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DONNÉES HISTOLOGIQUES SUR L'APPAREIL DIGESTIF ET LA DIGESTION DES ATLANTIDAE (PROSOBRANCHIA: HETEROPODA)[1]

Micheline Martoja[2] et Catherine Thiriot-Quiévreux[3,4]

RÉSUMÉ

La structure histologique de l'appareil digestif et ses modifications histophysiologiques au cours de la digestion sont décrits dans 6 espèces d'Atlantidae adultes. Les résultats sont interprétés sur le plan fonctionnel et discutés du point de vue de la systématique.

Le tractus digestif des Atlantidae comporte un oesophage faisant fonction de jabot, un estomac de volume réduit et un court intestin. Une paire de glandes salivaires tubulaires et une glande digestive (hépatopancréas) lui sont associées mais il est dépourvu de glandes oesophagiennes et rectales. L'appareil radulaire présente les caractères habituels connus chez les autres prosobranches.

Le tube digestif est totalement dépourvu de mucocytes. Quelques glandes unicellulaires sont réparties dans la paroi buccale et la partie antérieure de l'oesophage. Le jabot est le siège d'une sécrétion apocrine. L'activité glandulaire est minime dans l'estomac et nulle dans l'intestin.

Une glande salivaire est constituée d'un sac terminal, d'un tube glandulaire et d'un long canal collecteur. Le tube glandulaire est formé de cellules ciliées et de 3 types de cellules sécrétrices: cellules à sécrétion protéique, cellules à concrétions et mucocytes. Le canal collecteur se termine, au voisinage de la bouche, par un court segment muqueux.

Le parenchyme de la glande digestive rassemble des cellules principales, des cellules à ergastoplasme et des cellules à inclusions minérales dont l'autonomie en tant que lignées cellulaires est attestée par des données topographiques (emplacements distincts) et cytophysiologiques (cycles d'activité indépendants). La répartition des cellules à inclusions minérales représente un caractère spécifique et l'évolution se traduit par un groupement de plus en plus marqué de ces éléments.

Pour les cellules à sécrétion protéique des glandes salivaires, pour les cellules du jabot et pour les cellules à ergastoplasme de la glande digestive, la synthèse intracellulaire des sécrétions précède le repas. L'extrusion paraît déclenchée par l'arrivée du bol alimentaire dans les 2 premiers cas, par des facteurs internes, dans le dernier cas. Toutes ces cellules sécrètent probablement des enzymes digestives. Les cellules principales de la glande digestive ont un rythme inverse et leur fonction essentielle paraît être l'accumulation de lipides et glycoprotéines.

La structure de l'appareil digestif des Atlantidae présente un certain nombre de points communs avec celles des opisthobranches. Les caractères histologiques des glandes salivaires, qui sont très proches avec celles des Pyramidellidae, pourraient offrir un certain intérêt sur le plan de leurs affinités systématiques.

INTRODUCTION

Les Atlantidae présentent successivement, au cours de leur vie, 2 types de régimes alimentaires différents. Alors que les larves sont microphages, les adultes sont des carnassiers très souvent cannibales qui avalent, entières, d'énormes proies. Un changement aussi fondamental dans la biologie alimentaire est de nature à entraîner des modifications de l'appareil digestif. Or l'étude topographique des larves d'*Oxygyrus* et d'*Atlanta*, puis l'analyse des phénomènes survenant au cours de la metamorphose (Thiriot-Quiévreux, 1969, 1971) ont bien mis en évidence de telles modifications. Toutefois, leur aboutissement reste inconnu puisque, à l'exception de quelques indications sur l'anatomie

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microscopique (Furnestin, 1961) et d'une comparaison très succincte avec les Pterotracheidae (Gabe, 1962, 1966), il n'existe aucune donnée relative à l'histologie de l'appareil digestif des Atlantidae adultes.

En effet, les travaux anciens consacrés aux Heteropoda (Gegenbaur, 1855; Leuckart, 1855; Krasucki, 1911; Reupsch, 1912) comportent soit des descriptions anatomiques d'ailleurs très précises, soit des descriptions histologiques d'espèces n'appartenant pas à la famille des Atlantidae. Quant aux recherches récentes, elles concernent exclusivement deux genres de Pterotracheidae, *Pterotrachea* et *Firoloida* (Gabe, 1952, 1966).

Il nous a donc paru intéressant d'entreprendre l'étude histologique de l'appareil digestif et l'étude histophysiologique de la digestion dans le but de comparer l'organisation de l'adulte à celle de la larve et de dégager les caractères propres à ce groupe.

Les 6 espèces que nous avons examinées, *Oxygyrus keraudreni* Lesueur, *Protatlanta souleyeti* (Smith), *Atlanta fusca* Souleyet, *A. inflata* Souleyet (= *A. quoyana*), *A. peroni* Lesueur et *A. lesueuri* Souleyet, représentent les principales étapes phylogéniques de la famille des Atlantidae, étapes que des recherches récentes ont bien établies (Richter, 1961, 1969).

MATÉRIEL ET TECHNIQUES

Tous les animaux que nous avons étudiés proviennent de la Méditerranée. La majeure partie des représentants d'*Atlanta inflata* et d'*A. lesueuri* ont été obtenus dans le plancton de Banyuls-sur-mer (Thiriot-Quiévreux, 1971). Quelques individus d'*A. lesueuri* sont originaires du plancton de Villefranche-sur-mer. Les spécimens d'*Oxygyrus keraudreni, Protatlanta souleyeti, Atlanta fusca* et *A. peroni* ont été récoltés au cours d'une campagne océanographique en Méditerranée Orientale à bord de l'*Atlantis II* (Woods Hole Oceanographic Institution).

Les animaux vivants ont d'abord été triés puis isolés du plancton; l'état du tube digestif et notamment sa réplétion ou sa vacuité, a été noté pour chaque individu. Certains ont été mis en élevage en vue d'une étude histophysiologique. D'autres ont été fixés immédiatement.

Nous avons utilisé, pour la fixation, les mélanges de Bouin, Halmi, Carnoy et Baker. La plupart des pièces ont été incluses à la paraffine. Les coupes de 5 μm d'épaisseur ont été, dans tous les cas, étalées et montées en séries complètes. En raison de la petite taille des animaux (1 à 3 mm) et de la difficulté qui en résulte de réunir un grand nombre de coupes analogues nécessaires à la réalisation d'épreuves convenables, nous n'avons pas abordé d'étude à proprement parler, histochimique. Seules les quelques méthodes suivantes ont été appliquées:

Étude topographique: méthode à l'azan (Heidenhain) et coloration par la fuchsine paraldéhyde après oxydation permanganique suivie de coloration par l'hématoxyline-picro-indigocarmin (Gabe).

Caractérisation des composés "APS-positifs" et notamment des glucides: réaction à l'APS (Hotchkiss-McManus) suivie de coloration soit à l'hématoxyline, soit au bleu de toluidine à pH 4,5.

Caractérisation des mucopolysaccharides acides: réaction métachromatique au bleu de toluidine ou coloration au bleu alcian à pH 3,2 suivie de réaction à l'APS et d'une coloration à l'hématoxyline (Mowry).

Caractérisation des protéines: réaction à l'alloxane-Schiff sans coloration de fond (Yasuma & Ichicawa).

Caractérisation des protéines à groupements SH et SS: réaction au D.D.D. précédée ou non d'une réduction par le sulfure d'ammonium et sans coloration de fond (Barrnet & Seligman).

Caractérisation des anions: réaction de substitution à l'argent (Von Kossa).

Caractérisation des lipides hétérophasiques: coloration au noir Soudan de matériel formolé et post-chromé (Baker).

Caractérisation des chromolipoïdes: coloration au bleu de Nil suivie d'un traitement par l'eau oxygénée (Hueck).

Quelques individus d'*Atlanta inflata*, destinés à l'étude spectrographique, ont été fixés par le mélange de Carnoy. Devant être coupés avec leur coquille, sans décalcification préalable, ils ont été inclus non dans la paraffine, mais dans le mélange araldite-epon et débitées en coupes semi-fines à l'ultra-microtome. L'analyse a été faite à la microsonde électronique C.A.M.E.C.A. MS 46; nous renvoyons au mémoire de Galle (1965) pour l'exposé théorique et pratique de cette méthode.

Ont été recherchés par ce moyen, les éléments: Ca, K, Mn, Fe, S, P, Si, V, Zn, Cu, Na, Mg. Seules les données positives sont mentionnées au chapitre "Résultats."

Enfin, quelques radulas ont été examinées, après dissection, nettoyage et métallisation, au microscope électronique à balayage (type Cambridge S 4).

RÉSULTATS

DONNÉES ANATOMIQUES

Le tube digestif des Atlantidae s'étend depuis la bouche, située à l'extrémité du mufle, jusqu'à l'anus logé à l'avant de la cavité palléale (Fig. 1). La bouche s'ouvre sur la cavité buccale où débouchent, dorsalement l'oesophage, latéralement les 2 canaux salivaires et ventralement, l'appareil radulaire très développé qui se dévagine lors de la capture des proies.

Le tube digestif proprement dit peut être divisé en 3 segments. L'oesophage, très long, traverse tout le céphalopodium puis s'engage dans la partie ventrale de la masse viscérale, en longeant le muscle columellaire. Quand l'animal est en extension et à jeun, l'oesophage forme un mince tuyau presque droit, entre la bouche et la masse viscérale. Il se replie sur lui-même et décrit 2 ou 3 sinuosités au voisinage de cette dernière, si l'animal rentre dans sa coquille. Lorsqu'une proie est avalée, la partie antérieure de l'oesophage se dilate considérablement lors de son passage, mais retrouve aussitôt son diamètre initial. C'est alors la zone comprise entre le collier nerveux péri-oesophagien et la masse viscérale, qui s'élargit à son tour. Elle reste, quant à elle, dilatée pendant plusieurs heures (Richter, 1969; Thiriot-Quiévreux, 1969) et fait fonction de jabot. Le second segment du tube digestif, court et globuleux, est inclus tout entier dans la masse viscérale, au con-

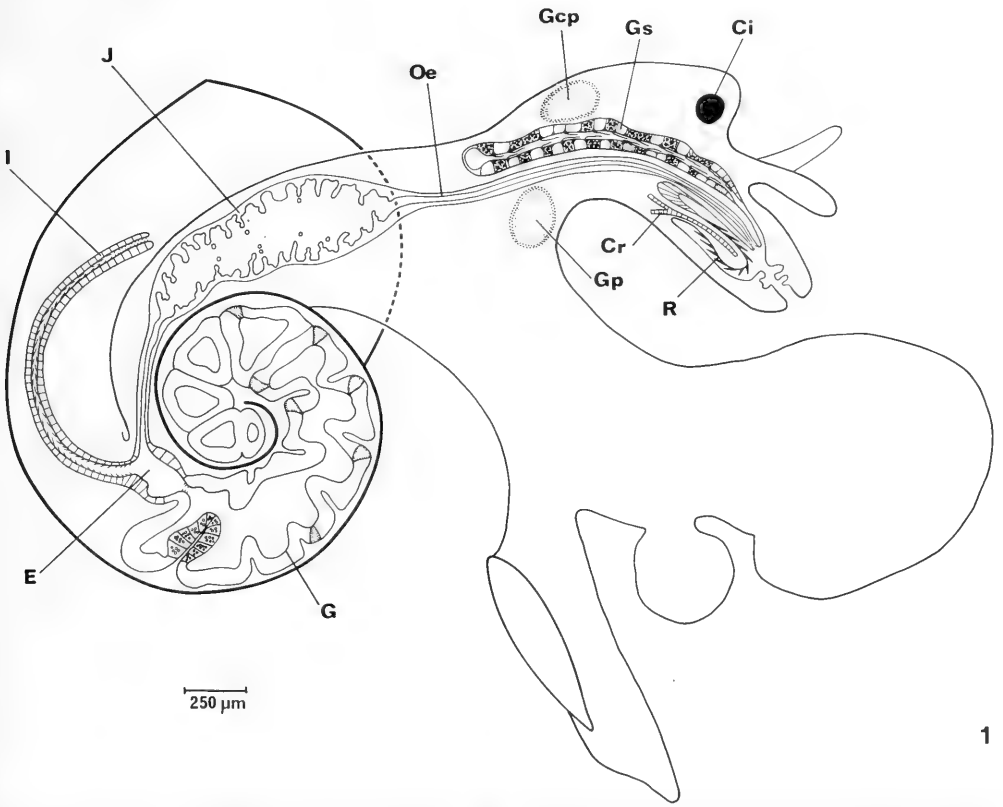


FIG. 1. Schéma de l'organisation de l'appareil digestif d'*Atlanta lesueuri* (les différents organes sont arbitrairement supposés dans un même plan). Ci: cristallin; Cr: cartilage radulaire; E: estomac, G: glande digestive: Gcp: ganglions cérébro-pleuraux; Gp: ganglions pédieux; Gs: glande salivaire; I: intestin; J: jabot; Oe: oesophage; R: radula.

tact de la gonade et de la glande digestive (hépatopancréas) avec laquelle il est en communication. De tels rapports anatomiques désignent ce second segment comme étant l'estomac. A partir de là, la direction générale du tube digestif se trouve ramenée vers l'avant. C'est au voisinage immédiat de l'orifice oesophagien que le troisième segment ou intestin émerge de l'estomac. Il est rectiligne, de calibre réduit, assez court et dorsal par rapport à l'oesophage. Sa zone orale, accolée à la face ventrale du rein, est intraviscérale tandis que sa région aborale est intrapalléale.

Deux types de glandes anatomiquement individualisées, les glandes salivaires et la glande digestive, sont annexées au tube digestif. Les glandes salivaires sont paires et asymétriques, la gauche étant de taille inférieure à la droite. Elles se présentent comme des tubes effilés à l'extrêmité antérieure. Elles traversent le collier périoesophagien et s'ouvrent dans la cavité buccale par l'intermédiaire de fins canaux. Transparentes, très mobiles, elles peuvent, selon les mouvements de l'animal, s'allonger notablement jusqu'à atteindre une longueur double de celle du mufle. La glande digestive, formée de 2 lobes dissymétriques, constitue à elle seule, la majeure partie du tortillon. Elle communique avec l'estomac par un seul et très large orifice, sans qu'il existe de canaux différenciés. Au cours de la digestion, des mouvements de va-et-vient du bol alimentaire peuvent être observés entre l'estomac et la glande digestive; de tels mouvements n'ont lieu que chez les individus en extension.

Il apparaît donc que l'appareil digestif des Atlantidae présente une structure anatomique simple. La netteté des connexions ne laisse aucun doute quant à l'interprétation de ses différents éléments. L'absence de glandes oesophagiennes et rectales, si fréquentes dans d'autres groupes de prosobranches, mérite d'être soulignée.

DONNEES HISTOLOGIQUES

I. LE TUBE DIGESTIF

1. Cavité buccale

Le volume compris entre l'orifice buccal et le point où se rejoignent l'appareil radulaire et l'oesophage, correspond à la cavité buccale dans laquelle débouchent aussi les 2 canaux salivaires.

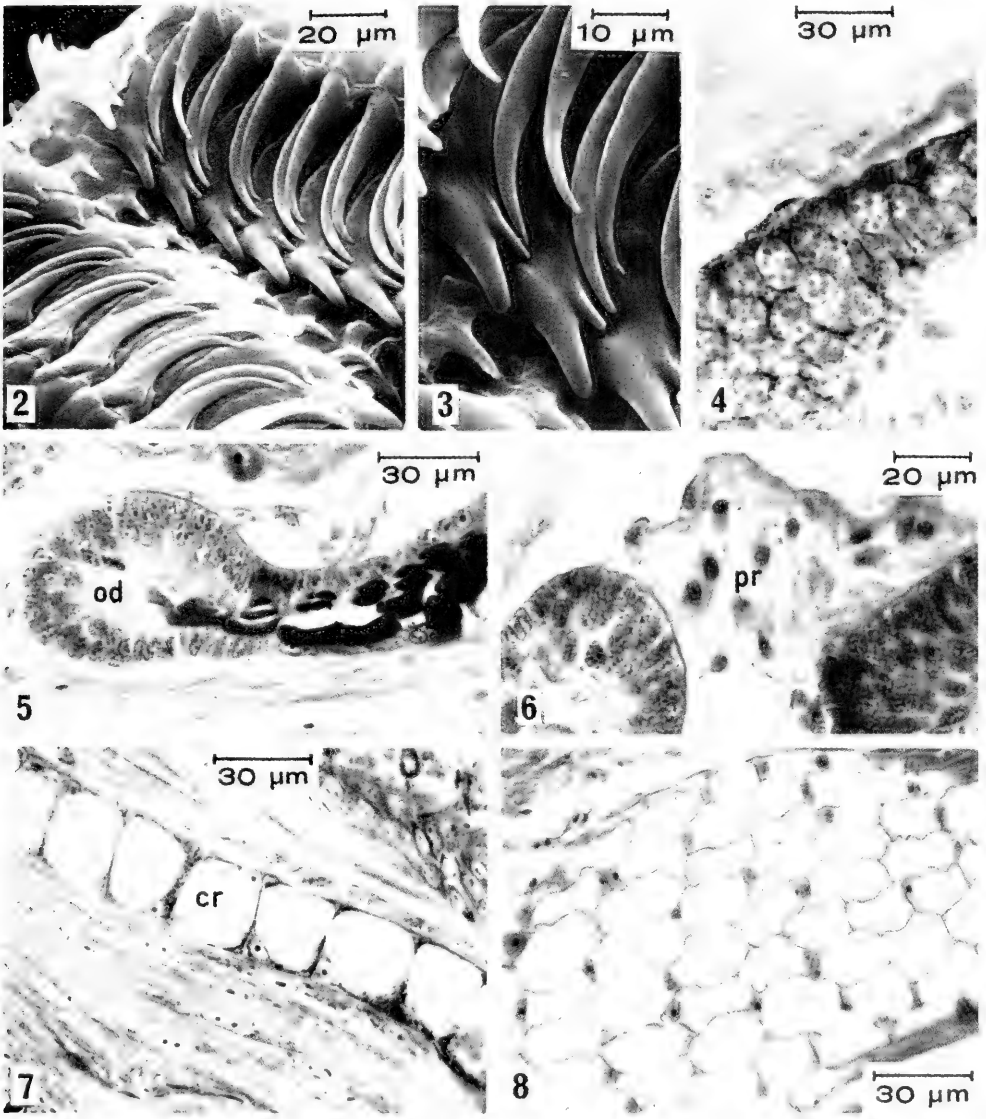
La paroi de la cavité buccale prolonge le tégument du mufle et les caractères histologiques de ce dernier y sont conservés en majeure partie. Elle comporte une musculeuse importante faite de fibres entrecroisées, une lame basale et un épithélium constitué de cellules assez hautes et dépourvues, pour la plupart, d'activité sécrétoire. Les différences les plus importantes par rapport au tégument concernent l'épaisseur de la lame basale et le nombre des cellules glandulaires incluses dans l'épithélium. La lame basale, très épaisse dans le tégument, devient beaucoup plus fine et moins plissée à l'intérieur de la bouche. Les cellules glandulaires deviennent très rares mais sont identiques aux glandes unicellulaires du tégument. Les unes sont des mucocytes typiques sécrétant des mucopolysaccharides acides. Les autres sont des cellules caliciformes à noyau basal et apex ouvert, remplies de gros grains APS-positifs, non métachromatiques, réagissant positivement à l'alloxane-Schiff et au D.D.D.; leur sécrétion est donc de nature protéique.

L'apex des cellules épithéliales, comme dans bien d'autres segments de l'appareil digestif, d'ailleurs, mériterait une étude ultra-structurale. Il est, en effet, recouvert d'une épaisse formation parfois épineuse d'aspect cuticulaire, qui va s'amincissant d'avant en arrière; elle est colorable par la fuchsine paraldéhyde et APS-positive. Chez certains individus cependant, la présence dans la cavité buccale, de structures filiformes à allure de cils, est nettement visible. Les rapports aussi bien que la nature exacte de cette "cuticule" et de ces "cils" ne peuvent être précisés au microscope photonique.

La cavité buccale ne présente, selon les genres ou les espèces étudiés, aucune différence notable. Chez *Oxygyrus* toutefois, les cellules épithéliales renferment de nombreux petits grains de pigment noir. Dans ce même genre, les évaginations de la cavité buccale où débouchent les canaux salivaires, sont bordées de quelques très grosses cellules remplies de grains ocres atteignant 1 μm de diamètre et rappelant d'assez près ceux de la glande digestive (cellules du type III) (Fig. 18).

Une mention particulière doit être faite au sujet du diverticule ventral de la cavité buccale qui s'enfonce sous le segment ré-

fléchi de la radula lorsque celle-ci est au repos. Son épithélium se place en regard des dents fonctionnelles et pourrait être qualifié de sub-lingual. Il est caractérisé par une intense activité glandulaire. Chez *Oxygyrus*, où ce caractère apparaît avec le plus de netteté, l'épithélium sub-lingual comporte, en alternance régulière, de grosses cellules sphériques à noyau basal remplies de grains de sécrétion et des cellules comblant les interstices, c'est-à-dire rétrécies dans leur zone médiane, à noyau apical et cytoplasme parsemé de granules de pigment noir (Fig. 4). L'ensemble est



FIGS. 2-8. Appareil radulaire.

2-3. *Atlanta peroni.* Radula photographiée au microscope electronique à balayage.
4. *Oxygyrus keraudreni* (APS-bleu alcian-hématoxyline). Détail de l'épithélium sub-lingual avec ses cellules glandulaires et ses cellules à pigments.
5. *Atlanta lesueuri* (Azan). Les odontoblastes (od) et les premières dents radulaires.
6. *Oxygyrus keraudreni* (APS-bleu alcian-hématoxyline). La papille radulaire (pr).
7. *Atlanta lesueuri* (APS-bleu de toluidine). Coupe sagittale du cartilage radulaire (cr).
8. *Atlanta lesueuri* (Azan). Coupe frontale du cartilage radulaire.

recouvert d'une cuticule épaisse. Les cellules glandulaires élaborent une sécrétion protéique comme les cellules caliciformes de la cavité buccale déjà mentionnées. Elles se raréfient au fur et à mesure que l'on progresse vers l'orifice buccal. Chez *Protatlanta,* l'alternance n'est pas aussi régulière et l'épithélium sub-lingual renferme moins de cellules glandulaires; il s'y mêle, par contre, des mucocytes. Dans le genre *Atlanta*, l'équipement glandulaire se réduit à une vingtaine de cellules et il n'y a pas de mucocytes.

2. Appareil radulaire

Outre la radula proprement dite, l'appareil radulaire comprend d'une part, la gaine radulaire, diverticule épithélial où sont élaborés les dents et le ruban qui les porte, d'autre part, un système de muscles, cartilage et conjonctif assurant le soutien et la mobilité de l'ensemble (Buchmann, 1924; Tesch, 1949). La radula, de type taenioglosse, comporte de part et d'autre de la dent médiane, une dent latérale et 2 marginales. Elle subit, au cours de l'ontogénie et de la phylogénie des Atlantidae, une évolution que Richter (1961) put établir en analysant les caractères spécifiques de la dent latérale. Nos examens de radula, au microscope à balayage (Figs. 2-3), confirment entièrement les descriptions de cet auteur. Par ailleurs, les caractères histologiques du système radulaire et leurs variations à travers le phylum des mollusques, one été longuement étudiés par Gabe & Prenant dont les conclusions ont été résumées dans une publication datée de 1958. Nous croyons donc superflu de donner à nouveau une description détaillée de l'organe et nous nous bornerons à dégager quelques traits caractéristiques de son organisation dans la famille des Atlantidae, non étudiée par Gabe & Prenant dans leur travail consacré aux Heteropoda (1950).

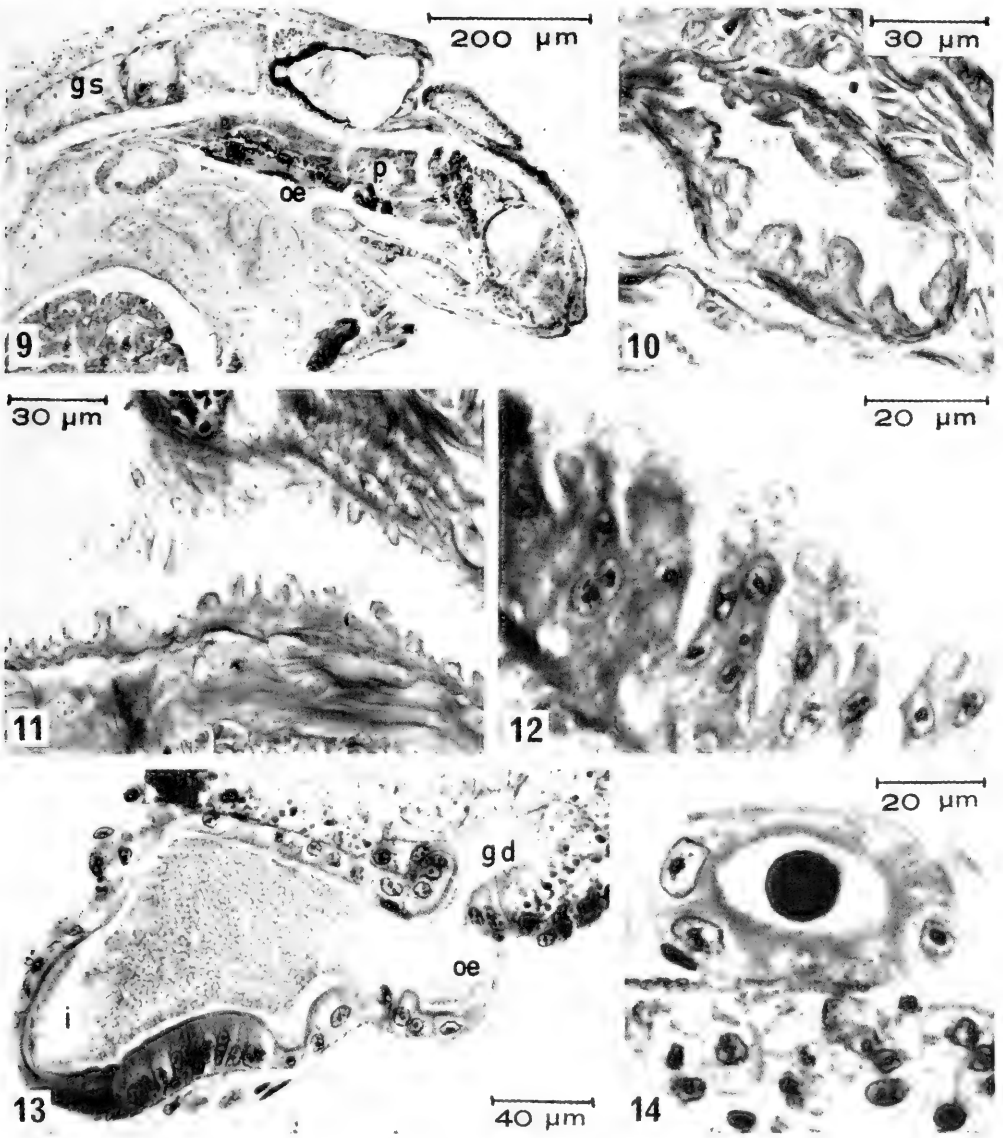
L'appareil radulaire atteint un développement considérable chez *Oxygyrus.* Son volume est encore très important chez *Protatlanta.* Il est, au contraire, relativement réduit dans *Atlanta.* Cette réduction de l'appareil radulaire affecte tous les éléments qu'il s'agisse du volume de la masse musculo-cartilagineuse, des dimensions des dents ou de la longueur de la gaine radulaire.

Dans tous les cas, les odontoblastes qui tapissent le fond de la gaine sont des cellules hautes et étroites, sans ergastoplasme visible, dépourvues aussi bien de glycogène que de sécrétions figurées ou d'inclusions minérales (Fig. 5). Ils sont reliés aux dents en voie d'élaboration par de fins tractus filiformes. L'épithélium inférieur est régulièrement aplati tandis que l'épithélium supérieur est plus haut et forme des franges qui s'intercalent entre les dents. Les caractères généraux de ces 2 épithéliums sont les mêmes que chez les autres Heteropoda. Les caractères histochimiques sont eux aussi très voisins; toutefois, les composés APS-positifs qui y ont été décrits par Gabe & Prenant (1958) n'apparaissent nettement chez aucun des Atlantidae examinés.

Les affinités tinctoriales des dents et leurs modifications sont comparables à celles des autres gastéropodes. Les dents les plus récentes sont cyanophiles, faiblement APS-positives et métachromatiques, c'est à dire colorables en violet par le bleu de toluidine. Elles deviennent ensuite érythrophiles et fortement APS-positives; des protéines riches en groupements SH et SS, décelables par les réactions à l'alloxane-Schiff et au D.D.D., s'y accumulent. Le bleu de toluidine les colore à ce niveau en bleu-vert, ce que nous considérons comme l'indice d'une minéralisation. Les dents achevées et fonctionnelles sont transparentes et chromophobes. Elle réagissent de façon positive à la méthode de Von Kossa mais l'intensité de la réaction est bien moindre que celle obtenue au niveau d'autres structures minéralisées telles que la coquille.

Le tissu musculaire n'offre aucune particularité. Le cartilage, au contraire, nous semble mériter quelque attention. Comme chez les autres Heteropoda, "son aspect rappelle à certains égards, celui d'un parenchyme végétal avec des parois assez minces" (Gabe & Prenant, 1950). Il n'est entouré, ici, d'aucune gaine fibreuse visible dans nos conditions d'observation. Lorsque le plan de coupe coïncide avec le plan sagittal de la lame cartilagineuse, le tissu apparaît formé d'une seule couche de volumineuses cellules cubiques et jointives (Fig. 7). Leur cytoplasme est pariétal et le noyau occupe l'un des angles; le centre est optiquement vide (Fig. 8). Chez *Atlanta,* ces cellules renferment un composé APS-

positif réparti en très petits grains. Bien que l'épreuve à la maltase n'ait pas été pratiquée, l'aspect morphologique de ce composé permet de supposer qu'il s'agit de glycogène. Le cartilage des individus d'*Oxygyrus* et de *Protatlanta,* que nous avons examinés, ne comportait ni glycogène ni inclusion figurée d'aucune sorte. Les espaces intercellulaires remplis d'un matériel cyanophile, APS-positif et métachroma-



FIGS. 9-14. Tube digestif.

9. *Atlanta inflata* (APS-bleu alcian-hématoxyline). Coupe sagittale d'un animal venant d'ingérer une proie (p); remarquer l'oesophage distendu (oe) et la glande salivaire (gs).
10. *Protatlanta souleyeti* (Azan). Zone antérieure de l'oesophage précédant les ganglions buccaux.
11. *Protatlanta souleyeti* (Azan). Zone moyenne de l'oesophage située entre les ganglions buccaux et le collier péri-oesophagien.
12. *Atlanta lesueuri* (Azan). Images de sécrétion apocrine dans le jabot.
13. *Atlanta lesueuri* (APS-hématoxyline). Coupe de l'estomac intéressant l'arrivée de l'oesophage (oe), le départ de l'intestin (i) et l'orifice de la glande digestive (gd).
14. *Atlanta lesueuri* (APS-hématoxyline). Coupe transversale de l'intestin.

tique, n'atteignent pas 0,5 µm de large et cette largeur est constante; leur développement est minime par rapport au volume cellulaire.

Chez *Oxygyrus* et *Protatlanta,* le segment aboral de la gaine est entouré d'un tissu conjonctif particulier comportant un feutrage de fibres métachromatiques et colorables par le bleu alcian. Quelques petites cellules ovoïdes sont disséminées entre les fibres (Fig. 6). Cette formation, par ses caractères histologiques, correspond à la papille radulaire décrite par Gabe & Prenant. Dans le genre *Atlanta,* la papille est réduite à quelques cellules emprisonnées dans une substance fondamentale plus homogène où les fibres apparaissent mal. Elle forme un cône dont le sommet s'étire en un fin filament rattachant l'extrémité de la gaine à l'apex de la masse musculo-cartilagineuse.

3. Oesophage

La limite antérieure de l'oesophage apparaît sans ambiguïté puisqu'elle s'établit d'après des connexions anatomiques et correspond au carrefour où se rejoignent le tube digestif et l'appareil radulaire. Sa limite postérieure est beaucoup moins précise et ne repose que sur des caractères histologiques (Fig. 9). La paroi oesophagienne est toujours constituée d'une musculeuse, d'une basale et d'un épithélium. Chacun de ces éléments est susceptible de varier, soit en fonction du niveau considéré, soit selon l'espèce.

Chez *Oxygyrus* et *Protatlanta,* l'oesophage peut être divisé en 3 segments. Le très court segment initial s'étend de la bouche jusqu'aux ganglions buccaux. Le segment moyen va des ganglions buccaux au collier nerveux péri-oesophagien qu'il traverse. Le segment postérieur débute immédiatement en arrière du collier et se prolonge jusqu'à l'estomac; c'est lui qui fait fonction de jabot.

Dans le segment initial (Fig. 10), la musculeuse, faite de fibres entrecroisées, est bien développée. Les cellules épithéliales sont assez larges, irrégulièrement hautes et portent une ciliature longue et flexueuse. Elles sont pourvues d'un gros noyau central, très pauvre en chromatine. Leur cytoplasme ne montre aucune basophilie et elles n'ont, sans doute, pas d'ergastoplasme. Elles ne renferment aucune sécrétion figurée. Au voisinage immédiat de la cavité buccale, quelques éléments glandulaires caliciformes sont inclus dans l'épithélium, Leur noyau et leur ergastoplasme occupent la base de la cellule; la sécrétion, de nature protéique, présente les mêmes caractères que dans la cavité buccale proprement dite. Le segment moyen diffère du précédent par une musculeuse un peu moins importante mais surtout par son épithélium. Celui-ci est formé de cellules plus hautes, plus étroites, n'adhérant entre elles qu'à la base et s'étirant librement vers la lumière. Leur noyau est souvent apical. Leur cytoplasme est acidophile et granuleux. Elles sont recouvertes d'un fin liseré épineux et cyanophile. Ces particularités donnent à l'ensemble un aspect dentelé (Fig. 11). Au niveau du segment postérieur, la musculeuse devient très réduite et discontinue. Elle est formée de fibres circulaires ou obliques non jointives. L'épithélium est fait de cellules plus volumineuses que dans le segment moyen. Ces cellules sont normalement bombées à l'apex. Elles s'étirent et s'aplatissent quand l'organe est en état de réplétion. Elles ont un gros noyau à chromatine lâche où le nucléole est bien visible. Des mitoses, rares d'ailleurs, peuvent être observées dans ce segment. Le cytoplasme granulaire est dépourvu de toute basophilie signalétique d'un ergastoplasme. L'immense majorité de ces cellules porte un revêtement APS-positif montrant une striation dans quelques cas favorables. A la différence de la "cuticule" de la cavité buccale, ce revêtement n'a que peu d'affinité pour la fuchsine paraldéhyde. Quelques cellules, pourvues de cils longs et grêles, sont groupées en une bande qui parcourt toute la longueur du jabot jusqu'à l'estomac.

Chez *Atlanta,* il n'est pas possible de distinguer trois segments oesophagiens. Il existe, comme chez *Protatlanta* ou *Oxygyrus,* un court segment initial cilié mais, au delà des ganglions buccaux, l'oesophage présente un aspect uniforme. La musculeuse, relativement importante dans la zone antérieure, se réduit progressivement. La lame basale, épaisse et sinueuse, traduit bien, par sa morphologie, les possibilités de distension de cet oesophage-jabot. L'épithélium est formé de cellules jointives jusqu'à mi-hauteur. Leur zone supérieure est, au contraire, libre de tout contact avec les cellules voisines et il en résulte que la surface épithéliale est fortement bour-

souflée. Le noyau se situe dans la moitié inférieure de la cellule. Le cytoplasme basal est érythrophile, dense, fibrillaire alors que dans la région apicale, il est clair et spongieux. Le revêtement apical apparaît d'autant mieux que la zone supérieure est moins dilatée.

Aucune des espèces examinées ne possède de glandes oesophagiennes unicellulaires, à l'exception des quelques éléments qui marquent la limite de la cavité buccale et qui ont déjà été mentionnés. L'oesophage ne comporte pas davantage de mucocytes. Il serait toutefois abusif de lui dénier toute fonction sécrétrice. En effet, chez certains individus, le renflement qui surmonte d'ordinaire les cellules et qui est pourvu d'un cytoplasme clair, se dilate et va jusqu'à former une bulle reliée seulement au corps cellulaire par un mince pédicule. Chez d'autres, la lumière oesophagienne contient de très nombreuses sphères cytoplasmiques isolées des cellules-mères tandis que l'épithélium, hérissé de pédicules rompus, présente une allure déchiquetée. Ces aspects autorisent à considérer que le jabot est le siège d'une sécrétion apocrine (Fig. 12).

4. Estomac

Lorsqu'il est vide, l'estomac n'est guère qu'un carrefour où se rejoignent l'oesophage, la glande digestive et l'intestin. En état de réplétion, son individualité est plus marquée et il forme une poche dilatée (Fig. 13). Sa structure histologique est simple. En effet, la musculeuse, déjà réduite autour de la région postérieure du jabot, semble inexistante. Le tissu conjonctif n'est représenté que par quelques fibrocytes; la basale est fine. La paroi gastrique est donc constituée presque exclusivement par un épithélium.

Dans les 3 genres, l'élément essentiel de cet épithélium est une cellule cubique, à cytoplasme acidophile et granuleux, sans ergastoplasme. Lorsque l'espèce est très pigmentée (*Atlanta fusca,* par exemple), le cytoplasme contient de minuscules grains de pigments probablement mélaniques. L'examen ultra-structural de l'apex de ces cellules présenterait certainement quelque intérêt, son étude précise dépassant les possibilités de la microscopie photonique. Dans certaines zones de l'estomac, il est représenté par un bordure APS-positive ne montrant aucune striation dans nos conditions d'observation. Dans d'autres zones, au contraire, il forme de longs filaments disposés sans orientation précise. L'extension et la répartition de ces zones varient d'un individu à l'autre ce qui pourrait être l'indice de leur caractère temporaire. Sous réserve de confirmation ultérieure, nous pensons que les cellules gastriques pourraient porter des microvillosités susceptibles de s'étirer ou de se rétracter en fonction du cycle digestif. Elles ne manifestent aucun signe d'activité glandulaire, n'accumulent aucune inclusion et ne montrent aucune image de sécrétion apocrine.

Quelques cellules appartenant à un second type forment une étroite bande dans la zone d'émergence de l'intestin. Elles sont 2 à 3 fois plus hautes que les précédentes. Les noyaux sont allongés parallèlement au grand axe cellulaire. Le cytoplasme supra-nucléaire, qui est spongieux, contient de petits granules ronds, APS-positifs, clairsemés au voisinage du noyau mais devenant de plus en plus nombreux vers l'apex. Ce dernier pose les mêmes problèmes d'interprétation que précédemment. Les grains de sécrétion sont plus nets chez *Oxygyrus* et *Protatlanta* que chez *Atlanta.*

Chez certains individus, de nombreuses cellules libres ovoïdes ou piriformes, à rapport nucléo-plasmique élevé, entourent l'estomac. Leur cytoplasme contient souvent des inclusions figurées dont les affinités tinctoriales sont identiques à celles du contenu stomacal. Certaines d'entre elles se rencontrent aussi, mais plus rarement, intercalées entre les cellules épithéliales de l'estomac. Ces cellules libres ont été observées dans toutes les espèces étudiées mais c'est chez *Protatlanta* qu'elles apparaissent avec le plus de netteté. En l'absence d'expérimentation, leur signification apparaît mal. Il nous paraît toutefois plausible de les rapprocher des amibocytes qui traversent la paroi de l'estomac et dont le rôle dans la digestion a été expérimentalement démontré chez un néogastropode (Martoja, 1964).

5. Intestin

Le segment terminal du tube digestif atteint un degré de réduction et simplification extrême qui concerne à la fois sa longueur, son diamètre et ses caractères histologiques. Il présente, en outre, une

structure uniforme et ne donne lieu à aucune subdivision.

La section de l'intestin est régulièrement circulaire sauf au voisinage de l'estomac où la paroi peut former un pli faisant saillie à l'intérieur de la lumière. La musculeuse paraissant absente, la paroi intestinal se réduit à une tunique conjonctive et un épithélium. Celui-ci est formé de cellules cubiques toutes identiques, à noyaux relativement gros et cytoplasme acidophile dépourvu d'inclusions. Elles portent à l'apex une ciliature très développée (Fig. 14).

L'intestin ne comporte ni cellules glandulaires, ni mucocytes à aucun niveau. Il se raccorde à la cavité palléale en formant une papille nettement marquée.

En conclusion, le tube digestif des Atlantidae montre, par rapport à celui des autres prosobranches, plusieurs particularités qui méritent de retenir l'attention. Il est, dans son ensemble, dépourvu de mucocytes; les quelques glandes unicellulaires incluses dans la région toute à fait antérieure élaborent des sécrétions protéiques. L'essentiel de son activité glandulaire est représenté par une sécrétion apocrine située au niveau de l'oesophage. Les apex cellulaires ont probablement une structure complexe.

II. LES GLANDES ASSOCIÉES AU TUBE DIGESTIF

1. Glandes salivaires

Les glandes salivaires sont des organes pairs ne montrant pas du point de vue de l'histologie, la dissymétrie qui se manifeste sur le plan anatomique. Leur importance varie selon l'espèce: c'est chez *Atlanta fusca* qu'elles sont le plus volumineuses et chez *Protatlanta souleyeti* qu'elles sont le plus réduites.

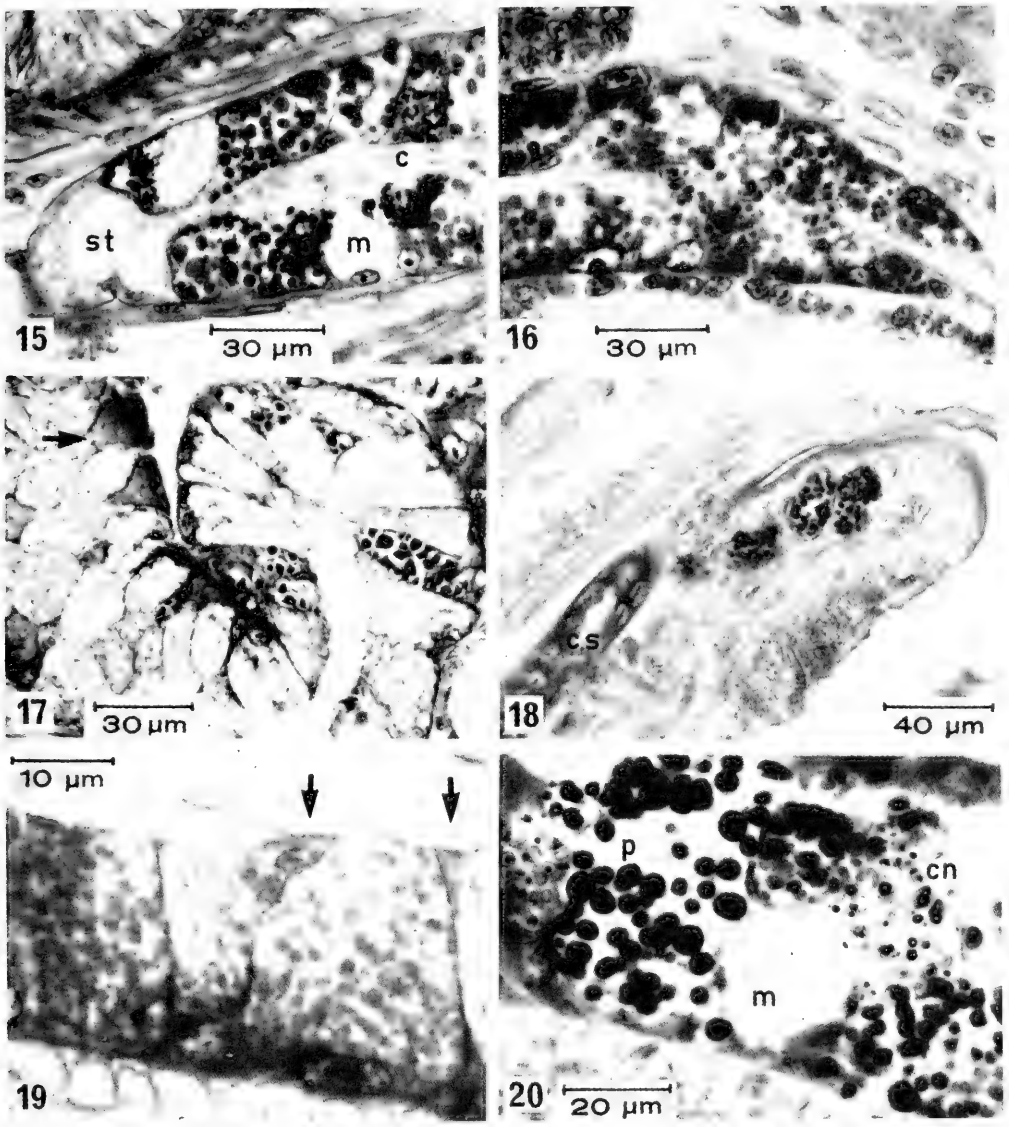
A l'extrémité borgne et postérieure correspond une sorte d'ampoule à paroi très fine que nous appellerons le "sac terminal" (Fig. 15). Un long segment à paroi épaisse, qui constitue la glande proprement dite, lui fait suite. Enfin, prolongeant cette zone glandulaire, vient un long canal salivaire, au calibre réduit (Fig. 16).

Le sac terminal occupe, par rapport au tube glandulaire, un volume minime. Il est constitué d'un épithélium pavimenteux reposant sur une lame basale bien visible, sans fibres musculaires sous-jacentes. Une coupe sagittale de ce sac intéresse environ une dizaine de cellules épithéliales dont la hauteur se situe autour de 3,5 μm. Les limites cellulaires n'apparaissent guère. Les noyaux sont bien développés et le cytoplasme est acidophile. Ces cellules ne semblent pas être le siège de phénomènes sécrétoires. Leur apex ne porte pas de ciliature visible en microscopie photonique.

Le tube glandulaire, comme le sac terminal, est entouré d'une lame basale et semble dépourvu de fibres musculaires. Sa lumière est tapissée, d'une part, d'éléments remplissant indiscutablement une fonction sécrétrice et, d'autre part, de cellules paraissant dépourvues d'une telle fonction. Le cytoplasme de ces dernières échappe souvent à l'examen mais leur présence est toujours attestée par une série de noyaux intercalés entre les apex des cellules glandulaires et comparables à ceux du sac terminal. Cette série se poursuit depuis le sac terminal jusqu'à l'émergence du canal salivaire. Il nous faut insister sur le fait que, si nous sommes en mesure d'affirmer l'existence de telles cellules dans toutes les espèces examinées, il nous est plus difficile d'en donner une description précise. Toutefois, dans les cas les plus favorables, il est visible que chacune d'entre elles envoie un fin processus cytoplasmique atteignant la lame basale (Fig. 19). Par ailleurs, la lumière des tubes renferme, à certains niveaux, de très longs cils et c'est à ces cellules qu'il convient de les rapporter. L'absence de ciliature à d'autres niveaux pourrait n'être qu'apparente, une ciliature très courte ou très fine étant susceptible de passer inaperçue.

Les cellules sécrétrices sont disposées en une seule couche régulière. Leur taille varie quelque peu d'une espèce à l'autre ou même selon les individus mais, pour un animal donné, toutes ont un volume équivalent. Les moins bien représentées sur le plan numérique, surtout chez *Oxygyrus* et *Protatlanta*, sont des mucocytes. C'est généralement à proximité de l'émergence du canal qu'ils sont les plus nombreux. Ce sont des cellules en forme d'outre dont le noyau, très volumineux se tient au voisinage de la lame basale. Il n'y a pas d'ergastoplasme visible et tout le corps cellulaire contient une substance disposée en réseau après les fixations que nous avons utilisées. Le réseau est cyanophile et colorable par le bleu alcian à pH 3,2. Il s'agit donc de mucopolysaccharides acides. Les autres

cellules sont prismatiques. A leur uniformité structurale évidente, s'oppose la dualité des inclusions qu'elles renferment. Elles sont pourvues d'un très gros noyau où la chromatine se présente en épais bâtonnets. La partie basale de la cellule est



FIGS. 15-20. Glandes salivaires.

15. *Atlanta peroni* (Fuchsine paraldéhyde-trichrome en un temps). Extrémité postérieure de la glande salivaire; remarquer le sac terminal (st), la ciliature (c) et un mucocyte (m).
16. *Atlanta lesueuri* (APS-bleu alcian-hématoxyline). Extrémité antérieure de la glande salivaire.
17. *Atlanta peroni* (APS-hématoxyline). Glande salivaire d'un animal à jeun; remarquer la coalescence des inclusions protéiques (flèche).
18. *Oxygyrus keraudreni* (APS-bleu alcian-hématoxyline). Le segment muqueux du canal salivaire (cs) et à droite les cellules à pigment ocre de la paroi buccale.
19. *Atlanta lesueuri* (Trichrome de Masson-Goldner). Détail de la glande salivaire; remarquer les cellules ciliées (flèche) intercalées entre les cellules glandulaires.
20. *Atlanta lesueuri* (Réaction au D.D.D., sans coloration de fond). Détail de la glande salivaire montrant les concrétions (cn), un mucocyte (m) et les grains de sécrétion protéique (p).

occupée par un ergastoplasme important dont le développement varie en fonction du cycle sécrétoire et dont la hauteur peut atteindre les 2/3 de la cellule. Dans la zone apicale, s'accumulent les inclusions figurées, semblables pour une même cellule mais très différentes d'une cellule à l'autre. Pour les unes, il s'agit de flaques plus ou moins étendues, parfois coalescentes, cyanophiles et colorables par la fuchsine paraldéhyde après oxydation permanganique. Elles réagissent de façon très positive à l'APS, à l'alloxane-Schiff, au D.D.D. avec ou sans réduction préalable, et sont donc de nature protéique (Fig. 20). Pour les autres, il s'agit de concrétions sphériques très réfringentes, voire biréfringentes dans certains cas. Des strates concentriques y deviennent visibles lorsqu'elles atteignent leur maximum de taille (2 à 3 μm). Les plus petites sont érythrophiles et faiblement APS-positives mais les plus grosses perdent ces caractères. Elles ne réagissent jamais à l'alloxane-Schiff ni au D.D.D. (Fig. 20). La réaction de Von Kossa, signalétique de la présence d'anions, y est négative, résultat qui peut être dû à une teneur trop faible pour être décelée.

L'allure morphologique des concrétions devait inciter à la recherche d'accumulations minérales par méthodes spectrographiques. L'analyse, faite sur les glandes salivaires d'*Atlanta inflata,* met en évidence l'existence d'une quantité très importante de phosphore et d'une certaine quantité de soufre. Le calcium est présent mais peu abondant: pour un même volume analysé, sa teneur est environ 6 fois moins élevée que dans les cellules à ergastoplasme ou les cellules à inclusions minérales de la glande digestive. On note, enfin, des traces de magnésium. Ces résultats n'ont, dans le cas particulier de la glande salivaire, qu'une valeur globale et concernent l'ensemble du tissu. La taille de l'organe et la dispersion des types cellulaires ne nous ont pas permis de situer exactement les points analysés en nous référant à une coupe colorée et adjacente. Il paraît toutefois plausible de rapporter l'excédent de phosphore à l'ergastoplasme, les quantités relatives de phosphore et de calcium ne pouvant s'expliquer par la seule présence de phosphate de calcium. Ce dernier est sans doute accumulé dans les concrétions. Quant à l'accumulation de soufre, nous sommes d'autant moins en mesure de l'interpréter que sa localisation se superpose à celle du calcium et ne semble donc pas correspondre aux sulfomucopolysaccharides des mucocytes. Une partie pourrait être engagée dans la trame organique des concrétions.

Les cellules à sécrétion protéique et les cellules à concrétion n'ont aucun emplacement fixe et se côtoient de façon quelconque le long du tube glandulaire. Leurs caractères nucléaires et cytoplasmiques sont identiques. Néanmoins, les différences très importantes existant entre les inclusions qu'elles élaborent portent à croire qu'elles appartiennent à deux lignées distinctes. Les données recueillies sur leur cycle d'activité, qui seront exposées plus loin, viennent à l'appui de cette hypothèse.

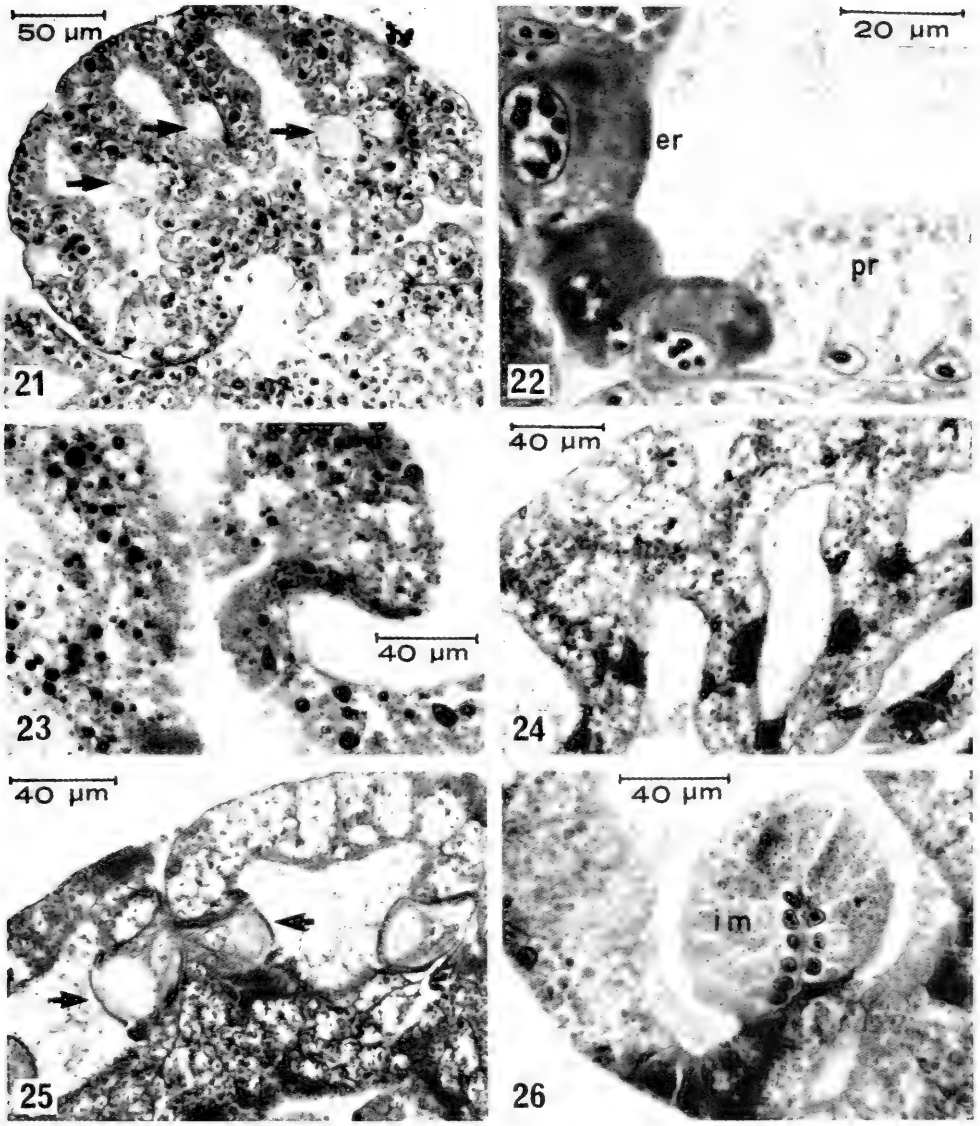
Le canal salivaire présente une section transversale circulaire dont le diamètre ne dépasse pas 12 μm. La lame basale est assez épaisse et il n'y a pas de musculeuse. L'épithélium simple est formé de cellules cubiques portant une ciliature dense et très développée. Il ne renferme aucune cellule glandulaire. Toutefois, entre le canal salivaire ainsi défini et la cavité buccale, s'interpose un segment muqueux long d'une dizaine de cellules environ. Les cellules ciliées y font place à des mucocytes typiques dont la sécrétion est constituée de mucopolysaccharides acides (Fig. 18).

2. Glande digestive (= hépatopancréas)

La glande digestive est une vaste poche débouchant dans l'estomac par un seul orifice cilié; elle est dépourvue de canaux collecteurs histologiquement différenciés. Au voisinage de l'estomac, elle n'est que partiellement cloisonnée par des replis de la paroi. Dans la zone postérieure, c'est à dire vers l'apex du tortillon, les cloisons se rejoignent pour délimiter des tubes.

Chaque tube est formé d'une seule assise de cellules assez hautes (30 μm environ), reposant sur une fine lame basale. La lumière des tubes est large si bien que les cavités représentent une fraction importante du volume de l'organe. Elles contiennent, en période de digestion, un matériel granuleux ou filamenteux et sont vides quand l'animal est à jeun. Le tissu conjonctif est aussi peu développé autour de la glande qu'entre les tubes. Aucune fibre musculaire n'a été détectée.

Trois types cellulaires constituent le parenchyme de la glande digestive. Nous les définirons avant d'envisager leur répartition



FIGS. 21-26. Glande digestive.

21. *Protatlanta souleyeti* (Azan). Vue générale de la glande digestive; remarquer les volumineuses cellules à inclusions minérales dispersées au sein du parenchyme (flèches).
22. *Atlanta lesueuri* (Azan). Détail de la glande digestive avec ses cellules principales (pr) et ses cellules à ergastoplasme (er).
23. *Atlanta inflata* (coloration au noir Soudan). Remarquer que les réserves lipidiques (en noir) sont incluses dans les cellules principales.
24. *Oxygyrus keraudreni* (APS-hématoxyline). Remarquer que les chromolipoïdes (en noir) se trouvent, au contraire, dans les cellules à inclusions minérales.
25. *Atlanta peroni* (APS-hématoxyline). Coupe sagittale de la glande digestive montrant les cellules à inclusions minérales de grande taille, disposées le long des cloisons intertubulaires (flèches). (Noter pour les chromolipoïdes, la différence par rapport à *Oxygyrus*).
26. *Atlanta lesueuri* (Azan). Coupe intéressant les cellules à inclusions minérales (im), de petite taille et groupées en un massif.

et leurs variations dans les 6 espèces étudiées.

2a. Les types cellulaires

Les cellules du premier type sont, et de très loin, les plus nombreuses (Fig. 22). Leur hauteur varie selon les phases de la digestion; elles deviennent très plates chez l'animal à jeun. Elles sont essentiellement caractérisées par une certaine pauvreté en acides nucléiques qu'il s'agisse d'ADN ou d'ARN. Les inclusions qu'elles renferment sont également très caractéristiques mais leur abondance est sujette à d'importantes fluctuations.

Le noyau est situé à la base de la cellule. Il est de dimensions modestes et ce n'est qu'à certains stades du cycle d'activité cellulaire, quand les inclusions sont peu nombreuses, qu'il est facile de l'observer. Son contour est irrégulier et la chromatine est répartie en petits grains. Un nucléole est souvent visible. Le cytoplasme, tout aussi réduit que le noyau, n'apparaît bien qu'après mise en oeuvre de colorants basiques comme le bleu de toluidine; il forme une pellicule au contact des membranes cellulaires latérales et quelques petits amas entre les inclusions. A l'apex de la cellule, les colorants acides ou la réaction à l'APS montrent une bande soit spongieuse, soit striée perpendiculairement à la lumière du tube. Il est probable que cette structure correspond, non à un second type de cytoplasme, mais à un système membranaire. Les deux aspects, striés ou spongieux, traduiraient alors des différences dans l'agencement des microvillosités, liées à leur activité.

Les inclusions qui remplissent la cellule sont très variables au sein d'un même élément mais l'existence de formes intermédiaires montre qu'il s'agit des stades évolutifs d'une même catégorie de grains. La variabilité se traduit par d'énormes différences de taille, de forme, de structure et d'affinités tinctoriales. Le diamètre de ces inclusions va de 1 à 6 μm. Les plus volumineuses sont arrondies, claires, hétérogènes et même granuleuses alors que les plus petites sont anguleuses, denses et plus intensément colorables. Après coloration à l'azan, il est possible d'observer une gamme de teintes allant du bleu pour les plus grosses au rouge vif pour les plus petites. Elles réagissent positivement à l'APS mais avec plus ou moins d'intensité. Il en va de même pour la coloration à la fuchsine paraldéhyde après oxydation permanganique en milieu acide. Les résultats des réactions à l'alloxane-Schiff et au D.D.D., avec ou sans réduction préalable, sont plus homogènes; ils montrent la présence d'une quantité notable de protéines à cystéine et cystine.

Dans les conditions ordinaires de fixation, il apparaît parfois une volumineuse vacuole qui refoule les autres inclusions. Il s'agit, en réalité, d'une enclave constituée de lipides complexes conservés sur coupes à la paraffine lorsque les pièces sont fixées par le formol et traitées par une solution de bichromate de potassium selon le procédé de Baker (Fig. 23). Fortement colorable dans ces conditions, elle est dissoute après la plupart des autres modes de fixation, d'où l'aspect de vacuole.

Certaines de ces cellules, presque toujours situées sous le tégument, contiennent de minuscules grains de pigment noir. Les grains de pigment, disséminés entre les autres inclusions, facilement décolorables par oxydation, sont sans doute des mélanines. Ils se trouvent en plus ou moins grand nombre selon les espèces ou même selon les individus. Ils existent aussi bien chez les très jeunes animaux que chez les adultes sexuellement mûrs. Ainsi, ils ne semblent pas représenter un pigment d'usure mais leur abondance constitue plutôt un caractère spécifique voire individuel; l'hypothèse émise pour *Pterotrachea* (Gabe, 1952) ne peut être reprise ici.

L'interprétation fonctionnelle des cellules de ce type pose des problèmes difficiles et encore très controversés mais leurs homologies, du point de vue de l'histologie comparée, apparaissent clairement. Elles présentent, en effet, des caractères très constants et ont été décrites chez tous les prosobranches examinés à cet égard. Elles ont reçu des noms divers tels que "cellules digestives" (digestive cells), cellules absorbantes, cellules à ferments, cellules cylindriques etc. . . Eléments dominants du tissu hépatopancréatique de tous les mollusques, nous proposons pour eux, le nom de **cellules principales**. Ce terme présente l'avantage de ne pas préjuger d'un rôle physiologique qui est loin d'être connu.

Les cellules du second type diffèrent en

tous points des précédentes. Elles sont peu nombreuses et, d'une manière très générale, plus volumineuses (Fig. 22). Lorsqu'elles sont intercalées entre les cellules principales, elles s'appuient largement sur la lame basale et ne prennent contact avec la lumière que par un étroit prolongement. La forme conique est moins évidente dans les espèces où elles sont groupées par trois ou quatre. Elles sont toujours pourvues de très gros noyaux situés en position centrale et certaines sont binuclées. Des mitoses ont été observées dans quelques cas. Chez *Atlanta lesueuri*, la taille des bâtonnets de chromatine suggère l'éventualité d'une polyploïdie. La richesse en ARN de ces cellules se manifeste à la fois par le développement de l'appareil nucléolaire et par celui de l'ergastoplasme qui est très dense et couvre toute la cellule. La réaction à l'alloxane-Schiff et celle au D.D.D. montrent une haute teneur en protéines et notamment en protéines soufrées; cette teneur varie de façon sensible d'une cellule à l'autre. A certains stades du cycle, il se forme des petits grains de sécrétion cyanophiles, APS-positifs et colorables par la fuchsine paraldéhyde après oxydation. Par ailleurs, la méthode de Von Kossa fait apparaître une multitude de très petits grains distincts des grains de sécrétion cyanophiles. Aux anions ainsi révélés correspond une importante teneur en calcium que nous avons mise en évidence par méthode spectrographique.

Ces cellules ne contiennent jamais de pigments. Etant presque toujours localisées contre le tégument, il est fréquent qu'elles soient entourées de cellules principales fortement mélanisées; dans tous les cas, le semis de grains de mélanine qui couvre les cellules voisines, s'interrompt à leur niveau. Le fait est particulièrement net dans des espèces très pigmentées comme *Atlanta inflata.* Elles ne renferment pas davantage de lipides figurés détectables dans nos conditions techniques. L'absence totale de "vacuoles" permet de croire que cette constatation n'est pas liée au procédé de détection mais que les lipides font réellement défaut.

Les homologies entre ces éléments et d'autres types cellulaires décrits chez les prosobranches apparaissent de façon nette. De nombreux auteurs les ont mentionnés (voir Fretter & Graham, 1962, et Owen, 1966) sans leur attribuer un nom précis. En raison de leur caractère cytologique le plus évident, nous les appelerons **cellules à ergastoplasme.**

Le troisième type cellulaire est représenté par des éléments clairs, de volume égal ou supérieur à celui des cellules principales. Contrairement aux deux catégories précédentes, ces cellules ont des caractères très différents selon l'espèce envisagée; leur trait commun est la présence constante de concrétions.

Leur noyau est, soit parfaitement ovale, soit au contraire très anguleux mais toujours pauvre en chromatine. Nous avons même observé, chez certains individus, des noyaux où la coloration au bleu de toluidine ne permettait la mise en évidence d'aucun ARN, seul apparaissant, alors, un nucléole unique. Ces divers aspects nucléaires n'ont pu être rattachés à aucune phase précise de l'évolution de la cellule. Le cytoplasme est absolument chromophobe dans la plupart des espèces, quelque peu basophile et relégué au pôle basal dans d'autres (*Atlanta peroni*). Le pôle apical, strié et APS-positif, est probablement garni de microvillosités.

L'étude des concrétions justifierait un examen ultrastructural et la mise en œuvre de méthodes histochimiques variées que nous n'avons pu envisager chez ces animaux de petite taille. Quelques arguments nous permettent toutefois de croire qu'elles représentent l'association de chromolipoïdes et de sphérocristaux minéraux. A certains stades de leur évolution, ce sont des grains minuscules, basophiles, APS-positifs, métachromatiques et colorables par le bleu alcian. Lorsque les coupes sont traitées uniquement par des colorants acides, méthode à l'azan, par exemple, ils ne sont pas colorés mais apparaissent grâce à une réfringence particulière. A d'autres stades, ces mêmes grains vont jusqu'à atteindre 3 ou 4 μm de diamètre; ils ont perdu toute basophilie et sont naturellement colorés en ocre (Fig. 24). Ils présentent alors une zonation qui s'organise autour d'un ou plusieurs centres et, seule, une très fine coque est faiblement APS-positive. Ils ne sont pas soudanophiles mais se colorent intensément par le sulfate de bleu de Nil et la teinte obtenue résiste à un séjour de 24 heures dans l'eau oxygénée à 20 vol. (méthode de Hueck). Ces caractères pourraient être ceux de chromolipoïdes dont le degré d'oxydation varierait selon les cellules.

L'analyse spectrographique des concrétions a été réalisée chez *Atlanta inflata,* sur matériel fixé au mélange de Carnoy, inclus à la résine et débité à l'ultra-microtome en coupes semi-fines. Cette analyse montre la présence de calcium, de phosphore et de soufre. Ont été recherchés également, le magnésium, le sodium, le cuivre, le zinc, le potassium, le manganèse, le fer, le silicium et le vanadium; les résultats de cette recherche ont été négatifs. L'absence de fer doit être soulignée puisque ce métal est mentionné dans les concrétions des Pterotracheidae (Gabe, 1952, 1966). La composante minérale des concrétions paraît donc être le phosphate de calcium. Le soufre pourrait être rapporté aux sulfomucopolysaccharides de la trame organique dont la présence est attestée par la métachromasie des concrétions et leur colorabilité par le bleu alcian. Il nous faut insister sur le fait que, en dépit de la présence de concrétions, la teneur en calcium de ces cellules n'est pas plus importante que celle des cellules à ergastoplasme des mêmes animaux analysées dans les mêmes conditions.

Toutes les concrétions d'une même cellule se trouvent à des phases identiques de leur évolution mais les diverses cellules d'une même glande représentent, au contraire, des stades variés, sauf chez *Atlanta lesueuri.* Il est donc certain que ces cellules évoluent encore chez l'adulte. Ce fait nous incite à croire que c'est à cette lignée qu'appartiennent certains éléments hauts, très étroits, à noyaux relativement gros et cytoplasme fibrillaire: la taille du noyau, la basophilie du cytoplasme, l'absence de sécrétion laissent supposer qu'il s'agit de cellules jeunes et indifférenciées. Elles sont dispersées chez *Atlanta fusca*, par exemple, mais se trouvent au contact des cellules à concrétions chez *A. peroni.* Cette répartition sur laquelle nous reviendrons, représente un argument supplémentaire pour les interpréter comme de jeunes cellules à concrétions. Il nous faut signaler, enfin, que nous n'avons jamais observé une éventuelle extrusion des concrétions.

Il ne semble pas que cette troisième catégorie cellulaire soit très répandue parmi les prosobranches mais elle est représentée chez les Pterotracheidae par des éléments décrits sous le nom de **cellules à inclusions minérales** (Gabe, 1952, 1966). C'est le terme que nous adopterons.

2b. La répartition des types cellulaires

Les 3 types de cellules qui viennent d'être définis existent, à l'exclusion de toute autre catégorie cellulaire, dans les 6 espèces d'Atlantidae considérées ici. Leur mode de répartition diffère selon les espèces mais il est remarquablement constant pour une espèce donnée (Fig. 27).

Les cellules principales (type I) qui constituent l'essentiel de la glande se retrouvent identiques à elles-mêmes depuis l'orifice gastrique jusqu'à l'apex du tortillon.

Les cellules à ergastoplasme (type II) se trouvent, elles aussi, depuis la chambre initiale partiellement cloisonnée jusqu'à l'extrémité borgne des tubes. Elles ne sont pas dispersées au hasard entre les cellules du type I mais sont disposées de façon privilégiée contre le tégument, dans la région pariétale des tubes glandulaires. La plupart se trouvent contre la face convexe du tortillon et quelques unes, contre la face concave. Ce n'est que lorsque l'hépatopancréas est très volumineux qu'on rencontre de telles cellules à l'intérieur de l'organe et encore y sont-elles peu nombreuses. Chez *Oxygyrus keraudreni*, les coupes, intéressant la région pariétale des tubes, montrent que celle-ci comporte un groupe unique de 4 ou 5 cellules à ergastoplasme. Dans les 5 autres espèces, ce groupe est scindé en 2 massifs séparés par quelques cellules principales. Chacun des massifs occupe alors, l'angle délimité par le tégument d'une part, la cloison intertubulaire, d'autre part.

Les cellules à inclusions minérales (type III) sont, quant à elles, distribuées d'une tout autre manière. Chez *Oxygyrus keraudreni* et *Protatlanta souleyeti*, elles sont disséminées entre les cellules principales sans donner lieu à aucun groupement particulier. Par ailleurs, elles existent à tous les niveaux, depuis la chambre initiale, jusqu'à l'apex du tortillon où elles deviennent toutefois beaucoup plus rares. Une disposition analogue est réalisée chez *Atlanta fusca* qui, à cet égard, se rapproche donc davantage d'*Oxygyrus* et de *Protatlanta* que des 3 autres espèces d'*Atlanta.* En effet, chez celles-ci, les cellules à inclusions minérales se groupent selon un mode propre à chaque espèce. Chez *Atlanta inflata,* la majorité d'entre elles recouvrent le sommet des cloisons, dans la chambre initiale; elles ne s'engagent que très peu

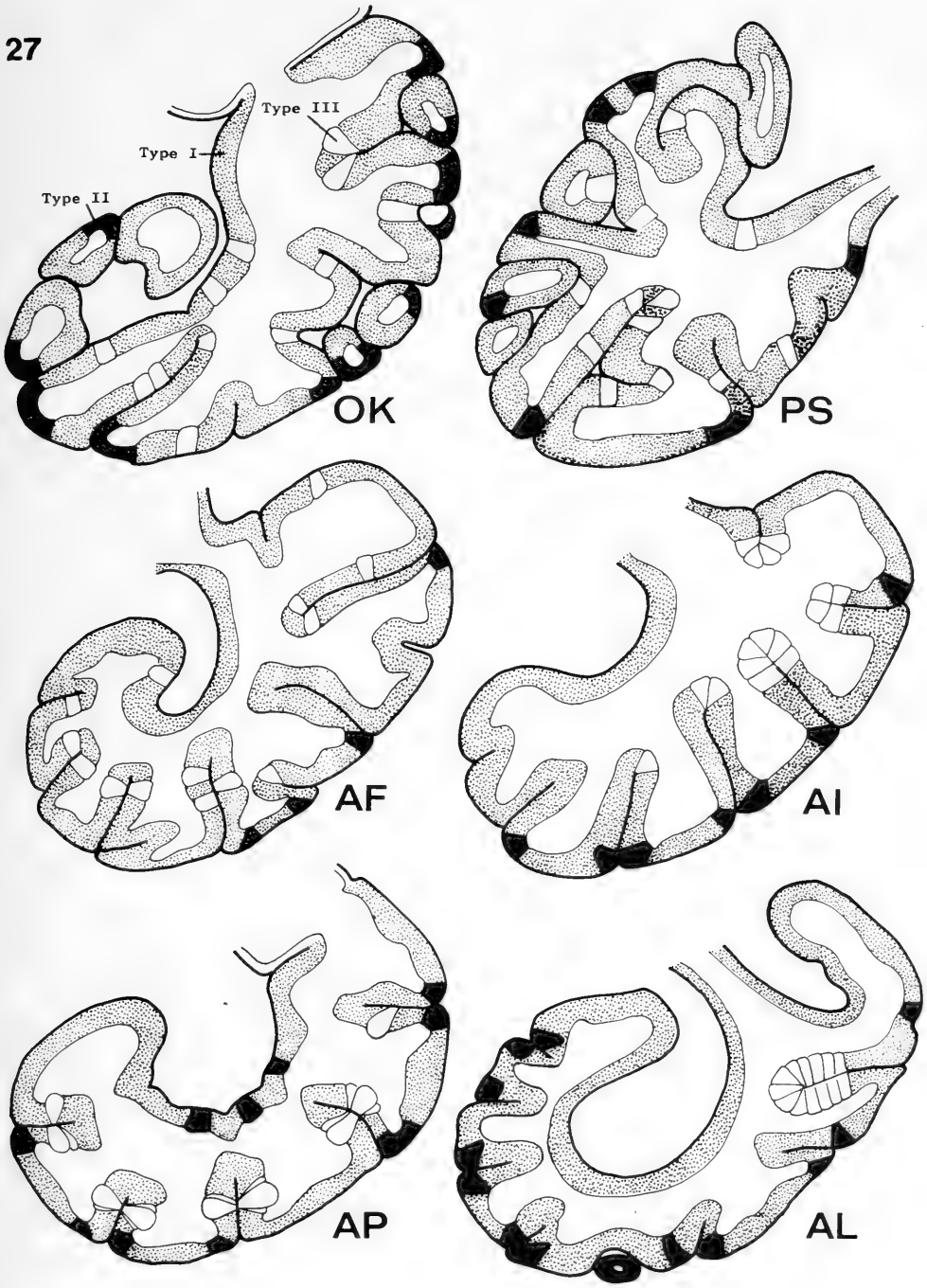


FIG. 27. Schéma de la répartition des 3 types cellulaires dans la glande digestive d'*Oxygyrus keraudreni* (OK), *Protatlanta souleyeti* (PS), *Atlanta fusca* (AF), *A. inflata* (AI), *A. peroni* (AP) et *A. lesueuri* (AL). Les cellules principales (type I) sont figurées en pointillé, les cellules à ergastoplasme (type II) en noir et les cellules à inclusions minérales (type III) en blanc.

dans les tubes. Chez *Atlanta peroni*, au contraire, elles ne se trouvent jamais au sommet des cloisons, mais seulement au flanc de celles-ci et leur aire de répartition s'enfonce profondément à l'intérieur des tubes. Elles sont disposées de telle sorte que les groupes se font face de part et d'autre de la lumière d'un tube ou de la cavité d'une crypte, dans la chambre initiale; ils sont adossés par paire de chaque côté des cloisons intertubulaires. En outre, il faut signaler que, chez *A. peroni*, et seulement dans cette espèce, chaque groupe est constitué d'éléments se trouvant à des stades différents de leur maturation. Le plus évolué et le plus volumineux étant au centre, le groupe prend une allure de bouquet. Enfin, l'étape ultime du groupement est atteinte chez *Atlanta lesueuri* où les cellules à inclusions minérales, forment un unique éperon situé face à l'orifice de l'estomac.

La répartition des différents types cellulaires telle qu'elle apparait sur coupes, dans les 6 espèces d'Atlantidae considérées ici, est schématisée sur la Fig. 27. Dans tous les cas, la coupe affecte la chambre initiale et parfois, son orifice dans l'estomac. Les données que nous venons d'exposer seront discutées ultérieurement mais il nous paraît opportun de souligner d'ores et déjà, l'originalité de la distribution des types cellulaires dans la glande digestive des Atlantidae, leur emplacement constant qui exclut toute possibilité de transformation d'un type en un autre et enfin, la tendance au groupement des cellules à inclusions minérales.

2c. Les variations spécifiques des types cellulaires

Les cellules principales présentent des caractères très voisins dans toutes les espèces d'Atlantidae et il n'y a pas lieu d'envisager, à leur sujet, de variations spécifiques.

Les cellules à ergastoplasme sont, chez *Oxygyrus,* plus plates et beaucoup plus larges que les cellules à inclusions polyédriques. Elles bordent la lumière sur une assez grande étendue et c'est probablement à cause de cette disposition que la bordure apicale est bien visible; elle apparaît striée. Les noyaux sont toujours gros et quelques mitoses ont été observées chez des individus jeunes. Chez *Protatlanta*, les cellules à ergastoplasme sont coniques et n'atteignent la lumière que par un étroit prolongement. Chez *Atlanta fusca,* elles sont profondément enfoncées entre les cellules à inclusions polyédriques et paraissent même très souvent, sous-épithéliales. Elles sont néanmoins reliées à la surface épithéliale par un processus filiforme. Chez *A. inflata* et *A. peroni,* elles sont plus superficielles mais toujours coniques. Chez *A. lesueuri,* l'une ou l'autre implantation peuvent se rencontrer. Les grains de sécrétion y sont plus gros que dans les autres espèces. Enfin, les noyaux sont très volumineux; la chromatine forme d'épais bâtonnets dont le développement suggère l'éventualité d'une polyploïdie.

Les cellules à inclusions minérales ont, chez *Oxygyrus,* un volume comparable à celui des cellules du type I. Les éléments jeunes à petits grains et les éléments à grains plus élaborés sont répartis de façon quelconque, au sein d'une même glande. Chez *Protatlanta,* les cellules à inclusions minérales sont nettement plus volumineuses que les cellules principales (Fig. 21). Comme précédemment, les stades à petits grains côtoient les stades à gros grains, sans répartition préférentielle. Chez *A. fusca,* les aspects sont très comparables à ceux de *Protatlanta.* Les étroites cellules à cytoplasme basophile qui, pensons-nous, représentent le stade initial de cette lignée, sont particulièrement visibles dans cette espèce. Les cellules à inclusions minérales d'*A. inflata* n'offrent aucun caractère particulier par rapport à *A. fusca,* sinon qu'elles peuvent devenir plus volumineuses. L'intérêt d'*A. peroni* dans l'étude des cellules à inclusions minérales, réside ainsi que nous l'avons mentionné, dans leur mode de groupement qui permet de suivre tous les stades de leur évolution. Dans un groupe donné, les cellules latérales, encore indifférenciées, sont extrêmement étroites, très basophiles et dépourvues d'inclusions. Puis viennent des cellules dont la zone apicale, désormais élargie, renferme des inclusions APS-positives dont l'allure n'est pas sans rappeler celles des cellules principales. La zone apicale continuant à se dilater, il y apparaît une plage claire à contenu pulvérulent, délimitée par l'ergastoplasme. Les cellules parvenues a maturité, qui forment l'axe du groupe, sont piriformes et très grosses (Fig. 25). L'ergastoplasme et le noyau, avec ses nombreux nucléoles, occupent la région basale effilée tandis que les inclusions sont concentrées

dans la zone renflée qui fait saillie dans la lumière. Ces inclusions ont parfois un aspect pulvérulent. Rappelons que l'ergastoplasme n'est décelable, dans les conditions d'observation de la microscopie photonique, que chez *A. peroni.* Chez *A. lesueuri,* les cellules à inclusions minérales restent de dimensions modestes, voisines de celles des cellules principales. D'aspect identique chez le même individu, il semble qu'elles soient toutes au même stade; les concrétions n'atteignent jamais un volume important (Fig. 26).

DONNÉES HISTOPHYSIOLOGIQUES ET INTERPRETATION FONCTIONNELLE

Une soixantaine d'individus appartenant presque tous à l'espèce *Atlanta inflata* ont été mis en élevage et fixés à des moments déterminés de leur cycle digestif, allant de quelques minutes à 5 jours après le repas. Rappelons, dans ce contexte, qu'un intervalle entre 2 repas d'environ 3 jours a pu être observé en élevage (Thiriot-Quiévreux, 1973).

La proie qui vient d'être ingérée reste pendant un certain temps suffisamment intacte à l'intérieur du jabot pour qu'il soit possible d'en effectuer la détermination sur coupes (Fig. 9). Deux à 3 heures après le repas, la proie est toujours dans le jabot mais ses tissus commencent à s'altérer puis à se dissocier en très petits fragments qui passeront dans l'estomac. La lyse se poursuit dans la cavité gastrique et le bol alimentaire y devient de plus en plus fluide ce qui se traduit sur coupes, par une texture de plus en plus uniforme. Au terme de l'évolution, le contenu de l'estomac présente un aspect filamenteux ou grenu; à ce stade, les cavités de la glande digestive contiennent un matériel identique à celui de la cavité gastrique. Dans la lumière de l'intestin, on n'observe jamais qu'un cordon dense et homogène.

L'examen de cette série d'animaux nous a montré, en outre, des modifications histologiques de l'appareil digestif survenant au cours du jeûne et des heures qui suivent le repas; les plus évidentes affectent les glandes salivaires, la glande digestive et le jabot. Nous en donnerons un aperçu succinct.

Après l'ingestion de la proie, les différences entre les 2 lignées cellulaires de la glande salivaire s'accentuent peu à peu jusqu'à devenir extrêmement sensibles chez l'animal à jeun. En effet, au cours du jeûne, les cellules à sécrétion protéique s'enrichissent en inclusions; les inclusions elles-mêmes s'élargissent et tendent à fusionner pour former des flaques homogènes (Fig. 17). Les concrétions de l'autre lignée cellulaire perdent, au contraire, toute colorabilité. L'ergastoplasme est très réduit dans les 2 lignées. Immédiatement après le repas, les cellules du premier type apparaissent très dégranulées; l'extrusion doit donc se produire au moment de l'ingestion de la proie. Nous n'avons pas observé de dégranulation pour les cellules à concrétions, non plus que l'extrusion de celles-ci. L'ergastoplasme redevient très visible pour les cellules des 2 types.

Le jeûne se traduit, au niveau des cellules principales de la glande digestive (type I), par une diminution progressive des inclusions polyédriques menant à leur disparition totale. Chez un animal n'ayant pas mangé depuis 5 jours, ces cellules sont très plates, vides et présentent un aspect spongieux. La restitution des inclusions polyédriques suit de quelques heures l'ingestion d'un repas. L'apparition des "vacuoles" correspondant aux enclaves lipidiques est plus tardive et ne s'observe que passé un délai de 24 heures après le repas. Les cellules à ergastoplasme (type II) se chargent de sécrétion au cours du jeûne. L'extrusion commence à se produire de 3 à 5 jours après le repas, sans que le jeûne soit interrompu. Elles sont donc déjà très dégranulées au moment où une nouvelle proie est ingérée. Les cellules à inclusions minérales (type III) paraissent moins affectées par le cycle digestif. Elles semblent certes particulièrement volumineuses chez l'animal à jeun mais, compte tenu de l'aplatissement des cellules principales, le phénomène pourrait n'être qu'apparent.

En ce qui concerne le tractus digestif proprement dit, nous n'avons décelé de modifications qu'au niveau du jabot. Dès que la proie y est parvenue, l'épithélium est distendu et très plat. Les sphères cytoplasmiques que nous interprétons comme une sécrétion apocrine ont disparu; il est vraisemblable de croire qu'elles se dissolvent, au contact du bol alimentaire, en libérant la composante active de leur sécrétion. De nouvelles sphères se reforment très tôt, dès que le bol alimentaire, ayant quitté le jabot, est parvenu dans l'estomac et la

glande digestive; elles sont surtout nombreuses dans la partie du jabot proche de l'estomac. Les cellules de l'estomac n'évoluent pas au cours du cycle digestif mais les accumulations d'amibocytes périphériques subissent certaines fluctuations. Les numérations de cellules qui auraient permis de préciser l'allure du phénomène en fonction du cycle digestif, n'ont pas été envisagées.

En conclusion, pour l'une des 2 catégories de cellules des glandes salivaires, pour les cellules du jabot et pour les cellules à ergastoplasme de la glande digestive, la synthèse intracellulaire des sécrétions se situe avant le repas. L'extrusion est conditionnée par l'arrivée du bol alimentaire pour les glandes salivaires et le jabot; elle en est indépendante et semble donc obéir à des facteurs internes pour les cellules à ergastoplasme de la glande digestive. Il est hautement probable que toutes ces cellules élaborent des enzymes digestives. Les caractères morphologiques généraux des cellules salivaires et des cellules à ergastoplasme de la glande digestive (ergastoplasme très développé, grains de sécrétion très comparables aux grains zymogènes) viennent à l'appui de cette hypothèse. Il est plus difficile de rapprocher les cellules du jabot d'un type cellulaire connu chez les vertébrés; on sait, en effet, que la sécrétion apocrine y est exceptionnelle. Les cellules principales de la glande digestive ont un rythme inverse de celui des cellules à enzymes. Il est évident que l'une de leurs fonctions consiste à accumuler des réserves. Quant au rôle des cellules à concrétions de la glande salivaire ou des cellules à inclusions minérales de la glande digestive, nos observations ne nous autorisent à formuler aucune hypothèse. Enfin, des cellules libres de type amibocytes interviennent sans doute dans les processus digestifs. Quelques aspects observés nous paraissent très suggestifs à cet égard mais la taille minuscule des animaux ne nous a pas permis de réunir des données expérimentales.

DISCUSSION

En abordant l'étude histologique de l'appareil digestif des Atlantidae, nous nous proposions de rechercher les modifications structurales et fonctionnelles corrélatives de la métamorphose, de préciser les aspects histophysiologiques de leur digestion, de comparer leur organisation à celle des autres Heteropoda et enfin, de dégager les caractères propres à cette famille. Ces différents points seront envisagés successivement.

1. Appareil digestif et digestion chez la larve et chez l'adulte

Les données relatives à l'appareil digestif des larves d'Atlantidae précédemment acquises (Thiriot-Quiévreux, 1969, 1971) et celles que nous venons de rapporter concernant les adultes permettent de comparer les 2 types d'organisation avec une certaine précision. Ainsi, l'essentiel des modifications morphologiques qu'entraîne la métamorphose se situe au niveau du tractus digestif proprement dit; la structure des glandes associées reste inchangée. En effet, les glandes salivaires, déjà mises en place chez la larve, subsistent chez l'adulte en gardant les mêmes caractères. C'est leur raccordement à la cavité buccale qui constitue, pour elles, l'acquisition principale au moment de la métamorphose. La glande digestive est, au cours des 2 phases, un sac cloisonné dont le parenchyme comporte les 3 mêmes catégories cellulaires. La répartition caractéristique de l'espèce est déjà fixée chez la larve. Le tube digestif, au contraire, se trouve profondément modifié. L'oesophage, simple canal cilié chez la larve, devient, tout autant qu'un jabot, un important organe glandulaire. L'estomac se simplifie en perdant sa cuticule et sa plaque dentée. L'intestin, où l'on pouvait reconnaître 3 segments, se simplifie plus encore, au point de se réduire à un fin conduit cilié de structure uniforme sur toute sa longueur.

Ces modifications morphologiques traduisent de nouvelles adaptations fonctionnelles correspondant au changement de régime alimentaire qui survient à la métamorphose. Un net déplacement des processus les plus importants de la digestion a lieu vers les régions antérieures de l'animal. La larve est dépourvue d'appareil masticateur et de glandes salivaires, ceux-ci n'étant pas fonctionnels à ce stade. Les courants ciliaires de l'oesophage conduisent les particules alimentaires directement à l'estomac où se trouve intégré, sous forme de cuticule et de plaque dentée, un dispositif de broyage. Chez l'adulte, l'appareil radulaire avec sa puissante musculature

prend le relai des courants ciliaires pour assurer la progression de la proie. C'est avant d'arriver dans l'estomac que celle-ci séjourne pendant plusieurs heurs au contact de la "salive" et des sécrétions du jabot, sans doute riches en enzymes. La digestion est donc déjà très avancée lorsque le bol alimentaire parvient à l'estomac, maintenant dépourvu d'appareil broyeur. Il est probable que le rôle de la glande digestive demeure inchangé comme ses caractères structuraux. Quant à l'intestin, la simplicité de son organisation incite à croire que ses fonctions sont moins diverses chez l'adulte que chez la larve.

2. Histophysiologie de la digestion chez les Atlantidae et chez d'autres prosobranches carnivores

La comparaison entre la physiologie de la digestion de la larve et celle de l'adulte ne peut guère être étendue au delà de ces quelques notions. De même, il est difficile d'établir, pour l'adulte, un schéma beaucoup plus précis que celui suggéré dans notre chapitre "Résultats". En effet, les aspects histophysiologiques du cycle digestif qui pourraient conduire à une interprétation définitive et indiscutable, sont mal connus chez les prosobranches. De nombreux travaux ont, certes, été consacrés à la digestion des mollusques (voir Owen, 1966, pour la bibliographie), mais la plupart d'entre eux procèdent de méthodes biochimiques ou portent sur des groupes autres que les prosobranches. Ceux-ci paraissent toutefois, présenter une certaine unité à cet égard et d'étroites analogies apparaissent entre les Atlantidae et d'autres prosobranches carnivores, les Nassariidae (Martoja, 1964). Les plus évidentes sont celles des cellules principales et des cellules à ergastoplasme de la glande digestive où le jeûne et la digestion entraînent des variations morphologiques identiques dans les 2 groupes. Le cycle des cellules à sécrétion protéique des glandes salivaires des Atlantidae se superpose également à celui de leurs homologues, décrit chez *Nassarius*. Il est plus curieux de constater qu'un rapprochement du même ordre peut être fait entre l'élaboration de la sécrétion du jabot des Atlantidae et celle de la glande oesophagienne (glande de Leiblein) des Nassariidae. Les glandes salivaires, la glande digestive, les cellules glandulaires à sécrétion apocrine de la région antérieure du tube digestif, qu'elles soient intra- ou extra-oesophagiennes, paraissent donc remplir un certain nombre de fonctions communes aux 2 groupes. La présence de cellules particulières aux Atlantidae (cellules à concrétions des glandes salivaires, cellules à inclusions minérales de la glande digestive) interdit cependant d'étendre cette notion à l'ensemble de ces organes. Ces fonctions peuvent, en effet, être multiples et certaines sont encore insoupçonnées. Dans ce contexte, il nous faut citer les très récents résultats de l'école de Falkmer (Davidson et col., 1971; Boquist et col., 1971) mettant en évidence des cellules à insuline dans la muqueuse gastro-intestinale de *Buccinum undatum*.

Le rôle des amibocytes dans la digestion, démontré chez les bivalves par Yonge dès 1926, mais très discuté depuis lors (voir Owen, 1966), paraît exister chez les Atlantidae. Ce rôle est considéré comme négligeable chez les prosobranches par Fretter & Graham (1962: 239). Toutefois, dans la famille des Nassariidae, les résultats expérimentaux appuient les vues de Yonge selon lesquelles les amibocytes traversent l'épithélium digestif en direction de la cavité gastrique, se chargent de métabolites et regagnent ensuite le milieu intérieur.

3. Appareil digestif des Atlantidae et des autres Heteropoda

La connaissance de l'appareil digestif des autres Heteropoda ne repose que sur des données statiques. Parmi eux, les Carinariidae n'ayant donné lieu à aucune étude histologique, cette connaissance se limite à la famille des Pterotracheidae dont les genres *Pterotrachea* et *Firoloida* ont été décrits par Gabe (1952, 1966). La compilation des résultats obtenus par Gabe et par nous-mêmes ne permet pas encore d'énoncer les caractères généraux de l'appareil digestif des Heteropoda. Il en ressort seulement que 2 caractères essentiels, à savoir l'absence de glandes oesophagiennes et la présence d'un jabot, sont communs aux 2 familles.

Au niveau du tractus digestif, la différence majeure entre les Pterotracheidae et les Atlantidae est représentée par une plus grande uniformité structurale, c'est-à-dire par une plus grande simplicité de l'intestin chez ces derniers. En effet, les glandes unicellulaires qui permettent de subdiviser en 3 segments l'intestin de *Pterotrachea* ou

de *Firoloida* n'ont leur équivalent dans aucune des espèces examinées. Certains caractères histologiques, comme l'absence de mucocytes, ne peuvent donner lieu à aucune généralisation à l'échelle de la superfamille puisqu'ils varient au sein même des Pterotracheidae; alors qu'ils sont abondants dans la partie antérieure du tube digestif de *Pterotrachea,* ils font défaut dans celui de *Firoloida* comme dans celui des Atlantidae. Le système radulaire est identique dans tous les cas mais on sait que, en dehors de la forme des dents, il est peu sujet à variations.

En l'état actuel de nos connaissances, il est impossible de dégager les caractères des glandes salivaires des Heteropoda. En effet, Gabe (1966) insiste sur le fait qu'elles ne sont pas ciliées chez les Pterotracheidae et ne fait aucune mention d'un sac terminal; or ce sont des particularités que nous tenons pour très importantes (voir ci-dessous). Des différences concernent également le nombre des catégories de cellules glandulaires. Gabe en décrit 1 seule chez *Pterotrachea*, 2 chez *Firoloida* et souligne l'absence de mucocytes dans les 2 genres. Les glandes salivaires des 6 espèces d'Atlantidae examininées ici comportent 3 catégories de cellules glandulaires parmi lesquelles, des mucocytes typiques.

Des constatations analogues s'appliquent à la glande digestive où l'homogénéité évidente de la famille des Atlantidae s'oppose à une déconcertante variabilité des Pterotracheidae. Gabe reconnaît la présence de 4 types cellulaires chez *Pterotrachea* et de 2 seulement chez *Firoloida* alors que nous en identifions 3 chez les Atlantidae. Les cellules principales (cellules à ferment de Gabe) sont identiques dans tous les cas et ne donnent lieu à aucune discussion. De même, les cellules à inclusions minérales ont une physionomie suffisamment particulière pour que les homologies soient établies sans difficulté; elles existent chez les Pterotracheidae comme chez les Atlantidae. Le problème des cellules à ergastoplasme se pose, au contraire, de manière complexe. Pourvues de sécrétions figurées, distinctes des autres types cellulaires par leur emplacement, leurs caractères cytologiques et leur cycle d'activité, elles constituent sans aucun doute, une lignée indépendante; elles ne peuvent donc correspondre aux cellules d'attente telles que Gabe les définit chez *Pterotrachea.* Il semble donc que ces cellules à ergastoplasme n'existent ni chez *Pterotrachea,* ni chez *Firoloida*, ce dernier ne possédant, selon Gabe, que des cellules principales (ou à ferment) et des cellules à inclusions minérales. Toutefois, il est certain qu'elles ne représentent pas une particularité des Atlantidae puisque des éléments comparables par leur morphologie et par leur cycle, ont été mis en évidence dans les Nassariidae ainsi que nous l'avons déjà mentionné. Nous soulignerons enfin que les mélanines présentes dans la glande digestive des Atlantidae sont incluses dans des cellules ayant tous les caractères morphologiques des cellules principales, parcourant le même cycle qu'elles et qu'il n'y a pas lieu d'interpréter comme une lignée autonome. Chez *Pterotrachea,* au contraire, les cellules à mélanine constituent, selon Gabe, une catégorie cellulaire spéciale.

4. Structure de la glande digestive et relations phylétiques entre diverses espèces d'Atlantidae

Dans le cas des Pterotracheidae, les divers types cellulaires de la glande digestive sont répartis de façon quelconque au sein du parenchyme. Chez les Atlantidae, au contraire, nous avons montré que la répartition des cellules à ergastoplasme (type II) et celle des cellules à inclusions minérales (type III) obéissaient à des règles très précises. Les cellules à ergastoplasme ne sont en aucun cas dispersées entre les cellules principales; elles se trouvent toujours sur le flanc des tubes et, pour la majorité des individus, contre la paroi de l'organe. Ce caractère observé dans les 6 espèces étudiées est certainement valable pour l'ensemble de la famille. Au contraire, la disposition des cellules à inclusions minérales diffère selon les espèces. Il paraît logique d'admettre que la tendance évolutive consiste en un groupement progressif de ces cellules et que les formes les plus primitives sont celles où elles sont dispersées. Les cellules à inclusions minérales sont réparties apparemment au hasard chez *Oxygyrus, Protatlanta* et *Atlanta fusca*; elles forment plusieurs massifs chez *A. inflata* et *A. peroni*; elles sont rassemblées en un groupe unique chez *A. lesueuri* qui représente donc, à cet égard, l'espèce la plus évoluée. Or les travaux de Richter (1961), consacrés à l'évolution de la radula, ont établi qu'il existait dans la famille des

Atlantidae 2 lignées phylogénétiques issues d'un ancêtre commun, *A. fusca*:

A. fusca → 1. *A. inflata—Protatlanta—Oxygyrus*
A. fusca → 2. *A. peroni—A. lesueuri*

Les données histologiques sont en accord avec l'existence de ces 2 lignées et les conceptions de Richter. La position d'*A. inflata,* toutefois, pourrait être discutée à la lumière de nos résultats puisque la tendance au groupement des cellules à inclusions minérales y est déjà très nette et que cette espèce pourrait s'insérer au début de la seconde lignée.

Significative sur le plan de la phylogénèse du groupe, la structure de la glande digestive l'est également sur le plan taxonomique. Son étude serait donc fructueuse dans la définition d'espèces difficiles à caractériser. On sait, et Tesch (1949) a insisté sur ce fait, que la systématique des Heteropoda présente des difficultés spéciales liées à la fragilité de leurs coquilles, à leur contractilité, etc. Certaines espèces sont encore mal définies. Par exemple, Tesch considère qu'*Atlanta gaudichaudi*, *A. peroni* et *A. inclinata* ne sont peut-être que les variétés d'une même espèce. Or la glande digestive d'*A. peroni* est si caractéristique que l'examen de cet organe dans les 2 autres formes apporterait sans doute la solution de ce problème.

L'évolution de la glande digestive à l'intérieur d'une même famille et l'intérêt taxonomique de ce tissu ne nous paraissent pas avoir été signalés dans d'autres groupes de gastéropodes.

5. Les caractères généraux de l'appareil digestif des Atlantidae ont-ils un intérêt systématique?

L'organisation de l'appareil digestif des Atlantidae retient l'attention sur le plan général de leurs affinités systématiques. La simplicité de cet appareil, qui représente son caractère le plus immédiat, pourrait être en relation avec la taille minuscule des animaux et c'est ainsi que Fretter (1948) interprète ce même caractère chez les Omalogyridae et les Rissoellidae. D'autres particularités pourraient être plus significatives. En effet, Fretter & Graham (1949), dans une monographie des Pyramidellidae, ont souligné que l'absence de glandes oesophagiennes et de gouttière oesophagienne dorsale, l'existence d'un jabot, la réduction de l'estomac et la faible longueur de l'intestin étaient propres aux opisthobranches. Or, tous ces caractères se trouvent réunis chez les Atlantidae. D'autres, plus spécialement histologiques, sont à prendre en considération. Par exemple, les glandes salivaires sont ciliées chez les Atlantidae comme chez de nombreux opisthobranches. Les apex cellulaires, qui portent à la fois des cils et un revêtement d'allure cuticulaire, sont identiques chez les Atlantidae et chez *Aplysia punctata* (Howells, 1942) alors qu'une telle disposition ne nous paraît pas fréquente chez les prosobranches. En outre, l'examen de nos propres préparations d'*Aplysia* nous a montré, au niveau du jabot, des images de sécrétion apocrine, tout à fait comparables à celles des Atlantidae; ce type de sécrétion est courant dans les glandes oesophagiennes des prosobranches (Martoja, 1964, 1971) mais n'a pas, à notre connaissance, été signalé dans l'oesophage proprement dit.

Le système radulaire se rapproche plus de celui des prosobranches. Gabe & Prenant (1958) indiquent que chez ceux-ci les odontoblastes sont nombreux et étroits et il en va de même chez les Atlantidae, alors qu'ils sont gros et peu nombreux chez les opisthobranches. La présence d'un cartilage radulaire est également considérée comme caractéristique des prosobranches. Toutefois, la distinction entre celui-ci et les amas de cellules de Leydig reconnus dans l'odontophore des opisthobranches, peut être difficile à établir. Cette difficulté existe dans le cas des Atlantidae. Les cellules cartilagineuses des mollusques (Gabe & Prenant, 1955) et les cellules de Leydig possèdent, en effet, de nombreux points communs; en outre, la substance fondamentale qui caractérise le cartilage et oppose donc les 2 tissus, occupe, chez les Atlantidae, un volume très réduit.

L'appareil digestif est donc construit sur le modèle opisthobranche tel que le conçoivent les auteurs actuels. Au schéma anatomique s'ajoutent des particularités histologiques qui tendent à établir le même rapprochement. On sait que d'autres organes d'Heteropoda donnent lieu à des constatations identiques et dès 1906, Pelseneer insistait sur le fait à plusieurs reprises. Il n'en est pas moins vrai que certains caractères sont, au contraire, de type prosobranche. Il nous paraissait nécessaire d'insister sur cette dualité qui peut

caractériser soit un "groupe-charnière", soit un groupe en pleine évolution.

Les Heteropoda ne sont pas les seuls prosobranches à manifester cette ambiguïté. A cet égard, il nous faut signaler l'extraordinaire ressemblance qui existe entre les glandes salivaires des Atlantidae et des Pyramidellidae. Le fait est d'autant plus intéressant que ces dernières, décrites et figurées par Fretter & Graham (1949), sont considérées comme très particulières (voir Fretter & Graham, 1962; Franc, 1968). Or, le sac terminal, les grandes cellules glandulaires, la couche superficielle de cellules ciliées, la rareté des mucocytes se retrouvent dans les 2 familles, en dépit de leur mode de vie et de leurs adaptations si différents. Il n'existe, en effet, aucun point commun entre la biologie des parasites de bivalves que sont les Pyramidellidae et celle de prédateurs pélagiques comme les Atlantidae. Tout phénomène de convergence paraissant dès lors exclu, est-ce dans une certaine parenté entre les 2 familles qu'il faut rechercher la cause de telles analogies? Cette éventuelle parenté s'étend-elle à d'autres familles? Il est probable que ces caractères ne sont pas l'apanage exclusif des Atlantidae et des Pyramidellidae. On sait déjà que les glandes salivaires sont également tubuleuses chez les Hydrobiidae, Rissoidae, Assimineidae, Calyptraeidae et Scalidae [Epitoniidae]. Leur étude histologique apporterait peut-être d'autres exemples de ce type de structure. Il est certes prématuré de considérer la glande salivaire comme un organe fondamental du point du vue de la systématique. On doit, toutefois, remarquer que certaines de ces familles ont quelques points communs et sont de position systématique douteuse. Quant aux Pyramidellidae, il est bien connu qu'ils cumulent eux-aussi, certains caractères des 2 sous-classes et sont considérés tantôt comme des opisthobranches (Fretter & Graham, 1949), tantôt comme des prosobranches (Franc, 1968).

Aucune solution ne saurait être apportée à ces questions en l'état actuel de nos informations car elle exige la connaissance détaillée des divers systèmes anatomiques des Atlantidae, des familles dont ils sont supposés issus et de celles auxquelles il conviendrait peut-être de les rattacher.

CONCLUSIONS

La métamorphose des Atlantidae coïncide avec un déplacement, vers les régions antérieures de l'animal, des processus fondamentaux de la nutrition (capture des proies, sécrétions d'enzymes digestives). Chez l'adulte, les manifestations histophysiologiques de la digestion sont, dans une large mesure, comparables à celles d'autres prosobranches carnivores.

L'appareil digestif des Atlantidae présente une remarquable unité de structure aussi bien anatomique qu'histologique. Cette unité n'est pas synonyme d'uniformité et ceci à tel point que les caractères spécifiques du parenchyme de la glande digestive pourraient avoir une valeur taxonomique. De plus, l'évolution de ce tissu reflète la phylogénie de la famille telle qu'on a pu l'établir d'après de tout autre critère.

L'organisation générale de l'appareil digestif est étonnament proche de celle des opisthobranches. Nos résultats montrent donc une certaine dualité dans les caractères anatomiques et histologiques des Atlantidae qui, à d'autres égards, sont des prosobranches typiques. Ils attirent aussi l'attention sur certaines particularités structurales peut-être significatives. C'est ainsi que les glandes salivaires pourraient représenter, selon nous, un organe-clé pour aborder l'étude des affinités systématiques des Heteropoda.

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ABSTRACT

HISTOLOGY OF THE DIGESTIVE SYSTEM AND DIGESTION IN THE ATLANTIDAE (PROSOBRANCHIA: HÉTEROPODA)

Micheline Martoja and Catherine Thiriot-Quiévreux

The histological structure of the digestive system and its histophysiological changes during digestion are described in the adults of 6 species of Atlantidae. The results are interpreted functionally and discussed from the point of view of systematics.

The digestive tract of the Atlantidae comprises an oesophagus functioning as a crop, a small stomach and a short intestine. A pair of tubular salivary glands and a digestive gland (hepatopancreas) are associated, but oesophageal and rectal glands are lacking. The radular apparatus has the usual prosobranch characters.

The digestive tract is totally devoid of mucous cells. Several unicellular glands are in the buccal wall and the anterior part of the oesophagus. There is an apocrine secretion in the crop. Glandular activity is minimal in the stomach and absent in the intestine.

A salivary gland comprises a terminal sac, a glandular duct and a long collecting duct. The glandular duct is made up of ciliated cells and of 3 types of secretory cells: cells secreting proteinaceous material, cells with mineral inclusions and mucous cells. The collecting duct ends near the mouth in a short mucous segment.

The parenchyma of the digestive gland comprises "principal cells," cells rich in ergastoplasm and cells with mineral inclusions. The distinctness of these 3 cell types is shown by their distinct localizations and by cytophysiological data (independent cycles of activity). The distribution of the cells with mineral inclusions is a species character, and these elements become more and more clustered in the course of evolution.

In the salivary gland cells secreting proteinaceous material, in the cells of the crop and in the cells rich in ergastoplasm of the digestive gland, intracellular synthesis of secretions precedes feeding. Release seems to be correlated with the arrival of the food bolus in the first 2 cases, and by internal factors in the last case. All these cells probably secrete digestive enzymes. The "principal cells" of the digestive gland have an inverse rhythm and their main function seems to be the accumulation of lipids and glycoproteins.

The structure of the digestive system of the Atlantidae shows some features in common with those of opisthobranchs. The histological characteristics of the salivary glands are very similar to those of the Pyramidellidae, which could be interesting from the standpoint of systematics.

ZUSAMMENFASSUNG

HISTOLOGIE VOM VERDAUUNGSSYSTEM UND DIGERIERUNG VON ATLANTIDAE (PROSOBRANCHIA: HETEROPODA)

Micheline Martoja und Catherine Thiriot-Quiévreux

Das Verdauungssystem der Atlantidae setzt sich zusammen aus einem Ösophagus, der als Kropf fungiert, einem kleinen Magen und einem kurzen Darm. Ein Paar schlauchförmiger Speicheldrüsen und eine Mitteldarmdrüse sind mit dem Darmkanal verbunden, der keine Ösophagus- und Rektum-Drüsen hat. Der Radula-Apparat weist die üblichen Eigenschaften auf, wie sie von anderen Prosobranchiern bekannt sind.

Der Verdauungskanal ist frei von Schleimzellen. Einzellige Drüsen sind in der Bukkalwand verstreut, wie auch in den vorderen Ösophagus-Partien. Im Kropf findet apokrine Sekretion statt. Die Drüsentätigkeit ist gering im Magen und fehlt im Darm.

Jede Speicheldrüse besteht aus einer terminalen Tasche, einem Drüsenschlauch und einem langen Sammelkanal. Der Drüsenschlauch ist aus bewimperten Zellen und 3 Typen sekretorischer Zellen aufgebaut: eiweissreiche sekretorische Zellen, solche mit mineralischen Einschlüssen und Schleimzellen. Der Sammelkanal endigt in der Mundgegend mit einem kurzen schleimzellenreichen Abschnitt.

Das Parenchym der Mitteldarmdrüsen besteht aus "Hauptzellen," "ergastoplasmareichen Zellen" und "Kalkzellen." Die Autonomie dieser 3 Zell-Streifen wird anhand topographischer (getrennte Lage) und zytophysiologischer Daten (voneinander unabhängige Zell-Zyklen) aufgezeigt. Kalkzellen sind ganz spezifisch gelegen, und mit der Evolution geht deren Zusammenballung einher.

In den eiweissreichen sekretorischen Zellen der Speicheldrüsen, in Kropfzellen und in ergastoplasmareichen Zellen der Mitteldarmdrüse findet die Sekretsynthese schon vor der Nahrungsaufnahme statt. Die Absonderung erscheint mit dem Eintreffen von Nahrung in den ersten beiden Fällen korreliert, hängt im dritten Fall jedoch von internen Faktoren ab. Höchstwahrscheinlich produzieren alle diese Zellen Verdauungsenzyme. Die wesentliche Funktion der Hauptzellen der Mitteldarmdrüse scheint die Aufnahme von Fetten und Glycoproteinen zu sein.

Die Struktur des Verdauungstrakts der Atlantidae hat Eigenschaften mit dem der Opisthobranchier gemein, und histologische Charakteristika von Speicheldrüsen sind denen von Pyramidellidae sehr ähnlich. Die phylogenetischen Schlussfolgerungen aus diesen Befunden werden diskutiert.

C.M.-B.

RESUMEN

HISTOLOGIA DEL SISTEMA DIGESTIVO Y DIGESTIÓN EN LOS ATLANTIDAE (PROSOBRANCHIA: HETEROPODA)

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El sistema digestivo de los Atlantidae se compone de un esófago funcionando como un buche, un estómago pequeño y corto intestino. No hay glándulas esofágicas ni rectales pero, asociado al canal hay un par der glándulas salivares tubulares. El aparato radular tiene el mismo carácter de otros prosobranquios.

Células mucosas estan ausentes pero glándulas unicelulares estan esparcidas en la pared bucal y en la porción anterior del esófago. En el buche se produce una secreción apocrina. La actividad glandular es baja en el estómago y ausente en el intestino.

Cada glándula salivar consiste de un saco terminal, un tubo glandular y un ducto colector largo. El tubo está formado por células ciliadas y 3 tipos de celulas secretoras: células proteinaceas, células con inclusiones minerales y células mucosas. El ducto colector termina cerca de la boca por un segmento mucoso corto.

El parénquima de la glándula digestiva consiste de "células maestras," "células ricas en ergastoplasma" y "células calcáreas." La autonomía de estos 3 grupos se demuestra por la topografía (localización distinta) y comprobaciones citofisiológicas (ciclos celulares independientes). Las células de calcio estan distribuidas específicamente y su agrupamiento es causado por evolución.

En las células proteinaceas secretoras de las glándulas salivares, en células del esófago, y en aquellas ricas en ergastoplasma de la glándula digestiva, la síntesis de secreción tiene lugar antes del paso de alimento. La descarga parece estar correlacionada con la llegada del alimento en los 2 primeros casos, pero en el último depende de factores internos. Con mucha probabilidad todas las células elaboran enzimas digestivas. La función esencial de las "células maestras" parece ser la de acumular reserva de lípidos y glicoproteinas.

La estructura del canal digestivo en Atlantidae tiene aspectos comunes con aquellas de los opistobranquios e histologicamente las caracteristicas de las glándulas salivares son muy similares a las de los Pyramidellidae; las implicaciones filogeneticas de esos aspectos se discuten.

J. J. P.

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EMBRYONIC DEVELOPMENT AND ORGANOGENESIS IN THE SNAIL *MARISA CORNUARIETIS* (MESOGASTROPODA: AMPULLARIIDAE). V. DEVELOPMENT OF THE NERVOUS SYSTEM[1]

Emile S. Demian[2] and Fouad Yousif[3]

ABSTRACT

The nervous system is ectodermal in origin. All nerve ganglia arise separately by proliferation and later delamination from the ectoderm, not by invagination. They become secondarily connected to one another by commissures and connectives developing as extensions from the peripheral layer of ganglionic nerve cells.

Rudiments of the cerebral, pedal, pleural and intestinal (parietal) ganglia arise almost simultaneously at a relatively early stage (*Stage V*). The cerebral ganglia develop from the ectoderm of the head plates. Rudiments of the pedal and pleural ganglia are separate at their inception. They later fuse (*Stage VI*) to form a pleuro-pedal ganglionic mass on each side. The 2 intestinal ganglia are symmetrical at the beginning, but they soon lose their symmetry as a result of torsion. The right ganglion crosses to the left over the gut and persists as the supraintestinal ganglion. The left or subintestinal ganglion shifts to the right and forward, and fuses with the right pleural ganglion (*Stage VIII*), thus obscuring the chiastoneury.

The paired buccal and single visceral (abdominal) ganglia start differentiating in *Stage VII*. The former develop from the ectodermal wall of the stomodaeum, while the visceral ganglion delaminates from the right wall of the visceral sac, then shifts to the left during torsion.

The statocysts develop early (*Stage V*) from 2 ectodermal invaginations on either side of the rudimentary foot. They later separate from the overlying ectoderm and statoconi appear in their lumina.

Contrary to earlier reports on related ampullariids, the osphradium proved to be ontogenetically older than the mantle and mantle cavity. It starts differentiating as a thickened ectodermal plate in the right wall of the visceral sac (*Stage V*). During torsion, it becomes engulfed in the mantle cavity and shifts to the left side, then is carried forward as the mantlegrow

The eyes develop late (*Stage IX*) as ectodermal invaginations which rapidly separate from the ectoderm to form closed vesicles. Their cells start differentiating before hatching to form the retina, in which pigment is deposited, and the inner cornea. The lens is secreted in the lumen of the eye and grows by addition of concentric layers of secretion.

INTRODUCTION

This is the 5th and last paper of a series dealing with the embryonic development and organogenesis of the ampullariid snail *Marisa cornuarietis* (L.), a potential predator and competitor of schistosome-transmitting snails.

The 1st part of the series (Demian & Yousif, 1973a) described cleavage and gastrulation and gave the general outlines of organogenesis during the 12 embryonic stages recognized; development of the alimentary system, of the circulatory and renal systems, and of the shell gland, mantle and respiratory organs were respectively dealt with in detail in the 2nd to 4th parts (Demian & Yousif, 1973b-d).

In the present paper, a detailed description is given of the embryonic development of the nervous system and sense organs in *M. cornuarietis*. Findings are compared with earlier information on the Ampullariidae and on other gastropods in general.

Observations were made on the same material and sets of serial sections that were used in all other parts of the series. The material and techniques have been described in the 1st part of the series (Demian & Yousif, 1973a), to which reference should also be made for the age,

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dimensions and diagnostic features of the 12 embryonic stages which are frequently referred to below.

KEY TO LETTERING ON FIGURES[4]

A	auricle
ANP	anal cell-plate
BG	buccal ganglion
BM	buccal commissure
BML	buccal muscles
BMS	buccal mass
CBN	cerebro-buccal connective
CG	cerebral ganglion
CM	cerebral commissure
CN	ctenidium
COI	inner cornea
COO	outer cornea
CPDN	cerebro-pedal connective
CPLN	cerebro-pleural connective
E	eye
EL	eye lens
ET	ectoderm
I	intestine
L	lung
LOC	lateral odontophoral cartilage
LPPG	left pleuro-pedal ganglionic mass
LPRN	left zygosis
LS	larval stomach
MS	mesoderm or mesenchyme cells
MTC	mantle cavity
MTE	mantle edge
NC	nerve cells
NF	nerve fibres
OE	oesophagus
OS	osphradium
OSG	osphradial ganglion
P	pericardium
PC	pericardial cavity
PDG	pedal ganglion
PDM	pedal commissure
PDN	pedal nerve trunk
PDP	pedal cell-plate
PLG	pleural ganglion
RIG	right intestinal ganglion
RPPG	right pleuro-pedal ganglionic mass
RS	radular sac
RTN	retina
SBG	subintestinal ganglion (former left intestinal ganglion)
SBN	subintestinal "nerve"
SBVN	subintestinal-visceral connective
SD	stomodaeum
SHG	shell gland
SOC	superior odontophoral cartilage
SOR	subradular organ
SPG	supraintestinal ganglion (former right intestinal ganglion)
SPN	supraintestinal "nerve"
SPVN	supraintestinal-visceral connective
STC	statocyst
STN	statoconi
TN	tentacle (rudiment)
V	ventricle
VG	visceral ganglion
VL	velum
VS	visceral sac

OBSERVATIONS

1. Nerve ganglia and commissures

All nerve ganglia in *Marisa cornuarietis* are ectodermal in origin and arise separately by cell-proliferation and subsequent delamination from certain thickened areas of the ectoderm. They become secondarily connected to one another by nerve commissures and connectives.

Rudiments of the cerebral, pedal, pleural and intestinal ganglia start to differentiate almost simultaneously as the embryo reaches *Stage V.* The cerebral ganglia (*CG*, Fig. 1A, B) arise from 2 symmetrical, ovoid, thickened, ectodermal areas (about 70 μm long) which become visible at this stage in the head or cephalic plates, already differentiated in the preceding stage (Demian & Yousif, 1973a) on the dorso-lateral sides of the embryo, above the level of the velum. The pedal ganglia (*PDG*) develop from 2 similar ectodermal plates (60 μm long) found on the sides of the foot rudiment. The pleural ganglia (*PLG*, Fig. 1A) originate from 2 smaller thickened plates (40 μm long) situated ventro-laterally at the place where the rudimentary foot and visceral sac meet. The 2 intestinal or parietal ganglia arise from 2 still smaller ectodermal plates which are symmetrically situated on either side of the embryo (see *RIG*, Fig. 1A), a little behind the rudimentary pleural ganglia (*PLG*).

[4]All drawings are of *Marisa cornuarietis* (L.). The general views are reconstructions, made from serial transverse and sagittal sections, of the nervous system and sense organs which are shown in transparency.

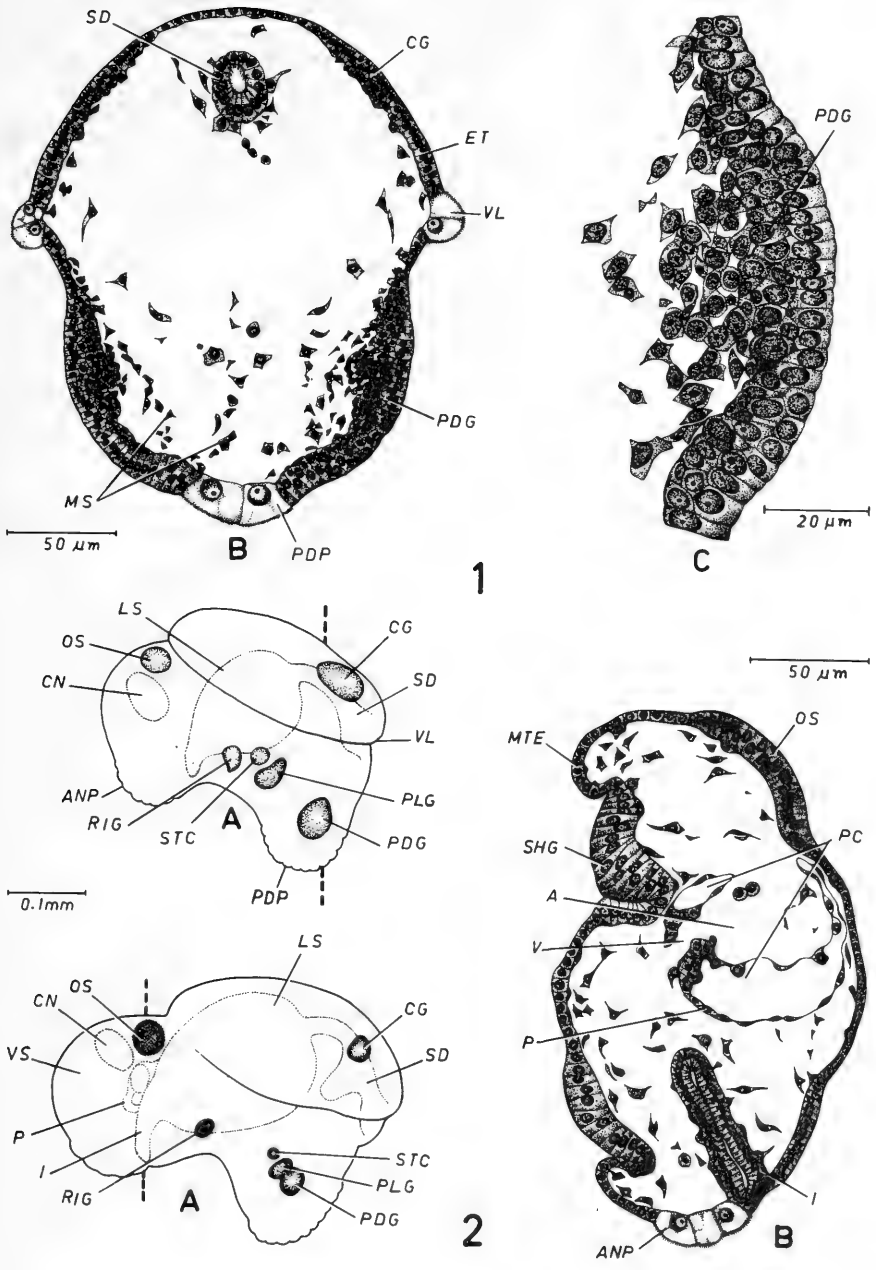

FIG. 1. A, Embryo in *Stage V*, right lateral view.
B, Transverse section of the embryo, same stage; plane of section is indicated by dashed line in A.
C, Enlarged portion of B, showing the rudiment of the pedal ganglion.

FIG. 2. A, Embryo in *Stage VI*, right lateral view showing all rudimentary ganglia found on the right side of the embryo.
B, Transverse section of the embryo, same stage; plane of section indicated by dashed line in A.

The cells in all these rudimentary plates are taller than neighboring ectodermal cells and their cytoplasm appears densely granular and somewhat more chromophilic. These cells proliferate rapidly so that the ectoderm soon becomes many-layered in these areas (Fig. 1C). The resulting cells start delaminating from the ectodermal layer in *Stage VI* to form compact masses of round, ovoid and irregular cells that gradually shift inwards below the ectoderm. The masses representing the rudiments of the cerebral ganglia (*CG*, Fig. 2A) come to lie dorso-laterally of the stomodaeum (*SD*). The rudiments of the pleural ganglia (*PLG*) moreover shift forward, approaching the rudiments of the pedal ganglia (*PDG*).

Rudiments of the 2 buccal ganglia and the unpaired visceral or abdominal ganglion start differentiating in *Stage VII* (Fig. 3). Those of the buccal ganglia appear as 2 small thickened areas in the wall of the stomodaeum, right behind the radular sac opening, and that of the visceral ganglion (*VG*) shows as a small, rounded, thickened area in the ectoderm forming the right wall of the visceral sac (*VS*). While the cells of the buccal ganglia remain attached to the ectodermal wall of the stomodaeum, those of the visceral ganglion rapidly delaminate from the ectoderm, forming a small compact mass in the primary body cavity, to the right of the rudimentary heart. In the same embryonic stage, rudiments of the pedal and pleural ganglia (*PDG, PLG*) of each side fuse into a single ganglionic mass.

Torsion begins at this stage (*Stage VII*). The only ganglia to be affected are the intestinal ganglia and the single visceral ganglion. The 2 intestinal ganglia start losing their symmetrical position as they become rotated anti-clockwise. The left ganglion (or subintestinal ganglion, *SBG*) shifts downward and approaches the median line below the larval stomach (*LS*, Fig. 3), while the right ganglion (or supraintestinal ganglion, *SPG*) shifts upward and a little backward to lie dorso-lateral to the larval stomach.

Nerve commissures and connectives start developing from this stage onward as thin cellular extensions of the rudimentary ganglia in the form of irregular strings arising from the peripheral ganglionic cells by proliferation. The strings from 2 ganglia advance gradually until they meet and form a rudimentary commissure. The 1st to appear (in *Stage VIII*, Fig. 4) is the connective between the supraintestinal ganglion (*SPG*) and the right pleural ganglion, already fused in the right pleuro-pedal ganglionic mass (*RPPG*). This connective runs almost vertically down the right side of the larval stomach (*LS*), and represents the supraintestinal "nerve" (*SPN*). The main posterior pedal nerve trunks (*PDN*) make their appearance also at this stage as 2 thin backward extensions of the rudimentary pedal ganglia.

In *Stage IX*, the subintestinal ganglion (*SBG*, Fig. 5) has completely fused with the right pleuro-pedal ganglionic mass (*RPPG*). The visceral ganglion (*VG*) has shifted a little forward, and 3 more connectives have developed. The first is the left zygosis (*LPRN*, Fig. 5) which represents a secondary pleuro-parietal connective extending between the supraintestinal (= parietal) ganglion (*SPG*) and the left pleural ganglion, already incorporated in the left pleuro-pedal ganglionic mass (*LPPG*). This connective runs downward to the left of the larval stomach (*LS*). The second is the supraintestinal-visceral connective (*SPVN*). (The subintestinal-visceral connective (*SBVN*) is not yet complete.) The third is a transverse connective representing the subintestinal "nerve" (*SBN*); it is established between the left pleural ganglion and the subintestinal ganglion (*SBG*) that has already fused with the right pleuro-pedal ganglionic mass (*RPPG*). The transverse pedal commissure (*PDM*) simultaneously forms between the 2 pedal ganglia, extending in front of the subintestinal "nerve" (*SBN*).

All nerve commissures and connectives are developed and well recognizable in *Stage X*: the cerebral commissure (*CM*, Fig. 7A) which extends transversely over the buccal mass between the 2 cerebral ganglia (*CG*), the paired cerebro-pedal (*CPDN*) and cerebro-pleural (*CPLN*) connectives passing out from the posterior tips of the cerebral ganglia to the corresponding portions of the right and left pleuro-pedal ganglionic masses (*RPPG, LPPG*), and the subintestinal-visceral connective (*SBVN*). The 2 buccal ganglia (*BG*) assume triangular outlines and also connect with each other through a thin buccal commissure (*BM*, Figs. 6, 7A), and with the 2 cerebral ganglia by 2 cerebro-buccal connectives (*CBN*, Fig. 7A).

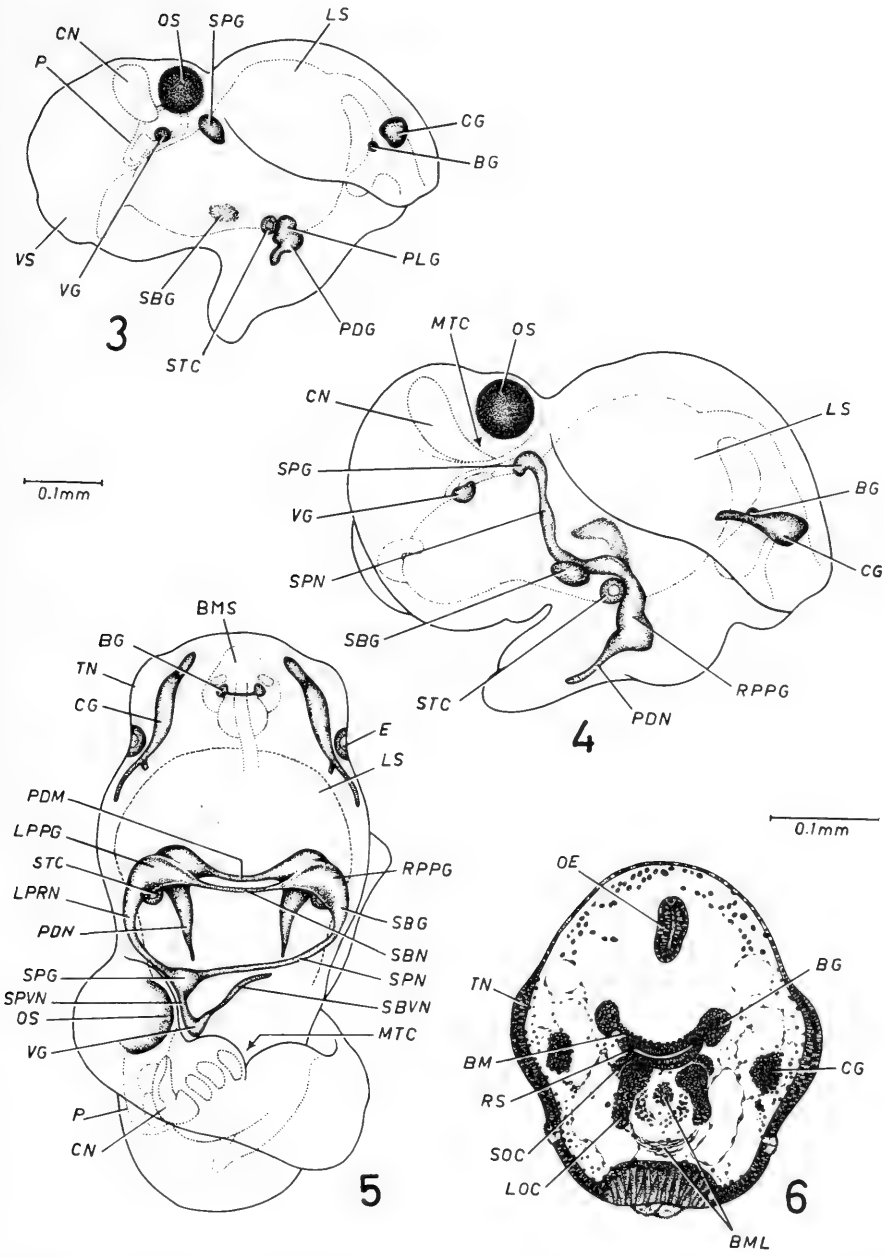

FIG. 3. Embryo in *Stage VII*, right lateral view. The left intestinal ganglion (now the subintestinal ganglion, *SBG*) is shown in transparency; the right intestinal ganglion (now the supraintestinal ganglion, *SPG*) has shifted dorsally.

FIG. 4. Embryo in *Stage VIII*, right lateral view. Ctenidium (*CN*) and osphradium (*OS*) are shown in the hollow of the incipient mantle cavity.

FIG. 5. Embryo in *Stage IX*, dorsal view. Ctenidium (*CN*) and osphradium (*OS*) shown in transparency inside the mantle cavity.

FIG. 6. Transverse section of the head region of the embryo in *Stage X* passing at the level of the buccal ganglia.

By the time the embryo reaches *Stage XII*, all nerve ganglia have attained their definitive shapes and positions, while the nerve commissures and connectives have become more fully developed and much thickened. The cerebral ganglia have shifted backward to lie dorsolateral to the buccal mass. The larval stomach has diminished greatly in size, and the oesophagus is much elongated. The supraintestinal ganglion has therefore come to rest on the left side of the oesophagus. The visceral ganglion lies below the left posterior edge of the mantle cavity. Some of the main nerves issuing from the cerebral ganglia, such as the tentacular, optic and statocyst nerves are also well differentiated at this stage.

The cells of most ganglionic masses start differentiating in *Stage X*: those at the periphery become enlarged and produce several protoplasmic processes extending inwards, towards the centre of the ganglionic mass. This peripheral layer of differentiated neurons thickens during further development so that, as the embryo reaches *Stage XII*, 2 regions or zones become well recognized in every ganglion: a thick outer zone of nerve cells (*NC*, Fig. 8) and a central fibrous core with nerve fibres (*NF*). The nerve commissures and connectives present a similar structure in cross section at this stage, and all of them as well as the nerve ganglia appear surrounded with thin sheets of mesenchymatous tissue, 1 or 2 cells thick, which will subsequently develop into connective tissue sheaths.

2. Statocysts

Rudiments of the statocysts (*STC*, Fig. 1A) differentiate early in *Stage V* as 2 small thickened ectodermal plates located on either side of the rudimentary foot, just above the rudiments of the 2 pleural ganglia (*PLG*). These ectodermal plates (*STC*, Fig. 9A) start invaginating in the same stage. The 2 invaginations deepen gradually during subsequent development (Fig. 9B), separate from the ectodermal layer, in *Stage VII*, and form 2 closed vesicles (Fig. 9C) below the ectoderm. Each vesicle measures about 30 μm in maximum length and has a thin wall of a single layer of columnar to cuboidal cells with large spherical nuclei.

The 2 rudimentary vesicles gradually gain in size during further development, become spheroidal and shift slightly forward, coming to lie in 2 small depressions on the inner surfaces of the pleuro-pedal ganglionic masses (*RPPG, LPPG*) in *Stage X* (*STC*, Fig. 7A, B). Meanwhile, their cells (Fig. 9D) develop short cilia on their free inner surfaces and a few transparent rod-like or dumbbell-shaped statoconi (*STN*) appear inside each vesicle. The statocysts measure about 65 μm in diameter in *Stage XII*, acquire a distinct outer sheath of mesenchyme cells and each receives a thin statocyst nerve from the cerebral ganglion of its side. It also now shows a somewhat wider lumen and a thin wall of cuboidal cells with vacuolated cytoplasm and ovoid central nuclei. After hatching, each statocyst gradually enlarges and secretes more statoconi within its lumen (Fig. 9E).

3. Osphradium

The osphradium is also ectodermal in origin and starts differentiating in *Stage V*, almost simultaneously with the statocysts. It first appears as a thickened ectodermal plate (*OS*, Fig. 1A) on the right dorsolateral side of the visceral sac rudiment, directly above the rudiment of the ctenidium (*CN*). This plate (*OS*, Fig. 2B, for *Stage VI*) consists of tall columnar cells with large ovoid nuclei and densely granular cytoplasm. The plate shifts gradually forwards, coming to lie in front of the gill rudiment (*CN*, Fig. 2A). Torsion, which begins at *Stage VII*, further causes the organ to move to the left of the median line in *Stage VIII* (*OS*, Fig. 4), and to be later (*Stage IX*, Fig. 5) engulfed in the mantle cavity (*MTC*). Meanwhile, the osphradium has considerably enlarged, attaining a diameter of about 0.1 mm. Some of its cells proliferate actively in the following stage, so that a distinct ganglionic mass is produced below the organ, representing the rudimentary osphradial ganglion (*OSG*, Fig. 7A, B).

In *Stage XI*, the osphradium has shifted further forwards and has become slightly raised off the inner epithelium of the mantle cavity. Two small invaginations appear on its 2 opposite sides. The organ has further enlarged in *Stage XII*, measuring about 0.2 mm in diameter, and develops 2 additional lateral invaginations. Its cells acquire long cilia and show a vacuolated cytoplasm and apical spherical

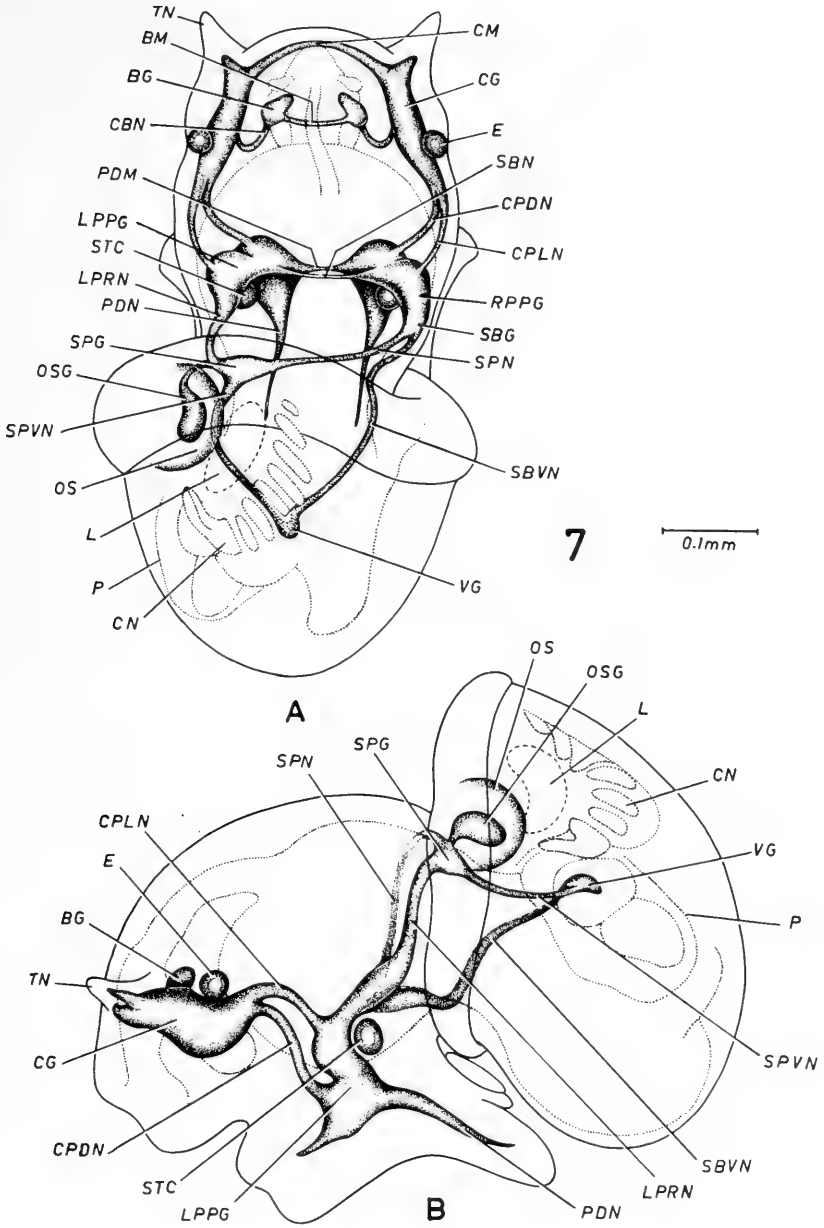

FIG. 7. A, B, Embryo in *Stage X*, dorsal and left lateral views.

nuclei. The connection between the osphradial ganglion and the left pleural ganglion is established at this stage through a thin osphradio-pallial nerve.

The osphradium further enlarges after hatching and its lateral ciliated invaginations deepen and increase gradually in number, until the organ assumes its definitive bipectinate form (see Demian, 1965).

4. Eyes

The eyes are the last to develop, also as ectodermal invaginations which later detach from the ectoderm. The eye rudiments (*E*, Fig. 5) are first noticed in *Stage IX* as 2 thickened ectodermal plates (each 35 μm in diameter) located on either side of the head vesicle, behind the rudimentary tentacles (*TN*). These plates become rapidly invaginated (*E*, Fig. 10A, B). As *Stage X* is reached, they have already constricted off, separated from the overlying ectoderm and transformed into 2 closed vesicles (*E*, Figs. 7A, B, 10C), each measuring about 30 μm in diameter. The cells in the inner or medial part of the wall of each optic vesicle are tall, columnar, with ovoid basal nuclei and a highly acidophilic cytoplasm. They will later form the retina (*RTN*, Fig. 10C). At this stage (*Stage X*), they start to secrete the eye lens (*EL*) as a thin homogeneous translucent material, in the lumen. This secretion stains brownish-red and violet after haematoxylin-eosin and Mallory's triple stain respectively. The cells of the lateral, outer walls of the eye vesicles are shorter, have central nuclei and will develop into the inner cornea (*COI*).

In *Stage XI*, the ectodermal layer behind each tentacle shows a small protuberance into which an eye vesicle has moved. The 2 eye vesicles have become more regularly rounded and each now measures about 40 μm in diameter. The retina cells (*RTN*, Fig. 10D) have become relatively taller and enclose ovoid nuclei located at different levels, while the much shorter cells of the inner cornea (*COI*) show basal nuclei. The lens (*EL*) has increased in diameter and lies within the inner or medial half of the lumen of the eye vesicle.

The ectoderm in a small area overlying each eye vesicle thins out to form the outer cornea (*COO*). This layer is composed of short cuboidal cells with rounded central nuclei.

The eyes have considerably enlarged in *Stage XII*. Two cell types are well recognizable in the retina at this stage: one with black pigment and the other devoid of pigment. The former have large spherical nuclei and broad apices loaded with dark pigment granules, while the latter are more or less fusiform, with attenuated apices and small central nuclei. The cells of the inner cornea now have a distinctly vacuolated cytoplasm. The lens is much enlarged, spheroidal and now occupies most of the space within the eye vesicle. It has obviously grown by addition of concentric layers of secretion to its outer surface.

DISCUSSION

As is well known, the Prosobranchia have a streptoneurous nervous system which is characterized by the concentration of the paired cerebral, pedal and pleural ganglia in a circumenteric ring. Distant from that ring are the sub- and supraintestinal ganglia (parietal ganglia) and the unpaired visceral (abdominal) ganglion. In addition, there is a pair of buccal ganglia on the buccal mass.

The right pleural ganglion generally gives off the supraintestinal nerve which crosses over the digestive tube to the left side to join the supraintestinal ganglion. The latter ganglion originally develops on the right side of the embryo but is shifted to the left side during torsion. Correspondingly, the left pleural ganglion gives off the subintestinal nerve which passes below the alimentary canal to the right side to join the subintestinal ganglion (originally on the left). A secondary connection, or zygosis, is further established between each pleural ganglion and the intestinal ganglion which comes to lie on the same side after torsion. From each of the 2 intestinal ganglia, an intestino-visceral connective extends backwards to join the visceral ganglion, thus completing the pleuro-visceral loop. As already indicated, the components of this loop cross as a result of torsion, thus establishing the streptoneurous condition or chiastoneury.

This general scheme is subject to several variations among different prosobranchs. The Ampullariidae, in particular, are characterized by the disappearance of the connective between the right pleural ganglion and the subintestinal ganglion. This brings

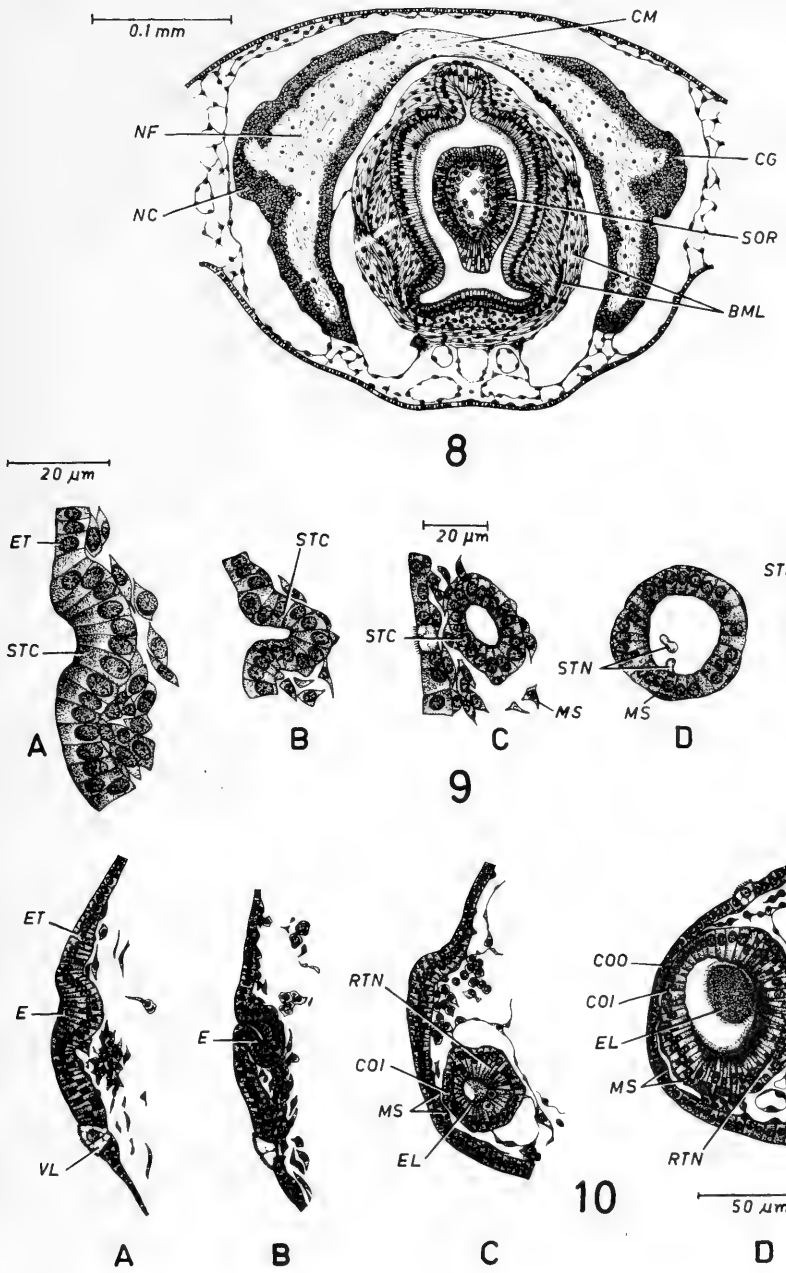

FIG. 8. Transverse section of the head region of the embryo in *Stage XII* passing through the cerebral ganglia.

FIG. 9. A-D, Transverse sections of the statocyst rudiment in *Stage V* (A), *Stage VI* (B), *Stage VII* (C), and *Stage X* (D).
E, Statoconi from the statocyst of a newly hatched snail.

FIG. 10. A-D, Transverse sections of the eye rudiment in *Stage IX* (A, B), *Stage X* (C), and *Stage XI* (D).

the latter ganglion in close contact with the right pleural ganglion, thus obscuring the crossed part of the pleuro-visceral loop and chiastoneury.

Whether the subintestinal ganglion was wanting or entirely fused with the right pleuro-pedal ganglionic mass in the Ampullariidae long remained subject to speculation. Bouvier (1887), from the departing nerves, theorized that the ganglion in question was completely fused with the right pleural ganglion in *Ampullaria*. Hägler (1923) and Prashad (1925) agreed with Bouvier's view. But factual support was not produced until Ranjah (1942) worked out the embryonic development of *Pila globosa*. The present work confirms that, in the Ampullariidae, the originally left rudimentary intestinal ganglion (i.e. the future "subintestinal" ganglion) shifts forwards during its early development and fuses with the rudiment of the right pleural ganglion.

Although the present description of the nervous system agrees with that for *P. globosa* made by Ranjah (1942) as regards the general pattern of development of the nervous system, it differs from his account in the following details:

1. Rudiments of the pedal and pleural ganglia of *Marisa cornuarietis* start differentiating simultaneously with those of the cerebral ganglia, not later as reported by Ranjah for *Pila*. Also, all 3 pairs of ganglia start developing in embryonic *Stage V* of *Marisa*, and not in much earlier stages. Moreover, the cerebral commissures and the cerebro-pedal and cerebro-pleural connectives are among the last commissures and connectives to develop in the embryo of *Marisa*, and are not the first to appear.

2. In *Pila*, the rudiments of the pedal and pleural ganglia of each side were described as being fused together from the beginning. In *Marisa* the authors observed the corresponding ganglia to arise separately and to remain separate for a short while before they fused into a pleuro-pedal ganglionic mass on each side.

3. The osphradium starts differentiating as an ectodermal thickening in the right wall of the visceral sac, before either torsion begins or the mantle cavity forms. It later becomes engulfed in the mantle cavity and shifted to the left side as a result of torsion. According to Ranjah, the osphradium is ontogenetically younger than the mantle cavity. The reason for this discrepancy, as mentioned before (Demian & Yousif, 1973d), is doubtlessly that Ranjah took the early rudiment of the ureter and renal vestibule of *Pila*, as described by the authors for *Marisa*, for a rudimentary mantle cavity.

In the almost unanimous view of previous authors, the nervous system in the Gastropoda is ectodermal in origin. Virtually all nerve ganglia arise by proliferation and later delamination from the ectoderm (Raven, 1966). It is only the cerebral ganglia which in some cases arise by a single or a paired invagination from the head plates. These invaginations form cerebral tubes, which, together with some neighbouring ectodermal cells, develop into the cerebral ganglia. Such a formation has been reported for *Patella* (Smith, 1935), *Vermetus* (Salensky, 1887), *Limax* (Meisenheimer, 1898), *Agriolimax* (Carrick, 1939) and *Achatina* (Ghose, 1962a). According to the last mentioned author, the pedal ganglia of *A. fulica* also develop by invagination, associated with delamination. In *Marisa* and in *Pila* (Ranjah, 1942), no invagination is involved in the development of the cerebral or any other ganglia.

It is also almost universally agreed that, in the Gastropoda, all nerve ganglia arise separately, and become secondarily connected to one another by commissures and connectives which develop as extensions from the peripheral layer of nerve cells of the nerve ganglia. *Marisa* is no exception in this respect. Among the few differing reports are those by Delsman (1914) for *Littorina* and by Heath (1916) for *Crepidula*, purporting that the buccal ganglia originated from the cerebral ones. Delsman moreover described the commissures in *Littorina* as developing from the centrally placed fibrous masses of the ganglia. Andersen (1924) held that the cerebral and pleural ganglia have a common origin in *Paludina* (= *Viviparus*).

As in *Paludina* and *Bithynia* (Erlanger, 1891, 1892, respectively), the 2 rudimentary intestinal ganglia in *Marisa* differentiate before the onset of torsion; hence they appear at first symmetrically placed on the right and left sides of the embryo. In some other cases they are asymmetrical from the beginning: in *Pomatias* (Creek, 1951) the corresponding ganglia do not

appear until torsion has proceeded 90° and in *Littorina* (Delsman, 1914) until torsion is complete.

Both Semper (1862) and Scott (1934, 1957) have described the statocysts in the embryos of various *Ampullaria* spp., but they did not describe the mode of development of these organs. In *Marisa*, as in *Pila* (Ranjah, 1942) and many other gastropods, such as *Patella* (Patten, 1886), *Paludina* (Bütschli, 1877; Erlanger, 1891) and *Bithynia* (Erlanger, 1892), the statocysts arise as ectodermal invaginations which are later constricted off and detached from the ectoderm. However, according to certain authors no invagination takes place in *Planorbis* (Rabl, 1879), in *Limax* (Henchmann, 1890; Meisenheimer, 1898), in *Physa* (Wierzejski, 1905), in *Littorina* (Delsman, 1914), and in *Lymnaea* (Raven, 1952). In these snails the statocysts are said to develop as solid masses by cell-proliferation from the ectoderm and to later develop central cavities.

Marisa also conforms with most other gastropods, such as *Paludina* (Erlanger, 1891), *Patella* (Smith, 1935), *Haliotis* (Crofts, 1938), *Limax* (Meisenheimer, 1898), *Physa* (Wierzejski, 1905), *Agriolimax* (Carrick, 1939), *Lymnaea* (Raven, 1952) and *Achatina* (Ghose, 1962b), as regards the mode of development of the eyes. They arise as ectodermal invaginations which later separate from the ectoderm to form closed vesicles. As regards *Littorina*, Delsman (1914), as for the statocysts, denied that invagination occurs and held that the eyes develop by cell-proliferation.

The eye lens in *Marisa*, as in *Pila globosa* (Ranjah, 1942) and in *Ampullaria polita* (Semper, 1862), is developed as a colourless secretion of the cells of the optic vesicle. However, the steady growth of that lens through the addition of concentric layers during development, which is evidenced in *Marisa* as in *Pila*, is opposed to the early view (Semper, 1862) of a fluid secretion that is transformed into the lens after the formation of the retina.

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ZUSAMMENFASSUNG

EMBRYONALEENTWICKLUNG UND ORGANOGENESE BEI DER SCHNECKE *MARISA CORNUARIETIS* (MESOGASTROPODA: AMPULLARIIDAE). V. ENTWICKLUNG DES NERVENSYSTEMS.

Emile S. Demian und Fouad Yousif

Das Nervensystem ist ektodermalen Ursprungs. Alle Nervenganglien gehen einzeln durch Hervorwölben und spätere Delamination aus dem Ektoderm hervor, nicht etwa durch Invagination. Erst sekundär werden sie miteinander durch Kommissuren und Konnektive verbunden, die sich dadurch bilden, dass sich Material aus der äusseren Schicht der Ganglionnervenzellen längsstreckt.

Erste Anlagen der Zerebral-, Pedal-, Pleural- und Intestinal- (Parietal-) Ganglien entstehen fast gleichzeitig auf einem verhältnismässig frühen Stadium (*Stadium V*). Die Zerebralganglien entwickeln sich aus dem Ektoderm der Kopfplatten. Anlagen der Pedal- und Pleuralganglien sind anfangs getrennt. Später verschmelzen sie (*Stadium VI*) miteinander, um jederseits einen Pleuropedalganglienkomplex zu bilden. Die beiden Intestinalganglien sind am Anfang symmetrisch, verlieren allerdings im Gefolge der Drehung alsbald ihre Symmetrie. Das rechte Ganglion wandert über den Darm nach links und verbleibt dort als Supraintestinalganglion. Das linke oder Subintestinalganglion schiebt sich nach rechts vorn und verschmilzt mit dem rechten Pleuralganglion (*Stadium VIII*) und verdeckt so die Chiastoneurie.

Die paarigen Buccal- und das einzelne Viszeral- (Abdominal-) Ganglion beginnen sich im *Stadium VII* zu differenzieren. Erstere entwickeln sich aus der ektodermalen Wand des Stomodaeums, während das Viszeralganglion sich aus der rechten Wand des Eingeweidesacks bildet und sich während der Drehung nach links schiebt.

Die Statozysten entwickeln sich früh (*Stadium V*) aus 2 ektodermalen Einstülpungen beiderseits der Fussanlage. Später trennen sie sich vom darüber liegenden Ektoderm, und Statokone erscheinen in ihren Hohlräumen.

Im Gegensatz zu früheren Berichten von verwandten Ampullariiden erwies sich das Osphradium als ontogenetisch älter als der Mantel und die Mantelhöhle. Es beginnt, sich als eine verdickte Ektodermpartie in der rechten Wand des Eingeweidesacks zu differenzieren (*Stadium V*). Erst während der Drehung wird es in die Mantelhöhle hineingeschoben und nach links gerückt, schliesslich mit dem Nachvornewachsen des Mantels in derselben Richtung mitgenommen.

Die Augen entwickeln sich spät (*Stadium IX*) als ektodermale Einstülpungen, die sich alsbald vom Ektoderm lösen, um geschlossene Bläschen zu bilden. Ihre Zellen beginnen vor dem Schlüpfen, sich zu differenzieren, und bilden die Retina mit Pigmenteinlagerungen und die innere Cornea. Die Linse wird in das Augenlumen sezerniert und wächst durch Anlagerung von Sekretschichten.

C. M.-B.

RÉSUMÉ

DÉVELOPPEMENT EMBRYONNAIRE ET ORGANOGENÈSE CHEZ L' ESCARGOT *MARISA CORNUARIETIS* (MESOGASTROPODA: AMPULLARIIDAE). V. DÉVELOPPEMENT DU SYSTÈME NERVEUX

Emile S. Demian et Fouad Yousif

Le système nerveux est d'origine ectodermique. Tous les ganglions nerveux apparaissent séparément par prolifération, puis plus tard par délamination de l'ectoderme et non par invagination. Ils sont secondairement reliés entre eux par des commissures et des connectifs qui se développent sous forme d'extensions à partir de la couche périphérique des cellules du ganglion nerveux.

Les ébauches de ganglions cérébraux, pédieux, pleuraux et intestinaux (ou pariétaux) apparaissent simultanément et à un stade relativement précoce (*stade V*). Les ganglions cérébraux se développent à partir de l'ectoderme des plaques céphaliques. Les ébauches de ganglions pédieux et pleuraux sont séparés à l'origine. Ils fusionnent plus tard (*stade VI*) pour former une masse ganglionnaire de chaques côté. Les 2 ganglions intestinaux sont symétriques au début, mais bientôt ils perdent leur symétrie à cause de la torsion. Le ganglion de droite passe a gauche par-dessus l'intestin et persiste sous forme d'un ganglion supraintenstinal. Celui de gauche ou sous-intestinal, se déplace sur la droite et en avant et fusionne avec le ganglion pleural droit (*stade VIII*), masquant ainsi la chiastoneurie.

La paire de ganglions buccaux et l'unique ganglion viscéral (abdominal) commencent à se différencier au *stade VII*. Les premiers se développent à partir de la paroi ectodermique du stomodeum, tandis que le ganglion viscéral se délamine à partir de la paroi droits du sac viscéral et qu'il se déplace ensuite vers la gauche au cours de la torsion.

Les statocystes se développent tôt (*stade V*) à partir de 2 invaginations ectodermiques sur chaque côté de l'ébauche de pied. Ils se séparent ensuite de l'ectoderme sus-jacent et des statocones apparaissent dans leur cavité.

Contrairement aux résultats des études précédentes sur des Ampullariidae voisins, on a mis en évidence que l'osphradie est ontogéniquement plus ancienne que le manteau et la cavité palléale. Elle commence à se différencier sous forme d'une mince plaque ectodermique dans la paroi droite du sac viscéral (*stade V*). Pendant la torsion, elle est englobée dans la cavité palléale et se déplace sur le côté gauche, ensuite elle s'achemine en avant pendant que le manteau s'accroît antérieurement.

Les yeux se développent tardivement (*stade IX*) sous forme d'invaginations ectodermiques, qui se séparent très vite de l'ectoderme pour former des vésicules closes. Leurs cellules commencent à se différencier avant l'éclosion pour former la rétine, dans laquelle du pigment se dépose, et al cornée interne. Le cristallin est sécrété par la cavité de l'oeil et s' accroît par addition de couches de sécrétion concentriques.

A. L.

RESUMEN

DESARROLLO EMBRIONARIO Y ORGANOGENESIS EN EL CARACOL *MARISA CORNUARIETIS* (MESOGASTROPODA: AMPULLARIIDAE). V. DESARROLLO DEL SISTEMA NERVIOSO.

Emile S. Demian y Fouad Yousif

El sistema nervioso es de origen ectodérmico. Todos los nervios ganglionales surgen separadamente por proliferación y luego delaminación del ectoderma, no por invaginación. Luego se conectan secundariamente unos con otros por comisuras y conectivos que se desarrollan como extensiones de la capa periferial de las células nerviosas ganglionales.

Rudimentos de los ganglios cerebral, pedal, pleural e intestinal (parietal) aparecen casi simultaneamente en un grado de crecimiento relativeamente temprano (*estado V*). El ganglio cerebral desarróllase del ectoderma de las placas cefálicas. Al comienzo, los rudimentos de los ganglios pedal y pleural estan separados; se fusionan luego (*estado VI*) para formar una masa pleuro-pedal a cada lado. Los dos intestinales son simétricos al principio, pero pronto pierden la simetría como resultado de la torsión. El ganglio derecho cruza a la izquierda sobre las vísceras y persiste como un ganglio supraintestinal. El izquierdo o subintestinal tuerce a la derecha y hacia arriba fusionándose con el ganglio pleural derecho (*estado VIII*), obscureciendo así la quistoneuria.

Los ganglios bucales pares, y el sencillo visceral (abdominal) comienzan a diferenciarse en el *estado VII*. El primero se desarrolla de la pared ectodérmica del stomadeum, mientras que el ganglio visceral es delaminado de la pared derecha del saco visceral, y tuerce hacia la izquierda durante la torsión.

Los estatocistos se desarrollan temprano (*estado V*) de dos invaginaciones ectodérmicas a cada lado del pié rudimentario. Esta último se desprende del superpuesto ectoderma y ectoconos aparecen en su lumina.

En contradición a lo que se habia indicado previamente para otros ampularidos relacionados, el osfradio demostró ser ontogeneticamente de aparición más temprana que el manto y la cavidad paleal. Comienza diferenciándose como una placa ectodérmica engrosada en la pared derecha del saco visceral (*estado V*). Durante la torsión es engolfado dentro de la cavidad paleal y movido a la izquierda, entonces, como el manto crece anteriormente, es llavado hacia adelante.

Los ojos tienen desarrollo tardío (*estado IX*) como invaginaciones ectodérmicas que se separan rápidamente para formar vesículas cerradas. Sus células empiezan a diferenciarse antes de la eclosión para formar la retina, en la cual se deposita pigmento, y la cornea interna. El lente es segregado en el lumen del ojo y crece por el agregado de capas concéntricas de secreción.

J.J.P.

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SYSTEMATICS AND BIOLOGY OF *THALA FLORIDANA* (GASTROPODA: VEXILLIDAE)

Virginia O. Maes[1] and Dorothy Raeihle[2]

ABSTRACT

Thala floridana (Dall, 1883) is limited to the Gulf of Mexico, Florida, the Bahama Islands and Bermuda. It has been incorrectly placed in the family Mitridae. The family Vexillidae, to which it belongs, is not closely allied to the Mitridae. *Thala floridana* has anatomical features which are not found in the Mitridae, such as a valve of Leiblein, paired accessory salivary glands, a gland of Leiblein, a pycnonephridian kidney, and reproductive features such as a blister-like egg capsule containing 1-4 eggs, and full capsule development of embryos.

Thala feeds on small gastropods which it kills with a penetrating poison which causes no trauma and which probably is secreted by the accessory salivary glands. The poison apparatus is not homologous with that of *Conus*.

Thala floridana becomes sexually mature at about 6 months, and lives at least 6 years. Its low rate of fecundity (about 60 eggs per year with a 10 month breeding season) must be offset by a high survival rate of its directly developing young. Distribution and abundance are probably limited by temperature requirements for reproduction.

INTRODUCTION

Thala floridana (Dall, 1883) is a small, inconspicuous brown snail common in shallow, protected bays of the Florida Keys but relatively uncommon elsewhere. It belongs to a genus which is ubiquitous but uncommon in warm seas around the world.

Studies of the genus have been based, for the most part, on dead-collected shells. Virtually nothing has been known of its anatomy or biology. Traditionally (and wrongly) the genus has been considered volutacean and placed in the family Mitridae.

Our study was stimulated by Raeihle's paper on *Thala floridana*'s reproductive habits (Raeihle, 1968). In this paper she noted that *Thala* stings its prey before feeding. Maes was interested in the evolution of the toxoglossan foregut and thought *Thala* might have a prototypic poison apparatus.

Information gathered on the reproduction and life cycle of this gastropod (Raeihle, 1968) suggested reasons for its local abundance and limited distribution. A study of its anatomy by Maes revealed the foregut of an unspecialized muricid-like neogastropod without a toxoglossan poison apparatus. The kidney structure was similar to that of muricids and buccinids, not mitres or toxoglossans.

SYSTEMATICS

Family **Vexillidae** Thiele, 1929

Vexillinae Thiele, 1929: 337, a subfamily of Mitridae.
Vexillidae Azuma, 1965: 53.
Vexillidae Ponder, 1972: 334.

Both Thiele and Azuma separated the vexillid and mitrid snails on radular differences alone. Ponder's more comprehensive anatomical studies demonstrated important differences such as a muricid-like foregut with secondary salivary glands and a conspicuous valve of Leiblein and a pycnonephridian kidney (Perrier, 1889: 242) in the vexillid genera. The mitrid genera Ponder studied lack the secondary salivary glands and many have developed a peculiar "epiproboscis". All Mitridae had the volutid type, meronephridian kidney.

In addition to anatomical differences, the 2 families produce different kinds of spawn. The spawn of many species and genera of Mitridae are known. They are all clusters of stalked capsules containing numerous eggs. The few species and genera of Vexillidae whose spawn are known produce solitary,

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blister-like capsules with few eggs (*Thala*, Raeihle, 1968; *Austromitra*, Ponder, 1972: 318, *Pusia*, Purtymun, 1974; *Pusia hanleyi* and *P. puella*, Maes & Raeihle, unpublished observations). The absence of knowledge of the spawn of all the large and often common Indo-Pacific *Vexillum* and *Pusia* species suggests that they also produce this type of solitary, inconspicuous spawn.

Separation of the 2 families is fully warranted by these anatomical and reproductive differences.

Genus **Thala** H. & A. Adams, 1853

Turricula (*Thala*) H. & A. Adams, 1853: 178. Placed in Mitridae; 5 species listed.

Thala, Tryon, 1882: 159. 16 species listed.

Micromitra Bellardi, 1888: 147.

Thala, Cossmann, 1899: 176. Designated *Mitra mirifica* Reeve, 1845, type-species. Placed *Micromitra* Bellardi in synonymy.

Pusia (*Thala*), Thiele, 1929: 338. Figured radula. Placed in Vexillinae.

Thala, Habe, 1943: 72, pl. 3, fig. 11. Figured radula of a Japanese species.

Thala, Wenz, 1943: 1285. Geologic range from the Eocene of Europe and ? Australia.

Mitromica Berry, 1958: 94 *Mitra solitaria* C. B. Adams, 1852, designated type-species.

Pusia (*Thala*), Cernohorsky, 1966:121. Thiele and Habe radula figures given.

Thala, Coan, 1966: 131. Designated type-species of *Micromitra*: *M. taurina* Bellardi, 1888.

Mitromica, McLean, 1967: 58. Radulae of Eastern Pacific species.

Thala, Sphon, 1969: 84. Placed *Mitromica* Berry in synonymy. Reviewed Recent distribution of the genus. Added a new species.

Thala, Cernohorsky, 1970: 58. Placed in subfamily Vexillinae. Distribution of genus: European Miocene (6 species with 5 synonyms), European Pliocene (1 species), Caribbean Recent (1 species), Eastern Pacific Recent (2 species with 3 synonyms), Indo-Pacific Recent (3 species with 18 synonyms).

The synopsis of the literature on *Thala* above gives some concept of the lack of knowledge of the status and distribution of the genus. It is a common Miocene fossil in Europe, where there are now no living species. Except for 1 Eastern Pacific Pleistocene species (Sphon, 1969) and 1 Western Atlantic Pleistocene species (Hoerle, 1970: 56), the genus is not known elsewhere as a fossil. Wenz's (1963: 1285) dubious Australian record was based on an extraneous species.

The absence of fossils is misleading. The rocky habitats preferred by many of the Recent species are unsuitable for fossil production. The recorded stratigraphic distribution of the genus is incomplete. It is probable that the "explosion" of species in Europe during Miocene times was accompanied by widespread dispersal. For example, the presence of homologous species on both sides of the Isthmus of Panama and on both sides of the old Caribbean land arc testify to the presence of *Thala* in that area by late Miocene or early Pliocene times at the latest (Fig. 15).

Recent records show a genus comprised of about 12 species. Several of the Indo-Pacific species are ubiquitous but uncommon. Of the 3 Eastern Pacific species

FIGS. 1-6. Shells of *Thala floridana*, all at approximately the same scale.

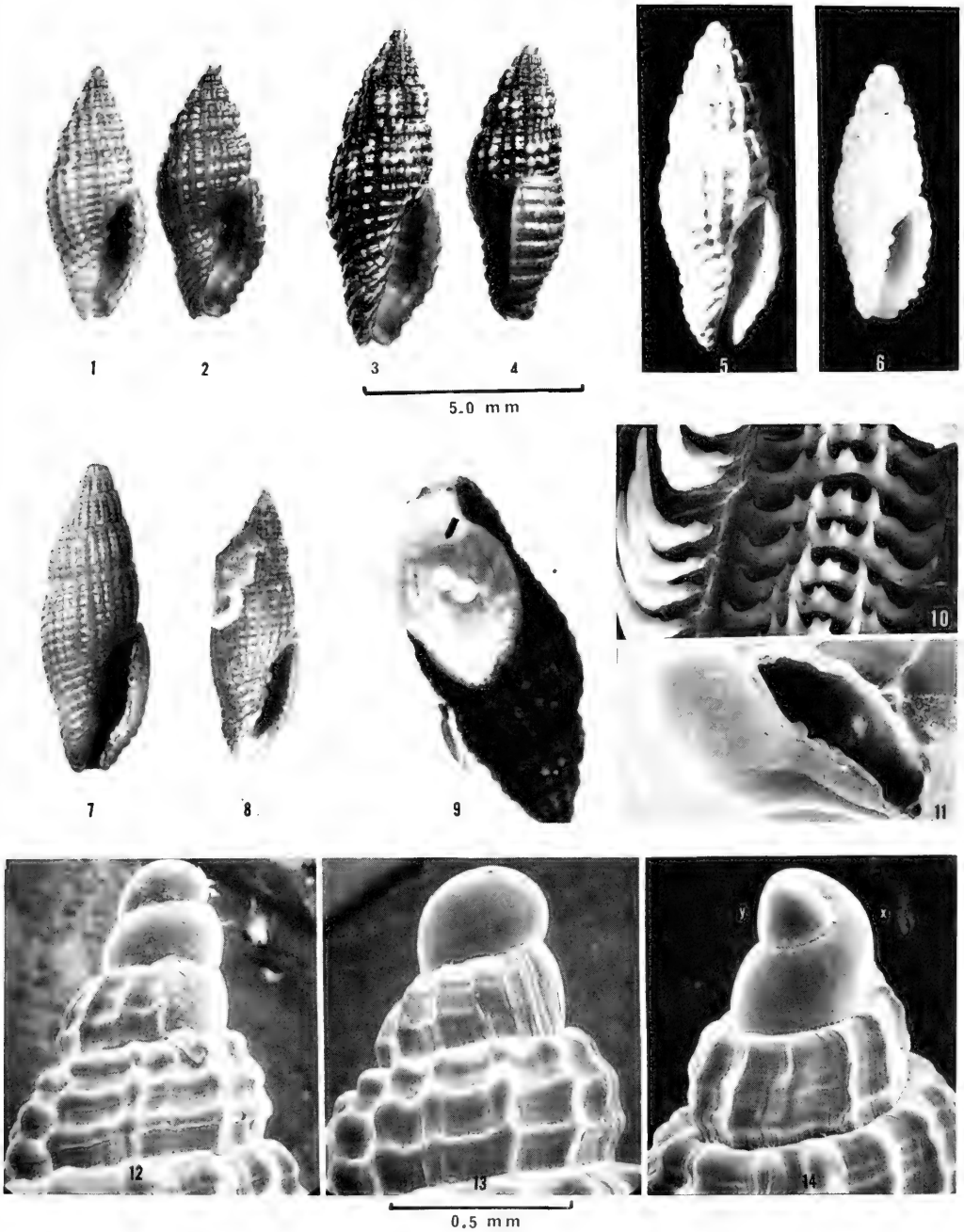
1. ANSP 285516, Isla Cancun, Quintana Roo, Mexico. 5.8 mm. long.
2. From the same locality and lot. 6.0 mm.
3. ANSP 220052, Bonefish Key, near Marathon, Florida. 8.2 mm.
4. From the same locality and lot. 7.3 mm.
5. Pleistocene fossil from the Glades Formation, 2 mi W of Ortona Lock, Caloosahatchie River, Florida. T. L. McGinty colln. 7.7 mm.
6. ANSP 315817, Shelly Bay, Bermuda. 6.0 mm.

FIGS. 7-8. Shells of *Thala foveata*. Same scale as above.

7. BM 39.10.22.7-18, non type material, St. Vincent, West Indies. 7.2 mm.
8. T. L. McGinty colln., Calliaqua, St. Vincent, West Indies. Bryozoan and worm tubes on spire. 6.3 mm.

FIG. 9. *Thala floridana* (6.5 mm long) attaching egg capsule to aquarium wall. Two eggs are under the center of the foot. The light reflection (arrow) is from the inner wall of the capsule. The dark slit to the left of the eggs is the ventral pedal pore which is visible only during oviposition.

FIG. 10. *Thala floridana* radula. ANSP 315495, shell 5.0 mm long, SEM, about 740X.



FIGS. 11-14. Protoconch and early teleoconch of *Thala*. SEM, all about 50X.

11. *T. floridana* 2 weeks after hatching. Note the 3 well-developed columellar plicae.
12. *T. gratiosa*, LACM A4052, intertidal, Bahía San Luis Gonzaga, Mexico. Note the concave scar of the protoconch lip.
13. *T. floridana*, ANSP 220052, Bonefish Key, near Marathon, Florida. Note the straight scar of the protoconch lip.
14. *T. floridana*, ANSP 303255, Quintana Roo, Mexico. The "x-y" axis was used to measure the diameter of the first whorl.

only 1, *Thala gratiosa* (Reeve, 1845), is moderately common and wide-ranging (San Diego, California, to Port Utria, Colombia; Sphon, 1969). The protoconch of one example of this species, studied with a scanning electron microscope, had a small first whorl and a concave scar of the protoconch lip (Fig. 12). This is suggestive of a free-swimming veliger stage unlike that of the subject of this study, *Thala floridana*. There are 2 species in the Western Atlantic (we disagree with Cernohorsky, 1970: 58, on their synonymy). *T. floridana* is fairly common but limited in distribution. *T. foveata* (Sowerby, 1874) is rare and has a remarkable distribution: the Caribbean island of St. Vincent and an Eastern Atlantic island, São Thomé, which lies near the equator off the coast of West Africa (Tomlin & Shackleford, 1914: 245, and S.P. Dance, written communication). This odd distribution suggests that *T. foveata* may be a relic of a pioneering Miocene species, a precursor of *T. floridana, T. gratiosa* and *T. solitaria* (C. B. Adams, 1852). Unfortunately it is quite rare. Almost all material in collections is poorly preserved and efforts to obtain living specimens were unsuccessful.

Raeihle's (1968) paper on the feeding and reproduction of *Thala floridana* is the only one on the biology of the genus. The few radula studies listed above represent the literature on the anatomy of the genus *Thala* in toto.

Thala floridana (Dall, 1883)
Figs. 1-6

Mitra (*Mitromorpha ?) floridana* Dall, 1883: 327, pl. 10, fig. 12. Key West, Florida, on reefs at low water. H. Hemphill, leg. 2 syntypes, USNM 35971.

Mitra floridana, Johnson, 1934: 129. Range given as Marco, Fla., to the Florida Keys.

Mitra floridana, M. Smith, 1937: 128, pl. 50, fig. 5, pl. 68, fig. 5. Range given as Card Sound to Key West and to Marco, Florida.

Mitra floridana, Raeihle, 1968: 36 Feeding and reproduction.

Thala floridana, Sphon, 1969: 85. Mentioned as the Atlantic "analogue" of *T. gratiosa*.

Thala foveata (Sowerby, 1874), Cernohorsky, 1970: 58. *T. floridana* considered a junior synonym.

Mitra cf. *floridana* Hoerle, 1970: 56. Listed as a Lower Pleistocene fossil from the Belle Glade Rock Pit, Palm Beach County, Florida.

Thala foveata, Waller, 1973: 38, 43, fig. 28. A small shell of *T. floridana* from 34 m off Bermuda.

The shell is small, 5 to 8 mm long, clathrate and biconic. Usually brown, it may be spotted or mottled white. A few shells are pure white. Definitive characters are: relatively large first whorl (diameter about 0.4 mm), paucispiral (1½ whorls) protoconch, convex whorls, relatively wide aperture with at least 3 plicae on the columella and small denticles inside the outer lip. The first spiral cord below the suture equals or is weaker than succeeding cords.

Thala floridana can be distinguished from its nearest relatives by the following shell differences: *T. foveata* (Figs. 7-8) has a smaller protoconch, a thickened cord immediately below the suture, flat-sided whorls and a narrower aperture; both *T. gratiosa* and *T. solitaria* are larger (10-17 mm long), have 3 protoconch whorls; *T. gratiosa* is also flat-sided, with a narrow aperture, being similar in outline to *T. foveata*.

Dall's confusion of *Thala* with the unrelated turrid genus *Mitromorpha* has been shared by many other workers. At least 3 Atlantic species, *Mitra haycocki* Dall & Bartsch, 1911, *Mitra* (*Thala*) *pleurotomoides* E. A. Smith, 1890, and *Mitra* (*Thala*?) *torticula* Dall, 1889, are toxoglossan Turridae, and not Vexillidae or Mitridae. It is, therefore, appropriate to point out differences between these genera here.

The shells of *Thala* and *Mitromorpha* are, as described above, small, biconic, clathrately sculptured and frequently brown or brownish. *Thala* always has 3 strong plicae on the columella and a proportionately higher spire. The columella of mitromorphine shells has 2 small denticles and the body whorl tapers anteriorly from the suture. This, and the squat spire give *Mitromorpha* shells a rather top-like appearance. Resemblance and confusion between the groups end with the shells. The foregut of *Mitromorpha* is typically toxoglossan, with a venom bulb and gland, lance-like marginal teeth, and lacking a valve and gland of Leiblein.

DISTRIBUTION

The distribution of *Thala floridana* is shown in Fig. 15. Fossil records of *T.*

floridana are known only from Florida formations. Aside from the published record of it in the Pleistocene Belle Glade Rock pit (Hoerle, 1970) there are several other specimens from another locality which may not be the same age. These are in the collection of Mr. Thomas L. McGinty, Boynton Beach, Florida. They come from 2 mi W of Ortona Locks, Caloosahatchie River, Glades County, Florida. Although both Hoerle and McGinty identified their shells as *Thala* cf. *floridana*, we believe they are true *T. floridana*. There is an interesting resemblance between one of the Ortona Lock shells (Fig. 5) and a Recent Bermuda example (Fig. 6).

The molluscan assemblages from these localities indicate environmental conditions similar to those now found off the ocean side of the Florida Keys (McGinty, 1970: 54).

Recent geographic distribution of the species is from Alacran Reef, off Yucatan (22°30′N, 89°45′W) to Destin, near Pensacola, on the NW coast of Florida. It has not been recorded from other Gulf coast states. Its distribution around Florida is more or less continuous as far north as Palm Beach on the E coast. It is also found along the NW coast of Cuba to Havana, and in the Bahama Islands and Bermuda. One dead shell was collected by Orcutt at Sal Trou, SE Haiti (18°13′N, 72°2′W). It is in worn condition and the protoconch is missing. A fairly long anterior siphonal canal and numerous (27) axial ribs indicate that it may have come from moderately deep water. This shell is in the collection of the U.S. National Museum of Natural History (USNM 439975).

Habitat requirements for *Thala floridana* appear to be: rather calm water with temperatures ranging between 18° and 33° C, a stone or shell for resting on and for attachment of egg capsules, and sufficient seaweeds to support an abundance of small gastropods for food. A favored habitat in the Florida Keys, where it is most common, is barely subtidal on weedy "ironshore" (limestone) rock with pockets of drifted sand. Here small colonies of 3-8 individuals can be found under a single coralline stone. Other habitats include *Thalassia* and other weedy substrates on sandy or oozy muds in depths down to about 90 m. The latter is an unusual depth for the species. The 1 lot we have seen from this depth contained some live-taken specimens. It is from the collection of the late Mr. Dan Steger, St. Petersburg, Florida (Steger colln. 1596) and was dredged from 40-50 fm (73-91 m), SW of Egmont Key, W Florida (approximately 27° 30′N, 84° 10′W).

The geographic distribution of *Thala floridana* reflects several aspects of its biology. To the N, the species is limited by inability of the adults to survive water temperatures below 18°C. *Thala* is rarely carried far and never in large numbers. Unlike species with planktonic larvae, it cannot repopulate, in summer, areas where the adults are killed by winter cold.

The southern limit is probably controlled by reproductive requirements. Our captive snails virtually ceased spawning when water temperatures rose to 27° C. A period of relatively cool temperatures is necessary for reproduction. The near coincidence of the southern limit to *Thala floridana*'s range and the 26° C. winter surface water isotherm are seen in Fig. 15.

The presence of this species, which develops to the crawling stage within the egg capsule, in isolated Bermuda is of interest. The similarity of Recent Bermuda and Pleistocene fossil Florida shells, mentioned earlier, suggests that *Thala floridana* has been in Bermuda for considerable geologic time. It could, however, have been transported there recently at the egg capsule stage under catastrophic circumstances. If a hypothetical weed-covered pebble or shell bearing several egg capsules were torn free in Florida or the Bahamas by a hurricane, it could drift to Bermuda within 20 days. (Drift and storm data from Robertson, 1964: 15, and U.S. Government Hydrographic Office, 1951: 16, 21, 34, 39.) This is well within the 22-30 days the developing embryos spend inside the firmly-attached capsule.

METHODS

Living *Thala floridana* were observed and collected in their natural habitat by both of us on several occasions in November and April in the Florida Keys and by Maes in March at Isla Mujeres off the Yucatan Peninsula.

All observations on spawn, growth and feeding were of captive specimens collected from Florida Bay at Crawl and Grassy Keys, near Marathon, Florida, or were 1st or 2nd generation captives of this stock.

FIG. 15. Distribution of *Thala floridana* and some influential factors. Recent water currents are shown by arrows (Scheltema, 1968, fig. 1); the 26° C minimum surface water isotherm is shown by a dashed line (Fuglister, 1947, pl. 14); shaded areas are Upper Miocene and Lower Pliocene land areas (Schuchert, 1935, Palaeogeographic map 15). Black dots are Recent and white circles are Pleistocene records of *T. floridana*. Some nearby occurrences of closely related species are "F" = *T. foveata*, "G" = *T. gratiosa* and "S" = *T. solitaria* (the latter two species from Sphon, 1969: 87).

Captive *Thala* were usually kept in groups of 6-12 adults in 20-30 cc of natural seawater in rectangular, covered plastic containers 12.5 X 8.5 X 6.0 and 8 X 6.5 X 3.5 cm. A small flat stone or clam shell was usually submerged in each aquarium. There were no water-circulating or aerating devices and the captives adapted well to occasional changes of New York or New Jersey seawater (about 3.1% salinity). Water temperatures were not controlled and were checked irregularly. Recorded temperatures ranged with room and season between 22° and 27° C. Extreme temperatures of 18° and 33° C were tolerated for short periods (less than 24 hr).

Feeding and egg-laying were observed with a 10X hand lens, under a Wild dissecting microscope and in still macrophotographs. Drawings of egg cases and developing larvae were made from photographs. A standard ocular micrometer mounted in a Wild dissecting microscope was used to make most of the measurements. The protoconch dimension measured is illustrated in Figs. 14 and 32 and was made at approximately 50X magnification. Observations of protoconchs and radulae were also made with a Jeolco JSM-2 Scanning Electron Microscope.

Anatomical studies were made of living specimens as well as material fixed in Bouin's and preserved in 70% ethanol. The most successful method of extending living specimens was to add 10% $MgCl_2$ until the animal became uncoordinated and then add Sevin (1 naphthyl N-methylcarbamate) dissolved in acetone and diluted in seawater (Carriker & Blake, 1959: 19). This usually extended the proboscis as well as the penis. It was difficult to kill and preserve animals in an extended position. Killing with hot Bouin's was the most successful method. Some of the fixed material was sectioned serially at 8-10 μm and stained with standard haematoxylin and eosin. A few were stained with Mallory Triple (Pantin, 1964: 41). Wherever possible, we have used the terminology of Fretter & Graham (1962) in the anatomical section of this paper.

Much of the material studied is in the collection of the Department of Malacology, Academy of Natural Sciences of Philadelphia. Additional material is in the British Museum (Natural History), the Los Angeles County Museum, and the collections of Mr. T. L. McGinty, Boynton Beach, Florida, and the late Mr. Dan Steger, St. Petersburg, Florida, and of the U.S. National Museum of Natural History.

MORPHOLOGY

The shell (Figs. 1-6, 9, 11, 13, 14)

A general description of shell shape, color and definitive characters of *Thala floridana* has been given in the systematic section of this paper. We are concerned here with the type and degree of shell variation. This is considerable, as one might expect in a species with numerous more-or-less genetically isolated micropopulations. To compare the degree of variation in unrelated characters we have used the coefficient of variability (methods of Cazier & Bacon, 1949: 364-372). In the following paragraphs we use S.D. = 1 standard deviation; C.V. = coefficient of variability.

Color. Shell color seems to be predominately controlled by the genetic resources of the original colonizing stock. Although almost any *Thala* color or pattern can be found in one large sample of a micropopulation, most geographic areas have a characteristic color pattern. W coast Florida shells are usually unmarked, warm brown. Florida Key shells are brown with white beads. Cuban shells are lighter brown with flames or splotches of white. Only the pure white shells are probably selected for ecologically. They occur in widely separated localities on white sand substrates (where ecologic data are known).

Size (Fig. 16). The longest shells measured 8.4 mm (Florida Keys and Cuba). We did not find sexually mature individuals smaller than 5.0 mm. The mean length of shells from 27 localities throughout the range was 6.5 mm (117 shells; S.D. = .79; C.V. = 12.02). The large coefficient of variability reflects, among other things, sexual dimorphism in the size of *Thala*. Females are usually larger than males.

Whorl counts varied from 5¼ to 6½ in adult shells. The mean count was 5.9 (89 shells; S.D. = .34; C.V. = 5.76). There was some positive correlation between size and whorl count at extreme lengths but shells of about 6 whorls (near the mean) varied in length from 5.5 to 7.3 mm. This is an expression of the sexual dimorphism mentioned above. Shell lengths of 12 females and 15 males from one micropopulation (Crawl Key, Florida) were: Females—largest

7.4, mean 6.5, smallest 5.9 mm. Males—largest 7.0, mean 5.9, smallest 5.0 mm. We did not determine whether the female is always the larger of copulating pairs as was the case in *Mitra idae* (Chess & Rosenthal, 1971).

Shape. Body and spire length are roughly equal in *Thala floridana* and the ratio was only moderately variable. We could not correlate spire length significantly with distribution, size or sex. When length of the body whorl was expressed as a percentage of total length, variation ranged from 41% (dredged, W Florida, 7.0 mm) to 59% (shallow water, NW Cuba). The mean ratio was 51% (118 shells; S.D. = 3.04; C.V. = 5.96).

Width of the shell was more variable and was negatively correlated with length. Long shells tended to be slender and short ones plump. This indicates that volume, not shape, is a more conservative (?important) character in the species. When width was expressed as a percentage of total length, variation ranged from 53% (Key West, Florida, 5.5 mm) to 30% (deep water off W Florida, 7.0 mm). The mean ratio of adults of all sizes from all parts of the geographic range was 39% (130 shells; S.D. = 3.42; C.V. = 8.77). An apparent sexual difference was merely a reflection of sexual size dimorphism. Large males had low W/L (32%, 7.0 mm), and smallish females were of mean dimensions (39%, 6.1 mm). Moreover, a frequency curve of this ratio showed no signs of bimodality.

Periostracum. Most shells are covered with a brown periostracum which, though thin and translucent, is very tough. It is sometimes eroded in muddy substrates. Brown shells that have lost their periostracum soon become chalky and greyish.

Sculpture of the teleoconch. The strength and spacing of axial cords is mainly influenced by rate of growth and habitat. It was the most variable shell character measured or counted. When our captive young snails were fed frequently and were growing rapidly, their axial cords were strong and widely spaced. The axials became smoother and more crowded as the snails reached sexual maturity and their growth slowed. Samples with adequate ecologic data suggested that shells from *Thalassia* substrates have smoother and more crowded axial and spiral cords than those from rocky bottoms. However, we did not have enough material to substantiate this.

The number of axial ribs on the body whorl varied from 33 (Abaco, Bahama Islands) to 14 (Yucatan) with a mean of 21.2 (71 shells; S.D. = 3.78; C.V. = 17.83). A scatter diagram of this character plotted against shell length is shown in Fig. 16.

Spiral cording was only slightly positively correlated with size and was only slightly less variable than the axial sculpture. Were it not for the tendency, mentioned above, to find more spiral and axial cords in shells from *Thalassia* substrates we might consider that spiral sculpture was controlled by random genetic factors. It is widely variable within a single micropopulation and is not affected by rate of growth.

The number of spiral cords on the body whorl ranged from 9 (several shells, Florida Keys) to 18 (shells from several geographic localities). The mean number of spiral cords was 12.3 (73 shells; S.D. = 1.95; C.V. = 15.85).

Protoconch (Figs. 11, 13, 14). The protoconch consists of about 1½ smooth, rounded brown whorls. The scar of the lip, i.e. the point where teleoconch growth commences, is straight, not concave as in many species with free-swimming veliger larvae. The diameter of the first whorl (x-y, Figs. 14, 32) varied from 0.48 mm (Florida Keys and Florida W coast) to 0.34 mm (Abaco, Bahama Islands). The mean diameter was 0.41 mm (82 shells; S.D. = .03; C.V. = 7.80). There was no correlation between the diameter of the first whorl and the ultimate size of the mature shell.

We consider the diameter of the first whorl the most meaningful dimension of *Thala* protoconchs. It correlates with egg size (Thorson, 1952: 282). It may possibly be influenced by the size of the parent (Chess & Rosenthal, 1971: 175). It is also influenced by the number of embryos in the capsule and the length of time spent in the capsule. (Single embryos and embryos spending longer periods in the capsule are usually larger.) In light of these diverse factors which influence the diameter of the first whorl, its coefficient of variability is surprisingly low.

External features of the head-foot

The external aspect of *Thala floridana* is not of great interest. It is not specialized for

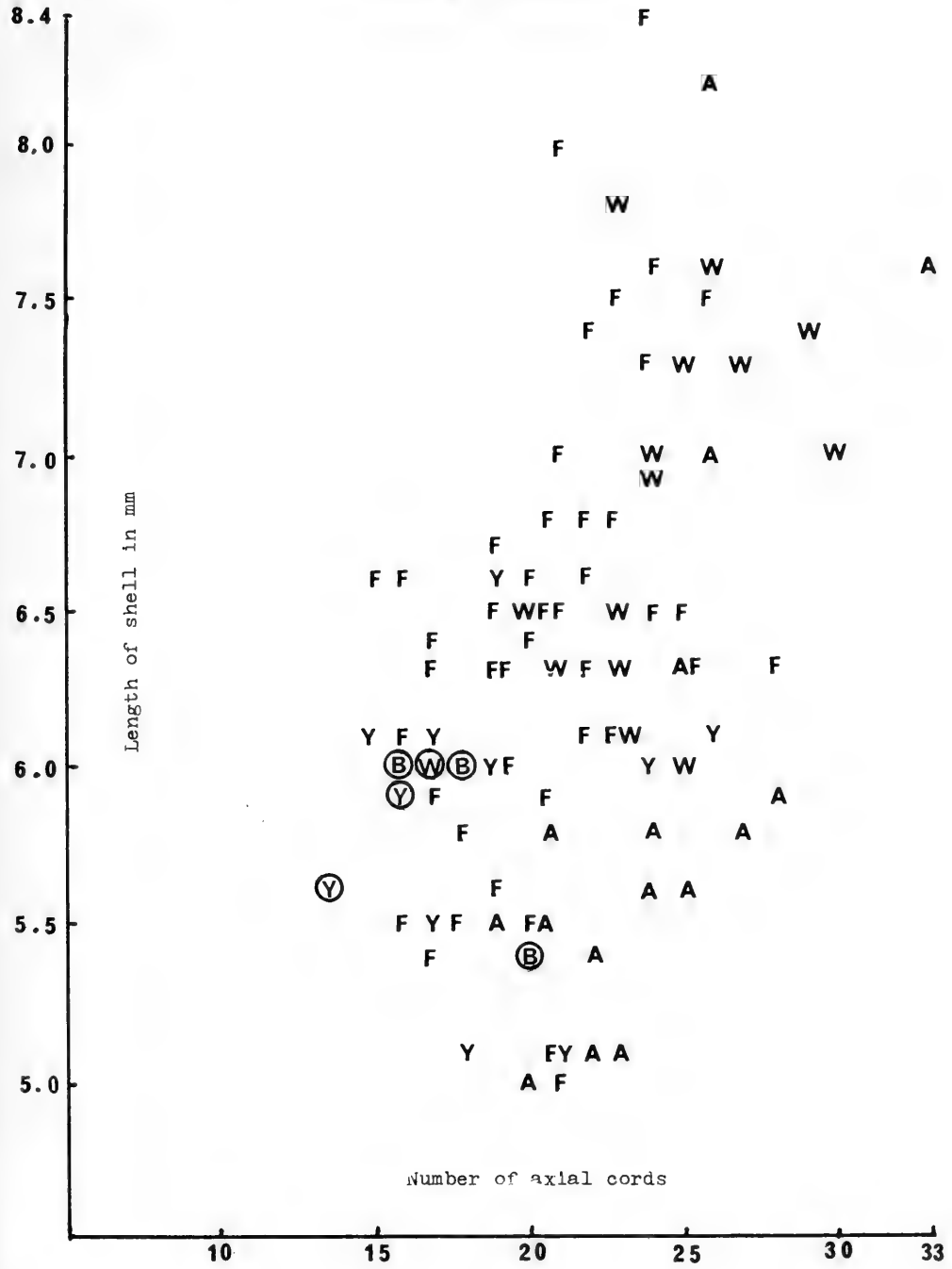


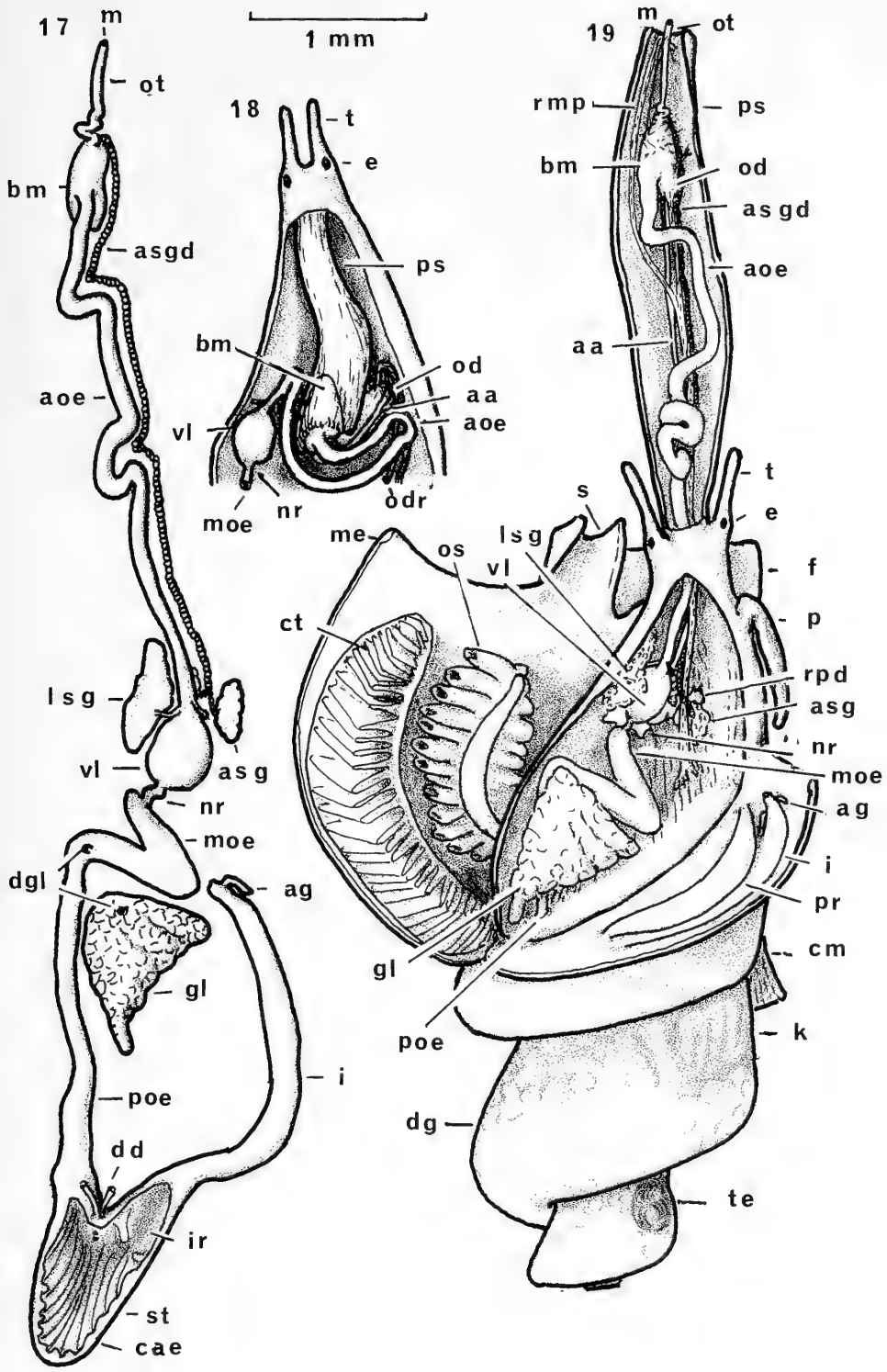
FIG. 16. Scatter diagram of some growth-related shell characters of adult *Thala floridana*. Adult size is given as the length of the shell. Speed of growth is shown by the number of axial cords, i.e. few cords = fast growth. A = Abaco, Bahama Islands; B = Bermuda; F = Florida Keys and E coast of Florida; W = Dry Tortugas and W coast of Florida; Y = Yucatan Peninsula. Pure white specimens from all localities had few ribs and are shown by a circled letter.

KEY AND INDEX TO LETTERING ON FIGS. 17-33

a	anus, Fig. 28.
aa	anterior aorta, Figs. 18, 19, 20, 22, 29.
ag	anal gland, Figs. 17, 19, 28.
alb	albumen, Fig. 30.
alg	albumen gland, Figs. 26, 27.
aoe	anterior oesophagus, Figs. 17, 18, 19, 20, 22.
apg	anterior pedal mucous gland, Fig. 25.
arv	afferent renal vessel, Figs. 28, 29.
asg	accessory salivary gland, Figs. 17, 19, 22, 25.
asgd	duct of accessory salivary gland, Figs. 17, 19, 20, 22.
au	auricle, Figs. 28, 29.
bacp	base of egg capsule, Figs. 30, 33.
bcp	bursa copulatrix, Figs, 25, 27, 28.
bg	buccal ganglion, Fig. 25.
bm	buccal mass, Figs. 17, 18, 19, 20, 22, 26.
cae	caecum of stomach, Fig. 17.
cm	columellar muscle, Figs. 19, 22, 23, 25, 26, 28.
cp	capsule gland, Figs. 26, 27, 28.
ct	ctenidium, Figs. 19, 25, 29.
dd	ducts of 2 lobes of digestive gland, Fig. 17.
de	developing eggs, Fig. 30.
dg	digestive gland, Figs. 19, 25, 29.
dgl	duct of gland of Leiblein, Fig. 17.
dodp	dorsal odontophoral protractor muscle, Fig. 20.
e	eye, Figs. 18, 19, 26, 32, 33.
ea	escape aperture, Figs. 30, 33.
f	foot, Figs. 19, 23, 25, 26, 29, 32, 33.
gl	gland of Leiblein, Figs. 17, 19, 29.
hg	hypobranchial gland, Figs. 25, 28, 29.
i	intestine, Figs. 17, 19, 25, 28.
ir	intestinal region of stomach, Fig. 17.
iwcp	inner wall of egg capsule, Figs. 30, 33.
k	kidney, Figs. 19, 25, 28, 29, 33.
ko	opening of the kidney into the mantle cavity, Fig. 28.
lodp	lateral odontophoral protractor muscle, Fig. 20.
lpl	left pleural ganglion, Figs. 21, 25.
lsd	opening of left salivary duct, Fig. 22.
lsg	left lobe of salivary gland, Figs. 17, 19, 23, 25.
m	mouth, Figs. 17, 19, 20, 25, 32.
mc	mantle cavity, Figs. 23, 28.
me	mantle edge, Figs. 19, 23, 25, 26, 33.
moe	mid-oesophagus, Figs. 17, 18, 19, 21, 25.
mu	muscle fibres, Fig. 22.
nr	position of nerve ring, Figs. 17, 18, 19.
od	odontophore, Figs. 18, 19, 20.
odc	odontophoral cartilage, Fig. 22.
odr	odontophoral retractor muscle, Figs. 18, 20, 22.
os	osphradium, Figs. 19, 23.
osg	osphradial ganglion, Fig. 29.
ot	oral tube, Figs. 17, 19, 20, 22.
otr	oral tube retractor muscle, Fig. 20.
ov	ovary, Fig. 27.
ovd	oviduct, Fig. 27.
owcp	outer wall of egg capsule, Figs. 30, 33.
p	penis, Figs. 19, 23, 24.
ped	penial duct, Fig. 23.
poe	posterior oesophagus, Figs. 17, 19, 25, 28, 29.
pr	prostate gland, Figs. 19, 24, 25.
ps	proboscis sheath, Figs. 18, 19, 20, 22, 23, 25.
rbg	right buccal ganglion, Fig. 21.
rcg	right cerebral ganglion, Fig. 21.
rcs	receptaculum seminis, Figs. 26, 27.
rmp	retractor muscle of the proboscis, Figs. 19, 20, 22.
rpc	renopericardial canal, Fig. 28.
rpd	right pedal ganglion, Figs. 19, 21, 22.
rs	radular sac, Fig. 22.
rsd	right salivary duct, Fig. 20.
s	siphon, Figs. 19, 33.
sbg	sub-oesophageal ganglion, Fig. 25.
sh	shell, Fig. 32.
sog	supra-oesophageal ganglion, Fig. 21.
st	stomach, Fig. 17.
sta	statocyst, Fig. 22.
t	tentacle, Figs. 18, 19, 25, 26, 29, 32.
td	testis duct, Figs. 24, 25.
te	testis, Figs. 19, 24.
tg	temporary egg groove, Fig. 26.
v	velum, Fig. 32.
va	vagina, Figs. 26, 27, 28.
vc	ventral channel, Fig. 27.
vd	vas deferens, Figs. 23, 24.
ve	ventricle, Fig. 28.
vl	valve of Leiblein, Figs. 17, 18, 19, 25.
x-y	diameter of first whorl of protoconch, Figs. 14, 32.

FIGS. 17-19. Alimentary system of *Thala floridana*.

17. Diagrammatic dorsal view. Proboscis extended. Right salivary gland removed. Gland of Leiblein moved to show position of the duct. Stomach opened dorsally.
18. Diagrammatic dorsal view with proboscis fully retracted. Salivary glands removed.
19. Dorsal view of extended foregut. Proboscis sheath opened and buccal mass turned to give a right lateral view. Mantle cut medially and the halves deflected laterally. Floor of the mantle cavity, right salivary gland and much of nerve ring cut away.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burrowing or clinging. Although moderately active when hungry, it is exceeded in crawling speed by many of its prey species. It is non-operculate.

Color. The translucent white head-foot is spotted and speckled with opaque white on the sides of the head, foot, tentacles and siphon (Florida and Yucatan). R. Robertson (unpublished communication) reported one animal from Abaco, Bahama Islands, with pale pink soft parts. Although these light-colored soft parts are conspicuous against the dark shell and the usually dark substrate, they are concealed by the cryptically-colored shell in a resting snail.

Foot. The sole of the foot is triangularly elongate and folds along a longitudinal median line (Fig. 29). It moves in monotaxic waves when the snail is crawling, and is heavily ciliated on the anterior half and less heavily ciliated posteriorly. There is a deep, glandular, mucus-secreting crease along the entire anterior margin (Fig. 25) and another glandular area a little anterior to the middle of the sole of the foot. This latter area is well developed in females and becomes pore-like during oviposition (Fig. 9).

Head. When at rest or not actively seeking prey, the head is narrow. The false mouth is a vertical slit between short tentacles. It widens by a factor of 3 when the proboscis is everted (Figs. 18, 19). Black eyes are set on the thickened base of each tentacle near the head. Distal to the head and eyes, the tentacles are quite plastic and can be stretched to double their resting length.

Siphon. Although virtually hidden by the shell of a resting snail, the siphon may be extended about 2 mm beyond the shell of an active one. It moves constantly, forward, back over the shell and from side to side, even when a snail is feeding. Through it, a hungry snail first detects the presence of prey. The snail may open the siphon ventrally from tip to mantle cavity but the siphon is usually closed as a tube.

Mantle. The mantle edge is thickened and light tan in color. This tan marking also rims the position of the ctenidium. The position of the ctenidium is also shown externally by a concentration of fine white opaque granules. Posteriorly the mantle becomes thin and translucent.

Alimentary system

General aspect and mode of function. *Thala floridana*'s pleurembolic proboscis is admirably adapted for its method of attack and feeding (Fig. 19). It is slender, flexible and can be extended a distance equal to the length of the individual's shell. This allows the attack to be made at a greater and less alarming distance, an advantage because *Thala* crawls at a slower pace than many of its prey species. The long proboscis allows *Thala* to feed deep in the tissues of prey which is often many times larger than the predator.

Prey is subdued by a venom which initially causes no signs of trauma but causes ataxia, paralysis and death usually within 4 minutes. The venom penetrates unbroken epidermis. (*Thala*'s pink buccal mass and radula are well back from the mouth during attack and the tip of the proboscis is unarmed.)

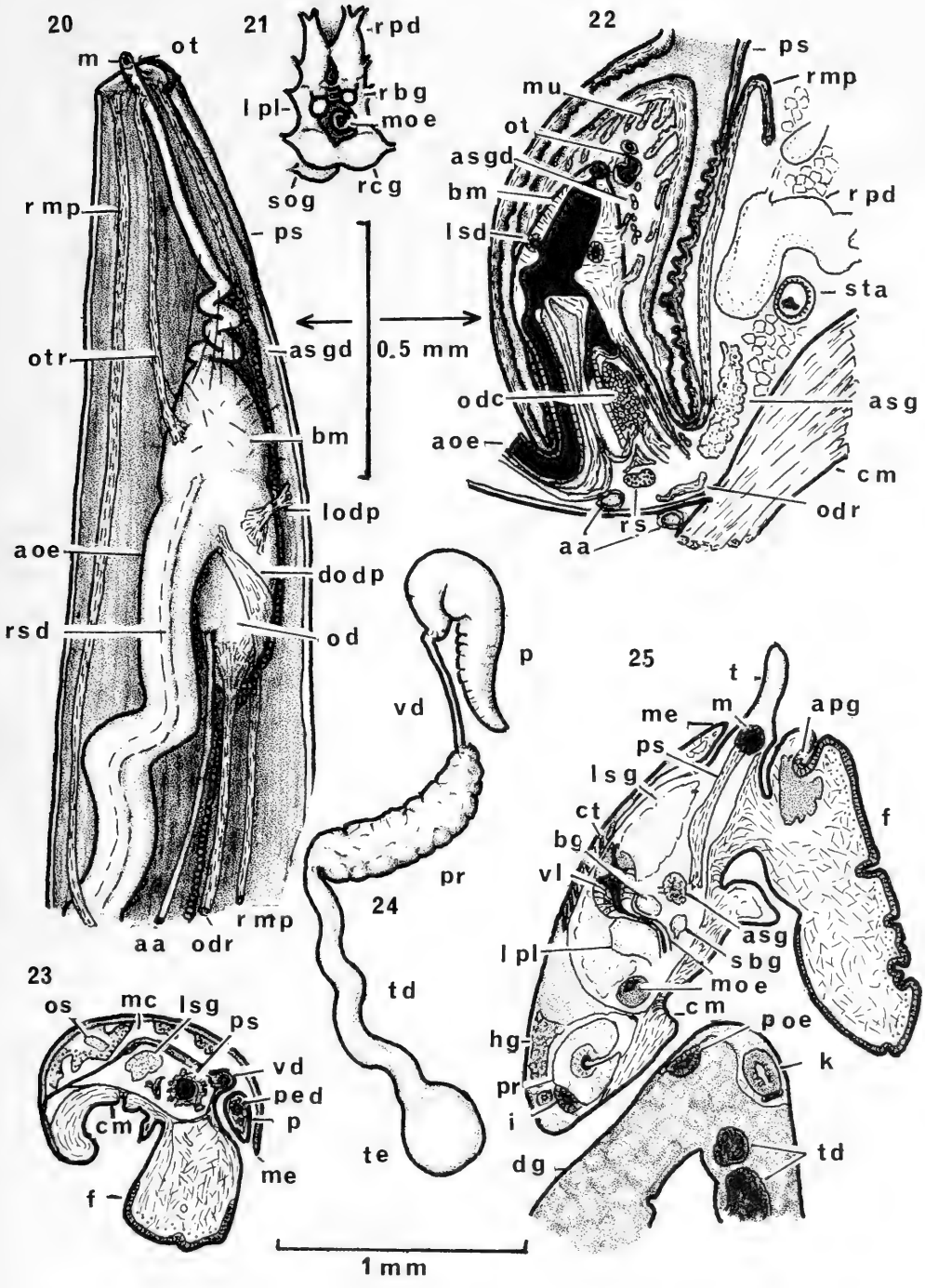
The source of the venom is probably the accessory salivary gland (Figs. 19, 22, asg). Although the lobes of the gland lie close to the nerve ring (nr, rpd) deep in the cephalic cavity, they open through fine muscular coiled ducts (or a duct?) into the oral tube (Figs. 20, 22, asgd, ot). Most of the muscle of these ducts is circular and the duct opening is anterior to the buccal mass and the ciliated portion of the buccal tube. This arrangement would be advantageous for jetting a secretion or toxin instantly and forcibly.

Martoja's fine histologic work on *Thais* foregut glands (1971: 251, 270) showed that

FIGS. 20-25. Alimentary system (continued), nerve ring and male reproductive system of *Thala floridana*.

20. Right lateral view of the extended oral tube and buccal mass enlarged to show major musculature.
21. Diagram of the nerve ring, dorsal view.
22. Dorso-lateral section of the retracted buccal mass. It was not as fully retracted as in Fig. 18.
23. Diagram of a transverse section of a male near the base of the penis to show the closed penial duct and laterally flattened outline. Viewed from the posterior.
24. Diagram of the male reproductive system. Dorsal view.
25. Diagram of a longitudinal section of a male at the level of the nerve ring to show partial fusion of the 2 lobes of the prostrate gland. Viewed from the right.

Figs. 21, 23-25 at same scale.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the secretion of the accessory salivary gland is probably a toxin and not digestive in function. Moreover, she found that the secreting, glandular part of this organ increased in size disproportionately as compared with non-glandular parts during growth of the animal. This could explain why our *Thala* were unable to subdue prey for 1 to 2 weeks after hatching.

The discovery of accessory salivary glands in many *Conus* which produce venom in another specialized gland (Marsh, 1971: 320) reveals the heterogeneity of the toxoglossan and *Thala*'s poison systems.

Thala's habit of feeding within the shell and tissue of its prey prevented observation of the proboscis tip and buccal mass of living animals. However, dissection showed that the massive odontophore could not pass through the narrow oral tube to the mouth and must function within the buccal cavity (Fig. 20, od, ot, m). A pump-like function is suggested by the bolster-like odontophoral cartilages, placement of the major muscles and heavy ciliation of the dorsal and lateral walls of the buccal cavity (Figs. 20, 22, odc, dodp, lodp). *Thala*'s minute radula (Fig. 10) probably has little function except to pass food particles from the buccal cavity to the oesophagus.

Thala probably feeds by sucking tissue from its prey. The suction pump action of the buccal mass upon a prey's tissue is increased by the small diameter of the oral tube. This hypothesis is supported by examination of prey when *Thala* has finished feeding. Prey parts such as the odontophore are cleaned of soft tissue but the radula membranes and teeth remain intact.

Thala floridana's diet of soft and liquid animal tissues is reflected in a simple digestive system. The elongate anterior part probably does little else than expedite the passage of food. The salivary glands are relatively large and there are many scattered mucous cells lining the buccal cavity to lubricate the food particles. The large valve of Leiblein also consolidates food for passage through the narrow nerve ring (Martoja, 1971: 284) (Fig. 17, aoe, lsg, bm, vl, nr).

Much of the digestion probably takes place after passage through the nerve ring and before entering the simple U-shaped stomach. The ventral channel of the mid-oesophagus is thick and glandular (Fig. 25, moe) and probably part of the function of the gland of Leiblein is digestive (Martoja, 1971: 282) (Figs. 17, 19, moe, gl, dgl).

The stomach is little more than a caecum of the intestine where food is held for final digestion and absorption. There are separate ducts opening from it to the 2 unequal lobes of the digestive gland (Fig. 17, st, dd).

Thala's diet produces scant fecal matter, which is lubricated by a concentration of mucous cells lining the intestinal arm of the stomach. There is a small anal gland of obscure function (Fig. 17, st, ir, ag).

Proboscis. The pleurembolic proboscis is everted only during hunting or feeding. When fully everted it can equal the length of the snail's shell. It is white and the pinkish buccal mass and large buccal aorta and oesophagus can be seen through its translucent walls. The buccal mass is situated about ½ the proboscis length behind the mouth in an attacking snail.

Proboscis sheath (Figs. 18, 19, 20, 22, 23, 25, ps). The proboscis sheath is thin-walled, with longitudinal muscle strands covered by a thinner layer of circular muscle. There are numerous mucous cells in its lining. Connectives (mu) run from its inner walls to the oral tube at the mouth (m) and anterior part of the odontophore (od).

Oral tube (Figs. 17, 19, 20, 22, ot). The thin, narrow oral tube has a thin layer of circular over longitudinal muscle. It is lined with a simple, non-ciliate cuboidal epithelium excepting immediately anterior to the buccal mass where the lining is ciliated. There are scattered mucous cells in the lining. The exceedingly fine duct or ducts of the accessory salivary gland (asgd) open near the distal end of the tube. Connective strands run from near the distal end of the tube to the walls of the distal end of the proboscis sheath. Connective strands and a retractor muscle (otr) also run to the anterior part of the buccal mass (bm). The oral tube enters the buccal cavity anteroventrally.

Buccal mass (Figs. 17, 18, 19, 20, 22, 26, bm). The outer walls of the buccal mass have thick layers of longitudinal and circular muscle as well as other variously-oriented muscle fibres. Anteriorly it is firmly laced to the wall of the proboscis sheath by numerous connectives but the posterior part is free. Posteriorly, corded muscle fibres, the short odontophoral protractor muscle (lodp) and the long odontophoral retractor muscle (odr) run to the sheath wall and to the columellar muscle respectively.

The oesophagus (aoe) with salivary ducts (lsd, rsd) buried in its walls opens dorsally

into the buccal cavity. The odontophore, with its massive odontophoral cartilages (odc) and minute vexillid radula, opens postero-ventrally. The large anterior aorta (aa) enters the odontophoral wall dorsally, anterior to the radula.

The floor of the buccal cavity is lined with non-ciliate cuboidal cells. The lateral and dorsal walls are strongly ciliate. There are scattered mucous cells in the lining as well as in the external epithelium of the buccal mass.

The radula (Fig. 10) is moderately long (about 0.35 mm) but narrow. It consists of 30-35 transverse rows of 2 simple lateral teeth and an arched central tooth bearing 5-9 cusps (15 specimens, Crawl Key, Florida). Cusps of the radula showed no signs of wear when investigated under high powers of the SEM. It was quite similar to radulae of other species of *Thala*: *T. gratiosa* (McLean, 1967, fig. 1), *T. jeancateae* (Sphon, 1969, text fig. 1), *T. ogasawarana* (Habe, 1943, pl. 3, fig. 11), *T. simulans* (Thiele, 1929, fig. 394).

Anterior oesophagus (Figs. 17, 18, 19, 20, 22, aoe). The anterior oesophagus is very long (2.5 mm in a 6.4 mm snail). The ducts of the salivary glands are buried in its wall on either side of the dorsal channel. The anterior part, the part which can be seen through the extended proboscis sheath, has thick layers of circular muscle over longitudinal strands. It is not attached to the proboscis sheath. The part which remains in the cephalic cavity is less muscular until immediately anterior to the valve of Leiblein (vl). The most muscular parts of the anterior oesophagus have a ciliated lining. The less muscular portions have not.

The anterior oesophagus of *Thala floridana* closely resembles that of the New Zealand species *Austromitra rubiginosa* in general plan except the former is much more elongate (Ponder, 1972: 315).

Salivary glands (Figs. 17,19, 23, 25, lsg). The 2 salivary glands are flattened and yellowish white in living material. The left gland coats much of the valve of Leiblein and part of the anterior oesophagus. The right gland covers the nerve ring and posterior part of the valve of Leiblein. The 2 glands are difficult to separate in dissection.

Short free ducts from the antero-ventral part of each gland enter the walls of the oesophagus just in front of the valve of Leiblein. Most of their course, however, is in the walls of the oesophagus. The ducts are lined with ciliated cells throughout their course from the glands to their openings on either side of the buccal cavity (Fig. 22, lsd).

Accessory salivary glands (Figs.17, 19, 22, 25, asg). The accessory salivary glands are of particular interest in *Thala* because they are the probable source of its venom (see p. 54). They are 2 thin oval lobes, whitish in life, which lie on the anterior surface of the pedal and pleural ganglia just anterior to the nerve ring (Fig. 22, rpd). Although they are only a few cells thick they are quite extensive (about 250 × 130 μm).

The ducts are extremely fine, muscular and tightly coiled. They rise from each lobe and meet under the anterior aorta and valve of Leiblein just in front of the nerve ring. It could not be determined whether these ducts (asgd) join at this point or whether they pass forward along the same course together for they are barely visible under the highest power of the dissecting microscope and their tight coils are difficult to follow in serial sections. The duct or ducts run forward under the cord formed by the anterior aorta, odontophoral retractor muscle and associated fibres. The duct becomes even finer just behind the odontophore where it passes forward ventral to the buccal mass. The duct or ducts (dsgd) enter the oral tube well forward of the buccal mass (Fig. 20, aa, odr, bm, ot). The course of the duct under the buccal mass to the oral tube was observed only in sections. The opening of the duct into the tube was not observed.

Histologically the accessory salivary glands of *Thala floridana* appear similar to those of other prosobranchs such as *Thais lapillus*. The larger glandular cells are outside a lining of muscle or connective tissue (Martoja, 1971: 269). The ducts are simple tubules of a circular muscle layer lined with non-ciliate epithelium.

Valve of Leiblein (Figs. 17, 18, 19, 25, vl). The valve of Leiblein is pyriform, muscular and large (diameter about 0.25 mm). It lies on the left side of the cephalic cavity directly above (anterior to) the nerve ring. It is shining, whitish and conspicuous in living material. It is opposite or slightly anterior to the buccal mass of a fully retracted proboscis and is partially covered by the salivary glands.

Histologically it is quite similar to the valve of Leiblein of *Thais lapillus* (Martoja, 1971: 260). It consists of an anterior

calcareous pad, which stains very dark purple in haematoxylin, surrounding numerous gland cells and a deep ciliate cone. Posteriorly the gland cells become elongate and the cilia shorter (Fig. 25, vl). A function of softening and consolidating food is suggested by its structure and position.

Mid-oesophagus (Figs. 17, 18, 19, 21, 25, moe). Immediately below (posterior to) the valve of Leiblein, the oesophagus narrows and is thin-walled as it passes through the nerve ring. It is round in section and non-ciliate. Below (posterior to) the nerve ring, the mid-oesophagus thickens, turns right and rises steeply to a dorsal position. This rise in the mid-oesophagus is the point of torsion of the gut of *Thala floridana*.

The course of torsion may be followed in serial sections. The walls of the ventral channel of the mid-oesophagus throughout the rise are thickly glandular and stain bluish purple in standard haematoxylin. This glandular area twists throughout this rise of the gut. Torsion is complete, the ventral channel having assumed a dorsal position, as the gut turns sharply left along the leading edge of the gland of Leiblein (Fig. 19, gl).

The mid-oesophagus is clasped by the gland of Leiblein as the oesophagus passes to the left side of the cephalic cavity. An extremely short duct enters at this point (Fig. 17, dgl).

Gland of Leiblein (Figs. 17, 19, 29, gl). The large (about 1.3 × 0.5 mm) triangular gland of Leiblein lies dorsally in the posterior part of the cephalic cavity. It is brown in life, and is rather similar to that of *Austromitra* (Ponder, 1972: 315) but is shorter and not as sharply folded. The gland is somewhat variable in individual *Thala*, particularly in the size and shape of the posterior "tail." Its size was much reduced in starved individuals.

A histological feature of interest was the large pale pink-staining (haematoxylin and eosin) spherical cells released by this gland. They crowded the lumen of the gland of well-fed individuals and were also found in the gut and stomach. They were not observed in emaciated snails.

The anterior part of the gland of Leiblein is almost fused to the mid-oesophagus. The duct between them is a mere common opening through the antero-ventral wall of the gland and the post-torsional wall of the oesophagus.

Posterior oesophagus (Figs. 17, 19, 25, 28, 29, poe). Posterior to the opening of the gland of Leiblein, the oesophagus loses its glandular lining. It becomes narrower and thin-walled, and passes on the left ventral side of the gland of Leiblein almost to the "tail." Here it dips below the gland and enters the visceral mass to the right of the gland of Leiblein just above the columellar muscle (Fig. 19, poe, cm). It is somewhat wider after entering the visceral mass but does not form a crop as in *Austromitra* (Ponder, 1972: 316).

Stomach (Fig. 17, st). The posterior oesophagus opens into the left side of a rather small U-shaped stomach. There is a rather deep caecum posteriorly (cae) with radially folded walls. There are no cuticularized areas. Two ducts from the lobes of the digestive gland (dd) enter between the arms of the U. The intestinal (right) arm of the U (Fig. 17) has many mucous cells in the lining which is not as strongly folded as the caecum. Two low ridges, typhlosoles, delineate this region but the low transverse ridge found by Ponder in the tunicate-feeding *Austromitra* was not apparent.

Digestive gland (Figs. 19, 25, 29, dg). The digestive gland is divided into 2 unequal lobes. The lesser, right lobe lies anterior to the intestinal part of the stomach. Its short duct loops down to enter the stomach just dorsal to the duct of the massive left lobe. The left lobe of the digestive gland forms much of the rest of the visceral mass.

Histological examination showed no dark-staining triangular cells (Fretter & Graham, 1962: 229) among the vacuolated digestive and ciliated cells. A few amoebocytes were found. Unfortunately, we cannot compare our material with Ponder's description (1972: 305, 316). He found amoebocytes containing green-staining granules in *Strigatella* (Mitridae) and none in *Austromitra* (Vexillidae). His material was Mallory's Triple-stained. Our sections prepared in this manner were from starved, atypical material.

Intestine and anal gland (Figs. 17, 19, 25, 28, i, ag). The thin-walled intestine leads from the right arm of the stomach ventral to the kidney (k). It opens in the posterior part of the right side of the pallial cavity. Its lining is strongly ciliated.

The anal gland is a single thin-walled tubule about 190 μm long. It is lined with

ciliated cells, and it opens into the intestine dorsally just inside the anal orifice.

Respiratory, vascular and excretory systems

The respiratory, vascular and excretory anatomy of *Thala floridana* was not worked out. The following notes on these systems are only recorded for possible future comparisons.

Ctenidium (Figs. 19, 24, ct). *Thala floridana* has a relatively large ctenidium composed of about 28 triangular leaflets. It occupies much of the posterior pallial cavity. There was a loose positive correlation between shell size and number of gill leaflets (7 specimens from Crawl Key, Florida, 7.4 mm - 34 leaflets, 6.0 mm - 24 leaflets).

Heart (Figs. 28, 29, au, ve). The positions of the auricle and ventricle relative to the kidney, mantle cavity and ctenidium are shown in the figures. The epidermis over the pericardial cavity is thin and easily ruptured in dissection.

The anterior aorta (Figs. 18, 19, 20, 22, 29, aa) is exceptionally large, about 0.1 mm in diameter. This is doubtlessly an adaptation to supply the considerable pressure needed to extend the long proboscis.

Kidney (Figs. 19, 25, 28, 29, k). The kidney in *Thala* is large (0.8 mm in a 7.9 mm snail) and is pycnonephridian, i.e. the primary and secondary folds of the kidney walls interdigitate. This character is of phylogenetic value in higher levels of classification. Perrier (1889: 242) found that many species of buccinid and muricid snails have pycnonephridian kidneys. All the marginellids, olives and toxoglossates he examined were meronephridian; the kidney folds were separate. Thus the former appears to be the more primitive condition.

Ponder (1972: 337) also found the character of the kidney significant at a high taxonomic level. Of the species of Vexillidae examined by him all were pycnonephridian and of the Mitridae, all were meronephridian. *Thala floridana* and its family, the Vexillidae, appear more closely allied to the Buccinidae and Muricidae than to the Mitridae on the basis of kidney structure. The functional significance of *Thala's* superimposed kidney escapes us.

Sensory and nervous system

The function and anatomy of these systems in *Thala floridana* were not studied in detail. They are fairly typical of an unspecialized neogastropod in having eyes, a large osphradium and a closely knit nervous system with fusion of several ganglia of the nerve ring.

Eyes (Figs. 18, 19, 26, 32, e). *Thala's* round black eyes lie on thickened regions near the base of the tentacles. They are sensitive to light and shadow. Their only function is probably defensive. A snail flinched or retracted depending upon the intensity of the shadow passing over it.

Osphradium (Figs. 19, 23, os). The osphradium is large (1.56 mm in a 5.9 mm snail). Living material is dark brown. It lies anterior to the ctenidium across the roof of the mantle cavity. The osphradium is second in importance only to the proboscis of a feeding *Thala*. The presence of prey initially is sensed through it. If the prey leaves no slime trail, the osphradium is used to locate it. After a successful attack it is probably chemoreception through the osphradium which triggers a feeding response in the predator and other *Thala floridana* in the vicinity.

Proboscis (Figs. 17, 19, 20). The proboscis is not ordinarily considered a part of the sensory system. *Thala*, however, frequently uses this organ to track and identify prey. The proboscis must be considered a part of its sensory repertory (see p. 65). A cursory examination did not reveal any exceptional development of sensory cells in the proboscis or foregut. Probably ordinary sensory cells in the buccal cavity are used to taste the prey's slime and slime trail.

Nerve ring (Figs. 21, 22, 25). *Thala's* nervous system is very concentrated. Most of the major ganglia constituting the nerve ring are lightly fused. Those that are not are coupled by very short connectives. They form a narrow ring around the oesophagus just posterior to the valve of Leiblein (Figs. 17, 19, nr, vl).

The cerebral, pleural and pedal ganglia are fused (Fig. 21, rcg, lpl, rpd). The buccal ganglia lie just under the anterior part of the valve of Leiblein, linked to each other and the cerebral ganglia by short connectives (Fig. 21, rbg, Fig. 25, bg). The long buccal nerves run through the proboscis to the buccal mass corded with muscle and other nerve fibres as well as the anterior aorta. The supra-oesophageal and sub-oesophageal ganglia are coupled posteriorly to the pleural

ganglia by short connectives (Fig. 21, sog, Fig. 25, sbg). A conspicuous osphradial ganglion lies just anterior to the pericardial cavity (Fig. 29, osg).

Reproductive system

Sexes are separate in *Thala floridana*. There are no indications that sex reversal takes place. Females are usually larger than males. Several large captive males that were more than 2 years old had an atrophied penis but showed no signs of a developing female system. Females produce eggs at an age of about 6 months.

Thala's reproductive system is similar to that in species of Vexillidae studied by Ponder (1972: 336, 337) with possibly one exception. During oviposition a small pedal pore was clearly visible in the middle of the female's foot (Fig. 9). We could not distinguish it at any other time in living, preserved or sectioned *Thala floridana* although this part of the foot is much folded and rich in mucous cells. Ponder reported that although Mitridae have an egg pore in the foot, Vexillidae do not. It is likely that the blister-like egg capsule of *Thala* (and Vexillidae) does not require the deep, glandular pore with which mitrid species mold and harden their high, stalked capsules.

Male system

Testis (Figs. 19, 24, te). The tubules of the testis form a discrete mass on the digestive gland that is similar to that in *Austromitra* (Ponder, 1972: 317).

Testis duct (Figs. 24, 25, td). The thin-walled duct opens from the testis ventrally near the right side. Its walls thicken and become longitudinally ridged as the duct nears the region of the kidney. The lining of the renal part of the duct becomes ciliate as it approaches the prostate. There is no reno-pericardial duct.

Prostate and vas deferens (Figs. 19, 24, 25, pr, and Figs. 23, 24, vd). The large prostate gland (about 1.0 × 0.3 mm) lies along the posterior margin of the mantle cavity. It is wrinkled exteriorly. Its 2 lobes are slit along a ventral line in the posterior part of the gland (Fig. 25, pr). This slit forms a very narrow opening into the posterior mantle cavity. The lobes of the anterior part of the gland are fused. The lining of the sperm channel or vas deferens of the fused portion of the prostate is more heavily ciliate than posteriorly.

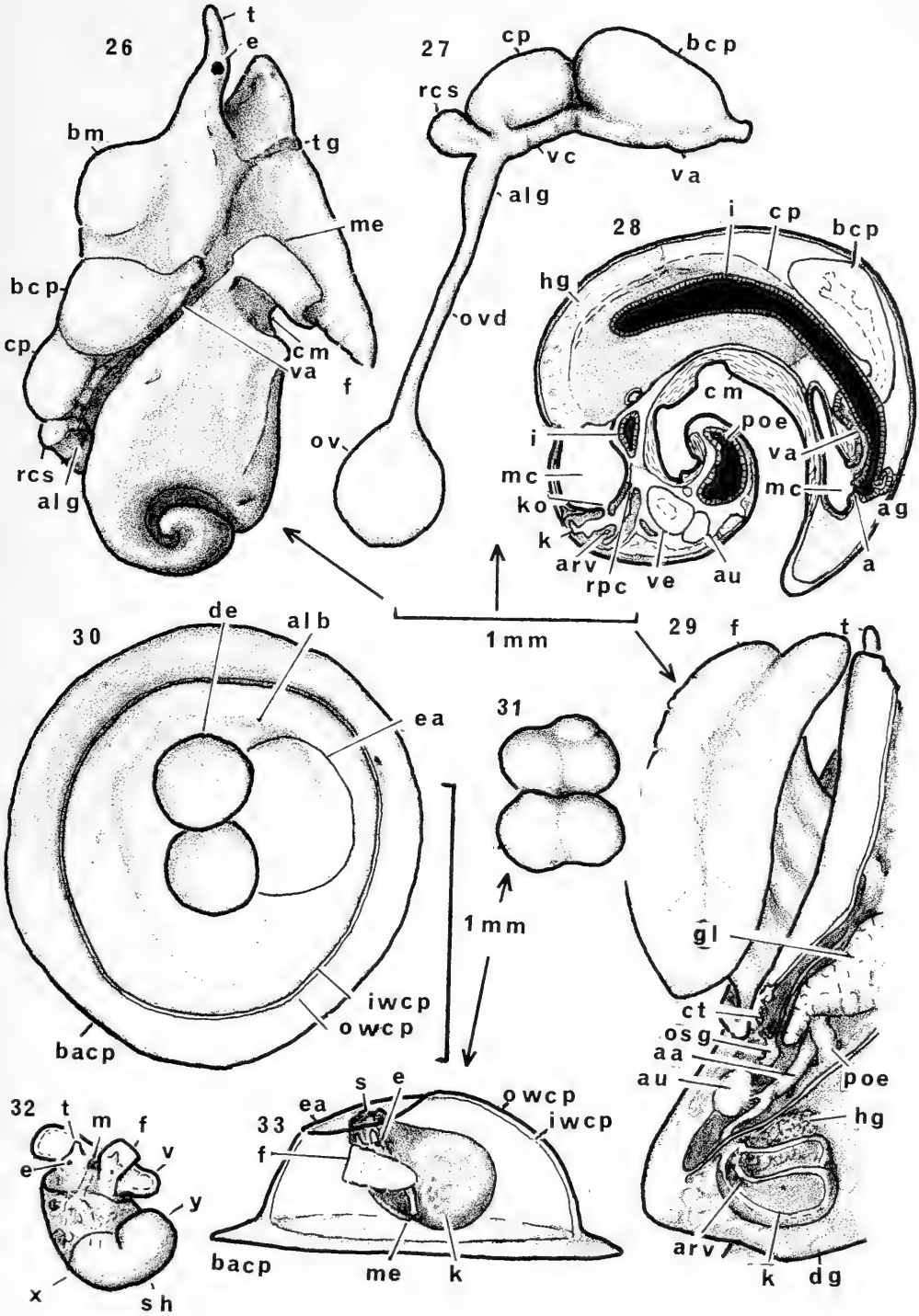
The vas deferens acquires a thin layer of muscle as it emerges from the prostate on the right side of the mantle cavity. It is about 50 μm in diameter. The vas deferens remains a thin-walled tube of approximately this diameter throughout its course down the right wall of the cephalic cavity to the base of the penis. Near the base of the penis, just behind the right tentacle, the vas deferens is enclosed in a small cluster of gland cells.

Penis (Figs. 19, 23, 24, p). The large penis (about 1.5 mm long) lies on the right side of the body just behind the right tentacle. Its base is level with the floor of the cephalic cavity. It is flattened ventro-laterally and tapers from its largest diameter (about 0.28 × 0.13 mm) near the curved point of attachment to a blunt point. The internal penial duct (Fig. 23, ped) is strongly ciliated

FIGS. 26-33. Female reproductive system, kidney, auricle, egg capsule, veliger and hatching young of *Thala floridana*.

26. A female dissected to show the anterior portion of the reproductive system and position of the temporary egg groove on the side of the foot. Mantle, ctenidium and hypobranchial gland have been removed. Viewed from the right.
27. Diagram of the female reproductive system. Dorsal view.
28. Diagram of a transverse section of a female at the level of the posterior limit of the mantle cavity to show the bursa copulatrix, vagina and genital opening. Kidney and heart are also shown. Viewed from the posterior.
29. Dissection to show the kidney and auricle. The mantle, part of the hypobranchial gland and almost all of the ctenidium have been removed. The kidney has been opened. Viewed ventrally, somewhat from the left.
30. Capsule and eggs immediately after oviposition on aquarium wall. Viewed through the base of the capsule.
31. A pair of developing eggs about 24 hr after oviposition. Blastomere formation has begun. Note that the undivided, presumably deutoplasmic lobes of the eggs are oriented oppositely.
32. Veliger removed from the capsule at 14 days. The bilobed velum is fully-developed. The foot is active. The shell is translucent white. The "x-y" axis was used to measure the diameter of the first whorl.
33. A hatching snail crawling through the escape aperture. The velar lobes have been resorbed. The shell is translucent brown.

Figs. 30-33 at same scale.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and is closed throughout its course to its opening on the pointed tip of the penis. There are no glandular cells in the penis other than mucous cells.

Female system

Ovary (Fig. 27, ov). The ovarian tubules are separate from the digestive gland. The ovary of one female contained a few developing ova. The largest ovum was about 0.30 mm in diameter and it was full of large yolk granules, which is not surprising in a species with rather lengthy (23-30 day) capsule development.

The upper and renal oviduct (Fig. 27, ovd) is short and thin-walled, and is lined with large cuboidal cells. There is no renopericardial canal.

Albumen gland (Figs. 26, 27, alg). The renal oviduct opens into the albumen gland where the latter curves about the columella ventral to the kidney. The gland is long (400 μm) and has a narrow lumen (75 μm in diameter). The lumen is lined with dark-staining mucoid-secreting cells. The ventral floor is thin, non-ciliate and contains a few mucous cells. A sphincter guards the anterior opening of the gland next to the receptaculum seminis.

Receptaculum seminis (Figs. 26, 27, rcs). The duct to the receptaculum seminis (ingesting gland) opens on the right side of the oviduct between the albumen and capsule glands. There are 2 folds in its wall as in *Austromitra* (Ponder, 1972: 318). The receptaculum seminis is large (600 $\times$ 750 $\times$ 65 μm) and somewhat triangular in shape. Unlike the vexillid and mitrid species studied by Ponder (1972: 309, 318, 322) the lumen of *Thala*'s receptaculum is not divided.

Sperm is undoubtedly stored in the receptaculum seminis for several days. The lumen of one female contained masses of both oriented and unoriented sperm, yet the ovaries did not contain well-developed ova. A few sperm were also found in the bursa copulatrix and the duct to the receptaculum. This female obviously had been recently inseminated. In the receptaculum of a female with a ripened ovum, sperm were aligned head to head along the long axis of the lumen. Some sperm were attached to the walls. A few had been ingested. Our captive females have produced viable eggs several days after all males were removed from the tank.

Capsule gland (Figs. 26, 27, 28, cp). The capsule gland is about 0.5 mm long. Unfortunately, our sectioned material of it was not good and we could not study the histology in detail. The anterior portion stained dark purple, the middle section was bright pink and the posterior part was purple when stained with haematoxylin and eosin. We did not work out details of the ventral channel.

Immediately anterior to the capsule gland was a short, ridged mucus-secreting area on the dorsal and ventral sides of the ciliate ventral channel. It stained a darker purple than the anterior section of the capsule gland.

Vagina (Figs. 26, 27, 28, va). The ciliate channel is continuous from the capsule gland to the vagina. The vagina is about 200 μm long, and the lumen is about 50 μm in diameter. The dorsal ridges are ciliate but ventrally the vagina is lined with a non-ciliate cuboidal epithelium. Anteriorly it becomes very muscular and opens into a short channel to the gonopore. This channel is very muscular and heavily ciliate.

The gonopore opens posteriorly on the right side of the mantle just behind the anus.

Bursa copulatrix (Figs. 26, 27, 28, bcp). The bursa copulatrix opens posterior to the gonopore and dorsal to the vagina. It is oval, about 1.0 mm long and about 0.27 mm in diameter. The walls are covered with a thin muscular layer. Interiorly there is a thick, folded layer of light-staining glandular tissue. There are a few mucous cells in the lining of the lumen.

Sperm is not retained in the bursa copulatrix for long. Only a few sperm were found in the bursa of one individual although masses of only partly oriented sperm were found in the duct and lumen of the receptaculum seminis.

LIFE CYCLE

Breeding habits and oviposition (Figs. 9, 26, 30, 33). Captive animals usually bred during the cooler months of the year when water temperatures ranged between 23° and 27° C. A few viable eggs were produced at 28° C by animals during their 2nd year in captivity. The presence of a mature male in a small colony of females took 10 days to induce oviposition but his removal a week later did not immediately halt it.

Oviposition in *Thala floridana* is solitary, unlike that in mitrid species whose capsules frequently are deposited in clusters with other individuals as well as their own. Even within the confinement of our small containers, *Thala* capsules were deposited separately. Before oviposition the female crawled away from other members of the colony and searched for a suitable substrate such as the top or side of a shell, stone or the aquarium floor or wall below water level. Algae, even calcareous forms, were not acceptable substrates. Deposition of an egg capsule took from 60 to 80 minutes. The following is an account of the deposition of one capsule viewed through the walls of an aquarium.

The egg is oval as it passes from the gonopore on the right side of the mantle cavity down a temporary groove in the side of the female's foot (Fig. 26, tg) to the cupped center of the sole of the foot. The rim of the snail's foot clings to the substrate. Muscles of the central area around the narrow slit or pore make wave-like motions around the egg, keeping the egg in motion. These motions slow somewhat after 17 min. At 20 min the wall of the capsule seems more solid and movements of the oval egg are confined to the central part of the capsule. The attaching base of the capsule is discernible (Fig. 30, bacp). At 25-27 min the wavelike motions of the muscles are very slow and mostly around the attaching base of the capsule; the egg is "balancing" in the middle of the case and is almost round. 65 min: the egg is quite round, and the base of the capsule is well-formed and slightly opaque. There were no changes in egg or capsule thereafter.

Females remain on the egg case for 15 min to 1 hour after deposition is completed. Then they constrict ½ of the foot and uncover ½ of the capsule. They twist to the other side and move away, and show no interest in the capsule or its site thereafter.

The capsule (Figs. 30, 33). The capsule is pustulate, oval, 1.6-2.5 mm at its greatest diameter. It is attached to the substrate by the basal membrane which extends as a flattened, irregular rim about 0.3 mm beyond the walls of the chamber. The domed egg chamber is approximately 0.75 mm high. It has an inconspicuous eccentric oval escape aperture (ea) about 0.4 mm at its greatest diameter. A fresh capsule contains considerable amounts of albumen (alb). The capsule remains more or less uncolored and transparent throughout the development of the embryos.

The egg capsule of *Thala floridana* is rather similar to that of the vexillid species *Austromitra rubiginosa* (Ponder, 1972: 319), *Pusia hanleyi* and *P. puella* (Maes & Raeihle, unpublished observations) and *P. cancellarioides* = *Mitra nodosa* (Purtymun, 1974).

Eggs and embryos (Figs. 9, 11, 30-33). Eggs of *Thala floridana* are spherical, creamy white and about 0.3 to 0.4 mm in diameter at oviposition. There are usually 1 or 2 eggs per capsule but sometimes there are 3. We have rarely had capsules with 4 eggs produce viable young.

Development takes 22-30 days but most young snails crawl from the capsule on the 23rd day. Development does not appear to be controlled entirely by temperature. Young snails from capsules deposited the same day in the same aquarium have emerged as many as 4 days apart.

Because development time varies, stages of development recorded below also varied:

12 hours ±, 2 cell cleavage.
48-49 hr, gastrulation.
5th day, elongates to ovoid shape.
6th-7th day, trochophore moves in capsule.
8th-9th day, formative shell.
9th-10th day, velar lobes forming. 11th-15th
11th-15th day, pigmentation of the shell begins in columellar area and suture of the body whorl.
13th-15th day, eyes and tentacles developing.
18th day, velar lobes at maximum development.
21st-22nd day, the velar lobes diminish and disappear, the foot becomes less translucent and more muscular, the shell deepens in color to a rich red-brown.
about 23rd day (see above), snail crawls from capsule, shell about 0.6 or 0.7 mm long.

Young *Thala floridana* emerge from the egg capsule as crawling, fully developed snails no matter what length of time they spend developing. This is unlike some nurse-egg-feeding species which hatch when their food supply is exhausted no matter what their stage of development (Thorson, 1950: 9). *Thala* young probably emerge from the egg capsule when the supply of albumen is exhausted but the gradual depletion of the albumen and its replacement with seawater regulates and triggers the appropriate developmental stages.

It is interesting to note that when there were 2 embryos in a single capsule they usually assumed a "head to tail" orientation even at earliest stages of development (Fig. 31).

Growth. Upon emerging from egg capsules the young snails have a smooth, brown shell with about 1½ whorls, 0.6-0.7 mm in length. There are 3 strong plicae on the columella (Fig. 11). Their head-foot is much like that of an adult in color and general shape. They have a radula of about 10 transverse rows of teeth. They hardly grow for about 2 weeks, after which they begin to feed and grow. They can survive almost a month of starvation during this post-emergence period. Growth before first feeding is recorded as incremental ridges of the lip (Fig. 13).

Normal juvenile snails begin appreciable growth with their first feeding and increase in length at the rate of about 1.0 mm a month. A 2 month old snail is 2 mm long, a 5 month old snail about 5 mm. When the individual reaches sexual maturity between 5 and 6 months of age the growth rate decreases to about 0.08 mm a month. Thus a mature snail grows only 1 mm longer during its 1st adult year. Rate of growth is even slower in succeeding years. The sexual difference of approximately 0.6 mm in mean shell length could be caused by males reaching sexual maturity as little as 2 or 3 weeks earlier than females. We have not investigated this idea.

When a snail was starved over a period of several weeks to a month, particularly during juvenile growth, the axial riblets at the shell lip became thick and crowded. When the snail fed regularly the axial riblets or cords were more widely spaced. Axial sculpture is a permanent record of the growth rate.

Age, mortality and fecundity

Age. Thala floridana may live 6 years or more. A few adults collected in November, 1968, lived well over 4 years in captivity. Of 5 specimens raised to maturity from a number hatched during the period January-June, 1969, 3 survived in October, 1973. Although fecundity was diminished, these 3 snails produced 6 young snails in June, 1973, alone.

Mortality. In specimens hatched in captivity there is high mortality caused by the artificial environment. Most die of desiccation after crawling high out of water. Young snails probably cannot emerge as abruptly in their natural habitat and this cause of mortality is not as serious. Predation is probably the principal natural cause of mortality. Adult shells collected at Crawl Key were sometimes drilled but were usually entire.

Fecundity. Egg production was highest during the 1st breeding season. We did not ascertain maximum or minimum production for individual snails. Average production for 4 females was 15 capsules a month during the breeding season. Projecting this from a 10 month breeding season and 1.6 eggs per capsule, our captive *Thala* produced an average of 60 eggs a year per snail. This is a very low level of productivity. However, as Mileikovsky (1971: 205) has shown, animals with abbreviated or no pelagic development are capable of maintaining high population levels by producing only 38 eggs a year.

Food and feeding

Food. Thala floridana preys opportunistically upon small gastropods. Table 1 contains the feeding record of 6 reasonably active adults for 3 months. The prey species listed are not given as a record of their natural prey. *Ilyanassa obsoleta*, for example, is not sympatric with *Thala*. The table shows size of prey and frequency of feeding. *Thala* will feed on snails much larger than shown (44 X its own bulk).

Most species of small gastropods (mostly herbivores) were acceptable as food. *Thala* killed and ate the easiest snail to catch. *Planaxis lineatus* and *Batillaria minima* often avoided capture by crawling faster than *Thala* and resting out of water. *Thala* did not hunt or feed out of water. *Thala* also fed on a few carnivores that were offered but there was no cannibalism. *Pusia* or marginellids were not eaten (see exception). As in many other poison-producing animals, *Thala* may be "immune" to its own toxin. *Pusia* and marginellids were observed to attack in a similar manner, and may possess a similar toxin and "immunity." Exceptionally, *Thala* did kill and eat newly hatched *Prunum*. Presumably, the *Prunum* had not developed a poison gland (see discussion of the accessory salivary gland, p. 54) and "immunity" to the toxin suggested above. Although hungry *Thala* did not scavenge even freshly killed snails, as many as 6 fed upon prey killed by 1 *Thala*. Some chemical signal related to the release of toxin in the environ-

TABLE 1. Feeding record of 6 adult *Thala floridana* in 1 container 12.5 X 8.5 X 6 cm for 3 months. The *Thala* measured 7.6 mm (♀), 6.4 mm (♀), 6.3 mm (♀), 5.8 mm (♀), 5.6 mm (♂) and 5.5 mm (♂). Prey species listed are: *Planaxis lineatus* (Costa, 1778), *Batillaria minima* (Gmelin, 1791), *Cerithium lutosum* (Menke, 1828) (+ *C. variabile* C. B. Adams, 1845) and *Ilyanassa obsoleta* (Say, 1822).

Time span	Food species offered	Prey chosen	Date killed
Nov. 1-4	*Planaxis* (7.1 mm) & *Ilyanassa* (6.7 mm)	*Ilyanassa*	Nov. 4
Nov. 4-8	*Planaxis* (7.1 mm) & *Ilyanassa* (6.6 mm)	*Ilyanassa*	Nov. 8
Nov. 8-12	*Planaxis* (7.1 mm) & *Batillaria* (12.8 mm)	*Batillaria*	Nov. 12
Nov. 12-15	*Planaxis* (7.1 mm) & *Batillaria* (8.8 mm)	*Batillaria* *	Nov. 14
Nov. 15-18	*Planaxis* (7.1 mm) (no alternative)	———	———
Nov. 18-Dec. 4	*Planaxis* (7.1 mm) & *Batillaria* (9.2 mm)	*Batillaria*	Dec. 4
Dec. 4-6	*Planaxis* (7.1 mm) & *Batillaria* (7.3 mm)	———	———
Dec. 6-9	*Planaxis* (7.1 mm) & *Ilyanassa* (7.2 mm) & *Batillaria* (7.3 mm)	*Ilyanassa* *	Dec. 9
Dec. 9-13	*Planaxis* (7.1 mm) & *Batillaria* (7.3 mm)	———	———
Dec. 13	*Planaxis* (7.1 mm) & *Ilyanassa* (6.5 mm) & *Batillaria* (7.3 mm)	*Ilyanassa*	Dec. 13
Dec. 13-23	*Planaxis* (7.1 mm) & *Batillaria* (7.3 mm)	*Batillaria*	Dec. 22
Dec. 23	*Cerithium* (11.5 mm) & *Ilyanassa* (6.5 mm)	*Ilyanassa* *	Dec. 23
Dec. 23-26	*Cerithium* (11.5 mm) (no alternative)	———	———
Dec. 26-27	*Cerithium* (11.5 mm) & *Batillaria* (6.3 mm)	*Batillaria*	Dec. 27
Dec. 27-30	*Cerithium* (11.5 mm) & *Batillaria* (9.1 mm)	*Batillaria*	Dec. 30
Dec. 30-Jan. 6	*Cerithium* (11.5 mm) & *Batillaria* (10.3 mm)	*Batillaria*	Jan. 6
Jan. 6-7	*Cerithium* (11.5 mm) & *Batillaria* (8.0 mm)	*Batillaria*	Jan. 7
Jan. 7-10	*Cerithium* (11.5 mm) & *Batillaria* (12.5 mm)	*Batillaria*	Jan. 10
Jan. 10-20	*Cerithium* (11.5 mm) & *Cerithium* (6.7 mm)	*Cerithium* (6.7 mm)	Jan. 20
Jan. 20-23	*Cerithium* (11.5 mm) & *Batillaria* (9.7 mm)	*Batillaria*	Jan. 22
Jan. 23-24	*Cerithium* (11.5 mm) & *Batillaria* (9.6 mm)	*Batillaria* *	Jan. 23
Jan. 24-31	*Cerithium* (11.5 mm) & *Cerithium* (10.1 mm)	———	———

*More than 1 *Thala* observed feeding on same prey.

ment appears to be necessary to induce feeding. The amount of food needed to maintain *Thala* was not determined because most prey were not completely consumed.

Adult *Thala* have survived starvation for 3 months. Serial sections of these animals showed serious loss of tissue in the foot, gland of Leiblein, digestive and reproductive glands. It is questionable if many recover from such prolonged fasts.

Hunting. *Thala* becomes aware of potential prey either by direct contact or chemoreception through the siphon with the osphradium. If prey is fairly close (50 mm) the proboscis is everted. If the prey is moving and leaving a slime trail, *Thala* follows the trail with its proboscis, probably by the taste of the slime. *Thala* was not observed following this trail out of water, however. If prey has been dropped into the tank on its back so that it leaves no slime trail, *Thala* locates it through the siphon alone. *Thala* touches (tastes the slime?) the prey's soft parts once with the proboscis before it attacks. Some potential prey frequently found with *Thala* in its natural environment seem to fear the presence of *Thala* and crawl quickly away. As stated above, they are safe from attack when they are out of water.

After a successful attack, *Thala* waits with its proboscis withdrawn until the prey is dead or immobile (usually in less than 4 min). The prey is usually fully immobile before the aperture can be sealed by its operculum. If the prey's aperture happens to become sealed, *Thala* is unable to feed.

CONCLUSIONS

Thala floridana is placed in the family Vexillidae on the basis of anatomical and reproductive criteria. It is not closely related to the Mitridae.

Related *Thala* species on both sides of the Isthmus of Panama, in the Caribbean basin and on the W coast of Africa, suggest a geologic history dating from the Miocene or early Pliocene in spite of a paucity of fossil records.

The Recent geographic distribution of *Thala floridana* follows a narrow belt from the Yucatan Peninsula, to Cuba, Florida, the Bahama Islands and Bermuda. It has been limited in the N by the adults' inability to withstand sub-18° C temperatures and to the S by their inability to reproduce at temperatures higher than 27°-28° C.

Habitat requirements are: relatively quiet waters that are barely subtidal to 90 m deep,

a few shells or stones for the attachment of egg capsules, and an abundance of small gastropods for food.

Shell characters are quite variable. Females of *Thala floridana* are slightly larger than males. Axial sculpture is partly affected by speed of growth. Well-fed young individuals grew stronger, more widely-spaced axial cords.

The alimentary system is that of an unspecialized neogastropod but it is admirably adapted to *Thala*'s mode of hunting and feeding. There is a long pleurembolic proboscis for attacking from a distance and feeding (probably sucking) on selected tissue deep in the body of the prey. A valve of Leiblein, paired accessory salivary glands, gland of Leiblein and pycnonephridian kidney give the anatomy of *Thala* a muricid-like aspect.

Thala floridana subdues prey up to 44 X its bulk with a quick-acting poison which penetrates unbroken epidermis. This poison is probably secreted by the accessory salivary glands. *Thala*'s poison apparatus is not homologous with that of *Conus*.

Reproduction involves capsule development. Young snails crawl out of their blister-like capsule about 23 days after oviposition. There may be 1-4 eggs per capsule but usually there are 1 or 2. Eggs are 0.3-0.4 mm in diameter and contain much yolk. Average production for a captive individual with a 10 month breeding season is 60 eggs a year.

Life span (in captivity) is at least 6 years. When *Thala* emerges from the capsule it is 0.6-0.7 mm long. It does not feed for a week or two. After it commences feeding, it grows about 1.0 mm a month until sexual maturity is reached after about 6 months. Growth slows thereafter to 1.0 mm or less per year.

Thala floridana's limited distribution is probably due to the exacting temperature requirements for reproduction. Where these requirements are met for a considerable part of the year (as in the Florida Keys), a superior rate of survival of the capsule-developed young maintains a high population level in spite of the low fecundity. When temperature requirements are met for a shorter period the lowered fecundity rate is inadequate to maintain a thriving population.

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LARVAL AND POST-LARVAL DEVELOPMENT OF THE GIANT CLAMS *TRIDACNA MAXIMA* AND *TRIDACNA SQUAMOSA* (BIVALVIA: TRIDACNIDAE)

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ABSTRACT

The larval development of *Tridacna maxima* and *T. squamosa* and the early post-larval development of *T. squamosa* are described. In both species the prodissoconch I is very large (length greater than 128 μm) and metamorphosis occurs at a relatively small size (length about 200 μm). Zooxanthellae do not appear until after metamorphosis. Each generation of giant clams is independently infected with the algal symbionts; the possible modes of infection are discussed. Shell deposition in juvenile *T. squamosa* is 1.5-2 times as great on the posterior and postero-ventral margins as on the anterior margin. This supports the concept that the form of tridacnids is, as in other monomyarian bivalves, best explained by differential growth.

INTRODUCTION

Morphological descriptions and the probable evolution of the Tridacnidae have been well treated (Yonge, 1936; Stasek, 1961) and recent work has clarified the role of the symbiotic zooxanthellae in the biology of these animals (Muscatine, 1967; Fankboner, 1971; Goreau et al., 1973). However, the question of the mode of transmission of the zooxanthellae from generation to generation has remained unanswered due to a lack of information on the early development of tridacnids, despite several reported attempts to spawn them (Stephenson, 1934; Rosewater, 1965). This study is an attempt to fill this gap and to elucidate the mechanism of development and possible evolution of the unique form of tridacnids.

During June-August, 1972, a field expedition to the Fiji Islands was conducted under the direction of Dr. Stephen Wainwright as part of a continuing program of investigation into the ecology and functional morphology of shallow water reef biota. The expedition was based on Nananu-i-Ra, an island 3 km N of Viti Levu, Fiji, within easy access of a large variety of reefs.

MATERIALS AND METHODS

Specimens of *Tridacna maxima* (Röding, 1798) were collected from patch reefs S of Nananu-i-Ra, Fiji, within 200 m of shore in 1-3 m of water. The majority of the *Tridacna squamosa* Lamarck, 1819, used in the spawnings were collected on the N edge of Thakau Savua reef N of Nananu-i-Ra (British Admiralty chart no. 801) in 5-8 m of water; 2 specimens came from Charybdis Reef, a drowned atoll NW of Viti Levu. The animals were held in a small plastic children's wading pool (2 m in diameter, 35 cm deep); a submersible pump supplied fresh sea water 6-10 hr/day. Species identifications follow Rosewater (1965); terminology in larval descriptions follows Chanley & Andrews (1971).

Spawning was initiated, in most instances, the day after capture; clams held for more than a week were extremely refractory to stimuli that caused freshly-caught clams to spawn. Stripped eggs, either fresh or held overnight at 8° C, were used to trigger the spawning reaction. To obtain uncontaminated eggs for the larval cultures, a *Tridacna* which was releasing eggs was removed from the wading pool and placed in a 14 l polyethylene container filled with sea water filtered through a 35 μm mesh screen. Approximately 3 min were allowed for sperm-contaminated water to wash off the shell and for the mantle cavity to flush; the water in this container and any eggs spawned during this period were discarded. After flushing, the animal was sequentially placed in two 14 l and one 27 l polyethylene container filled with

35 μm-filtered sea water and allowed to go through 1 spawning reaction in each container. The animal was then replaced in the wading pool and 1 ml of sperm-laden water from the wading pool was added to each container.

Larval cultures were kept under shelter, but at ambient air temperatures. The cultures were filtered daily through a 64 μm mesh plastic screen and the actively swimming larvae were separated from those at or near the bottom. The culture vessels were then washed with fresh water and a commercial (5.25%) sodium hypochlorite solution ("Clorox"), rinsed twice with fresh water, and refilled with fresh sea water filtered through a 64 μm mesh screen. No supplementary food was added to the cultures. The concentration of larvae in the cultures was kept below 1 per cc. After metamorphosis, the juveniles were held in an 11 l all-glass aquarium. The water in the aquarium was changed daily, but the aquarium was not cleaned. Samples of the eggs, embryos, larvae, juveniles, and adult mantle tissue were preserved in Carriker's fixative (1% formalin, 0.05% $NaHCO_3$ and 10% sugar in sea water). Samples of the larvae were taken daily, beginning with the formation of prodissoconch I and continuing through metamorphosis.

Sections of adult mantle tissues, eggs, larvae, and juveniles were obtained by post-fixing the specimens in Bouin's fluid for 24 hr to decalcify the shell and improve the staining properties of the soft tissues, double embedding in celloidin-paraffin, sectioning at 5 μm, and staining in eosin and Mallory's triple stain. Measurements of whole preserved larvae were made at 125X with a filar micrometer. Shells of larvae were prepared for scanning electron microscope (SEM) observation by soaking the larvae in a 0.05% sodium hypochlorite solution until the ligament dissolved and the valves could be separated. The larval valves were then washed twice with distilled water, dried overnight at 35° C, and vacuum-coated with gold-palladium alloy. The earliest prodissoconch I larvae of *Tridacna maxima* had not completed calcification of the valves, and it was necessary to wash the valves with acetone after the distilled water washes to dehydrate the organic component of the valves and prevent their collapse on air drying. SEM observations and photographs were done using a Jeolco JSM-S1 scanning electron microscope at 10 kv beam potential.

RESULTS

Spawning of *Tridacna maxima* was initiated twice, spawning of *Tridacna squamosa* 6 times (1 was spontaneous). The mean temperature of the water in which the animals spawned was 24.9 (± 0.7)° C. Spawning was most easily induced just after slack tide, on either a rising or falling tide; the introduction of eggs at this time often induced immediate spawning. Once, specimens of *T. squamosa* ignored the repeated introduction of stripped eggs over a period of 3 hr, yet, when the tide changed, immediately began to spawn. Neither species would spawn in response to the eggs of the other species.

Both species appeared to follow the same general pattern during spawning (for a more complete description, see Wada, 1954). Initially only sperm were released; spawning reactions occurred, at first, at approximately 30 sec intervals, gradually increasing to 5 min intervals. Sperm release continued for 1-1.5 hr; spawning of eggs then occurred for about the same period (giant clams are hermaphroditic; Wada, 1952, 1954). All animals more than about 15-20 cm in length produced both eggs and sperm; smaller animals produced only sperm. The eggs of both species were very susceptible to polyspermy, and the washing procedure described above was found to be essential if viable cultures were to be obtained. In the following descriptions, all times refer to time from fertilization.

Gametes. The eggs of *Tridacna maxima* ranged from 79.3-104.3 (mean 91.8 ± 8.6) μm in diameter less the membrane. The sperm heads were long and needle-shaped, ranging from 8.5-11.1 (mean 9.7 ± 0.7) μm in length, including the middle piece, and approximately 1 μm in diameter at the base. *T. squamosa* eggs ranged from 92.3-117.8 (mean 105.3 ± 12.3) μm in diameter less the membrane. The sperm were similar to those of *T. maxima* but slightly shorter, 7.4-9.4 (mean 8.1 ± 1.0) μm long. The length of the sperm flagellum was not measured for either species.

Embryology. The embryological development of *Tridacna maxima* was not followed.

A description of the embryology of *T. squamosa*, particularly the transition from the trochophore to the prodissoconch I larva, has been given elsewhere (LaBarbera, 1974).

Larval development—General. Although prodissoconch I (PD I) and prodissoconch II (PD II) shells are distinct in these species, the conventional distinctions between straight hinge and umbo larvae are of little use. Neither species develops a distinct umbo as a larva; even as juveniles the measured length of the straight hinge line did not differ significantly from that of PD I larvae. Chanley & Andrews (1971) also define the umbo stage as the stage where total length is greater than twice the straight hinge line length, but if this criterion is used selected individuals of *Tridacna squamosa* would be umbo larvae on day 2, while the whole larval population would be in the umbo stage by day 3. Depth measurements (the maximum right-

KEY TO ABBREVIATIONS ON FIGURES

a	anus
aa	anterior adductor
af	apical flagella
afr	anterior foot retractor
dg	digestive gland
e	esophagus
f	foot
g	gill
i	intestine
k	kidney
l	ligament
pa	posterior adductor
pfr	posterior foot retractor
s	stomach
ss	style sac
t	telotroch
tr	telotrochal retractor
v	velum
vr	velar retractors (numbered)
z	zooxanthellae

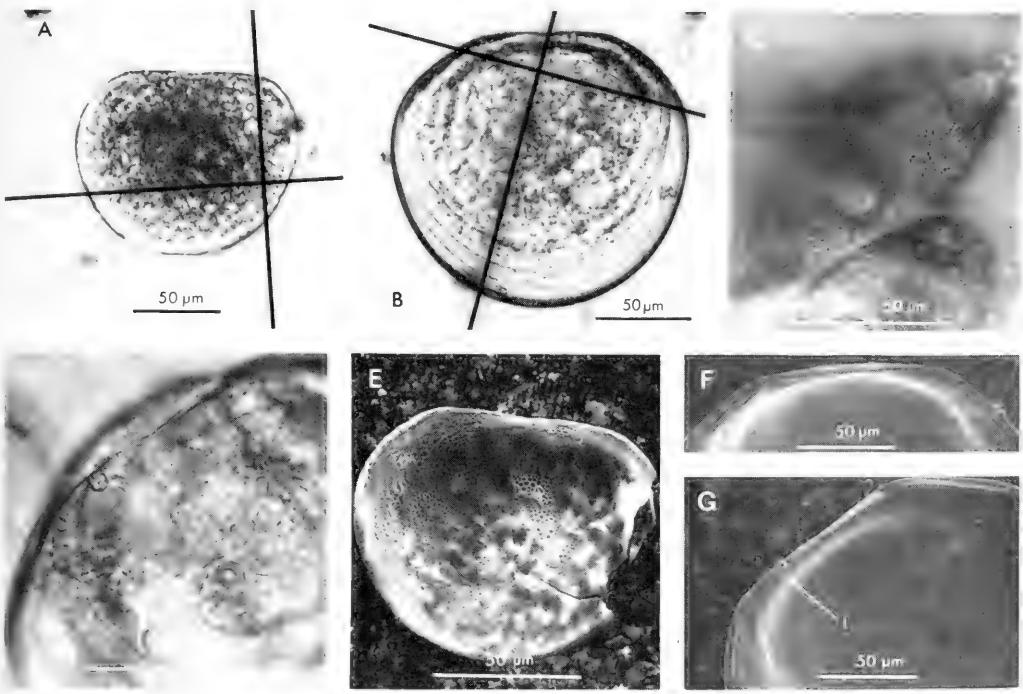

FIG. 1. Larval development of *Tridacna maxima*. A. Day 2 veliger, 128 × 103 µm. Anterior to the left. B. Pediveliger, day 14, 186 × 169 µm. Anterior to the left. C. Dorsal view of the hinge line of a day 2 veliger. Note the lack of hinge structures. D. Lateral view of late pediveliger hinge, day 15. The ligament is apparent. E. Right valve of day 2 veliger showing the undifferentiated hinge. F. Right valve, day 15 pediveliger. Note the lateral teeth and the spaces which serve as sockets for the teeth in the left valve. G. Left valve, day 15 pediveliger. Note the lateral hinge teeth and ligament. A-D, light photomicrographs; E-G, SEM photomicrographs.

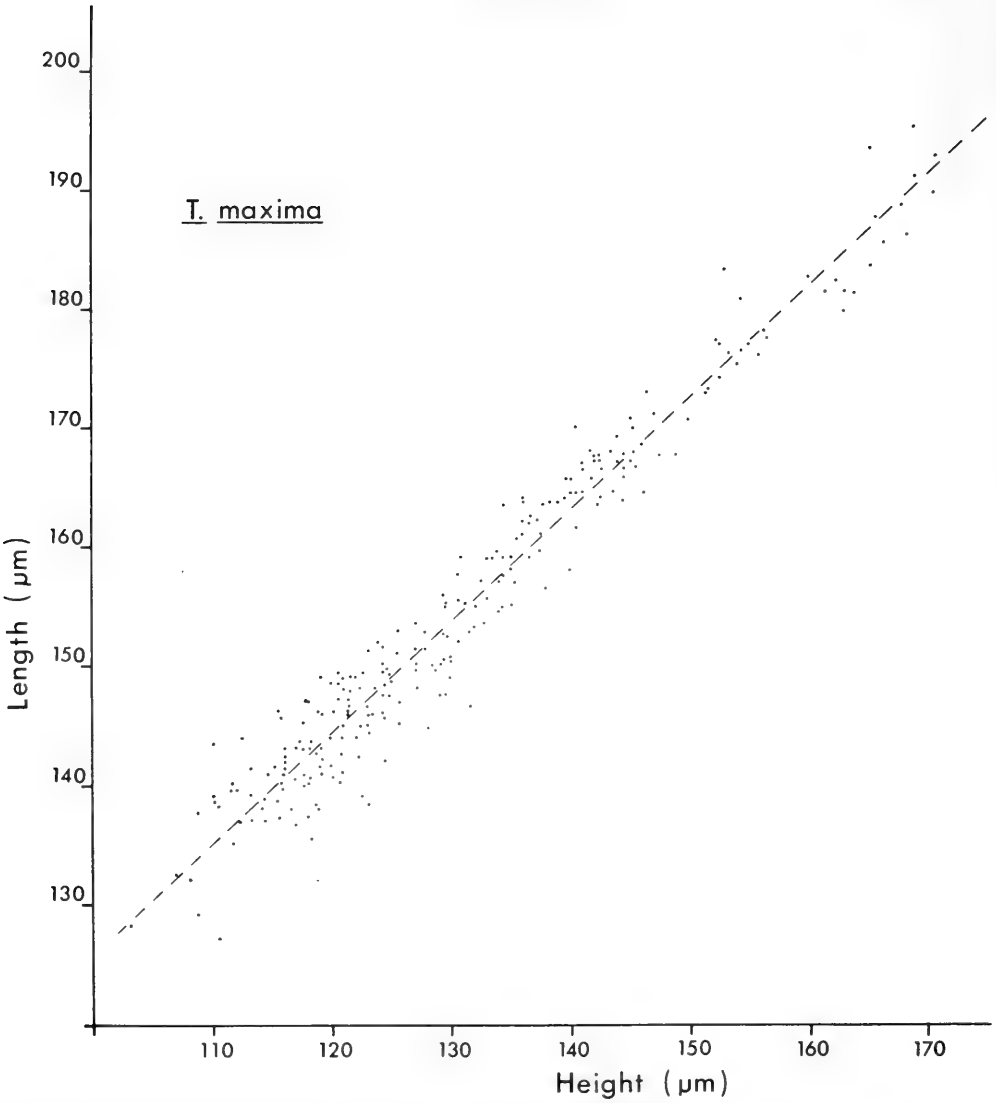

FIG. 2. Dimensions of larval *Tridacna maxima*. Each point represents a single animal. The dashed line represents the equation for the distribution, length = 0.93 (height) + 32.7; r = 0.98.

left dimension) were not made for either species of larva, but subjectively the larvae did not appear either more compressed or fatter than average for bivalve larvae.

Larval development—*Tridacna maxima.* Successful fertilization of *Tridacna maxima* eggs was accomplished on 10 June, 1972. The PD I larvae (day 2) ranged in length from 128-148 (mean 139 ± 3) μm; heights ranged from 103-119 (mean 113 ± 3) μm. Straight hinge line lengths ranged from 68-88 (mean 80 ±5) μm. The anterior shoulder was longer and sloped less steeply than the posterior shoulder; the anterior end was slightly pointed and longer than the posterior end (Fig. 1A). The posterior and ventral margins were evenly rounded. The majority of shell deposition during subsequent growth (Fig. 2) was along the ventral margins below the shoulders, lengthening and straightening the shoulders and making both the anterior and posterior ends of the pediveligers pointed.

Day 2 larvae have fully formed and functional larval retractor muscles and anterior adductor muscles (aa; Fig. 3A).

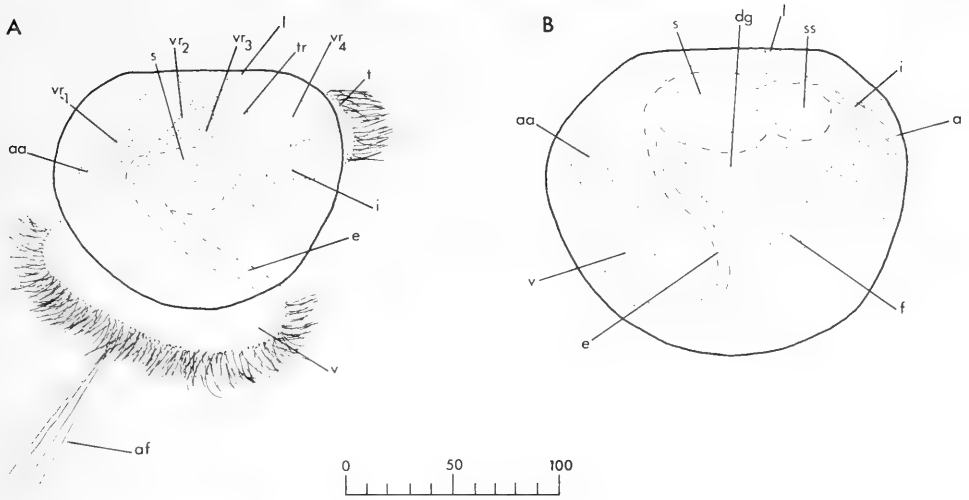

FIG. 3. Internal anatomy of larval *Tridacna maxima*. A. Day 2 protoveliger; the telotroch will be lost in a few hours. B. Pediveliger. Scale is in μm.

The esophagus (e) and stomach (s) are open and ciliated; the stomach is a simple sac. The intestine (i) during day 2 is a solid cylinder of cells lacking a lumen. The larvae are equipped with 4 apical flagella (af) on the velum; the telotroch has disappeared. No eyespot was noted. The hinge lacks larval hinge teeth, but a posterior internal ligament is present (Figs. 1C, 1E). The intestine becomes a hollow tube during day 3. The foot (f) begins to form on day 4 (mean length 144 ± 3 μm) and appears fully formed by day 5 (Fig. 3B). Gill primordia begin to appear on day 9 (mean length 180 ± 8 μm) as do the lateral hinge teeth; the posterior adductor appears on day 13.

The larval density in the cultures of *Tridacna maxima* began to decline on day 10 although there were no obvious signs of disease. Crawling larvae (Fig. 1B) were first observed on day 14, but this behavior may have been initiated earlier because, owing to a generator breakdown, no observations of living larvae were possible on days 12 or 13. The loss in numbers in the cultures which began on day 10 resulted in very few larvae achieving metamorphosis; metamorphosis apparently occurs at a length of 180-200 μm. Attempts to culture juvenile *T. maxima* failed. Lateral hinge teeth are fully formed by day 16 and the ligament is very prominent; the teeth in the right valve are separated from the margin of the valves by a space which acts as a socket for the teeth in the left valve (Figs. 1D, 1F, 1G).

Larval development—*Tridacna squamosa.* Cultures of *T. squamosa* were initiated twice, once on 6 July and again on 16 July, 1972; both cultures were successfully reared through metamorphosis. The following description and Fig. 7 are a composite of these two rearings.

PD I larvae (day 2) range from 141-159 (mean 152 ± 4) μm in length and 120-135 (mean 129 ± 3) μm in height. Straight hinge line lengths range from 65-84 (mean 76 ± 5) μm. The shape of the PD I larvae of *Tridacna squamosa* (Fig. 1A) is nearly identical to that of *T. maxima* (Fig. 4A), the only difference being that the posterior shoulder in *T. squamosa* slopes less steeply relative to the anterior than in *T. maxima*. The major difference besides size between the larvae of the 2 species is the position of the insertion on the shell of the 4th velar retractor (vr_4) (compare Figs. 3A and 5A). The esophagus (e) and gut of day 2 larvae are open and ciliated, but the intestine (i) is a solid cylinder which does not develop a lumen until day 3. The velum is equipped with 4 apical flagella derived from the apical flagella of the trochophore; the telotroch has disappeared (see LaBarbera, 1974, for a description of development up to this stage). No eyespot was noted. The anterior adductor and larval retractors are present and functional; the

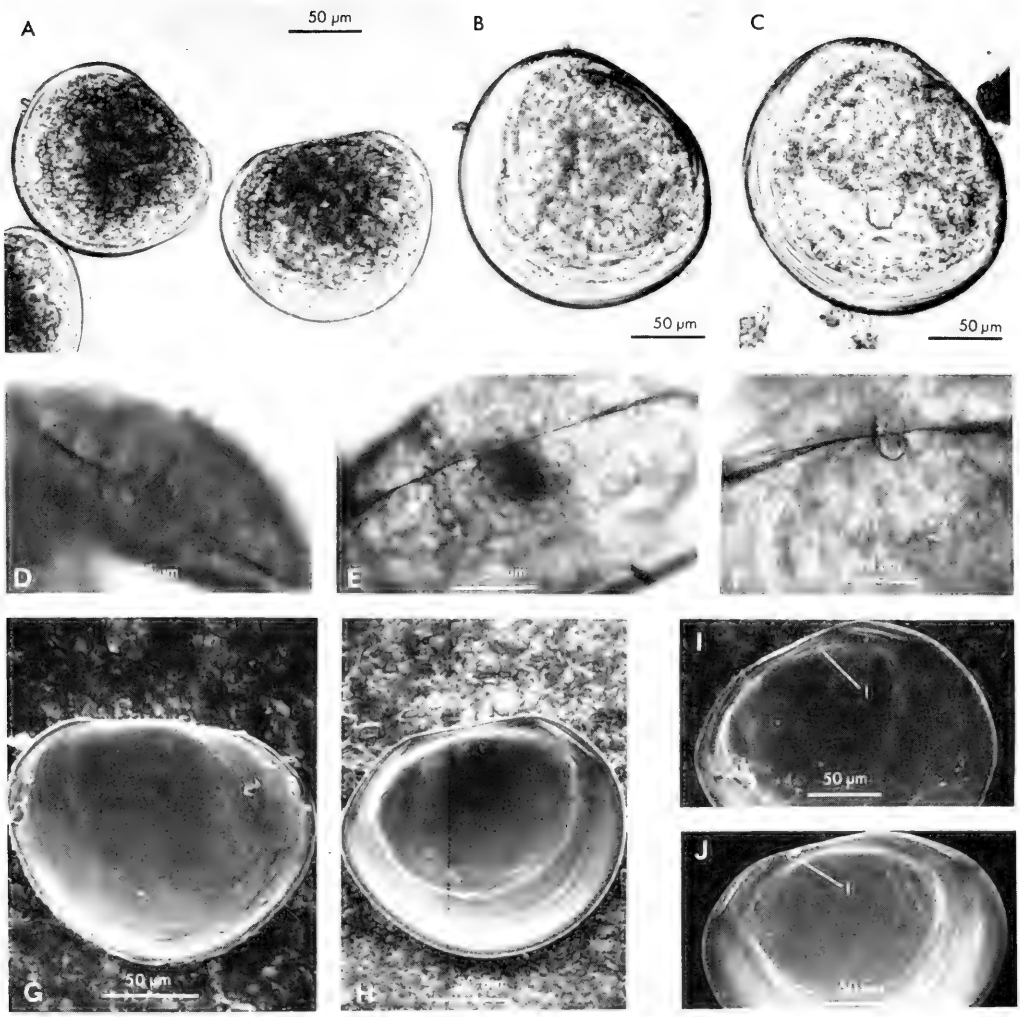

FIG. 4. Larval and post-larval *Tridacna squamosa*. A. Day 2 veligers, anterior ends facing each other. Left, 146 × 128 μm; right, 157 × 133 μm. B. Day 9 pediveliger, 193 × 171 μm. Anterior end to the left. C. Day 28 juvenile, 205 × 177 μm. Anterior end to the left. D. Dorsal view of the hinge, day 2 veliger. E. Dorsal view of the hinge, day 5 pediveliger. F. Posterior end of the hinge, day 28 juvenile. Note the prominent ligament. G. Left valve, day 2 veliger. Note the lack of hinge structures. H. Right valve, day 9 pediveliger. The hinge teeth are well formed; note the position of the ligament. I. Right valve, day 28 juvenile. Note the teeth, ligament, and spaces which act as sockets. J. Left valve, day 28 juvenile. Note the teeth and ligament. A-F, light photomicrographs; G-J, SEM photomicrographs.

hinge lacks teeth, but a posterior ligament is present (Figs. 4D, 4G). The foot begins to form on day 3 (mean length 157 ± 5 μm). By day 6 (mean length 178 ± 5 μm; Fig. 5B), the stomach (s) has differentiated into 2 sections, an anterior, lightly ciliated stomach, and a posterior, very heavily ciliated style sac. The 2 sections are separated by a slight constriction. Ducts from the digestive gland open into the stomach. Pediveligers (Fig. 4B) were observed crawling on day 9 (mean length 184 ± 4 μm); the foot is served by a complex network of muscles which attach to the shell dorsal to the anterior adductor muscle and the anus. No statocyst was seen. When crawling, the dorsoventral axis of the animal is vertical and the foot is straight, extending approximately 1 shell length beyond the valve margins. The tip of

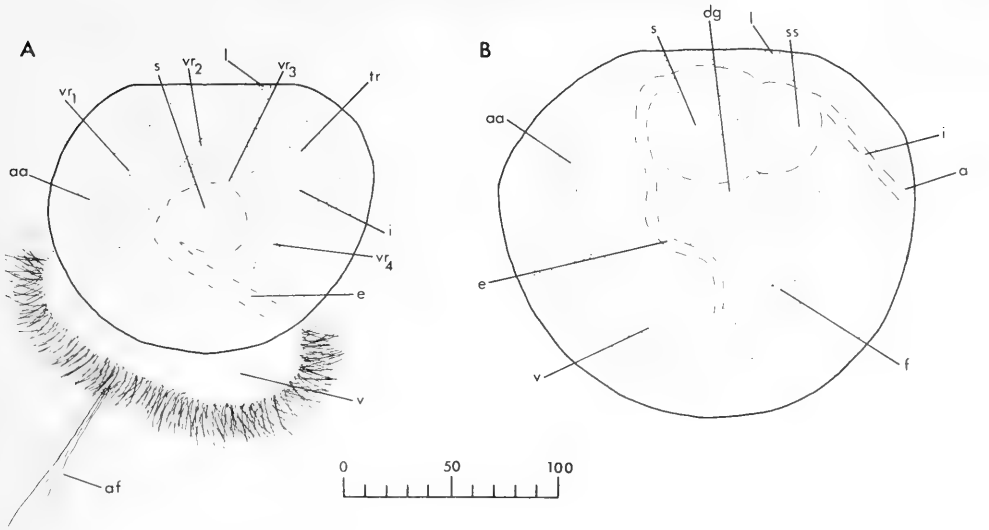

FIG. 5. Internal anatomy of larval *Tridacna squamosa*. A. Day 2 veliger; compare the configuration of the larval retractors shown on Fig. 3A. B. Pediveliger. Scale is in μm.

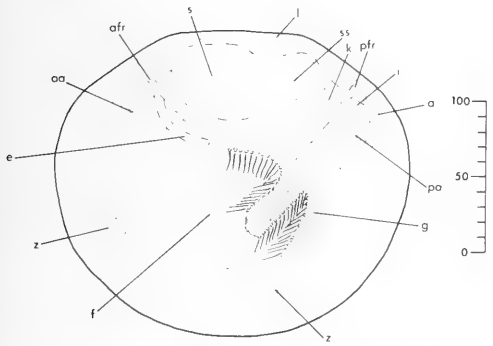

FIG. 6. Internal anatomy of early juvenile *Tridacna squamosa* (day 28). Note the well formed foot and gills. Scale is in μm.

the foot is apparently attached to the substrate and then retracted to effect crawling; no gliding movement was seen although the surface of the foot is ciliated. Lateral hinge teeth begin to form about day 9 (Fig. 4H), the posterior first and then the anterior. By day 10 both are formed and run the full length of the shoulders; the anterior tooth is consequently about 1/3 longer than the posterior. The teeth in the right valve are separated from the margin by spaces which function as sockets for the teeth in the left valve. Metamorphosis begins on day 10; metamorphosing animals range in length from 180-205 (mean 186 ± 9) μm. The gill primordia and posterior adductor begin to form just before metamorphosis; the gills form by the papillary mode (see Raven, 1958: 211). By day 28 (mean length 193 ± 17 μm) the juveniles possess a pair of gills; each, in lateral view, is folded in a "W" shape (Fig. 6, g). The hinge and prominent ligament (Fig. 4F) are compared with the 5 day condition (Fig. 4E). The hinge of the 28 day individual has prominent teeth (Fig. 4I, 4J). The mouth opens at the junction of the gills, and the esophagus leads directly to the stomach. The ventral surface of the stomach is ciliated, while the anterior, posterior, and dorsal surfaces are not.

Growth of the shell after metamorphosis is asymmetrical (Fig. 7). By measuring the distance between particular growth lines and the margin of the shell, it can be seen that shell growth on the posterior end is 1.5-2 times as fast as growth on the anterior end, the differing rates of shell deposition grading along the ventral margin. No byssal attachment was observed in any of the pediveligers or juveniles, although this may have been due to lack of a suitable substrate. No byssal notch is present by day 28, nor is there any indication of the plication of the valves or flat projecting spines typical of the adults.

Zooxanthellar acquisition. Sectioned and stained eggs of both species were inspected

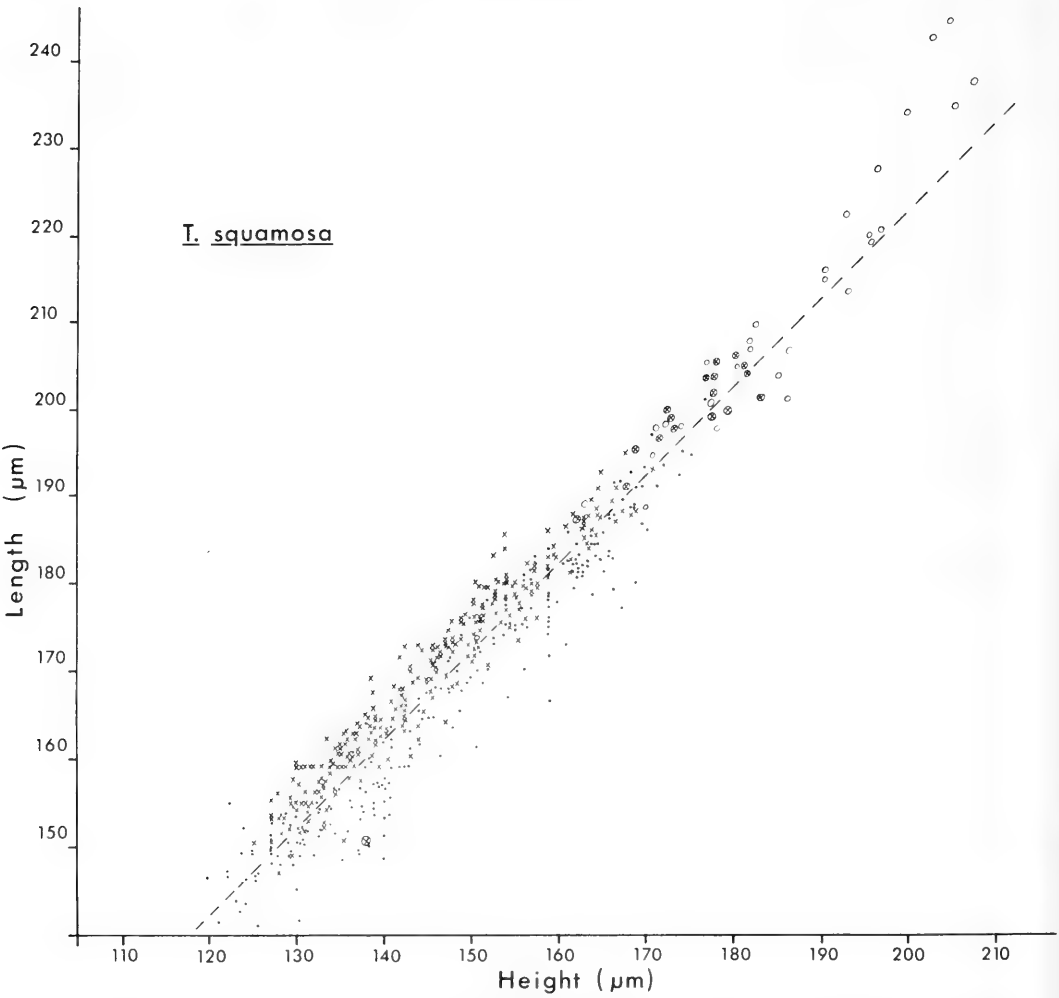

FIG. 7. Dimensions of larval and post-larval *Tridacna squamosa.* (●) = 6 July, 1972, spawning. (X) = 16 July, 1972, spawning. (○) = larvae and juveniles in day 28 sample. The dashed line represents the equation for the distribution, length = 1.00 (height) + 22.2; r = 0.97. Note departure of the juveniles from the regression line caused by differential shell deposition.

for the presence of zooxanthellae; frequent reference was made to sections of adult mantle tissue to verify the appearance of zooxanthellae under these conditions of fixation and staining. One hundred and thirty-seven *Tridacna maxima* eggs taken from the same spawning as the larvae described above were inspected; no zooxanthellae or structures which could reasonably be interpreted as inactive stages of zooxanthellae were seen. One hundred and sixty-three stripped eggs and 122 eggs from the 27 June, 1972, spawning of *T. squamosa* were also inspected with the same negative results. No zooxanthellae or identifiable zooxanthellar precursors were seen in any of the sections of larvae or newly metamorphosed juveniles of either species. Day 28 juveniles of *T. squamosa* did contain zooxanthellae, from 12 to over 100 algal cells per animal, primarily in the mantle but also in the digestive gland and pericardium. In the larger juveniles, the zooxanthellae were increasingly restricted to the mantle margins. The zooxanthellae appeared identical in all respects with the

zooxanthellae seen in sections of the adult mantle tissue. In several cases, zooxanthellae were seen in the process of fission.

DISCUSSION

Spawning. The low temperatures (mean 24.9° C) at which these species of *Tridacna* spawned, in 1 case spontaneously, contradicts previous reports that tridacnids will not spawn at temperatures below 30° C (Yonge, 1953a; Goreau et al., 1973), and supports Wada's (1954) contention that, in nature, temperature is probably not a critical factor for the spawning of these animals. The apparent effect of tidal phase on spawning reported here has not been previously noted.

Stephenson (1934) reported that *Hippopus hippopus* on the Great Barrier Reef spawned in January and that the gonads were spent and reduced during June and July, while the present study shows that *Tridacna maxima* and *T. squamosa* in Fiji are not only ripe during June and July, but are readily induced to spawn. These discrepancies may result from population differences, either induced or genetic, between Australian tridacnids and those of the more easterly Pacific islands, or may be due to generic differences, although it seems unlikely that both Stephenson (1934) and Yonge (1936) would have failed to report whether any of the Australian tridacnids were ripe during the winter months (June-August).

The 2 previous attempts at rearing larvae of tridacnids were probably unsuccessful for different reasons. Stephenson's (1934) attempt at artificial fertilization probably was unsuccessful because of failure of the germinal vesicle of the eggs to break down (see Loosanoff & Davis, 1963). My own attempts at artificial fertilization, both with and without treatment of the eggs with a 0.003 N solution of NH_4OH, did not yield any viable embryos. Rosewater's (1965) description of unsuccessful development of *Tridacna squamosa* eggs after a normal spawning is similar to my own observations of cultures where the eggs were polyspermic. Barriers to polyspermy seem to be poorly developed in tridacnids.

Larval development. No other species in the Tridacnidae have been successfully spawned and reared, but the larval development of some other members of the superfamily Cardiacea has been described. Due to uncertainties in identification of larvae described by the indirect method, only those studies where eggs or veligers were reared *in vitro* will be considered.

Lebour (1938) found that the PD I of *Cardium edule* was approximately 140 μm long; metamorphosis occurred at a length of about 300 μm. She also found the PD I of *Cardium scabrum* to be about 80 μm in length, with metamorphosis occurring at a length of 160 μm. The larvae possessed a distinct umbo at metamorphosis. Jørgensen (1946) modified these figures with his report that the PD I of *C. edule* ranged in length from 97-112 (mean 105) μm. Larvae were umbonate at a length of 175 μm, while metamorphosis occurred at 275-345 μm. Creek (1960) agreed with Jørgensen that the length of the PD I of *C. edule* was about 80 μm and that metamorphosis occurred at a length of 270 μm (at about 24 days after fertilization). According to Chanley & Andrews (1971), the PD I of *Laevicardium mortoni* is 80 μm long, increasing to 210-230 μm at metamorphosis. Round umbos develop at a length of about 120 μm, gradually becoming broadly rounded by a length of 150 μm. The hinge is undifferentiated except for a posterior ligament. The larvae of *Tridacna maxima* and *T. squamosa* are obviously highly modified from the cardiacean larval form in initial size, size at metamorphosis, and differentiation of the shell during the planktonic period. The sole characteristics which have apparently been retained are the posterior position of the ligament and the undifferentiated hinge (unlike Rees' (1950) cardiacean type).

The very large size of PD I and relatively small size at setting of both species of *Tridacna* described here indicates that these species normally have a very short free-swimming existence. The relatively long periods before metamorphosis reported here (at least 12 days for *T. maxima*, 10 days for *T. squamosa*) should be evaluated in light of the extremely adverse conditions under which these animals grew, i.e. extremely restricted food, large daily temperature fluctuations, and lack of a suitable substrate for induction of metamorphosis. Under natural conditions, these times might conceivably be halved.

Zooxanthellar infection. Stephenson (1934) failed to find zooxanthellae in eggs

in the gonads of *Hippopus hippopus*, and Yonge (1936) believed that the eggs were probably infected with zooxanthellae just before extrusion. In view of the highly developed symbiosis in these animals, it was indeed surprising to find no evidence of zooxanthellae prior to metamorphosis. However, in the other known bivalve with zooxanthellar symbionts, *Corculum cardissa*, the larvae also lack zooxanthellae prior to metamorphosis (Kawaguti, 1950). Exactly how the zooxanthellae are acquired by juvenile *Tridacna* is still unknown, but the number of possibilities is limited. The zooxanthellar symbiont in tridacnids is *Gymnodinium microadriaticum* (Freudenthal) (Taylor, 1969, 1971), a dinoflagellate known to produce several free-swimming stages, both *in vitro* (McLaughlin & Zahl, 1959; Freudenthal, 1962; Kevin et al., 1969; Taylor, 1969) and in nature (C. R. Stasek, personal communication). Infection may occur through 1 of these free-swimming stages. A 2nd possible mode of infection is implicit in the normal habitat of giant clams, namely coral reefs. The zooxanthellar symbiont of hermatypic corals is the same species of dinoflagellate as those found in giant clams (Taylor, 1969). Since corals under stress (Goreau, 1964) or, to a lesser degree, under superficially normal conditions where no stress is apparent (Yonge & Nicholls, 1931; Goreau et al., 1973) expell apparently healthy zooxanthellae embedded in mucus strings free into the water, it seems possible that young tridacnids might be infected by these non-motile stages as the mucus strings disintegrate. Either mechanism of infection implies some recognition mechanism in the giant clams to insure that the algal cell is phagocytized but not digested.

Post-larval development and the tridacnid form. The observation of differential growth along the shell margins of post-larval *Tridacna squamosa*, fastest along the posterior and postero-ventral margins, supports Stasek's (1961) contention that the form of tridacnids is more accurately expressed by the concept of differential growth than by rotation of the mantle-shell with respect to the body (Yonge, 1936). The areas of most rapid growth observed here are precisely those predicted by Stasek from a study of shell growth, utilizing growth lines as markers, in juvenile (length 1 mm or greater) *T. maxima*. The form of the Tridacnidae thus stems from a relative reduction by differential growth of the anterior regions of the body and shell comparable to the relative reduction of the anterior regions which has been postulated to account for the form of other monomyarian bivalves (Yonge, 1953b).

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SEXUALITY AND OTHER ASPECTS OF REPRODUCTION IN *ANODONTA* (PELECYPODA: UNIONIDAE)[1]

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ABSTRACT

The unionid subfamily Anodontinae contains several genera, principally Nearctic in distribution, among which occur considerable variations in life histories and sexual conditions. Eight species of *Anodonta* from the U.S.A. (viz., *A. californiensis, A. corpulenta, A. couperiana, A. gibbosa, A. hallenbeckii, A. imbecilis, A. peggyae* and *A. wahlamatensis*) were studied in order to identify and describe visceral sex, demibranch morphology, possible sex-reversal, age of sexual maturity, seasonal gonad activity, glochidial development and gravid periods, and adult life span.

Anodonta corpulenta, A. gibbosa and *A. wahlamatensis* were uniformly dioecious, whereas *A. californiensis, A. couperiana, A. hallenbeckii* and *A. peggyae* contained at least 1 kind of hermaphrodite in addition to males and females. Male-hermaphrodites (with a preponderance of testicular tissue over ovarian tissue) occurred in *A. couperiana, A. hallenbeckii* and *A. peggyae*, and female-hermaphrodites (with a preponderance of ovarian tissue, or with approximately equal amounts of male and female gonadal tissue) occurred in *A. californiensis* and *A. couperiana. A. imbecilis* consisted only of female-hermaphrodites and females; males were entirely lacking.

All 8 species exhibited the typical anodontine gill morphology. The non-marsupial demibranch (viz., the inner 2 in females and female-hermaphrodites, and all 4 in males and male-hermaphrodites) were undivided by secondary septa and had comparatively many filaments between successive primary interlamellar septa. The marsupial demibranchs (the outer 2 in females and female-hermaphrodites) were seasonally divided by secondary septa that produced temporary secondary water-tubes, resulting in a tripartite organization, and they had comparatively few filaments between successive primary interlamellar septa. Consistent correlation between the visceral sex (i.e., type of gonad present) and outer demibranch morphology in animals of different age classes from different seasons indicated an absence of sex-reversal.

Employment of the number of annuli on the shell suggested that species of *Anodonta* may not reach sexual maturity (i.e., become gravid) before 5 years of age. Studies of gonad activity in animals from monthly (*A. gibbosa, A. imbecilis* and *A. peggyae*, including 2 populations of the latter) or bimonthly (*A. couperiana*) samples showed that differences in oögenesis were less striking seasonally than those in spermatogenesis. Testicular activity in *A. couperiana* and *A. gibbosa* generated sperm-morulae (i.e., multinucleated figures of atypical spermatogenesis) from late fall into the following summer, produced typical spermatogenesis in late summer and provided mature spermatozoa in the early fall. In contrast, *A. imbecilis* had few sperm-morulae of irregular occurrence, a peak in typical spermatogenesis from summer to fall and abundant mature spermatozoa at all times. Animals of 1 population of *A. peggyae* displayed testicular activity similar to that of *A. imbecilis*, but those of the other population showed 2 consecutive cycles of activity in a year. Examination of the states of glochidial development revealed that *A. couperiana* and *A. gibbosa* are short-term, wintertachytictic breeders, *A. imbecilis* is a long-term, bradytictic breeder, and that *A. peggyae* can either be bradytictic or undergo 2 consecutive breeding cycles in a year. The adult life spans of the 8 species studied, judged from the number of annuli, varied interspecifically and intraspecifically. Males and females attained the same age in *A. californiensis, A. corpulenta, A. gibbosa* and 1 population of *A. peggyae,* whereas females reached a greater age in *A. couperiana, A. hallenbeckii, A. wahlamatensis* and a 2nd population of *A. peggyae*. Both males and females were older than any type of hermaphrodite in the same species.

Monoecious individuals displayed either of 3 states of gonadal differentiation, although most contained intermingled zones of male and female acini. The occurrence of hermaphroditism, in its various forms of glandular and ctenidial organization, does not coincide with conchological taxonomic groupings, nor do the present findings support views of the monoecious state as an adaptation to environmental conditions. The manifestations of hermaphroditism in mussels may be described, but the underlying genetic basis remains unknown.

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INTRODUCTION

Female and some hermaphroditic animals of the numerous species of the freshwater mussel family Unionidae Fleming undergo internal fertilization and incubate the developing young in the outer, marsupial demibranchs for varying periods of time, and most release glochidial larvae that are temporarily parasitic on the gills or fins of various species of fishes before assuming a free-living existence (Lefevre & Curtis, 1910a; Coker et al., 1921). However, a few exceptions have been reported: (1) Lefevre & Curtis (1911) stated that the glochidia of *Strophitus undulatus* (Say) [= *S. edentulus* (Say)] can metamorphose into juvenile mussels while still in the marsupial demibranchs and thus bypass a subsequent parasitic period, (2) Howard (1914) suggested that *Anodonta imbecilis* Say also displays similar direct development, and (3) Howard (1915) demonstrated the host of *Simpsoniconcha ambigua* (Say) to be not a fish but a salamander, *Necturus maculosus* (Rafinesque) [Proteidae].

Strophitus undulatus, A. imbecilis and *S. ambigua* are members of the unionid subfamily Anodontinae Ortmann (1910a), a group characterized in part as possessing marsupia which fill the entire outer demibranchs and form smooth pads without demarcation of the ovisacs (i.e., water-tubes, in which the embryos and subsequent larvae are brooded) by external sulci (Simpson, 1914). In addition, anodontine animals have been stated to be bradytictic breeders[2] (Ortmann, 1912). Species of the Anodontinae not only possess unique features among unionids, e.g., a tripartite organization of water-tubes and septa in the outer, marsupial demibranchs (cf. Fig. 5) but not in the non-marsupial demibranchs (Fig. 6), but also exhibit greater plasticity in life histories and sexual phenomena than do members of the other unionid subfamilies.

According to Sterki (1898a) and Ortmann (1911), the marsupial demibranchs of *Strophitus edentulus* contain a horizontal system of divided water-tubes and septa, whereas these elements are vertical in position in all other unionids. However, Heard & Fuller (in preparation) recently found that *S. rugosus* (Swainson) [= *S. edentulus*?] has the typical tripartite anodontine organization oriented vertically, i.e., dorso-ventrally, and that what had been interpreted as a horizontal structure consists of a vertical series of "perforations" in the interlamellar septa (Fig. 7). In addition, the posterior $\frac{1}{10}$ - $\frac{1}{5}$ of the outer demibranchs lacked marsupial organization. Ortmann (1911) also stated that in *S. edentulus* the secondary water-tubes vanish after the glochidia are expelled. Each ovisac was said to house a short, rather cylindrical gelatinous mass which contains the embryos and subsequent larvae. These masses, in which the glochidia (infective or metamorphosed?) are expelled, were termed "placentae" by Sterki and "placentulae" by Ortmann.

Placentulae are not produced in gravid animals of such other anodontine genera as *Alasmidonta* Say, *Anodonta* Lamarck, *Anodontoides* Simpson and *Lasmigona* Rafinesque (Ortmann, 1911), from which the glochidia are released either individually or in small groups in which the members are joined by intertwined larval filaments (Lefevre & Curtis, 1910a; Tucker, 1927), or individually or in groups agglutinated by a mucous secretion from the incubation chamber (Bouillon, 1955). Gravid animals in these genera also contain the tripartite marsupial organization in the outer demibranchs, the division being created by the seasonal appearance of a secondary septum on each side (lateral and medial) of the primary, central water-tubes (Ortmann, 1911). According to Ortmann, only the primary water-tubes serve as the ovisacs during incubation, but this concept will be modified later in this paper.

The contrasting reports concerning the life cycle of *A. imbecilis* are of particular interest. Howard (1914) stated that he found (1) juveniles, i.e., metamorphosed glochidia, in the marsupial demibranchs, (2) no natural "infections" of glochidia on what he considered to be the likely fish hosts, and (3) only difficult and incomplete experimental encystment of glochidia on these fishes. Allen (1924) also claimed to have found metamorphosed glochidia in the marsupial demibranchs, although Tucker (1927, 1928) reported no glochidial metamorphosis except after encystment on the fins of *Lepomis* (*Apomotis*) *cyanellus*

[2]Bradytictic animals, also called long-term or winter breeders, incubate young for most of the year, except for a part of the Nearctic summer. In contrast, tachytictic animals, also known as short-term or summer breeders, are gravid only during a part of the Nearctic summer.

Rafinesque, the green sunfish [Centrarchidae]. According to Allen, *A. imbecilis* has a very short (3-4 weeks), repetitive reproductive cycle, with an incubation period of even less duration than that displayed by tachytictic species (viz., members of the Pleurobeminae and Unioninae *sensu* Heard & Guckert, 1971). Accepting prior reports that the animals of *A. imbecilis* are hermaphroditic (refuted later in this paper) and might self-fertilize, and that their larvae lack a parasitic habit, Allen hypothesized that these features and such a very short reproductive cycle might be correlated with a more rapid growth rate and comparatively early attainment of sexual maturity in this species. None of Allen's contentions were confirmed by the present study.

A survey of "unionids"[3] for the occurrence of hermaphroditism has shown the monoecious condition to be common in the Anodontinae, and especially in *Anodonta* (cf. Van der Schalie, 1970; this paper, Table 1), although Bouillon (1955) previously stated that European species of *Anodonta,* none of which were named, are "dioïques mais dans les eaux stagnantes ce genre se montre souvent hermaphrodite." Van der Schalie listed only 4 "dominantly" hermaphroditic unionids, including 3 in the Anodontinae, while 16 other species were stated to contain "occasional" (or "sporadic") monoecious individuals in samples composed largely of dioecious animals.

Although serveral kinds of monoecious conditions in pelecypods have been described, much information concerning the nature of hermaphroditism in freshwater mussels (viz., Unionacea and Mutelacea) is still lacking. It is the purpose of this report to provide further data on this phenomenon and other aspects of reproduction in the Holarctic genus *Anodonta*.

LIST OF SPECIES AND LOCALITIES

Animals of 8 North American species of *Anodonta* were studied, 5 species from the southeastern U.S.A. and 3 from the western U.S.A. A total of 840 individuals were taken in 64 collections made between 1963 and 1969.

Subgenus *Anodonta*, s.s.

1. *A. californiensis* Lea. 1 collection (7 individuals): 11 October 1966. Mill Creek at Bartlett Springs Road, Colusa County, California.

[3]Species of *Amblema* Rafinesque, *Fusconaia* Simpson, *Gonidea* Conrad, *Quadrula* Rafinesque and *Tritogonia* Agassiz, as well as *"Elliptio" sloatianus* (Lea) [= *Elliptoideus sloatianus* (Lea)], listed in the Unionidae by Van der Schalie (1970), were considered by Heard & Guckert (1971) to be members of the Amblemidae Rafinesque.

TABLE 1. Recorded occurrences of hermaphroditism in the Unionidae: Anodontinae. All records are from the U.S.A. unless stated otherwise.

Species	Locality	Reference
Alasmidonta marginata (Say)[a]	Michigan & Tennessee	Van der Schalie, 1970
Anodonta anatina (Linnaeus)[a]	England	Bloomer, 1936
A. californiensis Lea[a]	California	*this paper*
A. corpulenta Cooper[a]	Tennessee	Van der Schalie, 1970
A. couperiana Lea[a]	Florida	*this paper*
A. cygnea (Linnaeus)[a]	England	Bloomer, 1930, 1934, 1935, 1939
A. grandis f. *footiana* Lea[a]	Michigan	Van der Schalie & Locke, 1941
A. hallenbeckii Lea[a]	Alabama	*this paper*
A. henryana Lea[b]	Texas	Ortmann, 1911
A. imbecilis Say,[c,d]	Pennsylvania	Sterki, 1898b; Ortmann, 1911
	Missouri	Utterback, 1915
	Michigan	Van der Schalie, 1966, 1970
	Florida & Alabama	*this paper*
A. peggyae Johnson[a]	Florida	*this paper*
Lasmigona complanata (Barnes)[a]	Michigan	Van der Schalie, 1970
L. compressa (Lea)[c]	Pennsylvania	Ortmann, 1911
	Michigan	Van der Schalie, 1966, 1970
L. subviridis (Conrad)[c]	eastern U.S.A.	Van der Schalie, 1966, 1970
Strophitus rugosus (Swainson)[a]	Michigan	Van der Schalie, 1970

[a]With males and females.
[b]Monoecious condition based only on inference, because of its alleged relationship to *A. imbecilis.*
[c]As hermaphrodites only.
[d]With females only.

2. *A. wahlamatensis* Lea. 1 collection (7 animals): 10 October 1966. Upper Blue Lake at State Highway 20, Lake County, California.

Subgenus *Pyganodon* Crosse & Fischer

3. *A. corpulenta* Cooper. 1 collection (14 individuals): 9 November 1969. Lake Mary, about 10 miles NE of Flagstaff, Coconino County, Arizona.
4. *A. gibbosa* Say. 10 collections (total of 53 individuals): monthly, except in June and August, 1965. Holmes Creek at Federal Highway 90, 4 miles W of Chipley, Holmes County, Florida.
5. *A. hallenbeckii* Lea. (a) 1 collection of 5 animals: 24 October 1963. Patsaliga Creek at Federal Highway 331, N edge of Luverne, Crenshaw County, Alabama. (b) 1 collection of 4 animals: 25 October 1963. Big Swamp Creek at State Highway 21, 1 mile SW of Hayneville, Lowndes County, Alabama. (c) 1 collection of 7 animals: 27 October 1963. Big Swamp Creek at Federal Highway 80, Lowndes County, Alabama. (d) 1 collection of 6 animals: 28 November 1963. Catoma Creek, 6 miles SW of Pike Road (village), Montgomery County, Alabama. (e) 1 collection of 9 animals: 1 December 1963. Cubahatchee Creek at Federal Highway 80, about 20 miles W of Tuskegee, Macon County, Alabama.

Subgenus *Utterbackia* F. C. Baker

6. *A. couperiana* Lea. (a) 6 bimonthly collections in 1965 (total of 372 individuals surveyed for gravidity; 10 per collection were sectioned). Myakka River at Myakka River State Park, about 18 miles SE of Sarasota, Sarasota County, Florida. (b) 2 collections (total of 16 animals): 16 August and 3 November 1968. Apalachicola River at Ocheesee Landing, about 6 miles N of Blountstown, Calhoun County, Florida.
7. *A. imbecilis* Say. (a) 9 collections (total of 70 individuals): monthly, except in January, April, June and August, 1964-1965. Lake Talquin (= reservoir of the Ochlockonee River) at Coe's Landing, about 13 miles W of Tallahassee, Leon County, Florida. (b) 5 collections (total of 41 animals): in March, May, June, July and November 1965. Gantt Lake (= reservoir of the Conecuh River) at Federal Highway 29, Clearview, Covington County, Alabama.
8. *A. peggyae* Johnson. (a) 12 monthly collections (total of 124 animals), 1963-1964. Lake Talquin (see under *A. imbecilis*, above), the type-locality. (b) 12 monthly collections (total of 102 individuals), 1964-1965. Holmes Creek (see under *A. gibbosa* above).

METHODS

One of the populations of *A. couperiana* was sampled every 2 months, and attempts were made to obtain animals of *A. gibbosa, A. imbecilis* and *A. peggyae* (both populations) each month for a calendar year in order to provide material for the study of seasonal aspects of reproduction.

All animals were narcotized with 10% sodium nembutal (= Diabutal), fixed either in Bouin's fluid or 10% formalin, and preserved in 70% alcohol or 1% propylene phenoxetol. Wedge-shaped pieces of the visceral mass containing the gonads were removed, dehydrated through an alcohol series, cleared in xylol and embedded in paraffin. Sections were cut at a thickness of 10 μm, stained in Harris' hematoxylin and counterstained with alcoholic eosin, and mounted with Canada balsam. Samples of the outer and inner demibranchs of each animal received the same treatment, but were immersed in a 1% solution of hydrochloric acid in 70% alcohol prior to embedding in order to decalcify any shelled larvae present. Gonadal sections were cut parasagittally from the outside inward so as to survey the width of the gonads for possible regional separation of the ovarian and testicular tissues in any hermaphrodites present. The demibranch sections were cut frontally from the axis (dorsal) downward, also to provide for examination of any possible regional variation. Five slides of each gonadal and demibranch sample were prepared, each containing sections from different locations.

The total length, height and width of each shell was measured (cf. Cvancara, 1963), and the occurrence of gravidity was recorded. The age of each individual was determined by counting the number of annuli on a single valve (see Chamberlain,

1931; Crowley, 1957; Ökland, 1963; Stansbery, 1967).

The incubating young in each gravid animal (about 3,000,000 in European species of *Anodonta, fide* Bouillon, 1955) were classified according to their comparative state of development. The seasonal occurrences of the general morphogenic stages (described on p. 96-97) were employed in determining the period of fertilization, the duration of incubation, the period of larval discharge, and the number of broods per year.

VISCERAL SEX

The sex of most unionids can be determined by the morphology of the outer demibranchs (see p. 87-88), or more precisely by the nature of the gonads[4]. The "visceral sex," defined by the kinds of gonads present, can be male, female or hermaphroditic. Coe (1943) arranged hermaphroditic conditions in pelecypods into 4 categories, principally according to the sequence of reproductive events (Table 2). In addition, monoecious unionids can be grouped as "♂ hermaphrodites" and "♀ hermaphrodites," depending in part on the relative preponderance of one type of gonadal tissue over the other, and in part on the morphology of the outer demibranchs (Table 2).

In the present investigation, the determination of the visceral sex of each individual showed that *A. imbecilis* (both populations) contained ♀ hermaphrodites (Fig. 1) and females; males and ♂ hermaphrodites were lacking (Table 3). *A. californiensis* was largely dioecious, although one animal was a ♀ hermaphrodite. *A. hallenbeckii*, and *A. peggyae* (Figs. 2-4) in both populations, were principally dioecious, but both also contained ♂ hermaphrodites. Two populations of *A. couperiana* were investigated; that from the Myakka River possessed only males and females (hermaphrodites were absent), whereas that from the Apalachicola River had females, ♀ hermaphrodites and ♂ hermaphrodites (males were lacking). *A. gibbosa* was entirely dioecious. *A. corpulenta* and *A. wahlamatensis* also lacked hermaphrodites, but the number of specimens (14 and 7, respectively) from a single sample each was small, and possibly rare monoecious animals may have escaped collection. Indeed, Van der Schalie (1970) previously reported the occurrence of hermaphrodites in *A. corpulenta*.

That *A. imbecilis* was found to contain females in addition to [♀] hermaphrodites is

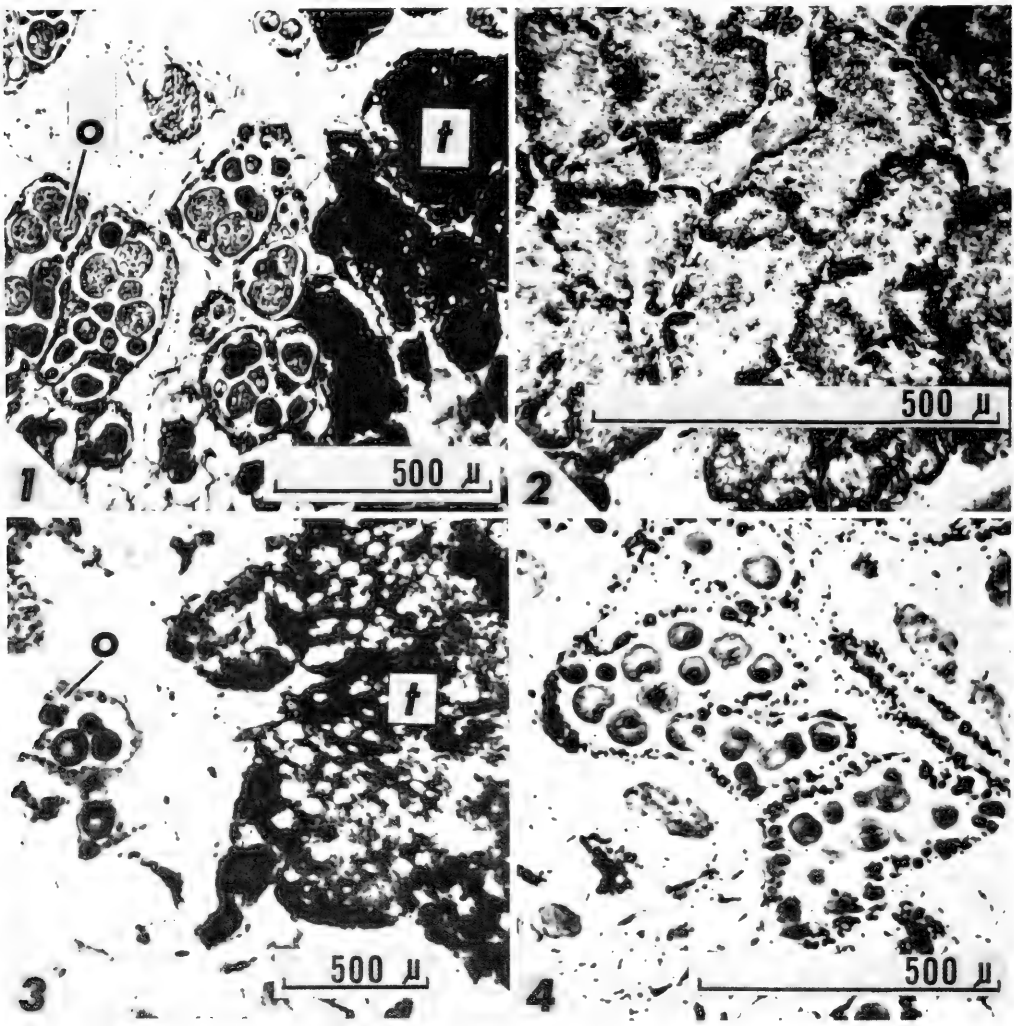
[4] *Anodonta cygnea* (Linnaeus), the type-species of the genus, is the only reported unionid in which the outer demibranch morphology and visceral sex may not always coincide (cf. Bloomer, 1934; p. 87 here).

TABLE 2. Classifications of pelecypod hermaphroditism (types 1-4 after Coe, 1943; types 5-6 used in this paper).

Type	Characteristics
1. Functional hermaphroditism a. normal[a,b] b. accidental or developmental[a,c]	1. Eggs and sperm produced simultaneously a. typically in monoecious species b. typically in dioecious species
2. Consecutive sexuality	2. Single sex-reversal, usually protandrous
3. Rhythmical sexuality	3. > 1 sex-reversal, usually protandrous
4. Alternative sexuality[a?]	4. Adults function seasonally as separate sexes; they may or may not reverse by the next reproductive season
5. ♂ hermaphroditism[a,b,d]	5. Predominance of testicular tissue; animals not gravid, with non-marsupial outer demibranch morphology
6. ♀ hermaphroditism[a,e]	6. Ovarian tissue slightly or greatly exceeding quantity of testicular tissue; animals with marsupial outer demibranch morphology, may become gravid

[a] Examples known in the Unionidae, including *Anodonta* (type 4 in *A. cygnea*?).
[b] Synonymous with "usual" and "dominant" *sensu* Van der Schalie (1966, 1970).
[c] Synonymous with "occasional," "partial" and "sporadic" *sensu* Van der Schalie (1966, 1970).
[d] Synonymous with accidental or developmental hermaphroditism (1.b.) in *Anodonta* spp.
[e] Synonymous with normal hermaphroditism (1.a.) in *A. imbecilis*, and with accidental or developmental hermaphroditism (1.b.) in other species of *Anodonta*.

in disagreement with the view, prompted by Sterki (1898a, 1898b) and perpetuated since by others (e.g., Ortmann, 1910a, 1911; Utterback, 1915; Allen, 1924; Baker, 1927, 1928; Van der Schalie, 1966, 1970), that this species is "normally" or "dominantly" hermaphroditic. Although Utterback considered that to be the case, he inconsistently listed data on males and females. Van der Schalie (1966) originally suggested that "...*Anodonta imbecillis* [sic] had representatives in Florida which were dioecious, indicating that such a wide ranging species may not be consistently hermaphroditic." These dioecious animals from the Hillsborough River in Hillsborough County, Florida, seen by me, actually belonged to *A. peggyae*. Van der Schalie (1970: 98) later stated that "...the difference in the sexual condition observed between the northern [Michigan] and southern [Florida] forms [of *A. "imbecillis"*], thought to be one of geographical strain, might be specific, a moot point." However, characteristic shell features, a distinctive geographical range and the different sexual composition support the



FIGS. 1-4. Histological sections of different visceral sexes in *Anodonta*. FIG. 1. ♀ hermaphrodite of *A. imbecilis* (gravid); Lake Talquin, 20 July 1963. FIG. 2. ♂ *A. peggyae*; Lake Talquin, 18 Jan. 1964. FIG. 3. ♂ hermaphrodite of *A. peggyae* (non-gravid); Holmes Creek, 24 Dec. 1964. FIG. 4. ♀ *A. peggyae* (non-gravid); Lake Talquin, 20 July 1963. o, ovarian tissue; t, testicular tissue.

TABLE 3. Numbers of animals according to their observed visceral sex. The numbers in parentheses represent gravid animals.

Species	Males	Hermaphrodites ♂	Hermaphrodites ♀	Females	Total no. examined
A. californiensis	5		1(0)	1(1)	7
A. corpulenta	7			7(4)	14
A. couperiana					
Myakka River	22			38(5)	60
Apalachicola River		5(0)	1(0)	10(0)	16
A. gibbosa	35			18(12)	53
A. hallenbeckii	10	1(0)[a]		20(18)	31
A. imbecilis					
Lake Talquin			34(12)	36(10)	70
Gantt Lake			24(9)	17(6)	41
A. peggyae					
Lake Talquin	80	1(0)		42(24)	123[b]
Holmes Creek	45	10(0)		47(38)	102
A. wahlamatensis	4			3(3)	7

[a]With 2 males and 3 females from Catoma Creek, Alabama.
[b]One animal, with 2 annuli on each valve, was sexually undifferentiated.

systematic validity of *A. peggyae*. Furthermore, through disc electrophoretic studies, Dr. John B. Burch of the University of Michigan (personal communication) found only a 75% similarity between foot muscle proteins of *A. imbecilis* from Michigan and *A. peggyae* from Florida (Lake Talquin topotypes).

DEMIBRANCH MORPHOLOGY

In describing anatomical features of several species of *Anodonta*, Ortmann (1911) contrasted the morphological organization common to all 4 demibranchs of males and the inner demibranchs of females with that of the outer demibranchs of females. Only the latter, which carry the incubating young and are therefore called "marsupial demibranchs," were stated to possess tripartite water-tubes; the non-marsupial demibranchs lacked this divided system. These observations, previously briefly noted by Ortmann (1910a, 1910b), were confirmed in the present study (Figs. 5-6), further refuting the opinion of Lefevre & Curtis (1910b) that such divided water-tubes do not exist.

It was also found here that as the marsupial demibranchs became laterally distended with near-infective glochidia, the secondary water-tubes united with the primary water-tubes (see Figs. 8-10, in a seasonal series). This finding is in contrast to Ortmann's (1911) report that the secondary water-tubes vanished *after* the discharge of the glochidia, and that only the primary, central water-tubes served as ovisacs.

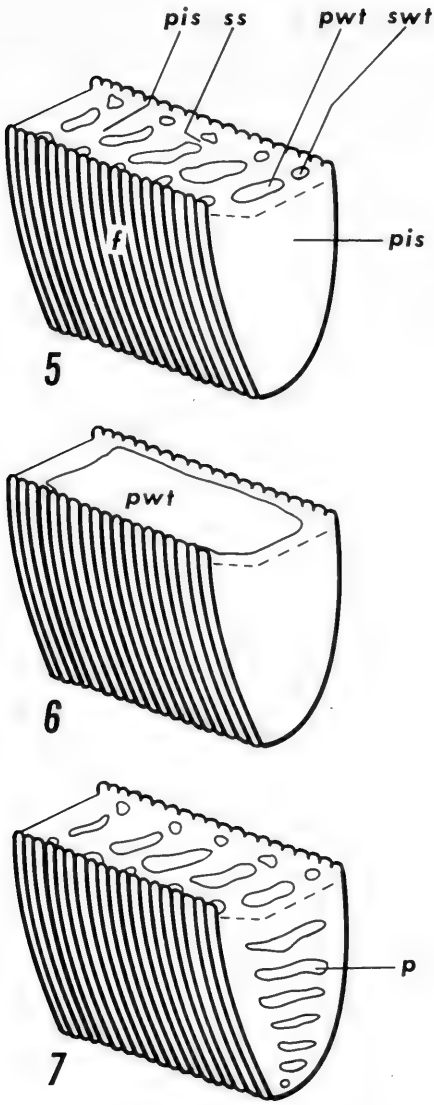
Ortmann (1911, 1912) and Bloomer (1934, 1936) noted that, in contrast to their more distant spacing in non-marsupial demibranchs, the primary interlamellar septa of marsupial demibranchs were comparatively close together. Indeed, Utterback (1915), among others, referred to the marsupial demibranchs as having "crowded septa." This dimorphism, apparently first detected by Peck (1877: shown in illustrations, but not described in the text), was confirmed here by determining the number of filaments between consecutive primary interlamellar septa: greater in non-marsupial demibranchs (Table 4; also compare Figs. 8 and 11).

Bloomer (1934, 1935, 1939) reported various hermaphroditic conditions in *A. cygnea*. At opposite ends of his monoecious series (visceral sex criterion) were forms in which the outer demibranchs were marsupial, and forms in which these demibranchs were non-marsupial[5]. The possible significance of these findings is discussed in the section on Sex-Reversal (p. 89).

Two kinds of monoecious animals were encountered in the present study: ♂ hermaphrodites and ♀ hermaphrodites, both initially identified by the visceral sex criterion (p. 85; Tables 2-3). None of the ♂ herma-

[5]Bloomer's distinction of the type of outer demibranchs present was based on septal spacing. Identification by the presence or absence of tripartite organization was not made.

phrodites were gravid; both non-gravid and gravid ♀ hermaphrodites were found, the non-gravid condition presumably reflecting age or seasonal variations in animals that probably were previously gravid or would have subsequently become gravid. All animals of *A. imbecilis*, ♀ hermaphrodites as well as females, possessed marsupial outer demibranchs (tripartite; crowded septa) and non-marsupial inner demibranchs (non-tripartite; distant septa) (Table 4). The single non-gravid ♀ hermaphrodite of *A. californiensis* had marsupial outer demibranchs. Males and females of *A. couperiana* from the Myakka River population had non-marsupial and marsupial outer demibranchs, respectively; the ♂ hermaphrodites from the Apalachicola River population had non-marsupial outer demibranchs, and although the single non-gravid ♀ hermaphrodite was discarded before a sample could be obtained it is hypothesized that such animals would have marsupial outer demibranchs as did the females. In *A. hallenbeckii* and *A. peggyae* only the females had marsupial outer demibranchs; the ♂ hermaphrodites and males had 4 non-marsupial demibranchs. The demibranchs of *A. corpulenta* and *A. gibbosa* were not examined histologically, and it is only assumed that the males and females had non-marsupial and marsupial outer demibranchs, respectively; no hermaphrodites were found among the animals of either species. The inner demibranchs were consistently non-marsupial in all males, ♂ hermaphrodites, ♀ hermaphrodites and females of each species.



FIGS. 5-7. Diagrammatic representations of anodontine demibranch morphologies. FIG. 5. Tripartite marsupial organization in *Anodonta*. FIG. 6. Non-marsupial organization in *Anodonta* and *Strophitus*. FIG. 7. Tripartite marsupial organization in *Strophitus rugosus* (Zukey Lake inlet, Livingston Co., Michigan, U.S.A.). f, filaments; p, perforation; pis, primary interlamellar septum; pwt, primary water-tube; ss, secondary septum; swt, secondary water-tube.

Van der Schalie's (1970) report on hermaphroditism in unionacean mussels was concerned only with the visceral sex condition, and no reference to the outer demibranch morphology of the monoecious animals was made. However, the legends to his photomicrographs of gonad sections of hermaphrodites often contain information on the relative proportions of ovarian and testicular tissue, and usually a notation about whether or not the animal was gravid, and some deductions can be made from his findings. For example, gravid hermaphrodites of *Anodonta corpulenta* and *Lasmigona complanata* were recorded, the latter "mostly female but with scattered spermatogenesis," both animals were probably ♀ hermaphrodites. Also listed were non-gravid hermaphrodites of *Alasmidonta marginata,* one of which was "evidently a female with patches of sperm," and *Anodonta grandis* form *footiana* that was "mostly male with only small amount of female tissue," the former may have been a ♀ hermaphrodite, and the latter a ♂ hermaphrodite. Van der Schalie consider-

TABLE 4. Dimorphism between the spacing of primary interlamellar septa in marsupial (tripartite) outer demibranchs and that in non-marsupial outer demibranchs of animals of different sexes in 6 species of *Anodonta*; based on numbers of filaments between consecutive interlamellar septa. Values for the inner, non-marsupial demibranchs of individuals of all visceral sex conditions were similar to those for the non-marsupial outer demibranchs. g, gravid animals; N, number of water-tubes examined; ng, non-gravid animals.

Species	Visceral sex	Tripartite organization	N	No. of filaments	
				Range	Mean
A. californiensis	male	no	57	6-20	12.3
	female; g	yes	15	4-9	6.4
	♀ hermaphrodite; ng	yes	10	2-8	4.3
A. couperiana	female; ng	yes	10	1-4	2.5
Apalachicola River	♀ hermaphrodite; ng	?*	—	—	—
	♂ hermaphrodite; ng	no	10	10-18	12.7
	male	no	20	10-30	17.9
Myakka River	female; ng	yes	12	2-4	2.6
	female; g	yes	12	3-6	4.5
A. hallenbeckii	male	no	18	14-27	19.1
	♂ hermaphrodite; ng	no	5	17-25	19.2
	female; g	yes	15	2-6	4.1
A. imbecilis	female; g	yes	27	1-6	2.4
(all Lake Talquin)	female; ng	yes	10	1	1.0
	♀ hermaphrodite; g	yes	50	1-8	3.7
A. peggyae	male	no	25	8-30	17.8
Holmes Creek	♂ hermaphrodite; ng	no	20	8-22	14.1
	female; g	yes	24	3-7	5.0
	female; ng	yes	8	3-6	4.9
	male	no	15	10-20	16.4
Lake Talquin	female; g	yes	26	2-10	5.5
	female; ng	yes	23	2-9	3.7
A. wahlamatensis	male	no	43	6-20	9.6
	female; g	yes	45	2-11	5.8

*The soft-parts of the single animal were discarded before a sample could be taken.

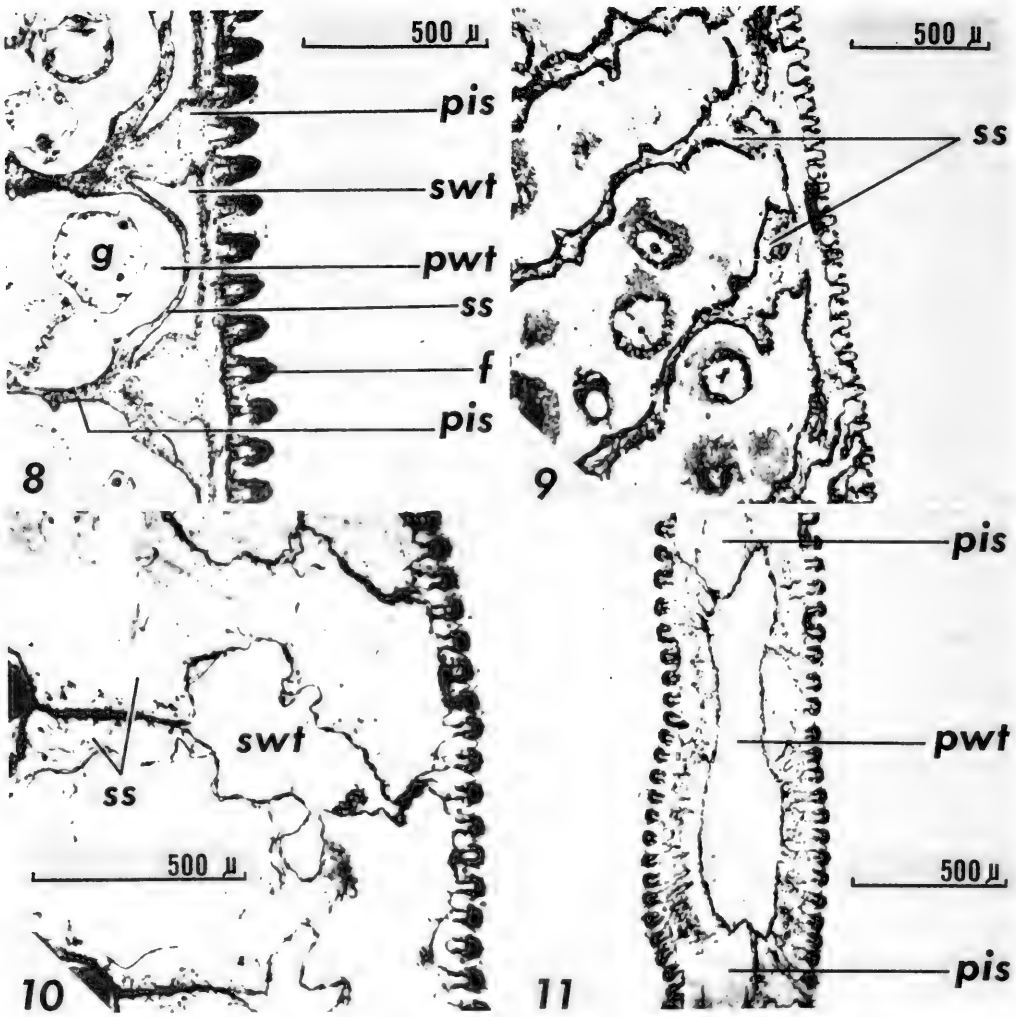
ed the monoecious individuals of these 4 taxa, and that of *Strophitus rugosus* ("mostly male with only a small amount of female tissue," but gravidity uncertain; perhaps a ♂ hermaphrodite), to be "occasional" hermaphrodites among largely dioecious samples. He listed *Anodonta imbecilis, Lasmigona compressa* and *L. subviridis*, as well as *Carunculina parva* (Barnes) [Unionidae: Lampsilinae], as the only species "in which hermaphroditism is the dominant condition"[6].

SEX-REVERSAL

Bloomer (1934) found that in *A. cygnea* the morphology of an individual's outer demibranchs was not always correlated with its visceral sex[7]. Although all females evidently had marsupial outer demibranchs, only some males had non-marsupial outer demibranchs; these demibranchs were marsupial in some individuals called males. The outer demibranchs in hermaphrodites were either marsupial (gravid), non-marsupial

[6]Among other unionaceans, no species of the Amblemidae is known to be at least predominantly monoecious. And although Van der Schalie (1966) reported just "occasional hermaphrodites" in the margaritiferids *Cumberlandia monodonta* (Say) [not cited by Van der Schalie, 1970] and *Margaritifera margaritifera* (Linnaeus), Heard (1970) found only hermaphrodites (visceral sex criterion) in a collection of 26 animals of *M. falcata* (Gould).

[7]Bloomer made several histological sections of gonad samples of *A. cygnea*, but most of his findings on the visceral sex of individuals were based on smear preparations. The latter is a less reliable technique for determining the presence of a hermaphroditic state, and especially for assessing the comparative abundance of ovarian and testicular tissues.



FIGS. 8-11. Frontal sections of *Anodonta* demibranchs showing the occurrence (FIG. 8), subsequent rupture (FIG. 9) and reappearance (FIG. 10) of secondary septa and secondary water-tubes in marsupial demibranchs, and the constant, non-tripartite organization of non-marsupial demibranchs (FIG. 11). FIG. 8. ♀ hermaphrodite of *A. imbecilis*; Lake Talquin, 20 July 1963. FIG. 9. ♀ *A. peggyae*; Lake Talquin, 16 May 1964. FIG. 10. ♀ *A. peggyae*; Holmes Creek, 15 May 1965. FIG. 11. ♂ hermaphrodite of *A. peggyae*; Lake Talquin, 18 Jan. 1964. g, developing glochidium; other abbreviations as in FIGS. 5-7.

(non-gravid) or "intermediate" (non-gravid), and Bloomer concluded that sex-reversal had occurred in this species.

Bloomer did not determine the ages of the specimens that he investigated, but he did record the total lengths of the shells. It was therefore possible to survey his data for indirect evidence of sex change or reversal with growth, an index of age. It appears that if sex-reversal did occur in Bloomer's animals, at least in some cases, it was independent of age; hermaphrodites in evidently varying stages and kinds, males and females of all sizes were reported[8], although most hermaphrodites were of larger size. In addition, Bloomer's (1946) observations on the seasonal sequence of events in the production and occurrence of sperm-morulae (see

[8]Such a condition might be expected in cases where more than one sex-reversal occurs in the life of an individual (see "Rhythmical sexuality" in Table 2).

below) and mature spermatozoa suggest that the possible sex-reversal is independent of seasonal influence.

Another aspect to be considered in examining the possibility of sex-reversal in *A. cygnea* is the occurrence of different sex compositions (i.e., associations of members of the different kinds of visceral sex conditions, apart from sex ratios) in different populations. Bloomer (1939) found the following associations, each characteristic of a separate population: males, females and hermaphrodites; males and hermaphrodites; females and hermaphrodites; and hermaphrodites only. Males and females never occurred together without hermaphrodites, and hermaphrodites were present in all populations. These relationships were apparently constant through at least several consecutive seasons; it is unknown whether the ratios changed with time. In the present study, *A. imbecilis* and *A. peggyae* showed no intraspecific variation in sex composition of the populations, although the ratios of the kinds of animals were different. However, a considerable difference in the sexual associations occurred between the 2 populations of *A. couperiana* (cf. Table 3). Van der Schalie's (1966, 1970) implication that *A. peggyae* may be a southern race of *A. imbecilis* is considered to be erroneous, although it may be that the northern (hermaphroditic only?) and southern (females and ♀ hermpahrodites) populations of *A. imbecilis* vary in sexual composition.

If none of the animals of *A. cygnea* had undergone sex change(s), Bloomer's observations can be explained in either of 2 ways. (1) A population of relatively stabile size, without significant emigration and immigration, might establish and maintain a characteristic sexual composition (regardless of possible changes in ratios), even through self-fertilization by hermaphrodites as concluded by Bloomer (1940, 1943)[9]. (2) It may be that *A. cygnea* contains males, ♂ hermaphrodites, ♀ hermaphrodites and females, with at least some, or even all, of these 4 kinds of individuals occurring in different populations.

The entire problem of the sexual nature of *A. cygnea* should be restudied, the hermaphroditic states described by Bloomer more precisely defined, and the mechanism of sex-reversal (if present) identified. The latter is made difficult by the lack of knowledge of this mussel's fish host(s), nature of genetic sex-determination and population genetics, and further by the time involved: several years between glochidial metamorphosis into a juvenile and the first "breeding."

It was found in the present study that the visceral sex of all individuals was consistently correlated with the morphology of the outer demibranchs, regardless of the season and the age of the animals. In those hermaphrodites with marsupial outer demibranchs the amount of ovarian tissue slightly (*A. imbecilis*) or conspicuously (*A. californiensis*, and *A. couperiana*?) exceeded the amount of testicular tissue in the sections, whereas the mass of testicular tissue greatly predominated in those hermaphrodites with non-marsupial outer demibranchs (*A. couperiana, A. hallenbeckii* and *A. peggyae*). It is therefore concluded that sex-reversal did not occur in the populations investigated.

SEASONAL ASPECTS OF REPRODUCTION

Sperm-Morulae

Organelles termed "sperm-morulae," named for their structural resemblance to the morular stage of ontogenetic development, may be observed in the testicular tissue of male (Fig. 12), ♂ hermaphroditic and ♀ hermaphroditic unionaceans. These multinucleate structures have previously been reported to occur in the marine pelecypod *Mya arenaria* Linnaeus [Myidae] (Coe & Turner, 1938; Stroganova, 1963; Ropes & Stickney, 1965; Shaw, 1965), as well as in the unionids *Anodonta anatina* (Bloomer, 1936; Stroganova, 1963), *A. cygnea* (Bloomer, 1930-1946), *A. grandis* form *footiana* (Van der Schalie & Locke, 1941), and *Unio pictorum* (Linnaeus) and *U. tumidus* (Philipsson) (both Stroganova, 1963). They are of widespread occurrence in the Unionacea, having been found in 43 species of 17 genera in a survey of the families Amblemidae, Hyriidae, Margaritiferidae and Unionidae (Heard, unpublished).

[9]On the other hand, the same concept might apply toward describing a characteristic sex composition for a population should at least some of the animals reverse their sexual condition at a constant rate, possibly with selection for or against one or more kinds of visceral sex if an imbalanced rate is present.

Sperm-morulae are seasonal in occurrence, being least abundant during the period of "typical" spermatogenesis[10] (Ropes & Stickney, 1965; confirmed here). Their origin has been attributed to "atypical" spermatogenesis (Coe & Turner, 1938; Stroganova, 1963; Ropes & Stickney, 1965), although there has been disagreement as to their fate. Coe & Turner (1938) reported that most sperm-morulae in *Mya arenaria* underwent cytolysis to provide nutrient supplies for the ensuing "typical" spermatogenesis, whereas some metamorphosed into mature spermatozoa; both conclusions were based on circumstantial evidence, and neither was documented. Bloomer (1946) also concluded that sperm-morulae in *Anodonta cygnea* generate mature spermatozoa, but without providing direct evidence.

Precise details of the origin, development, morphology and function of sperm-morulae are not yet clearly understood, although electron microscopic and cytochemical studies on *Villosa villosa* (Wright) [Unionidae: Lampsilinae] and *Anodonta peggyae* suggest that they do not undergo cytolysis in these species but instead complete metamorphosis to provide spermatozoa that are indistinguishable in morphology and size from those generated in the "typical" spermatogenic pathway, i.e., that containing "typical" meiotic figures (Heard & Thomas, in preparation). Nevertheless, the male germinal cycle in *A. couperiana* and *A. gibbosa* was found here to be seasonally different from that in *A. imbecilis* and *A. peggae* (see next section), and because the former 2 species contained many more sperm-morulae than did the latter 2, possibly not all of these structures generated mature spermatozoa. Whether or not the spermatozoa derived from sperm-morulae are viable is unknown at this time.

Spermatogenesis

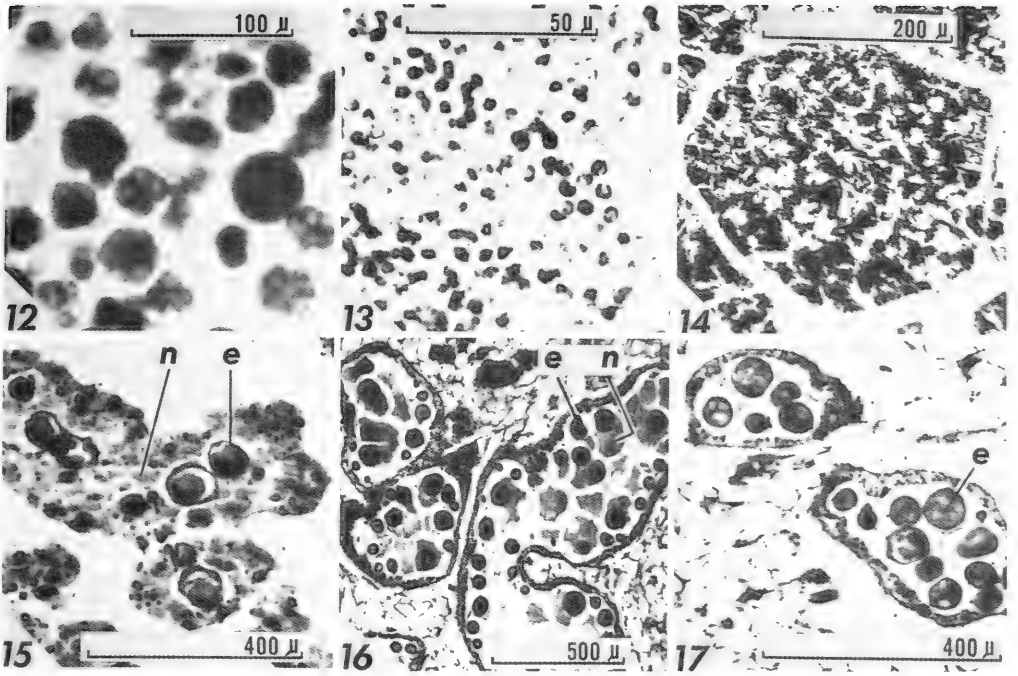
According to Bloomer (1946), animals of some English populations of *A. cygnea* contained comparatively few sperm-morulae and spermatozoa from January to May, showed a decline in the numbers of spermatozoa in May and June, underwent "development" of sperm-morulae in June and July, and contained large numbers of spermatozoa in July and August. The period of occurrence of "typical" spermatogenesis was not indicated. Bloomer (1940, 1943) previously stated that the release of spermatozoa was stimulated by direct sunlight and warmer water temperatures.

Possible interspecific and intraspecific seasonal variation in the occurrence of sperm-morulae (Fig. 12), typical spermatogenesis (Fig. 13) and mature spermatozoa (Fig. 14) was investigated here among 4 species: *A. couperiana, A. gibbosa, A. imbecilis* and *A. peggyae* (both populations). Although the cells of these 3 events were not absolutely mutually exclusive, they often appeared in distinct peak periods of abundance that were in seasonal sequence (see Table 5).

The "typical" spermatogenesis in *A. couperiana* and *A. gibbosa* was found to be confined to August and September, and spermatozoa appeared only in September. Sperm-morulae were predominant at all other times, usually alone filling the testicular tissue. In contrast, *A. imbecilis* and *A. peggyae* each showed considerable typical spermatogensis and numerous spermatozoa throughout the year, with animals of both species containing many fewer sperm-morulae than occurred in *A. couperiana* and *A. gibbosa*. However, the sperm-morulae, also present throughout the year, were observed to be more common in males and ♂ hermaphrodites of *A. peggyae* (both populations) than in the ♀ hermaphrodites of *A. imbecilis.*

No seasonal variation in the occurrences of sperm-morulae was detected between males (total of 125 specimens from both populations) and ♂ hermaphrodites (total of 11) of *A. peggyae*, although both kinds of animals from the Lake Talquin population consistently contained more sperm-morulae than did those from Holmes Creek. The Lake Talquin animals displayed 2 periods of typical spermatogenic, spermatozoan and sperm-morular abundance, whereas those from Holmes Creek showed only one (Table 5). The 2 peak periods of typical spermatogenesis in Lake Talquin animals occurred

[10] Typical and atypical spermatogenic pathways, giving rise to 2 different kinds of spermatozoa (viz., eupyrene, and oligopyrene or apyrene, respectively) that are functionally and usually morphologically distinct from each other, are known to occur simultaneously in most prosobranch gastropods (cf. Nishiwaki, 1964).



FIGS. 12-17. States of gonad activity in *Anodonta*. FIG. 12. Sperm-morulae in a ♂ *A. couperiana*; Myakka River, 30 Jan. 1965. FIG. 13. Typical spermatogenesis in a non-gravid ♂ hermaphrodite of *A. couperiana*; Apalachicola River, 16 August 1968. FIG. 14. Mature spermatozoa in a ♂ *A. gibbosa*; Holmes Creek, 21 Sept. 1963. FIG. 15. Early oögenesis in a non-gravid ♀ *A. couperiana*; Myakka River, 27 March 1965. FIG. 16. Intermediate oögenesis in a gravid ♀ hermaphrodite of *A. imbecilis*; Lake Talquin, 20 July 1963. FIG. 17. Mature eggs in a gravid ♀ *A. peggyae*; Lake Talquin, 20 July 1963. e, egg; n, nutrient matter.

TABLE 5. Seasonal events in the male germinal cycle in 4 species of *Anodonta* from North America.

		Peak occurrences		
Species	Locality	Typical spermatogenesis	Mature spermatozoa	Sperm-morulae
A. couperiana	Myakka River	Aug.—Sept.	Sept.	Dec.—July
A. gibbosa	Holmes Creek	Aug.	Sept.	Oct.—June
A. imbecilis	Lake Talquin	June—Nov.	year-around	irregular
A. peggyae	Lake Talquin	March—April,	May—June,	July—Aug.,
	Lake Talquin	July—Sept.	Oct.—Feb.	irregular
	Holmes Creek	April—Sept.	Oct.—Feb.	irregular

within the more extensive single period in Holmes Creek animals, but only the second period of spermatozoan and sperm-morular abundance in Lake Talquin coincided with the single one in Holmes Creek. The bimodal activity exhibited within the Lake Talquin population was not associated with differences in the ages of the animals, and was not related to differences between males (80 specimens) and ♂ hermaphrodites (only 1); it instead reflected 2 consecutive breeding cycles per year (see p. 96).

Bloomer's (1946) inference that in *A. cygnea* the sperm-morulae metamorphosed into mature spermatozoa was based on the observed disappearance of sperm-morulae just prior to the appearance of large numbers of spermatozoa (temporal occurrence of typical spermatogenesis not cited). This sequence was not observed here in *A. couperiana* and *A. gibbosa* (cf. Table 5). The evidence is less clear in *A. imbecilis* and *A. peggyae*, but it may be that in the animals of these 2 species the comparatively few

sperm-morulae found rapidly metamorphosed into spermatozoa independently of the season.

A comparison of the seasonal male germinal cycle in *A. gibbosa* and *A. peggyae* from Holmes Creek, and in *A. imbecilis* and *A. peggyae* from Lake Talquin, showed that these congeneric species were not simultaneously and identically synchronized with, or influenced by, environmental influence on gonad activity. The cycle in Holmes Creek was much more seasonally limited in *A. gibbosa* than in *A. peggyae*, and in Lake Talquin there was 1 cycle per year in *A. imbecilis* but 2 cycles per year in *A. peggyae*.

Oögenesis

The comparative state of ovarian activity was classified into several arbitrary categories: spent or seasonally inactive, early oögenesis (a few oögonia and much nutritive matter; Fig. 15), "intermediate" oögenesis (primary oöcytes and some nutritive matter; Fig. 16) and mature eggs[11] (primary oöcytes [?] only, nutritive matter vanished; Fig. 17).

Anodonta couperiana females from the Myakka River were inactive in January, showed early oögenesis in March, May and July, displayed intermediate oögenesis and mature eggs in September, and were spent in November. In the Apalachicola River population, females and the single ♀ hermaphrodite showed early oögenesis in early August; the females were spent in mid-November.

No females of *A. gibbosa* were found between mid-May and early October, and only inactive ovarian tissue occurred in the samples from the remaining months. The absence of mature eggs for most of the year coincided with the preponderance of sperm-morulae and lack of spermatozoa for much of that period.

In *A. imbecilis* from Lake Talquin, only the intermediate oögenic stage and mature eggs were found. Each occurred throughout the year in the ovarian tissue of both females and ♀ hermaphrodites, although there appeared to be a slight preponderance of mature eggs from December into March in members of the 2 sexual conditions. The Gantt Lake animals, available in fewer collections, coincided in ovarian activity with those from Lake Talquin.

Based on the seasonal sequence of spermatogenesis and larval development (see next section), it is concluded that Lake Talquin animals of *A. peggyae* underwent 2 reproductive cycles per year. However, although displaying only intermediate oögenesis and mature eggs throughout the year, females of that population showed a slightly greater activity in only 1 period: January into February. In *A. peggyae* from Holmes Creek, with just 1 reproductive cycle per year, intermediate oögenesis and mature eggs also occurred at all times; a slight peak in abundance appeared from late December into April.

The Incubation Period

Gravid animals in *Anodonta* have long been reported to exhibit a prolonged, bradytictic period of incubation, and sometimes to show a non-gravid interval between consecutive, annual breeding cycles (cf. Table 6).

Anodonta cataracta Say (Conner, 1907; Ortmann, 1909, 1912), *A. corpulenta* (Surber, 1912), *A. grandis* Say (Baker, 1928; Van der Schalie, 1938) and *A. implicata* Say (Conner, 1909) were found to have, during the Nearctic summer, a short but distinct non-gravid interval between consecutive "breeding seasons." In comparison, Baker (1928) and Van der Schalie (1938) reported the occurrence of gravid animals of *A. imbecilis* throughout the year, this species apparently lacking a non-gravid interval. Non-gravid animals of *A. cygnea* were reported only in July (Bloomer, 1930-1939), and the data may not be complete. *A. anatina* was reported to be gravid in July through December in England (Bloomer, 1936), and either this species has a comparatively long non-gravid interval, or the observations are perhaps again incomplete.

All of these reports concern only the seasonal presence of gravid animals, and such information does not reveal the number of

[11] Lillie (1901) demonstrated that in *Elliptio complanatus* (Dillwyn) [Unionidae: Pleurobeminae *sensu* Heard & Guckert (1971)] diploid primary oöcytes and not mature haploid ova were released from the ovaries, and that reduction-division of these cells did not occur until after sperm penetration (in the marsupial demibranchs). Because it is presently unknown whether this phenomenon is universal in the Unionidae, the most mature cells in the sections of ovarian tissue studied here will be referred to simply as "eggs."

TABLE 6. Known gravid periods in 13 species of *Anodonta* (from Baker, 1928; Bloomer, 1934, 1935, 1936; Conner, 1907, 1909; Ortmann, 1909; Surber, 1912; Van der Schalie, 1938; present observations).

Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
A. anatina							X	X	X	X		X
A. californiensis										X		
A. cataracta	X	X	X	X	X	(. . . interval[a] . . .)			X	X	X	X
A. corpulenta	X	X	X	X	(. . . . . interval[a] . . . . . .)					X	X	X
A. couperiana											X	
A. cygnea	X	X	X	X	X	X		X	X	X	X	X
A. gibbosa										X		X
A. grandis	X	X	X	X	(. . interval[a] . . . .)			X	X	X	X	X
A. hallenbeckii										X	X	X
A. imbecilis	X	X	X	X	X	X	X	X	X	X	X	X
A. implicata	X		X	X	X	(. . . interval[a] . . .)			X	X	X	X
A. peggyae	X	X	X	X	X	X	X	X	X	X	X	X
A. wahlamatensis										X		

[a]Interval, called "interim" by various authors, represents a non-gravid period between 2 consecutive reproductive cycles.

breeding cycles within a year. For instance, whereas *A. imbecilis* was found by Baker (1928) and Van der Schalie (1938) to be gravid throughout the year, Allen (1924) reported not just one but several reproductive cycles per year in that species.

In addition to recording the observed occurrences of gravid animals of *A. californiensis, A. corpulenta, A. couperiana, A. gibbosa, A. hallenbeckii, A. imbecilis, A. peggyae* and *A. wahlamatensis* in the present study (cf. Table 6), the incubating young in each of these animals were identified according to their comparative state of development (morphological stages described in next section).

The presence of gravid animals of *A. couperiana* and *A. gibbosa* only in the fall and winter suggests a "winter-tachytictic" breeding season hitherto unreported in the Unionidae. The indication of such a phenomenon is more reliable from *A. couperiana* (52 gravid Myakka River animals, all in November, among a total of 372 specimens examined from all 6 collections) than from *A. gibbosa* (12 of only 18 females were gravid: October and December). However, all gravid animals of both species contained only mature larval stages; no embryos or earlier larvae were found, and the rates of development and the more precise duration of incubation are not accurately known. Nevertheless, the seasonally confined occurrences of mature spermatozoa in both species (cf. Table 5) point to an autumnal period of fertilization, and thus suggest a rapid rate of larval development.

The presence of gravid Lake Talquin animals of *A. imbecilis* in all collections confirmed Baker's (1928) and Van der Schalie's (1938) earlier reports. Embryos appeared in March to May, early larvae from June to September, intermediate larvae in September to December, and mature larvae in January and February. This seasonal sequence, alike in the fewer Gantt Lake collections, seems to refute (at least for these populations) Allen's (1924) claim of several very short breeding cycles per year in this species. Nevertheless, the peculiar phenomenon of large numbers of mature eggs and sperm throughout the year in Lake Talquin (cf. Table 5) suggests that, although these gametes may not be chemically/physiologically differentiated or viable at certain seasons in that population, these cells may be functional during several consecutive periods per year in other populations (perhaps especially in other latitudes, Allen's study having been conducted in Iowa). Individuals of these other populations might thus undergo more than one reproductive cycle in a year. Such variation was found here in *A. peggyae* (see below). Seasonal investigation of gravid and non-gravid females and ♀ hermaphrodites of *A. imbecilis* revealed that there were no significant variations in gravid periods and developmental stages of incubating young between the Lake Talquin and Gantt Lake populations. Similarly, it was found that once the age of sexual maturity[12] was reached there was no significant variation in these features between animals of different age classes, re-

[12]"Sexual maturity" is defined here in terms of age when first gravid, rather than in terms of gonad development and activity (see p. 92-94).

gardless of whether the individuals were females or ♀ hermaphrodites.

Anodonta peggyae was gravid throughout the year in both populations. However, whereas the Holmes Creek animals displayed 1 breeding cycle in the year, the Lake Talquin individuals had 2. The latter group showed these 2 cycles both in terms of seasonal spermatogenesis (cf. Table 5) and comparative stages of embryonic and larval development. Gravid females undergoing one cycle contained embryos in March, early larvae in April, intermediate larvae in May and June, and mature larvae in July and August; those in the subsequent cycle contained embryos in September and October, early and intermediate larvae in November and December, and mature larvae in January and February. One individual from the September collection contained both embryos and mature larvae; all other gravid animals, in all species, contained only one developmental stage at a time, and most animals from the same month carried the same stage. In contrast to the Lake Talquin population, the gravid Holmes Creek females undergoing a single breeding cycle in the year contained embryos in March into July, intermediate larvae in August into December, and mature larvae in January and February.

Although there were differences in the number of breeding cycles per year between the Holmes Creek and Lake Talquin populations of *A. peggyae*, breeding cycles may not be influenced entirely by such conspicuous environmental factors as water temperature and the presence or absence of current because there were also such differences between the Lake Talquin populations of *A. imbecilis*, with 1 cycle per year, and *A. peggyae* with 2 cycles per year (see Tables 5 and 6).

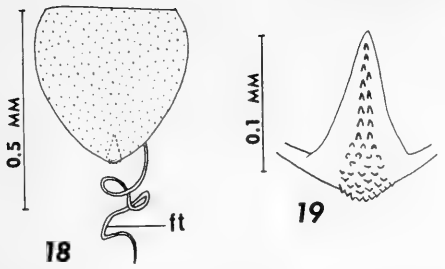
Seasonal observations were not possible for *A. californiensis*, *A. corpulenta*, *A. hallenbeckii* and *A. wahlamatensis*, although the presence of gravid animals of these species is noted in Table 6. *Anodonta californiensis* and *A. wahlamatensis* carried intermediate larvae in October, and *A. hallenbeckii* contained only mature larvae in late October, November and early December. The November animals of *A. corpulenta* were discarded before the development stage of incubating young could be made.

GLOCHIDIA

Glochidia, i.e., the mature and infective larvae, in *Anodonta* have been described and illustrated by Tucker (1927) and Bouillon (1955), among others, but most thoroughly by Inaba (1941). The subtriangular shell is punctated (Fig. 18), and the ventrally situated hooks bear numerous small spines (Fig. 19). Triangular, hooked glochidia are a feature of all species of the Anodontinae (Ortmann, 1912), although the prominent hooks are not a unique characteristic of this group of unionaceans, also occurring on the glochidia of some amblemids (at least the Indian species of *Indonaia* Prashad; cf. Prashad, 1918) and throughout the Hyriidae (Ortmann, 1921; McMichael & Hiscock, 1958; Parodiz & Bonetto, 1963), as well as in some species of the Unionidae: Unioninae s. s. (Ortmann, 1912, 1918). Another feature of the glochidia of many if not all species of *Anodonta* is the late appearance of a larval "thread" or "filament" (called a byssal thread by Bouillon, 1955); whether it occurs in other groups of the Anodontinae is not known.

The developmental continuum of incubating young observed in the present study was divided into several arbitrary stages in order to assist in determining the season of fertilization, the incubation period, the season of glochidial discharge and the number of broods generated per year. *Embryos* included those individuals from the zygote to the distinct appearance of the single adductor muscle, before the formation of the rudimentary shell; *early larvae* were characterized by the presence of a shell that lacked punctae and hooks; *intermediate larvae* possessed a punctated shell with only rudimentary hooks; and *mature larvae*, i.e., *glochidia*, displayed a punctated shell with well developed and spined hooks, as well as larval thread, and had broken free from the fertilization membrane that surrounded the individuals of the previous stages.

The seasonal observations indicate that in *A. couperiana* and *A. gibbosa* fertilization occurred in the late summer, and the short incubation period may not extend over the entire winter. In *A. imbecilis* and *A. peggyae* (Holmes Creek only, with 1 reproductive cycle per year), fertilization occurred in late winter, and the long incubation period lasted



FIGS. 18-19. Glochidial features of *Anodonta gibbosa*. FIG. 18. Mature larva, with filament-thread (ft) and punctated, subtriangular, ventrally hooked shell. FIG. 19. Ventral surface of spined hook.

until the following late winter. In the Lake Talquin population of *A. peggyae*, with 2 cycles per year, one fertilization occurred in the early spring, and incubation lasted until mid-summer; the second fertilization occurred in late summer, with incubation lasting until late winter. A search for mature glochidia in species of *Anodonta* in the southern United States should thus be made during the winter season, i.e., November-February.

In all species investigated here, the dorsal margin of the glochidial shell was straight, or nearly so, and its length was less than the total length which was found slightly above the middle of the valves (cf. Fig. 18). Inaba (1941) reported the sizes of the glochidial shells in *A. beringiana* Middendorff (0.296 mm total length × 0.296 mm high), *A. japonica* Clessin (0.258 × 0.232), *A. woodiana calipygos* Kobelt (0.298 × 0.297), *A. woodiana lauta* von Martens (0.303 × 0.268) and *A. "woodiana lauta tumens* Haas" (0.296 × 0.258), and in most of these species the total length was greater than the height. That relationship was found here only in *A. hallenbeckii* (0.285 × 0.266) and *A. peggyae* (0.261 × 0.256); the height exceeded the total length in *A. couperiana* (0.294 × 0.336), *A. gibbosa* (0.378 × 0.399) and *A. imbecilis* (0.228 × 0.233). The glochidia of *A. gibbosa* are the largest, and those of *A. imbecilis* the smallest, among those of all 10 taxa. The same relationship was found for the size of the hooks: 0.084 mm long in *A. couperiana*, 0.126 in *A. gibbosa*, 0.099 in *A. hallenbeckii*, 0.062 in *A. imbecilis* and 0.095 in *A. peggyae*.

There was no variation in the relative number or location of the punctae, none in the size and number of spines on the hooks[13], and apparently none in the nature of the larval thread among the glochidia of the different species studied here. Although the larval thread was loosely coiled, its comparative length could not be determined with confidence. There was also no difference in size or proportions between glochidia of the 2 populations of *A. peggyae*, and none between these larvae in females and ♀ hermaphrodites of both populations of *A. imbecilis*.

No metamorphosed glochidia, i.e., juveniles, were found in the marsupial demibranchs of *A. imbecilis* or the other species surveyed here.

AGE OF SEXUAL MATURITY AND LIFE SPAN

Van der Schalie & Locke (1941) concluded that animals of *A. grandis* form *footiana* did not become "sexually mature" until they had reached their second year of growth. In that instance, sexual maturity was defined in terms of gonad development while identifying the visceral sex of the animals.

In characterizing the Anodontinae, Stansbery (1967) reported that the mussels of this group ". . .are typically rapid growing, early maturing species having a relatively short life span. The extreme of this group in Lake Erie [Ohio, U.S.A.] is apparently *Anodonta imbecilis* Say, which matures in its second year but rarely lives to be 5 years of age." The criterion of maturity was not described in this example; the life span was estimated by counting the annuli on the shell.

Table 7 shows the age at the earliest observed sexual maturity (gravidity criterion) in animals of 15 populations representing 8 species. The number of annuli present in the youngest gravid animals ranged from 3 to 5 (4-6 years of age). This observation suggests that species of *Anodonta* mature at a greater age and state of growth than that reported by Stansbery (1967) for *A. imbecilis*. Although, as previously noted, there was no significant seasonal difference in the gravid periods of females and ♀

[13]The spines, correctly depicted by Inaba (1941), were directed medially, and clearly do not act as barbs to anchor the glochidium against dislodging. Although they would make penetration of the hooks more difficult, they might serve to further lyse the host tissue to stimulate cyst formation, and perhaps initiate rapid supply of nutrients.

TABLE 7. Ages of youngest gravid animals and observed life span in 8 North American species of *Anodonta*. Age in years = number of annuli + 1.

Species	No. of annuli in youngest gravid	No. of annuli in oldest animals			
			Hermaphrodites		
		Males	♂	♀	Females
A. californiensis	4[a]	4		2[b]	4
A. corpulenta	5	7			7
A. couperiana					
Myakka River	4	9			12
A. gibbosa	5[c]	15			15
A. hallenbeckii	4	13			15
A. imbecilis					
females					
Lake Talquin	5				12
Gantt Lake	4				8
hermaphrodites					
Lake Talquin	4			8	
Gantt Lake	3			9	
A. peggyae					
Lake Talquin	4	10	6		14
Holmes Creek	5	10	8		10
A. wahlamatensis	8[d]	9			10

[a]The only female in the collection.
[b]Non-gravid.
[c]Collections contained total of 2 non-gravid females with 4 annuli; none younger.
[d]Youngest animal available was a male with 6 annuli.

hermaphrodites of *A. imbecilis*, the majority of the youngest gravid animals were monoecious.

Also listed in Table 7 are the observed maximum numbers of annuli on the shells of the animals examined here. These values for most species varied between 7 and 15 (8-16 years in age[14]); the shells of *A. californiensis* were much smaller (and younger?) than those in museum collections. Animals of the southern (Florida, Alabama) populations of *A. imbecilis* lived longer than the northern one (Ohio) described by Stansbery (1967). Whereas there was little difference in the observed greatest ages between ♀ hermaphrodites of both populations of *A. imbecilis*, the females from Lake Talquin apparently lived 4 years longer than the hermaphrodites (and 4 years longer than the Gantt Lake females). A similar relationship occurred in *A. peggyae*, with no difference in the maximum age attained by males and females in the Holmes Creek population, and none between males from Lake Talquin and Holmes Creek; Lake Talquin females lived 4 years longer than Holmes Creek females, and 4 years longer than the males of both populations. There was no difference in the greatest ages between males and females of *A. californiensis*, *A. corpulenta* and *A. gibbosa*, and but little difference between those of *A. wahlamatensis*. Females survived longer than males in *A. couperiana* (by 3 years in the Myakka River) and *A. hallenbeckii* (by 2 years; composite values from all populations). In *A. peggyae* (both populations), the ♂ hermaphrodites were not as old as either the males or females. The ages of none of the animals of *A. couperiana* from the Apalachicola River could be determined with confidence, but there was no significant difference between the sizes of the females, ♀ hermaphrodite and ♂ hermaphrodites (males were lacking).

It must be noted, however, that relatively few younger and older animals were found during this study, and the data on earliest gravidity and greatest age may be incomplete. Furthermore, these features may not be species-specific, perhaps varying intraspecifically.

Even the oldest animals of all species displayed active gametogenesis (many with mature gametes, depending on the season), and most of the oldest females and ♀ hermaphrodites were gravid. These findings suggest the absence of a post-reproductive (or senility) period, mentioned by Stansbery

[14]Bouillon (1955) claimed a life span of 20-30 years in European species of *Anodonta*, none of which were identified by name.

(1967) as a feature of the Unionidae: Lampsilinae, as well as a potentially longer life span within the population.

SEXUAL DIMORPHISM OF THE SHELL

The possibility of sexual dimorphism of the shells of *Anodonta* was investigated by von Siebold (1837) and Weisensee (1916) for *A. cygnea* and by Hazay (1881) for *A. anatina*. It was concluded that females were significantly wider than males. Inasmuch as total length is often used as an index of size, Brummer (1932) and Brander (1954) employed the ratio of D:L (i.e., "diameter" [= width] to total length) in reporting dimorphic shell differences between males and females of *A. complanata* Rossmässler and *A. piscinalis* Nilsson. These investigations utilized size-frequency polygrams rather than statistical tests.

In the present study, mean sizes (based on width/total length X 100) of shells of individuals of different age classes and sexual conditions in *A. couperiana, A. gibbosa, A. imbecilis* and *A. peggyae* were determined, and the *t*-test for correlated means (cf. Snedecor & Cochran, 1967) was employed to assess the values. At the 5% rejection level, there was no statistically significant difference in size between the males and females of *A. gibbosa*, and none between females and ♀ hermaphrodites of *A. imbecilis* (Lake Talquin). Myakka River females of *A. couperiana* were significantly larger than males. The similarities and differences were constant for animals common to each age class; the same relationship was also found for *A. peggyae*.

In the Holmes Creek population of *A. peggyae*, there was no significant difference in size between males and females, and none between ♂ hermaphrodites and females, although the ♂ hermaphrodites were larger (though younger) than males. In contrast, Lake Talquin females were significantly larger than males. Also, Lake Talquin males and females were significantly larger than Holmes Creek males and females, respectively.

Although some sexual dimorphisms were found in the shells of *Anodonta*, none were of the conspicuous type well known in the Unionidae: Lampsilinae, in which the posterior part of the female shell is expanded in size and shape. Sexual dimorphism in *Anodonta* shells can be determined only by measurement and statistical testing.

DISCUSSION OF HERMAPHRODITISM

Glandular Differentiation

Pelseneer (1895) listed 4 "morphological forms" of hermaphroditism: (1) gonads with monoecious acini in which both eggs and sperm are produced, (2) gonads with intermingled zones of male and female acini, (3) gonads with male and female acini in regionally distinct and separate zones, and (4) distinct and separate male and female gonads in the same individual. A survey of Van der Schalie's (1970) recent report, and the present findings, indicates that the majority of the known hermaphroditic unionids belong to the first 2 categories, and it suggests that most of the monoecious animals are ♀ hermaphrodites (cf. Table 8).

The present study revealed that the ♂ hermaphrodites of *A. couperiana, A. hallenbeckii* and *A. peggyae*, as well as the ♀ hermaphrodites of *A. californiensis* and *A. couperiana*, were of Pelseneer's 2nd type, displaying intermingled dioecious acini. Only the ♀ hermaphrodites of *A. imbecilis* showed the regional differentiation of the 3rd type. Truly monoecious acini, reported in *A. corpulenta* by Van der Schalie (1970), were not found here.

Although he did not find monoecious acini in *A. cygnea*, Bloomer (1934), in his concept of sex-reversal in this species, suggested that acini containing sperm-morulae would subsequently be occupied by eggs. Should this type of transformation be documented, *A. cygnea* would exhibit an "asynchronous successive hermaphroditism" (cf. Bacci, 1951; Portmann, 1960) which, according to Pelseneer (1894), is a more primitive condition than that of "functional hermaphroditism" in which eggs and sperm are produced simultaneously.

Van der Schalie (1969, 1970) noted that in most hermaphroditic unionids one type of gonadal tissue was in a more advanced state of development and activity than the other, and that functional hermaphroditism was observed only in *Actinonaias ellipsiformis, Carunculina parva, Villosa iris* (all Lampsilinae) and *Anodonta imbecilis*. Functional hermaphroditism was verified here for *A. imbecilis*, and it was found that the eggs in ♂

TABLE 8. List of unionids displaying the monoecious states distinguished by Pelseneer (1895). Data drawn from Van der Schalie (1969, 1970: legends to photomicrographs) and the present study.

1. Hermaphroditic acini

Actinonaias ellipsiformis (Conrad)[a]
Alasmidonta marginata (Say)[a]
Anodonta corpulenta Cooper[a]
Carunculina parva (Barnes)[a]
Elliptio dilatatus (Rafinesque)[a]
Lasmigona complanata (Barnes)[a]
Lampsilis cariosa (Say)
Ptychobranchus subtentum (Say)[a]
Villosa iris (Lea)[a]

2. Intermingled zones of ♂ and ♀ acini

Anodonta californiensis Lea[a]
Anodonta couperiana Lea[a + b]
Anodonta grandis f. *footiana* Lea[b]
Anodonta hallenbeckii Lea[b]

2. (continued)

Anodonta peggyae Johnson[b]
Elliptio productus (Conrad)[b]
Lasmigona compressa (Lea)[a]
Leptodea laevissima (Lea)[a]
Pleurobema cordatum (Rafinesque)
Pleurobema c. coccineum (Conrad)[a]
Proptera alata (Say)[a]
Ptychobranchus fasciolaris (Raf.)[a]
Strophitus rugosus (Swainson)[b]

3. Regionally distinct and separate ♂ and ♀ acini

Anodonta imbecilis Say[a]

4. Separate ♂ and ♀ gonads in the same individual: none.

[a]Gravid or non-gravid, but with principally ovarian tissue; known or probably ♀ hermaphrodites.
[b]Non-gravid, and with principally testicular tissue; known or probable ♂ hermaphrodites.
*Members of the subfamily Anodontinae Ortmann.

hermaphrodites of *A. peggyae* were always smaller (= "poorly developed" or "suppressed" *sensu* Van der Schalie?) than those in females collected at the same time. However, observations on the monoecious animals of the other species is less conclusive. In *A. californiensis* and *A. couperiana* only sperm-morulae and early oögenesis were simultaneously present in the hermaphrodites, whereas in *A. hallenbeckii* both testicular and ovarian tissues were inactive in the single ♂ hermaphrodite.

Significance of Hermaphroditism

The known monoecious conditions in *Anodonta* do not coincide with conchological subgeneric groupings, although verification of these taxa as natural units is needed. However, the presence of hermaphroditism in various other unionaceans suggests that its occurrence, in its different forms, does not reflect phylogeny. Other explanations of the monoecious state have considered hermaphroditism to be an adaptation to environmental conditions.

Weisensee (1916) stated that in *A. cygnea* a dioecious relationship occurred in streams, whereas increased proportions of hermaphrodites appeared in standing waters. Unionids are, in general, stream- rather than lake-dwellers, and animals from lakes are typically smaller than animals of the same species from streams. A number of exceptions are known, however, including species of *Anodonta* which survive very well in standing water and not infrequently reach larger sizes in such environments.

Two populations of *A. peggyae* were studied here, one from a lotic environment (Holmes Creek) and one from a lentic environment (the Lake Talquin impoundment). The proportions of *male* hermaphrodites are in contrast to Weisensee's conclusion of ecological adaptation: the Lake Talquin population had a smaller proportion of monoecious animals (0.8%) than did the Holmes Creek population (9.8%). Both populations of *A. imbecilis* were from impoundments, and whether the proportion of the *female* hermaphrodites in a stream environment would be lower or higher than those observed here (48.5% in Lake Talquin; 58.5% in Gantt Lake) is not known.

Species of *Anodonta* have been referred to by Baker (1928) and others as "floaters" because these thin-shelled and thus comparatively light-weight animals can float in the water if an adequate amount of air becomes trapped between the valves. This phenomenon might be an adaptation to dispersal, especially if an individual was a ♀ hermaphrodite that had the capacity to self-fertilize and consequently serve as the beginning of a new population (assuming the presence of a suitable host for the glochidia). Nevertheless, such an event would not be advantageous unless it occurred in a stream.

According to Cole (1954:104), "Parthenogenesis, hermaphroditism and purely asexual reproduction may clearly offer some advantages under conditions that restrict the probability of contacts between the sexes." However, it may be noted that internal fertilization, even without copula-

tion, requires close proximity of members of a breeding population.

Ghiselin (1969), in reviewing hermaphroditism in parazoans and metazoans (freshwater mussels briefly noted on p. 98), stated that hermaphroditism "should" evolve under one or more of the following conditions: difficulty in finding a mate (for which a low density model was presented), beneficial size dimorphism between different sexes (size advantage model), and occurrence of small, genetically isolated populations (gene dispersal model). Too little information on unionid population dynamics is presently available for the use of any of these models in definitively interpreting the occurrence and nature of hermaphroditism in *Anodonta*.

Finally, Van der Schalie (1969) suggested genetic, hormonal or cytogenetic controls as reasons for the occurrence of hermaphroditism in its variable manifestations, but the nature of such possible mechanisms (if present) has yet to be investigated.

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INTRASPECIFIC VARIATIONS IN THE HEMOLYMPH OF *BIOMPHALARIA GLABRATA*, A SNAIL HOST OF *SCHISTOSOMA MANSONI*[1]

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ABSTRACT

An attempt was made to characterize the hemolymph of *Biomphalaria glabrata* with reference to "normal" intra-specific variation, i.e., both inter- and intra-strain differences. Total protein concentration, per cent hemoglobin, pH, and osmolality were studied. Seven geographic strains of *B. glabrata* were examined. In addition, observations were made on the hemolymph of *Biomphalaria straminea*, several strains of *Helisoma caribaeum*, and on *B. glabrata* subjected to infection with *Schistosoma mansoni* or to periods of starvation.

Intra-strain differences in total protein concentration and total hemoglobin concentration in *B. glabrata* appeared to be more closely related with snail size than with absolute age. Inter-strain variation in *B. glabrata* was also noted, but the differences were of the same magnitude as those from intra-strain samples. Significant differences in total protein concentration were observed, however, between the means of similar size *B. glabrata, B. straminea* and *H. caribaeum*.

The osmolality of the hemolymph from different size *B. glabrata* was similar as were the osmolalities of the hemolymph from similar size snails of different strains. However, all *B. glabrata* strains exhibited hemolymph osmolalities lower than observed in strains of *H. caribaeum*.

Infection with *S. mansoni* reduced the protein concentration of *B. glabrata* hemolymph. Differences were noted as early as 1.5-24 hr post-infection, with significant alterations occurring at about 11 days post-infection. To a lesser extent, starvation also depleted the protein content of the hemolymph.

INTRODUCTION

The hemolymph of *Biomphalaria glabrata*, and of other snails serving as hosts of schistosomes, has been subjected to considerable study (for literature see Michelson, 1966a). Until recently (Lee & Cheng, 1972), however, there has been a paucity of information with respect to "base-line" values of the various constituents of hemolymph or for its physico-chemical properties. Moreover, variations in amino acid composition and serologic activity of the hemolymph occur among geographic strains of *B. glabrata* (Gilbertson, Etges & Ogle, 1967; Gilbertson & Etges, 1967). Snails infected with *Schistosoma mansoni* also exhibit alterations in the composition and electrophoretic mobility of their hemolymph (Targett, 1962; Dusanic & Lewert, 1963; Pan, 1965; Gilbertson et al., 1967; Cheng & Lee, 1971).

We sought, therefore, to characterize the hemolymph of *B. glabrata* with reference to "normal" intra-specific variation, i.e., both inter- and intra-strain differences. Total protein concentration, per cent hemoglobin, pH, and osmolality were studied. In addition, observations were made on the hemolymph of *Biomphalaria straminea*, several strains of *Helisoma caribaeum*, and on *B. glabrata* subjected to infection with *S. mansoni* or to periods of starvation.

MATERIALS AND METHODS

Snails

Seven strains of *B. glabrata* were used: 2 from Puerto Rico (PR-1, PR-2), 4 from Brazil (BH, B-1, B-2, S-3), and a Puerto Rican-Brazilian hybrid (PR/B). Two of the strains (BH, PR/B) were albino. A Brazilian

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strain of *B. straminea*, and 3 strains of *Helisoma caribaeum* from Puerto Rico (257) and the Virgin Islands (CB, DB) were used in some studies. All the strains of *Biomphalaria* were susceptible to *Schistosoma mansoni* indigenous to the areas from which the snails originated. Except for *B. glabrata* (S-3) and *B. straminea*, the strains of *Biomphalaria* were also susceptible to our laboratory strain of Puerto Rican *S. mansoni*. The origin and maintenance of the snails have been described (Pan, 1965; Michelson, 1966b).

Intra-strain variations were studied in PR-1 snails, a strain of *B. glabrata* maintained in our laboratory for more than 15 years. The effect of size was examined in snails 6-9, 12-15, and 18-21 mm in diameter. Snails of similar age but of different size, and snails of similar size but of different age, were obtained by manipulating the density of the colony (Chernin & Michelson, 1957).

Infected *B. glabrata* were obtained by mass-exposing 30-35 snails, in 100 ml of water, to 350-500 *S. mansoni* miracidia. Snails were considered infected only if mother sporocysts were visible in their tissues or if cercariae emerged. When snails were used within a few hours or days of exposure, they were controlled by a replicate group, similarly exposed, and examined 14 days after exposure by the Chernin-Dunavan technique (1962).

For studies on the effects of starvation, 60 PR-1 snails (12-15 mm) were kept in a 5 gallon aquarium and fed romaine lettuce daily for 1 week. Fifteen snails, considered to be well-fed, were removed, bled, and their hemolymph tested to establish base-line values. The remainder of the snails were kept without food and groups were removed for bleeding after periods of 1, 7, and 14 days.

Determination of Total Proteins and Total Hemoglobin

Individual snails were bled as previously described (Chernin, 1963; Michelson, 1966b). The total hemolymph protein was estimated colorimetrically with the Folin-Ciocalteu phenol reagent (Kabat & Mayer, 1961). Each test required 5-20μl of hemolymph from individual snails, and samples were diluted with 2 ml of distilled water before use. Samples were examined with a spectrophotometer at 640 mμ and the optical densities compared with a calibrated curve prepared from standards of commercial crystallized bovine albumin. When we compared the technique with a micro-Kjedahl method (Williams & Chase, 1968), values varied from 5-8% lower.

A cyanmethemoglobin method (Clinical Methods Manual, Spectronic 20, Bausch and Lomb Co., 1965), employed to determine total hemoglobin, required 20μl of hemolymph from individual snails. Acuglobin(R) (Ortho Diagnostics), a commercial standard, served as control.

Values for total protein and total hemoglobin are expressed as grams per 100 ml of hemolymph.

pH Determinations

The pH of hemolymph from individual snails was determined by a Radiometer pH Meter 27 equipped with a E5021 micro-electrode unit (Radiometer A/S, Copenhagen). A minimum sample of 50μl was collected directly from the snail's pericardium into the micro-electrode and measured immediately.

Osmolality

Osmolality of the hemolymph was measured with a calibrated Wide Range Osmometer (Advanced Instruments Inc.). Since approximately 0.25 ml of hemolymph was required for each test, hemolymph was pooled from 2-4 of the larger snails and from 20 snails of the 6-9 mm group. Snails were bled after being air-dried, on paper toweling, for 30 min. A standard drying period was critical, since osmolality increased as the drying time lengthened. Samples of aquarium water were tested at the time snails were removed for bleeding.

RESULTS

Total Protein Concentration (TPC) and Total Hemoglobin Concentration (THC)

Intra-strain variation, associated with snail size but not age, was noted in the mean TPC of the PR-1 strain of *B. glabrata* (Fig. 1). Mean TPCs (in gm/100 ml) and their standard deviations were 0.90 ± 0.23, 1.62 ± 0.49, and 1.43 ± 0.42, for 6-9, 12-15, and 18-21 mm snails respectively. Differences between the mean TPC of the 6-9 mm group and the means of the other 2 groups were statistically significant ($P = < .001$).

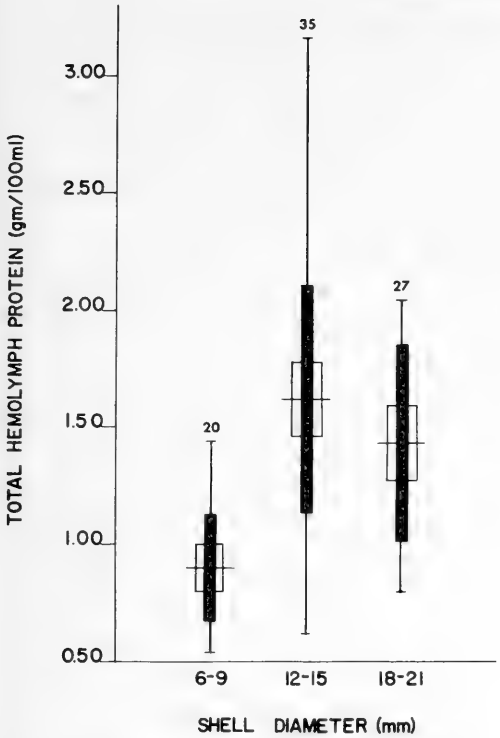

FIG. 1. Intra-strain variation of total hemolymph proteins from PR-1 *Biomphalaria glabrata.* In each size-group the thin vertical line represents the total variation of the samples; the broad portion of the line, one standard deviation on each side of the mean; the hollow rectangle, twice the standard error on each side of the mean; and the cross-bar, the mean. Numerals above each group represent the number of samples tested.

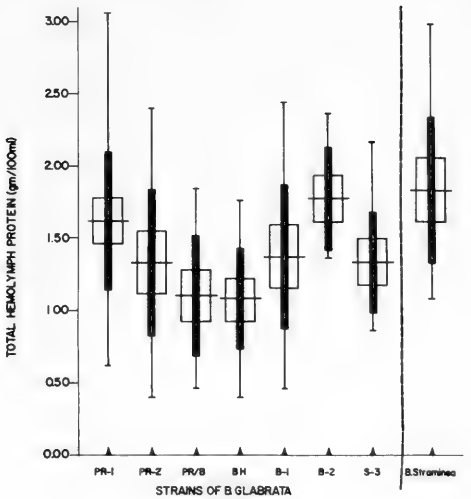

FIG. 2. Inter-strain and interspecific variation in total hemolymph proteins. All hemolymph samples were from 12-15 mm snails except those from *B. straminea,* which were from 6-9 mm snails. Thirty-five samples were tested from PR-1 snails, 20 samples from all others. Explanation of the diagram follows that given for Fig. 1.

The mean TPC of individual 12-15 mm snails was similar to those obtained by Chernin (1963) from pooled samples of hemolymph.

When snails of the same age (10 wks) but of different size (6-9 mm versus 12-15 mm) were tested, the larger snails again had a greater TPC (mean = 1.63 ± 0.40) than did the smaller (mean = 0.99 ± 0.28). Snails of similar size (12-15 mm) but of different ages (10 and 14 wks) had essentially the same mean TPCs (1.66 ± 0.38 and 1.61 ± 0.45 respectively).

B. glabrata from different geographic areas, all 12-15 mm, varied in mean TPC (Fig. 2). Except for strain B-2 (mean TPC = 1.77 ± 0.36), all strains had lower TPCs than the PR-1 strain. The lowest TPCs occurred in the 2 albino strains, PR/B and BH (mean = 1.10 ± 0.42 and 1.08 ± 0.35 respectively). The Puerto Rican strain studied by Gilbertson et al. (1967) had a higher TPC (2.08) than any we observed. The strain studied by Lee & Cheng (1972), possibly the same as our PR/B strain, had a TPC (1.23) comparable to our findings.

Although *B. straminea*, under natural conditions, may approach 15 mm diameter (Pan American Health Organization, 1968), snails from our laboratory colony seldom exceeded 9.5 mm. When strains of *B. glabrata* (12-15 mm) were compared with 6-9 mm *B. straminea*, the mean TPC of *B. straminea* exceeded that of any strain of *B. glabrata*, but not always at a significant level. However, when 6-9 mm *B. glabrata* (Figs. 1 and 2) were compared, the difference between the means was highly significant (*B. straminea* = 1.81 ± 0.51 and *B. glabrata* = 0.90 ± 0.23; P = < .001).

The TPCs of all 3 strains of *Helisoma caribaeum* were higher than in any strain or species of *Biomphalaria*. The mean TPCs for *H. caribaeum* were: DB (23 snails) = 3.55 ± 0.43; 257 (12 snails) = 3.05 ± 0.69; CB (12 snails) = 3.52 ± 0.59.

THC was determined only for the PR-1 strain, and considerable variation was noted among snails of the same size. The mean THC of 34 samples of hemolymph from individual snails 12-15 mm in size was 0.65 ± 0.23. Ten samples from 6-9 mm

snails and 15 samples for 18-21 mm snails had mean THCs of 0.39 ± 0.17 and 0.93 ± 0.28 respectively. Thus, hemoglobin represented 43% of the total hemolymph protein in 6-9 mm snails, 40% in the 12-15 mm snails, and 65% in the 18-21 mm snails.

pH Determinations

The pH of hemolymph from PR-1 snails 12-15 mm in diameter ranged from 7.62 to 7.90 (mean = 7.78 ± 0.09). In 18-21 mm snails, the pH ranged from 7.41 to 7.73 (mean = 7.59 ± 0.13). Twenty samples were tested from snails of each size group. The pH of the aquarium water, in which these snails were reared, was 7.31 at the time of sampling. Results from our individual samples were comparable to those of Chernin (1963) from pooled samples of hemolymph.

Osmolality

There appeared to be little difference in the osmolality of the hemolymph obtained from the PR-1 strain of *B. glabrata*, regardless of size, or from the various geographic strains of this species (Table 1). One strain of *H. caribaeum* (257) had a slightly higher mean osmolality, but did not differ appreciably from the strains of *B. glabrata*. Osmolality of the hemolymph did not appear to be influenced by the slight differences observed in the osmolality of the aquarium water, which was determined concurrently, in which the various strains were maintained.

TABLE 1. Osmolality of hemolymph from planorbid snails air-dried for 30 minutes.

Species and strains	No. samples and snails/ sample	Mean osmolality (mOsm/Kg)	Osmolality of aquarium water (mOsm/Kg)
Biomphalaria glabrata			
PR-1	3	114.2	8.5
6-9 mm	(20)		
12-15 mm	10 (2-4)	113.9±3.6	8.2-8.3
18-21 mm	11 (1-2)	116.7±6.4	8.8
B. glabrata			
PR-2	10 (3-4)	109.6±3.1	6.2
B. glabrata			
B-1	10 (3-4)	109.0±4.8	6.0-11.7
B. glabrata			
B-2	10 (3-4)	117.7±4.2	11.3-11.7
B. glabrata			
S-3	10 (3-4)	113.4±5.3	9.2-10.5
B. glabrata			
PR/B	10 (3-4)	109.9±5.3	9.0-14.0
B. glabrata			
BH	10 (3-4)	107.2±3.2	7.0
Helisoma caribaeum			
257	10 (3-4)	122.4±6.8	9.4-9.5

Starved and Infected Snails

Starved snails exhibited a gradual decrease in mean TPC (Table 2); however, differences between control and starved snails were not significant until the second week of starvation ($P = < .05 > .02$). Similarly, in snails infected with *S. mansoni* TPCs decreased significantly ($P = < .01$) at and after day 11 (Table 3).

In 5 samples from 12-15 mm cercaria-producing snails, infected for 41 days, the mean THC (0.72) was less than that of the controls. However, the hemoglobin increased from 40% to approximately 60% of the total hemolymph protein. In 7 snails infected for

TABLE 2. The effect of starvation on the total protein concentration of hemolymph from *B. glabrata* PR-1.

No. days snails starved	No. snails tested	Mean TPC (gm/100ml)
0 (control)	15	1.62 ± 0.49
1	15	1.48 ± 0.23
7	9	1.26 ± 0.33
14	12	1.05 ± 0.22

TABLE 3. The effect of *S. mansoni* infection on the total protein concentration of hemolymph from *B. glabrata* PR-1, 12-15 mm in diameter.

Time post-infection	No. individual samples	Mean TPC (gm/100 ml)
0 (control)	35	1.62 ± 0.49
1.5 hr*	20	1.42 ± 0.12
1 day**	20	1.13 ± 0.21
11 days	20	1.08 ± 0.20
20 days	6	0.53
39 days+	4	0.87
64 days+	19	0.48 ± 0.21

*Controls had an infection rate of 70% when crushed and examined 14 days post-infection.
**Controls had an infection rate of 95% when crushed and examined 14 days post-infection.
+Cercariae emerging.

16 days and reared in an aquarium with a water-pH of 7.33, the pH of the hemolymph was 7.54—essentially that of the controls.

DISCUSSION AND SUMMARY

In a given strain of *B. glabrata*, hemolymph from individual snails varied markedly in TPC and THC. This confirms, in part, the report of Gilbertson et al. (1967) on a Puerto Rican strain of *B. glabrata*. Cheng (1963, 1969) also noted variation in the TPCs of the hemolymph from 2 North American species of *Helisoma*. Intra-strain differences in TPC and THC in *B. glabrata* appeared to be more closely associated with snail size than with absolute age, suggesting the need to standardize size in studies of hemolymph. The failure of some workers to standardize the protein content of hemolymph from snails of different size has led to misinterpretations of electrophoretic patterns (Michelson, 1966a).

Inter-strain variation in TPC of *B. glabrata* was noted also, but these differences were of the same magnitude as those from intra-strain samples. The significant differences observed, however, in the mean TPCs from similar size *B. glabrata, B. straminea*, and *H. caribaeum* suggests a degree of generic and species specificity that may be of taxonomic value.

To our knowledge, the hemoglobin content of the hemolymph has been measured for only one other species of Planorbidae, *Planorbis corneus* (Sato, 1931); the hemoglobin content ranged from 1.43-2.3% versus 0.39-0.93% in *B. glabrata*. These differences may reflect differences in the oxygen tensions of the environments in which the snails were maintained (Fox, 1955).

The mean osmolalities of the hemolymph from the different sizes of *B. glabrata* (PR-1) were similar, a surprising finding in view of the significant differences noted between the mean TPC of the 6-9 mm snails and the larger size groups. This suggests that either the hemolymph proteins have little capacity for binding inorganic ions and that a Donnan equilibrium is not operative, or that the molecular size of the snail proteins exclude them from osmotic interaction. Lee & Cheng (1972), contrary to our observations, suggest that osmolality is greater in larger snails. Inasmuch as their observations were based on single determinations of pooled samples, it does not account for individual variation and may be misleading. The osmolality of samples from the various strains of *B. glabrata* were also similar to one another, and all had osmolalities less than observed in *H. caribaeum* or reported from species of *Lymnaea* (Potts & Parry, 1964; Pullin, 1971). Of considerable interest is the recent observation by Chernin (personal communication), that his basic salt solution minus bicarbonate (Chernin, 1963) has an osmolality of 117 mOsm/Kg—essentially that of the hemolymph of *B. glabrata*.

Changes in the protein and amino acid composition of the hemolymph have been observed in *S. mansoni*-infected *B. glabrata* (Dusanic & Lewert, 1963; Gilbertson et al., 1967; Lee & Cheng, 1972). Our data confirm these reports and also show that, to a lesser degree, starvation may deplete the protein content of the hemolymph. Dusanic & Lewert (1963) reported changes in the electrophoretic properties of the hemolymph from infected snails as early as 3 hr post-infection, and we, likewise, observed a reduction in the TPC of infected snails 1.5 and 24 hr after infection. There is no way of knowing if our observations and those of Dusanic & Lewert represent a related phenomenon. We believe, however, that these early reductions in TPC represent a true phenomenon and not merely an artifact of sampling, since almost identical results were obtained from 3 different groups of snails. One can hypothesize that this immediate reduction in TPC is due to leakage resulting from the penetration of miracidia.

Significant changes in TPC occurred by 11 days post-infection, and only 30-50% of the original TPC was detected in snails (infected 39 and 64 days) releasing cercariae. The absolute amount of hemoglobin in the hemolymph also decreased in infected snails, but the percent of hemoglobin increased.

Our data do not indicate any remarkable differences between the hemolymph of those strains of *B. glabrata* susceptible to our laboratory strain of *S. mansoni* and that from the refractory S-3 strain. The TPCs of the non-susceptible species, *B. straminea* and *H. caribaeum*, were, however, considerably greater than in *B. glabrata*. Our data do suggest that the generally recognized phenomenon of smaller snails being easier to infect than larger snails may be related to the lower TPCs of the smaller snails.

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ZUSAMMENFASSUNG

INTRASPEZIFISCHE VARIATION IN DER HÄMOLYMPHE VON *BIOMPHALARIA GLABRATA,* EINER ZWISCHENWIRTSSCHNECKE VON *SCHISTOSOMA MANSONI*

E. H. Michelson und Lorin DuBois

Es wurde der Versuch unternommen, die Hämolymphe von *Biomphalaria glabrata* unter Berücksichtigung "normaler" innerartlicher Variation, d. h. der Unterschiede sowohl zwischen Stämmen wie auch innerhalb einzelner Stämme, zu charakterisieren. Gesamtproteinkonzentration, prozentualer Hämoglobingehalt, pH und Osmolalität wurden untersucht. Geprüft wurden sieben geographische Stämme von *B. glabrata*. Ausserdem verwertet wurden Beobachtungsergebnisse an der Hämolymphe von *Biomphalaria straminea*, mehreren Stämmen von *Helisoma caribaeum,* und von *Biomphalaria glabrata*-Tieren, die einer *Schistosoma mansoni*-Infektion oder Hungerperioden ausgesetzt worden waren.

Unterschiede in den Gesamtkonzentrationen von Protein und Hämoglobin innerhalb desselben Stammes von *B. glabrata* erwiesen sich als eher mit der Grösse der Schnecken verknüpft als mit deren absolutem Alter. Verschiedenheiten zwischen den Stämmen von *B. glabrata* waren ebenfalls zu verzeichnen, doch lagen die Unterschiede in derselben Grössenordnung wie in einzelnen Proben desselben Stammes. Signifikant waren hingegen die Unterschiede in der Gesamtproteinkonzentration zwischen den Mittelwerten bei etwa gleichgrossen Tieren von *B. glabrata, B. straminea* und *H. caribaeum*.

Die Osmolalität der Hämolymphe von verschieden grossen *B. glabrata*-Tieren war etwa gleich, ebenso wie die Osmolalität der Hämolymphe etwa gleichgrosser Schnecken verschiedener Stämme. Immerhin wiesen alle *B. glabrata*-Stämme niedrigere Osmolalitätswerte in der Hämolymphe auf als *H. caribaeum*-Stämme.

Eine Infektion mit *S. mansoni* verringerte bei *B. glabrata* die Proteinkonzentration in der Hämolymphe. Unterschiede konnten bereits 1,5 bis 24 Std. post infectionem bemerkt werden, wobei besonders starke Veränderungen etwa 11 Tage p.i. auftraten. In geringerem Masse setzte auch Hungern den Proteingehalt der Hämolymphe herab.

C.M.-B.

RESUMEN

VARIACIONES INTRAESPECIFICAS EN LA HEMOLINFA DE *BIOMPHALARIA GLABRATA,* CARACOL HUESPEDE DE *SCHISTOSOMA MANSONI*

E. H. Michelson y Lorin DuBois

Con referencia a la variación intraespecífica "normal" de *Biomphalaria glabrata*, se intentó caracterizar la hemolinfa, tanto en las diferencias internas como en las externas de los linajes. Se estudió la concentración de proteína, porcentaje de hemoglobina, pH, y la osmolalidad. Siete razas geográficas de *B. glabrata* se examinaron, con observaciones adicionales en la hemolinfa de *B. straminea*, varios linajes de *Helisoma caribaeum* y, ejemplares de *B. glabrata* sujetos ya a infección con *Schistosoma mansoni* o a periodos de inanición.

Las diferencias intraraciales en las concentración total de proteínas y hemoglobina en *B. glabrata*, parecen tener relación más estrecha con el tamaño del animal que con la edad del mismo. Se notó también variación interacial, en *B. glabrata*, pero la magnitud de las diferencias fué igual a las ya mencionadas. Más significantes, sin embargo, fueron las diferencias en la concentración total de proteínas observadas entre los promedios de *B. glabrata, B. straminea* y *H. caribaeum.*

La osmolalidad de la hemolinfa en *B. glabrata* de diferentes tamaños fué similar a las de los otros linajes en caracoles del mismo tamaño. Pero todas las razas de *B. glabrata* mostraron osmolalidad linfática más baja que la observada en *B. caribaeum.*

La infección con *Schistosoma mansoni* redujo la concentración de proteína en la hemolinfa de *B. glabrata*. Se notaron diferencias tan pronto como 1.5-24 horas despues de la infección, con significantes alteraciones ocurriendo alrededor de los 11 días despues de la infección. En menor grado, la inanición consumió el contenido de proteína en la hemolinfa.

J.J.P.

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THE REPRODUCTIVE SYSTEM OF *BURSATELLA LEACHI PLEI* (OPISTHOBRANCHIA: APLYSIACEA) WITH SPECIAL REFERENCE TO ITS HISTOLOGY[1]

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ABSTRACT

The reproductive system of the sea hare *Bursatella leachi plei* (Aplysiidae, Notarchinae) was examined macroscopically and histologically. Oogenesis and spermatogenesis occur in the same acinus within the gonad, as in *Aplysia.* Spermatogenesis shows no unusual stages or structural modifications, although the mature spermatozoa in *Bursatella* do differ from those reported for *Aplysia* in having only 1 mitochondrial strand around the flagellum instead of 2. The reproductive organs were found generally to conform with those described for other aplysiids. There is, however, no pronounced prostate gland near the gonopore as reported for some aplysiids, but there is glandular tissue of possible prostatic function in the anterior hermaphrodite duct, as reported for another species (*Aplysia depilans*). A transmission electron microscopic study of allosperm storage in the spermatocyst revealed a penetration of the endothelial cell by the head of the allosperm. During this storage, a suspected fusion of sperm and endothelial membranes was not observed, these membranes being from 0.08 to 0.42 μm apart. The apparent variation in separation of the vaginal and oviducal channels within the spermoviduct in different aplysiid genera is discussed.

INTRODUCTION

The Aplysiidae are a circumtropical family of marine gastropods characterized by an external sperm groove and lateral extensions of the foot, the parapodia. The separation into 4 subfamilies (Aplysiinae, Dolabriferinae, Dolabellinae, Notarchinae) is based on the degree of development of the parapodia, the presence or absence of papillae on the body surface, and the presence or absence of a shell (Eales, 1944).

Much of the available information on the Aplysiidae is physiological (e.g., Geduldig & Junge, 1968; Takeuchi, 1968; Takeuchi & Chalazonitis, 1968) or taxonomic (e.g., Eales, 1944; Engel, 1936c), most of the work dealing with the genus *Aplysia*.

Few genera of the family other than *Aplysia* have been studied in detail anatomically, and therefore much work on these groups is needed to permit conclusions or conjectures on functional aspects and evolutionary trends within the family. Previous anatomical studies of aplysiids include those by Eales (1921, 1946, 1951), Eales & Engel (1935), Engel (1926, 1929, 1936a, 1936b), Marcus & Marcus (1962), McCauley (1960) and MacFarland (1966). However, these papers mostly serve in classification and there are few histological descriptions of the various organ systems. Since the penial complex has been shown to be taxonomically important in this group, that structure has been well documented in the older literature, while other organs of the reproductive system have been neglected until recently (Thompson & Bebbington, 1969; Beeman, 1970a).

The taxonomic literature on the monotypic aplysiid *Bursatella* de Blainville, 1817[3] (Notarchinae) is confused about the status of members of this taxon. Early authors (e.g., Cheeseman, 1878; Griffin, 1912; Engel, 1926) discussed subspecies of *Bursatella*. In 1935, Eales & Engel examined available specimens of *Bursatella*, reviewed the literature, and divided the species *leachi* de

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[3]Thiele (1931) listed *Bursatella* de Blainville, 1817, as an invalid synonym of *Notarchus* Cuvier, 1817, but Eales (1944) considered them separate genera on morphological grounds.

Blainville, 1817, into 6 geographical subspecies. These authors could not find morphological distinguishing characters and although they considered such a classification to be provisional, it still stands. A 7th subspecies has since been described by Bebbington (1969). The subspecies studied here, *B. l. plei* (Rang, 1828), ranges from the West Indies to the northern Gulf of Mexico.

Griffin (1912) studied the penis and posterior reproductive system of *Aclesia freeri* Griffin (= *B. l. leachi, fide* Eales & Engel, 1935). Henry (1952) briefly described *Bursatella leachi plei* morphologically, and also gave an account of larval development. Recently, Bebbington (1969) published observations on the radula, digestive tract and central nervous system along with a histological treatment of the various organs of the reproductive system in his new subspecies *B. l. guineensis*. Thompson & Bebbington (1969) did a detailed study of the structure and function of the reproductive systems in *Aplysia depilans*, *A. fasciata* and *A. punctata,* including allosperm storage and also for the first time using the transmission electron microscope. Much histological information was presented.

Beeman (1970a) discussed in detail the structure and function of the reproductive system of *Phyllaplysia taylori*. His excellent report included a scanning electron microscopic examination of sperm storage. In the same year, he used autoradiographic techniques to examine sperm storage and transfer in the same species (Beeman, 1970b). In the present paper, the reproductive system of *B. l. plei* is described macroscopically, histologically (using light and transmission electron microscopic techniques), and functionally.

MATERIALS AND METHODS

Specimens of *Bursatella leachi plei* used in this study were collected between 1967 and 1969 from the northern Gulf of Mexico at Turkey Point, Franklin County, Florida.

Dissection of unrelaxed, living animals resulted in the expulsion of purple "ink," in marked contractions of the body, and in the secretion of large quantities of mucus. Consequently, most animals intended for gross dissection were first relaxed (i.e., narcotized) with 1, or a combination of several of the following chemicals: magnesium sulfate, chloral hydrate, menthol, and tricaine methanesulphonate.

Specimens to be examined histologically under light and phase contrast microscopes were relaxed on the day of collection by the procedures described above; the relaxed animals (or tissues excised from them) were then fixed in Bouin's fluid, sea-water Bouin's fluid, alcohol-formalin-acetic acid (AFA), or sea water 1-2-3 Gomori's. The animals or tissues fixed in Bouin's were stored in that solution. Animals fixed in sea water 1-2-3 Gomori's or in AFA were washed in tap water and stored in 70% ethyl alcohol until used. Sea-water Bouin's was found to provide well-fixed material for the reproductive system.

For histological studies, fixed tissues were dehydrated, embedded in paraffin, sectioned at 5-10 μm, and stained with Harris' hematoxylin using alcoholic eosin or alcian blue as a counterstain. Alcian blue was used to test for the presence of acid mucopolysaccharides (see Steedman, 1950; Spicer, 1963).

Whole mounts were prepared from suspension of living sperm from the ampulla and the spermatocyst of living *Bursatella* in sea water. The sperm were examined under light and phase contrast microscopes. Fixed sperm were examined and photographed under phase contrast.

For electron microscopic studies, live animals were relaxed as described above, and then placed in 4% glutaraldehyde in Millonig buffer (pH 7.4) to fix the epidermal mucous glands before dissection. The excised tissues were placed in chilled, fresh 4% glutaraldehyde for 1 hour and fixed further in 1% osmium tetroxide in Millonig buffer (pH 7.4) for 1 1/2 hours. The tissues were then dehydrated in ethyl alcohol and embedded in Araldite.

Thin sections (about 50 nm) were cut on a Porter-Blum MT-2 ultramicrotome, placed on grids coated with formvar and carbon, stained with uranyl acetate and lead citrate, and examined with Phillips' 100 and Hitachi electron microscopes.

Line illustrations in this paper were made with the aid of a camera lucida.

OBSERVATIONS

The functional components of the reproductive system of *Bursatella* are shown in Fig. 1 (the fertilization chamber is internal

in the genital mass). Morphological and histological descriptions of these structures are given below. Comparisons with the corresponding organs of other aplysiids are made in the DISCUSSION, where differing terminologies and problems on the function of certain organs are also discussed.

1. Gonad (Ovotestis)

The conical, green ovotestis (Fig. 1, Ot) is located posteriorly, with its anterior surface closely applied to the dark brown surface of the digestive gland. The thin, translucent intestine (Fig. 1, I) forms coils around the digestive gland and also around the ovotestis so that this is partly obscured. The apex of the gonad points posteriorly. The gonad consists of a loose mass of spherical acini, about 0.1 mm in diameter, held together by a thin layer of squamous epithelium and by the ductules of the acini.

In a specimen collected in January, ova and sperm were being produced simultaneously in the same acini, although about 10% of the acini showed only sperm and 3% only ova. Gametogenic activity was not systematically studied in relation to the age of the animals. It was nevertheless noticed that spermatogenesis is most active in small animals, which show a higher percentage of acini with only sperm, while the highest oogenetic activity occurs after the peak of spermatogenesis. However, the proportions of ovarian, testicular, or hermaphroditic acini observed cannot be generalized because they have not been related to animal size.

Oogenesis. Developing oocytes (Fig. 2, Oo) are on the wall of the gonadal acinus. The oocytes resemble the mature ova, the major difference being their smaller size. An oocyte is about 71 μm long, with an oval nucleus approximately 28 μm long; it contains many eosinophilic spherules, the largest having a diameter of about 8 μm. The nucleolus, prominent in all stages of oogenesis, is about 8 μm in diameter.

Spermatogenesis. A transmission electron microscopic study of spermatogenesis was undertaken to describe the structure of the spermatogonia, spermatocytes, spermatids and mature spermatozoa. The ultrastructural changes are described below.

Spermatogonia. The spermatogonia (Fig. 3, Sg) rest on the basement membrane (BM) of the acinus. The membrane is 0.4 μm thick and contains a homogeneous array of electron dense granules. The spermatogonia, trapezoidal in shape and about 6 μm long, alternate with supporting cells (SuC) that are narrow basally and wide at the apical end, overlapping each adjacent spermatogonium. The oval spermatogonial nucleus contains a patchy chromatin network which is quite distinct and useful in identifying these cells. The nucleus (N) occupies much of the cell, leaving a sparse amount of cytoplasm containing a few scattered mitochondria (Mi).

As spermatogonial cells which are to undergo spermatogenesis migrate away from the basement membrane into the lumen of the acinus, they exhibit marked changes (Fig. 4): the spermatocytes (Sc) become spherical and smaller (5 μm) and the cyto-

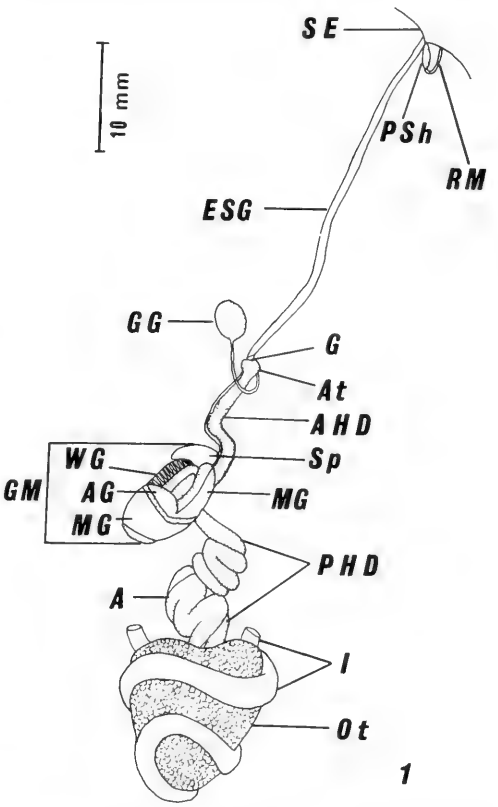


FIG. 1. Reproductive system of adult *Bursatella leachi plei* in dorsal view. A, ampulla; AG, albumen gland; AHD, anterior hermaphrodite duct; At, atrium; ESG, external seminal groove; G, gonopore; GG, gametolytic gland; GM, genital mass; I, intestine; MG, mucous gland; Ot, ovotestis; PHD, posterior hermaphrodite duct; PSh, penial sheath; RM, retractor muscle; SE, surface epithelium on head; Sp, spermatocyst; WG, winding gland.

plasm contains more mitochondria. The nucleus (N), however, continues to occupy most of the cell and the chromatin still forms a patchy network in the nucleus.

Spermatocytes. It was not possible to distinguish the 2 spermatocyte stages from one another ultrastructurally. Spermatocytes increase in cytoplasm, attaining a length of 5-10 μm. The nucleus is at one end of the cell and the chromatin becomes more homo-

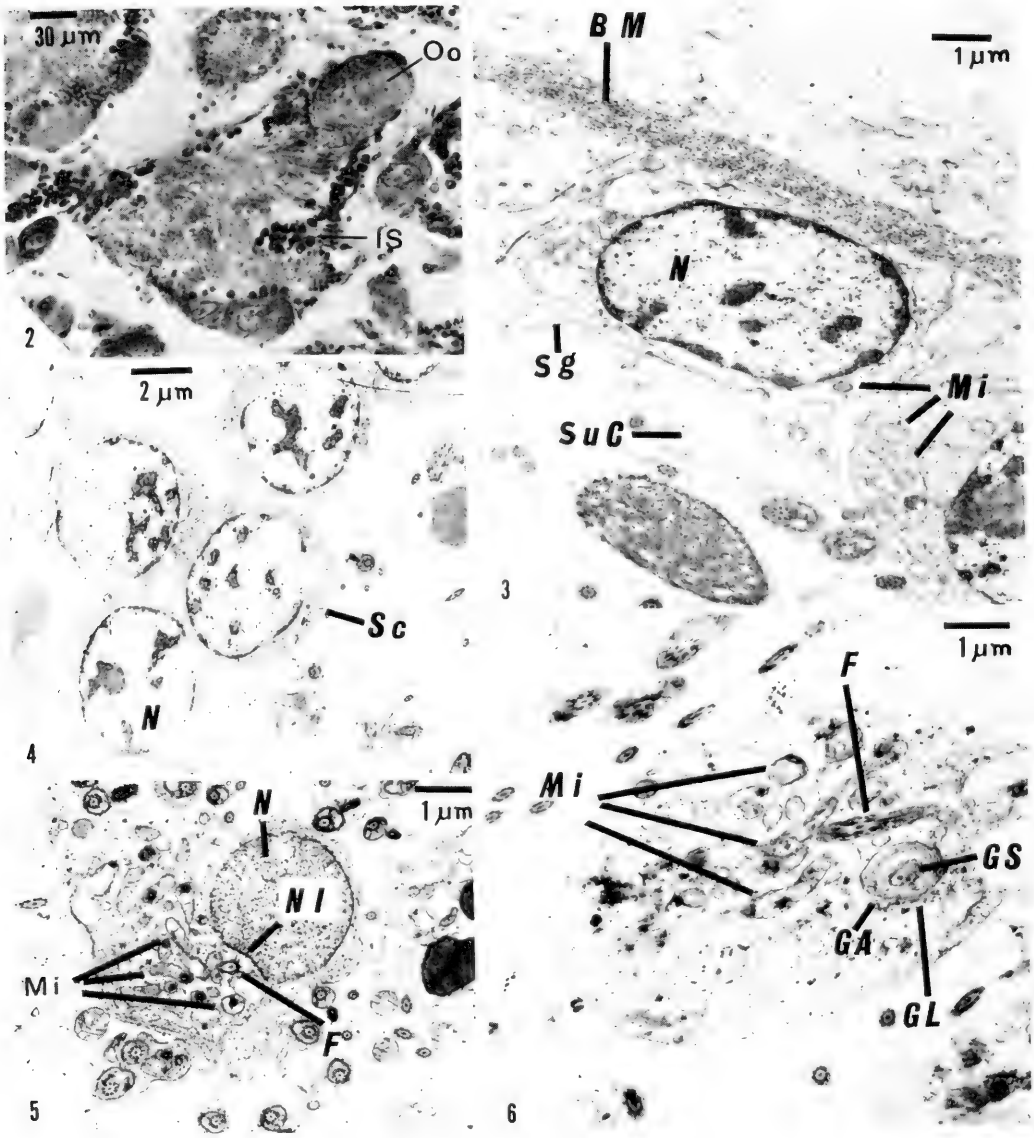


FIG. 2. An acinus containing immature spermatozoa (IS) and oocytes (Oo).

FIG. 3. Spermatogonial cell (Sg) on wall of acinus. Note the thickened basement membrane (BM) and interspersed supporting cells (SuC). N, nucleus; Mi, mitochondria.

FIG. 4. Early spermatocytes (Sc). The spherical cells each contain a large nucleus (N).

FIG. 5. Late spermatocyte. The developing flagellum (F) is near a nuclear indentation (NI). Mitochondria (Mi) surround the flagellum. N, nucleus.

FIG. 6. Cross section of a spermatid containing a prominent Golgi apparatus (GA) which consists of lamellae (GL) surrounding numerous spherules (GS). F, flagellum; Mi, mitochondria.

geneous; chromatin accumulates around the periphery of the nucleus. The mitochondria migrate to that area of the cell, fairly close to the nucleus, from which the flagellum will develop, immediately after mitosis of spermatocyte II. As the flagellum is formed, the adjacent part of the nuclear membrane is invaginated (Fig. 5, NI). While the late spermatocyte differentiates into the spermatid, the developing flagellum (F) lies adjacent to the nucleus (N), surrounded by numerous mitochondria (Mi).

Spermatids. At this penultimate stage the nucleus undergoes further alteration, initially manifest in the loss of a detectable membrane (Fig. 6). The flagellum (F) continues to develop, and the cell elongates as the flagellum lengthens. The mitochondria continue to surround this structure, along with a Golgi apparatus (GA) (especially prominent in all early spermatids) which is located near the base of the flagellum. The Golgi apparatus consists of parallel lamellae (GL) enclosing a secretory (?) body formed by numerous vesicles or spherules (GS) that vary in size and electron density. From then on the nuclear material begins to reaggregate, as evidenced by dark granules located around the flagellar base. As the excess cytoplasm is removed (by being cast off into the lumen of the acinus as an enucleate cell fragment), the spermatid nucleus or head (Fig. 7, N) becomes cigar-shaped and the chromatin aggregates into lamellae (Figs. 7, 8, CL). The developing sperm nucleus is surrounded by a roughly wrinkled cell membrane (Fig. 8, SM) and a decreasing layer of cytoplasm and a nuclear membrane. The flagellum passes backwards from a cone-shaped depression in the nucleus or head (Fig. 7, arrow). In cross-section the mitochondrial sheath which passes along the length of the flagellum and the developing sperm head (Fig. 9, SH) appears to be surrounded by a common, single row of closely-spaced microtubules (MT).

Mature spermatozoa. Anteriorly, the mature spermatozoon has an elongate helical nucleus. No acrosome was observed. The anteriormost portion of the long flagellum extends anteriorly beyond the posterior end of the nucleus which spirals around it. For the greater part of its length (except its posterior end) it is surrounded by a helically-wound mitochondrial strand, the mitochondrial sheath (Fig. 10, MiS). This sheathed portion, produced by the elongation of mitochondria during spermatogenesis, is often seen in electron microscopical sections to contain "bands" which represent the expanded cristae of the mitochondria. The sheathed portion is known as the middle piece. A thickened ridge along the border of the mitochondrial sheath is known as the spiral keel (SK). In cross section it appears as a dilation of the sheath. As in the later spermatids, the nucleus is surrounded first by a nuclear membrane and also by a cell membrane (= sperm membrane).

2. Posterior Hermaphrodite Duct (Gonoduct)

The posterior hermaphrodite duct originates in the anterodorsal region of the ovotestis as a result of the confluence of the acinar ductules. This duct (Fig. 1, PHD) serves to transport ova to the fertilization chamber (compare Fig. 11b, FC, for *Aplysia*) and to store and eventually transport sperm to the anterior hermaphrodite duct (AHD) and subsequently to the penis.

The whiteness of the posterior hermaphrodite duct facilitates its detection in a living animal. The duct is tightly coiled and rapidly increases in diameter as it passes along the dorsal surface of the digestive gland. This dilated portion is the ampulla (Fig. 1,A), or vesicula seminalis, i.e., the region of autosperm storage. As the posterior hermaphrodite duct approaches the genital mass (GM) it decreases in diameter and continues along the ventral surface of the genital mass, under the spermatocyst, and dorsoposteriorly over the albumen and mucous glands, disappearing into the fertilization chamber.

The inner lining of the posterior hermaprodite duct at the ampulla consists of simple ciliated columnar endothelial cells that have a height of 12 μm, a width of 5 μm, and an elongate nucleus 7 μm long (Fig. 12). Sections from this portion of the duct were stained with alcian blue to test for mucus. None of the cells stained positively.

From the genital mass to the fertilization chamber the posterior hermaphrodite duct exhibits a longer, ciliated epithelium (Fig. 13), the cells (36 μm high) being distinctly higher than in the ampulla. In this region the cells contain small, yellow spherules between the nucleus and the apical portion. These appear to be a secretion of the cell, but alcian blue positive mucus was not found in this area.

3. Genital Mass (Nidamental Complex)

The compact glandular mass formed by the aplysiid albumen, winding and mucous glands is referred to as the genital mass. Internally it contains the fertilization chamber. The genital masses of *Bursatella* and *Aplysia* are shown in Figs. 11a, and b, respectively.

Fertilization chamber. Soon after the posterior hermaphrodite duct reaches the

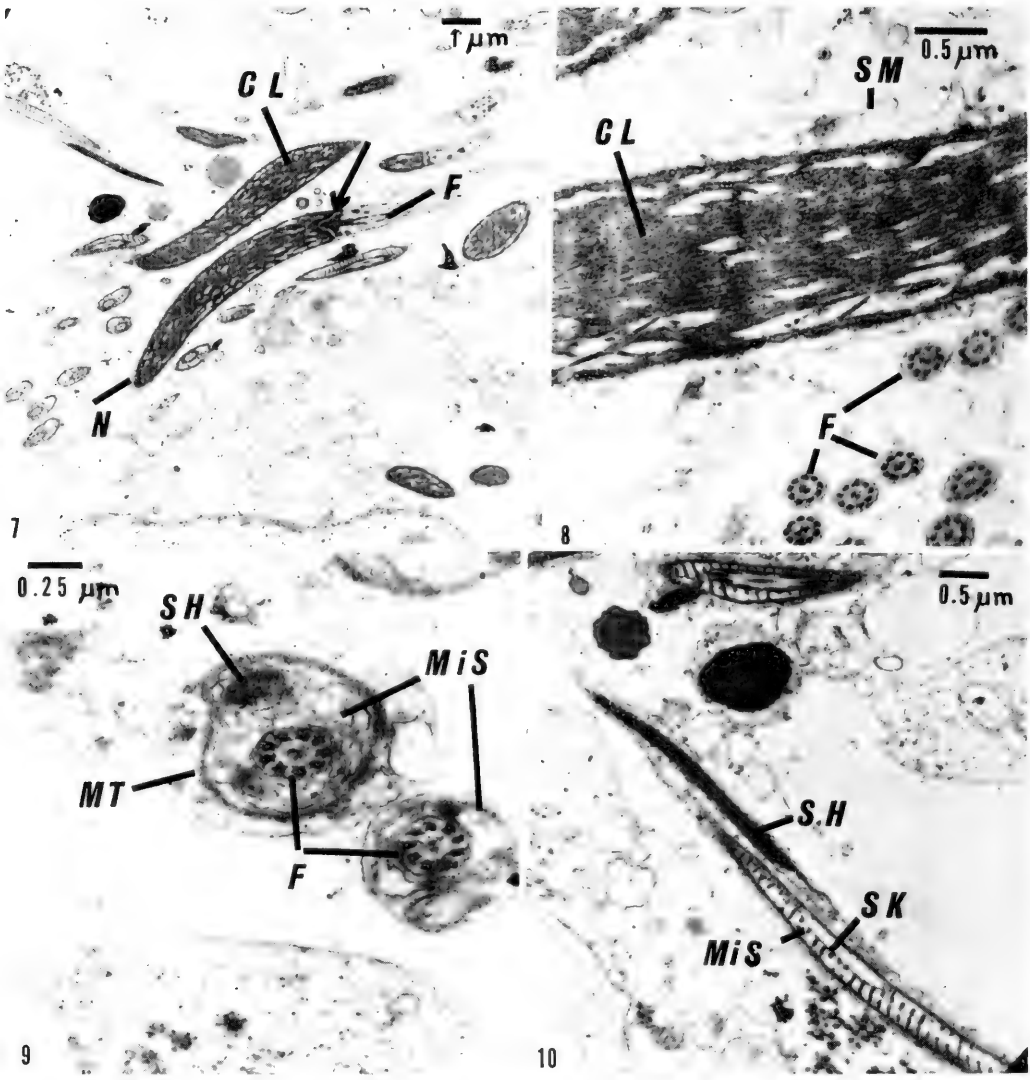


FIG. 7. Longitudinal section of the spermatid nucleus (N). The chromatin aggregates into lamellae (CL), some of which appear to occur in pairs. The arrow indicates an indentation of the nucleus at the insertion of the flagellum (F).

FIG. 8. Longitudinal section of the chromatin lamellae (CL) in the spermatid nucleus at higher magnification. Note the cell membrane of a spermatozoon (SM) and the cross sections of developing flagella (F). See also Fig. 9.

FIG. 9. Cross section of 2 developing spermatozoa. The large one is surrounded by a single row of microtubules (MT). A portion of the helically coiled sperm head (SH) can be seen. The mitochondrial sheath (MiS) is not yet well developed. The smaller spermatozoon is sectioned posterior to the sperm head. F, flagellum.

FIG. 10. Mature spermatozoon. The chromatin of the coiled sperm head (SH) is highly condensed. The spirally coiled mitochondrial sheath (MiS) bearing a spiral keel (SK) is seen.

genital mass it opens into a ciliated chamber, known as the fertilization chamber (Fig. 11b, FC), which also receives the opening of the albumen gland (AG) and the spermatocyst (Sp), and which gives off the winding gland (WG). The ova are fertilized in the fertilization chamber by allosperms from the spermatocyst.

Two morphologically and functionally distinct cell types are in the fertilization chamber endothelium: elongate ciliated cells and goblet-shaped secretory cells. The ciliated cells are columnar (about 40 μm high) and contain small nuclei and a finely granular cytoplasm which is highly eosinophilic and alcian blue negative. The second cell type found here is a goblet-shaped secretory cell varying from a true goblet shape to columnar depending on the secretory state of the cell. Typically large, oval nuclei (about 20 μm in length), within which are found 2 small nucleoli, are present. These cells constitute about 5% of the lining of the fertilization chamber.

Albumen gland. The albumen gland (Fig. 11a, AG), easily recognized by its brilliant orange in living animals and by its complicated internal parallel folds which are conspicuous in cross section, is surrounded by the white tube of the mucous gland.

The individual secretory cells forming the bulk of the endothelium are difficult to distinguish, due in part to their high affinity for eosin, and in part to the great abundance of secretory globules. These cells are elongate and are characterized by small, irregularly-shaped basal nuclei. The cell shape is usually distorted on account of the number of secretory globules, which vary greatly in diameter. These cells do not stain with alcian blue. Interspersed along them, at the apical ends, are small ciliated cells; the cilia extend into the lumen of the albumen gland. These cells probably provide currents for the passage, out of the gland, of the albumen that will coat the ova.

Winding gland. External examination of the genital mass reveals a white convoluted tubular mass near the spermatocyst. This structure, a tube of small diameter originating at the fertilization chamber, is the winding gland (Fig. 11b, WG), whose function is to coat the ovum with mucus after it has passed the mouth of the albumen gland (Thompson & Bebbington, 1969).

Two types of endothelial cells are in the lining of this gland (Fig. 14). One type is a simple, ciliated columnar cell (CC), 38 μm high, with a finely granular eosinophilic cytoplasm and very little secretory material. More conspicuous, however, are secretory cells (SeC) interspersed among them in varying abundance in different loops of the tubule. This 2nd non-ciliated cell type reaches its maximum profusion near the junction with the large mucous gland which is its continuation. At first sight this region of the winding gland appears to be a different gland, since one notices only the secretory cells. Closer scrutiny reveals that the non-secretory cells are also present, though not so conspicuously, and that they bear the cilia seen in this area.

The 2nd cell type stains intensely with hematoxylin and with alcian blue. Its goblet shape and its staining properties are presumably due to the amount and nature of the secretion contained in the cytoplasm. The cells become quite narrow at the base, where a large oval nucleus is present (Fig. 14).

All portions of the winding gland were found to be amply ciliated, presumably to transport the ova to the mucous gland. Muscle tissue capable of contracting the tubules, thus transportating the ova, was not found.

Mucous gland. The mucous gland (Figs. 11a,b, MG), the continuation of the winding gland, has a greater diameter. It is also white in the living animal, passes around the orange albumen gland, and merges with the oviduct channel in the light brown anterior hermaphrodite duct. Histologically it resembles the albumen gland (secretory cells alternating with apical ciliated cells).

The secretory cells are 71 μm high and contain a finely granular and eosinophilic cytoplasm. The secretory products are alcian blue positive. The nuclei of these cells are small (7 μm long) and are located close to the basement membrane (Fig. 15). The ciliated cells are at the distal end of the secretory cells and have long, slender connections extending to the basement membrane.

The mucous gland serves further to encapsulate the fertilized ova with more mucoid secretions in addition to the secretions from the winding gland (see Beeman, 1970a).

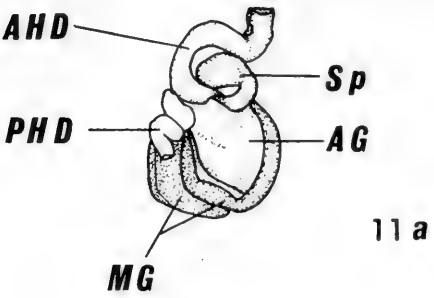
4. Spermatocyst (Seminal Receptacle; Spermatheca)

The spermatocyst (Figs. 11a, b, Sp) opens into the fertilization chamber, and is closely applied to the anterior surface of the genital

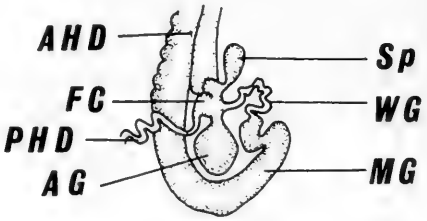
mass (Fig. 1, GM). In immature specimens it is translucent white, of small size and collapsed, while in mature animals it is opaque, quite firm and distended with allosperms. It is separated from the genital mass by a layer of connective tissue.

The cellular lining of the spermatocyst consists of simple columnar endothelium approximately 20 μm high (Fig. 16). The nuclei are typical of such endothelium, i.e. they are elongate (2 μm × 8 μm), and the chromatin is irregularly distributed throughout the nucleus, giving it a patchy appearance. One inconspicuous nucleolus was observed.

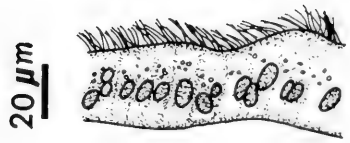
The cytoplasm of the cells is uniform in staining affinities for eosin except for a slightly higher affinity at the free end of the cell. Numerous alcian blue-negative vacuoles are scattered throughout the cytoplasm.



11a



11b



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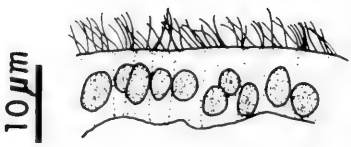

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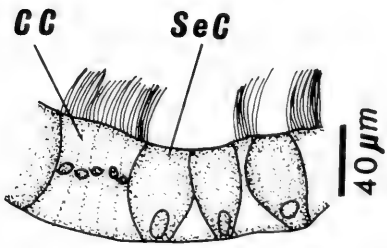

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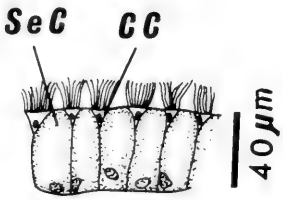

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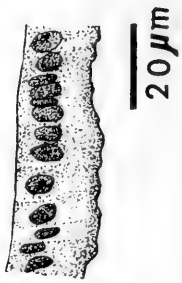

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FIG. 11.a, b. The genital mass of aplysiids. a, *Bursatella leachi plei*, dorsal view, slightly rotated clockwise, organs in situ. The fertilization chamber located internally near the base of the spermatocyst cannot be seen. b *Aplysia* sp. (from Eales, 1921). AG, albumen gland; AHD, anterior hermaphrodite duct; FC, fertilization chamber; MG, mucous gland; PHD, posterior hermaphrodite duct; Sp, spermatocyst; WG, winding gland.

FIGS. 12-16. Endothelial linings of *Bursatella* reproductive organs. 12, ampulla, composed of ciliated columnar cells. 13, posterior hermaphrodite duct near the fertilization chamber; the cells contain granules which may be secretory products. 14, winding gland. The distended secretory cells (SeC) are conspicuous and assume a goblet shape. 15, mucous gland; the apically located ciliated cells (SeC) are connected to the basement membrane by long, thin extensions. 16, spermatocyst; the ragged appearance of the free edge of the cells (right side) is caused by the numerous microvilli. CC, ciliated cell.

Underlying the endothelium is a layer of connective tissue beneath which is a layer of muscle tissue.

The apical end of the spermatocyst cell appears ragged in most sections. The allosperms are usually located about 10 μm away from the cell apex, having apparently broken away during treatment of the tissue.

In the electron micrographs, the apical end of the endothelial cell is seen to consist of numerous microvilli which extend into the lumen of the spermatocyst. Elongated mitochondria are abundant in this region of the cell. Also here are multi-vesicular bodies (Fig. 17, MVB), about 2 μm in diameter and enclosed in a unit membrane (UM)[4], which contain many small spherules of various electron densities. In addition to these organelles, osmiophilic granules ranging up to about 0.5 μm in diameter are frequent near the bases of the microvilli. These granules range from nearly transparent to very electron dense. Histochemical tests were not carried out to identify their composition, but their accumulation near the region where the embedded sperm heads are found may indicate a nutritive role for them. Adjacent endothelial cells are attached firmly to one another by well-developed septate desmosomes (Fig. 19, SD) and prominent terminal bars near the apical end of the cell.

Sections parallel to the microvilli reveal many spermatozoa in the lumen of the spermatocyst, cut in various planes (Fig. 18). The spermatozoa embedded in the endothelium were occasionally sectioned transversely. These embedded allosperms were sectioned in the head region, which suggests that they do not penetrate beyond their head. In one longitudinal view it was seen that only a portion of the head was embedded (Fig. 19, ESH).

Transverse sections of embedded spermatozoa provide most information about the relationship between the sperm head and the cell membrane surrounding the endothelial cells of the spermatocyst. The spermatozoon is surrounded by a cell membrane which is always structurally separated from that of the endothelial cell. No fusion of these membranes was ever observed. The sperm membrane (Fig. 20, SM) of the region of the embedded sperm head (ESH) anterior to the flagellum was found to be from 0.05 μm to 0.35 μm away from the infolded external cell membrane (EM) of the endothelial cell, the variation in distance being due to the folding of the outer cell membrane of the sperm head. Sections from posterior regions of the embedded sperm head (Fig. 21, ESH) contain both the flagellum (F) and the helically-wound nucleus. Here the membrane of the flagellum was more closely applied to the membrane of the endothelial cell (about 0.08 μm). In a posterior coil of the sperm head the distance between membranes (0.14-0.42 μm) was again greater and again comparable to that observed in the anterior region of the head (see Fig. 21).

5. Anterior Hermaphrodite Duct (Spermoviduct)

The anterior hermaphrodite duct (Fig. 1, AHD) passes from the genital mass to the gonopore (Fig. 1, G). Interiorly it has 3 more or less deeply invaginated folds: the internal seminal groove (Fig. 22, ISG), the oviduct (Ov), and the vagina (V). The first 2 channels are functionally but not morphologically separate throughout their length, whereas the vagina, in the middle region, is closed morphologically by the overlapping typhlosoles.

Anteriorly the lining of the lumen has 2 cell types: simple ciliated columnar endothelial cells and mucus-secreting cells. The endothelium of the internally folded vagina (Fig. 22, V) consists entirely of ciliated columnar cells (Fig. 23), none of which stain with alcian blue. The endothelium of the oviduct is less corrugated (Fig. 22, Ov) than that of the vagina. Its endothelial cells (Fig. 24) are distinct from those of the vagina in being higher and the nuclei being larger (11 μm long in the oviduct as against 6 μm in the vagina). Many of the oviduct cells contain a large secretion granule occupying most of the cytoplasm. This granule is composed of many very small spherules which cannot be resolved well with a light microscope. All of the spherules stain intensely with alcian blue. These cells alternate with small ciliated cells containing spherical nuclei.

[4] A membrane within or around a cell showing 3 layers at high magnifications. All cell membranes described in this paper were so constructed.

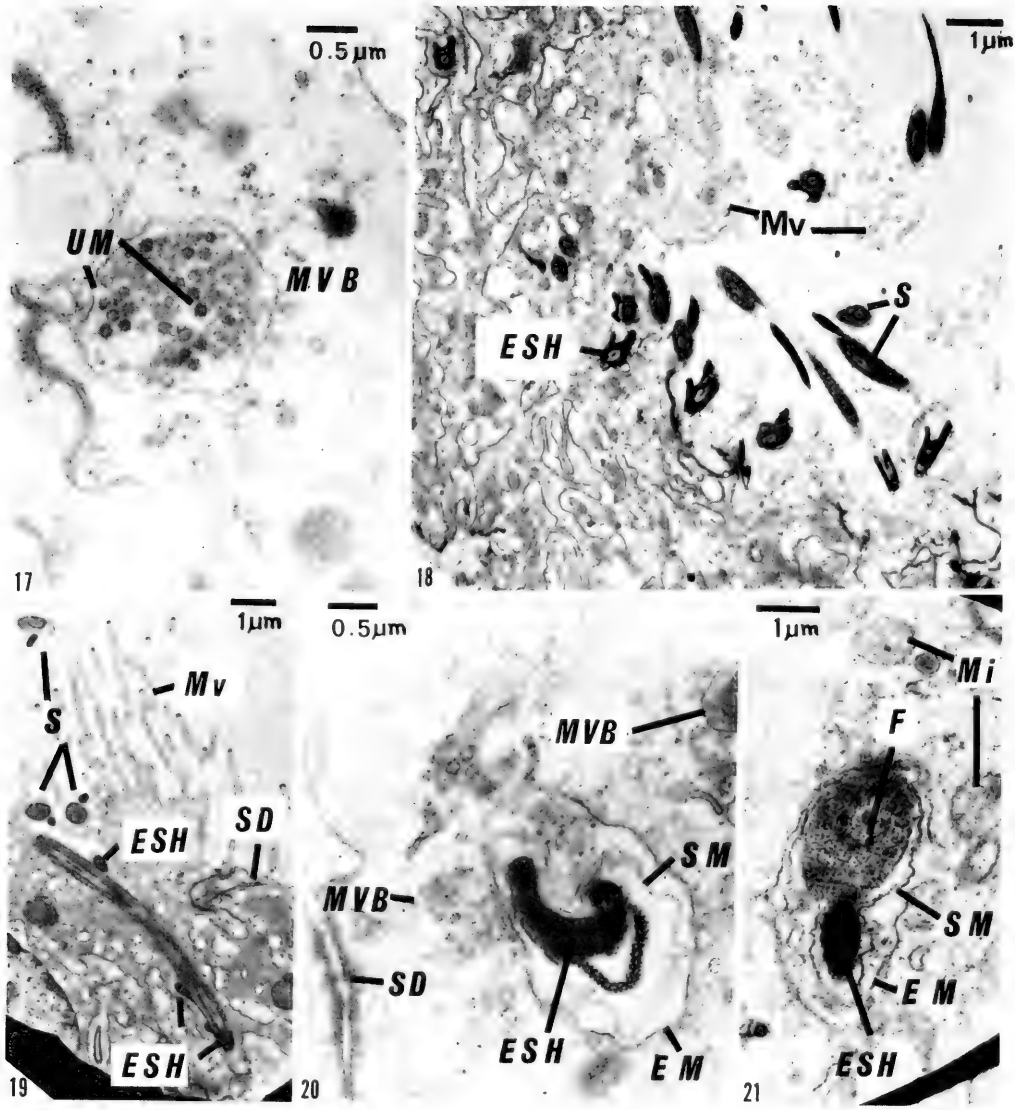


FIG. 17. A multi-vesicular body (MVB) in the apical end of the endothelial cell lining of the spermatocyst Membrane-bound spherules are within a unit membrane (UM).

FIG. 18. Spermatocyst endothelium, showing the relationship between spermatozoa and endothelium. The spermatozoa are buried in indentations of the endothelium. Cross sections of non-embedded spermatozoa and sperm flagella are in the lumen of the spermatocyst. ESH, embedded sperm head; Mv, microvilli; S, spermatozoa.

FIG. 19. Longitudinal section of head of embedded allosperm in spermatocyst endothelium. The coiled sperm head, of which several coils are seen, is not entirely embedded in the endothelial cell. ESH, embedded sperm head; Mv, microvilli; S, spermatozoa in cross section in lumen; SD, septate desmosome.

FIG. 20. Cross section of anterior portion of embedded sperm head (ESH). The membrane covering the sperm head (SM) and the endothelial cell membrane (EM) which surrounds the buried sperm head are not connected. A multi-vesicular body (MVB) is adjacent to the embedded sperm head. SD, septate desmosome.

FIG. 21. Posterior region of embedded sperm head (ESH). The sperm (SM) and endothelial cell (EM) membranes are not joined. The unit membrane of the sperm surrounding the flagellum (F) is also separated from the cell membrane. Mi, mitochondria of the endothelial cell.

The internal seminal groove (Fig. 22, ISG) is a simple fold, an incompletely covered deep channel lying between the oviduct and vagina. Its simple ciliated columnar endothelium (Fig. 26) is continuous with, and morphologically similar to, the vaginal endothelium. The seminal groove endothelium does not contain alcian blue positive secretions.

In the medial and posterior regions of the anterior hermaphrodite duct the internal seminal groove is surrounded by glandular tissue (Fig. 22, GE) (?prostate gland, see later under DISCUSSION). The alcian blue negative glandular cells of this mass are separated from the columnar cells of the seminal groove lining by a layer of connective tissue. The glandular cells are polygonal, 35 μm in diameter, highly granular, and strongly basophilic (Fig. 25).

The oviduct is widest posteriorly in the anterior hermaphrodite duct. Here it contains an additional cell type. Interspersed among the mucous cells, also found anterior to the region, are oval distended cells, 25 μm long, packed with alcian blue positive secretion granules. These cells, which open into the lumen of the oviduct, are oviducal mucous cells. They are more abundant near the genital mass. Serial sections of the mucous gland and the oviduct reveal a morphological similarity between the mucous cells of the oviduct and those of the mucous gland.

6. Atrium (Bursa Seminalis; ?Prostate)

The anterior hermaphrodite duct turns dorsally and dilates upon nearing the gonopore, forming a glandular swelling called the bursa seminalis by Eales (1921) and the atrium by Beeman (1970a) (Fig. 1, At) in other aplysiids. In *Bursatella* the simple ciliated columnar endothelial lining of this region (Fig. 27) is in numerous folds. Many of its cells contain secretory vacuoles, possibly containing mucous secretions, although alcian blue positive mucopolysaccharides were not observed in this endothelium (see DISCUSSION).

7. Gametolytic Gland (Bursa Copulatrix)

Dorsally there is a small spherical organ anterior to, and to the right of, the gonopore. This organ is the gametolytic gland (Fig. 1, GG) (bursa copulatrix of earlier authors), which in aplysiids, according to Eales (1921), Hirase (1929), McCauley (1960), Thompson & Bebbington (1969), and Bebbington (1969), removes "wastes" from the anterior hermaphrodite duct. The gland greatly enlarges as the animal matures. Leaving from the gametolytic gland posteriorly is a small duct, about 0.5 mm in diameter, which passes toward the gonopore and opens into the atrium after winding around it.

The cells of the gametolytic gland form a simple columnar endothelium. The cells are quite high (about 48 μm $\times$ 7 μm), and each contains an elongate (13 μm long) nucleus. A small, spherical nucleolus is present. The chromatin appears homogeneously distributed throughout the karyoplasm (Fig. 29). The alcian blue negative cytoplasm of the cell is quite complex and is differentiated into 3 distinct regions (Fig. 29): a fibrillar region (FR) between the basement membrane and the nucleus, a highly vacuolated region (VR) from the nucleus halfway to the apical end of the cell, and a deeply staining region (DSR) from there to the apical end. The cells are on a thick layer of muscular and connective tissue.

The duct of the gametolytic gland is lined with a simple ciliated columnar endothelium, the cells of which are much smaller (15 μm $\times$ 4 μm) than those of the gland proper (Fig. 28, 48 μm $\times$ 7 μm). The oval nuclei contain irregularly distributed chromatin. The cytoplasm is uniform in staining affinities and does not contain any noticeable vacuoles.

In most of the sections observed, the lumen of the gametolytic gland and its duct were filled with particulate matter, apparently waste material (gametes) removed from the vagina and oviduct during copulation.

8. External Seminal Groove

The external seminal groove (Fig. 1, ESG) is an open ciliated channel extending along the right dorsal surface of the animal from the gonopore to near the penis. Where the channel reaches the region of the penis (at the base of the right rhinophore), it becomes the seminal groove and passes into an invagination of the surface epithelium (the penial sheath) that surrounds the retracted penis and continues to the tip of the penis (Figs. 32, 33, ESG, SG).

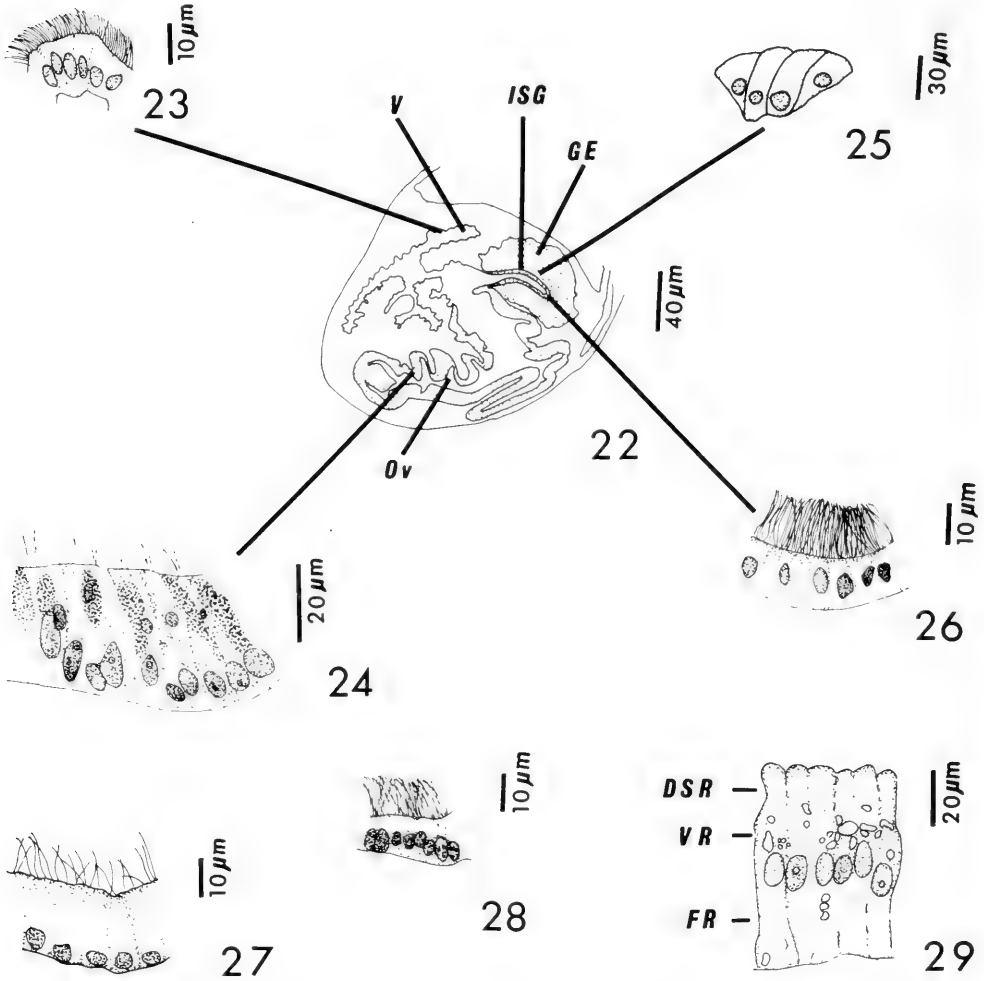
The seminal groove has a series of longitudinal folds which serve to funnel the

sperm to the penis. The changes in cross section of the groove as it passes anteriorly to the penial apparatus are illustrated in Figs. 30, a-c; 32.

The lining of the seminal groove is composed of a layer of simple ciliated columnar epithelium (alcian blue negative) with scattered secretory cells. The columnar cells are 14 μm high, 2 μm wide, and have an oval nucleus 5 μm high; numerous long (10 μm) cilia extend from them (Fig. 31) into the groove. The interspersed secretory cells have a large secretion vacuole at the apical end.

9. Penial Complex

The penis is usually found retracted within its sheath (see Fig. 32). The seminal groove on the penis is lined with a simple ciliated epithelium. The cells (18 μm high) are slightly higher than those of the posterior regions of the external seminal groove



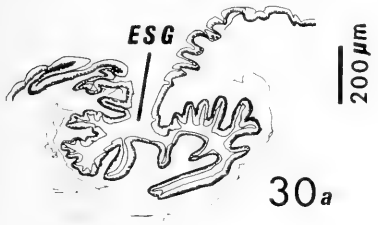
FIGS. 22-26. Cross section and tissues of the medial region of the anterior hermaphrodite duct. 22, cross section showing glandular endothelium (GE), internal seminal groove (ISG), oviduct (Ov), and vagina (V); 23, endothelium of vagina; 24, oviduct lining with large alcian blue positive secretion granules; 25, glandular endothelium (? prostate); 26, endothelium of the internal seminal groove.

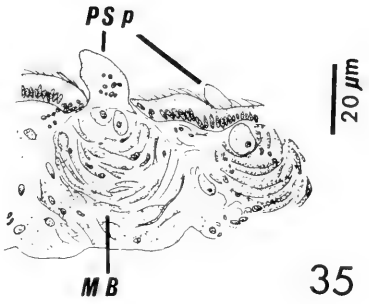
FIGS.27-29. Linings of organs at the anterior region of the anterior hermaphrodite duct. 27, atrium; 28, gametolytic gland duct; 29, gametolytic gland; note 3 regions in the high endothelial cells, a basal fibrillar region (FR), a vacuolated region (VR), and an apical deeply staining region (DSR).

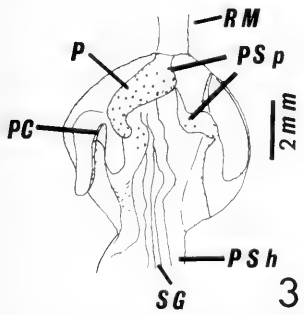
and contain more glandular (alcian blue negative) cells. The epithelium of the surface of the penis (Figs. 33, 34) is similar morphologically to that of the anterior region of the external seminal groove. Projecting from the surface of the penis are numerous spines arising from elongate muscle cells that form a bulbous base. Similar spines also line the penial collar. In section, the spines are sufficiently transparent for stained nuclei to be observed within (Fig. 35).

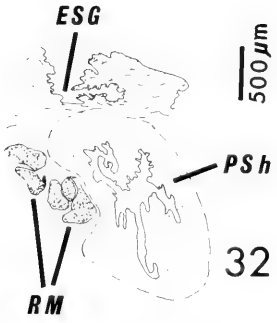
DISCUSSION

Gonad. In *Bursatella*, oogenesis and spermatogenesis occur randomly in the same acini, as is also the case in the 3 species of









FIGS. 30a-c, 31. Cross sections of external seminal groove (ESG); a, near gonopore; b, midway between gonopore and penis; c, in its anterior region. 31, Epithelial lining from region shown in Fig. 30b at higher magnification.

FIG. 32. Transverse section through head at base of right rhinophore, showing external seminal groove (ESG), and penial retractor muscles (RM), penial sheath (PSh), in cross section. The lumen of the penial sheath is the continuation of the external seminal groove. The retracted penis lies below the plane of section.

FIG. 33. Penial sheath opened to expose retracted penis and continuation of the seminal groove. Spines cover the penis and the collar which closely surrounds it. P, penis, PC, penial collar, PSh, penial sheath; PSp, penial spines; RM, retractor muscle; SG, seminal groove.

FIG. 34. Epithelial covering of penis.

FIG. 35. Section through penial wall showing penial spines (PSp) on a muscular base (MB).

Aplysia (*A. depilans, A. fasciata,* and *A. punctata*) investigated in this respect (Eales, 1921; Thompson & Bebbington, 1969).

Spermatozoon structure. In general appearance the mature spermatozoa of *Bursatella* are all alike (i.e., non-dimorphic) and resemble the Type II typical gastropod spermatozoa defined by Nishiwaki (1964): "head long and thread-like, and mitochondria disposed in a sheath around much of the tail." Although an acrosome is common in the spermatozoa of many gastropods, it apparently is lacking in aplysiids. This has been confirmed for *Bursatella leachi guineensis* (Bebbington, 1969). *Aplysia depilans, A. fasciata,* and *A. punctata* (Thompson & Bebbington, 1969), and *A. winneba* (Bebbington, 1969) and agrees with the findings for *Bursatella leachi plei* reported here.

The spermatozoon ultrastructure of 3 species of *Aplysia* described by Thompson & Bebbington (1969), i.e. helical nucleus without an acrosome, flagellum extending, anteriorly, nearly to the extremity of the spermatozoon head, and 2 mitochondrial strands (bounded by discrete membranes consisting of microtubules) spiraling around the flagellum, differs from that observed in *Bursatella leachi plei* only in the number of mitochondrial strands, there being 1 instead of 2 in *Bursatella*.

Posterior hermaphrodite duct. The distribution of ciliation in this duct appears to differ between aplysiids. The duct is entirely ciliated in *Bursatella*. Eales (1921) did not note cilia in the ampulla of *Aplysia punctata*, although Thompson & Bebbington (1969) later did. Eales reported a ciliated endothelium only for the part of the duct near the fertilization chamber, but later authors reported some ciliation for all parts of the posterior hermaphrodite duct. Thus, Marcus & Marcus (1957) observed cilia in the ampulla as well as near the fertilization chamber of *Aplysia brasiliana*, *A. dactylomela,* and *A. juliana*. Thompson & Bebbington (1969) reported 1/3–1/2 of the endothelium of the ampulla to be ciliated in 3 species: *A. depilans, A. fasciata*, and *A. punctata*, as well as all endothelial cells near the fertilization chamber. Working on *Phyllaplysia taylori* (Dolabriferinae), MacFarland (1966: 24) found a cuboidal endothelium with long cilia and large spherical nuclei throughout most of the duct, and low ciliated cells near the fertilization chamber. Working with this same species, Beeman (1970a) found much of the lining of the ampulla, and all of the lining near the fertilization chamber, to be ciliated. The cells of the ampulla and of the region near the fertilization chamber of *Bursatella* show no affinity for alcian blue. This, however, does not necessarily indicate a lack of mucus-secreting cells since alcian blue does not stain all mucoid substances but reveals only acid mucopolysaccharides. The area of the posterior hermaphrodite duct nearest the fertilization chamber of *Phyllaplysia taylori* has endothelial cells containing a yellow secretion. The abundance of these cells increases as the duct approaches the fertilization chamber (MacFarland, 1966). The secretions appear to be similar to those described here for *Bursatella*.

Fertilization chamber. The fertilization chamber of *Bursatella*, which is lined with a strongly ciliated endothelium, conforms with the description of this organ for *Bursatella leachi guineensis* (Bebbington, 1969), *Aplysia punctata* (Eales, 1921), and *Phyllaplysia taylori* (Beeman, 1970a).

Albumen, winding and mucous glands. In *Aplysia fasciata, A. depilans,* and *A. punctata* (Thompson & Bebbington, 1969), and in *Bursatella leachi guineensis* (Bebbington, 1969), the albumen gland is composed of 2 elements: non-ciliated columnar secretory cells alternating with small wedge-shaped ciliated cells, also here reported for *B. leachi plei*. Ciliated cells have not been reported from the albumen gland of *Phyllaplysia taylori* (MacFarland, 1966; Beeman, 1970a).

The winding and mucous glands in *Bursatella leachi plei*, as in other aplysiids, are histologically and functionally quite similar, the mucous gland being but a specialized portion of the winding gland. They both contain non-ciliated cells that produce mucous secretions, and ciliated cells that promote a unidirectional current through the glands. Thus in *B. l. plei* the 3 glands which coat the ova contain both secretory and non-secretory cells. These, however, are not always entirely similar. The secretory cells of the winding and mucous glands are alcian blue positive (indicating acid mucopolysaccharides) while those of the albumen gland are not. In the material examined, the secretory cells of the winding gland were striking in the degree of expansion that occurred during active secretion. The secretory cells

of the mucous gland can easily be differentiated from those of the albumen gland by their large size (71 μm high) and more finely granular and eosinophilic cytoplasm. The nuclei of these cells are small (7 μm long) and are located close to the basement membrane (Fig. 15). The apical ciliated cells and slender connections with the basement membrane of the albumen and mucous glands do not show any differences, whereas the ciliated cells of the winding gland extend down to the basement membrane extensively.

As the fertilized ova pass through the winding and mucous glands, stratified coats of mucoid substances are deposited on the ova and help to consolidate the string of egg capsules (see Beeman, 1970a on *Phyllaplysia taylori*). This secretion has also been discussed recently by Thompson & Bebbington (1969) for *Aplysia* spp.

In the 3 species of *Aplysia* examined by Thompson & Bebbington (1969) all cells of the winding gland are ciliated, while Beeman (1970a) found both ciliated and non-ciliated cells in the winding gland of *Phyllaplysia taylori*. McCauley's (1960) description is not clear; he apparently saw only ciliated cells in the winding gland of *P. taylori*.

Although the general structure of the aplysiid mucous gland has been found to be quite uniform (non-ciliated cells which secrete mucoid material and also current-producing ciliated cells), the distributions of the ciliated cells within the gland appear to differ considerably. In *Bursatella leachi plei* and *B. leachi guineensis* (Bebbington, 1969) these 2 cell types alternate with each other, as also in *Aplysia depilans, A. fasciata,* and *A. punctata* (Thompson & Bebbington, 1969), while in *Phyllaplysia taylori* the ciliated cells are restricted to a narrow groove within the gland (Beeman, 1970a).

Spermatocyst (seminal receptacle). The lining of the spermatocyst revealed by transmission electron microscopic techniques and described in the present study (viz., a simple columnar endothelium with a conspicuous brush border of microvilli) appears to be the typical aplysiid structure (see Bebbington, 1969; Thompson & Bebbington, 1969; Beeman, 1970a). The allosperms are stored in indentations of the endothelium and the microvilli may play an important role in this storage.

Early researchers, using light microscopy, were not able adequately to observe the ultrastructure of the endothelium. When viewed by that technique the microvilli form a "ragged" or "brush" border. As a result, McCauley (1960) and MacFarland (1966) described a ciliated columnar endothelium in the spermatocyst of *Phyllaplysia taylori*. The spermatozoon heads were said to lie between the endothelial cilia although some appeared to be buried in depressions of the endothelium. Eales (1921) figured a similar ciliated endothelium in *Aplysia punctata*. McCauley and MacFarland either misinterpreted the microvilli as cilia or were confused by the sperm flagella projecting from the endothelium. Judging from Bebbington's (1969) illustration there is, in *Bursatella leachi guineensis*, only 1 very large microvillus on each cell, whereas in my specimens there are many small ones.

According to Thompson & Bebbington (1969), means of storage and nutrition apparently differ within the genus *Aplysia*. In *A. depilans* and *A. punctata* each individual gamete is in contact with the endothelium. The allosperms of *A. fasciata* do not contact the endothelial cell, but are associated instead with a system of modified, dilated microvilli and anastomosing vesicles. In these 3 species of *Aplysia*, the allosperms are closely surrounded by small microvilli. In *B. l. plei* the allosperms are embedded in the endothelium of the spermatocyst, but the microvilli may not be as important for sperm nutrition and storage as in *Aplysia*.

It appears, then, that within the Aplysiidae there are at least 2 modes of allosperm storage: modification of the microvilli for supplying nutrition for the sperm (*Aplysia depilans, A. fasciata*, and *A. punctata*), and the penetration of the endothelium by the allosperms with the intimate association of the sperm head and the cytoplasm of the endothelial cell in *B. l. plei*. No ultrastructural modification of stored allosperms was observed in either *Aplysia* or *Bursatella*.

Anterior hermaphrodite duct (spermoviduct). This duct is morphologically adapted to transport allosperms to the spermatocyst (vaginal channel), to transport autosperms to the penis (internal seminal groove), and to convey the egg string to the common gonopore (oviducal channel). Among the Aplysiidae, the vaginal and oviducal channels, which lie close to each other, have become functionally separate. The vagina and oviduct in *Bursatella leachi plei* are partially

separated by an incomplete septum, as in *Aplysia punctata, A. depilans,* and *A. fasciata* (Eales, 1921; Thompson & Bebbington, 1969). Marcus & Marcus (1957) described muscular and connective tissue (a septum) separating the oviduct and vagina for a short distance in *A. brasiliana*, as did MacFarland (1966) for *A. californica.* In *Dolabella gigas* (Dolabellinae) the vagina is separated from the oviduct by an outgrowth of the duct wall which "almost but not quite divides the duct into 2 parts" (Eales, 1946). The anterior hermaphrodite duct of *Phyllaplysia taylori* is not morphologically divided into 2 completely separated ducts (McCauley, 1960). A comparative study of vaginal and oviducal separation among the Aplysiidae has not yet been carried out.

The histology of the vagina and oviduct is uniform in the members of the family studied so far. The pattern of alternating ciliated and nonciliated cells appears to be typical of aplysiids.

The internal seminal groove contains more glandular elements in its upper portion than it does in the distal atrium near the gonopore in *Bursatella leachi plei, B. l. guineensis*, and *Aplysia depilans*. This glandular area in the seminal groove has not yet received much attention and its function, presumably prostatic, and its variable development is in need of further investigation.

Atrium (bursa seminalis). The anterior hermaphrodite duct in *Bursatella leachi plei* terminates distally in a dilation which internally is lined by a glandular columnar endothelium. This region also receives the duct of the gametolytic gland. Eales (1921) termed a similar swelling in *Aplysia punctata* the bursa seminalis and suggested it was involved in copulation. Marcus & Marcus (1957) called the swelling in *Aplysia brasiliana* the clustered gland. The comparable dilation in *Phyllaplysia* was named the atrium by Beeman (1970a). The swelling at the junction of the gametolytic gland stalk and the anterior hermaphrodite duct is not equally conspicuous in the various species. Thompson & Bebbington (1969) describe it for *Aplysia fasciata* and *A. punctata* but reported it lacking in *A. depilans*. Concomitantly, a discrete lobate gland, identified as the prostate, was present in that area in the former 2 species while that gland was inconspicuous in the latter species, where, instead, more glandular tissue, also thought to be prostatic, was found to line the internal seminal groove. A similar weak development of the gland in the atrium coupled with stronger glandular development in the internal seminal groove prevails in *Bursatella leachi plei* and *B. l. guineensis* (Bebbington, 1969).

Gametolytic gland (bursa copulatrix). Eales (1921) reported a ciliated epithelium in this organ in *Aplysia punctata*, while according to Thompson & Bebbington (1969) it is non-ciliated in that, and in 2 other European species of *Aplysia*; it is also nonciliated in *Bursatella* (Bebbington, 1969; this paper). For *Phyllaplysia taylori*, McCauley (1960) reported cilia in this gland, but perhaps he observed the cilia in the beginning of the duct where they normally are present. Authors generally agree with Hirase (1929), who worked on *Dolabella*, that in the Aplysiidae this organ is not a "seminal receptacle," since it contains degenerating sperm and ova which seem to be absorbed there, perhaps through the action of secretions from the endothelial cells.

External sperm groove. The open ciliated sperm groove leading to the penis, first noted by Pruvot-Fol (1954) in several aplysiid genera, is characteristic of the family and apparently uniform in structure.

Penial complex. Aplysiids differ in the presence or absence of spines on the penis, penial collar, and preputium. The subject has been well treated by Eales (1944) in her review of the Aplysiidae. According to Eales & Engel (1935) and Eales (1944), the spines are on a muscular base or wart. Spines are not present in the Aplysiinae or Dolabellinae, may be present in the Dolabriferinae, and are always present on the penis and preputium or penial collar in the Notarchinae.

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ZUSAMMENFASSUNG

DIE FORTPFLANZUNGSORGANE VON *BURSATELLA LEACHI PLEI* (OPISTHOBRANCHIA: APLYSIACEA) MIT BESONDERER BERÜCKSICHTIGUNG IHRER HISTOLOGIE

Ronald F. Thomas

Die Fortpflanzungsorgane des Seehasen *Bursatella leachi plei* (Aplysiidae, Notarchinae) wurden makroskopisch und histologisch untersucht. Oogenese und Spermatogenese finden in demselben Acinus in der Gonade statt, wie bei *Aplysia*. Die Spermatogenese zeigte keine ungewöhnlichen Stadien oder strukturellen Modifikationen; allerdings unterschieden sich die reifen Spermatozoen von *Bursatella* von den bei *Aplysia* gefundenen, indem sie um die Geissel herum statt 2 nur einen Mitochondrienstrang besitzen. Generell stimmen die Fortpflanzungsorgane nach den Befunden mit den von anderen Aplysiiden beschriebenen überein. Es war jedoch nahe der Geschlechtsöffnung keine ausgesprochene Prostata vorhanden, wie von einigen Aplysiiden bekannt, sondern drüsiges Gewebe—möglicherweise mit Prostatafunktion—im vorderen Zwittergang, wie für andere Arten (*Aplysia depilans*) angegeben. Eine elektronenmikroskopische Studie zur Aufbewahrung der Fremdspermien in der Spermatocyste führte zu der Feststellung, dass die Fremdspermie mit ihrem Kopf in die Endothelzelle eindringt. Eine zunächst vermutete Verschmelzung der Membranen von Spermie und Endothelzelle während der Aufbewahrung war nicht zu beobachten. Die Membranen blieben zwischen 0,08 und 0,42 µm weit auseinander. Die offensichtliche Variation in der Trennung von Vaginal- und Ovidukt-Kanal innerhalb des Spermovidukts in verschiedenen Aplysiiden-Gattungen wird diskutiert.

C. M.-B.

RÉSUMÉ

L'APPAREIL REPRODUCTEUR DE *BURSATELLA LEACHI PLEI* (OPISTHOBRANCHIA: APLYSIACEA) AVEC ÉTUDE PARTICULIÈRE DE SON HISTOLOGIE

Ronald F. Thomas

L'appareil reproducteur de l'aplysie *Bursatella leachi plei* (Aplysiidae, Notarchinae) a été examiné macroscopiquement et histologiquement. L' ovogenèse et la spermatogenèse ont lieu dans le même acinus de la gonade, comme chez *Aplysia*. La spermatogenèse ne montre aucun stade inusuel ou de modifications structurales, bien que les spermatozoïdes matures de *Bursatella* diffèrent de ceux décrits chez *Aplysia* par le fait qu'ils n'aient qu'un filament mitochondrial autour du flagelle, au lieu de 2. Les organes reproducteurs sont conformes à ceux décrits chez les autres Aplysiidae. Il n'y a cependant pas une glande prostatique définie près du gonopore, comme cela a été indiqué pour quelques Aplysiidae, mais un tissu de fonction prostatique possible, dans la partie antérieure du canal hermaphrodite, comme cela a été indiqué chez d'autres espèces (*Aplysia depilans*). Une étude au microscope électronique de l'allosperme stocké dans la spermathèque révèle une pénétration de la cellule endothéliale par la tête de l'allosperme. Pendant ce stockage, une fusion suspecte du sperme et des membranes endothéliales n'a pas été observée, ces membranes ayant de 0,08 à 0, 42 µm d'épaisseur. L'apparente variation dans la séparation des canaux de vagin et de l'oviducte à l'intérieur du spermoviducte est discutée chez différents genres d'Aplysiidae.

A.L.

RESUMEN

EL SISTEMA REPRODUCTOR DE *BURSATELLA LEACHI PLEI* (OPISTHOBRANCHIA: APLYSIACEA) CON REFERENCIA ESPECIAL A SU HISTOLOGIA

Ronald F. Thomas

Se examinó, macroscopica e histológicamente, el sistema reproductor de la liebre de mar *Bursatella leachi plei* (Aplysiidae, Notarchinae). Ovogénesis y espermatogénesis ocurrieron en el mismo saco dentro de la gonada, como en *Aplysia*. La espermatogénesis no mostró estados fuera de lo comun ni modificaciones estructurales, aunque los espermatozoos maduros difieren de aquellos reconocidos en *Aplysia* por tener un sólo cordón mitocondrial, en lugar de 2, alrededor del flagelo. Se verificó que los órganos reproductores conforman generalmente con aquellos descriptos para otros aplysidos. No tiene, sin embargo, una glándula prostática pronunciada cerca del gonoporo como existe en algunos de ellos, pero hay tejido glandular de una posible función prostatica en el ducto hermafrodita anterior, como ha sido indicado para otra especie (*Aplysia depilans*). El estudio per microscopio electrónico de la reserva de alosperma en el espermatocisto, reveló una penetración celular endotelial por la cabeza del alosperma. Durante este proceso de reserva no se observó la fusión—que se habia sospechado—de las membranas endoteliales y espermáticas, estando tales membranas separadas de 0.08 a 0.42 μm. Se discute la variación aparente, en diferentes géneros de aplysidos, de la separación de los canales vaginal y oviductales dentro del espermoviducto.

J.J.P.

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ECOLOGIA DE UNA POBLACION DE "BERBERECHO" (*DONAX HANLEYANUS*) EN VILLA GESELL, ARGENTINA[1]

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RESUMEN

Donax hanleyanus es una especie compañera y subdominante en la comunidad de *Mesodesma mactroides* en las playas arenosas al norte de Mar del Plata, Argentina. Aunque presente en depósitos fósiles al sur de la región, su registro dentro de la fauna actual al sur se inicia a partir de 1962/63. Su dispersión reciente al sur del Río de la Plata procedente del litoral uruguayo debe atribuirse a condiciones oceanográficas favorables que hicieron posible que las larvas flanquearan el estuario. La colonización de las playas fué progresiva y consecuencia del transporte de larvas por corrientes de marea.

El "berberecho" habita preferentemente los niveles superiores del Piso Mediolitoral. Durante las pleamares se desarrolla una intensa actividad migratoria. Suelen producirse fenómenos de embancamiento en el Piso Supralitoral, lo que es causa importante de mortalidad masiva.

La densidad específica de la población varía local y estacionalmente, aumentando grandemente en los períodos de reclutamiento de nuevas generaciones.

Donax hanleyanus presenta en la zona de Villa Gesell 2 períodos de desove que pueden alterarse por factores aleatorios: uno de fines de invierno-comienzos de primavera (agosto-setiembre) y el otro estival (enero-febrero). Correlativamente hemos registrados dos períodos de reclutamiento: uno en octubre-noviembre y el otro en febrero-marzo. La diferenciación sexual se evidencia a los 2 meses de edad en los machos y a los 4 meses en las hembras. No existe un período de absoluto reposo gonadal.

La longevidad de *Donax hanleyanus* es de 3 años y su tasa de crecimiento de 1,83 mm/mes en el primer año de vida, 0,49 mm/mes en el segundo, y 0,02 mm/mes en el tercero.

INTRODUCCION

La "almeja mariposa o coquina," que en Argentina y Uruguay se ha dado en llamar "berberecho," *Donax hanleyanus* Philippi, 1845, habita las playas arenosas bonaerenses al norte de Mar del Plata. Si bien es una especie comestible no se halla sujeta a explotación comercial.

Es el único representante en Argentina de la familia Donacidae y su incorporación a la fauna actual es de muy reciente data. Castellanos & D'Ambrosi (1965) señalaron su presencia por primera vez en las playas de Mar de Ajó; sin embargo, Ihering (1907) y Camacho (1966) la citaron dentro de la fauna fósil del Pampiano y Post-Pampiano de la costa marítima al sur del Río de la Plata hasta Puerto Belgrano.

Lange de Morretes (1949), Barattini & Ureta (1960) y Ríos (1970) hicieron mención a su distribución geográfica; Bertullo et al. (1967) se ha referido a una nueva sustancia microbiana obtenida a partir de sus carnes; y por nuestra parte (Olivier & Penchaszadeh, 1968; Olivier et al., 1971) nos hemos referido al "berberecho" como especie compañera de la "almeja amarilla" (*Mesodesma mactroides* Deshayes) al estudiar la dinámica de las poblaciones de esta especie.

Las presentes investigaciones tratan de ofrecer un panorama de la biología y ecología de un pelecípodo que, además de ser poco conocido en nuestro medio, ofrece particular importancia por ser la especie subdominante en la comunidad de las playas arenosas de una amplia región. Por otra parte, su reciente incorporación a la fauna bonaerense permite observar interesantes fenómenos de colonización y dispersión, estabilización de las poblaciones, interacción con los organismos preexistentes y otros fenómenos bioecológicos.

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MATERIAL Y METODOS

El material estudiado procede de: a) campaña de evaluación de efectivos de "almeja amarilla" (*Mesodesma mactroides*); febrero de 1968; y b) muestreos mensuales realizados en los aledaños de la localidad de Villa Gesell (Provincia de Buenos Aires), desde enero de 1968 a febrero de 1970.

Para el estudio de la densidad de las poblaciones se utilizó la misma metodología que la descripta en un trabajo anterior (Olivier & Penchaszadeh, 1968). Para el estudio de la distribución vertical y de la estructura de la población se realizaron muestreos representativos al azar cavando en distintos sectores de la playa superficies de un 1/4 m cuadrado, tamizándose considerables volúmenes de arena para retener la totalidad de los individuos presentes.

La siguiente es la lista de los muestreos:

1968

11 de abril . . . . . .226 ind.
29 de mayo 110
28 de junio 151
31 de julio 227
6 de setiembre . . .208
7 de octubre 267
7 de noviembre . .375
6 de diciembre . .454

1969

7 de enero 505
10 de febrero 505
22 de marzo 473
28 de abril 273
30 de mayo 268
31 de julio 267
26 de agosto 113
24 de octubre 492
24 de noviembre . .414

1970

16 de enero 164
12 de febrero 550

ABREVIACIONES UTILIZADAS

De densidad específica media
De Pt densidad específica expresada en peso total
D máx. densidad especifica máxima
D recl. densidad de reclutamiento
F frecuencia
Lt largo total, en el sentido del eje antero-posterior
Ph. dec. peso húmedo, decalcificado
Ps dec. peso seco, decalcificado
Pt peso total, en vivo ó fijado en formaldehido 7%

HABITAT

Donax hanleyanus vive en densas poblaciones preferentemente en los horizontes Mediolitoral Medio y Mediolitoral Superior, desde Cabo San Antonio hasta Faro Querandí (Provincia de Buenos Aires); en forma aislada hemos registrado su presencia algunos kilómetros al sur de esta última localidad y en las playas de Punta Mogotes (Mar del Plata). La caracterización fisiográfica y oceanográfica de esta misma región ha sido referida con detalle en trabajos anteriores (Olivier & Penchaszadeh, 1968; Olivier et al., 1971).

El "berberecho" es un cavador superficial que no sobrepasa los 3-5 cm de profundidad; los sifones apenas se elevan por encima de la superficie de la arena. Las poblaciones se mantienen en la zona barrida por las olas gracias a mecanismos homeostáticos que determinan las migraciones mareales. En casos de fuertes vendavales se producen embancamientos o varazones de parte de la población en la playa distal y hasta el espaldón, causa importante de mortalidad masiva.

Las poblaciones de *Donax hanleyanus* forman bancos discontinuos que ocupan áreas de diferentes dimensiones. La fisiografía de las playas y las características de los sedimentos son los principales factores que afectan su distribución.

DISTRIBUCION GEOGRAFICA

Donax hanleyanus vive desde Río de Janeiro (Brasil) hasta Punta Mogotes (Argentina). Lange de Morretes (1949), Ríos (1970) y Barattini & Ureta (1960) citan su presencia para varias localidades de las costas brasileñas y uruguayas.

La colonización de las playas al sur del Río de la Plata comenzó entre 1960 y 1962 en que recibimos un primer lote de ejemplares de la localidad de Pinamar. Interpretamos que sus larvas planctónicas flanquearon la barrera geográfica que constituye el Río de la Plata favorecidas por condiciones oceanográficas especiales que posibilitaron su dispersión.

Sin embargo, *Donax hanleyanus* ha sido citada como fósil en el Pampiano y Post-Pampiano de Puerto Belgrano (Ihering, 1907) y para los mismos horizontes de toda la costa marítima al sur del Río de la Plata hasta Bahía Blanca por Camacho (1966). No deja de llamar la atención el hecho de que encontrándose fósil en depósitos tan recientes como el Querandino hasta luego desaparecido para reingresar a las comunidades costeras en los años pasados.

CARACTERES GENERALES DE LA ANATOMIA Y MORFOLOGIA

Donax hanleyanus (Fig. 1) posee una conchilla definidamente triangular, con los bordes distal y ventral finamente denticulados, y truncada posteriormente. Los dentículos marginales determinan una estriación radial que en ciertos casos se correlaciona con bandas coloreadas. El ligamento es totalmente externo.

La talla máxima observada fué de 33,5 mm Lt (24/XI/69). No obstante en las colecciones del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" existen dos conchillas de 40,1 y 37,9 mm Lt respectivamente, provenientes de Ilha do Governador (Brasil); un ejemplar de 36,0 mm de Playa Leblon (Brasil); un ejemplar de 38,4 mm Lt de Praya Peró, Cabo Frío (Brasil) y un ejemplar de 34,7 mm Lt de La Paloma (Uruguay). En Faro Querandí registramos una talla máxima de 35,2 mm Lt. Muy probablemente las diferencias de tallas apuntadas sea consecuencia de diferentes ritmos de crecimiento tal como ocurre en *Donax denticulatus* Linn. en Jamaica (Wade, 1968).

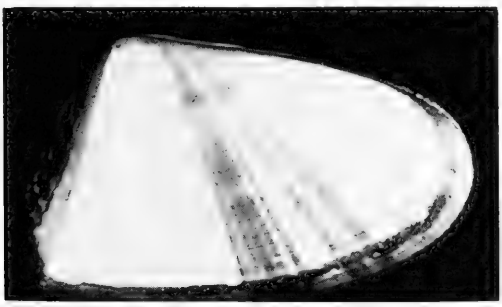


FIG. 1. Ejemplar adulto de *Donax hanleyanus* Philippi, 1845, procedente de Villa Gesell (Buenos Aires, Argentina). Lt = 30,8 mm.

La coloración de las conchillas es variable pudiéndose diferenciar 6 tipos principales: blanco con tonos grises, blanco con finas bandas marrones que forman un triángulo central, azul-violáceo en forma de tenues bandas, azul-violáceo más intenso, ocre y ocre-rojizo. La abundancia relativa de cada uno de los tipos parece no obedecer a causas locales.

El sifón inhalante (Fig. 2, si) posee 6 tentáculos primarios y 6 secundarios tal como ocurre en *Donax denticulatus* de acuerdo con las observaciones de Wade (1969) y en *D. gouldii* Dall de acuerdo con Pohlo (1967). Es de hacer notar que tanto estas ? especies como *D. hanleyanus* son suspensívoras por lo que la estructura sifonal permitiría la primera selección del material ingerido. No ocurre lo mismo con los telináceos sedimentívoros, como *Donax vittatus* Lamarck, en donde según Yonge (1949) ésta primera selección no es posible debido a la ausencia de estructuras especiales.

Los caracteres generales del manto son similares a los descriptos para *D. vittatus* (Yonge, 1949), *D. gouldii* (Pohlo, 1967), *D. striatus* Linn. y *D. denticulatus* (Wade, 1967a, b) excepción de las branquias y palpos labiales. En las dos primeras especies las branquias son grandes y los palpos labiales pequeños mientras que en *D. hanleyanus* cada branquia está constituida por 2 hemibranquias de las cuales la interna es la de mayor tamaño y los palpos labiales son laminares y ocupan una mayor porción de la cavidad del manto. Las escotaduras de los palpos labiales en *D. hanleyanus* son perpendiculares a la apertura bucal como ocurre en *D. denticulatus*. Las diferencias anatómicas señaladas se hallan en relación con el tipo de partículas que son capaces de ingerir cada una de las especies.

Por lo que respecta a *D. hanleyanus* es fundamentalmente suspensívora. El análisis de su contenido estomacal muestra una gran predominancia de detritos, en especial de origen vegetal, diatomeas, entre las que se destaca por su tamaño *Coscinodiscus*, y partículas de arena cuyo diámetro promedio oscila alrededor de los 150 μm. Accidentalmente hemos registrado la presencia de una probable larva de picnogónido de 640 μm.; sin embargo, en la cavidad paleal se acumulan abundantes granos de arena cuyo diámetro oscila en los 300 μm lo que evidencia la selectividad que realiza la apertura bucal y los palpos labiales.

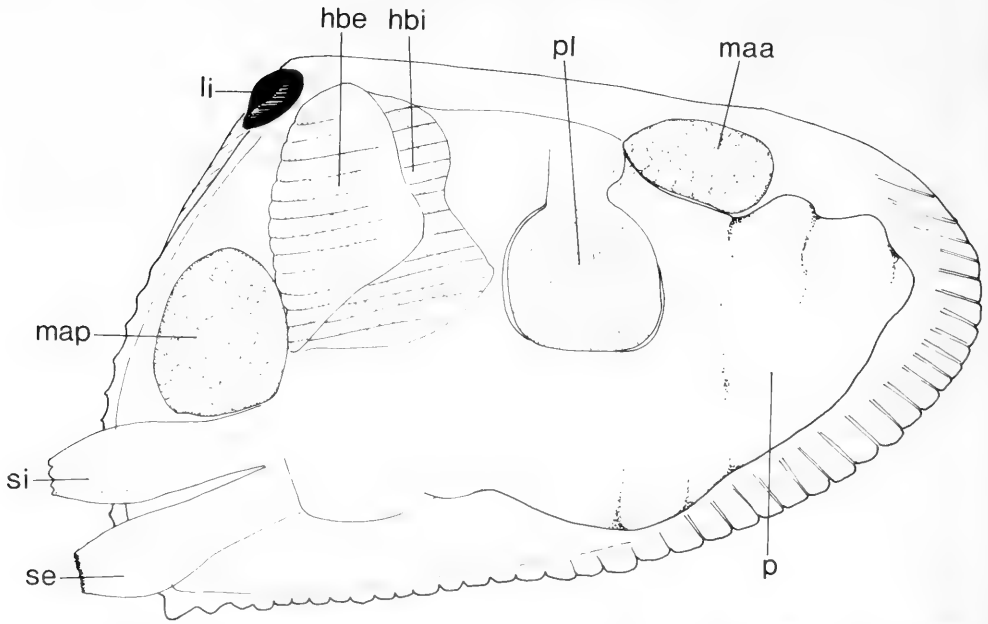


FIG. 2. Razgos anatómicos fundamentales en *Donax hanleyanus* una vez apartados las conchillas y el manto. **hbe**: hemibranquia externa; **hbi**: hemibranquia interna; **li**: ligamento; **maa**: músculo aductor anterior; **map**: músculo aductor posterior; **p**: pié; **pl**: palpos labiales; **se**: sifón exhalente; **si**: sifón inhalente.

BIOCENOSIS DE LAS PLAYAS ARENOSAS DE VILLA GESELL

La comunidad de las playas arenosas de la Provincia de Buenos Aires, al igual que las comunidades paralelas de regiones templadas y tropicales, posee una baja diversidad específica. Sin embargo pueden diferenciarse en ella una interesante diversidad de nichos ecológicos.

Las playas arenosas, que en apariencia se presentan como biotopos homogéneos, sufren continuas perturbaciones por acción de los factores ambientales. Las olas y las corrientes de marea, por ejemplo, provocan el lavado permanente del estran lo que limita la presencia de muchos organismos y causa, periódicamente, elevada mortalidad en otros. Las especies mejor adaptadas a estas condiciones de vida son cavadoras por lo que logran eludir, en parte, la acción limitante del medio. Otras por su parte, realizan migraciones mareales, por lo que no resultan apropiadas para caracterizar la zonación.

En las playas de Villa Gesell la comunidad tiene la composición específica que detallamos a continuación:

Mesodesma mactroides Deshayes. Es la especie dominante en número y biomasa. Su densidad específica media es de 458,7 ind./m² y la densidad específica máxima de 1.700 ind./m². La frecuencia alcanza al 97,82% y representa el 73,86% de la macrofauna. Es cavadora-profunda (hasta 40 cm), suspensívora (fitoplanctófaga-detritívora) y realiza migraciones mareales y estacionales desde el Horizonte Mediolitoral Superior hasta los niveles superiores del Piso Infralitoral.

Donax hanleyanus Philippi. Es la especie subdominante. Su densidad específica media llegó a 160,9 ind./m² y la densidad específica máxima a 2.496 ind./m². En épocas de reclutamiento hemos censado hasta 10.000 ind./m² de ejemplares juveniles. La frecuencia alcanza al 60,86% y representa el 25,91% de la fauna. Es cavadora-superficial (2-5 cm), suspensívora (fitoplanctófaga-detritívora) y realiza migraciones mareales entre los horizontes Mediolitoral Superior y Mediolitoral Medio.

Hemipodus sp. Es especie compañera que en trabajos anteriores (Olivier & Penchaszadeh, 1968; Olivier et al., 1971) hemos referido como *Glycera americana*

Leidy. Su densidad específica media es de 1,3 ind./m² y la máxima de 16 ind./m². La frecuencia es del 21,70% y representa el 0,21% de la fauna. Es cavadora-profunda (hasta 40 cm), sedimentívora y aparentemente no realiza migraciones rítmicas. Vive en el Horizonte Mediolitoral Medio.

Olivancillaria auricularia (Lamarck). Es también una especie compañera. Su densidad específica media es de 0,04 ind./m² y la máxima de 2 ind./m². La frecuencia llegó al 2,17% y representa el 0,006% de la fauna. Es cavadora superficial y carnívora (preda sobre las poblaciones de pelecípodos). Vive preferentemente en el Horizonte Mediolitoral Inferior y en los niveles superiores del Piso Infralitoral, aunque realiza migraciones mareales hacia el Horizonte Mediolitoral Medio.

Otros 2 gasterópodos, *Olivancillaria uretai* Klappenbach y *Buccinanops duartei* Klappenbach, también forman parte de la macrofauna acompañante; ambas son cavadoras superficiales y predatoras. De la primera especie hemos hallado siempre ejemplares aislados mientras que de la segunda suelen encontrarse agregaciones numerosas en las inmediaciones del Horizonte Mediolitoral Inferior en los meses estivales. Asimismo se destacan los anfípodos *Phoxocephalopsis zimmeri* Schell. y *Bathyporeiapus ruffoi* Escofet; los isópodos *Cirolana argentina* Giambiagi, *Macrochiridothea giambiagiae* Torti & Bastida y *Chaetilia argentina* Bastida & Torti; el poliqueto *Ophryotrocha* sp.; y larvas de Chironomidae. Ejemplares juveniles aislados de *Emerita brasiliensis* Schmitt fueron hallados en 2 oportunidades; fué este el primer registro para Argentina. Las especies más abundantes son *Cirolana argentina* y *Bathyporeiapus ruffoi*. La primera es cavadora muy superficial, de hábitos necrófagos y vive preferentemente en el Horizonte Mediolitoral Medio; la segunda, cuya etología ha sido detenidamente estudiada por Escofet (1973), es cavadora superficial, omnívora-detritívora y habita preferentemente el Horizonte Mediolitoral Inferior y los niveles superiores del Piso Infralitoral.

El sostén trófico de esta biocenosis es la producción fitoplanctónica y fitobentónica, a la que debe agregarse los detritos autóctonos y alóctonos de origen marino y terrestre.

Carreto (en Olivier et al., 1971) determinó la concentración de pigmentos fotosintéticos en las aguas de rompiente de Mar Azul, localidad aledaña a Villa Gesell, Durante el verano (diciembre-enero) se registraron los valores máximos de clorofila *a* (31,4 mg/m³), de clorofila *c* (11,5 mg/m³) y de carotenoides (31, 1 m-SPU/m³), mientras que en el invierno (junio-agosto) los valores descendieron apreciablemente (por ejemplo, el registro de clorofila *a* fué de 10-12 mg/m³). Las concentraciones de clorofila *b* fueron muy bajos a lo largo de todo el año. En lo que se refiere a los pigmentos detríticos (feofitina, feofórbidos) las máximas concentraciones corresponden al mes de diciembre en correlación con la mayor producción fitoplanctónica y la mayor actividad metabólica de los herbívoros.

Los consumidores primarios se hallan representados por los moluscos pelecípodos y el zooplancton. Entre los primeros la "almeja amarilla" (*Mesodesma mactroides*) y el "berberecho" (*Donax hanleyanus*) son principalmente fitoplanctófagos.

Son consumidores secundarios (carnívoros primarios) varios gasterópodos, peces y aves. Entre los caracoles malacófagos se destacan *Olivancillaria auricularia, O. uretai* y *Buccinanops duartei*, mientras que en horas de alta marea se alimentan también de moluscos algunos peces costeros como la "corvina" (*Micropogon opercularis*), la "burriqueta" (*Menticirrhus martinicensis*), la "corvina negra" (*Pogonias cromis*) y el "pejerrey" (*Austromenidia argentinensis*). También integran esta comunidad de playas arenosas algunas aves malacófagas tales como el "ostrero" (*Haematopus ostralegus*) y el "rayador" (*Rynchops nigra*).

También son consumidores secundarios, y en ciertos casos terciarios, otras aves carcinófagas, ictiófagas y necrófagas como son las "gaviotas," "gaviotines" y "chorlos playeros": *Larus ridibundus maculipennis, L. marinus, L. belcheri, Sterna trudeaui, S. paridisea, Pluvialis* sp., *Capella* sp. y *Charadrius* sp.

El esquema trófico de estas playas se completa con los isópodos y anfípodos que son preferentemente detritívoros y necrófagos aunque algunos de ellos suelen atacar otros animales vivos o moribundos. Entre estos se destacan *Cirolana argentina,*

Macrochiridothea giambiagiae, Chaetilia argentina, Bathyporeiapus ruffoi y *Phoxocephalopsis zimmeri.*

LA POBLACION DE *DONAX HANLEYANUS*

Dispersión y colonización de nuevas áreas

La incorporación de *Donax hanleyanus* a las comunidades del mediolitoral arenoso del norte de la Provincia de Buenos Aires plantea un caso muy interesante de colonización reciente de nuevas áreas por un organismo bentónico.

Como hemos hecho referencia, éste pelecípodo forma parte de la fauna fósil del Pampiano y Post-Pampiano desde el sur del Río de la Plata hasta Puerto Belgrano (Camacho, 1966). Su desaparición de la fauna actual argentina se habría producido a partir del Querandinense (Post-Pampiano) quizá como consecuencia de las repetidas transgresiones e ingresiones marinas que determinaron la inestabilidad de su habitat. Sin embargo, es preciso también tener en cuenta las grandes fluctuaciones en la densidad de las poblaciones de invertebrados mediolitorales en razón de factores ambientales aleatorios (Coe, 1953). Lo cierto es que *D. hanleyanus* no había sido registrado como componente actual de nuestra fauna litoral hasta el año 1965 (Castellanos & D'Ambrosi, 1965).

La colonización de su habitat ancestral en el litoral bonaerense debe explicarse como una consecuencia de la dispersión de sus larvas pelágicas por las corrientes de marea. Su diseminación hacia el sur ha sido paulatina alcanzando como límite austral conocido la localidad de Punta Mogotes (Mar del Plata). Sus larvas son transportadas muchos kilómetros de las poblaciones paternas, tal como ocurre con otras especies de pelecípodos (Coe, 1946; Coe & Fitch, 1950; Olivier & Penchaszadeh, 1968; Penchaszadeh, 1971).

El éxito de la colonización de nuevas áreas por *Donax hanleyanus* debe atribuirse a la interacción de varios factores ecológicos favorables: morfología y sedimentología de las playas, temperatura, salinidad, disponibilidades alimentarias y composición de la comunidad pre-existente.

Tanto los caracteres sedimentológicos del litoral bonaerense (arenas finas sin rodados y con escasos mantos de conchilla superficial) como así también las condiciones oceanológicas de la región (considerable aumento de la temperatura de las aguas en el verano por calentamiento local e influencia de la corriente cálida de Brasil y salinidad estable por ausencia de cursos importantes de agua dulce con desagüe en el mar) han favorecido la expansión de las poblaciones de "berberecho."

Por otra parte la competencia interespecífica con las densas poblaciones de *Mesodesma mactroides*, sólo se establece en lo relativo a la ocupación del espacio vital con sus juveniles. Las "almejas" adultas son cavadoras profundas mientras que *Donax hanleyanus* es cavador superficial. También se establece una segregación zonal: los bancos de "almeja amarilla" ocupan siempre niveles más inferiores del Piso Mediolitoral que sus juveniles y que *D. hanleyanus*. En épocas de reclutamiento simultáneo es posible observar como las crías de ambas especies se comportan como una única entidad frente a la migración mareal.

En cuanto a la disponibilidad de alimentos, si bien *Donax hanleyanus* posee el mismo nicho trófico que *Mesodesma mactroides*, la producción primaria de las aguas de rompiente de aquella región unida a una gran cantidad de detritos orgánicos (Carreto, en Olivier et al., 1971) son suficientes como para permitir la expansión de las poblaciones de ambas especies.

Zonación y migración

La distribución vertical de *Donax hanleyanus* en las costas bonaerenses (Fig. 3) varía en relación con factores ambientales aleatorios entre los que se destacan la morfología de las playas, la intensidad del oleaje y de las mareas, y las características sedimentológicas. Vive preferentemente en los niveles superiores del Piso Mediolitoral aunque es frecuente hallar agrupaciones densas en los niveles inferiores del Piso Supralitoral y ejemplares aislados en las zonas más altas del Piso Infralitoral.

Durante las horas de baja marea la población permanece inactiva y agrupada al azar en los horizontes Mediolitoral Superior y Medio. En las pleamares es dable observar intensa actividad migratoria de toda la población. Cuando el agua intersticial de

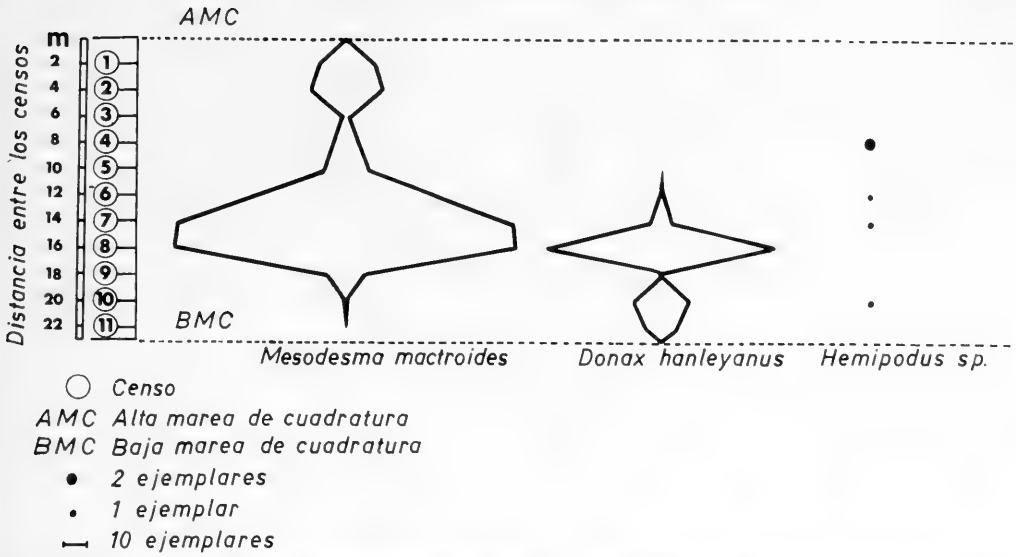


FIG. 3. Zonación de las poblaciones de *Donax hanleyanus* y *Mesodesma mactroides* en la región de Villa Gesell, localidad de Mar Azul.

los sedimentos aumenta hasta la saturación, *Donax hanleyanus* suele emerger activamente a la superficie. El lavado de las olas provoca entonces su desplazamiento hasta que el arrastre es frenado por el propio individuo utilizando el pié y los sifones extendidos. Estos desplazamientos no alcanzan a más de 2 o 3 m por vez aunque la migración continúa por largos períodos. Cava en la arena utilizando activamente su pié en forma de hacha. En cuanto a los juveniles ellos son removidos por la acción turbulenta de las olas.

A diferencia de lo expresado por Ansell & Trevallion (1969) de que *Donax incarnatus* Sowerby de la India y otras especies tropicales y subtropicales mantienen en forma permanente la misma posición relativa con el borde del agua, las poblaciones de *D. hanleyanus* permanecen durante las horas de baja marea embancadas en los niveles superiores del Piso Mediolitoral. Este comportamiento sería también diferente al registrado para *Donax trunculus* Linn. en Algeria (Moueza, 1972), que es descripto como pasivo en relación a los ritmos mareales.

Son estos fenómenos de zonación y migración los que permiten a las poblaciones de *Donax* en general, y a las de *D. hanleyanus* en particular, mantener un equilibrio dinámico en biotopos caracterizados por su inestabilidad.

En caso de fuertes tormentas suelen producirse en la región de Villa Gesell varazones o embancamientos de una buena parte de la población en los niveles inferiores del Piso Supralitoral. Los mecanismos homeostáticos quedan anulados y se producen mortalidades masivas por desecación que provocan marcados descensos en la densidad específica.

Otro factor que incide en la distribución normal de las poblaciones de *Donax hanleyanus* son las corrientes de retorno del oleaje. No sólo arrastran ejemplares, especialmente juveniles, hacia los niveles inferiores del Piso Mediolitoral, sino que suele producir agrupamientos desusados en los canalículos (*rill-marks*) y en las olladas de marea.

Densidad

La densidad específica de *Donax hanleyanus* en la zona de Villa Gesell es muy variable debido al fraccionamiento de la población en núcleos aislados y a la acción de factores ambientales, que ya hemos analizado.

Durante los años 1967/69 se realizaron un total de 46 censos ecológicos en la región de Villa Gesell-Faro Querandí donde el "berberecho" representa en número el 25,91% de la megalofauna (frecuencia en los censos 60,86%) con una densidad

media de 160,9 ind./m² (Olivier et al., 1971). Sin embargo, al considerar solamente los 28 censos en que se registró su presencia, la densidad específica media aumenta considerablemente hasta alcanzar 264 ind./m² (densidad máxima 2.496 ind./m²). En épocas de reclutamiento suelen producirse agrupaciones de ejemplares juveniles en áreas restringidas del estran donde la densidad específica suele sobrepasar los 10.000 ind./m².

En la localidad de Cariló, situada 10 km al norte de Villa Gesell, se realizaron en enero de 1968 censos ecológicos experimentales cuyos resultados promedios se resumen a continuación:

Densidad específica numérica	448 ind./m²
Densidad específica en peso total (Pt)	640 gr/m²
Peso húmedo decalcificado. .	161,6 gr/m² (25,25% del Pt)
Peso seco decalcificado	32,8 gr/m² (5,12% del Pt)

Reproducción

De los muestreos bioestadísticos periódicos se utilizó una submuestra de 20 ejemplares adultos (mayores de 20 mm Lt) que fueron fijados en formaldehido al 10% con el objeto de examinar el desarrollo gonadal de *Donax hanleyanus*. Algunas muestras debieron ser eliminadas debido a su deficiente conservación por lo que las observaciones sobre el ciclo sexual del "berberecho" sólo cubrieron un año (febrero de 1968 a febrero de 1969).

La gónada de *Donax hanleyanus* rodea la masa visceral y se extiende hasta la mitad del pié. Una vez aislada fué incluida en parafina y los cortes histológicos teñidos con hematoxilina-eosina.

Para el reconocimiento de los diferentes estadíos sexuales se siguió la metodología desarrollada por Christiansen (en Olivier et al., 1971) para *Mesodesma mactroides* y por Penchaszadeh (1971) para *Mytilus platensis*.

Los elementos sexuales de *Donax hanleyanus* (Fig. 4) pueden identificarse durante todo el año aun cuando, luego de los períodos de desove, se evidencian procesos de reabsorción tal cual ocurre en *Mesodesma mactroides* (Christiansen, op. cit.). Sin embargo, tomando en cuenta el diámetro de los ovocitos es posible diferenciar las distintas faces del desarrollo gonadal en el que se destaca la ausencia de un período de reposo absoluto que es característico en el ciclo sexual de *Mytilus platensis* (Penchaszadeh, 1971). El diámetro de los ovocitos maduros oscila entre 55 y 73 μm (Fig. 5). En síntesis hemos diferenciado 3 etapas del ciclo gonadal a saber:

1). *Vitelogénesis*: los ovocitos aumentan de diámetro hasta alcanzar la talla de la madurez sexual;

2). *Desove parcial*: una porción de los ovocitos son liberados mientras que los restantes entran en reabsorción;

3). *Recuperación gonadal*: simultáneamente con el proceso de reabsorción ovocitaria se reinicia la generación de nuevos ovocitos.

Hemos podido detectar durante el año estudiado 2 períodos de desove: uno de fines de invierno-comienzos de primavera (agosto-setiembre) y el otro estival (enero-febrero). Como consecuencia de ellos registramos asimismo 2 períodos de reclutamiento: uno en octubre-noviembre y el otro en febrero-marzo. Este último reclutamiento también fué registrado en el verano de 1970. Sin embargo nos ha llamado poderosamente la atención la ausencia de un reclutamiento masivo en el verano de 1968 y en la primavera de 1969. Ello coincide, en el primer caso, con la ausencia de desove y posterior reabsorción de los ovocitos, fenómeno revelado por el análisis histológico; en la primavera de 1969 no pudimos determinar el origen de la ausencia de reclutas ya que en julio los ovocitos se hallaban en estado de madurez avanzada. Una explicación a estas anomalías puede ser dada en virtud de que la región en que se realizaron nuestros estudios se encuentra en el límite austral de su distribución geográfica donde algunos factores ecológicos pueden actuar como limitantes.

Otro hecho interesante que puede inferirse de los estudios histológicos realizados es que la diferenciación sexual se evidencia a los 2 meses en los machos y a los 4 meses en las hembras. La talla de la primera maduración sexual fué registrada para individuos de 14,5 mm Lt aunque no constatamos evidencias de evacuación pero sí certeza de reabsorción ovocitaria.

Muy poca información acerca de la reproducción del género *Donax* es de nuestro conocimiento; la proporcionada por Nayar (1955) y Wade (1968) se basa en una metodología diferente a la que hemos

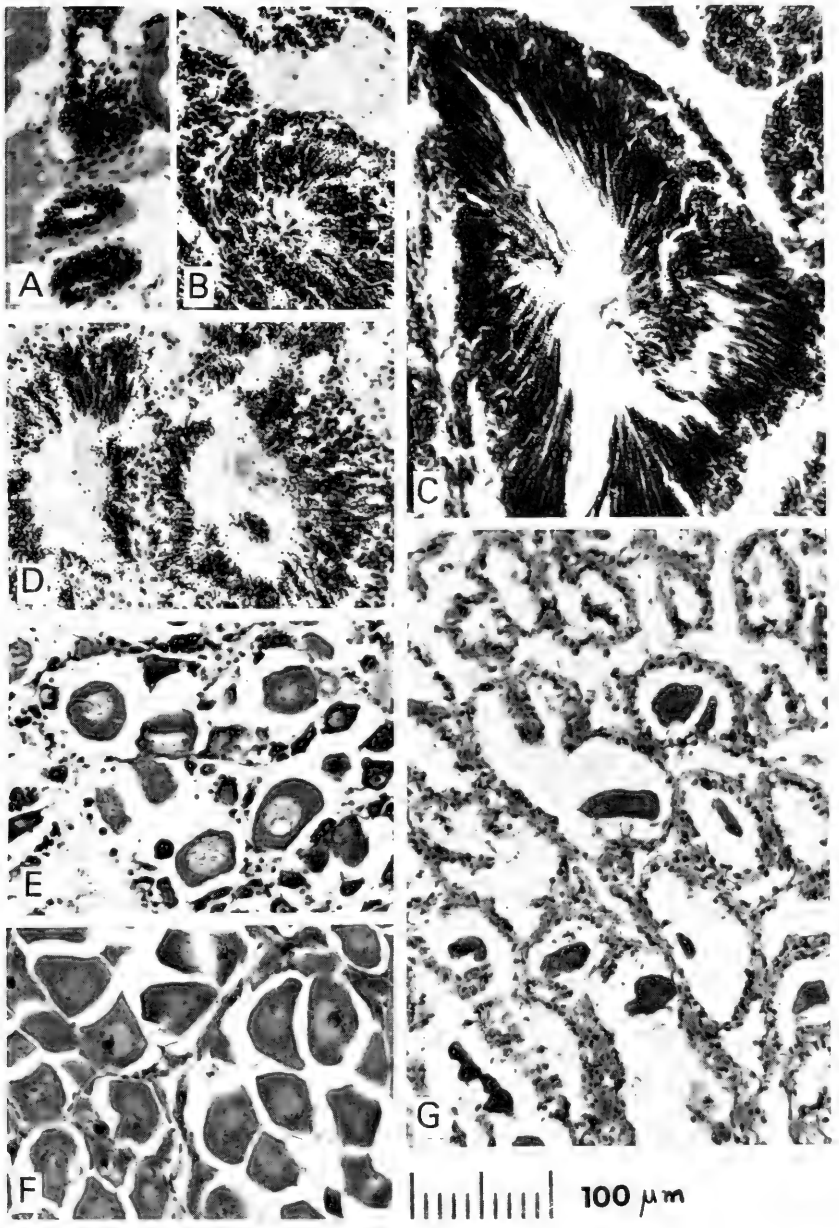


FIG. 4. Aspectos del ciclo gonadal de *Donax hanleyanus*. A. Macho de 2 meses de edad; primera formación de alveolos. B. Macho de 4 meses de edad, con formación de espermatocitos y algunas espermátidas. C. Macho en estadío de madurez avanzada; las espermátidas se encuentran alineadas radialmente. D. Macho en estadío de post-evacuación con activa reabsorción de elementos remanentes. E. Hembra de 5 meses de edad en maduración incipiente; gran cantidad de ovocitos en crecimiento se encuentran sobre las paredes de los alvéolos; se observan algunos ovocitos maduros. F. Hembra madura; los ovocitos ocupan toda la cavidad alveolar y presentan contornos poligonales. G. Hembra en estadío de post-evacuación con reabsorción de ovocitos remanentes y proliferación simultánea de células foliculares.

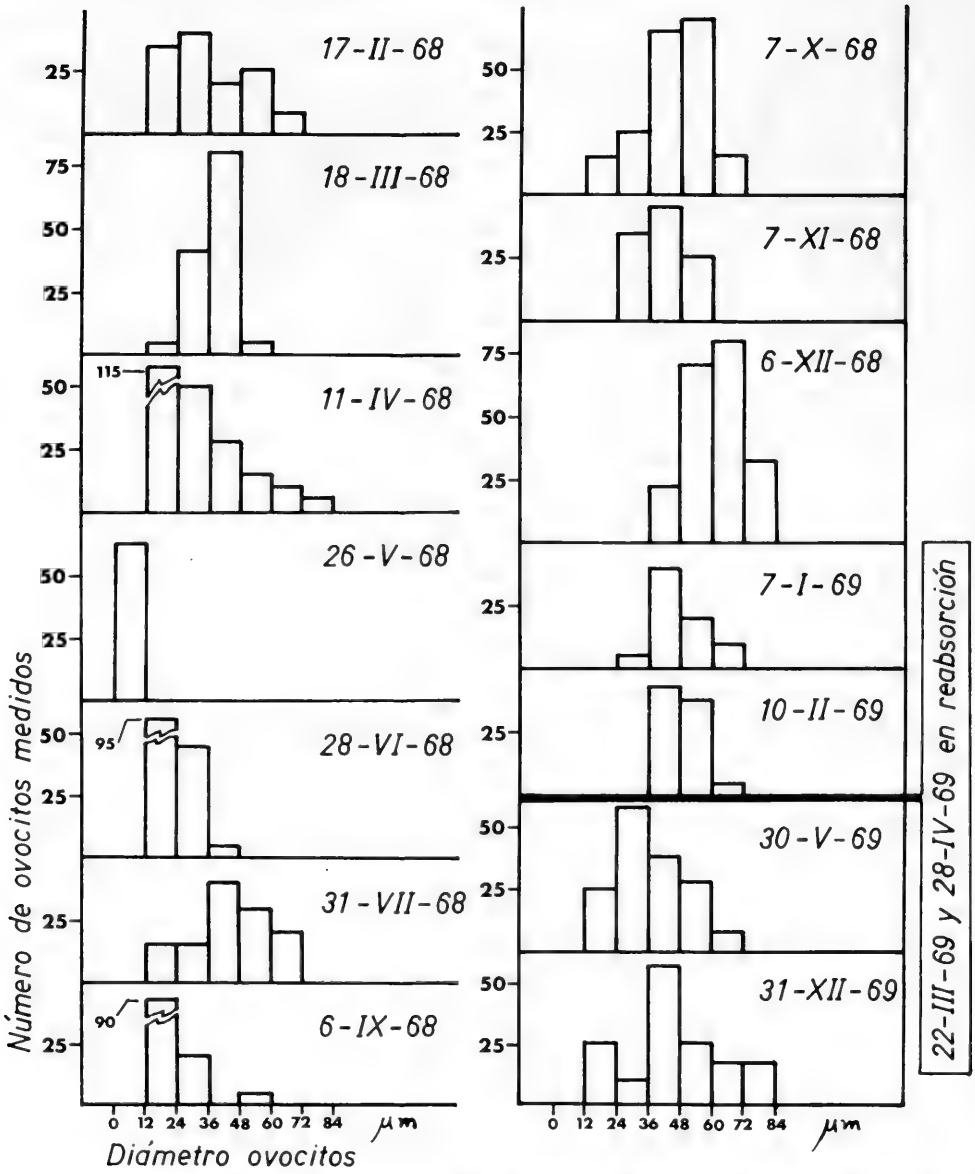
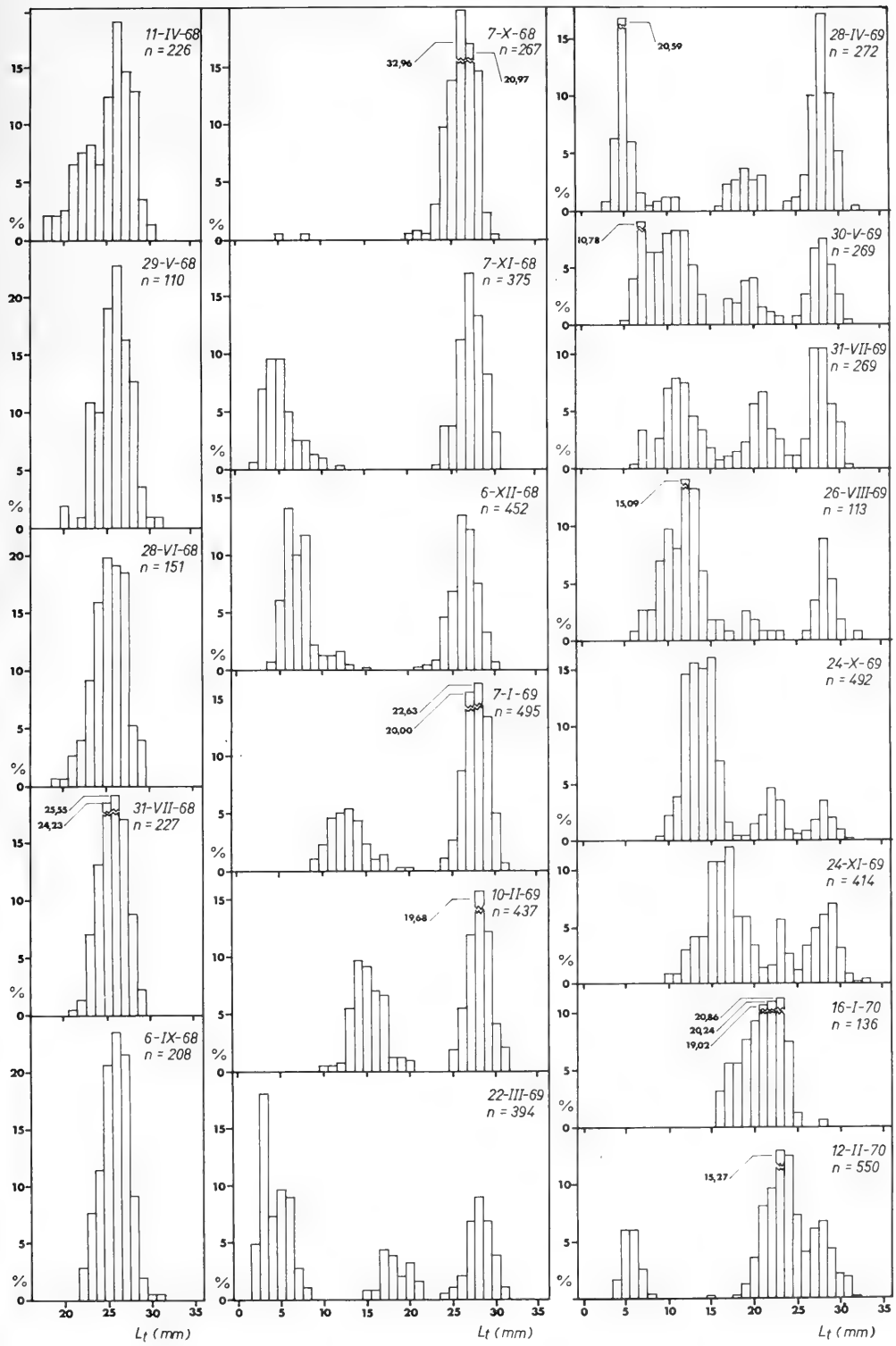


FIG. 5. Distribución mensual de la frecuencia de tallas de los ovocitos durante el ciclo sexual de *Donax hanleyanus*.

utilizado. El primero de estos autores estudiando *Donax cuneatus* Linn. en la India destacó que esa especie puede diferenciarse sexualmente a los 11 mm Lt. Alcanza el estado de madurez gonadal después de los 14 mm Lt (10 meses de edad) y desova por primera vez al año de edad. Por su parte Wade (op. cit.) al estudiar *Donax denticulatus* en Jamaica constató dos períodos de desove, uno en agosto y otro en enero, mientras que en febrero y julio se hallaba en estado de reposo o recuperación gonadal.

Comparando nuestros resultados con los

FIG. 6. Distribuciones originales de las frecuencias de talla en la población de *Donax hanleyanus* de Villa Gesell por clases de un milimetro en representación porcentual.


11-IV-68
n = 226
7-X-68
n = 267
32,96
20,97
28-IV-69
n = 272
20,59
29-V-68
n = 110
7-XI-68
n = 375
10,78
30-V-69
n = 269
31-VII-69
n = 269
6-XII-68
n = 452
15,09
26-VIII-69
n = 113
28-VI-68
n = 151
7-I-69
n = 495
22,63
20,00
24-X-69
n = 492
25,55
24,23
31-VII-68
n = 227
10-II-69
n = 437
19,68
24-XI-69
n = 414
6-IX-68
n = 208
22-III-69
n = 394
20,86
20,24
19,02
16-I-70
n = 136
15,27
12-II-70
n = 550
%
Lt (mm)

anteriores se hace evidente que la diferenciación sexual de *Donax hanleyanus* es mucho más temprana que la de *D. cuneatus*; que la madurez sexual se produce a una talla similar aunque a menor edad y que el primer desove es también coincidente (entre 11 y 15 meses de edad). En lo que respecta a comparación con *D. denticulatus* es evidente que en *D. hanleyanus* no existen los períodos de reposo sexual a que hace referencia Wade (1968).

Crecimiento

Para el estudio del crecimiento se utilizó el método del desplazamiento de picos modales en distribuciones de frecuencia de tallas a través del tiempo.

La Fig. 6 muestra la existencia de 3 períodos de reclutamiento muy bién marcados por la abundancia de ejemplares de muy pequeña talla: octubre de 1968, febrero de 1969 y febrero de 1970 (ya hemos hecho mención a las anomalías registradas en la reproducción en el verano de 1968 y la primavera de 1969).

En ese mismo histograma es posible visualizar que las dos primeras generaciones reclutadas alcanzan una talla modal de 22,5 mm Lt en los primeros 12 meses. De acuerdo con esta información es posible inferir que los individuos que en abril de 1968 tenían una talla modal de 23,5 mm Lt correspondían a la generación estival del año anterior, es decir que tenían 15 meses de edad; sin embargo, la estructura de esa generación no era homogénea por la presencia de individuos que evidentemente correspondían a generaciones anteriores. Estos desaparecieron en octubre y en febrero de 1969 la talla modal de aquella generación se había elevado a 28,5 mm Lt (2 años de edad) y en noviembre a 29,5 mm Lt (2 años y 9 meses de edad).

El ritmo de crecimiento de *D. hanleyanus*, a juzgar por los mismos desplazamientos modales (Fig. 7) es muy acelerado en los primeros meses de vida de tal forma que en el primer año alcanza las 2/3 partes de su talla máxima. Es probable que en otras áreas de su distribución geográfica estos índices sufran ciertas modificaciones. Tan es así que, comparando las estructuras de las poblaciones de "berberecho" de Mar Azul y Faro Querandí en enero de 1969, se manifestaba una pronunciada diferencia de las tallas máximas: 35,5 mm Lt en Faro Querandí y 31,5 mm Lt en Mar Azul (talla media: 31,83 mm Lt y 27,69 mm Lt respectivamente). Varios factores, entre los que podrían señalarse la disponibilidad de alimentos y densidad de las poblaciones, podrían incidir en estas apreciables variaciones.

La clave largo-edad de *Donax hanleyanus* para la localidad de Villa Gesell puede sintetizarse de la siguiente manera:

Edad 0 = 22,5 mm Lt
Edad 1+ = 28,5 mm Lt
Edad 2+ = 29,5 mm Lt (33 meses)

y las tasas mensuales de crecimiento

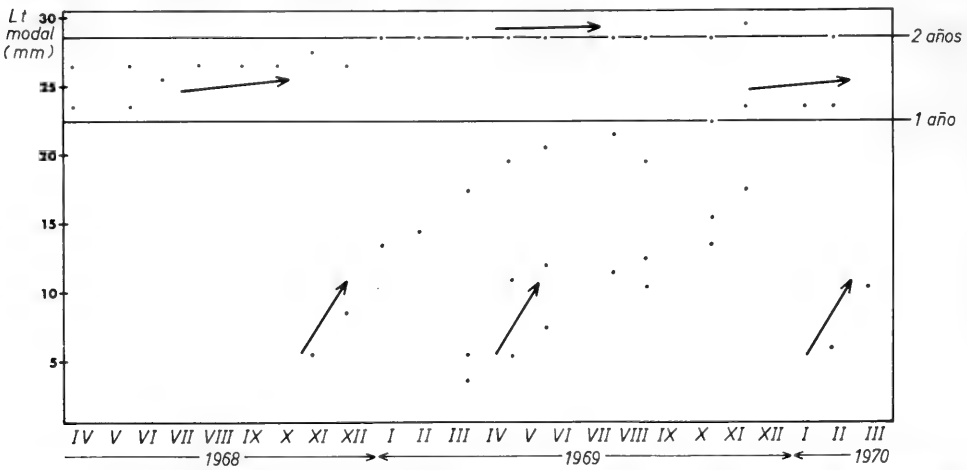


FIG. 7. Tasa de crecimiento de *Donax hanleyanus* de Villa Gesell y tiempo de cada generación en alcanzar una talla dada. Las rectas horizontales representan las tallas medias para cada edad y las flechas indican las distintas generaciones.

respectivas fueron de 1,83 mm, 0,49 mm y 0,02 mm. El crecimiento en el primer año de vida es muy semejante a los obtenidos por Lozada (com. pers.) para *D. denticulatus* en Venezuela, y para *Donax incarnatus* Sowerby de Shertallai, India (Ansell et al., 1972a, b).

Si bien no son comparables consignamos a continuación tasas de crecimiento máximo obtenidas para otras especies: *D. denticulatus*, 2,5-3,0 mm/mes en Jamaica (Wade, 1968); *D. cuneatus*, 1,75 mm/mes en India (Nayar, 1955); *D. variabilis* Say, 1,75 mm/mes en Texas, Estados Unidos (Loesch, 1957); y *D. tumidus* Philippi, 1,0 mm/mes en Texas, Estados Unidos (Loesch, 1957).

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ABSTRACT

ECOLOGY OF A POPULATION OF THE COQUINA CLAM *DONAX HANLEYANUS* AT VILLA GESELL, ARGENTINA

Pablo E. Penchaszadeh and Santiago R. Olivier

Donax hanleyanus is an associate and subdominant species in the community of *Mesodesma mactroides* in the sandy beaches north of Mar del Plata, Argentina. Although present in fossil deposits farther south, records of this species farther south in the Recent fauna began only in 1962/63. Its recent dispersal from the Uruguayan coast south of Río de la Plata must be attributed to favorable oceanographic conditions allowing the larvae to bypass the estuary. Colonization of the beaches was progessive and due to larval transport by ocean currents.

This coquina clam prefers to live at the upper levels of the midlittoral zone. During high tide there is intensive migration. Occasional stranding of individuals in the supralittoral zone is an important cause of mass mortality.

The density of the population varies both locally and seasonally, gradually increasing during periods of recruitment of new generations.

At Villa Gesell, *Donax hanleyanus* has 2 spawning periods: one in late winter and early spring (August-September), the other in summer (January-February). These periods can be altered by unpredictable climatic factors. Two corresponding periods of recruitment have been recorded: one in October-November and the other in February-March. Sexual differentiation is evident at age 2 months in males and 4 months in females. There is no period of complete gonadal inactivity.

D. hanleyanus lives 3 years and the rate of growth is 1.83, 0.49 and 0.02 mm/month for the first, second and third year respectively.

J.S.

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THE MOLLUSCS OF THE SEA OF GALILEE

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ABSTRACT

The small number of species living today in the Sea of Galilee can be explained only by the drastic geological events that occurred along the Jordan Rift Valley during the Pleistocene. The fresh-water faunas in the Central Jordan Valley were especially reduced following the post-Mindel, when most of the water bodies were eliminated, until as late as post-Würm. The fresh-water faunas were particularly impoverished during Würm time, when an extensive salt (= Lisan) lake existed along the Jordan Valley. Two major lakes remained after shrinkage of the salt lake: the Dead Sea in the south, and the Sea of Galilee in the north. The latter became fresh again in a rather short time (during post-Würm). The Sea of Galilee was repopulated only by species which survived around the formerly salt lake throughout the Würm. Moreover, the present Sea of Galilee does not maintain satisfactory environmental conditions for thin-shelled molluscs. The molluscs living in the lake proper are reduced to the following species: *Unio (Psilunio) semirugatus* Lamarck, *Unio (Limnium) terminalis* Bourguignat, *Corbicula fluminalis* (Müller), *Theodoxus jordani* (Sowerby), *Pyrgula barroisi* Dautzenberg, *Bithynia hawaderiana* (Bourguignat), *Melanopsis praemorsum* (Linnaeus), and *Melanoides tuberculata* (Müller).

Three main factors limit the distribution of molluscs in the lake: 1) the anaerobic zone; 2) the character of the bottom, and 3) storms and wave action.

Two biotopes are clearly distinguishable: one consists of gravel and cobble, on which the rock-dwellers live; the second consists of sands, silts and muds, in which the mud-dwellers live. The rock-dwellers are *Melanopsis praemorsum, Theodoxus jordani* and *Bithynia hawaderiana.* All the rest are mud-dwellers. No species strays from its proper biotope.

The abundance of the rock-dwellers, which are exclusively herbivorous, is determined by the high plant productivity of the littoral zone. The prosobranch populations grow densest where the aquatic vegetation is most luxuriant. The vegetation is greatly influenced by some edaphic factors and by the electrolyte content of the water. Hence a positive correlation may be drawn between the density of the rock-dwellers and the nutrient content of the water. The Jordan River has major influence upon the quantities of molluscs, supplying sediments, organic material, electrolytes and other nutrients enriching the eastern and southern shores. On the other hand, the principal limiting factor for molluscs in the lake are waves. After severe storms, most of the populations inhabiting the rocks perish, as do the mud-dwellers which remain close to the shore. Molluscs on small stones have greater chances of being swept away; indeed only juveniles are found on small stones.

The breeding season is restricted to the short period when the water temperature begins to rise from its lowest point, and when there is a sharp coincident decrease in salinity. Whether it is the water temperature or the salinity change which induces breeding is unknown; neither of these explain the shorter breeding season in the autumn when the water temperature is beginning to drop and the salinity increases.

Most of the prosobranchs presently inhabiting the Sea of Galilee are Tethyan relicts. *Bithynia* is the most ancient among them, having originated probably in the Palaeogene of Europe, and having invaded the Near East after the regression of the Paratethys towards the end of the Miocene. *Theodoxus* probably originated in the Sarmatic Province, and spread southward during the Pliocene, when it inhabited the already existing fresh waters of Syria-Israel and Mesopotamia. *Melanopsis* evolved in fresh water during this time, when the upper Miocene sea regressions occurred; it either originated in the Levantine province *in situ*, or invaded the area later from a Sarmatic origin. *Pyrgula* was established in the fresh waters of the Sarmatic province in the Pliocene, and invaded the Jordan system through the Orontes (Syria) in the late Pliocene or early Pleistocene.

INTRODUCTION

In the first part of this paper I discuss the geological history of the lake, especially the metamorphoses of the Central Jordan Valley, and the resultant effects on the malacofauna of the area. A survey of the palaeolimnology of the lake provides evidence to explain the small number of species, as well as their tolerance of environmental changes. There is little doubt that the few species of Recent molluscs are merely survivors of the critical periods of the valley's history since the Neogene and especially the Pleistocene.

Early investigation of the existing lake and the identification of its faunal assemblages led to much debate, but little interest was directed towards the geology and palaeontology of the Jordan Valley. Many hypotheses were given credence from only superficial understanding of the Jordan Valley's geological history. This lack of correlation impeded proper analyses of many basic problems inherent in a situation where the flora and fauna of 3 zoogeographic areas meet and overlap.

One of the first scholars to describe a part of the molluscan fauna of the Sea of Galilee was Bourguignat (1853), who based his study on material collected by M.F. de Saulcy. Locard (1883) employed the collection assembled by Ernest Chantre from Lake Homs and Lake of Antioch (Antakya, Turkey), as well as Bourguignat's collection from the Sea of Galilee, to revise the taxonomy of all Levantine fresh-water molluscs. Dr. N. Annandale visited the area in 1912 with the purpose of studying the Sea of Galilee; he subsequently forwarded the molluscs to Preston for analysis and description (1914). Preston complicated the study by describing no fewer than 17 species from a single population of *Unio terminalis,* and 5 species from one population of *Corbicula fluminalis;* at the same time, a few species common in the area today are missing from his inventories. Pallary paid a number of visits to the Levant and summarized his malacological interpretations in 2 volumes on the Syrian area (1929, 1939), and 1 volume on the Egyptian area (1909).

Blanckenhorn (1897) visited Palestine and Syria and contributed valuable descriptions of fossil and living molluscs of Syria and the Jordan Valley. Germain (1921, 1922) used the collections of Henri Gadeau de Kerville to produce 2 volumes considered to the present day as the definitive source of knowledge on the fresh-water and terrestrial molluscs of Syria and Palestine. Other scientists who indirectly contributed to our knowledge of the biology of the lake were Lartet (1878), Tristram (1884), and Barrois (1894).

I attempt to solve a few of the numerous problems connected with the origin of molluscs in the Sea of Galilee but am hindered, perforce, by the lack of information regarding their history in the Levant since the Neogene. The greater part of my discussion deals with the ecology and distribution of the molluscs in the lake, and will consider the primary influences of its physical qualities.

PALAEOLIMNOLOGY OF THE CENTRAL JORDAN VALLEY

From the numerous studies published to date on the origin of the Central Jordan Valley, two basic facts emerge clearly. The first is that the Valley was gradually deepened during its history and not long ago reached its maximal depth. Secondly, since the Valley was established by downward tectonic movements as early as the Neogene period, various water bodies have existed there more or less continuously throughout the Neogene and Pleistocene until the present. There has been a long history of various—sometimes drastic—metamorphoses in the nature of the water bodies, the geomorphology and the relief of the Jordan Valley. One of the resulting lakes is the present Sea of Galilee. The astonishingly low diversity of faunal elements inhabiting the lake, and the strange life cycles displayed by some in their tolerance of environmental alterations, are direct results of the extreme changes which have taken place since the Neogene.

During the early part of the Middle Pleistocene (= Mindel), no salt-water body remained in the Central Jordan Valley, as evidenced by the remains of an extensive fresh-water lake, known as the 'Ubeidiya Formation, found in this area. Large quantities of fresh-water molluscs, and fossil vertebrates (including fresh-water fishes and turtles) were found (Haas, 1966, 1968), as well as remains of very old human cultures. It has been suggested that these cultures were contemporaneous with Olduvai Bed II

(East Africa), a culture related to the early Middle Pleistocene (see Picard & Baida, 1966a, b; Tchernov, 1968a). This extended fresh-water lake (the 'Ubeidiya lake) existed for a long time, and was not immediately derived from the sea or saline waters. Analysis of the entire fauna suggests that a fresh-water fauna was established in the Valley long before. Connections with the sea would have been sealed. The diastrophic movements which occurred, probably during the Lower Pleistocene, resulted in the development of lakes in the already formed graben followed by the gradual freshening of the waters.

It is essential to inquire where the fresh-water molluscs originated in light of the fact that during the Miocene, and to a lesser extent in the Pliocene, this entire area was firmly connected with the Tethys. Even during Miocene times, when the graben was still in its incipient stage, some surrounding areas had fresh-water lakes. In such fresh-water sediments trionychids and crocodiles were found together with *Mastodon angustidens* and *Deinotherium bavaricum* (Savage & Tchernov, 1968). During the Miocene and Pliocene, fresh-water lakes also existed outside the developing graben, as in the Golan Heights, the Damascus district on the Syrian Plateau, the Orontes Valley and Lake Homs in Syria. Some of these lakes, which supported rich fresh-water faunas, were connected hydrologically with the developing Jordan Valley. Once isolation of the Jordan Valley from the Tethys occurred, these faunal elements could scatter and populate the freshening water bodies of the Valley. In the northernmost part of the graben, the Huleh basin, it appears that the penetration of sea water ceased earlier still. As this part of the Jordan Valley was of higher elevation as early as the Lower Pleistocene, and the general flow of water was southward, a permanent stock of fresh-water faunal elements was contained here for a long time. The fact that the Dead Sea area in the S. was lower than in the N. is proven by the isolated existence there of rock salt beds which are lacking in the north (Neev & Emery, 1967).

Por (1963) suggests that it was during the "wet pluvial periods [that] the Jordan Valley served as the gateway for penetration of tropical African elements towards the North." This does not coincide with the data that tropical elements existed in the Levant, and especially along the Asiatic Rift-Valley, at least since the Miocene. The Levant (and adjacent areas to the N.) was biogeographically connected until at least the late Miocene with both the Ethiopian and the Oriental units (Tchernov, 1968b). Later, tropical Africa was separated from the Palaeotropical regions by the development of the desert belt. Today, as well as during the Pleistocene, the tropical elements are only relicts, many of them isolated in special habitats. Furthermore, it does not appear that the invasion of Palaearctic elements into the area was limited to the post-glacial era as stressed by Por (1963). Palaearctic animals are known, for instance, as early as the early Middle Pleistocene 'Ubeidiya time (Haas, 1968), where they appear in the majority.

The fresh-water lakes already existing during the Miocene formed the primary habitation of fresh-water molluscs in the Near East, an element which was of triple geographical origin: African, southern Asian and Tethyan. Continental, semi-continental, and semi-marine basins established a continuous link with the African continent through N. Sinai and the Suez basin on one side, and with the E. through Mesopotamia on the other. The Jordan Valley was the meeting ground of the 2 major zoogeographical units, in addition to a major molluscan group originating from the Tethys.

During the long sedimentary 'Ubeidiya sequence in the Middle Pleistocene, a rich mollusc fauna was preserved in almost every layer. A portion of this assemblage was first investigated and thoroughly described as the *"Melanopsis* Stufe" by Blanckenhorn & Oppenheim (1927), and by Picard (1934) as the "Levantinische Stufe." Those Middle Pleistocene molluscs were subsequently redetermined by the writer. It seems that, in the case of some species, especially of the genus *Melanopsis,* too much splitting was done in the earlier studies; this will be discussed later in further detail. The list of the 'Ubeidiya mollusc fauna is as follows:

Theodoxus jordani (Sowerby)
Valvata saulcyi Bourguignat
Bithynia hawaderiana (Bourguignat)
Melanopsis praemorsum (Linnaeus)
Melanoides dadiana Oppenheim

Melanoides tuberculata (Müller)
Ancylus fluviatilis (Müller)
Planorbis planorbis (Linnaeus)
Gyraulus piscinarum Bourguignat
Unio (Limnium) terminalis Bourguignat
Unio (Psilunio) semirugatus Lamarck
Leguminaia chantrei Locard
Corbicula fluminalis (Müller)

A portion of the 'Ubeidiya sequence could have been contemporary with the "Hamarmar Formation" (Zak, 1967) in the Dead Sea area which continued for quite a long time thereafter, probably through the whole of Mindel, Mindel/Riss, and even (although without direct evidence) during part of Riss. When salt was later deposited in the Dead Sea area a fresh-water lake was already in existence in the Central Jordan Valley. This fact, however, does not indicate a dry climatic condition at that time. On the contrary, the faunistic evidence indicates (Haas, 1966, 1968; Tchernov, 1968a) that the lake was surrounded by dense vegetation, swamps, and woods.

Very little is known about the geological events occurring in the Central Jordan Valley during Mindel/Riss. Most probably the 'Ubeidiya lake contracted but did not completely disappear until early Riss. On the other hand, it is well established (Horowitz, 1968) that the Huleh basin, in the Upper Jordan Valley, maintained a fresh-water lake during the Riss. On its S. shores a rich assemblage of fossil molluscs and mammals was uncovered. The discovery of an advanced Acheulian culture site at Jisr-Banat-Yaqub demonstrates man's early occupation of this shore (Hooijer, 1959; Stekelis, 1960).

The total elimination of the fresh-water malacofauna in the Dead Sea occurred in post-Mindelian times, when the fresh-water body turned permanently salty. The only populations surviving to the present day were those left in springs or minute fresh-water bodies around the edges of the salt lake. Even now, in the Lower Jordan Valley, some very restricted mollusc populations survive in a few isolated springs. In contrast, in the Huleh basin a rich malacofauna is known which has suffered few changes and has continued to exist since the Riss without interruption (Picard, 1963). Although the old Huleh Lake regressed during Riss/Würm times (Horowitz, 1968), it continued as a fresh-water lake throughout the Würm until the present. The malacofaunal assemblage of Jisr-Banat-Yaqub (contemporaneous more or less with Mid- to Late Riss) does not differ basically from that of 'Ubeidiya, indicating that common characteristics were shared by the old 'Ubeidiya lake and the 'Riss-Huleh' lake. Those malacofaunal elements eliminated from the Central Jordan Valley continued to exist without many changes in the N. part of the valley. Comparison between the faunas of the Huleh basin and the Sea of Galilee proper is given in Table 1.

The fresh-water faunas in the Central Jordan Valley were especially reduced following the post-Mindel. After the elimination of the 'Ubeidiya lake, fresh-water bodies vanished from the area until as late as post-Würm. The fresh-water faunas were particularly impoverished during Würm time, when extensive areas of the Jordan Valley were filled with a huge salt lake extending from Ein-Hatzeva (S. of the Dead Sea) to the Sea of Galilee, the "Lisan lake". This lake came into existence about 70,000 yr. B.C. (somewhat earlier in its southern part). As almost no faunal remains have been found in the whole Lisan Stage, we do not know the aquatic fauna in the graben during the entire Würm. But the deposits confirm that "the water was hypersaline, though probably less so than the present Dead Sea" (Neev & Emery, 1967).

The Lisan lake disappeared at the end of the Würm, 20,000 yr. B.C., as a result of the general lowering of the water level in the graben due either to further tectonics, a sharp climatic change, or a combination of both—a point still in dispute.

Two major lakes remained following shrinkage of the Lisan lake—the Dead Sea in the S. and the Sea of Galilee in the Central Jordan Valley. The latter probably became fresh again in rather a short time. The possible existence of a few more small lakes between the 2 is still under discussion. Neev & Emery (1967) suggest a minor tectonic movement as the main cause for the disappearance of the Lisan lake and the resulting formation of the present Dead Sea. In the post-Würm the remaining fresh-water faunal elements in the surrounding Central Jordan Valley springs, rivers, and

TABLE 1. The rich malacofauna of the Huleh basin compared with the Sea of Galilee proper. Note the absence of pulmonates from the lake, but the presence of thick-shelled prosobranchs and bivalves.

HULEH BASIN	SEA OF GALILEE
Prosobranchia	
Theodoxus jordani (Sowerby)	*Theodoxus jordani* (Sowerby)
Valvata saulcyi Bourguignat	—
Bithynia hawaderiana (Bourguignat)	*Bithynia hawaderiana* (Bourguignat)
—	*Pyrgula barroisi* Dautzenberg
Melanopsis praemorsum (Linnaeus)	*Melanopsis praemorsum* (Linnaeus)
Melanoides tuberculata (Müller)	*Melanoides tuberculata* (Müller)
Pulmonata	
Lymnaea lagotis (Schrank)	—
Lymnaea palustris (Müller)	—
Planorbis planorbis (Linnaeus)	—
Gyraulus piscinarum Bourguignat	—
Ancylus fluviatilis (Müller)	—
Succinea pfeifferi Rossmässler	—
Bivalvia	
Sphaerium lacustre (Müller)	—
Pisidium casertanum (Poli)	—
Unio (Limnium) terminalis Bourguignat	*Unio (Limnium) terminalis* Bourguignat
—	*Unio (Psilunio) semirugatus* Lamarck
Corbicula fluminalis (Müller)	*Corbicula fluminalis* (Müller)

TABLE 2. The main palaeolimnological events in the Jordan Valley during the Pleistocene.

Age		Years B.P.	Lower Jordan Valley	Central Jordan Valley	Upper Jordan Valley
Post-Würm		-20,000	Dead Sea	Sea of Galilee	Huleh lake
Würm	Upper Pleistocene		Lisan Stage	?	
		-70,000			
Riss/Würm	—	-120,000		"Naharayim"	(contraction)
Riss	Middle Pleistocene			?	Old Huleh lake (= "*Viviparus* beds")
Mindel/Riss			Salt stage		
Mindel			"Hamarmar Formation"	'Ubeidiya Formation (Erq-el-Ahmar)	Jisr-Banat-Yaqub ("the tilted complex", Picard 1963)
	—	-500,000			
Günz/Mindel	Lower Pleistocene		"Amora Formation"	?	?
Günz					

pools began to repopulate the new Sea of Galilee. Thus the relatively new molluscan population of the Sea of Galilee, not older than 20,000 years (Table 2), represents the offspring of much older populations elsewhere in the graben. The Sea of Galilee was repopulated only by species which could survive in isolated habitats until the end of the Würm, and only very few were able to do so. The present Sea of Galilee does not maintain satisfactory environmental conditions for thin-shelled molluscs such as *Lymnaea, Planorbis,* etc. (see Table 1), as will be discussed in the next section. However, only a few species surviving in the immediate surroundings of the Central Jordan Valley were able to penetrate the new lake; hence the restricted number of mollusc species in the lake.

The sharp changes in the composition of the water bodies in the Jordan Valley have been a major influence upon the molluscs living there today. The few species in the Sea of Galilee are euryhaline, thick-shelled, and only rarely associated with water vegetation. In the shallow Huleh lake, where

little change has occurred since the Riss, many species are associated with water plants.

THE RECENT MOLLUSCS OF THE SEA OF GALILEE

Most studies of the molluscs of the Near East in general, and the Sea of Galilee in particular, were made at the beginning of this century. Many of the malacologists of that period, whether experiencing firsthand knowledge in the area, or merely studying the collections of others, were extreme "splitters" in their taxonomic practices. As a result, some dozens of species from this lake were named from a single population. Today, we must deal with an extreme number of species assigned to the malacofauna of the whole country.

Most of the mollusc species presently inhabiting the Sea of Galilee belong to old and conservative groups with very low rates of evolutionary change. During their histories they experienced extreme physicochemical changes in their environments; those which survived throughout are therefore unusually tolerant. It seems as if none of the species living in the lake, or in other areas of Israel, showed any specific changes during the whole of the Pleistocene; changes never rose above the intraspecific level. These highly adaptable species diverged into a variety of ecotypes and formed huge polymorphic groups. Despite the sharp changes of the environments in the water bodies of the Levant occurring since the Neogene, there were scarcely any specific changes in most of the genera "caught" and isolated in the graben. In addition, no sharp climatic fluctuations in Israel and the surrounding area have been proven (Tchernov, 1968b). Those climatic changes which did occur (whether correlated or not with the global glaciations) were too slight to affect the fresh-water faunas. If specific changes occurred at all in the Levant fresh-water molluscs, they were not the result of a changing climate. The general changes in the faunas were mainly the result of the major geomorphological changes occurring in the Levant since the Neogene and throughout the Pleistocene rather than a response to climatic fluctuations. These geomorphological changes had considerable impact, naturally, on the water bodies and their faunas.

Only 8 species of mollusc inhabit the lake—3 bivalves and 5 gastropods. More species were recognized by several earlier authors. Following the results of more than a hundred dredgings covering most of the lake's bottom, and from examination of the shores during the 5-year period, not a single specimen of the extraneous species mentioned earlier was found alive. A few of these species were represented by some shells (mostly empty), which, especially after storms, were swept into the lake by streams coming from the Upper Jordan and a few rivers around the lake. These were usually found at the end of the winter when water flow is at its maximum.

No endemic molluscs are known from the lake, but in the light of what has already been discussed endemics are not expected. However, there are some distinctive local varieties, especially of *Melanopsis*.

A descriptive systematic study is not the aim of this work. The following list of species is accompanied by a few comments on the systematics of some of the species.

The living species of the lake are as follows:

Family UNIONIDAE
Genus *Unio* Philipsson, 1788
Subgenus *Psilunio* Stefanescu, 1896
(= *Rhombunio* Germain, 1911)
Unio (Psilunio) semirugatus Lamarck, 1819

Israel and Syria are presumably inhabited by only 1 species, while towards Mesopotamia other closely related species are found. All of the various species of *Psilunio* or *Rhombunio* formerly mentioned from Israel and vicinity seem to belong to related populations of this same species, representing a very narrow range of variation. *Unio (Psilunio) homsensis* Lea, from Lake Homs in Syria, may differ from the Israeli form, but further studies are required to clarify this point. It seems that the *semirugatus* group borders upon Mesopotamia. It is possible that a broken topocline exists throughout the Near East, following roughly an E.-W. axis. Towards Mesopotamia *Psilunio* appears more elongate and narrow. *Unio (Psilunio) barroisi* Drouët is an elongate form living in the Orontes and Lake Homs. The Israeli form

has a strictly rhomboidal shell; it is much shorter and wider than the other Near Eastern forms. Located at the margin of the distribution of this subgenus, Israel has one, fairly constant species, whereas Mesopotamia, probably closer to the center of distribution, has more species. In Israel *Unio semirugatus* is not known outside the Sea of Galilee (Figs. 16, 18).

Subgenus *Limnium* Oken, 1815

Unio (Limnium) terminalis Bourguignat, 1852

This species is common in most of the fresh water bodies throughout the Near East which are less than meio-mesohaline (Dahl, 1956). It is absent from small springs or wadi streams. Prior to the intensive settlement during the 20th century, the main distribution in Israel included the whole Jordan water system, mainly Huleh lake, the Sea of Galilee, and most rivers of the coastal plain. Today it is confined almost exclusively to the Sea of Galilee, owing mainly to the water pollution of the other water bodies (Fig. 17).

Family CYRENIDAE

Genus *Corbicula* Megerle von Mühlfeld, 1811

Corbicula (Corbicula) fluminalis (Müller, 1774)

The Recent distribution of this species includes most of the Near East, from the Sarmatic province in the N., throughout the Levant and the Oriental areas. While restricted in North Africa to the Nile, it occupied the whole circum-Mediterranean region during the Quaternary. Its former and present distributions are given in detail by Germain (1921, 1922). It appears that, during the Pliocene and early Pleistocene, this species populated most of the fresh water bodies established after the regressing Tethys at the end of the Miocene.

As with *Unio terminalis,* this species occupied all the available larger water bodies in Israel, i.e., the Sea of Galilee and the remnant of Huleh lake. Formerly it also inhabited most of the rivers along the coastal plain (Figs. 14-15).

Family NERITIDAE

Genus *Theodoxus* Montfort, 1810

Subgenus *Neritaea* Roth, 1855

Theodoxus (Neritaea) jordani (Sowerby, 1836)

The Palaearctic region is inhabited by 2 major subgenera: *Theodoxus* s. s., and *Neritaea.* These probably separated at the end of the Miocene (when the Tethys regressed), and diversified especially in the Ponto-Aralo-Caspian province. The data show, however, that during the Pliocene *Neritaea* was already restricted to the Near East; *Theodoxus* s. s. occupied Asia Minor and Europe since the Oligocene. A common ancestor appears to have inhabited the whole Oligo-Miocene Tethys region, dividing thereafter into 2 main groups in the Sarmatic province—a zoogeographical boundary for many faunistic elements. According to Soós (1943), the distribution of *Theodoxus (Theodoxus) fluviatilis* is "from the northern shores of the [A]Egean, central Italy, Sicily and northern Spain, to the British Isles, the southern part of Scandinavia and Finland, and in Russia from Leningrad to the mouth of the Don; but it is absent from the water system of the Danube and the whole area of the upper reaches of the Rhine". These other areas are inhabited by other species of *Theodoxus* s. s.

Theodoxus (Neritaea) jordani inhabits the whole Near East, including Asia Minor, Mesopotamia and Egypt (the Nile). The only probable overlap in the distribution of this species with *Theodoxus* s. s. is in Turkey. Pallary (1929, 1939) mentioned *Theodoxus fluviatilis orientalis* from Mesopotamia (Ain Arouss, Bâhlik), a record which must be challenged because no one since has mentioned *Theodoxus fluviatilis* from the whole Mesopotamian region, and no one has implemented better criteria than shell morphology to establish whether the type-specimen from this unexpected locality is indeed a member of the *fluviatilis* group. *Theodoxus mesopotamica* Mousson, *Theodoxus euphratica* Mousson, and *Theodoxus cinctilla* von Martens were described from Mesopotamia as members of the *Neritaea* group, and are probably closely related to *Theodoxus jordani.* But a comparative study of these has never been done.

Israel is inhabited by *Theodoxus jordani* alone. A detailed study of this species is now in progress by Mrs. Dagan of the Department of Zoology, Hebrew University, Jerusalem (personal communication). There is great variability in shell morphology, body anatomy, radula and colour pattern in the Israeli populations. These variations are intraspecific. *Theodoxus macrii* Sowerby, often mentioned as a separate species from Israel, is a synonym, being within the limits of variation of *T. jordani*. Almost all water bodies of Israel are inhabited by *Theodoxus.* It seems to be absent from all areas never reached by the Neogene Tethys.

Of special interest is the extraordinary population of *Theodoxus* inhabiting the spring of Tabgha, Ein-Nur, near the Sea of Galilee, not far from Kefar Nahum (Figs. 19-20). This is an underground spring situated in almost complete darkness, with a nearly constant temperature of 28.4° C and a total salinity of about 3000 mg Cl/l; this spring is inhabited by Tethyan marine relicts such as the famous *Typhlocaris galilea* Calman.

According to Por (1962, 1963), the arthropod relicts of the Jordan Valley and other places in Israel are of Pliocene origin, when the Tethys was still connected with the evolving Jordan Valley (see also the earlier section on palaeolimnology). *Theodoxus,* although originally of marine origin, invaded this area much later from an open body of fresh water. This secondary invasion presumably took place when the lake was either dry or turning salty, probably during the Würm (= the Lisan Stage). At that time, surrounding water bodies were invaded by the remnants of fresh-water faunas, which found shelter there. Such a pattern holds true today along the Dead Sea shores. Judging from its anatomy and radula, the *Theodoxus* of Ein-Nur still closely resembles the *Theodoxus* of the lake. Moreover, it probably interbreeds with the populations inhabiting the other springs in the vicinity of the Tabgha area. However, this isolation was of such duration that interesting changes did occur. The population survives in almost absolute darkness, exploits a very restricted diet of algae, lives in a stable medium of salty hot water, has become almost transparent (lacking pigment in both shell and body), and is somewhat dwarfed. It is worth noting that the exposure of these transparent specimens to light for 2-3 months results in almost normal pigmentation of both epithelium and shell. This means that light is required for synthesis of pigments in *Theodoxus*. This subject is also being studied in more detail by Dagan (personal communication).

The other molluscs in the Ein-Nur spring are a dwarf form of *Melanopsis praemorsum* and *Hydrobia* sp. This *Melanopsis* population, possessing reduced pigmentation, is also a secondary invader from a fresh-water source. The same is true for *Hydrobia.* Only the arthropods are real relicts, as in a number of other water bodies in Israel (Por, 1962, 1963).

Considering the extreme variability of the shells, colour patterns, and the extreme isolation of the varied water bodies which it inhabits, the radula teeth of *Theodoxus* are surprisingly constant in shape throughout the country (Fig. 22).

Family VALVATIDAE
Genus *Valvata* O. F. Müller, 1774
Subgenus *Cincinna* Férussac, 1821
Valvata (Cincinna) saulcyi Bourguignat, 1853

This species is not a valid member of the lake malacofauna. Three individuals were found alive in the lake only once (May 27, 1964) at a depth of 31.5 m. This occurred when a small amount of oxygen remained from the aerobic period of the winter. This same year proved to be an exceptional one in respect to the periods of circulation within the lake. Together with the 3 specimens, many live plants were dredged from the bottom. All these organisms were brought into the lake by a strong current from the Jordan River following a severe storm; the oxygen remained at the lake bottom and kept them alive for some time. Only rarely has *Valvata* been found alive in small brooks running into the lake. Empty *Valvata* shells are found quite frequently in the lake, especially in winter.

Family TRUNCATELLIDAE
Subfamily Pyrgulinae
Genus *Pyrgula* Cristofori & Jan, 1832
Pyrgula barroisi Dautzenberg, 1894
(= *Pyrgula barroisi râbensis* Blanckenhorn, 1897)

Following the events which occurred in the Mediterranean area during the late Pliocene, especially in the Sarmatic province, the pyrgulines arose in the increasingly fresh water bodies of the Ponto-Aralo-Caspian region. From here they began to spread while radiating and speciating into several species and subgenera. Poliński (1932) pointed out that *Pyrgula (Xestopyrgula) bukowsky* Poliński from Lake Ochrid, and *Pyrgula (Xestopyrgula) pfeifferi* Weber from Lake Egerdir (Anatolia), are closely related to *Pyrgula (Xestopyrgula) barroisi* Dautzenberg. Judging by the radula (Fig. 24), *Pyrgula barroisi* is very different from *Xestopyrgula* and does not seem to belong to this subgenus. However, more detailed studies are needed to evaluate this relationship and to examine how far *Pyrgula barroisi* has deviated from the other pyrguline groups. It seems that from the original Sarmatic area 1 group extended W. to Europe. A 2nd group extended toward S. and E. Russia, while a 3rd group penetrated S. to Mesopotamia and to the Syrian and Israeli regions. It then split into small populations in small and isolated water bodies, but not long enough to allow new species to evolve. The Syrian and Israeli forms are very closely related. Only a few populations continued to survive to recent times. It is most probable, considering the present distribution in the Near East, that the group reached the Jordan Valley from the Orontes (Syria). However, *Pyrgula* has never been found in Israel outside the Sea of Galilee.

Dautzenberg (1894) was the first to record *Pyrgula* from the Near East (specimens were collected by Barrois in Syria and Palestine). Barrois emphasized that he dredged the material from a depth of 25 m. in the S. part of the lake. No wonder the material consisted, as Dautzenberg stressed, exclusively of empty shells! Preston (1914), in his list of species determined from Annandale's collection from the Sea of Galilee, mentioned *Pyrgula* as existing in the S. part of the lake, but again he says that the material consisted of empty shells only. The Sea of Galilee is the only place where it was found in Israel (Figs. 5-6, 9).

The variability of the shell is quite great, ranging from highly carinated (a single carina per whorl) to smooth specimens, from very oblong individuals to more bulliform types. The latter are only rarely found. The Syrian form, described by Blanckenhorn (1897) as *Pyrgula barroisi râbensis* (= *Pyrgula râbensis syriaca* Pallary, 1930) is much larger than the specimens described from the Sea of Galilee, and differs also in having fewer whorls. Pallary (1939) described another variant from Syria, namely *P. râbensis porrecta*, which is more elongate. Still in question, however, is the Mesopotamian form *Pyrgula euphratica*, which judging by the shape of the shell seems closely related to *Pyrgula barroisi.*

Family BITHYNIIDAE
Genus *Bithynia* Leach, 1818
Bithynia (Bithynia) hawaderiana Bourguignat, 1853

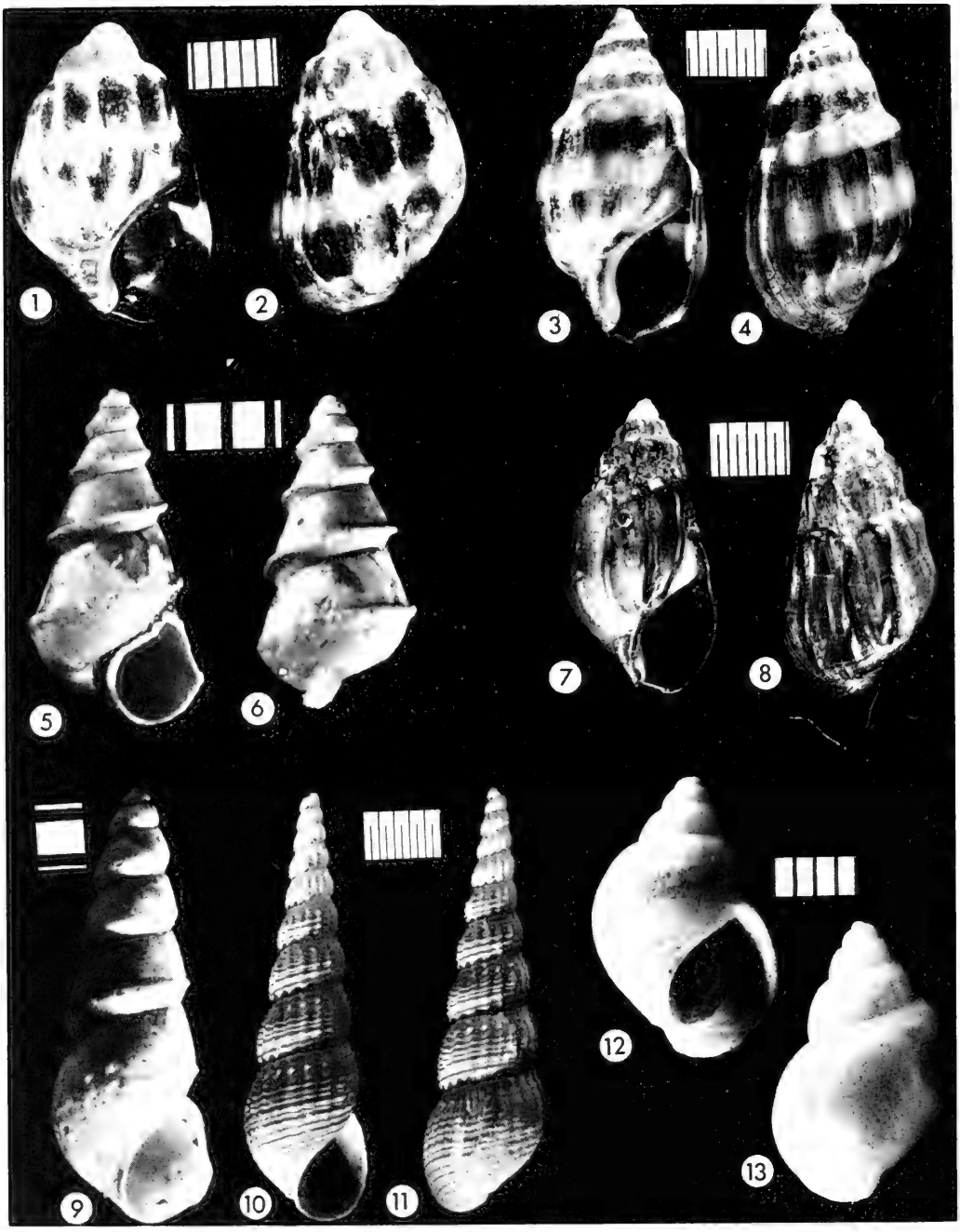
This mollusc occurs throughout the Near East; it is well represented in most of the larger water bodies. In general, it is not found in springs, swamps or small brooks, where as a rule *Hydrobia* takes its place.

The subgenus *Bithynia* invaded fresh water earlier than *Theodoxus* or *Melanopsis*, quite possibly as early as the Palaeogene. The Near East species is distinctly less euryhaline than either *Theodoxus* or *Melanopsis;* it is unable to survive in water bodies with a salinity higher than 1200 mg Cl/l. *B. hawaderiana* requires well-aerated (usually running), and clean fresh water. This may be why it is most common along the E. shore of the Sea of Galilee and in the Jordan River, which are places with strong water currents. It lives only under stones or rocks where it can penetrate and hide deep in cracks and holes. During winter or stormy periods it avoids the dangerous shores and retreats into deeper water where it searches for hard substrates.

Before the elimination of natural water bodies in Israel, *B. hawaderiana* was widespread in most rivers of the coastal plain, lake Huleh, Sea of Galilee and most of the Jordan River (Figs. 12-13). Its radular teeth are shown in Fig. 25.

Usually, the Israeli populations of *Hydrobia* and *Bithynia* do not occur together; *Hydrobia* is absent from large water bodies.

Family THIARIDAE
Subfamily Melanopsinae
Genus *Melanopsis* Férussac, 1807
Melanopsis (Melanopsis) praemorsum (Linnaeus, 1758)



FIGS. 1-2. *Melanopsis praemorsum.* Sea of Galilee. Shells like this from the W. side of the lake are lower, wider and more rounded than the shells from the E. ('En-Gev) population. Scale divisions 1 mm.
FIGS. 3-4. *Melanopsis praemorsum.* Sea of Galilee. Coloured shell from the E. side of the lake ('En-Gev population). Scale divisions 0.5 mm.
FIGS. 5-6. *Pyrgula barroisi.* Sea of Galilee. Zemah area, 15 m. Highly carinated shell. Scale divisions 1 mm.
FIGS. 7-8. *Melanopsis praemorsum.* Sea of Galilee. Black shell from the E. side of the lake ('En-Gev population). Scale divisions 0.5 mm.

The shoreline of the Tethys towards the end of the Miocene marks the limits of distribution of *Melanopsis* today. It was during this period that the Tethys underwent a rapid regression, severing its connection with the Atlantic Ocean, which resulted in its transformation into a series of saline, brackish to almost fresh-water lagoons. In most oligohaline water bodies (the condition of the Sea of Galilee today), some prosobranchs persisted in warm water, the most typical being *Melanopsis*. This is a circum-Mediterranean genus, widespread in Africa N. of the Sahara, but absent from the Nile complex where Ethiopian malacofaunal elements exist. *Melanopsis* is widespread in S. Europe, Catalonia, throughout the Italian peninsula (where it reaches the Po plain), the Balearic and Aegean Islands, Sicily, Greece, Rhodes and Cyprus. It is also common in most of the Ponto-Aralo-Caspian provinces, Turkey and southern Caucasia, where the rapid retreat of the Tethys at the end of the Miocene left many bodies of water. Elsewhere the genus is found throughout Mesopotamia and the Near East (Syria, Lebanon and Israel).

Later, during the Pliocene when the Gibraltar Strait reopened into the Atlantic Ocean and the Tethys again became a marine domain, isolated groups of *Melanopsis* were left in those water bodies which receded from the renewed Tethys as a re-established Mediterranean Sea. These forms underwent very slow speciation. *Melanopsis* seems to be very "stable". The isolation of the genus, however, in permanent or transitory water bodies varying in size and chemical properties allowed a high degree of intraspecific polymorphism.

Populations of *Melanopsis* are widespread in the entire Near East, including some of the most isolated springs deep in the desert. There are vast numbers of ecotypes; all, however, belong to *Melanopsis praemorsum* (Figs. 1-4, 7-8, 21-22). Their radular teeth are almost invariable (Fig. 26). While the species is firmly established in most of the water bodies of Syria, Lebanon and Israel, it has not yet been found in the Sinai Peninsula, except in Ein Kudeirat near the Israeli border.

As a fossil, the species is known from the early Middle Pleistocene 'Ubeidiya Formation (Picard, 1934), from the lake deposits of Jisr-Banat-Yaqub (Mindel) [see Table 2] (Picard 1963), and from the deposits of the old Huleh lake (Middle and Upper Pleistocene).

Subfamily Thiarinae
Genus *Melanoides* Olivier, 1804
Melanoides (Melanoides) tuberculata (O. F. Müller, 1774)

This species occupies most of the inland water bodies of the Near East, the Sinai Peninsula and N. and E. Africa. It is common in Israel in all the water bodies with muddy bottoms, and sometimes in oligohaline waters with a content of up to 4000 mg Cl/l.

Contrary to the situation with *Melanopsis* populations of Israel and North Africa (Llabador, 1935), more saline and hotter waters produce larger individuals of *Melanoides tuberculata*. Large numbers of very big specimens were found in quantity in oligohaline and relatively hot springs around the Dead Sea. In the Sea of Galilee or other colder, cleaner fresh-water bodies, the species appears in much reduced densities.

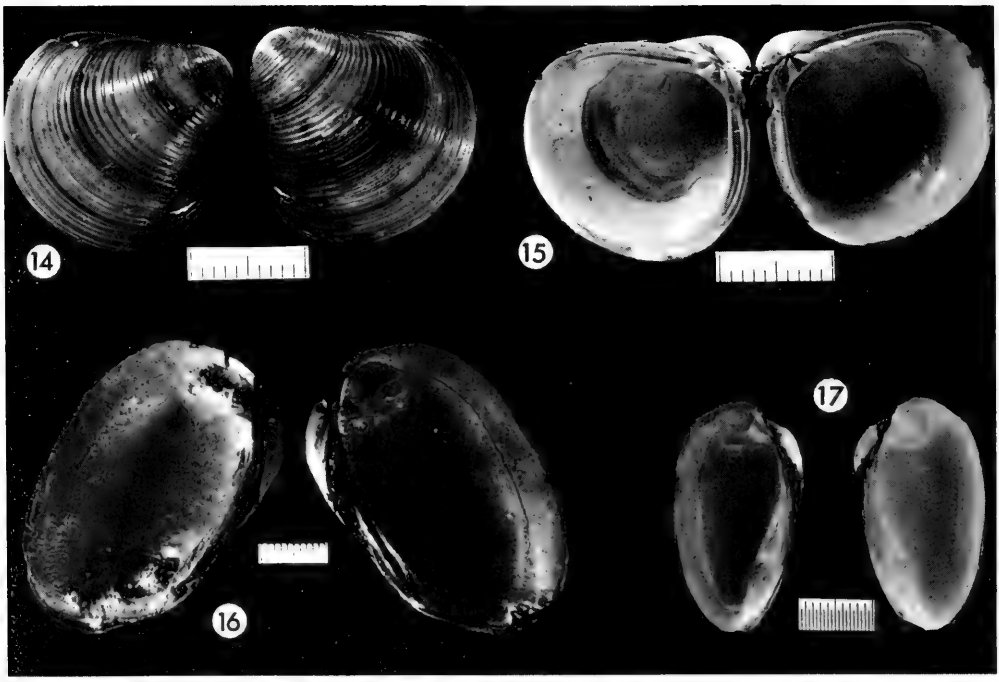
Except for size and shape differences, there is little variability in *Melanoides* of Israel and Sinai. The radular teeth (Fig. 27) are almost identical in most of the populations studied in Israel and Sinai. The shape of the shell (Figs. 10-11) is highly dependent on the special properties of the water body; any small change is reflected by the mantle; the radula is far less variable.

THE ECOLOGY AND DISTRIBUTION OF MOLLUSCS IN THE SEA OF GALILEE

The physical characteristics of the lake and its main habitats

As a result of the many distinctive changes undergone during the history of the lakes in the Central Jordan Valley (i.e. degrees of salinity, the nature of the littoral zone, the character of the bottom, etc.), and in comparison with other lakes,

FIG. 9. *Pyrgula barroisi.* Sea of Galilee. Zemah area, 10 m. Slightly carinated shell. Scale division 1 mm.
FIGS. 10-11. *Melanoides tuberculata.* Sea of Galilee. Ginnosar area, 5 m. Scale divisions 0.5 mm.
FIGS. 12-13. *Bithynia hawaderiana.* Sea of Galilee. 'En-Gev area. Scale divisions 1 mm.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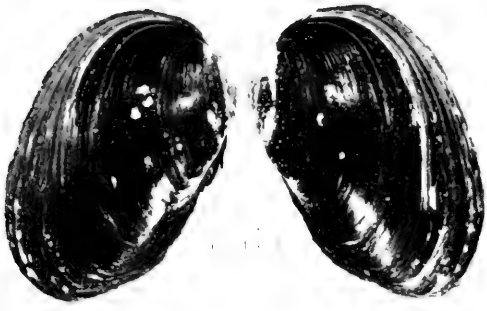
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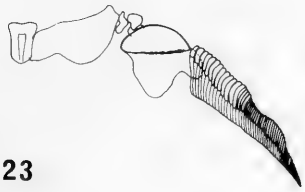

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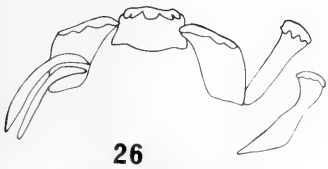

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FIG. 23. *Theodoxus jordani.* Sea of Galilee. Radula teeth: half of a transverse row.
FIG. 24. *Pyrgula barroisi.* Sea of Galilee. Radula teeth: half of a transverse row.
FIG. 25. *Bithynia hawaderiana.* Sea of Galilee. Radula teeth: half of a transverse row.
FIG. 26. *Melanopsis praemorsum.* Sea of Galilee. Radula teeth: whole transverse row. No radular differences were found between the costate form (*"Melanopsis costata"*) living in the open lake, and the smooth form inhabiting the brooks and springs around the lake. Whenever the 2 forms meet, extensive interbreeding takes place. .
FIG. 27. *Melanoides tuberculata.* A-Tor, S. Sinai, an extremely isolated spring. Radula teeth: half of a transverse row; teeth are identical with those in the population of the Sea of Galilee.

only a very small number of molluscan species survives; the gastropods are exclusively euryhaline prosobranchs.

The principal limiting factors determining the distribution of molluscs in the lake today are threefold: 1) the anaerobic zone; 2) the character of the bottom, and 3) storms and wave action.

As a consequence of an annual summer stagnation of 8 months, a zone sterile for molluscs is established below a depth of about 15 m. During the remaining 4 months the lake is of uniform temperature and aerobic, with water circulation beginning in December and ending in March. The pronounced stratification starts in April when the epilimnion absorbs most of the solar radiation, "while the hypolimnion is heated slowly and to a negligible degree" (Oren, 1957). Thus, while oxygen is available throughout the lake during the winter months the molluscs may penetrate a short distance into the summer stagnation zone. During the spring, when an anaerobic hypolimnion is re-established below 15 m, all the molluscs which had spread into this region die. Moreover, the anaerobic area is acid enough to dissolve the shells.

FIGS. 14-15. *Corbicula fluminalis.* Near Sea of Galilee. Tabgha area (near Kefar Nahum), 2 m. Scale divisions 1 mm.
FIG. 16. *Unio (Psilunio) semirugatus.* Sea of Galilee. Zemah area, 5 m. Scale divisions 1 mm.
FIG. 17. *Unio (Limnium) terminalis.* Sea of Galilee. Zemah area, 5 m. Scale divisions 0.5 mm.
FIG. 18. *Unio (Psilunio) semirugatus.* Sea of Galilee. Zemah area, 5 m. Scale divisions 1 mm.
FIGS. 19-20. *Theodoxus jordani.* Near Sea of Galilee. Tabgha spring. Scale divisions 0.5 mm.
FIGS. 21-22. *Melanopsis praemorsum.* Near Sea of Galilee. Tabgha spring (near Kefar Nahum); smooth form. Scale divisions 0.5 mm.

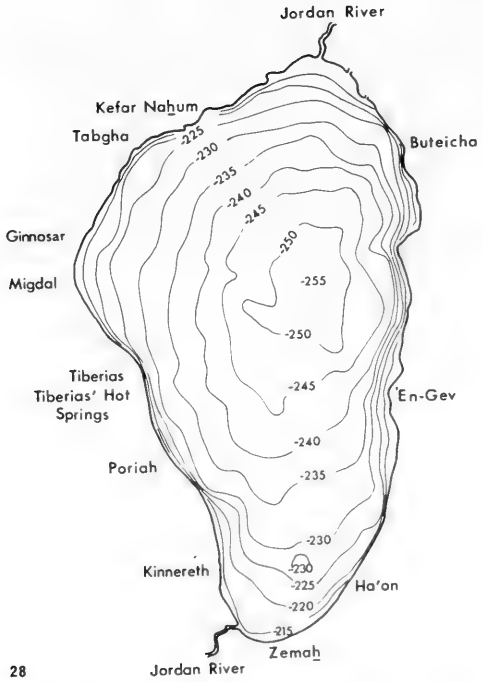


FIG. 28. Bathymetric map of the Sea of Galilee (after Oren, 1957), including the principal surrounding localities. Depths in m. Sea level of the lake is stated by Oren to be -210 m. Total length of the lake is ca. 6.5 km, and maximum width ca. 4.5 km.

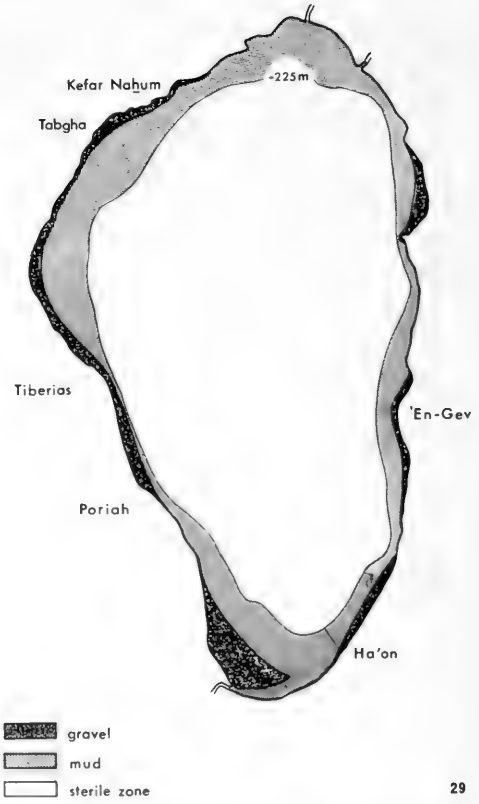


FIG. 29. The 2 main molluscan habitats in the Sea of Galilee: 1) the rocky littoral zone, composed mainly of cobbles, gravel, and pebbles not smaller than 15 cm; 2) the muddy zone (principally sublittoral—down to 15 m), composed of silts, coarse- to fine-grained sands, and clays. The zone sterile of moluscs is generally composed of marls.

The kind of bottom is an important factor determining the distribution of molluscs in the lake, especially along the W. shore. Down to a depth of 5 or sometimes 7 m (Kinnereth area, Fig. 28), the shores are generally covered with gravels and cobbles of a mean size of 15 cm (Fig. 29). Fine-grained gravels (with a mean size of 0.2 cm) disappear after a short distance. Gravels of a size of 15 cm are important for our discussion as this is usually the minimal size certain molluscs can use as a substrate or for shelter. Only in a few places along the W. shore of the lake are there interruptions in the gravels: immediately N. of Kinnereth (Figs. 28-29), where the gravels go to a depth of 1 m; 3 km N. of Kinnereth, where the shore is muddy and where there are no gravels for a short stretch, and N.E. of Kefar Nahum towards the entrance of the Jordan River into the lake, where the entire littoral zone is muddy and devoid of gravel.

On the E. side of the lake cobbles and gravels are much more scattered along the littoral zone (Figs. 28-29). Moreover, at places covered by gravels, the depth never surpasses 3-5 m. Gravels of the 15 cm size are restricted on the E. side of the lake to a limited area: from 6 km S. of 'En-Gev N. to el-Kursi. Farther to the N. gravel is no deeper than 2 m. Thus it forms a very narrow, rocky, littoral belt, notwithstanding that the E. littoral zones are shallower than those in the W. Farther to the N. the rocky zone completely disappears. The stretch from Ha'on to near the present outlet of the Jordan River is devoid of gravels as well. There are, in effect, 2 main isolated strips of gravels at present in the lake; one, much developed and extensive on the W. side, and one more restricted in area on the E. shore. The faunas of these 2 regions are isolated from each other.

The bottom of the lake in the anaerobic zone, from 15 m to 45 m max. depth, is muddy, composed mainly of clays, silts, and (rarely) sands, and usually lacks living molluscs (Fig. 29). In certain places mud occurs at much shallower depths. There is a sandy strip along the littoral of the E. shore (originating from the Neogene sandstone along the E. escarpment). It should be emphasized that silty sediments are scattered all along the S. half of the lake, while its N. portion has much finer sediments, mostly clay-mud. This is because transportation of material into the lake takes place predominantly from the N. inlet of the Jordan River and the discharge of a few other small rivers and brooks. The initial deposition of material occurs in the area around the Jordan's entrance. The deposits become thinner along the shores towards the S. and fill the entire bottom of the lake to a depth of -225 (or -15) m. No silty material, nor any other coarser sediments, are found deeper than -230 (or -20) m. The transition between the rocky zone (made of gravels and cobbles mixed with finer material) and the homogeneous mud is abrupt owing mainly to the fact that down to the depth of 10-15 m the shores are relatively steep.

Another interesting phenomenon along the littoral zone is the exposure of Lisan marls (Lisan Stage = Würm), mainly in the S.E. corner of the lake. Another exposure of marls of unknown origin, but probably of Upper Palaeolithic age, appears in the area N. of el-Kursi. These deposits were exposed by wave action and are too hard to be dug into by burrowing molluscs such as *Unio* or *Melanoides*. On the other hand, as both types of deposits are covered by water, a thin film of colloid-like material is formed at the contact with the water, creating an extremely smooth surface. This is too smooth for any mollusc to crawl on. Molluscs wandering by chance into these areas soon die. This shore lacks the rocks, stones, gravels or cobbles which offer a substrate for rock-dwelling molluscs. These marly littoral zones are devoid of molluscs, and form an almost absolute barrier between the E. and W. molluscan populations of the lake.

Another zone creating a similar barrier extends from the shore of Kefar Naḥum N.E. to the entrance of the Jordan River. This zone is composed of very soft clay-mud on which no rock-dwellers can move. Large masses of this mud are continuously discharged by the Jordan. Lack of wave action (E. winds are rare) prevents water circulation in this corner of the lake, and causes anaerobic conditions even close to shore. Thus, even burrowing mud-dwellers cannot live in this particular area. A very few rock-dwellers, living on boulders, are scattered along the shore.

Two biotopes are clearly distinguishable in the lake: one, consisting of gravel and cobble which we will call the rocky habitat and where the rock-dwellers live, and the second, consisting of sands, silts and muds, the muddy habitat, in which the mud-dwellers live. The rock-dwellers are: *Melanopsis praemorsum, Theodoxus jordani,* and *Bithynia hawaderiana.* The mud-dwellers are: *Unio (Limnium) terminalis, Unio (Psilunio) semirugatus, Corbicula fluminalis, Melanoides tuberculata,* and *Pyrgula barroisi.* No species strays from its proper biotope.

The rocky zone forms a very narrow strip along the shores, usually not deeper than 5 m. The rock-dwellers are restricted to this narrow, clear-cut, littoral strip, while the mud-dwellers appear in a separate strip of greater depth, but never deeper than 15 m or into the anaerobic zone. Waves are destructive to many animals, and are especially detrimental to molluscs. Throughout the year wave action is mainly directed (by W. winds) towards the E. shore of the lake. When E. winds occur (and, although quite rare, they are generally strong winds), strong waves reach the W. shore. Waves which are unusually strong sweep away the stones and gravels. Much stronger turbulence will cause large stones and cobbles to be swept away offshore. Once this has occurred, the many rock-dwellers attached to these stones are thrown ashore where they die. Indeed, after a severe storm, most of the populations inhabiting the rocks perish, as do the mud-dwellers which remain close to the shore. Molluscs on fine gravels have even greater chances of being swept away. Indeed, mature rock-dwellers are not found on small stones; only juvenile specimens are. A correlation is found between the age of a mollusc and the size of its rocky substrate. The chances of survival increase in positive correlation with the size of the substrate. One year old *Melanopsis* are

30a

FIG. 30a. Distribution of *Melanopsis praemorsum* in the Sea of Galilee.

30b

FIG. 30b. Distribution of *Theodoxus jordani* in the Sea of Galilee.

most frequent on stones measuring 5 × 5 × 5 cm. Analysis revealed an average of 10 juvenile specimens per stone, 6 individuals of an intermediate age, and only 1 mature specimen. On stones with dimensions of 10 × 10 × 10 cm, 6 juvenile specimens, 5 intermediates, and 3 adults were usually found. Stones with dimensions of 20 × 20 × 20 cm averaged only 3 juvenile specimens, 6 intermediates, and 8 adults.

The habits of *Theodoxus* help survival from storms because it is a much smaller creature, roundish in shape, and can easily penetrate small holes of stones and rocks. In addition, it can attach more firmly to the substrate. The same is true for *Bithynia*. Even when these molluscs are dislocated by storms, their chances for survival are higher because they remain inside their holes rather than being swept out into the lethal muddy bottom or the shore. Usually *Theodoxus* are on smaller stones than *Melanopsis*.

The comparative distribution of the molluscs in the lake

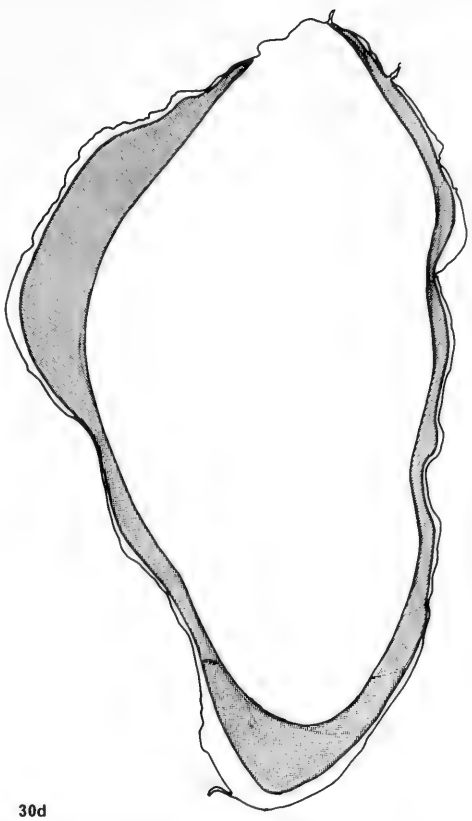
1. *Rock-dwellers*

Melanopsis praemorsum inhabits the entire rocky zone along the lake, from the shore down to 5 m; only a few specimens were found at greater depths (Fig. 30a). It is the most littoral form in the lake. In those areas where *Phragmites communis* lives, the main underwater stem is used as a substrate. (This is not used either by *Bithynia* or *Theodoxus*.) When the lake is calm and the weather hot and humid, *Melanopsis* creeps on stones above water close to shore. *Theodoxus,* on the other hand, is still common down to a depth of 5 m.

In the Tabgha area (Figs. 28-29), where the littoral bottom is steep and gravels are prevalent deep in the lake, a few *Melanopsis* live at a depth of 10 m. But N.E., not far from the inlet of the Jordan, the shores

30c

FIG. 30c. Distribution of *Bithynia hawaderiana* in the Sea of Galilee.



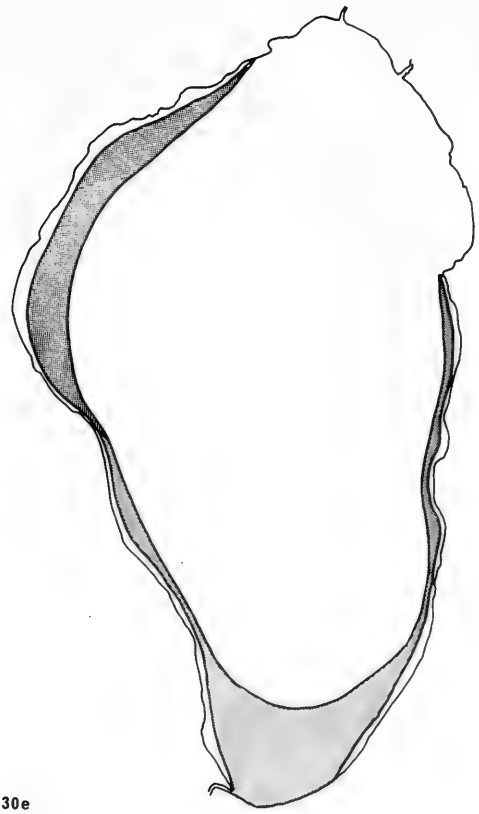
30d

FIG. 30d. Distribution of *Melanoides tuberculata* in the Sea of Galilee.

are extremely muddy, and the anaerobic conditions mentioned previously prevail even in shallow water. These conditions drastically reduce the molluscan population; the few rock-dwellers persist on the lake shore only where scattered cobbles are found, while the small number of mud-dwellers is restricted to the shallowest water. Near Ginnosar, *Melanopsis* also lives sporadically to a depth of 10 m.

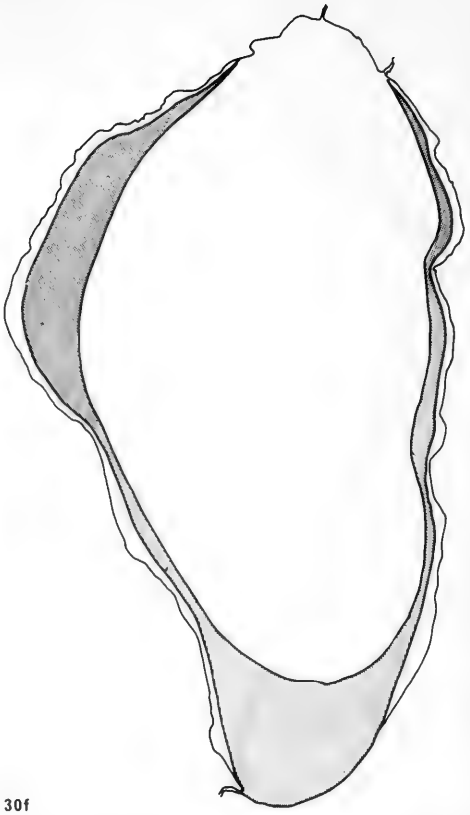
The distribution pattern of *Theodoxus jordani* differs considerably from that of *Melanopsis.* Small-sized gravels are more widespread at greater depths. As *Theodoxus* shelters among quite fine gravel (inhospitable to *Melanopsis*), it frequently occupies deeper zones where *Melanopsis* seldom is present (Fig. 30b). The inability of *Theodoxus* to crawl upon smooth sandy or clay bottoms exclude it from a variety of substrates acceptable to *Melanopsis.* It can, however, hide better in small holes. As it is both larger and cerithiform, *Melanopsis* is less able to use holes for shelter and is more easily detached. It does succeed, however, in crawling on smoother surfaces and sandy bottoms. Once turned upside down, *Theodoxus* cannot regain its normal position, whereas *Melanopsis* easily manages this. After one lifts a stone from the water with both species attached, all *Melanopsis* immediately loosen their hold and sink to the bottom where they begin to search for a new substrate. *Theodoxus,* on the contrary, remains tightly fixed inside small fissures and holes in the stone. In absolute numbers of specimens, *Theodoxus* far exceeds *Melanopsis.*

Bithynia hawaderiana is found attached exclusively, hidden in the lower part of its substrate. Like *Theodoxus,* it occupies small cracks and holes in rocks and gravels for protection against detachment by wave action. Its distribution in the lake is peculiar (Fig. 30c). While rare along the W. rocky shore, it does appear there at the



30e

FIG. 30e. Distribution of *Pyrgula barroisi* in the Sea of Galilee.



30f

FIG. 30f. Distribution of *Unio (Limnium) terminalis* in the Sea of Galilee.

lower depths; along the E. shore it is extremely common and occupies the whole of the rocky zone even at the banks of the lake.

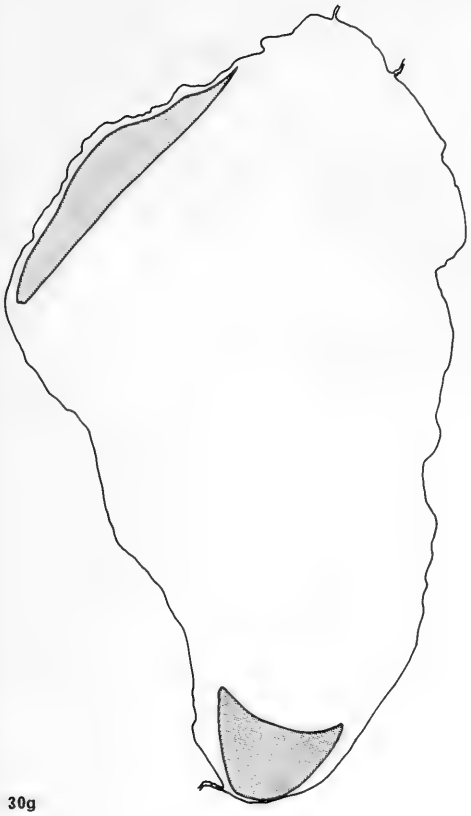
2. *Mud-dwellers*

Melanoides tuberculata is the most common species in the lake, existing in vast numbers everywhere on muddy bottoms. The population density is even greater in salty hot springs. In the N., where the Jordan River empties into the lake, it lives along the muddy shores (Figs. 28-29). In the Kefar Nahum area, it represents 50% of the entire molluscan population. Ranging from 3-12 m, it reaches its maximum number at the greater depths (Fig. 30d). At 'En-Gev, on the E. side of the lake where the bottom is very steep, it is present in the 2 m zone and reaches its maximum abundance at a depth of 9 m. In the Tiberias area, *Pyrgula barroisi* predominates down to a depth of 10 m where it is succeeded by *Melanoides.*

Quantitatively, the Zemah area in the S. part of the lake is rich in molluscs. Here *Melanoides* reaches its maximum abundance at 15 m, as in the Ginnosar area. In the Tabgha area, *Pyrgula* again predominates at 5 m, while *Melanoides* is more prevalent at 12 m.

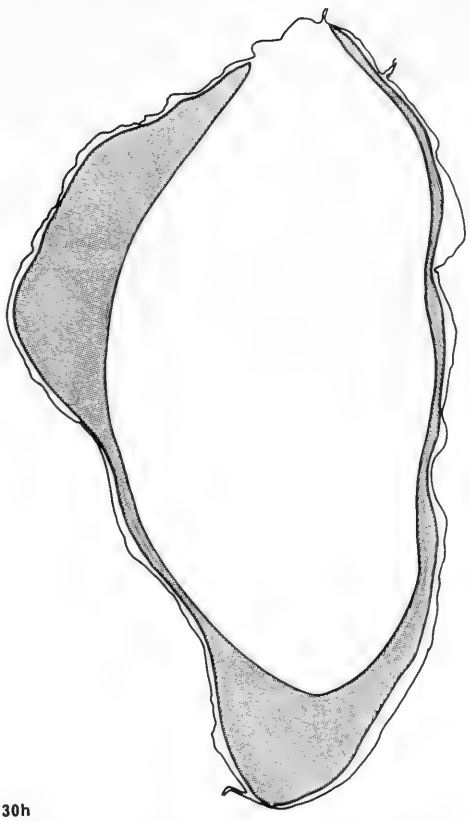
Melanoides usually sinks in the mud and makes very short foraging tours. In the laboratory it has never crawled more than 10 cm during a single night, and it never returns to its starting point as most rock-dwellers do.

In frequency *Pyrgula barroisi* is 2nd to *Melanoides.* It ranges between 5 and 10 m, appearing chiefly between 6 and 8 m (Fig. 30e). Compared with *Melanoides,* it occupies shallower bottoms and is, as a rule, more widespread along the W. and S. shores than in the N. Its behaviour is very similar to that of *Melanoides.* Being a



30g

FIG. 30g. Distribution of *Unio (Psilunio) semirugatus* in the Sea of Galilee.



30h

FIG. 30h. Distribution of *Corbicula fluminalis* in the Sea of Galilee.

smaller animal, it suffers higher mortality in storms.

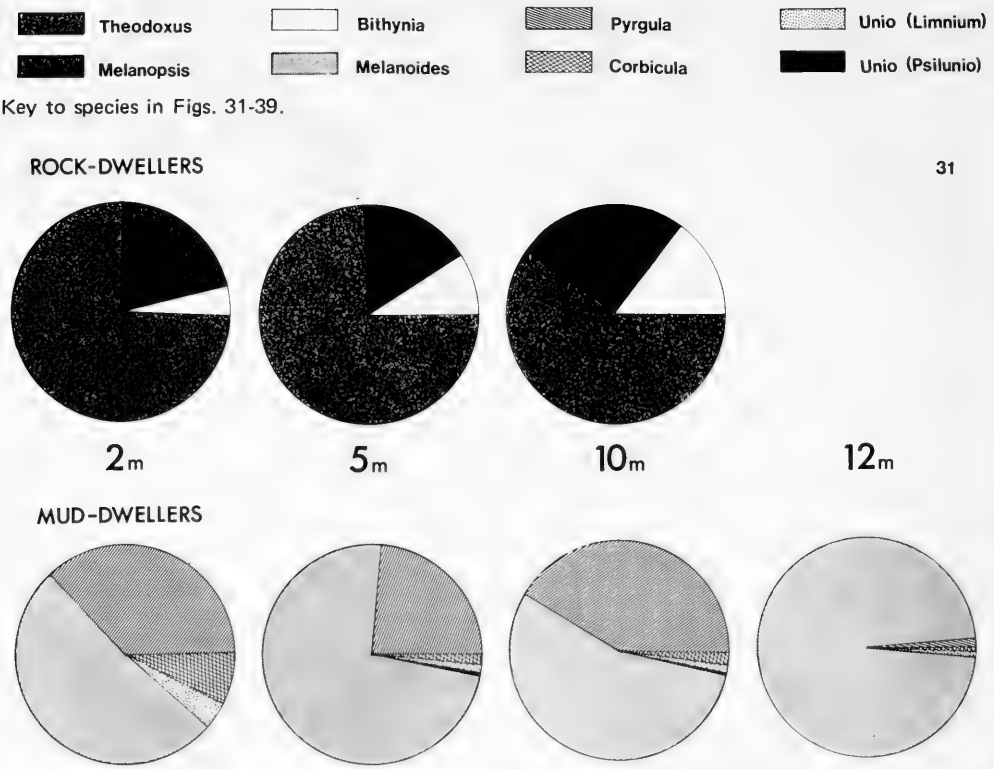
Unio (Limnium) terminalis (Fig. 30f) is likewise more common along the W. and S. sides of the lake, and is frequent at a depth of 5 m. In the 'En-Gev area it reaches its maximum density at a depth of 3 m, while in Kefar Nahum it only begins to appear at 3 m, reaching its maximum abundance at 6 m. At greater depths it vanishes rapidly. Quite rare in the Tiberias area, it only occurs deep; in the Zemah area it is common in an area devoid of gravels between 1 and 20 m. In both Zemah and Ginnosar the maximum numbers occur between 12 and 13 m. Around the muddy shores of the Jordan's influx, it lives very close to the shore and reaches its maximum abundance at 2 m, vanishing at 8 m where anaerobic conditions prevail.

Unio (Psilunio) semirugatus is the rarest mollusc in the Sea of Galilee; only a few specimens are occasionally found. It is absent from the E. part of the lake (Fig. 30g), appearing mainly in 2 localities: the Zemah area where it is most numerous, and from Ginnosar to Kefar Nahum. At Zemah it reaches its maximum abundance at 3 m, but it also is present in very small quantities at 18 m. At Ginnosar it is found in 5-8 m, and at Kefar Nahum at 5 m.

Corbicula fluminalis is distributed throughout the muddy zone at all depths, although it is not a common form in the lake (Fig. 30h). At Kefar Nahum it reaches its maximum abundance at 7 m, while at Tiberias and Ginnosar its maximum abundance is at 13 m. In these 2 areas it is fairly abundant; at Zemah it appears in higher quantities only at 15 m.

General distribution of molluscs in the lake

An attempt was made to determine relative abundance among the rock-dwellers and mud-dwellers as illustrated in Figs.



Key to species in Figs. 31-39.

FIG. 31. Relative abundance among the rock-dwelling and mud-dwelling molluscs at various depths below lake level in the Ginnosar area. The data in this and the following 8 figures are based on the numbers of living individuals in the samples.

31-33. Three main areas were considered: Ginnosar (Fig. 31) on the W. side of the lake, Zemah (Fig. 32) in the S. and 'En-Gev (Fig. 33) in the E.

Among the rock-dwellers of the Zemah area, the relative abundance of *Bithynia* increases with depth as the relative numbers of *Theodoxus* and *Melanopsis* decrease. *Melanopsis* occurs mainly near the shore, while *Theodoxus* reaches a depth of 11 m. Three sub-littoral zones are inhabited by the rock-dwellers: one close to the shore occupied mainly by *Melanopsis,* a middle zone (3-6 m) dominated by *Theodoxus*, and a deeper zone (6-11 m), where *Bithynia* is most prevalent. Beginning at 2 m, a constant ratio in the abundance of the mud-dwellers is apparent in the Zemah area. Only at the greater depths does *Melanoides* clearly dominate over the other species.

The situation is quite different in the Ginnosar area (Fig. 31), where a constant abundance ratio exists among the rock-dwellers down to 10 m; at deeper levels all forms disappear. The sharp differences between the 2 areas is accounted for by the contrasting bottoms. Coarse gravels and cobbles are widespread more or less homogeneously down to 10 m in the Ginnosar area, resulting in the constant abundance ratio of the rock-dwellers. In the Zemah area (Fig. 32) the big cobbles best suited for *Melanopsis* are only found along the shore; at deeper levels there are finer gravels unsuitable for *Melanopsis,* but which are appropriate for *Theodoxus* and *Bithynia.*

The mud-dweller *Melanoides* dominates throughout the Ginnosar area, its relative numbers increasing with depth. *Pyrgula* is found in relatively larger numbers between 2 and 10 m, but disappears at greater depths. The relative numbers of *Corbicula* and *Unio (Limnium) terminalis,* though

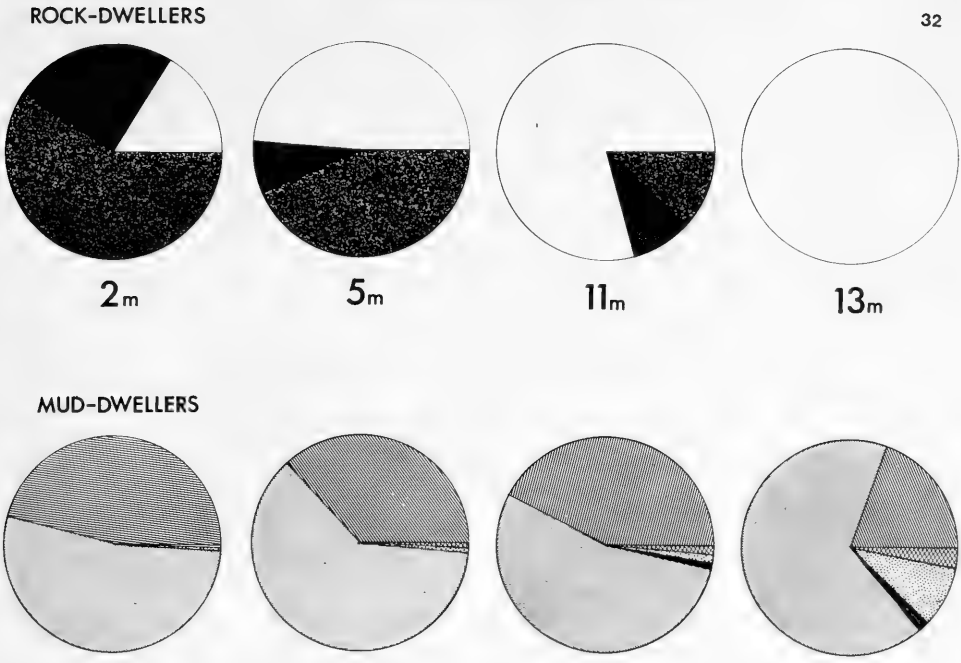


FIG. 32. Relative abundance among the rock-dwelling and mud-dwelling molluscs at various depths below lake level in the Zemah area. Key to species on p. 166.

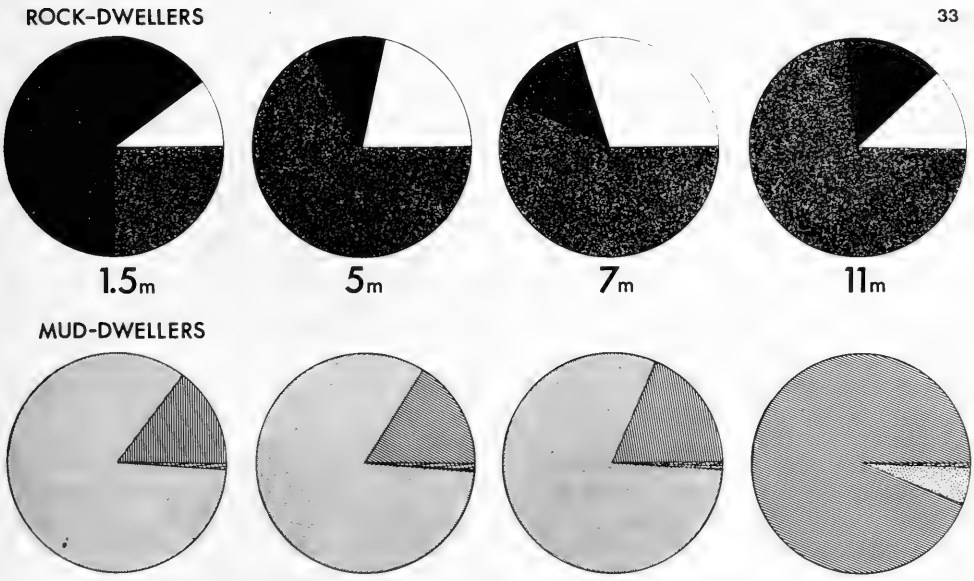


FIG. 33. Relative abundance among the rock-dwelling and mud-dwelling molluscs at various depths below lake level in the 'En-Gev area. Key to species on p. 166.

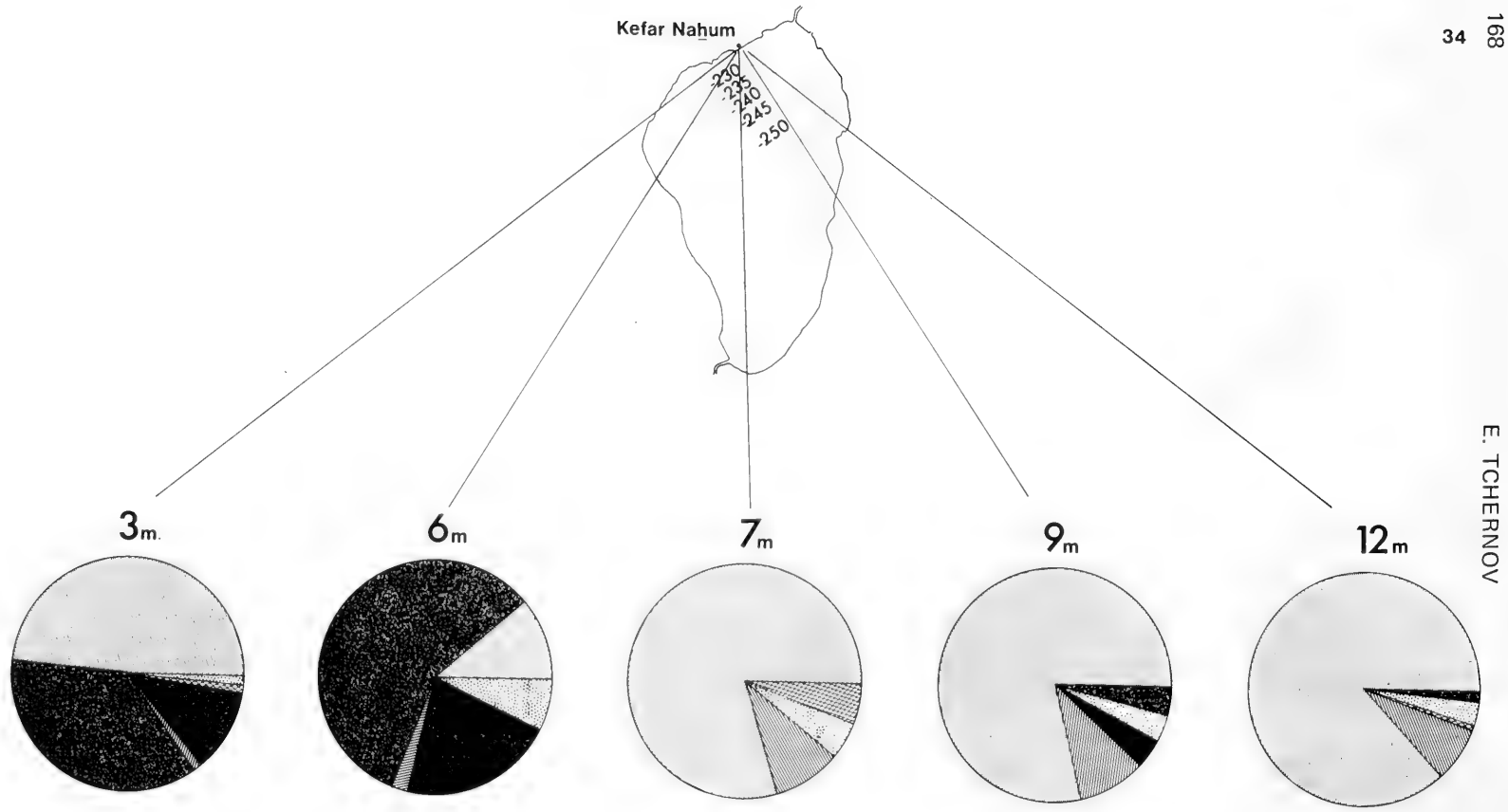


FIG. 34. Relative abundance of the molluscs at various depths below lake level in the Kefar Nahum area. Key to species on p. 166.

never high, decrease below 2 m. Only *Melanoides* is found below 10 m in this area.

In the 'En-Gev area (Fig. 33), 2 sublittoral zones inhabited by the rock-dwellers are clearly distinguishable: one close to shore where big cobbles are widespread and where *Melanopsis,* as expected, is dominant, and a 2nd zone, deeper than 2 m, characterized by fine gravels, and a predominance of *Theodoxus* and *Bithynia*. Unlike in other areas, it is worth noting that among the mud-dwellers *Melanoides* dominates only down to 7 m, quickly declining below this depth, giving way to *Pyrgula. Corbicula* and *Unio (Limnium) terminalis* are always relatively scarce in this area.

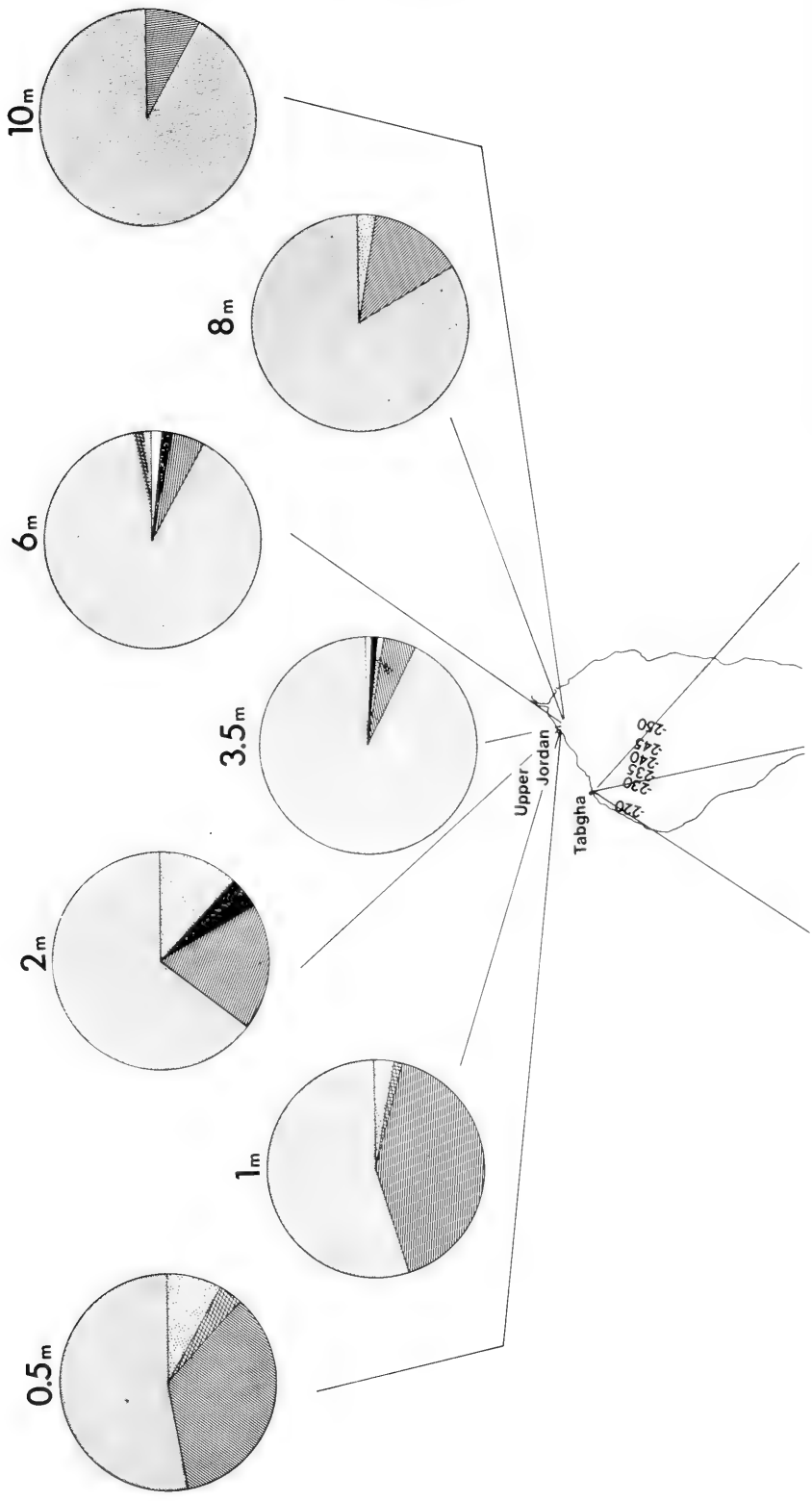
The abundance of the rock-dwelling prosobranchs, being exclusively herbivorous, is due to the high plant productivity of the littoral zone. The plants along the shores consist chiefly of epiphytic algae, but include Chlorophyceae as well. The prosobranch populations are largest where the aquatic vegetation is most luxuriant. The vegetation is greatly influenced by edaphic factors and by the electrolyte content of the water. Hence, a positive correlation may be drawn between the density of the rock-dwellers (*Melanopsis, Theodoxus* and *Bithynia*), and the nutrient content of the water. Indeed, the density of the rock-dwelling populations along the littoral zone distinctly increases along the E. side of the lake, where the nutrient content of the water is far richer than on the W. shore; this is because the prevailing W. winds frequently shift and move the water from W. to E., thereby enriching the E. littoral zone. As these westerly breezes are not strong enough to dislocate gravel, cobbles or rocks off the E. shore, the mortality rate caused by storms is not high. In contrast, when the rare E. winds develop, they are usually very strong, causing much damage and mortality along the W. shore. Although enrichment of the nutrients in the water along the W. shore takes place during these short periods of E. winds (usually not of more than 3 days' duration), the benefits are negligible compared with the widespread damage. Most of the fine- and medium-sized gravels and rocks, as well as even larger ones, are shifted, turned upside down, or thrown offshore, causing almost complete destruction of the molluscs. Worth noting is that the population density of the non-herbivorous mud-dwellers is also greatest along the E. shore as a result of the flow of organic materials from W. to E.

Fig. 34-42 show quantitative comparisons of species abundances in various areas and at various depths of the lake. Figs. 40-42 graph the quantitative abundances of empty shells of each group of species, using the absolute rather than the relative numbers of each species. Fig. 40 includes the mud-dwelling bivalves; Fig. 41 the mud-dwelling gastropods, and Fig. 42 the rock-dwelling gastropods.

Each point on the graphs (Figs. 40-42) represents 1 sample obtained with a Petersen grab (100 cm^3). Most of the samples were taken during winter, the only season when *Valvata* is found in the lake (often in very deep water). During summer, however, *Valvata* is restricted to the few water bodies which are associated with, and immediately connected to, the lake, i.e., the Upper Jordan, the Ginnosar River, the outlet of the lake into the Lower Jordan, and the Buteicha area on the N.E. shore of the lake.

One of the facts revealed by these graphs (Figs. 40-42) is the large quantity of gastropods as compared to bivalves. It is also remarkable that there are only 2 localities in the lake that are far richer in bivalves than elsewhere (Fig. 40), namely, the Zemah area in the S., and the Ginnosar area in the W. The most common bivalve is *Corbicula. Unio (Psilunio) semirugatus* is very rare. The clear reduction of *Corbicula* towards the N. part of the lake is noteworthy.

The lines of the graphs in Fig. 41, showing the abundance of the mud-dwelling gastropods *(Melanoides, Pyrgula* and *Valvata),* are more or less parallel with one another, becoming almost identical in the Zemah and Ginnosar areas where *Melanoides* is usually dominant. In the Ginnosar area the number of *Pyrgula* eclipses that of *Melanoides* at 10 m. Only in the Tiberias area is *Pyrgula* predominant at most depths. The quantities of *Pyrgula* are reduced towards the N. As mentioned above, I am not concerned in this study


10m
8m
6m
3.5m
2m
1m
0.5m
Upper Jordan
Tabgha
.220
.230
.235
.240
.245
.250

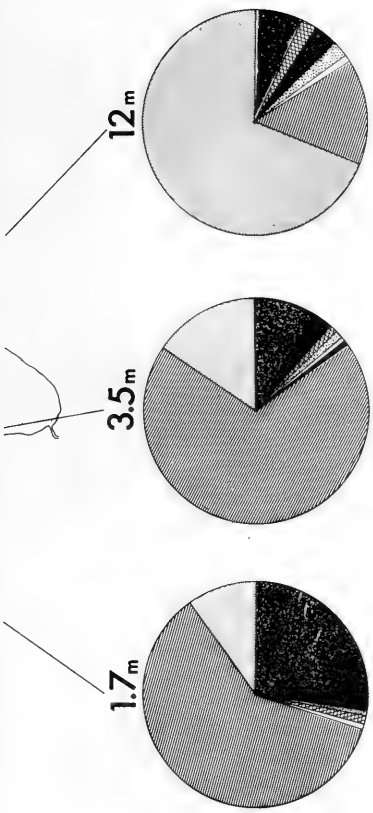


FIG. 35. Relative abundance of the molluscs at various depths below lake level in the Upper Jordan and Tabgha areas. Key to species on p. 166.

Valvata, because this species is occasionally washed into the lake during winter but is never permanently established. It is treated, therefore, as only a "winter visitor" of the lake. The graphs include *Valvata* in order to illustrate its abnormal distribution. Ecologically, its brief presence in the lake might affect its immediate surroundings to a negligible degree.

Rock-dwellers (Fig. 42) are most common along the E. shore, especially near 'En-Gev. The graphs usually show a single peak differing with each locality. In the Zemaḥ area, where the littoral zone is very shallow, they attain their maximum numbers at 7 m; at Tiberias and Ginnosar at 5 m; at Kefar Naḥum (a very steep littoral zone), at 3 m; and at 'En-Gev at 1.5 m. *Theodoxus* is the most common rock-dweller.

As a rule, the E. side of the lake has the greatest concentration of gastropods. Although *Melanopsis* is found in greater quantities at 7 m in the Zemaḥ area, it is proportionally dominant at 2 m, surpassed by *Bithynia* and *Theodoxus* at 7 m.

There is, as well, an increased quantity of gastropods towards the S. The Ginnosar area is richer in molluscs than nearby because it receives higher quantities of organic material and nutrients from the Ginnosar brooks (Amud, Rubeidiyeh and Hammam). This enrichment is especially effective during winter. The Jordan River has prime influence upon the quantities of molluscs, supplying sediments, organic material, electrolytes and other nutrients enriching the E. and S. shores.

REPRODUCTION AND LIFE CYCLES OF THE MOLLUSCS OF THE SEA OF GALILEE

All molluscs of the lake spawn at least once a year, during the spring. A few species breed both in spring and autumn, but the spring season is the main period. It is not yet clear whether the same individuals spawn twice a year, or if only an aberrant minority spawns in the autumn.

The breeding season of most species is confined to the short period when the temperature of the lake is beginning to rise from its lowest point; a sharp decrease in salinity coincides. Whether the water temperature, salinity change or both induce the

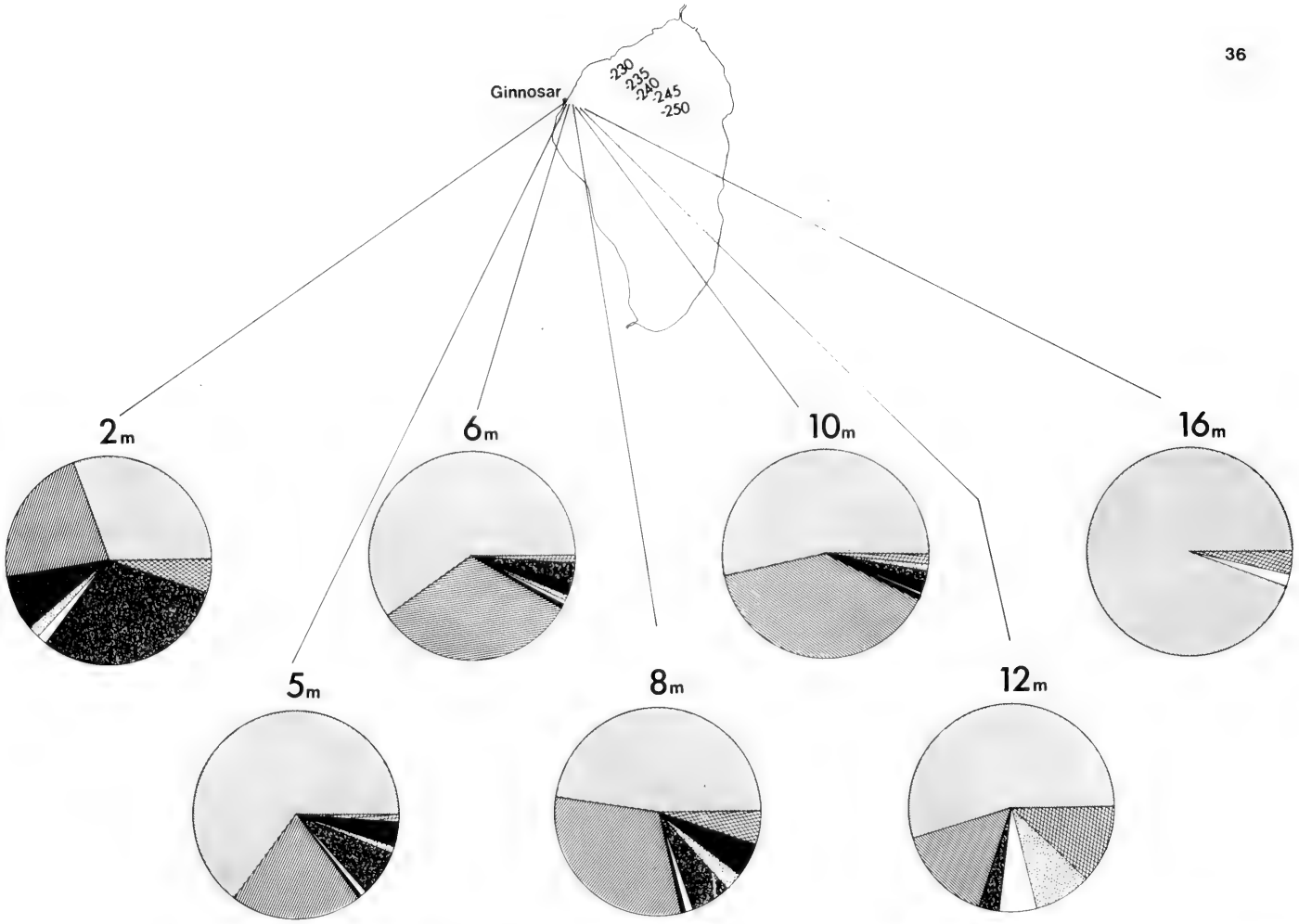


FIG. 36. Relative abundance of the molluscs at various depths below lake level in the Ginnosar area. Key to species on p. 166.

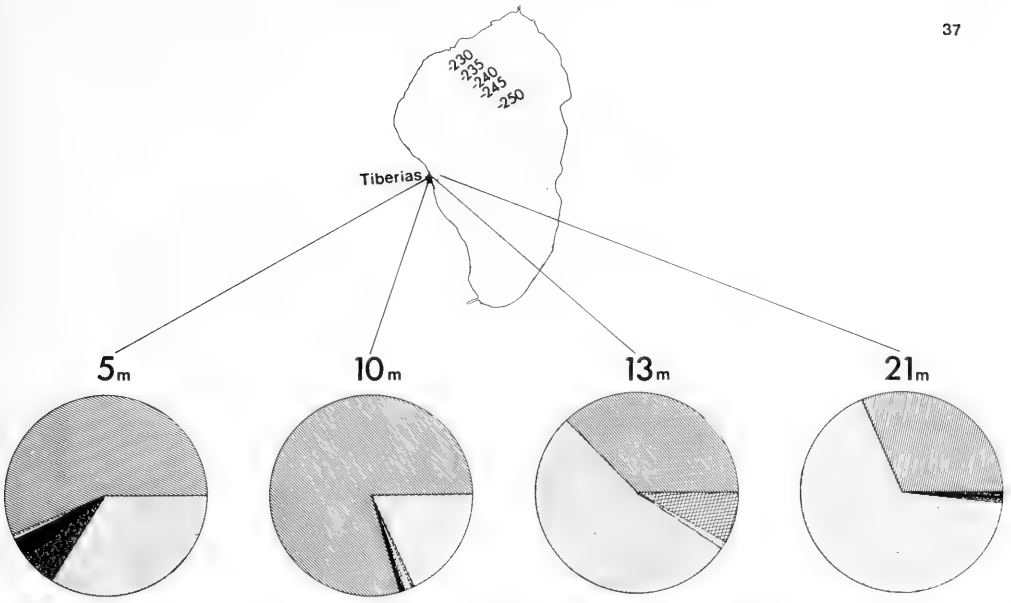


FIG. 37. Relative abundance of the molluscs at various depths below lake level in the Tiberias area. Key to species on p. 166.

breeding season is unknown. In any case, neither of these changes explains the shorter breeding season in the autumn when the water temperature is beginning to drop and the salinity is increasing (Fig. 43).

Theodoxus is the 1st to begin spawning, near the end of March or beginning of April—unless exceptionally low temperatures cause a brief delay. *Melanopsis* is more tardy, beginning to spawn usually in mid-April. The spawn of both species is fixed to hard substrates, including living shells of their own species (*Melanopsis* being the preferred substrate). The shells of other species are never used for this purpose. The flattened capsule of each species each contains 20-30 eggs. The general appearance of the capsules of both species is very similar. There are no distinguishing criteria before hatching takes place; convergence has developed here. Both *Melanopsis* and *Theodoxus* also lay eggs during autumn.

Bithynia spawns only once a year, throughout May. The eggs are laid 1 by 1 in 2 parallel rows of a maximum length of 1 cm. The eggs of 1 row alternate and interdigitate with those of the other row. The transparent eggs are usually laid under cobbles and rocks; shells of living animals are never used by this species. The young hatch a few days after spawn is laid, whereas those of *Theodoxus* and *Melanopsis* require 3-4 weeks to hatch. Thus the young of all these species hatch almost simultaneously during May (Fig. 43).

Eggs of *Pyrgula* have not been found so far, although young have occasionally been dredged from the bottom of the lake at the beginning of May. It may be assumed that the breeding season of *Pyrgula* also occurs during the early spring, probably in March.

The ovoviviparous *Melanoides tuberculata* lays its eggs in its mantle cavity during February or as early as the end of January. The young develop there for quite a long period, leaving the "mother" from the middle to the end of May, having already attained a length of 1.5-2.0 mm and produced at least 5 whorls. If these young contact a rough sandy substratum they are destroyed when the particles are agitated. Only on a muddy or very fine-grained substratum will they survive.

Our knowledge of the larval development of the bivalves in Israel in general, and the Sea of Galilee in particular, is extremely limited. We do know, however, that the development of glochidia occurs on most of the fishes inhabiting the lake, and that their dispersion occurs probably during late spring. Paperna (1964), studying

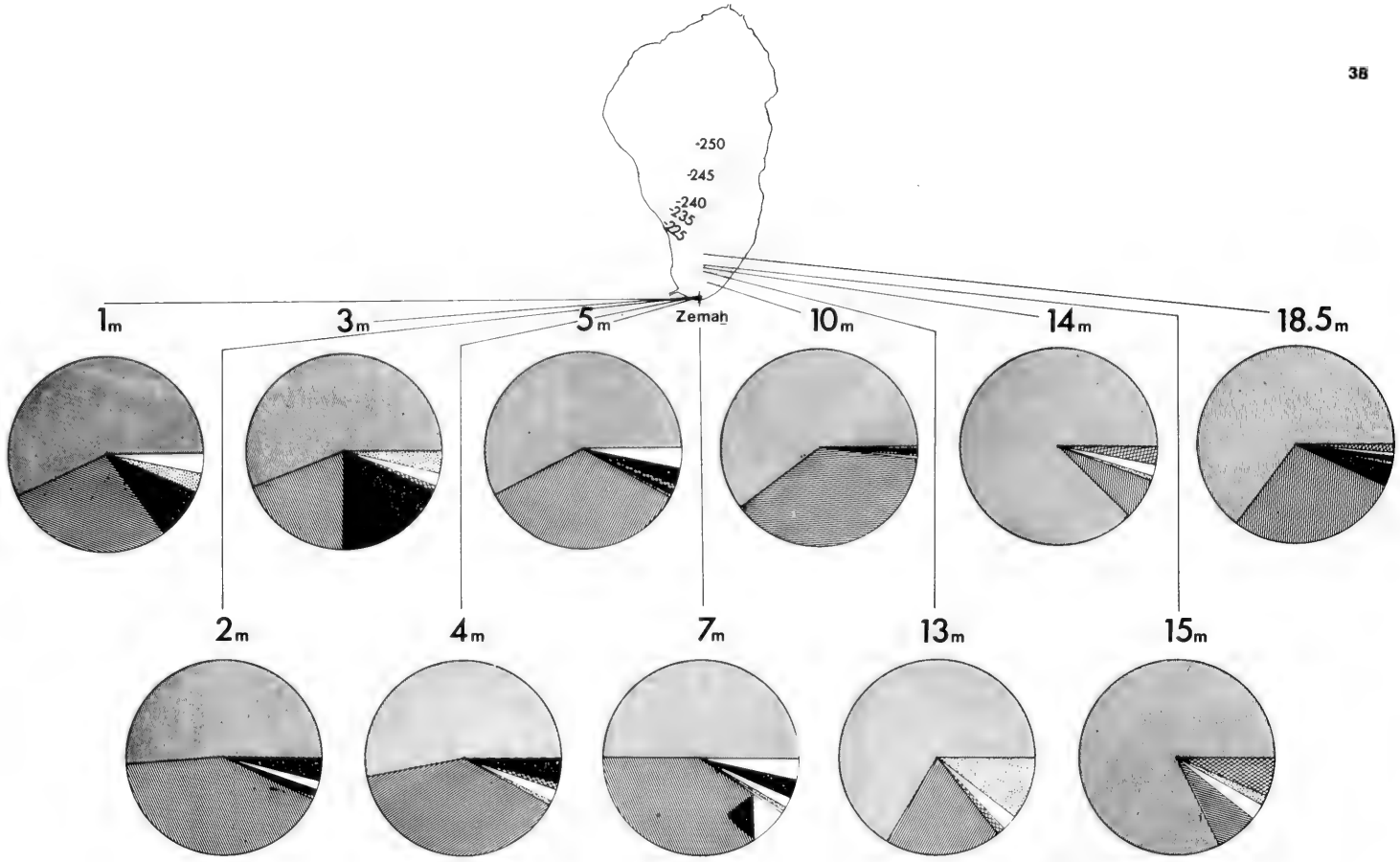


FIG. 38. Relative abundance of the molluscs at various depths below lake level in the Zemah area. Key to species on p. 166.

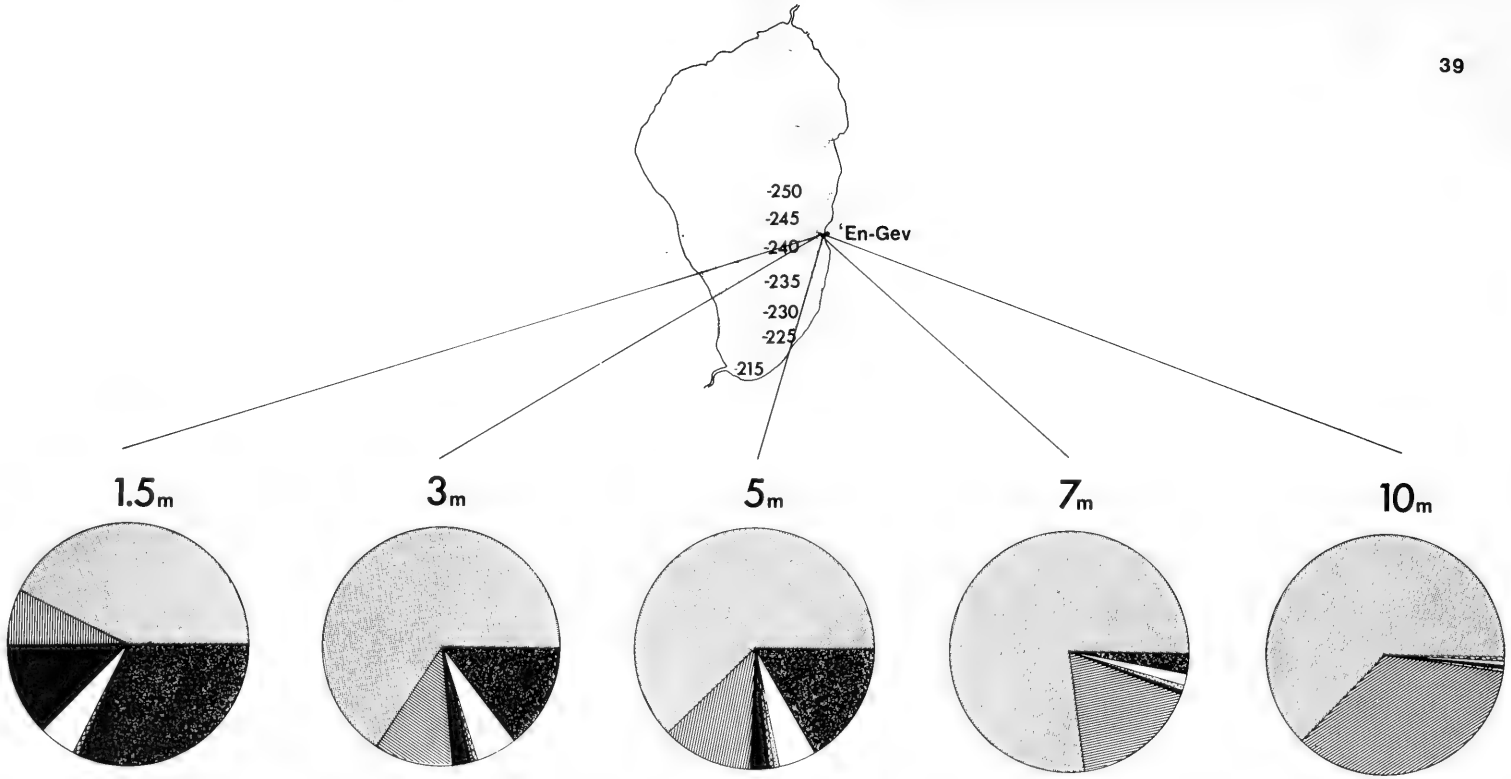


FIG. 39. Relative abundance of the molluscs at various depths below lake level in the 'En-Gev area. Key to species on p. 166.

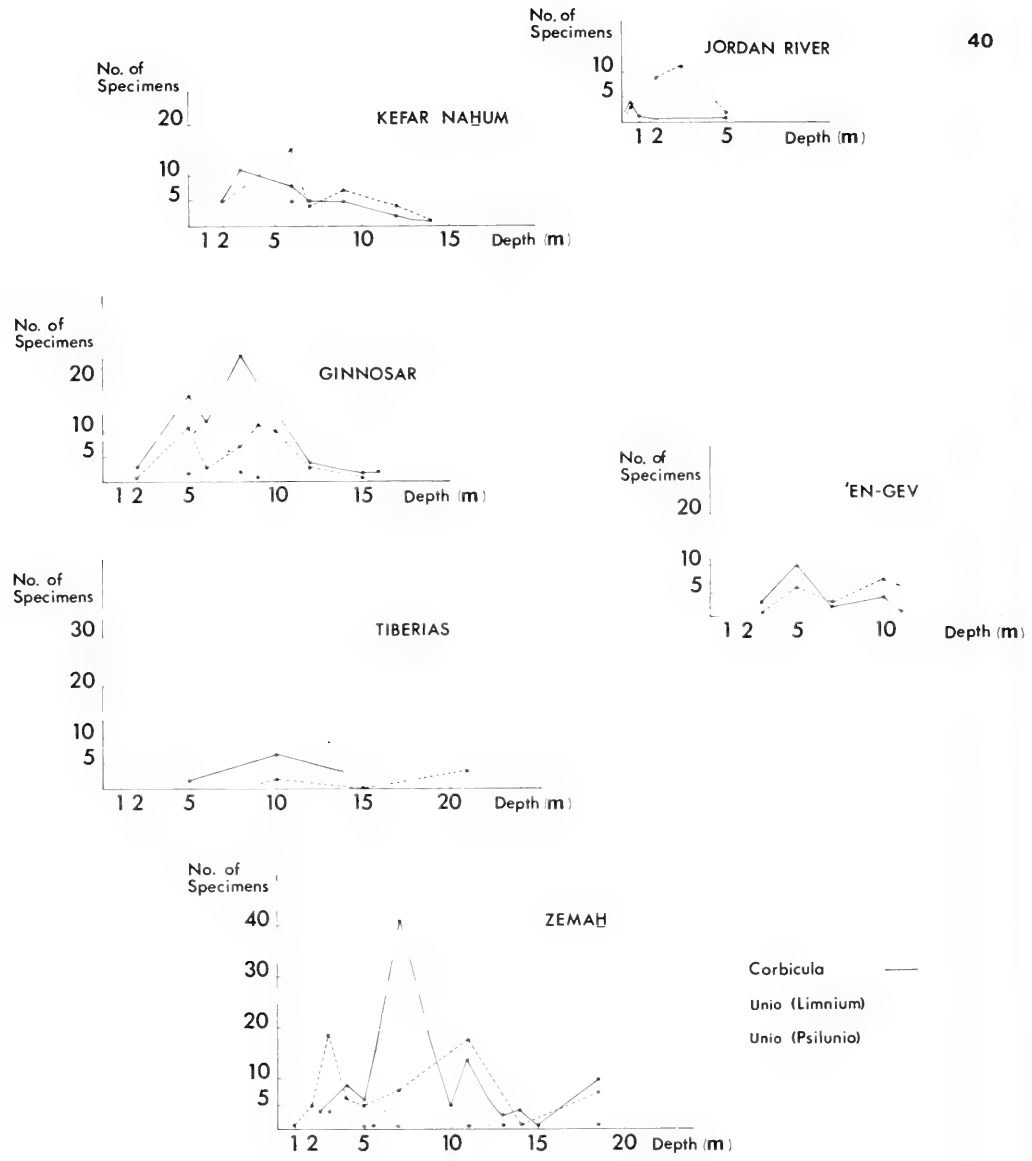


FIG. 40. The abundance of empty shells of the 3 mud-dwelling bivalves at various depths below lake level at 6 places around the Sea of Galilee.

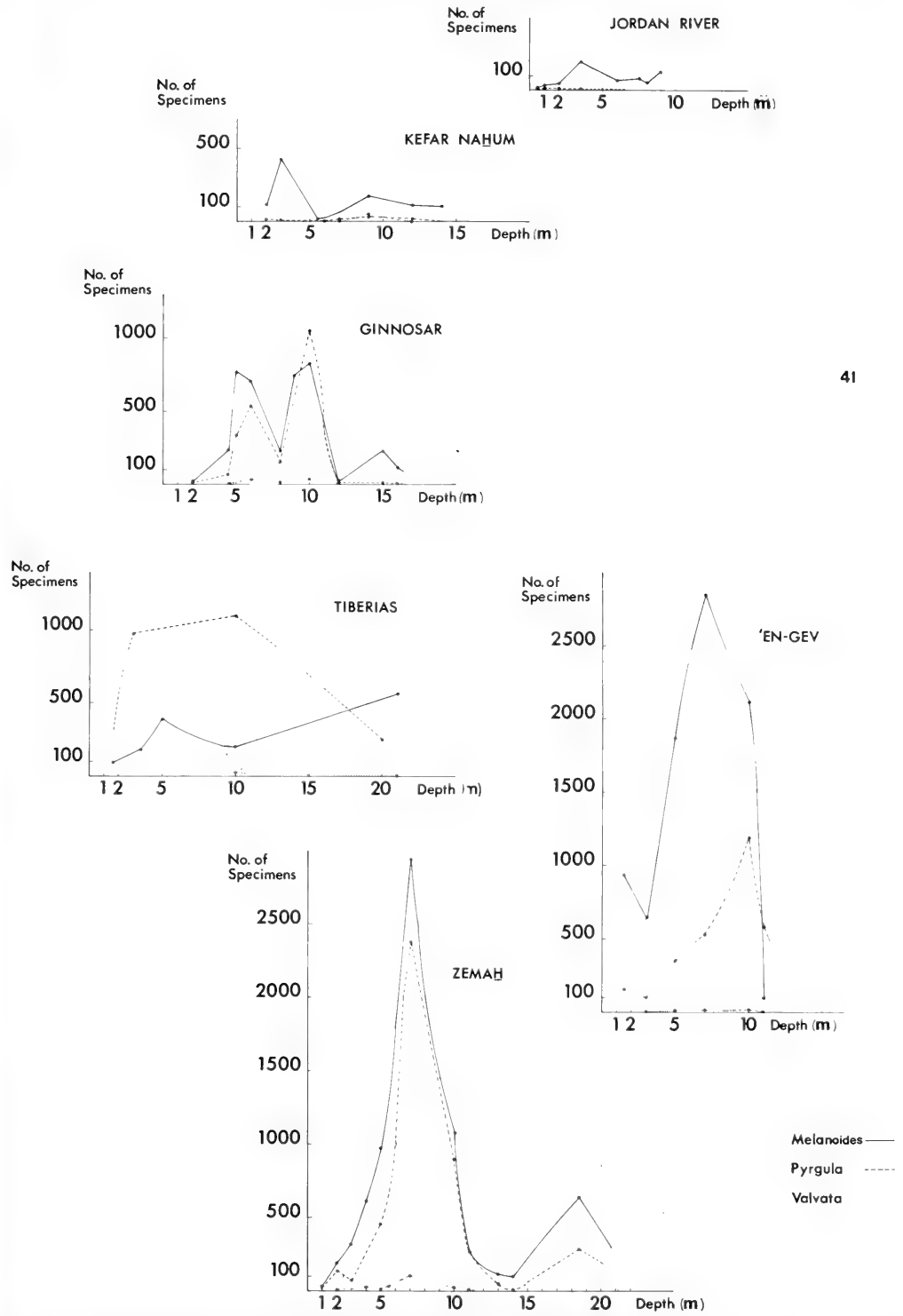


FIG. 41. The abundance of empty shells of the 3 mud-dwelling gastropods at various depths below lake level at 6 places around the Sea of Galilee. *Valvata saulcyi* is adventitious.

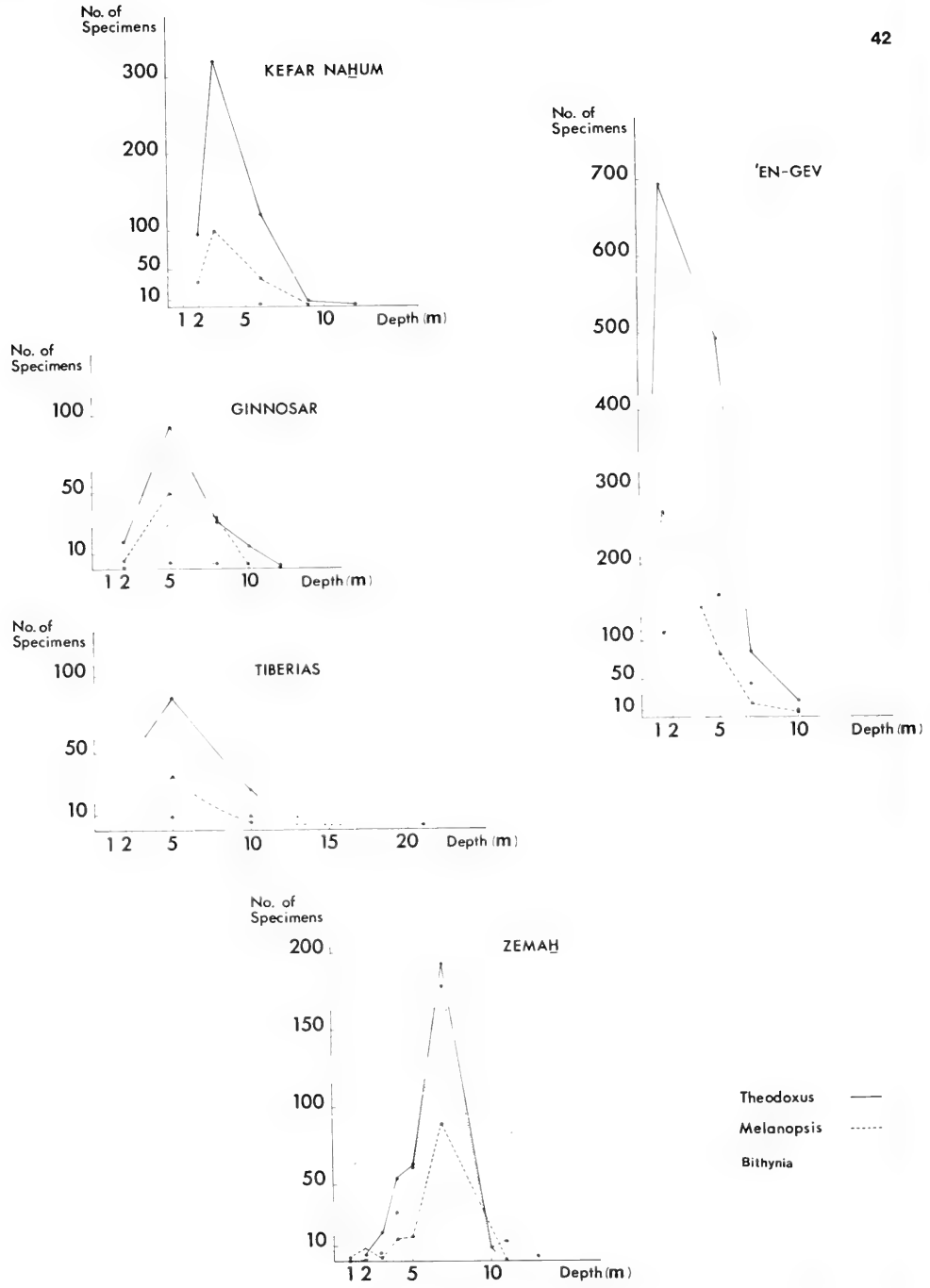


FIG. 42. The abundance of empty shells of the 3 rock-dwelling gastropods at various depths below lake level at 5 places around the Sea of Galilee.

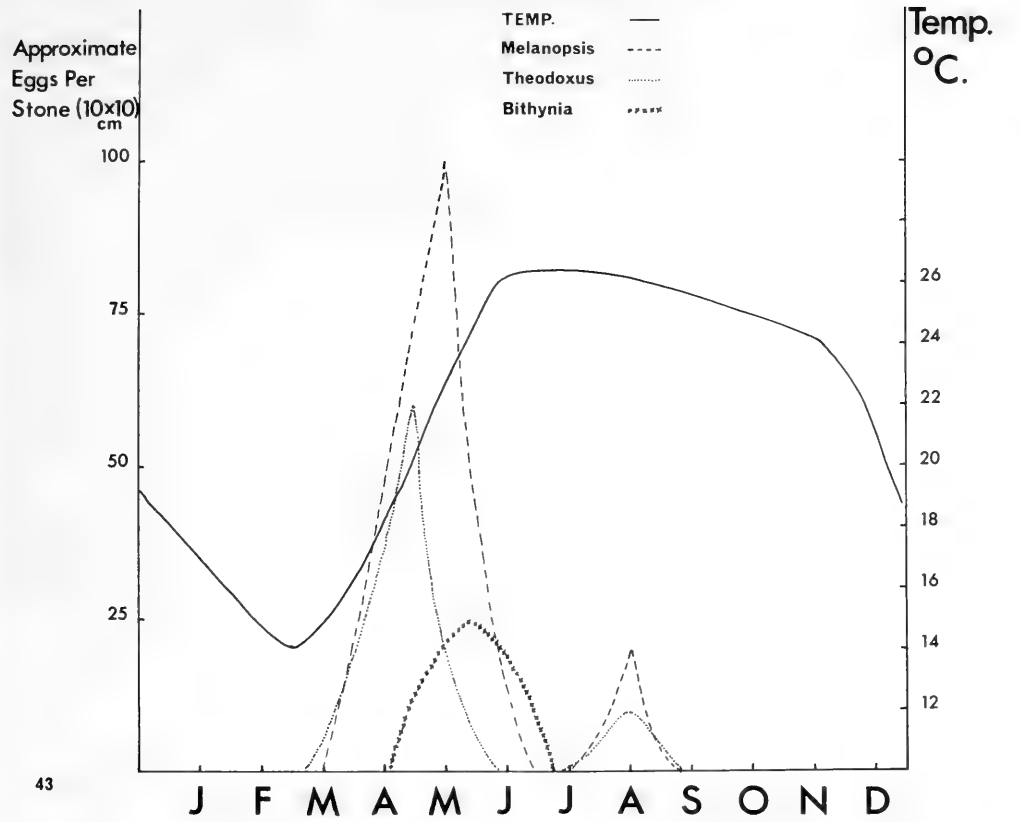


FIG. 43. Reproductive cycles of 3 of the gastropods in the Sea of Galilee.

the ectoparasites of fishes in Israel, came to the following conclusions concerning fishes infected by glochidia in the Sea of Galilee.

The larvae of *Unio* spend their marsupial stage within the inner demibranchs of the ctenidia. In their trochophore stage they leave via the exhalant siphon and attach themselves to the gills of one of the fishes listed in Table 3. This is their parasitic period during which they complete their veliger stage. They later leave their host and metamorphose for a benthic mode of life.

As the glochidia of Israel have never been distinguished specifically, little is known about their preference or specificity for particular fishes, or about their development and metamorphosis.

TABLE 3. Glochidial infestation of fishes in the Sea of Galilee. Data from Paperna (1964).

Infected fishes	Intensity of infestation by glochidia (%)
Acanthobrama terrae-sanctae	1.37 ± 1.37
Phoxinellus sp.	17.5 ± 6.4
Barbus canis	1 out of 4
Varicorhinus damascinus	6.6 ± 6.45
Tilapia zillii	33.3 ± 9.05
Tilapia nilotica	11.1 ± 7.45
Tilapia galilaea	10.5 ± 7.05
Tristramella simmonis	11.8 ± 7.8

ORIGIN OF THE MOLLUSCS IN THE SEA OF GALILEE

Although the record is not without uncertainties, it appears that most of the prosobranchs presently inhabiting the Sea of Galilee are Tethyan refugees. In general, it can be stated that wherever a strong regression of the Tethys occurred, leaving behind inland water bodies that became increasingly fresh, a new wave of prosobranchs invaded the fresh waters.

At the end of the Miocene, when a widespread process of freshening of water bodies was taking place, elements which had already occupied and were adapted to

fresh waters moved in large invasions in both directions between the Oriental regions and the Near East and Africa (see especially Steinitz, 1954, and Kosswig, 1955, 1967). At this time and during the Pliocene many fresh-water elements began to spread over large areas. It was at this period that most of the known fresh-water molluscs invaded Israel and its surroundings. Prior to this, inland waters were rare and intermittent in the Near East. Naturally, not all elements reached the extreme limits of Africa or India during this dispersive process. Some were only to reach the central Syrian-Israeli areas where the developing southern Palaearctic desert belt, although only in its early stage of formation during the Pleistocene, already served as a barrier to fresh-water elements.

Known from Europe since the Palaeogene, *Bithynia* is probably the most ancient fresh-water animal among the prosobranchs presently in the Sea of Galilee. Its exact origin, however, is difficult to trace. It probably developed and speciated in the wide lagunal regions of the Palaeogene, contemporaneous with *Planorbis pseudoammonius, Physa montensis,* and *Unio. Bithynia* could have invaded the Near East only after the regression of the Paratethys towards the end of the Miocene. As an "old" fresh-water element compared with other prosobranchs it is a stenokous and stenohaline animal.

The genus *Theodoxus* probably penetrated fresh water during the Oligocene, but the subgenus *Neritaea*, which is now characteristic of the Near East, arose later than *Theodoxus* s. s.; it probably originated in the Sarmatic province. From there it moved S. and S.E. during the Pliocene to the Syrian, Israeli and Mesopotamian areas. The Ponto-Aralo-Caspian province is the only area where the 2 above-mentioned subgenera overlap.

Melanopsis invaded fresh water later, probably during the Upper Miocene regression. Even in its Recent distribution, it traces the border of the Miocene Tethys. There is no evidence to support the suggestions that either *Melanopsis* developed in the Levantine province *in situ*, or that it occupied the area only later from a Mesopotamian or Sarmatic origin. On the contrary, as it occurred in numerous forms and varieties as early as the lower Middle Pleistocene in the Jordan Valley, we get the impression that even if it had not originated there an invasion and occupation of the area had taken place at a much earlier date, probably during the Pliocene.

The genus *Pyrgula* and its close relatives invaded fresh water relatively late, certainly not earlier than the Pliocene in the Sarmatic province. Once established, *Pyrgula* dispersed over wide areas in a short time. One of its routes to the S. was through the Orontes (Syria) into the Jordan Valley and to Mesopotamia. Upon reaching the Jordan Valley the way to the coastal plain was blocked, further confirmation of its late arrival in this area. The genus probably persisted in the Jordan Valley during the end of the Pliocene or early Pleistocene, but no fossils are known at present.

Melanopsis and *Theodoxus*, being older residents of the area, could occupy not only the coastal plain, but even N. Sinai and the mountainous springs in the southern Judean hills. It was impossible for any of the above-mentioned genera (*Theodoxus, Melanopsis, Bithynia* and *Pyrgula*) to reach Africa S. of the Sahara because the Levantine desert belt already existed before they invaded the area.

Before the Palaearctic was separated from the Palaeotropic zone (and the Ethiopian from the Oriental), and prior to the development of the Palaearctic desert belt, *Melanoides*, of tropical origin, and to a lesser extent *Cleopatra,* began to settle its southern regions. These genera were then cut off from their original areas at the end of the Miocene, after which the widespread Eurasiatic populations have steadily declined.

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ZUSAMMENFASSUNG

DIE MOLLUSKEN DES SEES TIBERIAS

Eitan Tchernov

Die betonte Artenarmut der heute im See Tiberias (= See Genezareth; = Galiläa-Meer) lebenden Mollusken ist nur durch die drastischen geologischen Vorgänge erklärbar, die sich während des Pleistozäns entlang dem Jordangraben abgespielt haben. Die Süsswasserfaunen im mittleren Jordantal reduzierten sich besonders im Anschluss an das Mindel/Riss-Interglazial, als die meisten Gewässer bis hin zum Post-Würm verschwanden. Besonders geschrumpft waren die Süsswasserfaunen während des Würms, als nämlich ein ausgedehnter Salz- (= Lisan) See das Jordantal entlang existierte. Auf das Schrumpfen des Salz- (= Lisan) Sees folgend entstanden zwei grössere endemische Seen: das Tote Meer im Süden und der See Tiberias im Norden, der in relativ kurzer Zeit (während des Post-Würms) wieder aussüsste. Wiederbesiedelt wurde der See Tiberias lediglich von Arten, die sich in unmittelbarer Nachbarschaft des ehemaligen Salzsees durch das Würm hindurch retten konnten. Darüberhinaus haben sich im See Tiberias ausreichende Umweltbedingungen für dünnschalige Mollusken bis zur Gegenwart nicht aufrechterhalten. Die heutzutage im See selbst lebenden Mollusken beschränken sich auf die folgenden Arten: *Unio (Psilunio) semirugatus* Lamarck, *Unio (Limnium) terminalis* Bourguignat, *Corbicula fluminalis* (Müller), *Theodoxus jordani* (Sowerby), *Pyrgula barroisi* Dautzenberg, *Bithynia hawaderiana* (Bourguignat), *Melanopsis praemorsum* (Linnaeus), und *Melanoides tuberculata* (Müller).

Hauptsächlich drei Faktoren begrenzen die Mollusken-Verbreitung im See: 1) die anaerobe Zone; 2) die Bodenbeschaffenheit; 3) Stürme bzw. Wellenschlag.

Zwei deutlich getrennte Biotope können klar unterschieden werden: einer besteht aus Kies und Kieselsteinen, an denen Felsbewohner sich festhalten; der andere besteht aus Sanden, Tonen und Schlamm, in denen Weichbodenbewohner leben. Bei keiner Art Kommt ein Verlassen des ihr eigenen Biotops vor. Die Felsbewohner sind *Melanopsis praemorsum, Theodoxus jordani* und *Bithynia hawaderiana.* Alle übrigen sind Weichbodenbewohner.

Die Häufigkeit der Felsbewohner, die ausnahmslos Herbivoren sind, wird bestimmt durch die wesentlich höhere pflanzliche Produktivität im Litoral. Die Prosobranchier-Populationen weisen eine höhere Dichte dort auf, wo die Wasservegetation üppiger ist. Die Vegetation wird weitgehend von einigen Bodenfaktoren und vom Elektrolytgehalt des Wassers beeinflusst. Somit dürfte eine positive Korrelation zwischen der Dichte der Felsbewohner und dem Nährstoffgehalt des Wassers bestehen. Der Jordan übt in erster Linie Einfluss auf die Menge der Mollusken durch die Versorgung mit Sinkstoffen, organischem Material, Elektrolyten und anderen Nährstoffen aus, mit denen die Uferzonen im Osten und Süden angereichert werden. Zum anderen stellen den westentlichen begrenzenden Faktor für das Molluskenleben im See die Wellen dar. Nach schweren Stürem gehen die felsbewohnenden Populationen grösstenteils zugrunde, ebenso wie jene Schlammbewohner, die sich in Ufernähe aufhalten. An kleineren Kieseln haftende Mollusken haben mehr Aussicht, fortgerissen zu werden; tatsächlich sind an kleinen Steinen sitzend nur juvenile Tiere zu finden.

Die Brutperiode ist beschränkt auf die kurze Zeit, da die Wassertemperatur von ihrem Minimum anzusteigen beginnt, womit ein abrupter Salinitätsabfall einhergeht. Ob die Brutperiode durch die steigende Wassertemperatur oder die Salinitätsänderung induziert wird, bleibt noch offen. Keine von beiden erklärt die kürzere Brutzeit im Herbst, wenn die Wassertemperatur zu fallen beginnt und der Salzgehalt wieder steigt.

Die meisten der gegenwärtig im See Tiberias lebenden Prosobranchier sind Tethys-Relikte. *Bithynia* ist das älteste von ihnen; er stammt wahrscheinlich aus dem europäischen Paläogen und drang in den Vorderen Orient nach dem Rückzug der Paratethys gegen Ende des Miozäns ein. *Theodoxus* entstand wahrscheinlich im Sarmat, breitete sich im Pliozän nach Süden aus, wo er die schon bestehenden Süsswässer von Syrien-Israel und Mesopotamien besiedelte. *Melanopsis* entwickelte sich während dieser Zeit in den Süsswässern als Resultat der Meeresregressionen des oberen Miozäns; sie entstand entweder im Levantin an Ort und Stelle oder eroberte dieses Gebiet später von dem sarmatischen Entstehungsgebiet aus. *Pyrgula* tauchte in den Süsswässern des sarmatischen Gebietes im Pliozän auf und fasste im Jordansystem auf dem Wege über den Orontes (= Asi-Fluss; Syrien) im späten Pliozän oder frühen Pleistozän Fuss.

C. M.-B.

RÉSUMÉ

LES MOLLUSQUES DE LA MER DE GALILÉE

Eitan Tchernov

La frappante rareté d'espèces vivant aujourd'hui en mer de Galilée ne peut être expliquée que par les violents évènements géologiques qui se sont produits le long du fossé d'effondrement du Jordan au Pleïstocène. Les faunes dulçaquicoles de la vallée centrale du Jordan furent surtout réduites après le post-Mindel, quand la plupart des masses d'eau furent éliminées jusqu'au post-Würm. Les faunes dulçaquicoles diminuèrent en particulier au Würm quand un vaste lac salé (= Lisan) s'étendit le long de la valée du Jordan. Deux principaux lacs endémiques suivirent la réduction du lac salé (= Lisan): la Mer Morte au Sud et la Mer de Galilée au Nord, qui redevint d'eau douce dans un temps relativement court (au post-Würm). Le repeuplement de la mer de Galilée ne le fut que par des espèces qui avaient pu survivre à la période salée du Würm. De plus, la présente mer de Galilée ne conserve pas des conditions d'environnement satisfaisantes pour les mollusques à coquilles fines. Les mollusques vivant actuellement dans le lac proprement dit sont réduits aux espèces suivantes: *Unio (Psilunio) semirugatus* Lamarck, *Unio (Limnium) terminalis* Bourguignat, *Corbicula fluminalis* (Müller), *Theodoxus jordani* (Sowerby), *Pyrgula barroisi* Dautzenberg, *Bithynia hawaderiana* (Bourguignat), *Melanopsis praemorsum* (Linné), *et Melanoides tuberculata* (Müller).

Trois principaux facteurs limitent la distribution des mollusques dans le lac: 1) la zone anaérobie, 2) les caractéristiques du fond, 3) les tempêtes et l'action des vagues.

On peut clairement distinguer 2 biotopes: l'un consiste en graviers et cailloutis, sur lesquels les saxicoles sont accrochés, l'autre consiste en sables, argiles et vases sur lesquels vivent les vasicoles. Aucune espèce ne s'écarte de son propre biotope. Les saxicoles sont *Melanopsis praemorsum, Theodoxus jordani* et *Bithynia hawaderiana.* Tous les autres sont des vasicoles.

L'abondance des saxicoles, qui sont exclusivement herbivores, est déterminée par la richesse végétale de la zone littorale. Les populations de prosobranches deviennent plus denses quand la végétation aquatique est plus luxuriante. La végétation est profondément influencée par certains facteurs édaphiques et la teneur de l'eau en électrolytes. A partir de là une corrélation positive peut être établie entre la densité des saxicoles et la teneur en matière nutritive de l'eau. La rivière Jordan a une influence primordiale sur les quantités de mollusques, en fournissant les sédiments, la matière organique, les électrolytes et autres substances nutritives qui enrichissent les rives est et sud. D'un autre côté, le principal facteur limitant pour les mollusques dans le lac sont les vagues. Après de grosses tempêtes, la plupart de la population habitant les rochers périt, ainsi que les vasicoles qui vivent près du bord. Les mollusques attachés sur les plus petits graviers ont les plus grandes chances d'être balayés; en fait, seulement les juvéniles s'attachent aux petites pierres.

La saison de reproduction est réduite à une courte période quand la température de l'eau commence à monter, à partir de son point le plus bas, et qui coïncide avec une nette décroissance de la salinité. On ne sait si c'est le changement de température ou de salinité qui détermine le moment de la reproduction; ni l'un ni l'autre n'explique la plus courte reproduction qui intervient en automne, quand la température commence à diminuer et que la salinité est en augmentation.

La plupart des prosobranches vivant actuellement dans la mer de Galilée sont des survivants de la Téthys. *Bithynia* est le plus ancien parmi eux, ayant son origine probable dans le Paléogène d'Europe, et ayant envahi le Proche Orient après la régression de la Paratéthys vers la fin du Miocène. *Theodoxus,* sans doute originaire de la province Sarmatique, s'étendit vers le sud pendant le Miocène, où il habita les eaux douces déjà existantes de Syrie-Israël et de Mésopotamie. *Melanopsis* évolua dans les eaux douces pendant cette période, résultat des régressions marines du Miocène supérieur; ou bien il était originaire de la province Levantine *in situ*, ou bien il envahit cette aire plus tardivement à partir d'une origine Sarmatique. *Pyrgula* était établi dans les eaux douces de la province Sarmatique au Pliocène et envahit le système du Jordan à travers les Orontes (Syrie) à la fin du Pliocène ou au début du Pleïstocène.

A. L.

RESUMEN

LOS MOLUSCOS DEL MAR DE GALILEA

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La notable escasez de especies vivientes en el Mar de Galilea sólo puede explicarse por los drásticos acontecimientos geológicos que ocurrieron en la quebrada del Valle del Jordán, durante el Pleistoceno. La fauna dulceacuícola del Valle del Jordán Central se redujo especialmente despues del pos-Mindel, cuando la mayoría de los cuerpos de agua desaparecieron durante un tiempo que duró hasta el pos-Würm. Esa fauna se restringió particularmente durante la deposición del Würm, cuando extensos lagos salados (= Lisan) existieron en el valle. Dos lagos principales y endémicos se formaron después de reducirse la salinidad (= Lisan) lacustre: el Mar Muerto en el Sur, y el Mar de Galilea en el Norte el cual retornó, en un proceso rápido, a ser de agua dulce, durante el pos-Würm.

El Mar de Galilea se repobló solamente con especies que pudieron sobrevivir en los alrededores del antiguo lago salado durante el Würm. Aun hoy el Mar de Galilea no mantiene condiciones de ambiente satisfactorias para moluscos de concha débil. Los moluscos vivientes, en el lago propiamente dicho, se reducen a las siguientes especies: *Unio (Psilunio) semirugatus* Lamarck, *Unio (Limnium) terminalis* Bourguignat, *Corbicula fluminalis* (Müller), *Theodoxus jordani* (Sowerby), *Pyrgula barroisi* Dautzenberg, *Bithynia hawaderiana* (Bourguignat), *Melanopsis praemorsum* (Linneo), y *Melanoides tuberculata* (Müller).

La distribución de los moluscos en el lago está limitada por tres factores principales: 1) la zona anaerobica; 2) constitución del fondo; 3) oleaje y tempestades.

Se distinguen, claramente, dos biotopos: uno consiste de cascajos y guijarros a los que se adhieren tres especies, *Melanopsis praemorsum, Theodoxus jordani* y *Bithynia hawaderiana;* el otro está formado por arenas y limos, donde se encuentran las especies de habitat barroso. No hay mezcla o invasión de especies de un biotopo dentro del otro.

La abundancia de individuos en el biotopo rocoso—los cuales son exclusivamente herbivoros—se determina por la mayor productividad vegetal en la zona litoral. Las poblaciones de prosobranquios crecen compactas donde la vegetación es más lujuriante. Tal vegetación esta en gran parte influenciada por algunos factores edáficos y por el contenido electrolítico del agua. De tal manera puede figurarse una correlación positiva entre la densidad de las especies que habitan entre las piedras y el contenido nutritivo del agua. El Río Jordán tiene influencia primaria sobre la cantidad de moluscos, aportando sedimentos, materia organica, electrolitos y otros nutrimentos que enriquecen las orillas oriental y meridional del lago. Por otra parte, el factor limitador principal para la existencia de los moluscos es el oleaje: después de severas tempestades las poblaciones en las zonas rocosas perecen, así como algunas del lago que estan cerca de la ribera. Individuos adheridos a los guijarros chicos estan más expuestos a ser acarreados fuera del agua; son precisamente los juveniles los que más se adhieren a las piedras pequeñas.

La reproducción está restringida al corto periodo en que la temperatura del agua comienza a elevarse desde el punto más bajo, coincidente con una marcada reducción en la salinidad. No se sabe si tales cambios son los que inducen a la función reproductora, así como tampoco puede explicarse otro periodo de reproducción más corto que tiene lugar en el otoño cuando la temperatura comienza a bajar y la salinidad aumenta.

La mayoria de los prosobranquios presentes en el Mar de Galilea son refugiados del antiguo Tethys. *Bithynia,* de más antiguedad entre ellos, y que probablemente tuvo su origen en el Paleogeno de Europa, invadió el Asia Menor despues de la regresión del Paratethys, hacia el final del Mioceno. *Theodoxus* se originó al parecer en la provincia Sarmática y se extendió al Sur durante el Plioceno, habitando las aguas entonces existentes de Siria-Israel y Mesopotamia. *Melanopsis* evolucionó en las aguas dulces durante esa época, resultando de la regresión del mar en el Mioceno Superior; pudo haber tenido su origen en la provincia Levantina *in situ* o, por ser originalmente Sarmático invadió más tarde aquella provincia. *Pyrgula* se estableció durante el Plioceno en la provincia Sarmática e invadió el desague del Jordan a través de Orontes (Siria) en el Plioceno Superior o Pleistoceno Inferior.

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SYSTEMATICS OF PROSOBRANCH GASTROPODS[1]

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ABSTRACT

The authors trace 5 main evolutionary lines within the class Gastropoda, and hence distinguish 5 principal taxonomic subdivisions, differing in the main characters of their structure. Three of these are, as a rule, united into the subclass Prosobranchia. However, the originality of morphological structure and direction of evolution in each of these 3 subdivisions are considered equivalent to those of the 2 other gastropod subclasses, the Opisthobranchia and Pulmonata. Three independent subclasses are therefore recognized among the prosobranch gastropods: Cyclobranchia, Scutibranchia and Pectinibranchia.

The Cyclobranchia (i.e. the former Docoglossa and some of the Paleozoic groups) present a particular line of evolution, demonstrable by their primitive, primarily symmetrical shell devoid of any incision or sulcus, by the archaic type of radular structure and movement, not shared by other Gastropoda, as well as by the structure of the reproductive system, stomach and nervous system, which are similar to those in Scutibranchia. Moreover, the asymmetry of the mantle complex, which the representatives of this group developed independently, the radula specialization, the development of the arterial bulbus and presence of the mantle nerve cords support the opinion that this group had a distinct type of evolution. From these considerations Cyclobranchia are set apart in a special subclass, embracing the orders Helcionellida, Archinacellida (formerly classified among the Monoplacophora) and Docoglossa. The evolutionary process was expressed morphologically within this group by the decrease in shell dimensions and sculpture, by the oligomerization of the radula, and by a reduction of the specialized breathing organs within the course of their development.

The rest of the Gastropoda originated from an ancient group of mollusks, evolving from primitive Cyclobranchia in the Cambrian period; these mollusks had a symmetrical mantle complex and a medially disposed fissure (selenizone) or sulciform projection.

The maintenance of symmetry of the mantle complex in the course of evolution, the parallel development of the fissure, the well developed epipodium and the absence of marked ganglia in the central nervous system, together with a marked development of symmetrical branchial ganglia permit unification of the orders Dicranobranchia, Fissobranchia and Macluritida into a separate subclass Scutibranchia. The evolution within Scutibranchia exhibits a tendency towards size reduction and decrease in degree of shell coiling, towards the separation and displacement of the selenizone from the peristome, a diminished importance of spiral sculpture as compared to axial sculpture, and the increase in size of the right kidney, due to its recently stabilized double function, that of excretion and of reproduction.

The subclass Pectinibranchia, including Monotocardia (Mesogastropoda and Neogastropoda) as well as Trochacea and Neritacea from Diotocardia (= Archeogastropoda) of former classifications, is phylogenetically the youngest and the most morphologically diverse; it has originated within Scutibranchia (most likely from Macluritida or their common ancestors).

Within Pectinibranchia 18 orders can be distinguished that share a common plan of structure and follow the general evolutionary trend of the whole subclass, but yet have a special line of evolution and a particular structure of shell, foot, digestive system, gill, central nervous system, reproductive system and ecology. From these 18 orders, the first to diverge were 2 groups, one now united in the superorder Pyramidellimorpha and the other comprising the superorder Turbinimorpha together with phylogenetically connected orders here combined in the new superorders Neritimorpha, Paludinimorpha, Littorinimorpha and Cerithiimorpha.

[1]MALACOLOGIA publishes this controversial paper because it synthesizes some current Russian thinking on the classification of prosobranchs, and because it discusses some work little known outside the U.S.S.R. The classification of the Neogastropoda advocated by W. F. Ponder in a recent issue of MALACOLOGIA (1974["1973"], 12(2): 295-338) differs drastically from that advocated here, in which the Neogastropoda are not even maintained as an order. Reviewers criticized the present paper for naming 6 new superorders without explicitly stated differences, for raising the ranks of some taxa without adequate explanation, and for naming 2 new suborders, 2 new superfamilies and 16 new families (including 2 replacement names) with in many cases too few distinguishing criteria. The overall reclassification of prosobranchs proposed here should elicit stimulating discussion. EDS.

The evolution of the Pectinibranchia, which often manifests itself similarly in different superorders and orders, is expressed morphologically by the: decrease of (particularly spiral) sculpture; formation of a siphonal process in absence of the epipodium; reduction of jaw; oligomerization of radula, accomplished differently in different groups; increase of mantle complex asymmetry; formation of a pectinate ctenidium and osphradium; transformation of right kidney into renal gonoduct; and concentration and integration of the central nervous system. Evolution within different subdivisions of the Pectinibranchia went a parallel way, from ancestral microphagy, sestonophagy and phytophagy toward detritophagy, saprophagy and predation, and, within the specialized forms, toward parasitism. In the mode of reproduction it went from external to internal fertilization, to direct development and ovoviviparity.

Some evolutionary parallelism is perceived in the development of the subclasses under consideration. It is morphologically expressed in the tendency towards increased asymmetry of structure, oligomerization of the radular apparatus, a greater complexity of the reproductive system and a more pronounced concentration of the nervous system. In ecology and distribution, the evolutionary parallelism within the subclass manifests itself in the change of habitats (from life in shallow waters and on hard substrates to life at greater depths, on mixed and soft substrates, within epifauna and, later, infauna), in the adaptation to fresh water and terrestrial life, in the expansion of distribution from tropical and subtropical latitudes toward temperate and cold regions.

The phylogenetically most advanced groups have the largest numbers of living species within all subclasses and orders.

The evolutionary process within the Gastropoda under consideration was uneven and intermittent. The most intensive stages in the process of formation occurred simultaneously within different groups in the Cambrian-Ordovician, Permian-Triassic and Cretaceous-Paleogene periods.

INTRODUCTION AND DISCUSSION

The erection and varying composition of numerous classifications of Gastropoda (Pelseneer, 1906; Thiele, 1925-26, 1929, 1931; Wenz, 1938-1944; Korobkov, 1955; Pchelintsev et al., 1960; Taylor & Sohl, 1962; Pchelintsev, 1963) shows that scientists have made many attempts to explain and to express taxonomically the peculiarities of structural types and the diversity of evolutionary trends in this large and complex group of mollusks.

Even the subdivision of Gastropoda into subclasses, which at first sight seems stable and fully established, has lately been criticized and revised. The independence of the subclasses Opisthobranchia and Pulmonata has been recently discussed in detail (Boettger, 1955; Morton, 1963, and others). As to the subclass Prosobranchia, which has been less frequently discussed from that point of view, it was long ago pointed out that it could be characterized by not 1 but by at least 2 structural plans.

This lack of uniformity in opinion results from the fact that the complex of morphological characters which is taken as a criterion for the division of the Gastropoda into subclasses comprises mostly peculiarities in their level of organization. Within the period of gastropod evolution there more than once originated groups in different phylogenetic branches that were convergent as to type and complexity of organization, so that similarity of structure is not an indispensable condition for phylogenetic relationship.

To reveal the phylogenetic relationships and compose a natural system one should investigate whether certain peculiarities of structure are characteristic of forms belonging to the same phylogenetic line, or if different lines may hold them equally, having inherited the said peculiarities from their common ancestors; besides, one should know whether the representatives of dissimilar groups have developed the same peculiarities by simple convergence.

Considering the main principle of characterization of the gastropod subclasses, we can observe the following inconsistency: the chiastoneury which seems characteristic of Streptoneura (= Prosobranchia) and serves as a criterion for setting them apart from the 2 other traditional subclasses (Opisthobranchia and Pulmonata which are sometimes united as the Euthyneura), can be observed, strictly speaking, among the representatives of each of these subclasses. The difference lies in the fact that the majority of the Prosobranchia retain this peculiarity and are streptoneural, while only few of them have reduced or completely lost it (e.g. *Cingulopsis*), whereas within the Euthyneura, only the lowest representatives still possess chiastoneury (Acteonidae, Chilinidae, etc.) while the

majority of the representatives have completely lost it. Moreover, the lack of chiastoneury within each of these subclasses may result from 2 independent processes, namely 1) from the shortening of the connectives, due either to greater concentration of the nervous system or, on the contrary, to the weakening of it, and 2) from detorsion.

The anterior position of the mantle complex, peculiar to Gastropoda, is lost within different subclasses, or is reduced to different degrees and for different reasons. This process is partly connected with the loss of primary symmetry in the mantle complex.

Two tendencies are distinguished in the evolution of the radula. The first manifests itself in a decrease in the number of teeth, from a considerable number (in rhipidoglossate forms), to 7 (in taenioglossate forms), to 2 (in toxoglossate forms), and even to 1 (in rachiglossate forms[2]). The diminution in the number of teeth could have developed independently, which can be illustrated by the fact that Epitoniidae and Janthinidae possess a multidental radula, Triphoridae and Choristidae a radula with more than 7 teeth, and Mathildidae, Omalogyridae and certain other families a paucidentate radula. A similar tendency in Docoglossa (the multidentate radula in Patellidae and the paucidentate one in Tecturidae) has already been discussed in the literature. The process of oligomerization within the Prosobranchia could have been accomplished in 2 ways: most frequently oligomerization manifests itself in the reduction and loss of marginal teeth; less commonly in the fusion of teeth, which is obvious in Lepetidae and highly probable in some Architectonicidae, as well as in Mitridae, Fasciolariidae and some other families.

The second tendency of radula evolution reveals itself in the predominance of the working part of the tooth accompanied by a reduction of its base, while the campilodont[3] rhipidoglossate and taenioglossate radulae independently transform into the orthodont[3] form in Ptenoglossa and Stenoglossa. The radula of some Architectonicidae (e.g. *Architectonica*) seems to be transitional; the tooth inflection is still noticeable.

It is a fact of some interest that among Opisthobranchia and Pulmonata, the lowest forms (Acteonidae, Auriculidae and Chilinidae) also possess a campilodont radula, and only some of the representatives of these subclasses later acquired an orthodont radula.

Therefore the docoglossan radula cannot be considered a result of the development of any known campilodont and orthodont radula and resembles only the monoplacophoran and loricate radulae; the radula of the Docoglossa should thus be regarded as keeping the ancestral gastropod features.

The type of movement of the docoglossan radula is distinct too and similar to that of the Loricata and, probably, of the Monoplacophora.

The main characteristics of all the gastropod subclasses could have been similarly discussed one by one, but the above-mentioned items will suffice to show that formal treatment of even those characteristics which seem obvious at first sight presents considerable difficulty and that they must be treated with caution. Having no intention to undertake a complete revision of the classification of gastropods, we shall here only examine the relations within the prosobranchs, considering that the solution of this problem may later facilitate the creation of an improved system for the other subclasses.

If we examine the structure and evolution of the prosobranch mantle complex, excepting only the Docoglossa, we can reach the following conclusion. As has been stated above, the strictly symmetrical mantle complex may be considered an ancestral character for the majority of the Gastropoda. The lowest Paleozoic bellerophontid must have possessed such a strictly symmetrical mantle complex. A characteristic peculiarity of this type of mantle complex was that the rectum opened between 2 ctenidia, which required a complex apparatus to supply the ctenidia with clean water and to remove the water contaminated with faeces from the

[2]In the original sense, as formulated by Gray (1853: 36), the rachiglossate radula has: "teeth on lingual membrane in a single central series." A radula with "three series" was originally named hamiglossate by Gray (1853: 34). Fischer (1880-1887) has united these terms, which may cause some confusion.

[3]In the campilodont radula (terminology of Macdonald, 1869) the tooth rises from a basal plate, forming a hook together with it, whereas in the orthodont radula the tooth does not have a true basal plate and is straight. ED.

mantle cavity. An apparatus of this type must have most efficiently worked among mollusks possessing a planospiral, vertically disposed, bilaterally symmetrical shell and a dilated aperture (Fig. 1).

Mollusks possessing such shells had 2 equal and symmetrical columellar muscles, as demonstrated by the bellerophontid muscle impressions (Knight et al., 1960). The collision of 2 symmetrical water currents directed from the right and left sides in the fore part of the mantle cavity caused the development of an apparatus capable of regulating the water current. Thus the bellerophontids developed a fissure (selenizone) in the shell-wall in the middle of the mantle cavity or, in the same place, a sulcus resembling a keel when viewed from outside.

When the shell became conispiral, water regulation became a more pressing necessity.

There could have existed 3 principles of water regulation: 1) by means of the

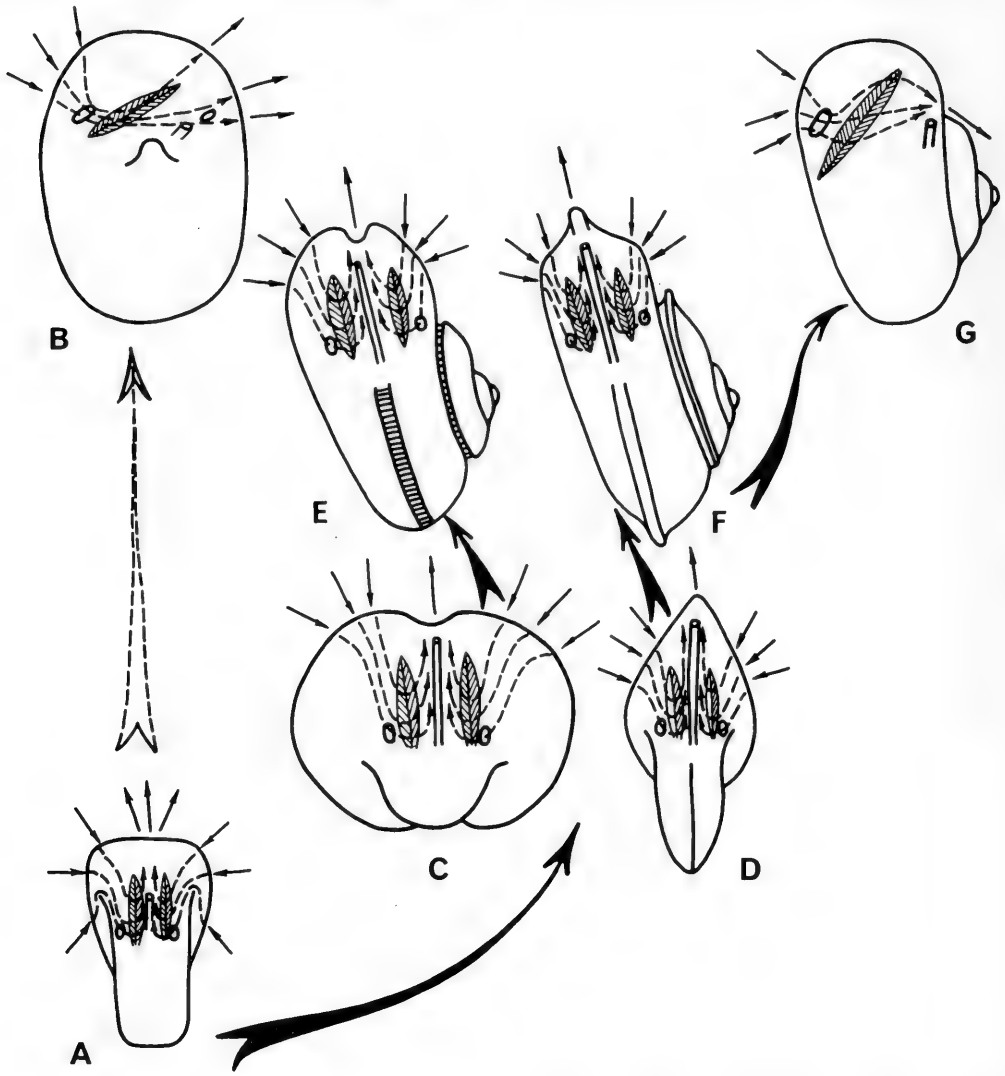

FIG. 1. The location of gills, osphradia and rectums in different groups of Prosobranchia in relation to the circulation of water in the mantle cavity: A, Helcionellida; B, Docoglossa; C, D, Bellerophontoidea; E, Fissobranchia; F. Macluritida; G, Anisobranchia.

reinforcement of the fissure developed by the bellerophontids; 2) by means of sulcus reinforcement; the primarily symmetrical structure of the mantle complex, especially the paired ctenidia and osphradia, the auricles and hypobranchial glands being in both cases preserved. But, hindered by the whorls, the water current on the left side, running from the basal border of the aperture, could not be equal to that on the right side, which caused a considerable difference in the size of the ctenidia on the right and the left sides in conispiral Zygobranchia (Woodward, 1901; Bouvier & Fischer, 1902; Crofts, 1929). The kidney asymmetry of the Zygobranchia, however, is apparently not related with water regulation, being a result of the double (excretory and reproductive) function of the right kidney. It must be noted that the development of a fissure caused a more effective water current regulation than the development of a sulcus could have given, which resulted in the survival of the fissuriform species until the Recent. 3) The third principle of water-regulation regards the use of the canal formed by the palatal and parietal walls of the last whorl. When the conispiral shell has its apex turned aside upward or somewhat backward, the water can enter the mantle cavity along the basal and the greater part of the palatal borders of the aperture, while it can leave the cavity near the anus, which is placed a little backward and to the right (in dextral forms). However, the anus must be displaced towards the upper suture of the body whorl, which inevitably causes the loss of the right ctenidium and destroys the symmetry of the mantle complex.

From the above considerations we conclude that 2 groups, Zygobranchia and Anisobranchia, usually classified among Diotocardia, doubtlessly belong to different phylogenetic lines, originating from common ancestors. Zygobranchia adopted fissure-development, including the separation of their working parts from the peristome, yet keeping the mantle complex symmetric. In Anisobranchia the anus became displaced toward the suture and they developed an asymmetry of the mantle complex. The second tendency found its further development in all Monotocardia, for which reason they can be connected with Anisobranchia.

The analysis of the central nervous system of these 2 groups similarly reveals the existence of 2 phylogenetic lines. The central nervous system of the Zygobranchia lacks separate ganglia, the nerve cells being disposed along the nerve cords; only in *Fissurella*, where the nervous system is at its highest concentration, is a supraintestinal ganglion formed. On the other hand, special branchial ganglia were developed to innervate the gills that are not, strictly speaking, connected with the central nervous system, and that secure gill function by means of a special complex apparatus.

In Anisobranchia, a marked concentration of nerve cells occurs in the ganglia, which is most notably expressed in the cerebral and pleural sections, though their nervous system is but weakly concentrated. The further evolution of this tendency leads to a characteristic system of ganglia in Monotocardia.

The study of other characteristics which are usually brought forward as convincing arguments for the union of Zygobranchia and Anisobranchia does not disprove the assumption that these groups had different types of development. On the other hand, the analysis of the tendencies of the morphological peculiarities in Anisobranchia and Monotocardia supports the view that they are phylogenetically akin, the former being ancestral to the latter.

Thus, the presence of 2 kidneys in both Anisobranchia and Zygobranchia and the absence of the right kidney in Monotocardia does not invalidate a relation between Anisobranchia and Monotocardia, as the latter sometimes do have a right kidney marked by an even stronger development (e.g., in *Circulus*; see Fretter, 1956) but performing a different function, wherefore it is called "the renal gonoduct". The fact that Anisobranchia have no pallial gonoduct does not run counter to the above point of view, as formation of a gonoduct has been observed more than once, and as there are groups among Monotocardia (Thiaridae) having no pallial gonoduct, while some of the highest Anisobranchia possess a primitive pallial gonoduct (*Calliostoma*). Some Monotocardia (Litiopidae, Janthinidae) possess a more or less developed epipodium, as well as the gastric caecum characteristic of a number of Monotocardia and even of Pulmonata. The fact that Anisobranchia possess a rudimentary vestigial right auricle[4] does not disprove their kinship with

[4]The terms "right" and "left" used in reference to the organs of the mantle complex and to the muscles refer to the post-torsional state of Gastropoda.

Monotocardia, as, after careful investigation, the same can also be discovered among the highly developed representatives of Monotocardia (see Spillmann, 1905). However, it must be emphasized that several independent phylogenetic branches of Monotocardia have originated from Anisobranchia, and that, if the latter are grouped together with Zygobranchia and separated from Monotocardia, such classification must be wrong, for the reason that when different groups of Monotocardia are derived from Diotocardia as if they were independent of each other, the phylogenetic unity of the system of Prosobranchia is destroyed.

While comparing Zygobranchia to Anisobranchia we excluded Docoglossa, which are often placed in Diotocardia.

If this comparatively restricted group is set against the 2 remaining groups of Diotocardia, it should be taken into consideration that its representatives can possess a vast number of peculiarities that have no connection with their phylogenetic relationship, but that result from specialization and that developed convergently with analogous peculiarities of other groups of prosobranchs, side by side with peculiarities having a phylogenetic value.

Therefore, it is important to give a detailed analysis of the structure of all the main docoglossan organs, as compared with the rest of the Diotocardia.

All Docoglossa (except *Propilidium*) possess a cap-like shell with the apex turned forward; they have no selenizone or sulcus, which characters separate them from the forms with cap-like shells of Zygobranchia (Fissurellacea)[5] that as a rule possess either a fissure (*Emarginula*), a perforation (*Fissurella*), or a sulcus clearly visible from the inner side of the shell (e.g. *Montfortia*). The fact that a cap-like shell may be formed from the bilaterally-symmetrical planospiral shell of bellerophon-like groups and from the conispiral shell of many other groups of Gastropoda is widely known. In both cases the spiral shell should be considered a primary type (Knight et al., 1960, and other authors). The columellar muscle in cap-like forms is usually horseshoe-shaped. However, we can obtain some data about the character and shape of the shell of the ancestors of Docoglossa. It is known that in gastropods with a conispiral shell the right columellar muscle functions alone. The horseshoe-shaped muscle of many cap-like forms has developed from this muscle. Conispiral Zygobranchia (Crofts, 1955) retain the left muscle as a rudiment, while Anisobranchia and Monotocardia have lost it. The formation of the horseshoe-shaped muscle of Docoglossa from 2 (left and right) columellar muscles, equally increasing after torsion (Crofts, 1955) doubtlessly proves that the ancestors of Docoglossa had a planospiral, bellerophon-like shell, devoid of any slit or sulcus.

A similar shell, which also had a tendency to dilate the preapertural part of the last whorl, was characteristic of the most ancient of all known Gastropoda, the correlated Cambrian families Coreospiridae and Helcionellidae. Helcionellidae had an almost cup-like shell. Probably it was "exogastric,"[6] like that of Docoglossa (Knight et al., 1960). Thus, the Bellerophontacea proper are to be regarded as a group derived from *Coreospira*-like forms, having developed after the slit or sulcus type.

By this character Coreospiridae and *Helcionella* are similar to Docoglossa, which brings them together and sets them apart from the Bellerophontacea, that developed in the direction of the Zygobranchia.

The deviation of the antero-posterior axis of the embryonic shell from that of the definitive one by an angle of about 20°, which was observed in the development of some Patellidae (Dodd, 1957), does not necessarily prove that the ancestors of Docoglossa were conispiral; it may have been caused by the clockwise rotation of some elements of the mantle complex, which will be discussed below.

The docoglossan mantle complex, with an unpaired ctenidium and a heart displaced to the left and forward, is at first sight similar to that of Anisobranchia; however, a detailed investigation reveals that this similarity is but slight and superficial.

The most important detail of mantle

[5]Following Recommendation 29A of the International Code of Zoological Nomenclature, the superfamily name endings have been changed to "-oidea" in the systematic part of the present work. When, however, discussing or quoting groups in the traditionally accepted sense, the customary ending "-acea" has usually been preserved.

[6]Coiled so as to extend forward over the head. ED.

complex asymmetry in Anisobranchia is represented by the reduction of the right ctenidium, which retains its position, and by the displacement of the anus, together with the nephropores, to the right.

In contrast, the asymmetry in Docoglossa results from the clockwise rotation of the ctenidium to the left by an angle of about 20°. Besides, the ctenidium-osphradium system is disrupted and the osphradia with the corresponding ganglia retain a strictly symmetrical position even after the reduction of one or even both of the ctenidia (Haller, 1894; Thiem, 1917a, b).

Consequently, the heart is displaced to the left and, after the reduction of the right ctenidium, it lies close to the base of the left ctenidium. Such an approach to the problem helps to explain the separation of the osphradia from the bases of the ctenidia in Docoglossa, which at first sight seems a paradox. Forbes' earlier observation (Forbes & Hanley, 1850) which, however, has not been verified by further investigation, that *Propilidium ancyloides* Forbes possesses 2 ctenidia, placed asymmetrically like those in *Acmaea*, would help to support our view.

The shifted position of ctenidia in Docoglossa results from the fact that the double water currents converging from 2 sides were replaced by a one-sided current, flowing from left to right. The water current along the inner border of the mantle, the site of the adaptive, secondary, mantle gills in Patellidae, is a further stage in the transformation due to the one-sided current.

The above data lead us to the conclusion that the mantle complex asymmetry in Docoglossa has developed independently from the asymmetry in Anisobranchia; the forms possessing a symmetrical mantle complex should be regarded as forms ancestral to Docoglossa. The problem as to what ancestors the forms with a one-sided water current were derived from is more difficult to solve; it is especially difficult to give details on development. However, the reason for the change in water currents should be sought in the same hydrodynamic difficulties which have caused the formation of the slit or the sulcus in Bellerophontacea.

The vascular system does not furnish sufficient evidence to enable us to expose the phylogenetic connections of Docoglossa since it is, in the main, of the same type as that of the other Diotocardia. We can only point out that the ventricle of Docoglossa is divided into 2 unequal parts; one functions as ventricle, the other is transformed into an arterial bulbus (Spillmann, 1905). This peculiarity of Docoglossa singles them out from the rest of the Prosobranchia.

The kidneys of Docoglossa are in all ways similar to those of the rest of Diotocardia. The right kidney is larger, as it has an excretive as well as a reproductive function.

However, the gonad in Docoglossa does not open into the renopericardial duct but directly into the kidney itself (Fig. 2). According to the system suggested by Pelseneer (1906) such a position would be secondary. This, however, is not convincing because Pelseneer's scheme was established for bivalve mollusks whose gonad opens into the renopericardial duct, on the basis of *Solemya* alone. Having considered this bivalve to be the most primitive of the Protobranchia, Pelseneer thought the position of the gonadal opening in that genus to be primary. At present, however, there is some cause to question whether *Solemya* is the most primitive representative of the Protobranchia. On the other hand, the monoplacophoran gonad opens directly into the kidney (Lemche & Wingstrand, 1959); moreover the gonad of *Haliotis* opens either into the kidney or into the renopericardial duct (Totzauer, 1902; Crofts, 1929) and that of *Pleurotomaria* immediately into the kidney (Woodward, 1901). Finally, the phylogenetic value of the relations between the kidney and the gonad should hardly be taken into consideration, as the kidney itself is separated from the renal-pericardic coelomic sac-like primordium in the course of development (D'Asaro, 1966) and both types of kidney and gonad connection reflect the union of the gonad with the coelom ancestral for Gastropoda. Anyhow, the difference in the character of kidney and gonad connection in Docoglossa and the majority of Prosobranchia ought to be considered proof of the peculiar line of evolution of Docoglossa.

The complicated reproductive system in Docoglossa went entirely its own way, independent of the rest of Prosobranchia. In the highest representatives (*Acmaea sybaritica* Dall, etc.) it resulted in the formation of a copulatory apparatus, which the other Diotocardia have never possessed.

The docoglossan radula is essentially different from the radula of the remaining Gastropoda because, when functioning, it

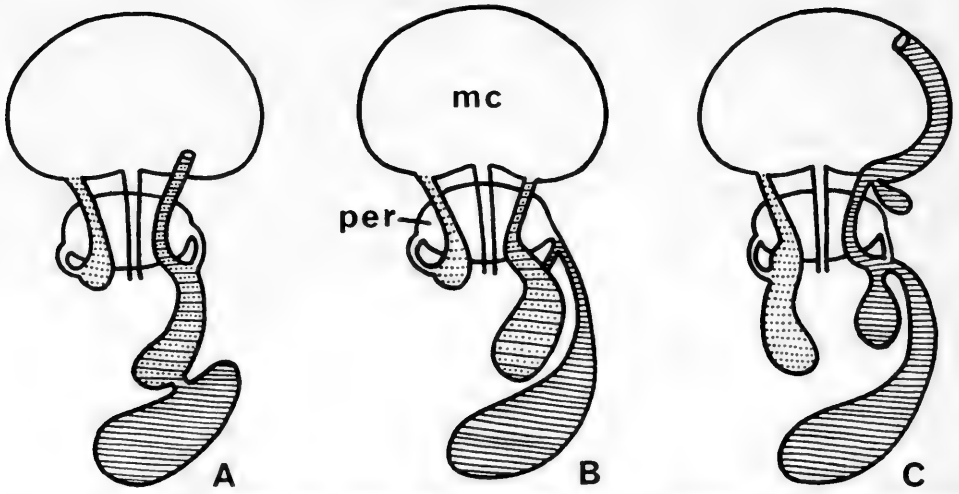

FIG. 2. The relationship between the gonad, kidney and pericardium in different groups of Prosobranchia. Organs having an excretory function are dotted, those having a reproductive function are horizontally lined; a combination of dotting and lining indicates a double function of a given organ. A, Cyclobranchia; B, Scutibranchia and lower Pectinibranchia (Anisobranchia); C, higher Pectinibranchia.

does not bend lengthwise; therefore during food-collection, each of its teeth moves only parallel to the longitudinal axis of the radula. (Its function has been described in detail by Ankel (1938).) In the remaining Prosobranchia, regardless of radular character (be it rhipidoglossate, taenioglossate, ptenoglossate or rachiglossate) and of the type of nutrition, the radula bends lengthwise, the central tooth being moved along with a slant to the axis, while the marginal teeth are drawn in an arc-shaped movement, the chords of the arcs being perpendicular to the radular axis, or at least forming a considerable angle with it (Ankel, 1938). The pulmonate radula movement is of almost the same type (Ankel, 1938) and the same applies to Opisthobranchia, though their radula differs slightly from the above type in that the radular row is only slightly differentiated into lateral and marginal teeth in the multidentate representatives, for which reason there is no marked difference in the trajectory of their movement. It is obvious that the type of radula movement in Docoglossa is more primitive than in the rest of Gastropoda; moreover, the central tooth, weakly developed in Docoglossa, becomes stronger in the course of transition of the radula to the type of movement characteristic of Gastropoda; it results in the differentiation of lateral and marginal teeth. On the other hand, a reverse transition from rhipidoglossate to docoglossate type is hardly probable; the reasons for the longitudinal bending of the radula are obscure and the phenomenon has never been observed among any of the gastropods with cap-like shells except Docoglossa. The reduction of the central tooth cannot be explained either, the more since the necessity of having one compels Docoglossa to form a secondary "central tooth" by means of merging the 4 lateral teeth (Lepetidae). Finally, we should point out, that besides motion, the character of the docoglossan radula is strikingly similar to that of Loricata and Monoplacophora; it has much in common with the latter in its structure (Lemche & Wingstrand, 1959). In the docoglossan radula there are also some peculiarities of specialization, particularly as regards the reduction in the number of teeth and in their differentiation.

According to Graham (1949), the stomach of the initial gastropod type was divided into 2 parts: the post-oesophageal part, into which opens the hepatopancreas, and the elongated part, where the protostyle is situated. The first part is thought to have had a chitinous lining and a caecum. However, it is doubtful whether the latter was actually present. In Zygobranchia the caecum is more weakly developed than in Trochidae (Fretter & Graham, 1962).

The lowest Bivalvia, the Protobranchia (Purchon, 1956), have no marked caecum;

finally, *Neopilina* has neither a caecum nor a chitinous lining (Lemche & Wingstrand, 1959).

From these facts we conclude that the stomach of the most primitive Gastropoda had no caecum and probably no chitinous lining, or, at best, one that was but weakly developed. The Docoglossa have a stomach of such a type, divided into 2 parts, devoid of caecum and chitinous lining and with a strictly terminal entrance (Haller, 1894; Thiem, 1917a, b). The difference lies only in the absence of the protostyle within Docoglossa.

The nervous system of Docoglossa is strongly reminiscent of that of Zygobranchia. Both are characterized by a weak development of the ganglia of the pleurovisceral cord, by the presence of special branchial ganglia (which are termed the osphradial ganglia in Docoglossa), by a considerable development of the labial ganglia and of a labial commissure. However, in addition to the above-mentioned characteristics, the nervous system of Docoglossa has a very typical peculiarity. Along the mantle margin, making up a circle, run 2 ganglionic nerve cords, which are connected with the symmetrical mantle nerves (Haller, 1894; Willcox, 1898; Thiem, 1917a, b). They are especially marked in *Acmaea*, s. l., and in *Lottia*, less marked in *Cellana*, and have not yet been observed in Lepetidae. Thiele's efforts (1895) to homologize them with the pleurovisceral cords of the chitons was subjected to justified criticism (Dogel', 1940; Ivanov, 1940). We consider the attempt to explain the formation of these cords by the ganglionization of the mantle nerves unfounded. If the latter hypothesis were accepted the fact that the mantle nerve cords in Tecturidae and Lottiidae are well developed while they are not observed in the phylogenetically more advanced forms could not be explained.

The above assumption is the more dubious, as the transformation of the cords into nervous connectives devoid of ganglionic cells is a common enough fact, whereas we have no reliable evidence of the reverse process. We consider it safer to explain the formation of the mantle cords by the concentration of the nervous plexus of the mantle border, which recurs in the representatives of many groups of Prosobranchia. The peculiarity of the mantle nerve cords in *Patella* supports this point of view (Haller, 1894), as in many respects they remind one of the nerve plexus.

To sum it up, the Recent Docoglossa have many characters that are more ancestral than those of the most primitive of the existing Zygobranchia, i.e. the primarily symmetrical shell without any slit or canal, and the radula and its type of movement. Besides, they have many peculiarities in common with Zygobranchia that testify to the descent of each of these groups from common ancestors, i.e. the connection of the gonad with the kidney, the stomach structure, the character of the central nervous system, and the development of branchial and labial ganglia. Moreover, Docoglossa have some peculiarities that show that they went their own way of development: the asymmetry of the mantle complex and its structure, the specialization and the decrease in and number of radular teeth, the absence of a protostyle and the formation of mantle nerve cords. Therefore, Docoglossa should be regarded as a separate phylogenetic line, the initial members of this line being the Cambrian Coreospiridae and Helcionellidae. This line is definitely more distant from the 2 groups (Zygobranchia and Anisobranchia plus Monotocardia) discussed above, each of the latter having more in common with one another than with Docoglossa.

We wish to emphasize that separation of the subclasses is based on those general morphological characters of organization which determine the possibility or impossibility of certain concrete adaptations. Thus, to mention only a few examples, in the forms with a peripheral throw of water in the mantle cavity (Scutibranchia) one ctenidium can never completely disappear; nor can any factor prevent ctenidium disappearance in the forms with water currents as they occur in the Pectinibranchia. The variety of teeth occurring in Pectinibranchia, Opisthobranchia and Pulmonata could have developed only on the basis of a radula bending lengthwise while the unbending radula of the Cyclobranchia (as well as that of the Loricata and Monoplacophora) could never have resulted in anything of this sort.

We are convinced that the 3 main phylogenetic lines under consideration as regards the independence of their evolution (disregarding some groups among them that are not yet fully investigated) are equal in importance to those of Opisthobranchia and

Pulmonata. Pulmonata have separated at an early stage of development of the mantle complex asymmetry (i.e., when one of the ctenidia was reduced and the anus was displaced toward the parieto-palatal canal). Later this group evolved toward a general reduction of the mantle cavity and its substitution by the pulmonary cavity, which, apparently, presented a special outgrowth of the mantle cavity (Régondaud, 1961a, b; Harry, 1964).

In Opisthobranchia the original asymmetry increased as a result of the increased detorsion, whereas, when the shell was reduced, the mantle cavity followed suit.

The present data on the evolution of karyotypes in gastropods (Nishikawa, 1962; Burch, 1965, 1967; Patterson, 1967) do not contradict the above considerations. The lower forms in each subclass usually have low numbers of chromosomes, the minima in prosobranchs, opisthobranchs and pulmonates being 7-9, 12 and 16 pairs of chromosomes respectively. In the course of evolution numbers increase in parallel in different subclasses. That, for example, in Scutibranchia the minimum number of reported chromosomes is as high as 16 may be explained by the fact that only high ranking families (Haliotidae and Fissurellidae) of this subclass have been studied. At the same time high numbers of chromosomes are generally reported in the more advanced subclasses and groups, the maximal haploid chromosome numbers being, in Pectinibranchia (n = 36), in Opisthobranchia (n = 18) and in Pulmonata (n = 34-36). In cases of polyploidy, though, there occur multiples of the basic numbers (n = 60 or 72).

In our opinion the above considerations are sufficient reason for regarding the 3 phylogenetic lines under discussion here as equal in rank with Opisthobranchia and Pulmonata, i.e. justifiably to represent subclasses of the class Gastropoda. Assigning to them their oldest names, we shall give the following characteristics of each subclass.

KEY TO LETTERING ON FIGS. 2-5

a	nerve anastomosis
ab	arterial bulb
an	anus
ao	aorta
asn	asymmetrical mantle nerve
au	auricle
br	branchial ganglion
c	cerebral arc/ganglion
ca	caecum of stomach
cm	columellar muscle
ct	ctenidium
e	eye
ep	epipodium
ept	epipodial tentacles
f	foot
fis	fissure of shell
frt	frontal tentacle
g	gonad
h	hepatopancreas
hg	hypobranchial gland
i	intestine
j	jaws
k	kidney
lc	labial commissure
m	mouth
mc	mantle cavity
mn	mantle nerve cords/ring
mt	free part of mantle
oe	oesophagus
oep	oesophageal pouches
op	operculum
os	osphradium
ov	oviduct
pe	penis
per	pericardium
pg	pedal nerve cord/ganglion
ph	pharynx
pl	pleural ganglion
pr	proboscis
r	rectum
rd	radula
s	shell
sb	subintestinal ganglion
sg	salivary gland
sgr	seminal groove
sip	siphonal process
sn	symmetrical mantle nerve
sph	siphon
spr	supraintestinal ganglion
sr	seminal receptacle
st	stomach
t	tentacle
ts	testis
ut	uterus
v	ventricle
vd	vas deferens
vg	visceral ganglion
z	right zygosis
♂	male orifice
♀	female orifice

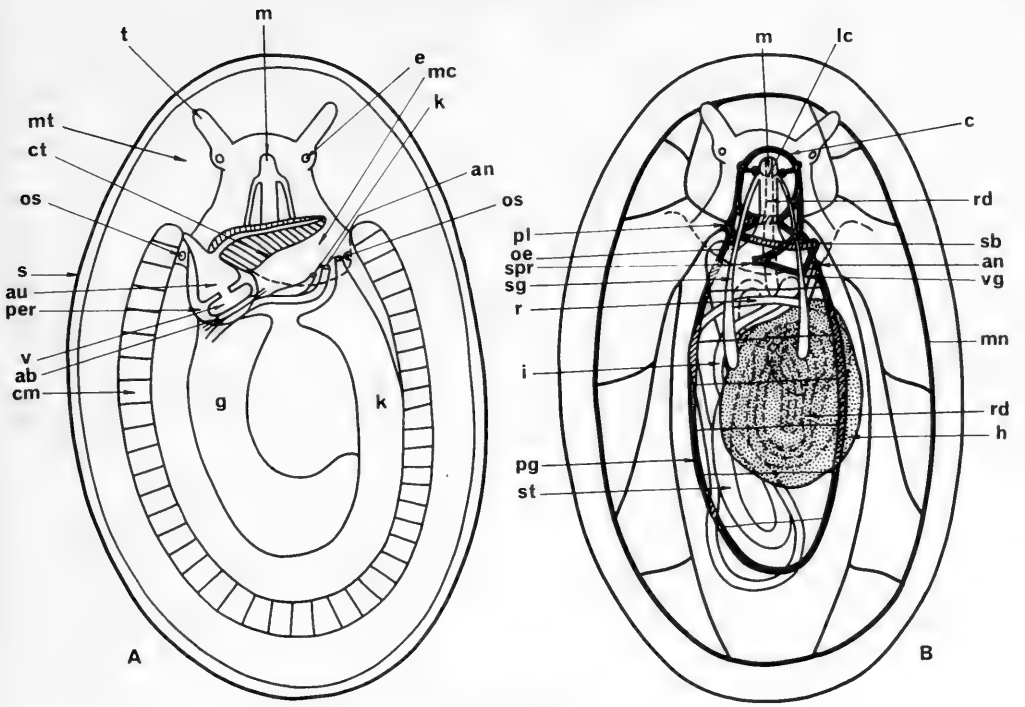

FIG. 3. General structural plan of Cyclobranchia (dorsal views).

SUBCLASS *CYCLOBRANCHIA* CUVIER, 1817 (Fig. 3)

(= Helcionellacea Wenz *sensu* Knight, Batten & Yochelson, 1960 + Archinacelloidea Knight & Yochelson, 1958 + Docoglossa Troschel, 1852).

The shell is primarily symmetrical, without any incision or sulcus, planospiral, endogastric[7], or cap-like with the apex displaced anteriorly, rarely posteriorly. The head bears one pair of tentacles. The epipodium is absent. The columellar muscle is originally paired; in cap-like forms it is horseshoe-shaped and develops from 2 muscle primordia. The mantle complex is primarily symmetrical; in Recent cap-like shell forms it is asymmetrical due to the clockwise rotation of the ctenidia and sometimes on account of the presence of the left ctenidium only, of the shift of the heart to the left and of the anus with the nephropores to the right. The osphradia retain their initially symmetrical position, the right osphradium occasionally disappears, the hypobranchial gland is absent. A circle of adaptive (secondary) mantle gills may be present. The heart has a well-developed left auricle, the right one being rudimentary; the arterial bulbus is present. There are 2 kidneys, the right kidney being larger and the gonad opening into it (not into its renopericardial duct). The reproductive system opens by a nephropore, the papilla of the right kidney sometimes continues into a long tube. Occasionally a copulatory apparatus of cephalic origin may also be present. Fertilization is mostly external. There are 2 pairs of salivary glands. The oesophagus is supplied with large sacs dilating into the gizzard. The radula is docoglossate, with many teeth in a transverse row in primitive forms, and a reduced number of teeth (6) in higher forms. When in motion the radula does not bend longitudinally and all teeth move only in one direction, coinciding with that of the movement of the whole radula. The stomach is divided into 2 parts, is devoid of protostyle, chitinous lining and caecum. In Recent forms, the rectum pene-

[7]Coiled so as to extend backward over the foot. ED.

trates the pericardium and not the ventricle. The central nervous system in higher forms has pronounced ganglia; Osphradial (branchial) ganglia and mantle nerve cords are present. There is no dialyneury.[8]

The subclass Cyclobranchia is divided into 3 orders, of which Docoglossa, with all their Recent forms, retain their generally accepted scope, but are given higher taxonomic rank.

Helcionellida, included in Tryblidiacea (= present class Monoplacophora) by Wenz (1938) and in Bellerophontida by Knight et al. (1960), are regarded as a separate order of Cyclobranchia. For the absence of the fissure on the shell in this Cambrian group, on the one hand, and the absence of any traces of metameric position of the internal organs, on the other hand, do not permit assignment to either Monoplacophora or Bellerophontida. However, a marked tendency towards reduction of the spire and a forward bend of the apex in the representatives of this group make it possible to include it in Cyclobranchia.

Taking into account the absence of any visible metamery in the muscles of *Archinacella* and similar forms, and the fact that at the apical end the muscular impression lies very close to the edge of the shell, leaving no place for the head, we consider the apical end of the shell to be their posterior, not anterior, end. It is a highly distinctive feature of Archinacellidae which obviously differentiates them from Monoplacophora, where they are usually placed (Knight &Yochelson, 1960; Horný, 1963a). That the contrapical portion of the shell in *Archinacellopsis patelliformis* (Hall) has 2 separate impressions which may be considered as impressions of radular muscles, furnishes further support for our view, already expressed in a recent study on the systematics of Monoplacophora (Starobogatov, 1970). The radulae of docoglossan type (in Monoplacophora and lower Gastropoda) are moved by a very strong system of muscles. The strongest of these, in Monoplacophora, are long radular muscles attached to the shell near the anterior edge of the muscular ring. Acmaeidae (= Tecturidae) and Patellidae have similar muscles, but their impressions are fused with the anterior ends of the horseshoe impression of columellar muscles.

For the above reasons we include the order Archinacellida in the gastropod subclass Cyclobranchia.

The evolution within Cyclobranchia, which proceeded in parallel to that in Scutibranchia, shows a tendency towards a smaller shell (with the average shell-length ranging from 55 mm in Patelloidea to 15 mm in Lepetoidea)[9], a less sculptured shell, oligomerization of the radula, manifested by fewer teeth per transverse row, the reduction of the specialized breathing organs, a larger renal papilla that began to protrude, the formation of a copulatory apparatus and a consequent transition to internal fertilization and ovoviviparity. The number of living species in Cyclobranchia does not exceed 350, of which only about 20 species belong to the phylogenetically youngest superfamily Lepetoidea. The most primitive of the recent representatives of the subclass live in the Indo-West-Pacific biogeographical region (about 120 species). Phylogenetically young representatives of the superfamily Tecturoidea and the majority of species of Lepetoidea are abundant in boreal waters (about 90 species). In the intertidal zone and in the extreme upper part of the sublittoral zone, i.e. on stony and rocky bottoms, the subclass shows the widest diversity of forms and the largest number of representatives. They live a semimobile life, feed on seasonal macrophyta and microphyta, scraping them off stones, and rarely on detritus. They appear to be mostly protandrous hermaphrodites.[10]

[8]Special arrangement of the nervous system with anastomosis of the pallial and visceral nerves, as in *Haliotis*. ED.

[9]The sizes of gastropod shells given here and later for different groups are based on an analysis of a total of over 20,000 dimensions, in part culled from the literature (Tryon & Pilsbry, 1880-1890; Philippi, Küster, Kobelt, Weinkauff, Clessin and Thiele, all in Martini & Chemnitz, 1846-1912) and in part from measurements from the collections of the Zoological Institute of the Academy of Science of the U.S.S.R. in Leningrad.

[10]At least there is no evidence for bisexuality in the Docoglossa, while there exist many records of protandry in representatives of this group (Willcox, 1898; Orton, 1920; Thorson, 1935, Bacci, 1948; Pellegrini, 1948; and others). Tecturidae, including *Acmaea*, are without exception hermaphrodites, as is also *Bathysciadium*. Consequently, until proof to the contrary is produced, we may assume that all Cyclobranchia are hermaphrodites.

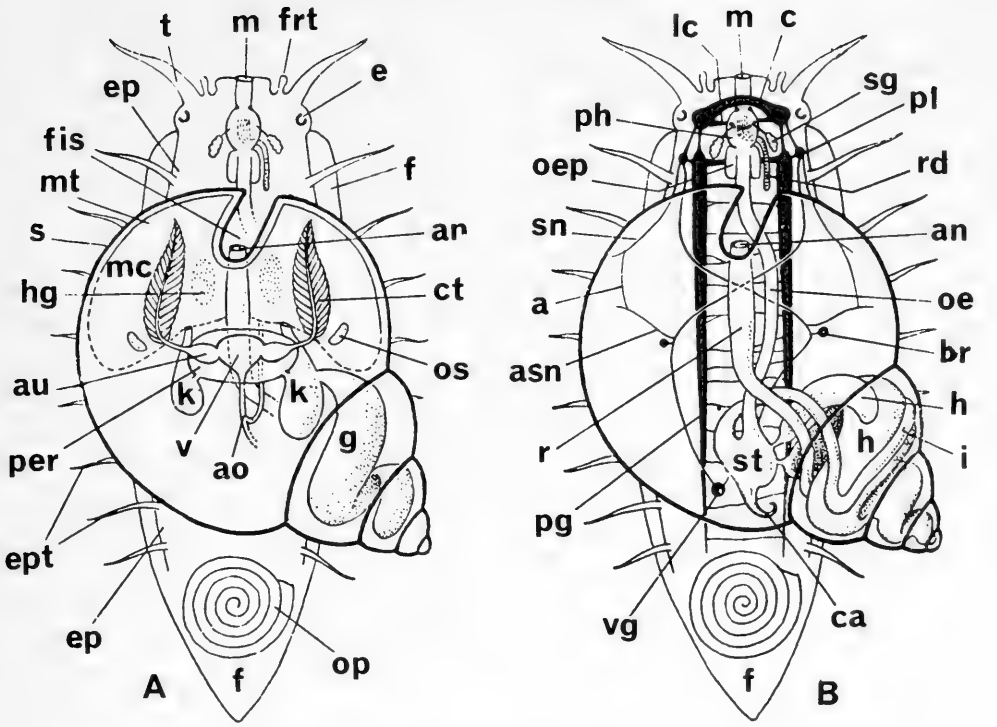

FIG. 4. General structural plan of Scutibranchia (from Ivanov, 1940).

SUBCLASS *SCUTIBRANCHIA* CUVIER, 1817 (Fig. 4)

(= Bellerophontina Ulrich & Scofield, 1897, excluding Helcionellacea + Zygobranchia Spengel, 1881)

The shell is either primarily symmetrical, planospiral, endogastric, often of a cap-like form, or conispiral; on the anterior periphery of the last whorl above the head there is always either an incision or a sulcus that appears as a peripheral keel when viewed from outside. In the course of growth, the incision may separate from the peristome, i.e. close to form a foramen and be displaced; in cap-like forms the foramen may become apical. The head has one pair of tentacles. The epipodium is well developed and is usually supplied with tentacles. The columellar muscle is paired; in primarily symmetrical planospiral forms the right and left muscles are equal; in cap-like forms they merge posteriorly to form a single horse-shoe-shaped muscle. In conispiral forms the left muscle is rudimentary, while the right muscle is well developed. The mantle complex is symmetrical, except that the right kidney is somewhat larger than the left. There are always 2 ctenidia in conispiral forms, the left always being larger than the right. The gonad opens into the right reno-pericardial duct and rarely into the right kidney. A copulatory apparatus is always absent. Fertilization is external. There is one pair of small salivary glands, located in the head. The oesophagus has a pair of oesophageal pouches. The rhipidoglossate radula is supplied with a great number of teeth, and, when in motion, is bent longitudinally with all its teeth moving in various directions that, except for the rachidian tooth, do not coincide with the direction of radula movement. The stomach has a caecum, a protostyle, and a chitinous lining. The rectum runs through the pericardium and the ventricle. The central nervous system has no prominent ganglia. Branchial ganglia are present, but no mantle nerve cords.

The subclass Scutibranchia is divided into 3 orders: Dicranobranchia, Fissobranchia and Macluritida, having different

shell characters, different times of origin and probably different anatomies. The order Dicranobranchia, which came into existence in the early Cambrian, includes the superfamily Bellerophontoidea and the superfamily Fissurelloidea. We think it reasonable to unite in one group the planospiral Bellerophontoidea, which became extinct in the Triassic, and the limpet-shaped Fissurelloidea, which appeared at that time, in particular if we take into account that the development of the latter group does not show any trace of a conispiral shell in their ancestors.

Besides, the presence in Fissurelloidea of a cap-like shell with a horseshoe-shaped columellar muscle developing from nearly equal rudiments (Crofts, 1955), its usual symmetry, and similarities in the location and size of the mantle complex, together with various progressive features in the structure of the nervous system, provide good reason to consider this group as derived from Bellerophontoidea, which had a planospiral endogastric shell. The Fissurelloidea are thought to continue the line of bellerophontid evolution side by side with Fissobranchia, which in the course of their evolution developed a conispiral shell and separated from bellerophon-like ancestors much earlier. That we find no noticeable transition between cap-like and Recent conispiral forms of Scutibranchia provides additional evidence in favor of this view. The order Fissobranchia, which is phylogenetically related to the Dicranobranchia, followed an independent line of evolution, due to the formation of the conispiral shell, while the symmetrical plan of structure of the mantle complex remained similar in the 2 orders. In general the scope of this order coincides with that of the superfamily Pleurotomariacea of other authors; the few modifications made are only within the order itself (see the notes).

The third order, Macluritida, that became extinct in the Triassic, exhibits a special line of evolution in the Scutibranchia. Its characteristic feature was a tendency to develop a depressed sulcus or a process instead of a fissure (selenizone) on the body whorl. This order may be considered ancestral to the subclass Pectinibranchia, the most primitive representatives of which could derive from Macluritidae or from their common ancestors. It is possible that the families of this order should be grouped in 2 independent orders: Macluritida, with a pseudosinistral shell (including the sole superfamily Macluritoidea), and Trochonematida, with a normal, dextral shell (including the remaining superfamilies). Such a classification would follow from Minichev & Starobogatov's (1971) considerations on the origin and evolution of heterostrophy.

To sum up the trends in the Scutibranchia: the evolution of this old subclass of Cambrian origin showed a tendency towards a smaller shell—in Recent forms the average height of shells vary (see footnote 9) from 91 mm in Pleurotomarioidea and Haliotoidea to 24 mm in Fissurelloidea; secondary reduction of the degree of shell coiling; less pronounced spiral sculpture (see footnote 12) and more prominent axial sculpture; further, as already stated, separation and displacement of the fissure from the peristome, the fissure itself growing smaller; and a larger right kidney serving a double function.

The number of Recent species of the subclass Scutibranchia does not exceed 450. More than half of them belong to the phylogenetically youngest superfamily Fissurelloidea. More than 43% of Recent representatives of the subclass live within the Indo-West-Pacific biogeographical region, which was not only the center of their evolution, but also that of their origin (see footnote 13). This idea is supported by the fact that the larger part of the superfamily Pleurotomarioidea, which is the most primitive of the Recent forms, live in the Indo-West-Pacific region (more than 68% of the species), while the superfamily Fissurelloidea, which is phylogenetically younger, is represented there by only 36% of its species.

The mollusks of this subclass live mostly in shallow waters on hard bottoms. They feed on algae and more rarely detritus. They are bisexual, and their pelagic larvae are a prominent feature in the course of development.

SUBCLASS *PECTINIBRANCHIA* BLAINVILLE, 1814 (Fig. 5)

(= Anisobranchia v. Ihering, 1876 + Monotocardia Mörch, 1865)

The shell is initially conispiral, sometimes with a secondary simplification, cap-like, tube-like or planospiral, always without

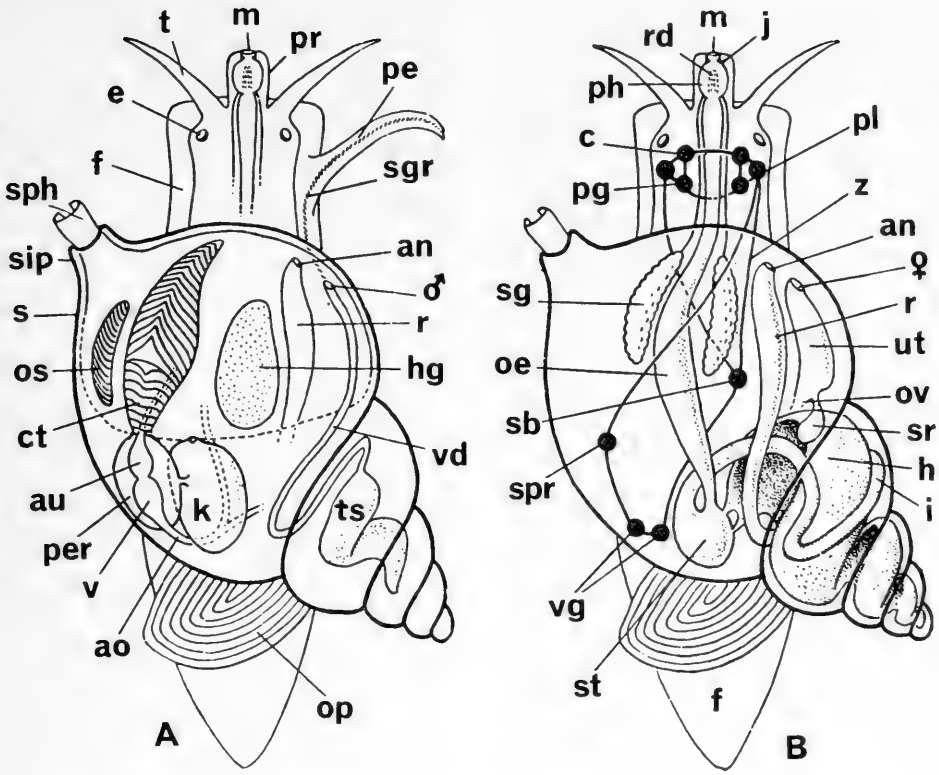

FIG. 5. General structural plan of Pectinibranchia (from Ivanov, 1940).

an incision. The head bears one pair of tentacles and sometimes has one pair of frontal lobes. The epipodium is only slightly developed, often completely absent. Only the right columellar muscle is present (in sinistral forms only the left). The horseshoe-shaped columellar muscle of cap-like forms develops from one muscle primordium. The mantle complex is sharply asymmetrical. The ctenidium and osphradium are unpaired (on the left in dextral forms). The hypobranchial glands are paired (very unequal), or more often single. Only one auricle is functional, corresponding to the only ctenidium; the other is rudimentary or completely invisible. There are 2 kidneys of which the right kidney (in dextral forms) is larger than the left, the gonad opening into the renopericardial duct; or the kidney may be completely incorporated in the reproductive system as the renal gonoduct. The reproductive system debouches either by the nephropore or continues further into the pallial gonoduct; a copulatory apparatus may also be present, arising either from the head or the foot. Fertilization is external or, more often, internal. There are 1 or 2 pairs of salivary glands; they are mostly large and situated behind the nerve ring. The oesophagus may have paired pouches, but, more often, lacks them. The radula is bent longitudinally when in action; it may be rhipidoglossate, consisting of a large number of rather homogeneous teeth, or it may have a smaller number of teeth per transverse row (7, 3, 2 or even 1). The stomach is with or without the caecum, and often has a protostyle or crystalline style. The rectum either penetrates the pericardium and the ventricle, or runs at a distance from these organs. The central nervous system has well developed and well pronounced ganglia. The lowest forms have the left branchial ganglion and show dialyneury, features absent in the highest forms. There are no mantle nerve cords.

The subclass is divided into 18 orders, characterized by a distinct structure of the shell, foot, mouth organs, gill, central nervous system, reproductive system and

distinctive ecology, the structural plan and direction of evolution being, in general, similar in all the orders. We shall not give a detailed analysis of all the characteristic features of each order, as the morphological and biological properties of their taxonomic representatives have already been given due and extensive consideration in the literature. We shall restrict the discussion of our classification only to those orders or parts of orders whose contents or position has been changed from that in the latest phylogenetic schemes.

Within the large subclass Pectinibranchia we may distinguish several phylogenetic branches, most comprising a few orders. All of them may have originated from the lowest Anisobranchia, which became extremely diversified in the Paleozoic. Each of these branches shows an independent development of the pallial gonoduct (as evidenced by the forms without a pallial gonoduct or at least by those with a longitudinally open pallial gonoduct in all the lines of evolution mentioned); they also show a concentration of the pedal nerve cords in the pedal ganglia and a change of the number of teeth per transverse row of the radula. There are 6 such phylogenetic branches for which we establish 6 superorders. Next to the superorder Turbinimorpha, which was ancestral to all the other groups and which includes only the order Anisobranchia and tentatively Lepetellida, we distinguish the following superorders: Neritimorpha (in content equal to the old superfamily Neritacea), Paludinimorpha (Architaenioglossa and probably Valvatacea), Pyramidellimorpha (heterostrophic forms together with Eulimacea and Ptenoglossa), Cerithiimorpha (Cerithiacea together with Stenoglossa = Hamiglossa and Toxoglossa, derived from them), and Littorinimorpha, comprising all the remaining groups, and considered as arising from forms that share many structural features with Turritellidae.

The ancestral order Anisobranchia, which is the most primitive in the subclass, retains its generally accepted scope with only minor modifications. The representatives of the order may have originated from old Scutibranchia as early as the Ordovician, and already by the Triassic had developed a great diversity of forms. Tentatively we here include the small order Lepetellida, following Moskalev (1971). However, its position and origin remain obscure and need further research.

Neritidae and related groups, forming a separate order Planilabiata in our scheme, show an independent line of evolution. The characteristic feature of this old order of supposedly Devonian origin is the relative complexity of its reproductive system, especially when contrasted with certain primitive elements in the structure of some other organs.

Viviparoidea and Cyclophoroidea, which may have appeared as early as the Carboniferous, form a special order Architaenioglossa. In the course of their evolution they adapted from marine life to that in fresh water and finally on land. The transition resulted in a longitudinally divided mantle cavity, in the reduction of the pectinate ctenidium and in the change from a ciliary semi-filtration type of feeding[11] to phytophagy and detritophagy.

The combination of progressive and primitive structural features and the presence of a bipectinate ctenidium freely protruding from the mantle cavity, features not observed in other Pectinibranchia, provide reason to separate the fresh-water Valvatoidea and possibly the marine Tornoidea in the special order Ectobranchia.

Turritelloidea and Vermetoidea, sharing some primitive structural features, and being an ancient, sufficiently specialized group of possibly Devonian origin, are placed in the separate order Protopoda. The characteristic features of these mollusks, which possibly might have been the ancestors of some other higher groups of Prosobranchia, are the absence of copulatory organs, the open pallial gonoduct, the elongated shell and semi-filtration feeding.

Littorinacea and Rissoacea in the generally accepted sense form one of the largest groups of prosobranchs, not only on account of the diversity of species with a distinctive morphology, but also because of their wide occurrence in shallow seas. They may be collected in one order, Discopoda, on the grounds of various common morphological features (such as a small shell with an esiphonate aperture, a rather complex repro-

[11] Ciliary semi-filtration feeding is the ability of prosobranchs to catch the seston carried over the surface of the bottom by the ctenidial cilia and to swallow it, agglutinating the organic particles with mucus.

ductive system, an alimentary system with a taenioglossate radula, which is in general similar in the 2 groups) and a uniform direction of evolution. They were specialized, mainly phytophagous gastropods which adapted to life on plants, colonized brackish and fresh waters and later dry land. The group is not ancestral to prosobranchs of other lines of evolution. It may have originated in the Triassic, its most probable ancestors being ancient Protopoda or some progenitors common to both. Taxonomically and morphologically, Discopoda have not been studied adequately because of their small size and diversity of form, and our classification of the order may need some corrections.

The group of families generally brought together to form the superfamily Strombacea has its own collateral line in the evolution of prosobranchs. Distinct from other Gastropoda having a taenioglossate radula, Strombacea have a peculiar shell, usually with processes, a divided foot with a metapodium, an operculum with a terminal nucleus and a distinctive structure of the radula and of the reproductive system. We think it reasonable to separate Strombacea in a special order Alata. The group probably originated at the juncture of the Triassic and Jurassic, from Protopoda or some common ancestor. Of great importance for the formation of the order was the adaptation of its representatives to life on soft bottoms in the marine epifauna; it resulted in the development of different types of shell processes to keep the shell on the surface of the bottom, and in the transition to active feeding on detritus.

Raising the Heteropoda—which in the course of their evolution assumed a planktonic way of life, with all the necessary adaptations—to the rank of an order appears reasonable and needs no additional comment.

The families Cymatiidae, Colubrariidae and Bursidae (= Ranellidae) are assembled in the superfamily Cymatioidea because of similar shells and morphology. Cassididae, Tonnidae and Ficidae (assembled in the superfamily Cassidoidea) form a special group of prosobranchs. This group of Cretaceous origin arose as an independent branch of evolution, and is probably phylogenetically connected with Protopoda or Alata. Development in this group was conditioned by the transition to (1) predation with the same taenioglossate radula, and (2) to a burrowing way of life. This independent direction of evolution, a characteristic shell, which is supplied with a siphonal canal, and the specific structure of the mantle and alimentary system make it possible to unite Cymatioidea and Cassidoidea in a special order Canalifera.

The superfamilies Vanicoroidea, Calyptraeoidea, Pedicularioidea, Cypraeoidea and Lamellarioidea, which mostly developed characteristic pelagic larvae, such as echinospirae, also show a special path of evolution. They have some morphological features in common and are combined in a special order Echinospirida. This large and complex group of mollusks may have appeared in the Triassic. Phylogenetically it is connected with the order Protopoda; in the course of its evolution it changed from a semi-filtration type of feeding to ectoparasitism (Vanicoroidea and Calyptraeoidea) or to predation (Cypraeoidea, Pedicularioidea and Lamellarioidea). Further characteristic features of the order are: a tendency towards reduction of the operculum; looser coiling of the whorls, resulting even in cap-like or ear-like shells; overgrowth of the shell by the mantle, resulting in complete disappearance of the external shell, or in the development of a thick, skin-like periostracum.

Phylogenetically closely connected with the above order are Naticacea, which may have appeared in the Triassic, and which developed independently as specialized predators. Naticacea are separated in a special order Aspidophora on the basis of an independent phylogenetic line of evolution, of having a distinctive shell, a propodium and a system of water-bearing vessels in the foot, and a special structure of the alimentary system (radula, acrembolic proboscis supplied with a drilling gland) and of the reproductive system.

Cerithiacea show an independent line of evolution in the Pectinibranchia. They may have appeared in the Triassic and, being a most productive group, they may have given rise to higher prosobranchs. The characteristic elongated shell with its tendency to develop a siphonal process, the operculum with its central nucleus, the character of the taenioglossate radula which shows a great variety of tooth form within this group, and

the absence of a copulatory apparatus make us separate Cerithiacea in the independent order Entomostoma.

The highest prosobranchs, which are generally brought together to make up the superfamilies Fasciolariacea, Buccinacea, Volutacea and Muricacea are in close and immediate phylogenetic relationship with the Entomostoma. This group of families, which probably appeared in the Cretaceous period, rapidly developed from detritophagy and saprophagy to specialized predation within a relatively short geological period of time. Apparently this transition brought about some reconstruction of the alimentary system, such as development of the oesophageal gland and the formation of the stenoglossan (rachiglossate) radula, with subsequent further oligomerization within the group, the development of the siphonal canal, which was always well pronounced, and the isolation of the reproductive system from the mantle cavity and the kidney. As far as the classification under discussion is concerned, the separation of this group of families in an independent order named Hamiglossa on the basis of priority needs no further consideration. It may be pointed out that Triphoridae, which show a kind of transitional link between Entomostoma and Hamiglossa, have a polydontous radula and are assigned to the suborder Rhiniglossa, and are the most primitive family in the order. The most progressive families are those in Muricoidea, which are equipped with the radula of a perfect predator, and in Cancellarioidea, with their tendency towards complete reduction of the radula. These are placed in the suborder Nematoglossa. Some further details about the order Hamiglossa are given in the notes.

Parallel to Hamiglossa there appeared a group of families usually united in the superfamily Conacea, which had the same Cretaceous origin and stemmed from the same ancestors. The characteristics of their external and internal morphology, the peculiar character of their development and the independent direction of their evolution provide sufficient reason for separating this group as a special order Toxoglossa. This order, consisting of specialized predators only, showed an evolutionary tendency towards oligomerization of the radula. The reduction proceeded parallel to, but unlike that in Hamiglossa, manifesting itself in a gradual disappearance of the rachidian tooth and of the middle lateral and marginal teeth, but not in the reduction and simplification of the lateral teeth. The most primitive families in the order, close to the lowest Hamiglossa are: Mitridae, Speightiidae, Thatcheriidae and Clavidae; the most advanced are Raphitomidae, Conidae and Terebridae.

The group of prosobranch gastropods which is generally comprised in the superfamilies Loxonematacea, Nerineacea, Pyramidellacea, Architectonicacea, Epitoniacea and Eulimacea, have an independent and distinctive line of evolution in the subclass Pectinibranchia. The morphological originality of this group, frequently mentioned in the literature, as well as the presence of heterostrophy in a number of its representatives, lead us to assume that its origin might be independent from that of the remaining Pectinibranchia. It is probable that, in the future, this group will be set apart as an independent subclass; but, for the time being, solely the reflections on the origin of heterostrophy (Minichev & Starobogatov, 1971) speak in favor of this assumption. We therefore refrain from categorical statements on this point and retain this group in Pectinibranchia. The group appeared as early as the late Cambrian or Ordovician, when differentiation of Pectinibranchia into orders was just starting. The group might have developed from common ancestors with Anisobranchia or even Opisthobranchia and Pulmonata. It is divided into a number of orders at different levels of evolution and specialization within the new superorder Pyramidellimorpha. The main trend in the evolution of these mollusks was the transition from free life and predation to commensalism, ectoparasitism and further to endoparasitism. Morphologically it gradually led to a smaller and reduced shell and radula, a more complex reproductive system, accompanied by an increased sexual dimorphism. The independence of the evolutionary line of this group is supported by a peculiar multidentate, weakly differentiated radula transitional between the campylodont and orthodont type in some representatives, while in others it is fully orthodont. This type of radular apparatus could develop only from the primitive multidentate radula. Loxonematacea (which probably are connected with Subulitacea) together with Pyramidellacea, Nerineacea and Architec-

tonicacea, which phylogenetically go back to Loxonematacea, are the oldest superfamilies of the group. Heterostrophy, perhaps a characteristic feature of primary forms which may have disappeared in some groups, a peculiar shell, an evolutionary tendency towards commensalism and ectoparasitism, and some common anatomical features, lead us to separate these superfamilies in a special order Heterostropha, with Subulitina, Entomotaeniata and Gymnoglossa as its suborders. The taxonomic position of Pyramidellacea, which are occasionally included in Opisthobranchia (Fretter & Graham, 1962) has caused many disputes and discussions. In our opinion the direct phylogenetic connection of Pyramidellacea with the above mentioned extinct mollusks, as well as with Architectonicacea, and of the latter group with Epitoniacea, contradict these views.

Epitoniacea and Janthinacea, which in the course of their evolution adapted to pelagic life, form a special group of gastropods that may have appeared at the juncture of the Triassic and Jurassic and developed from some ancestors held in common with Gymnoglossa. The character of the shell, the presence of the ptenoglossate radula in all the representatives, the absence of heterostrophy and the apparent evolutionary trends make it possible to unite these superfamilies in a special order Ptenoglossa.

Eulimacea (= Melanellacea), which are phylogenetically connected with the line of Subulitacea-Loxonematacea, are the most specialized group of the branch under consideration. These mollusks, lacking a radula and showing considerable morphological changes caused by the transition from commensalism and ectoparasitism to endoparasitism, are separated in the order Homoeostropha.

The evolution of the phylogenetic branches in the subclass Pectinibranchia had many features in common, which was often expressed by parallelism in each of the above mentioned phylogenetic branches. We observe: a common tendency towards weakening of shell sculpture in general and of the spiral sculpture in particular[12]; the formation, very often quite independently, of the siphonal process; disappearance of the epipodium; reduction of jaws; oligomerization of the radula, which took different forms in different groups and often led to its complete reduction in specialized mollusks; a more pronounced asymmetry of the mantle complex; formation of the pectinate ctenidium, attached to the mantle, and of the pectinate osphradium; transformation of the right kidney remnants into the renal gonoduct; formation and development of the pallial gonoduct and of the copulatory apparatus; concentration and integration of the central nervous system. The Pectinibranchia, which are the most highly developed subclass among Gastropoda, consist of about 12,000 Recent species. The 3 orders with the largest number of species are: the Anisobranchia (about 1,500), which are almost solely responsible for the diversity of the groups of the subclass, and the relatively young and phylogenetically advanced Hamiglossa and Toxoglossa (about 2,000 and 3,000 species respectively). More than half of the total number of species lives in the Indo-West-Pacific biogeographical region, which was the source of the high variety of forms of the subclass. As the most primitive representatives are also among them, this region was probably its center of origin[13]. This assumption is also supported by the fact that about 60% of all the Recent species of Anisobranchia and about 70% of Planilabiata live in tropical waters in the western part of the Pacific Ocean. The region of the present Mediterranean Sea and adjacent waters may also be considered to be an old center of form-building and evolution of the subclass Pectinibranchia. But that region is not so rich in forms and only about 20% of all species of the subclass live there now. The number of species of this subclass is about equal in all other biogeographical regions.

In temperate and cold waters only the highest of the phylogenetic lines discussed developed a considerable diversity of forms. The most developed are the species of the orders Echinospirida (about 90 species, i.e. about 36% of the total number of species of this group) and Hamiglossa (about 200

[12]The primary nature and great primitiveness of spiral sculptural elements of the gastropod shell have been well shown by Grabau (1928). From published data and from our own observations we could observe a decrease of spiral sculpture coupled with a relatively greater prominence of axial sculpture not only in phylogenesis but also in ontogenesis of pectinibranchs.

[13]This view is shared by a number of biogeographers, among them Ekman (1953); it applies also to crabs (Stephenson, 1962) and other groups of animals.

species, i.e. about 18% of the total for this group).

As to their biotopic preferences, the representatives of all the phylogenetic branches of the subclass exchanged, in the course of their evolution, rocky bottoms of shallow waters (the initial habitat of gastropods) for submerged plants, the open sea, epifauna of semi-hard bottoms and lastly for soft bottoms, migrating occasionally into the infauna; they also changed shallow water habitats for the deep sea and abyssal waters, and for fresh water and dry land. In fact, the majority of the representatives of the most primitive ancestral order Anisobranchia live on rocky bottoms in shallow waters, as also do the majority of species of the old order Planilabiata. They inhabit wide expanses of the littoral zone in tropical and subtropical latitudes, sometimes brackish and occasionally fresh waters. The species of the orders Architaenioglossa and Ectobranchia, which appeared in late Carboniferous or early Triassic times, live in fresh waters and on dry land. The species of the relatively old order Protopoda live mainly on hard, sandy, stony or rocky bottoms in shallow waters, while the younger orders Discopoda, Alata, Heteropoda, Canalifera, Echinospirida and Aspidophora, which are phylogenetically connected with Protopoda, inhabit vegetation such as leaves of underwater higher plants and thalli of algae, epifauna of semi-hard or soft bottoms, infauna, and pelagic communities. The phylogenetically youngest and highest orders Hamiglossa and Toxoglossa have the relatively highest percentages of species living in waters of considerable depth, on soft bottoms and in the infauna.

As for the type of feeding, the subclass clearly shows a tendency, parallel in different phylogenetic lines, of transition from initial microphagy, sestonophagy and phytophagy (in the majority of species of the orders Anisobranchia, Planilabiata, Architaenioglossa, Ectobranchia, Protopoda, Discopoda and Entomostoma) to detritophagy, saprophagy and predation (in the majority of representatives of the orders Alata, Heteropoda, Canalifera, Echinospirida, Aspidophora, Hamiglossa, Toxoglossa and Ptenoglossa). In the orders Heterostropha and Homoeostropha parasitism evolved and with it a special suctorial type of feeding.

Reproduction changed from external to internal fertilization; then, on account of a shortened pelagic stage, to the formation of egg capsules, to direct development and ovoviviparity.

The size of the shell, its change, and the direction of that change, are closely connected with the peculiarities of the ecology of a group in general and its type of feeding in particular. On the whole, in the course of its evolution, the subclass shows a tendency towards a larger shell because of the dominance of saprophages and predators at the top of different parallel evolutionary lines. The mean height of the shell (see footnote 9) in the ancestral order Anisobranchia is 18 mm, while in the phylogenetically younger orders Aspidophora and Alata it is 26 and 90 mm respectively in one line of evolution, and, in another line of evolution, in the most advanced groups of the subclass, i.e. the orders Hamiglossa and Toxoglossa, it is 40 and 28 mm respectively. Nevertheless the evolution of phytophagous forms showed a tendency towards a considerably smaller shell, while microphagous and sestonophagous forms showed almost no change, or tended towards a slightly larger shell. In the line of evolution Anisobranchia-Protopoda-Discopoda the mean height of the shell varies from 18 mm in the ancestral phytophagous group to 35 mm in sestonophagous Protopoda, and to 6 mm in phytophagous Discopoda. Within the last order the mean height of the shell changes from 10 mm in the superfamily Littorinoidea to 4 mm in the phylogenetically advanced superfamily Truncatelloidea. It should be noted, however, that in the course of their evolution predators and saprophages, which are in general larger than phytophages and sestonophages, within certain limits also show a tendency towards a smaller shell. In the order Hamiglossa, for example, the suborder Rhiniglossa has the smallest shell (the mean height of the shell being 10 mm), and Rachiglossa the largest (40 mm). Nematoglossa, being a phylogenetically younger group, show secondary diminishing of shell size (28 mm).

It is interesting to note that all 3 subclasses under consideration show much similarity in phylogeny and evolutionary trends. This similarity is revealed in parallel

evolutionary tendencies towards: more pronounced asymmetry and oligomerization of the radula; a more complex reproductive system, connected with the transition from external to internal fertilization, and from possessing a pelagic larva to direct development and ovoviviparity; also, the concentration and integration of the central nervous system. However, as has already been shown in the present paper, similar evolutionary problems were solved in different ways in the different subclasses, and results have not always been equally successful. It should be stressed here that convergence never involves those main morphological features that make the subclasses in question different from each other. Thus, in spite of the fact that limpet-like forms, which often had similar ways of life and similar manners of feeding, very often appeared in different subclasses, their internal morphology reflects the main morphological features of the corresponding subclasses. For example, the shape and function of the radula and some other peculiar structural features of Cyclobranchia differ very greatly from those in the cap-like forms of Scutibranchia and Pectinibranchia in spite of the similarity in their ecology, of the external shape of the shell and of the columellar muscle. The cap-like forms of Scutibranchia and Pectinibranchia are also very dissimilar morphologically, though the function of their radulae is in general the same. The above reflections support the evolutionary independence of the subclasses in question. The distribution of Recent species in the subclasses is in agreement with a well-known phylogenetic tendency for an increase in the number of species in phylogenetically advanced groups. Thus, the lowest number of species is found in the most archaic gastropods (Cyclobranchia) and the highest in the most progressive groups (Pectinibranchia, Opisthobranchia and Pulmonata).

In terms of ecology and distribution, the evolutionary parallelism in the subclasses finds its expression in: the transition from living on hard bottoms in shallow waters to living on mixed and soft bottoms at greater depths; in the change of the mode of feeding, i.e. in the transition from microphagy and phytophagy to detritophagy (in older groups) and to saprophagy and predation (in phylogenetically younger groups); in the extension of distribution from tropical and subtropical waters to temperate and cold regions; in an increase in the number of Recent species in the phylogenetically youngest groups. The tempo of form-building in the various phylogenetic groups of Gastropoda has been uneven. This observation is in agreement with the data on the evolution of other organisms. The form-building process was most active in the Cambrian-Ordovician, Permian-Triassic and Cretaceous-Paleogene, i.e. in the periods of increased tectonic alterations of the earth's crust and intensive changes of the planet's climate.

The parallelism in the evolutionary trends in various groups of prosobranchs is indicative not so much of phylogenetic relationship of the developing groups but rather of certain common traits of evolution then in progress that were closely connected with physical and chemical changes taking place in the course of the development of our planet.

The above considerations on the evolution of prosobranchs and on its main lines and the phylogenetic relationships between the different groups are reflected in the scheme of evolution and phylogeny presented here (Fig. 6) and in the subclasses, superorders, orders, suborders, superfamilies and families[14], listed below in their evolutionary sequence.

[14]It will be seen that a number of taxa have been elevated in rank and that a larger number of families are recognized, as we believe that the differences between the new and old families are in no case less than those met in the families generally accepted. By way of example, **Tibiidae** and Strombidae differ no less than Nassariidae and Buccinidae, or Buccinidae and Neptuneidae. Still more considerable are the differences between Pyramidellidae and Turbonillidae; in fact, the latter do not seem to be uniform and should probably be split into Turbonillidae and Odostomiidae as the differences in the glands of the reproductive system are as great as those between Planorbidae and Lymnaeidae. As regards the new family **Hemitomidae**, we find the differences from Emarginulidae and Fissurellidae important and our reasoning on the evolution of the Scutibranchia leads us to the conclusion that the Hemitomidae originated from other bellerophon-like ancestors.

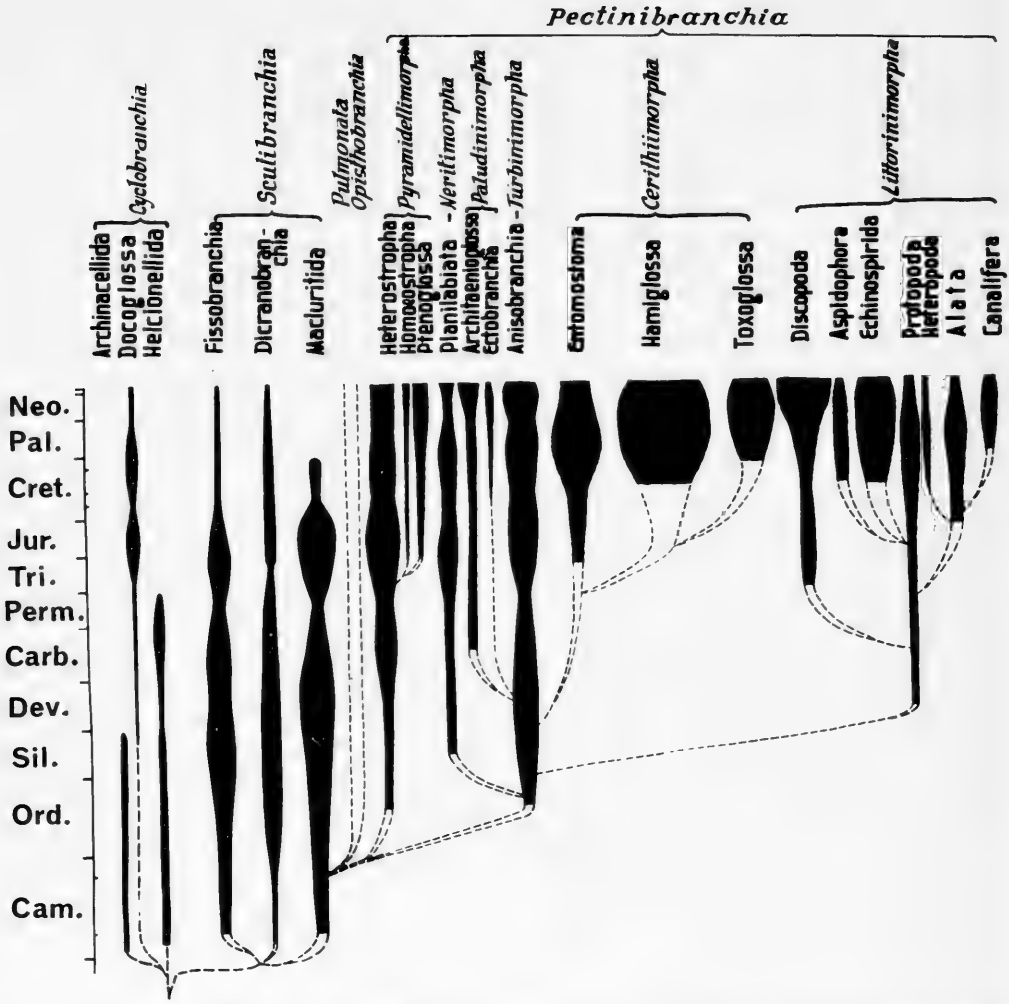

FIG. 6. Scheme of evolution and phylogeny of Gastropoda, particularly of prosobranch subclasses and orders (Opisthobranchia and Pulmonata are not considered in detail; Lepetellida are omitted). The width of the bands reflects the relative numbers of species in each phylogenetic branch at different geological times, from Cambrian to the Recent, calculated by the method of Schilder (1947).

SYSTEMATICS

Subclass CYCLOBRANCHIA Cuvier, 1817
- Order Helcionellida[15] Knight, Batten & Yochelson, 1960 (as Helcionellacea)
  - Superfamily Helcionelloidea Wenz, 1938 (note 1)
    - Coreospiridae Knight, 1947
    - Helcionellidae Wenz, 1938
  - Superfamily Metoptomatoidea Wenz, 1938 (note 2)
    - Metoptomatidae Wenz, 1938
- Order Archinacellida Knight & Yochelson, 1958
  - Archaeopragidae Horný, 1963
  - Archinacellidae Knight, 1956
  - (?) Hypseloconidae Knight, 1956
- Order Docoglossa Troschel, 1866 (note 3)
  - Superfamily Patelloidea Rafinesque, 1815
    - Damilinidae Horný, 1961
    - Nacellidae Thiele, 1891
    - Patellidae Rafinesque, 1815
  - Superfamily Tecturoidea Gray, 1847
    - Tecturidae Gray, 1847 (Acmaeidae)
    - Lottiidae Habe, 1944
    - Pectinodontidae Thiele, 1893
  - Superfamily Lepetoidea Dall, 1869
    - **Propilidiidae** fam. nov. (type-genus *Propilidium* Forbes & Hanley, 1849)
    - Lepetidae Dall, 1869
  - Superfamily Bathysciadioidea Dautzenberg & Fischer, 1900
    - Bathysciadiidae Dautzenberg & Fischer, 1900
  - (?) Superfamily Bathypeltoidea Moskalev, 1971
    - Bathypeltidae Moskalev, 1971

Subclass SCUTIBRANCHIA Cuvier, 1817
- Order Dicranobranchia Gray, 1821 (note 4)
  - Superfamily Bellerophontoidea McCoy, 1851
    - Sinuitidae Dall (in Zittel-Eastman), 1913
    - Grandostomatidae Horný, 1962
    - Temnodiscidae Horný, 1962
    - Tropidodiscidae Knight, 1956
    - Bucaniidae Ulrich & Scofield, 1897
    - Salpingostomatidae Koken, 1925
    - Carinaropsidae Ulrich & Scofield, 1897
    - Pterothecidae Wenz, 1938
    - Bellerophontidae McCoy, 1851
    - Cymbulariidae Horný, 1963
    - Knightitidae Knight, 1956
    - Euphemitidae Knight, 1956
  - Superfamily Fissurelloidea Fleming, 1822 (note 4)
    - Emarginulidae Gray, 1834
    - **Hemitomidae** fam. nov. (type-genus *Hemitoma* Swainson, 1840) [see footnote 14]
    - Fissurellidae Fleming, 1822

[15]Some authors of recent works (e.g. Knight et al., 1960) have attempted to treat the name endings of orders (-ida) and suborders (-ina) uniformly. If this is desired, the names of those orders and suborders of our system that do not have these endings may be transformed into: Docoglossida, Dicranobranchida, Fissobranchida, Anisobranchida, Planilabiida, Architaenioglossida, Ectobranchida, Protopodida, Discopodida, Prionoglossina, Alida, Heteropodida, Canaliferida, Inoperculina, Involutina, Aspidophorida, Entomostomida, Hamiglossida, Rhiniglossina, Rhachiglossina, Nematoglossina, Toxoglossida, Heterostrophida, Entomotaeniina, Gymnoglossina, Ptenoglossida, and Homoeostrophida.

Order Fissobranchia Stoliczka, 1868 (note 5)
- Superfamily Rhaphistomatoidea Koken, 1896
  - Sinuopeidae Wenz, 1938
  - Rhaphistomatidae Koken, 1896
- Superfamily Pleurotomarioidea Swainson, 1840
  - Eotomariidae Wenz, 1938
  - Lophospiridae Wenz, 1938
  - Luciellidae Knight, 1956
  - Phanerotrematidae Knight, 1956
  - Gosseletinidae Wenz, 1938
  - Portlockiellidae Batten, 1956
  - Catantostomatidae Wenz, 1938
  - Porcelliidae Broili, 1924
  - Rhaphischismatidae Knight, 1956
  - Phymatopleuridae Batten, 1956
  - Polytremariidae Wenz, 1938
  - Laubellidae Cox, 1960
  - Schizogoniidae Cox, 1960
  - Zygitidae Cox, 1960
  - Kittlidiscidae Cox, 1960
  - Temnotropidae Cox, 1960
  - Pleurotomariidae Swainson, 1840
  - Scissurellidae Gray, 1847
  - Trochotomidae Cox, 1960
- Superfamily Murchisonioidea Koken, 1896 (note 6)
  - Murchisoniidae Koken, 1896
  - Plethospiridae Wenz, 1938
- Superfamily Haliotoidea Rafinesque, 1815
  - Haliotidae Rafinesque, 1815

Order Macluritida Cox & Knight, 1960
- Superfamily Macluritoidea Fischer, 1885
  - Omphalocirridae Wenz, 1938
  - Macluritidae Fischer, 1885
  - Onychochilidae Koken, 1925
- Superfamily Euomphaloidea de Koninck, 1881
  - Helicotomidae Wenz, 1938
  - Euomphalidae de Koninck, 1881
  - Omphalotrochidae Knight, 1945
- Superfamily Pseudophoroidea S. A. Miller, 1889
  - Planitrochidae Knight, 1956
  - Euomphalopteridae Koken, 1896 (note 7)
  - Pseudophoridae S. A. Miller, 1889
- (?) Superfamily Clisospiroidea S. A. Miller, 1889
  - Clisospiridae S. A. Miller, 1889 (note 7)
- Superfamily Trochonematoidea Zittel, 1895
  - Trochonematidae Zittel, 1895 (note 7)

Subclass PECTINIBRANCHIA Blainville, 1814

Superorder **Turbinimorpha** nov.

Order Anisobranchia v. Ihering, 1876
- Superfamily Platyceratoidea Hall, 1859
  - Cyclonemidae S. A. Miller, 1889
  - Holopeidae Wenz, 1938
  - Platyceratidae Hall, 1859
- Superfamily Microdomatoidea Wenz, 1938
  - Microdomatidae Wenz, 1938
  - Elasmonematidae Knight, 1956

(?) Superfamily Codonocheiloidea S. A. Miller, 1889 (Craspedostomatacea) (note 8)
Craspedostomatidae Wenz, 1938
Brochidiidae Yochelson, 1956
Crossostomatidae Cox, 1960
Codonocheilidae S. A. Miller, 1889
Superfamily Anomphaloidea Wenz, 1938
Anomphalidae Wenz, 1938
Superfamily Oriostomatoidea Wenz, 1938
Oriostomatidae Wenz, 1938
Tubinidae Knight, 1956
Superfamily Paraturbinoidea Cossmann, 1916 (Palaeotrochacea) (note 9)
Palaeotrochidae Knight, 1956
Paraturbinidae Cossmann, 1916
Superfamily Turbinoidea Rafinesque, 1815 (note 10)
Turbinidae Rafinesque, 1815
Liotiidae Gray, 1850
Cyclostrematidae Fischer, 1885
Skeneidae Clarke, 1851
Phasianellidae Swainson, 1840
Superfamily Trochoidea Rafinesque, 1815
Ataphridae Cossmann, 1918
Angariidae Thiele, 1921
Trochidae Rafinesque, 1815
Calliostomatidae Thiele, 1924
Umboniidae H. & A. Adams, 1858
Stomatellidae Gray, 1840
Superfamily Eucycloidea Koken, 1896 (note 11)
Platyacridae Wenz, 1938
Cirridae Cossmann, 1916
Eucyclidae Koken, 1896 (Amberleyidae)
Notodelphinulidae Cox, 1960

Order Lepetellida Moskalev, 1971 (note 12)
Superfamily Lepetelloidea Dall, 1881
Lepetellidae Dall, 1881
Cocculinellidae Moskalev, 1971
Superfamily Addissonioidea Dall, 1882
Addissoniidae Dall, 1882

Superorder **Neritimorpha** nov.
Order Planilabiata Stoliczka, 1868 (note 13)
(?) Superfamily Cocculinoidea Dall, 1882
Cocculinidae Dall, 1882
Symmetrocapulidae Wenz, 1938
Superfamily Titiscanioidea Bergh, 1890
Titiscaniidae Bergh, 1890
Superfamily Hydrocenoidea Troschel, 1856
Hydrocenidae Troschel, 1856
Superfamily Neritoidea Rafinesque, 1815 (note 13)
(?) Plagiothyridae Knight, 1956
Neritopsidae Gray, 1847
Neritidae Rafinesque, 1815
Septariidae fam. nov. (type-genus *Septaria* Férussac, 1807)
Phenacolepadidae Pilsbry, 1895
Payettiidae Dall, 1924
Dawsonellidae Wenz, 1938

Deianiridae Wenz, 1938
Helicinidae Férussac, 1822

Superorder **Paludinimorpha** nov.
Order Architaenioglossa Haller, 1894
Superfamily Viviparoidea Gray, 1847
Viviparidae Gray, 1847
Pilidae Preston, 1915
(?) Pliopholygidae Taylor, 1966
Superfamily Cyclophoroidea Gray, 1847 (note 14)
Dicristidae fam. nov. (type-genus *Dicrista* Thompson, 1969)
Amphicyclotidae Kobelt & Moellendorff, 1897
Neocyclotidae Kobelt & Moellendorff, 1897 (Poteriidae Thiele, 1929)
Crocidopomidae Thompson, 1967
Megalomastomatidae Kobelt, 1902
Cyclophoridae Gray, 1847
Ferussinidae Wenz, 1938
Craspedopomatidae Kobelt, 1902 (Maizaniidae Tielecke, 1940)
Spirostomatidae Tielecke, 1940
Pupinellidae Kobelt, 1902
Pupinidae H. & A. Adams, 1855
Hainesiidae Thiele, 1929
Cochlostomatidae Kobelt, 1902
Diplommatinidae Stoliczka, 1871
Order Ectobranchia Fischer, 1884
Superfamily Valvatoidea Gray, 1840
Valvatidae Gray, 1840
Superfamily Tornoidea Sacco, 1896 (note 15)
Tornidae Sacco, 1896 (Adeorbidae; Vitrinellidae)

Superorder **Littorinimorpha** nov.
Order Protopoda Fischer, 1884
Superfamily Turritelloidea Woodward, 1851
Turritellidae Woodward, 1851
Superfamily Vermetoidea Rafinesque, 1815
Vermetidae Rafinesque, 1815
Tenagodidae Gill, 1871
Order Discopoda Fischer, 1884 (note 16)
Suborder Littorinina Pchelintsev, 1963 (as Littorinata) (note 17)
Superfamily Littorinoidea Gray, 1840
Lacunidae Gray, 1857
Littorinidae Gray, 1840
Superfamily Truncatelloidea Gray, 1840 (note 18)
Bithyniidae Gray, 1857
Pyrgulidae Brusina, 1881
Baicaliidae Fischer, 1885
Hydrobiidae Troschel, 1857
Lithoglyphidae Troschel, 1857
Emmericiidae Brusina, 1870
Fairbankiidae Thiele, 1928
(?) Tateidae Thiele, 1925
Stenothyridae Fischer, 1885
Truncatellidae Gray, 1840
Hyalidae fam. nov. (type-genus *Hyala* H. & A. Adams, 1852)

Littoridinidae Gray, 1857 (Pomatiopsidae Stimpson, 1865)
Benedictiidae Clessin, 1880
Fluminicolidae Clessin, 1880
Mexithaumidae Taylor, 1966
Lepyriidae Pilsbry & Olsson, 1951

Superfamily Pomatiasoidea Gray, 1852
Pomatiasidae Gray, 1852
Licinidae Pfeiffer, 1858 (Chondropomatidae) (note 19)

Superfamily Aciculoidea Gray, 1850
Aciculidae Gray, 1850

Superfamily Assimineoidea Fischer, 1885
Assimineidae Fischer, 1885

Superfamily Barleeioidea Gray, 1857
Barleeidae Gray, 1857

Superfamily **Alvanioidea** nov.
Alvaniidae fam. nov. (type-genus *Alvania* Risso, 1826) (note 20)

Superfamily Rissooidea Gray, 1847 (note 21)
Rissoidae Gray, 1847
Onobidae fam. nov. (type-genus *Onoba* H. & A. Adams, 1852)
Anabathronidae Coan, 1964
Rissoinidae Stimpson, 1865
Merelinidae fam. nov. (type-genus *Merelina* Iredale, 1915)
(?) Abyssochrysidae Tomlin, 1927 (note 22)

Superfamily Omalaxoidea Wenz, 1939
Omalaxidae Wenz, 1939
Circulidae Fretter & Graham, 1962

Superfamily Skeneopsoidea Iredale, 1915
Skeneopsidae Iredale, 1915

Superfamily Trachysmatoidea Thiele, 1925 (note 23)
Cingulopsidae Fretter & Patil, 1958
Eatoninidae fam. nov. (type-genus *Eatonina* Thiele, 1912)
Trachysmatidae Thiele, 1925

(?) Superfamily Rastodentoidea Ponder, 1966 (note 24)
Rastodentidae Ponder, 1966
Lironobidae Ponder, 1967

Superfamily Caecoidea Gray, 1847
Ctiloceratidae Iredale & Laseron, 1957
Caecidae Gray, 1847

Suborder **Rissoellina** nov. (note 16)
Rissoellidae Gray, 1850

Suborder Prionoglossa G. O. Sars, 1878 (note 16)
Omalogyridae G. O. Sars, 1878
(?) Orbitestellidae Iredale, 1917 (Microdisculidae) (note 25)

Order Alata Lamarck, 1809

Superfamily Stromboidea Rafinesque, 1815
Eustomidae Cossmann, 1906
Aporrhaidae Gray, 1850
Harpagodidae Pchelintsev, 1963
Tibiidae nom. nov. (for Rostellariidae) (note 26) [footnote 14]

Terebellidae Korobkov, 1955
Struthiolariidae Gabb, 1868
Colombellinidae Fischer, 1884
Strombidae Rafinesque, 1815

Superfamily Seguenzioidea Verrill, 1884 (note 27)
Seguenziidae Verrill, 1884

Order Heteropoda Lamarck, 1812 (note 28)

Superfamily Atlantoidea Deshayes, 1830
Atlantidae Deshayes, 1830

Superfamily Pterotracheoidea Férussac, 1819
Carinariidae Reeve, 1841
Pterotracheidae Férussac, 1819

Order Canalifera Lamarck, 1809

Superfamily Cymatioidea Iredale, 1913
Cymatiidae Iredale, 1913
Colubrariidae Cernohorsky, 1967
Ranellidae Gray, 1854 (Bursidae Thiele, 1925)

Superfamily Cassidoidea Latreille, 1825
Cassididae Latreille, 1825
Tonnidae Suter, 1913
Ficidae Conrad, 1867

Order Echinospirida Fretter & Graham, 1962 (as Echinospiracea) (note 29)

Suborder Inoperculata Fischer, 1884

Superfamily Vanicoroidea Gray, 1840
Fossaridae Troschel, 1861
Vanicoroidae Gray, 1840
Hipponicidae Troschel, 1861

Superfamily Calyptraeoidea Lamarck, 1809
Trichotropidae Gray, 1850
Lyocyclidae Thiele, 1925
Capulidae Fleming, 1822
Lamelliphoridae Korobkov, 1955
Xenophoridae Philippi, 1856
Calyptraeidae Lamarck, 1809

Suborder Involuta Fischer, 1884

Superfamily Cypraeoidea Rafinesque, 1815
Cypraeidae Rafinesque, 1815
Ovulidae Fleming, 1828

Superfamily Pediculariodea Gray, 1853 (note 30)
Triviidae Troschel, 1863
Pediculariidae Gray, 1853

Superfamily Lamellarioidea d'Orbigny, 1841
Velutinidae Gray, 1842
Lamellariidae d'Orbigny, 1841
(?) Pseudosacculidae Hirase, 1928

Order Aspidophora Fischer, 1884
Gyrodeidae Wenz, 1941
Globulariidae Wenz, 1941
Polinicidae Gray, 1847
Sinidae Wenz, 1941
Choristidae Verrill, 1882 (note 31)
Naticidae Forbes, 1838

Superorder **Cerithiimorpha** nov.

Order Entomostoma Blainville, 1824 (note 32)

Superfamily Purpurinoidea Zittel, 1895
Purpurinidae Zittel, 1895

Superfamily Planaxoidea Gray, 1850
Thiaridae Preston, 1915
Planaxidae Gray, 1850
(?) Brachytremidae Wenz, 1940
Superfamily Melanopsoidea H. & A. Adams, 1854
Melanopsidae H. & A. Adams, 1854
Modulidae Fischer, 1885
Superfamily Cerithioidea Férussac, 1819
Procerithiidae Cossmann, 1905
Eatoniellidae Ponder, 1965
Litiopidae Gray, 1847
Diastomidae Crosse & Fischer, 1893
Bittiidae Cossmann, 1906
Potamididae H. & A. Adams, 1854
Pachychilidae Troschel, 1857 (Pleuroceridae Fischer, 1885)
Paludomidae Gill, 1871
Syrnolopsidae Bourguignat, 1890
Cerithiidae Férussac, 1819
Superfamily Cerithiopsoidea H. & A. Adams, 1854
Cerithiopsidae H. & A. Adams, 1854
Eumetulidae fam. nov. (type-genus *Eumetula* Thiele, 1912)
Cerithiellidae nom. nov. (for Newtoniellinae Korobkov, 1960)
Seilidae fam. nov. (type-genus *Seila* A. Adams, 1861)

Order Hamiglossa Gray, 1853
Suborder Rhiniglossa G. O. Sars, 1878 (note 33)
Triphoridae Gray, 1847
Suborder Rachiglossa Gray, 1853
Superfamily Fasciolarioidea Gray, 1853
Fusinidae Wrigley, 1927
Fasciolariidae Gray, 1853
Superfamily Buccinoidea Rafinesque, 1815
Nassariidae Iredale, 1916
Vexillidae Thiele, 1929
Neptuneidae Troschel, 1869
Melongenidae Gill, 1871
Buccinulidae Powell, 1929
(?) Pseudolividae Thiele, 1929 (note 34)
Buccinidae Rafinesque, 1815
Superfamily **Beringioidea** nov. (note 35)
Anachidae fam. nov. (type-genus *Anachis* H. & A. Adams, 1853)
Beringiidae fam. nov. (type-genus *Beringius* Dall, 1879)
Superfamily Pyrenoidea Suter, 1913 (note 35)
Pyrenidae Suter, 1913
Superfamily Olivoidea Latreille, 1825 (note 36)
Olivancillariidae fam. nov. (type-genus *Olivancillaria* d'Orbigny, 1841)
Olividae Latreille, 1825
Harpidae Brown, 1849
Superfamily Marginelloidea Fleming, 1828 (note 36)
Marginellidae Fleming, 1828
Superfamily Volutoidea Rafinesque, 1815 (note 36)
Volutidae Rafinesque, 1815

Superfamily Muricoidea Rafinesque, 1815 (note 37)
Muricidae Rafinesque, 1815
Vasidae H. & A. Adams, 1853
Coralliophilidae Hoyle, 1888 (Magilidae Thiele, 1929)
Thaididae Jousseaume, 1888
Suborder **Nematoglossa** nov. (note 38)
Cancellariidae Gray, 1853
Admetidae Troschel, 1869
Order Toxoglossa Gray, 1853
Superfamily Mitroidea Swainson, 1831
Mitridae Swainson, 1831
Cylindromitridae Cossmann, 1899
Superfamily Conoidea Rafinesque, 1815
(?) Speightiidae Powell, 1942
(?) Thatcheriidae Powell, 1942
Clavidae Powell, 1942
Cochlespiridae Powell, 1942
Turridae H. & A. Adams, 1855 (note 39)
Raphitomidae Bellardi, 1875
Conidae Rafinesque, 1815
Pervicaciidae Rudman, 1969
Superfamily Terebroidea Mörch, 1852
Terebridae Mörch, 1852
Superorder **Pyramidellimorpha** nov.
Order Heterostropha Fischer, 1884 (note 40)
Suborder Subulitina Pchelintsev, 1963 (as Subulitata)
Subulitidae Lindström, 1884
Meekospiridae Knight, 1956
Suborder Entomotaeniata Cossmann, 1896
Superfamily Loxonematoidea Koken, 1889
Loxonematidae Koken, 1889
Palaeozygopleuridae Horný, 1955
Pseudozygopleuridae Knight, 1930
Zygopleuridae Wenz, 1938
Coelostylinidae Cossmann, 1909
Spirostylidae Cossmann, 1909
Superfamily Aclidoidea Thiele, 1925
Aclididae Thiele, 1925
Superfamily Pyramidelloidea d'Orbigny, 1840
Streptacididae Knight, 1931
Pyramidellidae d'Orbigny, 1840
Turbonillidae Locard, 1892 [footnote 14]
Superfamily Nerineoidea Zittel, 1873
Ceritellidae Wenz, 1938
Nerineidae Zittel, 1873
Nerinellidae Pchelintsev, 1960
Iteriidae Cossmann, 1896
Suborder Gymnoglossa Gray, 1853 (note 41)
Superfamily Mathildoidea Dall, 1889
Mathildidae Dall, 1889
(?) Superfamily Trochaclidoidea Thiele, 1929
Trochaclididae Thiele, 1929
Superfamily Architectonicoidea Gray, 1840
Cyclostremellidae Moore, 1966
Architectonicidae Gray, 1840
Toriniidae Troschel, 1863

Order Ptenoglossa Gray, 1853
- Superfamily Epitonioidea Berry, 1910 (note 42)
  - Acirsidae Korobkov, 1955
  - Epitoniidae Berry, 1910
- Superfamily Janthinoidea Lamarck, 1812
  - Janthinidae Lamarck, 1812

Order Homoeostropha Fischer, 1885
- (?) Superfamily Vellainelloidea Vasseur, 1880 (note 43)
  - Vellainellidae Vasseur, 1880
- Superfamily Pseudomelanioidea Fischer, 1885
  - Pseudomelaniidae Fischer, 1885
  - Glauconiidae Pchelintsev, 1953
  - Trajanellidae Pchelintsev, 1953
- Superfamily Eulimoidea H. & A. Adams, 1854 (Melanellacea)
  - Eulimidae H. & A. Adams, 1854
  - Stiliferidae Rosen, 1910
  - Asterophilidae Thiele, 1925 (note 44)
  - (?) Ctenosculidae Thiele, 1925
  - Paedophoropodidae Ivanov, 1937
  - Roseniidae Nierstrasz, 1913
  - Entoconchidae Fischer, 1883

NOTES

1. The category "superfamily" is used only when the families constituting an order or suborder can be assembled in more than one group. As regards the superfamily name endings (-oidea) see footnote 5.

2. Conchologically, the family Metoptomatidae is more similar to Helcionellidae than to Docoglossa; it therefore seems preferable to include it in the order Helcionellida.

3. The 3 generally accepted families of Docoglossa (Patellidae, Acmaeidae and Lepetidae) differ from each other so greatly as regards the structure of the mantle complex, the nervous system and the radula, that it appears more appropriate to consider them as 3 different superfamilies. The family Patellidae, in its commonly accepted scope, is divided into 2 independent families Nacellidae and Patellidae on the basis of anatomical data (Thiem, 1917a) and of its conchological peculiarities. In addition, we also include in this superfamily the family Damilinidae. Similarly the old family Acmaeidae Carpenter 1857, named by us Tecturidae in view of the independence of the genus *Tectura*, separates into 3 distinct families according to the development of their gills. The genus *Propilidium* Forbes & Hanley, 1849, is separated in an independent new family **Propilidiidae**, the characteristic feature of which is an apex which is markedly bent backwards and, according to Forbes (Forbes & Hanley, 1850), the presence of 2 ctenidia. The genus *Propilidium* needs taxonomic revision as some forms conchologically different from the type species are also included in it. The family Bathysciadiidae is placed in the order Docoglossa within a separate superfamily following Moskalev's (1971) opinion. Another superfamily tentatively placed here consists of the family Bathypeltidae which is very similar to the Bathysciadiidae in radula and shell.

4. Because of structural diversity of shells in the families Sinuitidae and Bellerophontidae, as given by Knight et al. (1960), we return to Wenz's (1938) families, accepting them with some modifications in view of recent data. Sharply different genera were included in the family Cyrtolitidae by Knight and his co-workers. As was shown by Horný (1965), the genus *Cyrtolites* undoubtedly belongs to Monoplacophora, not because its species have numerous muscle scars but rather because of the location of its single pair of shell (i.e. columellar) muscle impressions, which are found in the periphery of the last whorl. Probably *Cloudia* and *Trigyra* are also related to this genus. On the other hand, other genera and especially *Cyrtodiscus*, which have no lateral keels and have an extension below the spiral, undoubtedly belong to Bellerophontoidea and must be included in the family Temnodiscidae (Horný, 1963b). Parallelism in shell structure of spiral Monoplacophora

and the lowest Gastropoda has been noted in another instance, viz. in the pair *Sinuitopsis* (Monoplacophora) - *Sinuites* (Gastropoda) (Rollins & Batten, 1968). The subfamily Bucanellinae (especially *Bucanella*) is probably near to *Sinuitopsis* and consequently belongs to Monoplacophora.

The family Fissurellidae commonly includes 3 clearly separate groups, accepted here as independent families: Emarginulidae with a cap-like shell preserving some traces of spirality and having an incision on the front part of the peristome or, rarely, a subapical opening; **Hemitomidae** fam. nov. with a cap-like shell devoid of a marked incision, but having a noticeable sulcus running from the apex to the front part of the peristome that is clearly visible when viewed from within the shell; and Fissurellidae with an incision in the form of an apical of subapical perforation on the cap-like shell, which has no trace of spirality.

5. Some families are excluded from the superfamily Pleurotomarioidea (= Pleurotomariacea) to form independent superfamilies. The families Sinuopeidae and Rhaphistomatidae, the characteristic features of which are a weakly developed incision and a tendency towards the formation of a depression, protuberance or sulcus on the periphery of the last whorl, are separated as a special superfamily Rhaphistomatoidea. The taxonomic position of this superfamily is not clear and we include it in the order Fissobranchia only provisionally. This superfamily seems to be artificial and probably some of its representatives are related to the order Macluritida. The family Haliotidae is separated as a special superfamily Haliotoidea because its members have a distinctive ear-shaped shell and a number of incisions on the shell isolated from the shell margin. Phylogenetically this relatively young superfamily may be connected with the family Trochotomidae.

6. We consider Murchisonioidea to be a highly specialized group of Fissobranchia which has acquired some features common to Cerithioidea through convergence. The possibility of convergence of such kind occurring in the group is demonstrated by comparing Cerithioidea and Turritelloidea.

7. Euomphalopteridae and Trochonematidae, having no prominent fissure on the shell and only a canal, carina or depression on the body whorl, are doubtlessly connected with the branch Macluritidae-Euomphalidae, which has been separated as an independent order. Euomphalopteridae show a considerable conchological resemblance with Planitrochidae and Pseudophoridae (the genus *Crenilunula* is probably to be excluded from this family). The family Clisospiridae is only provisionally included in this order to form a special superfamily because this family may have developed from some pseudophorid ancestors.

8. The superfamily Codonocheiloidea (= Craspedostomatacea) is included in this group only provisionally in view of the conchological similarity of some of its genera with Turbinidae. The name has been changed according to the Law of Priority.

9. We use the name Paraturbinoidea instead of Palaeotrochacea according to the Law of Priority.

10. The families forming the traditional superfamily Trochacea fall into 2 distinct groups, one of which has Trochidae as its central family while the other includes Turbinidae. These families are now grouped in 2 superfamilies, Turbinoidea and Trochoidea, the former being considered more primitive than the latter in view of some similarity with Macluritida and of the necessity to include the highest Anisobranchia (*Calliostoma* in particular) in Trochoidea. The family Trochidae in its generally accepted scope is highly heterogeneous. It includes snails without pallial gonoducts (*Gibbula* and *Margarites*) and snails possessing one, though in a poorly developed form (*Calliostoma*) (see Fretter & Graham, 1962).

Taking into account the above considerations and the conchological peculiarities of different groups of genera we think it possible to raise the rank of the subfamily Calliostomatinae and consider it a separate family.

11. Recognizing the independence of the genera *Amberleya* and *Eucyclus*, we restore the oldest name for the family (and superfamily) i.e. Eucyclidae Koken, 1896, for Amberleyidae Wenz, 1938.

12. The arrangement of families of the order Lepetellida is given after Moskalev (1971). The superfamily Bathypeltoidea, however, has been tentatively placed in the cyclobranch order Docoglossa.

13. The superfamily Cocculinoidea (with the family Symmetrocapulidae) is included in the order Planilabiata after Moskalev (1971). The old superfamily Neritacea must be divided into 3 inde-

pendent ones: Titiscanioidea, Hydrocenoidea (both with a monaulic, but still very different female gonoduct), and Neritoidea (with a di- or triaulic female gonoduct). In the latter superfamily we set up a new family **Septariidae**, having a triaulic female gonoduct instead of the diaulic arrangement found in the Neritidae.

14. Anatomical differences between the groups of Cyclophoridae, s.l., are very great (Tielecke, 1940; Thompson, 1969) and comparable to the differences existing between Pilidae and Viviparidae. For this reason we treat the subfamilies accepted by these authors as separate families. We are also making some nomenclatorial changes: Maizaniidae Tielecke, 1940 = Craspedopomatidae Kobelt, 1902, and Poteriidae Thiele, 1929 = Neocyclotidae Kobelt & Moellendorff, 1897. Furthermore we add the family **Dicristidae** fam. nov., in members of which renal, bursal and pallial parts of the female gonoduct open independently into the mantle cavity (see footnote 16). The group Dendropupinae Wenz, 1938, judging by the shells of *Anthracopupa* and *Maturipupa*, belongs to the Carychioidea, subclass Pulmonata.

15. The family Tornidae (= Adeorbidae Monterosato, 1884; Vitrinellidae Bush, 1897) is included in the order Ectobranchia only provisionally, on the basis of anatomical data on *Tornus* (Woodward, 1899) which are somewhat inadequate.

16. The main group of the order Discopoda consists of families having a taenioglossate radula and either a single or a double pallial gonoduct. In the latter group these 2 gonoducts run distally from the end of the renal gonoduct, one being the usual glandular tube and the other either a ciliated groove or another tube running parallel to the first, and opening by a special orifice.[16] Gastropods with a complex hermaphroditic system go back to forms with a double pallial gonoduct. They form 2 independent groups with different structures of the reproductive system and of the radula. We therefore isolate these 2 groups as special suborders **Rissoellina** (new) and Prionoglossa, leaving the bulk of the other families of the order Discopoda in the suborder Littorinina.

17. Due to the vast diversity in structure of the reproductive systems of the gastropods formerly classified in the superfamilies Littorinacea and Rissoacea we divide the suborder into a considerably greater number (13) of superfamilies.

Among the members of the 2 old superfamilies one may distinguish 3 groups: (1) families whose members have a pallial gonoduct with equally thickened glandular walls (Aciculidae, Assimineidae and Barleeidae); (2) families with a pallial gonoduct with a longitudinal ventral ciliary groove separated, to a greater or smaller degree, from the glandular part (Littorinacea, Rissoidae and Hydrobiidae, in their former extent); and (3) families with a double pallial portion of the female reproductive system; in these, the glandular part has the same structure as in the 1st group; besides they have an independent ciliary groove (Skeneopsidae) or a separate duct (Cingulopsidae) running parallel to this part. Anatomical data (Rao, 1928; Krull, 1935; Fretter & Patil, 1958; Fretter & Graham, 1962; Jackiewicz, 1967) show that the families forming the 1st group are rather remote taxonomically and should be separated into 3 special superfamilies: Aciculoidea, Assimineoidea and Barleeioidea. The families of the 3rd group are provisionally placed in 2 superfamilies Skeneopsoidea and Trachysmatoidea (see also note 23) on conchological grounds. However, the taxonomic position of the genera of this group needs more detailed studies. The families of the 2nd group, which is the largest, may be divided into 5 superfamilies on the basis of the structure of the genital system: (1) the forms with a virtually unclosed pallial gonoduct (such as

[16]For a more precise homologization, the constituents of the reproductive system may be defined as having the following limits: the visceral gonoduct runs from the gonad to the gonopericardial duct, the renal gonoduct from the gonopericardial duct to the "bursal" duct; the pallial gonoduct runs distad from the "bursal" duct (or from the nephropore, where it is preserved transformed). Though the bursa (a name here used to designate the sac opening into the base of the pallial gonoduct in Discopoda) is of pallial origin, it cannot be considered a part of the pallial gonoduct; it is a rather special structure that appeared independently from the closing of the mantle folds. Probably it is a primary sperm-receiving reservoir, originally opening into the mantle cavity near the urogenital papilla (as is the case in Cocculinidae). The name "bursa" ("bursa copulatrix") is often applied to other sacs, such as the distal sac of the pallial gonoduct (which we call the spermatheca) or (in Entomostoma) to the sac opening in the middle of the pallial gonoduct. It is clear that neither organ has anything to do with the bursa of Discopoda.

Pomatiasidae) are included in a special superfamily Pomatiasoidea; (2) the forms having one gland in the pallial gonoduct and one gland in the renal gonoduct (Rissoidae, Onobidae, etc.) are included in the superfamily Rissooidea (see also notes 21, 22); (3) the group whose members have one gland in the pallial gonoduct and no gland in the renal gonoduct (Alvaniidae; see note 20) is separated as a new superfamily Alvanioidea; (4) families with 2 glands in the pallial gonoduct (Pyrgulidae, Baicaliidae and Hydrobiidae, s.l.) are included in the superfamily Truncatelloidea (see also note 18). (5) the old superfamily "Littorinacea" is the last superfamily of this group. To these 10 superfamilies we add another 3, as the structure of their shells and radulae prevents their inclusion in any of the above mentioned superfamilies in the suborder Littorinina. These are: the Caecoidea, the characteristic features of which are a closed pallial gonoduct and the presence of a penis, which has prevented us from including them in Cerithiacea; the Omalaxoidea, with the two families Omalaxidae and Circulidae (the characteristics of the latter family are found in Fretter (1956:381)), and, tentatively, the Rastodentoidea, with Rastodentidae (see also note 24) and Lironobidae.

18. The families included in the superfamily Truncatelloidea previously belonged either to Hydrobiidae, s.l., and Rissoidae or were considered independent (e.g. Baicaliidae). The families whose members have been studied anatomically are characterized by their reproductive systems as follows:

Bithyniidae. The bursa is present, but there is no seminal receptacle. The renal gonoduct is greatly thickened and has the shape of a long irregularly coiled tube. The ventral groove is separated by the folds of the glandular part, formed by 2 successive glands. The prostate is band-shaped and consists of diverticula opening into the vas deferens. The copulatory apparatus has 1 or 2 accessory glands (anatomical data of Bregenzer, 1916; Seshaiya, 1930; Krull, 1935; Lilly, 1953).

Pyrgulidae. The female reproductive system is somewhat similar to that of the previous family. But instead of a true seminal receptacle in the female renal gonoduct there is a pouch which does not differ histologically from the adjoining parts of the renal gonoduct. The prostate is kidney-shaped and consists of a great number of diverticula. The copulatory apparatus has no accessory glands (anatomical data of Kozhov, 1951; Radoman, 1955).

Baicaliidae. The female reproductive system has the same structure as in Pyrgulidae, but the renal gonoduct has several caeca serving as the seminal receptacle (anatomical data of Kozhov, 1951).

Hydrobiidae. The female reproductive system also has the same general structure, but the renal gonoduct is short, thin and almost uncoiled; there is a true seminal receptacle, which is not connected, however, with the bursa through a reservoir. The male reproductive system resembles that of Pyrgulidae (anatomical data of Quick, 1920; Robson, 1922; Krull, 1935; Fretter & Graham, 1962).

Lithoglyphidae. The glandular part of the female pallial gonoduct consists of 2 glands, and is separated from the ventral groove by several folds. There are 1-2 seminal receptacles. The renal gonoduct is greatly thickened and has the shape of a long irregularly bent tube. The male reproductive system is the same as in Pyrgulidae (anatomical data of Siebold, 1904; Krull, 1935; Krause, 1949; Radoman, 1955, 1963, 1965, 1966a, 1966b, 1967b; Bole, 1961, 1967).

Emmericiidae. The pallial gonoduct has 2 (?) glands and a ventral canal, separated by a fold and considerably dilated in the distal part. The bursa and the seminal receptacle are present. The renal gonoduct has the shape of a long, thick and coiled tube. The prostate is kidney-shaped and has a great number of diverticula. The copulatory apparatus has 2 accessory glands (anatomical data of Radoman, 1967a).

Truncatellidae. The pallial gonoduct of the female has 2 consecutive glands and a ventral groove, separated by a fold. The bursa and the seminal receptacle are present. Their ducts are connected to each other by a short duct; the bursa duct is also connected to the left kidney. The male reproductive system is the same as in Pyrgulidae (anatomical data of Vayssière, 1885; Fretter & Graham, 1962).

Hyalidae fam. nov. The glandular part of the female pallial gonoduct consists of 2 glands placed one after the other; the ventral groove is separated by a fold. The bursa is present; no seminal receptacle, but a spermatheca is present. The female genital pore is located midway on the pallial gonoduct. The shell is small, slender and smooth with a

stained periostracum (anatomical data of Johansson, 1950, on *Hyala*).

Littoridinidae (= Pomatiopsidae). Bursa and seminal receptacle are present. The pallial gonoduct of the female has 2 glands located one after the other. The ventral groove is set apart from the glandular part either completely or only in the distal half and closes to form a duct opening into a special orifice. The male reproductive system is as in Pyrgulidae (anatomical data of Robson, 1920, 1921; Li Fu-Ching, 1934; Krull, 1935; Itagaki, 1955; Van der Schalie & Dundee, 1956; Roth & Wagner, 1957; Patil, 1958; Roth, 1960; Davis, 1967).

Benedictiidae. Bursa and seminal receptacle are present; they adjoin each other closely, sharing a small area of wall which usually has a perforation or a connecting canal. The renal gonoduct is comparatively short and thin. The pallial gonoduct of the female has 2 glands one after the other. The ventral groove is set apart only by folds. The male reproductive system is as in Pyrgulidae (anatomical data of Kozhov, 1945, 1950).

The remaining families are included here on the basis of the structure of their shells and radulae. In the family Fluminicolidae are included, besides the type genus, a number of *Lithoglyphus*-like East Asiatic forms (*Lithoglyphopsis, Jullienia, Fenouilia, Lacunopsis* and *Wykoffia*); in the family Mexithaumidae, besides the type genus, *Potamolithus, Potamolithoides* and *Lithococcus*. The latter 2 families need careful anatomical and taxonomic study.

19. We use the name Licinidae and not Chondropomatidae according to the Law of Priority.

20. The new family **Alvaniidae** may be defined as follows: the shell is oval-conical, small, solid with reticular or, rarely, with only spiral sculpture and an oval aperture pointed upwards. The operculum is corneous, paucispiral, without any processes. The radular formula is 3.1.3. The rachidian and lateral teeth of the radula have large rounded cusps, the marginal teeth small cusps. No gland is present in the renal gonoduct of the female, but there is a widening. There are 1-2 seminal receptacles and a bursa; the ventral groove is set apart from the glandular part of the pallial gonoduct by several longitudinal folds. There is only 1 gland here. The prostate is cylindrical; the vas deferens is connected with the mantle cavity near the proximal end of the prostate (anatomical data of Johansson, 1956b).

21. The new family **Onobidae** differs from Rissoidae by the presence of a prostate and a connection between the vas deferens and anterior (not posterior as in Rissoidae) part of the mantle cavity. The shell is oval, oval-conical or top-shaped, either with dominant spiral sculpture or almost smooth, with a rounded or rounded-oval aperture that does not point upwards. The operculum is corneous, paucispiral. The radula is as in Rissoidae and Alvaniidae (anatomical data of Johansson, 1948; Fretter & Graham, 1962). To the Rissooidea we also add the families Anabathronidae (anatomical data of Ponder, 1967, 1968), Rissoinidae, whose anatomy was presented by Kosuge (1965) and **Merelinidae** fam. nov., the members of which differ from Rissoinidae by the presence of a prostate and by the subterminal position of the female aperture, which in Rissoinidae is located in the depth of the mantle cavity far behind the anus. Data on the anatomy of members of the Merelinidae are found in Ponder (1967, 1968). We also include in this family *"Rissoina" chathamensis* (Hutt.) because it has a prostate.

22. Because of the presence of a cephalic copulatory apparatus we exclude the family Abyssochrysidae from Cerithiacea and add it to Discopoda, where we provisionally include it in Rissooidea, guided by the characters of its shell.

23. We include in the superfamily Trachysmatoidea in addition to the family Trachysmatidae which has not been studied anatomically: Cingulopsidae, which are conchologically similar to Trachysmatidae, and **Eatoninidae** fam. nov., the members of which are similar to *Cingulopsis* in the structure of the reproductive system but differ by the absence a second pallial duct connecting the distal end of the renal gonoduct with the mantle cavity. Moreover, Eatoninidae differ from Cingulopsidae by the conical shell.

24. The family Rastodentidae (= Rastodenidae) is included provisionally in the Littorinina. Taxonomically, if the shell and radula are the guiding factors, it can be considered close to Lironobidae. It is to be stressed that the radula structure (Ponder, 1966, 1967) sets these 2 families apart from other Littorinina.

25. The family Orbitestellidae (= Microdisculidae) is provisionally included in this suborder following Thiele (1929).

26. The new name **Tibiidae** is used by us instead of Rostellariidae in view of the priority of the name *Tibia* Bolten in Röding, 1798 over *Rostellaria* Lamarck, 1799.

27. Some scientists (Thiele, 1929) place *Seguenzia* in Trochacea; others (Taylor & Sohl, 1962) have provisionally placed Seguenziidae in Cerithiacea. From the structure of the shell and the peculiar radula of a single representative of this family, which is very inadequately studied anatomically, we include it in the order Alata as a special superfamily.

28. The order Heteropoda is divided into 2 superfamilies. In one of them (Atlantoidea) we include forms with a developed shell and operculum; in the other (Pterotracheoidea), the forms with rudimentary shells.

29. The order Echinospirida is divided into 2 suborders, Inoperculata and Involuta, on the basis of their special structure, ecology and evolution. The characteristic feature of the suborder Inoperculata, which developed from a semi-filtrating mode of nutrition to ectoparasitism, is the transition from a spirally coiled shell to a cap-like external shell, often with a septum inside it. The suborder Involuta, which progressed to predation, is characterized by the formation of an involute or ear-shaped shell and by the mantle overgrowing the shell to the point even of complete enclosure of the shell.

30. We separate the superfamily Pedicularioidea (= Triviacea) following Schilder (1966), leaving the superfamily Lamellarioidea including only the families Lamellariidae, Velutinidae and, provisionally, Pseudosacculidae.

31. We provisionally include the family Choristidae in the order Aspidophora on the basis of shell characters and the shape of the radular teeth.

32. The order Entomostoma comprises groups that have usually been placed in Cerithiacea, as well as the Purpurinidae, transferred from the Littorinacea, as they are conchologically more similar to the lower Entomostoma. The old superfamily Cerithiacea remains highly heterogeneous even after we removed from it a number of families and assigned them to other orders. Its heterogeneous character becomes particularly evident when available anatomical data (Moore, 1898, 1899a, 1899b; Seshaiya, 1934; Johansson, 1947, 1953, 1956a; Morrison, 1954; Binder, 1959; Dazo, 1965) are analyzed. We therefore divide this superfamily into 4 smaller superfamilies. Into one of them, Planaxoidea, we place forms devoid of a true pallial gonoduct, having a ciliary mantle groove, and, besides, a special chamber for the incubation of eggs which is not of mantle origin. Two other superfamilies, Melanopsoidea and Cerithioidea, may be characterized as having a well developed but longitudinally unclosed pallial gonoduct. In Melanopsoidea, which comprise Melanopsidae and Modulidae, it is open only in females, which have a special ovipositor. In Cerithioidea it is not closed, or only partially closed in both sexes. In this superfamily we also include, next to Cerithiidae: Potamididae, Bittiidae, Pachychilidae (= Pleuroceridae), Paludomidae—which we consider an independent family in view of the marked differences between it and Pachychilidae in the structure of the female and male reproductive system—and Eatoniellidae, on the basis of Ponder's (1965, 1968) anatomical findings. Also included are families for which anatomical data are either very scanty or non-existent.

The family Cerithiopsidae cannot be included in any of the above 3 superfamilies because sperm transmission is carried out by spermatozeugmata, as in Ptenoglossa. We divide it into 4 families because of the vast diversity of its members, which we place in a 4th superfamily Cerithiopsoidea.

The family Cerithiopsidae, s.s., may be characterized by the presence of a multispiral protoconch, which differs markedly from the definitive shell by the steepness of coiling; a spirally nodular sculpture of the definitive whorls; a very weakly developed siphonal process with a wide canal; and characteristic radular teeth similar to those in Cerithioidea.

The family **Eumetulidae** fam. nov. has the following characteristic features: a paucispiral protoconch, spirally nodular sculpture of the definitive whorls and a wide apertural canal without a siphonal process. The radular teeth are wide and supplied with a great number of small cusps.

The characteristic features of the family **Cerithiellidae** nom. nov. (for Newtoniellinae Korobkov, 1960) are the following: a paucispiral protoconch; a spirally nodular structure of the definitive whorls;

the presence of a basal keel; a well developed oblique siphonal process and a radula furnished with hook-like lateral and marginal teeth and an almost square rachidian tooth bearing 1-5 cusps.

The family **Seilidae** fam. nov. is characterized by a paucispiral protoconch; smooth spiral sculpture of the definitive whorls; absence of the siphonal process accompanied by a wide apertural canal; and by a radula with a tricuspid rectangular rachidian tooth, several small tetragonal unicuspid lateral teeth and a very small hook-ended marginal tooth.

We expect that some of the families here included in the Entomostoma will be placed in other orders after careful anatomical studies.

33. Risbec (1955) showed anatomically that Triphoridae are closer to Stenoglossa than to Cerithiacea. This is also confirmed by the structure of the radula, which cannot be reduced from the taenioglossate type. Nevertheless, they cannot be included in the main group of Stenoglossa (i.e. Rachiglossa). We therefore separate it as a special suborder Rhiniglossa.

34. The subfamily Pseudolivinae, being rather far from other Olividae as to shell characters and differing greatly from them by their radula, is elevated to family rank, the more so as the remaining Olividae are also highly heterogeneous and should be divided into at least 2 families. On the basis of shell structure and radula we assign the family Pseudolividae to the superfamily Buccinoidea.

35. Columbellidae, s.l., are highly heterogeneous. They cannot be included in Buccinoidea. In our classification they are divided into 2 superfamilies: Beringioidea and Pyrenoidea. In Beringioidea, as seen by the anatomy of *Anachis*, males have no prostate and females have a renal albumen gland, the sperm receiving sac being situated in the distal part of the pallial gonoduct. In Pyrenoidea, as seen from the anatomy of *Mitrella lunata* (Say)[17] and *Pterygia= Columbella*, males have a prostate and females have neither albumen gland nor sperm receiving sac, the functions of which are performed by the pericardium (Marcus & Marcus, 1962). In the first of these superfamilies we distinguish 2 families. The new family **Beringiidae** may be described as follows: the shell is dilated and spindle-like; it has convex whorls, a wide, short siphonal process, which is slightly bent backwards, a relatively large embryonic shell and a well developed periostracum. Spiral sculpture clearly predominates over axial sculpture. The corneous operculum has a terminal nucleus and no ornamentation. The radula exhibits an edentate rachidian lamina and lateral laminae, which in general outline are similar to those in Pyrenidae. This young family, which may have appeared as late as the Miocene, inhabits cold and temperate waters in the Northern Hemisphere and is represented for the time being by 2 genera only, *Beringius* and *Liomesus*. **Anachidae**, the second new family of the Beringioidea, shows the following characteristics: the shell is spindle-shaped, either smooth or with axial ribs and spiral sculpture that is more prominent at the basal portion of the last whorl; the siphonal process is short, the palatal margin of the aperture is denticulate within; no prostate; the renal gonoduct of the male has a widening ("seminal vesicle"), the female has a renal albumen gland and a complicated spermatheca, opening into the distal portion of the pallial gonoduct; no gonopericardial duct in adults.

36. The studies by Olsson (1956) and Marcus & Marcus (1959) clearly show that Olividae, s.l., appeared and developed independently of Volutidae, with which they are often associated taxonomically, and parallel to Buccinoidea and Muricoidea. Following Olsson, we set apart Olividae, creating for them a special superfamily. Marginellidae are also separated as a special superfamily as they have an extremely peculiar radula (i.e., one with a single pluricuspid lamina) which is not derived from the radulae of Olividae or Volutidae. In the superfamily Olivoidea, we include next to Olividae and Harpidae, which are probably connected with Olividae, the new family **Olivancillariidae**, whose members differ from true Olividae by a peak-shaped shell with a short spire, by the presence of some additional cusps on the rachidian tooth of the radula and by a peculiar female reproductive system, in which the albumen gland, 2 sperm-receiving sacs and the gland of the pallial gonoduct have a common orifice opening into the posterior portion of the mantle cavity.

37. We include 4 families in the super-

[17]But the Northwest Pacific *Mitrella burchardi* (Dkr.) doubtlessly belongs to the family Anachidae (personal anatomical investigation).

family Muricoidea, among which Vasidae, which are usually placed among Volutacea, on account of a very peculiar structure of the shell and radula, and Thaididae, which, following Pchelintsev et al. (1960), we also consider an independent family, with Thaidinae (= Purpurinae Lamarck, 1809) and Rapaninae as subfamilies.

38. Cancellariidae and Admetidae are placed in a new suborder that we name **Nematoglossa** on the basis of: (1) distinct external and internal morphology; (2) more important yet, a most peculiar radula, differing greatly from that found in other representatives of the order Hamiglossa, and (3) a very characteristic direction in their evolution, showing a marked tendency towards complete reduction of the radula. Cancellariidae, having a strong shell with plicae on the columellar margin of the aperture, and possessing a radula, are phylogenetically older than Admetidae, that have no radula and a very thin shell, and should be considered a special family.

39. Powell (1942, 1964), who specialized in the taxonomy of the Turridae, s.l., attaches great importance to the shell and believes that the differences in the structure of the radula reflect different stages in the transition to the classical toxoglossate type, in which the rachidian and lateral teeth disappear completely. We doubt the validity of this approach on the one hand because in some forms the radula shows a specialized tendency towards stronger lateral (*Drillia*) or rachidian (*Leucosyrinx* and *Ptychosyrinx*) teeth. On the other hand, the features on which Powell has based his division of the Turridae into subfamilies may appear independently (Amitrov, 1968). We therefore divide the Turridae into 4 independent families: Clavidae, having laminar pluricuspid laterals and a small rachidian tooth (here belong the genus *Clavus* and a large part of the subfamily Clavinae as Powell understood it); Cochlespiridae, in which the lateral teeth have disappeared, whereas the rachidian exists in a highly developed form (here belong part of Powell's Cochlespirinae, probably the extinct genus *Cochlespira* and also the genera *Ptychosyrinx* and *Turridrupa*); Turridae, s.s., without lateral teeth, the rachidian being either rudimentary or completely absent, though the basal membrane of the radula is preserved; and Raphitomidae, having a radula of the classical toxoglossate type lacking lateral and rachidian teeth and also a basal membrane.

40. In the order Heterostropha we distinguish 3 suborders: Subulitina, Entomotaeniata and Gymnoglossa, characterized by an independent direction of evolution. In Entomotaeniata we place families with a turriform shell, often with a plicate columella, and with sloping excavations on the basal and palatal margins of the aperture. The characteristic features of its Recent representatives, in addition to those mentioned above, are a separated anterior part of the foot ("mentum"), a reduced radula, a more complex reproductive system (due mainly to hermaphroditism) and a considerably concentrated nervous system. The most specialized members of this group, Pyramidelloidea, have even been recently included in Opisthobranchia or Euthyneura. We are inclined to think, however, that all the features characteristic of Pyramidellidae discussed in support of this view (see Fretter & Graham, 1962) may have developed independently because of their small size and their peculiar mode of life or, in some cases, have been inherited from some ancestor common to them and to the lowest Opisthobranchia and Pulmonata. The suborder Gymnoglossa,[18] whose members retain their radula (which shows a gradually decreasing number of teeth), have comparatively simple alimentary and reproductive systems. The Subulitacea fail to fit in either of the other 2 suborders as it combines features of the Entomotaeniata and of the orders Ptenoglossa and Homoeostropha. For this reason we set it apart in a special suborder Subulutina. Heterostrophy occurs in the superfamilies Pyramidelloidea, Nerineoidea, and in the gymnoglossate Mathildoidea and Architectonicoidea. It does not occur in Aclididae and is not likely to be found in other groups. We may assume that in this order heterostrophy was inherited from some very remote ancestors that were also

[18]The term Gymnoglossa (naked tongue) was proposed by Gray (1853) for forms "with teeth and lingual membrane rudimentary or none." The taxon Gymnoglossa, however, included a number of heterogeneous groups, among which are the Architectonicidae. After the removal of most of these groups (e.g. Pyramidellidae, Tylodinidae, Cerithiopsidae, Cancellariidae, etc.) the name may now be retained for Architectonicidae, even though they do have a radula.

common to Opisthobranchia and Pulmonata, and lost many times within the order (see also Minichev & Starobogatov, 1971).

41. The families which we include in the suborder Gymnoglossa are distributed among 3 superfamilies: one of them contains the single family Mathildidae, which still retains a very strong rachidian tooth and has a characteristic shell, resembling that of Entomotaeniata; another includes Architectonicidae and similar forms, which have either markedly reduced or no rachidians, and in addition a top-shaped or planispiral shell. The Architectonicidae and Toriniidae, though, are rather heterogeneous as to their radulae and may have to be divided into a number of smaller families. The 3rd superfamily contains the Trochaclididae. This family certainly cannot be classified in the order Discopoda, where it would be included if we left it in the Rissoacea, following Thiele (1929); it may be placed either in Gymnoglossa or perhaps Ptenoglossa, standing somewhat apart. The problem can be solved only by careful anatomical studies of *Trochaclis* and of Architectonicidae.

42. Sharp distinctions in the form and degree of shell scalarity, in the shape of the shell and also in the form of the radular teeth allow us to distinguish 2 families in the superfamily Epitonioidea: Epitoniidae and Acirsidae. Both appeared at the juncture of the Triassic and Jurassic and evolved in parallel. Janthinidae may have developed from ancestors common with Epitoniidae.

43. This extinct group is excluded from Trochacea (now in the superorder Turbinimorpha) because of its shell shape and is provisionally placed in the order Homoeostropha as a separate superfamily.

44. Asterophilidae are included in this superfamily following Gruzov (1965). Ctenosculidae may also belong here, though available information on their anatomy does not constitute adequate proof.

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АБСТРАКТ

СИСТЕМАТИКА ПЕРЕДНЕЖАБЕРНЫХ МОЛЛЮСКОВ

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В пределах класса брюхоногих моллюсков авторы намечают 5 основных направлений эволюции и как следствие этого 5 главнейших таксономических подразделений, различающихся важнейшими особенностями строения. Три из них, как правило, объединяются в подкласс **Prosobranchia.** Однако своеобразие морфологической структуры и направления эволюции в каждом из свое трех подразделений рассматриваются как равноценные таковым у этих остальных подклассов брюхоногих т.е. у **Opisthobranchia** и **Pulmonata.** Вследствие этого переднежаберные моллюски разделяются на 3 самостоятельных подкласса **Cyclobranchia, Scutibranchia** и **Pectinibranchia.**

Cyclobranchia (т.е. **Docoglossa** в прежнем понимании и некоторые палеозойские группы) представляют собой особую линию эволюции, характеризующуюся примитивной первично-симметричной раковиной, лишенной вырезки или желобка, архаичным, не встречающимся у других брюхоногих типом строения и движения радулы, а также строением желудка, половой и нервной систем, которые у **Cyclobranchia** сходны с таковыми **Scutibranchia.** Кроме того асимметрия мантийного комплекса, развившаяся независимо у представителей этой группы, специализация радулы, развитие артериального бульбуса и наличие мантийных нервных стволов поддерживает мнение, что эта группа имеет свое направление эволюции. Исходя из этих доводов, **Cyclobranchia** выделяются в особый подкласс, включающий отряды **Helcionellida, Archinacellida** (ранее относимый к **Monoplacophora**) и **Docoglossa.** Эволюционный процесс в этой группе был морфологически выражен уменьшением размеров и степени развития скульптуры раковины, олигомеризацией радулы и редукцией специализированных органов дыхания в ходе эволюции.

Остальные брюхоногие происходят от древней группы моллюсков, возникших от примитивных **Cyclobranchia** в кембрийский период; эти моллюски имели симметричный мантийный комплекс и медиально расположенную вырезку (или желобообразный выступ).

Сохранение симметрии мантийного комплекса в ходе эволюции, параллельное развитие вырезки, хорошо выраженный эпиподий и отсутствие достаточно развитых ганглиев центральной нервной системы при заметном развитии симметричных бранхиальных ганглиев позволяют выделять отряды **Dicranobranchia, Fissobranchia** и **Macluritida** в особый подкласс **Scutibranchia.** Эволюция в пределах **Scutibranchia** выявляет тенденцию в ходе филогенеза к уменьшению размеров и степени закрученности раковины, к обособлению и смещению вырезки от края устья, к уменьшению роли спиральной скульптуры, при возрастании роли осевой и к увеличению размеров правой почки в связи с выполнением ею двоякой функции: выделительной и половой.

Подкласс **Pectinibranchia,** включающий **Monotocardia (Mesogastropoda** и **Neogastropoda),** а также **Trochacea** и **Neritacea** из **Diotocardia (=Archaeogastropoda)** прежних классификаций, филогенетически самый молодой и наиболее разнообразный по морфологическому строению, возник в недрах **Scutibranchia** (скорее всего от **Macluritida** или общих с ним предков).

В пределах **Pectinibranchia** выделяются 18 отрядов, характеризующихся общим планом строения и следующих основной эволюционной тенденции всего подкласса, но в то же время каждый из них представляет свою особую линию развития и имеет свои особенности строения раковины, ноги, пищеварительной системы, жабры, центральной нервной системы, половой системы и экологии. Из этих 18 отрядов наиболее ранней дивергенции подверглись две группы: одна, рассматриваемая здесь как надотряд **Pyramidellimorpha** и другая, представленная **Anisobranchia** (=надотряд

Turbinimorpha) вместе со связанными с ней филогенетически отрядами, объединенными здесь в новые надотряды **Neritimorpha, Paludinimorpha, Littorinimorpha** и **Cerithiimorpha.**

Эволюционное развитие подкласса, часто проявляющееся параллельно в разных отрядах и надотрядах, морфологически выражается в уменьшении степени развития скульптуры, (особенно спиральной), образовании сифонального выроста, исчезновении эпиподия, редукции челюсти, олигомеризации радулы, осуществляющейся в разных группах различными путями, усилении асимметрии мантийного комплекса, образовании гребенчатых ктенидия и осфрадия, превращении правой почки в ренальный гонодукт и концентрации и интеграции центральной нервной системы. Эволюция в пределах разных подразделений **Pectibranchia** шла параллельными путями от исходной микрофагии, сестонофагии и фитофагии к детритофагии, сапрофагии и хищничеству, а у специализированных форм и к паразитизму. В способах размножения она шла от внешнего оплодотворения к внутреннему, к прямому развитию и яйцеживорождению.

В развитии рассмотренных подклассов наблюдается эволюционный параллелизм. Он морфологически выражается в тенденции к увеличению асимметрии в строении, олигомеризации радулярного аппарата, усложнении половой системы и концентрации нервной системы. В экологии и распространении параллелизм в эволюции подклассов выражается в смене местообитаний (от жизни на мелководье и на жестких фациях к обитанию на больших глубинах, на смешанных и мягких фациях, в составе эпифауны и далее инфауны, в приспособлении к существованию в пресных водах и на суше), в расширении ареала от тропических и субтропических широт в сторону умеренных и холодных областей.

Филогенетически наиболее продвинутые группы включают наибольшее число нынеживущих видов среди всех подклассов и отрядов.

Эволюционный процесс у рассмотренных брюхоногих моллюсков был неравномерным и прерывистым. Этапы наиболее интенсивного формообразования, проходившего синхронно в разных группах наблюдались в кембрийский - ордовикский, пермский - триасовый и меловой - палеогеновый периоды.

ZUSAMMENFASSUNG

SYSTEMATIK DER PROSOBRANCHIER-SCHNECKEN

A. N. Golikov und Y. I. Starobogatov

Die Verfasser ziehen 5 Haupt-Entwicklungslinien innerhalb der klasse der Gastropoda und unterscheiden demzufolge 5 grundsatzliche taxonomische Unterabteilungen, die in wesentlichen Zügen ihres Baues voneinander abweichen. Drei davon werden in der Regel in der Unterklasse der Prosobranchia zusammengefasst. Jedenfalls wird die Besonderheit der morphologischen Struktur und die Entwicklungsrichtung bei jeder der 3 Unterabteilungen mit denen der anderen beiden Unterklassen gleichgestellt; dies sind die Opisthobranchia und die Pulmonata. Drei unabhängige Unterklassen werden also bei den Vorderkiemer-Schnecken unterschieden: Cyclobranchia, Scutibranchia und Pectinibranchia.

Die Cyclobranchia (Kreiskiemer, d.h. was man früher Docoglossa nannte, sowie einige der paläozoischen Gruppen) stellen eine besondere Entwicklungslinie dar, erkennbar an ihrer primitiven ursprünglich symmetrischen Schale ohne Einschnitt oder Rinne, dem ursprünglichen Typus der Radula-Struktur und -Bewegung, wie sie bei anderen Schnecken nicht vorkommen und ebenso an der Struktur des Geschlechtsapparates, Magens und Nervensystems, die bei den Cyclobranchia ähnlich wie bei der Scutibranchia sind. Darüber hinaus unterstütz die Asymmetrie des Mantelkomplexes, die die Vertreter dieser Gruppe unabhängig entwickelten, die Spezialisation der Radula, die Bildung des arteriellen Bulbus und das Vorhandensein der Mantel-Nervenstränge die Meinung, dass diese Gruppe eine besondere Entwicklung durchlaufen ist. Aus diesem Grunde werden die Cyclobranchia in eine besondere Unterklasse gestellt, die die Ordnungen Helcionellida, Archinacellida (die früher zu den Monoplacophora gerechnet wurden) und Docoglossa. Der Evolutionsprozess verlief in dieser Gruppe als abnahme der Schalen-dimensionen und ihrer Skulptur, Verminderung der Radula-Zähne und Reduktion der besonderen Atemorgane während des Verlaufs ihrer Entwicklung.

Die übrigen Gastropoden stammen von einer alten Molluskengruppe ab, die sich aus primitiven Cyclobranchia im Kambrium entwickelt hat, diese hatten einen symmetrischen Mantelkomplex und einen Schlitz in der Mitte oder eine rinnenförmige Bildung.

Das Beibehalten der Symmetrie vom Mantelkomplex während der Weiterentwicklung, die gleichzeitige Entwicklung des Schlitzes, das gut entwickelte Epipodium und das Fehlen gewisser ganglia im Zentralnervensystem zusammen mit einer deutlichen Bildung symmetrischer Kiemenganglien erlaubt die Vereinigung der Ordnungen Dicranobranchia, Fissobranchia und Macluritida in eine besondere Unterklasse Scutibranchia (Schildkiemer). Die Weiterentwicklung innerhalb der Scutibranchier zeigt die Tendenz zur Grössenabnahme und Verminderung der Windungen, zur Trennung und Verlagerunge des Schlitzes vom Mundsaum weg, zu Zurücktreten der Spiralskulptur gegen die Längsskulptur, zur Vergrösserung der rechten Niere wegen der neuerrungenen Doppelfunktion: Exkretion and Fortpflanzung.

Die Unterklasse Pectinibranchia (Kammkiemer), die die Monotocardia (Mesogastropoda und Neogastropoda) sowie Trochacea und Neritacea von den Diotocardia (= Archeogastropoda) der früheren Klassifikationen umfasst, ist phylogenetisch am jüngsten und morphologisch am mannigfaltigsten. Sie kommt von den Scutibranchia (höchstwahrscheinlich von den Macluritida oder hat mit diesen gemeinsame Vorfahren).

Innerhalb der Pectinibranchia können 18 Ordnungen unterschieden werden, die nach einem Plan gebaut sind, und die gleiche Entwicklungsrichtung wie die ganze Unterklasse haben, aber doch auch Besonderheiten in der Evolution, in der Schalenstruktur, Fuss, Verdauungstrakt, Kieme, Zentralnervensystem, Geschlechtsapparat und Ökologie. Von diesen 18 Ordnungen werden zwei Gruppen gebiltet, eine jetzt als Überordnung Pyramidellimorpha zusammengefasst, die andere umfasst die Überordnung Turbinimorpha zusammen mit stammverwandten Ordnungen die hier in die neuen Überordnungen Neritimorpha, Paludinimorpha, Littorinimorpha und Cerithiimorpha gestellt werden.

Die Gesamtentwicklung der Pectinibranchia, die sich ähnlich in verschiedenen Überordnungen und Ordnungen wiederholt, ist bezeichnet durch Nachlassen insbesondere der Spiralskulptur, Bildung eines Siphos statt des Epipodiums, Kieferreduktion, Verkleinerung der Radula die in verschiedenen Gruppen verschieden vor sich geht, Zunahme der Asymmetrie des Mantelkomplexes, Bildung einer Kammkieme und eines Osphradiums, Umbildung der rechten Niere zum Gonodukt, Konzentration und Integration des Zentralnervenystems. Die Entwicklung innerhalb der verschiedenen Untergruppen der Pectinibranchier verlaufen parallel von Mikrophagie, Sestonophagie und Phytophagie zur Detritophagie, Saprophagie, zum Beutefang und bei stark spezialisierten Formen zum Parasitismus. In der Fortpflanzung folgt auf äussere Befruchtung die innere, Aufgabe des Larvenstadiums und Ovoviviparie.

Parallelismus in der Entwicklung der betrachteten Unterklassen ist vorhanden. Er zeigt sich morphologisch in zunehmender Asymmetrie des Baues, Verkleinerung des Radulaapparates, Komplizierung der Fortpflanzungsorgane und stärkerer Konzentration des Nervensystems. In bezug auf Ökologie und Verbreitung zeigt sich die Parallelentwicklung innerhalb der Unterklassen im Wechsel des Lebensraumes (vom Leben im flachen Wasser und auf hartem Boden zum Leben in grösseren Tiefen auf gemischten und weichen Substraten, zwischen Epifauna und später Infauna), im Übergang ins Süsswasser und aufs trockene Land, in der Verbreitung von tropischen und subtropischen Breiten nach gemässigten und kalten Gebieten.

Die phylogenetisch höchstentwickelten Gruppen haben die grösste Zahl lebender Arten innerhalb allen Unterklassen und Ordnungen.

Der Entwicklungsprozess bei den betrachteten Schnecken war ungleichmässig und mit Unterbrechungen. Die Zeiten intensivster Artenbildung waren zugleich bei den verschidenen Gruppen vom Kambrium bis Ordovicium, vom Perm zur Trias und von der Kreide zum Paläogen.

H.Z.

RÉSUMÉ

SYSTÉMATIQUE DES GASTROPODES PROSOBRANCHES

A. N. Golikov et Y. I. Starobogatov

Les auteurs tracent 5 principales lignes évolutives dans la classe des Gastropoda, et à partir de là distinguent 5 principales subdivisions taxonomiques, qui diffèrent par les caractères essentiels de leur structure. Trois de ceux-ci sont, selon la règle, réunis dans la sous-classe des Prosobranchia. Cependant l'originalité de la structure morphologique et l'orientation évolutive dans chacune de ces subdivisions apparaissent comme équivalentes à celles des 2 autres sous-classes de Gastropodes, c'est-à-dire les Opisthobranchia et les Pulmonata. Trois sous-classes indépendantes sont en conséquence reconnues chez les prosobranches gastropodes: Cyclobranchia, Scutibranchia et Pectinibranchia.

Les Cyclobranchia (c'est-à-dire les anciens Docoglossa et quelques espèces des groupes Paléozoïques) présentent une ligne d'évolution particulière, mise en évidence par leur coquille primaire, primitivement symétrique, dépourvue de toute incision ou sulcus, par le type archaïque de la radula tant dans sa structure que son mouvement, caractères non partagés par tous les autres gastropodes, comme d'ailleurs la structure du système reproducteur, de l'estomac et du système nerveux, qui, chez les Cyclobranchia sont semblables à ceux des Scutibranches.

De plus, l'asymétrie du complexe palléal, qui se développe indépendamment chez les représentants de ce groupe, la spécialisation de la radula, le développement du bulbe artériel et la présence de cordons nerveux palléaux, font penser que ce groupe a un type d'évolution distinct. A partir de ces considérations, les Cyclobranchia ont été placés à part dans une sous-classe spéciale, qui embrasse les ordres Helcionellida, Archinacellida (précédemment classés parmi les Monoplacophora) et Docoglossa. Le processus d'évolution s'est morphologiquement exprimé à l'intérieur de ce groupe par la diminution des dimensions et de l'ornementation de la coquille, par une oligomérisation de la radula et par une réduction des organes spécialisés dans la respiration au cours de leur développement.

Le reste des gastropodes prend son origine à partir d'anciens groupes de mollusques, évoluant à partir de Cyclobranchia primitifs du Cambrien; ces mollusques ont un complex palléal symétrique et une fissure disposée médialement (sélenizone) ou projection sulciforme.

Le maintien de la symétrie du complexe du manteau au cours de l'évolution, le développement parallèle de la fissure, l'épipodium bien développé, l'absence de ganglions bien marqués dans le système nerveux central avec en même temps une symétrie bien nette des ganglions branchiaux, tous ces caractères ont permis l'unification des ordres Dicranobranchia, Fissobranchia et Macluritida en une sous-classe distincte, celle des Scutibranchia. L'évolution à l'intérieur des Scutibranchia montre une tendance à une réduction de la taille, à un moindre degré d'enroulement de la coquille, à une séparation et à un déplacement de la sélénizone par rapport au péristome, à la diminution de la sculpture spirale par rapport à la sculpture axiale, à l'augmentation de taille du rein droit due à la récente stabilisation de sa double fonction, celle d'excrétion et de reproduction.

La sous-classe des Pectinibranchia, comprenant les Monotocardia (Mesogastropoda et Neogastropoda) ainsi que les Trochacea et Neritacea parmi les Diotocardia (= Archeogastropoda) des précédentes classifications, est phylogénétiquement le plus récent et le plus diversifié morphologiquement; ses origines à l'intérieur des Scutibranchia (plus vraisemblablement des Macluritida ou de leurs ancêtres communs).

Chez les Pectinibranchia on peut distinguer 18 ordres qui partagent un plan commun de structure et suivent la tendance évolutive générale de l'ensemble de la sous-classe, mais qui ont déjà une ligne évolutive spéciale et une particulière structure de la coquille, du pied, de l'appareil digestif, des branchies, du système nerveux central et de l'appareil reproducteur, ainsi qu'une écologie différente. De ces 18 ordres, les premiers à diverger sont les 2 groupes suivants. L'un, maintenant unifié dans le superordre des Pyramidellimorpha et l'autre comprenant le superordre des Turbinimorpha et d'autres ordres voisins phylogénétiquement rassemblés dans les nouveaux superordres Neritimorpha, Paludinimorpha, Littorinimorpha et Cerithiimorpha.

Le développement évolutif des Pectinibranchia, qui se manifeste souvent de la même façon dans les différents ordres et sous-ordres, s'exprime morphologiquement par: diminution de la sculpture, surtout spirale; formation d'un processus siphonal en l'absence d'un épipodium; réduction de la mâchoire, oligomérisation de la radula, accomplies différemment dans les différents groupes; augmentation de l'asymétrie du complexe palléal; formation d'une cténidie pectinée et d'une osphradie; transformation du rein droit en gonoducte rénal; concentration et intégration du système nerveux central. L'évolution à l'intérieur des différentes subdivisions des Pectinibranchia suit une voie parallèle, depuis les ancestrales microphagie, sestonophagie et phytophagie, jusqu'aux détritophagie, saprophagie et prédation et, pour des formes spécialisées, jusqu'au parasitisme. Quant au mode de reproduction, il passe de la fécondation externe à l'interne, au développement direct et à l'ovoviviparité.

On peut percevoir un certain parallélisme évolutif dans le développement des sous-classes considérées. Il est exprimé par la tendance à l'augmentation de l'asymétrie de structure, l'oligomérisation de l'appareil radulaire, une plus grande complexité de l'appareil reproducteur et une concentration plus prononcée du système nerveux. En écologie et dans la répartition géographique, le parallélisme d'évolution entre les sous-classes se manifeste par un changement d'habitat (de la vie en eau peu profonde et sur substrat dur à celle à plus grandes profondeurs, sur fonds mixtes ou meubles, en tant qu'épifaune et plus tard d'endofaune), par l'expansion de la distribution des latitudes tropicales et subtropicales vers les régions tempérées et froides.

Les groupes les plus avancés phylogénétiquement ont le plus grand nombre d'espèces vivantes à l'intérieur de toutes les sous-classes et d'ordres.

Le processus évolutif à l'intérieur des Gastropodes considérés a été inégal et intermittent. Les stades les plus intenses dans le processus ont eu lieu simultanément dans différents groupes pendant les périodes Cambrien-Ordovicien, Permien-Triasique et Crétacé-Paléogène.

A.L.

RESUMEN

SISTEMATICA DE GASTROPODOS PROSOBRANQUIOS

A. N. Golikov y Y. I. Starobogatov

Los autores trazan 5 ramas de evolución principales dentre de la clase Gastropoda, distinguiendo así 5 subdivisiones taxonómicas mayores que difieren en los caracteres estructurales principales. Tres de estas se unen, corrientemente, en la subclase Prosobranchia; sin embargo, la originalidad de sus caracteristicas, y el sentido de la evolución en cada una de estas tres subdivisiones, tienen valor equivalente a los de las otras 2 subclases, Opisthobranchia y Pulmonata. Por consiguiente se reconocen aquí como tres subclases independientes: Cyclobranchia, Scutibranchia y Pectinibranchia.

Los Cyclobranchia (los llamados Docoglossa, y algunos de los grupos paleozoicos) presentan una evolución particular, demonstrable por su concha primitiva, simétrica y sin surco, por su arcaica estructura y movimiento de la rádula, tipo que no se encuentra en otros gastropodos, asi como también por la estructura de los sistemas reproductor y nervioso, y del estómago, que son similares a los de Scutibranchia. Además, la asimetría del complejo paleal que se desarrolló independientement, la especialización radular, presencia de cordones nerviosos en el manto, y desarrollo del bulbo arterial, soportan la opinión de que este grupo tuvo un tipo de evolución distinto. Estas consideraciones separan los Cyclobranchia en una subclase especial, que embraza los ordenes Helcionellida, Archinacellida (que antes se incluían en los Monoplacophora) y Docoglossa. El proceso evolutivo se demuestra morfológicamente por la redución en tamaño y escultura de la concha, la oligomerización de la rádula, y reductión de los órganos respiratorios especialidos.

El resto de los gastropodos tuvieron su origen en un antiguo grupo de los Cyclobranchia primitivos del Cámbrico; esos moluscos tenian un manto simétrico complejo, fisura media (selenizona) o proyección sulciforme.

El mantenimiento de la simetria de la complejo del manto durante la evolución, el desarrollo fisural paralelo, epipodio bien desarrollado, y la ausencia de ganglios bien marcados en el sistema nervioso central mientras qui tienen ganglios branquiales simétricos muy notables, permiten la unificación de los ordenes Dicranobranchia, Fissobranchia y Macluritida, en una clase separada, Scutibranchia. La evolución de los Scutibranchia muestra una tendencia hacia la redución de tamaño y grado en el arrollamiento de la concha, hacia la separación y desplazamiento de la selenizona de el peristoma, la diminución de la escultura espiral comparada con la axial, y el aumento en tamaño del riñón derecho debido a su doble función—de estabilización reciente—de excreción y reprodución.

La subclase Pectinibranchia, incluyendo Monotocardia (Mesogastropoda y Neogastropoda) así como Trochacea y Neritacea de los Diotocardia (= Archeogastropoda) de las clasificaiones corrientes, es la más jóven filogenéticamente y la más diversificada. Se originó dentro de los Scutibranchia (más probablemente de los Macluritida o sus antecesores comunes).

Dentro de los Pectinibranchia pueden distinguirse 18 ordenes con un plan de estructura común que sigue la linea evolutiva geral de la entera subclase, cada una con particularidades especiales y diversas estructuras de la concha, pié, sistema digestivo, branquias, sistema nervioso y reproductivo, así como ecología. De estos 18 ordenes, los primeros en divergencia fueron 2 grupos, uno ahora unido en el supeorden Pyramidellimorpha y el otro comprendiendo el superorden Turbinimorpha, junto con ordenes filogeneticamente relacionados combinados aquí en los nuevos superordenes Neritimorpha, Paludinimorpha, Littorinimorpha y Cerithiimorpha.

La evolución de los Pectinibranchia—que se manifiesta similarmente en diferentes ordenes y superordenes—se demuestra en la morfología de: la redución (particularmente espiral) de la escultura; formación de un proceso sifonal en ausencia del epipodio; redución de la mandíbula; oligomerización de la rádula que se produjo en forma distinta en los diferentes grupos; aumento de la asimetría del complejo paleal; formación de un ctenidium pectinado y osfradio; transformación del riñón derecho en un gonoducto renal; concentración e integración del sistema nervioso central. Esta evolución en los diferentes grupos de Pectinibranchia tomó caminos paralelos, desde una microfagia y sestonofagia ancestral y phytofagia, hacia detritofagia, saprofagia y predación, y, dentro de formas especializadas, hacia parasitismo. En el modo de reprodución pasaron de fertilizacion externa a interna, al desarrollo directo y ovoviparidad.

Un paralelismo evolutivo se percibe en las subclases consideradas. Esto se muestra morfológicamente en la tendencia hacia un aumento en la asimetría de la estructura, oligomerización del aparato radular, mayor complejidad del sistema reproductor, y una concentración más pronunciada del sistema nervioso. En ecología y distribución, tal paralelismo se manifiesta en los cambios de habitat (desde las aguas poco profundas sobre fondos duros, a la vida en las grandes profundidades de fondos blandos y mixtos, dentro de la epifauna y más tarde infauna), en la adaptación a las aguas dulces y vida terrestre, y en la expansión desde latitudes tropical y subtropicales hacia regiones templadas y frías.

Los grupos más avanzados filogenéticamente tienen el más grande numero de especies vivientes dentro de todas las subclases y en los ordenes.

La evolución de los gastropodos considerados fué despareja e intermitente. Los estados más intensos en el proceso formativo aparecieron simultaneamente dentro de los diferentes grupos en el Cámbrico-Ordoviciano, Permo-Triásico y el Cretáceo-Paleogeno.

J. J. P.

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ON THE FUNCTIONAL MORPHOLOGY AND ADAPTATIONS OF *ENTODESMA SAXICOLA* (BIVALVIA: ANOMALODESMACEA)

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ABSTRACT

The habits, major structural features and ciliary currents of *Entodesma saxicola* (Baird) are described. Apart from the morphological consequences of a permanently attached life within the confines of a crevice, *Entodesma* is a typical anomalodesmacean bivalve, its functional morphology being similar to that of related genera such as *Lyonsia* and *Pandora*. As a consequence of permanent attachment, *Entodesma* is heteromyarian with a much reduced foot, adapted for the production and placement of byssus threads.

INTRODUCTION

Entodesma saxicola (Baird) is one of the largest species of the order Anomalodesmacea. The specimens collected for the present study are more than 8 cm in length. The species is widely distributed along the Pacific coast of North America (Yonge, 1952), the present specimens being taken at low water mark in the rocky intertidal in gravel filled crevices, in which they are byssally attached throughout life, at San Juan Island, Puget Sound, Washington.

The genus was first described by Philippi (1845), who noted its irregular shape and habit of nestling in rock crevices and its association with sponges and coelenterates. *Entodesma saxicola* does not normally form an association with zoophytes, but is usually much distorted by the confines of its microenvironment.

Since Yonge's (1952) study, little new information has been published on this species. *Entodesma* is a member of the family Lyonsiidae and when undistorted resembles *Lyonsia* in general outline. It is biconcave, inequivalve, with the right valve overlapping the left; the umbones are anterior in position, while the posterior margin is laterally compressed and extended to enclose the short siphons.

The outer surface of the shell is ridged by both radial and concentric lines, but the dominant external feature is the thick fibrous brown periostracum. The shell valves are united along their entire dorsal margins by fused periostracum; elsewhere the shell margins are overlapped by a very thick layer of periostracum. This is particularly prominent posteriorly where, in the largest specimens, the periostracum extends more than 1 cm beyond the calcareous shell, and where it protects the siphons. Anteriorly and ventrally the overlap is somewhat less although extending at least 2 mm beyond the limit of the shell. Lyonsiids commonly incorporate sand grains within the periostracum and Yonge (1952) reports this in specimens of *Entodesma saxicola* he examined from Monterey, California. The present specimens have no incorporated sand grains. Internally, as in all lyonsiids, the shell is beautifully nacreous and opalescent with marked pallial and adductor muscle scars. The posterior adductor muscle scar is broad and somewhat irregular in outline and placed far anterior, halfway between the posterior margin and umbo (Fig. 1C); the anterior adductor muscle scar is smaller, bilobed and situated relatively ventral in position close to the margin. The pallial line is distant from the shell margin and there is a shallow posterior pallial embayment. Scars of retractor muscles associated with the foot are present dorsal to the adductor scars.

In post-larval life the animal is permanently attached by the byssus, the threads emerging from the very small, circular pedal aperture. Many animals have a conspicuous notch in the ventral shell margin, corresponding to the position of the byssus, entirely comparable to that described in another anomalodesmacean *Thracia distorta* (Allen, 1961a), a species which occupies a

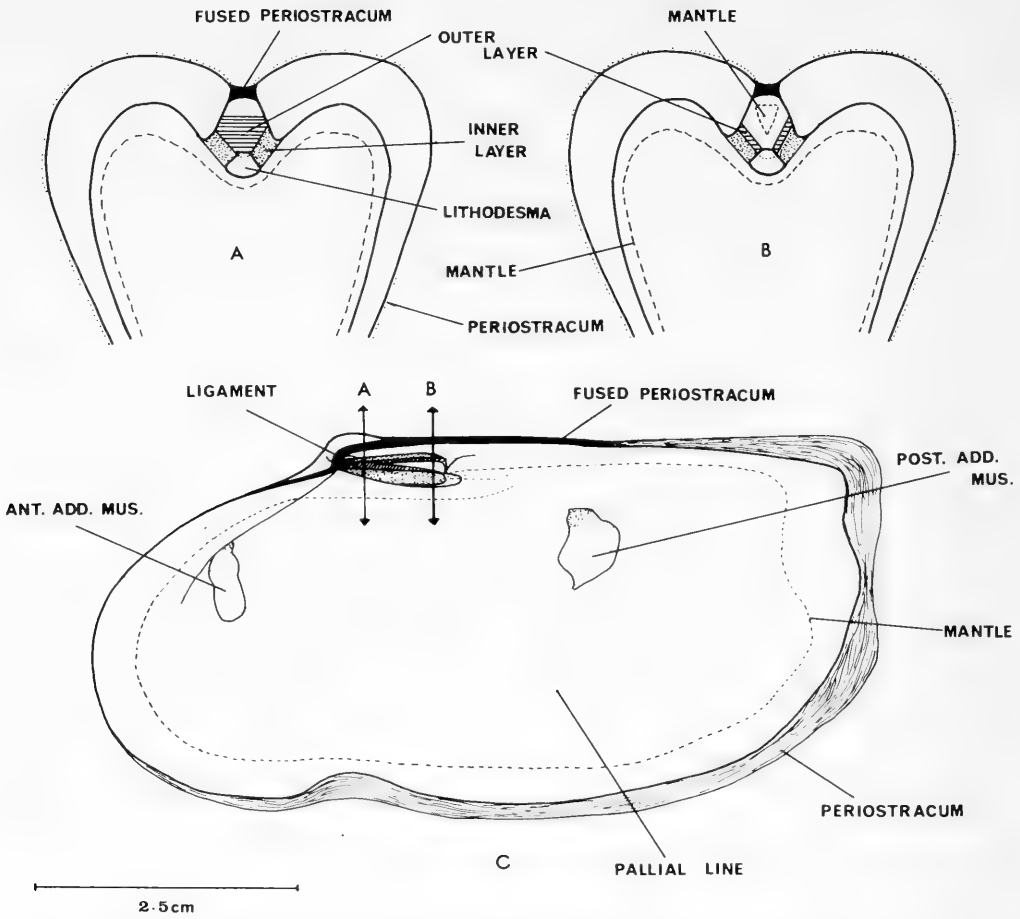

FIG. 1. A, B. Transverse sections through the ligament of *Entodesma saxicola*, cut at levels A & B as shown in C; C. Lateral view of internal shell surface of the right valve with the ligament intact.

comparable niche in the Eastern Atlantic littoral. Although only moderately heteromyarian, the condition in *Entodesma* strongly resembles that of *Mytilus* in that the posterior part of the mantle-shell is enlarged, extended and raised above the substratum. Correlated with this the anterior mantle cavity is restricted, the anterior adductor muscle is reduced in size and the body axis is directed forwards (Fig. 2). Yonge & Campbell (1968) consider that the heteromyarian condition is generally accompanied by a ventral flattening of the shell but here there is no sign of this; instead the valves are laterally compressed and somewhat boat-shaped when viewed laterally and are clearly adapted to a crevice or nestling habit.

Entodesma saxicola lacks hinge teeth, although an elongate lithodesma is present forming part of the opisthodetic ligament. The lithodesma is about one sixth or one seventh of the shell length, and is spatulate, triangular in cross section, with the apex uppermost. The remaining part of the ligament is composed of outer and inner layers overlain by fused periostracum. The ligament is V-shaped, the arms being united anteriorly beneath the umbos and diverging posteriorly (Fig. 1C). The outer and inner layers connect ventrally with the lithodesma while the outer latero-dorsal faces are attached to a raised, crescent-shaped chondrophore in each valve. At the apex of the V, the outer layer of the ligament forms, in cross section, a complete wedge between the 2 arms of the inner layer, but further back, like the inner layer, it is split into 2 separate arms (Fig. 1A, B). In addition, a small anterior outer layer extends from the

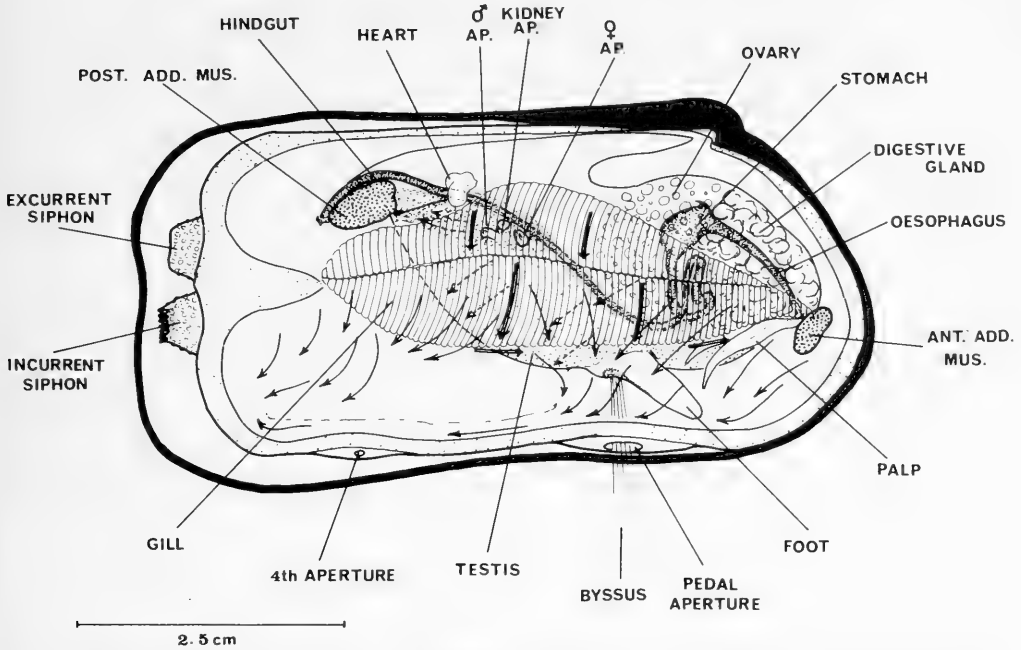

FIG. 2. Semidiagrammatic lateral view of *Entodesma saxicola* from the right side of the intact animal, to show the major features of the anatomy. Direction of ciliary currents is indicated by arrows:- dashed on body; double shaft on gill; single shaft on mantle.

umbo forwards, while a tongue of mantle tissue penetrates between the arms of the ligament from the posterior end. The latter secretes fused periostracum. This overlying fused periostracum must be of considerable significance in maintaining the correct alignment of the valves and preventing sheering of the ligament.

Opened living specimens give off a curious and characteristic acrid odour; a similar odour was observed earlier by one of us (JAA) during similar investigations into another anomalodesmacean, *Pandora inaequivalvis*.

Mantle

Fusion of the mantle edges is extensive and involves the inner lobe and much of the middle lobe (Yonge, 1952). The outer lobe, while tenuous, is greatly extended below the fused tissues. The periostracal groove is not well defined and periostracum appears to be secreted over a relatively broad band of the inner face of the extended mantle margin. The periostracum is much softer than in most bivalves, and many overlapping layers are secreted to produce the thickened margins of the shell. Ventrally, and in addition to the small pedal aperture, close to the posterior margin there is a minute 4th aperture (Fig. 2). Posteriorly, short incurrent and excurrent siphons are present which are similar in appearance and are a bright, deep orange-red in life. Mantle fusion separating the inner apertures of the incurrent and excurrent siphons is extended anteriorly into the mantle cavity close to the posterior limit of the posterior adductor muscle. The margin of the excurrent aperture lacks tentacles, while that of the incurrent is fringed with a ring of about 15 small orange tentacles which have a thickened collar just below the tip. The outer surfaces of both siphons are covered with small papillae (Fig. 2). The ciliary pathways on the mantle are generally ventral in direction, joining the rejectory tract at the pallial margin along which particles are carried to a position below the base of the incurrent siphon. There is a slight ridge posterior to the pedal aperture marking the dorsal side of the marginal rejection tract. Above this tract, to a position level with the ventral edge of gill and body, there is an area of mantle with little ciliation and particles dorsal to this area are deflected posteriorly around it (Fig. 2).

Foot

The foot is very small, almost cylindrical and pointed at its tip. It is not used for locomotion, the species being permanently attached. There is a functional byssus gland in the proximal part of the foot, the duct from which opens on the posterior side and continues as a median groove almost to the tip. The foot is positioned mid-centrally on the ventral side of the body. As in other bivalves with a well developed byssus gland, e.g., *Mytilus* and *Dreissena* (White, 1937; Yonge & Campbell, 1968), the pedal retractors tend to atrophy, while the byssus retractors, themselves specialized pedal muscles, dominate the pedal musculature (Fig. 3). In *Mytilus* and *Dreissena* 3 pairs of posterior byssal retractors are attached dorsally in a series close to the dorsal edge of the valves, while a pair of anterior retractors extends horizontally and attaches close to the anterior adductor muscle. *Entodesma* differs considerably from this condition and possesses only 1 pair of posterior byssal muscles, and these run together as a flattened strap from the foot postero-dorsally. Proximally they diverge and insert on the valves at either end of the posterior adductor muscle. There is a single pair of anterior pedal retractors and a single pair of anterior byssal retractors, the latter being much shorter than the posterior byssal retractors. The anterior byssal and pedal retractor muscles arise from the foot separately but converge and insert at a common point dorsal to the anterior adductor muscle (Fig. 3). The arrangement of the musculature is reminiscent of that of *Lithophaga* (Yonge & Campbell, 1968) in which the byssal retractors have become associated with movement for rock boring; however, here rock boring does not occur and the analogous number and disposition of the muscles is probably related to the crevice habit and the pattern of byssal attachment. The byssal threads themselves are numerous and produced in much the same manner as in *Mytilus* (Brown, 1952). However they are remarkably elastic, much more so than in any other bivalve that we have encountered.

Palps

The palps are small and triangularly strap-shaped. The ventral half of the inner surfaces is typically ridged transversely to the long axis of the palp although, unlike the condition in other bivalves, the dorsal half is non-ridged. While most bivalve palps have a smooth inner dorsal margin, it is rarely as

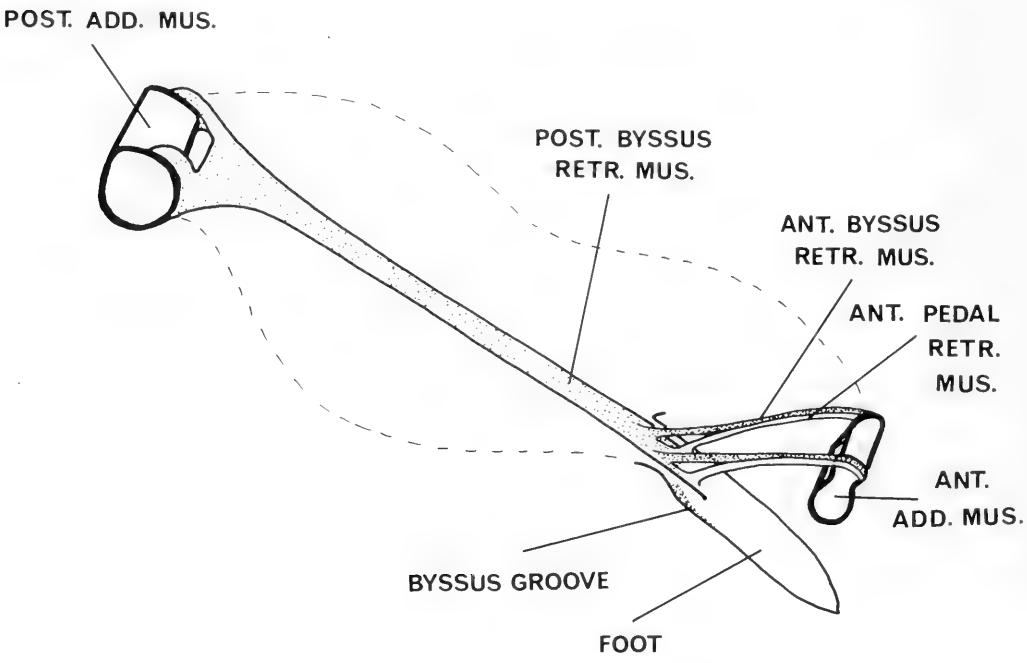

FIG. 3. *Entodesma saxicola*. Lateral view of foot and its associated musculature. X 2.

wide as seen here (Fig. 4A). In addition, a long ridge runs the length of the palp adjacent to the inner end of the transverse ridges. A very narrow marginal groove is present on both the ventral and dorsal edges of each palp. In the largest specimens there are approximately 100 of these transverse palp ridges. These are very deep and are vertical in attitude (Fig. 4B, C). Transverse sections show that the palps have a thick epithelium of elongate, ciliated cells overlying a connective tissue containing scattered muscle fibres and large mucous cells. The muscle fibres in the core of the ridges are not arranged in any clear order but predominately lie horizontal along the base and vertical across the depth of the palp. These muscles are probably concerned with the separation of the ridges which are extremely close set, and very erect in comparison with the condition in other bivalves. There are median ridges present along the length of the oral and aboral faces. The inner surface of the ridge on the aboral face is indented forming a deep groove (Fig. 4B). The rejectory tract at the crest of the ridge is not well defined. Directions of ciliary beat and manner of sorting are similar to those described earlier for the Lucinacea (Allen, 1958b). Other ciliary tracts on the palps are as follows:-

a) an aboral rejection tract along the ventral margin, particles passing along it fall off at the tip onto the rejection tracts of the mantle or body;
b) a similar but less dominant tract along the dorsal margin of the palp;
c) particles on the upper half of the inner face of the dorsal non-ridged area move towards the marginal groove and are rejected; those on the lower half move to the longitudinal ridge and cross this on to the ventral transversely ridged surface where they are sorted.

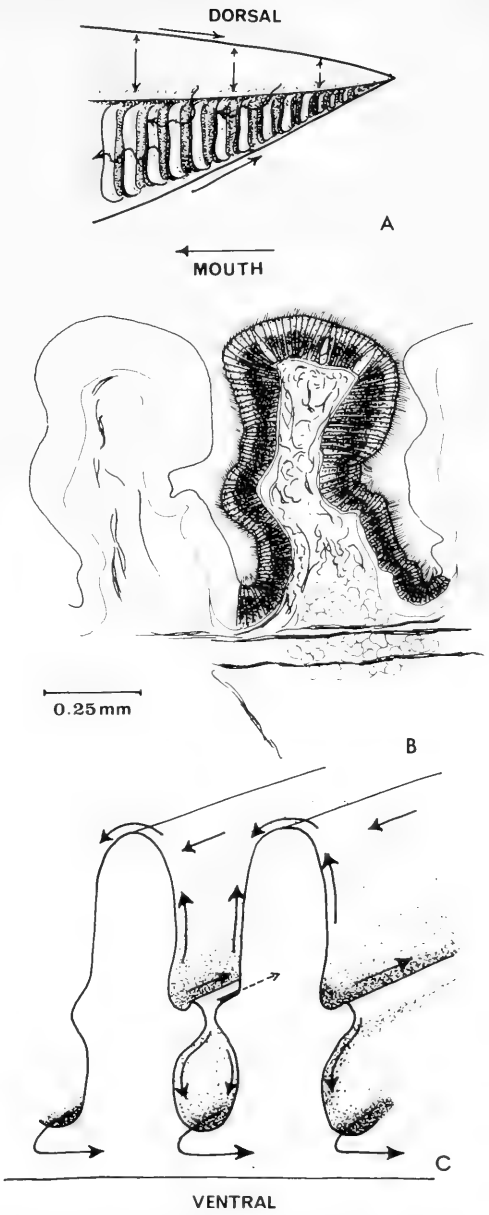

FIG. 4. *Entodesma saxicola*. A. Surface view of the inner face of a palp showing direction of ciliary currents; B. Transverse section of a palp ridge; C. Diagram of two adjacent palp ridges to show the direction of the ciliary currents.

Gills

The eulamellibranch gills are much modified. The ascending lamella of the outer demibranch is lost and the descending lamella is reflected dorsally. The latter is not as deep as that of the inner demibranch, particularly at its posterior limit where it skirts the ventral side of the posterior adductor muscle. It also stops short of the anterior limit of the inner demibranch. However, the gills are large and more than cover the body, their lateral area being little less than that of the mantle, internal to the pallial line (Fig. 2). The gills are deeply plicate, there being approximately 230 plicae/lamella. The number of filaments to

each plica is not constant, varying from 33 to 39, although the majority have 36. The axis is attached along the midline of the body, and afferent and efferent blood vessels, the axial nerve and a well defined block of longitudinal muscles run along its length. Associated with the gill axis and lying adjacent to the longitudinal muscle is a ciliated extension which contains gland cells and connective tissue.

We confirm Yonge (1952) in his observations on the ciliary currents of the gill; all particles travel to the ventral margin of the inner demibranch where they pass anteriorly to the region of the mouth.

Viscera

The ciliary currents of the body surface are all rejectory and postero-ventral in direction. Particles gather at the postero-ventral margin from where they fall on to the mantle. No ciliation was observed on the foot.

The course of the alimentary canal (Fig. 2) is similar to that of other lyonsiids except that 2, rather than 1, hind-gut loops are present anterior to the stomach. A long oesophagus opens into the anterior wall of the relatively small oval stomach. The combined style sac and mid-gut open from the ventral wall and extend vertically down to the junction of viscera with foot. From here the hind-gut makes 2 loops anterior to the style sac before passing to the right side and then taking a posterior dorsal course through the heart to the anus.

The stomach resembles that of *Pandora* (Allen, 1954), *Cleidothaerus* (Purchon, 1958) and *Lyonsia* (Narchi, 1968). There is a short dorsal hood present, and the gastric shield is extensive, covering much of the left and dorsal inner surfaces. The gastric shield is anchored in position by an anterior flange on the dorsal wall of the dorsal hood and a lateral flange on the left wall of the left pouch.

Dorsal to the lateral flange is a prominent recurved portion of the shield bearing a tooth on its inner, posterior rim. The ciliated region shows typical features of the anomalodesmacean stomach, e.g., posterior sorting area, acceptance tract, dorsal groove, and left and right apertures to the digestive diverticula (Fig. 5). The left aperture lies posterior but close to the left pouch. There are no apertures leading from the left pouch to the digestive diverticula although the cilia on the surface between the left duct and the left pouch beat towards the left pouch. Particles accumulating in the pouch are pulled along the groove in the gastric shield below the tooth and so towards the head of the style. Similarly, a narrow ciliated area adjacent and anterior to the recurved section of the gastric shield directs particles towards the head of the style. The apertures on the right side are 4 in number and are situated adjacent to the entrance of the oesophagus. In other descriptions of stomachs of species of Anomalodesmacea (Allen, 1954, 1958a; Purchon, 1958) at most only 2 apertures have been reported on the right side. Multiplication of apertures is undoubtedly related to the large size of the animal (Allen, 1958a; Purchon, 1958). Apart from the posterior sorting area that extends from the posterior end of the stomach to the dorsal hood, the remaining surface of the stomach is surprisingly free of ridged sorting areas (Fig. 5). The ridges leading from the apertures of the digestive diverticula to the mid-gut, which are a typical feature of the anomalodesmacean stomach, are few in number. Particles in the grooves between the ridges are passed to the mid-gut. On the flat ciliated area adjacent to the oesophagus cilia direct particles to the apertures beside the oesophagus. The perimeter of the oesophageal aperture is well defined with the oesophageal ridges terminating as small papillae. From the dorsal side of the oesophageal aperture, a dorsal groove crosses the anterior side of the stomach to the dorsal hood.

Gonads and kidney

As in the case of most members of the order Anomalodesmacea, *Entodesma saxicola* is a hermaphrodite. Ovary and testis are separate and paired, with each pair connected in the mid line. The mature testis lies ventral and occupies the major part of the body dorsal to the foot, and partly extends around the digestive gland to the oesophageal region. The ovaries are dorsal to the posterior part of the stomach. Both gonads open separately into the hyperbranchial cavity, on the postero-lateral body wall (Fig. 2). Both apertures are slits on a slightly raised papilla, the male pore being slightly dorsal and posterior to the female. As described by Yonge (1952), the apertures lie

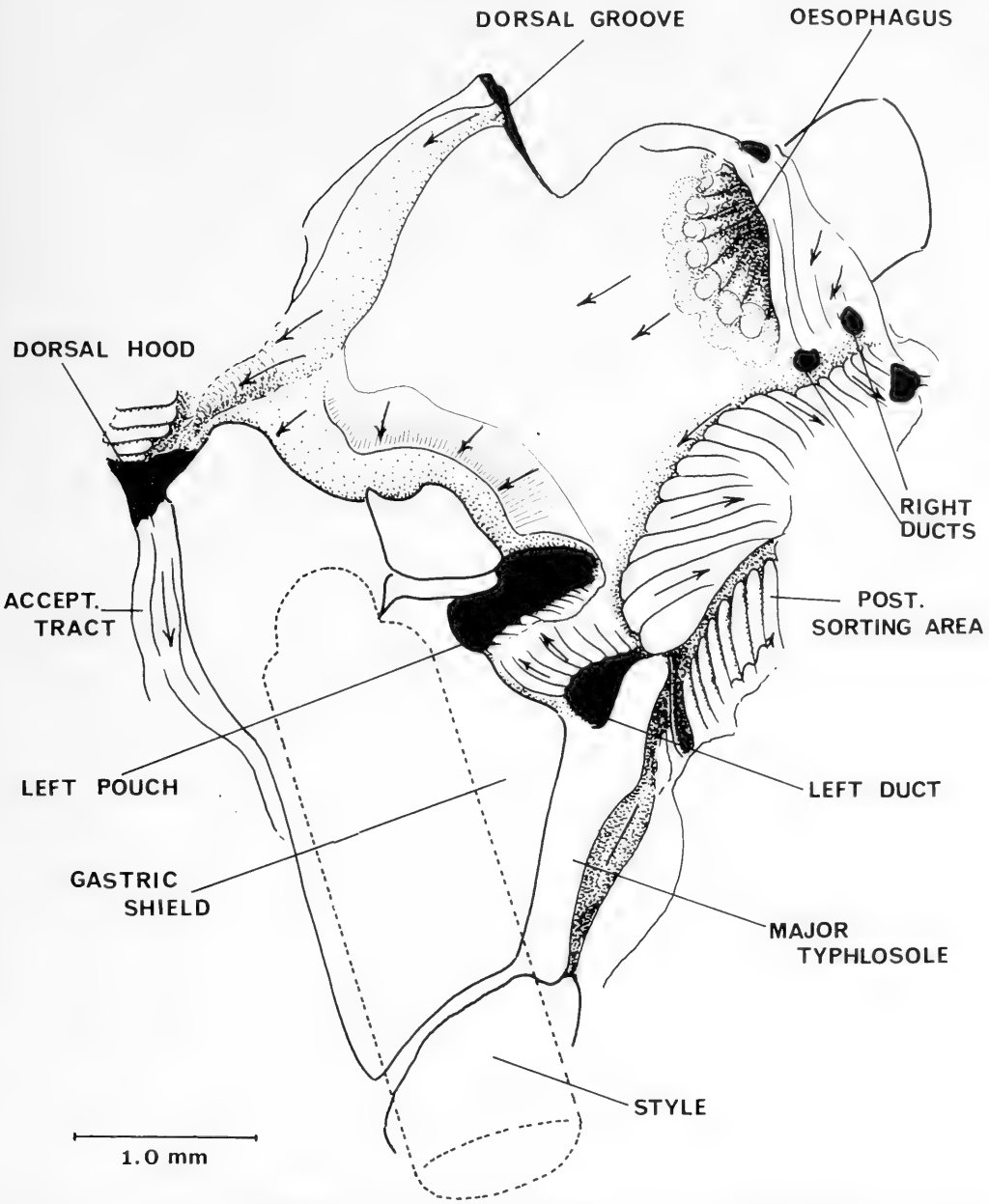

FIG. 5. The stomach of *Entodesma saxicola* opened longitudinally, the cut being made along the upper part of the right side.

close to and above the attachment of the margin of the inner demibranch to the body wall and below the gill axis. The area of the body wall between axis and gill attachment is ciliated and the cilia beat posteriorly towards the excurrent aperture. Specimens collected in the first week in September were ripe and contained immense numbers of ova. The mature ova measure 0.08 mm in length but are invested with a gelatinous coat giving an overall dimension of 0.17 mm × 0.14 mm. Eggs so coated appear typical of the Anomalodesmacea (Allen, 1961b, and personal observations).

The kidney is elongate, lying posterior to the ovary and opening into the hyper-

branchial cavity by an aperture which is covered by a flap of tissue. The kidney aperture lies posterior to that of the oviduct and dorsal to the male pore.

DISCUSSION

Yonge (1952) has discussed the form of *Entodesma* in relation to other members of the family Lyonsiidae and little can be added to his succinct and pertinent analysis of the effects of attachment on the symmetry of the animal. The functional significance of the 4th pallial aperture remains obscure. It is extremely small and observations on living specimens showed no clear function, either as an exit or an entrance to the mantle cavity.

Apart from its large size, *Entodesma* is in most respects a typical anomalodesmacean bivalve. It is probably the eastern Pacific counterpart of *Thracia distorta*, an intertidal and shallow sublittoral byssally attached anomalodesmacean of the eastern Atlantic that nestles in crevices and which becomes increasingly distorted as it grows and conforms to the confines of its microhabitat.

Because the animal is permanently attached, the foot is small and not used for locomotion. Its use is restricted to the formation of byssus threads and their attachment. Foot morphology, like that of mantle, shell and body, resembles that of *Mytilus*. As in the latter genus byssal retractor muscles dominate pedal musculature.

The elastic nature of the byssus threads, the thickened periostracum and firm attachment within crevices, make it ideally adapted to the exposed rocky littoral.

ACKNOWLEDGEMENTS

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MONOGRAPH ON *"LITHOGLYPHOPSIS" APERTA*, THE SNAIL HOST OF MEKONG RIVER SCHISTOSOMIASIS[1]

George M. Davis[2], Viroj Kitikoon[3], and Prasong Temcharoen[4]

ABSTRACT

We discuss the morphology, histology, ecology, distribution, systematics, and evolutionary relationships of *"Lithoglyphopsis" aperta* Temcharoen, the snail host of Mekong River *Schistosoma* sp., and part of a vast, complex, endemic hydrobiid fauna consisting of 11 genera and over 80 species.

"L." aperta is a member of the Hydrobiidae (as broadly outlined by Fretter & Graham, 1962), subfamily Triculinae (as defined by Davis, 1968b). *"L." aperta* cannot be assigned to *Lithoglyphopsis* because its shell and radula differ from those of the type-species, *L. modesta* (Gredler) from China, and because *L. modesta* is apparently more closely allied to other Mekong River genera in these traits. The female reproductive system of *"L." aperta* is similar to that of *Tricula burchi* Davis, a species from NW Thailand outside the Mekong River drainage. It is not possible to assign *aperta* to a named genus until the morphologies of numerous other hydrobiid taxa in the Mekong River are known.

"L." aperta is typically hydrobiid in grade of morphological organization, in the nervous, digestive, ctenidial and male reproductive systems. Differences from other hydrobiid taxa are in the female reproductive system and micromorphological features of the digestive tract. *"L." aperta* and species of *Tricula* from Thailand have a female reproductive system where sperm enter at the posterior end of the mantle cavity and travel to the bursa copulatrix via a spermathecal duct. These and related traits are the basis for the subfamily Triculinae. Hydrobiid taxa from Europe (Hydrobiinae s.s.) belong in a different phyletic line, where sperm enter the female reproductive system at the anterior end of the mantle cavity and travel via a ciliated groove in the pallial oviduct to the bursa copulatrix.

"L." aperta, as well as taxa of the Pomatiopsinae (e.g. *Oncomelania, Pomatiopsis*), differ from most known mesogastropods in lacking a hypobranchial gland. *"L." aperta*, other triculines, pomatiopsines and hydrobiines, as well as taxa studied in the Bithyniidae, Truncatellidae and Assimineidae differ from other mesogastropods, e.g. Viviparidae, Pleuroceridae, Littorinidae, etc., in that the salivary glands are dorsal to the nerve ring, i.e. do not pass through the nerve ring.

"L." aperta lives on solid substrata, particularly wood, shells and leaves in the Mekong River from Khemarat, Thailand, to the Cambodian border, 200 river miles downstream. The range probably extends another 100 river miles downstream to Kratie, Cambodia. It is an *"r"*-selected species by having a high density-independent mortality and using much of its resources for reproduction. The species is a colonizer in a river with severe annual floods. Females live less than 12 months; they apparently lay eggs in late January or February and die. In early March neither adults nor young can be collected. By mid or late March young suddenly flourish. The new generation does not mature until late May or June, after the beginning of the rainy season. The large bursa copulatrix, 63% the length of the pallial oviduct, is a unique feature of *aperta* and may help to maintain sperm during the peak flood months of August to November.

Three races of *"L." aperta* are described, differentiated by shell size, shape, sculpture, mantle pigment patterns, ecology, time of development, and minor aspects of anatomy. The beta race has been found only in the rapids of the Mun River; alpha and gamma races are extensively sympatric at Khemarat and Ban Dan in the Mekong River. The gamma race dominates at Khong Island. All 3 races can transmit the Mekong schistosome.

The Mekong schistosome is not *S. japonicum* but a sibling species probably evolved from a common ancestor, and which diverged well over a million years ago. The hypothesis is presented that the triculine and pomatiopsine taxa had common ancestry several million years ago. The fossil record indicates that triculine taxa and *Oncomelania* of the Pomatiopsinae existed in Burma in the Pleistocene. Several million years ago snails of both lineages probably transmitted schistosomes with less specificity than occurring today. Precursors of present day *Oncomelania hupensis* evolved with greater genetic affinity for schistosome transmission than did precursors to modern triculine taxa. With extinction of *Oncomelania* in

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the headwaters of the Mekong River during the Pleistocene, and with radiation of *O. hupensis* down the Yangtze River of China to Japan, Taiwan, the Philippines, and Sulawesi, the evolving snail-parasite interaction became highly specific, resulting in present day *S. japonicum* and the geographic subspecies of that parasite.

Triculine snails radiated in Burma, Thailand, Laos, and China. The present day Mekong schistosome appears to be a relict with limited distribution, transmitted by *"L." aperta* in a river, held in check by the vagaries of annual floods.

INTRODUCTION

Human schistosomiasis has been reported from the lower Mekong River in recent years (Barbier, 1966; Audebaud et al., 1968; Pathammavong, 1969; Sornmani et al., 1971; Iijima et al., 1971). The finding of this disease, which afflicts 200 million persons in the world, along the Mekong River evoked a strong reaction from those seeking to develop the water resources of the river.

Searches were made for the 1st intermediate host by the Faculty of Tropical Medicine of Mahidol University, Bangkok, and by World Health Organization teams (Iijima et al., 1971; Lo et al., 1971). Harinasuta et al. (1972) discovered that *"Lithoglyphopsis" aperta* Temcharoen (Hydrobiidae, Triculinae) from Khong Island, Laos (near the Cambodian border) could be experimentally infected. The life cycle was completed with cercariae shed from the snails and applied to mice, hamsters, and dogs (Sornmani et al., 1973). Subsequently, Kitikoon et al. (1973) found naturally infected *"L." aperta* in the Mekong River at Khong Island.

We have initiated intensive investigations of the biology of *"Lithoglyphopsis" aperta* because of its involvement with human schistosomes and because this species is part of a vast, endemic hydrobiid fauna that has previously been unstudied biologically and which has excited interest because of its intrinsic value in evolutionary studies. The quotation marks around *"Lithoglyphopsis"* indicate that *aperta* probably does not belong in the genus *Lithoglyphopsis.* This unresolved problem is taken up in the discussion section of the paper.

Eleven genera and over 80 species of Hydrobiidae, with an amazing variety of shell shapes and sculptural patterns, have been described from the Mekong River (Brandt & Temcharoen, 1971). These taxa represent the greatest assemblage of endemic hydrobiids within a single river or lake system known in the world. Aside from the original descriptions of shells and a few scanty notes on radulae, nothing is known of their biology. In the absence of anatomical data it is impossible to determine 1) variability within species, 2) limits of genera, and 3) relationships between Mekong River hydrobiids and extralimital hydrobiids.

One of us (Davis) has undertaken investigations of the Mekong River Hydrobiidae with several questions in mind. What is the temporal and spatial origin of the Mekong River hydrobiid fauna? How does this fauna relate to hydrobiids throughout the world? Are the Mekong River hydrobiids polyphyletic? What traits best serve to describe species, group species into genera, and assess lines of phylogeny? What are the relationships of vastly varying shell shapes and sculptural types to substrates, food, currents, seasonal fluctuations in the river, and temporal duration of the taxa in the Mekong drainage system? Is the capacity to transmit human schistosomes contained within a succinct lineage and can one establish a hypothesis to account for the molluscan host-parasite relationships seen in Asia today? Such a hypothesis would have to deal with the evolution of the host-parasite relationship leading both to the transmission of *Schistosoma japonicum* Katsurada in China by *Oncomelania hupensis* Gredler of the hydrobiid subfamily Pomatiopsinae, as well as the transmission of the Mekong schistosome by *"Lithoglyphopsis" aperta,* here classified in the hydrobiid subfamily Triculinae.

It has been increasingly obvious to current workers that traditional treatment of shells and radulae alone is insufficient to assess relationships within and between species, to define genera, or to gain insight into phylogeny. It has been adequately demonstrated that studies of complete male and female reproductive systems have yielded data giving insight into relationships in the Rissoacea (Johansson, 1939, 1956; Krull, 1935; Davis, 1968a, b). Characters of potential value for assessing systematic relationships may also be derived from the digestive system (Graham, 1939). The nervous, circulatory and excretory systems, however, are highly conservative in the Rissoacea and thus are of lesser value for lower

category systematics.

This paper is the first in a series dealing with the hydrobiids of the Mekong River. Anatomy and histology are used for comparisons with other taxa. Three races of *"Lithoglyphopsis" aperta* thus far found in the Mekong River are described. Anatomical data enable a further delineation of the subfamily Triculinae as defined by Davis (1968b), and a comparison with those other hydrobiids where anatomical data are available. Finally, *"Lithoglyphopsis" aperta* is compared with *Oncomelania hupensis,* the first intermediate host of *Schistosoma japonicum* in China, Japan, the Philippines and Sulawesi, on the basis of anatomy, distribution and evolution.

HISTORICAL REVIEW

After the first reports of human schistosomiasis in the lower Mekong River, several attempts were made to find the first intermediate host. It was taken for granted that the parasite was *Schistosoma japonicum* and thus, initially, the search was made for *Oncomelania.*

Results of such searches were summarized by Pathammavong (1969). *Wattebledia* (Bithyniidae) was found, but not *Oncomelania* (Hydrobiidae). *Wattebledia* is quite distantly related to *Oncomelania.* It is surprising that *Wattebledia* was so extensively collected and studied. The shell only vaguely resembles that of *Oncomelania* while the calcareous multispiral operculum clearly identifies *Wattebledia* as a bithyniid genus. Bithyniids are not naturally infected with mammalian or bird schistosomes (Malek, 1962; Ito, 1964). Efforts to infect *Bithynia tentaculata* with *Schistosoma haematobium* (Bilharz) Weinland, and *S. japonicum* failed (Stunkard, 1946).

In 1968, Brandt showed that hydrobiid snails were transmitting the Mekong schistosome and stated that *Hydrorissoia hospitalis* Brandt "was infected with miracidia from a human blood fluke in Laos. Specimens collected at Khong were found to be naturally infected with sporocysts of *Schistosoma."* In a later report (1970) Brandt stated that *Pachydrobia bavayi* Brandt "is now the first suspect among other species *(Manningiella, Hydrorissoia)* of being the first intermediate host of *Schistosoma japonicum. . . ."* This statement was based upon the observation that miracidia from eggs derived from a Laotian patient penetrated the snail.

Temcharoen (1971) noted that of all gastropods collected at Khong Island and exposed to miracidia of the Mekong *Schistosoma,* penetration was observed only with *Hydrorissoia hospitalis, Manningiella expansa* Brandt, *Pachydrobia bavayi,* and *Manningiella rolfbrandti* Temcharoen. But in all cases snails died before infections matured.

Penetration of a miracidium into a snail is no criterion for considering that species an intermediate host. Miracidia readily penetrate inappropriate snails (Chernin, 1968; Chernin & Perlstein, 1969) and even non-molluscan entities (Upatham, 1972; Upatham & Sturrock, 1973). Likewise, finding immature sporocysts is not sufficient evidence that a species is the first intermediate host for the Mekong schistosome. The reports (Brandt, 1968, 1970) were unworthy of publication because of insufficient data.

In 1968 and 1969, the World Health Organization sent a team consisting of a parasitologist and a malacologist to determine the extent of schistosomiasis in the Mekong Basin. Studies at Khong Island yielded *Schistosoma* sp. from dogs (Iijima et al., 1971). Lo et al. (1971) studied 10 species of operculate snails from Khong and found 26 types of larval trematodes including six furcocercous types. However, none of the latter resembled cercariae of human schistosomes. They suspected *Pachydrobia bavayi* to be the likely intermediate host for the Mekong schistosome.

The United States Agency for International Development granted the Smithsonian Institution funds in 1970 to undertake an analysis of water-borne disease problems in the Mekong River. A cooperative program was established with the Faculty of Tropical Medicine of Mahidol University, Bangkok.

The Smithsonian-Mahidol team placed emphasis on collecting hydrobiid snails from the Mekong and challenging the various species with miracidia of the Mekong schistosome. Miracidia were hatched from eggs passed by dogs from Khong Island infected with the Mekong schistosome. Also, snails from populations of various hydrobiids were crushed and examined to detect infections. As a result of these experiments, *"Lithoglyphopsis" aperta* was found to be a suitable first intermediate host of the Mekong

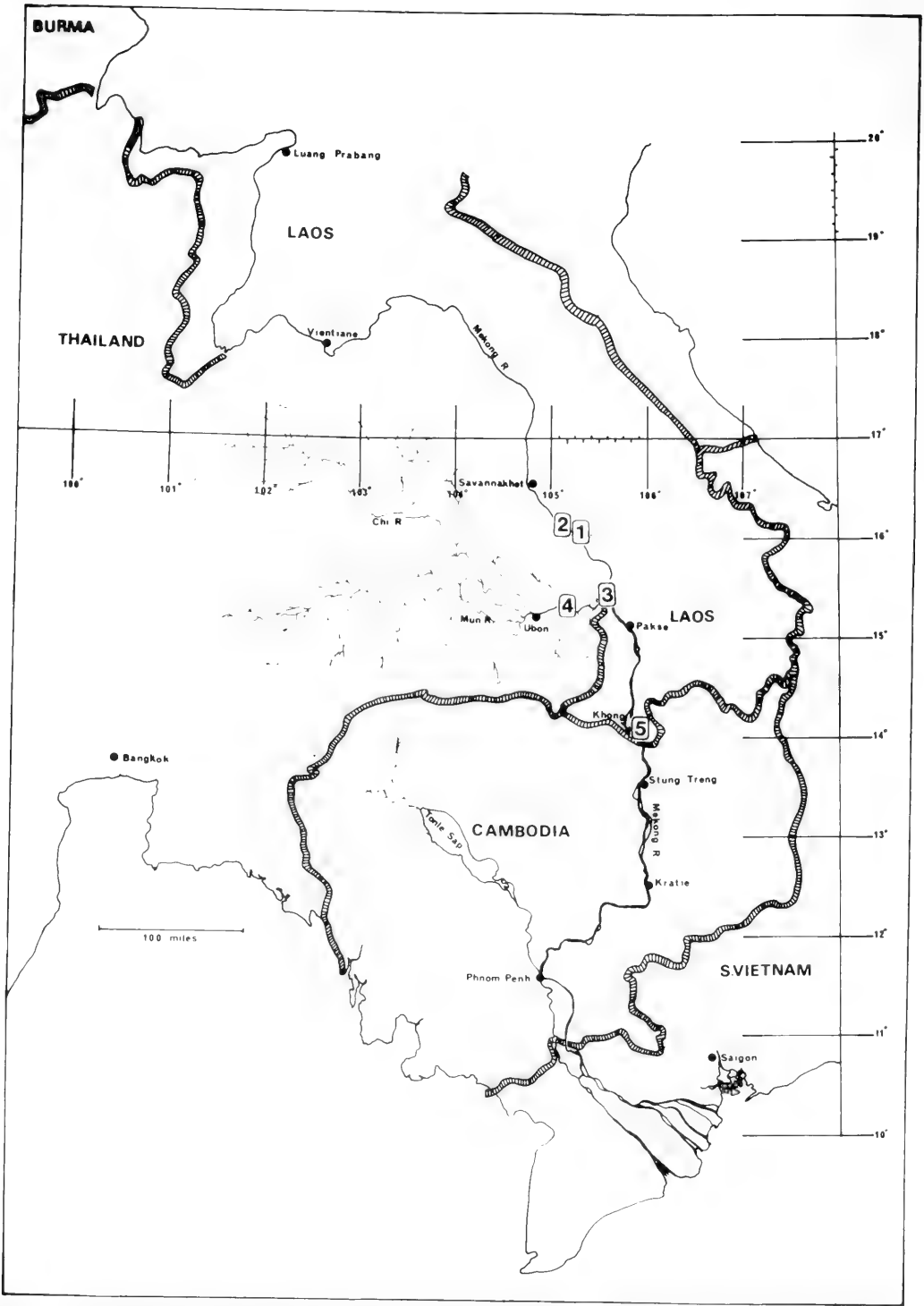


FIG. 1. Localities along the Mekong River where *"Lithoglyphopsis" aperta* has been collected. Alpha and gamma races have been collected together at localities 1 and 5. Beta race snails have thus far been found only at locality 4. Gamma race snails predominate at localities 2, 3 and 5.

schistosome (Harinasuta et al., 1972; Sornmani et al., 1973). Naturally infected snails were found at Khong Island near Ban Xieng Wang (Kitikoon et al., 1973).

LOCALITIES, DISTRIBUTION, AND HABITATS

Localities

Snails collected for this study came from the 5 localities shown on Fig. 1. Collections were, for the most part, made in March and April, 1973. One collection was made in June. The sites were selected because they were accessible by road (many parts of the Mekong River are accessible only by boat), and because they were known to be suitable localities for numerous triculine species (Brandt, 1968, 1970; Temcharoen, 1971).

A. Thailand, Ubon Ratchathani Province
   1. 2.5-3.0 miles below Khemarat Town, Ban Khee Lek (= Ban Khi Lek); 16°2′30″N, 105°17′30″E. Mekong River.
   2. Several miles above Khemarat. Mekong River.
   3. Ban Dan Village, small islands at mouth of the Mun River, 15° 19′15″N, 105°30′45″E. Mekong River.
   4. Amphoe Pibun Mangsahan, large island E. of Pibun Mangsahan (= Ban Sai Mun); 15°14′45″N, 105°17′30″E. Mun River.

B. Laos, Sithandone Province
   5. Khong Island; 14°7′30″N, 105° 51′45″E. Mekong River.

Type-locality

The type-locality of *"Lithoglyphopsis" aperta* Temcharoen (1971) is Ban Na on Khong Island, Laos (Fig. 2, site 4). Temcharoen (1971) gave the distribution as being between Cham Passak (3/4 the distance between Khong Island and Pakse (Fig. 1) and Sompamit Falls near Khone, Laos, at the Cambodian border).

The holotype and paratypes by original designation are in the collections of the Senckenberg Institute, Frankfurt-am-Main, Germany. One of us (Davis) has studied the types. The holotype conforms to the alpha race snails discussed in this paper. Part of the paratype series (SMRL 16282) is housed in the Academy of Natural Sciences of Philadelphia (ANSP 320061). Some of these paratypes are badly worn. Temcharoen (1971) collected only shells.

Distribution (Fig. 1)

Temcharoen's and our collections show that *"L." aperta* is distributed in the Mekong River from a point several miles upstream from Khemarat to the Cambodian border, i.e. Sompamit Falls near Khone. This is a distance of 154 direct miles, 200 river miles. We suspect the species lives as far S as Kratie, Cambodia, because schistosomiasis has been reported from this river town and because the hydrobiid fauna extends at least to Kratie. If this is eventually verified, the species is distributed over 300 river miles.

Habitats and Life Cycle

Rainy and dry seasons are pronounced in the Mekong Basin. Heavy rains usually begin about early June. The river rapidly rises 40 to 60 ft and becomes a raging torrent. With the cessation of rains in November to December, it falls again most markedly in late November. Lowest water levels occur in April.

Young *"L." aperta* are found in mid to late March. Snails having 3.0-3.5 whorls and a shell 1.3 mm long have been found on 22 March 1973 near Khemarat. By late April the majority of the snails have 4.0-4.5 whorls and a length of 2.8 mm. Full maturity occurs from late May probably to late June, coinciding with the beginning of the rainy season.

At locality 1, Ban Khee Lek, rock outcroppings and islands cause the river to narrow. Gamma race snails were found on 14 April 1973, massed on sticks and rocks at 0.5-1.5 m depth in moderate to swift current near the Thailand shore side of islands at Ban Khee Lek. Later, on 5 June, the water had risen and the current was swifter. Alpha race snails were found underneath the rocks at about 1.5-2.0 m. Only 1 gamma race snail was found in this collection.

A pure population of gamma race snails was collected upstream from Khemarat on 5 June (locality 2). Snails were under rocks in about 2 m of water. They could only be collected by diving for rocks. The snails were only half-grown.

The channel running between the 2 principal islands at locality 3 was about 1 m

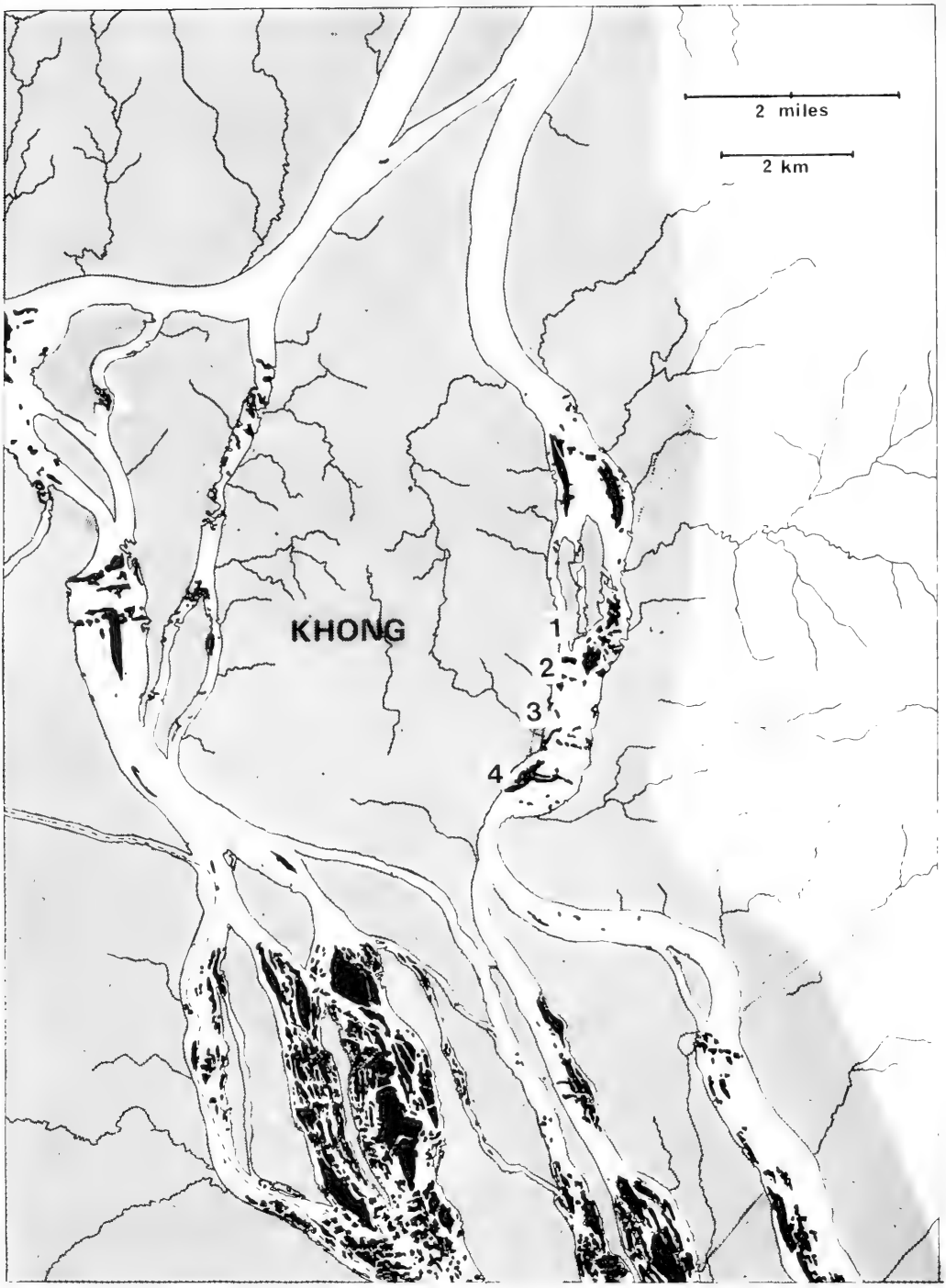


FIG. 2. Khong Island with 4 collection sites frequently visited for *"Lithoglyphopsis" aperta* and other hydrobiids. 1. Laotian Army camp; 2. infection site at a section of Muong Khong (Khong Town) called Ban Xieng Wang; 3. Government Hospital and Thomas Dooley House; 4. Ban Na, the type-locality. Note the thousands of small islands (in black) at the southern end of Khong Island through which the river percolates during the dry season.

deep at low water. There was little current. Collections on 18 April 1973, yielded thousands of half-grown gamma race snails. These were massed on sticks, clam shells and rocks. A few alpha race snails were found with 3.5-5.5 whorls. Mud-coated egg capsules of *"L." aperta* were plastered on the shells of some of the snails.

Both alpha and gamma races have been collected from Khong Island. The gamma race predominates along the eastern side of the island. Snails are found in shallow water on rocks, leaves and sticks which rest on the mud substrate. Occasionally snails are found in the mud itself, under rocks. Water may be only 4-5 cm deep, with little or no current, and warm, i.e. 26° to 27°C. The shallow environment is quickly changed with the onset of heavy rains when a strong current develops. Then snails are found beneath rocks. Habitats are totally inaccessible at the height of the rainy season.

Four collection sites on Khong Island are shown in Fig. 2. *"L." aperta* was found at all 4 sites. Human infections with the Mekong schistosome appear to be derived principally from site 2 where people frequent the shallows to bathe, wash clothes, and defecate. The center of Khong Town is less than 1/4 mi SW of site 2.

METHODS

Anatomical data on the alpha race were derived from snails collected at locality 1 (Fig. 1) on 5 June 1973. Shells of this population have the Academy of Natural Sciences of Philadelphia catalog number 331949. Data on the gamma race were obtained from snails collected at Khong Island (locality 5) and maintained in the laboratory of the Faculty of Tropical Medicine in Bangkok until they matured. Dissections of alpha race snails were done in Philadelphia; gamma race snails were studied in Thailand. No shells of the laboratory-maintained gamma populations survived to be catalogued after the anatomical study. During the course of this anatomical study, no live beta race snails were seen.

Anatomical procedures employed are those given in detail by Davis & Carney (1973). Aqueous solutions of neutral red and methylene blue were used as vital stains for studying the reproductive system. The nervous system was dissected out in a dilute solution of Bouin's fixative. Radulae were mounted unstained in CMC-10, a non-resinous mounting medium.

Confirmation of duct openings was made by studying histological sections. The serial sections were cut at 7 μm and stained in hematoxylin and eosin.

MORPHOLOGY

Shell

A summary of shell traits distinguishing the 3 races is given in the first 5 traits listed in Table 11.

ALPHA RACE (Table 1, Fig. 3A-B).—

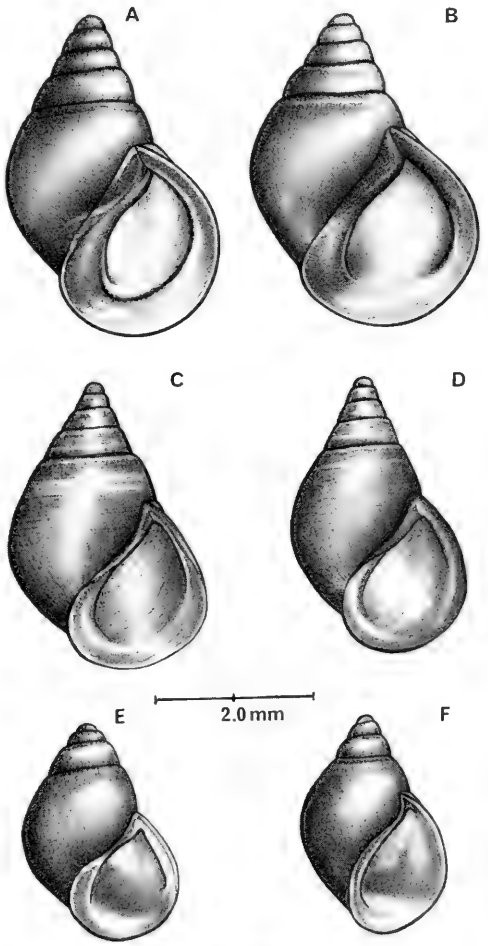


FIG. 3. Shells of the 3 races of *"Lithoglyphopsis" aperta.* A-B, alpha race, ANSP catalog number 331949; C-D, beta race, ANSP no. 332316; E-F, gamma race, ANSP no. 330925.

TABLE 1. Analyses of shells from living animals of alpha race *"Lithoglyphopsis" aperta* (measurements in mm).

Shell trait**	Females		Males		S.D.	P
	$\bar{X}$	Sd	$\bar{X}$	Sd		
6.0 whorls (No. = 9)						
Length	4.20	0.11	4.03	0.10	N	>0.05
Width	2.79	0.08	2.72	0.16	N	>0.05
Length of body whorl	3.15	0.11	2.81	0.30	S	<0.05
Aperture length	2.62	0.09	2.49	0.10	S	<0.01
Aperture width	2.13	0.09	1.96	0.10	S	<0.01
6.5 whorls (No. = 8)						
Length	4.22	—	4.18	0.06	N*	—
Width	2.81	—	2.90	0.27	N*	—
Length of body whorl	3.26	—	2.90	0.22	S*	—
Aperture length	2.69	—	2.60	0.08	N*	—
Aperture width	2.19	—	2.03	0.08	S*	—

*Probably, only 2-3 shells of 6.5 whorl females were found.
**Shells were destroyed after measurement to procure the animals for anatomy. Remaining shells in The Academy of Natural Sciences of Philadelphia, no. 331949.
N, not significantly different.
No., number of shells measured.
P., probability level.
S, significantly different.
Sd, standard deviation.
S.D., significant difference.
$\bar{X}$, mean.

Shells of mature animals possess 6.0-6.5 whorls and are 4.20 ± 0.11 mm long. Other shell dimensions are given in Table 1. The whorls are shouldered and increase regularly in size. Some young have a concave outline for the first 3 or 4 whorls. There is no spiral microsculpture. Sculpture consists of fine axial growth lines.

The body whorl is inflated; the aperture is pyriform, produced adapically like a beak. A distinct crease or groove runs from the adapical limit of the peristome into the shell following the contour of the body whorl. The peristome is complete and edged with brown periostracum. The inner lip is expanded over the base of the shell; it is often wide, sharp at the end and keel-like. The outer margin of the aperture, 0.63 ± 0.06 mm in width, is transparent and glistening. Internal to that margin the aperture is chalky white.

Young shells are translucent and yellowish; adult shells are opaque and white. The periostracum is olivaceous. Shells with 6.0 whorls dominate the adult population. In this size class males and females differ significantly in length of body whorl, aperture length and width.

BETA RACE (Table 2, Fig. 3C-D).—Shells of mature animals have 6.0-6.5 whorls and are significantly smaller than those of the alpha race. The greatest length observed for an uneroded shell with 6.5 whorls is 3.81 mm. Shells also differ from those of the alpha race in having flat-sided whorls or a smoothly concave spire outline. The suture is very shallow. Raised spiral microsculpture is pronounced in 58% of the shells, faint in 25% and absent in 17% (40 specimens).

GAMMA RACE (Table 2, Fig. 3E-F).—Animals mature with a shell primarily of 5.5 whorls; few reach 6.0 whorls. Females taken from Khong Island and maintained in the laboratory for several months matured with an average shell length of 2.93 mm (standard deviation, 0.16 mm; standard error of the mean, 0.06 mm). An insufficient number of males was available for comparison.

Living mature animals have thus far not been collected and preserved in the field to enable accurate shell measurements. Several collections of dead shells were made at Khemarat (locality 1). The shells were collected in pockets in the river where currents had deposited them. Their position with regard to living immature snails suggested that they were of the same population but of a previous generation. Data from 2 of these populations are given in Table 2. Shell apices were so badly eroded that shell lengths were not measured. Mature shells

TABLE 2. Shell dimensions of beta and gamma race *"Lithoglyphopsis" aperta.* Males and females are mixed.

Whorls	Length	Width	Lbw	Lap	Wap
Beta Race—ANSP 332316+					
Complete Shells					
6.0	3.44	2.00	2.63	1.88	1.31
6.5	3.81	2.56	2.94	2.31	1.81
Eroded Shells					
6.0 est. (No.=8)	——*	2.23 ± 0.13	2.68 ± 0.10	2.06 ± 0.13	1.52 ± 0.12
6.5 est. (No.=11)	——	2.46 ± 0.11	2.95 ± 0.04	2.34 ± 0.07	1.73 ± 0.06
Gamma Race—ANSP 330925					
5.5 to 6.0 (No.=7)	——	2.29 ± 0.17	2.68 ± 0.18	2.11 ± 0.22	1.66 ± 0.19
Gamma Race—ANSP 327506					
5.0 est. (No.=7)	——	1.91 ± 0.20	2.32 ± 0.12	1.76 ± 0.17	1.44 ± 0.14

*Eroded, measurement useless.
±, Standard deviation.
+, catalog number in The Academy of Natural Sciences of Philadelphia.
Lap, length of aperture. No., number of shells measured.
Lbw, length of body whorl. Wap, width of aperture.

were readily recognized because of the fully developed aperture with pronounced parietal shelf and keel-like appearance of the edge of the expanded inner lip. Estimates of whorl number were derived from the 1 or 2 nearly entire shells.

As seen in Table 2, from Fig. 3E-F, and from the data on laboratory-reared specimens, there is great variability in shell size of mature gamma race snails. This has been observed both within and between populations. As seen in Table 2, the length of body whorl and width of gamma race snails (ANSP 330925) equaled those of eroded beta race snails with the same estimated whorl number. Most populations of gamma race snails seen, however, have been significantly smaller. Influence of sex on shell size in the beta and gamma races has yet to be determined.

The whorls are slightly convex and thus there is only a shallow suture. The base of the inner lip meets the base of the shell in a sharp keel. The translucent outer margin of the aperture is 0.25-0.30 mm wide; the area within the aperture is the usual chalky white. There is a tendency in this race to have a less developed beak-like adapical projection of the aperture and a less developed parietal shelf as compared with alpha race snails. Shells have no spiral microsculpture.

External Features

The gamma race is unique among Mekong River hydrobiids by having 4 black pigment spots on the mantle which are clearly seen through the body whorl when the animal is withdrawn (Fig. 4F), or emerged and moving on the substrate (Fig. 5). Approximately 10% of the population has a variable pigment pattern such as shown in Fig. 4A-E.

By contrast, the alpha and beta races are devoid of pigment spots. Instead, alpha race snails have a dusting of melanin on the mantle over the region of the ctenidium. In some individuals the pigment is denser on the mantle following along each gill leaflet.

Head, neck, and foot regions of the races studied are not dusted with black melanin or with yellow-orange pigment as are many Mekong River hydrobiids. The dorsal aspect of the head-snout is rather transparent; there are a few scattered white granules about the medial aspect of the eye, on the snout, and along the tentacles (Fig. 9). There is no omniphoric groove or suprapedal fold (illustrated in Davis, 1967) on the lateral aspect of the head-foot region. One can readily see the pigmented cerebral and pleural ganglia through the epithelium when studying the dorso-lateral aspects of the head (Fig. 9).

Tentacles are elongate and broadly rounded at their tips. They are lightly ciliated and without pronounced tufts or clusters of cilia. The sole of the foot is white. When extended, its length varies from 2.5-2.9 mm. At rest, the length is about 2.0

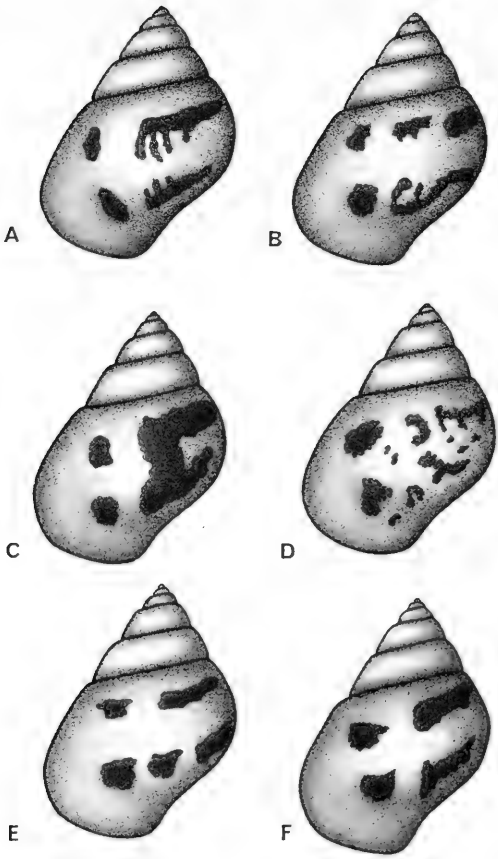
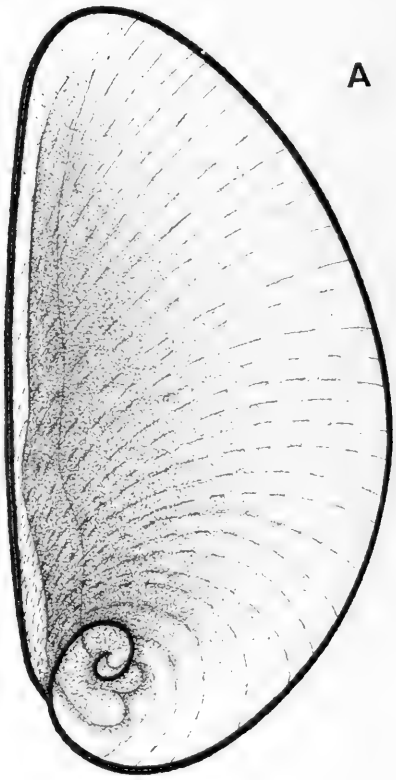


FIG. 4. Variation in pigment patterns on the mantle as seen through the shell of gamma race snails.

mm. The posterior end is rounded; the anterior end is blunt, 1.2 mm wide, and has the typical rissoacean mucous slit across the entire front edge (see Davis, 1966, fig. 4a). Viewing the antero-dorsal edge of the foot, one can observe, in alcohol-preserved specimens, characteristic mucous glands (Fig. 6B). The mid-central gland is largest of these. Results of histological studies of these glands are given in Fig. 16F-I. The central gland projects farthest upward into the pedal haemocoel. The highly secretory nature of the gland cells is seen particularly well in Fig. 16G. These glands, which pour their mucous secretions into the anterior pedial slit, are more pronounced in this species than in other taxa in which these glands have been studied, i.e. *Tricula* and *Oncomelania hupensis*.

The dorsal aspect of the stomach and digestive gland are densely pigmented with melanin. Salmon pink granules give the posterior areas of the living animal, especially the digestive gland, a pink sheen.



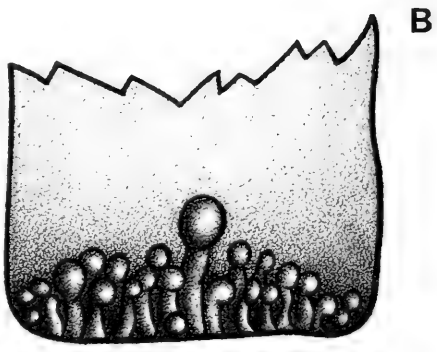


FIG. 6. A. Operculum, 1.20 mm long, from a gamma race individual. B. Glands along the anterior edge of the foot as seen (dorsal view) through the epithelium of an alcohol-preserved specimen. Note that the central gland is longest. See Fig. 16, F-I.

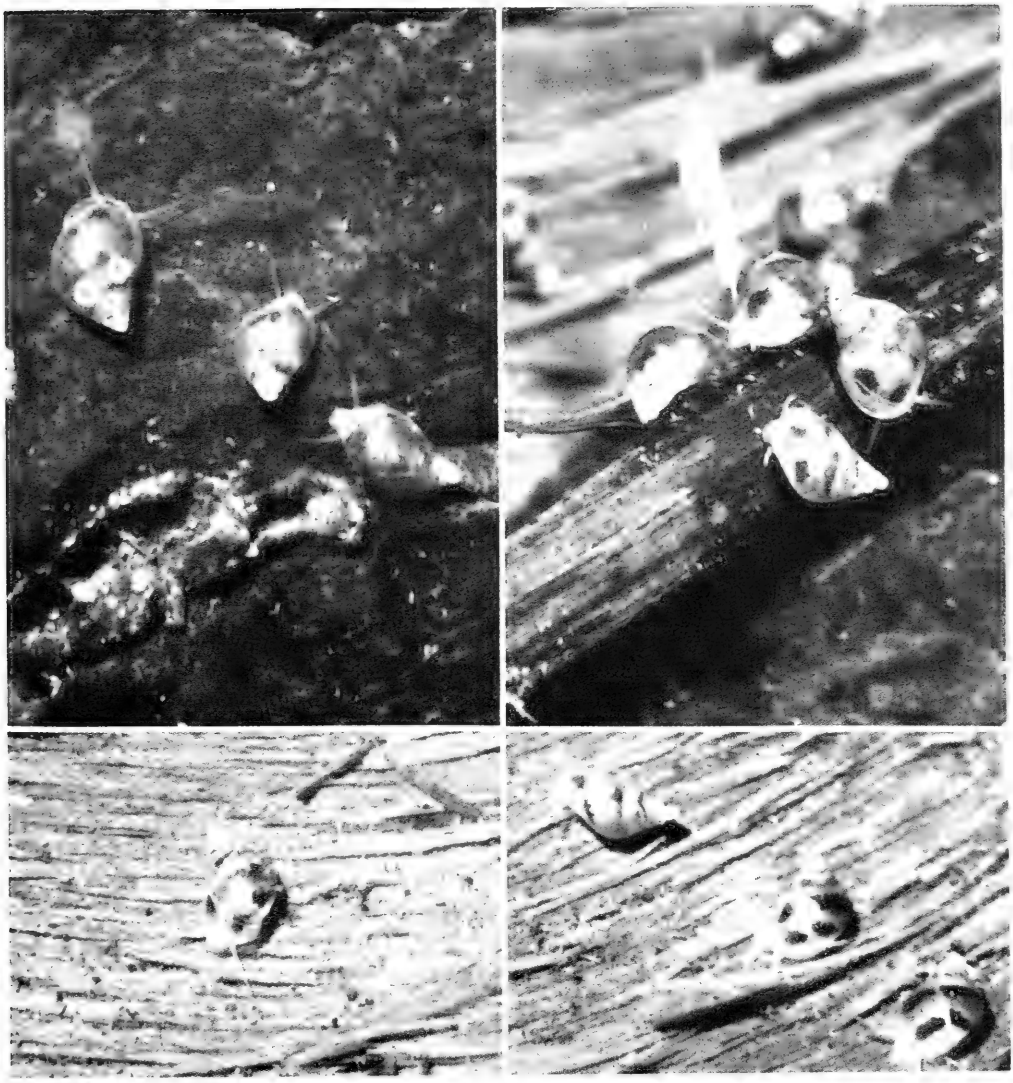


Fig. 5. Gamma race snails crawling over the substrate.

Operculum (Fig. 6A)

The operculum is thin, corneous and paucispiral. The nucleus is eccentric, nearly marginal. In gamma race snails, the left posterior margin spirals out over the columellar edge of the operculum. Growth striations are very faint. Dimensions are given in Table 3.

The operculum of alpha race snails differs slightly from that of the gamma race in that the edge of the operculum has a smooth contour, i.e. the growth spiral from the nucleus does not extend out beyond the columellar edge. As seen in Table 5, the operculum is larger than that of the gamma race, a correlate of greater shell size.

Mantle Cavity (Figs. 7, 9)

Structures in the mantle cavity are typically rissoacean. There is sexual dimorphism in the number of gill filaments; males have fewer (Tables 3-4). The length of the row of gill filaments is 1.83 mm ± 0.47 in the gamma race and 2.10 mm ± 0.17 in the alpha race. Correlated with this is the greater number of gill filaments in the alpha race (Tables 3-5).

TABLE 3. Dimensions (mm) or number of non-neural organs and structures of gamma race *"Lithoglyphopsis" aperta.*

Organ or structure		No.	$\bar{X}$	Sd	Range
Operculum	L	5	1.20	0.01	1.18-1.22
	W	4	0.68	0.03	0.68-0.70
Gill filaments					
males		4	26.8	6.07	20-34
females		9	35.7	2.17	32-40
Buccal mass	L	1	0.60	—	—
Osphradium	L	2	0.85	—	0.80-0.90
	W	1	0.14	—	—
Prostate	L	3	1.33	0.15	1.20-1.50
	W	1	0.56	—	—
Verge	L	3	2.03	0.20	1.85-2.25
Pallial oviduct	L	3	1.73	0.32	1.50-2.10
	W	1	0.34	—	—
Bursa copulatrix	L	3	1.09	0.10	1.00-1.20
	W	2	0.31	—	0.30-0.32

L, length. W, width.
No., number of snails. $\bar{X}$, mean.
Sd, standard deviation.

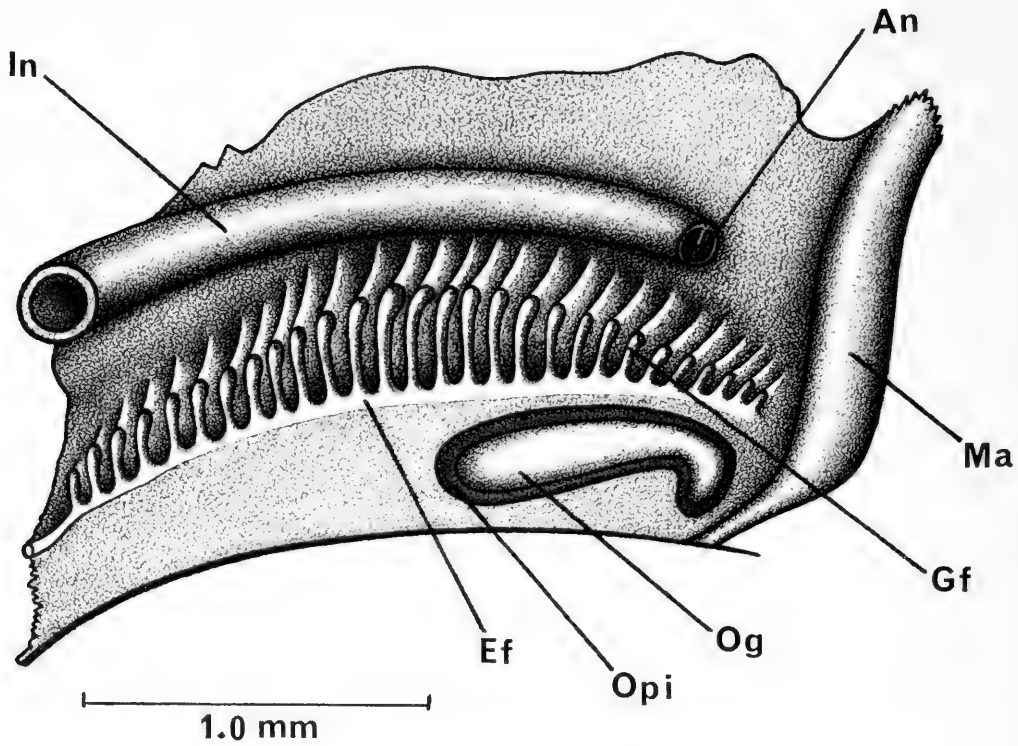


FIG. 7. Anterior end of the mantle cavity opened to reveal the relationships of the intestine, ctenidium, osphradium and mantle edge. **An**—anus; **Ef**—efferent branchial vessel; **Gf**—gill filament of the ctenidium; **In**—intestine; **Ma**—mantle edge; **Og**—osphradial ganglion; **Opi**—osphradial pit.

TABLE 4. Dimensions (mm) or numbers of non-neural organs and structures of alpha race *"Lithoglyphopsis" aperta.*

Organ or structure		No.	$\bar{X}$	Sd	Range
Operculum	L	6	1.62	0.09	1.48-1.72
	W	6	0.92	0.06	0.85-1.02
Gill filaments					
males		10	43.6	3.66	38-48
females		4	49.8	1.50	48-51
Osphradium	L	4	1.01	0.08	0.96-1.14
	W	3	0.21	0.06	0.16-0.29
Prostate	L	8	1.18	0.25	0.85-1.45
	W	8	0.36	0.08	0.21-0.48
Verge	L	8	1.63	0.33	1.16-2.42
Gonad	L	9	1.96	0.39	1.57-2.42
(m)	W	4	0.44	0.06	0.41-0.48
(f)	L	3	0.61	—	0.61-
Digestive gland	L	12	2.96	0.57	1.82-3.63
(m + f)	W	9	0.70	0.15	0.48-1.02
Pallial oviduct	L	6	2.26	0.14	2.06-2.42
	W	6	0.29	0.20	0.15-0.68
Bursa copulatrix	L	7	0.84	0.20	0.61-1.09
	W	7	0.16	0.07	0.12-0.29

f, female. No., number of snails. $\bar{X}$, mean.
L, length. Sd, standard deviation.
m, male. W, width.

TABLE 5. Statistical comparison of lengths or numbers of selected structures of the alpha and gamma races of *"Lithoglyphopsis" aperta.*

Organ or structure	Significant difference	P.	Alpha race has greater (G) lengths or numbers	Difference is correlated (+) with larger size of alpha race
Operculum	+	0.01	G	+
Gill filament no.				
males	+	0.01	G	+
females	+	0.01	G	+
Osphradium	+	0.01	G	+
Prostate	—	0.10		
Verge	—	>0.01		
Pallial oviduct	—	>0.01		
Bursa copulatrix	—	>0.01		

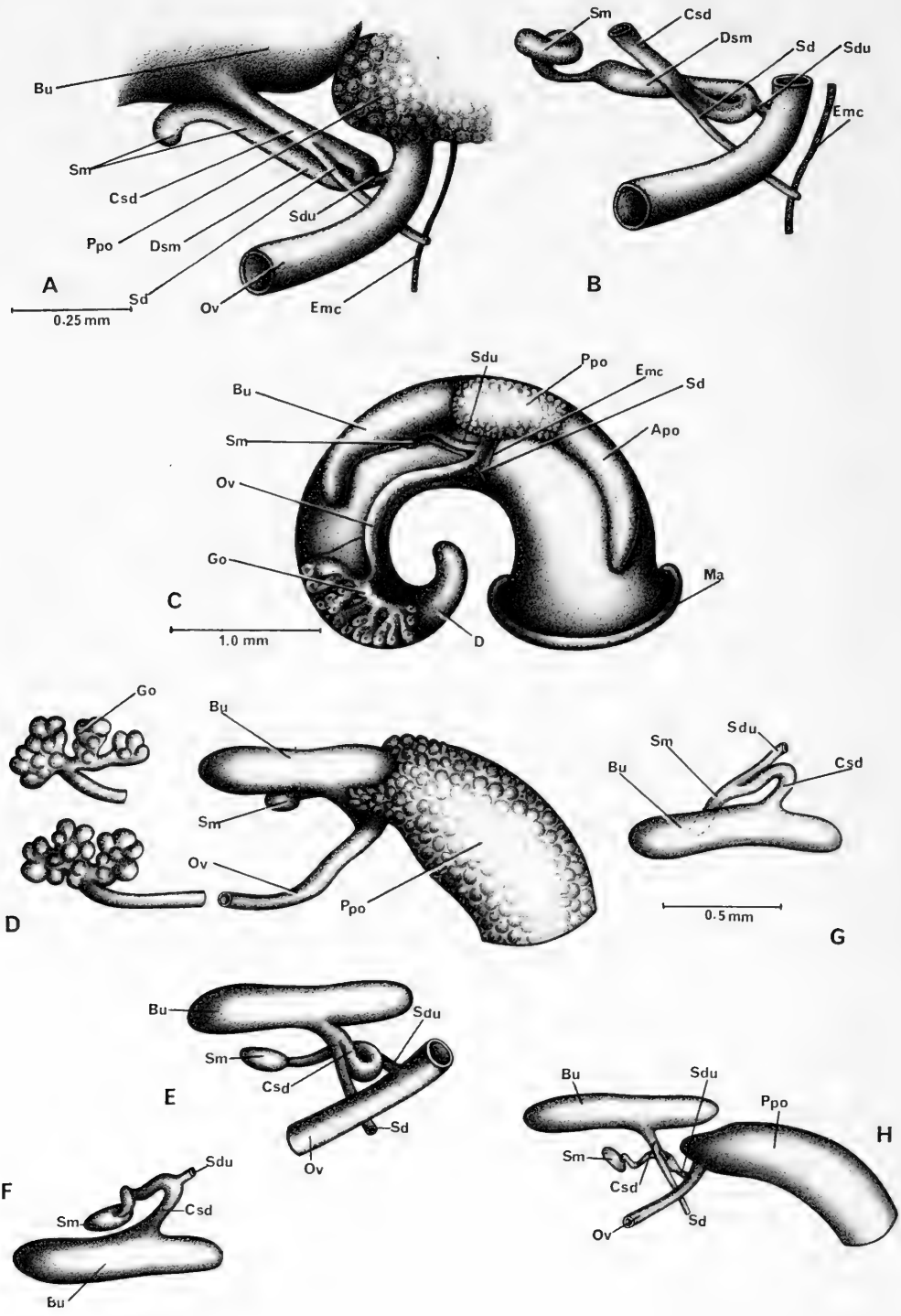
+, yes.
—, no.
P, probability level.

The histological structure of the ctenidium is shown in Fig. 16C-E. The basal shaft of each gill filament is unciliated while the expanded distal end of each filament has coarse, thick cilia. The overall structure is typical for the Hydrobiidae.

The osphradium is elongate and cylindrical. It begins at the mantle collar and extends back along the ctenidium. Its length is 46% the length of the ctenidium (measurements from 10 individuals).

Digestive System Exclusive of Radula (Figs. 7, 9, 10, 15, 16)

The ground plan is typically hydrobiid. A cross section through the head close to the mouth reveals the typically dorsal food channel (Df) and jaws (Ja) composed of chitinous plates (Fig. 15B). Posterior to the short stretch of oral tube is the buccal mass containing the odontophoral apparatus (Fig. 15C). The longitudinal section shows the


Bu
Sm
Csd
Ppo
Dsm
Sdu
Sd
Ov
Emc
A
0.25 mm
B
Sm
Csd
Dsm
Sd
Sdu
Emc
C
Sdu
Ppo
Emc
Sd
Bu
Sm
Apo
Ov
Go
Ma
D
1.0 mm
Go
Bu
Sm
Ov
Ppo
D
Sdu
Sm
Bu
Csd
0.5 mm
G
Bu
Sdu
Sm
Csd
Sd
Ov
E
F
Sdu
Sm
Csd
Bu
H
Bu
Sdu
Ppo
Sm
Csd
Ov
Sd

entire radula from tip of radula sac to the bending plane over the cartilage (Ca). The salivary glands, a single pair, are unbranched simple tubes which run back dorsal to the nerve ring. Ducts of the gland are shown in Fig. 16A.

The esophagus has a pronounced dorsal food groove bounded on each side by a pronounced dorsal fold. Just posterior to the cerebral ganglia several smaller folds appear in the region where the dorsal food groove is located (Fig. 15D) and the right dorsal fold becomes less pronounced until it resembles the other folds of the esophagus. Thus, only the left dorsal fold persists, as a structure twice the size of the other 8 to 9 folds. Torsion in the gut, which occurs just posterior to the cerebral ganglia, is seen by following the rotation of the left dorsal fold to a ventro-lateral position.

The stomach is like that described in *Oncomelania, Pomatiopsis,* and other hydrobiids. The topography of the ventral surface is shown in Fig. 10A, B, D. The section shown in Fig. 15E shows both the entrance of the deeply crypted esophagus (Es) into the stomach and passage from the stomach to the digestive gland (Ed).

The intestine leaves the stomach at the left ventro-lateral aspect of the style sac, coils as a U-shaped tube over the end of the style sac, and then doubles back to run anteriorly to the end of the mantle cavity. There is no slit-like communication between the style sac and the intestine. The whole length of the U-shaped portion of intestine contains an extremely pronounced typhlosole (Fig. 15G). This highly ciliated structure undoubtedly serves to send a constant stream of particles to the fecal pellet compressor located in the sharp bend where the intestine begins to run anteriorly.

The extremely strong and well-organized cilia of the style sac are shown in Fig. 15F (top row of cells) in contrast to the less organized cilia lining the roof of the anterior chamber of the stomach which slightly overlies the style sac (lower row of cells).

Radula (Fig. 11, gamma race female)

The radula is typically taenioglossate. Radular dimensions and counts of teeth are given in Table 6. Numbers of cusps on each of the 4 different teeth are quite variable, as documented in Table 7. The most generalized formulas for the alpha and gamma races are given in Table 8.

Although its shell is longer, the alpha race has a significantly shorter radula than the gamma race. There are, however, significantly more teeth on the radula (Table 6). The width of the base of the central tooth of the alpha race is greater.

No alpha race snail has been found with a central tooth formula of $\frac{4\text{-}1\text{-}4}{5\text{-}5}$, but this formula predominates in 67% of the radulae of gamma race snails. The most characteristic features of this species are: 1) the 4 to 7 cusps on the basal lateral angle of the central tooth; 2) the largest basal cusps of the

FIG. 8. Female reproductive system. The whole reproductive system in the uncoiled snail (minus head) is shown in Fig. 8C. The ventral surface of the snail is exposed. Key reference points are the anterior end of the mantle cavity (Ma) and the posterior end of the mantle cavity (Emc). The reproductive system is drawn as seen through the epithelium of the living animal.

A-B. Expanded views of the ducts associated with the bursa copulatrix (Bu) and posterior pallial oviduct (Ppo) with the snail's epithelium and kidney tissue removed. Variation in twisting of the U-shaped duct running from the bursa to the seminal receptacle is shown.

A-C were drawn from gamma race snails. D-H were drawn from alpha race snails.

D-F. The tissues of the posterior pallial oviduct shown in D are stripped away in E to reveal the interrelationships of ducts. In F, the bursa was rotated 180° to expose the nature of the coiling of the duct of the seminal receptacle and the origin of the sperm duct (Sdu).

G. The bursa rotated as in F but in this individual the seminal receptacle is a blind duct and the sperm duct is very elongate, arising near the seminal receptacle instead of the usual position at the end of the duct of the seminal receptacle.

H. An immature individual. Note the positional relationship of the anterior end of the bursa copulatrix. and the pallial oviduct. Compare with Fig. 17 C-E.

Figs. 8A and B are at the same scale, and so are Figs. 8D-H.

Apo—anterior pallial oviduct;
Bu—bursa copulatrix;
Csd—common sperm duct;
D—digestive gland;
Dsm—duct of the seminal receptacle;
Emc—posterior end of the mantle cavity;
Go—gonad;
Ma—anterior end of the mantle;
Ov—oviduct;
Ppo—posterior pallial oviduct;
Sd—spermathecal duct;
Sdu—sperm duct;
Sm—seminal receptacle.

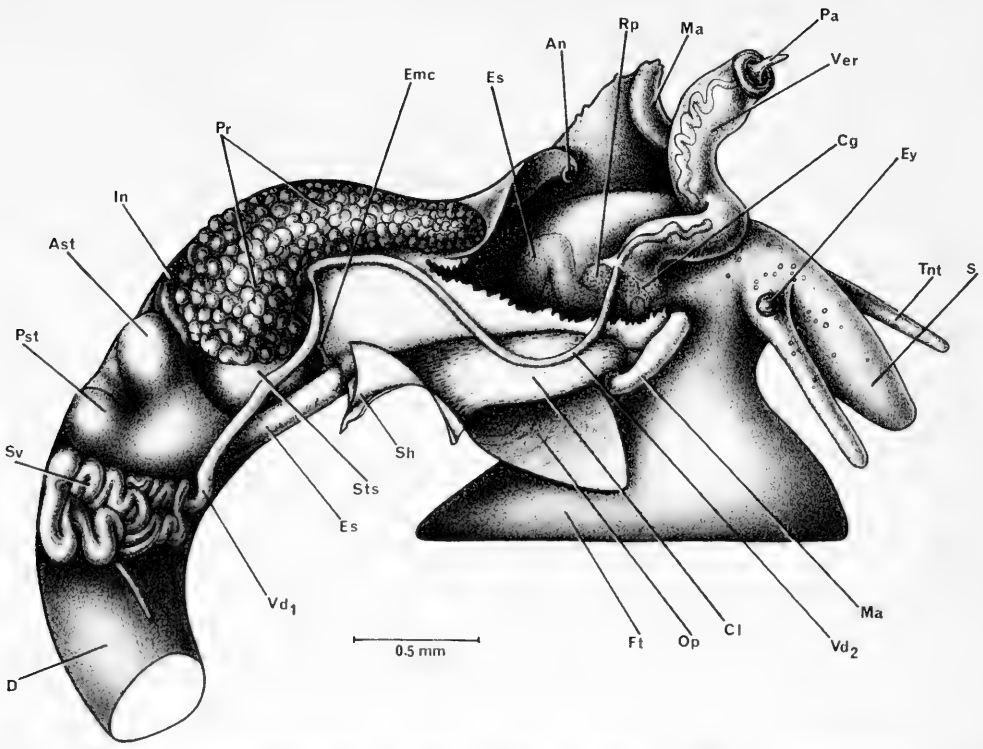


FIG. 9. Male snail of the gamma race uncoiled to reveal the ventral surface. The digestive gland (D) has been partially removed and the gonad is not shown. The mantle cavity has been opened to show the anus (An), origin of the penis (Ver = verge), and structures readily seen beneath the epithelium of the neck such as the esophagus (Es), right pleural ganglion (Rp) and cerebral ganglion (Cg). Note that the prostate (Pr) overlies the posterior end of the mantle cavity (Emc) and that the seminal vesicle (Sv) consists of very heavy coils pressed against the posterior chamber of the stomach (Pst).

An—anus;
Ast—anterior chamber of the stomach;
Cl—columellar muscle;
Cg—cerebral ganglion;
D—digestive gland;
Emc—posterior end of the mantle cavity;
Es—esophagus;
Ey—eye;
Ft—foot;
In—intestine;
Ma—anterior edge of the mantle;
Op—operculum;
Pa—papilla;
Pr—prostate;
Pst—posterior chamber of the stomach;
Rp—right pleural ganglion;
S—snout;
Sh—shell;
Sts—style sac;
Sv—seminal vesicle;
Tnt—tentacle;
Vd_1—posterior section of the vas deferens;
Vd_2—anterior section of the vas deferens;
Ver—verge.

central tooth arise from the face of the tooth; 3) the central anterior cusp of the central tooth is flanked by 3 or more cusps, and 4) the lateral tooth usually has 4 or more cusps on the inner side of the dominant cusp.

Female Reproductive System (Fig. 8A-H)

The system is rissoacean in that there is an interrelationship of bursa copulatrix, seminal receptacle, and a bipartite pallial oviduct (i.e. albumen gland [Ppo] and capsule gland [Apo]). The reproductive system is shown in Fig. 8C in relation to the general body shape and regions. Points for orientation are the mantle edge (Ma), posterior end of the mantle cavity (Emc), and digestive gland (D).

When the living animal is pinned out to expose its uncoiled ventral surface and stained with neutral red, one observes an amazingly large bursa copulatrix (Bu), the pallial oviduct (Ppo and Apo), gonad (Go) and oviduct (Ov) extending to the posterior section of the pallial oviduct (Ppo). A vague

TABLE 6. A comparison of radular traits of alpha and gamma race *"Lithoglyphopsis" aperta* using 9 individuals of each.

Radular trait	alpha race $\bar{X}$	alpha race Sd	gamma race $\bar{X}$	gamma race Sd	S.D.	P.
Length*	0.41	0.016	0.65	0.04	S	<0.01
Width	0.06	0.002+	0.09	0.03	S	<0.01
No. rows of teeth	103.8	3.73	77.9	4.09	S	<0.01
No. rows forming	7.4	2.15	9.3	3.16	N	>0.10
Width of base of central tooth	0.031**	0.001	0.027	0.001	S	<0.01

* Measurements in mm.
** No. radulae = 10.
+, highly invariable width resulting in an extremely low standard deviation.
N, not significantly different.
P, probability level.
S, significantly different.
Sd, standard deviation.
S.D., significant difference.
$\bar{X}$, mean.

impression of a tube from the bursa copulatrix running towards the oviduct is seen. Careful dissection, with removal of membranes, kidney tissue, and excessive glandular tissue of the posterior pallial oviduct, reveals a unique arrangement of tubes (Fig. 8A-B).

Sperm enter the system from within the posterior recess of the mantle cavity (Emc) and travel in the spermathecal duct (Sd, called receptacular duct in Davis, 1968b) to enter the common sperm duct (Csd). The spermathecal duct is very pronounced and easily dissected to the end of the mantle cavity. Sperm then travel to the bursa copulatrix (Bu) or to the seminal receptacle (Sm). The spermathecal duct runs dorsal to, and at right angles to the oviduct.

The bursa copulatrix is unusual for a hydrobiid because of its great length and bulk. It is, on the average, 63% the length of the pallial oviduct in the alpha and gamma races. In *Tricula* it is 24-25% (Davis, 1968b); in *Oncomelania* it is 18-24% (Davis & Carney, 1973). The anterior end is, in mature animals, slightly overgrown by the filmy glandular tissue of the posterior pallial oviduct (Fig. 8C, D). In immature animals (Fig. 8H) the anterior end of the bursa is antero-lateral to the posterior end of the pallial oviduct.

Substructures of the bursa copulatrix and its relationship to the pallial oviduct in early development are seen in histological sections (Fig. 17 A-E). Internally, the bursa has highly secretory columnar cells. Vacuoles with secretory product dominate the cells and are seen from the basal nucleus to the point of disruption into the lumen (Fig. 17G). It is clearly seen in Fig. 17C-E that the anterior end of the bursa is anterolateral to the end of the posterior pallial oviduct. When the latter matures as the fully secretory albumen gland it will surround the anterior end of the bursa as shown in Fig. 8C, D.

There is a greater tendency in the alpha race (Fig. 8D) for the bursa to be deeply embedded in the mature albumen gland. Contrast the condition seen in the gamma race (Fig. 8C).

A pronounced key trait of this species is the U-shaped common sperm duct (Csd,

TABLE 8. Formulae for the most common cusp arrangements in *"Lithoglyphopsis" aperta.*

Tooth	Formula	% Radulae with formula
	Alpha race	
Central	$\frac{4(5)\text{-}1\text{-}(5)\text{-}4}{6\text{-}6}$	100
Lateral	5(6)-1-6	66
Inner marginal	18-21	100
Outer marginal	15-17	100
	Gamma race	
Central	$\frac{4\text{-}1\text{-}4}{5(6)\text{-}(6)5}$	89
Lateral	4-1-4(5)	89
Inner marginal	17-20	100
Outer marginal	15-17	100

TABLE 7. The various cusp arrangements in the 4 types of taenioglossate teeth from the radulae of 7 alpha race and 9 gamma race *"Lithoglyphopsis" aperta.*

Central (% of radulae)			Lateral (% of radulae)		
anterior cusps / basal cusps	alpha	gamma	Cusps	alpha	gamma
4-1-4 / 5-5	—	67	4-1-5	17	67
			4-1-4	—	67
4-1-4 / 6-6	57	56	5-1-6	50	—
			5-1-4	—	44
5-1-5 / 6-6	57	44	6-1-6	33	—
			4-1-3	—	22
5-1-5 / 5-5	29	44	3-1-5	—	22
			3-1-4	—	22
5-1-5 / 7-7	29	—	4-1-6	17	—
			4-1-7	17	—
3-1-3 / 5-5	—	33	5-1-7	17	—
			5-1-8	17	—
3-1-3 / 6-6	—	33	6-1-7	17	—
			5-1-5	17	11
3-1-3 / 7-7	14	—	7-1-6	17	—
			7-1-7	17	—
4-1-4 / 7-7	—	11	5-1-3	—	11
4-1-4 / 4-4	—	11			

Inner Marginal (% of radulae)			Outer Marginal (% of radulae)		
No. cusps	alpha	gamma	No. cusps	alpha	gamma
18	67	33	16	57	89
21	67	22	17	57	67
17	17	56	15	71	44
20	50	22	18	43	—
19	33	33	19	29	—
22	33	33	14	—	22
15	—	22	13	—	11
24	22	—	12	—	11
16	17	—			
23	17	—			
25	—	11			

FIG. 10. Male reproductive system. Alpha race, A-G; gamma race, H.

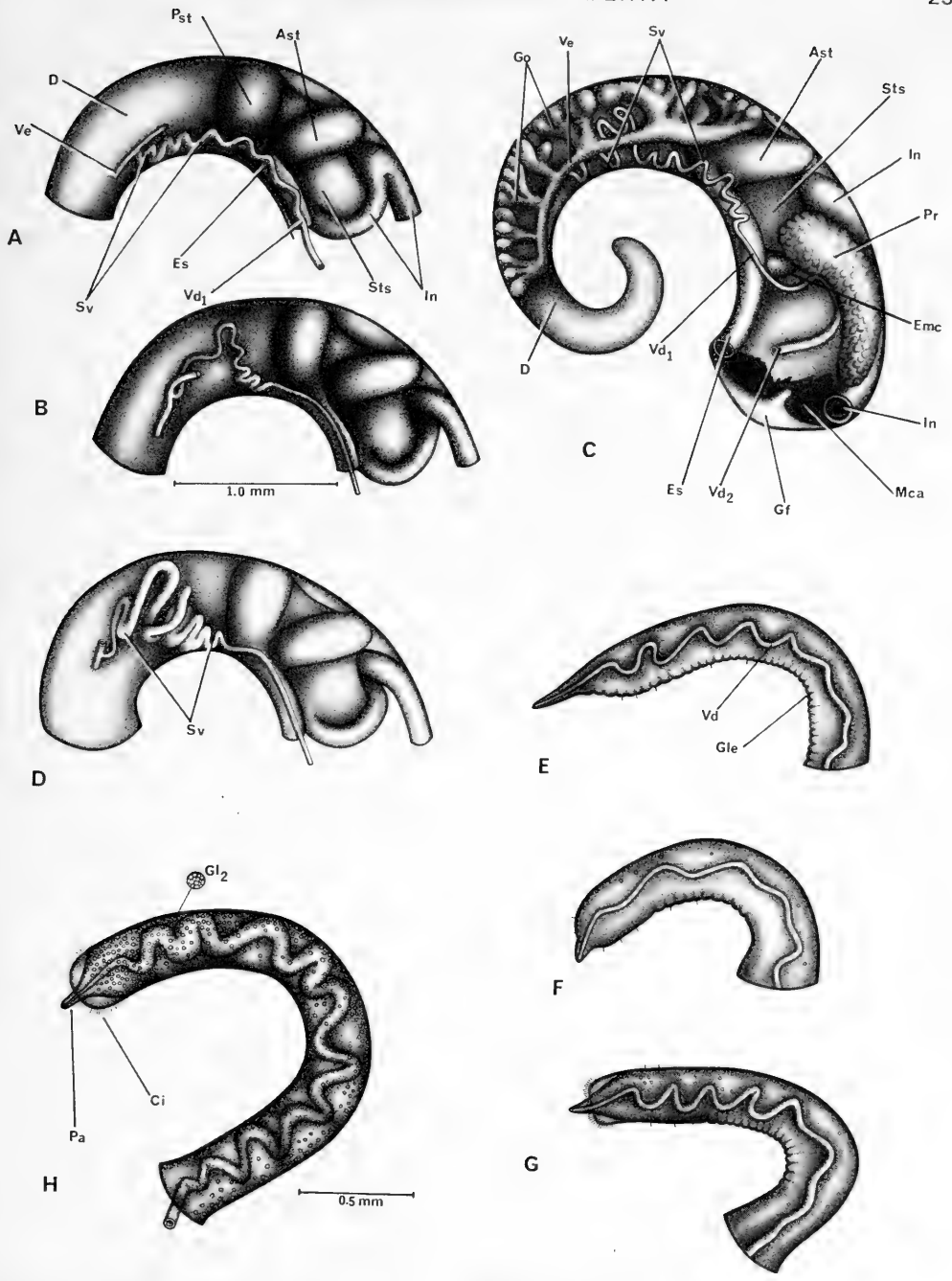
A, B, D. Variation in coiling of the seminal vesicle (Sv) shown from different individuals.

C. An uncoiled snail with the ventral surface exposed. The anterior end has been sliced off to reveal the mantle cavity (Mca), the intestine (In) and a gill filament (Gf). The loosely coiled seminal vesicle (Sv) is shown in relation to the gonad.(Go). Note that the anterior end of the gonad overlies the posterior chamber of the stomach.

E-G. Various stages in the development of the verge in alpha race snails. In E there is no papilla, only a slender prong without retractile musculature. In F there is an incipient papilla. Cilia are lacking in these early developmental stages although some solitary non-motile cilia are seen. Full development is shown in G, with a fully retractile papilla and ciliary bands.

H. Verge from gamma race snail with numerous $G1_2$ type glands, cilia and retractile papilla.

Figs. 10A-D are at the same scale, and so are Figs 10E-H.



Ast—anterior chamber of the stomach;
Ci—cilia;
D—digestive gland;
Emc—posterior end of the mantle cavity;
Es—esophagus;
Gf—gill filament;
Gle—glandular scalloped edge of the verge;
Gl_2—gland type 2 of the verge;
Go—gonad;
In—intestine;
Mca—mantle cavity;
Pa—papilla;
Pr—prostate;
Pst—posterior chamber of the stomach;
Sts—style sac;
Sv—seminal vesicle;
Vd_1—posterior section of the vas deferens;
Vd_2—anterior section of the vas deferens;
Ve—vas efferens.

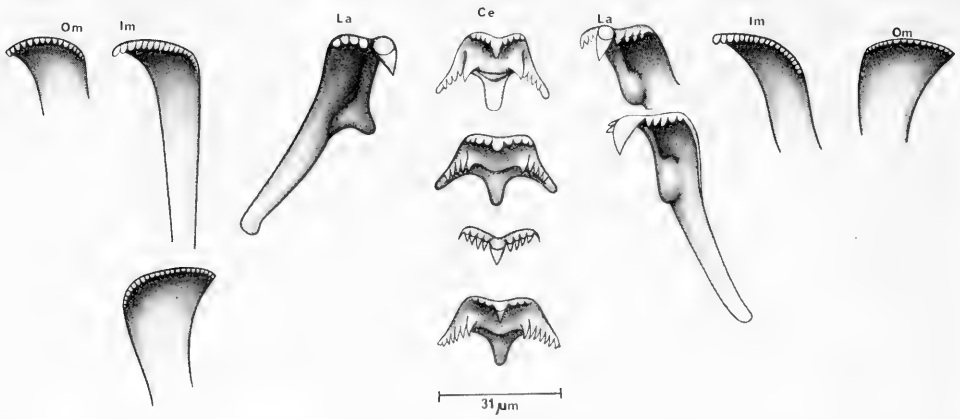


FIG. 11. Isolated teeth from the radula of gamma race *"Lithoglyphopsis" aperta* but arranged according to their relative position on the radular ribbon. The width of the central tooth at the base is, on the average, 31 µm (see Table 8). **Ce**—central tooth; **Im**—inner marginal tooth; **La**—lateral tooth; **Om**—outer marginal tooth.

Fig. 8A, B, E, G, H). The duct leaves the anterior end of the bursa as shown in histological section (Fig. 17C, D, H). The anteriorly directed arm of the U receives the spermathecal duct which opens directly into it, i.e. the spermathecal duct does not run as a tube-within-a-tube into the bursa. Near the bend of the tube, the sperm duct (Sdu) connects the common sperm duct with the oviduct (Fig. 8B).

The posteriorly directed arm of the common sperm duct (Csd) is the duct of the seminal receptacle. The whole of the U-shaped Csd is heavily ciliated as shown in Fig. 17F, I. The opening of the Csd into the seminal receptacle is shown in Fig. 17E, F, I, J. The Csd may be twisted in various ways as seen in Fig. 8A, B, E.

The seminal receptacle (Sm) is quite variable. In the gamma race the Sm may be nothing more than a continuation of the Csd (Fig. 8A). In the alpha race the simple condition is rarely seen. A simple tube-like seminal receptacle is usually correlated with an underdeveloped reproductive system (Fig. 8G). The seminal receptacle of the alpha race usually is a discrete sac-like structure clearly distinguished from the Csd (Fig. 8E, F, H). Histology of the seminal receptacle (Fig. 17E, F, J) reveals a simple unciliated cuboidal epithelium.

The posterior pallial oviduct (Ppo) appears highly glandular in gross dissection (Fig. 8C, D) and functions as the albumen gland. It is sharply set off from the smooth, firm anterior pallial oviduct (Apo) which functions as a capsule gland. The opening of the oviduct into the posterior pallial oviduct is shown histologically in Fig. 17D (pointer 1). The opening of the sperm duct into the oviduct occurs just before the latter enters the posterior pallial oviduct.

Histological analysis of the spermathecal duct (Sd) shows it to be an open ciliated duct from the Csd to the end of the mantle cavity (Sd, Fig. 17K). The Sd invariably passes dorsal to the oviduct. There is no pronounced musculature surrounding the Sd.

The ovary consists of 2 or 3 groups of lobes in both races (Fig. 8D). Oocytes can mature in the ovary before the ovary becomes greatly lobed (Fig. 17L). The characteristics of fully mature oocytes can be seen in Fig. 17N, O. The extremely dense nucleolus is noteworthy. No differentially stained cytoplasm was observed. Oil droplets were not pronounced.

Eggs leave the oviduct 1 at a time; they are coated with fine sand granules by the foot and subsequently attached to shells or other hard substrates.

The dimensions of organs of this system are given in Tables 3 and 4. The races do not differ significantly in lengths of pallial oviduct or bursa copulatrix (Table 5; $P > 0.01$).

Male Reproductive System (Figs. 9, 10)

The male reproductive system has the standard hydrobiid ground plan. The verge (Ver, Fig. 9) arises from the side of the neck to the right of the mid-line and behind the right tentacle. The living animal carries the

verge tightly coiled over the neck. It has no appendages. As shown in Figs. 9 and 10G, H, the mature verge has an eversible papilla. The anterior end is covered by cilia (Ci).

In alpha race snails a transition has been observed from a non-papillate verge to one with a fully eversible papilla. Fig. 18B, D, shows a longitudinal section through a mature verge. The vas deferens (Vd) is convoluted. Muscles (Ms) to retract the papilla (Pa) are fully developed.

The verge of some animals is relatively undeveloped and probably not functional although the prostate and testes are mature. As seen in Figs. 10E and 18I, the musculature to retract the papilla and cilia have not developed. The tip of the verge is drawn out and cannot be retracted. An intermediary stage has been observed (Figs. 10F and 18F) where the musculature is partially developed and cilia-bearing cells have begun to differentiate. The papilla, however, cannot be withdrawn.

Of the gamma race snails thus far seen, none had immature stages of papillar retraction or cilia.

The base of the verge is shown in Fig. 18G, H. The sections are through the verge just as it arises from the neck. In such genera as *Oncomelania* and *Tricula,* where very thick layers of circular muscles surround the vas deferens, one finds the ejaculatory duct in this region. No such layers were found around the basal vas deferens (Vd) of the verge of either race of *"Lithoglyphopsis" aperta*.

In gamma race snails the anterior end of the verge is packed with prominent $G1_2$-type glands (Fig. 10H; see Davis, 1967; Davis & Carney, 1973). These thin out along the convex curvature of the verge. Such glands are sparse in the verges of alpha race snails (Fig. 10E-G). The basal concave edge of the verges from gamma race snails is smooth and firm, indicating a low degree of glandular development in that region (Fig. 10H); it is crenulated and more glandular in alpha race snails (Fig. 10E-G). Glands in this crenulated area are $G1_3$-type, as illustrated in Davis, 1967; Davis & Carney, 1973.

The intra-verge vas deferens is central, thick, and undulating.

In both races the prostate (Pr, Figs. 9, 15A) overlies the posterior end of the mantle cavity. The posterior section is ventral to the style sac of the stomach so that the prostate hides the style sac from view when dissecting from the ventral side.

The seminal vesicle (Sv, Figs. 9, 10A-D, 18E) is differently arranged in the 2 races. In the gamma race it is a mass of heavy coils pressed against the anterior edge of the digestive gland and against the posterior edge of the stomach (Fig. 9). The length of the mass equals the diameter of the digestive gland (0.6-0.7 mm), while the width of the mass varies from 0.2-0.4 mm. The situation in the alpha race is shown in Fig. 10A-D. The coils of the seminal vesicle are loose and traverse the mid-ventral area of the digestive gland or the left ventro-lateral edge. While the condition of loose coils is seen in over 80% of the individuals, the condition shown in Fig. 10D is seen in some fully mature males of maximum size. Even in these cases, with the seminal vesicle swollen with sperm (Fig. 18D), neither the extent of coiling nor the position of the coils approaches those found in gamma race snails.

The gonad is similar in the 2 races (Go, Fig. 10C); it nearly fills the length of the digestive gland. There are 8-10 branches arising from the vas efferens. The anteriormost lobes expand anteriorly beyond the digestive gland and rest upon the ventral aspect of the posterior chamber of the stomach. The lobes drain into a vas efferens (Ve) from which the seminal vesicle (Sv) arises at about mid-gonad. The seminal vesicle may arise from a slightly more posterior position.

Histological sections of the gonad are given in Fig. 18A, E. It can be seen that the lobes are wide, 2 or 3 draining into the vas efferens. Although the females studied were not fertilized and many had immature reproductive systems, the gonads of the males were, for the most part, mature, i.e., loaded with spermatocytes, spermatids and clusters of ripe sperm. Sections of the loosely coiled seminal vesicle (Sv) are shown in Fig. 18D; the seminal vesicle is loaded with sperm.

Organ dimensions are given in Tables 3 and 4. The alpha and gamma races differ significantly in length of prostate but not in length of verge (Table 5).

Nervous System (Figs. 12-14)

The nervous system is typically hydrobiid. Measurements of the lengths of the primary neural structures are given in Table 9. The races are similar. Distinctive aspects of the nervous system of this species are:

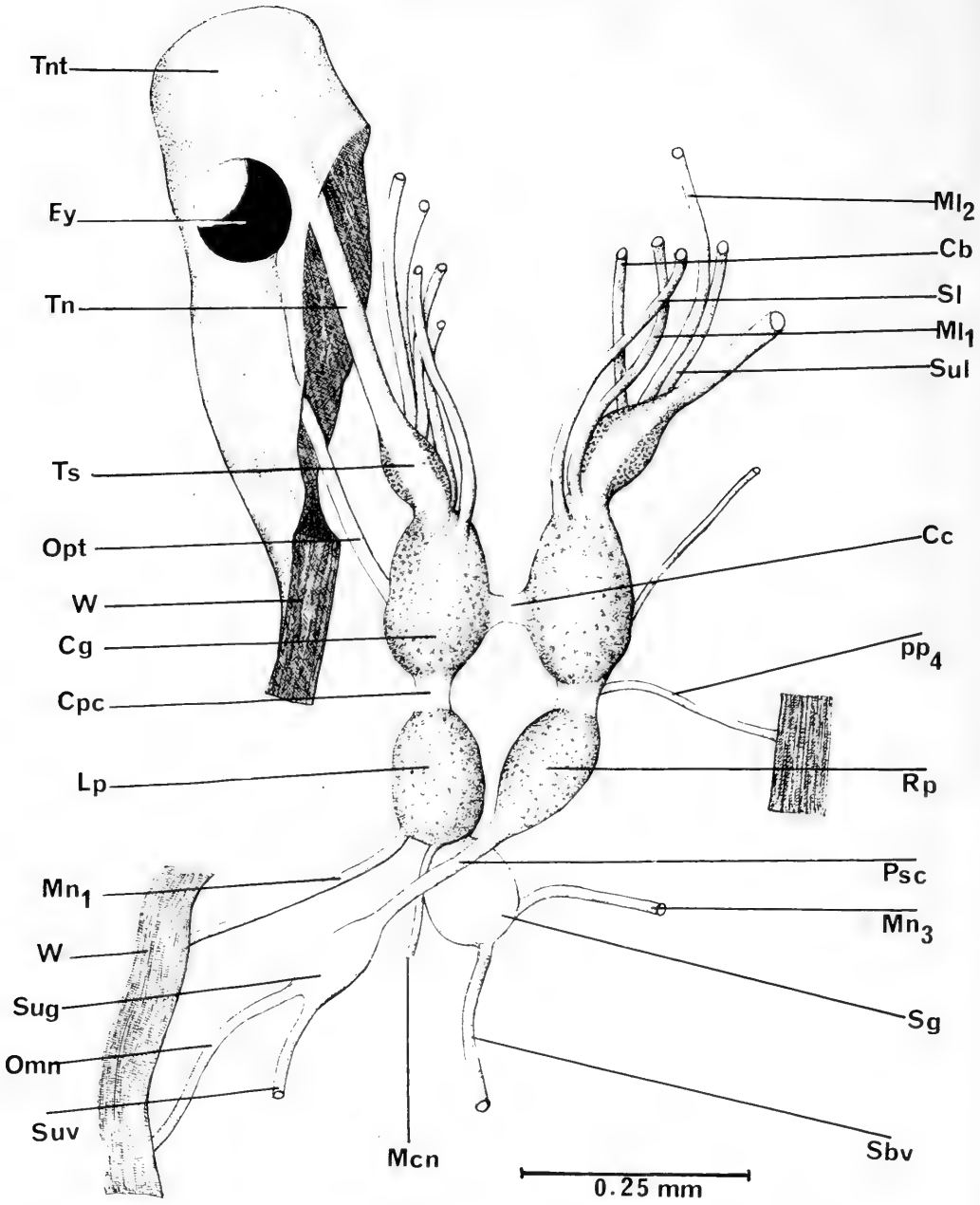


FIG. 12. Central nervous system seen from dorsal aspect. Note the great amount of melanin on the cerebral (Cg) and pleural (Rp and Lp) ganglia as well as the swelling of the tentacular nerve (Ts). A portion of the tentacle (Tnt) is shown.

1) There is heavy pigment on the cerebral and pedal ganglia, and usually also on the pleural ganglia. 2) The origin of the tentacular nerve is far anterior on the cerebral ganglion, and the tentacular nerves have prominent pigmented swellings (Ts, Fig. 12). 3) The pedal commissure is elongate compared with that known in other hydrobiids (Pc, Fig. 14). 4) In some individuals the pleural ganglia are not tightly fused against the cerebral ganglia, i.e. there is a distinct cerebro-pleural connective (Cpc, Fig. 12).

General intrapopulation variation in neural structures is similar to that discussed by Davis & Carney (1973).

Histological sections (Fig. 16A, B) reveal the darkly pigmented cerebral and pedal ganglia. Note the elongate pedal commissure (Fig. 16B). The statocyst (Stc) with a single statolith is shown in Fig. 16B.

A condition where the connectives are short relative to the size of the animal and size of the nervous system is considered an advanced or highly evolved state. This is based on the assumption that a condensed nervous system is more efficient in neuromuscular coordination and neuro-regulatory functions. By contrast, elongate connectives and a "loose" nervous system is considered primitive (Fretter & Graham, 1962).

Few drawings of hydrobiid and rissoid nervous systems exist where one can find a measurement scale or have confidence that the drawings were accurately proportioned. Where data seem accurate, taxa of the 2 families appear to vary considerably in the lengths of the osphradio-mantle nerve and the supraesophageal connective.

In order to assess the degree of condensation of the supraesophageal nerve tract, particularly the closeness of the supraesophageal ganglion to the right cerebral ganglion, we have established the length of the connective divided by the sum of the lengths of the right pleural ganglion, the pleuro-supraesophageal connective, and the supraesophageal ganglion. Data derived from this study and the literature are given in Table 10. The higher the value, the greater the relative length of the connective. As seen from the data, in spite of different shell lengths, taxa of the Pomatiopsinae and Triculinae thus far studied have rather similar values, ranging from 0.40 to 0.49. We consider this length intermediate. The connective of taxa placed in the Hydrobiinae varies from elongate in *Hydrobia* (50 to 63% of the total length) to short in *Lithoglyphus* (7%). The 1 species of *Rissoa* for which data were available has a connective of rather intermediate length. The connective of *Littorina littorea* (Linnaeus) is exceptionally elongate.

DISCUSSION

Races or Species?

The summary of differences between the 3 races of *"Lithoglyphopsis" aperta* given in Tables 5 or 11 or discussed in the text suggest that there may be 3 species. Differences include shell size and microsculpture, pigment patterns, radular traits, coiling of the seminal vesicle, and attributes of the verge.

Further weight is given to the hypothesis that the taxa are either species or subspecies when one considers factors of environment and differential rates of maturation. The beta race has only been found at 1 locality, the Mun River below Pibun Mangsahan. The Mun River flows into the Mekong River at the islands near Ban Dan, locations inhabited by gamma race *"L." aperta.* Living beta race snails were collected from the undersides of boulders in swift rapids at Ban Hin Lart near

Cb—cerebro-buccal connective;
Cc—cerebral commissure;
Cg—cerebral ganglion;
Cpc—cerebro-pleural connective;
Ey—eye;
Lp—left pleural ganglion;
Mcn—mid-columellar nerve;
Ml_1—median labial nerve—1;
Ml_2—median labial nerve—2;
Mn_1—mantle nerve—1;
Mn_3—mantle nerve—3;
Omn—osphradio-mantle nerve;
Opt—optic nerve;
pp_4—lateral nerve—4;
Psc—pleuro-supraesophageal connective;
Rp—right pleural ganglion;
Sbv—subvisceral connective;
Sg—subesophageal ganglion;
Sl—supralabial nerve;
Sug—supraesophageal ganglion;
Sul—sublabial nerve;
Suv—supravisceral connective;
Tn—tentacular nerve;
Tnt—tentacle;
Ts—swelling of the tentacular nerve;
W—left wall of the neck.

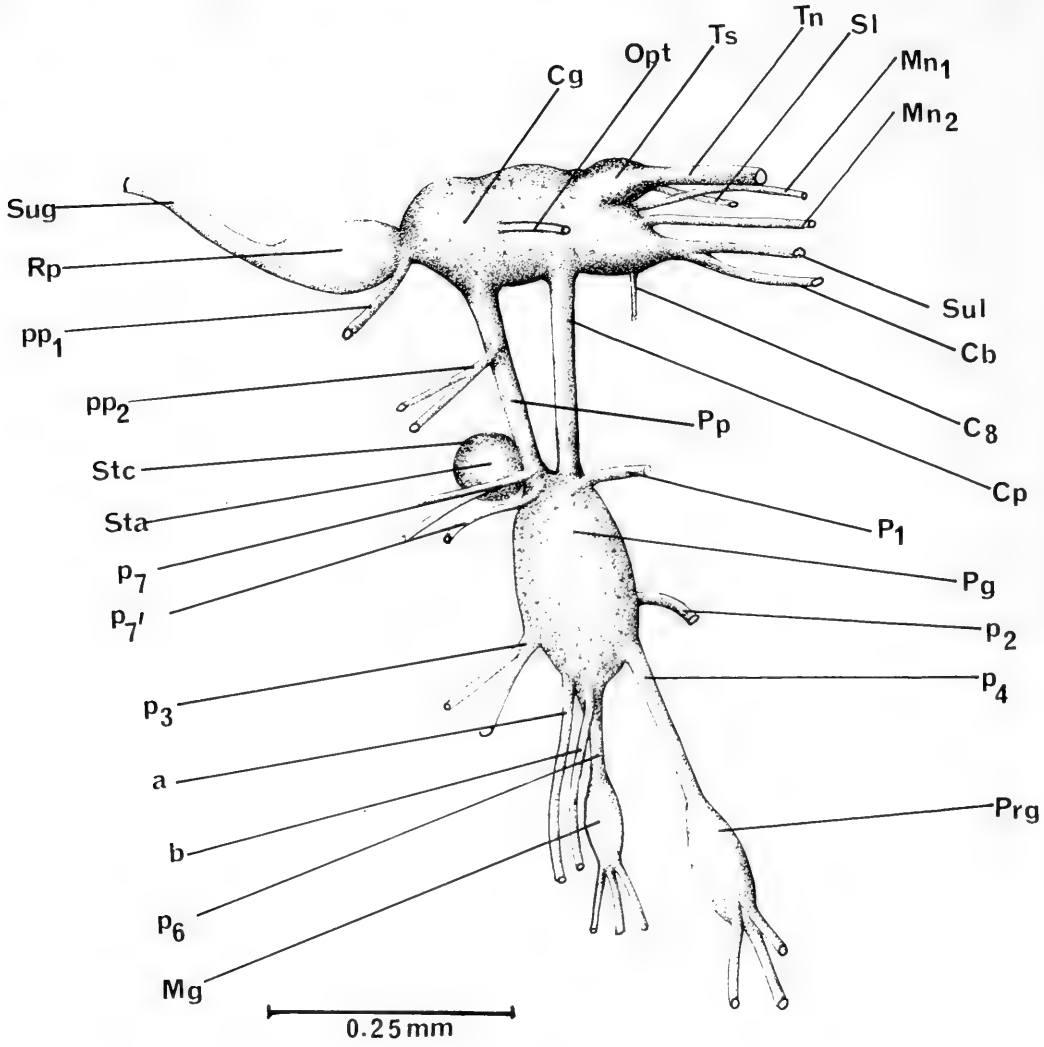


FIG. 13. Lateral view of the cerebro-pedal nerve complex.

a—nerve from p_6;
b—nerve from p_6;
c_8—cerebro-tensor nerve;
cb—cerebro-buccal connective;
Cg—cerebral ganglion;
Cp—cerebro-pedal connective;
Mg—metapodial ganglion;
Mn_1—median labial nerve—1;
Mn_2—median labial nerve—2;
Opt—optic nerve;
P_1—lateral retractor nerve;
P_2—nerve to antero-ventral wall of the pedal haemocoel;
P_3—major lateral nerve of the pedal ganglion;
P_4—propodial connective;
P_6—metapodial connective;
P_7—dorso-lateral pedal nerve;
P_7'—secondary dorso-lateral pedal nerve;
Pg—pedal ganglion;
pp—pleuro-pedal connective;
pp_1—lateral nerve—1;
pp_2—lateral nerve—2;
Prg—propodial ganglion;
Rp—right pleural ganglion;
Sl—supralabial connective;
Sta—statolith;
Stc—statocyst;
Sug—supraesophageal connective;
Sul—sublabial nerve;
Tn—tentacular nerve;
Ts—swelling of the tentacular nerve.

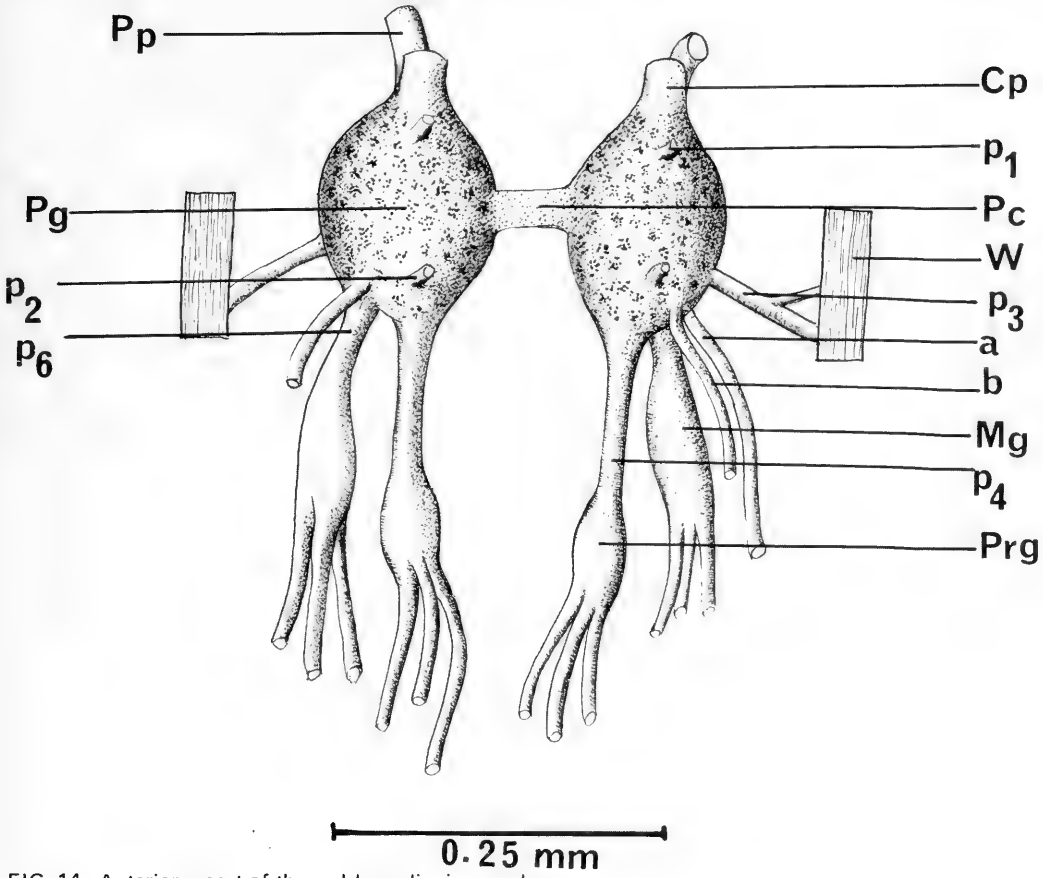


FIG. 14. Anterior aspect of the pedal ganglionic complex.

a—nerve from p_6;
b—nerve from p_6;
Cp—cerebro-pedal connective;
Mg—metapodial ganglion;
p_1—lateral retractor nerve;
p_2—nerve to antero-ventral wall of the pedal haemocoel;
p_3—major lateral nerve of the pedal ganglion;
p_4—propodial connective;
p_6—metapodial connective;
Pc—pedal commissure;
Pg—pedal ganglion;
Pp—pleuro-pedal connective;
Prg—propodial ganglion;
W—wall of the pedal haemocoel.

TABLE 9. Measurements (mm) of lengths of neural structures of gamma race *"Lithoglyphopsis" aperta*.

Structure	No.	$\bar{X}$	Sd	Range
Cerebral ganglion	4	0.23	0.02	0.20-0.24
Cerebral commissure	2	0.045	——	0.04-0.05
Pleural ganglia				
Right	4	0.12	0.02	0.10-0.14
Left	4	0.12	0.01	0.10-0.12
Pleuro-supraesophageal connective	4	0.16	0.04	0.10-0.20
Supraesophageal ganglion	4	0.12	0.02	0.10-0.14
Osphradio-mantle nerve	3	0.26	0.05	0.20-0.30
Subesophageal ganglion	3	0.11	0.01	0.10-0.12
Pedal ganglion	2	0.18	——	0.16-0.20
Pedal commissure	3	0.07	0.002	0.06-0.08

No., number of snails.
Sd, standard deviation.
$\bar{X}$, mean.

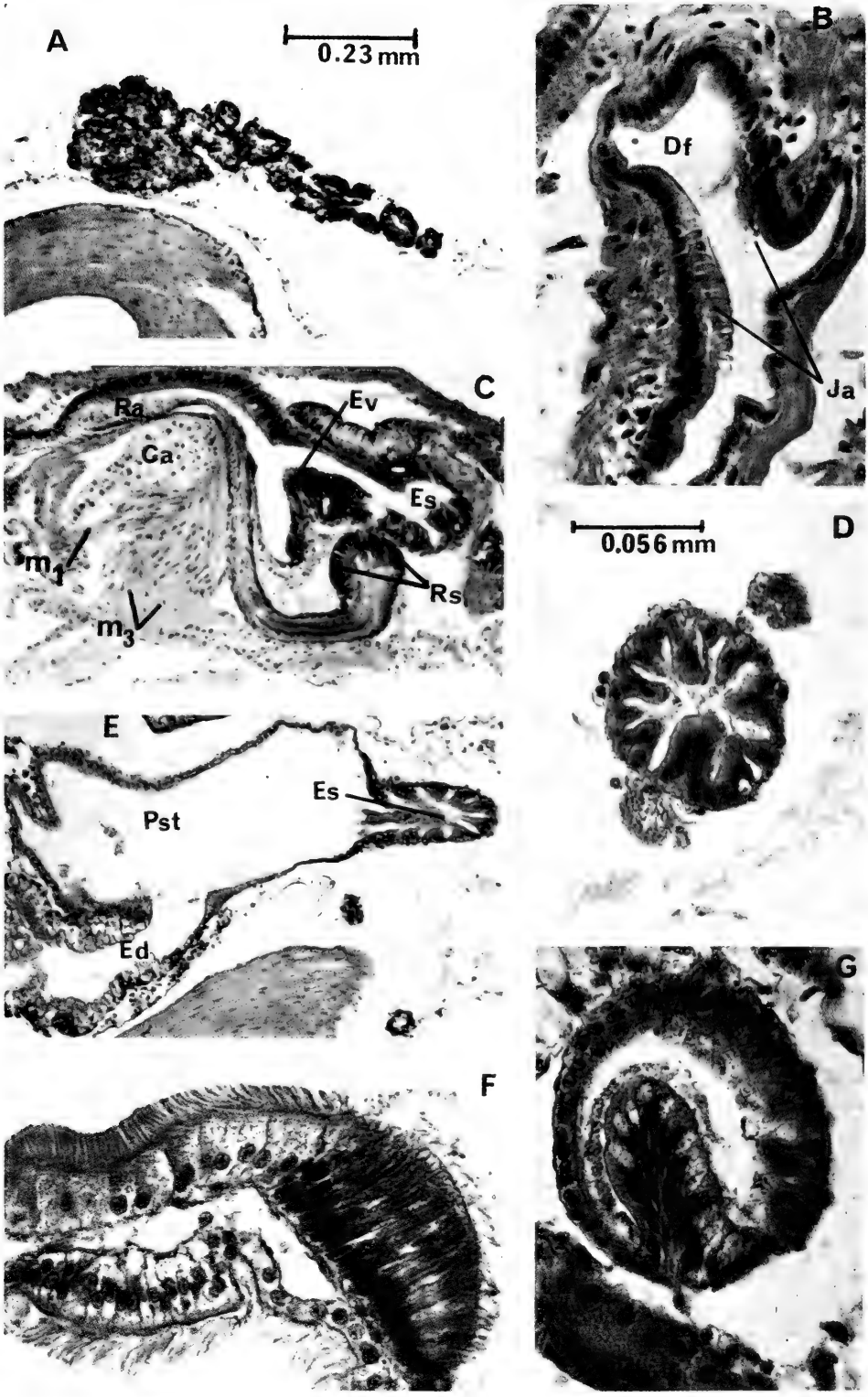

A
0.23 mm
B
Df
Ja
C
Ra
Ga
Ev
Es
m_1
m_3
Rs
D
0.056 mm
E
Es
Pst
Ed
F
G

TABLE 10. The RPG* ratio for selected hydrobiid, rissoid, and littorinid taxa.

Taxon	Reference	RPG
Hydrobiidae		
Triculinae		
Tricula bollingi Davis	Davis, 1968b	0.47
"Lithoglyphopsis" aperta Temcharoen	this paper	0.40
Pomatiopsinae		
Oncomelania hupensis chiui (Habe & Miyazaki)	Davis, 1968a	0.49
O. h. lindoensis Davis & Carney	Davis & Carney, 1973	0.40
Pomatiopsis lapidaria (Say)	Davis, 1967	0.42
Hydrobiinae		
Bythinella dunkeri (Frauenfeld)	Bregenzer, 1916	0.18
Hydrobia ulvae (Pennant)	Krull, 1935	0.63
Hydrobia ventrosa (Montagu)	Krull, 1935	0.50
Lithoglyphus naticoides (Fér.) Pfeiffer	Krause, 1949	0.07
Semisalsa dalmatica Radoman	Radoman, 1974	0.36
Rissoidae		
Rissoa inconspicua Alder	Johansson, 1939	0.32
Littorinidae		
Littorina littorea (Linnaeus)	Johansson, 1939	0.72
Littorina littorea (Linnaeus)	Fretter & Graham, 1962	0.84

*The length of the pleuro-supraesophageal connective divided by the sum of the lengths of the supra-esophageal ganglion, pleuro-supraesophageal connective and right pleural ganglion.

Ban Sai Mun on 26 April 1974. About 10% of the shells were full-sized as shown by the thickening of the outer lip of the shell. The reproductive systems, however, were too rudimentary for anatomical analysis. During this same low water period, alpha and gamma races were found at Khemarat and Ban Dan, clustered on sticks, shells and small stones in shallow quiet water or in a slow current. Gamma race snails collected from Ban Dan during the same week were only 1/3 grown; those collected from Khong Island in mid-May, 1974, were not yet 1/2 grown.

Alpha race snails collected from Khemarat in June 1973 had fully developed shells and nearly mature reproductive systems. Some males had reached sexual maturity. Gamma race snails from Khemarat, collected at the same time, were about half grown.

It thus appears that sympatry of the alpha and gamma races at several localities is made possible by a differential rate of growth and maturation which might create a barrier to cross breeding.

What are the factors that weaken the case for species status for the 3 taxa? There are several populations where snails were fully mature. These are most difficult to obtain, as full sexual maturity occurs in late May or in June after the rainy season has begun and populations are several meters under swift current. The data presented here for

FIG. 15. Histology of the male reproductive system (A) and digestive system (B-G).
A. Prostate in an early stage of development with the columellar muscle seen below.
B. Oral aperture sectioned through the jaws (Ja).
C. Buccal mass featuring the odontophore apparatus with cartilage (Ca), radula (Ra), radular sac (Rs) and intrinsic muscles m_1, m_3.
D. Cross section of the esophagus.
E. Section showing the entrance of the esophagus (Es) into the stomach, and the entrance of the stomach (Ed) into the digestive gland.
F. Heavily ciliated columnar cells lining the style sac are shown above while less densely organized cilia shown below line the roof of the anterior chamber of the stomach.
G. Cross section of the intestine with pronounced typhlosole.
Figs. 15A, C and E are at the same scale, and so are Figs. 15B, D, F, and G.

Ca—cartilage;
Df—dorsal food groove;
Ed—entrance of stomach to the digestive gland;
Es—esophagus;
Ev—esophageal valve;
Ja—jaws;
m_1—lateral cartilage tensor;
m_3—odontophore divaricator;
Pst—posterior chamber of the stomach;
Ra—radula;
Rs—radular sac.

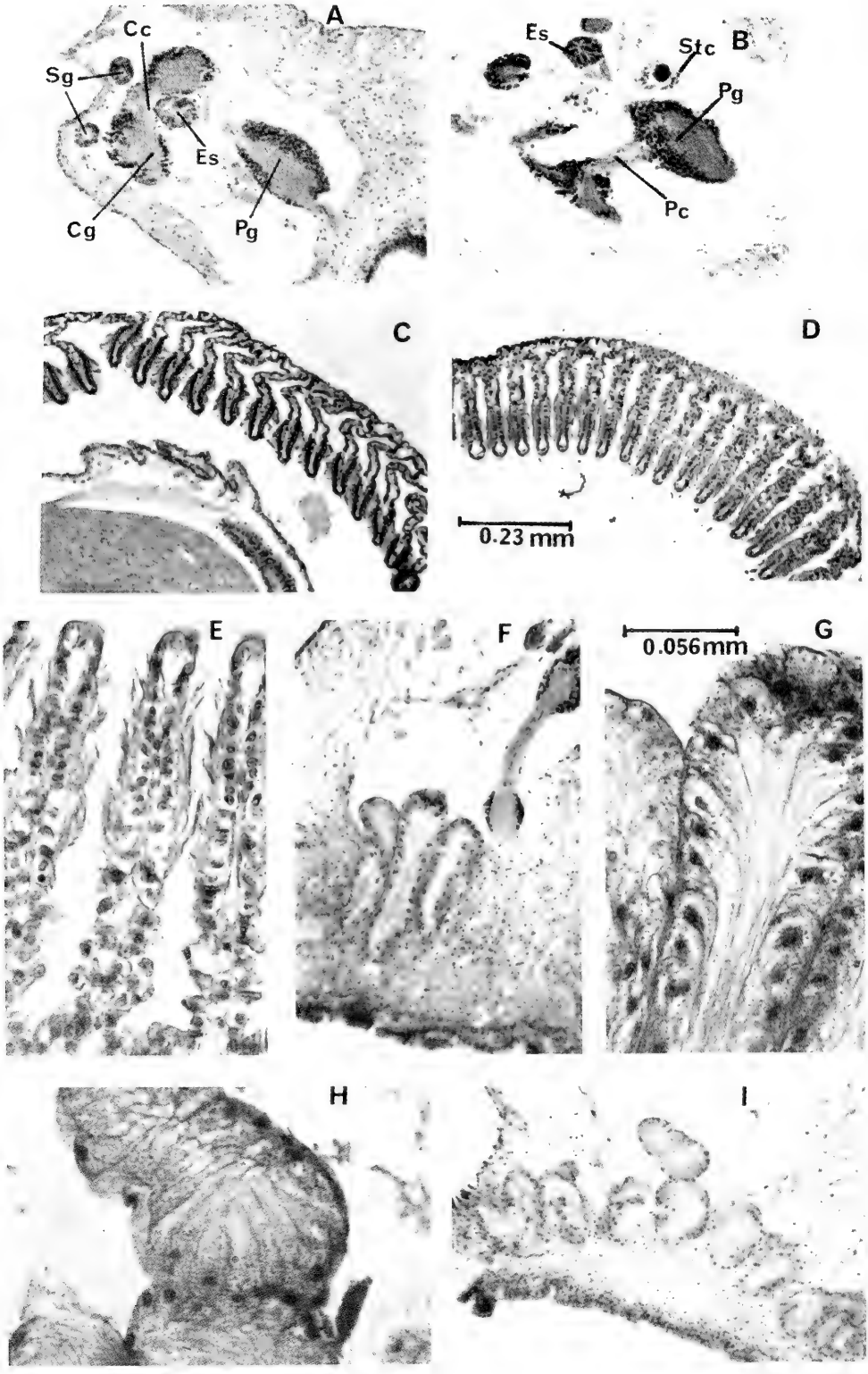

A
Cc
Sg
Es
Cg
Pg
B
Es
Stc
Pg
Pc
C
D
0.23 mm
E
F
0.056mm
G
H
I

TABLE 11. Summary of differences between the races of *"Lithoglyphopsis" aperta*. See text for details.

Trait	alpha	beta	gamma
1. Shell length (mm)	3.15-3.26	2.94-2.95	2.68
2. No. whorls	6.0-6.5	6.0-6.5	5.5-6.0
3. Concave outline to spire	–	+	–
4. Shouldered whorls	+	–	+
5. Shell microsculpture	–	+	–
6. Pigment spots on mantle	–	–	+
7. Contour operculum smooth and continuous	+	?	–
8. Length of ctenidium (mm)	2.10	?	1.83
9. No. gill filaments	44-50	?	27-36
10. Radular length (mm)	0.41	?	0.65
11. No. rows central teeth on radula	104	?	78
12. Width central tooth (mm)	0.031	?	0.027
13. Central tooth formula			
$\frac{5\text{-}1\text{-}5}{6\text{-}6}$	+	?	–
$\frac{4\text{-}1\text{-}4}{5\text{-}5}$	–	?	+
14. Seminal receptacle a discrete sac	+	?	–
15. Seminal vesicle a coiled mass against digestive gland	–	?	+

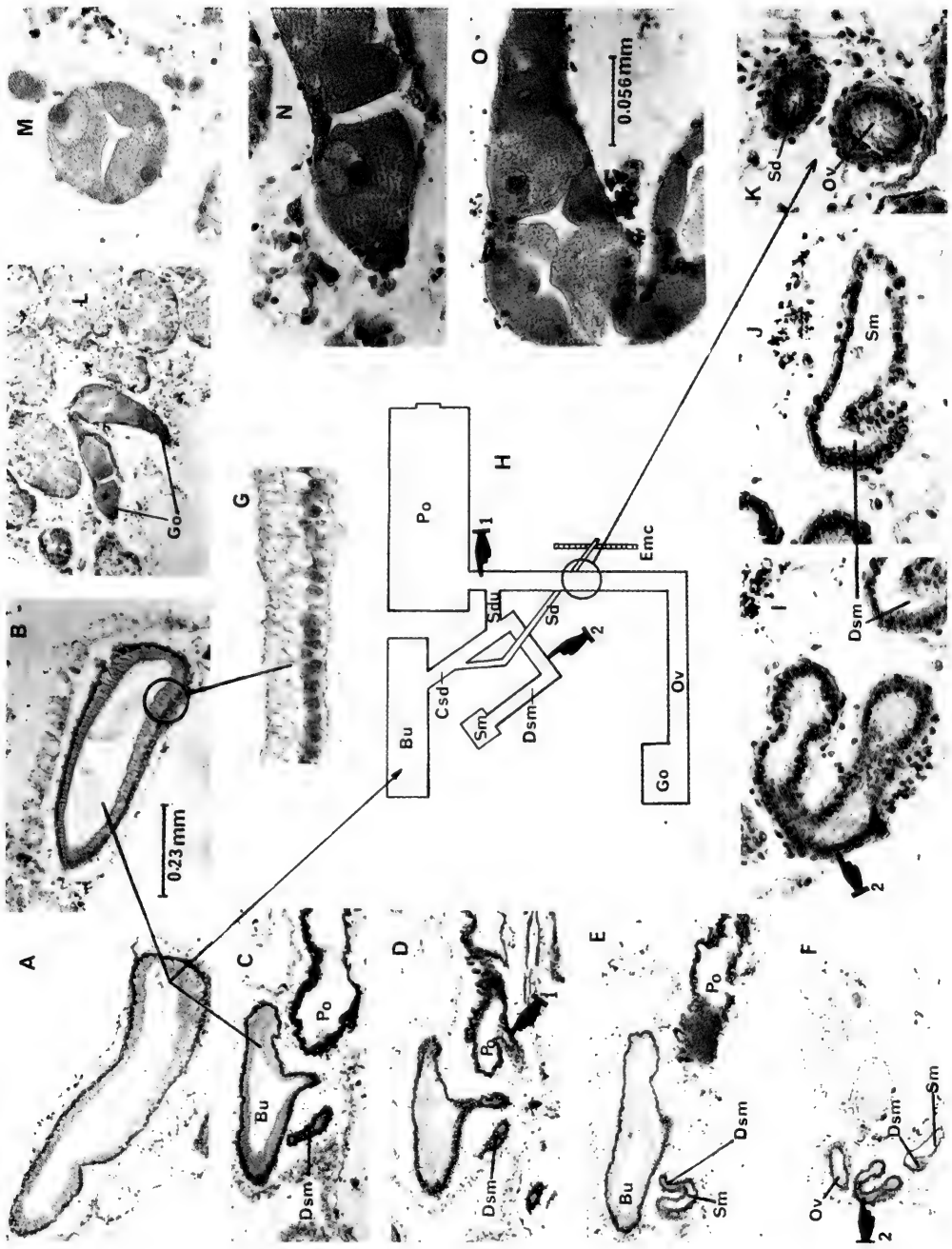
+, yes or has.
–, no or does not have.
?, unknown.

the alpha race snails were from specimens collected at Khemarat when the water was rapidly rising. Only a few males had reached maturity while females had not attained maximum development of the reproductive system. Data for the gamma race were obtained from those snails surviving to maturity in the laboratory. To date, it has not been possible to complete the life cycle of these snails in the laboratory, since culture methods have not yet been worked out.

Arguments against separate species status are: 1) There are indications that there is some cross breeding between alpha and gamma races. Nearly mature snails collected at Sompamit Falls near the Cambodian border in mid-May 1974 had a size and shape intermediate between these races. Also, the pigment pattern was irregular, varying from a wide grey bar to several disrupted splotches. Few individuals had the pronounced 4 to 5 dots of black pigment characteristic of the gamma race. 2) Differences in verge, coiling of the seminal vesicle, and position of the bursa copulatrix in relationship to the albumen gland section of the pallial oviduct (Ppo) appear, in part, to reflect differences in the stages of ontogeny and maturity between the races. 3) One should be cautious in using unique pigment patterns to characterize species. For example, Davis & Carney (1973) described a unique pigment pattern of a subspecies belonging in the *Oncomelania hupensis* species complex. 4) Variation in size, sculpture, pigment patterns, and radular formulae are known to be controlled at the infraspecific level in taxa of the Pomatiopsinae, a sub-

FIG. 16. Histology of ganglia, ctenidium, and pedal glands.
A. Section through the head showing cerebral ganglia and one pedal ganglion (Pg). Note the heavy melanization of the ganglia. The ducts of the salivary glands are seen (Sg) and the esophagus (Es).
B. Section through the head-foot region revealing the pedal commissure (Pc) which is especially long in this species. Note the statocyst (Stc).
C-D. Sections through the ctenidium.
E. An enlargement of three gill filaments.
F-I. Sections of the mucous glands at the anterior edge of the foot shown in Fig. 6B. The central gland is elongate and projects into the pedal haemocoel. Enlargements of these glands are given in G and H.
Figs. 16A-D, F and I are at the same scale, and so are Figs. 16E, G and H.

Cc—cerebral commissure;
Cg—cerebral ganglion;
Es—esophagus;
Pc—pedal commissure;
Pg—pedal ganglion;
Sg—duct of salivary glands;
Stc—statocyst.



Bu—bursa copulatrix;
Csd—common sperm duct;
Dsm—duct of seminal receptacle;
Emc—posterior end of the mantle cavity;
Go—gonad;
Ov—oviduct;
Po—pallial oviduct;
Sd—spermathecal duct;
Sdu—sperm duct;
Sm—seminal receptacle.

family closely allied geographically, and possibly genetically, to the Triculinae (Davis, 1967; 1968a; 1968b; 1971; Davis & Carney, 1973; Davis & Ruff, 1974). For example, Davis & Ruff (1974) demonstrated that ribbing in *Oncomelania* is controlled by a dominant gene and that the degree of ribbing appears to be controlled by multiple alleles. Likewise, the variation in microsculpture in a single population of the beta race suggests control by multiple alleles.

Variation in cusp formulae in polytypic *Oncomelania hupensis* is notorious (Davis & Carney, 1973). The same magnitude of variation is seen for *"L." aperta* in Table 7. It is expected that, as more populations of *"L." aperta* are studied, apparent differences between races will lessen.

The tradition in malacology has been to present cusp formulae from 1 row of teeth from 1 radula (Bartsch, 1936). Little attention to variation is usually given (Brandt, 1968, 1970; Thompson, 1968). However, if variability is not adequately studied, one may repeat mistakes exemplified by Bartsch (1936) who separated taxa, now considered *Oncomelania hupensis,* into various genera and species on the basis of cusp formulae. For example, he considered *Katayama* to have 3-3 basal denticles on the central tooth while *Oncomelania* and *Schistosomophora* had 2-2. He stated that the anterior cusps of the central tooth numbered 3 in *Katayama.* We know today that a population of *O. h. quadrasi* (previously considered *Schistosomophora quadrasi*) can have a central tooth formula of $\frac{1\text{-}1\text{-}1}{3\text{-}3}$, $\frac{2\text{-}1\text{-}2}{3\text{-}3}$, or $\frac{1\text{-}1\text{-}1}{2\text{-}2}$. The anterior edge of the central tooth of *O. h. nosophora* (Robson) (previously considered *Katayama nosophora*) can have 1-1-1 or 2-1-2 cusps.

Davis & Carney (1973: 32) suggested that cusping in *Oncomelania* is under genetic control, that patterns of variability in cusp formulae serve to characterize populations, and that the distribution of those genes governing cusp formation could be analyzed by population studies. It is possible that cusp formation on the central tooth of the radula is governed by 2 genes, where 1 gene governs anterior cusps while the 2nd controls basal cusps (anterior and posterior numbers vary independently). Interaction between the alleles of these genes could account for variability scored for the central tooth seen in Table 7. The formula can vary on the same radula, indicating lack of rigid control in the individual. However, one formula may be present in 2% of population A and of 50% of population B. This difference is reproducible, i.e. on the population level, variability appears to be held within genetically defined bounds from 1 year to the next. Individual versus population variability is open to techniques of analysis of variance.

Species Easily Confused with "L." aperta

One species, *Manningiella conica* Temcharoen (1971), has been confused with *"L." aperta.* Shells of *M. conica* are illustrated in Fig. 19. Temcharoen (1971) stated that the species looks like young *aperta;* as the anatomy was not described, the species was only tentatively placed in *Manningiella. M. conica* was described as having a shell

FIG. 17. Histology of the female reproductive system. The schematic representation (H) of the reproductive system was derived from Fig. 8.

A, B. Longitudinal sections of the bursa copulatrix (Bu). These bursas are fully developed and ready to function. The highly secretory columnar cells with dense basal nuclei and pronounced vacuoles are seen in G.

C-E. The positional relationships of the bursa, pallial oviduct (Po), and seminal receptacle (Sm) are shown in the sections of three different levels. Note that the pallial oviduct has not matured. Fertilization has not occurred because the bursa and the seminal receptacle are devoid of sperm. The entrance of the oviduct into the pallial oviduct is shown in D (1; compare with H).

F, I. The pronounced U-shaped tube from the bursa to the seminal receptacle (2) is greatly ciliated throughout. One arm of the tube is the duct of the seminal receptacle (Dsm, E, F, I, J).

E, F, J. The sac-like seminal receptacle is composed of simple unciliated cuboidal cells.

K. Cross section of the greatly ciliated oviduct (Ov) and ciliated spermathecal duct (Sd) at a position close to the posterior end of the mantle cavity (Emc). Compare with H.

L. The ovary (Go) embedded in the digestive gland in a relatively early stage of development as it is unbranched. However, it contains mature oocytes.

M-O. Cross section of the ovary with three oocytes. Enlargement of the oocytes, compared with these shown in L, is given in M-O. Note the markedly dense nucleolus in the mature oocytes.

Figs. 17A-F and L and are at the same scale, and so are Figs. 17G, I-K, M-O.

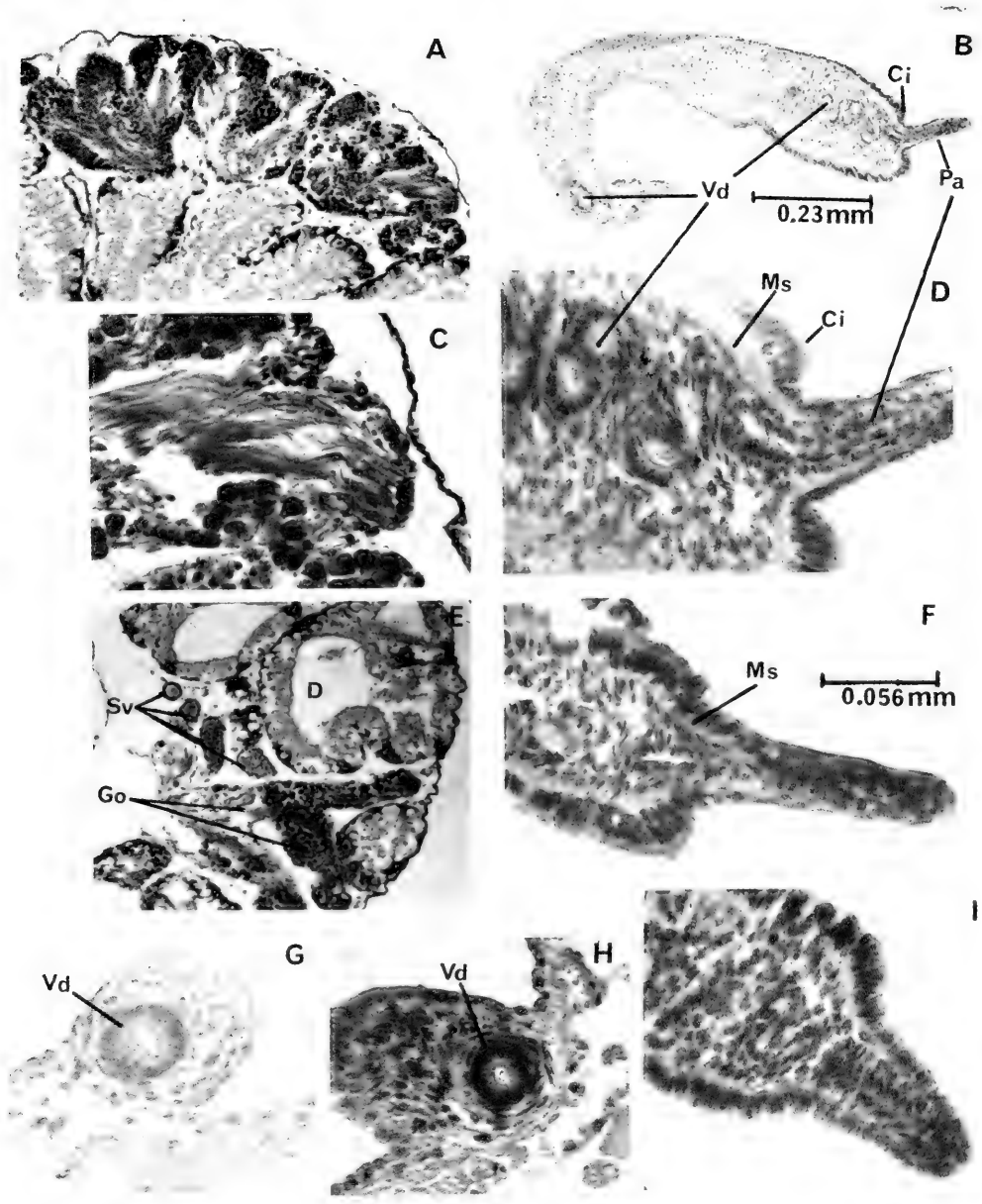


FIG. 18. Histology of the male reproductive system.

A. Lobes of the testis packed with spermatids and sperm.

B. Longitudinal section through the verge showing the pronounced papilla and some coils of the vas deferens.

C. Masses of sperm and spermatocytes.

D. Enlarged view of B showing the ciliated cells (Ci), the fully-developed papilla retractor muscles (Ms) and the vas deferens (Vd).

E. A section demonstrating regions of the sperm-packed, coiled seminal vesicle (Sv).

F. Anterior end of verge in which the papilla is not yet retractible and the papilla retractor muscles have not yet become fully developed. A verge with a very undifferentiated papillar area is shown in I.

G-H. The vas deferens (Vd) where it leaves the neck and enters the base of the verge. Note that there are sparse circular muscles surrounding the vas deferens.

Figs. 18A, B and E are at the same scale, and so are Figs. 18C, D, F-I.

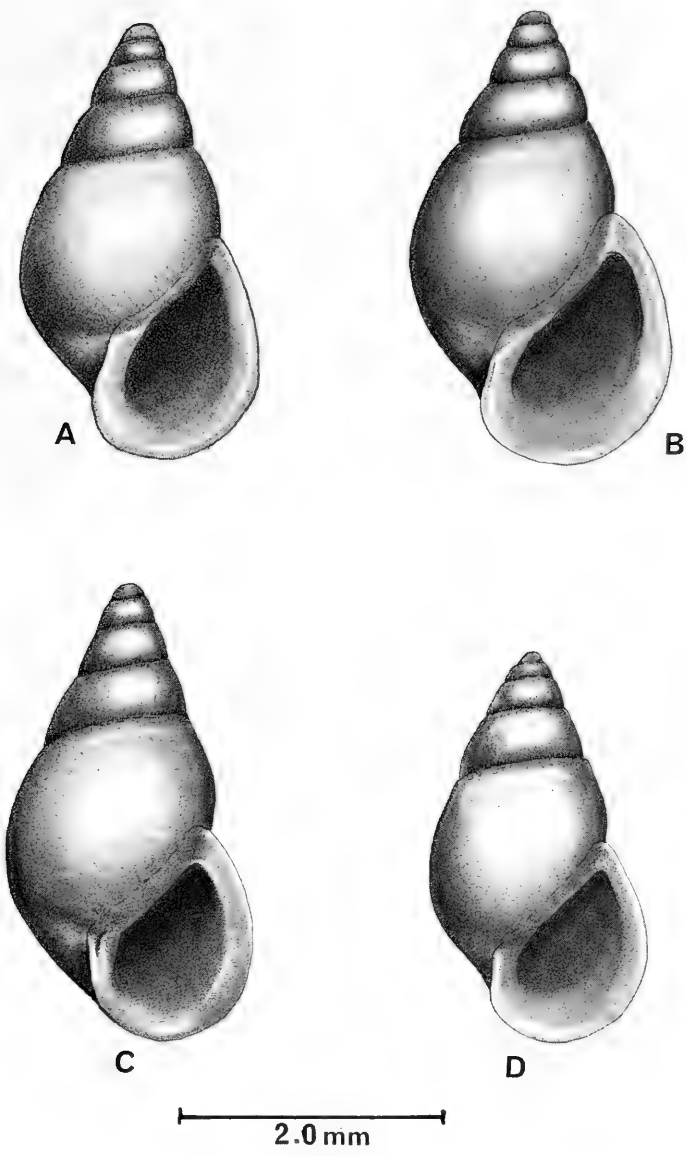


FIG. 19. Shells of *Manningiella conica*. Khong Island; location 5, site 3, 25 May 1973. ANSP 332467.

Ci—cilia;
D—digestive gland;
Go—gonad:
Ms—muscles;
Pa—papilla of the verge;
Sv—seminal vesicle;
Vd—vas deferens.

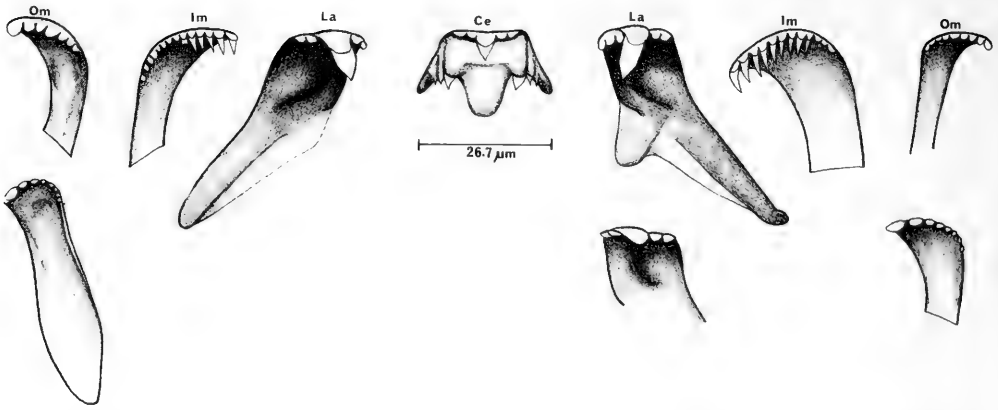


FIG. 20. Isolated teeth from the radula of *Manningiella conica* but positioned as one would observe them on the radular ribbon. The width of the central tooth at the base is, on the average, 26.7 μm. Abbreviations the same as for Fig. 11.

length of 3.0 to 3.8 mm. The length/width ratio is 1.8 ± 0.1. The shell is smooth and lacks spiral microsculpture; there are delicate axial growth lines. The 5 whorls increase regularly, the aperture is large and somewhat expanded; the umbilicus is closed. The mantle edge of some individuals can have black pigment bars or specks, but these are not grouped as 4 or 5 distinct spots as in gamma race *"L." aperta.*

The radula is distinctive. The face (basal plate) of the central tooth is rectangular and the basal cusps arise primarily from the face of the tooth (Fig. 20); the smallest basal cusp arises from the lateral angle. The radular formula is $\frac{2\text{-}1\text{-}2}{3\text{-}3}$, 3(2)-1-2, 11-13, 8-10. The central tooth formula $\frac{2\text{-}1\text{-}2}{4\text{-}4}$ was found only on a few teeth of one radula. The width of the central tooth at the base was 2.67 μm ± 2.4 (standard deviation); (n = 7).

M. conica was most frequently collected by sieving sand at the shore of Khong Island, an environment devoid of *"L." aperta.* Like *"L." aperta, M. conica* matures late, i.e. during the onset of the rainy season in June. For this reason it has not yet been possible to obtain mature animals for anatomical study in order to clarify the generic status of *M. conica.*

"L." aperta differs from *M. conica* in that the shell is wider, the length/width ratio being 1.50 ± 0.1. The lip is widely flaring and expanded in *"L." aperta.* The gamma race has distinct pigment spots while the alpha race is devoid of pigment. The lateral angle of the central tooth of *"L." aperta* bears 4-5 teeth; only 1 cusp arises from the face of the tooth. The general radular formula for *"L." aperta* is $\frac{4(5)\text{-}1\text{-}(5)4}{6(5)\text{-}(5)6}$, 4(5)-1-5(6), 17-21, 15-17. *"L." aperta* clings to hard surfaces on a substrate tending towards mud.

One other species, *Pachydrobia bavayi* might be confused with *"L." aperta* or with *M. conica.* The young of *P. bavayi* have a shell very similar in all respects to that of immature *M. conica.* The adult, however, is much larger, reaching a length of 5.0-7.8 mm. *P. bavayi* has no pigment dots or black bars on the mantle. The mantle appears bright pink. However, some pink color is seen on the mantle of both *M. conica* and some *"L." aperta.*

Radular Structure and the Generic Status of "Lithoglyphopsis" aperta

The genus *Lithoglyphus* Hartman (1821) has previously been considered to have taxa in Europe, Asia and Africa (Thiele, 1928, 1929; Wenz, 1939). The type-species, *L. naticoides* (Fér.) Pfeiffer (1828) is European. The designation of *L. naticoides* as type-species is discussed in Appendix I. Placement of taxa from diverse geographic regions in the genus is based on shell similarity, i.e. these freshwater snails have globose to cap-shaped, fairly thick shells.

Thiele (1928), studying the radula of *L. naticoides* and Asian *"Lithoglyphus",* noted that the central tooth formula of the former

was $\frac{3\text{-}1\text{-}3}{3(4)\text{-}(4)3}$ while that of some species (i.e. *L. tonkinianus* Bavay & Dautzenberg and *L. modesta* (Gredler) of the latter had $\frac{0\text{-}1\text{-}0.}{2\text{-}2}$ Accordingly, Thiele (1928) created the genus *Lithoglyphopsis* and designated *L. modesta* type-species.

The rather globose shell of *Lithoglyphopsis modesta* is unlike the ovate-conic shell of *"L." aperta.* That they are not congeneric is shown by the structure of the central tooth of the radula. The 1, large, smooth anterior cusp of *L. modesta* corresponds to the condition seen in the Mekong River hydrobiid genera *Pachydrobiella, Hydrorissoia,* and *Lacunopsis.* The radula of *"L." aperta* more closely resembles that of *Lithoglyphus naticoides,* a convergent similarity as discussed below. The radular illustration presented by Temcharoen (1971) is not of *"L." aperta.* It is definite that the radulae studied here came from snails corresponding to his taxon. It was on the basis of his radular drawing that he placed the species in *Lithoglyphopsis.*

While the radula is of limited value for characterizing higher taxa and assessing relationships between taxa, it is often of value for defining species and genera. Where several species of a hydrobiid genus have been studied carefully, we note that the ground-plan of the radula has been uniform for the genus. It is of course true that several genera may have the same ground-plan, e.g. the radular structure of *Hubendickia* and *Paraprososthenia* is similar. However, congeneric species do not have vastly different radular structures. A species with a central tooth like that of *L. modesta* would not belong in the same genus with a species having a central tooth as in *"L." aperta.*

It is premature to create a new monospecific genus for *"L." aperta.* Too few data are available for the numerous hydrobiid taxa of the Mekong and Yangtze Rivers. Thus, *aperta* is temporarily left in *"Lithoglyphopsis."* The problem of generic placement will be solved when we know more of the anatomy of several species of each of the hydrobiid genera in the Mekong. The specific information needed is on the anatomy of the female reproductive system. This will be correlated with shell, radula, and habitat characters. Much of the problem would be clarified by anatomical data from Yangtze River *Lithoglyphopsis* and *"Lithoglyphus."*

Subfamily Status

Because of similarity in shell structure, several authors but prominently Thiele (1928, 1929), placed *Lithoglyphopsis, Lacunopsis, Pachydrobia, Pachydrobiella, Paraprososthenia* and *Tricula* of SE Asia and China in the tribe Lithoglypheae or subfamily Lithoglyphinae. This was followed by Brandt & Temcharoen (1971).

The subfamily name "Lithoglyphi," based on the genus *Lithoglyphus,* was given by Troschel (1857) to *Lithoglyphus, Assiminea,* and *Tomichia.* Troschel's subfamily was based on 1 character, namely the presence of 2 or more basal cusps on either side of the central tooth. The "Hydrobiae" had only 1 basal cusp on each side. Fischer (1885) followed Troschel in using this trait to separate the Lithoglyphinae from the Hydrobiinae. Subsequent history of the use of the name Lithoglyphinae is reviewed by Taylor (1966).

Krull (1935), Krause (1949), and Radoman (1966) studied the anatomy of *L. naticoides.* Comparisons show that *Tricula* and *"L." aperta* belong in a different phyletic line.

The subfamily Triculinae of Annandale (1924) was redefined by Davis (1968b). Its differential characters include how sperm enter the female reproductive system and the morphology of the system. The Triculinae is an Asian subfamily which includes *"L." aperta,* where sperm enter at the posterior end of the mantle cavity and travel to the bursa copulatrix through the spermathecal duct. This passage may be via the pericardium or it may bypass the pericardium. In the subfamily Hydrobiinae (contrasted with the Triculinae in Fig. 21) to which *Lithoglyphus* of Europe is assigned, sperm enter the pallial oviduct at the anterior end of the mantle cavity and travel to the bursa via a ciliated gutter. There is no spermathecal duct. It is thus evident that there is a fundamental difference between female reproductive systems in these 2 subfamilies. Characteristics of the male reproductive system are of little value in defining these subfamilies. For example, numerous taxa of both have a simple verge with 1 duct.

Similarities in the structure of the central tooth of *"L." aperta* and *Lithoglyphus naticoides* are superficial and derived by

convergent evolution.

Relationships of "Lithoglyphopsis" aperta *Within the Rissoacea*

Higher Category Relationships—*"L." aperta* conforms to the grade of anatomical organization which is rissoacean and hydrobiid. On the basis of mode of sperm entrance into the female reproductive system and the ontogeny of the female reproductive system it is evident that the Triculinae differ from the Hydrobiinae phylogenetically.

A duct leading from the upper end of the pallial oviduct to the proximal end of the mantle cavity is known from only a few non-triculine mesogastropods. Creek (1953) described such a duct in the terrestrial littorinacean *Acicula fusca* (Montagu). Johansson (1953) reported its occurrence in the marine cerithiacean *Triphora perversa* (Linnaeus); Fretter & Graham (1962) discuss its presence in the marine rissoacean *Barleeia rubra* (Montagu).

Johansson (1953) and Fretter & Graham (1962) considered the connection between the oviduct and proximal end of the mantle cavity to reflect a primitive state. Only in the Triculinae has a morphological ground plan evolved where the primitive route of fertilization has been uniformly retained. The triculine taxa possibly differ from the above named taxa in that there is evidence of a close association between the spermathecal duct and pericardium, e.g. sperm reach the spermathecal duct of *Tricula bollingi* Davis by passing through the pericardium.

The salivary glands of *"L." aperta* are dorsal to the cerebral commissure and have their origin anterior to the nerve ring. Fretter & Graham (1962) and Ponder (1973) make a point of differentiating monotocardian gastopods from neogastropods by stating that the ducts of the salivary glands run through the nerve ring in the former while the glands and ducts are in front of the cerebral commissures and thus do not pass through the nerve ring in the latter.

"L." aperta, however, is not unique among monotocardian gastropods. The dorsal anterior position of the duct is seen in the Pomatiopsinae (Davis, 1967, 1968a) and Assimineidae [*Assiminea brevicula* (Pfeiffer)], Truncatellidae [*Truncatella guerinii* A. & J. B. Villa], Bithyniidae [*Bithynia manchurica* Bourguignat], and Hydrobiidae [*Amnicola limosa* (Say)] (dissected by Davis along with *"L." aperta* specifically for this trait). Too few papers dealing with rissoacean anatomy give details on the interrelationships of organs, and thus the status of the salivary glands relative to the cerebral commissures is unknown for over 50 taxa discussed in the literature (Henking, 1894; Bregenzer, 1916; Robson, 1920, 1921, 1922; Krull, 1935; Johansson, 1939, 1956; Krause, 1949; Lilly, 1953; Radoman, 1955a, 1955b, 1974; Dundee, 1957; Bole, 1970, 1971; Winterbourn, 1970; Pezzoli & Girod, 1971).

It is not appropriate to use the trait in question to differentiate monotocardian gastropods from the neogastropods. Contrary to the explanation given by Fretter & Graham (1962), it is evident that in certain lineages of mesogastropods there was a backward shift of the cerebral ganglion-commissure complex *not* accompanied by a backward shift of the salivary glands and correlated elongation of the salivary ducts.

"L." aperta does not possess a hypobranchial gland, in contrast to the usual mesogastropod condition. The same lack of this gland is observed in the pomatiopsines *Oncomelania* and *Pomatiopsis.* Too few rissoacean taxa have been examined for this trait to make useful statements concerning the distribution of the hypobranchial glands among the various families.

The Triculinae are most closely allied with the Pomatiopsinae both in anatomy and zoogeography. One of us (Davis) considers the subfamily Pomatiopsinae to have evolved from the same basal stock giving rise to both *"L." aperta* and *Tricula.* This is an important consideration as *Oncomelania hupensis* of the Pomatiopsinae and *"L." aperta* of the Triculinae transmit human, Asian schistosomes. While the ancestral Triculinae were aquatic, the present day Pomatiopsinae are amphibious or terrestrial. The adaptation to the amphibious-terrestrial environment is seen in the pedal crease of the foot and the step-like mode of progression; both traits resulted from bearing the weight of the turreted shell in the absence of water. The aquatic Triculinae move by ciliary glide. Both pomatiopsine and triculine snails lay eggs singly and coated with sand grains or mud. The central tooth of the radula of the Pomatiopsinae closely resembles that of certain taxa now placed in the Triculinae, e.g., *Manningiella conica* (Fig.

20).

The pomatiopsine female reproductive system (Fig. 21) could have been derived from the triculine condition seen in *"L." aperta* and *Tricula burchi* Davis (Fig. 22). The bursa would have rotated 90° to 180°, bringing the conditions shown in Fig. 22A to those given in Fig. 22B, i.e. bringing the openings of the spermathecal duct and sperm duct into the bursa from the left ventro-lateral side to the right anterolateral aspect. With the rotation, the spermathecal duct elongated along the pallial oviduct to open at the anterior end of the mantle cavity. The duct of the seminal receptacle migrated to open directly into the oviduct. Continued rotation of the bursa yielded the pomatiopsine condition (Fig. 22C). It is a distinct advantage to pomatiopsine snails to have the opening of the spermathecal duct at the anterior end of the mantle cavity rather than at the posterior end when one considers the mechanics of copulation in the amphibious or terrestrial environment.

Oncomelania hupensis is the most widespread and abundant representative of the Pomatiopsinae in Asia. As discussed by Davis (1971) and Davis & Carney (1973), fossil *Oncomelania* have been found in Pleistocene beds of the northern Shan States of Burma (Annandale, 1919). This establishes that *Oncomelania* has existed in an arc overlapping the Mekong and Yangtze Rivers. From this area taxa of the genus radiated to Japan, the Philippines, and Sulawesi (= Celebes).

It is, of course, possible that the Pomatiopsinae evolved independently of the Triculinae. The presence of a gonopericardial duct in *Oncomelania* and *Pomatiopsis* of the former subfamily (Davis, 1967) and absence of the duct in the latter may support this view.

The pomatiopsine female reproductive system could not have been derived from the hydrobiine type described in the section on "Subfamily Status". The spermathecal duct of the former did not arise by closure and separation of the ciliated ventral groove of the pallial oviduct of the latter. In the Hydrobiinae the ciliated gutter is formed during ontogeny by the closure of the open pallial oviduct (Johansson, 1956). In the Pomatiopsinae (e.g. *Oncomelania hupensis*) one of us (Davis) has observed that the pallial oviduct forms by cavitation in a solid core of developing tissue and the spermathecal duct elongates from a bud of the bursa copulatrix.

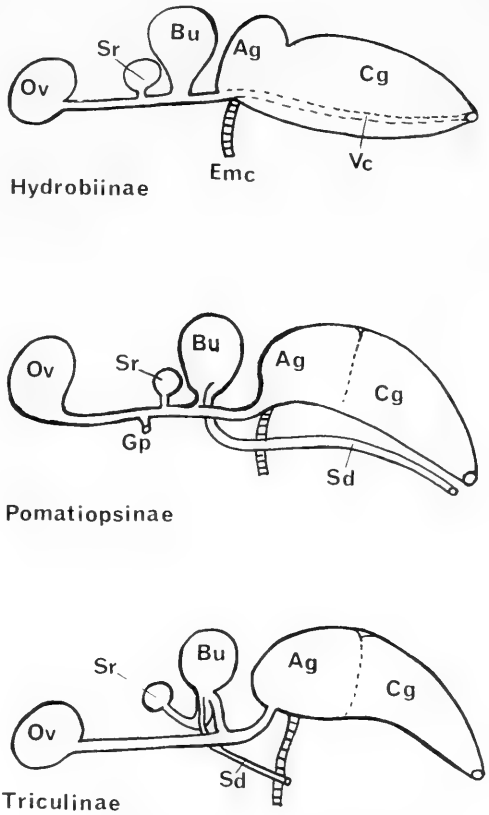


FIG. 21. Schematic drawings of the female reproductive systems of three subfamilies of the Hydrobiidae showing essential similarities and differences.

Ag—albumen gland = posterior pallial oviduct;
Bu—bursa copulatrix;
Cg—capsule gland = anterior pallial oviduct;
Emc—posterior end of the mantle cavity;
Gp—gonopericardial duct;
Ov—ovary;
Sd—spermathecal duct;
Sr—seminal receptacle;
Vc—ventral channel of the pallial oviduct.

Lower Category Relationships—*"L." aperta* is, of taxa thus far known, most closely related to *Tricula burchi*. In both *"L." aperta* and *T. burchi* there is a U-shaped common sperm duct from the bursa copulatrix to the seminal receptable. In both taxa the spermathecal duct (labeled Rd in Davis, 1968b) bypasses the pericardium and joins the common sperm duct close to the bursa copulatrix.

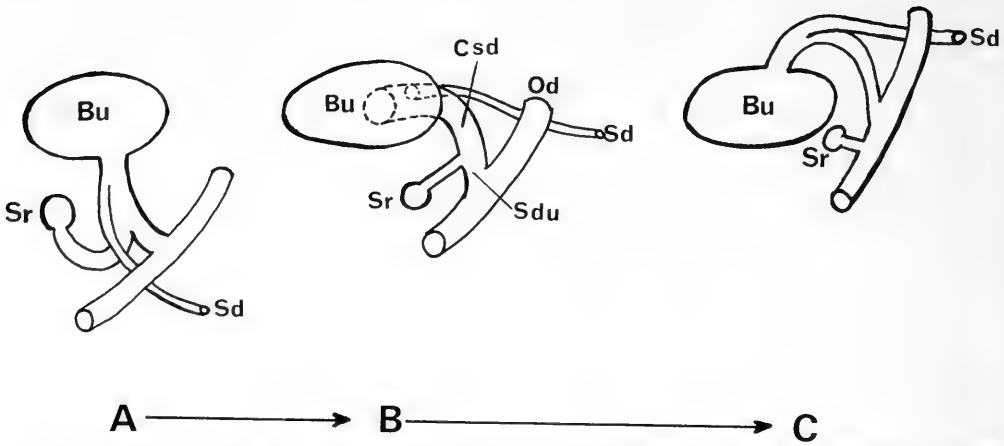


FIG. 22. The hypothetical sequence of events by which the arrangement of ducts and organs of the female reproductive system seen in the Triculinae today (A) modified to produce the condition seen in the present-day Pomatiopsinae (C). The bursa copulatrix in A rotated through 90° (B) to 180° (C), bringing the opening of the spermathecal duct (Sd) to the right antero-lateral edge of the bursa. The seminal receptacle (Sr) migrated to open from the oviduct (C).

A. Triculinae.
B. Intermediate stage.
C. Pomatiopsinae.

Bu—bursa copulatrix;
Csd—common sperm duct;
Od—oviduct;
Sd—spermathecal duct;
Sdu—sperm duct;
Sr—seminal receptacle.

The close relationship to *Tricula burchi* suggests that *Tricula* might be a suitable genus for *"L." aperta.* Unfortunately, the anatomy of the type-species of *Tricula* Benson (1843), i.e. *T. montana* Benson (1843), is unknown. *T. montana* has not been found since it was discovered in Bhimtal, India (Prashad, 1921 a, b; Rao, 1928). The anatomical concept of *Tricula* is currently based on *T. burchi* and *T. bollingi* (Davis, 1968b).

"L." aperta differs from *T. burchi* and *T. bollingi* in several characters. Species placed in *Tricula* have turreted shells with 5 or more whorls, the inner lips are simple, sharp, and not reflected over the base, the length to width ratio is 2.0 to 2.26, and there is no columellar shelf. There is no eversible papilla in the verge of either *T. burchi* or *T. bollingi.* As previously mentioned, the taxa differ from *"L." aperta* in size and shape of the bursa copulatrix and the relative position of the seminal receptacle to the bursa. The central tooth of *Tricula* has a "basal bar" not seen in *"L." aperta.*

Tricula bollingi differs from both *"L." aperta* and *T. burchi* in that the seminal receptacle does not arise from the common sperm duct, but from the oviduct. Also, the spermathecal duct enters the pericardium and there is a passage from the pericardium to the rear of the mantle cavity.

Aside from *"L." aperta* and *T. burchi,* the bursa copulatrix and seminal receptacle have separate openings into the oviduct in rissoids and hydrobiids thus far studied.

We consider the fundamental condition or primitive state of triculine snails to be seen in the morphology of *"L." aperta* and *T. burchi,* i.e. where there is a common sperm duct through which the bursa copulatrix and seminal receptacle communicate independent of the oviduct. The sequence in the secondary and tertiary derived states involves the migration of the seminal receptacle to open into the oviduct posterior to the opening of the duct of the bursa. A third stage, not yet observed, would have the seminal receptacle lost and the storage of sperm within the coils of the oviduct. Also, a stage might be found fixed in some living species where the seminal receptacle opens into the duct running from the bursa into the oviduct.

Histological Data

Histological data presented here are baselines for comparisons with other Mekong River hydrobiids and rissoaceans in general. Very few papers have been published illustrating even limited histological aspects of rissoacean taxa. Henking (1894) presented a few drawings of sections through the buccal mass of *Hydrobia ulvae* (Pennant). Bregenzer (1916) gave an excellent account of *Bythinella dunkeri* with 28 drawings of sections. Vague information is given by Robson (1920) for *Potamopyrgus jenkinsi* (Smith), by Robson (1921) for *Oncomelania hupensis nosophora* (Robson), and by Robson (1922) for *Hydrobia ventrosa* (Montagu). Johansson (1939) provided numerous photographs and drawings of sections for 4 species of Rissoidae. Krause (1949) gave an excellent account of the anatomy of *Lithoglyphus naticoides* which included 12 drawn sections.

From the information available, it appears that there are differences between rissoacean snails in micro-morphology of the digestive system. Graham (1939) summarized the available data on the alimentary canal of style-bearing prosobranchs. In *Hydrobia ventrosa, H. ulvae,* and *Pomatopyrgus jenkinsi* the dorsal food channel of the esophagus is bounded by dorsal folds so high that they contact the opposite wall, thereby seeming to divide the tube into 3 chambers. The posterior esophagus has numerous folds, 1 of which is a continuation of the left dorsal fold. In *Bythinella dunkeri* (Frauenfeld) the dorsal food groove of the anterior esophagus is closed ventrally by the meeting of the ends of the dorsal folds; the posterior esophagus is thrown into folds.

In *"Lithoglyphopsis" aperta* the dorsal food groove of the anterior esophagus is almost closed ventrally except that the ends of the dorsal folds do not quite meet. The left dorsal fold continues to the stomach, while the right 1 becomes indistinguishable from the several other folds which are about 1/2 the height of the left dorsal fold. The transition occurs posterior to the nerve ring. The persistence of the left dorsal fold as a structure twice the size of the other 8 to 9 folds is thus far unique among hydrobiid snails. It has yet to be determined whether these traits described for *"L." aperta* are species-specific or characteristic of all triculine snails. The functional significance of these folds is unknown. It is important to determine if differences between triculine taxa occur, and if these differences correlate with different ecological conditions, particularly food preferences.

The intestine and style sac intercommunicate via a slit in *Bithynia tentaculata* (Linnaeus) and *Rissoa parva* (da Costa) (Graham, 1939), a condition not seen in *"L." aperta.*

There are few precise data on the typhlosole of the intestine. *"L." aperta* has an extremely pronounced typhlosole, extending from the style sac to the pellet compressor (Fig. 15C). The pellet compressor is located in the bend of the intestine where it turns to run to the anterior end of the mantle cavity. Dundee (1957) states that the typhlosole of *Pomatiopsis lapidaria* (Say) extends beyond the pellet compressor to an area opposite the posterior end of the gill; Van der Schalie & Dundee (1956) reported this also for *P. cincinnatiensis* (Lea).

From the limited data available it appears that the micromorphology of the esophagus of *"L." aperta* and the extent of the typhlosole fit a general hydrobiid pattern, but certain aspects are distinctive of this species. It remains to be seen if these traits are characteristic of the Triculinae.

Our histological data on *"L." aperta* confirm that the spermathecal duct opens at the rear of the mantle cavity and opens directly into the common sperm duct. It does not travel as a tube-within-a-tube to the bursa copulatrix. In *Oncomelania* the spermathecal duct and sperm duct both enter the spermathecal sheath for a short distance before they enter the bursa (Css, fig. 27, Davis, 1969a). The wrapping of these ducts in a sheath is here considered to be derived from the sheathless state because the tubes are not wrapped in *"L." aperta,* because morphology of the bursa-seminal receptacle complex in *"L." aperta* is considered, and because we feel that *Oncomelania* evolved from early triculine stock where taxa had an *"L." aperta*-like bursa-seminal receptacle complex.

Analysis of the ontogeny of the penis sheds light on how the papillate condition is derived from the "simple" penis. The degree of papilla formation corresponds to the degree of development of the penial muscles at the free end of the penis attaching to the blunt nipple-like tip (Fig. 18 I, F, D, B). As the muscle bundles thicken, strands extend into the papilla and the papilla becomes more slender. Muscles bunch up around the

base of the papilla essentially forming a cylinder through which the papilla can be retracted.

Nervous System

Clearly, more data from additional triculine and pomatiopsine species are needed to confirm or reject the hypothesis indicated by the available data that there is no relative reduction of the supravisceral connective in taxa of these subfamilies. As the species increase in size, so does the connective.

We consider the relative length of the supraesophageal connective thus far seen in the triculine-pomatiopsine lineage to be intermediate in the Rissoacea (Table 10). In the Hydrobiinae there is a great spectrum of values ranging from elongate connectives *(Hydrobia)* to near fusion of supraesophageal and right pleural ganglia *(Lithoglyphus).* Thus there is, in the monophyletic assemblage of the Hydrobiinae, a distinct trend towards concentration of the nervous system. Brackish-water *Hydrobia* is considered most like the rissoacean marine ancestor of the Hydrobiinae. *Bythinella* is a more highly evolved type while *Lithoglyphus* represents the most advanced condition. The latter genera inhabit fresh water.

We consider the Littorinidae to be more generalized in its nervous system than the Rissoidae or Hydrobiidae because of the very elongate connective (the RPG ratio being 0.72 in *Littorina littorea*) as seen in Johansson, 1939, and 0.84 as seen in Fretter & Graham, 1962). The former ratio was derived from measuring a photograph of the dissected nervous system; the latter was derived from a drawing.

It has yet to be learned if triculine snails radiating into environments requiring specialization have evolved a more concentrated nervous system. For example, do species of *Lacunopsis* which resemble (in shell) *Lithoglyphus* of Europe and which live in rapids have a concentrated nervous system? Have arboreal pomatiopsine snails likewise evolved such a nervous system?

Conservative- and Non-Conservative Organ Systems

Our anatomical and histological data reveal a conservative hydrobiid ground plan in the circulatory, excretory, nervous, digestive and male reproductive systems. The arrangement of folds in the esophagus of *"L." aperta* is a variant within the hydrobiid ground plan and thus far unique.

As is evident from the discussions of the female reproductive systems of the Triculinae, Pomatiopsinae, and Hydrobiinae, this system is non-conservative. Aside from the fact that the females of the 3 subfamilies have a bursa, seminal receptacle, and pallial oviduct, there is no common ground plan. Where data are available for pomatiopsine and triculine taxa (Davis, 1967, 1968a, b, 1969a; Van der Schalie & Dundee, 1956) it is evident that this 1 organ system has changed markedly in taxa radiating into new environments and geographic regions. We have yet to see an end to the variation of how the bursa, seminal receptacle, spermathecal duct and oviduct interconnect. It is evident that selective pressures adapted reproductive strategies to very different ends in coping with new environments while feeding strategies (as seen in the structure of the digestive system) were adapted to the same end, i.e. feeding structures did not diversify but held to the same general type. This is the converse of the course of events in the neogastropod radiation where reproductive structures are quite similar from genus to genus or between families, while fore-gut structural differences are profound.

We need both qualitative and quantitative data for organ systems in order to provide data of value for systematics in the Rissoacea, i.e. shell, and reproductive, digestive, and nervous systems, as well as external features of the head-foot region and mantle cavity structures. It takes little additional effort to record quantitative data while observing qualitative aspects of an organ, e.g. recording dimensions of major organs. It is obvious that such measurements must be made with regard to a well established marker indicating stage of development, e.g. using only fully mature animals where the shell has reached maximum development.

It is important to be able to compare taxa in the relative sizes of organs. While this is obvious to a student of vertebrate biology or one investigating races of mankind, it has been generally ignored by students of molluscan systematics and evolution. It should be obvious that when taxon A has a shell length of 5 mm and a length of pallial oviduct of 2.0 mm while congener B has a

shell length of 4 mm and a pallial oviduct 2.5 mm long, quantitative analysis is of value in discriminating between taxa. In the absence of the quantitative data one has a usual assessment; the shells differ in size, the external aspects of the pallial oviduct are the same. Obviously, meaningful information is lost. With such data one can often make assessments of subtle infraspecific variation. This was done by Davis & Carney (1973) in distinguishing *O.h. lindoensis* of Sulawesi from small subspecies of *O. hupensis* from Taiwan and the Philippines.

While quantitative data serve to characterize a taxon and increase the data base for inter-taxon comparisons, they are also of value for analyses of function or evolutionary strategies for coping with the environment, obtaining energy, reproduction, etc. For example, the length of the osphradium of *"L." aperta* is 46% of the length of the ctenidium. The relative length of the osphradium in other Hydrobiidae (where known, Davis, 1969a) varies from 26 to 40%. With the length of shell as a standard of size, the relative length of the osphradium is 24% in *"L." aperta* as against 8 to 13% in *Oncomelania minima, O.h. chiui,* and *O.h. formosana.* The estimated value for *Tricula burchi* and *T. bollingi* is 10%. A quick check of the osphradia of taxa of other hydrobiid genera in the Mekong River showed that they, likewise, had an elongate osphradium. *Tricula,* closely allied genetically to *"L." aperta* but outside the Mekong River drainage, has a short osphradium as indicated above. The elongate osphradium correlates with habitation of the Mekong River. A hypothesis to explain this is that: The Mekong River has an exceptional silt burden. Sensory perception with a small nerve center might be ineffectual under such conditions. Enhancement of sense discrimination where silt burden could overload the sensory system might be achieved by increasing the volume of the nerve elements in the osphradium. The elongation of the osphradial ganglion would cause an increase in surface area and volume and hence cause a markedly increased capacity for sensory perception. That there is a selection advantage for an elongate osphradium is shown by the fact that the species checked of such divergent Mekong dwelling genera as *Hubendickia* and *Pachydrobia* possess the elongate osphradium.

Quantitative Data, Ecological Parameters, and "r"-Selection

Analysis of quantitative data for the bursa copulatrix and pallial oviduct shows that the former is 63% the length of the latter. In other hydrobiids (where known) the % varies from 18 to 25. The pallial oviduct of *"L." aperta* and these other hydrobiids has a length relative to shell length of 54 to 66%. Correlated with the extremely large bursa is a correspondingly large seminal receptacle-common sperm duct complex. We suggest that these relative size differences are related to ecological parameters and reproductive strategy.

"Lithoglyphopsis" aperta, when found in nature, are gregarious and extremely limited in movement. They are found densely crowded on solid objects such as sticks, shells, and stones. Populations of growing young are extremely dense, e.g. 10 per cm^2 on a stick or shell. Because of their substrate preference and their tendency to move little while grazing, it is evident that the population in a given area is composed of those snails hatching within the area. During their growth to maturity there is probably little recruitment from extralimital areas and nearly zero emigration. As snails mature, and with increased flooding from July on, some snails are probably transported on sticks to different localities.

The species has 1 breeding cycle per year. We have collected no living specimens, but thousands of dead shells, in early March. Newly hatched young are collected in April. The following are probable: 1) Females lay their eggs in late January or early February and subsequently die. Eggs are coated with sand grains and attached to hard substrates such as shells of living mollusks, sticks, stones, shells of dead animals. The numerous shells of dead animals collected in March probably do not come from animals dying in November or December, but in January and February. The raging currents which scour the river bottom would sweep these downstream; they would be ground to small particles by the action of sand and pebbles carried in the current. Also, the shells collected in March are in the same area where the populations of young are found in April. 2) The young crowd every piece of substrate available, e.g. surfaces of leaves, sticks, etc. Young seem to be substrate limited, as there are frequently scant solid objects in the area,

otherwise composed of silt, mud or mud-sand. Many do not reach maturity, as evidenced by the fact that collecting these animals by fine sieves, empty *"L." aperta* shells of 3.0 whorls are common.

Males mature ahead of females, i.e. in May. By mid-May, alpha race females have oocytes in the gonad. We project that full maturity in females is reached in late June or possibly in early July, and that copulation occurs at this time when the river level has begun to rise. If the reproductive pattern follows what is known for *Oncomelania hupensis* and generally for hydrobiids, once copulation has occurred females can store sperm for prolonged times in the seminal receptacle. Sexual dimorphism, frequently seen in hydrobiids, is usually represented by a smaller shell in males; the shells have one half to a full whorl less than that of the female. This is correlated with a more rapid maturation rate of the males. There is no selective pressure on males for prolonged life beyond copulation. It is suspected that males die before females in *"L." aperta.* This is the case in *Manningiella expansa* Brandt which also lives in the Mekong River. We note that functional males of *M. expansa* have not been found in late April or May although functional females have been found. The indication is that the reproductive system deteriorates, the penis atrophies, that the small males die off before the females. Likewise, in *Pachydrobia,* we have seen females with functional reproductive systems in April; males were fewer in number, the verges were atrophied and the rest of the reproductive system was degenerating.

The indications are that female *"L." aperta,* once fertilized, store sperm and do not release oocytes for fertilization during the six months of great environmental trauma when the Mekong River is in flood. As the animals have limited mobility and are substrate-limited it is almost certain that large numbers of the population are swept away and destroyed annually. We have seen areas heavily populated one year that were totally disrupted the following year due to the floods. The extremely large bursa-seminal receptacle complex would thus be necessary to store copious quantities of sperm in the viable state and manage this resource throughout the environmentally disrupted period by continuously destroying weakened or inviable sperm. The bursa copulatrix functions in regulating the catabolism of sperm. The bursa of hydrobiids, after fertilization has occurred, is full of a brown-yellow mass of sperm in various stages of decomposition and elimination. Snails surviving the period of trauma by location in rock crevices and beneath rocks unmoved by the floods produce prodigious numbers of young per female and thus need a large reservoir of viable sperm. The dense populations of young seen in April and May substantiate the high reproductive capacity per female.

Populations are often restricted to several small patches within a larger area. This is due to discontinuity of suitable substrates and of relatively sheltered areas characterized by a slow current and zone of deposition. For example, 1 population at Ban Khee Lek of Khemarat was located within an area of 4,000 m^2 and another population was not found until 1/2 mi upstream. In other regions such as Khong Island, the population may be continuous for 2-3 miles along the shore of the island with nodes of increased density reflecting a greater abundance of suitable substrates in protected shallow water areas. It has thus been evident over 4 years of collecting *"L." aperta* from various regions in the Mekong River that certain areas in the river are relatively stable over a number of years as evidenced by *"L." aperta* being found in the same locality year after year. Other regions are unstable in that the population is found at a locality 1 year and not in the next, the difference attributed to complete alteration at the locality due to flooding.

Taking these facts as a group it is evident that *"L." aperta* has 2 major "strategies" for survival. 1) The species acts as a colonizer, living in unstable habitats which may be destroyed and new ones created. The mechanism for invasion of a freshly created suitable environment must be the survival of some individuals or encapsulated eggs on dead shells or sticks which are swept by the gentler currents in the periods prior to, or after peak flooding. The sand grain encrusted eggs are sturdy. There must be a strong selection for such egg capsules because all the triculine snails in the Mekong thus far observed have this trait. *"L." aperta* is a colonizer or fugitive species in the sense of Wilson (1965) in that it survives . . . "indefinitely within the kaleidoscopically changing environments of single regions." By considering the fugitive species concept one

may account for the origin of the genetic differences seen in the 3 races and the invasion of new environments as exemplified by the beta race. An additional reason (to the ones previously given) that the races are probably not species derive from Wilson's (1965) speculation that a colonizer which permits speciation generates its own competitors which reduces the rate of——or potential to——colonize. Considering the predictable annual cycle of environmental disruption in the Mekong River it would seem to be a distinct selective advantage for survival if trends toward speciation were dampened. However, considering the number of species of other triculine genera which are also likely colonizers it is probable that a balance has been achieved between the ability to speciate and the ability to colonize and to maintain gene flow with other transient populations, thus assuring survival. 2) *"L." aperta* is an *r*-strategist (MacArthur, 1962; MacArthur & Wilson, 1967; Hairston et al., 1970) in that there is a high density-independent mortality, apparently much of its resources are applied towards reproduction, the energy expended per young produced is very low, and the number of young produced per time is very high compared with pomatiopsine species.

King & Anderson (1971) discussed the fact that there are simultaneously *r* and *k* components in selection and their interaction with regard to genotype and initial population structure determines the pattern of population growth and changes in gene frequencies. They demonstrated via simulations that as the number of breeding cycles for each environmental cycle is reduced, the *r*-components come ". . . to determine both equilibrium gene frequencies and population size." In their model the threshold for *r*-selection was 13 breeding cycles per environmental cycle. *"L." aperta* has 1 breeding cycle per environmental cycle and thus clearly is within King & Anderson's (1971) concept of an *r*-selected species.

The *k*-components of selection in *"L." aperta,* i.e. density dependent factors, are active during the growth phase when young increase in size on a limited substrate and crowding occurs. Not all young will survive to maturity; there is not sufficient room. There is then selective pressure in relation to those surviving to reproduce.

Transmission of Mekong Schistosoma *sp.*

One of us (Kitikoon) has established (unpublished) that all 3 races of *"L." aperta* can experimentally transmit the Mekong schistosome. We consider this schistosome to be a different species than *S. japonicum.* The interaction between the Mekong schistosome and *"L." aperta* is highly specific. The Mekong schistosome and *S. japonicum* have probably evolved from a common ancestor.

The evolution of host-parasite interactions involves sets of complex factors. On the one hand it is clear that molluscan genes operating at the interspecific level control the potential for schistosome miracidia to successfully penetrate and infect a population of snails. This has been established for *Schistosoma mansoni* Sambon of Africa and South America (Richards, 1970), and *S. japonicum* of Asia (Chi et al., 1971; Davis & Ruff, 1974). On the other hand it is clear that genetic factors inherited by the parasite are important if a successful infection in the snails is to occur (Wright, 1974).

Schistosoma japonicum is transmitted by subspecies of *Oncomelania hupensis* of the Pomatiopsinae. There are populations on Taiwan of *O.h. formosana* which lack genes for transmission (Davis & Ruff, 1974). Only *O.h. hupensis* of mainland China and *O.h. chiui* of Taiwan have populations through which all geographic strains of *S. japonicum* can be transmitted.

Lo et al. (1971) have shown that no subspecies of *O. hupensis* can be infected with the Mekong schistosome. This indicates that the Mekong parasite does not have genes enabling penetration and infection of polytypic *Oncomelania hupensis* and that the genetic composition of *O. hupensis* marshals against infection. This does not negate the potential of miracidia of *S. japonicum* to infect *"L." aperta.* Even if the latter should be demonstrated, it is evident that the Mekong parasite is now genetically isolated from *S. japonicum* by its inability to develop in *O. hupensis.*

Iijima et al. (1971) studied adult Mekong schistosome worms and compared them with the Japanese strain of *S. japonicum.* They concluded that the Mekong schistosome is different from all strains of *S. japonicum.* It would appear that the Mekong schistosome is a sibling species of *S. japonicum* because

of the general morphological resemblance. We note, however, that the eggs of the Mekong parasite are smaller and rounder; the worms are significantly longer than those of *S. japonicum;* the ovaries are relatively larger.

The ecology of transmission is different. *S. japonicum* is transmitted by an amphibious snail. Transmission can occur in dew-wet fields of rice, in small drainage ditches and pools. *"L." aperta* is found only in the river, one which is in flood for much of the year. As *"L." aperta* grows to infective size and matures in late May or June, man can become infected only in the dry season from perhaps late May to June or July, and after the September peak floods, from December to late February when the adults die. With the May rains, the river rises some 40 ft and becomes a raging torrent. The current is too swift for man or animal to venture into the river and is too swift to enable the delicate larval cercariae to infect man. It appears that the annual floods keep this parasite in balance as a relict species from Khong Island to Kratie, Cambodia. That the parasite is not more prevalant throughout the range of *"L." aperta* is probably due to the patchiness and population dynamics of the species discussed earlier, which are so tightly coupled with the hydrodynamics of the Mekong River.

The Mekong schistosome and *S. japonicum* probably evolved from a common ancestor. Several million years ago both triculine and pomatiopsine snails existed in an arc from India to the upper Yangtze drainage. As pomatiopsine snails evolved from the early triculine-pomatiopsine stock, genes governing the transmission of a generalized schistosome parasite were inherited by some taxa of both lineages of snails. Genetic control over transmission would not have been nearly as specific as it is today. With time, as new species and genera of snails evolved, genes governing transmission would have become more restricted to some taxa than to others. Precursors to present day *Oncomelania hupensis* evolved with a greater genetic affinity for schistosome transmission while only a few triculine snails retained genes for transmission.

With extinction of *Oncomelania* in the headwaters of the Mekong during the Pleistocene, and with the subsequent radiation of *Oncomelania hupensis* throughout the Yangtze basin, Taiwan, the Philippines, Sulawesi and Japan, the evolving interaction with the parasite, now *S. japonicum,* became highly specific. As the snail evolved so did the parasite if it were to survive in the snail (Davis, 1969b). As the subspecies of *O. hupensis* altered genetically in the separated regions of its range, so did the parasite. The strains of *S. japonicum* occurring today differ somewhat in morphology, egg dimensions, pathogenicity, etc.

The triculine snails radiated both into the Mekong and the Yangtze. As far as we know today, the human schistosome of the Mekong is transmitted only by *"L." aperta. Tricula* and *"L." aperta* are allied in having genetic potential to transmit mammalian schistosomes, as Davis (1969a) found an undescribed mammalian schistosome in *T. bollingi*. It has yet to be discovered whether species of *"Lithoglyphus"* of China are involved in schistosome transmission or have potential to transmit the Mekong schistosome. Much has yet to be learned of *Tricula* from India, Burma, and China regarding the potential to transmit schistosomes.

APPENDIX I

DESIGNATION OF THE TYPE-SPECIES OF *LITHOGLYPHUS*

Hartman (1821: 57) listed *"Lithoglyp. eburneus"* in his catalog of German gastropods. His footnote indicates that *eburneus* is a manuscript name and, without description, a nomen nudum ["(Megerle ab Mühlfeld) nov. spec."].

Pfeiffer (1828) formally described a manuscript name of Férussac, i.e. *Paludina naticoides,* and the manuscript name *Lithoglyphus fuscus* of Ziegler, i.e. *Paludina fusca.*

Cristofori & Jan (1832) list both *naticoides* and *fusca* under *Paludina (Lithoclypus). "Lithoclypus"* is an error for *Lithoglyphus.*

Herrmannsen (1846) designated *L. naticoides* as type of the genus *Lithoglyphus* preceding Gray's (1847) designation of *L. fuscus.* Subsequent authors have used *naticoides* (Fér.) Pfeiffer as the type-species (e.g. Stimpson, 1865; Thiele, 1929; Wenz, 1939).

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Histological preparations were made by Mr. Edward Kepner and Ms. H. Hopkins. All drawings except those of the shells were made by one of us (Davis). Final rendering of the nervous system was done by Mr. Pluem Kidkian of the Faculty of Tropical Medicine, Bangkok. Final rendering of the other anatomical drawings was done by Ms. Vicky Pritchard. The shells of *"L." aperta* were done entirely by V. Pritchard while those of *M. conica* were done by Ms. H. Hopkins.

The manuscript was typed and edited by Ms. Margie Skedzielewski.

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OPEN COILING IN RECENT GASTROPODS

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ABSTRACT

Open coiling in gastropod shells is a condition in which successive whorls are detached but still coiled at a fairly uniform logarithmic rate. It is extremely rare as either a specific or subspecific characteristic in Recent snails and appears to be confined to the Prosobranchia even in terrestrial and fresh-water forms. We examine open coiling in the context of a general model of the geometry of coiling in molluscs developed by Raup. Existing open coiled forms do not appreciably add to the relatively small proportion of theoretically available coiling morphologies that gastropods actually employ. Evolution toward open coiling appears to approach rapidly the limits of adaptation for mobile species. More extensive whorl detachment is associated with either irregular coiling and sessility or the evolution of a nearly straight but still regularly formed shell. The selective significance of open coiling in any individual Recent species is unclear, but it is doubtful that the phenomenon represents a simple case of convergence. It probably evolved independently in several prosobranch lineages to fill dissimilar environmental roles. Some open coiled species have been quite successful either in terms of surviving through geological time or having a broad geographical range.

INTRODUCTION

The shells of most living gastropods are tightly coiled and show extensive overlap of successive whorls. Coiling increases compactness which facilitates locomotion, and whorl overlap strengthens shells and conserves shell material. Both coiling and whorl overlap have figured importantly in the adaptive radiation of shelled gastropods into a tremendous variety of ecological roles. However, in a few taxa, certain species have secondarily evolved open coiling, a condition in which successive whorls are detached. In this paper we review the occurrence of open coiling in Recent gastropods and comment on some of its evolutionary implications.

The degree of regularity of whorl detachment varies enormously in gastropods. Some of the more common forms are shown in Fig. 1. Simroth (1896-1907) introduced the term "alloiostrophy," apparently to include the complete spectrum of forms from simple detachment of the body whorl found in *Ceratodiscus* (Fig. 1a) and numerous other pulmonates to the completely solute condition found in vermetids and several other prosobranchs (e.g. see Fig. 1b-e). Yochelson (1971), in discussing open coiling in Paleozoic gastropods, suggested that either of the terms "disjunct" or "uncoiled" should be applied both to cases of detachment of the body whorl and to forms in which most or all whorls are detached but growth is very irregular such as found in the vermetids. He proposed that "open-coiled" be applied to cases of whorl detachment where coiling still conforms closely to a logarithmic spiral.

Problems of open coiling in gastropods can be treated in the context of a general model of coiling in molluscs developed by Raup (1961, 1962, 1966). The basic geometry of the coiled shell can be described using four parameters: shape of the generating curve (S), rate of whorl expansion (W), distance of the whorls from the axis of coiling (D), and translational rate of whorls along the axis of coiling (T). If whorl cross sectional shape (S) is assumed to remain constant (say always circular), then all theoretically possible coiling geometries can be visualized as the space within a three dimensional coordinate system, the axes of which are W, D, and T. Raup (1966) defined a surface within this coordinate space that separates a region of whorl overlap which is occupied predominately by univalves from a region in which whorls do not overlap which is occupied predominately by bivalves. Open coiling, or lack of whorl overlap, will occur in planispiral ($T = 0$) shells if either D or W are large enough to prevent whorl contact. In downward spiralling helicoid species ($T > 0$) it can occur either according to the

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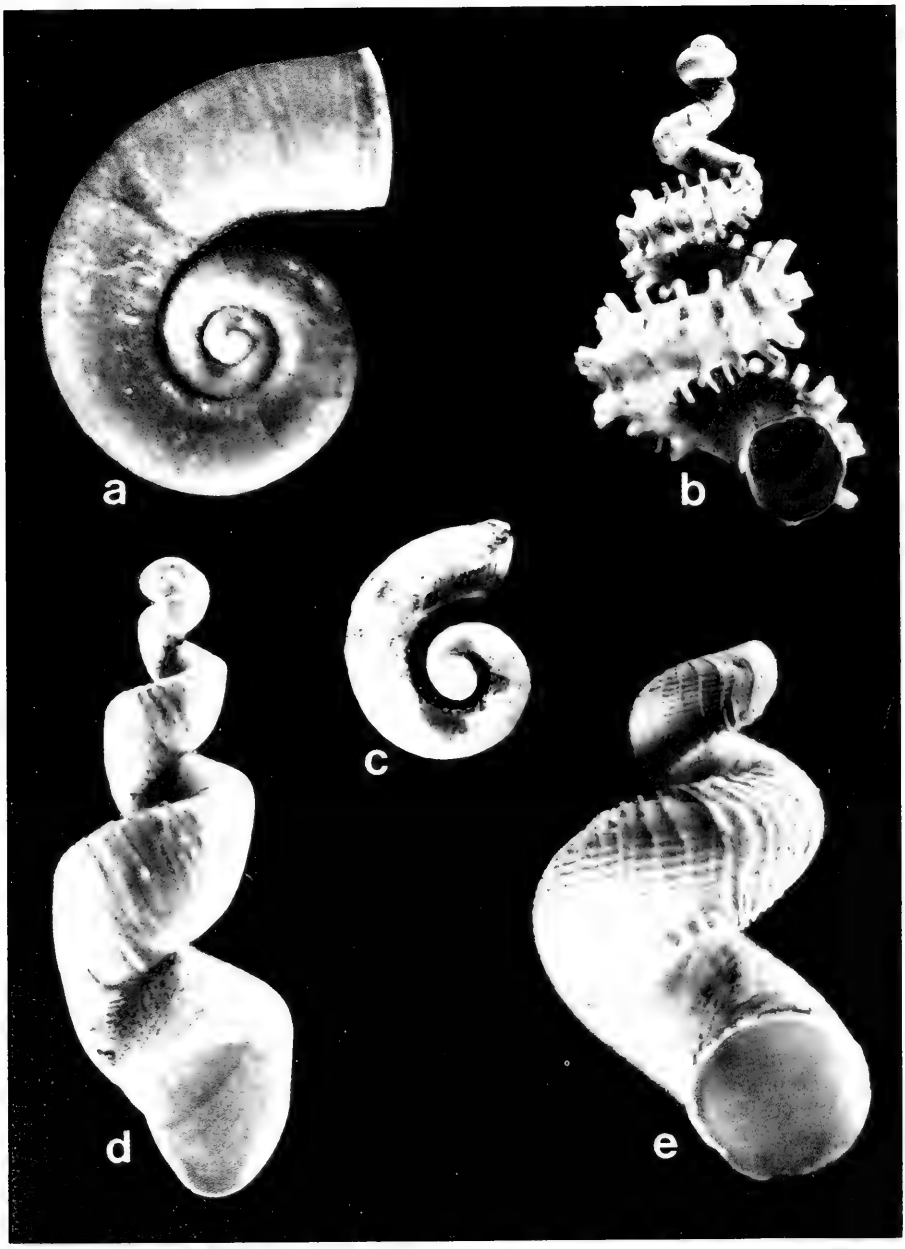

FIG. 1. (a). *Ceratodiscus solutus* Simpson & Henderson, La Ferrière, Haiti, diameter = 4.3 mm, United States National Museum 490059. (b). *Blaesospira echinus* (Pfeiffer), El Queque, Viñales, Cuba, height = 9.0 mm, Museum of Comparative Zoology 193509. (c). *Balambania cornu* (Moellendorff), Kanoan, Siquijor Island, Philippine Islands, diameter = 2.5 mm, Museum of Comparative Zoology 21945. (d). *Baicalia stiedae* (Dybowski), Lake Baikal, U.S.S.R., height = 8.5 mm, Museum of Comparative Zoology 58668. (e). *Epitonium nitidum* (Verrill & Smith), *Travailleur* Station 3, off Portugal, height = 5.5 mm, Museum National d'Histoire Naturelle, Paris 642.

same criteria or if the rate of whorl translation is sufficiently high to prevent contact of successive whorls.

Raup (1966) showed that coiling geometries actually observed in molluscs (and brachiopods) are confined to a relatively small portion of theoretically available forms, and ranges of coiling morphologies utilized by different classes of molluscs tend to be non-overlapping within the potential space. Interesting evolutionary questions can be formulated either from the perspective of the selective pressures which might constrain a taxon to occupy a particular region in the model, or how coiling geometry could be optimized to fulfill some environmental role. Using this approach, Raup (1967) performed an elegant analysis of the theoretical morphology of coiling in planispiral ammonoids. Raup & Stanley (1971) compared density contours on a bivariate plot of actual W and D values for ammonoid genera to adaptive landscapes in the sense of Sewall Wright. Areas of high densities on such plots can be thought of as adaptive peaks and sparsely occupied or unoccupied regions as adaptive valleys.

MATERIALS AND METHODS

Systematic literature on Recent gastropods was surveyed for records of open coiling. Many of the references cited are rather obscure and should in themselves be of interest to students of molluscan morphology. We confined our study to forms that are open coiled according to Yochelson's definition. This approach permitted us to consider open coiling in terms of Raup's model which is based on a logarithmic spiral. Other coiling strategies are discussed in terms of their departure from the constraints of the model. We present only cases in which open coiling appeared to be a specific or subspecific characteristic. The numerous cases of open coiling or uncoiling that arise occasionally as either aberrant individuals or small semi-isolated populations are mentioned in the discussion but not treated in detail. We did not include limpet forms which are, technically speaking, open coiled because of their very high whorl expansion rates, but which deviate from the basic logarithmic model by marked compensatory growth required to ensure firm attachment to hard surfaces (Raup, 1966).

Values of W, D and T were calculated according to criteria outlined by Raup (1966, 1967) from measurements made from photographs or drawings provided in publications where open coiled species were reported. In general, planispiral forms were figured in lateral views and helicoid forms in apertural views. W and D in the planispiral shells were obtained by using the same methods that Raup (1967: 44) applied to planispiral ammonoids except that D could be determined directly since the inner margins of whorls were visible. In downward spiralling forms the axis of coiling was first located as carefully as possible and then W was found as above and D was calculated from measurements taken on the last whorl where the inner margin is visible. D was often either zero or some small value (e.g. see Fig. 1b, d, e). "Translation rate is equal to the calculated ratio of movement of the center of the generating curve along the coiling axis to movement away from the coiling axis" (Raup, 1966: 1181). In open coiled forms the center of the generating curve (i.e. center of whorl cross-section) can be located from apertural views since both the outer and upper (or lower) margins of whorls are visible. The center of the generating curve lies at the intersection of perpendicular lines that extend inward from these points. We calculated T as the ratio of the distance that the center of the generating curve moved down the coiling axis to the difference in its distance away from the axis per half whorl of coiling.

Several difficulties were encountered in measuring the geometric parameters. Illustrations of the shells were generally small and were not oriented in such a way as to permit precise location of the axis of coiling and center of generating curve in all cases. This problem was further complicated by the fact that the axis of coiling is often not straight as Raup's basic model assumes. The model (Raup, 1961) also assumes that the geometric parameters S, W, D, and T remain constant throughout shell growth; but as Gould (1969) pointed out, many species (including some analyzed here) grow allometrically. To minimize these problems we took the mean of measurements on several whorls whenever possible. Another shortcoming of our method is that measurements on a single individual cannot reflect the important population variation in any of the parameters. Because of small sample sizes,

measuring problems and the fact that some features of coiling deviate slightly from the restrictions of Raup's model, the data on coiling parameters plotted below should be accepted as approximate.

RESULTS

Records of species that have open coiled shells according to the above mentioned criteria are listed in Table 1 along with general habitat information and references. Only 15 open coiled species were found in the literature on Recent gastropods. All are prosobranchs and are confined to 10 families of mesogastropods and one family (Cancellariidae) of neogastropods (classification according to Taylor & Sohl, 1962). The frequency of open coiling among the Prosobranchia is 7.5×10^{-4} (15 spp./20,000 spp.), and 4.0×10^{-4} (15 spp./37,500 spp.) among the Gastropoda as a class. Estimates of the number of species in these taxa were taken from Boss (1971). It is likely that some references to open coiling were overlooked. But even taking this probable source of error into account, the frequency of this mode of coiling is exceedingly low.

Values of W, D and T for the 15 species are plotted in Fig. 2 (compare to fig. 7 in Raup, 1966: 1187). The curved surface in Fig. 2 separates a region where whorls overlap below it (occupied by most gastropods) from a region where whorls do not overlap (i.e. open coiling) above it. Forms directly on the surface would have successive whorls just touching. Four species that are planispiral (Nos. 9, 10, and 11 in Table 1), or nearly so (No. 7), exhibit open coiling that results primarily from high values of D. Nine helicoid species (Nos. 1, 4, 5, 6, 8, 12, 13, 14, and 15) show open coiling that arises from unusually high translation rates. Two species (Nos. 2 and 3) are open coiled according to both criteria. The species do not appear to segregate according to general habitat (i.e. marine, land, or fresh-water) and most species lie relatively close to the surface that separates tightly coiled from open coiled forms.

TABLE 1. Species of Recent gastropods that exhibit open coiling.

Family	Genus and species[1]	Locality	Habitat[2]	Reference
Cyclophoridae	1. *Distropis biroi*	Stephansort, New Guinea	T	Soós, 1911; Wenz, 1938
	2. *Cyclosurus mariei*	Mayotte Is., Comores	T	Morelet, 1881; Wenz, 1938
Valvatidae	3. *Valvata sincera*	Northwestern Ontario, Canada	F	Hyatt, 1880; Clarke, 1973
Chondropomidae	4. *Blaesospira echinus*	Western Cuba	T	Crosse, 1890
Hydrobiidae	5. *Baicalia stiedae*	Lake Baical, U.S.S.R.	F	Dybowski, 1875; Kozhov, 1936, 1963
Littoridinidae	6. *Ecpomastrum mirum*	Lake Titicaca, So. Amer.	F	Haas, 1957
Assimineidae	7. *Balambania aries*	Cebu, Philippine Is.	T	Crosse, 1891; Wenz, 1938
Turritellidae	8. *Callostracum gracilis*	Cape Verde Is.	M	Maltzan, 1883; Smith, 1909
Architectonicidae	9. *Spirolaxis exquisita*	Caribbean Sea	M	Dall & Simpson, 1901
Trichotropidae	10. *Lyocyclus solutus*	Indian Ocean, off Southeast Africa	M	Thiele, 1925
	11. *Lyocyclus aethiopicus*	Indian Ocean, off Southeast Africa	M	Thiele, 1925
Cancellariidae	12. *Extractrix milleri*	Pacific Ocean, off Costa Rica	M	Keen, 1971
Epitoniidae	13. *Epitonium nitidum*	Atlantic Ocean	M	Rex & Boss, 1973
	14. *Epitonium revolutum*	Funafuti Atoll, Pacific Ocean	M	Hedley, 1899
	15. *Epitonium echinaticostum*	Caribbean Sea	M	Clench & Turner, 1951

[1]Numbers associated with species are used to plot the species against parameters of shell coiling in Fig. 2.
[2]The symbols T, F and M indicate terrestrial, fresh-water and marine benthic habitats respectively.

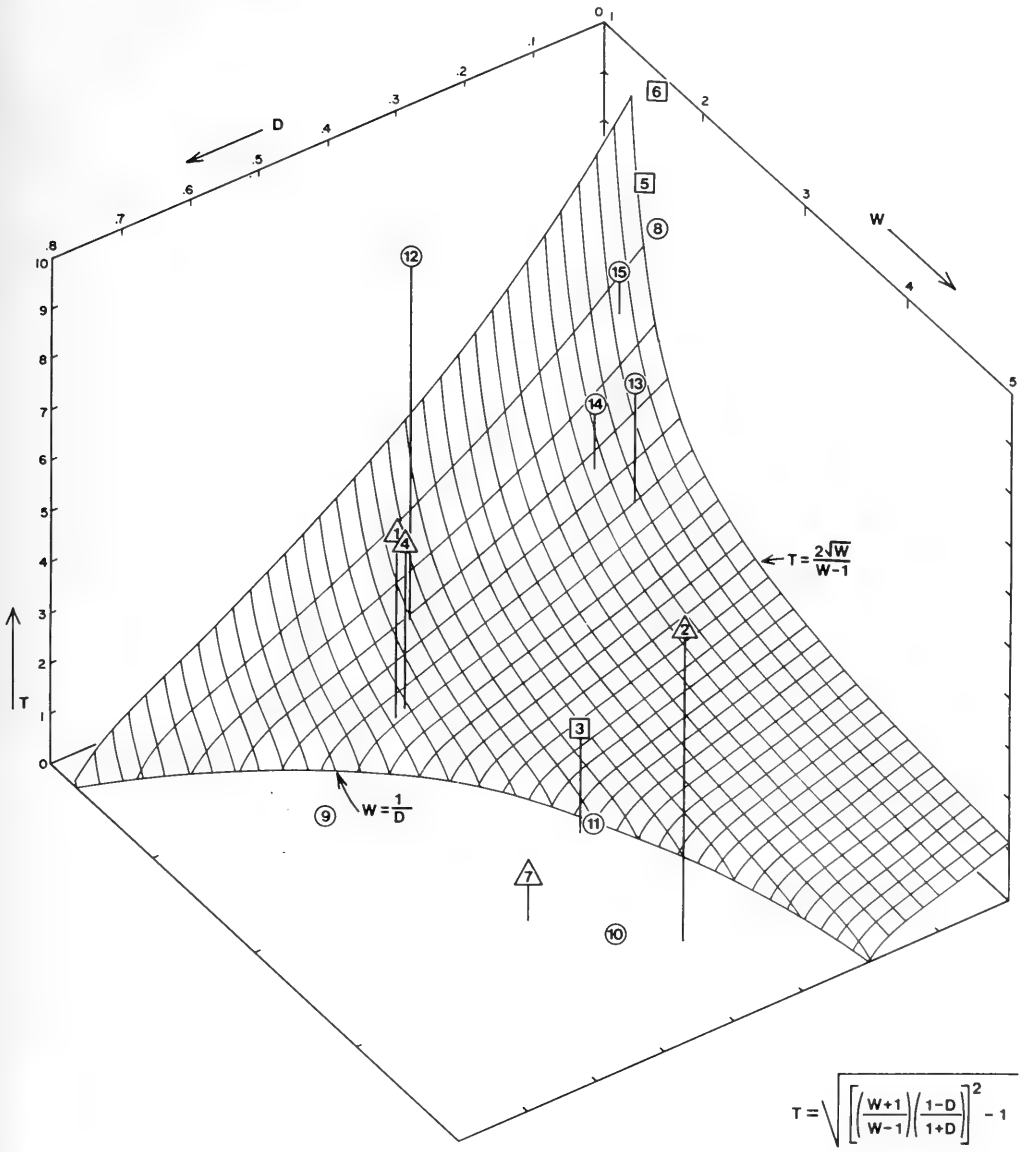

FIG. 2. Three-dimensional plot of W, D and T for 15 species of open coiled gastropods. Numbers representing species are from Table 1. Triangles, squares and circles represent terrestrial, fresh-water and marine benthic habitats respectively. The curved surface separates a region where whorls overlap below it from a region where whorls do not overlap (i.e. open coiling) above it. Forms on the surface would have whorls just touching. The equation for the surface is given in the lower right corner. Equations $W = 1/D$ and $T = 2\sqrt{W}/W-1$ are functions for the intersection of the curved surface with the W–D and W–T planes. Points 6, 5 and 8 lie on the W–T plane ($D = 0$) and points 9, 10, and 11 on the W–D plane ($T = 0$). Locations of other points are indicated by the heights of their stems (reflecting T values) and by the intersection of their stems with the W–D plane below the curved surface. The diagram was first constructed by computer and then reproduced by an artist.

DISCUSSION

The 15 open coiled Recent gastropods occupy only a small region in Raup's theoretically habitable morphological space. Open coiled forms do not substantially increase the proportion of this space that is occupied by the majority of gastropods, though at least 8 species (Fig. 2) do extend the T axis beyond 4.0, the maximum value considered by Raup (1966). The 15 species, either as a whole or as phylogenetic or ecological sub-groups, do not appear to occupy any peripheral novel "adaptive peaks" above the surface that separates tightly coiled from open coiled shells. Both the extreme rarity of open coiling and the close proximity of most open coiled forms to the tightly coiled region in Fig. 2 suggest that the condition of open coiling approaches the limits of adaptation for most shelled gastropods. This limitation may result not only from loss of functional adaptive advantages gained by being tightly coiled, but also from competitive pressure from members of other phyla such as annelids, which exploit very successfully sessile tube-dwelling niches that completely open coiled gastropods would presumably be best suited for. Vermetid gastropods, which are often close to being completely uncoiled, have a very worm-like life style being both sessile and ciliary suspension feeders. By uncoiling extensively vermetids are able to conform to irregular substrates and increase their own surface area for cementation (Gould, 1966). In soft bottom environments uncoiling permits the rapid rate of upward growth necessary to keep their suspension feeding mechanism free of sediment and maximally exposed to suspended organic material (Gould, 1968).

Yochelson (1971) noted a morphological gap in open coiled Paleozoic gastropods between those species in which the shell is nearly straight or only slightly curved and those that have very strongly curved shells. There seemed to be no species showing an intermediate degree of open coiling. This gap represents part of the unutilized morphological space in Raup's model. The dichotomy in the extent of open coiling applies to Recent species as well. Nearly straight shells are found in the family Caecidae and a shell of only slight but still regular curvature is found in the hydrobiid *Orygoceras* sp. where it appears to be an adaptation for mobility in an interstitial environment (Taylor, 1974). Yochelson (1971), following Flower (1955), suggested the possibility that this gap may be bridged by "saltation." The genetic evidence on coiling presented below suggests that alleles (or combinations of genes at different loci) for at least strongly curved open coiled forms are carried in some populations at low frequency and selectively favored in certain environments. Both selectionist and mutationist scenarios can be invoked to explain the evolution of straight shelled forms, but experimental and comparative evidence in support of either hypothesis is lacking. It seems clear that intermediate forms would be strongly selected against in any case. Evidently the limits of adaptation are approached rapidly with even a relatively slight degree of regular open coiling. Beyond this the strategies employed by Recent species involve either a sessile existence and more phenotypic plasticity in coiling or the evolution of a straight shell. The mobility required by snails whether they are active predators or grazing herbivores would be severely impeded by an intermediate condition of open coiling. Clarke (1973) observed that individuals of even the moderately open coiled subspecies of *Valvata sincera* (Table 1) seemed to have unusual difficulty in moving their shells.

The selective significance of open coiling in any of the species treated here is very uncertain since little is known of their habits. However, the general appearance of some species and the biological characteristics of the taxa to which they belong permit some speculation. Open coiling and protruding spines in *Blaesospira* (Fig. 1b) suggest the hypothesis of predator avoidance since an effectively larger and spine-covered snail would be more difficult to consume than compact and relatively smooth forms. Land snails are known to be common prey of birds, mammals and insects (Taylor, 1894-1900), though no observations of predation on *Blaesospira* have been reported to our knowledge. Two of the fresh-water species, *Valvata sincera* and *Baicalia stiedae* and 1 of the marine species, *Callostracum gracilis*, belong to families (Valvatidae, Hydrobiidae [Baicaliidae], and Turritellidae respectively) that are known to contain suspension-feeding representatives (Jørgensen, 1966). If these 3 species are suspension feeders as well, then their open coiling could be adaptive for reasons presented by Gould

(1966, 1968) above. Three marine species, *Epitonium nitidum* (Fig. 1e), *E. revolutum* and *E. echinaticostum* belong to the family Epitoniidae, members of which are ectoparasites on anthozoans (Robertson, 1963). Both their open coiling and axial ribs or lamellae (probably broken off *E. nitidum* during dredging; Rex & Boss, 1973) may function to anchor individuals of these 3 species firmly in the substratum adjacent to their hosts.

It seems likely that selection in the form of biological interactions as well as the animal-sediment relationships stressed by paleontologists plays an important role in maintaining open coiling in Recent species. It is doubtful that open coiling among all 15 species can be regarded as a simple case of convergence related to a sedentary mode of life as in the case of uncoiled marine mesogastropods (Gould, 1966), especially since 4 of the species are land-dwelling where a sessile existence for a snail is unlikely and suspension feeding is precluded. With respect to relative mobility it may be significant that open coiled snails are quite small (e.g. see Fig. 1) as are caecids and *Orygoceras*, and that most open coiling involves a high rate of translation rather than unusually high distance of whorls from the axis of coiling. Large mobile snails, if open coiled, would encounter difficult problems of balancing the shell and surface friction. Among small snails that are open coiled, it may require less effort to pull forward or otherwise control or balance a high spired shell that is moderately open coiled because of a high rate of translation than to balance or move in any way a nearly planispiral open coiled shell such as *Balambania* (Fig. 1c). Eleven of the species (73%) live in an aquatic environment where added buoyancy may partially offset the difficulty of transporting an open coiled shell.

It is puzzling that open coiling in Recent snails is phylogenetically confined to the Prosobranchia even in land and fresh-water habitats that are heavily dominated by pulmonates. Within the prosobranchs certain genera such as *Epitonium* seem to show a propensity for open coiling. Certain other wentletrap-like epitoniids not treated here have shells with whorls that are just touching or slightly solute but with sculptural varices that impinge upon successive whorls (e.g. see Clench & Turner, 1951). Open coiling is known to occur sporadically in the pulmonate genera *Planorbis, Gyraulus, Lymnaea, Helix*, and *Biomphalaria* (Férussac, 1819-1832, 1822; Porro, 1838; Piré, 1871; Van den Broeck, 1872; Taylor, 1894-1900; Hofmann, 1924; Schlesch, 1927; Sprick, 1927; Basch, 1968; Gasull, 1971; Lisický, 1972). Many of the examples in these papers were adults, so open coiled individuals are not completely selected out of populations at young stages. Richards (1970) showed that open coiling in *Biomphalaria glabrata* was a heritable sublethal genetic effect and that crosses involving open coiled individuals produced high mortality in the progeny. Stelfox (1968) actually obtained open coiled *Helix aspersa* by selectively inbreeding unusually high spired (but still tightly coiled) specimens found in his garden. Yet there seem to be no open coiled pulmonate species. Both the experiments and numerous sightings in nature suggest that many pulmonate populations carry rare genes for open coiling and that coiling is well canalized as we might expect of any highly adaptive trait. Unfortunately, we know of no such observation on prosobranchs. However, Clarke (1973) reported that *Valvata sincera* has various populations that are either tightly coiled, open coiled, or mixed, again suggesting that open coiling is a trait with a genetic basis that is carried in a species population and favored in suitable habitats.

Whatever the adaptive advantages of open coiling, it appears to have sometimes been a successful strategy in terms of survival where it has occurred. Clarke (1973) reported *Valvata sincera* from the Late Wisconsin age of the Pleistocene, and *Epitonium revolutum* is known from the Late Miocene (Ladd, 1972). The genus *Extractrix* also has a fossil representative, *E. extractrix* in the Miocene (Korobkov, 1955). The family Micromelaniidae contains several extinct fresh-water representatives that lived during the Late Tertiary, including *Streptocerella sokolovi* (Andrussov, 1902), *Avardaria andrussowi* (Ali-Zade, 1932; Kolesnikov, 1950) and the genus *Baglivia* which underwent an adaptive radiation during the Lower Pliocene (Brusina, 1892, 1902; Wenz, 1926) that produced at least 4 open coiled species similar in appearance to the hydrobiid (baicaliid) *Baicalia stiedae* shown in Fig. 1d. The nearly straight shelled *Orygoceras* sp., also a hydrobiid, is known from the Late Tertiary of both southeastern Europe and northwestern United States (Taylor, 1974).

The success of *Epitonium nitidum* is indicated by its broad geographic range which includes both the eastern and western North Atlantic Ocean and a bathymetric distribution extending from the continental shelf to abyssal depths (Rex & Boss, 1973).

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THE SYSTEMATICS AND DISTRIBUTION OF *LOLIGO* (CEPHALOPODA, MYOPSIDA) IN THE WESTERN NORTH ATLANTIC, WITH DESCRIPTIONS OF TWO NEW SPECIES[1]

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ABSTRACT

The common squid *Loligo pealei* Lesueur, 1821, lives on the continental shelf and slope of the North and South American continents from Nova Scotia to the Gulf of Venezuela. Statistical analyses show that 1) females have a wider gladius and fewer gill filaments than males; there also is slight but statistically significant sexual dimorphism in 3 other characters; 2) populations vary but there are no clines in 50 anatomical measurements. However, southern *L. pealei* (Caribbean Sea-Gulf of Mexico) differ in the following ways from northern *L. pealei* (eastern United States Atlantic coast): 1) gill length increases faster in relation to mantle length in the southern squid; 2) there is more variation in the hectocotylus and number of buccal lappets in the southern squid.

Variation in *Loligo pealei* appears greater in areas of sympatry with *L. plei* (= *Doryteuthis plei*); much of this variation takes the form of greater resemblance to *L. plei*. These 2 species overlap in almost all characters. The ratio of the greatest width of the gladius vane to the greatest width of the free rachis can be used to distinguish the 2 species. The geographic range of each species is redefined.

Two new species of *Loligo* are described: *Loligo ocula*, a large-eyed species caught at 256-362 m in the Caribbean Sea and between Cuba and the Bahamas, and *Loligo roperi*, a small species from the Caribbean.

The 4 species are compared. In many characters they show the following relationships: *Loligo ocula* is most similar to *L. pealei*; *L. pealei* is also similar to *L. plei*; *L. plei* is most similar to *L. pealei*, but is also similar to *L. roperi*; *L. roperi* is the most distinctive of the 4 species.

Loligo roperi matures at a small size and then apparently ceases growing or does not survive spawning; it may be a somewhat neotenic relative of *L. plei*. The larger eyes in *L. ocula* (and correspondingly larger head and mantle width) may be an adaptation to living at depths greater than are typical for the Loliginidae.

In the western North Atlantic, the greatest species diversity for both *Loligo* and the Loliginidae occurs in the Caribbean Sea. A key to these 4 species of *Loligo* of the western North Atlantic Ocean is given.

INTRODUCTION

Interest in *Loligo pealei* Lesueur, 1821, as a fisheries resource for bait and food, and as a source of large axons for neurological research, has stimulated many studies—chiefly of populations that occur between Cape Hatteras and Nova Scotia.

The purpose of this study is to clarify the systematic status of a taxonomically confused group of commercially important cephalopods. Considerable variation has been noted in *Loligo pealei*; some specimens of *L. pealei* are so similar to some specimens of *L. plei* Blainville, 1823, that misidentifications often occur in spite of existing keys (Voss, 1956: 91). Verrill (1880, 1881), Arnold (1962), LaRoe (1967), and Voss (personal communication) have suggested that variation in *L. pealei* is geographic. This study examines variation in *L. pealei* and describes and compares the 3 other species of *Loligo* which are partially sympatric with *L. pealei.*

Loligo pealei is the most widely distributed of the neritic squid in the western Atlantic (LaRoe, 1967), where it has been reported to extend from Nova Scotia (Mercer, 1970a) to Colombia (LaRoe, 1967). This is a latitudinal distance of more than 35 degrees and includes the Caribbean Sea, the Gulf of Mexico, and the Atlantic coast of North America (Fig. 1).

[1]Part of this investigation was done in partial fulfillment of the requirements for the degree of Master of Science, University of Maryland.

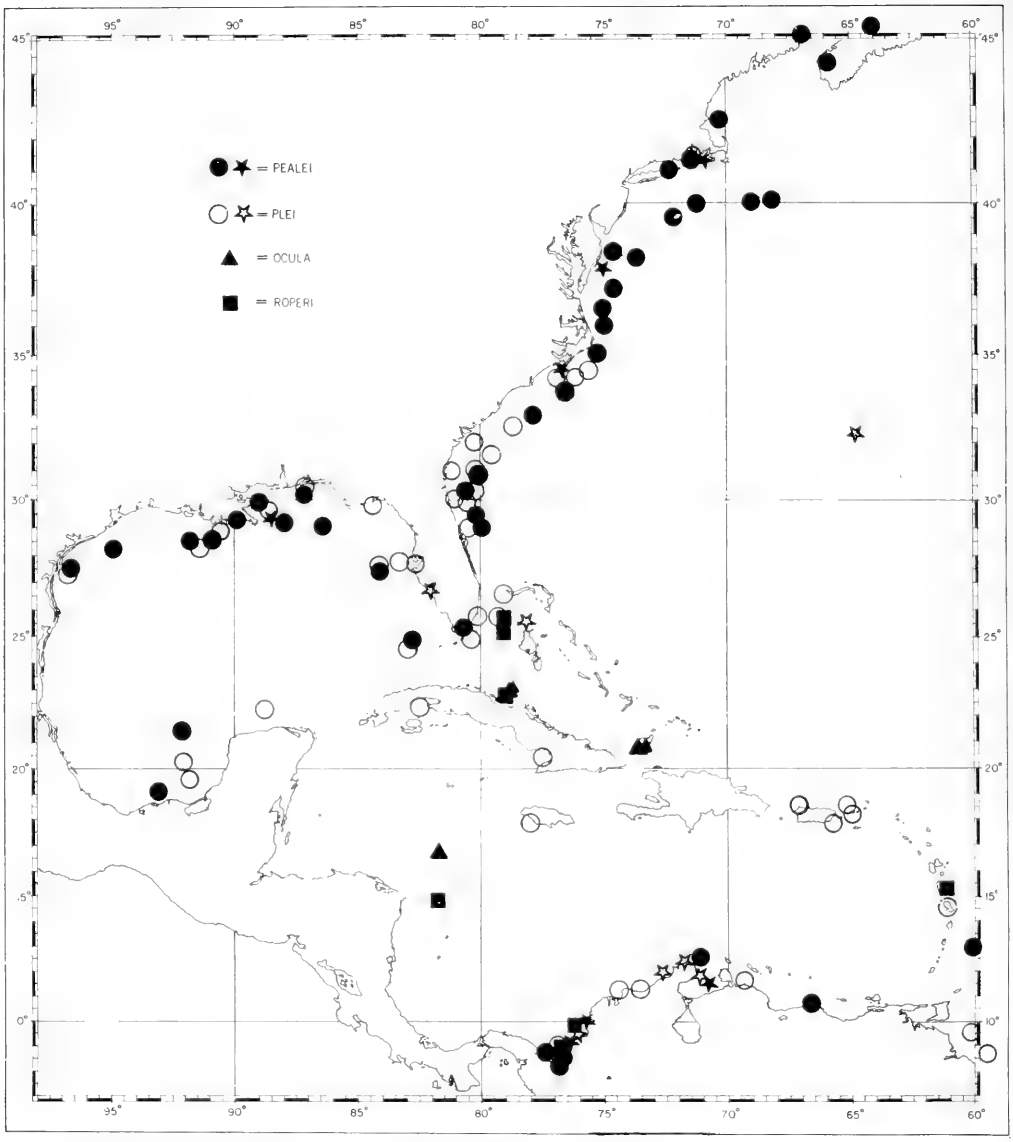


FIG. 1. Map showing location of statistical samples of *Loligo pealei* and *L. plei* and other records of capture of *L. pealei, L. plei, L. ocula,* and *L. roperi.*

MATERIALS AND METHODS

MATERIALS: All material studied is listed in the species descriptions or in Appendix A. Most of the material for this study was provided by the Smithsonian Institution. Material was also provided by the Marine Biological Laboratory of Woods Hole, the Rosenstiel School of Marine and Atmospheric Sciences at the University of Miami, the Florida State Board of Conservation, the National Marine Fisheries Service, and J. Ewald of the Fisheries Research and Development Project, Food and Agricultural Organization of the United Nations.

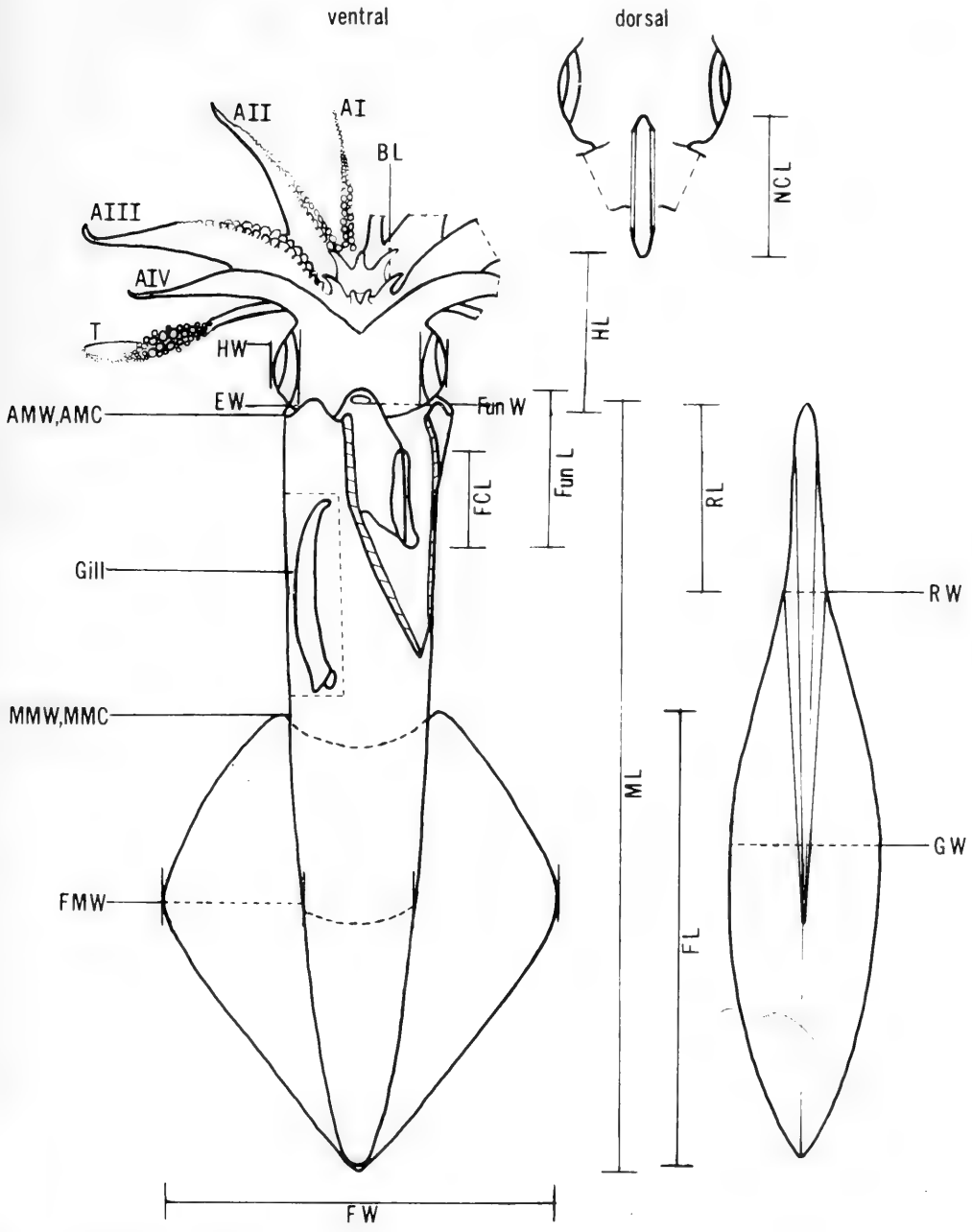


FIG. 2. Diagram of measurements.

DESCRIPTION OF MEASUREMENTS: Most of the measurements in the following list are shown in Fig. 2. Dorsal, ventral, anterior and posterior refer to orientation of the adult in life.

MEASUREMENTS:

AL arm lengths measured from proximal-most sucker to arm tip on right arms. (Left arm measured if a right one was missing. Only right ventral arm of males used because left ventral male arm is hectocotylized.)

ALI length of 1st or dorsal arm.

ALII length of 2nd arm.

ALIII length of 3rd arm.

ALIV length of 4th or ventral arm.

AMC mantle circumference measured at anterior border (opening).

AMW mantle width at anterior border (opening) with mantle held as cylindrical as possible.

ASW I, II, III, IV greatest width of largest sucker on right (left if right arm is missing) arms I-IV.

BE distance between median borders of eyes with head compressed.

ED greatest diameter of white eyeball visible externally through cornea.

FCL greatest length of entire right funnel cartilage.

FL fin length from point on dorsal mantle midway between fin insertion, to posterior body tip.

FMW mantle width coincident with widest point of fins.

Fun L ventral funnel length from midpoint of anterior opening to midpoint of posterior border.

Fun W greatest width of anterior funnel opening measured by spreading dividers as widely as possible inside orifice.

FW greatest width of both fins between lateral-most points.

Gill F number of outside filaments on right gill.

Gill L length of right gill from proximal attachment of branchial vein to gill tip.

Gill W greatest width of right gill.

GW greatest width of vane of gladius.

HAL length of hectocotylized arm.

HCL length of hectocotylus from its origin proximally to arm tip.

HL head length from anterior tip of nuchal crest to juncture of dorsal arms.

HW greatest head width at level of eyes with head strongly ventro-dorsally compressed between two fingers.

LD diameter of dissected lens.

ML length of mantle from anterior tip of mid-dorsal point to posterior body tip.

MMC mid-mantle circumference at level of fin insertion.

MMW mid-mantle width at level of fin insertion.

NCL greatest length of entire nuchal cartilage.

RL length of free rachis.

RW greatest width of rachis of gladius.

TCL length of right tentacular club (left if right club is missing) from proximal-most sucker to tip.

TL length of right (left if right tentacle is missing) tentacle from origin between A III and IV to tip.

TSW greatest width of largest sucker on right (left if right tentacle is missing) tentacle.

COUNTS:

ASI, II, III, IV total number of suckers on right arms I, II, III, IV (left arm used if part of right arm missing).

BLS 1,2,3,4-5,6,7 number of suckers on each buccal lappet (counting counter-clockwise beginning with mid-dorsal lappet).

H number of modified suckers on hectocotylus in the dorsal row that are less than 1/2 the size of their partners in the ventral row.

HAS total number of suckers

on hectocotylized arm from proximal-most modified sucker to arm tip.

TSR number of transverse rows of suckers across right (left if right tentacle is missing) tentacular club (4 suckers in each row).

For convenience, males were considered mature if spermatophores were present in Needham's sac, and females were counted as mature if the ovaries were filled with eggs; since this method is inadequate in recently spent animals, the lengths of penises and female accessory nidamental glands were recorded.

Most measurements were made with dividers and a ruler with 0.5 mm divisions, and were recorded to the nearest mm. Sucker widths were measured with a micrometer caliper with 0.05 mm divisions and recorded to the nearest 0.1 mm.

AMC and MMC were measured with a steel tape with 1 mm divisions. Because the mantle wall is often very flaccid, circumference probably is a more accurate measurement than width. Both measurements were made because MW is widely used by others.

Arm tips and gills were stained with methyl blue solution to facilitate counting of suckers and gill filaments. The largest suckers were removed from the right 3rd arms and the tentacles of 52 specimens of *Loligo pealei* and 10 specimens of *L. plei* and glued to cardboard slides with a numbered grid for comparison of dentition. Spermatophores were mounted on glass slides with Turtox CMC-10 mounting medium; after several months they deteriorated.

Gladius length was not measured because of the difficulty in removing the entire gladius intact from many specimens and because gladius length is almost the same as ML which is measured directly over the gladius.

Other measurements taken initially but discontinued include the number of muscle strands in the fin (too difficult to count) and the number of suckers from the base of the arm to a point on the arm equal to 1/5 ML (results influenced by AL:ML). The following measurements were discontinued because the results did not show any useful pattern: the number of suckers on the basal half of the arm, the angle of the vane of the gladius at its origin on the rachis, distance between the insertion of the fins, and dimensions of the funnel valve.

STATISTICAL ANALYSES: Data were analyzed on the UNIVAC 1108 at the Computer Science Center of the University of Maryland with canned computer programs. The BMDO2D and BMDO3D (Dixon, 1970) were used to obtain means, standard deviations, correlation coefficients, sums of squares and cross plots.

Many characters of *Loligo pealei* change with growth. Haefner (1964) found that indices (dividing by ML) of FW, FL, MW, HL, and HW change with growth in *L. pealei*. Since it was impossible to get samples of equal size for comparison, an analysis of these characters that would eliminate the effect of differences due to growth was made. Covariance (ANCOVA) analyses were done with the Manova program (Biometric Laboratory, no date). This program allowed the analysis of the factors of geographic location and sex simultaneously and printed out means, standard deviations, variance and covariance tables, F values, probabilities for F values for regressions and factors, grand means, deviations of factor means from grand means, and within regression coefficients and intercepts.

When a significant F value was found, a Studentized Range Q test (Snedecor & Cochran, 1969: 272-274) was used to find significant differences between factor means. Differences between 2 regressions were tested by the method of Snedecor & Cochran (1969: 432-435).

Analyses were made using ML and FCL as independent variable and covariate. ML is the commonly used measure of standard length in squid. FCL was used because FCL shows higher correlations with many characters than ML does (Tables 4 and 5), because fewer inequalities of variance occur with FCL than with ML, and because of the results of the preservation experiment (discussed below). In those cases in which similar results were obtained with analysis using ML and FCL, ML is the independent variable shown in graphs illustrating this study because ML is the common measure of standard length. Statistical results (analysis of covariance and regression equations) are given in Appendix B.

EFFECTS OF PRESERVATION

Preservation with formalin has been found to shorten the length of fishes. For example, *Oncorhynchus* shrank 3% after 12 hours in 3.8% formalin and 1% more after 30-40 days; further changes in length were insignificant (Parker, 1963). *Oncorhynchus* shrank 4.6-6.8% after 5.5 months in 10% formalin; about 80% of the total decrease occurred in the first 24 hours.

In the squid *Loligo pealei* and *Lolliguncula brevis*, Haefner (1964) reported more than 5% shrinkage in the length of arms and tentacles after preservation in 5% formalin.

Methods of preservation of most samples available for this study were suspected to be different; this could cause artificial differences in measured characters. I was able to collect only 2 fresh samples; one, consisting of 44 specimens, was divided into 3 parts and preserved by 3 different methods. Covariance analyses were made to determine if differences in techniques of preservation caused significant differences in any measurements. The methods of preservation were: 1) 9 specimens (86-188 mm ML) were kept on ice and refrigerated for 2 days before being preserved in 10% formalin. After 16 days they were rinsed and placed in 40% isopropyl alcohol. 2) 22 specimens (76-244 mm ML) were preserved in 10% formalin immediately after capture, then rinsed and placed in isopropyl alcohol 2 days later. 3) 13 specimens (130-234 mm ML) were preserved in 10% formalin immediately after capture, then rinsed and placed in isopropyl alcohol 16 days later.

Results of this experiment are shown in Table 1. When formalin preservation is delayed (method 1), the size of AL II and TL are statistically significantly larger when either ML or FCL are used as covariates.

FCL is also statistically significantly greater under method 1 with ML as covariate. The following results are probably related to the relationship between ML and FCL. Statistically significant difference in these variables depends on which of the 2 covariates is used with them. When ML is used as covariate (but not when FCL is used as covariate) the following measurements are statistically significantly higher in method 1, when formalin preservation is delayed, than in methods 2 and 3: HL, ALI, ALIII, ALIV, TCL, ASW III, Fun L, and Fun W. Sucker widths of the other arms were not tested but it is likely that they would show similar results.

When FCL is used as covariate (but not when ML is used as covariate) the following measurements are statistically significantly smaller when formalin preservation is delayed: FL, FW, MMW, and NCL. In order to eliminate bias between specimens which have been preserved differently, it is necessary to use the covariate (ML or FCL) with which the measurement has shown no preservation differences.

TABLE 1. Measurements of *Loligo pealei* significantly affected by differences in the method of preservation ($p < 0.05$).

Measurement	Covariate*	Significant difference between adjusted means in mm		Sample size		
		Method 1 minus Method 2	Method 1 minus Method 3	Method 1	Method 2	Method 3
ALII	ML	12.1	8.6	9	16	10
ALII	FCL	6.8	—	9	16	—
TL	ML	49.3	39.7	8	21	12
TL	FCL	39.5	29.4	8	21	12
FCL	ML	2.0	—	9	16	—
HL	ML	6.0	—	9	16	—
ALI	ML	10.2	6.6	9	16	10
ALIII	ML	11.0	9.6	9	16	10
ALIV	ML	8.8	7.3	9	16	10
TCL	ML	8.7	7.2	8	21	12
ASWIII	ML	0.32	—	9	16	—
Fun L	ML	2.6	—	9	16	—
Fun W	ML	1.7	—	9	16	—
FL	FCL	−16.9	−16.2	9	16	10
FW	FCL	−10.2	—	9	16	—
MMW	FCL	−2.2	−3.5	9	16	10
NCL	FCL	−2.3	—	9	16	—

*Covariance was effective in all cases. P less than 0.001 for F test of mean square due to regression.

HW, AMW, MMC, Gill L, and GW show no significant preservation differences using either ML or FCL as covariates. There are no significant differences between methods 2 and 3 for any measurements.

Differences in preservation did not affect tests for sexual dimorphism since both sexes were present in all samples. Effects of preservation would have to be considered in comparing geographically different population samples since these were preserved differently by different collectors. Past descriptions of *Loligo pealei* and probably other species of squid may be biased in the measurements which are affected by preservation differences.

A more comprehensive experiment to determine the full extent of preservation differences would be worthwhile. A larger sample should be tested. Delays in fixation of 1 week or even 2 weeks should be tested as preservation is sometimes delayed that long when squid are iced or frozen on board ship and not preserved in formalin until port is reached.

This experiment did not show 1) whether both covariates, FCL and ML, shrink less when preservation is delayed but FCL shrinks even less than ML, or 2) whether both shrink more when preservation is delayed, but ML shrinks even more than FCL. An experiment including measurements of fresh specimens would be necessary to determine this. FCL is a measurement made directly upon a rigid structure and it is unlikely that it shrinks much with preservation. ML is a fairly reliable measurement because it is made where the mantle overlies and is rigidly supported by the attached rigid chitinous gladius. ML was measured on 7 specimens before and after immediate fixation; preservation caused as much as 6% shrinkage. LaRoe (1967) found shrinkage in 15 immediately preserved specimens averaged 1.2% with a maximum of less than 2.5%. The entire gladius was removed from some specimens and it is often a few mm shorter than the ML measured before removal. Such removal of the supporting gladius shortens the mantle.

The Smithsonian Institution has many specimens collected by A. E. Verrill between 1875 and 1880. Verrill, in his publications, listed many of the measurements of these specimens along with remarks on their preservation (Verrill, 1881). I found 6 of these specimens with Verrill's identifying numbers still tied to them and in 1972 remeasured them twice. The specimens were originally 124-254 mm ML and bear Verrill's numbers: DD♀, HH♀, IV♀, 8V♂, d♂, and c♂. Table 2 shows the results. These specimens had been stored in 70% ethanol for 92-97 years between the time of Verrill's measurements and mine. The sample is very small. I cannot know how my methods of measurements differed from Verrill's; however there was sometimes a greater difference between my 2 measurements than between mine and Verrill's. Mantle length shrank slightly. Fin width was shorter or the same in 5 specimens and slightly wider in one. Head width and tentacular club length were greater. Mantle width and circumference were less in 4 specimens and greater in 2. Change in the other measurements was more inconsistent.

The small change in mantle length agrees with Parker's (1963) and Burgner's (1962) report that in the fish *Oncorhynchus* most shrinkage in length occurs only in the first day after preservation. While delay in preservation affects some measurements of squid, well-kept museum specimens may not change greatly in morphometrics following the changes which occur at death and initial preservation.

TABLE 2. Morphometric changes in *Loligo pealei* after 92 years of storage in 70% ethyl alcohol.

Measurement	n	Average difference between Verrill and Cohen measurements, mm	Effect	Average change %	Greatest single change %
Mantle length	6	−1.9	shorter	1.0	1.6
Fin length	6	−1.7	inconsistent	2.8	12.0
Fin width	6	−3.3	shorter	3.6	6.8
Head width	5	+3.0	wider	9.9	19.0
Mantle width	6	−1.4	inconsistent	12.0	13.0
Mantle circumference	6	−3.4	inconsistent	5.5	13.0
Tentacular club length	5	+1.6	longer	7.9	20.0
Tentacular sucker width	3	0.0	inconsistent	0.0	9.1
Arm III sucker width	3	−0.17	inconsistent	6.4	20.0

SYSTEMATICS

Loligo pealei Lesueur, 1821
(Figs. 3-4)

Loligo pealeii Lesueur, 1821: 92-94, pl. 8.—Férussac & d'Orbigny, 1834-48, pl. 11.—Drew, 1911: 327-359; 1919: 379-418.

Loligo pealei Lesueur.—Férussac & d'Orbigny, 1834-48: 311-312.—Verrill, 1880: 292-293; 1881: 308-343, pl. 29, figs. 1-4, pl. 37, figs. 1-3, pl. 39, fig. 4, pl. 40, pl. 41, pl. 45, figs. 3-4.—Voss, 1956: 112-115, fig. 5; 1962: 1; 1973: 24-25.—Dillon & Dial, 1962: 156-166.—Summers, 1968: 366-367; 1969: 202-216; 1971: 189-201.—Summers & McMahon, 1970: 389-396.

Loligo pallida Verrill, 1873: 635-636, pl. 20, figs. 101, 101a; 1874: 169-170, figs. 54-55; 1880: 293.

Loligo pealei Lesueur var. *borealis* Verrill, 1880: 284-295; 1881: 308, 316-317, pl. 37, fig. 2, pl. 41, fig. 1.

Loligo pealei Lesueur var. *pallida* Verrill.—Verrill, 1881:308, 317-318, pl. 34, figs. 1-4, pl. 37, figs. 9-11, pl. 40, fig. 1.

Loligo pealii Lesueur.—Verrill, 1874: 170-172.—Williams, 1909: 1-92.—Stevenson, 1934: 4-7, figs. 1-2.—Adam, 1937: 62-63, fig. 16.—Arnold, 1962: 53-57.

DIAGNOSIS: Ratio of greatest width of vane of gladius to greatest width of free rachis 2.4-2.9 in males, 2.7-3.7 in females; hectocotylus originating in distal 1/3-1/4 of left ventral arm, not extending to arm tip, not more than about 12 suckers in dorsal row less than 1/2 the size of their ventral counterparts, at least some modified suckers of dorsal row with narrow bases.

DESCRIPTION: *Mantle* long, moderately slender, cylindrical, tapering to a posterior rounded point. Anterior mantle width 14-37% of ML (25-315 mm ML); anterior mantle circumference 39-44% of ML (95-244 mm ML); longer specimens more slender. Ventrolateral lobes on mantle opening short and pointed (point approximately 90° angle, usually slightly acute, sometimes slightly rounded); dorsal lobe larger than lateral lobes, with rounded point. Low, narrow mid-ventral ridge present (mostly in males).

Fins rhomboid, sides fairly straight, widest point curved and slightly anterior of midpoint of fin length; fins united posterior to tip of mantle; width about 34-56% of ML (45-315 mm ML); length about 44-64% of ML (45-314 mm ML); width about equal to length; ratio of length to width = 0.812-1.88 (64-315 mm ML). Fins relatively longer and more narrow in longer specimens; anterior lobes well-developed.

Funnel well-developed, set in deep funnel groove. Funnel opening level with eyes. Lateral adductor muscles conspicuous, strong, rod-like; anterior adductors thin, sheet-like. Dorsal funnel organ large; posterior limbs broadened anteriorly, tapering posteriorly to blunt, rounded points, lateral borders curved more than medial borders; apical papilla minute and rounded or pointed at tip. Ventral pads oblong, shorter than dorsal organ. Funnel valve broad, blunt or bluntly rounded, with thin curved lateral flaps.

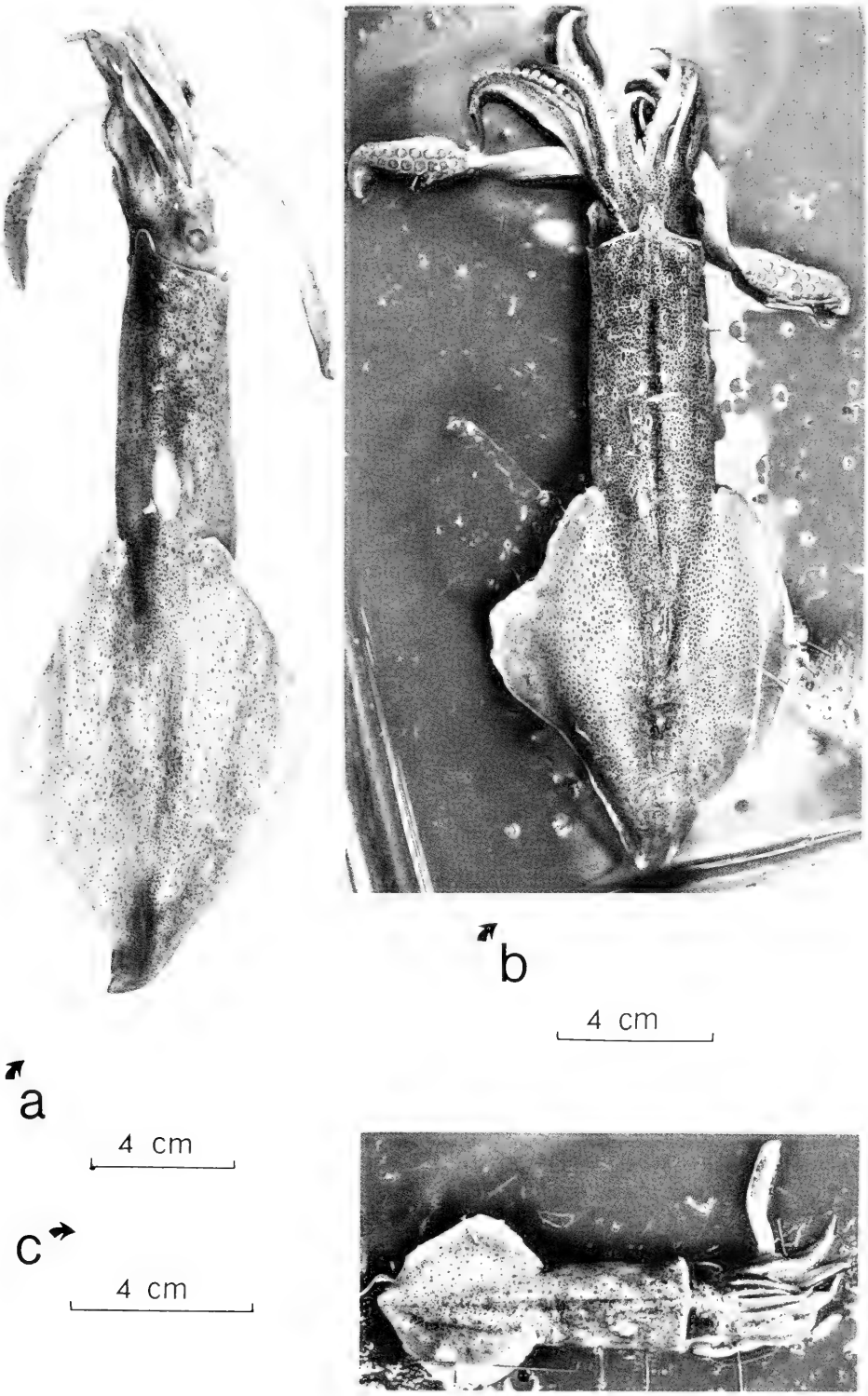
Funnel locking-cartilage long (about 10-18% of ML, 60-314 mm ML), straight, compliment of funnel lock. Longitudinal ridge low and narrow.

Head width about 12-33% of ML (45-314 mm ML); length about 10-30% of ML (70-315 mm ML); head relatively smaller in longer specimens; nuchal cartilage long, about 13-22% of ML (60-273 mm ML), cartilage relatively shorter in longer specimens, straight, broader anteriorly, embedded in muscle except for anterior and posterior ends which taper to blunt or rounded points; shallow central groove, lateral ridges distinct.

Eyes oval, covered by cornea, pupil round. Diameter of externally visible eyeball about 8-18% of ML (25-237 mm ML). Diameter of dissected lens about 2-6% of ML (72-291 mm ML). Dark, rarely greenish, crescent along dorsal border of eye. Aequiferous pore at anterior edge of cornea.

Arm order usually III>II>IV>I or III>IV≥II>I, occasionally III>II>I>IV, III>IV>I>II, III>I>II>IV, II>III>I>IV, II>IV>III>I, IV>III>II>I, IV>II>III>I. Length of arm I about 19-50% of ML; length of arm II about 22-50% of ML; length of arm III about 26-45% of ML; length of arm

FIG. 3. Examples of *Loligo pealei* showing variation in relative proportions of mantle and fin; **a**, ♂, 214 mm ML; *Cynthia*, Cohen statistical sample no. 20; **b**, ♀, 179 mm ML; Cohen spec. no. 8, stat. sample no. 1; **c**, ♂, 70 mm ML; York Spit Light, Chesapeake Bay, 2 July 1968.


b
4 cm
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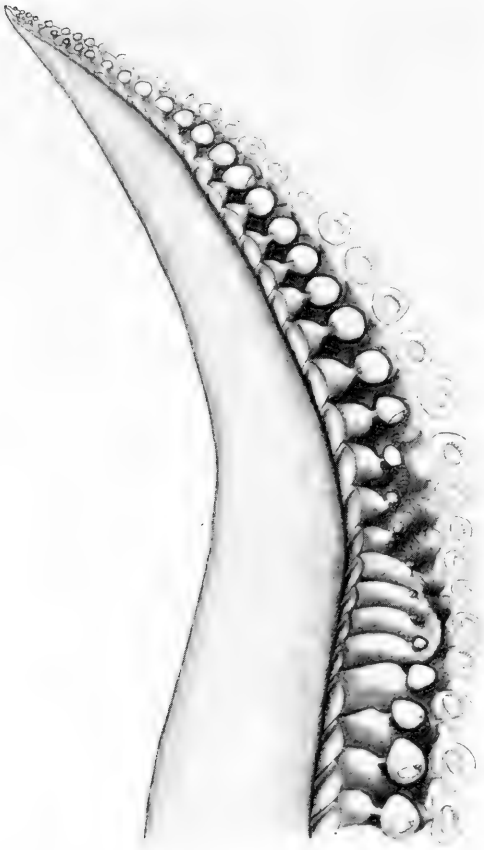

FIG. 4. *Loligo pealei* hectocotylus; 244 mm ML; *Cynthia,* Cohen spec. no. 272, statistical sample no. 13; distal 20 mm (distal third) of arm shown.

IV about 22-38% of ML (60-315 mm ML). Arm III robust, IV, II less robust, I least robust, very slender. Swimming keels third-best developed on arm I, flaring before midpoint, decreased to very low distally; very low, weak on arm II, decreased distally; best-developed on arm III, flared before midpoint, decreased gradually distally; second-best developed on arm IV, 2 keels decreased gradually distally, dorsal keel better-developed, dorsal keel of arm IV and keel of arm III arising from same area at base of arms. Protective membranes well-developed, particularly ventral membranes on arms I, II, III; poorly developed, particularly dorsal membrane, on arm IV; trabeculae long, strong, except on arm IV, arise from base of sucker stalks, form high points along membranes. Suckers biserial. Distad increase in size of about 5-10 proximal-most suckers on arms I, II, III, sometimes IV; gradual decrease in size of succeeding suckers; rapid decrease in size of suckers on arm III following about 20th-25th sucker. Number of suckers on arms increases with mantle length; number of suckers on arms I, II, III about equal, about 10 more suckers on arm IV than on other arms; about 65-125 suckers on arm I, about 70-125 suckers on arms II, III, about 84-132 suckers on arm IV (40-315 mm ML). Width of suckers on arms in order III≥II≥I≥IV.

Arm sucker dentition variable. Teeth usually present on distal 1/2 of tooth ring only. Proximal 1/2 of tooth ring usually low, broad plate, occasionally rippled, rarely defined into about 10-20 tiny blunt teeth. About 6-10 teeth on distal 1/2 of arm I; about 7-12 teeth on distal 1/2 of arm II; about 6-11 teeth on distal 1/2 of arm III; about 5-8 teeth on distal 1/2 of arm IV. Teeth shape and pattern varies, tips of teeth usually blunt or rounded, apparently never pointed; teeth sometimes square, center 1-4 teeth often narrowest, teeth decrease in size laterally, pattern not always symmetrical.

Left ventral arm *hectocotylized* (Fig. 4), modification in distal 1/3 to 1/4 of arm, chiefly in dorsal sucker row, does not extend to tip of arm; usually only 10-12 suckers in the dorsal row less than 1/2 the size of their ventral counterparts (range of variation observed 5-17). About 34-61 suckers proximal to hectocotylus, proximal-most about 6-24 suckers increasing slightly in size distally, followed by suckers of slightly decreasing size. About 52-82 suckers distal to origin of hectocotylus; hectocotylization originates proximally with about 2-5 suckers in the dorsal row diminishing in sucker size and increasing in pedicel height, followed by 1-4 tiny suckers on long pedicels, followed by 2-5 tiny suckers on pedicels of decreasing height, followed by 5-8 suckers of increasing size; ventral suckers in modified area reduced slightly, at least twice the size of their dorsal counterparts, pedicels normal; suckers distal to modified area normal in both rows except dorsal suckers often slightly smaller than ventral suckers. Central area of arm in modified area raised, puffy and folded with central ridge connecting the folded bases of the arms.

Tentacles robust. Clubs expanded, about 20 to 38% of ML (60-315 mm ML). Clubs with 30-45 transverse rows of 4 suckers each (20-315 mm ML). Distinct carpal cluster

absent, suckers in ill-defined carpal area small, biserial, only about 1-3 suckers; no carpal knobs. Often only 3 small suckers in proximal-most row of manal suckers; distal rows tetraserial; suckers gradually increase in size; lateral manal suckers smaller than medial suckers; about 12-17 medial suckers on manus greatly enlarged; manus terminates rather abruptly; distal-most 1 or 2 transverse rows of manal suckers decrease in size, lateral suckers more equal in size to medial suckers, ventral lateral sucker becomes larger than dorsal lateral sucker of same transverse row and this size difference sometimes continues for as many as 14 rows of the dactylus. Dactylus distinct, slender, suckers tetraserial, numerous, minute, decreasing in size distally; distal-most 2 transverse rows often triserial and biserial. Tip with narrow, suckerless flange. Swimming keel short and inconspicuous on stalk, along at least distal 1/2 of stalk aborally, increases in size on club particularly on distal 1/3 of manus, broadest along dactylus, diminishes at distal tip. Lateral angles distinct on oral surface and continue as broad, heavily supported protective membranes along club, diminish significantly along dactylus; dorsal membrane slightly smaller than ventral membrane along manus and insignificant along dactylus. Broad trabeculae between lateral suckers, usually broaden laterally as a fan shape, arise from common base of lateral suckers, particularly the distal sucker; contribution from proximal sucker also in many larger specimens. Width of largest tentacular sucker almost always larger than width of largest sucker on arm III; ratio of width of largest sucker of tentacle to width of largest sucker on arm III: 0.72-2.1.

Club sucker dentition variable. About 8-30 teeth, usually about 20, on sucker rings of carpal area, varying from blunt to pointed, graded in size; teeth on 1/2 of ring very small, sometimes only a rippled edge, about 4-13 large teeth. About 20-35 teeth on largest lateral manal suckers; teeth usually pointed, graded in size, sometimes alternating large and small teeth; teeth at outer edge of ring larger and usually more pointed than inner teeth. About 35-65 teeth on largest medial manal suckers; teeth usually pointed, usually triangular in shape, points sometimes slightly curved; patterns of teeth arrangement vary, teeth often arranged in a pattern of alternating large and small teeth, many specimens have at least some teeth arranged in a trinary pattern in the following sequence: large tooth, small tooth, medium tooth, small tooth, large tooth; occasionally teeth are of almost equal size. Proximal dactylar sucker rings with about 16-22 pointed teeth, graded in size; about 6-10 larger teeth.

Gladius long, rather wide (about 10-20% of ML, 23-224 mm ML), feather-shaped; anterior tip with weak flexible acute point; rachis stiff, free rachis length about 7-33% of ML (23-224 mm ML); median ridge and strong lateral rods on rachis, continue in center of vane, fuse beyond midpoint of vane, extend length of gladius. Additional lateral colored bands often occur near edge of vane; these bands rarely thickened into a weak to strong lateral rod in males; lateral edges of vane usually thin and weak. Sides of vane usually curved (fairly straight in some males); vane usually tapers at both ends, widest point in central area. Rachis rather narrow, gladius rather wide; ratio of greatest width of vane to greatest width of rachis about 2.4-3.2 (2.1 in one specimen).

Buccal lappets usually 7 (rarely 6, 8, 9); 7 buccal connectives, 7 supporting rods, suckers present on each lappet (maximum of 19); total suckers on all lappets about 35-113 (44-315 mm ML). Connectives of buccal membrane attach to dorsal, dorsal, ventral, ventral borders of arms I-IV respectively.

Beaks. Rostrum of upper beak curved, strong, sharp, long (but short in comparison to length of hood and rostral lamella); weak, thin, lightly pigmented, notch separates rostrum and rostral lamella (jaw angle recessed); cutting edge of rostral lamella straight; palatine lamella weak, large, long, deep, pigmented anteriorly, dorsal crest only slightly curved. Rostrum of lower beak shorter than upper beak, pointed, heavily pigmented, inner edge curved, jaw angle obtuse but nearly 90°; rostral lamellae narrow, short, wing lobate, thin; gular lamella large, crest strong, posterior corner pointed, moderately curved.

Radula with 7 transverse rows of teeth; rachidian with long central pointed tooth, pointed lateral cusps; 1st lateral tooth pointed with pointed lateral cusp; 2nd lateral tooth pointed, longer than first, no lateral cusp; 3rd lateral tooth long, curved, scythe-shaped; marginal plaques present.

Spermatophore with sperm mass of about 74-79% of total length, cement body about

7-9% of total length (153-291 mm ML), total length about 4-13 mm (70-291 mm ML). Oral connection of cement body cylindrical, narrows at oral end.

Gill length about 23-34% of ML (55-315 mm ML). Number of filaments on 1 side of gill increases with ML.

Color (in alcohol). Reddish-brown chromatophores present on entire mantle, larger and more closely-spaced on dorsal side, particularly in mid-dorsal region; present only on dorsal side of fins; cover entire head, more closely-spaced dorsally, particularly proximal to eyes; present on collar and funnel, on outer sides of arms, tentacles, trabeculae and protective membranes of arms I, II, III, tentacles. Dark crescent over dorsal borders of eyes. Reddish-brown anterior mid-dorsal longitudinal indentation.

HOLOTYPE: Deposited at the Academy of Natural Sciences of Philadelphia, but missing (Voss, 1962).

TYPE LOCALITY: South Carolina?

DISTRIBUTION: Continental shelf and slope of the E coast of the North and the N coast of the South American continents from Nova Scotia to the Gulf of Venezuela; very rare occurrences off islands near continents in the Bahamas and Caribbean. See Fig. 1. Dip-netted at the surface and taken in bottom trawls down to 393 m.

DISCUSSION:

Nomenclature: Loligo pealei was described by Lesueur (1821), who named it after R. Peale, manager of the Philadelphia Museum and source of the original specimens. Mr. R. Peale probably was the naturalist, Rubens Peale, son of Charles Wilson Peale, painter of portraits of George Washington (Malone, 1934).

The original spelling is *Loligo pealeii*, which is the correct spelling according to Article 32 of the *International Code of Zoological Nomenclature* (1964: 32-33), although according to Article 31A, the recommended ending for a patronymic specific name is a single *"i"*. The commonly used spelling for this species is now *L. pealei*. The International Commission on Zoological Nomenclature is now considering a request (Smith, Stuart & Conant, 1971: 250-252) to revise Article 32 to permit or require usage of the single *"i"* ending for a species-group name regardless of its original spelling. Smith et al. pointed out that the single *"i"* was required by the 1961 Code, is in better conformance with the rules of classical Latin, and is increasingly popular among taxonomists. I prefer the single *"i"* ending and will use it pending a decision by the Commission. The species name has also been spelled *L. pealii* (Ghiretti, 1966: 202; Williams, 1909) and *L. peali* (Brown, 1956: 153).

Loligo pealei commonly is known as the long-finned, common or winter squid (Lyles, 1968).

Geographic distribution: Loligo pealei is found as far N as Nova Scotia, Canada. The most northern specimen which I have identified is a juvenile (10.6 mm ML) collected in Minas Basin, Nova Scotia (USNM collection). Stevenson (1934) observed spawning schools of *L. pealei* in New Brunswick, Canada. The most southeastern *L. pealei* which I have identified are 10 mature specimens from the Gulf of Venezuela, Venezuela. Only 4 Loliginidae from Guiana, 6 from Mar del Plata, Brazil, and 4 from Rio Grande do Sul, Brazil, were available to me. They are not *L. pealei* and there are no reports of *L. pealei* from that far S. Francisco Palacio, University of Miami (personal communication) found no *L. pealei* in a collection of squid from Brazil; the bulk of his material came from the area between Rio de Janeiro and São Paulo. The 4 specimens from Guiana are probably *Loligo surinamensis* Voss (1974).

Voss (1973) states that the range of *Loligo pealei* is the continental shelf from Cape Cod S to Florida and the Gulf of Mexico, and possibly into the Caribbean Sea. On a map showing the distribution of *L. pealei*, Voss (1971: 309-310) showed *L. pealei* distributed along the E coast of the United States as far N as New York and present along the shores of the islands of the Caribbean Sea, the Bahama Ids., and Bermuda. However, Voss (1960: 420) found no *L. pealei* in collections from Bermuda; he also suggested that those squid from Bermuda listed as *L. pealei* by Verrill might have been *L. plei*. All 10 of the Bermuda *Loligo* specimens in the collection of the National Museum of Natural History are *L. plei*. Voss (1955: 83) listed *L. pealei* as recorded from Cuba by other sources but did not give the sources. LaRoe (1967: 23) gave the range of *L. pealei* as Massachusetts to Colombia, but also listed *L. pealei* from the islands cited by Voss. All of LaRoe's records from islands were citations from

other authors which were not listed in his literature citations. All of the specimens examined and identified by LaRoe were from the continental shelf or slope. I have been unable to find evidence in the literature that *L. pealei* lives anywhere but on the continental shelf and upper slope. In searches of the collections at the University of Miami (in 1970 and 1973) and the Smithsonian Institution (1970-73) I found only 2 samples of *L. pealei* collected from island areas. These are 2 males from Eleuthera, Bahamas, and 3 males from Bridgetown, Barbados (USNM collections). These islands, although oceanic, are not distant from continents. I believe that these 5 squid represent rare strays and that *L. pealei* normally lives only on the continental shelf and slope.

It has been easiest for me to obtain large samples from waters between Beaufort, North Carolina, and Cape Cod, but this could be due to factors other than relative abundance. *Loligo pealei* is common to abundant on the continental shelf off the E coast of the United States (Serchuk & Rathjen, 1974); the remainder of the range of *L. pealei* has not been as intensively surveyed yet. According to LaRoe (1967), *L. pealei* is most common in the New England area. Only scattered individuals occur in the Gulf of Mexico and Caribbean Sea, according to Arnold et al. (1974), citing LaRoe (1967) and a personal communication from Mercer. No evidence has been given to support this statement. I examined 1 lot of 20 specimens from a station in the Gulf of Mexico and 1 lot of 163 specimens from the Caribbean (Table 6; Appendix A). Samples of more than 2-3 specimens from either Florida coast were not available and *L. pealei* probably is uncommon there. *L. pealei* has been found chiefly where the continental shelf is broad, with one exception—the coast of Colombia.

Loligo pealei is fished off the E coast of the United States by Canada, Spain, Italy, Cuba, West Germany, East Germany, USSR, Poland, the United States and others (Vovk, 1969; Rathjen, 1973). Japanese trawlers have averaged 10 or more tons per fishing day (Rathjen, 1973). About 90% of the New England squid catch is *L. pealei* (Summers, 1967). The total New England squid catch for 1973 was about 56,000 tons (123 million lb.) (Lux, Handwork & Rathjen, 1974). U.S. fishermen in 1973 caught well over 2 million lbs. (Rathjen, 1974). The fall apparent total abundance is calculated to average 60 thousand tons (Serchuk & Rathjen, 1974).

The distribution of populations of *Loligo pealei* in the western North Atlantic Ocean between Cape Hatteras and Nova Scotia has been analyzed from the results of year-round trawling studies or surveys by Summers (1969, 1971), Vovk (1969) and Serchuk & Rathjen (1974). Vovk's report is based on 3,420 trawls made during 24 expeditions between 1958 and 1968. Summers based his analysis on 4 cruises made between 1966 and 1968. Serchuk & Rathjen based their findings on 2,537 otter trawl stations from 1967-1971.

Populations of *Loligo pealei* occur in shallow waters of the continental shelf from Cape Hatteras to Cape Cod in summer months when spawning takes place. In fall, the species is dispersed in waters less than 110 m deep (Serchuk & Rathjen, 1974). Summers (1969), Vovk (1969) and Serchuk & Rathjen (1974) have shown that autumn populations migrate offshore into the deeper waters of depressions in the continental slope. The autumn offshore migration takes place at later dates at localities farther S. Furthermore, the northern limit of distribution occurs 600 km farther S in winter than in summer (Summers, 1969). Probably the inshore-offshore and N-S migrations are related to the avoidance of water temperatures of 8°C or lower (Summers, 1969). Vovk (1969) correlated concentrations to temperatures between 9-12°C in the depressions of the continental slope. In winter, bottom temperatures are higher there than on the continental shelf. Serchuk & Rathjen (1974) confirmed the findings of Summers and Vovk and found that in all seasons the best catches of squid were consistently made at locations where the temperature was above 10°C (10-12°C in spring and 10-14°C in fall) and are greatly diminished in strata with bottom temperatures below 8°C.

In mid-winter, populations of *Loligo pealei* are caught at depths between 28-366 m with peak abundance at 110-183 m; larger squid predominate with increasing depth (Summers, 1969; Serchuk & Rathjen, 1974). In spring relatively large concentrations of squid occur at 111-183 m; they are seldom taken in less than 55 m and never obtained in shallow waters N of Chesapeake Bay (Serchuk & Rathjen, 1974).

Populations of *Loligo pealei* are caught in canyons S of 40° N latitude from December to January at greater depths between Hudson and Veatch canyons than in the more southern canyons. Between March and May the greatest concentrations shift northward from Baltimore to Wilmington to Hudson and later Veatch and Hydrographer canyons (Vovk, 1969).[2] The squid leave the canyons in summer and migrate inshore to spawn.

Fertilized eggs of *Loligo pealei* in southern New England are deposited in masses from June to September; peak deposition takes place in June and July. Egg masses have been found attached to seaweed or other supports near Woods Hole (Verrill, 1874) and to wooden shipwrecks at a depth of 240 m off New Jersey (Bulloch, 1969). According to Summers (1971), hatching occurs mainly in July and November. Young *L. pealei* are very abundant in the surface waters off southern New England during July and August (Verrill, 1874). The newly hatched young closely resemble the adults and do not undergo metamorphosis. The juveniles are planktonic; the adults are nektonic.

Loligo pealei is generally demersal but disperses upwards into the water column at night; adults are observed swimming near the surface at night in summer (Summers, 1969). Daytime catches are about 9 times larger than nighttime catches; at night the squid may leave the bottom to pursue food (such as euphausids) which are known to migrate in a similar fashion (Serchuk & Rathjen, 1974). Recently hatched squid gather at the surface of an aquarium attracted by light.

The many other studies of *Loligo pealei* include: embryology (Arnold, 1964, 1965a, 1965b, 1965c, 1968a, 1968b, 1971), developmental rate (McMahon & Summers, 1971), spermatophores (Drew, 1919; Austin, Lutwak-Mann & Mann, 1964), breeding behavior (Drew, 1911; Arnold, 1962), morphology compared with *Lolliguncula brevis* (Haefner, 1964; Dillon & Dial, 1962), anatomy (Verrill, 1881; Williams, 1909), breeding seasons and growth rates (Summers, 1968, 1971), maturity (Vovk, 1972b), feeding habits (Vovk, 1972a), useful manual of laboratory techniques (Arnold et al. 1974), chromatophores (Mirow, 1972), locomotion (Ward, 1972).

Loligo pealei has been captured in the same bottom trawls (not closing nets) with *L. plei* and *L. roperi* as shown in Table 3.

Sexual dimorphism: Analysis of covariance showed that the sexes are significantly different statistically in many characters, but these differences are very small and graphed values overlap. Sexual differences are distinctive in only 2 characters: females have a broader gladius vane and fewer gill filaments than do males. See Figs. 5 and 6.

Tests of sexual differences using ML as covariate sometimes showed statistically significantly different variances between male and female samples. When the tests were repeated using specimens of only 120-200 mm ML, the variances were then not significantly different.

When either ML or the length of the funnel cartilage is used as the covariate, the adjusted means for the following measure-

[2]Black and Witch Canyons mentioned in the translation of Vovk's paper are probably mistranslations of Block and Veatch Canyons, which appear on Coast and Geodetic Survey Maps (1967) of the region.

TABLE 3. Location of trawls containing 2 or more loliginid species.

Collector, sta. no.	Location	Date	*Loligo ocula*	*Loligo pealei*	*Loligo plei*	*Loligo roperi*	*Lolliguncula brevis*
Choco 38	9°3.5′N, 76°28′W	18 May 1969		x	x	x	
J. Ewald	Gulf of Venezuela	2 Mar. 1971		x	x		
Delaware II							
D-72-25 9	34°39′N, 75°39′W	27 Oct. 1972		x	x		
D-72-25 4	35°11.5′N, 75°12′W	27 Oct. 1972		x	x		
D-72-25 24	34°13′N, 76°53′W	29 Oct. 1972		x	x		
J. Ewald	Gulf of Venezuela	1 Mar. 1971			x		x
Oregon II							
10858	22°59′N, 78°43′W	13 Dec. 1969	x			x	
Pillsbury							
406	8°49.2′N, 77°21.2′W	17 July 1966		x		x	
352	8°20.1′N, 76°53.6′W	11 July 1966		x		x	

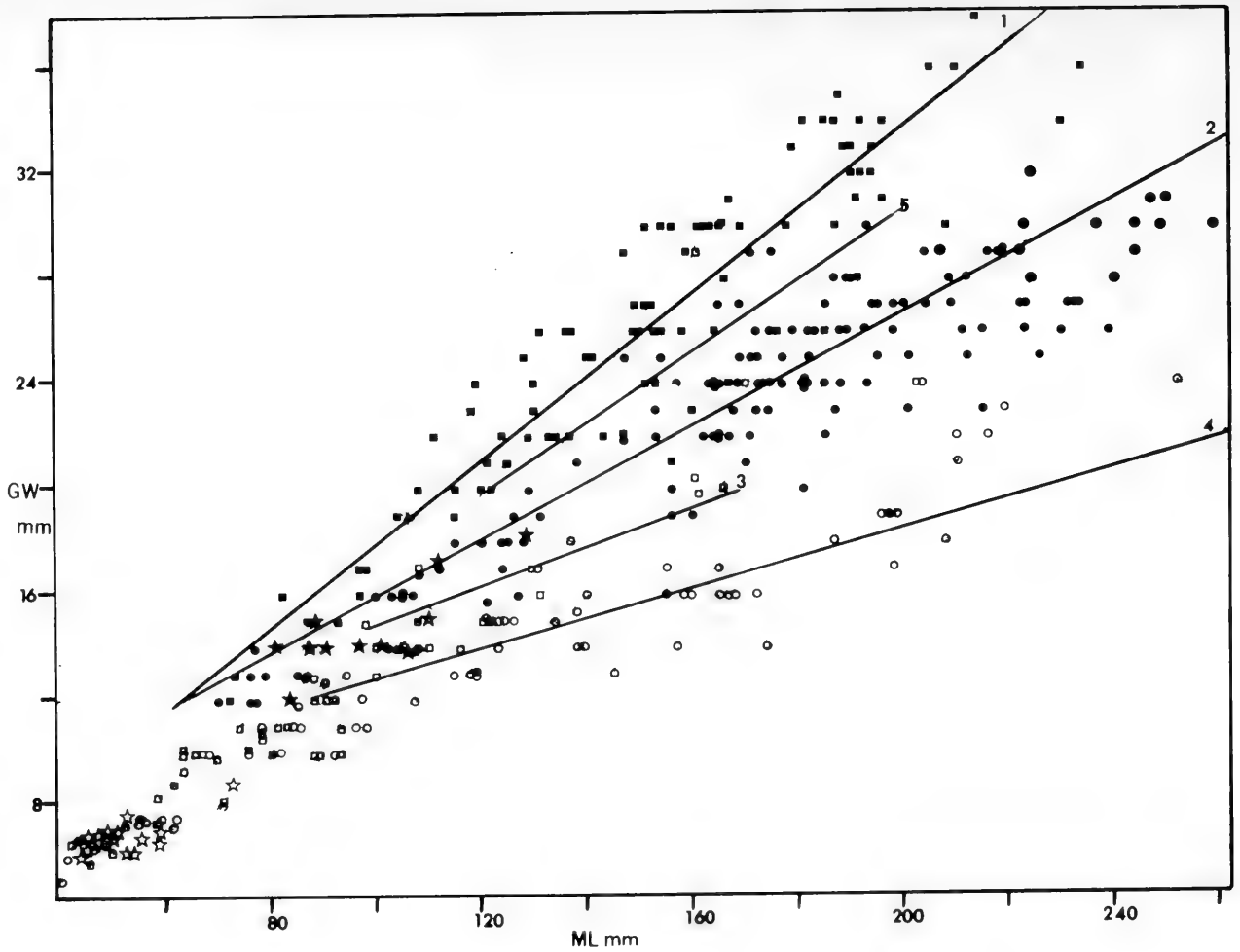

FIG. 5. The regression of greatest width of gladius upon mantle length (GW:ML). *Loligo pealei*: ♀ = solid squares, regression line no. 1; ♂ = solid circles, regression line no. 2. *L. plei* ♀ = open squares, regression line no. 3; ♂ = open circles, regression line no. 4. *L. ocula* = solid stars. *L. roperi* = open stars. *L. pealei* 120-200 mm ML only (used to test sexual dimorphism), regression line no. 5.

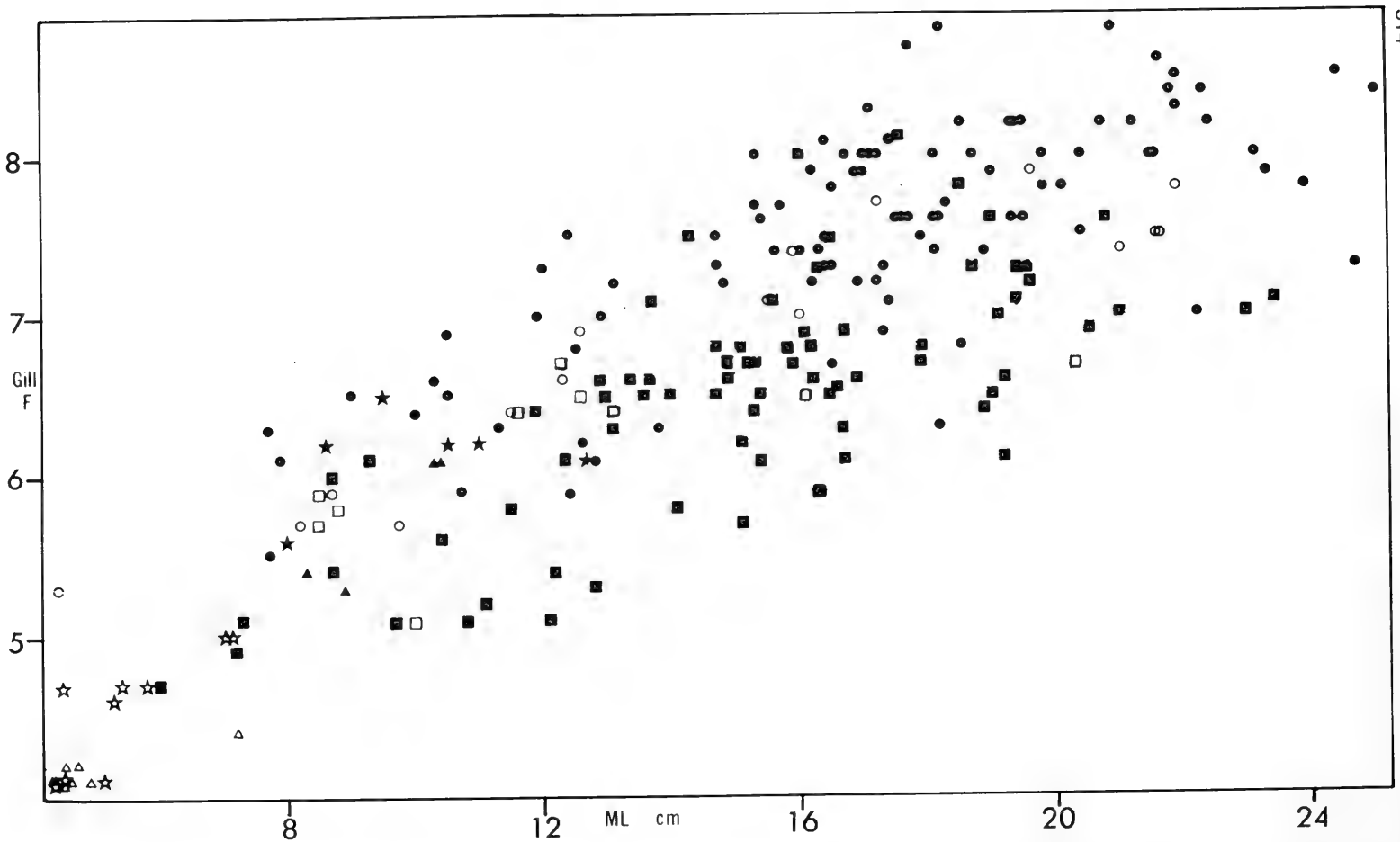

FIG. 6. The regression of the number of gill filaments upon mantle length (Gill F:ML). *Loligo pealei*: ♀ = solid squares, ♂ = solid circles. *L. plei*: ♀ = open squares, ♂ = open circles. *L. ocula*: ♀ = solid triangles, ♂ = solid stars. *L. roperi*: ♀ = open triangles, ♂ = open stars.

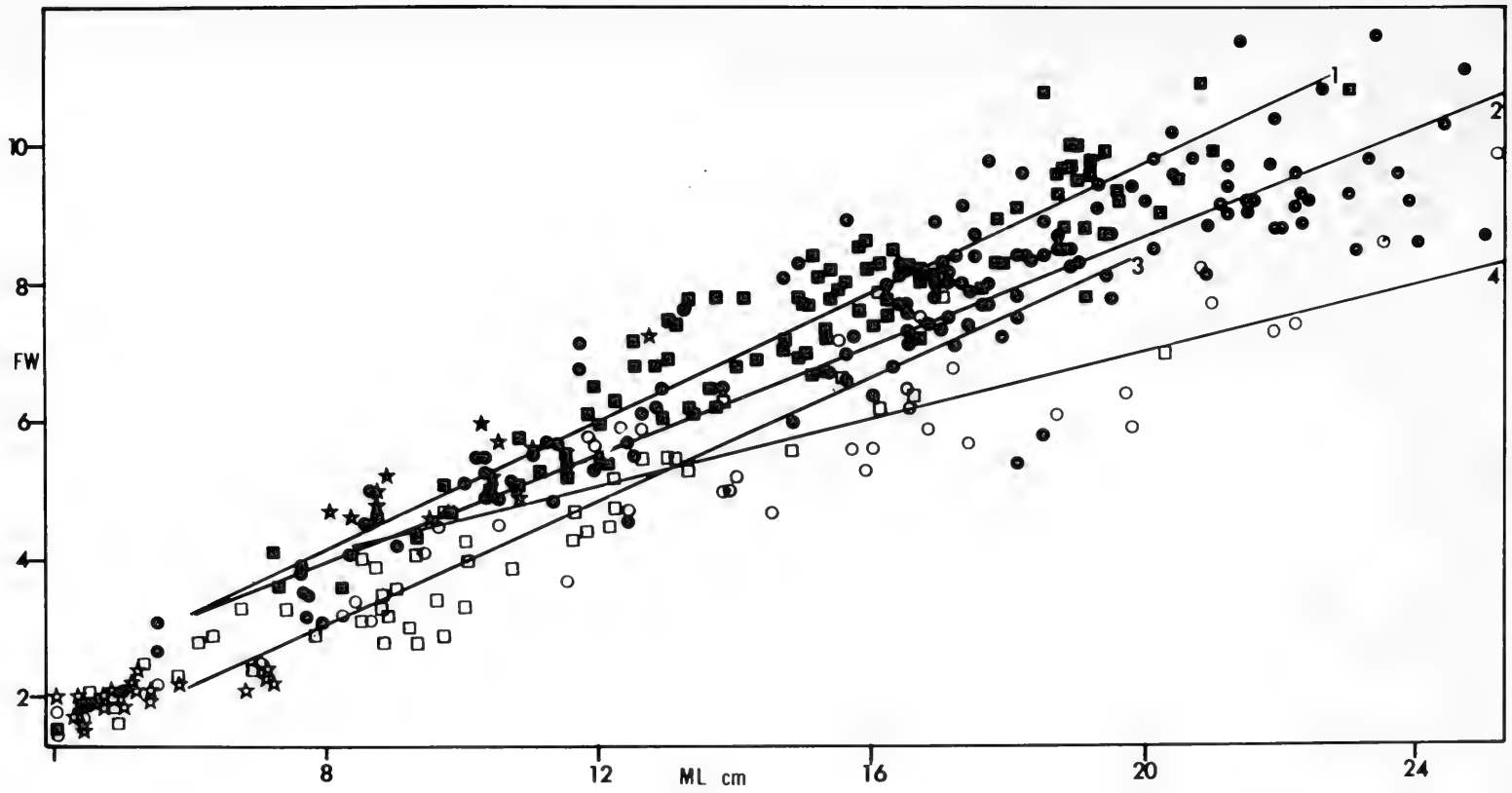

FIG. 7. The regression of fin width upon mantle length (FW:ML). *Loligo pealei*: ♀ = solid squares, regression line no. 1; ♂ = solid circles, regression line no. 2. *L. plei*: ♀ = open squares, regression line no. 3; ♂ = open circles, regression line no. 4. *L. ocula* = solid stars. *L. roperi* = open stars.

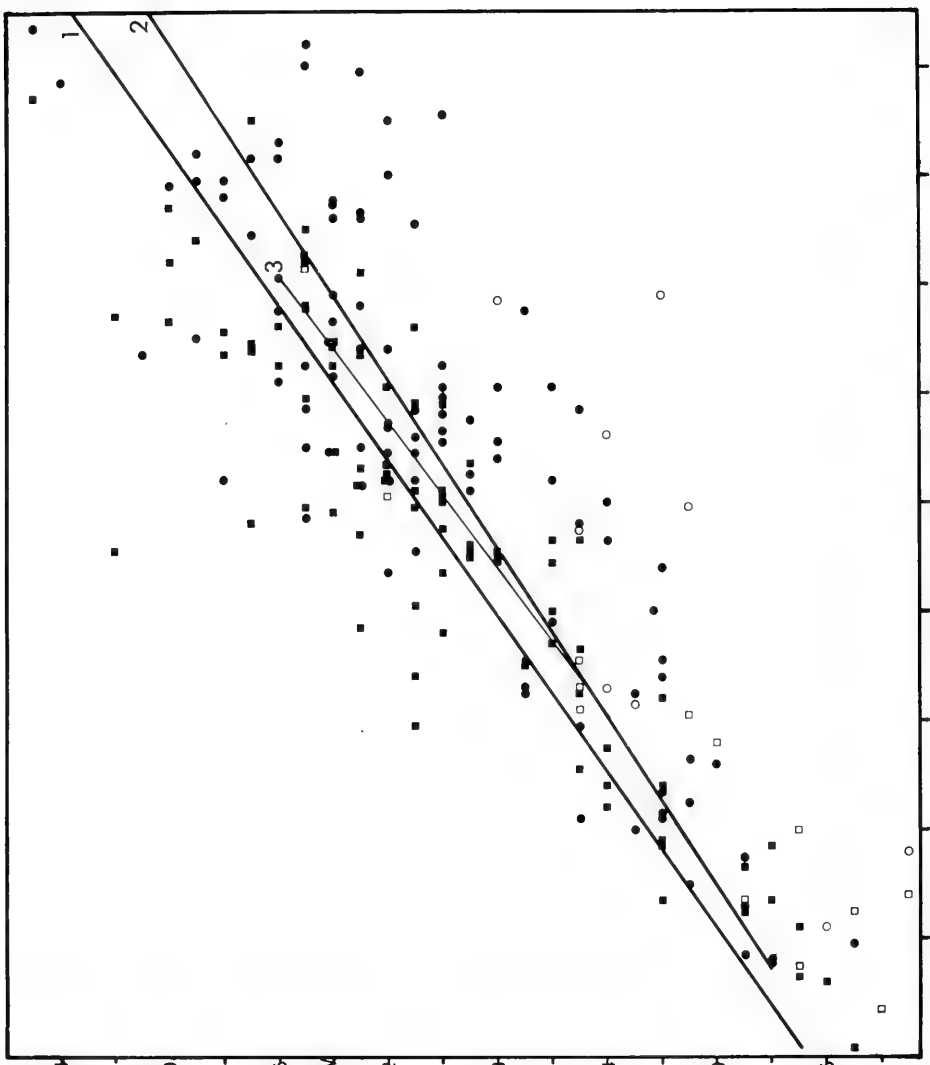

FIG. 8. The regression of mid-mantle width upon mantle length (MMW:ML). *Loligo pealei*: ♀ = solid squares, regression line no. 1; ♂ = solid circles, regression line no. 2. *L. plei*: ♀ = open squares, ♂ = open circles. *L. pealei* 120-200 mm ML only, regression line no. 3.

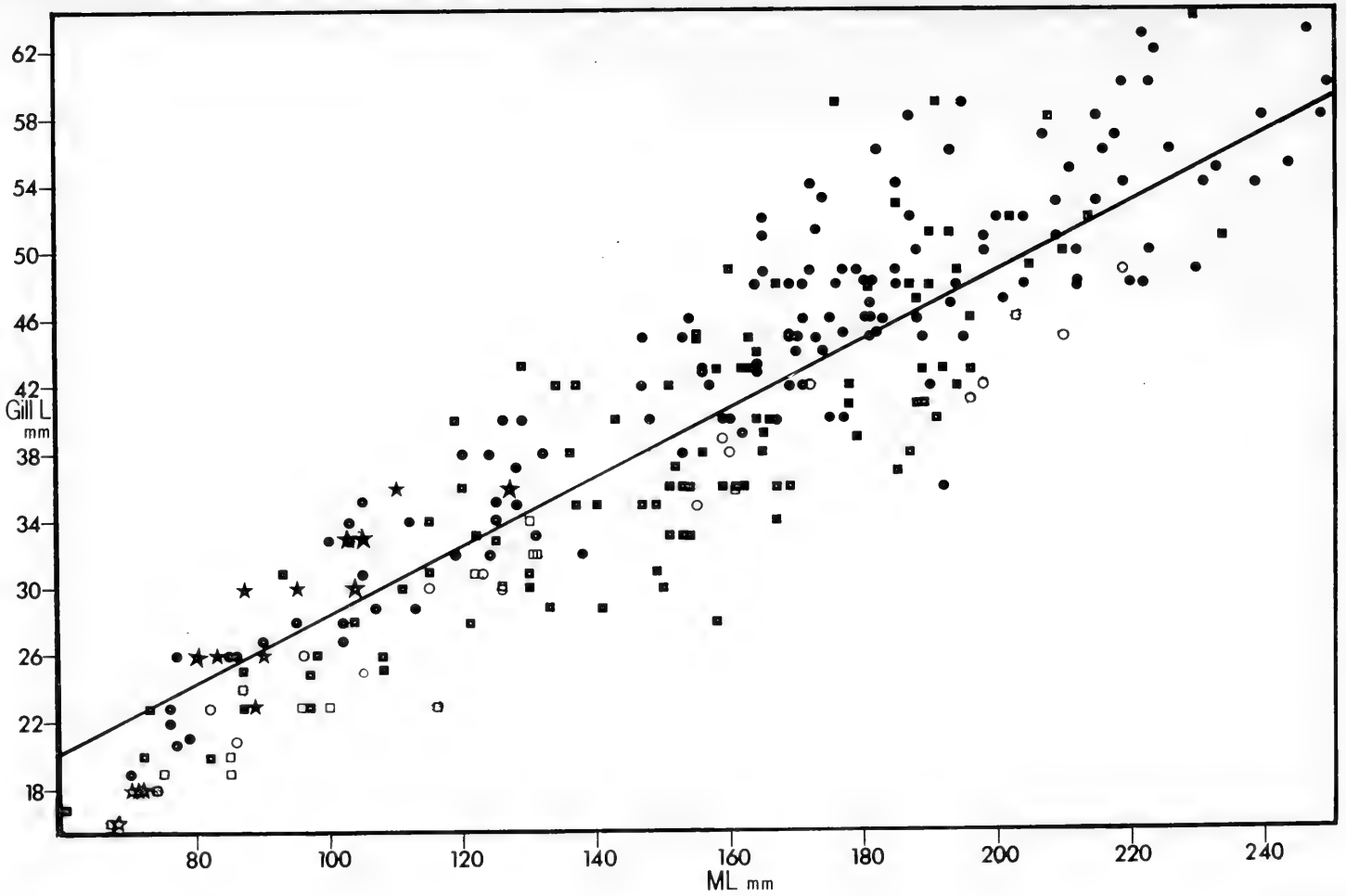

FIG. 9. The regression of gill length upon mantle length (Gill L:ML). *Loligo pealei*: ♀ = solid squares, ♂ = solid circles. *L. plei*: ♀ = open squares, ♂ = solid circles. *L. ocula*: solid stars. *L. roperi*: open stars. Regression line for *L. pealei* only.

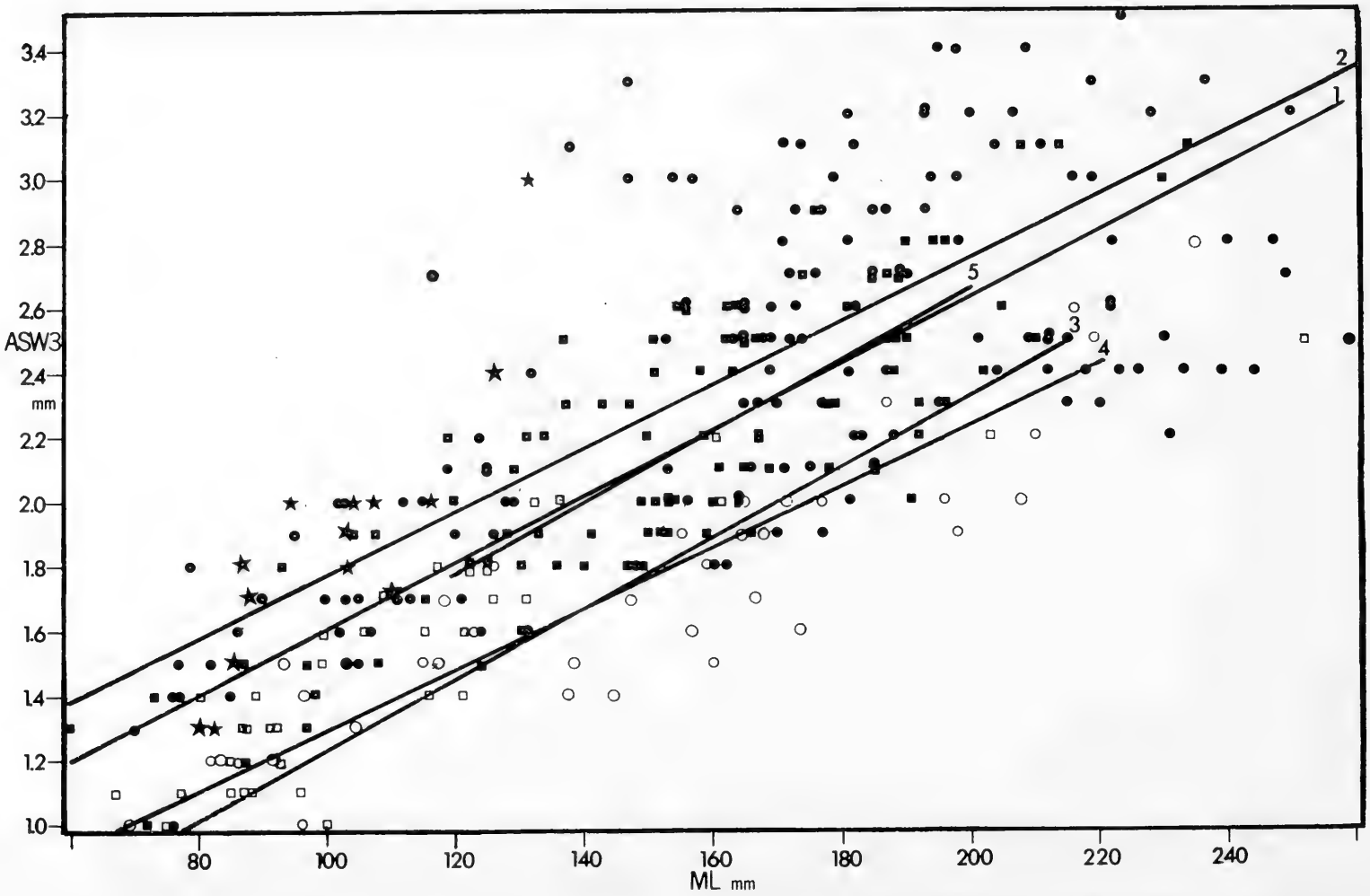

FIG. 10. The regression of the greatest sucker width of arm III upon mantle length (ASW III:ML). *Loligo pealei*: ♀ = solid squares, regression line no. 1; ♂ = solid circles, regression line no. 2. *L. plei*: ♀ = open squares, regression line no. 3, ♂ = open circles, regression line no. 4. *L. ocula* = solid stars. *L. roperi* = open stars. *L. pealei* 120-200 mm ML only, regression line no. 5.

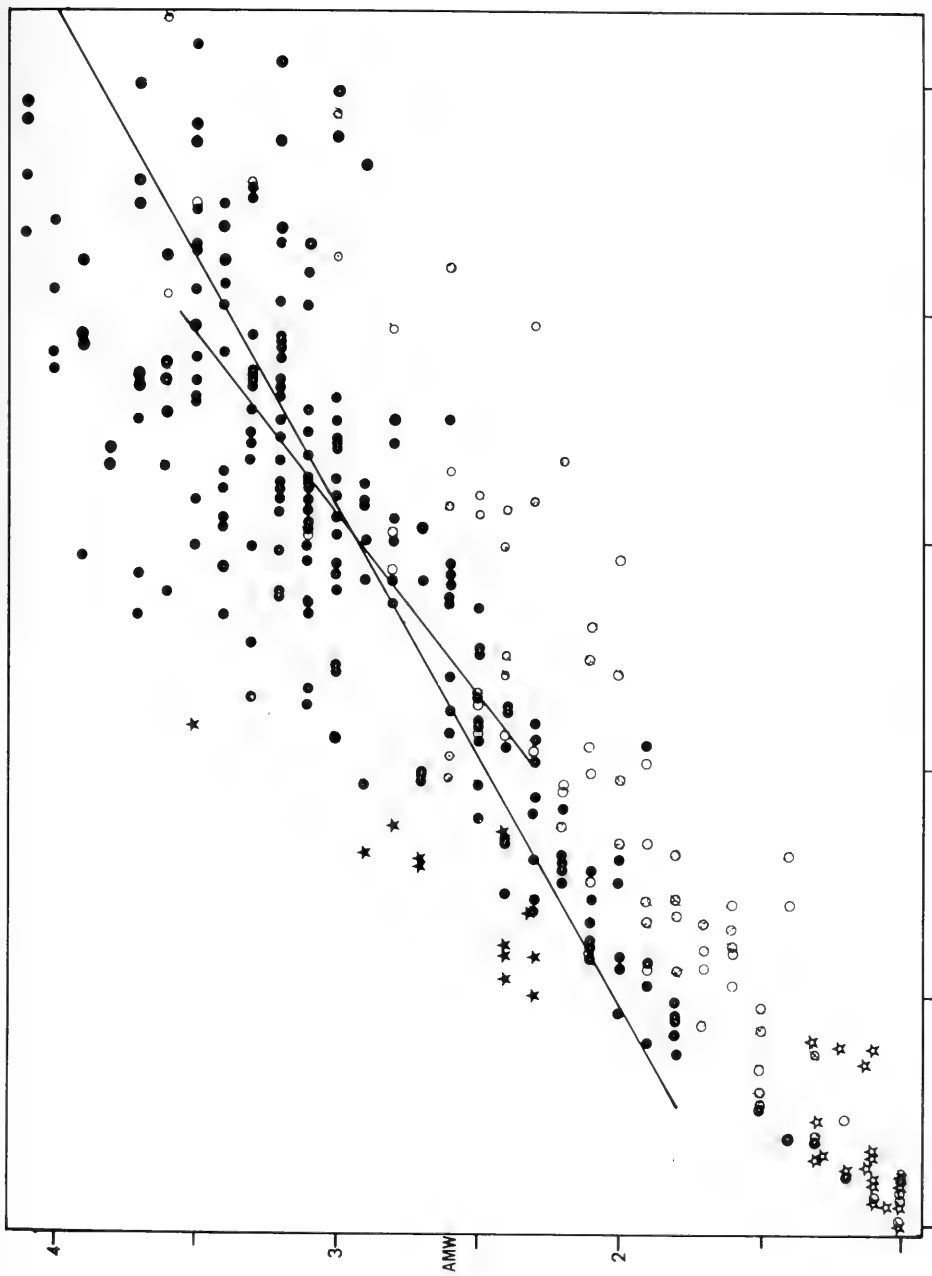

FIG. 11. The regression of anterior mantle width upon mantle length (AMW:ML). *Loligo pealei* = solid circles. *L. plei* = open circles. *L. ocula* = solid stars. *L. roperi* = open stars. Both regression lines for *L. pealei* (short line used to test sexual dimorphism).

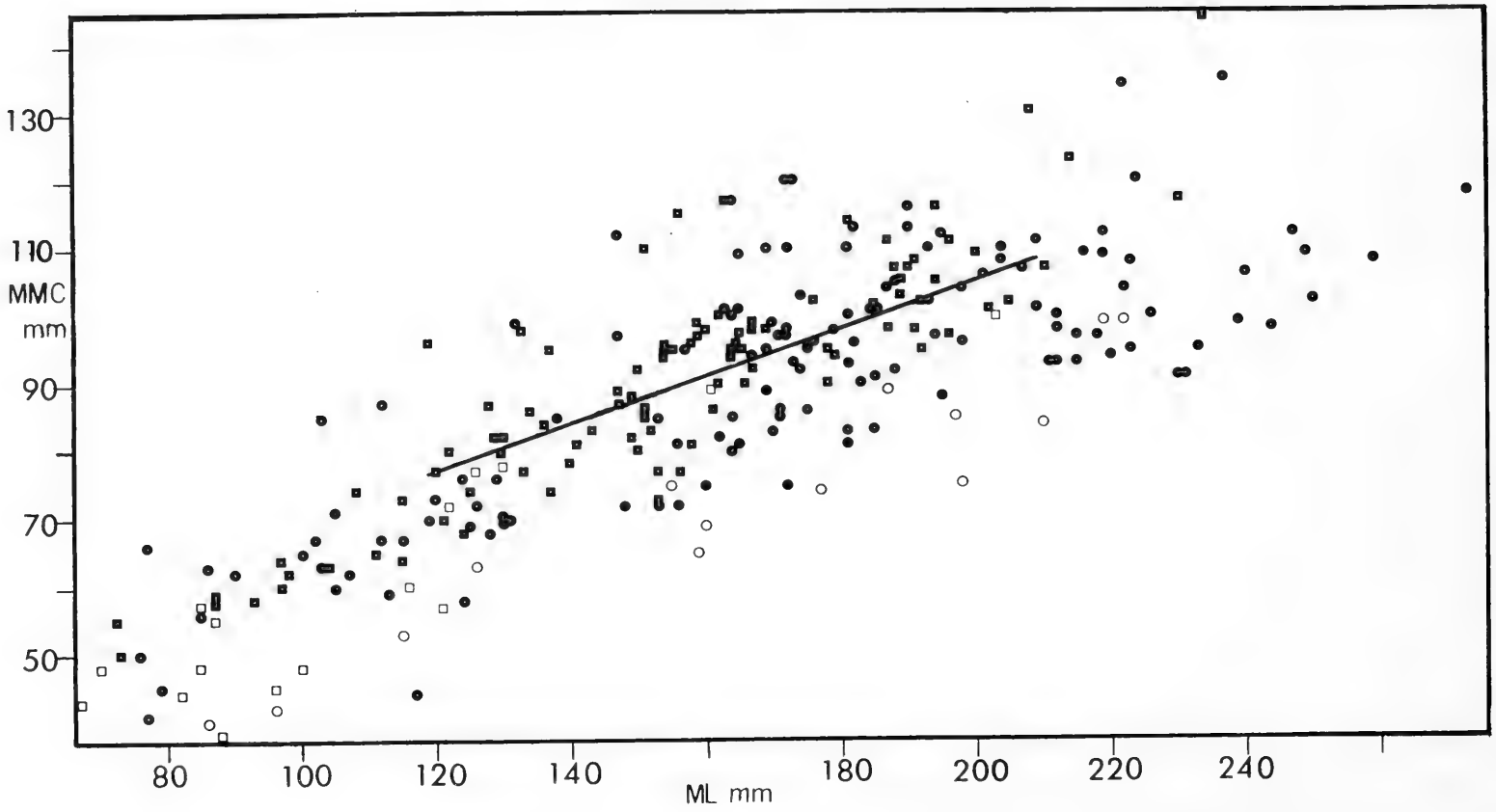

FIG. 12. The regression of mid-mantle circumference upon mantle length (MMC:ML). *Loligo pealei*: ♀ = solid squares, ♂ = solid circles. *L. plei*: ♀ = open squares, ♂ = open circles. Regression line for *L. pealei* only.

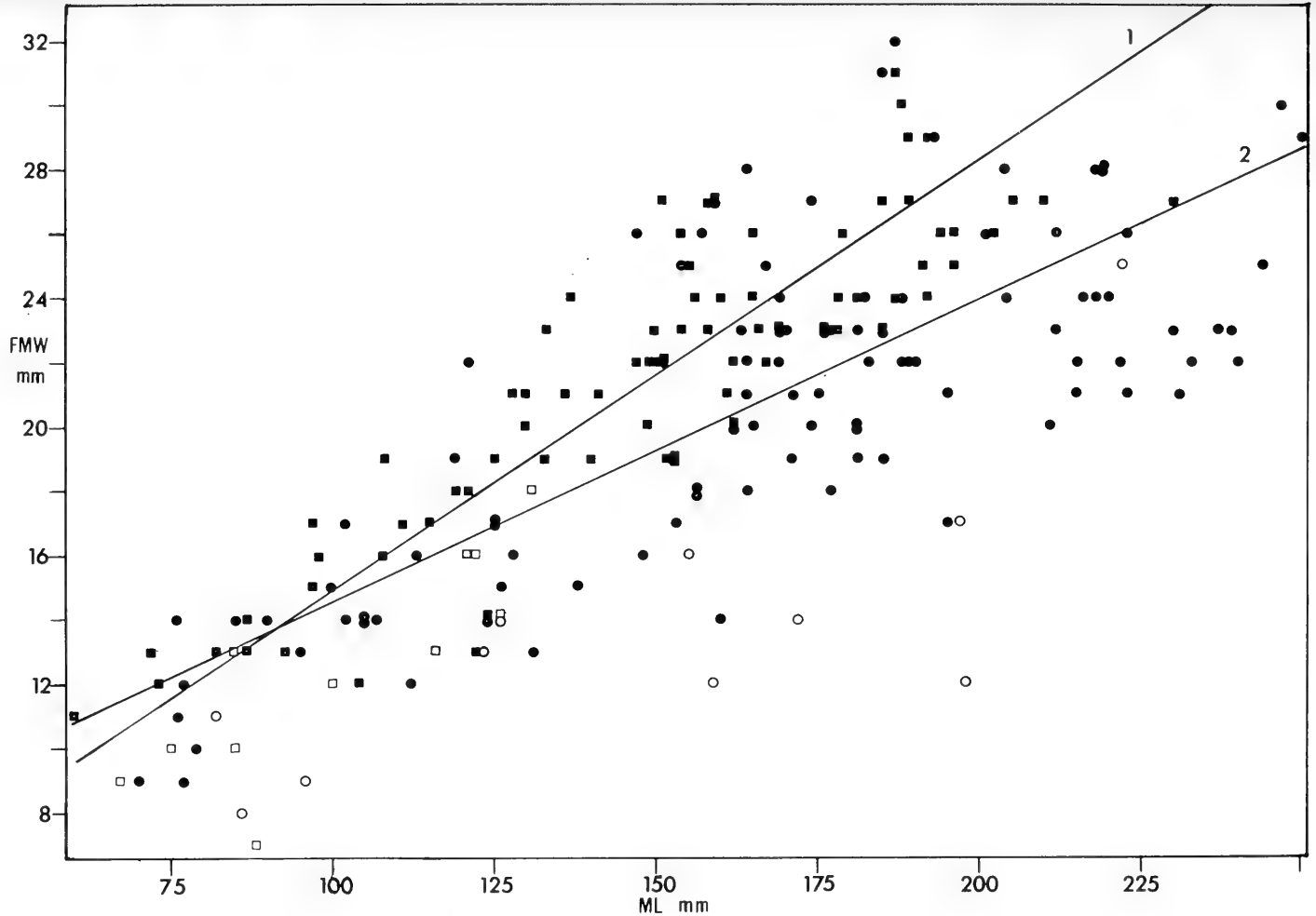

FIG. 13. The regression of mantle width coincident with widest point of fins upon mantle length (FMW:ML). *Loligo pealei*: ♀ = solid squares, regression no. 1; ♂ = solid circles, regression no. 2. *L. plei*: ♀ = open squares, ♂ = open circles.

ments are statistically significantly higher in females than in males: fin width, mid-mantle width, gladius width; and the following show statistically significantly higher means in males than in females: gill length, the number of gill filaments, and the widths of the suckers on arms II, III, and IV. See Figs. 7-10. The differences are most pronounced in gladius width and the number of gill filaments.

In addition, regression coefficients are statistically significantly different for fin width and the width of the mantle at mid-fin length, when ML is used as the independent variable. These 2 characters increase faster in respect to increasing ML in females than they do in males. Females appear to have a higher regression coefficient also for gladius width:ML, but variance differences made a statistical test invalid.

There are probably no real differences in mantle width between the sexes except posterior to the fin insertion. While mid-mantle width:ML shows significant difference between the sexes, regressions on ML of mid-mantle circumference, as well as anterior mantle width and circumference do not (Figs. 11-12). There is considerable overlap between the sexes in these characters. Mid-mantle circumference is a more accurate measurement than mid-mantle width. The higher regression of mantle width at mid-fin length:ML in females is probably due to swelling of the posterior part of the mantle with eggs in mature ripe females (Fig. 13).

With the length of the funnel cartilage as covariate (but not with ML as covariate) females have higher adjusted mean head width and nuchal cartilage length, and males have higher adjusted mean fin length, arm I length and arm I sucker width. Broad overlap of values occurs in these characters.

No sexual dimorphism occurs in the following measurements using either ML or length of the funnel cartilage as covariates: head length, distance between the eyes, funnel length, funnel width, tentacular club length, tentacular sucker width, length of arms II, III, IV, and number of suckers on each arm. While there is a low correlation between the number of suckers on arms and ML, the analysis of covariance showed that the regression is significant. No sexual dimorphism is observed in the teeth of the largest suckers on either the third arm or the tentacular club.

More males than females have a longitudinal mid-ventral ridge and it is more pronounced in males. Some large mature males have longitudinal, reddish-brown chromatophore stripes extending posteriorly near the ventro-lateral margins of the mantle opening.

Verrill (1881: 314-316) examined many specimens of *Loligo pealei* from between Long Island Sound and Cape Ann, Massachusetts, and he reported that the gladius is wider in females than in males. In mature females the broad portion of the gladius lies above the full ovary and may help support or protect the large mass of eggs in a ripe female. Verrill stated that the ratios of head circumference to ML, fin width to ML, tentacular sucker width to ML and arm I length to ML are larger in females than males. While the ratios varied he found no overlap between sexes for these ratios with the exception of tentacular sucker width to ML.

Testing for sexual dimorphism in all geographic samples of *Loligo pealei* together, I found that the mean of fin width adjusted for ML is indeed statistically significantly larger in females than in males, but with considerable overlap (Fig. 7). There is no statistically significant difference for head width:ML; tentacular sucker width:ML; and arm I length:ML. Males have longer 1st arms than females using length of funnel cartilage as covariate, but values overlap so much that this is not apparent on a graph.

Verrill asserted, without giving the figures, that all arms are longer and all of the suckers usually distinctly larger in females. There is no statistically significant difference in the lengths of arms II, III, IV, and males have longer 1st arms and larger suckers (Fig. 10). Verrill felt that preservation changes might mask sexual dimorphism. However, preservation probably affects most characters of males and females alike, altering ratios and regressions alike.

Females have shorter gills with fewer filaments than males which suggests that females may have a lower oxygen requirement. Males are more active in mating (Drew, 1911; Arnold, 1962), but females produce and lay 3500-6000 eggs (Summers, 1971). Other relative differences in activity are not now known for the 2 sexes.

Maturity and growth: The smallest male found with spermatophores was 61 mm ML (*CHOCO* station 38, off Colombia, May 18,

1969) and the largest without spermatophores was 219 mm ML (*A.E. VERRILL*, Martha's Vineyard, Massachusetts, Oct. 8, 1970). The smallest female found with eggs was 73 mm ML (*OREGON II* station 223, off Colombia, Nov. 28, 1968) and the largest found without eggs was 208 mm ML (*A.E. VERRILL*, Martha's Vineyard, Massachusetts, Oct. 8, 1970). The relationship of maturity to water temperature will be discussed under geographic variation.

The hectocotyli of 126 males (49-315 mm ML) were examined. Males as large as 54 mm ML (*CYNTHIA*, off Virginia, May 18, 1971) have no hectocotylus. Partial hectocotylization is present in immature males as small as 47 mm ML (*PILLSBURY* station 352, off Colombia, July 11, 1966) and as large as 76, 85, and 90 mm ML (*CYNTHIA*, off Virginia, June 15, 1971). In the last 3 specimens about 6 suckers on the dorsal row are 1/2 the diameter of their partners on the ventral row and their stalks are more elongate. The dorsal suckers in the region of the future hectocotylus are like their ventral partners on the left arm IV of small males (less than ca. 45-70 mm ML). The hectocotylus appears to be formed by differential growth of the dorsal suckers in the future region of the hectocotylus.

Within the ML range considered in this study (60-315 mm), many measured characters do not appear to change much in size with increasing ML. Although these correlations are very low, all except the number of transverse rows of tentacular suckers are statistically significant for the sample size (Tables 4-5), which means that these characters do increase slightly with increasing ML within the range considered.

Many measured characters show high correlations (Table 5). The lengths of the arms and tentacular club and sucker diameters are all highly correlated with each other. The mantle width and head width appear similarly related. That these correlated characters may not be independent of each other should be considered when making comparisons between animals. These correlations could represent common genetic control.

A few abnormalities were noted in the arrangement of arm suckers in *Loligo pealei*. A total of 215 arms was examined. In a female (154 mm ML, Martha's Vineyard, Massachusetts, July 1971) the sucker-bearing surface of the right arm II is interrupted in one place by a convergence of the 2 lateral epidermal surfaces across the suckered ventral surface of the arm. In a female (150 mm ML, *CYNTHIA*, off Virginia, May 18, 1971) the biserial arrangement of suckers on the right ventral arm is replaced in 4 suckers near the basal portion of the arm with a left, right, right, left arrangement. A total of 119 arms was examined. A male (315 mm ML) *CYNTHIA*, off Virginia, May 18, 1971) has a hectocotylized arm with 3 suckers instead of 2 in one row at one point on the arm. A total of 118 hectocotyli were examined. Bradbury & Aldrich (1971) observed this arrangement in a specimen of *Illex illecebrosus*.

Abnormal numbers of buccal lappets and other variations in the hectocotylus were also observed and are discussed next under geographic variation.

Geographic variation: Eleven samples of populations of *Loligo pealei* from 5 geographic areas were statistically analyzed for geographic variation. The samples are listed in Table 6 and shown as stars in Fig. 1. Comparison was made of more than 50 different counts, measurements or observations. Most of these are listed in the description of measurements. When the study had been partially completed the following measurements were no longer made for an entire population sample but for only 10 specimens (5 males and 5 females) in each sample: distance between the eyes; anterior and mid-mantle widths; mantle width at fin insertion; number of suckers on arms I, III, IV; width of suckers on arms I, II, IV, and

TABLE 4. Some characters in *Loligo pealei* with a correlation of less than 0.6 with mantle length.

Character	Mantle length		Funnel cartilage length	
	r	N	r	N
TSR	0.214	76	0.749	73
TL	0.312	221	0.491	218
BLS 7	0.347	116	0.355	115
1	0.318	117	0.287	116
2	0.397	118	0.477	117
3	0.264	118	0.318	117
4-5	0.440	117	0.417	116
6	0.322	117	0.338	116
Fun W	0.428	217	0.553	217
HAS	0.400	118	0.514	117
HS	0.321	118	0.353	117
AS I	0.568	115	0.705	114
II	0.555	215	0.679	214
III	0.585	119	0.706	118
IV	0.356	119	0.492	118
TCL	0.598	220	0.725	216
Gill W	0.517	172	0.618	171

TABLE 5. Correlations greater than 0.8 between measurements of *Loligo pealei* (sample sizes in parentheses).

	ML	FCL	NCL	FL	FW	HW	MWA
ML		0.915(232)	0.924(228)	0.994(232)	0.924(175)	0.832(225)	0.838(196)
FCL	0.915(232)		0.943(228)	0.897(228)	0.904(226)	0.904(225)	0.891(192)
NCL	0.924(228)	0.943(228)		0.911(224)	0.885(222)	0.892(221)	0.877(188)
FL	0.994(232)	0.897(228)	0.911(224)		0.917(175)		0.821(192)
FW	0.924(175)	0.904(226)	0.885(222)	0.917(175)			
HW	0.832(225)	0.904(225)	0.892(221)				0.892(191)
AMW	0.838(199)	0.891(192)	0.877(188)	0.821(192)			
MMW	0.852(179)	0.891(175)	0.889(171)	0.839(175)		0.872(175)	0.899(179)
AMC	0.843(228)	0.903(228)	0.907(224)	0.825(224)	0.864(222)	0.922(221)	0.924(118)
MMC	0.809(225)	0.885(225)	0.874(221)		0.871(220)	0.892(218)	0.900(185)
Gill L	0.891(232)	0.869(228)	0.889(226)	0.875(228)		0.809(225)	0.816(193)
GW	0.785(217)*	0.830(216)			0.861(210)	0.810(210)	0.803(179)
AL I							
II							
III		0.822(218)	0.816(214)				
IV							
ASW I		0.834(130)	0.820(126)			0.838(129)	0.817(123)
II						0.816(129)	
III		0.818(230)	0.821(226)			0.857(227)	0.844(196)
IV						0.803(129)	

	MWM	MCA	MCM	Gill L	GW	AL I	AL II
ML	0.852(179)	0.843(228)	0.809(225)	0.891(232)			
FCL	0.891(175)	0.903(228)	0.885(225)	0.869(228)	0.830(216)		
NCL	0.889(171)	0.907(224)	0.874(221)	0.889(226)			
FL	0.839(175)	0.825(224)		0.875(228)			
FW		0.864(222)	0.871(220)		0.861(210)		
HW	0.872(175)	0.992(221)	0.892(218)	0.809(225)	0.810(210)		
AMW	0.899(179)	0.924(118)	0.900(185)	0.816(193)	0.803(179)		
MMW		0.907(171)	0.929(169)	0.812(176)	0.836(162)		
AMC	0.907(171)		0.951(225)	0.849(224)	0.811(212)	0.812(214)	0.854(221)
MMC	0.929(169)	0.951(225)		0.801(221)	0.819(209)		
Gill L	0.812(176)	0.849(224)	0.801(221)				
GW	0.836(162)	0.811(212)	0.819(209)				
AL I		0.812(214)					0.96(87)
II		0.854(221)				0.96(87)	
III	0.815(166)	0.875(214)	0.808(211)	0.823(215)		0.953(210)	0.96(87)
IV		0.862(213)				0.96(87)	0.971(213)
ASW I		0.862(126)	0.817(126)			0.866(118)	0.884(127)
II		0.826(126)				0.906(118)	0.903(127)
III		0.861(226)		0.811(230)		0.918(216)	0.915(224)
IV		0.824(126)				0.876(118)	0.871(127)

	AL III	AL IV	ASW I	ASW II	ASW III	ASW IV
ML						
FCL	0.822(218)		0.834(130)		0.818(230)	
NCL	0.816(214)		0.820(126)		0.821(226)	
FL						
FW						
HW			0.838(129)	0.816(129)	0.857(227)	0.803(129)
AMW			0.817(123)			
MMW	0.815(166)					
AMC	0.875(214)	0.862(213)	0.862(126)	0.826(126)	0.861(226)	0.824(126)
MMC	0.808(211)		0.817(126)			
Gill L	0.823(215)				0.811(230)	
GW						
AL I	0.953(210)		0.866(118)	0.906(118)	0.918(216)	0.876(118)
II	0.96(87)	0.971(213)	0.884(127)	0.903(127)	0.915(224)	0.871(127)
III		0.975(208)	0.896(120)	0.900(120)	0.922(219)	0.881(120)
IV	0.975(208)		0.883(118)	0.900(118)	0.925(216)	0.881(118)
ASW I	0.896(120)	0.883(118)		0.952(134)	0.944(134)	0.948(134)
II	0.900(120)	0.900(118)	0.952(134)		0.966(134)	0.952(134)
III	0.922(219)	0.925(216)	0.944(134)	0.966(134)		0.941(134)
IV	0.881(120)	0.881(118)	0.948(134)	0.952(134)	0.941(134)	

*Male GW = 0.819(126); female GW = 0.909(88).

TABLE 6. Samples of *L. pealei* used for statistical analysis.

Sample no.	N	Location	Date	Depth m	Collector, no.	Specimen,* no.
1	17	Menemsha Bight, Martha's Vineyard, Mass.	30 July 1970	7	Cohen, *Captain Bill IV*	1-17
3	14	Menemsha Bight, Martha's Vineyard, Mass.	4 Sept. 1969	20	Summers, *A. E. Verrill*	18-28, 54-56
4	24	Vineyard Sound, Mass.	8 Oct. 1970	13-15	Summers, *A. E. Verrill*	70-93
12	30	Vineyard Sound, Mass.	14 July 1971	—	*Captain Bill IV*	242-271, 280
13	44	37°50-55′N, 75°10-20′W	18 May 1971	8-20	Cohen, *Cynthia,* 1-3	272-279, 281-316
20	17	37°50′N, 75°10′W	15 June 1971	20	Sweeney, *Cynthia,* 3	323-339
8	28	4 mi. S of Beaufort Bar, Beaufort, N.C.	24 Sept. 1970	13	Schwartz, *Machapunga*	160-187
2	20	29°29′N, 88°37′W	26 Jan. 1970	8	*Oregon II,* 10886	29-48
9	11	9°37′N, 76°01′W	28 Nov. 1968	10	*Oregon II,* 223	201-202
		9°45′N, 75°45′W	28 Nov. 1968	7	*Oregon II,* 219	203-208
		10°N, 75°44′W	27 Nov. 1968	11	*Oregon II,* 214	198-200
11	22	9°3.5′N, 76°28′W	18 May 1969	10	*Choco,* 38	190-197, 317-319
		9°31′N, 76°10.6′W	15 May 1969	10	*Choco,* 25	209-219
10	10	Gulf of Venezuela (NW)	2 Mar. 1971	—	J. Ewald	232-240

*All specimens are in the National Museum of Natural History (United States National Museum), Washington, D.C.

the tentacular club; number of gill filaments; and number of suckers on buccal lappets. Preliminary analysis indicated that these measurements were not useful enough for the purposes of this study to justify the time spent measuring them. Also mantle width is closely correlated with mantle circumference; distance between eyes with head width; number of suckers on arms I, III, IV with the number on arm II; and width of the suckers on arms I, II, IV with the width of the suckers on arm III.

Comparison of the first samples of populations from different geographic locations showed clinal differences in several characters. However, when I later examined new material, I found that 2 samples from the same locality often differ more from each other than they do from a sample from another locality. This is true of characters affected by differences in preservation as well as those unaffected by such differences. Table 7 shows some variables in which 2 samples from Woods Hole differed more from each other than from samples from other localities.

Only 2 characters show any statistically significant geographic variation: gill length

TABLE 7. Comparisons of adjusted means showing greater differences between samples of *Loligo pealei* from the same locality than from other localities.

Measurement	Covariate	Martha's Vineyard, Mass.				Other locality		
		Sample 4		Sample 12				
		$\bar{X}$ mm	N	$\bar{X}$ mm	N	$\bar{X}$ mm	N	
Gill L, F*	ML	43.2	11	33.4	11	35.1	7	Colombia
GW, F	ML	23.0	11	27.4	11	25.9	7	Colombia
ASW III, F	FCL	2.2	11	2.0	11	1.9	7	Colombia
AS II	ML	109	23	96	30	106	24	Beaufort, N.C.
FCL	ML	21.8	23	20.5	30	21.4	24	Beaufort, N.C.

*F = Female.

and the number of transverse sucker rows on the tentacular club. The regression coefficients of gill length on funnel cartilage length show a statistically significant difference ($p < 0.05$) between samples from the E coast of the United States and samples from the Gulf and Caribbean Sea (Fig. 14). Gill length increases faster relative to increasing funnel cartilage length in samples from the Gulf and Caribbean Sea than in samples from the U.S. E coast. Faster growth of gills may be correlated with a lower oxygen content in the waters of the warmer part of the range of *Loligo pealei*. Roper (1969) found correlations between increased gill size and number of filaments and lower oxygen concentrations for *Bathyteuthis* and noted that similar correlation had been found for some fish. However, increase in gill length also could be correlated with a

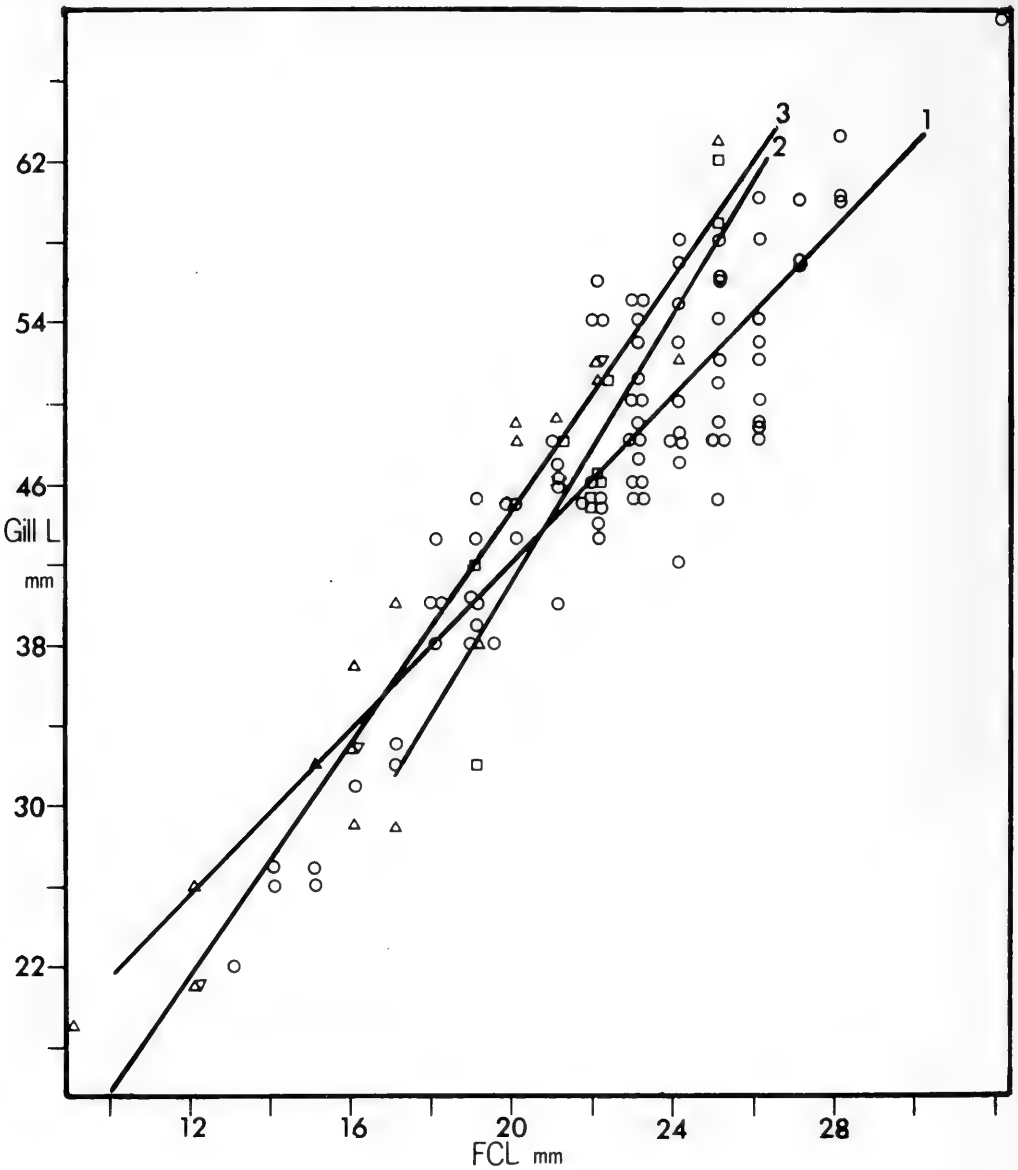

FIG. 14. The regression of gill length upon funnel cartilage length (Gill L:FCL) in males of *Loligo pealei*. Eastern coast of United States = open circles, regression no. 1. Gulf Coast of United States = open squares, regression no. 2. Caribbean Sea = open triangles, regression no. 3.

higher metabolic rate in warmer waters. Voss (1967) and Robson (1925) suggested that decreased respiratory surface in deep-sea octopods was correlated with lower temperature and lower metabolic rate. Walters (1961) suggested the same for some bathypelagic fishes.

It is surprising to find that the regression coefficient for Gill L:FCL is higher for the northern Gulf of Mexico sample than for the Caribbean samples. Ekman (1953) felt that the northern Gulf is more similar to warm temperate regions like Beaufort, North Carolina, than to the tropical Caribbean Sea. Intense cold spells have killed fishes in the northern Gulf about once every 14 winters (Leipper, 1954). On the other hand summer surface waters are about 28°C throughout the Gulf (Leipper, 1954). The regression of Gill L:FCL may be related more to summer temperatures than to winter ones or may be the result of the relatively smaller sample size tested.

In contrast to Gill L:FCL, the number of gill filaments in relation to ML appears to be lower in males (no large females available) from the Caribbean than in males from northern samples.

Table 8 shows a cline in the mean number of transverse sucker rows (TSR) on the tentacular club for samples of populations from the eastern Atlantic coast of the United States, northern Gulf of Mexico, and the Caribbean Sea. A significant difference ($p < 0.05$) exists only between the samples from the Caribbean versus the samples from the Gulf of Mexico and the eastern Atlantic coast of the United States. Furthermore, the means of smaller geographic regions are not perfectly arrayed in a cline and the standard deviations show that the geographic areas overlap in TSR (Table 9). Therefore, there is no meaningful geographical difference in TSR.

No other characters show geographical clines in means, means adjusted by covariance, or in regression coefficients. However the Caribbean samples differ from samples from other regions not only in gill length but also show increased variability, particularly in the hectocotylus. The hectocotylus is 1 of the 2 nonoverlapping characters differentiating *Loligo pealei* from *L. plei.* (Figs. 4, 20). In most *L. pealei* only 10-12 suckers in the dorsal row are hectocotylized; the rest of the distal dorsal suckers are equal in diameter to those in the ventral row. In *L. plei*, reduction of the suckers of the dorsal row extends to the tip of the arm. In all geographic samples of *L. pealei*, except the one from Beaufort, there are some specimens with more than 12 suckers somewhat reduced in diameter distal to the 10-12 hectocotylized suckers. The 3 Caribbean samples have the most specimens with greater reduction of the dorsal row (11 of 44 males).

TABLE 8. Possible geographic variation in number of sucker rows on the tentacular club of *Loligo pealei.*

Region	Sample size	Sucker rows		Significance
	N	$\bar{X}$	±S	
East Coast U.S.	63	38.4	1.99	
Gulf Coast U.S.	15	36.0	2.3	NS
Caribbean Sea	22	35.4	2.3	$P < 0.05$

TABLE 9. Possible geographic variation in number of sucker rows on the tentacular club of *Loligo pealei.*

Locality	Sample size	Sucker rows		Significance
	N	$\bar{X}$	±S	
Cape Cod, Mass.	61	39.1	2.3	
Assateague, Va.	20	38.6	1.6	NS
Beaufort, N.C.	11	38.6	2.2	NS
Venezuela	8	36.5	1.4	$P < 0.05$
Louisiana	16	36.1	2.2	NS
Colombia	19	34.7	2.4	NS

There is only 1 other sample in which similar reduction in sucker size occurs in several specimens. In a sample from Assateague, Virginia (no. 13), 6 out of 17 males have suckers reduced in diameter in addition to the usual 10-12. However, in the other Assateague sample, reduction occurs in only 1 out of 34; therefore only 7 out of 51 specimens from Assateague samples show increased dorsal reduction of sucker diameter.

Furthermore, 2 specimens from the Caribbean Sea have hectocotylized arms bearing dorsal suckers only 1/2 of the diameter of the ventral suckers from the origin of the hectocotylus to the tip of the arm. Five specimens from the Caribbean have an unusual reduction in the size of a few ventral suckers at the origin of the

hectocotylized portion of the arm.

The Caribbean samples appear to have more variation in FW:ML and greater overlap with the FW:ML of *L. plei* than in samples from other areas. However, the analysis of covariance does not show statistically significant differences in these characters between the Caribbean samples of *Loligo pealei* and other samples of *L. pealei*.

A familial character for the family Loliginidae is the presence of 7 buccal lappets. Variation was observed in 12 Caribbean specimens; 164 were examined. One specimen out of 20 examined from the Gulf of Mexico had an abnormal number; none of 132 examined from the east coast of the United States, and 12 of 164 from the Caribbean had an abnormal number. One Louisiana and 3 Colombia specimens have 6 lappets, 8 Colombia specimens have 8, and one Colombia specimen has 9. Nine Colombia specimens were from 1 station (*Pillsbury* 357), where a total of 104 *Loligo pealei* were collected. Lesueur (1821) said that the type specimen from South Carolina had 6 lappets; the type is missing (Voss, 1962).

The margins of the vane of the gladius are usually unthickened although often pigmented. In 6 male *Loligo pealei* of 580 examined, the margin of the vane of the gladius is thickened into a lateral rib equal in thickness to the thickest ribs observed in *L. plei*. These 6 males are: 2 from off North Carolina (223 mm ML, *OREGON II* station 10675; 314 mm ML, *SILVER BAY* station 1219); 1 from off Louisiana (244 mm ML, *OREGON II* station 10858); and 3 from off Colombia (181 mm ML, *CHOCO* station 25; 121 mm, 127 mm ML, *PILLSBURY* station 352). The gladius of the *SILVER BAY* specimen is indistinguishable from that of *L. plei*; it is the only *L. pealei* gladius which I have seen with an index of less than 2.4 for the ratio of vane width to rachis width. The index of 2.1 should identify it as *L. plei*; but its hectocotylus is clearly that of *L. pealei*. This is discussed further in the section on Comparison of Species.

Maturity occurs at a somewhat smaller size in Caribbean specimens than in specimens from other localities. Samples for this study are not random samples of the entire size distribution of each population. The smallest mature males and females respectively found in each sample are: Caribbean 61, 73 mm; Louisiana 138, 133 (however, no smaller specimens are included in the sample), Assateague 86, 87; and Cape Cod 131, 141. The smallest mature Cape Cod specimens were captured in summer. Late fall samples from Cape Cod include immature specimens as large as 190 mm ML (and perhaps 219 mm ML). Summers (1971) believes that large immature autumn squid are representatives of a November brood of the previous year in that region.

Loligo pealei seems to mature at a smaller size in warmer waters. Thompson (1968) states that this is true of many animals and that in addition, animals grow faster at a warmer temperature but reach a smaller maximum size. Embryos of *L. pealei* develop faster at warmer temperatures (McMahon & Summers, 1971). The largest specimens of *L. pealei* are found in the cold part of the range. Summers (1968) recorded a maximum ML of 465 mm. I have seen only one male greater than 200 mm ML and no females larger than 128 mm ML from the warmer waters of the range of *L. pealei*.

According to Summers' (1971) theory, absence of large specimens in the Caribbean could be explained by a longer or year-round breeding season along with death of all *Loligo pealei* after spawning. Death follows spawning in *L. opalescens* (Fields, 1965). Summers believes that the largest males of *L. pealei* are those which missed spawning because they were hatched late in the previous season and were immature or unable to compete successfully for females during the next spawning season. However, as Summers & McMahon (1970) and Summers (1971) said, there is as yet no evidence for breeding mortality. *L. pealei* did not die immediately in studies of spawning in an aquarium (Arnold, 1962). In the currently most successful attempt to keep *L. pealei* alive in an aquarium, 246 squid survived for an average of only 7.4 days (maximum 58 days) and 120 squid survived for an average of 10.3 days. Survival was lower for squid which had reached maturity and for those which bred in captivity (Summers, McMahon & Ruppert, 1974). *L. pealei* observed spawning in nature did not die but left the spawning site after 4 days spent hovering near the eggs (Stevenson, 1934). No mass mortality of *L. pealei* has been described in nature.

Since Gulf and Caribbean squid have been taken in as shallow waters in winter months as in summer, seasonal migrations to deep

waters may not occur in the warm part of the range of *Loligo pealei*.

No systematic studies have been made of the distribution and life history of populations of *Loligo pealei* in the Gulf of Mexico and Caribbean Sea. *L. pealei* has been collected at depths of 8-393 m in the Gulf and at depths of 0-73 m in the Caribbean (Table 6, Appendix A). Gravid females were present in samples collected in January from Louisiana and in November from Colombia. Summers (1969) linked seasonal migrations of *L. pealei* to avoidance of winter temperatures below 8°C north of Cape Hatteras. Temperatures as low as 8°C do not occur in the Gulf and Caribbean.

The possibility remains that populations in the warm waters may be adapted to a different critical temperature, but little seasonal variation exists in the surface waters of the Caribbean and surface temperatures remain about 25-28°C. The thermocline at 100-200 m (Gordon, 1966) is below the depth at which *Loligo pealei* has been found to occur. However, Gordon said that upwelling occurs off Colombia and Venezuela; it may expose the populations there to colder water. While summer temperatures in the Gulf of Mexico are tropical, winter temperatures are usually 17-19°C with colder inshore temperatures some years (Leipper, 1954).

Verrill established varieties and subspecies of *Loligo pealei* based upon morphological differences between geographically adjacent populations in New England.

Verrill (1873) described *Loligo pallida* as a distinct species, but in 1881 he reduced it to a variety of *L. pealei* and distinguished it from the typical form of *L. pealei* by its shorter and wider body, broader and larger caudal fin, and larger suckers, especially those of the tentacular club. *L. pealei* var. *pallida* was common in Long Island Sound while the typical form *L. pealei* was common in both Long Island and Vineyard Sound. Considerable overlap exists in the ranges of the ratios Verrill listed for the 2 subspecies.

Verrill (1880) described *Loligo pealei borealis* from off Cape Ann, Massachusetts Bay, but after examining a larger series of specimens he changed it from a subspecies to a geographical variety because he observed specimens showing a gradation between the subspecies and the typical form (Verrill, 1881).

Variation in behavior (presumed to be related to geographic range) was described by Arnold (1962) who observed the establishment of male breeding hierarchies for *Loligo pealei* in an aquarium. Specimens captured in Rhode Island were more aggressive than larger ones from Cape Cod.

I found no evidence of geographical variation in the morphology of samples from New England. Verrill's subspecies are invalid.

LaRoe (1967) reported that there was wide variation in *Loligo pealei*, but little of statistical importance. However, he concluded that 2 large populations of *L. pealei* exist, one in the Caribbean Sea and one from New England waters. Although LaRoe felt that there is clinal variation in some characters between these 2 populations, he suggested that the populations could be 2 allopatric species with ranges meeting at the Yucatan Peninsula, Mexico.

I did not find clinal variation in *Loligo pealei*. Caribbean samples differ only slightly from other geographic samples; they differ little from samples from the Gulf of Mexico. LaRoe's conclusions were based upon smaller samples.

The geographic range of *Loligo pealei* is great, extending from the tropical waters of the Caribbean to the subtemperate waters of Nova Scotia. This represents the largest geographical distribution and greatest range of environmental temperature adaptation of any loliginids in the western North Atlantic. However, no indication of clinal geographic variation exists in the morphology of *L. pealei* although nonmorphological geographic variation remains a possibility and there are small differences in some characters between samples from the Gulf and Caribbean compared with those from farther N.

The species is composed of morphologically variable populations. Whether the variation is phenetic or genetic in origin is not known. The species may be variable as an adaptation to the range of environmental variation it encounters throughout its range, particularly temperature. The nonclinal variation may be brought about through genetic mixing of all populations. This could occur through migrations of adults or movement of planktonic young by currents. *Loligo pealei* is known to migrate seasonally in the northern part of its range, probably in avoidance of temperatures below 8°C. However, large populations have been found in

winter as far N as approximately 40° N latitude, so not all members of the species migrate to the Caribbean Sea in winter and there is no evidence that any migrate that distance. How far adults can and do migrate is not known because tagging experiments have thus far been unsuccessful (Summers, 1971, and personal communication). The planktonic young may be carried for considerable distances by currents. The coastal current system of the North American continent is complex, particularly off the eastern coast of the United States (Bumpus & Lauzier, 1965; Gordon, 1966), with many changes throughout the year particularly in the waters close to shore.

The apparently greater variation in Caribbean populations may be related to sympatry with *Loligo plei*; this is discussed later in the comparison of species.

Loligo ocula Cohen, new species
(Figs. 15-20)

MATERIAL: Holotype: ♂, 105 mm ML; *Oregon II* sta. 10858; 22°53′N, 78°43′W; 276 m; 15 Dec., 1969; USNM 727093. Paratypes: 2 ♂ juv., 80, 86 mm ML; *Oregon II* sta. 10858; 22°53′N, 78°43′W; 276 m; 15 Dec., 1969; USNM 727094.—1 ♂, 95 mm ML; 1 ♂ juv., 110 mm ML; 3 ♀ juv., 83-104 mm ML; *Oregon II* sta. 10850; 20°49′N, 73°26′W; 311 m; 13 Dec., 1969; USNM 727098.—1 ♂, 108 mm ML; *Oregon II* sta. 10849; 20°50′N, 73°23′W; 311 m; 13 Dec., 1969; USNM 727097.—1 ♀, 89 mm ML; *Oregon II* sta. 10178; 16°43′N, 81°53′W; 256 m; 16 Nov., 1968; USNM 727096.—2 ♂, 87 mm, 127 mm ML; *Oregon II* sta. 10859; 23°04′N, 78°46′W; 362 m, 15 Dec., 1969; USNM 727095.

DIAGNOSIS: Eye large, diameter of externally visible eyeball about 15-21% of ML (Fig. 19); lens large, diameter of dissected lens about 6-8% of ML (Fig. 20); hectocotylus originating in distal 1/3 to 1/4 of left ventral arm, not extending to arm tip; all modified suckers of dorsal row with broadly triangular bases.

DESCRIPTION: Specimens examined: 80-127 mm ML. *Mantle* cylindrical, tapers posterior to fin insertion to a blunt point. Anterior mantle width rather broad, width 22-29% of ML (Fig. 11); anterior mantle circumference 67-89% of ML; longer specimens more slender. Ventro-lateral lobes on mantle opening short and pointed (point approximately 90° angle); dorsal lobe at least as large as lateral lobes, with rounded point; low, narrow mid-ventral ridge present in males. *Fins* rhomboid, widest point curved and slightly anterior to midpoint of fin length, fins united at posterior end of mantle; width about 45-59% of ML; length 43-54% of ML; width about equal to length, ratio of length to width = 0.783-1.18, fins relatively longer and more narrow in longer specimens; anterior lobes well-developed. *Funnel* well-developed, set in deep funnel groove. Funnel opening level with eyes. Lateral adductor muscles conspicuous, strong, rod-like; anterior adductors thin, sheetlike. Dorsal funnel organ large; posterior limbs broadened anteriorly, tapering posteriorly to blunt, rounded points, lateral borders curved more than medial borders; apical papilla minute and rounded or pointed at tip. Ventral pads oblong, shorter than dorsal pad. Funnel valve broad, bluntly rounded, with thin curved lateral flaps.

Funnel locking-cartilage strong, somewhat long, cartilage length 16-17% of ML (Fig. 21); straight, posterior tip curved dorsally, shallowly grooved. Entire cartilage bordered by thin flange. Mantle locking cartilage straight, compliment of funnel lock. Longitudinal ridge low and narrow.

Head large, width about 24-34% of ML (Fig. 22); length about 19-28% of ML; head relatively smaller in longer specimens; nuchal cartilage long (about 18-23% of ML) (Fig. 23), relatively shorter in longer specimens, straight, broader anteriorly, embedded in muscle except for anterior and posterior ends which taper to rounded points; shallow central groove, lateral ridges distinct. Eyes oval, large, diameter of externally visible eyeball 15-21% of ML (Fig. 19), relatively smaller in longer specimens, covered by cornea, pupil round. Lens large, diameter of dissected lens 6-8% of ML (Fig. 20). Dark, sometimes greenish crescent along dorsal border of eye. Aequiferous pore at anterior edge of cornea.

Arm order III≥IV≥II>I or III≥II≥IV>I; length of arm I about 20-34% of ML; length of arm II about 29-42% of ML; length of arm III about 35-42% of ML; length of arm IV about 31-40% of ML. Arm III most robust; arms II, IV less robust; arm I least robust, very slender. Swimming keels low, weak, especially on distal 1/2 or 1/3 of arm II; higher, better developed on 2/3 to 3/4 of arm I; best developed on arms III and IV

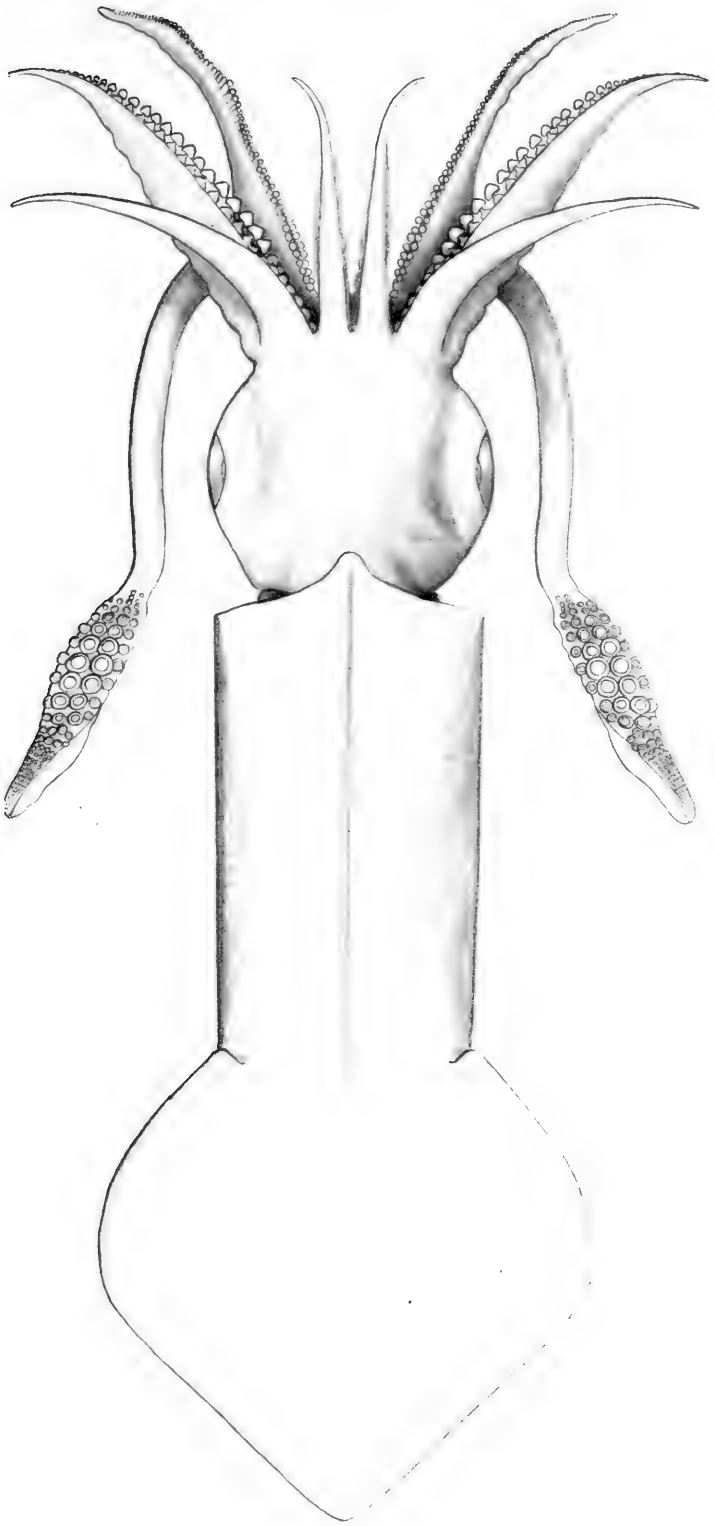

FIG. 15. *Loligo ocula* Cohen, n. sp., holotype; ♂, 105 mm ML, *Oregon II* sta. no. 10858; fins partially drawn from ♀, 104 mm ML, *Oregon II* sta. no. 10850.

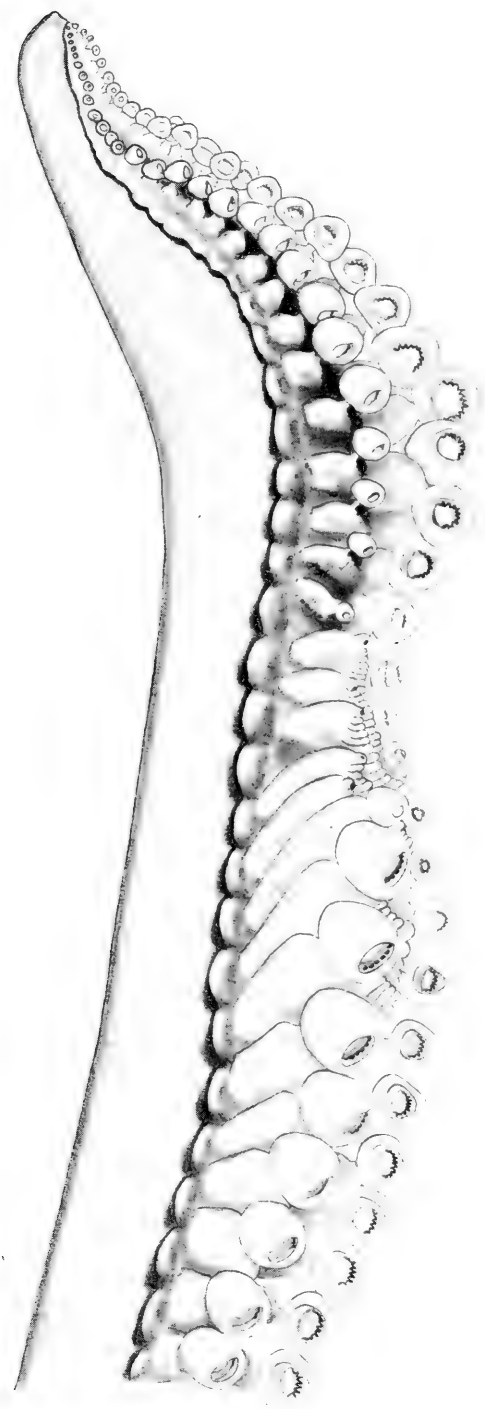

FIG. 16. *Loligo ocula* Cohen, n. sp., hectocotylus; holotype, 105 mm ML; *Oregon II* sta. no. 10858; distal 25 mm (distal 45%) of arm shown.

FIG. 17. *Loligo ocula* Cohen, n. sp., gladius; holotype, ♂, gladius length 105 mm, *Oregon II* sta. no. 10858.

where they extend full length of arms; 2 keels on arm IV, dorsal keel of arm IV and keel of arm III arising from same area at base of arms. Protective membranes well-developed, particularly ventral membranes of arms I, II, III; ventral membrane of arm IV least developed; trabeculae long, strong, arise from between bases of sucker stalks, form high points along membranes, less well-developed on arm IV.

Suckers biserial. Number of suckers on arms increases with mantle length; arms I, II, III with about equal numbers of suckers (about 90-100 at 80-95 mm ML, 95-105 at 95-105 mm ML, 105-110 at 127 mm ML); arm IV with about 10 more suckers than other arms. Width of suckers on arms in order III≥II≥I≥IV.

Arm sucker dentition variable (Fig. 18). Teeth present on distal 2/3 of tooth ring. Low, broad, sometimes rippled plate on proximal 1/3 of tooth ring. Arm I with about 7-14 teeth; arm II with about 8-14 teeth; arm III with about 9-11 teeth; arm IV with about 7-8 teeth. Variation in teeth shapes and patterns but arms I, II, and III

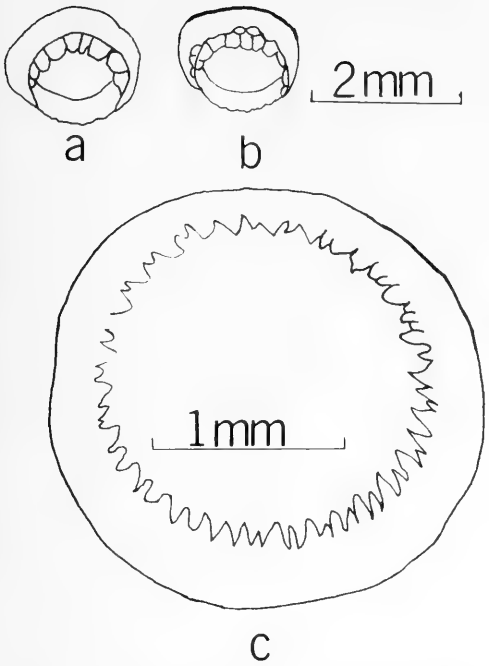

FIG. 18. *Loligo ocula* Cohen, n. sp. **a**, teeth ring of largest sucker on arm III; holotype, ♂, 105 mm ML, *Oregon II* sta. no. 10858; **b**, teeth ring of largest sucker on arm III; other specimen; **c**, teeth ring of large mid-manal sucker on tentacular club; holotype.

often with the following pattern: central 2 teeth of tooth row most narrow, next 2 lateral teeth on either side of central pair increasingly wide; next lateral teeth of decreasing size. Arm IV with irregular patterns but with narrowest teeth near center of tooth row. Tooth shape on all arms varies from very low and blunt in some specimens to longer with blunted points. Smaller tooth rings with relatively narrower teeth.

Left ventral arm *hectocotylized* (Fig. 16), modified in distal 1/3 to 1/4 of arm; modification chiefly in dorsal sucker row, does not extend to tip of arm; only 10-12 suckers in dorsal row less than 1/2 the size of their ventral counterparts. About 33-45 suckers proximal to hectocotylus. Hectocotylization originates proximally with 2-5 suckers of dorsal row larger than their ventral counterparts and on increasingly long, widely triangular pedicels; followed by 5-7 dorsal suckers of rapidly diminishing size on long, large, broadly triangular pedicels of slowly diminishing size distally; ventral suckers in this area diminish in size also but less so and on unmodified pedicels shorter than their dorsal counterparts; ventral suckers at least twice the size of dorsal ones. Suckers of both rows increase in size again distally. Distal tip of arm fairly normal in appearance; suckers of both rows gradually diminish in size; dorsal suckers often slightly smaller than their ventral counterparts. Central area of arm in modified area raised, puffy and folded with central ridge connecting the folded triangular bases of the arms.

Tentacles robust. Clubs expanded, about 24-35% of ML. Clubs with about 32-39 transverse rows of 4 suckers each. Distinct carpal cluster absent, suckers in ill-defined carpal area small, biserial, only about 2-5 suckers; no carpal knobs. Often only 3 small suckers in proximal-most row of manal suckers; distal rows tetraserial; suckers gradually increase in size; lateral manal suckers smaller than medial suckers; medial manal suckers arise distal to the carpal suckers; about 10-16 medial suckers on manus greatly enlarged; manus terminates rather abruptly, distal-most 1 or 2 rows of manal suckers decrease in size, lateral suckers become more equal in size to medial suckers, ventro-lateral sucker becomes large relative to medial suckers of same transverse row. Dactylus distinct, slender, suckers tetraserial, numerous, minute, decreasing in size distally; suckers in approximately first 10 rows graded in size transversely, ventro-lateral sucker largest, dorso-lateral sucker smallest in each transverse row; distal-most 2 transverse rows often triserial and biserial. Tip with narrow, suckerless flange. Swimming keel short and inconspicuous on stalk, along at least distal 1/2 of stalk aborally, increases in size on club, particularly on distal 1/3 of manus, broadest along dactylus, diminishes at distal tip. Lateral angles distinct on oral surface and continue as broad, heavily supported protective membranes along club, diminish significantly along dactylus. Broad trabeculae between lateral suckers, usually broaden laterally in the shape of a fan, arise from common base of lateral suckers, particularly the distal sucker. Largest suckers on club larger than largest suckers on arm III; ratio of width of largest tentacular sucker to width of largest sucker on arm III = 1.1-2.0.

Club sucker dentition variable (Fig. 18). About 24-30 teeth, usually 24, on sucker rings of carpal area; teeth usually bluntly

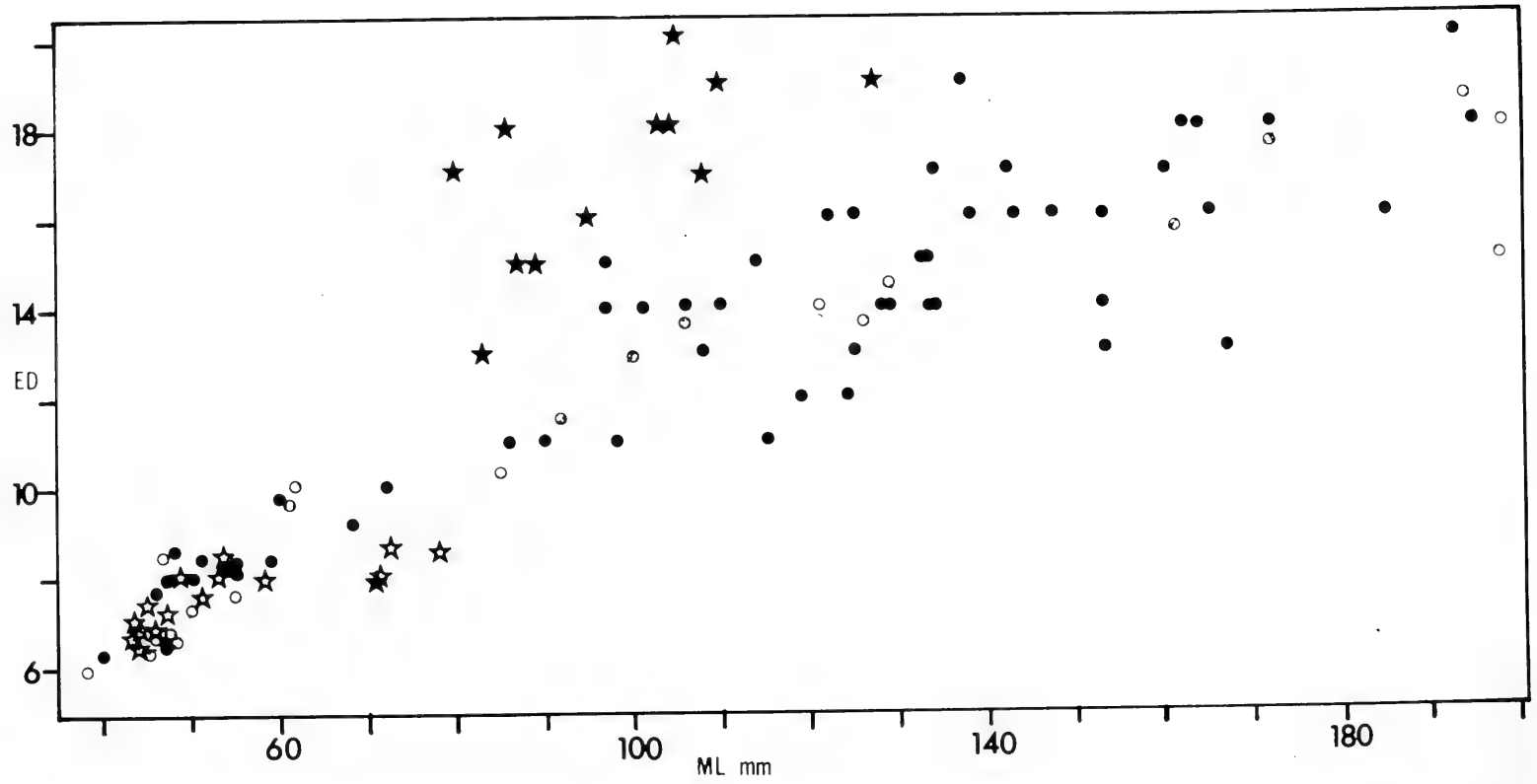

FIG. 19. The regression of diameter of externally visible eyeball upon mantle length (ED:ML). *Loligo pealei* = solid circles. *L. plei* = open circles. *L. ocula* = solid stars. *L. roperi* = open stars.

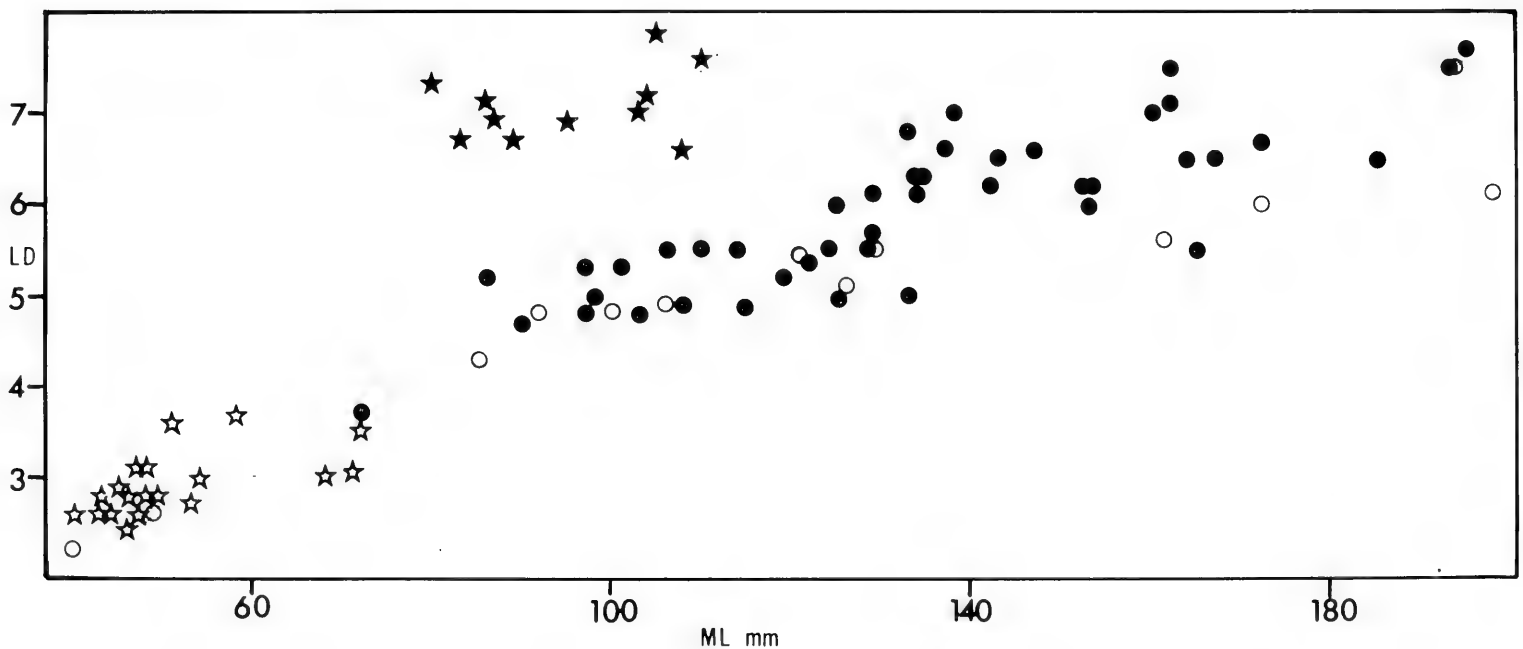

FIG. 20. The regression of diameter of dissected lens of eye upon mantle length (LD:ML). *Loligo pealei* = solid circles. *L. plei* = open circles. *L. ocula* = solid stars. *L. roperi* = open stars.

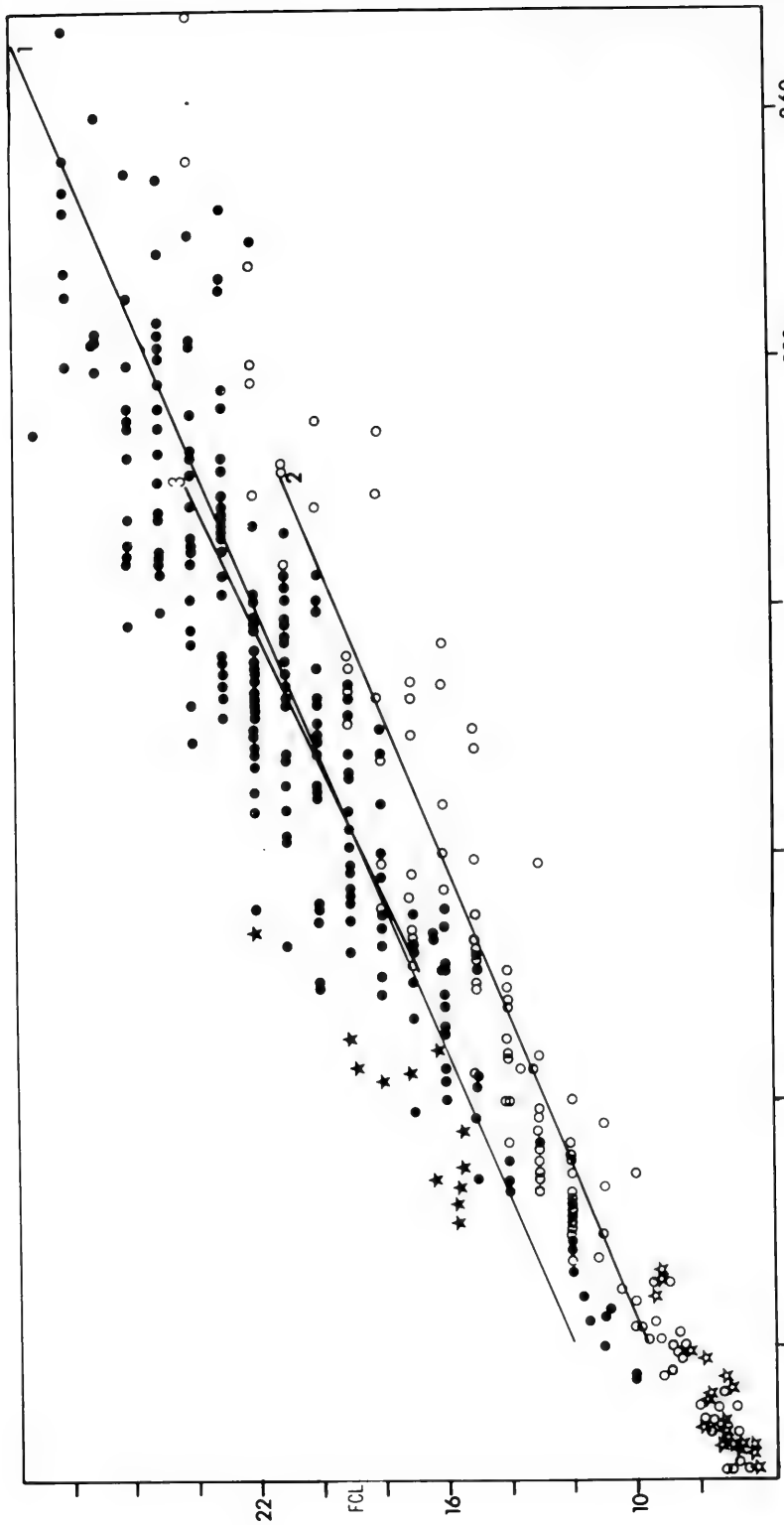

FIG. 21. The regression of funnel cartilage length upon mantle length (FCL:ML). *Loligo pealei* = solid circles, regressions nos. 1, 3 (120-200 mm ML only); *L. plei* = open circles, regression no. 2. *L. ocula* = solid stars. *L. roperi* = open stars.

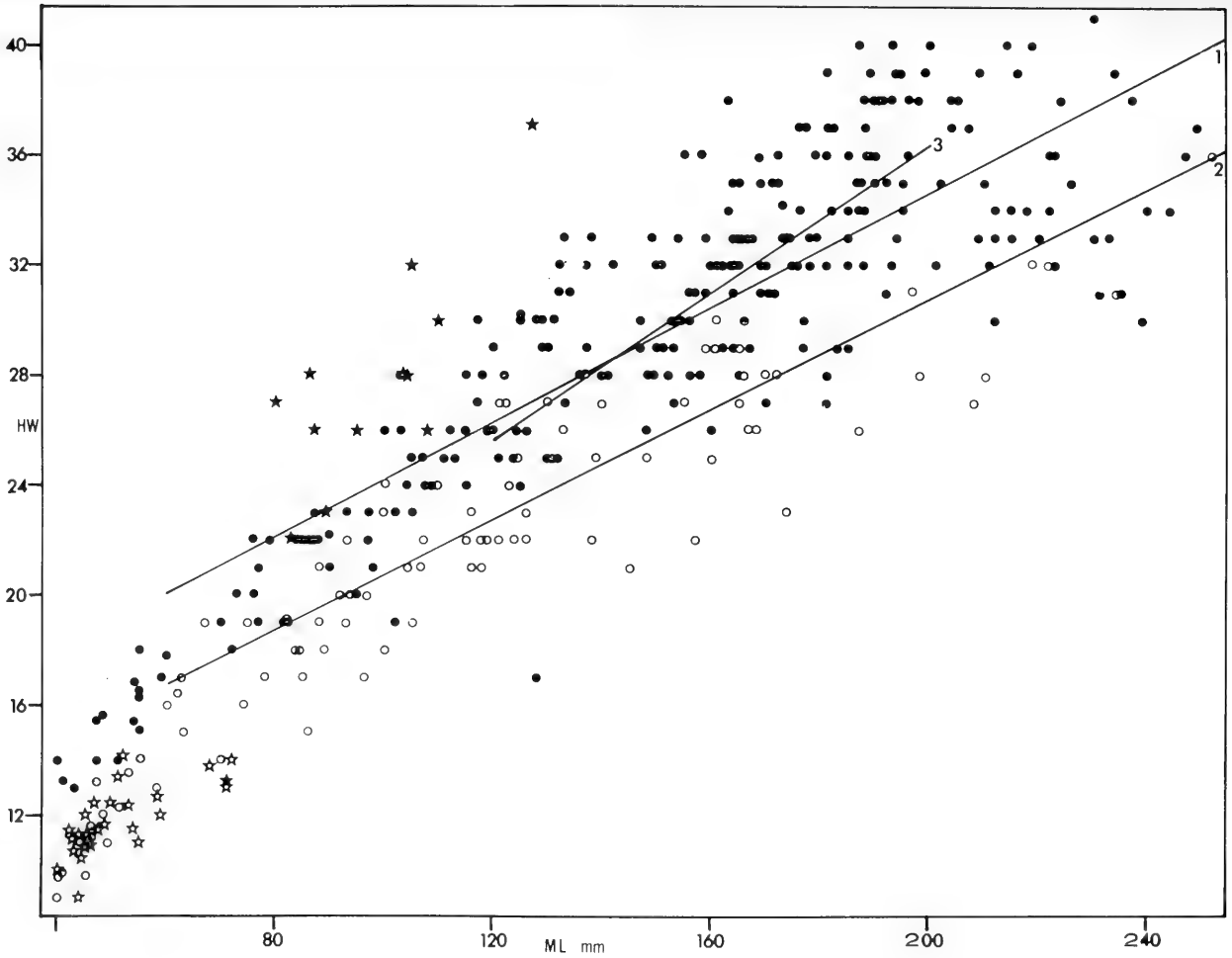

FIG. 22. The regression of head width upon mantle length (HW:ML). *Loligo pealei* = solid circles, regressions nos. 1, 3 (120-200 mm ML only). *L. plei* = open circles, regression no. 2. *L. ocula* = solid stars. *L. roperi* = open stars.

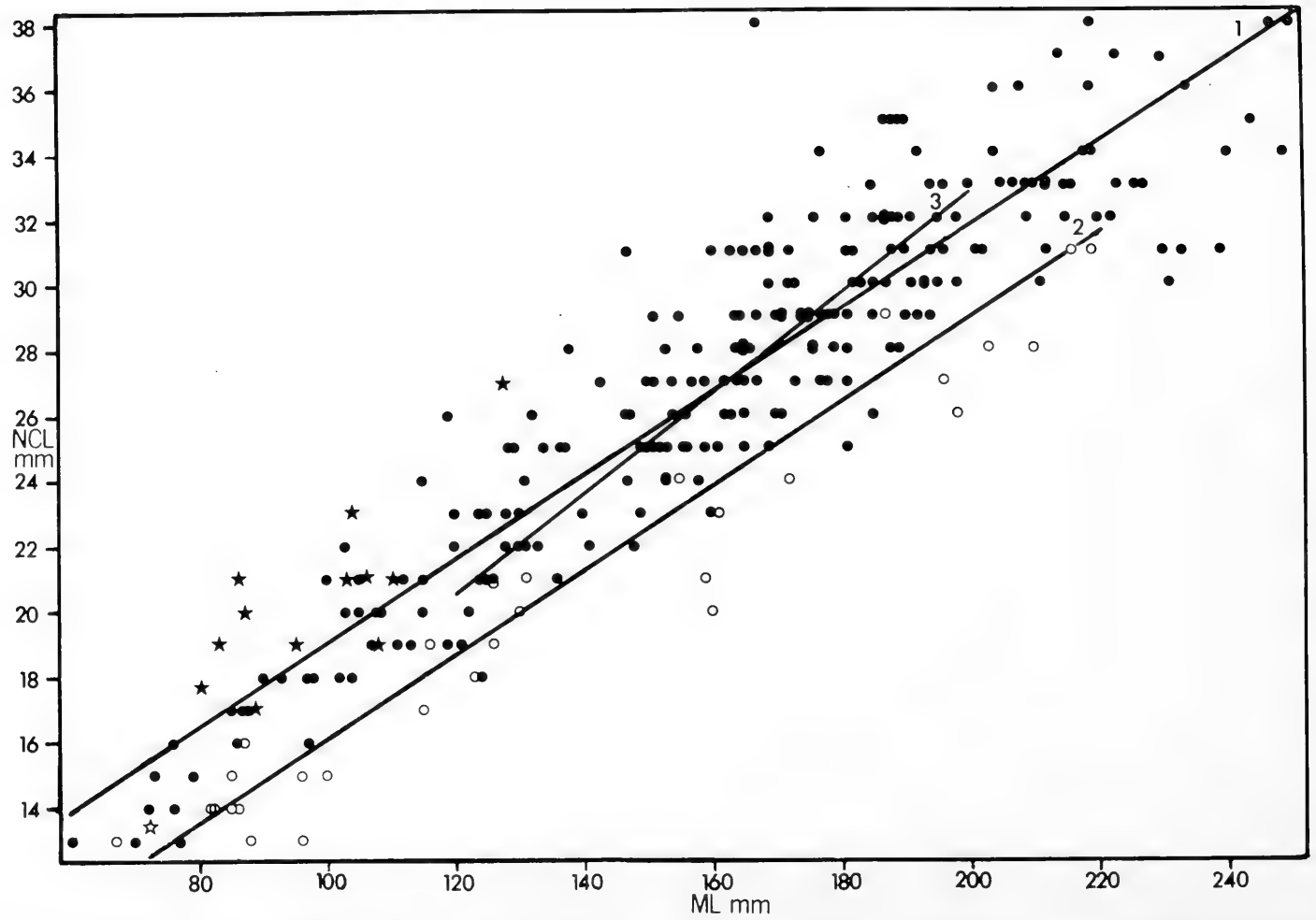

FIG. 23. The regression of nuchal cartilage length upon mantle length (NCL:ML). *Loligo pealei* = solid circles, regressions nos. 1, 3 (120-200 mm ML only). *L. plei* = open circles, regression no. 2. *L. ocula* = solid stars. *L. roperi* = open stars.

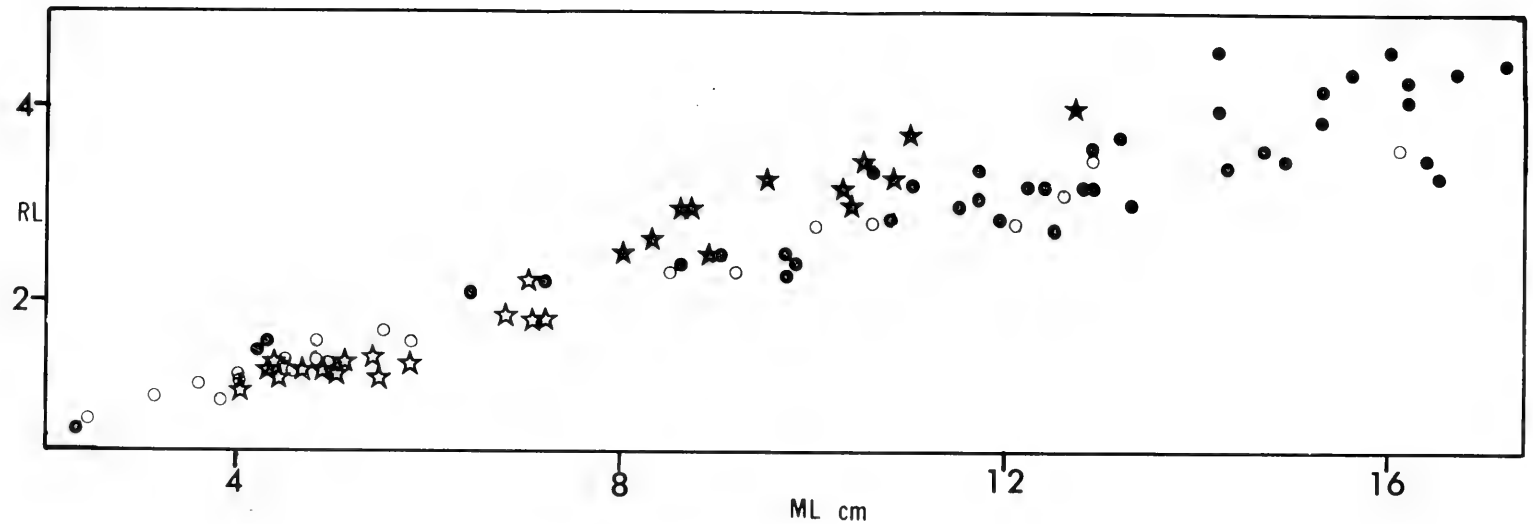

FIG. 24. The regression of rachis length upon mantle length (RL:ML). *Loligo pealei* = solid circles. *L. plei* = open circles. *L. ocula* = solid stars. *L. roperi* = open stars.

pointed, varying from blunt to pointed; teeth graded in size, proximal teeth larger, usually more pointed than distal teeth. About 15-27 teeth on proximal-most lateral suckers; about 23-35 teeth on largest lateral suckers; about 15-25 teeth on distal lateral suckers; teeth usually pointed, points often curved, sometimes bluntly rounded instead of pointed; teeth graded in size, and sometimes alternating large and small; teeth at outer edge of ring larger and usually more pointed than inner teeth. About 22-28 teeth on proximal-most medial manal suckers (first 1-3); about 35-60 teeth on largest medial manal suckers; about 22 teeth on distal medial manal suckers; teeth usually pointed, usually triangular in shape, points sometimes slightly curved, sometimes bluntly rounded, often with alternating large and small teeth (a pattern of large tooth, small tooth, medium-sized tooth, small to medium-sized tooth, medium tooth, large tooth and a pattern of large, small, small, large each observed once). About 20 usually pointed (sometimes stubby and rounded) teeth on proximal dactylar sucker rings; about 8 teeth larger and usually more pointed than others.

Gladius (Fig. 17) long, rather wide (width about 13-17% of ML), feathershaped; anterior tip with weak flexible acute point; rachis stiff, free rachis long, about 28-35% of ML (Fig. 24); median ridge and heavy lateral rods on rachis, continue in center of vane, fuse beyond midpoint of vane, continue to tip. Vane tapers at both ends from widest point in central area, edges thin, posterior tip pointed and thin. Rachis rather narrow, vane rather wide; ratio of greatest width of vane to greatest width of rachis about 2.4-2.9.

Buccal lappets usually 7 (8 in holotype: left dorsal lappet doubled); ventral pair united at base and with fewer suckers; suckers present on all lappets; total suckers on all lappets 45-64. Connectives of buccal membrane attach to dorsal, dorsal, ventral, ventral borders of arms I-IV respectively.

Beaks. Rostrum of upper beak curved, strong, sharp, long (but short in comparison to length of hood and rostral lamella), heavily pigmented; dorsal hood weak, thin, lightly pigmented; notch separates rostrum and rostral lamella (jaw angle recessed); cutting edge of rostral lamella slightly curved, smooth, small convex curve adjacent to rostrum; palatine lamella weak, large, long, deep, pigmented anteriorly, dorsal crest only slightly curved. Rostrum of lower beak shorter than upper beak, pointed, heavily pigmented, inner edge curved; rostral lamellae narrow, short, with wing lobate, thin; gular lamella large, crest strong, posterior corner pointed, moderately curved.

Radula with 7 transverse rows of teeth; rachidian with long central pointed tooth and pointed lateral cusps; 1st lateral tooth pointed, with pointed lateral cusp; 2nd lateral tooth pointed, curved on outer side, longer than first, no lateral cusp; 3rd lateral tooth long, curved, scythe-shaped; marginal plaques present.

Spermatophore with sperm mass of about 70-80% of total length, cement body about 7-13% of total length, total length about 6-14 mm. Cone at oral end of cement body cylindrical, narrows at oral end.

Gill length about 26-35% of ML. Number of filaments on one side of gill increases with ML, about 53-56 at 80-90 mm ML, 61-65 at 95-127 mm ML.

Color (in alcohol). Reddish-brown chromatophores cover entire mantle, more widely spaced ventrally; present only on dorsal side of fins and more widely-spaced laterally; cover entire head, more closely-spaced proximal to eyes; present on exposed part of funnel and collar; present on outer side of arms and tentacles. Dark, sometimes greenish crescent over dorsal border of eyes. Dark mid-dorsal longitudinal indentation extends from mid-dorsal mantle point to just posterior of fin origin, more than 1/2 of ML.

HOLOTYPE: United States National Museum (727093). Paratypes: United States National Museum (727094, 727095, 727096, 727097, 727098).

TYPE LOCALITY: 22°53′ N; 78°43′ W on edge of Grand Bahama Bank about 45 mi N of Punta Alegre, Cuba; *Oregon II* station 10858, 15 December 1969, 276 m.

DISTRIBUTION: Caribbean Sea: between Cuba and Great Bahama Bank; S of Great Inagua Id., Bahama Ids.; off continental shelf, E of Honduras (Fig. 1). Taken in bottom trawls at depths of 256-362 m. This species has been caught together with *Loligo roperi* (Table 3).

ETYMOLOGY: The Latin word "*oculus*" means eye, and refers to the large, prominent eyes of *L. ocula.*

DISCUSSION: The holotype of *Loligo ocula* has 8 buccal lappets (all of the others have 7). While 7 buccal lappets is a familial

character for the Loliginidae, aberrations in the number of lappets occur as noted here in *L. plei* and in *L. pealei* (including its holotype).

Fig. 6 indicates that females may have fewer gill filaments than males. However more specimens are necessary to verify that this is as true of *Loligo ocula* as it is of *L. pealei*.

Loligo plei Blainville, 1823
(Figs. 25-26)

Loligo pleii Blainville, 1823: 132-133.—Férussac & d'Orbigny, 1834-48, pl. 16.
(?)*Loligo brasiliensis* Blainville, 1823.—Férussac & d'Orbigny, 1834-48: 313-314.
Loligo plei Blainville.—Férussac & d'Orbigny, 1834-48: 312-313.—d'Orbigny, 1853: 42-45.
Doryteuthis plei (Blainville).—Naef, 1912: 742.—Adam, 1937: 63-67, figs. 18-22; 1941: 132-133.—Rees, 1950:111-113, pl. 14.—Voss, 1956: 116-118, fig. 6, b-d.

DIAGNOSIS: Ratio of greatest width of vane of gladius to greatest width of free rachis 1.5-2.4, vane of mature males with thickened rod-like margins; hectocotylus originating in distal 1/4 to nearly 1/2 (not more than 50%) of left ventral arm, extending to arm tip, at least 1/2 (but less than 70%) of the suckers in the dorsal row less than 1/2 the size of their ventral counterparts.

DESCRIPTION: *Mantle* long, slender, cylindrical, tapering to a posterior acute point. Anterior mantle width about 11-25% of ML (49-348 mm ML); anterior mantle circumference 35-68% of ML (44-348 mm ML), longer specimens more slender. Ventro-lateral lobes on mantle opening short and pointed (point approximately 90° angle); dorsal lobe longer than lateral lobes, with rounded point; low, narrow, mid-ventral ridge often present, particularly on males.

Fins rhomboid, sides fairly straight, widest point curved and slightly anterior of midpoint of fin length; fins united posterior to tip of mantle; length (35-58% of ML, 40-348 mm ML) about equal to width (33-45% of ML, 40-348 mm ML), fins relatively longer and more narrow in long specimens, ratio of length to width is about 0.765-1.66; anterior lobes well-developed.

Funnel well-developed, set in deep funnel groove. Funnel opening level with eyes. Lateral adductor muscles conspicuous, strong, rod-like; anterior adductors thin, sheet-like. Dorsal funnel organ large; posterior limbs broadened anteriorly, tapering posteriorly to blunt, rounded points, lateral borders curved more than medial borders; apical papilla minute, very inconspicuous, pointed. Ventral pads oblong, shorter than dorsal pad. Funnel valve broad, shallowly curved or blunt with thin curved lateral flaps.

Funnel locking-cartilage long (about 7-18% of ML, 60-348 mm ML), straight, posterior end slightly wider and curved dorsally, shallowly grooved. Mantle locking-cartilage straight, compliment of funnel lock. Longitudinal ridge low and narrow.

Head width about 10-41% of ML, length about 10-22% of ML (44-348 mm ML), head relatively smaller in large specimens; nuchal cartilage long (about 11-19% of ML, 44-348 mm ML), relatively shorter in long specimens, straight, broader anteriorly, embedded in muscle except for anterior and posterior ends which taper to blunt or rounded points; shallow central groove, lateral ridges distinct. Eyes oval, covered by cornea, pupil round. Diameter of externally visible eyeball about 14-19% of ML (40-319 mm ML), diameter of dissected lens about 2-7% of ML (40-348 mm ML). Dark crescent along dorsal border of eye. Aequiferous pore at anterior edge of cornea.

Arm order III≥IV≥II>I or III>II≥IV>I; length of arm I about 16-26% of ML; length of arm II about 23-31% of ML; length of arm III about 25-37% of ML; length of arm IV about 21-32% of ML (44-348 mm ML). Arm III robust, arms IV, II less robust, arm I least robust, very slender. Swimming keels 3rd best developed on arm I, flaring before midpoint, decrease to very low distally; very low and weak on arm II, decrease distally, best-developed on arm III, flared before midpoint, decrease gradually distally; 2nd-best developed on arm IV, 2 keels decrease gradually distally, dorsal keel better developed; dorsal keel of arm IV and keel of arm III arise from same area at base of arms. Protective membranes well-developed, particularly ventral membranes on arms I, II, III; poorly developed, particularly dorsal membrane on arm IV; trabeculae long, strong, except on arm IV, arise from base of

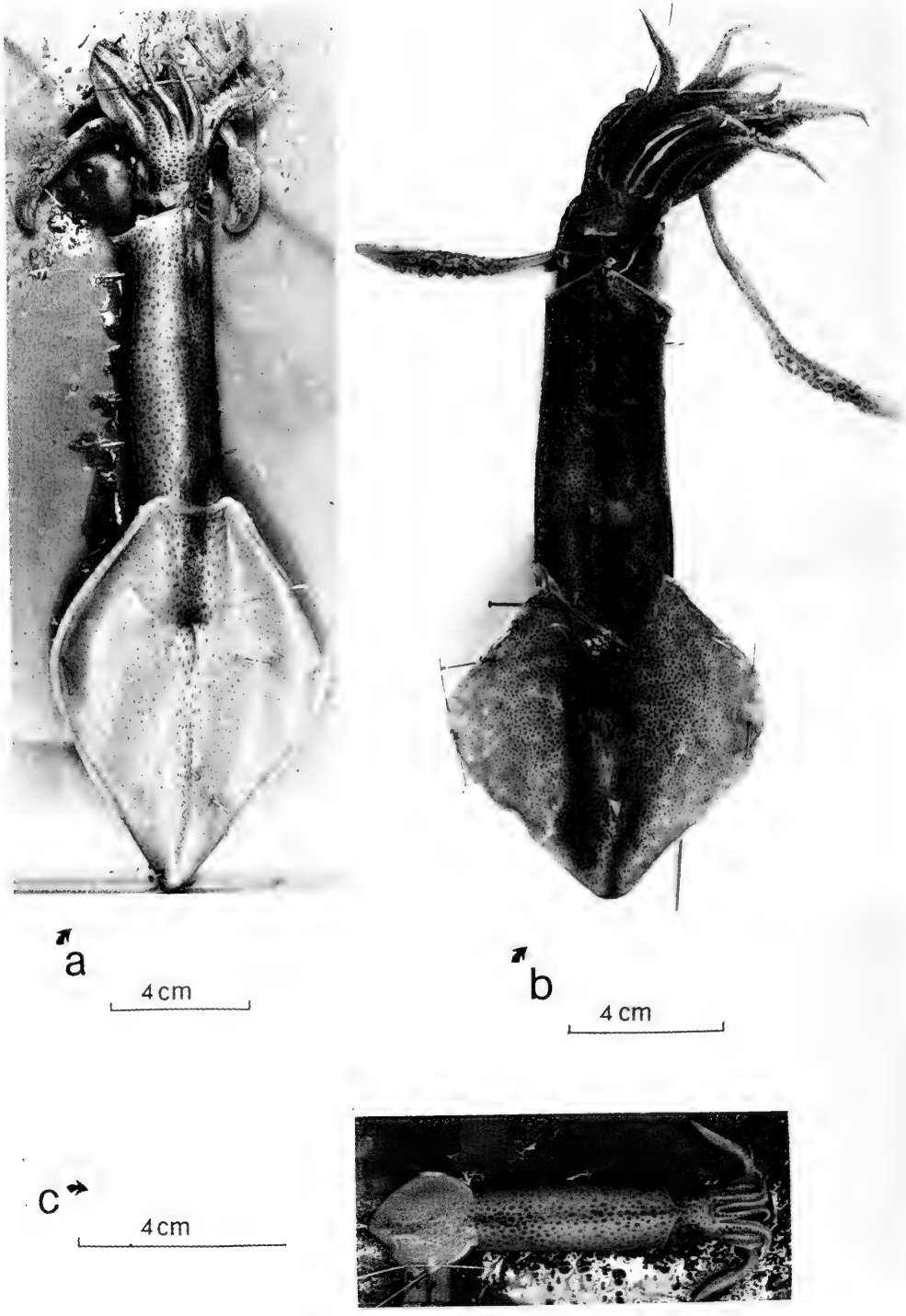

FIG. 25. *Loligo plei.* **a**, ♂, 200 mm ML; Oregon sta. no. 6777; **b**, ♀, 161 mm ML, *H. Cortez*, FSBC no. I2131; **c**, ♀ juv., 69 mm ML, *Geronimo*, cr. 6, no. 8.

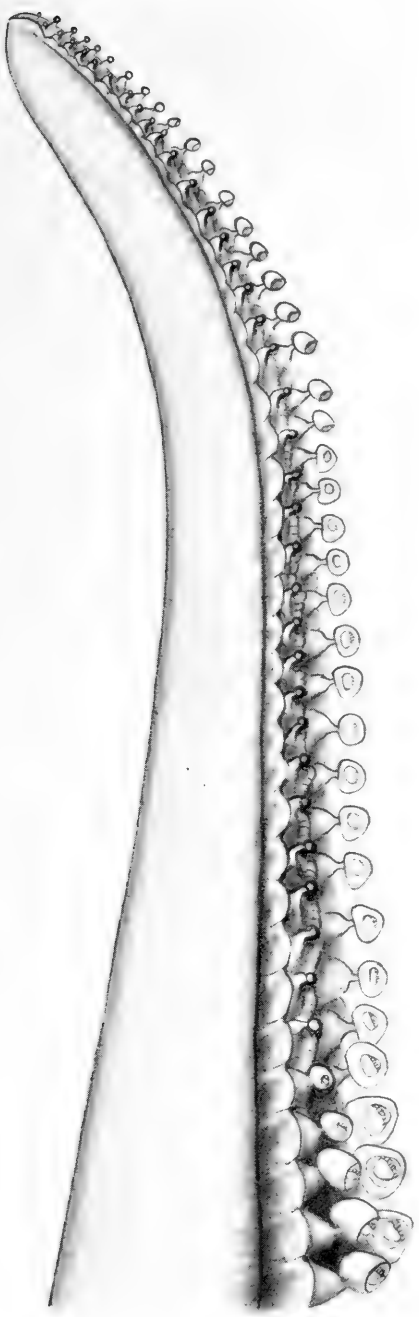

FIG. 26. *Loligo plei* Blainville; hectocotylus; ♂, 194 mm ML; *Choco* sta. no. 50; distal 34 mm (distal half) of left ventral arm.

sucker stalks, form high points along membranes. Suckers biserial. About 5 to 15 proximal-most suckers on arms I, II, III, sometimes IV increase in size distally, followed by gradual decrease in size of suckers; rapid decrease in size of suckers on arm III following about 20-34th sucker. Number of suckers on arms increases with mantle length; about 50-120 suckers on arm I, about 70-120 on arms II, III, about 90-130 on arm IV (40-348 mm ML). Width of suckers on arms in order III≥II≥I≥IV.

Arm sucker dentition variable. Teeth present on distal 1/2 of tooth ring (absent rarely, apparently worn down). Low, narrow plate on proximal 1/2 of tooth ring. About 5-10 teeth on each arm. Teeth shapes and patterns vary; tips of teeth usually blunt or rounded; teeth sometimes square, center 1-4 teeth often narrowest, lateral teeth decrease in size, pattern not always symmetrical. Some or all teeth very pointed on some or all suckers of right ventral arm (IV) of some males; teeth usually blunt on proximal-most suckers.

Not more than 1/2 of left ventral arm *hectocotylized* (about 26-50%; 38-348 mm ML) (Fig. 26). Modification usually in dorsal sucker row only, extends to arm tip. About 4-8 proximal-most suckers in dorsal row increase slightly in size distally, followed by about 5-12 decreasing slightly in size distally; followed by hectocotylized suckers rapidly diminishing in size of suckers while increasing in height of pedicels; all succeeding suckers in dorsal row with minute suckers (much less than 1/2 the size of their ventral counterparts), on small, narrow triangular pedicels (only about 3-4 proximal-most modified suckers on enlarged pedicels); about 42-82 suckers (dorsal and ventral rows) distal to origin of hectocotylus (about 52-69% of total suckers on arm; 38-348 mm ML). Central area of arm with low folds and low ridge in hectocotylized area.

Tentacles robust. Clubs expanded, about 19-29% of ML (44-348 mm ML). Clubs with 27-38 transverse rows of 4 suckers each (31-348 mm ML). Distinct carpal cluster absent, suckers in ill-defined carpal area small, biserial, only about 1-4 suckers; no carpal knobs. Often only 3 small suckers in proximal-most row of manus; distal rows tetraserial, suckers gradually increase in size; about 10-14 medial suckers on manus greatly enlarged; lateral manal suckers smaller than medial suckers; manus terminates

rather abruptly; distal-most 1 or 2 transverse rows of manal suckers decrease in size, ventro-lateral sucker usually larger than dorso-lateral sucker in distal row of manus and for as many as 14 rows of dactylus. Dactylus distinct, slender, suckers tetraserial, numerous, minute, decreasing in size distally; distal-most 2 transverse rows often triserial and biserial. Tip with narrow, suckerless flange. Swimming keel short and inconspicuous on stalk, along at least distal 1/2 of stalk aborally, increases in size on manal region of club, broadest along dactylus, diminishes at distal tip. Lateral angles distinct on oral surface and continue as broad heavily supported protective membranes along club, diminish significantly along dactylus particularly on dorsal side. Broad trabeculae between lateral suckers, usually broaden laterally in the shape of a fan, arise from common base of lateral suckers particularly the distal sucker, slight contribution from proximal sucker also in many larger specimens. Width of largest sucker greater than width of largest sucker on arm III (ratio of width of largest sucker of tentacle to width of largest sucker on arm III: 1.29 to 2.09).

Club sucker dentition variable. Sucker rings of carpal area with about 10-30 teeth (rarely none), varying from blunt to pointed, graded in size, teeth on 1/2 of ring very small, sometimes only a rippled edge, about 5-12 large teeth. Teeth of lateral manal suckers usually pointed, teeth graded in size, sometimes large and small teeth alternate, teeth at outer edge of ring larger and usually more pointed than inner teeth; largest lateral suckers with about 17-25 teeth. Teeth of medial manal suckers usually pointed, usually triangular in shape, points sometimes slightly curved, sometimes rounded, teeth rarely worn down to rounded stubs; patterns of teeth arrangement vary, teeth often arranged in a pattern of alternating large and small teeth, occasionally almost equal in size, very rarely teeth arranged in trinary pattern described in *Loligo pealei*; largest medial manal suckers with about 26 to 46 teeth. Proximal dactylar sucker rings with about 15 to 20 teeth, usually pointed, sometimes blunt or rounded stubs, graded in size, about 5 to 10 teeth larger than rest (specimens examined: 92-319 mm ML).

Gladius long, slender (width about 7-22% of ML, 40-348 mm ML), feather-shaped; anterior tip with weak flexible acute point; rachis stiff, free rachis length about 18-33% of ML (40-280 mm ML); median ridge and strong, thick lateral rods on rachis continue in center of vane, fuse beyond midpoint of vane, extend length of gladius. Additional lateral rods usually border most of vane, strongest in large mature males, weakest, sometimes rather indistinct (only a thickened stripe) in immature females, posterior portion often only a colored stripe. Rachis rather wide, vane rather narrow; ratio of greatest width of vane to greatest width of rachis about 1.5-2.4 (38-348 mm ML). Vane tapered at both ends, greatest width in males usually near anterior shoulders of vane, greatest width in females near center of vane, sides of vane fairly straight (curved in many females). Posterior tip pointed and thin.

Buccal lappets usually 7 (rarely 5 or 6), 7 buccal connectives, 7 supporting rods. Suckers (maximum 16) present on each lappet, total suckers on all lappets about 16-66, rarely fewer (suckers may have fallen off). Connectives of buccal membrane attach to dorsal, dorsal, ventral, ventral borders of arms I to IV respectively (specimens examined 44-348 mm ML).

Beaks. Rostrum of upper beak curved, strong, sharp, long (but short in comparison to length of hood and rostral lamella), heavily pigmented; dorsal hood weak, thin, lightly pigmented, notch separates rostrum and rostral lamella (jaw angle recessed); cutting edge of rostral lamella slightly curved, smooth, small convex curve sometimes adjacent to rostrum; palatine lamella weak, large, long, deep, pigmented anteriorly, dorsal crest only slightly curved. Rostrum of lower beak shorter than upper beak, pointed, heavily pigmented, inner edge slightly curved, jaw angle obtuse but nearly 90°; rostral lamellae narrow, short, wing lobate, thin; gular lamella large, crest strong, posterior corner pointed, moderately curved.

Radula with 7 transverse rows of teeth; rachidian with long central pointed tooth and pointed lateral cusps; 1st lateral tooth pointed and with pointed lateral cusp; 2nd lateral tooth pointed, longer than 1st, no lateral cusp; 3rd lateral tooth long, curved, scythe-shaped; marginal plaques present.

Spermatophore with sperm mass of about 51-77% of total length, cement body about 8-15% of total length; total length about 4-13 mm (62-280 mm ML). Oral connection of cement body cylindrical, narrows at oral

end.

Gill length about 20-32% of ML (44-348 mm ML). Number of filaments on gills increases with ML, number of filaments on one side of gill 53-84 (44-348 mm ML).

Color (in alcohol). Reddish-brown chromatophores present on entire mantle, larger and more closely-spaced on dorsal side, particularly in mid-dorsal region, often arranged in longitudinal stripes on anterior ventral-lateral mantle of large, mature males; present only on dorsal side of fins; cover entire head, more closely-spaced dorsally, particularly proximal to eyes; present on collar and funnel, on outer sides of arms, tentacles, trabeculae and protective membranes of arms I, II, III, and tentacles. Dark crescent over each dorsal border of eye. Mid-rib of gladius visible externally as an anterior reddish-brown, mid-dorsal indentation.

HOLOTYPE: Muséum National d'Histoire Naturelle, Paris.[3]

TYPE LOCALITY: Martinique, Lesser Antilles.

DISTRIBUTION: Continental shelf and slope of the E coast of the North and South American continents from Cape Hatteras (very rarely Rhode Island) to Fortaleza, Brazil (LaRoe, 1967); Bermuda; islands of the Bahamas and the Caribbean Sea (Fig. 1). Taken by dip net at the surface; in bottom trawls at depths of 3-366 m.

DISCUSSION:

Nomenclature: *Loligo pleii* is the original spelling by Blainville (1823), but *L. plei* is the commonly used spelling and the species was actually named after a Monsieur Plée. Pending a decision on the request to the Commission by Smith, Stuart & Conant (1971), I will use *plei*.

Geographic Distribution: Four *Loligo plei* were caught off Newport, Rhode Island, in 1880: a mature male, 84 mm ML, and 2 immature females, 63 and 93 mm ML (USNM no. 51271, *FISH HAWK* sta. no. 800, 16 August, 1880); and a mature male, 107 mm ML (USNM no. 33189). I know of no other *L. plei* caught N of Cape Hatteras. The temperatures for *FISH HAWK* no. 800 were: bottom and surface 20°C. Station records for 1874-1887 of the *FISH HAWK, SPEEDWELL*, and *BLUELIGHT* indicate that these temperatures are not unusual in August. However, these squid must represent rare northern strays. A similar rare northern record for the tropical species *Sepioteuthis sepioidea* at Woods Hole, Mass. in July, 1938, is reported by Mercer (1970b) who suggested that it was carried northward by the Gulf Stream.

Loligo plei has been caught in the same bottom trawls as *L. pealei* and *L. roperi*, with *L. pealei* alone, and with *Lolliguncula brevis* (Table 3).

Sexual dimorphism: Some sexual dimorphism is obvious in *Loligo plei*. The vane of the gladius is wider in females (11-22% of ML, 42-203 mm ML) than in males (7-11% of ML, 40-348 mm ML) (Fig. 5). The vane of female gladii usually has curved, tapered margins with weak lateral ribs; the widest point is near the center of the vane. Male gladii usually have straighter

[3]Since the text was completed I have had the opportunity to visit the Muséum national d'Histoire Naturelle in Paris, where I examined a specimen which is probably the holotype designated by Blainville. This specimen is a mature male *L. plei*, 156 mm ML, collected by M. Plée in Martinique. Unfortunately the specimen does not bear a label that specifies it as the type. Blainville (1823: 132-133) gave a short, 119 word description of *L. plei*; he did not list the measurements or illustrate his specimen. However Blainville stated that his specimen was sent to him from the seas of Martinique by M. Plée and that it was kept in the collection of the Muséum national d'Histoire Naturelle. The specimen which I examined agrees with Blainville's description. In particular it has no teeth on the sucker rings of the arms nor on the largest mid-manal tentacular suckers. This is very unusual in *L. plei*; I have seen only 1 other specimen which lacked teeth. This may be an artifact of preservation or a natural wearing of the teeth. Blainville stated that the chitinous ring of the suckers of his specimen was whole or entire; I believe that he meant that it was smooth or lacked teeth.

I cannot be absolutely certain that this is Blainville's original specimen because occasionally in the past, original specimens may have been replaced by more attractive specimens. However this specimen fits the brief original description. It is a mature male, and though old, it is in fairly good condition. Therefore I must assume that this specimen is indeed the holotype of *L. plei*.

Counts and measurements are as follows: ML 156 mm; FL 76 mm; FW 49 mm; AMW 21 mm; FCL 15 mm; NCL 21 mm; HL 18 mm; ED 10 mm; AL I 30 mm; AL II 35 mm; AL III 38 mm; AL IV 36 mm; the hectocotylus is 11 mm in length and extends to the tip of the left ventral arm which is 34 mm in length; the hectocotylized arm bears 86 suckers of which about 48 suckers are present in the hectocotylized area; about 33 transverse rows of suckers on the tentacle club; no teeth on largest mid-manal suckers; broadly triangular, widely-spaced, pointed teeth on smaller proximal mid-manal suckers; mid-manal suckers about twice the size of lateral manal suckers; RL 31 mm; RW 7 mm; GW 12 mm; lateral edge of vane of gladius thickly ribbed; suckers present on all buccal lappets.

margins with stronger lateral ribs; the widest point is anterior to the midpoint. Ventral longitudinal ridges on the mantle are more often present in males than in females. Mature males often have ventro-lateral stripes of chromatophores. The sexes of *L. plei*, unlike those of *L. pealei*, do not appear to differ in gill length or number of gill filaments (Fig. 6). Statistical analysis of sexual dimorphism was not made.

Maturity: LaRoe (1967) found gravid *Loligo plei* during all months but June and August. *L. plei*, unlike many other squid may not die after spawning but continue to grow and spawn again. Roper (1965) described spawning in an aquarium by one *L. plei*; it spawned a 2nd time after 4 days and remained healthy for nearly a week. Waller & Wicklund (1968) observed spawning underwater and saw no mortality. Spermatophores are present in males ranging in size from 38 mm ML (*GILL* cruise 4, sta. no. 19, off eastern Florida) to 348 mm ML (*CHOCO* sta. no. 11, off Colombia, 3 May, 1969); eggs are present in females ranging in size from 42 mm ML (USNM no. 575445, off Georgia, 1957) to 203 mm ML (*CHOCO* sta. no. 11, off Colombia). Apparently immature males and females as large as 139 mm ML (USNM no. 577080, off Puerto Rico, 26 Oct., 1966) and 90 mm ML (USNM no. 574327, off Georgia) respectively were observed.

Surprisingly, single trawl hauls have caught small mature *Loligo plei* along with much larger immature ones. Immature *L. plei* 52-91 mm ML (hectocotylus not fully developed) were caught with a mature male *L. plei*, 55 mm ML (spermatophores present, hectocotylus developed) off South Carolina in June (USNM no. 575408). Immature *L. plei* 80-138 mm ML were caught with mature *L. plei* 52-61 mm ML off Georgia (USNM no. 574327). Many immature *L. plei* 37-91 mm ML were caught with 3 mature *L. plei* 48-78 mm ML off North Carolina in October (*DELAWARE II* sta. no. 10). I could find no morphological differences between mature and immature specimens; I believe they belong to the same species. Why did the squid of the same area not mature at the same time? Since these were open nets some specimens may have been caught while the net was being retrieved. The mature and immature squid may have originated in different waters of different temperatures and somehow come together later on. I will discuss possible implications for speciation later in comparing *L. plei* with *L. roperi*.

Geographic variation: A familial character for the family Loliginidae is the presence of 7 buccal lappets. Some variation was observed in *Loligo plei* as well as in *L. pealei* and *L. ocula*. Four specimens of *L. plei* have missing buccal lappets; 155 specimens were examined. A 166 mm female caught off North Carolina (*SILVER BAY* sta. no. 1222) has 6 lappets. Three of the 10 specimens from Bermuda have missing lappets. These 3 specimens lack the 3rd, the 4th, and the 4th and 5th lappets respectively. The unusual percentage of abnormalities in the number of buccal lappets could be due to the isolation of what is probably a small population of *L. plei* at Bermuda. *L. plei* probably was introduced to Bermuda from the S (Voss, 1960). It is likely that it arrived from the West Indies via the Gulf Stream as have many shore fishes (Collette, 1962) and invertebrates (Ekman, 1953). Collette (1962) noted character differences between mainland stocks of shore fishes and their endemic derivatives or populations at Bermuda which could be correlated with scarcity of food in the Sargasso Sea around Bermuda. Collette also found that endemism is less than 4% in shore fishes—probably because of continued influx of individuals via the Gulf Stream. *L. plei* of Bermuda do not differ in most respects from the populations of other localities, and planktonic young and nektonic adults may be reintroduced to Bermuda frequently.

Loligo roperi Cohen, new species
(Figs. 27-30)

MATERIAL: Holotype: ♂, 70.8 mm ML; *Geronimo* sta. 8-26; 25°42.5′N, 79°20′W, off Bimini, Bahama Ids.; night light; 6 June, 1966; USNM 727777. Paratypes: 2 ♂, 67.9, 70.5 mm ML; *Geronimo* sta. 8-26; 25° 42.5′N, 79°20′W; off Bimini, Bahama Ids.; night light; 6 June, 1966; USNM 727776.—3 ♂, 16 ♀, 44.3-58 mm ML; *Oregon II* sta. 187; 14°49′N, 81°39′W; 48 m; 19 Nov. 1968; USNM 727775.—1 ♀, 72 mm ML; *Oregon II* sta. 10858; 22°59′N, 78°43′W; 278 m; 15 Dec. 1969; USNM 727774.—3 ♂, 2 ♀, 44-58 mm ML; *Choco* sta. 6902-38; 9°3.5′N, 76°28.5′W; 55 m; 18 May 1969; USNM 727773.—2 ♂, 1 ♀, 40-45 mm; *Pillsbury* sta. 352; 8°20.1′N, 76°53.6′W; 55-51 m; 11 July 1966; Univ.

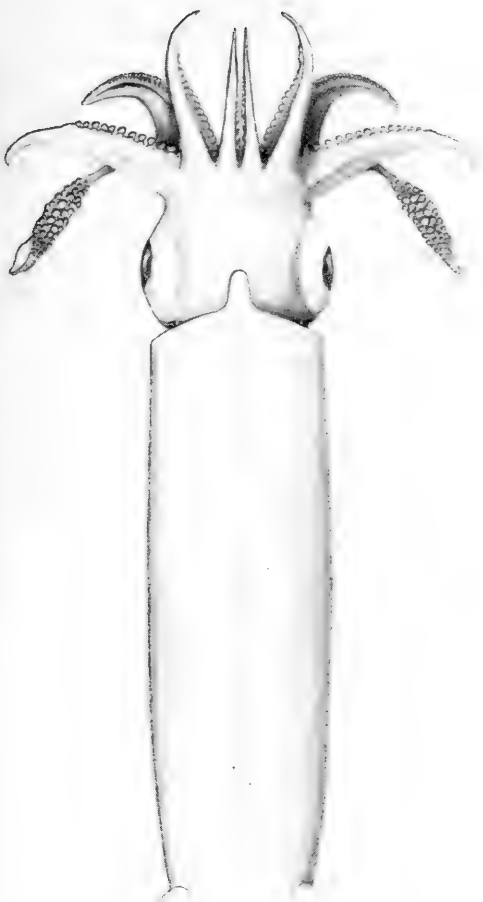

FIG. 27. *Loligo roperi* Cohen, n. sp.; holotype, ♂, 70.8 mm ML; *Geronimo* sta. no. GE-8-26.

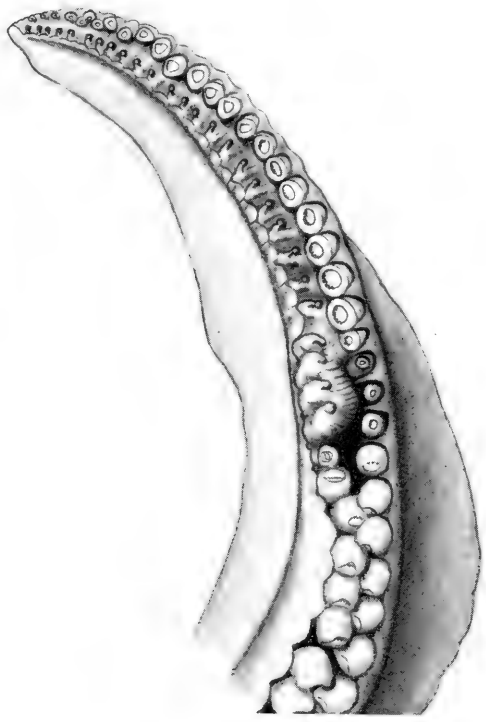

FIG. 28. *Loligo roperi* Cohen, n. sp.; hectocotylus; holotype, ♂, 70.8 mm ML; *Geronimo* sta. no. GE-8-26; entire arm (arm length 14.8 mm).

Miami. Other material: 26 ♀, 44-50 mm ML; *Oregon II* sta. 187; 14°49′N, 81°39′W; 48 m; 19 Nov. 1968; USNM 727772.—1 ♀, 44 mm; *Oregon II* sta. 223; 9°37′N, 76°1′W; 55 m; 28 Nov. 1968; USNM 727771.—1 ♀, 46 mm ML; *Silver Bay* sta. 2477; 25°13′N, 79°13′W; 366 m; 8 Nov. 1960; USNM 575884.—1 ♂, 53 mm ML; off Woodbridge Bay, Dominica, B.W.I.; night light; 13 Nov. 1964; USNM 575874.—3 ♀, 40-43 mm ML; 8°49.2′N, 77°21.2′W; dip net; 17 July 1966; Univ. Miami.

DIAGNOSIS: small (none observed larger than 72 mm in ML), mature at small size (mature males of 44 mm ML, mature females of 43 mm ML); tentacular clubs with not more than 25 transverse rows of suckers in 4 longitudinal series containing not more than 105 suckers total; hectocotylus occupies over 50% of the distal part of the left ventral arm, extends to tip of arm, about 80% (77-89%) of the suckers of the dorsal

FIG. 29. *Loligo roperi* Cohen, n. sp.; gladius; ♂, gladius length 44 mm, Cohen spec. no. 17; *Oregon II* sta. no. 187.

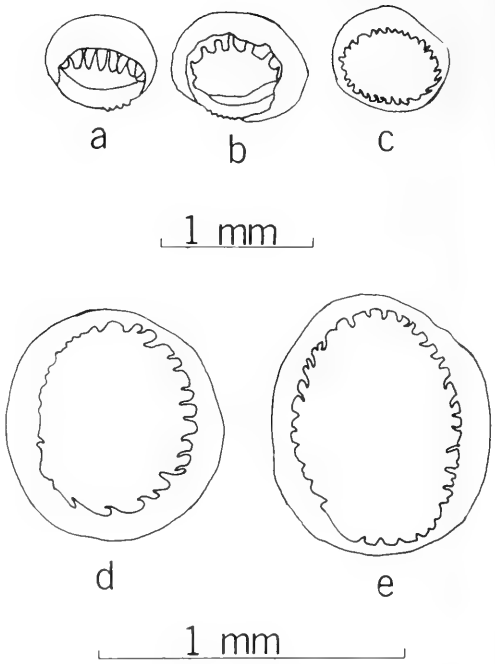

FIG. 30. *Loligo roperi* Cohen, n. sp.; teeth ring of largest sucker on arm III: **a, b** (holotype); teeth rings of large mid-manal sucker of tentacular club: **c, d** (holotype), **e.**

row modified: minute suckers upon broadly triangular pedicels; no suckers on ventral lappets of buccal membrane, not more than about 6 suckers total on buccal membrane, ventral lappets short, often do not extend beyond membrane, 5-7 lappets but 7 buccal connectives and 7 supporting rods.

DESCRIPTION: *Mantle* long, slender, cylindrical, tapers to a posterior acute point (30-35°). Mantle broadest anteriorly in males, broadest near midpoint in mature females (corresponding interiorly to posterior portion of accessory nidamental glands, anterior portion of egg mass); anterior mantle width about 16-26% of ML (40-72 mm ML), greatest mantle width in mature females about 18-27% of ML (40-72 mm ML), longer specimens of both sexes more slender. Ventro-lateral lobes on mantle opening short and pointed (point approximately 90° angle); dorsal lobe longer than lateral lobes, with rounded point; low, narrow ventral ridge present on males.

Fins rhomboid, curved lateral and anterior margins give a somewhat heart-shaped or oval appearance to fins of some specimens (mostly females); widest point curved and

anterior to or at midpoint of fin length; fins united posterior to tip of mantle; length (33-39% of ML, 40-72 mm ML) about equal to or slightly less than width (31-50% of ML, 40-72 mm ML), fins relatively large in short specimens, ratio of length to width = 0.7-1.17 (40-72 mm ML); anterior lobes well-developed.

Funnel well-developed, set in deep funnel groove. Funnel opening level with eyes. Lateral adductor muscles conspicuous, strong, rod-like; anterior adductors thin, sheet-like. Dorsal funnel organ large; posterior limbs broadened anteriorly, tapering posteriorly to blunt, rounded points, lateral borders curved more than medial borders; apical papilla minute and bluntly pointed at tip. Ventral pads oblong, shorter than dorsal pad. Funnel valve broad, blunt, with thin curved lateral flaps.

Funnel locking-cartilage long (about 13-16% of ML, 40-72 mm ML), straight, posterior end slightly wider and curved dorsally, shallowly grooved. Mantle locking-cartilage straight, compliment of funnel lock. Longitudinal ridge low and narrow.

Head width about 19-27% of ML; length about 12-25% of ML (40-72 mm ML), head relatively small in large specimens; nuchal cartilage long (about 15-19% of ML, 40-72 mm ML), straight, broader anteriorly, embedded in muscle except for anterior and posterior ends which taper to rounded and blunted points respectively; shallow central groove, lateral ridges distinct. Eyes oval, covered by cornea, pupil round. Diameter of externally visible eyeball about 11-16% of ML, diameter of dissected lens about 3-6% of ML (40-72 mm ML), eye relatively small in large specimens. Dark, sometimes greenish crescent along dorsal border of eye. Aequiferous pore at anterior edge of cornea.

Arm order III≥IV≥II>I or III≥II≥IV>I; length of arm I about 14-27% of ML; length of arm II about 18-34% of ML; length of arm III about 20-38% of ML; length of arm IV about 18-36% of ML (43-72 mm ML). Arm III robust, arms II, IV less robust, arm I least robust. Swimming keels well-developed on arm I, flaring before midpoint, decreasing to very low distally; very low, weak on arm II, decrease distally; best-developed on arm III, flare before midpoint, decrease gradually distally; well-developed on arm IV, 2 keels, decrease gradually distally, dorsal keel better developed, dorsal keel of arm IV and keel of arm III arise from same area of base of arms. Protective membranes well-developed, particularly ventral membranes on arms I, II, III; ventral membrane on arms II, III broadest adjacent to largest suckers; poorly developed, particularly dorsal membrane on arm IV, trabeculae long, strong, except on arm IV, arise from base of sucker stalks, form high points along membranes. Suckers biserial. About 5 proximal-most suckers of arm I increase slightly in size distally. About 5-9 proximal-most suckers on arms II, III increase in size distally; 10-12 suckers large; succeeding suckers decrease in size, decrease sometimes rapid following 20-24th sucker. 1-2 proximal-most suckers on arm IV often smaller than 2nd or 3rd sucker, succeeding suckers decrease in size distally. About 41-54 suckers on arm I; about 53-62 suckers on arm II; about 56-65 suckers on arm III; about 60-76 suckers on arm IV (43-72 mm ML). Arms I, IV sometimes with about 10 less and more respectively than arms II, III. Width of suckers on arms in order III>II≥I≥IV.

Arm sucker dentition variable (Fig. 30). Teeth present on distal 1/2 of tooth ring. Low plate on proximal 1/2 of tooth ring. Arm I with about 5-7 usually blunt or bluntly-rounded, sometimes square teeth; central 2-4 teeth sometimes pointed, narrower, often longest; lateral teeth decrease in size. Arm II with about 7-10 teeth; shape ranges from all teeth blunt to all teeth pointed except lateral-most teeth; central 2-4 teeth usually longer, narrower and more pointed than lateral teeth which decrease in size; arm III with 6-8 teeth, shape varies from all blunt to only lateral teeth blunt, central 2-4 teeth usually longer, narrower and more pointed than lateral teeth which decrease in size; arm IV with 3-5 blunt or pointed teeth on distal 3rd of small tooth ring, low broad plate on proximal 2/3 of tooth ring; teeth equal in size or central teeth longer. Smaller distal tooth rings on all arms with relatively narrow teeth.

More than 1/2 of the left ventral arm *hectocotylized* (about 57-62%, 44-71 mm ML) (Fig. 28). Modification, chiefly in the dorsal sucker row, extends to arm tip. About 2-5 proximal-most suckers in the dorsal row equal in size (1st sucker may be smaller); about 1-7 proximal-most suckers in ventral row equal in size; about 1-7 succeeding suckers in dorsal row decrease in size distally; about 2-10 succeeding suckers in ventral row decrease in size distally; next

succeeding suckers in dorsal row minute, on enlarged pedicels, 3-5 pedicels most enlarged, 1-2 adjacent ventral suckers very tiny followed distally by about 3-6 large ventral suckers of either increasing or equal size; all succeeding suckers of both rows decrease in size distally, suckers of dorsal row minute (more distinct than proximal 8 most modified suckers), on triangular pedicels. Hectocotylized arm with about 68-86 suckers, 58-68 suckers distal to origin of hectocotylus (about 77-89% of total suckers on arm, 44-71 mm ML). Central area of arm adjacent to about 3-7 most modified suckers raised as a central ridge connecting bases of dorsal suckers.

Tentacles robust. Clubs expanded, about 14-21% of ML (40-72 mm ML). Clubs with 19-24 transverse tetraserial rows of suckers (40-72 mm ML). Distinct carpal cluster absent, suckers in ill-defined carpal area small, biserial, only about 1-4 suckers; no carpal knobs. Often only 3 suckers in proximal-most row of manal suckers, distal rows tetraserial, suckers increasing in size, about 8-12 medial suckers on manus greatly enlarged; lateral manal suckers smaller than medial suckers; manus terminates rather abruptly, distal-most 1 or 2 transverse rows of manus decrease in size, ventro-lateral sucker becomes large relative to medial suckers. This pattern of transverse gradation of sucker size with ventro-lateral sucker the largest, medial suckers smaller, dorso-lateral sucker smallest, continues for about 5-10 rows of dactylus. Dactylus distinct, short, slender, suckers tetraserial, minute, decreasing in size distally, distal-most 2 transverse rows often with 3 and 2 suckers. Tip with narrow, suckerless flange. Swimming keel short and inconspicuous on stalk, along at least distal 1/2 of tentacular stalk aborally, increases in size on manal region of club, broadest along dactylus, diminishes at distal tip. Lateral angles distinct on oral surface and continue as broad heavily supported protective membranes along club, diminish significantly along dactylus particularly on dorsal side. Weak trabeculae between lateral suckers, usually broaden and disappear laterally in the shape of a fan; arise from common base of lateral suckers; ventral ones sometimes stronger, absent on dorsal side of dactylus. Largest suckers on club usually slightly larger than largest suckers on arm III; ratio of width of largest tentacular suckers to width of largest suckers on arm III = 0.8-1.3 (40-70 mm ML).

Club sucker dentition variable (Fig. 30). Sucker rings of carpal area usually with low, broad plate on proximal 1/2 of tooth ring, about 8 weak, usually pointed teeth on distal 1/2 of tooth ring, teeth graded in size, sometimes no teeth on entire ring or only blunt stubs on distal 1/2 of ring. Proximal-most lateral manal suckers often with low, broad plate on inner 3rd to 1/2 of tooth ring, sometimes toothed around entire margin, about 5-15 usually pointed or triangular, sometimes curved blunt or bluntly-rounded teeth; teeth usually spaced, graded in size occasionally with tiny teeth between larger ones, largest teeth on lateral margin. Largest lateral suckers toothed around entire margin, about 14-30 pointed, narrow or triangular, sometimes curved teeth, graded in size; about 5-12 much larger teeth, on lateral margin; teeth on inner margin often minute, teeth usually spaced, sometimes with small teeth between large ones. Large medial manal suckers with about 25-46 usually pointed triangular teeth of varying sizes; teeth sometimes with rounded tips; large teeth separated by spaces and/or 1-4 smaller teeth of varying height, no regular pattern, occasionally with trinary pattern as follows: large tooth followed successively by small, medium, small and large tooth, but each ring exhibiting variety of patterns, distal-most mid-manal suckers with large teeth on disto-ventral margin of tooth ring. Proximal dactylar sucker rings with about 9-20 teeth graded in size, about 4-8 much larger narrower teeth on distal-ventral margin of tooth ring; teeth fragile, minute, merely a ripple or missing from 1/4 to 1/2 of proximal-dorsal margin of tooth ring; teeth narrow or triangular, pointed, sometimes curved, usually spaced, occasionally with small teeth between a few large teeth.

Gladius (Fig. 29) long, slender (width about 11-15% of gladius length, 40-72 mm ML), feather-shaped; anterior tip with weak flexible acute point; rachis stiff; free rachis length about 24-32% of gladius length (about 22-33% of mantle length, 40-72 mm ML); median ridge and slender lateral rods on rachis continue in center of vane, weaken posteriorly, converge and become indistinguishable near posterior tip. Lateral rods of vane and central ribs of vane joined by diagonal striations, central ends of striations anterior to lateral ends. Rods weaker in females than in males. Ratio of greatest

width of vane to greatest width of rachis about 1.9-2.6 (40-72 mm ML). Vane tapered at both ends, sides straight, greatest width in males usually near anterior shoulders of vane, vane gradually narrows posterior to that point; greatest width in females nearer center of vane, located along straight sides between shoulders and midpoint; vane in females does not narrow noticeably until posterior tip. Posterior tip of vane pointed and thin.

Buccal lappets 5-7, 7 buccal connectives, 7 supporting muscular rods (rarely lacks 1); ventral pair of lappets ill-defined, united basally or entirely, often absent in mature females and incorporated into ventral buccal pad on inner surface of buccal membrane for receiving spermatophores; rest of buccal membrane with many inner folds, spermatophores deposited around entire inner side of membrane. Other 5 lappets short, do not project much beyond buccal membrane. Suckers few, 0-3 on each lappet, not more than a total of about 6 on all lappets; suckers usually present on ventro-lateral lappets, rare on 3 dorsal lappets, apparently never present on ventral pair. Connectives of buccal membrane attach to dorsal, dorsal, ventral, ventral borders of arms I-IV respectively (specimens examined 40-72 mm ML).

Beaks. Rostrum of upper beak curved, strong, sharp, long (but short in comparison to length of hood and rostral lamella) heavily pigmented, notch often separates rostrum and rostral lamella (jaw angle acute or recessed); cutting edge of rostral lamella straight or curved; palatine lamella weak, large, long, deep, slightly pigmented, dorsal crest shallowly curved, slight indentation in lateral wall. Rostrum of lower beak shorter than upper beak, pointed, heavily pigmented, inner edge straight or slightly jagged, jaw angle obtuse, nearly 90°; rostral lamella nearly straight, narrow, short, wing lobate, thin; gular lamellae large, weak, not ridged, posterior corner pointed or with curved point; hood and rostrum short in comparison with wing length and gular lamella length.

Radula with 7 transverse rows of teeth; rachidian with long central pointed tooth and pointed lateral cusp; 1st lateral tooth pointed, sometimes narrow, with pointed lateral cusp; 2nd lateral tooth pointed, longer than 1st, no lateral cusp; 3rd lateral tooth long, curved, scythe-shaped; marginal plaques present.

Spermatophore with sperm mass of about 68-75% of total length, cement body about 13% of total length, total length about 3 mm in specimens (44-53 mm ML). Oral connection of cement body funnel-shaped.

Gill length about 21-31% of ML. Number of filaments on one side of gill 41-50 (40-72 mm ML).

Color (in alcohol). Reddish-brown chromatophores present on entire mantle, larger and more closely-spaced on posterior half of dorsal side; few ventrally; present only on dorsal side of fins, more widely-spaced laterally; cover entire head, more closely-spaced dorsally, particularly proximal to eyes; few and only on exposed part of funnel and collar; on outer side of arms and tentacles, form longitudinal line on arms IV, sometimes III. Dark, sometimes greenish crescent over dorsal border of eye. Reddish-brown mid-dorsal longitudinal indentation varying in length, sometimes extends posteriorly almost to fins.

HOLOTYPE: United States National Musuem (727777). Paratypes: United States National Museum (727773, 727774, 727775, 727776); University of Miami.

TYPE LOCALITY: 25°42.5'N, 79°20'W off Bimini Id., Bahama Ids.; *GERONIMO* station 8-26, 6 June 1966, night light.

DISTRIBUTION: Continental shelf of Caribbean: off Nicaragua and Colombia; Antilles; Dominica; Bahama Ids.: Bimini and Old Bahama Channel between Cuba and Great Bahama Bank. Taken by dip net at the surface at night; in bottom trawls at depths of 48-304 m.

ETYMOLOGY: This species is named for Dr. Clyde F. E. Roper, curator in the mollusk division at the Smithsonian Institution and to whom the author is deeply indebted for guidance during preparation of her master's thesis and this publication.

DISCUSSION: *Loligo roperi* has been caught in bottom trawls with *L. pealei* and *L. plei*, with *L. pealei* alone, and with *L. ocula* (Table 3).

Some sexual dimorphism occurs in the width and shape of the vane of the gladius, in the width of the mantle, in the shape of the fins, and in a mid-ventral ridge. The margin of the vane is straighter in males, more tapered in females. The width of the vane is 12-15% of ML in females, 11-14% in males. The point of greatest width of the mantle often lies between the anterior opening and the fin insertion in females; in males

TABLE 10. Comparison of western North Atlantic *Loligo* species. The mantle length examined is given in parentheses in mm.

Character	Species			
	ocula	*pealei*	*plei*	*roperi*
Gladius:				
GW:RW	♀ 2.4-2.9 ♂ 2.5-2.7 (80-127 for all characters)	♀2.7-3.7 (87-188) ♂ 2.4-2.9 (55-244)	1.5-2.4 (38-348)	♀ 2.1-2.6 ♂ 1.9-2.3 (40-72 for all characters)
GW:ML	13-17%	10-20% (28-314)	7-22% (40-319)	11-15%
RL:ML	28-35%	7-33% (23-224)	18-33% (40-280)	22-33%
vane edge (outline)	curved	curved; ♂ sometimes straight	straight; ♀ often curved	straight
vane edge (thickness)	thin	thin; rarely ribbed	ribbed; sometimes weakly	ribbed
Hectocotylus:				
modification extends to tip?	no (some slightly reduced)	no (some slightly reduced)	yes	yes
origin of hectocotylus to arm tip—% of arm length	25-33%	25-33%	26-50%	57-62%
origin of hectocotylus to arm tip—% of total arm suckers	54-62%	47-69%	52-69%	77-89%
Tentacle club: no. of transverse rows of suckers	32-39	30-45 (20-315)	27-38 (31-348)	19-24 (40-72)
TCL:ML	24-35%	20-38% (60-315)	19-29% (44-348)	14-21%
Eye:				
ED:ML	15-21%	8-18% (25-237)	14-19% (40-319)	11-16%
LD:ML	6-8%	2-6% (72-291)	2-7% (40-348)	3-6%
Fins:				
FL:ML	43-54%	44-64% (45-314)	35-58% (40-348)	33-39%
FL < ½ ML		less than 55 mm ML	less than 95 mm ML (many in range 95-192 mm ML)	all
FW:ML	45-59%	34-56% (45-315)	33-45% (40-348)	31-45%
FCL:ML	16-17%	10-18% (60-314)	7-18% (60-348)	13-16%
HW:ML	24-34%	12-32% (25-314)	10-41% (40-348)	19-27%
HL:ML	19-28%	9.5-30% (70-315)	10-22% (44-348)	12-25%
AMC:ML	67-89%	39-78% (60-315)	35-68% (44-348)	
AMW:ML	22-29%	14-33% (45-315)	11-25% (49-348)	16-27%
Buccal lappets: total suckers	45-64	35-113	16-66	0-6
suckers on ventral lappets	yes	yes	yes	never
Gills:				
GL:ML	26-35%	23-34%	20-32%	21-31%
no. of filaments	53-127	55-91 (55-315)	53-84 (44-348)	41-50

TABLE 10. Cont.

Character	Species			
	ocula	*pealei*	*plei*	*roperi*
Arms:				
ALI:ML	20-34%	19-50%	16-26%	14-27%
ALII:ML	29-42%	22-50%	23-31%	18-34%
ALIII:ML	35-42%	26-45%	25-37%	20-38%
ALIV:ML	31-40%	22-38% (60-315)	21-32% (44-348)	18-36%
No. of suckers:				
AI	90-110	60-125	50-120	41-54
AII	90-110	70-125	70-120	53-62
AIII	90-110	70-125	70-120	56-65
AIV	95-120	84-132 (40-315)	90-130 (40-348)	60-76

it is more often at the anterior opening. The fins of most males are more rhombic in shape than those of most females. In males the anterior margin of the fin is usually straight; in females it is more often curved. Males have a mid-ventral ridge on the mantle.

COMPARISON OF SPECIES

IDENTIFICATION: Since *Loligo* is a myopsid squid, the lens of each eye is completely covered by a cornea; this easily differentiates it from superficially similar oegopsid squid which always have an oval opening in the skin around the eyes, exposing the lens to sea water. Table 10 and graphs in Figs. 5-7, 9-11, 19-24 compare the 4 species of *Loligo* found in the western North Atlantic Ocean. The hectocotylus quickly identifies mature male *L. plei* and *L. roperi* and distinguishes them from *L. pealei* and *L. ocula* (Figs. 4, 16, 26, 28). In all 4 species the left ventral arm is modified, but modification extends to the tip of the arm only in *L. plei* and *L. roperi*. Modification (hectocotylization) is defined for these purposes as reduction of dorsal suckers to less than 1/2 the size of the ventral counterparts. In *L. plei* the hectocotylus occupies less than 1/2 of the arm (less than 70% of the dorsal suckers); in *L. roperi* the hectocotylus occupies more than 1/2 (at least 55%) of the arm (more than 75% of the dorsal suckers). *L. roperi* is the smallest and most distinctively different of the 4 species. All sexes and sizes of *L. roperi* above 20 mm ML can be identified by the small number of suckers on the tentacles, arms, and buccal lappets, and by the small number of filaments on the gills (Table 10). The largest *L. roperi* examined (72 mm ML) do not have more than 24 transverse rows (of 4 suckers each) of tentacular suckers, while *L. pealei* and *L. plei*, longer than 20 mm ML, have at least 28 rows of tentacular suckers. *L. roperi* shorter than 40 mm ML were not available and may have even fewer suckers and gill filaments. All *L. ocula* examined were at least 80 mm ML; they have at least 32 rows of tentacular suckers. The tentacular clubs of *L. roperi* are also correspondingly shorter than those of the other species. The buccal lappets of *L. roperi* do not bear more than 6 suckers altogether and the ventral pair bear no suckers at all; the buccal lappets of the other 3 species bear more than 16 suckers, and always bear suckers on the ventral pair.

All sizes and sexes of *Loligo ocula* and *L. pealei* can be distinguished from *L. plei* by comparison of the ratio of greatest gladius width (vane width) to greatest rachis width (Table 10). The width of the vane is at least 2.4 times that of the rachis in *L. ocula* and *L. pealei* but is less than 2.4 times that of the rachis in *L. plei* which has both a relatively narrower vane and a wider rachis. Furthermore because the vanes of mature *L. pealei* and *L. plei* are wider in females than in males, the difference between mature *L. pealei* and *L. plei* in this ratio is greater between members of the same sex. Small immature specimens can be separated by this character. This ratio can be determined either by removing and measuring the gladius or by measuring it in place as follows: make an antero-posterior cut along the mid-ventral line. Then either:

1) gently insert finger under gladius, free-

ing it from its attachment along the mid-dorsal line of the mantle. Remove and measure gladius, or

2) gently insert finger between internal organs and gladius, freeing organs from the gladius which lies dorsal to them. Use dividers to determine the relative vane width:rachis width without removing the gladius.

Loligo ocula most closely resembles *L. pealei*; these 2 species are the most difficult of the 4 to differentiate. They differ most in relative size of eyes; the eyes are noticeably larger in *L. ocula*. Measure the diameters of the externally visible eyeball and of the dissected lens. In *L. ocula* the diameter of the dissected lens is at least 6% of ML; in the other species it is 6% or less. Since growth is allometric, the differences are more apparent on a graph (Figs. 19, 20). The modified suckers in the hectocotylus of *L. ocula* are all based upon broadly triangular pedicels, while those of *L. pealei* are, at least in part, based upon narrow pedicels. In addition *L. ocula* usually has a larger head and a longer free rachis, funnel cartilage, and nuchal cartilage than the other 3 species; these characters however show considerable overlap (Figs. 21, 23, 24).[4]

COMPARISON OF *LOLIGO PEALEI* AND *L. PLEI*: *Loligo pealei* and *L. plei* overlap in all characters examined except the hectocotylus and (with one exception among 580 examined) the ratio of greatest gladius width to greatest rachis width. A comparison of Figs. 3 and 5 shows how similar the 2 species, particularly the females, appear. The hectocotylus of *L. plei* extends to the tip of the arm and in *L. pealei* does not (Figs. 4, 26). However, in many *L. pealei* slight reduction of suckers extends distal to the modified area. In some cases this slight reduction extends to the arm tip. But in *L. pealei* the distal suckers in the dorsal row are always more than 1/2 the size of their ventral counterparts. Table 10 shows that other characters overlap extensively. Since these species of *Loligo* have allometric growth, a better comparison can be made with graphs than indices. The graph plotting fin length against ML shows that fin lengths are similar in all 4 species for specimens shorter than about 65-70 mm ML (Fig. 31). In larger specimens, *L. pealei* and *L. ocula* have the longest fins, *L. plei* shorter fins and *L. roperi* the shortest fins, but there is considerable overlap. The difference increases with increasing ML in *L. pealei* and *L. plei*; above about 170 mm ML there is no overlap between the 2 species, but the regression in *L. plei* is curved upward for the longest specimens, so that in specimens over 300 mm ML, *L. plei* and *L. pealei* apparently have a similar fin length. It is helpful in differentiating the 2 species to note that the fin length is equal to or greater than half the ML in specimens of *L. pealei* longer than 55 mm ML; but in *L. plei* is less than 1/2 the ML in many specimens shorter than 192 mm ML and all specimens shorter than 95 mm ML.

In plots of the lengths of the funnel cartilage, gladius width, anterior mantle width, head width and possibly fin width against ML (Figs. 5, 7, 11, 21, 22), the species show overlapping differences in specimens greater than 65 mm ML: *Loligo ocula* is relatively larger in these characters, *L. pealei* next largest, *L. plei* smaller, and *L. roperi* smallest. The differences become more marked in larger specimens.

LaRoe (1967) also found that *Loligo pealei* and *L. plei* overlapped considerably in most characters. LaRoe listed the most effective characters for separation of *L. pealei* and *L. plei* as the hectocotylus, the relative width of the gladius, and the relative lengths of the fin and funnel cartilage. Adam (1937) stated that the 2 species differ in mantle width and fin length. While these indices show differences, because growth is allometric and values overlap, they are not as useful in separating the 2 species as are the hectocotylus and the ratio of gladius width to rachis width. Compare Figs. 3 and 25.

Voss (1956) and Adam (1937) used the gladius to distinguish between the 2 species. Mature *Loligo pealei* usually possess a gladius with a broad vane and curved borders that are not thickened. *L. plei* usually has a

[4]Since this paper was submitted, a 5th species of *Loligo* from the western North Atlantic has been described: *Loligo surinamensis* Voss, 1974. This species, which has been found only off Surinam, most closely resembles *L. pealei*. Apparently only the males of *L. pealei* and *L. surinamensis* may be distinguished and by only 2 characters in which they never overlap. The mid-portion of the right ventral arm of male *L. surinamensis* bears sharply pointed teeth; there are apparently never any pointed teeth on the suckers of the right ventral arm of *L. pealei*. In *L. surinamensis* the modified portion of the hectocotylized arm consists of flattened, broadly triangular pedicels forming distinct lappets; in *L. pealei* at least some of the modified pedicels are narrow, rather rounded, not broadly triangular.

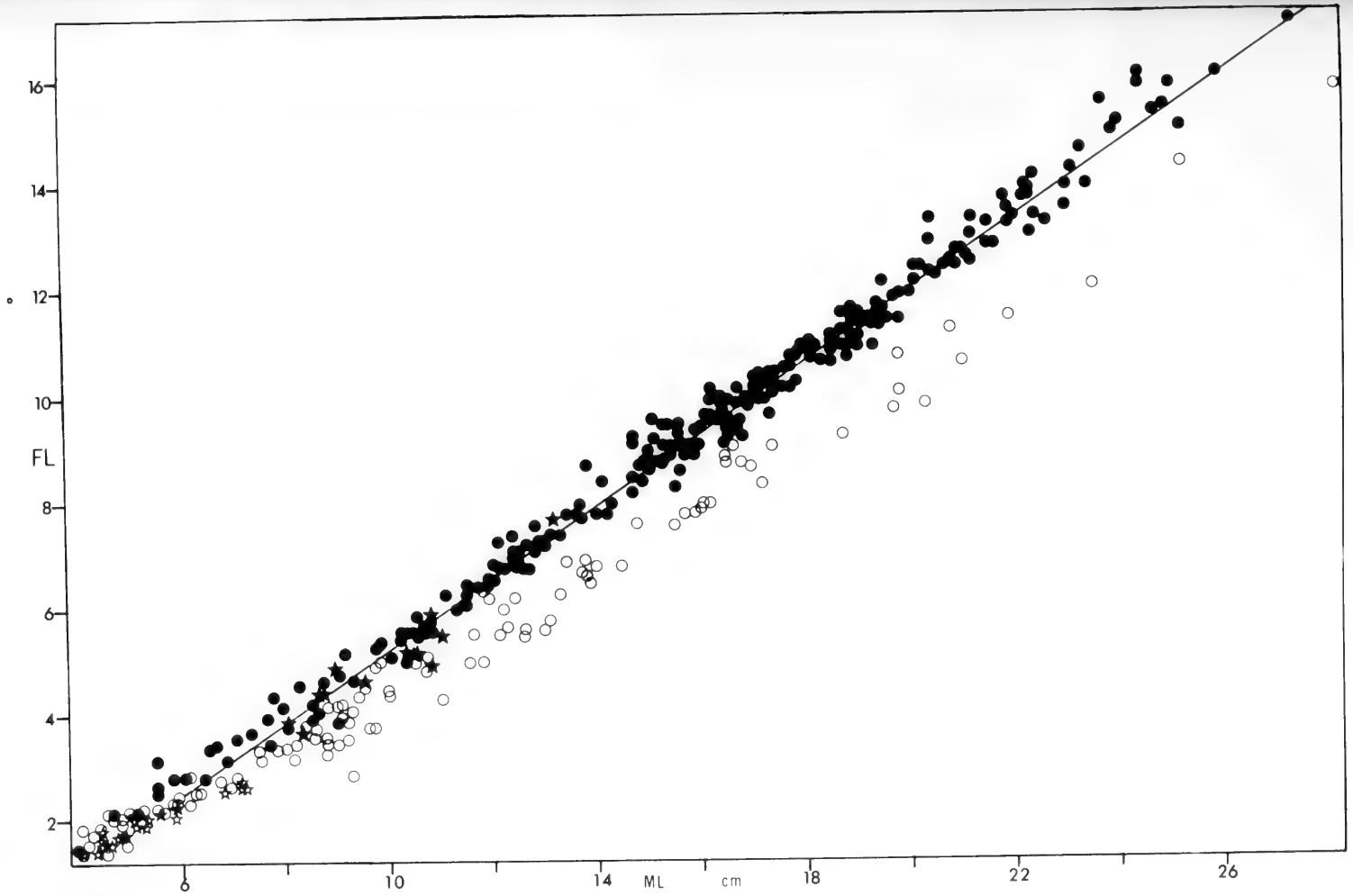

FIG. 31. The regression of fin length upon mantle length (FL:ML). *Loligo pealei* = solid circles and regression line. *L. plei* = open circles. *L. ocula* = solid stars. . *L. roperi* = open stars.

gladius with a narrower blade and straight, thickened borders. However, pigmented but unthickened stripes occur along the margin of many *L. pealei* gladii: 29% of 258 examined have at least a faint stripe; the darkness of the stripe varies considerably. Seven male *L. pealei* of 580 examined have the vane of the gladius with the margin thickened into a lateral rib equal (in some) or almost equal in thickness to any observed in *L. plei*. Some male *L. pealei* have fairly straight edges and small female *L. plei* often have edges that are more curved and scarcely thickened or not at all, in the smallest females. Lateral ribs on the gladius are useful but not reliable by themselves in distinguishing *L. plei* from *L. pealei*.

Voss (1956) and Adam (1937) also use differences in the dentition of the largest tentacular suckers to distinguish between the 2 species. *Loligo pealei* sometimes has a unique trinary pattern of teeth. This pattern has the following sequence: large tooth, small tooth, medium-sized tooth, small tooth, and large tooth. The teeth of the largest tentacular rings of both species often occur in an alternating large and small pattern. Examination of one of the largest tentacular suckers from each of 43 *L. pealei* selected from almost the entire range of distribution showed that the trinary pattern is present in part of the sucker ring of 24, is absent in 15, and doubtful in 4. Of the 15 lacking the pattern, 9 have at least a partial pattern of large-small alternating teeth and 6 have teeth of about equal size. In the 4 doubtful ones the pattern is best described as alternating large and small teeth. The shapes of the teeth are very variable and only the 24 with the trinary pattern are distinct from most *L. plei* teeth patterns. The trinary pattern was also observed in 2 *L. roperi* (20 examined) and 1 *L. plei* (10 examined); it is thus not a useful character.

Ventral ridges occur in males of both species as reported by LaRoe (1967). Of 218 *Loligo pealei* examined, a ventral ridge is at least partially present in 50% and 15% have prominent ridges. Females of *L. pealei* have ridges though they are less prominent. The ventral stripes of chromatophores on the mantle are present on large males of both species, not *L. plei* alone. Ventral stripes occur in 29% of 258 *L. pealei* examined. The darkest stripes occur in the largest males of *L. plei*, but the intensity of the stripes varies considerably. Stripes are not a useful character.

Analyses of covariance were made comparing 13 characters in *Loligo pealei* and *L. plei* (Table 11).

Seven characters show highly significant differences and 6 none. The 2 species are statistically significantly different but overlap in fin length, fin width, head width, gladius width, length of the funnel and nuchal cartilages, and sucker width on arm III (with ML as covariate). There is no significant difference between the 2 species in anterior mantle width, gill length, and number of gill filaments (with ML as covariate), nor with funnel length and length of

TABLE 11. Comparisons of *Loligo pealei* and *L. plei*.

Measurement	Covariate	Adjusted $\bar{X}$ of *L. pealei*		Adjusted $\bar{X}$ of *L. plei*		Significant difference between $\bar{X}$s, p less than
		mm	N	mm	N	
FL	ML	75.3	75	63.4	12	0.001
FCL	ML	18.3	75	16.8	12	0.001
FW	ML	66.3	75	57.8	12	0.001
HW	ML	28.2	75	25.7	12	0.003
NCL	ML	22.9	75	21.2	12	0.006
Fun L	FCL	18.7	75	19.6	12	NS
AL I	FCL	35.2	75	33.4	12	NS
AL III	FCL	46.7	75	47.8	12	NS
TCL	FCL	33.4	75	36.9	12	NS
AMW	ML	30.8	58	25.4	58	NS
F Gill L	ML	33.9	98	31.2	13	NS
F Gill F*	ML	62.3	77	64.0	10	NS
F GW	ML	22.8	22	17.0	22	0.005
M GW	ML	23.9	37	16.9	37	0.005
M ASW III**	ML	2.6	37	1.9	37	0.005

*Variance differences made male results inconclusive.
**F = female, M = male.

arm III (with length of funnel cartilage as covariate). Mantle width was used instead of circumference because this is the measurement used by other workers.

There is no noticeable difference between the spermatophores of the 2 species. Spermatophores of 16 specimens of *Loligo pealei* from 3 locations and 4 specimens of *L. plei* were mounted on slides. Spermatophores taken from 2 specimens of *L. pealei* differ as much from each other as they do from those of *L. plei*. In addition, 16 separate measurements of the spermatophores of 2 *L. pealei* and one *L. plei* were compared and in these also, differences are greater between the 2 specimens of *L. pealei* than between the 2 species. Measurement of additional spermatophores did not seem profitable.

Loligo pealei inhabits waters with a wider temperature range than does *L. plei*. *L. plei* appears not to share the coldest part of the range of *L. pealei*. *L. pealei* does not share the non-continental or most southern parts of *L. plei*'s range.

In the area in which *Loligo plei* is sympatric with *L. pealei*, LaRoe (1967) believed that *L. plei* occurred in slightly shallower depths than *L. pealei*. Although my data are not from a systematic, unbiased year-round sampling of the area, they do suggest that this is incorrect. Off the SE coast of the United States *L. pealei* were caught at 0-154 m and *L. plei* at 0-366 m. In the northern Gulf of Mexico *L. pealei* were caught at 8-393 m and *L. plei* at 0-80 m. In the southern Caribbean *L. pealei* were caught at 0-73 m and *L. plei* were caught at 0-101 m. See Appendix A. They have been caught in the same trawls (Table 3).

In mating behavior no clear differences have yet been observed between *Loligo pealei* (Drew, 1911; Arnold, 1962) and *L. plei* (undersea observations by Waller & Wicklund, 1968). In both species the males compete for females, display color changes while driving off other males, and mate in the same 2 positions. These features have also been observed in some other members of the Loliginidae, as well as some more distantly related squid. More detailed observations have been made of *L. pealei* than of *L. plei*; these include specific patterns of coloration, formation of male breeding hierarchies, and egg mass or egg mass-like objects as a stimulus to mating. The courtship patterns of *Sepioteuthis sepioidea* (a loliginid) are similar but differ in the following ways from those of *L. pealei*: *S. sepioidea* is not stimulated by egg masses and has different courtship color patterns (Arnold, 1965b). Detailed study of *L. plei* may also reveal specific mating behavior.

I have seen no evidence of hybridization or introgression in the morphology of the 264 *Loligo plei* which I examined. However in *L. pealei* I have seen variations in the hectocotylus and even more so in the gladius which show resemblance to the hectocotylus and gladius of *L. plei*. These were described in the discussion of variation in *L. pealei*. The *L. pealei* with gladii very similar to those of *L. plei* were found in areas of sympatry.

The apparently greater variation in Caribbean populations of *Loligo pealei* (described earlier) may be related to sympatry with *L. plei*. The 2 species have been collected in the same trawls and have similar breeding behavior. Neither species shows character displacement, but rather *L. pealei* exhibits suggestions of higher variability and closer resemblance in some characters to *L. plei*. Rare introgression is a possibility but is not established.

Because the 2 species are so similar morphologically, they are here considered congeneric. *Loligo plei* was described as a *Loligo* (Blainville, 1823) and later placed in the new genus *Doryteuthis* by Naef (1912) who did not designate a type-species. Voss (1956, 1960) and later Adam (1937, 1941) and others have followed Naef. LaRoe (1967) placed *plei* in *Loligo* because of its similarity to *L. pealei*. *Doryteuthis* is more similar to *Loligo* than are other genera, but determination as to whether or not it deserves separate generic status awaits study of all of the species of *Doryteuthis*. The affinities of the 4 known western North Atlantic species support the acceptance of *plei* as a *Loligo*. *L. plei* is so close to *L. pealei* that if *plei* is placed in *Doryteuthis*, *L. roperi* must be placed in a new genus. *L. roperi* is the most distinctive of the 4 species.

VARIATION: Some sexual dimorphism occurs in all 4 species. Statistical analysis of variation was made only of samples of *Loligo pealei*, the most variable species. Lateral ribs of the blade of the gladius are stronger in males than in females of *L. roperi* and *L. plei*; they are present only rarely in males, never in females of *L. pealei*, and are not present in the 12 *L. ocula* available to me. The margin of the blade of the gladius is

straighter in males, more tapered in females of *L. pealei, L. plei*, and *L. roperi*. The blade is noticeably wider in females than in males of *L. pealei* (statistically significant difference) and *L. plei*; it is slightly wider in some females of *L. roperi*; it shows no apparent sexual dimorphism in the 12 *L. ocula*. In mature females the broad portion of the gladius lies above the full ovary and may help support or protect the large mass of eggs in a ripe female.

The presence of eggs is probably the reason that in the region of the mantle posterior to the fin insertion, mature females of *Loligo pealei, L. plei,* and *L. roperi* are sometimes wider than males.

In *Loligo pealei* females have about 10 fewer gill filaments than do males (statistically significant difference) of the same ML. Females of *L. ocula*, and *L. roperi* larger than about 65 mm ML, seem also to have fewer gill filaments than do males; there were not enough specimens of either to be certain. Sexes of *L. roperi* smaller than about 65 mm ML and all *L. plei* show no sexual dimorphism in gill filaments. The dimorphism in *L. pealei* suggests that in *L. pealei* the females may have a lower oxygen requirement (as discussed earlier).

A mid-ventral ridge on the mantle is much more common in males than in females of *Loligo plei* and *L. pealei*; it is apparently present only in males of *L. roperi*. Ventral longitudinal reddish-brown chromatophore stripes are present only in some mature males of *L. plei* and *L. pealei*.

Fin shape is slightly dimorphic in *Loligo roperi*: most males have fins which are more rhombic and less curved in outline than those of the females.

Some sexual dimorphism has been reported for other Loliginidae. The males of *Loligo opalescens* Berry, 1911, a closely related species on the Pacific coast of the United States, have longer arms and larger heads than females (Fields, 1965). Fields concludes that these differences are sufficient for visual sexual discrimination by the squid. In the 4 species of *Loligo* considered here, sexual differences in fin width and arm sucker width are not sufficient for visual or field determination of sexes by man. Although statistically significantly different in *L. pealei*, there is a great overlap of values between the 2 sexes even when these are regressed on ML. The differences probably do not contribute to visual sexual differentiation by *L. pealei* or the other species of *Loligo* considered here.

Greater fin width in females than in males was reported also for *Loligo vulgaris* (Férussac & d'Orbigny, 1834-48), which lives along eastern Atlantic shores. In *Alloteuthis africana* Adam, 1950, a loliginid which occurs off the W coast of Africa, females have wider bodies than males. Unlike *L. pealei*, the females of this species have a smaller head and tail than males and the sexes differ in the shape of the ventral arm suckers (Adam, 1952).

As already noted several authors suggest that geographic variation occurs in several characters of *Loligo pealei*; their suggestions are not supported by the results of this study. I found no clines in 50 anatomical measurements made on *L. pealei*. Southern *L. pealei* (Caribbean Sea-Gulf of Mexico) differ in the following ways from northern *L. pealei* (eastern United States Atlantic coast): 1) gill length increases faster in relation to mantle length in the southern squid; 2) there is more variation in the hectocotylus; 3) they apparently mature at a smaller size. Abnormal numbers of buccal lappets occur in *L. plei* collected in Bermuda and in *L. pealei* collected in the Caribbean. As already noted, variation in *L. pealei* appears greatest in areas of sympatry with *L. plei*; much of this variation takes the form of greater resemblance to *L. plei*.

Geographic variation has been reported for several species in the family Loliginidae. Geographic variation in the following characters in *Lolliguncula brevis* was observed: fin length, fin width, sucker size and arrangement, sucker dentition (Voss, 1956); and fin length, fin width, and arm length (LaRoe, 1967). Sasaki (1929) presented weak evidence that *Loligo edulis nagasakensis* and *L. edulis grandipes* are distinct subspecies. Clarke (1962) found some geographic variation in the darkening of beaks of *Loligo vulgaris* Lamarck, 1799, *L. forbesi* Steenstrup, 1856, and *Sepioteuthis lessoniana* Lesson, 1830. I did not find geographic variation in any of the above characters in *L. pealei*.

Several species-specific characters in *Loligo roperi* are characters that vary in *L. pealei*. The number of buccal lappets vary occasionally in *L. pealei* and *L. plei*; in *L. roperi* the lappets are smaller and bear fewer suckers than in the other 3 species. The number of gill filaments are fewer in female

than male *L. pealei*; in both sexes of *L. roperi* they are fewer than in the other 3 species. The amount of modification of the hectocotylized arm varies in *L. pealei*; it is greater in *L. roperi* than in the other 3 species.

AFFINITIES: The 4 species of *Loligo* considered here arrange themselves in the following general order of resemblance: *L. ocula, L. pealei, L. plei* and *L. roperi*. This has been noted already in plots of the length of the funnel cartilage, head width, anterior mantle width, gladius width against ML and possibly fin width; and in the fin length and percentage of modification in the hectocotylized arm (*L. pealei* and *L. ocula* are about the same in the last 2 respects) (Figs. 5, 7, 11, 21, 22, 31). *L. ocula* is very similar morphologically to *L. pealei* and differs principally in having larger eyes. *L. ocula* apparently lives in deeper water than *L. pealei*. It is probably closely related to *L. pealei* and may have evolved larger eyes as an adaptation to living in a deeper habitat with less light than that of *L. pealei*. The enlarged head and wider mantle may have evolved in harmony with the eyes—the head to accommodate the larger eyes and the wider mantle opening to accommodate the wider head. The 2 species so far as is now known are allopatric; *L. pealei* strays only extremely rarely from the continental shelf and slope; *L. ocula* usually occurs near islands and in deeper water than *L. pealei*. *L. pealei* and *L. ocula* may be sympatric on the continental shelf off Honduras; *L. ocula* has been captured there, but *L. pealei* has not. Whether or not they are also separated by any reproductive barriers is not now known. Possibly *L. ocula* is, or its ancestors were, a subspecies of *L. pealei*. I think that the morphological differences are consistent and extensive enough to conclude that they are separate species.

Loligo pealei and *L. plei* differ in more characters than do *L. pealei* and *L. ocula*. *L. roperi* differs from the other 3 in even more characters. It is closer in most characters (length of the funnel cartilage, fin length, head width, anterior mantle width, gladius width) to *L. plei* than to the other species; in the ratio of gladius width to rachis width, *L. roperi* lies between *L. plei* and *L. pealei*.

Loligo roperi is sympatric with all 3 species but apparently has a smaller geographic range than *L. pealei* and *L. plei*. It has been captured in trawls with *L. plei* and *L. ocula*.

Several things suggest that *Loligo roperi* may be an early-maturing (perhaps somewhat neotenic) relative of *L. plei*. *L. roperi* matures at a small size and apparently does not grow as large as the other species; 72 mm ML is the largest observed. It has much fewer suckers on the arms and tentacles and fewer gill filaments (Fig. 6) than do equally small specimens of the other 3 species; apparently when *L. roperi* reach 40 mm ML (or possibly less) there is no further increase in suckers and little in gill filaments. Furthermore, while the mantle length continues to increase, specimens greater than 50 mm ML (only 12 were examined) show no increase in anterior mantle width, fin width, eye diameter, and lens diameter, and relatively less increase in gladius width and head width than the other species (Figs. 5, 7, 11, 19, 20, 22). In the other 3 species there is continuous increase in all of these characters with increasing ML.

Loligo plei have been found mature at a ML as small as 38 mm and immature at a ML as great as 139 mm. As already discussed, *L. plei* probably do not die immediately after spawning. Catches of *L. plei* sometimes contain small mature specimens with larger immature ones; the small mature specimens can reproduce earlier than the larger immature ones. If there were a genetic basis for early maturity in these specimens, and if it were coupled with death after spawning, there would be a chance for genetic isolation of 2 subspecific groups—early maturers and later maturers. If the early maturers survive spawning and later mate with later maturers, the groups would not be genetically isolated. In comparing small, mature *L. plei* with both small, immature *L. plei* and with large mature and immature *L. plei*, I found no morphological differences which would indicate that separation between early and late spawners is now occurring. I suggest that *L. roperi* could have become separated as a species from *L. plei* or its ancestors in this manner, particularly if ancestors died after spawning. It would be interesting to know how much their niches differ. *L. roperi* probably cannot eat the same food as the larger *L. plei; L. roperi* has a smaller geographic range than *L. plei; L. roperi* may have a narrower niche than *L. plei*.

There are probably 2 ways in which a species of squid can mature at a small size and also attain a relatively large size: 1)

survival after a first spawning followed by continuing growth and later spawnings (*Loligo plei* and *L. pealei* may use this strategy); 2) spawning linked to an environmental cue such as temperature change; delay in spawning for some populations until they reach a larger size; death after spawning (*L. pealei* probably uses this strategy, at least in the temperate part of its range; *L. plei* may also use it in the small temperate part of its range). A 3rd strategy is one spawning occurring within a relatively narrow size range followed by death (this is apparently the strategy of *L. roperi*, which lives only in the tropics). This is mere speculation. Studies of the biology of the tropical populations of these *Loligo* have not been made; such studies, as well as observations of live animals, would be useful.

DIVERSITY: Two species of Loliginidae belonging to different genera are also partially sympatric with the 4 species of *Loligo* discussed in this paper. *Lolliguncula brevis* has been caught on the continental shelf and in estuaries from Delaware Bay to Rio de Janeiro, Brazil, and is found in lower salinities than the other loliginids (LaRoe, 1967). It has been caught in the same trawls with *Loligo plei*. In *Lolliguncula brevis* the body is relatively shorter and wider than in *Loligo* and the fins are round or eliptical (not rhomboidal) and wider than long. *Sepioteuthis sepioidea* has been caught in tropical waters from Villegas, Venezuela, to Cape Canaveral, Florida, and in the Bahamas, Bermuda, St. Martins of the Netherlands Antilles, and Cozumel, Mexico (LaRoe, 1967). It has fins which extend the length of the mantle except in tiny newly-hatched specimens (LaRoe, 1967).

All 7 of the western North Atlantic loliginids live in the Caribbean Sea; this sea has the greatest species diversity of the western North Atlantic for not only the genus *Loligo* but the family Loliginidae. Five species: *Loligo pealei, L. plei,* and *L. roperi, Lolliguncula brevis*, and *Sepioteuthis sepioidea* live on the continental shelf off Panama and Colombia. *Loligo plei, L. ocula, L. roperi*, and *Sepioteuthis sepioidea* (and very rarely *L. pealei*) are found off the islands of the Caribbean. *L. surinamensis* Voss is reported off Surinam by Voss (1974). The Gulf of Mexico has only 3 loliginids: *L. pealei, L. plei*, and *Lolliguncula brevis*. Three species live in the Bahamas: *Loligo plei, L. roperi*, and *Sepioteuthis sepioidea* (and very rarely *L. pealei*). Two are found off Bermuda: *L. plei* and *Sepioteuthis sepioidea*. Four species live off the east coast of Florida: *L. plei, L. pealei, Lolliguncula brevis*, and *Sepioteuthis sepioidea. S. sepioidea* is only rarely found farther north. *Loligo plei* is only rarely found north of Cape Hatteras, and *Lolliguncula brevis* is only rarely found north of Delaware Bay, leaving only 1 species—*L. pealei*—off New England and southern Canada.

The Caribbean Sea (in particular the Panama area) thus seems to be the area of greatest species diversity for the Loliginidae and the genus *Loligo* in the western North Atlantic. There is less diversity in the Gulf of Mexico and increasingly less N of Florida, although there is considerable diversity on the E coast of Florida. The greatest diversity is thus in the most tropical, probably most environmentally stable part of the region. In the genus *Loligo*, the 2 apparently more specialized members—*L. roperi* and *L. ocula*—occur only in the tropical North Atlantic; the apparently more variable species—*L. pealei* and *L. plei*—have a wider geographic range extending over a wider environmental range. *L. pealei* seems to be the most variable of these species and it has the greatest geographic range covering the widest range of environmental factors—particularly temperature.

KEY TO THE SPECIES OF *LOLIGO* IN THE WESTERN NORTH ATLANTIC OCEAN[5]

1. Left ventral arm hectocotylized (mature males) 2

   Left ventral arm not hectocotylized 5

2. Hectocotylus extends to tip of arm (diameter of distal suckers of dorsal row less than 1/2 that of their ventral counterparts; Figs. 26, 28) 3

   Hectocotylus does not extend to tip of arm (diameter of distal suckers of dorsal row equal or nearly equal to that of their ventral counterparts) 4

[5]See Table 10 for more comparative data.

3. Hectocotylus occupies less than half of arm (26-50% of arm length; 52-69% of total number of suckers of arm; Fig. 26); suckers on ventral buccal lappets . . . . . *L. plei*

   Hectocotylus occupies more than half of arm (57-62% of arm length; 77-89% of total number of suckers of arm; Fig. 28); no suckers on ventral buccal lappets . . . . . *L. roperi*

4. Eye unusually large (diameter of externally visible eyeball 15-21% of ML, diameter of dissected lens 6-8% of ML (Figs. 19-20); bases of hectocotylized suckers all broadly triangular (Fig. 16) . . . . . *L. ocula*

   Eye not unusually large (diameter of externally visible eyeball 8-18% of ML, diameter of dissected lens 2-6% of ML (Figs. 19-20); bases of at least some hectocotylized suckers narrowly triangular (Fig. 4) . . . . . *L. pealei*

5. No suckers on ventral buccal lappets; total number of suckers for all buccal lappets fewer than 7; fewer than 25 transverse rows (of 4 suckers each) of suckers on tentacular club . . . . . *L. roperi*

   Suckers on ventral buccal lappets; total number of suckers for all buccal lappets more than 15; more than 26 transverse rows of suckers on tentacular club 6

6. Ratio of greatest width of blade of gladius to greatest width of free rachis 1.5-2.4; lateral margin of vane usually thickened and rod-like (fin length less than 1/2 of ML in specimens less than 95 mm ML, often less than 1/2 ML in specimens less than 190 mm ML; Fig. 31) . . . . . *L. plei*

   Ratio of greatest width of blade to greatest width of free rachis 2.4-3.7; lateral margin of vane usually thin although often slightly darkened (fin length more than 1/2 of ML in specimens greater than 55 mm ML; Fig. 31) 4

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APPENDIX A. Specimens of *Loligo pealei* and *L. plei* identified for this study.

A. Loligo pealei:

No. of specimens	Location	Depth, m	Date	Collector, number	Present location	Number
1	Minas Basin, Nova Scotia	—	X, 1970	Petersen	USNM[1]	—
3	Chesapeake Bay, Va.	13	VII, 1968	—	USNM	—
2	off Grand Id., La.	—	VI, 1938	—	USNM	574174
20	28°18′N, 91°26′W	12	I, 1970	—	USNM	—
1	27°48′N, 97°W	155	III, 1917	—	USNM	576938
1	off Rockport, Tex.	—	1951	Baughman	USNM	574693
2	S. of Tortugas, Fla.	102	VII, 1932	64-32	USNM	576929
1	Orient, Long Id., N. Y.	—	VI, 1939	Erdman	USNM	575922
3	Bridgetown, Barbados	0–2	VI, 1969	—	USNM	—
1	30°16′N, 87°15′W	—	—	—	USNM	576921
1	Delaware Bay	—	1881	—	USNM	576928
1	Stonington, Conn.	—	1966	Morrill	USNM	576243
3	Woods Holl, Mass.	—	XI, 1885	Edwards	USNM	577076
2	Beaufort, N.C.	—	1950	Dundee	USNM	574616
2	off Grand Id., La.	—	VI, 1938	38-2	USNM	576926
1	off Cape Ann, Mass.	—	V, 1880	U.S. Fish. Comm.	USNM	576801
6	off Newport, R.I.	—	1880	U.S. Fish. Comm.	USNM	576787
1	Vineyard Sound, Mass.	—	V, 1880	U.S. Fish. Comm.	USNM	576840
1	Vineyard Sound, Mass.	—	V, 1880	U.S. Fish. Comm.	USNM	576841
2	Vineyard Sound, Mass.	—	1875	U.S. Fish. Comm.	USNM	—
1	Vineyard Sound, Mass.	—	V, 1880	U.S. Fish. Comm.	USNM	576839
1	Vineyard Sound, Mass.	—	V, 1880	U.S. Fish. Comm.	USNM	576842
6	Woods Hole, Mass.	—	VI, 1885	—	USNM	50576
2	Vineyard Sound, Mass.	—	VI, 1876	—	USNM	576784
25+	off Beaufort, N.C.	13	V, 1970	*Machapunga*	USNM	—
1	Chandaleur, La.	18	I, 1938	*Pelican*	USNM	574321
1	28°36.5′N, 90°55′W	18	III, 1938	*Pelican*, 33	USNM	574325
1	Woods Holl, Mass.	—	1885	*Albatross*	USNM	50575
47	9°3.5′N, 76°28.5′W	57	V, 1969	*Choco*, 38	USNM	—
16	35°11.5′N, 75°12′W	37	X, 1972	*Delaware II*, 4	NMFS[2]	—
19	34°39′N, 75°39′W	123	X, 1972	*Delaware II*, 9	NMFS	—
46	34°2.5′N, 76°14.5′W	154	X, 1972	*Delaware II*, 20	NMFS	—
2	33°43.5′N, 77°13.5′W	31	X, 1972	*Delaware II*, 24	NMFS	—
10+	38°30′N, 74°53′W	62	VIII, 1967	Va. Inst. Mar. Sci., T165	USNM	—
10+	37°55′N, 74°28′W	58	VIII, 1967	Va. Inst. Mar. Sci., T159	USNM	—
10+	36°36′N, 75°6′W	30	VIII, 1967	Va. Inst. Mar. Sci., T186	USNM	—
10+	36°5′N, 74°52′W	88	VIII, 1967	Va. Inst. Mar. Sci., T189	USNM	—
10+	35°51′N, 75°30′W	22	XII, 1967	Va. Inst. Mar. Sci., T238	USNM	—
12	38°2′N, 74°46′W	29	IX, 1967	Va. Inst. Mar. Sci., T217	USNM	577083
2	36°4′N, 74°45′W	137	V, 1967	Va. Inst. Mar. Sci., 65-1	USNM	577082
4	36°51′N, 74°41′W	88	VIII, 1967	Va. Inst. Mar. Sci., T181	USNM	577075
1	33°48′N, 76°42′W	46	IX, 1959	*Silver Bay*, 1220	USNM	—
2	33°43′N, 76°45′W	55	IX, 1959	*Silver Bay*, 1219	USNM	—
1	30°56.5′N, 80°20′W	37	XII, 1963	*Silver Bay*, 5416	USNM	—

APPENDIX A. Cont.

A. Loligo pealei: cont.

No. of specimens	Location	Depth, m	Date	Collector, number	Present location	Number
1	33°N, 78°2′W	0	XII, 1960	*Silver Bay*, 2536	USNM	—
1	29°45′N, 80°9′W	0	XI, 1957	*Silver Bay*, 215	USNM	—
1	21°30′N, 92°23′W	158	VI, 1970	*Oregon II*, 11006	USNM	—
1	20°17′N, 92°7′W	72	VI, 1970	*Oregon II*, 11005	USNM	—
13	36°22′N, 74°48′W	110	VII, 1969	*Oregon II*, 10670	USNM	—
2	28°40′N, 91°20′W	26	I, 1970	*Oregon II*, 10888	USNM	—
3	10°7′N, 75°44′W	60	XI, 1968	*Oregon II*, 10214	USNM	—
3	36°11′N, 74°58′W	38	VII, 1969	*Oregon II*, 10675	USNM	—
2	19°10′N, 92°55′W	174	VI, 1970	*Oregon II*, 10995	USNM	—
7	28°18′N, 91°26′W	69	I, 1970	*Oregon II*, 10882	USNM	—
1	28°16′N, 91°26′W	69	I, 1970	*Oregon II*, 10883	USNM	—
1	8°50′N, 76°38′W	46	XI, 1968	*Oregon II*, 10245	USNM	—
4	19°16′N, 92°50′W	274	VI, 1970	*Oregon II*, 10996	USNM	—
1	29°17′N, 88°2′W	194	VIII, 1970	*Oregon II*, 11138	USNM	—
3	10°5′N, 75°40′W	44	XI, 1968	*Oregon II*, 10215	USNM	—
3	28°54′N, 86°26′W	366	II, 1970	*Oregon II*, 10898	USNM	—
3	35°46′N, 74°59′W	55	VII, 1969	*Oregon II*, 10681	USNM	—
10+	36°17′N, 74°52′W	73	VII, 1969	*Oregon II*, 10673	USNM	—
2	35°19′N, 74°59′W	124	VII, 1969	*Oregon II*, 10694	USNM	—
2	35°21′N, 74°58′W	82	VII, 1969	*Oregon II*, 10696	USNM	—
4	35°41′N, 74°54′W	73	VII, 1969	*Oregon II*, 10682	USNM	—
4	29°9′N, 88°15′W	393	VI, 1969	*Oregon II*, 10647	USNM	—
8	8°51′N, 76°51′W	73	XI, 1968	*Oregon II*, 10246	USNM	—
6	9°37′N, 76°1′W	55	XI, 1968	*Oregon II*, 10223	USNM	—
3	28°17′N, 94°58′W	46	VIII, 1966	U.S.F.C., 8	USNM	576320
1	27°36′N, 84°13′W	80	II, 1966	*H. Cortez*, EJ-66-10	FSBC[3]	11597
1	8°49.2′N, 77°21.2′W	0	VII, 1966	*Pillsbury*, 406	UMML[4]	—
10	8°0.1′N, 76°50′W	4	VII, 1966	*Pillsbury*, 357	UMML	—
89	8°20.1′N, 76°53.6′W	53	VII, 1966	*Pillsbury*, 352	UMML	—
1	8°49.2′N, 77°21.2′W	0	VII, 1966	*Pillsbury*, 406	UMML	—
163	8°0.1′N, 76°50.3′W	20	VII, 1966	*Pillsbury*, 357	UMML	—
1	9°51′N, 75°58′W	51	V, 1964	*Oregon*, 4885	UMML	—
3	27°37′N, 96°39′W	46	XI, 1950	*Oregon*, 153	UMML	31.317

Statistical samples are listed in Table 6.

B. Loligo plei:

1	Jekyl Id., Ga.	—	VI, 1932	Lindner	USNM	574857
5	St. John, Virgin Ids.	0	III, 1958	S.I. Bredin Exp.	USNM	576085
4	30°16′N, 87°15′W	—	—	*Grampus*	USNM	576921
4	18°32.15′N, 65°18.45′W	366	II, 1933	Johnson-Smithsonian	USNM	577096
1	Tortugas, Fla.	26	VII, 1932	Schmitt, 56	USNM	576917
2	off Grand Id., La.	—	VIII, 1930	Burkenroad	USNM	574548
18	off Sea Id., Ga.	—	VIII, 1931	Berry	USNM	574327
2	29°40′N, 80°23′W	77	X, 1953	*Gill*, 4-19	USNM	—
20	Great Stirrup Cay, Bahamas	16	I, 1967	Waller, *Deep Diver*	USNM	576456
1	Tortola, Virgin Ids.	0	III, 1958	Schmitt, 4a-58	USNM	576081
7	Gulf of Venezuela	—	1-3, 1971	Ewald, 23	USNM	—
1	Tortola, Virgin Ids.	0	IV, 1956	Schmitt, 115-56	USNM	576241
4	6°38′N, 55°35′W	44	VII, 1957	*Coquette*, 311	USNM	575573
1	Sarasota, Fla.	0	IV, 1949	U.S. Fish Wildlife	USNM	574856
1	Panacea, Fla.	4	IV, 1967	Rudloe	USNM	576911
2	So. Carolina?	—	V, 1966	McCain	USNM	576444
4	off Beaufort, N.C.	0	VIII, 1915	Badger	USNM	574654
2	off Beaufort, N.C.	—	1950	Dundee	USNM	574616
1	30°13′N, 88°26′W	5	VIII, 1967	*George M. Bowers*, 8034	USNM	—
2	30°32′N, 87°14′W	9	—	*George M. Bowers*, 8031	USNM	—
1	30°23′N, 87°15′W	7	VIII, 1967	*George M. Bowers*, 8022	USNM	—
1	30°23′N, 87°15′W	—	VIII, 1967	*George M. Bowers*, 8019	USNM	—
1	St. Davis, Bermuda	—	I, 1931	—	USNM	575199
1	St. Georges Harbor, Bermuda	0	X, 1967	—	USNM	576902
3	St. Georges Harbor, Bermuda	0	X, 1967	*Trident*	USNM	576903
1	Flatts Inlet, Bermuda	—	I, 1968	—	USNM	—
1	Flatts Inlet, Bermuda	—	XI, 1967	—	USNM	—
1	Smiths Parish, Bermuda	—	V, 1969	JB-H	USNM	—

APPENDIX A. Cont.

B. Loligo plei: cont.

No. of specimens	Location	Depth, m	Date	Collector, number	Present location	Number
1	Harrington Sound	—	VIII, 1969	JB-H	USNM	—
1	Bermuda Biol. Sta., Bermuda	—	V, 1951	Baily	USNM	575766
1	9°3.5′N, 76°28′W	10	V, 1969	*Choco*, 38	USNM	—
15	12°27.7′N, 71°44′W	7	VI, 1969	*Choco*, 50	USNM	—
5	12°N, 72°16′W	5	V, 1969	*Choco*, 11	USNM	—
3	Gulf of Venezuela	—	III, 1971	Ewald	USNM	—
3	32°34′N, 78°46′W	8	VI, 1957	*Combat*, 424	USNM	575408
5	30°8′N, 80°49′W	31	I, 1957	*Combat*, 202	USNM	575446
5	32°34′N, 78°46′W	44	VI, 1957	*Combat*, 424	USNM	575408
1	34°39′N, 75°5′W	366	XI, 1956	*Combat*, c-171	USNM	575441
1	29°N, 80°41′W	18	IV, 1940	*Pelican*, 209-5	USNM	574166
1	28°39.5′N, 91°4.5′W	18	1938	*Pelican*, 81-2	USNM	574320
2	28°39.5′N, 91°4.5′W	18	1938	*Pelican*, 81-2	USNM	574662
8	18°25′N, 67°12′W	—	X, 1966	*Geronimo*, 7-2	USNM	577080
3	off Newport, R.I.	7	VIII, 1880	*Fish Hawk*, 800	USNM	51271
1	off Newport, R.I.	—	1880	—	USNM	33189
1	29°56.5′N, 80°51.5′W	26	V, 1960	*Silver Bay*, 2087	USNM	—
2	17°51′N, 66°8.5′W	37	X, 1959	*Silver Bay*, 2640	USNM	—
1	33°N, 78°40′W	27	X, 1959	*Silver Bay*, 1361	USNM	—
2	34°13.5′N, 76°36.5′W	33	IX, 1959	*Silver Bay*, 1236	USNM	—
1	34°0.5′N, 76°21′W	57	IX, 1959	*Silver Bay*, 1233	USNM	—
1	34°1′N, 77°8′W	27	IX, 1959	*Silver Bay*, 1223	USNM	—
2	33°57.5′N, 77°1.5′W	29	IX, 1959	*Silver Bay*, 1222	USNM	—
4	33°41′N, 77°40′W	0	IX, 1959	*Silver Bay*, 1209	USNM	—
2	34°31′N, 76°51′W	20	IX, 1959	*Silver Bay*, 1259	USNM	—
1	34°40′N, 76°23.5′W	15	IX, 1959	*Silver Bay*, 1251	USNM	—
1	34°21′N, 76°29′W	18	IX, 1959	*Silver Bay*, 1243	USNM	—
3	33°32′N, 77°30.5′W	26	IX, 1959	*Silver Bay*, 1208	USNM	—
1	34°7′N, 77°19′W	24	IX, 1959	*Silver Bay*, 1224	USNM	—
1	29°55′N, 80°38′W	0	VI, 1960	*Silver Bay*, 2139	USNM	—
1	34°24′N, 76°23′W	20	IX, 1959	*Silver Bay*, 1261	USNM	—
2	33°56′N, 77°20′W	27	IX, 1959	*Silver Bay*, 1215	USNM	—
1	34°16′N, 77°34′W	13	IX, 1959	*Silver Bay*, 1226	USNM	—
1	34°55′N, 76°9′W	18	IX, 1959	*Silver Bay*, 1255	USNM	—
1	34°46′N, 76°12.5′W	22	IX, 1959	*Silver Bay*, 1265	USNM	—
1	33°55′N, 77°52.5′W	9	IX, 1959	*Silver Bay*, 1211	USNM	—
1	34°10.7′N, 76°15′W	40	IX, 1959	*Silver Bay*, 1245	USNM	—
1	33°58.5′N, 76°22′W	82	IX, 1959	*Silver Bay*, 1234	USNM	—
2	34°19′N, 77°19.5′W	18	IX, 1959	*Silver Bay*, 1228	USNM	—
1	33°43′N, 76°45′W	55	IX, 1959	*Silver Bay*, 1219	USNM	—
4	8°51′N, 76°51′W	73	XI, 1968	*Oregon II*, 10246	USNM	—
1	20°17′N, 92°7′W	66	VI, 1970	*Oregon II*, 11005	USNM	—
2	8°43′N, 59°10′W	73	IV, 1969	*Oregon II*, 10499	USNM	—
3	8°43′N, 59°10′W	73	IV, 1969	*Oregon II*, 10500	USNM	—
1	29°42′N, 88°40′W	16	V, 1958	*Oregon*, 2193	USNM	575648
10+	19°36′N, 91°47.5′W	44	VIII, 1951	*Oregon*, 425	USNM	575108
2	24°46′N, 82°59′W	46	I, 1951	*Oregon*, 237	USNM	575104
3	30°44′N, 81°12′W	15	I, 1967	*Oregon*, 6324	USNM	—
4	25°24′N, 79°15′W	296	V, 1966	*Oregon*, 6094	USNM	—
5	34°17′N, 77°18′W	20	VI, 1967	*Oregon*, 6761	USNM	—
1	34°13′N, 77°15′W	24	VI, 1967	*Oregon*, 6763	USNM	—
13	29°29′N, 80°11′W	37	XI, 1972	*Delaware II*, 113	NMFS	—
1	34°39′N, 75°39′W	123	X, 1972	*Delaware II*, 9	NMFS	—
2	35°11.5′N, 75°12′W	37	X, 1972	*Delaware II*, 4	NMFS	—
14	33°43.5′N, 77°13.5′W	33	X, 1972	*Delaware II*, 31	NMFS	—
55	34°33.5′N, 75°47′W	91	X, 1972	*Delaware II*, 10	NMFS	—
8	31°24′N, 80°37′W	24	XI, 1972	*Delaware II*, 85	NMFS	—
4	34°13′N, 76°53′W	31	X, 1972	*Delaware II*, 24	NMFS	—
6	31°29′N, 80°7.5′W	38	XI, 1972	*Delaware II*, 80	NMFS	—
1	31°6′N, 80°57′W	18	I, 1967	*Oregon*, 6328	NMFS	—
1	11°39′N, 69°22′W	101	X, 1965	*Oregon*, 5640	NMFS	—
1	32°54′N, 78°38′W	35	I, 1967	*Oregon*, 6376	NMFS	—
2	32°2′N, 80°21′W	18	I, 1967	*Oregon*, 6339	NMFS	—
1	32°55′N, 78°54′W	24	VI, 1967	*Oregon*, 6777	NMFS	—
1	9°35′N, 75°44′W	33	XI, 1968	*Oregon II*, 10226	NMFS	—
10+	Egmont Key, Fla.	9	I, 1966	*H. Cortez*, EJ6634 EJ6630	FSBC	11742 11718

APPENDIX A. Cont.

B. Loligo plei: cont.

No. of specimens	Location	Depth, m	Date	Collector, number	Present location	Number
1	27°36'N, 84°13'W	80	II, 1966	*H. Cortez*, EJ6647	FSBC	11960
19	Tampa Bay, Fla.	6	II, 1966	*H. Cortez*, EJ6666	USNM	–
2	9°30'N, 60°15'W	117	VII, 1968	*Pillsbury*, 699	UMML	–

[1]USNM = U.S. National Museum (National Museum of Natural History), Smithsonian Inst., Washington, D.C.
[2]NMFS = National Marine Fisheries Service, Woods Hole, Mass.
[3]FSBC = Florida State Board of Conservation, St. Petersburg, Fla.
[4]UMML = University of Miami Marine Laboratory.

APPENDIX B. *Loligo* statistics.

Fig. no.	Regression no.	Species	Y	X	Regression	N	
5	1	*L. pealei*	♀GW	♀ML	Y=2.0+0.1585Xmm	81	
	2	*L. pealei*	♂GW	♂ML	Y=5.2+0.1074Xmm	89	
	5	*L. pealei*	GW	ML	Y=3.5+0.135Xmm	70	(120-200 mm ML only)
			Sexes differ (ANCOVA $p < 0.001$)				
	3	*L. plei*	♀GW	♀ML	Y=7.5+0.07364Xmm	12	
	4	*L. plei*	♂GW	♂ML	Y=7.1+0.0567Xmm	12	
		Species differ (ANCOVA $p < 0.001$)					
6		*L. pealei*	Gill F	ML	Y=48.0+0.134Xmm	173	
			Sexes differ (ANCOVA $p < 0.001$)				
7	1	*L. pealei*	♀FW	♀ML	Y=4.5+0.4649Xmm	70	
	2	*L. pealei*	♂FW	♂ML	Y=8.6+0.3945Xmm	93	
			Sex regressions differ ($p < 0.025$)				
	3	*L. plei*	♀FW	♀ML	Y=–5.2+0.4543Xmm	16	
	4	*L. plei*	♂FW	♂ML	Y=22.2+0.2401Xmm	10	
		Species differ (ANCOVA $p < 0.001$)					
8	1	*L. pealei*	♀MMW	♀ML	Y=8.6+0.1403Xmm	72	
	2	*L. pealei*	♂MMW	♂ML	Y=8.5+0.1293Xmm	79	
			Sexes differ (ANCOVA $p < 0.003$)				
9		*L. pealei*	Gill L	ML	Y=8.1+0.204Xmm	208	
			Sexes differ (ANCOVA $p < 0.001$)				
10	1	*L. pealei*	♀ASWIII	ML	Y=0.59+0.0102Xmm	81	
	2	*L. pealei*	♂ASWIII	ML	Y=0.79+0.0098Xmm	89	
	5	*L. pealei*	ASWIII	ML	Y=0.46+0.011Xmm	70	(120-200 mm ML only)
			Sexes differ (ANCOVA $p < 0.007$)				
	3	*L. plei*	♀ASWIII	ML	Y=0.14+0.0109Xmm	8	
	4	*L. plei*	♂ASWIII	ML	Y=0.36+0.0094Xmm	12	
11		*L. pealei*	AMW	ML	Y=11.6+0.113Xmm	175	
		L. pealei	AMW	ML	Y=4.2+0.157Xmm	70	(120-200 mm ML only)
12		*L. pealei*	MMC	ML	Y=30.8+0.365Xmm	218	
13	1	*L. pealei*	♀FMW	♀ML	Y=5.3+0.093Xmm	73	
	2	*L. pealei*	♂FMW	♂ML	Y=1.5+0.134Xmm	78	
14	1	*L. pealei*	♂Gill L	FCL	Y=0.104+2.1Xmm	62	(Eastern Coast U.S.)
	2	*L. pealei*	♂Gill L	FCL	Y=–25.2+3.326Xmm	10	(Gulf Coast U.S.)
	3	*L. pealei*	♂Gill L	FCL	Y=–13.1+2.898Xmm	17	(Caribbean Sea)
21	1	*L. pealei*	FCL	ML	Y=7.4+0.083Xmm	218	
	2	*L. plei*	FCL	ML	Y=4.8+0.0814Xmm	20	
22	1	*L. pealei*	HW	ML	Y=14.1+0.105Xmm	208	
	3	*L. pealei*	HW	ML	Y=9.7+0.133Xmm	70	(120-200 mm ML only)
	2	*L. plei*	HW	ML	Y=10.9+0.0997Xmm	20	
23	1	*L. pealei*	NCL	ML	Y=6.2+0.1274Xmm	175	
	3	*L. pealei*	NCL	ML	Y=2.4+0.152Xmm	70	(120-200 mm ML only)
	2	*L. plei*	NCL	ML	Y=3.2+0.1282Xmm	20	
31	1	*L. pealei*	FL	ML	Y=–15.0+0.6748Xmm	223	
	2	*L. plei*	FL	ML	Y=–14.2+0.5572Xmm	38	

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A NATURAL POPULATION OF *HELISOMA DURYI* IN BRAZIL[1]

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ABSTRACT

A well established natural population of *Helisoma duryi* (Wetherby) was recently found in central Brazil, where it was introduced probably with aquatic plants conveyed by aquarists. A morphological description based on the observation of 10 specimens is presented, involving the shell, cephalopodal mass, mantle organs, reproductive system and buccal apparatus.

INTRODUCTION

Helisoma is a historically Nearctic genus of the molluscan family Planorbidae whose occurrence in the Neotropical region has been frequently recorded. The genus has been spreading from North America through the filter bridge of Middle America, having also reached several Antillean islands. In South America *Helisoma* has been found breeding naturally, west of the Andes, in Peru (*Planorbis peruvianus* Broderip, 1832), Ecuador (*Planorbis equatorius* Cousin, 1887) and Colombia (Paraense, unpublished).

An undoubtedly wrong record of *Helisoma peruvianum* in Brazil appears in Baker's monograph (1945, pl. 141, figs. 31, 32). In fact, until recently no species of *Helisoma* had been found in any of the significantly large areas of this country carefully surveyed during the last 20 years. The present paper is thus the first reliable record of the occurrence of this genus in Brazil.

In August, 1972, a sample of planorbids from Lagoa da Pedra, a lake connected with the river Canabrava, in the district of Santa Rosa, municipality of Formosa, State of Goiás, was brought to this institute by our collectors. Dissection of these specimens showed that several of them belonged to the species *Helisoma duryi* (Wetherby, 1879). A few days later I visited the same breeding place, finding a flourishing population of this species (including a large proportion of albinos), in sympatry with *Biomphalaria straminea, B. schrammi, Drepanotrema anatinum, D. lucidum* and *Plesiophysa ornata,* besides ancylids, physids and ampullariids.

MATERIAL AND METHODS

Ten of the largest specimens of *H. duryi* were dissected for anatomical study. To avoid retraction into the shell, to which the helisomas are particularly prone when touched, each specimen was previously placed in a finger bowl containing 100 ml of a 0.2% solution of nembutal in dechlorinated tap water. After 6 hours they were well extended and motionless. They were then carefully picked up with a forceps, the shell aperture upward, and gradually plunged in hot water at 70°C for about 45 seconds, showing practically no reaction to manipulation. Once dead, the animal body was gently pulled by the foot with a small dentate forceps, so as to disconnect the insertion of the columellar muscle. The whole animal having been drawn out of the shell, which remained unbroken, it was preserved in Railliet-Henry's fluid (formalin 5 ml, acetic acid 2 ml, and 0.6% aqueous sodium chloride 93 ml) for further dissection.

Histological observations were made on cross sections of some specimens fixed in Bouin's fluid, embedded in paraffin and stained with hematoxylin and eosin.

[1]Contribution from the Schistosomiasis Snail Identification Center for the Americas, maintained under the auspices of the University of Brasília, the Pan American Health Organization and the Ministry of Health of Brazil.

OBSERVATIONS

1. Shell (Fig. 1A-F)

The largest shell is 18 mm in diameter and 8.5 mm in width at the aperture (5.5 mm at the beginning of the outer whorl), and has 5 whorls. The whorls increase in diameter rather rapidly. The right side is vortex-shaped, showing a very deep central depression at the bottom of which the apical whorl is almost completely hidden; on this side the whorls are rounded and separated by a deep suture. The left side is shallowly depressed; its wall is bluntly angular on the outer whorl, the angulation getting sharper and sharper toward the apical whorl and lying very near the suture, or even coinciding with it, on the inner whorls. If the left angulation coincides with the suture, the inner whorls altogether form a flattened surface; in any case, however, the lateral surface of the whorls is plainly exposed on the left. The periphery is rounded and somewhat shifted to the right. The aperture is heart-shaped or deltoid, usually transverse, and has an angular left lip; it may be directed forward, or more or less deflected to the left or, less frequently, to the right. The growth lines are well marked, giving the shell a conspicuously striated appearance; in addition to them, there may be coarser lines forming rings and rib-like thickenings. There is neither punctation nor spiral striation. The shells were examined by transmitted light under the stereomicroscope, showing no internal lamellae. The shell of newly hatched specimens, nearly 0.8 mm in diameter and 0.7 mm in width, has about 1¼ whorls and shows a delicate structure similar to that of *Biomphalaria* (see, for instance, Paraense & Ibañez, 1964: 253).

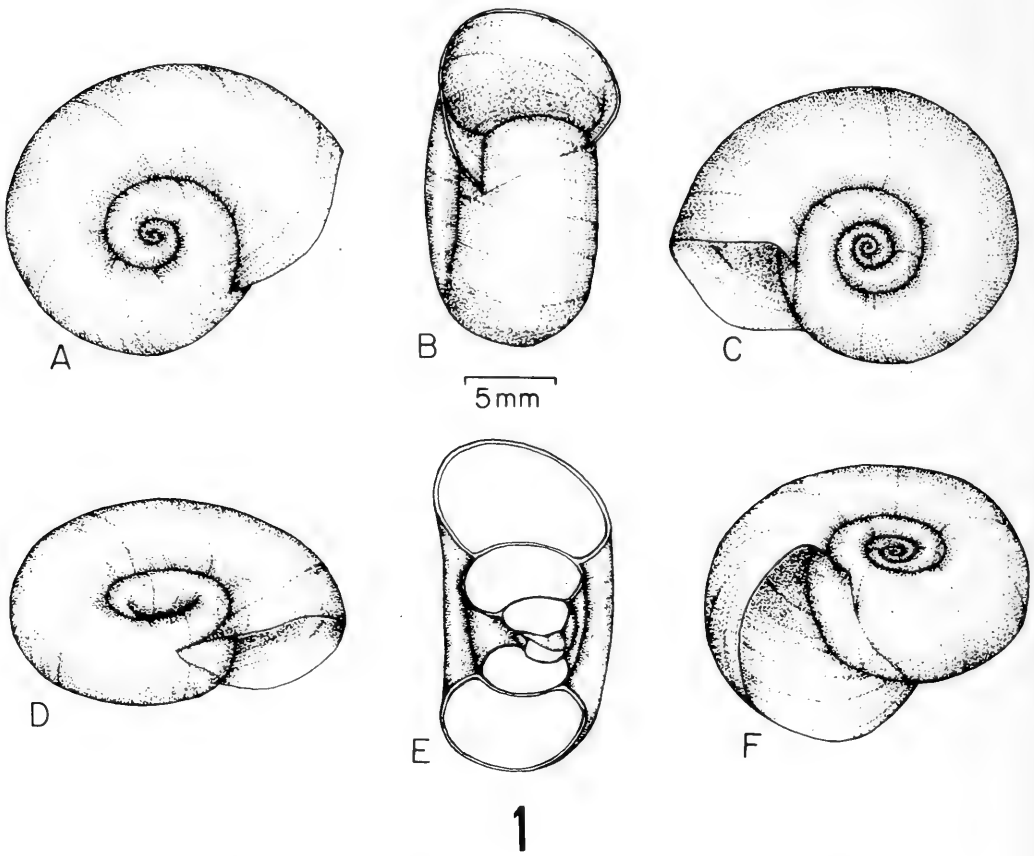


FIG. 1. Shell of *Helisoma duryi*. A, Right lateral view. B, Ventral view. C, Left lateral view. D, Dextroventral view. E, Diametrical section. F, Sinistroventral view.

2. Cephalopodal mass and mantle organs

The crawling animal carries its shell somewhat leaning to the left. The foot is oblong, with rounded corners at its front end and a narrower back end showing an ogival outline. The cephalopodal mass is diffusely dark brown and sprinkled throughout with minute whitish dots. A darker line runs along the unpigmented edges of the foot and velum. The pulmonary wall is blotched with dark gray. In the freely moving animal the heart can be seen beating in the first quarter of the outer whorl. The ventral surface of the renal tube shows a renal ridge similar to that of *Biomphalaria glabrata* (see Paraense & Deslandes, 1959), but much more prominent and (at least in the present sample) without a particular pigmentation. As in *Biomphalaria,* there are a pulmonary lamella (consisting of a dorsolateral ridge which folds down at the back of the pulmonary cavity to continue into a rectal ridge) and a leaf-like pseudobranch traversed lengthwise by the tip of the rectal ridge. The cephalopodal mass, the pulmonary wall and the rectal ridge, and less noticeably other organs, show a bluish green pigmentation either diffuse or concentrated in discrete dots, and more conspicuous in albino specimens. Such pigmentation gradually disappears after fixation.

3. Reproductive system (Figs. 2-12 and 14)

The ovotestis is composed of more or less 50 transverse rows of about 8-10 diverticula at the cephalic end, gradually decreasing to 1-2 at the caudal end. Although most diverticula are unbranched, there is a significant number of bifurcate and trifurcate units. The ovotestis of one specimen was thoroughly dissected, showing 228 diverticula, of which 160 were unbranched, 50 bifurcate, 17 trifurcate and 1 quadrifid. The diverticula are usually elongate (finger-like or club-shaped), converging toward the collecting canal so as to show a fan-like disposition in cross-sections of the ovotestis. The proximal segment of the ovispermiduct is very short and frequently hidden by the caudal diverticula of the seminal vesicle. The latter is moderately sinuous, chiefly at the caudal half, and beset with parietal diverticula which vary in shape from knob-like to finger-like; the elongate diverticula may be unbranched or subdivided. The distal segment of the ovispermiduct also shows parietal diverticula similar to those of the seminal vesicle, but smaller, nearly always unbranched, confined to the dorsal wall and devoid of spermatozoa. The ovispermiduct opens through the caudal pole of the carrefour, whereas the duct of the albumen gland opens through the opposite pole.

The albumen gland is squarish and covers the dorsal surface of the stomach and the transverse segment of the prointestine. The oviduct follows a crooked course at its first portion, and then runs forward nearly straight. At its cephalic end it expands into a pouch of plicate walls (pouch of the oviduct) which continues into the nidamental gland. The latter is longer and much wider than the oviduct. It gradually narrows forward to merge with the uterus. The vagina has an upper cylindric portion followed by an enlarged lower portion which communicates with the spermatheca. The spermatheca has a club-shaped body merging in a narrow duct of variable length, the distal portion of which gradually widens down to its attachment to the right wall of the vagina. The spermatheca tends to be longer than either the prostate or the penial complex.

The spermiduct begins as a flattened tube parallel to the oviduct, and narrows very gradually as it runs forward. It then crosses diagonally the right surface of the pouch of the oviduct, where it lies in a furrow of variable depth. After leaving that furrow it runs straight for a short distance, and then puts forth a few (about 5-7) prostatic diverticula, the stalks of which are usually widely spaced (Fig. 7). The diverticula branch repeatedly, so that each of them looks like a compact arborescent cluster of intermingling tubules (Figs. 4-6), very difficult to separate from each other and from the branches of neighboring diverticula. About 450 final branches were counted in a thoroughly dissected prostate. The prostate, represented by a series of multibranched diverticula, extends over the right side of the nidamental gland, occupying the space between the fore margin of the pouch of the oviduct and the top of the spermatheca, a small area of the latter being usually in contact with the foremost prostatic diverticula (Fig. 8). The vas deferens, narrower than the distal portion of the spermiduct, may be considered as formed by two segments, about the same width, a proximal one from the prostate to the left wall of the

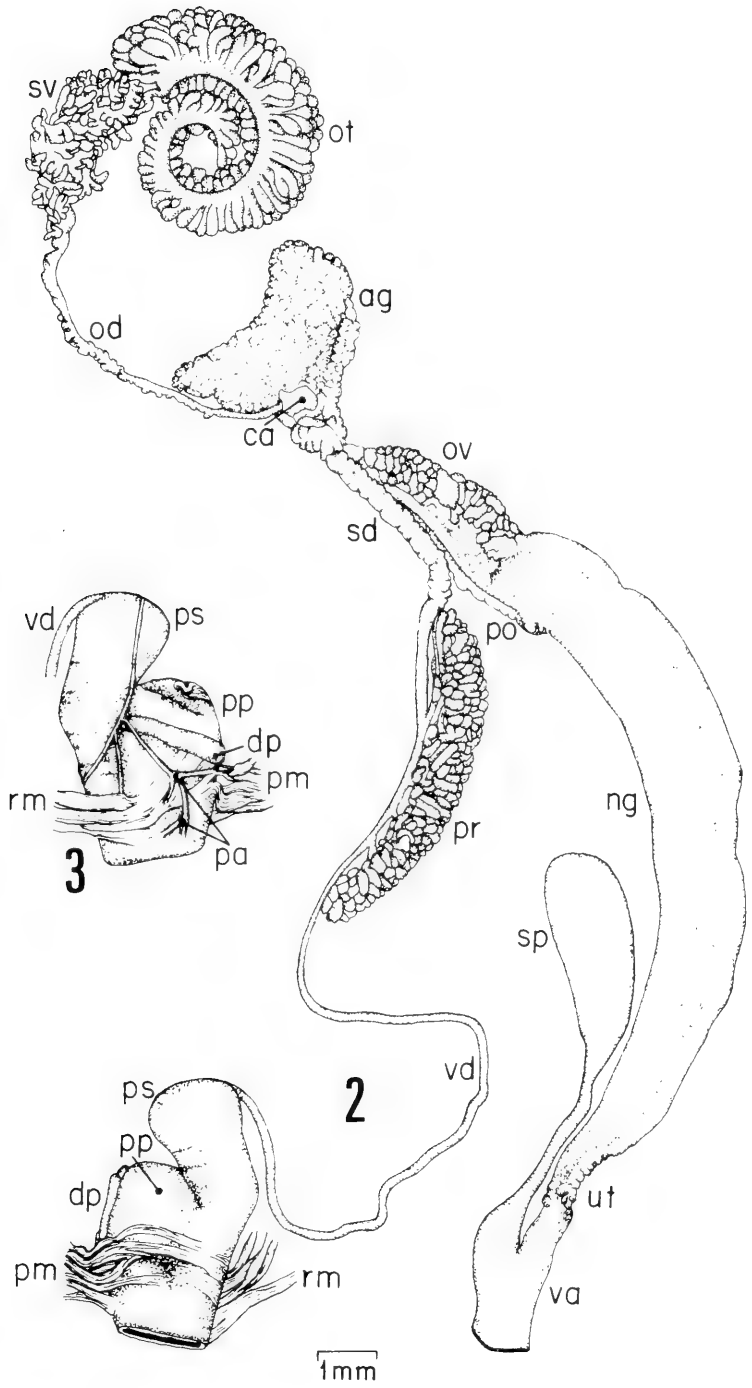
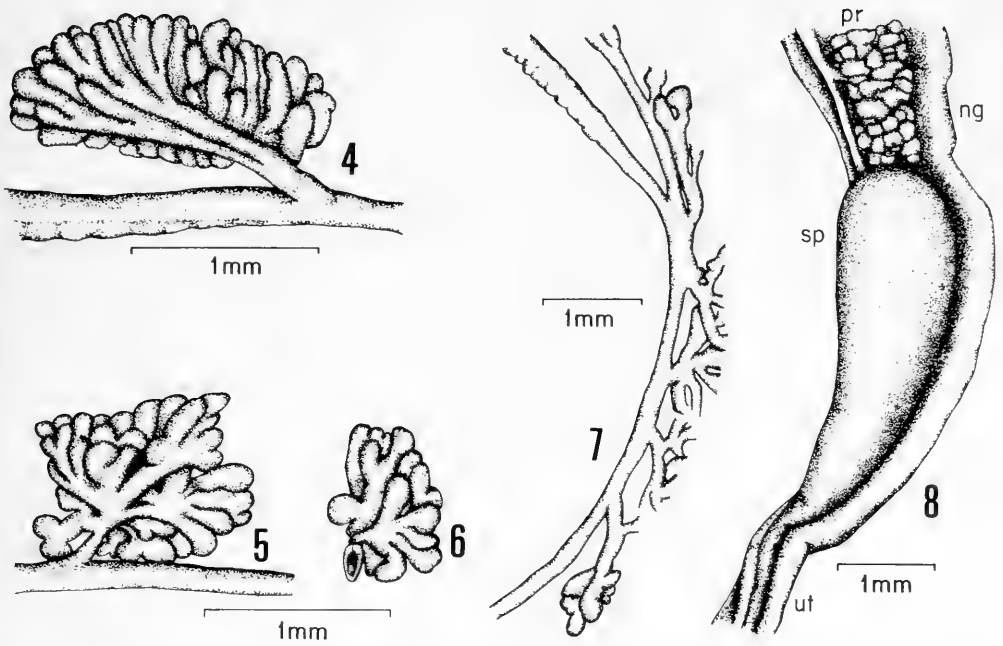


FIG. 2. Reproductive system of *Helisoma duryi*. FIG. 3. Penial complex, dorsal view. **ag**—albumen gland; **ca**—carrefour; **dp**—duct of preputial organ; **ng**—nidamental gland; **od**—ovispermiduct; **ot**—ovotestis; **ov**—oviduct; **pa**—preputial artery; **pm**—protractor muscle of prepuce; **po**—pouch of oviduct; **pp**—prepuce; **pr**—prostate: **ps**—penis sheath; **rm**—retractor muscle of prepuce; **sd**—spermiduct; **sp**—spermatheca; **sv**—seminal vesicle; **ut**—uterus; **va**—vagina; **vd**—vas deferens.

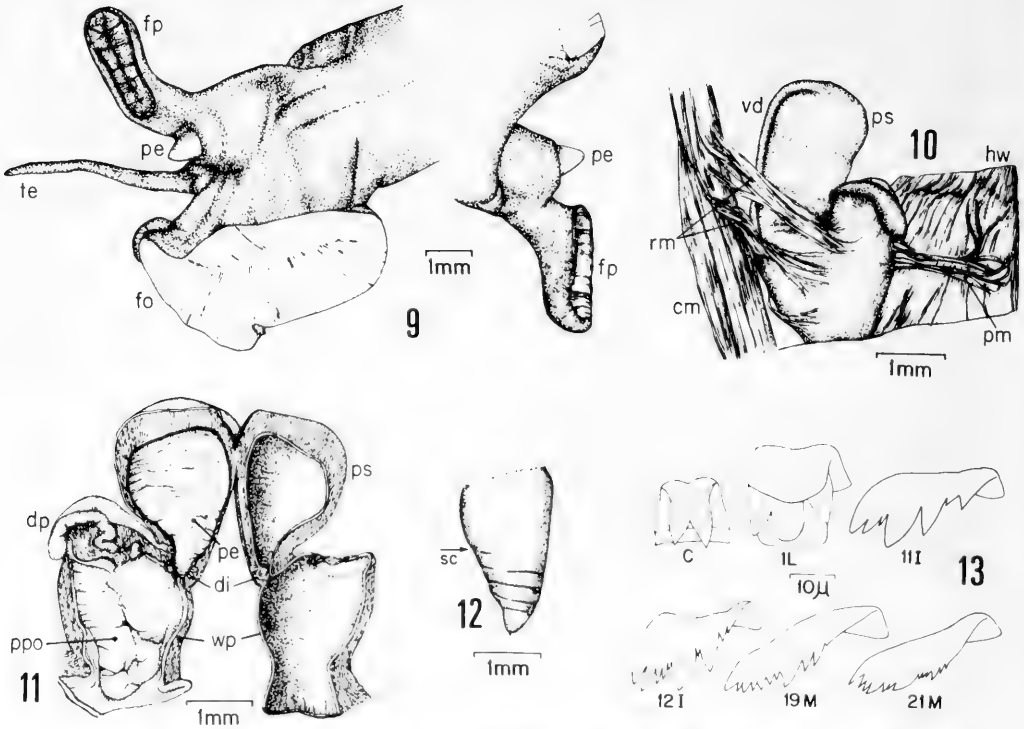


FIGS. 4-8. Organs of *Helisoma duryi.* 4, Hindmost prostatic diverticulum. 5, Foremost prostatic diverticulum. 6, Interproximal view of prostatic diverticulum. 7, Stems of prostatic diverticula. 8, Relation between foremost prostatic diverticulum **(pr)** and spermatheca **(sp)**; **ng**—nidamental gland; **ut**—uterus.

snail's head, and a distal one from this point to the top of the penis sheath and, sometimes, increasing in width as it approaches its distal end. The penis sheath is pear-shaped, with a globular top and a narrower basal portion continuous with the prepuce. Externally the penis sheath is marked off from the prepuce by a constriction; internally the 2 organs show a smooth wall and are separated by a well developed diaphragm (Fig. 11, di). The wall of the prepuce shows a lateral swelling produced by the preputial organ, with a central umbilication corresponding to the site of attachment of that organ. The preputial organ hangs from the inner wall of the prepuce, to which it is attached by a short stalk. It accommodates to the preputial cavity much like a closed boxing glove (Fig. 11, ppo). When extended through the preputial outlet, it shows a foot-like free portion (Fig. 9), with a sole which acts as a sucker in playing a hold-fast function during copulation (Malek, 1952; Pace, 1971). The preputial organ is greatly variable in shape owing to its great extensibility and contractivity. It has a duct which originates in the depression near the distal end of the sole, runs to the stalk and pierces the wall of the prepuce. Then it coils free in the blood sinus outside the penial complex (Figs. 2, 3 and 11, dp), perforates the wall of the penis sheath just above the diaphragm (Fig. 11, dp), and opens into the sheath lumen. The penis (Fig. 12) is cone-shaped and shows at its point a small papilla provided with a very minute stylet. The sperm canal opens laterally, about midway between the base and the tip of the penis (Figs. 12 and 14, sc). Attached to opposite sides of the outer preputial wall, there are a retractor muscle, directed caudally, which merges with the columellar muscle (Figs. 2, 3 and 10, rm), and a protractor muscle, directed dorsally which attaches to the midline on the inner wall of the head cavity (Figs. 2, 3 and 10, pm); each muscle consists of several bundles of fibers. The preputial artery ramifies over the surface of the prepuce and penis sheath, giving cross-connected branches as shown in Fig. 3.

4. Buccal apparatus

The jaw is similar to that of *Biomphalaria,* showing a T-shaped outline, with a transverse crescent-like upper piece connected at each end with a more slender



FIGS. 9-13. Organs of *Helisoma duryi.* 9, Cephalopodal mass with extruded preputial organ (**fo**—foot; **fp**—foot-like portion of preputial organ; **pe**—penis; **te**—tentacle). 10, Penial complex, with retractor muscle (**rm**) merging in columellar muscle (**cm**) and protractor muscle (**pm**) attached to head wall (**hw**), **vd**—vas deferens. 11, Penial complex, internal view (**di**—diaphragm; **dp**—duct of preputial organ; **pe**—penis; **ppo**—preputial organ; **ps**—penis sheath; **wp**—wall of prepuce). 12, Penis: sperm canal outlet (**sc**) indicated by arrow. 13, Teeth from the 30th row of a radula with 165 transverse rows; the numbers indicate position in the transverse row, counting from the central tooth (**C**, central; **L**, lateral; **I**, intermediate; **M**, marginal).

vertical lower piece. The buccal sac is pear-shaped and similar to that of *Biomphalaria.* The salivary glands are free from the nerve ring, and are joined behind. The radula shows, as an important characteristic, a roundly blunt mesocone in the lateral teeth (Fig. 13, 1L), contrasting with the entocone and the ectocone which are broadly aculeate.

DISCUSSION

The occurrence of *Helisoma duryi* in an isolated area of central Brazil is undoubtedly due to its having been introduced, most likely with aquatic plants conveyed by aquarists.

Comparing the present material with Pilsbry's (1934) and Baker's (1945) descriptions and figures, I concluded that it belongs to the species *Helisoma (Seminolina) duryi* (Wetherby, 1879). Its preputial organ shows a short external duct, a feature considered by Baker (1945) to be characteristic of the subgenera *Seminolina* and *Helisoma,* s.s., in contradistinction to a much longer duct in the subgenera *Pierosoma* and *Planorbella.* Distinction between *Seminolina* and *Helisoma,* s.s., may be based again on the comparative length of the mentioned duct, which, in the former, is about twice as long as in the latter. An additional difference is in the mesocone of the lateral teeth of the radula, which is bluntly rounded in *Seminolina* and spade-like in *Helisoma,* s.s.

If the identification of the present species is correct, some disagreement between the anatomical description above and that given by Baker (1945) should be mentioned.

The prostate of *Seminolina* is described by Baker (1945:130) as "oblong, over 2 mm in length composed of many diverticula arranged in fan-like rows. A section of the

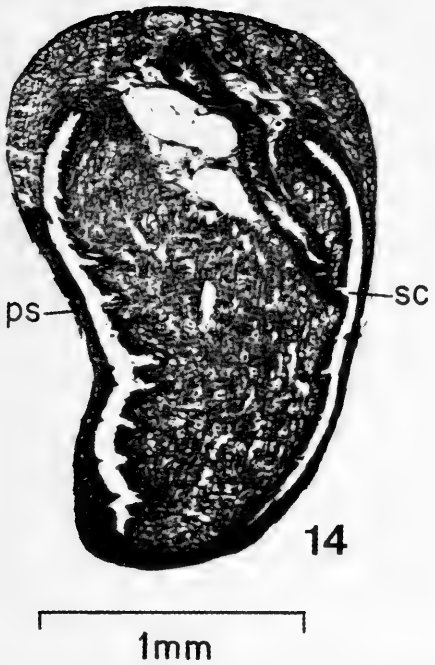


FIG. 14. Longitudinal section of penis and penis sheath of *Helisoma duryi* (ps—penis sheath; sc—sperm canal outlet).

prostate near the middle shows sixteen rows of club-shaped diverticula. The prostate diverticula discharge into a separate duct, the prostate duct, with which the sperm duct connects posteriorly and the vas deferens anteriorly." In the present material the prostate may show an oblong outline in contracted specimens, but in relaxed ones it is decidedly elongated (Fig. 2, pr). The diverticula are subdivided and their branches are so closely intermingled that they are difficult to disentangle (Figs. 4-6). Such diverticula are far from club-shaped and arranged in fan-like rows. They discharge through their stems directly into the spermiduct (Fig. 7), not into a separate prostatic duct. Prostatic diverticula directly attached to the spermiduct were also seen in *H. duryi* by Ferguson & Gerhardt (1956).

The preputial organ, called penial gland by Pilsbry (1934) and Baker (1945), is less complicated than described and figured by these authors. If the specimens are previously relaxed with nembutal, the organ may extend through the preputial outlet, showing the shape depicted in Fig. 9, and agreeing perfectly with Malek's (1952) Fig. B, Plate II, of *H. duryi.*

Baker (1945) considers the muscle attached to the right wall of the prepuce a retractor muscle, and that attached to the left wall a supporting muscle. Since support is a characteristic function of connective tissues, and since contractility (which brings about retraction and protraction) is a muscular property, it seems evident that those musclar bundles are respectively retractor and protractor muscles.

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RÉSUMÉ

UNE POPULATION NATURELLE D'*HELISOMA DURYI* AU BRÉSIL CENTRAL

W. Lobato Paraense

Une population naturelle bien établie d'*Helisoma duryi* (Wetherby), introduite probablement avec des plantes aquatiques importées, a été trouvée récemment au Brésil Central. Dans ce travail sont décrits la coquille, la masse céphalopodale, les organes palléaux, le système reproducteur et l'appareil buccal de 10 exemplaires disséqués.

RESUMEN

UNA POBLACION NATURAL DE *HELISOMA DURYI* EN EL BRASIL CENTRAL

W. Lobato Paraense

Una población natural bien establecida de *Helisoma duryi* (Wetherby), introducida probablemente con plantas acuáticas importadas, ha sido hallada recientemente en el Brasil Central. En este artículo se describen la concha, la masa cefalopodal, los órganos paleales, el sistema reproductor y el aparato bucal de 10 ejemplares disecados.

MALACOLOGIA, 1976, 15(2): 377-399

BENTHIC MOLLUSCAN ASSEMBLAGES IN RELATION TO SEDIMENT GRADIENTS IN NORTHEASTERN LONG ISLAND SOUND, CONNECTICUT[1]

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ABSTRACT

Associations of sublittoral benthic mollusks occurring along a gradual sediment texture gradient in NE Long Island Sound (Fishers Island Sound), U.S.A., are defined using cluster analysis. Stations were selected to include a sediment gradient from silt through very coarse sand but within a small geographical area where "between station" differences in temperature and salinity are minimal. Groups of stations produced by the Classification Analysis were contiguous along the sediment gradient and highly correlated with parameters of sediment texture. The molluscan associations which correlate with these groups are defined as "very fine sand," "medium sand" and "coarse sand" associations. These groups of species are characterized respectively as deposit-feeders, siphonate infaunal suspension-feeders, and short- or non-siphonate suspension-feeders. Diversity as measured by the Shannon-Wiener function (H') was a reflection primarily of the evenness component of diversity (J). Along the sediment texture gradient, H' was affected by high dominance (D) in soft sediments, and seasonal changes in dominance at intermediate sediment textures.

Factors accounting for high dominance and low evenness in very fine sediments are discussed, and it is argued that this reflects the homogeneity of the energy resource (organic matter), the reduced pool of potential competitors, and the severely seasonal thermal environment. Sediment-correlated species associations in this area appear to be fairly stable and predictable within a framework of seasonal variability in the degree of dominance exhibited by certain species. The Classification procedure is useful in grouping stations along a gradual environmental continuum for the purpose of diversity analysis. It is not argued that these groups comprise rigid, non-overlapping associations or communities.

INTRODUCTION

The "structure" of benthic communities, i.e. the specific organisms present and their relative abundances, varies in conjunction with gradual changes along environmental gradients. The resulting continuum (Mills, 1969) of species distributions implies the absence of precise boundaries separating such communities except at points where the environmental gradients steepen to form natural or habitat separation. The benthic fauna at points along a gradient can be characterized by species composition and diversity (Sanders, 1956, 1958, 1960) and predictable aggregations of species recur where requisite conditions prevail.

The possibility of comparing the species composition and diversity of communities with similar environmental characteristics, but at different geographical locations, or at the same location over an extended period of time, has implications in studying the effects of pollution on marine ecosystems, as well as the effects of natural environmental factors on community structure. However, data presently available on species composition of benthos are inadequate as a predictive tool in the evaluation of the effects of environmental gradients on benthic communities. The primary goal of this study was to determine the species structure and diversity of sublittoral benthic molluscan associations within Fishers Island Sound (FIS). The distribution of species as well as associations of species will be correlated with the gradient in sediment grain size. This type of analysis will be of particular interest because FIS is an area with a remarkably wide range of sediments but little variability in temperature and salinity (except in shoal areas influenced by the several small rivers which empty into the Sound). Consequently, within FIS, sediment texture is hypothesized to be the primary environmental correlate of species composition.

[1]Contribution No. 114 of the Marine Sciences Institute, University of Connecticut.

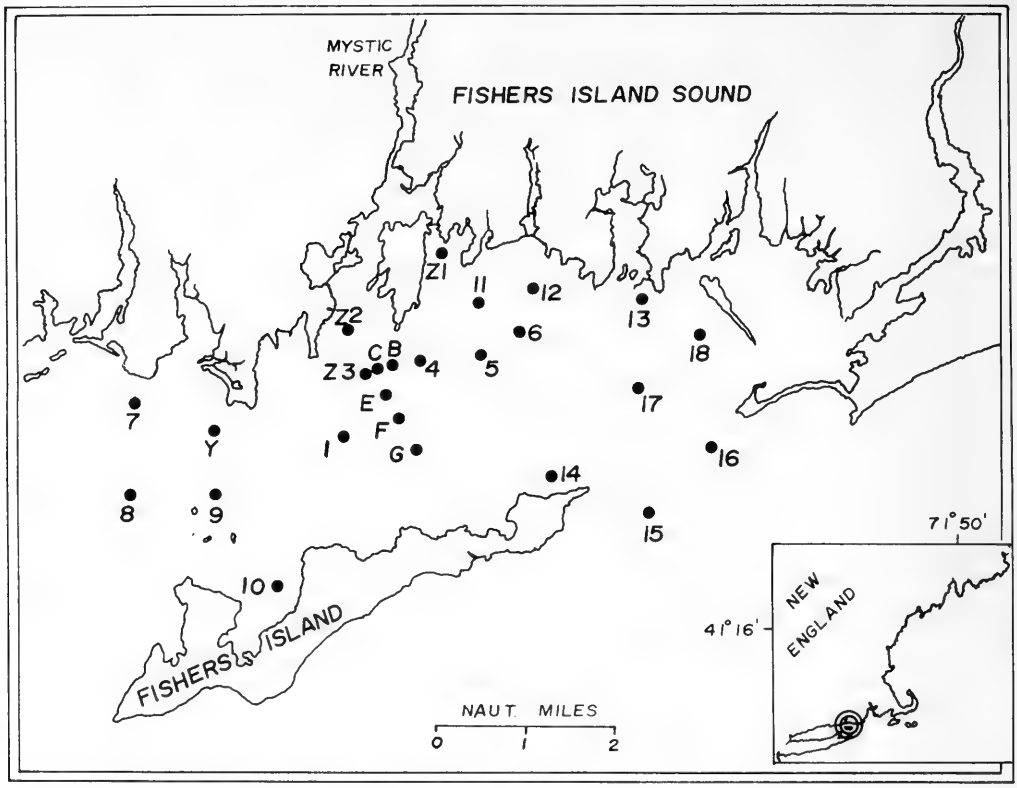

FIG. 1. Research area. Solid circles indicate location of sampling sites.

METHODS AND MATERIALS

Fishers Island Sound (Fig. 1), forming the northeastern portion of Long Island Sound, is bounded by Fishers Island on the S and NE Connecticut on the N. Continuous with Long Island Sound to the W, FIS is confluent with Block Island Sound to the E via several shallow passages. Two small rivers empty into FIS, the Pawcatuck and Mystic, but their major influence on salinity is restricted to the shoals and bays along the N shore. At most other locations throughout the Sound, salinity is relatively constant between 29 and 31°/₀₀ (Clark, 1971). Tidal currents through FIS originate in Block Island Sound and flow westward (U.S. Department of Commerce, Coast and Geodetic Survey, Tidal Current Charts Long Island Sound to Block Island Sound, Series 544). As these currents are generally rapid, the prevailing sediments in the Sound are fairly coarse. However, the presence of shoals, small islands and bays provides areas where finer sediments accumulate. In most areas, water temperature varies seasonally from approximately 2-3° C to 25° C. However, temperature variation between stations is insignificant except in very shallow water.

Stations were selected to provide the maximum sediment gradient excluding locations on flats and bays along the N shore where salinity levels drop below 29°/₀₀. All stations are sublittoral, ranging in depth from 4 to 30 m MLW.

Bottom samples were taken at 3 seasons, Spring, Late Summer and Winter (June, August, 1972; January, 1973). Bottom grab samples were collected using a 0.1 m^2 weighted Petersen Grab. At each station, a minimum of 3 grabs were taken and the contents pooled. Sediments were returned to the laboratory and screened using a 1 mm mesh sieve. Because of the problem in sampling the range of sediments encountered with the available sampling device (Petersen Grab), as well as the lack of knowledge on the degree of contagion exhibited for almost all benthic molluscan species, it was decided

not to attempt to express the faunal abundance data in terms of biomass.

Organisms retained on the 1 mm sieve were fixed in neutralized formalin and stained with Rose Bengal. Complete samples were stored in the laboratory for identification and enumeration of mollusks.

Small amounts of sediment were retained at the time of collection for subsequent sediment texture analysis. The silt-clay fraction was determined by means of standard pipette analysis (Krumbein & Pettijohn, 1938) following agitation of the wet sediment samples in 3% sodium hexametaphosphate (Calgon) solution (Folk, 1968). The coarser fraction, retained on a 0.062 mm screen, was sieved through a nested series of screens at 0.5 phi intervals (U.S. Standard Series) on a Ro-Tap shaker, and each screen fraction was weighed to the nearest 0.1 g. The following sediment parameters were determined: mean and median particle size, percent clay, percent silt and clay; percent gravel; degree of sorting; skewness. Sediment statistics follow Folk (1968).

It was frequently impossible to return to the same stations with precision because of weather conditions. Consequently, each sample is treated separately and no assumption is made that stations are precisely replicated at different seasons.

Several sampling and analytical designs have been successfully applied in the analysis of benthic associations. These include repetitive sampling at fixed stations within a single biotope (Sanders, 1960), sampling over a sediment gradient at fixed stations (Sanders, 1958; Lie, 1968; Nichols, 1970; Stephenson, Williams & Lance, 1970; Field, 1971; Day, Field & Montgomery, 1971; Young & Rhoads, 1971; Wade, 1972; Hughes, Peer & Mann, 1972; Boesch, 1973), random and repetitive sampling over a sediment gradient with subsequent grouping of stations with similar biotopes (O'Connor, 1972). In many of these studies similarity among stations in a sampling grid was determined using coefficients of similarity (or dissimilarity) and the resulting similarity matrices further analyzed by multivariate methods including ordination and/or analysis. Environmental factors incorporated into such studies include the degree of tidal exposure on rocky shores (Field & McFarlane, 1968), depth and turbulence (Field, 1971; Day, Field & Montgomery, 1971), distance from shore (Hughes & Thomas, 1971) and sediment texture (Field, 1971; Nichols, 1970; Hughes, Peer & Mann, 1972; Boesch, 1973; Gage, 1974).

The attractive features of a randomized sampling plan notwithstanding, a scheme involving repetitive sampling at fixed stations over a predetermined sediment gradient was selected as most appropriate in the present study. The primary factor in this choice was the great variability in sediment texture over short distances, which made it necessary to return, as precisely as possible, to the same stations in order to guarantee the inclusion of the maximum sediment gradient. Since the gradient in sediment texture was to be correlated with the distribution of individual species as well as associations of species, a means of classifying the collections into units for comparison was advantageous. Thus, a community classification procedure was selected as the most fruitful approach.

A Q-mode analysis was carried out in which all pairs of stations were compared on the basis of their species composition. Similarity coefficients were calculated among all pairs of stations using the Czekanowski coefficient (Bray & Curtis, 1957):

$$C_z = 2W/(A+B)$$

where A is the sum of the measure of abundance of all species at a given station a; B is the sum of the measures of abundance of all species at station b; and W is the sum of the lower of the two abundance values for each species common to the two samples being compared. Note that when the measure of abundance is the percent of each species, $C_z = W$. W is the sum of the lesser of the 2 percentages of each species shared between 2 stations. This value is subsequently referred to in this paper as the **Percentage of Similarity** or **PS** (Southwood, 1968). This formulation emphasizes dominance. Therefore, a second derivative of C_z was calculated in which A is the number of species at station a; B is the number of species at station b; and W is the number of species common to both a and b. Used in this way, as a binary coefficient, C_z reduces to the **Dice** coefficient (Hall, 1969), which is equivalent to Sorenson's quotient of Similarity (Sorenson, 1948). This coefficient eliminates all relative abundance data and weights all species equally.

The similarity data were clustered using

the unweighted pair-group method of Sokal & Michener (1958) in which the level that a member joins an existing cluster is based on the average similarities of all existing members of the cluster of the original similarity matrix (Hazel, 1970).

Three aspects of species diversity were considered in this study: the relative contribution of the several components of species diversity; the possible existence of diversity gradients along sediment texture gradients; and seasonal variability in diversity. The components of species diversity measured include **Species Richness** (Number of species per station); **Community Dominance** ($D = y_1 + y_2$) where y_1 and y_2 are the percentage values of the two most abundant species (McNaughton, 1968); Shannon's information formula for **Species Diversity** ($H' = -\Sigma p_i \log_2 p_i$) where p_i is the proportion of individuals belonging to the i^{th} species; and **Evenness** ($J = H'/H_{max}$) where $H_{max} = \log_2 S$ and S = No. Species (Pielou, 1969).

The role of the sediment texture gradient in affecting diversity was determined by correlation analysis carried out separately for August and January.

RESULTS

The results of the sediment texture analysis are shown in Appendices 1-3. The original 12 stations in June were increased to 22 stations in August and January. Cumulative sediment curves for selected stations (Fig. 2) indicate a fairly wide range in sediment texture although almost all stations contain sediments predominantly in the sand range. The overall sediment gradient in the study area ranges from very coarse sand (< 0 phi) to predominantly silt and clay (> 4 phi). However, as seen in Fig. 2, variability in the percent composition of gravel or silt-clay exists among stations with similar values of central tendency (mean, median, mode). This variability is reflected in high standard deviations (i.e. poorly sorted sediments) and may be of significance in the distribution patterns of specific invertebrates.

Extreme variation in sediment parameters such as the percent of silt and clay (2-64%) and percent of gravels (0-60%) characterizes the study area. In general, the soft-bottom stations in FIS lack the very large components of silt-clay noted by Sanders (1958, 1960) in central Long Island Sound and Buzzards Bay. FIS stations with mean sediment values in the silt-clay range (> 4.0 phi) have silt-clay components from 28 to 64% ($\bar{x} = 41.6\%$). All such sediments are poorly sorted in FIS.

Approximately 40% of stations sampled are characterized by fine to very fine sediments (phi 2.5-4.0) with silt-clay components ranging about 7-26% ($\bar{x} = 15.5\%$). About 23% of locations are characterized by predominantly medium sand (phi 1.0-2.0); the percentage of silt-clay ranges about 1-17% ($\bar{x} = 5.5\%$). Only a very few of these stations have sorting coefficients of less than 1.0 phi (moderately sorted). The remainder are poorly to very poorly sorted. Stations with bottom sediments in the coarse range (phi 0-1.0) have silt-clay values from 3-12% ($\bar{x} = 5.4\%$). Stations with mean values of less than 0 phi (very coarse sand) are areas subjected to high velocity tidal currents. In general, these sediments are very poorly sorted. Although gravel components may dominate these sediments, silt and clay are present at levels of 2-4%.

Numerical analysis

The initial suite of 14 stations sampled in June was analyzed using the PS similarity coefficient followed by Q-mode cluster analysis. On the basis of this analysis, two inshore stations characterized by *Zostera* (Z1, Z2) were discarded for the purposes of this study because of the unique effects of eelgrass on species composition. With the exception of 1 other station, the remaining 11 collections appeared to form 3 weak clusters of stations. Based on these preliminary results, a 2nd suite of samples was collected in August, 1972. All of the original areas were resampled, and the number of stations was increased to 24. As in June, a Q-mode cluster analysis using PS was calculated. These results are shown in Fig. 3a. Station Z1 (not clustered) and Station 18 appear to be only very weakly associated with any of the other stations. The remaining stations clustered into 3 groups, designated A, B, and C. However, as will be noted below, the anomalously large number of stations comprising group B result from dominance at these stations of a single species, *Tellina agilis*. Consequently, a Dice similarity matrix for August was recon-

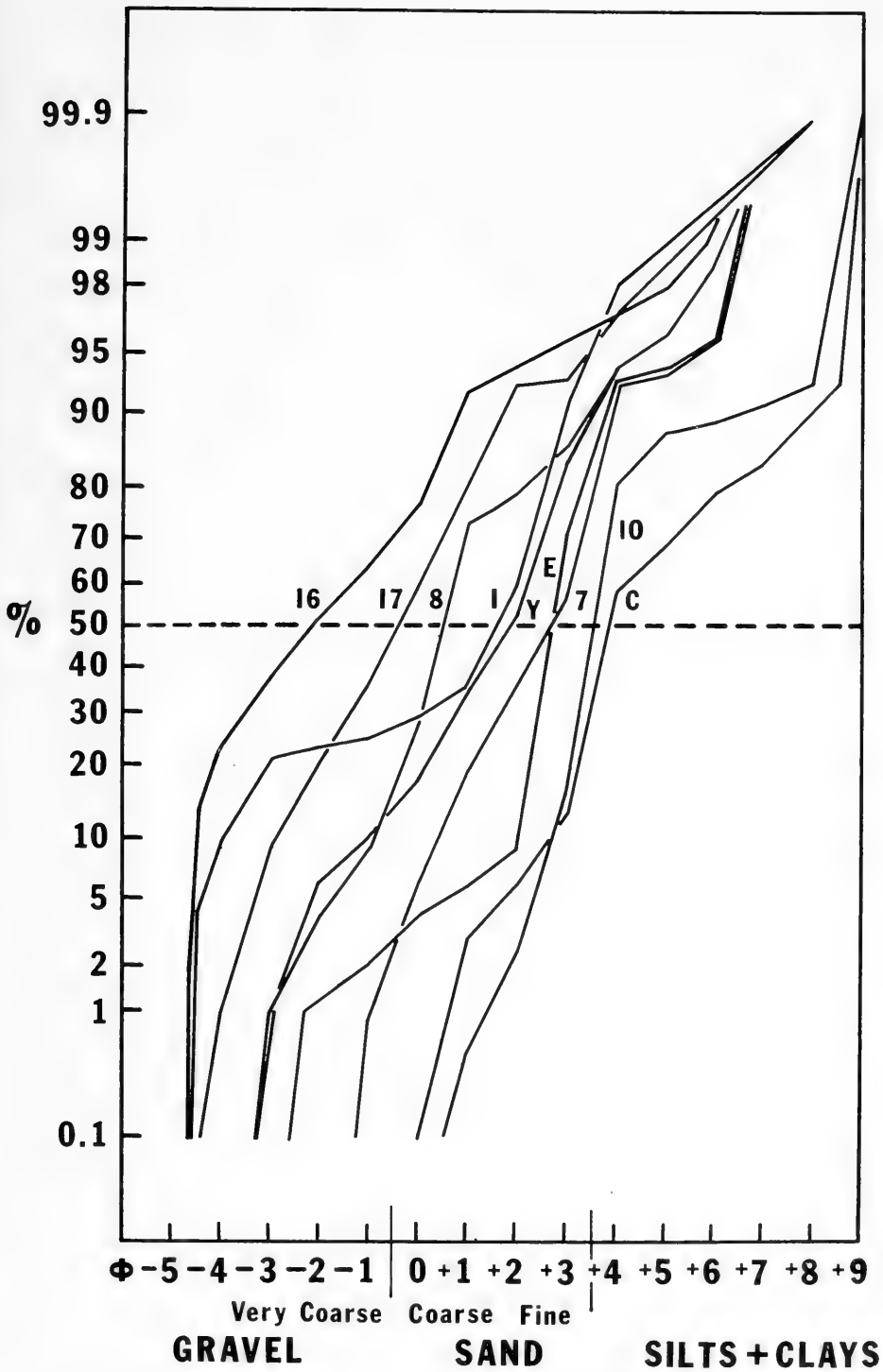

FIG. 2. Cumulative sediment curves at 9 stations, August (1972), selected to show the overall sediment gradient in the study area. The dotted line indicates the median (50%).

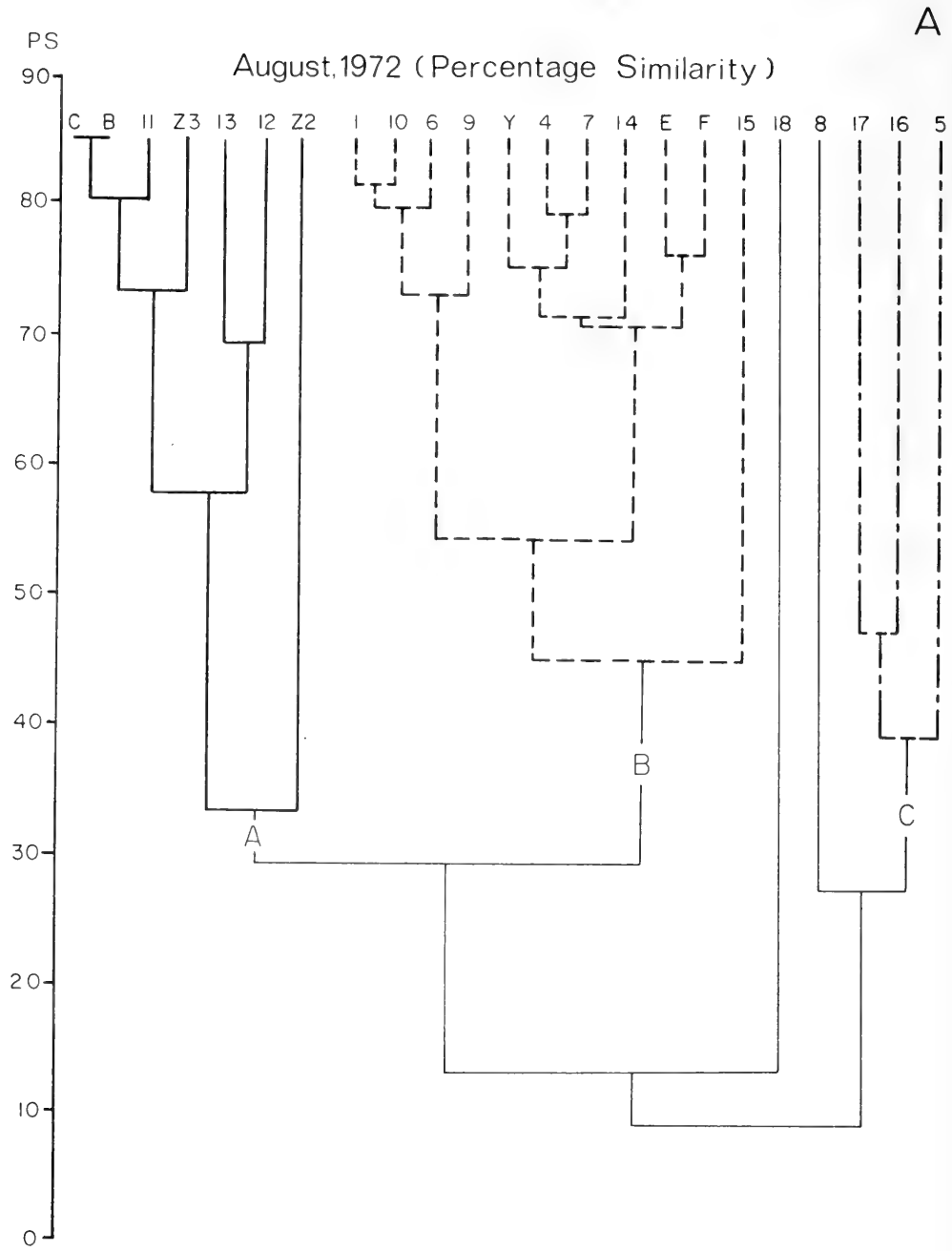

FIG. 3A. Q-mode phenogram of stations collected in August, 1972, based on PS similarity coefficients.

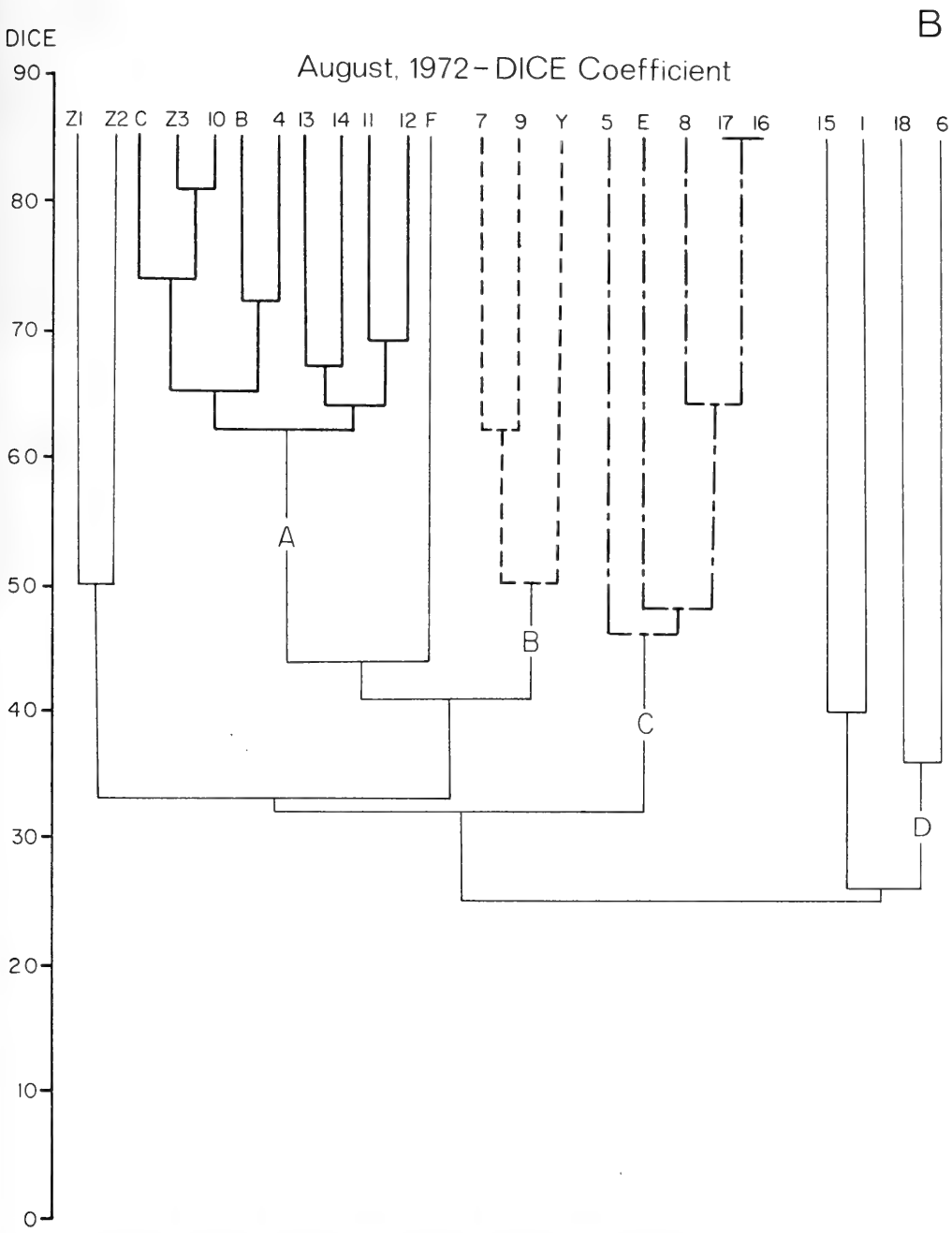

FIG. 3B. Q-mode phenogram of stations collected in August, 1972, based on Dice similarity coefficients.

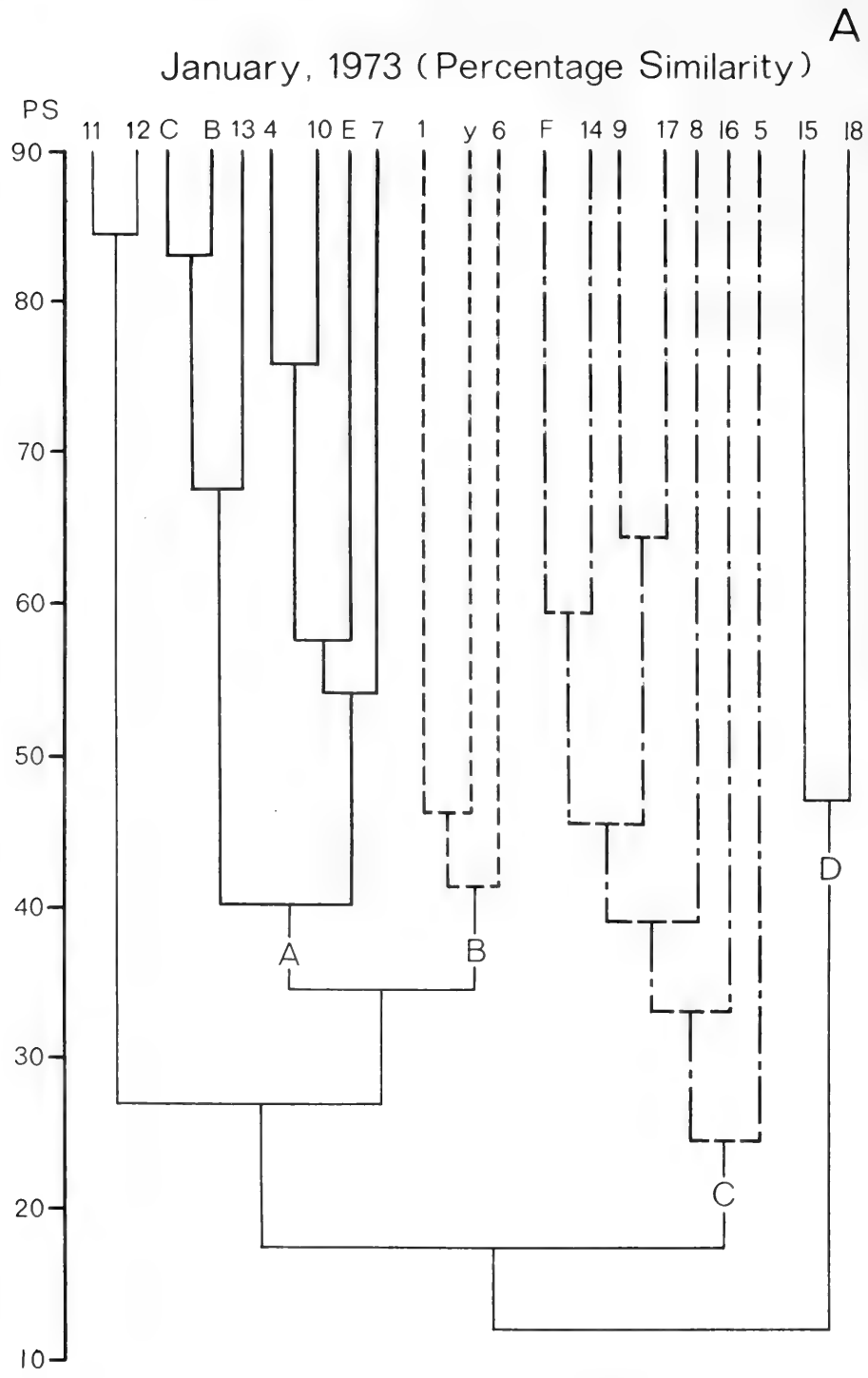

FIG. 4A. Q-mode phenogram of stations collected in January, 1973, based on PS similarity coefficients.

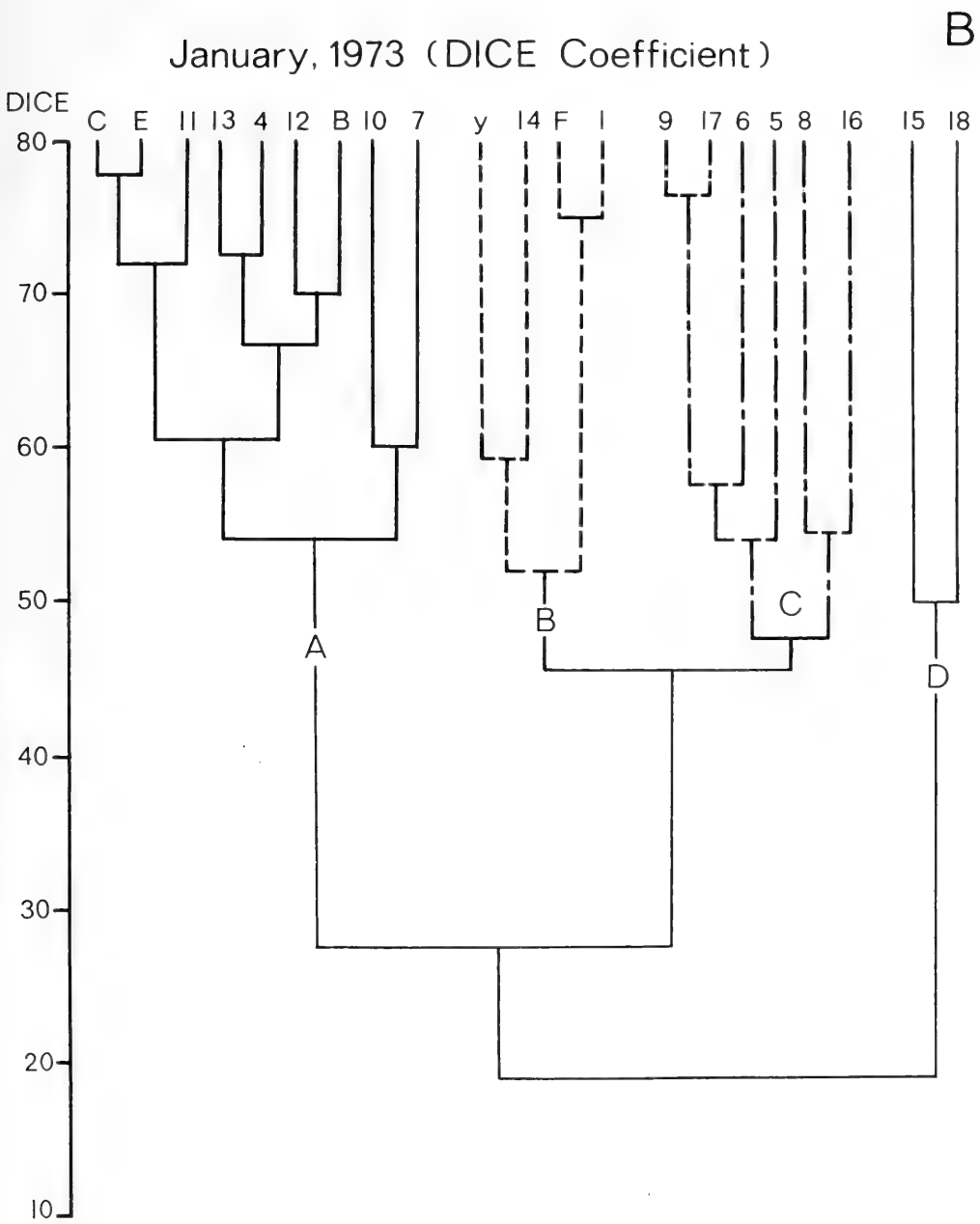

FIG. 4B. Q-mode phenogram of stations collected in January, 1973, based on Dice similarity coefficients.

structed and clustered (Fig. 3B). Note that the effect of the Dice Coefficient is to reduce the size of group B. Several of the stations formerly in group B are relocated in groups A and C; and 4 stations are set off with little apparent affinity with the others. The latter group is designated group D (Fig. 3B).

A 3rd suite of stations sampled in January, 1973, was clustered utilizing both PS and Dice Coefficients. These results are shown in Figs. 4A, B). The clustering of Dice Coefficients (Fig. 4B) results in 4 rather well defined groups, designated A, B, C and D. The clustering of PS values for these data also results in 4 groups (A-D) plus a pair of stations (11 and 12) which are weakly associated with 2 of the above groups (Fig. 4A). There is generally good agreement in the composition of the groups generated by the similarity coefficients, although some discrepancies are apparent. One interesting difference is the linkage between groups A and B in the PS cluster. In the Dice cluster, group B is more closely linked with C than with A.

Species composition and group correlation

A total of 52 species of sublittoral mollusks was encountered, not including nudibranchs which were not included because of their high degree of association with epibenthos, and because of problems in the identification of preserved and contracted animals. In Table 1, these species are listed and ranked by frequency of occurrence in samples, and by numerical abundance. The species comprising each of these 4 faunal groups (A, B, C and D), their relative abundance and percent composition are shown in Appendix 4.

The groupings of stations produced by the Dice Coefficient cluster analysis, which reflect similarity in species composition, are clearly correlated with sediment texture as shown in Fig. 5. The solid line is fitted visually and indicates the correlation between median particle size and the percent of silt-clay. The stations comprising group A occur in fine to very fine sand (median particle size less than 4 Ø) and silt-clay levels generally well above 10%. The group B stations are associated with fine to medium sands (3 Ø-1.4) and silt-clay levels of about 5-15%. The group C stations are mostly coarse sand (less than 1 Ø) with silt-clay levels of 2-10%. The stations comprising group D range from fine to coarse sand (2.5-0.5 Ø) but at very low levels of silt and clay (less than 3.5%).

Fig. 6 shows the distribution and relative abundance of 18 of the more common mollusks in relation to median sediment size in FIS. The shading patterns identify these species with 1 of 3 groups, A, B or C. Note that the abundance patterns of 3 of the species, *Pandora gouldiana, Lunatia triseriata* and *Anachis translirata*, are not correlated with sediment texture (except that they do not usually occur in the soft mud locations). Of these, *Lunatia*, and probably *Anachis*, are predators and the suspension feeder *Pandora* seems to occur in all sandy sediments.

The species of Group A, with the exception of *Tellina* and *Solemya*, correspond to the mollusk component of the *Nucula/Nephthys/Yoldia* infaunal mud community described by Sanders (1956, 1958, 1960) in Long Island Sound and Buzzards Bay. Thus, group A may be considered an extension of this benthic association into very fine sand sediments.

The species composition of group B stations is more variable than in group A but *Tellina agilis* is highly dominant. Negative characteristics include the absence or uncommon occurrence of *Nucula, Tornatina* and *Cylichnella*.

The group C stations, which occur primarily in coarse sand with significant amounts of gravel, are characterized by the non-siphonate bivalves indicated in Fig. 6 plus *Crassinella mactracea* and *Musculus discors*. Note also the continued presence of *Tellina* (Appendix 4).

The stations designated as Group D are low diversity, high energy habitats with populations of *Spisula solidissima*. Too few of these stations are represented in this study to allow any further generalizations.

Diversity

The measures of diversity, i.e. Species Richness (SR), Dominance (D), Evenness (J) and the Shannon index (H′), as determined for each station in August (1972) and January (1973), are listed in Appendix 5. In the present analysis, each of these diversity measures was correlated with 3 sediment variables: median sediment particle size (MPS), the percent of silt-clay (PSC) and the percent of gravel (PGR). Since, over the

TABLE 1.

Species ranked by abundance	Species ranked by frequency of occurrence in samples	No. samples present	Total no. specimens	Rank by abundance
1. *Tellina agilis*	1. *Tellina agilis*	53	1337	1
2. *Nucula proxima*	2. *Nucula proxima*	33	1186	2
3. *Turbonilla nivea/stricta*	3. *Lyonsia hyalina*	33	129	8
4. *Tornatina canaliculata*	4. *Turbonilla nivea/stricta*	31	668	3
5. *Solemya velum*	5. *Pitar morrhuana*	28	58	16
6. *Mysella planulata*	6. *Mitrella lunata*	27	118	9
7. *Cylichnella oryza*	7. *Tornatina canaliculata*	27	224	4
8. *Lyonsia hyalina*	8. *Anachis translirata*	25	88	12
9. *Mitrella lunata*	9. *Lunatia triseriata*	23	48	19
10. *Ensis directus*	10. *Nassarius trivittatus*	23	87	13
11. *Astarte undata*	11. *Ensis directus*	22	94	10
12. *Anachis translirata*	12. *Astarte undata*	21	89	11
13. *Nassarius trivittatus*	13. *Pandora gouldiana*	19	28	24
14. *Cardita borealis*	14. *Solemya velum*	19	193	5
15. *Turbonilla interrupta*	15. *Cylichnella oryza*	18	142	7
16. *Pitar morrhuana*	16. *Yoldia limatula*	17	52	18
17. *Spisula solidissima*	17. *Mercenaria mercenaria*	15	27	25
18. *Yoldia limatula*	18. *Cardita borealis*	15	73	14
19. *Lunatia triseriata*	19. *Macoma tenta*	13	30	23
20. *Crenella decussata*	20. *Cerastoderma pinnulatum*	13	36	21
21. *Cerastoderma pinnulatum*	21. *Turbonilla interrupta*	11	66	15
22. *Mytilus edulis*	22. *Mysella planulata*	10	158	6
23. *Macoma tenta*	23. *Petricola pholadiformis*	10	18	28
24. *Pandora gouldiana*	24. *Spisula solidissima*	9	55	17
25. *Mercenaria mercenaria*	25. *Eupleura caudata*	8	8	35
26. *Musculus discors*	26. *Mytilus edulis*	8	32	22
27. *Aligena elevata*	27. *Musculus discors*	8	26	26
28. *Petricola pholadiformis*	28. *Urosalpinx cinerea*	7	9	34
29. *Mulinia lateralis*	29. *Astarte castanea*	7	12	30
30. *Astarte castanea*	30. *Mulinia lateralis*	6	15	29
31. *Nucula delphinodonta*	31. *Nucula delphinodonta*	6	12	31
32. *Crassinella mactracea*	32. *Aligena elevata*	4	19	27
33. *Modiolus modiolus*	33. *Modiolus modiolus*	4	9	33
34. *Urosalpinx cinerea*	34. *Hiatella arctica*	4	7	37
35. *Eupleura caudata*	35. *Crassinella mactracea*	4	11	32
36. *Hiatella arctica*	36. *Haminoea solitaria*	3	4	37
37. *Haminoea solitaria*	37. *Odostomia* sp.	3	3	38
38. *Odostomia* sp.	38. *Crenella decussata*	3	38	20
39. *Alvania* sp.	39. *Gemma gemma*	2	1	51
40. *Polinices heros*	40. *Cumingia tellinoides*	2	1	52
41. *Anachis avara*	41. *Alvania* sp.	2	3	39
42. *Busycon canaliculata*	42. *Anachis avara*	2	2	41
43. *Philine sinuata*	43. *Polinices heros*	2	3	40
44. *Crepidula fornicata*	44. *Busycon canaliculata*	2	2	42
45. *Epitonium rupicola*	45. *Philine sinuata*	2	2	43
46. *Rictaxis punctostriatus*	46. *Crepidula fornicata*	1	2	44
47. *Polinices duplicatus*	47. *Epitonium rupicola*	1	1	45
48. *Diaphana minuta*	48. *Rictaxis punctostriatus*	1	1	46
49. *Siliqua costata*	49. *Polinices duplicatus*	1	1	47
50. *Musculus niger*	50. *Diaphana minuta*	1	1	48
51. *Gemma gemma*	51. *Siliqua costata*	1	1	49
52. *Cumingia tellinoides*	52. *Musculus niger*	1	1	50

entire sediment spectrum, very few of these diversity components show a significant correlation with sediment texture, the correlation matrices are not reproduced here although several significant correlations will be discussed below.

There are, however, very significant linear correlations between the diversity components (SR, J, and D) and the Shannon index H′ (Table 2). Note that the strongest correlation is between D and H′ ($r = > 0.9$). Thus, community dominance in FIS is an excellent correlate of H′, and is clearly a better predictor of diversity than SR, the other independent measure. Note also in Table 2 the large seasonal difference in the correlation relating H′ to SR. Thus, the correlation based on combined August and January data is lower than either August or January measured separately. This is accounted for

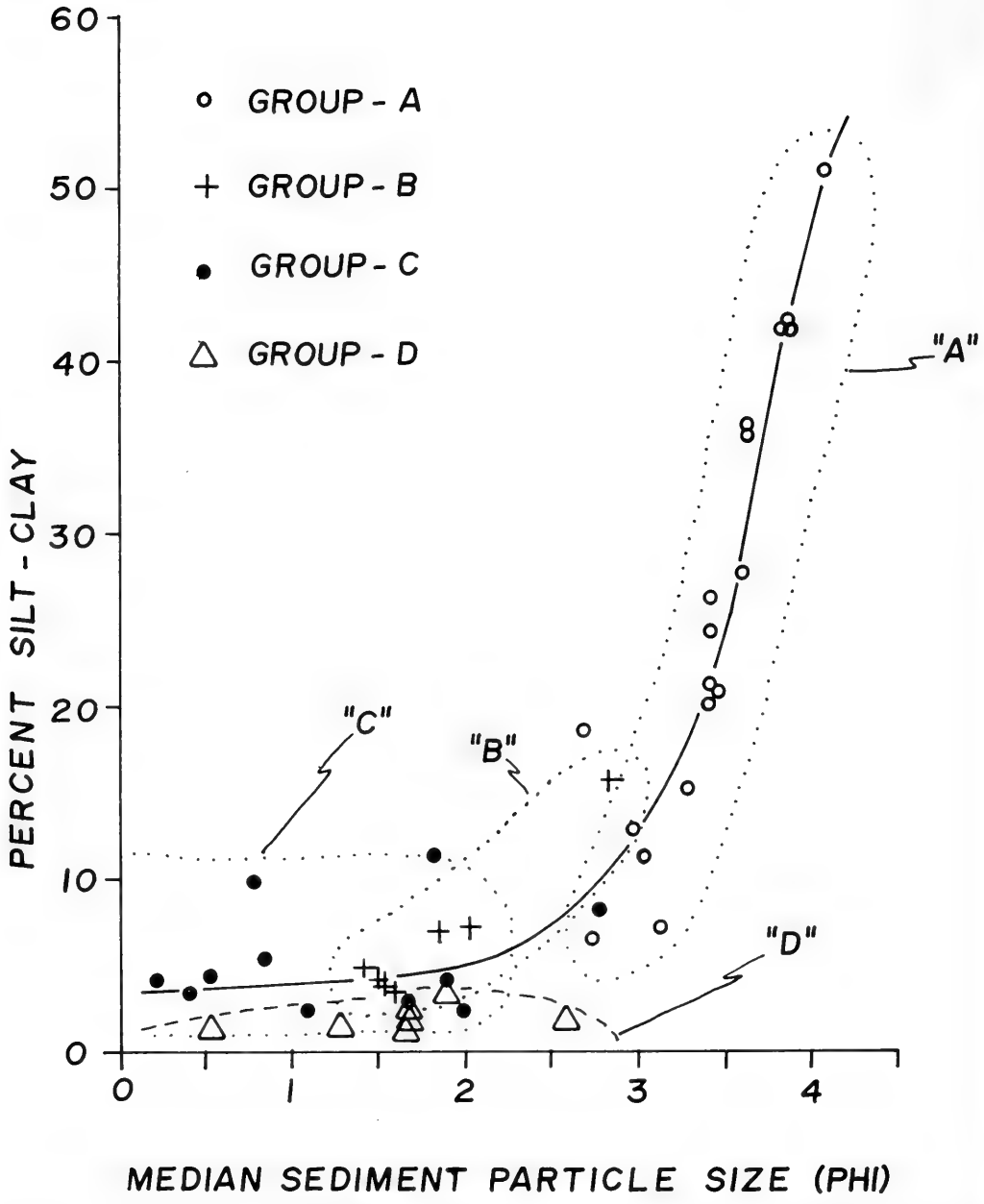

FIG. 5. Relationship between the sediment texture gradient (% silt-clay, and median particle size) and the distribution of stations in cluster groups A-D. Each point represents a single sampling station and date (August, 1972, and January, 1973). Group designations are based on the Dice Similarity Coefficients.

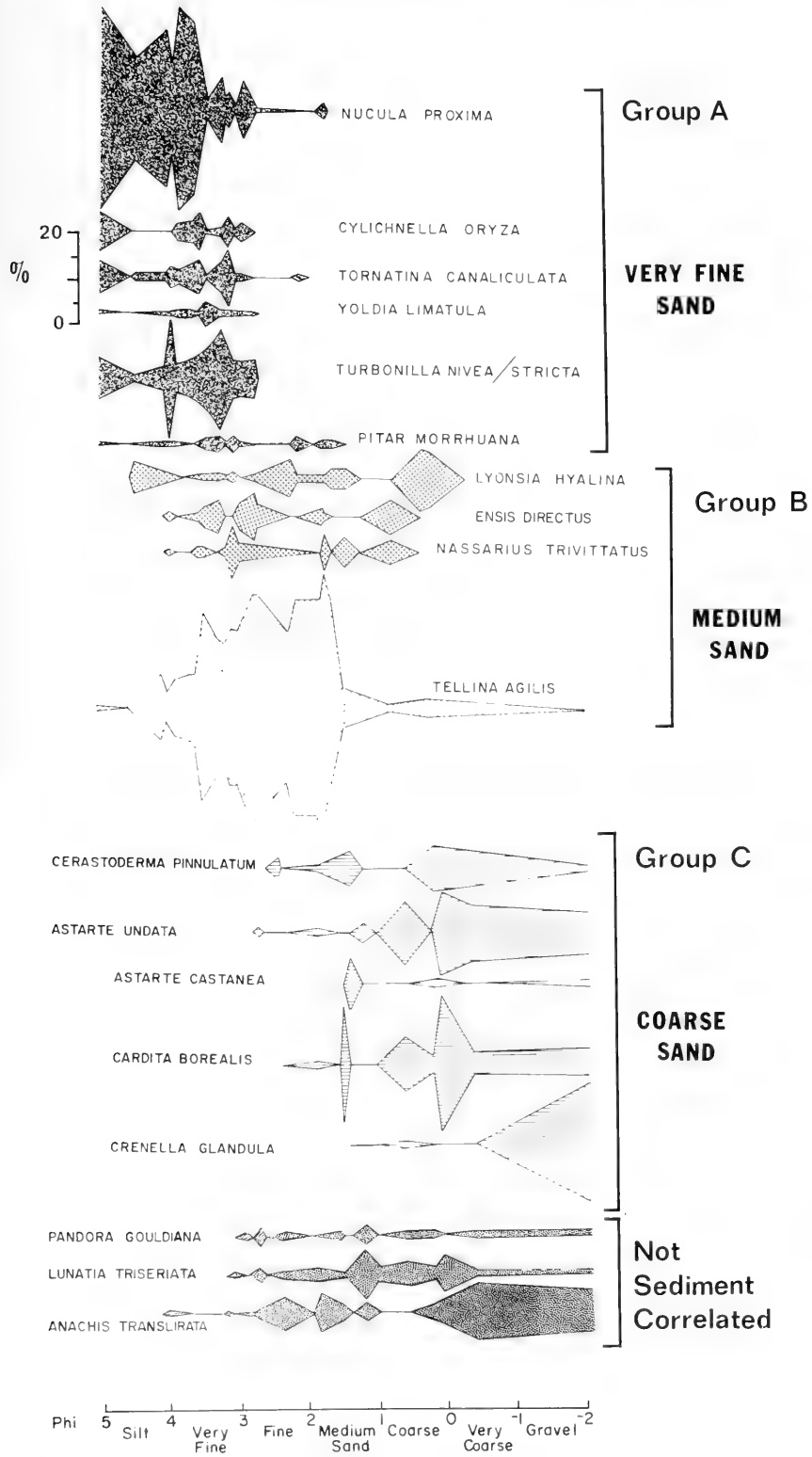

FIG. 6. Relative abundance of the 18 most common species in relation to the sediment texture gradient. The upper 6 species are characteristic of group A stations (very fine sand); the following 4 species are more characteristic of fine to medium sand (Group B); the next 5 species occur in coarse to very coarse sediments (Group C); the last 3 species are widely distributed in all but the finest sands. Thickness of the abundance polygons is proportional to the percentage contribution of the species to the total fauna at a series of stations encompassing the total sediment gradient.

TABLE 2. Regressions of Species Diversity (H′) as a function of 3 diversity components: Species Richness (SR), Evenness (J), Dominance (D).

		r	p
Species Richness			
August	H′ = 0.923 + 0.112 (SR)	0.714	0.001
January	H′ = 0.801 + 0.171 (SR)	0.790	0.001
Combined	H′ = 1.039 + 0.124 (SR)	0.659	0.01
Evenness			
August	H′ = 0.011 + 3.395 (J)	0.730	0.001
January	H′ = −0.374 + 3.786 (J)	0.766	0.001
Combined	H′ = −0.059 + 3.440 (J)	0.769	0.001
Dominance			
August	H′ = 5.029 − 0.041 (D)	−0.946	0.001
January	H′ = 4.783 − 0.038 (D)	−0.938	0.001
Combined	H′ = 4.847 − 0.039 (D)	−0.944	0.001

by a distinct decline in SR at most stations between August 1972 and the following January.

In addition to seasonal changes in SR, there were also important shifts in dominance. However, these seasonal changes do not occur across the entire sediment spectrum. Seasonal changes in diversity are summarized in Table 3 in which data for all stations within a group have been pooled. In interpreting this table, it is important to remember that both H′ and J are derived values, i.e. both are based on the relative importance of the 2 independent correlates SR and D. Evenness (J) is strongly correlated inversely with dominance (D). It is evident that diversity as measured by H′ is higher in coarse sand habitats (Group C) than in finer sediments (Groups B and A) and that this is primarily a reflection of reduced dominance in these collections. Neither H′ nor D undergo significant seasonal shifts in Group C although a very small, though statistically significant, shift in J is evident.

Seasonal shifts in diversity (H′) in the medium sand stations (Group B) are primarily effected by changes in dominance of a single species, *Tellina agilis*, with resulting effects on the evenness component (J). Seasonal changes in SR are not statistically significant.

In the fine sand habitats comprising Group A we find little seasonal variation. Thus, changes in H′ and D between August and January are not statistically significant although significant but rather small shifts do occur in J and SR.

It is evident from these data that diversity in FIS is predominantly a function of dominance. Therefore, an attempt to clarify sediment-diversity relationships in this study is essentially an inquiry into the role of sediment texture in affecting community dominance. The complicating factors in these relationships include the fact that 2 species contribute to high dominance; both occur at different places along the sediment spectrum; and both are independent of each other with regard to seasonal changes. As a consequence, correlation matrices generated to determine the correlation between the various components of diversity and sediment texture yield few significant results. This problem was partially overcome by dividing the entire sediment spectrum into 2 parts: fine to medium sands (Dice Groups A and B); coarse to very coarse sands (Dice groups C and D). Table 4 summarizes those statistically significant sediment-diversity correlations which resulted from these correlation matrices.

Only those sediment-diversity cor-

TABLE 3. Seasonal group diversity patterns. The 3 groups are based on Dice similarity coefficient cluster analysis.

		AUGUST			JANUARY	
		n	Mean ± s.d.	P*	n	Mean ± s.d.
GROUP A FINE SAND	Diversity (H′)	9	2.31 0.27	NS	9	2.46 0.57
	Dominance		70.61 6.29	NS		62.80 12.84
	Evenness (J′)		0.61 0.07	0.05		0.74 0.12
	Species Richness		13.67 1.89	0.05		11.00 2.54
GROUP B MEDIUM SAND	Diversity (H′)	3	1.83 0.24	0.05	4	3.02 0.44
	Dominance		77.15 5.38	0.05		49.62 13.83
	Evenness (J′)		0.59 0.04	0.05		0.82 0.05
	Species Richness		8.67 1.25	NS		12.75 2.95
GROUP C COARSE SAND	Diversity (H′)	5	2.93 0.57	NS	6	3.03 0.15
	Dominance		50.08 14.44	NS		45.64 5.35
	Evenness (J′)		0.76 0.11	<0.1		0.88 0.05
	Species Richness		13.40 3.26	NS		10.83 0.90

*Significance values based on t-tests comparing January and August means.
NS = not significant at p = 0.05 level.

TABLE 4. Statistically significant sediment-diversity correlations (P = 0.05).

	August	January
Fine to medium sand (groups A & B)[1]		
Median sediment particle size: H′	(0.539)[2]	−0.570
Median sediment particle size: SR	0.767	(−0.392)
Percent silt-clay: D	(−0.171)	0.550
Percent silt-clay: H′	−0.558	(0.391)
Percent gravel: SR	−0.678	(0.246)
Coarse to very coarse sand (groups C & D)[1]		
Median sediment particle size: D	0.685	(−0.292)
Median sediment particle size: H′	−0.637	(0.247)
Percent gravel: SR	0.810	(0.309)

[1]Station designations based on Dice coefficient cluster analysis.
[2]( ) = not significant at p = 0.05.

relations which were significant at the P = 0.5 level in either August or January are included in Table 4. If a significant correlation occurred in only 1 month, e.g. August, the coefficient of correlation is also listed for the other month, January, but in parenthesis, thus indicating the absence of a significant correlation. Also, in interpreting Table 4, it is necessary to recall that median sediment particle size (MPS) is expressed in phi (Ø) units, i.e. increasing Ø denotes decreasing sediment particle size. Note that in fine to medium sand (Groups A and B), there were no significant correlations between H′ and either MPS or percent silt-clay (PSC) in August. However, by January, we find that H′ declines significantly with decreasing particle size (increasing Ø), and increasing PSC. Likewise, there is no correlation between dominance (D) and PSC in August, but in January D increases significantly with increasing PSC. These shifts are explained by the sharp decline in the abundance of *Tellina* which occurred between August and January. The significant correlations between gravel content (PGR) and decreasing diversity (H′ and SR) which occur in August disappear in January, and their explanation is problematic.

In coarse sands (Groups C and D), H′ decreased in August with decreasing particle size (increasing Ø) while D increased. However, these same correlations are not statistically significant in January, again suggesting that *Tellina* played a controlling role in these shifts. There is an indication in Table 4 that SR responds differently to increased gravel content in finer sediments as compared with coarser sediments. The positive correlation between increasing gravel and SR in coarse sand suggests that increasing gravel content is salutary to the survival of the predominantly epifaunal species occurring in these areas. On the other hand, in fine sediments, increasing gravel has no positive importance to the predominantly deposit-feeding species present, and may indeed be a correlate of other environmental factors detrimental to such species. Thus, SR is negatively correlated with PGR in Groups A and B in August (no significant correlation in January).

DISCUSSION

The bottom sediments of Fishers Island Sound are predominantly sandy but with a gradient ranging from very fine sand with high proportions of silt and clay at 1 extreme to coarse sand mixed with gravel at the other. The results of the Q-mode cluster analysis of stations encompassing this gradient indicate the existence of several groups of stations which are correlated with sediment texture. These groups are identified on the basis of similarity in species composition and are considered to be operational communities for the purposes of this analysis. However, groups of stations generated by a cluster analysis do not prove the existence of discrete communities along a sediment gradient. Evidence to support the identity of such groups as communities would include: a) the recurrence of such groups at other locations under comparable environmental and zoogeographical conditions; b) the demonstration of community boundaries along gradual environmental gradients; c) the characterization of such communities on the basis of recurring patterns of diversity and trophic structure.

Of the operational communities defined in the present study, Group A comes closest

to fulfilling these criteria. The degree of association between stations comprising Group A and the molluscan component of the *Nucula/Nephthys/Yoldia* (N/N/Y) community in Buzzards Bay (Station R; Sanders, 1960) is indicated in Table 5. Group A stations are compared individually with Station R using the PS similarity coefficient. The stations in column 1 are then ranked by the degree of association with Buzzards Bay. The stations of group A most similar to Buzzards Bay have PS values of 68% which are comparable to within-habitat values reported by Sanders. Table 5 also shows, however, that this ranking of stations is highly correlated with increasing mean particle size of sediments.

Kendall's coefficient of rank correlation, calculated for all seasons separately, indicates a significant correlation linking the decline in *Nucula* abundance with increasing sediment particle size and decreasing % silt-clay. Both parameters correlated equally well with *Nucula* importance (June: % silt-clay, Tau = 0.600, $P = \angle 0.01$, n = 6; mean particle size, Tau = 0.600, $P = \angle 0.01$, n = 6; August: % silt-clay, Tau = 0.611, $P = \angle 0.01$, n = 9; mean particle size, Tau = 0.722, $P = \angle 0.01$, n = 6; January: % silt-clay, Tau = 0.441, $P = \angle 0.05$, n = 9; mean particle size, Tau = 0.555, $P = \angle 0.01$, n = 9). Thus, these data show that although the species composition of group A stations is virtually identical to the *Nucula/Nephthys/Yoldia* community, quantitative differences exist which are correlated with sediment texture within this habitat. *Nucula* declines with increasing sediment particle size, and *Tellina* increases.

As noted above, the stations comprising Group B are associated with fine to medium sand. The faunal composition of these stations is quite variable although characterized by several siphonate species including *Tellina agilis, Ensis directus, Lyonsia hyalina* and *Nassarius trivittatus*. It is evident that group B partially overlaps the "sand bottom" community described by Sanders (1958). All of the molluscan species reported by Sanders for Buzzards Bay also occur at group B stations except *Nucula delphinodonta, Laevicardium mortoni* and *Natica pusilla*. Likewise, the sediments of the Buzzards Bay stations overlap Group B although the silt-clay values in Buzzards Bay tend to be higher.

In FIS, in sediments below 2 phi (greater than 0.250 mm median particle size) the species composition of mollusks gradually shifts toward a coarse sand association consisting of a set of characteristic species including *Cerastoderma pinnulatum, Astarte undata, A. castanea, Cardita borealis* and *Crenella glandula*. (Appendix 4 Group C). No sharp boundaries separate the medium and coarse sand associations. Several medium sand species such as *Tellina* and *Lyonsia* occur also in somewhat coarser sediments; and some of the coarse-sand species such as *Cerastoderma* and *A. undata* may occasionally occur in medium to fine sand. The habitat of Group C occurs in areas of rapid tidal currents. The fauna consists primarily of epibenthic species such as *Mytilus, Modiolus* and *Anachis* as well as short-siphoned or non-siphonate suspension feeders such as *Astarte* spp., *Cardita, Crenella* and *Crassinella*.

TABLE 5. Group A stations ranked by association with Station R, Buzzards Bay (PS)

Station	PS*	Mean particle size (phi)
C June	67.7	5.47
C Aug.	67.6	4.73
11 Aug.	59.4	4.59
B Aug.	59.2	4.32
Z3 Aug.	49.7	4.57
13 Aug.	43.3	4.10
Z3 June	31.7	4.46
B June	30.8	4.19
E June	29.8	3.33
12 Aug.	28.6	3.16
4 June	19.6	3.22
4 Aug.	14.1	3.32
14 Aug.	10.0	3.10
7 June	9.9	4.27
10 Aug.	9.4	3.96

Kendall's coefficient of rank correlation: Tau = 0.676, ts = 3.52, Prob. of occurrence by chance alone = 0.0005.
*FIS stations ranked in order of decreasing similarity (PS) to Buzzards Bay, Sta. R.
PS = similarity coefficient.

I conclude that although gradual changes in faunal composition occur in conjunction with gradual sedimentary gradients, an ecologically reasonable, if arbitrary, classification of the faunal gradient into operational associations of species is possible. These associations are not perceived as defining communities with rigid, non-overlapping boundaries, but rather as contiguous but overlapping assemblages designated as "very fine sand," "medium sand" and "coarse sand" associations. These will probably recur in the northwest Atlantic

where comparable sedimentary and hydrographic conditions prevail but confirmation of the validity of this prediction must await future research in this area.

Driscoll & Brandon (1973) present evidence for the existence in Buzzards Bay of 3 "fine-grained" species associations (biofacies) which they consider as subdivisions of the *Nucula/Nephthys* community. Two of these ("offshore" and "nearshore") facies occur in sediments of very fine sand and fine sand, respectively, and their fauna is very similar to that of FIS in comparable sediments. However, a remarkable and unexplained feature of these locations is the near complete absence of *Nucula proxima* in spite of mean silt-clay concentrations of about 32% for both facies. In FIS, such silt-clay levels occur in locations with mean particle sizes of 3.5 phi or greater, and *Nucula* is abundant. A 3rd association of mollusks reported by Driscoll & Brandon was designated the "open bay" facies and occurs in sediments of generally medium to coarse sands. This was considered to be analogous to Sanders' *Ampelisca* assemblage. The authors note the absence of selective deposit feeders, which is true also in the present study at comparable sediment textures. Likewise, there is a general correlation between the mollusks present in FIS and Buzzards Bay in similar sediments although several important species in FIS are not included in Buzzards Bay. These include *Astarte undata, A. castanea* and *Cardita borealis.* A most remarkable difference is the absence from Driscoll's assemblage of the ubiquitous *Tellina agilis*, a species found at virtually all sites in FIS. The total sediment gradient reported by these authors is smaller than at FIS, and their fine-grained biofacies are interpretable as occurring in the zone of overlap between the very fine sand and fine sand associations of FIS (Groups A and B). Likewise, their "open bay" facies occurs in the zone of overlap between the medium and coarse sand assemblages in FIS (Groups B and C).

Patterns of diversity observed in FIS strongly emphasize the role of dominance (D). Since D is highly correlated in a reciprocal way with J ($r = -0.83$ in August; -0.71 in January), H′ is predominantly a function of evenness. The 2 species of importance as dominants were *Nucula proxima* and *Tellina agilis*. The sediment ranges of these species broadly overlap but as noted above, *Nucula* is most abundant in the finest sediments and declines in importance as sediments become coarser and the silt-clay component decreases. *Tellina*, on the other hand, becomes increasingly dominant as the sediment texture shifts from predominantly silty sand to medium sand. In coarser sediments, *Tellina* also decreases. Although *Nucula* is evidently dominant in appropriate sediments throughout the year, *Tellina* underwent a sharp decline in abundance between August and January.

In fine to medium sands (Groups A and B) the seasonal dominance by *Tellina* was the controlling factor affecting the evenness component of diversity. In August, high *Tellina* dominance particularly in the medium sand portion of the spectrum counter-balanced the "permanent" dominance of *Nucula* in fine to very fine sediments. Consequently, there were no significant correlations between sediment texture and diversity since a high degree of dominance by 1 species or the other was present over the entire sediment spectrum. In January, however, with the natural disappearance of most of the *Tellina* juveniles present in August, the role of *Nucula* as the dominant species in the finer sediments became evident in the sediment-diversity correlations (Table 4), and H′ did increase with increasing sediment particle size (and decreasing silt-clay content). In other words, the role of *Nucula* in affecting diversity was effectively masked in August by the temporary abundance of *Tellina*.

In the coarse sediments (Groups C and D), *Tellina* played an equally important role. In August, the strong correlations between decreasing sediment particle size and decreasing H′ were due primarily to dominance by *Tellina* in the medium sand portion of the sediment spectrum. With the decline of *Tellina* in January, there correlations became statistically insignificant.

These data, as well as Table 3, imply that the major seasonal changes affecting diversity occur in the medium sand portion of the sediment gradient, and that at the extremes of the sediment continuum, i.e. silty-sands and gravelly sands, diversity is less variable.

In addition to its effects on diversity, the superdominance by *Tellina* significantly reduced the usefulness of the PS similarity coefficient in discriminating between some pairs of stations because the percentage

overlap between stations due to *Tellina* alone masked underlying differences in species composition. The parallel use of a binomial coefficient such as the Dice coefficient was helpful in this study in assaying these affects.

The consistent dominance of bottom assemblages occurring in very fine sediments by species such as *Nucula* or *Yoldia* is a phenomenon of considerable ecological interest. Why are aggregations of species in such sediments more likely to be dominated by 1 or 2 species than aggregations in coarser bottoms? Sanders (1958) noted that this tendency is brought about in part by trophic relationships. Benthic animals which feed on very small particles of detritus occur most abundantly in areas where these particles (silts, clays, organic material, bacteria) are most abundant. Such animals include deposit-feeders as well as some suspension-feeders. Mud sediments accumulate in places where sluggish currents allow the deposition of fine sediment particles. Thus, the existence of such a habitat implies a degree of environmental stability. Levinton (1972) has argued that the deposit-feeding communities which occur in such habitats are highly buffered and that their food supply is predictable. He concludes that "species structures due to competitive interactions should be important in deposit-feeding communities" because food will be a limiting factor which will result in competition. Presumably these evolutionary processes would result in increased diversity. Yet apparently this has not occurred. Rather, such communities are usually highly dominated by a relatively few abundant deposit-feeding species and the diversity is consequently lower than in coarser sediments (Sanders, 1960).

In spite of the apparent stability of currents and food supply, thermal variability remains a severe factor in all inshore habitats (Sanders, 1958) and this environmental instability can be expected to depress the evolutionary processes which could increase diversity. Another factor having the same effect is the homogeneity of very fine sediments as compared with coarser sediments. Competition among deposit-feeding species, which would produce a subdivision of the available energy resource (niche differentiation), can be expected to proceed more slowly where the resource to be divided is very homogeneous.

Diversity within a community can only be increased by the addition of more species, or by a shift in the relative abundances of species to induce greater evenness. In boreal and temperate mud communities, however, the sources of potential competitors are limited. The richer protobranch fauna present in deeper waters has not colonized inshore sediments, perhaps because of the thermal instability noted above. This leaves only the fauna of inshore suspension feeders as a source of potential competitors but there is probably a limited selective advantage for such species to move down the sediment gradient from medium or fine sand into mud. Neither food nor space is likely to be limiting to infaunal suspension feeders. Furthermore, the negative effects of the activities of deposit-feeders (Rhoads & Young, 1970) can also be expected to have a depressing effect on the colonization of mud by suspension feeders. Thus, the great dominance of inshore mud communities by a few deposit-feeders results from homogeneity of the energy resource (very fine sediment rich in organic materials), a reduced pool of potential competitors, and a severe thermal environment. In spite of the apparent stability of the environment in terms of food resources and currents, the species structure is reminiscent of stress environments in which a few abundant species dominate the community. This is not to imply that suspension feeders are incapable of adapting to mud. The existence of such adaptations are well documented (e.g. by Stanley, 1970). Rather, the selective benefits accruing to suspension feeders are likely to be offset by the evolutionary costs of doing so in an environment of severe thermal instability.

In FIS, communities occurring in coarse sediments (Group C) are characterized by lower dominance, greater evenness and higher H′ than in fine sediments (Table 3). In considering the factors which interact to affect evenness in coarser sediments, it is useful to distinguish between infaunal (usually siphonate) suspension feeders and epifaunal or shallow infaunal (usually non-siphonate or short siphonate) suspension feeders. The former occur in fine to medium sand and their life modes depend on the ability to burrow below the surface of the sand. The latter species may burrow or may be entirely epifaunal but if burrowing occurs, the animals must have the mobility

to maintain contact with the overlying water in the face of potentially shifting sediments. Infaunal sand dwellers are perhaps more protected from casual (i.e. nonspecialized) predators. Such species must, however, be well adapted for maintaining position below the sediment surface while feeding. Thus, a capacity for rapid vertical movement may be more important than the capacity for horizontal mobility. Furthermore, such species must have the capacity to suspension-feed in sands with at least 5-15% silt/clay. Epifaunal and shallow infaunal, short-siphonate species, on the other hand, have little or no problem with silts and clays but are more exposed by their position to predation, and must be well adapted for maintaining position in the face of strong water currents. Further, their relationships to sediment may require larger sediment particles for attachment.

Levinton (1972) has speculated that the seasonal variation in abundance of many suspension-feeding bivalves living in sandy sediments is caused by seasonal variability (and hence unpredictability) in the phytoplanktonic food source, and that these animals have evolved means of rapidly increasing their numbers in response to periods of food abundance. The resulting "explosion" would be evidenced by increased dominance of the sand-bottom community by such species. In FIS, the phenomenon of superdominance was observed to occur in medium sand sediments in the summer of 1972 involving *Tellina agilis*. While the cause of this is unclear, Levinton's argument that food supply is the root cause is unsatisfactory. In the first place, no remarkable explosions in abundance of other suspension or deposit-feeding species were observed. Moreover, while it is clear that phytoplankton production is seasonally variable, it is less clear that this leads to great instability since the periods of maximal abundance and scarcity occur with considerable predictability. For example, the oyster *Crassostrea virginica* is a suspension-feeding bivalve cited by Levinton as an example of enormous year to year fluctuations in larval settlement. Yet, in the substantial literature devoted to oysters, there are no data indicating that this phenomenon is due to fluctuations in food supply of adults or larvae. It seems more likely to me that the explanations for this phenomenon are to be found in the environmental factors affecting survival of larval and post-larval stages, particularly predation and the random removal and destruction of larvae and spat by physical factors.

SUMMARY

1. The distribution of sublittoral benthic Mollusca was studied in Fishers Island Sound (NE Long Island Sound). A Q-mode cluster analysis of the stations encompassing a sediment gradient from very fine through very coarse sand was carried out at 3 seasons, late Spring, late Summer and late Winter, using 2 similarity coefficients (Percentage of Similarity and Dice).

2. Based on similarity analysis of Mollusca among stations, groups of stations generated by the cluster analysis were correlated with sediment texture. Three of 4 cluster groups (A-C) replace each other along the sediment gradient as follows: Group A, very fine sand and silt/clay levels from 10-60%; Group B, fine to medium sand and silt/clay levels of 5-15%; Group C, coarse to very coarse sand with silt/clay levels less than 10%. A fourth group of stations (D) occurred in fine to coarse sand at silt/clay levels of less than 5%.

3. The above groups of stations, with their characteristic fauna are considered as operational communities. Group A is virtually identical to the *Nucula/Nephthys/Yoldia* community described by Sanders (1956, 1958, 1960); Group B is similar to the sand-bottom community described by Sanders (1958); Group C is a hitherto uncharacterized association of predominantly short or non-siphonate suspension feeders occurring in coarse to very coarse sand. Group D stations occur in areas of severe tidal surge and have very few species. *Spisula*, however, occurs in such areas.

4. Diversity as measured by H′ and J′ is higher in coarser sand than in the very fine sediments, and these differences are primarily due to differences in community dominance. At intermediate sediment textures, seasonal variability in dominance brings about large seasonal changes in J′ and H′. Much of this fluctuation is accounted for by a single species, *Tellina agilis*. Species Richness is similar in very coarse and very fine sands, but varies seasonally, particularly in fine to medium textured sediments.

5. It is suggested that the low evenness

and high dominance observed in very fine sands and silts may reflect the homogeneity of the primary energy resource (organic matter), the reduced pool of potential competitors, and the severe thermal environment. The relative roles of these factors need to be determined by further research.

6. In evaluating the cause for increased evenness and decreased dominance in coarse sediments, a distinction is drawn between predominantly infaunal siphonate suspension feeders which prevail in fine to medium sand, and the predominantly non-siphonate or short-siphonate suspension-feeders which prevail in coarse sand. Selective pressures are quite different.

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APPENDIX 1. Sediment parameters (phi values)—June, 1972.

Station	Mean	Median	% Clay	% Silt-clay	% Sand	% Gravel	Sorting*	Skewness
1	1.27	2.28	4.2	5.9	89.2	5.4	1.34	FS
4	3.22	3.23	6.7	11.7	87.6	0.8	1.39	FS
5	0.19	0.30	3.0	4.1	72.7	23.1	1.73	NS
6	0.09	1.53	2.5	3.0	84.1	12.4	1.85	CS
7	4.27	3.47	13.5	33.4	65.9	0.7	2.47	FS
B	4.19	3.60	10.4	31.1	68.7	0.1	1.69	FS
C	5.47	4.97	19.6	64.2	35.6	0.2	2.28	FS
E	3.33	3.27	7.5	14.0	86.0	0	1.18	SFS
F	0.30	1.47	9.3	12.0	59.0	29.3	3.89	CS
G	0.47	1.33	4.9	6.4	63.4	30.7	2.97	CS
Y	1.69	3.12	10.3	17.3	62.8	20.1	3.76	CS
Z3	4.46	4.04	11.0	50.6	49.4	0	1.67	FS

*Inclusive graphic standard deviation (σ I).
Symbols: CS = coarse skewed; FS = fine skewed; NS = nearly symmetrical; SCS = strongly coarse skewed; SFS = strongly fine skewed.

APPENDIX 2. Sediment parameters (phi values)—August, 1972. Skewness symbols as for Appendix 1.

Station	Mean	Median	% Clay	% Silt-clay	% Sand	% Gravel	Sorting	Skewness
1	0.10	1.66	2.0	2.6	72.0	25.4	2.75	SCS
4	3.32	3.29	6.1	15.1	84.5	0.5	1.24	SFS
5	0.49	0.85	3.6	5.2	74.7	20.1	1.90	NS
6	1.67	1.77	2.6	3.3	94.1	2.6	0.86	CS
7	2.55	2.84	6.3	15.7	83.3	0.9	2.05	CS
8	0.97	0.42	3.4	7.1	85.2	7.7	1.92	SFS
9	0.03	1.48	3.0	3.8	70.9	25.3	2.44	SCS
10	3.96	3.47	8.7	20.7	79.2	0.1	1.35	SFS
11	4.59	3.63	12.0	36.7	63.3	0	1.72	SFS
12	3.16	3.03	5.8	11.4	88.5	0.1	1.34	SFS
13	4.10	3.60	5.2	27.8	72.1	0.1	1.48	SFS
14	3.10	3.14	3.8	7.1	92.8	0	0.74	FS
15	1.62	1.72	0.4	1.8	96.1	2.0	0.82	CS
16	1.83	2.00	2.2	2.4	34.4	63.1	2.20	SCS
17	0.42	0.24	2.5	4.0	60.3	35.6	1.94	CS
18	2.49	2.55	1.8	1.9	97.8	0.2	0.50	SCS
B	4.32	3.69	11.2	35.7	64.4	0	1.74	SFS
C	4.73	3.87	13.6	42.2	57.8	0	2.01	SFS
E	2.86	2.83	4.3	8.2	89.2	2.6	1.07	FS
F	2.12	2.25	3.9	6.9	86.4	6.7	1.62	CS
Y	1.59	1.85	4.0	6.9	82.6	10.5	2.09	CS
Z3	4.57	4.09	10.5	51.2	48.7	0.1	1.58	SFS

APPENDIX 3. Sediment parameters (phi values)—January, 1973. Skewness symbols as for Appendix 1.

Station	Mean	Median	% Clay	% Silt-clay	% Sand	% Gravel	Sorting	Skewness
1	1.36	1.38	2.8	4.9	87.3	7.8	1.40	NS
4	3.12	2.98	5.4	12.8	87.2	0	1.23	SFS
5	0.37	0.53	2.5	4.2	74.6	21.2	1.76	NS
6	1.72	1.86	2.7	4.0	91.6	4.4	1.00	CS
7	2.65	2.69	6.5	18.5	79.6	1.9	2.28	FS
8	0.07	0.76	3.9	9.6	44.8	45.6	3.64	CS
9	1.10	1.81	5.4	11.3	67.5	21.2	3.06	CS
10	3.82	3.41	8.1	20.4	78.4	1.2	1.42	SFS
11	3.88	3.43	8.2	26.3	73.4	0.3	1.75	SFS
12	3.95	3.44	7.9	24.2	75.8	0	1.49	SFS
13	4.36	3.86	10.1	42.8	57.2	0	1.63	SFS
14	1.50	1.54	2.3	3.9	92.2	3.8	0.99	NS
15	0.33	0.55	1.0	1.1	67.3	31.5	2.12	SCS
16	0.91	1.13	2.4	3.4	44.9	51.7	2.26	SCS
17	1.37	1.67	1.8	2.8	37.0	60.1	2.11	SCS
18	1.51	1.33	1.5	2.1	92.0	6.0	1.19	NS
B	3.81	3.41	7.6	21.4	78.7	0	1.41	SFS
C	4.64	3.87	12.4	42.1	57.9	0	1.79	SFS
E	2.74	2.73	3.7	6.5	93.5	0	0.83	FS
F	1.37	1.56	2.3	3.7	89.0	7.2	1.38	CS
Y	1.96	2.06	3.6	7.1	86.7	6.1	1.89	NS
Z3	1.50	2.82	2.9	0.6	75.8	20.6	2.41	SCS

APPENDIX 5. Components of species diversity.

AUGUST Station	H′	J	D	SR
C	2.09	0.56	75.1	13
B	2.25	0.63	69.4	12
11	2.22	0.62	72.8	12
13	2.41	0.63	73.1	14
10	1.78	0.46	84.0	15
4	2.23	0.60	68.7	13
14	2.49	0.62	66.9	16
12	2.57	0.74	61.4	11
7	1.77	0.56	78.5	9
E	1.84	0.61	75.4	8
Z3	2.76	0.67	64.0	17
16	3.23	0.77	50.0	18
Y	2.16	0.65	70.0	10
6	1.28	0.46	88.4	7
1	1.04	0.37	90.2	7
9	1.57	0.56	83.0	7
5	3.16	0.85	37.5	13
8	2.90	0.78	52.7	13
17	3.50	0.90	34.8	15
18	1.45	0.78	82.3	4
15	2.02	0.87	64.3	5
F	Not sampled			

JANUARY Station	H′	J	D	SR
C	1.93	0.64	74.8	8
B	2.28	0.67	44.8	10
11	1.50	0.47	83.8	9
13	2.58	0.78	61.1	10
10	3.23	0.79	44.8	17
4	2.90	0.81	51.7	12
14	3.53	0.86	39.2	17
12	1.82	0.87	77.2	10
7	2.79	0.75	59.3	13
E	3.08	0.93	48.1	10
Z3	Not sampled			
16	2.97	0.89	40.5	10
Y	2.70	0.81	56.5	10
6	2.90	0.81	50.0	12
1	2.49	0.75	68.7	10
9	3.19	0.96	44.0	10
5	2.84	0.85	51.6	10
8	3.03	0.84	50.0	12
17	3.25	0.94	37.5	11
18	0.85	0.42	94.6	4
15	1.75	0.87	77.7	4
F	3.36	0.88	34.0	14

APPENDIX 4. Species composition. Groups A-D (excluding rare species).

Species	GROUP A June	Aug.	Jan.	Total	%	GROUP B June	Aug.	Jan.	Total	%	GROUP C June	Aug.	Jan.	Total	%	GROUP D June	Aug.	Jan.	Total	%
Tellina agilis	95	657	159	911	24.8	25	128	41	194	48.4	6	17	23	46	8.9		91	1	92	50.5
Nucula proxima	277	600	274	1151	31.4		4	5	9	2.2				1	0.2					
Turbonilla (n/s)	161	142	316	619	16.9	6	10		16	4.0	1	4		5	1.0					
Tornatina canaliculata	76	57	104	237	6.5															
Solemya velum	31	47	41	119	3.2	6		2	8	2.0		2		2	0.4		4		4	2.2
Mysella planulata	15	3	4	22	0.6											1			1	0.5
Cylichnella oryza	69	51	22	142	3.9															
Lyonsia hyalina	20	17	1	38	1.0	4	5	11	20	5.0	6	10	20	36	6.9	2	4		6	3.3
Mitrella lunata	5	13	38	56	1.5	2	3	4	9	2.2		27	15	42	8.0			3	3	1.6
Ensis directus	8	45	7	60	1.6		15	9	24	6.0	1	8		9	1.7		1		1	0.5
Astarte undata						1	6	9	16	4.0	12	29	27	68	13.1		2		2	1.0
Anachis translirata	3	5	2	10	0.3	2	2	22	26	6.5	3	23	11	37	7.1	1		1	2	1.0
Nassarius trivittatus	8	16	23	47	1.3	6	4	1	11	2.7	3	3	7	13	2.5		6		6	3.3
Cardita borealis								9	9	2.2	20	22	20	62	11.9					
Turbonilla interrupta	17	19		36	1.0	2			2	0.5	5			5	1.0	1			1	0.5
Pitar morrhuana	12	21	8	41	1.1		1	10	11	2.7			1	1	0.2		1		1	0.5
Spisula solidissima			1	1	0.1	1		1	2	0.5		1	6	7	1.3		2	35	37	20.3
Yoldia limatula	20	25	6	51	1.4		1		1	0.2										
Lunatia triseriata	2	5	1	8	0.2		1	13	14	3.4	8	5	5	18	3.5		1	35	2	1.0
Crenella decussata												37	1	38	7.3					
Cerastoderma pinnulatum							2	5	7	1.7		15	9	24	4.6		3		3	1.6
Mytilus edulis		6		6	0.2							5	6	12	2.3	19			19	10.4
Macoma tenta	2	7	1	10	0.3							13	2	15	2.9		3		3	1.6
Pandora gouldiana	1		5	6	0.2	2	1	2	5	1.2	3	5	9	17	3.3					
Mercenaria mercenaria	1	5	13	19	0.5	1			1	0.2			3	3	0.6					
Musculus discors		1		1	0.1		5		5	1.2		10	10	20	3.8					
Aligena elevata	3	18	1	22	0.6			1	1	0.2										
Petricola pholadiformis		1	6	7	0.2	2		3	5	1.2	1		3	4	0.8					
Mulinia lateralis	5	5	5	15	0.4															
Astarte castanea												3	2	5	1.0		6	2	8	4.4
Nucula delphinodonta	12	10		22	0.6															
Crassinella mactracea												7	4	11	2.1					
Modiolus modiolus												8	1	9	1.7					
Urosalpinx cinerea			5	5	0.1			2	2	0.5		2	1	3	0.6		1		1	0.5
Eupleura caudata	1		2	3	0.1	1	1	1	3	0.7	1			1	0.2					
Hiatella arctica												5		5	1.0					
				3665					401					519					182	

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VERTICAL DISTRIBUTION AND BURROWING BEHAVIOR OF THE FINGERNAIL CLAM, *SPHAERIUM TRANSVERSUM*[1]

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ABSTRACT

Small fingernail clams, *Sphaerium transversum* (Say), occurred as deep as 16 cm in the substrate in Pool 19 of the Mississippi River; clams over 3.0 mm long occurred only in the upper 2.6 cm of substrate. Penetration was deepest in soft clayey silt and shallowest in coarse sand. At Lake Texoma, Oklahoma, newborn *S. transversum* were placed in plastic tubes containing a substrate and allowed to burrow under various experimental conditions.

In these experiments, newborn clams burrowed to a maximum depth of 24 cm in sandy-mud (85% sand) and to 11 cm in mud. Some newborn clams burrowed 6 cm deep in mud in 12 hours but burrowing continued for 24 to 48 hours. Clams reburrowed after being brought to the substrate surface. Clam density seemed to have no effect on depth of clam burrowing. Clams born in a pan of lake water burrowed deeper than clams born in the substrate.

Newborn clams that burrow may enter a "resting-state." Maintenance of a segment of the clam population deep in the substrate may prevent excessive losses during periods of heavy predation, disease or unfavorable water conditions.

INTRODUCTION

Fingernail clams are frequently abundant in benthic freshwater communities and are important in the aquatic food web. In Pool 19 of the Mississippi River, in extreme southeastern Iowa (91° 23'W, 40° 33'N), *Sphaerium transversum* (Say) is important in the diets of diving ducks (Thompson, 1973), fish (Jude, 1968; Ranthum, 1969) and leeches (Gale, 1973). Few, if any, freshwater areas in the Mississippi flyway are as heavily used by lesser scaup (*Aythya affinis*) as is Pool 19, and abundance of fingernail clams in Pool 19 (Gale, 1969) may be one of the reasons. Thompson (1973) observed hundreds of thousands of lesser scaup using Pool 19 twice yearly; food studies indicated that scaup fed almost entirely on *S. transversum*.

Little has been published on the vertical distribution of fingernail clams in substrates. Gilmore (1917) stated that *S. simile* buries itself 2.5 cm or more below the substrate surface, but he did not elaborate. Rawson (1930) found nearly all benthic organisms in the upper 2 cm of substrate in Lake Simcoe, but it is not clear whether *Pisidium* and *Sphaerium* were present in the samples. In Selenter Lake, Lenz (1931) found *Pisidium* sp. from 10 to 12 cm below the substrate surface, with greatest density between 4 and 6 cm. Cole (1953) mentioned only 1 small *Sphaerium* sp. 3 to 4 cm below the substrate surface in Douglas Lake. In laboratory experiments, Meier-Brook (1969) found that 2 of 3 species of *Pisidium* lived below the substrate surface. He did not indicate the depth of burrowing, but pointed out that the clams burrowed into the substrate dorsal side down.

The objectives of my study were (1) to describe vertical distribution of *S. trans-*

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versum in Pool 19 of the Mississippi River and (2) further to investigate its burrowing behavior with laboratory experiments.

PROCEDURES

Samples for the study of vertical distribution of clams in Pool 19 were collected with a frozen-core sampler (Shapiro, 1958). In July 1967, 8 cores were collected at 7 sampling stations (described by Gale, 1969: 9-15). After examination of these cores revealed a need for additional samples from clay-silt substrates, 4 additional cores were collected within enclosures which prevented vertebrate predation (Gale, 1969: 155-165). Two more samples were taken at transect 3, station 6, in October 1968 to determine if vertical distribution in fall 1968 was similar to that observed in summer 1967. No differences in vertical distribution were detected in these 2 samples.

Cores, 3.18 cm in diameter and 8-20 cm long, were frozen *in situ*, removed from the river and taken frozen to the laboratory. Before examination, the tubes were rinsed with hot water, and the frozen substrate was forced onto toweling and thawed at room temperature. The towels absorbed excess moisture as the samples melted, leaving the cores damp but firm, with sediments intact. Cross sections, 1.3 cm thick, were cut from the cores and screened through a No. 25 (U.S. series equiv.) sieve. Differential freezing rates of water and substrate caused the upper portion of the cores to be slightly distorted and frozen with a convex contour. Determination of the upper 1.3 cm of substrate was consequently somewhat subjective, but it is unlikely that measurement errors greater than 0.3-0.4 cm would have resulted. Also, the substrate may have been compacted slightly by the sampler.

Core freezing took 5-15 min, and some clams might have changed position in the substrate. Extensive movement was unlikely because clams typically respond to disturbances by clamping their valves together rather than moving away. As a check, 2 unfrozen core samples were taken with plexiglass tubes, at transect 5, station 2. The unfrozen cores were quickly removed from the tubes and divided into sections about 4.0 cm long. It was impossible accurately to divide the unfrozen cores into shorter sections under field conditions. Numbers and sizes of clams in the unfrozen samples were similar to those in comparable strata in frozen cores.

A series of 5 laboratory experiments was conducted at the University of Oklahoma Biological Station on Lake Texoma in 1970. In all experiments newborn clams were allowed to burrow inside opaque plastic tubes filled with substrate. Substrates were later removed from the tubes, sectioned, screened and the location of the clams determined and recorded. Experiments were conducted in a concrete holding tank in an air-conditioned laboratory with a continuous flow of aerated lake water. Water temperatures, usually 25-27°C, fell to 23°C on July 18, when the supply of lake water was interrupted.

Tubes holding substrates were 28 cm lengths of rigid-walled (polyvinyl chloride) plastic plumbing pipe with an inside diameter of 3.0 cm. These tubes were filled with substrates to about 2.5 cm from the top. The lower ends of the tubes holding sand and some with sandy-mud were blocked with paraffin to retain the substrate. Substrates used in experiments included mud from the banks of Pennington Creek and windblown sand from a field near the biological station. The composition of the mud, determined by the Bouyoucos hydrometer method, was 56% silt, 20% clay and 24% very fine sand (less than 0.125 mm in diameter). The sand was washed and screened through a No. 40 (U.S. Standard Sieve Series) sieve. The sand was of 3 size fractions: medium sand (0.250-0.500 mm diameter), 11%; fine sand (0.125-0.250 mm), 68%; very fine sand (0.063-0.125 mm), 21%. Sandy mud was produced by mixing the sand with the mud to bring the percentage of sand to stated levels.

Adult clams were placed in pans of lake water until enough young for experimentation were born, usually within 48 hours. Young clams were pipetted into vials of lake water until the desired number was reached (see section on LABORATORY EXPERIMENTS), and then poured into substrate tubes immersed vertically in the holding tank.

To locate clams after experimentation, the tubes and their substrates were frozen in a dry ice-alcohol bath. Freezing took 5-10 min. Cores were then removed as described for field samples. Sections approximately

1.25 cm thick were cut from the cores and screened through a No. 40 sieve. Mean penetrations were calculated on the assumption that clams occurred at the middle of each section of substrate. Data for pairs of consecutive sections of substrate were combined for presentation in all tables except Table 6.

Experiments were initiated as follows: A and B on June 17; C on June 30; D on July 16; and E on July 14, 1970. Parents of clams used in experiments A, B and C were collected in Pennington Creek, about 3 km south of Tishomingo, Oklahoma, on June 10, 1970. Parents of clams in experiment D were collected in Briar Creek, about 12 km northwest of Willis, Oklahoma, on July 8, 1970 (Gale, 1973).

From 93 to 97% of the small clams used in experiments A through E were recovered in the substrate tubes. The missing clams either crawled out of the substrate tubes or else fell outside the tubes as they were poured in.

VERTICAL DISTRIBUTION IN SUBSTRATES IN THE MISSISSIPPI RIVER

In Pool 19, clams were unevenly distributed in the substrate, with smaller clams being deeper than large ones (Table 1). At birth, clams average between 2.0 and 2.4 mm in length whereas adults often exceed 13 mm (Gale, 1969). Most of those greater than 3.0 mm in length were in the upper 1.3 cm of substrate, and all were within the upper 2.6 cm. Clams deeper than 2.6 cm in the substrate averaged 2.1 mm in length, with the longest being 2.7 mm.

Clam density was greatest in the upper 1.3 cm of substrate where 32% of the clams occurred, followed closely by the density at 2.6 to 3.9 cm which contained 24%. One clam occurred in the stratum 15.6 to 16.9 cm below the substrate surface. Maximum and mean penetration of clams was greatest in soft clayey silt, inside enclosures, and least in sand.

Since 59% of the clam population occurred deeper than 2.6 cm in the substrate, their presence at this depth is of considerable importance. Small clams, less dense than sand or silt, did not passively sink into the substrate. Conceivably, mature clams might burrow into the substrate, discharge young, and then move back to the substrate surface. Such a procedure would require several migrations because offspring are discharged periodically. Moreover, if

TABLE 1. Numbers and lengths of *Sphaerium transversum* at various depths in the substrates at 8 stations in Pool 19, Mississippi River. Data for T3S6B (Transect 3, station 6B) are totals for 2 samples taken in October 1968. All other samples were taken in July 1967. Data for T3S6A and T5S2 are totals for 3 samples. At other stations a single sample was taken. Notice that smaller clams occurred deeper than larger ones. N, number of clams; $\bar{x}$, mean clam length; R, range in length in mm.

		Sand		Clay-sand			Clay-silt			
Stations		T3S6A	T3S6B	T3S7	T3S4	T3S8	T3S9	T3S10	T4S1	T5S2
Depth cm	N	111	8	30	20	24	15	9	2	32
0-2.6	$\bar{x}$	5.0	5.0	4.4	4.0	6.0	4.3	6.1	6.5	5.7
	R	2.0-9.3	2.1-7.7	1.9-7.1	1.9-7.0	2.0-10.2	2.0-7.1	3.1-8.1	3.1-9.8	1.9-11.1
	N	74	8	49	29	36	2	9	0	20
2.6-5.2	$\bar{x}$	2.3	2.1	2.2	2.1	2.2	2.0	2.1		2.0
	R	2.0-2.7	1.7-2.2	1.7-2.6	1.7-2.5	1.9-2.6	1.9-2.1	1.9-2.4		1.8-2.2
	N	5	1	1	0	4	19	0	4	42
5.2-7.8	$\bar{x}$	2.1	2.0	2.1		2.1	1.9		2.0	2.1
	R	1.8-2.3	—	—		1.9-2.2	1.6-2.2		1.9-2.2	1.8-2.2
	N	0	0	0	---	0	0	0	21	22
7.8-10.4	$\bar{x}$								2.0	2.1
	R								1.7-2.3	1.9-2.5
	N	---	0	---	---	---	---	---	14	2
10.4-13.0	$\bar{x}$								2.1	1.9
	R								1.9-2.2	1.9-2.0
	N	---	0	---	---	---	---	---	1	1
13.0-15.6	$\bar{x}$								2.1	2.1
	R								—	—
	N	---	---	---	---	---	---	---	0	1
15.6-18.2	$\bar{x}$									2.1
	R									—

large clams burrowed into the substrate to discharge young, some would probably have been found deeper than 2.6 cm in the cores. Thus, it seems most likely that young clams were discharged from their parents within the upper 2.6 cm of substrate, and then burrowed.

LABORATORY EXPERIMENTS

How and why small clams became buried in the substrate could not be determined by field observations, and the following laboratory experiments were conducted to explore the problem.

Experiment A was designed to discover (1) whether young clams burrow into the substrate and if they do, (2) how fast and how deep they penetrate and (3) how long they remain burrowed. Twenty newborn clams were added to each of 21 mud-filled tubes. Three tubes were randomly selected and examined at each of the intervals of 0.5, 1, 2, 4, 8, 16 and 32 days.

Young clams usually burrowed out of sight within seconds of their release on the substrate surface. Within 12 hours 73% of the clams had burrowed more than 2.5 cm into the substrate; 19% had burrowed 5.0-7.5 cm deep (Table 2). Increased mean and maximum penetrations in 1 and 2-day samples suggest that some clams continued to burrow for a few days. Differences between days, however, were not significant at the 0.05 level of confidence using the "F" test.

Experiment B investigated clam penetration in relation to substrate type. Eighteen tubes were filled with substrate. Three tubes each were filled with the following: mud (containing 24% sand), sand and mixtures of sandy-mud with 39, 55, 70 and 85% sand. Twenty clams were released on the substrate surface of each tube. Replicates of 6 tubes were randomly selected and examined after 4, 7 and 16 days.

Because differences between replicates (days) were not significant at the 0.05 level of confidence, the data were combined in Table 3. Mean and maximum clam penetrations were greatest in sandy-mud (85% sand) and least in mud. The difference between treatment means (substrate types) was significant at the 0.01 level of confidence. Clams might have burrowed deeper than 25.0 cm if the tubes had been longer, but only in the sandy-mud (85%) were any clams within 3 cm of the bottom.

Experiment C was run to determine whether clams which have burrowed into the substrate will reburrow if returned to the substrate surface. Sandy-mud (75% sand) was placed in 3 tubes. Sand or sandy-mud was substituted for mud in most experiments after it was found that clams burrowed into them. Filling tubes and screening samples was faster using sandy materials. Ten clams obtained at depths of 5-23 cm in a core of sand, where they had lived 3 days, were placed on the substrate surface of each tube. One tube each was examined after 5, 10 and 20 days. Upon examination, 12

TABLE 2. Vertical distribution of newborn clams (% total) in experiment A after various lengths of time. Totals based on 3 cores each. There was no statistically significant difference in burrowing between successive time periods.

Depth in substrate (cm)	Days in substrate						
	0.5	1.0	2.0	4.0	8.0	16.0	32.0
0 - 2.5	26	28	25	36	33	33	18
2.5- 5.0	54	35	28	20	24	35	67
5.0- 7.5	19	23	38	28	26	24	15
7.5-10.0	0	14	5	7	17	7	0
10.0-12.5	0	0	4	0	0	2	0
12.5-15.0	0	0	0	0	0	0	0
15.0-17.5	0	0	0	0	0	0	0
17.5-20.0	0	0	0	0	0	0	0
20.0-22.5	0	0	0	0	0	0	0
22.5-25.0	0	0	0	0	0	0	0
Mean penetration (cm)	3.9	4.1	4.6	4.2	4.6	4.1	3.6

TABLE 3. Vertical distribution of newborn clams (% total) in various concentrations of sand in experiment B. Totals based on 3 cores each, after 4, 8 and 16 days. There was no statistically significant difference in burrowing between successive time periods.

Depth in substrate (cm)	Percent sand					
	100	85	70	55	39	24
0 - 2.5	34	12	19	14	25	32
2.5- 5.0	19	5	12	18	32	44
5.0- 7.5	19	15	23	14	25	19
7.5-10.0	3	13	26	21	13	5
10.0-12.5	7	20	2	14	5	0
12.5-15.0	3	15	16	9	0	0
15.0-17.5	2	12	0	7	0	0
17.5-20.0	12	5	0	2	0	0
20.0-22.5	0	0	2	0	0	0
22.5-25.0	0	3	0	0	0	0
Mean penetration (cm)	6.2	12.4	9.2	8.1	4.7	3.7

clams were found in tube C3 and 8 in C2. Likely 2 of the clams intended for tube C2 were placed in tube C3 by mistake. Substrates in experiment C, as in other experiments, had been screened to remove all clams before the experiment started.

The clams did reburrow (Table 4). Clams placed in tubes C2 and C3 were obtained from a depth of 5.0-7.5 cm in the sand. Several of these burrowed deeper the 2nd time than they had the 1st. The difference may have been due to the use of sandy-mud instead of sand in tubes for reburrowing.

Experiment D was to determine if clam density affects clam penetration. Sand was placed into 18 tubes. Fifty clams were placed into each of 3 tubes and 10 clams in each of the other 15, producing densities of 70,741 and 14,148 clams/m^2, respectively. Densities of over 100,000 clams/m^2 sometimes occur in the natural environment (Gale, 1973), but 70,000 clams/m^2 is a very high density. Young clams in replicates 1 and 2 came from adults collected in Pennington Creek on July 14, and those in replicate 3 came from clams collected in Briar Creek on July 8. Tubes were examined after 7 days.

TABLE 4. Vertical distribution of newborn clams (% total) in 3 cores after reburrowing in sandy mud for 5, 10 and 20 days in experiment C.

Depth in substrate (cm)	Day	5	10	20
	Tube	C1	C2	C3
0 - 2.5		11	0	33
2.5- 5.0		11	13	17
5.0- 7.5		22	25	8
7.5-10.0		0	13	17
10.0-12.5		44	50	17
12.5-15.0		0	0	8
15.0-17.5		11	0	0
17.5-20.0		0	0	0
20.0-22.5		0	0	0
22.5-25.0		0	0	0
Mean penetration (cm)		8.7	8.9	6.1

Clam density had no apparent effect on penetration (Table 5). In replicates 1 and 2, clams in 10 tubes with low density penetrated an average of 2.8 cm in the substrate; clams in the 2 tubes with high density penetrated 3.5 cm. Clam penetration in replicate 3 was much less, with means of 0.8 and 0.6 cm, suggesting differences in the parental stocks.

Experiment E was to determine if young clams born in a substrate tube (and not handled) penetrate to the same depth as young born in a pan of lake water (and subsequently handled). Sand was added to 15 tubes and 1 adult *S. transversum* was placed into each of 10 tubes. Ten newborn clams were placed into each of the 5 remaining tubes. Adults were removed after 6 days and all tubes were examined after 9 days. All adults were still in the upper 2.5 cm of substrate when removed. A few had burrowed out of sight and were located by gently probing the substrate with a broom straw.

Clams born inside substrate tubes penetrated somewhat less than those born in a pan of lake water (Table 6).

DISCUSSION

Results of experiment A indicate that burrowing begins immediately after the

TABLE 5. Vertical distribution in sand of young clams (% total) in high and low densities; experiment D. Numbers of tubes examined are in parentheses.

	Replicates 1 and 2[a]		Replicate 3[b]	
Depth in substrate (cm)	high (2) density	low (10) density	high (1) density	low (5) density
0 - 2.5	52	64	98	100
2.5- 5.0	17	18	2	0
5.0- 7.5	12	5	0	0
7.5-10.0	8	7	0	0
10.0-12.5	8	4	0	0
12.5-15.0	1	1	0	0
15.0-17.5	0	0	0	0
17.5-20.0	0	0	0	0
20.0-22.5	0	0	0	0
22.5-25.0	0	0	0	0
Mean penetration (cm)	3.5	2.8	0.8	0.6

[a]Parents of clams collected in Pennington Creek (July 14).
[b]Parents of clams collected in Briar Creek (July 8).

TABLE 6. Vertical distribution of clams (% total) born in substrate tubes (E1-E10) or in a pan of lake water (E11-E15) in experiment E.

Depth in substrate (cm)	Tubes E1-E10	Tubes E11-E15
0 -1.3	90	52
1.3-2.6	10	34
2.6-3.9	0	7
3.9-5.2	0	7
Mean penetration (cm)	0.8	1.5

clams are born and is nearly completed within 12 hours. Not all newborn clams burrowed deeply into the substrate; some remained near the surface or at intermediate depths in all experiments. Moving about in the substrate would seem a waste of energy unless the clams were moving to the surface to feed and then reburrowing. It is doubtful that clams feed during their stay deep in the substrate since clams from the 32-day sample were no larger than clams in the 0.5-day sample. Furthermore, in another experiment, clams were placed into 68-cm long tubes containing about 26 cm of sand, and 16 cm of sand was poured on top of them. None of the clams was in the upper 16 cm of sand after 10 days, indicating that young clams did not migrate upward, although they survived the experiment.

How long clams can remain buried was only partially determined, but clearly they may remain buried for a month or longer. Newborn clams in the natural environment seem to remain buried for several weeks or months; otherwise, the majority of small clams would not consistently occur deep in the substrate as they did in cores from Pool 19.

In experiments A and B, the 104 clams that burrowed deepest averaged 1.88 mm in length, the same size as the 84 clams in the upper 2.5 cm. Maximum depth of penetration does not seem related to size of newborn clams.

Results of experiment C revealed that clams that burrow into the substrate retain the tendency to reburrow, if uncovered, for at least 3 days and perhaps much longer.

Substrate effects

The depth to which newborn clams burrow is determined, at least in part, by the nature of the substrate. In Pool 19 clam penetration was least in sandy substrates and greatest in soft clayey silts such as those inside enclosures at T4S1 and T5S2 (Table 1). The fact that clam penetration was greatest inside enclosures suggests that the enclosures might somehow have affected penetration. Siltation, for example, may have been greater inside enclosures than elsewhere, but little if any siltation occurred inside the enclosures. More likely, clam penetration was greater at T4S1 and T5S2 because they were backwater stations containing soft sediments several cm deep. The clayey silt substrate at station 10, on the other hand, was unusually firm, particularly in lower strata; the firmness may have restricted clam penetration (Table 1).

Results of laboratory experiment B (Table 3), where clams penetrated deepest in sandy mud, seem to conflict with field observations in Pool 19. The coarser sand in Pool 19 (primarily 0.250-1.000 mm in particle diameter), however, was probably more difficult to penetrate than sand used in experiment B (primarily 0.125-0.250 mm diameter). Newborn clams may have been unable to dislodge the larger sand grains. Mud in cores from Pool 19, with the exception of that at station 10, seemed softer and likely was penetrated more easily than mud in experiment B. Mud in Pool 19 samples was composed primarily of clay particles with lesser amounts of silt and virtually no sand (Gale, 1969: 13). Mud in experiment B, as described earlier, was primarily silt with substantial amounts of very fine sand. Why clams should burrow deeper in some substrates than in others is not certain, but penetration may be deepest in substrates offering least resistance.

A greater amount of interstitial water in the substrate may facilitate burrowing. Meier-Brook (1969) found that some species of *Pisidium* obtain water through interstitial spaces in the substrate and discharge it through the hole produced by burrowing. Some of my observations to be discussed later suggest that interstitial water is not important as a source of food or oxygen for newborn *S. transversum.*

Other environmental effects

In Pool 19, I was unable to relate maximum depth of penetration to density of small clams in the cores (Table 1). In experiment D, clam density seemed to have no effect on depth of penetration (Table 5).

The large difference between replicate 3 and replicates 1 and 2 probably reflects a difference in young clams used. Newborn clams in replicates 1 and 2, from Pennington Creek, were relatively large (many were over 2.5 mm long) and most were unusually brown; they were held in a pan of lake water in the laboratory for a maximum of 2.5 days before experiment D was initiated. Clams in replicate 3 were much smaller and had a more characteristic pinkish color. They had been held in the laboratory up to 8 days before experimentation. Clams collected in Briar Creek were unusually slow in discharging young and some never yielded many. It seems likely that large clams from Briar Creek (collected July 8) were not gravid, and only small adults were giving birth. A sample of 10 large adult clams collected at the same site in Briar Creek on July 23 were all heavily parasitized with rediae and were not gravid. Parasitism and a concomitant lack of embryos have been reported by Wenke (1965) and Gale (1973) in *S. transversum* and by Heard (1965) and Meier-Brook (1970) in some species of *Pisidium*. One might contend that clams in replicate 3 did not burrow deeply because they were retained too long in the pan where they were born, but few clams were in the pan more than 3 days because their parents were slow in giving birth to them.

The differences in penetration might reflect environmental differences in the habitats where the clams were obtained. Both groups of newborn clams faced similar environments in the laboratory where they were born. The behavior of newborn clams, however, may reflect the prenatal environment within the branchial chamber of the parent. Clams in Pennington Creek were obtained from mud substrates in sluggish, shallow water that received several hours of direct sunlight daily. Clams in Briar Creek, on the other hand, came from a sandy substrate in shaded water with considerable current. Dissolved oxygen levels were probably lower and water temperatures higher in Pennington Creek. Considering the environmental differences encountered by clam populations in the 2 creeks, it would not be surprising if the 2 groups differed physiologically, genetically and behaviorally.

The young of clams from Briar Creek may have been born prematurely. In earlier experiments (Gale, 1969: 95), 80% of the test adults gave birth during the first 40 hours of confinement; the young born early were larger than those born later. Extra-marsupial embryos (those no longer within a marsupial sac) are usually larger and better developed than intra-marsupial embryos and are born first. In experiment D, few young were born during the first 5 days suggesting that those born later may have been intra-marsupial young. Effects of such possible premature birth upon postnatal behavior is not known.

In experiment E, clams born in a pan of lake water penetrated deeper than clams born inside substrate tubes (Table 6). Being born in a pan of water (or handling associated with it) seems to affect the behavior and perhaps the metabolism of young clams. In earlier experiments in Pool 19 (Gale, 1969: 107-135), many young clams born inside growth chambers grew to maturity, but during the same period many clams born in a pan of river water and then transferred to growth chambers failed to grow for 33 days; the clams seemed to have been in a resting state. Possibly, the stimulus producing a resting state in newborn clams might also cause them to burrow deeply into the substrate.

Clams were in tubes E11 and E15 for 9 days, ample time for maximum penetration to have occurred. Most clams were probably in tubes E1 to E10 nearly as long, since most should have been born within 48 hours after their parents were placed in the tubes. Because parental clams were removed 3 days before the tubes were examined, all clams were at least 3 days old. Mean clam penetration in experiment E was 0.8 and 1.5 cm (Table 6), much less than the mean of 6.2 cm observed in experiment B (Table 3). In experiment D, newborn clams from the same group of parents as those used in experiment E burrowed to mean depths of 3.5 and 2.8 cm (Table 5). The main difference between the clams in experiments D and E seems to have been the length of time spent in the pan where they were born. Clams in experiment D were in the pan up to 2.5 days, while those in experiment E were in the pan 3 hours or less. Seemingly, duration in the pan in some way affects subsequent clam behavior. Although the prenatal environment may affect postnatal behavior, as suggested earlier, it is clear from experiment E that the postnatal environment may also modify postnatal behavior.

Resting periods

Previously, I found that some newborn *S. transversum* could survive at least 2 weeks in sealed containers in anaerobic conditions. Such clams seemed to be in a resting state because they kept the shell closed and the hearts beat only a few times per minute. Two observations suggest that clams buried deep in the substrate, in laboratory experiments, were in a resting state. First, all clams in experiment A contained empty guts and seemingly were not feeding when frozen. Second, the shells of many clams, especially those deep in the substrate, became very dark during experimentation, probably as a result of anaerobic conditions.

Calyculate clams (i.e. with capped beaks) in Pool 19 seem to have been born in autumn and may have overwintered deep in the substrate. Clams born in summer usually are not calyculate and may begin to grow immediately, rather than burrowing into the substrate. Yet, July core samples (Table 1) contained many clams deep in the substrate. Two explanations could account for this discrepancy. First, clams deep in July core samples may have been born in spring (April and May); second, some clams born from June through August could begin to grow immediately, but others could burrow into the substrate and not grow. The latter possibility seems most likely since some clams in experiments A through E did not burrow into the substrate. Not all newborn clams undergo an initial resting period before they start to grow, nor do all newborn clams need to burrow deeply into the substrate. In earlier experiments (Gale, 1969: 107-135), some clams reared in approximately 1 cm of substrate grew to large size in about a month. These clams could not have burrowed deeply nor could they have spent much time in a resting state.

In October and November, substantial numbers of very small calyculate clams appeared in Pool 19, suggesting that some of the clams which had been dormant had begun to grow.

Energy considerations

The fact that newborn clams seem to burrow deepest in substrates offering least resistance suggests that energy expenditures may be an important consideration. However, the results of experiment C seem to indicate that energy depletion is not the mechanism, or not the only mechanism, regulating depth of clam penetration. The clams which had previously burrowed were held in vials of lake water for only a few minutes before being transferred to the second series of tubes to reburrow; the clams were not observed to filter-feed during this time. Yet, these clams had sufficient energy to reburrow and presumably sufficient energy left to resurface.

Survival value

Why *S. transversum* burrows deeply into the substrate remains undetermined, but deep penetration could be a means of self-regulating population levels. When clam populations are high, placement of newborn clams deep in the substrate would be a convenient and relatively safe storage area, precluding increased competition for food, space and other essentials. Growth and subsequent reproduction would be delayed, further reducing problems of overpopulation. Although initial density of newborn clams in experiment D had little effect on subsequent penetration into the substrate, density of adult clams might be an important factor.

There are several possible advantages to maintaining a segment of the clam population deep in the substrate. First, clams deep in the substrate may avoid being swept away during periods of stream turbulence. Second, they may escape periods of intensive fish, duck or leech predation. Third, disease organisms, parasites and temporary accumulations of noxious materials in the water might be avoided. Observations of a captive population of *S. transversum* in Pool 19 substantiated the belief that clams deep in the substrate may escape unfavorable conditions. In a population of several thousand, nearly all clams near the substrate surface were killed by unknown causes; small clams deep in the substrate were alive and seemed normal.

It may be that *S. transversum* evolved in temporary or vernal ponds where burrowing into bottom sediments during dry periods was necessary. In temporary ponds in Southern Michigan, Kenk (1949) usually found that only those young *Sphaerium occidentale* that were buried in the pond

bottom survived the dry season. Thomas (1963) came to similar conclusions studying *Sphaerium partumeium* in temporary ponds. Seemingly, such a trait would be lost after the clams moved from temporary ponds to permanent bodies of water, but this trait would likely persist if it offered survival value to compensate for the resultant delay in growth and the extra energy expenditures of burrowing into the substrate.

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LOCOMOTION IN THE GASTROPODA: FUNCTIONAL MORPHOLOGY OF THE FOOT IN *NERITINA RECLIVATA* AND *THAIS RUSTICA*[1]

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ABSTRACT

The mechanics and parameters of pedal waves are redefined and discussed. The foot of *Neritina reclivata* (Say) contains longitudinal, transverse and diagonal muscles. There are 3 types of mucocytes in the foot: anterior, epithelial and sub-dermal. *Neritina* crawls by means of monotaxic retrograde waves. These waves are the result of the combined action of transverse and longitudinal muscles. The foot of *Thais rustica* (Lamarck) contains longitudinal, transverse, diagonal and dorso-ventral muscles. *Thais* crawls using alternate ditaxic direct waves; the longitudinal muscles produce these waves. Supplementary observations of the types of locomotion employed by over 60 species of gastropods were combined with observations of previous workers to determine the factors affecting locomotion in the Gastropoda. These factors are: size, form, habitat and phylogeny. The inter-relationship of these parameters varies within the class.

INTRODUCTION

The predominant mechanisms of locomotion employed by gastropods are muscular pedal waves and cilia. Pedal waves have been classified as direct or retrograde depending on the direction of propagation. Direct waves move in the same direction as locomotion, that is, posterior to anterior, whereas retrograde waves move in the opposite direction, that is, anterior to posterior.

There is no theory accounting for the function of direct and retrograde waves; therefore, an understanding of gastropod locomotion is incomplete. There are few papers containing detailed observations of wavelength, timing and the diagonal orientation of pedal waves. The effects of ecological factors, such as gravity, wave shock and habitat upon locomotion have hardly been considered.[2]

The purpose of this study was to determine the mechanism of production of direct and retrograde waves and to gain insight into the factors affecting, and the functional advantages of, the different types of locomotion employed by gastropods. Observations of locomotion were correlated with the anatomy of the foot in *Thais rustica* (Lamarck, 1822), and *Neritina reclivata* (Say, 1822), examples of gastropods with direct and retrograde waves, respectively. In addition, observations of over 60 other species of gastropods were made to determine the types of locomotion.

HISTORICAL RESUME

Early controversies on gastropod locomotion concerned the force needed to re-extend the longitudinal muscles of the foot during the passage of a pedal wave. Simroth (1879) thought that an 'extensile musculature' was responsible for re-extension of contracted muscles. Carlson (1905), Jordan (1905) and Robert (1907) believed that extension was the result of muscular contraction and hydrostatic pressure. Dubois & Vlès (1907) postulated that adhesion to the substratum and locomotion were due solely to muscular action and discounted the role of cilia, mucus and blood pressure. All of these theories were based upon the assumption that the longitudinal muscles provided the primary force

[1]Publication No. 23 of the Tallahassee, Sopchoppy & Gulf Coast Marine Biological Association.
[2]After acceptance of this manuscript, the author learned of a paper then in press by S. Miller dealing with a similar topic (Miller, 1974).

in locomotion, although little was known about the actual arrangement of pedal muscles.

Vlès (1907) was the first person to classify the types of muscular locomotory waves, dividing them into direct and retrograde waves. He further classified locomotion according to the number of waves present across the width of the foot: 1 series of waves being monotaxic, 2 being ditaxic and 4 being tetrataxic.

Parker (1911) subdivided ditaxic waves into alternate and opposite forms: alternate waves are out of phase and opposite waves are in phase. He also proposed another type of muscular locomotion, arhythmic, that was later found by Copeland (1919) to be due to cilia. Biederman (1905) postulated that pedal waves are convexities of the surface of the foot, while Parker (1911) suggested that the waves are concave. Parker's suggestion was later verified experimentally by Olmsted (1917) and Lissmann (1945).

Lissmann (1945, 1946) investigated the internal and external forces that produce locomotion in 3 species of gastropods exhibiting direct waves. Studying the interrelationship of various portions of the foot, he concluded that forward thrust is developed in the area between the anterior and central regions of the foot, while tension is developed in the area between the posterior and central regions.

Jones & Trueman (1970) studied the locomotion of *Patella vulgata*, which employs retrograde waves in locomotion. In the absence of longitudinal muscles in the foot, they hypothesized that the dorsoventral muscles and the hydrostatic skeleton provide the locomotory forces in *Patella*.

PARAMETERS OF PEDAL WAVES

The parameters of pedal waves are illustrated in Fig. 1. The wave-length is defined here as the distance between the leading and following interfaces of the wave. I have defined the leading interface of the wave to be the first edge to appear on the foot. Therefore, the leading interface of a direct wave is towards the anterior end of the foot while the leading interface of a retrograde wave is towards the posterior end of the foot.

Unfortunately, the terms used previously to describe the external events of a pedal wave conflict with the terms used to describe the actions of the pedal musculature, which are internal events. I will use the terms elongation and compression, instead of extension and contraction, for the external events of a wave. Extension and contraction will be used in conjunction with the pedal musculature.

MATERIALS AND METHODS

Living specimens of *Thais rustica* were obtained from Phipp's Park, Palm Beach, Florida and were kept in a 15 gallon aerated aquarium. Specimens of *Neritina reclivata* were obtained from the Wakulla River, Wakulla County, Florida. They were kept in a 2 gallon aerated aquarium. Visual observations of locomotion in the horizontal plane were made through the bottom of a small glass chamber with the aid of a mirror and a hand lens. Observations in the vertical plane were made with a Wild dissecting microscope mounted horizontally. Sixteen mm black and white films were made of *Thais* crawling vertically.

Sections were prepared by relaxing the animals in magnesium chloride isotonic with the ambient water and fixing them in Bouin's fluid. The specimens were sectioned at 7 μm in paraffin and stained in Mallory's triple stain. Several sections from each series were stained in Alcian Blue G8X and Periodic Acid Schiff (PAS) as a test for mucus.

OBSERVATIONS

Neritina reclivata

Anatomy and Histology. The foot of *Neritina reclivata* is dorso-ventrally flattened and has a metapodial lobe (MP) that rises from the postero-dorsal margin of the foot, forming a pocket in which the shell of the animal rests when the foot is extended (Fig. 2). Anteriorly there is a transverse cleft (TC) that is bordered by a narrow lip (Figs. 2, 4). There are 3 types of mucocytes in the foot. The anterior mucocytes (AM) are arranged in longitudinal bundles with a duct running from the center of each bundle to the dorsal region of the transverse cleft (Fig. 4). The bundles of mucocytes are separated from one another by numerous longitudinal

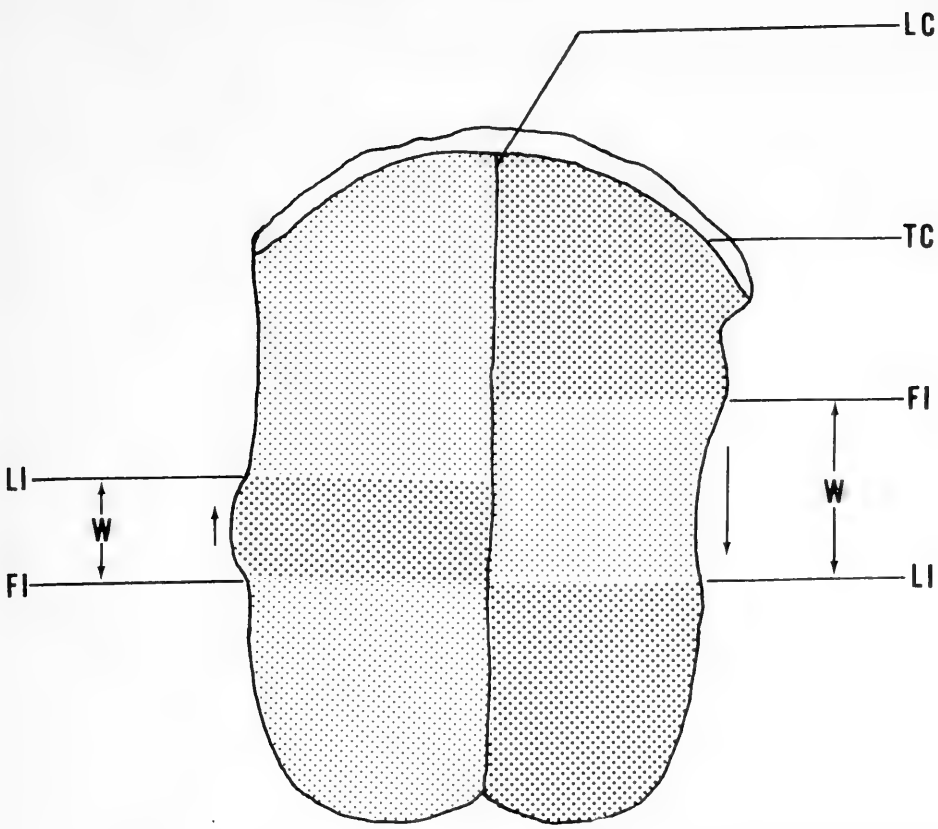

FIG. 1. Hypothetical snail foot showing various parameters of pedal waves on a ditaxic sole. A direct wave is on the left while a retrograde wave is on the right. The arrows closest to the foot show the direction of wave propagation. The leading interface of the retrograde wave is towards the posterior end of the foot because the wave is moving in that direction. FI = following interface; LC = longitudinal cleft; LI = leading interface; TC = transverse cleft; W = wavelength.

muscles (Fig. 5, LM). The subdermal mucocytes (Fig. 4, SD) are large and elliptical, lying dorsal to the epithelium of the sole; each cell has a duct leading to the exterior. These cells are unevenly distributed throughout the ventral portion of the foot. They are heavily concentrated in the anterior region, where they lie ventral to the anterior mucocytes, and decrease in number towards the posterior end of the foot. Both anterior and sub-dermal mucocytes stain positively with Alcian Blue. The epidermis is composed of ciliated columnar cells and mucocytes in alternation with one another. The epithelial mucocytes gave negative results with PAS and Alcian Blue. According to Mowry (1963) the PAS reaction is an indication of neutral glycoprotein while Alcian Blue indicates acidic mucopolysaccharide. Staining with Mallory's suggested that the production of mucus in individual mucocytes is cyclical since some mucocytes stained while others contained vacuoles, possibly filled with mucus in some non-staining stage of formation.

The pedal nervous system of *Neritina* resembles that of *Nerita* as described by Bouvier (1887). The paired pedal ganglia lie in the large hemocoel between the head and foot. Each ganglion gives rise to 3 nerves on its antero-ventral margin. These nerves enter the foot separately and branch in the anterior region of the foot. The large pedal cords (Fig. 2, PNC) arise on the posterior margin of each ganglion and course posteriorly into the foot. Each cord lies in a hemocoelic space and sends lateral branches into the pedal musculature. The cords are not connected by commissures.

The paired columellar muscles of *Neritina* appear equal in diameter although Bourne (1908) stated that the right one is larger.

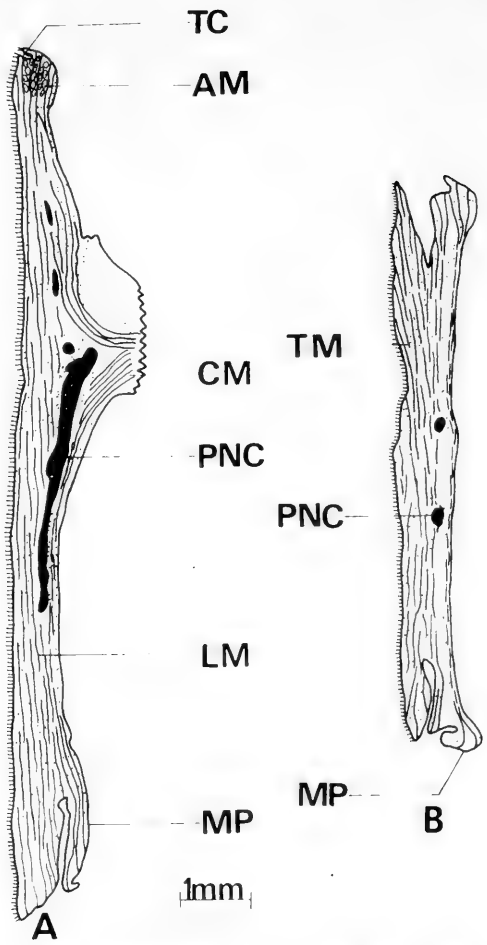

FIG. 2A: Parasagittal section of the foot of *Neritina reclivata;* B: cross section. AM = anterior mucocytes; CM = columellar muscles; LM = longitudinal muscle; MP = metapodium; PNC = pedal nerve cord; TC = transverse cleft; TM = transverse muscle. Muscles in cross section are indicated by stipple.

Each muscle has 2 slips, one going to the head, the other to the foot. The portions of the muscles entering the foot are further divided into anterior and posterior branches. The smaller anterior branches originate on the anterior dorsal margin of the foot and serve to retract the front of the foot when the animal withdraws into its shell. The posterior branches lie above the pedal nerve cords, inserting on the operculum and splaying into the metapodium and posterior tip of the foot (Fig. 2).

The intrinsic pedal musculature is composed of 3 main groups: longitudinal, transverse and diagonal. Dorso-ventral muscles are lacking except for a few small fibers along the front end of the foot. Longitudinal muscles (Fig. 2, LM) are uniformly distributed throughout the foot; in frontal section (Fig. 3) these muscles are parallel to the lateral margins of the foot. The transverse muscles (TM), in frontal section, do not extend straight across the foot; at either extremity they are curved concavely toward the ends of the foot; in the middle they extend straight across except near the lateral margins where they are curved posteriorly (Fig. 3). There are 2 layers of transverse muscles in the metapodium, 1 above and 1 below the columellar muscles. The diagonal muscles (DM) extend forward from the mid-line of the foot to the lateral and anterior margins. Along the center of the foot these muscles overlap and continue posteriorly across the midline for a short distance. The distribution of transverse, longitudinal and diagonal muscles throughout the foot is unequal. Transverse and diagonal muscles predominate in the anterior region while longitudinal fibers predominate in the posterior region. Although the relationship of the muscles with respect to the margins of the foot is probably constant, the orientation of the muscles shown in Fig. 3 is altered somewhat as the foot becomes elongated during locomotion. The entire foot is permeated by connective tissue which appears to sheath each individual muscle fiber.

Locomotion. Neritina reclivata crawls using monotaxic retrograde waves that propel the animals by elongation and then compression of the tissues of the foot. The sole of the foot is spotted with many small pigment granules that served as markers during my observations of the crawling animal. Elongation occurs along the leading margin of each wave, the foot remaining expanded to the following margin of the wave where the foot is compressed to its resting condition. As a wave passes a given area of the foot the dorso-lateral margins, adjacent to the wave, are compressed towards the center of the sole and remain so until the wave passes. The forces of elongation and compression must be equal, otherwise the foot would either become greatly elongated or compressed and such is not the case. These forces are not equal in their overall effect on locomotion throughout the foot. At the extreme anterior margin of the foot, forward movement is effected only by

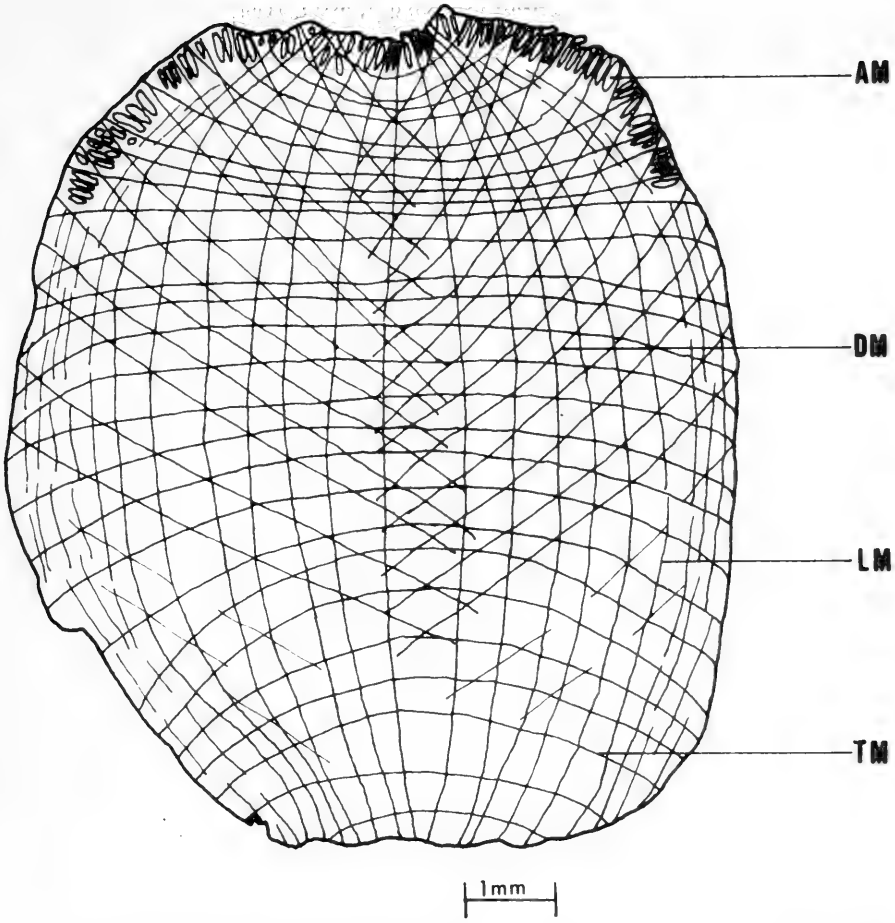

FIG. 3. Frontal section of the foot of *Neritina reclivata*. AM = anterior mucocytes; DM = diagonal muscles; LM = longitudinal muscles; TM = transverse muscles. The density of the muscles has been reduced to clarify the figure.

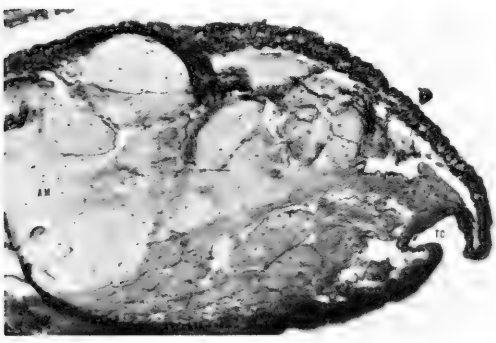

FIG. 4. Sagittal section of the anterior tip of the foot of *Neritina reclivata*. AM = anterior mucocytes; SD = sub-dermal mucocyte; TC = transverse cleft. The sole of the foot is towards the lower edge of the figure.

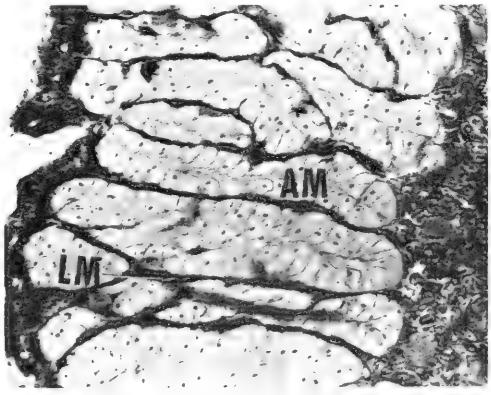

FIG. 5. Frontal section of the anterior mucocytes of *Neritina reclivata* showing the longitudinal muscles separating the mucocytes. AM = anterior mucocytes; LM = longitudinal muscle.

a force of elongation, the force of compression serving to restore the foot to its resting state. At the extreme posterior margin, forward movement is effected only by a force of compression, the force of elongation serving to expand the foot so that compression can occur. Observations on the remainder of the foot showed that forward movement is effected equally by elongation and compression.

The orientation of a wave changes as it progresses along the foot. Each begins as an elongation of the anterior medial portion of the foot (Fig. 6A). The interface between the area of forward elongation and pedal adhesion is curved concavely towards the anterior end of the sole. This curvature is maintained over the anterior third of the foot. As the wave moves posteriorly past the anterior third, the wave front straightens except for the lateral margins which continue to curve anteriorly. The following margin of the wave begins to form in the anterior central region at the same instant that the leading interface of the wave straightens (Fig. 6C). When the wave reaches the posterior 1/2 of the foot the orientation of the interfaces changes so that they are curved concavely towards the posterior end of the foot.

The shape of the anterior region of the foot while at rest (Fig. 6D) is a direct result of the form of the waves. The anterior lateral margins continue to be pushed forward by the elongation at the leading interface of the wave while the antero-central portion of the foot is compressed and attached to the substratum. As a result of this movement, the lateral margins are pushed ahead of the central margin of the foot. The length of a wave remains constant along the foot except at the anterior and posterior margins where the wavelength is increasing and decreasing respectively. Although the orientation of the interfaces changes over the length of the foot the movement of the epithelium within the wave remains constant and is always forward.

At any instant there is only 1 complete wave on the foot although this wave may be composed of 1 single wave in the middle of the foot or 2 half waves in the anterior and posterior regions (Fig. 6 D&A, respectively). The anterior and posterior ends of the foot move forward simultaneously (Fig. 6); the anterior end by elongation and the posterior end by compression. The extremities cease

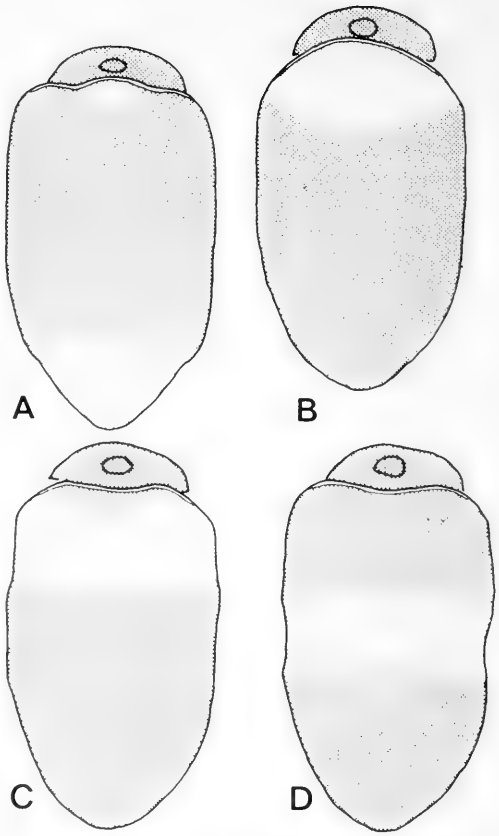

FIG. 6. Diagram of the pedal waves of *Neritina reclivata.* The waves are indicated by the lighter stipple. In "A" one wave is leaving the foot at the posterior end, while another wave is beginning at the anterior end. "B" through "D" follow the course of the wave at the anterior end in "A" as it moves posteriorly along the length of the foot. The anterior end of the foot is towards the top of the page.

their forward movement at the same time, which is an indication that the period of elongation is equal to that of compression.

Neritina has 2 methods of turning. Turns less than 90° are executed by postural orientation of the anterior end of the foot in the direction of the turn. Turns greater than 90° were rarely observed but are accomplished by a combination of retrograde and direct waves. The 1/2 of the foot on the same side as the turn moves backward by means of direct waves while the side of the foot opposite the turn moves forward using retrograde waves. Due to the opposite directions of movement of the 2 sides of the foot, the waves both start at the front of the foot and move over the sole in the normal

manner. The leading interfaces move along the foot together; however, the following interfaces are out of alignment because the direct wave is 1/2 the wavelength of the retrograde wave. The side of the foot possessing direct waves bulges laterally as each wave passes any given point. The epithelium is folded within the direct wave.

Thais rustica

Anatomy and Histology. The foot of *Thais* is blunt in front and tapered in the rear. Two clefts, longitudinal and transverse, are present on the sole. The longitudinal cleft (Fig. 7C, LC) divides the major portion of the sole in half and extends from the posterior tip of the foot to the region just posterior to the transverse cleft (TC). The pore of the accessory boring organ (ABO) opens into the anterior end of the longitudinal cleft. The organ lies within a cavity dorsal to the pore (Fig. 7) and is composed of gland cells and muscle fibers. It is extended only when the animal is chemically boring. As in *Neritina*, there are 3 kinds of mucocytes in the foot. The ciliated epithelium (Fig. 8) is composed of mucocytes (EM) and columnar cells (CC) in alternation with one another except in the longitudinal cleft where the mucocytes are less numerous. Differential staining of mucocytes (EM) and the epithelial cells (CC) indicated that the mucocytes are unciliated.

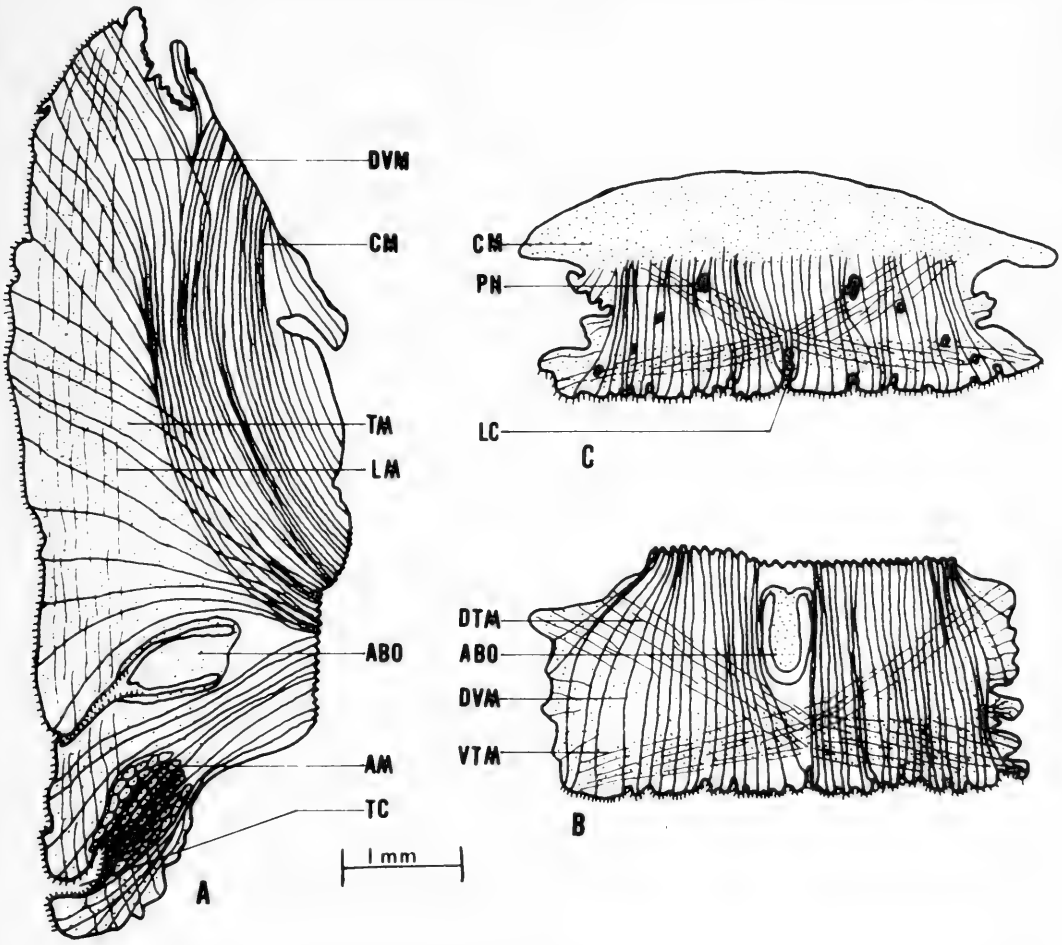

FIG. 7A: Sagittal section of *Thais rustica* foot. B & C: cross sections. ABO = accessory boring organ; AM = anterior mucocyte; CM = columellar muscle; DTM = dorsal transverse muscles; DVM = dorso-ventral muscles; LC = longitudinal cleft; LM = longitudinal muscles; PN = pedal nerve cord; TC = transverse cleft; TM = transverse muscles; VTM = ventral transverse muscles. Muscles in cross section are indicated by stipple.

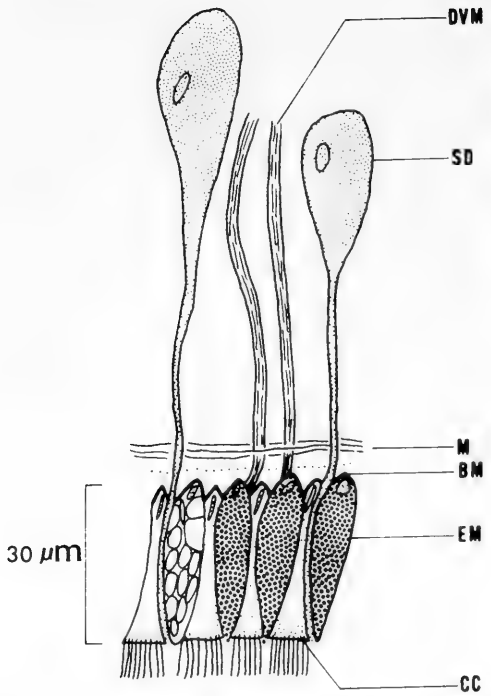

FIG. 8. Composite diagram of the foot epithelium of *Thais rustica*. BM = basement membrane; CC = columnar epithelial cell; DVM = dorso-ventral muscle; EM = epithelial mucocyte; M = muscle fiber; SD = sub-dermal mucocyte. In *Neritina*, the epithelium is 20 μm thick.

FIG. 9. Sagittal section of *Thais rustica* foot showing the transverse cleft and anterior mucocytes. AM = anterior mucocytes; TC = transverse cleft. The sole of the foot is to the lower edge of the figure.

These mucocytes stain positively with Alcian Blue and PAS, except for those in the longitudinal cleft which stain positively only with PAS. The sub-dermal mucocytes (SD) are present along the entire sole except for the region above the longitudinal cleft and anterior to the transverse cleft. The transverse cleft (TC) extends completely across the anterior end of the foot (Figs. 7, 9). The epithelium of the transverse cleft is ciliated and is lacking in mucocytes. The dorsal margins of the cleft are permeated by ducts from the anterior mucocytes. The individual anterior mucocytes are smaller and less organized than those in *Neritina*. The sub-dermal and anterior mucocytes stain positively with PAS.

The pedal nervous system is similar to that of other neogastropods. The pedal ganglia are connected by a short commissure and lie in the hemocoel between the foot and head. There are anterior and posterior groups of nerves emerging from each ganglion. The anterior group consists of about 10 fibers which originate on the antero-ventral margin of each ganglion and lie in a straight line running anterior to posterior. These nerves enter the foot separately and branch into the anterior 1/2 of the foot. There are many small branches of the anterior nerves concentrated along the posterior margin of the transverse cleft. The posterior group of nerves consists of about 15 fibers from each ganglion. These fibers are narrower than the anterior ones and originate on the posterior margins of the ganglia. The posterior nerves enter the foot as 2 bundles, one from each ganglion, rather than as single fibers. The bundles lie in blood sinuses and run postero-ventrally into the foot. There are 8 main bundles of nerves in the posterior 1/2 of the foot. These bundles result from a splitting of the 2 larger bundles after they enter the foot. The smallest bundles lie near the ventro-lateral margins of the foot; the bundles gradually increase in diameter dorso-medially (Fig. 7).

The 4 main groups of muscles within the foot are columellar, transverse, longitudinal and diagonal. The columellar muscle is divided into 2 parts. The bulk of the muscle originates on the operculum, extending forward to the 'waist' of the foot where it turns dorsally and passes into the body. The rest of the columellar muscle originates on what appears to be the basement membrane of the ventral epithelium of the foot; these fibers are present throughout the foot and are termed dorso-ventral muscles (DVM). In the posterior part of the foot the dorso-ventral muscles join the main bulk of the columellar muscle before it enters the body. In the anterior region, the dorso-ventral

muscles join the cephalic branches of the columellar muscle before uniting with the main body of the muscle.

The transverse muscles (TM) run straight across the foot (Fig. 10) except in the posterior region where they are curved concavely toward the posterior end of the foot. Because of this curvature, the lateral ends of the transverse muscles are perpendicular to the margins of the foot. In cross section (Fig. 7B&C) the transverse fibers can be divided into dorsal and ventral groups, both of which are oriented diagonally in the transverse plane. The ventral groups (VTM) are closest to the sole near the lateral margins, rising above the sole as they approach the center of the foot where they lie dorsal to the longitudinal cleft. The dorsal groups (DTM) are oriented in such a way that they are closest to the sole in the central region of the foot and extend dorsally to the lateral margins.

The longitudinal (LM) and diagonal (DM) muscles are horizontal in the sagittal plane and are restricted to the lower 1/2 of the foot. Single longitudinal muscle cells do not appear to run the entire length of the foot although this may be an artifact of sectioning. In frontal section (Fig. 10), the longitudinal fibers are straight except along the postero-lateral margins where they are curved. There are a few muscle fibers in the postero-lateral regions of the foot that are not horizontal but curve downward from the operculum to the ventral region where they run parallel to the longitudinal fibers. The orientation of the diagonal fibers is best seen in frontal section (Fig. 10). These fibers are more dense in the anterior region of the foot and extend forward from the center of the foot to the lateral and anterior margins. The muscles do not stop at the mid-line of the foot; the result is a narrow region in the center of the foot where diagonal muscles from each 1/2 of the foot overlap. Each individual muscle fiber appears to have a sheath of connective tissue.

Locomotion. Thais rustica crawls using alternate ditaxic direct waves that propel the animal by compression, then elongation of the tissue of the foot. Observations of compression and elongation within a wave were aided by the presence of numerous folds in the epithelium of the sole; these folds are diagonal and extend posteriorly from the mid-line to the lateral margins of the foot (Fig. 11). The locomotory waves

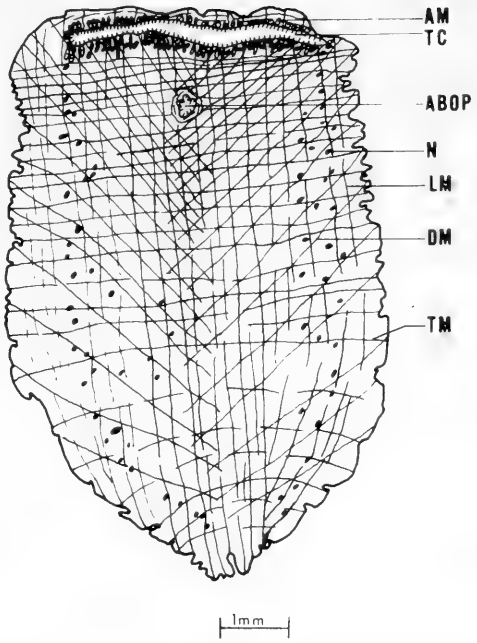

FIG. 10. Frontal section of *Thais rustica* foot. ABOP = pore of the accessory boring organ; AM = anterior mucocytes; DM = diagonal muscle; LM = longitudinal muscle; N = nerve; TC = transverse cleft; TM = transverse muscle. The density of the muscles has been reduced to clarify the figure.

move along the foot nearly parallel to the folds; temporary folds are also produced during the process of compression and disappear during elongation. When the diagonal folds were used as reference points, compression was observed to occur at the leading interface of the wave while elongation occurred at the following interface; the middle zone of the wave was fully compressed. Movement of the epithelium is directly towards the anterior end of the foot and not in the antero-lateral direction of wave propagation. The lateral margins of the foot bulge out during the passage of a wave. As is the case in *Neritina* the posterior margin of the foot is moved forward by compression whereas the anterior margin is advanced by elongation. As a pedal wave leaves the front of the foot, expansion of 1/2 of the anterior tip of the foot occurs simultaneously.

The timing of the waves is described beginning with a stationary animal. The animal begins to crawl when a wave is formed on the postero-median margin of the foot (Fig. 11A, wave 1). When wave 1

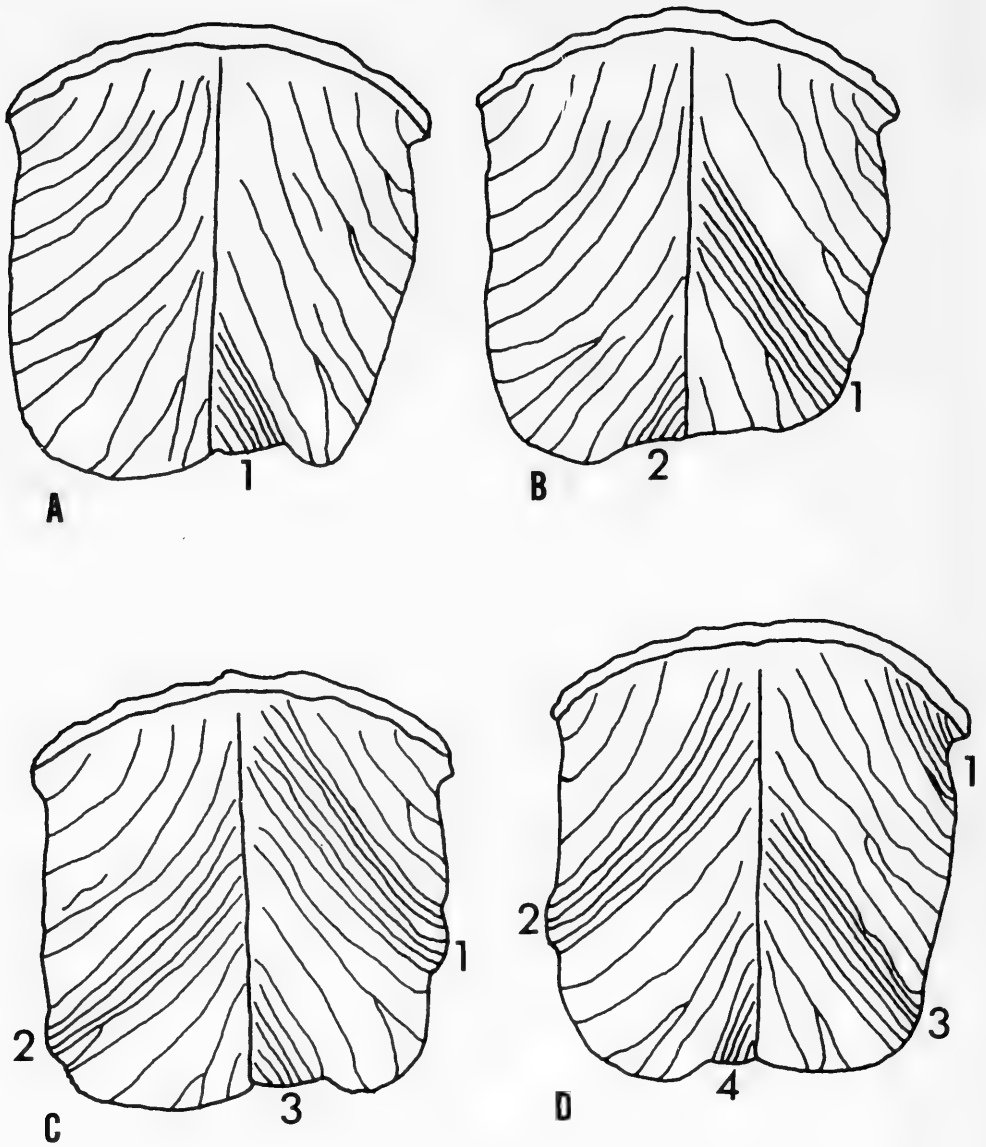

FIG. 11. Diagram of the pedal waves of *Thais rustica*. The sequence starts as if the animal were just beginning to crawl (A) and continues in "B" and "C" until wave number 1 reaches the anterior end of the foot in "D". The waves are numbered to show the timing of pedal waves on alternate sides of the foot. The anterior end of the foot is towards the top of the page.

reaches the halfway point in its trip along the foot, wave 2 forms on the opposite half of the foot. As the 1st wave reaches the anterior mid-line of the foot, and wave 2 is at its halfway point, wave 3 is formed on the same side as wave 1. Wave 4 is formed as wave 1 reaches the anterior lateral margin of the foot, wave 4 being on the same side as 2. Thus the anterior margin of 1/2 of the sole and the posterior margin of the other 1/2 move forward at the same time. The wavelength remains constant except for the appearance and disappearance of waves at the posterior and anterior ends of the foot. The orientation and distance between consecutive waves is constant.

Thais turns by bending the foot. During locomotion, the anterior lip of the transverse cleft is continuously moving in an undulatory manner. This movement is indepen-

dent of the movement of the waves and results in an opening and closing of the transverse cleft. The anterior end of the foot is folded so that the longitudinal cleft is at the apex of the fold when the animal is stationary. This fold is tucked into the shell along with the head giving the posterior portion of the foot, which remains in contact with the substratum, a circular outline.

DISCUSSION

Locomotion in *Neritina reclivata* is a result of the combined action of transverse and longitudinal muscles. Elongation, occurring at the leading interface of the wave, is brought about by contraction of the transverse muscles. This was deduced from the curvature of the leading interface of the wave, which is parallel to the transverse muscles, and the compression of the lateral margins of the foot within a wave, an event that occurs simultaneously with expansion. Compression, occurring at the following interface, is brought about by contraction of the longitudinal muscles, as was deduced from the re-extension of the transverse muscles when compression occurs.

Although contraction of the transverse muscles is the primary force causing extension of the longitudinal muscles, there is probably some force of extension provided by the contraction of longitudinal muscles at the following interface of the wave. The supposition that the transverse muscles at the following interface of a wave are partially extended by contraction of transverse muscles at the leading margin of a wave is possibly valid.

To summarize, contraction of the transverse muscles serves 3 functions in a retrograde wave: 1) to move the foot forward by expansion of the pedal sole, 2) to extend the longitudinal muscles and 3) possibly, to aid in re-extension of transverse muscles that are already contracted at the following margin of a wave. The functions of the longitudinal muscles are: 1) to move the foot forward by compression of the pedal sole, 2) to re-extend the transverse muscles to their resting length and 3) possibly, to aid in re-extension of the longitudinal muscles at the following margin of a wave that are already contracted.

When turning, *Neritina* uses a combination of direct and retrograde waves; 1/2 of the foot moves backward with direct waves, while the other 1/2 of the foot moves forward with retrograde waves. Reverse locomotion on the 1/2 with direct waves is initiated by contraction of the longitudinal muscles at the anterior end of the foot. This contraction moves that portion of the foot towards the rear and extends the transverse muscles on that side via the hydrostatic skeleton. These events were inferred from the creasing of the epithelium and the bulge at the lateral margins of the foot. The longitudinal muscles at the following interface of the wave are probably re-extended through contraction of the transverse muscles and by contraction of longitudinal muscles at the leading interface of the wave.

It would be conceptually convenient if locomotion in *Thais rustica* involved a reversal of the sequence of internal events that occur in retrograde waves in *Neritina* since the mechanisms are the converse of one another. Such is not the case, especially with respect to the transverse muscles, because of the diagonal orientation of the waves in *Thais*. The following analysis was based on the observed absence of transverse and diagonal displacement of the epithelium within a wave. The relative displacements of the diagonal and transverse muscles is generalized in Figs. 12 & 13 in that the angle of deformation of the transverse and diagonal muscles could be altered by varying the wavelength and spacing of the muscles.

Movement of the tissue in a forward, rather than a diagonal direction, leaves little doubt that compression of the tissue, the initial event in a wave, is caused by the longitudinal muscles. The transverse muscles are extended from their resting length by the diagonal orientation of the waves (Fig. 12). The amount of extension undergone by the transverse muscles is equal to the secant of the angle between the former and latter positions of the muscle (Fig. 12B). The tension on the diagonal muscles is reduced as a wave passes over them (Fig. 13). The amount of contraction of the diagonal muscles is equal to the cosine of the angle between the former and latter positions of the muscles (Fig. 13B). In my opinion, the transverse and diagonal muscles do not contribute significantly to forward locomotion because the transverse distance between the longitudinal muscles is constant. Because the transverse muscles are

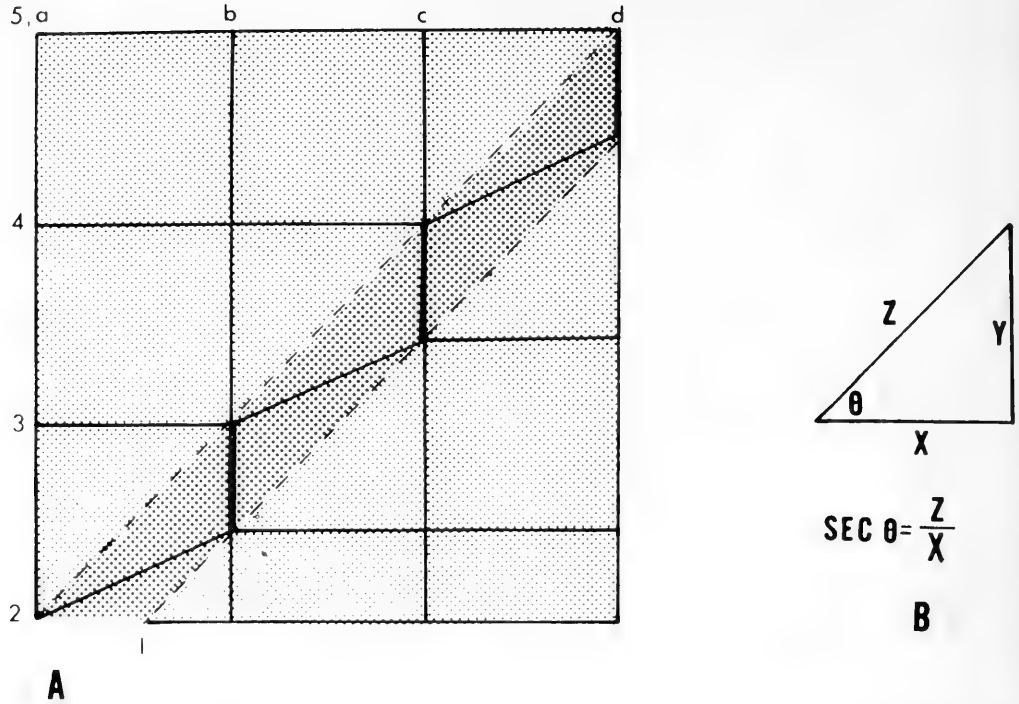

FIG. 12A: Diagram illustrating the longitudinal displacement of the transverse muscles during locomotion in *Thais rustica* as viewed in frontal section. The anterior midline of the foot is at the upper right. The direction of wave propagation is towards the upper left of the page. Transverse muscles are represented by the horizontal lines. The wave is indicated by the darker stipple. B: diagram showing the amount of extension undergone by a transverse muscle during the passage of a wave. x = resting length of a transverse muscle; y = the forward displacement of the right end of the muscle; z = the length of a transverse muscle within a wave; Θ = the angle between z and x; sec = amount of extension of the transverse muscles.

incapable of producing elongation, the longitudinal muscles serve as their own extensors and are responsible for compression and elongation within a wave.

The only problem that remains to be discussed is the extension of the anterior margin of the foot. The margin does not move forward until a wave has passed off the sole. Analysis of films showed that there is a lateral bulge present at the anterior end of the foot when a wave leaves the sole. This bulge disappears as the tip of the foot moves forward. The transverse muscles are probably extended as a result of the hydrostatic pressure created by contraction of the longitudinal muscles across the tip of the foot. Referring to Fig. 12, one can imagine that, as the wave progresses, muscle 4 will be moved forward; when the wave passes off the foot point 4 *a* will be extended laterally because all of the longitudinal muscles between 4 and 5 will be contracted. Therefore, when muscle 4 contracts, the hydrostatic skeleton will extend the longitudinal muscles and the tip of the foot.

The use of a flat pedal sole for locomotion and adhesion, as is common in the Gastropoda, requires the presence of mucus for lubrication and adhesion. The presence of several types of mucocytes in the foot suggests the possibility that the products of these cells are responsible for more than one function. The location of the anterior mucocytes and the movement of the anterior margin of the foot during locomotion leaves little doubt that these cells secrete a lubricating mucus. The subdermal mucocytes probably serve the same function, especially in *Neritina* in which they are more concentrated in the anterior 1/2 of the foot. There is no evidence that the epithelial mucocytes secrete an adhesive mucus although its acidic qualities might aid in surface preparation of some sort. The mucus that serves as a lubricant may also have adhesive properties because the foot is attached to the substratum in those areas not immediately under a wave. Suction

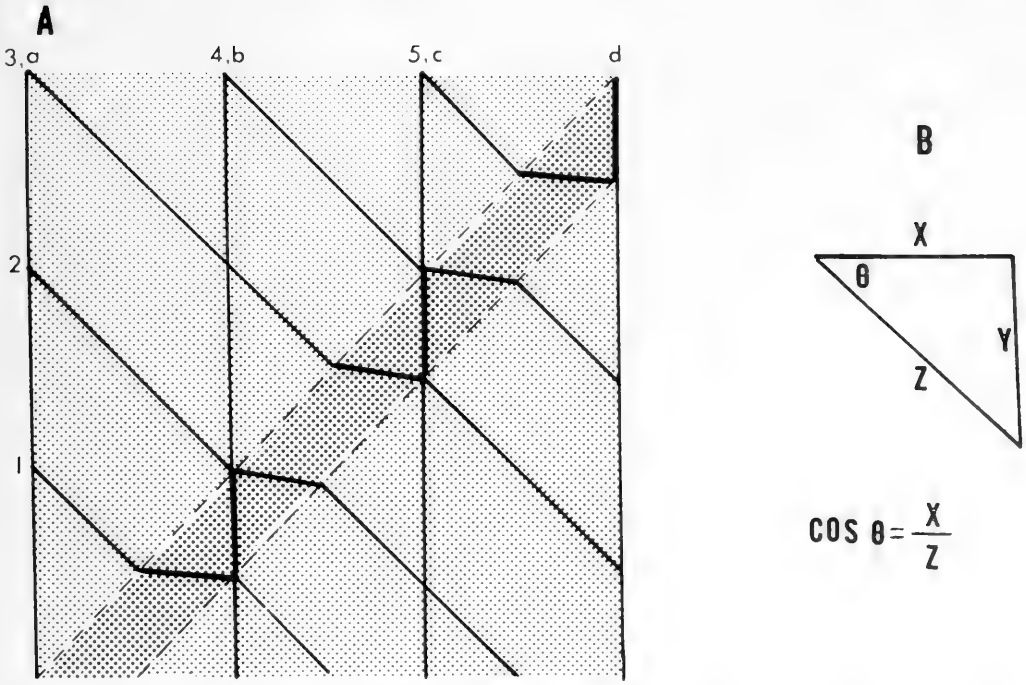

FIG. 13A: Diagram illustrating the displacement of the diagonal muscles during locomotion in *Thais rustica* as viewed in frontal section. B: diagram showing the amount of contraction undergone by the diagonal muscles. z = the resting length of the diagonal muscles; x = the length of the diagonal muscles within a wave; y = the forward displacement of the right tip of the muscle; cos = amount of contraction of the diagonal muscle. Other symbols the same as in Fig. 12.

appears to play a role in pedal adhesion when *Thais* and *Neritina* are at rest because the foot is nearly circular in outline, a shape that is ideally suited for suction. In addition, the center of the sole lifts off the substratum when an attempt is made to dislodge the animal; I have observed the same phenomenon in *Murex fulvescens, Nerita* spp., *Cymatium parthenopeum* and *Liguus fasciatus*.

Jones & Trueman (1970) concluded that locomotion in *Patella vulgata* is the result of the contraction of the dorso-ventral muscles. Personal observations on *Siphonaria pectinata* suggest a mechanism of locomotion similar to that described for *Patella*. The occurrence of 3 different mechanisms of muscular interaction to produce locomotion among 4 unrelated gastropods implies that the detailed patterns of locomotion have evolved independently in *Neritina, Thais, Siphonaria* and *Patella* and that the same mechanism may have evolved convergently in species of similar form such as *Patella* and *Siphonaria*.

When size, form, habitat and phylogeny are taken into consideration, several generalizations can be made concerning the occurrence of particular modes of locomotion. I concur with Elves (1961) that ciliary locomotion predominates in small gastropods. Examples are to be found in the Rissoacea, the Cerithiacea, *Epitonium, Trivia, Nassarius, Marginella* and *Anachis*. There are exceptions: *Littorina ziczac* is small, yet has muscular waves. This is probably in relation to its habitat and will be discussed later.

The form of the animal also has some bearing on the mode of locomotion. Species with high-spired shells typically crawl using a ciliary-B mode of locomotion that is characterized by the alternate movement of the foot and shell (see APPENDIX). The correlation is so strong in extant forms that I am confident that extinct forms with a similar kind of shell crawled in the same manner. The supposed close phylogenetic relationships among the Murchisoniacea, Loxonematacea and Cerithiacea, as well as the Nerineacea and the Pyramidellacea, enhance this view (Cox, 1960). A functional

relationship between locomotion and form is clear in this situation. Those species with a high-spired shell have a very small foot in relation to their overall size: in *Cerithium floridanum* the foot is 1/3 the length of the shell. The foot is so small that the shell cannot be carried upright but must be dragged behind the foot. This results in the uneven mode of locomotion that typifies these forms. The use of cilia to advance the foot is related to its small size.

The presence of muscular pedal waves in gastropods is, in some cases, a function of habitat and the size of the animal (Elves, 1961). Terrestrial gastropods generally employ pedal waves during locomotion. The correlation is probably a function of the weight of the animal since a given mass weighs more on land than in water, thus reducing the effectiveness of cilia as a means of terrestrial locomotion. The only exceptions known are *Discus rotundatus* (Elves, 1961), *Acicula fusca* (Creek, 1952) and certain zonitaceans (Pilsbry, 1946). All of these animals employ cilia as a means of locomotion, are very small and occupy moist micro-habitats. The significance of direct waves in pulmonates is unclear. The shorter wavelength of direct waves in comparison with retrograde waves may have been a factor in the selection of this mode because a shorter wavelength may encounter less frictional resistance from the substratum.

Gastropods living in the rocky intertidal zone often have retrograde waves. Examples include *Littorina, Nerita, Tegula* and patelliform genera. The presence of pedal waves in these forms is probably related to a greater reliance upon adhesion in agitated water as muscular waves enable a snail to keep a portion of its foot firmly attached to the substratum while at the same time moving forward, thus increasing its adhesion during locomotion. The predominance of retrograde waves may be a function of greater suction produced by such waves. Jones & Trueman (1970) recorded negative pressures under the pedal waves of *Patella vulgata*. Their observations also showed that the direct waves, produced when the animal turns, have a shorter wavelength than the retrograde waves. The same is true in *Tegula, Neritina* and *Siphonaria* (personal observations). If the vertical displacement of both types of waves is the same, then the total amount of force occurring under a direct wave may be less due to its smaller surface area. Therefore, the occurrence of retrograde waves in forms where adhesion is at a premium may be a function of suction under the wave.

The ability to turn using a combination of waves is restricted to *Patella* (Jones & Trueman, 1970), *Tegula* (Robert, 1907 and personal observation), *Siphonaria* and *Neritina* (personal observations). The ability to crawl backwards occurs in *Patella, Fissurella* (Olmsted, 1917), *Tegula* and chitons (Parker, 1911). All of these animals live in the rocky intertidal zone except for *Neritina*. The ability to turn by a combination of waves or crawl in reverse is probably of considerable advantage in the habitat of these animals in that the habitat is topographically rugged. In addition, the ability to turn around in one's own diameter may be advantageous in homing. The advantage to *Neritina* is more obscure. *Neritina* probably evolved from ancestors in the rocky intertidal zone but turning in the manner described may still be of advantage because *Neritina* inhabits narrow blades of grass which may restrict normal turning. Clearly, the ability to turn using a combination of waves is not due to any structural limitation of the foot in *Tegula* and *Neritina* as both animals can turn in the normal manner by a postural bending of the foot. In *Siphonaria* (personal observations) the foot is solid and is not capable of bending to any great extent; in addition, the foot is restricted to the aperture of the shell. Therefore, in *Siphonaria*, and probably other patelloids, the ability to turn with a combination of waves may be a result of the structure of the foot as well as the restrictive habitat.

The relationship of phylogeny to locomotion differs among taxa. There is little variation in locomotion below the generic level; this lack of variation may be the result of genetic stability in some instances, as in *Murex*, or of constancy in size, habitat and form. Above the generic and family level the influence of phylogeny varies considerably. The apparent constancy of locomotion in the Neritacea is probably the result of genetic stability since the examples in the Appendix have different habitats and sizes.

In summary, the relative importance and the interrelationship of size, form, habitat and phylogeny in determining the mode of locomotion varies within the class. In some instances certain combinations of ecological factors seem to be of primary importance

while in others the phylogenetic relationships of the animals involved overrides ecological variation.

APPENDIX

The following list is a compilation of the types of waves employed by gastropods I have observed. The reader is referred to a similar compilation by Miller (1974) for additional data. Some references omitted by her are also included here. I have followed the classification of Taylor & Sohl (1962) except that I have separated the Euthyneura into Opisthobranchia and Pulmonata.

Abbreviations: Ret = retrograde, Dir = direct, M = monotaxic, D = ditaxic, Cil = ciliary. Those animals with a 'B' under the ciliary column crawl by extending the foot forward with cilia while the shell is stationary. When the foot has ceased forward motion the shell and body are brought forward by contraction of the columellar muscle. Animals with the abbreviation 'R' are able to crawl backwards using the type of locomotion noted while those with a 'T' are able to turn using a combination of waves as was described for *Neritina*. An 'S' designates an animal with a longitudinal cleft on the pedal sole. I have observed those species followed by an asterisk.

		Ret		Dir		Cil	Notes
		M	D	M	D		
PROSOBRANCHIA							
Archaeogastropoda							
Fissurellacea							
Fissurellidae							
Fissurellinae							
Fissurella rosea (Gmelin)	*	+					
Diodorinae							
Diodora cayenensis (Lamarck)	*	+					
D. dysoni (Reeve)	*	+					
Patellacea							
Acmaeidae							
Acmaea digitalis Eschscholtz	*		+				
Trochacea							
Trochidae							
Tegula funebralis (A. Adams)	*		S		T		
Calliostoma bairdi (Verrill & Smith)	*		S				
C. jujubinum (Gmelin)	*		S				
Turbinidae							
Turbo castaneus Gmelin	*				S		
Astraea americana (Gmelin)	*		S				
Neritacea							
Neritidae							
Nerita tessellata Gmelin	*	+					1
N. peloronta Linné	*	+					
N. versicolor Gmelin	*	+					
N. fulgurans Gmelin	*	+					
Neritina reclivata (Say)	*	+			T		
Helicinidae							
Helicina spp.	(Pilsbry, 1948)	+					
H. angulata C. B. Adams	(Brown, 1910)	+					
H. orbiculata (Say)	*	+					
Mesogastropoda							
Viviparacea							
Ampullariidae							
Pomacea paludosa Say	*					+	
Littorinacea							
Littorinidae							
Littorina irrorata (Say)	*		S				

		Ret M	Ret D	Dir M	Dir D	Cil	Notes
L. ziczac (Gmelin)	*		S				
L. angulifera (Lamarck)	*		S				
L. planaxis (Philippi)	*		S				
L. scutulata Gould	*		S				
Tectarius muricatus (Linné)	*(Abbott, 1954)		S				
Echininus nodulosus (Pfeiffer)	*(Abbott, 1954)		S				
Nodilittorina tuberculata (Menke)	*(Abbott, 1954)		S				
Pomatiasidae							
Chondropoma dentatum (Say)	(Pilsbry, 1948)				S		
Pomatias (= Cyclostoma) sp.	(Parker, 1911)				S		
Adamsiella variabilis (C. B. Adams)	(Brown, 1910)				S		
A. ignilabris (C. B. Adams)	(Brown, 1910)				S		
A. irrorata Gloyne	(Brown, 1910)				S		
Colobostylus jayanus (C. B. Adams)	(Brown, 1910)				S		
C. banksianus (Sowerby)	(Brown, 1910)				S		
C. bronni (C. B. Adams)	(Brown, 1910)				S		
Tudora armata (C. B. Adams)	(Pilsbry, 1948)				S		
Annularia fimbiatula (Sowerby)	(Pilsbry, 1948)				S		
Rissoacea							
Aciculidae							
Acicula (= Acme) fusca (Beck)	(Creek, 1952)					+	
Bithyniidae							
Lyogyrus sp.	*					+	
Cerithiacea							
Cerithiidae							
Cerithium floridanum Mörch	*					B	2
Potamididae							
Batillaria minima (Gmelin)	*					B	2
Cerithidea scalariformis (Say)	*					B	
Pleuroceridae							
Pleurocera sp.	*					B	
Modulidae							
Modulus modulus (Linné)	*					+	3
Turritellidae							
Turritella communis Risso	(Yonge, 1946)					B	4
Epitoniacea							
Epitoniidae							
Epitonium angulatum (Say)	*					B	
Lamellariacea							
Eratoidae							
Trivia pediculus (Linné)	*					+	
Cypraeacea							
Ovulidae							
Neosimnia uniplicata (Sowerby)	*					+	
Calyptraeacea							
Calyptraeidae							
Crepidula maculosa Conrad	*			+			
Naticacea							
Naticidae							
Polinices heros (Say)	(Trueman, 1968)			+		+	5
Tonnacea							
Cymatiidae							
Cymatium parthenopeum (Von Salis)	*		+				
Neogastropoda							

		Ret M	Ret D	Dir M	Dir D	Cil	Notes
Muricacea							
Muricidae							
Muricinae							
Murex rubidus F. C. Baker	*		+				
M. fulvescens (Sowerby)	*		+				
M. florifer Reeve	*		+				
M. beaui Fischer & Bernardi	*		+				
M. pomum (Gmelin)	*		+				
Muricopsis ostrearum (Conrad)	*		+				
Purpurinae							
Urosalpinx perrugata (Conrad)	*		+				
Eupleura sulcidentata Dall	*		+				
Thais rustica (Lamarck)	*				S		
Thais haemastoma Link	*				S		
Buccinacea							
Buccinidae							
Cantharus cancellarius (Conrad)	*		+				
C. tinctus (Conrad)	*		+				
Melongenidae							
Melongena corona (Gmelin)	*		+			+	6
Busycon contrarium (Conrad)	*		+			+	
B. spiratum (Lamarck)	*		+			+	
Pyrenidae							
Anachis avara (Say)	*					+	7
Mitrella lunata (Say)	*					+	
Nassariidae							
Nassarius vibex (Say)	*					+	
Fasciolariidae							
Fasciolaria tulipa (Linné)	*		+				
F. hunteria (Perry)	*		+				
Pleuroploca gigantea (Kiener)	*		+				
Volutacea							
Olividae							
Oliva sayana Ravenel	*				+	+	8
Marginellidae							
Prunum apicinum (Menke)	*					+	9
Cancellariidae							
Cancellaria reticulata (Linné)	*					+	
Conacea							
Conidae							
Conus floridanus Gabb	*					+	
Terebridae							
Terebra dislocata (Say)	*					B	
Turridae							
Polystira albida (Perry)	*					+	
Kurtziella limonitella (Dall)	*		•			+	
OPISTHOBRANCHIA							
Anaspidea							
Aplysiacea							
Aplysiidae							
Notarchinae							
Bursatella leachi plei Rang	*					+	
Dolabriferinae							
Phyllaplysia zostericola McCauley	(McCauley, 1960)		+				10
Phyllaplysia sp.	*		+				

		Ret M	Ret D	Dir M	Dir D	Cil	Notes
Sacoglossa							
Oxynoacea							
Oxynoidae							
Oxynoe sp.	*					+	
Entomotaeniata							
Pyramidellacea							
Pyramidellidae							
Pyramidella crenulata (Holmes)	*					+	11
Odostomia impressa (Say)	*					+	
Turbonilla portoricana Dall & Simpson	*					B	
T. hemphilli Bush	*					B	
PULMONATA							
Basommatophora							
Patelliformia							
Siphonariidae							
Siphonaria pectinata (Linné)	*		+		T		
S. alternata Say	*		+		T		
Ancylacea							
Ancylidae							
Laevapex sp.	*					+	12
Physidae							
Physa fontinalis Draparnaud	(Elves, 1961)					+	
Planorbidae							
Helisoma sp.	*					+	
Biomphalaria glabrata (Say)	*					+	
Lymnaeacea							
Lymnaeidae							
Lymnaea peregra (Müller)	(Elves, 1961)					+	
Ellobiacea							
Ellobiidae							
Melampinae							
Melampus bidentatus Say	*			+			
Otinidae							
Otina otis Gray	(Vlès, 1913)		+				13
Stylommatophora							
Orthurethra							
Pupillacea							
Pupillidae							
Gastrocopta armifera (Say)	(Pilsbry, 1948)			+			
Vertigo ovata Say	(Pilsbry, 1948)			+			
Valloniidae							
Vallonia pulchella (Müller)	(Pilsbry, 1948)			+			
V. costata (Müller)	(Pilsbry, 1948)			+			
Heterurethra							
Succineacea							
Succineidae							
Succinea ovalis Say	(Pilsbry, 1948)			+			
Sigmurethra							
Holopodopes							
Rhytidacea							
Haplotrematidae							
Haplotrema concavum (Say)	(Pilsbry, 1946)			+			
Bulimulacea							
Bulimulidae							
Bulimulinae							

		Ret M	Ret D	Dir M	Dir D	Cil	Notes
Drymaeus multilineatus (Say)	(Pilsbry, 1946)			+			
Orthalicinae							
Liguus fasciatus Fischer & Crosse	*			+			
Urocoptidae							
Urocoptis turneri Pilsbry	(Pilsbry, 1946)			+			
U. pallidula Torre	(Pilsbry, 1946)			+			
Cochlodinella poeyana (d'Orbigny)	(Pilsbry, 1946)			+			
Achatinacea							
Spiraxidae							
Euglandina rosea (Férussac)	*			+			
Aulacopoda							
Endodontacea							
Endodontidae							
Discus rotundatus (Müller)	(Elves, 1961)					+	
Arionidae							
Arion sp.	(Vlès, 1907)			+			
Zonitacea							
Zonitidae							
Zonitinae							
Oxychilus spp.	(Pilsbry, 1946)			+			
Retinella electrina (Gould)	(Pilsbry, 1946)			+			
R. indentata (Say)	(Pilsbry, 1946)			+			
Mesomphix inornatus (Say)	(Pilsbry, 1946)			+			
Vitrinizonites spp.	(Pilsbry, 1946)			+			
Paravitrea multidentata (Binney)	(Pilsbry, 1946)					+	
Euconulinae							
Euconulus fulvus (Müller)	(Pilsbry, 1946)					+	
E. chersinus (Say)	(Pilsbry, 1946)					+	
Gastrodontinae							
Ventridens spp.	(Pilsbry, 1946)					+	
Striatura exigua (Stimpson)	(Pilsbry, 1946)					+	
Zonitoides arboreus (Say)	(Pilsbry, 1946)					+	
Z. nitidus (Müller)	(Elves, 1961)					+	
Milacidae							
Milax sowerbii (Férussac)	(Barr, 1926)			+			
Limacidae							
Limax sp.	(Vlès, 1907)			+			
Deroceras reticulatum (Müller)	(Pilsbry, 1948)			+			
Holopoda							
Helicacea							
Helicidae							
Helix sp.	(numerous authors)			+			14
Helix aspersa (Müller)	(Parker, 1937)	+		+			
Helminthoglyptidae							
Helminthoglypta dupetithouarsi (Deshayes)	(Carlson, 1905)	+		+			
	(Parker, 1937)	+		+			
Hygromia simularis (Férussac)	(Olmsted, 1917)			+			
Polygyracea							
Polygyridae							
Triodopsis sp.	*			+			

NOTES

1. Parker (1911) described *Nerita tessellata* as having opposite ditaxic waves in which the waves progressed down the lateral margins of the foot in phase with one another. I am convinced that nerites have monotaxic waves. Parker was probably misled because the waves are extremely difficult to see in the middle of the foot.

2. *Cerithium, Batillaria* and *Cerithidea* all crawl by extending the foot with cilia and then bringing the shell forward. In these genera the foot becomes elongated as it is extended. When the shell is brought forward the foot is contracted muscularly to its resting shape.

3. Even though *Modulus* is in the Cerithiacea it has a somewhat trochiform shell. As a result it crawls in a normal ciliary fashion rather than a ciliary-B as was described in note 2.

4. Yonge (1946) described the burrowing of *Turritella communis* although he failed to describe the mechanism by which the foot moves forward. I have hypothesized that it moves its foot forward by means of cilia due to its phylogenetic position and its small size. This would make its locomotion ciliary-B.

5. Copeland (1922) found that *Polinices* employs cilia when crawling upon the substratum. Direct waves were employed when resistance was encountered, as in burrowing. Trueman (1968) described another type of burrowing mechanism that was employed simultaneously with muscular pedal waves. It consists of expansion of the propodium into the substratum followed by contraction of the columellar muscle which pulls the mesopodium and shell forward. This mechanism is classified as an elongated retrograde wave.

6. Observations on *Busycon* and *Melongena* indicate that they generally crawl by means of cilia. I have observed them using ditaxic retrograde waves when crawling up the side of an aquarium. These waves are slow and have a long wavelength so that they are difficult to see.

7. *Anachis avara* crawls with a combination of cilia and muscular contractions when resistance is encountered. The sequence begins when the anterior 2/3 of the foot extends anteriorly. This is accomplished by cilia. When the anterior 2/3 is completely extended the anterior tip of the foot acts as a holdfast and the foot, along with the shell, is brought forward.

8. When crawling on glass or on sand *Oliva* employs cilia as a means of locomotion. When burrowing, the animal employs direct monotaxic waves. These waves start in the middle of the foot and move forward, the posterior 1/2 is either dragged passively forward or advances with the aid of cilia.

9. *Prunum* uses a ciliary-B type of locomotion when crawling beneath the sand. The anterior end of the foot, which is normally blunt, is folded to form a point as the foot moves forward. When the foot stops and the shell is carried forward, the anterior margin of the foot is unfolded to act as a holdfast.

10. McCauley (1960) described the locomotion of *Phyllaplysia* but failed to state that this animal crawls using monotaxic retrograde waves. My observations indicate that locomotion is initiated by the elongation of the anterior 3/4 of the foot. This elongation occurs simultaneously with transverse compression of the foot. When elongation is complete the anterior tip of the foot acts as a holdfast and the foot is compressed. As in elongation, the compression is simultaneous and the foot comes to rest in an elliptical shape at which time the process starts again. The posterior 1/4 of the foot does not undergo elongation or compression. It serves as a holdfast while expansion occurs and is drawn passively forward during compression. In this system of locomotion the wavelength is equal to the active region of the foot.

11. Although *Pyramidella* has a high-spired shell it crawls in a continuous, rather than an intermittent, fashion because its shell is so light that the animal is able to hold it above the substratum.

12. Even though *Laevapex* is patelliform it crawls by means of cilia, as opposed to retrograde waves which are used by most patelliform gastropods. This is probably a function of the small size of the animal as it is less than 1 cm in length.

13. *Otina* and *Siphonaria* are the only pulmonates known to me to use retrograde waves. They are both patelloid and live in the rocky intertidal zone.

14. Carlson (1905) and Parker (1937) described a 'galloping' mode of locomotion

for *Helix*. It consists of a large retrograde wave that appears simultaneously with the monotaxic direct waves, which are the normal means of progression.

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INTRASPECIFIC VARIATIONS IN GROWTH, BIRTH PERIODS, AND LONGEVITY OF *MUSCULIUM SECURIS* (BIVALVIA: SPHAERIIDAE) NEAR OTTAWA, CANADA

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ABSTRACT

Samples were collected at least once a month for 1 to 3 years from 4 diverse habitats near Ottawa, Ontario, Canada, to provide a basis for research on the growth, birth period and life span of *Musculium securis* (Prime). Analyses of the life history samples and the results from laboratory and field experiments showed that growth of newborn begins in the spring and is usually completed within 60-70 days. Births of young occur in early summer and/or late summer-early autumn. The species usually has a life span of approximately 1 year. Intrapopulation variations in growth, and to some extent birth periods and longevity, are more pronounced in temporary aquatic habitats than permanent aquatic habitats. Interpopulation transplants of *M. securis* indicate that growth may be adaptively modified.

INTRODUCTION

This study examines some life history aspects of 4 populations of *Musculium securis* (Prime) near Ottawa, Ontario, Canada. Two populations were inhabiting temporary forest ponds, 1 was from a river, and the 4th was from a permanent pond.

The objectives of the study were to investigate possible intraspecific variations in growth, birth periods, and longevity of *Musculium securis.* Although life history studies of sphaeriids are numerous (Gilmore, 1917; Thiel, 1926; Monk, 1928; Foster, 1932; Mitropolskji, 1965; Gale, 1969; Avolizi, 1971; Zumoff, 1973), few have taken into account the intraspecific variations in life history. Heard (in press) has briefly described some life history aspects of *M. securis*, although his observations were qualitative and non-seasonal.

STUDY AREAS

Mackie (1973) has described the study areas in detail. Only brief descriptions of the 4 habitats are given below.

One temporary pond is located in a deciduous forest near Carp, Ontario, and is called Carp Pond. The pond is approximately $100 \times 150\ m^2$ in area, with a maximum depth of 1 m. White elm (*Ulmus americana*), black willow (*Salix nigra*), and red maple (*Acer rubrum*) are the most common trees scattered throughout the pond. The most abundant single macroinvertebrate in Carp Pond is *Musculium securis.* Other common species include the gastropods *Helisoma anceps, Gyraulus parvus, Physa gyrina*, and *Lymnaea elodes*, the amphipod *Hyalella azteca*, the isopod *Asellus* sp., the anostracan *Eubranchipus* sp., and several species of Chironomidae, Culicidae and Trichoptera.

The 2nd temporary pond is located south of Greely, Ontario, and is called Greely Pond. Willows (*Salix* spp.), trembling aspen (*Populus tremuloides*), white elm, and red maple are the most common tree species within the pond. The maximum depth of the

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pond is 0.8 m and has an area of approximately 300 × 300 m. *Sphaerium occidentale* and *Musculium securis* are the most abundant macroinvertebrates with the former being approximately twice as numerous as the latter. Other common benthic organisms include *Physa gyrina, Lymnaea elodes, Hyalella azteca, Asellus* sp., Diptera and Trichoptera. Both Carp Pond and Greely Pond are usually dry from August to November.

The 3rd population occurs in Britannia Bay of the Ottawa River near Ottawa, Ontario. Larger populations of *Musculium securis* occur in the mud of the 3-4 m depths than in the fine sand of the 0-3 m depths where other sphaeriids (*Musculium transversum* and *Sphaerium striatinum*) predominate. Mackie (1971) found approximately 100 species of benthic macroinvertebrates in Britannia Bay. Unlike the other habitats, Britannia Bay has many fish species, including catfish (*Ictalurus punctatus*), pike (*Esox lucius*), walleye (*Stizostedion vitreum*), and yellow perch (*Perca flavescens*).

The 4th habitat studied is a large permanent pond called Lac Bourgeois, which is situated in the Gatineau Hills near Hull, Quebec. The pond is surrounded by a hardwood forest composed mainly of maples (*Acer* spp.) and oaks (*Quercus* spp.), measures approximately 200 × 450 m and has a maximum depth of 3 m. Having a contagious distribution in Lac Bourgeois, *Musculium securis* is confined to a small area (4 × 8 m) on the E shore in the shade of several small willow trees. *Gyraulus parvus, Physa gyrina, Lymnaea elodes, Hyalella azteca,* and several species of Diptera, Odonata and Trichoptera are also common in Lac Bourgeois.

MATERIALS AND METHODS

The post-larval growth, birth periods and longevity of *Musculium securis* were determined from seasonal field collections and from clams maintained in the field and in the laboratory.

Seasonal field collections

Seasonal field collections were taken from each population at usually 2 week intervals in the summer and 4 week intervals in the winter. For the life history studies, random quantitative samples were taken from Britannia Bay with a standard Ekman grab (15 × 15 cm, with screen on top) and qualitative samples from the remaining habitats with an ordinary domestic sieve. Seasonal quantitative estimates of the Carp Pond population were taken with the Ekman grab. The sizes of samples needed to show differences between means of shell lengths of different populations at $p < 0.05$ were determined from the sample size formula of Simpson et al. (1960: 196). The specific dates of collections and the sample sizes are shown in Fig. 3.

All clams used for life history studies were preserved immediately in 70% ethanol. Since some clams prematurely released their young, individuals greater than approximately 3 mm in length were isolated and put into vials containing 70% ethanol. For each clam in the seasonal field collections, lengths and heights were measured in mm to 2 decimal places with a Precision Tools and Instruments Co. Ltd. microscope micrometer, model 14.

In plotting seasonal size-frequency distributions of *Musculium securis* from each population, 13 length classes of 0.49 mm increments were used (length class 1 = 0-0.49 mm, 2 = 0.50-0.99 mm, 3 = 1.00-1.49 mm, . .12 = 5.50-5.99 mm, and 13 = > 6.00 mm). To allow comparisons of the histograms, the frequency in each length class is shown as a percentage of the total number in each sample.

The birth periods and longevities of *Musculium securis* for each population were determined from the size frequency histograms. These were confirmed by maintaining clams in the field.

Weights were taken of more than 200 clams selected at random from various field collections and representing all length classes of adults. The soft tissue was removed from the shells of each individual by hand and both shell and tissue were dried in an oven at 60°C. Total weight (shell plus tissue) and shell weight only for each clam was determined in grams to 6 decimal places with a Sartorius microbalance.

Maintenance of M. securis *in the laboratory and field*

Adults were maintained in the field and laboratory to complement the life history studies based on seasonal field collections. As defined by Heard (in press), in the maintenance of adults, young are born but

they are not kept alive to investigate their life cycles.

Growth tubes, prepared from plastic vials 45 mm wide × 70 mm high (Mackie, 1973), were used to maintain adults in the field. Racks, made from 1 cm-thick Plexiglas sheet, were cut and drilled to hold 20 growth tubes.

For life history studies, a rack of 20 tubes was put into each of Carp Pond, Britannia Bay, and Lac Bourgeois on May 9, 1972. Greely Pond was not investigated in this way (it was first examined on June 6, 1972). Each growth tube contained one newborn and substrate (1 cm deep) from the habitat in which the tube was placed. The lengths of adults were measured at approximately 2 week intervals until their deaths. Newborn were counted and removed as soon as they appeared in each tube. The numbers of litters produced by each parent were also noted.

Interpopulation transplants were done to determine if the growth rates, birth periods, and longevities of *Musculium securis* had environmental or genetic bases. Newborn *M. securis* from each habitat were isolated and maintained in growth tubes in each of the other habitats (except Greely Pond) as well as its own. Lengths of these clams were measured at approximately 2 week intervals until their deaths.

Adults from Carp Pond, Britannia Bay, and Lac Bourgeois were also maintained in the laboratory. Since *Musculium securis* would grow only in the presence of tree foliage, only substrate and leaves from Carp Pond were used. "Pyrex" dishes, 100 mm in diameter × 50 mm deep, were used as growth dishes. Five *M. securis* newborn from each habitat were put into each of the 3 dishes. Three replicates were made of each dish containing 5 *M. securis*, 50 g of air dry Carp Pond soil, 2 g of air-dried white elm leaves, and chlorine-free tap water. The lengths of adults were recorded at frequent intervals, and the total number of young produced in each dish was recorded.

Statistical procedures

Since all growth curves of *M. securis* reached an asymptotic value on approximately the 70th day, asymptotic regression formulae were fitted to the growth data. The modified exponential, $Y = A+BR^x$, gave the best fit to hyperbolic growth curves but transgeneration of this regression to the logistic equation, $1/Y = A+BR^x$, gave the best fit to sigmoid growth curves. The coefficient A is the asymptotic value or the maximum length (mm) attained, B is the distance between the asymptotic value and the value of Y when $x = 0$ (i.e. the increment in growth since birth), and R is the ratio of successive differences along the curve.

The logistic regression is merely a modified exponential in terms of the reciprocals of the Y values. That is, A in the logistic expression equals 1/A of the modified exponential (when $x = 0$ and $B = 0$). Also, B of the logistic equation equals 1/Y - 1/A of the modified exponential (when $x = 0$). Therefore, to compare coefficients between the 2 curves, it was necessary to make the appropriate conversions. A Fortran computer program was used to calculate the asymptotic regression of *Musculium securis* in all growth experiments. The program, described by Dixon (1971: 297-311), is called "BMD 06R."

Results of the growth experiments are reported in figures and tables. There were no significant differences ($P > 0.05$) in the growths of *Musculium securis* between replicates, as determined by the Student's *t* test (Simpson et al., 1960: 178) on A and B of the regressions. Therefore, the growth curves of *M. securis* are plotted as average observed growth in length within replicated dishes. Significant differences between mean asymptotic values (A) and between growth increments since birth (B) of different growth curves are presented in tables. However, as indicated above, it was necessary to make the appropriate inversion of the coefficient of the logistic expression back to the modified exponential and to express Y and the coefficients in terms of the original units of measurements. Therefore, the A and B values of the logistic expression $1/Y = A+BR^x$, were re-inverted so that $A' = 1/A$ ($x = 0$, $B = 0$) and $B' = 1/(1/Y-A)$. The inversions are indicated in the tables with the expression $1/Y' = A' + B'R^x$.

RESULTS

Growth

The length-height relationships of shells of *Musculium securis* from the 4 populations are shown in Fig. 1. Individuals of all

populations studied had similar ($P < 0.01$) length-height relationships. In general the length was 1.2 times the height.

The relationship between growth in shell length and total dry weight of *Musculium securis* is shown in Fig. 2. Shell weight accounted for over 90% of the total weight. All populations studied had similar length-weight relationships.

Carp Pond—The seasonal size-frequency distributions of *Musculium securis* in Carp Pond for the 3 years of study are shown in Fig. 3. Adult (post-larval clams) in the 1st collection (May 25, 1970) were arbitrarily designated the P_1 (1st parental) generation. All larvae contained within these parents (adults carrying young) were called collectively, the F_1 (1st filial) generation. The adult sample of May 25 was unimodal and the shift of this mode was easy to follow in the frequency plots through July, after which these P_1 died. Parents of length class 10 were present in late May but were not gravid (carrying shelled larvae) until mid-June when even length class 9 was gravid, indicating that gravidity was a function of both incubation time and size of parent.

A P_2 (2nd parental) generation (length class 4, Fig. 3) appeared in early July, giving the sample a bimodal distribution. Bimodality occurred only in the month of July with the P_1 generation dying in late July or early August when the pond was drying up. Only newborn (length classes 3, 4, and 5) estivated during the summer months. Water appeared in the pond again by November 15 and the newborn hibernated until early May, 1971 when growth ensued. Similar events occurred in 1971 as in 1970 with a P_3 generation appearing in late June.

In 1972 a P_4 generation appeared in mid-July as in previous years but the pond did not dry up and the bimodal distribution persisted until mid-October. Moreover,

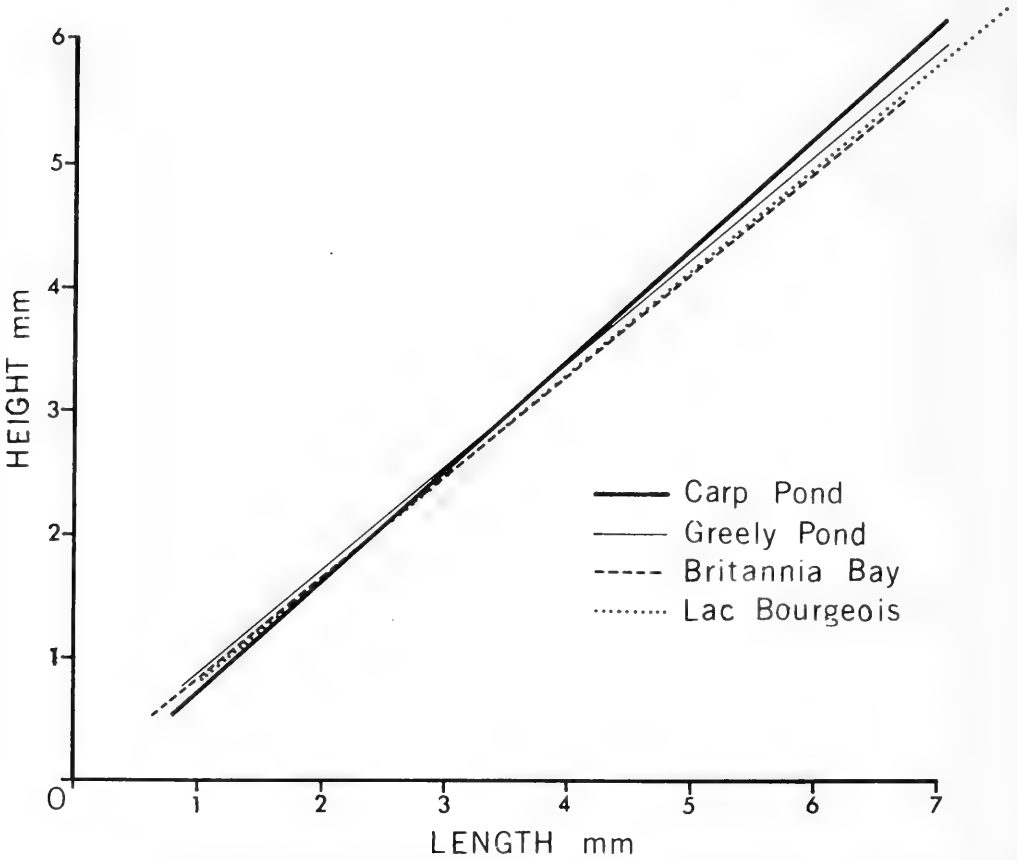

FIG. 1. The shell length-height relationship of *Musculium securis* in Carp Pond (Y = –0.22+0.90X, N = 158, r = 0.98), Greely Pond (Y = –0.18+0.88X, N = 130, r = 0.98), Britannia Bay (Y = –0.09+0.84X, N = 175, r = 0.99), and Lac Bourgeois (Y = –0.13+0.86X, N = 150, r = 0.98).

growth of the P_4 generation began in late August so that the hibernating generation consisted of several length classes of adults.

Greely Pond—The seasonal size-frequency distribution of *M. securis* in Greely Pond (Fig. 3) is similar to that for Carp Pond in 1972-1973. Newborn dominated the hibernating generation (November to April) but several other length classes were also present.

Britannia Bay—Samples collected from Britannia Bay in 1970 exhibited a bimodal distribution of length classes for the P_1 generation (Fig. 3). This bimodal character is more clearly seen in the P_2 generation of 1972 samples and indicates the simultaneous presence of 2 generations. However, on the basis of calyculism where calyculate adults are of the 1st generation and uncalyculate

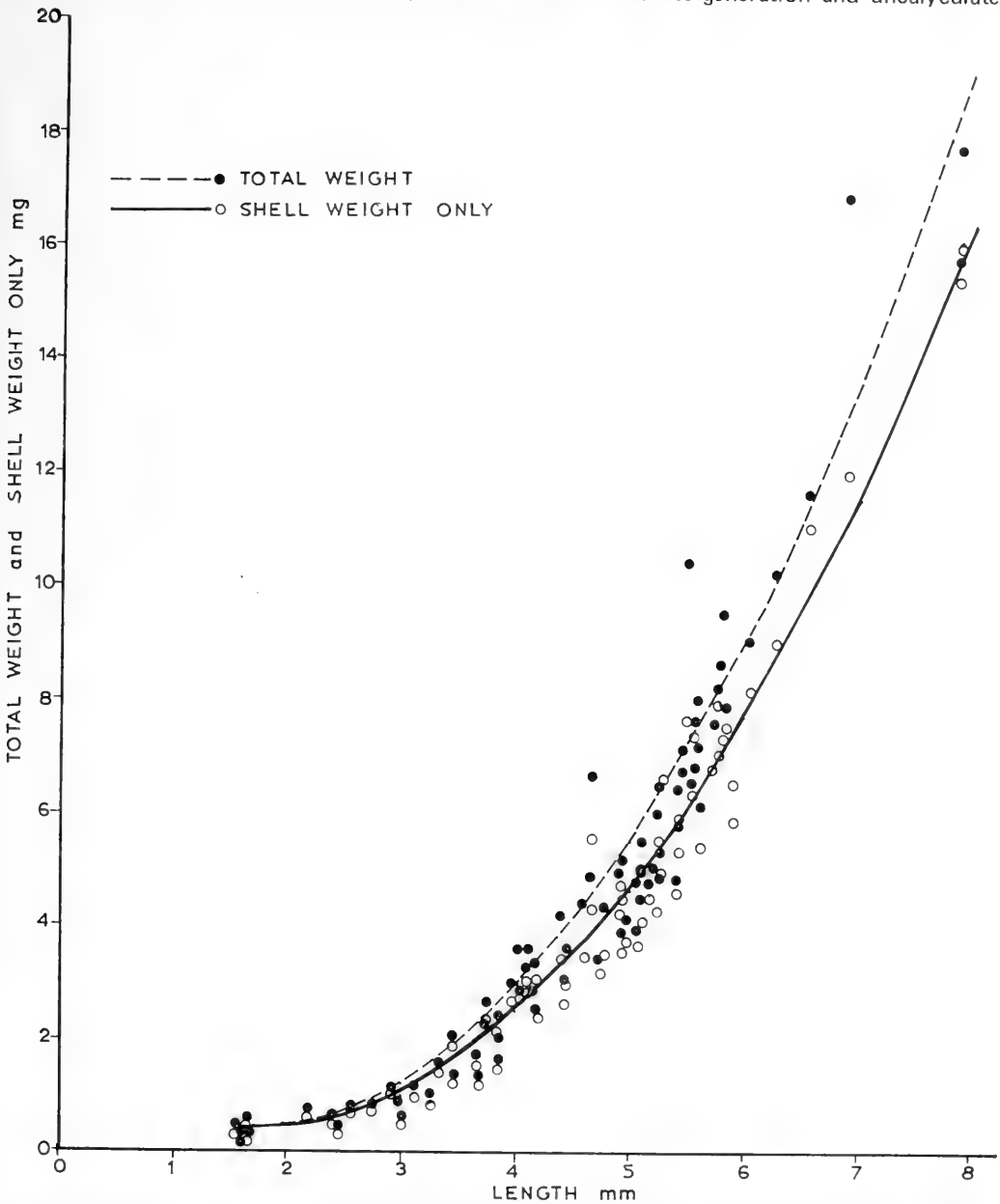

FIG. 2. Relation between total dry weight and shell length ($Y = 1.86 - 1.63x + 0.47x^2$, $N = 80$, $r = 0.92$) of *Musculium securis* from Carp Pond.

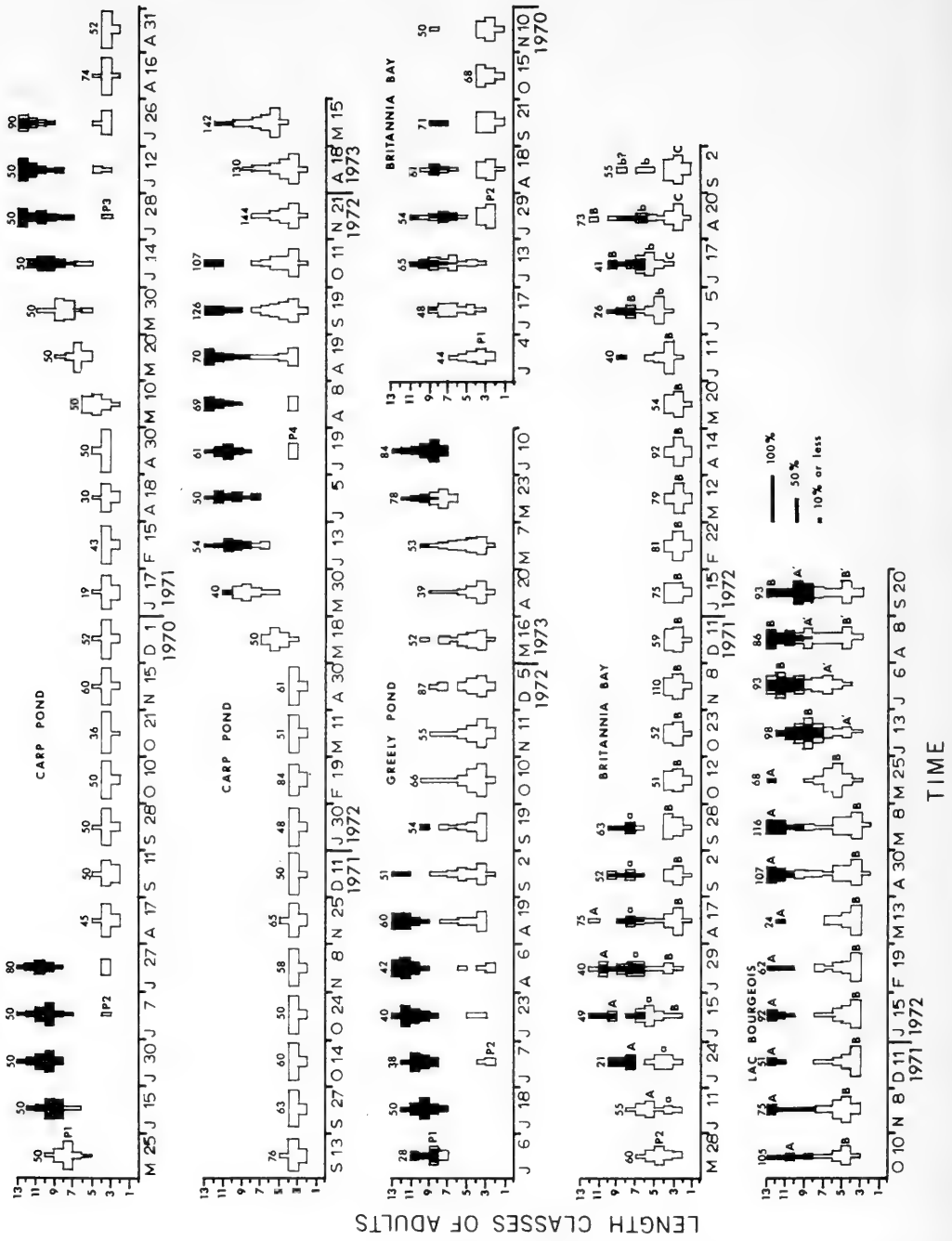

FIG. 3. Seasonal size-frequency distribution of *Musculium securis* in Carp Pond (from May 25, 1970 to May 15, 1973), in Greely Pond (from June 6, 1972 to June 10, 1973), in Britannia Bay (from June 4, 1970 to September 2, 1972) and in Lac Bourgeois (from October 10, 1971 to September 20, 1972). Length classes 1-12 represent length increments of 0.50 mm, size class 13 includes lengths greater than 6.00 mm. Black areas denote gravid adults. Numbers above each histogram represent the sample sizes. For further explanation, see text.

are of the 2nd generation of the year (Mackie & Qadri, 1974), only 1 generation of the calyculate adults was present until June 24 and the population consisted of slow-growing (mode a) and fast-growing (mode A) individuals. Measurements of the lengths of calyculae showed that newborn of lengths greater than 1.35 mm had growth rates similar to those of other populations whereas those less than 1.00 mm long appeared to have much slower growth rates. There was also a 4 week lag in growth of *M. securis* in Britannia Bay, which can probably be attributed to the lag in temperature increase of the water (Mackie, 1973).

A trimodal distribution with modes a, A, and B occurred in the 1971 samples collected on July 15, July 29, and August 17 (Fig. 3). The 3rd mode (B) represents the P_3 generation. Mode B was also composed of slow-growing (mode b) and fast-growing (mode B) individuals which were clearly seen in the sample of July 5, 1972. The fast-growing adults of 1971 were not gravid until they attained lengths of 2.50-3.00 mm. Mode A individuals had disappeared by September 1971 and only slow-growing individuals of the P_2 generation and newborn of the P_3 generation were present until June 11, 1972. However, some members of the P_3 generation had grown to maturity by late September, as indicated by the absence of calyculae. The hibernating generation thus consisted of newborn of the P_3 generation and also of a P_4 generation (mode C).

These results were confirmed by the maintenance of adults in growth tubes in Britannia Bay. Newborn from the P_2 generation with calyculae longer than 1.35 mm had grown rapidly and some had produced young precociously early in July. These precocious young had grown to maturity by September to give birth to another generation. The newborn of this new generation were significantly smaller ($P < 0.05$) than those of lengths greater than 1.35 mm and did not give birth to young.

Lac Bourgeois—A bimodal size-frequency distribution (modes A and B, Fig. 3) was characteristic of the fall and winter populations in Lac Bourgeois. Mackie and Qadri (1974) have given the relative proportions of newborn, calyculate, uncalyculate, and annulated adults in the samples. The fall and winter populations must have been born in the summer months of 1971 since calyculae were absent on the adults. Spring and summer populations of 1972 consisted of calyculate adults that were probably born in the fall and/or winter of 1971, and of uncalyculate and uncalyculate-annulated adults that were probably born in the summer of 1972 and 1971, respectively. The modes, therefore, represent adults born in the summer months (mode A) and adults born in the fall and winter months (mode B). By February 19, 1972, all parents had released their extra-marsupial larvae so that mode A′ probably represents the birth of 2nd (and probably 3rd) litters of extra-marsupial larvae. Mode B′ represents adults that were probably born in late July, 1972. Presumably, mode B would have disappeared in the fall of 1972 and the size-frequency distribution then would have been similar to that of October, 1971.

Seasonal plots of mode B showed that the growth of *Musculium securis* in Lac Bourgeois during the spring and summer was rapid and did not appear to differ from the growth of clams in other populations except for the slow-growing adults of Britannia Bay. However, the growths of *M. securis* in growth tubes in Lac Bourgeois did differ significantly ($P < 0.05$) from those grown in Britannia Bay (Table 1); also, no significant differences in growth were observed between the Lac Bourgeois and Carp Pond clams reared in growth tubes.

Birth period

The Carp Pond population had only 1 birth period per year. Births of extra-marsupial larvae in 1970 and 1971 occurred immediately before the disappearance of water from the pond in late July. Upon birth, the newborn burrowed 1-8 cm below the soil where they estivated until November when they began hibernation. The birth period in 1972 extended from late July to mid-October when most parents died in both Carp Pond and Greely Pond (Fig. 3).

There were 2 birth periods per year in the Britannia Bay population. Some young were born in July-August. Those born in early July grew rapidly and produced a litter in September.

Births occurred throughout the year in Lac Bourgeois, although newborn dominated the winter population, suggesting that many births occurred in late fall or early winter. Another birth period probably occurred in

TABLE 1. Asymptotic growth data for the regressions $Y = A + BR^x$ and $1/Y = A + BR^x$ of adults of *Musculium securis* transplanted into Carp Pond, Britannia Bay, and Lac Bourgeois. The A and B values of the logistic equation are transformed to permit tests of significant differences among all groups. Means side-scored by the same line are not significantly different at P = 0.05. Twenty specimens were put into each habitat but only N number matured.

Populations transplanted from:	Growth form	Mean and standard deviation ( ) of asymptotic regression data for $Y = A + BR^x$ and $1/Y = A + BR^x$ (or $1/Y' = A' + B'R^x$)					
Lac Bourgeois into:		Amm		Bmm		R	
Britannia Bay (N = 16)	1/Y	0.151	(0.033)	0.477	(0.033)	0.980	(0.0044)
	1/Y′	6.42	(0.72)	−5.94	(0.68)		
Lac Bourgeois (control) (N = 18)	1/Y	0.161	(0.015)	0.469	(0.015)	0.989	(0.0036)
	1/Y′	6.21	(0.62)	−4.68	(0.60)		
Carp Pond (N = 16)	1/Y	0.166	(0.009)	0.465	(0.010)	0.986	(0.0028)
Carp Pond into:	1/Y′	6.02	(0.34)	−4.50	(0.33)		
Britannia Bay (N = 17)	1/Y	0.162	(0.021)	0.464	(0.020)	0.985	(0.0038)
	1/Y′	6.18	(0.80)	−4.65	(0.76)		
Carp Pond (control) (N = 17)	1/Y	0.164	(0.010)	0.463	(0.010)	0.985	(0.0021)
	1/Y′	6.09	(0.34)	−4.58	(0.33)		
Lac Bourgeois (N = 16)	1/Y	0.172	(0.030)	0.457)	(0.030)	0.978	(0.0051)
	1/Y′	5.82	(0.94)	−4.37	(0.90)		
Britannia Bay into:							
Britannia Bay (control) (N = 18)	1/Y	0.188	(0.014)	0.439	(0.012)	0.983	(0.0051)
	1/Y′	5.32	(0.38)	−3.81	(0.32)		
Lac Bourgeois (N = 15)	Y	4.63	(0.73)	−2.19	(0.68)	0.989	(0.0035)
Carp Pond (N = 14)	Y	4.44	(0.58)	−2.00	(0.54)	0.985	(0.0023)

July since the August 8 collection was dominated by size class 5 (Fig. 3).

Data from the maintenance of adults in all habitats, except in Greely Pond, supported the above results. Births occurred in the growth tubes during late July in Carp Pond, in early July and mid-September in Britannia Bay, and in late July in Lac Bourgeois. The young born early in Britannia Bay growth tubes grew rapidly and produced a mid-September litter. Similar results were obtained when adults from Carp Pond and Lac Bourgeois were transplanted into Britannia Bay, and when the newborns from each of these populations were maintained in the laboratory. Therefore, in each population, parents usually gave birth about 60-70 days after their own birth.

The earlier newborn were usually born with a smaller size than those born later in the temporary habitats and with a larger size than those born later in the permanent aquatic habitats. Newborn that appeared in early July in Carp Pond and Greely Pond were of length classes 3 and 4 whereas those born later were of length class 5. Conversely, newborn born in July in Britannia Bay were of length classes 3 and 4 whereas those born in late summer were of length class 2.

The births of a total of 28 extra-marsupial larvae from 7 parents were observed. It took 1 parent approximately 18 min to release 4 young. All parents had released their young within 45 min. During the birth of young, the parent usually laid on its side with the valves slightly gaping and the siphons either fully extended or relaxed. Prior to birth, the extra-marsupial larvae moved almost continuously within the parent. This action may have severed the attachment of the byssal stalk from the foot of the larva. Heard (in press) has suggested that the byssal stalk, which is produced in the byssal gland in the foot of the prodissoconch larva during its development (Mackie, Qadri & Clarke 1974), prevents precocious birth of young. This tends to support the contention of Yonge (1962) that the byssus is a larval characteristic and its retention into adult life is a neotenous feature of bivalve evolution. After freeing itself from the byssal stalk the extra-marsupial larvae were always released via the anal siphon, usually "head-first." In this manner the foot of the larva usually preceded the body proper, and grasped either the parent's shell or the substrate to pull itself out. When the larvae were released with the posterior end first, the parent appeared to "spit" them out by first extending its siphon and then suddenly retracting it. It is not known what factors were responsible for inducing birth of extra-marsupial larvae.

Longevity

Analyses of the size-frequency histograms (Fig. 3) show that *M. securis* lived for approximately 1 year in each habitat. The life span was extended for only 3 months with the persistence of an aquatic environment in Carp Pond in 1972. The longevity of *Musculium securis* in the maintenance studies was 80-100 days when newborn were permitted to grow immediately after birth. The life span was increased significantly by maintaining newborn in a cold room at 5°C for 4 months and then growing them at 18°C for 80-100 days.

Interpopulation transplants

The results of the transplantations (Fig. 4, Table 1) show that the growth of Carp Pond and Lac Bourgeois adults in their own habitats did not differ significantly when transplanted into other habitats. The growths of Britannia Bay adults in Britannia Bay did, however, differ ($P < 0.05$) from those transplanted in Carp Pond and Lac Bourgeois.

Approximately 25% of the Britannia Bay adults, as well as adults from Carp Pond and Lac Bourgeois transplanted into Britannia Bay, produced young in early July. These adults matured into uncalyculate adults that produced a litter in September. Newborn that appeared near the end of July and early August did not continue growth in the fall in any of the populations.

Most of the 1st generation adults died by early August and those that were still alive in August did not grow substantially in September (Fig. 4). Dissection of the larger adults that were alive in September (mainly uncalyculate adults) showed that all extramarsupial larvae had been released and that the other larval stages appeared to be too immature to be born before the onset of cold weather.

DISCUSSION AND CONCLUSIONS

Intraspecific variations in the life history of Musculium securis

The data demonstrate intraspecific variations in growth, birth periods, and longevity. These variations were present at both the intrapopulation and interpopulation levels, and as in many mollusks, particularly gastropods (Hunter, 1961, 1964), were determined partly by environmental and partly by endogenous factors.

The environmental influence was present

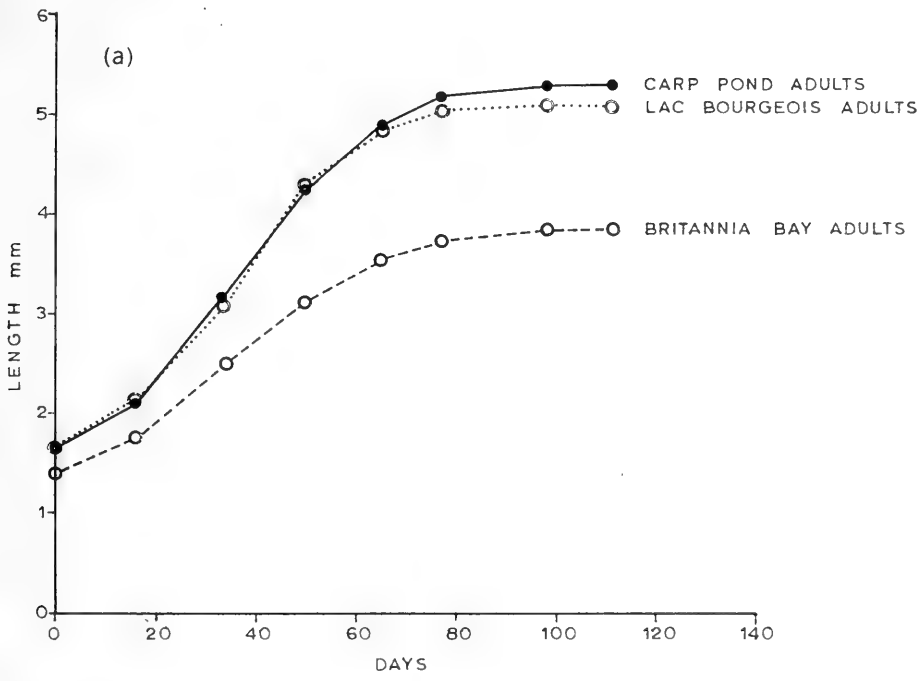

FIG. 4(a). Caption on p. 442.

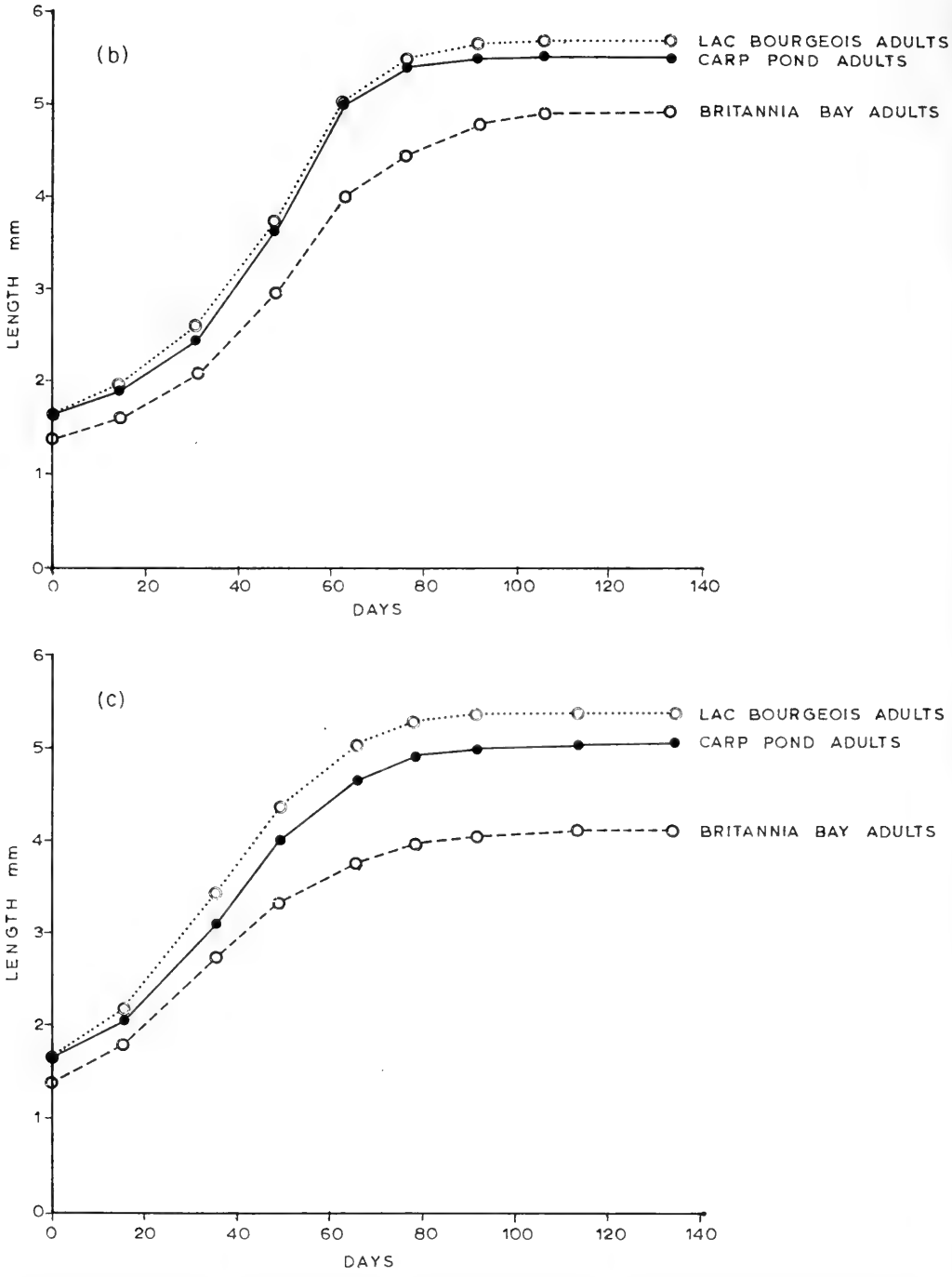

FIG. 4. Growth in shell length of newborn *Musculium securis* from Carp Pond, Britannia Bay, and Lac Bourgeois transplanted into (a) Carp Pond, (b) Britannia Bay and (c) Lac Bourgeois, Day 0 = May 9, 1972. Means are plotted as text indicates.

in Carp Pond where large amounts of rainfall in the summer of 1972 (Mackie, 1973) had a significant effect on the growth and hence the size-frequency distribution of the summer-born individuals. In 1970 and 1971 the newborn laid dormant and estivated from August to November. However, in 1972 water from high rainfall remained in the pond during this period and the newborn started growing immediately after birth (late July). In the permanent habitats there was no estivation period and the large amount of rainfall in 1972 had no apparent effect on the growth and seasonal size-frequency distribution of *M. securis*. Consequently, rainfall had a greater effect on the growth of *M. securis* in the temporary than in the permanent aquatic habitats.

The temporary aquatic habitats often had unimodal size-frequency distributions while the permanent aquatic habitats had bimodal, and sometimes trimodal size-frequency distributions of adults. Bimodality resulted from 2 different phenomena. In Britannia Bay the bimodal character was the result of differences in growth rates of slow- and fast-growing adults. The fast-growing adults produced young in mid-July so that the remainder of the summer was represented by 3 modes (C, b, B; Fig. 3). Lac Bourgeois had 2 overlapping generations, 1 represented by adults born in early summer and the other by adults born in late fall or early winter.

The transplant studies indicated that the growth of individuals in the Britannia Bay population was slower than those of other populations. By correlating the lengths of calyculae or umbones (i.e. lengths of newborn at birth) with maximum length attained, a correlation coefficient (r) of 0.87 was obtained (Fig. 5). Thus larger newborn usually attain greater maximum lengths than smaller newborn. The average length of newborn in Britannia Bay was 1.36 mm; this would explain the smaller average maximum length attained in Britannia Bay than in other habitats where newborn were usually longer than 1.65 mm.

Water temperature may also be an important factor in the growth of Britannia Bay clams. Mackie (1973) showed that the growth of *Musculium securis* began at approximately 10°C and probably occurred at optimum rates near 18°C. Mackie (1973) also showed that these temperatures were reached approximately 4 weeks later in Britannia Bay than in other habitats. Therefore, the slow rate of temperature increase may have been a factor in the reduced growth of Britannia Bay clams. Also, since the Britannia Bay population had 4 weeks less time in which to produce young, it would be to the advantage of the population to select for smaller newborn. In this context the growth of Britannia Bay clams may be adaptively modified to temperature. Hunter (1961) also attributed variations in breeding among several populations of snails to variations in water temperature; he further showed that the pattern of life cycle, though varying within the species, seemed to remain constant within each population and indicated some genetic stability through adaptive modification.

The growth and seasonal size-frequency distribution has been described for several sphaeriids but only a few have been demonstrated to display intraspecific variation within and/or among habitats. Thomas (1963, 1965) studied a population of *Musculium partumeium* in a temporary habitat and also found that summer growth varied with the amount of rainfall; adults attained greater lengths and the newborn which usually estivated upon birth and laid

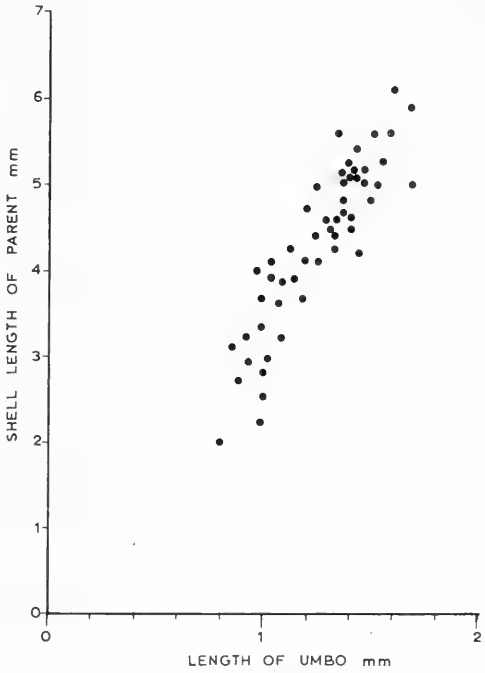

FIG. 5. The relationship between length of umbo (mm) and shell length of parents (mm) in *Musculium securis*. Correlation coefficient (r) = 0.87.

dormant showed more growth in a summer of high rainfall than in summers of low rainfall. The present study indicates that the estivating populations of *M. securis* consisted only of newborn. However, Thomas (1963) showed that the estivating populations of *M. partumeium* consisted of adults of lengths 1-5 mm, although newborn were the most numerous. Intraspecific variations were also noted by Avolizi (1971) but he concluded that interspecific differences in life-cycle and growth between *Sphaerium striatinum* and *S. simile* were greater than intraspecific differences.

There was only 1 birth period per generation of *Musculium securis* adults. The birth period was usually of 2-4 weeks duration. Only 1 generation and hence 1 birth period was usually present in the temporary aquatic habitats whereas 2 generations and 2 birth periods were present in the permanent aquatic habitats.

The birth period of the Carp Pond population extended throughout July in all 3 years of study but both the numbers of birth periods and the birth period would probably have changed in 1973. By May 15, 1973 (Fig. 3) some adults were already gravid and probably would have produced young in June 1973. If young were produced early in June, there would probably have been sifficient time for these young to grow and reproduce before the pond dried up in August, 1973. The probability of 2 overlapping generations occurring in 1973 would increase if the pond did not dry up or if the summer aquatic season was longer than usual.

The birth periods of the fast-growing adults in the Britannia Bay population were during July and September and of the slow-growing adults during August. Young born in late July and early August did not grow until the following spring, as was typical of newborn in temporary aquatic habitats. Since only newborn estivated in the temporary ponds it is reasonable to assume that only individuals of this size class were capable of (or adapted to) estivation. If only newborn can survive estivation there would appear to be greater survival value if a genetic determinant for "temporary cessation of growth at birth" was selectively favored during evolution of the species. Conversely, there would seem to be greater survival value in a permanent aquatic habitat if a genetic determinant for "temporary cessation of growth at birth" was not so favored. Speculating on this basis, *Musculium securis* may have evolved in a temporary aquatic habitat since the newborn in Britannia Bay and Lac Bourgeois did not continue growth immediately upon birth in late July, as shown in the interpopulation transplant studies. Further, the data indicated that interpopulation variations in time and number of birth periods tended to be greater than intrapopulation variations.

Interpopulation variations in birth periods appear to be greater in other sphaeriids compared to *Musculium securis*. For example, Foster (1932) cited the birth period of *Sphaerium striatinum* as December but Avolizi (1971) reported June and July as the months of greatest "spat-fall" for the same species. The birth rate of *S. simile* was highest during the winter and summer months as reported by Zumoff (1973) but during late June-early July and late fall according to Avolizi (1971). *Sphaerium corneum* has been reported to produce 2 generations; Thiel (1926) cited the birth periods as early summer and autumn but Mitropolskji (1966) as no distinct boundaries between the 2 birth periods.

The life span of *Musculium securis* was typically 12 months in all habitats investigated here. However, the life span was increased to 15-16 months in the temporary aquatic habitats after a summer of high rainfall. This increase in longevity had a significant effect on such other life history aspects as the seasonal size-frequency distribution and the birth periods as discussed earlier.

On the basis of the number of annuli on the valves, Heard (in press) suggested that the maximum life span of *Musculium securis* was three years. Using this technique, Lac Bourgeois adults, which had 1 annulus, would have been in their second year of life. However, results from field and laboratory studies clearly showed that these annulated adults were in their first year of life and lived for only approximately 12 months. Therefore, "annuli" may not always represent annual rest periods. This is particularly true of clams that live in temporary habitats where water levels fluctuate from one month to the next. Heard (in press) recorded maximum possible life spans of several other sphaeriids and his predicted values (on the basis of the number of annuli) were invariably higher than those observed by investi-

gators using other techniques. For example, Avolizi (1971) and Foster (1932), on the basis of length class distributions, reported an 18-24 and 12 month life span, respectively for *Sphaerium striatinum*, but Heard predicted a maximum 5 year life span; by marking and recapture, Herrington (1948) showed that the life span of *S. occidentale* in temporary ponds was at least 3 years but Heard predicted 6 years.

To recapitulate, intraspecific variations in the growth of *Musculium securis* were related to environmental pecularities. Interpopulation differences were primarily attributable to intrapopulation variations in growth of *M. securis* in the less stable temporary habitats and probably to adaptive modification in the more permanent aquatic habitats. In the latter instance it was proposed that *M. securis* evolved in a vernal habitat and through adaptive modification of some of its growth patterns (e.g. size of young at birth) adapted to different environmental conditions in habitats of more permanence. On the other hand, certain characteristics, such as birth period and longevity, appeared to be under greater genetic control and the species showed little adaptive plasticity in these qualities. Hence, the birth period was usually 60-70 days after the onset of growth of newborn and death of the parents usually occurred shortly after the birth of their young. Mackie, Qadri and Clarke (in press) have also demonstrated adaptive plasticity in some reproductive features of *M. securis.* The selective advantages of adaptive plasticity has been discussed at length for other mollusks by Hunter (1961), Hubendick (1954) and Waddington (1953 a,b,c).

ACKNOWLEDGMENTS

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THE KARYOTYPE OF *BIOMPHALARIA GLABRATA*, THE SNAIL VECTOR OF *SCHISTOSOMA MANSONI*[1]

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ABSTRACT

Karyotyping was done on the mitotic metaphase chromosomes obtained from the embryos of *Biomphalaria glabrata.* The 18 chromosome pairs were identified and classified into 6 groups. The diploid cell has 10 pairs of metacentric, 4 pairs of submetacentric, 2 pairs of acrocentric and 2 pairs of telocentric chromosomes. The pair number 8 with secondary constriction can be used as a marker in genetic experiments.

INTRODUCTION

Chromosome numbers and cycles of many snails belonging to the family Planorbidae have been reported previously (Burch, 1960b; Natarajan et al., 1965; Patterson & Burch, 1966). These reports were based on observations of the meiotic divisions, where individual identification of the chromosomes was not possible. The chromosome number of *Biomphalaria glabrata*(Say), the intermediate host of *Schistosoma mansoni*, has been reported as 18 haploid (Burch, 1960a), also based on the meiotic stages. No details on chromosome analysis have been published. In this paper, karyotype analysis based on mitotic metaphase chromosomes is presented.

MATERIALS AND METHODS

Studies were done on *Biomphalaria glabrata* that were originally from Puerto Rico, and which were susceptible to infection with *Schistosoma mansoni*. The information on mitotic divisions is based on material from embryos and that of meiosis from preparations of ovotestis. The egg sacs with young embryos were wiped with alcohol, and collected into a large sterile petri dish with sterile spring water (commercial, bottled) to which one ml of penicillin-streptomycin solution had been added. After 1 min in this mixture, egg sacs were transferred to another large petri dish with modified *Drosophila* medium (Hansen, 1974).

Embryos were dissected from egg sacs and the embryos from 15-20 egg sacs were pooled and homogenized in a sterile glass tissue homogenizer. The homogenate was transferred to a sterile centrifuge tube and spun at 500 g for 5 min. The supernatant was discarded and the pellet resuspended in 10 ml of fresh medium, to which 1 ml of 0.04% colchicine was added and incubated at 27°C for 45 min. The cell suspension was then centrifuged at 500 g for 5 min, and after discarding the supernatant, the pellet was subjected to hypotonic treatment with 3 ml of sterile distilled water (1 part medium and 5 parts distilled water can also be used) for 10 min at room temperature. To this, 3 ml of fixative (3 parts methanol and 1 part glacial acetic acid) was gradually added. After 10 min this was centrifuged for 5 min and the pellet resuspended in 3 ml of fresh fixative. Finally the cells were resuspended in a small amount of fresh fixative depending on the size of the pellet. The slides were prepared by squirting a drop of the cell suspension on to a cold wet slide and quick air drying.

The ovotestis was dissected from the adult snail by pulling it out of the central whorl after making a quick incision through the outer two whorls with fine forceps. It was then immediately fixed in 45% acetic

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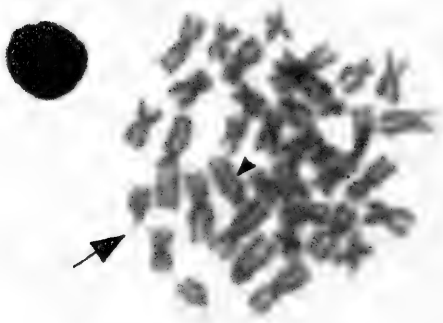
acid for 15 min. Squashes were made from the fixed material according to the technique described elsewhere (Raghunathan & Voge, 1974). Chromosome preparations from ovotestis can also be made in the same way as for the embryos described above, by making a cell suspension.

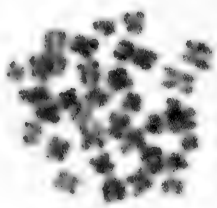
The permanent slides were stained with Giemsa in tap water (1:10) for 3-5 min, rinsed with tap water and air dried.

RESULTS

In the mitotic stages the prophase, metaphase, and telophase are clearly evident. In the prophase the chromosomes can be seen as long threads. As the prophase proceeds to metaphase, the chromosomes progressively shorten and become thicker (Figs. 1-2). The centromeres can be distinguished from the onset of metaphase. From the metaphase plates the chromosomes ($2n = 36$) can be classified into metacentric, submetacentric, acrocentric and telocentric depending on the centromeric position, according to the method of Levan et al. (1964). In this paper the chromosomes are primarily classified on the basis of centromeric position and size. There are altogether 10 metacentric, 4 submetacentric, 2 acrocentric and 2 telocentric chromosome pairs (Table 1). These are further assigned to groups A-F (Fig. 3). Group A comprises chromosome pairs 1-3, all of which are metacentric and large; pair 1 is the largest and can easily be identified. Pairs 2 and 3 can be distinguished by size and also by the nature of the centromeric region. In pair 2 this area appears like a tube connecting the long and short arms; whereas in chromosome pair 3, the chromatids appear to be crossing over in the centromeric region. Pairs 4-7, which are all submetacentric, are grouped under category B. There is a gradation in size from pair 4-7. Group C contains chromosome pairs 8 and 9, both



1



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FIGS. 1-2. Mitotic metaphase spreads of *Biomphalaria glabrata* from the embryonic cells, ×2100. 1. Secondary constrictions in pair 8 (thin arrow) and satellites on pair 9 (thick arrow) are prominent.

TABLE 1. Classification of *Biomphalaria glabrata* chromosomes into groups A-F on the basis of size and centromeric position.*

Group	Size	Centromeric position	Chromosome pair number	Number in a diploid cell
A	large	metacentric	1	
	medium	metacentric	2, 3	6
B	medium	submetacentric	4-7	8
C	medium	telocentric	8	
	small	telocentric	9	4
D	small	metacentric	10-13	8
E	small	acrocentric	14, 15	4
F	smallest	metacentric	16-18	6
			Total	36

*Classification according to Levan et al., 1964.

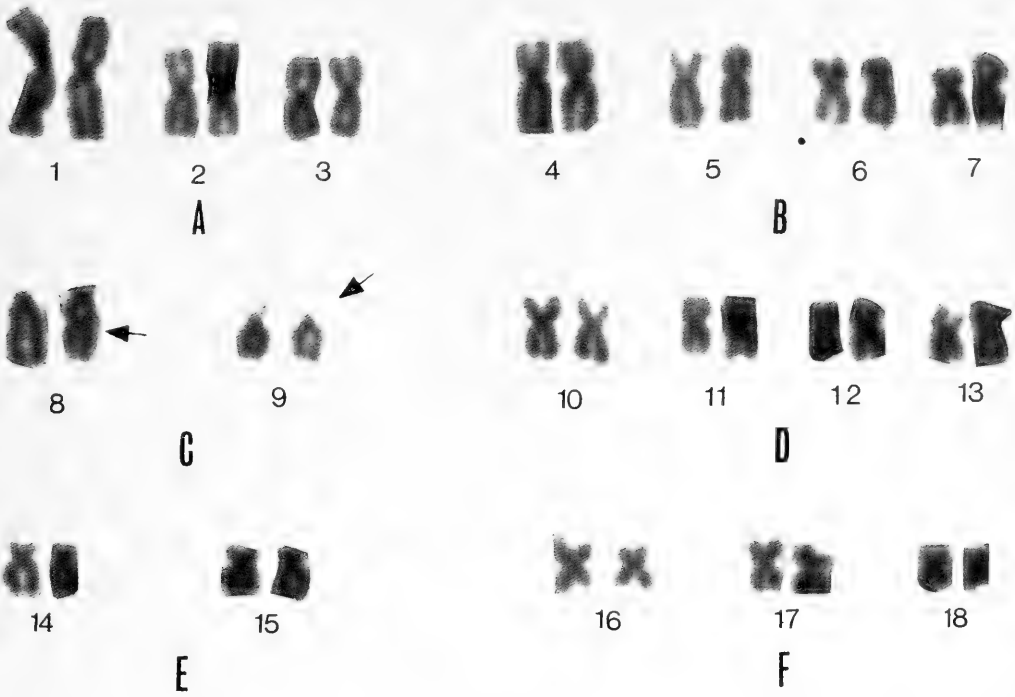

FIG. 3. Karyotype of mitotic metaphase chromosomes shown in Fig. 1, divided into 6 groups A-F. A. Metacentric pairs 1-3. B. Submetacentric pairs 4-7. C. Telocentric pairs 8 and 9 are shown by arrows. D. Metacentric pairs 10-13. E. Acrocentric pairs 14 and 15. F. Metacentric pairs 16-18.

telocentric. Pair 8 is large and has a secondary constriction (Figs. 1, 3) on both homologues but more prominent in one of the chromosomes of the pair. Pair 9 has satellites at the end of their telomeres, which can be seen only in a few chromosome complements. This pair can be easily distinguished from pair 8 by its small size and absence of secondary constrictions, even when the satellites are not seen. Group D has 4 metacentric pairs 10-13 and these can be distinguished from each other by their size. Group E comprises pairs 14 and 15, which are both acrocentric. In pair 15, the left chromatid appears to cross over the right one at the centromeric region. Group F contains 3 metacentric chromosome pairs 16-18. The chromosome pairs 16 and 18 can be identified by their large and small size respectively, and 17 by one of its chromatids appearing swollen at the ends, which stain dark.

Several stages of 1st meiotic prophase, and metaphase I are observed from the ovotestis preparations. The chromosome cycle observed here is basically the same as that of other pulmonate snails described previously.

DISCUSSION

Because of the small size of mitotic chromosomes it is rather difficult to study their morphology, unless the preparations are very good. The most suitable spreads are those in which the chromatids are separated, showing clearly the centromeric position. This can be attained only when the time schedule for metaphase arrest, hypotonic treatment, and fixing is adhered to strictly. The chromosome pairs 1, 4, 8-10, 15 and 18 are easily recognizable even in bad preparations. Chromosome pair 9 is the nucleolus organizer.

Since identification of the individual chromosomes is now possible, future studies on various banding patterns (C, G, and R) would be very useful for genetic studies. It has been suggested from the genetic studies on this mollusk that there are five different linkage groups in this species (Richards, 1973), but its location on any particular chromosome is not known. The presence of a secondary constriction on pair 8, and satellites on pair 9, make these chromosomes useful markers in genetic studies.

ACKNOWLEDGMENTS

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[1]Named as new but already named this by Olsson (1970).

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