forme n'a rien d'exceptionnel, elle est de plus en plus adoptée dans la plupart

des congrès, et je pense que vous n'aurez pas de peine à vous y plier. Afin de remédier à son principal inconvénient qui est l'impossibilité de discuter longuement après chaque communication, des séances de discussion ont été prévues à d'autres moments, principalement pendant les soirées, et grouperont chacune les personnes qui s'intéressent à un sujet; au cours de ces séances des questions pourront être posées aux auteurs de communications, mais la conversation pourra aussi prendre un tour plus général sans trop de restriction de sujet ni de temps. Les présidents des séances de discussion auront toute latitude de les organiser et de les diriger. Cette partie de notre activité pourrait bien se révéler l'une des plus intéressantes.

En parcourant vos programmes, vous avez pu constater que les sujets traités dans les nombreux travaux présentés sont très variés et que les domaines sont bien équilibrés; la physiologie est beaucoup mieux représentée que dans les congrès précédents; seule la paléontologie est peu traitée. En ce qui concerne les conférences principales, l'une (Boss) est un sujet de systématique très général, l'autre (Streiff) traite d'un aspect de la physiologie des Mollusques qui a des incidences dans tous les autres domaines. L'excursion au Jura montrera aux paléontologues les formes fossiles quaternaires de la craie lacustre et des tufs de la Combaz, tandis que les écologistes pourront constater les changements de peuplement avec l'altitude, l'exposition et le substrat. Ainsi, je pense que tous les goûts seront satisfaits et j'espère qu'avec votre contribution le congrès qui s'ouvre sera un succès dans son genre.

PRESIDENTIAL ADDRESS - ENGLISH SUMMARY

Ladies and Gentlemen,

Welcome to the IV. European Malacological Congress. Our meeting is honoured by the presence of representatives of the State and City of Geneva: M. le Conseiller d'Etat Chavanne et Mme le Conseiller Administratif Girardin. Several other organizations are also officially represented at the Congress.

The number of congressists is a reflection of the development and growing influence of UNITAS. One hundred and seventy-four participants have registered, coming from 31 countries. I greet especially those who come from other continents.

Since the last congress, the following well-known malacologists are deceased: Prof. Fritz Haas of Chicago, Prof. Siegfried Jaeckel of Berlin, and Prof. Gunnar Thorson of Helsingør.

This year, the composition of our assembly is well balanced by the presence, for the first time, of an important French participation. This is due to the recent foundation of the Société Française de Malacologie (S.F.M.), which is closely linked with the Unitas and brings us in contact with the French malacologists. This new French society has developed quickly and has already held a congress in September 1970. It issues a new publication called "Haliotis". Another malacological society has been founded: the Israelian Malacological Society, which also has already held a colloquium and has its own review "Argamon". We greet the birth of these new societies and wish them a long and fruitful development, following the example of the Deutsche Malakologische Gesellschaft, which has celebrated in 1969 its 100th year of existence. These events show the lively expansion of malacological research.

Cooperation by the different malacological societies with the UNITAS is active and satisfactory: The Société Française de Malacologie has contributed materially to the present Congress. The Società Malacologica Italiana has proposed a place for the next congress; the 3 Italian, Dutch and German societies have nominated candidates for our next council of the UNITAS MALACOLOGICA EUROPAEA.

We feel the need to improve the coordination between the Councils of the main

malacological societies, and UNITAS ought to play an important part in this effort. This is the reason for a meeting of the Council members of malacological societies during this congress.

Another meeting in connection with the Congress is the one of museum curators in charge of mollusc collections, which took place yesterday and which I think I may say has been pleasant and fruitful. The Continental Faunistic Commission of the S.F.M. will take advantage of the Congress to hold a meeting, and so will the directors of malacological reviews.

It is the duty of UNITAS to make a stand against any action which spoils the environment, and especially against over-collecting of molluscs (see fly-leaf entitled "Malacologists and the protection of molluscs").

The Congress itself will not comprise several parallel sections, so that every participant will be able to attend all the lectures which interest him. This implies a rather short time for speeches, and will require some discipline on the part of the speakers, but this is the way things are in most congresses. To avoid the main drawback, i.e., the fact that it is impossible to discuss each lecture within speaking time, discussion sessions have been provided at a later moment; they will bring together people interested in each particular subject; the speakers can then be asked questions and the resulting talks can extend to more general considerations without being restricted too much as regards topics or time. The chairmen will be given great liberty in organizing and leading these discussions according to their judgement.

Besides the lectures, a few scientific exhibits from participants are being displayed in the Museum.

The subjects dealt with by the lecturers are varied and rather well-balanced. Only in paleontology are there rather few lectures. One of the main conferences deals with systematics and the other with physiology. On the other hand, the excursion in the Jura will interest paleontologists and ecologists. So we expect that all kinds of interests will be satisfied and hope that, with your active participation, this Congress will be a success.

ANREDE DES VORSITZENDEN - DEUTSCHE ZUSAMMENFASSUNG

Meine Damen und Herren,

Seien Sie willkommen zum IV. Europäischen Malakologen-Kongress. Wir haben die Ehre, die Anwesenheit von Vertretern des Staats und der Stadt Genf zu begrüssen, nämlich M. le Conseiller d'Etat Chavanne und Mme le Conseiller Administratif Girardin. Auch verschiedene andere Organisationen sind hier offiziell vertreten.

Die Zahl der Kongressisten zeigt Entwicklung und Ausstrahlen der UNITAS. Es haben sich 174 Teilnehmer angemeldet, die von 31 Ländern kommen. Ich möchte hier besonders diejenigen begrüssen, die von anderen Kontinenten kommen.

Seit dem letzten Kongress sind folgende bekannte Malakologen gestorben: Prof. Fritz Haas, von Chicago, Prof. Siegfried Jaeckel, von Berlin, und Prof. Gunnar Thorson, von Helsingør.

Dieses Jahr erfreuen wir uns der Teilnahme einer bedeutenden französischen Delegation. Dies verdanken wir der vor einiger Zeit erfolgten Gründung der Société Française de Malacologie (S.F.M.), welche mit der UNITAS enge Beziehungen pflegt und uns somit mit unseren französischen Kollegen in Verbindung setzt. Diese neue französische Gesellschaft hat sich rasch entwickelt und hat bereits im September 1970 einen Kongress abgehalten. Sie veröffentlicht eine Zeitschrift unter dem Titel "Haliotis". Es wurde noch eine andere malakologische Gesellschaft gegründet, die Israelian Malacological Society, die schon ein Kolloquium abgehalten hat und ein

Blatt "Argamon" erscheinen lässt. Wir begrüssen die Gründung dieser neuen Gesellschaften und wünschen ihnen eine lange und fruchtbare Laufbahn, wie zum Beispiel diejenige der Deutschen Malakologischen Gesellschaft, welche im 1969 ihren hundertsten Jahrestag feierte. Diese Ereignisse beweisen die lebhafte Entwicklung der malakologischen Forschung.

Es besteht zwischen den verschiedenen malakologischen Gesellschaften und der UNITAS eine rege und erfreuliche Mitarbeit: Die Société Française de Malacologie hat dem heutigen Kongress finanziell beigetragen. Die Societa Malacologica Italiana hat vorgeschlagen, den nächsten Kongress in Italien zu beherbergen. Die italienische, die holländische und die deutsche Gesellschaften haben für den nächsten Vorstand der UNITAS MALACOLOGICA EUROPAEA Kandidaten angemeldet.

Es scheint nötig, dass die Mitarbeit zwischen den Vorständen der wichtigsten malakologischen Gesellschaften verstärkt wird, und wir glauben, dass die UNITAS hier eine führende Rolle spielen könnte. Deshalb ist im Laufe dieses Kongresses eine Zusammenkunft der Vorstandsmitglieder der malakologischen Gesellschaften vorgesehen.

Im Zusammenhang mit dem Kongress wurde gestern eine Sitzung von den mit der Verwaltung von Molluskensammlungen beauftragten Museumskustoden abgehalten, von der ich glaube, sagen zu dürfen, dass sie angenehm und fruchtbar gewesen ist.

Die Kontinentale faunistische Kommission der S.F.M. wird die Gelegenheit des Kongresses benutzen, um eine Sitzung abzuhalten, und ebenso die Direktoren der malakologischen Zeitschriften.

Es ist eine Pflicht für die UNITAS, gegen alles, was die natürliche Umgebung zerstört, Stellung zu nehmen, und insbesondere gegen die übermässige Aufsammlung von Mollusken (siehe Separat-Blatt unter dem Titel "Die Malakologen und der Mollusken-Schutz").

Der Kongress selber ist nicht in verschiedenen parallelen Sektionen eingeteilt, damit jeder Teilnehmer alle ihn interessierenden Vorträge hören kann. Das bedingt eine ziemlich kurze Sprechzeit und wird den Rednern eine gewisse Disziplin auferlegen, aber das ist wohl der Fall in den meisten Kongressen. Um den grössten Nachteil, nämlich die Unmöglichkeit einer Diskussion gleich nach dem Vortrag, vorzubeugen, wurden Diskussions-Sitzungen auf einen späteren Zeitpunkt festgesetzt. Dann können die Leute, die für ein besonderes Thema gemeinsam Interesse haben, dem Redner Fragen stellen, was eine Erweiterung der Diskussion auf einer breiteren Basis, ohne allzugrosse Objekt- oder Zeiteinschränkung, ermöglichen wird. Es wird dem Vorsitzenden überlassen, die Diskussion nach seinem Gutdünken zu organisieren und zu führen.

Ausser den Vorträgen werden im Museum einige wissenschaftliche Demonstrationen von Teilnehmern vorgezeigt.

Die von den Rednern vorgebrachten Themen sind mannigfaltig und ziemlich gut verteilt. Allein in der Paläontologie gibt es nur wenig Vorträge. Der erste Hauptvortrag bezieht sich auf Systematik und der zweite auf Physiologie. Andrerseits wird der Jura-Ausflug für Paläontologen und Oekologen besonders Interesse bieten. Wir glauben somit den verschiedenen Interessen eines jeden Teilnehmers zu entsprechen und hoffen, dass dank Ihrer aktiven Anteilnahme unser Kongress erfolgreich verlaufen wird.

E. BINDER

PROCEEDINGS OF THE GENERAL ASSEMBLY OF UNITAS MALACOLOGICA EUROPAEA

by the Secretary, Dr. A. Zilch

The 1971 meeting of the General Assembly of UNITAS MALACOLOGICA EUROPAEA took place at the Geneva Natural History Museum on Saturday, September 11, at 5:00 p.m. 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 June 9, 1971, 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. Binder, the President, presented a report on the work of UNITAS since the last General Assembly.

In November 1969, the "Proceedings of the Third European Malacological Congress, Vienna 1968" were published by the Department of Mollusks of the Vienna Natural History Museum and the Institute of Malacology, Ann Arbor, as vol. 9 no. 1 of "Malacologia". Copies were sent to all participants of the Congress and to all other members of UNITAS.

Four members of the Council of UNITAS met in Frankfurt am Main on May 24, 1969, for a first discussion of the preparation of the Geneva Congress. A meeting of all members of the Council took place in Basle on December 19, 1970. Dr. Binder reported on the subjects discussed in these meetings and pertaining to the general policy of UNITAS, especially on the matters of eventual honorary members, of admission conditions of new members and on the position of UNITAS concerning the protection of mollusks (see point 9 of this report).

Up to the date of the General Assembly, 27 new members joined UNITAS. Three members died (H. Modell in 1969, Dr. F. Haas in 1969, Prof. Dr. G. Thorson in 1971). Five members resigned, and one membership was cancelled. Thus, the number of members increased from 139[1] on September 6, 1968, to 157 on September 11, 1971.

The 157 members consisted of:

Ordinary members (personal 121, collective 10). 131
Corresponding members (all personal). 26

They came from 30 countries:

a) Ordinary members in 20 countries:
Austria (2), Belgium (2), Denmark (6), Egypt (1), France (22), Germany (12), Great Britain (20), Hungary (2), Israel (2), Italy (13), Morocco (2), Netherlands (21), Norway (3), Poland (1), Portugal (4), Rumania (2), Sweden (4), Switzerland (8), Turkey (2), Yugoslavia (2).

b) Corresponding members in 9 countries:
Australia (2), Brazil (1), Canada (1), Ethiopia (1), Ghana (1), New Zealand (1), Nigeria (2), South Africa (1), U.S.A. (16).

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[1] In "Malacologia", 9(1): 17, the number 140 was published; one ordinary personal member who had applied for membership at the assembly did not confirm his application in writing.

3. Statement of accounts by the Treasurer

Dr. Forcart, the Treasurer, presented the following statement of accounts (in Swiss Francs) for the period from August 9, 1968, to August 26, 1971. The statement had been audited by Dr. Toffoletto and, in absence of Mr. Dance, by Mr. Girod.

	S. Fr.
Income	6,742.08
Expenditure	5,037.70
Excess of Income	1,704.38
Assets Schweizerischer Bankverein (E.H. 941085)	7,020.12
Balance 8.8.1968	5,315.74
Balance 26.8.1971	7,020.12
Excess	1,704.38

4. Approval of acts of councillors

The acts of the councillors for the period from 1968 to 1971 were approved.

5. Postal ballot on new councillors for the period 1971-1974

Three statutory proposals had been received by the Secretary for the election of the new Council. These were submitted by the Società Malacologica Italiana, the Nederlandse Malacologische Vereniging, and the Deutsche Malakozoologische Gesellschaft. The Council of UNITAS agreed to these proposals. They were mailed as a ballot to all 121 ordinary personal members on July 21 and 22, 1971, in accordance with paragraph 11 of the Rules. At the General Assembly the following result of the voting in which only 63[2] members had participated was announced:

	yes	no	abstention
President:			
Dr. F. Toffoletto, Italy	62	-	1
Vice President:			
Dr. B. Salvat, France	(16+)[3] 19	2	2
Dr. A. C. van Bruggen, Netherlands	(16+)[3] 27	5	2
Secretary:			
Dr. O. E. Paget, Austria	62	-	1
Treasurer:			
Dr. P. Jung, Switzerland	60	-	3
Member of Council:			
J. F. Peake, B.Sc., England	59	-	2

Thus, the following office holders were elected members of Council:

President: Dr. F. Toffoletto (Milan, Italy)
Vice President: Dr. A. C. van Bruggen (Leiden, Netherlands)
Secretary: Dr. O. E. Paget (Vienna, Austria)
Treasurer: Dr. P. Jung (Basle, Switzerland)
Member of Council: J. F. Peake, B.Sc. (London, England)

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[2]4 voting papers were mailed too late and reached the Secretary only after the date of the General Assembly.

[3]On 16 voting papers both nominations for the office of the Vice President were marked with a cross.

6. Election of auditors for the period 1971-1974

The following members were appointed auditors: Mr. J. M. Gaillard, Paris, and Mr. A. Girod, Milan.

7. Subscription for the period 1971-1974

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

8. Year and place of the next Congress

The President-Elect, Dr. Toffoletto, invited the members of UNITAS to the next Congress in Milan in 1974. The invitation was accepted.

9. Other business

a) List of Malacologists and Bibliography:

At the last General Assembly in 1968, Dr. Paget had been authorized to make further efforts at completing the projects as mentioned under numbers 2, 4, and 5 in the Résumé of the Presidential Address published in the Proceedings of the Third European Malacological Congress p 14. In the meantime the "List of European Malacologists 1971" has been published and can be obtained from Dr. Oliver Paget, Naturhistorisches Museum, Burgring 7, A-1014 Wien, Austria (price: 5 international reply coupons). Bibliographies for the years 1969 and 1970 are also obtainable, free of charge. The 1971 bibliography is being prepared. The project foreseen under No. 5 is underway and results shall be published in due time.

b) Protection of Mollusks:

The draft resolution submitted by the drafting commission was discussed and unanimously adopted after some minor changes. (See page 16.)

COMPTE RENDU DE L'ASSEMBLEE GENERALE DE L'UNITAS MALACOLOGICA EUROPAEA

par le Secrétaire, Dr. A. Zilch

L'Assemblée générale de 1971 de l'UNITAS MALACOLOGICA EUROPAEA s'est tenue à Genève, au Muséum d'Histoire Naturelle, le samedi 11 septembre à 17 h. Nous remercions M. G. I. Crawford d'avoir bien voulu en assumer la présidence.

L'assemblée s'est déroulée conformément à l'ordre du jour qui avait été envoyé à tous les membres le 9 juin 1971 en application de l'art. 8 des statuts de l'UNITAS.

1. Confirmation de nouveaux membres

L'admission des nouveaux membres, dont la liste était annexée à l'ordre du jour, a été confirmée.

2. Rapport du Président sur l'activité de l'UNITAS

Le Président, Dr. Binder, a présenté son rapport sur l'activité de l'UNITAS depuis la dernière assemblée générale.

Les "Proceedings of the Third European Malacological Congress, Vienna 1968" ont été publiés en novembre 1969 par le Département des Mollusques du Musée d'Histoire Naturelle de Vienne et par l'Institute of Malacology, Ann Arbor, comme vol. 9 No. 1 de "Malacologia". Tous les participants au Congrès et tous les autres membres de l'UNITAS en ont reçu un exemplaire.

Quatre membres du Conseil de l'UNITAS se sont réunis le 24 mai 1969 à Francfort sur le Main pour une première discussion sur la préparation du Congrès

de Genève. Puis tous les membres du Conseil ont tenu séance à Bâle le 19 décembre 1970. Le Dr. Binder rappela les principaux sujets discutés au cours de ces séances et concernant la politique générale de l'UME, notamment la question d'éventuels membres honoraires, les modalités d'admission des nouveaux membres et l'attitude de l'UME face au problème de la protection des Mollusques (voir point 9 de l'ordre du jour).

27 nouveaux membres ont adhéré à l'UNITAS en cours d'exercice. Trois membres sont décédés (H. Modell en 1969, Dr. F. Haas en 1969, Prof. Dr. G. Thorson en 1971). Cinq membres ont démissionné et un fut exclu. Ainsi, le nombre des membres a passé de 139[1] le 6 septembre 1968 à 157 le 11 septembre 1971. Ce chiffre de 157 comprenait:

Membres ordinaires (individuels 121, collectifs 10). 131
Membres correspondants (tous individuels) 26

(Pour la répartition par pays, se référer à la version anglaise)

3. Présentation des comptes par le Trésorier

Le Trésorier, Dr. Forcart, présenta les comptes (établis en francs suisses) pour la période allant du 9 août 1968 au 26 août 1971. Ces comptes avaient été vérifiés par le Dr. Toffoletto et, en l'absence de Mr. Dance, par M. Girod.
(Pour le relevé de compte, voir la version anglaise)

4. Décharge au Comité

Décharge fut donnée au Comité pour sa gestion pendant la période de 1968 à 1971.

5. Election du nouveau Comité pour la période 1971-1974

Pour l'élection du nouveau Comité, le Secrétaire a reçu trois propositions statutaires, soumises respectivement par la Société Malacologique Italienne, la Société Malacologique Néerlandaise et la Société Malacologique Allemande. Le Comité de l'UNITAS a approuvé ces propositions. Elles furent soumises par poste aux 121 membres individuels ordinaires les 21 et 22 juillet 1971, conformément à l'art. 11 des statuts. Le résultat de la votation, à laquelle 63[2] membres seulement avaient participé, fut proclamé à l'assemblée générale.
(Pour le détail, se référer à la version anglaise)

6. Election des vérificateurs des comptes pour la période 1971-1974

Les membres suivants ont été désignés comme vérificateurs des comptes: M. J. M. Gaillard, Paris, et M. A. Girod, Milan.

7. Cotisations pour la période de 1971 à 1974

Les cotisations actuelles de 10 francs suisses par an pour les membres ordinaires et de 5 francs suisses par an pour les membres correspondants ont été maintenues.

8. Date et lieu du prochain Congrès

Le Président élu, Dr. Toffoletto, invita les membres de l'UNITAS à venir à Milan pour le prochain Congrès en 1974, invitation qui fut acceptée.

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[1] Le vol. 9(1) de "Malacologia" indiquait, en page 17, le nombre de 140; un membre ordinaire individuel qui avait demandé son admission lors de l'assemblée, n'a pas confirmé sa demande par écrit.

[2] 4 bulletins de vote expédiés trop tard n'ont atteint le Secrétaire qu'après la date de l'assemblée générale.

9. Divers

a) Liste des Malacologues et bibliographie:

A la dernière assemblée générale en 1968, le Dr. Paget avait été chargé de poursuivre la réalisation des projets indiqués sous 2, 4 et 5 dans le Résumé du Discours présidentiel (Proc. Third Europ. Malac. Congr., p 14). La "Liste des Malacologues européens 1971" a été publiée dans l'intervalle. Elle peut être obtenue auprès du Dr. Oliver Paget, Naturhistorisches Museum, Burgring 7, A-1014 Wien, Oesterreich (5 coupons-réponse internationaux). Les bibliographies pour les années 1969 et 1970 (littérature européenne seulement) sont également disponibles, gratuitement. La bibliographie pour 1971 est en préparation. On continue à s'occuper du projet mentionné sous chiffre 5; les résultats seront publiés en temps utile.

b) Protection des Mollusques:

Le projet de résolution soumis par la commission de rédaction ad hoc a été discuté et adopté à l'unanimité après modifications. (Voir page 16.)

BERICHT ÜBER DIE GENERALVERSAMMLUNG DER UNITAS MALACOLOGICA EUROPAEA

vom Sekretär, Dr. A. Zilch

Die Generalversammlung 1971 der UNITAS MALACOLOGICA EUROPAEA fand am Samstag, dem 11. September, um 17 Uhr im Naturhistorischen Museum der Stadt Genf statt. Wir danken Herrn G. I. Crawford, dass er wieder das Amt des Chairman übernommen hat.

Die Versammlung folgte der Tagesordnung, die am 9. Juni 1971, gemäss § 8 der Satzung der UNITAS, an alle Mitglieder verschickt worden war.

1. Bestätigung neuer Mitglieder

Die neuen Mitglieder der UNITAS (Anlage der Tagesordnung) wurden bestätigt.

2. Tätigkeitsbericht des Präsidenten

Der Präsident, Dr. Binder, gab einen Bericht über die Tätigkeit der UNITAS seit der letzten Generalversammlung.

Im November 1969 sind die "Proceedings of the Third European Malacological Congress, Vienna 1968" als Band 9 Nummer 1 der "Malacologia" von der Mollusken-Sektion des Naturhistorischen Museums Wien und dem Institute of Malacology, Ann Arbor, veröffentlicht worden. Jeder Kongressteilnehmer und jedes weitere Mitglied der UNITAS hat ein Exemplar erhalten.

Diejenigen Vorstandsmitglieder der UNITAS, die zur Feier des 100jährigen Bestehens der Deutschen Malakozoologischen Gesellschaft in Frankfurt am Main anwesend waren, sind am 24. Mai 1969 zu einer ersten Besprechung der Vorbereitungen des Genfer Kongresses zusammengekommen. Eine Sitzung aller Vorstandsmitglieder hat am 19. Dezember 1970 in Basel stattgefunden. Dr. Binder berichtete über die besonderen Punkte, die auf dieser Sitzung erörtert worden sind, vor allem das Problem des Molluskenschutzes.

Bis zum Zeitpunkt der Generalversammlung sind der UNITAS 27 neue Mitglieder beigetreten. Drei Mitglieder sind verstorben (H. Modell 1969, Dr. F. Haas 1969, Prof. Dr. G. Thorson 1971). Fünf Mitglieder haben ihren Austritt erklärt, und ein Mitglied wurde gestrichen. Dadurch ist die Zahl der Mitglieder von 139[1] am 6.

[1] In "Malacologia", 9(1): 17 ist die Zahl 140 veröffentlicht worden; ein persönliches ordentliches Mitglied, das sich auf der Versammlung um die Mitgliedschaft beworben hatte, hat trotz mehrfacher Aufforderung eine schriftliche Beitrittserklärung nicht abgegeben.

September 1968 auf 157 am 11. September 1971 angewachsen.
(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 9. August 1968 bis zum 26. August 1971. Die Rechnungsführung ist von Herrn Dr. Toffoletto und, in Abwesenheit von Herrn Dance, von Herrn Girod geprüft worden.
(Vgl. die Zusammenstellung in der englischen Fassung.)

4. Entlastung des Vorstandes
Der Vorstand (1968-1971) wurde entlastet.

5. Wahl des neuen Vorstandes für die Periode 1971-1974
Für die Wahl des neuen Vorstandes sind drei satzungsgemässe Vorschläge beim Sekretär eingegangen, die von der Società Malacologica Italiana, der Nederlandse Malacologische Vereniging und der Deutschen Malakozoologischen Gesellschaft eingereicht wurden. Der Vorstand der UNITAS hat sich diesen Vorschlägen angeschlossen. Die Stimmzettel sind am 21. und 22. Juli 1971, gemäss § 11 der Satzung, an alle 121 persönlichen ordentlichen Mitglieder abgeschickt worden. Auf der Generalversammlung wurde das Ergebnis der Wahl, an der sich nur 63[2] Mitglieder beteiligt haben, bekanntgegeben und damit der neue Vorstand der UNITAS gewählt.
(Vgl. die Zusammenstellung in der englischen Fassung.)

6. Wahl der Rechnungsprüfer für die Periode 1971-1974
Zu Rechnungsprüfern wurden ernannt: Herr J. M. Gaillard, Paris, und Herr A. Girod, Mailand.

7. Mitgliedsbeitrag für die Periode 1971-1974
Die jährlichen Beitragsraten von 10.00 S. Fr. für ordentliche Mitglieder und 5.00 S. Fr. für korrespondierende Mitglieder wurden nicht geändert.

8. Jahr und Ort des nächsten Kongresses
Der gewählte Präsident, Dr. Toffoletto, hat die Mitglieder der UNITAS für den nächsten Kongress 1974 nach Mailand eingeladen. Diese Einladung wurde angenommen.

9. Verschiedenes
a)Liste der europäischen Malakologen und Bibliographie: Auf der letzten Generalversammlung 1968 war Dr. Paget beauftragt worden, sich um die Weiterführung der Vorhaben zu bemühen, die unter den Punkten 2, 4, und 5 in dem "Résumé" der "Presidential Address" (Proc. Third Europ. Malac. Congr., p 14) erwähnt sind. Inzwischen ist die "Liste der europäischen Malakologen 1971" erschienen. Sie kann bezogen werden von Dr. Oliver Paget, Naturhistorisches Museum, Burgring 7, A-1014 Wien, Österreich (5 Internationale Antwortscheine). Die Bibliographien für die Jahre 1969 und 1970 (nur europäische Literatur) stehen ebenfalls zur Verfügung (kostenlos). Die Bibliographie für 1971 ist in Vorbereitung. Das unter Punkt 5 erwähnte Vorhaben wird fortgesetzt; Ergebnisse werden zur gegebenen Zeit veröffentlicht.
b)Schutz der Mollusken: Der von der betreffenden Redaktionskommission vorgeschlagene Text eines Entschlusses wurde kiskutiert und nach einigen Veränderungen einstimmig angenommen (Siehe Seite 16).

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[2]4 Stimmzettel sind zu spät abgeschickt worden und erreichten den Sekretär erst einige Tage nach der Generalversammlung.

COMPTE-RENDU DE LA REUNION DE FAUNISTIQUE CONTINENTALE, le 10 septembre 1971

Une réunion de travail sur les méthodes de collecte de données faunistiques dans le milieu continental avait été demandée par la Société Française de Malacologie. La participation, au Congrès de Genève, du Dr J. Heath, responsable anglais du "European Invertebrate Survey" ("Cartographie des Invertébrés Européens"), a permis de donner à cette réunion une portée coordinatrice internationale.

Les 28 malacologistes qui participèrent à cette réunion appartenaient aux pays suivants: Allemagne Fédérale, Australie, Finlande, France, Grande Bretagne, Hongrie, Norvège, Pays Bas, Suède et Suisse. Après l'exposé du Dr Heath sur les méthodes utilisées par l'"European Invertebrate Survey", plusieurs collègues prirent la parole pour décrire les méthodes employées, dans leur pays, par leurs Sociétés malacologiques ou par leurs Instituts de Recherche, pour annoncer les résultats obtenus, pour évoquer les problèmes non encore résolus et pour signaler les projets en cours.

Les collègues présents à cette réunion ont, finalement, souhaité que les méthodes de cartographie préconisées par l'"European Invertebrate Survey" (représentation de la distribution d'une espèce à l'aide de signes ponctuels sur des cartes UTM muettes), soient adoptées par les malacologistes comme elles l'ont été par les entomologistes. Ils ont enfin exprimé le désir de voir se former une commission européenne patronée par UNITAS MALACOLOGICA EUROPAEA. L'Assemblée générale de l'UNITAS, au cours de sa réunion du 11 septembre, a approuvé la création de cette commission et a confié les travaux de coordination à quatre responsables: MM. H. Ant (Allemagne Féd.), H. Chevallier (France), M. Kerney (G. B.) et H. Waldén (Suède). Ces quatre chercheurs se sont entendus pour prendre contact avec des collègues continentalistes d'autres pays afin de constituer une Commission Faunistique Continentale Européenne, regroupant, si possible, un réprésentant de chaque pays européen.

H. Chevallier
Muséum National d'Histoire Naturelle
55, rue Buffon, Paris 5e, France

WORKING CONFERENCE ON DISTRIBUTION MAPPING
September 10th 1971

This meeting was organised by the Commission Faunistique Continentale of the Société Française de Malacologie and was attended by 30 Congress members. The countries represented were France, Federal Germany, Switzerland, Netherlands, Sweden, Norway, Finland, Hungary, Australia and Great Britain.

The methods being used by the European Invertebrate Survey for the production of maps of Europe were described by J. Heath. This project uses a 50 Km square derived from the UTM grid as the basic recording unit. Advanced data processing facilities are available at the Biological Records Centre, Monks Wood Experimental Station which, together with Professor Leclercq's Department of Zoology, Gembloux, Belgium, is acting as coordinating centre.

M. H. Chevallier then explained the techniques being used by the Société Française de Malacologie for their survey. The use of the various recording sheets was explained in detail.

Dr. M. Kerney of the British Conchological Society detailed the methods being used for their Atlas project which aims at producing complete species lists for each 10 Km square in Britain. A species list Field Card is used by the recorders for entering their data which, after checking, is transferred to a 'Master' card for each square. These are then processed and maps made by the Biological Records Centre. Some provisional maps have already been published. The data from this scheme will be made available to the European Invertebrate Survey.

The German project was outlined by Dr. H. Ant who said that they had also encountered the problems of identification mentioned by M. H. Chevallier. He said that they had now adopted the UTM grid as the basis for recording, although this had entailed converting much data from an earlier system.

For the Netherlands Dr. Butot reported that originally mapping had not been carried out using the UTM grid, but that workers in his country had now changed over to that system.

Dr. H. Walden described the very detailed work which has been carried out in Sweden where mapping was at an advanced stage. Unfortunately very little had yet been done in Norway. A proposal to form a Scandinavian biological data bank was under discussion.

The meeting concluded by forwarding to the General Assembly of UNITAS MALACOLOGICA EUROPAEA a resolution that U.M.E. should sponsor and co-ordinate a scheme to map the molluscs of Europe in collaboration with the European Invertebrate Survey. This resolution was later unanimously adopted by the meeting on Saturday, September 11th, 1971. The General Assembly appointed a committee comprising Dr. M. Kerney (U.K.), Dr. H. W. Walden (Sweden), Dr. H. Ant (Germany (FR)) and M. H. Chevallier (France) to implement the resolution.

J. Heath
Biological Records Centre
Monks Wood Experimental Station
Abbots Ripton, Huntingdon, England

MALACOLOGISTS AND THE PROTECTION OF MOLLUSCS

Numerous species of molluscs are in the process of disappearing or are becoming rare. In 1968, the American Malacological Union held a symposium on the endangered species of North America, which came to the general conclusion that rarefaction is mostly due to the destruction or alteration of the environment.

In South Africa, forest molluscs in the Capetown area disappear and are replaced by species accidentally imported from Europe. In tropical Africa, many species will unavoidably disappear if the felling of the rain forest goes on. This is especially serious from a scientific point of view, for many species are being destroyed even before they are known, which makes the study of phylogeny impossible. In this way, very interesting speciation cases escape analysis while they might have given precious information on the mechanism of this process. In some parts of Australia, the fauna is no longer to be found except in cemeteries where the sheep cannot penetrate and therefore have not been able to alter the environment.

As regards marine molluscs, Mr. Torchio, in a conference given at the Congress of the Società Malacologica Italiana in 1970, has shown how rapidly pollution by fuel and by particles suspended in the water is eliminating the fauna, principally the molluscs, from the coasts of the Mediterranean Sea. In a session of June 1971, the American Western Society of Malacologists has dealt, among other subjects, with the preservation of the marine environment from the malacological point of view.

The impoverishment of the fauna due to the degradation of the environment is a problem which concerns all biologists, and it is as biologists that we must strive with energy against this tendency whenever there is an opportunity. There would be no reason to put this problem on the agenda of a specifically malacological congress if it had not an aspect in which we are particularly concerned: Where the environment has not yet been destroyed and where molluscs are still abundant, they are endangered by overcollecting, especially with sales in view. This applies above all to marine molluscs. This activity has developed to a considerable extent in the course of the last fifteen years, owing to the multiplication of the number of amateurs, and still more to the extension of the means at disposal: organized travelling, fast speedboats, easy scuba diving within reach of nearly everybody. Many divers collect all that they see, without discrimination and without consideration. Others make a living out of it, plundering methodically and completely; then they move to another place and start afresh. Traders pay them and sell the shells to numerous collectors who are scarcely ever moved by scientific considerations, but are rather interested in the rarity of the species.

Faced with this problem, malacologists find themselves in an ambiguous position: Collectors have always existed and have furnished many museums with their first scientific collections. Scientists were among the first to profit by the use of scuba diving apparatus. Museums often have applied to shell dealers, many of whom are efficient and reliable in their information. Thus it is not easy for us to stand up unanimously against this activity of collecting molluscs. It is nevertheless evident that this process leads to deplorable excesses which reverberate on the ecological balance of the environment so that we run the risk of being deprived of good scientific material. For this reason, the president of U.M.E., Dr. E. Binder, took advantage of the IV. European Malacological Congress to raise this problem so that it may be examined by all interested malacologists present.

A meeting was held on the evening of September 8, attended by 56 congress members, to discuss the different aspects of the question and find a way in which to intervene.

The meeting came to the decision to ask the help of the councils of all malacological societies and of amateur shell-clubs in influencing the interest of their members and altering their perspective as to shell-collecting. A drafting committee was appointed to prepare a resolution to be circulated among malacological societies and published in malacological journals as the official stand of UNITAS MALACOLOGICA EUROPAEA in this matter. As a result, the general Assembly on September 11 adopted the following resolution:

RESOLUTION ON THE PROTECTION OF MOLLUSCS
adopted by the General Assembly of U.M.E., 11 September 1971

UNITAS MALACOLOGICA EUROPAEA (U.M.E.), representing malacologists and conchologists in Europe, is much concerned by the rapidly increasing destruction of the natural environment. It therefore supports all measures being taken to avoid and reduce this destruction.

As Malacologists, we are particularly concerned with molluscs. Therefore, U.M.E. urges all who are concerned throughout the world to accept responsibility for ensuring the future existence of Mollusca and their habitats.

We, the members of U.M.E., realize that this will necessitate a curtailment of collecting activities, but we are sure that, as responsible naturalists, all conchologists and malacologists will wish to support appropriate conservation measures. U.M.E. therefore urges that, for any purpose whatsoever, only about the minimum number of specimens shall be collected. Observation as well as photography of living specimens in their natural habitats may be a much more rewarding activity than mere collecting. This applies equally to the work of the amateur and the professional. Such an approach to field studies would result in the acquisition of much of the information which is so urgently needed to ensure the success of the efforts being made to conserve these animals.

PAPERS and ABSTRACTS

of the

FOURTH EUROPEAN MALACOLOGICAL CONGRESS

(Geneva, 7-11 September 1971)

MALACOLOGIA, 1973, 14: 19-27

PROC. FOURTH EUROP. MALAC. CONGR.

PALEOCENE MOLLUSKS FROM EWEKORO, SOUTHERN NIGERIA[1]

O. S. Adegoke

Department of Geology, University of Ife
Ile-Ife, Nigeria

INTRODUCTION

Marine macrofossil-bearing strata of Paleocene age show a patchy distribution all over the world. Among the best known circum-Atlantic/Tethyan sections may be mentioned the Danian beds at Faxe, Denmark (Ravn, 1933; Rosenkrantz, 1960), and at Copenhagen (Ravn, 1939; von Koenen, 1885); the Montian beds in Belgium (Briart and Cornet, 1871; Cossmann, 1908, 1913, 1924; Vincent, 1930); the Ranikot beds of India (Cossmann and Pissarro, 1909, 1927; Douvillé, 1928, 1929; Vredenburg, 1929; Cox, 1930); the lower Mokattam beds of Egypt (Oppenheim, 1903, 1906); the Midway Group of the American Gulf Coastal Plain (Harris, 1896; Gardner, 1933); the Kangilia and Agatdal formations of West Greenland (Rosenkrantz, 1970), the Maria Farinha beds of Pernambuco, Brazil (White, 1887; Penna, 1965), and the Soldado Formation of Trinidad (Rutsch, 1943).

Fossiliferous marine Paleocene has also been reported from scattered West African localities, the best known being the Landana beds of Congo (Vincent, 1913; Miller, 1951); various localities in Senegal (Tessier, 1952), Morocco (Salvan, 1954), Soudan (Douvillé, 1920); the Adabion and Togblekové beds in Togo (Oppenheim, 1915; Furon, 1948) and the Apatuema beds of Ghana (Cox, 1952).

In Nigeria, marine macrofossil-bearing Paleocene is represented in the southwest by the Ewekoro Formation, a shelly limestone exposed in the quarry of the West African Portland Cement Company Limited at Ewekoro (Fig. 1).

Until the initiation of the present series of studies by the writer in 1967, little was known about the macrofauna of the Ewekoro Formation. Reyment (1966a) described a fragmentary *Cimomia* from the quarry which he erroneously assigned to *Cimomia landanensis* (Vincent). He mentioned also the occurrence of *Deltoidonautilus togoensis* (Oppenheim). More recently, Adegoke and Dessauvagie (1970) described a new *Campanile, C. nigeriense* from the Quarry.

A recently completed study (Adegoke, in preparation) has led to the recognition of over 220 species of macrofossils in the quarry material. This well preserved fauna (see Plates 1 and 2) is dominated by microform mollusks. The Ewekoro quarry thus becomes one of the most fossiliferous Paleocene sections recorded to date. The present paper reviews the salient aspects of the fauna.

STRATIGRAPHY

The Ewekoro Formation at the type locality consists of about 12.5 metres of shelly limestone. It is sandy near the base and grades into the underlying Abeokuta Forma-

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[1] This paper is based on research carried out while the writer held a Visiting Research Associateship at the Smithsonian Institution, Washington, D. C. The opportunity to use the Museum and other facilities is gratefully acknowledged. Thanks also are due to the University of Ife, Nigeria for financial support. The completed monograph, including the description of new taxa will be published in the Smithsonian Contributions to Paleobiology.

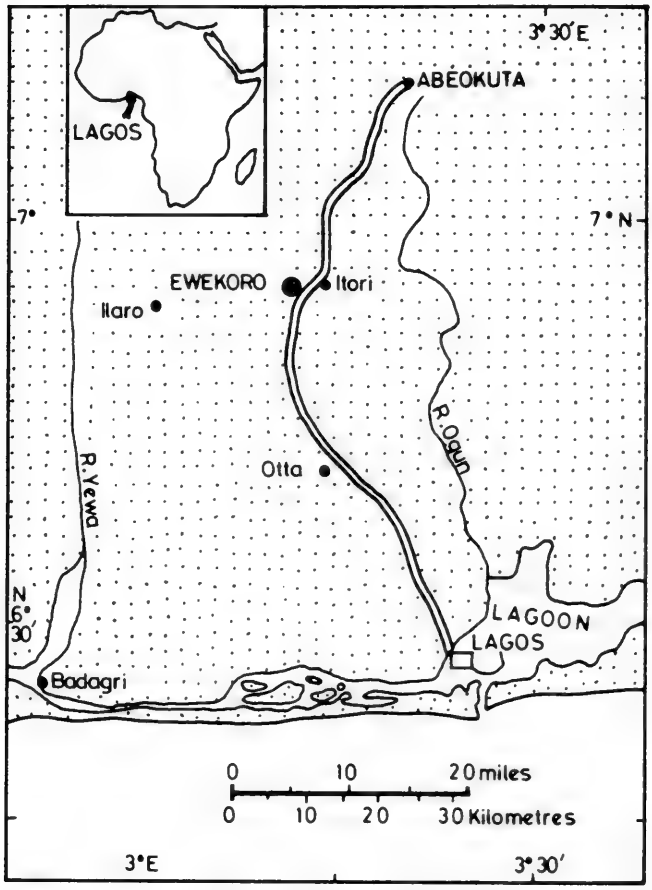


FIG. 1. Map of western Nigeria showing location of Ewekoro.

tion (Fig. 2). The formation was formally named by Jones (1964) who included within it the overlying shale which has subsequently been referred by Ogbe (1971) to the Akinbo Formation. Details of the stratigraphy and petrography of the Formation were published by Adegoke and others (1971) who erected three microfacies units, the Sandy Biomicrosparite at the base, overlain by the Shelly Biomicrite and the Algal Biosparite. More recently, Ogbe (1972) proposed a fourth unit, the Red Phosphatic Biomicrite, represented by thin erosional remnants, less than 1 metre in thickness overlying the Algal Biosparite. Most of the fossils studied were preserved in the Shelly Biomicrite.

FAUNA

The Ewekoro macrofauna contains over 200 determinable species, most of which are new. The fauna is dominated by mollusks (gastropods ca. 125 species, pelecypods ca. 70 species, nautiloids 6 species, scaphopods 3 species). Corals are represented by 7 species many of which are new. Of 5 echinoid species collected, only 3 referred to the genera *Togocyamus*, *Cassidulus* and *Thylechinus* are determinable. A probable crinoid stem fragment was also collected. Arthropods were abundantly represented by fragmentary ambulatory appendages of the cosmopolitan Tertiary genus, *Callia-*

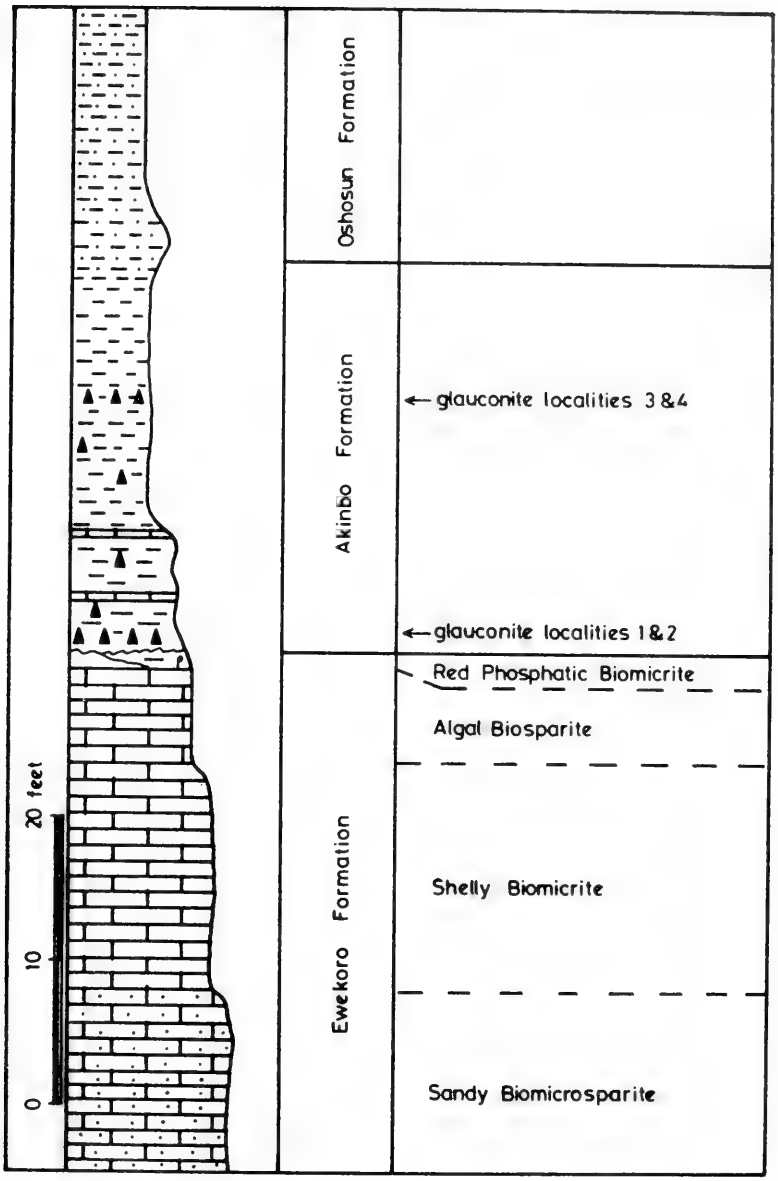


FIG. 2. Stratigraphic Section of Strata exposed in the Ewekoro quarry. Note location of the radiometrically dated glauconite samples.

nassa. Vertebrates were sparsely represented by teeth and denticles of *Myliobatis*, *Odontaspis* and other unidentified sharks and rays.

The molluscan assemblage is dominated by gastropods not only in species diversity but also in total number of individuals. The gastropod-pelecypod ratio is about 2 to 1, whereas their numerical ratio is over 10 to 1.

The greatest gastropod diversity is seen among the submicroscopic size (1-3 mm) forms. Genera such as *Pseudomalaxis*, *Heligmotoma*, *Pseudoliva*, *Rimella*, *Cerithiopsis*, *Sycostoma*, *Mesalia* and *Haustator* showed remarkable species diversity though

PLATE 1

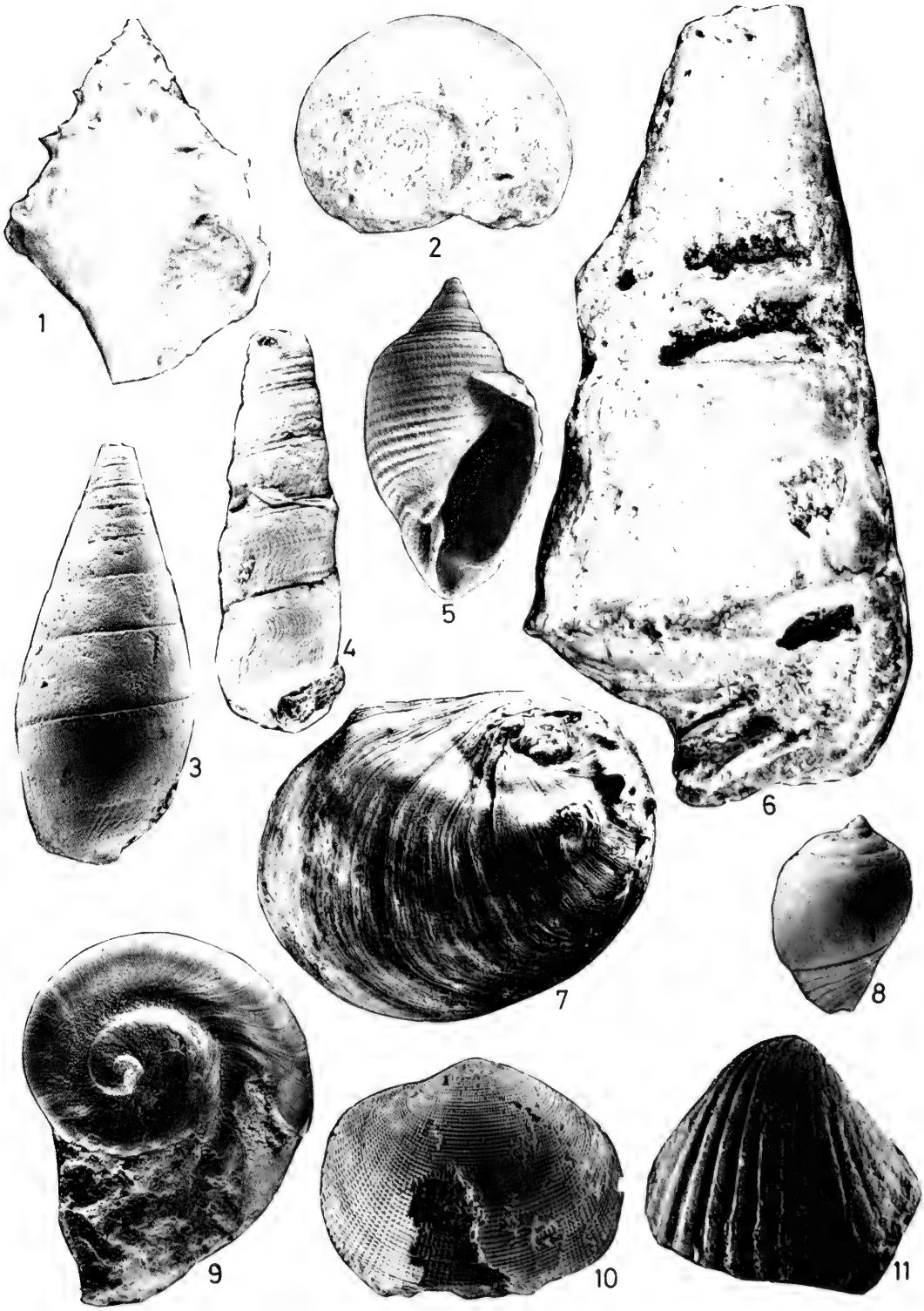
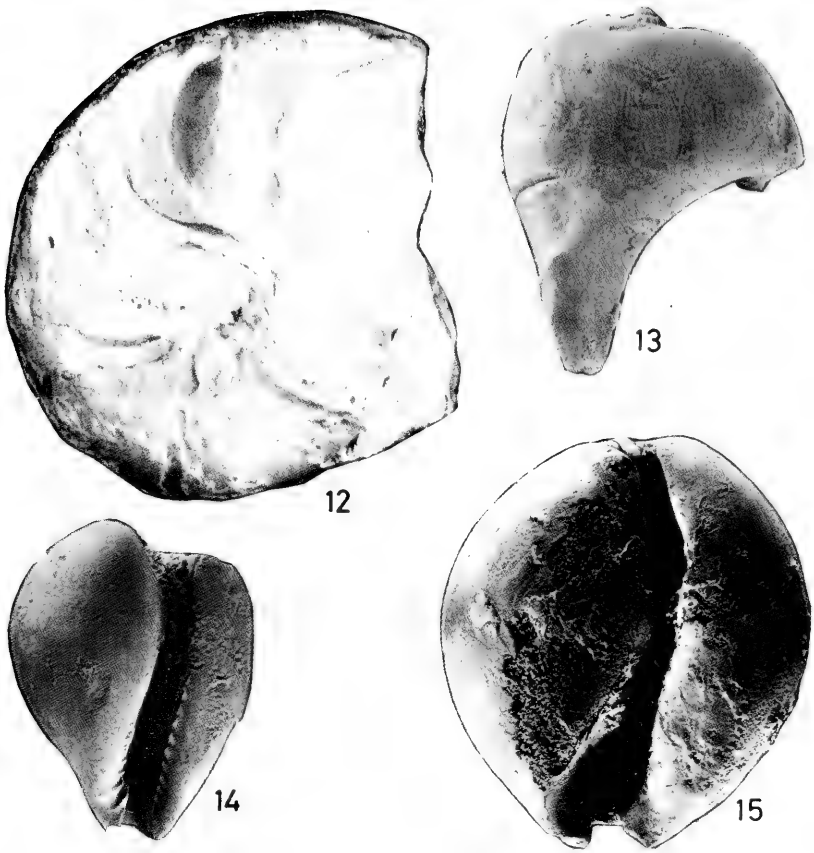


PLATE 2



EXPLANATION OF PLATES

(Abbreviations: UIMG = University of Ife Museum of Geology;
USNM = United States National Museum)

FIG. 1. *Clinuropsis diderrichi* Vincent, UIMG no. 153, X1.
FIG. 2. *Gisortia brevis* Douvillé, UIMG no. 152, X1.
FIG. 3. ?*Clavocerithium* n. sp., USNM no. 174744, X2.
FIG. 4. *Torquesia adabionensis* Oppenheim, USNM no. 174741, X1½.
FIG. 5. *Tornatellaea* (*Ravniella*) *africana* Furon, USNM no. 174745, X7.
FIG. 6. *Campanile nigeriense* Adegoke and Dessauvagie, UIMG no. 20, X1.
FIG. 7. *Velates* n. sp., USNM no. 174740, X1.
FIG. 8. *Pseudoliva* (*Buccinorbis*) n. sp., UIMG no. 159, X1½.
FIG. 9. *Heligmotoma* n. sp., USNM no. 174747, X1.
FIG. 10. *Fimbria subdavidsoni* Furon, USNM no. 174755, X1½.
FIG. 11. *Venericardia* (*Venericor*) n. sp., UIMG no. 158, X1½.
FIG. 12. *Cimomia* n. sp., UIMG no. 128, X1.
FIG. 13. *Pseudoliva* (*Buccinorbis*) n. sp., USNM no. 174753, X1½.
FIG. 14. *Cypraea* n. sp., UIMG no. 155, X1½.
FIG. 15. *Eocypraea* n. sp., UIMG no. 150, X1.

rarely accompanied by a commensurate numerical abundance. Among the most abundant species may be mentioned *Pseudaulicina simplex* Furon, *Strepsidura kerstingi* Oppenheim, *Clinuropsis togoensis* (Oppenheim), *Volutilithes uniplicata* Furon, *Solariella* n. sp., *Clavilithes* (*Cosmolithes*) n. sp. and *Pseudoliva* n. sp.

Bivalves are in general less diverse and less numerous than gastropods. The genera *Ostrea*, *Venericardia*, *Macrocallista*, *Corbula*, *Glycymeris* and *Cardium* showed a diversity both in number of species and (except for *Glycymeris*) in number of individuals. *Cardium zechi* Oppenheim and *Corbula* n. sp. were numerically the most abundant.

The nautiloid fauna is diverse and represents one of the most diverse and most abundant known for strata of comparable age. This renders unnecessary Reyment's (1966a) suggestion that empty nautiloid conchs were supplied to the coasts of Nigeria and Togo *via* a hypothetical north-drifting paleo-oceanographic current from the Cabinda enclave in Angola. Besides, the most abundant Ewekoro species are forms with very large body chambers more than one and a half whorls long. According to the results of Reyment's (1958) biostratonomic experiments, such forms would rarely stay afloat for the 3,500-4,000 kilometres between the Cabinda enclave and the Nigeria-Togo shoreline.

TETHYAN AFFINITIES

The great similarity between West African Paleogene faunas and those of distant Tethyan provinces of India, Egypt and the Gulf Coastal United States has attracted the attention of many earlier workers (see Newton, 1922; Cox, 1930; Davies, 1934). This coupled with the gross dissimilarities between these faunas and those of neighbouring North African and European areas led Douvillé (1920), for example, to refer to them as an Indo-African fauna.

The Tethyan affinity of the Ewekoro fauna was stressed by the writer (Adegoke, 1972a, 1972b). This is confirmed by the presence in it of the following genera commonly associated with the Tethyan seaway (see Palmer, 1967): *Nummulites*, *Gisortia*, *Velates*, ?*Terebellum*, *Carolia*, *Campanile*, *Crommium*, *Venericardia*, *Fimbria*, etc. (see Plates 1 and 2). In addition, a few specimens of a new genus previously referred to ?*Clavocerithium* (see Palmer and Brann, 1966) were also collected.

Until recently, *Nummulites* was considered absent from West Africa south of Senegal and the area was, in fact, mapped as part of the "non-nummulitic facies" by Davies (1934). The record of a new species of *Nummulites* (Sachs and Adegoke, in press) from Ewekoro is significant not only because it further extends the range of the genus in West Africa (see Blondeau, 1966) but also confirms the suggested connection of the West African Paleogene basins with the Tethyan sea *via* a trans-saharan epeiric seaway (see Reyre, 1966; Adegoke, 1969).

Further evidences of close Tethyan affinity are furnished by the parallel development of species of *Strepsidura*, *Torquesia*, *Mesalia*, *Collonia*, *Heligmotoma*, *Solariella*, *Cardita*, etc., between Ewekoro and the contemporaneous Tethyan faunas of the Ranikot beds of India and the Mokattam beds of Egypt. Comparable species of *Calyptraphorus*, *Surcula*, *Volutilithes*, *Buccinorbis*, *Mesalia*, *Cimomia*, *Venericardia* and *Cucullaea* also occur in Ewekoro and the Midway Group of the United States Gulf Coastal Plain.

AGE OF THE EWEKORO FORMATION

Apart from Fayose and Asseez (1971), all workers to date assign the Ewekoro Formation to the Paleocene. The former assigned an Eocene age to the formation on the basis of a single record of *Pseudohastigerina* in a limestone facies penetrated by

a borehole located a few kilometres from the Ewekoro quarry. Their claim has subsequently been disregarded because the log of the borehole showed that no sample was collected from the interval from which *Pseudohastigerina* was presumably recorded.

Reyment (1966b) and Ogbe (1972) recorded the following planktonic formaminifera from the Ewekoro Quarry: *Globorotalia acuta* Toulmin, *G. velascoensis* (Cushman), *G. varianta* (Subbotina), *G. pseudobulloides* (Plummer) and *Globigerina triloculinoides* (Plummer). These suggest a Paleocene age.

Ostracods from the formation were recently re-examined by Dr. M. E. Omatsola of the Paleontological Institute, Uppsala who identified 31 species. He considered the assemblage diagnostic of the upper Paleocene (Omatsola, 1970, personal communication).

Apart from the affinities of the Ewekoro macrofauna with faunas of well known Paleocene horizons discussed earlier, a few diagnostic Paleocene species occur at Ewekoro. *Clinuropsis diderrichi* Vincent, first recorded in the Paleocene of Landana, Congo (Vincent, 1913) has been found in contemporaneous strata in Togo, Ghana and Senegal (see Cox, 1952; Tessier, 1952). It was also recorded in the Soldado rock in Trinidad (Rutsch, 1943). *Ornatellaea* (*Ravniella*) *africana* Furon, a common Ewekoro form belongs to a subgenus which according to Rosenkrantz (1970) is so far known to be restricted to the lower Paleocene. The pelecypod *Fimbria subdavidsoni* Furon, also common at Ewekoro is virtually indistinguishable from *F. davidsoni* (Deshayes) from the Thanetian of the Paris Basin (see Farchad, 1936). It should also be mentioned that the Paleocene index echinoid, *Togocyamus seefriedi* Oppenheim occurs abundantly in the Ewekoro Formation.

Finally, radiometric (K-Ar) age determination of glauconites in the Akinbo shale which *disconformably* overlies the Ewekoro Formation (see Fig. 2) yielded a date of 54.45 ± 2.7 million years (Adegoke and others, 1972). This age closely corresponds to the Paleocene-Eocene transition of Berggren (1969) and conclusively proves that the underlying Ewekoro Formation cannot be younger than late Paleocene.

SUMMARY

A fauna containing over 200 determinable species has been recorded from the Paleocene Ewekoro Formation of southwestern Nigeria. The fauna shows strong genetic affinities with contemporaneous Tethyan faunas of India (Ranikot beds), Egypt (Mokattam beds), United States Gulf Coastal Plain (Midway Group), Trinidad (Soldado Rock) and West Africa (Togo, Ghana, Senegal and Landana).

The Tethyan affinity is confirmed by the presence of *Nummulites*, *Gisortia*, *Velates*, ?*Terebellum*, *Carolia*, *Campanile*, *Crommium*, *Venericardia* and *Fimbria*.

The Paleocene age is confirmed on the bases of planktonic foraminiferal, ostracode and macrofossil evidences as well as a radiometric age of 54.45 ± 2.7 million years obtained for glauconitic beds which overlie the Ewekoro formation disconformably.

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PROC. FOURTH EUROP. MALAC. CONGR.

FAUNENGESCHICHTLICHE BEDEUTUNG DER ALTPLEISTOZÄNEN MOLLUSKENFAUNA VON UNGARN

E. Krolopp

Ungarische Geologische Anstalt
Budapest, Ungarn

Die Wurzeln unserer Molluskenfauna reichen bis auf das Ende Tertiär zurück. Obwohl uns aus dem Pliozän des Karpaten-Beckens 41, auch heute noch lebende, Arten bekannt sind, weicht die spättertiäre Gastropodenfauna von der heutigen trotzdem wesentlich durch die ausgestorbenen beziehungsweise "exotischen" Arten, sogar Gattungen ab (Krolopp, 1969).

Es ist daher verständlich, dass für die Faunenentwicklung die frühren Stufen des Quartärs (unteres Pleistozän) von entscheidender Bedeutung sind.

Aus dem unteren Pleistozän von Mittel- und Westeuropa sind schon lange solche ausgestorbenen oder dort heute nicht lebenden Arten bekannt, die Beziehungen zu dem Süden und Südosten aufweisen oder auch heute noch im Süden leben. Das Karapaten-Becken, das in Richtung Süden und Südosten offen war, stellte ein Gebiet von Schlüsselbedeutung für die altpleistozäne Verbreitung dieser Arten, für die Fixierung ihrer Bewegungen in der Zeit dar.

Da ich in jüngster Zeit Gelegenheit hatte, die Molluskenfauna von zahlreichen altpleistozänen Lokalitäten zu bearbeiten, deren Alter mit vertebratenpaläontologischen Angaben genau bestimmt werden konnte, erhielt ich auch faunengeschichtlich wertvolle Daten.

Aus den altpleistozänen terrestrischen Steh- und Flusswasserablagerungen konnte ich eine Gesamtzahl von 102 Arten bestimmen.

Die meisten terrestrischen Arten sind bereits heute lebende Formen von grossem Verbreitungsareal. Neben diesen bedürfen einer besonderen Erwähnung zwei *Gastrocopta*-Arten, von denen eine die aus dem älteren Teil des unteren Pleistozäns der Tschechoslowakei und Osterreich bekannte *Gastrocopta serotina* Lož. (Ložek, 1964) ist, die andere eine neue, noch nicht beschriebene Art aus dem jüngeren Altpleistozän darstellt. Die beiden *Gastrocopta*-Arten können als altpleistozäne Relikte der im Pliozän von Mitteleuropa ziemlich weit verbreiteten Gattung betrachtet werden, die jedoch sich gut von den pliozänen Arten unterscheiden lassen.

Die von Ložek beschriebene Art *Zonitoides sepultus* Lož. war ausser einigen tschechoslowakischen Lokalitäten nur aus Schmiechen (Deutschland) bekannt (Ložek, 1964). Jetzt wurde sie auch im jüngeren Altpleistozän von Ungarn angetroffen.

Schlieslich möchte ich bemerken, dass aus dem unteren Altpleistozän eine *Parmacella*-Art bekannt geworden ist. Die Gattung lebt - wie bekannt - in Südeuropa und im Raume des Kaukasus (Zilch, 1959-60).

Das sind also im Vergleich mit den heutigen fremde Elemente der altpleistozänen terrestrischen Gastropodenfauna von Ungarn.

Die Basommatophoren der ungarischen altpleistozänen Ablagerungen sind im Allgemeinen auch heute noch lebende, weit verbreitete Arten. Von den Besonderheiten ist eine *Gundlachia*-Art am interessantesten. Es ist bekannt, dass in den letzten Jahren aus Mittel- und Südwesteuropa zahlreiche solche Angaben über Ancyliden bekannt wurden, die mit den Vertretern der subtropisch-tropischen Gattung *Gundlachia* beziehungsweise *Ferrissia* verglichen wurden (Zilch-Jaeckel, 1962, Mirolli, 1960, Wautier-Odiévre, 1961, Pintér, 1968). Ein Teil der Vorkommen könnte zwar auf

Einschleppen zurückgeführt werden, aber nach meiner soeben erwähnten Angabe, hat die Gattung *Gundlachia* im unteren Pleistozän im Karpaten-Becken noch gelebt. Sie war also Mitglied der Fauna von Mitteleuropa. Da zur dieser Zeit auf unserem Gebiet auch noch die gegenwärtig in Südeuropa verbreitete *Parmacella* lebte, kann man die südwesteuropäischen Angaben über die Gundlachien als Vorkommen einer Gattung zu deuten, die sich in den jüngeren Stufen des Pleistozäns nach Süden zurückgezogen hat und dort noch immer lebt.

Eine andere Merkwürdigkeit unserer altpleistozänen Basommatophoren-Fauna ist eine *Acella*-Art. Die zoogeographischen Beziehungen dieser, mit *Lymnaea* verwandten, Gattung sind vorderhand nicht geklärt, da zur Zeit uns lediglich aus Nordamerika einige lebende Vertreter der Gattung bekannt sind (Zilch, 1959-60). Da aber in den pliozänen Ablagerungen des Karapaten-Beckens auch mehrere Vertreter der Gattung angetroffen wurden, ist es wahrscheinlich, dass die altpleistozäne Art mit einem von diesen generisch zu verbinden sei.

Die Prosobranchiaten-Arten der altpleistozänen Fauna sind zumeist aus jenen fluviatilen Ablagerungen zum Vorschein gekommen, die in einer Wechsellagerung mit Stehwasser-Sedimenten unter der Oberfläche der Grossen Ungarischen Tiefebene eine über 800 m mächtige pleistozäne Schichtenfolge bilden. Im Laufe der malakologischen Untersuchungen der Bohrkerne hat es sich herasgestellt, dass der grösste Teil der Schichtenfolge vom Altpleistozän stammt und die mächtigkeit der jungpleistozänen Schichten ein Maximum von 100 m erreicht. Die Gliederung der Sedimentfolge in diese zwei Komplexe wurde gerade durch die Untersuchungen der Molluskenfauna ermöglicht (Krolopp, 1970). Unter den altpleistozänen fluviatilen Schnecken gibt es nämlich - neben den heute lebenden Arten - einige Formen, die im Quartär ausgestorben sind und schon in den jungpleistozänen Ablagerungen nicht angetroffen werden können.

Von diesen möchte ich zunächst *Viviparus böckhi* (Halav.) erwähnen, die wahrscheinlich eine endemische altpleistozäne Art des Karapaten-Bekens ist, aber eine nahe Verwandtschaft zu den aus Dnjester-Terrasen beschriebenen *Viviparus*-Formen aufweist (Tschepalyga, 1971). Eine andere Merkwürdigkeit ist eine noch nicht beschriebene *Bithynia*-Art, die grösser als *Bithynia tentaculata* (L.) ist und ein charakteristisches excentrisches Operculum besitzt. Eine Ebenfalls neue Art ist eine *Hydrobia*, die verwandtschaft mit den pliozänen Prososthenien aufweist.

Zur Gruppe der ausgestorbenen Arten gehört auch noch eine Muschel, *Pisidium clessini* Neum., die auch aus den mittelpleistozänen Ablagerungen bekannt ist.

Eine andere Gruppe der altpleistozänen fluviatilen Formen bilden solche Arten, die aus den alt- und mittelpleistozänen Interglazialen vom westlichen Mitteleuropa beziehungsweise von Westeuropa bekannt sind, aber in den jüngeren pleistozänen und rezenten Faunen dieser Gebiete fehlen (Steusloff, 1953), während sie in den im Karapaten-Becken befindlichen Flüssen des Wassersystems der Donau und in Südost-Europa auch heute noch leben (z.b.: *Fagotia acicularis* (Fér.), *Fagotia esperi* (Fér.), *Theodoxus danubialis* (C.Pfr.)). Auf Grund der erwähnten Angaben hat es sich erwiesen, dass diese Arten - offenbar wegen klimatischer Effekte - auch im Karapaten-Becken in den fluviatilen Ablagerungen seit dem Mindel-Glazial fehlen, aber im Holozän wieder erschienen.

Etwa einen Übergang zwischen den beiden Gruppen bildet die Muschel *Corbicula fluminalis* (Müll.), die zwar in Vorder- und Mittelasien auch heute noch lebt, in Europa aber ausgestorben ist, während sie in den altpleistozänen und älteren mittelpleistozänen Schicten von Mittel- und Westeuropa an zahlreichen Stellen angetroffen wurde (Zilch-Jaeckel, 1961). Aus ungarischen Tiefbohrungen wurde sie ebenfalls an mehreren Stellen bekannt.

Die Arten der altpleistozänen fluviatilen Fauna von Ungarn stimmen also mit

jenen überein, die uns auch schon früher als characteristische altpleistozäne Mollusken von Mittel- und Nordwest-Europa bekannt waren. Andere Arten lassen sich jedoch in eine Verwandschaft mit den westlichen Formen bringen. So dürfte unsere Art *Viviparus böckhi* (Halav.) vielleicht mit *V. diluvianus* (Kunth), beziehungsweise *V. d. glacialis* (S. V. Wood) verwandt sein. Die in unserem Altpleistozän häufige Art der Gattung *Theodoxus* vereinigt die Merkmale von *Th. danubialis* (C.Pfr.) und *Th. prévostianus* (C.Pfr.) in sich. Die aus dem unteren Pleistozän des Rheinlandes bekannte *Th. serratiliniformis* (Geyer) kann man vielleicht als ihren westlichen Vertreter nehmen, während *Th. prévostianus* (C.Pfr.) selbst ihre in Thermalquellen und in Quellen von ständiger Temperatur erhalten gebliebener und an die dortigen Verhältnisse angepasste Form zu sein scheint. Hier sei noch erwähnt, dass in unserem altpleistozänen Material die Merkmale der Arten *Fagotia acicularis* (Fér.) und *F. esperi* (Fér.) noch vermischt vorkommen, was auf ihre geneinsame Herkunft hinweist, worauf an Hand eines ungarischen Pliozän-Materials früher auch schon Bartha hingewiesen hat, der die Art *Melanopsis fuchsi* Handm. für den gemeinsamen Vorfahren dieser beiden Arten hielt (Bartha, 1956).

Die altpleistozäne Molluskenfauna von Mitteleuropa benötigt weitere Untersuchungen, damit die Verwandtschaftsbeziehungen geklärt werden können. Allerdings kann das gegenwärtig laufende Studium des in den letzten Jahren gefundenen reichen ungarischen Mareriales neue wertvolle Angaben zu diesen Untersuchungen liefern.

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SUMMARY

With its extinct or "exotic" species and even genera, the Latest Tertiary mollusc fauna of Central Europe differs considerably from the now-living forms. The Middle

Pleistocene fauna, however, is essentially identical with the contemporary one. Accordingly, the Lower Pleistocene was crucial for faunal evolution.

Open to the S and SE, the Carpathian Basin in Central Europe was a key area on the path of northward proliferation of southerly forms during the interglacials. Therefore the analysis of the 102 mollusc species identified in recent years in the Lower Pleistocene sediments of Hungary supplies data that are important for both the understanding of the fauna of the older member of the Pleistocene and the faunal history of Central Europe as a whole. In this connection it is worth mentioning that the present writer could show the presence of the genera *Parmacella* and *Gundlachia* in the Lower Pleistocene of Hungary (and, consequently, of Central Europe). The last-mentioned data imply, at the same time, a new approach to the explanation of the occurrences of *Gundlachia* and *Ferrissia* in Europe. Surprisingly enough, among the Lower Pleistocene forms the features of some species, readily distinguishable at present, are still mixed, indicating their origin from a common ancestor (e.g., *Fagotia acicularis* (Fér.) and *Fagotia esperi* (Fér.) or *Theodoxus danubialis* (C.Pfr.) and *Th. prévostianus* (C.Pfr.), respectively).

MALACOLOGIA, 1973, 14: 33-37

PROC. FOURTH EUROP. MALAC. CONGR.

THE EARLIEST OCCURRENCE OF *MACOMA BALTHICA* (L.) AS A FOSSIL IN THE NORTH SEA DEPOSITS

P. E. P. Norton and G. Spaink

Zoology Dept., Glasgow University, Scotland and
Netherlands Geological Survey, Haarlem, Netherlands

ABSTRACT

Macoma balthica is found first in the late Baventian of Mundesley, Sidestrand, West Runton and Sheringham, in Norfolk. It occurs by derivation in Pastonian sites close to these, but not elsewhere in the East Anglian 'Crag' succession. An hypothesis is offered, explaining this on tectonic grounds. Records of *M. balthica* from the Calabrian of Italy and the 'Icenien' of Holland are considered incorrect. A brief discussion of the paleogeography and immigration times of *M. obliqua, M. praetenuis* and *M. calcarea* is also given.

PALEOGEOGRAPHY

The *Macoma* species, *M. obliqua, M. praetenuis, M. calcarea* and *M. balthica,* appeared newly in the North Sea Basin deposits in the Pliocene and early Pleistocene time. Their points of origin and route of immigration are unknown to us. Discussion may begin with paleogeographic concepts of the later Tertiary time. There are differing claims for what the paleogeography was. Strauch (1971) considers that Atlantic and Scandic marine provinces existed. A land barrier, the Thule Province, separated them. It ran from Greenland to Europe and included Iceland, the Faroes and Britain. The Atlantic province included that part of the Atlantic Ocean which is bounded by the continental shelf of Ireland, Iceland, the southern tip of Greenland and eastern North America. Deep gulfs extended into the present Mediterranean Sea and Davis Strait. The Scandic province included what is now the Greenland and Barents seas, connecting northward with the North Eurasian Basin and extending southward into the North Sea as a narrow gulf. Other workers claim that the later Tertiary paleogeography was substantially similar to the present. The North Sea and *proto* English Channel were connected across the present Pas de Calais. There was an open connection from the North Sea to the Atlantic as at present. Spaink's findings (unpublished) on the evolution of the Astartidae would support the latter paleogeographic reconstruction. The *Macoma* evidence inclines us to keep both theories in mind. *Macoma* species were, at any rate, evolving in the North Sea and Arctic seas at this time.

MACOMA OBLIQUA (Sowerby)

In the Coralline Crag of England, which was forming during the Pliocene, is found *Macoma obliqua.* The diagnostics of this species as compared with the other species of *Macoma* mentioned here have been given and figured by Spaink & Norton (1967) and are not repeated here. *M. obliqua* is extinct today. Its Pliocene range also included the Scaldisien of the Netherlands and Belgium.

By the beginning of the Pleistocene it appears that, even if the Scandic and Atlantic provinces had been separate previously, they were now united and so were the Pacific and Arctic Oceans. The Bering Strait had been submerged during the Beringian trans-

gression (Hopkins 1967). Foraminiferal studies of the East Anglian Crag deposits (Funnell 1961) indicate that the Pas de Calais Strait became closed during the early Pleistocene. It is inferred by van Voorthuysen (1954) that tectonic movements caused rising of the land in the southern North Sea at this time. The Pas de Calais Strait was open during the time of deposition of the Waltonian and Newbournian Red Crag and the early Ludham Crag. When the Butleyan Red Crag and the Norwich Crag Series above the early Ludham Crag were being deposited, the Strait was closed. (It is not yet known whether the Ludham Crag may be correlated with any part of the Red Crag Series).

MACOMA PRAETENUIS (Leathes) and *M. CALCAREA* (Gmelin)

In the topmost Pliocene of the Netherlands and Belgium and in the earliest Pleistocene (Waltonian) of England occurs *Macoma praetenuis*. *Macoma calcarea* appears shortly afterward, in the Netherlands' 'Icenien' and the English Newbournian. *M. praetenuis* occurs also in the Icelandic succession at Tjörnes, beginning just below the currently recognised Pliocene-Pleistocene boundary (in Horizon 13/1 of Strauch (1963); *M. calcarea* was present earlier).

Macoma species also reached the Mediterranean, where in the marine Calabrian deposits Moroni (1967) found a shell named by her as *M. balthica* though on the basis of her figure we judge it to be a form of *M. obliqua*.

In the early Pleistocene North Sea Deposits there is evidence for cycles of climatic change, indicated by procession from temperate to subarctic vegetation (West 1968) and Foraminifera (Funnell 1961). After the Pas de Calais Strait finally became land, the North Sea appears to have become rather shallow and brackish in the East Anglia region. The Southeastern part (the present Netherlands and Belgium) rather soon became nonmarine. Zagwijn (1963) found that in the Western Netherlands the 'Icenien' sea receded and continental conditions began during a late cool phase (Pollen Subzone TC4c) of the Tiglian Interglacial. Zagwijn (personal communication) suggests this may be correlated with the (East Anglia) Thurnian. The East Anglian basin remained marine much longer (Spaink & Norton 1967).

MACOMA BALTHICA (Linnaeus)

A new *Macoma* species, *M. balthica*, is first recorded from marine deposits of the late Baventian on the north coast of Norfolk. Pollen spectra in clays of this Stage indicate open heath oceanic vegetation (West 1961) and similar pollen occurs in clays associated with the *Macoma balthica* deposits. *M. balthica* is not found in Baventian deposits elsewhere in East Anglia. Preliminary findings (Beck, personal communication) of the U.E.A. Research Boreholes programme allow us to speculate that the north and south parts of the deposition basin were separated by a chalk ridge running northeast towards Halesworth (Fig. 1). The Northern Basin subsided during Ludhamian times. Both parts, except for North Norfolk, subsided during Thurnian, Antian and Baventian times. The sea level was lowered glacio-eustatically during the Thurnian and Baventian. In late Baventian times a local marine transgression in North Norfolk allowed the incursion of a marine fauna in which *M. balthica* is the most frequent species (Norton 1967). Deposits of 'Weybourne Crag' at Sheringham, Sidestrand, West Runton and grey shelly deposits with *M. balthica* in borings at Mundesley, represent this phase. The succeeding Pastonian was a time of regression on the North Norfolk coast, with deposition of thick estuarine silts. In these conditions the *M. balthica* stocks, with the rest of the 'Weybournian' fauna, retreated. Later Pastonian, and younger, 'Weybourne Crag' deposits on the North Norfolk Coast were formed by reworking of the primary Baven-

TABLE 1

East Anglia Stages (*Temperate Stages italicised*)	Pas de Calais Strait	*Macoma* arrivals	Netherlands Stages (Correlation not guaranteed)
Pastonian	Closed	(reworking)	Eburonian
Baventian	Closed	*M. balthica*	Eburonian
Antian	Closed		Tiglian in nonmarine facies
Thurnian	Closed		Tiglian in nonmarine facies
Ludhamian (top)	Closed		Tiglian in marine facies
Ludhamian (lower)*	Open		Tiglian in marine facies
Butleyan Red Crag*	Closed		no pollen in Red Crag
Newbournian Red Crag	Open	*M. calcarea*	no pollen in Red Crag
Waltonian Red Crag	Open	*M. praetenuis*	no pollen in Red Crag
Coralline Crag (Pliocene)	Open	*M. obliqua*	Scaldisian

*As mentioned in the text, the relationship between the Ludham Crag and Red Crag is not understood and this table should not be read either as correlating them, or as stating that the Pas de Calais Strait closed twice.

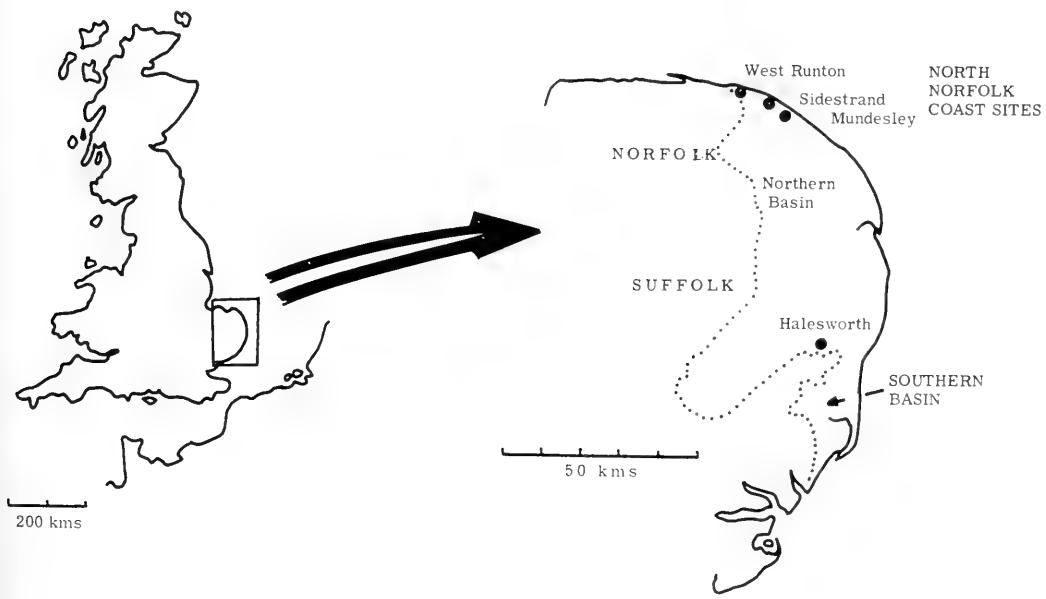

FIG. 1. Sketch-map of East Anglia showing the 2 main basins on the Crag base.

tian material. The 'Weybourne Crag' deposits are diachronous. The Pastonian sea spread over the rest of the Northern Basin and Southern Basin. Silts alone were deposited in the Northern Basin. Mollusca were living in the Southern Basin. *M. balthica* has never been found in the shelly deposits here though the molluscan assemblages at some sites (Norton 1970) show that conditions would have been suitable for it. Apparently this species had become locally extinct and did not recolonise after its short incursion in the Baventian.

Some records of *M. balthica* in the Netherlands Pliocene or Early Pleistocene were published by Lorié (1885). Heering (1950) summarises them. This gave rise to the term 'Weybournien' for the top part of the 'Icenien' (Tesch 1942). Examination of these shells (Spaink & Norton 1967) shows that all are wrongly determined. They should be *M. calcarea*, *M. obliqua* or *M. praetenuis*. A few shells are correctly determined but belong to a much younger horizon mistakenly recorded as 'Icenien'. The use of the term 'Weybournien' in the Dutch succession has therefore been discontinued, which is fortunate as we (*op. cit.*) have inferred that it cannot be placed later than Tiglian TC4c which is similar to the Thurnian in East Anglia whereas the East Anglia 'Weybourne Crag' is Baventian, Pastonian or Cromerian.

After the brief occurrence of *M. balthica* in the East Anglia Pleistocene and the Pastonian and Cromerian reworking of its shells, follows the remainder of the Cromer Forest Bed Series and the first glaciation of this region, the Lowestoftian (which may be equivalent to the Elsterian). Following the Elsterian in the Netherlands, are found the marine deposits of the Holsteinian Interglacial, in which *M. balthica* is abundant, as it has been in suitable deposits ever since.

ACKNOWLEDGEMENTS

We thank Dr R. G. West, whose palynological studies form the basis of the dating of the Crag Deposits mentioned, for kindly informing us of unpublished results of his work.

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MALACOLOGIA, 1973, 14: 38

PROC. FOURTH EUROP. MALAC. CONGR.

PHYLOGENETICAL INVESTIGATIONS IN THE NEOGENE ASTARTIDAE OF THE SOUTHERN NORTH SEA BASIN

Gerard Spaink

Geological Survey of the Netherlands
Haarlem, Holland

ABSTRACT

In the Pliocene deposits of the southern North Sea basin the family of Astartidae is an important group of Mollusca (Bivalvia) consisting of more than 15 species. These Astartidae can be divided into several taxonomical groups. In most of these groups the *Astarte* species can be arranged into pairs. The members of each pair have the same characters in contrast and one is always older than the other. The older member has a relatively thick, convex compressed and comparatively small shell, while the younger one has a relatively thin, flat and more oval shell, which is bigger. It follows that during the Pliocene epoch the Astartidae increased in size.

The young form may be an adjusting form from the old form, following the constant decrease of average temperature during the Pliocene. At the end of the Pliocene the average temperature fell lower and the Arctic influence became stronger. All Neogene Astartidae in the southern North Sea basin died out rather suddenly, except those species which extended to the open Atlantic coast as well as inhabiting the southern North Sea basin. They were able to migrate to the South and they still occur in the Mediterranean and along the Atlantic coasts of Western Europe. Next the Arctic Astartidae were able to migrate to the South and occupy the southern North Sea basin with other taxonomical groups which have nothing to do with the Neogene groups. Although some of these Arctic species come close together morphologically, no radiations into pairs, as with the Neogene species, occur.

A possible explanation of the cause of the radiation in the Neogene Astartidae is discussed.

The point of view that the Neogene Astartidae occur in morphologically similar pairs has its consequences for the nomenclature. The members of the pairs should be named to reflect this. Instead of *Astarte omalii* and *Astarte basteroti* we should write *Astarte omalii omalii* and *Astarte omalii basteroti*, and so on.

MALACOLOGIA, 1973, 14: 39-46

PROC. FOURTH EUROP. MALAC. CONGR.

MINERALOGY AND BIOGEOCHEMISTRY OF CALCAREOUS OPERCULI AND SHELLS OF SOME GASTROPODS[1]

O. S. Adegoke

Department of Geology, University of Ife
Ile-Ife, Nigeria

INTRODUCTION

The nature and structure of the operculum of gastropods and its probable equivalence to various other molluscan structures have received the attention of malacologists since Adanson (1757) first alluded to its homology with the second valve of pelecypods. Gray (1850) independently arrived at the same conclusion and, citing evidences based on morphology, mobility and growth pattern, he concluded that the operculum was a modification of the other shell of the gastropod, analogous to the second valve of the pelecypod, and secreted by the opercular mantle.

The idea was revived in recent years by Duges (1829), Fleischmann (1932), who concluded that the operculum and shell are opposed organs, left and right, and also by Pruvot-Fol (1954) who regarded the operculum as a ventral replica of the gastropod dorsal valve, homologous to the byssus of pelecypods and the aptychus and anaptychus of some ammonites.

Opponents of the suggested homology include Lamarck (1801), de Blainville (1825), Houssay (1884), Fischer (1940) and Kessel (1941). Unlike the proponents, the latter emphasized the distinctness in origin of the two structures - the shell being a product of the mantle while the operculum is produced by the foot - and their conclusions were grounded mainly on embryological and ontogenetic evidences (see especially Houssay, 1884 and Kessel, 1941).

In the present study, mineralogic and biogeochemical data are presented on the shells and the calcareous operculi of nineteen prosobranch species representing seven genera, *Astraea*, *Turbo*, *Lunella*, *Nerita*, *Neritina*, *Puperita* and *Natica* (see Pl. 1 and Table 1). The study is significant in that it provides quantitative proof that major differences exist between the two structures.

ANALYTICAL TECHNIQUES

The analysed shells were initially cleaned under a binocular microscope to remove all adhering epiphytes and foreign inorganic particles. The specimens were crushed to increase the surface area and treated with commercial Clorox to remove the organic matrix. The residue was thoroughly washed, dried, ground by hand in a mortar and passed through a sieve with 100 meshes per inch. Large specimens were ground in their entirety, whereas two or more specimens of smaller shells were ground together

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[1]Most of the analytical data reported here were obtained when the writer held a postdoctoral fellowship at the California Institute of Technology, Pasadena, California. The writer thanks Professor Heinz A. Lowenstam, Margaret Dekkers and Elizabeth Bingham. The specimens illustrated on Plate 1 were kindly supplied by Dr. Rosewater of the Smithsonian Institution, Washington, D. C.

TABLE 1. Summary of analytical data

Species	Weight (gm)	% Aragonite		% Mg		% Sr	
		Shell	Operculi	Shell	Operculi	Shell	Operculi
Astraea longispina (Bermuda)	4.57	100	35	0.01	0.67	0.16	0.14
	8.71	100	28	0.01	0.88	0.15	0.14
	12.42	100	26	0.01	0.91	0.15	0.13
	23.68	100	13	0.01	1.06	0.16	0.13
Astraea undosa (California)	-	100	100	0.02	0.09	0.15	0.17
	-	100	100	0.03	0.11	0.14	0.16
Turbo setosus (Palau)	0.99	100	100	0.01	0.03	0.14	0.15
	3.35	100	100	0.01	0.02	0.16	0.14
	5.12	100	100	0.01	0.01	0.16	0.14
Turbo chrysostomus (Palau)	8.28	100	100	0.01	0.02	0.16	0.14
	15.54	100	100	0.01	0.03	0.16	0.13
	21.42	100	100	0.01	0.01	0.16	0.14
	24.73	100	100	0.02	0.03	0.14	0.13
	25.99	100	100	0.01	0.03	0.16	0.12
	26.69	100	100	0.01	0.03	0.14	0.12
Turbo argyrostomus (Palau)	31.59	100	100	0.01	0.03	0.15	0.14
Lunella smaragda (New Zealand)	0.65	100	100	0.01	0.05	0.15	0.14
	1.02	100	100	0.01	0.05	0.17	0.12
	2.29	100	100	0.01	0.06	0.16	0.16
Nerita peloronta (Bermuda)	2.96	68	100	0.32	0.04	0.18	0.51
	3.32	71	100	0.32	0.03	0.18	0.50
	4.34	67	100	0.30	0.03	0.22	0.50
Nerita tessellata (Bermuda)	-	56	100	0.49	0.05	0.16	0.43
	0.12	54	100	0.48	0.06	0.17	0.37
	0.46	48	100	0.48	0.05	0.16	0.37
	0.75	51	100	0.46	0.04	0.17	0.40
	0.89	51	100	0.51	0.08	0.17	0.43
	1.35	64	100	0.39	0.03	0.17	0.49
	1.46	45	100	0.54	0.04	0.17	0.41
	2.07	75	100	0.26	0.05	0.18	0.46
	2.43	63	100	0.36	0.05	0.16	0.36
	2.47	62	100	0.39	0.04	0.16	0.45
	3.16	70	100	0.28	0.03	0.16	0.45
Nerita albicilla (Palau)	3.35	76	100	0.27	0.05	0.18	0.31
	3.41	72	100	0.27	0.05	0.16	0.31
	3.47	69	100	0.34	0.05	0.17	0.31
Nerita polita (Palau)	8.18	75	100	0.35	0.03	0.20	0.40
	11.22	73	100	0.30	0.05	0.17	0.39
Nerita plicata (Palau)	0.13	63	100	0.55	0.04	0.18	0.36
	0.18	64	100	0.51	0.04	0.19	0.38
	0.23	66	100	0.58	0.05	0.23	0.38
	0.28	67	100	0.45	0.04	0.15	0.33

Table 1 (cont.)

Species	Weight (gm)	% Aragonite		% Mg		% Sr	
		Shell	Operculi	Shell	Operculi	Shell	Operculi
Nerita plicata	1.24	73	100	0.31	0.03	0.19	0.45
	1.39	77	100	0.41	0.04	0.23	0.46
	2.25	70	100	0.39	0.04	0.17	0.44
	2.40	64	100	0.44	0.04	0.22	0.45
	2.46	73	100	0.34	0.04	0.16	0.48
	3.86	73	100	0.35	0.04	0.17	0.46
Nerita picea (Palau)	1.12	68	100	0.58	0.05	0.21	0.42
	2.51	73	100	0.38	0.05	0.22	0.40
	5.58	78	100	0.30	0.05	0.25	0.46
Nerita senegalensis (Nigeria)	-	79	100	0.02	0.08	0.15	0.18
Neritina sp. (Palau)	0.08	94	100	0.01	0.04	0.23	0.76
	0.64	96	100	0.01	0.02	0.25	0.64
	0.73	97	100	0.01	0.02	0.29	0.52
Puperita pupa (Grand Cayman)	0.12	93	100	0.04	0.07	0.16	0.31
	0.15	95	100	0.06	0.07	0.17	0.27
	0.19	92	100	0.04	0.07	0.18	0.27
	0.22	94	100	0.05	0.08	0.16	0.30
	0.23	94	100	0.04	0.09	0.16	0.30
	0.32	94	100	0.05	0.07	0.18	0.28
	0.37	95	100	0.05	0.06	0.16	0.27
	-	93	100	0.05	0.06	0.17	0.30

to obtain powders large enough for analyses.

A representative portion of the sieved sample was removed for analyses. Aragonite percentages were determined by X-Ray diffraction as described by Lowenstam (1954). Percentage strontium and magnesium were estimated by the emission spectrographic and X-ray fluorescence techniques as described by Lowenstam (1961).

RESULTS AND DISCUSSION

The analytical results are shown in Table 1. No attempt is made to convert the Mg and Sr values to parts per million or to estimate mole percent of the carbonate because the study is interested merely in comparing the relative proportions between shell and operculum. Average values were used to plot the graphs shown in Figures 1 and 2.

Mineralogy

It has long been established that molluscan shells are either entirely aragonitic or composed of varying proportions of calcite and aragonite. The aragonite-calcite ratio is primarily affected by temperature, less so by the physiology of the organism and water chemistry (see Lowenstam, 1960). The effects of these factors on the values shown in Table 1 have been largely offset by comparing values for shells and operculi of the same individuals.

As emphasized by Kessel (1941), the operculum is largely aragonitic (see Fig. 1).

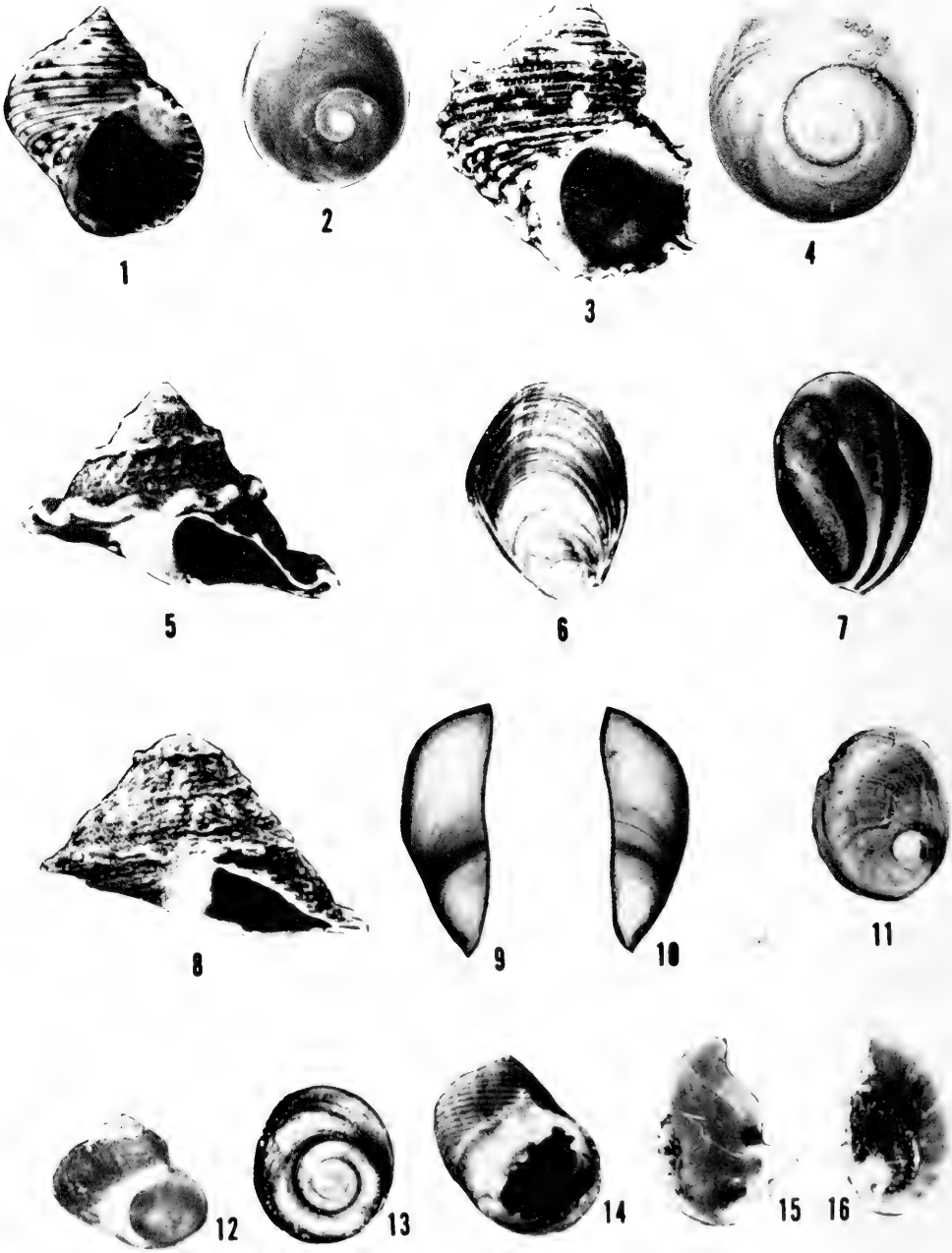

PLATE 1

FIGS. 1, 2. *Turbo setosus,* X1. FIGS. 3, 4. *Turbo chrysostomus,* X1. FIGS. 5–7. *Astraea undosa.* 5, shell X1; 6, 7, operculum X2. FIGS. 8–11. *Astraea longispina.* 8, shell X1; 11, operculum X 2; 9, 10, polished section of operculum showing dominantly calcitic initial portion X 4. FIGS. 12, 13, *Lunella smaragda.* 12, shell X 1; 13, operculum X 2. FIGS. 14–16. *Nerita peloronta.* 14, shell X 1; 15, 16, operculum X 2.

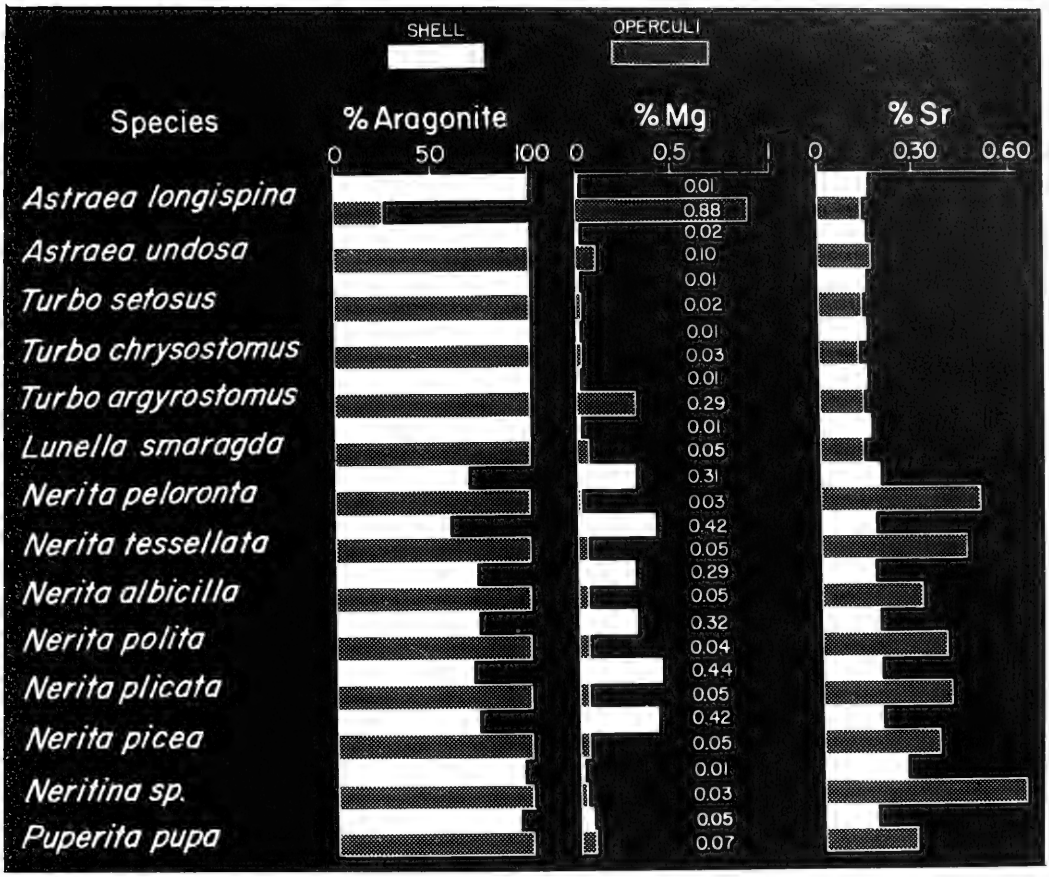

FIG. 1. Graph showing Aragonite, Magnesium and Strontium contents of the shells and operculi of the species analysed.

The only exception in this study is that of *Astraea longispina* which is dominantly calcitic (Figs. 1, 2). The proportion of calcite was found to increase directly with age (Figs. 2C, 2D), attaining a maximum of about 87% in the largest analysed specimen. The shell is, however, entirely aragonitic (Fig. 2C).

The neritids analysed (*Nerita*, *Neritina* and *Puperita*) were equally significant. The shell is bimineralic with varying proportions of calcite and aragonite (Fig. 1). The operculi, however, uniquely have 100 percent aragonite. These two groups conclusively show that gross physiological differentiation, demonstrated by mineralogic differences, exists between the secretions of the mantle and foot of the same gastropod.

Astraea undosa, *Natica*, the species of *Turbo* and the closely related *Lunella* have monomineralic shell and operculum.

Magnesium content

The biogeochemistry of Magnesium was discussed in detail by Chave (1954) and was aptly summarized by Lowenstam (1960). Both support a mineralogic control of Mg content in which the calcitic structure accommodates a considerably larger amount of Magnesium in solid solution than the aragonitic structure. Turekian and Armstrong (1960), however, contended that generic affinity is more important than crystal form.

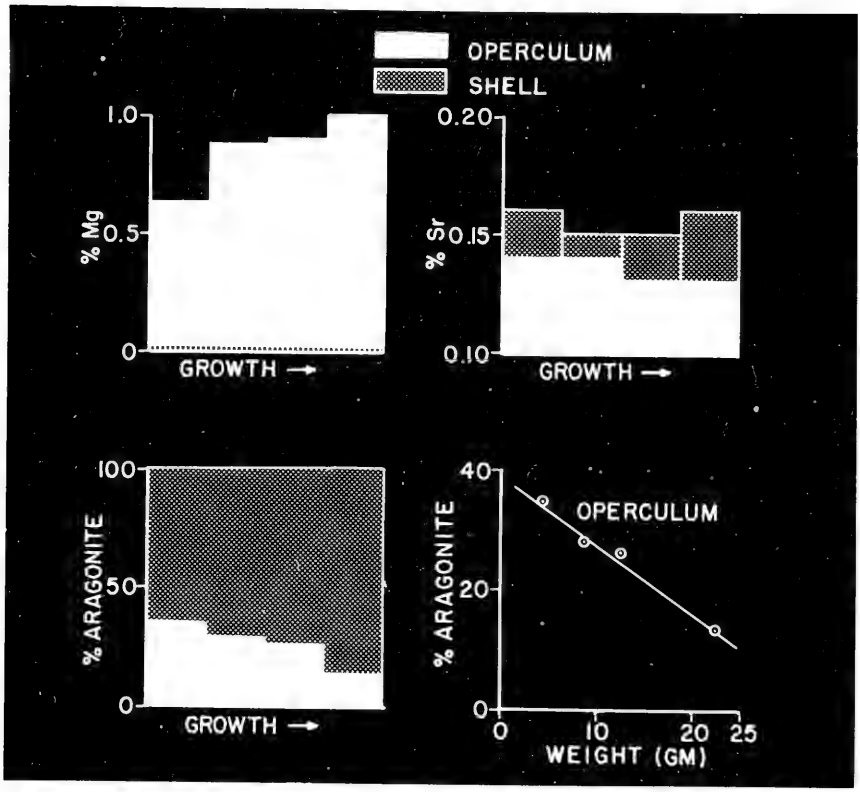

FIG. 2. Analytical data on *Astraea longispina* showing: A, Mg content, B, Sr content and C, Aragonite content of shells and operculi relative to age. D, Graph showing the inverse relationship between aragonite content of the operculum of *A. longispina* and the growth stage.

The major differences in Mg values recorded in the bimineralic species studied here can be directly correlated with differences in mineralogy (see Fig. 1). For example, the entirely aragonitic shell of *Astraea longispina* shows a Mg content of about 0.01 percent whereas the dominantly calcitic operculum of the same specimens show a range between 0.67 and 1.06 percent (Fig. 2A). The completely aragonitic neritid operculum, by contrast, shows a low Mg content (0.02-0.09 percent), whereas their calcitic shells show a range between 0.26 and 0.58 percent. In both *Neritina* and *Puperita* with low calcite content (3-8 percent) in the shell, the Mg value is comparably low in shell and operculum.

These results indicate that the Mg content is influenced more by mineralogy than generic affinity.

The entirely aragonitic species offer better examples for studying the biogeochemical differences between shell and operculi. Though the Mg content of both structures is expectedly low, the operculi consistently show higher Mg values than the shells (see Fig. 1).

Strontium content

The Strontium content of calcareous shells is, in general, affected by the same factors which influence the Mg content. The effect of the crystal form is different in that the aragonitic structure accommodates more Sr in solid solution than the calcitic structure (Odum, 1957; Lowenstam, 1960). Turekian and Armstrong (1960), however,

favored generic control.

Among the neritids, the aragonitic operculi show higher Sr values (0.27-0.76 percent) than the calcite-bearing shells (0.15-0.29 percent), thus substantiating Odum's (*op. cit.*) and Lowenstam's (*op. cit.*) views. The fact that the operculum of *Neritina* and *Puperita* have almost twice as much Sr as the shell despite the low calcite content (3-8 percent) of the latter, coupled with the virtually identical Sr content of the aragonitic shells and the dominantly calcitic operculi of *Astraea longispina* (see Table 1) indicate that generic affinity may be as important as crystal form in the distribution of Sr.

SUMMARY

Though the suggested homology of operculi and shells of gastropods and the supposed equivalence of both to the valves of pelecypods is no longer accepted, little quantitative data have been published on the subject. Nineteen calcareous operculi-secreting prosobranch species representing seven genera (*Astraea*, *Turbo*, *Lunella*, *Nerita*, *Neritina*, *Puperita* and *Natica*) were examined minerallogically by X-ray diffraction and biogeochemically by X-ray fluorescence and emission spectrographic methods. The results confirm the existence of major differences between the two structures.

The operculi (except that of *Astraea longispina*) shows 100 percent aragonite even when the associated shell contains a fair proportion of calcite.

Strontium concentration is consistently lower in shells (0.13-0.23%) than in operculi, with the highest concentrations (0.31-0.76%) occurring in the neritid operculi. Magnesium concentration is, on the average, lower in shell (0.01-0.08%; 0.26-0.58% in calcite-bearing neritid shell) than in operculi (0.01-0.11%). The highest concentration of 0.67-1.06% was recorded in the calcite-bearing operculi of *Astraea longispina*.

The data support a mineralogic control of Mg content as proposed by Chave (1954) and Lowenstam (1960) but contradict the generic control supported by Turekian and Armstrong (1960). The Sr content, however, seems equally influenced by both factors.

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MALACOLOGIA, 1973, 14: 47-51

PROC. FOURTH EUROP. MALAC. CONGR.

TRANSFERT DU CALCIUM A TRAVERS L'EPITHELIUM DU REPLI OPERCULAIRE CHEZ *ASTREA RUGOSA* L. (TURBINIDAE)

Jean Vovelle

Histologie et cytologie des Invertébrés marins
Université de Paris VI, France

Le "repli operculaire" qui peut recouvrir aux deux tiers l'opercule calcifié du Gastéropode *Astrea rugosa* (Turbinidae) apparaît comme un matériel histologique favorable pour démontrer l'évidence du transfert de calcium à travers une partie de son épithélium. Des travaux antérieurs nous ont familiarisé avec le problème de la composante protéique tannée de l'opercule des Prosobranches et nous savons qu'*Astrea* en donne une variante intéressante par son opercule oligogyre sous-jacent à la galette aragonitique dont l'élaboration nous retient présentement. Mais si la zone de l'épithélium pédieux dorsal immédiatement antérieure à la surface d'insertion du disque operculigère révèle une chimie spécifique où l'on peut démontrer les composantes protéique, aromatique et phénolasique de la lame organique inférieure, la zône en croissant réfléchi qui la précède vers l'avant de l'animal, cette face interne, concave, du repli operculaire, ajustable au front de croissance de l'opercule calcaire, est logiquement seule concernée par la traversée d'un calcium que nous allons reconnaître comme labile, sous forme soluble, et que par conséquent les techniques histochimiques courantes échouent à mettre en évidence. Le recours à divers artifices d'histochimie et de radioautographie à l'échelle de la microscopie photonique ou électronique, ou d'histoenzymologie, permet de tourner la difficulté et de marquer les étapes de son passage.

HISTOCHIMIE

On a pratiqué dans un premier temps sur coupes à la paraffine de pièces fixées par les liquides appropriés (alcool-chloroforme, alcool-formol selon la formule de Mc Gee Russell) les techniques les plus classiques de détection du calcium ionique insoluble: aux métaux lourds (Stoelzner, Von Kossa), aux laques (purpurine, rouge nucléaire solide et alizarine selon les protocoles de Mc Gee Russell), au rhodizonate de sodium. Leur réponse est toujours négative, sauf parfois pour indiquer une légère pellicule apicale superficielle dans les plissements de l'épithélium de la face concave du repli. Cette réponse négative est tout à fait cohérente avec celle que l'on connaît au niveau des territoires de l'épithélium palléal impliqués dans la sécrétion de la fraction minérale de la coquille.

La technique récente de Kashiwa (1966) au Glyoxal bis (2.hydroxyanil) (=GBHA) permet d'envisager la chélation du calcium soluble sous réserve qu'il soit maintenu totalement ou partiellement en place par les techniques préliminaires. Pratiquée sur coupes au cryostat de tissus frais elle donne une réponse positive dans toute la zone conjonctive sous-épithéliale du repli operculaire, sous forme de traînées intensément colorées, et se retrouve plus discrètement soulignant la bordure en brosse de l'épithélium.

Puisqu'il s'agit évidemment de calcium ionique soluble, dont l'emploi de la micro-incinération, pratiquée sur coupes au cryostat de tissus frais, assure, au niveau même de l'épithélium, la présence dans des spodogrammes trop grossiers pour apporter des indications supplémentaires, on aurait pu imaginer le recours aux techniques de précipitation par l'acide oxalique pour sa caractérisation ultérieure. Décevant en

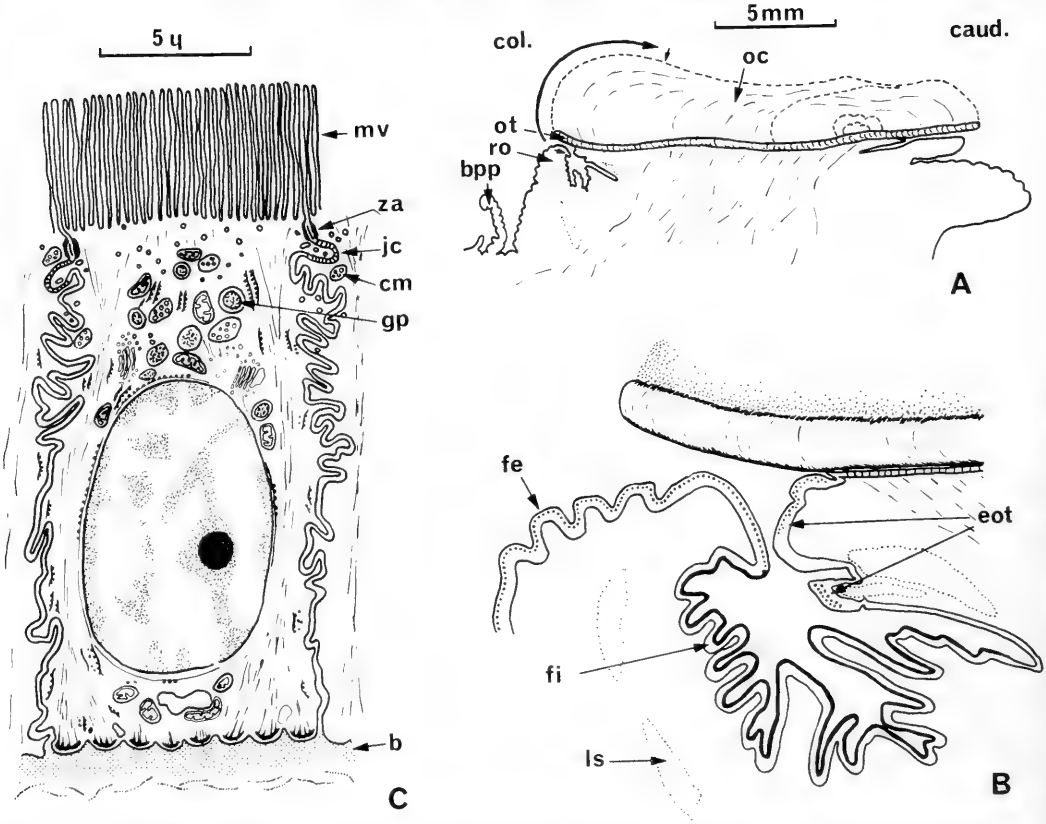

FIG. 1. A, Coupe sagittale de la zone dorsale operculigère du pied; bpp: bourrelet palléal postérieur; col: région columellaire; caud: région caudale; oc: opercule calcaire; ot: opercule protéique tanné; ro: repli operculaire. B, Détail de la région antérieure columellaire et du repli operculaire; eot: épithélium sécréteur de l'opercule protéique tanné; fe: face externe pigmentée du repli operculaire; fi: face interne sécrétrice de l'opercule calcaire; ls: lacunes sanguines. C, Organisation ultrastructurale d'une cellule de la face interne du repli operculaire; b: basale; cm: corps multivésiculaires; gp: granulations pigmentaires; jc: jonction cloisonnée; mg: microvillosités; za: *zonula adhaerens*.

microscopie optique le procédé connait un certain succès dans sa transposition en microscopie électronique (Carasso et Favard-1966; Kniprath-1971) lorsqu'il s'agit d'animaux dulçaquicoles mais son usage pour notre matériel marin était d'emblée aléatoire.

Nous avons préféré nous adresser à la transposition électronique d'une technique aux métaux lourds (acétate de Pb, cf. Carasso et Favard-1966) dont l'intérêt essentiel est de procéder à une substitution sur pièce, préalable aux procédures de déshydratation et d'enrobage, et par conséquent de fournir un état meilleur de conservation en place du métal substitué, observable à l'échelle ultrastructurale. Nous avons suivi le protocole des auteurs précités, et observé sur microscope Hitachi HS 7 et U 11 B des coupes ultraminces avec ou sans post-coloration selon la formule de Reynolds. La post-coloration permet de retrouver des images plus satisfaisantes et plus proches du plan d'organisation cytologique (dont nous avons déjà rendu compte par ailleurs), en éliminant un fin précipité généralisé d'ailleurs significatif. Les localisations plus massives qui subsistent dans ces conditions concernent un précipité important entre les microvillosités de la bordure en brosse, des dépôts en réservoirs dilatés au niveau de la portion subapicale des espaces intercellulaires, caractérisée par sa *zonula adhaerens* et ses jonctions cloisonnées, et des dépôts plus discrets mais réguliers

dans toute la partie inférieure des espaces intercellulaires, jusqu'à la basale et au conjonctif sous-jacents qui présentent par endroits des accumulations considérables du métal substitué.

RADIOAUTOGRAPHIE

Le recours aux techniques de radioautographie a été développé à partir de l'emploi du Ca 45, utilisé sous forme de chlorure et injecté dans la région dorsale du pied en solution aqueuse à 20 mC/mg d'activité spécifique (la taille des animaux et la précarité de l'installation empêchent d'ajouter, comme Istin et coll.-1970, l'élément marqué au milieu ambiant). Après une survie de deux jours l'animal est sacrifié et la pièce fixée suivant les cas pour la microscopie optique à l'alcool formol, ou, pour la microscopie électronique, soit à la glutaraldéhyde à 3 p.100 dans le tampon phosphate à pH 7, soit suivant la technique à l'acétate de plomb de Favard et Carasso. Les images obtenues en microscopie photonique ont le mérite de souligner la dissymétrie des deux versants externe et interne du repli operculaire. La seule face interne présente une réponse importante dans le conjonctif sous-jacent et, très intensément, au niveau de la bordure en brosse épithéliale. L'itinéraire suggéré dans le conjonctif est moins superficiel que l'étape terminale indiquée par la méthode histochimique au GBHA et, sur des images d'exposition suffisante, certaines cellules conjonctives apparaissent renforcées.

Les quelques images obtenues en microscopie électronique doivent leur rareté à la nécessité imprévue d'une longue exposition (2 mois et demi) et les impacts radioactifs observables concernent essentiellement les zones de jonction intercellulaires subapicales de l'épithélium du repli interne: dans quelques cas elles se superposent précisément aux corps multivésiculaires abondants à leur voisinage.

HISTOENZYMOLOGIE

L'histoenzymologie des phosphomonoestérases a le double mérite de nous proposer l'existence de processus enzymatiques impliqués dans ce transfert du calcium et de différencier grâce à eux formellement les deux faces externe et interne du repli operculaire, suivant une ligne de séparation dont la radioautographie en microscopie photonique suggérait déjà l'importance.

La recherche des phosphomonoestérases alcalines non spécifiques a donné des résultats convergents par les deux méthodes utilisées (de Gomori au nitrate de cobalt et de Pearse aux colorants azoïques couplés) sur coupes à la paraffine ou au cryostat avec légère post-fixation formolée. Elle correspond à une réponse positive élective au niveau de la bordure en brosse apicale de l'épithélium de la seule face concave du repli, alors que la face externe reste réfractaire.

L'adénosine triphosphatase, démontrée par les deux méthodes de Wachstein et Meisel et de Padykula et Herman sur coupes au cryostat avec légère post-fixation formolée fournit une réponse superposable à la précédente, qui se complète dans la zone apicale sous-jacente à la bordure en brosse par la mise en évidence d'un système supplémentaire de granulations. Elles seules subsistent dans les contre-épreuves, notamment par mise en oeuvre du 2-3-dimercapto-1-propanol (BAL) qui bloque l'activité phosphatasique non spécifique de la bordure en brosse. On a pu supposer leur rapport avec les structures mitochondriales, mais les images de ces organites qu'on a pu leur superposer, fournies tant par la microscopie photonique (fuchsine d'Altmann), que par la microscopie électronique, concernent également, bien qu'à un degré moindre, la région basale de la cellule épithéliale. Exclusivement apicales, deux catégories de formations restent à considérer comme support de l'ATPase: les formations

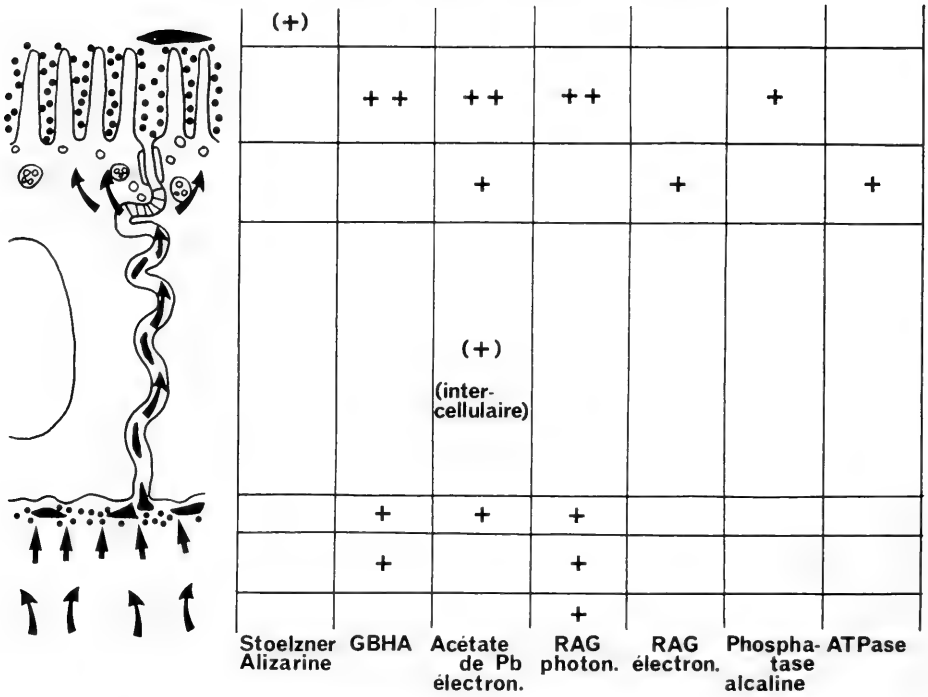

FIG. 2. Tableau interprétatif du passage du calcium au niveau de l'épithélium de la face interne du repli operculaire.

sphérulaires "pigmentaires" (à conchoporphyrine), bien plus rares au niveau de la face interne de l'épithélium que dans sa face externe, et les "corps multivésiculaires" signalés par le microscope électronique.

Malgré les images imparfaites qu'elle nous a fournies, la transposition ultrastructurale de la technique de Wachstein et Meisel confirme la mise hors de cause des mitochondries et semble impliquer de préférence les corps multivésiculaires.

CONCLUSION

En somme, dans le domaine de l'histochimie et de la radioautographie, aussi bien à l'échelle photonique qu'électronique, les images que nous avons pu obtenir, toutes dépendantes de conditions diverses du maintien en place préalable d'un calcium prioritairement sous forme ionique soluble, fournissent des états plus ou moins satisfaisants, mais qui se manifestent heureusement comme des jalons complémentaires.

Le tissu conjontif sous-jacent, jusqu'à la basale de l'épithélium de la face interne du repli, affirme son rôle de vecteur et assure l'origine endogène de la substance minérale. L'amorce d'une précipitation de cette dernière apparait dans les intervalles des microvillosités de la bordure en brosse de cet épithélium particulier: on est assurés d'ailleurs de la présence de phosphomonoestérase alcaline non spécifique à ce niveau. Entre les deux, la traversée de l'épithélium proprement dit privilégie, à l'échelle untrastructurale, les espaces intercellulaires jusqu'aux dispositifs de jonction sub-apicaux. Ces données, cohérentes avec ce qu'on sait du transport des liquides à travers les épithéliums (cf. Diamond et Torney-1966), sont comparables à celles par exemple que Neff a fourni récemment à propos des glandes calcifères d'un Serpulidé.

Au niveau de la zone apicale sous microvillositaire de l'épithélium des corps multivésiculaires ou des formations vacuolaires interviennent, qui elles aussi peuvent rappeler les images de Neff ou de Kniprath, et qui dénoncent l'ultime transport actif du calcium secrété.

SUMMARY

The "opercular fold" of *Astrea rugosa* secretes the calcareous piece overlying the protein operculum. Only epithelium of the internal opercular surface is crossed by the labile calcium ions. Presence of the calcium cannot be detected using standard histochemical techniques. The specific technique of Kashiwa using GBHA shows localization of soluble calcium at the level of the epithelial brush border, as well as on the basal lamina and the underlying connective tissue. The lead acetate staining method for electron microscopy also demonstrates the presence of calcium, implicating the intercellular spaces up to their subapical junction and finding again the accumulations at the level of the *basal lamina*, just as the precipitates on the microvilli. The use of calcium 45 for radioautography in photonic microscopy illustrates the role of the vehicle of the connective tissue and the elective elimination of the cation at the level of the epithelial brush border of only the internal side. The histoenzymological research of the nonspecific phosphomonoesterases and of the ATPase also allows us to detect this precisely defined region. Radioautography at the level of ultrastructures marks out the final active transfer of calcium in the apical zone under microvilli of this privileged epithelium.

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MALACOLOGIA, 1973, 14: 53-61

PROC. FOURTH EUROP. MALAC. CONGR.

MANTLE ACTIVITY FOLLOWING SHELL INJURY IN THE POND SNAIL *LYMNAEA STAGNALIS* L.

Lucy P. M. Timmermans

Zoological Laboratory, University of Utrecht, The Netherlands[1]

ABSTRACT

Histological and histochemical studies were carried out on the mantle of *Lymnaea stagnalis* at various intervals after a shell defect.

In the mantle area underlying the damaged shell area, the epithelial cells become elongated and show an increased content of RNA and alkaline phosphatase. At first (3 and 5 days after a shell defect), the stimulated area is considerably larger than the exposed region. Afterwards (8-16 days) the area of activated epithelium is restricted to the exposed mantle area. Peroxidase is demonstrated in the exposed mantle epithelium and in the repaired shell membrane.

These results indicate that the mantle epithelium plays an important role in shell repair. The appearance of peroxidase in the exposed mantle epithelium and in the repaired shell points to the formation of tanned periostracum proteins after shell damage.

INTRODUCTION

During normal growth of snails, the increase in mantle area is coupled with an increase in shell area. It is now generally accepted that the shell is to be considered as a secretion product of the mantle, especially the mantle border, and that each layer of the shell is secreted by a definite region of the underlying mantle.

In the mantle border of *Lymnaea stagnalis* (Fig. 1) a few sharply defined zones can be distinguished in the outer epithelium with histochemical methods for RNA, alkaline phosphatase and peroxidase (Timmermans, 1969). The high content of RNA in zones 1 and 2 indicates that these areas are involved in protein synthesis, required for the formation of the periostracum. It is assumed that the enzyme peroxidase, which is present in this region only, plays a part in the tanning of periostracum proteins. The RNA in zone 3 may be involved in the formation of the inner layer of the periostracum. The formation of the calcareous layers is ascribed to zones 4 and 5. These zones, but not the periostracum-forming cells of zones 1-3, contain the enzyme alkaline phosphatase which therefore is assumed to play a role in calcium deposition. Next to alkaline phosphatase this region contains glycogen, carbonic anhydrase, ATP-ase and enzymes of the citric acid cycle, but not RNA and peroxidase.

Generally, damage to the shell is followed by repair of the damaged region. However, it is still an unsolved question whether the periostracum is repaired, when a shell defect is not in contact with the mantle border. According to Simroth & Hoffmann (1928), Kessel (1933) and others, the periostracum in Gastropods is not repaired. On the other hand, Beedham (1965) reports that in lamellibranchiates a true periostracum is repaired after damage to the shell.

Repair of a shell defect is carried out by the mantle, and it may be assumed that during shell repair the mantle tissue, underlying the damaged area, shows an increased activity. The increased activity might be manifested by an enlargement of the epithelial cells underlying the damaged shell area and by an increased enzyme activity in these cells. It is also possible that amoebocytes play an important role in shell

[1]Present address: Zoological Laboratory, Agricultural University, Wageningen, The Netherlands.

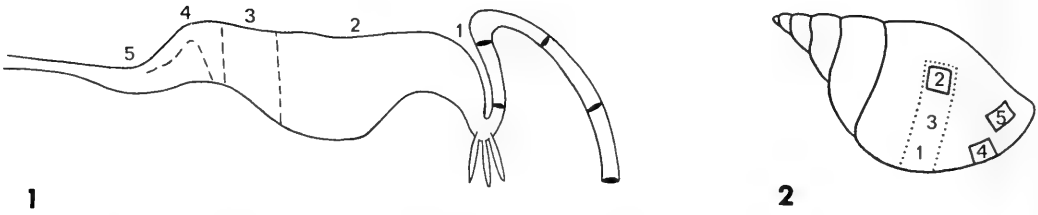

FIG. 1. Transverse section through the mantle of *Lymnaea stagnalis* to illustrate the localization of the chemical compounds and enzymes. Zone 1 + 2, RNA, peroxidase; Zone 3, RNA; Zone 4, alkaline phosphatase; Zone 5, alkaline phosphatase, glycogen, carbonic anhydrase, ATP-ase, cytochrome oxidase, succinate dehydrogenase (and other dehydrogenases).

FIG. 2. Shell of *Lymnaea stagnalis*, schematic drawing to illustrate the location of the fragments. 2,4,5, removed shell fragments; 1,2,3, (dotted line): mantle segment, used for histological and histochemical examination.

repair by carrying repair material to the damaged region (Wagge, 1951; Abolins-Krogis, 1963, 1968). If the periostracum is not repaired, particularly those enzymes will show an increased activity which are concerned with calcium secretion, as the calcium layers only contain a small amount of organic matrix. If, on the other hand, a periostracum is actually repaired, the appearance of compounds and enzymes can be expected which are involved in the formation of periostracum proteins. These considerations made it desirable to investigate : 1. whether the epithelial cells underlying the damaged shell area become enlarged; 2. whether the amounts of RNA and alkaline phosphatase increase; 3. whether peroxidase is present. A positive reaction for peroxidase may be an indication that the periostracum is repaired, whereas a negative peroxidase reaction may mean that no periostracum material has been formed.

MATERIAL AND METHODS

For the experiments snails of the same age (4 months) were used, which had been reared in the laboratory. Shell-fragments of 0.5 - 0.6 cm^2 were removed with a dentist drill. The fragments were selected from the border of the shell and from areas to which the mantle edge could not be retracted (Fig. 2).

At intervals from one hour to 21 days after the removal of the shell-fragments snails were anaesthesized (Joosse and Lever, 1959) and segments of the mantle were excised for fixation as shown in Fig. 2 (dotted line). The slices consist of mantle border (1), tissue from below the removed shell area (2) and the tissue in between both mantle areas (3). Equivalent mantle segments of control snails were used for comparison.

Mantle slices were fixed at 1, 2, 3, 5, 24 hours and at 3, 5, 7, 8, 12, 15, 16 and 21 days after inflicting shell damage. After each period at least three experimental snails and three control snails were used. The height of the epithelium was measured with an ocular micrometer.

The mantle slices were freeze-dried or fixed in acetone at 4° C followed by embedding in paraffin. Also fixation in formol-calcium at 4° C, followed by cryostat sectioning has been applied. The sections were stained with hemalum eosin for histological examination and with methylgreen-pyronin (Brachet, 1953) for the detection of RNA. The azo dye method of Pearse (1960, 1968) was used for the demonstration of alkaline phosphatase; the activity of peroxidase was investigated with the benzidine blue method (v. Duyn, 1955) after formalin fixation and cryostat sectioning.

TABLE 1. Size of cells and content of RNA, alkaline phosphatase and peroxidase in the mantle epithelium underlying a damaged shell area.

Time after shell damage in days	Height of cell in μ		RNA		Alkaline Phosphatase		Peroxidase	
	exper.	control	exper.	control	exper.	control	exper.	control
3	8-12	6-8	+/++	tr	tr/+	+		
5	15-18	6-8	++/+++	tr	++	+		
7/8	24-30	6	+++	tr	++	tr		
12	24-30	6-8	+++/++++	tr	+++	tr	++	-
15/16	24-32	6-8	+++	tr	++	+	++	-
21	20-30	6-8	++/+++	tr	+/++	tr		

++++
+++ intense reaction
++ distinct reaction
+ moderate reaction
tr weak reaction

Acetone fixation followed by paraffin embedding was preferred as routine method for the detection of RNA and alkaline phosphatase, as with this method clear and comparable histological pictures were obtained from the long slices of mantle tissue. Although the alkaline phosphatase activity may be slightly less after acetone fixation, the same distribution pattern was obtained as in freeze-dried or cryostat sections, though incubation periods had to be prolonged. The peroxidase method was only carried out at 12-16 days after damage of the shell.

RESULTS

Repair of the damaged shell area

After removing a marginal portion of the shell (Fig. 2, nr. 4 or 5) the snail retracted the mantle border up to the damaged area, where new shell material was added. After a few days the removed part was completely replaced. The removed portion was restored more rapidly than an equivalent area of normal shell was formed. When a fragment of shell was removed so far from the edge that it was impossible for the snail to retract the mantle border up to the damaged area (Fig. 2, nr. 2), repair also takes place but distinctly slower. The first sign of repair in *Lymnaea stagnalis* was often visible three days after removal of the shell-fragment. It was a thin proteinaceous layer which already contained calcium carbonate crystals. In many cases however, the regeneration membrane[2] appeared later.

Histology and histochemistry of the mantle underlying the damaged shell area.

The results are represented in Table 1. The shell defect was situated near or above the kidney; the underlying mantle epithelium was compared with equivalent epithelium

[2]The membrane formed in the damaged area of the shell.

FIG. 3. Size of cells and activity of alkaline phosphatase in the mantle epithelium, 12 days after shell injury. A, Exposed mantle epithelium; intense activity of alkaline phosphatase in the apical parts of the cells; cell height 24–30 μ. Note that also the nuclei are enlarged considerably. B, Equivalent mantle area of control snail; no activity of alkaline phosphatase; cell height 6–8 μ (azo dye method, freeze-dried sections, x700).

of control snails. In all investigated snails the epithelium of the mantle border showed an intense reaction of alkaline phosphatase and RNA which indicates that the snails were actively secreting shell material at the time of fixation (Timmermans, 1969). Within 24 hours after damage of the shell, no enlargement of the cells was observed. The amount of alkaline phosphatase and RNA was small and did not differ from the controls.

Three days after damage to the shell, the mantle epithelium had enlarged from the mantle edge up to and including the damaged area. The cell length was 8-12 μ, whereas in control snails the cell length was 6-8 μ. The amount of RNA had increased considerably in the whole epithelium, whereas the activity of alkaline phosphatase was weak, even less than in control snails.

Five days after damage of the shell the epithelium was considerably thickened over its whole length from the mantle edge up to and including the damaged area. The cell length was 15-18 μ, an increase of more than 50% compared with control snails. The

amount of RNA had increased considerably in the whole slice and the activity of alkaline phosphatase had increased too.

Seven and eight days after damage of the shell the epithelium was thickened up to 24-30 μ, the cells were three or four times as large as in control snails. In this group the area of cell enlargement and increased activity was restricted to the epithelium underlying the damaged shell area. This epithelium contained a large amount of RNA and a distinct activity of alkaline phosphatase.

Twelve, fifteen, sixteen days after damage of the shell. The area of cell elongation and activity was restricted to the epithelium underlying the damaged shell area. In this area the length of the cells was 24-30 μ (Fig. 3A), i.e., three or four times as large as in the epithelium of control snails (Fig. 3B). The thickened epithelium showed intense reactions for RNA and alkaline phosphatase (Fig. 3A).

Twelve and sixteen days after damage of the shell a group of snails was fixed in formol calcium and the peroxidase reaction was carried out. The exposed epithelium showed an intense reaction, whereas the mantle epithelium of control snails remained unstained. A positive reaction was also obtained in the regeneration membrane.

Twenty-one days after damage of the shell, cell elongation was restricted to the exposed area of the mantle. The epithelium showed less activity, compared to 12 and 16 days after damage. The length of the cells was 20-30 μ, the amount of RNA and alkaline phosphatase had decreased, but was still considerable.

In many cases, the mantle epithelium underlying the damaged shell area was injured and appeared to have vanished. In these cases the "wound" area was filled up with a large number of cells. These might be amoebocytes carrying repair material to the damaged shell. However, alkaline phosphatase and RNA have never been detected in these cells, whereas the epithelium surrounding the wound was thickened and contained large amounts of RNA and alkaline phosphatase.

DISCUSSION

The mantle

After damage to the shell at some distance from the mantle border, an increased activity is noticed in the outer mantle epithelium resulting in an enlargement of the cells and an increasing content of RNA and alkaline phosphatase. At first, the whole epithelium from the mantle border up to and including the repair area is activated. Clearly, the stimulated portion of the mantle is considerably larger than the area in contact with the shell defect. Afterwards, beginning 8 days after shell damage, the area of activated epithelium becomes restricted to the region underlying the damaged shell area. The signs of increased activity were not observed before three days after shell damage and at that time a regeneration membrane containing calcium salts is mostly present already. This indicates that the repair processes had started earlier though they could not be detected with the applied methods. Abolins-Krogis (1963) observed in *Helix* changes in the mantle tissue related to shell repair within three hours after shell damage. However, she did not observe RNA, alkaline phosphatase and cell elongation in the mantle epithelium. According to her, (1963, 1968) the mantle and the digestive gland in *Helix* are activated after damage of the shell and repair material and calcium are transported by amoebocytes from these regions towards the damaged part of the shell. Also Wagge (1951), Wagge & Mittler (1953) and Kapur & Gupta (1970) report amoebocytes to be involved in shell repair in land snails. The results obtained in the present study, and also those of Durning (1957) for *Helix* and of Beedham (1965) and Saleuddin (1967, 1969) for *Anodonta*, indicate clearly that the mantle epithelium plays an important role in shell repair. The increase in RNA indicates that proteins are synthesized which are necessary for the matrix of the re-

generation membrane; the increase in alkaline phosphatase may be connected with calcium deposition and the appearance of peroxidase indicates that the secreted proteins are tanned. A fair amount of RNA and alkaline phosphatase in the epithelial cells of the mantle after damage of the shell, is reported by Durning (1957) for *Helix* and by Saleuddin (1967) for *Anodonta*. Saleuddin (1969) found a twofold increase in activity of alkaline phosphatase.

The increase in RNA and alkaline phosphatase and the appearance of peroxidase in the exposed epithelium proves that this epithelium is capable of transformation and of obtaining functions normally restricted to specific cell groups of the mantle border. Moreover, RNA and peroxidase, on the one hand, and alkaline phosphatase, on the other hand, which in the mantle edge are contained in separate cell groups, are located in the same cells in the repair area. Beedham (1965) observed in *Anodonta* too that different shell-forming functions are performed by one and the same type of cells in the repair area. First the cells become elongated and form a periostracum and prismatic layer. At that time they resemble histologically and histochemically the cells in the periostracum-forming region. Afterwards, these cells resume their normal shape while repairing the inner calcareous layer. The same phenomenon was described with electron microscopy by Kawaguti and Ikemoto (1962) for the bivalve *Musculus*. Taylor and Kennedy (1969) showed in *Anodonta* that periostracum and prismatic sheets can also be formed spontaneously in the nacreous layer of undamaged shells. Beedham concluded from his observations that the relationship which normally exists between the different shell layers and the secretory epithelial zones of the mantle are not specific and unalterable. The present study shows that this is also true for a representative of the gastropods. The possibility of the underlying epithelium being destroyed after damage to the shell in *Lymnaea stagnalis*, so that cell elongation and the appearance of peroxidase would be properties of new cells and not newly acquired properties of existing cells, must be rejected. Shortly after damage a large area of epithelium reacts with elongation and with the appearance of new compounds, whereas the "activation" is only afterwards restricted to the epithelium underlying the damaged area.

According to Beedham, in *Anodonta* the periostracum is repaired after damage to the shell. In *Lymnaea stagnalis* the presence of peroxidase in the exposed epithelium suggests that in this snail also the periostracum is repaired. However, histological and histochemical investigations indicate that in the regeneration membrane two types of lamellae are formed; one type is histologically and histochemically similar to the matrix of the calcareous layers, the other may have the same properties as the periostracum (to be published). These results suggest that periostracum material is actually formed, but probably not a true periostracum.

Source of calcium

The calcium necessary for shell repair has been supposed to be provided by the neighbouring areas in the shell (Wagge, 1951), by calcium cells of the digestive gland (Wagge, 1951; Abolins-Krogis, 1961, 1968), by calcium cells situated in the connective tissue of the mantle (Durning, 1957; Guardabassi and Piacenza, 1958; Tsujii, 1960; Abolins-Krogis, 1963) and by the food (Wagge, 1951; Bierbauer, 1957). Wagge (1951) observed in *Helix* that calcium is not deposited in the shell when food is lacking. Bierbauer (1957) observed in histochemical and quantitative investigations in *Helix* that the amount of calcium in the digestive gland and mantle is not diminished during shell regeneration and that in springtime and summer when feeding conditions are good, regeneration is accomplished in much shorter time than in winter. Shell repair was accelerated by injections of calcium. Bierbauer (1957) concluded from these observations that in *Helix* the calcium, neces-

sary for shell repair is derived from the food and not supplied by the calcium cells of the mantle and digestive gland. In *Lymnaea stagnalis* it has been shown in experiments with calcium-45 added to the water that calcium is rapidly deposited in the shell, particularly in the shell edge, whereas in the calcium cells of mantle and digestive gland only a limited amount is deposited (Timmermans, 1969). This indicates that in this animal under normal circumstances the calcium cells do not provide the calcium for the shell of fast growing snails; it may be assumed that also for shell repair, the necessary calcium is supplied by the surrounding water or by the food. According to Van Der Borght and Van Puymbroeck (1966) nearly all the calcium obtainable from the food is extracted by *Lymnaea stagnalis* but nevertheless about 80% of the acquired calcium is derived directly from the water. This calcium is taken up against an electrochemical potential gradient (Van Der Borght & Van Puymbroeck, 1964).

Calcium transport

Wagge (1951), Wagge and Mittler (1953) and Abolins-Krogis (1963, 1968) supposed that in *Helix* calcium and other repair material is transported by amoebocytes, which migrate into the exposed surface of the mantle and which secrete and calcify the repair membrane. In *Lymnaea stagnalis* such transport was not observed. In the area underlying the damaged shell region in this animal, a large accumulation of small cells is observed only when the epithelium is damaged too. However, positive reactions were not obtained in these cells with the applied histochemical methods. The fact that these cells are observed only in areas of damaged epithelium and not below the surrounding activated epithelium or in an exposed mantle area with intact epithelium suggests that these cells have a protective function against inflammation. The manner in which calcium and other repair material is transported to the exposed epithelium in *Lymnaea stagnalis* still remains to be solved.

ACKNOWLEDGEMENTS

I wish to thank Prof. Dr. Chr. P. Raven for his valuable criticism and critical reading of the manuscript; Mrs. J. Akkermans-Kruyswijk for careful technical assistance and Mr. H. van Kooten and co-workers for preparing the photographs.

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RESUME

ACTIVITE DU MANTEAU PENDANT REGENERATION DE LA COQUILLE CHEZ L'ESCARGOT *LYMNAEA STAGNALIS* L.

Lucy P. M. Timmermans

Des études histologiques et histochimiques ont été appliquées au manteau de *Lymnaea stagnalis* à intervalles divers après ablation d'un fragment de coquille.

Dans la région du manteau, située au-dessous de la fracture de la coquille, l'épithelium s'est épaissi montrant une augmentation d'ARN et de phosphatase alcaline. Au début (3 à 5 jours après la fracture), la région activée était considérablement plus étendue que l'épithelium au-dessous de la fracture. Plus tard (16-18 jours) l'activité s'est limitée à la région découverte. L'enzyme peroxidase a été détectée dans l'épithelium découvert et dans la fraction régénerée de la coquille.

Ces resultats ont montrés l'importance de l'épithelium du manteau pour la régénération de la coquille. L'apparition de peroxidase dans l'épithelium découvert et dans la fraction régénerée de la coquille, a indiquée que des proteines tanneés ont été formées après fracture de la coquille.

MALACOLOGIA, 1973, 14: 63-79

PROC. FOURTH EUROP. MALAC. CONGR.

A NEW THEORY OF FEEDING AND DIGESTION IN THE FILTER-FEEDING LAMELLIBRANCHIA

Brian Morton

Department of Zoology, The University of Hong Kong

ABSTRACT

Recent observations regarding the feeding and digestive processes of the filter-feeding Lamellibranchia do not find accord with the currently accepted concept of continuous and simultaneous feeding and digestion in these animals.

A new theory embracing both the old and the new facts is put forward in which these processes are considered to be rhythmic in nature.

INTRODUCTION

Amongst the Bivalvia, the Lamellibranchia form a relatively homogenous grouping that most taxonomists agree are distinct from the Protobranchia, e.g., Ridewood (1903), Pelseneer (1911), J. E. Morton (1967), Owen (1959), Purchon (1959), Yonge (1959). The Septibranchia are linked by some with the Lamellibranchia, e.g., Newell (1965), J. E. Morton (1967), but not by others, e.g., Pelseneer (1911), Purchon (1960, 1962).

In the primitive Protobranchia the digestion of food is considered to be mainly extra-cellular (Owen, 1956), whilst there is a paucity of information on the feeding and digestive processes of the scavenging Septibranchia (Yonge, 1928).

The Lamellibranchia (constituting the majority of the Bivalvia) exhibit a wide variety of form and exploit a wide range of aquatic environments. They do, however, possess many common features not the least of which is that they are mostly filter-feeders and that the process of digestion is both extra-cellular and intra-cellular.

The processes of feeding and digestion in the Lamellibranchia are considered to be continuous and simultaneous. Owen (1966) states that "the more or less continuous mode of feeding which characterises the majority of bivalves would seem to preclude a synchronous activity of the digestive system." Purchon (1968) can also be quoted as reporting that "It is generally considered that feeding and digestion are continuous processes in bivalves, new food material being added all the time, and unwanted material being as constantly eliminated by passage into the mid gut." Purchon (1971) has, however, subsequently suggested, in the light of new evidence, that these processes may not be continuous and that a reappraisal of current thought on this subject is called for.

Owen (1955) showed how such a continuous system could operate, and there can be little doubt that the components of the feeding and digestive processes he elucidated do operate in the Lamellibranchia. This is not questioned. The purpose of this paper is to demonstrate that these component processes do not necessarily occur simultaneously and continuously and to show that feeding and digestion in the Lamellibranchia is a dynamic process.

THE PRESENT THEORY

It is generally assumed that members of the Lamellibranchia are filtering suspended or deposited material from the water continually, this process being the function of the ctenidia.

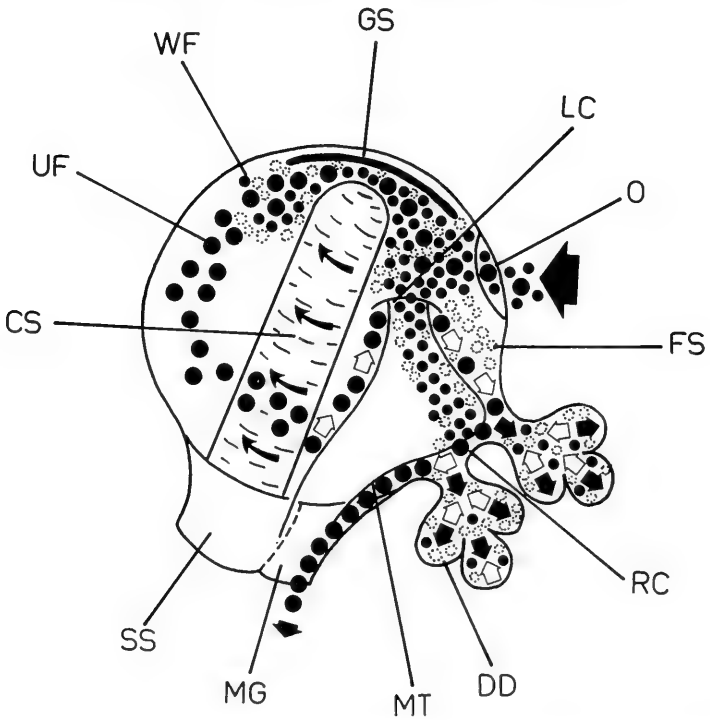

FIG. 1. A diagrammatic representation of the suggested functioning of the stomach and digestive diverticula of the Eulamellibranchia, CS, Crystalline style; DD, Digestive diverticula; FS, Fragmentation spherules; GS, Gastric shield; LC, Left caecum; MG, Mid gut; MT, Major typhlosole; O, Oesophagus; RC, Right caecum; SS, Style sac; UF, Large unwanted particles; WF, small food particles. (After Owen, 1955.)

As the water is passed through the ctenidia exchange of oxygen and carbon dioxide takes place and particulate material is abstracted and passed either up or down the gill lamellae to be concentrated in mucoid strings and passed anteriorly. Large particles are removed by ciliary sorting mechanisms on the ctenidia and also by powerful ciliary tracts on the mantle and visceral mass and passed posteriorly to be ejected as pseudofaeces via the inhalant opening. From the ctenidia particles are passed to the labial palps where further rigorous sorting takes place. Finally, particles of a suitable size are passed to the mouth where they are ingested (Atkins, 1936, 1937a, b, 1938).

In the stomach the mucoid food string becomes wound around the crystalline style (Fig. 1, CS) which acts as a capstan, winding in the string. The tip of the style revolves against the gastric shield (GS) and it is assumed that this action mechanically breaks up the food material; the style dissolves as it rotates, releasing extra-cellular enzymes bound up in its matrix. Since the style is continually dissolving distally it must be continually secreted at its basal end. As the food is broken up it is subjected to further sorting in the stomach and large indigestible particles are passed to the mid gut (MG) in the intestinal groove of the major typhlosole (MT). Small particles are continually being passed to the digestive diverticula (DD) where they are phagocytosed, subjected to intra-cellular digestive processes and finally assimilated. Waste from the diverticula is passed back to the stomach in fragmentation spherules (FS) which probably break up and aid in the primary extra-cellular digestion of newly arriving food material by release of small quantities of enzymes derived from the digestive diverticula.

TABLE 1. A summary of the species of lamellibranchs in which rhythmicity has been detected. The environmental variables to which the rhythms have been correlated have also been indicated with the authority.

Species	Rhythms detected	Authority
A. Freshwater		
Anodonta cygnea	Endogenous	Barnes, 1952, 1955
Anodonta cygnea	Daily	Sálanki, 1964; Sálanki & Vero, 1969
Unio pictorum	Daily	B. S. Morton, 1970b
Hyridella australis	Daily	Hiscock, 1950
Dreissena polymorpha	Daily	B. S. Morton, 1969b
B. Marine		
Venus mercenaria	Daily	Thompson, 1970
Venus mercenaria	Daily	Bennett, 1964
Venus mercenaria	Daily, monthly, 27-day	Brown *et al.*, 1956
Crassostrea virginica	Tidal, daily, monthly, 27-day	Brown, 1954; Brown *et al.*, 1956
Crassostrea virginica	Tidal	Haskin, 1964
Crassostrea virginica	Tidal	Carriker, 1951
Crassostrea virginica	Tidal	Kunkle, 1957
Crassostrea virginica	Tidal	Nelson, 1918, 1920, 1925, 1933
Crassostrea virginica	Tidal, daily	Loosanoff & Nomejko, 1946
Ostrea edulis	Tidal, daily	B. S. Morton, 1971
Cardium edule	Tidal	B. S. Morton, 1970a
Cerastoderma (=*Cardium*) *edule*	Tidal	Farrow, 1972
Arctica islandica	2x Daily (Tidal ?)	Winter, 1969, 1970
Mytilus edulis	Tidal	Gompel, 1937
Mytilus edulis	Tidal	Rao, 1954
Mytilus californianus	Tidal	Rao, 1953
Modiolus modiolus	2x Daily (Tidal ?)	Winter, 1969, 1970
Modiolus demissus	Tidal	Nagabhushanam, 1963
Macoma balthica	Tidal	B. S. Morton, 1970c
Macoma balthica	Tidal	Thorpe, 1972
Donax semignosus	Tidal	Mori, 1938, 1950
Donax denticulatus	Tidal	Trueman, 1971
Scrobicularia plana	Tidal	Thorpe, 1972
Mya arenaria	Tidal, daily, monthly	Dicks (pers. comm.)
Lasaea rubra	Tidal	J. E. Morton, 1956
Lasaea rubra	Tidal	McQuiston, 1969
Teredo navalis	Daily	B. S. Morton & McQuiston, 1973
Pecten jacobaeus	Daily	Sálanki, 1966
Lithophaga lithophaga	Daily	Sálanki, 1966

RHYTHMICITY IN THE LAMELLIBRANCHIA

Occurrence

Examination of the literature reveals that many lamellibranchs possess rhythms of activity (Table 1).

Pavlov (1885) first noted that the spontaneous activity of the adductor muscles of *Anodonta* assumed a regular periodicity. Marceau (1906, 1909) later showed that very many lamellibranchs of widely differing structure and mode of life exhibited a rhythmi-

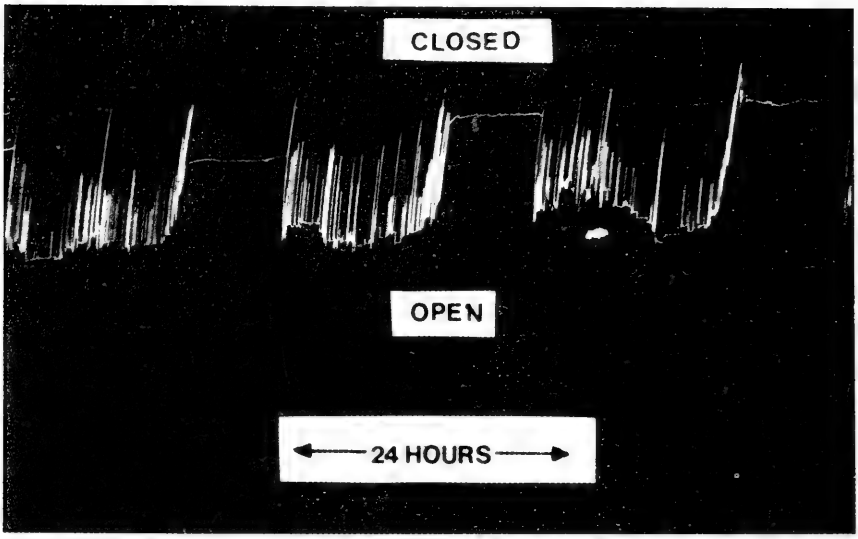

FIG. 2. A kymograph record of the activity of *Dreissena polymorpha*.

cal activity of the adductors. Subsequent research has shown that in most cases the rhythms so described can be correlated in some adaptive fashion with the rhythm of the environment. *Anodonta* apparently possesses an endogenous rhythm (Barnes, 1952, 1955) although recently Sálanki (1964) and Sálanki & Vero (1969) have suggested that this species may also possess a rhythm related to the phases of night and day.

Littoral lamellibranchs are affected by the rhythm of the tide and can be expected to respond to such environmental extremes. What is of interest, however, is that fresh water and sub-littoral forms also possess rhythms of activity and inactivity related to another environmental variant - night and day.

Monthly or semi-lunar cycles of activity are produced by the summation of tidal and diurnal rhythms in littoral bivalves, and may play an important role in the timing of breeding in these genera, as will be discussed later.

Nature

The rhythmical nature of lamellibranch behaviour has been recorded in various ways, e.g., by measuring the variation in water propulsion (siphoning) (Hopkins, 1936; Rao, 1953, 1954) or oxygen consumption (Gompel, 1937) but by far the most revealing method is to record the shell valve movements directly by means of a kymograph (Barnes, 1955; Koshtoyants & Sálanki, 1957). In every case which has been studied it has been shown that the period of activity is characterised by rapid phasic contractions, whilst the period of rest is characterised by either closure or gaping of the shell valves (Fig. 2) according to the species (Marceau, 1906, 1909). The phasic contractions rapidly close the shell valves, but relaxation of the adductor muscles allows the elastic ligament to force the shell valves open. This process is repeated many times during the period of activity. The "quick" portion of the adductor muscles might be responsible for phasic adductions whilst the "catch" portion of the adductor muscles might be responsible for the maintained closure of the shell valves during the quiescent period. In those lamellibranchs which gape during their quiescent period it would seem the "catch" mechanism is only used when the animal is disturbed.

Effect

The phasic contractions characteristic of the period of activity serve as a pump. Rapid closure of the shell valves forces filtered water (lacking in oxygen but rich in carbon dioxide) out of both inhalant and exhalant apertures and pseudofaeces and faeces out of the inhalant and exhalant apertures respectively. Opening of the valves again, reduces the pressure in the mantle cavity relative to the outside and fresh water enters via the inhalant aperture. Sâlanki & Lukacsovics (1967) have shown that *Anodonta* is rapidly filtering at this time and that oxygen consumption is also high.

During the period of quiescence the shell valves either close or gape according to the genus (Marceau, 1906, 1909). Whichever action is utilised the effect is the same, the water in the mantle cavity is not replenished by muscular action and filtration all but ceases. Sâlanki & Lukacsovics (1967) have shown for *Anodonta* that filtration is minimal and oxygen consumption negligible at this time. It has also been shown for *Dreissena* that filtration ceases at this time (B. S. Morton, 1970e) and in *Cardium edule* and *Teredo navalis* (B. S. Morton, 1970a; B. S. Morton & McQuiston, 1973) that the pH of the fluid in the mantle cavity falls, indicating that it is being depleted of oxygen and greatly enriched with carbon dioxide. Koch & Hers (1943) reported a similar rhythmicity in siphonal activity and oxygen uptake in *Anodonta* and Galtsoff (1964) and Sâlanki & Lukacsovics (1967) have recommended that shell valve activity be taken into account when studying filtration in lamellibranchs.

The regularity of these alternating processes of adduction and of quiescence in so many lamellibranchs precludes artefacts and to the contrary suggests that it is extremely important and is an intrinsic lamellibranch character.

FILTER FEEDING

It has been shown in many bivalve genera that the rhythmical nature of the adduction of the shell valves has a profound effect upon feeding. The phasic adductions characteristic of the period of activity greatly enhance the food trapping mechanisms by constantly replenishing the water in the mantle cavity. It has been considered that the ctenidia themselves were solely responsible for the inhalant stream; it now seems likely that this action is supplemented by the pumping motion of the shell valves. The long periods of quiescence observed in lamellibranchs limit feeding while the shell valves are shut or gaping. It would seem therefore that a high level of filter feeding in the Lamellibranchia is not necessarily continuous.

FUNCTIONING OF THE STOMACH AND DIGESTIVE DIVERTICULA

Unless such genera possess mechanisms for converting an irregular supply of food material into a constant stream then their digestive processes can not be continuous and simultaneous. It can be assumed that shortly after the last phasic adduction of a period of activity the mantle cavity is comparatively free of particulate material and all acceptable material has been passed to the stomach. In rare exceptions food may be stored in special organs associated with the stomach, e.g., the appendix of the Teredinidae. However, as will be discussed later the appendix generally has quite a different function. For most lamellibranchs it must be assumed that the cessation of feeding has a profound effect upon the digestive process.

The stomach contents

It has been shown for *Ostrea edulis* (B. S. Morton, 1971) that the constituents of the stomach fluids change considerably over the tidal cycle. The same is true for the appendix of *Teredo navalis* (B. S. Morton & McQuiston, 1973).

When *Ostrea* is feeding the stomach is full of ingested material. At the start of feeding this is in the form of distinct mucoid food strings. These strings are not present for long and it is not considered that the style is continually winding in food chains as previously thought. Later the food disappears from the stomach and for a short time the stomach fluid is relatively clear. Still later the stomach begins to fill with fragmentation spherules derived from the digestive diverticula; eventually these too disappear and food begins to enter the stomach with the recommencement of feeding.

Diurnal changes were also observed in the appendix of *Teredo navalis* and these reflected the changes occurring in the much smaller stomach, and showed a close similarity to the changes observed in the stomach of *Ostrea*, with the additional complication of the presence of wood fragments in the former (B. S. Morton & McQuiston, 1973).

The crystalline style

One of the most important single factors that has led to the acceptance of a concept of continuous feeding and digestion in the Lamellibranchia was the belief that the slow dissolution of the crystalline style released a constant supply of the enzymes that effect extra-cellular digestion of food material in the stomach. Constant dissolution assumed constant secretion at the basal end (J. E. Morton, 1952). Mitra (1901), however, believed the dissolution of the style to be periodic. Nelson (1918, 1920, 1925, 1933) showed that the style of *Ostrea virginica* was not always present and that on a rising tide it was a large firm rod, but on a falling tide it was reduced to an amorphous gelatinous mass. He further showed that the style of *Ostrea* could be reformed in 15 minutes. J. E. Morton (1956) similarly showed that the style of *Lasaea rubra* was formed and dissolved during every tidal cycle. Owen (1966) has stated that the style of lamellibranchs dissolves when the animals are kept out of water, under anaerobic conditions (also noted by Berkeley (1923)) or when the 2 valves are clamped together. Under natural conditions littoral animals are out of water at low tide; anaerobic conditions exist in the mantle cavity at certain times (i.e., during the quiescent phase) and very often lamellibranchs clamp their shell valves together for long periods of time.

My own studies on *Dreissena polymorpha*, *Cardium edule* and *Ostrea edulis* (B. S. Morton, 1969b, 1970a, 1971) have shown that the style dissolves either just before or during the early stages of feeding. This agrees with the findings of J. E. Morton (1956) on *Lasaea*. In *O. virginica* (Nelson, 1920), *O. edulis* (B. S. Morton, 1971) and *Lasaea rubra* (J. E. Morton, 1956) the style dissolves completely. This is not so in *D. polymorpha* and *C. edule* (B. S. Morton, 1969b, 1970a) in which it only partially dissolves. The enzymes of the crystalline styles of numerous lamellibranchs are well documented (Owen, 1966; Purchon, 1968) but since the style only dissolves occasionally these enzymes are released only intermittently and consequently extra-cellular digestion in the stomach is rhythmic too. The site of secretion of the matrix of the style is now generally assumed to be the typhlosole, e.g., List (1902), Nelson (1918), Lazier (1924), Graham (1931), Goreau *et al.* (1966), B. S. Morton (1969a, 1970a,d), Giusti (1970). The ciliated cells of the style sac itself probably only serve to rotate the style though they may also be responsible for the secretion of some enzymes.

The laminar nature of the style (Nelson, 1918; Kato & Kubomura, 1954; B. S. Morton, 1969a, 1970a) suggests that it is secreted intermittently. It is now postulated that at the time of secretion (Fig. 3,A), style material is poured into the style sac and coats the surface of the style; this has the effect of pushing the style forward, and this process is aided by the cilia which rotate the style. Eventually the newly produced style material solidifies and secretion stops. Dissolution begins (Fig. 3,B) and ceases when the thin basal end of the style is no longer in contact with the cilia of the style sac and cannot be pushed forward any further. This process in all probability occurs in those

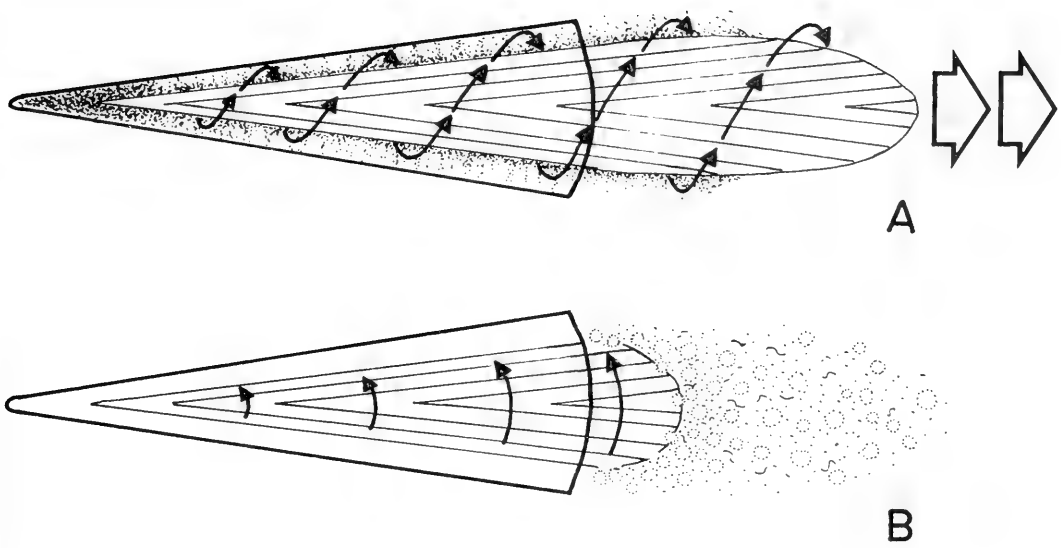

FIG. 3. A diagrammatic representation of the 2 processes of (A) secretion and (B) dissolution of the crystalline style of the Lamellibranchia.

bivalves in which the style does not dissolve completely, and accounts for the known facts regarding the lengthening and thickening of the style. In those bivalves in which the style dissolves completely, e.g., *Ostrea* and *Lasaea*, the process is much simpler although probably the same principles are involved; the style is secreted at one time and dissolved at another.

One of the commonest misconceptions regarding the crystalline style of lamellibranchs is that it is the most acid organ in the gut (Yonge, 1925, 1926a). In bivalves examined subsequently (B. S. Morton, 1969b, 1970a, 1971) the style has been approximately neutral, or at the most only slightly acid. The digestive diverticula appear to be the most acid region of the gut and in most species (but not in *Ostrea edulis*), the style does not buffer the stomach contents. This is true for *Dreissena* and *Cardium* where the pH of the stomach fluids varies widely over the course of the diurnal and tidal cycle respectively (B. S. Morton, 1969b, 1970a). In *O. edulis* the pH of the stomach contents remain fairly stable over the tidal cycle.

The gastric shield

The gastric shield of the Lamellibranchia is largely restricted to the left dorsal wall of the stomach. It has generally been regarded as protecting the stomach wall from the abrasive effect of the rotating crystalline style, though it may (Yonge, 1949) assist in

the trituration of stomach contents. Halton & Owen (1968) have shown that the gastric shield of the protobranch *Nucula sulcata* is enzymatically active. They further suggest that the gastric shield of lamellibranchs may also be enzymatically active, an observation supported by the recent work of McQuiston (1970), and not simply an inert protective structure. Should it subsequently be proven that the gastric shield generally plays an active role in digestion it is possible that this function would be closely associated with the functioning of the crystalline style and as such similarly regulated.

The sorting areas of the stomach

Purchon (1956, 1957, 1958, 1960) has made an especial survey of the stomach in the Bivalvia. In the Lamellibranchia the stomach possesses sorting areas that principally function by removal to the mid gut of large or indigestible particles leaving a suspension of fine particles for primary extra-cellular digestion by enzymes liberated by the style and subsequent transmission to the digestive diverticula for intra-cellular digestion.

Since it has been shown that lamellibranchs are not continually feeding, food is not always in the stomach and it therefore follows that the sorting areas are not always sorting potential food material. This is particularly true for the eulamellibranch sorting area type C (Reid, 1965b) in the digestive caeca. It is probable that in this organ the sorting mechanism manipulates food at one time and waste material at another.

The appendix

As noted earlier the contents of the appendix of *Teredo navalis* vary systematically over the course of 24 hours. Wood is always present, but at certain times either fragmentation spherules or filtered material too large to be digested are also found. As in *Ostrea* particulate material other than fragments of wood never occurs simultaneously with the fragmentation spherules. It appears that the appendix of *Teredo* serves partly as a temporary store of unusable or unwanted material and perhaps also as a reserve of potential food material. Purchon (1960) and Reid (1965b) have suggested the former function for the appendix of the Tellinacea which is homologous with the appendix of the Teredinidae (Yonge, 1949). Reid (1965b) further suggested that contraction of the adductor muscle periodically emptied the appendix of *Lima hians*.

The digestive diverticula

The digestive diverticula of the Lamellibranchia all possess a striking similarity. Their function has been elucidated by Yonge (1926b) and Owen (1955) who subsequently (Yonge, 1939; Owen, 1956) also showed that they differ fundamentally from those of the Protobranchia.

The digestive diverticula are organs of absorption and intra-cellular digestion (List, 1902; Vonk, 1924; Yonge, 1926b; Owen, 1955; Dinamani, 1957; Saleuddin, 1965; Sumner, 1966a,b; B. S. Morton, 1969a, 1970a,d). Mansour (1946), Mansour & Zaki (1946) and Mansour-Bek (1946) also considered them to be organs of secretion. It was considered by Owen (1955) that this secretory function could be derived from the disruption of fragmentation spherules, carrying the waste products of intra-cellular digestion, in the stomach. Subsequently Sumner (1966a,b) and McQuiston (1969) attributed a secretory function to the basiphil cells or "nests of young cells" of Yonge (1926b) which were considered to be responsible for the replacement of old spent digestive cells and the formation of new tubules (Yonge, 1926b; J. E. Morton, 1956; B. S. Morton, 1969b, 1970a,b,c, 1971).

Owen (1970) has now apparently clarified the issue and shown that the "nests of young cells" are composed of two cell types, one of which is secretory, the other perhaps being responsible for the replacement of both secretory and absorptive cells.

The location of the digestive diverticula in relation to the stomach varies from species to species, but in the Lamellibranchia they are mainly restricted to caeca. In many, but not all cases, the openings to the digestive diverticula are associated with an in-pushing of the major typhlosole which projects into the duct leading to the diverticula (Sorting area type C (Reid, 1965b)). Particles of food enter the caeca where they are transported to the openings of the ducts. It was assumed that small particles were continually entering the ducts and that the digestive diverticula were continually absorbing fluid and phagocytosing small particles. It was necessary to postulate a two way flow in the ducts supplying the diverticula in order to explain how the waste products of digestion could pass out while food material was entering. The counter-current theory (Owen, 1955) explained how this system could operate. Undoubtedly the principle underlying this theory is correct. The food entering the ducts does travel in the "upper" part of the duct and waste does travel out of the diverticula in the "lower" part of the tube (Mathers, 1972). The system, however, is not necessarily a counter-current since food is not necessarily entering the diverticula at the same time that waste is leaving the diverticula. It has now been established for *Dreissena*, *Cardium*, *Anodonta*, *Macoma*, and *Ostrea* (B. S. Morton, 1969b, 1970a,b,c, 1971) that the digestive diverticula undergo a pattern of cytological changes that is related to the feeding and digestive rhythm. This pattern closely approximates to that demonstrated by J. E. Morton (1956) and subsequently confirmed by McQuiston (1969) for *Lasaea* and the stages can be defined as 1) Formation, 2) Absorption and phagocytosis, 3) Digestion, 4) Breakdown, 5) Development and Formation (1). To this sequence must now be added the secretory function described by Sumner (1966a,b), McQuiston (1969) and Owen (1970). The enzymes are probably secreted prior to or during the absorptive phase.

During breakdown of the diverticula, the absorptive cells disintegrate releasing fragmentation spherules which pass into the stomach. Owen (1955) has suggested that their disruption in the stomach may aid primary extra-cellular digestion. This is probably true for some genera, e.g., *Lasaea rubra* (J. E. Morton, 1956), but since they are probably more acid than the organ that produces them, they may more importantly, also initiate style dissolution. pH may not be solely responsible for dissolution of the style at this time since the proteinaceous style (Bailey & Worboys, 1960) would be liable to dissolve if a protease were present (Reid, 1965a). Such a protease could be found in fragmentation spherules containing excess intra-cellular proteases derived from the digestive diverticula (Yonge, 1923; Rosen, 1949; Ganapati & Nagabhushanam, 1956).

Movement of food and waste in the stomach

Ciliary mechanisms have been considered as the main propulsive source for the movement of particles in the stomach of lamellibranchs. It has, however, been shown that the cilia at the opening of the caeca into the stomach usually beat out of the caeca thereby apparently hindering the entry of food material, but also probably more importantly, thereby preventing blockage of the openings (Purchon, 1955). Since the counter-current theory explaining the two way passage of material in the ducts of the diverticula may not necessarily function as originally envisaged since the inhalant and exhalant streams are separated temporally as well as spatially, it is necessary to find an alternative mechanism to account for the transport of material between the stomach and the digestive diverticula.

The tubules of the digestive diverticula are surrounded by a meshwork of muscle fibres. Owen (1955), Millar (1955) and J. E. Morton (1956) have all suggested that contraction of these muscles would expel waste from the diverticula. The last two authors report observing this action in *Ostrea* larvae and in *Lasaea* respectively. Reid (1965b) has suggested that the appendix of *Lima* is emptied by the contraction of the adductor

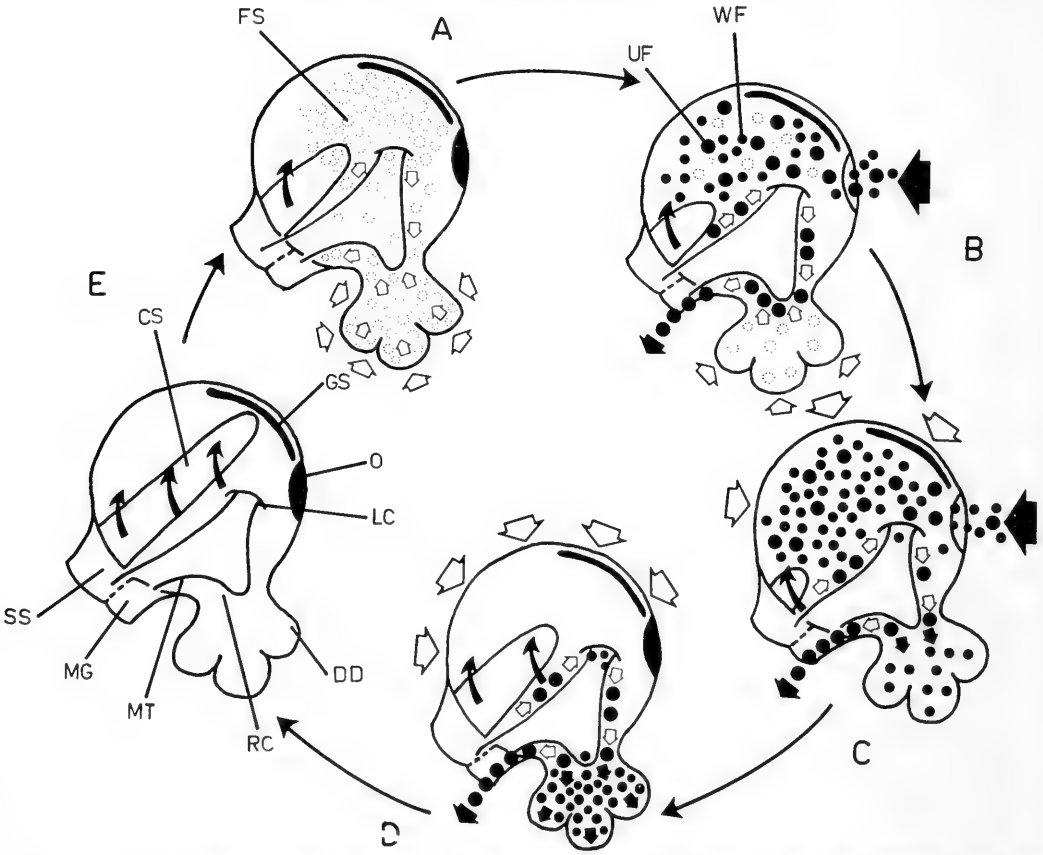

FIG. 4. Diagrammatic representations of the stomach in the Lamellibranchia showing how the digestive processes can be divided into a number of phases. (For lettering see Fig. 1.)

muscles, whilst the appendix of *Teredo* could be emptied by nothing other than by muscular activity (Purchon, 1960).

Possibly rapid phasic adductions of the adductor muscles at the time of feeding in lamellibranchs may also serve the subsidiary function of squeezing the products of extra-cellular digestion in the stomach into the diverticula, and at other times contractions of the muscle fibres investing the diverticula may help to pass waste materials into the stomach. As originally postulated by Graham (1949), Owen (1953) and Purchon (1955) opposing muscular forces acting on a fluid medium may be the principal agency for the transference of particulate material from one part of the alimentary tract to another in the Lamellibranchia.

DISCUSSION

Critical analysis of the available information suggests that the currently accepted theory of a steady state in feeding and digestion in the Lamellibranchia cannot account for many of the changes observed in the feeding and digestive processes and which are of a cyclical nature.

For those species examined the following sequence of events has been determined.

The animal feeds for a period of time. This action is characterised by rapid phasic contractions of the adductor muscles which serve to pump water into and out of the mantle cavity, thereby supplementing the inhalant ciliary currents produced by the

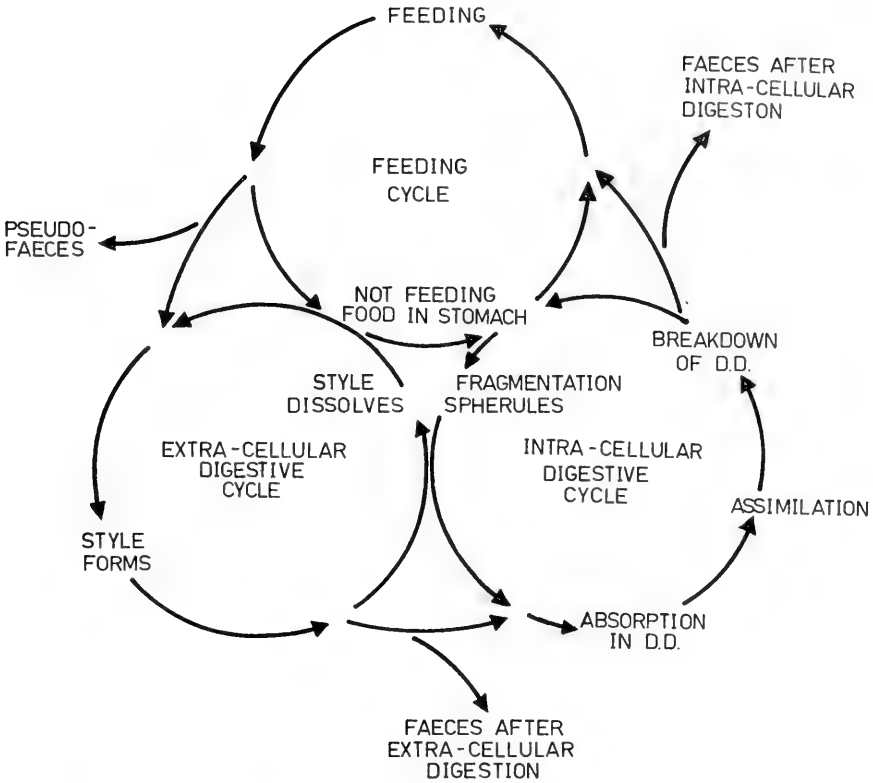

FIG. 5. A schematic representation of the rhythmic nature of the feeding process and extracellular and intracellular digestive mechanisms in the Lamellibranchia.

ctenidia. The ctenidia also serve to effect the filtration of the water once it is in the mantle cavity and to initially sort the food. Material of an acceptable size is passed to the labial palps for further rigorous sorting and ultimately selected material is transported to the mouth for ingestion.

The food arrives in the stomach at a time when the style (Fig. 4,CS) has either wholly or partly dissolved (Fig. 4, A), e.g., *Ostrea edulis* (B.S. Morton, 1971) or the arrival of food in the stomach initiates style dissolution (Fig. 4, B), e.g., *Dreissena polymorpha* (B.S. Morton, 1969b). In the former case the dissolution of the style is considered to have been caused by the arrival in the stomach of the fragmentation spherules (FS) derived from the digestive diverticula (DD). In the stomach the enzymes released from the dissolving style act upon the food to break it up. The partly digested food is then sorted in the stomach, large unwanted particles (UF) are passed to the mid gut (MG) in the intestinal groove of the major typhlosole (MT) (Fig. 4, B,C,D) and food material of an acceptable size is passed to the digestive diverticula for further extra-cellular digestion (Owen, 1970), absorption and phagocytosis, intra-cellular digestion and final assimilation. Passage of food material into the diverticula may be assisted by the phasic contractions of the adductor muscles that are occurring at this time.

When the animal ceases to feed (Fig. 4, D) (during the period of adductor quiescence) the mouth (O) may shut, remaining waste is passed to the mid gut and remaining food passed to the diverticula. The final closing action of the shell valves probably also removes the last pseudofaeces from the mantle cavity. The crystalline style now reforms and the epithelium of the digestive diverticula commence the process of breakdown (Fig. 4, E) eventually passing assimilated products to the rest of the body and producing fragmen-

tation spherules which are ultimately passed to the stomach (Fig. 4, A) probably by contraction of the meshwork of muscle fibres surrounding each digestive tubule. The digestive diverticula reform in preparation for another cycle whilst the fragmentation spherules begin to act upon the now fully formed style causing it to dissolve once again.

The process varies, as would be reasonably expected in such a diverse assemblage of animals, but the essential principle (Fig. 5) is evident in all those examined, and is usually regulated by an environmental rhythm.

It would seem to be generally accepted that the evolution of the Lamellibranchia occurred in the shallow coastal waters. Such animals would have been subjected to the twin environmental rhythms of the tide and night and day. These rhythms are apparently retained in modern littoral lamellibranchs (Table 1). Adaptive radiation of the Lamellibranchia into the sublittoral zone of the sea and into fresh waters removed the effect of the tide. Sublittoral forms now possess diurnal rhythms only. Similarly modern fresh water forms also possess diurnal rhythms although *Anodonta* may have taken the process one step further and evolved an endogenous rhythm; feeding as the necessity arises. Apparently the Lamellibranchia have retained either the primitive feeding mechanisms related to the tidal cycle or have transferred their feeding rhythm to the subsidiary rhythm of night and day. In littoral lamellibranchs, e.g., *Crassostrea virginica* (Brown *et al.*, 1956), *Ostrea edulis* (B. S. Morton, 1971) and *Mya arenaria* (Dr. B. Dicks, pers. comm.), it has also been suggested that summation of the tidal and daily rhythms produce a third rhythm related to the phases of the moon. Brown *et al.* (1956) have shown this rhythm to be of 14.8 days duration, being thus semi-lunar.

Spawning and the liberation of larvae in *Ostrea edulis* occurs at fortnightly intervals in relation to the phases of the moon (Korringa, 1947; Knight-Jones, 1952). This confirmed the earlier work of Orton (1926) who showed that in this species young larvae are more abundant in the gills of the adult immediately after the full moon whilst mature larvae showed peaks of abundance later. A lunar periodicity in spawning has also been shown for *Chlamys opercularis* (Amirthalingham, 1928) and *Pecten maximus* (Mason, 1958). The triggering mechanism for the release of larvae or gametes may be synchronised by the semi-lunar rhythm built up by the summation of the tidal and diurnal rhythms. Temperature may also play a role in ensuring that the gametes or larvae are not liberated in the wrong lunar cycle. Such a mechanism has obvious survival values.

It would appear that rhythmicity in the Lamellibranchia is widespread, regardless of the habitat and is important in correlating the various components of the complex feeding and digestive cycle.

SUMMARY

It has hitherto been believed that in the filter-feeding Lamellibranchia the processes of feeding and digestion were both held in a steady state. Careful study of both of these processes in a number of genera, both freshwater and marine in relation to the time factor, has shown this view to be untenable. These processes comprise a rhythmic sequence of phases related to environmental rhythms. Two alternate phases can be detected. In the first food is collected, filtered, selected and passed to the stomach. Food collection then ceases and the accumulated food material is digested. The complex organs of feeding and digestion in the Lamellibranchia are co-ordinated to a fine degree and the processes they initiate achieve a refinement hitherto unsuspected. Feeding and digestion in the Lamellibranchia is a dynamic process both temporally and spatially.

ACKNOWLEDGEMENTS

I would like to thank Professor G. Owen, Professor R. D. Purchon and Sir Maurice Yonge F. R. S. for their constructive criticism of the first draft of the manuscript of this paper.

Much of my own research embodied in this paper was undertaken when I was a research student with Professor Purchon and subsequently as a research associate at the Marine Laboratory of Portsmouth Polytechnic.

I have benefited greatly from discussions with many people, but I would particularly like to thank Dr. Peter Russell and Dr. Rob McQuiston.

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PROC. FOURTH EUROP. MALAC. CONGR.

THE INFLUENCE OF TEMPERATURE ON THE GROWTH RATE OF *BULINUS (BULINUS) TROPICUS* (KRAUSS) AND *LYMNAEA NATALENSIS* KRAUSS (MOLLUSCA: BASOMMATOPHORA)

J. F. Prinsloo and J. A. van Eeden

Snail Research Group of the Medical Research Council
Potchefstroom University for C. H. E., Potchefstroom, South Africa

It is no unusual experience for the freshwater malacologist who goes collecting snails, to end up with a wide range of sizes of the same species taken from the same pool at the same time, and it has almost become customary to regard such specimens as representing generations of different ages. A series of small specimens from a particular area is, furthermore, often identified as dwarfed representatives of a normally larger species and their small size is then vaguely attributed to possibly suboptimal conditions under which they might have lived. However logical these claims may be, their validity has, in our opinion, not yet been tested carefully enough.

The data discussed in this paper were collected during a laboratory investigation of the influence of temperature on such aspects as survivorship, reproduction rate and capacity for increase in *Bulinus (Bulinus) tropicus* (Krauss) and *Lymnaea natalensis* Krauss which was reported on by Prinsloo & Van Eeden (1969). The experimental set-up was, therefore, the same as that described in the report cited above. Growth rate was measured in terms of increase in mass and for this purpose all the snails in the experimental populations were weighed at monthly intervals commencing at 1.5 months from date of hatching. Thirty to thirty-five specimens of each species were reared from egg masses of the same age at each of the selected temperatures.

GROWTH RATE

The average mass per specimen at successive ages and at the different temperatures tested are given in Table 1 and the growth curves based on these data are reproduced in Figs. 1 and 2.

The data in the table and figures given reveal certain interesting differences between the 2 species. Throughout the experiment *Bulinus tropicus* enjoyed a mass advantage over *Lymnaea natalensis* at 27°, 25° and 21°C but at 18° and 15°C the latter species grew faster than the former right from the beginning (Table 1). In *B. tropicus* (Fig. 1) the mass increase at 18° and 15°C remained almost negligible up to 1.5 months and at 15°C this trend was maintained up to 2.5 months. It is, furthermore, evident that the rate of average mass increase per specimen increased with rising temperature and was best at 27°C. At both 27° and 25°C all the snails had died out before 4.5 and 5.5 months respectively. Egg deposition at these 2 temperatures, as also at 21°C, started almost simultaneously. This occurred before 1.5 months from the time of hatching and seems, at all the temperatures tested, to have been linked with an average mass of 0.02-0.04 g per specimen which, at 18° and 15°C, was respectively reached 1 and 2 months later than at the other temperatures. The best average mass increase (0.06-0.08 g per specimen per month) was also recorded at 27°, 25° and 21°C during the period between 1.5 and 2.5 months.

In *Lymnaea natalensis* (Fig. 2), as in *Bulinus tropicus*, the average monthly rate of mass increase at 15°C remained negligible up to 2.5 months after hatching but

TABLE 1. Monthly average mass in grams per specimen of *Lymnaea natalensis* and *Bulinus tropicus* reared at constant temperatures.

Age in months	Species	Temperature in °C				
		27	25	21	18	15
1.5	*L. natalensis*	0.0182	0.0253	0.0169	0.0203	-
	B. tropicus	0.0441	0.0455	0.0243	0.0051	-
2.5	*L. natalensis*	0.0321	0.0405	0.0452	0.0598	-
	B. tropicus	0.1198	0.1286	0.0935	0.0421	-
3.5	*L. natalensis*	-	0.0656	0.0758	0.1269	0.0569
	B. tropicus	0.1782	0.1572	0.1452	0.0912	0.0423
4.5	*L. natalensis*	-	0.0906	0.1401	0.1902	0.1203
	B. tropicus	-	0.1980	0.1748	0.1298	0.0822
5.5	*L. natalensis*	-	-	0.1803	0.2262	0.1953
	B. tropicus	-	-	0.2170	0.1734	0.1272
6.5	*L. natalensis*	-	-	0.1682	0.2475	0.2534
	B. tropicus	-	-	0.2455	0.2260	0.1780

from this age onwards it rose more steeply at this than at any of the other temperatures. In fact, the general trend was for the rate of mass increase to improve with decreasing temperature which is exactly the opposite of what we experienced in the case of *B. tropicus*. All the specimens at 27°C died out before reaching an age of 3.5 months. This is 1 month sooner than it had occurred in *B. tropicus* which, therefore, survived both 27°and 25°C better. The best average rate of mass increase (0.07 g per specimen per month) was recorded at 18°C during the period between 2.5 and 3.5 months, i.e., both later and at a lower temperature than in *B. tropicus*.

MASS DISTRIBUTION

In spite of the fact that all the experimental snails were hatched from egg masses deposited during the same 24 hour period the mass varied from specimen to specimen from the moment of hatching. That this would be so could already be detected in many egg masses before hatching. The snails could consequently be arranged in a series of mass groups of 12 mgm intervals as was done in Figs. 3-8. At 1.5 months (Fig. 3 and Table 2) the phenomenon of mass distribution was more marked for *Bulinus tropicus* than for *Lymnaea natalensis* and the percentage egg masses revealing it was distinctly highest at 27° and 25°C. At this age *B. tropicus* was differentiated into larger numbers of mass groups than *L. natalensis* at all the temperatures except 18°C at which temperature the latter species outnumbered it. At. 2.5 months (Fig. 4) the numbers of mass groups had increased for both species but this was particularly noticeable for *B. tropicus* at 27°C where, already, 12 mass groups were recorded. The histograms in Fig. 4 moreover reveal that the mass groups had, from the time represented by Fig. 3, moved towards the right, i.e., in the direction of the heavier groups, noticeably faster in the case of *B. tropicus* than that of *L. natalensis*. At 18°C, however, the latter species still had an advantage over the former. While the overall picture at 3.5 (Fig. 5) months was more or less similar to the one at 2.5 months, with *L. natalensis* maintaining its advantage at 18°C where 14 mass groups could be recorded, this species started gaining on *B. tropicus* also at 15°C.

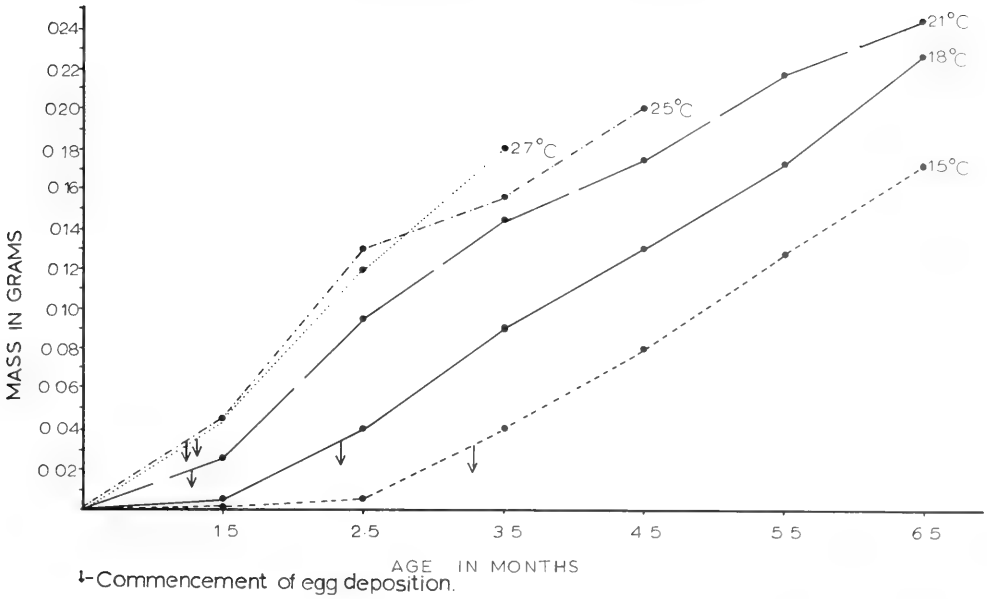

FIG. 1. Graphic presentation of the average growth rates per month of populations of *Bulinus tropicus* reared at constant temperatures.

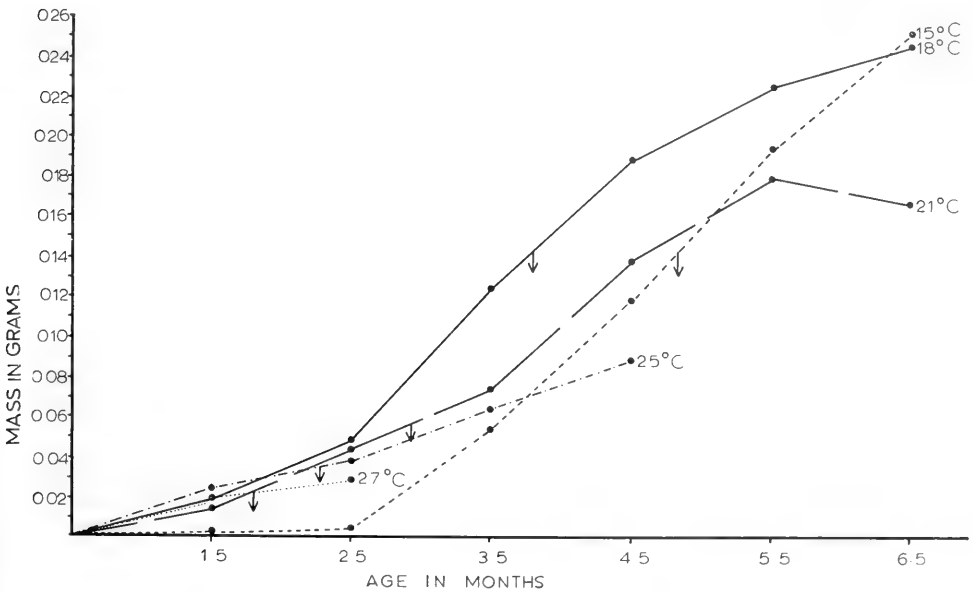

FIG. 2. Graphic presentation of the average growth rates per month of populations of *Lymnaea natalensis* reared at constant temperatures.

The most interesting novelty at 4.5 months (Fig. 6) was the large number of mass groups recorded for both species (16 each) at 21° C, the small number for *Lymnaea natalensis* at 25°C and the fact that, at 21° C, this species had gained on *Bulinus tropicus* with regard to mass increase. Towards the end of the experiment (Figs. 7, 8), however, the numbers of mass groups of *B. tropicus* had decreased considerably com-

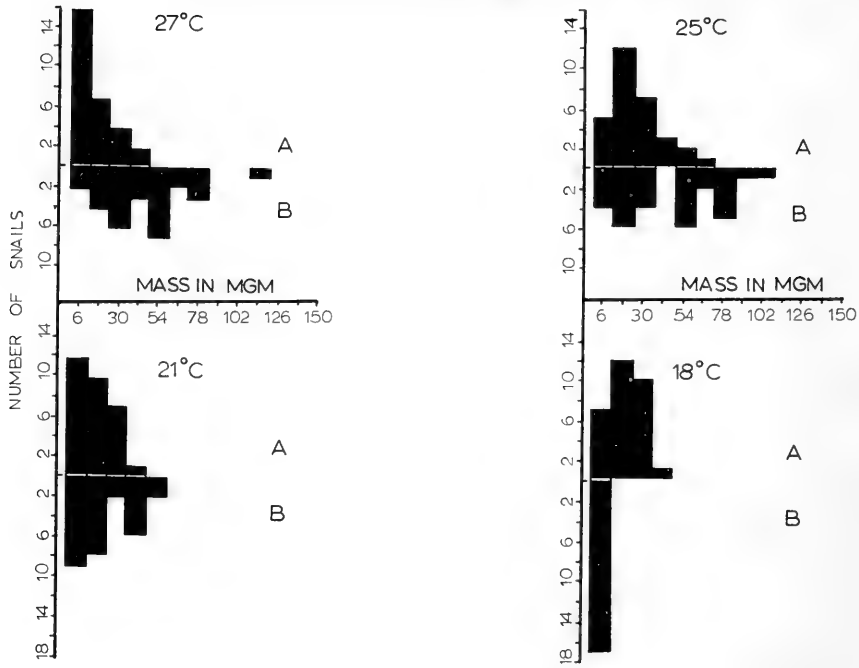

FIG. 3. Mass distribution in experimental populations of *Lymnaea natalensis* (A) and *Bulinus tropicus* (B) reared at constant temperatures. Age 1.5 months.

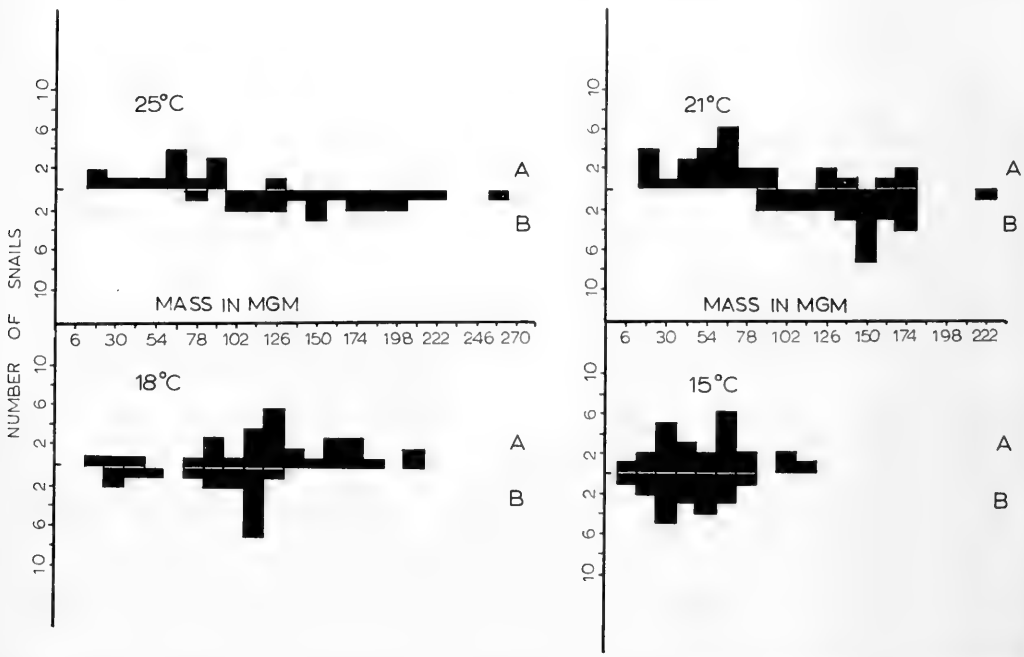

FIG. 4. Mass distribution in experimental populations of *Lymnaea natalensis* (A) and *Bulinus tropicus* (B) reared at constant temperatures. Age 2.6 months.

TABLE 2. Number of mass groups and mass range (mgm/specimen) in experimental populations of *Bulinus tropicus* and *Lymnaea natalensis* reared at different constant temperatures.

Age in months	Species	A mass groups B mass range in mg/spec.	Temperature in °C 27	25	21	18	15
1.5	*L. natalensis*	A mass groups	4	6	4	4	-
		B mass range	6-42	6-66	6-42	6-42	
	B. tropicus	A mass groups	8	8	5	1	-
		B mass range	6-114	6-102	6-54	6-6	
2.5	*L. natalensis*	A mass groups	6	9	8	9	-
		B mass range	6-102	6-114	6-90	6-102	
	B. tropicus	A mass groups	12	8	7	5	-
		B mass range	62-198	78-174	54-126	18-66	
3.5	*L. natalensis*	A mass groups	-	8	11	14	9
		B mass range		18-126	18-174	18-210	6-114
	B. tropicus	A mass groups	-	13	9	8	7
		B mass range		78-258	90-222	30-126	6-78
4.5	*L. natalensis*	A mass groups	-	3	16	12	11
		B mass range		78-102	30-246	30-270	30-198
	B. tropicus	A mass groups	-	9	16	10	7
		B mass range		114-270	78-270	30-210	18-114
5.5	*L. natalensis*	A mass groups	-	-	12	13	14
		B mass range			42-258	42-320	66-310
	B. tropicus	A mass groups	-	-	9	10	7
		B mass range			78-282	30-320	54-166
6.5	*L. natalensis*	A mass groups	-	-	9	13	14
		B mass range			54-222	102-342	138-354
	B. tropicus	A mass groups	-	-	8	8	7
		B mass range			174-380	42-380	90-222

pared with those of *L. natalensis*. This was particularly obvious at 15°C (Fig. 8) where no bulinid specimen of over 222 mg was still alive at the termination of the experiment. This contrasts strongly with the large numbers for *L. natalensis* at 18° and 15°C, viz., 13 and 14 respectively (Fig. 8). It is of interest to note that even at 5.5 months the populations of both species still contained specimens which, at all the temperatures still in operation, had not yet grown to beyond 54 mg.

The numerical data on which Figs. 3-8 are based are reproduced in Table 2, from which one gets the impression that whereas the number of mass groups tended to increase with age in *Lymnaea natalensis*, they reached a peak in *Bulinus tropicus* at 4.5 months and then gradually decreased again towards 6.5 months. It is certainly tempting to conclude that the differentiation into different mass groups must in some

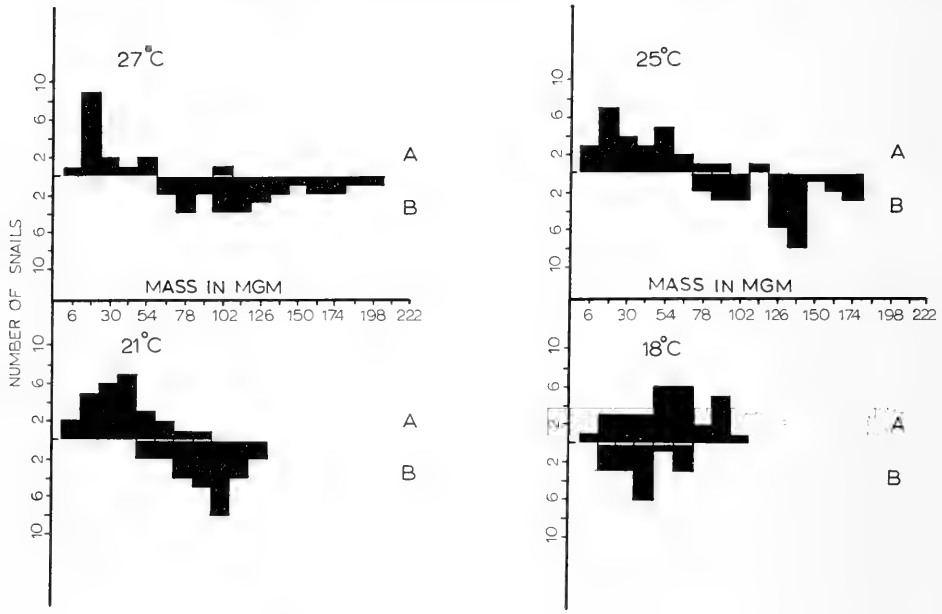

FIG. 5. Mass distribution in experimental populations of *Lymnaea natalensis* (A) and *Bulinus tropicus* (B) reared at constant temperatures. Age 3.5 months.

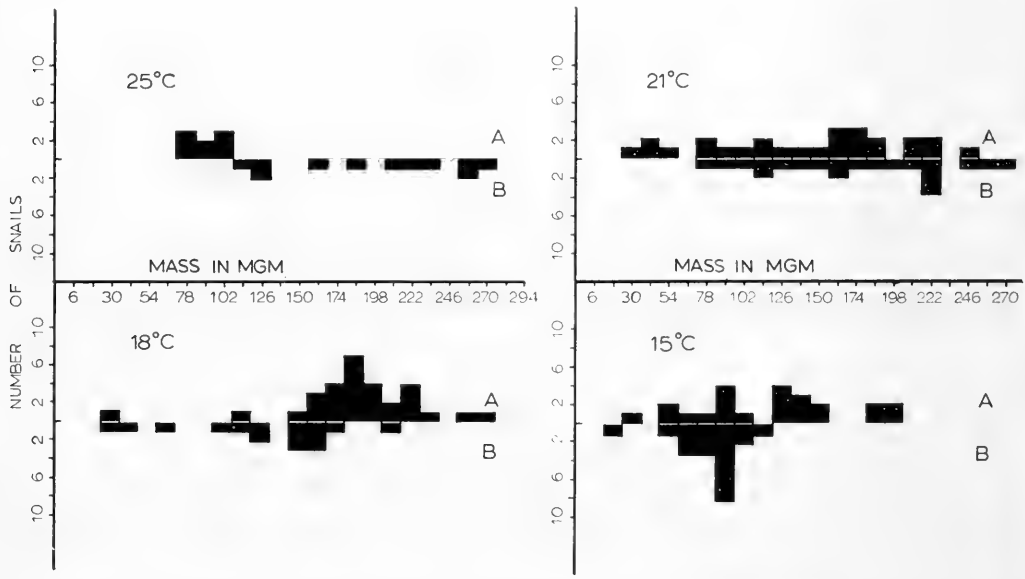

FIG. 6. Mass distribution in experimental populations of *Lymnaea natalensis* (A) and *Bulinus tropicus* (B) reared at constant temperatures. Age 4.5 months.

way have been correlated with conditions of accelerated growth. Observations apparently supporting this view are the following: (a) In both species the periods of maximum mass increase per month and the largest number of mass groups coincided. In *L. natalensis* this was after 2.5 and in *B. tropicus* before 2.5 months. (b) The largest

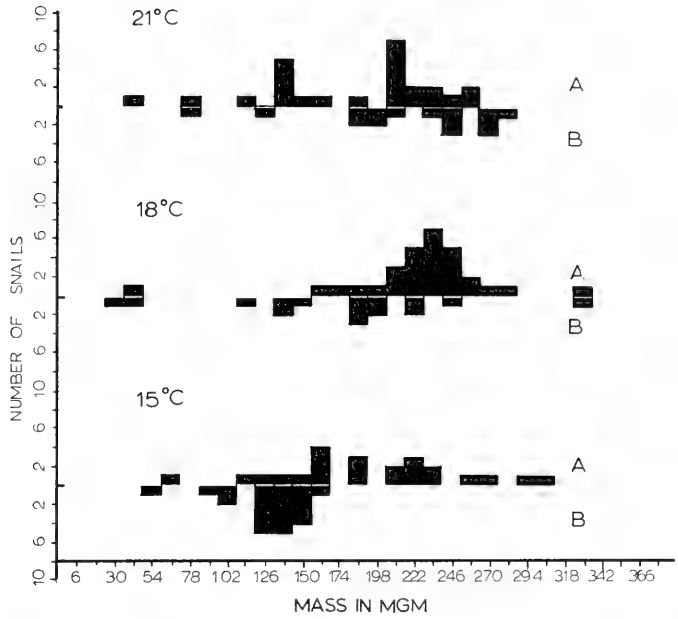

FIG. 7. Mass distribution in experimental populations of *Lymnaea natalensis* (A) and *Bulinus tropicus* (B) reared at constant temperatures. Age 5.5 months.

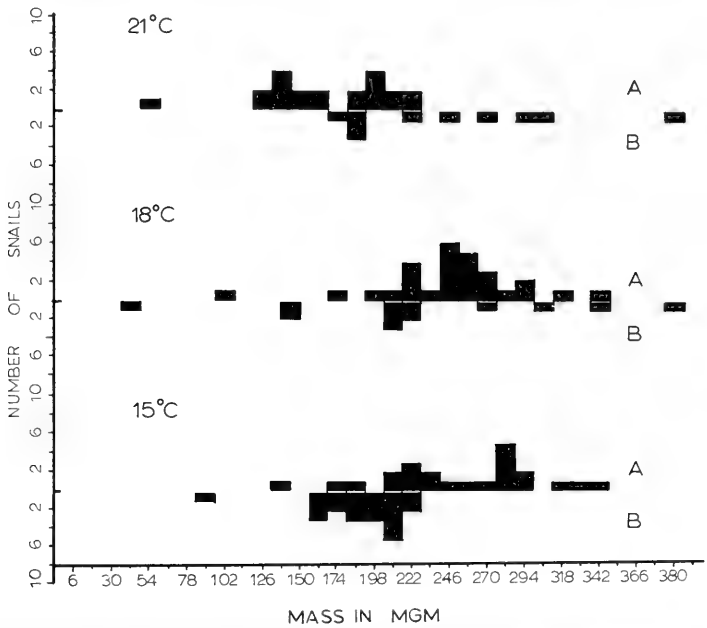

FIG. 8. Mass distribution in experimental populations of *Lymnaea natalensis* (A) and *Bulinus tropicus* (B) reared at constant temperatures. Age 6.5 months.

numbers of mass groups were often established at those temperatures which, also on other grounds, could be regarded as the most favourable for the species concerned. For *B. tropicus* these temperatures were 27° and 25°C for as long as the snails lived at these temperatures and 21° and 18°C from 4.5 months onwards. The corresponding

temperatures for *L. natalensis* were 21° and 18°C and up to 4.5 months and 18° and 15°C from then onwards.

DISCUSSION

The differences in growth rate at the same constant temperatures between *Bulinus tropicus* and *Lymnaea natalensis* lead to the same conclusions as were reached by Prinsloo & Van Eeden (1969) on the basis of the finite rate of increase, intrinsic rate of natural increase, nett reproductive rate and mean generation time determined for these species. The high growth rate of *B. tropicus* at 27°, 25° and 21°C underline the fact that this species must be well adapted to surviving under the semi-arid conditions which prevail in many parts of South Africa where summer temperatures are generally high and the available habitats are subject to intermittent drying up. These climatic conditions naturally call for the capacity to survive high temperatures and to grow and reproduce rapidly as soon as the temperature starts rising after winter. The findings for both species invalidate the assumption that different size groups in the same population necessarily represent different generations of the same species for at 6.5 months the mass per specimen ranged from 90 to 222 mg for *B. tropicus* and from 138 to 342 mg for *L. natalensis* in spite of the fact that none of the specimens could have differed in age more than 24 hours. A temperature of 15°C may, on the evidence of our data, certainly be regarded as suboptimal for *B. tropicus*. And yet, at the end of 6.5 months some of the specimens kept at this temperature had grown to 222 mg. Compared with the maximum mass of 380 recorded for any specimen of *B. tropicus* in our experiment, a specimen of 222 mg could not, in our opinion, be described as dwarfed. In fact, excluding one small specimen, the sizes of the specimens at 15°C and 6.5 months ranged from 162 to 222 mg so that the modal class specimens although admittedly smaller than at the higher temperatures, could still be described as fair sized.

SUMMARY

Five populations each of *Bulinus tropicus* and *Lymnaea natalensis* were reared at constant temperatures of 27°, 25°, 21°, 18° and 15°C. The 2 species differed noticeably in their growth response to the different temperatures and the resulting differentiation into different mass groups.

ACKNOWLEDGEMENTS

This investigation was made possible by financial assistance received from the South African Council for Scientific and Industrial Research.

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MALACOLOGIA, 1973, 14: 89-91

PROC. FOURTH EUROP. MALAC. CONGR.

STUDIES ON THE PERMEABILITY OF THE SEPTATE JUNCTION IN THE KIDNEY OF *HELIX POMATIA* L.

P. F. Newell and J. M. Skelding

Department of Zoology, Westfield College
London University, NW3 7ST, U.K.

It has long been suspected that the snail kidney is a functional analogue of the vertebrate glomerular nephron (Vorvohl, 1961; Martin, Stewart & Harrison, 1965). It is clear that in some gastropod molluscs the primary filtration process occurs in the heart (Picken, 1937; Van Aardt, 1968; Bonga & Boer, 1969). Recently Andrews & Little (1971) have provided the first ultrastructural evidence for the presence of podocytes in the epithelium covering the outer (pericardial) surface of the ventricle in the terrestrial prosobranch, *Poteria*. These are similar to the podocytes of Bowman's capsule in the vertebrate kidney. The ultra-filtrate is conveyed to the kidney through the reno-pericardial canal.

In pulmonate land snails primary urine formation takes place in the kidney sac, but a recent ultra-structural survey of the kidney sac of *Achatina achatina* (Skelding, 1972a, b) failed to reveal any structural equivalent of the vertebrate glomerular podocytes. This study showed that the cells of the kidney sac (nephrocytes) are joined by septate desmosomes composed of an intermediate junction and a septate junction. In the intermediate junction the intercellular space is patent, whereas in the septate junction the lateral plasma membranes are joined across the intercellular space by a series of regularly spaced bars, or septae. It is widely held that septate desmosomes prevent the movement of particles, including ions and water through the intercellular spaces between adjacent cells. If this is so, and if there is no specialised filtration site, by what route does fluid leave the blood vascular system and make its way into the lumen of the kidney sac? Skelding has proposed that the assumption that septate junctions are invariably "tight" may be incorrect and that they do not form an impenetrable barrier to fluid movement in the nephrocytic epithelium lining the kidney sac in *A. achatina*. The permeability of the septate junctions in the kidney sac of *Helix pomatia* to horse-radish peroxidase and lanthanum has been studied by Newell and Skelding (1972) to test this hypothesis.

The permeability of the junction to horse-radish peroxidase

Hydrated active snails, approximately 30 g fresh weight, received 100 mg of horse-radish peroxidase in 0.1 ml of distilled water by injection into the ventral sinus. The animals were sacrificed at timed intervals after the injection and slices of the kidney sac tissue were fixed by immersion in 2% gluteraldehyde in 100 mM/1 sodium phosphate buffer, pH 7.6, for 30 minutes. The tissue was washed overnight in buffer solution and then incubated in 0.1% 3-3'diamino benzidine reagent containing 0.01% hydrogen peroxide in 100 mM/1 tris-HCl buffer at pH 7.6, according to the method of Karnovsky (1967). The tissues were postfixed in 1% osmium tetroxide in phosphate buffer for 2 hours. They were subsequently dehydrated, and embedded in TAAB resin. Some tissue samples were taken from snails which had not been previously injected with peroxidase. These control samples were incubated in exactly the same way as the peroxidase-injected material.

Micrographs showed that the injected peroxidase leaves the blood capillary and passes into the connective tissue underlying the nephrocytes. The nephrocytic basal

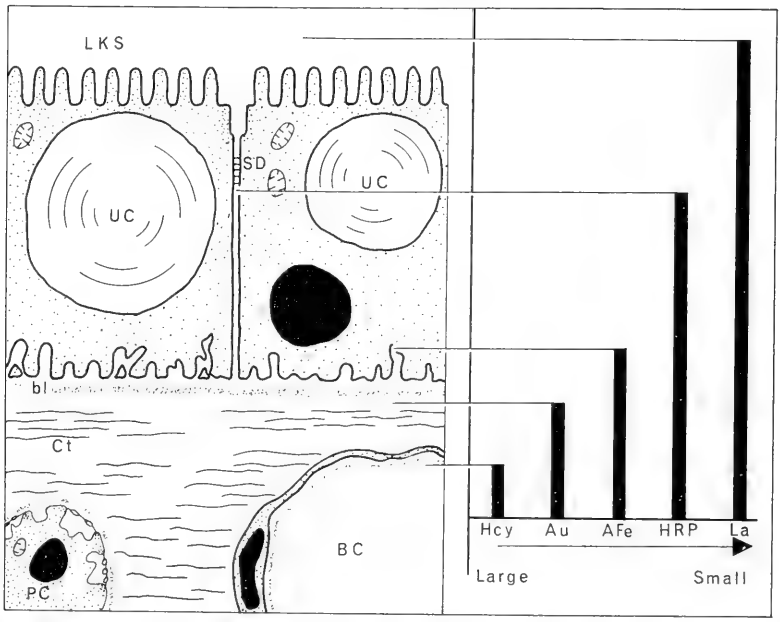

FIG. 1. Diagram of the nephrocytic epithelium of a pulmonate land snail. The graph shows the mobility of various molecules through the epithelium from a blood capillary. In *Achatina achatina* the capillaries are permeable to colloidal gold and ferritin, but the gold is excluded from passage into the intercellular spaces between the nephrocytes by the basal lamina (Skelding, 1972a). In *Helix pomatia* the capillaries are permeable to peroxidase, which enters the intercellular spaces between the nephrocytes but is excluded from the septate junctions. Lanthanum penetrates the septate junctions.

Au, colloidal gold; AFe, ferritin; BC, blood capillary; bl, basal lamina; Ct, connective tissue; Hcy, haemocyanin; HRP, horse-radish peroxidase; La, lanthanum; LKS, lumen of kidney sac; PC, pore cell; SD, septate desmosome; UC, urate crystal.

lamina is permeable to peroxidase and the latter passes into the intercellular spaces between the nephrocytes. The peroxidase was not detected beyond the septate junction and was absent from the intercellular spaces between the septae (see diagram). Comparison with the controls showed that intrinsic peroxidase activity was confined to mitochondria.

The permeability of the junction to lanthanum

Active, hydrated snails, approximately 30 g fresh weight, were sacrificed and the kidney was perfused with a solution containing 2% gluteraldehyde and 1% lanthanum nitrate brought to pH 7.7 with NaOH. Small slices of the kidney were fixed for 2 hours in fresh fixative containing lanthanum. The tissues were then post-fixed for 2 hours in 2% osmium tetroxide solution containing lanthanum in cacodylate buffer, pH 7.7. Finally, the tissue was dehydrated in alcohol and embedded in TAAB resin. The sections were examined without staining with heavy metals.

Lanthanum was clearly visible throughout the intercellular spaces between the nephrocytes. At the apex of the cells the lanthanum had, in some cases, penetrated through part, or the whole of, the septate region of the intercellular junction. Lanthanum was also infrequently present in the intermediate junction, which may mean that some areas of the septate junction are permeable to this molecule. Oblique sections of septate junctions infiltrated with lanthanum showed that the septae are parallel

corrugated sheets which seemed in all respects similar to those described from the gill of the fresh water mussel, *Elliptio complanatus*, by Gilula, Branton & Satir (1970).

When lanthanum is applied to tissues at the time of fixation the results must be treated with caution; it cannot be assumed that the permeability of the tissues remains unaltered during fixation. However, the absence of peroxidase from the septate junction seems to imply that peroxidase molecules do not diffuse into the septate junction as a post-fixation artefact. The size of the particle determines whether or not it penetrates the junction. If this is so, then the kidney sac lamella is a series of barriers of decreasing porosity from the blood capillary to the apex of the nephrocytic epithelium. Skelding (1972a) showed that the blood capillaries within the kidney sac of *Achatina achatina* are impermeable to haemocyanin, but partially permeable to colloidal gold and ferritin particles (ca. 100Å diameter and 90Å respectively). The basal lamina supporting the kidney sac cells is impermeable to colloidal particles yet permeable to ferritin, which penetrates the intercellular spaces only in the lower third of the cell height.

The present study shows that smaller particles including horse-radish peroxidase (M.W. 40,000) can fill the whole of the intercellular space. Lanthanum, which is known to penetrate gaps as small as 20Å, gains access to the lumen of the kidney sac. Thus, the fluid contained in the intercellular spaces between the nephrocytes originates from the blood, and might enter the urine by passage through localised areas of the septate junctions. A similar proposal has been made by Karnovsky (1967) to explain the formation of lymph by vertebrate capillaries.

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MALACOLOGIA, 1973, 14: 93-96

PROC. FOURTH EUROP. MALAC. CONGR.

STUDIES ON THE RENAL PHYSIOLOGY OF *ACHATINA ACHATINA* (L.)

John M. Skelding

Department of Zoology, Westfield College
London, NW3, U.K.

The kidney of the stylommatophoran pulmonate molluscs has attracted the attention of workers interested primarily in nitrogen metabolism; but the role of the renal organ in salt and water balance has received scant attention. The Stylommatophora are of considerable interest in that their renal physiology might usefully be compared with that of other invertebrates which have exploited the land habitat. Useful comparisons can be made also with their close aquatic relatives, the freshwater Basommatophora.

In freshwater snails the first-formed, or primary urine, originates in the pericardium, by pressure filtration of the blood through the wall of the heart (Picken, 1937; Bonga & Boer, 1969; Van Aaardt, 1968). The ultrastructural basis for this process in the terrestrial prosobranch *Poteria* has recently been described by Andrews & Little (1971). In terrestrial pulmonates, urine formation takes place in the kidney sac. Vorvohl (1961) demonstrated that in *Archachatina ventricosa* and *Helix pomatia*, the primary urine can be collected from a catheter inserted into the kidney sac, while a catheter simultaneously inserted into the pericardium yields only a very meagre fluid flow. Martin, Stewart & Harrison (1965) demonstrated that when inulin is injected into *Achatina fulica*, it appears in the urine at a similar concentration to that present in the blood. They showed also that when back pressure is applied to the ureter there is a resulting diminution in urine flow rate. The formation of urine ceases when the back pressure exceeds 12 cm of water.

Taken together these observations appear to support the conclusion that the kidney in land snails functions in a similar manner to the vertebrate glomerular kidney; that is, filtration of the blood by hydrostatic pressure leads to the formation of a primary urine which is identical with the blood, except in the absence of compounds of very high molecular weight. The final urine is subsequently elaborated by reabsorptive and secretory processes. However, there are several objections to this conclusion.

1)The appearance of the renal test substance, inulin, in the urine is probably not incontrovertible evidence that it is formed as a consequence of filtration under hydrostatic pressure. The Malpighian tubule of *Calliphora*, which is known to form primary urine by a secretory process (Berridge & Oschman, 1969), is also able to excrete inulin, albeit with a U/B of 0.5 (M. Phillips, pers. comm.). The isolated salivary glands of *Helix aspersa* secrete saliva following addition of the hormone 5-hydroxytryptamine. When ^{14}C-carboxy-inulin is added to the bathing medium, it appears in appreciable quantities in the saliva (Skelding, unpubl.). Some secretory tissues are therefore permeable to inulin.

2)Some secretory processes may be susceptible to applied back pressure. Ramsay (1954) has shown that the Malpighian tubules of *Dixippus* cease urine formation when the applied back pressure exceeds 20 cm of water. Maddrell (1969) has reported that back pressure lessens the rate of urine formation by the Malpighian tubules of *Rhodnius*, *in vitro*.

Before we can be certain that the land snail kidney is a functional analogue of the vertebrate glomerular kidney, the following criteria should be satisfied.

a) The primary urine and the blood should be identical in composition with respect

to ions and small organic molecules.
b) The extent to which large molecules are prevented from entering the urine from the blood should be a function of their molecular size.
c) Within the kidney, a morphological site or route should exist, where the blood and urine are brought into intimate proximity, and where filtration of the blood might take place.
d) A hydrostatic pressure gradient in excess of the colloid osmotic pressure of the blood should exist across this site which favours the movement of fluid from the blood into the urine.

In the case of the land snail kidney all of the above criteria remained to be demonstrated at the time of the initiation of the present study. The author has investigated aspects of the physiology and the ultrastructure of the kidney in *Helix pomatia* and *Achatina achatina* to determine whether they satisfy these criteria. Only those experiments with *A. achatina* are described here.

Hydrated animals received injections of the renal test substance, inulin. Fluid samples were removed from the various regions of the kidney and ureter by means of silica micropipettes. A blood sample was also taken. The concentrations of Na^+, K^+, Ca^{++}, Mg^{++}, Cl^- and HCO_3^- were determined, with melting point and ^{14}C-inulin activity, in the urine and blood samples. The ionic composition, osmotic pressure and inulin concentration of the urine could be compared with identical parameters in the blood, and provided clues to the nature of the processes underlying the elaboration of the final urine.

Pericardial fluid and primary urine in the kidney sac are similar in composition to the blood with respect to most ions, osmotic pressure and concentrations of inulin. Calcium and magnesium concentrations are elevated in the blood compared with the pericardial fluid and primary urine, possibly as a consequence of cation-binding by the blood proteins. These observations satisfy the first criterion, set out above. As the fluid moves along the ureter ions (mainly Na^+ and Cl^-) are reabsorbed together with some water, and the urine becomes progesssively more hypotonic compared with the blood. The final urine, in the distal region of the secondary ureter, represents two-thirds of the volume which entered the kidney in the form of primary urine. Approximately 86% of the calcium, 80% of the sodium and 64% of the chloride are reabsorbed. Potassium enters the urine in the secondary ureter, and there is an overall small net secretion of this cation into the urine. Bicarbonate ions persist in the final urine at a similar concentration to that present in the blood, so that this anion contributes significantly to the overall osmotic pressure of the final urine. Under conditions of hydration the osmotic pressure of the final urine is approximately one half that of the blood.

A group of hydrated animals was injected with inulin and was subsequently subjected to desiccation until they had lost 10% of their total live weight. Samples of blood and urine from the various regions of the kidney were taken for analysis. The osmotic pressure and the concentration of all the measured anions and cations in the blood increase during dehydration. These increases are matched by similar increases in the ionic concentration of the pericardial fluid and the primary urine. The animals continue to form a strongly hypotonic urine which contains about twice the concentration of potassium present in the blood. *Achatina achatina* responds to dehydration by reabsorbing a larger proportion of the water from the primary urine. Almost 70% of the water, together with 90% of the sodium and chloride are reabsorbed from the primary urine, while 80% of the potassium is excreted.

Herbivorous animals, whose main dietary cation is potassium, are likely to find sodium, the major blood cation, in short supply in their food. If, during dehydration, the animals were to excrete sufficient sodium in the urine to keep the blood concen-

tration constant, upon rehydration a similar amount of sodium would have to be ingested. The animals do not form a hypertonic urine, and they continue to conserve salt when dehydrated, even though the salt concentration of the blood increases. Under natural conditions the animals may be alternately subjected to conditions of hydration and dehydration over short time intervals. By conserving salt even when they are dehydrated, the animals avoid the need to ingest large amounts of salt, when subsequently water becomes plentiful and the animals are rehydrated. The unusual tolerance of the tissues to varying salt concentrations is undoubtedly of considerable selective advantage to these animals.

The ability of the kidney to discriminate between particles on the basis of their molecular size was tested as follows. Dextran molecules of 2 molecular size ranges were injected into the blood of 2 groups of experimental animals. The ability of the kidney to exclude these compounds from the urine was determined by comparing the concentrations of dextran in urine and blood (U/B ratio). Low molecular weight dextran (Mol.Wt. 16,000-19,000) enters the urine at a similar rate to inulin, that is, the U/B ratio is approximately 1. The U/B ratio of high molecular weight dextran (60,000-90,000 Mol. Wt.) in the primary urine of *Achatina achatina* is 0.58 ± 0.05. (Mean ± S.D., 6 animals). Clearly a restriction to the movement of particles into the urine operates in the size range 19,000-90,000 Molecular weight. This is equivalent to an Einstein-Stokes radius of 30-40Å. The high permeability of the snail kidney compared with vertebrate kidneys may be functionally related to the high molecular weight of the major blood protein, haemocyanin (Mol.Wt. 8.9×10^6).

Electron microscopical investigations revealed that no direct structural analogue of the vertebrate glomerulus or of the basommatophoran epicardial podocytes exists in *Achatina achatina*. It is therefore concluded that fluid reaches the urinary space from the blood capillaries by crossing the nephrocytic epithelium which lines the kidney sac. The fluid which bathes the base of the nephrocytes is haemocyanin-free and presumably originates by ultrafiltration of the blood through the walls of the fenestrated capillaries in the so-called blood space. The basal lamina underlying the nephrocytes is impermeable to colloidal gold particles approximately 100Å in diameter, but is permeable to ferritin molecules. Ferritin does not enter the final urine in significant amounts, so the basal lamina is probably too coarse a filter to be responsible for the final filtration process. The further movement of ferritin is restricted by the extracellular mucopolysaccharide which coats the basal and lateral plasma membranes. It is proposed that the septate junctions between the nephrocytes are "leaky" and contain pores or discontinuities in their structure through which fluid from the intercellular spaces gains access to the urinary space (Skelding, 1972).

The kidney sac epithelium may be functionally analogous to the vertebrate capillary endothelium; in the latter, the so-called tight junctions (*zonula occludens*) contain pores through which lymph passes into the interstitium. It might be speculated that the degree of leakiness of the septate junction in various epithelia is related to their physiological function. Where highly permeable epithelia are required, the intercellular junctions are entirely absent (visceral epithelium of Bowman's capsule, crayfish coelomosac, epicardial cells in *Poteria*). Where a diffusely permeable epithelium is required (nephrocytes of *Achatina*, vertebrate myocardial and skeletal capillaries) the intercellular junctions may contain pores. This hypothesis has been tested by Newell & Skelding (1973a, b). Frömter & Diamond (1972) have recently shown that in many vertebrate fluid-transporting epithelia the route of passive ion permeation is through the so-called tight junctions. Moreover, these authors have also suggested that water and small non-electrolytes, including inulin, may pass across epithelia by the same route.

That a filtration process is involved in urine formation in the land snail kidney seems undeniable. At the present time there is little direct evidence that filtration

is brought about by arterial pressure. The possibility that a secretory process is involved cannot be entirely eliminated.

The role of the ureter in reabsorption is reflected in its ultrastructure. The epithelium lining the duct is composed of cells which bear an apical microvillous border. The lateral plasma membranes are thrown into vertical folds which are continuous with invaginations of the basal plasma membrane. Adjacent cells therefore interdigitate in a complex fashion. The cytoplasmic folds contain large numbers of mitochondria and considerable accumulations of glycogen. The cells thus support a series of vertical, extracellular, fluid-filled channels. Diamond & Bossert (1967) have proposed that intercellular channels in fluid-transporting epithelia support standing osmotic gradients and are the route whereby fluid passes across the cells.

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MALACOLOGIA, 1973, 14: 97-106

PROC. FOURTH EUROP. MALAC. CONGR.

MICRO-BIOCHEMICAL AND PHYSIOLOGICAL STUDIES ON AN IDENTIFIED SEROTONERGIC NEURON IN THE SNAIL *HELIX POMATIA*

Neville N. Osborne [1]

Wellcome Laboratories of Pharmacology
Gatty Marine Laboratory, University of St. Andrews, Scotland

INTRODUCTION

The work described in this paper is divided into 2 parts, the 1st of which deals with the identification of a giant serotonergic neuron in the metacerebral ganglia of *Helix pomatia*. This work was initially undertaken to measure the serotonin content of an identifiable neuron and also to study the precise subcellular localisation of the amine. The 2nd part of the paper is concerned with the composition of amino acids and related substances in the giant metacerebral serotonergic cell. To demonstrate the chemical heterogeneity of nerve cells, the amino acids and related substances were also determined in the circumoesophageal ganglia and a giant neuron of the buccal ganglia which lacks serotonin.

I. LOCALISATION AND ESTIMATION OF SEROTONIN IN THE GIANT METACEREBRAL CELL

It is important to know the exact localisation of serotonin (5-hydroxytryptamine) in nervous tissue in order to interpret its physiological role. Previous work on nervous tissue of molluscs (see Cottrell & Laverack, 1968; Cottrell & Osborne, 1970) shows that serotonin is probably localised in small granular vesicles in the cell cytoplasm, but confirmation of this has proved difficult, mainly because it has not been possible to study tissue known to contain serotonin and no other monoamines. However, information is now available (Cottrell & Osborne, 1970) describing the serotonin distribution in the cytoplasm of a neuron situated in the metacerebral ganglion of the slug *Limax maximus*. It was decided to investigate the localisation of serotonin in the analogous cells of the metacerebral ganglia of the snail *Helix pomatia*.

Using standard methods of amine-fluorescence histochemistry (Corrodi & Jonsson, 1967), a pair of giant yellow fluorescing cells can be localised in the metacerebral ganglia of *Helix pomatia* (Fig. 1). These cells had already been discovered by Osborne & Cottrell in 1971. The first object was to ensure that this yellow fluorescence was specific to serotonin and this was judged by the criteria of colour, reducibility, fading and absence without paraformaldehyde sublimation. Since some neurons in the snail are thought to contain serotonin as well as dopamine (Kerkut, Sedden & Walker, 1967), it was decided to examine the nature of the amine-fluorescence in giant metacerebral neurons of snails which had been pretreated with drugs known to interfere with the metabolism of different monoamines. The results of this study are shown in Table 1, and they support the view that serotonin is localised in the giant neurons and furthermore that the neurons do not contain any primary catecholamines.

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[1] Present address: Max-Planck-Institut für Experimentelle Medizin, Arbeitsgruppe Neurochemie, 3400 Göttingen, Hermann-Rein Strasse 3, Germany.

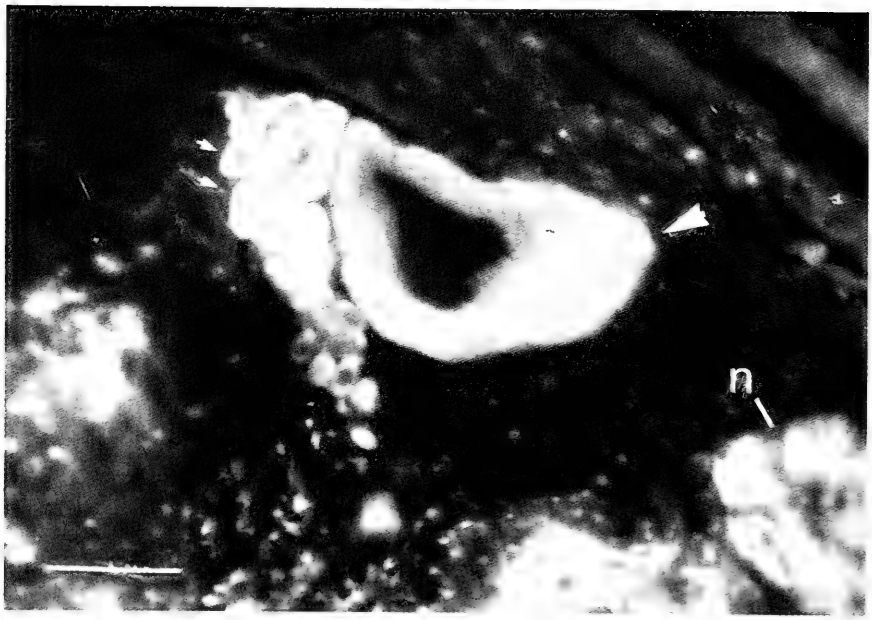

FIG. 1. Section through a metacerebral ganglion of *Helix pomatia* processed by the histochemical method for demonstrating monoamines. Situated near the giant serotonergic neuron (large arrow head) which appears yellow in colour is a group of small green fluorescing cells (small arrow heads). Parts of the neuropile (n) contain green-yellow fluorescing fibre. (The bar represents 100 μ.)

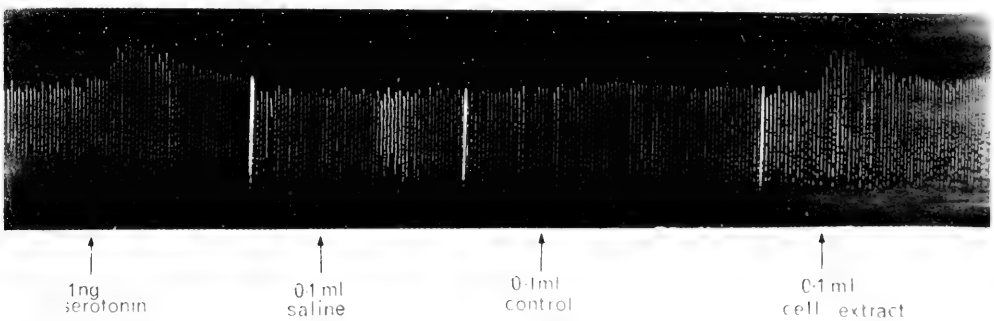

FIG. 2. Response of an isolated *Helix aspersa* heart to serotonin, to snail saline, to an extract prepared from individually isolated giant serotonin-containing cells and to a similarly prepared extract from an equivalent number of non-fluorescing cells from the buccal ganglia (control).

Using an isolated snail heart preparation which is known to be very sensitive to serotonin but insensitive to catecholamines (Cottrell & Osborne, 1969), the serotonin content in individually dissected neurons was measured (Fig. 2). From the results of a number of experiments the amine content was estimated at 0.6 ng/cell. This result was substantiated using a microchromatographic method (Osborne, 1971). In this procedure the brains from 4-8 animals are perfused with radioactive 5-hydroxy-tryptophan for at least 7 hours, the giant neurons then dissected and chromatographed. Chromatography was performed on 3x3 cm polyamide layers (Carl Schleicher & Schüll) in an ascending fashion, using either methyl acetate/isopropanol/ammonia

TABLE 1. Summary of the effects of various drugs on the yellow fluorescence of the serotonergic neuron of *Helix pomatia*. Two mg of each drug were administered over a period of 30 hours before observation.

Name of drug	Effects	Effect on yellow fluorescence of giant cell
Reserpine	Depletes amines from molluscan nervous tissue	All fluorescence eliminated
p-Chlorophenyl-alanine	Reduces 5-HT content by inhibiting the enzyme tyrosine hydroxylase in vertebrates.	Colour of fluorescent still yellow although intensity reduced
α-methyl-m-tyrosine	Reduces CA content by inhibiting the enzyme tyrosine hydroxylase in vertebrates	No change in colour and intensity of fluorescence
5-HTP	Precursor of 5-HT in molluscs	Intensity of yellow fluorescence increased
DOPA	Precursor of CA's in molluscs	No change in colour and intensity of fluorescence
Nialamide	Monoamine oxidase inhibitor in vertebrates	Slight increase in intensity of yellow fluorescence
NSD 1024	DOPA decarboxylase inhibitor in molluscs	Yellow fluorescence very slightly reduced

25% (9:7:5) or butanol/chloroform/acetic acid (4:1:1), exposed to formaldehyde vapour and viewed under ultraviolet light. By scraping off the spot corresponding to different substances and counting the radioactivity associated with each of them, it became clear that the giant metacerebral cells take up radioactive 5-hydroxytryptophan and convert part of it to serotonin.

Electron microscopy of the cells' cytoplasm revealed, as in *Limax maximus* (Cottrell & Osborne, 1970), the presence of large numbers of vesicles (Fig. 3a) together with elongated mitochondria, lysosome-like particles and other structures reported in molluscan neurons. Tissue fixed and processed by the method of Wood (1965, 1966) for detecting amines, contained electron dense reaction products in the small granules (Fig. 3) and, in some instances, in the lysosome-like particles. Prior injection of reserpine or p-chlorophenylalanine greatly reduced the number of granules in the serotonin-containing cell.

DISCUSSION

For the following reasons it is concluded that of all the monoamines, serotonin alone was present in giant metacerebral cells. Firstly, when processed by amine-histochemistry the giant neuron fluoresced yellow, an indication of serotonin, and the fluorescence formed was relatively unstable to ultraviolet light. Secondly, pretreatment of snails with drugs known to interfere with the metabolism of different monoamines showed that the yellow fluorescence in the cytoplasm of the neuron was derived solely from serotonin. Thirdly, extracts from giant neurons could take up radioactive 5-hydroxytryptophan and convert it to a substance which in 2 different solvents has the same chromatographic mobility as pure serotonin.

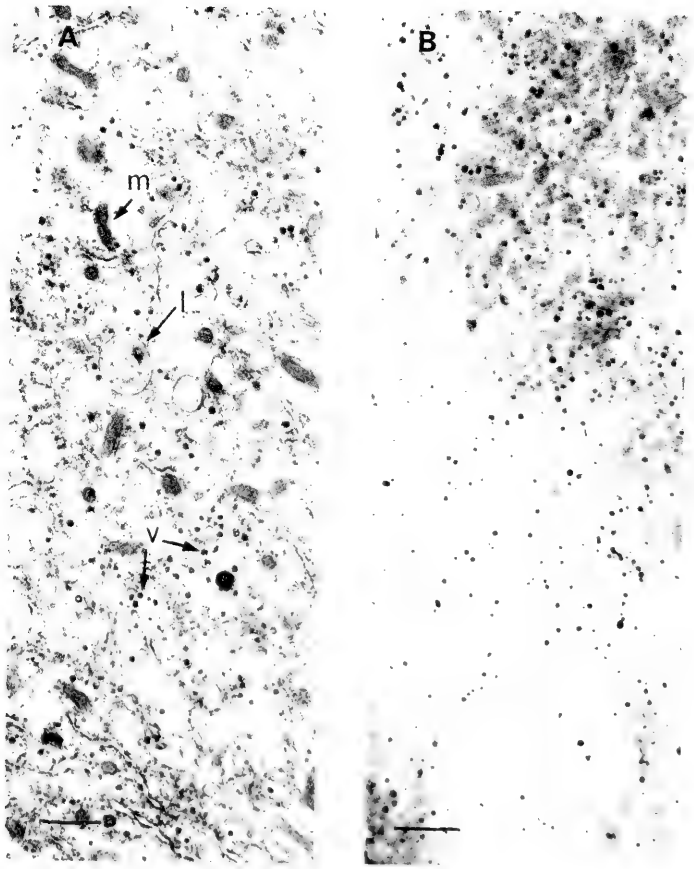

FIG. 3. A, Electron micrograph of part of the cytoplasm from a giant serotonin cell fixed in glutaraldehyde and osmium and stained with lead citrate and uranyl acetate. The most conspicuous organelles in the cytoplasm are small granular vesicles (v) which have an average diameter of 60–120 nm, mitochondria (m), and lysosome-like structures (l). B, A similar part of another giant serotonin cell processed by the Wood's method. The electron-dense deposits represent sites of serotonin (localisation). These are the same size as the centres of the granular vesicles. (The bar represents 0.5 μ.)

From a number of bioassay and chromatographic experiments the serotonin content of a single cell was estimated to be 0.6 ng. Since the total volume of the giant cell of *Helix* is about 1.2 nl and the cell's nucleus, which contains no serotonin, occupies about 1/5 of this, it is estimated that the concentration of serotonin in the cytoplasm of the cell soma is 3.5×10^{-3}m. This concentration is of the same value as that calculated to exist in the giant cell of *Limax maximus* (Cottrell & Osborne, 1970).

The localisation of serotonin in granules in the cytoplasm of the giant neuron of *Helix pomatia* is like that already observed in the giant serotonergic neuron of *Limax maximus* (Cottrell & Osborne, 1970). Granules of similar dimensions have been suggested to bind catecholamines and serotonin in nerves of the snail heart (Cottrell & Osborne, 1969), catecholamines in bivalve ganglia (Cottrell, 1967) and serotonin in the Retzius cell of the leech (Rude, Coggeshall & Van Orden, 1969). It is therefore suggested that serotonin is sequestered within the small granules.

Preparations stained for the ultrastructural localisation of amines only rarely showed dense reaction products in the lysosome-like particles. A detailed study was not undertaken as in the case of *Limax maximus*, where a seasonal variation in the localisation of the amine was observed (Cottrell & Osborne, 1970). In connection with this observation it was often noticed that tissue fixed and stained by standard methods of electron microscopy showed the occurrence of small granulated vesicles within the lysosome-like structure of the giant serotonergic cell.

II. AMINO ACIDS AND RELATED COMPOUNDS IN ISOLATED NEURONS

Appreciable amounts of amino acids occur in the nervous system. It is generally accepted that these are predominantly concerned with general metabolic processes and with the maintenance of water and ion distributors across cellular membranes. However certain amino acids may also function as synaptic transmitters. Recent papers catalogue the many instances where particular amino acids have been inferred to be potential transmitter substances.

Neuhoff and co-workers (for details and references see Osborne, Briel & Neuhoff (1971) and Osborne (1972)) have recently described a microchromatographic method for the detection of amino acids in as little as 0.1 mg of nervous tissue. The method involves the reaction of the -OH or $-NH_2$ groups of amino acids and related substances with dansyl chloride (1-dimethylamino-naphthalene-5-sulfonyl-chloride) to form intensely fluorescent dansyl substances which can then be separated by microchromatography using certain solvent systems. This process detects as little as 1 pico mole of amino acid, which is extremely sensitive compared with other methods. This was the method used to analyse the distribution of amino acids and related substances in the brain, the metacerebral serotonergic giant neurons and a pair of non-serotonergic giant neurons from the buccal ganglia of *Helix pomatia*. The aim of this study was to reveal the heterogeneity of neurons with the snail brain with respect to content of amino acids and related substances.

Radioautograms and maps showing the occurrence of ^{14}C-dansylated substances in the brain of *Helix* are shown in Fig. 4. The radioactivity associated with each spot is shown in Table 2. A number of points of interest concerning the amino acid distribution in the brain have been discussed elsewhere (Osborne, Briel & Neuhoff, 1971), but of special significance is the occurrence of GABA, which had previously been thought to be absent from gastropod tissues.

A comparison of the amino acids and related substances in the brain, and of the metacerebral serotonergic neurons and the nonserotonergic neurons in the buccal ganglia is shown in Table 2. Generally the distribution of dansylated substances in the cell types is similar; GABA for example is present in each but in low concentrations. The serotonergic cell however contains less ornithine and more glycine than the buccal cells.

The results also show the existence of high levels of serotonin in the metacerebral giant cells when compared with the whole brain, and confirm the absence of the amine in the buccal cells. In this connection, the presence of the unknown substance (spot 15) is of interest, for it occurs in large amounts in the serotonergic cell and to a lesser extent in the whole brain. Initial experiments suggested that the substance could be 5-hydroxytryptophan. It is known that the serotonergic neurons can take up tritiated 5-hydroxytryptophan and convert it to serotonin.

The occurrence and distribution of 5-hydroxyindole in gastropods would seem to indicate that this substance is a metabolite of serotonin. Besides occurring in the whole brain and, to a greater extent, in the serotonergic neurons, 5-hydroxyindole is also present in the integument of the slug *Arion ater* (Osborne, Briel & Neuhoff,

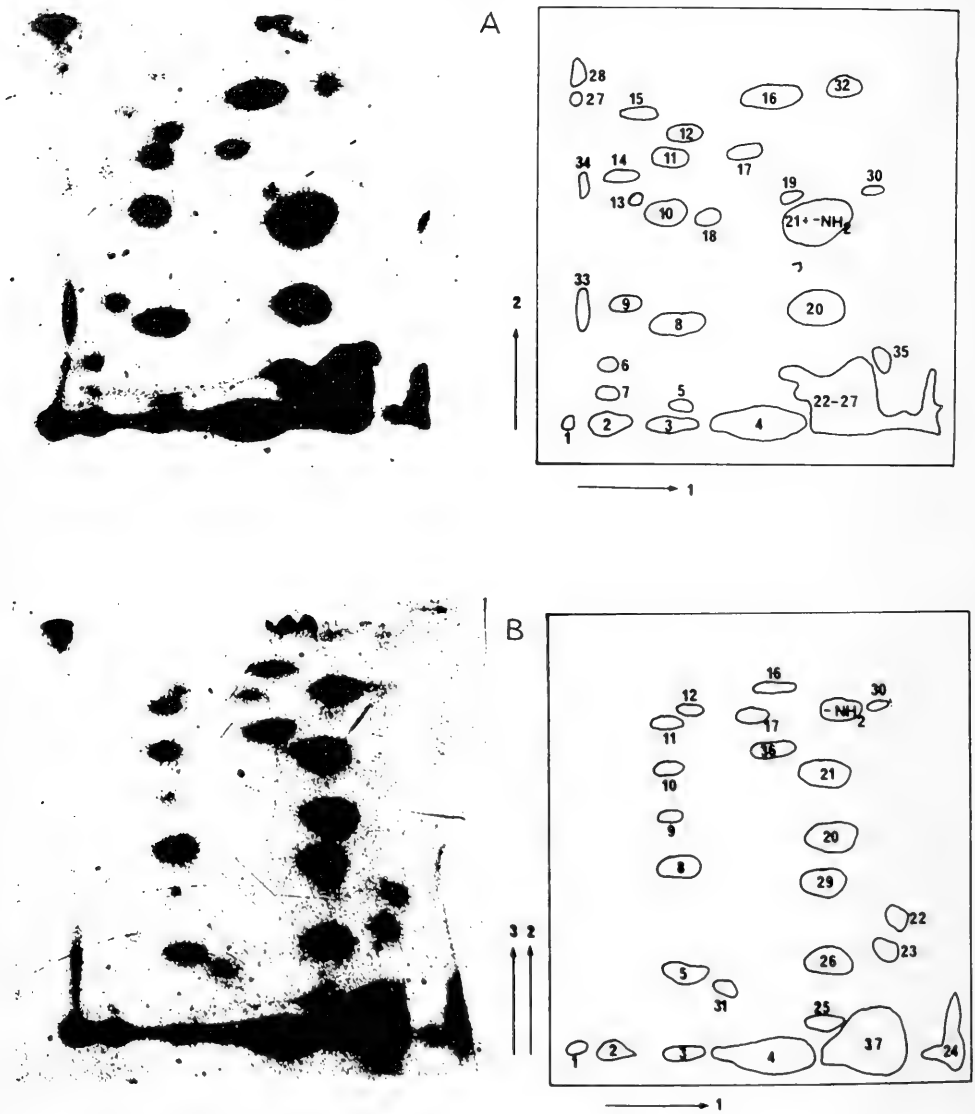

FIG. 4. Autoradiograms of microchromatograms and maps of substances in the brain (circumoesophageal ganglia and connectives) of *Helix pomatia* after having reacted with ^{14}C-dansyl-chloride. A, After chromatography in 2 systems; B, after chromatography in 3 systems. The direction of chromatography is indicated by the arrows. First direction water/formic acid (100:3), 2nd direction benzene/acetic acid (9:1), 3rd direction ethyl acetate/methanol/acetic acid (20:1:1). Each microchromatogram measures 3 x 3 cm. The numbers on each map corresponding to the dansyl compounds are shown on Table 2. Unmarked spots on chromatograms belong to impurities of ^{14}C-dansyl-chloride.

1971), in which part waste products of metabolism are often present. It is worth noting that attempts to detect the closely related substance, 5-hydroxyindole acetic acid, in gastropod nervous tissues have proved unsuccessful (Osborne & Cottrell, 1970).

TABLE 2. Composition of dansylated compounds when separated by microchromatography on polyamide layers. Results expressed as residues per 100 total residues.

Spot No.	Substances	Brain	Metacerebral serotonergic neuron	Buccal non-serotonergic neuron
1	Starting point	-	-	-
2	Unknown substance	-	-	-
3	Taurine	0.67	-	-
4	Dansyl-OH	-	-	-
5	N-Tyrosine	0.31	1.71	1.11
6	Tryptophan	0.36	1.91	0.31
7	N-Serotonin	0.42	8.63	-
8	Ornithine	1.09	3.01	1.52
9	Bis-lysine	0.42	0.83	2.88
10	Phenylalanine	1.79	3.39	3.98
11	Leucine	1.31	2.46	4.32
12	Isoleucine	0.88	1.44	2.82
13	Bis-Histidine	1.64	-	-
14	Bis-Tyrosine	0.31	0.31	0.19
15	Unknown substance (5-HTP?)	0.47	5.68	-
16	Proline	0.72	2.77	2.81
17	Valine	1.01	1.38	4.03
18	Methionine	0.73	0.69	0.66
19	GABA	0.38	0.30	0.65
20	Glycine	3.61	6.07	7.38
21	Alanine + Dansyl-NH_2	17.97	30.79	31.72
22	Glutamine + Threonine	4.11	3.06	3.26
23	Asparagine + Serine	3.0	2.21	3.01
24	Argenine, ε-Lysine, α-amino-histidine and cystine	42.72	7.16	9.36
25	Aspartic Acid	1.67	0.36	0.49
26	Glutamic Acid	5.03	1.10	1.57
27	Bis-Serotonin	0.34	0.63	-
28	5-Hydroxyindole	0.72	0.61	-
29-37	Unknown substances	8.32	13.50	18.23

DISCUSSION

It has been stressed that in order to understand more about the nervous system, chemical analysis must be done on repeatedly identifiable isolated neurons rather than on brain tissue, which often contains a heterogeneous population of neurons as well as glia and muscle tissue (Rose, 1968; Giacobini, 1969). The 1 giant serotonin-containing neuron in each metacerebral ganglion of *Helix pomatia* is known to make direct synaptic contact with at least 2 of the 3 repeatedly identifiable giant neurons which lack biogenic amines in the buccal ganglia (Cottrell, 1970a). All the available data suggest that the serotonin within these metacerebral neurons is used as a transmitter substance (Cottrell, 1970a, b; Cottrell & Osborne, 1970). The giant metacerebral neuron and the buccal neuron therefore represent 2 different types of nerve cells.

The most striking feature of these results is the high level of serotonin, 5-hydroxyindole and unknown substance (5-hydroxytryptophan?) in the metacerebral cell, and to a lesser extent in the whole brain, yet their complete absence from the buccal cells. This observation confirms the chemical heterogeneity of neurons within the gastropod brain. The distribution of other dansylated substances in the serotonergic and buccal cells is similar but for 2 exceptions. The serotonergic cells contain less ornithine and more glycine than the buccal cells. The significance of this discovery has still to be established.

Finally mention must be made of the exact chemical content of each cell type. Isolation of cells by free-hand dissection can incur a number of errors, particularly from contamination. Furthermore, the cell membrane can be damaged during the dissection, thus allowing leakage of chemicals from the cells and subsequently destroying the integrity of the neuron. There is also evidence that methylene blue causes 'release' of chemicals from the cells (for details see Briel, Neuhoff & Osborne, 1971). It is for these and other reasons that a further number of experiments are required before deciding upon the exact chemical content of each cell type. In practice this might prove impossible should the chemical content of each neuron depend upon the activity of the individual snail.

SUMMARY

There is a giant serotonin-containing neuron in the metacerebral ganglion of the snail *Helix pomatia*. Further evidence for the presence of serotonin and the absence of catecholamines was obtained by observing the effects of different drugs on the amine fluorescence. Moreover, biological assay and microchromatography of cell extracts provided independent evidence for the existence of serotonin in the neurons, and the amount of amine was estimated at 0.6 ng/cell. The serotonergic neurons were also shown to take up tritiated 5-hydroxytryptophan and to convert the substance to serotonin. Results from electron microscopic cytochemistry revealed that serotonin is sequestered in small granular vesicles and also sometimes associated with lysosome-like particles.

Microchromatography of dansylated substances in the brain, the metacerebral serotonergic neurons and the non-serotonergic neurons in the buccal ganglia disclosed the chemical heterogeneity of neurons within the snail brain. 5-hydroxyindole, serotonin and an unknown substance were all present in the metacerebral cells, and to a lesser extent in the brain, but absent from the buccal cells. The serotonergic metacerebral cells also contained less ornithine and more glycine than the buccal cells. Generally, however, the distribution of the other amino acids was similar in both cell types.

ACKNOWLEDGEMENT

The work reported in the 1st part of this paper was carried out in collaboration with Dr. G. A. Cottrell to whom the author is gratefully indebted. The work in the 2nd part of the paper was accomplished in conjunction with Professor V. Neuhoff and Dr. G. Briel. The author is also grateful to the Royal Society of London for a travel grant.

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RESULTATS EXPERIMENTAUX SUR LA FIXATION DU ZINC-65 PAR *ANODONTA CYGNEA* (LINNAEUS)

L. Foulquier, P. Bovard et A. Grauby

C.E.N. - Cadarache, France

RESUME

Le zinc-65 est un corps radioactif induit qui se retrouve principalement dans les dèchets des réacteurs nucléaires; il est fortement concentré par les organismes vivants en particulier par les mollusques. Le développement des installations nucléaires le long du Rhône a conduit les auteurs à étudier la fixation du zinc-65, (sous forme de chlorure), par *Anodonta cygnea*.

Deux expériences sont décrites: La première concerne l'étude dynamique, par la mesure radioactive des animaux vivants, de l'absorption et de la désorption du zinc-65 par les anodontes en fonction de la variation de la teneur en zinc-65 de l'eau. La fixation du zinc-65 par ces bivalves, qui semble être proportionnelle à la teneur en zinc-65 de l'eau, est un phénomène rapide; on obtient un pic maximum d'activité dès le 3ème ou 4ème jour après la contamination. Dans un circuit d'eau inactive la perte du zinc par les anodontes est relativement lente; la période biologique est de l'ordre de 31 jours.

La deuxième expèrience est une étude de la fixation du zinc-65 par les différents organes de l'Anodonte après avoir contaminé l'eau d'un aquarium contenant du sédiment. On constate une décroissance très rapide de l'activité de l'eau au profit du sédiment. Après 59 jours l'eau contient 0,2% de la quantité de zinc-65 introduite, les anodontes 6,2% et le sédiment 93,6%.

Pendant toute l'expérience les activités spécifiques des tissus mous et de la coquille sont variables selon les individus mais demeurent à l'intérieur de certaines limites. L'activité des liquides internes baisse en fonction de la décroissance de l'activité de l'eau. L'hémolymphe a toujours une activité spécifique nettement supérieure à celle du liquide palléal et extrapalléal. En fonction de leurs activités spécifiques décroissantes, les organes internes se classent ainsi:

1) branchies
2) palpes
3) siphons
4) bord du manteau
5) masse viscérale
6) masse musculaire

Le facteurs de concentration, représentant le rapport entre l'activité de l'organe et l'activité de l'eau, à l'équilibre, sont en moyenne les suivants:

Animal total	= 955	Branchies	= 7 840
Coquille	= 230	Palpes	= 2 530
Parties molles	= 3 220	Siphons	= 3 140
Liquides internes	= 30	Bord du manteau	= 2 880
Sang	= 50	Masse viscérale	= 2 620
		Masse musculaire	= 2 470

La distribution du radio-zinc dans l'organisme se répartit ainsi:

Par rapport à l'activité de l'animal total		Par rapport à l'activité des tissus mous	
Coquille	= 10 %	Masse visséral	= 40%
Tissus mous	= 88,5%	Branchies et palpes	= 35%
Liquides internes	= 1,5%	Manteau	= 15%
		Masse musculaire	= 10%

Les Anodontes fixent très fortement le zinc-65 et peuvent eventuellement servir comme indicateur du niveau de la contamination du milieu. La coquille retient essentiellement le zinc-65 par des mécanismes d'adsorption. Par contre les branchies et la partie externe du manteau sont des organes de fixation et de stockage préférentiels; l'hémolymphe semble jouer un rôle essentiel dans le transport du zinc.

INTRODUCTION

A cause de leurs besoins en eau les Centrales nucléaires s'installent le long des fleuves et des rivières utilisés comme exutoire naturel des grands volumes d'effluents faiblement radioactifs. Les corps ainsi rejetés rentrent dans les cycles biogéochimiques et il est donc particulièrement important d'étudier leur fixation par les organismes aquatiques. Nous avons vu que les bivalves constituent, de ce point de vue, des témoins biologiques interessants [1]. Nous présentons ici quelques résultats expérimentaux concernant la fixation du zinc-65 par *Anodonta cygnea* (L.).

Le zinc est un oligoélément important en écologie [2]. Le zinc-65, qui peut servir de traceur pour l'étude du cycle du zinc stable, est un corps produit par la radioactivité induite à partir des sels dissous. Ce phénomène se réalise après les explosions nucléaires sousmarines. Par exemple, dans les îles Marshall, on décèle la présence de radioactivité un an à deux ans après les explosions et, en particulier dans les bivalves [3]. Mais on trouve aussi du zinc-65 dans les déchets des réacteurs nucléaires; d'importantes quantités de zinc-65 sont véhiculées par la Columbia River [4], et les teneurs sont parfois notables le long des côtes et dans les estuaires [5].

Par ailleurs, le zinc est un produit fortement concentré par les organismes d'eau douce ou marins [6] [7]. Les mollusques, en particulier, sont de bons indicateurs de la présence de zinc-65 [4] [7] [8] [9] [10].

CONDITIONS EXPERIMENTALES

Les contaminations expérimentales sont réalisées avec du chlorure de zinc en solution HCl (N = 0.1) sans entraîneur (la teneur en zinc stable influe sur le niveau de la contamination des organismes). La période du zinc-65, émetteur γ, est de 245 jours. Dans tous les résultats nous avons tenu compte de la décroissance physique du radioélément en effectuant les corrections nécessaires.

Les mesures sont faites sur un sélecteur d'amplitude monocanal, (la sonde est constituée d'un syntibloc SC^3N^{50} 1' 3/4 2'').

L'eau est prélevée par pipettage, placée dans des tubes de 10 cm^3 et comptée directement dans un cristal-puits. La mesure des animaux s'effectue selon deux procédés différents; les courbes de la dynamique de la contamination et de la décontamination sont obtenues par la mesure des animaux vivants; à différents intervalles de temps les échantillons sont prélevés, lavés et comptés, de telle sorte que chaque point de la courbe représente une valeur moyenne; les animaux sont placés dans le compteur de manière à ce que les conditions de géométrie soient les plus voisines possibles. Pour les mesures réelles de l'activité, les organes sont disséqués, pesés frais[1] et placés dans les tubes de comptage, les coquilles sont préalablement broyées.

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[1] Les rapports $\frac{\text{Poids frais}}{\text{Poids sec}}$ sont en moyenne les suivants:

Animal total = 4,5	Manteau = 17	Masse musculaire = 10
Tissus mous = 10	Branchies = 7,7	Masse viscérale = 13
Coquille = 1,1		

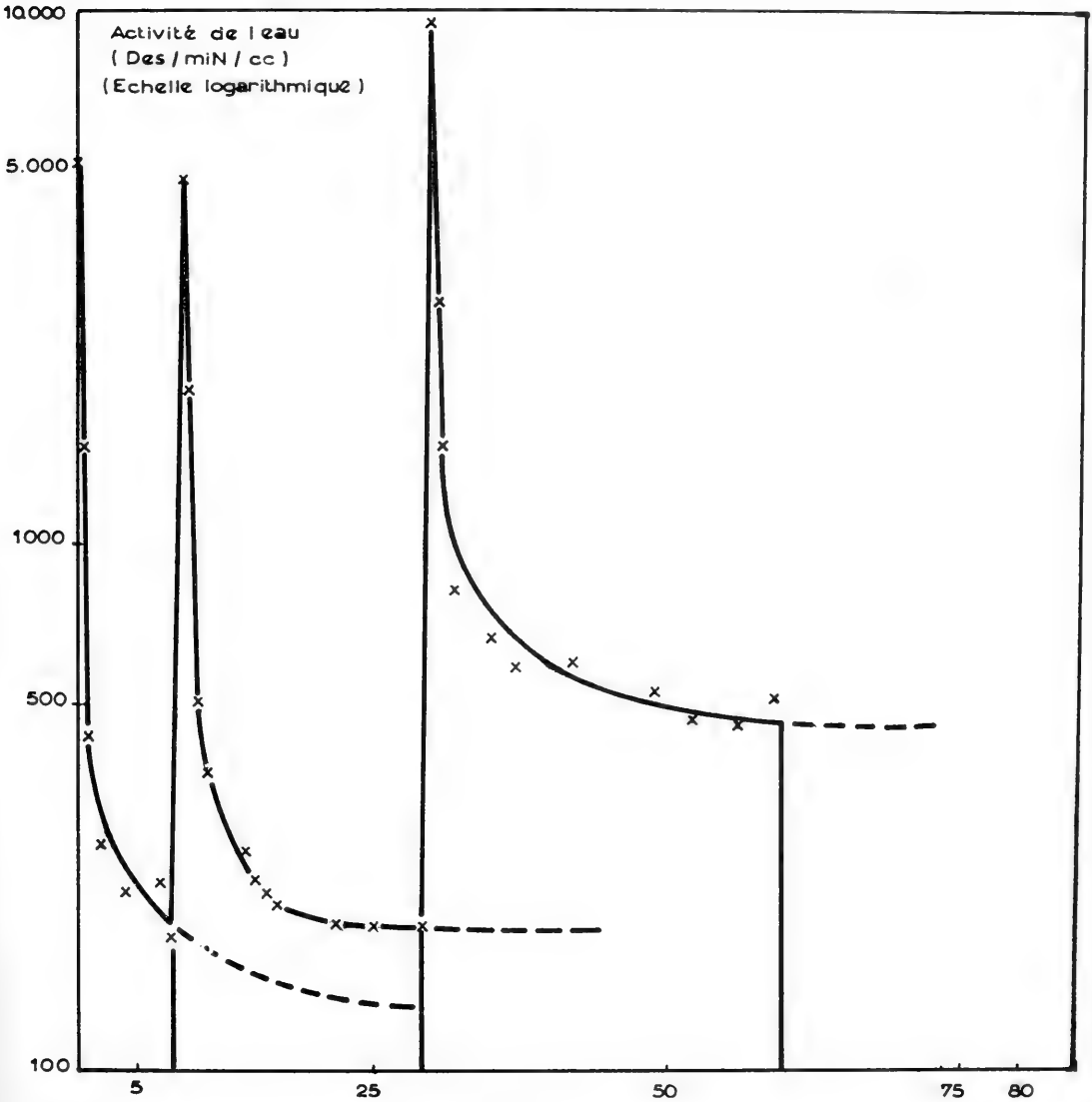


FIG. 1. Variations de la teneur en zinc-65 de l'eau.

Les aquariums expérimentaux sont climatisés à 16°C ± 1°C. Nous utilisons toujours la même eau et le même sédiment provenant du Rhône. L'eau renferme entre 3 et 10 µg/litre de zinc et le sédiment entre 0,5 et 2 mg/100 g.

RESULTATS

ETUDE DYNAMIQUE DE L'ABSORPTION ET DE LA DESORPTION DU ZINC-65 PAR LES ANODONTES

Dans un aquarium contenant trente litres d'eau et du sédiment nous avons placé cinq anodontes. Après avoir laissé le bac se stabiliser pendant 15 jours nous avons entrepris l'expérience. Elle consiste à faire varier en fonction du temps la teneur en zinc-65 de l'eau et à suivre l'évolution de l'activité des anodontes. La Fig. 1 et

TABLEAU 1. Variations de la teneur de l'eau en zinc-65 en fonction du temps.

Temps	Des/min/cc	Processus expérimental
1 heure	5 100	→ 1ère contamination
6 heures	1 500	
1 jour	430	
2 jours	270	(3,5 µCi/litre soit 7 800 Des/min/cc)
4 "	220	
7 "	230	
8 "	180	
9 jours (1 heure)	4 830	→ 2ème contamination
9 " (6 heures)	1 940	
10 " (36 ")	500	
11 " (2 jours)	370	
14 " (5 ")	260	
15 " (6 ")	230	(3,3 µCi/litre soit 7 400 Des/min/cc)
16 " (7 ")	220	
17 " (8 ")	210	
18 " (9 ")	220	
22 " (13 ")	190	
25 " (16 ")	190	
29 " (20 ")	190	
30 " (1 heure)	9 500	→ 3ème contamination
30 " (6 heures)	2 840	
31 " (1 jour)	1 510	
32 " (2 jours)	810	
35 " (5 jours)	660	
37 " (7 ")	590	(3,9 µCi/litre soit 8 900 Des/min/cc)
42 " (12 ")	600	
49 " (19 ")	530	
52 " (21 ")	470	
56 " (25 ")	450	
59 " (28 ")	510	
60 jours ↓ 90 jours	≃ 0	→ -Décontamination (Introduction des anodontes dans un circuit d'eau inactive)

le Tableau 1 montrent le processus de l'expérience. Après chaque contamination l'activité de l'eau augmente très rapidement et décroît également vite ensuite. Il semble que l'on atteigne un état d'équilibre environ 30 jours après la contamination. Remarquons que chaque fois que l'on apporte du zinc-65 l'activité spécifique de l'eau se stabilise à un niveau plus élevé. Il doit se produire des phénomènes de saturation progressive au niveau du sédiment. Il s'en suit que plus le milieu reçoit de zinc-65 plus les anodontes vivent dans une eau de radioactivité élevée et, par conséquent,

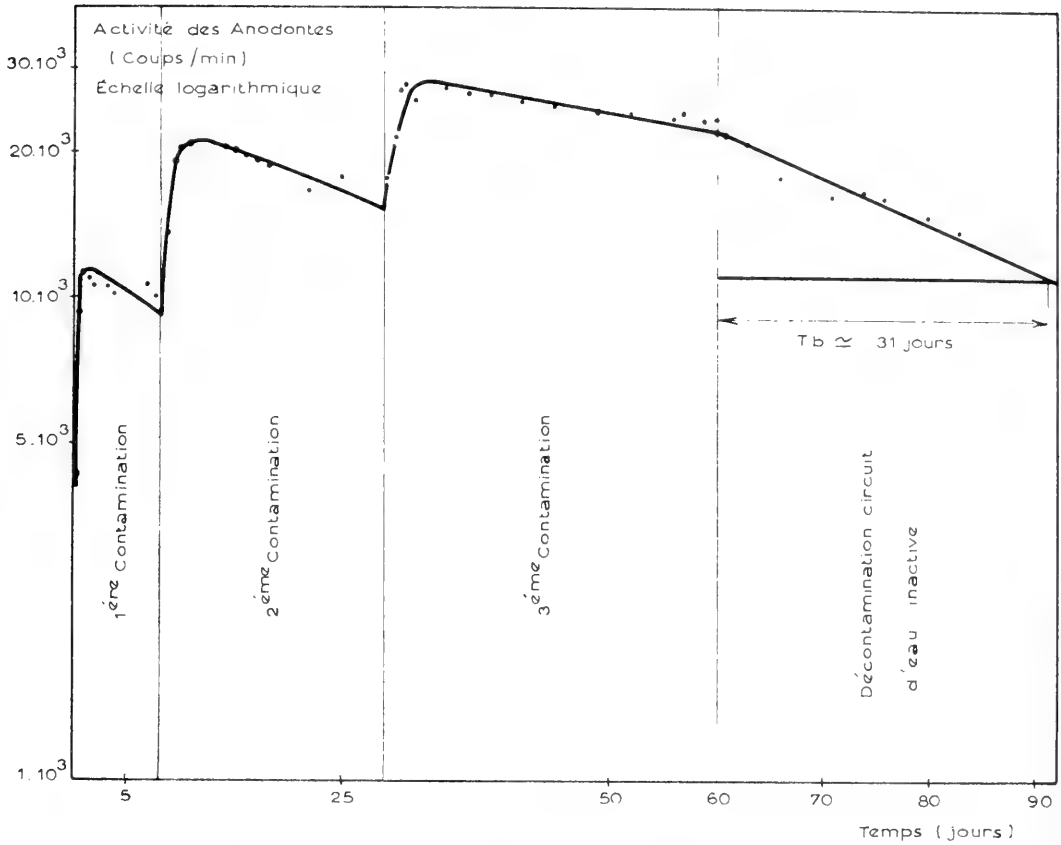


FIG. 2. Dynamique de l'absorption et de la désorption du zinc-65 par les anodontes en fonction de la variation de la teneur en zinc-65 de l'eau.

leur propre niveau de contamination augmente.

C'est effectivement ce que l'on observe en mesurant régulièrement la teneur en zinc-65 des animaux vivants (Fig. 2, Tableau 2).

En ce qui concerne la contamination nous pouvons observer, compte tenu des écarts individuels importants, qu'il est difficile d'obtenir un état d'équilibre et, qu'en tous les cas, pour l'atteindre, le temps doit être très long. Il semble même que la décroissance de l'activité des anodontes après chaque contamination soit moins rapide. Ceci confirme les résultats de Keckes obtenus sur *Mytilus galloprovincialis* qui montrent que la perte de zinc dépend du temps d'exposition des animaux au zinc-65 [11] [12]. Le phénomène le plus général réside dans la rapidité de la fixation du zinc-65. Chipman et Col. sur des truites montrent la rapidité des échanges [13]; sur des coquilles saint-Jacques, Borough et Col. montrent que deux heures sont suffisantes pour atteindre un pic d'activité [14]. L'accumulation de zinc-65 est proportionnelle à la concentration de l'eau, ce qui est conforme aux résultats de Pauley et Nakatani [15].

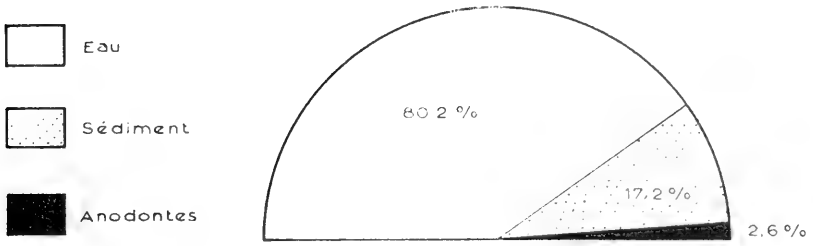
En plaçant des anodontes dans un circuit d'eau inactive, la perte de zinc semble s'effectuer selon une courbe uniforme et correspond à une période biologique de l'ordre de 31 jours. D'après Young et Folson, en transportant des moules (*Mytilus galloprovincialis*) d'une zone contaminée vers une zone inactive la baisse de la con-

TABLEAU 2. Evolution de l'activité totale des Anodontes en fonction de la variation de la teneur en zinc-65 de l'eau.

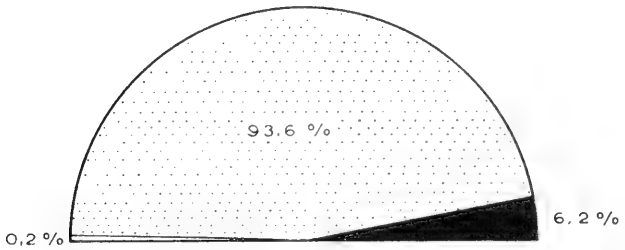
Temps	Activité des Anodontes en coups/minute (comptage des animaux vivants)						X*
1 heure	3 340	4 080	3 640	5 580	4 490	1ère contamination	4 230
6 heures	9 650	10 860	7 610	9 320	9 890		9 460
24 heures	10 060	13 550	10 140	10 710	11 680		11 230
30 heures	9 430	13 560	9 790	10 750	12 110		11 130
2 jours	9 330	12 250	10 300	10 250	11 150		10 600
54 heures	9 390	11 850	10 880	10 100	11 110		10 570
4 jours	8 290	11 390	10 380	9 650	10 860		10 220
7 jours	7 980	10 780	10 850	9 580	13 620		10 780
8 jours	7 280	9 950	9 930	8 610	13 320		10 010
9 jours (1h)	10 480	13 490	13 970	12 140	18 180	2ème contamination	13 630
9 " (6h)	17 040	19 650	18 510	16 220	21 350		18 550
10 " (36h)	17 920	21 300	20 410	17 380	23 730		20 150
11 " (2 j)	17 280	21 540	21 350	18 330	25 260		20 970
14 " (5 j)	16 730	23 001	20 750	17 240	24 080		20 780
15 " (6 j)	15 760	21 190	20 490	16 590	24 300		20 070
16 " (7 j)	15 580	20 000	20 000	16 640	23 580		19 560
17 " (8 j)	15 140	20 710	18 350	16 150	23 230		19 090
18 " (9 j)	13 890	19 690	18 420	15 830	22 090		18 580
22 " (13 j)	12 620	18 160	16 500	14 000	19 760		16 880
25 " (16 j)	13 110	18 650	16 400	13 800	20 890		17 820
29 " (20 j)	13 000	19 500	16 110	13 920	21 230		17 900
30 jours (1h)	16 900	24 460	22 [illegible]	18 5[illegible]	25 360	3ème contamination	21 960
30 " (7h)	23 030	29 [illegible]	28 [illegible]	23 620	33 200		27 550
31 " (1 j)	22 590	29 [illegible]	27 [illegible]	23 190	33 570		27 330
32 " (2 j)	20 920	29 210	26 080	22 520	26 160		25 230
35 " (5 j)	25 260	28 990	24 810	21 340	32 020		27 060
37 " (7 j)	20 730	30 180	25 740	21 720	33 [illegible]		26 800
39 " (9 j)	18 860	30 000	24 520	21 520	32 650		26 500
42 " (12 j)	19 160	29 140	24 400	20 870	31 770		25 100
45 " (15 j)	18 640	28 480	22 [illegible]	20 180	30 600		25 400
49 " (19 j)	17 700	27 460	22 210	19 300	29 380		24 400
52 " (21 j)	17 760	27 240	21 930	19 740	29 110		24 600
56 " (25 j)	16 720	27 280	21 [illegible]	17 [illegible]	27 600		23 800
57 " (26 j)	17 [illegible]	27 120	20 [illegible]	17 930	27 540		24 100
59 " (28 j)	17 160	26 180	20 540	16 8[illegible]	26 260		23 250
60 " (29 j)	17 380	25 780	21 040	17 550	26 190		23 600
60 jours (6h)	15 220	17 400	14 [illegible]	21 550	20 240	Décontamination	22 600
61 " (1 j)	14 [illegible]	15 690	13 240	20 360	20 170		21 700
63 " (3 j)	13 540	14 830	12 370	19 040	17 960		20 100
66 " (6 j)	11 480	12 960	15 100	14 490			17 600
70 " (10 j)	10 [illegible]	11 580	13 910	13 070			16 300
74 " (14 j)	10 720	12 050	14 370				16 500
76 " (16 j)	9 590	12 760	13 300				16 000
80 " (20 j)	9 040	12 600					14 800
83 " (23 j)	8 740	11 390					13 880

* Dans cette colonne les résultats sont donnés en tenant compte de la décroissance physique du zinc-65.

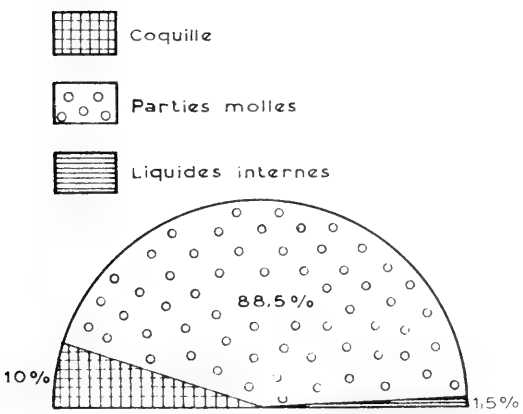
centration en zinc s'exprime par une exponentielle simple correspondant à une période biologique de l'ordre de 76 jours [16]; dans les mêmes conditions avec *Crassostrea gigas* Seymour trouve une période de 300 jours [17]; d'après des informations non publiées de Price la période ne serait pour *Mercenaria mercenaria* que de 30 jours [2]; par contre, Harvey qui a travaillé sur *Lampsilis radiata* distingue une période rapide voisine de 3,5 jours et une lente de 40 jours [18].



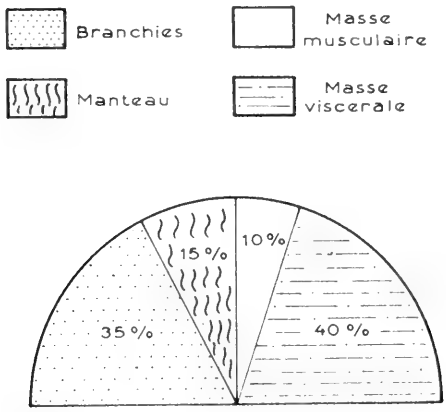
Graphique n° 1 Constitution de l'aquarium
(Poids total ≃ 87 200g)



Graphique n° 2 Répartition de l'activité à la fin de l'expérience
(Activité totale ≃ $6223 \cdot 10^5$ Des/min.)



Graphique n° 3
Par rapport à l'activité totale de l'animale
(Activité moyenne: ≃ $2900 \cdot 10^3$ Des/min)



Graphique n°4
Par rapport à l'activité totale des parties molles
(Activité moyenne: ≃ $2000 \cdot 10^3$ Des/min)

GRAPHIQUES 1-4. Distribution du radiozinc dans l'anodonte.

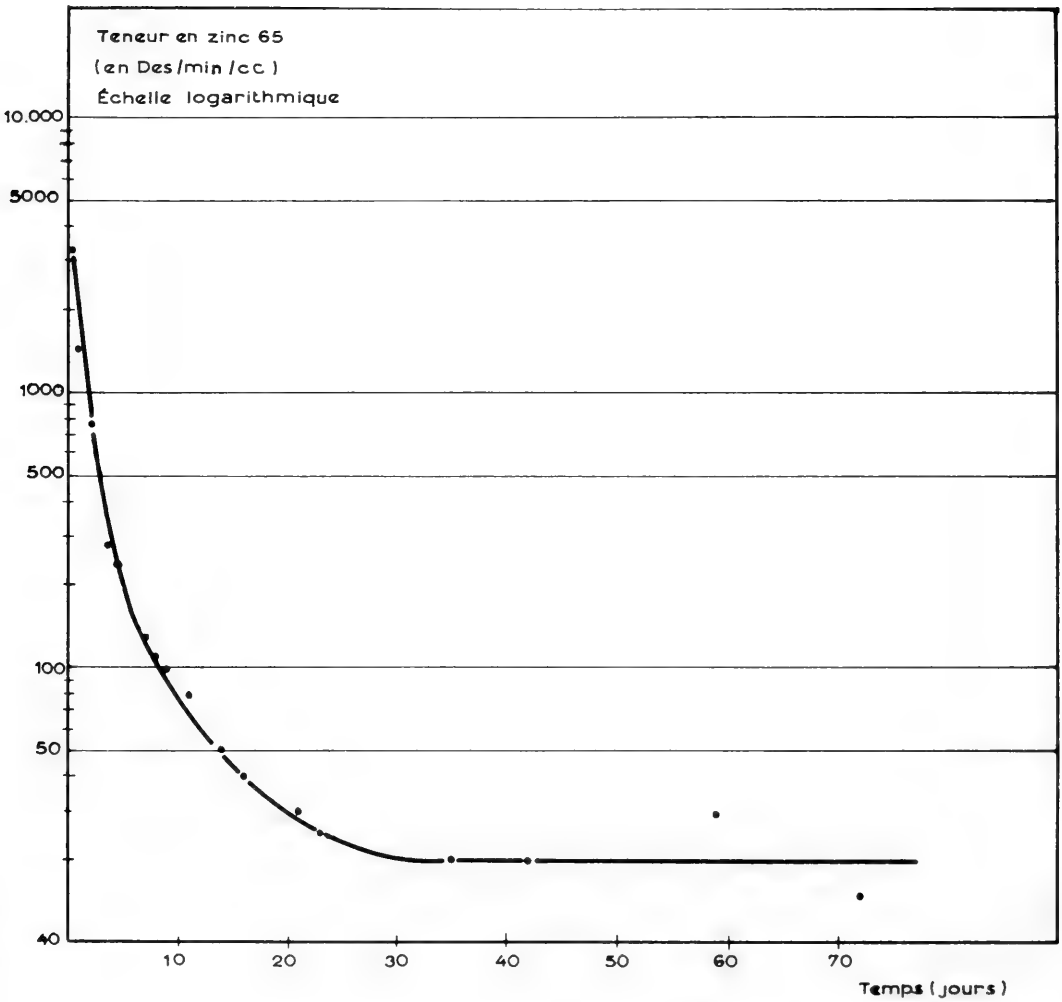


FIG. 3. Evolution de l'activité de l'eau.

Nous retiendrons essentiellement de cette expérience que la fixation du zinc-65 par les anodontes est intense et rapide puisqu'on obtient un pic d'activité dès le 3ème à 4ème jour, cette fixation est d'autant plus importante que l'activité de l'eau est élevée. La perte de zinc est un processus relativement long qui, pour être saisi dans toute sa complexité, devra être complété par l'étude la la période biologique de chaque organe.

ETUDE QUANTITATIVE DE LA FIXATION DU ZINC-65 PAR LES ANODONTES ET DE SA REPARTITION

Dans un aquarium contenant 70 litres d'eau et 15 kg de vase, on place 18 anodontes (graphique 1). On contamine l'eau de l'aquarium à 4 μCi/litre, soit une activité totale de 6223.10^5 des/min. L'expérience dure 59 jours. Il est intéressant de voir dès maintenant comment se répartit le zinc-65 en fin d'expérience dans les différents constituants de l'aquarium (graphique 2). L'activité des anodontes représente environ

TABLEAU 3. Evolution de l'activité de l'eau.

Temps	Activité de l'eau (Des/min/cc)
Instant de la contamination	8 890
4 heures	3 340
1 jour	1 440
2 jours	790
3 "	280
4 "	240
7 "	130
8 "	110
9 "	100
11 "	80
14 "	50
16 "	40
21 "	30
23 "	25
35 "	20
42 "	20
59 "	30
72 "	15

$38\,400.10^3$ des/min. Ainsi, la majeure partie du zinc-65 a été retune par le sédiment.

1. Evolution de l'activité de l'eau

Le Tableau 3 et la Fig. 3 montrent la décroissance très rapide de l'eau qui tend vers un état d'équilibre. A la fin de l'expérience nous avons effectué plusieurs prélèvements de vase qui nous ont donné les résultats suivants, en des/min/g frais: 17 400; 18 000; 26 800; 16 000; 24 200; 26 700; 12 500; 23 500; 16 600; 21 000. L'activité totale du sédiment est d'environ 583.10^6 des/min. La distribution du zinc dans le sédiment n'est homogène ni en surface ni en profondeur.

Ces résultats correspondent à ceux trouvés par Rowe & Gloyna [19]. Remarquons qu'une partie du zinc reste en solution et qu'une autre peut se fixer sur tous les fins matériaux en suspension. En plus des mécanismes d'échanges ioniques entre l'eau et le sédiment, il se produit de simples phénomènes d'adsorption.

2. Teneur en zinc-65 de l'animal total, de la coquille, des tissus mous et des liquides internes

a) Evolution des activités spécifiques

Les Fig. 4 et le Tableu 4 montrent la très grande variabilité des résultats que l'on obtient d'un échantillon à l'autre. Ces écarts individuels sont de l'ordre de 1 à 4. Le résultat principal réside cependant dans le fait que la coquille et les tissus mous fixent très rapidement le zinc et que cette fixation se maintient par la suite à l'intérieur de certaines limites (Fig. 4B et 4C). L'activité spécifique des liquides internes décroît en fonction de la baisse de celle de l'eau mais lui demeure toujours supérieure (Fig. 4D).

Au niveau de la coquille la fixation du zinc-65 est due essentiellement à des mécanismes d'adsorption [3] [6] [7] [12]. Par contre les tissus mous présentent une grande affinité pour le zinc et ce sont des phénomènes métaboliques qui dominent [15] [18].

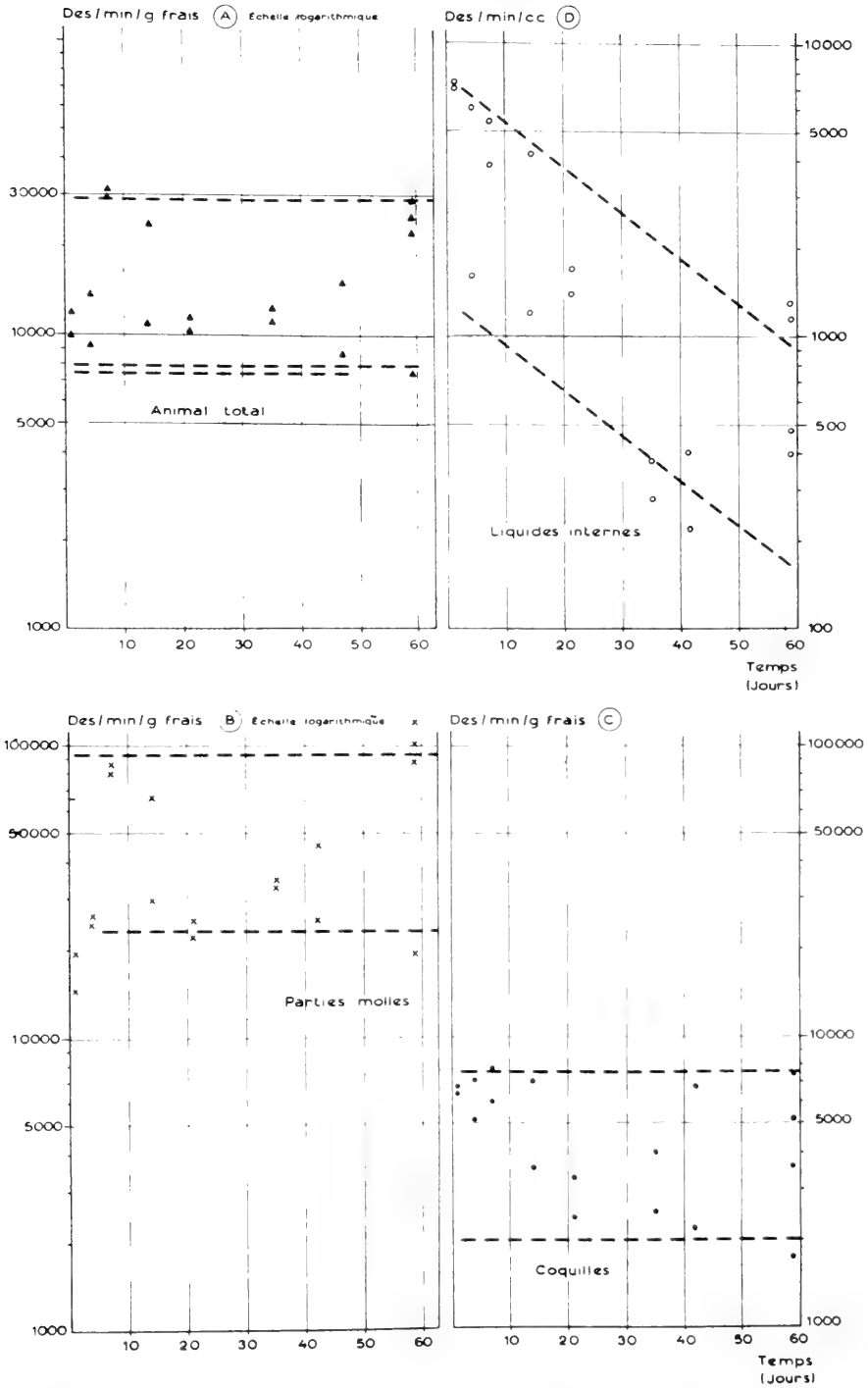


FIG. 4. Teneur en zinc-65 de l'animal, des liquides internes, des parties molles et de la coquille en fonction du temps.

TABLEAU 4. Evolution de l'activité spécifique de l'animal total, de la coquille, des parties molles et des liquides internes en fonction du temps.

Temps	Activités spécifiques (Des/min g frais ou cc)			
	Animal total	Coquille	Parties molles	Liquides internes
1 j	10 000 - 12 150	6 570 - 6 870	14 690 - 19 400	7 100 - 7 470
4 j	9 290 - 13 770	5 200 - 7 180	24 370 - 26 400	1 650 - 6 120
7 j	30 000 - 31 200	7 970 - 6 000	85 500 - 80 890	5 400 - 3 900
14 j	11 600 - 24 290	3 690 - 7 070	29 340 - 67 600	1 200 - 4 490
21 j	10 600 - 11 660	2 420 - 3 310	22 130 - 25 100	1 480 - 1 790
35 j	12 450 - 11 040	4 090 - 2 590	34 570 - 33 500	280 - 380
42 j	8 790 - 15 090	6 890 - 2 260	25 620 - 46 500	221 - 400
59 j	26 200 - 7 640 28 700 - 29 390	3 670 - 5 170 7 560 - 1 790	120 000 - 19 300 88 100 -100 800	480 - 400 1 180 - 1 310

TABLEAU 5. Distribution du zinc-65 dans l'organisme en fonction de l'activité totale de l'animal.

Temps	Pourcentage de zinc-65 contenu dans chaque organe en fonction de l'activité totale de l'animal		
	Coquille	Parties molles	Liquides internes
1 jour	16 - 17,5	59 - 65	25 - 17,5
4 jours	17 - 14	76 - 70	7 - 16
7 jours	6 - 4	85 - 90	8 - 6
14 jours	9 - 8	87 - 84	4 - 8
21 jours	6 - 6,5	90 - 88	4 - 5,5
35 jours	9 - 7	90 - 91,5	1 - 1,5
42 jours	27 - 5	72 - 94	1 - 1
59 jours	4 - 19,5- 6 - 1,5	95-78,5-92-96,5	1 - 2 - 2 - 2

b) Distribution du radiozinc

Le graphique 3 et le Tableau 5 montrent qu'en fin d'expérience la majeure partie du zinc-65 se trouve dans les tissus mous. Selon la composition physico-chimique de l'eau, l'espèce, et les conditions expérimentales les phénomènes d'adsorption peuvent être plus ou moins intenses. Parfois la coquille peut retenir plus de 60% du zinc-65. Ce peut être le cas, par exemple, lorsque l'expérience est poursuivie dans un milieu ne contenant pas de sédiment; dans ce cas, en effet, la surface de la coquille offerte à l'adsorption est beaucoup plus importante.

Dans cette question de la distribution du zinc-65 dans l'organisme, plusieurs auteurs ont montré, sur des bivalves marins, toute l'importance de la teneur en zinc-stable [8] [10] [13] [20] [21] [22]. Différentes analyses permettent de montrer que, pour les parties molles, le zinc-65 suit le métabolisme du zinc stable [15] [23][2]. La distribution du zinc-65 correspond à celle du zinc stable.

3. Teneur en zinc-65 des principaux organes internes

a) Evolution des activités spécifiques

Lors de chaque prélèvement d'anodontes nous avons disséqué les principaux organes internes et mesuré leurs activités spécifiques respectives (Tableau 6). Malgré les écarts individuels, on constate une fixation rapide du zinc-65 qui atteint un maximum d'activité dès le 7ème jour puis se maintient par la suite. Si on considère les activités spécifiques décroissantes des organes, à partir du moment où l'eau est à l'"équilibre", c'est-à-dire au 35ème jour, elles se classent de la manière suivante:

- Branchies (avec des valeurs supérieures pour les branchies internes)
- Siphons
- Palpes
- Bord du manteau (le reste du manteau ayant une activité nettement plus faible)
- Masse viscérale
- Masse musculaire

Ainsi les organes intervenant dans le transfert des particules et dans la filtration de l'eau ont des teneurs en zinc-65 particulièrement fortes de même que le bord du manteau. Ces résultats concordent avec ceux trouvés sur des mollusques marins et, en particulier, avec les expériences conduites par Pauley et Nakatani [7] [12] [13] [15] [22]. Notons, par ailleurs, que le sang (ou hémolymphe) a une activité spécifique élevée et toujours nettement supérieure à celle du liquide extrapalléal. (Certaines mesures donnent également des teneurs en zinc-65 élevées pour le coeur).

On peut donc conclure que la filtration de l'eau, les échanges osmotiques et certains processus métaboliques au niveau intestinal et au niveau du manteau jouent un rôle particulièrement important dans la fixation du zinc. Les siphons et les palpes interviennent dans la collecte des particules en suspension qui passent ensuite dans le tractus digestif, le sang transporte ensuite le zinc vers les épithéliums des branchies et du manteau. Au niveau des branchies il doit se produire également des phénomènes d'adsorption par le mucus qui les recouvre. Pour ce qui est du manteau Istin a montré le rôle de l'anhydrase carbonique localisée à la périphérie; or cette enzyme contient du zinc [24]. D'autres enzymes d'ailleurs renferment du zinc.

b) Distribution du radiozinc

Si on ne considère que l'activité totale des tissus mous, la distribution du zinc s'effectue conformément aux résultats donnés dans le tableau 7 et le graphique 4. Ces résultats correspondent à la teneur en zinc stable des différents organes [15].

4. Les facteurs de concentration

Ils représentent la valeur du rapport, à l'équilibre, entre l'activité spécifique de l'animal ou de ses organes avec celle de l'eau. C'est une donnée particulièrement importante dans le domaine de la protection sanitaire car elle exprime la capacité de fixation des radioéléments par une espèce.

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[2]Sur Unio la distribution du zinc stable est de 0,25 à 0,79% du poids sec dans les tissus mous et de 0,001 à 0,018 dans la coquille.

TABLEAU 6. Activités spécifiques des organes internes en fonction du temps (Des/min/g frais).

Organes \ Temps jours	1	4	7	14	21	35	42	59	Moyenne
Liquides internes	7 100 7 470	1 650 6 120	5 400 3 930	1 210 4 490	1 480 1 795	280 380	220 400	480- 400 1 190- 1 310	580
Liquide extrapalléal	720 2 950	160 920	5 200 4 020	570 4 550	580 880	105 170	90 95	380- 180 1 570- 1 230	480
Liquide palléal	7 150 7 060	280 5 330	4 340 1 016	740 470	840 730	60 230	145 90	360- 130 50- 1 020	260
"Sang"	11 600 11 300	4 520 9 260	7 020 4 940	1 300 5 740	2 920 3 560	440 570	370 690	850- 810 1 680- 1 950	920
Branchies totales	17 640 31 720	52 370 57 900	109 000 122 140	64 570 124 230	39 500 36 900	121 420 53 520	42 040 159 400	313 500- 58 800 118 000-273 300	142 500
Branchies internes	35 900 33 120	64 200 54 960	252 600 263 400	71 240 223 900	53 900 50 920	118 400 64 800	43 680 160 000	471 400- 74 820 335 200-326 600	199 400
Branchies externes	11 360 29 580	43 700 62 630	73 100 71 070	59 460 59 670	32 500 27 990	126 400 43 460	39 730 158 600	201 580- 47 050 62 360-221 800	112 600
Manteau total	9 350 16 400	11 480 11 750	63 470 55 080	24 620 51 920	14 510 27 140	22 450 12 960	16 630 43 460	90 190- 10 620 54 280- 64 750	39 400
Bord du manteau	19 750 9 600	11 100 14 100	58 800 40 840	29 700 50 170	23 150 37 390	11 940 16 780	13 230 74 390	124 320- 17 090 79 230- 80 050	52 100
Reste du manteau	6 440 15 800	11 400 10 870	55 050 45 440	19 500 42 820	11 250 21 450	24 390 11 350	16 620 38 540	70 000- 7 920 28 980- 44 400	30 300
Siphons	16 650 35 900	12 920 13 860	104 500 77 880	48 900 97 500	31 750 59 920	17 540 17 560	24 610 44 460	78 350- 28 600 154 000- 90 460	56 900
Masse musculaire totale	16 870 13 800	15 120 9 350	49 760 39 190	25 830 57 470	25 030 33 400	14 480 24 230	13 950 29 170	67 220- 22 210 97 220- 89 620	44 700
Muscles adducteurs	12 610 13 000	5 920 6 240	43 500 33 300	23 [illegible]	[illegible]	9 950 18 600	9 400 24 060	52 480- 6 300 68 430- 79 [illegible]	33 700
Masse viscérale	10 800 16 300	21 530 27 370	91 390 82 060	22 [illegible] 56 700	19 440 18 190	25 170 41 170	27 630 33 690	85 490- 10 550 84 970- 73 700	47 800
Palpes	138 200 149 200	151 860 152 240	151 190 125 300	86 400 [illegible]	110 040 34 700	28 700 33 800	31 840 65 470	52 290- 41 340 63 700- 52 170	45 200

TABLEAU 7. Distribution du zinc-65 dans les organes en fonction de l'activité totale des tissus mous.

Temps	Pourcentage de zinc-65 contenu dans chaque organe en fonction de l'activité totale des tissus mous			
	Branchies et palpes	Manteau	Masse musculaire	Masse viscérale
35 jours	42 - 22 -	16 - 9 -	4 - 10 -	38 - 59 -
42 jours	26 - 33 -	16 - 18 -	6 - 9 -	52 - 40 -
59 jours	44 - 45 - 37 - 35 -	16 - 13 - 15 - 14 -	8 - 16 - 14 - 15 -	32 - 26 - 34 - 34 -
Moyenne	35	15	10	40

Nous avons porté les principaux résultats dans le tableau 8 ils ne font d'ailleurs que confirmer la capacité de fixation plus ou moins grande d'un organe pour le zinc. Notons simplement que les valeurs obtenues sont particulièrement fortes, et supérieures à celles des bivalves marins, mais restent, comme en milieux marins, nettement inférieures à celles correspondant au facteur de concentration du zinc stable.

Pour le zinc stable les moules ou les huitres peuvent avoir des facteurs de concentration de l'ordre de plusieurs milliers; 14 600 pour *Crassostrea gigas*, 17 000 pour *Pecten japonicus*, 40 000 pour *Ostrea edulis* [7] [17] [20]. Pour *Lampsilis* sp., Harvey donne un facteur de concentration pour les tissus mous voison de 4 100 [18]. Si les anodontes contiennent entre 0,2 et 0,4 mg/g de zinc et l'eau douce environ 10 μg/litre, le facteur de concentration pour le zinc stable se situe entre 12 000 et 24 000.

CONCLUSION

Ces premiers résultats nous donnent des informations dans trois domaines différents et nécessitent pour chacun d'eux des approfondissements.

Sur le plan sanitaire, nous avons pu observer une fixation rapide et importante du zinc-65 par les anodontes qui est fonction de la teneur en zinc-65 de l'eau. La période biologique relativement longue est voisine de 31 jours. Il faut cependant noter que, compte tenu de la très forte capacité de rétention du zinc par le sédiment, la quantité restant disponible pour une contamination éventuelle des organismes est faible. Le Facteur de Concentration de l'anodonte est voisin de 950 mais peut dépasser 7 000 pour les branchies. La capacité de filtration de l'eau permet à ces bivalves d'atteindre rapidement un pic d'activité [8]. Il semble d'ailleurs que la quantité de zinc-65 absorbée soit en relation directe avec le volume d'eau filtrée [25]. Les bivalves, et les anodontes en particulier, peuvent servir d'indicateurs de la présence de zinc-65 dans l'eau et contribuer à l'établissement des concentrations maximales admissibles [10].

Sur le plan physiologique, le zinc-65 peut servir d'indicateur pour suivre le métabolisme du zinc. Nous avons vu que des organes jouent un rôle particulier dans ce domaine. Des mécanismes d'échanges et d'adsorption s'établissent au niveau des branchies; les siphons et les palpes interviennent dans la collecte des particules; l'hémolymphe joue le rôle de transporteur du zinc vers les épithéliums du manteau. Ces études sont à poursuivre en utilisant, en particulier, les méthodes autoradiographiques.

Sur le plan biologique et écologique, les questions essentielles résident dans la voie d'entrée du zinc et dans le rôle des facteurs du milieu. En effet, le zinc soluble peut

TABLEAU 8. Facteurs de concentration du zinc-65 de l'Anodonte et de ses différents organes en fonction du poids frais.

Organes / Temps	Animal total	Coquille	Tissus mous	Liquides internes	Sang	Branchies totales	Palpes	Manteau total	Bord du manteau	Reste du manteau	Siphons	Masse muscul.	Muscles adduct.	Masse viscér.
35 j.	655	215	1 819	15	23	6 390	1 506	1 181	628	1 283	923	752	523	1 324
	580	136	1 760	20	30	2 [illegible]	1 [illegible]	664	[illegible]	[illegible]	[illegible]	1 [illegible]	[illegible]	[illegible]
42 j.	442	262	1 348	12	12	2 [illegible]	1 [illegible]	875	690	5 [illegible]	1 [illegible]	734	409	1 [illegible]
	538	126	2 585	22	25	8 [illegible]	3 [illegible]	2 414	1 132	2 [illegible]	2 [illegible]	1 [illegible]	1 [illegible]	1 671
59 j.	1 [illegible]	204	2 [illegible]	20	42	17 [illegible]	2 [illegible]	5 [illegible]	5 [illegible]	2 [illegible]	1 [illegible]	3 [illegible]	2 [illegible]	4 [illegible]
	424	287	1 072	22	45	5 [illegible]	2 [illegible]	910	949	440	1 [illegible]	1 224	591	955
	1 [illegible]	420	4 [illegible]	[illegible]	93	[illegible]	3 [illegible]	2 015	4 [illegible]	1 [illegible]	3 [illegible]	5 [illegible]	3 [illegible]	4 720
	1 [illegible]	100	5 [illegible]	[illegible]	108	19 [illegible]	2 [illegible]	2 [illegible]	4 [illegible]	2 [illegible]	2 [illegible]	[illegible]	[illegible]	[illegible]
Moyenne	955	230	3 220	30	50	7 [illegible]	2 [illegible]	2 170	2 [illegible]	[illegible]	3 [illegible]	2 [illegible]	1 [illegible]	2 [illegible]

pénétrer par simple échange entre l'eau et l'organisme; lorsqu'il est adsorbé il peut être ingéré par l'intermédiaire des particules organiques ou minérales. Par ailleurs, des facteurs du milieu tels la turbidité, la température ou la composition chimique de l'eau peuvent, en variant, modifier la capacité de fixation des organismes.

Des protocoles expérimentaux bien appropriés doivent permettre de répondre à ces questions.

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SUMMARY

RESULTS OF EXPERIMENTS ON ZINC-65 FIXATION BY *ANODONTA CYGNEA* (L.)

Zinc-65 is an induced radioactive substance found mainly in the waste products of nuclear reactors; it is accumulated in highly concentrated form by living organisms, molluscs in particular. The development of nuclear plants along the Rhone has led the authors to study Zinc-65 fixation (in chloride form) by *Anodonta cygnea*.

Two experiments are described: The 1st concerns the dynamic study, by means of radioactive measuring of the living shellfish, of Zinc-65 absorption and desorption by anodontae, in terms of the varying Zinc-65 content of the water. Zinc-65 fixation by these bivalves appears proportional to the Zinc-65 content of the water, and is a rapid phenomenon: a maximum activity peak is obtained on the 3rd or 4th day following contamination. In an inactive water circuit, the anodontae lose the zinc relatively slowly, and the biological period is about 31 days.

The 2nd experiment is a study of Zinc-65 fixation by the various organs of the anodonta after contaminating the water in an aquarium containing sediment. The activity of the water is seen to decrease very rapidly, whereas the activity of the sediment increases. After 59 days, the water contains 0.2% of the quantity of Zinc-65

introduced, the anodontae 6.2% and the sediment 93.6%.

Although the specific activities of the soft tissues and the shell vary from one specimen to another throughout the whole experiment they remain within particular limits. The activity of the internal liquids decreases as the activity of the water decreases. The haemolymph always has a distinctly greater specific activity than the palleal and extrapalleal liquid. The classification of the internal organs, in terms of their decreasing specific activities, is as follows:

1) Gills
2) Palps
3) Siphons
4) Mantle edge
5) Visceral mass
6) Muscular mass

The average concentration factors representing the proportion between the activity of the organ and the activity of the water, in a state of balance, are as follows:

Entire shellfish	≃ 955	Gills	≃ 7240
Shell	≃ 230	Palps	≃ 2530
Soft parts	≃ 3220	Siphons	≃ 3140
Internal liquids	≃ 30	Mantle edge	≃ 2880
Blood	≃ 50	Visceral mass	≃ 2620
		Muscular mass	≃ 2470

The radio-zinc's distribution in the organism is as follows:

With respect to the activity of the entire shellfish		With respect to the activity of the soft tissues	
Shell	≃ 10 %	Visceral mass	≃ 40%
Soft tissues	≃ 88.5%	Gills and palps	≃ 35%
Internal liquids	≃ 1.5%	Mantle	≃ 15%
		Muscular mass	≃ 10%

Anodontae fix Zinc-65 very strongly and can be used, if necessary, as indicators of environmental contamination. The shell keeps the Zinc-65 mainly through adsorption mechanisms. On the other hand, the gills and the outer part of the mantle are the organs preferred for fixation and storage; the haemolymph seems to play an essential part in transporting the zinc.

MALACOLOGIA, 1973, 14: 125-127

PROC. FOURTH EUROP. MALAC. CONGR.

THE ROLE OF THE RELATIVE SUSCEPTIBILITY OF SNAILS TO INFECTION WITH HELMINTHS AND OF THE ADAPTATION OF THE PARASITES IN THE EPIDEMIOLOGY OF SOME HELMINTHIC DISEASES

J. C. Boray

Department of Parasitology, University of Zürich[1,2]

The presence of specific intermediate hosts is essential for the development of some helminths which may cause serious diseases in man and animals. The occurrence, distribution and epidemiology of these diseases depend greatly on the geographical distribution of the intermediate hosts and on their relative susceptibility to the parasites. All digenetic trematodes have 1 or more intermediate hosts, the first of which is always a snail, and they also have single or multiple definitive host-species. During the evolutionary process and speciation of various trematodes a distinct biological balance has developed between the hosts and parasites. The free-living stages exposed to adverse effects of the environment are usually produced in enormous numbers (up to 50,000 eggs per day by a single *Fasciola hepatica*). However the 1st larval stages often have to find highly specific intermediate snail hosts. During the 1st parasitic stages a parthenogenetic multiplication occurs resulting in the release of large numbers of the 2nd free-living stage. A single *Lymnaea truncatula* may produce a total of 300-4000 metacercariae of *F. hepatica* which are relatively resistant to adverse environmental conditions. The output of the relatively short lived *Schistosoma mansoni* cercariae in *Biomphalaria glabrata* is 1000-3000 daily. *Dicrocoelium dendriticum* produces fewer but more resistant eggs but a large number of 1st intermediate snail hosts are available for their larval development and asexual multiplication.

The relative susceptibility or resistance of the intermediate and/or definitive hosts to the various parasites is another factor, which plays a most important role in maintaining the biological balance ensuring the survival of both the host and the parasites. Members of the family Dicrocoeliidae show little specificity in their 1st intermediate hosts. Many species belonging to several families of Stylommatophora have been found to be good hosts for the larval development of *Dicrocoelium dendriticum*. There is also little host specificity in the definitive hosts and the epidemiology of dicrocoeliosis is more dependent on the highly specific 2nd intermediate ant-hosts or on other ecological factors. Little host specificity has been found in the relationships of some nematodes (Metastrongylidae, *Angiostrongylus cantonensis* and *A. vasorum*) and cestodes (Davaineidae) to their intermediate snail-host (Stylommatophora), but those parasites are more specific in their definitive hosts. The medically important groups, such as Schistosomatidae and Fasciolidae, are more host specific in the snails (Planorbidae and Lymnaeidae, Basommatophora) than they are in their definitive hosts. In most parts of the world *Fasciola hepatica* is transmitted by *Lymnaea truncatula* and *F. gigantica* by *L. auricularia* s.l. or by varieties of these insufficiently distinctive to be regarded as separate species. A certain species of planorbid or *Oncomelania* snail host is essential for the larval development of various *Schistosoma* spp., and the availability of a suitable intermediate host is further complicated by the different

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[1]Winterthurerstrasse 260, CH 8057 Zürich, Switzerland

[2]Present address: Research Centre, Ciba-Geigy Ltd., Western Rd., Kemps Creek, N.S.W., Australia

TABLE 1. Host-parasite relationship between *Lymnaea* and *Fasciola* spp.

Absolute resistance:	No larval development	
Age resistance:	Development only in young snails	Termination of infection full development of few larvae
Relative disparity:	Full development in adult snails	Low infection rate - Slow development of few larvae Low infection rate - High mortality of snails High infection rate - High mortality of snails
Normal relationship:	Full development in adult snails	High infection rate - Low mortality of snails

susceptibility of infra-specific variations of species-complexes of snails to different races of the parasites.

It has been shown that some geographical or microgeographical races of planorbid or lymnaeid snails, although susceptible, are not equally competent intermediate hosts for different species or strains of Schistosomatidae or Fasciolidae. This relative disparity is an important limiting factor in the distribution of a disease (ref.: Jordan & Webbe, 1969; Boray, 1969). A considerable effort has been devoted to experimental work showing host parasite disparity between infra-specific variations of schistosomes and snails (Files & Cram, 1949; Hunter *et al.*, 1952; De Witt, 1954; Hsü & Hsü, 1960, 1967; Wright, 1962; Paperna, 1968 and most recently Webbe & James, 1971). However, it has been shown in laboratory experiments by Boray (1967, 1969) that in newly formed relationships between trematodes and an unusual snail host, the adaptation of the trematode can occur rapidly as a result of passage, such as the European *Fasciola hepatica* in the Australian *Lymnaea tomentosa* and the Australian *F. hepatica* in *L. tomentosa* from New Guinea, or rather slowly, such as *F. hepatica* in *L. peregra*, the latter showing a strong age resistance. Boray (1969) concluded that in newly formed relationships between trematodes and an unusual snail host, the adaptation of the trematode might occur very rapidly as a result of passage if the snails have a degree of susceptibility in their adult stage.

Various manifestations of a relationship between lymnaeid snails and *Fasciola* spp. (Table 1) may be similar in other snail-trematode relationships. It would be most important that similar studies should be carried out with the medically important schistosome-snail combinations showing relatively low susceptibility. In some of the less competent race combinations within established specific relationships the disparity may be only temporary. Most trematodes have a long life span in their definitive hosts, and if some fasciolids were introduced by domestic animals or some schistosome strains were introduced by movements of human populations into new areas, they may adapt readily to a relatively less susceptible snail through passages, thus creating new problems in disease control.

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MALACOLOGIA, 1973, 14: 129-133

PROC. FOURTH EUROP. MALAC. CONGR.

EFFETS DE LA CASTRATION CHIRUGICALE SUR LE TRACTUS GENITAL ET LA PONTE CHEZ LES AEOLIDIIDAE: APPLICATION A LA COMPREHENSION DES MECANISMES DU CONTROLE ENDOCRINE DE LA SEXUALITE

J. Tardy

Laboratoire de Biologie et Biochimie Marines
Université de Poitiers, France

A la suite des interventions que j'ai pratiquées chez les Aeolidiidae[1], j'ai pu noter quelques faits qui méritent d'être signalés et discutés à la lumière des observations faites dans d'autres groupes, en particulier récemment, chez les Prosobranches par Streiff (1967), Streiff et Le Breton (1970 a et b) et chez les Basommatophores, par Harry (1965) et par Brisson (1970 et 1971). Sans faire l'exégèse des nombreux travaux effectués chez les Pulmonés et les Prosobranches, résumons les résultats auxquels ont abouti les recherches: pour les uns, le tractus est indépendant de la gonade, pour les autres, au contraire, la dépendance serait étroite. En fait, comme l'exprime Streiff (1970 c), la contradiction ne pourrait être qu'apparente, car les travaux sur les Prosobranches portent sur la différenciation, les autres sur le fonctionnement du tractus glandulaire.

Mes observations permettent d'affirmer cette opinion. Auparavant, il convient de remarquer qu'aucun Aeolidiidae castré ne dépose la moindre ponte et qu'il faut attendre, chez ceux qui régénèrent, l'émission des ovocytes pour que se restaure le processus. Pourtant, dans les conditions d'élevage, des pontes sans germe ou partiellement pourvues de germes sont parfois déposées par des *Aeolidiella alderi* indemnes. Quelquefois les oeufs sont éclatés: la ponte renferme alors un véritable cordon de vitellus qui n'évolue pas et devient vite la proie de bactéries.

Selon les espèces, chez les Basommatophores castrés, des pontes sans germes sont déposées assez souvent ou rarement (Brisson, 1970-1971).

Cependant, comme l'a observé cet auteur chez les Basommatophores, et moi-même chez les Aeolidiidae, l'instinct d'accouplement subsiste (au moins chez certains individus).

Que révèlent la dissection et l'étude histologique du tractus génital chez les Aeolidiens castrés définitivement?

1) Tractus mâle: Le pénis semble peu affecté par la castration; par contre le spermiducte montre des variations importantes du développement des épithéliums glandulaires, surtout dans sa partie proximale (prostatique).

2) Tractus femelle: Les glandes responsables de la formation de la ponte demeurent parfois à l'état d'ébauches (Fig. 1) et n'acquièrent pas de différenciation cytologique; plus généralement elles ont un volume normal ou sont hypertrophiées. Dans ces deux cas elles présentent un aspect cytologique pathologique.

Les cellules prennent une forme sphérique, se détachent et tombent dans la lumière où elles forment un coagulum nécrotique qui remonte parfois vers la glande gamétolytique où il est phagocyté par l'épithélium qui augmente considérablement d'épaisseur.

Cet aspect des glandes nidamentaires se retrouve chez tout sujet ne produisant

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[1]Sept types principaux d'intervention représentant plus de 150 observations individuelles, portant sur *Aeolidia papillosa, Aeolidiella glauca, Ae. sanguinea* et surtout sur *Ae. alderi*.

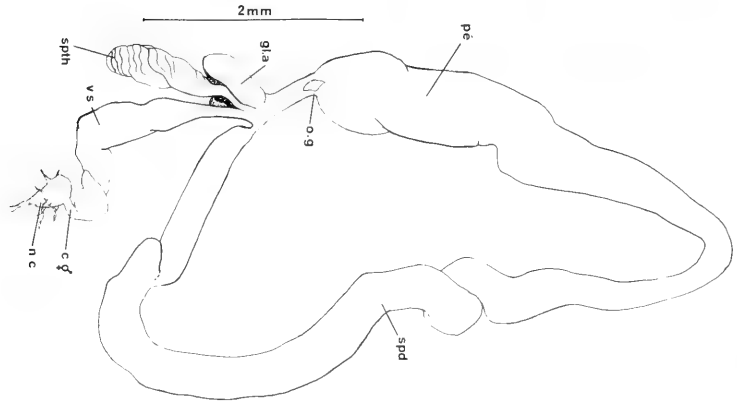

FIG. 1. Tractus génital d'*Aeolidiella glauca* récoltée et opérée alors qu'elle était en phase juvénile et sacrifiée 66 jours plus tard: Le tractus mâle, la vésicule séminale et la spermathèque sont normalement développés. Par contre, les glandes annexes femelles sont totalement indifférenciées et n'ont pas évolué.

c. ♂ : Canal hermaphrodite, gl. a. : glandes annexes; n. c. : nodule cicatriciel au niveau de la section du canal hermaphrodite; o. g. : orifice génital; pé: pénis; spd: spermiducte; spth: glande gamétolytique; vs: vésicule séminale.

plus de gamètes à la suite de diverses interventions, en particulier chez les individus en régénération, dont les glandes étaient déjà fonctionnelles lors de l'opération. Dans ce cas, une partie de l'épithélium semble alors proliférer et remplacera probablement la portion en voie de nécrose.

Lorsque ces glandes étaient encore juvéniles à la castration, elles subissent un retard considérable dans leur développement si la gonade régénère. A la suite de ces observations nous pouvons supposer que l'absence totale du dépôt de la ponte pourrait s'expliquer par une double action de la castration: blocage de la différenciation glandulaire lorsque l'opération a lieu assez tôt, ou bien si celle-ci survient après la différenciation glandulaire, perturbation du fonctionnement entraînant une dégénérescence plus ou moins marquée des glandes nidamentaires.

Dans ce cas, comme l'a exprimé Brisson (1970 et 1971) à propos des Basommatophores, il semble bien que le fonctionnement normal de ces glandes ne soit pas sous le contrôle hormonal de la gonade, mais dépende plutôt de son bon fonctionnement exocrine: en effet si l'on implante une gonade à un individu préalablement castré, ou bien si l'on sectionne le canal hermaphrodite à un individu indemne, la glande nidamentaire s'hypertrophie et dégénère.

Le blocage de la différenciation glandulaire du tractus par la castration montre bien qu'il y a, chez les Gastéropodes, une action hormonale de la gonade qui agit directement ou indirectement sur la cytodifférenciation du tractus femelle et peut-être également sur celle du tractus mâle.

Un autre point est particulièrement frappant et suggestif: il apparaît nettement que les tractus mâle et femelle évoluent indépendamment (Fig. 1 et 2). Ces dernières observations sont, elles aussi, en accord avec les remarquables travaux de Streiff (1967), qui a montré *in vitro* chez les Prosobranches que le développement du tractus mâle et du tractus femelle est régi par des substances hormonales différentes, émises, pour le premier, par le tentacule, pour le second, par le système nerveux.

Chez *Calyptraea sinensis*, Prosobranche à hermaphrodisme successif, Streiff (1967) a montré par des associations en cultures d'organes que l'évolution du tractus femelle est déclenchée par une substance hormonale émise par les ganglions céré-

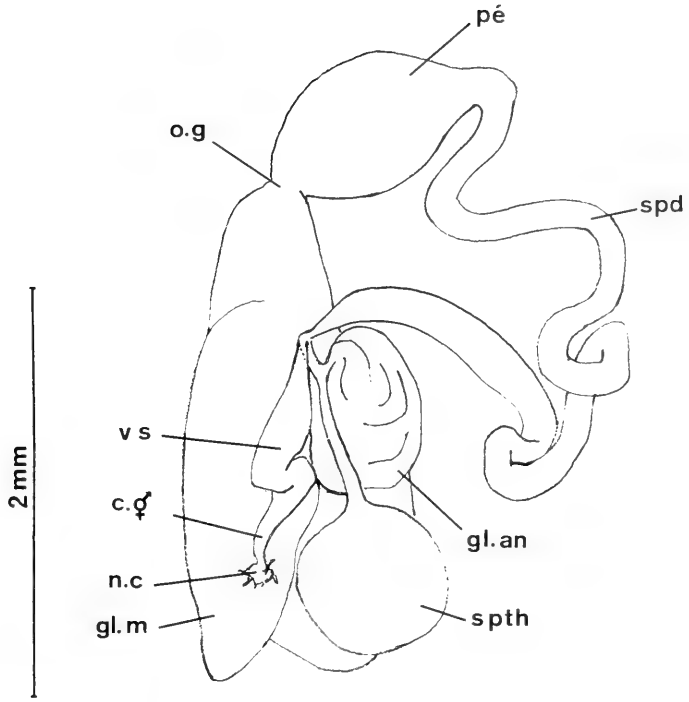

FIG. 2. Tractus génital d'*Aeolidiella alderi* opérée alors qu'elle était en fin de phase juvénile et fixée 115 jours plus tard. La partie mâle est cytologiquement différenciée mais faiblement développée; le pénis est sub-normal, les glandes annexes sont différenciées. gl. m: glande muqueuse: gl. a. : glande de l'albumine (pour les autres abréviations, se reporter à la Fig. 1).

broïdes pendant un temps très court, lorsque se produit le changement de sexe. A la suite de cette impulsion la cytodifférenciation se poursuit d'elle-même.

Ce résultat explique parfaitement, à mon sens, les observations faites chez les Pulmonés et les Nudibranches où les individus castrés présentent un tractus cytologiquement différencié ou non, si l'on admet l'hypothèse suivante: c'est la gonade qui provoque par l'intermédiaire du cerveau l'émission d'une ou de plusieurs substances inductrices du développement du tractus femelle.

Si la castration survient *avant* que la gonade ait déclenché cette émission, le tractus reste juvénile; dans le cas contraire, le tractus acquiert une cytodifférenciation fonctionnelle, mais son fonctionnement est plus ou moins fortement perturbé par l'absence de production de gamètes.

L'impulsion hormonale doit survenir très tôt, car la majorité des individus que j'ai castrés ont un tractus développé. D'autre part, bien que Brisson ait opéré des individus aussi jeunes que possible, il n'a jamais observé d'inhibition du développement du tractus chez les Basommatophores. Seul Harry (1965) semble y être parvenu.

D'autre part, il est possible que lors de l'organogénèse naturelle le massif mésodermique soit l'inducteur morphogénétique direct ou indirect du tractus femelle. Par contre, il ne semble pas être le déterminant morphogénétique du tractus mâle ainsi que le montrent les expériences *in vitro* pour les Prosobranches (du moins directement) et les cas d'aphallie, (règle courante chez certaines races de *Bulinus* par exemple) de biphallie symétrique ou autres anomalies constatées de temps en temps chez divers Pulmonés.

En résumé, il semble hors de doute que la gonade soit à l'origine des mécanismes

de fonctionnement du tractus. Son rôle serait indirect; il déterminerait l'élaboration d'une ou de plusieurs hormones par le système nerveux. Celle(s)-ci provoquerai(en)t: (1) la cytodifférenciation du tractus femelle, (2) très probablement celle du tractus glandulaire mâle.

Enfin pour prouver la réelle indépendance de la morphogenèse du tractus chez les formes hermaphrodites, (où le déterminant génétique est probablement éliminé) il serait intéressant de supprimer l'ébauche gonadique de larves avant que ne se forme le bourgeon ectodermique. Une telle opération est très difficile à réaliser, mais elle est susceptible d'apporter des résultats déterminants.

SUMMARY

SURGICAL CASTRATION OF THE GENITAL TRACT AND THE SPAWN OF THE AEOLIDIIDAE: AN ATTEMPT TO UNDERSTAND THE MECHANISMS OF SEXUAL ENDOCRINE CONTROL

Surgical castration in the Aeolidiidae has given the following results: 1) No spawn is ever laid by these castrated sea-slugs; 2) From the cytological point of view, after a certain amount of time, the female tract can have one of two opposite appearances: a) glandular differentiation does not appear, or, b) most of the time, differentiation does appear.

In the case of differentiation there is a hypertrophic female tract, the elements of which are usually and in greater part degenerated, and fall into the lumen. They then seem to go to the "gametolytic gland" where they are probably digested.

3) Observation also shows that male and female tracts of the same animal can have an opposite cytological aspect, either differentiated or not. This fact confirms that each one depends on a different endocrine control for cytological differentiation as Streiff (1967) has shown in the prosobranchs.

All of these observations are discussed and compared with the results obtained with other gastropods. They suggest some modifications of the diagram proposed to explain the mechanisms which control differentiation, maturation, and interactions of the different parts of the tract.

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PROC. FOURTH EUROP. MALAC. CONGR.

STUDIES OF THE ENDOCRINE CONTROL OF THE REPRODUCTIVE TRACT OF THE GREY FIELD SLUG *AGRIOLIMAX RETICULATUS*

N. W. Runham, T. G. Bailey and A. A. Laryea

Department of Zoology, University College of North Wales
Bangor, Caernarvonshire, U.K.

INTRODUCTION

Pulmonate slugs are protandric hermaphrodites. Many species complete 1 breeding cycle, then die, but some may complete 2 such cycles, e.g., *Milax gagates* (Galangau, 1964). In very young animals the simple sac-like gonad is full of apparently undifferentiated cells. As the animals get older the gonad becomes increasingly lobed, then first oocytes become visible followed by differentiating sperm and nutritive cells. At first the oocytes enlarge slowly while there is very rapid production of large numbers of sperm. When most of the sperm have been shed the ova mature. Reproductive tract maturation is very closely related to this sequence in the gonad. The prostate gland matures preparatory to the male phase of the gonad and functions at copulation. Egg laying is preceded by the maturation of the albumen and oviducal glands. In most species, e.g., *Arion ater* (Lusis, 1961; Smith, 1966), there is a very clear separation of the male and female phases of the cycle, but in *Agriolimax reticulatus* there is often some overlap (Runham & Laryea, 1968).

The relation between the gonad and reproductive tract has been extensively studied by Laviolette (1954). Using various arionid and limacid species with well defined seasonal breeding periods he carried out an extensive series of organ transplants. The gonad or the reproductive tract from a species at one stage of development was transplanted into the body cavity of another species which at that time of year was at a different stage of its reproductive cycle. Laviolette observed that an immature tract transplanted into a 'mature' animal showed a marked enlargement. He deduced, therefore, that there was a hormone in the blood which controlled the maturation of the reproductive tract.

In this study *Agriolimax reticulatus* was used as it will breed all the year round, so all stages of reproductive maturation are available in the one species. It is also usually available in large numbers and can be maintained in the laboratory fairly readily.

MATERIALS AND METHODS

Agriolimax reticulatus were collected from various localities within a 3-mile radius of the Department. Most of the larger animals used for operations were collected from the wild, but as small animals are very difficult to collect laboratory cultures were set up for these. The cultures were maintained in either polystyrene sandwich boxes or polythene washing-up bowls, in both cases filled to a depth of 3-5 cm with sterile soil and having a small aperture covered with gauze in the cover. Animals were usually fed on carrot but also occasionally on lettuce, and cleaned at least twice a week. The only difficulty encountered with the cultures was at the start of the experiments when there was a very high incidence (about 90%) of infection with *Tetrahymena* in locally collected animals. It was found to be impossible to control this parasite, which can be transmitted in the egg, but luckily, for no apparent reason, the incidence of infection in the local population later fell to a very low level.

For all operations the slugs were anaesthetised with carbon dioxide (Bailey, 1969). They were then placed on moist filter paper on the stage of a Zeiss Stereomicroscope III with foot-operated focussing control. Fine forceps, needles and de Wecker iridectomy scissors were the only instruments required for the operations.

a) Sampling the gonad. A small cut was made in the body wall at the point A (Fig. 1); the very deeply pigmented gonad was located and a small piece removed.

b) Castration. The gonad was located as in a); then it was carefully separated from the digestive gland by tearing the connective tissue sheaths and membranes. The main difficulty with this operation is avoiding damage to the overlying rectum particularly when the gonad is pulled out from beneath it. Once the gonad has been separated from the surrounding tissues it is pulled, if possible forwards, then the hermaphrodite duct is cut and the gonad removed. In some cases the gonad had to be removed in 2 pieces because of its size, the region posterior to the rectum and the region anterior to it. Occasionally there are rather small and isolated groups of acini at the anterior edge of the gonad and these were easily left behind. This was always checked at the conclusion of the experiment. Regeneration of the gonad from the cut end of the hermaphrodite duct occurs as in other slugs (Laviolette), but very rarely was there any sign of differentiation by the end of the experiment.

c) Transplants. The transplants (see below) were manipulated under medium and taken up into the end of a trochar needle. A small hole was cut in the body wall at point B (Fig. 1), the trochar inserted and the transplant injected. The body was held against the tip of the trochar when it was removed in case the transplant adhered to the needle.

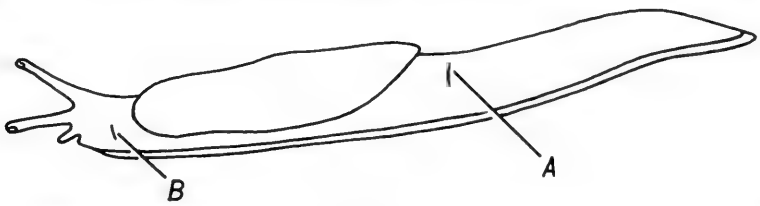

FIG. 1. *Agriolimax reticulatus*. A, position of the incision for removal of the gonad; B, position of the incision for the injection of the transplant.

In none of these operations were any sutures needed in the body wall. After the operation the animals were transferred individually or in small groups to disposable petri dishes lined with moistened filter paper and containing a piece of carrot. Animals were usually wandering around the dish within 30 minutes of operation.

The transplants were obtained from very small animals that had a reproductive tract in the earliest stage of differentiation. After anaesthesia animals were dissected under either Hedon-Fleig saline or organ culture medium (Bailey, 1972). The common duct, in some cases with the albumen gland attached, was removed and cut into 2-7 pieces, one of which was immediately fixed, while the others were transplanted. Transplanting occurred 10-60 minutes after dissection.

At the end of the experiment anaesthetised animals were opened along the length of the body and the transplant searched for in the haemocoel, particularly in the region of the brain and buccal mass. In some cases where the transplant had formed a large swollen cyst it was readily found, but in castrates the very small pieces of tract were exceedingly difficult to discover. The transplant together with the host gonad and sometimes the reproductive tract were fixed.

Tissues were either fixed in susa, washed and dehydrated in cellusolve and embedded in ester wax, or fixed in buffered osmium and embedded in Araldite. Ester wax sections (7 μ) were stained with Azan and 1-3 μ Araldite sections were stained with

toluidine blue. The stages in the maturation of the gonad and reproduction tract have been described elsewhere (Runham & Laryea, 1968).

RESULTS

It was hoped originally to produce quantitative data for the enlargement of the glands and for any histological changes resulting from transplanting. For the following reasons this proved to be impossible. Because of a lack of clear separation of the male and female stages in this species the determination of some stages in the development of the gonad was less accurate than with others. No problems were encountered with the spermatocyte, spermatid, early sperm, late oocyte and post-reproductive stages. The separation of late sperm and early oocyte stages however is dependant on the relative quantities of sperm and oocytes and the size of the latter. In some late sperm stages, with large amounts of sperm present, only a few oocytes were visible - far fewer than normal - probably indicating that in these animals some egg laying had taken place before the more normal loss of the majority of the sperm. Because of variations in the relative proportions of oviducal and prostate gland tissue along the length of the common duct (i.e., oviducal gland predominates at the top of the common duct and prostate gland at the bottom) it was impossible to quantify the changes in the relative proportions of the 2 glands in the small transplants. Frequently the 2 open ends of the transplanted common duct became sealed and secretion by the glands led to the formation of a considerably swollen cyst with greatly distorted glands. A subjective qualitative assessment was therefore developed to assess the changes following transplanting with the above features taken into account.

During normal maturation of the reproductive tract the prostate gland develops first. Diverticulae are formed which enlarge, and then the cubical epithelium becomes underlain by cells which differentiate into a number of different types of secretory cell. Only when secretion has appeared in the prostate does differentiation of the oviducal gland begin. Cells appear beneath the cubical epithelium lining of the oviducal gland which differentiate to become grossly distended with secretion.

Castrated animals were left for a week to recover from the operation and then a piece of common duct from a very young animal was transplanted into the haemocoel. Due to the very small size of these transplants they were only recovered from 6 animals, but in no case was there any increase in size of the common duct after 10 days compared to the controls. The results from 3 series of experiments on normal hosts are given in Tables 1, 2 and 3. When a tract from a very young animal, showing only the earliest stages in the differentiation of the prostate gland, was transplanted into the haemocoel of an animal at a later stage of development and left there for 10 days, rapid transformation of the transplant occurred. In the spermatid stages there was a slight enlargement, while in early sperm and the earliest of the late sperm stages development of the prostate was pronounced (Fig. 2). During the very late sperm stage both the oviducal and prostate glands matured. In the oocyte stages the oviducal gland shows maximum enlargement and secretion while the prostate gland enlarges slightly (Fig. 3). In the post-reproductive stages the oviducal gland alone matured. In normally developing common ducts the oviducal gland matures only after the prostate gland has completed its maturation.

DISCUSSION

As the transplants were left free in the haemocoel, the factors causing the observed changes must be blood-borne, i.e., they are hormones. The results obtained indicate the existance of 2 hormones, one responsible for the maturation of the prostate gland

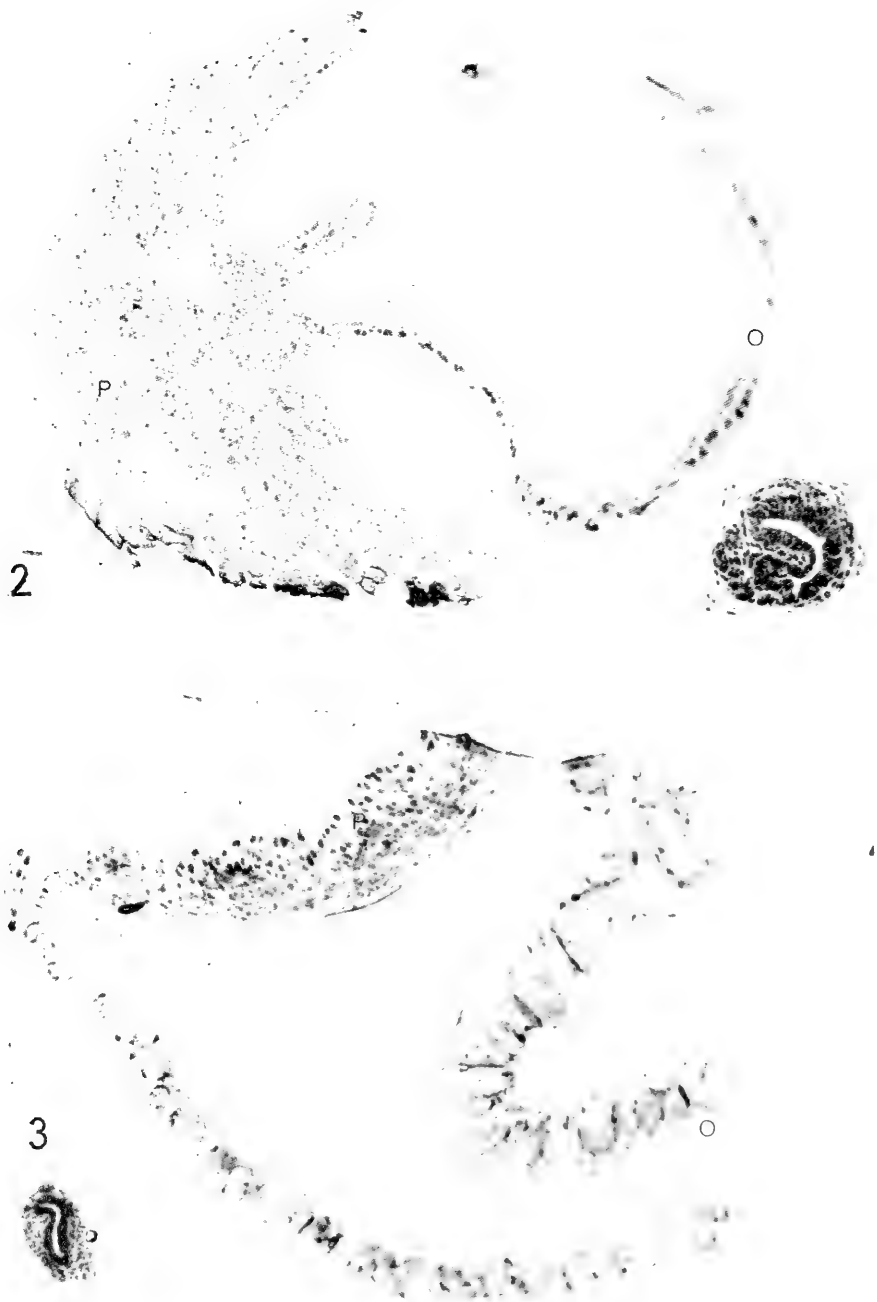

FIG. 2. *Agriolimax reticulatus*. Common duct transplant 10 days after placing in the haemocoel of an early male stage host. Inset, control piece of common duct fixed at the time of transplanting. P, prostate gland; O, oviducal gland.

FIG. 3. *Agriolimax reticulatus*. Common duct transplant 10 days after placing in the haemocoel of an early female stage host. Inset, control piece of common duct fixed at the time of transplanting. P, prostate gland; O, oviducal gland.

TABLE 1. *Agriolimax reticulatus*. Fate of pieces of immature common duct transplanted into the haemocoel of older animals.

Series 1

Host Stage	Prostate Gland		Oviducal Gland		Common Duct	
	% Expansion	Secretion	% Expansion	Secretion	Male Characteristics	Female Characteristics
D	150	-	-	-	+	-
D	300	-	-	-	+	-
D	300	-	500	+	+	+
D	500	-	500	-	++	+-
E	600	-	-	-	++	-
E	1,650	++	-	-	++++	-
E	1,500	+	-	-	++++	-
E	700	++	700	+	+++	+
E	4,000	++	4,000	++	++++	++
E	200	+	2,000	+++	+	+++
F	400	-	?	+++	+	+++
G	4,000	++	4,000	+++	++++	++++
G	1,000	-	1,000	++	++	+++
G	300	+++	1,500	++++	++	++++
G	200	+-	400	+++	+	+++
H	350	++	1,000	++++	++	++++
H	150	++	2,500	++++	+	++++
H	0	++++	?	++++	+	++++
H	0	-	1,000	++++	-	++++

Stages of maturation of the host gonad are:- D early spermatozoon, E late spermatozoon, F early oocyte, G late oocyte, H post-reproductive. The amount of secretion is indicated by the number of + symbols and the absence of secretion by -. The male characteristics of the common duct is a subjective assessment based on the percentage expansion, amount of secretion and the histology of the prostate gland; while the female characteristics is similarly based on the oviducal gland.

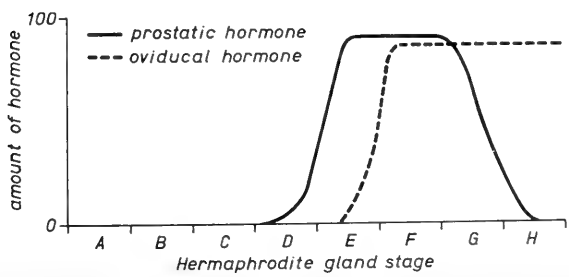

FIG. 4. *Agriolimax reticulatus*. Suggested timing for the secretion of prostatic and oviducal hormones in relation to the stage of development of the hermaphrodite gland. A, undifferentiated; B, spermatocyte; C, spermatid; D, early spermatozoon; E, late spermatozoon; F, early oocyte; G, late oocyte; H, post-reproductive.

TABLE 2. *Agriolimax reticulatus*. Fate of pieces of immature common duct transplanted into the haemocoel of older animals.

Series 2

Host Stage	Prostate Gland		Oviducal Gland		Common Duct	
	% Expansion	Secretion	% Expansion	Secretion	Male Characteristics	Female Characteristics
D	400	-	500	-	+	+
E	0	?	0	0	-	-
E	500	-	400	-	++	-
E	200	+	0	-	++	-
E	800	+	0	-	++	-
E	150	+-	1,000	+-	+	++
E	0	+++	500	+-	++	+
E	400	-	200	-	++	-
E	250	-	?	-	+	-
F	400	-	200	-	+	-
F	300	-	700	+	+	++
G	500	+-	600	++	++	+++
G	150	-	300	?	+	+
G	500	-	500	?	+	+
G	400	-	1,000	++++	+	++++
H	1,000	-	1,000	+++	++	+++
H	700	+	3,000	++++	++	++++
H	0	-	1,000	++++	-	++++
H	0	-	1,600	++++	-	++++

Stages of maturation of the host gonad are:- D early spermatozoon, E late spermatozoon, F early oocyte, G late oocyte, H post-reproductive. The amount of secretion is indicated by the number of + symbols and the absence of secretion by -. The male characteristics of the common duct is a subjective assessment based on the percentage expansion, amount of secretion and the histology of the prostate gland; while the female characteristics is similarly based on the oviducal gland.

and the other for the oviducal gland (Fig. 4). The prostate hormone appears during the late spermatocyte or at the beginning of the spermatid stage and reaches a maximum during the spermatozoan stages. During the late sperm stage, at about the time the amount of prostatic secretion begins to decrease, the oviducal hormone appears and rapidly reaches its maximum. Prostatic hormone appears to be present only in small amounts during the oocyte stages and may be absent from post-reproductive animals.

The processes leading to the maturation of the glands are complex and involve at least the following processes: cell proliferation, with cell migration leading to tissue

TABLE 3. *Agriolimax reticulatus*. Fate of pieces of immature common duct transplanted into the haemocoel of older animals.

Series 3

Host Stage	Prostate Gland		Oviducal Gland		Common Duct	
	% Expansion	Secretion	% Expansion	Secretion	Male Characteristics	Female Characteristics
D	200	-	200	-	+	-
E	300	-	0	-	++	-
E	250	++	250	-	++	-
E	300	++	0	-	++	-
E	400	++	300	+	++	+
E	300	+-	1,000	+	++	++
E	300	+	500	-	++	+
E	300	++	200	++	++	++
E	600	++++	200	-	++++	-
E	300	++++	400	+	++++	++
E	?	?	500	++++	-	++++
E	300	++	400	++++	++	++++
E	400	++	600	++++	++	++++
E	300	+	400	++++	++	++++
E	500	++	500	++++	++	++++
E	300	++	10,000	++++	++	++++
F	150	-	400	-	-	+
F	300	-	600	++++	+	++++
H	0	+	10,000	++++	+	++++
F	150	+	400	++++	++	++++
H	500	+-	1,000	++++	+	++++

Stages of maturation of the host gonad are:- D early spermatozoon, E late spermatozoon, F early oocyte, G late oocyte, H post-reproductive. The amount of secretion is indicated by the number of + symbols and the absence of secretion by -. The male characteristics of the common duct is a subjective assessment based on the percentage expansion, amount of secretion and the histology of the prostate gland; while the female characteristics is similarly based on the oviducal gland.

and organ differentiation, and cell differentiation leading to the formation of secretion by the cells. In the transplants, even in the short period of 10 days, massive enlargement and differentiation both of tissues and cells took place. In some cases it was obvious that differentiation of the cells could occur apparently independently of the other processes. Thus several examples were noted of cell differentiation in the prostate without any apparent increase in the size of the gland compared to the controls; and in addition other examples were found where enormous enlargement of the gland occurred with no, or very little, secretion being formed in the cells. There are several possible explanations for this phenomenon. The effect of the hormone may vary

with its concentration, or formation of secretion is controlled by a different hormone to that controlling organ differentiation. In the case of the prostate gland it is even possible that the oviducal hormone may affect formation of prostatic secretions. Not enough data was however available for an analysis of this problem.

Laviolette (1954) clearly demonstrated that the maturation of reproductive tracts of a variety of limacid and arionid slugs were under hormonal control. This study confirms and extends Laviolette's findings, indicating at least in *Agriolimax reticulatus* that not less than 2 hormones are involved in the maturation of the common duct. The albumen gland was also found by Laviolette to be under hormonal control. In our experiments information on the albumen gland was obtained only in the first series of experiments, and in these enlargement of the gland and the formation of secretion occurred in the latest of the spermatozoan stage and in all the oocyte and post-reproductive stages. This would perhaps indicate that the albumen gland is also influenced by the oviducal hormone.

The source of these hormones is unknown. Laviolette injected extracts of the gonad into various slugs but the reproductive tract did not appear to be affected. Preliminary organ culture experiments (Bailey, 1973) indicate that when the gonad and reproductive tract are cultured in close proximity no maturation changes can be observed in the reproductive tract. However, when the brain, gonad and reproductive tract are cultured close together then maturation changes can be observed in the cells of the reproductive tract. When Laviolette transplanted gonads from mature slugs into castrated immature slugs, maturation of the host reproductive tract resulted. There is therefore tentative evidence that factors are produced by the gonad which cause the brain to produce the prostatic and oviducal hormones.

Further experimental studies are clearly needed to clarify the details of hormonal control of the reproductive tract of slugs.

SUMMARY

An extensive series of organ transplants using the slug *Agriolimax reticulatus* indicate the existence of 2 hormones. When immature common ducts are transplanted into the haemocoel of older animals the changes observed in the transplants clearly reflect the stage in the reproductive maturation of the host. It is concluded that 1 hormone controls differentiation and enlargement of the prostate gland, the 2nd hormone controls the oviducal gland. No changes were observed in common ducts transplanted into the haemocoel of castrated animals. It is suggested that these hormones are produced by the brain.

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MALACOLOGIA, 1973, 14: 143

PROC. FOURTH EUROP. MALAC. CONGR.

THE ANATOMY OF *CAVOLINIA INFLEXA* (PTEROPODA)

Joyce E. Rigby

Queen Elizabeth College, University of London
Campden Hill, London W. 8, England

ABSTRACT

Living and preserved specimens of the thecosomatous pteropod, *Cavolinia inflexa* have been examined, in the young and mature stages. Illustrations of their locomotion and anatomy were presented, and special attention has been given to the elaboration of lateral lobes from the mantle margin which probably act as balancing structures and accessory surfaces for food collection. A further account of this work will be published elsewhere.

MALACOLOGIA, 1973, 14: 143

PROC. FOURTH EUROP. MALAC. CONGR.

FUNCTIONAL MORPHOLOGY OF THE VERTICORDIIDAE (BIVALVIA)

J. A. Allen

Dove Marine Laboratory, Cullercoats, North Shields
Northumberland, England

ABSTRACT

The Verticordiidae are restricted to the deep-sea. They have a characteristic trapezoidal shape and usually measure less than 1 cm total length. They lie close to the surface of the sediment so that the mantle apertures with their arborescent papillate fringing tentacles are level with the sediment surface. The tips of the papillae are glandular, the adhesive secretion of which is used in the capture of prey. The latter includes copepods and large diatoms. Food is conveyed to the mouth via the gills. The gill filaments are reduced in length and form a pair of vertical ciliated channels leading to the mouth which is surrounded by a large, posteriorly directed funnel formed by the greatly modified palps and lips. Oesophagus and stomach are highly muscular and form a crushing organ. The stomach is lined with scleroprotein, apart from a narrow ventral ciliated gutter leading to a short style sac.

MALACOLOGIA, 1973, 14: 144-146

PROC. FOURTH EUROP. MALAC. CONGR.

CONVERGENT EVOLUTION IN PULMONATE RADULAE

Alan Solem

Field Museum of Natural History, Chicago, Illinois, U.S.A.

ABSTRACT

Optical examination of radulae is limited by the very shallow depth of field inherent to the light microscope. This has necessitated mounting the radula in a flattened position between two pieces of glass and viewing the squashed specimen from directly above using transmitted light. Where the radula is folded under, a glimpse of the side of a tooth may be obtained, but normally it is possible to see only the cusp outlines. Where the cusps are large, they extend backwards over the anterior end of the basal plate in the next row, effectively concealing any structures on the basal plate.

The Scanning Electron Microscope has an effective range of magnification between 14X and 100,000X, its depth of field is 300X to 500X that of optical systems, and its resolving power is 12X to 100X greater. When coupled with the ability to tilt the specimen from 0°-90° (with the Cambridge Stereoscan but not the Jeolco SEM) and rotate it continuously, far more information can be obtained concerning radular structure and function.

To obtain this information requires abandoning previous methods of viewing. The radula should be torn and twisted so that lateral views of individual teeth can be seen. It should be folded so that in part the teeth

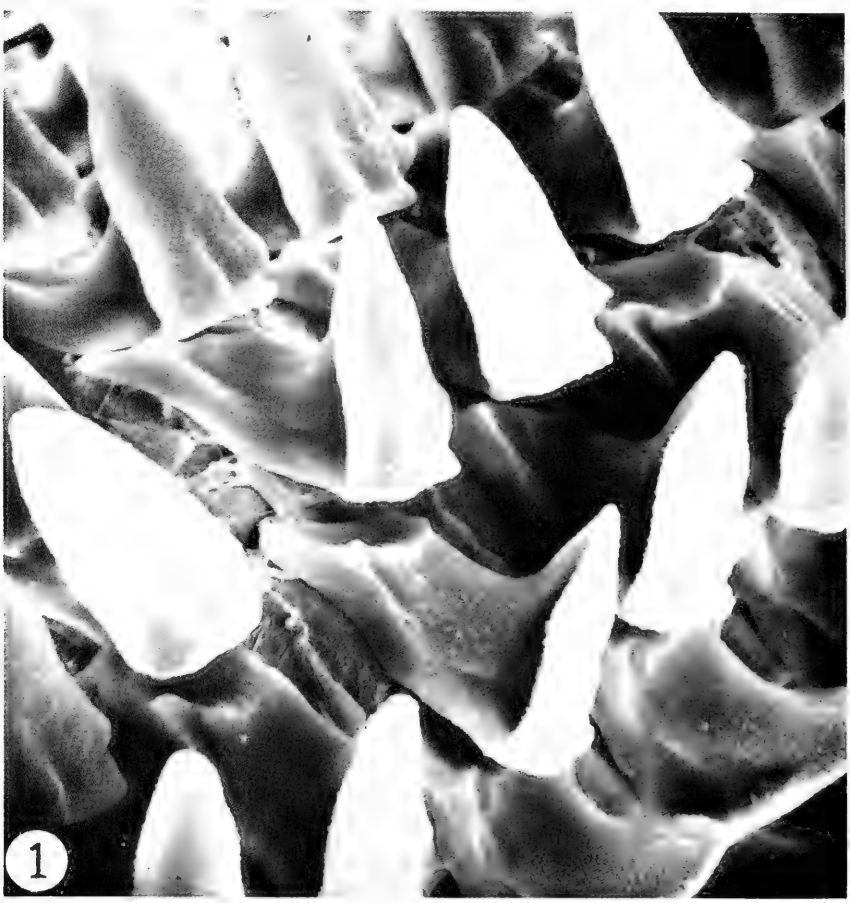
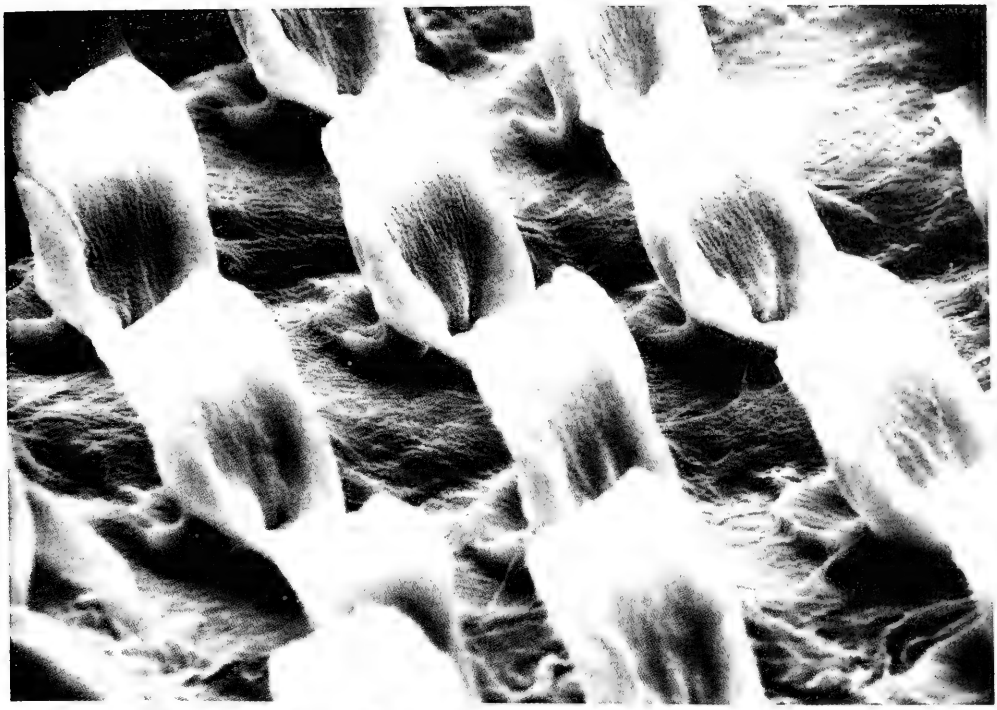
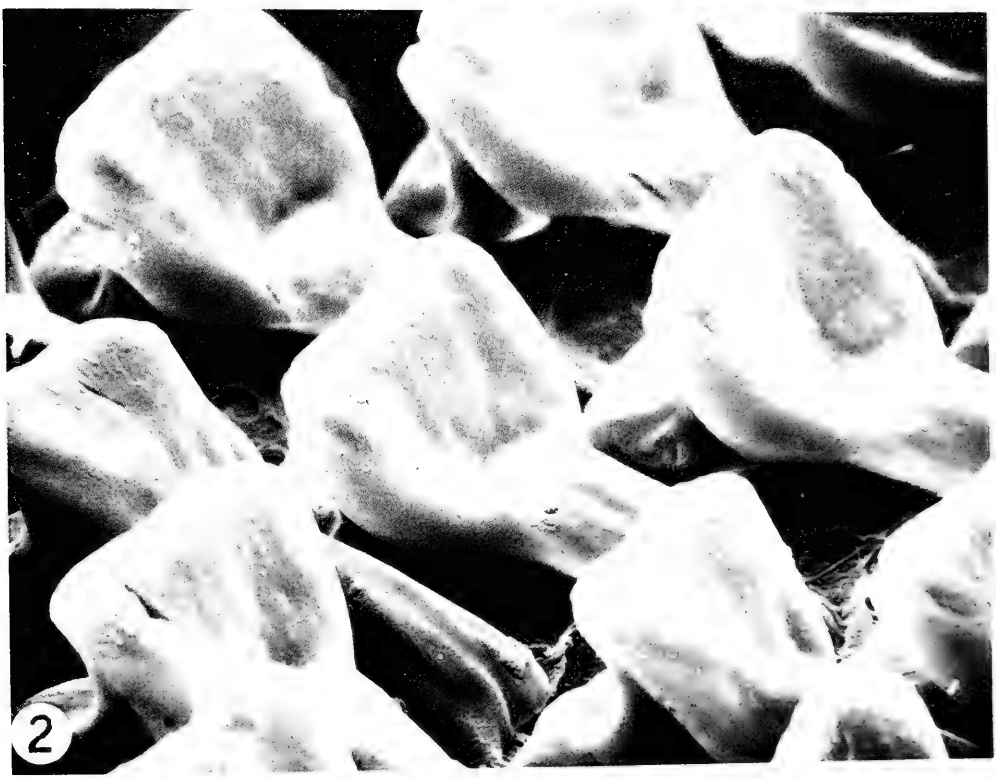


FIG. 1. Lateral teeth from the radula of an undescribed West Australian desert camaenid at 1,075X.

FIG. 2. Upper. Lateral teeth from the posterior end of the radula in *Papuina phaeostoma medinensis* I. Rensch from Lossu Village, Kavieng, New Ireland, Bismarck Archipelago at 1,280X. Lower. Worn lateral teeth from the anterior end of the same radula at 1,475X.

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will be elevated as in a feeding stroke, while elsewhere the teeth lie flat as when they occupy the posterior section of the buccal cavity. Since the depth of field obtainable with the Scanning Electron Microscope substantially exceeds the field of view dimensions, examination from angles other than the traditional vertical study is possible and highly advantageous.

Preliminary use of the Scanning Electron Microscope in the study of pulmonate radulae has revealed a number of significant facts. Most important of these is the existence of a stress support system between the rows of teeth. This occurs in a number of families, but varies widely between members of the same family and cannot be used to recognize higher taxonomic units. The basic functioning of this support system is as follows. When a cusp encounters resistence in cutting or scraping against a food source, the stress is transmitted to the anterior part of the tooth which is forced down against the basal plate of the tooth in the next anterior row. If this tooth is balanced on the odontophoral cartilage tip, then the tip will act as a fulcrum, transferring downward pressure on the base to upward pressure on the cusp. Thus resistance encountered by one tooth will be applied to the basal plate of the next tooth to come into contact with the food source. The process may actually aid the cutting action of this second tooth. Such a mechanism where the action of one tooth aids the work of the next is highly efficient.

When the teeth are viewed from about a 45° angle at a place where the radula has been bent so that the sides of some basal plates can be seen (Fig. 1), the nature of this support system and overlap becomes clear. The example used is an undescribed species of camaenid from Western Australia. These are lateral teeth shown at a magnification of 1,075X. The tooth at the lower left is resting against the support ridges on the next basal plate, as it would under conditions of stress, while the tooth in the center is obviously not under stress and is removed from the basal plate contact.

To date, this phenomenon has been observed in members of the Achatinellidae, Enidae, Pupillidae, Punctidae, Charopidae, Endodontidae, Partulidae, Cerionidae, Bulimulidae, Achatinidae, Caryodidae, Camaenidae, Succineidae, Polygyridae and Helicidae. The details of the support system differ more widely within families than between families in some cases. Thus it cannot be used as a means of determining phyletic relationships. The general presence of this mechanism in herbivorous taxa suggests that it may be one of the prime reasons for the successful radiation of land snails.

In carnivorous taxa there is another problem. The long, often sickle-shaped teeth must be folded flat when not in use, then elevated to essentially a vertical position in order to slice into the prey. In taxa such as *Euglandina*, the anterior end of the tooth is truncated into a supporting plate that rests against the odontophore when the tooth is elevated.

Other problems that are being investigated using the Scanning Electron Microscope include convergent evolution in the cusp structure of algal scraping snails, and varying patterns of tooth wear shown by snails living under different conditions. In a species of *Papuina* from the Bismarck Archipelago, for example, the newly formed lateral teeth (upper part of Fig. 2) are markedly elevated, with broad, spade-like cusp. At the anterior end of the same radula (lower part of Fig. 2) the cusps have been worn down to less than half their original height. Scratch lines are clearly visible on the remnant upper edge. The upper figure is at 1,280X magnification, while the lower figure is slightly larger at 1,475X.

Use of the Scanning Electron Microscope will revolutionize study of radular structure and function. The data cited above represents only the very first glimpses of knowledge that can be obtained by use of this instrument.

MALACOLOGIA, 1973, 14: 147-165

PROC. FOURTH EUROP. MALAC. CONGR.

SCANNING ELECTRON MICROSCOPE STUDIES OF GASTROPOD RADULAE

T. E. Thompson and A. Bebbington

Zoology Department, University of Bristol, England

INTRODUCTION

Traditional methods of preparing the gastropod radula for microscopical examination are well known. In a recently published variant of these, the radula is freed from the buccal mass by first boiling in caustic potash, washing with 70% alcohol, and then mounting flat on a microscope slide in polyvinyl lactophenol containing the stain lignin pink (Thompson, 1958). That publication included a photomicrograph probably showing the maximum that can be achieved by optical microscopy of small opisthobranch radulae. A photograph of part of the much larger radula of *Aplysia* as seen with the light microscope has been given by Bebbington & Thompson (1968). Most accounts of radulae, however, are restricted to drawings such as those given by Bebbington (1969) for *Bursatella*.

The traditional methods of preparation are imperfect when one tries to understand the functional morphology of the opisthobranch radula, because it is necessary to squash the preparation. The results of squashes are unpredictable and can, moreover, distort or alter the natural relationships of the teeth. The scanning electron microscope (SEM) permits the examination and photography of radulae without elaborate preliminary preparation and without squashing or fragmentation. A clear picture of three-dimensional morphology can therefore be obtained which enlightens more mundane methods of observation.

The principles on which the SEM is based have been described by Oatley, Nixon & Pease (1965). Runham & Thornton (1967) used the technique to examine the radulae of *Patella vulgata* and *Agriolimax reticulatus*. Thompson & Hinton (1968) described observations on some opisthobranch radulae: *Aeolidia papillosa*, *Facelina auriculata*, *Archidoris stellifera* and *Cadlina laevis*; and also on the shell sculpture of several species of *Philine*. Runham (1969), in the Proceedings of the Third European Malacological Congress, reported on the radulae of *Agriolimax reticulatus* and *Nucella lapillus*. Thompson (1972) in a paper on eastern Australian Pleurobranchomorpha showed the radular teeth of *Berthellina citrina*, *Pleurobranchus peroni* and *Euselenops luniceps*, and, more recently (Thompson, 1972), illustrated the radulae of *Casella atromarginata* and *Chromodoris amoena*. Solem (1970) in a review of the malacological applications of the SEM introduced pictures of some features of the shell surface. Recently, Robertson (1972) has used the SEM to study the shells of planktonic larval marine gastropods, and Bebbington (1972) has published photographs of the radulae and penial spines of *Notarchus punctatus* and *Bursatella leachi savigniana*.

MATERIALS AND METHODS

The specimens from which the radulae were obtained were collected from a number of localities in the United Kingdom; at Arcachon, France; from various marine sites in Queensland and New South Wales, Australia; from the Friday Harbor Laboratories, U.S.A.; from Naples, Italy, and from Kenya, East Africa.

A total of 36 species have been examined in order to assess the value of the SEM for studies of gastropod radulae. Thirty-three of these were opisthobranchs, 2 were

prosobranchs and 1 was a pulmonate:

Phylum Mollusca
Class Gastropoda
Sub-class Prosobranchia
Order Neogastropoda
Conus geographus (Pl. 1), *Conus marmoreus* (Pl. 2)
Sub-class Opisthobranchia
Order Bullomorpha
Bullina lineata (Pl. 3a,b), *Haminea navicula*, *Hydatina physis* (Pl. 3c,d)
Order Aplysiomorpha
Aplysia parvula (Pl. 4a,b), *Aplysia dactylomela* (Pl. 4c,d), *Aplysia depilans*, *Bursatella leachi leachi.* (Pl. 7d), *Bursatella leachi savigniana*, *Dolabella auricularia* (Pl. 5a,b), *Dolabrifera dolabrifera* (Pl. 6), *Notarchus punctatus* (Pl. 7a,b), *Stylocheilus longicauda* (Pl. 7c)
Order Pleurobranchomorpha
Berthellina citrina, *Euselenops luniceps*, *Pleurobranchus peroni*
Order Sacoglossa
Elysia bennetti (Pl. 8a)
Order Nudibranchia
Sub-order Dendronotacea
Dendronotus frondosus (Pl. 9c,d)
Sub-order Arminacea
Armina californica (Pl. 10)
Sub-order Doridacea
Casella atromarginata (Pl. 11c,d), *Cadlina laevis*, *Chromodoris amoena* (Pl. 12a), *Chromodoris loringi* (Pl. 12b), *Hypselodoris bennetti*, *Hypselodoris infucata* (Pl. 12d), *Kalinga ornata* (Pl. 13), *Onchidoris bilamellata* (Pl. 8b), *Polycera capensis* (Pl. 14c,d), *Rostanga arbutus* (Pl. 11a,b), *Triopha carpenteri* (Pl. 14a,b)
Sub-order Aeolidacea
Aeolidia papillosa, *Facelina auriculata longicornis* (Pl. 9b), *Hermissenda crassicornis* (Pl. 12c), *Pteraeolidia semperi* (Pl. 9a)
Sub-class Pulmonata
Order Onchidiacea
Onchidium damelii (Pl. 5c,d)

Material for the SEM was freed from the gastropod body by dissection of the buccal mass followed by boiling in caustic potash, washing with 70% alcohol; and then the radula was dried, mounted on a metal stub with "Durafix", and finally coated with a thin layer of gold-palladium (Thompson & Hinton, 1968). The preparations were examined using a Cambridge Stereoscan microscope kindly made available by the Long Ashton Research Station. Technical assistance from Mrs Elizabeth Parsons is gratefully acknowledged. The opportunity was taken to examine the visual effects of rotating and tilting the coated specimens so as to understand and anticipate the foreshortening and other illusory effects which may bedevil the interpretation of SEM micrographs.

CONCLUSIONS

The scanning method is rapid and same-day photographs may be obtained from urgent material. The radula is not damaged in any way by the preparative or other techniques and may be subsequently re-examined in the SEM or even cleared and mounted in balsam or polyvinyl lactophenol for optical microscope study.

The specimen in the SEM can be rotated and tilted while under observation (Pls. 2, 3, 10), and this helps enormously the building up of a three-dimensional appreciation of radular morphology. It also helps to avoid the pitfalls which can result from light-microscope observations made solely upon squashed specimens mounted on a glass slide.

While observations with the higher magnifications of the SEM can be valuable, for instance to demonstrate the beading on the fine subdivisions of the teeth of *Rostanga arbutus* (Pl. 11b), or the denticulated cutting faces of the *Elysia bennetti* radular teeth (Pl. 8a), the greatest applicability of the technique to functional morphology (e.g., Pls. 8b, 14) is evident in the low to medium range of magnification (x 40 up to x 400).

The SEM can allow the discovery of new radular details. In the teeth of *Conus geographus* (Pl. 1) a series of pores set in amongst a row of lateral barbs probably correspond to the problematic exit-pores through which the granular cone-venom reaches the exterior. These are invisible with the light microscope, whatever method of preparation may be attempted.

SEM montage-photographs permit a clear picture to be built up of the radular variation within a taxon. For instance, we have been especially interested in the Aplysiomorpha, many representative genera of which we have now investigated (Pls. 4, 5, 6, 7). As Eales (1944) has pointed out, radular patterns change more rapidly during the course of evolution than deeply seated characters like the nervous system. Within the Aplysiidae the radula of the 2 genera in the Aplysiinae (*Syphonota*, *Aplysia*) resemble one another closely, with their wide multidenticulate median teeth and biserrate laterals (Pl. 4). The Dolabellinae (*Dolabella*) have little resemblance to this type for the central tooth is narrow and reduced and the scythe-shaped laterals are without denticulations (Pl. 5a,b). The 3 genera of the Dolabriferinae (*Dolabrifera*, *Petalifera* and *Phyllaplysia*) have, however, an easily recognisable type of radula with wide median teeth and two-pronged laterals with or without accessory denticles (pl. 6). The Notarchinae (*Notarchus* (Pl. 7a,b), *Stylocheilus* (Pl. 7c), *Barnardaclesia*, and *Bursatella* (Pl. 7d)) are an odd group, in which the wide multidenticulate median tooth resembles that of the Aplysiinae but the lateral teeth do not. In *Notarchus* (Pl. 7a,b) the laterals are unique in their symmetry and denticulated margins while, in the remaining genera of the Notarchinae, such teeth may be considered to be derived from the Dolabriferinae type with its two-pronged lateral. The outer laterals may be degraded and the outer prong may be greatly reduced, resulting in teeth each of which possesses a rather long single cusp with lateral denticles, a tooth-type characteristic of *Stylocheilus* (Pl. 7c), *Barnardaclesia* and *Bursatella* (Pl. 7d) but found in no other member of the Aplysiidae.

Like most new techniques of observation, the results obtained from the SEM pose more questions than presently have been answered, in relation to the functional morphology of the radula. Two representative questions raised by the photographs presented here can be summarised thus:

1) What is the adaptive significance of the narrow (often uniseriate) radula possessed by many opisthobranchs which feed upon coelenterates? *Hermissenda crassicornis* (Pl. 12c), *Aeolidia papillosa* (Thompson & Hinton 1968), *Facelina auriculata* (Pl. 9b) and *Pteraeolidia semperi* (Pl. 9a) all feed on coelenterates and possess stout jaws and a denticulate horseshoe-shaped tooth-type. *Dendronotus frondosus* attacks closely similar prey and the narrow radula of a large adult has the formula 40 x 10.1.10 (Pl. 9c,d). Whatever the evolutionary pressures which have guided the ancestors of these forms towards radular narrowing they have, strangely, not acted similarly on the primitive dendronotacean nudibranch *Tritonia hombergi*, which also feeds upon coelenterates (chiefly *Alcyonium*), but possesses, as well as stout cutting jaws, a broad radula of a primitive kind (Thompson, 1962). Plainly, observations like these pre-

sented graphically in the form of SEM micrographs, can stimulate further research into the detailed functioning of the buccal mass and associated organs during the manipulation and ingestion of the prey in eolidiform and tritoniform nudibranchs.

2) Why should radular morphology be so variable in the sponge-eating dorid nudibranchs? Apart from the fact that the radula is usually broad in such forms, they have little in common so far as tooth-shape is concerned. This can be seen clearly in the micrographs (Pls. 11, 12, 13). In *Chromodoris amoena* (Pl. 12a) the radula is broad, reaching a formula in a 26 mm adult specimen of 82 x 98.1.98; all the teeth are denticulate. Near the mid-line of the radula, where the vestigial median teeth are detectable, the denticles are not prominent and the principal cusp of each tooth is short and hooked. Towards the side of the radula, each tooth becomes long and slender and the denticles appear more functional. The extreme marginal teeth, however, are again squat and the principal cusp and the denticles are approximately equal in size. In *Hypselodoris infucata* (Pl. 12d) the broad radula reaches a formula of 73 x 97.1.97 (30 mm adult specimen). The teeth near the middle of the radula are hooked and deeply bifid. In extreme lateral teeth the cusps are rudimentary, but supplementary denticles could be detected along the hinder face of each tooth. In *Casella atromarginata* (Pl. 11c,d) the formula of a 50 mm specimen was 252 x 52.0.52. The most central teeth bear 4 or 5 denticulations on each side of the cusp but these are confined to the outside of succeeding teeth and are lacking in extreme laterals. In *Kalinga ornata* (Pl. 13) the rather uniform teeth are erect, multifid hooks. Finally, in *Rostanga arbutus* (Pl. 11a,b), the broad radula (52 x 48.0.48 in a 9 mm specimen) consists of lateral teeth of a simple hooked type bearing a few small denticles while the marginal teeth are elongate and produced distally to form an erect cluster of fine beaded rods. All these species (and, of course, many more) are known to feed upon siliceous sponges. Why should animals with similar diets have such a variety of tooth morphology? Perhaps the diets, or the methods of manipulation and ingestion, are not so uniform as has been thought.

SUMMARY

The scanning electron microscope has been used by the authors to study the radulae of some 36 species of gastropod molluscs of which 24 species are illustrated in the present paper. The usefulness of the scanning electron microscope in such studies is discussed together with some conclusions and questions raised by the information gained.

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ADDENDUM

Since this paper was prepared, 3 important articles on radular fine structure have appeared. Kohn, Nybakken & Van Mol (1972) investigated the tooth of the vermivorous toxoglossan *Conus imperialis*, in which the tooth unit consists of an enrolled chitinous tube, very different from our interpretation of *C. geographus* and *C. marmoreus*. Thiriot-Quiévreux (1973) studied the taenioglossan radulae of various planktonic heteropods and her paper includes some electron micrographs of high quality and great usefulness to students of the group. Finally, Solem (1973), who studied pulmonate radulae from snails of the Charopidae, Enidae and Partulidae, has shown that patterns of interlock between radular teeth in adjacent rows are present, and his SEM studies have enabled him to propose that evolutionary convergence in cusp form has occurred in the Enidae and Partulidae.

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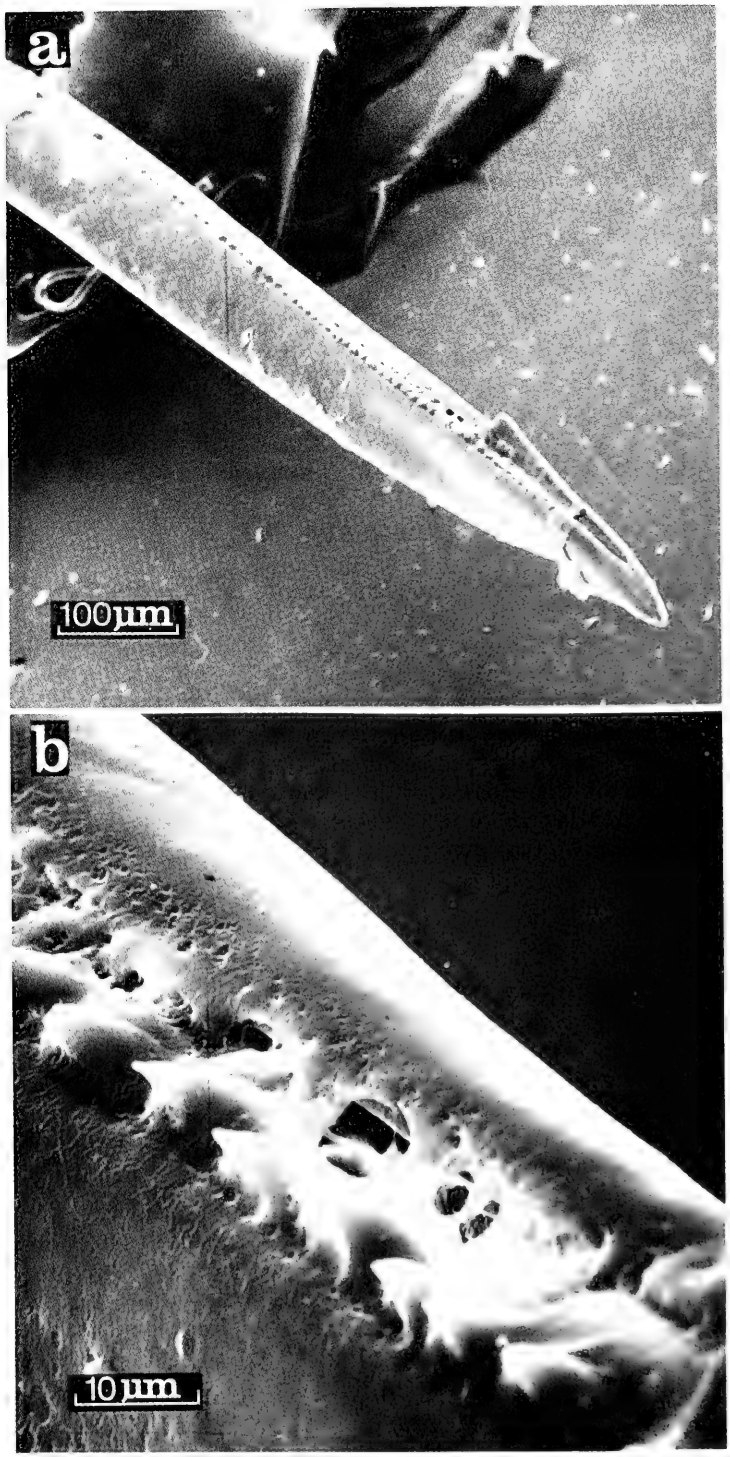

PLATE 1. *Conus geographus*, tooth of an adult cone from Great Barrier Reef, June 1968, showing in a, various barbs, and in b, fine barbs and associated venom exit-pores.

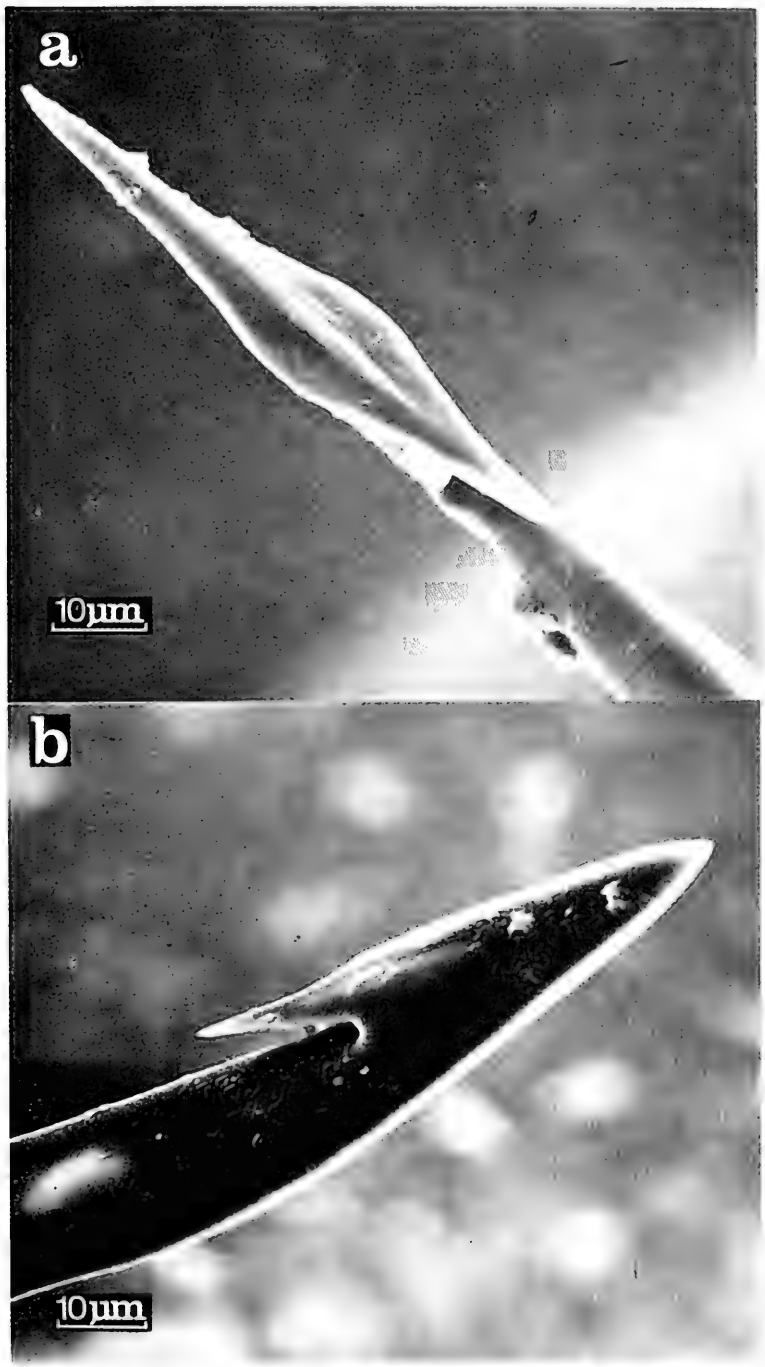

PLATE 2. *Conus marmoreus*, tooth of an adult cone from the Great Barrier Reef, June 1968, showing, a and b, different aspects resulting from specimen-rotation in the SEM.

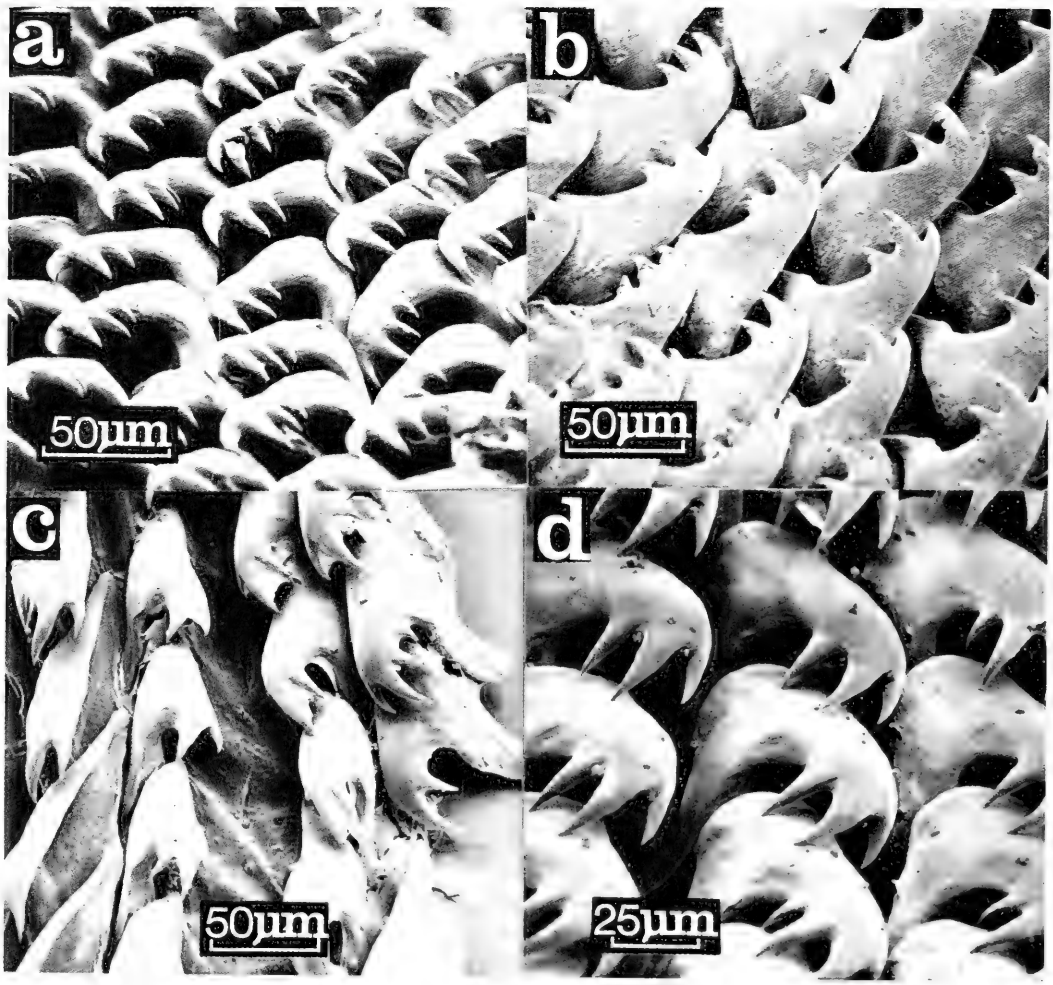

PLATE 3. a and b, *Bullina lineata*, shell-length 13 mm, Long Reef, N.S.W., Australia, May 1968, showing the effect of specimen-rotation in the SEM; c and d, *Hydatina physis*, shell-length 22 mm, from the same locality, showing how specimen-tilt in the SEM can alter the apparent aspect of the radular teeth.

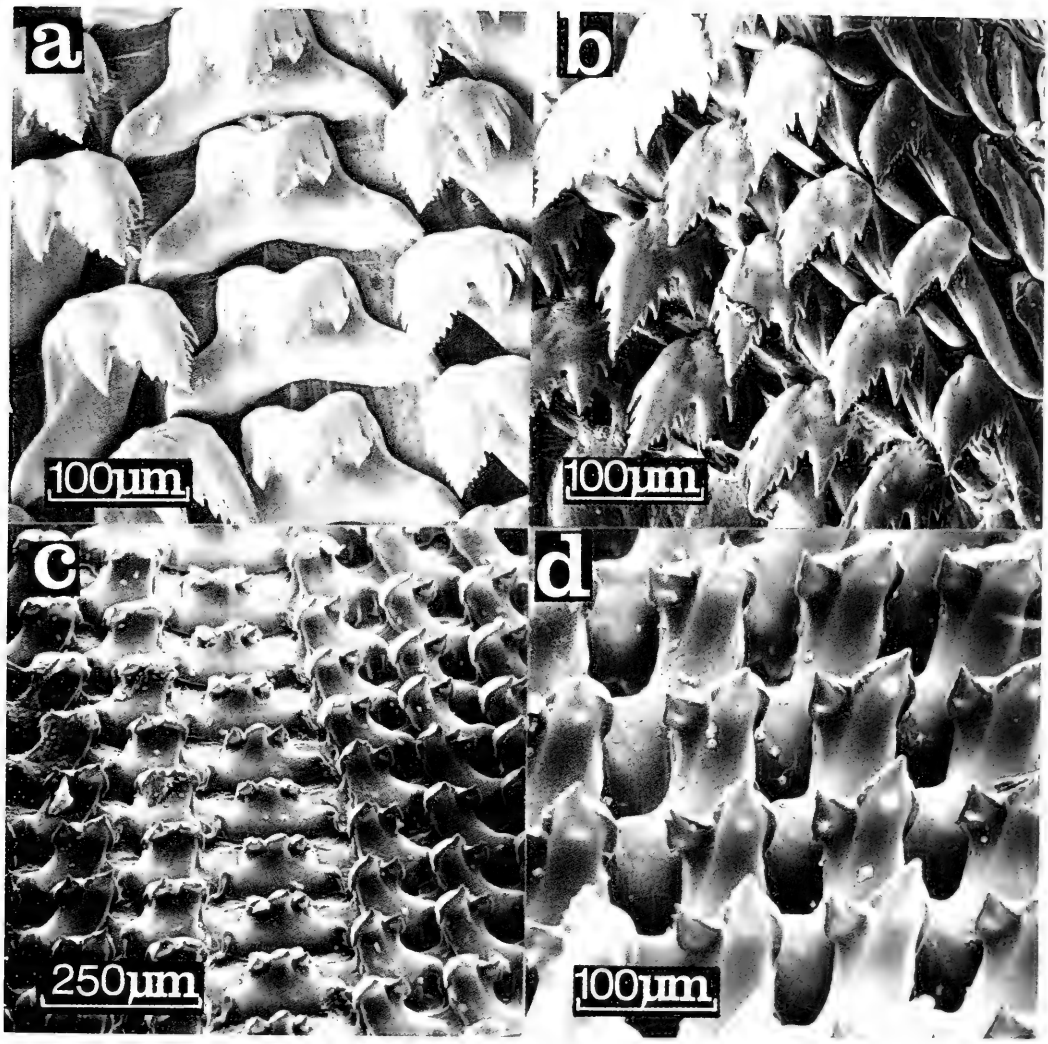

PLATE 4. a and b, *Aplysia parvula,* weight 5.3 g (in alcohol), Sydney Harbour, N.S.W., Australia, February 1968; c and d, *Aplysia dactylomela,* weight 180 g (in alcohol), from the same locality, March 1968.

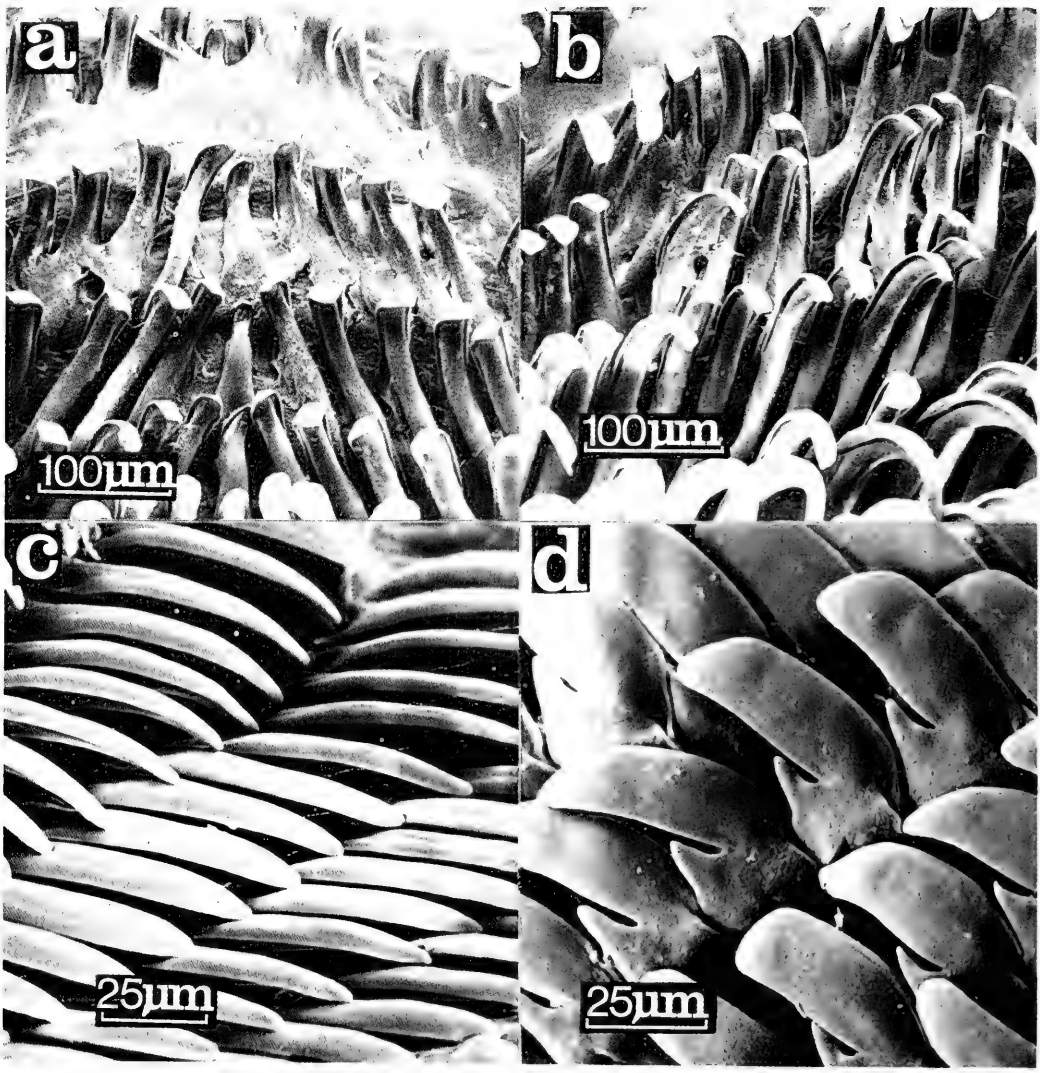

PLATE 5. a and b, *Dolabella auricularia,* weight 25.1 g (in alcohol), Moreton Bay, Queensland, Australia, July 1968; c and d, *Onchidium damelii,* length 3 cm (in alcohol), Pitt Water, N.S.W., Australia, April 1968.

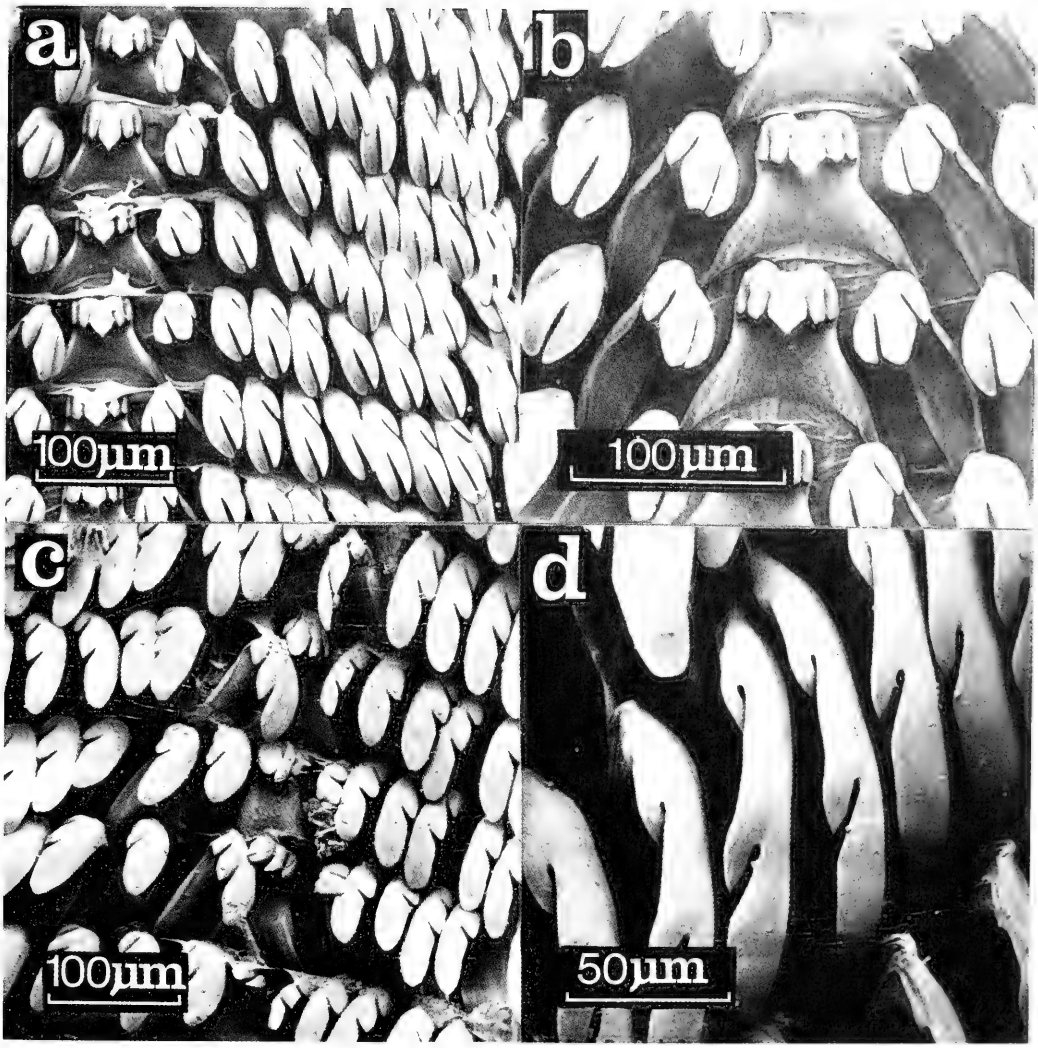

PLATE 6. a and b, *Dolabrifera dolabrifera,* weight 2.2 g (in alcohol), Kenya, East Africa, August 1970; c and d, *D. dolabrifera,* weight 18.1 g (in alcohol), Long Reef, N.S.W., Australia, February 1968.

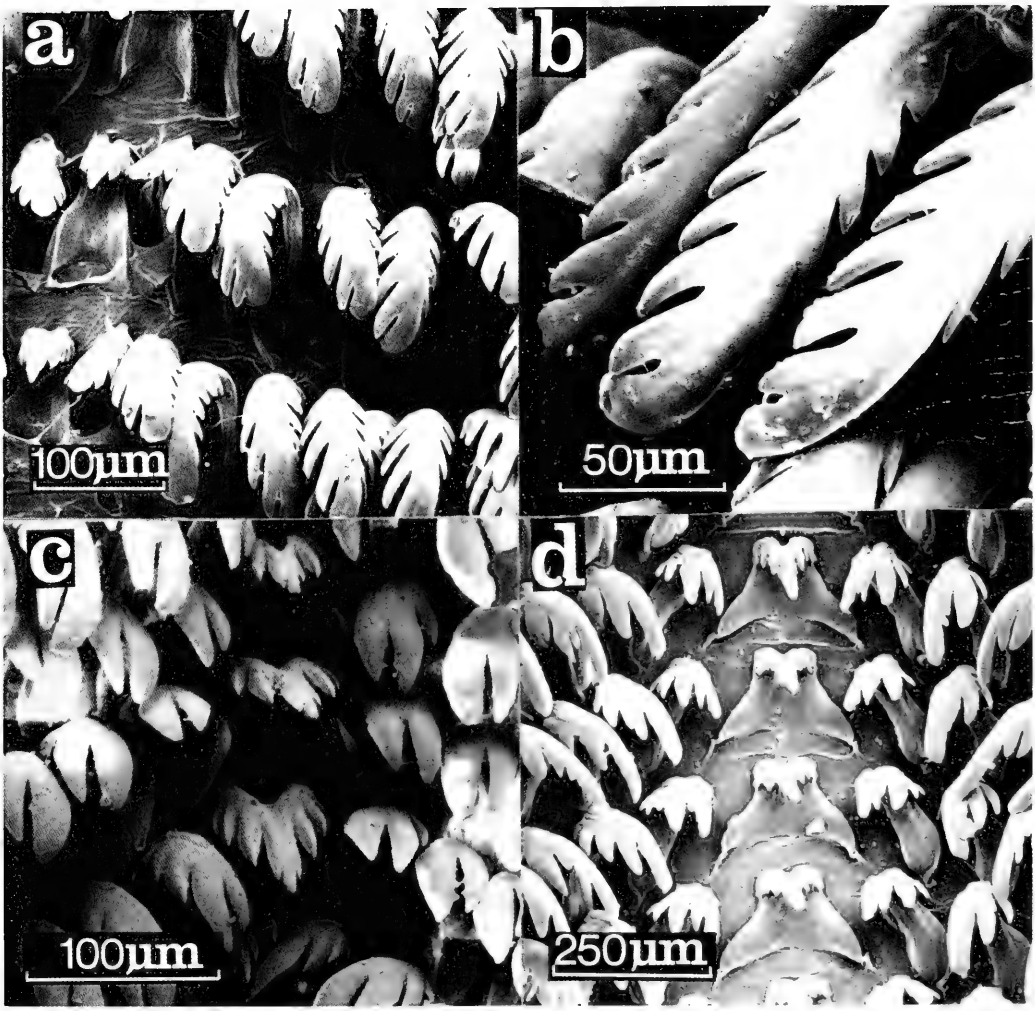

PLATE 7. a and b, *Notarchus punctatus*, weight 7.8 g (in alcohol), Naples, Italy, 1970; c, *Stylocheilus longicauda*, weight 0.09 g (in alcohol), Johnson's Reef, Eastern Australia, January 1963; d, *Bursatella leachi leachi*, weight 40 g (in alcohol), Myora, Queensland, Australia, June 1968.

PLATE 8. a, *Elysia bennetti*, length 25 mm (in alcohol), Great Barrier Reef, June 1970; b, *Onchidoris bilamellata*, length 26 mm (in alcohol), Helford Passage, Cornwall, U.K., March 1971.

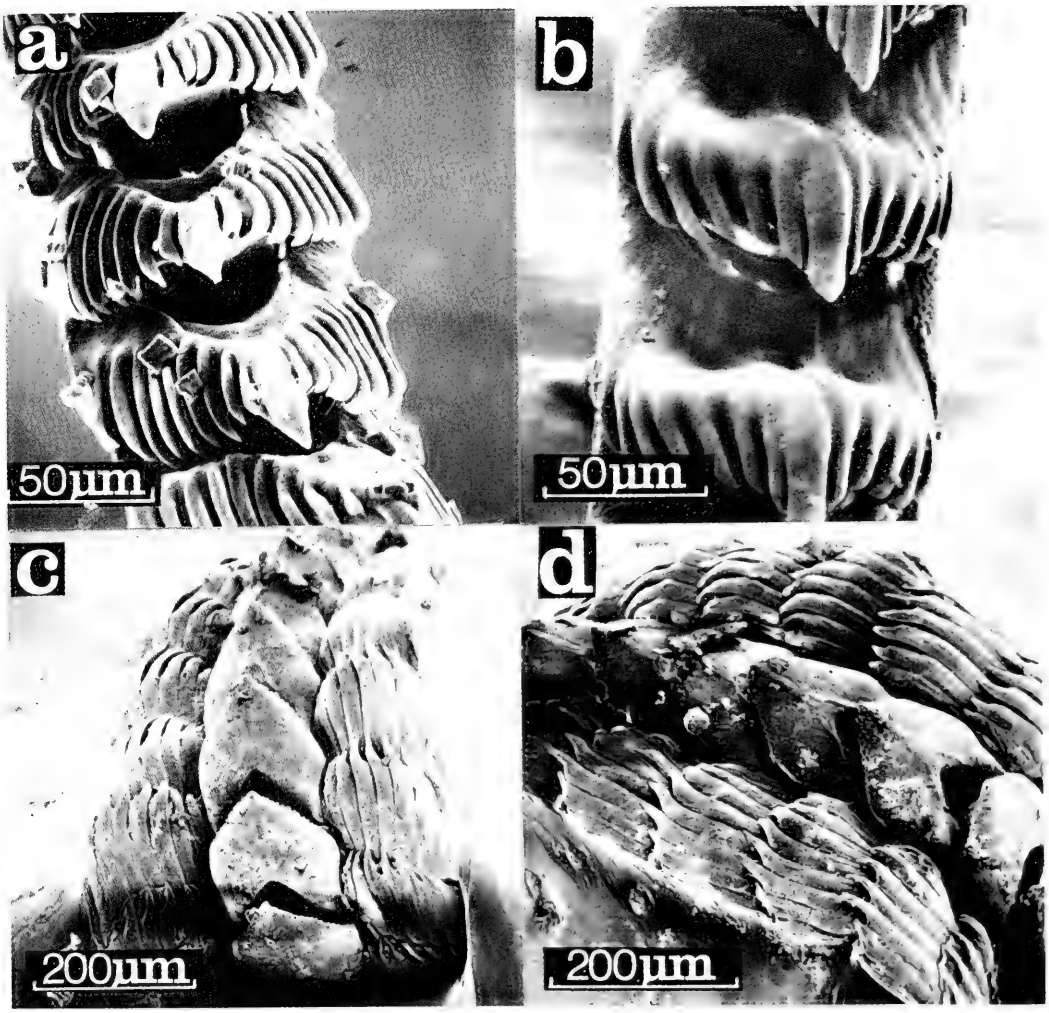

PLATE 9. a, *Pteraeolidia semperi*, adult from Botany Bay, N.S.W., Australia, March 1968; b, *Facelina auriculata longicornis*, length 3 cm alive, Falmouth Cornwall, U.K. (photograph by H. E. Hinton, F.R.S.); c and d, *Dendronotus frondosus*, adult from Plymouth, Devon, U.K., June 1971.

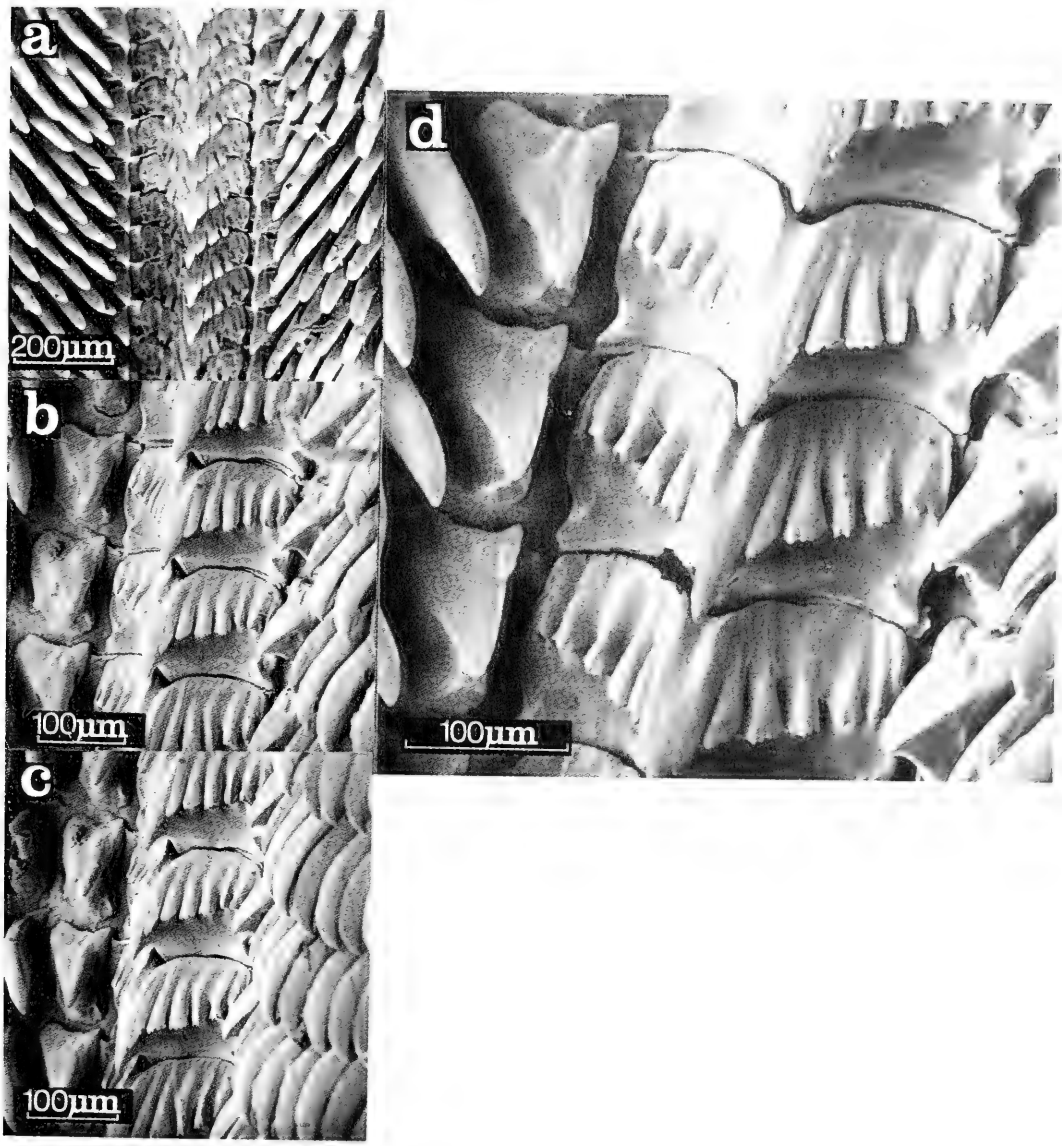

PLATE 10. a-d, *Armina californica,* length 6 cm (in alcohol), dredged off the San Juan Islands, U. S. A., August 1969, showing the apparent effects of altering the SEM specimen-tilt mechanism.

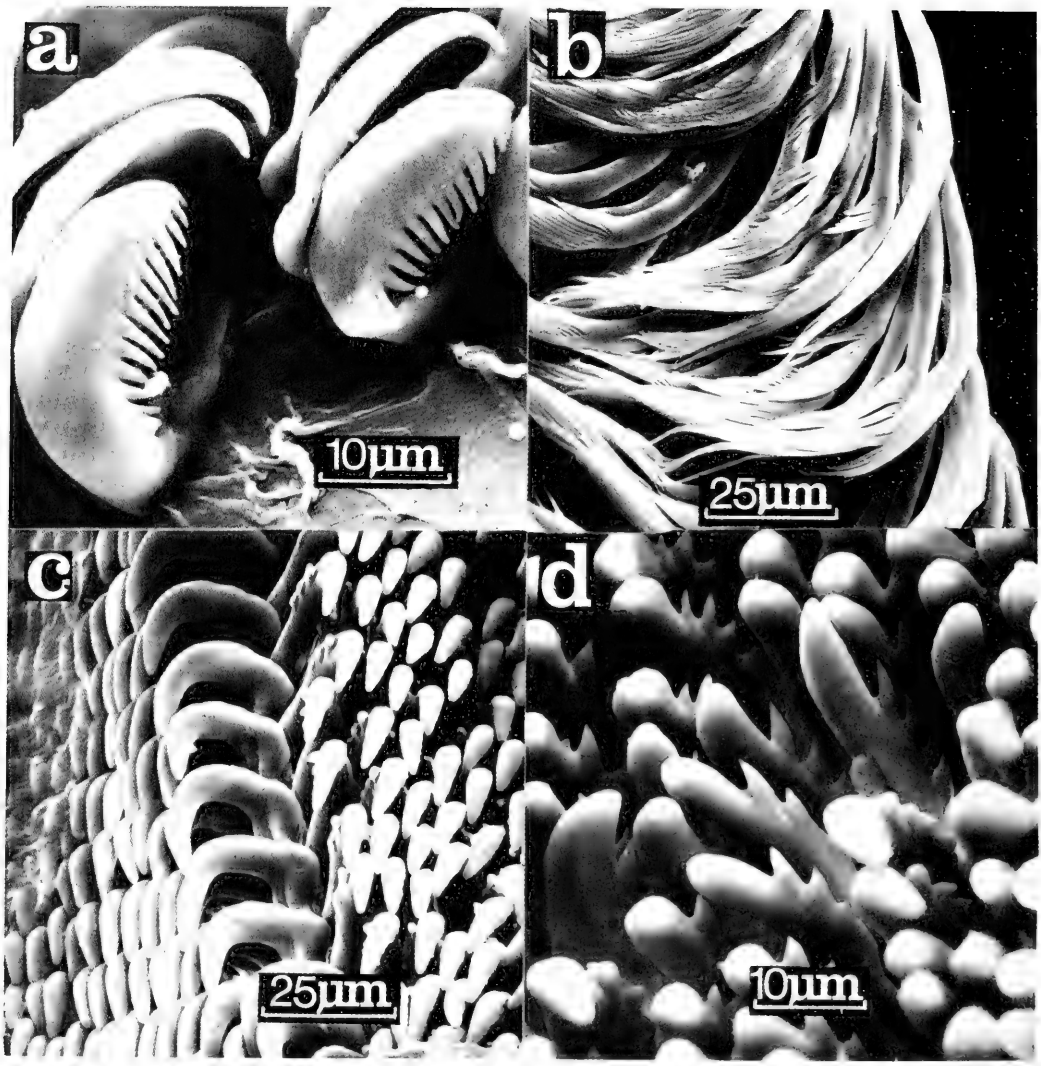

PLATE 11. a and b, *Rostanga arbutus*, length 8 mm alive, Long Reef, N.S.W., Australia, February 1968; c and d, *Casella atromarginata*, adult from Botany Bay, N.S.W., Australia, March 1968.

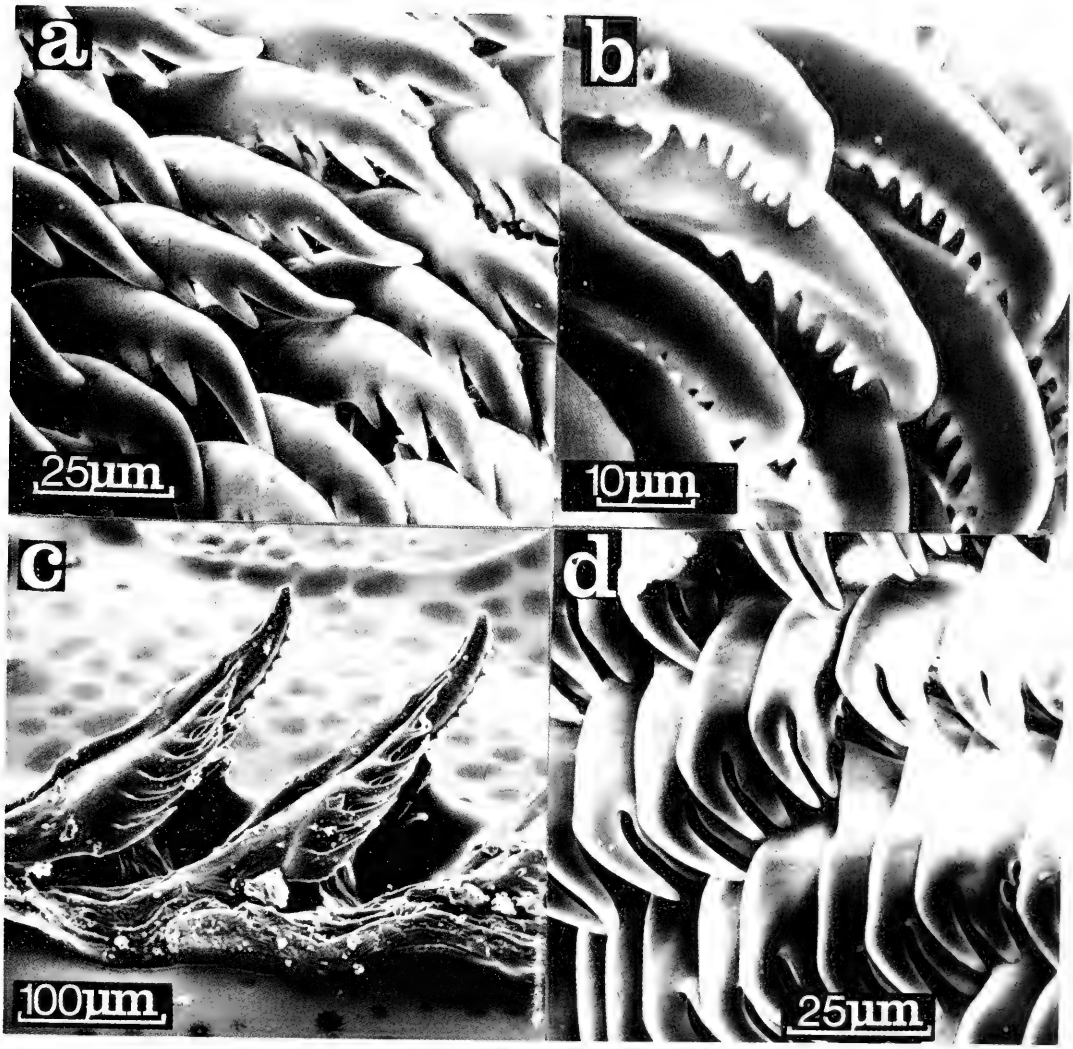

PLATE 12. a, *Chromodoris amoena,* length 26 mm (in alcohol), Botany Bay, N.S.W., Australia, March 1968; b, *C. loringi,* adult, from the same locality; c, *Hermissenda crassicornis,* length 45 mm, San Juan Island, U.S.A., June 1969; d, *Hypselodoris infucata,* adult from Myora, Queensland, Australia, June 1968.

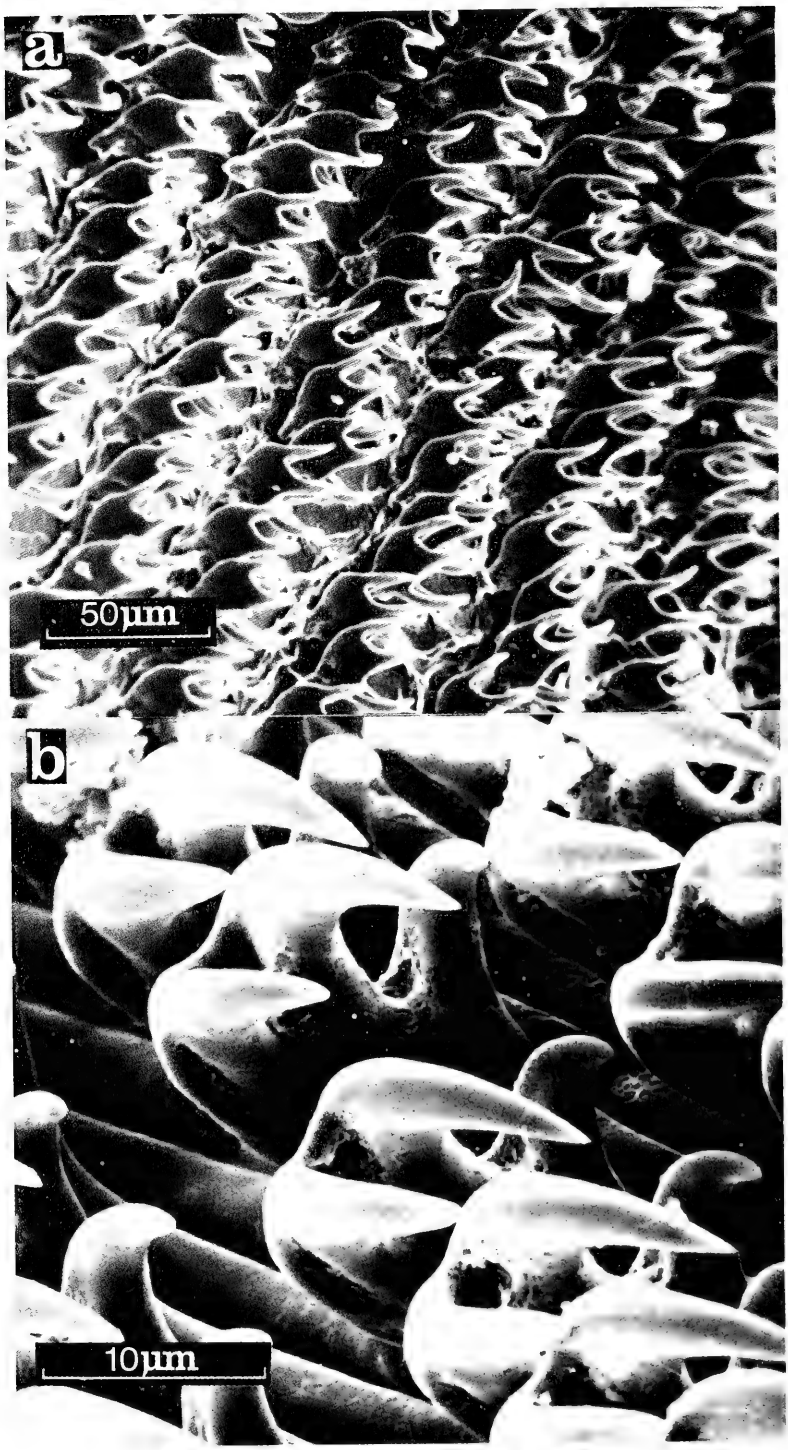

PLATE 13. a, *Kalinga ornata*, length 45 mm (in alcohol), S. E. Queensland, Australia, December 1937; b, *K. ornata*, length 60 mm (in alcohol), from the same locality.

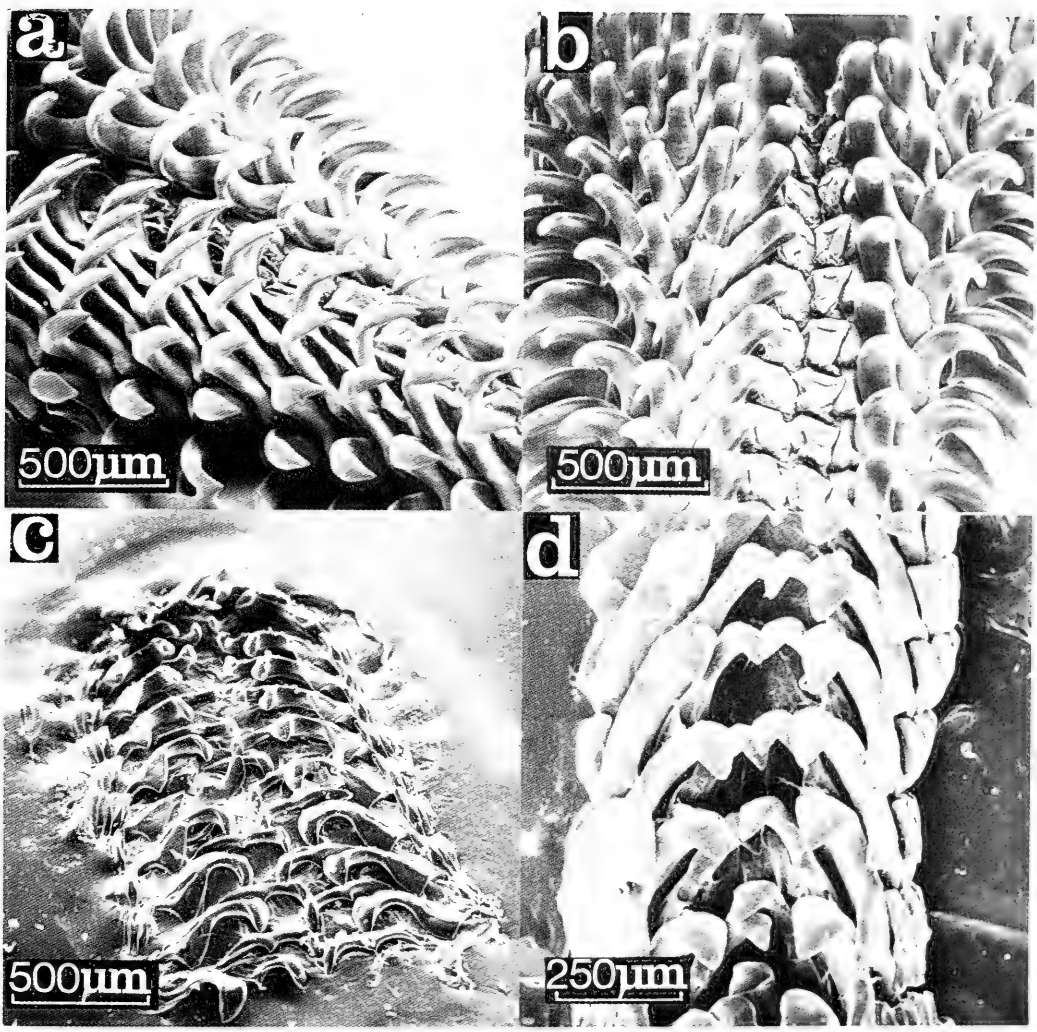

PLATE 14. a and b, *Triopha carpenteri,* length 9 cm alive, dredged off the San Juan Islands, U.S.A., July 1969; c and d, *Polycera capensis,* length 3 cm alive, Sydney Harbour, N.S.W., Australia, March 1968.

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THE RADULA OF THE CHAETODERMATIDAE (APLACOPHORA, CHAETODERMATIDA)

Amelie H. Scheltema

Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, U.S.A.

ABSTRACT

The aplacophoran family Chaetodermatidae (genera *Falcidens* and *Chaetoderma*) has a radula consisting of a single cone-shaped structure in connection with a pair of teeth. The genus *Falcidens* has, as well, a plate with 2 extensions that wrap around the paired teeth.

One species of each genus is known to feed on foraminifera.

The buccal mass bears many similarities to the gastropod buccal mass: it is covered distally by a subradular membrane connected to the radula; it lies in a buccal cavity; it contains a pair of bolsters, from which run muscles to the radula and subradular membrane; it has a blood sinus surrounding a sac of epithelial cells which secrete the cone-shaped tooth.

This sac is considered to be a radula gland homologous to that of other mollusks. It lies between and above the bolsters, as in other mollusks. At its proximal, blind end are 4 large odontoblasts.

The cone-shaped tooth is considered to be a fused, permanent, continuously secreted radula. Scanning electron photomicrographs support this view.

MALACOLOGIA, 1973, 14: 167-206

PROC. FOURTH EUROP. MALAC. CONGR.

EUTHYNEURAN AND OTHER MOLLUSCAN SPERMATOZOA

T. E. Thompson

Zoology Department, University of Bristol, U.K.

ABSTRACT

Spermatozoa of Euthyneura possess a variable number of spiral structures along the tail. These were investigated using both conventional methods of preparation for electron microscopy and freeze-etching techniques. Spermatozoa of *Acteon* possessed 4 distinct mitochondrial spiral keels, those of *Aplysia* and *Bursatella* had only 2, while in the nudibranchs only 1 keel was detectable.

The situation in the pulmonates is variable, the arrangement in the Stylommatophora investigated being similar to the nudibranchs, while the Basommatophora investigated possessed a multiplicity of helical structures in the sperm-tail.

CONTENTS

INTRODUCTION

Serious interest in molluscan spermatozoa began with the publication in 1906 of Retzius's splendid monograph, in which he described and illustrated the structure (using bright-field optical microscopy) of the gametes of numerous molluscs. These pioneering studies have often been ignored by later workers. One example of this was documented by Thompson & Bebbington (1970) in reviewing different published interpretations of the structure of the complex aplysiid spermatozoon. Both Tuzet (1940) and Franzén (1955) ignored Retzius's description of this type of gamete in their published reviews, yet the electron microscope shows (Thompson & Bebbington, 1969) that Retzius had in fact provided a description no less accurate than those of later light-microscopists. Retzius's microscopical investigations without doubt represent the highest possible level of achievement in optical studies of live metazoan spermatozoa. Fortunately, modern techniques of fine-structure investigation have resulted in methods such that we do not have to be as skilled as Retzius to achieve worthwhile results. Standard techniques of transmission electron microscopy, which can be learnt and applied by a novice after a short period of training, enable the research worker to go deeply into details of cell substructure that the optical microscopists could only guess at. New methods of preparation for electron microscopy, such as freeze-etching, allow the investigator to have the advantage of a physical (not chemical) technique of fixation, especially useful in studies of complex cells like spermatozoa (Koehler, 1970; Thompson, 1971). Finally, and most important of all, the application of techniques of ultrastructural cytochemistry with great brilliance by André, Personne & Anderson (key references listed by Personne & Anderson, 1970) has enabled a serious start to be made in understanding the functioning of various parts of the spermatozoan body. It may be added that the application of certain techniques of simple physics to the study of scale-models of molluscan spermatozoa has proved to be rewarding in trying to understand the functional morphology of euthyneuran gametes (Thompson, 1966).

The principal conclusions to be drawn from Retzius's survey of molluscan spermatozoa were that there was considerable heterogeneity in shape and size; that all the normal (i.e., fertilizing or eupyrene) gametes were capable of motility; that helical modifications of acrosome, nucleus, and principal-piece were encountered in many species; and that the spermatozoa of the primitive groups (such as bivalves and chitons), with external fertilization, were apparently less specialized morphologically than those of the more advanced, internally fertilizing groups (such as the higher gastropods).

Franzén (1955) investigated a greater variety of molluscan spermatozoa and fully established these conclusions. His paper is a model of patience and thoroughness and he clearly showed that, to use his own words, "the morphology of the sperm within the Mollusca can be said to stand in a certain relation to the biology of fertilization. The primitive type of sperm is retained in forms which discharge their sperms freely into the water. In the cases where an internal fertilization takes place or where the sperms are delivered in the immediate vicinity of the female genital opening, the sperm differs morphologically more or less from the primitive type." These morphological modifications chiefly affect the head and the middle piece and are "obviously connected with the different nature of the medium at the place where the sperm is in quest of the egg."

Other workers have contributed towards the understanding of the structure and functioning of the sub-cellular constituents of the advanced spermatozoon of the Opisthobranchia (Thompson, 1966; Thompson & Bebbington, 1969, 1970; Thompson, 1971) and in the Prosobranchia and Pulmonata (reviewed by Personne & Anderson, 1970, and by

Favard & André, 1970). Many of these publications have included observations on spermiogenesis, invaluable in attempts to define the homology of the spermatozoan organelles throughout the Mollusca. According to Favard & André (1970) the changes which occur in the spermatid mitochondria during spermiogenesis in the pulmonates represent the most extreme mitochondrial transformation and re-modelling yet detected in animal gametes. The mitochondria of the young spermatid assemble around the centriolar cone to the rear of the nucleus, before fusing to form a continuous sheath which extends rearward, enveloping the flagellum. In this very complete fusion of mitochondrial elements, the matrices of the cristae and both internal and external membranes all merge. Most of the bulk of this large mitochondrial derivative (which may come to occupy about 95% of the volume of the spermatozoon) is made up of a proteinaceous crystal composed of particles 90Å in diameter. According to Favard & André (1970) this crystal is traversed by 2 or more helically coiled canals of 2 different kinds. One of these they term the major helix (André, 1962) and this type is filled with glycogen during the last phase of spermiogenesis (Personne & André, 1964). The other type is the secondary helix and is derived from the matrix areas of the original mitochondrion. Using cytochemical methods Favard & André report findings showing Krebs cycle activities in the secondary helix, cytochrome activities in the body of the crystal, and phosphorylase activity in the major helix (based upon photographs supplied by Anderson & Personne). These results appear to be derived entirely from studies of the stylommatophoran *Helix*. There is known to be considerable morphological diversity in euthyneuran spermatozoa. For instance, in *Planorbis* there are known to be 2 major helices, compared with 1 in *Helix*. In *Planorbis* both of these are known to contain glycogen (Personne & Anderson, 1970). In *Testacella* there are 3 helices: 1 is a glycogen canal and the others contain condensed matrix material (André, 1959).

After an exhaustive investigation into spermiogenesis in the pulmonate *Succinea*, Hickmann (1931) concluded that: "concerning the functional significance of the spiral arrangement of the sperm of pulmonates we are very much in the dark." Thanks to the work of André, Anderson and Personne, we now know that these spirals are connected with the provision of substrates for the metabolism of the flagellar axoneme. But this explanation raises more questions. Why should the configuration of these materials be a spiral one? Why should the spiralling components of the mitochondrial derivatives stand out as prominent ridges upon the surface of the sperm tail? Are these mitochondrial helices related geometrically and functionally to the spiral structures often distinguishable on the head of various spermatozoa among the higher molluscs? In a paper published in 1966, I proposed that a simple answer could be offered to these questions. This proposal came out of an investigation into the locomotion of active allosperms of the opisthobranch *Archidoris pseudoargus* by means of ciné-photomicrographic techniques. It will be necessary at this point to summarize some of the results obtained. During swimming, thrust was provided by flagellation of the kind described by Gray (1955, 1958) in echinoid and mammalian spermatozoa, with a series of propagated waves originating in the neck and progressing down the tail. So far as could be ascertained, the waves originating in the sperm-neck are uniplanar and approximately symmetrical on the 2 sides. (In abnormally moving individual spermatozoa, encountered occasionally, the waves originate at the rear and pass forwards, resulting in sperm-progression backwards). As normal *Archidoris* allosperms progress forwards they spin in a clockwise direction when viewed from the front. This spinning may exceed 8 rev/s. As a sperm moves forward the spinning spiral mitochondrial keel (of which there is only 1 in nudibranchs such as *Archidoris*) gives rise to the illusion of short-period waves passing backwards along the tail (similar to the waves apparent on a rotating barber's pole). In the abnormal individuals

referred to above this is reversed.

It seemed likely that the spinning of motile spermatozoa of *Archidoris* is brought about by the spiral mitochondrial keel and the spiral shape of the head itself, through their differential alterations of the moving spermatozoon's resistance to torque. To test whether such a keel could function in this way a preliminary glass model was constructed to scale and towed in water. This was found to spin so long as forward motion continued, and, in short, reproduced some of the features of normal spermatozoan motility. This was of indefinable significance, however, because of the disparity between the Reynolds number of the spermatozoon/seminal fluid and the glass model/tap-water systems. To obtain further evidence, a number of models were constructed more accurately, using nylon thread and glass, and these were towed at 5 cm/h through glycerol at temperatures ranging from 5 to 19°C. In these experiments the Reynolds number was found to be acceptably close to that calculated for the natural system. In the trials, the sperm model when in motion rotated (up to 1 1/2 spins/h) upon its long axis in a clockwise direction when viewed from the front, thus giving experimental support for the hypothesis advanced above. What appears to be true for spermatozoa of *Archidoris* may well apply more widely to other euthyneurans with external helical keel-like modifications, namely that such structures by their differential alteration of the moving gamete's resistance to torque convert uniplanar flagellation into helical progression of the spermatozoon. The advantages of spinning progression are uncertain. It may allow faster progression in the female tract; it may even facilitate oocyte-penetration during the process of fertilization *in vivo*.

A number of other issues have emerged following recent studies of various molluscan gametes. Stringer (1963) in attempting to use sperm-morphology as a guide to phylogenetic affinity, stated that the "spiral form of the spermatozoa" is found only in the pulmonate gastropods. This is certainly untrue, and leads to the conclusion that guidelines are needed to help students of molluscan evolution to use information about spermatozoa wisely. Bayne (1970) investigated the fine-structure of spermatozoa of the slug *Agriolimax reticulatus* and found the axoneme to consist of a 9 + 2 arrangement but the 9 outer moieties were single, not double as in typical metazoan flagella, whereas other workers (summarized by Giusti, 1969) have reported a 9+9+2 axoneme and have described α fibres of the doublet type. Clearly, this is a field where further study is needed. Another problem demanding fine-structural study is the claim, by Martin *et al.* (1970), that spermatozoan heads of *Octopus dofleini* possess superficially disposed sheaths of glycogen. These are the kinds of issues that have stimulated the present investigations, but it is certainly not yet possible, regrettably, to give more than partial answers to some of the questions that they raise.

The present paper reports on my work on various molluscan spermatozoa, in an effort to synthesize the known extraordinarily wide range of gamete morphology in the phylum, as well as to explore some new techniques of examination of small cells and sub-cellular structures.

MATERIALS AND METHODS

Living spermatozoa were examined by various methods of optical microscopy, sometimes after vital dyeing with neutral red or janus green. Most of the routine work was carried out using a Wild M11 phase-contrast microscope (Pl. 1A). Fluorescence microscopy after staining with acridine orange was useful in distinguishing the acrosome in difficult material. Zeiss interference microscopy was excellent for studying fine helical structures on the head in living spermatozoa, but the more simple Zeiss Nomarski microscope is little inferior in performance using such cells (Pl. 1B-D). Straightforward bright-field optical microscopy is poor for the study of small

cells such as molluscan gametes and it is a matter for surprise and admiration that the early work of Retzius (1906) was carried out solely by this method. Considerable insight into the structure of fresh gametes could be obtained by allowing them to dry out gradually, in a bubble of air trapped beneath a conventional cover-glass, while a close watch was kept upon the changes which began after cell-death. The nucleus frequently bursts rather readily in such pathological preparations, enabling a close scrutiny to be made of the more robust acrosome and centriolar cone. The advantages of some of these techniques can be compared in Plate 1. The nucleus itself could be characterized and studied best after fixation of a gamete-smear on a glass slide in the vapour of acetic acid and staining in haemalum or any other standard nuclear dye.

Material for the electron microscope was sometimes examined whole, sometimes sectioned in Araldite, and sometimes processed by the freeze-etching method. A) Whole mount preparations were made by allowing living gametes to dry down on a copper grid, in an atmosphere saturated with the vapour of either osmic acid or formaldehyde. After 3 hours the grid was washed in distilled water, dried and examined. The micrographs obtained (Pl. 2) show gamete silhouettes but occasionally surface or internal details can be discerned by careful focusing of the microscope (Pl. 2C, F, G) and adjustment of photographic exposures. B) Material for sectioning was fixed in phosphate-buffered 25% glutaraldehyde with added sucrose, washed in the buffer, then post-fixed in 1% osmic acid in the buffer. Araldite sections were stained with saturated uranyl acetate in 70% alcohol. C) Existing methods (such as those outlined above) for investigating the spatial relationships at the ultrastructural levels of cells and of sub-cellular structures have at least 2 disadvantages. 1) Chemical fixation results in unpredictable, sometimes capricious damage to the specimen. 2) Cytological three-dimensional reconstruction is difficult even when serial sectioning has been mastered. The technique of freeze-etching, devised by Steere (1957) and refined by Moor (1964) as an adjunct to transmission electron microscopy of biological and medical materials, offers a helpful alternative to the older preparative methods. Moor's technique is novel in that it is a purely physical preparation of the specimen, thus providing a useful check on preparative methods which involve chemical fixation. Considerations of space preclude a detailed account of the freeze-etching method and the interested reader is referred to my paper on the application to molluscan ultrastructure research of the Balzers 360M freeze-etching plant (Thompson, 1971). Electron micrographs obtained in this way (Pls. 3C, 11-14) have a three-dimensional quality which is strikingly reminiscent of micrographs from the scanning electron microscope (Thompson & Hinton, 1968) but of course far better resolution can be obtained using a transmission electron microscope. This three-dimensional appearance is not spurious, and genuinely allows a rapid, accurate appreciation of spatial relationships. Some of the micrographs presented here illustrate this point. They enable an immediate understanding of the shape of some of the components of the euthyneuran sperm-tail. It can be exceedingly laborious to build up such a clear picture of this kind of cell by reconstruction of serial sections. The only insurmountable defect of the freeze-etching method at present is the fact that certain organelles do not survive the preparation well. The α and β fibrils of flagella, for instance, become difficult to discern.

The live animals studied were obtained in Bristol or during working visits to laboratories in Australia, Britain, France and the U.S.A. Table 1 lists the species examined, their source, and the principal methods of investigation.

GENERAL CHARACTERISTICS OF MOLLUSCAN SPERMATOZOA

Molluscan male gametes are all elongated motile cells. In most species the fully mature spermatozoa are morphologically uniform but in certain prosobranch gastro-

TABLE 1. Material

Species	Source*	Examined optically**	Whole mount electron microscopy+	Sectioned for electron microscopy++	Freeze-etched†
Acanthochitona crinitus	Arcachon	x	x		
Transennella tantilla	Friday Harbor	x			
Gibbula cineraria	Plymouth	x	x		
Gibbula umbilicalis	Plymouth	x			
Acteon tornatilis	Rhossili	x	x	x	
Bulla ampulla	Myora	x	x	x	
Hydatina physis	Long Reef	x	x		
Haminea virescens	Friday Harbor	x			
Odostomia columbianus	Friday Harbor	x	x		
Odostomia sp.	Friday Harbor	x	x	x	
Dolabella auricularia	Myora	x			
Dolabrifera dolabrifera	Long Reef	x	x	x	
Bursatella leachi	Myora	x	x		
Phyllaplysia taylori	Friday Harbor	x	x		
Aplysia punctata	Plymouth	x	x	x	x
Aplysia depilans	Arcachon	x	x	x	x
Umbraculum sinicum	Long Reef	x	x	x	
Pleurobranchus peroni	Long Reef	x	x	x	
Berthella plumula	Plymouth	x	x	x	
Tritonia festiva	Friday Harbor	x	x		
Dendronotus iris	Friday Harbor	x	x		
Archidoris pseudoargus	Cornwall	x	x	x	x
Cadlina laevis	Cullercoats	x	x		
Hermissenda crassicornis	Friday Harbor	x	x		
Armina californica	Friday Harbor	x	x		
Planorbarius corneus	Bristol	x	x		x
Lymnaea peregra	Bristol	x	x	x	x
Lymnaea stagnalis	Bristol	x	x		x
Physa fontinalis	Bristol	x	x		x
Physa gyrinus	Bristol	x			
Hedleyella falconeri	Queensland	x	x		
Onchidium damelii	Pitt Water	x	x	x	
Helix aspersa	Bristol	x	x		
Helix pomatia	Bristol	x	x		x
Ariolimax columbianus	Friday Harbor	x	x		
Loligo opalescens	Friday Harbor	x	x		

*Plymouth Sound, Cornwall, Bristol, Cullercoats, Rhossili in U.K.; Arcachon in France; Friday Harbor, U.S.A.; Myora in Queensland, Long Reef and Pitt Water in N.S.W., Australia.

**Wild M11 phase microscope; Zeiss Nomarski photomicroscope.

+Dried in Os_2O_4 or HCHO vapour.

++Fixed in buffered glutaraldehyde; postfixed in Os_2O_4.

†Method described by Thompson, 1971.

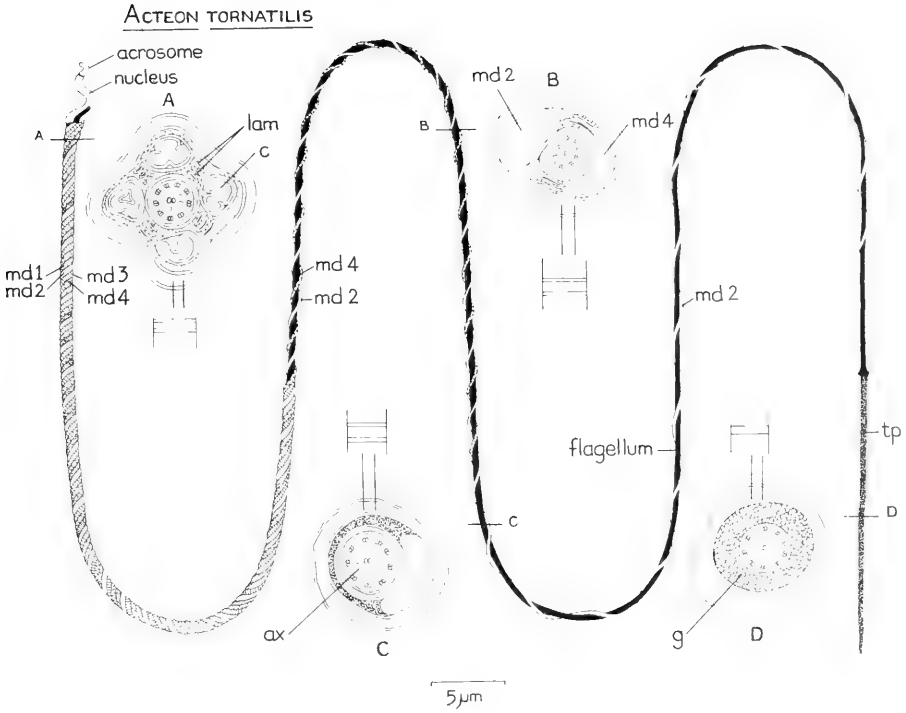


FIG. 1. Spermatozoon of *Acteon tornatilis*.

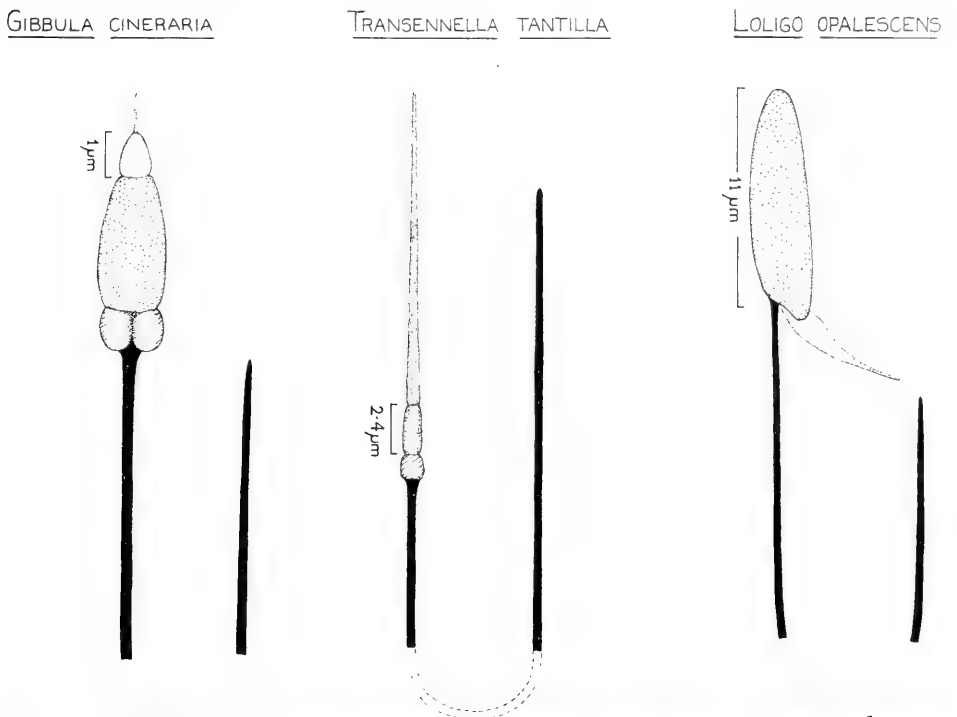


FIG. 2. Spermatozoa of *Gibbula cineraria*, *Transennella tantilla* and *Loligo opalescens*.

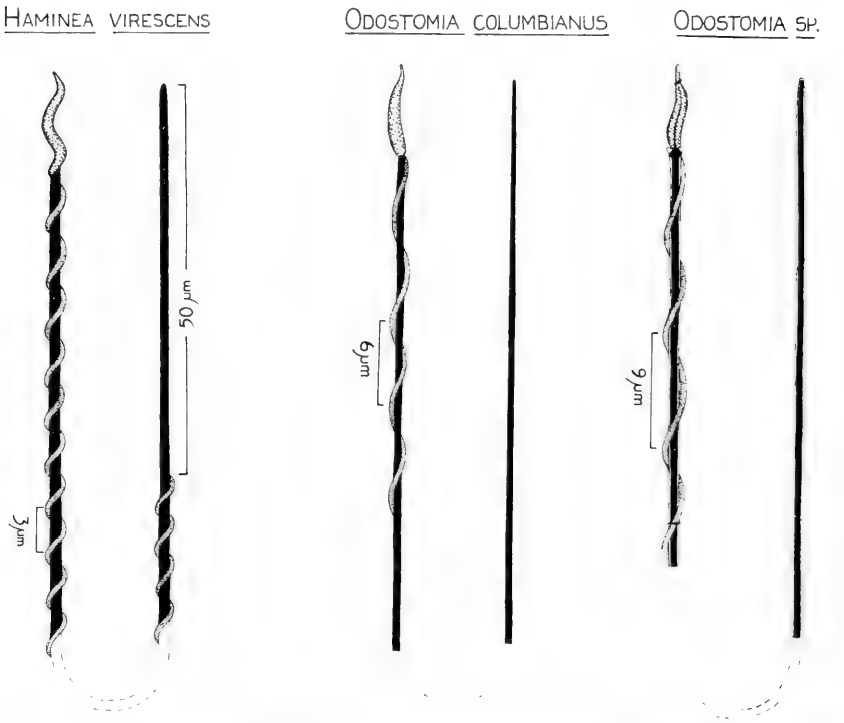


FIG. 3. Spermatozoa of *Haminea virescens*, *Odostomia columbianus* and *Odostomia* sp.

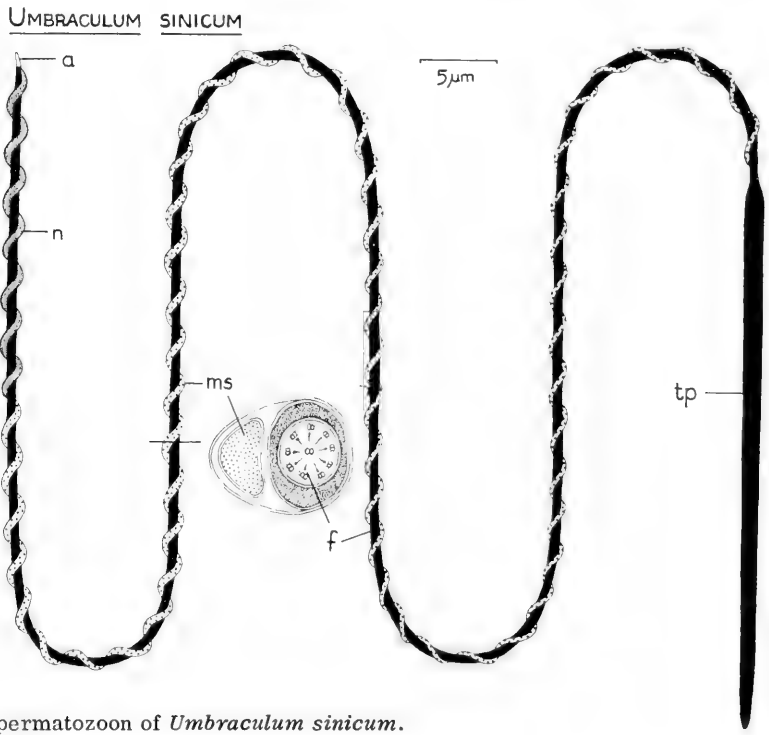


FIG. 4. Spermatozoon of *Umbraculum sinicum*.

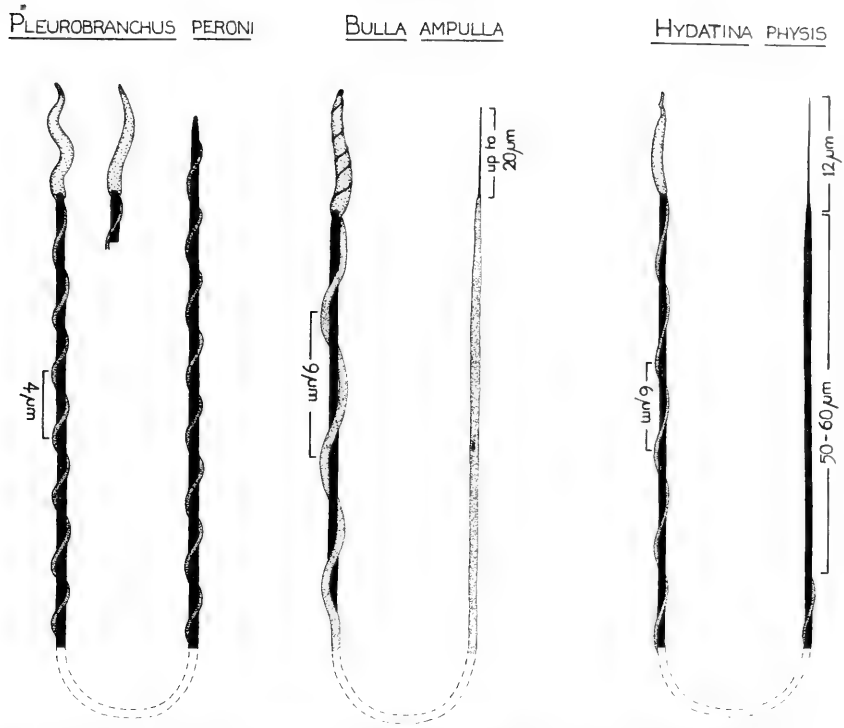


FIG. 5. Spermatozoa of *Pleurobranchus peroni*, *Bulla ampulla* and *Hydatina physis*.

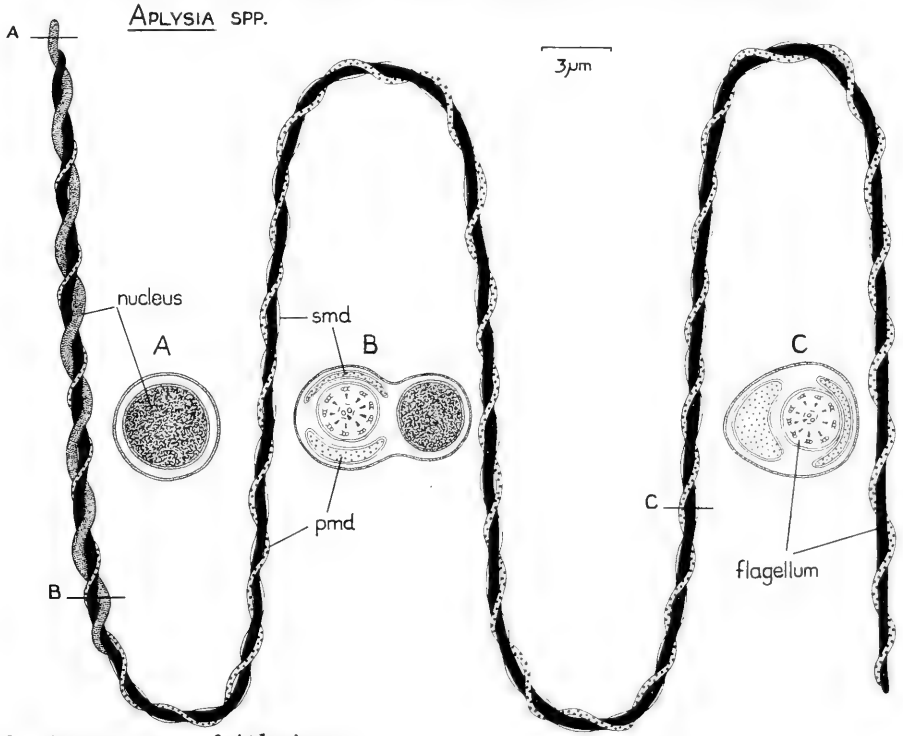


FIG. 6. Spermatozoon of *Aplysia* spp.

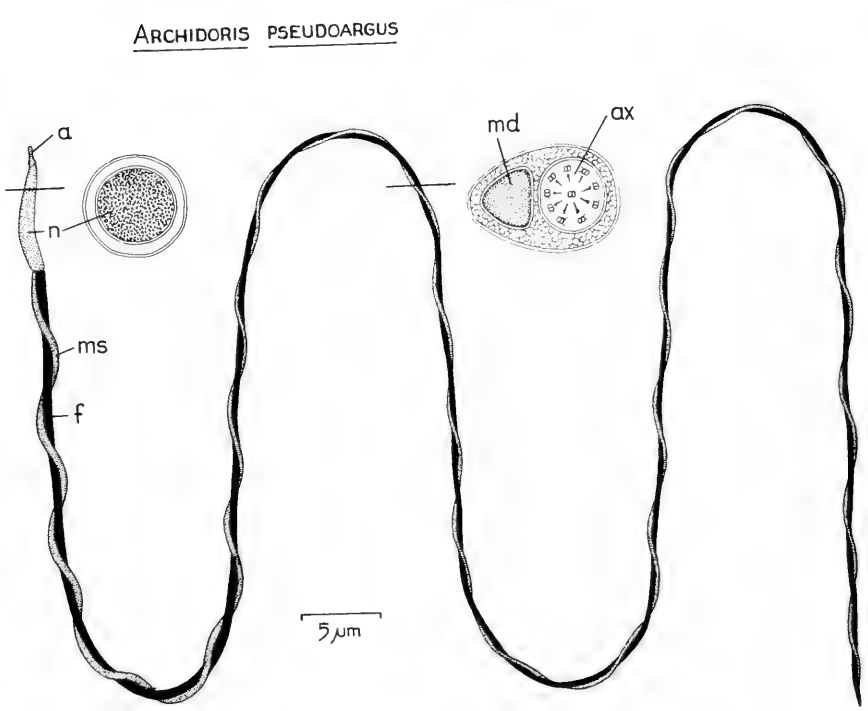


FIG. 7. Spermatozoon of *Archidoris pseudoargus*.

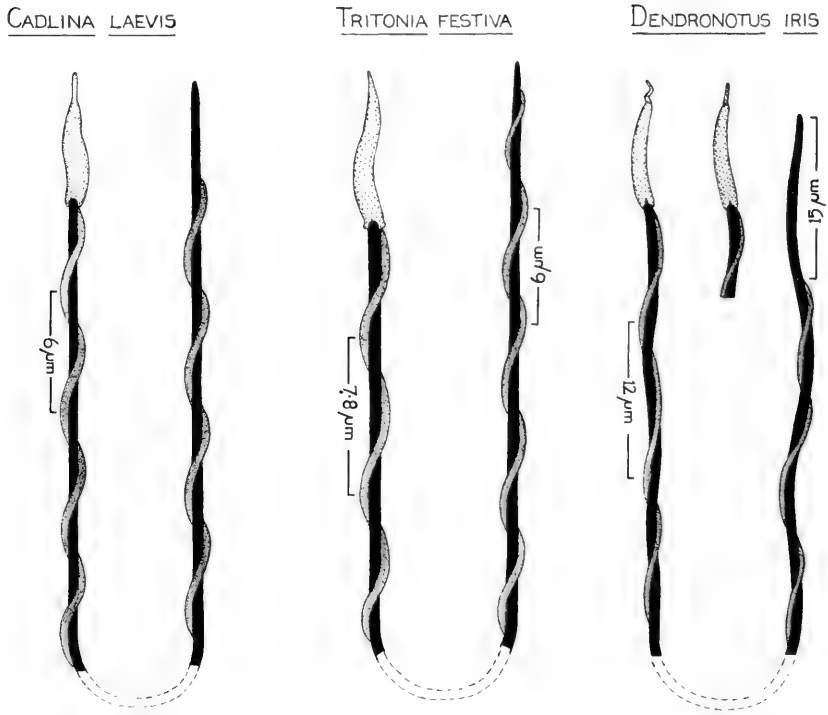


FIG. 8. Spermatozoa of *Cadlina laevis*, *Tritonia festiva* and *Dendronotus iris*.

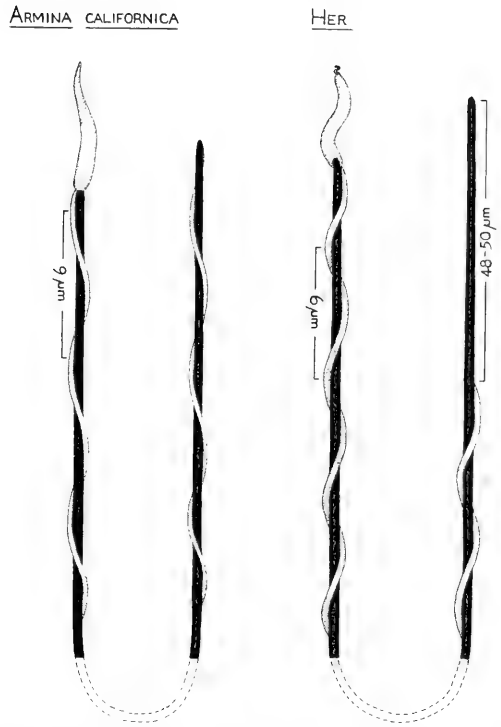


FIG. 9. Spermatozoa of *Armina californica* and *Hermissenda crassicornis*.

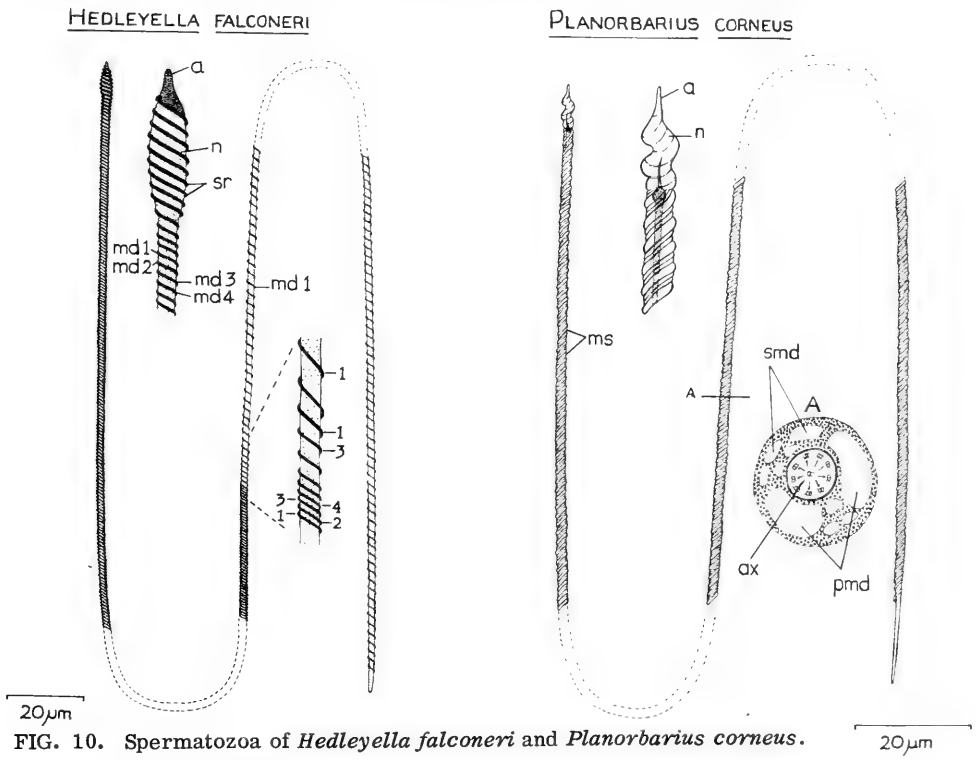


FIG. 10. Spermatozoa of *Hedleyella falconeri* and *Planorbarius corneus*.

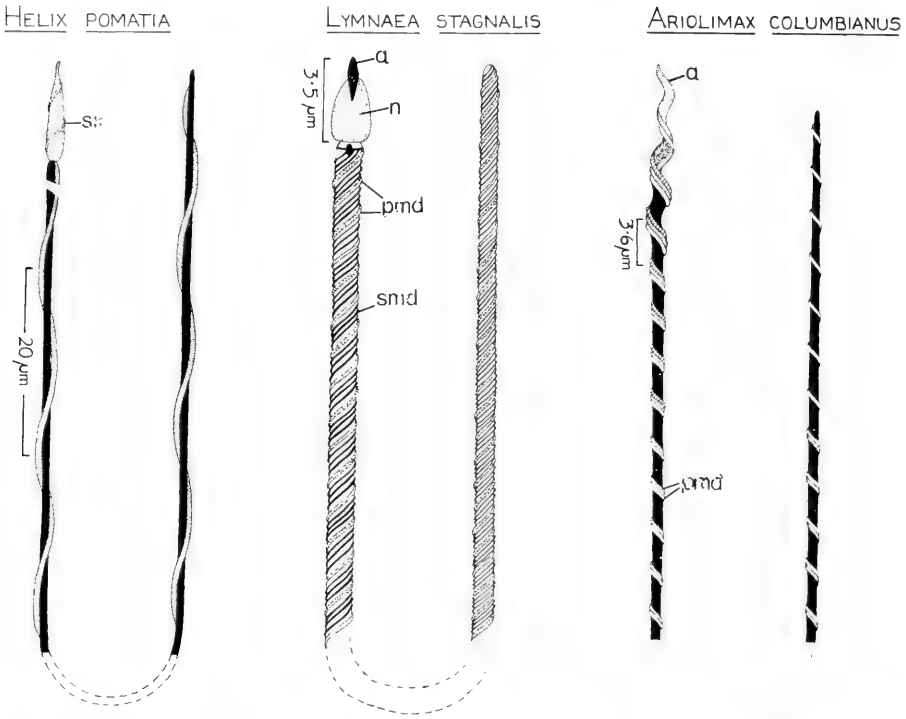


FIG. 11. Spermatozoa of *Helix pomatia*, *Lymnaea stagnalis* and *Ariolimax columbianus*.

pods dimorphism occurs. The normal kind of gamete is then said to be eupyrene, while the novel kind is incapable of participating in egg-penetration or in amphimixis, and, being virtually devoid of nuclear chromatin, is said to be oligopyrene or apyrene. Details of the structure and functioning of these atypical spermatozoa are outside the scope of the present paper; the subject has been reviewed by Nishiwaki (1964) and by Hyman (1967). Throughout the present paper the term spermatozoon refers only to eupyrene gametes.

Table 2 shows the sizes of spermatozoa of various molluscs. It is often axiomatic in discussions of gamete size to stress that the male or micro-gamete is always much smaller than the female or mega-gamete, and this is of course true, *but only in terms of biomass*. If linear dimensions are compared it is often found that sperm-length greatly exceeds ovum-diameter. The smallest molluscan spermatozoa are those of chitons, bivalves, and, perhaps surprisingly, cephalopods (with the exception of the 500 μm long gametes of the giant North Pacific *Octopus dofleini*). In most of these forms there is no clear correlation between adult-size and sperm-size. On the other hand, within the pulmonate gastropods considerable evidence exists that the largest species do predictably possess the longest spermatozoa. The largest sperm so far reported for any mollusc occurs in the giant Queensland forest snail *Hedleyella falconeri* (Fig. 10). Perhaps this apparent positive correlation will prove to be spurious; all that will be needed will be the discovery of several species of small pulmonates which possess spermatozoa more than 1 mm in length.

The basic type of spermatozoon found in the Mollusca (Franzén, 1955) is possessed by externally fertilizing species such as the gastropod *Gibbula cineraria* (Pls. 2A, 5; Fig. 2) (see also the excellent paper of Personne & Anderson, 1970). The length overall was approximately 60 μm. The head of a freshly-shed spermatozoon measured

TABLE 2. Size of molluscan spermatozoa.

Species	Length in μm	Source (P - Present Paper)
Acanthochitona crinitus	65	P
Lepidopleurus asellus	79	Franzén, 1955
Lepidochitona cinerea	33	P
Chaetoderma nitidulum	90	Franzén, 1955
Nucula sulcata	58	Franzén, 1955
Crassostrea virginica	40	Galtsoff & Philpott, 1960
Unio pictorum	39	Franzén, 1955
Thracia papyracea	64	Franzén, 1955
Transennella tantilla	66	P
Gibbula umbilicalis	50	P
Gibbula cineraria	60	P
Hydrobia ulvae	100	Franzén, 1955
Onoba striata	140	Franzén, 1955
Turritella communis	115	Franzén, 1955
Caecum glabrum	120	Franzén, 1955
Triphora perversa	140	Franzén, 1955
Velutina velutina	90	Franzén, 1955
Pomatias elegans	135	P
Nassa reticulata	150	Franzén, 1955
Acteon tornatilis	230	P
Diaphana minuta	215	Franzén, 1955
Cylichna cylindracea	200	Franzén, 1955
Bulla ampulla	106-115	P
Hydatina physis	155	P
Odostomia columbianus	250	P
Odostomia sp.	750-876	P
Haminea navicula	240	Dupouy, 1960
Haminea virescens	264-270	P
Akera bullata	260	Franzén, 1955
Dolabella auricularia	275	P
Dolabrifera dolabrifera	350	P
Aplysia depilans	155-158	Thompson & Bebbington, 1969
Aplysia fasciata	182-185	Thompson & Bebbington, 1969
Aplysia punctata	215-228	Thompson & Bebbington, 1969
Bursatella leachi	180	P
Umbraculum sinicum	225	P
Pleurobranchus peroni	180-190	P
Berthella plumula	440	P
Tritonia hombergi	280	Thompson, 1961
Tritonia festiva	180-190	P
Dendronotus iris	288	P
Archidoris pseudoargus	208-210	Thompson, 1966
Onchidoris muricata	300	Franzén, 1955
Armina californica	222-228	P
Hermissenda crassicornis	204-210	P
Planorbarius corneus	720	P
Lymnaea stagnalis	690	P
Lymnaea peregra	550	P
Onchidium damelii	420	P
Succinea ovalis	420	Hickman, 1931

Table 2 (Continued)

Species	Length in μm	Source (P - Present Paper)
Hedleyella falconeri	1140-1400	P
Physa fontinalis	375	P
Physa gyrinus	350	P
Achatina fulica	750	P
Helix aspersa	655	P
Helix pomatia	850	P
Ariolimax columbianus	265	P
Eledone moschata	195	Franzén, 1967
Loligo forbesi	69	Franzén, 1955
Loligo pealii	50	Austin *et al.*, 1964
Loligo opalescens	51-54	P
Octopus dofleini	500	Martin *et al.*, 1970

4.2 μm in length; it was divided externally into 3 regions clearly visible with phase-contrast microscopy (Pl. 5). In a late spermatid, in which the nucleus is still swollen, having as yet not become completely condensed, the anterior acrosomal moiety and the posterior mitochondrial moiety could be readily distinguished (Pl. 5, s). This mitochondrial middle piece consists of 4-6 globular mitochondria (5-6 according to Personne & Anderson, 1970) surrounding the centriolar cone, from which the simple flagellum takes its origin. After such spermatozoa have been exposed to egg-water the acrosome can be seen to have discharged (Fig. 2), giving rise to a 1 μm acrosomal filament. These observations were confirmed using the slightly smaller gametes of *Gibbula umbilicalis*, and are in line with observations by Dan (1956) on other archaeogastropods (*Scutus*, *Turbo*, *Tegula*, *Monodonta*, *Calcar*, *Lunella* and *Clypidina*). In normal fertilization of marine invertebrates, this acrosomal reaction plays a key role in species-specific recognition, accomplished at the sub-cellular level in primitive molluscs.

The spermatozoa of chitons, also externally fertilizing forms, are rather similar, in that the flagellum is again rather simple and placed in contact with the mitochondria at the centriolar cone. The length of the spermatozoon of *Acanthochitona crinitus*, for instance, is approximately 65 μm, of which the head constitutes 10 μm (Pl. 2H). Approximately 1/2 of the head-length is taken up by the slender, tapering acrosome (described previously for *Lepidochitona* by Retzius (1906) and Rothschild & Tyler (1955)), which in the chitons does not alter appreciably during egg-water tests in the laboratory. The 4 globular mitochondria lie asymmetrically at the rear of the nucleus; these organelles are easily displaced.

The spectacular acrosomal reaction of some bivalve mollusc sperm is now well documented, especially in *Mytilus* (Niijima & Dan, 1965; Galangau, 1969), and in *Barnea* (Pasteels & Harven, 1962) in which the gametes are in many ways similar to those of the gastropod *Gibbula*, described above. In the North American bivalve *Transennella tantilla*, however, the proportions of the various parts of the head are strikingly different (Fig. 2). The head is 17-18 μm in length, occupying nearly 1/4 of the total length of the cell. But the nucleus itself is of normal size and shape, about 2.4 μm in length, while the undischarged acrosome is fully 15 μm in length. The mitochondrial middle piece is extremely small, only 1 μm long. This gamete resembles morphologically that of a mesogastropod rather than that of *Mytilus* or *Gibbula*.

These gametes described above are very simple in plan and are found, as Franzén (1955) has stressed, in externally fertilizing molluscs. The spermatozoa of cephalopods

are of the same general kind except in *Octopus dofleini martini*, however, even though these advanced forms have evolved a system of courtship and copulation. In *Loligo opalescens* (Fig. 2), for example, the proportions of nucleus, mitochondrial middle piece and flagellum (Martin *et al.*, 1970) are similar to those encountered in, for instance, *Gibbula* or *Mytilus*. There are important differences, however. It can be seen from the diagram (Fig. 2) of *Loligo opalescens* that the mitochondrial moiety (forming a spur in many cephalopods, but not in *Octopus dofleini* (Martin *et al.*, 1970)) and the centriolar cone are asymmetrical and, to a great extent, structurally independent of one another. No acrosome could be detected by optical microscopy, although known to be present in *Octopus vulgaris* (Galangau, 1969) and in *O. dofleini* (Martin *et al.*, 1970). A diminution in the importance and size of the acrosome would be expected in animals such as cephalopods in which species-specific recognition occurs as the result of adult and spermatophoral physiological and behavioural factors, rather than at the level of the cell or of sub-cellular constituents, as occurs in non-copulating molluscs.

In the cephalopods the evolution of spermatophoral packaging during copulation, and the concomitant lack of need for spermatozoan flagellation during the act of transfer, or for dynamic acrosomal participation in species-specific recognition, have led to the retention of a male gamete of an apparently rather primitive type.

In higher molluscs of the Gastropoda, however, the evolutionary acquisition of systems of copulation, and, in the highest forms, of functional simultaneous hermaphroditism, has been accompanied by radical changes in the structure of the spermatozoa. From the examples shown us by the cephalopods, we might expect the loss of the acrosome and the retention of a simple flagellum and its fuel-system, the short mitochondrial mid-piece. Instead, we find the acrosome to be retained and even greatly enlarged, as in *Theodoxus* and its allies (Retzius, 1906; Hanson, Randall & Bayley, 1952; Galangau, 1969; Giusti, 1969; personal observations), while the mitochondria and flagellum have increased tremendously in importance. The mitochondria may form prominent spiralling ridges, while their cristae become transformed in various ways (André, 1962), increasing the intimacy of their association with the axoneme of the flagellum, and the axoneme itself may become transformed from the primitive 9 + 2 arrangement to the 9 + 9 + 2 system characteristic of the higher (internally fertilizing) vertebrates (Bradfield, 1955) and of many insects (for instance, in the fire-ant *Solenopsis* (Thompson & Blum, 1967)). As Fawcett & Phillips (1970) point out, there is currently a concensus of opinion that such outer "coarse" $_{Y}$ fibres represent additional motor elements which have evolved in connexion with spermatozoan locomotion in a more viscous medium. The nucleus remains the least modified structure in these higher gastropods although it may become pierced throughout its length by the flagellum (Retzius, 1906; Walker & Macgregor, 1968; Galangau, 1969). Moreover, it will be seen that in *Cipangopaludina* (Yasuzumi & Tanaka, 1958), *Aplysia*, *Umbraculum* and many other euthyneurans, the nucleus itself becomes helically coiled, a phenomenon found elsewhere in the insect *Dahlbominus* (Wilkes & Lee, 1965), in some fish and birds (Stanley, 1971; McFarlane, 1963) and in the toad *Xenopus laevis* (personal observations).

As the structures derived from the spermatid mitochondria became enlarged in the spermatozoa of higher gastropods, so too does the amount of food material enclosed within the gametes during late spermiogenesis. In some cases the predominant food reserve of ripe autosperms has been identified as glycogen (Personne & André, 1964; Anderson & Personne, 1970). What purpose such reserves possess during the normal functioning of the reproductive organs is far from clear. In internally fertilizing Mollusca it might be expected that exogenous sources of energy, like the fructose of mammalian seminal plasma, would be needed, but not endogenous mitochondrial

glycogen. It is only in gametes of externally fertilizing animals that the metabolic substrates must all be endogenous.

It is also strange that modifications, such as the 9 + 9 + 2 axoneme, the greatly elongated tail, and the posterior extension and intimate disposition of the mitochondrial derivatives, should be found in those very gastropods which, because they possess behavioural and mechanical devices designed to bring about internal fertilization, make the least demands on the locomotory powers of their male gametes. These and other observations lead to the recognition of a remarkable paradox, namely, that in those molluscs in which sperm motility might be considered important, the gametes have a small flagellum of the 9 + 2 type, tiny mitochondrial fuel-stores and the necessity to move considerable distances through a hostile external medium. On the other hand, in the majority of those molluscs in which the male gametes have need of their own means of propulsion solely during the moments during which they penetrate the protective investments of the egg, the spermatozoa are equipped with a greatly enlarged flagellum of the 9 + 9 + 2 type and relatively enormous mitochondrial and other fuel-stores.

The remainder of this paper will be devoted to a description of some of the structural details of the spermatozoa of higher gastropods. At the present time they do not enable the resolution of the paradox outlined above. They may, however, contribute to the accumulation of the essential basic functional morphological information. What is next needed is more information about the behaviour of the spermatozoon while it is actually approaching and entering the egg, together with an analysis (in media of a controlled range of viscosities) of the pattern of utilization of the endogenous metabolic substrates present in the allosperms of the euthyneuran gastropods.

EUTHYNEURAN SPERMATOZOA

A. BULLOMORPHA

Acteon tornatilis (Fig. 1; Pls. 3B, 4)

Each spermatozoon from the vesicula seminalis measured approximately 230 μm in life, of which the head accounted for 4 μm (including a 2 μm long acrosome). The head exhibited a helical twist of about 2 full turns (Pl. 3B). After staining with acridine orange, live gametes gave a strong green emission detected with the fluorescence microscope, but the acrosome did not under any circumstances fluoresce. If subjected to hypertonic sea water or other serious osmotic stress, the nucleus readily exploded, showing the true shape of the acrosome (Pl. 4A), and revealing that the centriolar region of the flagellum normally fits into a pit (1 μm in depth) in the rear of the nucleus.

The tail is divided into a mitochondrial mid-piece and a posterior mitochondria-free tail-piece (Fig. 1; Pl. 4B). This division was not detectable by optical microscopy and was therefore missed by Franzén (1955). Another important difference along the tail is that the mid-piece is ensheathed by 2 unit-membranes (Pl. 4C, E) whereas the tail-piece has only 1 unit-membrane. The morphogenesis of this remarkable phenomenon would be of considerable interest. In the mid-piece, 4 mitochondrial derivatives run a spiral course (Pl. 4A, ms) around the axoneme, which is itself ensheathed by a strong, closely adherent membrane, and consists of 9 doublets surrounding a central pair. Some evidence was obtained that coarse γ fibres were present outside the doublets, but only in the initial proximal region of the axoneme. The diameter of the axoneme was (in sectioned material) 0.25 μm, approximately equal to the maximal girth of each of the 4 major mitochondrial derivatives.

The 4 mitochondria are greatly elongated (Fig. 1, md; Pl. 4G, ms). They originate in the neck of the gamete and spiral around the axoneme for varying distances (Fig. 1).

In the neck, the 4 moieties can be distinguished but at a level approximately 60 μm down the tail only 2 moieties are present, and after a further 60 μm only 1 mitochondrial ridge spirals around the tail, having a crest to crest length of 2.6-2.8 μm (Fig. 1). So far as fine-structure is concerned, each mitochondrion has some similarity to a somatic organelle, possessing recognizable cristae (Pl. 4C, E, mc), but, towards the rear, each mitochondrion becomes more solid, its lumen being restricted, so that cristae may no longer be found (Pl. 4D). Flattened vesicular structures of unknown significance or homology lie between the mitochondria, (Pl. 4C, E, lm), and may be observed in some longitudinal sections to join the outer membranes of adjacent mitochondria.

Behind the mitochondrial mid-piece of the tail, and marked off from it by a line of disjunction (Pl. 4B, zd), is the tail-piece, through the centre of which runs the axoneme to the tail tip (Fig. 1; Pl. 4F, ax). The girth of the tail is similar in mid-piece and tail-piece regions. In the tail-piece, the axoneme lacks a distinct bounding membrane (Pl. 4D, F), the cell wall consists of only 1 unit-membrane (Pl. 4G, arrowed), and the space around the axoneme is packed with granules, probably of glycogen (Anderson & Personne, 1970).

Bulla ampulla (Fig. 5; Pl. 2G)

The sperm-length overall was 106-115 μm, of which the nucleus took up 8 μm. On its anterior tip was the tiny conical acrosome, less than 1 μm in length. The banana-shaped nucleus smoothly continued the pitch and wavelength of the single mitochondrial spiral keel of the tail. The wavelength of this spiral was 9 μm (Fig. 5). The nucleus was ridged externally, the ridges spiralling around the head (shown diagrammatically in Fig. 5). In fact, ultrastructural observations on sections passing through the sperm-head reveal that 5-11 individual ridges may be present, as indicated in whole-mount preparations (Pl. 2G, hg).

Although only 1 major mitochondrial spiral could be detected on the tail, sections revealed a much smaller, second, subsidiary mitochondrial derivative travelling back from the neck for a short distance. This could not be shown in Fig. 5. The mitochondrial spiral peters out approximately half way back along the tail, leaving 50 μm of the tail at the rear exhibiting no helical structures. At the extreme rear tip, a short length of more or less naked axoneme protrudes conspicuously (Fig. 5).

Hydatina physis (Fig. 5; Pl. 2E) and *Haminea virescens* (Fig. 3).

These gametes, as can be seen from the illustrations, differ only slightly from the spermatozoon of *Bulla ampulla*, described above. As can be seen in Fig. 3, the spermatozoon of *Haminea virescens* is very different from Dupouy's (1960) description of *H. navicula*. Dupouy does not illustrate or mention any helical tail structures, and this omission, together with his claim that these gametes are polymorphic (as is known to occur in certain prosobranch gastropods) urgently requires re-investigation.

B. PYRAMIDELLOMORPHA

Odostomia sp. (Fig. 3; Pl. 8D, E, F)

The length varied greatly, extremes being 750-876 μm, of which the head occupied 7.3 μm. The cylindrical acrosome was about 1.8 μm in length. The slightly curved nucleus led smoothly into the characteristic pitch and wavelength of the single mitochondrial spiral keel. The wavelength was 9.0 μm; there were about 45 helices in all, leaving naked the rearmost 1/2 - 1/3 of the tail. Shoulder-like structures surrounding the neck were prominent features (Fig. 3). Such structures in gastropod sperms are sometimes misleadingly called "ring centrioles." A more elusive feature was a possible intra-nuclear filament, more obvious in some preparations than

others. Fine-structure studies indicate that the appearance of a filament in this situation is in fact spurious.

Sections through ovotesticular spermatozoa (Pl. 8D, E, F) show that vestigial cristae are present in the single mitochondrial derivative (ms) and that numerous membranous vesicles (similar to those described above for *Acteon*) form a packing around the axoneme (Pl. 8E, lm). No glycogen could be detected in any of the preparations.

Odostomia columbianus (Fig. 3).

The spermatozoa of this species were smaller, 250 μm in length, than those of the above, and showed other important differences. The wavelength of the single mitochondrial spiral keel was 6 μm but the spiral consisted of only 3-4 full turns so that by far the greatest length of the tail lacked the mitochondrial sheath. Differences of a minor kind were also evident in both the head and neck (Fig. 3).

These observations strongly support Franzén's (1955) contention that the pyramidellids possess spermatozoa clearly belonging to the euthyneuran type.

C. PLEUROBRANCHOMORPHA

Umbraculum sinicum (Fig. 4; Pls. 6B, 8A)

The overall length of these remarkable gametes was approximately 225 μm, of which the helically disposed nucleus occupied 22 μm. Pl. 8A illustrates that the nucleus (n) spirals around the axoneme (ax), shown diagrammatically in Fig. 4. A cylindrical acrosome, less than 1 μm in length, projected from the front of the spermatozoon. The flagellum travels from the rear of this acrosome to the posterior tip of the tail. The 7 helices of the nuclear spiral are continued smoothly rearwards down the tail by the single mitochondrial spiral keel. The wavelength of these spirals was 3.0-3.5 μm. The mitochondrial keel consisted of about 50 helices. The terminal 35 μm of the tail lacked spiral features and was distinctly swollen (Fig. 4; Pl. 6B, tp). Unfortunately no sections pass through this tail-piece, in the limited amount of material presently available for study, but it is inferred that this swollen region of the tail is homologous with the glycogen-filled tail-piece of *Acteon* (Fig. 1, tp).

Pleurobranchus peroni (Fig. 5; Pl. 8C)

The spermatozoa of *Pleurobranchus* are very different from those described above for *Umbraculum*.

The length overall was 180-190 μm, of which the nucleus accounted for 7-7.5 μm. The acrosome was less than 1 μm in length. The acrosome, nucleus, and tail form integrated parts of a smoothly helical configuration, the pitch and wavelength being rather uniform from 1 end of the cell to the other. The wavelength of these helices was approximately 4.5 μm. The number of helices exhibited by the nucleus was, surprisingly, variable in different specimens, sometimes 1 full turn, sometimes 2 (Fig. 5). The total number of spirals visible along the length of the whole cell was 45-46.

Ultrastructural observations (Pl. 8C) show the nucleus to be ridged (5 prominent ridges were visible in transverse sections through the sperm-head), very different from the circum-flagellar helical nucleus of *Umbraculum* (compare Figs. 4 and 5). The single prominent mitochondrial spiral keel contained granular material, probably glycogen (Pl. 8C, g), and similar material could be found around the axoneme fibres near the neck. The centriolar region of the axoneme is located deep within a conical crypt in the rear of the nucleus.

Berthella plumula

Although rather larger than the spermatozoa of *Pleurobranchus*, gametes of *B. plumula* agree closely, and, like *P. peroni*, are very different from those of *Umbraculum*.

D. APLYSIOMORPHA

This account is based chiefly upon published findings (Thompson & Bebbington, 1969, 1970) dealing with *Aplysia*, but comparative observations have since been made on spermatozoa of other aplysiomorphs. As has been stressed (Thompson & Bebbington, 1970) the spermatozoa of aplysiids have in the past been misinterpreted in various ways, and this is, perhaps, not surprising in view of their structural complexity.

Aplysia spp. (Fig. 6; Pls. 7, 9B)

Three North Atlantic species were investigated; these were *Aplysia depilans*, *A. fasciata* and *A. punctata*. Only minor differences were noted between these species. In overall length the gametes ranged from 155-228 μm. The nucleus is a cylinder, 0.2-0.4 μm in diameter, which forms a helix (Pl. 9B) of 5-7 turns. The nucleus extends to the anterior tip of the head; no acrosome could be detected. The flagellum originates just behind the anterior extremity of the head, and extends over nearly the whole length of the cell. In sections through the flagellum, the familiar 9 peripheral fibre-doublets could be recognised. Radial material extends from each fibre-doublet towards the central pair of fibrils, around which is a set of struts of unknown function. The diameter of the flagellum was approximately 0.22 μm. Two mitochondrial strands spiral around the flagellum; they are disparate in girth. Only the larger strand is clearly visible in live spermatozoa under phase-contrast microscopy; it forms a projecting spiral keel (Fig. 6; Pl. 7, pmd), while the other moiety is detectable only in sectioned material (Fig. 6; Pl. 7, smd). These may be termed the principal and subsidiary mitochondrial derivatives. The former contains quantities of granules (see Thompson & Bebbington, 1969, pl. 8A-E), believed to be glycogen.

Dolabella auricularia (Pl. 8B), *Dolabrifera dolabrifera*, *Bursatella leachi* and *Phyllaplysia taylori*

Optical and electron microscopic studies of these aplysiids showed their gametes to conform to the plan described above for *Aplysia*. One noteworthy feature is that in *Dolabella* (Pl. 8B) regular transverse rungs divide up the principal mitochondrial derivative; these rungs (which are less easy to detect in the other species) are presumably derived during spermiogenesis from the mitochondrial cristae of the spermatid nebenkern.

E. NUDIBRANCHIA

This account is based chiefly upon published findings (Thompson, 1966) dealing with *Archidoris*, but more recent observations on this and other nudibranchs have been added.

Archidoris pseudoargus (Fig. 7; Pls. 1, 9A, 10, 11A).

The appearance of mature spermatozoa under various conditions of optical microscopy is shown in Pl. 1. The overall length is 208-210 μm, of which the banana-shaped head takes up 8-9 μm. Pl. 9A shows the head in lateral view, with the short acrosome on the anterior tip. Samples of autosperms and allosperms were subjected to a variety of tests using preparations of egg-water (employing eggs from the ovotestis)

and controls in sea water, but no acrosomal reaction could be induced. The bulk of the sperm-head was occupied by the nucleus, whose contents were coarsely striated, the long axes of most of the striae being coincident with that of the sperm (Pl. 10). The nucleus was bounded by a nuclear membrane and the whole head ensheathed by the stout cell-membrane, continuous with that of the tail. The superficial spiral filament mentioned and illustrated in my 1966 paper is now thought to be spurious, although the whole head is in life curved in such a way as to hint at a helical pattern (Fig. 7). Details of the centriolar cone are described reasonably accurately in that paper and will not be repeated here.

The tail is illustrated diagrammatically in Fig. 7 and a micrograph of a freeze-etched preparation is shown in Pl. 11A. The cytoplasm of the tail is bounded by a fine spirally striated sheath. The axis of the tail consists of a central fibre-doublet with a ring of 9 peripheral doublets; the diameter of the axoneme in sections is 0.17 μm. The axis is bilaterally symmetrical and the plane of symmetry remains unaltered along the length of the tail. The spirally keeled mitochondrial derivative (Fig. 7; Pl. 11A) commences just behind the head and winds (in a clockwise direction when viewed from the front) to the tip of the tail. The wavelength of the spiral varies from 5 to 11 μm after different methods of preparation for electron microscopy, but is constant along any individual sperm-tail. The crest to trough amplitude also shows individual variation; but superimposed upon this is a diminution in amplitude from neck to rear. The mitochondrial derivative possesses a lumen, 0.25 μm wide at its maximum, filled after fixation with a loosely coagulated material, not glycogen granules.

Observations on activation, behaviour and storage of spermatozoa of *Archidoris* have been published elsewhere (Thompson, 1966).

Tritonia festiva (Fig. 8; Pl. 2F), *Dendronotus iris* (Fig. 8), *Cadlina laevis* (Fig. 8), *Armina californica* (Fig. 9) and *Hermissenda crassicornis* (= *H. opalescens*) (Fig. 9)

The illustrations show a close similarity in these nudibranchs, selected as examples from all the major subdivisions of the group, to the spermatozoa of *Archidoris pseudoargus*. Of course, sizes and proportions vary from species to species, but the basic plan remains, in the nudibranchs, the same. Only the shape of the acrosome shows significant variation. In the majority of the nudibranchs this structure forms a short, straight rod, as in *Archidoris*, but in some species, for instance, of *Hermissenda* and of *Dendronotus*, the acrosome may be helically disposed. In *Dendronotus iris* (Fig. 8) a proportion of the gametes have a helical acrosome, while in the remainder this organelle is straight; the significance of this remarkable dimorphism is not understood. In *Hermissenda crassicornis* is found another feature of uncertain importance; the mitochondrial helix terminates approximately 50 μm from the tail tip (Fig. 9).

F. PULMONATA

Planorbarius corneus (Fig. 10; Pls. 2B, 3C, 12, 13A), *Physa gyrinus*, *P. fontinalis* (Pl. 11C), *Lymnaea peregra* and *L. stagnalis* (Fig. 11; Pl. 11B)

In these basommatophoran species, already the subjects for productive research (Selman & Waddington, 1953; Anderson & Personne, 1970), the spermatozoa appear to show a high degree of uniformity.

In *Planorbarius corneus*, for example, the length overall was 720 μm, of which the tiny head accounted for only 6.5 μm, including the 1.5 μm acrosome. The nucleus had a spiral twist (Fig. 10) as well as bearing superficial helical ridges and grooves (Pl. 2B, hg). The centriolar cone fits into a deep pit situated in the rear of the nucleus (Fig 10). The axoneme, with its basic pattern of 9 + 2 elements (9 + 9 + 2 just behind the head, as shown in Pl. 12), is ensheathed by a thick layer of granular material

(glycogen), through which spiral numerous organelles (Pl. 13A, ms). None of these stands out to form a spiral keel of the type found in the Opisthobranchia, but the largest and most conspicuous are a pair of strong mitochondrial elements (Fig. 10; Pls. 12, 13A). Numerous other elements, probably also mitochondrial derivatives, spiral with these and may be studied in freeze-etched preparations.

In other species, only minor differences could be discovered. In *Lymnaea stagnalis* (Fig. 11; Pl. 11B), for example, the nucleus was not markedly spiral in overall shape, and the superficial helical grooves were exceptionally shallow. Such differences are essentially quantitative rather than qualitative. Perhaps more important is the fact that in certain species (*Lymnaea peregra*, for example) a glycogen-filled tail-piece may be found, posterior to the region of spiralling mitochondrial derivatives.

Achatina fulica, *Helix pomatia* (Fig. 11; Pls. 6A, 13B, 14A, B), *Onchidium damelii* (Pl. 2C), *Ariolimax columbianus* (Fig. 11; Pl. 2D) and *Hedleyella falconeri* (Fig. 10; Pl. 3A)

In the Stylommatophora there is an astonishing amount of variability of sperm type, more than has been found in any other comparable group of molluscs. They range from gametes which resemble those of the aplysiids (as in *Ariolimax*), through some which superficially recall those of Basommatophora (as in *Hedleyella*), to the streamlined nudibranch-like spermatozoa of the higher stylommatophorans (such as *Helix*). Bayne (1970) was certainly in error when he wrote that in general the spermatozoa of pulmonates are "practically identical."

In *Helix pomatia*, the overall length of the spermatozoon was approximately 850 μm, of which the head took up 12 μm, including the tapering acrosome 2 μm in length. A single mitochondrial spiral travels back from the neck to the tail tip. These helices have a wavelength of approximately 20 μm. The axoneme (consisting proximally of 9 + 9 + 2 elements, distally of only 9 + 2, according to Grassé *et al.*, 1956) is surrounded by densely granular periaxial material (glycogen), in which are located a spiralling series of pits. Into these pits fit similarly disposed pegs projecting inwards from the outer case of the sperm-tail, as shown in Pl. 14A, B. The shape and some details of the texture of the material constituting the helical principal micochondrial derivative are displayed especially well by the freeze-etching method (Pl. 14A, B). The elongated, banana-shaped head bears faint superficial spiral markings. The gametes of *Onchidium damelii* and *Achatina fulica* were, except for details of size and proportion, rather similar to those of *Helix*.

The spermatozoa of *Hedleyella falconeri* are the longest possessed by any mollusc, measuring 1140-1400 μm, of which the head accounts for only 10 μm, including an acrosomal projection 1.5 μm in length. The nucleus exhibited several helical superficial ridges and grooves (Pl. 3A, hg), clearly visible with light microscopy. These grooves, which were 0.6 μm apart, continued smoothly into the neck blending with the spiral ridges surrounding the tail (Pl. 3A, ms). The tail ridges, believed to be mitochondrial derivatives by analogy with what is known of other euthyneuran gametes, are 4 in number (Fig. 10 md 1-4) for approximately 230 μm, but thereafter 3 of these moieties peter out so that the remainder of the flagellum is surrounded by only 1 spiralling ridge (Fig. 10).

The gametes of the American N.W. Pacific forest slug *Ariolimax columbianus* provide a useful comparison and gave quite close agreement with the work of Bayne (1970) on the fine-structure of a European species of related slug. In *A. columbianus* the overall length was 265 μm, of which the helically disposed nucleus occupied 11 μm, including the 3 μm anteriorly situated acrosome (Fig. 11). An anterior prolongation of the nucleus accompanies the acrosome and is shown in Pl. 2D. Overlapping the middle and rear part of the nuclear helices are a pair of mitochondrial derivatives which continue rearwards down the tail, winding round the flagellum. The total number of spirals counted along the whole length of the gamete was 63-64.

CONCLUSIONS

In the Euthyneura, *Acteon* shows the basic type of spermatozoon from which the others may have been derived. In *Acteon*, each spermatozoon possesses 4 distinct mitochondrial derivatives which pursue a spiral course around the flagellum. These all exhibit rung-like lamellar cristae. A posterior non-helical tail-piece contains endogenous food-stores in the form of closely packed glycogen granules.

In scattered examples from higher groups of Euthyneura (*Umbraculum*, *Lymnaea*) such a discrete tail-piece is retained, but in most other euthyneuran spermatozoa the tail-piece has been abolished and the glycogen is contained within 1 or more of the helically wound mitochondrial derivatives. The entire length of the tail or principal-piece in the higher Euthyneura corresponds to the middle piece of *Acteon*.

Endogenous food-reserves are most conspicuous in the Pulmonata and in the lower opisthobranchs and least developed in the Nudibranchia.

In *Acteon* the tail-piece is surrounded by a single unit-membrane, but in the mitochondrial middle piece there are 2 such discrete membranes. The morphogenesis of this remarkable difference is obscure, as also is the situation in other gastropods.

In *Acteon* the nucleus exhibits incipient helical coiling. In scattered examples among the higher Euthyneura (*Aplysia*, *Umbraculum*, *Ariolimax*) this is exaggerated and the nucleus in some of these forms has come to be wound around the centriolar cone. The tendency towards nuclear coiling, like that towards the possession of various helical configurations in the tail, is a characteristic of euthyneuran sperm in general.

In the higher Opisthobranchia a trend is detectable towards a reduction in the number of mitochondrial derivatives visible along the tail, so that in *Aplysia* there are only 2 (one of these is vestigial), while in the nudibranchs there is only 1 principal mitochondrial derivative.

In the Pulmonata a trend is detectable towards an increase in the number of separate mitochondrial helices, up to a maximum of 7.

In some euthyneuran orders (for instance, the Basommatophora, Aplysiomorpha and the Nudibranchia) the spermatozoa show a relatively uniform morphology, whereas in others (for instance, the Pleurobranchomorpha or the Stylommatophora) there is a great deal of heterogeneity.

Gross sperm-morphology is useful in the taxonomy of gastropods only in allocating dubious forms to either the Streptoneura or the Euthyneura, so that such criteria clearly confirm the euthyneuran affinities of the Pyramidellomorpha. It is not useful in attempts to decide, whether, for instance, the Onchidiidae or the Succineidae are opisthobranchs or pulmonates.

The greatest areas of ignorance at present surround the function of the endogenous food-reserves of euthyneuran spermatozoa, the hydrodynamics *in vivo* of external form in these helically wound gametes, the behaviour of gastropod male gametes during egg-penetration and amphimixis and the function of the acrosome in internally fertilizing molluscs.

ACKNOWLEDGEMENTS

I am deeply grateful for help at various stages of this work to Mr Alan Britton, Mrs J. Milton and Mr G. H. Brown. My colleague Mr W. L. Maxwell has kindly read and commented helpfully on the paper during its preparation. This research has been supported by grants from the Royal Society, the Leverhulme Trust and the Science Research Council.

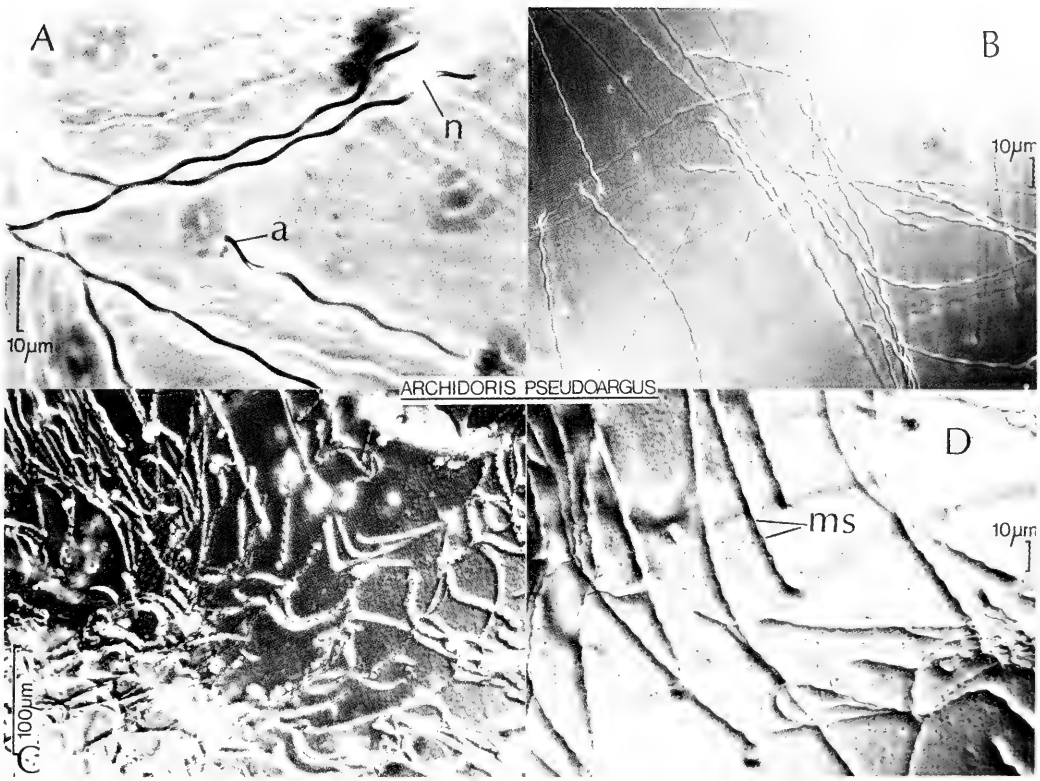


PLATE 1. Optical microscopy of *Archidoris pseudoargus* spermatozoa.

A, Wild phase-contrast x100 oil; sperm in sea water.

B, Zeiss Nomarski x40; sperm in sea water.

C, Zeiss Nomarski x16; sperm drying in a bubble.

D, Zeiss Nomarski x40; sperm drying in a bubble.

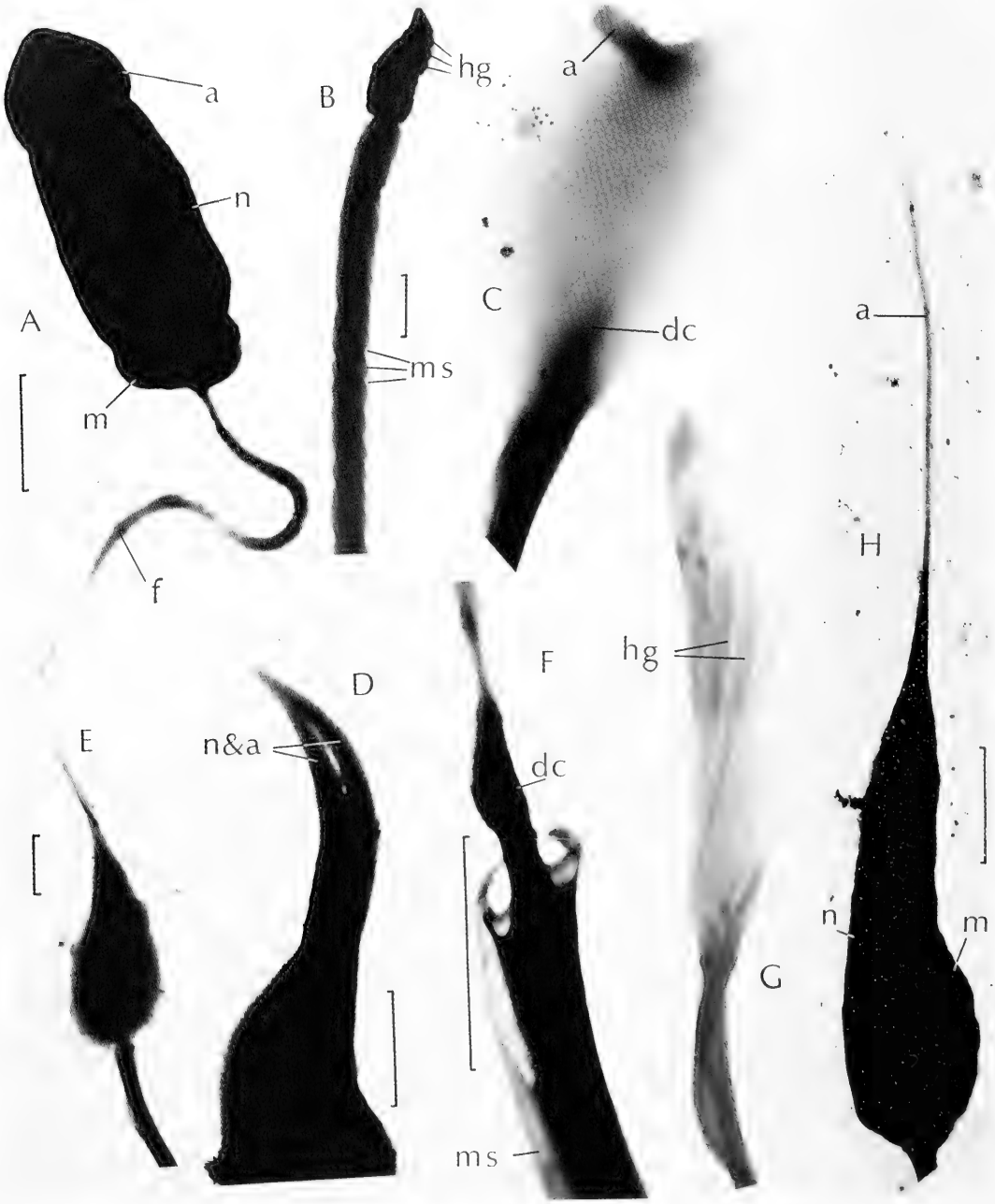


PLATE 2. Electron micrographs of head structures of chiton and gastropod spermatozoa, dried in the vapour of osmic acid or formaldehyde. The scale in each case represents a true 1 μm.

A, *Gibbula cinevaria*; B, *Planorbarius corneus*; C, *Onchidium damelii*; D, *Ariolimax columbianus*; E, *Hydatina physis*; F, *Tritonia festiva*; G, *Bulla ampulla*; H, *Acanthochitona crinitus*

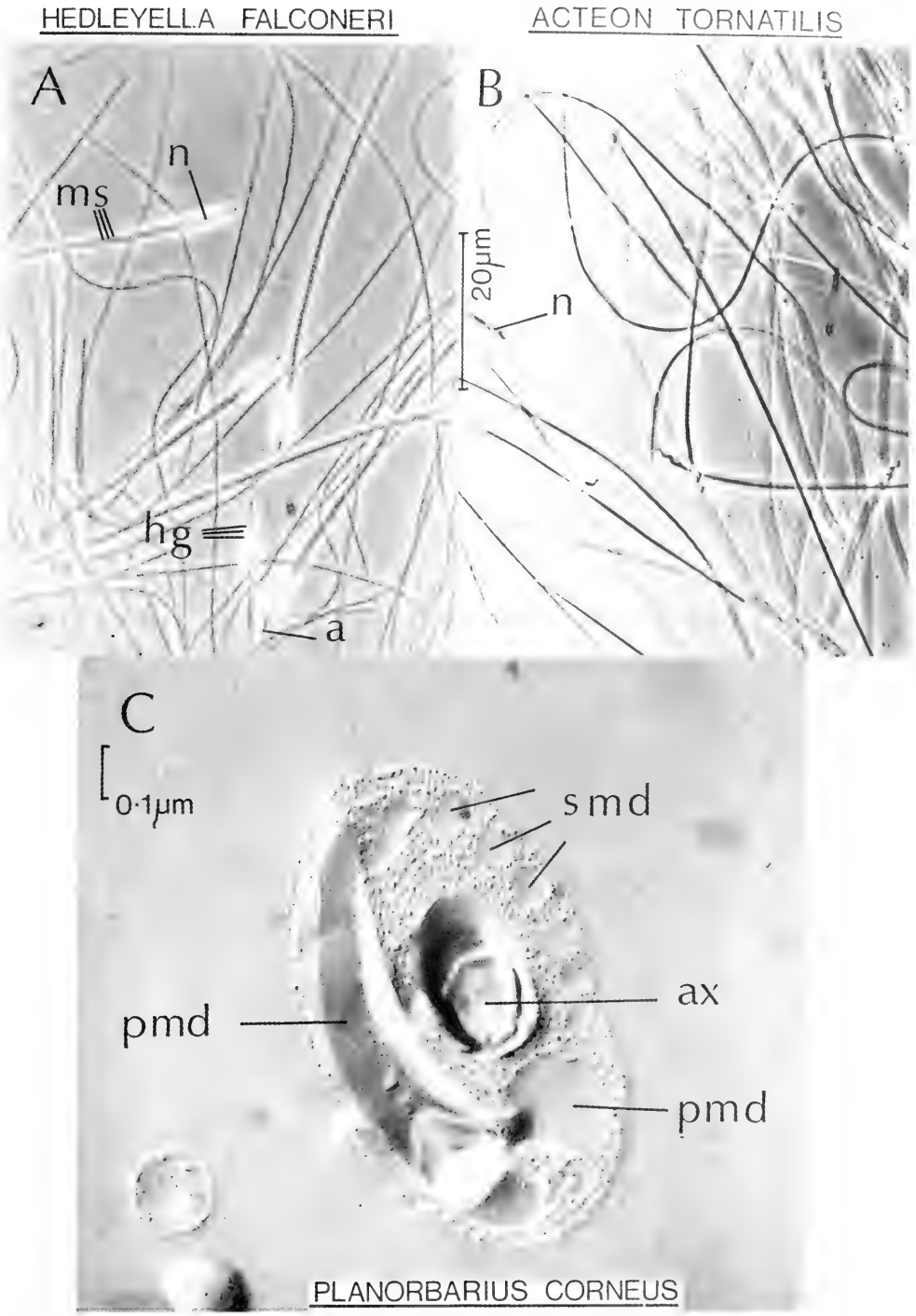


PLATE 3. Spermatozoa of euthyneuran gastropods.

A, phase-contrast optical micrograph, *Hedleyella falconeri*; B, phase-contrast optical micrograph, ***Acteon tornatilis***; C, electron micrograph of a freeze-etched replica, *Planorbarius corneus*.

PLATE 4. Electron micrographs of spermatozoa from *Acteon tornatilis* taken from the wide hermaphrodite duct (=vesicula seminalis). The scale in each case represents a true 1 μm.

A, whole spermatozoan head, dried in osmic acid vapour; the nucleus has disintegrated, revealing the more durable acrosome and distal centriole. Four mitochondrial derivatives of equal size spiral around the flagellum.

B, whole spermatozoon, region of disjuncture between the middle and tail-pieces.

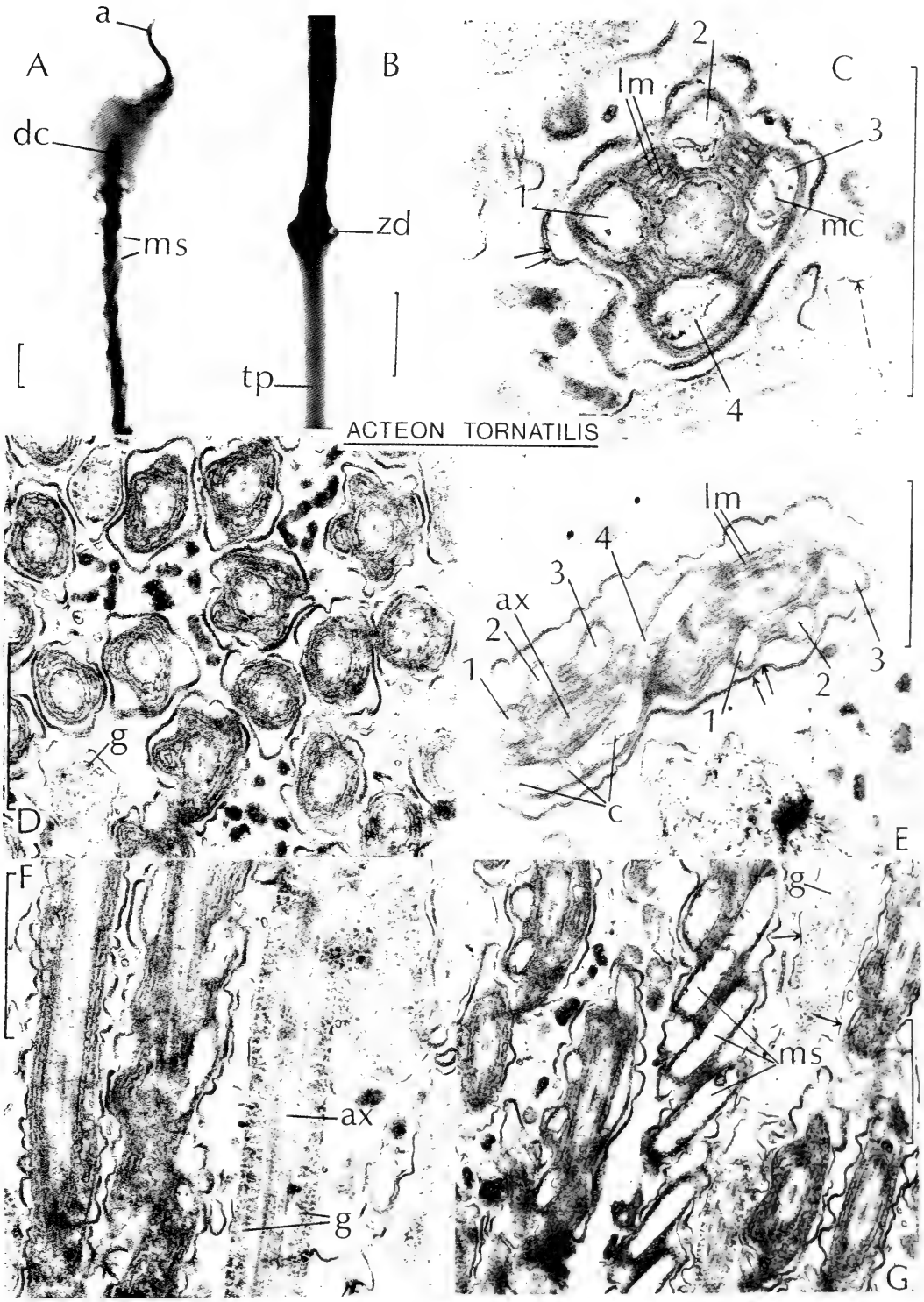
C, transverse section through the tail just behind the head, showing the 4 equal mitochondrial derivatives (numbered) with their distinct cristae. The cell membrane is double, i.e., consists of 2 unit membranes (solid arrows). By contrast, in an oblique L.S. of part of the tail-piece of another spermatozoon, the cell membrane may be seen to consist of only 1 unit membrane (interrupted arrow).

D, transverse sections through numerous sperm-tails, mostly through the mid-piece, (showing 4, 3, 2 or 1 mitochondrial derivatives), 2 passing through the tail-piece and showing the periaxial layer of glycogen.

E, longitudinal sections through part of a sperm-tail in the mid-piece, showing typical cristae and the flattened lamellae that run between the 4 mitochondrial derivatives.

F, longitudinal sections through sperm-tails, the 2 on the left being through the mid-piece, the others through the tail-piece and showing the periaxial layer of glycogen.

G, longitudinal sections through sperm-tails, showing the mitochondrial spirals, and the glycogen layer of a section through a tail-piece, with its single cell membrane (arrowed).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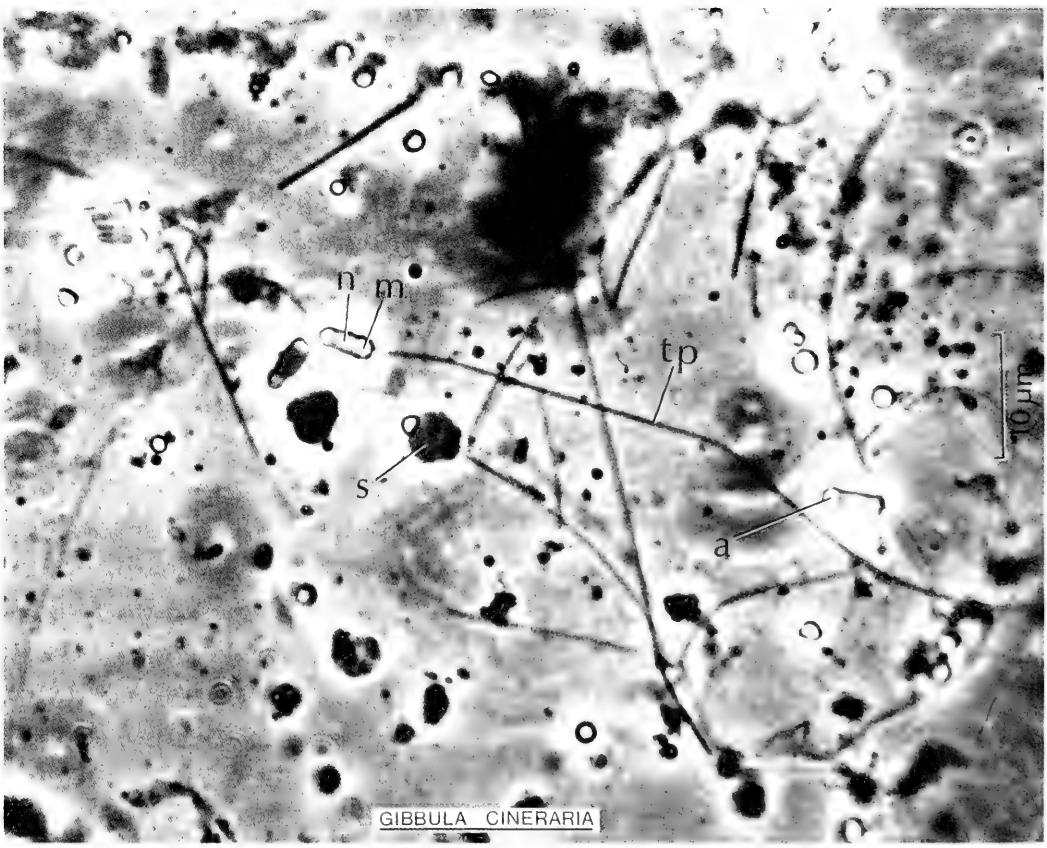


PLATE 5. Optical micrograph (phase-contrast) of living spermatozoa and late spermatids of *Gibbula cineraria*.

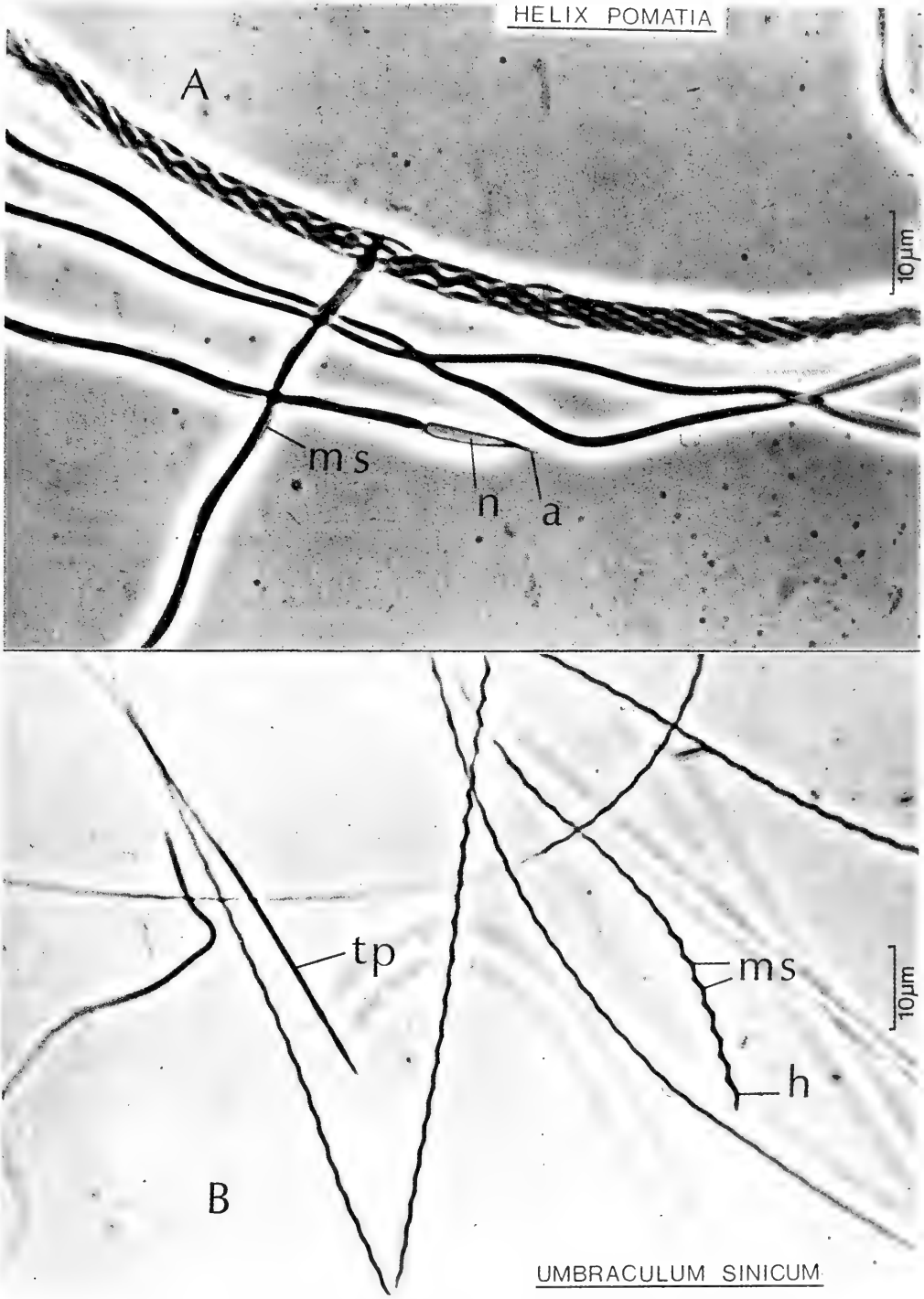


PLATE 6. Optical micrographs (phase-contrast) of living euthyneuran spermatozoa.

A, *Helix pomatia*; B, *Umbraculum sinicum*

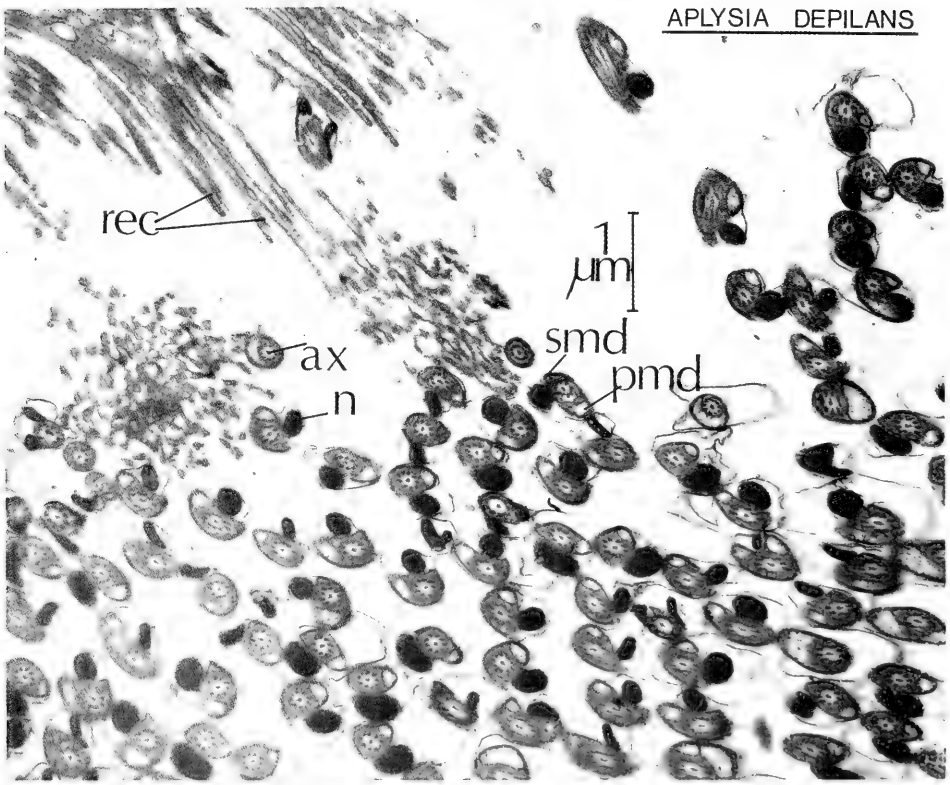
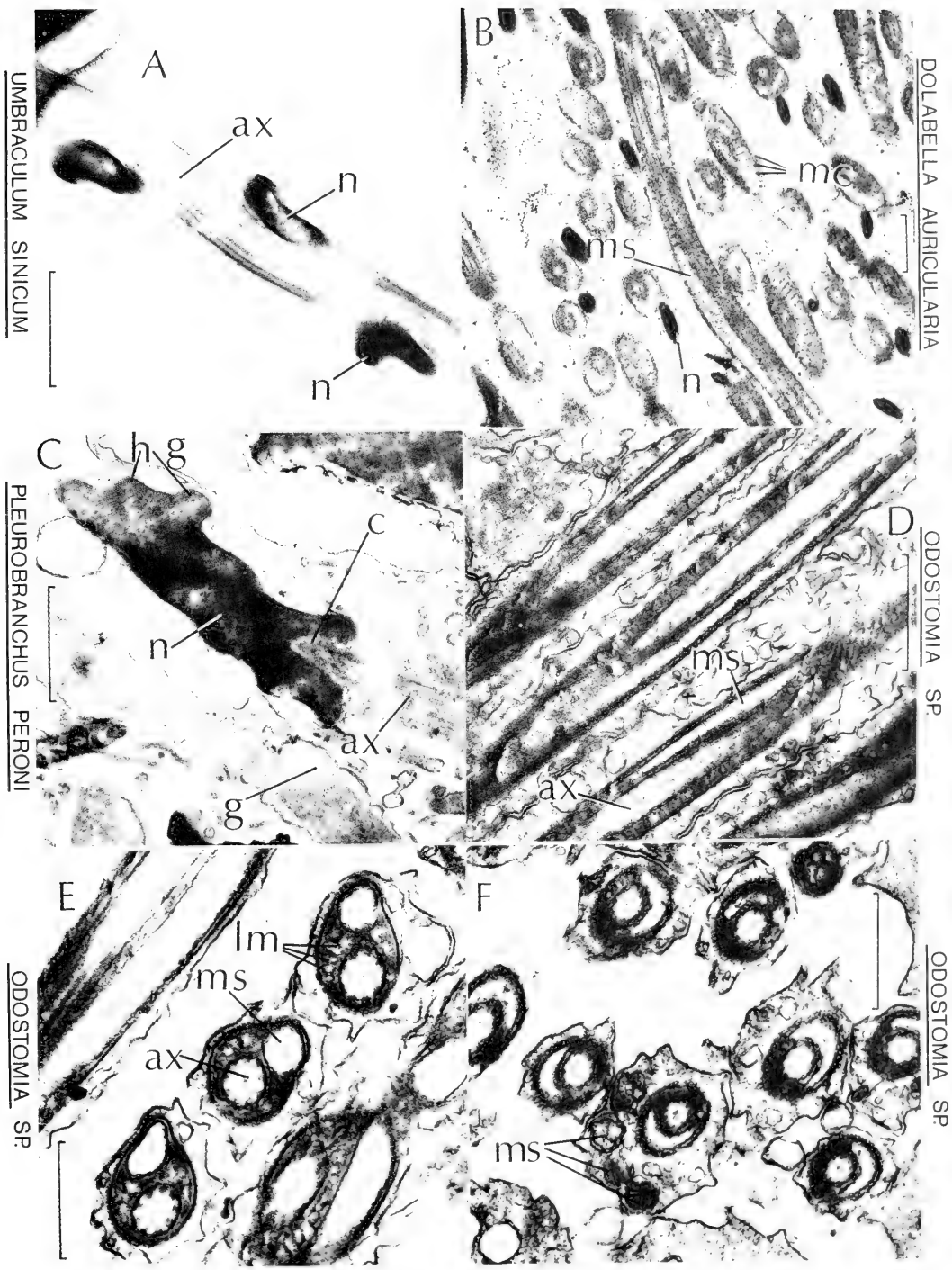


PLATE 7. *Aplysia depilans* allosperms. Section through the receptaculum seminis of a mated specimen, showing many sperm-heads cut transversely. The head contains 2 mitochondrial derivatives (of disparate sizes) and the nucleus, spiralling around the axoneme.

PLATE 8. Electron micrographs of sections through spermatozoa of Euthyneura. The scale in each case represents a true 1 µm.

A, longitudinal section through part of the head of a seminal vesicle autosperm of *Umbraculum sinicum*, showing the nucleus spiralling around the axoneme. B, sections through allosperms in the receptaculum seminis of a mated adult *Dolabella auricularia*, showing a single mitochondrial derivative, with conspicuous transverse cristae spiralling around the axoneme. Several sperms are sectioned through the head and show the helical nucleus at various levels. C, section through the vesicula seminalis of *Pleurobranchus peroni*, passing longitudinally through a nucleus with its conspicuous post-nuclear embayment within which the centrioles are situated. D-F, various sections through the ovotestis of a mature *Odostomia* sp. from the Pacific N. W. of the United States of America showing various features of spermatid fine-structure.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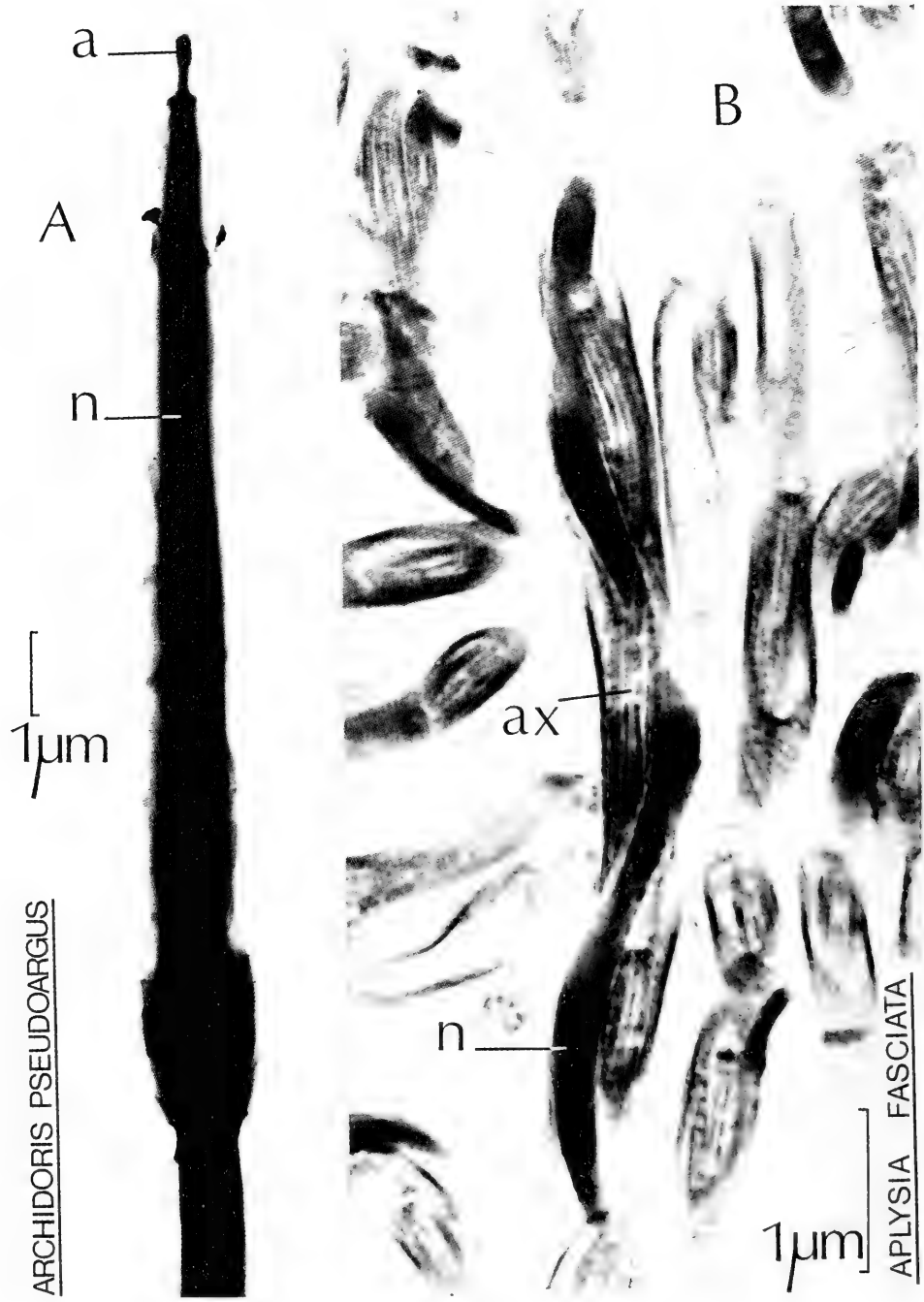

PLATE 9. Spermatozoa of euthyneurans.

A, whole head of autosperm of *Archidoris pseudoargus*, dried in osmic acid vapour.
B, section through allosperms of *Aplysia fasciata*, showing the nucleus spiralling around the axoneme in the head region.

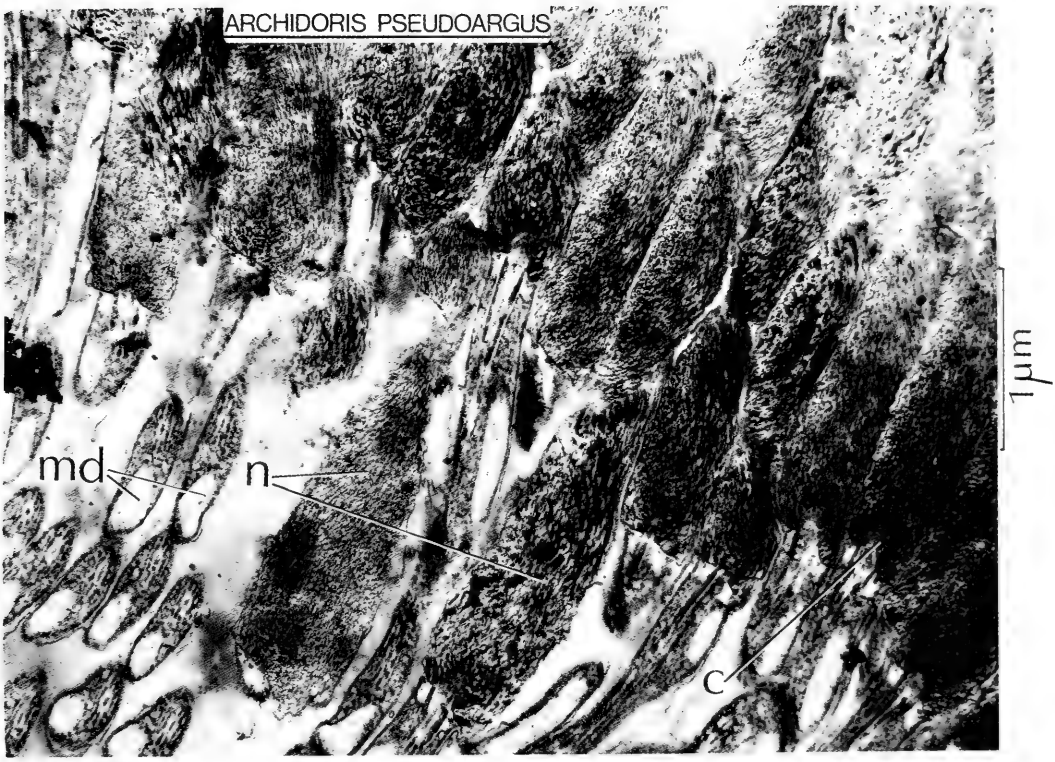

PLATE 10. *Archidoris pseudoargus* allosperms. Section through the receptaculum seminis of a mated specimen, showing masses of orientated spermatozoa with nuclear material condensed into coarse longitudinal threads and the post-nuclear recess containing the centrioles. The tail contains the axoneme with the helically wound single mitochondrial derivative (md).

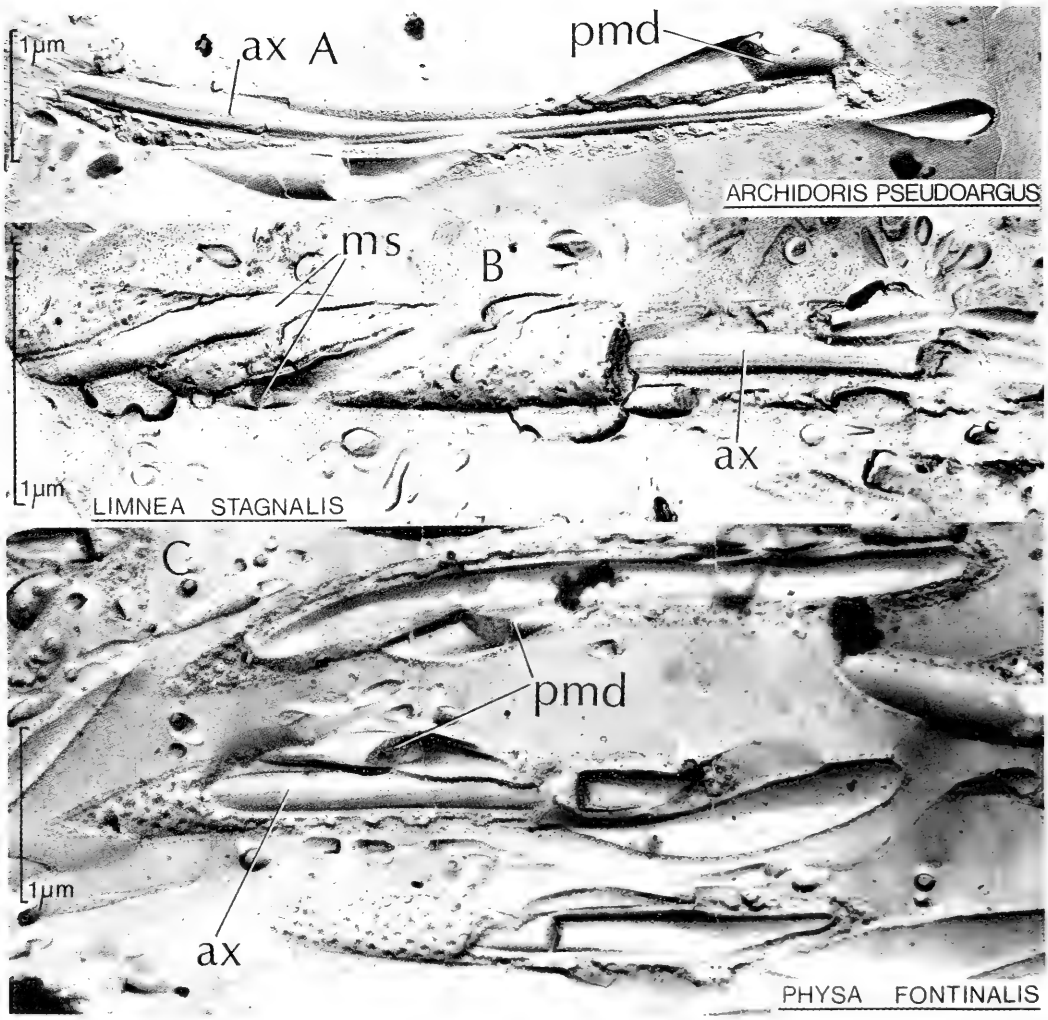

PLATE 11. Electron micrographs of freeze-etched replicas of seminal vesicle autosperms of euthyneuran gastropods, showing details of the helical configuration of the tail and the pustular texture of the periaxial packing material.

A, *Archidoris pseudoargus*

B, *Lymnaea stagnalis*

C, *Physa fontinalis*

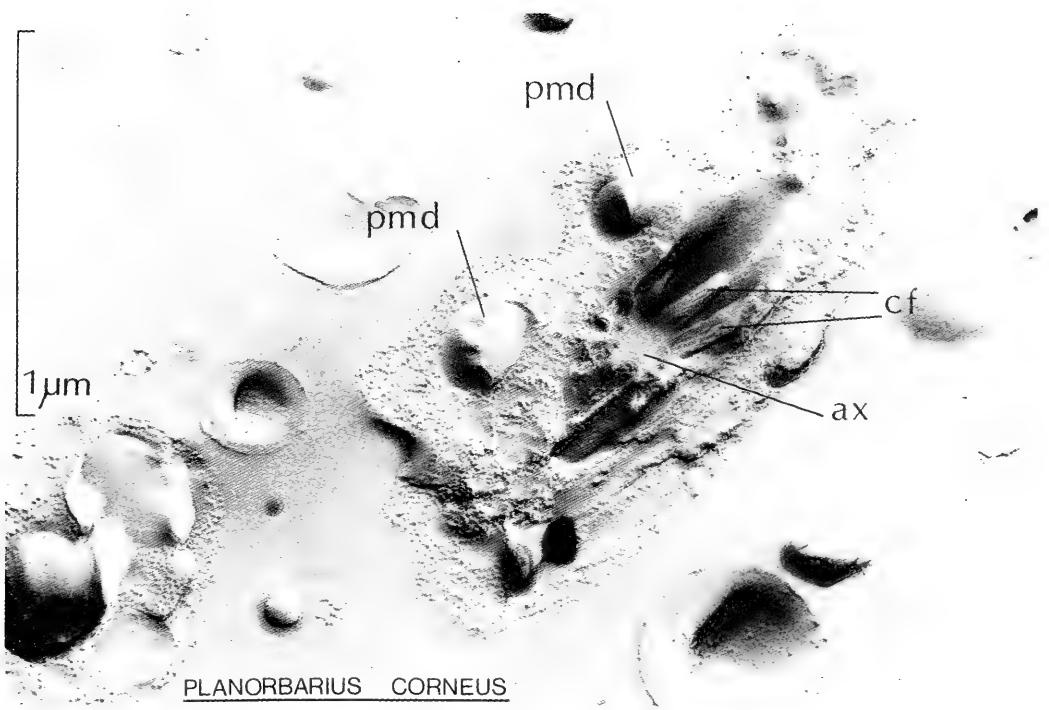

PLATE 12. Electron micrograph of a freeze-etched replica of autosperms of *Planorbarius corneus*. The specimens show structures of the tail region, just behind the neck.

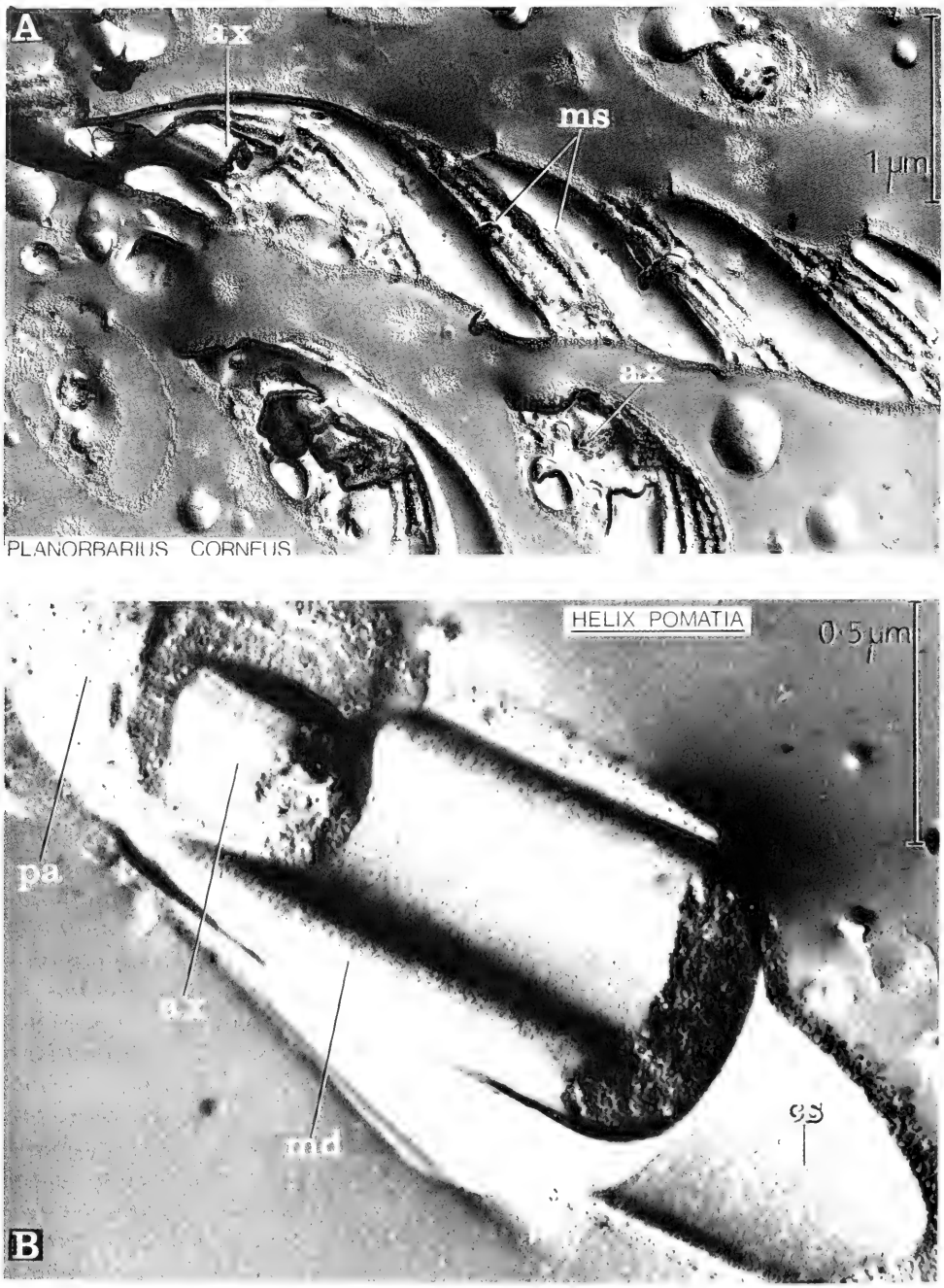

PLATE 13. Electron micrographs of freeze-etched replicas of seminal vesicle autosperms of euthyneuran gastropods, showing details of helical structures in the tail.

A, *Planorbarius corneus*
B, *Helix pomatia*

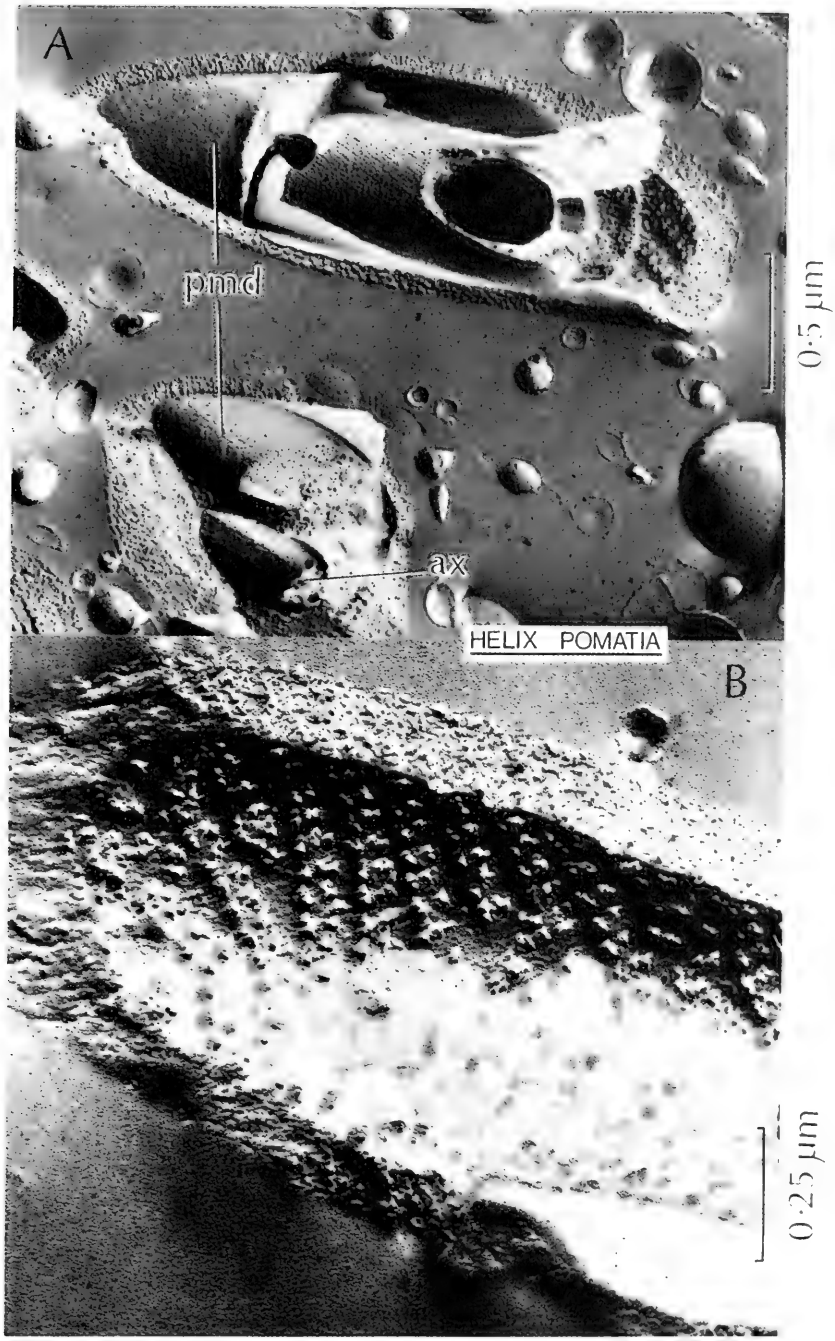

PLATE 14. Electron micrographs of freeze-etched replicas of autosperms of *Helix pomatia*.

A, showing 2 spermatozoa exposed in the tail region; B, showing the interior surface of the periaxial material with its characteristic pustulose appearance.

ABBREVIATIONS USED IN THE ILLUSTRATIONS

a, acrosome; ax, axoneme; c, centriolar area; cf, coarse γ fibres; cs, cell sheath; dc, distal centriole; f, flagellum; g, glycogen; h, head; hg, helical grooves; lm, lamellae; mc, mitochondrial cristae; md, mitochondrial derivative; ms, mitochondrial spirals; n, nucleus; pa, periaxial material; pmd, principal mitochondrial derivative; s, spermatid; sm, mitochondria of spermatid; smd, subsidiary mitochondrial derivative; sr, superficial ridges; tp, tail-piece; zd, zone of disjunction.

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ADDENDUM

Since this paper was prepared, further information has been obtained relating to the fine structure of spermatozoa of *Acteon tornatilis*. These gametes had presented many puzzling features, especially concerning the nature and homologies of the various unit-membranes along the tail. It has now proved possible to obtain and study longitudinal sections through the crucial areas, namely, the neck (Pl. 15)[1] and the zone of disjunction between the mitochondrial mid-piece and the tail-piece (Pl. 16). Slight osmotic swelling during the fixation of these preparations has clarified the relationships between the various membranes. The micrographs (Pls. 15 and 16) show for the first time that the inner unit-membrane of the mid-piece sheath is continuous, both in the neck and at the posterior zone of disjunction, with the outermost unit-membrane of the mitochondrial axonemal sheath in the mid-piece. The functional significance of this morphological continuity is not clear, but it may have been dictated by morphogenetic aspects of spermiogenesis. It should be rewarding to study sperm-maturation in *Acteon*. Unfortunately, it is a marine mollusc of sporadic occurrence and living material is difficult to obtain.

In the last 2 years, my colleague Mr. W. L. Maxwell has carried out a survey of spermiogenesis in cephalopod molluscs. His studies on *Eledone cirrhosa* demonstrate a spermatozoon differing from the primitive type in that the head (both nucleus and acrosome) are helically wound, the axoneme possesses a 9+9+2 arrangement of fibrils, and the mature gamete reaches a length of 550 μm. Glycogen deposits occur solely in the tails of the spermatozoa of the octopod *Eledone*. Maxwell's studies on decapods show a range of gamete length from 46 μm (*Loligo forbesi*) to 120 μm (*Eusepia officinalis*). These decapod sperm differ from those of other molluscs in that the mitochondrial portion of the mid-piece is separated from the axoneme by a complex folding of the plasmalemma. There appear to be no glycogen deposits in mature spermatozoa of decapod cephalopods.

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[1]For Plates 15 and 16, see p 443-444.

MALACOLOGIA, 1973, 14: 207-213

PROC. FOURTH EUROP. MALAC. CONGR.

ARTCHARAKTERISTISCHE FEINSTRUKTUREN BEI NUDIBRANCHIERN[1]

Luise Schmekel

Max-Planck-Institut für Zellbiologie, Tübingen und Zoologische Anstalt der Universität Basel

ABSTRACT

The fine structure of different cells of the epidermis, cerebropleural ganglia, digestive gland and reproductive organs has been investigated in 12 species of nudibranchs from the Gulf of Naples. Some cells, like the gland cells of the mucous gland, possess a similar ultrastructure in all species studied. Other cells show species-specific differences. Such species-specific features are found mainly among the differentiations of the plasmalemm, among telosomes and mature secretion products, e.g., the definitive, mature form of the prostate granules is species-specific. Developmental stages of secretion granules and lysosomes agree in most species.

Vor mehr als 25 Jahren hat der Tübinger Zoologe Alfred Kühn (1946) elektronenmikroskopisch die einzelligen Schmetterlingsschuppen von einem Spanner und einer Mehlmotte untersucht. Er fand erhebliche Strukturdifferenzen zwischen beiden Arten und meinte, es müsse lohnend sein, diese Unterschiede in den verschiedenen systematischen Gruppen zu verfolgen und daran die Schmetterlingssystematik zu prüfen. Das Thema dieses Vortrages reicht also bis in die Frühzeit der Elektronenmikroskopie zurück. Dennoch werden Sie, als Sie es hörten, zunächst einen Augenblick gestutzt haben. Bei Protozoen sind artcharakteristische Strukturen auf Zellniveau evident und uns allen vertraut. Aber bei Metazoen? Da fällt uns eine Reihe von aus der Lichtmikroskopie her vertrauten, oft von Art zu Art verschiedenen Differenzierungen ein, wie Blutzellen von Vertebraten oder Nesselkapseln von Hydroiden. Darüberhinaus aber sind wir alle geneigt, mit zunehmender mikroskopischer Auflösung und dem Übergang vom Lichtmikroskop auf das Elektronenmikroskop eine zunehmende Strukturübereinstimmung anzunehmen und vom Huhn auf die Vertebraten, von *Aplysia* auf die Mollusken zu schliessen. Weithin geschieht das mit vollem Recht. Golgiapparat, Mitochondrien, Mikrotubuli scheinen von funktionellen Differenzen abgesehen überall gleich gebaut, Zilien nach dem gleichen 9+2 Schema angelegt, usf. Gibt es darüber hinaus etwas, worin sich die Muskelzelle der Art A von einer Muskelzelle der Art B unterscheidet? Ja etwas, worin sich übereinstimmend die Muskel- und Nervenzelle einer Art A von Muskel- und Nervenzellen der Art B unterscheiden?

Das gibt es, soweit ich bei den mir vertrauten Mollusken und Seeigeln sehe. Und das in diesen beiden Gruppen beobachtete scheint zu einem guten Teil auch für die übrigen Metazoen zu gelten. Artcharakteristische Strukturen finden sich in beiden Stämmen bevorzugt unter den Differenzierungen der Zelloberfläche (1), unter den Sekreten (2) und unter den Lysosomen (Hetero- und Autotelosomen) (3). Die Bilder, die ich Ihnen zur Demonstration zeigen werde, stammen alle von Nudibranchiern aus dem Golf von Neapel und betreffen meist Gattungs- und keine Artunterschiede, weil die Geinheiten

[1]Mit Unterstützung durch die Deutsche Forschungsgemeinschaft und den Schweizerischen Nationalfond zur Förderung der Wissenschaften.

von Artunterschieden in 10 Minuten nicht aufzuzeigen sind (Material und Methodik vgl. Schmekel, 1971).

1. Wir hörten zu Anfang von der Schmetterlingsschuppe. Bei den Nudibranchiern spielen derartige Differenzierungen der Zelloberfläche eine weit geringere Rolle als bei den Insekten und betreffen z. B. die Ausbildung des Mikrovillisaumes. Ob die Mikrovilli lang oder kurz sind, kann z. T. funktionsabhängig sein, ob sie verzweigt, unverzweigt sind oder ein Reusenwerk bilden, ist artcharakteristisch. Ein Beispiel soll hier genügen. In der Mitteldarmdrüse der Aeolidoidea kommen neben anderen Zellen regelmässig zwei Zelltypen vor: phagozytierende Zellen, welche bei allen von mir untersuchten Arten unspezifisch sind und eine durchaus 'nichtssagende' Oberfläche besitzen - und ausserdem Zellen mit einem hoch differenzierten Mikrovillisaum. Diese letzteren Zellen scheinen u. a. Substanzen pinocytotisch aus dem Mitteldarmdrüsenlumen aufzunehmen. Die Ausbildung ihres Mikrovillisaumes variiert von Art zu Art. *Coryphella pedata* (Montagu, 1815) zeigt schlauchförmige, unverzweigte, relativ locker stehende Mikrovilli. *Trinchesia granosa* Schmekel, 1965 trägt über jeder Zelle ein dichtes Polster mehrfach verzweigter und untereinander anastomosierender Mikrovilli (Abb. s. Schmekel & Wechsler, 1968).

2. Sekretgrana und Vakuolen können bei den Nudibranchiern vollkommen unspezifisch gestaltet sein. Zu diesen mit unseren heutigen Methoden morphologisch unspezifischen Sekreten gehört z. B. dasjenige der Becherzellen in der Epidermis, der Mucuszellen im Ovidukt (Schmekel, 1971), aber auch die Vakuolenkörper in den Vakuolenzellen der Aeolidierepidermis. Die Vakuolenkörper sehen bei allen Aeolidoidea gleich aus (Schmekel & Wechsler, 1966, Abb. 6 und 13), fehlen aber bei den Doridoidea. Wir haben hier also gruppentypische, nicht aber artcharakteristische Gebilde vor uns. Sekrete können andrerseits aber auch in hohem Masse spezifisch strukturiert sein, wie z. B. im vorderen Genitalsystem das Sekret der Prostata (Abb. 1-4).

Als Prostata wird bei den Nudibranchiern der drüsige Abschnitt des männlichen Ausführweges bezeichnet. Die Prostata kann eine einfache Gangerweiterung sein oder eine abgesetzte Drüse. Ihr Epithel ist einschichtig. Merokrine Drüsenzellen und bewimperte Stützzellen wechseln einander ab. Das Sekret der Drüsenzellen besteht aus einer feinst flockulären, 'hellen' Komponente und einer osmiophilen, granulären Komponente. Beide Komponenten liegen bei manchen Arten in getrennten Zellen (*Chromodoris*), bei anderen in gesonderten Vakuolen in einer Zelle (*Peltodoris*, Abb. 1) oder aber zusammen in einer Vakuole (*Coryphella*, Abb. 4b). Flockuläres Material und osmiophile Grana werden, ohne ihre Struktur zu ändern, ins Prostatalumen abgegeben (Abb. 2a, 4b), wo sie unverändert bis zur nächsten Kopula erhalten bleiben. Sie dienen während der Kopulation dazu, die Autospermien zu einem festen Spermienballen zu verkleben. Bei allen Arten lassen sich die ersten, überall gleich aussehenden, osmiophilen Primär-Grana im Bereich des Golgi-Apparates beobachten (Abb. 2). Die weitere Reifung führt bei allen 12 bisher untersuchten Arten zu durchaus verschieden strukturierten Sekreten, die auf verschiedene Weise ausgeschleust werden. Bei *Trinchesia coerulea* (Montagu, 1804) (Abb. 2a) bleiben die osmiophilen Primärgrana als kleine Einzelgrana erhalten und werden meist einzeln ins Lumen abgegeben, indem die Vakuolenmembran des Granum mit dem apikalen Plasmalemm verschmilzt und beim Öffnen zum Teil des Plasmalemms wird. Bei *Trinchesia ocellata* Schmekel, 1965 (Abb. 3) wachsen die Primärgrana homogen zu Grana mit einem erheblich grösseren Durchmesser als bei *Trinchesia coerulea* heran. Bei *Flabellina affinis* (Gmelin, 1791) (Abb. 4a) wird die Vakuole zuerst stärker erweitert als das Granum und später unregelmässig weiteres osmiophiles Material angelagert, bis zuletzt pro Vakuole ein

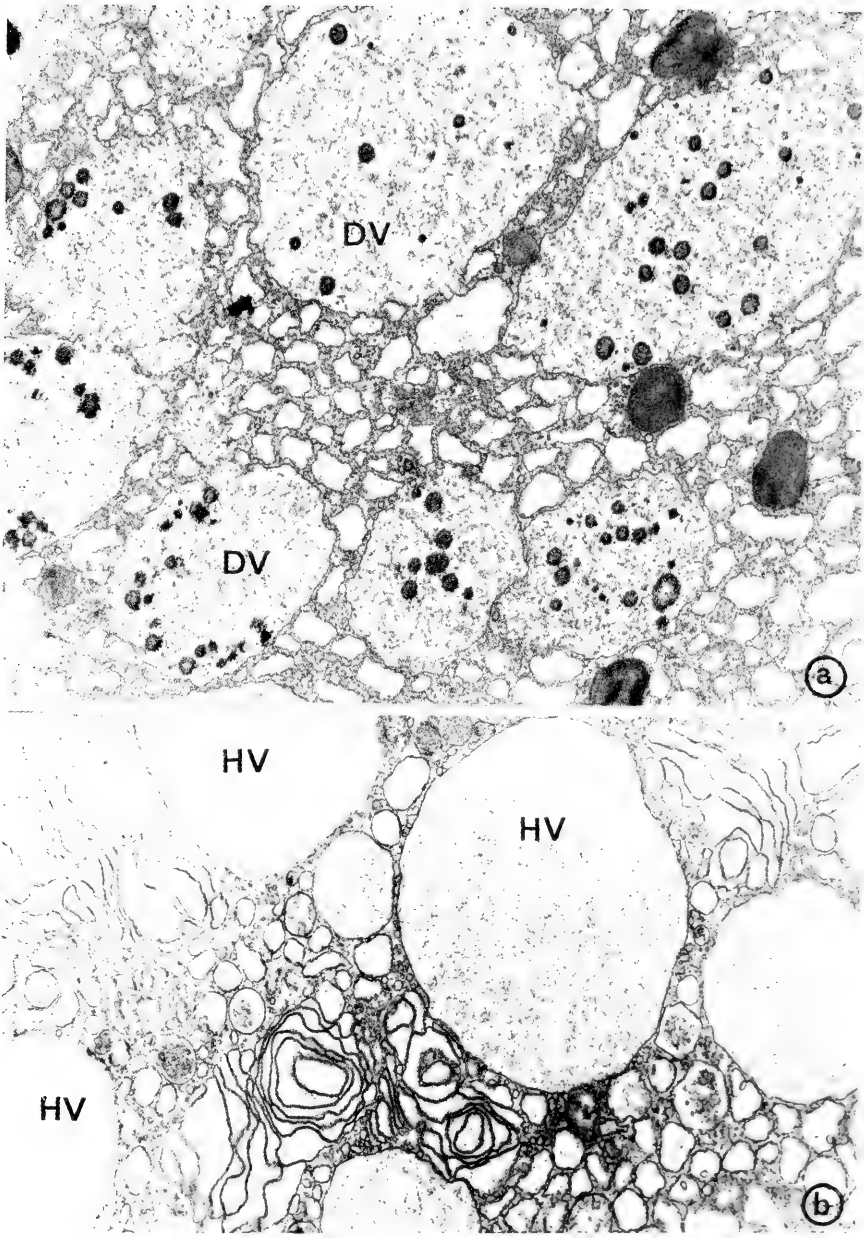

ABB. 1. *Peltodoris atromaculata*, Prostata. Dunkle Sekretvakuolen DV mit osmiophilen Grana (Abb. 1a, Vergr. 17500 x) und helle Vakuolen HV mit feinst flockulärem Material (Abb. 1b, Vergr. 21600 x) aus verschiedenen Regionen einer Zelle.

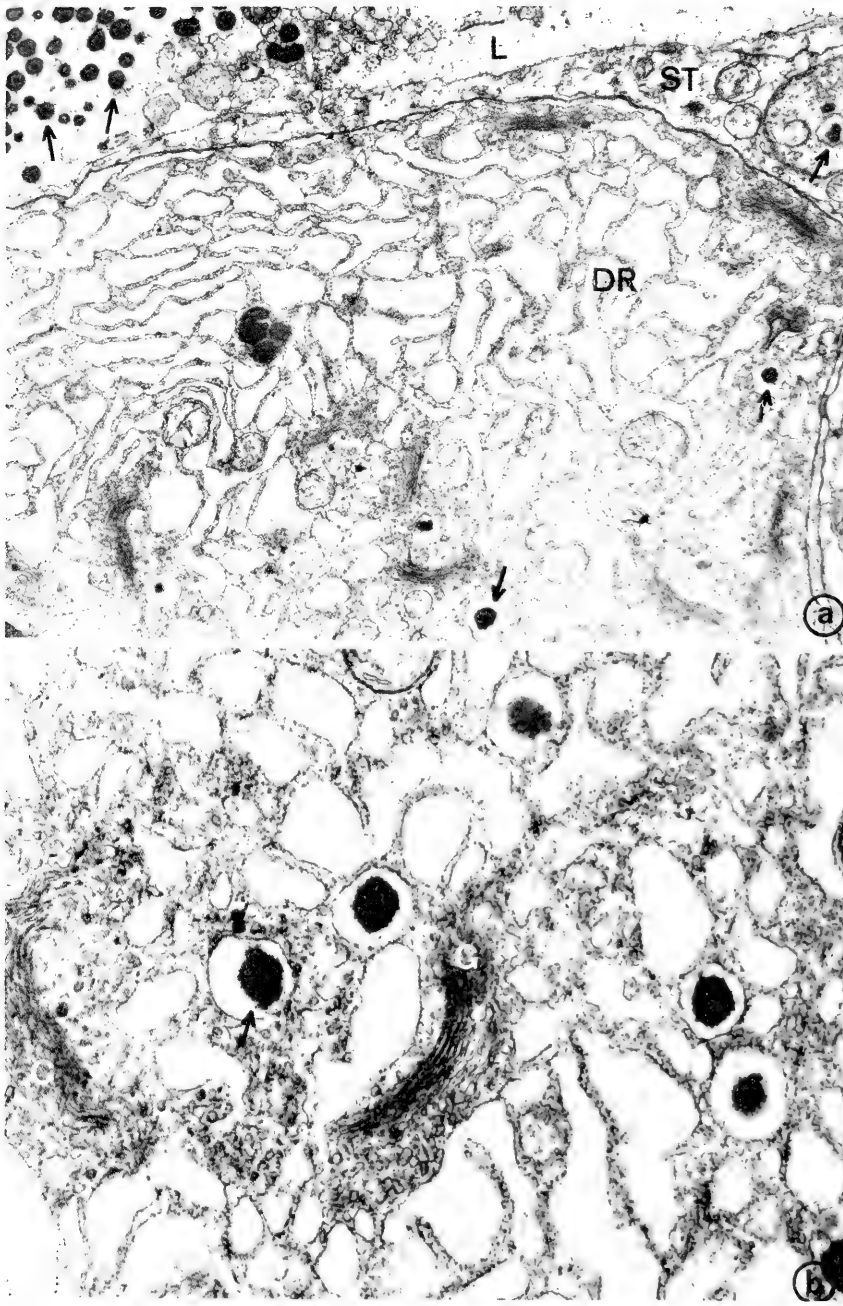

ABB. 2. *Trinchesia coerulea*, Prostata. Kleine osmiophile Sekretgrana SG im Drüsenlumen L (Abb. 2a, Vergr. 9000 x) und im Bereich des Golgiapparates G (Abb. 2b, Vergr. 24000 x). DR Drüsenzelle, ST Stützzelle.

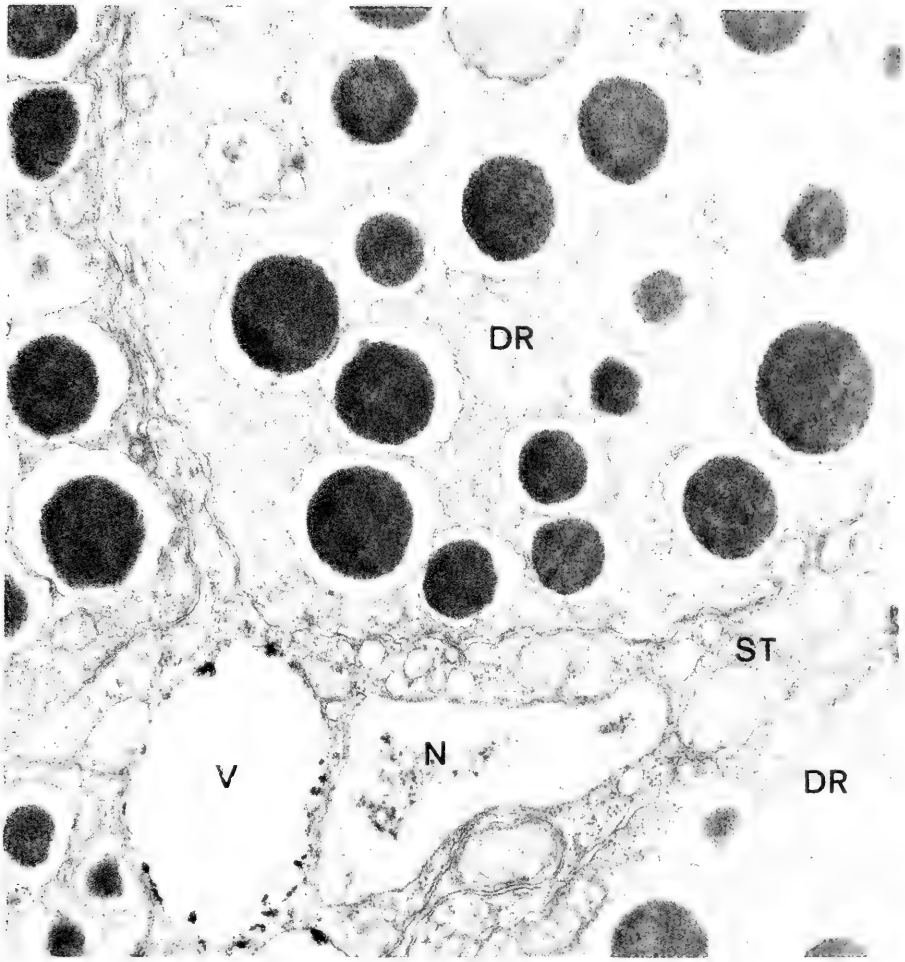

ABB. 3. *Trinchesia ocellata,* Prostata. Grosse osmiophile Sekretgrana SG in den Drüsenzellen DR. N Kern und V Vakuole einer Stützzelle ST (Vergr. 24000 x).

grosses, oft noch unregelmässig osmiophiles Granum vorhanden ist. Bei *Coryphella pedata* (Montagu, 1815) (Abb. 4b) werden nach und nach in der sich vergrössernden Vakuole immer mehr osmiophile Einzelgrana angesammelt und gleichzeitig flockuläres, helles Material angereichert. Die Einzelgrana verschmelzen nicht miteinander, sondern die Vakuolen mit vielen Grana gelangen in den Zellapex, wo die Vakuolenmembran aufgelöst wird, so dass eine einzige grosse, apikale Ansammlung von osmiophilen Grana und flockulärem Material entsteht. Die Ausschüttung erfolgt durch einfache Öffnung des Plasmalemms. Damit genug der ausserordentlich vereinfacht vorgetragenen Beispiele.

3. Wir kommen nun zum dritten Bereich, in dem Artunterschiede zu erwarten sind, den Lysosomen. Ich darf zunächst kurz die Nomenklatur erläutern, de Duve & Wattiaux (1966) folgend:

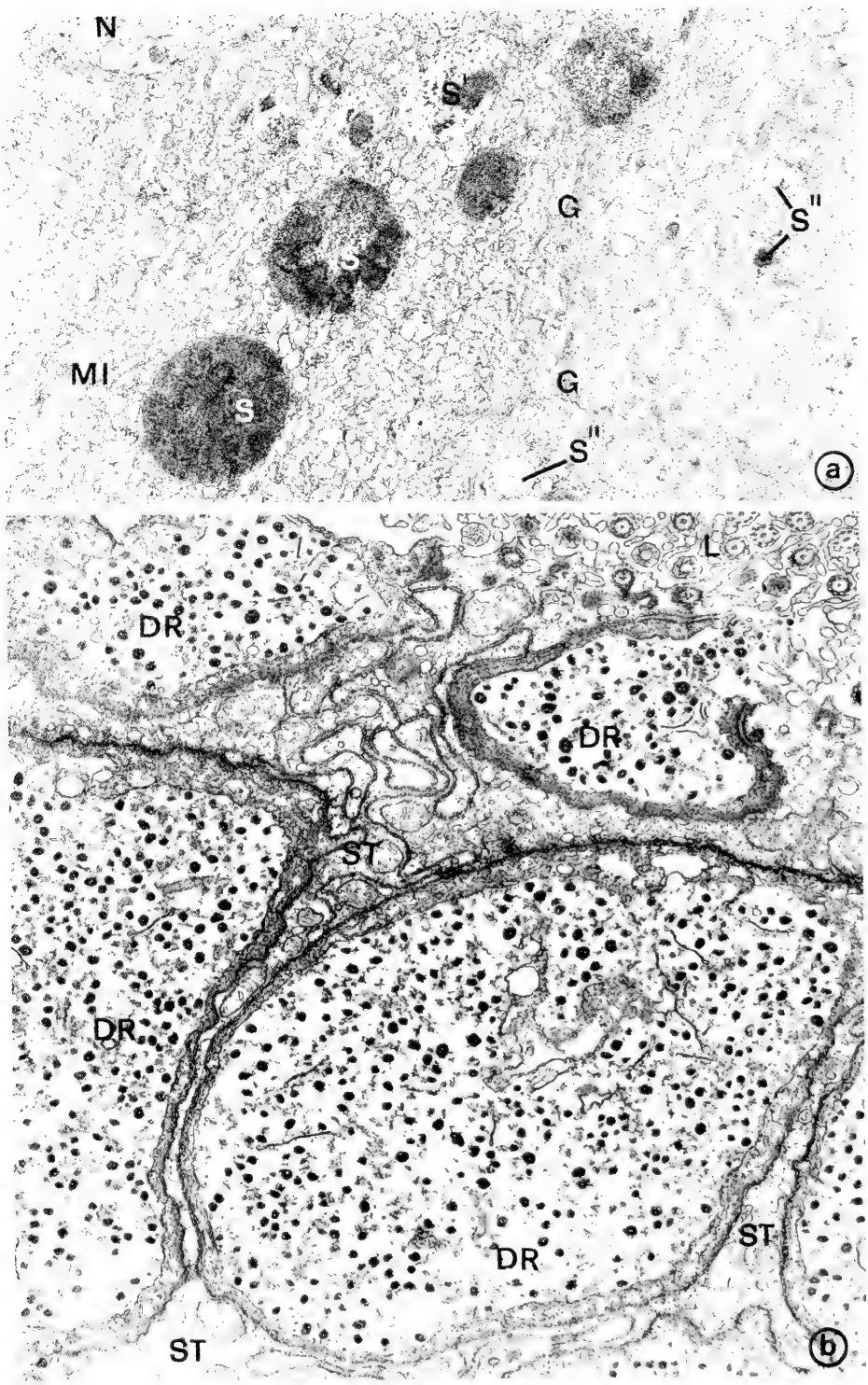

ABB. 4. Flabellinidae, Prostata. Abb. 3a *Flabellina affinis* (Vergr. 3000 x), reife S, halbreife S' und junge S'' Sekretvakuolen. G Golgizone, MI Mitochondrium, N Kern. Abb. 3b *Coryphella pedata* (Vergr. 16800 x), apikale Ansammlung von osmiophilen Grana und feinstflockulärem Material in den Drüsenzellen DR. ST Stützzellen, L Drüsenlumen.

Primäre Lysosomen sind im Bereich des Golgiapparates liegende kleine Vesikel, die saure Hydrolasen enthalten. Der Inhalt dieser Vesikel kann zur Verdauung von zellfremder oder zelleigener Substanz verwendet werden. Im ersten Fall entsteht aus dem primären Lysosom und der Phagozytosevakuole ein Heterolysosom, im zweiten Fall aus primärem Lysosom und zelleigenem Material ein Autolysosom. Heterolysosom und Autolysosom werden zu einem häufig keine oder nur noch schwache saure Phosphataseaktivität zeigenden Telosom verdaut. Das Telosom kann ausgeschieden werden. Wird es in der Zelle behalten, wird es oft weiter kondensiert zu einem Postlysosom. Die Telo- und Postlysosomen zeigen nun, worauf für *Helix* z. B. schon Mercer 1963 hingewiesen hat, häufig in verschiedenen Geweben einer Art das gleiche Aussehen und unterscheiden sich von denen einer zweiten Art. Artcharakteristisch strukturierte Telosomen finden sich bei Nudibranchiern z. B. meist in grösserer Anzahl in den Riesennervenzellen der Cerebropleuralganglien, kommen in geringerer Zahl aber auch in den kleineren Nervenzellen und den Gliazellen vor (Schmekel & Wechsler, 1968). Autolysosomen lassen im Unterschied zu den Telosomen i. allg. keine spezifischen Merkmale erkennen. Wichtig ist hier also wieder, was wir schon für die osmiophilen Primärgrana des Prostatasekretes beobachtet haben: artcharakteristisch ist nicht das Genesestadium, sondern das Speicherstadium, bzw. das Stadium, in dem die Kondensierung unterbrochen wird.

Lysosomen und Sekrete sind Teil des Vakuolenapparates der Zelle. Fassen wir zusammen, so sind feinstrukturelle Unterschiede also als Differenzierungen der Zelloberfäche zu erwarten oder bei Material, das vorübergehend oder dauernd im Vakuolenapparat der Zelle gespeichert wird. Organellen des Elementarstoffwechsels zeigen dagegen bei den Nudibranchiern i. allg. keine spezifischen Feinstrukturen.

Ich danke der Stazione Zoologica di Napoli für die guten Arbeitsbedingungen in Neapel.

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MALACOLOGIA, 1973, 14: 215-220

PROC. FOURTH EUROP. MALAC. CONGR.

THE BIOLOGY OF THE ARCHITECTONICIDAE, GASTROPODS COMBINING PROSOBRANCH AND OPISTHOBRANCH TRAITS

Robert Robertson

Academy of Natural Sciences of Philadelphia, Pennsylvania, U.S.A.

The Architectonicidae (or "Solariidae") are a small, specialized family of primarily tropical marine gastropods that are of particular phylogenetic interest and importance because they combine prosobranch traits such as streptoneury with various opisthobranch traits. This paper reviews what has been learned to date about architectonicid higher category relationships. Studies are still in progress on their biology, specifically their systematics, ecology, life history, anatomy, histology, functional morphology and cytology (the latter aspects are being done in collaboration with Dr. George M. Davis). Most of our work is based on the tropical western Atlantic species *Heliacus cylindricus* (Gmelin).

The family is a cohesive, well-defined group and consists of 3 principal genera: *Architectonica* (or "*Solarium*"), *Philippia* and *Heliacus* (or "*Torinia*"). Their shells range in shape from high trochoidal and narrowly umbilicate (*Gyriscus*) through discoidal and widely umbilicate to forms with disjunct, planispiral whorls (*Spirolaxis*). The genera have been variously divided into 2 subfamilies or even families; such divisions greatly overemphasize opercular or radular differences (among which there admittedly is structural diversity).

There is little published anatomical information on architectonicids. The best work is Bouvier's (1886); Risbec (1955) and Merrill (unpubl.) have also studied their anatomy.

Thiele (1929) grouped the family among the mesogastropods in the Cerithiacea primarily on the basis of Bouvier's work. Taylor & Sohl (1962) named a superfamily Architectonicacea, placed this in the Mesogastropoda, but noted that it and the Mathildidae "may prove to be primitive shelled Euthyneura." As long ago as 1928, Kuroda transferred the Architectonicidae to the opisthobranchs, but without stated reasons. More recently, Habe & Kosuge (1966) and Kosuge (1966) have grouped the Architectonicidae, Mathildidae, Epitoniidae, Janthinidae and Triphoridae in a new order or suborder, the Heterogastropoda, which they placed between the Neogastropoda and Basommatophora; they dispensed with subclasses and placed the Entomotaeniata (Pyramidellidae) and Cephalaspidea after the Basommatophora. This classification is unsatisfactory because the relationships between Triphoridae and the other 4 families seem highly tenuous and because the other families are separated from their nearest relatives (mesogastropods, pyramidellids and cephalaspids).

As has long been known, the Architectonicidae have hyperstrophically coiled larval shells (Robertson, 1963b). If the Pyramidellidae are to be considered opisthobranchs (Fretter & Graham, 1949, 1962), the Architectonicidae, Mathildidae and Cyclostremellidae (Moore, 1966) remain the only living families with this character that are still classified with the prosobranchs. It was this character plus the pigmented mantle organs of larval pyramidellids that initially led Thorson (1946) to suggest that these are tectibranchs. Thorson later (1957) observed that larval Epitoniidae (or "Scalidae") have similarly pigmented mantle organs, and even though epitoniids lack hyperstrophically coiled larval shells, he hinted that these too might be tectibranchs. Earlier, Knight *et al.* (1954) had already placed the "Scalacea" with the opisthobranchs, but without stated reasons.

All the known similarities between architectonicids and epitoniids are listed in Table 1. The information is partly from the literature and partly from unpublished data as noted. Similarities 4, 5 and 6 may be correlated with feeding habits, and similarities 8 and 9 are acknowledged to be inexact. Nevertheless, this many similarities seem to indicate that the 2 families are related. The relationships between architectonicids and pyramidellids seem closer, there being at least 7 uncorrelated and exact similarities (Table 2). Risbec (1955) was also impressed by similarities between these 2 families.

All the known prosobranch and opisthobranch traits of architectonicids are listed in Tables 3 and 4. Again, the information is partly from the literature and partly from unpublished data as noted. A fact to be stressed is that there are exceptions to nearly all the criteria by which opisthobranchs are distinguished from prosobranchs, and thus that there is no clearcut separation or objective way of defining the 2 subclasses. Architectonicids combine a nearly equal number of traits of each subclass. They also combine at least 1 trait unknown among prosobranchs (Table 4, trait 7) with 1 trait unknown among opisthobranchs (Table 3, trait 5). Architectonicids also have distinctive and highly specialized traits (Table 5), which make it unlikely that they gave rise to any other group. On the basis of shell matrix proteins, Ghiselin *et al.* (1967) believed *Architectonica* to be "an excellent precursor for the opisthobranchs and pulmonates." The other living families that show a complex web of interrelationships between prosobranchs and opisthobranchs (combining various proportions of traits of both) include: Pyramidellidae, Mathildidae, Cyclostremellidae, Epitoniidae, Janthinidae, Rissoellidae, Omalogyridae and Acteonidae. More comparative information is particularly needed on the Mathildidae and Cyclostremellidae.

Excluding these transitional groups, it must be acknowledged that prosobranchs and opisthobranchs show divergent evolutionary trends. Opisthobranchs probably diverged polyphyletically from lower mesogastropods, and the transitional groups help to show the sequence of evolutionary changes that occurred during the divergence.

Gastropods have commonly been divided into prosobranchs, opisthobranchs and pulmonates, but Boettger (1955) has advocated combining the latter 2 as the subclass Euthyneura. There would be as much reason to combine prosobranchs (Streptoneura) and opisthobranchs. I prefer to retain the 3 subclasses, but with the reservation that they can only be separated arbitrarily.

TABLE 1. Similarities between Architectonicidae and Epitoniidae:

1. Eyes near surface in swellings at outer bases of the tentacles.
2. Streptoneury [note 1].*
3. Long acrembolic proboscises.
4. Postlarval feeding associations with coelenterates [note 2].
5. Esophagus cuticularized [note 3].
6. Some architectonicids with ptenoglossate-like radulae [note 4].
7. Pigmented mantle organs [note 5].
8. Hermaphroditism (but epitoniids protandric?).
9. Chalazae (but in epitoniids these connect capsules containing numerous eggs, and the capsules are not in gelatinous masses).

*See Notes on p 218, 219.

TABLE 2. Similarities between Architectonicidae and Pyramidellidae:

1. Long acrembolic proboscises.
2. Pigmented mantle organs [note 5].
3. Juxtaposed (dorsal and ventral) longitudinal ciliated tracts in mantle cavities [note 6].
4. Simultaneous hermaphroditism [note 7].
5. Spermatophores (some species in both groups) [note 8].
6. Chalazae connect capsules containing single eggs within gelatinous egg masses [note 9].
7. Hyperstrophically coiled larval shells [note 10].

TABLE 3. Prosobranch traits of Architectonicidae and exceptional opisthobranchs (Pyramidellidae included) with same traits:

1. Entrance to mantle cavities directed anteriad, gills anterior to hearts and auricles anterior to ventricles (*Acteon, Ringicula, Cylichna* and Pyramidellidae, the latter usually without gills [note 11]).
2. Spires of shells not reduced and bodies retractile into shells (various Cephalaspidea, all Pyramidellidae and some Thecosomata).
3. Opercula present in adults (*Acteon,* Pyramidellidae, *Retusa,* Spiratellidae and Peraclididae).
4. Streptoneury [note 1] (*Acteon, Ringicula* and *Toledonia*).
5. Eyes near surface in swellings at outer bases of tentacles (no known opisthobranchs).
6. Osphradia present [note 1] (*Acteon,* Diaphanidae and Pyramidellidae).
7. Long acrembolic proboscises (Pyramidellidae).
8. Salivary glands non-tubular [note 12] (some nudibranchs, etc).
9. Velum with 4 long lobes [note 17] (any opisthobranchs?).

TABLE 4. Opisthobranch traits of Architectonicidae, with exceptional prosobranchs (Epitoniidae included) with same traits:

1. Feet very wide and with median anterior cleft (various prosobranchs).
2. Tentacles slightly flattened, and ventrally ciliated and channeled (any prosobranchs?) [note 13].
3. Gills foliobranch [note 1], and main pallial water currents created by pair of longitudinal ciliated tracts (latter in *Omalogyra*).
4. Pigmented mantle organs [note 5] (*Omalogyra,* Epitoniidae, etc.).
5. No esophageal glands (*Omalogyra,* Epitoniidae, etc.).
6. Simultaneous hermaphroditism [note 7] (*Acmaea rubella, Cocculina, Omalogyra, Rissoella, Valvata* and Lamellariidae [note 14]).
7. Chalazae connect capsules within gelatinous egg masses [note 9] (no known prosobranchs).
8. Hyperstrophically coiled larval shells [note 10] (Cyclostremellidae and Mathildidae, but these could be opisthobranchs).

TABLE 5. Some of the apparently unique characteristics or specializations of the Architectonicidae (some may occur only in *Heliacus*):

1. Ciliated omniphoric groove extends onto right side proximal outer surface of proboscis [note 15].
2. Ciliated dorsal crest divides exceptionally deep mantle cavity longitudinally (a superficially similar crest exists in viviparids), and all organs except the osphradium are adjacent to or open into the right chamber [note 1].
3. Uppermost duct in dorsal crest extends through nerve ring to a pore at middle of sole, from which a tough, elastic mucus thread is continuously extruded [note 15].
4. No penis; instead, long, coiled, tubular spermatophores [note 8].
5. Opercula paucispiral to multispiral, lamellate and conical, with peg projecting into foot (those of some Cyclophoridae are superficially similar).
6. False spire of hyperstrophically coiled protoconch projects into teleoconch umbilicus, and protoconch and teleoconch axes slightly different [note 10] (also in Cyclostremellidae).
7. Intraspecific larval shell size bimodality [note 16].
8. Arrested growth in an early postlarval stage (recorded as a distinct growth line on older shells) [note 17].

NOTES

1. *Architectonica:* Bouvier, 1886; *Heliacus:* Robertson & Davis, unpubl.
2. *Heliacus* spp. with zoanthiniarians (Robertson, 1967a; Marche-Marchad, 1969), *Philippia* (*Psilaxis*) with scleractinians (Robertson *et al.*, 1970), and *Philippia* (*Philippia*) with actiniarians (Robertson & W. F. Ponder, unpubl.). The food of *Architectonica* remains unknown. My (1963a) hypothesis that all Epitoniidae feed on coelenterates has been strengthened by subsequently published information (Fager, 1968; Morton & Miller, 1968; Robertson, 1970a; Albergoni *et al.*, 1970).
3. Robertson, 1970b.
4. Architectonicid radulae range in structure from modified taenioglossate (5 teeth per transverse row in *Heliacus*) to ptenoglossate-like (with numerous teeth per transverse row in *Architectonica*) [Troschel, 1861, 1875; Thiele, 1928; Robertson, 1970b; Merrill, unpubl.]. The latter could be convergent with epitoniid radulae: a consequence of identical food.
5. I intentionally use this vague terminology for the structure or structures that have been called a larval excretory organ (kidney) in larval opisthobranchs and a hypobranchial gland in adult epitoniids. Both in architectonicids and in pyramidellids I have observed these organs to be retained from the larva through metamorphosis and throughout life, and the same probably occurs in epitoniids. These usually darkly pigmented organs, so conspicuous in the larvae, become associated with the hypobranchial gland or gill in the adults. The pigment they release may be repugnatorial. Further work is needed on the structure and function of these organs at different life history stages and in different groups to determine whether they are homologous.
6. *Heliacus* and *Odostomia*, s.l.: Robertson, unpubl.
7. Both specimens of a pair of *Heliacus cylindricus* at Bermuda were found to have ripe spermatozoa in the gonad; earlier, they had been transferring spermatophores and one of them had laid an egg mass (Robertson, unpubl.). Anatomical confirmation of simultaneous hermaphroditism in this and other architectonicids is still needed.
8. *Heliacus cylindricus* and *H. perrieri* (Rochebrune): Robertson, unpubl. Pyramidellidae: Höisaeter, 1965; Robertson, 1967b and unpubl.

ACKNOWLEDGEMENTS

I thank Drs. George M. Davis, Vera Fretter, Alastair Graham and Henning Lemche for helpful discussions. These persons do not necessarily agree with all the views stated here. Part of the work was supported by National Science Foundation Grant GB-7008.

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notes cont.

9. *Philippia* (*Psilaxis*): Robertson, 1970b; *Heliacus cylindricus* and *H. perrieri:* Robertson, unpubl.

10. Robertson, 1963b, 1964. In architectonicids, hyperstrophic coiling is abnormally retained throughout life: Robertson & Merrill, 1963.

11. Risbec (1955) found a reduced gill in 1 pyramidellid.

12. *Architectonica:* Bouvier, 1886; Risbec, 1955.

13. *Heliacus:* Robertson, unpubl.; the tentacles of *Architectonica* apparently are channeled medially (Bouvier, 1886).

14. Confirmation is needed that the hermaphroditism in some of these prosobranchs truly is simultaneous and not protandric.

15. *Heliacus cylindricus:* Robertson & Davis, unpubl.

16. *Architectonica nobilis* Röding and eastern Pacific *Heliacus architae* (O. Costa): Robertson, unpubl.; *Philippia* (*Psilaxis*) *radiata* (Röding): Robertson, 1970b; *P.* (*P.*) *krebsii* Mörch: Robertson, 1964 and unpubl. There seems to be some genetic basis for the dimorphism.

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MALACOLOGIA, 1973, 14: 221-222

PROC. FOURTH EUROP. MALAC. CONGR.

A COMPARATIVE STUDY OF SOME POLISH AND AMERICAN LYMNAEIDAE: AN ASSESSMENT OF PHYLOGENETIC CHARACTERS

J. B. Burch

Museum of Zoology, The University of Michigan
Ann Arbor, Michigan 48104, *U.S.A.*

ABSTRACT[1]

Electrophoretic and immunological studies show that the Polish *Stagnicola corvus* and the North American *Stagnicola palustris elodes* are very closely related in regard to their foot muscle proteins. These and their nearly identical shells are regarded to be indicative of their common ancestry; their similar shells are not the result of parallel evolution. Likewise, Polish *Lymnaea stagnalis* and the North American subspecies *L. stagnalis jugularis* (=*appressus*) are very closely related, but neither shows close affinities to either of the *Stagnicola* species. *Stagnicola corvus* has in common with *L. stagnalis* a multifolded prostate gland, and like *L. stagnalis*, it lacks appendices at the proximal ends of both the uterus and the prostate gland. However, these anatomical peculiarities do not seem to relate *S. corvus* more closely to *L. stagnalis* than to other *Stagnicola* species. These anatomical characters, rather than the shell characters, must be the result of parallel evolution. Or more probably (by inference from characters of other lymnaeids), a stagnicoline ancestor with tricuspid lateral teeth, a unifolded prostate gland, and lacking a penial swelling, as well as lacking proximal appendices on the uterus and prostate gland, gave rise to 2 stocks of stagnicoline snails. In one stock, the endocones and mesocones of the lateral radular teeth merged (or the endocones were reduced to obsolescence), the penis developed a stronger holdfast "knot," and appendices developed in the proximal parts of the uterus and prostate glands. Nevertheless, these modifications were only minor evolutionary changes, and a corresponding evolution of basic structural foot muscle proteins did not take place. Descendants of this stock occur in Eurasia, and they are apparently the only *Stagnicola* group found in North America. The other stock did not migrate from Eurasia, and retained the tricuspid condition of the first lateral radular teeth, and did not develop uterine and prostatic appendices or a well-developed penial "knot." However, the prostate gland became more highly folded. From this second stock *Lymnaea* s. str. may have evolved, retaining certain anatomical characters in the ancestral condition, but diverging significantly in shell shape, some anatomical characters, and especially in proteins (as evidenced by foot muscle).

The patterns of characters and their evolution in the apparently ancient and now widely distributed family Lymnaeidae are very complex, and assessment of the importance of morphological characters, in every case, should be aided by auxiliary studies using immunological, electrophoretic, or other modern taxonomic methods.

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[1]Published *in extenso* in: Zool. zh., 1971, 50(8): 1158-1168, coauthored with G.K. Lindsay and P.T. LoVerde.

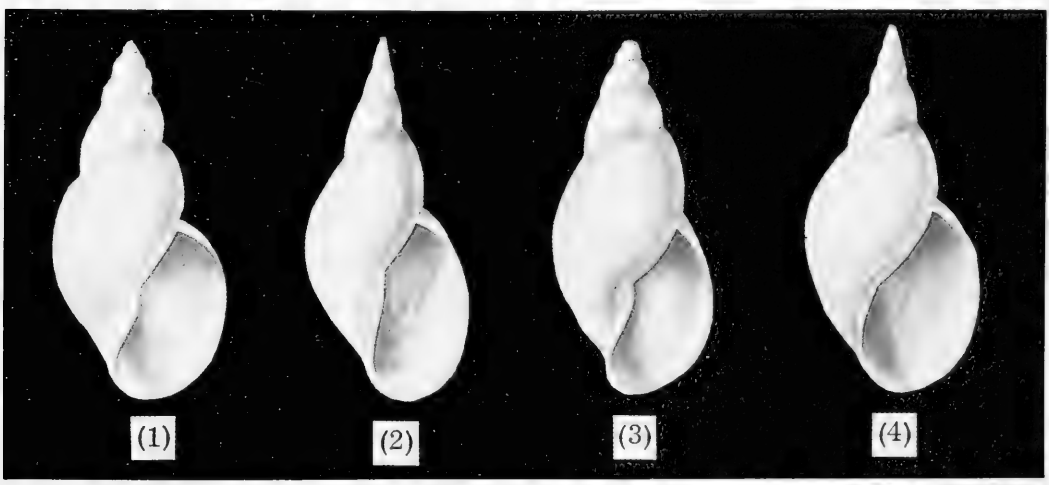

FIG. 1. Shells of American and Polish lymnaeid species used in this study. (1) *Stagnicola palustris elodes* (x2) [U.S.A.]; (2) *Lymnaea stagnalis jugularis* (x1) [U.S.A.]; (3) *S. corvus* (x2) [Poland]; (4) *L. stagnalis* (x1.2) [Poland].

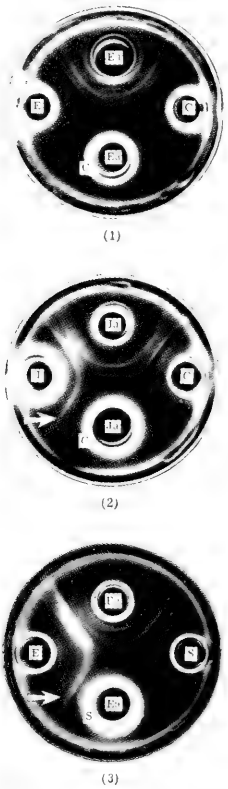

FIG. 2. Precipitin reactions of North American and Polish lymnaeid snails. Arrows point to "non-identity" reactions. E = *Stagnicola palustris elodes* antigen, Ea = *S. p. elodes* antiserum, C = *S. corvus* antigen, S = *Lymnaea stagnalis* antigen, J = *L. stagnalis jugularis* antigen, Ja = *L. s. jugularis* antiserum. (1) *S. corvus* antigen x *S. p. elodes* antiserum. (2) *S. corvus* antigen x *L. s. jugularis* antiserum. (3) *L. stagnalis* antigen x *S. p. elodes* antiserum.

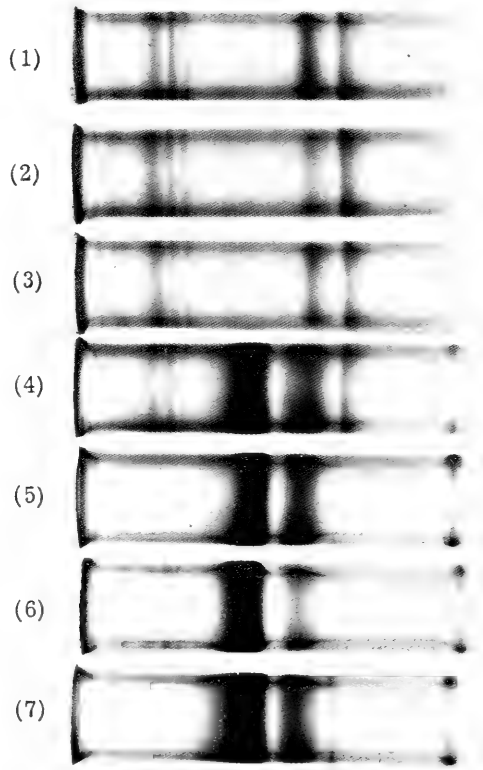

FIG. 3. Acrylamide gel columns (the bottom "separating" gel only) showing esterase separations from snail foot muscle proteins. (1) *Stagnicola palustris elodes*, U.S.A. (2) Separation of a mixture of foot muscle extracts of *S. p. elodes* and *S. corvus*, Poland. (3) *S. corvus*. (4) Separation of a mixture of foot muscle extracts of *S. corvus* and *Lymnaea stagnalis jugularis*, U.S.A. (5) *L. s. jugularis*. (6) Separation of a mixture of foot muscle extracts of *L. s. jugularis* and *L. stagnalis*, Poland. (7) *L. stagnalis*.

MALACOLOGIA, 1973, 14: 222

PROC. FOURTH EUROP. MALAC. CONGR.

PROBLEMS OF GENERIC PLACEMENT IN AUSTRALIAN LAND MOLLUSCS

Brian J. Smith

National Museum of Victoria, Melbourne, Victoria, Australia

ABSTRACT

Because of its large land area, its wide range of habitats from tropical rainforests to large desert areas and because of its relatively complete geographical isolation, Australia has an extensive, varied and largely endemic land mollusc fauna. However, even though a fairly large amount of work has been carried out on this fauna, there is still a large measure of confusion of its taxonomic state, particularly at the generic level. This is caused by 2 factors. Firstly, Iredale erected a large number of genera with little or no proper generic description and with no attempt at revision of the groups. Secondly, the type specimens of many of the type species of the Iredalean genera and of the genera from which they were separated are held in overseas institutions, principally in Europe and Britain. It is intended to attempt to clarify the positions of all Iredalean genera in a series of revisionary papers, firstly for the land molluscs and hopefully eventually for all the Iredale genera in doubt.

MALACOLOGIA, 1973, 14: 223-232

PROC. FOURTH EUROP. MALAC. CONGR.

THE USE OF ECOLOGICAL DATA IN THE ELUCIDATION OF SOME SHALLOW WATER EUROPEAN *CARDIUM* SPECIES

P. J. C. Russell[1] and G. Høpner Petersen[2]

INTRODUCTION

Throughout the last 2 centuries there has been much controversy concerning the validity of various *Cardium* species, in particular *C. glaucum* Bruguière, due to both the lack of ecological data and the widely accepted use of the morphological characters of shell material alone as a basis for their classification (Russell, 1969). The resulting confusion was highlighted recently by the description of a new species from Danish waters (*Cardium hauniense*), which had been identified as *C. exiguum* Gmelin for more than a century (Petersen & Russell, 1971a). The nomenclatural problems within this genus have already been dealt with by us at this Congress; however, it should be noted that the present nomenclature is based on the acceptance of *C. aculeatum* L. as the type species of the genus name *Cardium* (Lamarck, 1799).

It will be shown that by the combination of field observations, laboratory tolerance tests and field transplant experiments considerable insight may be gained into the taxonomic and ecological interrelationships of the species.

MATERIALS AND METHODS

Our studies involved *Cardium edule* L., *C. glaucum*, *C. exiguum* and *C. hauniense* Petersen & Russell (1971a), which were identified using the methods of Petersen (1958), Russell (1969) and Petersen & Russell (1971b).

Detailed accounts of the methods involved may be seen from Russell (1969) and thus only a brief summary will be given. The preferred habitat of each species was found by measuring parameters, such as salinity, temperature, exposure, exposure to air, tidal amplitude, etc., of the environments of many populations covering as wide a geographical range as possible. The tolerances of the species to those parameters which may be limiting their distributions were tested under controlled laboratory conditions, using samples from populations having similar environmental histories; populations consisting of 2 species were used frequently for direct comparisons thus avoiding non-genetic adaptations (Kinne, 1964). To test the conclusions reached from the laboratory tests, large numbers of cockles were transplanted to sites differing only in certain required respects and their survival recorded. If the transplanted cockles grew they provided a unique opportunity to check the validity of the use of certain shell features by taxonomists wishing to separate the species.

RESULTS

Field observations: From our field observations the preferred habitats of the 4 species (Table 1) show marked differences.

Laboratory tolerance tests: The type of information gained from tolerance tests can be seen from the following results:

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[1]Portsmouth Polytechnic Marine Laboratory, Ferry Road, Hayling Island, Hants, PO11 ODG, U. K.

[2]University Zoological Museum, Universitetsparken, 15, Copenhagen. Ø Denmark.

TABLE 1. The habitat preferences and habits of the species, based on field observations.

	C. edule	*C. glaucum*	*C. exiguum*	*C. hauniense*
Salinity range (°/oo)	15 - 35	4 - 100	20 - 35	8 - 12
Temperature range (°C.)	3 - 25	0 - 32	3 - 25	0 - 25
Exposure to air (as % time)	0 - 40	0 - 5	0 - 5	0
Habitat exposure	Estuarine	Lagoon	Estuarine/ Lagoon	Lagoon
Tidal amplitude (m.)	0.2 - 10	Zero - 5	Zero - 10	Zero - 0.1
Habit	Buried in substrate	Buried or on surface	Attached by byssus	Attached by byssus

TABLE 2. The salinity tolerances of the species based on samples from various habitats.

	Site	Habitat	Salinity (°/oo) Tolerances Lower LS_{50}	Upper LS_{50}
C. edule	Lille Strand	20	12.5	38.5
C. glaucum	"	20	14.5	39.5
C. exiguum	Portsmouth	30	24.0	39.0
C. hauniense	Dybso Fjord	11	9.0	13.0
C. glaucum	Orford	10	3.7	30.5
C. glaucum	Etang de l'Arnel	52	22.5	82.5

TABLE 3. The upper lethal temperatures of 2 species under conditions of different seawater availability.

Seawater availability (ml / day)	Upper lethal temperature (LT_{50} in °C.)	
	C. edule	*C. glaucum*
200	18.7	31.4
1,000	31.4	32.2

TABLE 4. The susceptibility of 2 *Cardium* species, originating from homogeneous and heterogeneous populations, to 'cockle-water.'

	Tidal Amplitude (m)	Survival time (days)		Susceptibility
		Membrane Filtered 'Cockle-water'	Membrane Filtered 'Seawater'	$\frac{\text{Control}}{\text{Test}} \times 100$
C. glaucum	0	85.0 +	93.8 +	110
C. glaucum	0.2	47.8	97.8	204
C. edule	0.2	53.8	114.4	213
C. edule	4	58.8	87.0	148

Salinity. Table 2 shows the results of 3 comparative experiments. The salinities in which 50% of the sample died (LS_{50}) were read off from salinity/response curves constructed from the survivals of the cockles in various salinities after a given time. In contrast to *Cardium edule* and *C. glaucum*, between which no inherent difference in salinity tolerance can be seen, *C. exiguum* and *C. hauniense* exhibit markedly different salinity tolerances. The significance of the latter result can be seen from a comparison with the overlapping tolerances of 2 populations of *C. glaucum* despite the fact that their environmental salinities differed to a greater extent.

Temperature. Field observations suggested that *Cardium edule* was absent from areas liable to summer water temperatures in excess of 25°C. Temperature tolerance tests demonstrated this clearly (Table 3). However, in another test, in which more water was made available to the cockles, the upper LT_{50} was markedly higher. Thus temperature was significant only in conjunction with seawater availability.

Stagnation. From the field observations it appeared that *Cardium edule*, in contrast to *C. glaucum*, required a tidal amplitude in excess of 0.2 m, suggesting that the former required the removal from its vicinity of a toxic metabolite. To test this theory the survivals of samples of *C. edule* and *C. glaucum* from homogeneous and heterogeneous

TABLE 5. The survival and shell features of *Cardium edule* and *C. glaucum* after transplantation to different environments.

	Widewater lagoon		Chichester harbour	
	C. edule	*C. glaucum*	*C. edule*	*C. glaucum*
survival (%)	0	70	87	96
posterior shell margin	crenulate	straight	crenulate	almost straight
internal ribbing	present	present	absent	absent
Periostracum thickness	thin	thick	thin	thick
Mean shell height (as % increase)	16.7	36.6	48.2	48.7

TABLE 6. The geographical distribution of the species. (+ = present; - = absent)

	C. edule	*C. glaucum*	*C. exiguum*	*C. hauniense*
Eastern Baltic	-	+	-	-
Central Baltic	-	+	-	+
Western Baltic	+	+	-	+
Kattegat	+	+	+	-
North Sea	+	+	+	-
Channel	+	+	+	-
North eastern Atlantic	+	+	+	-
Mediterranean	-	+	+	-
Black Sea	-	+	+	-

populations in seawater, in which *C. edule* had been living for a given time (cockle-water), were checked. The results (Table 4) demonstrated an inherent difference between the species; samples of *C. glaucum* from stagnant (i.e., non-tidal) lagoon conditions are less susceptible to cockle-water than those from tidal waters, whereas

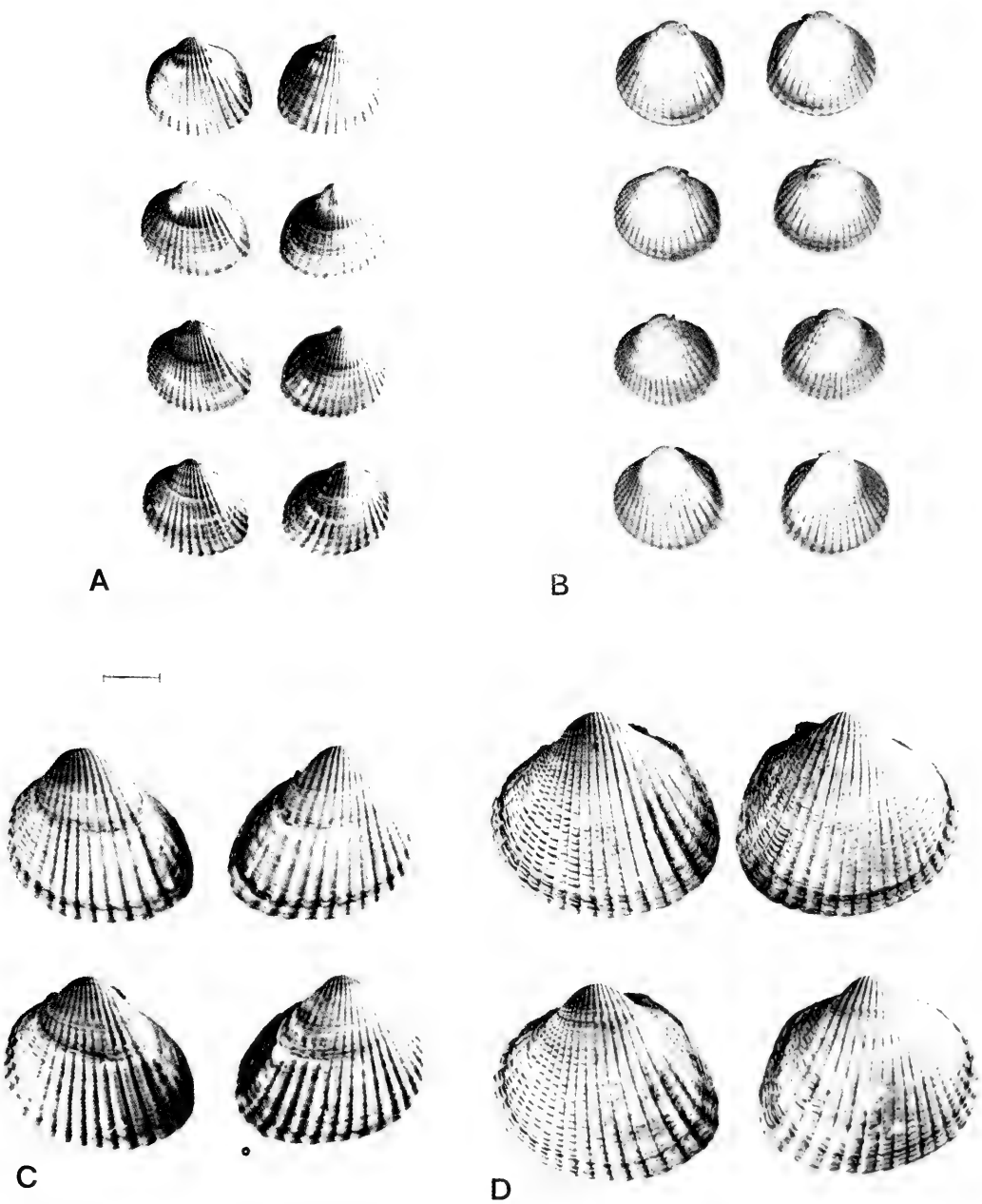

PLATE 1

A, *Cardium glaucum,* before; B, *Cardium edule*, before; C, *Cardium glaucum,* 18 months after transplanting to Langstone Harbour; D, *Cardium edule*, 18 months after transplanting to Langstone harbour. Scale = cm.

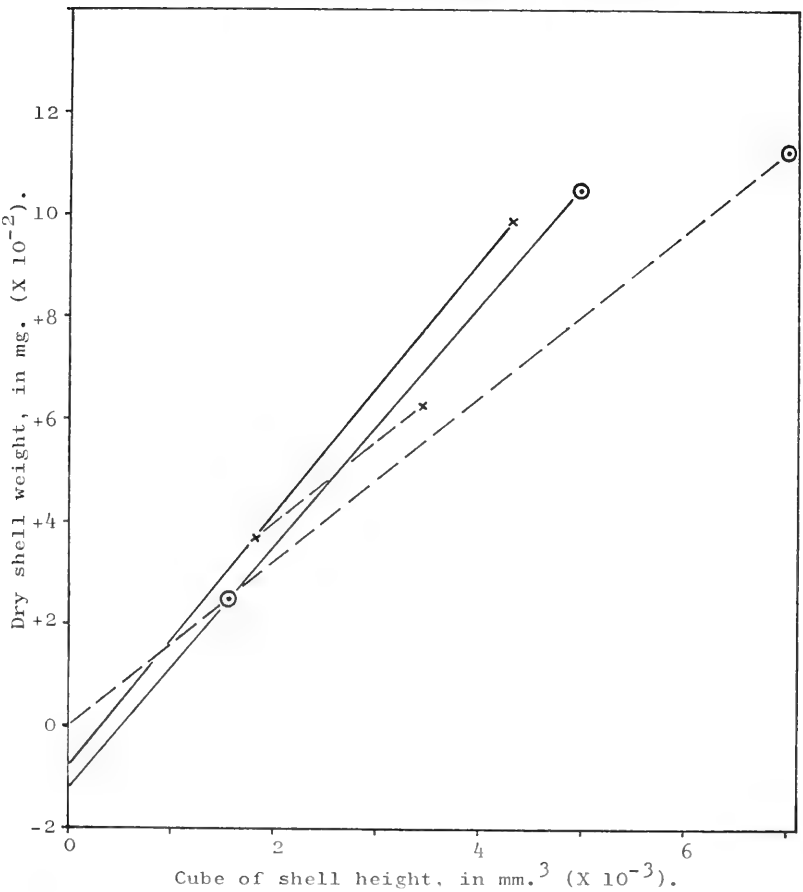

FIG. 1. Mean dry shell weight against the cube of mean shell height for transplanted *Cardium edule* (X) and *C. glaucum* (O), at Ellenore (———), a tidal mud flat, and Widewater (- - -), a nontidal lagoon.

samples of *C. edule* from less tidal waters are *more* susceptible than those from fully tidal estuaries.

Field transplant experiments

By careful site selection it is possible to test the validity of both the conclusions reached from the laboratory tests and the use of various features in the identification of the species. Considering the results of a transplant of samples of young *Cardium edule* and *C. glaucum* to 2 sites having approximately the same salinities and temperatures but different tidal amplitudes (Table 5), it can be seen that both the survival of the cockles and certain shell features are dependent more on the different environments than on the species themselves (Pl. 1). Further information may be gained from a more quantitative approach; for example, from a graph of mean shell weight against the cube of shell height (Fig. 1) it can be seen that the slopes of the lines (i.e., the rates of increase of shell weight with shell height or shell thickness) of the 2 species are parallel at each site. Thus shell thickness is dependant to a marked extent on the environment and, consequently, associated features, like internal ribbing are of no value in the identification of *C. edule* and *C. glaucum*.

Geographical distribution

Having predicted which environmental parameters are limiting the habitat occupation of the species, their geographical distributions can be proposed (Table 6). The absence of a species from any large area, for example the Mediterranean, is impossible to prove but all the evidence to date agrees well with their suggested distributions (Russell, 1971). It is of interest that the range of each pair of closely related species almost covers the entire European coast.

INTERSPECIFIC RELATIONSHIPS

A close relationship between *Cardium edule* and *C. glaucum* is shown by the following features:

Hybridisation

In the laboratory, hybrid larvae which are viable at least to metamorphosis have been reared from gametes originating from homogeneous populations (Kingston, verbal commun.). However, in nature apparent hybrids (i.e., cockles with shell characters intermediate between the species) represent only 2 or 3% of some heterogeneous populations. Boyden (1971) accounted for this by demonstrating a displacement of spawning times in a mixed population, *Cardium glaucum* following some weeks after *C. edule*. Kingston (verbal commun.) has shown that this displacement only occurs in mixed populations and Russell (in prep.) has shown that it occurs when a mixed population is created by transplantation.

Character displacement

In heterogeneous populations some morphological features of the shell in *Cardium glaucum* appear to exhibit the phenomenon of character displacement (Brown & Wilson, 1956); for example:

(a) Despite the larger variation of the mean rib number in *Cardium glaucum* (20.8-27.2) compared with that in *C. edule* (22.5-25.6) from homogeneous populations, data from mixed populations show that the mean rib number in *C. glaucum* is always significantly less than that in *C. edule* (Table 7). The mean rib numbers of each species from partly mixed and partly unispecific populations (Table 8) show that it is the mean rib number in *C. glaucum* which is displaced and not that in *C. edule*.

(b) Some techniques for separating the species do not always hold good for the identification of individuals within unispecific populations, for example the ligament length/shell width ratio (Petersen, 1958). A shift in the plots representing *Cardium glaucum* towards those of *C. edule* occurs when data based only on unispecific populations are compared with data based only on mixed populations (Russell, 1969).

A close relationship between *Cardium exiguum* and *C. hauniense* is seen from their similar habits linked with the ability of the adult cockles to produce byssus; a feature not so far observed for any other *Cardium* species. No living mixed population has as yet been found, but it is proposed to investigate the possibility of hybridisation in the laboratory.

CONCLUSION AND DISCUSSION

From the field observations we conclude that each of the 4 *Cardium* species tends to occupy a different habitat, although each is capable of coexisting with at least 1 of the others; *C. glaucum*, the species tolerating the widest range of habitat, can coexist with all of the other species under various environmental conditions. It has been

TABLE 7. Mean rib number in *Cardium edule* and *C. glaucum* from mixed populations.

Origin of Sample	Mean rib number (no. counted) *C. edule*	*C. glaucum*	Significantly different at P less than
R. Roach estuary	22.24 (62)	20.58 (62)	0.001
R. Crouch estuary	23.44 (35)	21.79 (65)	0.001
Pughavn	24.04 (57)	23.28 (48)	0.05
Ørø	24.62 (50)	23.04 (50)	0.001
Vellerup	24.10 (70)	22.60 (162)	0.001
Nykobing	23.75 (20)	22.04 (46)	0.001
Lynaes	23.75 (30)	23.12 (36)	0.05
Jaegerspris	24.25 (46)	22.91 (30)	0.001

shown previously (Petersen & Russell, 1971b and Russell, 1972) that on both morphological and ecological grounds *Cardium edule* and *C. glaucum*, and *Cardium exiguum* and *C. hauniense*, may be considered as 2 pairs of very closely related species or siblings.

From the laboratory tolerance tests we conclude that the allopatric distributions of *Cardium exiguum* and *C. hauniense* are maintained by the marked difference in their salinity tolerances. The allopatric[3] part of the distribution of *C. glaucum* (i.e., the Mediterranean basin and the majority of the Baltic) is preserved by the inability of *C. edule* to tolerate a low tidal amplitude, especially at high temperatures, and not its relative stenohalinity as suggested most recently by Muus (1967).

Over the sympatric[3] part of their distributions ecological isolation is almost complete; *Cardium glaucum*, being unable to occupy the typical estuarine environment of *C. edule*, possibly due to the inability of their larvae to withstand even moderate exposure (Kingston, verbal commun.) is limited to lagoon habitats. However, in habitats like the shallow semitidal Danish fjords where neither stagnation nor summer water temperatures are excessive the species can be found together. Under such

[3]Note that our usage of the term sympatric follows that of Kohn & Orians (1962) rather than that of its originator (Mayr, 1942).

TABLE 8. Mean rib number in *Cardium edule* and *C. glaucum* in unispecific and mixed populations at Pughavn and Vellerup.

Locality	Population Composition	Mean rib number (no. counted)		Significantly different at P less than
Pughavn	Only *C. edule*	23.68	(63)	no sig. difference
	Both *C. edule* and *C. glaucum*	24.04	(57)	
		23.28	(48)	0.05
Vellerup	Both *C. edule* and *C. glaucum*	24.11	(70)	0.001
		22.60	(162)	
	Only *C. glaucum*	23.56	(50)	0.001

conditions hybridisation is reduced to a minimum by the displacement of the spawning time in *C. glaucum* (Boyden, 1971). Also under these conditions *C. glaucum* exhibits character displacement, emphasising the morphological differences between the species.

Kohn & Orians (1962) pointed out that morphological character displacement may lead to the members of those populations sympatric with a closely related species being described as a distinct species. They cited the case of *Agelaius bicolor* Audubon, which was in fact *A. phoeniceus* from those areas where its distribution overlapped that of a sibling, *A. tricolor*, but nevertheless survived in the literature for over 50 years (Mailliard, 1910). Despite the fact that the character displacement in *Cardium glaucum* is nothing like so obvious as the plumage displacement in the male *A. phoeniceus*, similar invalid species, based on samples of *Cardium glaucum* taken from areas where this species is sympatric with *C. edule*, have been erected (Russell, 1972); for example, Reeve (1845) distinguished *C. lamarcki* from *C. belticum* Beck and it was not until more than a century had passed that they were finally amalgamated by Petersen (1958). It should be noted that until quite recently taxonomic studies of these cockles were based on shells in museum collections rather than on freshly collected material and thus the large morphological variation in *C. glaucum* served to confuse rather than elucidate the problem of its taxonomic status. However, it is of interest that the partly sympatric siblings were resolved before the allopatric siblings *C. exiguum* and *C. hauniense*, exemplifying the fact that character displacement results in sympatric siblings differing more from each other than closely related allopatric species (Brown & Wilson, 1956).

The suggestion by Purchon (1939) that transplant experiments would prove useful in the resolution of the taxonomic position of the 'varieties of *Cardium edule*' was indeed valid. However, it should be remembered that their use is limited to the study of siblings whose adults, at least, can coexist in the same habitat; thus with allopatric

species the testing of their survivals in a number of different habitats may be an unrewarding prerequisite.

Finally we suggest that this ecological approach, which has clarified the taxonomic position of these 4 *Cardium* species and accounted for their distributions, might well be applicable to other closely related species in this and other genera of marine bivalves.

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PROC. FOURTH EUROP. MALAC. CONGR.

THE NOMENCLATURE AND CLASSIFICATION OF SOME EUROPEAN SHALLOW-WATER *CARDIUM* SPECIES

G. Høpner Petersen[1] and Peter J. C. Russell[2]

ABSTRACT

The nomenclature for the genus *Cardium* depends on the acceptance of the 2 following designations of type species:

A. *Cardium aculeatum*, Linné 1758, selected by Lamarck 1799, accepted by Bucquoy, Dautzenberg & Dollfus, 1892.

B. *Cardium costatum*, Linné 1758, selected by Children 1823, accepted by Kennard, Salisbury & Woodward 1931.

The 2 possibilities for nomenclature are demonstrated in Table 1. In this abstract we follow Bucquoy, Dautzenberg & Dollfus to retain the well known name *Cardium*. The 4 shallow-water species *C. edule*, *C. glaucum*, *C. exiguum* and *C. hauniense* are placed in the same genus as *C. aculeatum*. Table 2 shows that morphological characters alone cannot allow grouping. *C. aculeatum* can be separated from the 4 shallow-water species on the basis of size and vertical distribution.

TABLE 1

Taxon: v

to be divided into

Taxa: x - y - z

Taxon x includes:
larger species: *Cardium aculeatum*, *C. tuberculatum*, *C. echinatum*, *C. paucicostatum*, *C. erinaceum*.
smaller species: *C. papillosum*, *C. minimum*, *C. ovale*, *C. scabrum*, *C. parvum*, *C. simile*, (*C. elegantulum*), (*C. pinnatulum*).

Taxon y includes:
C. edule, *C. glaucum*.

Taxon z includes:
C. exiguum, *C. hauniense*.

The nomenclature of these taxa depends on the type-species designation for the genus *Cardium*. Two possibilities exist:

A. *C. aculeatum* is the type-species, then
v = *Cardium sensu latu*
x = *Cardium* s.s., y = *Cerastoderma*, z = *Cerastobyssum*.

B. *C. costatum* is the type-species, then
v = *Cerastoderma sensu latu*
x = *Acanthocardia*, y = *Cerastoderma* s.s., z = *Cerastobyssum*.

Note for the x taxon.

This taxon is a pool, which we at present can only group into the larger and the smaller species. It includes the *Cardium aculeatum*, which is the type-species of *Acanthocardia* and eventually also of *Cardium*. We do not consider the 2 north and northwest Atlantic species *elegantulum* and *pinnatulum* (see Clench, W. J. & L. C. Smith, 1944: The family Cardidae in the western Atlantic. Johnsonia, 1(13): 32 p, p 12) to be included into our y taxon (= *Cerastoderma*).

Note for the y taxon.

It is of no doubt that *Cardium edule* is the nominal type-species for the genus name *Cerastoderma*, Poli.

Note for the z taxon.

None of the 2 species included have been designated as type-species for a genus. However the name *Cardium exiguum* is in trouble with the genus *Parvicardium* (see Petersen, G. Høpner & Peter J. C. Russell, 1972, A proposed termination to the widely accepted junior synonymy of *Cardium parvum* Phillippi to *C. exiguum* Gmelin. J. Conchol., 27: 397-400). We call the z taxon *Cerastobyssum* and designate *C. hauniense* to be the type-species for *Cerastobyssum*.

[1]Zoological Museum, Copenhagen, Denmark

[2]Marine Laboratory, Hayling Island, Hants, England

TABLE 2

	C. exiguum	*C. hauniense*	*C. glaucum*	*C. edule*	*C. aculeatum*
Shell characters:					
furrowed ribs	+	-	-	-	+
projections on ribs	knots	knots-spines	scales	"steps"	knots-spines
thick periostracum	+	-	+	-	-
raised ligament	-	-	+	+	+
keeled shell	+	-	-	-	-
rib number	20-22	23-30	17-32	19-29	20-22
max. length, mm	15	10	50	60	100
no. of teeth in right hinge:					
anterior	2	1	2	2	2
cardinal	2	2	2	2	2
posterior	1	1	2	2	1
Ecological characters:					
S‰ tolerance in ‰	25-35	6-12	3-100	15-35	?
habitat preference	tidal-lagoon	lagoon	lagoon	tidal	?
use of byssus by adults	+	+	(+)	-	?
horizontal distribution	Mediterr.-Norway	Baltic	Mediterr.-Norway	Morocco-Iceland	Mediterr.-North Sea
vertical distribution in m	0-55	0-40	0-50	0-10	50-2000
occurs with	gl. ed.	gl.	ex. ha. ed.	ex. gl.	?
larval development	egg capsules	egg capsules	free spawning	free spawning	?
Other characters:					
nice electrophorese	-	+	-	-	?
tailing electrophorese	+	-	+	-	?
has been confused with	-	ex. gl.	ex. ed.	-	-
was type designated for	*Parvicardium*	*Cerastobyssum*	*Parvicardium*	*Cerastoderma*	*Cardium Acanthocardia*

(ex. = *C. exiguum;* ha. = *C. hauniense;* gl. = *C. glaucum;* ed. = *C. edule;* ac. = *C. aculeatum.*)

Table 1 presents a proposed classification of the cockles (Cardiidae) living in the Mediterranean Sea, the Baltic Sea and the coastal waters from Greenland to Spain; however the Caspian Sea is excluded and thus *Didacna*, *Monodacna* and *Adacna* are not considered.

For the shallow-water *Cardium* species, Table 2 demonstrates that by use of any particular character it is possible to pair up almost any combination of 2 species. Two groups are formed, 1 based on presence of 2 posterior lateral teeth in the right valve (*edule* + *glaucum*) and 1 based on the adults climbing with a byssus (*exiguum* + *hauniense*).

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MALACOLOGIA, 1973, 14: 235-241

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A PRELIMINARY REPORT ON SYSTEMATICS AND DISTRIBUTION OF THE GENUS *ERVILIA* TURTON, 1822 (MESODESMATIDAE, BIVALVIA)

Louise A. de Rooij-Schuiling

Rijksmuseum van Natuurlijke Histoire, Leiden, Netherlands

INTRODUCTION

This is a preliminary report on the systematics and distribution of the genus *Ervilia*. A more extensive and documented revision of all the species of the Mesodesmatidae will be published later (De Rooij-Schuiling, 1974).

The species of the genus *Ervilia*, created by Turton in 1822, have typical mesodesmatid characters, viz., the possession of a feeble outside ligament, a strong resilium and the structure of the hinge. Their distribution is tropical and subtropical.

DIAGNOSIS OF THE MESODESMATIDAE

The Mesodesmatidae have equivalved shells from a small to moderately large size (max. length 3-140 mm) and of a subtriangular, ovate or subtrigonal-inequilateral shape. The umbones are mostly posterior. The external ligament is short and feeble, but there is a stout resilium fitted in a deep resilifer. The hinge is rather solid. In each valve a single cardinal is present. In the left valve there is 1 lateral on each side of the umbo fitting between the 2 opposite laterals of the right valve. The pallial sinus is variously developed, even absent in some genera.

TAXONOMY OF THE GENUS *ERVILIA* TURTON, 1822

Ervilia Turton, 1822: 55. Type species *Mya nitens* Montagu, 1808: 165.
Rochefortina Dall, 1924: 88. Type species *R. semele* Dall, 1924: 88.
Spondervilia Iredale, 1930: 402. Type species *Ervilia australis* Angas, 1877: 175, pl. 26, fig. 21.

Dall first described in 1924 a tiny shell from Oahu. He placed it in *Rochefortina*, a new subgenus of *Rochefortia*, and named it *R. semele*. In 1938 he synonymized this species with *Ervilia sandwichensis* Smith, 1885, thereby raising *Rochefortina* to a genus. *R. sandwichensis* is, however, a species which differs only on specific level from its nearest relative, *Ervilia bisculpta* Gould, 1861. So *Rochefortina* Dall, 1924 becomes a junior subjective synonym of *Ervilia* Turton, 1822 (De Rooij-Schuiling, 1972).

In 1930 Iredale created the new genus *Spondervilia* for the *Ervilia*'s from the Australian area. This genus was based on *Ervilia australis* Angas, 1877 as type species. However, contrary to Iredale's views, *Ervilia australis* and *E. bisculpta* are conspecific, and there is no difference between the specimens of the Australian and the Japanese populations. Because *E. bisculpta* differs only on the species level from other *Ervilia*'s, *Spondervilia* Iredale, 1930 is a junior subjective synonym of *Ervilia* Turton, 1822 (De Rooij-Schuiling, 1972).

DIAGNOSIS OF THE GENUS *ERVILIA*

Small mesodesmatids (max. size of recent species: length 15 mm; height 9 mm). Shell elongate-ovate to triangular, mostly inequilateral. Umbo on the anterior side.

The dorso-anterior side is straight to slightly convex, anterior, ventral and posterior sides are rounded. Some species have white, others coloured shells; the periostracum is nearly always completely worn off. The surface can be smooth and glossy with concentric growth lines only, or it can have distinct concentric ridges. But in all species radial sculpture is present, although in some species only on very few specimens. Although denied by some authors (Lamy, 1914: 12; Davis, 1967: 233), the *Ervilia*'s do have 2 lateral teeth in the right valve. The pallial sinus is deep and the pallial line is looped posteriorly on the ventral side of the sinus (see Fig. 5).

DISTRIBUTION OF THE GENUS

Ervilia seemed to appear suddenly in Europe during the Eocene. Their fossils are found in many of the sediments of the Thetys Sea: in Poland, Austria, France, North Italy and even in South Italy. The distribution of the fossils is mostly along the margin of the distributional area of the Recent species. It is strange to notice that they do not occur in the Mediterranean in recent times. I have as yet no explanation for this phenomenon. They have a really good adaptability, as is evident by their occurence in both the Atlantic Ocean and the Red Sea.

Ervilia nitens (Montagu, 1808) (Figs. 1 and 5)

Mya nitens Montagu, 1808: 165.
Ervilia nitens (Montagu); Turton, 1822: 56, pl. 19, fig. 4.
Ervilia concentrica Gould,* 1862: 281.
Ervilia subcancellata Smith, 1885: 80, pl. 6, fig. 2-2b.
Ervilia maculosa Dall, 1896: 26.
Ervilia californica Dall, 1917: 414.
Ervilia rostratula Rehder, 1944: 189, pl. 19, fig. 1-2.

*Holmes described in 1860 a fossil *Ervilia* and named it *Mesodesma concentrica*. According to Davis (1967) it is conspecific with *Ervilia concentrica* Gould. I do not want to express an opinion now because I have not yet made a thorough study of the fossils.

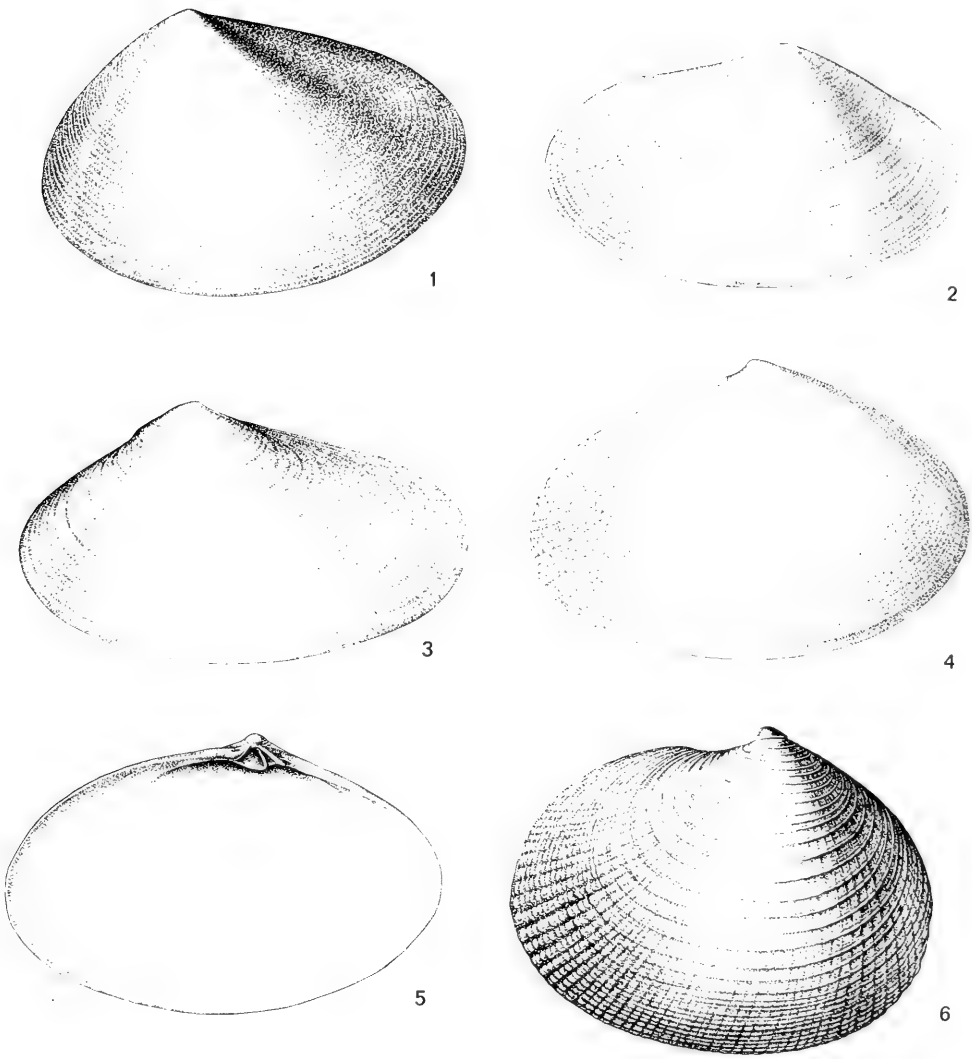
Diagnosis:

Medium sized *Ervilia* (max. length 9 mm, height 6 mm). Shell ovate to triangular. The appearance of the apex is variable. Sometimes, especially in pink specimens, the outline is rounded, hardly disturbed by the umbo. Sometimes the umbo projects conspiciously. All intermediate forms do occur. Shell white to pink. Concentric ridges all over the shell. If radial sculpture is present it is distinct but not as deep as the concentric ridges. Radial sculpture is mostly only present on the posterior side; however, sometimes it is found on the anterior side as well.

Remarks:

Ervilia nitens was first described from specimens found in Durban, Scotland. These few valves are so often mentioned in the literature that the species is considered British by many authors, even recently. I think, however, that Forbes & Hanley (1853: 345) were probably right in supposing that sailing ships brought them from the West Indies in their ballast sand which they put down in the Scotch harbour, thereby bringing these Caribbean molluscs to places far from their habitat.

The species is so very pluriform that it was described as 6 species. The synonymy of *Ervilia maculosa* with *E. concentrica*, and of *E. rostratula* with *E. subcancellata*,



FIGS. 1-6. *Ervilia* species. FIG. 1. *Ervilia nitens*. Left valve of type specimen of *E. californica*. San Pedro, California. Nat. size: 6.5 mm long, 4.5 mm high. FIG. 2. *Ervilia castanea*. Right valve. Portinho, Portugal. Nat. size: 12 mm long, 7 mm high. FIG. 3. *Ervilia scaliola*. Left valve. Ras Matarma, Red Sea. Nat. size: 6 mm long, 3.5 mm high. FIG. 4. *Ervilia bisculpta*. Right valve. Shionomisaki, Japan. Nat. size: 4.6 mm long, 3.2 mm high. FIG. 5. *Ervilia nitens*. Innerside left valve of type specimen of *E. maculosa*. Cape Lookout, North Carolina. Nat. size: 4.7 mm long, 3.0 mm high. FIG. 6. *Ervilia sandwichensis*. Right valve. Oahu, Sandwich Islands. Nat. size: 3.0 mm long, 2.3 mm high.

had also occurred to J. D. Davis (pers. comm., 1969). The study of the type specimens and of great amounts of material of this species from localities all over the western part of the Atlantic Ocean has convinced me that there is only 1 species in that region (Chart 1).

Ervilia castanea (Montagu, 1803) (Fig. 2)

Donax castanea Montagu, 1803: 573, pl. 17, fig. 2.
Capsa castanea, Turton, 1822: 128, pl. 10, fig. 13.
Ervilia castanea, Chenu, 1843: 3.

Diagnosis:

Large *Ervilia* (max. length 12 mm, height 6 mm). Shell elongate-ovate, mostly inequilateral. The dorsal posterior side is mostly slightly concave. The valves are light brown. The pigmentation of the shell is often radial. The smooth surface is glossy and has concentric growth lines only. A few specimens have a distinct but very shallow radial sculpture as well.

Remarks:

The material I have seen of this species suggests that it has its relict distribution around the Azores. I think this may be the only Recent habitat, whereas material found in other localities has been brought there by sea currents (Chart 1).

Ervilia scaliola Issel, 1869 (Fig. 3)

Ervilia scaliola Issel, 1869: 53, pl. 1, fig. 2.
Ervilia purpurea Deshayes, manuscript name.

Diagnosis:

Large *Ervilia* (max. length 15 mm, height 9 mm). Shell elongate-ovate, mostly inequilateral. The dorsal posterior side is mostly slightly concave. The shells are white to deep purple. The colour of the shell has mostly a radial pattern. The surface is mostly smooth with growth lines only and sometimes superficial radial structure. Some specimens have concentric ridges and obvious radial sculpture on both the anterior and posterior sides.

Remarks:

This species lives mostly in sea water with an extremely high salinity, viz., about 45‰ in the Red Sea and up to 55‰ in parts of the Persian Gulf. The shells from these areas are almost invariably smooth with growth lines and very superficial radial sculpture only. Specimens from the only locality with a lower salinity known to me, viz., Karachi have obvious concentric and radial sculptures (Chart 1).

Ervilia bisculpta Gould, 1861 (Fig. 4)

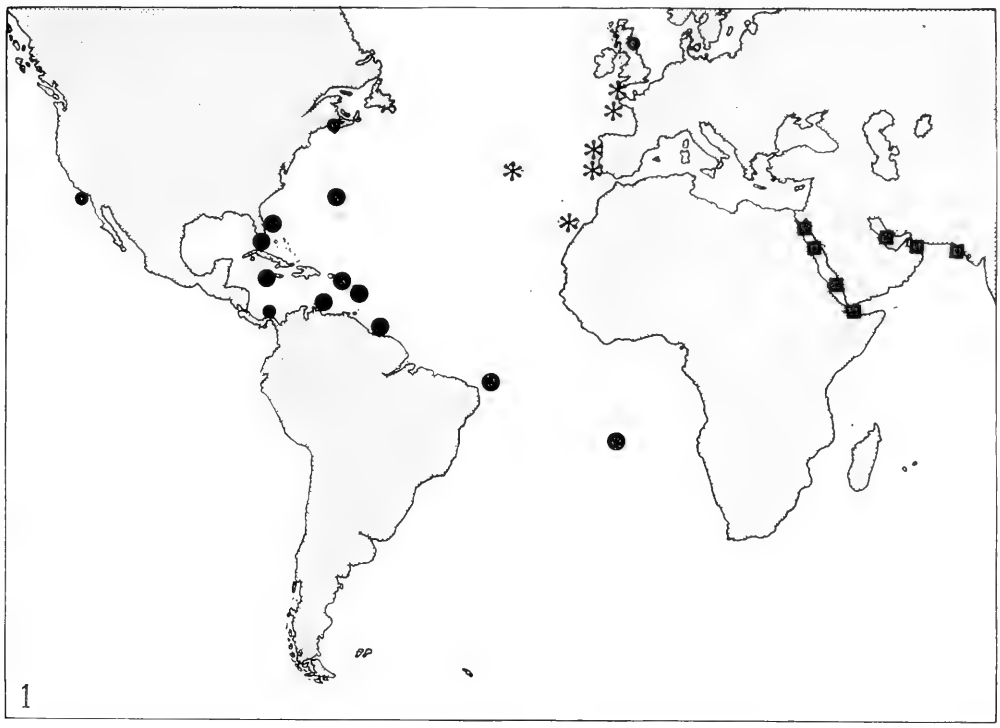
Ervilia bisculpta Gould, 1861: 28.
Ervilia livida Gould, 1861: 28.
Ervilia japonica Adams, 1862: 224.
Ervilia australis Angas, 1877: 175, pl. 26, fig. 21.
Ervilia ambla Dall, Bartsch & Rehder, 1938: 171, pl. 44, fig. 5-8.

Diagnosis:

Small *Ervilia* (max. length 7 mm, height 4 mm). Shell elongate-ovate to triangular, often equilateral. Anterior and posterior dorsal margins straight to slightly convex. The shells are white, often with an ivory shade. Concentric ridges all over the surface and very deep radial sculpture on both the anterior and posterior sides.

Remarks:

The study of type specimens and of material from many localities has convinced me that the species *Ervilia livida*, *E. japonica*, *E. australis* and *E. ambla* are conspecific



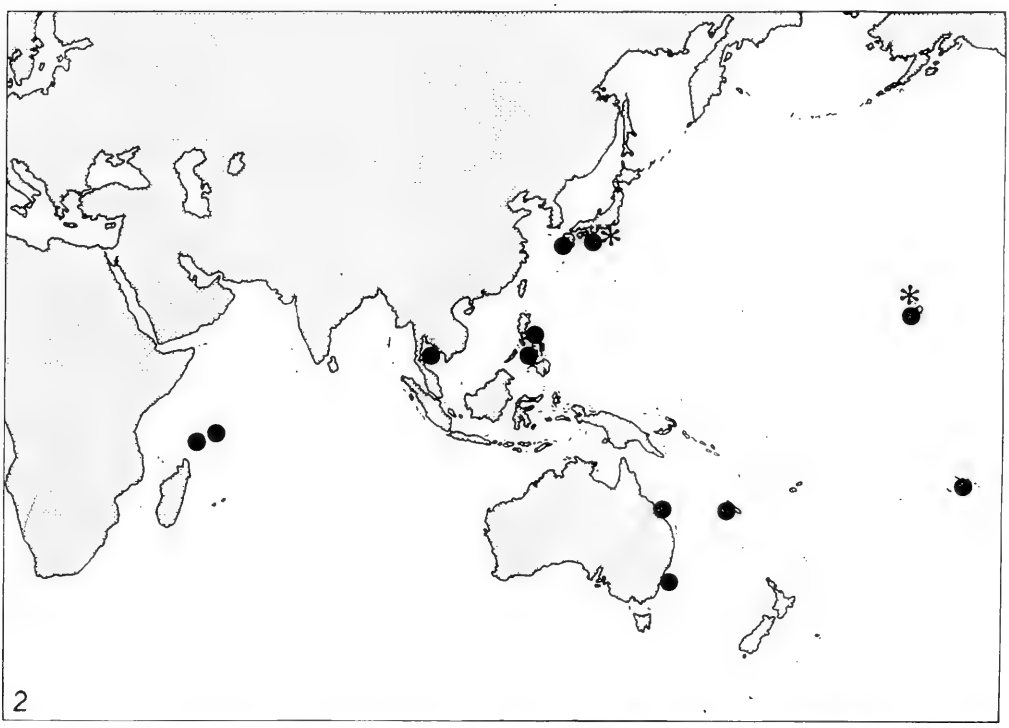


CHART 1. ●*Ervilia nitens*, ●*Ervilia nitens*, dubious loc., ✱*Ervilia castanea*, ■*Ervilia scaliola*.
CHART 2. ●*Ervilia bisculpta*, ✱*Ervilia sandwichensis*.

with *E. bisculpta*. The species has a much wider distribution than formerly was assumed. In the localities near the Seychelles and Amirante Islands it approaches the area of *E. scaliola*, thus forming a more or less continuous area of distribution for the genus (Chart 2).

Ervilia sandwichensis Smith, 1885 (Fig. 6)

Ervilia sandwichensis Smith, 1885: 81, pl. 25, fig. 5-5b.
Rochefortia (Rochefortina) semele Dall, 1924: 88.
Rochefortina sandwichensis Dall, Bartsch & Rehder, 1938: 169.

Diagnosis:

Tiny *Ervilia* (max. length 3 1/2 mm, height 2 1/2 mm). Shell rounded ovate. The posterior side is somewhat expanded in the dorsal direction, thus forming a small cavity in the posterior dorsal margin, near to the umbo. Because of this the dorsal laterals do not quite reach the umbo. The umbo projects distinctly from the dorsal side. The surface of the white valves has both deep concentric ridges and deep radial sculpture all over the shell.

Remarks:

This rare species is only known from the Sandwich Islands and Japan (Chart 2).

Principal localities

Ervilia nitens: Dunbar, Scotland; St. Helena; Fernadez de Noronha; Dutch Guyana; St. Martin, Antilles; Guadeloupe; Barbuda; Lake Worth; Bermuda; San Pedro, California.
Ervilia castanea: Falmouth; Treen; Porthcurno; Scilly Islands; Roscoff; Portinho; Setubal; Canaries; Azores.
Ervilia scaliola: Karachi; Persian Gulf; Gulf of Bahrein; Djibouti; Dahlak; Ras Matarma; Gulf of Akaba; Bitter Lakes.
Ervilia bisculpta: Mast Head Island; Port Jackson; New Caledonia; Society Islands; Sandwich Islands; Shionomisaki; Kagoshima; Philippines; Gulf of Thailand; Seychelles; Amirante Islands.
Ervilia sandwichensis: Honolulu; Shionomisaki.

ACKNOWLEDGEMENTS

This study was partly made possible by grants from The Netherlands Foundation for the Advancement of Tropical Research (WOTRO), The Royal Netherlands Academy of Sciences and The Ter Pelkwijk Fund.

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MALACOLOGIA, 1973, 14: 242-243

PROC. FOURTH EUROP. MALAC. CONGR.

DIE GATTUNG *MELANOPSIS* FERUSSAC 1807 AUF NEUKALEDONIEN

Ferdinand Starmühlner

1. *Zoologischen Institut der Universität Wien, Österreich*

ZUSAMMENFASSUNG

Die Gattung *Melanopsis* ist rezent einerseits von den Küstenländern des Mittelmeeres (mit verwandten Gattung, z.B. *Fagotia* und *Amphimelania* auch an Reliktstandorten in Mittel- und Südsteuropa) bis nach Iran, andererseits im Südwestpazifik in Neukaledonien und Neuseeland verbreitet. Nach Sunderbrinck (1929) dürften sich die Cerithiidae und Thiaridae (=Melaniidae) im unteren Trias von ausgestorbenen Pseudomelaniidae ableiten. Im oberen Jura dürfte es schliesslich zur Aufspaltung der rezent rein marinen Cerithiidae und der rezent brackisch oder limnisch lebenden Thiaridae gekommen sein. Am Übergang zwischen Kreide und Tertiär spalten sich die Melanopsinae von den übrigen Thiaridae ab, wobei es zum Übergang von marinen Litoralformen zu Brackwasser-bzw. Süsswasserformen gekommen sein dürfte. Zahlreiche *Melanopsis*-Arten, darunter auch die neukaledonischen Arten, zeigen auch heute noch eine Toleranz zu Brackwasser, d.h. sie sind von reinen Süsswasserabschnitten der Flüsse bis zu den brackischen Flutrückstaugebieten anzutreffen.

Nach Bubnoff (1956) bildete im Alttertiär das äquatoriale Mittelmeer noch einen durchlaufenden Gürtel von Mexiko über Gibraltar und den Südsaum Eurasiens bis zu den Sunda-Inseln, Neuguinea und Neuseeland, wobei alte Massive die Tethys in einzelne Stränge zerlegte. In dieser Zeit wird von den Geologen auch die Auffaltung von Neukaledonien aus marinen Sedimenten der papuanischen Geosynklinale von Neuguinea bis Neuseeland zwischen Australien und dem allmählich im Meer untertauchenden Tasmania-Kontinent angenommen (Le Borgne, 1964). Es ist daher möglich, dass dabei, die im Küstensaum der Tethys von Eurasien vorkommenden Melanopsiden in eine neuseeländisch - neukaledonische, bzw. mediterran-vorderasiatisch Gruppe aufgespalten wurden.

Die langzeitige Isolierung der Gattung auf Neukaledonien führte bei der Variabilität der Schalengrösse, -form, und -färbung zur Ausbildung zahlreicher Schalenvarietäten, die von den älteren Konchyliologen als eigene Arten beschrieben wurden. Bei der Durchsicht der Arbeiten von Morelet, Gassies, Crosse und Reeve findet man über 25 neukaledonische Arten beschrieben. Bereits Brot (1874) fasste diese Arten in seiner Monografie über die Melaniaceen auf drei Gruppen, die *Melanopsis frustulum* Morelet 1856/57-Gruppe, die *Melanopsis brevis* Morelet 1857-Gruppe und die *Melanopsis mariei* Crosse 1869-Gruppe zusammen. Pérès (1945/46) und Franc (1956) beliessen nach dem Studium des Schalenmaterials im Pariser Museum 6, bsw. 7 Arten für Neukaledonien.

Nach den Serienaufsammlungen der Österr. Neukaledonien-Expedition 1965 und anatomischen Studien lassen sich auf Neukaledonien zwei Arten, *Melanopsis frustulum* und *M.* (*Zemelanopsis*) *mariei* aufstellen, wobei erstere, mit stark variabler Schale, in 6 verschiedene Formen zerfällt, die aber durch deutlich Übergänge verbunden sind. Anatomisch lassen sich die Formen nicht unterscheiden, ja es ist kaum möglich deutliche anatomische Unterschiede zu den mediterranen Arten zu finden (Starmühlner, 1970). So besitzen die neukaledonischen *Melanopsis*-Arten wie alle bisher untersuchten mediterranen, bzw. iranischen Arten sowohl beim ♀ als beim ♂ eine offene Genitalrinne, die von einer hohen Falte überdeckt wird, in der rechten äussersten Mantelbodenhälfte. Das Weibchen besitzt eine drüsige Laichgrube (Ovipositor) am Übergang zwischen Mantelhöhlenboden in die äussere Fussfläche. Der Medianzahn der Radula zeigt bei *M. frustulum* die Formel 2/3+1+2/3, der Lateralzahn 1/2+1+1/2, innerer Marginalzahn mit 4-5, äusserer Marginalzahn mit 4, seltener 5 kleinen Dentikeln. Bei *M.* (*Zemelanopsis*) *mariei* ist die Zahl der Nebendentikel des Lateralzahnes etwas grösser, die Formel lautet demnach 2/3+1+4/5, äusserer Marginalzahn mit 5, innerer Marginalzahn mit 6 Dentikeln. Die Radula entspricht bei *M.* (*Zemelanopsis*) *mariei* mehr der neuseeländischen *M.* (*Zemelanopsis*) *trifasciata*, der die Art auch in der Schalenbildung, mit rasch zunehmenden Umgängen, sehr nahe kommt.

Im Anschluss an Pérès (1945/46) wurden 6 Formen von *Melanopsis frustulum* nach forma (Form und Grösse der Schale), modus (Art und Höhe des Gewindes) sowie coloratus (Färbung) unterschieden.

1) *M. frustulum* f. *normalis* (*-cylindrus*), m. *normalis-corrosus*, col. *maculatus*
2) *M. frustulum* f. *normalis* (*-curta*), m. *normalis-corrosus*, col. *fasciatus*
3) *M. frustulum* f. *normalis-curta*, m. *minor-corrosus*, col. *fasciatus*
4) *M. frustulum* f. *normalis-cylindrus*, m. *normalis-corrosus*, col. *multistriatus*
5) *M. frustulum* f. *normalis-cylindrus*, m. *normalis-corrosus*, col. *fasciatus* (et *fuscus*)
6) *M. frustulum* f. *curta-cylindrus*, m. *minor-corrosus*, col. *fasciatus*

Die ersten zwei Formen sind durch deutliche Übergänge verbunden und besiedeln die Urwaldbäche und -flüsse der zentralen Gebirge, die gegen die West, bzw. Ostküste abfliessen. Die 3. Form ist eine Zwerg- bzw. Kümmerform der 2.Form und findet sich isoliert ausschliesslich in zwei kleinen Seen (Lac en 8 und Grand Lac) in der Hochebene des südlichen Serpentingebietes in Gewässern mit äusserst geringem Mineralsalz-und Nährstoffgehalt (El_{20}:56 Mikro-Siemens) Die Formen 4-6 sind durch Übergänge verbunden und die subzylindrische Ausbildung des letzten Umganges gekennzeichnet. Es finden sich aber auch Übergänge zu den Formen 1-3 mit mehr spindelförmigem letztem Umgang. Sie besiedeln ausschliesslich die Unterläufe, bzw. Mündungsgebiete der Bäche und Flüsse und finden sich häufig, wenigstens zeitweise, in Brack-

wasser.

Melanopsis (*Zemelanopsis*) *mariei* wurde nur in den Fliessgewässern im Süden Neukaledoniens im Bereich der Serpentin-Macchie gefunden. Am Rande von Urwald und Macchie tritt die Art in gemischten Populationen mit *M. frustulum* f. *norm.-curta*, m. *norm.-corr.*, col. *fasciatus* auf. Die Arten lassen sich dabei leicht nach der Art der Zunahme der Windungen unterscheiden. Wie bereits erwähnt, steht *mariei*, nach der Form der Schale, der neuseeländischen Art *M.* (*Zemelanopsis*) *trifasciata* sehr nahe.

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MALACOLOGIA, 1973, 14: 244-246

PROC. FOURTH EUROP. MALAC. CONGR.

ON A POLYPLACOPHORA DESCRIBED BY MONTEROSATO

B. Sabelli

Istituto di Zoologia dell'Università, Bologna, Italia

ABSTRACT

About 2 years ago I began to review the Mediterranean Polyplacophora. During these studies I checked the types of *"Chiton"* (*sensu lato*) described by Monterosato. Thanks to the kind offices of Mr. Settepassi, whom I wish to thank, I was able to study the original specimens preserved in the Monterosato collection, now located in the Zoological Museum of Rome. This time I will describe only *C. phaseolinus*, 1 of the 4 species of the Sicilian malacologist. Monterosato (1879) settled this species according to about 30 specimens from Arenella, a locality near Palermo (Sicily) (Fig. 1). Only a small number of these specimens are now in the author's collection, and another specimen, with a manuscript label of Monterosato, was given to him by A. Costa. I was able to study the species on the basis of cited specimens and also on about 10 others, corresponding to types (Figs. 2, 3) which were found by Dr. Spada and Prof. Franchini in 1968, 1969 and 1970. So it was possible for me to examine isolated valves and microscopical preparations of perinotum.

As already observed by Monterosato (1879), this species belongs to the genus *Chiton*. This is substantiated by 2 characters: its pectinate insertion plates and the thick rhomboid scales of perinotum. The esthetes also are typical of the genus *Chiton*. The shell is more narrow than in *C. corallinus*, with which it was often confused; it is not carinated, is on the average smaller (5-7 mm) than in the 2 congeneric species (*C. olivaceus* and *C. corallinus*) and is a pale green colour, sometimes with some whitish stains (the specific name *phaseolinus* is due to its colour).

The tegmentum of intermediate and posterior valves (Fig. 4b, c) has 2 evident small elevated lateral areas. The sculpture is absent or sometimes is made up of 2-3 scars which are similar in shape to those of *Callochiton achatinus*.

The articulamentum of the head valve has an insertion plate cut into a very variable number of pectinated teeth (8-14) (Fig. 4d), that of the posterior valve always has 8-9 teeth (Fig. 4f). The insertion plates of the intermediate valves (Fig. 4e) are divided into 2 teeth by an incision. The triangular apophyses (Fig. 4b, c, e, f) extend medially to the point of nearly joining; they are like indentations in the jugal zone.

The esthetes (Fig. 5) have an arrangement like those of *Chiton olivaceus* and *C. corallinus:* generally in the lateral areas there are about 8 micresthetes around an evidently larger megalesthete. In the median area the esthetes are more scarce than in the lateral areas and the size difference between micro-and megalesthetes decreases.

Gills of the adanal type are present along the whole length of the foot.

Dorsally the perinotum (Fig. 6a) has ellipsoid scales much more elongated than the ones of *Chiton olivaceus* and *C. corallinus*, and the scale surface is covered by a high number of ribs perpendicular to its major axis. Between these ribs there are irregular concentric wrinkles (Fig. 6b). A spiculose fringe is present and between the spicules we can observe long and subtle bristles like those described by Blumrich (1891) in the perinotum of *C. olivaceus*.

The morphological characters now cited are, in my opinion, sufficient to confirm the validity of the species. In addition, there are ecological data which distinguish this species from its congeneric ones. In fact the specimens of Monterosato (1879), Costa and others I cited before were collected between 1 and 4 meters depth. So it is clear that this species lives in shallow waters; on the contrary, *Chiton corallinus*, with which it is easily mistaken at a superficial analysis, lives in deeper waters (more than 15 m).

On the basis of the 5 recent findings of *Chiton phaseolinus*, the distribution of this species is to be extended to Lampedusa (Cala spugne, 1 specimen, 1968), Pantelleria (Scauri, 1 specimen, 1968), Camerota (Salerno, 2 specimens, 1969), Mazzarò (Taormina, 6 specimens, 1970), Capo de Gata (Southern Spain, 1 specimen, 1970). The species probably lives in Italy on all coasts of Sicily and on the Tirrenic coast of Calabria and Campania.

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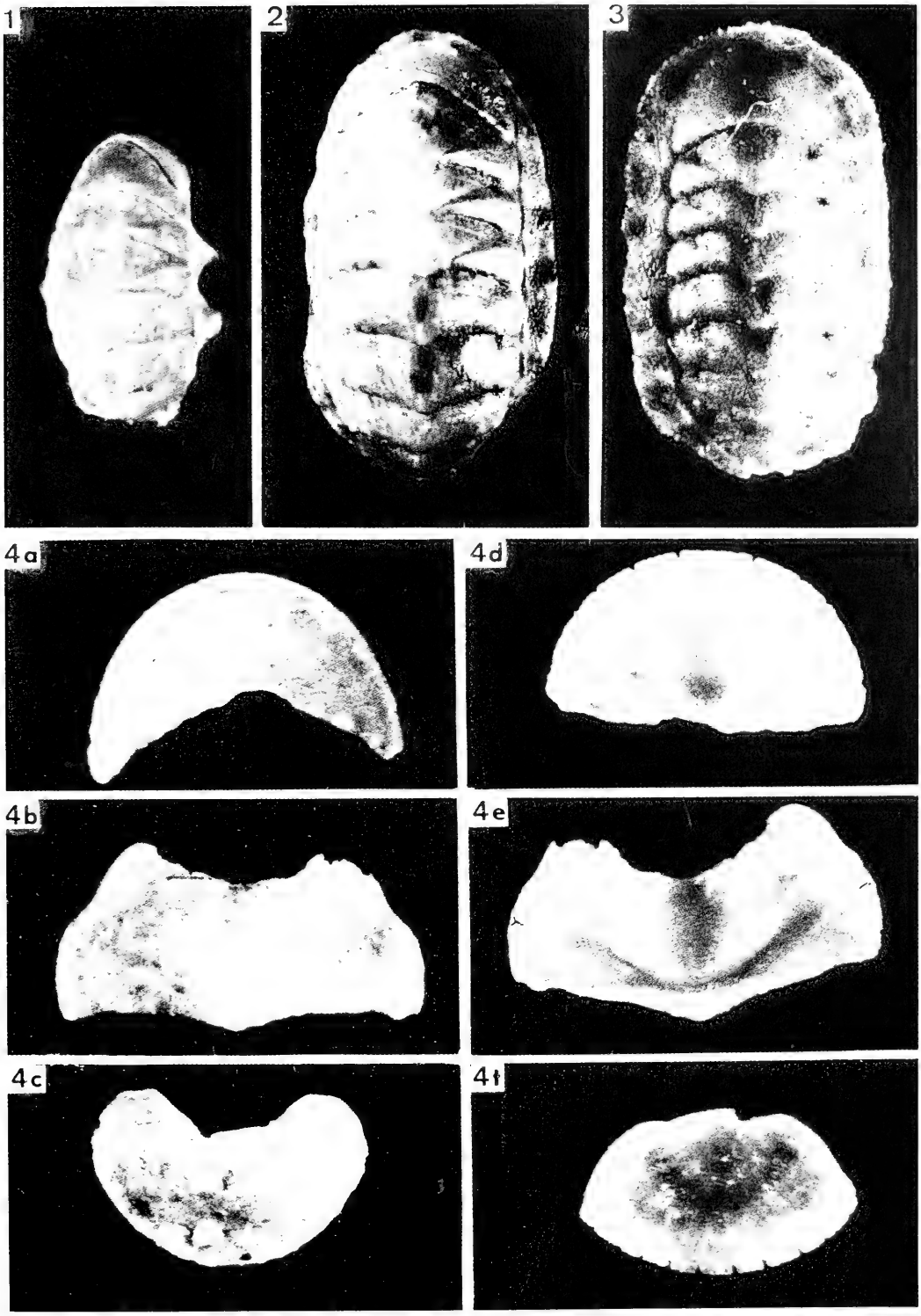
FIG. 1. Specimen from the Monterosato collection (Arenella), 7x. FIG. 2. Specimen from Pantelleria (Scauri) legit Spada, 1968, 12x. FIG. 3. Specimen from Camerota (Salerno) legit Spada, 1969, 10x. FIG. 4. Isolated valves of a specimen from Mazzarò (Taormina), about 20x. a, dorsal view of the 1st valve; b, dorsal view of the 4th valve; c, dorsal view of the 8th valve; d, ventral view of the 1st valve; e, ventral view of the 4th valve; f, ventral view of the 8th valve.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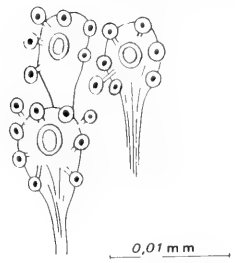

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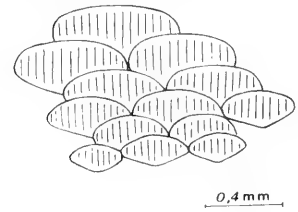
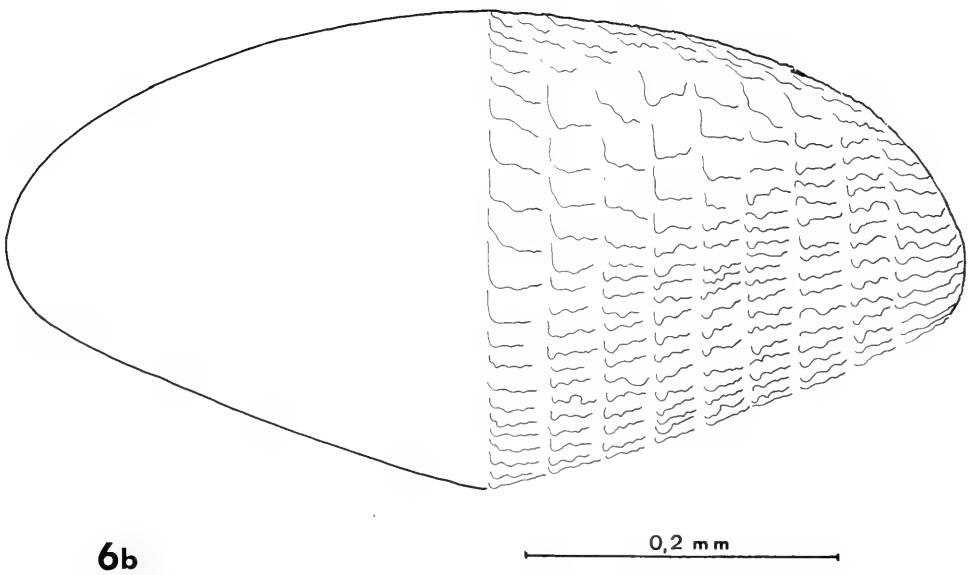


6a



6b

FIG. 5. Esthetes of the lateral area.

FIG. 6. a, Scales of the upper surface of the perionotum. b, Detail of a scale of the upper surface of the perinotum.

MALACOLOGIA, 1973, 14: 247-270

PROC. FOURTH EUROP. MALAC. CONGR.

THE SPECIES COMPLEX OF *DIPLODON DELODONTUS* (LAMARCK) (UNIONACEA - HYRIIDAE)

J. J. Parodiz

Carnegie Museum, Pittsburgh, Pennsylvania, U.S.A.

ABSTRACT

The relationships among 6 species of the genus *Diplodon,* belonging to the superspecific complex of *D. delodontus* (Lamarck), were studied to clarify their identification; a full conchological revision was made from which some species names, formerly placed in synonymy, were revalidated. The species here recognized are: *Diplodon delodontus* (Lamarck 1819); *D. delodontus wymani* (Lea 1860); *D. solisianus* (d'Orbigny 1835); *D. uruguayensis* (Lea 1860); *D. martensi* (Ihering 1893); *D. expansus* (Küster 1856); and *D. paulista* (Ihering 1893). Their distribution includes the Paraná-Uruguay-La Plata river system in South America (southern Brazil, northeastern Argentina and Uruguay); since such a system (as we know it today) did not exist before the Pleistocene epoch, the occupation of the area and process of speciation took place very rapidly and close to the Recent, which explains the great affinity still shown by the species. Many hybrids within the populations were detected. Species sympatry, overlapping large portions of their areas of dispersion, precludes any subspecific treatment of the taxa (except in the case of *D. delodontus wymani*). Populations of different species are co-habitants of the same ecological niches; therefore the variations frequently found are not always phenotypical but rather genetical due to crossbreeding. The concept of superspecies is applicable to the *D. delodontus* group, being a monophyletic one of very closely related species, and their genetic affinities allow for recurrent hybridization.

Species of the *Diplodon delodontus* group inhabit the middle and lower sections of the Paraná River, the Uruguay River and tributaries of the La Plata River system in South America, covering the areas of Southern Brazil, northeastern Argentina and Uruguay. In the present study, 6 species and 1 subspecies are recognized as belonging to this group or superspecies.

In the abundant literature on the genus, the taxonomy included about 50 nominal taxa for the group. Names were given to individual variations, ecological forms, clines and especially various hybrids populations. Among the 7 recognized taxa, some "variations" which appeared recurrently were identified as caused by crossbreeding; the lack of a prevalent evidence of allopatry in such intermediate forms precluded any subspecific consideration, except only in 1 case, of *Diplodon delodontus wymani* (Lea).

Two or more different populations were found at short intervals at the same locus and ecological niches, and this not only renders it ineffectual to class them as "ecological forms," but actually they represented either different species or hybrid populations.

As it has been demonstrated with other naiads from North America by a number of authors, and especially among the more recent ones, by Henry van der Schalie and David Stansbery, species which participate in environmental conditions of great similarity frequently show also similarity on their external characteristics, even when their relationships may be not too close, while at different locations one same species may have peculiarities of form, color or other shell characters, and can be

recognized clinally and ecologically. Such phenomenon obviously produced taxonomic confusion among the less known South American groups, a confusion which lasted many years. Sometimes, the differences found according to location are not simply phenotypical; van der Schalie has shown (1941) that specimens transferred from their habitat in rivers to be reared in lacustrine environments, preserved the features of the former, and this is an indication that the characteristics have also a genetic constituency.

Many of the named species of the genus *Diplodon* were placed in synonymy on embryological bases, i.e., by similarities of the glochidia. But the fact that 2 entirely dissimilar adult populations have larval stages that look alike is not an indication of conspecificity, because many of the characters with specific value may not become conspicuous until an advanced stage in the development of the individual. In well formed but still very young shells, differences can be detected which even when in their glochidial stage were undistinguishable. The great importance of glochidial identification is at the genus, subgenus or species-group level.

Hybridization in mollusks is an occurrence which until recently received not enough attention. In gastropods, among which hybridization is even less known than among bivalves, several studies have recently dealt with the subject (e.g., the perfectly demonstrated hybridization by Owen, McLean & Meyer (1971) among several species of *Haliotis* from California). In bivalves, an interesting case of hybrid *Tellina* was disclosed by Boss. In freshwater bivalves, especially, their system of reproduction affords conditions very favorable to crossbreeding. In groups of species whose genetic constituency is of great affinity and monophyletic, and with populations largely sympatric, hybridization may not only be feasible, but frequent. Masculine gametes of 2 or perhaps more closely related species fertilizing a single female individual may result in offspring which are heterozygous as well as homozygous.

For the purposes of identification, hybrids, as individuals or as populations, are recognized if the parental species involved are well known to the taxonomist in their most prevalent characteristics, as well as in their range of variation of distribution. Synonymies were usually made on second hand references, or analysis not careful enough, of original descriptions produced early last century, and this commentary is valid too for species which were created after 1900.

The *Diplodon delodontus* group, with the complexity of its populations, leads us to the concept, which applies to it, of the superspecies. Simplifying other more elaborate definitions, the superspecies is a non-taxonomic (that is, not for nomenclatorial purposes) monophyletic group of very closely related species. The species recognized in our particular group are: *Diplodon solisianus* (d'Orbigny 1835), *D. uruguayensis* (Lea 1860), *D. martensi* (Ihering 1893), *D. expansus* (Küster 1856), *D. paulista* (Ihering 1893), *D. delodontus* (Lamarck 1819) and *D. delodontus wymani* (Lea 1860).

The following hybrids, as individuals or populations, have been detected:

Diplodon delodontus delodontus
x *D. solisianus*
x *D. d. wymani*
x *D. uruguayensis*
x *D. martensi*

Diplodon uruguayensis
x *D. martensi*
x *D. expansus*

Diplodon expansus
x *D. paulista*

Diplodon delodontus delodontus (Lamarck 1819); Figs. 1, 6, 7, 8

Unio delodonta Lamarck, 1819: 77. Delessert, 1841: pl. 12, fig. 7. Catlow & Reeve, 1845: 58, No. 69. d'Orbigny, 1846: 605. Hupe, in Castelnau, 1857: 82. Formica Corsi, 1901: 449, No. 132.

Unio delodon Martens, 1868: 193, 212. Strobel, 1874: 71.

Unio delodontes Doering, 1875: 66 (Buenos Aires, Montevideo, Paraná, Corrientes).

Unio delodontus Sowerby, in Reeve, 1864/67: fig. 288. Küster, 1861: 234, pl. 88, fig. 5. Clessin, 1888: 171. Paetel, 1890: 150.

Unio lacteolus Lea, 1834: 40, pl. 8, fig. 19 (and 1834 Observations: 152, pl. 8, fig. 19 - type loc. Rio de la Plata). d'Orbigny, 1835: 34 (*lacteola*). Lea, 1867: 22. Ihering, 1893: 117. Ortmann, 1921: 518-523, 547, 548 (in part). Simpson, 1914: 1227. Simpson and Ortmann used Lea's *lacteolus* because they considered *delodonta* to be "unidentifiable." Lea, subsequent to his description, compared *lacteola* with the types of *delodonta* and declared them identical (see Synopsis 1836 y 1852). Also d'Orbigny, who apparently had access to Lamarck's materials, identified his own collected specimens as *delodonta*.

Unio divaricatus Lea, 1834a: 64, pl. 9, fig. 24 and 1934b: 176. 1870: 49, 116. Simpson, 1900: 878. Lea indicated *divaricatus* from Egypt! as *Margarita* (*Unio*) 1836, and *Margaron* (*Unio*) 1870. Catlow & Reeve, 1845: 58, No. 74.

Unio rudus Lea, 1859: 187. 1860a: 16 (type loc. Rio de la Plata), 1860b: 84, pl. 43, fig. 146. Küster, 1861: 261, pl. 88, fig. 1. Doering, 1875: 45 (*rudis*, probably from Paetel, 1890). Ihering, 1893: 117 (*rudis*). Simpson, 1900: 875. *U. rudus* corresponds to the typical form of *Diplodon delodontus*.

Unio firmus Lea, 1866: 33; 1868: 267, pl. 34, fig. 82; 1869: 27, 28, same figures (type loc. "South America": Uruguay River near Salto). 1870: 45 (as *Margaron firmus*). Ihering, 1893: 98, 105. Simpson, 1900: 875. Marshall, 1923: 4 (as compared with *podagrosus* which is *uruguayensis*). Haas, 1916: 4. Bonetto, 1961: 17 (as *Diplodon*). The named "Var." *firmus boettgeri* Ihering, 1893 = *martensi* (see Parodiz, 1968 and Mansur, 1970).

Unio paraguayensis Lea, 1866: 34; 1868: 271, pl. 35, fig. 85 and 1869: 31, same plate and figure. (Type loc. "Paraguay"). It is unlikely that the specimens so called by Lea came from Paraguay; they look very much like the form he described as *peculiaris* (which is a hybrid): *delodontus* x *uruguayensis*. Martens' (1895: 34) "*Unio paraguayanus*" is probably the same.

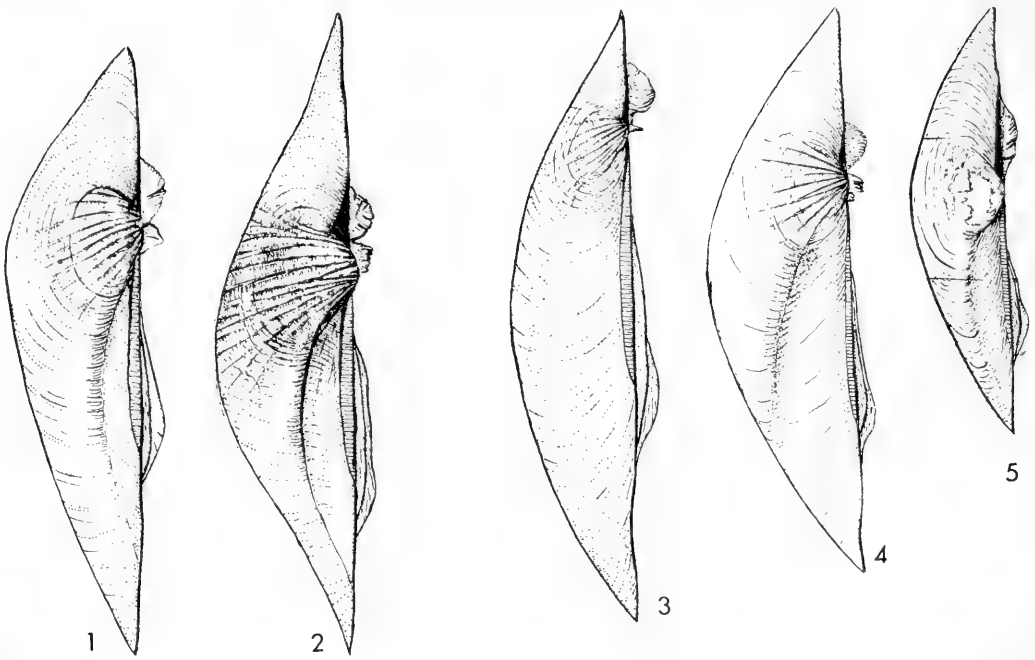
Diplodon firmus, Simpson, 1900: 874 ("more solid than *peculiaris*"); 1914: 1233 ("allied to '*paraguayensis*'"). Bonetto, 1966: 40 (under *rhuacoicus*).

Diplodon charruanus in part, by authors, not *Unio charruana* d'Orbigny 1835. Haas, 1930: 190. Barattini, 1951: 239. Castellanos, 1960: 88.

Diplodon rhuacoicus in part, by authors, not *Unio rhuacoica* d'Orbigny 1835. Bonetto, 1964: 325; 1965: 40.

Diplodon delodontus, Simpson, 1900: 873. Haas, 1930: 182, 190 (in part). Barattini, 1951: 240. Bonetto, 1954: 40; 1959: 47; 1965: 43. Bonetto, Pignalberi & Maciel, 1962: 170. Bonetto & Ezcurra, 1963: 17. Castellanos, 1960: 88. Parodiz & Bonetto, 1963: 17. Figueiras, 1965: 233. Olazarri, 1966: 24 (in part). Parodiz, 1968: 410. Mansur, 1970: 60. Parodiz, 1971: 34 (Amer. malacol. Union, ann. Reps.).

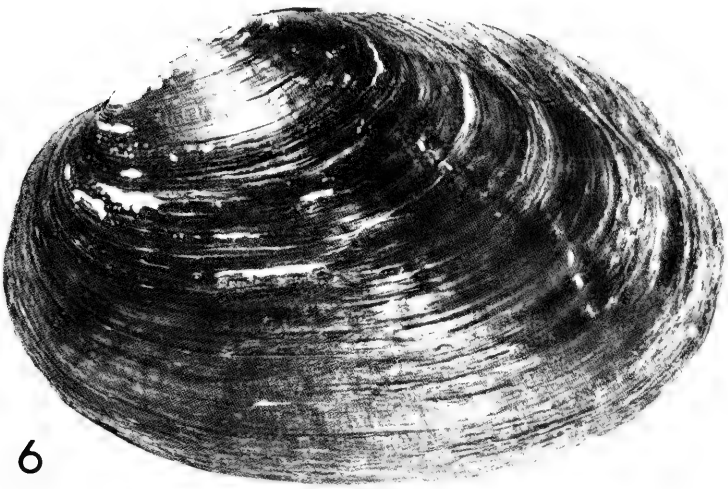
In the synonymy of *Diplodon delodontus* were included also (by Haas 1930 and subsequent authors) several names which do not belong there: *Unio ampullaceus* Lea 1866 and *D. podagrosus* Marshall 1923, both equal to *D. uruguayensis; U. fokkesi* Dunker 1853, a hybrid form between *D. uruguayensis* and *D. expansus; U. browni* Lea 1856, a synonym of *D. rhombeus* Wagner 1827; also, *D. smithi* Marshall 1917, under *D. delodontus* by Bonetto (1954, 1965), is equal to *D. burroughianus*.

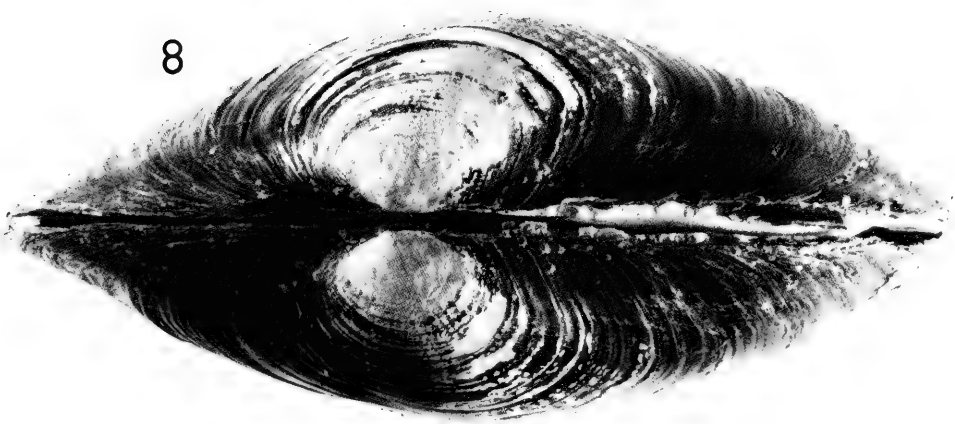


FIGS. 1-5. Umbonal views of left valves of *Diplodon*. FIG. 1. *Diplodon delodontus delodontus* (Lam.). FIG. 2. *Diplodon solisianus* (d'Orbigny). FIG. 3. *Diplodon delodontus wymani* (Lea). FIG. 4. *Diplodon uruguayensis* (Lea). FIG. 5. *Diplodon expansus* (Küster).

Comparing descriptions and illustrations, I agree with Haas (1930) and Bonetto (1955, 1965) to include *Unio paraguayensis* Lea 1866 in the synonymy of *Diplodon delodontus delodontus*. However, collections from the region between São Paulo and the Paraguay River (a gap of about 500 miles, from where intermediate forms of this group are scarcely known) are needed to establish the status of *D. paraguayensis;* the only sample of this form, mentioned by Haas as *delodontus*, is a single valve from Concepción, Paraguay.

Complete description. Shell elliptical, anterior margin normally rounded from the end of the very short lunule to the ventral margin, which is straight in the larger specimens and somewhat curved in the smaller ones. Dorsal margin descending obliquely, or in a slight curve, from the umbos to the posterior margin, which begins approximately at the middle of the dorsal wing; the connection of these 2 margins form an obtuse angle. The posterior margin meets the ventral one at a point below the lower half of the shell; here again a slight angle may be formed, or both posterior and ventral margins fuse into a continuous curve. These angles are variable according to the individuals, the longer ones being more elliptical, the shorter ones more rhomboidal. The dorsal slope below the wing is rounded, but sometimes a weak carina is insinuated. The valves are inflated from the umbo to the middle of the shell, and from that point become rapidly compressed toward the center of the ventral margin, where some radial rugosities appear; the major inflation is posterior to the umbo, a little below the slope. The umbos are prominent in relation to the anterior end, but low in comparison with the ligamental area; the umbonal disk, however, is rather outstanding on account of the lateral inflation. The umbonal sculpture consists of 13, occasionally 15, ribs regularly distributed but extending below the line of the beginning of the anterior margin (that is, no lower than the lunule). There is also a microsculpture





FIGS. 6, 7. *Diplodon delodontus* (Lam.). Paraná River near Santa Fe, Argentina. FIG. 8. *Diplodon delodontus*. Gerontic specimens from Lujan River at Pilar, Argentina (MACN 11570). All 1/2 size.

of concentric lines between the ribs, and sometimes for each 4 or 5 of these costular lines there is one stronger one which crosses the ribs, forming minute nodules (but this is not a reliable diagnostic feature). There are 3 or 4 of these concentric costulae per mm. Three of the main ribs radiating from the tip of the umbo are coalescent; the 2 on the side meet a short distance from the tip forming a V, and the central one unites with them at the angle. In all cases such sculpture is not as strong and not so conspicuous as in *Diplodon solisianus*. The rest of the shell is very rugose, with coarse concentric folds of growth and some radiating lines centrally which are strictly cuticular. The color of the periostracum is very clear brown at the centre of the shell, but it becomes very dark toward the margins, principally on the posterior slope in a mixture of dark green with dark chestnut. The ligament is rather narrow, with its insertion a little posterior to the middle of the lateral teeth, not deep. The narrow lunule is not always well marked. The interior of the shell is pure white (for which Lea called it *U. lacteolus*) and iridescent toward the anterior and posterior margins.

Hinge: Left valve with pseudocardinals divided into 2 conic pieces, the anterior one larger with sharp crenulated edge, and the posterior one an acutely pointed tooth; between them there is a deep fossa divided by an internal bar, and the entire surface of this fossa is rugosely striated. At the base of the anterior denticle there is a deep circular cavity corresponding to the anterior retractor, separated from the anterior adductor by the wall of the tooth base which falls, perpendicularly, to the adductor scar, which is semicircular and confluent to the elongated inferior scar. There are 2 parallel, arcuate, lateral teeth, of which the lower one is wider, ending at the posterior adductor, which is very shallow.

The right valve has its pseudocardinal bifurcated in a longitudinal oblique direction, the lower part of it forming a thick, large and rugose tooth; the upper part is just a narrow bar.

The umbonal cavity has 4 or 5 irregular and rather large mantle muscle scars. A short but relatively wide interdentum is noticeable. A line, visible inside the valves and running from the umbo to the adductor, corresponds to the external dorsal ridge. The depressed exterior middle area of the anterior portion shows inside as a thickening. The pallial line is well impressed.

Type locality. In Lamarck's description the habitat was unknown. D'Orbigny collected the species at several localities on the Uruguay and La Plata Rivers. The synonyms *U. lacteolus* Lea and *U. rudus* Lea were described from the La Plata River; *U. divaricatus* and *U. firmus* Lea were described from the Uruguay River. The species is more abundant in the southern half of the Uruguay River and the lower course of the Paraná. The locality Brazil (Rio Grande do Sul) mentioned by Mansur (1970) was taken from Martens, Simpson and other authors, but apparently no actual specimens were examined.

Distribution. Rio Batel, west of Goya, Corrientes, Argentina (d'Orbigny). Paraguay River at Concepción (Haas)! Haas also indicated "North of Patagonia," probably from a specimen with a wrong label.

Materials observed at the Carnegie Museum. Laguna Guadalupe, Santa Fe, Argentina; Arroyo Urquiza S. of Colón, Entre Rios, Argentina; Arroyo Guaviyú, S. of Salto, Uruguay; Arroyo Malo, Paysandú and Arroyo Miguelete, Colonia, Uruguay. In the Museo Argentino de Ciencias Naturales, Buenos Aires, gerontic specimens from the Lujan River, prov. of Buenos Aires (Fig. 8).

Dimensions. Fifty specimens were measured from the lot of Arroyo Guaviyú: length 64.2-84.5, mean 72.6 mm; height 35.4-52.9, mean 46 mm; width 24.1-36.3, mean 30.8 mm; distance from umbo to anterior margin 12.1-23.9, mean 17.5 mm. The largest specimen observed was from Laguna Guadalupe: length 95, height 60, distance

from umbo to anterior margin 25 mm; it represents a typical, oversized *Diplodon delodontus*.

Individual variations. The most variable external features of *Diplodon delodontus* are shell length and the angulosity of the posterior margin; in some specimens the margin is almost rounded (as in what Lea called *U. rudus*), but in the majority the degree of angulosity differs. The color varies less, and a few shells in a population may be olive-green, especially in the area around the umbo. The hinge varies more according to age, the older hinges obviously stronger, but in individuals not especially old, but short, it is also strong. Sometimes the larger piece of the pseudocardinal of left valve has a longitudinal sulcus, giving the impression of a trifid tooth, but such a feature is not frequent.

The most constant feature in this species is its general shape, within the limits of moderate variations, and the peculiar very rugose surface of concentric furrows, thickened at the lines of growth. Also, the anterior and ventral margins show an imbricate aspect, with stronger rugosities on the posterior margins.

Evidently, the above description and observations of the typical *Diplodon delodontus* correspond to what have been clearly described by Lea as *U. lacteolus* and *U. rudus*. *Unio fokkesi* Dunker, which most authors synonymized under *delodontus*, might be that species, but the type in the Senckenberg Museum, figured by Haas, has a different shape and it is with all probability a hybrid of other east-northern forms. *Unio divaricatus* Lea, erroneously described as from Egypt, is a *Diplodon delodontus* (but not of typical form); Drayton's figure of the umbonal sculpture (pl. 9, fig. 5) is exaggerated.

Hybrids. In comparison with other species of the complex, *Diplodon delodontus* offers less numbers of individual hybrids in its populations, and yet, the types of such hybrids show a greater mixing. From the Paraná to the Uruguay River across Entre Rios, and down to La Plata River at Colonia, the populations of *D. delodontus* are relatively uniform, agreeing with the typical pattern. In the southern localities, however, specimens are smaller but still typical and distinguishable from the subspecies *D. delodontus wymani*. The 2 subspecies have been easily identified by most authors; when intermediates are found there is no doubt that these are hybrids. At Arroyo Malabrigo, Santa Fe, populations of *D. delodontus delodontus* hybridize with *D. solisianus*, this last species being dominant; the umbos, sculpture and posterior slope of the hybrids are like those in *D. solisianus*, but the rugose surface and thickness is as in *D. delodontus*, although more compressed. In no way is it possible to consider such forms as clinal, because there is no gradual modification of characters through a large area; the individual hybrids occur only in the zone of overlap of both species. Although they may reappear in other places in their typical forms, there is always one species dominant over the other, and *D. delodontus* recedes where *D. solisianus* is abundant, and vice versa.

Mature glochidia in *Diplodon delodontus delodontus* are found from April to November. The glochidia, according to Bonetto, are of large size (although not so large as those of *D. paulista*), of about 1/3 mm, and present scarce variability. The marsupium occupies the entire free gill.

*Diplodon delodontus wymani** (Lea 1860); Figs. 3, 9-11

Unio Wymanii Lea, 1860: 90; 1863a: 17, 25, pl. 42, fig. 289; 1863b: 381 (same pl. and fig.); 1867: 23. Sowerby, in Reeve, No. 449. Martens, 1868: 193. Doering, 1875: 45 (*wymani*).

Margaron (Unio) Wymanii Lea, 1870: 35, 103, 137.

Unio delodonta, Ihering, 1893: 117.

Diplodon wymanii, Simpson, 1900: 874; 1914: 1230 (Simpson noted: "extremely

close to *apprimus"*, which is *D. uruguayensis*). Haas, 1916: 12, 47. Castellanos, 1965: 104.

Diplodon felipponei Marshall, 1917: 381, pl. 50, figs. 1-3, pl. 51, fig. 1. Ortmann, 1921: 520 (as *lacteolus*) = *d. wymani* x *d. delodontus*.

Diplodon lacteolus, Ortmann, 1921: 518, 519 (in part).

Diplodon (Cyclomya) paranensis funebralis, Haas, 1931: 36 (in part, not *funebralis* Lea 1860; from Arroyo del Gato, La Plata).

Diplodon delodontus wymanii, Haas, 1930: 192 (in part). Bonetto, 1954: 41; 1964: 325. Bonetto & Ezcurra, 1962: 35. Castellanos, 1960: 89, pl. 2, fig. 13. Figueiras, 1965: 233. Olazarri, 1966: 18, 21, 24 (in part).

Diplodon delodontus wymani, Barattini, 1951: 240. Parodiz, 1968: 5, 11, 16. Mansur, 1970: 62.

*Spelling corrected according to Art. 32 ii, Appendix D II of the International Commission on Zoological Nomenclature.

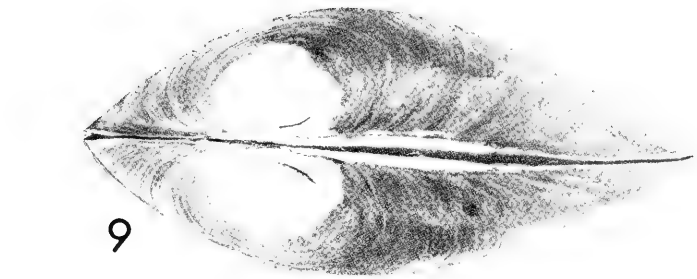
Although the type locality was given as Uruguay River, *Diplodon delodontus wymani* inhabits only the lower portion of that river and the same portion in the Paraná, being more characteristic of the Paraná Delta, La Plata River and its affluents in the Buenos Aires province. Many references to "Uruguay" are due to its having been confused with *D. uruguayensis*. Thus, it can be differentiated easily geographically as a subspecies from *D. delodontus delodontus*, which may be found overlapping with it in the marginal areas.

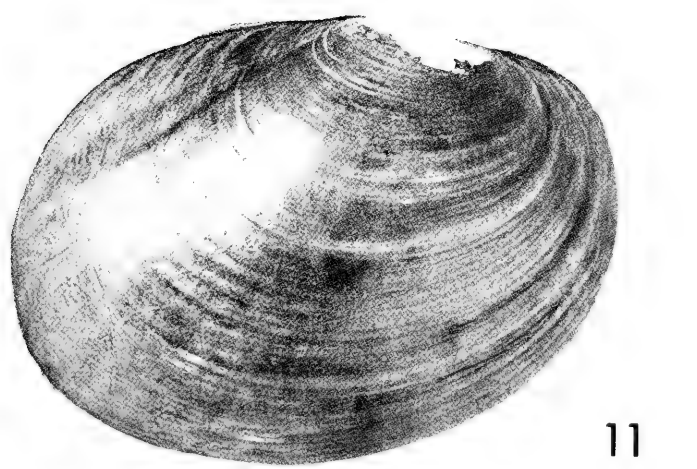
Lea's description suffices to identify the subspecies without difficulty, in spite of certain undefined expressions (the adverb "somewhat" was used 4 times). A characteristic not mentioned by Lea, but which shows well in its figure, is the thinness of the periostracum, dehiscent principally at the margins; the periostracum is also more brilliant than in *Diplodon delodontus delodontus*. Sowerby's (in Reeve) fig. 449 was indicated as taken from one of Lea's specimens, but the greenish coloration is exaggerated.

Of all the forms in the *Diplodon delodontus* complex, *D. delodontus wymani* has the flattest valves, and its contour forms an almost perfect arch with slopes equally descending on both sides, and its umbo is placed in a more anterior position than that in any of the others. The figure of *D. felipponei* in Marshall (1917) represents the typical form of *D. delodontus wymani*. The lateral teeth in *D. delodontus wymani* are thinner and sharper than in *D. delodontus delodontus* and, compared with *D. uruguayensis*, there is practically no interdentum.

Apparently *Diplodon delodontus wymani* is not an abundant but a rather scarce subspecies, and its records in collections are few (when those of *D. uruguayensis* labelled as *D. d. wymani* are eliminated). In the marginal areas where *D. delodontus delodontus* and *D. delodontus wymani* overlap, the typical *delodontus* form is always more abundant, so that when crossbreeding occurs, it shows predominantly in the progeny, and since the parents are conspecific, there is more probability of the fertility diminishing the genetic gap than in other hybrids. That might account also for the proportional scarcity of *D. delodontus wymani*. Therefore only hesitantly can the crossbreeding be termed true hybridization, a designation more fitting when the condition is produced by 2 properly differentiated species.

Haas (1930) united *Diplodon apprimus* (Lea) with *D. delodontus wymani*, but the former name corresponds to an oversized *D. uruguayensis*. As for *D. felipponei* Marshall, its author recalled that it "mimics" *D. delodontus wymani* (it is not *D. paranensis* or *D. funebralis* as referred by other authors); it is, as its type (in the U.S. National Museum) figured by Marshall shows, one of the hybrids, with a shape agreeing with that of *D. delodontus wymani*, but with surface and inflation closer to





FIGS. 9-11. Type of *Diplodon felipponei* Marshall = typical *Diplodon delodontus wymani* (Lea). 1/2 size.

D. delodontus delodontus, for which Ortmann included it in "*D. lacteolus*."

Materials at Carnegie Museum. Typical specimens are from Arroyo Los Gatos, North of city of La Plata, Buenos Aires province. From Arroyo Las Tunas (affluent of Tigre River, Paraná) there is a hybrid with *D. delodontus delodontus*. There are many specimens from Paraná River at Sta. Fe.

The majority of the typical populations examined at the Museo Argentino de Ciencias Naturales at Buenos Aires are from the Paraná Delta and southwest (Figs. 12, 13); also hybrids (Fig. 16).

The specimen observed by Ortmann from a "pond along the Negro River, Uruguay" (collected in 1912 by J. Haseman) and referred as *Diplodon uruguayensis*, is a young of *Diplodon delodontus wymani*, extra-limital.

Diplodon uruguayensis (Lea 1860); Figs. 4, 14, 15

Unio uruguayensis Lea, 1860: 90; 1863: 388, pl. 45, fig. 298; 1863a: 241, pl. 45, fig. 298. Sowerby, in Reeve, 1868: pl. 84, fig. 448 ("Uruguay Riv."). Doering, 1875: 45. Paetel, 1890: 171.

Unio piger Lea, 1860: 90; 1863: 23, pl. 45, fig. 296. Sowerby, in Reeve, 1868: pl. 84, fig. 445. Doering, 1875: 45. Martens, 1868: 212. (Under *D. delodontus wymani* by Haas, 1931 and Castellanos, 1960; under *charruanus* by Bonetto, 1964).

Unio apprimus Lea, 1866: 34; 1868: 263, pl. 33, fig. 78; 1869: 23, pl. 33, fig. 78. Simpson 1900: 874. (Under *D. wymani* by Simpson, 1914, by Haas, 1931 and by Castellanos, 1960; under *D. uruguayensis* by Ortmann 1922).

Unio ampullaceus Lea, 1866: 34; 1868: 269, pl. 35, fig. 83 (type locality "South America" -Paz); 1869: 29, pl. 35, fig. 83. (Under *D. delodontus* by Haas, 1931; under *D. charruanus* by Castellanos, 1970).

Unio peculiaris Lea, 1866: 33; 1868: 265, pl. 34, fig. 80; 1869: 25, pl. 34, fig. 80.

Unio caipira Ihering, 1893: 98, pl. 4, fig. 9i, h ("Southern Brazil"). Nehring, 1894: 83. Bonetto, 1965: 44 (under *D. delodontus expansus*). = *D. uruguayensis* x *D. expansus*.

Margaron (Unio) uruguayensis Lea, 1870: 46, 103, 136.

Margaron (Unio) apprimus Lea, 1870: 46, 102, 111.

Margaron (Unio) ampullaceus Lea, 1870: 53, 102, 110.

Margaron (Unio) piger Lea, 1870: 46, 102, 128.

Margaron (Unio) peculiaris Lea, 1870: 47.

Diplodon apprimus, Simpson, 1900: 874; 1914: 1231. Haas, 1916: 12 (under *D. delodontus wymani*).

Diplodon ampullaceus, Simpson, 1900: 874; 1914: 1230. Haas, 1916: 11. Ortmann, 1921: 518 as *D. burroughianus*?

Diplodon piger, Simpson, 1900: 875; 1914: 1236. Bonetto, 1965: 50 under D. *charruanus*.

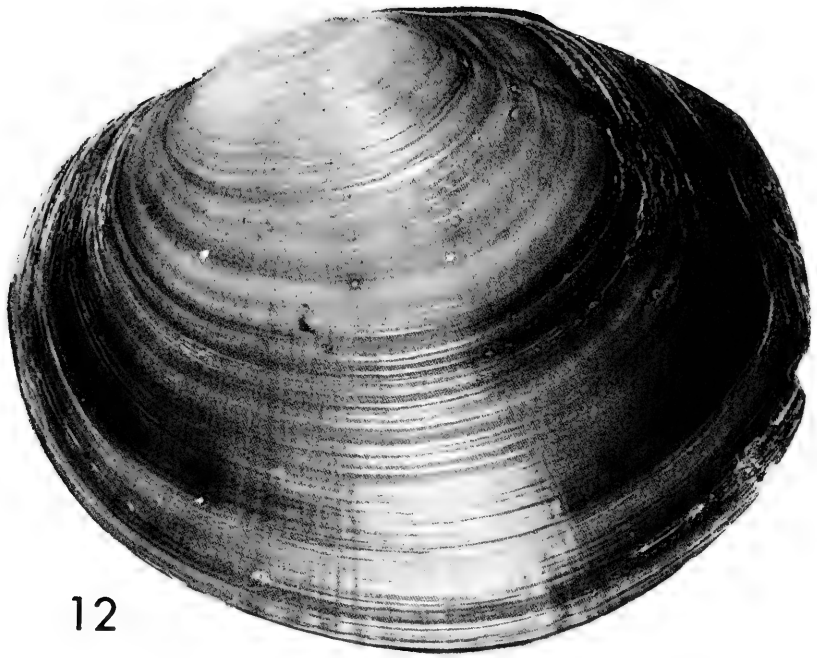
Diplodon delodontus (in part), Barattini, 1951: 240.

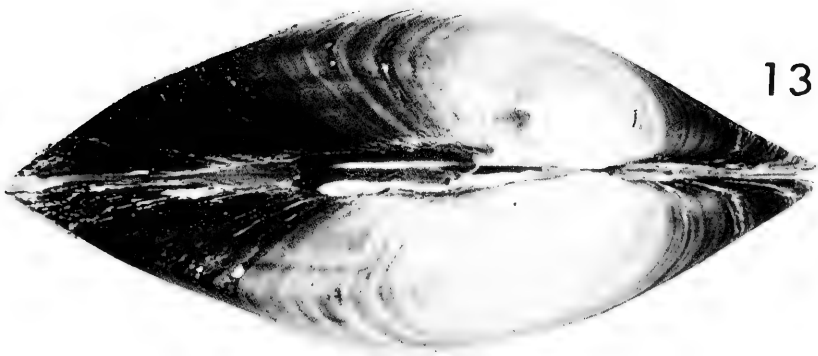
Diplodon delodontus wymani (in part), Barattini, 1951: 240. Castellanos, 1960: 89. Bonetto, 1965: 43, 50. Figueiras, 1965: 234. Olazarri, 1966: 24.

Diplodon charruanus (in part), Bonetto, 1964: 327; 1965: 50. Figueiras, 1965: 238. Castellanos, 1960: 88. Bonetto & Ezcurra, 1962: 31, 39. Olazarri, 1966: 26.

Diplodon uruguayensis, Simpson, 1900: 875; 1914: 1234. Ortmann, 1921: 512, 547. Parodiz, 1968: 3, 9, 11. Mansur, 1970: 65, 66.

The original description agrees entirely with the specimens identified by Ortmann in 1921 as *Diplodon uruguayensis* from the Rio Negro in Uruguay. This is a solid species, thick, inflated, with umbos rather flat and the hinge strong, easily distinguishable from *D. delodontus wymani*.





FIGS. 12-13. *Diplodon solisianus* (d'Orbigny). Aged specimens from La Plata River (MACN 10662) in which the axial costulae have been smoothed.

Distribution. Common in the Uruguay River and tributaries, but found also in rivers of southern Brazil up to the Tietê, where it hybridizes with *Diplodon expansus* (Ihering named the latter populations *Unio caipira*, of which a paratype is at the Carnegie Museum; it is not related to *D. ellipticus* as Simpson thought.) *U. apprimus* Lea is an extreme clinal stage, of large size, in the western distribution of the species, and it cannot be associated with *D. delodontus wymani* as several authors have indicated, but, as Ortmann considered it, belongs to *D. uruguayensis*.

Materials at the Carnegie Museum. Uruguay: Rio Uruguay, Rio Negro, Rio Queguay, and Arroyo Artilleros near Colonia. Argentina: Arroyo La Leche, Colón, Entre Rios. Brazil: Camaquam, Guahyba, Jacuhy and Cachoeira rivers in Rio Grande do Sul; also Rio Tietê, São Paulo (*D. caipira* = *D. uruguayensis* x *D. expansus*).

Unio fokkesi Dunker 1853 and *Diplodon trivialis* Marshall are also hybrids with *D. expansus*, as indicated by Mansur (1970), both from Southern Brazil (the locality "Rio de la Plata" given by Dunker to *U. fokkesi* is not correct).

In the Senckenberg Museum there are specimens received from Ihering (No. 11301) which are *Diplodon uruguayensis* x *D. delodontus* from the Camaquam River; also there are several lots of *D. uruguayensis* labelled by Ihering as *U. lacteolus*, *U. apprimus* and *U. wymani*, and by Bonetto as *D. charruanus*.

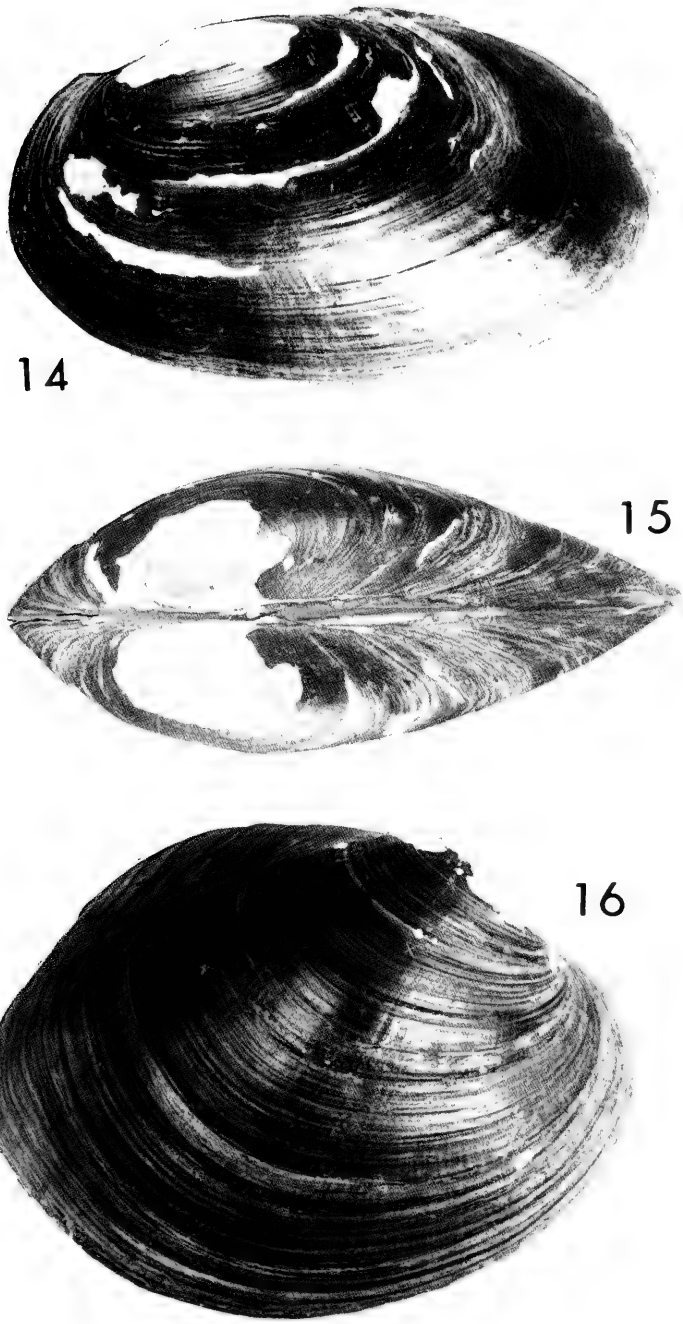
Typical specimens in Figs. 14, 15 are from the Uruguay River at Paysandú (MACN 15307).

The character of the hinge, as Ortmann indicated, changes with age, the pseudocardinals becoming more stumpy.

In coloration, *Diplodon uruguayensis* resembles *D. piceus*, but the size is greater, more inflated, thicker, with stronger hinge and very wide and thick prismatic area (this last character is conspicuous, even in populations of *D. uruguayensis* x *D. delodontus*). A clinal variation resulting in heavier shells occurs in southern Brazil, inhabiting rapid streams and having umbos much eroded, but in those better preserved the umbonal ribs appear stronger than in *D. piceus*.

Ortmann separated *Diplodon uruguayensis* and *D. piceus* (he called the latter *D. charruanus*) collected simultaneously at the same place (Ponds of Santa Isabel, Rio Negro, Uruguay) by J. Haseman in 1909. Also the glochidia which Ortmann mentioned from these specimens as *D. charruanus* (and by Bonetto, 1961: 24) actually belong to *D. piceus*. Under *D. piceus*, Ortmann (1921: 506) included a number of different species: *D. charruanus*, *D. rhuacoicus* and *D. aethiops*. On the other hand, the glochidia studied by Bonetto from specimens in the Museu Paulista (and labelled by Ihering as *U. aethiops* Lea) from the Camaquam River are *D. parallelipipedon aethiops* (Lea); corresponding specimens of the same lot distributed by Ihering are at the Carnegie Museum (see Parodiz, 1968: 12). From these considerations and the corrected identifications, the glochidia of *D. piceus* (=*D. charruanus* after Ortmann, not d'Orbigny) must be of direct development in the subgenus *Rhipidodonta*, unrelated to *D. uruguayensis* and unlikely would hybridize with it.

Dimensions (mean in mm):	Length	Height	Width	No. specimens
Southern Brazil				
Camaquam River (1)	72	46.5	30	3
Camaquam River (2)	70.5	41	28.5	13
Camaquam River (3)	73	47	30	1
Guaiba River	71	47	39	1
Uruguay				
Rio Negro	75	45	35	6
Santa Ana	62	37	28	19
Uruguay River	69	41	31	1
San José *uruguayensis* x *delodontus*	63	38.5	28	7
Mean of 51 specimens	70.7	47	32.7	



FIGS. 14–15. *Diplodon uruguayensis* (Lea). Uruguay River, near Paysandú, Uruguay (MACN 15307). FIG. 16. Hybrid *Diplodon solisianus* x *wymani*. Rio de la Plata.

Diplodon solisianus (d'Orbigny 1835); Figs. 2, 12, 13, 16-18 (hybrids)

Unio solisiana d'Orbigny, 1835: 34, No. 12; 1842: 604, pl. 69, figs. 1-3. Sowerby, in Reeve, 1868: No. 508, pl. 93 (fig. from d'Orbigny's specimens in British Museum). F. Corsi, 1900: 449 (fig. 32 under *soliciana* is *Diplodon paranensis funebralis* (Lea)). Doering, 1876: 6.

Diplodon solisianus, Simpson, 1900: 887; 1914: 1287.

Diplodon (*Bulloideus*) *solisianus*, Haas, 1931: 38. Castellanos, 1960: 27, pl. 5, figs. 4, 8.

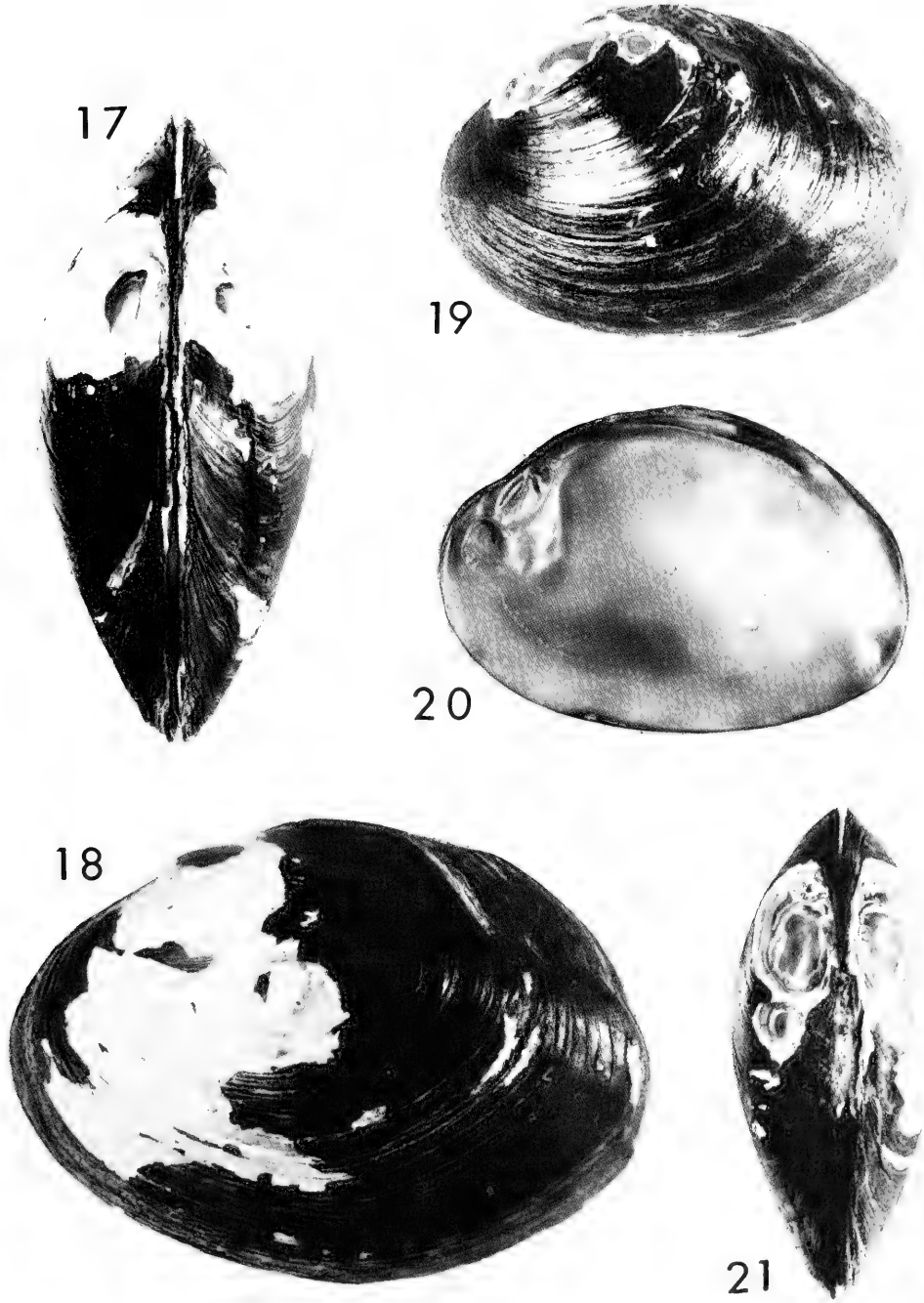
Diplodon (*Rhipidodonta*) *variabilis*, Bonetto, 1965: 47. Figueiras, 1965: 236, 237. Olazarri, 1966: 25 (*solisiana*).

Diplodon solisianus, Parodiz, 1968: 10, 16, 20.

Complementary description. Shell oval, but less elliptical and more rounded than in *Diplodon delodontus;* anterior-dorsal margin with small but well formed lunule, after which it descends in a continuous rounded line with the anterior margin; from the middle of the anterior margin the line descends rapidly and obliquely toward the ventral margin, which curves upward; the union of the ventral and posterior margins forms a rounded angle a little below the middle of the shell; from there the posterior margin is rather straight affected only by a slight undulation at the point where the posterior ridge ends. The dorsal margin is almost straight along the ligamental section and then descends obliquely to meet the posterior margin; the posterior ridge is well marked with a (sometimes double) carination, above which the wing is higher and thinner than in *D. delodontus;* viewed from the top the posterior dorsal margin shows an escutcheon; sometimes also the wing has very faint flutings. The umbos are larger, more prominent and higher than in *D. delodontus*, with stronger radial sculpture, further apart and more inclined to project into rugosities over the rest of the shell; the 2 central bars form a large V, in contrast with the short V of *D. delodontus;* although the number of bars is equal in both species, in *D. solisianus* they are stronger near the beginning of the posterior ridge; the microscopic concentric striae on the umbo are very profuse. The concentrically striated lines of growth are not as coarse as in *D. delodontus*. The color at the center and upper part of the shell is olive-green, paler in juvenile specimens, but around the margins and posterior wing the color is dark brown; sometimes there are alternating bands of the 2 colors. The periostracum near the umbo peels easily. The greater inflation of the valves, instead of being back and posterior to the umbo as in *D. delodontus*, is more to the center and the compression toward the margins is more noticeable; the mark of the ligament insertion above the lateral tooth is similar, but shorter. The cavity under the umbo is deep. Hinge: left valve with pseudocardinal bifid or trifid (usually appearing as having 2 teeth, but they are united by a superior ridge), the posterior division directly under the umbo, stronger, but these characteristics are variable; the laterals have a sinuous line, curved upward at the middle and then descending, and ordinarily more separated from the pseudocardinals than in *D. delodontus*, thus forming a perfect interdentum. On the right valve the pseudocardinals are, in general, stronger. The anterior adductor scars are smaller but deeper than in *D. delodontus;* the pallial line, as well as the posterior adductor, is less marked.

Type locality. D'Orbigny indicated several localities in the vicinity of the La Plata River and Maldonado. The name *solisianus* refers to the Solís River of Uruguay, which empties at Maldonado (derived from Juan de Solís, discoverer of La Plata River in 1515). Maldonado should be selected as the type locality, although today the species seems to be less common there than on the west side.

Materials observed. Province of Santa Fe: Arroyo Malabrigo, near Roman (where it lives sympatrically with *D. delodontus*), Carnegie Museum; Province of Buenos Aires: Arroyo Los Cuervos, Ramallo; Arroyo Los Pozos, 50 km SW of Buenos Aires



FIGS. 17-18. Hybrid *Diplodon solisianus* x *delodontus*. Paraná River at Santa Fe, Argentina. FIGS. 19-21. *Diplodon expansus* (Küster). Ibicuy del Norte Island, Paraná River, Paraguay (MACN).

city, both in the Carnegie Museum; Rio de la Plata, Museo Argentino de Ciencias Naturales. Castellanos (1960) reported the species from several small streams in the vicinity of La Plata.

Diplodon solisianus can be easily distinguished from *D. delodontus*. Its anterior dorsal half is somewhat similar (more oblique in *D. solisianus*), but its posterior half is decidedly subquadrate; its shape is always higher and shorter, more compressed, with more prominent umbos and radial sculpture stronger. In some more angulated individuals of *D. delodontus*, the angle is at the posterior side of the base, while *D. solisianus* is more rounded at the point, and the angle appears higher near the middle line; also the posterior dorsal margin forms in *D. solisianus* an almost right angle at the wing.

Individual variations. Young specimens are sometimes more elongated, with radial ribs and the posterior ridge more marked; they turn more inflated with age.

Diplodon solisianus seems to be less common than its allied species in large rivers, and it usually appears in small creeks. From "lagunas" of northern Santa Fe where *D. solisanus* co-habits with *D. delodontus*, hybridization can be detected in more elongated specimens which grow thicker, but the populations are largely distinct and, although sympatric, where the populations of *D. delodontus* increase, those of *D. solisianus* decrease; hybrids have been observed when the 2 populations are in the same proportion. In the south (Arroyo Los Pozos) a lot consisting of 3 specimens shows 2 of them closer to the typical *D. solisianus*, and the 3rd is shaped like *D. delodontus wymani*. Specimens like these are usually labelled simply as *wymani* or *delodontus* in collections. This species has also been mistaken for *D. paranensis*, *D. paranensis funebralis* or *D. fontaineanus;* but apart from their embryological differences (*D. solisianus* has parasitic glochidia, while the *D. paranensis* group has direct development), *D. paranensis* is very circular in shape and its only angulosity is at the posterior wing, with very shallow adductors and umbos considerably smaller; *D. paranensis funebralis* is very flat, with an umbo so advanced that there is practically no anterior dorsal margin, and the line of the anterior margin is almost vertical.

Distribution. The range of *Diplodon solisianus* is along the southern part of the Paraná River and tributaries of the Plata. Apparently it is absent in the Uruguay River drainage. It probably covered a larger area in pre-Pleistocene times before the formation of La Plata drainage. The last Pleistocene ingression, Querandinan, separated the populations at both sides of the present La Plata estuary. Although *D. solisanus* and *D. delodontus* overlap greatly in their areas of the Paraná, *D. solisianus* does not appear in the province of Entre Rios as *D. delodontus* does; more collecting in that area, however, may prove the extension of its range.

Sowerby (in Reeve) figured a specimen of *Diplodon solisianus* from d'Orbigny's materials in the British Museum (the collection of that museum contains the holotype, and 11 paratypes, but the localities of Buenos Aires and Maldonado have been mixed). That illustration differs from the figure by d'Orbigny, but agrees completely with our observed specimens from Arroyo Malabrigo, except for the reference by Sowerby (followed by other authors) to the divergent umbonal ribs, for which an acclaration is in order: d'Orbigny only indicated 10-12 ribs, without mention of divergence; it was Sowerby who added "a few slantingly divergent subradiating ribs which in the suborbicular form delineated by d'Orbigny extend over the entire surface." Such reference indicates only that the ribs radiate and diverge *from* the beak; subsequent coalescence of central ribs were not considered in the original description of many species. It must be also noted that illustrations in d'Orbigny's work, especially those by Annedouche, were not always very accurate, especially in regard to hinge characters and colors. Sowerby's figure is closer to the actual specimens, even if the sinuosity of the ventral margin is somewhat exaggerated.

Diplodon subquadratus Marshall has been indicated (Castellanos, 1960) as belonging to *D. solisianus;* the specimens illustrated by Castellanos as such are truly *D. solisianus*, but *D. subquadratus* is more inflated posteriorly, with weaker hinge line, wider prismatic area, and its type locality is Paysandú, Uruguay, from where many collections have been made without *D. solisianus* being yet found. *D. subquadratus* belongs to the group (and it is probably a synonym of) *D. variabilis* (Maton).

Dimensions (means of lots):	Length	Height	Width
Arroyo Malabrigo, Santa Fe, 21 specimens	62.8	46.5	23.7
"Lagunas" near Arroyo Malabrigo, 5 specimens	81	60.5	33
Arroyo Los Pozos, Buenos Aires, 3 specimens	82	63	32
Small specimen from Arroyo Los Cuervos, Buenos Aires	50	41	20.5
Mean of Total	68.9	52.7	27.3

These figures show that, in comparison with *Diplodon delodontus*, *D. solisianus* is shorter, higher and more compressed.

One specimen in the Seckenberg Museum (No. 3859) from La Plata River and labelled "paratype" (!) of *Diplodon solisianus* - ex-Copenhagen Museum from Ihering's collection) - is but a very young and thin individual of *D. variabilis* (Maton), inflated and with a different hinge. Haas, however, identified the true *D. solisianus* (No. 11431) from La Plata River.

Hybrids of *D. solisianus* x *D. delodontus* from the Paraná River at Santa Fe are shown in Figs. 17, 18.

Diplodon martensi (Ihering 1893)

Unio martensi Ihering, 1893: 100, pl. 4, fig. 10.

Unio firmus boettgeri, Ihering, 1893: 105, pl. 4, fig. 2 (as "*granosus multistriatus*", Haas, 1930: 32 and Bonetto, 1965: 37).

Unio sebastiani Ihering, *in litt.* (label Senckenberg Museum), *nomen nudum.*

Diplodon binneyi Simpson, 1900: 878 (as *Diplodon*, from Lea's *Unio binneyi*, 1845: 165, "southern U.S.A."); see acclaration by Parodiz, 1968: 2.

Diplodon suppositus Simpson, 1914: 1245 (named, but undescribed, by Ihering, 1893). (As *D. rhuacoicus* by Haas, 1930). Marshall, 1917: 385, pl. 51; Bonetto, 1961: 33. Zanardini, 1965: 6, 9. Figueiras, 1965: 238. Morretes, 1949: 19.

Diplodon santa-mariae Simpson, 1914: 1270. Ortmann, 1921: 495. Marshall, 1917: 386, pl. 52, fig. 6, pl. 55, figs. 1-4. Morretes, 1949: 20. Haas, 1930: 180 (under *D. rhuacoicus*). Bonetto, 1965: 39 (under *D. granosus multistriatus*).

Diplodon decipiens Ortmann, 1921: 499, pl. 36, figs. 3, 6, pl. 45, fig. 4, pl. 48, fig. 7. Haas, 1930: 180 (under *D. rhuacoicus*). Bonetto, 1964: 325 and 1965: 44 (under *D. delodontus expansus*).

Diplodon imitator Ortmann, 1921: 469, 491-500, pl. 34, figs. 5, 7. Bonetto, 1961: 16. Figueiras, 1965: 235 (in part).

Diplodon simillimus Ortmann, 1921: 495-500, pl. 35, figs. 3, 6, pl. 45, fig. 2. Haas, 1930: 180 (under *D. rhuacoicus*). Bonetto, 1961: 11.

Diplodon vicarius Ortmann, 1921: 496, pl. 35, figs. 7, 8, pl. 36, figs. 1, 2. Haas, 1930: 180 (under *rhuacoicus*). Bonetto, 1961: 10; 1965: 39 (under *D. granosus multistriatus*).

Diplodon rhuacoicus, Haas, 1930: 180. Castellanos, 1960: 68 (in part). Bonetto, 1961: 18 (under *D. piceus*); 1965: 40. Figueiras, 1965: 225. Parodiz, 1968:

9, 15. Mansur, 1970: 77. (The last 2 references under *D. rhuacoicus* proper, not in part.)

Diplodon granosus multistriatus, Haas, 1931: 32. Bonetto, 1964: 324 and 1965: 39.

Diplodon delodontus expansus, Bonetto, 1964: 325 (in part).

Diplodon charruanus, Olazarri, 1966: 26 (in part).

Diplodon martensi, Simpson, 1900: 882; 1914: 1266. Haas, 1930: 180 (under *D. rhuacoicus*). Parodiz, 1968: 7, 14, 15. Mansur, 1970: 74.

Simpson, in a transcription of the description (1914), said that the shell of this species is rhomboid, little wider behind, with posterior ridge low and base line a little curved at the middle. I have observed the last character in paratypes of the nominal species *D. simillimus* and *D. decipiens*, which occurs on specimens living in fast running waters and stony substratum.

Type locality. The only clearly stated location given by Ihering was Taquara in the Vacahy river drainage, Rio Grande do Sul; Haas (under *Diplodon rhuacoicus*) referred also the "type" of *D. martensi* as Rio Grande do Sul, not São Paulo, which Ihering referred with the mark "?".

The intricate synonymy of *Diplodon martensi* includes several names given by Ortmann and Simpson as presumable new species, which are only parts of clinal variations. More complicated is its assumed relationship with *D. rhuacoicus*, under which (in part) it was placed by Haas and Bonetto (the confusion originated in Sowerby's figure of *D. charruanus* as *D. rhuacoicus*, and under that name, afterwards *D. martensi*, as well as *D. piceus*, and even *D. parallelipipedon aethiops*, were wrongly subordinated).

The shape of *Diplodon martensi* is very elongated-oval with the anterior and posterior margins well rounded, except for a slight angulosity at the posterior end. *Diplodon rhuacoicus* is more inflated and solid, narrower and well angulated behind, and the umbos are more prominent. The hinge teeth in *D. martensi* are reduced (in comparison with *D. rhuacoicus*) and are of the same type found in *D. decipiens*, *D. vicarius*, etc.: the left valve has a small pseudocardinal tooth with rugosities under and behind it, but such a character is variable and the teeth may grow stronger as in *D. simillimus;* in *D. rhuacoicus* the pseudocardinal in the left valve is always large with a conspicuous supplementary tooth behind.

The relationship of *Diplodon martensi* is closer to *D. expansus* and *D. paulista* than to *D. rhuacoicus*, in color, periostracum, flatness of valves and hinge; for all these characters, Bonetto placed the synonym *D. decipiens* under *D. expansus*. On the other hand, the synonymy given by the same author for "*D. granosus multistriatus*" (including *D. vicarius*, *D. santamariae* and *D. decipiens*) needs modification, because *D. granosus* (Bruguiere) from the Guianas is entirely different from *D. multistriatus*, which corresponds to *D. ellipticus* Wagner (Lea himself, in 1870: 31, found out that his *Unio multistriatus* was a perfect synonym of *U. ellipticus*); of the figures given by Haas (1930-1931) as *D. granosus multistriatus*, Abb. 24-26 agree with *D. ellipticus*, while fig. 28 is *D. martensi;* fig. 29, which is the type of *U. pfeifferi* Dunker, is an entirely different shell not belonging to this group.

While *Diplodon martensi* seems to be a species well distributed in southern Brazil (São Paulo, Paraná, Rio Grande do Sul), *D. rhuacoicus* is a very rare one, a fact already stated by d'Orbigny in 1846. Its habitat is reduced to small streams of southern Uruguay (Maldonado and especially Canelones), with some eastern isolated morphological variations (Cerro Largo), to which Marshall gave the names *D. pilsbryi* and *D. yaguaronis*. The larvae studied by Bonetto from northern specimens such as *D. rhuacoicus* very unlikely correspond to this species, but are more probably *D. martensi;* thus the glochidia of the real *D. rhuacoicus* might belong to the group of *D. charruanus*,

i.e., may be characterized by direct development. There are populations in Canelones which appear to hybridize with *D. charruanus*, but no indications of crossbreeding with *D. martensi* or *D. uruguayensis* have been found for *D. rhuacoicus*.

The materials of *Diplodon martensi* observed in the Carnegie Museum correspond to the original lots described as *D. decipiens*, *D. vicarius*, *D. simillimus* and *D. imitator*, and complete references can be found in Ortmann's 1921 work. Ortmann said that *D. martensi* was "impossible to identify" on account of its doubtful type locality. On the other hand, Ortmann declared that the 4 species he described were "extremely similar" and "very close" (1921: 494, 496, 499, 501).

Diplodon expansus (Küster 1856); Figs. 5, 19-21

Unio expansus Küster, 1856(9): 149, pl. 43, fig. 5.

Unio effulgens Lea, 1857a: 94; 1857b: 303, pl. 28, fig. 18; 1870: 35, etc. (as *Margaron*). Simpson, 1900: 879 (as *Diplodon*).

Unio eurhynchus Küster, 1861: 237, pl. 79, fig. 5 (loc. unknown).

Unio greeffeanus Dunker (*in litt.*), Ihering, 1893: 96, pl. 4, fig. 8.

Unio aethiops piracicabana Ihering, 1893: 102 (*U. aethiops* Lea is a subspecies of *parallelipipedon*). Simpson, 1900: 874.

Unio guahybae Ihering (*in litt.*: specimens so labelled were distributed by Ihering to many collectors). Simpson, 1900: 892 (as *Diplodon*). This reference is according to Haas and Bonetto. [Of "*Unio bischoffi*" and "*U. sanctipauli*" both Ihering's *in litteris*, I have no other knowledge but the indication by Haas (1930) that they may belong to *D. expansus*; they are *nomina nuda*].

Diplodon mimus Simpson, 1914: 1249. Morretes, 1949: 19. Marshall, 1917: 383, figs. 3-6.

Diplodon mogymirim Ortmann, 1921: 520, pl. 37, figs. 4-7, pl. 46, fig. 5, pl. 48, fig. 2. Morretes, 1949: 19.

Diplodon granosus multistriatus, Haas, 1931: 32. Bonetto, 1965: 39 (these references, in part, correspond to *D. mimus*).

Diplodon delodontus expansus, Haas, 1930, 192, fig. 15. Bonetto, 1954: 41; 1964: 325; 1965: 44. Bonetto & Drago, 1966: 122. Zanardini, 1965: 8, 9, fig. 1. Figueiras, 1965: 233. Zilch, 1967: 124.

Diplodon expansus, Ihering, 1910: 107, 134. Simpson, 1914: 1231. Bonetto, 1960: 48, 50; 1961: 13, 14. Parodiz, 1968: 66. Mansur, 1970: 65.

Type locality. Conigo River at Nova Friburgo, state of Rio de Janeiro, Brazil.

Although the species is well known from rivers of southernmost Brazil in Rio Grande do Sul, its greater abundance is in the Tieté River in the vicinity of Piracicaba, São Paulo.

Although the inclusion by most authors of *Unio greeffeanus* (Dunker) Ihering in the synonymy of *Diplodon expansus* (Ortmann also referred it very close to his *D. mogymirim*) is acceptable, the figure of this species in Ihering (1893, pl. 4, fig. 8) shows a peculiar radiation on the umbo, which in actual specimens (always found with eroded umbos) is almost impossible to detect. But the type of *U. greeffeanus* in the Senckenberg Museum leaves no doubt of their conspecificity. Küster's description (he credited it to Jean Charpentier) is lean in clear-cut characters, and while he said the cardinals are "rather strong", the description of *U. effulgens* indicated "teeth small"; these are 2 extremes in variation I found in populations of *D. mogymirim*, but the cardinals usually are strong. Simpson's observations that *D. expansus* (its figure is in Küster) looks more like an Australian rather than a South American shell is pertinent, because in some localities, as in the Ivai River, the shells are very thin and rough-surfaced (as in *Hyridella australis*); other *Diplodon* also have such peculiar aspect, as in the *D. chilensis* group; but the majority of the Tieté River materials are rather solid and polished, as those which Ihering called *U. piracicabana*, identical with *D. greeffeanus-mogymirim*.

The materials of *Diplodon expansus* revised in the Carnegie Museum, includes the lots of types and numerous paratypes of *Diplodon mogymirim* (for which complete references and measurements are found in Ortmann, 1921), plus 1 specimen labelled by Ihering (from Geret Coll. of Paris) as *"Unio Wymanni"* (a hybrid individual of *D. expansus* x *D. uruguayensis*, very strong and inflated), and 3 specimens from Ivai River, Paraná (received from Bonetto as *"D. granosus"*) collected by Zanardini in 1960, which are of small size, thin and fragile.

According to Bonetto (1961: 13), who found differences with *Diplodon delodontus* in the shape of glochidia, *D. expansus* would be "a well differentiated subspecies." On the other hand, the same author (1964: 324) considers that the elements attributable to *D. delodontus expansus* are "considerably heterogeneous" and "the situation [is] not clear enough." Such a statement was justified by the number of names involved in the synonymy. But among the "subspecies" subordinated to *D. expansus*, several have been discarded: *D. enno* Ortmann = *D. rotundus enno; D. delodontus pilsbryi* = *D. rhuacoicus; D. fontaineanus deceptus* Simpson = *D. rotundus gratus* (see Parodiz, 1968: 16, 18); as for *D. imitator* and *D. decipiens*, see above under *D. martensi*.

The lectotype selected for *Diplodon mogymirim* (for which the complete description by Ortmann serves also for *D. expansus*) corresponds to the specimen ♂ No. 9, figured on plate 37, fig. 4a, b, c; the allotype ♀ No. 38, fig. 7a, b. These specimens were not measured in Ortmann's table but are among the larger; the largest (not figured) was length 68, height 45, width 26 mm. Females are somewhat larger and stronger than males, but not always; in overall features *D. expansus* seems to be less variable than other species in the group, except when under very unfavorable environments where the individuals remain small. Young specimens are very light in color and more rounded.

The lunule in *Diplodon expansus* is very narrow and sometimes concave. In the left valve there is a single pseudocardinal (occasionally with a small supplementary cusp) and 2 short and parallel cusps in the right valve. In older specimens I have observed transposition of teeth (an abnormality which has been studied by van der Schalie on North American naiads) with the single tooth on the right valve. Pseudocardinals are placed anteriorly to the umbo, under the lunule, and there is a long, curved, narrow and marginated interdentum. The lateral teeth are short but strong. All muscles scars are very well impressed. As a whole, the hinge plate differs from that of *D. uruguayensis* in which the teeth are closer to the *D. delodontus* type. Some females of *D. expansus*, when old and heavy, offer an aspect resembling *D. uruguayensis*, but the characteristics of the teeth denounces the difference. The mark of ligamental insertion is placed closer to the end of the laterals and the cartilage extends under the umbo.

Of *Unio guahybae* Ihering (*in litt.*), which I included, following Haas and Bonetto, in the list of names under *Diplodon expansus*, most probably does not belong here. I have specimens labelled by Ihering from the Guahyba River (or Guaiba, according to Maria Cristina Mansur, of Porto Alegre, from whom I have also received excellent lots of this form) in which the hinge is of the *D. rotundus* Wagner type, with a subtrapezoidal shape; it might constitute a valid form between *D. rotundus rotundus* and *D. rotundus fontaineanus* d'Orb.; however, it is still undescribed.

An extreme southwestern locality for *Diplodon expansus* was registered on specimens of the Museo Argentino de Ciencias Naturales (Buenos Aires) collection, from the Ibicuy Island, on the Paraná River, Paraguay, 25 km east of Encarnación and south of Carmen. The specimens have the umbos mostly eroded, due to the rapid water of the Paraná River in that area. Apart from the relatively larger size, they are identical with those of the original lot of *D. mogymirim*, (see Figs. 19-21). The Ibicuy Island on the Upper Paraná should not be confused with the island of same name in the Paraná Delta.

Diplodon paulista (Ihering 1893)

Unio paulista Ihering, 1893: 93, pl. 4, fig. 7.
Diplodon delodontus expansus, Haas, 1930: 192. Bonetto, 1964: 325; 1965: 44.
Diplodon paulista, Simpson, 1900: 873; 1914: 1229. Ortmann, 1921: 501, pl. 46, fig. 1, pl. 47, fig. 1. Bonetto, 1961a: 14; 1961b: 49. Parodiz, 1968: 9, 18.

For a complete, detailed description of this species, including anatomy and glochidia, see Ortmann (1921).

Type Locality. Tieté River, at Piracicaba, São Paulo, Brazil (Lectotype in Senckenberg Museum; paratypes Carnegie Museum). Other materials in the Carnegie Museum are from Sapina, São Sebastio, Mogy das Cruzes and Mogy Mirim, all of São Paulo.

This species differs from *Diplodon expansus* in its more elongated shape, being more depressed, with posterior margin more angulated and narrower front; it is also less solid, the periostracum is not marked, and it is green, not chestnut as in *D. expansus*, and the nacre is more bluish. Additional differences are: the smaller and more triangular pseudocardinals and the thinner and longer laterals with sharp edges reaching below the umbo and without noticeable interdentum.

Ortmann did not compare this species with his *Diplodon mogymirim* (=*D. expansus*), assuming that the differences were obvious. It is sympatric with it and found at the same localities living together, for which any subspecific or ecological consideration of differences is out of order.

The specimens I observed at the Senckenberg Museum (Nos. 3872 and 3873), types and paratypes, agree in all details with those in the Carnegie Museum studied by Ortmann, but are of larger size.

SYNOPSIS OF DISTRIBUTION

Species typical of the lower Paraná and La Plata rivers: *Diplodon delodontus delodontus*, north to Paraguay; *Diplodon delodontus wymani*, La Plata River and its affluents in the Buenos Aires Provinces; *Diplodon solisianus*, west bank of La Plata River and affluents up to Santa Fe - now rare in Uruguay.

Species typical of Southern Brazil up to Sao Paulo: *Diplodon martensi*, Rio Grande do Sul and São Paulo (also eastern Uruguay); *Diplodon expansus*, São Paulo (Rio Janeiro?) east to Paraguay; *Diplodon paulista*, São Paulo.

Species typical of Uruguay: *Diplodon uruguayensis*, Central and northern Uruguay into Rio Grande do Sul. In Uruguay, all species (except *D. expansus* and *D. paulista*) overlap.

The La Plata River system, which includes the vast area of the Paraná-Paraguay-Uruguay drainages, did not come into existence (as we know it at present) until the Pleistocene epoch (see Parodiz, 1969: 34). Therefore, the expansion of *Diplodon* southwards and the correlative speciation was a very rapid process on which account the species still maintain very close affinity and overlapping areas, resulting in recurrent crossbreeding.

RESUMEN

Las relaciones entre seis especies de *Diplodon*, pertenecientes al complejo superespecífico de *D. delodontus* (Lam.), se estudiaron para aclarar el problema que plantea sus identificaciones. La completa revisión conchológica de cada especie demostró que varias de ellas -nominalmente consideradas sinónimos en trabajos previosdebe rehabilitarse. Las seis especies aqui reconocidas son: *Diplodon delodontus* (Lamarck 1819); *D. delodontus wymani* (Lea 1860); *D. uruguayensis* (Lea 1860); *D. martensi* (Ihering 1893); *D. expansus* (Küster 1856); *D. solisianus* (d'Orbigny 1835); *D. paulista*

(Ihering 1893).

La distribución comprende el sistema fluvial del Paraná, Uruguay y La Plata; desde que tal sistema -tal como lo conocemos hoy- se formó recién en el Pleistoceno, la ocupación del área y el proceso de especiación fueron de operación muy rápida e inmediata al Reciente, lo que explica la gran afinidad de constitución genética demostrada por repetidos cruzamientos. Existe acusada simpatría en la superposición de grandes áreas de distribución en cada especie, lo que impide el reconocimiento de subespecies (excepto en el caso de *Diplodon delodontus wymani*); por otra parte, la co-habitación de un mismo nicho ecológico por distintas especies, demuestra que la "variaciones" frecuentemente consideradas ecológicas, no son tanto fenotípicas como genotípicas debido a hybridización. El concepto de superespecie es perfectamente aplicable al grupo de *D. delodontus*, siendo este monofilético y manteniendo sus especies tal afinidad como para permitir cruzamientos recurrentes.

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PROC. FOURTH EUROP. MALAC. CONGR.

DIE GATTUNG *BYTHINELLA* UND DIE GATTUNG *MARSTONIOPSIS* IN WESTEUROPA, 1. WESTEUROPÄISCHE HYDROBIIDAE, 4[1]. (PROSOBRANCHIA)

Hans D. Boeters

Rumfordstr. 42, *D*-8 *München* 5, *Deutschland*

(1) *Bythinella*

1851 Les Bithinelles Moquin Tandon, J. Conchyliol., 2: 237 [*nom. nud.*].
1855 *Bythinella* Moquin Tandon, Hist. natur., 2: 515 und 516. Typus: *Bulimus viridis* Poiret, 1801. Typuswahl: Stimpson (1865: 44).
1892 *Bicarinatiana* Fagot, Bull. Soc. Ramond, 27: 27-28 [*nom. obl.*]. Typus: *Paludina bicarinata* Des Moulins, 1827. Typuswahl: Fagot (1892: 28).
1929 *Brachypyrgula* Polinski, Glas Srpske Kral. Akad., 137: 153. Monotypus: *Paludina bicarinata* Des Moulins, 1827.
1931 *Pyrgobythinella* Germain, Mollusques, 2: 627. Monotypus: *Hydrobia carinulata* Drouet, 1868.

Bemerkungen: Es wurden nur geringfügige anatomische Unterschiede zwischen *viridis*, dem *Bythinella*-Typus, einerseits und *carinulata*, dem *Pyrgobythinella*-Typus, sowie *bicarinata*, dem *Brachypyrgula*-Typus, andererseits ermittelt. Da auch eine befriedigende conchologische Abgrenzung von *viridis* und *carinulata* nach heutigen Kenntnissen nicht möglich ist, wird *Pyrgobythinella* als jüngeres Synonym von *Bythinella* s. str. angesehen. Das gleiche gilt für *Brachypyrgula*, da die conchologische Eigenartigkeit von *bicarinata* allein für eine Abtrennung von *Bythinella* s. str. nicht ausreicht.

B. (*B.*) *viridis*
Abb. 1, 24-25, 35

1801 *Bulimus viridis* Poiret, Aisne: 45-46. Loc. typ.: "Le ruisseau qui tombe en cascade de la montagne au bas de laquelle est situé le moulin de Veau, proche Chartreuve" bei Chéry-Chartreuve, Aisne.

Kiemenlamellen: 19-20 (BOE 386/1-2♀♀, 11-12♂♂); Osphradium nicht hahnenkammförmig (BOE 386/1-2♀♀, 11-12♂♂). - Darm: 1 Z-förmige Schlinge hinter dem Magen mit 8-9 Kotballen hinter der Schlinge (BOE 386/1-2♀♀); der U-förmige Knick hinter der Schlinge ist beim ♂ spitz V-förmig ausgebildet (BOE 386/11♂). — Penis: in der Ruhelage etwa so lang wie die Drüsenrute (Abb. 25 = BOE 386/11). — Weiblicher Genitraltrakt: Ovidukt vor der Einmündung des Receptaculum seminis mit 1 Z-förmigen Schlinge, 1 Receptaculum seminis, Bursa copulatrix U-förmig (Abb. 24 = BOE 386/1,2).

Untersuchtes Material und Vorkommen: BOE 386 = Rheokrenen (11,5°C; mit *Potamopyrgus jenkinsi*) am Abluss der Fontaine St. Martin und Abfluss (9,5°C) dieser Fontaine an der Strasse von Dravegny nach St. Gilles ca. 4,5 km nö. Chartreuve.

Typen: Syntypen (?) MW/5, D/3.

Verbreitung: *viridis* dürfte in Westeuropa der älteste Name eines Taxons der Gattung *Bythinella* sein. Die Art und ihre Verbreitung muss bis zu ihrer Wiederbeschreibung in dieser Arbeit als so gut wie unbekannt angesehen werden. Daran ändert es nichts,

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[1]Siehe 1: *Avenionia*, Arch. Molluskenk., 96: 155-165; 2: *Microna*, Arch. Molluskenk., 100: 113-145; 3: *Corrosella*, J. Conchyliol., 108: 63-69.

dass für *viridis* nach ihrer Beschreibung durch Poiret überall aus Westeuropa Fundorte angegeben worden sind. Die Ermittlung der Verbreitung von *viridis* steht erst am Anfang, da bisher von *viridis* weder Typen abgebildet worden sind noch der Versuch unternommen wurde, sie vom locus typicus wiederzubeschreiben. Ihre Abgrenzung gegen die benachbarte *carinulata* ist problematisch (vgl. unter *B.* (*B.*) *carinulata*).

Fundortkatalog (Abb. 35): Aisne: Barzy und Chartèves (Lallemant & Servain 1869: 43) [49,0/3,5°]. — Chartreuve bei Chéry-Chartreuve (Poiret 1801: 45-46) [49,2/3,6°].

B. (*B.*) *carinulata*
Abb. 2-5, 26-27, 35

1801 *Turbo griseus* Vallot, Exercise: 6 [*nom. obl.*]. Loc. typ.: "Fontaine de Champmol", Dijon, Côte-d'Or (Vallot, 1827: 71).

1868 *Hydrobia carinulata* Drouet, Mém. Acad. imp. Sci. Arts b.-L. Dijon, (2) 14(1866/67): 122. Originalfundorte: "fontaine de Larrey, près Dijon (type)! fontaine des Chartreux, à Dijon! fontaine de Velars! source de la Norges! la Douix, à Châtillon-sur-Seine! [sämtlich Côte-d'Or]...dans l'Aube et la Haute-Marne...de l'est, notamment de la Moselle."

1869 *Paludinella turgidula* Paladilhe, Rev. Mag. Zool. pure appl., (2) 21: 275-277, T. 20, F. 1-2. Originalfundorte: "Outre la localité de Billy-lès-Chanceaux (Côte-d'Or)...aussi dans le département de l'Aube, aux environs de Bar-sur-Seine et des Riceys."

1876 *Paludinella scalarina* Paladilhe, Rev. Sci. natur., 5: 334-335. Loc. typ.: "près de Châtillon-sur-Seine (Côte-d'Or)."

1882 *Bythinella turgida* Locard, Catalogue: 227.

1893 *Bythinella burgundina* Locard, Conchyliologie: 80. Loc. typ.: "dans les puits de Châtillon-sur-Seine (Côte-d'Or)."

1931 *Bythinella* (*Pyrgobythinella*) *carinulata*, Germain, Faune, 2: 628.

Synonymie: Nach dem Studium von Syntypen von *burgundina* und *scalarina* und Topotypen von *turgidula* sind diese jüngere Synonyme von *carinulata* (vgl. Abb. 2-5); dafür spricht auch die weite Verbreitung, die Drouet für *carinulata* angibt. Hingegen handelt es sich nach dem Studium von Topotypen von *cylindracea* Paladilhe, 1869 [*Belgrandia*] und Syntypen von *lanceolata* Locard, 1893 [*Belgrandia*], *riparia* Locard, 1893 [*Belgrandia*], *sequanica* Paladilhe, 1870 [*Belgrandia*] und *tricassina* Locard, 1893 [*Belgrandia*] vermutlich um eine andere Art. Offen bleibt, um was es sich bei *bourguignati* Locard, 1893 (: 88) [*Bythinella*] non *bourguignati* Locard, 1884 [*Paulia*] (1893: 92) handelt.

Kiemenlamellen: 11-12 bei ♂♂ (BOE 148/11-12), 21-22 bei ♀♀ (BOE 148/1-3); Osphradium nicht hahnenkammförmig (BOE 148/1-3 ♀♀). — Penis: in der Ruhelage etwa so lang wie die Drüsenrute (Abb. 27a-b = BOE 148/12 bzw. 11). — Weiblicher Genitaltrakt: Ovidukt vor der Einmündung des Receptaculum seminis mit 1 Z-förmigen Schlinge, 1 Receptaculum seminis, Bursa copulatrix J-förmig (Abb. 26 = BOE 148/1, 2).

Untersuchtes Material: BOE 148 = Quellteich in Norges-la-Ville, Côte-d'Or.

Typen: *carinulata:* Syntypen nicht ermittelt, Topotypen BOE 148 (Norges), 277 a-b und 290 a (Verlars); *griseus:* Syntypen nicht ermittelt; *turgidula:* Syntypen PA, Topotypen BOE 144 (Bar-sur-Seine); *scalarina:* Lectotypus PA (Etiketten: "*Paludinella* n.sp. Châtillon s. Seine Boutigny d." und "*Paludinella scalarina* Pal. 1876 Châtillon s. Seine Bout. d."); *burgundina*: Lectotypus MP und Paralectotypen MP/3.

Vorkommen: Limnokrenen.

Verbreitung: Côte-d'Or, Yonne und Aube. Die Abgrenzung gegen *viridis* ist problematisch; beispielsweise will Drouet (1868: 121) *viridis* im Verbreitungsgebiet von

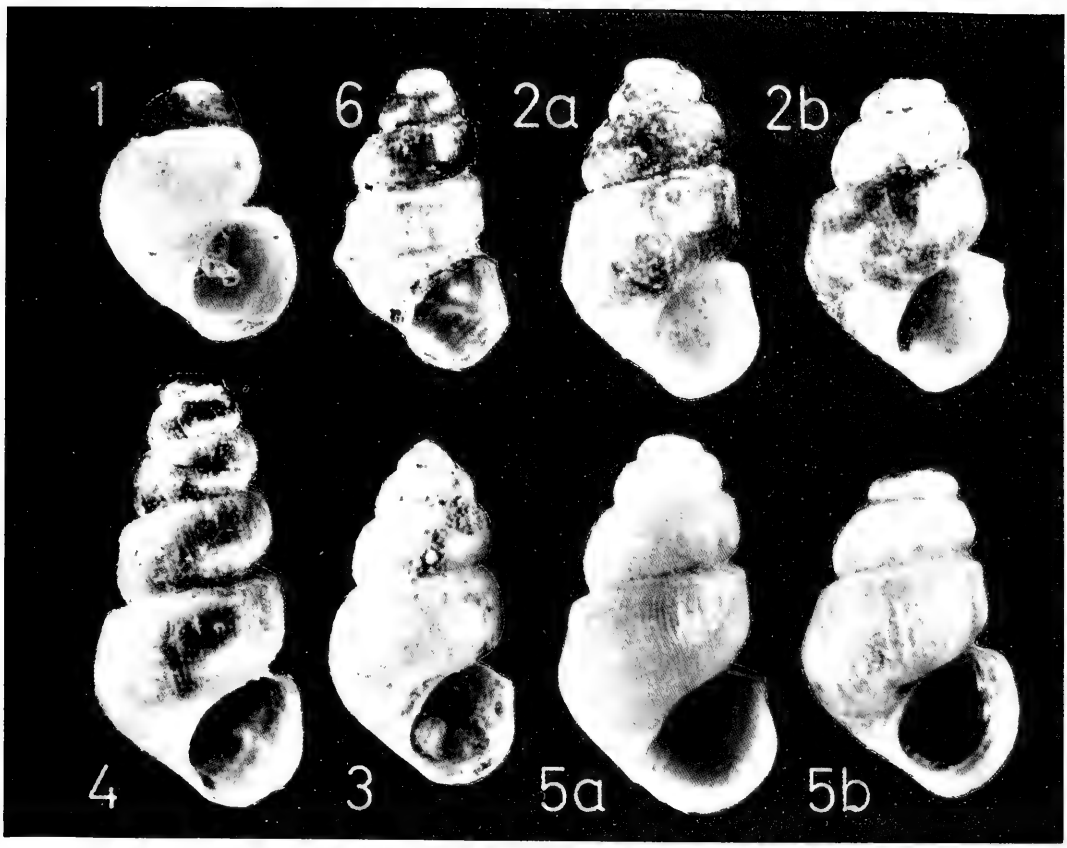

ABB. 1. *Bythinella viridis* (Syntypus (?) von *Bulimus viridis* Poiret; D). Chéry-Chartreuve, Aisne.

ABB. 2-5. *Bythinella carinulata*. Abb. 2. (Topotypen von *Hydrobia carinulata* Drouet; BOE 148). Norges-la-Ville, Côte-d'Or. Abb. 3. (Lectotypus von *Bythinella burgundina* Locard; MP). Châtillon-sur-Seine, Côte-d'Or. Abb. 4. (Lectotypus von *Paludinella scalarina* Paladilhe; PA). Châtillon-sur-Seine, Côte-d'Or. Abb. 5. (Topotypen von *Paludinella turgidula* Paladilhe; BOE 144). Bar-sur-Seine, Aube.

ABB. 6. *Bythinella bicarinata* (Topotypus von *Paludina bicarinata* Des Moulins; BOE 289). Couze-et-St.-Front, Dordogne.

Vergrösserung 1:15.

carinulata und wollen Lallemant & Servain (1869: 43) *turgidula* = *carinulata* im Verbreitungsgebiet von *viridis* gefunden haben.

Fundortkatalog (Abb. 35): Côte-d'Or: Quelle in Beaune (BOE 152, 47°1'55"/4°49'35") [47,0/4,8°]. — Velars-sur-Ouche (Drouet 1868: 122) [47,3/4,9°]. — Dijon (Vallot 1827: 71, *viridis;* Drouet 1868: 122) [47,3/5,0°]. — Norges-la-Ville (Drouet 1868: 122) [47,4/5,0°]. — Billy-lès-Chanceaux (Paladilhe 1869: 276, *turgidula*) [47,5/4,7°]. — Châtillon-sur-Seine (Vallot 1827: 71, *viridis;* Drouet 1868: 122; Boutigny nach Paladilhe 1876: 335, *scalarina;* Beaudouin nach Locard 1893: 80, *burgundina*) [47,8/4,5°]. — Yonne: Châtel-Censoir (Caziot 1907: 253) [47,5/3,6°]. — Aube: Riceys (Paladilhe

1869: 276, *turgidula*) [47,9/4,3°]. — Fontaine du Cris zw. Jully-sur-Sarce u. Villemorien (BOE 142); Quelle zw. Polisot u. Bar-sur-Seine links der Seine (BOE 143) [48,0/4,3°]. — Bar-sur-Seine (Paladilhe 1869: 276, *turgidula*) [48,1/4,3°]. — Quellen im Val-d'Arlette n. Arsonval (BOE 140) [48,2/4,6°]. — Sonstiges: Haute-Marne und Moselle (wo? Drouet 1868: 122).

B. (B.) reyniesii
Abb. 9-13, 30-32

1851 *Hydrobia reyniesii* Dupuy, Hist. natur., 5: 567-569; 6: T. 28, F. 6. Originalfundorte: "environs de Cauterets, au Four à chaux..., près de Mahourat, près du lac de Gaube,...dans la vallée du lac d'Estom...aux environs de Bagnères-de-Bigorre", Hautes-Pyrénées.

1874 *Paludinella baudoni* Paladilhe, Ann. Sci. natur., Zool., (6) 1: 32-33, T. 3, F. 9-10. Loc. typ.: "à la source de la Pique, port de Venasque (Gironde [!])", Haute-Garonne.

1875 *Paludinella andorrensis* Paladilhe, Ann. Sci. natur., Zool., (6) 2: 13-14, T. 21, F. 24-26. Originalfundorte: "dans le val d'Andorre,...en Catalogne, dans les environs de Ribas."

1877 *Paludinella darrieuxii* Folin & Berillon, Bull. Soc. Borda Dax, 2: 208, T. 3, F. 3-5. Loc. typ.: "ad fontem nomine Bente d'Arneguy [Fontaine de Besslé nach Granger 1897: 259] circum St-Jean-Pied-de-Port", Basses-Pyrénées.

1890 *Paludinella darrieuxii*, Folin, Naturaliste, (2) 12: 200, 2 Abb.

1891 *Bythinella baudoniana* Bofill, Crón. cient., 318: 7.

Bemerkungen: Wie ein Vergleich des Lectotypus von *darrieuxii* mit der Originalabbildung von Folin und Berillon zeigt, wurde *darrieuxii* von diesen Autoren unzutreffend abgebildet. Nach einem conchologischen und anatomischen Vergleich und aufgrund des Vorkommens handelt es sich bei *darrieuxii* um ein jüngeres Synonym von *reyniesii*. Auch *andorrensis* und *baudoni* sind nach dem Studium von Syntypen als jüngere Synonyme von *reyniesii* anzusehen.

Kiemenlamellen: 17-20 bei ♂♂ (BOE 195/11, 362/11-12), 20-22 bei ♀♀ (BOE 195/1, 362/1-2); Osphradium hahnenkammförmig (BOE 195/1 ♀ und 11 ♂, 362/11 ♂). — Darm: Bei ♂♂ und ♀♀ 1 Z-förmige Schlinge hinter dem Magen (BOE 362/1-2 ♀♀ und 11-12 ♂♂) mit (etwa) 11 Kotballen hinter der Schlinge (BOE 362/13 ♂); bei ♂♂ vor der Spitze des ruhenden Penis Richtung After 1 V-förmiger Darmknick (BOE 362/11-13). — Penis: In der Ruhelage fast so lang oder kürzer als die Drüsenrute (Abb. 30 = BOE 195/11, Abb. 32 = BOE 362/11, 13). — Weiblicher Genitaltrakt: Ovidukt vor der Einmündung des Receptaculum seminis mit 1 Z-förmigen Schlinge, 1 Receptaculum seminis, Bursa copulatrix J-förmig (Abb. 31 = BOE 362/1, 2).

Untersuchtes Material: BOE 195 = Quelle im Thermenpark von Bagnères-de-Bigorre, Hautes-Pyrénées; BOE 362 = gefasste Quelle ca. 300 m nö. der Kirche rechts an der Strasse nach St.-Jean-Pied-de-Port in Arnéguy, Basses-Pyrénées.

Typen: *reyniesii:* Syntypen nicht ermittelt, Topotypen BOE 195-197 und 288 (alle Bagnères-de-Bigorre); *baudoni:* Lectotypus PA und Paralectotypus PA/1 (Etiketten: "*Paludinella Baudoni* (Gironde)" und "*Paludinella Baudoni* PAL. 1873 Source de la Pique Port de Vénasque (Gironde) Ind. Baud. d."); *andorrensis:* Syntypen BOU/zahlreich; *darrieuxii:* Lectotypus BE (Etiketten: "Fontaine Bente d'Arneguy près St. Jean Pied de Port" und "*Paludinella darrieuxii* Fol. et Beri." und "Lecto Type [vermutlich unveröffentlicht]"), Topotypen (?) BOE 362-363.

Vorkommen: Rhoekrenen auf vorzugsweise kalkarmen Formationen (11,5°C, BOE 195, gelegentlich mit *Potamopyrgus jenkinsi* und *Microna* sp., BOE 362-363).

Verbreitung: Über die Pyrenäen und vermutlich das Massif Central (Abb. 23, nördlich bis an die Côte-d'Or?) weit verbreitet.

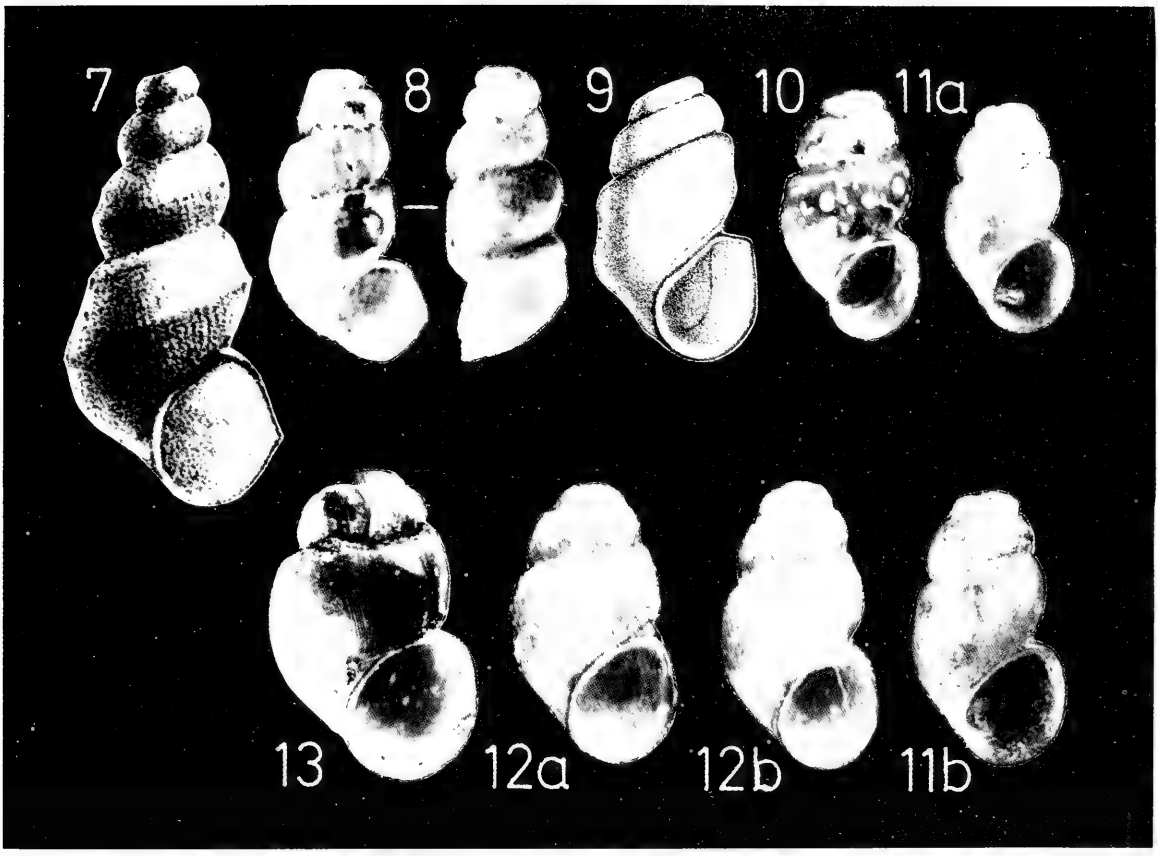

ABB. 7-8. *Bythinella pyrenaica*. Abb. 7. (Die F. 12 von *Pyrgula pyrenaica* Bourguignat in Bourguignat, 1861: T. 15 wurde auf 57 mm vergrössert, was einer Vergrösserung der natürlichen Gehäuselänge gemäss T. 15, F. 11 im Verhältnis 1 : 15 entspricht). Abb. 8. (Lectotypus von *Pyrgula pyrenaica* Bourguignat; BOU). Bagnères-de-Bigorre, Hautes-Pyrénées.

ABB. 9-13. *Bythinella reyniesii*. Abb. 9. (Die F. 4 von *Paludinella darrieuxii* Folin & Berillon in Folin & Berillon, 1877: T. 3 wurde auf 38 mm verkleinert, was einer Vergrösserung des nach Folin & Berillon, 1877: 208 "2 mm 5" langen Gehäuses im Verhältnis 1 : 15 entspricht). Abb. 10. (Lectotypus von *Paludinella darrieuxii* Folin & Berillon; BE). Arneguy, Basses-Pyrénées. Abb. 11. (Topotypen von *Hydrobia reyniesii* Dupuy; BOE 195). Bagnères-de-Bigorre, Hautes-Pyrénées. Abb. 12. (Syntypen von *Paludinella andorrensis* Paladilhe; BOU). Les Escaldes, Andorra. Abb. 13. (Lectotypus von *Paludinella baudoni* Paladilhe; PA). Port de Venasque, Haute-Garonne. Vergrösserung 1:15.

B. (B.) bicarinata
Abb. 6, 28-29

1827 ***Paludina bicarinata*** Des Moulins, Bull. Hist. natur. Soc. linn. Bordeaux, 2: 26-27, T. Loc. typ.: "dans la petite rivière de Couze, près Lalinde, arrondissement de Bergerac", Dordogne.

1838 ***Paludina tricarinata*** Potiez & Michaud, Galérie, 1: 256, T. 26, F. 21-22 [*nov. nom.* pro *bicarinata*].

1892 ***Bythinella (Bicarinatiana) bicarinata,*** Fagot, Bull. Soc. Ramond, 27: 27-28.

1929 ***Brachypyrgula bicarinata,*** Polinski, Glas Srpske Kral. Akad., 137: 153.

Kiemenlamellen: 20 (BOE 366/3 ♀, 11-12 ♂♂). — Penis: in der Ruhelage etwas länger als die Drüsenrute (Abb. 29 a = BOE 366/11, Abb. 29b = BOE 366/12). — Weiblicher Genitaltrakt: Ovidukt vor der Einmündung des Receptaculum seminis mit 1 gelblichen Z-förmigen Schlinge, 1 Receptaculum seminis, proximaler Teil der Anhangdrüse relativ schwach ausgebildet (Abb. 28 = BOE 366/1, 2).

Typen: Syntypen nicht ermittelt, Topotypen D/1 (Dupuy 1851: 578, Astre 1921: 262) und BOE 289 und 366.

Untersuchtes Material, Vorkommen und Verbreitung: Bisher nur vom locus typicus, einer Limnokrene (Waschhaus) am Couze-Ufer, bekannt (18°C).

B. pyrenaica
Abb. 7-8

1861 *Pyrgula pyrenaica* Bourguignat, Rev. Mag. Zool. pure appl., (2) 13: 530-531, T. 15, F. 11-13. Loc. typ. (restr.): "dans la fontaine ferrugineuse de Bagnères-de-Bigorre (Hautes-Pyrénées)."

Bemerkungen: Durch Polinski (1929: 154) wurde *pyrenaica* neben *stancovici* Polinski, 1929, den Typus von *Micropyrgula*, gestellt. Die Anatomie von *stancovici* wurde von Radoman (1955) beschrieben. Bei *pyrenaica* handelt es sich jedoch um keine *Micropyrgula*, sondern um eine *Bythinella*, die von Bourguignat irreführend abgebildet wurde; der Lectotypus zeigt den für *Bythinella* typischen schräg aufsitzenden Apex.

Unklar ist, um was es sich bei *paludestrinoides* Paladilhe, 1869 [*Hydrobia*] und *bigorriensis* Paladilhe, 1869 [*Belgrandia*] handelt, die beide wie *pyrenaica* in einer "source ferrugineuse" bzw. "fontaine ferrugineuse, près de Bigorre (Hautes-Pyrénées)" gefunden wurden.

Typen: Lectotypus BOU.

Vorkommen und Verbreitung: *pyrenaica* ist seit ihrer Beschreibung an den von Bourguignat angegebenen Orten nicht wiedergefunden worden. Die Quelle, zu der die Avenue de la Fontaine Ferrugineuse in Bagnères-de-Bigorre führt, beherbergt keine *Bythinella;* in Rheokrenen unterhalb dieser Quelle findet man nur *reyniesii*.

BESTIMMUNGSSCHLÜSSEL

Mit diesem Schlüssel wird der Versuch unternommen, innerhalb einer Gattung der Hydrobiidae eine Arten-Bestimmung ausschliesslich aufgrund anatomischer Merkmale durchzuführen. Der Schlüssel kann jedoch nicht mehr als eine Anregung geben, da die Konstanz der ihm zugrundeligenden Merkmale ungewiss ist.

1 Bursa copulatrix etwa oval . . . . . *bicarinata*
- Bursa copulatrix etwa wurstförmig. 2

2 Bursa copulatrix etwa U-förmig. . . . . *viridis*
- Bursa copulatrix etwa J-förmig 3

3 Anhangdrüse des ♀ distal erst im letzten Viertel ab Einmündung des Ovidukts deutlich verjüngt, ruhender Penis nicht kürzer als die Drüsenrute. . . . . *carinulata*
- Anhangdrüse des ♀ distal etwa ab Einmündung des Ovidukts spitz auslaufend, ruhender Penis kürzer als die Drüsenrute. . . . . *reyniesii*

(2) *Marstoniopsis*

1936 *Marstoniopsis* van Regteren Altena, Basteria, 1: 64-73. Typus: *Hydrobia steinii* Martens, 1858. Typuswahl: van Regteren Altena (1936: 69).

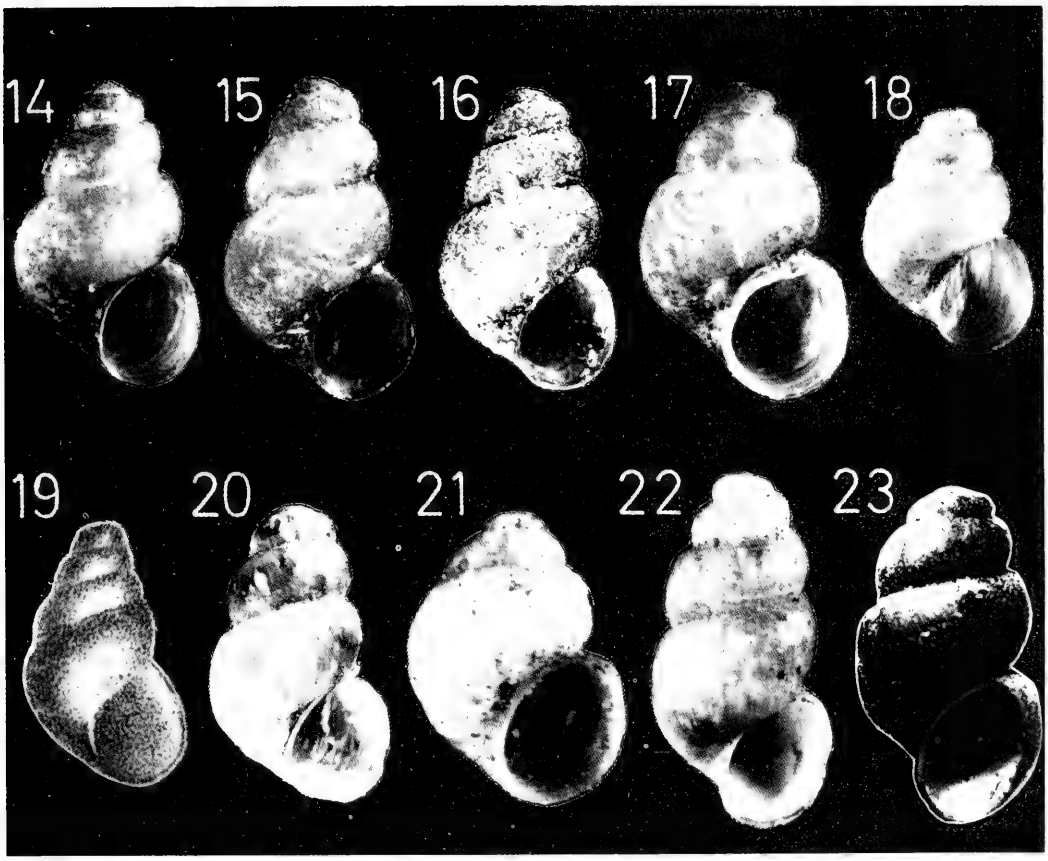

ABB. 14–17. *Marstoniopsis scholtzi*. Abb. 14. (Topotypus von *Hydrobia scholtzi* A. Schmidt; SMF 114 559). Marienau, Schlesien. Abb. 15. (SMF 114 527). Bach bei Tegel (Berlin). Abb. 16. (Syntypus von *Paludinella armoricana* Paladilhe; PA). Nantes, Loire-Atlantique. Abb. 17. (Paratypus von *Amnicola steinii pallida* Krausp; SMF 142 367). Kostivere, Estland.

ABB. 18. *Marstoniopsis insubrica* (Topotypus von *Paludina insubrica* Küster; BOE 128 ex Wüthrich). Muzzano, Tessin.

ABB. 19–20. *Bythinella abbreviata*. Abb. 19. (Die F. 53 von *Paludina abbreviata* Michaud in Michaud, 1831: T. 15 wurde auf 35 mm vergrössert, was einer Vergrösserung des in F. 52 in natürlicher Grösse dargestellten Gehäuses im Verhältnis 1 : 15 entspricht). Abb. 20. (Syntypus von *Paludina abbreviata* Michaud; PA). Lyon, Rhône.

ABB. 21. *Bythinella* sp. (BOE 413 c ex Geissert). Arbois, Jura.

ABB. 22. *Bythinella pupoides* (Topotypus von *Paludinella pupoides* Paladilhe; BOE 384). Thoiry, Ain.

ABB. 23. *Bythinella reyniesii* (?) (Das von Germain, 1931: T. 19, F. 549 in einer Vergrösserung von "x 20" abgebildete Gehäuse wurde auf 44 mm entsprechend einer Vergrösserung im Verhältnis 1 : 15 verkleinert). Mont d'Or Lyonnais, Rhône.

Vergrösserung 1:15.

Differenzierende Merkmale: Anders als bei *Bythinella* (Bregenzer 1915: 252) mit einem schwefelgelben Fleck oberhalb der Augen (E. A. Smith 1901: 192, Van Regteren Altena 1936: 65, 69), Kieme der ♀♀ mit etwa 27 Lamellen (vgl. unten) gegenüber 22 und weniger bei *Bythinella* (vgl. oben und Bregenzer 1915: 246, T. 16 F. 2 ♀), Drüsenrute (vgl. unten und Van Regteren Altena 1936: 73, Abb. 3a) gedrungener als bei *Bythinella* (vgl. oben und Literaturzusammenstellung in Boeters 1970: 117), der Ovidukt ist nach eigenen Untersuchungen anders als bei *Bythinella* in unübersichtlicher Weise nach Annäherung an die Anhangdrüse mit dieser verwachsen (wobei bereits Krull 1935: 444 die Struktur von Bursa copulatrix und Receptaculum seminis nur z. T. aufklären konnte), Unterschiede im Nervensystem gegenüber *Bythinella* bei Krull (1935: 424), Laich nicht wie bei *Bythinella* einfach-linsenförmig (Lauterborn 1904: 86, Bregenzer 1915: T. 16, F. 13, Jungbluth 1971: Abb. 31a-c), sondern mit einem Kiel (Jackson & Taylor 1904: 10, Abb. 3-5, Van Regteren Altena 1936: 65, 75, Abb. 1), Vorkommen in sauerstoffärmerem Wasser als *Bythinella* (*scholtzi* wurde von Ziegeler 1935: 57 im Aquarium gezüchtet).

M. scholtzi
Abb. 14-17, 33, 36

1850 *Bythinia acuta*, Stein, Berlin: 95, non T. 3, F. 5.
1853 *Paludina* sp., Scholtz, Schlesien, 2. Aufl., Suppl.: 13-14.
1856 *Hydrobia scholtzi* A. Schmidt, Z. ges. Naturw., 8: 158. Loc. typ.: "Wiesengräben zwischen Breslau und Marienau".
1857 *Hydrobia scholtzi*, A. Schmidt, Verzeichnis: 42.
1858 *Hydrobia steinii* Martens, Arch. Naturgesch., 24: 183-184, T. 5, F. 9. Originalfundorte: "am Ufer des Tegelsees zwischen Berlin und Spandau" und "in der Havel bei Pichelsberg".
1869 *Paludinella armoricana* Paladilhe, Rev. Mag. Zool. pure appl., (2) 21: 278-279, T. 20, F. 5-6. Loc. typ.: "dans l'Erdre, près de Nantes", Loire-Atlantique.
1901 *Paludestrina taylori* E. A. Smith, Ann. Mag. natur. Hist., (7) 7: 191-192. Loc. typ.: "canal at Dukinfield, Cheshire".
1936 *Amnicola steinii pallida* Krausp, Eesti loodus.: 196-200. Loc. typ.: "Estonia, the district of Harjumaa, Kostivere, at the beginning of the subterranean river of the Jõelähtme-River".

Bemerkungen: Stein führte 1850 Funde von "*Bythinia acuta* Drap." bei Berlin an, Scholtz 1853 "*Paludina* spec. nova?" aus der Umgebung Breslaus. Beide Angaben hatten Neubeschreibungen zur Folge. Jedoch wurde das Scholtzsche Material schon 1856 durch A. Schmidt mit dem Namen *scholtzi* belegt, während die Beschreibung von *steinii* mit dem Steinschen Material durch Martens erst 1858 erfolgte. Clessin erkannte (1884: 480), dass es sich um Synonyme handelt; er gab jedoch dem jüngeren Namen *steinii* den Vorrang: "Scholtz hat seine Beschreibung wahrscheinlich nach unvollendeten Exemplaren entworfen." Damit wurde die bis zum heutigen Zeitpunkt vor allem im deutschsprachigen Schrifttum verbreitete Unterdrückung des nomenklatorisch gültigen und älteren Namens *scholtzi* begründet. Hingegen wird in der jüngeren englischen Literature die Art richtig als *scholtzi* geführt (z.B. Census 1951: 179, Fretter & Graham 1962: 642, Ellis 1969: 271).

Radula: (?Lindström 1868: T. 3, F. 9, der Penis F. 8 zeigt keine Drüsenrute! Johansen 1918: Abb. 10, T. Benthem Jutting 1933: Abb. 68, Krull 1935: 413, Van Regteren Altena 1936: 66, Abb. 2, Verdcourt 1948: Abb. 8-11). — Kiemenlamellen: ♂♂ 21 (BOE 274/11), ♀♀ 28 (BOE 274/1-2). — Penis: Drüsenrute etwa halb so lang wie der Penis (Van Regteren Altena 1936: 73, Abb. 3a, Abb. 33 = BOE 274/11, 12). — Weiblicher Genitaltrakt: Krull konnte die Struktur von Bursa copulatrix und Receptaculum seminis

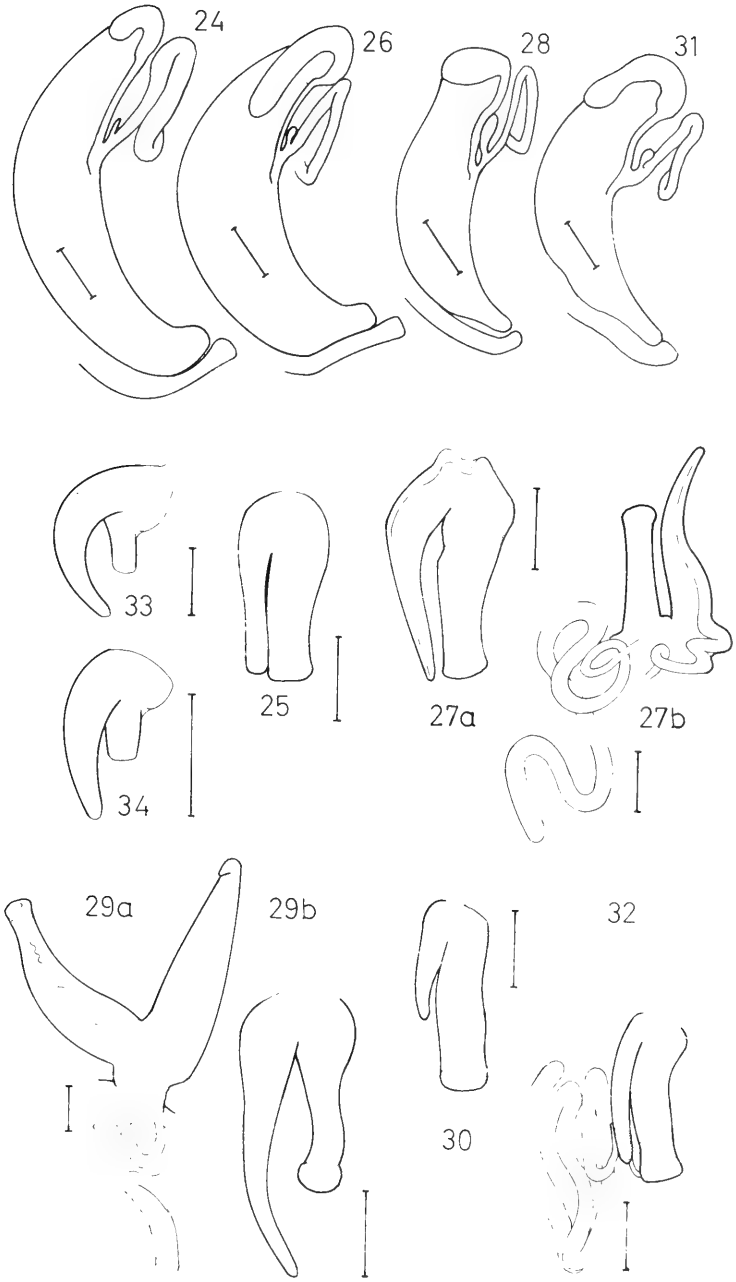

ABB. 24-25. *Bythinella viridis* (BOE 386). Zwischen Chéry-Chartreuve und St. Gilles, Aisne. ABB. 26-27. *Bythinella carinulata* (Topotypen von *Hydrobia carinulata* Drouet; BOE 148). Norges-la-Ville, Côte-d'Or. ABB. 28-29. *Bythinella bicarinata* (Topotypen von *Paludina bicarinata* Des Moulins; BOE 366). Couze-et-St.-Front, Dordogne. ABB. 30-32. *Bythinella reyniesii*. Abb. 30. (Topotypus von *Hydrobia reyniesii* Dupuy; BOE 195). Bagnères-de-Bigorre, Hautes-Pyrénées. Abb. 31-32. (Topotypen (?) von *Paludinella darrieuxii* Folin & Berillon; BOE 362). Arneguy, Basses-Pyrénées. ABB. 33. *Marstoniopsis scholtzi* (BOE 274 ex Meier-Brook). Langsee (Kiel-Elmschenhagen). ABB. 34. *Marstoniopsis insubrica* (SMF 4 649). Lago Maggiore.

Vergleichsstrecke 0,25 mm.

nicht völlig aufklären (1935: 444); nach eigenen Untersuchungen ist der Ovidukt nach Annäherung an die Anhangdrüse in unübersichtlicher Weise mit dieser verwachsen (BOE 274/1).

Untersuchtes Material: BOE 274 = Langsee, Kiel-Elmschenhagen, Meier-Brook leg.

Typen: *scholtzi:* Topotypen SMF 114 559/11; *steinii:* Syntypen nicht ermittelt; *armoricana:* Syntypen PA/zahlreich; *pallida:* Syntypen SMF 142 367/7.

Verbreitung:

(1) Grossbritannien. Die in der Literatur verbreitete Ansicht, dass *scholtzi* aus Nordamerika nach Europa eingeschleppt worden sei, geht auf E. A. Smith (1901: 191) zurück und trifft nicht zu. Diese irrige Ansicht wurde dadurch begünstigt, dass E. A. Smith die bis 1901 rezent nur vom Kontinent bekannte *scholtzi* beim Erstnachweis für Grossbritannien nicht erkannte und als *taylori* neu beschrieb. Smith's Ansicht wurde in jüngster Zeit von D. W. Taylor (1966: 173) und Ellis (1969: 271) richtig gestellt; *taylori* wurde von E. A. Smith anhand rezenten Materials beschrieben, — nicht nach einem fossilen Fund, wie S. G. A. Jaeckel (1962: 49, 1967: 97 Fussnote 112) entnommen werden muss, wenn er schreibt: "+ *Amnicola taylori* (Smith 1901)... ausgestorben u. durch... [*Marstoniopsis steinii* = *scholtzi*] ersetzt." Ferner ist an diesem Zitat richtigzustellen, dass nach Van Regteren Altena (1936: 70) und Ellis (1969: 271) *scholtzi* [und nicht *taylori*!] im Holozän in Grossbritannien erloschen ist, jedoch durch "reintroduction from its area in the northwestern part of the European continent in historical time" (Van Regteren Altena 1936: 70, "recent importation" nach Ellis 1969: 271) heute in Grossbritannien wieder vorkommt.

Ein Argument, das gegen dieses zwischenzeitliche Erlöschen sprechen könnte, ist die Tatsache, dass von *Mercuria* sp. (=*Pseudamnicola confusa* auct.) bisher nichts analoges berichtet wird; diese Art kommt gleichfalls in Grossbritannien vor und begleitet *scholtzi* stellenweise, — zumindest auf dem westlichen europäischen Kontinent (Paladilhe 1869: 279).

(2) Frankreich. *Marstoniopsis* wurde bisher aus Frankreich noch nicht rezent angegeben. Jedoch stellt *armoricana* ein Synonym von *scholtzi* dar; *armoricana* wurde am locus typicus mit *sarahae* Paladilhe, 1869 [*Amnicola*] = *Mercuria* sp. vergesellschaftet angetroffen. Nach dem Gehäuse kann es sich auch bei *curta* Paladilhe, 1874 [*Paludinella*] um ein Synonym von *scholtzi* handeln.

Fundortkatalog (Abb. 36): rezent: Loire-Atlantique: Nantes (Letourneux nach Paladilhe 1869: 279, *armoricana*) [47,2/-1,6°]; pleistozän: Charente-Maritime: Celles-sur-le-Né (Bourdier 1942: 473, *steinii*) [45,6/-0,4°]. —Dordogne: Condat [-le-Lardin oder -sur-Tricou oder -sur-Vézère?] (Bourdier 1942: 473, *steinii*).

M. insubrica
Abb. 34, 36

1853 *Paludina insubrica* Küster, *Paludina,* 2: 77-78, T. 13, F. 20-21. Loc. typ: "Lago di Muzano bei Lugano".

1859 *Bythinia insubrica stabilei* Stabile, Atti Soc. geol. res. Milano, 1(1855/59): 167 und 182. Loc. typ.: "lago di Muzzano".

1968 *Marstoniopsis insubrica,* Boeters, Mitt. bad. Landesver. Naturk. Naturschutz, NF 9: 755 und 765.

Bemerkungen: Die von Boeters (1968: 765) vertretene Auffassung, dass *insubrica* nicht wie bisher (Alzona & Alzona Bisacchi 1939: 143, Toffoletto 1964: 209) bei *Pseudamnicola,* sondern bei *Marstoniopsis* einzuordnen ist, wird folgendermassen begründet: *insubrica* weist (anders als *lucensis,* der Typus von *Pseudamnicola*) wie *scholtzi,* der Typus von *Marstoniopsis,* einen schräg aufsitzenden Apex und eine Drüsenrute am männlichen Kopulationsorgan auf; auch kommt *insubrica* wie *scholtzi* in stehenden

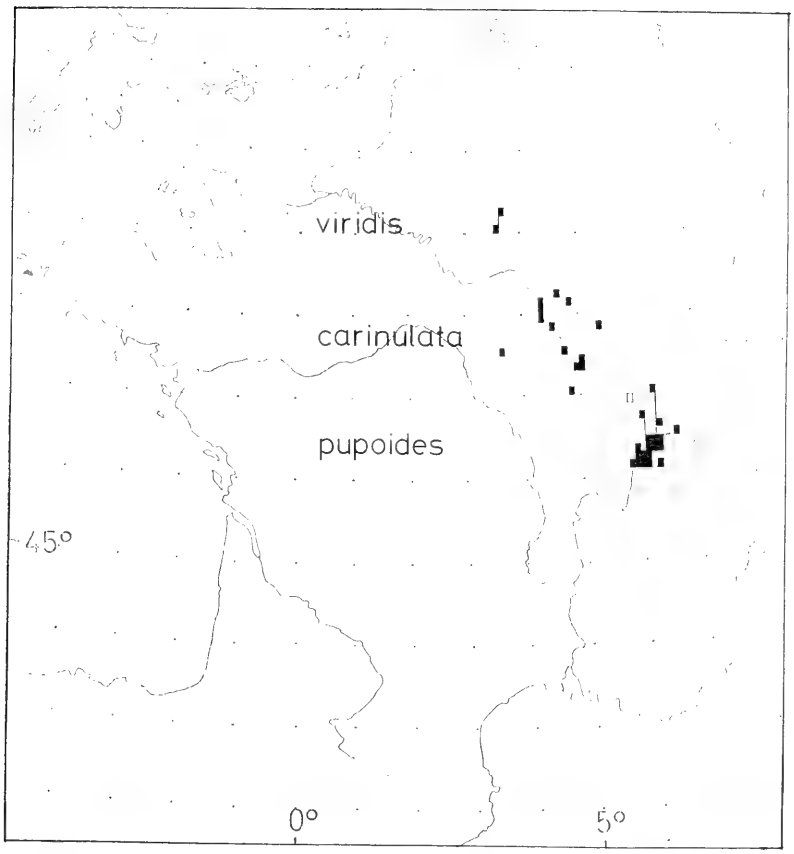

ABB. 35. Verbreitungsgebiete von *Bythinella viridis*, *B. carinulata* und *B. pupoides*. Die Abbildung beruht auf den Fundortkatalogen, vgl. die Erläuterungen unter (4).

Gewässern vor.

Es bleibt zu klären, ob *scholtzi* nicht nur eine geographische Rasse von *insubrica* darstellt; eine Verbindung zu den *scholtzi*-Vorkommen des Balkans kann nicht von vornherein ausgeschlossen werden. Von S. H. Jaeckel & Klemm & Meise (1958: 175) wird *scholtzi* als nord-, mittel- und (nicht etwa südost- sondern glatt:) südeuropäisch bezeichnet. (Bei weiterer Bearbeitung südeuropäischer *Marstoniopsis*-Vorkommen wären auch *lacustris* Hadžišče, 1958 [*Bythinella*] und *macedonica* Hadžišče, 1958 [*Belgrandia*], von welcher der Autor die zapfenartige [!] Drüsenrute hervorhebt, zu überprüfen.)

Radula: Mittelplatte mit 2 Lateraldentikeln (BOE 95/1). — Kiemenlamellen: (etwa) 3 vor, 12 am, 6 hinter dem Osphradium Richtung Mantelrand, insgesamt (etwa) 21 bei ♂♂(SMF 4 649/1 ♂). — Penis: Drüsenrute etwa halb so lang wie der Penis (Abb. 34 = SMF 4 649/1).

Untersuchtes Material: BOE 95 = Lago di Muzzano, Wüthrich leg., SMF 4 649/10 = Isola dei Pescatori im Lago Maggiore, Gaschott leg.

Typen: *insubrica* und *stabilei:* Topotypen BOE 95.

Verbreitung: Südalpenrandzone.

Fundortkatalog (Abb. 36): Schweiz: Lago di Muzzano (Stabile nach Küster 1853: 78, Stabile 1859: 167, Wüthrich nach Boeters 1968: 765) [45,9/8,9°]. — Italien: Lago Maggiore

(Imhof 1901: 58, *cylindrica*, Gaschott 1931: 35, *Bythinella* sp., Nocentini nach Toffoletto 1964: 209) [45,9/8,5° und 46,0/8,6°]. — Lago di Garda bei San Vigilio (Gittenberger in litt.) [45,5/10,7°]. — Castel Goffredo (Genist) (F) [45,2/10,4°]. — Lago di Levico (SMF 142 364, *steinii*) [46,0/11,2°].

(3) *Bythinella* oder *Marstoniopsis abbreviata*
Abb. 19-20

1831 *Paludina abbreviata* Michaud, Complément: 98, T. 15, F. 52-53. Loc. typ.: "Lyon, dans les alluvions du Rhône."

Bemerkungen: Zur Anregung der Diskussion um die Identifizierung von *abbreviata* wird im folgenden die Frage aufgeworfen, ob es sich möglicherweise um einen Vertreter von *Marstoniopsis* handelt.

Aufgefundene Syntypen (Abb. 20) stimmen gut mit Michaud's Abbildung (Abb. 19) überein. Sie lassen sich bisher keiner *Bythinella* im Einzugsgebiet der Saône und Rhône bei Lyon zuordnen: - *reyniesii* (?, Abb. 23) der Ausläufer des Massif Central rechts der Saône und Rhône bei Lyon (Fischer 1880: 298 und 1885: 307, Locard 1877: 515, *viridis*, Germain 1931: XII, T. 19, F. 549 und XIV, T. 23, F. 595, *brevis*) kommt *abbreviata* nicht nahe, bezüglich des Habitus und Vorkommens auf vorzugsweise kalkarmen Formationen eher *dunkeri;* - *carinulata* (Abb. 2-5) unterscheidet sich durch seine kantigen Umgänge und kommt nach heutigem Wissen nicht sehr nah an Lyon heran (Abb. 35); - *pupoides* (Abb. 22) hat schlankere Gehäuse und kommt nach gegenwärtigen Kenntnissen gleichfalls nicht sehr nah an Lyon heran (Abb. 35 auf Basis von Boeters 1968: 763, Abb. 72); auch eine weiterer von Geissert im Jura (Abb. 35 leeres Kästchen) gesammelte *Bythinella* (-*viridis*? Abb. 21), deren artliche Zuordnung noch zweifelhaft ist, kommt nicht in Betracht.

Die aufgefundenen Syntypen zeigen vielmehr einen *Marstoniopsis*-ähnlichen Habitus (vgl. Abb. 14-16 mit 20). Man könnte daran denken, dass *abbreviata* im Gebiet der Seenplatte (Les Dombes) zwischen Saône und Rhône nördlich Lyon vorkommt. Dazu machte Ogerien (1863: 544) in seiner Histoire naturelle du Jura unter dem Namen *viridis* die bemerkenswerte und bisher ungeklärte Angabe: "plaine, AC [assez commune]".

Typen: Syntypen PA/6 (Etikett: "*Paludinella abbreviata* Jura typus ex auctore"). In Lyon (Forcart 1959: 7, Dance 1966: 294) und Brive-la-Gaillarde (Collot 1911: 94) wurden keine Syntypen ermittelt.

NAMEN UND TYPUSFESTLEGUNGEN

In dieser Arbeit werden folgende Namen erwähnt (in ihr festgelegte Typen sind in Klammern angegeben): *andorrensis*, *armoricana*, *baudoni* (Lectotypus), *baudoniana*, *bicarinata*, *bigorriensis*, *bourguignati* [*Bythinella* non *Paulia*], *burgundina* (Lectotypus), *carinulata*, *curta*, *cylindracea*, *darrieuxii* (Lectotypus), *griseus*, *insubrica*, *lanceolata*, *pallida*, *paludestrinoides*, *pupoides*, *pyrenaica* (Lectotypus), *reyniesii*, *riparia*, *scalarina* (Lectotypus), *scholtzi*, *sequanica*, *stabilei*, *steinii*, *taylori*, *tricarinata*, *tricassina*, *turgida*, *turgidula* und *viridis*.

Fundortkataloge: Bei der Angabe der geographischen Koordinaten und bei der Kartographierung (Abb. 35-36) wurde das von Boeters (1968: 756, 1970: 114) gewählte System benutzt.

Sammlungen:

BE = Sammlung Berillon, Musée d'Histoire Naturelle, Bayonne (Frankreich); BOE = Sammlung Boeters, München (Deutschland); BOU = Sammlung Bourguignat, Muséum d'Histoire Naturelle, Genève (Schweiz); D = Sammlung Dupuy, Muséum d'Histoire Naturelle, Toulouse (Frankreich); F = Sammlung Falkner, München (Deutsch-

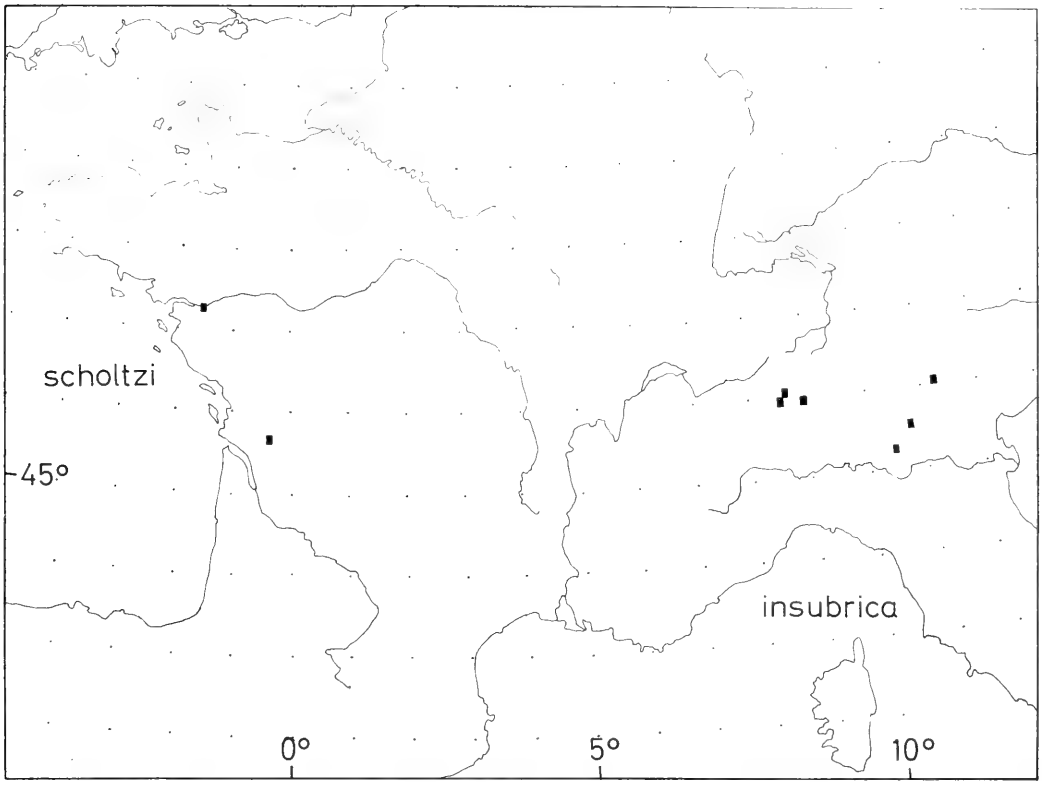

ABB. 36. Verbreitungsgebiete von *Marstoniopsis scholtzi* und *M. insubrica*. Die Abbildung beruht auf den Fundortkatalogen, vgl. die Erläuterungen unter (4).

land); MP = Muséum National d'Histoire Naturelle, Paris (Frankreich); MW = Naturhistorisches Museum, Wien (Österreich); PA = Sammlung Paladilhe, Faculté des Sciences, Montpellier (Frankreich) und SMF = Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main (Deutschland).

Den Herren Dr. E. Binder (Genève), H. Chevallier (Paris), G. Falkner (München), F. Geissert (Sessenheim), E. Gittenberger (Leiden), Prof. Dr. R. Legendre (Montpellier), Dr. O. Paget (Wien) und Dr. A. Zilch (Frankfurt am Main) danke ich für die grosszügige Unterstützung mit Material und Informationen, Herrn F. Geissert darüber hinaus für das Résumé.

RESUME

L'espèce-type du genre *Bythinella*, *Bulimus viridis*, ainsi que les quatre Prosobranches pyrguloides d'Europe occidentale (*Hydrobia carinulata*, *Paludinella darrieuxii*, *Paludina bicarinata* et *Pyrgula pyrenaica*) ont été identifiés au moyen de syntypes et de topotypes. Il en résulte que *H. carinulata*, *P. darrieuxii* et *P. bicarinata* sont à considérer comme représentants du genre *Bythinella* s. str. La position systématique de *P. pyrenaica* au sein du genre *Bythinella* reste indécise.

La preuve a pu être apportée que *Paludina insubrica* appartient au genre *Marstoniopsis* (Boeters 1968: 755).

Le nombre des lamelles branchiales est plus élevé chez les ♀♀ de *Marstoniopsis* que chez celles de *Bythinella*. L'on peut distinguer les ♀♀ et les ♂♂ aussi bien des

Bythinella que des *Marstoniopsis* par l'étude du parcours intestinal, sans avoir recours à la destruction de la coquille.

Des syntypes de *Paludina abbreviata* ont été trouvés; le mode de leur test ressemble à celui des *Marstoniopsis*. L'identification de *P. abbreviata* reste encore problématique.

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MALACOLOGIA, 1973, 14: 287-289

PROC. FOURTH EUROP. MALAC. CONGR.

ELECTROPHORESIS AS A SUPPORT FOR THE IDENTIFICATION OF VARIOUS AFRICAN *BIOMPHALARIA*

Gudrun Wium-Andersen

Danish Bilharziasis Laboratory, Charlottenlund, Denmark

ABSTRACT

Esterases from the hepato-pancreas of African *Biomphalaria* spp. have been examined by means of starch-gel electrophoresis. On the basis of esterases it was possible to separate the following species determined from their morphological characters: *B. pfeifferi* (Krauss), *B. alexandrina* (Ehrenberg), *B. camerunensis* (Boettger) and *B. sudanica tanganyicensis* (Smith). *B. alexandrina wansoni* Mandahl-Barth is identical with *B. camerunensis* in regard to the esterase pattern.

The esterases emphasize the conformity found in shell morphology between *Biomphalaria alexandrina* from Ismailiya and *B. sudanica tanganyicensis*. In *B. alexandrina* esterases varied from one population to another, while they were completely constant in all *B. pfeifferi* populations examined. This variability parallels a great variation in susceptibility to infection with *Schistosoma mansoni* (Sambon) found in the populations of *B. alexandrina* examined, and a constant susceptibility to infection with *S. mansoni* in the populations of *B. pfeifferi* examined.

It is a well known fact that species of the genus *Biomphalaria* act as intermediate hosts of *Schistosoma mansoni*, which causes the intestinal form of human bilharziasis.

Some of the African species of *Biomphalaria* show great variation in shell morphology as well as in anatomy, which impedes the classification of the species. As a supplement to the morphological characters I have used biochemical methods. In the beginning I have examined esterases from the hepato-pancreas by using starch-gel electrophoresis for the purpose of achieving a better understanding of the taxonomy within the genus and also hoping to get some information as to whether the differences in susceptibility within a certain species can be correlated to different infraspecific forms.

Fig. 1 shows the sample localities: *Biomphalaria alexandrina* from 8 localities, *B. pfeifferi* from 4 localities, *B. camerunensis* from 4 localities near Kinshasa in Congo, *B. alexandrina wansoni* from 2 localities near Kisangani and *B. sudanica tanganyicensis* from Mwanza in Tanzania. Fig. 2 shows a diagram of the esterase bands found in the examined *Biomphalaria* species. In *B. pfeifferi* I have found 6 esterase bands, 2 of which move towards the cathode and the remaining towards the anode. The maximum number of esterase bands found in *B. alexandrina* was 11. However, with this technique *B. alexandrina* from Ismailiya did not show the same bands in the B-series, but instead 2 more powerful ones with a quite thin band in between moving a little faster towards the anode. These 3 bands are almost confluent. In all other *B. alexandrina* populations B_1, B_2, and B_3 were always present. In *B. camerunensis* the technique shows 8 esterase bands. *B. alexandrina wansoni* is identical with *B. camerunensis*. Unfortunately there was only a limited number of specimens of *B. sudanica tanganyicensis* at my disposal, but the examined specimens show bands in the B-series identical with those of *B. alexandrina* from Ismailiya.

I have found that the populations of *Biomphalaria pfeifferi* from Ethiopia, Katanga and Uganda are identical and all bands appear with a frequency of 100%. The Rhodesia

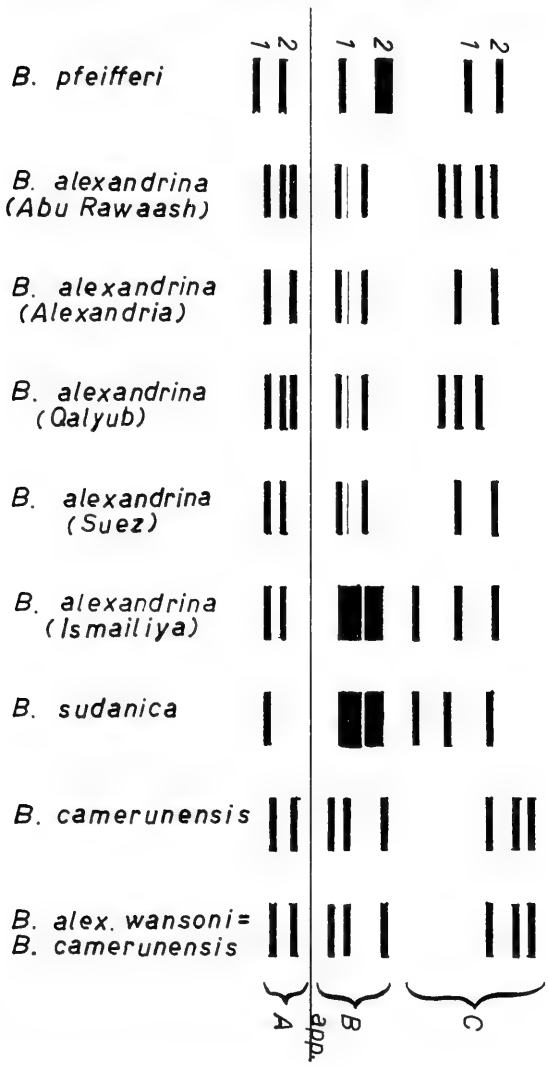

FIG. 1. Collecting localities for the examined African *Biomphalaria*.

population was similar to the 3 mentioned, apart from the lacking band A_1.

The variation in the esterase pattern in *Biomphalaria alexandrina* is very great from one population to another. The Ismailiya population can always be distinguished from the others by the presence of C_1. All *B. camerunensis* populations examined are identical and they do not differ from the *B. alexandrina wansoni* populations.

The esterases suggest that the 3 species *Biomphalaria pfeifferi*, *B. sudanica tanganyicensis* and *B. camerunensis* identified on morphological characters are well established species, as they have different esterases, as opposed to *B. alexandrina*, in which the variability makes the state less clear.

Different populations of *Biomphalaria alexandrina* vary in their susceptibility to *Schistosoma mansoni* from Egypt and elsewhere, whereas populations of *B. pfeifferi* from geographically widely separated localities all have the same high susceptibility to all strains of *S. mansoni*.

The results obtained demonstrate a correlation between uniform esterase pattern and high susceptibility of *Biomphalaria pfeifferi*, whereas in *B. alexandrina* there is a

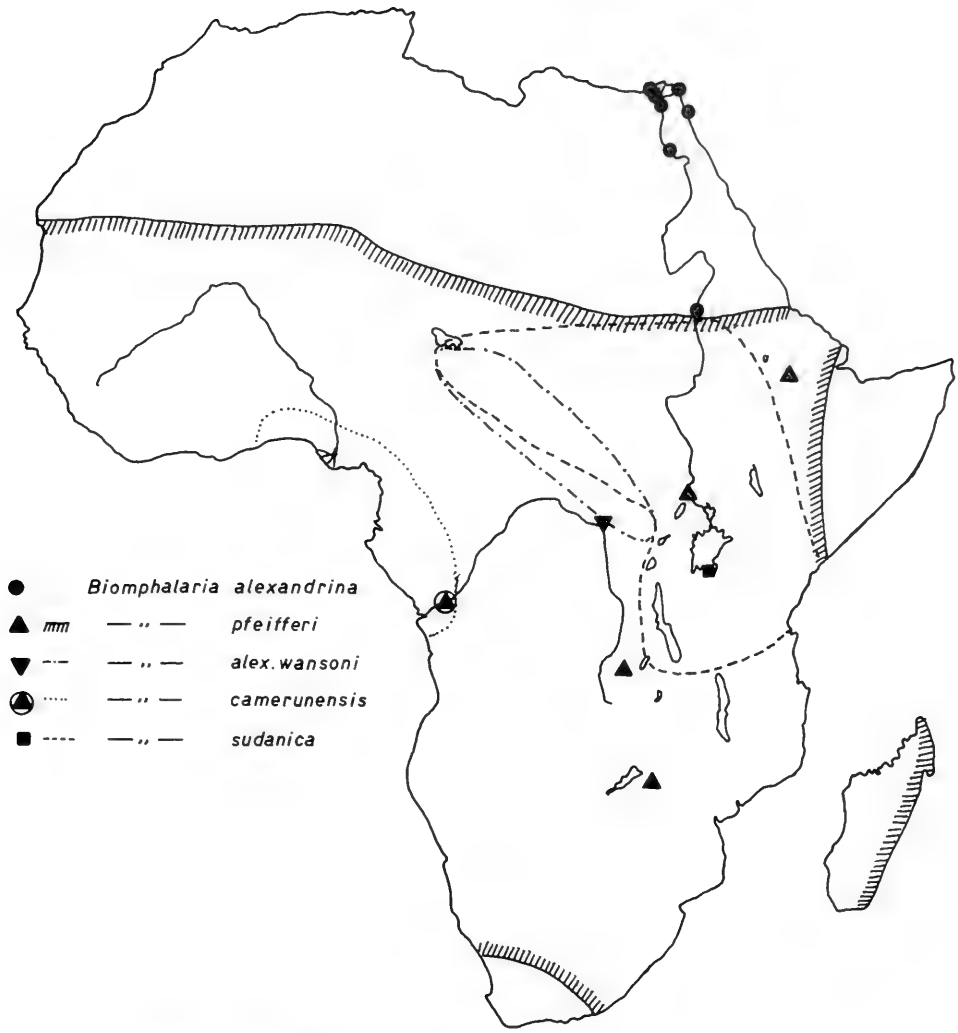

FIG. 2. The esterase bands found in African *Biomphalaria*.

great variation both in the esterase pattern and in the susceptibility to *Schistosoma mansoni*. These results are remarkable considering the much wider geographical distance between the *B. pfeifferi* localities than between those of the *B. alexandrina* populations.

The *Biomphalaria alexandrina* population from Ismailiya resembles *B. sudanica* in shell shape, length of central teeth and in the esterase pattern. Now the question arises whether this population should be considered as an isolated population of *B. sudanica*. Perhaps the peculiar distribution of *B. alexandrina*, its variation in susceptibility, the unstable morphological characters and the esterases suggest that *B. alexandrina* should rather be regarded as a hybrid between *B. pfeifferi* and *B. sudanica*. In any case, the great variation in *B. alexandrina* indicates that this species is most probably a species in evolution.

In morphological characters *Biomphalaria alexandrina wansoni* is closely related to *B. camerunensis* and they have identical esterases. I think that *B. wansoni* must be regarded as an inland form of *B. camerunensis* and not as a subspecies of *B. alexandrina*.

MALACOLOGIA, 1973, 14: 291-301

PROC. FOURTH EUROP. MALAC. CONGR.

THE MINUTE SHELL STRUCTURE OF THE GLOCHIDIUM OF SOME SPECIES OF THE GENERA *UNIO*, *POTOMIDA* AND *ANODONTA* (BIVALVIA, UNIONACEA)

Folco Giusti

Institute of Zoology, Siena, Italy

INTRODUCTION

Anyone who has read or even leafed through texts on Unionacea systematics will easily understand the reason for this research which I have undertaken. In fact, the systematics of this group of molluscs is in chaos, particularly at the level of species. This systematic disorder is caused principally by the fact that the Unionacea, like most bivalves, do not possess a structure which gives valid characteristics so that the different species may be classified with any certainty. The only structure useful for classification, the shell, is in fact very variable, as it is subject to environmental factors, and so does not lend itself to a sure identification. In the past, exactly as has happened in all the other groups of molluscs, the study of the shells only has led to the creation of an incredible number of species, with the result that, if the place where they were taken is not considered, it is practically impossible to distinguish one species from another. Thus my attention was drawn to young bivalves, and in particular to those larval forms known everywhere as "glochidia." It seemed logical that larval forms which are highly differentiated, as in the glochidium, possessing as they do a small rather complicated embryo shell, would provide on further study characteristics useful not only for testing the validity of the classification of the different species, but also for the clarification of the interrelations between the different genera.

The shell and the attachment structures of the glochidium of *Unio*.

My research began with a study of the glochidium of a population of *Unio* living on the outskirts of Pavia. According to Zilch (1967), the species should be *U. elongatulus glaucinus* Porro, but in the past it has at times been called *U. requieni* and at other times *U. pictorum* or *U. athesinus*.

The shell of the glochidium is made of 2 triangular valves, the mirror image of each other, held together by a ligament (Fig. 1). Under the scanning electron microscope at low magnification it is already possible to make out that the outer surface of the 2 valves is not smooth, but covered with numerous evenly-distributed protuberances (Figs. 2 and 4). In many places the valve surface is furrowed as well with numerous small hollows (Figs. 3 and 4). Finally, on examining fragments of valves, it is possible to make out that the shell is made of 2 parts. One is external, like a thin skin, with the above described protuberances on the outside, and one is internal, of a crystalline aspect, full of numerous holes (Figs. 2 and 3). The hollows noticed on the surface of the valves originate in the furrowing of the external skin following the holes of the crystalline layer. In both valves, the attachment structure is situated on the anterior apex and is made up of a margin possessing numerous pointed spines (Figs. 8 and 9). Closing the valves the margins fold towards the inside, fastening the spines firmly into the tissues of the host fish (Figs. 10 and 11). The apex of each valve, all around the spiny margin, has small very dense spines for a short stretch (Fig. 11).

The shell and the attachment structures of the glochidium of *Potomida*.

The research was carried out on the larval forms of *Potomida littoralis littoralis* (Lamarck) from the river Ebro, Spain[1]. In this species which, according to Zilch (1967) belongs to the subfamily Quadrulinae of the Unionidae, there has been found a particular kind of glochidium. Its shell in fact has an hemispherical shape and lacks a spiny margin like that seen in *Unio*. There are only small spines distributed all along the edge of the 2 valves (Fig. 12). On the other hand the sculpture of the external surface of the valves strongly resembles that seen in *Unio* (Fig. 6). The external protuberances, as seen in *Unio* (Fig. 5), completely cover the smallest spines of the attachment edge (Fig. 7).

The shell and the attachment structures of the glochidium of *Anodonta*.

My research on the glochidium of *Anodonta* was carried out on materials coming from 2 different distant populations of *Anodonta*, the one from Lake Maggiore and the other from Lake Trasimeno (Italy). Nowadays these 2 populations, distinguished in the past by many different names, should be considered as belonging to 1 single species, *Anodonta cygnea* (Linnaeus) according to Zilch (1967). The shell of the glochidium of *Anodonta*, even if of greater size (about 300 μ long), appears as in *Unio*, in a triangular shape with 2 valves of equal size, held together by a ligament (Fig. 13). In this case, too, the external surface of the valves is not smooth, both the glochidium of the 2 different populations having numerous hairy excrescences. These are very thick near the base of the shell (Fig. 15), but they become more and more rare towards the central part of the valve where they are found in parallel rows (Figs. 14 and 16). Near the anterior apex of the shell the protuberances described are even rarer and less obvious.

As seen in *Unio*, the shells of the glochidium of *Anodonta* are also found to consist of 2 parts, one external, a very thin layer, the other internal, much thicker and of crystalline aspect (Figs. 17 and 19). There are many holes in the latter (Figs. 18 and 19). The numerous hollows which are seen on the outer surface of the valves (Figs. 13, 14 and 16) originate in the wrinkling of the external layer over the holes in the crystalline layer. The attachment structure of the glochidium of *Anodonta* is made in the same way in the 2 populations I examined, but *Anodonta* has certain characteristics which differ from those described in *Unio*. On each valve they consist of an apical margin that is covered with long pointed spines (Figs. 20, 23, 24, 25 and 26). There are fewer spines than in *Unio*, both at the base of the spiny margin and on the spiny margin itself (Figs. 21 and 22).

CONCLUSIONS

Besides giving simple information concerning the morphology of the shell and the attachment structure of the valves of the glochidium I examined, I belive I have also shown their importance. The material I examined is too scant to give any practical result, but the field is open, and with the help of European malacologists and others from the rest of the world, I hope to be able to examine other materials and so begin a comparison of the data obtained and attempt making use of these in a revision of the classification of Unionidae.

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[1]My sincere thanks to Dr. Adolf Zilch from Frankfurt, who sent me the material.

SUMMARY

The shell and the attachment structure of the glochidia of some species belonging to the genera *Unio*, *Potomida* and *Anodonta* have been examined with the scanning electron microscope. The author points out that the number and disposition of the attachment spines and the external sculpture of the surface of the shell seem to offer sufficient characteristics to be used in the systematical study of these bivalves.

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FIG. 1. The shell of the glochidium of *Unio elongatulus glaucinus*. The ligament (L) holding together the 2 valves (V). 720x.

FIG. 2. The shell of the glochidium of *Unio elongatulus glaucinus*. In this fragment it is possible to see the external part of the shell like a thin skin (E) and the internal one of crystalline aspect (I). 3,000x.

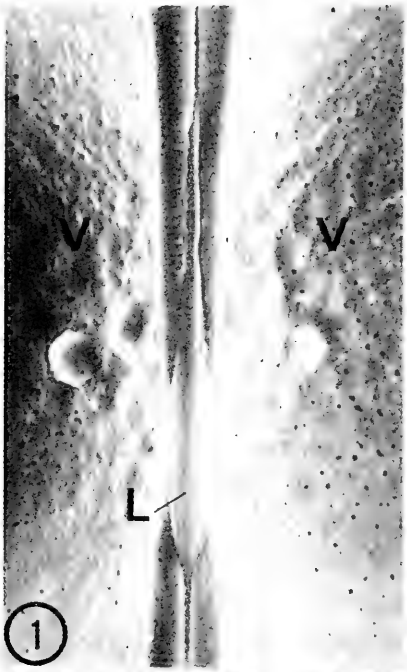
FIG. 3. The shell of the glochidium of *Unio elongatulus glaucinus*. Fragment showing 2 of the holes of the internal crystalline layer externally closed by the "thin skin" like layer. 10,000x.

FIG. 4. The shell of the glochidium of *Unio elongatulus glaucinus*. The outer surface of the "thin skin" layer is covered with numerous little protuberances. The hollows (H) on the surface originate in the furrowing of the "thin skin" following the holes of the crystalline layer. 10,000x.

FIG. 5. The shell of the glochidium of *Unio elongatulus glaucinus*. The "thin skin" layer is extended to completely cover the smallest spines of the attachment structure. 10,000x.

FIG. 6. The shell of the glochidium of *Potomida littoralis littoralis*. The outer surface of the shell is covered with numerous little protuberances. 16,000x.

FIG. 7. The shell of the glochidium of *Potomida littoralis littoralis*. The external little proturberances completely cover the spines of the attachment edge. 16,000x.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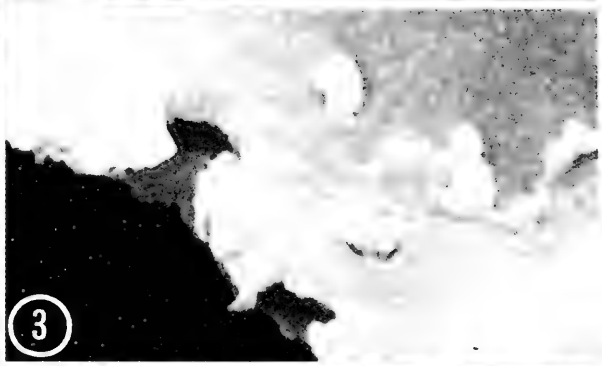
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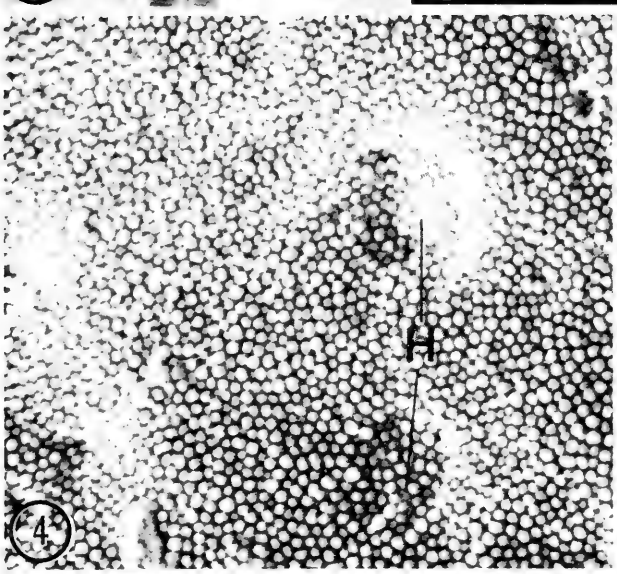
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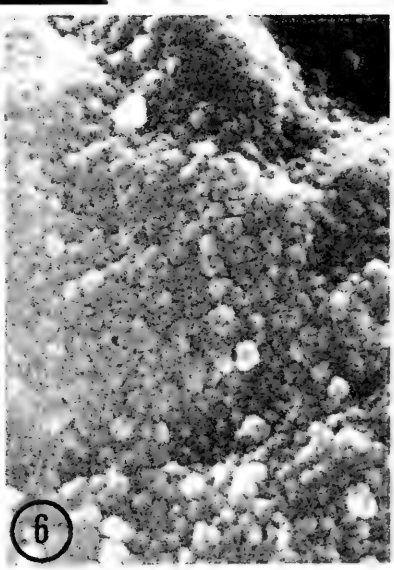
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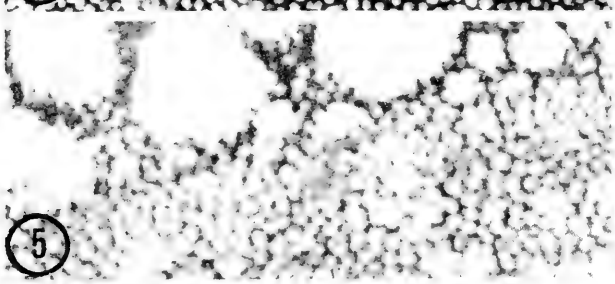
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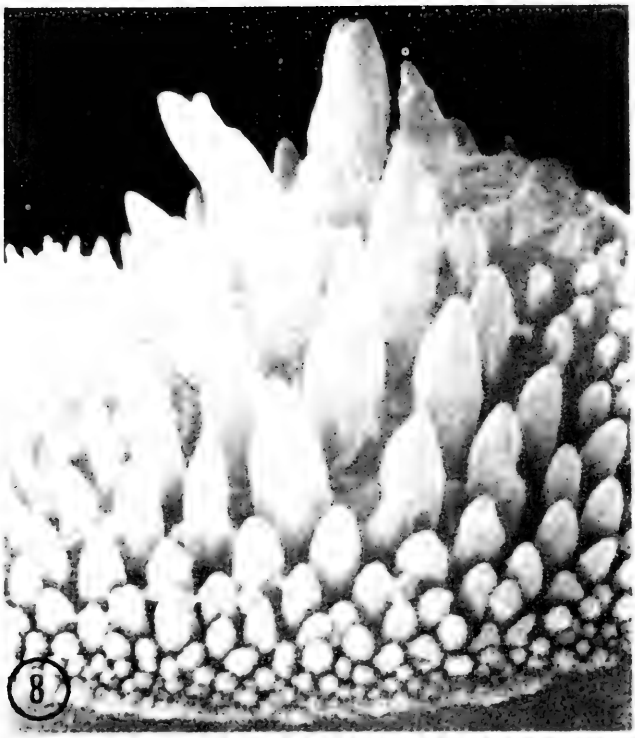
FIG. 8. The attachment structure of the glochidium of *Unio elongatulus glaucinus*. On the anterior apex of a valve there is the initial portion of the attachment structure possessing numerous pointed spines. 3,000x.

FIG. 9. The attachment structure of the glochidium of *Unio elongatulus glaucinus*. The initial portion of the attachment structure of the 2 valves of a glochidium. 1,350x.

FIG. 10. The attachment structure of the glochidium of *Unio elongatulus glaucinus*. Side view showing the spiny margin of the attachment structure folded towards the inside of the valve cavity. 1,000x.

FIG. 11. The attachment structure of the glochidium of *Unio elongatulus glaucinus*. The spiny margin with numerous rows of spines. 2,000x.

FIG. 12. The attachment edge of the glochidium of *Potomida littoralis littoralis*. The spiny structure is lacking; numerous small spines are distributed all along the edge of the valves. 1,000x.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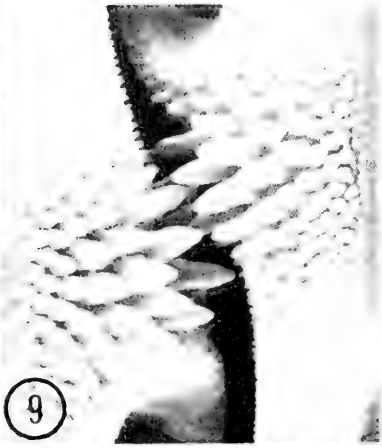
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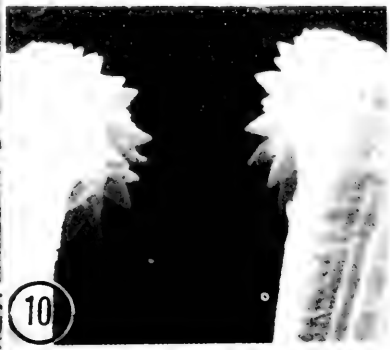
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FIG. 13. The shell of the glochidium of *Anodonta cygnea* from Lake Trasimeno (Italy). 230x.

FIG. 14. The shell of the glochidium of *Anodonta cygnea* from Lake Trasimeno (Italy). The outer surface of the "thin skin" layer has, in the central part of the valves, numerous hairy excrescences in parallel rows. The hollows originate in the wrinkling of the external "thin skin" layer over the holes of the internal crystalline one. 10,000x.

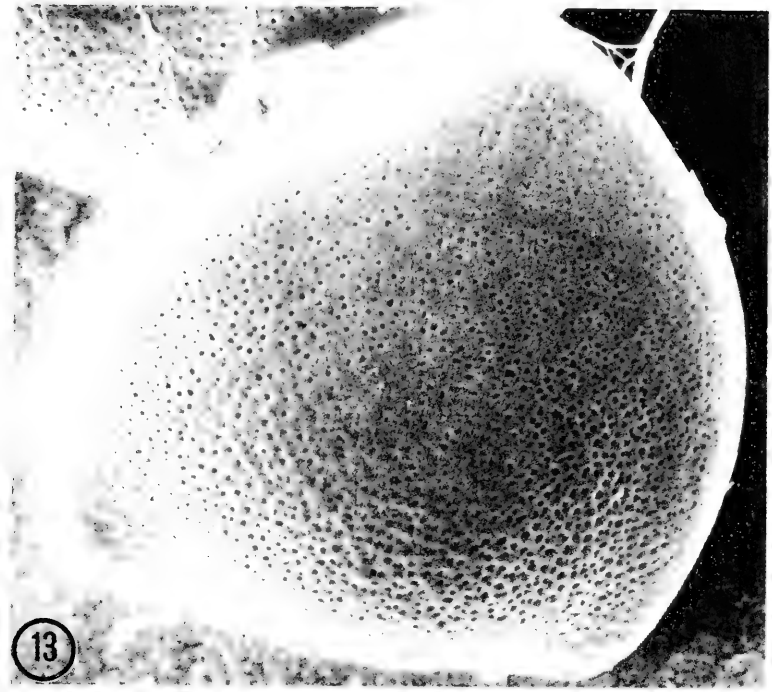
FIG. 15. The shell of the glochidium of *Anodonta cygnea* from Lake Trasimeno (Italy). Near the base of the shell the hairy excrescences are very thick. 15,000x.

FIG. 16. The shell of the glochidium of *Anodonta cygnea* from Lake Maggiore (Italy). The hairy excrescences have the same shape and disposition as those seen on the outer surface of the "thin skin" layer of the glochidium of *A. cygnea* from Lake Trasimeno (Italy). 10,000x.

FIG. 17. The shell of the glochidium of *Anodonta cygnea*. In this fragment it is possible to see the 2 layers constituting the valves; the external one like a "thin skin" (E) and the internal one of crystalline aspect (I). 10,000x.

FIG. 18. The shell of the glochidium of *Anodonta cygnea*. Numerous holes are in the internal crystalline layer of the valves. 1,700x.

FIG. 19. The shell of the glochidium of *Anodonta cygnea*. The internal crystalline layer of the valves (I) of the glochidium is still present in the initial portion of the shell (S) of a young *Anodonta*. 3,000x.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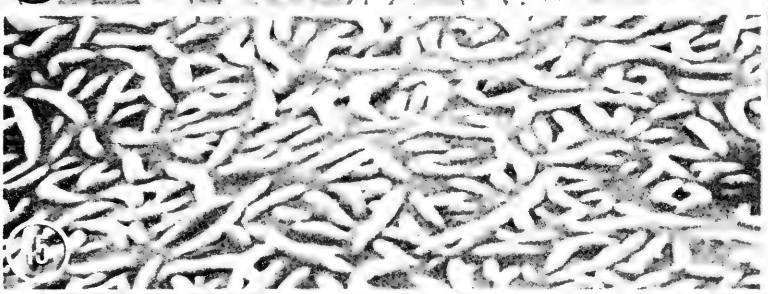
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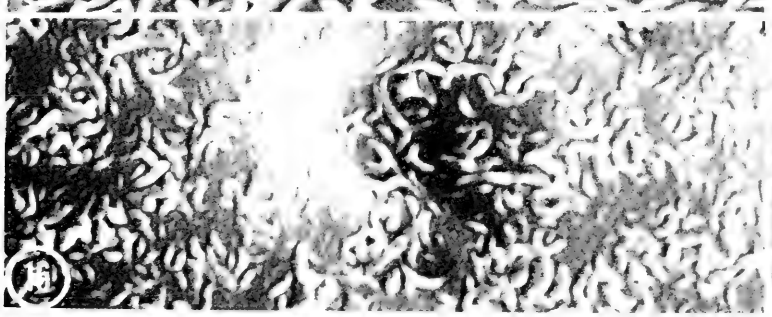
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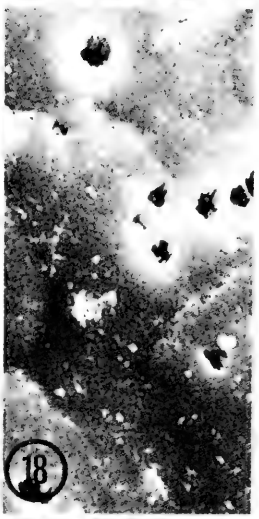
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FIG. 20. The attachment structure of the glochidium of *Anodonta cygnea*. On the anterior apex of a valve there is the initial portion of the attachment structure. The spines are fewer than in *Unio*. 2,600x.

FIG. 21. The attachment structure of the glochidium of *Anodonta cygnea*. The spiny margin is folded towards the inside of the valve cavity. 870x.

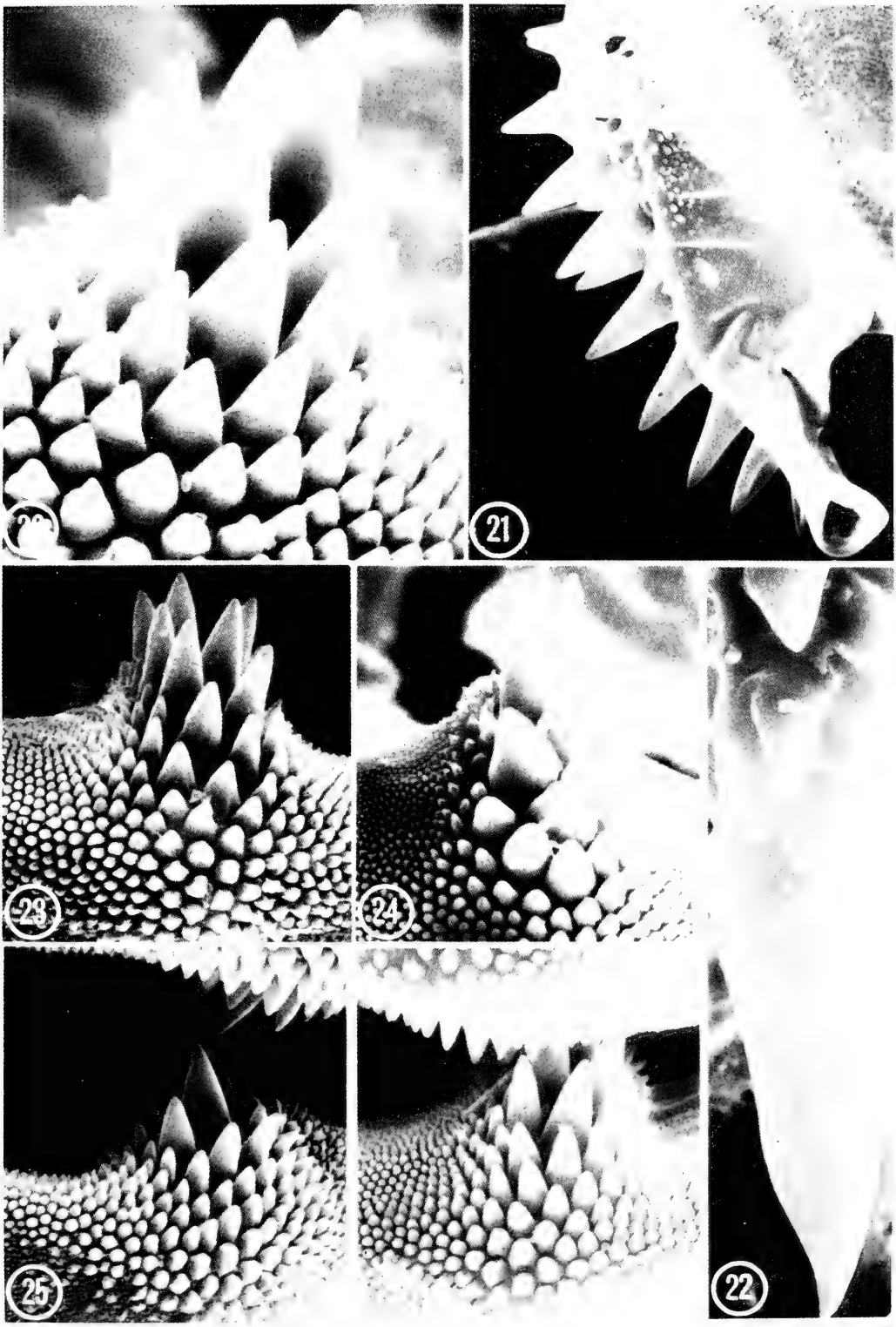
FIG. 22. The attachment structure of the glochidium of *Anodonta cygnea*. Few spines are on the spiny margin. 1,500x.

FIG. 23. The attachment structure of the glochidium of *Anodonta cygnea* from Lake Maggiore (Italy). The initial portion. 1,000x.

FIG. 24. The attachment structure of the glochidium of *Anodonta cygnea* from Lake Trasimeno (Italy). The initial portion. 1,000x.

FIG. 25. The attachment structure of the glochidium of *Anodonta cygnea* from Lake Maggiore (Italy). The initial portion. 1,000x.

FIG. 26. The attachment structure of the glochidium of *Anodonta cygnea* from Lake Trasimeno (Italy). The initial portion. 1,000x.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SPECIES ISOLATION IN SYMPATRIC POPULATIONS OF THE GENUS *DIPLOMMATINA* (GASTROPODA, PROSOBRANCHIA, CYCLOPHORIDAE, DIPLOMMATININAE)

John F. Peake

British Museum (Natural History), London, England

ABSTRACT

A study of sympatric populations of *Diplommatina* species in Malaya and the Solomon Islands indicates that the distribution of the morphological features exhibited by these taxa can be interpreted in terms of maintaining or reflecting species isolation, both genetical and ecological. The morphological characters considered are shell size, direction of coiling and shell shape. Selection or competitive exclusion favors divergence of these features amongst coexisting populations.

Examples of sympatric populations of closely-related species of snails and slugs are numerous, indeed, the molluscan faunas of many isolated islands can be characterised by this phenomenon. These faunas could have arisen through autochthonous evolution from a few initial propagules or by multiple colonisations of a number of closely-related taxa each possessing high probabilities for successful dispersal. Studies of island faunas thus provide abundant opportunities for investigating the strategems involved in maintaining species isolation, both genetical and ecological. Yet with a few exceptions there have been remarkably few attempts to analyse the evolution or the distribution of sympatric populations of non-marine molluscs in such terms.

The molluscan fauna of a series of isolated limestone hills in Malaya exhibit a pattern typical of island faunas. A number of genera are represented by groups of closely-related species. Purchon & Solari (1968) have suggested that the occurrences of these taxa show a random pattern, as the number of species recorded for each hill fit a Poisson distribution, this type of pattern resulting from the interaction of a number of random variables. The purpose of this paper is to analyse the distribution of one of the genera, *Diplommatina*, that occurs on these limestone hills and to amplify the study by including data from another area, the Solomon Islands. It will be suggested that the results can only be interpreted satisfactorily in terms of interactions between sympatric populations and that this factor is important in determining the distribution patterns of the taxa included in the genus.

Groups of sympatric species occur throughout the range of the genus *Diplommatina*, from India in the west to Samoa in the east. These small prosobranch snails exhibit a number of diverse shell forms and it is the distribution of these morphological forms that provides a means of demonstrating interactions between coexisting populations. A number of subgenera have been recognised on the basis of these differences in shell morphology and the genus has been separated from the closely-related taxon *Palaina* on the presence or absence of a parietal denticle in the aperture of the shell. The taxonomic status of these groups is open to doubt and for that reason within the context of this paper all the species are referred to a single genus *Diplommatina sensu latu*.

Detailed information is available for populations of *Diplommatina* species from only

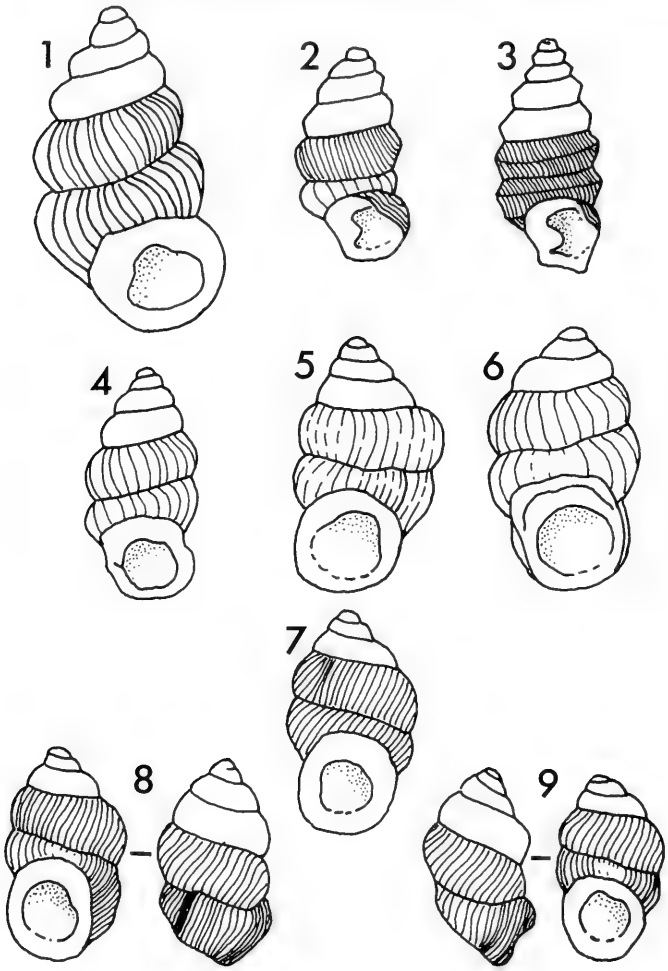

FIG. 1. Species of *Diplommatina* from the Solomon Islands, figures to illustrate diversity of shell form; as no specific epithets are available (see text) shells are identified by locality. 1, Nuhu, Guadalcanal; 2, Nuhu, Guadalcanal; 3, 12 kilometres south of Wainoni, San Cristobal; 4, Mount Austen, near Honiara, Guadalcanal; 5, Mount Austen, near Honiara, Guadalcanal; 6, Nuhu, Guadalcanal; 7, 12 kilometres south of Wainoni, San Cristobal; 8, Mount Austen, near Honiara, Guadalcanal (apertural and lateral views); 9, 20 kilometres south of Wainoni, San Cristobal (apertural and lateral views).

2 areas, the Solomon Islands and Malaya. The data for the Solomon Islands are based on collections made by the author while a member of a Royal Society expedition (June to December 1965) and by Dr. P. J. M. Greenslade during his tenure in the local Department of Agriculture. All the collections were made in rainforest (Peake, 1967, 1968). The majority of specimens were found in leaf litter either in gullies, between the buttresses of tree trunks or in small clefts and ledges on steep slopes. Records from other habitats include arboreal sites, for example, the basal leaf rosettes of both *Pandanus* and *Asplenium* plants. No distinction could be detected between the species composition of the molluscan faunas existing on different geological formations. In contrast, the data for *Diplommatina* in Malaya refers to faunas from precipitous

TABLE 1. Distribution of *Diplommatina* species in the Solomon Islands; only samples containing more than a single species included. Distribution scored as representation of dextral (D) or sinistral (S) forms in different size classes (see text for reasons). Species with overlapping size parameters joined by vertical boxes.

Island	Locality	Size class			
		1	2	3	4
Guadalcanal	Mount Austen	D	D S	S	D
	Nuhu	D	D S	D	
	Tambulusu		S		
San Cristobal	Huni River		S	D	
	2 km East of Huni River		S	D	
	Ultrabasics near Wainoni	S	S	D	D
	12 km South of Wainoni, Camp Site	S	D S	D	D
	80 m altitude	S		D S	D
	240 m altitude	S	D		
	400 m altitude	S		D	
	20 km South of Wainoni East side of river	S		D S	
	West side of river	S	D	D S	
Malaita	Maramiske	S		D	
Santa Ysabel	Fulkora Point		S	S	
Choiseul	Wagino	S	S		

limestone hills; records for other habitats being extremely rare and then only from localities at high altitudes (Laidlaw, 1949; Peake unpubl.). In this context the hills are considered as islands of almost bare rock and comparatively sparse vegetation isolated by alluvial deposits which often support forest vegetation (Tweedie, 1961). Information for Malaya is based on the published records of Laidlaw (1949), Tweedie (1961), Benthem Jutting (1960) and Berry (1965), supplemented with occasional information from museum collections.

For each population shell size is indicated by the simple measurements of maximum height and breadth, while shell shape is scored for direction of coiling and shell form. An indication of the diversity of shapes (Figs. 1 and 2) is provided by a very simple classification. The direction of coiling, whether dextral or sinistral, is constant for species in samples from the Solomon Islands, but Tweedie (1961) has recorded from Malaya a few sinistral individuals amongst predominately dextral populations, although the converse has not been observed.

SOLOMON ISLANDS

Specimens of *Diplommatina* were collected on 11 islands in the archipelago, but samples containing more than a single species were obtained from only 5 (see Table 1). The systematics and nomenclature of these taxa have not been finalised and, therefore, in this paper specific epiphets have not been given (see Fig. 1). Samples with the highest diversity of species were always associated with the thickest and more stable deposits of litter and in such habitats a maximum of 5 species were found coexisting. Within these collections up to 4 distinct size classes are recognizable in any single sample, although usually a smaller number are represented. These groups are identified on the basis of shell height and breadth (see Figs. 3 and 4). They are clearly defined and, typically, no overlap between adjacent groups has been discovered, even though the constituent species may vary.

Occasionally, however, the size parameters for 2 species are superimposed or overlap to form a single group or unit, but again the isolation of the size classes from adjacent groups is maintained. In those instances where the parameters for size overlap, there is always clear morphological separation of the species on the basis of shell shape. At the simplest level this consists of one species being dextral, the other sinistral.

MALAYA

A similar empirical relationship of shell size and shape is exhibited by populations from the limestone hills in Malaya; the data are summarised in Table 2. A limitation has been imposed by the utilisation of a variety of sources for this information. Thus shell height is the only parameter used to indicate shell size and often there is only a single measurement available. For the latter the criteria for deciding potential range of each size class, and therefore overlap, are based on extrapolation from the data for the Solomon Islands. It is impossible to distinguish populations which are truly coexisting in time or space; they can only be described as being found together on a particular hill. This is probably not a serious limitation and many of the hills are quite small. In a few instances the published records for closely adjacent hills have been amalgamated. Even with these restrictions the data are sufficient to corroborate the results from the Solomon Islands and permit the analysis to be extended.

Information is available for 28 localities and these provide evidence for a maximum of 5 species coexisting and being divided into 4 size classes. There are 6 examples of 2 species with the parameters for size being superimposed or overlapping; in each case one species is dextral, the other sinistral. Amongst these pairs there is further evidence of morphological divergence. The shell of all the dextral species conform to 2 rather similar shapes (see Fig. 2, types 1 and 2), while many of the sinistral taxa deviate from these patterns and have a different and indeed rather bizarre form (Fig. 2, type 3). This contrast is emphasised by comparing 2 groups of sinistral species, those overlapping and those not overlapping on the size classes of dextral taxa. The former (4 species) includes all the morphological forms of type 3, while the latter (3 species) approach closer to the form of the dextral species types 1 and 2. Thus differences in direction of coiling appear to be reinforced by divergence in shell shape.

The only possible exceptions to the correlation between shell size and direction of coiling are provided by the records of 2 dextral species coexisting; these are *Diplommatina nevilli* and *D. streptophora* on hill number 10 and *D. nevilli* and *D. ventriculus* on hill number 6 (see Table 2). *D. nevilli* exhibits the widest size range recorded for any species found in Malaya, while *D. streptophora* has only been found on 2 hills.

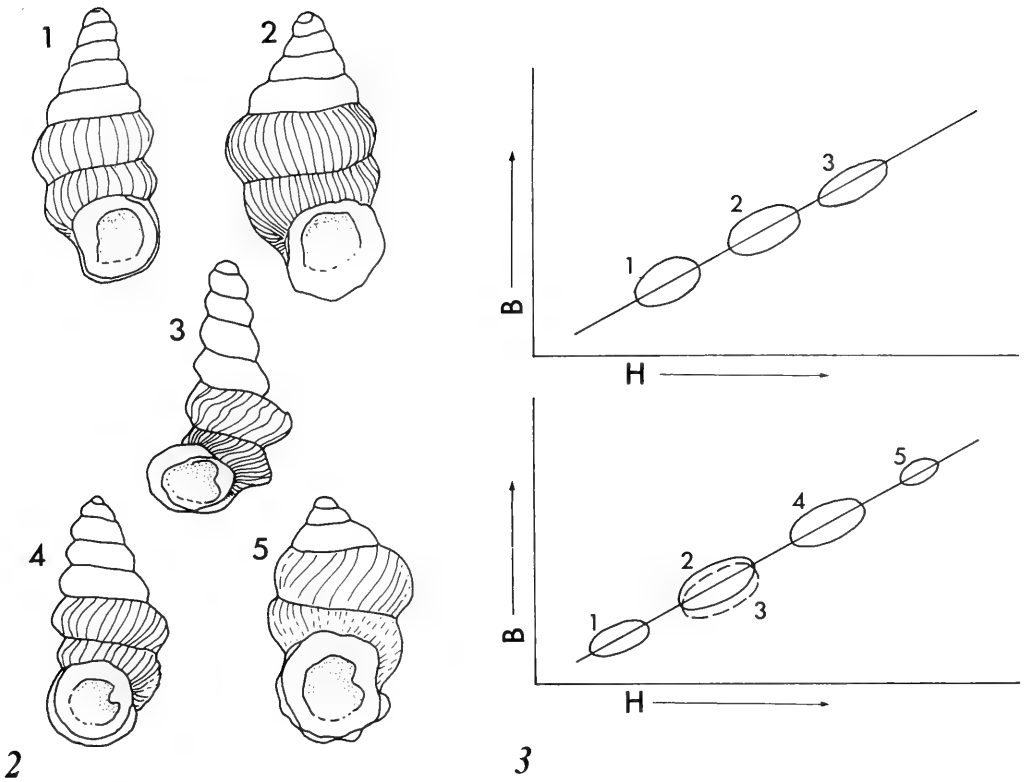

FIG. 2. Malayan species of the genus *Diplommatina*: a classification of shell shape.

Type	Direction of coiling	
	Dextral	Sinistral
1	*D. nevilli* (1)	*D. acme* (4)
2	*D. streptophora* (2)	*D. tweediei* (5)
3	-	*D. attenuata* (3)

FIG. 3. Diagrammatic representation of the distribution of size classes in samples. H, shell height; B, shell breadth. Upper figure, 3 species divided into 3 size classes; Lower figure, 5 species divided into 4 size classes; size parameters for 2 species overlapping to form a single group.

The range of shell height for *D. nevilli* is 1.82 to 3.45 mm, but for *D. streptophora* there is only a single recorded measurement of 2.5 mm. Where the 2 coexist on hills 6 and 10 the size of *D. nevilli* is at the extreme upper limit and, therefore, exhibits the greatest possible divergence, within the size range, from that known for the other species. Thus the limited data available provides no evidence that the size ranges of these 2 dextral species overlap. The information for *D. nevilli* and *D. ventriculus* from hill number 6 is also ambiguous. Measurements for *D. ventriculus* from that hill are not available and, therefore, the shell height given is extrapolated from that

for a limited number of records. There is no reason to presume that the shell size of this species does not vary as does that of *D. nevilli* (see discussion).

DISCUSSION

The significance of variations in the shape of the shell of non-marine molluscs has frequently been questioned. Although correlations between physical factors of the environment and shell shape have been demonstrated by various authors (e.g., Rensch, 1932; Gould, 1969) evidence for interactions between species influencing these features is limited. A notable exception has been the studies on *Partula* by Clarke & Murray (1969).

In this study an empirical relationship has been demonstrated for the distribution patterns exhibited by the different morphological forms of *Diplommatina*. Shells of coexisting populations are separated by size and shape, the latter being direction of coiling and shell form. In the few species that have been dissected it is obvious that these variations are not correlated with differences between the sexes. Confirmation is provided by the observation that many taxa have been found either isolated as single populations or not consistently associated with other forms. Morphologically similar populations have not been found coexisting. It must, therefore, be concluded that either competitive exclusion is operating for such species or natural selection favours divergence subsequent to initial colonisation. The outcome after initial colonisation is probably not predictable and both could occur on different occasions or in distinct areas of the species range. Moreover there is no evidence that dispersal is a limiting factor to the distribution of, at least, some species of *Diplommatina;* the small size of these snails must increase the probability of successful dispersal and colonisation (Peake, 1969).

Size also varies under different physical regimes. Records of a single species from 1 island in the Solomon Islands, where there is no other species of *Diplommatina*, demonstrates that size decreases with increasing altitude. The magnitude of this variation is not equivalent, however, to the difference between the means of size classes recorded from other islands in the archipelago. This variation is consistent with the correlation demonstrated by Berry (1963) for differences in shell size of *D. nevilli* and annual rainfall in the different areas. The height of the shells was shorter in areas where the annual rainfall was highest. In the Solomon Islands an increase in altitude would be associated with an increase in the wetness of the environment. This comparison illustrates a distinction between the climates of the 2 regions; the Solomon Islands can be described as continuous wet, while that for Malaya shows wide variations with many areas being described as seasonally wet or with irregular periods of drought (Peake, 1968). Therefore, it may be postulated that variations in shell size attributable to differences in climate would be greatest in Malaya compared with the Solomon Islands. This appears to be true for comparisons between *D. nevilli* and taxa from the Solomons, but whether it applies to other species from Malaya is unknown. For populations of *Diplommatina* from Malaya the variation in shell size with climate makes the interpretation of shell morphology in relation to other factors more complex. In the Solomon Islands, however, where the climate is more constant this type of variation is not so important.

The differences in shell size and shape exhibited by populations of *Diplommatina* from the Solomon Islands are interpreted in terms of promoting species isolation, both ecological and genetical. The distribution of species in Malaya supports such an hypothesis, but with an additional complication produced by variation of shell size with differences in climate. The relative importance of the morphological features in maintaining, reflecting or reinforcing isolation cannot be determined without more

TABLE 2. Distribution of *Diplommatina* species on limestone hills in Malaya; species arranged according to size. Shell type: classified into 3 groups (see Fig. 1). Direction of coiling: D, dextral; S, sinistral. Shell height: range of available measurements given and where a mean is available then it is included in brackets. Data and localities for hill numbers 1-27 follow Laidlaw (1949) and for numbers 28-33 follow Berry (1965). Species with overlapping size parameters joined by vertical boxes. Note: *D. nevilli* appears in the table in 7 separate places depending on the shell height recorded for different populations.

Shell type	Direction of coiling	Shell height (mm)	Species	Individual limestone hills: 1 2 3 5 6 7 8 9 10 11 12 13 14 15 16 17 20 21 22 24 26 27 28 29 30 31 32 33
2	D	1.5	*D. crosseana* Crosse	7 8 9 10
2	D	1.7	*D. maduana* Laidlaw	27 29 30
1	D	1.82-2.1 (1.97)	*D. nevilli* Crosse	16
1	S	2.0	*D. diminuta* Mlldff	7 8 9
2	D	2.0	*D. demorgani* Laidlaw	20 30 31
1	D	1.9 -2.17 (2.03)	*D. nevilli* Crosse	15 21
3	S	2.05	*D. attenuata* Laidlaw	21
1	S	2.2	*D. acme* Laidlaw	1 3
2	D	2.25	*D. seimundi* Laidlaw	12 13
1	D	2.25-2.45 (2.32)	*D. nevilli* Crosse	7
2	D	2.4	*D. pentaechma* Laidlaw	27 28 29 31
1	D	2.3 -2.5 (2.43)	*D. nevilli* Crosse	11
2	D	2.5	*D. streptophora* Laidlaw	6 10
1	D	2.47-2.67 (2.5)	*D. nevilli* Crosse	1 5
3	S	2.6	*D. superba* Godwin-Austen	8 9 10
1	D	2.5 -2.85 (2.7)	*D. nevilli* Crosse	2 3 8 9
3	S	3.0	*D. parabates* Laidlaw	6
2	S	3.0	*D. tweediei* Laidlaw	27
1	D	2.6 -3.45 (3.07)	*D. nevilli* Crosse	6 10
3	S	3.25	*D. lenggongensis* Tomlin	6
2	D	3.3	*D. ventriculus* Mlldff	1 5 6 7 8 9 10 12 13 14 16 17
1	D	3.9 -4.9	*D. canaliculata* Mlldff	12 13 20 21 22 24 26 27 28 29 30 31 32 33

ecological information and breeding experiments. However, the patterns shown by these variations in shell morphology demonstrate the selective advantages of such differences. Further evidence for selection is provided by comparing the distances separating adjacent size classes in samples from the Solomon Islands. Where the direction of coiling is the same for adjacent groups the distances tend to be greater than for adjacent groups where the direction of coiling is different (see Fig. 4). Selection favours greater divergence of size in populations with convergence of other morphological features.

It can be postulated that the presence of morphological differences between the species, for example size, could lead to differentiation in the ecological niches occupied; niche is used here in Hutchinson's sense (1965). Populations of such species could coexist without spatial separation, as they could utilise different resources or elements of the environment. Hutchinson (1965) has indicated that differences in size of the order of 130:100 would be sufficient to allow different proportions of the available food supply to be taken. The differences between the mean points of the size classes of *Diplommatina* are of this order and in many cases greater when comparisons are made between populations with shells having the same direction of coiling. However, this relationship does not hold for populations with different direction of coiling. If the differences between size classes reflect variations in the niches occupied, are the morphological features associated with similar ecological disparity?

Ecological information for *Diplommatina* is limited. The structure of the radula indicates that all the species belong to a similar feeding type; they are probably all grazers. In the Solomon Islands the disjunct and very limited distributions displayed by many species suggest specialised ecological requirements, but this type of information is not conclusive. Differential dispersal of snails in the litter, during torrential rainstorms, might give rise to such a pattern (Peake 1968). Observations on a species of a related genus *Opisthostoma* (Berry 1962) indicated that the distances between the small, but numerous, varices on the shell each represent a single day's growth. Species of *Diplommatina* exhibit differences in this feature and, therefore, it is presumed differences in the growth patterns and life cycles. The possibility of predators acting as agents selecting different shell forms or limiting the possibilities of competition must not be discounted, for potential predators do exist. Ants have been recorded carrying small snails and on the Malayan hills there are a variety of carnivorous snails belonging to the pulmonate family Streptaxidae.

It is tempting to extrapolate from data from the pulmonate genus *Partula* and postulate that direction of coiling is important in maintaining sexual isolation. Clarke & Murray (1969) have demonstrated that where the distributions of 2 typically sinistral species overlap there is a gradual change in the population of one to become predominately dextral and thereby reduce interbreeding.

If the hypothesis is correct that the differences in shell morphology are important in maintaining isolation between species, then this isolation probably cannot be considered as either genetical or ecological, but as a combination of both. It is possible to speculate further on the importance of variations in size of taxa like *Diplommatina nevilli*. Different populations of this species, although similar in shape, exhibit a wide divergence in size, with supposed 'dwarf forms' being recognised. Although such variations can be correlated with climate, are these populations conspecific with variations in size being genetically determined and reflecting exploitation of different niches? If so, do they represent stages in incipient speciation?

ACKNOWLEDGEMENTS

The author is indebted to the Trustees of the British Museum (Natural History) and to the Royal Society for enabling him to participate in an expedition to the Solomon Islands. To G. Smith and Miss M. Elsmore thanks must be expressed for considerable

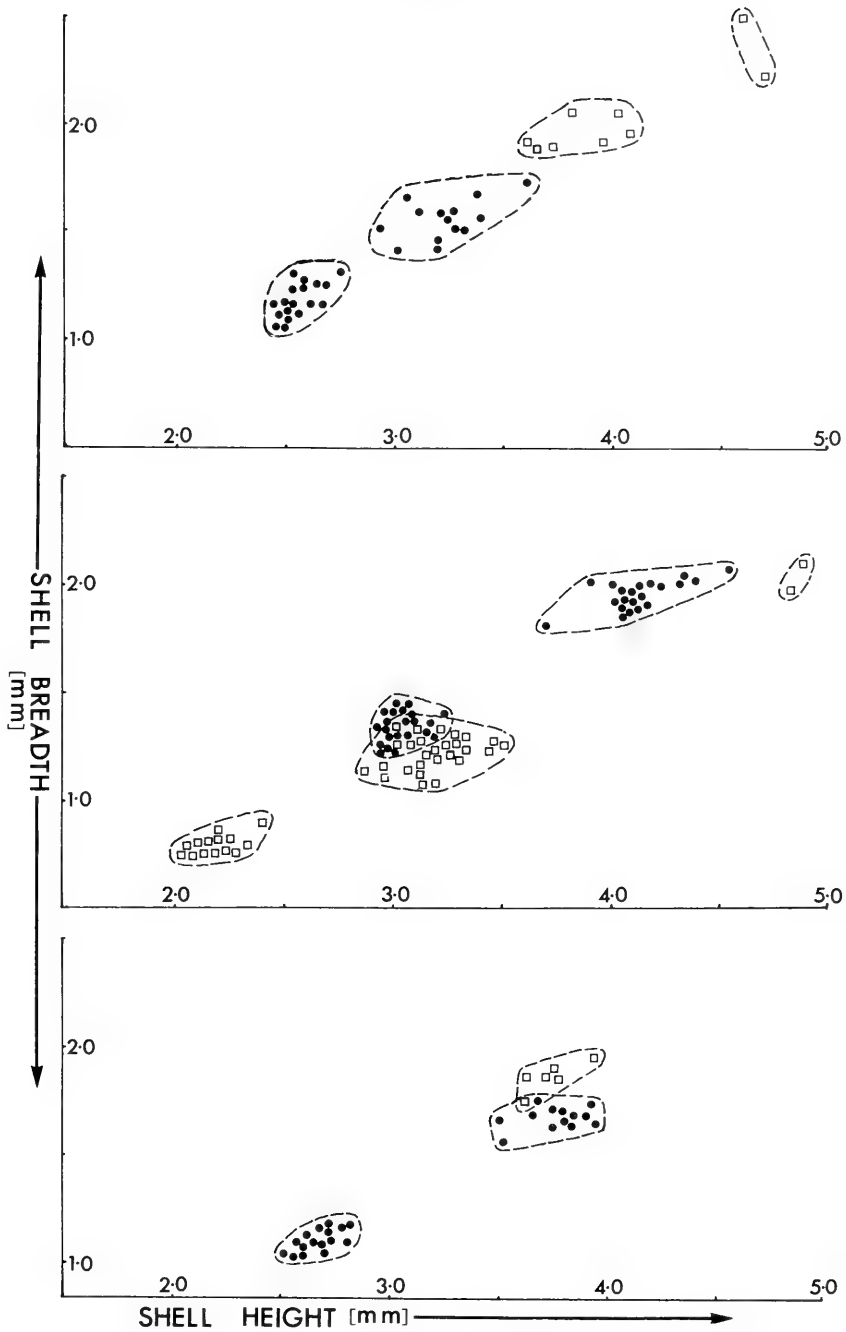

FIG. 4. Distribution of size classes in 3 samples from the Solomon Islands. Open squares, dextral forms; solid circles, sinistral forms. Upper figure, 4 species illustrating none overlapping size classes. Sample from Ultrabasic rocks, near Wainoni, San Cristobal. Centre figure, 5 species with the size parameters for 2 overlapping to form a single group. Sample from Mount Austen, near Honiara, Guadalcanal. Lower figure, 3 species with size parameters for 2 overlapping to form a single group. Sample from 20 kilometres south of Wainoni, San Cristobal. Note: not all the specimens included in a sample are represented on these figures, but all records would be contained within the dotted lines.

assistance in measuring and analysing the samples of *Diplommatina*.

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MALACOLOGIA, 1973, 14: 313-319

PROC. FOURTH EUROP. MALAC. CONGR.

POLYMORPHISME DU TEST DE *POTAMOPYRGUS JENKINSI* (E. A. SMITH, 1889) EN MILIEU SAUMATRE OU LACUSTRE[1]

Guy Réal

Institut de Biologie Marine, Arcachon, France

RESUME

Le test de *Potamopyrgus jenkinsi,* gastéropode Hydrobiidae des eaux douces ou saumâtres, peut présenter trois aspects; individus portant un test sans ornementation; individus présentant un test orné d'une carène continue ou enfin d'épines.

L'auteur passe en revue les hypothèses émises quant aux facteurs, génétiques ou écologiques, susceptibles d'être à l'origine de ces ornementations. Il apporte en outre une contribution personnelle relative à l'observation de 35 stations, douces ou saumâtres, du Sud Ouest de la France, dont il a régulièrement suivi la composition durant plusieurs années. Il conclut à la difficulté qu'il y a d'interpréter la nature et la fréquence des ornementations en fonction du seul facteur salinité.

Potamopyrgus jenkinsi Smith est un Hydrobiidae récent pour l'Europe; l'espèce est actuellement encore en pleine expansion. Le problème de l'ornementation du test, qui reste à élucider, est un des sujets sur lequel beaucoup d'auteurs ont travaillé. Des observations sur le terrain, tant en milieux saumâtres que lacustres, permettent d'apporter un certain nombre de précisions.

I. VARIATIONS MORPHOLOGIQUES DU TEST

Dés la création de l'espèce, on s'aperçut que les divers spécimens de *Hydrobia jenkinsi* Smith = *Potamopyrgus jenkinsi* (Smith) présentaient des variations morphologiques du test. Très rapidement les auteurs créèrent des variétés en rapport avec ces variations. La coquille peut, en effet, présenter 3 aspects:

- test à spire totalement dépourvue de toute ornementation
  = animaux à test lisse - variété *"ecarinata"* (Jenkins, 1889)
- test à spire présentant une carène
  = animaux à test caréné - variété *"carinata"* (J. T. Marshall, 1889)
- test à spire présentant une ligne de denticules ou épines
  = animaux à test à épines - variété *"aculeata"* (Overton, 1905)

Cette terminologie est actuellement abandonnée. On a vainement essayé de vérifier, par des élevages, le caractère héréditaire de ces ornementations; on tend aujourd'hui à penser qu'elles sont en relation non pas seulement avec des facteurs génétiques, mais également avec les conditions écologiques externes.

Enfin tous les intermédiaires entre le type caréné et le type à épines existent. La carène peut être réduite à une simple bande, même à peine visible, ou au contraire être très accentuée et donner une forme anguleuse à la spire en dessinant une véritable crête. La carène se situe approximativement sur le tiers supérieur des tours de spire et toujours parallèlement à leur ligne de suture. Les épines se situent exacte-

[1]Je suis heureux de remercier Monsieur le professeur Amanieu qui est à l'origine de ce travail.

ment au même emplacement, elles sont généralement assez régulières, parfois accolées par groupe. Entre les épines, la carène est souvent faible ou même absente.

Les deux formes, carénées et à épines, ne sont donc pas nettement distinctes. Dans certains cas, il semble même qu'il apparaisse d'abord une carène, les épines se développant ultérieurement.

II. PRINCIPAUX RESULTATS ANTERIEURS

Welch (1898) avait constaté "la présence d'exemplaires carénés en eaux saumâtre et l'absence d'ornementation chez les animaux en eaux douce". Cette observation fut reprise par Seifert (1935) qui confirma, en 1938, que non seulement les individus carénés se trouvaient en eau saumâtre mais que le pourcentage de sujets carénés était en rapport très net avec la teneur en NaCl; ainsi "pour une salinité de 3‰ on avait plus de 50% d'individus carénés avec quelques uns à épines et à une salinité de 5‰ il n'y avait plus que 30% de lisses, 50% avait une carène et 20% des épines". Steusloff (1939) confirma cette interprétation; Adam (1942) écrit "tandis que le matériel provenant d'eau saumâtre comprend toujours un certain pourcentage de spécimens à coquille carénée ou même épineuse, celui provenant d'eau douce se compose exclusivement d'animaux à coquille lisse". Récemment Grossu (1966), après une étude statistique, constatait que dans les régions à salinité élevée, la majorité des exemplaires étaient carénés, tandis que l'on observait la situation inverse dans les régions plus lacustres.

En revanche, d'autres auteurs estiment qu'il n'y a pas de relation directe entre l'ornementation de *Potamopyrgus jenkinsi* et la salinité du milieu; ainsi selon Robson (1926), Boycott (1929) et Warwick (1946), les formes ornées se trouvent indistinctement en eau douce et en eau saumâtre. D'autres auteurs enfin, tout en admettant que, généralement, le milieu saumâtre héberge des individus ornés signalent de nombreuses exceptions, notamment Bondesen & Kaiser (1950), Lucas (1959-1963) et Mars (1961). Mais selon Petit & Veuillez (1962) "il est d'autre part un fait qui paraît certain, c'est que dans les eaux encore voisines du littoral, mais qui sont parfaitement douces, il n'y a plus d'individus carénés. Nous ne pouvons citer que 2 exemples mais ils sont nets". Pour terminer ce rapide tour d'horizon sur les observations des auteurs concernant l'ornementation en rapport avec le milieu je citerai Mars (1961) "en revanche, on ne semble pas avoir signalé de stations saumâtres (plus de 1‰ par mélange avec de l'eau de mer, distinction importante) où les populations soient toujours non carénées à 100%".

III. OBSERVATIONS PERSONNELLES

A. Formation de l'ornementation

J'ai constaté que ni un nouveau-né, ni même un jeune des toutes premières semaines, ne présentent jamais la moindre trace de carène: en général l'ornementation apparaît seulement à partir de la taille 1,5 mm parfois plus, rarement moins. Quelques rares auteurs font état du nombre de tours de spire lors de l'apparition de la carène. Ainsi selon Boycott (1929) "les jeunes coquilles sont parfaitement lisses sur 2 spires au moins; la carène et les épines commencent sur la 3ème ou 4ème spire". De même Petit & Veuillez (1962) écrivent "la carène commence généralement sur le 3ème tour de spire et peut s'étendre jusqu'au tour médian. Dans certains cas assez rares, on peut constater, sur le même tour, l'amorce d'une autre carène et parfois d'une 3ème entre la première et la suture." Ces deux auteurs sont, je pense, les seuls qui signalent une carénation multiple (c'est à dire 2 et même 3 carènes entre deux lignes de suture, donc sur le même tour de spire). Malheureusement il n'y a ni photographie

ni dessin pour illustrer ce cas. J'ai moi même trouvé deux individus qui semblaient présenter une deuxième carène parallèle à la première. Les photographies no 1 et no 2 montrent le même individu avec le début et la fin de cette carène supplémentaire.

J'ai également trouvé 3 individus dont la carène, d'un type nouveau, présente un décrochement brutal qui la décale parallèlement à la ligne de suture. La photographie no 3 représente ce cas extrêmement rare de carène, le seul que j'ai observé sur plus de 20.000 individus et qu'il serait intéressant de retrouver.

En revanche, j'ai constaté souvent des ornementations qui s'esquivaient pour réapparaître plus loin mais toujours dans le même alignement.

Enfin la photographie no 4, inédite, présente un intérêt particulier en montrant que les modifications du milieu, se répercutant sur l'accroissement de la coquille, peuvent stopper net la fabrication de la carène à un moment précis. En effet, comme on peut le remarquer sur ce document à l'endroit où la coquille présente un accident dans la zone d'accroissement correspond l'arret brutal, complet et définitif de la carène.

B. Stations prospectées et analyse comparative

Pourtour du Bassin d'Arcachon (Gironde)

Dans cette région, 23 stations situées dans des étangs saumâtres, des zones d'estuaires sujettes au jeu de la marée, et enfin dans les ruisseaux donnant dans le Bassin d'Arcachon, ont été régulièrement suivies:

13 stations sont en eau douce (ruisseaux ou mares) - 10 en eau saumâtre (étangs et estuaires)

Pour les stations saumâtres, à chaque prélèvement la salinité de l'eau a été recherchée par la méthode Harvey (solution de NO3Ag à 27,25 gr/litre et 10 ml d'eau à analyser). Certaines de ces stations furent régulièrement suivies pendant 6 années voire 8 pour l'une d'entre elles.

Région du sud ouest de la France (Arcachon jusqu'au Pyrénées)

12 stations ont été prospectées, toutes en eau douce.

Au total c'est donc 35 stations qui ont été étudiées. J'ai constaté:

— que sur les 25 stations en eau douce, il y en a 19 qui présentent des individus ornés tandis que seulement 6 renferment des populations à test lisse à 100%.

— que sur les 10 stations saumâtres il y a une population où les tests sont à 100% lisses et que 3 ne présentent que 1% environ de tests ornés.

— de plus les stations où le pourcentage global d'individus carénés sur plusieurs prélèvements est le plus fort, se trouvent toujours être des stations en eau douce.

— En ce qui concerne les populations à fort pourcentage d'exemplaires à épines, photographie no 5, c'est également dans des stations en eau douce que j'ai pu les récolter. Au contraire, les stations saumâtres ne présentent que peu ou pas d'individus avec des épines bien développées.

C. Polymorphisme des populations en fonction du milieu

1) La présence d'eau salée n'entraine pas obligatoirement la présence de l'ornementation. Une station appelée "réservoir de Chabaud" a été suivie pendant des années: l'eau y fut constamment saumâtre avec une amplitude importante de variations de la salinité comme le montre la Fig. 1. Or, dans cette station, sur environ 10.000 individus que j'ai examinés, aucun ne montra jamais la moindre ornementation.

2) La présence d'eau salée n'est pas indispensable pour l'observation d'individus à coquille ornée. Dans le Sud Ouest de la France, à plusieurs kilomètres du littoral j'ai trouvé jusqu'à plus de 70% d'individus ornés et sur le pourtour du Bassin d'Arcachon un petit ruisseau d'eau douce contenait une population ornée, en majorité à épines, à plus de 95%, mais elle était assez clairsemée. (Je n'ai récolté que 1.024


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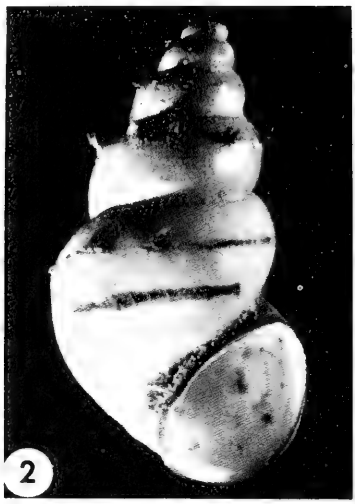
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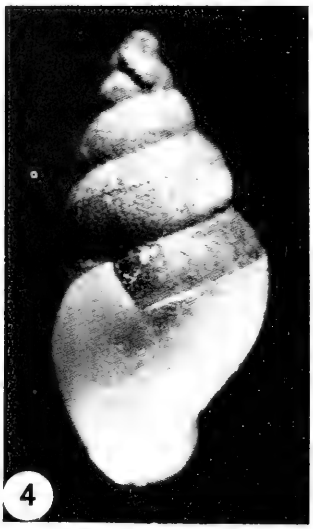
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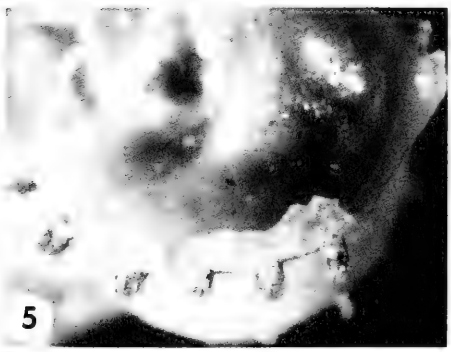
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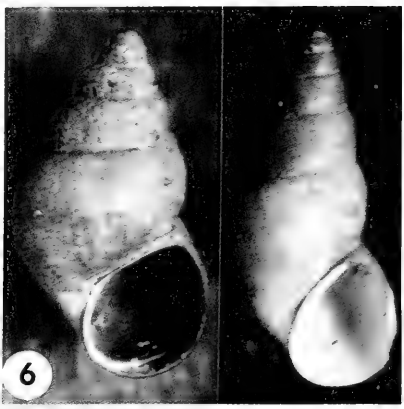
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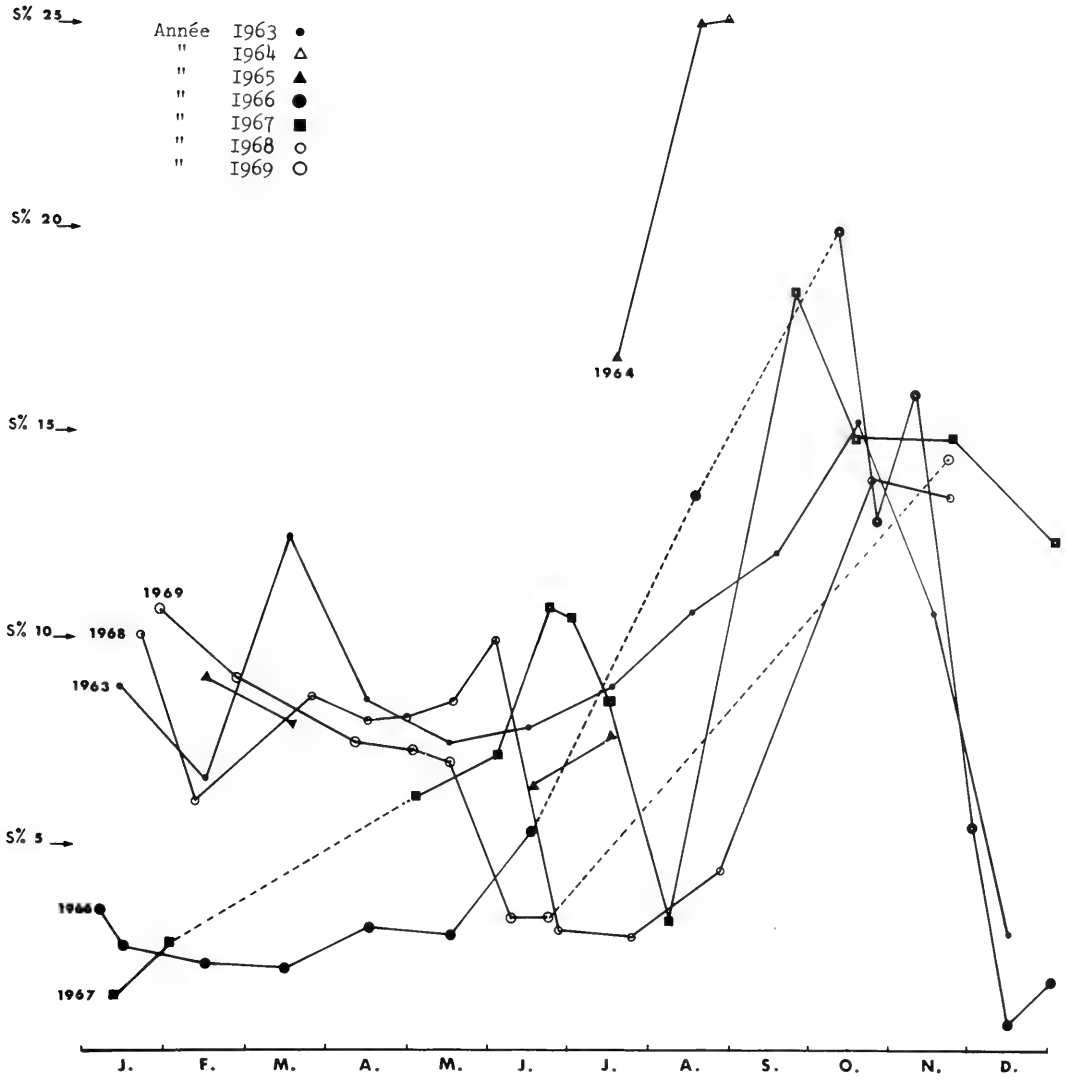

FIG. 1. Réservoir de Chabaud: Courbes des salinités, Année 1964: 3 dosages; Année 1965: 4 dosages. Remarque: deux dosages consécutifs mais séparés par une longue période sont reliés par une ligne en pointillé.

PHOTOGRAPHIE 1, 2. Ces deux photographies du même test montrent le début et la fin de la deuxième carène qui est plus légère qu'une carène habituelle. On peut également remarquer que sur le dernier tour de spire les épines cessent et que seule demeure une carène.

PHOTOGRAPHIE 3. Test avec une carène dont l'axe se trouve brutalement décalé par rapport à la ligne de suture.

PHOTOGRAPHIE 4. Test présentant un arrêt brutal du développement de la carène correspondant à une zone de modification dans l'accroissement de la coquille.

PHOTOGRAPHIE 5. Test découpé pour montrer les épines de profil.

PHOTOGRAPHIE 6. Ces 2 tests montrent la variation de l'indice longueur/largeur que l'on peut rencontrer entre 2 populations.

individus en 8 prélèvements ce qui est peu comparativement à la densité de la plupart des stations prospectées.)

3) Des populations situées en eau douce permanente et lisses à 100% existent et sont quelquefois stabilisées dans le temps.

Une population a été suivie pendant plus de 8 ans sans modification. Elle a été découverte par M. Amanieu en 1962 et est suivie depuis cette date; les individus y sont grands (jusqu'à 5,7 mm) et toujours lisses.

4) Des populations situées en eau saumâtre permanente et lisses à 100% existent et sont quelquefois stables au cours du temps. Une population a été suivie pendant 7 années avec plus de 70 prélèvements, sans jamais montrer un seul individu présentant la moindre ornementation.

5) Je n'ai pas trouvé de populations présentant une ornementation à 100%. Des auteurs ont signalé des populations ornées à 100%. Il faudrait que quelques unes de celles-ci soient étudiées dans le temps et en précisant les conditions écologiques.

6) D'après mes observations sur le terrain, les collections d'eau saumâtre dont la salinité moyenne est élevée, ne renferment pas un pourcentage d'individus ornés plus important que d'autres où la salinité est faible.

7) Les plus forts pourcentages d'individus ornés se trouvent, d'après mes récoltes, dans les eaux douces.

8) Dans une même population, je n'ai pu relever de différence sensible de la taille maximum entre les individus lisses et carénés.

9) Des variations de taille, d'épaisseur de la coquille, de teinte, d'importance de la ponte, d'indice longueur/largeur du test existent chez certaines populations mais sont difficiles à schématiser de manière démonstrative. La plus frappante est certainement le rapport longueur/largeur de la coquille (photographie no 6).

CONCLUSIONS

Ces observations permettent de comprendre pourquoi les divergences des auteurs sont aussi fréquentes même actuellement. D'une part, il faut considérer que l'espèce est capable de s'installer dans des biotopes extrêmement variés: dans la mesure où l'on travaille en milieu saumâtre, le facteur salinité peut apparaître déterminant pour la présence de l'ornementation. D'autre part, les stations citées en eau douce paraissent le plus souvent être à populations lisses mais elles sont encore peu nombreuses et souvent récentes.

Je crois qu'il est encore nécessaire que quelques malacologistes continuent à suivre les populations qu'ils connaissent; ainsi, par la confrontation des résultats basés sur de longues observations sur le terrain, on arrivera à cerner le problème de l'ornementation.

C'est dans cet esprit que j'ai entrepris récemment de transplanter des populations bien connues dans des milieux différents de leur habitat d'origine; malheureusement de telles expériences se heurtent à la difficulté qu'il y a à assurer une surveillance fréquente des animaux ainsi transplantés.

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MALACOLOGIA, 1973, 14: 321-325

PROC. FOURTH EUROP. MALAC. CONGR.

CONIDAE WITH SMOOTH AND GRANULATED SHELLS

Henry E. Coomans

Zoological Museum, Amsterdam, The Netherlands

Ornamentation of the shell in the Conidae is very scarce. A number of species have small nodules at the shoulder, others have longitudinal ridges at the base of the last whorl. *Conus sulcatus* Hwass has spiral grooves over the whorls; this characteristic is also found in a few other species, e.g., *C. austini* Rehder & Abbot, *C. granulatus* Linné. In general the Cone shells are smooth.

It has been known for a long time that some *Conus* species can be found in 2 phenotypical different forms: the normal smooth shell, and the shell of the other form is covered with spiral rows of granulations over the last whorl. Martini (1773, Conchylien-Cabinet, vol. 2, p 273) described a granulated *Conus ammiralis* Linné as "Conus Architalassus granulatus." The name was used properly by Meuschen (1787, Museum Geversianum, p 346) as *Conus ammiralis granulatus* (Fig. 1), and this name was used by a number of authors (cf. Dautzenberg, 1937, p 21-22).

Chemnitz (1788, Conchylien-Cabinet, vol. 10, p 83) described "Conus Terebellum violaceum granulatum," which is a granulated *Conus glans* Hwass (Fig. 2). Lamarck (1822, Anim. s. Vert., vol. 7, p 514) mentioned this form as *Conus glans* var.b *granulata*. Dautzenberg (1937, p 129, pl. 1, fig. 11) also recognized a variety *tenuigranulata*, which should have smaller granulations. However, we consider *tenuigranulata* Dautzenberg a synonym of *C. glans* forma *granulata* Lamarck.

Hwass (in Bruguière, 1792) described and figured *Conus arenatus* with a variety C "Testa granulosa" (Fig. 3), which was supposed to come from the Philippines.

Reeve (1843, Conch. Icon., vol. 1, *Conus* spec. 197b) described a granulated form of *Conus senator* (=*C. planorbis* Born) with the "shell entirely granulated."

Wils c.s. (1969 cont., p 60) described *Conus catus* var. *granulata* from Malaita, Solomon Islands.

The authors mentioned above considered the smooth shell as the normal species, while the granulated specimens were varieties. A contrary opinion was held by Sowerby II (1857, Thes. Conchyl., vol. 3, *Conus*, p 2, pl. 1, figs. 6-7) who described *Conus deburghiae* (Fig. 4) as a granulated species, which had also a smooth variety.

During 1967-1968 the *Conus* collection of the Zoological Museum in Amsterdam was revised by E. X. Maier, under supervision of the author. In his report Maier (1969) mentioned the occurrence of granulated forms in the following species: *C. achatinus* Hwass; *C. ammiralis* Linné (Fig. 1); *C. arenatus* Hwass (Fig. 3); *C. bandanus* Hwass; *C. chaldeus* Röding; *C. furvus* Reeve; *C. glans* Hwass (Fig. 2); *C. litoglyphus* Hwass; *C. lucidus* Wood (Fig. 5); *C. musicus* Hwass (Fig. 6); *C. planorbis* Born; *C. striatellus* Link; and *C. vitulinus* Hwass. Except for *C. lucidus* from the Eastern Pacific, all these species belong to the Indo-Pacific faunal province. According to Marsh (1964, p 146, pl. 21, fig. 7) the population of *C. chaldaeus* from Hawaii is granulated; the specimens from other places in the Pacific are smooth.

Although it was well known that a number of Conidae are found with smooth and with granulated shells, as discussed above, some granulated Conidae were described as distinct species. The granulated *Conus verrucosus* Hwass (Fig. 8) from the West Indies is now united with the smooth *C. jaspideus* Gmelin. Modern authors consider *verrucosus* a variety or subspecies of *C. jaspideus;* both can be found together at the same locality (Abbott, 1958, p 17, map 10). The *C. jaspideus* complex was discussed

by Abbott (l.c., p 88-91, pl. 3), who included many more *Conus* names in this complex.

Reeve (1843, Conch. Icon., vol. 1, *Conus* spec. 115) already mentioned that *Conus elventinus* Duclos was a granulated variety of *C. mindanus* Hwass. However, other granulated Conidae were described by Reeve as distinct species. *Conus metcalfii* Reeve is now considered by most authors to be the granulated form of *C. magus* Linné, and *C. rivularis* Reeve (Fig. 10) represents the granulated form of *C. boeticus* Reeve (Fig. 9).

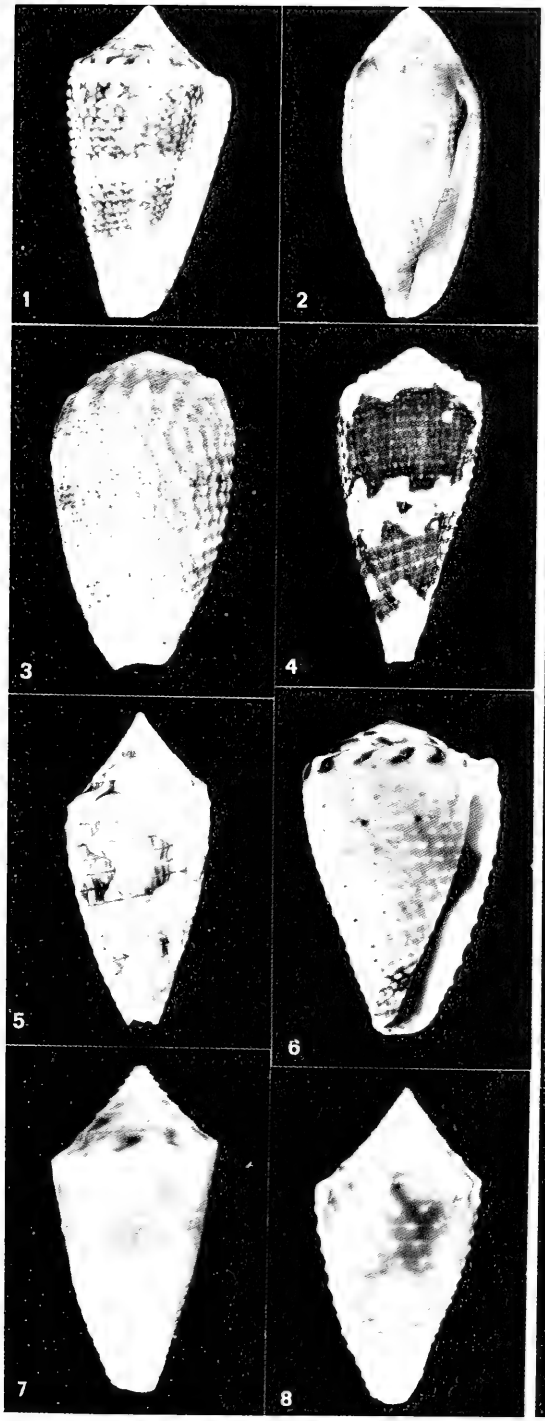
Other species pairs have been treated until now as 2 distinct species, and we suggest that they are the smooth and granulated forms of 1 single species. The smooth *Conus sugillatus* Reeve (Fig. 11) and the granulated *C. muriculatus* Sowerby II (Fig. 12) represent only 1 species. Since *muriculatus* was described in 1833 and *sugillatus* in 1844, the name of the granulated form has priority over the normal smooth shell. *Conus flavidus* Lamarck and the granulated *C. frigidus* Reeve (=*maltzianus* Weinkauff) may belong to 1 single species, although some further differences between these can be mentioned: *frigidus* has a rounded shoulder, a higher and straight spire which is spirally grooved, and a pink color, whereas *flavidus* is yellow.

Conus puncticulatus Hwass (=*C. pygmaeus* Reeve) (Fig. 13) from the southern Caribbean has a granulated form which is known as *C. pustulatus* Kiener (Fig. 14).

It remains questionable whether the smooth *Conus bocki* Sowerby III, known from the Moluccas, and the sulcated *C. sulcatus* Hwass from China, belong to 1 species, comparable to the smooth and granulated Conidae. The occurrence of smooth and sulcated forms is known from other species; Abbott (1958, pl. 3, fig. i) mentioned a spirally grooved form of *C. jaspideus*.

Two West Indian species, the smooth *Conus mappa* Lightfoot (Fig. 15), syn. *cedonulli* Hwass, *dominicanus* Hwass, *insularis* Gmelin, and the granulated *Conus aurantius* Hwass (Fig. 16) are considered by some authors (van Mol, Tursch & Kempf, 1967; Holeman & Kohn, 1970) as 1 single species. However, after studying a large number of specimens in several museums and private collections, Maier (1969) and the author are convinced that they represent 2 distinct species on the following grounds:

FIG. 1. *Conus ammiralis* Linné forma *granulatus* Meuschen, length 36 mm, Indonesia, Moluccas. (All photographs by L. A. van der Laan, Zoological Museum Amsterdam)
FIG. 2. *Conus glans* Hwass forma *granulata* Lamarck, length 43 mm, Indonesia, Amboina Is.
FIG. 3. *Conus arenatus* Hwass forma *granulosa* Hwass, length 21 mm, Indonesia, Moluccas.
FIG. 4. *Conus deburghiae* Sowerby II, length 54 mm, Indonesia, Moluccas.
FIG. 5. *Conus lucidus* Wood, granulated form, length 25 1/2 mm, Galapagos Is., Santa Cruz.
FIG. 6. *Conus musicus* Hwass, granulated form, length 18 mm, Indonesia, Moluccas.
FIG. 7. *Conus jaspideus* Gmelin, length 21 mm, West Indies.
FIG. 8. *Conus jaspideus* forma *verrucosus* Hwass, length 24 mm, Bahamas, N. Bimini.
FIG. 9. *Conus boeticus* Reeve, length 25 1/2 mm, Indonesia, Moluccas.
FIG. 10. *Conus boeticus* forma *rivularis* Reeve, length 34 mm, Indonesia, Moluccas.
FIG. 11. *Conus muriculatus* forma *sugillatus* Reeve, length 44 mm, Indonesia, Moluccas.
FIG. 12. *Conus muriculatus* Sowerby II, length 34 1/2 mm, Indonesia, Moluccas.
FIG. 13. *Conus puncticulatus* Hwass, length 23 mm, Netherlands Antilles, Curaçao.
FIG. 14. *Conus puncticulatus* forma *pustulatus* Kiener, length 22 mm, Netherlands Antilles, Curaçao.
FIG. 15. *Conus mappa* Lightfoot, length 49 1/2 mm, West Indies.
FIG. 16. *Conus aurantius* Hwass, length 40 mm, West Indies.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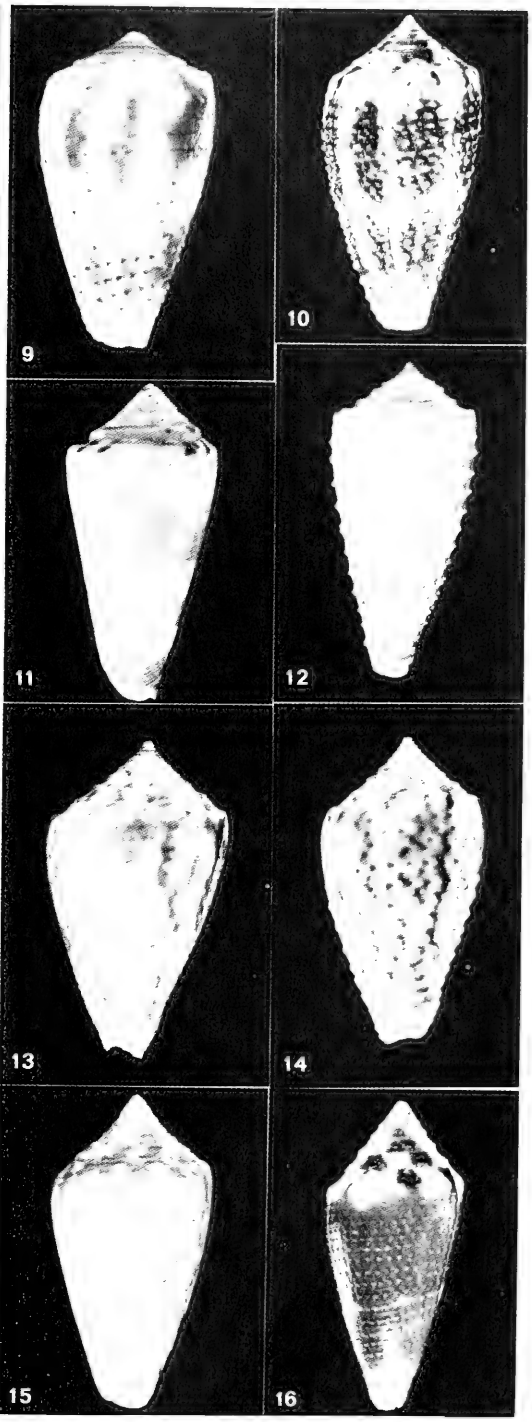
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Conus mappa (Fig. 15)	*Conus aurantius* (Fig. 16)
Shell wide (*C. regius* type)	Shell slender
Length to 60 mm	Length to over 70 mm
Spire with small nodules	Spire with larger nodules
Shoulder smooth	Shoulder nodulated
Last whorl smooth	Last whorl granulated
Color pattern very variable	Color pattern more uniform
Spiral whorls with some very fine longitudinal grooves	Spiral whorls smooth, except for growth lines
Wider distribution in the Caribbean	Distribution limited to southern Caribbean
In deeper water	In shallow water

The occurrence of granulated forms in the Conidae is not related with any zoogeographical province, since they are known from the Indo-Pacific, the West Indies, and the Panamic faunal province. The species in which we have found granulated forms do belong to a number of subgenera in the genus *Conus* (*Conasprella*, *Chelyconus*, *Puncticulis*, *Leptoconus*, etc.); hence there is no relation between granulation and subgenus. All species discussed here are recent Conidae; however, also in fossil Conidae the occurrence of granulated forms is known. G. Spaink from the Dutch Geological Survey informed me that the 2 fossil Conidae found in the Netherlands, *Conus dujardini* Deshayes and *C. antidiluvianus* Bruguière, both from the European Miocene, are found with smooth and with granulated shells.

Suggestions that smooth and granulated shells are connected with sexual dimorphism can be withdrawn, and it cannot be proved that different ecological conditions develop granulated shells. It seems more plausible that granulations are produced by mutations, in which case they deserve the status of a variety.

As far as is known to me, granulated specimens are only known from the Conidae, and not from the related families in the superfamily Toxoglossa, the Terebridae and the Turridae.

Dr. F. Starmühlner informed me that similar phenomena can be observed in the genera *Neritina* and *Melanopsis*. Some *Neritina* species are known with smooth and with spined shells, while the shell in *Melanopsis* can be unicolored or multicolored in the same species. These cases are related to the ecological circumstances, i.e., fresh and brackish water. The specimens from brackish water are smooth (*Neritina*) resp. unicolored (*Melanopsis*); in fresh water they become spined resp. multicolored.

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MALACOLOGIA, 1973, 14: 327-331

PROC. FOURTH EUROP. MALAC. CONGR.

A 16-YEAR SURVEY OF *CEPAEA* ON THE HUNDRED FOOT BANK

C. B. Goodhart

University Museum of Zoology, Cambridge, England

INTRODUCTION

The Hundred Foot Bank is a dead straight and highly uniform earthen dyke running beside the artificial New Bedford ("Hundred Foot") River across the fens, some 20 kilometres northwest of Cambridge. It was originally built in 1652, when the fens were first drained for cultivation, but it has been reconstructed at various times and most recently in 1947-48, after a disastrous flood which left the bank as an island, with water on both sides, for upwards of 3 months. After this, the bank was heightened and levelled, mostly with silt dredged from the river, and it was re-seeded with grass in 1948, which is lightly grazed by cows and cut each summer. Over the past 20 years there has been some increase in weeds (nettles, cow parsley and thistles, mainly), but these are kept under control by spraying from the air, and the bank still appears to be remarkably uniform ecologically along its whole length.

It supports a very abundant population of *Cepaea nemoralis* (Linnaeus), which shows significant variation in the frequency of different morphs over quite short distances, apparently unrelated to any vegetational or other ecological differences which, anyway, are minimal. I first surveyed the snail colony in 1952, taking samples at 200 metre intervals along 2 miles (3.2 kilometres) of the bank (Goodhart, 1962, which also gives a detailed description of the habitat, with photographs). But it was evident that these samples had been taken too far apart for there to be any correlation between neighbouring collections; and marking-recapture studies showed that the mean displacement of individual snails was only about 6 metres a year, the maximum observed being 16 metres.

SAMPLING PROCEDURE

So in 1953 a new series of samples were taken from 64 stations, exactly spaced and measured with a surveyor's chain, at intervals of 1/8 furlong (27 1/2 yards = 25.15 m) along 1 mile (1609 m) of the bank, being the northern half of the 2-mile section examined in the previous year. All the stations were measured from an origin at 440 yards from the southern end, which was immediately opposite a ditch junction on the other side of the road beside the bank, its grid coordinate reference being 408767 on Sheet 52/47 of the 1/25,000 Ordnance Survey map.

Each sample comprised 50 adult *Cepaea nemoralis*, taken from the eastern face of the bank only, snails being less abundant on the western (river) face, which is partially submerged when the water is high in the winter. Four samples of 50 were collected in the months of May, June, July and August, from the 8 stations, starting with the southernmost, at 200 m intervals, and 2 samples of 50 each were collected in May and August from the 8 intermediate stations at 100, 300, 500, etc., metres, with 1 sample of 50 being taken from each of the 3 stations at 25 m intervals between these others.

Exactly the same sampling procedure was followed in 1961, nearly all the samples being collected within a week of the corresponding one 8 years before. This was repeated in 1969, except that as I was unable to start collecting until June the dates did not match so precisely those of the other 2 years. As well as being measured with

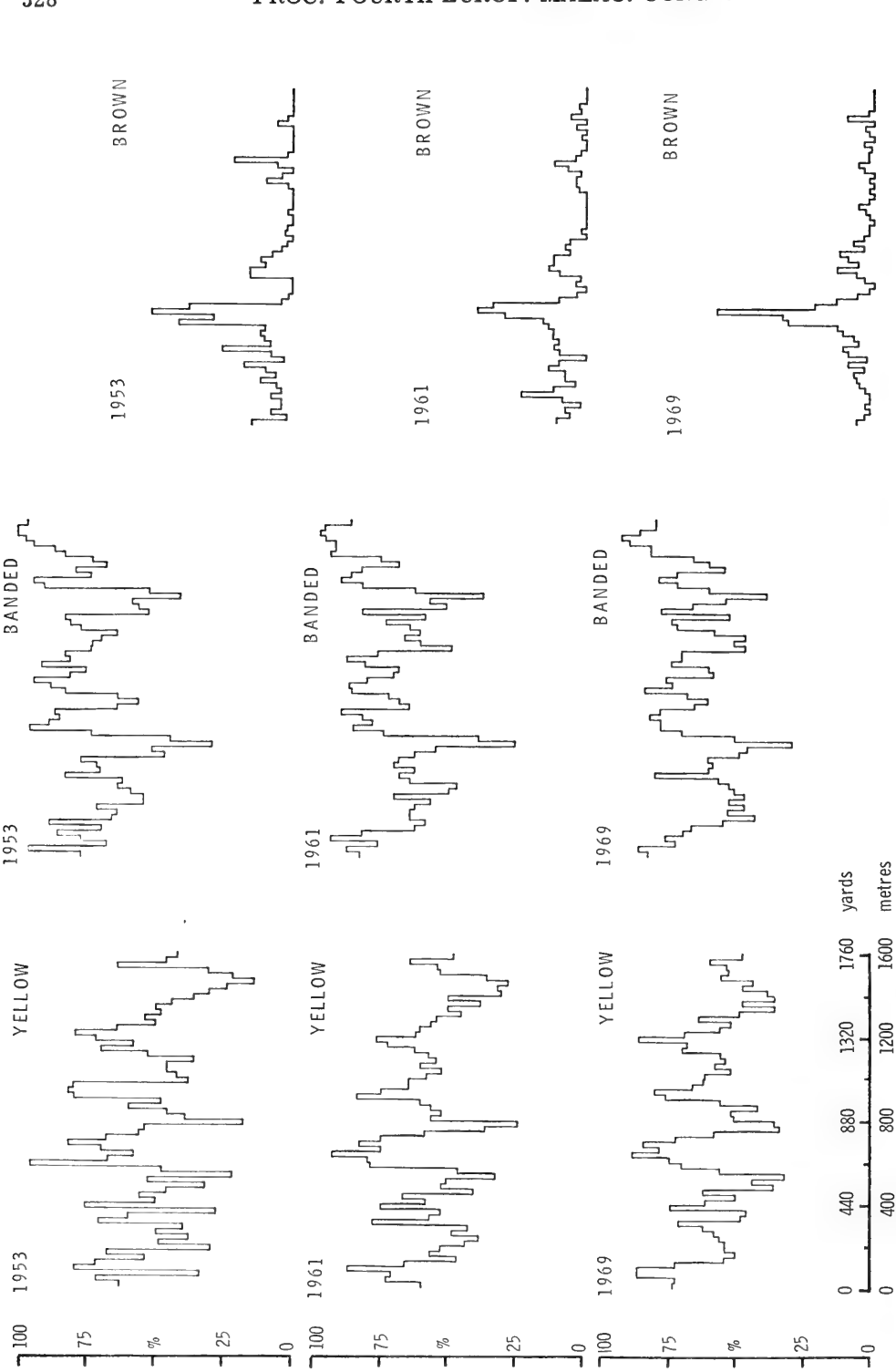

FIG. 1. Percentages of 3 phenotypes of *Cepaea nemoralis* along 1600 m of the Hundred Foot Bank in the years 1953, 1961 and 1969. Each of the 64 columns is 25 m from the next.

the chain, many of the positions could be related to fixed landmarks and I do not think that any of the collecting stations could have been misplaced by more than a metre or so over the whole 16 years.

POPULATION NUMBERS

In 1952 the *Cepaea nemoralis* population was very abundant indeed, ranging from about 5 to over 20 adults per square metre on the eastern slope of the bank, probably because all the rats, which seem to be the principal predators, had been drowned in the floods 5 years before. Since 1952 numbers have been more than halved, but the snails are still very plentiful and there seems to have been little change since 1961. Many rat-predated shells can now be found, but thrushes' anvils have only rarely been seen, and thrushes do not normally live in these open fens. Other birds, especially rooks, probably also feed upon the snails.

Cepaea hortensis (Müller) occurs only on one short section of 200 m of the bank between the stations at 300 and 500 m from the southern end, where it has never comprised more than 10% of the total *Cepaea* population. It was found along these 200 m which appear to be ecologically the same as the rest of the bank, in 1953, 1961 and 1969, and there is no evidence of any significant change in its numbers relative to *C. nemoralis* over this period.

GENETIC VARIATION AND STABILITY

By way of illustration, Fig. 1 shows the percentages along the bank of 3 common phenotypes. These are Yellow shells, homozygous $C^{\underline{Y}}C^{\underline{Y}}$ and recessive to Pink and Brown; Banded shells, homozygous $B^{-}B^{-}$ and comprising all shells with any bands, recessive to Unbanded; and finally Brown shells, which because of a linkage disequilibrium in this colony are all Unbanded, carrying the dominant allele $C^{\underline{b}}$. It will be seen that there are large fluctuations in the proportions of these phenotypes along the bank, ranging from under 20% to over 90% for Yellow; from just over 20% to 100% for Banded; and from 0 to 58% for Brown shells.

A number of regular clines in morph frequency over distances of a few 100 m can be seen and, although there are some signs of a levelling out of the troughs and peaks of these fluctuations between 1953 and 1961, the main outlines have been preserved with remarkable constancy over the 16 years. Most of the between-years variation is within the range of the 4 monthly samples taken from the 8 stations at 200 m intervals in each year (not shown in Fig. 1), which themselves showed no signs of any regular seasonal trends. None of this can be related to any observable ecological differentiation in what looks like an unusually uniform habitat. A similar state of affairs is found with all the other phenotypes which have been studied.

LINKAGE DISEQUILIBRIUM

Apart from the linkage disequilibrium already mentioned, resulting in a complete absence of Banded Brown shells, as is found in most other British colonies of *Cepaea nemoralis*, on the Hundred Foot Bank there is also a significant deficiency of Unbanded Pink shells, compared with Yellows. That is so along the whole 1600 m studied, except at one point 550 m from the southern end where in 1953 there was a highly significant *excess* of Unbanded Pinks. It was still there, and significant at the 5% level, in 1961; but by 1969, although there was still a small excess of Unbanded Pinks at this point, it was much reduced and well short of statistical significance. Whether the effect is being eliminated by selection, or simply swamped by immigration in

from either side, cannot be determined.

There also seemed in earlier years to have been a significant excess of Fused Bands among Pink shells, though this is now less well marked than it was before. Indeed, there may have been an overall decrease in band fusion, the inheritance of which is complex and not properly understood. If so, this probably constitutes the only major change in the colony over these 16 years, and one which presumably would have resulted from natural selection, though probably not by predators.

AUTOCORRELATION WITH DISTANCE

Fig. 2 shows the results of a computer study in which each of the 64 stations was correlated with its next neighbour at 25 m, then the next but one at 50 m, and so on, for their percentages of the same 3 phenotypes, namely Yellow, Banded and Brown. This shows significant correlation between samples collected 25 m apart, and usually also at 50 m, but beyond that correlation sinks rapidly to nil; it will be seen also that the histograms remained remarkably similar over the whole 16 years. This is another indication of the extremely low vagility of *Cepaea nemoralis* populations.

CONCLUSIONS

These observations show that important differences in the genetic composition of *Cepaea nemoralis* populations living in very similar habitats can be maintained unchanged for considerable periods of time, apparently without any differential environmental selection whether by visual predation or by adaptation to vegetational, edaphic, or micro-climatic differences, all of which seem to be minimal in this unusually uniform habitat. For example, the small-scale "area effect" for Brown shells, extending along about 100 m of the bank and quite sharply delimited (see Fig. 1) cannot possibly be attributed to any micro-climatic effect such as the ponding of cold air, which possibly favours this morph in some other situations (Cain, 1968).

Of course the *Cepaea* on the Hundred Foot Bank must be subject to natural selection, like all other natural populations, but there is little reason to suppose that this, in so far as it is due to the external environment, should operate differently at different points along the bank, or that it could be responsible for the observed differences in the polymorphism of the snail population.

A more likely explanation may be that snail numbers were much reduced during the flooding and re-building operations in 1947-48, and that chance differences ("founder effects") then arising in the surviving nuclear populations along the bank persisted during the subsequent great expansion in numbers, which reached its peak in about 1952. The fact that these local differences in morph frequency have now been maintained more or less unchanged for nearly 25 years, in the face of selection in a uniform environment, suggests that some genetic co-adaptation may have occurred and that the genetic differences between different sections of the colony, which will have had their origin in chance founder effects, may now be being maintained by selection. But this will be of an internal genotypic nature (and the occurrence of linkage disequilibria shows that this must be operating, at least to some extent), rather than being due to selective differences in the external environment. It remains to be seen whether selection for co-adaptation will be strong enough to outweigh the levelling effects of migration, slow as that certainly is. So far, most of the quite sharp local differentiation in morph frequency seems to have been quite stable. A similar mechanism has already been proposed (Goodhart, 1963) as a possible explanation for some of the large-scale "area effects" seen in other populations.

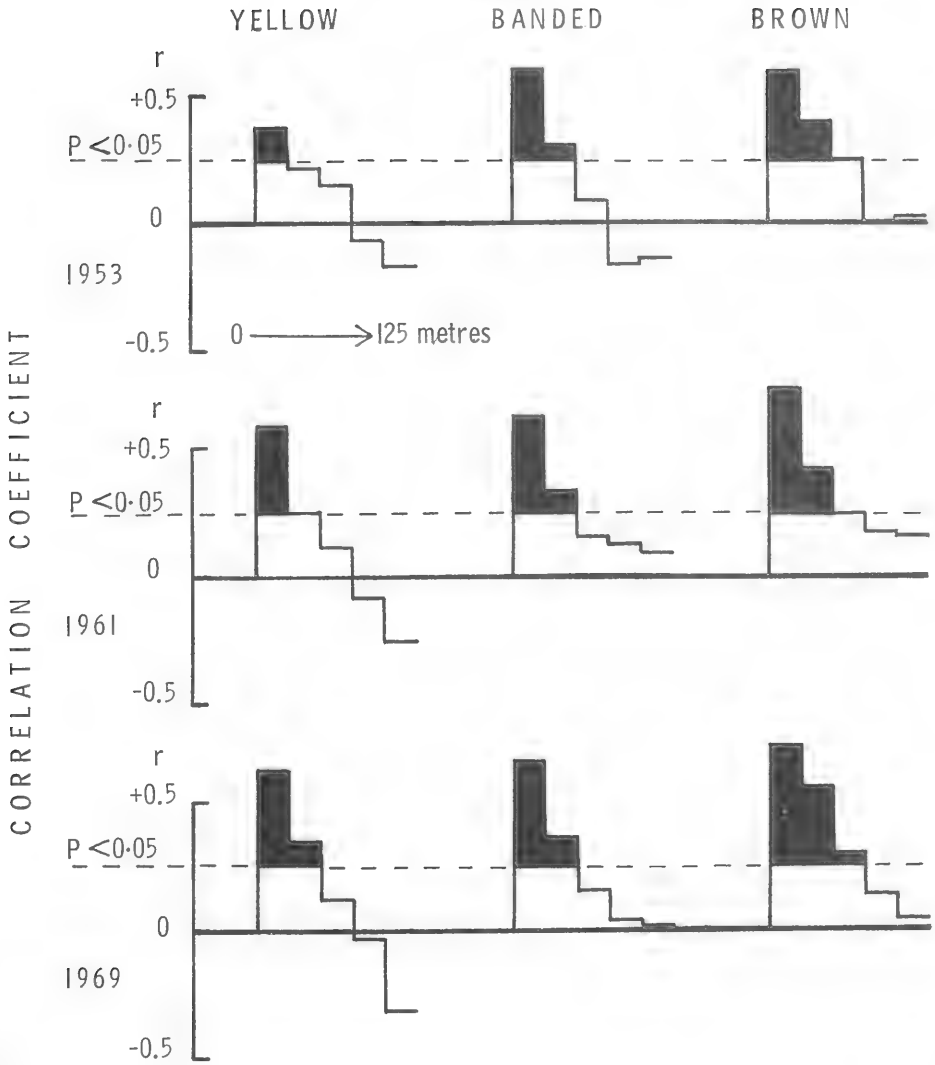

FIG. 2. Correlation coefficient (r) for each of the 64 samples in Fig. 1 with its next neighbour at 25 m, its next but one at 50 m, and so on to 125 m, for the percentages of the 3 phenotypes in the samples, in 1953, 1961 and 1969.

SUMMARY

Significant local differences over distances of about 100 m in the polymorphism of a linear colony of *Cepaea nemoralis* living in an extremely uniform habitat, on an artificial river bank, have been maintained unchanged over 16 years. These are regarded as comparable with the larger "area effects" observed in other populations of this species, and it is suggested that they may be due to genetic co-adaptation resulting from founder effects when numbers were reduced, rather than to differential selective forces in the external environment.

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PROC. FOURTH EUROP. MALAC. CONGR.

ASPECTS GENERAUX DU POLYMORPHISME DE LA COULEUR DU PERISTOME CHEZ *CEPAEA HORTENSIS* EN FRANCE

M. A. Guerrucci[1]

Ecole Normale Supérieure, Laboratoire de Zoologie, Paris, France

Contrairement aux individus de l'espèce *Cepaea nemoralis* qui sont assez généralement caractérisés par la coloration brune de leur péristome, les *C. hortensis* ont le plus souvent un péristome blanc. Dans un assez grand nombre de colonies de *C. hortensis* il existe cependant aussi des coquilles à péristome coloré en brun, en brun clair ou en rose.

Le caractère péristome coloré se retrouve chez *Cepaea hortensis* dans la plupart des régions de France, avec des fréquences très variables. Pour faire apparaître les différences entre ces régions on a estimé, pour un certain nombre d'entre elles, la fréquence moyenne du caractère péristome blanc. Les différentes valeurs obtenues, reportées sur la carte de France (Fig. 1), montrent l'existence d'une variation géographique importante.

C'est dans la vallée de la Loire, particulièrement entre Tours et Blois, où certaines colonies présentent parfois moins de 10% de péristomes blancs que la fréquence moyenne du caractère est la plus faible. Sa valeur varie peu le long de cette vallée, mais elle augmente, en revanche, assez rapidement dans les régions voisines. Elle atteint 90% dans le Pyrénées, en Normandie, dans le Nord et dans l'Est. Cette prépondérance des péristomes blancs dans les régions périphériques est en accord avec les observations effectuées en Espagne, en Angleterre, aux Pays Bas et en Allemagne, où la présence d'individus à péristome coloré est signalée comme rare.

La variation clinale du caractère péristome blanc est parfois très sensible à l'échelle locale. Le phénomène est particulièrement net en Touraine où la fréquence des péristomes blancs augmente progressivement vers l'amont des vallées du Cher et de l'Indre, affluents de la Loire (Fig. 2). La fréquence du caractère atteint même 100% dans les populations les plus éloignées.

Dans la vallée de l'Aube, il est possible de distinguer, parmi les populations étudiées, un groupe situé à l'ouest d'Arcis-sur-Aube, distant de 15 kilomètres environ d'un autre groupe situé à l'est. La fréquence moyenne du caractère péristome blanc, qui est de 60% à l'ouest, passe à 83% dans le secteur oriental (Fig. 3). Les deux groupes d'échantillons diffèrent significativement en ce qui concerne ce caractère ($P < 10^{-4}$). Toutefois le gradient apparaît moins nettement qu'en Touraine. Il est en effet dissimulé par les variations assez notables de la fréquence d'une colonie à l'autre.

Les écarts observés entre les fréquences peuvent être attribués en partie à des fluctuations d'échantillonnage ou encore à des phénomènes de dérive, d'autant plus que les échanges entre populations demeurent très limités, car la plupart d'entre elles sont distantes de plusieurs kilomètres. En outre, comme le caractère péristome blanc est souvent assez étroitement associé à d'autres caractères de coloration de la coquille, sa fréquence peut se trouver en partie conditionnée par celle des caractères qui lui sont associés.

L'importance des fluctuations de la fréquence du caractère dans les populations situées à l'intérieur d'un secteur limité est mise en évidence sur les histogrammes de

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[1]Adresse postale: Laboratoire de Zoologie ENS, 46 rue d'Ulm, Paris 5e, France.

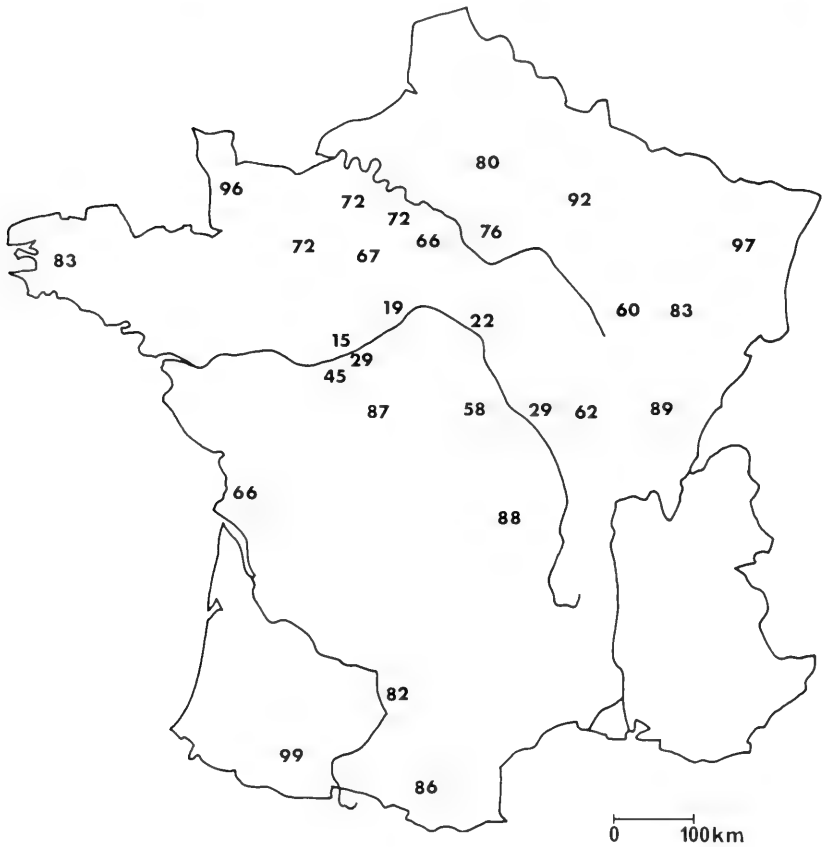


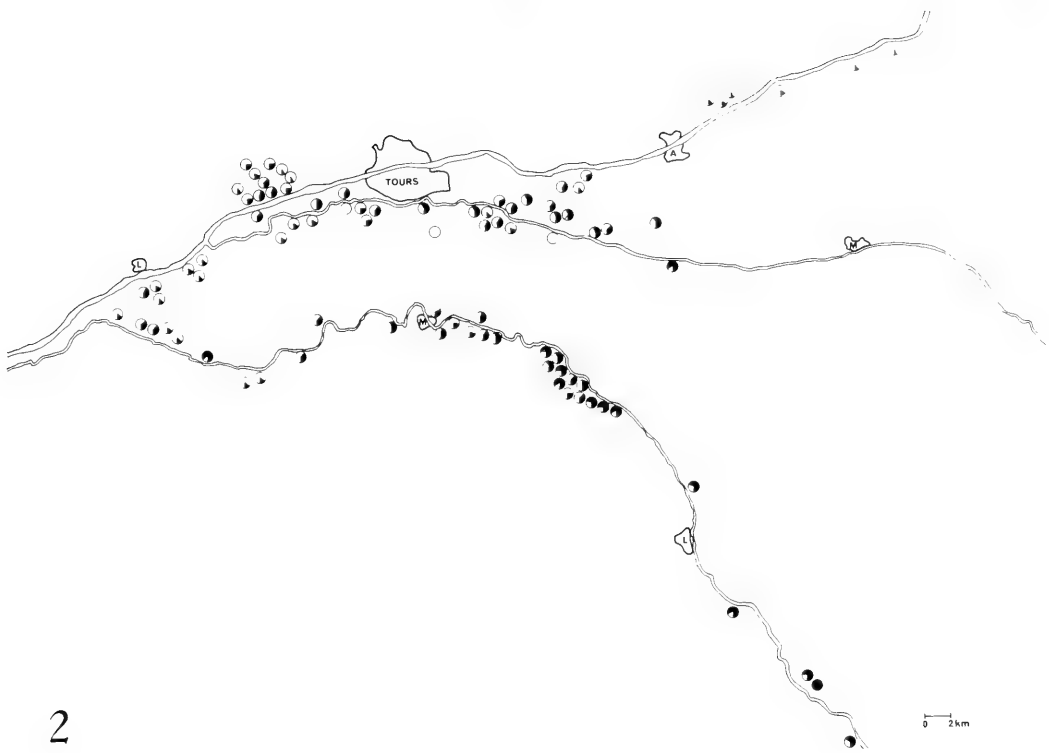
FIG. 1. Fréquences régionales moyennes (en %) du caractère Péristome blanc.

la Fig. 4. Dans les différents secteurs de la vallée de la Loire observés, la fréquence oscille entre 0 et 40%. Les variations sont de même amplitude dans chacun des deux groupes de populations de la vallée de l'Aube, ainsi que dans la vallée de l'Eure. Dans le département de la Marne la fréquence du caractère est presque toujours supérieure à 90%; elle atteint même 100% dans plusieurs populations.

Au total, les distributions correspondant à chacun des secteurs sont assez homogènes et montrent que, localement, la fréquence du caractère péristome blanc est relativement stable; l'estimation de la fréquence moyenne à l'intérieur d'une région est donc une bonne image de la fréquence du caractère dans ces régions.

La variation clinale de la fréquence d'un caractère n'est pas un phénomène rare et, chez de nombreuses espèces continentales, il est courant qu'un ou plusieurs caractères présente de semblables variations. D'autres gradients ont d'ailleurs été mis en évidence chez *Cepaea hortensis*, en particulier pour le sytème de bandes 10305 (12). De telles variations géographiques sont généralement en relation avec une variation graduelle des facteurs climatiques de l'environnement. Cependant l'aspect rayonnant du cline rend difficile à priori l'hypothèse l'une simple action sélective par des facteurs climatiques car, dans des régions présentant des caractéristiques climatiques aussi différentes que le Nord, l'Est, le Sud et le Sud-Ouest de la France, le caractère se présente avec des fréquences identiques.

Le gradient mis en évidence peut être rapproché des observations concernant la



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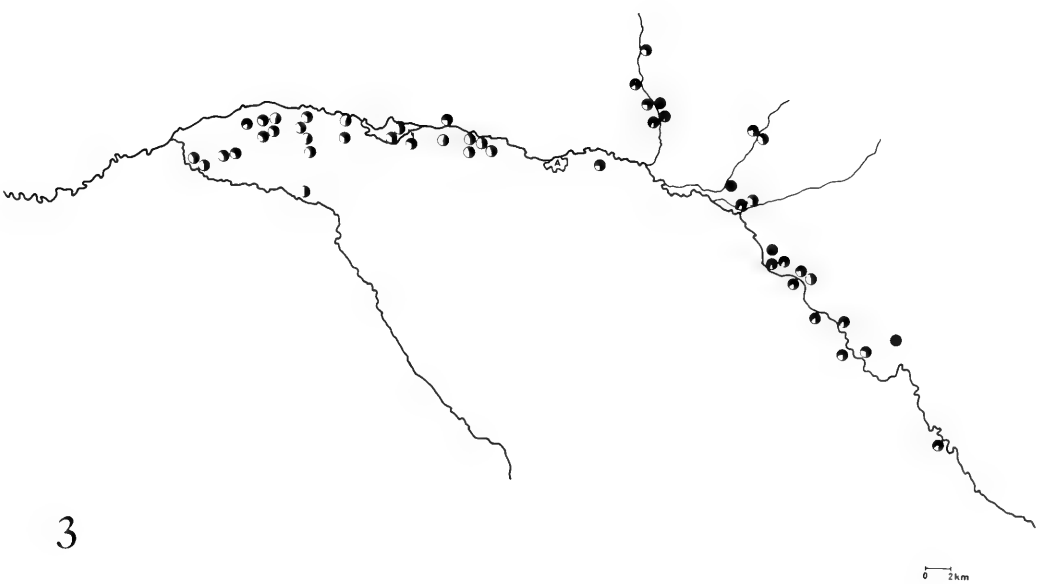

3

FIG. 2. Fréquence du caractère Péristome blanc dans les populations de Touraine.

FIG. 3. Fréquence du caractère Péristome blanc dans les populations de la vallée de l'Aube.

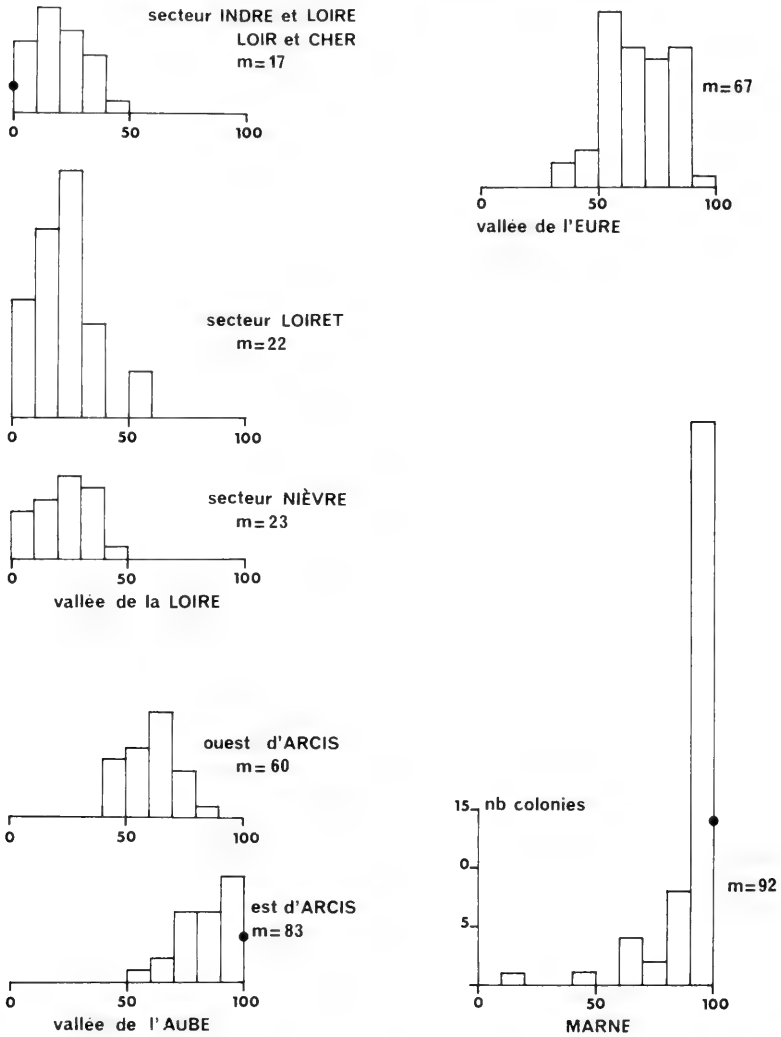

FIG. 4. Distribution des fréquences du caractère Péristome blanc à l'intérieur de différents secteurs géographiques. - en abcisse : fréquence (en %) du caractère Péristome blanc; - en ordonnée : nombre de colonies (le repère placé sur l'axe de ordonnées indique le nombre de colonies où la fréquence du caractère est de 0% ou de 100%).

répartition du caractère péristome blanc chez *Cepaea nemoralis*. Ce caractère est sans doute contrôlé par un gène P_A récessif par rapport au gène P_N qui détermine la coloration normale du péristome (3.8). Il est rare parmi les individus de cette espèce et n'a été recontré avec une fréquence importante que dans des régions isolées ou à la limite de l'aire de répartition [ouest de l'Irlande, (5.6.9.), Ecosse, (1), nord de l'Allemagne (13.14), Pyrénées (2.10)]. Il est possible d'envisager que le gène P_N, apparu au centre de l'aire de distribution, ait été favorisé et soit parvenu à éliminer progressivement son allèle sauf dans les régions où les populations sont relativement isolées. Cain a effectivement pu observer dans certaines localités du sud de l'Angleterre une diminution de la fréquence du caractère péristome blanc entre le néolithique et l'époque actuelle (4).

Etant donné l'étroite parenté génétique entre les deux espèces on est tenté de retenir un hypothèse semblable pour interpréter les variations observées chez *Cepaea hortensis*. Il faudrait alors supposer soit qu'une mutation du gène s'est produite en un point bien déterminé de l'aire de l'espèce et s'y est répandue dans les populations, soit qu'il y a eu, à une époque donnée, une introgression entre les deux espèces. Cette dernière hypothèse est étayée par la similitude plus grande de la coquille des deux espèces dans le centre de la France, à tel point que, dans les populations mixtes la seule observation de la coquille ne permet souvent pas de l'identifier. Le caractère ainsi apparu chez *C. hortensis* aurait ensui te, comme chez *C. nemoralis* mais avec une réussite moins totale, diffusé à travers les diverses populations.

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SUMMARY

In contrast to individuals of the species *Cepaea nemoralis* which are generally characterized by their brown lip, *C. hortensis* more often possesses a white lip. However in France shells with a brown, light brown or pink lip also occur in a relatively large number of *C. hortensis* colonies.

The spatial distribution of the average frequency for the white lip estimated in a certain number of French regions shows the existence of a significant geographic variation. The frequency of the white lip, very rare in the Loire valley, gradually increases in the neighboring regions and reaches 90% in the Pyrenees, in Normandie, in the north and the east. The preponderance of white lip observed in the peripheral regions corresponds to the results reached in England, in the Netherlands, in Germany and in Spain where the presence of colored lip individuals has been noticed as a rare event.

One can also observe at a local level the clinal variation of the phenotype. The frequencies of the white lip are however relatively stable within a limited sector.

MALACOLOGIA, 1973, 14: 339-343

PROC. FOURTH EUROP. MALAC. CONGR.

AN EXAMINATION OF THE DISTRIBUTION OF SHELL PATTERN IN *LITTORINA SAXATILIS* (OLIVI) WITH PARTICULAR REGARD TO THE POSSIBILITY OF VISUAL SELECTION IN THIS SPECIES

Charles Pettitt

Manchester Museum, The University, Manchester, England

ABSTRACT

Previous reports of crypsis in prosobranchs are briefly reviewed. Preliminary data are presented which indicate that *Littorina saxatilis* with patterned shells tend to be associated with backgrounds upon which they are cryptic. The suggestion is made that visual selection, probably by birds or crabs, must be considered as a factor influencing this distribution.

INTRODUCTION

The rough winkle, *Littorina saxatilis* (Olivi 1792), is highly polymorphic for a number of shell characters such as shape, sculpture and shell thickness. However, it is probably the striking variation in the colour and pattern of the shell in this species which has attracted most attention from malacologists. The colours found range from white through grey, fawn, brown, purple, red, orange and yellow to black. After a careful study of numerous shells it has proved possible to score the varieties of shell ground colour using 7 broad colour classes. Some interesting variations in percentage frequency of the different ground colours have been found in contiguous populations and in serial samples; these results will be reported in detail elsewhere.

In addition to differing ground colours, patterns composed of 1 or more colours or shades superimposed on a different ground colour or shade are also frequent. These patterns may consist of well defined bands (1 or 2, rarely 3); such shells were scored as B^+. Continuous or interrupted lines and a great variety of flecks, hyphens, spots, patches, tessellations, flammules and zigzags, etc., also occur; these shells were all scored as 'tessellate' (T^+). The possibility that these morphs might show associations with the nature of the background was thought to be worth investigating.

Very few earlier references to crypsis in intertidal prosobranchs have been found. Cooke (1895) mentions 3 examples of what he considered to be protective colouration, 1 in the tropical *Littorina* (=*Tectarius*) *pagodus*, which closely resembled its background rock; another in some black and white banded *Thais lapillus* at Newquay, on rocks which were variegated with white and other colours; and finally he noted that *L. obtusata* closely resembled the bladders of *Fucus vesiculosus* upon which it lived. This crypsis of *L. obtusata* was also remarked upon by Walton (1915), and has been found to apply also to snails on *Ascophyllum nodosum* (pers. observ.).

Blaney (1904), studying *Thais* from a number of islands off Maine, U.S.A., found the bright yellow morph to predominate over the other kinds on Yellow Island, where the rocks were yellow or reddish. Colton (1916), again working with *Thais*, this time at Mount Desert Island, Maine, found more light coloured shells on red rocks than on black rocks, although yellow was equally common on both. He also offered a small amount of evidence showing a tendency for banded *Thais* to be associated more with striped schist than with plain red granite.

The observations of all these authors were based on small numbers of shells. However, Cain & Sheppard (1950), in their classic paper on selection in the polymorphic

land snail *Cepaea nemoralis*, found a strong correlation between the amount of variegation of the habitat background and the amount of banding of the shells; this observation has since been thoroughly confirmed. It was therefore decided to examine from a similar standpoint some accumulated data on the relative frequencies of banded and tessellate morphs of *Littorina saxatilis* from various habitats.

MATERIALS AND METHODS

Eleven populations from 8 localities on the west coast of England and Wales were scored. It was found possible to divide the habitats from which the samples had been collected into 'variegated': e.g., rocks or, particularly, groynes covered in barnacles and small seaweeds, or rocks with many flecks and veins of contrasting colour in them; and 'non-variegated': monochrome rockfaces and boulder shores.

It was further possible to divide the habitats into 'open': rockfaces or groynes sides where the snails are exposed to view for a considerable part of the time, and 'concealed': such as rocks with many crevices, or, particularly, shores where boulders piled up 2 or more deep allow the snails to spend much of their time hidden from view under or between the boulders.

It was noticed while collecting that banded shells, particularly white banded ones, tend to be conspicuous on both variegated and non-variegated shores, whereas tessellate shells were conspicuous on non-variegated but tended to be cryptic against variegated ones. No concealed but variegated shore was found.

RESULTS

Table 1 gives the numbers of banded and of tessellate shells, together with the total sample size for each of the 11 samples; in 3 of the localities samples were taken from 2 different but contiguous backgrounds. The relative frequency between each of the 2 factors for both the morphs may be summarised thus:

	B^+	T^+
variegated	high	high
unvariegated	low	low
open	low	high
concealed	high	low

The summed percentage frequency of the 2 morphs found on the various combinations of habitat type are given in Table 2.

The frequency of banding was significantly higher in samples from variegated and from concealed shores ($p < 0.001$ for both). Highly significant heterogeneity in banding exists between the various samples ($X^2_{10} = 521.15$; $p << 0.001$). The heterogeneity of banding was determined between the 3 combinations of habitat type found, using summed data; this heterogeneity was significant ($X^2_2 = 93.86$; $p < 0.001$), and was caused mainly by the association of banded shells with open variegated and with concealed variegated shores, while shells on open unvariegated shores tended to be unbanded.

However the residual heterogeneity was still highly significant ($X^2_8 = 521.15 - 93.86 = 427.29$), indicating that other factors are involved also in determining the distribution of these morphs.

The frequency of tessellation was significantly higher in samples from variegated backgrounds and from open shores ($p < 0.001$ for both). There was significant heterogeneity in tessellation between the various population samples ($X^2_{10} = 5231.28$; $p << 0.001$). The heterogeneity of tessellation was determined between the 3 combinations of habitat type, using the summed data; this heterogeneity was significant ($X^2_2 = 326.12$; $p << 0.001$), and was due chiefly to the association of tessellate shells

TABLE 1. Frequency of banded and tessellate morphs on different backgrounds.

Population	Habitat description	Habitat type	Frequency		Sample size
			B^+	T^+	
Red Reef	red rock with streaks and spots of white	variegated open	7	8	87
Hoylake	fawn/grey boulders	unvariegated concealed	17	8	357
Mumbles	grey rockface	unvariegated open	1	2	99
Mumbles	grey boulders	unvariegated concealed	7	0	121
Llanfairfechan	groyne with barnacles	variegated open	204	55	771
Llanfairfechan	fawn boulders	unvariegated concealed	92	19	264
Amroth	brown/grey boulders	unvariegated concealed	2	5	94
Amroth	groyne with barnacles	variegated open	28	270	906
Oxwich	grey rockfaces	unvariegated open	7	0	606
Port Eynon	grey boulders	unvariegated concealed	5	0	56
Port Erin	black rockfaces	unvariegated open	1	5	50
		Totals:	371	372	3411

TABLE 2. Percent frequency of banded and tessellate morphs on different backgrounds.

	Concealed shores	Open shores
variegated appearance		mean T^+ = 18.9% S.D. = 7.2 N. = 1764 mean B^+ = 13.5% S.D. = 7.1
unvariegated appearance	mean T^+ = 3.6% S.D. = 1.4 N. = 892 mean B^+ = 13.8% S.D. = 6.4	mean T^+ = 0.9% S.D. = 3.0 N. = 755 mean B^+ = 1.2% S.D. = 0.4

with variegated open shores; populations in the other 2 habitat types tended to be non-tessellate.

Once more, however, the residual heterogeneity was highly significant (X^2_8 = 5231.28 - 326.12 = 4905.16), indicating that other factors again must be involved in determining the distribution of this morph.

DISCUSSION

The data here presented indicate that there is a tendency for patterned shells to be associated with habitats where they are most cryptic, although obviously much more information is needed before any firm conclusions can be drawn.

In the absence of any evidence that shell colour is either linked to, or has a pleiotropic relation to, the other variable characters such as shell thickness, sculpture, resistance to desiccation, etc., the only selective force likely to be of importance in governing the distribution of the colour morphs of *Littorina saxatilis* is visual selection. From a review of the predators of this species (to be published elsewhere) it is apparent that the most important visual selectors of the snails are birds and crustaceans, particularly crabs.

Giesel (1970) found the limpet *Acmaea digitalis*, in a panmictic unit, to be dimorphic, with light and dark morphs. The dark morphs were associated with dark rocks, and the light morphs with rocks encrusted with white barnacles. The young of each morph settle equally on both substrates and the bimodal distribution of the adults appears to be established by visual selection of the young snails by shore birds.

As *Littorina saxatilis* is viviparous the explanation of the association found of B^+ and T^+ morphs with different substrates cannot be exactly the same. The spat of *L. saxatilis* tend to remain in the vicinity of the parent, and the active dispersal rate of the adults is slow, about 0.5 to 10 m per year (Herdman, 1890; Gowanloch & Hayes, 1926; Lami, 1937; Berry, 1961; James, 1968). Thus if the frequencies of T^+ were initially identical on, say, a plain rockface and a continuous barnacle encrusted rockface, visual selection would alter this equality; assuming T^+ to be inherited, the increased frequency of T^+ on the barnacle face, and the reduced frequency on the plain rock would tend to be maintained by later generations, whether the selection was intermittent or even ceased altogether.

As the number of samples in the present study is small, the possibility cannot be dismissed, however, that these morphs may have become initially associated with their present backgrounds by chance. Again, tessellate and non-tessellate morphs may initially actively select a cryptic background, as do the light and dark morphs of the moth *Biston betularia* (Kettlewell, 1955).

However, the present results indicate that visual selection should be considered as a factor determining the distribution of the tessellate and banded colour morphs of *Littorina saxatilis*.

ACKNOWLEDGEMENTS

I thank Dr. L. M. Cook for his helpful suggestions and criticisms at all stages of the preparation of this paper, and especially for his assistance with the statistical work.

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MALACOLOGIA, 1973, 14: 344

PROC. FOURTH EUROP. MALAC. CONGR.

PREDICTION OF THE NUMBER OF COLOR MORPHS IN POPULATIONS OF *LIGUUS FASCIATUS*

Michael A. Rex[1]

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.

ABSTRACT[2]

Liguus fasciatus is a highly polymorphic arboreal pulmonate inhabiting small islands called hammocks in southern Florida and hardwood groves in Cuba and Haiti. The present study concerns those living on hammocks in Long Pine Key, Florida. Hammocks are islands of tropical hardwood vegetation surrounded by sparse sandy pine wood or swamp. In Long Pine Key, hammocks range in size from 0.34 to 43.80 acres. The *Liguus* material, collected in 1931 by W. J. Clench and W. S. Schevill, included 9 color morphs: *eburneus*, *cingulatus*, *roseatus*, *castaneozonatus*, *deckerti*, *luteus*, *ornatus*, *testudineus*, *marmoratus* (see Pilsbry, 1946).

Computerized stepwise multiple regression analysis (Dixon, 1968) was performed to determine whether the number of color morphs in populations of *Liguus* living on 48 individual hammocks in Long Pine Key could be predicted by any of the following set of independent variables: X_1, hammock area; X_2, distance to the largest hammock; X_3, distance to the largest hammock > 20.0 acres (there were 6 hammocks of this size); X_4, distance to nearest hammock; X_5, size of nearest hammock. Variables X_2 - X_5 were thought to measure isolation. The statistic R^2 estimates the variance in the dependent variable (number of color morphs) "explained" by the combined effects of the independent variables.

The regression as a whole provided a significant prediction of the number of morphs ($R^2 = .39$, $F_{(5, 42)} = 5.372$, $P < .01$). A significant positive correlation existed between the number of morphs and hammock area (contribution to $R^2 = .30$, $t_{(42)} = 4.5705$, $P < .001$; but variables measuring isolation, with the exception of X_2, proved insignificant. Distance to the largest hammock (X_2) was significant (contribution to $R^2 = .07$, $t_{(42)} = 2.2924$, $P < .05$), but subordinate to the effect of area.

I infer from the relative ineffectiveness of isolation variables to predict the number of morphs in the multiple regression and the general widespread distribution of morphs in this group of hammocks that inter-hammock migration is extensive, but that its contribution to maintaining polymorphism is strongly mediated by hammock size. Polymorphism is evidently not random as Pilsbry (1912, 1946) suggested. Some form of selection appears to reduce the color variation of populations on small hammocks. What the selective agent(s) might be is uncertain. One possibility is that the various morphs are aposematically (Eisner & Wilson, 1970) or cryptically colored and that smaller hammocks support less variable populations because they afford fewer possibilities for aposematic or cryptic associations to avoid visual predators. Predators on *Liguus* include several birds (Simpson, 1929) and the opossum (Pilsbry, 1946).

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[1]Present address: University of Massachusetts - Boston, Boston, Massachusetts, U.S.A.

[2]Published *in extenso* in Breviora, 1972, 391: 1-15.

MALACOLOGIA, 1973, 14: 345-347

PROC. FOURTH EUROP. MALAC. CONGR.

LITHOPHAGA LITHOPHAGA (L.) (BIVALVIA) IN DIFFERENT LIMESTONE

Karl Kleemann

I. Zoologisches Institut der Universität Wien, Austria

The purpose of this study is to determine the boring rate of *Lithophaga lithophaga* (L.) with respect to different kinds of limestone, in field and laboratory investigations. Up to the present time, no experiments have shown the influence of the different morphological texture and the chemical composition of limestone on the boring rate. Hodgkin (1962) put specimens of *L. plumula kelseyi* Hertlein & Strong 1946 in holes bored in limestone rock as well as in non-calcerous mudstone in order to determine whether they bore by some sort of chemical or mechanical means. By this approach he provided a successful method.

The author prepared 8 different limestone rocks with holes 12 mm wide and 30 mm deep according to the method of Hodgkin, 1962. 1) These are samples from the area investigated at Rovinj, Yugoslavia: BA and BRbl originate from the island Banjole; V is a boulder from the Vestar-bay. 2) The samples III, II, W, GM and KK are not from Rovinj; they consist of calcite as the above-mentioned, without showing essential chemical differences with regard to further components (mainly quartz), with the exception of KK, which is interspersed with ferric-oxide-hydrates (Limonite).

The rocks are determined by X-ray diffraction and thin-sections. Each sample contains 3 mussels approximately 30 mm long marked by etching numbers on the shell and the measures and weight of each mussel are recorded. Field investigations are adapted to obtaining the boring rate under most natural conditions in order to bring them into relation with the laboratory results observed. A plastic sliding-gauge is used for measuring the depth of the holes. A measuring scale is used to determine the volumes. The samples are checked at intervals of 12 weeks.

In the 1st period (in the fall) the minimal boring rate in the field shows an increase ranging from 1-3 mm and 0.1-0.25 ml. In the 2nd period (in the winter) 1/3 to 1/2 of that amount is measured and in the 3rd period (in the spring) even lower values are obtained as a result of specimens having died due to sedimentation.

In the laboratory, too, the boring rate decreases from period to period, which is due to the fact that the physical condition of the mussels becomes weaker as there is no nourishment. In the 1st period, the boring rate yields an increase of 0.4-1.5 mm and 0.04-0.09 ml. This corresponds perhaps to half the boring rate in proportion to the same interval in the field or equals the 2nd period in the field. In the laboratory, the boring rate decreases in the 2nd and 3rd period even faster; for a series of smaller mussels (20 mm average in holes 8 mm in diameter), slightly higher values are obtained in relation to the increase of depth. The increase of volume is nearly the same compared with mussels in holes of 12 mm in diameter (Fig. 1).

Micron-sized and highly porous calcite of the samples BA and BRbl, as well as very few pores and no texture showing calcite of the sample V, yield higher values than the marble W, having no pores and centimicron-sized grains with distinct twin-laminations, caused by pressure, and rounded quartz-grains. The dense calcites III and II show lower values. The marble GM and limestone KK, which is a micron-sized dense calcite, richly interspersed with fossils and ferric-oxide-hydrates, yield the lowest values.

The results obtained do not allow a conclusive interpretation as to the texture of limestone. Pores, being present, seem to be an obvious factor in facilitating deminer-

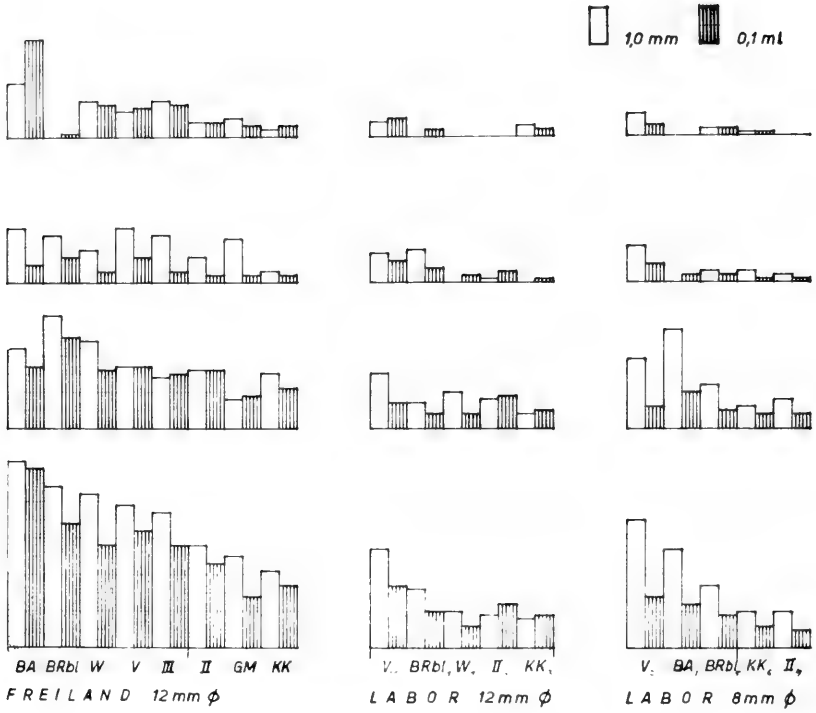

FIG. 1. Boring rates of *Lithophaga lithophaga* in various types of limestone (see text for types) in the field (Freiland) and laboratory (Labor).

alisation. (Bindings between the grains, which have to be dissolved, are not so strong. Dilution at the contact-sheet between mantle and substrate does not take place; on the contrary, the enlarged surface leads to a greater degree of demineralization.) The micron-sized matrix yields a faster boring rate than the deci- or centi-micron-sized matrix. (Smaller grains are dissolved more easily than bigger ones.) How does the sample W with its centi-micron-sized matrix and relatively numerous quartz-grains fit in here, whereas GM, being marble too, yields the lowest values besides KK? Probably the ferric-oxide-hydrates are the cause of the lowest boring rate together with the influence of twinned one-crystals and tectonical cracks, which are filled with recrystallized calcite. (The significance of the chemical composition is more distinct than the matrix/grain/fabric-relation (Kleemann, 1972, dolomite compared with calcite).)

The boring rate is not related to the growth rate of the mussels (which is approximately 1 decimal less) but equals the boring rate of other organisms in the "Endolithion" (Riedl, 1966). (Compare with Neumann, 1966 about the boring rate of the sponge, *Cliona lampa*.)

If we take into account the short time of investigation in relation to the age of fully-grown mussels (according to the growth rate results the age of mussels was estimated up to 80 years (Kleemann, 1972, 1974)) and the fact that their holes are quite often considerably longer (12 cm), and if we can transfer the problem to the field with varying ecological conditions involved, it can be said that the texture of carbonate rock is decisive for the rate of bio-corrosion which in the samples investigated ranges from 4.3-12.9 mm/year.

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MALACOLOGIA, 1973, 14: 348

PROC. FOURTH EUROP. MALAC. CONGR.

STUDIES ON THE DISTRIBUTION AND ECOLOGY OF *LYMNAEA TRUNCATULA* INTERMEDIATE HOST OF *FASCIOLA HEPATICA* IN PORTUGAL

Maria de Lourdes Sampaio Xavier, João Fraga de Azevedo and Maria Alice Mattos dos Santos

Instituto Nacional de Saúde "Dr. Ricardo Jorge" Largo 1 de Dezembro, Porto Portugal

ABSTRACT

In the present paper we report our findings during 3 years concerning the distribution and population dynamics of *Lymnaea truncatula*, intermediate host of *Fasciola hepatica* in Portugal.

Contrary to former belief this species proved to be common in fascioliasis areas, mainly in the north of the country, where we found not only the highest rate of infection in animals, but also a continuous increase in the number of human cases. The initial failure to find this species in the mentioned areas has to be attributed to the minute size of this amphibious snail in its various habitats and to the insufficient knowledge of these habitats and snail populations dynamics.

This is particularly true for the provinces of Alentejo and Algarve (south part of Portugal), where the general ecological circumstances (especially the climate) are unfavourable for the development of fascioliasis, though it occurs there in some restricted areas where the microclimate is favourable to the development of *Lymnaea truncatula*.

MALACOLOGIA, 1973, 14: 348

PROC. FOURTH EUROP. MALAC. CONGR.

THE ROLE OF TEMPERATURE IN THE ECOLOGY AND DISTRIBUTION OF THE SNAIL, *LYMNAEA STAGNALIS*

Henry van der Schalie and Elmer G. Berry

Museum of Zoology, The University of Michigan, Ann Arbor, Michigan, U.S.A.

ABSTRACT

Forty or 50 years ago the large circumpolar pond snail, *Lymnaea stagnalis*, was common in southern Michigan. This species has now disappeared throughout the southern half of this state. It was used extensively for studies in parasitology, genetics and functional anatomy. Recent laboratory studies, designed to stress this snail at various temperatures to measure differences in growth and reproduction, indicate that it may be quite sensitive to heat budgets. The data appear to indicate that this sensitivity may be responsible for its disappearance from lower southern Michigan and explain the shrinking of its present range to the upper part of the Lower Peninsula.

MALACOLOGIA, 1973, 14: 349-354

PROC. FOURTH EUROP. MALAC. CONGR.

WASSERMOLLUSKEN-ZONOSEN IN DEN MOORWALDERN *ALNION GLUTINOSAE* (MALCUIT) DER UNGARISCHEN TIEFEBENE

Karl Bába

Zoologischer Lehrstuhl der Pädagogischen Hochschule, Szeged, Ungarn

Während der letzten Jahre habe ich in einem umgrenzten Areal der Ungarischen Tiefebene zwischen Duna und Tisza (im Eupannonicum) die Isolierungsmöglichkeiten der Molluskenzönosen nach Vegetationsbeständen studiert. Die Vegetation hat sich hier wegen der Wasserablassungen stark verändert. Natürliche Moorwälder gibt es hier kaum noch, früher machten diese Waldassoziationen die dominierende Vegetation des Alföld aus. Ich habe mich mit ihnen beschäftigt, weil in ihnen die ursprüngliche Fauna fortlebt.

Die Molluskenzönosen der Erlen-Eschen-Aschweiden-Moorwälder habe ich, um die Abweichungen darzutun, mit den Wasserzönosen wasserbestandener, sandiger Moorwiesen (*Molinion coeruleae*) verglichen. Nach Ansicht der Phytozönologen stellt diese Pflanzenassoziation einen den Moorwäldern vorausgehenden Zustand dar. Weitere, vergleichsweise untersuchte Gewässertypen waren tote Tiszaarme, Erdgruben, Natrongewässer und Reisfelder.

Von jedem der 47 untersuchten Wasserbiotope habe ich mit Hilfe von je zehn 25 cm-Quadraten Proben eingeholt und das Material der Sammlungen aufgrund von 11.975 Individuen mathematisch bewertet. Mit der Ramsay-Pőcs'schen Formel nahm ich Artenidentitäts- sowie Dominanz- und Konstanzidentitätsberechnungen vor und kontrollierte sie mit der chi^2-Signifikanzprobe. Als Wahrscheinlichkeitsniveau der Signifikanz wählte ich aufgrund der sich aus der Methode ergebenden theoretischen Erwägungen 5%. (pH-Daten siehe an Tabelle 1.)

Von den Gewässertypen sind nur die toten Tiszaarme ständig mit Wasser versehen. Die Moorwälder, mit Ausnahme der Moorwiesen, weichen nicht nur in ihrer Artenzahl und der Zusammensetzung ihrer Charakterarten, sondern auch mathematisch in ihrer Artenidentität von den einzelnen Sammelstellen anderer Gewässertypen ab. Die meisten Arten kamen aus den Moorwäldern und den toten Tiszaarmen (je 37 Arten mit 3232 bzw. 5884 Individuen) und die wenigsten (8 bzw. 1 Art) aus Natrongewässern und Reisplantagen zum Vorschein. Die einzelnen Gewässertypen bieten für die massenhafte Vermehrung verschiedener Arten optimale Bedingungen und sind daher aufgrund ihrer Artenzusammensetzung bzw. ihrer konstanten, dominanten Arten gut auseinanderzuhalten. In den Moorwäldern und toten Tiszaarmen fand ich nur eine gemeinsame konstant-dominante Art: die *Bithynia tentaculata* (wegen ihrer Eventualität in die Tabelle nicht aufgenommen (Tabelle 1)).

Zwischen den Zönosen der Moorwiesen und Moorwälder besteht eine Artenidentität, dies zeigen auch die 6 gemeinsamen konstantdominanten Arten. Beachtenswert ist dies, weil zwischen den Pflanzenassoziationen der *Molinion coeruleae*- und *Alnion glutinosae*- Bestände auch geobotanische Sukzessionszusammenhänge bestehen.

Die Ursache für die Unterschiede zwischen den Gewässertypen bzgl. Artenzusammensetzung und Individuenzahl erblicke ich - da es sich um weitverbreitete Arten handelt - in der abweichenden Nahrungszusammensetzung (die von der Zusammensetzung und dem Zustand der Vegetation und dem Wasser-pH abhängt).

Den Unterschied zwischen den Wassertypen der Moorwälder und der ebenfalls artenreichen toten Flussarme zeigt der Umstand, dass aus den Moorwäldern mehrere konstante, Detritus fressende Schneckenarten und 12 Muschelarten zum Vorschein kamen, während in den toten Armen die Pflanzenfresser dominieren. Die gefundenen

Muschelarten bilden in den Moorwäldern 32% der Gesamtindividuenzahl und in den toten Armen nur 1%.

Nur aus den Moorwäldern kamen *Segmentina nitida* f. *distiquenda* und *Musculium lacustre* f. *hungaricum* zum Vorschein. Den grösseren Anteil der Moorwälder-Mollusken (24=42%) machen wärmebeanspruchende oder wärmetolerierende Tiere mit weiten Toleranzgrenzen aus. Wegen der wechselnden Wassertiefe und der durch die Beschattung seitens der Bäume temperaturmässig aufgeteilten, gegliederten Wasserfläche leben hier auch einige in Ungarn heute schon seltene Arten mit engen Toleranzgrenzen, wie z.B. *Valvata naticina*, *Bithynia leachi*, *Bathyomphalus contortus*, *Pisidium supinum* und *P. milium*. Die Molluskenarten der Moorwälder kommen - entgegen anderen Gewässern - nicht nur in den Uferregionen massenhaft vor.

Für die quantitativen Verhältnisse ist charakteristisch, dass in den toten Flussarmen die Individuenzahl der konstanten Arten ein Mehrfaches jener der übrigen Arten beträgt, während in den Moorwäldern die quantitativen Verhältnisse der konstant-dominanten Arten ausgeglichener sind.

Typisch für die Struktur der Zönosen in den Moorwäldern ist, dass ihre Artenzahl an wasserarmen Stellen 10-11 und an wasserreichen 21-24 beträgt. Die Gesamtindividuenzahl in den Aschweidenbeständen beträgt 148-175, in den Klimaxwäldern 271-460 (einmal sogar 1036), in den Moorwäldern 11; auf den Moorwiesen können 6 Arten - entsprechend dem Zustande der Pflanzensukzessionen konstant-dominant werden (Tabelle 1.). Charakteristish für die Moorwälder ist, dass in ihnen auch mehr als zwei Arten absolute Konstanz erreichen können. Hier fehlen die Arten mit mittlerer Konstanz (50-60%). Die grosse Zahl der über eine hohe Charakteristik verfügenden Arten zeigt, ähnlich wie bei den Landzönosen beobachtet, die Prozesse der Umwandlung der Zönosen an. In den wasserreichen Moorwäldern zeigt die hohe Zahl der jugendlichen Individuen im Verhältnis zur Gesamtindividuenzahl (69-82%) die Stabilität der Zönosen an.

Die Basis meiner Untersuchungen bildeten die Pflanzenassoziationen und die ihnen entsprechenden elementaren Molluskenzönosen, die Synusien. Die Molluskensynusietypen sind in Pflanzenassoziationsserien nach Pflanzenassoziationen im folgenden angegeben. In Klammern sind nach den Namen der Molluskensynusien die ebenfalls charakteristischen subkonstant-subdominanten Arten angeführt.

Reisplantagen

Physa fontinalis - *Radix peregra* f. *ovata*, *Physa fontinalis* - *Radix peregra* f. *ovata* - *Gyraulus albus*

Erdgruben entlang der Tisza

Planorbarius corneus, *Planorbarius corneus* - *Lymnaea stagnalis* (*Musculium lacustre*) *Planorbarius corneus* (*Lymnaea stagnalis*), *Lithoglyphus naticoides* - *Lymnaea stagnalis*, *Radix peregra* f. *ovata* (*Lymnaea stagnalis*, *Planorbis planorbis*)

Natrongewässer

Anisus spirorbis

Pflanzen-Assoziationen der toten Tiszaarme

a) *Hydrocharietalis* Tx. et Prsg. *Hydrochari-Stratiotetum* fac.: *Ceratophylletosum demersi* Kárpáti: *Gyraulus albus* - *Planorbarius corneus* (*Armiger crista*, *Lymnaea stagnalis*),
b) *Potametalia* W. Koch. *Myriophyllo* - *Potametum myriophylletosum spicati* Soó: *Bithynia tentaculata* (*Radix peregra* f. *ovata*). *Nymphaeetum albo-luteae nymph-*

TABELLE 1. Liste der konstant-dominanten Arten.

Artenname	1 pH 5,8 6,5–5,7	2 6,5–8,5	3 7,5–8,5	4 7,5–9	5 7,5–8	6 6,5–7
1. *Viviparus contectus* (Millet)	+	+				
2. *Viviparus viviparus* (L.)	⊞	⊞	+			
3. *Viviparus acerosus* Bourguignat		+	⊞			+
4. *Valvata cristata* O. F. Müll.	⊞	+				⊞
5. *Valvata pulchella* Studer	+				+	+
6. *Valvata piscinalis* (O.F. Müll.)	+	+	+			
7. *Valvata naticina* Menke	+	+				
8. *Lithoglyphus naticoides* (C. Pfeiffer)			+			
9. *Bithynia tentaculata* (L.)	⊞	+	+			⊞
10. *Bithynia leachi* (Sheppard)	+	+	+			+
11. *Aplexa hypnorum* (L.)	⊞	+				
12. *Physa fontinalis* (L.)		⊞			⊞	+
13. *Physa acuta* (Drap.)		+	+			
14. *Galba truncatula* O.F. Müll.	⊞	+	+			
15. *Stagnicola palustris* (O.F. Müll.)	+	+				+
16. *Radix auricularia auricularia* (L.)		+	+			+
17. *Radix peregra* (O.F. Müll.)	+	+	+		+	
Radix peregra f. ovata (Drap.)	+	⊞	⊞		⊞	+
18. *Radix ampla* (Hartm.)		⊞	+			
19. *Lymnaea stagnalis* (L.)		⊞	⊞		+	
20. *Planorbis planorbis* (L.)	⊞	+	+			⊞
21. *Planorbis carinatus* (O.F. Müll.)		+				
22. *Anisus septemgyratus* (Rossm.)	⊞	+				+
23. *Anisus leucostomus* (Millet)	+	+				
24. *Anisus spirorbis* (L.)	⊞	+	+	⊞	+	⊞
25. *Anisus vortex* (L.)	+	+				+
26. *Anisus vorticulus charteus* (Held)	+	+	+			⊞
27. *Bathyomphalus contortus* (L.)	+					+
28. *Gyraulus albus* (O.F. Müll.)	+	⊞	+		⊞	
29. *Gyraulus laevis* (Alder)	+	+				+
30. *Armiger crista* (L.)	+	⊞			+	+
31. *Segmentina nitida* (O.F. Müll.)		+	+			⊞
Segmentina nitida f. distiquenda Gredler	⊞					
32. *Hippeutis complanatus* (L.)	+	+	+			
33. *Planorbarius corneus* (L.)	+	⊞	⊞			+
34. *Acroloxus lacustric* (L.)	+	⊞				+
35. *Gundlachia Uni* sp. (Wouteri)		⊞				
36. *Unio tumidus f. decurvatus* (Rossm.)			+			
37. *Anodonta cygnea f. zellensis* (Gmelin)		+				
38. *Spaerium corneum* (L.)	+	+				+
39. *Musculium lacustre* (O.F. Müll.)		+	+			+
Musculium lacustre f. hungaricum Hazay	+					
40. *Pisidium henslowanum* (Sheppard)		+				
41. *Pisidium supinum* (A. Schmidt)	+					
42. *Pisidium milium* (Held)	⊞					+
43. *Pisidium subtruncatum* (Malm.)	+					
44. *Pisidium nitidum* (Jenyns)	+					
45. *Pisidium pulchellum* (Jenyns)	+					
46. *Pisidium personatum* (Malm.)	+					
47. *Pisidium obtusale* (C. Pfeiff.)	⊞					+
48. *Pisidium casertanum* (Poli)	⊞					+
49. *Pisidium hibernicum* (Westerlund)	+					
Artenzahl	37	37	22	1	8	25
Dominante konstante Arten	11	10	4	1	3	6

Legenda: 1, *Alnion glutinosae* (Malcuit); 2, Toter Tiszaarm; 3, Erdgruben entlang der Tisza; 4, Natrongewässer; 5, Reisplantagen; 6, *Molinion coeruleae* W. Koch

aetosum Kárpáti: *Sphaerium corneum - Viviparus viviparus. Nymphaeetum albo-lutaea* Nowinski: *Gyraulus albus - Gyraulus crista* (*Acroloxus lacustris*). *Trapetum natantis* Müller & Görs: *Hippeutis complanatus - Acroloxus lacustris* (*Radix peregra* f. *ovata*). *Nymphaeetum albo-luteae Trapa natans* Soó: *Viviparus viviparus - Planorbarius corneus.*

c) *Phragmitetalia* W. Koch. *Scirpo-Phragmitetum medioeuropaeum* Tx. fac.: *typhetosum*, (*Potamogeton crispus*): *Gyraulus cristata, Physa fontinalis - Radix ampla, Radix peregra* f. *ovata, Planorbarius corneus, Lymnaea stagnalis - Radix ampla, Lymnaea stagnalis - Planorbarius corneus.*

d) Komplex-Pflanzen-Assoziation *Hydrochari - Stratiotetum stratiotetosum* (Langendonck), *Nymphaeetum albo-luteae* Nowinski Komplex: *Gundlachia wouteri? - Acroloxus lacustris* (*Gyraulus albus*). *Nymphaeetum albo-luteae* Nowinski fac.: *Syum latifolium, Myriophyllo-Potametum* Soó Komplex: *Gyraulus albus - Gyraulus crista* (*Acroloxus lacustris - Bithynia tentaculata*). *Caricetum elatae* W. Koch, *Nymphaeetum albo-lutaea* Nowinski fac.: *Lemno-Utricularietum* Komplex: *Gyraulus albus - Galba truncatula - Gyraulus crista* (*Bithynia tentaculata, Hippeutis complanatus*). *Scirpo-Phragmitetum schoenophetosum* Soó *Nymphoidetum peltatae* (Allorge) Komplex: *Acroloxus lacustris - Planorbarius corneus. Scirpo-Phragmitetum* W. Koch, *Nymphaeetum albo-luteae* Nowinski Komplex: *Gyraulus albus - Gyraulus crista. Scirpo-Phragmitetum-typhoetosum angustifoliae* Soó, *Nymphaeetum albo-luteae* Nowinski Komplex: *Gyraulus crista - Acroloxus lacustris. Scirpo Phragmitetum sparganietosum* Soó, *Nymphaeetum albo-luteae* Nowinski Komplex: *Valvata piscinalis - Gyraulus albus - Acroloxus lacustris.*

Sandige Moorwiesen und Moorwälder

Molinion coerulae (Malcuit): *Valvata cristata - Bithynia tentaculata, Valvata cristata - Planorbis planorbis.*

Calamagostri - Salicetum cinereae Soó & Zólyomi fac.: *Carex elongatae: Bithynia tentaculata - Valvata cristata* (*Sphaerium corneum*), fac.: *Phragmites: Sphaerium corneum - Bithynia tentaculata* (*Planorbarius corneus*), fac.: *Carex acutiformis: Segmentina nitida - Planorbis planorbis* (*Anisus septemgyratus*), fac.: *Lastea thelypteris: Segmentina nitida - Planorbis planorbis - Anisus septemgyratus* (*Bithynia tentaculata, Valvata cristata*).

Fraxino pannonicae - Alnetum hungaricum Soó & Komlósi fac.: *Carex acutiformis, C. riparia, C. elatae: Bithynia tentaculata - Valvata cristata*, fac.: *Hottonietosum, Carex remota, Urtica dioica: Galba truncatula - Pisidium obtusale* (*Pisidium casertanum, Valvata cristata, Stagnicola palustris*).

Die im Abschnitt "Sandige Moorwiesen und Moorwälder" angeführten Synusien gehören dem *Valvata cristata - Bithynia tentaculata - Pisidium obtusale* - Malakosozion an.

Fraxino pannonicae - Alnetum hungaricum Soó & Komlódi fac. *Dryopteris* Konsozion: *Anisus spirorbis - Aplexa hypnorum* (*Viviparus contectus*).

Ein von den übrigen abweichendes, montanes Synusium am nördlichen Rande der Ungarischen Tiefebene (Alföld): *Dryopteridi - Alnetum* Klika. fac: *Thelypteridetosum palustris: Pisidium casertanum - P. milium - P. hibernicum* (*Anisus spirorbis, Segmentina nitida*).

Obzwar die einzelnen Moorwälder sich in verschiedenen Phasen der Vegetationssukzession befinden, besteht zwischen ihnen doch eine starke, 56-65%-ige, Konstanz- und Dominanzidentität. Die Zusammengehörigkeit der Zönosen ist auch malakozönologisch nachweisbar. Die häufigsten Charakterarten der vom Gesichtspunkte der Sukzession jüngeren Aschweidenbestände sind, ähnlich wie im Falle der Moorwiesen, vorwiegend *Valvata cristata, Bithynia tentaculata, Planorbis planorbis* und *Segmentina*

nitida. In den Klimax-Erlen-Eschen-Moorwäldern erscheinen neben den Scheckearten auch *Pisidium obtusale*, *Pisidium casertanum* oder andere konstant-dominante Muschelarten.

KONKLUSION

Die in eine Sukzessionsreihe einfügbaren Biotope, von den Moorwiesen bis zu den Moorwäldern, unterscheiden sich strukturell - und dementsprechend aufgrund ihrer Identitätsziffern auch nach der Zusammensetzung ihrer Sammelstellen - mathematisch von anderen Gewässertypen.

Die von den Moorwiesen bis zu den Moorwäldern reichende Sukzessionsreihe lässt sich in ein in Richtung der Sukzession zeigendes Sozion (*Valvata cristata - Bithynia tentaculata - Pisidium obtusale*) und in ein wegen des Austrocknens auf die Regression hindeutendes Konsozion (*Anisus spirorbis - Aplexa hypnorum*) aufteilen. Die die Sukzessionsreihe zusammenfassende zönologische Kategorie, das Sozion, ist im Gegensatz zu anderen Gewässertypen mit der Gesamtheit der gemeinsam vorkommenden hochcharakteristischen Arten zu kennzeichnen (Charakterarten). Diese Arten sind: *Valvata cristata*, *Planorbis planorbis*, *Anisus septemgyratus*, *Segmentina nitida*, *Pisidium obtusale*, *Pisidium casertanum* und die hochfidelitative *Viviparus contectus*, bzw. *Anisus vorticulus*.

Die Untersuchung der Pflanzenzönosen und der Molluskenzönosen dürfte auch bei der Bewertung der Molluskenperiode des Pleistozän verwertbar sein.

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SUMMARY

WATER MOLLUSCA COENOSES IN MARSH-WOODS: *ALNION GLUTINOSAE* (MALCUIT) IN THE GREAT HUNGARIAN PLAIN

The water Mollusca coenoses (w.m.c.) of *Alnus*, *Fraxinus* and *Salix cinerea* in marsh-woods (m.w.), sandy-soiled marsh-meadows (m.m.) and other water types found now but in traces in the territory between the Danube and Tisza are compared and their separability according to the vegetation is investigated. The coenological collections are evaluated with a mathematical method. The calculations are checked

with significance test chi^2. The constant, dominant species change according to water types and states of plant succession (Table 1). The molluscan synusia of plant associations are given in the text. In m.w., not so as in other water types, more than 2 species can be absolutely constant. Besides the water snails fed mainly on detritus, the dwarf shells form 32% of the total individual number, while in other waters their number is not even as high as 1%. The w.m.c. of m.w. and m.m. significantly differ from other water types in species constancy and dominance identity, having at the same time between themselves a high degree of species identity. Common constant species: 6. The m.w. and m.m. are, according to the plant coenologues, in a connection of succession.

MALACOLOGIA, 1973, 14: 355-370

PROC. FOURTH EUROP. MALAC. CONGR.

SOME WOODLAND MOLLUSC FAUNAS FROM SOUTHERN ENGLAND

R. A. D. Cameron

Department of Biological Sciences, Portsmouth Polytechnic, Portsmouth, England

INTRODUCTION

The only comprehensive account of the habitats of British terrestrial molluscs is that of Boycott (1934). His approach, for the most part, was to attempt to define the range of habitats occupied by each species, and to relate this to environmental variables. Many of the British species (nearly half the total), proved to have very wide ranges of habitat. As Boycott himself realized, the broadness of many habitat-ranges was the result of geographical variation in habitat preference within Britain. Recent studies (Cameron, 1970; Cameron & Palles-Clark, 1971) confirm this, showing that the habitats occupied by one species may change considerably over short distances (10-50 km) as a response to quite small changes in climate.

Work in some other European countries, starting with the pioneer work of Favre (1927), has a different approach: determining the number and variety of species found in particular environments (Walden, 1965). This approach, especially when conducted in a quantitative manner, has yielded interesting results (Ant, 1969; Kornig, 1966; Walden, 1955; Wareborn, 1969), suggesting the existence of characteristic molluscan assemblages associated with various habitats. This study follows the pattern of these investigations, but in a very restricted range of habitats in a small, zoogeographically homogenous area: deciduous woodlands on the chalk hills of Sussex and Hampshire.

THE AREA AND HABITATS STUDIED

The map (Fig. 1) shows the area and localities sampled. All sites are on the South Downs, a range of Cretaceous chalk hills rising gently from the coastal plain to an east-west scarp 200-250 m a.s.l. The north-facing slopes of the scarp are steep (usually ca. 30°); those on the south-facing dip slopes are varied, and there are plateau areas with very gentle slopes.

The climate is mild by British standards. Annual rainfall varies from 29 inches (725 mm) on the lower southern slopes to 39 inches (975 mm) on some parts of the scarp. Mean monthly temperatures range from 17.0°C in July to 5.5°C in January (Meteorological Office, 1952).

Substantial parts of the South Downs are wooded, but many woods, especially on the dip slopes, are recent plantations, mostly of conifers. The mature deciduous woods are usually dominated by beech (*Fagus sylvatica*), which is sometimes the sole canopy species, but ash (*Fraxinus excelsior*) is also frequent and is a co-dominant with beech in some woods. Oaks (*Quercus* spp.), sycamore (*Acer pseudoplatanus*) and various introduced conifers occur sporadically. Many woods lack a secondary layer of woody plants; where it is present it is usually of yew (*Taxus baccata*) and occasionally of hazel (*Corylus avellana*), hawthorn (*Crataegus* spp.) or elder (*Sambucus nigra*).

In most sites, the tree canopy is very dense and ground cover scanty, especially in pure beechwoods on the scarp, where 90% or more of the ground may be devoid of vegetation. In all the scarp woodlands, and in many of the others, the most abundant herb is dog's mercury (*Mercurialis perennis*) with Solomon's seal (*Polygonatum multiflorum*) and wild garlic (*Allium ursinum*) being locally abundant on wetter slopes.

On the acid soils of the gentlest slopes, blackberry (*Rubus fruticosus* agg.) usually dominates. Small clearings and other recently disturbed areas are often covered with stinging nettle (*Urtica dioica*) or willowherbs (*Epilobium* and *Chamaerion* spp.).

On the scarp, steepness and lack of herbaceous cover result in unstable soil surfaces; the soil is usually shallow and there is much chalk debris at the surface. All measurements of soil pH at the surface in scarp sites were greater than 7.0. On the gentler slopes the soil is deeper; brown earth soils with no chalk visible at the surface. In a few sites, thin layers of clay overlie the chalk.

Due perhaps to the softness of the rock, there are no natural crags or boulders, even on the steepest slopes. The porosity of the rock tends to minimize both surface run-off and waterlogging, and none of the sites are very wet.

All woods in the area are to some extent man-made and are subject to some disturbance in the form of forestry activities and the clearing of paths and rides for shooting and rearing pheasants. A few of the woods on the gentle slopes show signs of coppicing. These activities are more frequent on the dip slopes, and many sites on the scarp have not been disturbed for some time - trees have been allowed to die and fall, with no signs of thinning or clearing. Forestry records (Brown, 1953) indicate that even these woods are planted (at least in part), and it seems doubtful if beech is the natural dominant of any British woodlands (Godwin, 1956; Pennington, 1969).

METHODS

For each site, an area of ca. 1000m^2 was chosen in a wood so that (a) it did not include any wood-edge, and (b) it was covered, as far as possible, by a canopy of mature trees. In each such area, molluscs were searched for and collected by hand, the search lasting for 1 hour in each case. In addition, small amounts of soil and litter were taken from over each area, to a volume of about 1.5 l, and removed for examination in the laboratory. A colourimetric determination of pH was made on soil from the top 1 cm at each site, together with a brief description of the vegetation.

Material brought back to the laboratory was dried and passed through a series of sieves, the smallest mesh being 0.5 mm. Any material passing through this was discarded and the remainder as searched for molluscs with the aid of a binocular microscope.

The combination of these 2 methods of collecting yields consistent and repeatable qualitative results for snails, but quantitiative estimates of abundance based on searching in the field are unreliable. This method is retained in order to ensure adequate representation of the larger and less populous species. The results for slugs are much less satisfactory, and it is clear that only a small proportion of the slug fauna has been discovered in some cases (Wareborn, 1969). Nearly all samples were made in dry weather, it being too dark inside some woods to search effectively during rain. The samples were made between June and September (so that plant-cover could be assessed at the time of sampling), in 1968, 1969 and 1970.

RESULTS

Table 1 shows shows the site characteristics of each sample made. Table 2 lists the mollusc fauna of each site. It is evident from Table 2 that there are differences between sites both in numbers of species found and in species composition. The analysis which follows refers only to snails; the slugs are discussed briefly at the end.

Variation in number of species per site

Table 3 shows the mean number of species per site in categories defined by topography, soil pH, and plant cover. Samples from the scarp have a higher mean than

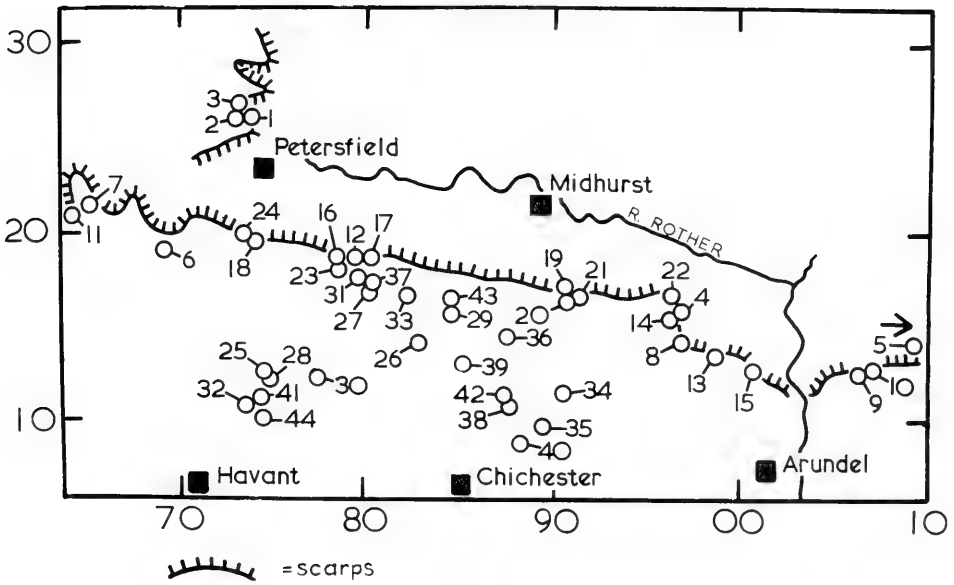

FIG. 1. A map showing the study area and sample sites. The British Ordnance Survey 10 km grid is shown in the margins.

TABLE 1. Habitat characteristics of the samples mentioned in the text.

Scarp Samples:	1 - 24.
Bare ground 90%+:	2,4,8,10,13,14,16,18,19,21.
Intermediate (50-90% bare ground):	1,3,9,12,15,17,20,22,23.
Covered (0-50% bare ground):	5,6,7,11,24.
Rubus fruticosus present:	11,15.
Non scarp Samples:	25-44.
Soil pH: 7.0+ :	25,26,27,28,30.
6.0- 7.0 :	29,31,32,33,34,35,36,37,38,39.
5.0- 6.0 :	40,41,42,43,44.
Rubus fruticosus present	29,35,36,38,39,40,41,42,43,44.

TABLE 2. The occurrence of species of snails and slugs in the samples. Nomenclature follows Ellis (1969). *Cochlicopa lubrica* is an aggregate species (Quick, 1954) and both segregates occur; some specimens were lost, and so segregation has not been done systematically. *Arion circumscriptus* and *A. ater* are also aggregates; no dissections were carried out.

Species	Sites																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Snails																						
Pomatias elegans	+	+	+	+	+		+	+	+	+		+	+	+	+	+	+	+	+	+	+	+
Acicula fusca	+	+	+	+	+			+		+		+	+	+	+		+	+	+	+	+	+
Carychium tridentatum	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Cochlicopa lubrica	+				+	+	+	+	+	+	+	+		+	+	+	+	+	+	+		
Abida secale													+						+			
Acanthinula aculeata		+	+	+		+	+	+					+					+				
Ena obscura		+		+	+					+	+	+	+		+	+	+	+	+	+		+
Marpessa laminata	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Clausilia bidentata		+	+	+	+	+	+		+			+	+	+	+		+		+	+	+	+
Clausilia rolphii	+		+		+			+		+		+	+	+		+	+	+		+	+	
Cecilioides acicula		+							+		+											
Helicodonta obvoluta	+	+						+		+		+		+		+	+			+	+	+
Helicigona lapicida			+														+		+	+		
Arianta arbustorum										+					+				+			
Cepaea hortensis	+	+	+			+	+			+	+	+		+		+	+		+	+	+	
Helix aspersa			+	+	+		+	+	+	+		+	+	+	+	+	+	+	+	+		+
Cepaea nemoralis					+			+	+	+			+	+	+	+			+		+	+
Hygromia subrufescens																						
Hygromia striolata		+	+		+	+				+	+	+	+		+	+		+	+			
Hygromia hispida	+		+	+	+					+	+	+	+	+		+	+	+	+	+	+	+
Monacha cantiana																				+		
Punctum pygmaeum	+	+		+				+				+	+	+	+						+	+
Discus rotundatus	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

Species	Sites																					
	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Snails																						
Pomatias elegans	+	+	+	+		+	+	+	+	+	+	+		+			+					
Acicula fusca		+						+						+			+					
Carychium tridentatum	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+				
Cochlicopa lubrica	+	+	+	+		+				+	+			+	+					+	+	
Abida secale																						
Acanthinula aculeata						+				+												
Ena obscura	+		+		+	+	+	+			+		+	+								
Marpessa laminata	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+			+	+
Clausilia bidentata	+	+		+	+	+	+		+		+		+	+	+							+
Clausilia rolphii	+	+	+			+					+			+								
Cecilioides acicula																						
Helicodonta obvoluta									+													
Helicigona lapicida																						
Arianta arbustorum																						
Cepaea hortensis		+	+	+		+		+	+			+	+					+				
Helix aspersa	+	+	+			+		+			+	+	+	+				+				
Cepaea nemoralis	+			+		+	+	+			+	+	+			+						
Hygromia subrufescens															+							
Hygromia striolata	+	+	+		+	+								+			+	+		+	+	
Hygromia hispida			+	+	+				+		+	+			+		+	+				
Monacha cantiana												+										
Punctum pygmaeum	+	+	+																			
Discus rotundatus	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

TABLE 2. (Cont.)

Species	Sites																																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Snails (cont.)																																												
Euconulus fulvus		+	+	+		+	+	+				+	+		+	+			+		+			+		+	+			+	+	+	+			+	+		+	+	+	+	+	+
Vitrea contracta	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+			+	+		+							
Vitrea crystallina													+																									+	+		+		+	+
Oxychilus cellarius	+	+	+	+	+	+	+	+	+	+			+	+	+	+		+	+	+	+	+	+	+		+		+	+		+	+	+	+	+		+	+	+					+
Oxychilus alliarius	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+		+	+	+	+	+	+	+		+	+	+	+	+	+	+	+
Oxychilus helveticus			+	+			+			+																														+				
Retinella radiatula																																+		+				+			+		+	+
Retinella pura	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+		+	+		+	+	+	+			+			
Retinella nitidula	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+		+	+	+	+	+	+		+	+	+	
Vitrina pellucida	+	+	+			+	+		+		+	+	+	+	+	+		+	+		+		+		+	+	+			+	+				+		+	+	+			+		
Number of species	17	20	21	18	18	15	17	16	15	21	15	21	23	20	20	20	18	18	22	18	19	17	19	18	17	16	13	17	10	16	13	12	15	13	14	14	14	11	13	10	7	7	9	8
Slugs																																												
Arion intermedius						+															+										+		+											
Arion circumscriptus	+			+			+				+							+												+	+	+						+						+
Arion hortensis	+			+					+	+		+	+	+	+	+	+							+	+			+		+		+									+			
Arion subfuscus																+	+				+		+							+					+		+	+			+			
Arion ater	+											+	+		+	+	+		+	+		+	+	+					+		+		+										+	
Milax sowerbyi							+																																					
Limax maximus	+		+	+					+					+	+	+	+	+							+		+		+	+			+					+	+					
Limax cinereoniger			+			+				+		+	+				+		+	+		+	+										+											
Lehmannia marginata													+					+			+	+		+				+					+					+			+			+
Agriolimax reticulatus					+		+																								+				+									

TABLE 3. Variation in mean number of species of snail per site with topography, soil pH and vegetation cover at ground level.

Category of Site	Mean number of species per site	Number of sites
Scarp sites with bare ground	19.7	10*
Intermediate scarp sites (10-50% cover)	18.4	9
Covered scarp sites (50-100% cover)	16.6	5*
All Scarp sites	18.6	24**
Non-scarp sites (a)pH 7.0+	15.8	5**
(b)pH 6.0-7.0	12.9	10**
(c)pH 5.0-6.0	8.2	5**

**all significantly different from each other at $p<0.05$.
*significantly different, $p<0.02$, (Wilcoxon, Mann, Whitney test in each case).

the others, even than those elsewhere with alkaline soils. Within dip-slope samples, samples with the highest soil pH values have the highest mean. Within the scarp samples, there are smaller differences in mean number of species between sites with differing amounts of ground cover. The barest sites have the highest mean, and the most covered the lowest.

The degree of similarity of species composition between sites

A measure of the similarity in species composition between sites has been obtained by calculating a Simple Matching Index (S.M.I.) for each sample with respect to each of the others in turn (Sokal & Sneath, 1963). The matrix produced has been reduced to a dendrogram (Fig. 2) by successively combining the S.M.I.'s of the most similar sites remaining in the matrix (Sokal & Sneath give details of procedure). The S.M.I. takes into account similarities between sites produced by absence of a species from both, as well as presence in both. If a set of very dissimilar faunas were compared, the use of such an index would be misleading, as absence may be caused by a variety of different factors. In this case, where a small number of factors appear to be effective and the faunas are broadly similar, such an index seems more useful than one based on presence alone, since absence of a species from any 2 sites is likely to relate to

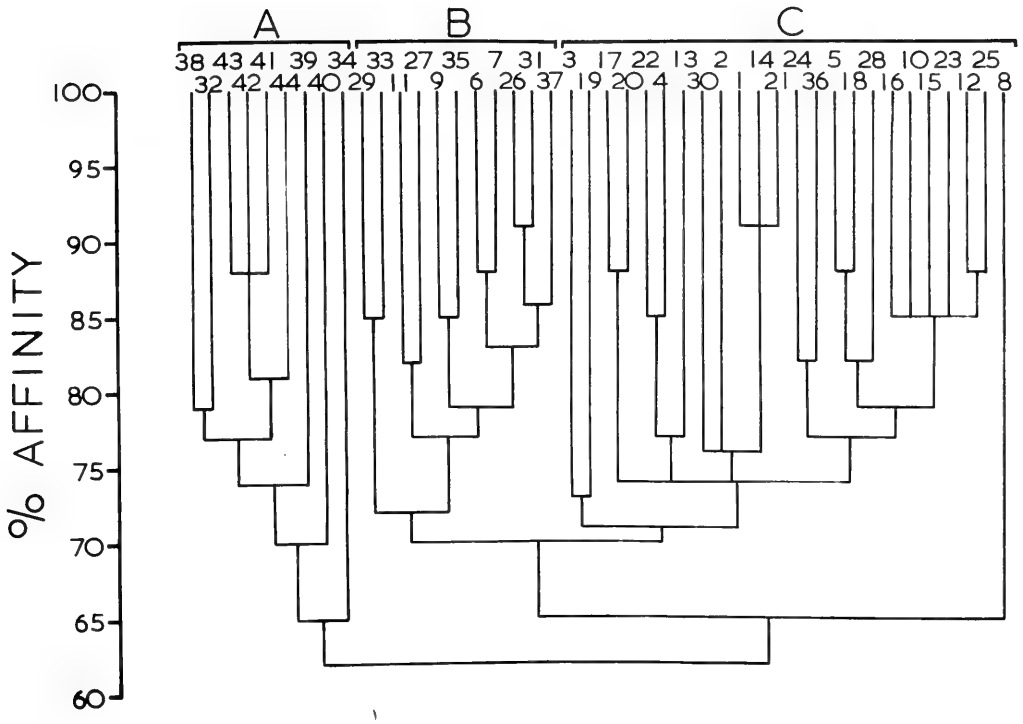

FIG. 2. A dendrogram showing the levels of affinity connecting the samples, based on the Simple Matching Index.

TABLE 4. Distribution of samples from each faunal group (A, B, C) with respect to environmental factors mentioned in the text.

Groups	A	B	C
Number of sites	9	11	24
Scarp samples	0	4	20
Non-scarp samples	9	7	4
Scarp samples:			
(a) bare ground	-	0	10
(b) Intermediate	-	1	8
(c) Covered	-	3	2
Mean pH of non-scarp samples	5.7	6.5	7.0
Samples with *Rubus*	6	3	3

TABLE 5. Frequency of occurrence (%) of each species in each faunal group: 1, species restricted to Group C; 2, species restricted to group A; 3, "Universal" species; 4, Species more frequent in B and C than A; 5, Species most frequent in A; 6, rare species (less than 4 occurrences).

		GROUPS		
	SPECIES	A	B	C
1	*Acicula fusca*	11	0	83
	Clausilia rolphii	0	9	75
	Helicodonta obvoluta	0	0	50
	Helicigona lapicida	0	0	18
	Helix aspersa	0	27	88
	Punctum pygmaeum	0	0	54
2	*Vitrea crystallina*	55	0	4
	Retinella radiatula	66	0	0
3	*Marpessa laminata*	77	100	100
	Discus rotundatus	100	100	100
	Oxychilus alliarius	100	100	83
	Retinella nitidula	77	81	100
4	*Carychium tridentatum*	44	100	100
	Cochlicopa lubrica agg	33	63	71
	Clausilia bidentata	11	90	71
	Cepaea hortensis	11	54	62
	Cepaea nemoralis	33	45	54
	Vitrea contracta	11	81	96
	Oxychilus cellarius	55	90	79
	Oxychilus helveticus	11	0	13
	Retinella pura	33	90	92
	Pomatias elegans	33	54	100
	Acanthinula aculeata	11	18	29
	Ena obscura	0	45	75
	Hygromia hispida	33	54	67
	Hygromia striolata	44	27	62
	Vitrina pellucida	33	81	58
5	*Euconulus fulvus*	77	63	54
6	*Abida secale*	0	0	8
	Cecilioides acicula	0	18	4
	Arianta arbustorum	0	0	12
	Hygromia subrufescens	0	9	0
	Monacha cantiana	11	0	4

the same factor in each case.

For further analysis, the sites have been split into 3 large groups, an arbitrary level of affinity being chosen for the purpose (70%). Three samples are not connected to others at this level. Samples 34 and 40 are clearly closer to Group A (Fig. 2) than to the others. Sample 8 is related to Groups B and C. Inspection of individual S.M.I.'s indicate closer affinities with sites in Group C than Group B, and it is assigned to the former group.

Table 4 shows the properties of sites in each group in relation to topography, soil pH and plant cover. It is evident from the table that each group of sites has distinctive

TABLE 5a. Number of occurrences of slug species in each faunal group.

Species	A	B	C
Arion intermedius	0	3	1
**Arion circumscriptus*	3	3	4
Arion hortensis	2	1	13
Arion subfuscus	2	2	5
**Arion ater*	1	3	11
Milax sowerbyi	0	0	1
Limax maximus	2	4	10
Limax cinereoniger	0	2	9
Limax marginatus	3	2	9
Agriolimax reticulatus	0	3	1

*Aggregate species not segregated by dissection (Ellis, 1969).

habitat features; similar snail faunas tend to occur in sites with similar environments. The number of sites and the amount of environmental information is too small to attempt explanation of small groups of sites with closer affinities.

Group A sites are characteristically acid; the commonest herb recorded is *Rubus fruticosus* agg. Group C sites, the richest in species, are nearly all on the scarp, and nearly all alkaline. Scarp sites with bare ground predominate. The Group B sites are intermediate in character.

The occurrence of individual species

The 3 affinity groups described above are strongly related to the various habitat categories described earlier. This implies that variation in mean species number between categories is, at least in part, the consequence of the same species being eliminated in each site. This can be examined by comparing the frequency of occurrence of each species in each group (Table 5). Inspection of the table shows that this is indeed the case. Some species occur in almost all sites in all groups; a larger number are almost exclusive to Group C and 2 to Group A. Most of the rest are more frequent in B and C than in A, but the magnitude of the difference varies. Although a few species reach their highest frequency in Group B, there is no real evidence that any species is particularly characteristic of that group.

Slugs (Table 5)

The general trend seen amongst snails, for species to be most frequent in Group C, is present also in the slugs. Group A has the least species recorded from it, and those that do occur tend to be less frequent than in Group C. *Arion hortensis* and *Limax cinereoniger* in particular are more frequent in Group C than elsewhere.

DISCUSSION

Character of the Faunas studied

The influence of soil pH

The association of snail-faunas rich in individuals and species with alkaline soils is well known (Atkins & Lebour, 1923; Boycott, 1934; Valovirta, 1968). The relationship is not direct, available calcium in the soil being more specific (Burch, 1955). Calcium available in leaf litter may be much more than would be inferred from soil pH, especially in acid soils (Wareborn, 1969). No measurement of available calcium was made in this study, but the very direct contribution made by underlying calcareous rock to conditions at the soil surface means that pH is probably a reasonable assessment of calcium availability. Soil reaction may also be indicative of certain structural properties of soil important to molluscs (Lozek, 1962).

The reduction in average numbers of species with increasing acidity is marked, the more noticeably since all sites have mull soils with no perennial accumulation of litter. Fall-off in species numbers with acidity is not so rapid in some Pyrenean woods (Cameron, unpubl.) and many woodlands on acid soils have more species than are recorded here (Favre, 1927; Boycott, 1934; Valovirta, 1968; Wareborn, 1969), even though many of those studied are much further north.

As might be expected (Boycott, 1934), many of the species which vanish or are much reduced in Group A are large, thick shelled species usually restricted to calcareous districts- *Pomatias elegans*, *Helicigona lapicida* and *Helix aspersa*. Some species on the edge of their range in Britain are also known to be calcicole there:- *Helicodonta obvoluta* (Cameron, 1972), *Clausilia rolphii* (Boycott, 1934) and *Abida secale* (Kerney, 1962). Other snails regarded as mildly calcicole also show varying reductions in occurrence: *Cepaea hortensis* and *C. nemoralis*, *Ena obscura*, *Carychium tridentatum* and *Acanthinula aculeata* (Boycott, 1934). The reduction of *Vitrea contracta* in Group A is paralleled by an increase in its congener *V. crystallina* - the change may relate to dampness rather than soil acidity (Kuiper, 1964).

There are, however, a number of species whose occurrence is not explained by reference to soil pH. *Punctum pygmaeum* and *Clausilia bidentata* are both more tolerant of acid conditions than many other species showing less reduction in Group A (Boycott, 1934), while *Marpessa laminata*, one of the most frequent species in all groups, is more calcicole than many species which diminish considerably in Group A. The other dominant species in Group A, however, including *Retinella radiatula*, *Vitrea crystallina* and *Euconulus fulvus* are all species tolerant of mildly acid conditions (Boycott, 1934). Amongst slugs only *Arion hortensis* is thought to favour calcareous soils (Boycott, 1934); it does reach its highest frequency in Group C.

The nature of the molluscan faunas

Study of the groups of sites produced by analysis of the S.M.I. matrix shows that particular sets of environmental conditions tend to contain specific molluscan faunas. Inspection of Wareborn's (1969) and Kornig's (1966) results, also from woods, suggests a similar conclusion. Such a conclusion would be expected on general ecological principles, but in the circumstances of this study the result has a special significance. All sites here have suffered from human interference, and in such sites one might expect the fauna to reflect accidents of recolonization or recent destruction. The high levels of affinity, especially for Group C sites, suggest that they have reached an approximately natural state in which all available niches have been filled by the appropriate species; disturbance is no longer the main determinant of faunal composition (but see below).

The difference between the 3 groups are such that A and B do not have their own characteristic species, but are merely impoverished versions of C. Of the 33 species of snail found in the study, only 2 are missing from Group C (Table 6): *Retinella radiatula* is frequent in A sites; *Hygromia subrufescens* occurs once only (in a Group B site). Of the 5 dominant (occurrence 75%+) species in Group A 4 are also dominant in Groups B and C, and the remaining 1, *Euconulus fulvus*, is not uncommon in them. Only *Vitrea crystallina* and *R. radiatula* are at all specific to Group A. In other studies of woodland molluscs over a range of soil acidity, there are often more signs of a distinctive acid soil fauna, especially when density as well as occurrence is considered (Walden, 1955; Valovirta, 1968; Wareborn, 1969).

The effect of disturbance on the faunas

The woods of the dip-slopes show most signs of disturbance. The effects of this disturbance are hostile to snails; compaction of the soil and removal of timber so that little is left to rot are possibly the worst (Boycott, 1934). The presence of naturally fallen timber on the scarp sites is a good indicator for *Helicodonta obvoluta* (Cameron, 1972), a species known to be adversely affected by disturbance. Of the other species regarded by Boycott as anthropophobes, *Acicula fusca*, *Limax cinereoniger* and *Hygromia subrufescens* occur here, the last only once, but the other anthropophobe slug, *Limax tenellus* (Müll) is apparently absent. *A. fusca* is here restricted to Group C sites, but this cannot be attributed to soil pH, as it can occur in undisturbed acid woodlands (e.g., Torc Woods, Kerry; Boycott, 1934). The same argument applies to *L. cinereoniger*. Since there is some evidence of plantation and management all over this area, the idea that *L. cinereoniger* is restricted to primaeval forest (Boycott, 1934; Quick, 1949) is not entirely correct.

Inspection of Table 6 shows that there is a much higher proportion of "rare" (occurrence less than 50%) species in Group A than in the others. This could be, in part, an artifact due to low population densities of the species concerned, but it suggests that the occurrence of many species in Group A is due to accidents of destruction or recolonization. This suggestion runs counter to the argument in the above section, and it is possible that S.M.I. is not the most appropriate index of affinity for Group A, because absences in common will in fact contribute far more to the intra-group indices than presences, unlike the situation within Groups B and C.

Disturbance could also explain the variation in numbers of species per site in scarp woodlands with ground cover. The dense canopy of mature beech trees often prevents the development of ground-flora. Dense carpets of *Mercurialis perennis* indicate a higher than average light intensity, which could be caused by thinning. *Mercurialis* itself is certainly no deterrent to snails; many rest and feed on it, and some show a strong preference for it in laboratory food trials (Frömming, 1954; Grime & Blithe, 1969; Grime, Dearman & McPherson-Stewart, 1968).

Comparison with other faunas

Other woodlands in Britain

There is no systematic account of the faunas of woodland in Britain, but there are many accounts of the faunas of individual woods. The most appropriate comparisons are with other calcareous woods: from chalk (Ellis, 1942), Jurassic Limestones (Boycott, 1934; Salisbury, 1946), Carboniferous Limestones (Stratton, 1956; Kerney & Fogan, 1969; Cameron, unpubl.), and calcareous tufa in an otherwise acid situation (McMillan, 1954). The similarity between these faunas and those on the South Downs is considerable. Many of the sites above, however, hold more species than are found in any one site on the South Downs, and if non-calcareous woods are considered as

well (Boycott, 1934; Stratton, 1951, 1956 and 1964; Langmead, 1949; Lloyd-Evans, 1958), the overall list of snails recorded from woodland is much larger than that given here. There are a variety of probable reasons for the absence of the extra species.

Variations in geographical distribution. *Lauria anglica*, *Helix pomatia*, *Acanthinula lamellata*, *Clausilia dubia* and *Vitrea diaphana* are all absent from the whole area studied, most being northerly species in Britain (Ellis, 1951; Kerney & Fogan, 1969). *Ena montana* has not been found in the area recently although it used to be there (Boycott, 1934). Conversely, *Helicodonta obvoluta* is found only in the study area, and is absent from the rest of Britain (Cameron, 1972).

The occurrence of cliffs, rocks and open scree. The study area, unlike many of the others, lacks natural areas of bare rocks or boulders. Two species often associated with rocks occur rarely in the area: *Abida secale* (Kerney, 1962; Long, 1970) and *Helicigona lapicida* (Stratton, 1956). Other rock-loving species found in other woods are completely absent - *Balea perversa*, *Lauria cylindracea* and *Pyramidula rupestris*. *Azeca goodalli* may also belong here, or in the next group (Adam, 1960).

Dampness. The sites in this study are comparatively dry. One species common in wet woodland, *Arianta arbustorum*, is very rare on the South Downs (Cameron & Palles-Clark, 1971). Another, *Vitrea crystallina*, is usually replaced by *V. contracta* in drier sites (Kuiper, 1964), and is here restricted to the more acid sites. *Columella edentula*, *Carychium minimum*, *Zonitoides nitidus*, *Agriolimax laevis*, *Succinea putris* and *Monacha granulata*, all absent from my sites, occur in many of the others, especially in the wetter sites. All are common in wet places, and many are restricted to them (Boycott, 1934; Watson & Verdcourt, 1953).

Openness. *Pupilla muscorum*, *Vallonia excentrica* and *Helicella caperata*, species usually found in open situations, occur in a few sites elsewhere. Descriptions of the sites do not indicate whether clearings are present.

Extreme acidity. *Zonitoides excavatus*, the only calcifuge snail in Britain (Boycott, 1934) is found in some of the most acid woods elsewhere.

Comparisons with other European woodland faunas

The study area lies in the broad climatic zone of rich mixed deciduous woodlands. Direct comparisons with continental faunas from the same zone is difficult, because of variations in the geographical distribution of species within that zone, and because the British fauna is impoverished as a result of isolation following the loss of the land connection (Beirne, 1952). In many cases the same genera are represented by different species, but one cannot yet assume that they are ecological replacements.

In the Netherlands, the richest woods evidently support a fauna very similar to those of Group C, especially if woods in the exceptionally rich Limburg region are included (Bruijns, Altena & Butot, 1959). As with the British woods, the list is much longer than that obtained here; detailed inspection of lists for each site would be necessary to see if the same factors operate. Some of the poorer woodland associations resemble those from Group A sites.

There are also similarities with several types of German beechwood. The *Melico-Fagetum* and *Carici-Fagetum* of Ant (1969) show strong resemblances to South Downs beechwoods (*Carychium minimum* in this paper is an aggregate, so *C. tridentatum* is possibly present (Ant, pers. comm.)), with many species of high constancy in common. In central Germany, the Staudenbuchenwalder of Kornig (1966), and in particular the Hangbuchenwalder which form a sub-division of the former, contain mollusc faunas very similar to those reported here (Table 7). They are usually on slopes and have highly calcareous soils. Unlike the beechwoods studied by Ant (1969), they are appreciably richer in species than those from the South Downs.

The mountain forests of Geneva (Favre, 1927) also show similarities to those of the

TABLE 6. Numbers of species of given levels of frequency occurring in each faunal group.

Frequency	GROUPS		
	A	B	C
100-75	5	10	13
74-50	3	5	10
49-25	8	4	1
25-1	7	4	6
Total	23	23	31
Absent	10	10	2

TABLE 7. A comparison of the most frequent (75%+) species in the Staudenbuchenwalder of Kornig (1966) and Group C sites in this study. + = frequency 75% or more, 50+ = frequency between 50 and 75%, rare = frequency less than 25%, - = absent. *Acicula polita* and *Helix aspersa* are treated as potential ecological equivalents of *A. fusca* and *H. pomatia*.

	Staudenbuchenwalder	Group C
Ena montana	+	-
Ena obscura	+	+
Marpessa laminata	+	+
Clausilia bidentata	+	50+
Discus rotundatus	+	+
Retinella nitidula	+	+
Retinella pura	+	+
Oxychilus cellarius	+	+
Vitrea contracta	+	+
Perforatella incarnata	+	- (absent in Britain)
Hygromia hispida	+	50+
Helicodonta obvoluta	+	50+
Helix pomatia	+	- (*H. aspersa* +)
Acicula fusca	- (*A. polita* rare)	+
Clausilia rolphii	-	+
Oxychilus alliarius	rare	+
Carychium tridentatum	50+	+
Pomatias elegans	-	+

South Downs; *Retinella nitidula* and *Marpessa laminata* are the most frequent species in these woods, and *Discus rotundatus* is obviously common (it is omitted from the list of woodland molluscs (Favre, p 322), but it is clear from the following text that it occurs frequently in woods). This list evidently represents a fairly diverse range of woodland types. The maximum number of species found in any one site was 31, surprisingly lower than figures for several British sites (Boycott, 1934; Stratton, 1956).

Deciduous and mixed woods, especially the more eutrophic ones, in southern Sweden, also have faunas containing many species (or more northerly representatives of the same genus, e.g., *Discus ruderatus*) found in South Downs faunas (Lundgren, 1954; Walden, 1955; Wareborn, 1969), but the dominant species are usually smaller than those of England (*Retinella radiatula* (=*Nesovitrea hammonis*, Walden 1966), *Euconulus fulvus*, *P. pygmaeum*), and genera such as *Columella* and *Vertigo* are well represented. Many of these woods must be much less disturbed, or present more niches (e.g., rocks, screes and clearings) than the Group A sites of this study, for many sites with acid soils have much richer faunas. Rather similar faunas, poorer in Helicids, come from central Finland (Valovirta, 1968).

This study demonstrates that certain narrowly defined habitats in Britain do have characteristic faunas, which can be compared with similar ones in such a way that reasonable explanations can be offered for the differences. Such studies are lacking in Britain, yet they form a useful basis for more quantitative work on the role of molluscs in the woodland ecosystem (e.g., Mason, 1970). They permit the conclusions of such work, which is laborious to carry out in more than a few sites at once, to be extended with confidence to a wider area.

SUMMARY

1) A survey of the molluscan faunas of 44 deciduous woodland sites in Southern England has been carried out.

2) Analysis of faunal affinities using the Simple Matching Index indicate the existence of 3 types of fauna: type A, sparse faunas associated with low soil pH and some disturbance; type B, intermediate and type C, rich faunas associated with high soil pH and minimal disturbance.

3) The high levels of affinity between faunas in Group C and the high proportion of frequently occurring species (occurring in 50% or more of the sites examined) reflect the similarity of habitat between sites and the minimal effect of disturbance on faunas.

4) The absence of various species found in other British woodlands is tentatively explained.

5) The faunas are compared with those from various European woodlands, some of which are extremely similar.

ACKNOWLEDGEMENTS

Thanks are due to Dr. L. M. Cook for computing the S.M.I.'s for me and for discussion of indices of affinity; to Mr. F. Haynes and Dr. D. I. Morgan-Huws for botanical information and ideas and to Dr. M. P. Kerney, who kindly read a draft of this paper. I should also like to thank Miss J. Switzer for facilities provided at Portsmouth Polytechnic.

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PROC. FOURTH EUROP. MALAC. CONGR.

PRELIMINARY REPORT ON THE MOLLUSCA OF THE BENTHIC COMMUNITIES OFF TEMA, GHANA

J. Edmunds and M. Edmunds

Department of Zoology, University of Ghana, Legon, Ghana

ABSTRACT

Preliminary results from a survey of the bottom communities off Tema, Ghana, are discussed. Most of the bottom is of soft deposits, but there is a reef at 10 m and a second, more fragmentary, reef at 20 m. The dominant molluscs on the 10 m reef are herbivores and species which browse on sedentary animals such as sponges and polyzoa, but there are rather few species of active carnivores. The 20 m reef has a very similar fauna to the 10 m reef but with rather fewer algae and associated herbivores.

Of the soft deposit communities 2 of the most interesting are composed of sandy silt overlaid with colonial foraminiferans, *Julienella* and *Schizammina*. These have very rich faunas of molluscs with abundant ciliary feeders (*Turritella* and bivalves) in the silt. There is an unusually rich variety of carnivores in these communities including many species of Toxoglossa. The reason why there are so many carnivores in this otherwise very uniform habitat whilst there are so few in the much more diverse reef is not known. Nudibranchs, however, are much more abundant on the reef than in the foraminiferan communities, since they browse on sponges, polyzoa and hydroids which can only grow on the reef.

INTRODUCTION

The offshore fauna of Ghana has been studied by Buchanan (1954, 1958), Buchanan & Anderson (1955) and Bassindale (1961), all of whom concentrated on the fauna of the soft deposits off Accra. At present, Mr. W. Pople of the Zoology Department and Dr. D. John of the Botany Department at the University of Ghana are surveying a limited area off Tema (35 km east of Accra). The survey is being carried out in considerable detail by diving in the shallower regions and by dredging in deeper water. The aim of the study is to work out the patterns of distribution of the fauna and flora, and to investigate the interactions between the various species. This report covers the more common species of mollusc collected during the survey. They were identified from the publications of Nicklès (1950, 1955), Knudsen (1952, 1956), Eales (1957), Edmunds (1968) and Tebble (1966). We are grateful to Dr. J. Knudsen for help with identifying the more difficult shelled molluscs. The work is still in the preliminary stages and has been hampered in 1970 and 1971 by the boat having been rammed and sunk in Tema harbour. Collections since then have been less regular.

The coast of Ghana east of Cape Three Points runs west-south-west to east-north-east with fault planes both parallel to the coast and due west-east. Tides are small (with a maximum difference at Spring tide of 1.5 m), but waves are high and there are considerable underwater currents eastwards, and a long shore drift results in changes in the distribution of the sand. From Tema eastwards the coast is rocky with patches of sand especially at the outlets of lagoons. The rock forms a platform from low tide level to about 10 m depth, then the bottom shelves more steeply. From East Tema Rocks a reef, Vernon Bank, runs eastwards into Kpone Bay. It is at a depth of about

10 m, and, except at its western end where it joins the shore, there is a deeper area, up to 16 m, between it and the 10 m shore platform (Fig. 1). From observation underwater, it appears that this reef is the remains of an old shoreline, composed of rock which probably lies along an east-west fault plane. It would have been flooded, together with the lagoon it enclosed, when the sea level rose. The western end of this reef shelves downwards on its seaward side, but further east it forms a prominent cliff. Beyond the reef the bottom slopes gently to a depth of 20 m where there are fragmentary remains of another reef which is composed largely of *Dendropoma* and is possibly an old shoreline. Beyond this the sea bottom slopes gradually to 40 m depth, then drops away more suddenly to 100 m which is the edge of the continental shelf. There is some evidence of another reef at about 30 m depth, as gorgonians and sponges have been dredged from here, but no more is known about it.

The areas studied are: 1) the 10 m Kpone reef (Vernon Bank), which is studied mainly by SCUBA diving; 2) the deeper 20 m reef, which is studied by diving and dredging; 3) the soft deposits between the 2 reefs and beyond the 20 m reef to a depth of about 40-50 m. These areas can only conveniently be studied by dredging. The communities living in these soft deposits will be discussed only briefly in this paper.

The 10 m reef (Kpone reef)

The most common species of mollusc on the 10 m Kpone reef are herbivores and browsing carnivores, as one would expect in an area where there are many sea weeds, sponges, gorgonians, polyzoa and small tunicates (but rather few corals). Herbivores found are listed in Table 1. *Alaba cullierети* feeds, and is usually found, on *Sargassum* which characteristically grows in sandy areas of the reef, in contrast to *Fissurella nubecula* which scrapes hard surfaces and occurs only on the rocky areas of the reef. *Aplysia winneba* Eales also occurs on the reef. Individuals of this species from 2 to 6 mm long have been collected feeding on *Laurencia majuscula* (Harvey) and one was subsequently reared until 30 mm long when identification was possible. The food preferences of the other herbivores are not known.

Ciliary feeders on the reef are shown in Table 2. Except for the gastropod *Crepidula porcellana*, all are fixed bivalves. *Ostrea spp.* are rare but occur in groups of several individuals. *Pteria sp.* lives attached to the gorgonian *Lophogorgia*. Hole-living species such as *Notirus irus* and *Saxicava arctica* are probably more common than they appear from the samples, and a large species of *Lithophaga* may occur since it has been found on the 20 m reef.

Browsers of sessile animals are shown in Table 3. From observations on species found elsewhere, *Triphora sp.* probably eats sponges (Fretter, 1951), and *Erato prayensis* tunicates (Fretter & Graham, 1962). The food of *Mathilda* is not known, and further work needs to be done on these species. *Rostanga sp.* and *Chromodoris gracilis* are probably sponge feeders and may be found almost anywhere on the reef where sponges occur. The food of the common reef and intertidal *Doriopsilla albolineata* is not known. Several dorids feed on polyzoa, for example *Onchidoris sp.* eats *Stylopoma duboisi*, and *Corambe sp.* eats *Membranipora*. *Trinchesia sp.* and *Doto sp.* are hydroid browsers - *Doto* being particularly common on hydroids growing on *Sargassum*.

There is a notable absence of carnivores on the reef, especially when compared with the fauna of the deeper water off Tema. Table 4 lists the commonest carnivores, but the food preferences of most are not known. At low tide *Cantharus viverratus* has been found eating a moribund sea urchin. In the laboratory a large *Cassis spinosa* rasped away at the starfish *Oreaster clavatus* Müller & Troschel; and *Tritonalia fusiformis* is suspected of having bored holes in *Alaba cullierети*. In Hawaii, *Bursa* eats polychaetes (Houbrick & Fretter, 1969), and species of *Chrysallida* are known to be external parasites of bivalves (Fretter & Graham, 1962). The taxonomy of the several

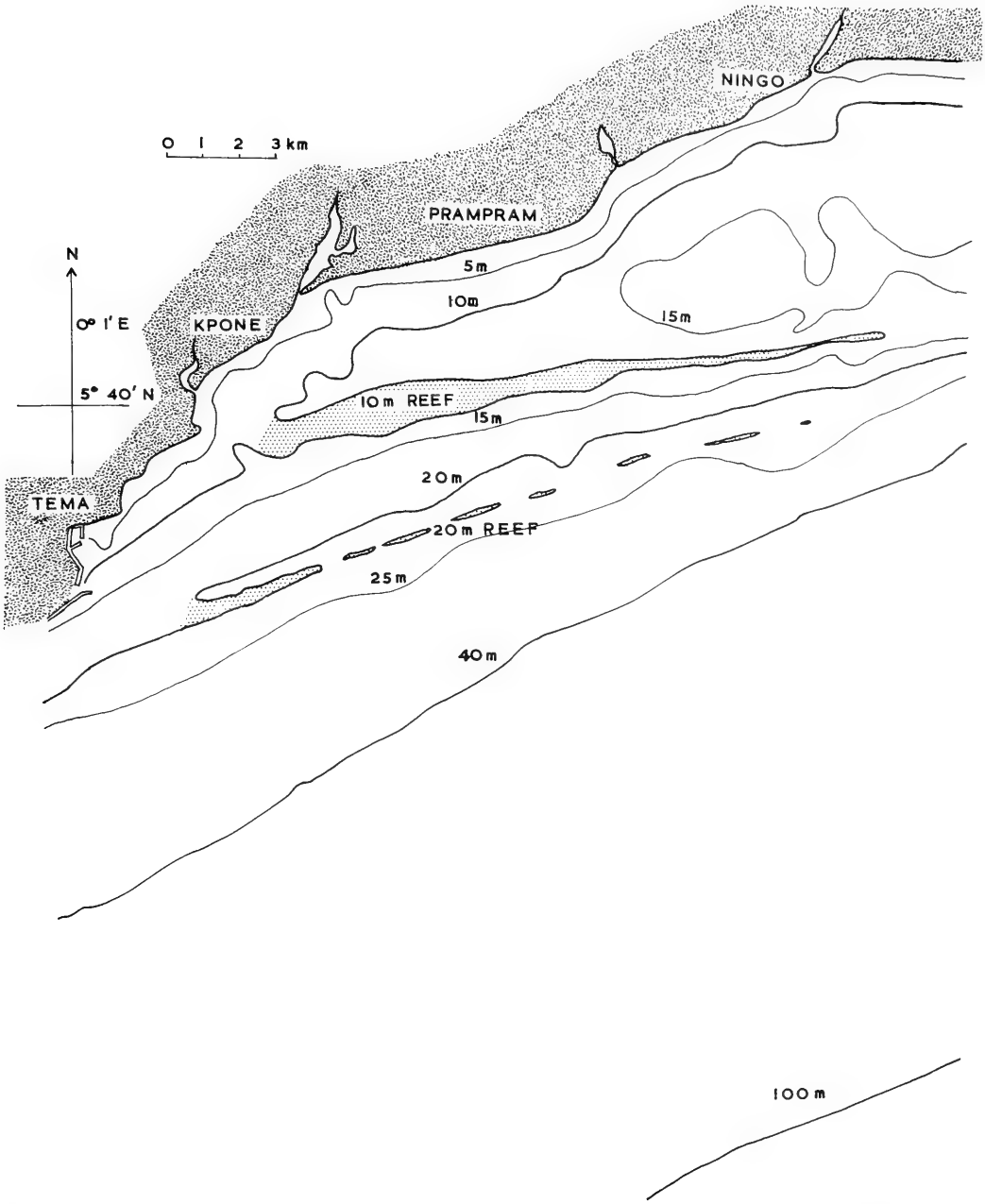

FIG. 1. Map of the Tema area, Ghana, showing the positions of the 10 and 20 m reefs.

species of *Nassa* has not been worked out, but they are probably scavengers.

The sandy areas of the reef are devoid of molluscs - the only ones recorded are *Turritella ungulina* (Linnaeus) and *Terebra grayi* E. A. Smith, but the area is not regularly sampled by divers. *Aplysia dactylomela* Rang and *A. fasciata* Poiret have both been found buried in the sandy crevices of the reef with only the mantle and its water currents visible. Presumably they are protected from predators, but this

TABLE 1. Herbivores of the 10 m reef.

Common on the reef, rare elsewhere	Occasional on the reef, occasional or rare elsewhere
Solariella canaliculata E. A. Smith	*Rissoina sp.*
Fissurella nubecula Linnaeus	*Calliostoma* (2 spp.)
Alaba cullicreti Dautzenberg	*Columbella rustica* (Linnaeus)

TABLE 2. Ciliary feeders of the 10 m reef.

Common on the reef, rare elsewhere	Occasional on the reef, occasional or rare elsewhere
Beguina senegalensis (Reeve)	*Arca noë* Linnaeus
Spondylus senegalensis Schreibers	*Pteria spp.*
	Crepidula porcellana Lamarck
	Notirus irus (Linnaeus)
	Saxicava arctica Linnaeus
	Ostrea spp.

TABLE 3. Browsers of the 10 m reef.

Common on the reef, rare elsewhere	Common or occasional both on the reef and elsewhere
Triphora sp.	*Erato prayensis* Rochebrune
Mathilda canariensis Dautzenberg	Occasional on reef, rare elsewhere:
Philine sp.	
Doriopsilla albolineata Edmunds	*Okenia impexa* Marcus
Chromodoris gracilis (Rapp)	*Rostanga sp.* (probably *R. rufescens* Iredale and O'Donoghue)
Onchidoris sp.	*Trinchesia sp.* (probably *T. albopunctata* Schmekel)
Doto sp.	*Janolus sp.*
	Corambe sp.

TABLE 4. Carnivores of the 10 m reef.

Common both on the reef and elsewhere	Rare on the reef
Tritonalia fusiformis (Gmelin)	*Thais haemastoma* (Linnaeus)
Nassa spp.	*Conus ambiguus* Reeve
Occasional on the reef, rare elsewhere:	*Tritonalia decussata* (Gmelin)
	Murex gravidus Hinds
Marginella sp.	*Cassis spinosa* Gronovius
Cantharus sp.	*Cantharus viverratus* (Kiener)
Bursa pustulosa Reeve	*Fusus sp.* (probably *F. boettgeri* von Maltzan)
Drupa nodosa C. B. Adams	
Chrysallida sp.	

behaviour does not appear to have been recorded before.

The fauna of this reef, especially the carnivores, shows affinities to that of the shore and shallow sublittoral. *Thais haemastoma*, *Cantharus viverratus*, *Tritonalia decussata* and *Conus ambiguus* all occur commonly on the shore as well as on the reef. The herbivores *Fissurella nubecula* and the rarer *Cerithium atratum* Born as well as the bivalve *Pinna rudis* (Linnaeus) also occur both on the reef and intertidally. Other reef species which can be found in the shallow sublittoral include *Beguina senegalensis*, *Triphora sp.*, *Mathilda canariensis*, *Alaba cullereti*, *Arca noë* and *Doriopsilla albolineata*. This is hardly surprising since the reef can be considered as a submerged rocky promontory of the shore. However, being at 10 m depth, some species which are common in deeper water are also found on the reef. Thus *Tritonalia fusiformis* and some species of *Nassa* are common on the reef as well as deeper, and *Erato prayensis*, *Rissoina sp*, one species of *Calliostoma* and *Crepidula porcellana* also occur in both areas. A few other deep water species are found on the reef rarely.

The 20 m reef

The fauna of the 20 m reef is not as well known as that of the 10 m reef, but it appears to be very similar except for having fewer algae and associated herbivores, as one would expect in view of the lower light intensity there. A few species, however, occur here which are absent from the 10 m reef, e.g., *Cardium kobelti* von Maltzan, *Gari fervensis* (Gmelin) and *Drillia pyramidata* (Kiener).

The soft deposits

The large area of sea bottom that is not reef has a variety of communities based on sand, mud or shell gravel, but the only ones mentioned here are the *Julienella foetida* Schlumberger and *Schizammina spp.* foraminiferan communities. Here the greyish mud is overlaid with pieces of siliceous material formed by the colonial foraminiferans, and the fauna here is far richer than in apparently similar deposits but without foraminiferans. Presumably the foraminiferans provide an additional solid substrate which is important for many of the species. The dominant ciliary feeder of the community is *Turritella annulata* Kiener, with the bivalves *Cardium kobelti*, *Pitaria tumens* (Gmelin) and *Cultellus tennuis* Gray also common in the mud, and *Calyptraea chinensis* (L.) on the surface. Scavengers (*Phos grateloupianus* (Petit) and *Nassa spp.*) are very numerous, and there is an incredible number of predatory gastropods such as *Murex spp.*, *Oliva flammulata* Lamarck, *Philine aperta* L., and the toxiglossans *Turris undatiruga* (Bivona), *Asthenotoma spiralis* (E. A. Smith), *Drillia spp.*, *Clavatula spp.*, *Terebra spp.* and *Conus spp.* There is also a great variety of hermit crabs, the majority living in shells of *Turritella* that have been bored by one of the carnivorous gastropods. The richness of the molluscan fauna in this apparently uniform habitat contrasts strikingly with the relative paucity of the shelled molluscan fauna in the more varied habitat of the reef. The food of the large number of toxiglossans is not immediately obvious, and further work in this area would be very interesting.

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MALACOLOGIA, 1973, 14: 377-383

PROC. FOURTH EUROP. MALAC. CONGR.

RECORDINGS OF THE HEART RATE AND ACTIVITY OF MOLLUSCS IN THEIR NATURAL HABITAT

E. R. Trueman, J. G. Blatchford, H. D. Jones and G. A. Lowe

Department of Zoology, University of Manchester, M13 9PL, U.K.

ABSTRACT

A method is described of continuously recording and analysing the heart rate and activity of molluscs in their natural habitat. The effect of change of temperature and valve closure on the heart rate of *Isognomon* illustrate the techniques. The possibility of developing these methods to employ sessile molluscs as environmental sensors is discussed.

INTRODUCTION

Much past work on the heart rate, e.g., Welsh, 1961; Pécsi, 1968, and activity, e.g., Salánki, 1966, of Mollusca has been carried out in the laboratory, recordings commonly being made on kymographs. Knowledge of the physiological ecology of littoral molluscs is derived from observations of their distribution and also from experiments carried out largely in the laboratory (Newell, 1964). However, the development of electronic recording techniques, e.g., Trueman, 1967; Salánki & Vêrô, 1969, allows experiments to be carried out in the natural environment with minimal disturbance to normal activity. Control experiments over long periods may be conveniently carried out in the laboratory using the same recording technique.

This paper consists of a description of the recording technique used, illustrated by extracts from recordings of *Chiton*, *Patella*, *Isognomon* and *Anodonta*, which show the effect of temperature change or valve closure on the heart rate. A technique of analysing the large amount of data that may be obtained is described and its use is discussed.

METHODS

Vêrô & Salánki (1969) have described a method of continuously recording the movement of the valves of *Anodonta* while in the natural environment. This involved the attachment of coils of fine wire to the valves and allowed Salánki & Vêrô (1969) to study the diurnal rhythms of activity of this mussel. It is, however, convenient to record both heart rate and valve movements simultaneously by use of an impedance pneumograph connected to a multichannel pen recorder both commercially available from Narco Biosystems Inc. The impedance pneumograph, which was originally designed to monitor chest volume in mammals, has proved to be an extremely versatile transducer. A small oscillating current (25 Kc/s, 2μA) is passed between a pair of fine platinum or silver wire electrodes and any changes in impedance that occurs between them is converted into a voltage signal. This is amplified to drive a pen in the recorder (Fig. 1a). The electrodes may be attached 1 to each valve of a bivalve to record shell movements or inserted into the pericardial cavity through fine holes drilled through the valves to monitor heart rate additionally. The electrodes are then sealed in place by wax (Fig. 2). Changes in impedance are recorded in respect of heart beat, valve movements and possibly pedal and rectal movements. Mussels

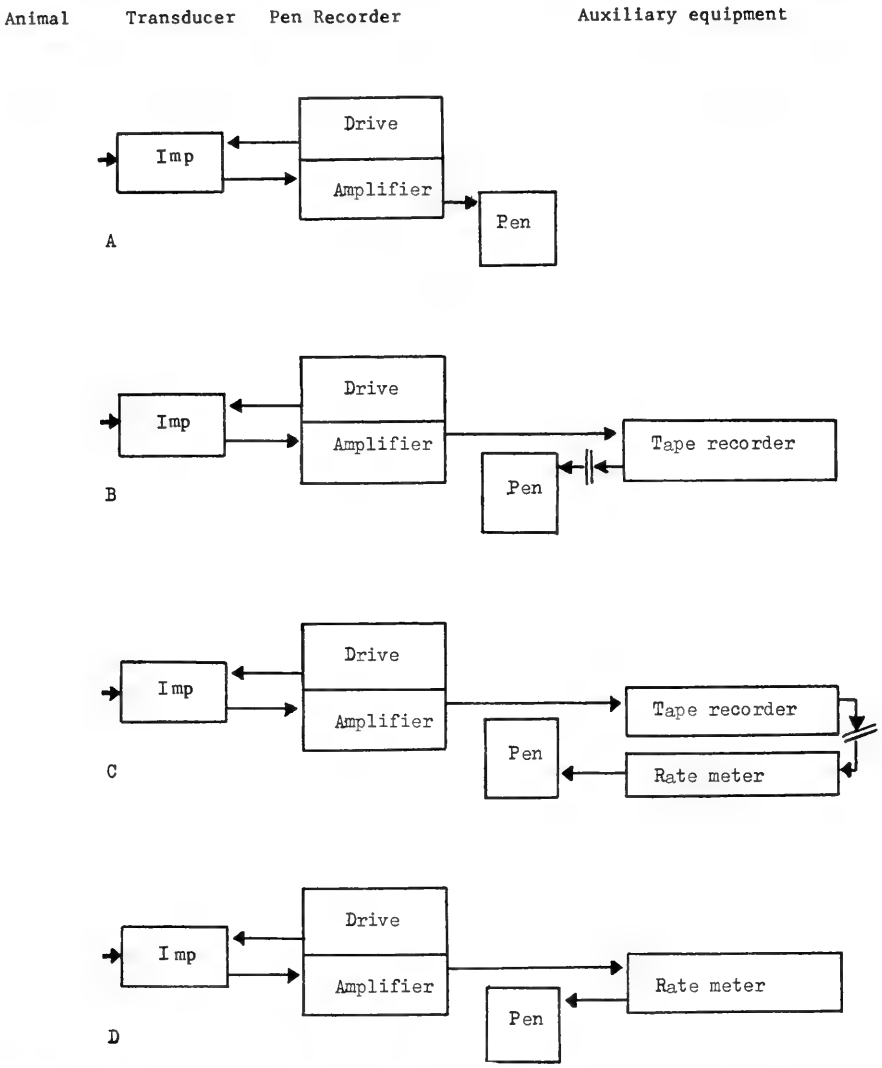

FIG. 1. Diagram showing different recording techniques. The animal (left) is connected to an impedance pneumograph transducer (Imp). Recording equipment comprises transducer drive (Drive), signal amplifier (Amplifier) and pen output (Pen). Broken line after tape recorder indicates replay of tape at any time after recording.

with electrodes inserted in this manner have been used for recordings for at least several weeks in the field and several months in the laboratory. Recordings of pressure in the pericardium and electrocardiographs confirmed that the heart beat was being satisfactorily recorded. This general technique and the same transducer may be used to record activity in any part of small sessile invertebrates, e.g., barnacles (Blatchford, 1970), dependent on the position of implantation of the electrodes.

The electrodes were joined to the impedance pneumograph by fine twin core flexible screened cable (Fig. 1a). Lengths of up to 100 m are used so that the mollusc can be in the sea some distance away from the recording instrument. The number of animals sampled continuously was limited to the number of pneumographs and recording

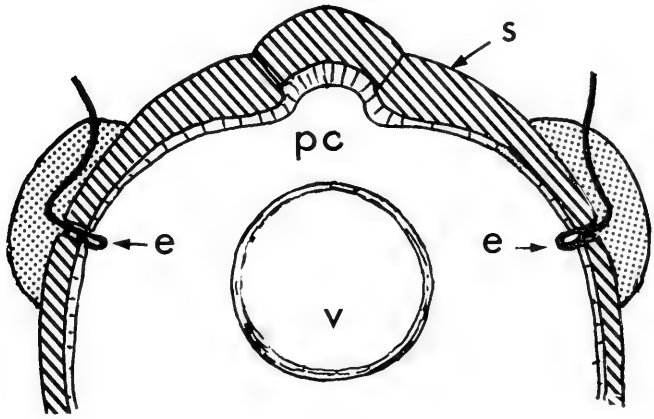

FIG. 2. Diagram of transverse section of the pericardium (pc) of a bivalve showing location of electrodes (e) passing through the shell (s) on either side of the ventricle (v) and embedded in wax (stipple).

channels available on the pen recorder.

Using this technique recordings of heart beat such as shown in Fig. 3 were obtained. Analysis of these traces is easy over relatively short periods and, although examination of continual recordings of long duration is feasible, it is rather exhausting. One modification involves the replacement of the usual pen output by a long playing tape recorder (Phillips ANA - LOG 7) (Fig. 1b) which can store up to 7 channels of information on tape and runs for about 12 hours unattended. Such tapes can be analysed at a later date either by means of sample periods being transferred to paper or by means of a Nielson Instantaneous Ratemeter (Devices Instruments Ltd) (Fig. 1c). It is possible to analyse tapes very rapidly by speeding up the tape recorder provided a steady record has been obtained free of electrical interference. When the ratemeter output is fed into the pen recorder a time/rate curve is produced (Fig. 4). Finally this system may be modified to record the heart rate instantaneously by elimination of the tape recorder (Fig. 1d).

EXPERIMENTAL RESULTS

The regular rhythm of the heart beat is typically recorded from a bivalve as shown for *Isognomon* (Fig. 3c) either during continual immersion in the sea or in the laboratory. These recordings may be readily obtained from all species of bivalves. Similar recordings may be taken from polyplacophorans and gastropods (Figs. 3a and b) with the electrodes inserted through the shell into the pericardium about 1 cm apart. This technique also gave perfectly satisfactory results with bivalves, although electrodes are generally placed 1 through each valve. No problems were encountered in using this technique on the large West Indian *Chiton tuberculatus* L. except that it was difficult to drill through the thick and tough shell. Recordings were also easily obtained from *Patella vulgata* L. (Jones, 1968), but gastropods with coiled shells are more difficult. It is possible to produce traces from the heart of *Helix*, but movement of the viscera within the shell when the foot is protracted makes the technique very difficult in this class.

The amplitude of heart beat recorded remains at approximately the same amplitude for successive beats due to the impedance change between a pair of electrodes being

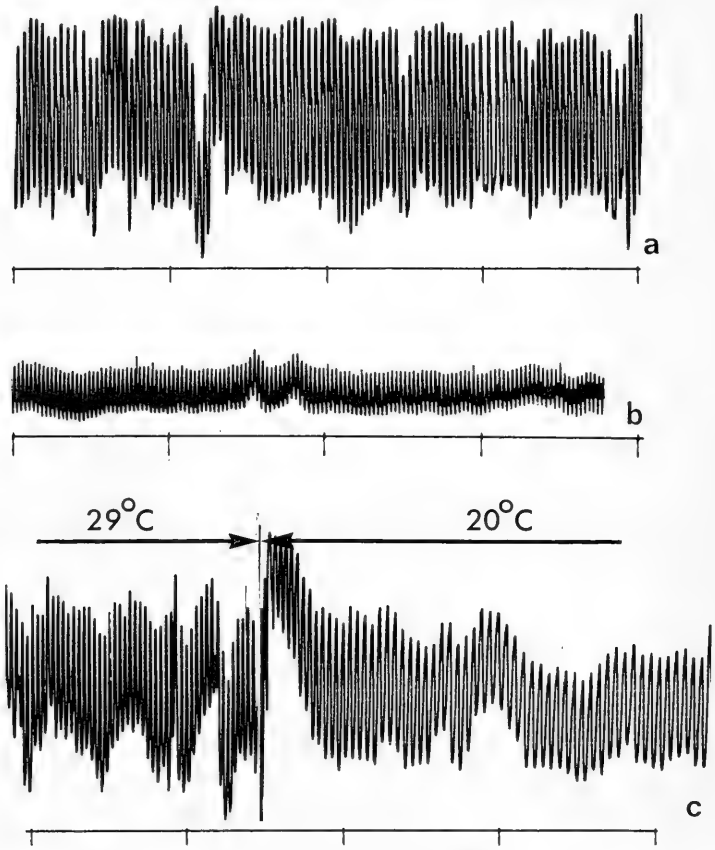

FIG. 3. Examples of recordings of the heart beat of a, *Chiton tuberculatus*; b, *Patella vulgata*; c, *Isognomon alatus*. The latter shows the immediate effect of change of temperature on heart rate. Time traces in minutes.

constant for similar contractions. It is not possible to calibrate the traces in respect of amplitude of deflection, but it is reasonable to assume that an increased amplitude of deflection represents a larger contraction and a greater heart output. This commonly occurs after a littoral bivalve, e.g., *Cardium*, has been reimmersed by the tide (Trueman, 1967). However, with a constant amplitude of contraction the base line of the recordings may fluctuate. A downward deflection of the trace indicates a reduction of impedance between the electrodes and conversely an increase for an upward swing. Thus adduction of the valves of Bivalvia gives rise to a negative spike (Fig. 5 A) whereas pedal retraction may produce a positive deflection in all classes. The latter is probably shown centrally in the recording from *Patella* (Fig. 3b).

During continual immersion many bivalves exhibit little change in heart rate in respect of tidal or light changes (Trueman & Lowe, 1972) but respond rapidly to changes in water temperature. This is shown for *Isognomon alatus* (Gmelin) in respect of a rapid drop in temperature (Fig. 3c). Fig. 4 illustrates a slow rise of temperature for *Anodonta*, recorded by thermistor probe, the recording being made on tape (Fig. 1c) and played back onto paper at a higher speed so as to display events taking place over 160 min. in 5 min. The heart beat at the beginning and near the end of the recording (Fig. 4 A and B) was recorded as a check on the ratemeter values. *Anodonta cygnea* proved particularly suitable for use with the ratemeter since it gave

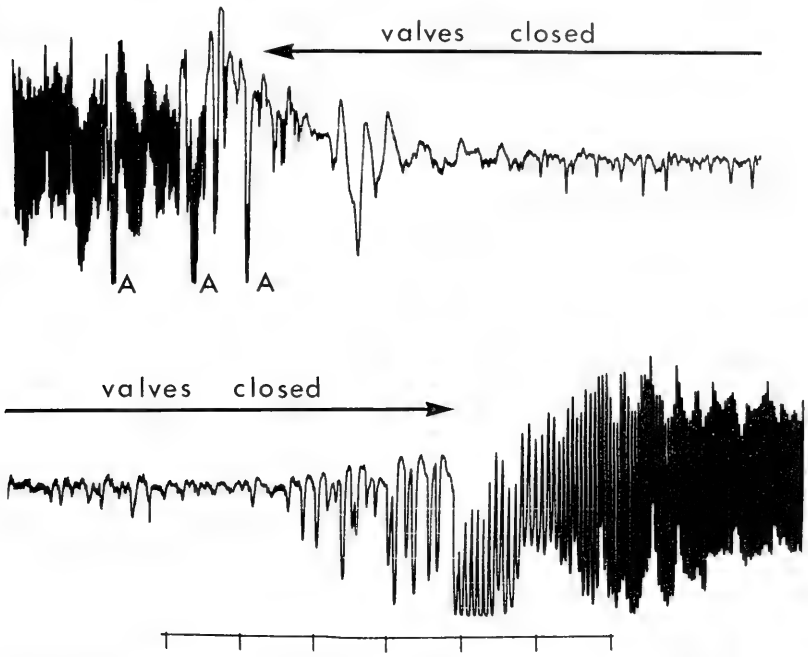

FIG. 4. Recordings of heart rate (beats/min.) using ratemeter and temperature (°C) if ubgakebt water current showing the effect of raising the temperature over a period of 160 min. Actual heart beat at beginning and end of period shown in A and B respectively.

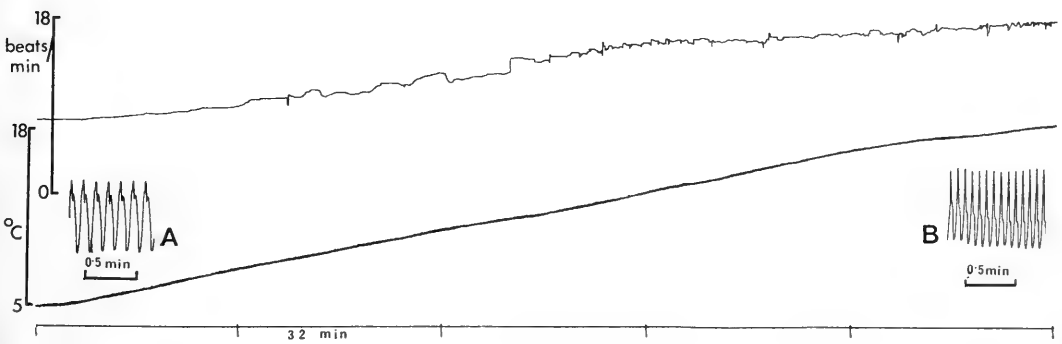

FIG. 5. Field recording of heart beat of *Isognomon alatus* during a spontaneous period of valve closure with consequent suppression of the heart. The lower trace follows the upper with an interval of 5 min. Time trace in minutes. A, adduction of valves.

a heart record with a steady base line and near constant amplitude. Traces showing major fluctuations as in Fig. 5 are as yet unsuited for this technique for they require continual adjustment of the ratemeter.

Long term recordings of bivalves constantly immersed may commonly show little short term fluctuation of activity but in some, e.g., *Isognomon alatus*, the valves may

remain closed for a short time. This occurs after several adductions, and the heart almost completely ceases to beat. It may be noted that the heart commences to beat more strongly before the valves reopen, possibly to ensure circulation of the blood through the gills to meet the new inhalent water current (Trueman & Lowe, 1971). Analysis of these valve movements over 7 day periods shows little obvious correlation to environmental factors and more exhaustive recordings are required to investigate this feature further.

DISCUSSION

The techniques described afford a means of long term monitoring of the activity of sessile invertebrates in their natural habit. Some results of preliminary investigations are already available (Helm & Trueman, 1967; Jones, 1968; Trueman & Lowe, 1971) and it is hoped to considerably extend these in the near future by use of the ratemeter technique. Before such recordings can be understood in terms of the animal's response to environmental change, extensive laboratory recordings are required under constant conditions so that the effect of isolated factors such as temperature, light, salinity or food may be studied. The results of some such investigations are already in press (Lowe & Trueman, 1972; Coleman & Trueman, 1971).

One of the snags of this method is that a continuous record is obtained of a single animal or, even if several channels of the recording equipment are used, only of a small number of animals. Preliminary experiments indicate that it may be possible to monitor up to 12 animals on a single channel by automatically switching from one to another. This would enable a statistically significant section of a population to be sampled over long periods and the seasonal effects of breeding and fluctuating food supplies to be studied.

Preliminary experiments with *Anodonta* have indicated that the normal heart rate and activity is suppressed when water is chlorinated. Further studies are clearly required on the effects of environmental changes and of pollution. If the heart rate and activity of bivalves are sensitive to pollutants then it is tempting to suggest that these animals could be used as living environmental sensors. But this will require the development of the techniques described here and a much greater understanding of the animals' reactions to environmental changes.

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PROC. FOURTH EUROP. MALAC. CONGR.

RECHERCHES SUR L'ECHAUFFEMENT DE *CEPAEA NEMORALIS* (L.) PAR L'ENERGIE RAYONNEE

M. C. Garcia

Laboratoire de Zoologie, Ecole Normale Supérieure, Paris, France

Des observations dans la nature ont amené à penser que les températures extrêmes supportées par les *Cepaea nemoralis* dans quelques milieux aux conditions climatiques ou microclimatiques assez rudes pourraient être à l'origine d'une action sélective du milieu vis-à-vis de quelques phénotypes. C'est pour essayer de répondre en partie à cette hypothèse que nous avons entrepris cette étude.

Nous avons fait, fondamentalement, deux types d'expériences: d'une part, l'échauffement d'escargots placés directement au soleil, d'autre part, l'étude de la variation de leur température, par l'action de l'énergie rayonnée par une ampoule Mazdasol de 150 à 300 watts, placée dans une enceinte en bois. Nous avons considéré non seulement les animaux vivants mais aussi deux séries d'essais d'échauffement de coquilles vidées de leurs corps et constituant des échantillons statistiquement homogènes quant à la taille, à la hauteur et au poids, c'est-à-dire donc aussi quant à l'épaisseur de la coquille; il est évident que, dans ces conditions, on écarte encore tous les éléments concernant la variabilité du corps de l'animal, due notamment à sa masse et à sa pigmentation, aussi bien qu'à son comportement physiologique. Pour notre étude nous avons choisi deux séries de coquilles, les premières de la race des Pyrénées, grandes et épaisses, les autres de petite taille et de faible calcification, et nous les avons remplies d'un certain volume d'agar-agar à 2% (3,5 cc pour la première série; 2 cc pour la seconde).

Dans les expériences d'ensoleillement direct, on utilisa à chaque fois un lot d'individus de taille approximativement égale, appartenant à différents phénotypes d'une même population. Les escargots étaient attachés à une plaque en bois par des bracelets en caoutchouc, l'apex tourné vers le haut. Les expériences furent toujours réalisées au mois de juillet entre 11 et 16 heures et permettaient l'enregistrement de la température du pied au moyen de thermocouples introduits dans les coquilles (Fig. 1).

Dans tous les autres cas, nous avons utilisé une enceinte en bois à dimensions variables selon le type d'expérience; au plafond, on plaçait une ampoule Mazdasol et l'on disposait à la base une plaque circulaire - plan de travail - sur laquelle avaient été creusées, au préalable, de petites encoches où l'on attachait les escargots (Fig. 2 à 4).

Dans les expériences de type I, l'échauffement se fait par intermittence, c'est-à-dire qu'il y a un mécanisme thermostaté qui coupe le courant de l'ampoule chaque fois que la température de la sonde, placée à l'intérieur de l'enceinte, atteint un certain niveau. Nous avons utilisé une enceinte de 44 x 44 x 58 cm avec une ampoule de 150 ou 250 watts et adopté des températures allant de 39 à 42°C; l'homogénéisation thermique au niveau des emplacements à escargots se faisait au moyen d'un mouvement circulaire uniforme du plan de travail (2,5 tours/min.).

Dans les expériences de type II, on disposait d'une grande enceinte (61 x 61 x 104 cm), d'une ampoule de 300 watts et d'un élément étalon pour le contrôle thermique; on enregistrait la température de quelques individus placés à des endroits du plan de travail soumis à un même échauffement. On a considéré des escargots à épiphragme épais et d'autres ne renfermant pas d'épiphragme calcifié.

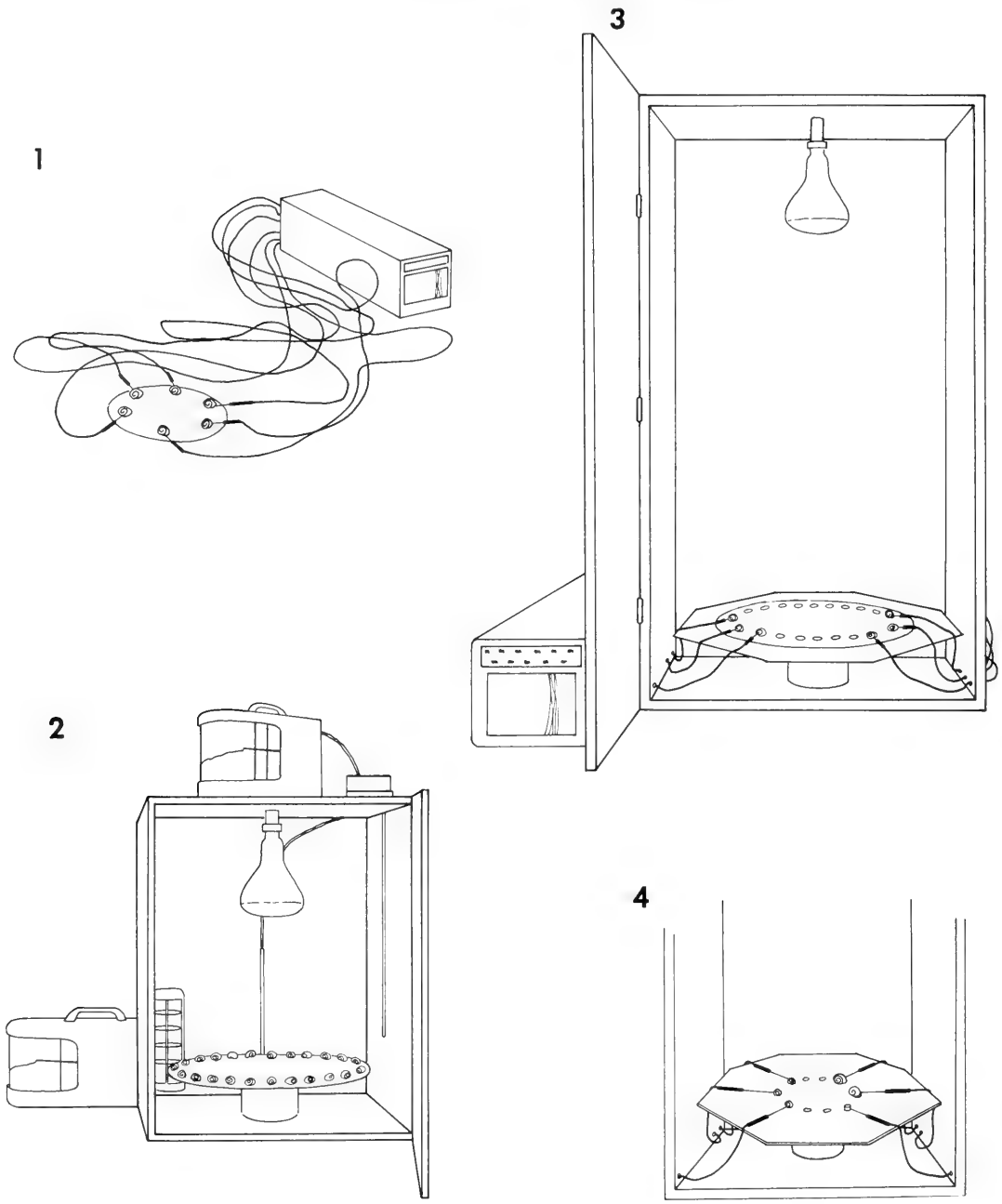


FIG. 1. Schéma du dispositif utilisé dans les expériences d'échauffement d'escargots par le soleil avec enregistrement de température.

FIG. 2. Schéma du dispositif utilisé dans les expériences de type I.

FIG. 3. Schéma du dispositif adopté dans les expériences de type II.

FIG. 4. Plan de travail utilisé dans les expériences d'échauffement de coquilles.

TABLEAU 1. Mortalité totale observée chez des escargots des Basses Pyrénées soumis à échauffement par l'énergie rayonnée par une ampoule Mazdasol, pendant 15 jours après l'expérience.

	Jaunes		Roses	
	00000	12345	00000	12345
Population Y (Sauveterre)	$\frac{36}{60}$ (60,0%)	$\frac{37}{60}$ (61,6%)	$\frac{0}{60}$ (0 %)	$\frac{32}{60}$ (53,3%)
Population D (St Gladie)	$\frac{16}{30}$ (53,3%)	$\frac{20}{30}$ (66,6%)	$\frac{22}{30}$ (73,3%)	$\frac{23}{30}$ (76,6%)
Population E (Mauléon)	$\frac{4}{30}$ (13,3%)	$\frac{20}{30}$ (66,6%)	$\frac{15}{30}$ (50%)	$\frac{30}{30}$ (100%)

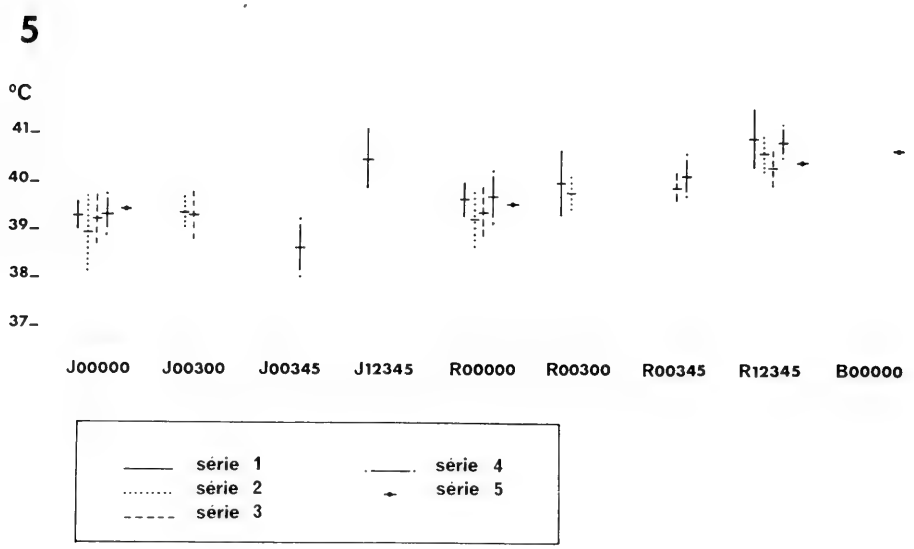
Les expériences de type III ne durent que 12 à 18 min., pendant lesquelles la plaque fait seulement 2 tours; il s'agit d'un échauffement intensif sans enregistrement. L'enceinte est petite (44 x 44 x 58 cm), l'ampoule de 250 watts.

Pour l'échauffement des coquilles on a repris la grande enceinte (61 x 61 x 104 cm). Des éléments utilisés comme étalon nous ont permis de déterminer, au préalable, les emplacements soumis à un même échauffement et de choisir deux groupes de trois encoches chacun, à l'intérieur desquels les conditions d'échauffement étaient identiques. Nous avons donc considéré ensemble les deux séries de coquilles, en sachant que l'une des séries subirait un échauffement plus intense.

Les résultats obtenus (mortalité immédiate, mortalité totale 15 jours après l'expérience, température des individus, perte de poids) sont, au premier abord, très hétérogènes; on trouve en effet des populations où la mortalité se traduit par des chiffres presque opposés pour les différents phénotypes. Parfois, dans des populations très rapprochées géographiquement, d'une même région naturelle, on en trouve une dont un phénotype a une réponse tout à fait inattendue, soit une mortalité en masse, soit, précisément, une résistance à toute épreuve. Ne pouvant pas présenter et discuter ici tous ces résultats, nous nous bornerons à en donner un exemple, celui de trois populations des Basses Pyrénées distantes entre elles de moins de 30 km et à caractères morphologiques identiques (Tableau 1).

Les données obtenues concernant les températures montrent que les formes rayées s'échauffent plus fortement que les sans bandes et que, lorsqu'on compare les phénotypes roses et jaunes, les premiers subissent souvent un plus grand échauffement (Fig. 5, 6); cependant, d'autres caractères particuliers de chaque coquille (épaisseur, intensité de coloration de fond, taille) jouent un rôle aussi important et sont certainement, en partie, l'une des raisons de l'hétérogénéité observée.

La forte épaisseur de la coquille constitue une bonne protection contre la chaleur et les individus déshydratés et à épiphragme bien calcifié, s'ils sont bien protégés contre le dessèchement, sont aussi ceux qui accusent les températures les plus



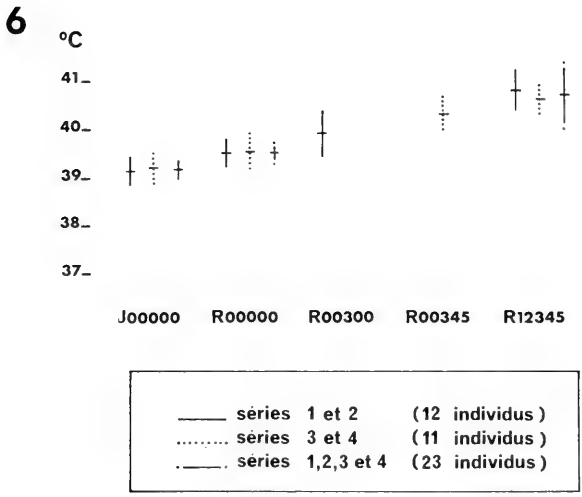


FIG. 5. Représentation graphique des températures enregistrées pendant l'échauffement solaire direct d'escargots de la population de Asson (Hautes-Pyrénées). Le trait horizontal correspond à la moyenne ($m \pm s_m$).

FIG. 6. Représentation graphique des températures enregistrées pendant l'échauffement solaire direct d'escargots de Asson (Hautes-Pyrénées). Grouppement des résultats de différentes series. Le trait horizontal correspond à la moyenne ($m \pm s_m$).

élevées pendant l'échauffement. Ils perdent, en effet, moins de poids pendant l'échauffement mais les formes les plus hydratées trouvent dans la perte d'eau un moyen de régulation de température, si minime soit-elle, qui peut les protéger dans certaines limites.

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RESUME

Pour essayer de déceler l'importance de l'ensoleillement chez les différents phénotypes de *Cepaea nemoralis* L., on a réalisé plusieurs expériences d'échauffement d'escargots de cette espèce, soit par l'énergie solaire directe, soit par le rayonnement d'une ampoule Mazdasol de 150 à 300 watts. On s'est intéressée à plusieurs aspects: mortalité survenue, variation de la température du pied, perte de poids. On a encore considéré deux séries de coquilles, homogènes quant à la taille et au poids, vidées de leurs corps et remplies d'agar-agar à 2% et déterminé leur échauffement différentiel.

Les résultats obtenus sont très hétérogènes mais on peut dire que, dans l'ensemble, les formes avec bandes s'échauffent plus fortement que les formes sans bandes, de même que les phénotypes roses par rapport aux jaunes. D'autres facteurs importants sont aussi l'épaisseur et la taille de la coquille, aussi bien que l'état hydrique de l'animal.

MALACOLOGIA, 1973, 14: 391-392

PROC. FOURTH EUROP. MALAC. CONGR.

ASPECTS OF FEEDING AND GROWTH IN LAND SNAILS

June E. Chatfield

Department of Biology, Portsmouth College of Education
Locksway Road, Portsmouth, U.K.

Although general accounts of food materials are given in the literature, there is relatively little work giving precise details of eating habits of land snails. The present paper investigates feeding and growth in 2 species of helicid snails, one *Monacha cantiana* (Montagu) which lives in open habitats and the other, *Hygromia striolata* (Pfeiffer) which is to be found in both open edge habitats and in woodlands. In some situations (e.g., roadside banks) these 2 species are abundant together in the same plant community.

Microscope studies of faecal strings and gut contents from populations of these 2 snails near Reading, Berkshire, showed that they had fed on a variety of food plants including both green and decaying leaves; the type of food ingested varied with the time of year. More green food was taken during summer.

Some experiments were set up to test the growth of young *Monacha cantiana* and *Hygromia striolata* on various food materials. The snails were collected from a nettle patch on Portsdown Hill near Portsmouth during September and November 1970. They were kept in petri dishes and provided with food, moisture and chalk. The foods were green leaves of *Armoracia rusticana* (horseradish), lettuce, beech litter, oak litter and filter paper; each snail had access to only 1 type of food. The lip of the shell was marked with black waterproof ink and subsequent growth of new shell measured using a calibrated micrometer eye-piece.

The results of the experiments (Fig. 1) showed that only specimens of *Monacha cantiana* and *Hygromia striolata* which had fed on green leaf material showed any

TABLE 1. Food plants identified in the gut contents of *Monacha cantiana* and *Hygromia striolata* feeding in their natural habitat. The snails were collected from a number of sites in Berkshire and Surrey.

Monacha cantiana	*Hygromia striolata*
Urtica dioica	*Urtica dioica*
Lamium album	*Lamium album*
Anthriscus sylvestris	-
Heracleum sphondylium	-
Cirsium arvense	-
Glechoma hederacea	*Glechoma hederacea*
-	*Mercurialis perennis*
-	*Fagus sylvatica* litter
Brachypodium pinnatum	-
Dactylis glomerata	-
Grasses undetermined	Grasses undetermined
Flower petals	-
Fungal hyphae	Fungal hyphae

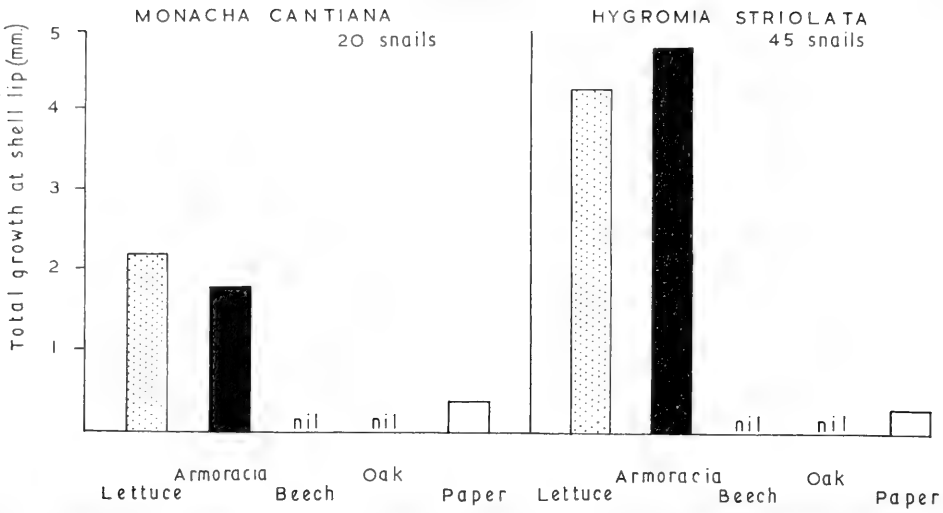

FIG. 1. Diagram to show the total growth at the shell lip of *Monacha cantiana* and *Hygromia striolata* during 3 weeks at 9-22 C. The specimens of *Monacha cantiana* were 6.5-11.5 mm shell diameter and *Hygromia striolata* were 5.0-10.0 mm.

continued growth of new shell. No growth was recorded in specimens feeding on beech or oak litter and negligible growth on filter paper. All the food materials were acceptable and readily ingested by the snails. Growth of snails kept on leaf litter was restored when the diet was changed to lettuce.

It is evident from this investigation that the snails will eat most available food materials in their environment, but different foods ingested in the same quantity have different growth potential.

RESUME

Cet exposé décrit des recherches sur la nourriture et la croissance des deux espèces d'escargots helicidés, *Monacha cantiana* et *Hygromia striolata*, qui habitent les talus au bord des routes.

Les jeunes escargots étaient nourris d'un seul genre de nourriture, d'humidité et de craie. Afin de mesurer la croissance consécutive, on marqua le péristome de la coquille avec de l'encre. Les deux espèces grandissaient lorsqu'elles mangeaient des feuilles vertes de laitue et de raifort. Cependant, nourries de feuilles mortes de hêtre ou de chêne, elles ne grandissaient point et nourries de papier filtre, elles grandissaient très peu. Néanmoins les jeunes escargots acceptaient et mangeaient toute les nourritures qu'on leur offrait. Ceux qu'on avait nourris de feuilles mortes de hêtre ou de chêne recommencèrent à grandir dès qu'on leur offrit de la laitue.

MALACOLOGIA, 1973, 14: 393-395

PROC. FOURTH EUROP. MALAC. CONGR.

DER EINFLUSS VON TEMPERATUR UND PHOTOPERIODE AUF DEN LEBENSZYKLUS EINIGER SÜSSWASSERPULMONATEN[1]

Gerhard Imhof

II. Zoolog. Institut, Universität Wien, Austria

ABSTRACT

The infraspecific variability in life-cycles of freshwater pulmonates raises the question about the influence of temperature and photoperiodism on growth and reproduction. Groups of 4 species of lymnaeids and planorbids reared under controlled conditions showed some capacity for active growth regulation in relation to temperature within the range prevailing during the warm season - this capacity being developed during the early postembryonic growth. Above specific threshold values there is no correlation between temperature level and the intensity of spawning. Photoperiodism does not influence growth, but lengthening of daylight stimulates spawning in lymnaeids, and if combined with a rise in temperature, in planorbids, too. Whereas growth and reproduction continues steadily under constant conditions, distinct activity periods exist in the natural life-cycle which can be induced by imitating the natural course of seasonal climatic conditions in the laboratory. These results lead to the conclusion that the natural life-cycle is controlled by a sequence of climatic conditions, and that any intrinsic seasonal rhythm must be synchronized by the periodicity of temperature and daylight to become effective.

ZUSAMMENFASSUNG

Wie aus Arbeiten verschiedener Autoren der letzten 2 Jahrzehnte bekannt ist, zeigen die Lebenszyklen der Süsswasserpulmonaten eine starke infraspezifische Variabilität, welche sich auf die Anzahl der Generationen pro Jahr, die Jahreszeit des stärksten Wachstums und der Reproduktion, sowie die bei Beginn der Eiablage erreichte Grösse erstreckt. Zur Klärung der Frage, wieweit klimatische Faktoren für die Steuerung der Lebenszyklen von Populationen verschiedener Standorte verantwortlich sind, wurden experimentelle Untersuchungen über den Einfluss von Temperatur und Photoperiodik auf Wachstum und Reproduktion in Aquarienkulturen unter kontrollierten Bedingungen durchgeführt.

Kohorten von *Lymnaea stagnalis* L., *L. peregra* f. *ovata* Drap., *Planorbarius corneus* (L.) und *Planorbis planorbis* (L.), die vom Ei an bei optimalem Futterangebot unter verschiedenen konstanten Temperaturen aufgezogen wurden, zeigten eine partielle Temperaturunabhängigkeit des Wachstums (Abb. 1). Die Reaktionen auf gebotene Temperaturänderungen im Verlauf des Heranwachsens legen ferner die Schlussfolgerung nahe, dass zumindest eine Anzahl von Süsswasserpulmonaten der gemässigten Zone innerhalb des vorherrschenden sommerlichen Temperaturbereiches zu aktiver Wachstumsregulation befähigt sind, welche jedoch erst postembryonal ausgebildet wird. Hinsichtlich der Reproduktion bestehen artspezifische Schwellenwerte (zwischen 7° und 12°), unterhalb welcher keine Eiablage stattfindet. Oberhalb derselben wurde keine Korrelation zwischen Beginn und Intensität der Eiproduktion einerseits und der herrschenden Temperatur andererseits gefunden. Während die Tageslichtlänge auf das Wachstum keinen unmittelbaren Einfluss ausübt, zeigten Vergleiche zwischen Kulturen bei Langtag (16 Std.) und solchen bei Kurztag (8 Std.) bei den Lymnaeiden eine reproduktionsfördernde Wirkung des Langtags. Die Eiablage wird auch durch Tageslichtverlängerung stimuliert, ebenso wie durch Temperaturerhöhung, wobei jedoch erstere dominiert, wie kombinierte Versuche zeigten. Bei allen Arten wirkt eine Kombination von Temperaturerhöhung und Tageslichtverlängerung stark stimulierend. Gleichzeitig wurde eine Koppelung zwischen Reproduktion und Wachstum festgestellt, indem induzierte Intensivierung bzw. Abschwächung der Reproduktion eine gleichsinnige Reaktion des Wachstums bewirkt.

Während unter konstanten Bedingungen das Wachstum kontinuierlich verläuft, und die Reproduktion über lange Zeit mit unregelmässigen Intensitätsschwankungen andauert, kann durch künstliche Imitation des natürlichen Jahresganges von Temperatur und Photoperiode der natürliche Lebenszyklus mit distinkten Aktivitätsphasen induziert werden, wie dieser für jede Art aus demographischen Studien im natürlichen Wohngewässer der Versuchstiere (Schilfgürtel des Neusiedlersees/Österreich) bekannt ist (Abb. 2). Aufgrund der experimentellen Ergebnisse lässt sich der natürliche Lebensablauf als eine Folge von Reaktionen auf klimatische Bedingungsabfolgen erklären, und zwar bei der einjährigen Art *L. ovata* vollständig, und bei den übrigen, 2-jährigen Arten (mit je einer frühjährlichen Reproduktionsperiode in den beiden aufeinanderfolgenden Jahren) mit Ausnahme der sommerlichen Stagnation. Als Ursache für letztere kommen neben Erschöpfung nach frühjährlicher Aktivitätskonzentration v.a. ein endogener Jahresrhythmus in Betracht, welcher jedoch nur bei Synchronisation durch den natürlichen Jahresgang von Temperatur und Photoperiode wirksam werden kann.

[1] Die ausführliche Publikation dieser Untersuchungen wird vorraussichtlich in "Oecologia" 1974 erscheinen.

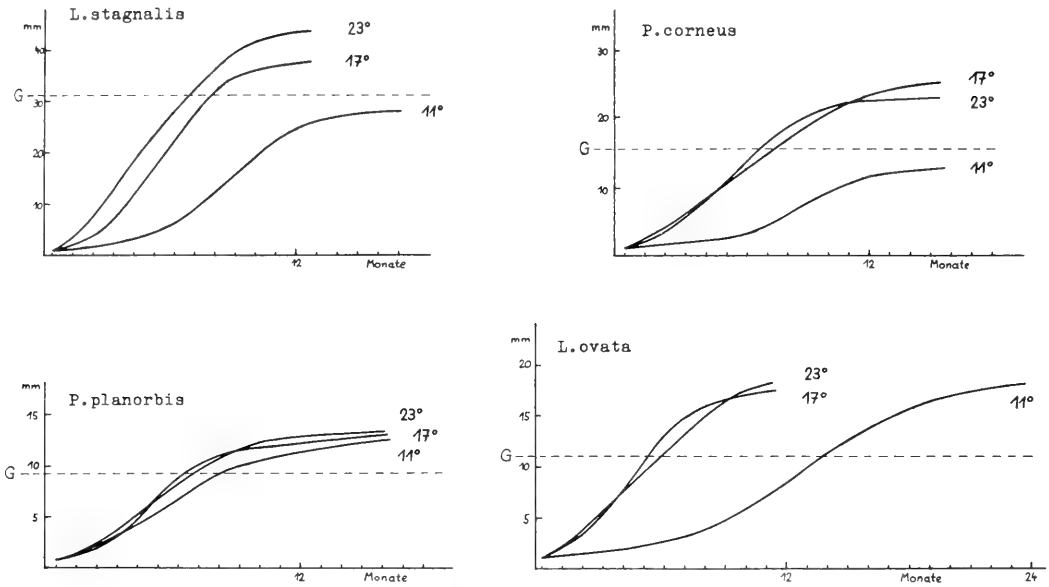

ABB. 1. Mittlere Wachstumsverläufe unter konstanten Bedingungen. Ordinate: lineare Gehäusegrösse; G = mittlere Grösse bei Beginn der Eiablage. - Bei der Versuchstemperatur 5° findet kein Wachstum statt.

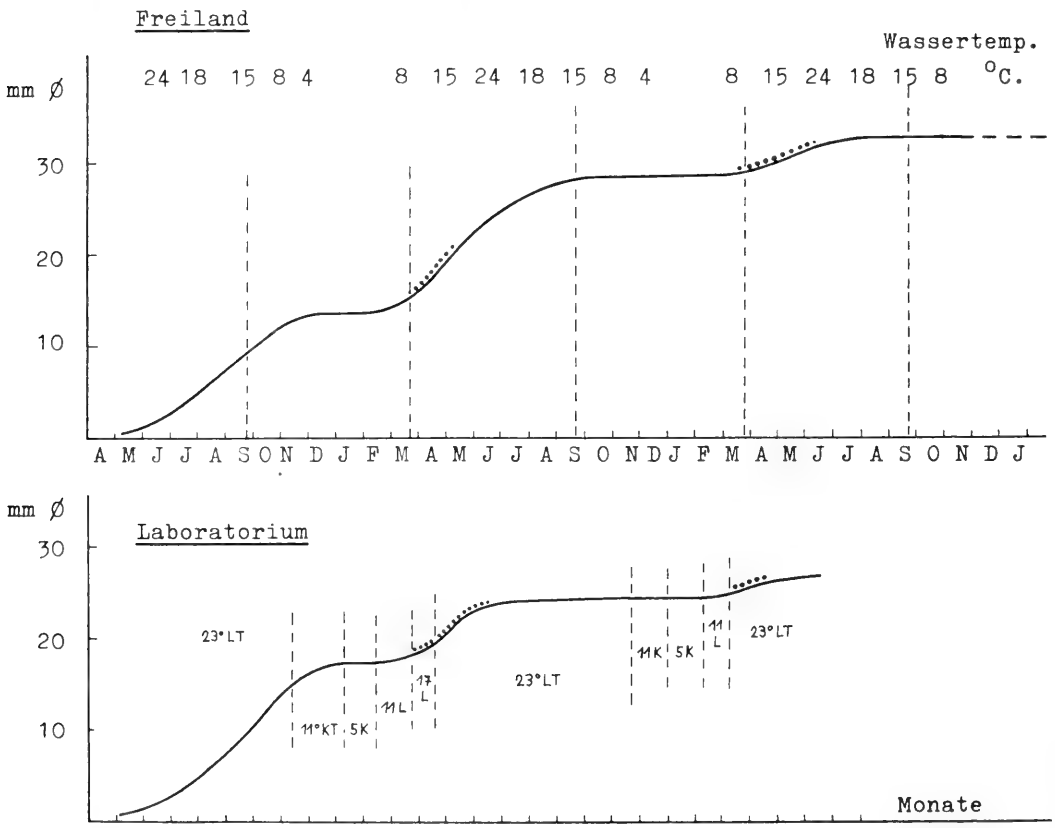

ABB. 2. Vergleich der Wachstumsverläufe und Reproduktionsperioden (Punktierung) einer Generation von *Planorbarius corneus* im Freiland und im Laboratorium (K = Kurztag; L = Langtag).

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MALACOLOGIA, 1973, 14: 395-396

PROC. FOURTH EUROP. MALAC. CONGR.

ACTIVITY PATTERNS OF *LYMNAEA STAGNALIS* (L.) IN RELATION TO TEMPERATURE CONDITIONS: A PRELIMINARY STUDY[1]

S. C. McDonald

Museum of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A.

ABSTRACT

Life is a low-temperature phenomenon. Other things being equal, below-normal temperatures are less damaging to the biochemical integrity of an organism than above-normal temperatures. For this reason, the rapidly expanding use of rivers and lakes for domestic and industrial cooling purposes poses a threat to aquatic life and necessitates the study of the effect of elevated temperatures upon aquatic organisms.

Temperature is an environmentally relevant aspect of an organism's life. It is a major parameter of virtually all biological activities, affecting chemical reaction rates which in turn affect an organism's physiology and ultimately its behaviour. Yet, the thermal problem facing aquatic organisms is not particularly the avoidance of biochemical damage from temperature extremes but rather the maintenance of effective organic integrity by regulating the balance among the rates of various chemical activities. This regulation in poikilotherms, such as the cold-water snail *Lymnaea stagnalis*, must manifest itself in behavioural responses or in changes in activity rates since poikilotherms passively follow the environmental temperature and expend virtually no energy on thermoregulation.

In general, research on the effects of different temperatures on mollusks has dealt with geographic distribution, relative abundance and physiological responses, particularly growth and reproduction. A neglected area of study is that of behavioural responses (Welch & Wojtalik, 1968); especially lacking are quantitative studies of behavioural responses. The aim of this experiment is to provide such a quantitative study.

The long-range objective of this study is to ascertain, quantitatively, the behavioural responses of the cold-water snail *Lymnaea stagnalis* to optimal and to sublethal elevated temperature regimes. The more limited objectives of the preliminary study herein summarized were to ascertain the activity patterns of adult *L. stagnalis:* (1) at an optimal temperature of 20°C, (2) at a sublethal elevated temperature of 30°C; (3) during light and dark phases at each of these 2 temperature regimes; and (4) to test for acclimation to elevated temperature with time. The choice of 20°C as the optimal temperature was based on experimental results obtained by E. G. Berry and Henry van der Schalie (pers. comm., 1969), who found that this temperature was close to the optimum for survival, growth and reproduction for *L. stagnalis* from northern Michigan. The sublethal elevated temperature, 30°C, is reasonably close to the thermal maximum of 35°C ascertained by the author for this population of *L. stagnalis*, as well as being a convenient temperature since most biochemical reaction rates double with each 10°C increase in temperature.

In this preliminary study, 10 snails were maintained at 20°C for 7 days and the temperature was then increased 1°C per hour, a rate consistent with most normal heating records, to 30°C at which temperature the snails were maintained for an additional 7 days. The temperature was then again increased 1°C per hour to the thermal maximum of 35°C and held at this temperature for 3 days, at the end of which time all the snails were dead. Throughout these 17 days, the activities of the snails were recorded on time-lapse

[1]Supported by a research grant (5 T1 AI 41) from the National Institute of Allergy and Infectious Diseases, U. S. Public Health Service.

film at the rate of 1 frame each 30 seconds. The variables measured were temperature, oxygen content, barometric pressure and food supply; the light regime was 12 hours light-12 hours dark.

As a 1st step to interpreting behavioural responses, diurnal activity patterns: breathing, copulating, feeding, ovipositioning, resting and 4 forms of movement (crawling on substrate, floating, gliding on surface film and twisting at the surface with shell uppermost), as well as all snail interactions were analyzed for 3 of the snails at 2 days of each temperature regime. Since the rate of acclimation to higher temperatures is usually rapid, frequently occurring in less than 24 hours (Brett, 1946), it was decided to compare the 2nd day at each temperature, a time at which acclimation should not yet be complete and a later day, the 6th day at each temperature, to ascertain if acclimation occurred with time. Such a form of acclimation would seem a logical adaptation since aquatic organisms are often rhythmic and should be adapted in phase with the normal day (Welch & Wojtalik, 1968) and with the progression of the seasons.

A detailed analysis of the activity patterns of all 10 snails on the 1st day of the study had shown that sequences and rates of activity patterns of individual snails were so different as to preclude summing results or comparing activity patterns of different snails under different temperature regimes and to warrant the detailed analysis of the activity patterns of individual snails through various temperature regimes.

Among the results suggested by this analysis of individual snails are: (1) that overall, the percentage of time spent breathing increased with an increase in temperature; (2) that the percentage of time spent in breathing may be less at night under optimal temperature conditions, but that under conditions of sublethal elevated temperature this tendency may be reversed; (3) that the percentage of time spent in feeding, while greater in darkness by a factor of 2 to 3 under optimal temperature conditions, became markedly reduced under elevated temperature conditions, so that the percentage of time spent feeding under elevated temperature conditions was about the same for both the light and dark phases; (4) that the proportion of time spent in actual movement was usually between 60 and 65% throughout the diurnal cycle showing no change with increase in temperature; but (5) that the rate of change from one activity pattern to another was greatly accelerated by the elevated temperature regime; this was more marked on the 2nd day than on the 6th day (suggesting that, in this aspect, acclimation occurred with time), and moreover (6) that the increase in temperature induced a rhythmicity to certain of the activity patterns, chiefly the set: breathing - crawling - resting - crawling - breathing, so that the actual length of time spent in each of these individual activity patterns was relatively constant whether the set was repeated over a period of 15 minutes or over one of several hours; and (7) that under both temperature regimes, individual snails were observed to be able to distinguish and follow their own slime trails and that although this was observed rather often at 20°C it was a more pronounced occurrence at the elevated temperature, particularly with regard to the set of patterns: breathing - crawling - resting - crawling - breathing, where a snail would be observed repeatedly to follow its own trail between its resting place and the surface of the water.

In order to interpret the above results in a more detailed manner, the activity patterns of more snails are being analyzed for the 4 days already discussed as well as for the 1st days at 20°C, 30°C and 35°C. Moreover, additional studies are now underway to determine the effects of constant versus fluctuating acclimation temperatures on the responses of *Lymnaea stagnalis* to a wide range of sublethal elevated temperatures. These studies are being conducted in a simulated stream and are the next step before taking these studies to an actual field situation. The results of these analyses will be computerized so that more complicated facets of behaviour such as sequential analysis of activity patterns, social interactions and their effect on copulation, and circadian rhythms may also be analyzed.

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MALACOLOGIA, 1973, 14: 397-400

PROC. FOURTH EUROP. MALAC. CONGR.

ISLAND SIZE AND SPECIES DIVERSITY IN PACIFIC ISLAND LAND SNAILS

Alan Solem

Field Museum of Natural History, Chicago, Illinois, U.S.A.

Recent years have seen the development of theoretical biogeography (see MacArthur & Wilson, 1967). Since Preston's demonstration of a close relationship between the size of an area and the number of species inhabiting it, 2 additional biogeographical concepts have become almost axiomatic. First, that faunas have a saturation level, a maximum number of species that can live in a particular place. Second, the MacArthur-Wilson theory that areas will achieve faunal equilibrium, a balance between colonization by new species and some extinction among those already present.

These propositions were developed using data from taxa that represent human introductions, that show rapid colonization and turnover rates, that have a low ratio of island size to species survival area, or where local speciation is absent or at a bare minimum. In their study of the Polynesian ant fauna, Wilson & Taylor (1967) showed that when only the tramp species, those introduced by commerce, were considered, the species-area model was highly predictive, but that inclusion of the native ants found on the islands of American and Western Samoa resulted in skewing the curve drastically upwards.

The Pacific Island land mollusks show perhaps a 95% level of specific endemism, frequently with only 1 of 2 islands or even part of an island comprising the entire range of a species. Studying their patterns of species-area diversity permits examining the situation under conditions of maximal local differentiation where colonization rates apparently are very low. In addition, the Pacific basin is both ancient and stable, with islands having been present since at least the mid-Mesozoic. While virtually none of the islands would have been present for the entire period, there have been specks of dry land present throughout this era and some islands may have a 50,000,000 year history. Evidence from the deep core drillings on Bikini and Eniwetok has demonstrated that there has been more than 5,000' of subsidence in Micronesia since the beginning of the Tertiary, while sea floor mapping has revealed numerous sunken guyots that formerly were elevated stepping stones for dispersal. The great age of the area, high endemicity, and great local speciation present a considerable contrast to the very young islands with rapidly shifting faunas that were used to establish the basic theoretical concepts.

Full testing of species-area diversity requires comprehensive sampling and study of the faunal elements concerned. Unfortunately, while comprehensive samples of the Pacific Island land snail fauna have been made, most of these have not been studied and reported on in the literature. For example, there are 31 described taxa of Hawaiian endodontoid land snails, but collections in the Bishop Museum contain 199-205 species from Hawaii (Solem, unpubl.). Slightly less than 1/6 are recorded in the literature. Fortunately, several of the numerically most important taxa found on the Pacific Islands have been monographed or reviewed utilizing modern systematic concepts and collection resources. The Achatinellidae (Cooke & Kondo, 1960), Partulidae (Kondo, 1968), endodontoid taxa (Solem, in press), and the 2 limacoid families (Helicarionidae and Zonitidae, see H. B. Baker, 1938, 1940, 1941) were used in a comprehensive survey of species diversity on many islands.

In addition, there are some islands whose fauna has been monographed or from which sufficiently extensive collections were available that the total land snail diversity

TABLE 1. Species-area relationships for selected islands

Island	Area in miles^2	Land snail families	Observed species diversity	Calculated diversity	
				$S=10A^{0.27}$	$S=18.6A^{0.63}$
Lord Howe	5	9	51	15	51
Rapa	14.2	8	100	21	99
Upolu	430	10	44	51	848
Oahu	604	8	395	56	1,045
Viti Levu	4,011	10	58	94	3,464

TABLE 2. Mean number of land snail species

Island area in miles^2	under 1,000' elevation	over 1,300' elevation
4.9-8	9.5	34.3
10-15	9.5	31.5
18-28	12.5	20.0
34-60	7.0	16.5
100-225	8.0	21.8

could be estimated with some accuracy. These include Upolu, Western Samoa (Garrett, 1887 and collections made by the author in 1965), Rapa (collections in the Bernice P. Bishop Museum), Lord Howe Island off Australia (Iredale, 1944 as modified by study of collections made in 1963 and type material in the Australian Museum, Sydney to reduce Iredalean species multiplication), Viti Levu, Fiji (Germain, 1932 and collections made in 1971), and Oahu, Hawaiian Islands (data from many sources).

The contrasts in relative species abundance for the well sampled islands are striking, as is their lack of conformity to the predictive formula $S = CA^z$ (where S is the number of species, C a variable constant, A refers to island area, and z is a second variable constant). In its most frequently used form, C is 10 and z is 0.27. Table 1 lists the islands, their areas, the number of native land snail families present, the observed species abundance, the abundance predicted by $S = 10A^{0.27}$, and the numbers predicted by an adjustment in both C and z so that the observed species numbers for both Rapa and Lord Howe Island would be produced. It is obvious that the relative abundance of species does not correlate with island area. This difference cannot be attributed to a new faunal element wiping out forms that are an important group elsewhere. Both Viti Levu and Upolu have the prosobranch family Poteriidae; Lord Howe Island, Upolu and Viti Levu have the prosobranch family Diplommatinidae; Lord Howe and Viti Levu have the Bulimulidae; and Succineidae are found on both Upolu and Oahu. Otherwise the family groups are essentially the same.

If Rapa and Lord Howe Island are assumed to be saturated, then the other islands are markedly "underdiversified."

The question of correlation between island factors and snail diversity does not lie

in terms of area alone. By using data from the recently monographed families, it was possible to gain information of partial species diversity for 57 Polynesian and Micronesian islands (excluding the Hawaiian chain). When the islands were grouped by size, there was a 3 step diversity: under 4 square miles, low diversity; 4.9-225 square miles, a higher, but unchanging level of diversity; 400-4,000 square miles, a slight increase over the 2nd stage. When the islands were grouped by elevation: under 700 feet, low diversity; over 920 feet, high diversity; over 4,300 feet, slight increase in diversity probably associated with these islands being 10 times the size of those in the next lower group.

If island area and elevation are combined in a single analysis (Table 2), it is evident that the primary correlations indicative of high land snail species diversity are: 1) elevation of more than 1,300 feet; and 2) island size between 4.9 and 15 square miles. Two additional correlations can be made: 1) islands nearer the New Guinea-Indonesian core region have markedly lower diversity than islands of equal size located farther out in the Pacific; and 2) more isolated islands such as Lord Howe, Mangareva and Rapa have far greater species level diversity than islands of the same size located within an archipelago.

It is quite probable that predation by the native ants on Viti Levu and Upolu has limited snail diversity, since on Oahu and many Polynesian islands, which lacked any native ants, it is evident that the introduced ants have decimated the native fauna. The meaning of the approximately 1,000 foot elevation triggering higher diversity probably relates to moisture supplies. Higher islands have proportionately much greater rainfall than do lower islands, and islands of under 1,000 feet elevation may have too little or too infrequent rainfall. The isolated islands may attain greater diversity because of less frequent colonization by either competitors or predators. Similarly, the greater land snail diversity on islands 4.9-15 square miles in size may result from absence of competition from some nonmolluscan group or by the absence of some predators that require more than 15 square miles to maintain a breeding population.

All of the above speculations require field observations and experimental data for substantiation or refuting. They may serve to provide a stimulus for further work on the problem of explaining the very different patterns of snail diversity found on Pacific Islands from that predicted by the species-area model and equilibrium theory.

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MALACOLOGIA, 1973, 14: 401-408

PROC. FOURTH EUROP. MALAC. CONGR.

POSSIBLE COMPETITIVE DISPLACEMENT AND EVIDENCE OF HYBRIDIZATION BETWEEN TWO BRAZILIAN SPECIES OF PLANORBID SNAILS[1]

F. S. Barbosa

The World Health Organization, Parasitic Diseases
Division of Communicable Diseases, Geneva, Switzerland

ABSTRACT

Occasional introduction of *Biomphalaria straminea* in an area known for several years to be inhabited exclusively by *B. glabrata*, allowed the study of the behaviour of these closely related planorbid species competing in the same body of water. *B. glabrata* was totally eliminated and substituted by *B. straminea* within a period of 3 years. Four mixed forms collected in the area were interpreted as inter-species hybrids. These however had disappeared by the following year, thus showing their inability to perpetuate themselves in nature. The substitution of *B. glabrata* by *B. straminea* was considered as a possible case of competitive displacement, although only suggestions were made as to the forces which may have favoured *B. straminea*.

INTRODUCTION

The Planorbidae are freshwater snails living in a variety of habitats around the world. Those belonging to the genus *Biomphalaria* are limited in their distribution to the African and American continents and to South West Asia. In the Americas, *Biomphalaria* distribution ranges from the southern part of North America, through Central America, on down to the southern part of South America. On this continent 17 *Biomphalaria* species have been recognized, most of them occurring in the tropical regions. These snails have received special attention since some of them serve as intermediate hosts of schistosomiasis mansoni, an important human disease in several tropical regions of the world.

In north-eastern Brazil, the 2 snail intermediate hosts of *Schistosoma mansoni* are *Biomphalaria glabrata* (Say) and *B. straminea* (Dunker). *B. glabrata* is found in many islands of the West Indies, and in the north and east of South America (Venezuela, Surinam, French Guyana and Brazil), between the latitudes 20°N and 26°S. *B. straminea* exists in Paraguay, Venezuela, the Guyanas and Brazil reaching to about 20°S.

Biomphalaria glabrata and *B. straminea* differ from each other in their morphological features. The differences are few but conspicuous. The genitalia and the renal tube present reliable means of differentiation between the 2 species. The following specific characteristics are considered of particular value. The vagina of *B. glabrata* shows a prominent pouch while that of *B. straminea* presents a typical vaginal corrugation. The ovotestis diverticula in *B. glabrata* are predominantly trifurcate but may be divided into from 2 to 5 branches and only exceptionally may be unbranched. In *B. straminea*, the ovotestis diverticula are usually unbranched, though sometimes bifurcate and occasionally trifurcate. This species lacks a renal ridge which is present in *B. glabrata*. Conchological features are of limited value because they are

[1]This study was carried out by the Research Center "Aggeu Magalhães," Recife, Brazil.

less reliable than the anatomical ones for species identification purposes.

Although *Biomphalaria glabrata* and *B. straminea* occur in the same areas of the coastal region of the State of Pernambuco, these closely related species are very seldom found in the same body of water (Barbosa & Olivier, 1958).

Interspecific crosses have been obtained in the laboratory between allopatric as well as sympatric species of planorbid snails. It has also been shown that the 2 species dealt with in this paper are able to hybridize under laboratory conditions (Barbosa, 1960 and PAHO/WHO, 1968).

The present study was undertaken to determine the circumstances in which isolating mechanisms could be broken down in nature, and to investigate the possible significance of this fact. Much knowledge was gained on the behaviour of the 2 species when competing in the same body of water. The occasional occurrence of certain conditions were found to be of particular value to the present studies.

GENERAL INFORMATION ON THE STUDY AREA

The geographical region known as north-east Brazil includes different physiographical zones. The physiography of Pernambuco is more or less the same as that of north-east Brazil. It has a narrow coastal zone, followed by a zone of low rolling hills which is about 50 to 80 km wide and is continued by a high inland plateau. The littoral zone is just a narrow, sandy strip of land, covered by typical vegetation, and spotted by dunes and mangrove areas. The middle zone was originally covered by tropical forests, now mostly destroyed. The inland plateau, called *caatinga*, is a rough, stony, semi-arid zone with short, spiny vegetation having deciduous leaves. Limited zones with a specific type of vegetation are called *cerrados*.

The temperature in the littoral and forest zones averages about 27°C all the year round, and over a period of 14 years the mean monthly rainfall as given by Olivier & Barbosa (1955) has been : March 156 mm; April 253 mm; May 374 mm; June 293 mm; July 215 mm; and August 161 mm. During the remainder of the year the average monthly rainfall varies from 26 mm to 66 mm. This shows the marked seasonal rainfall cycle in these regions.

Recife, the capital of the state of Pernambuco, is situated on the seacoast, at 8°3'S and 34°51'W. The present study was carried out in a limited area of about 6 km^2 situated on the outskirts of Recife. This low-lying area is mostly covered by coarse grass though parts are irrigated for the cultivation of vegetables. A slow-moving stream crosses it from west to east in the direction of the mangrove swamps. The stream has its source about 6 km inland on a low hill.

At the beginning of the dry season, i.e., usually by the end of September, the water level falls. About a month later there is no more standing water in the fields and at this time aestivating snails, protected by grass or debris, were easily found on the soil. During the wet season, usually from May to September, the fields are filled with water and at the end of the rainy season large populations of *Biomphalaria glabrata* were found all over the area. Most of the active snails were found in the irrigation ditches.

METHODS

From 1952 to 1955 several routine checks were made of the entire area, although at irregular intervals, in order to collect snails needed in different types of laboratory work. *Biomphalaria glabrata* was the only species found in the area. However, in November 1956 a small colony of *B. straminea* was accidentally found thriving in the upper part of the stream crossing the study area, thus providing the author with the

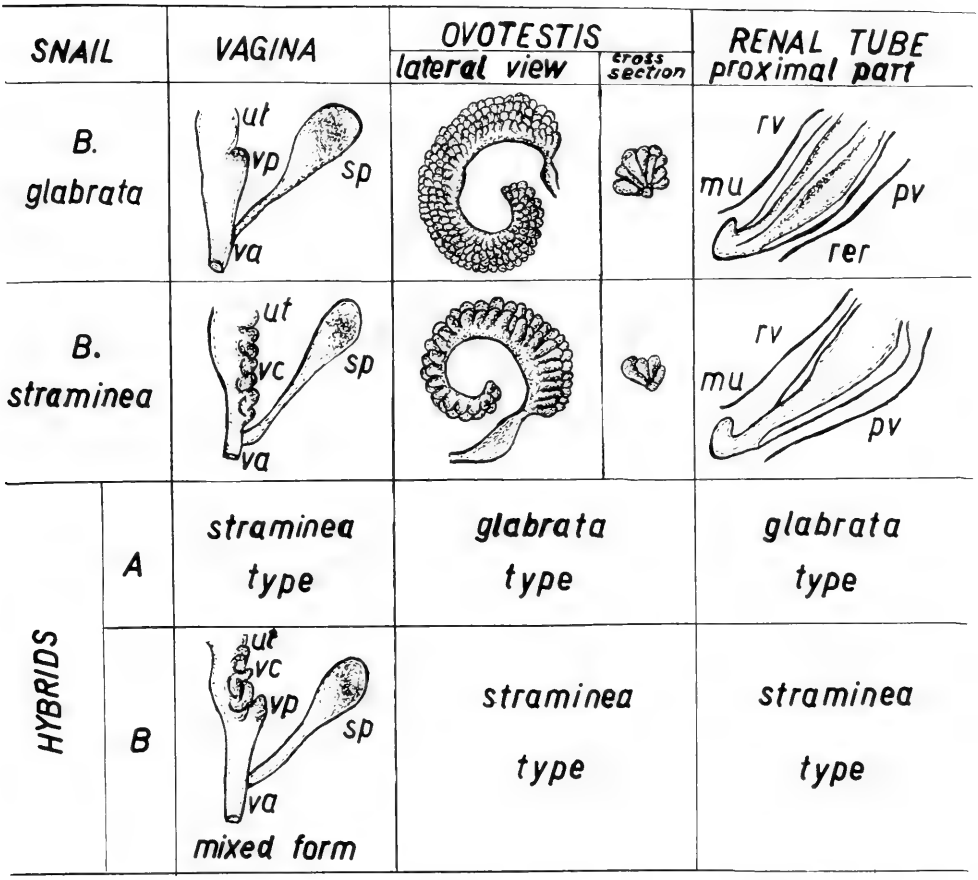

FIG. 1. Comparison of the anatomy of *Biomphalaria glabrata* and *B. straminea* and their hybrids. mu, meatus of ureter; pv, pulmonary vein; rer, renal ridge; rv, renal vein; sp, spermathecal sac; ut, uterus; va, vagina; vc, vaginal corrugation; vp, vaginal pouch.

opportunity of studying the balance between the 2 snail populations. Working on the assumption that the heavy rains of the next wet season would carry the snails downstream, the area was kept under particularly close observation. From 1957, when the 1st specimens of *B. straminea* were found in the study area, until 1960, snails were systematically collected every year during the month of September. A random sample of 10% of the snails collected was dissected for anatomical studies in 1957 and 1958. This figure was raised to 50% in 1959 and 1960. The snail densities were measured once a year during the month of September, just after the rainy season when the snail populations attain higher levels. During 4 weeks (20 working days) 2 carefully trained field workers covered the entire area and collected the snails by using a standard snail scoop consisting of a large perforated metal cup which was dipped into the water every 10 steps down to the bottom of the ditches. The number of snails thus collected was recorded per dip and their average number could then be calculated. Results are presented as "snails per dip." To determine the infection rates, the snails were exposed to a strong source of artificial light for 1 hour during the appropriate time of day, after which they were examined for cercariae.

TABLE 1. Snails collected and examined in the study area during the period 1957-1960.

Year	Snails Collected		Snails examined									
					B. glabrata			*B. straminea*			Mixed forms (hybrids)		
	Total	Per dip	Total	%	Total	Per dip	% infected with *S. mansoni*	Total	Per dip	% infected with *S. mansoni*	Total	Per dip	% infected with *S. mansoni*
1957	3831	19.1	383	10	345	17.1	7.2	38	1.9	0	-	-	-
1958	3503	19.4	350	10	9	0.5	0	337	18.7	0	4	0.2	0
1959	2404	13.3	1202	50	-	-	-	1202	13.3	0	-	-	-
1960	3984	19.7	1892	50	-	-	-	1892	19.7	0.2	-	-	-

RESULTS

Following the discovery of the 1st small colony of *Biomphalaria straminea* in November 1956, the snails were seen migrating to small ditches in the area which drained to the stream's head. At the beginning of 1957 several well established colonies of *B. straminea* were breeding in the ditches all around the head of the stream. The 1st systematic collection made in September 1957 revealed that *B. straminea* had arrived in the low-lying area inhabited by *B. glabrata*. Out of 383 snails collected in the area and examined, 38 were *B. straminea*. It was furthermore observed that all 38 specimens of *B. straminea* came from the same ditch.

During the same period of the following year (1958), 350 snails were examined. *Biomphalaria straminea* was now the predominant species and was found throughout the area. Special attention was paid to the possibility of encountering intermediate forms. The results were as follows: 337 *B. straminea*, 9 *B. glabrata* and 4 intermediate forms. The intermediate forms were submitted to careful morphological studies, which took into consideration the 3 main anatomical characteristics known to be of primary importance in distinguishing the 2 species, i.e., the external surface of the vagina, the branching diverticula of the ovotestis and the upper surface of the renal tube. Two types of mixed forms were seen: A showed a vagina of the *B. straminea* type and glabrata-like ovotestis and renal tube, while B exhibited a vagina of mixed type (i.e., with corrugation plus a pouch) and ovotestis and renal tube of the *straminea* type (Fig. 1).

In 1959 and 1960 only typical *Biomphalaria straminea* were found in the area. For those 2 years random sampling of the snails collected having been increased to 50%, 1202 and 1892 snails were examined respectively, and the 1959 results were confirmed by those obtained in 1960.

Table 1 gives the results for the 4 years 1957-1960.

DISCUSSION

The substitution of a natural population by another, even within restricted limits as in the present study, shows that the balance between the 2 populations was broken in favour of 1 of them. This is a well-known phenomenon which especially occurs when 2 closely related species are involved. The results of the study suggest a competitive displacement of *Biomphalaria glabrata* by *B. straminea*. The ecology of these planorbid snails is not sufficiently known to provide a satisfactory explanation for the gradual replacement of *B. glabrata* by *B. straminea*. Both species are found in a variety of habitats and presumably have similar or identical requirements. The fact that these 2 species, although inhabiting the same region, are never or very seldom found together in the same breeding place (Barbosa & Olivier, 1958) can be explained by the old principle revised by De Bach (1966): "Different species which co-exist indefinitely in the same habitat must have different ecological niches; this is, they must not be ecological homologues." Although the above statement remains true as an ecological principle some evidence has been brought to show that it cannot be generalized. It has been shown that when the environment is not completely uniform in space or in time, prolonged or even indefinite co-existence of competitors is possible.

Pielou (1969) had recently demonstrated that mathematically the indefinitive coexistence of the competing species in a state of stable equilibrium is possible and that, theoretically, co-existence of ecological homologues can happen. On the other hand the well-known classical laboratory experiments of Park (1954) with mixed populations of the flour beetles *Tribolium confusum* and *T. castaneum* are interpreted by Pielou (1969) as an example of competitive displacement between species which

are not ecological homologues.

Although in the present study the phenomenon can be tentatively explained in terms of competitive displacement, the forces favouring *Biomphlaria straminea* remain unknown. Two possibilities can be suggested to explain the break of the population stability of *B. glabrata:* 1) *B. straminea* is much less susceptible to infection with *Schistosoma mansoni*, and this human trematode, which was prevalent in the area, has a definite killing effect on the snails it infects; 2) It has been suggested that *B. straminea* is more resistant to dessication than *B. glabrata*, and the area has a natural cyclic dry season. The above 2 factors might have favoured *B. straminea* in the course of the competitive displacement.

The fact that natural selection may favour an unsusceptible strain of the snail host living together with a susceptible one was pointed out by Hubendick (1958), although at that time he considered this no more than a theoretical possibility. Very recently Richards (1970), studying the genetics of *Biomphalaria glabrata* in the laboratory, suggested that the combination of unsusceptibility to *Schistosoma mansoni* with drought-resistance could speed up the process of favourable selection in temporary habitats. Commenting on the above paper Wright (1971) states that such studies provide a most important basis for a possible method of biological control of schistosomiasis, although he mentions several potential complications that may occur in nature from a purely malacological view of the problem. In the present paper field evidence is brought to show that a snail species combining partial susceptibility to *S. mansoni* with higher drought-resistance can displace in a temporary habitat another species known to be highly susceptible and less resistant to drought.

The genetic relationships among the planorbid snails are not completely understood. Planorbid snail species are known to hybridize under laboratory conditions. In fact it has been shown that in this group interspecific crossings are not uncommon. Experimental crosses between *Biomphalaria straminea* and *B. glabrata* from the same region with the production of fertile offspring, have been recorded (Barbosa, 1960 and PAHO/WHO, 1968). After the prolonged contact of these 2 species in nature, few specimens were found to show the mixed morphological characteristics of interspecific hybrids. Although, in the present instance, the genetic barrier could not completely prevent interspecific hybridization, it is evident that an effective barrier between the 2 species does exist, since the natural hybrids did not perpetuate themselves in nature. The occurrence of occasional hybrids between sympatric species is not a sufficient argument to place in doubt the validity of regarding their parent forms as distinct species.

The only other instance of mixed forms of planorbid species found in nature is that reported by Barbosa (1964) in the State of Rio de Janeiro, Brazil. Out of 498 specimens of *Biomphalaria tenagophila* collected in the area, 2 showed a typical renal ridge which is considered as a specific feature of *B. glabrata.* In 8 other specimens poorly developed renal ridges were found. These observations, although difficult to interpret, suggest the possibility of natural hybridization between the 2 species.

Methods of vector control other than the application of pesticides have lately been coming to the attention of public health workers. The possibility of using different predators, parasites and competitors in the control of the snail intermediate hosts of schistosomiasis is still under consideration. A review of biological control of trematode diseases was recently made by Wright (1968). Although investigations have not been encouraging, some optimistic reports are coming from Puerto Rico (Ruiz-Tiben, Palmer & Ferguson, 1969) on the ability of *Marisa cornuarietis* to act as both predator and competitor of *Biomphalaria glabrata*, the local intermediate host of *Schistosoma mansoni.* A recommendation that studies be continued to assess the value of biological control of the snail intermediate hosts of the schistosomes was recently made by a WHO Expert Committee (1967).

The present paper has shown that a population of 1 species of planorbid snail was accidentally replaced by another. This offers wider perspectives for studies on interaction between freshwater snail species. The phenomenon is not rare in nature (De Bach, 1966) and, besides its basic importance in ecology and evolution, may have substantial significance in the practical field of schistosomiasis control. If we are, on the one hand, largely ignorant of the requirements and behaviour of the planorbid snails, of their homologies and heterogeneities, in other words of their ecological niches, we do know, on the other hand, that some species of *Biomphalaria* are very closely related to one another both morphologically and genetically (Barbosa, 1960 and PAHO/WHO, 1968). In connexion with the foregoing we wish to stress the need for carrying out basic ecological and genetic studies in order to define the characteristics of the natural populations of snail intermediate hosts of schistosomiasis.

RESUME

POSSIBILITE DE DEPLACEMENT COMPETITIF ET MISE EN EVIDENCE D'HYBRIDATION ENTRE DEUX ESPECES BRESILIENNES DE MOLLUSQUES PLANORBIDES

L'introduction occasionnelle de *Biomphalaria straminea* dans une région connue depuis des années comme habitée exclusivement par *B. glabrata* a permis l'étude du comportement de ces deux espèces très voisines de Planorbidés en compétition dans la même pièce d'eau. *B. glabrata* a été totalement éliminé et remplacé par *B. straminea* en moins de trois ans. Quatre formes mixtes récoltées dans la zone de l'étude ont été considérées comme des hybrides; toutefois, elles ont disparu au cours de l'année suivante, prouvant ainsi leur incapacité à se reproduire d'elles-mêmes dans les conditions naturelles. Le remplacement de *B. glabrata* par *B. straminea* est considéré comme un cas probable de déplacement compétitif et des hypothèses sont formulées, concernant les facteurs qui ont pu favoriser *B. straminea*.

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MALACOLOGIA, 1973, 14: 409

PROC. FOURTH EUROP. MALAC. CONGR.

EASTWARD AND WESTWARD DISPERSAL OF TROPICAL PROSOBRANCH LARVAE ACROSS THE MID-ATLANTIC BARRIER

Rudolf S. Scheltema

Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, U.S.A. 02543

ABSTRACT[1]

The dispersal of larvae over long distances depends upon the velocity of ocean currents and the duration of planktonic development. Plankton collections made throughout the tropical Atlantic show that the larvae of shoalwater species from the continental shelf are regularly carried for long distances, and that they can be found in every major ocean current. The larvae of stenothermal tropical forms are carried westward from West Africa on the North and South equatorial currents and eastward from Brazil along the equatorial undercurrent. The genus *Bursa* is an interesting example, as its teleplanic forms are commonly found in both the tropical surface and undercurrent systems. An estimate of the duration of larval life and a knowledge of the current velocity suggest regular exchange of *Bursa* larvae between the continents of South America and Africa.

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[1]The complete text is published under the title "Eastward and Westward dispersal across the tropical Atlantic Ocean of larvae belonging to the genus *Bursa* (Prosobranchia, Mesogastropoda, Bursidae)." Inter. Rev. Gesamten Hydrobiol., 57(6): 877-887.

MALACOLOGIA, 1973, 14: 409

PROC. FOURTH EUROP. MALAC. CONGR.

THE DISTRIBUTION OF THE LAND MOLLUSCS IN THE UPHEAVAL AREA IN THE QUARKEN, AN ARCHIPELAGO IN THE GULF OF BOTHNIA

Ilmari Valovirta

Zoological Museum, University of Helsinki, Finland

SUMMARY[1]

The study area is right at the centre of the land upheaval area in the Northern Baltic, where the earth's crust is rising at a rate of ca. 100 cm a century. The upheaval phenomenon is most evident in the shallow sea area, where new islets continually appear and the area of the existing islands enlarges. This study concerns the distribution and dispersal of 38 land mollusc species living on the islands, which have risen out of the sea. What are the patterns of age diversity, area diversity and isolation diversity at the species and population levels? What are the 1st species to occupy the islets as they emerge, and how quickly can they do so? As the age of an island can be calculated, it is possible to tell the maximum time that a land mollusc species needs to reach the island by some means of passive dispersal (but allowing for the gap between the emergence of the island and the time at which it provides the minimal requirements of the species). There are 385 sample plots on the study area, and the number of mollusc specimens collected is over 50,000.

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[1]A detailed account of this study will be published in "Annales zoologici Fennici."

MALACOLOGIA, 1973, 14: 411-413

PROC. FOURTH EUROP. MALAC. CONGR.

THE EUROPEAN INVERTEBRATE SURVEY

John Heath

Biological Records Centre, Monks Wood Experimental Station, Abbots Ripton Huntingdon, England

The value of detailed distribution maps of species as aids to nature conservation, ecology and natural history was first clearly demonstrated when the "Atlas of the British Flora" was published in 1962. The methods developed for the production of these botanical maps have now been refined and are being used by the Biological Records Centre, which is part of the Nature Conservancy's Monks Wood Experimental Station near Huntingdon, for the preparation of maps of various animal groups. For the maps of Britain the basis of all the schemes is to indicate by means of a conventional symbol the presence of each species in each 10 km square of the appropriate map grid, i.e., British National Grid, Irish Grid or Universal Transverse Mercator Grid. The use of grid squares means that comparisons of one area with another are always made using units of equal size. As there are 3600 such squares in the British Isles the mapping of a group of 100 species could involve the handling of upwards of 2 million individual records. In addition to field records, museum and literature records are frequently used as supporting data. Each record of a particular species is stored on magnetic tape at the Atlas 2 computer centre in Cambridge. The records are entered and access to them is by means of a remote teletype terminal at Monks Wood. For map making a special set of 80 column punch cards is prepared by the computer. These cards then produce the map mechanically on a specially modified electric typewriter (IBM 866) controlled by an automatic card reading machine (IBM 836).

In planning a mapping scheme, whether it be for a continent the size of Europe, or a small island, 2 main factors govern the size of the recording area. The 1st consideration must be the fineness of detail required to give a proper picture of the distribution of the organism concerned, and the 2nd is the number of recorders available for the survey. As the maps must obviously be as up-to-date as possible, the survey period should be kept as short as possible. For Britain, it is considered that 10 years is a realistic time for a survey involving 1,000 recorders, i.e., with each recorder being responsible for an average of four 10 km squares. With smaller areas in Britain the tetrad (2 km x 2 km square) has been adopted by botanists for county floras, and entomologists are using a square of 5 km x 5 km for such mobile insects as the Lepidoptera. At the county (province, canton) level these are considered to give sufficient detail for the pattern of distribution to be resolved. However, on small islands where there is a great diversity of habitat it may be desirable to use a 1 km or even 500 m square as the standard recording unit.

The collection of data for the British National schemes is usually organised by the relevant national biological society, e.g., the Conchological Society is responsible for the mapping of Mollusca, whilst the Biological Records Centre advises, processes the data, and produces the maps. When organizing field recording, the aim should be the compilation of species lists, as complete as possible, for each of the squares being used as the basis of the scheme. For this purpose 3 special cards can be used, namely 1) a Field Card, normally 20 cm x 13 cm, on which is printed the species list of the group concerned in alphabetical order, with the names abbreviated if necessary. In use the recorder completes 1 of these cards for each square by crossing through

the name of the species being recorded; 2) an Individual Record Card (a specially printed punch card which can be handled directly by the data processing machinery) on which 1 species can be recorded from 1 square, together with other information, e.g., status, rarity, stage, etc. and 3) a One Species Card, again 20 cm x 13 cm in size, on which 1 species can be recorded from any number of squares. For each square a Field Card can be used as a Master Card on which all the records received from the square can, after checking, be summarized. In this way duplication can be eliminated. The distribution maps can then be plotted either mechanically, or by hand directly from the master cards. A unique feature of this method is that at the same time situation maps can be produced showing the completeness of the survey by indicating (using a suitable scale) the number of species recorded in each square. Thus meaning can be given to incomplete data.

When using this method all the recorder is asked to do is to record the presence of the species in a square printed on a map of the area. No counting of individuals or other sophisticated recording techniques are needed and therefore it gives a standard method which can be used by anyone able to identify the organisms being surveyed. This considerably reduces the sampling errors which frequently complicate the assesment of the results of biological surveys. To ensure absolute accuracy for every record is impossible, but checks can be made by 1) referring records to a local expert who will indicate those which require verification, 2) by specialist examination of material from the critical groups and 3) by noting and checking outlying records when maps are produced. Lists of critical species have been prepared for all the groups which are being surveyed by the Biological Records Centre, and Guides to the Identification of these, containing illustrated keys, are being produced. Additionally training courses for amateur naturalists are organised each year which provide basic instruction in the techniques of identification and field sampling methods.

These surveys also result in the identification of those species in need of protection. Repeat surveys carried out at regular, e.g., 5 year, intervals enable changes in distribution and status to be shown. With these sort of data a much more effective case can be made for the introduction of conservation legislation by the authorities than with existing subjective assessments of possible threats to wildlife.

The success of these British schemes resulted in 1965 in the setting up of the international project for mapping European vascular plants with a secretariat in Helsinki and in 1969 the initiation jointly by the Biological Records Centre and Professor Jean Leclercq at Gembloux, Belgium of the European Invertebrate Survey.

The objectives of this are: 1) the compilation of lists of verified zoogeographic data which can be used for map making and statistical studies; 2) the publication and interpretation of distribution maps based on the U.T.M. grid, with 50 km squares being used for all Europe and 10 km or 5 km squares for those countries and regions where more detailed surveys have been carried out; and 3) to encourage the setting up of records centres in all countries.

Already 4 parts of the Atlas Provisoire des Insectes de Belgique and 1 part of the Atlas Provisoire des Arthropodes non Insectes de Belgique and the 1st part of the Provisional Atlas of the Insects of the British Isles have been published. Records centres have been or are being set up in France, Belgium, Netherlands, Luxembourg, Germany, Denmark, Sweden and Finland. The Biological Records Centre at Huntingdon together with Prof. Leclercq's department at Gembloux are acting as co-ordinating centres. All invertebrate zoologists, both professional and amateur, are invited to participate in this project. Of all the group of plants and animals the mollusca are probably the easiest to survey and I hope that one of the results of this conference will be the setting up of an integrated European scheme to map this group.

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MALACOLOGIA, 1973, 14: 414

PROC. FOURTH EUROP. MALAC. CONGR.

VORSCHLÄGE ZUR ERFASSUNG DER MITTELEUROPÄISCHEN MOLLUSKEN

H. Ant

Hamm, Deutschland

ZUSAMMENFASSUNG

Die faunistische Erforschung Europas ist in vielen Gebieten und für manche Tiergruppen schon recht weit gediehen. Die zunehmende Einengung natürlicher Biotope lässt es geboten erscheinen, eine genaue Erfassung aller Arten und ihrer Verbreitung so schnell wie möglich in Angriff zu nehmen. Dieses Problem ist in Europa bereits verschiedentlich erörtert worden; auch sind Ansätze für eine Kartierung der Wirbellosen vorhanden. Es sei erinnert an die Floristische Kartierung Mitteleuropas, die Erfassung der Wirbellosen in England und Frankreich sowie der Beginn einer Kartierung und Erfassung der Mollusken Englands.

Es scheint daher dringend erforderlich zu sein, dass die UNITAS MALACOLOGICA EUROPAEA ein allgemeines Programm zur Erfassung aller europäischen Mollusken aufstellt. Hier wird vorgeschlagen: 1, Zusammenarbeit der bereits tätigen Organisationen, Institutionen oder Privatpersonen; Bildung einer besonderen Kommission. 2, Aufstellung einer Check-List für Europa. 3, Erarbeitung von genauen Arbeitsanweisungen und Arbeitsunterlagen (Kartenmaterial etc.). 4, Aufstellung einer Liste der Arten, deren Kartierung vordringlich erscheint (z.b., *Vertigo moulinsiana*, *Margaritifera margaritifera*, *Candidula unifasciata*). Hierbei sollten vor allem Arten Berücksichtigung finden, deren Biotope gegenwärtig und in Zukunft besonders gefährdet sind.

MALACOLOGIA, 1973, 14: 415-418

PROC. FOURTH EUROP. MALAC. CONGR.

SUR QUELQUES *PISIDIUM* HAUT-ALPINS

*Adrien Jayet

Laboratoire de Paléontologie, Université de Genève, Suisse

La faune des *Pisidium* alpins est très mal connue; les observations demeurent sporadiques, elles demandent en effet de forts déplacements à des altitudes variées et sur des distances considérables. Ces faits expliquent dans une certaine mesure le manque d'intérêt des malacologistes pour ce groupe de Lamellibranches; nos propres observations ont été faites au cours d'excursions géologiques.

Les matériaux que nous utilisons ont été récoltés par Jules Favre, par ses collaborateurs, enfin par nous même; ils sont déposés au Museum d'histoire naturelle de Genève, les déterminations sont celles de J. Favre.

Les notes qui suivent sont, par la force des choses, très incomplètes. En les publiant nous avons pour but essentiel d'attirer l'attention sur le groupe des *Pisidium*, leur étude systématique apporte aussi bien dans le domaine de la Biologie que dans celui de la Paléontologie une multitude de précieux renseignements.

La zone alpine qui nous retiendra est comprise entre 2000 et 2800 m. La caractéristique en est que les nappes d'eau sont recouvertes de glace pendant une grande partie de l'année, très spécialement la sous-zone de 2500-2800 m. Cette dernière est située au-dessus de la limite des arbres tandis que la sous-zone 2000-2500 m est presque toujours dans la région des forêts. Au point de vue géographique les localités indiquées se rapportent à la zone pennique du Valais, aux Grisons et à la Haute-Savoie.

Les nappes d'eau fréquentées par les *Pisidium* sont des lacs, souvent de dimensions très réduites, des marais, des ruisseaux de caractère torrentiel, enfin des mares artificielles et des fossés. Jusqu'à présent aucune recherche n'a été faite, à ma connaissance, dans la zone profonde des lacs alpins. Nos documents proviennent donc seulement de la zone littorale ou encore des eaux peu profondes des cours d'eau.

Dans la zone pennique du Valais, les sédiments, dérivant de roches métamorphiques, sont des sables, ils sont peu favorables et ce n'est que dans les plages limoneuses et terreuses, au voisinage de la végétation que l'on peut trouver des *Pisidium*.

Pour l'instant nos connaissances se bornent à trois espèces, soit: *P. casertanum* Poli, *P. hibernicum* Westerlund, *P. personatum* Malm. Ce nombre très faible d'espèces s'augmentera certainement par la suite comme semble le prouver la découverte de *P. lapponicum* Clessin en Engadine, de *P. nitidum* Jenyns dans le lac Champex, etc.

Répartition en verticale. Des 17 localités d'où proviennent les *Pisidium* haut-alpins de la collection J. Favre, 8 sont comprises entre 2000-2500 m et 9 au delà soit de 2500-2800 m. Nous indiquons ci-dessous et pour chaque espèce ces localités par ordre d'altitude croissant.

Pisidium casertanum Poli

Amont de Mauvoisin 2002 m (Val de Bagnes, Valais), Champlong 2200 m (V. d'Entremont, Valais); Valsorey 2350 m (V. d'Entremont, Valais); Val Scarl 2350-2400 m (Grisons); Chanrion 2470 m (V. de Bagnes, Valais); Stellisee 2453 m (région de Zermatt, Valais); Combe des Planards 2550 m V. d'Entremont, Valais; Schwartzsee 2556 m (r. de Zermatt, Valais); Ofenpass 2600 m (Grisons); Riffelsee 2780 m (R. de Zermatt, Valais).

Pisidium hibernicum Westerlund

Col. d'Anterne 2000 m (Haute-Savoie); Valsorey 2350 m (V. d'Entremont, Valais);

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*Deceased

Schwartzsee 2556 m (r. de Zermatt, Valais); Forclettaz 2600 m (Val d'Annivers, Valais).

Pisidium personatum Malm

Les Vergys 2000 m (Haute-Savoie); Stellisee 2543 m (r. de Zermatt, Valais); fond de la combe des Planards 2800 m (V. d'Entremont, Valais).

Morphologie

La coquille des *Pisidium* haut-alpins est le seul élément dont nous avons eu à nous occuper, elle est très semblable à celle des espèces de la plaine. Il faut toutefois signaler quelques différences entre les unes et les autres. Dans la plaine les différentes formes ou variétés se groupent autour de trois principaux modes de variation: a) formes typiques, b) formes pondéreuses, c) formes rabougries.

Chez les *Pisidium* haut-alpins nous n'avons pas constaté de formes pondéreuses, celles-ci exigent des températures régulièrement élevées et une forte teneur de l'eau en carbonate de calcium. Nous n'avons pas non plus constaté de formes très rabougries, ce qui signifie que les *Pisidium* se situent au voisinage du type.

Toutefois il se dégage d'un examen détaillé un certain nombre de traits communs à tous les *Pisidium* de haute altitude, traits qui les distinguent de ceux de la plaine. Notre attention avait été attirée par J. Favre sur un trait caractéristique de *P. hibernicum* haut-alpin, il avait appelé cette forme *P. hibernicum* var. *giganteum* mais sans en donner une description, nous compléterons ce point ci-dessous. A la suite de la remarque de J. Favre nous nous sommes demandé si les deux autres espèces ne présenteraient pas aussi des formes plus grandes que le type et tel est bien le cas.

P. casertanum Poli

Les individus adultes du Valsorey mesurent 4 à 4,8 mm avec une moyenne de 4,3 mm. Par contre les formes de la plaine mesurent 3,5 à 4 mm pour les formes typiques. Il semble donc bien que les *P. casertanum* alpins soient plus grands que leurs congénères de la plaine.

P. hibernicum Westerlund var. *giganteum* J. Favre

Les dimensions des adultes de Valsorey (2350 m) varient de 3,2 à 3,8 mm. Par contre le type de la plaine mesure de 2,5 à 3 mm, ce qui justifie bien l'appellation de J. Favre. Nous ajoutons la diagnose succinte suivante: test mince, stries d'accroissement déjà visibles sur la protodyssoconque, forme un peu moins équilatérale que le type, par conséquent un peu plus allongée dans le sens transversal.

P. personatum Malm

D'après J. Favre les individus que nous avions récoltés à la combe des Planards à 2800 m correspondent à une "curieuse forme à galbe ovale". Les dimensions varient de 3,5 à 4 mm avec une moyenne de 3,7 mm. Là encore la forme alpine diffère du type de plaine qui mesure 3 à 3,6 mm.

La tendance des *Pisidium* haut-alpins à une augmentation de la taille est donc générale, elle entraîne de part et d'autre du crochet une certaine inégalité, la partie antérieure étant plus développée que la postérieure; en d'autres termes elle devient moins équilatérale.

Il s'agit maintenant d'examiner un problème important. A considérer le climat alpin on doit penser qu'il se rapproche plus que d'autres de celui qui devait régner à la fin de l'extension glaciaire (fin du Würm, période dite Dryas des palynologues). Lors de cette période les conditions climatiques sont rudes, elles se traduisent pour les *Pisidium* par une modification de la croissance de la coquille, Celle-ci se fait par à coups, ce sont des arrêts de croissance ou d'une façon plus simple des irrégularités de croissance. Elles déterminent un profil irrégulier en zig-zag alors que ce

dernier est régulièrement convexe chez les formes normales. Dans la plaine, les espèces atteintes d'irrégularités de croissance sont celles du Pléistocène récent, on les considère souvent comme des espèces reliques. Ce sont *P. lapponicum* Clessin (ou *P. obtusale* C. Pfeiffer var. *lapponicum* Clessin), *P. hibernicum* Westerlund, *P. lilljeborgi* Clessin.

Des trois espèces haut-alpines, c'est donc *P. hibernicum* qui devrait présenter le phénomène des arrêts de croissance, or nous constatons qu'il n'en est rien ou plus exactement que ces irrégularités sont si faibles qu'elles se fondent dans celles des stries d'accroissement.

Un autre caractère est celui de la charnière. Celle des *Pisidium* haut-alpins est toujours mince, les dents cardinales et latérales sont développées normalement mais sans exagération, leur allure se rapproche un peu de celle des formes rabougries de la plaine.

En résumé, les formes de haute altitude se distinguent de celles de la plaine par leurs dimensions un peu plus fortes, leur coquille et leur charnière minces. Elles sont d'allure très uniformes et ne présentent pas la gamme de variations que l'on observe ailleurs, elles témoignent donc d'un biotope particulièrement homogène.

Age de la pénétration des *Pisidium* dans la région alpine

Il est difficile de connaître exactement les phases du peuplement actuel des Alpes, qu'il s'agisse de la faune ou de la flore. On peut toutefois supposer qu'il s'est effectué au cours du retrait glaciaire würmien. La géologie indique pour le glacier du Rhône un front glaciaire en amont de Villeneuve qui pourrait correspondre à la période magdalénienne. Ce serait alors au cours de la période suivante, au Mésolithique que se situeraient les principales étapes du retrait glaciaire dans la vallée du Rhône valaisan et ce serait aussi l'âge du peuplement des Alpes par la végétation et par les faunes.

Une constatation vient à l'appui de cette manière de voir. Dans la plaine les formes reliques disparaissent à la fin du Pléistocène avant le Mésolithique quoique certaines se soient maintenues dans des milieux particulièrement favorables tels que le Léman. La raison de la pauvreté en *Pisidium* des régions haut-alpines pourrait bien s'expliquer par le fait que le retrait glaciaire a été particulièrement tardif dans les hautes régions.

Un autre fait vient appuyer cette opinion; à l'heure actuelle c'est le *P. casertanum* que pénètre partout dans les nappes d'eau crées artificiellement, fossés, canaux, petits lacs artificiels. Le même fait s'observe dans des régions d'altitude moindre, Jura, Salève, etc. D'après J. Favre (1927) ce *Pisidium* est rare dans les dépôts postglaciaires anciens, c'est donc pour les Alpes une espèce d'introduction relativement récente mais qui manifeste un grand pouvoir d'extension, la liste des localités qui le contiennent en fait foi; il est encore possible que la période actuelle de réchauffement lui soit particulièrement favorable.

CONCLUSIONS

Les espèces de *Pisidium* haut-alpins sont peu nombreuses, les observations ne donnent à ce jour que trois espèces soit *P. casertanum*, *P. hibernicum*, *P. personatum*, mais les recherches futures augmenteront certainement ce nombre.

Tous les milieux aquatiques de la zone 2000-2800 m peuvent abriter des *Pisidium*, toutefois les milieux sableux leur sont contraires.

Au point de vue morphologique, les *Pisidium* haut-alpins présentent des formes un peu plus grandes que celles de la plaine, la variété *giganteum* de *P. hibernicum* en est un bon exemple. La coquille est mince, la charnière étroite, avec les dents cardinales et latérales elle rappelle un peu celle des formes rabougries de la plaine.

Il n'y a pas ou très peu d'irrégularités de croissance.

Le peuplement des Alpes en *Pisidium* s'est probablement poursuivi pendant l'extrême fin du Pléistocène, au cours du Mésolithique et des périodes plus récentes. Le *P. casertanum* est le plus répandu et son extension se poursuit actuellement tandis que *P. hibernicum* fait figure d'espèce relique. Le *P. personatum* reste encore le plus mal connu.

Il faut insister sur l'intérêt que présenteraient des recherches systématiquement poursuivies, les quelques observations exposées ci-dessus doivent être considérées comme un aperçu très incomplet et en quelque sorte préliminaire.

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MALACOLOGIA, 1973, 14: 419-425

PROC. FOURTH EUROP. MALAC. CONGR.

DISTRIBUTION PATTERNS OF THE GENUS *GULELLA* (GASTROPODA PULMONATA: STREPTAXIDAE) IN SOUTHERN AFRICA

A. C. van Bruggen

Department of Systematic Zoology of the University
c/o Rijksmuseum van Natuurlijke Historie, Leiden, Holland

The genus *Gulella* L. Pfeiffer 1856 consists of small (length of shell 1.5-22 mm) carnivorous snails which as a rule belong to the cryptofauna of various types of forest and savanna. The genus is distributed over much of sub-Saharan Africa and adjacent islands except in really arid areas; however, some species have even been obtained in Somalia and South West Africa. Outside Africa the genus is sparsely represented on the Comoro Is., Aldabra Is., Seychelles Is., Mauritius and Madagascar. The shells are usually pupiform and as a rule supply stable and reliable characters, mainly in the arrangement and number of denticles and other processes in the aperture, and in the shape and costulation of the shell. Radula and genitalia so far have contributed little of real taxonomic value. The genus is very diverse and hundreds of species are known from the African continent. Connolly's monograph (1939) enumerates 123 species south of the Zambezi and Cunene Rivers which number is approximately correct because of additional species and (expected) synonymies. The synonymy ratio (cf. Boss, 1971: 83, 86) appears to be low and stands at 1.4/1, but may increase to 1.5/1. The present author has undertaken a revision of these species and the results given below are in the nature of a summary interim report on distribution data.

The distribution of the genus in Southern Africa is shown in Fig. 1. Only marginal localities marking the western limits have been indicated. The main range of *Gulella* in the southern parts of Africa lies east of the line Swellendam-Somerset East-Cradock-Middelburg (C.P.)-Bloemfontein-Kroonstad-Potchefstroom-Rustenburg-Mount Mohapaani[1]-Blouberg-Matopos-Khami-Victoria Falls. Outside this area we have only 3 records for 1 species from South West Africa (Otavi Highlands, Omaruru District, Diab River) and 1 for a closely allied form from the dry parts of the north-central Cape Province (Prieska). South West Africa is malacologically comparatively well-known so that *Gulella* may occur here only in scattered localities. Lack of records west of the line on the map is probably due to the lack of suitable habitats and perhaps in addition to a dearth of collectors. Much of Botswana (Bechuanaland), South West Africa and the northwestern districts of the Cape Province are obviously too arid for *Gulella*, while on the other hand species of the genus may be expected to occur in certain malacologically poorly explored regions of Botswana (e.g., Ngamiland) and South West Africa (e.g., Caprivi Strip). Most of the area inhabited by *Gulella* in Southern Africa has a rainfall in excess of 20 inches (= 500 mm) per annum, although obviously a lower rainfall definitely does not prevent a few species from surviving in sheltered localities (e.g., Kruger National Park). Attention is drawn to the course of the line in Fig. 1, which line only pretends to be an approximation as regards the local western boundary of the genus. In the southern part of the range the real boundary is probably the watershed of the Drakensberg range separating the fairly

[1]Not in Botswana (Bechuanaland), but in the Transvaal (*fide* Van Bruggen, 1969: 28); *Gulella miniata* (Krauss) therefore has to be expunged from the Botswana list (Van Bruggen, 1966a: 110), so that there are at present as yet no records for the genus from that country.

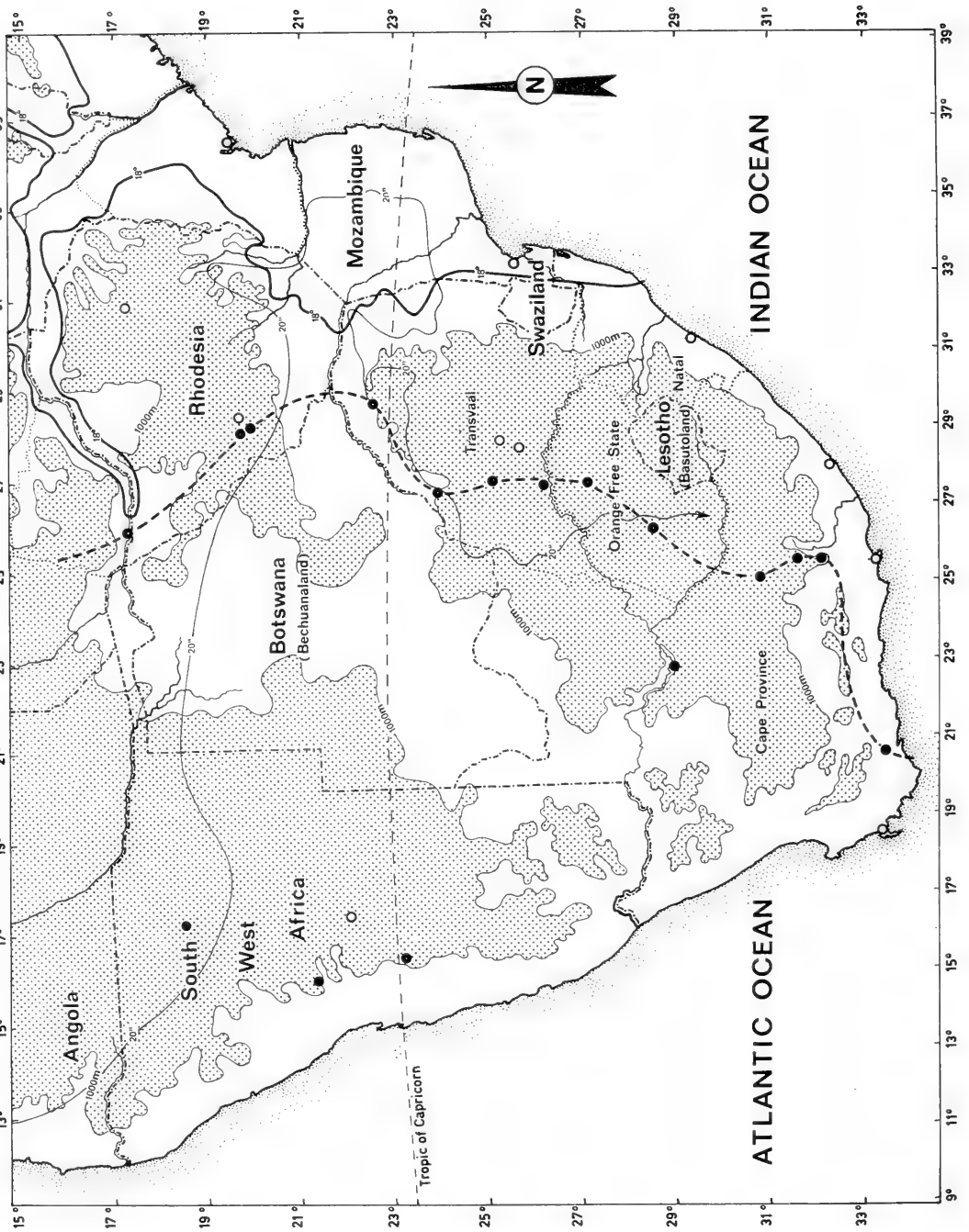

FIG. 1. Map of Southern Africa showing the western limits of the genus *Gulella* (heavy broken line); note 4 isolated localities west of the line. Contour line of 1000 m, isohyet of 20 inches = 500 mm mean annual rainfall, and mean 18°C July isotherm also indicated. H. Heijn del.

humid eastern coastal area and the dry Karoo northwest of the mountains, while in the eastern Transvaal the boundary may follow the various isohyets very closely. Actually the Limpopo River valley on the borders of the Transvaal and Rhodesia forms an arid corridor, thereby interrupting the distribution of various fauna elements on both sides of the river. Consequently the line between the Blouberg and the Matopos should follow part of the 20 inches isohyet eastward around the Limpopo River through Mozambique rather than connect the above 2 localities with an almost straight line.

Scattered occurrence west of the line may be explained by a reduction in rainfall since the last pluvial or hypothermal (cool-humid) period (cf. Van Bruggen, 1969: 75). Therefore one might consider occurrence outside the main range to be of a relict nature. Indeed, the 1 species from South West Africa, the status of which is as yet uncertain (for the time being recorded s.n. *Gulella caryatis diabensis* Connolly), is probably closely allied to a fairly widely distributed species which is adapted to comparatively arid conditions as shown by its distribution along the western limits of the genus in South Africa. Incidentally, this is the species recorded from Prieska: *G. caryatis* (Melvill & Ponsonby).

East of the line there is a fair to large amount of rainfall and various types of vegetation exist suitable to species of *Gulella*. The genus is of tropical origin and there is a rapid decline in number of species from north to south in a markedly narrowing belt along the east coast east of the main watershed in the form of the Drakensberg range. Approximately 50 species occur in the Cape Province, many of which only penetrate as far south as the northeastern part of the province (Pondoland). The southernmost record for the genus is at about 34°S (Swellendam).

Although it may seem somewhat dangerous to draw up distribution patterns of small snails in Southern Africa, one should realize that this part of Africa is comparatively well-collected in this respect; hundreds of specimens in a very large number of samples, mainly belonging to the Natal Museum (Pietermaritzburg, South Africa), warrant at least careful consideration.

Only 5 species or 4% of the total are not endemic to the Southern African subregion, i.e., are also found north of the Zambezi River. *Gulella rhodesiana* (Connolly) is only found in the northern Transvaal and on both banks of the Zambezi at the Victoria Falls. The other 4 are among the few really widely distributed species, viz., *G. gouldi* (Pfeiffer) from the eastern Cape Province (Bathurst: 33°30'S 26°50'E) to Zululand (Ndumu Game Reserve, Ndumu hamlet: 27°56'S 32°16'E), and the Usambaras (about 5°09'S 38°36'E) in continental Tanzania; *G. planidens* (Von Martens) from the Rhodesia-Mozambique eastern escarpment (Lundi and Vila Péry respectively) to continental Tanzania, Uganda and Congo-Kinshasa, and westward to Senegal (probably the most widely distributed species in the genus if not in the family[2]); *G. sexdentata* (Von Martens) from Zululand to Tanzania (including Zanzibar); *G. vicina* (Smith) from the Rhodesian eastern escarpment (Mount Selinda) to Kenya, Uganda and Congo-Kinshasa.

Three of these (if not all) are to be divided into well-marked subspecies, *Gulella gouldi* even into geographically widely separated forms (2 in Southern Africa, 1 in Tanzania), which fact may also be due to changes in the climate of Africa. Generally variation on a subspecific level is uncommon among Southern African *Gulella*, only 8 such species at present being known: the 4 above-mentioned non-endemic and widely distributed species in addition to *G. caryatis* (see above), *G. crassidens* (Pfeiffer), *G. darglensis* (Melvill & Ponsonby) and *G. elliptica* (Melvill & Ponsonby). A few more such species may be discovered in the course of current investigations.

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[2]The greatest distance over which the range of *Gulella planidens* extends is approximately 6000 km or 3800 miles; compare *G. vicina* with about 2500 km or 1500 miles.

All above non-endemics, except for *Gulella gouldi*, belong to the tropical element in Southern Africa, i.e., are unknown south of the Limpopo and Tugela Rivers. Incidentally, the distribution pattern of *G. gouldi* in South Africa is a typical "collector's pattern" in Natal; it closely follows the coastal road where there is a string of seaside resorts from the southern borders of the province to the banks of the Tugela River, while from Durban inland it follows the main road through Pietermaritzburg to Johannesburg. Nevertheless it somehow conveys a picture of the distribution of the species and allows for more or less reliable extrapolation as to its occurrence outside the main roads. One may, for example, expect it to occur throughout much of the lower parts of Natal and Zululand, which may also apply to its range in the eastern Cape Province (cf. Van Bruggen, 1969: 44, fig. 15).

Roughly 20% of the species are at present only known from their type localities, which may be due to poor collecting but also to endemism, particularly with reference to physiographical conditions. Many endemic species do not conform to a geographical pattern and may indeed be poorly collected taxa; on the other hand certain patterns are quite obvious and are moreover confirmed by similar patterns in other groups of animals. The broken Drakensberg range in the Transvaal, Rhodesia and Mozambique shows some striking patterns as far as *Gulella* is concerned. Four separate regions are isolated by low-lying and much drier country: south and north of the Olifants River, the Zoutpansberg area and the Rhodesia-Mozambique eastern escarpment, each with 2-5 endemics in addition to 0-5 other species. The major part of these regions is over 1000 m or 3000 ft. Thus a fair number of species with numberous processes and intricate patterns in the aperture and with a very limited distribution (frequently at higher altitudes) probably are products of geographical isolation. An example of this is *G. viae* Burnup, a minute costulate species known only from about 2500 to 8000 ft. in parts of the Drakensberg range in Natal and the Transvaal.

The relationships of such endemic species are sometimes complicated and therefore not easily explained. Some species showing unique dental patterns are obviously so highly specialized that it is clear that these species are taxonomically more or less isolated and speculation as to their ancestry seems premature. Others clearly show relationships, such as those of the widely distributed and intricately interrelated *Gulella infans* (Craven) group, which probably has various derivatives in the upland forests.

There is also possibly a relationship between *Gulella crassilabris* (Craven), *G. distincta* (Melvill & Ponsonby) and *G. sibasana* Connolly (Fig. 2). These species are largely allopatric, except for the 1st 2 which occur side by side in the central districts of the Kruger National Park (Van Bruggen, 1966b: 385, fig. 64), thereby proving their separate identities. It is possible that these species are derived from a common ancestor, although it is a moot point whether the forest dweller *G. sibasana* is closer to the ancestor than the 2 inhabitants of the much drier and somewhat lower areas. In view of the fact that Southern Africa now experiences an interpluvial (warm-dry) period (Van Bruggen, 1969: 75) it may be more plausible to consider *G. crassilabris* and *G. distincta* offshoots of *G. sibasana* rather than otherwise. In this case the mountain forest environment has certainly a longer and more continuous history than the much drier mid- and lowlands of the Transvaal, or, conversely, when the forest contracted with the onset of another dry period *G. crassilabris* and *G. distincta* must have adapted themselves in geographically separated areas to a drier climate and resultant vegetation, which allowed them to stay where they were and possibly even to increase their range, thereby coming in contact with each other in the eastern Transvaal (Kruger National Park). In this context we may perhaps consider the *G. sibasana* complex a superspecies.

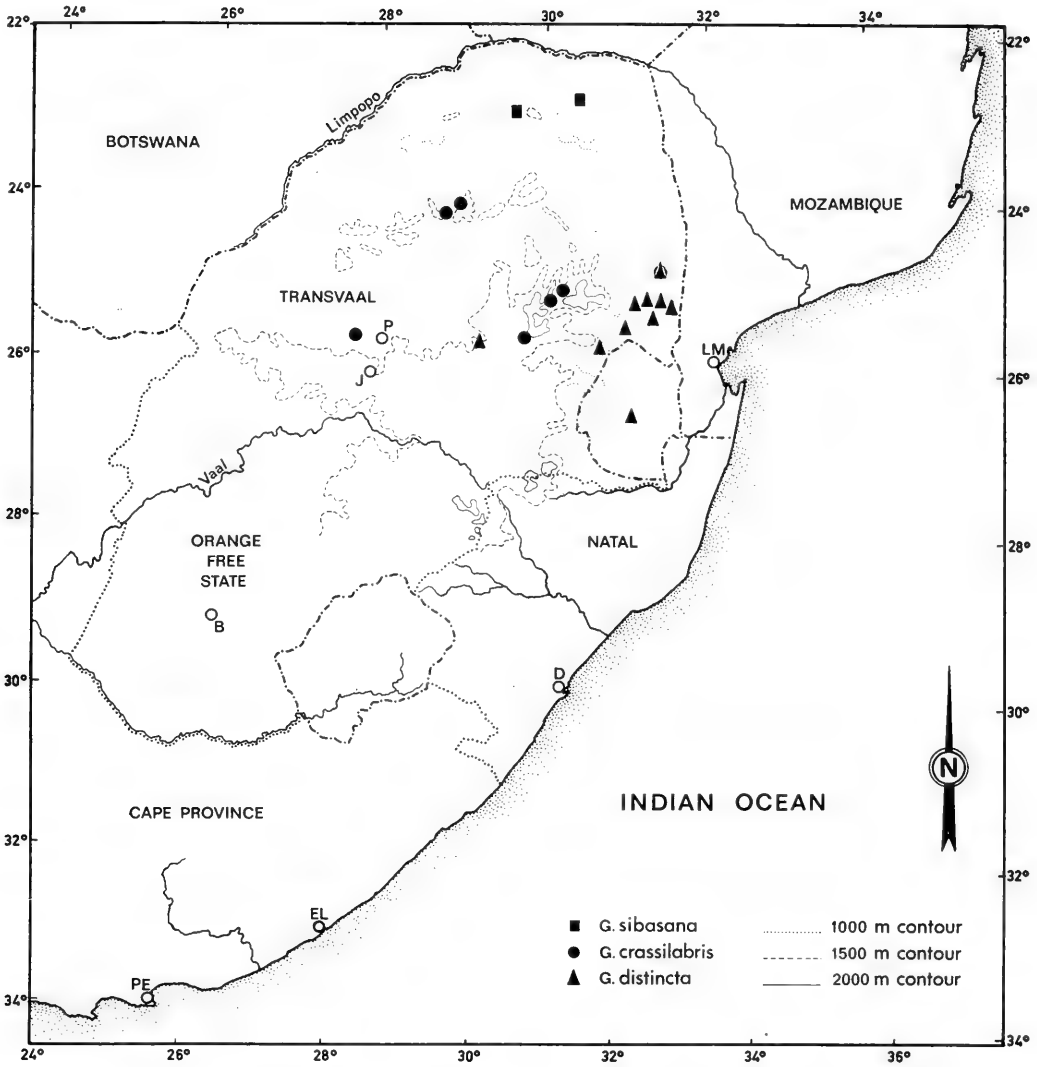

FIG. 2. Distribution of *Gulella sibasana* Conn., *G. crassilabris* (Crvn) and *G. distincta* (M. & P.). Abbreviations of towns: B, Bloemfontein; D, Durban; EL, East London; J, Johannesburg; LM, Lourenço Marques; P, Pretoria; PE, Port Elizabeth. H. Heijn del.

It is interesting to check on some general principles of evolutionary biology as regards the Southern African species of *Gulella*. Important characters are apertural dentition and costulation of the shell. Many species are clearly marked by showing more or less prominent ribbing, others being smooth or almost so. Some costulate species, however, have populations with weakly costulate to even practically smooth shells. Here the question arises whether species with smooth shells belong to more primitive stock than species with costulate shells. Primitive streptaxids probably had smooth shells with little apertural dentition (see, e.g., Van Bruggen, 1967). Some of the widely distributed species, such as the above-mentioned *G. planidens* and *G. sexdentata*, indeed have smooth shells, while on the other hand *G. planti* (Pfeiffer) (smooth) and *G. zuluensis* Connolly (faintly costulate) both have a very limited distri-

bution. These 2 species are also comparatively large and have only 2-3 processes in the aperture. This may lead to the conclusion that both are possibly derived taxa having had as yet no time to expand their range or perhaps are adapted to a unique situation. A 3rd possibility is that they have ceased to exist elsewhere. *G. planti* is Southern Africa's largest species (shell length up to 21.5 mm). Generally one finds that species with large shells (length 12 mm and over) have a restricted distribution, which also applies to other parts of Africa. Incidentally, the majority of these large species seems to dwell in the uplands of Africa.

The *Gulella infans* group consists of species with small shells and few processes in the aperture; both costulate and smooth shells are represented here, even sometimes within the same species. The wide distribution of the *G. infans* group correlated with limited dentition, frequently smooth shell, and small size may indicate that this group represents a somewhat primitive or ancient element in the genus. Convergent evolution, leading to almost identical types of shell, cannot be excluded here. Some West African and a Madagascar species are conchologically close to the *G. infans* group but may be only distantly related.

Rensch (1932) has shown that sculpture in general is more marked in dry and warm than in cooler and more humid areas. In the case of *Gulella* this may also be a complicating factor. The one form in arid South West Africa is decidedly more costulate than its nearest allies in less arid environments (see above). On the other hand many forest dwelling endemics are markedly costulate and probably are derived from smooth species, which only shows that the picture is really much more complicated.

Finally, is there perhaps a correlation between the dental pattern in the aperture and the costulation of the shell? As a working hypothesis one may predict a positive correlation between a smooth shell and a limited apertural dentition, or, conversely, a costulate shell with an intricate pattern of processes in the aperture. Both types are difficult to delimit. A preliminary survey of the Southern African species revealed that about 2/3 of the species do indeed show a positive correlation between dental pattern and sculpture of the whorls. However, all in all this is perhaps not quite sufficient to prove the point in question.

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RESUME

MODELES DE DISTRIBUTION DU GENRE *GULELLA* (GASTROPODA PULMONATA: STREPTAXIDAE) EN AFRIQUE AUSTRALE

Le genre *Gulella* est très répandu dans le sud-est de l'Afrique australe (environ 125 espèces). Sur la carte (Fig. 1) la ligne en traits interrompus indique la limite occidentale du genre; à l'ouest de cette ligne on ne connait que quatre localités. Seulement quatre espèces (*G. gouldi*, *G. planidens*, *G. sexdentata* et *G. vicina*) se trouvent aussi au nord du Zambèze. Les autres sont endémiques et souvent très localisées. *G. sibasana*, *G. crassilabris* et *G. distincta* sont peut-être originaires d'un ancêtre commun (Fig. 2). Le groupe de *G. infans* comprend des espèces de petite taille, avec une ouverture à peu de dents; ce groupe est très répandu de sorte qu'il peut être relativement primitif ou ancien. Les coquilles d'environ deux tiers des espèces de l'Afrique australe montrent une corrélation positive entre le nombre (et le développement) des dents à l'ouverture et la présence ou l'absence d'une sculpture sur les tours (ornementation sous forme de côtes ou de stries).

MALACOLOGIA, 1973, 14: 426

PROC. FOURTH EUROP. MALAC. CONGR.

DIE FORMEN VON *ABIDA SECALE* (DRAPARNAUD) IN DEN ÖSTLICHEN PYRENÄEN

E. Gittenberger

Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands

ZUSAMMENFASSUNG[1]

Die Gehäuse von *Abida secale* (Draparnaud) variieren im grössten Teil des Verbreitungsgebietes der Art, das von Spanien ostwärts bis in Ungarn reicht, fast nur in den Massen und im Habitus. Die Gestaltung der Mündung und der Mündungsarmatur ist dabei auffallend konstant.

Im östlichen Teil der Pyrenäen hingegen ist eine erstaunlich grosse, geographisch bedingte, Variabilität vorhanden, die sich nicht auf Habitus und Masse beschränkt. Nur durch ein paralleles Studium von Morphologie und geographischer Verbreitung der verschiedenen *Abida*-Populationen werden die Zusammenhänge deutlich.

Es ergibt sich, dass einige stark differenzierte Formen, die immer als Arten betrachtet wurden, als Unterarten zu *Abida secale* gestellt werden müssen auf Grund der genetischen Zusammenhänge, die sich in Vorkommen und Verbreitung von Uebergangsformen zeigen. Aus gleichen Gründen müssen zwei *Abida*-Formen, die ohne Uebergänge zusammenleben zu *A. secale* gestellt werden. Sie hängen indirekt, durch weitere Formen, zusammen.

Die Art wird als eine genetische Entität gesehen. Im Rahmen einer Behandlung der taxonomischen Gliederung einiger *Delima*-Formen bemerkt Nordsieck (1969: 274), dass ". . . bei vielen Arten offenbar die Fortpflanzungsisolation noch unvollständig ist, also die morphologische Differenzierung schneller vonstatten ging als der Erwerb isolierender Mechanismen" und spricht etwas weiter von Formen, die "wegen der morphologischen Differenzierung" als verschiedene Arten aufzufassen sind. Eine solche, morphologische Begründung des Artbegriffs wird abgelehnt.

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MALACOLOGIA, 1973, 14: 426

PROC. FOURTH EUROP. MALAC. CONGR.

ZOOGEOGRAPHY OF THE PLEUROCERINE FRESHWATER SNAILS

Joseph P. E. Morrison

U. S. National Museum of Natural History, Washington, D. C., U.S.A.

ABSTRACT

The Amphimelaniinae of Europe, Melanatriinae of Africa, Paludominae of Asia, and the Pleurocerinae of North and Central America are confluent as 1 subfamily, with identical female egg-laying structures. The detailed pattern of egg-laying and the egg-mass is still considered a generic character. The Pleurocerinae are thus primarily Holarctic.

The Recent pleurocerids of Europe (from the Danube System) are now incorrectly called *Amphimelania*. The name *Holandriana* Bourguignat May 1884, with the type species *Melania holandri* C. Pfeiffer 1828, precedes *Amphimelania* Fischer 1885 and should be used.

The closely related Family Melanopsidae includes *Melanopsis* of Europe, North Africa to Iraq and of New Caledonia. *Zemelanopsis* of New Caledonia and New Zealand re-covers the apical whorls with an added covering of periostracum (and shell layers) effectively hiding the 4 first whorls of the shell.

The Melanopsidae of the Danube and Dniester River Systems are now incorrectly called *Fagotia*. The names of Bourguignat 1877, including *Esperiana* (type *esperi*), were reported by Bourguignat (May, 1884, p 3), before he placed the same group 1st under *Fagotia* on p 30. As the earliest name, *Esperiana* must be used for this genus. *Microcolpia* Bourguignat 1884, p 49, will remain as a subgenus for *Esperiana* (*Microcolpia*) *acicularis* Ferussac.

MALACOLOGIA, 1973, 14: 427

PROC. FOURTH EUROP. MALAC. CONGR.

A PROGNOSIS IN THE SPREAD OF THE GIANT AFRICAN SNAIL TO CONTINENTAL UNITED STATES

Albert Raymond Mead

University of Arizona, Tucson, Arizona, U.S.A.

ABSTRACT

The giant African snail, *Achatina fulica*, has been on the move from its east African home for over 150 years. That it had not become established in any continental site in the Western Hemisphere until recently is virtually a biological enigma. Its 1st point of establishment in the Western Hemisphere was in the Hawaiian Islands in 1936. In spite of the most intensive control and quarantine measures ever initiated against this pest, it is still spreading. It was not until 1969 that it was found thoroughly ensconced in North Miami and Hollywood, Florida. Since then, over 17,000 specimens have been collected and destroyed at an expense of over $ 80,000. The population is being contained but currently is holding at the "irreducible minimum." Every feasible control measure except biological control has been initiated and carried through by qualified personnel on a rigid program. This snail pest never has been eradicated in any place in the world where it has become established as a population. There is now the best chance that man has ever had successfully to contain and eventually eradicate this largest major land snail pest. The next 12-24 months will doubtless prove decisive. If the present program fails, it is predicted that *A. fulica* will eventually spread north to the Carolinas and west, through the Gulf states, spottedly through the Southwestern "desert" states, and into southern California; from these areas it easily could spread to the Caribbean islands, Mexico, Central and South America. The phenomenon of natural population decline, manifested in virtually all of the older populations that have been examined, holds the key to eventual practicable control.

MALACOLOGIA, 1973, 14: 429-430

PROC. FOURTH EUROP. MALAC. CONGR.

MOLLUSQUES DES ILES TUBUAI (AUSTRALES, POLYNESIE) COMPARAISONS AVEC LES ILES DE LA SOCIETE ET DES TUAMOTU

Bernard Salvat

Laboratoire Biologie Marine et Malacologie
Ecole Pratique des Hautes Etudes, Muséum Paris, France[1]

L'Archipel des îles Tubuai, ou Australes, entre 144 et 154° de longitude Ouest comprend sept îles disposées selon un axe Nord-Ouest - Sud-Est traversant le tropique du Capricorne. Entre l'île la plus occidentale, Maria, et la plus orientale, l'îlot de Bass, s'échelonnent les cinq principales îles de l'Archipel: Rimatara, Rurutu, Tubuai, Raevavae et Rapa. Cet ensemble se situe au Sud-Est et au Sud des Archipels de la Société (îles hautes volcaniques dont Tahiti et Bora-Bora), des Tuamotu (îles basses ou atolls dont Rangiroa, Raroia, Mururoa) et des Gambiers (îles hautes dont Mangareva, Aukena).

Les deux principales îles méridionales de l'Archipel des Tubuai, Raevavae et Rapa, sont intéressantes du point du vue écologique et biogéographique car l'une présente un climat tropical alors que l'autre possède un climat tempéré. Ces deux îles ont été l'objet, en avril-mai 1968, de prospections malacologiques[2].

Raevavae, île volcanique de 9 km de longueur, possède des récifs frangeants et un lagon entouré par un récif barrière presque continu. Cette île est située à la même latitude (23° Sud) que les Gambiers. Comparativement à la faune de ces dernières îles, la faune du lagon de Raevavae est bien plus pauvre en nombre d'espèces alors que la faune des récifs extérieurs est analogue, peu de différence pouvant être notée. Des études précédentes (Salvat 1970a, b) ont montré que les Mollusques caractéristiques des récifs extérieurs, supprimer du récif barrière des îles volcaniques Gambiers (23° latitude Sud) comme de la bordure océanique de l'atoll de Fangataufa (22° de latitude Sud) dans les Tuamotu, sont les mêmes: *Turbo setosus* (Gmelin, 1791), *Nerita plicata* Linne, 1758, *Littorina coccinea* (Gmelin, 1791), *Vermetus maximus* Sow., 1825, *Drupa grossularia* (Röding, 1798), *D. horrida* (Lamarck, 1816), *D. morum* Röding, 1798, *D. ricinus* (Linne, 1758), *Morula granulata* (Duclos, 1832), *Strigatella litterata* (Lamarck, 1811), *Conus chaldaeus* Röding 1798, *C. ebraeus* Linne, 1758, *C. miliaris* Hwass, 1792, *C. nanus* Broderip, 1833 et *C. sponsalis* Hwass, 1792. A l'exception de deux d'entre elles, *Tectarius grandinatus* et *Conus nanus*, toutes ces espèces peuvent être récoltées sur les récifs extérieurs de Raevavae où on note toutefois, comparativement aux Gambiers et à Fangataufa, la rareté de *Turbo setosus* dans la zone frontale du récif, de *Conus sponsalis* sur les platiers et de *Littorina coccinea* sur les blocs de la zone supérieure. En revanche, quelques espèces inexistantes ou inhabituelles sur les récifs extérieurs des Gambiers ou de Fangataufa sont bien représentées sur les platiers externes de Raevavae: *Drupa elata*, *Cantharus undosus*, *Latirus nodatus*, *Peristernia nassatula* et *Nerita morio* (voir Salvat, 1971).

Rapa, par 27° 5 de latitude Sud, est en dehors de la zone intertropicale et la température des eaux superficielles, si elle permet la croissance de certains coraux, ne conduit pas à la construction d'édifices récifaux importants; il n'y a ni récif frangeant,

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[1]Egalement - Antenne de Tahiti B. P. 562, Papeete.

[2]Recherches réalisées dans le cadre de conventions entre la DIR.C.E.N./S.M.C.B. et le Muséum de Paris.

ni récif barrière mais une pente littorale avec colonies coralliennes. La faune malacologique marine est considérablement plus pauvre qu'à Raevavae, 4° de latitude plus au Nord. Sur les 80 espèces de Mollusques testacés, Gastropodes et Bivalves, recensées dans cette dernière île, il ne nous a été donné de n'en retrouver que 10: *Nerita plicata*, *Nerita morio*, *Drupa morum*, *D. ricinus*, *Morula granulata*, *Siphonaria* sp., *Modiolus auriculatus*, *Chama asperella*, *Gafrarium pectinatum*, *Tellina rugosa*. Il convient de citer encore 6 espèces non récoltées à Raevavae mais par ailleurs communes dans les îles de la Société, des Gambiers, et des Tuamotu et qui doivent se trouver, selon toute vraisemblance, à Raevavae: *Planaxis lineatus*, *Cerithium morus*, *Peristernia* cf. *sulcata*, *Malleus maculosus*, *Crassostrea cucullata* et *Cardita variegata*. Signalons enfin 2 espèces du genre *Patella* en cours d'étude et 3 espèces que nous considérons présentement comme nouvelles, appartenant à deux familles: Turbinidae et Muricidae. Indiquons, de plus, la présence à Rapa d'un Polyplacophore et d'un Céphalopode octopode. Notre inventaire faunistique se ramène donc à 23 espèces malacologiques.

On remarquera que sur 4 familles d'Archaéogastropodes représentées dans les îles de la Société, des Tuamotu et à Raevavae, trois possèdent des représentants à Rapa (Patellidae, Neritidae, Trochidae, absence de Turbinidae). Sur 6 familles de Mésogastropodes (Littorinidae, Vermetidae, Cerithiidae, Strombidae, Cypraeidae, et Naticidae) une seule est encore représentée (Cerithiidae)[3]. Pour les Néogastropodes, s'il existe à Rapa des Muricidae et des Mitridae, nous n'avons en revanche récolté aucune espèce de Buccinidae, de Conidae ou de Terebridae.

Le substrat rocheux intertidal est dominé par les Patelles, les Polyplacophores et les Nerites et il présente des caractéristiques de zone tempérée avec notamment une couverture algale bien développée qui n'existe pas dans les îles aux latitudes plus faibles. Les quelques espèces de Muricidae (*Drupa*, *Morula*), très abondantes sur les récifs extérieurs d'îles plus septentrionales, n'existent à Rapa qu'en quelques localités où une plateforme de roche volcanique au niveau de la mer permet l'installation d'algues, notamment de Sargasses, recréant ainsi un biotope analogue à des récifs frangeants.

ABSTRACT

The littoral marine fauna of the Raevavae and Rapa islands of the Australs Archipelago south of Tahiti has been investigated. In the tropical Raevavae island the abundance of the fauna of the external reef is nearly similar to that found in the Society Islands or Tuamotu, the main difference being noted in the lagoon where a poorer fauna was found. On the other hand, in Rapa where no fringing reef nor outer barrier-reef are to be found, the fauna is much poorer, mainly in mollusks of which 23 species only have been collected.

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[3]Une ou 2 espèces de *Cypraea* seraient présentes que nous n'avons pas rencontrées.

MALACOLOGIA, 1973, 14: 431-432

PROC. FOURTH EUROP. MALAC. CONGR.

SOME ASPECTS OF THE DISTRIBUTION OF THE MARINE MOLLUSCS OF WEST AFRICA

J. Knudsen

Zoological Museum, University of Copenhagen, Denmark

ABSTRACT

It is well known that the endemic West African fauna extends from a rather narrow border zone, beginning at about 15°N and fading off in the region between 10° and 20°S. A conspicuous element of the Mediterranean-Lusitanean fauna extends its range into the West African region. Most species seem to penetrate a relatively short distance south of the border zone just mentioned, while some are found throughout the entire West African region, thus being common to both regions. The proportion of Mediterranean-Lusitanean species in the northern part of the West African region may be put at 25-30%.

A survey of Barnard's papers (1958-69) on the marine molluscs of South Africa shows that many earlier records of species occurring both in West and South Africa are erroneous, based on either misidentification or erroneous locality data. The number of well established cases of species occurring in both areas is very low.

Thus the relations of the West African fauna to its 2 neighboring faunas are very different. This may to a great extent be explained in terms of larval ecology. Transport of pelagic larvae of molluscs from the Mediterranean-Lusitanean region to the West African is greatly facilitated through the Canary Current. On the other hand, the Benguela Current area with its low temperatures probably constitutes a major obstacle for an intrusion of larvae of benthic molluscs from the South African region (and the Pacific region), and possibly the Congo river's discharge of both fresh water and sediment adds to the effect.

Less conspicuous fauna elements show aberrant distributional patterns: 1) Circumtropical (may not include East Pacific); 2) Circumtropical (may not include West Atlantic); 3) Amphi-Atlantic; 4) Indo-Pacific - West African, absent from South Africa.

Many well studied examples of the above-mentioned categories can be found in the monographs published in "Johnsonia" and "Indo-Pacific Mollusca" and in other recent taxonomic works (Burgess, 1970; Fischer-Piette & Delmas, 1967; Turner, 1966). Veligers from 10 amphi-Atlantic species of prosobranchs were collected from the open ocean, and, thus, Scheltema (1971) was able to conclude that long-distance dispersal of larvae takes place. By consulting a number of the recent monographs already referred to, I have found that distributional patterns of the above-mentioned 4 categories occurring in systematic groups not dealt with by Scheltema (l.c.) in many cases, may be explained by special means of spreading. Several species live attached to mangrove or other plant material or bore into wood. Such forms may easily be transported with the oceanic current systems. Several cases are obviously misidentifications or they belong to "critical" taxonomic groups which have not been subjected to recent study on a world wide or oceanic scale.

Scheltema (l.c.) states that frequent long-distance dispersal of larvae may facilitate the gene flow between widely separated populations, and that the degree of morphological differentiation between eastern and western Atlantic populations of gastropod species having amphi-Atlantic distributions would be expected to bear an inverse relationship to the frequency with which the larvae of these species were found in the open sea. On consulting the above-mentioned papers it seems quite obvious that populations on both sides of the Atlantic are conspecific while in other cases morphological differences at the specific or the subspecific level are found.

Differences at the subspecific level may be found between populations in the Indo-Pacific and the East Atlantic. A few examples may be mentioned: *Littorina scabra scabra* (Linnaeus, 1758) is widely distributed in the Indo-West Pacific region, while the subspecies *L. s. angulifera* (Lamarck, 1822) occurs in morphologically identical populations on both sides of the Atlantic (Rosewater, 1970). *Dosinia exoleta exoleta* (Linnaeus, 1758) is distributed in the East Atlantic from about 68°N to off the Congo. *Dosinia e. amphidesmoides* (Reeve, 1850) is an Indo-West Pacific subspecies (Fischer-Piette & Delmas, l.c.). Future taxonomic revisions may reveal many similar examples.

The West African region may be subdivided into 3 zones (Williams, 1968): 1) western tropical zone (from about 11°N to Cape Palmas, about 8°W; 2) central upwelling zone (from Cape Palmas to the region west of Lagos, about 3°E); and 3) eastern tropical zone (from west of Lagos to Cape Lopez, about 1°S). The zones north and south of these 3 are termed north transitional and south transitional zone, respectively.

The 2 tropical zones are characterized by having surface temperatures always exceeding 24°C, with rather small seasonal fluctuations. The upwelling zone has temperatures showing considerable annual fluctuations (up to 10°C).

The distribution of some species may be explained by the differences in environmental conditions prevailing in these zones. Thus Burgess (l.c.) records 4 species of *Cypraea* restricted to the western tropical zone, and the distribution of some species of *Marginella* shows the same pattern. There are also examples of species apparently being confined to the eastern tropical zone.

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MALACOLOGIA, 1973, 14: 432

PROC. FOURTH EUROP. MALAC. CONGR.

LES MOLLUSQUES BATHYALS DU GOLFE DE TARENTE

Pietro Panetta

Istituto Sperimentale Talassografico Taranto, Via Roma 3
I-74100 *Taranto, Italie*

RESUME

L'Albatros, dans les années 1966-1969, a effectué 9 croisières dans le golfe de Tarente, en prélevant 500 échantillons dans l'espace compris entre la côte et 35 milles au large. La zone bathyale, comprise entre 200-1000 m, est assez restreinte le long de la côte salentine, tandis qu'elle est assez étendue le long de la côte calabraise. On peut remarquer une alternance de fonds boueux et vaseux, ceux-ci formant une grande extension jusqu'aux grandes profondeurs.

La faune est très dispersée, pauvre en espèces avec prédominance de Polychètes; elle est caractérisée par une association de *Cyclammina cancellata* et de *Nassa limata* Chemn., *Bullaria utricula* (Brocchi), *Nucula tenuis aegeensis* (Fbs.), *Abra alba* (Wood), *Lissactoeon exilis* Fbs., *Trophonopsis carinata* (Biv.) et *T. richardi* (Dautz. & Fisc.). A partir de 400-500 m, on peut remarquer beaucoup de coquilles de Ptéropodes: *Cavolinia tridentata* Forsk., *C. trispinosa* Les., *Cleodora pyramidata* Les. et *Styliola recta* Les. De nombreuses espèces rares de Mollusques ont été découvertes: *Malletia obtusa* (Sars), *Cuspidaria costellata* (Des.), *Pleurotomella pycnoides* (Dautz. & Fisc.), *Pleurotoma macra* (Watson) et *Pleurotomella bairdi* Verril & Smith.

La faune malacologique bathyale du golfe de Tarente est une faune atlantique très pauvre qualitativement. Les espèces sont pour la plupart euribathyales, mais il y a aussi des abyssales.

MALACOLOGIA, 1973, 14: 433-437

PROC. FOURTH EUROP. MALAC. CONGR.

QUELQUES CAS DE DIPHYOIDIE OBSERVES SUR DES MOLLUSQUES CONTINENTAUX[1]

Louis Chaix

Département d'Anthropologie, Université de Genève, Suisse

Une coquille affectée du phénomène de diphyoidie montre une tendance à une scission transverse et médiane de son test (Fig. 1). Certains mollusques fossiles montrent cette morphologie particulière en tant que caractère spécifique comme certains Gastéropodes du Trias (*Emarginula*) ou actuels comme *Scissurella*. Il est à remarquer que cette échancrure présente des dimensions très variables. Plusieurs Brachiopodes fossiles sont également diphyoides, les plus caractéristiques étant *Eospirifer* du Silurien et *Dictyothyris* du Jurassique. Il est à remarquer que sur les gastéropodes et les brachiopodes cités, on ne peut pas parler de position de la scissure transverse et médiane, puisqu'elle est longitudinale, le test de ces mollusques étant assimilable à une valve. En étudiant les tests de certains mollusques continentaux dulcicoles, Lamellibranches et Gastéropodes, nous avons constaté des caractères morphologiques rappelant cette diphyoidie. La plupart de nos observations ont été faites sur de petits Lamellibranches du genre *Pisidium*, provenant de sondages dans les sédiments post-glaciaires du Bassin Lémanique. De nombreuses valves présentent une ébauche de scissure plus ou moins développée dans la partie médiane de la coquille (Fig. 2). Ce sillon peut être faible ou assez profond et se retrouver sur la face interne de la valve. Dans d'autres cas, il se réduit à un lacis de rainures sinueuses, mais dont le sommet occupe toujours une position médiane (Fig. 3). Ce sillon peut être limité au bord de la coquille ou s'étendre très haut dans la région du crochet. Un fait qui nous a paru important, c'est la position médiane de cette échancrure, quel que soit son degré. La majorité des cas observés se rapporte aux espèces *Pisidium nitidum* Jen. et *Pisidium milium* Held. Sur quelques exemplaires complets conservés dans la craie lacustre, nous avons pu voir que cette diphyoidie affectait les deux valves d'une manière absolument symétrique. Notre matériel provenait de sondages à but paléontologique et nous avons jugé utile de calculer le pourcentage d'individus diphyoides d'un échantillon à l'autre. Sur le graphique suivant (Fig. 4) on peut voir, replacée dans un cadre chronologique, cette évolution du phénomène. Nous avons également observé cette

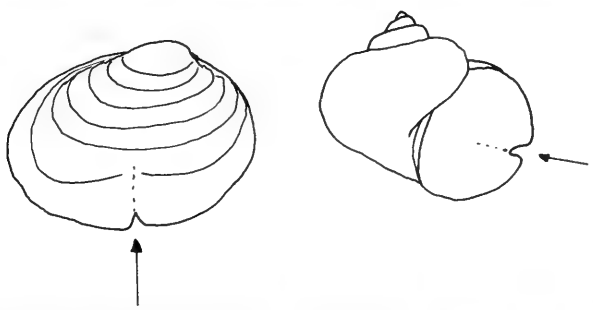
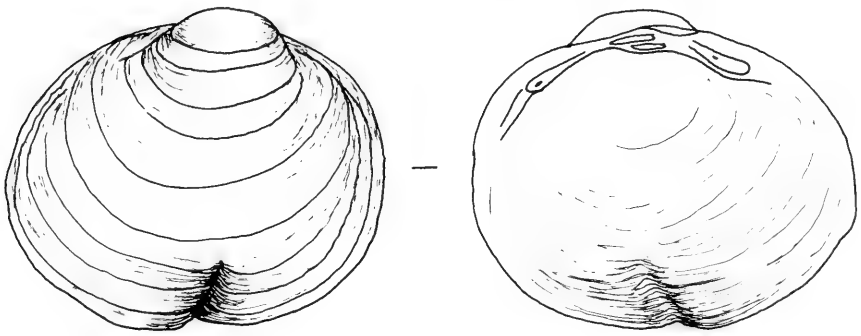
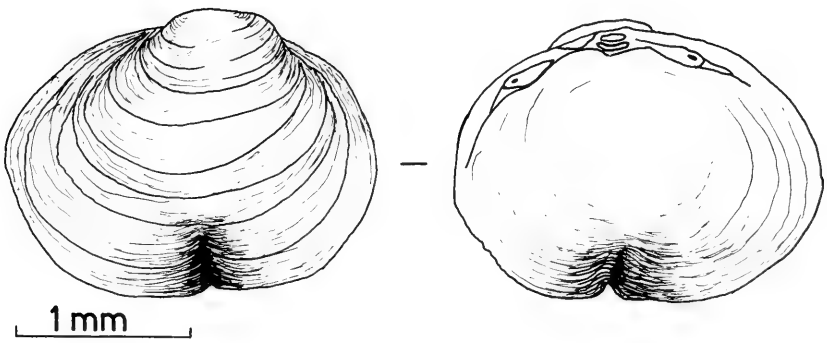


FIG. 1. Une coquille affectée du phénomène de diphyoidie montre une tendance à une scission transverse et médiane de son test.

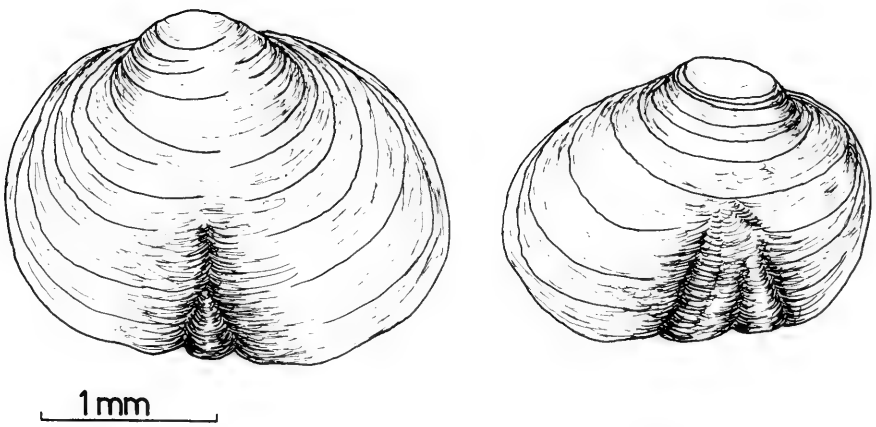
[1]A la mémoire du Professeur Ad. Jayet.



Pisidium nitidum Jen.



2 Pisidium milium Held.



3 Pisidium nitidum Jen.

FIG. 2. En haut: *Pisidium nitidum* Jen.; en bas: *Pisidium milium* Held.
FIG. 3. *Pisidium nitidum* Jen.

Ech.	Total	N.diph.	% diph.	Ech.	Total	N .diph.	% diph.
I	I	0	0	I7	I52	I6	I0,5
2	I	o	0	I8	I5I	24	I5,8
3	II	0	0	I9	I43	I3	9,I
4	2	0	0	20	I56	II	7,0
5	7	2	28,5	2I	I57	I0	6,3
6	I20	o	0	22	225	I9	8,4
7	65	7	I0,7	23	2I3	II	5,I
8	73	4	5,4	24	33	5	I5,I
9	I44	I7	II,9	25	I	00	0
I0	95	I8	I8,9	26	0	0	0
II	28I	48	I7,0	27	I36	4	2,9
I2	247	44	I7,7	28	I92	2	I,0
I3	I33	30	22,5	29	66	0	0
I4	77	7	9,0	30	II4	0	0
I5	I56	46	29,5	3I	I	0	0
I6	I77	6	3,3	32	I8	I	5,5

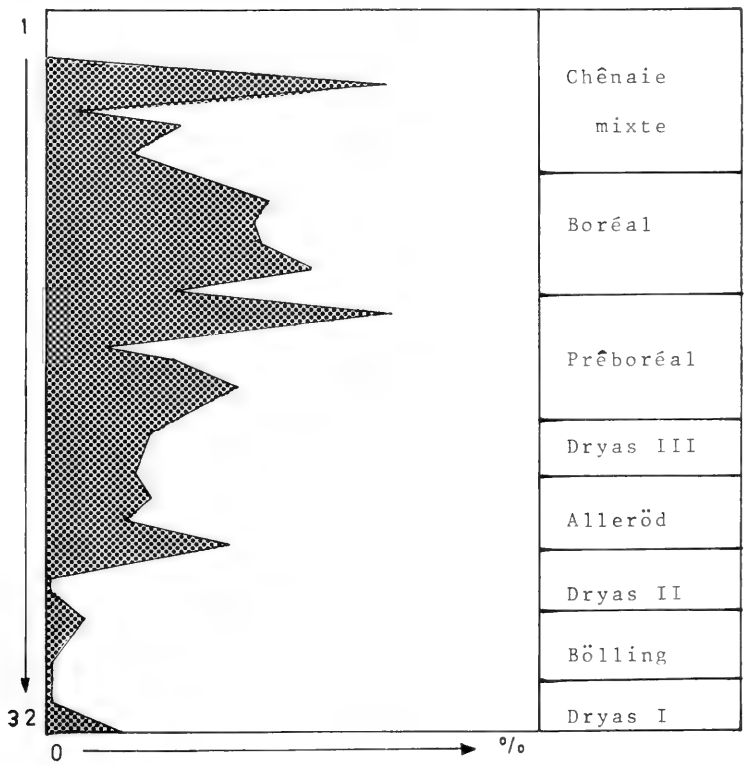


FIGURE 4

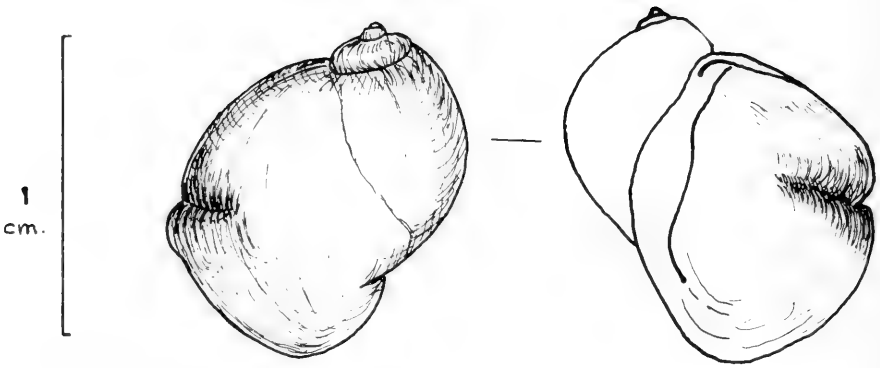


FIG. 5. *Radix auricularia* L.

diphyoidie sur un gastéropode actuel du Rhône, *Radix auricularia* (L.). Ici, comme nous l'avons fait remarquer plus haut, le sillon est longitudinal et correspond à un certain rebroussement des stries d'accroissement (Fig. 5). On remarquera également la position médiane de l'échancrure du labre.

Plusieurs auteurs ont tenté d'expliquer ce phénomène. Certains, comme Bourguignat, ont fait une espèce de ces individus diphyoides sous le nom de *Pisidium sinuatum*. Nous avons aussi remarqué dans certaines collections de musées des exemplaires d'Unionidés présentant cette particularité et portant des noms spécifiques tels que *Unio sinuata* Lam. ou *Unio sinatus* Lam. et provenant de la Loire ou de la Garonne. J. Favre, en 1927, a signalé certains individus de *Lymnaea stagnalis* possédant des incisions plus ou moins développées du bord palléal. Geyer a évoqué une action de lacération mécanique du manteau et d'autres auteurs (Mermod, 1930) ont signalé la présence d'une grande quantité de cercaires. Mais tous ces faits ont été constatés dans de très faibles proportions (1 ou 2%), alors que les calculs que nous avons effectué sur le produit de nos sondages montrent de forts pourcentages, jusqu'à 29,5% de diphyoides. Nous pensons que l'hypothèse d'une lacération mécanique si localisée est à rejeter. La position toujours semblable de l'échancrure nous semble avoir une autre origine. L'attribution spécifique différente donnée à de tels individus nous semble également arbitraire, la diphyoidie pouvant apparaitre sur des mollusques de genres différents. L'influence des divers paramètres du milieu mériterait une étude approfondie de même qu'une approche génétique du problème. Kuijper nous signalait récemment qu'il n'avait jamais observé cette diphyoidie sur les embryons de *Pisidium*, et d'autres observations signalent que l'échancrure des gastéropodes du genre *Scissurella* n'apparait que chez les individus adultes. Seule une étude biologique pourrait apporter une solution au problème que nous nous sommes posé face au nombre important de *Pisidium* aberrants des niveaux post-glaciaires que nous avons étudiés.

SUMMARY

Diphyoidy is a morphological character affecting the mollusc's shell. The diphyoidic shell shows a transversal furrow in the mesial part of the valve. We have observed a similar fact on fossil lamellibranchs from borings through post-glacial deposits in the Lemanic area. The species concerned are *Pisidium nitidum* Jen. and *Pisidium milium* Held. The shell shows a mesial furrow more or less developed, alone or

forming a network of grooves; we must remark that the point of junction of these grooves is always mesial. A similar observation was made on a recent living species of lymnaeid (*Radix auricularia* L.). We have computed the percentages of diphyoides during the post-glacial times. At present, no explication can be advanced for the diphyoidy. Some authors have made new species with diphyoid molluscs, like Bourguignat with *Pisidium sinuatum*, and we have seen in collections unionids named *Unio sinuata* Lam. or *Unio sinatus* Lam. We think that it is not a specific character, but a morphological change affecting several genera and species. Other authors, like Geyer, have spoken about mechanical tearing, but the constantly mesial position of the furrow seems to indicate another origin. Finally, it has been observed in a number of cases a lot of cercaria in the liver of diphyoid lymnaeids. But this number represents only a low percentage (1 or 2%) while our results show a higher percentage (up to 29.5%). To conclude, only a biological survey of ecological parameters, still to be determined, will open the way to a solution of this problem.

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MALACOLOGIA, 1973, 14: 438

PROC. FOURTH EUROP. MALAC. CONGR.

NOTES ON THE ORNAMENTATION OF MOLLUSK SHELLS

J. J. Oberling

Naturhistorisches Museum Bern, Switzerland

ABSTRACT

Five types of relationships between elements of shell ornamentation (sculpture and colouring) have been studied by the author. Three of these types (associated, correlated and independent) have been described at some length in an earlier paper (Oberling, 1968). The 2 remaining types, the contrasting subordinate and exclusion types, are considered here. In both cases we have a primary element whose presence influences the behaviour of the secondary element. The primary element often pertains to the sculpture, the secondary to the colouring.

In *Harpa harpa* L., where the black dashes are restricted to the varices, we have an example of the subordinate type of relationship, the presence of the dashes being subordinate to that of the primary elements, the varices. In *Harpa major* Röd., where coloured lobes occur only where varices are absent, we have an example of the exclusion type of relationship, as the coloured lobes may be considered excluded wherever varices are present.

Exclusion can also be found within the colour pattern itself. Examples cited include the 2-component pattern of *Neritina virginea* L., where the transverse lines are interrupted by the primary lobate units, whose presence excludes that of the lines. Or the 1-component system of *Conus marmoreus* L. where the earlier secreted ovate units often overlap later secreted ones, which in effect means that secretion of the latter is prevented until that of the earlier is concluded: the earlier units are here the primary units whose presence excludes that of portions of the latter. The same thing is true for *Oliva porphyria* L., where tents at any one place can only be secreted after completion of earlier tents or zigzags.

A study of various *Oliva porphyria* as well as other members of the genus strongly suggests that the tents are merely the tips of zigzags whose bases are excluded by previously secreted pattern elements. Occasional short, empty and regular "exclusion intervals" between the slopes of a tent and the origins of succeeding tents would moreover appear to indicate that the exclusion or inhibition effect of earlier secreted structures over later may at times persist awhile even after secretion of the former. Absence of such "domination" of earlier over later elements is seen in the case of crossing tents and zigzags in *Tapes litteratus* L.

Another topic of interest in shell ornamentation, here especially studied in respect to colouring, concerns the orientation of pattern elements. The orientations studied by the author might be resumed as follows:

Orientation constant: a) radial, and b) concentric; Orientation not highly variable: c) transverse, and d) crossed-oblique; Orientation highly variable: e) curving or lobate, with change of orientation relatively regular; f) irregular, with change of orientation haphazard.

a), b) and c) are already well known; d) under different and somewhat inadequate or cumbersome names has been mentioned by Wrigley (1947) and Neumann (1959). It refers to the common tendency for colour patterns to be secreted in 2 directions of about equal but opposite obliquity. This crossed-oblique tendency may be reflected in various ways: we may have figures that are irregularly distributed on the shell surface, but may themselves be 2-directional, as in various *Lioconcha;* or elements that are themselves irregular may have a crossed-oblique distribution (i.e., the spots on *Natica millepunctata* Lm.).

In the e) case, forming lobate and related figures, the shift of the area of secretion along the mantle margin tends to accelerate in a logarithmic manner up to the completion of the figures. True, fully developed lobate patterns have not been found in pelecypods.

f) irregular patterns seem to occur only where the colour pattern is influenced by a sculpture that shows such an orientation, as in *Helix aspersa* Müll.

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MALACOLOGIA, 1973, 14: 439

PROC. FOURTH EUROP. MALAC. CONGR.

EFFECT OF *MARISA CORNUARIETIS* ON *BULINUS TRUNCATUS* POPULATIONS UNDER SEMI-FIELD CONDITIONS IN EGYPT

Emile S. Demian and Erian G. Kamel

Department of Zoology, Faculty of Science, Ain Shams University, Cairo, Egypt

ABSTRACT

Earlier laboratory investigations have indicated that the South American ampullariid snail *Marisa cornuarietis* acts as a potential antagonist and efficient predator of *Bulinus truncatus*, the transmitter of urinary bilharziasis. A study has been made of the effect of *M. cornuarietis* on 4 populations of *B. truncatus*, exactly matching control populations in size, number and season of nurture. The observations were made in a series of artificial earth-lined ditches with continuously flowing Nile water. Quantitative estimation of the densities of the experimental and control populations was made by standard fortnightly samplings with a dip net.

Significant reductions in density of the experimental populations, as compared to the control populations, were observed after an initial period of 3 - 4 months, and *Bulinus truncatus* was completely eliminated from the experimental ditches in 5 - 8 months. The results suggest that *Marisa cornuarietis* could be of great value as a biological control agent against natural populations of *B. truncatus* in Egypt. This semi-field study is being continued at various density levels of the 2 competing species.

MALACOLOGIA, 1973, 14: 439

PROC. FOURTH EUROP. MALAC. CONGR.

DIE ÖKOLOGISCHEN GRUNDLAGEN DER PRÜFUNGSMETHODEN VON MOLLUSKIZIDEN

D. Godan

Biologische Bundesanstalt für Land- und Forstwirtschaft, Institut für Zoologie, Berlin-Dahlem, Deutschland

ZUSAMMENFASSUNG

In feuchten Gebieten und regnerischen Jahren treten Landgastropoden als Schädiger von Kulturpflanzen auf. Ihre mit Köderpräparaten vorwiegend noch auf Metaldehydbasis durchgeführte Bekämpfung ist reich an Problemen. Der häufig beobachtete geringe Erfolg beruht darauf, dass die verschiedenen autökologischen sowie auf die Schnecke einwirkenden Umwelt-Faktoren in ihrer Wechselwirkung und Verknüpfung mit abiotischen Bedingungen nicht berücksichtigt werden. Sie sind bei den Prüfungsmethoden in Rechnung zu stellen, um Fehlbeurteilungen des Molluskizids im Hinblick auf dessen Anwendung in der Praxis zu vermeiden. Köder- und Toxizitätseffekt sind abhängig von Spezies, Alter, Grösse, Aktivitätsrhythmus und Verhalten der Schnecke, von Gewöhnung und Lernvermögen.

Temperatur, Feuchtigkeit und Licht beeinflussen Wasserhaushalt, Aktivität und Erholung vergifteter insbesondere Nacktschnecken. Auch sind Menge und Art der Nahrung in dem Biotop und Beschaffenheit der Bodenoberfläche wichtig. Erdschollen und dichter Bewuchs (aufliegende Blätter) bieten Versteck-und somit Schutzmöglichkeiten. Hohe Feuchtigkeit begünstigt die Erholung, während Trockenheit und Sonneneinstrahlung bei gleichem Vergiftungsgrad der Schnecken tödlich wirken, so dass dasselbe Molluskizid ohne Kenntnis von Biologie, Physiologie und Umwelteinflüsse in dem einen Fall als unwirksam, aber in dem anderen als hochtoxisch beurteilt wird, was falsche Schlüsse für die Praxis ergeben kann.

Der Vortrag mit obigem Titel ist ungekürzt im Nachrichtenblatt Deutsch. Pflanzenschutzd., Braunschweig, 24(3): 35-37, 1972, erschienen.

MALACOLOGIA, 1973, 14: 440

PROC. FOURTH EUROP. MALAC. CONGR.

A NEW INJECTION FLUID FOR MALACOLOGISTS

Ko Bun Hian

University of Reading, England

SUMMARY

The Injection Fluid. The injection fluid is made up of a plastic adhesive and an artist's oil-base paint of the desired colour stirred thoroughly into acetone to give a fluid with a final viscosity of 1.8 poise ± 10% (low sheer rate 25 sec^{-1}). The following adhesives have been found satisfactory: Uhu, Dia-mend, Bostik 1 and Sellobond. Mix any one of these adhesives in equal volume with acetone, then add enough oil paint to obtain a dense colour. One advantage of this fluid is that specimens injected can be embedded and sectioned, and the fluid in the vessels and sinuses show well in stained sections. In sections of the salivary glands of *Dolabella* vessels only 16 microns in diameter are evident.

Method of injecting. In *Dolabella* every single specimen requires about 10 to 20 cc of the fluid, which is sucked into a syringe with a No. 18 hypodermic needle. A clogged needle can be washed in acetone. If the injection is to be made into the efferent branchial vessel the gill is first stretched to expose it fully and to locate the deep groove which lies on the dorsal side of the vessel. The needle is now inserted into the vessel and as the fluid is injected it goes directly to the heart, then to the various organs. Care, however, must be taken to keep the needle in its position for at least 5 minutes after the injection to give the fluid time to set and prevent it from flowing out of the wound. A successful injection is one in which no liquid flows to the reverse direction. Once assured of this, preserve the specimen in 4% formalin. The animal will be ready for dissection and study after 3 hours (Fig. 1).

FIG. 1. Injected specimen of *Dolabella auricularia* (Humphrey) to show arteries associated with cerebral ganglia. The thickest nerve has a diameter of 0.4 mm.

MALACOLOGIA, 1973, 14: 441

PROC. FOURTH EUROP. MALAC. CONGR.

HISTORICAL ASPECTS OF ALPHEUS HYATT'S WORK ON FOSSIL CEPHALOPODS

Ralph W. Dexter

Department of Biological Sciences, Kent State University, Kent, Ohio, U. S. A.

SUMMARY[1]

Alpheus Hyatt (1838-1902) studied natural history under Louis Agassiz. From 1867 to the end of his life, Hyatt was in charge of the fossil cephalopod collection at the Museum of Comparative Zoology. He was a consultant in paleontology for the U. S. Geological Survey and a part-time professor of zoology and paleontology at the Massachusetts Institute of Technology and Boston University. In 1870 he became custodian for the Boston Society of Natural History (the title was later changed to that of curator) and he held that position for life. Between 1872-73, he studied the fossil cephalopod collections in the museums of Europe and the fossil gastropods at Steinheim, Germany.

Hyatt published about 50 papers and monographs on fossil cephalopods. The 1st of importance was "The Fossil Cephalopods of the Museum of Comparative Zoology" (1865) which included 24 new genera and 127 new species. One of the most important of his theoretical papers was "On the parallelism between different stages of life in the individual and those in the entire group of the molluscous order Tetrabranchiata" (1867). He and E. D. Cope independently developed what became known as the Law of Acceleration and Retardation which resembled the biogenetic law of Haeckel. Hyatt belonged to the Neo-Lamarckian school of thought. Hyatt's evolutionary interpretation of fossil cephalopods has been questioned by modern students. While his theoretical work has been discarded, he made solid contributions to the classification of fossil cephalopods and stimulated research in the evolutionary development of that group.

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[1] Published *in extenso* in: Malacol. Rev., 6(1): 38-40.

Addendum to T. E. Thompson, "Euthyneuran and other molluscan spermatozoa", p 167-206, this issue of Malacologia.

PLATE 15. Electron micrograph of autosperm of *Acteon tornatilis*, passing through the neck and showing the outer unit-membrane (interrupted arrows) of the cell, and the points (solid arrows) where the inner unit-membrane is continuous with the outer unit-membrane of the axonemal mitochondrial sheath. The scale represents 0.1 μm.

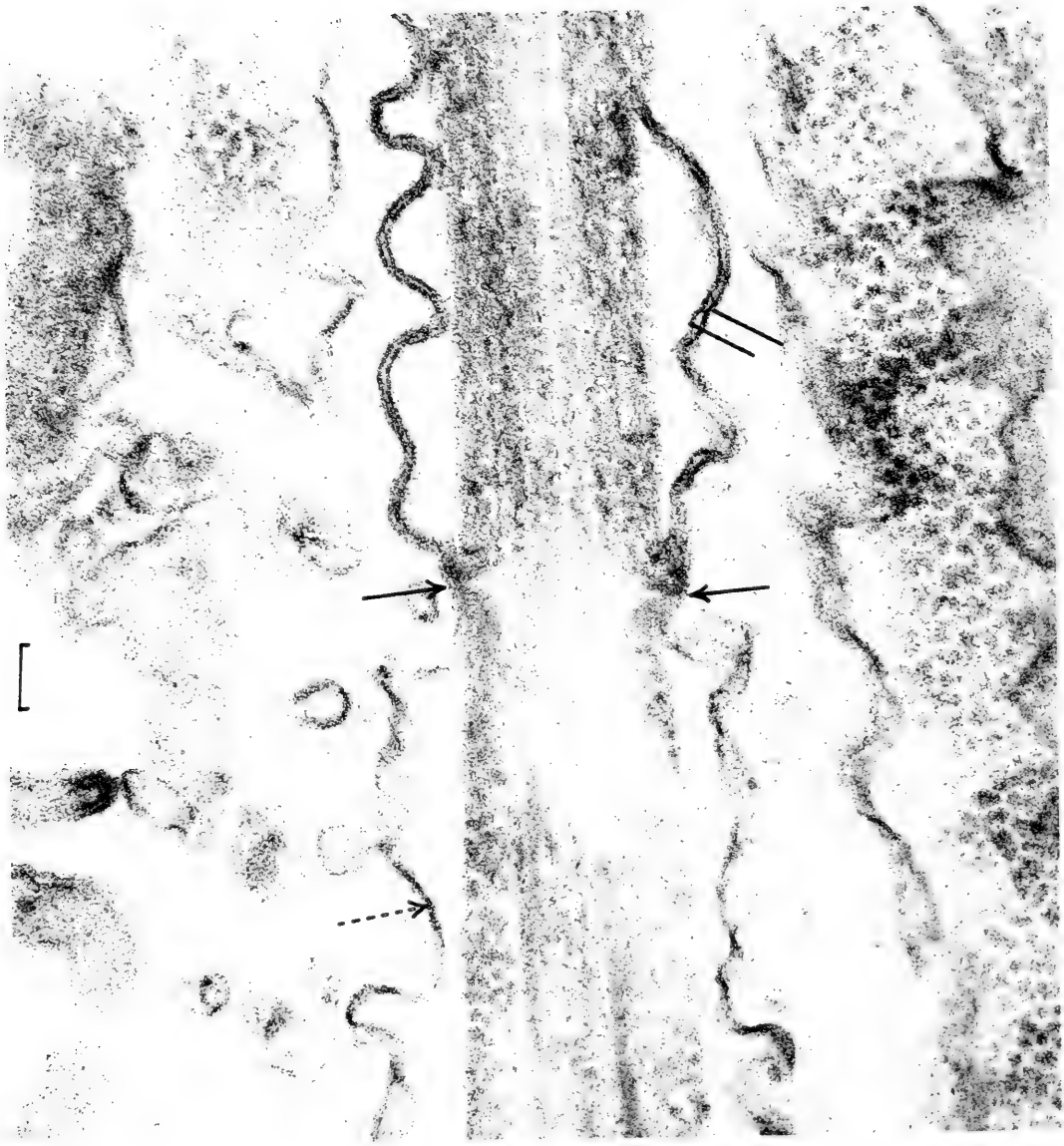

PLATE 16. Electron micrograph of autosperm of *Acteon tornatilis*, passing longitudinally through the zone of disjunction (solid arrows) between the mitochondrial mid-piece (top of the page) and the glycogen-filled tail-piece. An interrupted arrow indicates the single unit-membrane of the tail-piece, while a pair of oblique lines indicates the double membrane system of the mid-piece. The scale represents 0.1 μm.

EXHIBITS

The following exhibits were displayed by Congress members:

T. Gascoigne. Demonstration of the dissection of the nerve collar of *Alderia modesta*.

Ko Bun Hian. A new injection fluid for malacologists: 2 injected specimens of *Dolabella auricularia*, with explanatory drawings.

P. Newell and J. M. Skelding. The structure and functioning of the kidney of *Achatina* and *Helix*; photos and graphs.

O. E. Paget. Models of *Neopilina*, *Achatina* and molluscan larvae, manufactured by the Museum of Natural History in Vienna.

I. Richter. Color drawings of Nudibranchia from the western Mediterranean.

T. Thompson. Freeze-etch technique applied to the study of molluscan spermatozoa structure; photographs.

SOCIÉTÉ FRANÇAISE DE MALACOLOGIE, Commission de Faunistique continentale. Method of distribution mapping of terrestrial Mollusca.

J. Heath. Method of distribution mapping by the European Invertebrate Survey.

ADEGOKE, O. S., University of Ife, Ile-Ife, Nigeria.
AELLEN, Villy, Directeur du Muséum d'Histoire naturelle, CH-1211 Genève 6, Suisse.
ALLEN, John A., Dove Marine Laboratory, Cullercoats, North Shields, Northumberland, England.
ALVAREZ, Julio, Instituto de Entomologia, Gutierrez Abascal 2, Madrid 6, Espana.
ANSELL, A., Scottish Marine Biological Association, P.O. Box 3, Oban, Scotland.
ANT, H., Wielandstr. 17, D-47 Hamm, Deutschland.
BÁBA, K., Pädagogische Hochschule, Aprilis 4.u.6. Szeged, Hongrie.
BACKHUYS, W., Natuurhistorisch Museum Kastanjesingel 107, Rotterdam 3012, Nederland.
BARBOSA, F., OMS, Maladies Parasitaires, Av. Appia, CH-1211 Genève, Suisse.
BEBBINGTON, A., Redland College and Zoology Dept., University of Bristol, England.
BINDER, E., Muséum d'Histoire naturelle, CH-1211 Genève 6, Suisse.
BOETERS, Hans D., Rumfordstr. 42, D-8 München 5, Deutschland.
BOETTGER, C. R., Güldenstr. 40B, D-33 Braunschweig, Deutschland.
BOLLING, W., Luitpoldstr. 33, D-8600 Bamberg, Germany-West.
BONETTO, Argentino, Jose Maciá 1933, Santo Tome, Santa Fe, Rep. Argentina.
BORAY, J. C., Institut für Parasitologie, University of Zürich, Suisse.
BOSS, K. J., Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 021381, U.S.A.
BOUCHET, P., Faculté des Sciences, Rennes, France.
BRÖNNIMANN, P., Laboratoire de Paléontologie, Université de Genève, CH-1211 Genève 4, Suisse.
BRUGGEN, A. C. van, Dept. of Systematic Zoology of the University, c/o Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Leiden, Nederland.
BULLOCK, Robert C., Harvard University, Cambridge, Massachusetts 021381, U.S.A.
BURCH, J. B., Museum and Department of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A.
BUTOT, L. J. M., Rijksinstituut voor Natuurbeheer, Kasteel Broekhuizen, Leersum (Utr.), Nederland.
CAMERON, R., Dept. of Biological Sciences, Portsmouth Polytechnic, Portsmouth, U.K.
CHAIX, L., Dept. d'Anthropologie, Université de Genève, 12, rue G. Revilliod, CH-1227 Genève, Suisse.
CHATFIELD, J., Dept. of Biology, Portsmouth College of Education, Locksway Road, Milton, Portsmouth, England.
CHETAIL, M., Laboratoire d'Anatomie Comparée, Faculté des Sciences, 7, quai Saint-Bernard, F-75 Paris 5ème, France.
CHEVALLIER, H., Muséum national d'Histoire naturelle, 55, rue de Buffon, F-75 Paris 5ème, France.
CONCI, C., Museo Civico di Storia Naturale, Corso Venezia 55, I-20121 Milano, Italia.
COOMANS, H. E., Zoologisch Museum Amsterdam, Plantage Middenlaan 53, Amsterdam -C, Nederland.
CRAWFORD, G., Stanton's Hall, Blindley Heath, Lingfield, Surrey, England.
DE JONG-BRINK, M. M., Dept. of Biology, Free University, P.B. 7161, Amsterdam, Nederland.
DEMIAN, E. S., Dept. of Zoology, Ain Shams University, Cairo, Egypte, R.A.U.
DEXTER, R. W., Dept. of Biological Sciences, Kent State University, Kent, Ohio 44242, U.S.A.
DUNDEE, D. S., Dept. of Biology, Louisiana State University, New Orleans, Louisiana, U.S.A.

EALES, N. B., Littledown, Colliers Lane, Kingwood, Henley on Thames, Oxon, England.
EDMUNDS, M., Dept. of Zoology, University of Ghana, Box 67, Legon, Ghana.
EEDEN, J. A. van, Potchefstroom University, Dept. of Zoology, Potchefstroom, Republic of South Africa.
FISCHBERG, M., Station de Zoologie, 154, route de Malagnou, CH-1224 Genève, Suisse.
FORCART, L., Zürcherstrasse 9, CH-4000 Basel, Suisse.
FOULQUIER, L., Centre d'Etudes Nucléaires de Cadarache, B.P. 1, F-13 St.-Paul-lez-Durance, France.
FRANCHINI, D. A., Via Cremona 37, I-46100 Mantova, Italia.
GAILLARD, J. M., Laboratoire de Malacologie, Muséum national d'Histoire naturelle, 55, rue de Buffon, F-75 Paris 5ème, France.
LOPES-RODRIGUES GARCIA, M. C., Ecole Normale Supérieure, Laboratoire de Zoologie, 46, rue d'Ulm, F-75 Paris 5ème, France.
GASCOIGNE, T., Biology Department, Alleyns School, Townley Road, E. Dulwich, London SE 22, England.
GERBER, V., Naturhistorisches Museum, Bernastrasse 15, 3005 Bern, Suisse.
GHISOTTI, F., Via Giotto 9, I-20145 Milano, Italie.
GIROD, A., Via Savona 94/A, I-20144 Milano, Italie.
GISMANN, A., 19, rue 12, Maadi, Egypte, R.A.U.
GITTENBERGER, E., Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Leiden, Nederland.
GIUSTI, F., Istituto di Zoologia Università, via Mattioli 4, Siena, Italie.
GODAN, D., Biologische Bundesanstalt für Land -u. Fortswirtschaft, Institut für Zoologie Berlin-Dahlem, Königin-Luise-Str. 19, 1 Berlin 33, Deutschland.
GOODHART, C. B., Cambridge University, Dept. of Zoology, Downing Street, Cambridge, England.
GUERRUCCI, M.-A., Ecole Normale Supérieure, Laboratoire de Zoologie, 46, rue d'Ulm, F-75 Paris 5ème, France.
HADŽIŠČE, S., Hidrobiološki Zavod, Ohrid, Jugoslavija.
HEATH, J., Biological Records Centre, Monks Wood Experimental Station, Abbots Ripton, Huntingdon PE17 2LS, England.
HEPPELL, D., The Royal Scottish Museum, Chambers Street, Edinburgh EH1 1JF, Scotland.
HETTICK, L., 933 Lynnwood Dr., Bartlesville, Oklahoma 74003, U.S.A.
HOLME, N. A., Marine Biological Association Plymouth, The Laboratory, Citadel Hill, Plymouth, England.
HUBENDICK, B., Naturhistoriska Museet, Box 11049, 40030 Göteborg, Sweden.
HURST, A., University of St. Andrews, Gatty Marine Laboratory, St. Andrews, Fife, Scotland, U.K.
IMHOF, G., II. Zoolog., Universität Wien, Dr. K. Luegerring 1, A-1010 Wien, Autriche.
JANUS, H., Staatliches Museum für Naturkunde in Stuttgart, Schloss Rosenstein, D-7 Stuttgart 1, Deutschland.
*JAYET, A., Laboratoire de Paléontologie, Université de Genève, CH-1211 Genève 4, Suisse.
JOOSSE, J., Dept. of Biology, Free University, P.B. 7161, Amsterdam, Nederland.
JUNG, P., Naturhistorisches Museum, Augustinergasse 2, CH-4051 Basel, Suisse.
KEARNEY, A., The Agricultural Institute, Ballinrobe, Co. Mayo, Ireland.
KERNEY, M., Dept. of Geology, Imperial College, London S.W. 7, England.
KLEEMANN, K., I. Zoolog. Institut der Universität Wien, Dr. Karl Luegerring 1, A-1010 Wien, Autriche.

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*deceased

KNUDSEN, J., Zoologisk Museum, Universitetsparken 15, DK-2100 Copenhagen Ø, Danmark.
KO BUN HIAN, Dept. of Zoology, University of Reading, Whiteknights, Reading RG6 5AJ, England.
KROLOPP, F. E., Ungarische Geologische Anstalt, Népstadion u. 14, Budapest, XIV, Ungarn.
KUIJPER, Wim W. J., De Lannoystraat 101, Den Haag, Nederland.
KUIPER, J. G. J., 121, rue de Lille, F-75 Paris 7ème, France.
LEMCHE, H., Zoologisk Museum, Universitetsparken 15, DK-2100 Copenhagen Ø, Danmark.
LLEWELLYN JONES, Joan, Seaview Avenue, West Mersea 2036, Essex, England.
LLEWELLYN JONES, John E., Soham Grammar School Cambridgeshire, 16, Brierley Walk, Cambridge CB 3N4, England.
McDONALD, S. C., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A.
MATTOS DOS SANTOS, M.-A., Junta de Investigacões do Ultramar, Rua Presidente Wilson, 6-4° dir., Lisboa 1, Portugal.
MAXWELL, W. L., Bristol University, 28 Woodfield Rd., Bristol BS6 6JQ, England.
MEAD, A. R., Dept. of Biological Sciences, University of Arizona, Tucson, Arizona 85721, U.S.A.
MEIJER, T., Philip Vingboonsstraat 50, Amsterdam 16, Nederland.
MELLO, M. D. A. de, 8, rue des Lilas, CH-1202 Genève, Suisse.
MERCER, M. C., Fisheries Research Board of Canada, Biological Station, Water St. East, St. John's, Newfoundland, Canada.
MERMOD, G., 22, Avenue Soret, CH-1203 Genève, Suisse.
MILLER, W., Dept. of Biological Sciences, University of Arizona, Tucson, Arizona 85721, U.S.A.
MISSET, M.-T., Muséum d'Histoire naturelle, CH-1211 Genève 6, Suisse.
MOENS, R., Station de Zoologie appliquée de l'Etat, 5800 Gembloux, Belgique.
MONGIN, D., Centre National de la Recherche Scientifique, 9, rue de Mezieres, F-75 Paris 6ème, France.
MORRISON, J. P. E., U.S. National Museum, Smithsonian Institution, Washington D.C. 20560, U.S.A.
MORTON, B., Dept. of Zoology, University of Hong-Kong, Hong-Kong.
MOUEZA, M., Institut Océanographique d'Alger, Jetée Nord, BP 90, Alger Bourse, Alger, Algérie.
NATTKAEMPER, G., II. Zoologisches Institut Wien, Luegerring 1, A-1010 Wien, Autriche.
NEWELL, P., Zoology Department, Westfield College, Kidderpore Avenue, London NW 3, England.
NICOLAY, K., Via Tomacelli, 146-IV P, 00186 Roma, Italie.
NIEUWENHUIS, J. G. B., Bentincklaan 37a, Rotterdam-4, Nederland.
NIJSSEN-MEYER, J., Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Leiden, Nederland.
NORRIS, A., City Museum, Municipal Buildings, Leeds 1, England.
NORTON, P. E. P., Zoological Department, University of Glasgow, Glasgow W.2, Scotland.
NUUS, J. G., Zee-Aquarium Delfzijl, De Paap 10, Delfzijl, Nederland.
OBERLING, J. J., Naturhistorisches Museum, 15 Bernastrasse, CH-3005 Bern, Suisse.
ØKLAND, J., Dept. of Limnology, University of Oslo, Blindern, Oslo 3, Norway.
ØKLAND, K. A., Dept. of Limnology, University of Oslo, Blindern, Oslo 3, Norway.
OSBORNE, N., Gatty Marine Laboratory, University of St. Andrews, St. Andrews, Fife, Scotland.

PAGET, O. E., Naturhistorisches Museum, Burgring 7, A-1014 Wien, Österreich.
PANETTA, P., Instituto Sperimentale Talassografico Taranto, Via Occlavio 64, I-74100 Taranto, Italie.
PARODIZ, J. J., Section of Invertebrates, Carnegie Museum, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213, U.S.A.
PEAKE, J. F., Dept. of Zoology, British Museum (Natural History), Cromwell Road, London S.W. 7, England.
PETERSEN, G. H., Zoologisk Museum, Universitetsparken 15, 2100 Kobenhavn, Danmark.
PETITJEAN, M., Université Paris V11, 26, rue de Bretagne, F-78 Versailles, France.
PETTITT, C., Manchester Museum, The University, Manchester, M/C M13 9PL, England.
PEZZOLI, E., Via Fornari 48 I-00146 Milano, Italie.
PICKRELL, D. G., Congleton R.D.C., 47, West Way, Holmes Chapel, Cheshire, England.
POSTMA, N., St. Annastraat 94, Nijmegen, Nederland.
REAL, G., Institut de Biologie Marine, 2, rue du Pr. Jalyet, F- 33 Arcachon, France.
RENAULT, L., Institut Océanographique d'Alger, Jetée Nord, BP 90 Alger Bourse, Alger, Algérie.
REX, M., Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.
RICHARDOT, M., C.N.R.S., 140, Cours Emile Zola, F-69 Villeurbanne, France.
RICHTER, I., Ta'bor Utca 13, Kiskunhalas, Hongrie.
RIGBY, J. B., Queen Elizabeth College, Campden Hill, London W. 8, England.
ROBERTSON, R., Academy of Natural Sciences of Philadelphia, Nineteenth and The Parkway, Philadelphia, Pennsylvania 19103, U.S.A.
ROOIJ-SCHUILLING, L. A. de, Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Leiden, Nederland.
RUNGGER, D., Station de Zoologie expérimentale, Université de Genève, 154, route de Malagnou, CH-1224 Genève, Suisse.
RUNGGER-BRAENDLE, E., Laboratoire de Génétique animale et végétale, 154, route de Malagnou, CH-1224 Genève, Suisse.
RUNHAM, N., Zoology Dept., University College of North Wales, Bangor, Caernarvonshire, Wales, U.K.
RUSSELL, J. C., Portsmouth Polytechnic, The Marine Laboratory, Ferry Road, Hayling, Hants, PO 11ODG, England.
SABELLI, B., Istituto di Zoologia, Via San Giacomo 9, Bologna, Italie.
SALVAT, B., Laboratoire de Malacologie, 55, rue de Buffon, F-75 Paris 5ème, France.
SALVAT, F., Laboratoire de Biologie Marine et Malacologie, 55, rue de Buffon, F-75 Paris 5ème, France.
SAMPAIO XAVIER, M. L., Escuela Superior de Higiene "Dr. Ricardo Jorge", Largo 1 de Dezembro, Porto, Portugal.
SCHALIE, H. van der, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104, U.S.A.
SCHELTEMA, R., Wood's Hole Oceanographic Institution, Wood's Hole, Massachusetts 02543, U.S.A.
SCHELTEMA, Amélie, Wood's Hole Oceanographic Institution, Wood's Hole, Massachusetts 02543, U.S.A.
SCHMEKEL, L., Max-Planck-Institut für Zellbiologie, Melanchthonstr. 36, BRD 74 Tübingen, Deutschland.
SCHUITEMA, A. K., Zee-Aquarium Delfzijl, De Paap 10, Delfzijl, Nederland.
SETTEPASSI, F., Via G. Caccini 1, Roma 00198, Italia.
SKELDING, M., Dept. of Zoology, Westfield College, Kidderpore Avenue, London, N.W. 3, England.

SLIGGERS, B., Rijks Geologische Dienst, Spaarne 17, Haarlem, Nederland.
SMITH, M., National Museum of Natural Sciences, Ottawa KIA OM8, Canada.
SMITH, Brian J., Curator of Invertebrates, National Museum of Victoria, 285-321 Russell Street, Melbourne, Victoria 3000, Australia.
SNELI, J.-A., Biologisk stasjon, N-7001 Trondheim, Norway.
SOLEM, A., Field Museum of Natural History, Lake Shore Drive at Roosevelt Road, Chicago, Illinois 60605, U.S.A.
SPADA, G., Via S. Felice 26, I-40122 Bologna, Italia.
SPAINK, G., Rijks Geologische Dienst, Spaarne 17, Haarlem, Nederland.
SPOEL, S. van der, Inst. for Taxonomic Zoology, Plantage Middenlaan 53, Amsterdam, Nederland.
STARMÜHLNER, F., I. Zoolog. Institut der Universität, Luegerring 1, A-1010 Wien, Österreich.
STREIFF, W., Laboratoire de Zoologie, Université de Caen, 2, rue de Beny, F-14 Caen, France.
TARDY, J., Laboratoire de Zoologie, Faculté des Sciences de Poitiers, F-86 Poitiers, France.
TESKEY, M., P.O. Box 239, Big Pine Key, Florida 33043, U.S.A.
TESTUD, A.-M., Muséum national d'Histoire naturelle, 55, rue de Buffon, F-75 Paris 5ème, France.
THIRIOT-QUIEVREUX, C., Centre Océanographique de Bretagne, B.P. 337, F-29-N-Brest, France.
THOMPSON, T. E., Zoology Department, University of Bristol, Bristol, England.
TIMMERMANS, L. P. M., Zoologisch Laboratorium, Janskerkehof 3, Utrecht, Nederland.
TOFFOLETTO, F., Via Eugenio Chiesa 4, I-20122 Milano 233, Italia.
TRUEMAN, E. R., Dept. of Zoology, The University, Manchester M13 9PL, England.
URK, R. M. Van, Rijksmuseum van Natuurlijke Historie, Leiden, Nederland.
VALOVIRTA, I., Zoological Museum, University of Helsinki, P. Rautatiekatu 13, 00100 Helsinki 10, Finland.
VERY, J.-M., Laboratoire de Paléontologie, Ecole des Sciences de la Terre, Université, CH-1211 Genève 4, Suisse.
VOVELLE, J., Université Paris V1, Histologie et Cytologie des Invertébrés Marins, Faculté des Sciences, 7, quai St-Bernard, F-75 Paris 5ème, France.
WALDEN, H. V., Naturhistoriska Museum, S-400 30 Göteborg 11, Sweden.
WARWICK, T., Zoology Department, Edinburgh University, Westmains Road, Edinburgh, U.K.
WIRTH, U., Zoolog. Institut, Katharinestr. 20, D-7800 Freiburg i. Br., Deutschland.
WIRTH-SANGMEISTER, B., Beethovenstr. 24, D-7800 Freiburg, Deutschland.
WIUM-ANDERSEN, G., Danish Bilharziasis Laboratory, Charlottenlund, Danmark.
WUETHRICH, M., Oberfeldstr. 32, CH-3067 Boll, (Bern) Schweiz.
WYSOCZANSKI, C., 16, rue du Levant, F-74 Annemasse, Hte-Savoie, France.
ZANINETTI, L., Laboratoire de Paléontologie, Université de Genève, CH-1211 Genève 4, Suisse.
ZILCH, A., Senckenberg Museum, Senckenberg-Anlage 25, D-6 Frankfürt/M. 1, Deutschland.

ADDRESS CHANGES OF AUTHORS

BARBOSA, F. S., Universidade de Brasilia, Faculdade de Ciências da Saude, Brasilia D.F. 70000, Brésil.
CAMERON, R. A. D., Dept. of Extramural Studies, University of Birmingham, P.O. Box 363, Birmingham B15 2TT, U.K.
EDMUNDS, J. and EDMUNDS, M., Dept. of Biological Sciences, University of Exeter,

Hatherly Laboratories, Prince of Wales Road, Exeter, Devon, U.K.
RUNHAM, N.W., BAILEY, T. G. and LARYEA, A. A., Biologisch Laboratorium, Vrije Universiteit, De Boelelaan 1087, Amsterdam-Buitenveldert, Nederland.
SCHMEKEL, Luise, Zoologisches Institut der Westfälischen Wilhelms-Universität, D-44 Münster (Westf.) Hüfferstrasse 1.
TARDY, J., Laboratoire de Biologie et Biochimie marines, IUT de la Rochelle, B.P. 536, rue de Roux, 17000 La Rochelle, France.

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