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UNITAS MALACOLOGICA EUROPAEA

IV European Malacological Congress

The Fourth European Malacological Congress will be held in Geneva, Switzerland, from September 7 to 11, 1971. It will follow a one-day meeting of museum curators in charge of Mollusca, devoted to the discussion of curatorial problems and collaboration. The meetings will take place in the new Museum of Natural History and in the University buildings. All malacologists are cordially invited.

The Congress fee is S. Fr. 30.- (about U S $ 7.00) for members and corresponding members of U.M.E., S. Fr. 40.- (about U S $ 9.00) for non members, and S. Fr. 15.- (about U S $ 3.50) for students and accompanying persons.

Accommodation will be arranged by the Tourist office in hotels and the Student hostel.

If you are interested and have not received the circulars, please contact the president, Dr. E. Binder, for more detailed information.

Address: IV European Malacological Congress
Museum of Natural History
CH- 1211 Geneva 6, Switzerland

MALACOLOGISTS INTERESTED IN AFRICA. --- During the last week in November 1969, a meeting was held at the Musée Royal de l'Afrique Centrale, Tervuren, Belgium, which was attended by various people interested in the study of land and freshwater mollusks of Africa, south of the Tropic of Cancer, including Madagascar (Malagasy), the adjacent islands and part of Arabia. This group decided to issue a newsletter once a year, beginning in the spring of 1970, giving names and addresses of researchers interested in this region, as well as lists of their papers and current researches, notes on the location of African type specimens in museums, proposed expeditions to Africa, specialized bibliographies and addresses for inquiries. This newsletter will be called *ACHATINA*. Copies of it will be available at no cost to *bona fide* workers who cooperate in this scheme. The terms of reference will be restricted to taxonomy and zoogeography; medical aspects will be outside the area of interest. A long term project is to compile an annotated bibliography of all the papers dealing with non-marine molluscs of this area.

Those interested should contact Dr. J.-J. VAN MOL, c/o Section des Invertébrés non Insectes, Musée Royal de l'Afrique Centrale, Tervuren, Belgium.

MALACOLOGIA

Proceedings of the

American Malacological Union

Symposium on

Rare and Endangered Mollusks

PAPERS

on the

RARE AND ENDANGERED MOLLUSKS OF NORTH AMERICA

Edited by Arthur H. Clarke

National Museum of Natural Sciences
National Museums of Canada
Ottawa

Based on a *Symposium on the Rare and Endangered Mollusks of North America*
sponsored by the American Malacological Union and presented on
July 16, 1968 at Corpus Christi, Texas

FOREWORD

The papers presented here document crisis situations which will be of concern to all persons who care about the preservation of our unique North American fauna. Through expanded industrial development, increased water pollution, widespread habitat disruption, and over-collecting, more than 400 native species of mollusks are in imminent danger of extinction. At least 1000 others will soon be endangered if present trends continue.

All of the scientists who participated in the American Malacological Union's *Symposium on Rare and Endangered North American Mollusks* possess special knowledge and several of them are among our most distinguished malacologists. All of the assessments, presented here, are therefore authoritative. Excerpts from some of the papers speak for themselves.

"We are left with the inescapable conclusion that we are gradually destroying upwards of a thousand endemic species of freshwater mollusks." (David H. Stansbery).

"There is a [large] complex of hydrobiid gill-breathing snails in North American brackish water that is headed for extinction even before the species are scientifically described or named." (Joseph P. E. Morrison).

"About 1953, land clearing and the building of fishing camps and other tourist attractions eliminated just about all of the hammock land [on Lower Matecumbe Key] and, of course, a few more color forms of *Liguus* peculiar to this key. The same type of destruction has occurred along the entire series of Keys from near Miami to Key West." (William J. Clench).

"Among the [marine] species that are being over-collected in certain limited areas are *Strombus gigas*, *Cassis madagascariensis*, *Pleuropoca gigantea*, *Cyrtopleura costata*, *Cymphoma gibbosum*, *Melongena corona*, and edible clams, scallops and oysters." (R. Tucker Abbott).

"Viewed from the most pessimistic angle, it might be stated that all land mollusks indigenous to the western part of the United States are endangered to some degree." (Allyn G. Smith).

The objectives of the symposium and of this publication are to call attention to the present threats to species survival, to make available within a single reference preliminary lists of our rare and endangered mollusks, and to provide some basis for their planned conservation. Corrections and necessary additions to these lists are solicited. Individuals and organizations are urged to do what they can to conserve and protect our endangered native species and to preserve them from destruction.

A. H. C.

CONTENTS

1. INTRODUCTION

The magnificent freshwater mollusk fauna of southeastern North America was discovered by C. S. Rafinesque, Thomas Say, Isaac Lea, T. A. Conrad, and other celebrated naturalists who, between 1816 and 1850, described hundreds of unique new species from that region. Influenced by a benign climate, varying topography, abundant calcium and fortunate geological history, a hundred million years of uninterrupted evolution had produced there the most diverse and luxuriant freshwater molluscan fauna known to exist on earth.

As the country became more densely populated streams were dammed; cattle, sewage and industrial wastes poisoned the waterways; and, one after another, rivers became unfit for mollusks and other aquatic animals. During the nineteenth and twentieth centuries most of the rivers became partially or wholly polluted and their mollusk faunas were destroyed (see paper by D. H. Stansbery, this publication). For example the Powell, Clinch, Holston, French Broad and Hiwassee rivers, all major tributaries of the upper Tennessee River, were previously unsurpassed for their rich mollusk populations. By 1950 only the Clinch and portions of the Powell remained unspoiled.

On June 10, 1967 a retaining wall collapsed at Carbo, Virginia sending 130 million gallons of toxic industrial waste flooding into the Clinch River. In Virginia alone an estimated 163 million fish were killed. Effects of the poison on the mollusk fauna were then unknown but the worst was feared.

Malacologists have long been aware of the gradual depletion of the North American fauna but most had felt, with some justification, that nothing could be done. But the call for action signalled by the Clinch River disaster was too imperative to ignore. On July 31, 1967 an Executive Council of the American Malacological Union appointed the writer as Chairman of a Committee to recommend action for the preservation of the rare and endangered mollusks of North America.

Clearly the first assignment of the Committee was to assess the problem and to identify those species of mollusks which are now rare and in danger of extinction. It was decided that a symposium on this subject should be held during the next annual AMU meeting and its results published. During the next few weeks malacologists possessing special knowledge of the survival status of marine, freshwater and terrestrial mollusks of both eastern and western North America were asked to participate. The response was most gratifying. All of the workers who were asked to present papers promptly accepted and most of the invited discussants also agreed to help.

The *Symposium* took place on July 16, 1968 in Corpus Christi, Texas during the 34th annual meeting of the American Malacological Union. Carefully prepared papers from 14 malacologists were read. Audience participation was enthusiastic and much valuable supplementary information was thereby brought forth.

All of the contributed papers which have been released by their authors for publication are presented here. Some have been revised but most are printed essentially as they were delivered. These collected papers constitute the first attempt to enumerate the rare and endangered mollusks of North America or, for that matter, of any continental molluscan fauna.

The purpose of this publication is to focus attention on the species mentioned and to stimulate corrective action wherever possible. Every land management agency of national, regional, and local governments is invited and requested to do what it can. "Individuals, organizations, and interested agencies are urged to employ all means available to them toward achieving greater security for all wildlife. Only by united appropriate action will we prevent other species from joining the list of those now extinct." (1966, *United States Department of the Interior, Resource Bulletin*, 34: iii).

It had been hoped that the *Symposium* might also provide some basis for planned conservation or, if necessary, for propagation of these species. Fundamental information of this sort has already been published by the U.S. Department of the Interior's Bureau of Sport Fisheries and Wildlife (*op. cit.*) for the rare vertebrates of North America and by the International Union for Conservation of Nature and Natural Resources (1966, the *Red Data Books*) for rare mammals and birds of the World. We had proposed to use these works as models. It was soon obvious that although the geographical distribution of most rare North American mollusks is reasonably well-known (often to their detriment) we know almost nothing about the ecology, life history or population structure of most of them. Critical areas for research are therefore plainly indicated.

Biologists are becoming increasingly convinced that our generation has a profound obligation to conserve our natural environment for the practical and esthetic benefit of future generations of man. Some are also deeply concerned with our moral obligation to preserve rare species for the benefit of the species themselves. Either cause is more than sufficient and it is proper that the American Malacological Union should assume a leading role in fostering the conservation of our North American molluscan fauna.

A. H. C.

MALACOLOGIA, 1970, 10(1): 9-22

AMERICAN MALACOLOGICAL UNION SYMPOSIUM
RARE AND ENDANGERED MOLLUSKS

2. EASTERN FRESHWATER MOLLUSKS (I) THE MISSISSIPPI AND ST. LAWRENCE RIVER SYSTEMS

by David H. Stansbery

The Ohio State Museum of The Ohio Historical Society
Faculty of Population and Environmental Biology of
The Ohio State University, Columbus, Ohio 43210, *U.S.A.*

THE EXTENT OF THE FAUNA

The conditions for speciation of stream dwelling animals has been nearly ideal in eastern North America for many million years. One of the results has been the origin of what is probably the richest freshwater mollusk fauna in the world. While true of nearly all groups of freshwater mollusks represented, it is especially striking in the stream forms: 1) the river snails of the Family Pleuroceridae and 2) the naiads of the Family Unionidae. Tryon (1873: XXXVII) notes that:

> "We have, in North America, nearly five hundred recognized species of shells belonging to the various genera of Strepomatidae [= Pleuroceridae]. So considerable a moiety of these are to be found to be inhabitants of the upper Tennessee River and its branches in East Tennessee and North Alabama, and of the Coosa River in the latter State, that we quite agree with Mr. Lea in regarding that region as the great centre of this kind of animal life."

It should be added that these species are endemic to eastern North America and most probably outnumber the combined melanian species of the rest of the world.

The abundance of naiads or "unios" in both species and numbers of individuals proved to be no less spectacular. In his synopsis of the naiads of the world Simpson (1900: 505) recognizes:

> "about one thousand species and 82 varieties of Unionidae. . . Of these 533 species and 55 varieties belong in North America. . ."

Subtracting the few western North American species we find that eastern North America has roughly half the known species of river snails and half the known species of naiads in the world and together they total about a thousand species. With a very few exceptions these species are found nowhere else in the world.

A RESUME OF THE POST-COLUMBIAN HISTORY OF THE FAUNA

Although the prehistoric North American Indians utilized prodigious quantities of these mollusks (Stansbery, 1966: 42) their harvests apparently had little effect on the survival of these species. A comparison of the shells recovered from prehistoric mounds and midden heaps with pioneer lists reveals that the species composition of our streams had not changed appreciably for at least six to eight thousand years prior to pioneer settlement.

The factors which have been responsible for the decimation of our freshwater mollusks have increased in both number and intensity as our population has grown. With the initial clearing of the forests and tilling of the soil great quantities of humus-rich topsoil was washed into our streams. This loss to early agriculture was also a loss to stream life through a reduction of dissolved oxygen and an increase in organic acids. The removal of topsoil decreased the ability of the land to hold water, hence

producing greater floods in the wet seasons and dryer droughts in the dry part of the cycle. Each exaggerated extreme took its toll of stream life. Over a century ago Higgins (1858: 550) wrote:

> "Gentlemen who collected the shells of this vicinity in early times, found many species in great abundance which have at this day either totally disappeared or are represented by occasional straggling specimens, and all species, with but few exceptions, have gradually decreased in numbers, . . This remarkable decrease and extinction among the mollusca, may, to a great degree be accounted for, when we consider the immense change which the surface of the country has undergone. The change of the wilderness into a highly cultivated country, the immense area of forest which has yielded to the plow; the decrease in the volume of the water in our rivers and creeks,. . ."

The fine silts and clays which followed the topsoil into our streams may well have had a smothering effect on some species by the simple effect of clogging of gills or stimulating excess mucus secretion. In the early days the rivers were commonly the direct recipients of lumbermill sawdust, brewery slops, and slaughterhouse refuse (Trautman, 1957: 18). With the coming of community sewage systems, raw domestic sewage was added without benefit of treatment. The discovery of new energy resources in the form of coal and petroleum led directly to an upsurge of technology and a mushrooming of industry. Not only did the mining and drilling operations add new pollutants in increasing amounts to our waters but the industries they supported contributed a whole new spectrum of soluble and insoluble wastes to our already overloaded rivers.

Ortmann (1909) was so moved by the wholesale destruction of mollusks and crustaceans that he wrote a paper on "The destruction of the fresh-water fauna in western Pennsylvania." In addition to polluting industries of many diverse kinds he also cites the "*damming up of certain rivers*." He notes that:

> "By this process [damming] the rivers, which originally possessed a lively current, with riffles, islands, etc., have been transformed into a series of pools of quiet, stagnant water, ... It is most destructive to mussels, most of which require a lively current. Dams also prevent free migration, for instance of fishes, and thus they must be an obstacle to the natural restocking of the rivers..."

Ortmann seems to have been the first biologist to correctly diagnose the true effect of impoundments on stream life. It is easy to understand why he, being the first, grossly underestimated the effects damming could have on our stream life. It is to be regretted that many biologists (perhaps most) have yet to recognize that nearly all of the exceedingly rich freshwater fauna of eastern North America evolved in or adjacent to a riffle or shoal habitat. To the extent that we change our streams into long chains of lakes -- to this extent do we eradicate this unique biological heritage.

More and more in recent years sand and gravel firms have turned to the alluvial deposits of our stream beds as a source of materials. These operations in addition to the dredging involved in stream channel "improvement" and quarry washing operations have their effect felt for miles downstream. For reasons as yet unknown, a dredged section of stream will not regain a naiad fauna for as much as a decade or more.

The advent of the chemical pesticide industry over the past twenty years has given additional cause for concern since the bulk of most of these toxins are washed into our streams. Their precise effects on our freshwater mollusks have yet to be documented in detail.

Malacologists over the years have not been blind to the increasingly damaging effects man has had on our stream environments and the organisms living there. Ortmann followed his work in Pennsylvania (which formed the basis of his 1909 paper cited above) with a survey of the naiads of the upper Tennessee Drainage System. At the

conclusion of his paper (Ortmann, 1918: 525) he records:

> "In view of the gradual, slow but steady, deterioration of the fauna in consequence of stream-pollution, there is great danger that the fauna will largely become destroyed, and that it will be impossible, in the future, to duplicate this collection."

I have collected the upper Tennessee with some thoroughness. Ortmann's fear has been largely realized. The rivers which make up the headwaters of the Tennessee (Powell, Clinch, Holston, Nolichucky, French Broad, Little Tennessee and Hiwassee) are, in large part, destroyed. Where the fauna has not been greatly reduced or eliminated by pulp mill liquors, salt plant effluent, wood extracting plants, paper mills, etc., the high dams of the Tennessee Valley Authority have done so. There are still a few streams, however, having something which approaches the original fauna. The Powell and Clinch Rivers just above Norris Reservoir still afford conditions where the industrious collector may take as many as thirty species from a single site. How long these conditions will last cannot be predicted but I suspect not very long. There is already agitation for additional dams on both rivers and concerted efforts are being made to industrialize this section of "Appalachia." I would not be surprised to witness the eradication of most elements of the Cumberlandian Fauna within the next several decades. We have excellent reason to expect it.

In 1924 Ortmann brought the influence of damming on the naiad fauna at Mussel (Muscle) Shoals to the attention of American scientists with an article in *Science*. He expressed the concern that the richest of all known naiad sites (at least 70 species in 31 genera) was being destroyed. Efforts to assess any changes in that particular fauna since Ortmann's day have been made (Stansbery, 1964: 25). Extensive collecting produced specimens of less than half of the original fauna. Over the five years since that time Professor Paul Yokley of Florence State College has made every reasonable effort to add to the recent list. His persistent labors with commercial collecting gear and SCUBA equipment have resulted in the recovery of single specimens of four additional species.

Mr. Billy Isom informs me that the original Mussel Shoals lie today beneath 19 feet of muck behind Wilson Dam, at the bottom of Wilson Reservoir. The "glory of the mussel shoals" discovered originally by Conrad (1834: 12) and lamented by Ortmann (1924: 565) has indeed become history.

In more recent times Van der Schalie (1938, 1945, 1947, 1958, 1960) has been outspoken in his criticism of dams and pollution and has cited evidence which abundantly supports his position. The impoundment of the lower Tennessee, known as Kentucky Lake, has been studied by Bates (1962: 232). He found the faunal assemblage of the old river channel to be essentially the same as the pre-impoundment composition. All individuals so taken were found to be adults (10+ years) with juveniles being absent. It would seem that impounding either stopped effective reproduction or the survival of the young in these populations leaving only the pre-impoundment individuals to live out their life expectancies. More recent collections from the same area support this conclusion.

We are left with the inescapable conclusion that we are gradually destroying nearly a thousand endemic species of freshwater mollusks. This fauna was millions of years in coming into being and is in the process of being eliminated in only a century or two. -- And all this before we have even begun to seriously investigate their potential value.

RARE AND ENDANGERED SPECIES

It should be noted at the outset that my knowledge of the status of standing-water species in general, and non-naiad species in particular, is too scant to determine which are either rare or endangered today. Although the stream forms, especially the naiads,

are far better known, the observations offered below are obviously only as valid as the extent of my field experience and that of my several colleagues.

A "rare and endangered species" is defined, for the purposes of this paper, as any species which is known living today from only one or a very few populations having a restricted range. Even though a species may be reduced to an estimated 10% or less of its former abundance it is not included unless it fits the above criteria.

For some species the time for concern appears to be past. A number of species of the Genus *Dysnomia* Agassiz (= *Epioblasma* Rafinesque) have not been collected alive nor have fresh specimens of their shells been found in nature for at least half a century despite a concerted effort to find them. They are included here (see Pls. 1 and 2) in order to give a reasonably complete record and with the hope that one or more surviving populations may yet be discovered. Such species are, however, presumed extinct and shall be so listed until valid evidence of their continued existence is obtained.

CLASS GASTROPODA

Subclass PULMONATA
Order BASOMMATOPHORA
Family PHYSIDAE
Family LYMNAEIDAE
Family PLANORBIDAE
Family ANCYLIDAE
Subclass PROSOBRANCHIA
Order MESOGASTROPODA
Family VIVIPARIDAE
Family VALVATIDAE
Family HYDROBIIDAE
Family PLEUROCERIDAE

Insufficient data for Evaluation of Species Status

Genus *Io* Lea, 1831.

Io fluvialis Say, 1825. A few relict populations remain in the Powell, Clinch, and Nolichucky Rivers. It is absent from most of its former range.

Genus *Lithasia* Haldeman, 1840. (Includes *Angitrema* Hald.)

Most of the small stream species still persist in isolated localities. Most of the large river species are either extinct or existing as very small populations in the rapid water below dams.

Genus *Pleurocera* Rafinesque, 1819.

Many headwater species still persist although most of the species characteristic of large rivers are either greatly reduced or extinct.

Genus *Goniobasis* Lea, 1862.

Most of the species of this typical headwater genus still survive.

Genus *Eurycaelon* Lea, 1864.

A few populations of at least one species yet survive in the headwaters of the Tennessee River system.

Genus *Anculosa* Say, 1821. (= *Leptoxis* Raf.)

Some species of this genus may still be found in numbers on the rocky riffles of many medium to small streams of the southern part of the Ohio River system in Kentucky, Tennessee and Virginia.

Genus *Spirodon* Anthony, 1873. (= *Mudalia* Haldeman, 1840, of authors)

The few species of this genus still survive in rivers of the east central Atlantic drainage and in the headwaters of the New and Holston rivers of the Mississippi basin.

CLASS BIVALVIA

Order UNIONOIDIA

Family MARGARITIFERIDAE Ortmann, 1911.

Cumberlandia monodonta (Say, 1829).

Remnants of this species still live in the Powell and Clinch Rivers with scattered individuals in the Tennessee River proper. The Green River of Kentucky has at least one small population but the only population of substantial size presently known is found in the Gasconade River of the Ozark Plateau in Missouri.

Family UNIONIDAE (Fleming, 1828) *sensu* Ortmann, 1911.

Subfamily AMBLEMINAE Morrison, 1955.

Fusconaia cuneolus (Lea, 1840).

A single population remains in the Clinch River in Virginia.

Fusconaia edgariana (Lea, 1840).

Small relict populations remain in the Clinch and Paint Rock Rivers. The only known population of size is in the Powell while one persisting until 1967 in the lower Elk River, Tennessee, has apparently since been destroyed by quarry washings.

Quadrula intermedia (Conrad, 1836).

A few scattered small populations yet remain in the Powell, Clinch and Duck Rivers. Known until recently from the Elk River, Tennessee.

Quadrula sparsa (Lea, 1841).

This form stands between *Q. metanevra* and *Q. intermedia* but merges with neither. A single population remains in the Powell River in Tennessee.

Quadrula cylindrica (Say, 1817).

The big river form *cylindrica* appears to be reduced to a few populations in the Ouachita Mountains of Arkansas and Oklahoma, but the headwater form *strigillata* still lives in a number of small headwater populations of the Ohio system.

Plethobasus cicatricosus (Say, 1829).

Known today from a population in the Tennessee River below Wilson Dam in Alabama.

Plethobasus cooperianus (Lea, 1834).

Occasional specimens are still taken from the Tennessee River in Tennessee and Alabama.

Lexingtonia dolabelloides (Lea, 1840).

Individuals rarely taken yet in the Powell, Clinch and Holston Rivers. Duck and Paint Rock Rivers have small local populations.

Pleurobema clava (Lamarck, 1819).

This once common widespread Ohioan species still remains in several small disjunct headwater populations in Ohio. Occasional specimens are taken in the Wabash River of Indiana and the Green River of Kentucky.

Pleurobema pyramidatum (Lea, 1831).

In recent years this naiad has been found only in the Green River of Kentucky, the Clinch River above Norris Reservoir, and rarely from the Tennessee River proper.

Lastena lata (Rafinesque, 1820).

Although extirpated from nearly all its former range this species still lives in the Green River at Munfordville, Kentucky, and the Clinch River above Norris Reservoir. A population in the Elk River persisted until 1967.

PLATE 1. Extinct Unionidae

FIG. 1. *Dysnomia flexuosa* (Rafinesque, 1820). OSM 10369.1, male, "Ohio River," 18_?, length = 58 mm.

FIG. 2. *Dysnomia flexuosa* (Rafinesque, 1820). OSM 10369.2, female, "Ohio River," 18_?, length = 69 mm.

FIG. 3. *Dysnomia stewardsoni* (Lea, 1852). OSM 10371.2, male, "Tuscumbia, Ala.," 18_?, length = 39 mm, from Henry Moores Collection.

FIG. 4. *Dysnomia stewardsoni* (Lea, 1852). OSM 10371.4, female, "Tuscumbia, Ala.," 18_?, length = 35 mm, from Henry Moores Collection.

FIG. 5. *Dysnomia arcaeformis* (Lea, 1831). OSM 10364, male, "Tenn. River, Alabama," 18_?, length = 35 mm.

FIG. 6. *Dysnomia arcaeformis* (Lea, 1831). OSM 10363, female, "Holston River, Tenn.," 18_?, length = 38 mm, from Henry Moores Collection.

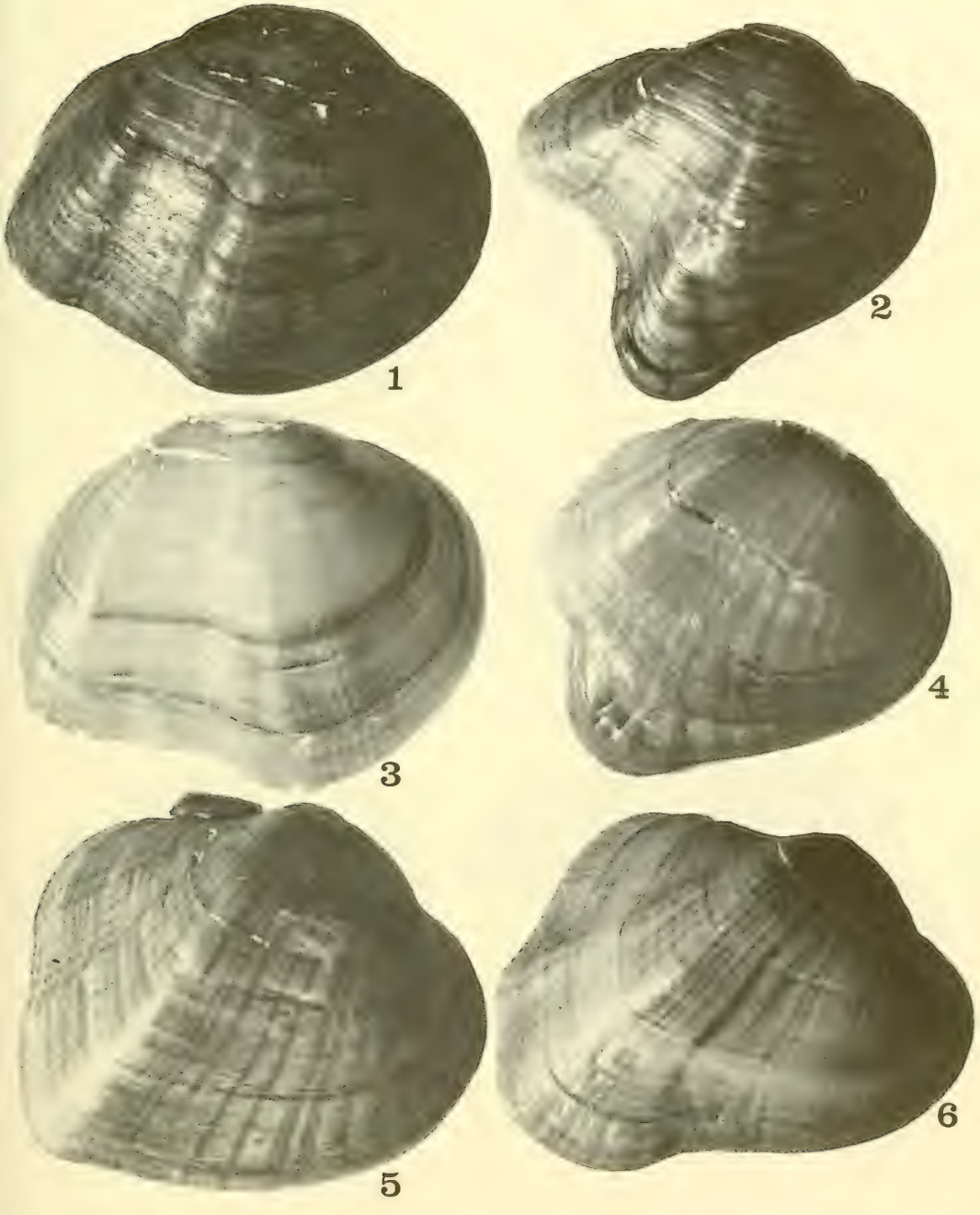
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PLATE 2. Extinct Unionidae

FIG. 1. *Dysnomia personata* (Say, 1829). OSM 10379.1, male, "Ohio River, Cin., O.," 18_?, length = 40 mm, from Henry Moores Collection.

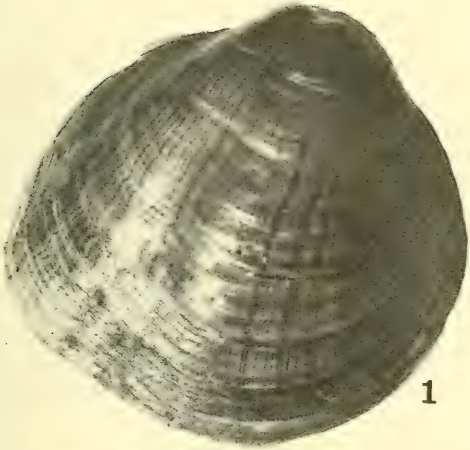
FIG. 2. *Dysnomia personata* (Say, 1829). OSM 10370.1, female, "Ohio River," 18_?, length = 46 mm, from Henry Moores Collection.

FIG. 3. *Dysnomia lenoir* (Lea, 1843). OSM 20208.4, male, Stones River 1.2 miles west of Couchville, Davidson Co., Tenn., 2 Sept. 1965, length = 33 mm.

FIG. 4. *Dysnomia lenoir* (Lea, 1843). OSM 20208.1, female, Stones River 1.2 miles west of Couchville, Davidson Co., Tenn., 2 Sept. 1965, length = 27 mm.

FIG. 5. *Dysnomia propinqua* (Lea, 1857). OSM 4078, male, locale unknown, 18_?, length = 35 mm.

FIG. 6. *Dysnomia sampsoni* (Lea, 1861). OSM 10395, male, "Wabash," 18_?, length = 41 mm.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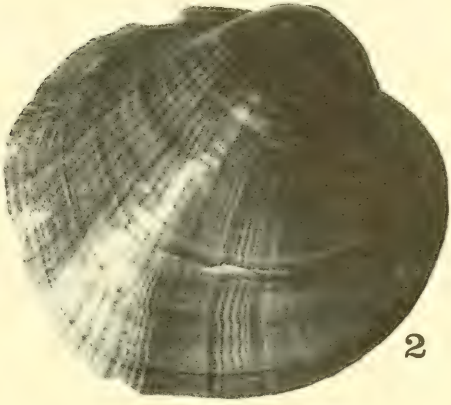
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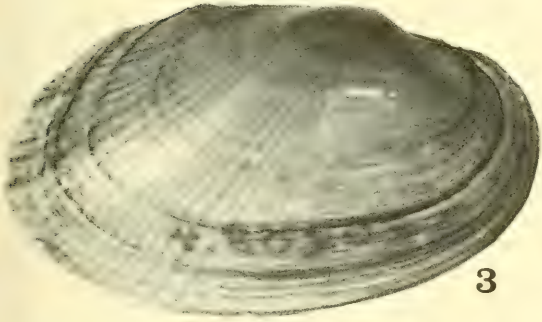
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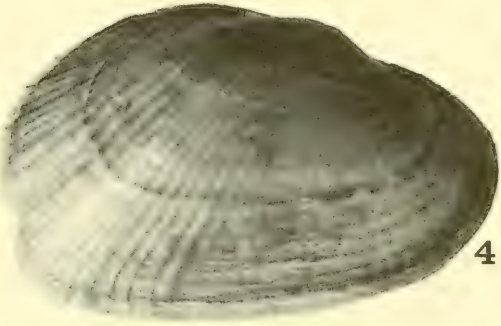
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Subfamily ANODONTINAE (Swainson, 1840) sensu Ortmann, 1910.

Pegias fabula (Lea, 1836).

Never common, this species has become increasingly rare in recent years. Its range appears to have been reduced to a few isolated populations in the upper Cumberland River tributaries.

Simpsoniconcha ambigua (Say, 1825).

A species sporadic in distribution and seldom found in numbers anywhere in recent years. Its habitat in the silt beneath relatively large flat rocks may render its rareness more apparent than real.

Arkansia wheeleri Ortmann and Walker, 1912.

This species of the streams flowing out of the Ouachita Mountains has apparently never been found in numbers. The only recent record is from Kiamichi River in Oklahoma.

Subfamily LAMPSILINAE (von Ihering, 1901) *sensu* Ortmann, 1910.

Ptychobranchus subtentum (Say, 1825).

Remnant populations may still remain in the Rockcastle River of the upper Cumberland and the Duck River of the lower Tennessee. Two substantial populations are today found in the Powell and Clinch Rivers above Norris Reservoir.

Cyprogenia aberti (Conrad, 1850).

The range of this species has apparently been reduced to the Black and Ouachita Rivers of Arkansas.

Dromus dromus (Lea, 1834).

Formerly found throughout the Cumberlandian Faunal Region this species is now restricted to the Powell and Clinch Rivers just above Norris Reservoir.

Obovaria retusa (Lamarck, 1819).

A population still living in the impounded lower Tennessee had apparently not reproduced since impoundment and is expected to die out. The only known breeding population of this once widespread species is a small one in the Green River near Munfordville, Kentucky.

Leptodea leptodon (Rafinesque, 1820).

This species, rare since its discovery, has now all but disappeared east of the Mississippi River. In the last half century single specimens have been taken from the Green River of Kentucky, the Ohio River near Cincinnati, the Meramec River of Missouri, the Kiamichi River of Oklahoma and several each from the Gasconade River in Missouri and the Saline River of Arkansas. The expression "widespread and everywhere rare" fits this species perfectly.

Proptera capax (Green, 1832).

Although largely if not entirely gone from the entire Ohio River drainage, this species still survives in the White and St. Francis Rivers of Arkansas.

Carunculina glans (Lea, 1831).

The typical *C. g. glans* of the Ohioan Faunal Zone appears on the verge of extinction while its Cumberlandian counterpart *C. g. moesta* exists in some numbers in several headwater streams of the Cumberland Plateau and the Southern Appalachians.

Carunculina cylindrella (Lea, 1868).

A population of this exceedingly rare species still lives in the Paint Rock River system of northern Alabama.

Conradilla caelata (Conrad, 1834).

Originally found throughout the upper Tennessee this rare species is now restricted to several small populations in the Powell, Clinch and Duck Rivers of that region.

Villosa trabalis (Conrad, 1834).

The typical form *V. t. trabalis* may still be found in the Cumberland River just below the Cumberland Falls and in the Rockcastle River nearby. The purple nacred *V. t. perpurpurea* seems restricted to the upper Clinch River where it is very rare and to Copper Creek, one of its tributaries.

Villosa ortmanni (Walker, 1925).

Never known outside the Green River system in the Mammoth Cave region of south central Kentucky. Common today only in the vicinity of Munfordville.

Lampsilis orbiculata (Hildreth, 1828).

The typical form *L. o. orbiculata* may still be taken occasionally from the Tennessee River below Wilson Dam and Guntersville Dam and very rarely from its type locality, the Muskingum River in Ohio. The *L. o. higginsi* is known living today only from the upper Mississippi River. Related forms from the Gasconade, Black and Sabine Rivers of the Ozark-Ouachita are also rare and may constitute a third species or subspecies of this interesting complex.

Lampsilis virescens (Lea, 1858).

Never a common species nor widely distributed, *L. virescens* is found today only in the Paint Rock River of Alabama. Dredging operations there may render this species extinct within the year.

Dysnomia flexuosa (Rafinesque, 1820). Pl. 1, Figs. 1, 2.

This species has not been collected since 1900 in spite of repeated efforts to find it. It was apparently a species of shallow riffles in big rivers, a habitat which has been totally eliminated. It is presumed **extinct.**

Dysnomia arcaeformis (Lea, 1831). Pl. 1, Figs. 5, 6.

The entire range of this species is now under a series of impoundments. It has not been collected in over half a century and hence is presumed **extinct.**

Dysnomia lenior (Lea, 1843). Pl. 2, Figs. 3, 4.

The last known population of this species is now covered by the Priest Reservoir on the Stones River in Tennessee. The only records of this species during the last 50 years were from this site. It is presumed **extinct.**

Dysnomia sulcata (Lea, 1829).

The big river *D. s. sulcata* form having a purple nacre may be extinct but the white nacred *D. s. perobliquus* is still occasionally found in streams tributary to western Lake Erie or Lake St. Clair.

Dysnomia haysiana (Lea, 1834).

This rare species is today apparently restricted to that part of the Clinch River from St. Paul to Dungannon, Virginia, a distance of only about ten miles.

Dysnomia personata (Say, 1829). Pl. 2, Figs. 1, 2.

I know of no collections of this species made in this century. It is an Ohioan species once found in the shallows of the Ohio and a few of its largest tributaries. It is presumed **extinct.**

Dysnomia stewardsoni (Lea, 1852). Pl. 1, Figs. 3, 4.

A rare species even before the impoundments and apparently not collected in the last half century. It is presumed **extinct.**

Dysnomia lewisi (Walker, 1910).

Recorded from both the Tennessee and Cumberland River Systems up until the construction of Wolf Creek Dam on the Cumberland and the TVA Dams on the Tennessee. It has not been collected in over 20 years and hence is presumed **extinct.** *D. lewisi* is figured by Walker, 1910, *The Nautilus* 24(4): Pl.3, Figs. 3-5 and by Neel & Allen, 1964, *Malacologia* 1(3): 451.

Dysnomia biemarginata (Lea, 1857).

The big river *D. b. biemarginata* form has not been collected during this century and presumably has been extinct for some time. The headwater *D. b. turgidula* form was recently rediscovered in the Elk River of Tennessee but quarry washing operations in the summer of 1967 apparently destroyed most or all of the naiads in this area. It may yet be rediscovered in some undamaged tributary.

Dysnomia florentina (Lea, 1857).

The form *D. f. florentina* is apparently gone from the entire Tennessee System except for the South Fork Holston River in Virginia. A closely related species or subspecies, *D. f. walkeri*, has its range reduced to the lower Stones and Red Rivers of the Cumberland River system.

Dysnomia torulosa (Rafinesque, 1820).

Typical *D. t. torulosa* are still occasionally collected in commercial operations on the lower Ohio River (Kentucky-Illinois) (Parmalee, 1967) and from the Nolichucky River near its mouth in western Tennessee. It is gone throughout the rest of its previous range. The smooth headwater subspecies, *D. t. rangiana*, persists as a few populations in smaller streams in the Ohio and lower Great Lakes systems. In the southern Appalachians one may still find an occasional specimen of *D. t. gubernaculum* but it is apparently restricted to the Clinch River and is rare even there.

Dysnomia propinqua (Lea, 1857). Pl. 2, Fig. 5.

Never known outside the Tennessee System, this species has not been collected in over half a century. It is similar to both *D. torulosa* and *D. sampsoni* but apparently does not merge with either. It is presumed **extinct**.

Dysnomia sampsoni (Lea, 1861). Pl. 2, Fig. 6.

A smooth inflated form of the lower Wabash River which appears to merge with *D. t. rangiana* and may be simply a variant of that subspecies. It has not been collected for over 50 years and may well be extinct in spite of the relatively good condition of this river.

A review of the status of the 103 species of naiads now known from the Ohio River drainage system reveals that 41 readily qualify listing as rare and endangered and, of this latter number, at least 8 species are presumed to be extinct. All 8 species believed to be extinct are members of the Genus *Dysnomia* Agassiz (= *Epioblasma* Rafinesque). Species of this genus are characteristic of the riffle (or shoal) habitats of high gradient streams and the 8 extinct forms were recorded, with rare exception, from riffles of our largest rivers. This specific type of habitat has all but disappeared from the Ohio basin and is being further reduced with the construction of new and higher dams.

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Discussion of Dr. Stansbery's Paper

by Arthur H. Clarke

The eastern regions not considered by Dr. Stansbery or Dr. Heard, the North Atlantic Watershed and the Canadian Interior Basin, contain mostly widespread species whose ranges extend into undeveloped, sparsely settled regions. Although many local mollusk populations there have been killed by pollution, the species themselves are not yet endangered.

A possible exception may be the unionid *Alasmidonta heterodon* (Lea), a small, rare species known only from 5 river systems, *viz.* the Peticodiac in New Brunswick, the Connecticut and the Housatonic in New England, the Delaware in Pennsylvania and the Rappahannock in Virginia. Expansion of industrial pollution could eliminate this

species. There are no early records of its occurrence elsewhere and its discontinuous distribution may indicate that it is becoming extinct through natural causes.

According to the literature some species within the Canadian Interior Basin (i.e., the Hudson Bay Watershed combined with the Arctic Watershed) have been taken only at one or a few localities and might be presumed to be rare. Recent work (Clarke, in press) has shown that most of them are not rare and that some are even abundant. For example, *Acroloxus coloradensis* (Henderson), previously known only from 4 lakes in the Rocky Mountains, has been found in 5 other localities in eastern Canada and may be widely distributed. *Physa jennessi jennessi* Dall, previously recorded only from its type locality near Bernard Harbour in the Canadian Arctic has now been collected from about 30 localities along the arctic mainland coast and near both sides of Hudson Bay. It appears to be a common arctic species. *Physa jennessi skinneri* Taylor, another presumably rare taxon, is now known from approximately 100 localities within the Canadian Interior Basin alone and should be considered abundant. Of the 103 species and subspecies now recognized from that region none now appear to be in danger of extinction by man.

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AMERICAN MALACOLOGICAL UNION SYMPOSIUM
RARE AND ENDANGERED MOLLUSKS

3. EASTERN FRESHWATER MOLLUSKS (II) THE SOUTH ATLANTIC AND GULF DRAINAGES

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INTRODUCTION

The eastern United States contains over 50 major drainage systems, as well as many smaller ones, between the St. Croix River on the Maine - New Brunswick, Canada, border and the Rio Grande River on the Texas - Mexico border. In addition, the interior drainages contribute to the very extensive Mississippi River and Great Lakes - St. Lawrence River watersheds.

The coastal drainages have been designated by Simpson (1900) and H. & A. van der Schalie (1950) as comprising the Atlantic and Apalachicolan, as well as part of the Interior Basin (= Mississippian), faunal regions for unionid mussels. The Atlantic region has been divided into a northern and a southern element, with the Potomac River drainage employed as the demarcation between the 2 parts. This report will cover the freshwater gastropods and bivalves of the South Atlantic Region from the Potomac River in Maryland to the St. Marys River on the Georgia - Florida border, peninsular Florida, the Apalachicolan Region, and the southern-most portion of the Interior Basin (i.e., the Alabama River system west to the Rio Grande drainage in Texas).

Unfortunately, there are significant gaps in our knowledge of the taxonomy, phylogenetic relationships, and geographical and ecological distribution of the mollusks of many of the drainages. Efforts have been made in recent years to correct our ignorance, and it is hoped that the effect of this symposium will be to stimulate both further and more intensive research in these areas.

THE NATURE OF THE FAUNA

In general, the streams flowing into the Atlantic Ocean and Gulf of Mexico contain rather endemic mollusk elements. Each region or subregion is characterized by the presence and/or absence of various genera and species, and even within a single region striking differences in the fauna may occur from one stream to another.

For example, one-half of the entire mollusk fauna of the Apalachicolan Region is endemic (e.g., *Notogillia* Pilsbry and *Quincuncina* Ortmann), about one-quarter also extends to the north and west, and the remaining nearly one-quarter extends southward into central Florida (Clench & Turner, 1956). Examining the mussel fauna (Unionidae) separately, one finds that one-fourth of the species are endemic, another quarter are related to eastern (South Atlantic) species, and half of the species have western (Interior Basin) affinities (van der Schalie, 1940).

Within this same Apalachicolan Region, different drainages often have different assemblages of mollusks, i.e., vary in the numbers and kinds of species present. In comparing the elements of the whole region, Clench & Turner (1956) clearly point out that the Apalachicola River (with its major tributaries, the Flint, Chattahooche and Chipola rivers) contains the greatest total number of species, the largest number of

species endemic to the region, and the largest number of species endemic to any single one of the drainage systems. In contrast, the Suwannee River drainage has fewer total species, has a proportionately smaller fauna which is endemic to the region, and altogether lacks species endemic to that drainage.

These relationships of endemism (both between and within regions) appear to occur throughout the coastal drainages in the eastern United States, while widespread species typify (in part) the much larger Interior Basin. If one compares freshwater mollusks regionally, however, it becomes immediately clear that the South Atlantic and Apalachicolan faunas are depauperate in relation to those of the southern part of the Interior Basin (particularly as concerns the large Alabama River system).

THE NATURE OF THE AREA

The drainage systems of the South Atlantic Region, peninsular Florida, the Apalachicolan Region and the southern part of the Interior Basin traverse one or more of the following physiographic provinces (as listed and described by Fenneman, 1938): Appalachian Mountains/Highlands, Valley and Ridge, Blue Ridge, Piedmont Plateau and Coastal Plain (both the Atlantic and Gulf portions). Short streams are usually confined to the Coastal Plain, while larger drainage systems may have tributaries flowing through several provinces. For example, the Coosa River tributary of the Alabama River system originates in the Blue Ridge and flows through the Valley and Ridge Province and the Piedmont Plateau before entering the Alabama River proper in the northern Gulf Coastal Plain. Another tributary, the Tombigbee River, flows largely through the Gulf Coastal Plain (a tributary of its own, the Black Warrior River, originates in the Appalachian Highlands) where it joins the Alabama River proper only about 25 miles from the Gulf of Mexico.

Striking differences in the freshwater mollusk fauna(s) occur between and occasionally within, different physiographic provinces. The Piedmont Plateau has a very sparse fauna, and most of the species of the rich fauna of the Coosa River occur in the Valley and Ridge Province. And frequently, the Coastal Plain assemblage is quite distinct from the composition found upstream in another province.

These phenomena are mentioned here to point out that within a single faunal region distinct elements of the biota may be found in different "zones" of the same drainage. These faunal elements may reflect a variety of circumstances, such as (1) a group which is adapted to living in small stream conditions versus a large river habitat, (2) an area which is comparatively "more favorable" for such factors as type and/or quantity of food or substrate conditions, or (3) preclusion of a part or all of the fauna because of industrial pollution.

Such generalities are frequently made to explain the presence or absence of species in/from an area without more specific information. It is particularly common to blame pollution for the absence of some or all biota, and while this conclusion may often be valid it is nearly always based on superficial observation. More detailed information concerning ecological requirements and hazards are in effect lacking, and such data are desirable for all species, and in particular for those which are localized in distribution and can be considered rare and/or endangered.

CHANGES IN THE FAUNA

It should be clear to all that the freshwater mollusk fauna(s) of the eastern United States has been altered and is continuing to change at an amazing rate, often in a disadvantageous direction.

The following categories of circumstances and the accompanying specific examples

reflect largely personal observations; a few conditions were taken from the literature. Further information is currently being assembled on the freshwater mollusks of peninsular Florida and the drainages of the South Atlantic Region, principally by the workers at Harvard's Museum of Comparative Zoology. More complete data will be provided when their studies are published.

Species of Decreased Abundance/Distribution

The natural ranges of many species of plants and animals are diminishing, largely due to human alteration of the environment(s). This circumstance is demonstrated, in part, by the reduced abundance of organisms in an area. Unless at least a few breeding individuals can be maintained, the population will become extinct. And if this course is followed by numerous populations, the species may be summarily reduced in its geographic distribution and perhaps eventually experience total extinction.

Pomacea paludosa Say (Gastropoda: Pilidae) occurs in southern Georgia and Alabama and throughout Florida. Because of the activities of the U.S. Army Corps of Engineers, large tracts of the Everglades in southernmost peninsular Florida have been drained. One result of this action has been the destruction of this snail's habitat, and consequently their numbers have decreased in this region. Similarly, the Florida kite, a bird which preys upon *P. paludosa* in the Everglades, is diminishing in numbers.

Another example concerns two unionid clams. In 1963 *Anodonta imbecilis* Say and *A. peggyae* Johnson occurred in approximately equal numbers in Lake Talquin (the type locality of *A. peggyae*!), a reservoir of the Ochlookonee River, Leon-Gadsdon County, Florida. Since that time, however, *A. imbecilis* has become all but extinct and *A. peggyae* has become drastically reduced in numbers in the impoundment. This situation has evidently been wrought principally by the Florida Fresh Water Fish and Game Commission which has administered rotenone to the reservoir to remove a pest fish, the grizzard shad (= *Dorosoma cepedianum*). After such treatment, the shore is littered with numerous decaying bivalves of several species.

Clench & Turner (1956) state that *Goniobasis albanyensis* Lea (Gastropoda: Pleuroceridae) probably formerly occupied the entire Apalachicola River system but that it now is confined to the Flint and Chattahoochee tributaries. Farming and consequent silting is listed as the cause of the decline not only of *G. albanyensis* but also of *G. boykiniana* (Lea) which is considered nearly extinct.

Notogillia wetherbyi Dall (Gastropoda: Hydrobiidae) is recorded by Clench & Turner (1956) as inhabiting the St. Johns, Suwannee and Apalachincola drainage systems. It has also been discovered as fossil along the McBride's Slough tributary of the Wakulla River in Wakulla County, Florida. For unknown reasons, it is extinct in that drainage now.

Extinct Species

Although several fossil species of freshwater mollusks have been described from the South Atlantic and Gulf Coastal drainages, very few have become extinct in comparatively recent times.

Ordinarily, a list of such species would include those of the genus *Tulotoma* Haldeman (Gastropoda: Viviparidae). However, in the past few years intensive collecting by Mr. Herbert Athearn of Cleveland, Tennessee, has located 1 living population each of 2 species, *T. angulata* (Lea) and *T. magnifica* (Conrad), in the Coosa River tributary of the Alabama River. The Coosa River is crossed by a number of dams, and the attendant impoundments as well as silting and pollution have served to drastically alter the original aquatic fauna(s). Consequently, the 2 populations of *Tulotoma* may represent the last remnants of this genus.

Among the pleurocerid snails, Clench & Turner (1956) list *Goniobasis catenoides*

(Lea), known only from the Chattahoochee River at Columbus, Georgia, as extinct, "apparently ... exterminated by river silt."

Extinct Communities

On occasion, one may find that a habitat previously visited has been destroyed and that the assemblage of mollusks at that site has been eliminated.

We are fortunate indeed to have such faunal lists as that prepared by Hinkley (1906) for the Yalobusha River (and other drainages) and that by Frierson (1911) for the Pearl River (in part), both in Mississippi. The Yalobusha and Pearl drainages presently receive substantial industrial effluents, and the former faunas at Grenada and Jackson (respectively) have been obliterated. Further downstream, beyond the recovery zone, one may again find elements of the fauna that formerly resided upstream. In the Pearl River at Columbia, Mississippi, approximately 100 miles downstream from Jackson, one can collect over 20 species of unionid mussels. But only upstream from the bridge (U.S. Hwy. 98), because immediately under the bridge the stream again receives an odorous contribution, the Columbia sewage. A striking zonation can be observed, and no mussels occur below the source of the effluent.

More horrifying still are examples of the extinction of the fauna of nearly entire drainages. A paper mill at Foley, Florida, voids its wastes into the Fenholloway River about 15 miles from the Gulf of Mexico. The entire fauna and flora of the main channel has been totally destroyed, and only remnants remain in the unaffected small tributaries. A similar situation, involving phosphate mining pollution, has effected the decimation of the fauna in the main channel of the Peace River in peninsular Florida.

DISCUSSION (THE ENDANGERED FAUNA)

The overall changes in the freshwater mollusk fauna(s) of the eastern United States brought about by human activities have been immense, although only a few examples have been cited here.

Examination of a drainage map of the United States reveals a paucity of natural lakes in the Atlantic and Gulf coastal states as compared to those of the northern areas which felt the impact of glaciation, one effect of which was to scour out depressions which became lake basins. Evidently the evolution of freshwater gastropods has followed accordingly. The majority of aquatic pulmonates are in the north, and most prosobranchs occur in the south. Nearly the entire fauna of the south is composed of gilled species, and as such it is more susceptible to disruption of the aquatic environment than the lunged basommatophorans of the northern lakes.

Most gilled aquatic mollusks are stream-dwellers, and they are affected if the stream is altered in some way such as by (1) dam construction and impoundment of stream water to provide recreational facilities, better navigation, and/or a source of electric power, (2) industrial pollution which affects the chemical content of the water (by robbing the stream of dissolved oxygen, adding toxic materials, and/or adding normally non-toxic materials in toxic quantities), and/or by (3) extensive farming which through erosion will increase the silt content of streams, a process tending to progressively destroy the aquatic fauna.

Although Birmingham, Alabama, lies several hundred miles upstream from the Gulf of Mexico and numerous dams occur along the Alabama-Coosa River waterway, attempts have been made to promote this city as a seaport. The aquatic mollusks of the drainage have already been extensively damaged by impoundment-production (as well as by silting and pollution), yet further efforts are underway to construct additional dams (with locks), threatening the remaining species.

Industrial plants are continually arising alongside or near streams, and while attempts to encourage conservation are everywhere these days there are too few and/or too weak laws to punish or correct violations. Plans for the construction of a paper mill on the Apalachicola River between Bristol and Blountstown, Florida, are now under consideration. Unless measures are taken for adequate treatment of the effluents, we will most certainly lose the mollusks of the main channel, particularly *Glebula rotundata* (Lamarck) (Pelecypoda: Unionidae), a large stream species which finds its eastward limit in this drainage.

The southern states are comparatively agricultural (e.g., cotton, peanuts, tobacco), and soil conservation must be practiced not only for human benefit of continued crops but also for the perpetuation of the aquatic fauna. Silting is often said to affect mollusks by interfering with their respiration and/or feeding, and by altering the substrate disadvantageously. Specific evidence, particularly of an experimental nature, is largely lacking, however.

One can and must conclude that all of our freshwater mollusks, not only those of the eastern United States, are endangered. The factors which have partially or totally destroyed such faunal elements continue to plague us. Particular concern should be afforded not only rare and/or diminishing species (e.g., the unionids *Pleurobema collina* (Conrad) of the James River, Virginia, and the Tar River, North Carolina; and *Elliptio spinosa* (Lea) of the Altamaha River drainage in Georgia (Boss & Clench, 1967)), but also those which are greatly restricted in range even though they may be abundant in it (e.g., the unionids *Elliptio mcmichaeli* Clench & Turner and *Quincuncina burkei* Walker of the Choctawhatchee River system in southern Alabama and the Florida panhandle (Clench & Turner, 1956)). If such streams are sufficiently changed in some way, these endemic forms will vanish.

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Discussion of Dr. Heard's Paper

by Herbert D. Athearn

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My field work on the freshwater mollusks of the Gulf of Mexico drainage region began in 1941 and has been carried on intensively since 1954. During that period collections were made at about 500 stations. Many species were found to be abundant, others are common, and some are rare or very rare and have been found on only one or a few occasions. Other species previously reported from the region have never been collected by me.

Some species have apparently become very rare or perhaps even extinct during the past few years because of water pollution, dam construction or other habitat disruption. Dam construction on the Coosa River has eliminated almost all riffle habitats and has been particularly destructive to the rich, endemic fauna which previously flourished there.

Several of these now rare and endangered, or possibly extinct, species have already been mentioned by Dr. Heard. Unfortunately an additional large number should also be inserted into the preliminary list. These are as follows:

SOUTHERN AND CENTRAL TEXAS DRAINAGES

UNIONIDAE
- *Fusconaia friersoni* B. H. Wright 1896
- *Fusconaia lananensis* Frierson 1901
- *Fusconaia ridelli* Lea 1861
- *Quadrula aurea* Lea 1859
- *Lampsilis bracteata* Gould 1866

LOWER MISSISSIPPI AND ATCHAFALAYA RIVER TRIBUTARIES

PLEUROCERIDAE
- *Lithasia hubrichti* Clench 1965
- *Anculosa arkansensis* Hinkley 1915

UNIONIDAE
- *Margaritifera hembeli* Conrad 1838
- *Fusconaia missouriense* Marsh 1901
- *Arkansia wheeleri* Walker & Ortmann 1912
- *Ptychobranchus occidentalis* Conrad 1836
- *Lampsilis streckeri* Frierson 1927
- *Dysnomia florentina curtisi* Utterback 1915
- *Dysnomia lefevrei* Utterback 1915

TOMBIGBEE - ALABAMA - COOSA RIVER SYSTEM

NERITIDAE
- *Lepyrium showalteri* Lea 1861

VIVIPARIDAE
- *Lioplax cyclostomatiformis* Lea 1844

AMNICOLIDAE
Clappia cahabensis Clench 1965
Clappia clappi Walker 1909
PLEUROCERIDAE
Pleurocera foremani Lea 1842
Pleurocera showalteri Lea 1862
Goniobasis alabamensis Lea 1861
Goniobasis bellula Lea 1861
Goniobasis brevis Lea 1842
Goniobasis bullula Lea 1861
Goniobasis caelatura stearnsiana Call 1886
Goniobasis cahawbensis fraterna Lea 1864
Goniobasis capillaris Lea 1861
Goniobasis clausa Lea 1861
Goniobasis crenatella Lea 1860
Goniobasis fusiformis Lea 1861
Goniobasis gibbera H. H. Smith, Goodrich 1936
Goniobasis hartmaniana Lea 1861
Goniobasis haysiana Lea 1842
Goniobasis impressa Lea 1841
Goniobasis jonesi Goodrich 1936
Goniobasis lachryma Anthony, Reeve 1861
Goniobasis laeta Jay 1839
Goniobasis macglameriana Goodrich 1936
Goniobasis olivula Conrad 1834
Goniobasis pilsbryi Goodrich 1927
Goniobasis pupaeformis Lea 1864
Goniobasis pupoidea Anthony 1854
Goniobasis pygmaea H. H. Smith, Goodrich 1936
Goniobasis vanuxemiana Lea 1842
Gyrotoma alabamensis Lea 1860
Gyrotoma amplum Anthony 1860
Gyrotoma cariniferum Anthony 1860
Gyrotoma excisum Lea 1843
Gyrotoma hendersoni H. H. Smith, Goodrich 1924
Gyrotoma incisum Lea 1843
Gyrotoma laciniatum Lea 1845
Gyrotoma lewisi Lea 1869
Gyrotoma pagoda Lea 1845
Gyrotoma pumilum Lea 1860
Gyrotoma pyramidatum Shuttleworth 1845
Gyrotoma spillmani Lea 1861
Gyrotoma walkeri H. H. Smith, Goodrich 1924
Anculosa choccoloccoensis H. H. Smith, Goodrich 1922
Anculosa clipeata H. H. Smith, Goodrich 1922
Anculosa coosaensis Lea 1861
Anculosa foremani Lea 1842
Anculosa formosa Lea 1860
Anculosa griffithiana Lea 1841
Anculosa ligata Anthony 1860
Anculosa melanoides Conrad 1834
Anculosa modesta H. H. Smith, Goodrich 1922

Anculosa picta Lea 1860
Anculosa showalteri Lea 1860
Anculosa taeniata Conrad 1834
Anculosa torrefacta H. H. Smith, Goodrich 1922
Anculosa vittata Lea 1860

ANCYLIDAE

Rhodacmea cahawbensis Walker 1904
Rhodacmea filosa Conrad 1834
Rhodacmea gwatkiniana Walker 1917
Rhodacmea rhodacme Walker 1917
Neoplanorbis carinatus Walker 1908
Neoplanorbis smithi Walker 1908
Neoplanorbis tantillus Pilsbry 1904
Neoplanorbis umbilicatus Walker 1908
Amphigyra alabamensis Pilsbry 1906

UNIONIDAE

Fusconaia rubidula Frierson 1905
Quadrula archeri Frierson 1905
Quadrula stapes Lea 1831
Pleurobema aldrichianum Lea 1858
Pleurobema altum Conrad 1854
Pleurobema avellana Simpson 1900
Pleurobema concolor Lea 1861
Pleurobema decisum Lea 1831
Pleurobema favosum Lea 1856
Pleurobema fibuloides Lea 1859
Pleurobema furvum Conrad 1834
Pleurobema hagleri Frierson 1900
Pleurobema hanleyanum Lea 1852
Pleurobema hartmanianum Lea 1860
Pleurobema instructum Lea 1861
Pleurobema interventum Lea 1861
Pleurobema irrasum Lea 1861
Pleurobema johannis Lea 1859
Pleurobema lewisi Lea 1861
Pleurobema meredithi Lea 1858
Pleurobema murrayense Lea 1868
Pleurobema perovatum Conrad 1834
Pleurobema rubellum Conrad 1834
Pleurobema simulans Lea 1874
Pleurobema showalteri Lea 1860
Alasmidonta mccordi Athearn 1964
Strophitus alabamensis Lea 1861
Ptychobranchus foremanianum Lea 1842
Ptychobranchus greeni Conrad 1834
Obovaria curta Lea 1859
Plagiola lineolata Rafinesque 1820 (secure elsewhere)
Lampsilis altilis Conrad 1834
Lampsilis perovalis Conrad 1834
Lampsilis perpasta Lea 1861
Villosa propria Lea 1865
Dysnomia metastriata Conrad 1840

Dysnomia othcaloogensis Lea 1857
Dysnomia penita Conrad 1834

EASTERN GULF DRAINAGES: ESCAMBIA TO SUWANNEE RIVER

UNIONIDAE
Margaritifera hembeli Conrad 1838
Quincuncina burkei Walker 1922
Megalonaias boykiniana Lea 1840
Pleurobema pyriforme Lea 1857
Elliptio sloatianus Lea 1840
Alasmidonta triangulata Lea 1858
Medionidus penicillatus Lea 1857
Lampsilis australis Simpson 1900
Lampsilis binominata Simpson 1900
Lampsilis haddletoni Athearn 1964
Lampsilis jonesi van der Schalie 1934

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AMERICAN MALACOLOGICAL UNION SYMPOSIUM
RARE AND ENDANGERED MOLLUSKS

4. WESTERN FRESHWATER MOLLUSKS

by Dwight W. Taylor

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(Editor's Summary)

Dr. Taylor discussed in detail the nature of the fauna and the changes which are occurring. The full text of his paper is not available for publication but his list of recently extinct and/or rare and endangered species (status uncertain, and only those already named) is as follows:

Valvata virens Tryon, 1863. Clear Lake, and a lake near Watsonville, California.
Fontelicella idahoensis (Pilsbry, 1933). Snake River, southwestern Idaho.
Pyrgulopsis nevadensis (Stearns, 1883), Pyramid Lake, Nevada.
Durangonella mariae Morrison, 1945. Valley of Mexico.
Durangonella seemanni (Frauenfeld, 1863). Durango City, Mexico.
Planorbella traskii (Lea, 1856). Lakes in southern San Joaquin Valley, California.
Menetus opercularis (Gould, 1847). Mountain Lake, San Francisco, California.
Physa columbiana Hemphill, 1890. Columbia River below The Dalles, Oregon-Washington.
Physa humerosa Gould, 1855. Upper Gila River, Arizona-New Mexico.
Physa virginea Gould, 1847. Mountain Lake, San Francisco, California.

Discussion of Dr. Taylor's Paper

by Harold D. Murray

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Dr. Taylor has carefully and accurately analyzed the numerous causes of the changes in the molluscan fauna of Western North America. Perhaps his most succinct statement is "...the greatest handicap to evaluating the endangered species is the general lack of knowledge of the fauna." That statement needs no further elaboration.

The definition of "Western North America" used by Dr. Taylor is adequate for the purposes and discussion he presents. This author would be inclined to extend the eastern border of his definition into the Great Plains possibly as far east as longitude 100. This eastward extension is possible not because of faunal similarities to the far western area but because the same factors in faunal changes also apply there.

This author is impressed by the vivid references to the rich endemic fauna of Cuatro Cinegas in northeastern Mexico. I wonder how many similar such habitats exist in the vast area of western United States.

I disagree with but one of Dr. Taylor's comments. He states that no field evidence of deleterious effects of introduced species of mollusks have been observed. At present, I know of one example located 30 miles north of San Antonio, Texas. *Melanoides tuberculatus* and *M.* (*Thiara*) *graniferus* have invaded the type locality of *Goniobasis comalensis* Pilsbry 1886 to the extent that *G. comalensis* is now extremely

difficult to find where it was once common. Furthermore, several other habitats where *G. comalensis* was once common are now predominately occupied by one or both of the above introduced species. It is possible that either *M. tuberculatus* or *M. graniferus*, or both, could in time find their way to some of the localities of endemic native species to which he refers and have serious effects.

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AMERICAN MALACOLOGICAL UNION SYMPOSIUM
RARE AND ENDANGERED MOLLUSKS

5. EASTERN LAND SNAILS

by William J. Clench

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The preservation of our land mollusks is an almost impossible task. The allocation of small as well as large areas as National Parks or National and State forests will in a measure preserve some of our species. Other than in a limited number of cases, it would be impossible to prevent the extermination of certain species or races which have a very restricted distribution. What has occurred on the Lower Florida Keys is parallel if not similar to what has taken place over much of North America. Most of the area composing the Lower Florida Keys was and is privately owned and as such is subject to the whims, one way or another, of the owner of the property. A classic example is that of Lower Matecumbe Key, about midway in the Lower Keys.

I first saw this key during the winter of 1929. At that time Lower Matecumbe was relatively undisturbed. There was, of course, both the auto road and the Florida East Coast Railroad, both of which had a right-of-way cut through the length of the key. Hammock land was rather extensive and *Liguus* were abundant. About 1935 a very severe hurricane completely destroyed a group of beach hammocks along with *Liguus solidus dohertyi* Pflueger, a color form known only from these small hammocks. About 1953, land clearing and the building of fishing camps and other tourist attractions eliminated just about all of the hammock land and, of course, a few more color forms of *Liguus* peculiar to this Key. This same type of destruction has occurred along the entire series of keys from near Miami to Key West.

In general, the loss of our land mollusks is not due to pollution but to land clearing, strip mining, fire and other factors which destroy or completely change the natural habitat. At this time we have but little control over many of these factors.

Pesticides and weed killers cause an element of pollution, perhaps only in local areas where they are used, so far as it concerns the land mollusks. Both of these may be far more serious as a pollution problem in our freshwater streams due to surface run-off. In the North, during winter months, tons of salt are used to keep the highways free from ice. This same salt becomes a most important pollutant when carried into our roadside streams and ponds. Even trees and other vegetation along the highways are killed by the salt.

With relatively few exceptions most of our eastern land mollusks possess a fairly large distributional range. As a consequence, many or most of these species will be under "protective custody" in our National and State Parks and Forests.

Species and subspecies with a restrictive range or those known from but a single locality are far more difficult to protect. We are probably even unaware of the existence of many unique populations which need protection.

Factors given above will also hold for most of the West Indies. Rapid air transportation is making most of these tropical islands easily accessible and shortly these will be subjected to the ever increasing pressure of the tourist.

A curious factor which is detrimental to colonies of *Cerion* in Cuba is the quest for "sharp" sand for concrete and cement work. *Cerion* lives only along the upper strand line in Cuba and it is here where this type of commercial sand occurs. As a consequence areas along this strand line are completely destroyed. Bulldozers cut down as much as 6 feet into jumble of coral rock and sand, destroying the vegetation of bushes and small trees, and of course the colonies of *Cerion*.

Discussion of Dr. Clench's Paper

by Dee S. Dundee

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In considering rare and endangered eastern land snails, several questions come to mind. First, what exactly does rare mean? Does it mean those which once had a wide distribution but now are restricted to a few places? Or does it mean those that always have been restricted to a few places where they continue to maintain the population at a high level? Or does it mean those that have a wide range as a species but have the individuals widely scattered within that range? Or, does it mean all of these? One must resolve these questions before he can set about thinking clearly of the problem at hand.

Once a decision is reached about the meaning of rare, one must ask, if it is rare, then is it necessarily endangered? After wrestling with these questions and discussing them with my colleagues, I find that I am still confused. Therefore, I have had arbitrarily to select, as being rare, those snails which are, for one reason or another, now limited to one area (a State or less). I have decided that, even though they are rare, they are not necessarily endangered. Upon these premises I shall proceed with my comments.

Here we should consider some other questions: first, what will cause the extinction of any species? Dr. Clench has mentioned a few things: climatic factors such as hurricanes, the clearing of land by man, strip mining, fire, pesticides. There are, of course, many others such as other types of climatic changes, soil changes, biological introductions, and so on. Second, what general types of snails are most likely to disappear? Assuming that edaphic factors such as climate and soils remain somewhat constant (they never do) in the near future, it would appear, as Dr. Clench has pointed out, that those snails having a restricted range or those from a small locality, or in some cases, the larger, more conspicuous forms would be most likely to disappear. Those ranging widely over much of eastern North America may have their populations depleted by man, but they should survive and most probably will adapt to the new environments created by man (e.g., where did all of those which now live in flower and vegetable gardens and lawns live prior to 1609?). Next we must ask, which of the eastern land snails then are likely to become extinct? Or which, if any, should we protect? Here we must use our arbitrary decisions as to what is rare and, if it is rare, is it endangered. I have checked through the land snails of eastern North America and have arrived at the following possibilities. Dr. Clench mentions only one, *Liguus*, which is truly North American. I believe that others *may* also be considered. I certainly am *not* proposing that we include all of these in a list of rare and endangered forms. I only ask that my colleagues consider these in the light of their experiences and help me decide.

(After the session various malacologists contributed deletions and additions and the following list is the result.)

Pomatiasidae:	*Opisthosiphon bahamensis* (Pfeiffer)	Florida
Oleacinidae:	*Varicella gracillima floridana* (Pilsbry)	Florida
Polygyridae:	*Triodopsis soelneri* (Henderson)	North Carolina
	Stenotrema hubrichti Pilsbry	Illinois
	Polygyriscus virginianus (P. R. Burch)	Virginia
	Polygyra hippocrepis (Pfeiffer)	Texas

Pupillidae:	*Bothriopupa variolosa* (Gould)	Florida & Yucatan
	Sterkia eyriesi rhoadsi (Pilsbry)	Florida
Sagdidae:	*Hojeda inaguensis* (Weinland)	Florida Keys - Bahama Islands
Zonitidae:	*Vitrinizonites uvidermis* (Pilsbry)	North Carolina, Tennessee
	Pilsbryana tridens (Morrison)	Oklahoma, Texas
	P. aurea (Baker)	Tennessee
	Paravitrea roundyi (Morrison)	Oklahoma
	P. variabilis (Baker)	Tennessee, Oklahoma
	P. aulacogyra (Pilsbry & Ferriss)	Arkansas
	Clapiella saludensis (Morrison)	South Carolina
Bulimulidae:	*Liguus fasciatus* (Müller)	Florida
	Orthalicus reses (Say)	Florida
	O. floridensis (Pilsbry)	Florida
	Drymaeus dormani (Binney)	Florida
	D. dominicus (Reeve)	Florida
Cerionidae:	*Cerion incanum* (Binney)	Florida

It is very difficult to really decide if some of these are endangered; one really needs to be working with the groups to know for sure.

A final question, and one which will be very unpopular, is this: should we worry about our rare species of eastern land snails? When one considers that the molluscs are a very old group dating back 600 million years, one must realize that there surely have been many species which lived and became extinct in that much time. Many of them doubtlessly were as desirable as those about which we now are concerned. In fact, those which concern us now may have taken the places of some of the earlier ones. Perhaps the destruction of these present day forms is merely the next evolutionary step in the scheme of things with man being the evolutionary agent. A prominent ecologist has pointed out that, despite the fact that man is severely changing the landscape, there *are* organisms adapting to those changes and filling the niches of those wiped out by the changes. This whole question is a very philosophical one and has many ramifications but it *is* one which we should consider. Dr. Clench pointed out in his opening statement that the preservation of land molluscs is an almost impossible task.

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AMERICAN MALACOLOGICAL UNION SYMPOSIUM
RARE AND ENDANGERED MOLLUSKS

6. WESTERN LAND SNAILS

by Allyn G. Smith

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INTRODUCTION

Viewed from the most pessimistic angle, it might be stated that all land mollusks indigenous to the western part of the United States are endangered to some degree. The rapid growth of the West has been spectacular and indications are that this will be accelerated in the future. While this is particularly true of the States west of the Rocky Mountains, to a much lesser degree has it affected Alaska, western Canada and Mexico, but even in these broad areas such growth is beginning to be felt. This massive advance in civilization, brought about by what amounts to a population explosion, brings with it the construction of more and ever wider freeways for motor traffic; bigger and higher dams that cause the flooding of beautiful, scenic cañons; bigger airports and similar projects that take over more and more wild land, scar the countryside and destroy land-snail habitats right and left. Developers are creating new towns and housing projects. The industrial trend is creating a movement from the central cities into outlying areas. This, with the air pollution and garbage disposal problems that result, bodes ill for the future of many western land snails, none of which can survive out of their natural habitats. There are a few species of land mollusks that do tolerate the advance of civilization - *Helix aspersa*, *Oxychilus cellarius* and several species of slugs to mention a few. But these are European immigrants and are not pertinent to this discussion.

The future picture does, however, have some bright spots. The western national, state and local parks provide habitats for many snail species. Those living in these areas are definitely not endangered and hopefully never will be. We are only just beginning to wake up to the need to preserve more wild areas for the enjoyment of future generations of people, and public opinion, prodded by an increasing number of conservation-minded folks, seems to be moving in this direction, however slowly. This augurs well for the extension of the great western park systems, the creation of "green belts," and the setting aside of wilderness areas safe from the incursion of loggers, miners, cattle men, resort developers and others of like ilk whose interest in the preservation of our natural resources leaves something to be desired.

Another bright spot for the future well-being of indigenous land snails is the western "lay of the land," with its vast mountainous and desert areas. Much of these are so inaccessible and incapable of "improvement," or the climatic conditions are so adverse, that the so-called advance of man and his works is prevented or at least severely limited and will remain so. Land snails that live in such areas will continue to do so without habitat interference.

Fortunately, also, the ranges of many western land snail species are sufficiently extensive geographically so that the liklihood of wiping them out completely is remote. There is a danger here, however, for future malacological studies dealing with ecology and with species evolution. The possibility of eliminating certain local races of widespread species through habitat destruction is imminent, especially where such races occupy limited areas.

Again, the relatively few collectors especially interested in land mollusks at present are not liable to endanger a species; but this may not be so true in the future. There is an ever-present danger from the over-collecting of some forms having an extremely limited distribution or living in micro-habitats not occurring anywhere else. Danger to such forms can and should be minimized in the interests of science. Land snail collectors can reduce this danger if they will operate with discretion, with a weather eye on the need to allow a race or a colony to perpetuate itself.

RARE AND ENDANGERED WESTERN LAND SNAILS

I can say, at the outset, that at present I know of no western land snail species that is so rare or endangered to the degree that exists, for example, in the case of the California Condor, the California Clapper Rail or the Trumpeter Swan. There may well be such but the west is a big country and includes thousands of square miles where I have not done any appreciable amount of collecting. Thus, I can comment only on those areas and those species with which I have had some familiarity starting in the year 1910, with the hope that others will be able to fill in the gaps.

Perhaps the most practical way to approach the subject is to use Pilsbry's two-volume monograph on the *Land Mollusks of North America* (*North of Mexico*), 1939-1948, published by the Academy of Natural Sciences of Philadelphia, taking the groups, family by family, and commenting on species known to be rare, or that appear to be in some danger of extinction. This, of necessity, will not cover species described since the Pilsbry Monograph was published - one of the gaps mentioned above.

For the sake of brevity in the following list, code letters are used, as follows:

R - Rare occurrence in nature (not because merely hard to collect);
L - Limited or local in geographic distribution;
E - Endangered or possibly endangered for stated reasons.

LIST OF SPECIES

Family HELMINTHOGLYPTIDAE

Monadenia

M. fidelis group. Widespread with many localized subspecies. Safe in redwood parks.

M. f. celeuthia Berry. R - L. Upper Rogue River valley.
M. f. pronotis Berry. R - L. Near Crescent City, Calif.
M. f. leonina Berry. R - L. Along Klamath River, Calif.
M. f. klamathica Berry. R - L. A high dam on the Klamath River could eliminate this and the preceding subspecies.

M. infumata group. Many localized races. Generally safe in redwood parks.

M. i. alamedensis Berry. R - L - E, by industrial development and housing expansion along the eastern shore of San Francisco Bay.

M. mormonum group. Many local races. Generally safe in mountain areas.

M. m. buttoni (Pils.). R - L - E, by construction of both high and low dams causing cañon flooding.
M. m. cala (Pils.). L. Safe in Calaveras Big Tree Park.
M. m. loweana Pils. R - L.
M. m. hirsuta Pils. R - L - E, from possible over-collecting.

M. troglodytes Hanna & Smith. R - L. Recently found living.

M. circumcarinata (Stearns). R - L. Possibly a relict species nearing extinction. Not found living in recent years.

M. hillebrandi (Newc.) & ssp. *yosemitensis* (Lowe). R - L. Safe in Yosemite and Kings River National Parks. A high dam across the Merced River below the Yosemite Park boundary could eliminate a local race.

Helminthoglypta

H. tudiculata series. Fairly widespread. Many local races and subspecies. Generally safe in mountain habitats.

H. t. grippi (Pils.). R - L.

H. t. angelena Berry. L - E, by industrial expansion.

H. cypreophila series. Widespread, and generally safe in mountain habitats.

H. allynsmithi (Pils.). R - L. A high dam across the Merced River Cañon could eliminate this species.

H. hertleini Hanna & Smith. R - L.

H. nickliniana series.

H. californiensis (Lea). L. The typical small form is practically gone from the type locality, a small off-shore islet being destroyed by wave action, but is safe in Pt. Lobos State Park.

H. berryi Hanna. R - L - E. Possibly nearing extinction as a relict species. Could be endangered further by over-collecting.

H. n. awania (Bartsch). R - L. Safe in Pt. Reyes National Seashore.

H. n. bridgesi (Newc.). L - E, by industrial and building expansion.

H. n. contracostae (Pils.). L - E, at the type locality from resort expansion or over-collection. The habitat for the race *arnheimi* on the east side of San Francisco Bay has been completely destroyed by industrial expansion.

H. arrosa series. Widespread and generally not endangered. Many local forms, coastal and inland.

H. a. holderiana (Cooper). L - E, by industrial expansion on the east side of San Francisco Bay.

H. a. miwoka (Bartsch). R - L. Safe in Pt. Reyes National Seashore.

H. a. pomoensis A. G. Smith. R - L. Some danger from logging operations.

H. a. mailliardi Pils. R - L.

H. ayresiana series. Limited to Santa Barbara Channel Islands. E, on San Miguel Id., the type locality, from U.S. Navy operations. The ssp. *sanctaecrucis* Pils. in no present danger on Santa Cruz Id.

H. walkeriana (Hemphill) and ssp. *morroensis* (Hemphill). R - L.

H. dupetithouarsi series.

H. dupetithouarsi (Desh.). An unnamed, dwarf race on an offshore islet (type locality of *H. californiensis*) is probably extinct from wave erosion of its micro-habitat.

H. cuyama Hanna & Smith. R - L.

H. benitoensis Lowe. R - L. Safe in Pinnacles National Monument.

H. sequoicola consors (Berry). L - E, by expansion of farming and industrial operations.

H. cuyamacensis series. Mostly in mountain habitats.

H. c. lowei (Bartsch). R - L.

H. c. avus Bartsch. R - L.

H. c. venturensis (Bartsch). R - L.

H. c. paiutensis Willett. R - L.

H. callistoderma (Pils. & Ferriss). R - L - E, possibly by a high dam across the lower Kern River Cañon.

H. orina Berry. R - L.

H. tularensis series. Mountain habitat. R. Mostly safe in Sequoia National Park.

H. napaea series. L. Mountain habitat. Safe in national parks. (Mohave desert

series). R - L. Several species with desert habitat. Not in danger at present.

H. traski series. Many subspecies and races. Mostly mountain habitat.

H. t. misiona Chace. R - L.

H. t. coelata (Bartsch). R - L.

H. t. coronadoensis (Bartsch). R - L - E, from over-collecting in island habitat.

H. t. pacoimensis Gregg. R - L.

H. t. fieldi Pils. R - L.

H. t. phlyctaena (Bartsch). R - L.

H. t. willetti (Berry). R - L - E, possibly by severe forest fires.

H. t. tejonis Berry. R - L.

H. carpenteri (Newc). R - L. Desert habitat.

H. similans Hanna & Smith. R - L. Desert habitat.

H. petricola series. Several species and subspecies. R - L.

H. stageri (Willett). R - L.

H. inglesi Berry. R - L.

H. lioderma Berry. R - L.

H. ferrissi Pils. R - L. A large race safe in Kings Cañon National Park.

H. proles series. Mountain habitats. Two subspecies. Generally safe in national parks.

H. euomphalodes Berry. R - L.

H. tularica (Bartsch). R? - L. A "lost" species.

Micrarionta. The southern and Lower California species, of which there are many, are confined to the Santa Barbara Channel Islands or to desert mountain habitats. *M. stearnsiana* (Gabb) is a mainland species and there are others in Lower California. Most are limited in distribution. Living specimens of desert species are rare and difficult to collect for the most part. Those that might be endangered at present are:

M. rufocincta (Newc.) and ssp. *beatula* Ckll. E, from resort expansion on Santa Catalina Id.

M. facta (Newc.). E. May be extinct on San Nicolas Id.

M. kelletti (Fbs.). L - E, from possible destruction of its cactus-patch habitat on Santa Catalina Id.

M. tryoni carinata Hemphill. R - E, especially on San Nicolas Id.

Sonorella. Widely distributed, as a genus, but many species, subspecies and local races have extremely limited distributions. Usually occurring in colonies but living specimens often rare and difficult to collect, as they are subterranean. Some forms are no doubt in possible danger from over-collecting or other causes. Dr. Walter B. Miller has studied the group recently and is in a better position than I to indicate species that may be endangered.

Humboldtiana. Mountain snails confined in the U.S. to the Texas border, extending south at least as far as Mexico City. U.S. species seem to be relatively rare but apparently not in danger.

Oreohelix. Mountain snails widespread in the West. Generally colonial and common, with many species, subspecies and local races. As a group, the Oreohelices do not appear to be in any particular danger although some forms having extremely limited distributions may be potentially endangered.

O. avalonensis (Hemphill). E, if not already extinct, the single known colony having been wiped out by the original collector many years ago.

Polygyrella. Fairly wide distribution in relatively unpopulated country.

Ammonitella. A relict genus, possibly on the way to extinction, though common at present, where found.

A. yatesi and ssp. *allyni* Chace. L - E, from possible over-collecting. The subspecies seems safe in a national park.

Polygyroidea. Possibly another relict genus. Mountain habitat.

P. harfordiana (J. G. Cooper). R - L. Safe in Mariposa Big Trees, the type locality, although it appears to be becoming increasingly rare there because of its extremely limited habitat. Also occurs in Merced River Cañon below Yosemite Park, where it could be endangered by a high dam.

Glyptostoma. Several southern California species and subspecies, all except *G. newberryanum* (W. G. B.) being localized and rare.

G. gabrielense Pils. L - E, from industrial development in the Dominguez Hills, near Los Angeles, but probably safe in Elysian Park, Los Angeles.

Family POLYGYRIDAE

Trilobopsis. Generally occurs in a mountainous habitat, in relatively unpopulated areas.

T. loricata series. Several subspecies, all more or less limited in distribution but not thought to be endangered.

T. trachypepla Berry. R - L.

T. roperi series.

T. roperi (Pils.). R - L.

T. tehamana (Pils.). R - L.

T. penitens (Hanna & Rixford). R - L - E, as type locality inundated by Folsom Reservoir. A new locality for this species discovered in 1968, which also may be in trouble from a resort developer.

Triodopsis.

T. devia (Gld.). E, because of industrial expansion in the Seattle area. May not be in danger elsewhere in its range.

T. mullani series. Many subspecies and local races in a mountainous habitat, generally in unpopulated country. In no present danger, as a group.

T. sanburni W.G.B. R - L.

T. populi (Van.). E. A high dam on the Snake River at Hell's Cañon may put this species in danger.

Allogona. Western species in no particular danger. Widespread in Pacific Northwest east of the Cascades in U.S. and Canada.

A. ptychophora solida (Van.). L - E, from a possible high dam at Hell's Cañon.

Vespericola. Many species and subspecies, plus local races, most not being in any present danger although the habitats of some are being restricted.

V. columbiana series.

V. c. depressa (Pils. & Henderson). R - L.

V. hapla (Berry). R - L.

Ashmunella. Mountain snails in Arizona and New Mexico. Many species, subspecies and local races. Generally colonial. I am not familiar with their abundance or rarity at the present time. Most seem not in danger, as a group, although some may be in danger from over-collecting.

Family SAGDIDAE

Thysanophora. Widespread in the Southwest and in Mexico (including Baja California).

Microphysula. Fairly widespread distribution. In no present danger.

Family BULIMULIDAE

Bulimulus. Western species (Pacific Southwest, Mexico and Baja California) occupy mountainous or desert mountain habitats. In no particular danger.

Family UROCOPTIDAE

Holospira. Numerous species in Arizona and New Mexico. Generally colonial in mountainous terrain. I am not familiar with forms that are presently rare, although some have limited distributions. Probably not endangered at present.

Coelocentrum. Several species and subspecies on islands in Gulf of California and in Baja California. Probably not endangered, as most are remote.

Family ACHATINIDAE

Rumina. Introduced into Arizona and California.

Cecilioides. Introduced into California.

Family HAPLOTREMATIDAE

Haplotrema. Numerous western species and subspecies. Smaller forms usually rare.

H. duranti (Newc.). Santa Barbara Channel Ids. only. R - E.

H. catalinense (Hemphill). R - L. Santa Catalina Id. only.

H. keepi (Hemphill). R - L.

H. transfuga (Hemphill). R - L.

H. voyanum (Newc.). R - L. No typical specimens found in recent years. May be extinct.

H. v. humboldtense Pils. R? - L?. Unknown to me. Possibly not related to true *H. voyanum*.

Family ZONITIDAE

Euconulus. Small; widespread. Mountainous habitat. Not in danger.

Oxychilus. Several introduced species. Adapts to civilization.

Retinella. Small mountain snails. Generally rare and seasonal. Probably not in danger.

Pristiloma. Small; seasonal. Numerous western species. Probably not endangered.

P. stearnsi (Bland). R.

P. pilsbryi Vanatta. R.

P. idahoense Pils. R.

P. arcticum (Lehnert). R.

P. a. crateris Pils. R - L.

P. lansingi (Bland). R.

P. johnsoni (Dall). R.

P. nicholsoni H. B. Baker. R - L.

P. shepardae (Hemphill). R - L. Island distribution only.

P. orotis (Berry). R - L.

P. gabrielinum (Berry). R - L.

P. wascoense (Hemphill). R - L.

P. subrupicola (Dall). R.

P. s. spelaeum (Dall). R - L. Not a true cave snail.

Hawaiia. Small; widespread. Not in danger.

Striatura. Small; widespread. Not endangered.

Vitrina. Widespread in mountains at higher elevations. Not in danger.

Megomphix. Shells similar to *Haplotrema*.

M. hemphilli (W. G. B.). R.

M. lutarius H. B. Baker. R - L.

M. californianus A. G. Smith. R - L.

Family ENDODONTIDAE

Anguispira. One common western form in Pacific Northwest and British Columbia. Not in danger.

Discus. Small mountain snails. Not endangered.

D. marmorensis H. B. Baker. R - L.

D.? selenitoides (Pils.). R - L. Safe in Yosemite Park.

Helicodiscus.

H. singleyanus (Pils.). R.

H. eigenmanni arizonensis (Pils. & Ferriss). R.

H. salmonaceus W.G.B. R - L.

Speleodiscoides.

S. spirellum A. G. Smith. R - L. Not a cave snail. Found living for the first time in 1967. May not be an endodontid.

Punctum. Small; generally widespread. Western species not endangered.

Radiodiscus. Small. Mountain habitat. Western species not in danger.

Family SUCCINEIDAE

Oxyloma. Western species probably not endangered.

O. nuttalliana (Lea). R.

O. n. chasmodes Pils. R - L.

O. haydeni kanabensis Pils. R - L.

O. hawkinsi (Baird). R.

Succinea. Western species generally not endangered.

S. rusticana Gld. R.

S. lutella Gld. R. In Arizona and New Mexico.

S. gabbi Tryon. R.

S. californica Fischer & Crosse. R. In Baja California.

S. oregonensis Lea. An unknown species.

Quickella. Western species not worked out taxonomically.

Family VALLONIIDAE

Vallonia. Western species not endangered.

V. gracilicosta Reinhardt. R - L. In western states.

V. albula Sterki. R - L. In western states.

Planogyra.

P. clappi (Pils.). R.

Cionella.

C. lubrica (Müller). R - L. In western states.

Family PUPILLIDAE

Gastrocopta
Chaenaxis
Pupoides
Pupilla
Vertigo
Sterkia

Many western species and subspecies, some with limited ranges (e.g., *Chaenaxis* and *Sterkia*). Not considered to be particularly endangered, especially in mountainous and desert habitats.

Family CARYCHIIDAE

Carychium.

C. exiguum (Say). R - L.

C. occidentale Pils. R.

Family TRUNCATELLIDAE

Truncatella.

T. simpsoni Stearns. R - L.

C. californica Pfeiffer. R - L.

The above list is, as stated earlier, far from complete. It omits any detailed mention of species living in western Canada (especially the northern provinces), Alaska and Arctic North America, whose status is not known to me. Similarly, I am not familiar with the extensive land snail fauna of Mexico (south of the Sonora Desert), or of Central America, where little collecting has been done in recent years. For such areas, much of which is largely unexplored conchologically, it probably can be stated categorically that the species living there are in no particular present danger.

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7. EASTERN MARINE MOLLUSKS

by R. Tucker Abbott

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The survival problems confronting marine species, although somewhat similar to those facing the land and fresh-water forms, are quite different in severity, manner of endangerment and nature of possible remedial measures.

Marine mollusks do not appear to be endangered in the same sense as are many birds, mammals and fresh-water mollusks. In my considered judgement, there are few, if any, marine species of mollusk, anywhere in the world, being led to extinction because of the activities of man. This, however, is mainly because the distribution of every species of marine mollusk is either very extensive over many hundreds of linear miles, or, in the case of a few highly endemic species, at least extended over many hundreds of square miles. Furthermore, bathymetric ranges in sublittoral species give additional protection.

Although no accurate figures are available, and, indeed, there is need for new studies along these lines, I would not hesitate to say that the well-known high mortality rates of marine mollusks are largely due to natural causes. Probably less than 1% of the annual death rate of all marine mollusks is due to the activities of man. Commercial fisheries would probably account for the greatest cause of man's reduction of mollusk populations; pollution and other environmental changes made by builders and engineers would probably come second; and shell collectors would make a very poor third.

From the distributional records being made by several research fisheries' boats and by casual dredging samplings by amateur conchologists and commercial shrimp trawlers, it would appear that there is a population band of *Macrocallista maculata* running from Alabama to central west Florida and from North Carolina to central east Florida, anywhere from 1 to 8 miles in width at depths ranging from 6 to 60 feet. This represents about 6,000 square miles of high density Calico Clam populations. The species, incidentally, extends through the Caribbean to Brazil. One might hazard a guess that about 2 billion bushels of this clam die every 5 years. Old age, fish, "red-tide," cold water, fungal diseases and shifting bottoms probably account for most of these deaths. Of the 2 billion bushels, I doubt if shell collectors account for more than 1,000 bushels, and most of these would be specimens cast ashore after storms. A similar situation exists for the vast majority of the marine mollusks.

Are some marine species being over-collected? Yes. Especially, locally; and especially the larger and edible species. Are they in danger of becoming extinct? No. Is over-collecting bad? Yes, because it reduces the density of the populations in certain areas to the extent that they are no longer available in commercial quantities (in the case of oysters, scallops, clams and edible whelks) or no longer present in sufficient numbers to satisfy the normal, modest requirements of hobby collectors. Among the species that are being over-collected in certain limited areas are *Strombus gigas* (the Pink Conch), *Cassis madagascariensis* (the Helmet Shell), *Pleuroploca gigantea* (the Horse Conch), *Cyrtopleura costata* (the Angel Wing), *Cyphoma gibbosum* (the Flamingo Tongue), *Melongena corona* (the King's Crown) and edible clams, scallops and oysters. Of all these species, the first 3 (*Strombus*, *Cassis* and *Pleuro-*

ploca) are the least able to replace their numbers, and are becoming comparatively uncommon, but certainly not extinct.

In addition to over-collecting, and I refer mainly to that created by commercial fisheries' activities and professional shell gatherers who sell to shell dealers, far-reaching and much more serious consequences can descend upon shore mollusks and, of course, other forms of marine life, by major engineering projects of man or by mass pollution of coastal waters by heavy metals, major heat transfers, massive oil spillage or altered currents. The filling of extensive marsh lands by real estate developers robs the coastal offshore waters of their life-giving source of nutrients. What's bad for a *Melampus* marsh snail is bad for a coastal shelf *Junonia*.

What practical protective measures are possible? Space does not permit me to discuss national pollution and conservation problems. Agencies of the United States government and well over 500 private foundations and organizations, such as the National Wildlife Federation and the Welder Wildlife Foundation, are actively working on these matters.

Over-collecting can be reduced by shellfishery laws and the dissemination of information among shell collectors. I have studied the shellfishery laws of each state, and in 1961 I published a digest of the laws of 24 of the U.S. states and Canadian provinces that have salt-water coasts (*How to Know the American Marine Shells*, Signet Key Book, KT 375, New American Library, Inc., N. Y., p 197-203). In this I said, "The laws were not created to annoy tourists or shell collectors or to interfere with students of marine life. Unfortunately, the regulations vary from state to state, and in many instances they are ambiguous, scientifically inaccurate, and self-contradictory. We recommend 3 general rules for collectors: cooperate with local wardens; ask local fishermen or ocean-front property owners about local restrictions; don't collect live oysters at any time. Beware of Sunday "blue law" restrictions, especially in eastern Canada and New Jersey. You may write to the director of fishery agencies for special collecting permits. Most states will issue them cheerfully without cost."

Many clubs are encouraging the conservation of mollusks. The Sanibel-Captiva club in Florida was the first to initiate a program of local education by publishing posters, flyers and booklets on "Don't Be a Pig." Other clubs have distributed "collecting creeds," urging members to take small samplings, rather than to pick up every specimen seen. Authors of popular articles and books are now urging the general public to collect in moderate numbers. These measures are helpful in local areas. In some good collecting spots you can find a choice specimen only because a thoughtful and courteous collector was there just before your visit.

One of the most successful systems of protecting our wildlife was championed by President Theodore Roosevelt, who began our system of National Parks and Wildlife Preserves. This is an ideal mechanism of ensuring reasonable protection to undersea life in many areas. There are several underwater parks in America, the first being the Key Largo Coral Reef Preserve, opened in Florida in 1960. The Department of Mollusks at the Academy of Natural Sciences has made surveys in such island groups as the Seychelles, Indian Ocean, with a view towards outlining the methods of establishing underwater preserves that will not interfere with the rights and livelihood of the local people. Other governments, as in Malaya, British Honduras and the Bahamas, are now taking active steps to protect sea life for future generations.

Discussion of Dr. Abbott's Paper

by Joseph Rosewater

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It is refreshing to learn that in regard to our marine mollusks it is unlikely that any species is endangered due to man's activities. I should like to make the point, however, that it may not always be possible to make a subjective determination on the probability of the extinction of a species. The fossil record tells us that long before the appearance of man millions of once living species had already ceased to exist. We are relatively sure that this is continuing, and in the case of such cryptic animals as mollusks, probably largely undetected.

What causes it? Probably many things, such as unsuccessful competition between species, changes in climate or in other characteristics of the habitat. It may be that there is inherent in each species a sort of evolutionary "time piece" which "runs down" at last. This is an enormous simplification which one day may be elaborated and more fully understood. The "running down," however, could certainly be hastened or delayed by a multiplicity of factors, many of which man may influence especially in the light of his recent population growth.

Persons, such as ourselves, who collect forms of life intensively and specifically may do well to approach the task thoughtfully. It is true that if we did not collect them the individuals would eventually die anyway. But if we collect every visible specimen of a species from a unit area, we may be upsetting the "balance of nature" in that spot. And if we destroy the habitat by turning rocks which we do not replace, etc., we may be sure that we have created havoc in that spot.

What can be done? Dr. Abbott has made what are probably the most effective suggestions to assure us of a continuing source of enjoyment in our hobby and work. Obey local collecting regulations; collect moderately and intelligently; support conservation efforts. To these I would like to add another suggestion which may appear questionable at first but which may be understandable upon reflection: avoid subjective measures which bring about major changes in the environment or species composition, for these have in the past, and almost certainly will in the future, upset evolution.

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8. WESTERN MARINE MOLLUSKS

by A. Myra Keen

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Having contacted several collectors who might know of any West Coast mollusks that are both rare and endangered, I am pleasantly surprised to come up with nearly negative findings. It is true that we have rare species. We also have areas and habitats that are threatened. As yet there seem to be few if any species qualifying in both categories.

I had thought that perhaps *Norrisia norrisi*, a trochid snail that feeds on the blades of giant kelp, might be in a precarious state, for the extent of the kelp beds has markedly diminished in southern California; also, commercial harvesting removes much of the annual production. However, Mr. John Fitch reports that although in places where pollution and sea urchins have destroyed the kelp, the snail is rare or missing, around some of the offshore islands and in untainted coastal waters it is still abundant.

The great hazard to marine populations on the Pacific Coast is not so much to certain species as it is to the whole ecosystem, especially in the shallow bays. This West Coast, characterized by a steep continental shelf and slope, has only a few bays, and most of the species that have adapted to the bay environment tend to be widespread in geographic range. If only part of the bays were threatened, the assemblages might be expected to survive in other areas. However, the pressure of human populations and the obsession on the part of developers to fill or radically modify the few bays that are here is cause enough for alarm. Pollution from industrial wastes, from sewer outfalls, and (most hazardous of all) from agricultural pesticide runoff has already had considerable effect on the marine fauna, and as it increases can cause enormous havoc. The voice of the conservationists is being raised, but here, as elsewhere in the country, the cry is yet too feeble to influence the expansionist planners.

Commercial development of shellfish resources on the West Coast has been limited by several factors. Oysters were introduced into San Francisco Bay nearly a century ago from the Atlantic coast, for the native oyster, which had thrived there, is too small for marketing. Within a few years pollution had built up so much that the oysters became unsafe for food. The industry continues, however, in a few other sites along the coast, importations now being of spat from Japan. With the oysters came several Atlantic and Japanese molluscan species, accidentally. Some have flourished -- for example, *Ilyanassa obsoleta* -- but so far as I know none has been a special threat to native species as so often happens with introduced forms. Because it is in the interests of the industry to keep bay waters clean, the industry is, on the whole, on the side of conservation.

A canning industry, based on such West Coast food clams as the razor clam, *Siliqua patula*, burgeoned in the 1920's from Washington to Alaska, but this enterprise soon foundered because the shellfish could not reproduce fast enough to supply the demands the canners were making. Some clam beds have never recovered, but there was a large enough breeding population so that the species have managed to survive.

I shall give a review of the situation for the one intertidal species, a littorinid, that comes close to qualifying as endangered. It could easily be wiped out with only a

slight habitat change. For a time its numbers decreased markedly, and as it has a limited range, its condition was precarious.

The status of *Algamorda newcombiana* (Hemphill, 1876)

For the following notes on the situation of *Algamorda newcombiana* (family: Littorinidae), I am indebted to Mr. Robert Talmadge, who has been making observations on the species for about thirty years.

This small snail is virtually restricted to Humboldt Bay, in northern California. It lives on the lower stems of a marsh succulent, *Salicornia*, or in the muddy substrate immediately below. Its optimal distribution is at or slightly above mean high tide level, so that it is submerged in sea water only a few hours per year and, because of the heavy rainfall of the region, is more apt to be wetted by fresh than by salt water.

In the 1930's, when Mr. Talmadge's studies began, the species was distributed over a stretch of about 10 miles along the bay margins, present wherever there was *Salicornia* but tending to be in uneven clusters of dense populations thinning out laterally. During the 1940's and 1950's several sawmills were actively operating in the area. By 1961 most of the snails were gone, and only a mass of half-burned sawdust could be found blanketing their habitat. Small isolated colonies survived in parts of the bay where the sawdust was less pervasive, but the prospects at this time seemed dim for the species.

Upon my recent inquiry as to status of the snail, Mr. Talmadge revisited the bay in February 1968. He found a few colonies doing well in both the south and the north ends of the bay. Some of the sawdust layer has broken up, and mud is again evident in places. Some of the normal associates such as arthropods and the marsh snail *Phytia* were present again, even where *Algamorda* was not. It would seem, therefore, that habitat recovery is taking place. Several of the sawmills have been abandoned and others have converted to a type of work not producing sawdust. Thus, the menace to estuarine life here is lessening. *Algamorda* may again be able to expand to its former extent, barring further pollution factors. Possibly the re-occupation of its range might be hastened by judicious transplanting as soon as the environment, through decay and flushing away of the sawdust, has again returned to normal.

Discussion of Dr. Keen's Paper

by William K. Emerson

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I concur with Dr. Keen's conclusion that there are apparently no species of west American marine mollusks facing biological extinction. However, as Dr. Keen has pointed out, it is the basic ecosystem of the shallow water bays, especially those of southern California, that is endangered. The severe modification of these bays by man for commercial and recreational purposes requires that one must look to northern Baja California, Mexico to find an essentially undisturbed bay-fauna of the Californian faunal province. San Quintin Bay, which is situated some 150 miles south of San Diego, is an example of such an embayment (Gorsline & Stewart, 1962).

Fortunately, most of the shallow-water, marine inhabitants of the bays of southern California occur as populations living offshore in shallow water at depths that are below effective wave action. A case in point is the Giant Smooth Cockle, *Laevicardium*

elatum (Sowerby), a southern ranging species that was reported living in San Diego Bay at the turn of the century (Kelsey, 1907). Apparently as a result of man-made changes of the environment of the bays of southern California, this species is now restricted along this coast to quiet offshore waters. Populations of this species are now known to occur between Seal Beach and Huntington Beach, off the California coast (Fitch, 1953). Farther south, this cockle, which ranges from San Pedro to Panama, can be found living in the intertidal zone (Keen, 1958).

It appears likely that most of the marine elements of the bays of southern California would be re-populated by the offshore-larvae of the presently missing species. The re-establishment of these species seemingly will occur only when the bays are allowed to return to their former environmental status. Partial success in re-establishing these species by natural faunal succession has apparently been achieved in Mission Bay at San Diego, where the bay environment was modified extensively for recreational purposes, but where certain areas are being retained as natural preserves (Morrison, 1957).

It is, however, the truly estuarine species, which require brackish water and extensive mud flats, that appear at the present time to be in danger of extinction locally. The destruction of the tidal flats by land fill and the changing of the salinity of the water by the channelling of the runoff of freshwater from the few rivers and streams of the area into unnatural flood control systems has largely eliminated some elements of the brackish water fauna in the larger bays. Although the brackish water element constitutes only a small part of the fauna, we must make an effort to conserve this endemic assemblage by retaining some of the existing natural areas of the bays when we undertake to modify them further for the "benefit" of mankind.

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9. BRACKISH WATER MOLLUSKS

by J. P. E. Morrison

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Brackish water mollusks may be divided into 2 groups. Those with the more primitive life histories have a free swimming veliger stage that permits scattering of individuals in each generation to all available and suitable estuarine habitats. The second group has "crawl-away" young. Its species are thereby assured continuation in one-way current-swept localities, but spread of the population is restricted to immediately contiguous habitats.

In North America man continues to unconsciously endanger and to ignorantly exterminate brackish water species every time a marina is "built," "dug," "dredged" or "improved" in an estuary situation. In the same way, today's real-estate developments with land-fills and dredged or blasted canals, designed to increase the number of water-front lots for sale, are deadly to estuarine species. Another modern water "conservation" plan to impound fresh waters in lowland reservoirs by damming estuaries, prevents effective mingling with saline waters, and so narrows or destroys the brackish water habitat.

Brackish water mollusks (with pelagic larvae) such as the Salt Marsh Snail *Melampus bidentatus*, the mactrid clam *Rangia cuneata* and the Virginia Oyster *Crassostrea virginica*, are not now in danger of extinction. Local populations may be extinct, but *Melampus bidentatus* still lives from southeastern Quebec to Yucatan. *Rangia cuneata* is locally abundant from Chesapeake Bay, Maryland to the Laguna Terminos, Campeche. The Virginia Oyster is still harvested commercially from New Brunswick to Campeche.

Some widespread species such as the ovo-viviparous marsh clam *Cyrenoida floridana* and the tiny snail *Hydrobia jacksoni* may be exterminated locally whenever conditions are arbitrarily changed by man. Such local populations could only be replaced by reintroduction from (relict) undisturbed populations in other areas.

There is a complex of hydrobiid gill-breathing snails in North American brackish waters that is headed for extinction even before the species are scientifically described or named. *Littoridinops tenuipes* is the only named species among hundreds which belong to the group. Some have been made extinct by a single hurricane which changed the salinity of the waters in their restricted local habitat. A pair of species are known to have been wiped out of existence when their brackish water "lake" was filled in the construction of one airport facility in Maryland. Others are so localized in range that a single marina development is known to have made a half dozen species extinct. The direct importance of these minute species (with crawl-away young) to man is nil except in that they form part of the food chain. They serve as food for shrimps, crabs and fishes in these brackish waters. With the extinction of even a small fraction of the food chain the production of sea-foods from the estuaries is modified.

Since estuarine and littoral habitats are the greatest proportionate source of sea-foods man must examine critically every "improvement" that modifies and inevitably decreases his own food supply. Note that the Virginia Oyster is today commercially re-seeded or re-planted in many regions in an effort to prevent such a decrease of food resource. In the lagoons of Campeche, the Virginia Oyster has been deliberately replanted into "reefs" for centuries to maintain the harvest.

10. SUMMARY

In spite of differences in mode and degree of endangerment of the mollusks within the regions discussed, some features are common to all. In general those species whose survival is most in jeopardy occur only within small geographical areas which are undergoing urbanization, industrialization or other ecological disruption. Moreover, numbers of species have recently become extinct or are on the threshold of extinction which were not even suspected of being imperiled. A much larger number will soon follow if effective programs for their protection are not soon initiated.

The survival status of large segments of the freshwater molluscan fauna is particularly precarious, especially within the southeast and south-central portions of North America. In all, approximately 185 species and subspecies have been cited as rare and endangered. An additional 9 species, 8 *Dysnomia* (pp 19-20, pl. 1, 2) and 1 *Goniobasis* (*G. catenoides*, p 25), are now almost certainly extinct. These figures do not include the gastropods of the American Interior Basin because their status has not been determined. Scores of Pleuroceridae and many other snails from that region are probably also endangered or recently extinct.

Numerous terrestrial species are imperiled. Some 45 species and subspecies, about half in the East and half in the West, are apparently rare and endangered. A much larger number, particularly in the West, are also rare and/or highly localized. Many of these may soon have to be added to the list of endangered taxa.

Fortunately marine mollusks are relatively secure. Only *Almagorda newcombiana* (p 52) is known to be endangered. Some local populations of the more conspicuous species are being over-collected but since most of these also occur in subtidal or other relatively inaccessible regions, or are widely distributed, the species themselves are still safe.

Brackish-water mollusks, like freshwater mollusks, are vulnerable to pollution and habitat disruption. Widespread species are not in danger but hundreds of highly endemic species, especially Hydrobiidae, are in great danger.

Future challenges to species survival may be even more intense. The recent Santa Barbara disaster has shown that massive pollution from oil may menace whole communities of species. Effects of pesticides and radioactive waste products may be even more pervasive. Critics of the proposed sea-level canal in or near Panama have even predicted that if unrestricted faunal interchange is permitted between the oceans much of the tropical eastern Pacific fauna may be wiped out from competion with Caribbean species possessing superior adaptive features. Fortunately this problem is now under investigation by a number of workers.

Recently Mr. H. D. Athearn has revisited the Clinch River and has found that the rich mollusk fauna there is still in a healthy condition. Miraculously, it was apparently unharmed by the temporary severe pollution in 1967.

The recent deaths of millions of fish in the Clinch River was a most regrettable accident. That accident, however, engendered this *Symposium*. If students are now encouraged to study the endangered mollusks of North America and if heightened general awareness of our obligation to conserve our fauna coupled with suitable remedial action now result, the net effect of that accident will have been supremely beneficial to the preservation of our native molluscan fauna.

A. H. C.

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MUSSELS (UNIONIDAE) OF THE RED RIVER VALLEY IN NORTH DAKOTA AND MINNESOTA, U. S. A.

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ABSTRACT

Thirteen species of mussels inhabit the Red River of the North and 18 of its tributaries in eastern North Dakota and western Minnesota. These species, in 10 genera, are: *Fusconaia flava* (Rafinesque), *Amblema costata* Rafinesque, *Quadrula quadrula* Rafinesque, *Lasmigona compressa* (Lea), *L. costata* Rafinesque, *L. complanata* (Barnes), *Anodonta grandis* Say, *Anodontoides ferussacianus* (Lea), *Strophitus rugosus* (Swainson), *Proptera alata* (Say), *Ligumia recta latissima* (Rafinesque), *Lampsilis siliquoides* (Barnes) and *L. ventricosa* (Barnes). Eight mussel species have been collected from the Red River, and 1-13 species from each of its tributaries. The 4 most common species are *Lasmigona complanata, Anodonta grandis, Anodontoides ferussacianus* and *Lampsilis siliquoidea*. Five species, *Amblema costata, Quadrula quadrula, Proptera alata, Ligumia recta latissima* and *Lampsilis ventricosa*, are generally characteristic of the larger rivers in the Red River Valley. *Lasmigonia compressa* and *Anodontoides ferussacianus* are generally indicative of smaller rivers in the Valley.

The mussel fauna of the Red River Valley, which is part of the Hudson Bay drainage, originated from that of the Mississippi River system. The Valley fauna, however, constitutes only 26% of that of the Mississippi.

Four ecological factors are presumably of primary importance in restricting the distribution of mussels in the Red River Valley. These are: prolonged lack of river flow, high chloride content, water pollution and possibly high turbidity.

INTRODUCTION

Previous work and purpose

Little but species lists have previously been published for the mussels of the Red River drainage in North Dakota and Minnesota. Owen (1852: 177), during a geological reconnaissance, reported observing very abundant mussels in the Red River, below the mouth of the Red Lake River, in July, 1848. He listed the following species as most common: *Unio plicatus* [= ? *Amblema costata* Rafinesque], *U. quadrulus* [= *Quadrula quadrula* Rafinesque], *U. alatus* [= *Proptera alata* (Say)], *U. gibbosus* [= ? *Ligumia recta latissima* (Rafinesque)], and *U. crassus* [= ? *Lampsilis siliquoidea* (Barnes)].

In 1858, Lea listed 9 mussel species from the Red River of the North at 50° N. lat.; if the latitude is correct, the locality would be in the vicinity of Winnipeg, Manitoba. Species given by Lea were: *Unio rubiginosus* Lea [= *Fusconaia flava* (Rafinesque)], *U. undulatus* Barnes [= *Amblema costata* Rafinesque], *U. asperrimus* Lea [= *Quadrula quadrula* Rafinesque], *Anodonta decora* Lea [= *Anodonta grandis* Say], *Anodonta ferussaciana* Lea [= *Anodontoides ferussacianus* (Lea)], *U. alatus* Say [= *Proptera alata* (Say)], *U. rectus* Lamarck [= *Ligumia recta latissima* (Lamarck)], *U. luteolus* Lamarck [= *Lampsilis siliquoidea* (Barnes)] and *U. occidens* Lea [= *Lampsilis ventricosa* (Barnes)]. Dawson (1875: 350) listed 7 mussel species for the Red River; his species, or the

presumed equivalents of his species names, did not differ from those of Lea (1858), with the exception of *Unio spatulus* Lea [= *Ligumia ellipsiformis* (Conrad): = ? *Ligumia recta latissima* (Lamarck)]. Grant (1885: 115-119) listed and remarked upon 8 species of mussels from the Red River, Wilkin County, Minnesota. His species, or the equivalents of his species names, were previously given by Lea (1858) with the exception of *Anodonta edentula* Say [= *Strophitus rugosus* (Swainson)]. In addition to those species listed by Lea (1858) and the previously mentioned authors, Dall (1905) noted the following species for the Red River drainage: *Quadrula heros* (Say) [= *Megalonaias gigantea* (Barnes)], *Quadrula plicata* (Say) [= *Amblema peruviana* (Lamarck)], *Symphynota complanata* (Barnes) [= *Lasmigona complanata* (Barnes)] and *Lampsilis gracilis* (Barnes) [= *Leptodea fragilis* Rafinesque].

Wilson & Danglade (1914: 12) listed 10 species of mussels from 5 stations on the Otter Tail River (= "Red River") in Minnesota. Species not mentioned previously by Owen (1852), Lea (1858) or Dall (1905) were *Anodonta pepiniana* Lea, *Symphynota costata* (Rafinesque) [= *Lasmigona costata* (Rafinesque)] and *Quadrula coccinea* (Conrad) [= *Pleurobema cordatum coccineum* (Conrad)]. Coker & Southall (1915: 15), in a survey for commercial mussels, reported 6 species from the Red River at Fargo and 4 species from the Sheyenne River at Lisbon. Only one species listed, *Quadrula pustulosa* (Lea) (at Fargo), was different from those already cited above by earlier workers. Winslow (1921: 15) listed 5 mussels from North Dakota and only 2, *Lampsilis luteola* (Lamarck) [= *Lampsilis siliquoidea* (Barnes)] and *Lasmigona compressa* (Lea), from a river of the Red River Valley (Sheyenne River). Dawley's (1947: 679) survey of Minnesota aquatic mollusks included a listing of 10 mussel species for the Red River and 11 for the Red Lake River. Tuthill's (1962, 1963) lists of North Dakota mollusks included mussels of the Red River Valley. Clarke's (1964) summary of the mollusks of the Hudson Bay Watershed includes all of the species which I have taken from the Valley.

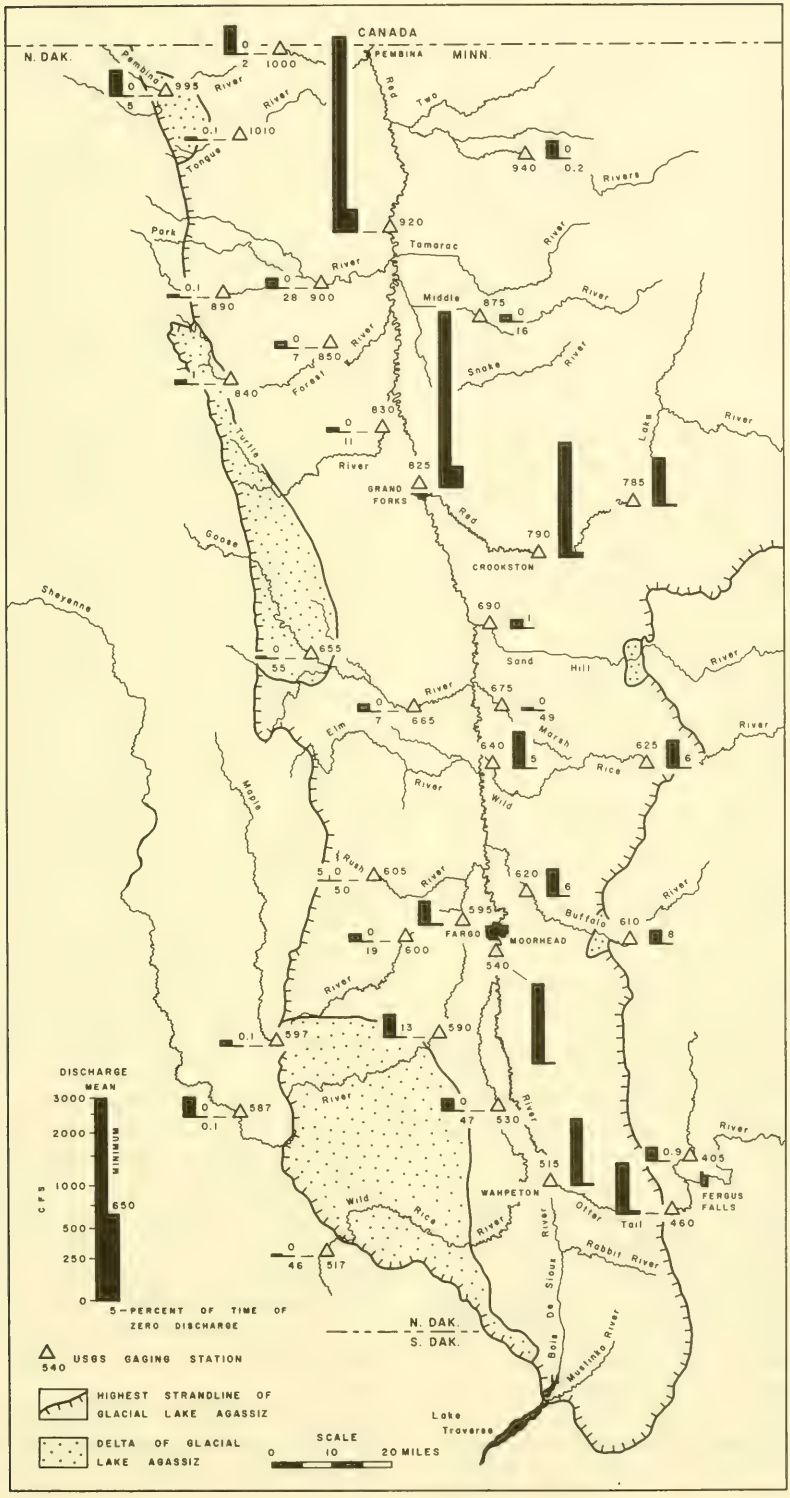
Since 1964, my students and I have studied the distribution and ecology of mussels in the Valley (Cvancara & Harrison, 1965; Cvancara, 1966; Cvancara, Heetderks & Iljana, 1966; Cvancara, 1967 and Norby, 1967.

The main purpose of this paper is to present the known mussel fauna and its distribution in the Red River Valley of North Dakota and Minnesota. Also, those ecologic factors presumed to inhibit the distribution of mussels are evaluated.

Geologic setting, climate and river discharge

The term "Red River Valley," as used herein, refers to a glacial lacustrine plain or basin on both sides of the Red River of the North in eastern North Dakota and western Minnesota. Its boundary is defined as the highest strandline (Herman "beach") of glacial Lake Agassiz (Fig. 1). The Red River and its tributaries are part of the Hudson Bay

FIG. 1. Map of the Red River Valley showing stream discharge at U. S. Geological Survey gaging stations. Discharge values are for the 10 year span from October 1, 1955 to September 30, 1965. The left hand bar portrays the mean discharge for each station whereas the right hand bar shows the minimum discharge. Figures above the bars indicate discharges under 10 cu. ft./sec. that are not readable on the scale; where minimum discharge was zero, figures below the right hand bar indicate the percent of time that zero discharge has occurred. Discharge data were taken from U. S. Geological Survey (1961-1966a, 1961-1966b and 1964c). The highest strandline of glacial Lake Agassiz is from Leverett (1932) and from Colton, Lemke & Lindvall (1963); the deltas of glacial Lake Agassiz are from Upham (1895).


CANADA
N. DAK.
PEMBINA
MINN.
Pembina River
Tongue River
Park River
Red River
Two Rivers
Tamarac River
Middle River
Snake River
Forest River
Turtle River
Goose River
Sheyenne River
Loon River
GRAND FORKS
CROOKSTON
Sand Hill River
Elm River
Marsh River
Rice River
Wild Rice River
Maple River
Ruth
Buffalo River
FARGO
MOORHEAD
WAHPETON
Otter Tail River
FERGUS FALLS
Rabbit River
Bois De Sioux River
Mustinka River
Lake Traverse
N. DAK.
S. DAK.
DISCHARGE
MEAN
MINIMUM
CFS
3000
2000
1000
500
250
0
650
5 — PERCENT OF TIME OF ZERO DISCHARGE
USGS GAGING STATION
HIGHEST STRANDLINE OF GLACIAL LAKE AGASSIZ
DELTA OF GLACIAL LAKE AGASSIZ
SCALE
0 10 20 MILES

drainage and drain northward.

Only a relatively small part of the maximum extent of glacial Lake Agassiz, which was about 80,000 square miles (Elson, 1967: 37), occupied North Dakota and Minnesota. During the interval of about 12,500 - 9,000 years ago, 4 or 5 episodes of the lake occurred in the now general Red River Valley area (Elson, 1967: Table 6 and Fig. 6). The geology and geological history of Lake Agassiz in the United States and over its entire extent has been summarized recently by Laird (1965) and Elson (1967), respectively.

Sediments over much of the Red River Valley consist of silt and clay, deposited in lake water perhaps up to 200 - 700 feet deep (Elson, 1967: 45). Marginal to the Valley are linear ridges of sand and gravel, commonly referred to as "beaches." Sand and gravel bodies in the form of deltas also occur at the extreme margins of the Valley, those at the eastern side poorly defined (Fig. 1). Glacial till generally occurs peripherally and beneath the lake-associated sediments.

Local relief in the Red River Valley, excepting incised stream valleys, generally is only a few to several feet. In the Grand Forks area (Fig. 1), for example, the local relief is only 1 - 15 feet per square mile.

Along the axis of the Red River Valley, the regional slope is very low. Using the cities of Wahpeton, Fargo, Grand Forks and Drayton (at the U.S. Geological Survey (USGS) gaging station 920, Fig. 1) as control points, I have calculated the regional slope to be as follows: 1.9 ft/mile (Wahpeton to Fargo), 1.1 ft/mile (Fargo to Grand Forks), and 0.53 ft/mile (Grand Forks to Drayton). The average of these slopes is only 1.2 ft/mile.

Visher (1954: 365) has classified the climate of eastern North Dakota and western Minnesota, including the Red River Valley, as "Dry Subhumid." In this region evaporation is usually in excess of precipitation (Visher, 1954: 364). The average annual runoff in the Valley is only about one inch (Miller, Geraghty & Collins, pl. 10).

Temperature and precipitation data for Wahpeton, Fargo, Grand Forks and Pembina are given in Table 1. The average temperature and precipitation for the Valley is 41° F and 20.6 inches, respectively, as calculated from data in Table 1. These data also show a temperature range of 144° (-42 - 102° F) and a precipitation range of 23.4 inches (12.9 - 36.3). The average temperature gradient was calculated as 1.6° F/degree latitude; this gradient, as computed between the 4 cities, appears to decrease northward.

Table 4 shows average water temperatures for selected stations in the Valley. These data suggest that average water temperatures, as exemplified by those at Grand Forks and Fargo (Tables 1 and 4), are about 10° higher than average air temperatures.

Discharge values for many localities are shown in Fig. 1. At a glance one can see that the principal tributaries of the Red River are the Otter Tail, Sheyenne, Buffalo, Wild Rice (Minnesota), Red Lake and Pembina, listed in a downstream direction. The Red Lake River is the largest tributary, and effectively doubles the discharge of the Red River at Grand Forks.

Below Grand Forks, at USGS gaging station 920 (in city of Drayton), the mean discharge of the Red River is nearly 3,000 cu. ft./sec. (Fig. 1). This discharge is appreciable although the gradient is very low. Between Grand Forks and Drayton, I have calculated the river gradient as 0.26 ft/mile; between Grand Forks and Fargo, and Fargo and Wahpeton, the gradients are 0.53 ft/mile and 0.85 ft/mile, respectively. The average of these gradients, from Wahpeton to Drayton, is only 0.55 ft/mile. Gradients of the rivers transverse to the Valley axis, however, are generally considerably higher, at least in their upper reaches.

Parts of several streams have low minimum discharge values and are also characterized by relatively long periods

TABLE 1. Temperature and precipitation data* (1955-1965) for 4 localities in the Red River Valley

		Years												
		1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	Aver. 11 yrs.	Variance
TEMPERATURE (°Fahrenheit)														
Pembina	max.	96	94	92	95	97	94	99	91	92	98	97		
	mean	37.7	37.6	39.3	39.5	45.0	38.8	39.8	35.8	40.5	41.9	--*	39.6	6.62
	min.	-42	-36	-30	-27	-30	-27	-32	-39	-33	-30	-32		
Grand Forks	max.	98	96	96	102	97	96	99	94	92	100	101		
	mean	39.0	38.4	39.8	40.8	39.9	39.9	41.4	39.6	42.6	41.0	38.3	40.1	1.75
	min.	-30	-28	-30	-26	-30	-22	-27	-32	-28	-25	-30		
Fargo	max.	99	99	98	101	102	100	99	97	96	98	100		
	mean	40.6	40.1	41.8	42.4	41.8	40.4	42.4	41.3	42.9	41.9	38.0	41.2	1.85
	min.	-27	-26	-27	-23	-24	-31	-27	-34	-28	-24	-35		
Wahpeton	max.	98	99	96	101	101	99	99	92	94	97	100		
	mean	42.8	42.1	43.8	44.5	44.0	42.9	44.3	41.5	40.9	43.5	40.8	42.9	2.90
	min.	-32	-26	-27	-26	-18	-26	-24	-29	-25	-20	-30		
TOTAL PRECIPITATION (Inches)														
Pembina		24.4	16.5	22.1	13.8	20.7	16.3	13.1	22.6	15.6	23.6	--*	18.9	16.3
Grand Forks		21.5	19.6	25.7	17.8	20.0	19.9	18.9	20.8	12.9	27.4	27.8	21.1	17.6
Fargo		17.4	17.0	25.0	20.9	18.2	19.0	17.8	26.6	14.2	18.3	24.0	19.9	13.2
Wahpeton		18.8	22.2	26.2	17.7	18.4	22.6	15.8	36.3	21.1	19.2	27.5	22.3	20.0

*The 1965 average temperature and total precipitation values for Pembina are not included because data for 5 months were lacking. All data were taken from U. S. Weather Bureau, 1955-1966, and U. S. Weather Bureau, 1965.

of zero discharge. Several gaging stations (Fig. 1) show a minimum discharge of 10 cu. ft./sec. or less. A few stations in North Dakota (station 517, 530, 605 and 655) indicate no flow for about half the time. Under the condition of zero discharge, sections of a river are reduced to stagnant, elongate ponds.

MATERIALS AND METHODS

Field work was done during the summers of 1965 and 1966. Mussels were collected by 2 methods: by hand and with a crowfoot dredge.

Hand-picking was by far the most effective method; it was used in all the tributaries and along the banks of the Red River. In water of low turbidity a Turtox Fishscope, which is an aluminum alloy cylinder measuring 24 inches in length by 6 inches in diameter fitted with a glass plate, aided in locating mussels. In turbid waters, mussels were located by feel with hands and feet. With experience, a mussel could often be distinguished from a pebble by the feet, even through thick rubber waders. The length of bottom examined, for each station, was determined by pacing. Usually 1/2 - 2 hours were spent in hand-picking and all mussels noted were gathered and counted. The numbers were converted to mussels per hour and used in constructing Fig. 8. Counts were made for each species, and a presumedly representative series was taken for each. Sex was determined in the sexually dimorphic species.

An 8-foot crowfoot dredge was dragged from a 17-foot canoe for all Red River stations, in addition to hand-picking along the banks. The crowfoot dredge consisted of a pipe 2 inches in diameter with 1 1/2-foot chains spaced at 6-inch intervals. Each chain was fitted with 2 back-to-back hooks fashioned from a single piece of heavy wire.

On the Red River and 18 of its tributaries, 119 stations were checked for mussels (Fig. 2). Generally, about 5 stations were selected for each tributary, including, where feasible, 1-2 stations just outside of the lake plain. Such rivers as the Mustinka, Rabbit and Marsh in Minnesota, and the Rush in North Dakota were not sampled. They did not behave like true rivers, for I observed no flow in them during the summer of 1966, a wet year.

The water was analyzed by about one dozen chemical tests (see p 16) and also for turbidity, at most stations, in the field, with a Hach Chemical Company portable chemical kit (Model DR-EL). With few exceptions, all tests were made at 3-5 stations for each tributary during the same day. All dissolved oxygen and free carbon dioxide tests were made during daylight hours.

Field data also included observations on the bottom (Table 2), width and depth of stream, shading of banks, associated animal life and aquatic vegetation.

Shell measurements were made with vernier calipers on specimens with 4 or more growth annulae. Of the sexually dimorphic species, only shells of the males were measured. Length (L) was taken as the greatest length parallel to the hinge line; height (H) was taken as the greatest dorso-ventral measurement at right angles to the hinge line; and width (W) was the greatest measurement taken across both valves.

RESULTS

Mussel species

A complete taxonomic treatment for each species, including generic and specific descriptions and synonymies, seems unwarranted here. In the diagnoses for the following 13 species, for brevity, generic and specific characters are not differentiated. A diagnosis includes those characters that permit ready distinction of one species from all others in the Red River Valley.

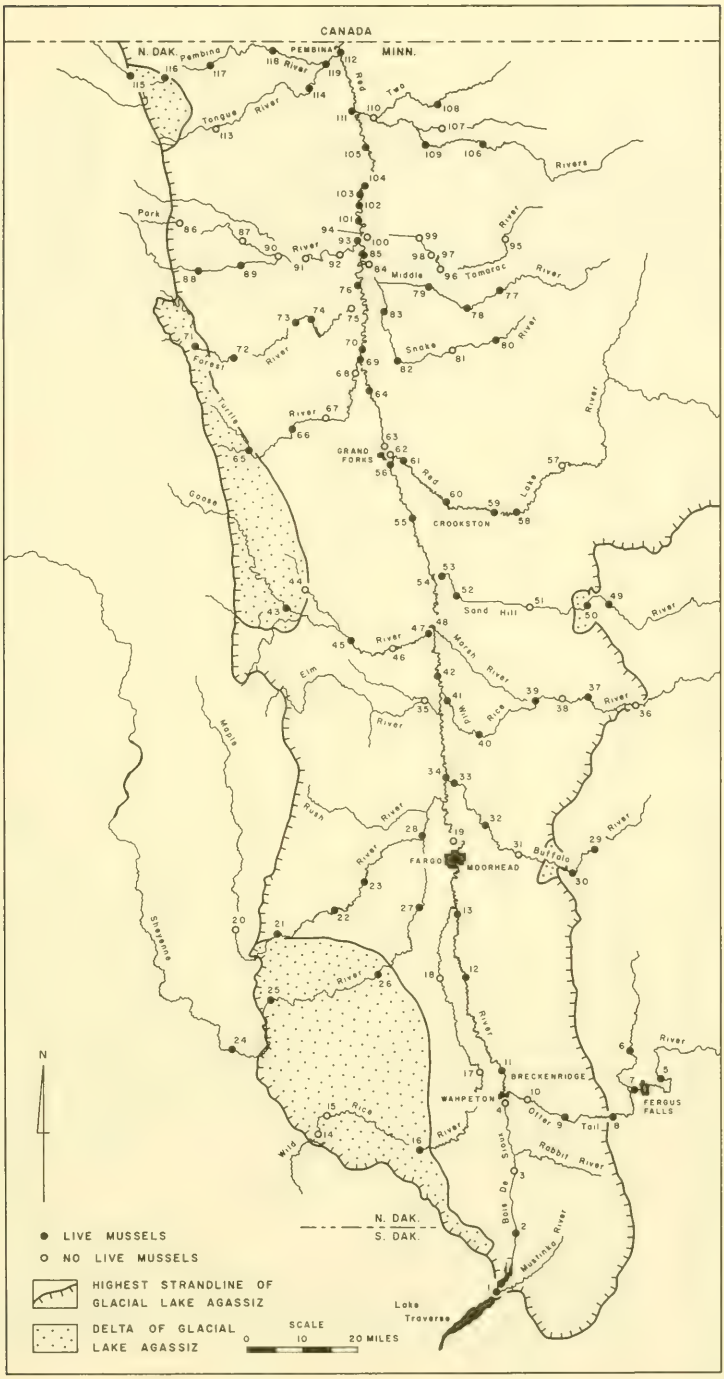


FIG. 2. Map of mussel stations in the Red River Valley. The explanation of Fig. 1 gives sources for the highest strandline and deltas of glacial Lake Agassiz. Locality descriptions of stations and predominant bottom type at each are given in Table 2.

TABLE 2. Mussel stations* in the Red River Valley with predominant bottom type at each

Station	Location	Predominant Bottom
1 (A114)*	Bois de Sioux R., 8 mi SE Rosholt, N. Dak. (7 1/4 mi WSW Wheaton, Minn.)	Sandy, clayey mud**
2 (A115)	Bois de Sioux R., 1/4 mi E White Rock, N. Dak. (1/2 mi W Boisberg, Minn.)	Gravelly (pebbly) sand
3 (A116)	Bois de Sioux R., 2 3/4 mi NE Fairmount, N. Dak. (7 1/2 mi W Campbell, Minn.)	Sandy, muddy (pebble to boulder) gravel
4 (A126)	Bois de Sioux R., 1 1/4 mi SE center Wahpeton, N. Dak. (1 mi S center Breckenridge, Minn.)	Sandy, silty mud
5 (A77)	Otter Tail R., 3 3/4 mi ENE center Fergus Falls, Minn.	Sandy gravel
6 (A98)	Pelican R., Elizabeth, Minn.	Sandy, (pebble) gravel
7 (A78)	Otter Tail R., 1 3/4 mi SW center Fergus Falls, Minn.	Sandy, (pebble) gravel
8 (A95)	Otter Tail R., 7 3/4 mi SW center Fergus Falls, Minn.	Sandy, (pebble) gravel
9 (A96)	Otter Tail R., 6 mi SSW Foxhome, Minn.	Sandy, (pebble) gravel
10 (A97)	Otter Tail R., 4 mi ESE center Breckenridge, Minn.	Gravelly (pebbly) sand
11 (A127)	Red R., 4 1/4 mi N center Wahpeton, N. Dak. (4 1/4 mi NNW center Breckenridge, Minn.)	Sandy, (pebble) gravel
12 (A128)	Red R., 2 1/2 mi E Christine, N. Dak. (1 mi NW Wolverton, Minn.)	Muddy, (pebble) gravel
13 (A129)	Red R., 1 1/4 mi E Wild Rice, N. Dak. (1 3/4 mi WNW Rustad, Minn.)	Sandy mud
14 (--)	Wild Rice R., 6 mi N Geneseo, N. Dak.	Gravelly (pebbly) sand
15 (--)	Wild Rice R., 6 1/2 mi SW Wyndmere, N. Dak.	Muddy sand
16 (A113)	Wild Rice R., 4 mi N Hankinson, N. Dak.	Muddy sand
17 (--)	Wild Rice R., 2 3/4 mi NE Dwight, N. Dak.	Sandy, clayey mud
18 (A112)	Wild Rice R., 1 3/4 mi W Christine, N. Dak.	Clayey mud
19 (A130)	Red R., 5 3/4 mi SE Harwood, N. Dak. (4 mi NNW center Moorhead, Minn.)	Clayey mud
20 (A106)	Maple R., 5 mi SW Alice, N. Dak.	Sandy gravel
21 (A105)	Maple R., 6 1/2 mi SE Alice, N. Dak.	Gravelly (pebbly) sand
22 (A103)	Maple R., 6 3/4 mi N Leonard, N. Dak.	Sandy mud

TABLE 2 (contd.)

Station	Location	Predominant Bottom
23 (A104)	Maple R., 1 1/2 mi ENE Durbin, N. Dak.	Sandy, clayey, mud
24 (A107)	Sheyenne R., 4 3/4 mi SSE center Lisbon, N. Dak.	Sandy, (pebble) gravel
25 (A109)	Sheyenne R., 1 mi S Anselm, N. Dak.	Gravelly (pebbly) sand
26 (A110)	Sheyenne R., 7 mi WNW Walcott, N. Dak.	Sand
27 (A111)	Sheyenne R., 1 1/2 mi SW Horace, N. Dak.	Muddy sand
28 (A108)	Sheyenne R., 3 3/4 mi SW Harwood, N. Dak.	Muddy sand
29 (A90)	Buffalo R., 2 3/4 mi ENE Hawley, Minn.	Sandy, (pebble) gravel
30 (A91)	Buffalo R., 3 1/4 mi SSW Hawley, Minn.	Sandy, (pebble) gravel
31 (A92)	Buffalo R., 2 1/2 mi ENE Glyndon, Minn.	Gravelly (pebbly) sand
32 (A93)	Buffalo R., 7 1/4 mi NW Glyndon, Minn.	Muddy sand
33 (A94)	Buffalo R., Georgetown, Minn.	Sandy, clayey mud
34 (A131)	Red R., 6 1/4 mi ENE Argusville, N. Dak. (1 1/2 mi NW Georgetown, Minn.)	Sandy, clayey mud
35 (--)	Elm R., 6 1/4 mi ESE Kelso, N. Dak.	Clayey mud
36 (A79)	Wild Rice R., 1/4 mi SW Faith, Minn.	Sandy, (pebble) gravel
37 (A81)	Mashaug Creek, 1 3/4 mi NNW Twin Valley, Minn.	Sandy, (pebble) gravel
38 (A80)	Wild Rice R., 5 3/4 mi WNW Twin Valley, Minn.	Sandy, (pebble) gravel
39 (A82)	Wild Rice R., 2 mi ESE center Ada, Minn.	Gravelly (pebbly) sand
40 (A83)	Wild Rice R., 7 1/2 mi SE Hendrum, Minn.	Sand
41 (A84)	Wild Rice R., 2 mi N Hendrum, Minn.	Sandy, clayey mud
42 (A133)	Red R., 7 1/2 mi SSE Caledonia, N. Dak. (1 mi E Halstad, Minn.)	Sandy, clayey mud
43 (A99)	Middle Branch Goose R., 4 3/4 mi WNW Portland, N. Dak.	Sandy, (pebble) gravel
44 (--)	North Branch Goose R., 5 1/4 mi N Portland, N. Dak.	Muddy sand

TABLE 2 (contd.)

Station	Location	Predominant Bottom
45 (A100)	Goose R., 6 mi WNW Hillsboro, N. Dak.	Muddy sand
46 (A101)	Goose R., 2 1/4 mi ENE Hillsboro, N. Dak.	Muddy sand
47 (A102)	Goose R., Caledonia, N. Dak.	Sandy gravel
48 (A135)	Red R., 1 1/2 mi NE Caledonia, N. Dak. (2 3/4 mi NW Shelley, Minn.)	Muddy gravel
49 (A85)	Sand Hill R., 2 1/2 mi NW Rindal, Minn.	Gravelly (pebbly) sand
50 (A86)	Sand Hill R., 3/4 mi ESE Fertile, Minn.	Sandy, (pebble) gravel
51 (A87)	Sand Hill R., 2 mi ESE Beltrami, Minn.	Muddy, gravelly sand
52 (A88)	Sand Hill R., 2 3/4 mi NE Nielsville, Minn.	Gravelly (pebbly) sand
53 (A89)	Sand Hill R., 1/2 mi WSW Climax, Minn.	Sandy gravel
54 (A134)	Red R., 11 1/4 mi E Buxton, N. Dak. (2 mi W Climax, Minn.)	Sandy, clayey mud
55 (A132)	Red R., 8 mi ESE Thompson, N. Dak. (7 1/4 mi WSW Fisher, Minn.)	Sandy, clayey mud
56 (A59)	Red R., Lincoln Park, Grand Forks, N. Dak. (2 1/2 mi S center E. Grand Forks, Minn.)	Sandy, silty mud
57 (A41)	Red Lake R., 3 1/2 mi W Red Lake Falls, Minn.	Sandy, (pebble) gravel
58 (A64)	Red Lake R., 3 3/4 mi E center Crookston, Minn.	Sandy gravel
59 (A65)	Red Lake R., downstream edge dam, Crookston, Minn.	Gravelly (pebbly) sand
60 (A66)	Red Lake R., W edge Fisher, Minn.	Gravelly sand
61 (A67)	Red Lake R., 2 1/2 mi ESE center E. Grand Forks, Minn.	Sandy mud
62 (--)	Red R., downstream side mouth Red Lake R., Grand Forks, N. Dak.	Sandy, clayey mud
63 (A58)	Red R., N edge Grand Forks, N. Dak.	Silty mud
64 (A57)	Red R., 3 1/3 mi ENE Manvel, N. Dak.	Sandy mud
65 (A69)	Turtle R., 3 mi NE Larimore, N. Dak.	Gravelly sand
66 (A70)	Turtle R., 2 1/2 mi SW Mekínock, N. Dak.	Gravelly sand

TABLE 2 (contd.)

Station	Location	Predominant Bottom
67 (--)	Turtle R., 3 3/4 mi E Mekinock, N. Dak.	Muddy, gravelly sand
68 (A73)	Turtle R., 4 mi N Manvel, N. Dak.	Silty mud
69 (A56)	Red R., 6 3/4 mi NNE Manvel, N. Dak. (1 1/2 mi SSW Oslo, Minn.)	Sandy mud
70 (A55)	Red R., 3 3/4 mi E. Poland, N. Dak. (NW edge Oslo, Minn.)	Sandy mud
71 (A43)	Forest R., 1/2 mi S Fordville, N. Dak.	Gravelly sand
72 (A42)	Forest R., 2 mi N Inkster, N. Dak.	Silty, gravelly sand
73 (A44)	Forest R., 2 1/4 mi SW Minto, N. Dak.	Sand
74 (A45)	Forest R., 2 1/2 mi ESE Minto, N. Dak.	Sandy mud
75 (--)	Forest R., 3 mi ENE Warsaw, N. Dak.	Sandy mud
76 (A54)	Red R., 6 2/3 mi NE Warsaw, N. Dak.	Sandy mud
77 (A36)	Middle R., 12 mi W Newfolden, Minn.	Sandy gravel
78 (A38)	Middle R., 4 3/4 mi ESE Argyle, Minn.	Gravelly sand
79 (A60)	Middle R., 3 mi NW Argyle, Minn.	Clayey mud
80 (A37)	Snake R., 7 1/2 mi ENE Warren, Minn.	Sandy gravel
81 (A72)	Snake R., WSW edge Warren, Minn.	Muddy sand
82 (A61)	Snake R., 1 1/2 mi S Alvarado, Minn.	Clayey mud
83 (A62)	Snake R., 7 3/4 mi NNE Oslo, Minn.	Clayey mud
84 (A63)	Snake R., 10 3/4 mi WSW Stephen, Minn.	Silty mud
85 (A53)	Red R., 8 mi E Oakwood, N. Dak. (11 1/2 mi WSW Stephen, Minn.)	Sandy mud
86 (--)	Middle Branch Park R., 1 2/3 mi N Edinburgh, N. Dak.	Sandy gravel
87 (A41)	Middle Branch Park R., 3 1/2 mi S Hoople, N. Dak.	Gravelly, sandy mud
88 (A40)	South Branch Park R., 2 1/4 mi WNW Park River, N. Dak.	Sandy gravel

TABLE 2 (contd.)

Station	Location	Predominant Bottom
89 (A39)	South Branch Park R., 5 1/2 mi ENE Park River, N. Dak.	Sandy gravel
90 (--)	Park R., 3 mi NW Grafton, N. Dak.	Gravelly mud
91 (A46)	Park R., 2 mi ENE Grafton, N. Dak.	Sandy mud
92 (--)	Park R., 3 mi ENE Oakwood, N. Dak.	Sandy mud
93 (A52)	Red R., 7 mi ENE Oakwood, N. Dak.	Sandy, clayey mud
94 (A51)	Red R., 8 3/4 mi NE Oakwood, N. Dak.	Clayey mud
95 (A35)	Tamarac R., 6 mi W Strandquist, Minn.	Sandy gravel
96 (A32)	Tamarac R., 4 mi SSE Stephen, Minn.	Gravelly (pebbly) sandy mud
97 (A31)	Tamarac R., 1/4 mi SSE Stephen, Minn.	Gravelly (pebbly) sandy mud
98 (A33)	Tamarac R., downstream edge dam at Stephen, Minn.	Gravelly (pebbly) sandy mud
99 (A34)	Tamarac R., 3 1/4 mi NNW Stephen, Minn.	Muddy gravel
100 (--)	Tamarac R., 11 3/4 mi WNW Stephen, Minn.	Clayey mud
101 (A50)	Red R., 2 1/2 mi SSE Drayton, N. Dak.	Clayey mud
102 (A49)	Red R., 1 1/2 mi ENE Drayton, N. Dak.	Clayey mud
103 (A48 & A140)	Red R., 2 2/3 mi NNE Drayton, N. Dak. (1 3/4 mi N Robbin, Minn.)	Clayey mud
104 (A47)	Red R., 4 1/2 mi NNE Drayton, N. Dak.	Clayey mud
105 (A68)	Red R., 3 1/3 mi NE Bowesmont, N. Dak.	Silty mud
106 (A122)	S. Branch Two Rivers, SW edge Lake Bronson, Minn.	Sandy, (pebble) gravel
107 (--)	Middle Branch Two Rivers, 5 3/4 mi E Hallock, Minn.	Sandy, (pebble) gravel
108 (Å123)	North Branch Two Rivers, 2 1/4 mi SW Lancaster, Minn.	Sandy, (pebble) gravel
109 (A124)	South Branch Two Rivers, 3 3/4 mi SSE Hallock, Minn.	Gravelly (pebbly) sand
110 (A125)	Two Rivers, 7 1/2 mi WNW Hallock, Minn.	Sandy, clayey mud

TABLE 2 (contd.)

Station	Location	Predominant Bottom
111 (A139)	Red R., 1 3/4 mi E Joliette, N. Dak. (8 3/4 mi WSW Northcote, Minn.)	Sandy clayey mud
112 (A138)	Red R., SE edge Pembina, N. Dak. (SW edge St. Vincent, Minn.)	Clayey mud
113 (A136)	Tongue R., NW edge Akra, N. Dak.	Gravelly (pebbly) sand
114 (A137)	Tongue R., 5 3/4 mi E. Bathgate, N. Dak.	Clayey mud
115 (A117)	Pembina R., 6 1/2 mi W Walhalla, N. Dak.	Sandy, (pebble) gravel
116 (A118)	Pembina R., 1 1/4 mi SSW Walhalla, N. Dak.	Sandy, (pebble) gravel
117 (A119)	Pembina R., 1/2 mi N Leroy, N. Dak.	Gravelly (pebbly) sand
118 (A120)	Pembina R., 2 1/2 mi E Neche, N. Dak.	Sand
119 (A121)	Pembina R., 2 3/4 mi SW Pembina, N. Dak.	Muddy sand

*Station numbers correspond to those shown on Fig. 2. In parentheses following station numbers are accession numbers of the Department of Geology, University of North Dakota.

**Mud is a sediment composed of silt and clay.

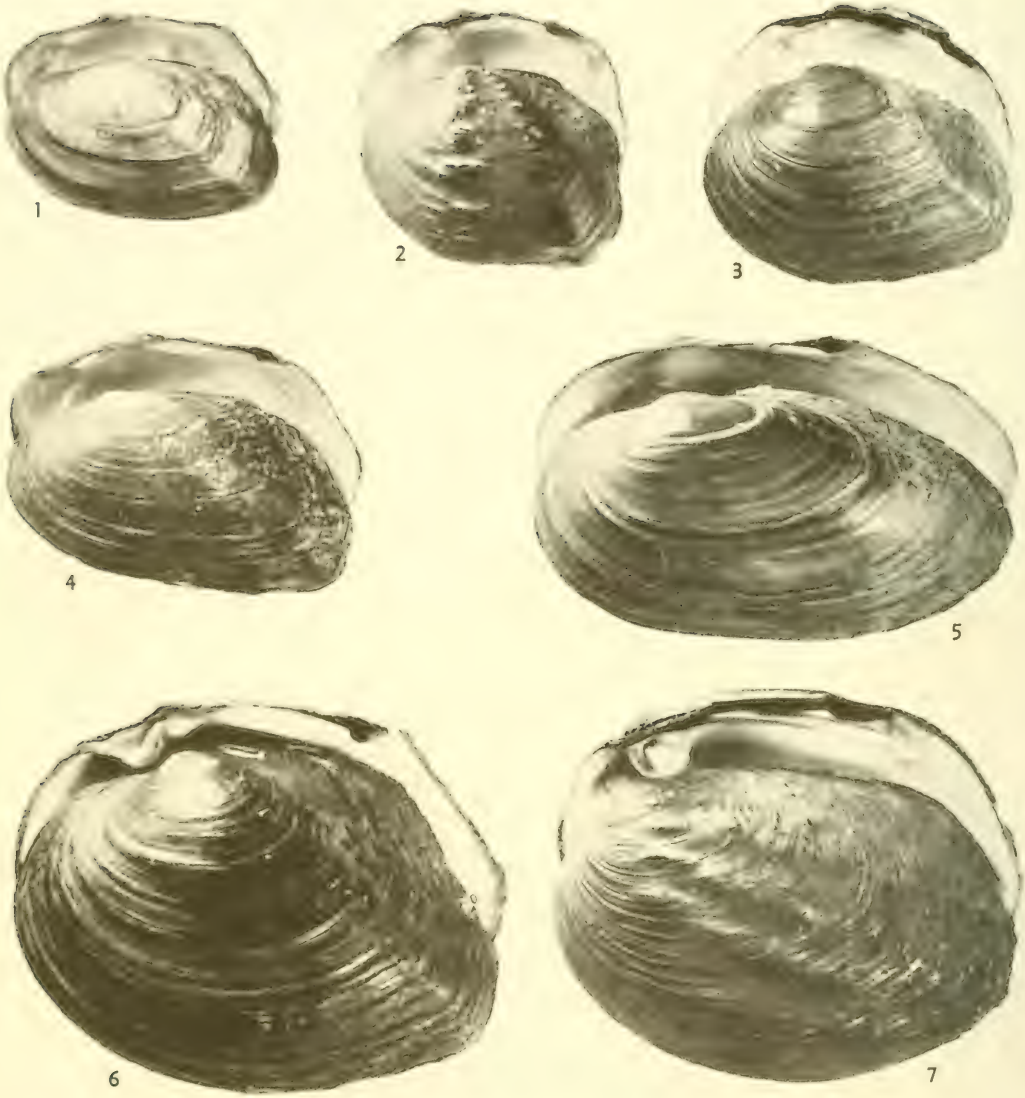


PLATE 1. (All figures are X1/2; locality numbers correspond to those shown on Fig. 2 and listed in Table 2. Catalog numbers are those of the paleontological collection of the Department of Geology, University of North Dakota.)

1. *Lasmigona compressa* (Lea), Pembina River, locality 115, UND Cat. No. 13001. 2. *Quadrula quadrula* Rafinesque, Red Lake River, locality 59, UND Cat. No. 13002. 3. *Fusconaia flava* (Rafinesque), Buffalo River, locality 30, UND Cat. No. 13003. 4. *Lasmigona costata* Rafinesque, Red Lake River, locality 57, UND Cat. No. 13004. 5. *Anodonta grandis* Say, Forest River, locality 71, UND Cat. No. 13005. 6. *Lasmigona complanata* (Barnes), Sheyenne River, locality 26, UND Cat. No. 13006. 7. *Amblema costata* Rafinesque, Sheyenne River, locality 24, UND Cat. No. 13007.

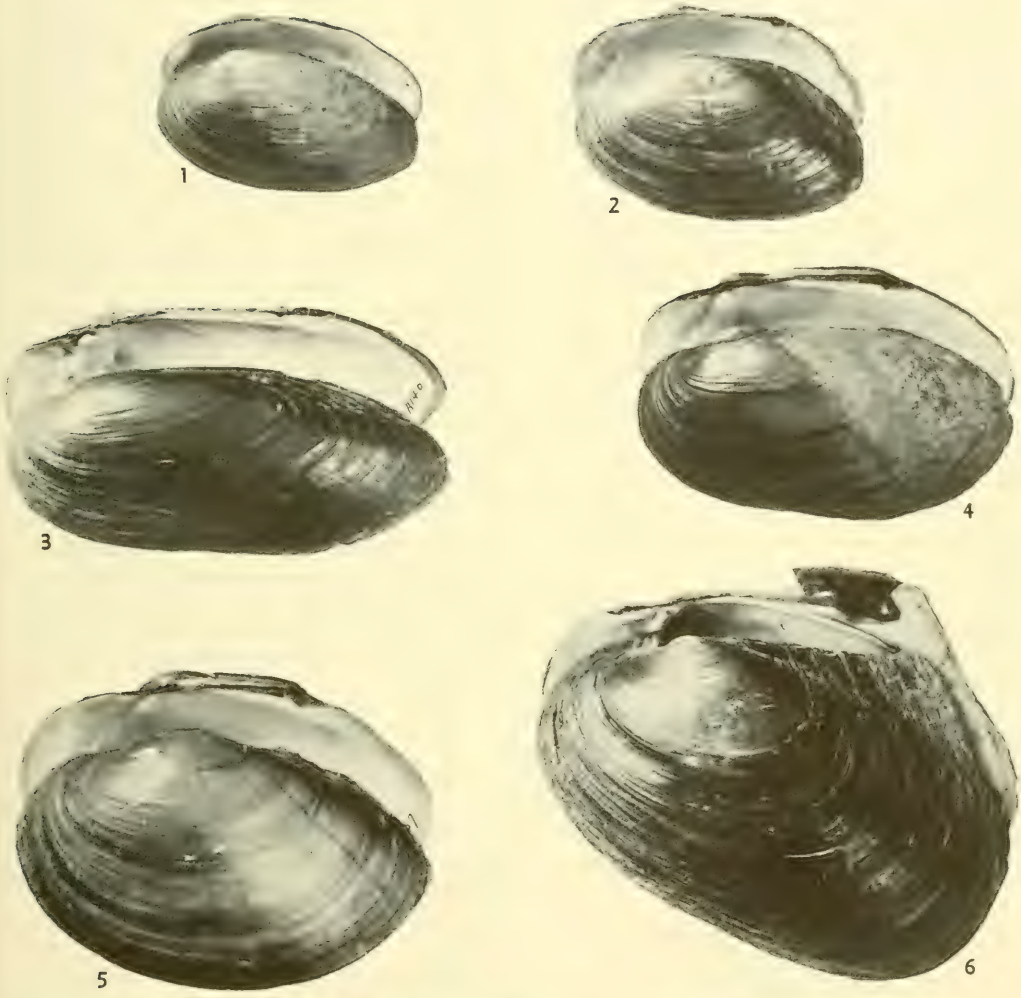


PLATE 2. (All figures are X1/2; locality numbers correspond to those shown on Fig. 2 and listed in Table 2. Catalog numbers are those of the paleontological collection of the Department of Geology, University of North Dakota.)

1. *Anodontoides ferussacianus* (Lea), Sand Hill River, locality 49, UND Cat. No. 13008. 2. *Strophitus rugosus* (Swainson), Pembina River, locality 116, UND Cat. No. 13009. 3. *Ligumia recta latissima* (Rafinesque), Red River, ♂, locality 103, UND Cat. No. 13010. 4. *Lampsilis siliquoidea* (Barnes), Buffalo River, ♂, locality 30, UND Cat. No. 13011. 5. *Lampsilis ventricosa* (Barnes), Red River, ♂, locality 11, UND Cat. No. 13012. 6. *Proptera alata* (Say), Red River (not collected alive), locality 105, UND Cat. No. 13013.

Family Unionidae
Subfamily Unioninae
Fusconaia flava (Rafinesque)
"Wabash pig toe"
Plate 1, Fig. 3

Diagnosis. Shell subtriangular, smooth; posterior ridge moderately prominent, roundly angled; shallow, radial depression anterior to posterior ridge; beak sculpture of fine to moderate, subconcentric ridges. Hinge complete, of coarse teeth; nacre white or salmon-colored.

Measurements. Shells (32) varied in length from 48 to 119 mm (average 78 mm), had H/L ratios of 0.60-0.78 (average 0.68) and W/H ratios of 0.45-0.76 (average 0.59).

Remarks. *Fusconaia flava* was collected alive from 7 rivers and 13 stations (Table 3; Fig. 3). Its distribution appears to be erratic but related to the relatively larger rivers in the Valley. This species was usually taken from a firm bottom of sandy gravel or gravelly sand, but it occurred also on a sandy mud bottom at stations 76 and 111 (Fig. 3).

The largest and thickest-shelled specimens were collected at station 8, which included the largest and most thick-shelled specimens of *Strophitus rugosus* and *Ligumia recta latissima*. Shells of *Amblema costata* and *Anodonta grandis* were also relatively large and thick from this locality. Specimens with a salmon tinge to the nacre were collected from only stations 25 and 39 (Fig. 3).

Amblema costata Rafinesque
"Three ridge"
Plate 1, Fig. 7

Diagnosis. Shell subrhomboidal, may be subovate, with coarse diagonal ridges that may also be present on postero-dorsal area; beak sculpture of fine to moderate, concentric ridges. Hinge complete, with coarse teeth; nacre white, may be purplish or pinkish on posterior part of shell.

Measurements. Shells (42) varied from 74 to 145 mm in length (average 110 mm), had H/L ratios of 0.56-0.77 (average 0.64) and W/H ratios of 0.40-0.72 (average 0.59).

Remarks. *Amblema costata* was collected alive from 5 rivers and 13 stations (Table 3; Fig. 3); it is associated with the larger rivers in the Valley. Greatest numbers of individuals were taken at stations 24, 25, 58 and 59. This species was usually collected from a firm bottom of sandy gravel or gravelly sand, but it occurred also on a mud bottom at stations 54, 101, 103 and 112 (Fig. 3). Ridges on the postero-dorsal area of the shell are either poorly developed or lacking on most specimens examined from the Valley.

Clarke & Clench (1966) have suggested that *Amblema plicata* is a "stunted ecophenotype" of *A. costata*, and a senior synonym; therefore, it should take precedence and serve as the type species of *Amblema*. This approach is subjective and the ruling of Opinion 840 of the International Commission on Zoological Nomenclature (1968: 339) does not specifically suppress *A. costata* Rafinesque, 1820 for *A. plicata* (Say), 1817. Therefore, I shall continue to use *A. costata* for the conspicuously costate mussel in the Valley.

Quadrula quadrula Rafinesque
"Maple leaf"
Plate 1, Fig. 2

Diagnosis. Shell subquadrate to subrhomboidal, with many pustules; median, shallow, radial depression; beak sculpture of fine, double-looped ridges. Hinge complete, with coarse teeth; nacre white.

Measurements. Shells (15) varied from 56 to 97 mm in length (average 72 mm), had H/L ratios of 0.70-0.81 (average 0.76) and W/H ratios of 0.46-0.61 (average 0.54).

Remarks: This species was collected alive from only the 2 largest rivers and 7 stations in the lower part of the Valley (Table 3; Fig. 3). *Quadrula quadrula* was taken from sandy gravel, gravelly sand and mud. It occurred with one or all

TABLE 3. Occurrence of mussels in the Red River and 18 of its tributaries. Species are indicated as collected alive (X), represented only by empty shells (0), or from river terrace sediments and interpreted as fossils (F). Tributaries, as read from left to right, are arranged from south to north.

Taxon	Red R.	Otter Tail R., Minn.	Wild Rice R., N. Dak.	Sheyenne R., N. Dak.	Maple R., N. Dak.	Buffalo R., Minn.	Wild Rice R., Minn.	Goose R., N. Dak.	Sand Hill R., Minn.	Red Lake R., Minn.	Turtle R., N. Dak.	Forest R., N. Dak.	Snake R., Minn.	Middle R., Minn.	Park R., N. Dak.	Tamarac R., Minn.	Two Rivers, Minn.	Tongue R., N. Dak.	Pembina R., N. Dak.
UNIONINAE																			
Fusconaia flava	X	X		X	0	X	X		X	X	F						0		
Amblema costata	X	X	X	X		0	X			X									
Quadrula quadrula	X			F						X									
ANODONTINAE																			
Lasmigona compressa		0		X			0		X	X	F	X					0		X
Lasmigona costata		0								X									
Lasmigona complanata	X	X	0	X	X	X	0	0	X	X	X	X				0	X	X	X
Anodonta grandis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	0	X	X	X	X
Anodontoides ferussacianus		X		X	X	X	X	0	X	X	X	X	X	X	X	X	X	X	X
Strophitus rugosus	0	X		X		0	0		X	X	F	X					0		X
LAMPSILINAE																			
Proptera alata	0			F			0			X									
Ligumia recta latissima	X	X		F			0		0	X									
Lampsilis siliquoidea	X	X	0	X	0	X	X	0	X	X	X	X		X	0	X	X	X	X
Lampsilis ventricosa	X	X		X			0		X	X							0		

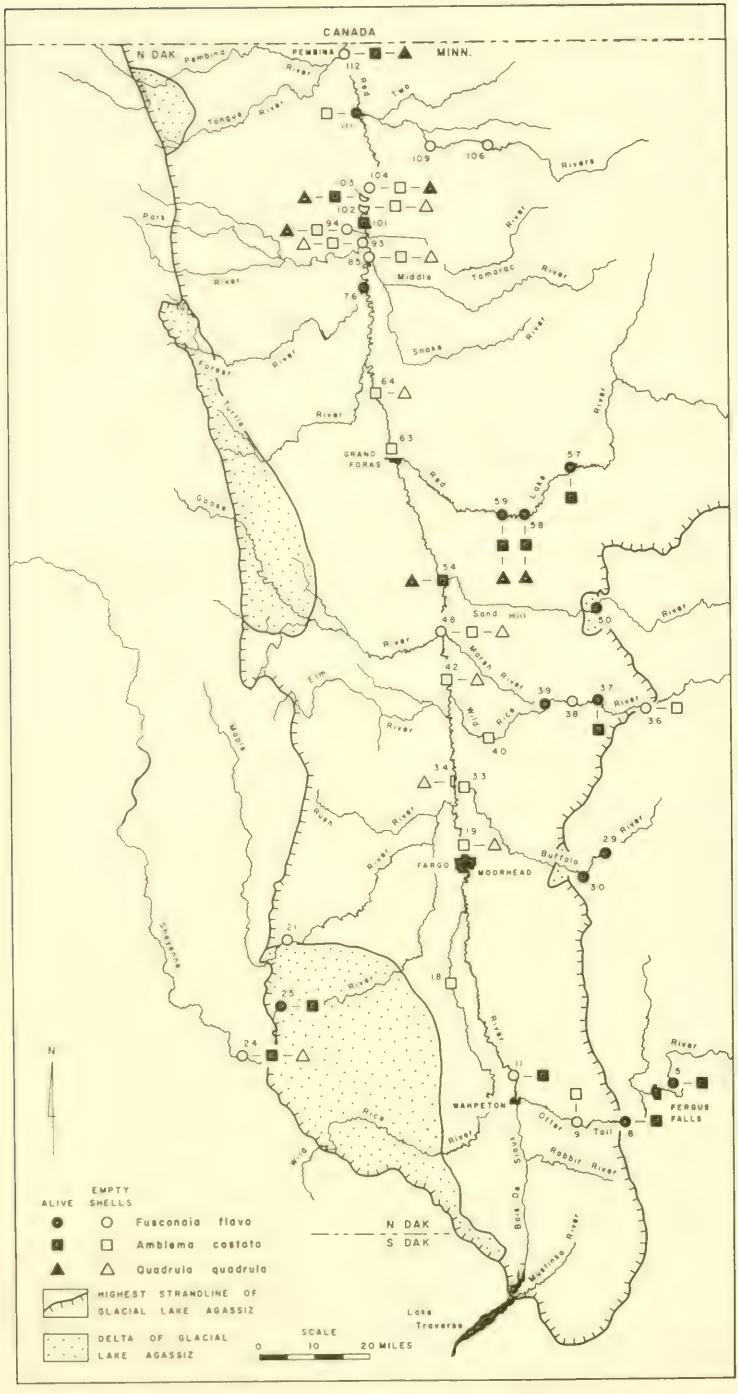


FIG. 3. Distribution map of *Fusconaia flava* (Rafinesque), *Amblema costata* Rafinesque and *Quadrula quadrula* Rafinesque in the Red River Valley. Stations are as in Fig. 2; for glacial Lake Agassiz features see Fig. 1.

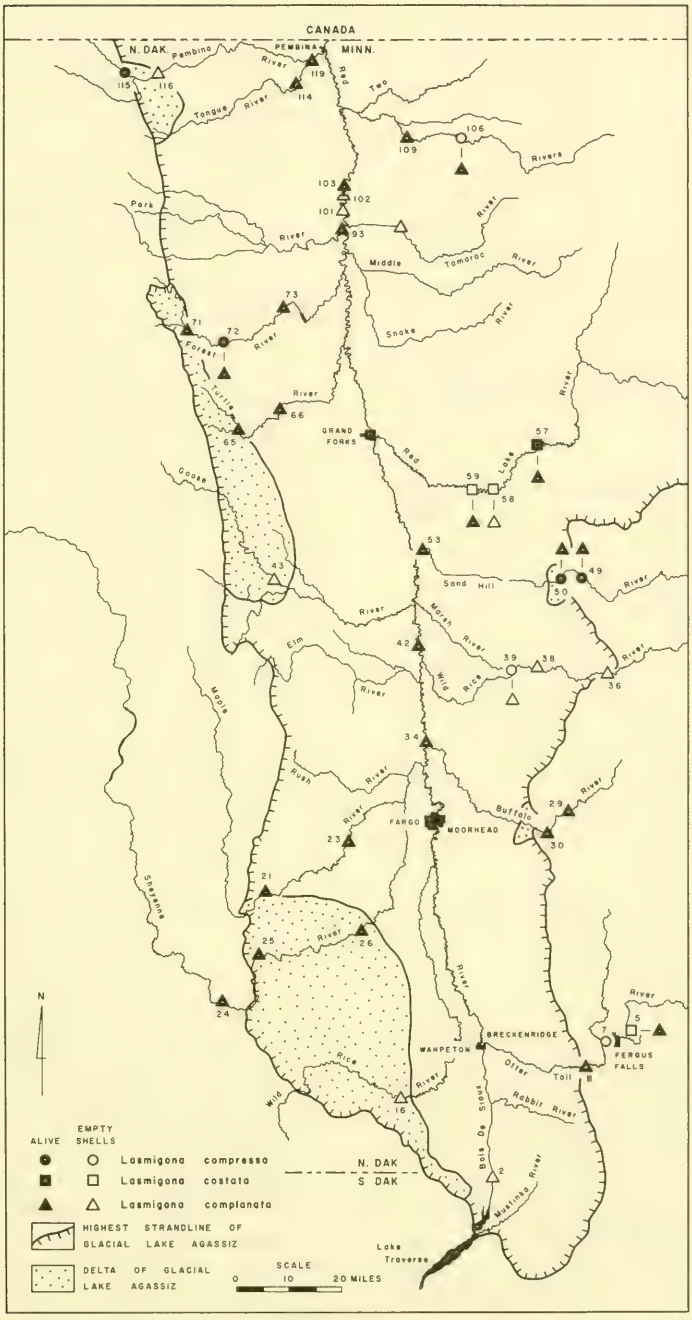


FIG. 4. Distribution map of *Lasmigona compressa* (Lea), *L. costata* Rafinesque and *L. complanata* (Barnes) in the Red River Valley. On October 21, 1967, *L. compressa* was also collected alive from the Red Lake River about 8 air miles east-northeast (upstream) of station 57. Stations are as in Fig. 2; for glacial Lake Agassiz features see Fig. 1.

of the species: *Amblema costata*, *Proptera alata*, *Ligumia recta latissima* and *Lampsilis ventricosa*.

Subfamily Anodontinae
Lasmigona compressa (Lea)
Plate 1, Fig. 1

Diagnosis. Shell subrhomboidal, posterior margin biangulate, smooth; beak sculpture of fine, irregular, double-looped ridges. Hinge complete, with fine teeth; nacre white or salmon or cream-colored, especially near beaks.

Measurements. Shells (6) varied from 70 to 96 mm in length (average 82 mm), had H/L ratios of 0.56-0.70 (average 0.60) and W/H ratios of 0.46-0.56 (average, 0.50).

Remarks. This species was collected alive during the study from only 3 rivers and 4 stations (Fig. 4). Later, it was taken also from the Sheyenne River above station 24 and the Red Lake River above station 57 (Table 3; Fig. 4). Further collecting has revealed its occurrence at several more localities in the Forest River, although not in large numbers. *Lasmigona compressa* is generally characteristic of smaller rivers or the upper parts of larger rivers in the Valley. It seemed to prefer a gravelly sand or sandy gravel bottom.

Lasmigona costata Rafinesque
"Fluted shell"
Plate 1, Fig. 4

Diagnosis. More elongate than *Lasmigona compressa*, with radial costae or ridges on postero-dorsal part of shell. Moreover, double-looped ridges on beak are coarser, and only moderate pseudocardinals (no laterals) are present on hinge.

Measurements. Shells (6) varied from 73 to 109 mm in length (average 90 mm), had H/L ratios of 0.52-0.59 (average 0.56) and W/H ratios of 0.48-0.60 (average 0.52).

Remarks. This species was collected alive from only the Red Lake River at 1 station (station 57, Fig. 4). Here, the bottom was of sandy pebble gravel. Empty shells of this species were collected from 2 other stations on the Red Lake River, and 1 station on the Otter Tail River (station 5). Wilson & Danglade (1914: 12) said *Lasmigona costata* was one of the 3 principal commercial species of the Otter Tail River.

Lasmigona complanata (Barnes)
"White heel splitter"
Plate 1, Fig. 6

Diagnosis. Larger, higher and with more distinctly double-looped beak ridges than in *Lasmigona compressa* and *L. costata*. Also, differs from *L. compressa* in lacking lateral teeth, and from *L. costata* in lacking costae or ridges on postero-dorsal part of shell.

Measurements. Shells (45) varied from 85 to 166 mm in length (average, 122 mm), had H/L ratios of 0.61-0.76 (average 0.69) and W/H ratios of 0.35-0.61 (average 0.50).

Remarks. This species is one of the 4 most common in the Valley (Table 3; Fig. 4), and occurs in both small and large rivers. It seemed to prefer a bottom of sandy gravel and gravelly sand but was found also on sandy mud and mud. The largest and thickest shells were collected from stations 24, 25 and 42 (Sheyenne and Red Rivers).

Anodonta grandis Say
"Floater"
Plate 1, Fig. 5

Diagnosis. Shell elongate, subovate, thin, smooth; beak sculpture of fine to moderate, distinctly double-looped ridges. Hinge teeth lacking; nacre variable, white, bluish white, greenish yellow and orange-pink.

Measurements. Shells (75) varied from 76 to 160 mm in length (average 116 mm), had H/L ratios of 0.46-0.66 (average, 0.55) and W/H ratios of 0.50-0.81 (average 0.61).

Remarks. This species is the most common in the Valley and was collected alive from all rivers but the Park (Table 3; Fig. 5). Consequently, it was taken from all types of bottom, but more

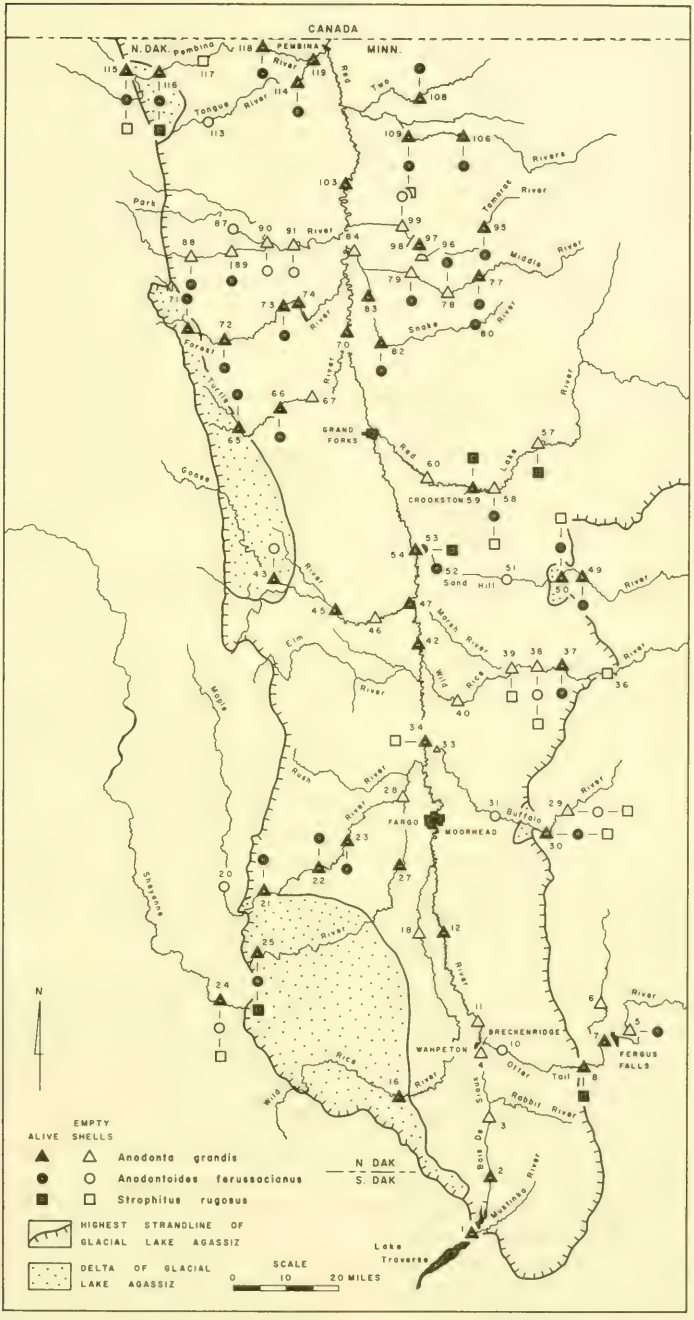


FIG. 5. Distribution map of *Anodonta grandis* Say, *Anodontoides ferussacianus* (Lea) and *Strophitus rugosus* (Swainson) in the Red River Valley. On September 8, 1966, *Strophitus rugosus* was also collected alive from the Forest River about halfway between stations 72 and 73. Stations are as in Fig. 2; for glacial Lake Agassiz features see Fig. 1.

frequently from sandy gravel and gravelly sand than from muddy sand or mud.

Several specimens of an *Anodonta* collected from the Maple River (stations 21, 22 and 23) were shorter (relative to height) and with more centrally-placed beaks than in typical *A. grandis*. However, early growth stages showed little deviation from normal *A. grandis*, and plots of H/L against length and posterior length (beak to posterior margin)/L against length showed overlap of points. Both of these factors suggest that the differences noted are not taxonomic. Perhaps some pathological or parasitic condition inhibited the posterior growth of certain individuals, resulting in shorter specimens with more centrally-placed beaks.

Clarke (1966: 25) has placed the *Anodonta* of the Valley into the subspecies *A. grandis grandis*. He stated that it extends northward to central Saskatchewan.

Anodontoides ferussacianus (Lea)
"Cylindrical paper shell"
Plate 2, Fig. 1

Diagnosis. Smaller than *Anodonta grandis;* beak sculpture of fine, concentric ridges.

Measurements. Shells (26) varied in length from 48 to 81 mm (average, 63 mm), had H/L ratios of 0.44-0.67 (average 0.54) and W/H ratios of 0.57-0.90 (average 0.68).

Remarks. This species is one of the 4 most common in the Valley (Table 3; Fig. 5), and is generally characteristic of smaller rivers or the upper parts of larger rivers. It was collected from a variety of bottom type, but mostly from sandy gravel and gravelly sand. *Anodontoides ferussacianus* occurs commonly with *Anodonta grandis*, and in marginal, uppermost stream conditions, either or both of these species are usually the only mussels present.

Strophitus rugosus (Swainson)
"Squaw foot"
Plate 2, Fig. 2

Diagnosis. Shell elongate, subovate to subelliptical, smooth; beak sculpture of coarse, concentric ridges. Hinge incomplete, only with rudimentary pseudocardinals (slight tubercles); nacre white or bluish white, commonly cream or salmon-colored, especially near beaks.

Measurements. Shells (5) varied in length from 60 to 109 mm in length (average 81 mm), had H/L ratios of 0.50-0.61 (average 0.55) and W/H ratios of 0.55-0.66 (average 0.61).

Remarks. This species is not common in the Valley; it was taken alive from 6 rivers but only 7 stations (Table 3; Fig. 5). It seems to be characteristic of the larger tributaries of the Valley, and was not found in the Red River. *Strophitus rugosus* seemed to prefer a firm bottom of sandy gravel or gravelly sand.

Subfamily Lampsilinae
Proptera alata (Say)
"Pink heel splitter"
Plate 2, Fig. 6

Diagnosis. Shell subovate, with prominent dorsal wing; sexually dimorphic; smooth; beak sculpture of fine, double-looped ridges. Hinge complete, with moderate teeth; nacre purple or pink.

Measurements. Shells (4♂) varied in length from 97 to 145 mm (average, 119 mm), had H/L ratios of 0.66-0.72 (average 0.70) and W/H ratios of 0.36-0.44 (average 0.39).

Remarks. This species was collected alive from only the Red Lake River at 3 stations, although empty shells were taken at several stations on the Red River (Table 3; Fig. 6). It occurred on 3 different types of bottom, sandy gravel, gravelly sand and sandy mud.

Ligumia recta latissima
"Black sand shell"
Plate 2, Fig. 3

Diagnosis. Shell very elongate, subelliptical; sexually dimorphic; smooth; periostracum very dark; beak sculpture of fine, double-looped ridges. Hinge complete, of moderate teeth; nacre white or pink to purple.

Measurements. Shells (29♂) varied in

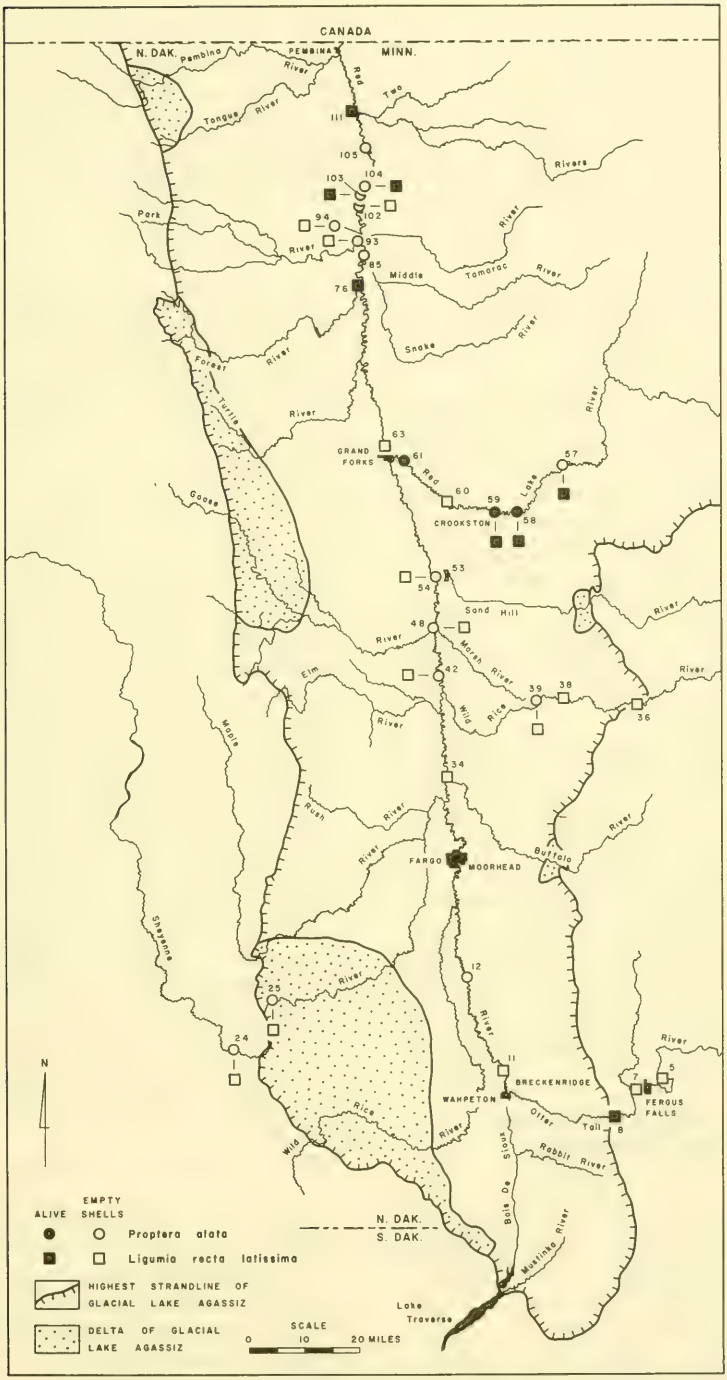


FIG. 6. Distribution map of *Proptera alata* (Say) and *Ligumia recta latissima* (Rafinesque) in the Red River Valley. Stations are as in Fig. 2; for glacial Lake Agassiz features see Fig. 1.

length from 103 to 127 mm (average, 112 mm), had H/L ratios of 0.38-0.46 (average 0.43) and W/H ratios of 0.50-0.68 (average 0.57).

Remarks. *Ligumia recta latissima* was collected alive from only 3 rivers at 8 stations (Table 3; Fig. 6). It is characteristic of the largest rivers in the Valley. This species was taken on bottoms of sandy gravel, gravelly sand, sandy mud and mud.

Lampsilis siliquoidea (Barnes)
"Fat Mucket"
Plate 2, Fig. 4

Diagnosis. Shell elongate, subovate to subelliptical; sexually dimorphic; periostracum yellowish or brownish, commonly with green rays; smooth; beak sculpture of fine, chevron-like (or wavy, double-looped) ridges. Hinge complete, with moderate teeth; nacre white.

Measurements. Shells (253 ♂) varied in length from 65 to 120 mm (average, 90 mm), had H/L ratios of 0.40-0.67 (average 0.52) and W/H ratios of 0.48-0.94 (average 0.65).

Remarks. Second to *Anodonta grandis*, this species was the most frequently found in the Valley (Table 3; Fig. 7). Consequently, it was taken from both large and small rivers and all types of bottom from gravel to mud; however, it was collected at most stations from sandy gravel, gravelly sand and sandy mud. It occurred commonly and in large numbers along the banks of the Red River, usually associated with *Lampsilis ventricosa*.

Lampsilis ventricosa (Barnes)
"Pocketbook"
Plate 2, Fig. 5

Diagnosis. Higher than *Lampsilis siliquoidea* with more elevated beaks; also sexually dimorphic; beak sculpture with coarser, indistinctly double-looped ridges; hinge teeth coarser.

Measurements. Shells (38♂) varied in length from 82 to 130 mm (average 99) had H/L ratios of 0.57-0.71 (average 0.62) and W/H ratios of 0.52-0.74 (average 0.62).

Remarks. This species was collected alive from 5 of the largest rivers in the Valley at many stations (Table 3, Fig. 7). It was found most frequently on a bottom of sandy mud or mud but also commonly on sandy gravel. *Lampsilis ventricosa* was commonly associated with *L. siliquoidea* along the banks of the Red River but in lesser numbers than that species.

Concentrations of mussels

An idea of concentrations of mussels in the Valley, all species taken collectively, can be gained from Fig. 8. This map might prove useful should commercial exploitation of mussels be contemplated there.

In the Red River, more individuals appear to occur in the lower reaches near the U.S. - Canada border. Just below the largest city complexes of Fargo-Moorhead and Grand Forks - East Grand Forks, mussels are presumably absent, but concentrations increase generally downstream from them. Few mussels occur above Fargo - Moorhead with the exception of the upper reaches of the Bois De Sioux River where only 1 species was taken alive (*Anodonta grandis*).

Tributaries of the Red River commonly show a decrease of mussel individuals downstream. The Park, Forest and Turtle Rivers apparently have no live mussels in their lower reaches. The Wild Rice, Goose and Park Rivers in North Dakota, and the Tamarac, Middle and Snake Rivers in Minnesota are particularly poor in mussels. High in both individuals and species is the Red Lake River, the best tributary for mussels in the Valley.

Bottom and turbidity

Bottom sediments generally vary from gravel and sand at or near the margins of the lake plain to primarily silt and clay (collectively, mud) at or near the axis of the Valley (Table 2). Bottom type is closely allied with turbidity and generally is directly reflected by it.

Turbidity in the tributaries generally increases downstream as the bottom sediment becomes finer (Fig. 9). Values

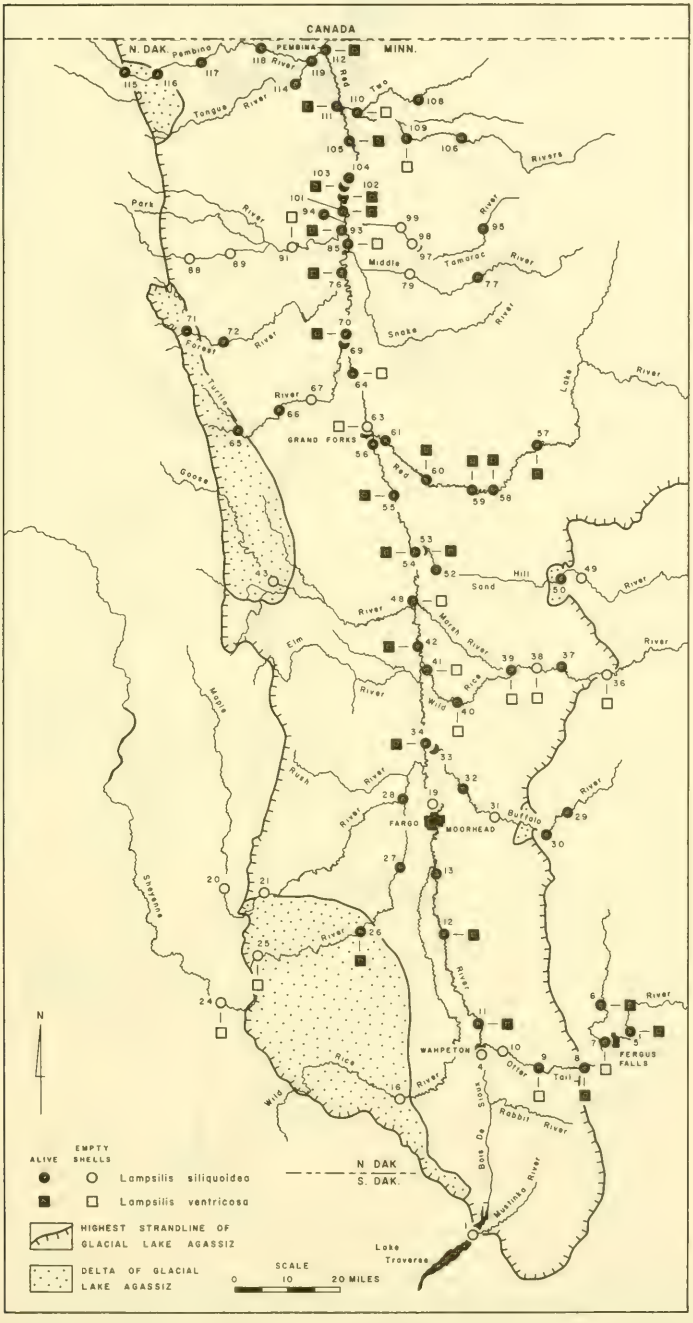


FIG. 7. Distribution map of *Lampsilis siliquoidea* (Barnes) and *L. ventricosa* (Barnes) in the Red River Valley. Stations are as in Fig. 2; for glacial Lake Agassiz features see Fig. 1.

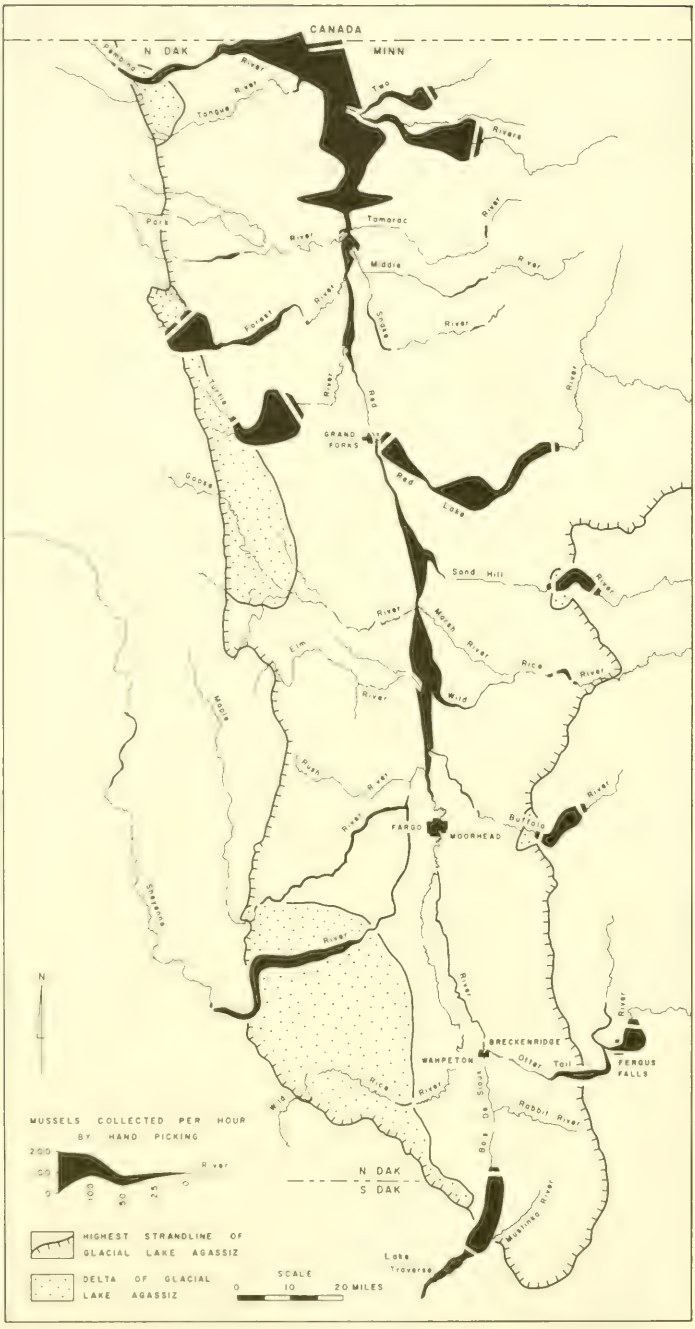


FIG. 8. Map of the relative abundance of individual mussels in the Red River Valley. The width of each dark band on a river is equivalent to the numbers of mussels collected per hour by hand-picking. Dark bands show breaks where control is lacking and the mussel concentrations are inferred. Stations used for control are shown on Fig. 2.

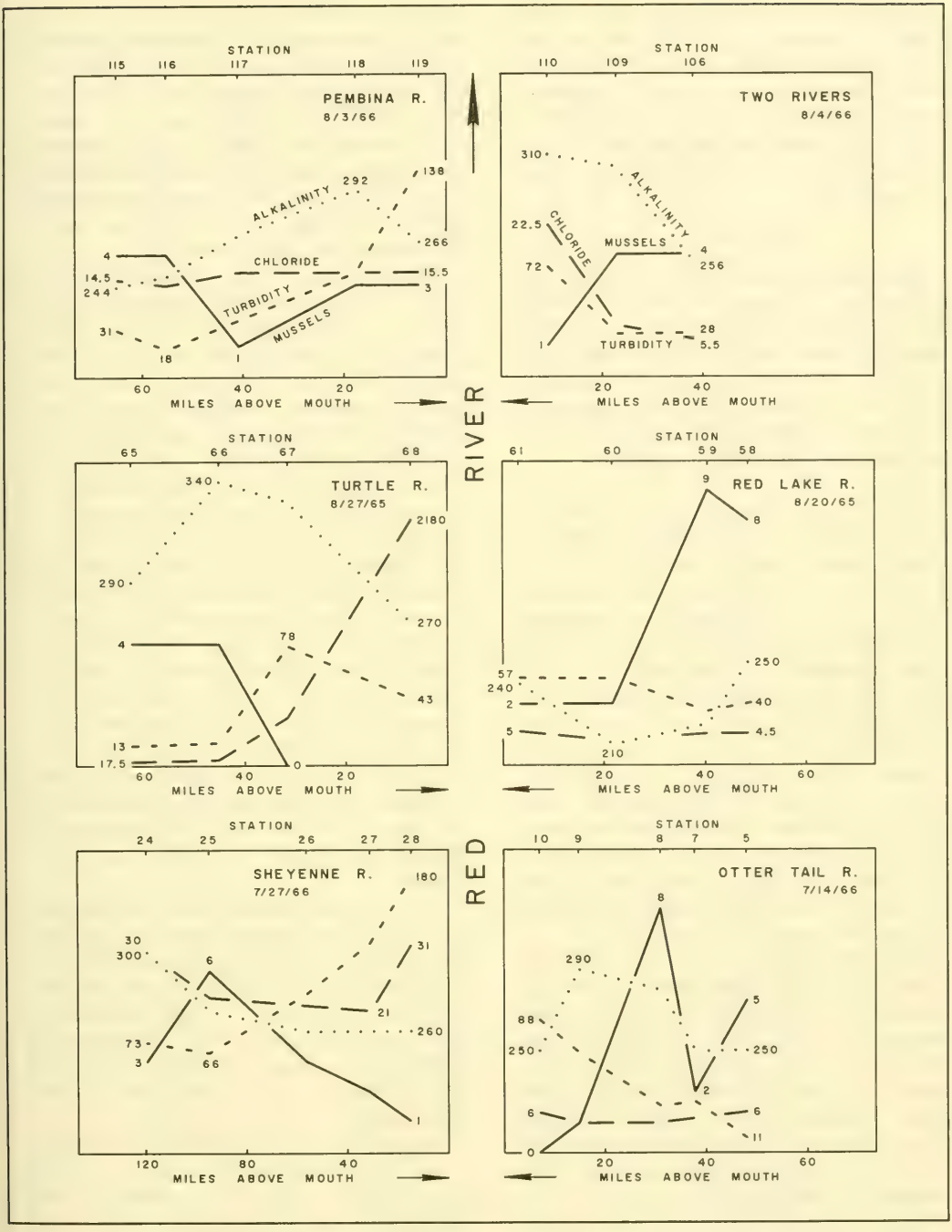


FIG. 9. Variation with station position of total alkalinity, total chlorides, turbidity and mussel species for 6 tributaries of the Red River, from measurements made in July and August, 1965 and 1966. Chemical values are in ppm and turbidity is in Jackson turbidity units (JTU). Arithmetic scales were used for all factors plotted except total chlorides, which are plotted on a logarithmic scale. Station numbers correspond to those shown on Fig. 2. Arrows point downstream.

(in Jackson turbidity units, JTU) varied from 11 (station 5) to 285 (station 52) with considerable fluctuation. In the Red River, turbidity is consistently high with relatively less fluctuation, and values of 65-240 JTU were measured. Secchi disk readings were correspondingly low, from 0.50 to 1.0 ft.

Chemical data

Generally, chemical factors vary with discharge. Therefore, the Red River, with a relatively high discharge, exhibits relatively less variability in the concentration of chemical ions. Tributaries of the Red, however, with less and generally more fluctuating discharge, are characterized by greater chemical variability.

Total dissolved solids for a few selected localities are listed in Table 4. Values range there from 150 to 1,110 ppm (both extremes for the Sheyenne River). The relationship of chemical variability to discharge can be perceived if one compares extreme values of total dissolved solids and discharge for each of 2 gaging stations on the Red and Sheyenne Rivers.

Water was analyzed for dissolved oxygen, free carbon dioxide, pH, total chloride, nitrate and nitrite content, phenolphthalein and total alkalinity, calcium and total hardness, and iron. Values obtained during the summers of 1965 and 1966 are summarized below.

Dissolved oxygen and free carbon dioxide, in the Red River, varied from 6.5 (stations 63 and others) to 9.1 ppm (station 11) and from 2.4 (station 62 and others) to 19.2 ppm (station 103), respectively. In the tributaries, oxygen and carbon dioxide ranged from 5.3 (station 39 and others) to 14 ppm (station 29) and from O (station 2 and others) to 33 ppm (station 32), respectively.

Values of pH in the Red River were from 8.0 (station 34 and others) to 8.3 (station 11). In the tributaries, pH varied considerably more, from 7.5 (station 6) to >9.2 (station 2).

Total chloride values showed relatively little variability in the Red River, from 6.5 (station 12) to 37.5 ppm (station 94). In the tributaries, however, marked extremes were present, from 3.5 (station 60) to 2180 ppm (station 68). Variation in chloride content with station is shown for 6 tributaries in Fig. 9. Total chloride is seen to increase markedly downstream in the Turtle River. High chloride values were noted also in the lower reaches of the Forest and Park Rivers.

Nitrate and nitrite content in the Red River ranged from 0.65 (station 13) to 2.75 ppm (station 104) and from 0.000 (station 12 and others) to 0.014 ppm (station 94), respectively. In the tributaries, these same factors varied from 0.00 (station 65) to 5.1 ppm (station 96) and from 0.000 (station 3 and others) to 0.046 ppm (station 17), respectively.

Phenolphthalein and total alkalinity in the Red River were from 0 (station 12 and others) to 10 ppm (station 48) and from 188 (station 12) to 300 ppm (station 64 and others), respectively. In the tributaries, these same factors varied from 0 (station 5 and others) to 60 ppm (station 51 and others) and from 118 (station 2) to 450 ppm (stations 44 and 53), respectively. Phenolphthalein alkalinity, at most mussel stations, was zero. Variation in total alkalinity at different stations is shown for 6 tributaries in Fig. 9; no readily apparent trends are present.

Calcium and total hardness values for the Red River ranged from 90 (station 12) to 180 ppm (station 85) and from 230 (station 19 and others) to 330 ppm (station 54), respectively. In the tributaries these factors varied from 65 (station 5) to 600 ppm (station 68) and from 170 (station 58) to 1050 ppm (station 68), respectively.

In the Red River, iron values were from 0.38 (stations 62 and 63) to 0.86 ppm (station 93). Iron values in the tributaries varied from 0.07 (stations 44 and 81) to 1.04 ppm (station 52).

DISCUSSION AND CONCLUSIONS

Thirteen species of mussels, arranged in 10 genera, are presently known to in-

TABLE 4. Total dissolved solids and water temperatures, with mean discharge, for selected U. S. Geological Survey gaging stations* in the Red River Valley

USGS Gaging Station*	River	Mean Discharge (cu. ft./sec.)	Min.	Total Dissolved Solids (ppm) Mean	Max.	Water Temp. (Aver.)	Water Years** and (No. of Observations)
460	Otter Tail	295.0	221	244	267	--	61, 65 (4)
540	Red (Fargo)	607.5	175	333.4	650	51.3	56-65 (246)
560	Sheyenne	30.5	150	399.8	1,110	49.9	56-65 (238)
587	Sheyenne	92.8	204	500.2	907	49.9	57-65 (214)
610	Buffalo	27.6	---	381	---	--	65 (1)
790	Red Lake	1385.0	191	273	388	--	64-65 (12)
825	Red (Grand Forks)	2478.0	170	333.5	540	50.2	57-65 (238)
885	Park (Homme Reservoir)	--	475	543	666	--	58-59 (6)
995	Pembina	181	187	451	822	47.4	62-63, 65 (66)

*Locations of gaging stations are shown on Fig. 1. Data were taken from U. S. Geological Survey, 1960-1963, 1964a, 1964b, 1965, 1966a and 1966b. Gaging station 885 is half a mile upstream from station 890 (Fig. 1).

**From October 1 to September 30.

habit the rivers and streams of the Red River Valley (Table 3). Dawley (1947: 679) also reported 2 other species, *Obliquaria reflexa* and *Actinonaias carinata*, but I have not been able to verify their occurrence. Later, Dawley (written communication, dated January 20, 1967) indicated that the reported occurrences of these 2 species from the Red River are probably in error. Additions that I have been able to make to Dawley's list (: 679) are *Quadrula quadrula*, *Lasmigona compressa* and *Anodontoides ferussacianus* for the Red Lake River and *Lasmigona complanata* for the Red River. I have not taken *Strophitus rugosus* and *Proptera alata* alive from the Red River as she reported.

Generally, the larger the river, the more mussel species it will contain. Exceptionally, the Red River has 8 species, whereas the Red Lake River, its largest tributary, has yielded the total mussel fauna of 13 species (Table 3). Other tributaries have from 1 (Park River) to 9 species (Sheyenne River). In the lower part of the Sheyenne River, *Lasmigona compressa* was not observed; however, it has been collected above station 24 (Fig. 2; Norby, 1967: 19) and therefore was included in Table 3.

The 4 most common species are *Lasmigona complanata*, *Anodonta grandis*, *Anodontoides ferussacianus* and *Lampsilis siliquoidea* (Table 3). Two species, *Lasmigona costata* and *Proptera alata*, were taken alive from only a single river, the Red Lake (Figs. 4, 6). *Quadrula quadrula* was collected alive from only the Red and Red Lake Rivers (Fig. 3).

The distribution of certain species shows a relation to river size. The species taken usually from the larger rivers in the Valley include *Amblema costata*, *Quadrula quadrula*, *Proptera alata*, *Ligumia recta latissima* and *Lampsilis ventricosa* (Figs. 3, 6 and 7). Three of these species, *Quadrula quadrula*, *Proptera alata* and *Ligumia recta latissima* are common throughout the main mussel-bearing reaches of the Mississippi River (van der Schalie & van der Schalie, 1950: 457). Two species, *Lasmigona compressa* and *Anodontoides ferussacianus*, are generally indicative of smaller rivers or the upper parts of larger rivers in the Valley.

The Red River Valley mussels represent a modified Mississippi River system fauna in that the 13 species in 10 genera of the Valley are a sharp reduction from the 50 species in 29 genera of the Mississippi and its tributaries (determined from van der Schalie & van der Schalie, 1950: 454-456). The Valley fauna is basically one pertaining to the uppermost Mississippi and its tributaries. Only 4 Valley species, *Quadrula quadrula*, *Lasmigona complanata*, *Proptera alata* and *Ligumia recta latissima* are common throughout the main Mississippi River (van der Schalie & van der Schalie, 1950: 457).

The causes for the faunal limitation are not clear. Perhaps the range in size, or maximum size, of water body (river) is a significant factor. Rivers of the Red River Valley are not as large nor as varying in size as those of the Mississippi Valley. Consequently, fewer habitats are available, resulting in a smaller mussel fauna. Availability of suitable rivers is reflected in part by average annual runoff, which is directly related to the amount of precipitation in an area. The average annual runoff is 7.2 inches in the Upper Mississippi drainage basin but only 1.6 inches in the part of the Hudson Bay drainage basin concerned in the United States (Miller, et al., 1962, Pl. 9).

Mussels must have entered the Valley from the south via its upper reaches during confluence over a divide now separating the present Mississippi and Hudson Bay drainage basins (van der Schalie, 1939: 254; 1945: 359). This migration must have occurred during at least part of the existence of glacial Lake Agassiz via River Warren (its valley presently occupied by the Minnesota River), the southern outlet of the Lake. Dawley (1947: 680) has noted the presence of *Amblema costata*, *Lasmigona com-*

planata, *Ligumia recta latissima*, *Lampsilis siliquoidea* and *L. ventricosa* in glacial Lake Agassiz sediments. Whether the 8 remaining mussel species of the Valley migrated into it during glacial or post-glacial time is uncertain. I am presently concerned with the time of first arrival of certain mussel species in the Valley. The study will necessitate considerable search for mussels in Lake-associated sediments and species found at known levels will need to be correlated to events at the southern outlet of the Lake (Matsch & Wright, 1967).

Transfer of mussels is probably still occurring between the Mississippi system and the Valley. Big Stone Lake, the source of the Minnesota River, and Lake Traverse, the ultimate source of the Red River, are separated by but a few miles. Dawley (1947: 680) has pointed out that these 2 lakes are connected at times of very high water.

Restrictive ecological factors

Physical. Bottom type seems to have little significant effect in limiting the distribution of mussels. Certain mussels apparently prefer a specific bottom, but most mussels in the Valley have been found on a variety of sediment, indicating a relatively wide tolerance to bottom type. Also, many species seem to tolerate both firm and soft bottoms (e.g., *Lampsilis siliquoidea* on gravel or sand in most of the tributaries and in soft mud along the banks of the Red River). A shifting bottom is a different matter. In practically no instance have I taken live mussels from a rippled, moving bottom.

High turbidity, correlated with a finer bottom, may be a limiting factor in the lower reaches of several tributaries, where it increases (Fig. 9). This increase is commonly associated with a decrease in the number of mussel individuals (Fig. 8) and species (Fig. 9). However, the Red River is highly and consistently turbid and yet harbors large numbers of mussels.

River discharge is probably a significant limiting physical factor. Rivers with higher discharge generally contain more mussel species and those with a low or sporadic discharge generally have fewer (Fig. 1, Table 3). No flow for long periods may notably restrict or exclude mussels from certain parts of rivers. This is perhaps true in the lower reaches of the Tamarac, Middle and Snake Rivers, where flow may be interrupted continuously for longer than 7 and 8 months (MacLay, Winter & Pike, 1965). Stagnation for long periods is probably also inhibiting in parts of the Wild Rice and Goose Rivers in North Dakota (Fig. 1), where discharge is zero about half the time. Such a situation may be detrimental to mussels because of lowered dissolved oxygen, increased concentrations of dissolved salts, and increased predation accompanying the lowering of the water level.

Chemical. Of the chemical factors measured, a high chloride content appears to restrict significantly the occurrence of mussels. Relatively high chloride values occur in the lower reaches of the Park, Forest and Turtle Rivers, a high of 2180 ppm having been measured in the Turtle River (Figs. 2, 9). In this region of high chloride values, I have taken no live mussels. The high chloride content is thought to be the result of saline ground water seepage from Cretaceous rocks of the Dakota Group (Upham, 1895: 527). Saline soils in this region also relate to high chloride values of the river water (Cvancara & Harrison, 1965, Figs. 1, 2).

The prohibitive effects, if any, of other chemical factors are uncertain. The relatively high total alkalinity and hardness of water in the Valley should be 2 chemical factors conducive to the propagation of mussels.

Biological. Biological factors have been considered only partially in this study, but they may be of as much or more significance than the other factors. Fish hosts may be of prime importance in the distribution of mussels, and have a greater influence than bottom type.

This inference is made from the occurrence of many species on different types of bottom; I believe that, if other conditions are suitable, the bottom probably will not be prohibitive and that mussels occur in a stream not far from where they left the fish host as larvae. After leaving the fish host, they are presumably concentrated or grouped locally, at least in small rivers, into areas of relatively higher water velocity (Cvancara et al., 1966).

Food, although not separately evaluated, seemed to be generally available. Predation, notably by the raccoon and muskrat, is presumably a biological factor of secondary importance.

Pollution. Industrial, municipal or domestic pollution, although not as serious as in many other sections of the United States, appears to restrict mussels in parts of the Valley. I have not taken live mussels just below the urban complexes of Fargo - Moorhead and Grand Forks - East Grand Forks (Fig. 2), and attribute their presumed absence there to pollution. The apparent absence of live mussels at the downstream edge of Stephen, Minnesota, on the Tamarac River (station 98) and just below Fairmount, North Dakota, on the Bois De Sioux River (station 3) is presumably also the result of poor water quality.

An example of recent, possible pollutional effects is found just below the American Crystal Sugar Company plant near Drayton, North Dakota. On August 24, 1965, before the plant began operation, an assistant and myself collected from a 312-yard-long strip, 160 yards below the sugar plant effluent channel and along the opposite (right) bank (station 103.) In one hour we picked 351 mussels. One year later (August 19, 1966), after the sugar plant had been operating during the autumn and winter, we collected from exactly the same part of the river, recovering only 97 mussels per hour, which corresponds to a reduction in mussels of approximately 75%.

The least polluted part of the Red River is from about Drayton (USGS gaging station 920, Fig. 1) to the Canadian border (Gallagher et al., 1965). The near absence of pollution is apparently reflected by the greater concentration of mussels in that section of the river (Fig. 8).

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RÉSUMÉ

MOULES D'EAU DOUCE (UNIONIDAE) DE LA RED RIVER VALLEY DU NORD DAKOTA ET DU MINNESOTA, U. S. A.

A. M. Cvancara

Treize espèces de Moules d'eau douce habitent la Red River du Nord et 18 ses tributaires du Nord Dakota et de l'Ouest du Minnesota. Ces espèces, appartenant à 10 genres, sont: *Fusconaia flava* (Rafinesque), *Amblema costata* Rafinesque, *Quadrula quadrula* Rafinesque, *Lasmigona compressa* (Lea), *L. costata* Rafinesque, *L. complanata* (Barnes), *Anodonta grandis* Say, *Anodontoides ferussacianus* (Lea), *Strophitus rugosus* (Swainson), *Proptera alata* (Say), *Ligumia recta latissima* (Rafinesque) *Lampsilis siliquoidea* (Barnes) et *L. ventricosa* (Barnes). Huit espèces ont été collectées de la Red River, et 13 espèces de chacun de ses tributaires. Les 4 espèces les plus communes sont *Lasmigona complanata, Anodonta grandis, Anodontoides ferussacianus* et *Lampsilis siliquoidea.* Cinq espèces, *Amblema costata, Quadrula quadrula, Proptera alata, Ligumia recta latissima* et *Lampsilis ventricosa* sont généralement caractéristiques des plus grandes rivières, tandis que *Lasmigona compressa et Anodonta ferussacianus* le sont des plus petites rivières de la Red River Valley.

La faune de moules d'eau douce de la Red River Valley, qui fait partie du drainage de la baie d'Hudson, tire son origine de celle du réseau hydrographique du Mississippi. La faune de la Valley, cependant, comporte seulement 26% de celle du Mississippi.

Quatre facteurs écologiques sont vraisemblablement de première importance dans la restriction de la distribution des espèces dans la Red River Valley. Ce sont: les longues périodes sans courant, la haute teneur en chlorures, la pollution de l'eau et peut-être la forte turbidité.

A. L.

RESUMEN

ALMEJAS (UNIONIDAE) DEL RED RIVER EN DAKOTA DEL NORTE Y MINNESOTA, E. E. U. U.

A. M. Cvancara

Trece especies de almejas habitan el Red River del Norte y 18 de sus tributarios, en el este de Dakota del Norte y oeste de Minnesota. Estas especies, pertenecientes a 10 géneros son: *Fusconaia flava* (Rafinesque), *Amblema costata* Rafinesque, *Quadrula quadrula* Rafinesque, *Lasmigona compressa* (Lea), *L.costata Rafinesque, L. complanata* (Barnes), *Anodonta grandis* Say, *Anodontoides ferussacianus* (Lea), *Strophitus rugosus* (Swainson), *Proptera alata* (Say), *Ligumia recta latissima* (Rafinesque), *Lampsilis siliquoidea* (Barnes) y *L. ventricosa* (Barnes). Ocho especies fueron colectadas en el Red River y 13 especies en cada uno de los tributarios. Las cuatro especies más comunes son *Lasmigona complanata, Anodonta grandis, Anodontoides ferussacianus,* y *Lampsilis siliquoidea.* Otras cinco, *Amblema costata, Quadrula quadrula, Proptera alata, Ligumia recta latissima* y *Lampsilis ventricosa* son generalmente caracteristicas de los grandes ríos en el valle del Red River. *Lasmigona compressa* y *Anodontoides ferussacianus* generalmente indicadoras de ríos menores.

La fauna de almejas en este valle que es parte de cuenca de la Bahia de Hudson, tuvo su origen en aquella del sistema del Rio Mississippi, pero constituye sólo un 26% de la de ese río.

Se indican cuatro factores ecológicos, presumiblemente de primera importancia en la restricción de la distribución de las almejas en el valle del Red River, que son: falta prolongada de corriente en el río, alto contenido de cloro, corrupción de las aguas y posiblemente la elevada turbidez.

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АБСТРАКТ

МОЛЛЮСКИ (UNIONIDAE) ИЗ ДОЛИНЫ РЕД РИВЕР,
СЕВЕРНАЯ ДАКОТА И МИННЕСОТА

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Тринадцать видов моллюсков известны в Ред Ривер на севере и в 18 ее притоках на востоке Северной Дакоты и западной Миннесоты. Эти виды, относящиеся к 10 родам, следующие: *Fusconaia flava* (Rafinesque), *Amblema costata* Rafinesque, *Quadrula quadrula* Rafinesque, *Lasmigona compressa* (Lea), *L. costata* Rafinesque, *L. complanata* (Barnes), *Anodonta grandis* Say, *Anodontoides ferussacianus* (Lea), *Strophitus rugosus* (Swainson), *Proptera alata* (Say), *Ligumia recta latissima* (Rafinesque), *Lampsilis siliquoidea* (Barnes), и *L. ventricosa* (Barnes). Из них 8 видов были собраны в Ред Ривер и от 1 до 13 видов в каждом из ее притоков. Из них 4 вида наиболее обычны, это: *Lasmigona complanata, Anodonta grandis, Anodontoides ferussacianus* и *Lampsilis siliquoidea*. Пять видов: *Amblema costata, Quadrula quadrula, Proptera alata, Ligumia recta latissima* и *Lampsilis ventricosa*, - характерны для более крупных рек долины Ред Ривер, а 2 вида, *Lasmigona compressa* и *Anodontoides ferussacianus*, обычны для мелких речек этого района.

Фауна моллюсков долины Ред Ривер, являющейся частью бассейна Гудзонова залива, берет свое начало от малакофауны речной системы Миссисиппи. Фауна моллюсков долины Ред Ривер составляет лишь 26% последней.

Четыре экологических фактора имеют, по видимому, основное значение, ограничивающее распространение моллюсков в долине Ред Ривер: протяженность рек, высокое содержание хлоридов, загрязнение воды и, возможно, большая ее мутность.

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HERMAPHRODITISM AMONG NORTH AMERICAN FRESHWATER MUSSELS[1]

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ABSTRACT

Information on the extent of hermaphroditism among the freshwater mussels of the rich naiad fauna of the U.S.A. is fragmentary. In this study the gonads of 1,871 specimens belonging to 97 species in 32 genera were histologically examined, using the paraffin block technique for sectioning. Only 4 species in 2 unionid subfamilies were shown to be dominantly hermaphroditic (monoecious); 3 in the Anodontinae: *Anodonta imbecillis, Lasmigona compressa* and a close relative *L. subviridis* and 1 in the Lampsilinae: *Carunculina parva.*

Sporadic hermaphrodites were found in another 22 species or forms belonging to 17 genera in 2 families. Usually such individuals appear to be predominantly of one sex, with only a small amount of gonad tissue of the opposite sex. One ambisexual specimen was found in the Margaritanidae, in *Margaritifera margaritifera,* among 24 specimens sectioned representing 2 genera and species. In the Unionidae accidentally monoecious individuals occurred in all 3 subfamilies. Among the Unioninae, with 567 specimens (34 species, 11 genera) examined such individuals were found in 9 species (or forms) of 5 genera, i.e., in *Elliptio dilatatus, E. productus, Fusconaia ebenus, F. flava, Gonidea angulata, Pleurobema cordatum, P. c. coccineum, Quadrula quadrula* and *Tritogonia verrucosa.* In the Anodontinae, with a total of 479 specimens (20 species, 5 genera) sectioned, sporadic hermaphrodites were demonstrated in 5 species belonging to 4 genera, of which 2 are the genera also containing the predominantly hermaphroditic species; i.e., they occurred in: *Anodonta corpulenta, A. grandis footiana* and *Lasmigona complanata* as well as in *Alasmidonta marginata* and *Strophitis rugosus.* In the Lampsilinae, with a total of 801 specimens (41 species, 14 genera) sectioned, the condition was detected in 7 further species representing 6 genera, i.e., in: *Actinonaias ellipsiformis, Lampsilis cariosa, Leptodea laevissima, Proptera alata, Ptychobranchus fasciolaris, P. subtentum* and *Villosa (Micromya) iris.*

This rather extensive survey of American naiades shows that they are generally dioecious. Whether or not hermaphroditism appears in animals confronted with difficult environmental conditions, as has been previously suggested, remains an open question.

One of the best summary analyses of sexual differentiation among pelecypod mollusks was published by Coe (1943). He indicated that among the 10,000 odd species of bivalves about 400 were known to deviate from the strictly dioecious or unisexual condition and stressed that in these every grade of sexual differentiation and of ambisexuality was found. Hermaphroditism could be complete, partial or occasional. Among the normally hermaphroditic (ambisexual, mo-

[1]This paper was read at the Second European Malacological Congress, Copenhagen, August, 1965 and abstracted in Malacologia, 1966. It has now been brought up to date in minor details.

noecious) marine species studied, some exhibited alternative sexual phases, including functional hermaphroditism. Not only could species of the same genus differ considerably in sexuality but there existed variability in different individuals of the same species or in single individuals at different periods of life. Similarly, the distribution of ovogenic and spermatogenic tissues also showed great variation. The observed variability is attributed to the interplay between multiple hereditary sex differentiating mechanisms and environmental factors, though evidence as to the influence of the latter yet needed further and more direct experimental proof.

As regards freshwater mussels, the sphaeriids are all known to be hermaphroditic, but relatively little is known about the extent of hermaphroditism in the larger forms. As late as 1926, Pelseneer noted that the number of freshwater mussels investigated in this respect was not great. That the unionid *Anodonta* may show the condition has been known for a long time. Weisensee (1916), in a scholarly article on the sex of *Anodonta*, thoroughly reviews the observations made since the time of Leeuwenhoek in 1722: he states (on p 275):

> "Seit der Arbeit von Lacaze-Duthiers über den Genitalapparat der Lamellibranchiaten wurde die Frage nach der Geschlechtsverteilung bei *Anodonta* nicht mehr zum Gegenstand eingehenderer Untersuchungen gemacht. Seit diesem Zeitpunkt war man der Ansicht - und diese Ansicht finden wir in fast allen heutigen Lehrbüchern vertreten - dass sowohl *Anodonta* als auch Unio in der Regel getrenntgeschlechtlich seien."[2]

Hermaphroditism in British *Anodonta* was intensively studied by Bloomer (1930, 1934, 1935, 1939). Pelseneer (1920) quotes Schierholz's report of *Margaritifera* as an occasional hermaphrodite in Germany. In the U.S.A. Sterki (1898) recognized hermaphroditism in 3 unionids: *Anodonta imbecillis*, *Carunculina parva* and *Fusconaia flava*. In the latter 2 genera for the first time Ortmann (1912) noted, however, that most of the Unioninae have separate sexes. The histology of the gonads of *Carunculina parva* was later studied by Tepe (1943).

The aim of the present study was to investigate the extent of hermaphroditism among the numerous species of freshwater mussels (Unionacea) and, if possible, to gain information on factors that may serve to induce hermaphroditism. During the past several years material was collected from widely distributed locations, and 1,871 specimens belonging to 97 species (or forms) in 32 genera (Table 1) were histologically examined. The distribution of these species as to family group was as follows: 2 species in the Margaritanidae; and, in the Unionidae, 34 species in the Unioninae, 20 in the Anodontinae and 41 in the Lampsilinae.

The specimens were anaesthetized (usually in sodium nembutal) and killed and fixed (mostly in Bouin's fluid). They were then serially sectioned in paraffin and stained with haematoxylin and eosin.[3]

RESULTS

In the present study, only 4 unionid species have been found to be dominantly hermaphroditic (Tables 1, 2), while sporadic, sometimes partial hermaphrodites were found in 22 species distributed in all families and subfamilies (Tables 1,

[2] Translation: "Since Lacaze-Duthiers' [1894] work on the genital apparatus of the lamellibranchs, the question of sex distribution in *Anodonta* has not been made the object of further detailed investigation. The general view held since that time - a view to be found in almost all textbooks today - is that *Anodonta*, as well as *Unio*, are, as a rule, of separate sexes."

[3] The investigation is continuing. To date another 2000 specimens have been quick frozen and sectioned with a cryostat (a microtome designed to cut frozen tissue). So far, no essential differences from the results reported in this paper have been found.

TABLE 1. North American freshwater mussels sectioned to determine sex (97 species; 32 genera)

Species	Nos. sectioned
MARGARITANIDAE (2 species; 2 genera)	
Cumberlandia monodonta (Say)	12
**Margaritifera margaritifera* (Linnaeus)	12
	24
UNIONIDAE (95 species; 30 genera)	
Unioninae (34 species; 11 genera)	
Amblema boykiniana (Lea)	5
Amblema costata (Rafinesque)	15
Amblema costata plicata (Say)	1
Amblema neislerii (Lea)	6
Amblema peruviana (Lamarck)	1
Amblema perplicata (Conrad)	6
Cyclonaias tuberculata (Raf.)	20
Elliptio buckleyi (Lea)	6
Elliptio complanatus (Dillwyn)	5
Elliptio crassidens (Lamarck)	22
**Elliptio dilatatus* (Raf.)	68
Elliptio fraternus (Lea)	8
**Elliptio productus* (Conrad)	9
Elliptio sloatianus (Lea)	6
Elliptio strigosus (Lea)	6
Elliptio tuomyi (Lea)	6
Fusconaia barnesiana (Lea)	6
**Fusconaia ebenus* (Lea)	35
**Fusconaia flava* (Raf.)	68
Fusconaia succissa (Lea)	34
**Gonidea angulata* (Lea)	12
Lexingtonia dolabelloides (Lea)	7
Megalonaias gigantea (Barnes)	2
Plethobasus cooperianus (Lea)	1
Plethobasus cyphyus (Raf.)	1
**Pleurobema cordatum* (Raf.)	38
**Pleurobema cordatum coccineum* (Conrad)	35
Pleurobema pyriforme (Lea)	8
Pleurobema strodeanum (B. H. Wright)	7
Quadrula cylindrica (Say)	4
Quadrula pustulosa (Lea)	23
**Quadrula quadrula* (Raf.)	85
Quadrula quadrula speciosa (Lea)	2
**Tritogonia verrucosa* (Raf.)	9
	567
Anodontinae (20 species; 5 genera)	
Alasmidonta calceolus (Lea)	86
**Alasmidonta marginata* (Say)	48
Alasmidonta undulata (Say)	4
Anodonta couperiana Lea	6

Table 1 (contd.)

Species	Nos. sectioned
Anodontinae (contd.)	
**Anodonta corpulenta* Cooper	35
Anodonta californiensis Lea	6
**Anodonta grandis footiana* (Lea)	12
Anodonta cataracta Say	2
Anodonta hallenbeckii Lea	1
***Anodonta imbecillis* Say	105
Anodonta marginata Say	6
Anodonta suborbiculata Say	5
Anodontoides ferussacianus (Lea)	38
Arcidens confragosus (Say)	14
**Lasmigona complanata* (Barnes)	3
***Lasmigona compressa* (Lea)	25
Lasmigona costata (Raf.)	8
***Lasmigona subviridis* (Conrad)	2
**Strophitus rugosus* (Swainson)	64
Strophitus undulatus (Say)	9
	479
Lampsilinae (41 species; 14 genera)	
**Actinonaias ellipsiformis* (Conrad)	206
Carunculina corvunculus (Lea)	6
***Carunculina parva* (Barnes)	14
Carunculina vesicularis (Lea)	15
Dysnomia compacta (Lea)	1
Dysnomia triquetra (Raf.)	8
Lampsilis anodontoides (Lea)	10
Lampsilis anodontoides floridensis (Lea)	1
**Lampsilis cariosa* (Say)	7
Lampsilis claibornensis (Lea)	27
Lampsilis clarkiana (Lea)	1
Lampsilis dolabraeformis (Lea)	5
Lampsilis excavata (Lea)	7
Lampsilis fasciola (Raf.)	44
Lampsilis hydiana (Lea)	6
Lampsilis siliquoidea (Barnes)	41
Lampsilis siliquoidea rosacea (DeKay)	18
Lampsilis splendida (Lea)	11
Lampsilis subangulata (Lea)	6
Lampsilis tampicoensis (Lea)	6
Lampsilis ventricosa (Barnes)	20
Lampsilis ventricosa cohongoronta (Ort.)	8
Leptodea fragilis (Raf.)	18
**Leptodea laevissima* (Lea)	72
Ligumia nasuta (Say)	26
Medionidus simpsonianus Walker	9
Obliquaria reflexa Rafinesque	10
Obovaria subrotunda (Raf.)	3
Plagiola lineolata (Raf.)	5
**Proptera alata* (Say)	14

Table 1 (contd.)

Species	Nos. sectioned
Lampsilinae (contd.)	
Proptera purpurata (Lamarck)	2
**Ptychobranchus fasciolaris* (Raf.)	22
**Ptychobranchus subtentum* (Say)	18
Truncilla donaciformis (Lea)	11
Truncilla truncata (Raf.)	1
Villosa (Micromya) fabalis (Lea)	4
**Villosa (Micromya) iris* (Lea)	77
Villosa (Micromya) lienosa (Conrad)	11
Villosa (Micromya) nebulosa (Conrad)	4
Villosa (Micromya) ogeecheensis (Conrad)	9
Villosa (Micromya) vibex (Conrad)	17
	801
	1,871

*Occasionally hermaphrodites

**Dominantly hermaphrodites

3). Some of these species are discussed in the following. Data illustrating the gonadal picture in 27 specimens belonging to 23 species or forms are given in the legends to the figures.

I. Margaritanidae

Margaritifera margaritifera
(Linnaeus)
Fig. 4

This long-lived circumpolar pearl producing mussel is interesting in several respects. Comfort (1957) wrote: "If the 100-year estimate of longevity in *M. margaritifera* (L.) is correct, it is the longest-lived invertebrate known. A life span of this order in the wild would imply an exceedingly low adult mortality." Subsequently Hendelberg (1960) reported that the species could live, at least, 116 years. As already indicated, Schierholz (quoted by Pelseneer, 1920) found 1 hermaphrodite among 80 specimens from northern Germany that he sectioned, while Hendelberg (1960) failed to find any in a series of 20 specimens from arctic Sweden.

In 1962 I collected *Margaritifera* from Pole Cat Creek in Yellowstone National Park, Wyoming, U.S.A. One of a series of 12 specimens sectioned was hermaphroditic (Fig. 4).

II. Unionidae

a. Unioninae

Paraffin sections were made of 567 specimens of this subfamily, representing 34 species. While none were found to be regularly hermaphroditic, 9 were found to be occasionally so, as detailed in Tables 1 and 3. Ortmann (1912) had already clearly stated that most of the Unioninae had separate sexes. He also noted that the gonadal tissues of these mussels were highly colored, showing various tints of orange, pink or bright crimson. While it has been stated that this coloring is associated with egg production, Ortmann's studies (: 244) would indicate that the color may be found in males as well as females. He asserts that there is "no relation of these colors to sex." My own observations corroborate his statement.

Fusconaia flava
(Rafinesque)
Figs. 8, 9

So far as I can determine, Sterki (1898) was the first and only one to indicate that this species "had a few acini producing ova in the gonad charged with copious sperm." The distinction, he explained, was particularly easy because of the bright crimson color of the ova. The animal's visceral mass indeed often shows a striking coloration. In the spring of 1962, a large collection of *Fusconaia flava* was made in the headwaters of the Grand River in Michigan. Some animals in this series were orange, others white. When an equal number of each were sectioned, the proportion of males and females was about equal, which tends to support the view that visceral coloration is not associated with sex. The hermaphroditic individuals figured were taken in 1959 and 1960 from Ore Creek, a tributary in the Saginaw drainage.

b. Anodontinae

In this subfamily 479 specimens representing 20 species were sectioned (Table 1). Of these, 8 species had hermaphroditic gonads: in 3 of these species or forms the condition was found to be dominant (Tables 1, 2); in the 5 others the condition is rare (Tables 1, 3). Four of the species showing hermaphroditism are discussed below.

Anodonta imbecillis Say[4]
Fig. 1

Again Sterki (1898) was the first to notice that all of the specimens of *Anodonta imbecillis* he examined were gravid. He found "ova and sperma in various proportions." The species is reported to be dominantly monoecious. It is also of interest that 3 characteristics, i.e., the hermaphroditic state, the lack of elevated umbones and the supposed metamorphosis without parasitism, induced F. C. Baker (1927) to establish the genus *Utterbackia*. However, Mary Tucker (1928) showed clearly that *Anodonta imbecillis* does have a normal fish host, the green sunfish, *Apomotis cyanellus*.

Many years ago, (1940) I made serial sections of specimens of this species from the Ann Arbor, Michigan, area. It was evident that the acini composing the male elements were characteristically located along the sides of the visceral mass and were not as widely distributed as the acini containing the eggs. More recently I examined animals considered to belong to this same species, from Hillsboro River in Florida. It came somewhat as a surprise to find that the sexes of that population were separate. In a recent paper, Johnson (1965) reports a hitherto unrecognized species of *Anodonta*, which he calls *A. peggyae*, also giving Hillsboro River as one of the localities. This report suggests that the difference in the sexual condition observed between the northern and southern forms, thought to be one of geographical strain, might even be specific, a moot point. Johnson, incidentally, corrects the spelling of the specific name *imbecillis* to *imbecilis*.

Anodonta grandis footiana (Lea)
Fig. 15

Observations by Boycott and Oldham led Bloomer (1930, 1934, 1935, 1939) to extensively investigate the sex conditions of *Anodonta cygnea* (L.) in the British isles. From the structure of the gonad he suspected possible sex reversal (1934). Studying the ratios of males, females and hermaphrodites in various populations (1939) he found these constant for, but varying between, populations. His stimulating papers aroused our curiosity and our interest in *Anodonta grandis* Say, the most common North American species, about which, in contrast to *A. imbecillis*, no information was available. As reported by van der Schalie & Locke (1941), gonads of a lake form of this species, *A. grandis footiana* were sectioned and hermaphroditism was

[4]The related species *Anodonta henryana* Lea and *A. gibbosa* Say have not been sectioned in this study, but from preliminary examination it would seem that they are not monoecious.

TABLE 2. The only North American naiades in which hermaphroditism is the dominant condition

Families	Species
MARGARITANIDAE	none
UNIONIDAE:	
Unioninae	none
Anodontinae	*Anodonta imbecillis* Say (Fig. 1) *Lasmigona compressa* (Lea) (Fig. 2) *Lasmigona subviridis* (Conrad)
Lampsilinae	*Carunculina parva* (Barnes) (Fig. 3)

TABLE 3. Species of North American naiades in which hermaphrodites were occasionally found

MARGARITANIDAE

Margaritifera margaritifera (Linn.) (Fig. 4)

UNIONIDAE

Unioninae

Elliptio dilatatus (Raf.) (Figs. 5, 6)
Elliptio productus (Conrad) (Fig. 7)
Fusconaia flava (Raf.) (Figs. 8, 9)
Fusconaia ebenus (Lea)
Gonidea angulata (Lea) (Fig. 17)
Pleurobema cordatum (Raf.)
Pleurobema cordatum coccineum (Conrad) (Figs. 10, 11)
Quadrula quadrula Raf.
Tritogonia verrucosa (Say) (Fig. 12)

Anodontinae

Alasmidonta marginata (Say) (Figs. 13, 14)
Anodonta corpulenta Cooper (Fig. 16)
Anodonta grandis footiana (Lea) (Fig. 15)
Lasmigona complanata (Barnes) (Fig. 18)
Strophitus rugosus (Swainson) (Fig. 19)

Lampsilinae

Actiononaias ellipsiformis(Conrad) (Figs. 20, 21)
Lampsilis cariosa (Say) (Fig. 22)
Leptodea laevissima (Lea) (Fig. 23)
Proptera alata (Say) (Fig. 24)
Ptychobranchus fasciolaris (Raf.) (Fig. 25)
Ptychobranchus subtentum (Say) (Fig. 26)
Villosa (*Micromya*) *iris* (Lea) (Fig. 27)

FIGS. 1 - 9. Gonadial tissues of some North American naiades showing various degrees of hermaphroditism (stain: haematoxylin and eosin).

FIG. 1. *Anodonta imbecillis* (Say). Huron River, above Ypsilanti, Washtenaw Co., Michigan. May 25, 1940. Henry van der Schalie, Collector. Specimen: 5 years old. Normal hermaphrodite with male and female tissues separated so that male gonad is found along the upper and outer sides of the visceral mass. (Original photomicrograph taken at X 100).

FIG. 2. *Lasmigona compressa* (Lea). Ore Creek, 5 mi. below Hartland, Michigan. June 9, 1959. Henry van der Schalie, Collector. Specimen: 82 mm long, 5 years old, gravid. A typical and normal hermaphrodite with eggs in one follicle and sperm developed in another. (Taken at X 125).

FIG. 3. *Carunculina parva* (Barnes). Tennessee River, Station 3, near New Johnsonville, Tennessee. October 16, 1964. John M. Bates, Collector. Specimen: 27.5 mm long, 8 years old, not gravid. A normal hermaphrodite with male and female follicles separate. (Taken at X 125).

FIG. 4. *Margaritifera margaritifera* (L.). Pole Cat Creek, just south of Yellowstone Park, Wyoming. August 15, 1962. Henry van der Schalie, Collector. Specimen: 34 mm long, 5 years old, not gravid. Note that male and female follicles are separate. (Taken at X 125).

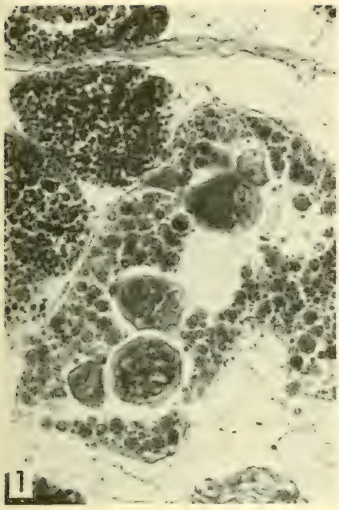
FIG. 5. *Elliptio dilatatus* (Raf.). Cranberry Creek, Byron, Shiwassee Co., Michigan. June 5, 1961. Henry van der Schalie, Collector. Specimen: 67 mm long, 8 years old, not gravid. Mainly female, but with male tissue developing in female follicles; eggs seem to be developing normally. (Taken at X 125).

FIG. 6. *Elliptio dilatatus* (Raf.). French Creek, trib. Allegheny River, 5 mi. north of Meadville, Pennsylvania. July 17, 1961. MacKenzie Keith, Collector. Specimen: 4 years old, 61 mm long, gravid. Spermatogenesis clearly evident in female follicles. (Taken at X 125).

FIG. 7. *Elliptio productus* (Conrad). Savannah River, above Route 301 bridge, south of Allendale, S. Carolina. June 24, 1964. John M. Bates, Collector. Specimen: 59 mm long, 6 years old, not gravid. A small amount of normal female tissue present in a preponderantly male specimen. (Taken at X 125).

FIG. 8. *Fusconaia flava* (Raf.). Ore Creek, 1 mi. northwest of Hartland, Livingston Co., Michigan. May 22, 1960. Henry van der Schalie, Collector. Specimen: 74 mm long, 12 years old, not gravid. A female with only a small amount of spermatogenesis in wall of follicles. (Taken at X 125).

FIG. 9. *Fusconaia flava* (Raf.). Ore Creek at Clyde Road, below Hartland, Livingston Co., Michigan. June 25, 1959. Henry van der Schalie, Collector. Specimen: 68 mm, 11 years old, not gravid; predominantly male with only small foci of female tissue and eggs tending to be suppressed. (Taken at X 100).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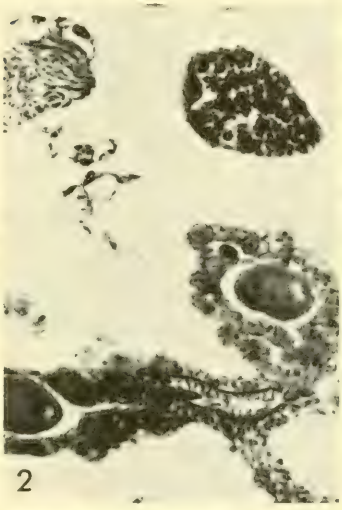
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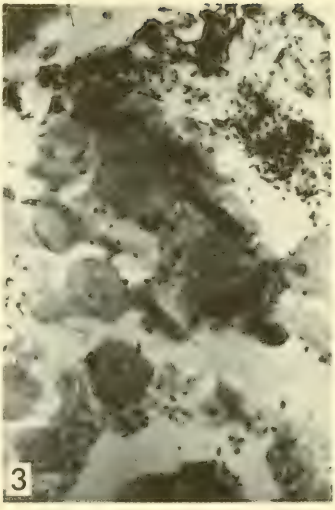
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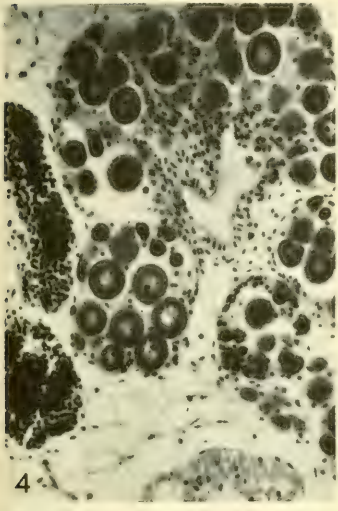
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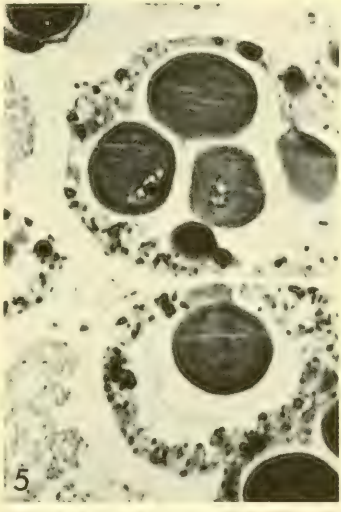
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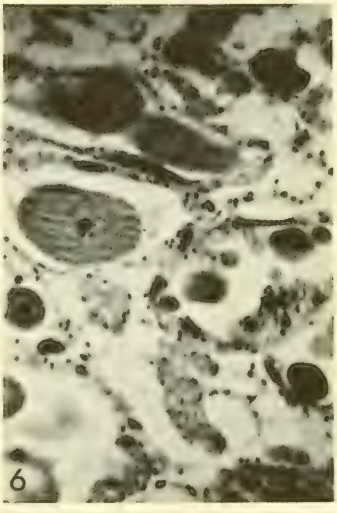
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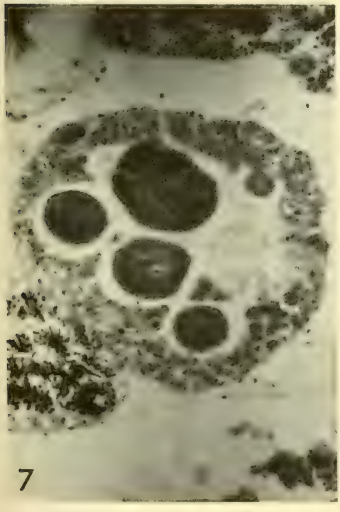
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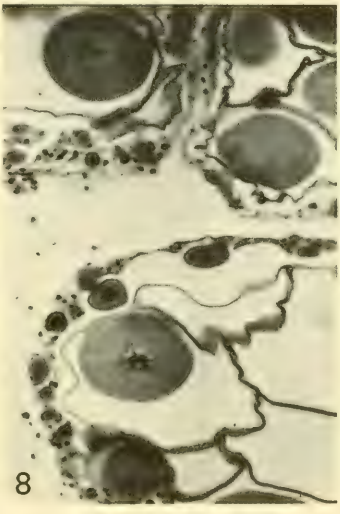
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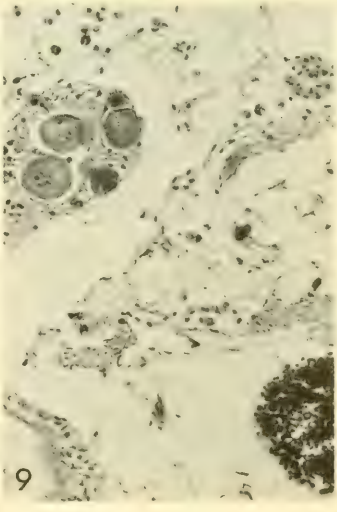
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FIGS. 10-18. Gonadial tissues of some North American naiades showing various degrees of hermaphroditism (stain: haematoxylin and eosin).

FIG. 10. *Pleurobema cordatum coccineum* (Conrad). South branch Cranberry Creek at Byron, Shiawassee Co., Michigan. Nov. 21, 1960. Henry van der Schalie, Collector. Specimen: 35 mm long, 3 years old, not gravid; mostly female tissue with only a small amount of discrete male follicles. (Original photomicrograph taken at X 100).

FIG. 11. *Pleurobema cordatum* (Raf.). Tennessee River, above New Johnsonville, Tennessee. Nov. 11, 1963. John M. Bates, Collector. Specimen: 80 mm long, 17 years old, not gravid; appears to be about half male and half female with eggs poorly developed in follicles with spermatogenesis in walls. (Taken at X 100).

FIG. 12. *Tritogonia verrucosa* (Raf.). Guadalupe River, 1/2 mi. west of Sequin, Guadalupe Co., Texas. August 22, 1962. John M. Bates, Collector. Specimen: 66 mm long, 5 years old, not gravid; mainly female with patches showing spermatogenesis. (Taken at X 125).

FIG. 13. *Alasmidonta marginata* (Say). River Raisin, Sharon Hollow, Washtenaw Co., Michigan. July 20, 1962. Henry van der Schalie, Collector. Specimen: 41 mm long, 3 years old, not gravid; evidently a female with patches of sperm developing in walls of follicles; eggs do not seem normal in development. (Taken at X 125).

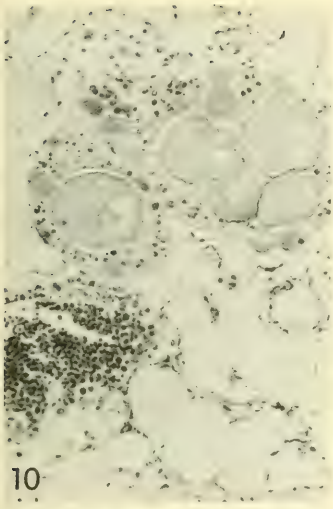
FIG. 14. *Alasmidonta marginata* (Say). Powell River, at U.S. 25 E, Claiborne Co., Tennessee. June 23, 1961. B. Dazo and H. van der Schalie, Collectors. Specimen: 62 mm long, 10 years old, not gravid; evidently sex quite mixed so that many egg follicles have spermatogenesis in walls with eggs often suppressed in development. (Taken at X 125).

FIG. 15. *Anodonta grandis footiana* (Lea). Zukey Lake, Lakeland, Livingston Co., Michigan. May 11, 1940. Henry van der Schalie, Collector. Specimen: 7 years old; mostly male with only small amount of female tissue which seems to be normal in development. (Taken at X 125).

FIG. 16. *Anodonta corpulenta* Cooper. Tennessee River, slough along river at mile 97.7, near New Johnsonville, Tennessee. October 16, 1964. John M. Bates, Collector. Specimen: 81 mm long, 5 years old, gravid; eggs do not appear to be developing normally and spermatogenesis appears in walls of some follicles. (Taken at X 125).

FIG. 17. *Gonidea angulata* (Lea). Snake River, near Bliss, Idaho. August 18, 1962. Henry van der Schalie, Collector. Specimen: 117 mm long, 15 years old, not gravid; a typical hermaphrodite with both male and female tissues well developed. (Taken at X 125).

FIG. 18. *Lasmigona complanata* (Barnes). River Rouge, Michigan. October 1, 1962. Carol Geake, Collector. Specimen: 170 mm long, 12 years old, gravid; the gonad appears to be mostly female but with scattered spermatogenesis in the walls of many follicles. (Taken at X 125).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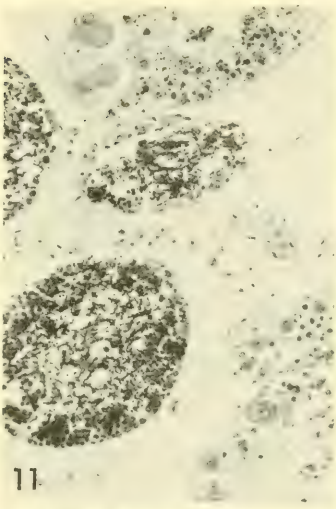
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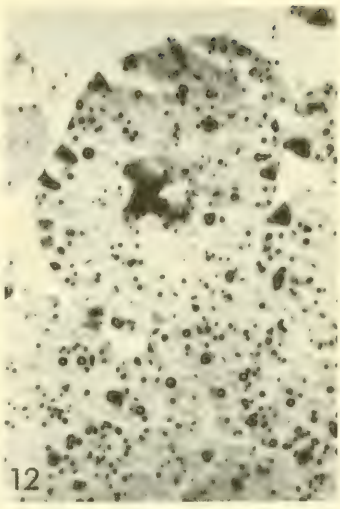
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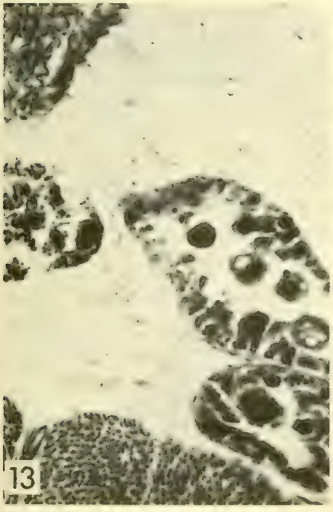
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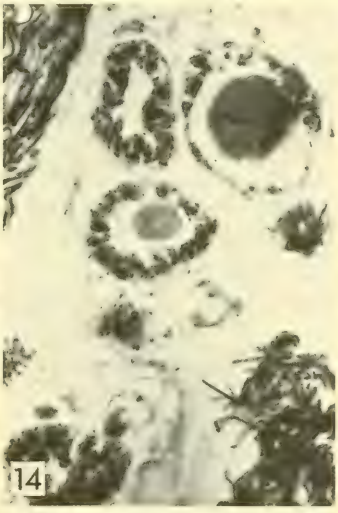
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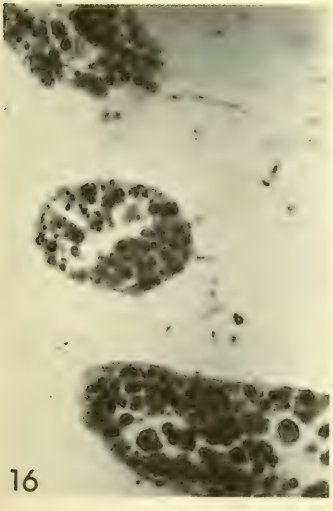
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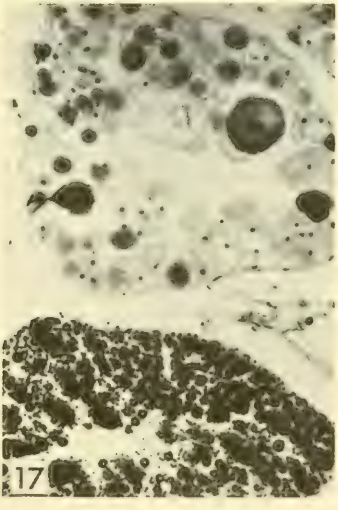
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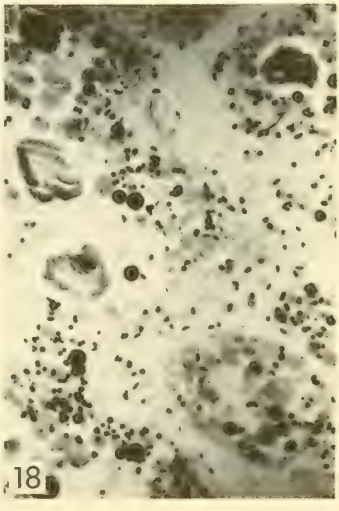
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FIGS. 19-27. Gonadial tissues of some North American naiades showing various degrees of hermaphroditism (stain: haematoxylin and eosin).

FIG. 19. *Strophitus rugosus* (Swainson). Inlet to Zukey Lake, Livingston Co., Michigan. July 14, 1960. Bonifacio Dazo, Collector. Specimen: 56 mm long, 4 years old, gills not clear as to gravid state; mostly male with only a small amount of female tissue. (Original photomicrograph taken at X 125).

FIGS. 20 & 21. *Actinonaias ellipsiformis* (Conrad). Ore Creek, at Clyde Road, near Hartland, Livingston Co., Michigan. Henry van der Schalie, Collector. Specimen: 67 mm long, 10 years old, not gravid; one of most unusual hermaphrodites observed in that male and female tissues quite thoroughly mixed. (Taken at X 125).

FIG. 22. *Lampsilis cariosa* (Say). Potomac River, Point of Rocks, near Frederick, Maryland. September 22, 1962. John M. Bates, Collector. Specimen: 100 mm long, 8 years old, not gravid; eggs in poor development but in discrete follicles; some spermatogenesis in walls of poorly developed female follicles. (Taken at X 125).

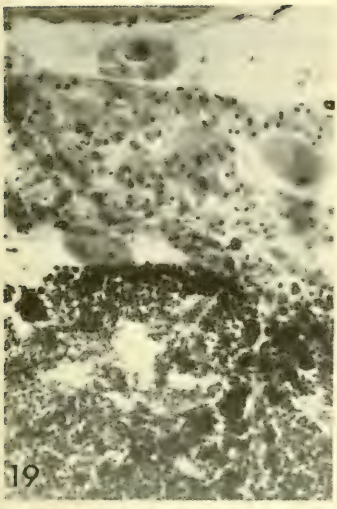
FIG. 23. *Leptodea laevissima* (Lea). Tennessee River, at mile 97.7 near New Johnsonville, Tennessee. October 16, 1964. John M. Bates, Collector. Specimen: 55 mm long, 3 years old, gravid; mostly female but with small foci of what appears to be developing sperm. (Taken at X 125).

FIG. 24. *Proptera alata* (Say). Lake Erie, at 32 feet depth near Middle Sister Island, Ohio. August 22, 1962. Yarl Hiltunen, Collector. Specimen: 66 mm long, 5 years old, gravid; mainly female tissue but with a hermaphroditic trend shown by an incipient spermatogenesis. (Taken at X 100).

FIG. 25. *Ptychobranchus fasciolaris* (Raf.). Little Portage River, above Toma Road, Washtenaw Co., Michigan. Bonifacio Dazo, Collector. Specimen: 69 mm long, 9 years old, gravid; mainly female but with small areas of spermatogenesis scattered throughout the glandular masses. (Taken at X 125).

FIG. 26. *Ptychobranchus subtentum* (Say). Powell River, at U.S. 23 E, Claiborne Co., Tennessee. August 23, 1961. B. Dazo and H. van der Schalie, Collectors. Specimen: 82 mm long, 15 years old, not gravid; a female with clear-cut patches of male tissue with follicles showing poor development of eggs. (Taken at X 125).

FIG. 27. *Villosa (Micromya) iris* (Lea). River Raisin, Sharon Hollow, Washtenaw Co., Michigan. July 20, 1962. Norman Reigle, Collector. Specimen: 33 mm long, 3 years old; female with gills about spent; mainly female, but with unusually abundant spermatogenesis appearing in walls of many female follicles. (Taken at X 100).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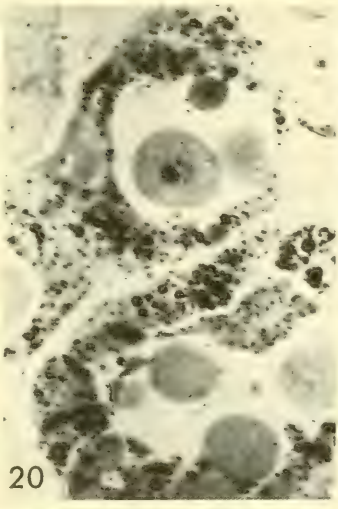
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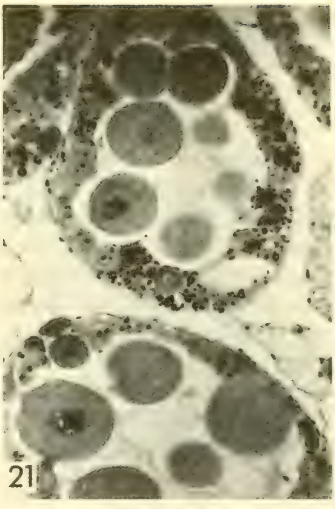
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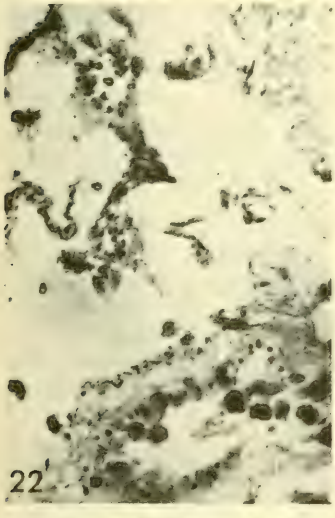
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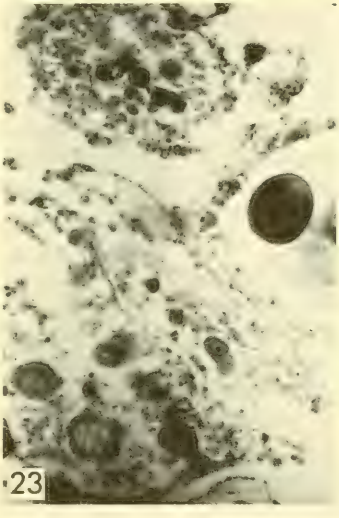
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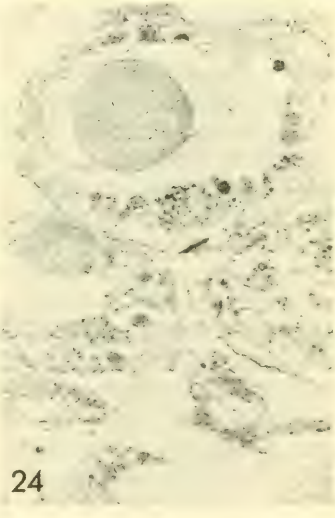
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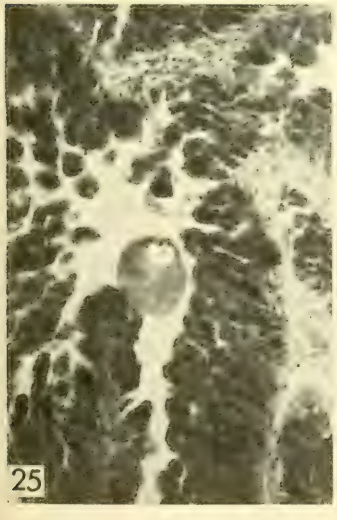
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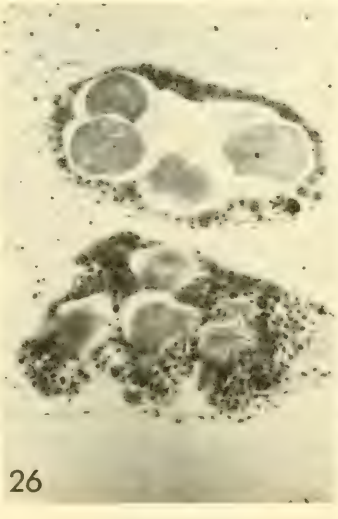
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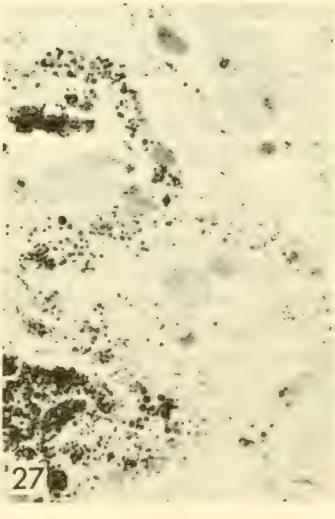
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demonstrated in 2 out of 14 specimens.

Lasmigona compressa (Lea) and *L. subviridis* (Conrad)
Fig. 2

All 25 specimens of *Lasmigona compressa* collected from several creeks in Michigan were hermaphroditic. This species is widespread and unique in that it is able to occupy very minute creeks and streams - places in which often no other mussels are found.

A closely related eastern species of similar ecology, *L. subviridis*, has also been found for the first time to be dominantly hermaphroditic (2 out of 2 examined). The relationship of these 2 species is uncertain.

Strophitus rugosus (Swainson)
Fig. 19

Among others, a series of 64 specimens was collected in a creek connecting 2 lakes in Livingston County, Michigan, in every month of the year. The hermaphroditic condition was observed in only 1 specimen. There was a clear-cut separation between the male and female tissues. The animal was collected on July 14, 1960, and there were sufficient eggs in a normal state to indicate that the specimen was a functional hermaphrodite.

c. Lampsilinae

In this subfamily 801 specimens representing 41 species were sectioned (Table 1); 8 species belonging to 7 genera were found to be hermaphroditic; one, *Carunculina parva* was regularly ambisexual (Tables 1, 2) and 7 species were occasionally so (Tables 1, 3).

Carunculina parva (Barnes)[5]
Fig. 3

Hermaphroditism in this species was reported at an early date (Sterki, 1898). Tepe (1943) carefully studied the histology of the gonads. He reported the occasional presence of hermaphroditic acini that contained eggs as well as sperm and made the following statement regarding this condition:

"In most instances it was observed that eggs enclosed in male follicles were smaller (20-24 microns) than eggs from strictly female follicles (40-100 microns). The eggs in essentially male follicles were free from germinal epithelium, and their small size does not seem to indicate immaturity. Both eggs and spermatozoa appeared mature in all the individuals, which would seem to indicate that this hermaphroditic condition does not represent a phase in a periodic sex reversal."

Our studies on 14 individuals from the Tennessee River show essentially the same conditions. All individuals examined were hermaphrodites; 2 of them also had acini with both eggs and sperm.

Actionaias ellipsiformis (Conrad)
Figs. 20, 21

In an earlier study (H. & A. van der Schalie, 1963) some 200 specimens of this species were collected over an extended period. It was found that the gonads remained undifferentiated for the first 2 years. All specimens 2 years old or older were either distinctly male or female, except for one hermaphrodite. This specimen was the largest (68 mm) of a series of 25 individuals taken late in June from Ore Creek, Livingston Co., Michigan, of which 13 were gravid and 12 non-gravid. It was originally considered a female because the lower posterior portion of the outer gill showed a small amount of marsupial tissue. At that time the animal was reaching the end of the spring glochidial shedding period, but there was enough gill modification to show it was functioning as a female. Its hermaphroditic condition was not discovered until the gonads were sectioned, when it was found

[5]Two other species of *Carunculina*, *C. corvunculus* (Lea) and *C. vesicularis* (Lea), collected in southern states, were not found to be monoecious.

that male and female tissue was quite thoroughly mixed.[6] This mussel, with 10 annuli on the shell, was the oldest of the series. On the chance that this hermaphroditic condition might be associated with senescence, the other large specimens of this series were reexamined, but results were negative.

Villosa (*Micromya*) *iris* (Lea)
Fig. 27

A specimen of this species has also been found to have similarly mixed gonad tissue,[6] simultaneously producing eggs and sperm.

DISCUSSION

Hermaphroditism in mollusks is supposed to be derived from an originally dioecious condition. Some authors emphasize that the condition tends to appear in situations when the animal is confronted with difficulties in its normal reproductive activity. Hence hermaphroditism might be an adaptive mechanism, giving the species some evolutionary advantage.

Now that almost 100 North American naiad species have been studied, it has become evident that among this large and highly evolved group relatively few are regularly hermaphroditic. Essentially the situation is similar to that in the marine lamellibranchs in which also there are comparatively few species that are monoecious. Among the naiades, only the Anodontinae and the Lampsilinae appear to have species in which the condition occurs regularly and only 4 species are involved: 3 in the former subgenus and 1 in the latter. All of the sporadic cases that were detected in 22 species or forms clearly belong to the category that Coe (1943: 156) considered as accidental or developmental ambisexuality. Under this heading he stated:

"Even in species which are otherwise strictly of separate sexes there may be an occasional individual with functional hermaphroditism. These can all be considered as resulting from deviations in the developmental processes due to a failure of the sex-differentiating mechanism to function normally. The proportion of spermatogenic and ovogenic tissues in the gonad is highly variable, some individuals having approximately equal parts of both sexual types, while others are principally one sex, with but few cells characteristic of the opposite sex. This type of sexuality is more common in the pelecypods than in most other groups of animals and it occurs frequently in young individuals at the first reproductive season. In certain local races of oviparous oysters, clams and mussels it is possible to determine whether the initial sexual phase is normal or accidental."

In the present study specimens from species found to be regularly hermaphroditic presented a "normal" histological picture, with male and female tissues, resp. acini separate, a situation that was also encountered in *Margaritana*, *Strophitus* and *Gonidea*. The other occasional hermaphrodites, however, were as a rule predominantly of one sex, with only some tissue or cells of the other sex developing in or among the follicles of the dominant sex.

The various occasional hermaphrodites detected were certainly not restricted to, or prevalent in, young individuals. But Coe does not quote only age as a factor connected with modification of the sexual state. Temperature, resp. season, and several other factors have also been incriminated. Thus, for instance, nutritional disturbances of the Bombay oyster apparently resulted in an increased proportion of males, whereas in years and locations favoring rapid growth, Virginia oysters had a large proportion of females. Habitat has been

[6]The unusual condition of the gonads of the 2 specimens here quoted has been recently discussed (van der Schalie, 1969). It was stressed that the simultaneous production of eggs and sperm is quite uncommon among freshwater mussels.

considered to play a role: Weisensee (1916: 292) claimed to have observed that the dioecious condition was normal for *Anodonta cygnea* living in rivers, while those living in impounded waters tended to be hermaphroditic.

In other instances variation is attributed to heredity per se: Coe (1943) reports races with different heredity in the Virginia oyster. Bloomer (1939) reports populations of *Anodonta cygnea* in which hermaphroditism was relatively more common than in others in a constant manner. From the findings reported in this survey, it appears quite possible that wide-ranging species, such as *Anodonta imbecillis*, may not be hermaphroditic throughout their whole range, so that northern forms may differ in this respect from the southern representatives (?*A. peggyae*). Such a regional difference was recently shown to exist (van der Schalie, 1965) in a freshwater gastropod, *Campeloma*, which in the northern United States is parthenogenetic, no males being known from that region.

Though interesting to speculate on, Weisensee's contention as to a direct influence of the environment would, according to his own testimony, need much additional investigation before it could be plausibly substantiated. Although a wide cross-section of the North American mussel fauna has now been sampled, including mussels living in streams as well as in lakes, it has not been possible so far to demonstrate any environmental factor that would indicate any causal relation with sexuality. The extent of ambisexuality and the mechanisms producing it still remain open questions. Studies would need to be intensified so as to cover species in greater detail, i.e., at different ages, seasons and localities. Such investigations are not easy because gonad smears or sections must be made to discover hermaphroditism and ample material must be procured. While it would be of interest to explore factors (chemical, physical, etc.) that might perhaps serve to induce sex changes in the naiades, this group unfortunately does not lend itself readily to laboratory experiments. However, investigations are continuing. Arrangements have been made for the procurement of *Margaritana* from the Rocky Mountain regions of the U.S.A. during the active season of the year, and a study to determine the sex ratios of several commercially important mussels is being conducted by the University of Michigan in Kentucky Lake, Tennessee, and in the Muskingum River in Ohio.

ACKNOWLEDGEMENTS

Several of our staff and students assisted with preparing the thousands of paraffin blocks and cutting thin sections that made this investigation possible. Some of the sections were made by my wife, Annette; others were made by Khan Tandaraporn, Barbara Peckham, Susanne Pauly, Jane Phelps and Paula Levy. Colleagues and students generously contributed live specimens for proper fixation and preservation; among them mention should be made especially of John M. Bates, William H. Heard, Bonifacio Dazo and Robert Wakefield. The photographs were made with the assistance of Vera Farris, Louis P. Martonyi and Gene K. Lindsay.

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RÉSUMÉ

L'HERMAPHRODISME CHEZ LES MOULES D'EAU DOUCE D'AMÉRIQUE DU NORD

H. van der Schalie

Les informations sur l'existence de l'hermaphrodisme parmi les moules d'eau douce de la riche faune des U.S.A., sont fragmentaires. Dans cette étude, les gonades de 1871 exemplaires appartenant à 97 espèces et 32 genres ont été examinées histologiquement, par la technique des coupes à la paraffine. Seulement 4 espèces parmi 2 subfamilles des unionides se sont montrées essentiellement hermaphrodites (monoïques); 3 chez les Anodontinae: *Anodonta imbecillis*, *Lasmigona compressa* et (espèce toute proche) *L. subviridis;* 1 chez les Lampsilinae: *Carunculina parva.*

Des hermaphrodites accidentels ont été trouvés chez 22 autres espèces ou formes, appartenant à 17 genres et 2 familles. En général, de tels individus ont généralement un sexe dominant, avec seulement une faible quantité de tissus de l'autre sexe. Un spécimen ambisexué a été trouvé chez les Margaritanidae, chez *Margaritifera margaritifera*, parmi 24 spécimens sectionnés représentant 2 genres et espèces. Chez les Unionidae, des hermaphrodites accidentels se rencontrent dans les 3 subfamilles. Parmi les Unioninae, sur 567 spécimens (34 espèces, 11 genres) examinés, de tels individus ont été trouvés dans 9 espèces (ou formes) et 5 genres, soit: *Elliptio dilatatus*, *E. productus*, *Fusconaia ebenus*, *F. flava*, *Gonidea angulata*, *Pleurobema cordatum*, *P. c. coccineum*, *Quadrula quadrula* et *Tritogonia verrucosa.* Parmi les Anodontinae, sur un total de 479 spécimens (20 espèces, 5 genres) sectionnés, des hermaphrodites accidentels ont été mis en évidence chez 5 espèces appartenant à 5 genres, dont 2 sont des genres comportant aussi des espèces hermaphrodites; c.a.d. qu'ils se rencontrent chez: *Anodonta corpulenta*, *A. grandis footiana* et *Lasmigona complanata* ainsi que chez *Alasmidonta marginata* et *Strophitus rugosus.* Chez les Lampsilinae, avec un total de 801 spécimens (41 espèces, 14 genres) sectionnés, le phénomène a été à nouveau trouvé chez 7 espèces représentant 6 genres, c.a.d. chez: *Actinonaias ellipsiformis*, *Lampsilis cariosa*, *Leptodea laevissima*, *Proptera alata*, *Ptychobranchus fasciolaris*, *P. subtentum* et *Villosa* (*Micromya*) *iris.*

Ce relevé, à peu près complet des moules d'eau douce américaines, montre qu'elles sont généralement dioïques. La question reste toujours posée de savoir, si oui ou non, l'hermaphrodisme apparaît chez des animaux placés dans des conditions de milieu difficiles, comme cela a été antérieurement suggéré.

A. L.

RESUMEN

HERMAFRODITISMO EN ALMEJAS DE AGUA DULCE DE NORTE AMERICA

H. van der Schalie

La información existente acerca de la amplitud del hermafroditismo en la rica fauna de naiades de U.S.A. es fragmentaria. Para el presente estudio se examinaron las gonadas de 1871 ejemplares pertenecientes a 97 especies de 32 géneros, usando cortes de bloques de parafina. Sólo 4 especies, en dos subfamilias de uniónidos, mostraron ser dominantemente hermafroditas (monoicos); 3 en los Anodontinae: *Anodonta imbecillis*, *Lasmigona compressa* y (la estrechamente emparentada) *L. subviridis*, y 1 en los Lampsilinae: *Caranculina parva.*

En otras 22 especies o formas, pertenecientes a 17 géneros y 2 familias, se encontraron hermafroditas esporádicos. Usualmente estos individuos parecen ser predominantemente de un sexo, con sólo una pequeña cantidad de tejido gonadal del sexo opuesto. Un ejemplar ambisexual se encontró en Margaritanidae, en *Margaritifera margaritifera*, entre 24 ejemplares seccionados que representaban 2 géneros y especies. En los Unioninae, individuos accidentalmente monoicos aparecieron en las 3 subfamilias. Entre los Unioninae con 567 ejemplares (34 especies, 11 géneros) examinados, tales individuos se encontraron en 9 especies (o formas) de 6 géneros: *Elliptio di latatus*, *E. productus*, *Fusconaia ebenus*, *F. flava*, *Gonidea angulata*, *Pleurobema cordatum*, *P. c. coccineum*, *Quadrula quadrula*, y *Tritogonia verrucosa*. En los Anodontinae, con un total de 479 ejemplares (20 especies, 5 géneros) seccionados, hermafroditas esporádicos se mostraron en 5 especies de 4 géneros, de los cuales 2 géneros son los que también contenian las especies predominantemente hermafroditas; las 5 especis son: *Anodonta corpulenta*, *A. grandis footiana*, *Lasmigona complanata*, *Alasmidonta marginata* y *Strophitus rugosus*. En los Lampsilinae con un total de 801 especimenes (41 especies, 14 géneros) seccionados, la condición fue detectada en otras 7 especies representantes de 6 géneros: *Actinonaias ellipsiformis*, *Lampsilis cariosa*, *Leptodea laevissima*, *Proptera alata*, *Ptychobranchus fasciolaris*, *P. subternum* y *Villosa* (*Micromya*) *iris*.

Esta inspección de un caracter mas bien extensivo de los naiades americanos, muestra que ellos son generalmente dioicos. Queda aun por resolver la cuestión si el hermafroditismo aparece o no en los animales que confrontan condiciones ambientales dificiles.

J. J. P.

АБСТРАКТ

ГЕРМАФРОДИТИЗМ У СЕВЕРО-АМЕРИКАНСКИХ ПРЕСНОВОДНЫХ МОЛЛЮСКОВ

Г. ВАН-ДЕР ШЕЙЛИ

О гермафродитизме среди пресноводных наядид, фауна которых в США очень богата, известно очень мало. В настоящей статье рассматриваются результаты гистологического изучения гонад этих моллюсков, полученных от 1871 экземпляра 97 видов из 32 родов. Для срезов использовались парафиновые блоки.

Лишь 4 вида из 2 подсемейств унионид были преимущественно гермафродитными (однодомными). Это 3 вида из Anodontinae: *Anodonta imbecillis*, *Lasmigona compressa* и близкородственный *L. subviridis* и один вид из Lampsilinae *Carunculina parva*.

Спорадический гермафродитизм был отмечен у 22 видов или форм, относящихся к 17 родам и 2 семействам. Обычно такие особи с виду кажутся однополыми, лишь с небольшой частью гонады противоположного пола. Одна двуполая особь была найдена среди Маргаритинид- *Margaritifera margaritifera*, из 24 экземпляров, на которых были сделаны срезы, представляют 2 вида и вида. Из Unionidae случайно однодомные особи были встречены во всех трех подсемействах. Среди просмотренных 567 экземпляров (34 вида и 11 родов) такие особи были найдены у 9 видов (или форм) из 5 родов. Это: *Elliptio dilatatus*, *E. productus*, *Fusconaia ebenus*, *F. flava*, *Gonidea angulata*, *Pleurobema cordatum*, *P. c. coccineum*, *Quadrula quadrula* и *Tritogonia verrucosa*.

Из 479 изученных экземпляров Anodontinae (20 видов и 5 родов), спорадический гермафродитизм был отмечен у 5 видов из 4 родов. Из них 2 относились к родам, также имеющим преимущественно гермафродитные виды. Это: *Anodonta corpulenta A. grandis footiana* и *Lasmigona complanata*, а также *Alasmidonta marginata* и *Strophitus rugosus*. Из Lampsilinae был изучен 801 экземпляр (41 вида из 14 родов); указанные выше особенности отмечены у 7 видов из 6 родов, а именно: *Actinonaias elipsiformis, Lampsilis cariosa, Leptodea laevissima, Proptera alata, Ptychobranchus fasciolaris, P. subtentum* и *Villosa* (*Micromya*) *iris*.

Эти довольно экстенсивные исследования американских наядид показали, что они являются преимущественно раздельнополыми. Вопрос о том, появляется ли гермафродитизм у животных в трудных условиях существования, остается пока открытым.

Z. A. F.

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COMPARATIVE ECOLOGY OF THE SNAILS *PHYSA GYRINA* AND *PHYSA INTEGRA* (BASOMMATOPHORA: PHYSIDAE)[1,2]

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ABSTRACT

A comparative study was made on 2 freshwater pulmonate snails, *Physa gyrina* Say and *P. integra* Haldeman, in the Lake Okoboji area, Dickinson County, Iowa to investigate the local distribution of each species and its causes.

P. integra was found to be a characteristic inhabitant of rocky lake shores and of vegetated off-shore areas of lakes to depths of at least 3 meters, but was totally absent from ponds. Dense populations of *P. gyrina* were found in ponds, in rocky lake shore areas and in habitats of intermediate types, but always in very shallow water. In field populations of both species, growth and reproductive activity was greatest in the spring (April through June), there was considerable mortality during the summer, and growth was slight during the winter. *P. gyrina* was consistently the more rapidly growing species in field and laboratory, but laboratory grown *P. integra* usually reached reproductive maturity slightly sooner (often under 2 months). In the laboratory, both species produced an average of 200-300 eggs per snail per month during the peak period of reproduction (4 months in *P. gyrina,* 6 months in *P. integra*).

Stomach analyses and extensive laboratory observations on food preference suggest that both species consume a wide variety of food materials, determined chiefly by what can be scraped loose and ingested; food habits are not appreciably different. Dispersal rates of *P. gyrina* were significantly higher than those of *P. integra* in the laboratory and in the field. The 2 species behaved similarly under the following circumstances: in a temperature gradient chamber they moved away from the cold end (11° C) and tended to move toward, but not into, the heated end (38°-40° C); both moved freely through a wide range of temperatures. When wave action was heavy in rocky shore areas, they moved to the lower or otherwise protected surfaces of the stones. They came to the surface regularly for aerial breathing when in very shallow water. *P. integra* in deeper water, however, had the mantle cavity filled with water and could remain submerged throughout the life cycle.

P. gyrina can withstand high temperatures (35° and 40° C), and also the effects of drying, for a significantly longer period of time than can *P. integra*. Partly for this reason *P. integra* is excluded from ponds. The large size and rapid growth rate of *P. gyrina* with the resultant need for atmospheric oxygen, may limit this species in summer to very shallow water, while the smaller,

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[1]Adapted from a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Iowa.

[2]The work was supported through a National Science Foundation Cooperative Graduate Fellowship, 1961-63.

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slower-growing *P. integra* is not so restricted. *P. integra* may be restricted to the more stable conditions of lakes (as compared with ponds) partly also because of its slower growth rate, a potentially longer period of reproduction, and slower rate of dispersal in response to changing environmental conditions.

INTRODUCTION

In considering any species of animal in relation to its environment, the following questions arise: (1) Where is the animal found? (2) Why is it found in some habitats and not in others?

Comparative studies of closely related species are of value in dealing with these questions, because they lead us to determine what factors are limiting for one species but not for another. Where there are differences in geographic or local distribution between related species, explanations can be sought in terms of limiting factors. A comparative approach may guide us in choosing what factors to study.

Two species of freshwater pulmonate snails, *Physa gyrina* Say and *Physa integra* Haldeman, were chosen for this study with the above considerations in mind. The adults of the 2 species can be distinguished readily from external morphology alone. Both species occupy a wide geographic range centering broadly in the Great Lakes region of North America, and are common species in the Lake Okoboji area of northwest Iowa, where most of the field work for this study was done. In the study area, the 2 species are found together in rocky lake shore habitats. Only *P. gyrina* is found in ponds, and only *P. integra* in the vegetated offshore areas of lakes. The purpose of the investigation was to determine as precisely as possible the similarities and differences in local distribution in the 2 species, and to attempt to explain these similarities and differences.

The methods used include a wide variety of field and laboratory techniques. These will be described in some detail under the headings to which they pertain. Very briefly, the methods include: (1) qualitative and quantitative sampling in various habitats; (2) laboratory and field experiments designed to measure the behavior and tolerance of the 2 species in response to specific factors, such as food, temperature and drying; (3) life history studies in the field and the laboratory; and (4) observations, in field and laboratory, on locations, orientation and attributes of behavior of the 2 species.

The facilities of the Iowa Lakeside Laboratory, Milford, Iowa, were used for a large part of the work reported here.

THE TWO SPECIES

The taxonomy of the large genus *Physa*, at least in its North American representatives, is at present in a rather doubtful state. The statement of Goodrich & van der Schalie (1939), "No general rules have been laid down as yet that are helpful toward a certain and confident determination of the species of *Physa*," is still valid today. Baker (1928), in his monograph, *The Fresh-water Mollusca of Wisconsin*, describes some 50 species and varieties of *Physella* (= *Physa*). Wurtz (1949) suggests that a large proportion of these should be reduced to synonymy. With the vary large number of names associated with what may be only a relatively few species, the geographic and local distribution of any "species" of *Physa* is at best uncertain, and the proper label to attach cannot now be determined with certainty.

Geographic and Local Distribution

Baker (1928) states that *Physa gyrina* occurs "from the Arctic regions south to Alabama and Texas." Clench (1926) claims, on the other hand, that the species does not extend south of the Ohio River or southern Missouri. The catalogue of the mollusk collection at the University of Michigan has some listings for *P. gyrina* from points as divergent

as Nova Scotia and Prince Edward Island in the northeast to Florida in the southeast and California in the west. Whether these all represent correct listings is doubtful, but it can be said with some confidence that the species has an extensive geographic range.

Baker (1928) cites Crandall (1901) as giving the distribution of *P. integra* as "from the Great Lakes to the Gulf, occupying a belt from central Arkansas to central Kansas." He adds that it has not been reported from south of the Ohio River, but is common in several states from New York west to South Dakota. The University of Michigan collection has listings from such divergent areas as Quebec, New York, Alabama, Texas, Colorado, Wyoming, and N. W. Territory, Canada (Great Slave Lake). The limits of the range of this species are again uncertain, but the range is apparently extensive and covers much of the geographic area where *P. gyrina* may also be found.

Baker (1928) says of *P. gyrina* that "it appears to be characteristic of slow-moving and stagnant bodies of water, in shallow water, usually on a mud bottom." DeWitt (1955) describes the species as being "a typical inhabitant of temporary and permanent ponds." Listings for this species in the University of Michigan collection include a large number of entries from creeks, rivers, lakes and ponds. H. B. Baker (1922) gives some useful ecological notes on the species as it occurs in Dickinson County, Michigan, noting that it occurred abundantly in several stagnant, muck-bottomed ponds, along the marshy shore of a lake, and also in a stream with a rocky and gravel bottom and with a fairly swift current. Goodrich & van der Schalie (1939) also report on *P. gyrina* collected from several creeks, brooks, rivers, ponds and a lake, noting that many of the habitats were mucky and stagnant and were sometimes filled with aquatic vegetation. The picture that emerges is that this is primarily a pond species, but one which can also live in streams and lakes having a variety of other ecological conditions.

P. integra is found, according to Goodrich & van der Schalie (1944) "more often . . . in streams than in quiet waters." The same authors (1939) report this species from a number of creeks, rivers and brooks, at least some of these habitats having a stony or a gravel substratum. The University of Michigan collection has listings for *P. integra* from a large number of rivers, creeks and lakes. Baker (1928) reports it from lakes (including Green Bay, Lake Michigan), on substrata of mud, clay, sand, gravel or boulders, in water ranging from 5 cm to 3 m deep. H. B. Baker (1922) found the species on water lilies (*Nymphaea advens*) in a lake; he also records a "variety" of *P. integra* as being abundant along the shore of a river, in shallow water with a swift current and a substratum of sandy clay. The impression that emerges here is that this species lives in streams and lakes on a variety of substrata, but that, unlike *P. gyrina*, it is absent from ponds.

Both *P. gyrina* and *P. integra*[4] occur in abundance in the lakes area of northwest Iowa (Fig. 1). *P. gyrina*, at least, is common also in other parts of the state. The 2 species overlap in their distribution in lake habitats; my observations confirm *P. gyrina* as a characteristic pond inhabitant and *P. integra* as being absent from ponds. A full discussion of the local distribution of the 2 species will be presented under "Habitats" (p 130 ff.).

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[4]The latter species is listed in a recent paper by Bovbjerg & Ulmer (1960) as *Physa sayii*. Examination of numerous specimens, including the anatomy of the male genitalia, and of much of the relevant literature, has convinced me that this designation (and that of a similar form from Douglas Lake, Michigan, as *P. sayii crassa*) is in error. *P. sayii* appears to belong in a subgenus separate from these forms. (See p 119-121).

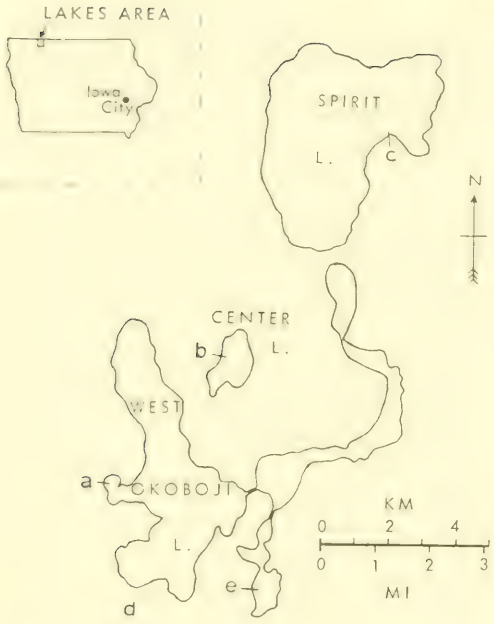

FIG. 1. Lakes area of northwestern Iowa (approximate location indicated on map, upper left) where much of this study was carried out. Several locations from which *Physa* were studied are: (a) Little Miller's Bay, West Okoboji Lake, Iowa Lakeside Laboratory; (b) western shore, Center Lake; (c) Big Stoney Point, Spirit Lake; (d) Garlock Slough; (e) Lower Gar Lake.

Morphology

Because of the confusion surrounding the taxonomy within the genus *Physa*, some discussion of the morphology of the 2 species is in order.

External Characteristics (Figs. 2, 3)

Adults of the 2 species differ in size, shape and color of shell and animal body. *P. gyrina* is the larger species. I have found a few specimens with shells up to 25 mm long, while a *P. integra* shell 14 mm long can be considered an unusually large one. Fig. 2 shows fairly large shells of adult *P. gyrina* (14-15 mm long) and *P. integra* (10-11 mm).

In *P. integra* the ratio of width to length of the shell is greater (see biometric analysis below). The body whorl and whorls of the spire are more convex and the "shoulder" between the spire and body whorl is also a characteristic difference from the rather smooth transition between these shell parts in *P. gyrina*.

The shell of *P. integra* is typically paler in color than is that of *P. gyrina*. The outer lip of the aperture is often thickened and whitish in the former species, and there may be additional white stripes ("rest marks" or varicose bands) running longitudinally elsewhere on the shell. The shell of *P. gyrina* not only is darker, but the thickenings of the lip of the aperture and elsewhere on the shell are, if present, dark brown.

The body of *P. integra* (Fig. 3), like the shell, is typically light-colored. The foot is often yellowish, and the body light-colored from above, though it often has a dark band over the dorsal part of the mantle which can be seen through the shell. In contrast, *P. gyrina* is typically quite heavily pigmented, both ventrally on the foot and through the shell dorsally. As these characters are highly variable for both species, they are not in themselves very reliable.

The most reliable criteria for distinguishing the 2 species by external morphology relate to width-length ratios, convexity of body whorls and whorls of spire (related to the more deeply impressed sutures between whorls in *P. integra*), and the degree of shouldering between body whorl and spire.

Biometric Analysis

Although average and maximum sizes were consistently greater for *P. gyrina* than for *P. integra*, sizes were too variable in both species to yield meaningful statistical comparisons. Data on width-length ratios, however, do provide meaningful comparisons.[5] Table 1 summarizes some of these data for the 2 species, along with information on habitats, number of snails in the samples, and size range of shells. Snails selected

[5]Tests of significance referred to in this paper were performed using the t distribution.

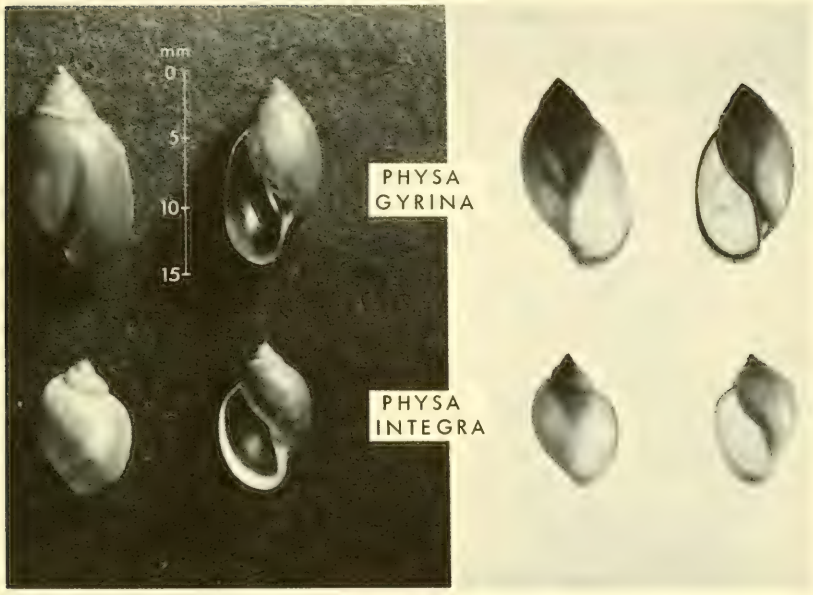

FIG. 2. Shells of the 2 species of *Physa*. Note the differences in size, shell shape, and convexity of the body whorl and whorls of the spire. Note also the whitish outer lip of the aperture of *P. integra* (2nd figure from lower left), and the dark outer lip of *P. gyrina* (upper extreme right figure).

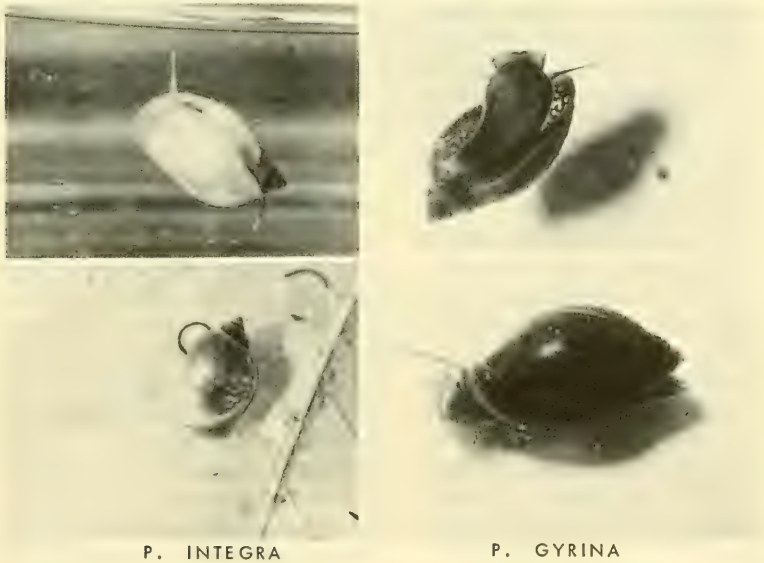

FIG. 3. Live specimens of the 2 species of *Physa*. Note the darker color, both dorsally and ventrally, of *P. gyrina*. Approximate shell lengths of snails: upper l., 10 mm; lower l., 8 mm; upper r., 12 mm; lower r., 16 mm.

TABLE 1. Biometrics

Species of *Physa*	Habitats*	Sample size	Shell length in mm	Width-length ratios of shells
P. integra	2 Lakes: (Center L. & Spirit L. - rocky shore area)	106	7.6 → 12.5 $\bar{X}$ = 9.7	0.65 ± 0.03**
	W. Okoboji L. (Little Miller's Bay - in offshore vegetation)	50	5.3 → 7.4 $\bar{X}$ = 6.0	0.63 ± 0.02
P. gyrina	2 Ponds: (Clear Creek & Garlock Slough)	154	9.6 → 24.2 $\bar{X}$ = 14.2	0.55 ± 0.02
	Spirit Lake (rocky shore area)	94	7.1 → 17.8 $\bar{X}$ = 9.6	0.59 ± 0.02
	W. Okoboji L. (Little Miller's Bay - periphery)	50	9.3 → 15.9 $\bar{X}$ = 11.0	0.59 ± 0.02

*See Fig. 1 for locations of these habitats.

**In the above table and elsewhere in this paper, the number following the ± sign indicates the standard deviation of the sample.

for measurement were representative samples of adult populations (shell length over 5 mm in *P. integra* and over 7 mm in *P. gyrina*) in the selected habitats. Measurements were made to the nearest 0.1 mm, using a vernier caliper.

Data are given on 5 samples of snails, 2 of *P. integra* and 3 of *P. gyrina;* width-length ratios vary somewhat within as well as between species. Analysis of the data shows a significant difference between species, and likewise between pond and lake populations of the same species in the case of *P. gyrina*.[6] The probability of any of these differences occurring by chance alone is in each case well under 0.001.

P. integra samples taken from Center Lake and Spirit Lake (Table 1) were analyzed separately and yielded nearly identical width-length ratios. The same is true of samples of *P. gyrina* from 2 ponds (Table 1), even though these ponds are nearly 300 miles (480 km) from each other (Clear Creek Pond near Iowa City, Garlock Slough adjacent to Lake Okoboji in northwest Iowa). Also, the width-length ratios of *P. gyrina* from one of these, Clear Creek Pond, were found to be identical in the following instances: (1) a May 1962 sample of 51 snails averaging 11 mm in length and ranging from 9.6 to 13 mm, and (2) a June 1962 sample of 65 snails averaging 17.5 mm and ranging from 15 to 24 mm in length. These data appear to conflict with DeWitt's (1954a) observation that, during growth in later life in this species, there is "a change from longitudinal to lateral expansion" of the shell.

Two conclusions can be drawn from these data: (1) There are clear-cut differences between the 2 species in width-length ratios, differences that are not only apparent subjectively but can also be revealed statistically. (2) Intra-specific differences in these ratios are also present, especially in *P. gyrina*.

[6]Comparable differences in these ratios in laboratory reared *P. gyrina* whose parents were collected, respectively, from a pond and from a lake, suggest that the difference in width-length ratio has, within this species, a genetic basis.

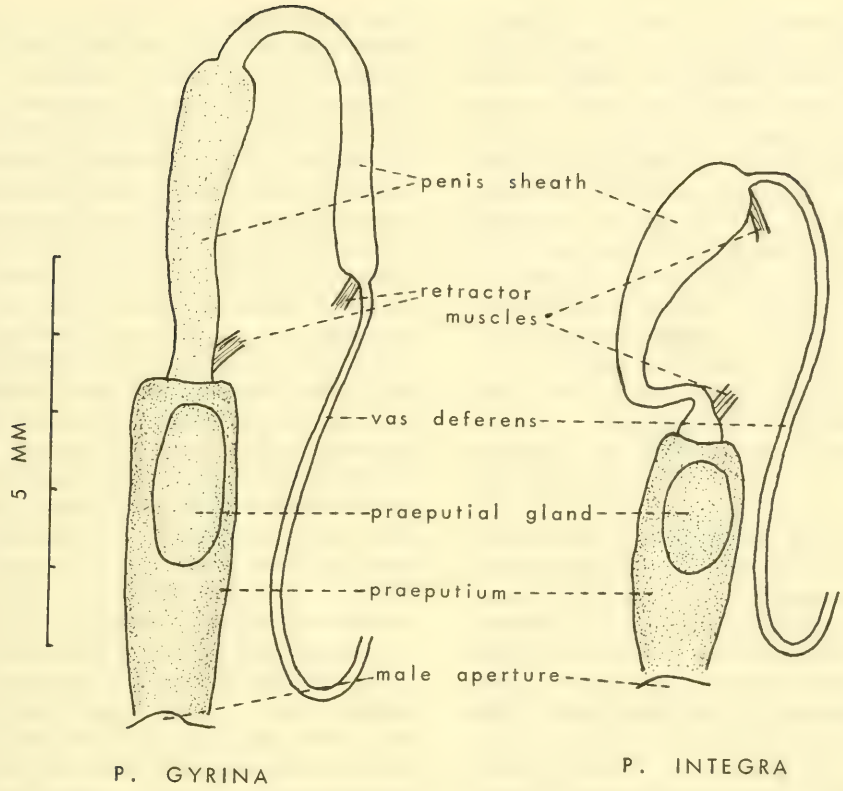

FIG. 4. Male genitalia of *Physa gyrina* and *P. integra* (anterior portion only), shell lengths 15 mm and 11 mm respectively. Note, in *P. gyrina,* the much longer penis sheath, composed of 2 distinct portions separated by a constriction, and the characteristic granular appearance of the basal portion. In *P. integra,* note the constriction and the characteristic kink near the base of the penis sheath.

Gross Anatomy of the Male Reproductive System (Fig. 4)

Differences in the male genitalia of the 2 species provided a useful criterion for checking identifications made initially on the basis of external characteristics. These structures can be exposed quite easily by making an incision on the left side of the animal behind and above the head. Dissections of the male genitalia of both species were made, from time to time, on more than 100 snails of all sizes and from various habitats. Although there were variations, especially those associated with differences in size and reproductive maturity, all specimens (except very small ones) could be placed with confidence in either of 2 categories on the basis of differences in length and form of the penis sheath, as illustrated in Fig. 4. In *P. gyrina* the penis sheath is elongated and has a prominent constriction between lower pigmented and upper portions; that of *P. integra* lacks the constriction, is shorter, lacks pigmentation, and typically has a sharp kink at its base. In none of the specimens did there appear to be intermediates between these 2 forms, and the features of external morphology and those of the male reproductive system consistently showed the expected correlation.

Subgeneric Systematics

The male genitalia provide a helpful criterion for species identification in *Physa*, but their use for this purpose has

definite limitations. A number of species resemble *P. gyrina* in having an elongated penis sheath with a prominent median constriction, while others are similar to *P. integra* in having a much shorter penis sheath without the constriction (Fig. 4; & Baker, 1928, Fig. 190). These differences in the length and form of the penis sheath may, however, provide a valid basis for grouping the majority of American species - certainly most of those in the Great Lakes region - into 2 subgenera. *P. gyrina* and *P. integra* would be representative of these subgenera.

The idea of subdividing the American *Physa* into subgenera is not new. Haldeman (1842) proposed names and defined the following subgeneric sections: *Physella*, "with branchiae, shell globose," with type *P. globosa; Physodon*, "columella toothed," with the type *P. microstoma; Diastropha*, "shell umbilicated, no fold." Baker (1926), while dismissing the characters given by Haldeman as trivial, thought it appropriate to retain the names *Physella* and *Physodon*, which he emended. Baker proposed that the name *Physella* should replace the name *Physa* in North America on the grounds that the North American forms differed anatomically from the European. Further, he proposed that the names *Physella* and *Physodon* be used also as subgeneric names, under the genus *Physella*. He described these subgenera (see below), and placed all of the Wisconsin species under one or the other of them.

Baker's (1926) use of the names *Physella* and *Physodon* was declared invalid by Clench (1930),[7] who added that there seemed to be no justification anatomically, as yet, to split the genus *Physa* - as represented by most of the European and American forms - "into groups worthy of generic or subgeneric headings." While granting the validity of the objections to Baker's use of the names *Physella* and *Physodon*, I believe that what the names designate are real entities. I base this opinion upon: (1) examinations, particularly of the male systems, of snails from some 50 different populations, mostly from Michigan and Iowa but including other scattered localities in the United States and Canada as well; (2) a study of Baker's (1928) illustrations and descriptions of this organ system. Shell characters as described below are highly variable and may be unreliable; the male genitalia, however, exhibit features which are conservative and, I believe, diagnostic for distinguishing major subgenera.

In Baker's subgenus *"Physella,"* the male system closely resembles that of *P. gyrina* (Fig. 4) in having a long penis sheath - often nearly twice the length of the praeputium - with a definite constriction midway along its length. Baker (1928) describes the group as follows: "Shell large, usually rather thin, the columella twisted and with a plait or ridge; genitalia with the penis sheath having a constriction in the middle dividing it into two parts." Based on the shells I have examined, I would add that there tends to be a rather smooth transition between body whorl and spire of the shell (Fig. 2, upper figures) and that the apex is often somewhat blunt. Baker (1928) gives descriptions, and in most instances figures, conforming to

[7]Clench (1930) states that an examination of Haldeman's original specimens of *P. globosa* - the type of *Physella* Haldeman, which Baker also selected - show them to be "materially different from any other known American *Physa*"; thus "the name *Physella* ... must be retained only for the single species *Physa* (*Physella*) *globosa*, and not be used in the generic sense for many of the North American forms. ... Haldeman's name *Physodon* (1842, p 39) and its emendation by Baker is untenable for subgeneric use as the main character for which the name was established, on the presence of columellar teeth, is not a constant character at all and at best can only be considered of specific value" (Clench, 1930).

the male genitalia as described above, for the following forms: *P. ancillaria* Say, *P. vinosa* Gould, *P. sayii* Tappan, *P. warreniana* Lea, *P. chetekensis* Baker, *P. bayfieldensis* Baker, *P. obrussoides* Baker, *P. gyrina* Say and *P. elliptica* Lea. I have similar evidence for some of the above plus the following: *P. parkeri* "Currier" DeCamp,[8] *P. magnalacustris* (Walker) and *P. remingtoni* Clench. Whether all of these forms represent valid species may be doubted (Wurtz, 1949). However, the available evidence, particularly that based on the male genitalia, suggests that the forms listed are part of a natural grouping.

In the subgenus "*Physodon*," as defined by Baker, the male system closely resembles that of *P. integra* (Fig. 4) in that the penis sheath is short - never much longer than the praeputium - and is not subdivided into 2 parts by a central constriction. Baker (1928) gives the following description: "Shell small, usually rather thick and solid, the columella smooth without distinct twisted plait; genitalia without constriction in center of penis sheath, which gradually enlarges." Again from my own observations, I would add that the shell usually has a shouldered appearance, with a very evident angle between body whorl and whorls of the spire, and that the apex of the spire is usually fairly sharp (Fig. 2, lower figures). Baker (1928) gives descriptions and figures conforming to the male system, as described above, for *P. integra* Haldeman and *P. walkeri* Crandall. I have additional evidence of the same type for *P. michiganensis* Clench and *P. anatina* Lea. All of the above forms are evidently representative of a natural grouping which differs in shell characters, and particularly in the male genitalia, from the "*Physella*" group.

In summary, Baker's (1928) concept of grouping the American species of *Physa* into 2 major subgenera appears to be basically sound. Further exploration of this concept, focussing initially on characters of the male genitalia, should aid us in gaining a better understanding of the systematics of this difficult group.

Life History

Considerable life history information is available on *P. gyrina* (DeWitt 1954a, b, c, 1955) and on other species of *Physa*, notably the European *Physa fontinalis* (Frömming, 1956; DeWit, 1955; Duncan, 1959; Hunter, 1961a, b). Reproduction, early development and fecundity have also been studied intensively in *P. gyrina* (DeWitt, 1954a, b, c) and the anatomy and physiology of the reproductive system in *P. fontinalis* (Duncan, 1958, 1959).

No such work is available for *P. integra*.

The aim of this section is twofold: (1) to report, for comparative purposes, the results of life history studies on both field and laboratory populations of *P. gyrina* and *P. integra;* and, while doing so, (2) to fill this particular gap in our knowledge concerning *P. integra*.

Scope and Techniques of Investigation

Comparative data were collected on times of breeding, length of reproductive periods, size composition of natural populations, growth rates, life spans and fertility (egg production) in the 2 species.

For securing field data, snails of both species were collected at monthly inter-

[8] Examination of *P. parkeri* specimens from Douglas Lake, Michigan, suggests a possible error in Baker's figure (1928, Fig. 186, p 422) of the male genitalia of this species; the penis sheath is actually - in these specimens - of the same basic type as in *P. gyrina*, rather than like that of *P. integra* as Baker's figure indicates.

vals from selected habitats by methods which are described in detail below (p 130). A special effort was made to get representative samples, including all sizes of snails and in representative proportions. Also, notes were made on the presence and abundance of egg masses at the sites of these collections each month.

To supplement the field data, snails of each species were cultured in small (5 liter) aquaria at room temperatures (averaging 20° - 23° C). Green lettuce and dried maple leaves were the usual food source. The aquaria were aerated continuously, and uniform and continuous illumination from overhead fluorescent lights was maintained.

All snails were measured with a vernier caliper, those in the laboratory being measured alive and then returned to the aquaria in which they were being cultured.

Field Populations

Little Miller's Bay *P. gyrina* and *P. integra:*

Life history studies were made on populations of both species in Little Miller's Bay, West Okoboji Lake, Dickinson County, Iowa (Fig. 5). The *P. gyrina* were from the extreme edge of the bay (station 1), where there was a sand substratum and much allochthonous material; there was some emergent vegetation, notably *Scirpus*. The *P. integra* were from station 5, 60 m from shore, water depth 1.8 m; the snails were on the dense growth of *Ceratophyllum demersum* and other submerged vascular plants above a substratum of mud (see p 135 for a brief description of the Little Miller's Bay area).

The *P. gyrina* population (Fig. 6) grew little during the winter, but showed rapid growth from April through June,[9] and produced many eggs in May and a new generation in June. There was considerable mortality among the larger snails,

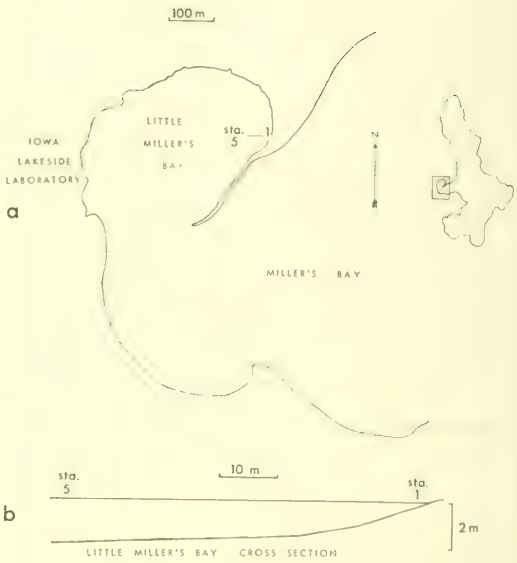

FIG. 5. a, The Little Miller's Bay study area in West Okoboji Lake (see Fig. 1 for geographic location). b, In the cross sectional diagram, vertical exaggeration is 2.5 x.

P. gyrina was dominant at station 1, along the east shore of the bay. Only *P. integra* was found at station 5, 60 m from shore, and in all the more central portions of the bay. Miller's Bay area map after that of D. M. Kelly (unpublished).

12 mm or more in length, in July and August.

In the *P. integra* population (Fig. 7) there was slight growth from March to April, but considerable growth from April to June. Egg production occurred in a great burst in May, and young snails (1-2 mm) were present in great numbers in June. There was much mortality of the larger snails, 4-8 mm long, by June, and all of this older generation were dead by July 1st. No more eggs were found at that time. Even with warmer water temperatures and continued growth of vegetation, the *P. integra* did not grow or reproduce as much during the summer as in the spring. However, there was

[9] For growth rates of various populations see p 126-130 & Fig. 10.

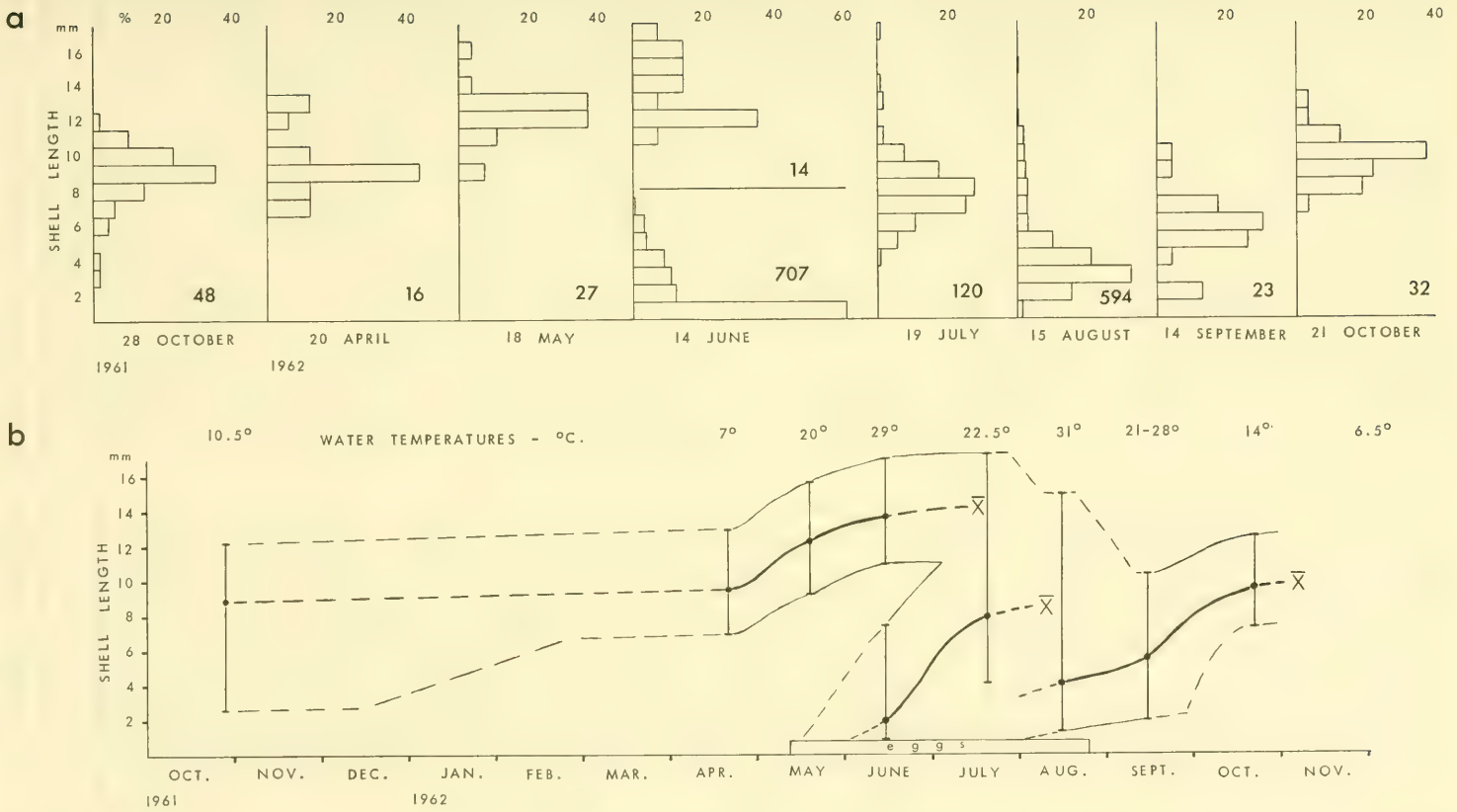

FIG. 6. Seasonal changes in shell size of *Physa gyrina* from station 1 (see Fig. 5), Little Miller's Bay. a, Relative proportions (%) of different sized snails, in shell length to nearest mm. From representative samples collected from October 1961 through October 1962. Numbers in bold face type (here and in Figs. 7 and 8) to the lower right of each graph represent total numbers of snails per sample. In June, young and adult components of the population are represented separately (divided by horizontal line), each as 100%. The young far exceeded the adults in absolute numbers. b, Same data as in a, presented as mean ($\bar{x}$) and range ($\dagger$) of shell size, showing monthly size changes throughout the year. Note water temperatures, and the spring and summer period of egg production (peak in May). Broken lines represent periods when exact nature of population changes is uncertain.

some egg production again in August and September, and many very young snails were found in September. Little or no growth occurred between October and February. The small maximum size (4-8 mm) and early mortality of the "adult" snails of this population may be atypical for *P. integra*. Such atypical features can perhaps be explained on the basis of peculiarities in the ecology of Little Miller's Bay, e.g., relative isolation of the bay and seasonal succession toward a vegetation-choked pond-like environment which becomes inhospitable for *P. integra* - particularly for the larger snails - by midsummer. Whatever the peculiarities of this life history pattern, it appears to have survival value for the population as a whole, in that the bay supports and maintains a large population of the species.

The life histories of these species are similar here in that both show a peak of growth and reproductive activity in the spring and early summer, suffer considerable mortality, particularly among the larger specimens, during the summer, and grow very little during the winter months. They differ in that *P. gyrina* have much faster growth rates (during the periods when they are actively growing) and attain much larger absolute sizes than do *P. integra*. Another difference was the 100% mortality of the older generation of *P. integra* by the end of June; such mortality did not occur in *P. gyrina* until July and August.

Clear Creek Pond *P. gyrina:*

For comparative purposes, life history data are presented on a pond population of *P. gyrina*. This pond, about 5 miles (8 km) west of Iowa City in Johnson County, Iowa, is small (about 50 m long and 30 m wide in the widest part), has a substratum of silt and clay, is bordered on 2 sides by a fairly open woodland, and by a cultivated field and a gravel road on the other 2 sides, and its basin is formed by part of an old ox-bow of Clear Creek; at times of flooding the overflow from the stream enters the pond. Environmental conditions, relating to depth and area covered by the water, temperature, turbidity, amount and character of the vegetation, animal life and other factors are extremely variable, much more so than in lake habitats. In depth, for example, the range was from a maximum of more than 1 m after a 20-cm (8-inch) rain in July 1962, to no water in September and October 1962. More typically, the depth ranged from about 30 to 60 cm, and the pond contained some water continuously from at least October 1961 to early September 1962. The small size of the pond, its constantly fluctuating conditions, and particularly the fact that the *P. gyrina* population was a thriving one during most of the period of study, make it desirable to compare the life history here with that in Lake Okoboji.

The Clear Creek Pond *P. gyrina* (Fig. 8) grew slightly during the winter (1961-62). A tremendous burst of egg production in early April was followed in turn by a very rapid growth in the previous year's population. By early May, many tiny young snails of the new spring generation had appeared, and these and the previous year's crop continued to grow rapidly until June. Egg production ceased sometime before the end of May. During June and July there was considerable mortality, and the largest snails were eliminated from the population. The rate of growth of the spring generation diminished greatly during July and August. A general decline in numbers of snails between June and August indicated high mortality among all size classes. In June, several hundred snails could be collected readily in a few minutes; in August, an hour's search yielded about 150 snails. A brief period of egg production in August was followed by a gradual drying of the pond. Drying followed by freezing had, by early November, killed most of the snails. Some survived through the winter, for in early April (1963), when water from previously melted snow and ice had refilled the pond, a few live if weather-beaten *P. gyrina* (along with small numbers of egg masses)

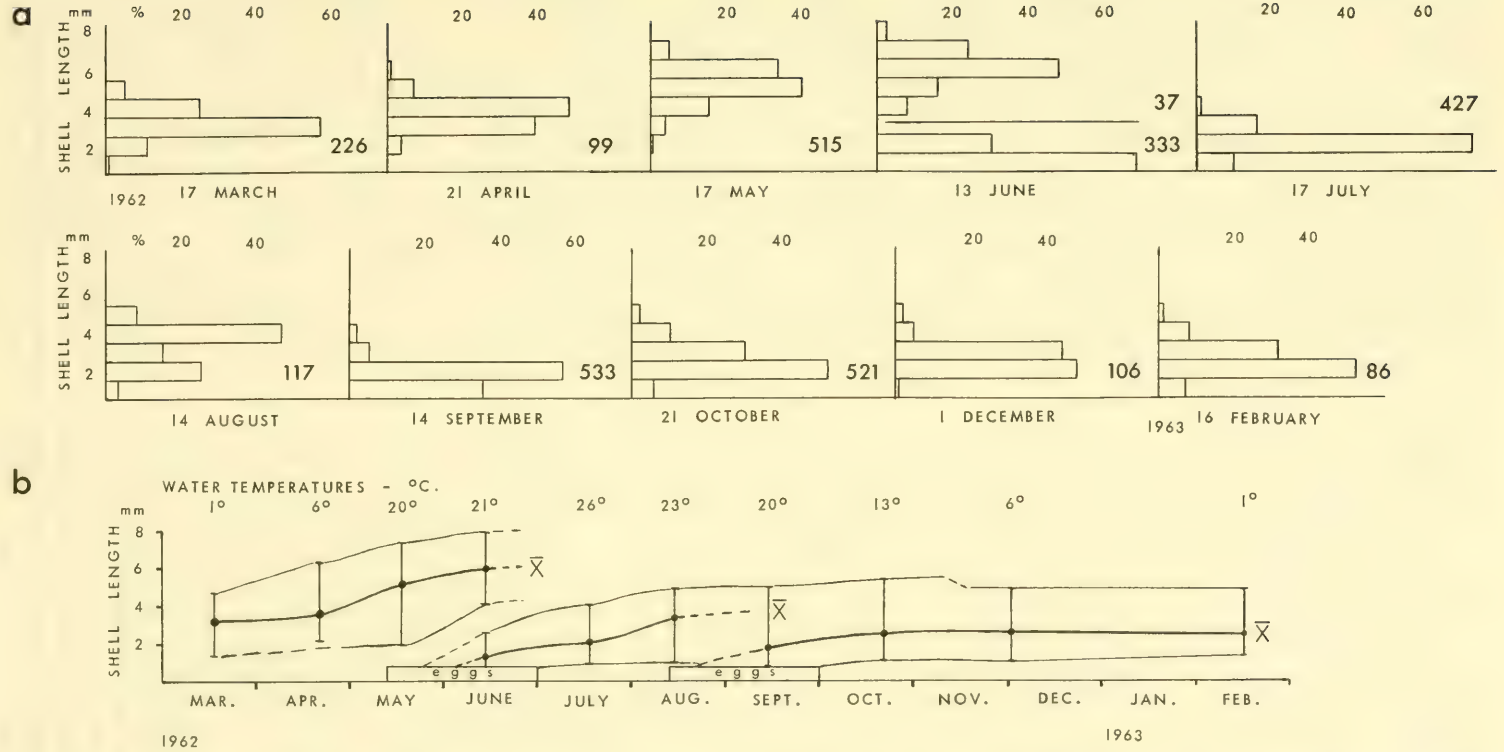

FIG. 7. Seasonal changes in shell size of *Physa integra* from station 5 (see Fig. 5), Little Miller's Bay. a, Relative proportions (%) of different sized snails, in shell length to nearest mm, from representative samples collected from March 1962 through February 1963. In June, young and adult components of the population are represented separately (divided by horizontal line), each as 100%. The young far exceeded the adults in absolute numbers. b, Same data as in a, presented as mean ($\bar{x}$) and range ($\overset{\bullet}{\underset{\bullet}{|}}$) of shell size, showing monthly size changes throughout the year. Note water temperatures, and periods of egg production in May-June and August-September (peak in May). Broken lines represent periods when exact nature of population changes is uncertain.

were collected there.

The life history pattern of the pond *P. gyrina* is similar to that of the Little Miller's Bay *P. gyrina* in most respects, such as the slight growth during the winter, the great upsurge of growth and reproduction in the spring, and the heavy mortality during the summer. The patterns differ in that the eggs appeared in the pond a month earlier than in the lake (due perhaps in part to the fact that the ice melted from the pond nearly 3 weeks earlier than from the lake), the spring growth rates were more rapid in the pond, and egg production stopped completely in the pond for a long period during the summer. Also, the maximum size reached by the pond *P. gyrina* (shells up to 25 mm long in May and June) was greater than in the lake (17 mm in June and July).

DeWitt's (1955) study of *P. gyrina* in a pond (Scio) in Michigan shows a life history pattern basically similar to that described here for the same species. Differences in details, such as the timing of reproduction, growth rates and mortality patterns, are probably a reflection of differences both in regional climatic factors and in conditions peculiar to the local habitats.

Laboratory Populations

Fig. 9 shows comparative growth rates in the 2 species during a 3 month period after hatching, from January to April 1963. Parent stock for both these populations was collected from Big Stoney Point on Spirit Lake (see Fig. 1) in late November 1962. The basis for these studies was 130 eggs of *P. gyrina* and 126 of *P. integra*. Approximately 32 young snails were grown in each of 8 aquaria during the first 2 months of the study, after which the numbers were reduced to 16 snails per aquarium, a total of 64 snails of each species, representative of all sizes in the population, being selected for further study.

Growth rates of the 2 species (Fig. 9) averaged about the same (up to about 3.2 mm shell length) during the first 30 days. After 2 months *P. gyrina* were slightly longer on the average (5.4 compared with 5.0) mm) and were considerably so in maximum length (7.8 compared with 6.1 mm); this divergence had widened markedly after 3 months (mean shell lengths: 7.6 mm against 5.9 mm). Growth rates during the first 9 weeks after hatching averaged .69 mm per week in *P. gyrina* and .54 mm per week in *P. integra*. By comparison, DeWitt's (1954a) data for *P. gyrina* reared in isolation reveal a faster average growth rate of 1.60 mm per week for the first 7 weeks after hatching; the rate thereafter slowing greatly to .1 mm or less per week. In our populations the variability in size became progressively greater in *P. gyrina* than in *P. integra*. Both species had produced some eggs before they were 2 months old. *P. integra*, which reaches reproductive maturity when about 5 mm long, reached this stage slightly earlier than did *P. gyrina*, which becomes mature when the shell is about 7 mm long (see also DeWitt, 1955).

Separate populations of the 2 species, grown over longer periods of time, were also measured at monthly intervals. Portions of the growth curves of these populations are shown in Fig. 10. (1) During a 6-month period (January to June 1962) a laboratory population of 15 *P. gyrina* (parents collected from Clear Creek Pond) increased in shell length from an average of 2 mm to 12 mm, or by 10 mm in all, with a mean rate of growth of 1.7 mm per month (.39 mm per week). Divided into 2-month intervals, the growth rates averaged as follows: first 2 months, 2.6 mm per month; second 2 months, 1.5 mm per month; third 2 months, 0.8 mm per month. (2) During a 10-month period (November 1961 to September 1962) a laboratory population of 13 *P. integra* (collected as small snails from Big Stoney Point, Spirit Lake) increased in average shell length from 4.3 to 10.5 mm, a total growth of 6.2 mm, and a nearly constant mean rate of 0.62 mm per month (.15 mm per week). These

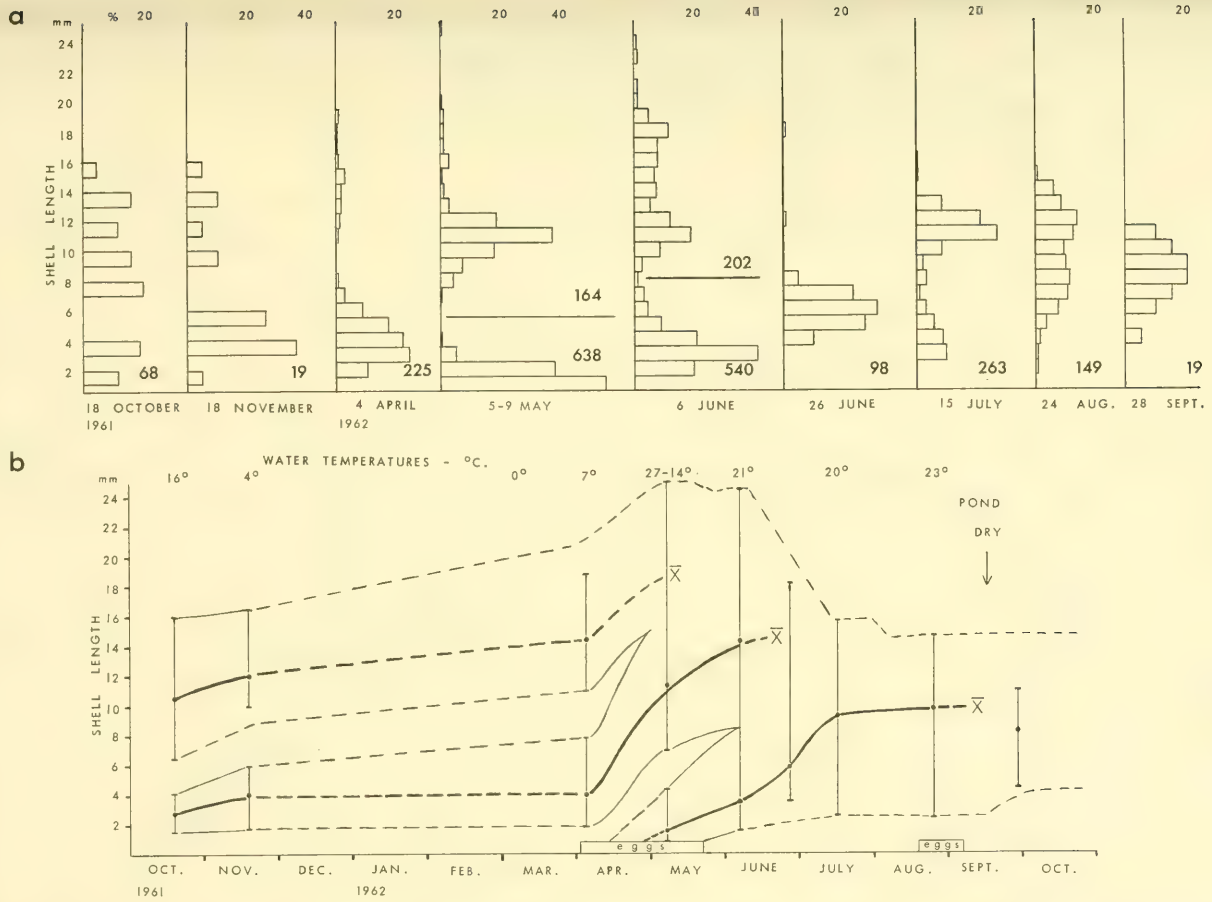

FIG. 8. Seasonal changes in shell size of *Physa gyrina* in Clear Creek Pond near Iowa City, Iowa. a, Relative proportions (%) of different sized snails, in shell length to nearest mm, from representative samples collected from October 1961 through September 1962. In May and on June 6th, young and adult components of the population are represented separately (divided by horizontal line), each as 100%. The young far exceeded the adults in absolute numbers. b, Same data as in a, presented as mean ($\bar{x}$) and range (⊕) of shell size, showing monthly size changes throughout the year. Note water temperatures, and periods of egg production in April-May and late August to early September (peak in April). Broken lines represent periods when exact nature of population changes is uncertain.

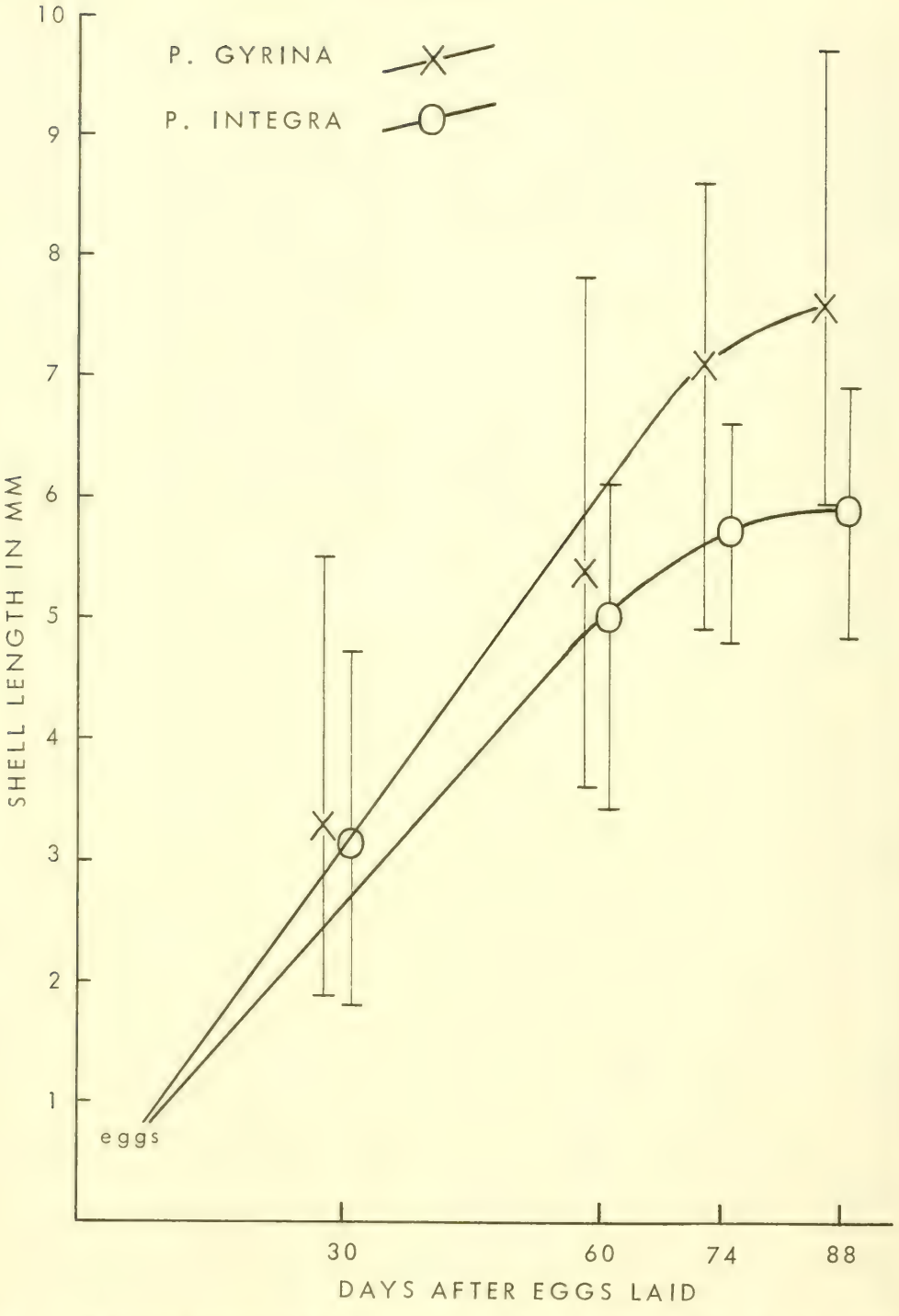

FIG. 9. Laboratory growth rates of *Physa gyrina* and *P. integra* during the first 3 months after hatching, showing mean shell length and range for each species. Parents of both populations were collected from Spirit Lake (Big Stoney Point).

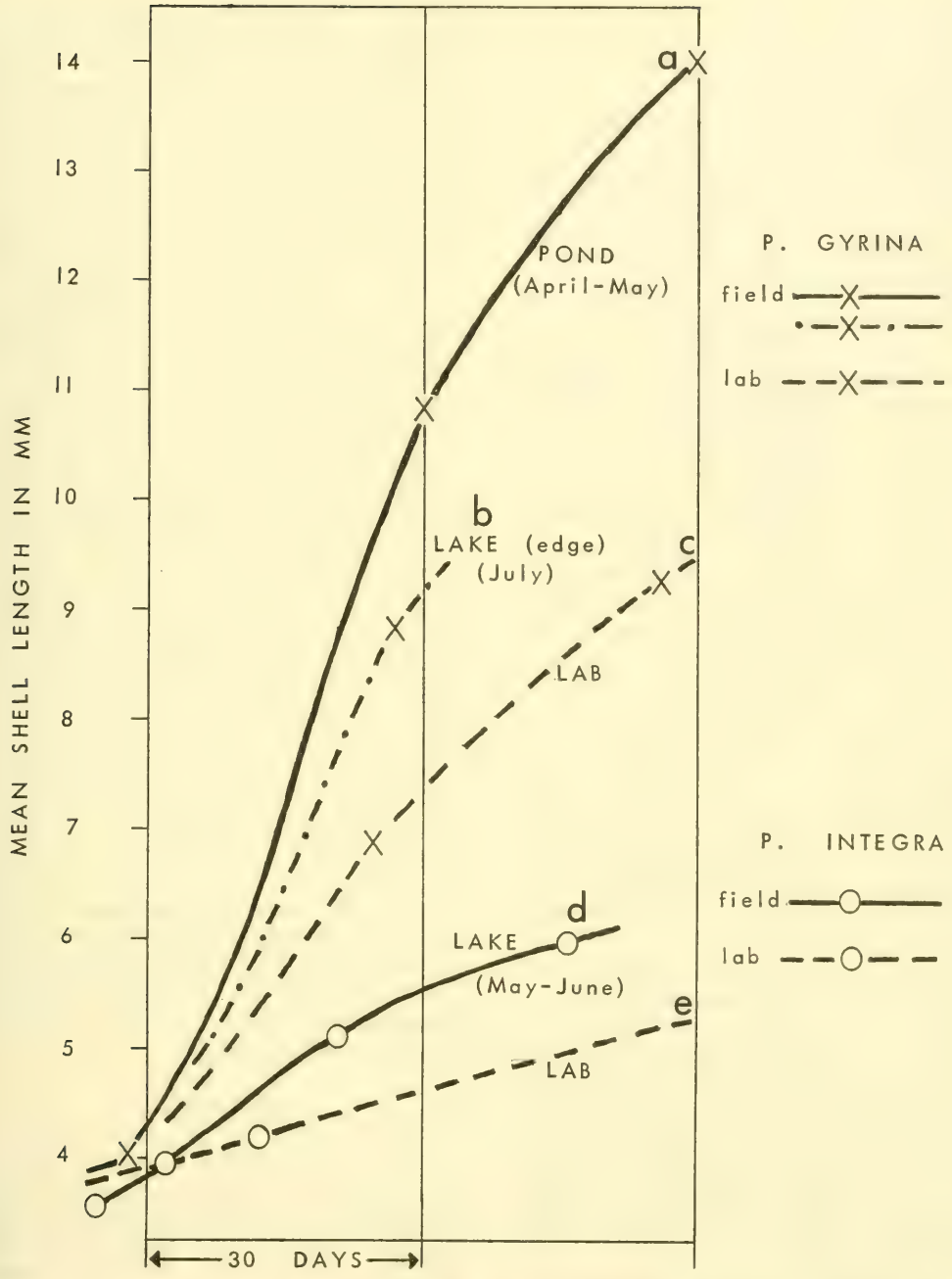

FIG. 10. Growth rates of 5 populations of *Physa*, beginning at 4 mm mean shell length and continuing for a 2-month period. a, Clear Creek Pond *P. gyrina*, April-May 1962 (see Fig. 8). b, Little Miller's Bay *P. gyrina*, July 1962 (see Fig. 6, station 1). c, Laboratory reared populations of 15 *P. gyrina*; parent stock from Clear Creek Pond. Laboratory temperatures, 20-23° C. d, Little Miller's Bay *P. integra*, May-June 1962 (see Fig. 7, station 5). e, Laboratory reared population of 13 *P. integra*, collected as young snails from Spirit Lake (Big Stoney Point). Laboratory temperatures, 20-23° C.

data indicate a much slower but also much more constant growth rate for *P. integra* than for *P. gyrina* in these populations.

Comparative Growth Rates in Field and Laboratory

Fig. 10 shows growth rates, for a 2-month period, of 5 populations (each discussed previously) of snails representing both species. These data, if truly representative, indicate that *P. gyrina* is a much more rapidly growing species than is *P. integra*. Particularly striking is the growth of the pond *P. gyrina* from a mean shell length of 4 mm to nearly 11 mm, a net gain of about 7 mm (1.6 mm per week), during a 30-day period in April. In comparison, the Little Miller's Bay *P. integra*, with a net growth of hardly over 1.5 mm (4 - 5.5 mm, at .35 mm per week) during a 30-day peak period in May, appears to be a slowly growing snail, indeed. Laboratory populations of both species were, in these examples, considerably less rapid in their growth rates than were their field counterparts: laboratory-reared *P. gyrina* had a net gain in shell length of slightly over 3 mm in a 30-day period (.7 mm per week), while laboratory-reared *P. integra* grew very slowly, although at a steady rate, with a net gain of 0.7 mm per month (.16 mm per week).

Egg Production

Fig. 11 shows the monthly egg production in laboratory populations of 15 *P. gyrina* (parents from Clear Creek Pond) and 13 *P. integra* (collected as small snails, Big Stoney Point, Spirit Lake). Both populations were grown under the laboratory conditions described previously (p 122). All egg masses were removed at weekly intervals, and the eggs counted throughout the reproductive life of the populations.

The data (Fig. 11) show high egg production in both species, lasting for 6 months (24 weeks) between March and August 1962 in *P. gyrina*, and for 9 months (36 weeks) between December 1961 and August 1962 in *P. integra*. Peak production was reached in the *P. gyrina* population during the 2nd month, and in *P. integra* during the 3rd month. Half of the eggs had been laid by the *P. gyrina* population in slightly over 2 months, while in *P. integra* this halfway point was reached about the middle of the 4th month. Both species produced an average of 200 - 300 eggs per snail per month through much of the reproductive life of the population. The very high productivity of the last surviving *P. gyrina* individual during the last month is noteworthy; it suggests that a few highly fecund snails could also have been responsible for most of the egg production earlier.

These results on egg production differ from those of DeWitt (1954b, c) chiefly in the greater total number of eggs laid per snail and in the higher proportion of the total life span during which reproduction occurred. For example, DeWitt (1954c) found that 6 *P. gyrina* reared together produced an average of 272 eggs per snail during a reproductive period occupying 38% (131 days) of a total life span of 346 days. In the present study, total egg production per snail averaged over 700 in *P. gyrina* and more than 1000 in *P. integra*. The total reproductive period of the *P. gyrina* population was 163 days, or 63% of the maximum life span of 260 days; that of *P. integra* was 243 days, again over 60% of the (estimated) maximum life span. A few days of unusually hot weather late in August 1962 may have hastened the death - and thereby shortened the post-reproductive period - of the remaining snails of both species.

HABITATS

The purpose of this section is to discuss in some detail the habitats and microhabitats where each species was located; and, for selected spots, the numbers in which they were found. Qualitative and quantitative samples, and a study of seasonal changes in local distribution, are included.

Qualitative Samples in the Field

Techniques

Qualitative samples of snails were

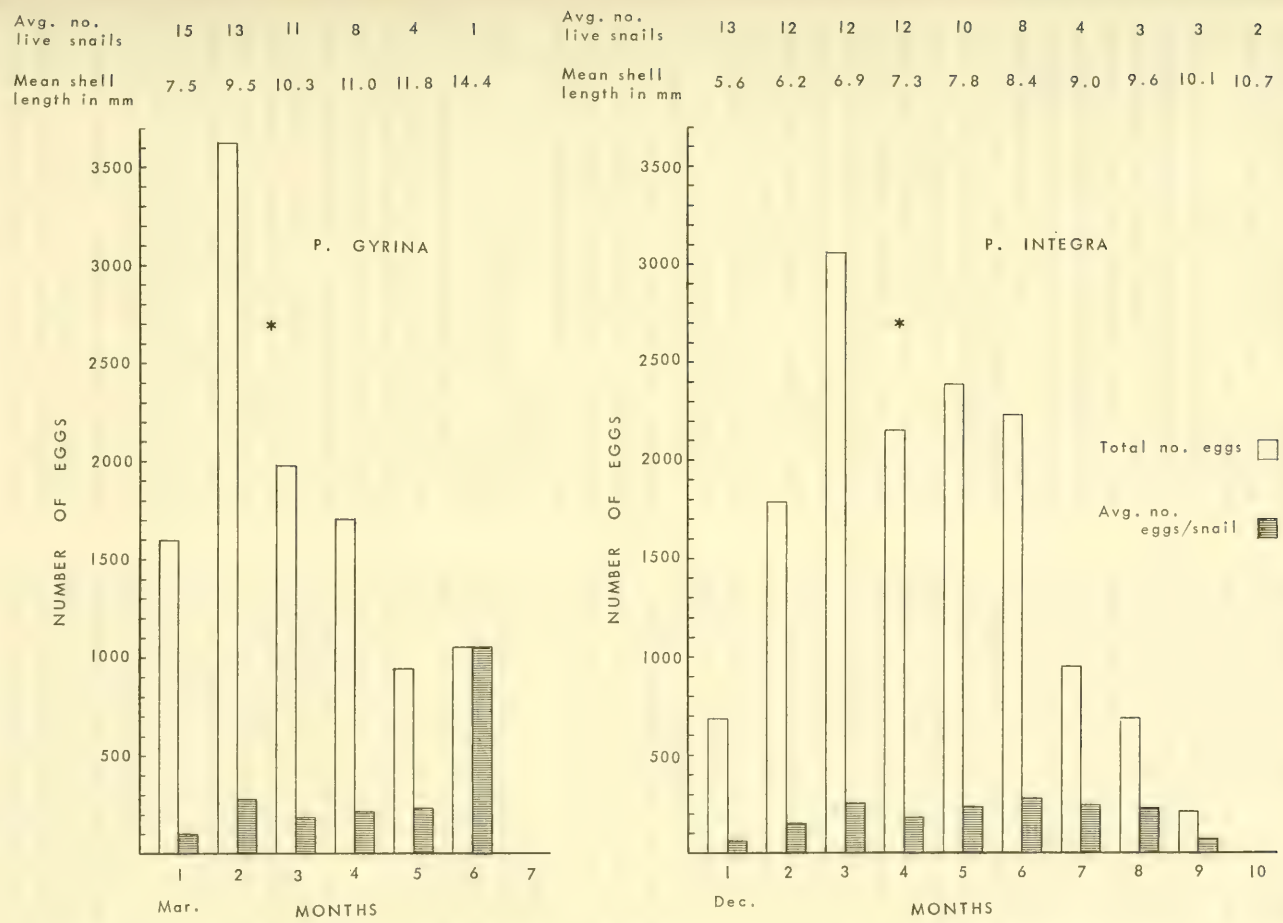

FIG. 11. Egg production during monthly (28 day) periods, in laboratory populations of adult *Physa gyrina* and *P. integra*, through entire reproductive life. Asterisk (*) represents approximate time when half of the total egg production of the population has been achieved. Note that this occurred after the 2nd month of egg-laying in *P. gyrina* and during the 4th month in *P. integra*. The last *P. gyrina* died during the 7th month of egg production, the last *P. integra* at the end of the 10th month.

usually collected by hand from stones, sticks, leaves, green or decaying vegetation or other materials. In pond habitats a dip net was also used. In water too deep for wading, a grappling hook or an Ekman dredge was used from a boat, the choice of instrument depending on the substratum characteristics and on the quantity and kind of vegetation present. The same instruments were operated through a hole in the ice during winter. Materials collected by means of these tools were later sorted for snails on shore or in the laboratory. A series of graded screens was used for washing the bottom materials collected with the Ekman dredge. Notes on such factors as depth, distance from shore, substratum, types and density of vegetation, temperature, hardness of the water, and wave action or currents were recorded, and the snails were usually killed and fixed in formalin (a 10% solution) for future reference. Selected snail samples were relaxed in a nembutal solution, according to a method suggested by van der Schalie (1953), and were then killed and fixed for later anatomical studies.

Types of Habitats

Samples were taken from a variety of lakes, temporary and permanent ponds, ditches and streams. Most of these habitats were in the region immediately around Lake Okoboji in Dickinson County, Iowa (Fig. 1). In this area there are a large number of lakes and ponds of various sizes and types, but streams are rather few in number and type. A limited amount of sampling was also done from ponds and streams in the area immediately around Iowa City, Johnson Couty, Iowa.

Lake habitats sampled were mostly along the shore, and ranged from steep, wave-beaten boulder shores, on one extreme, to quiet, stagnant, mud-bottomed, gently sloping pond-like borders of small bays on the other. Intermediate in character were moderately sloping, wave-washed cobble shores, and others with a gravel or sand substratum, sometimes grading into mud. Offshore habitats included a relatively shallow, mud-bottomed, vegetation-choked bay, areas ranging from gravel to mud with only sparse or no vegetation, and profundal bottom ooze.

Pond habitats also varied, though less so than those of lakes. In size the ponds ranged from small shallow puddles to large sloughs several hundred acres in extent. Some were transitory wet places, others semi-permanent aquatic habitats. Some were crowded with emergent vegetation such as *Typha* or *Carex*, others had dense growths of submerged *Utricularia* or *Ceratophyllum*, and in others vascular plants were sparse or lacking. Most were in rather open prairie country, but some were in wooded areas. Some were roadside ditches, others oxbows along streams, still others undrained depressions in otherwise fairly level farm land. Substrata varied, but were usually of silt or clay.

The few streams that were sampled were all rather turbid, currents varied from fairly swift to sluggish, and substrata were of cobbles, gravel, sand or silt, or of some combination of these materials.

Characteristic Habitats of the Two Species

Of the various habitats surveyed in this study, *P. integra* was a characteristic species in 2 general types: rocky shores and vegetated offshore areas of lakes. In the shore habitat, the substratum was typically of cobble-sized stones, the slope was usually moderate, there was typically a good growth of algae on the stones, and wave action ranged from slight to heavy. In the vegetated offshore areas, the snails were found on the vegetation: mainly *Ceratophyllum demersum*, *Myriophyllum exalbescens*, *Ranunculus longirostis*, various *Potamogeton* species, and perhaps other submerged aquatics; the vegetation ranged from dense to fairly sparse; the depth ranged from less than 50 cm to more than 3 m; and the substratum was of sand or mud.

Certain contrasts between these 2 *P. integra* habitats should be noted. In the shore habitat the snails were on the stones, while in the deeper vegetated habitat they were very largely on the vegetation. Along the shore they had easy access to the surface for air breathing, while in deeper water that access was, at best, more difficult; my failure to find snails on the surface film in these offshore areas suggested that in these habitats they do not come to the surface.

A contrast was seen in the *P. integra* populations themselves: the individuals of the shore-dwelling populations reached a considerably larger size than did those of the offshore populations.

All of these differences deserve careful attention, particularly as they relate to food, oxygen requirements and behavior in the species.

The types of habitats in which *P. integra* were not found should also be well noted. Included in this negative category were the zones of lakes too deep to support rooted vegetation, and particularly all types of ponds (see discussion under "Conclusions").

In sharp contrast, *P. gyrina* is a characteristic and obviously successful pond species. It was found on a variety of materials such as boards, sticks, decaying weed stems, leaves, filamentous algae, on the substratum itself, and on the surface film. Summer populations of *P. gyrina* were restricted largely to the edges of these ponds, often in water less than 10 cm deep. On warm, sunny days, water temperatures in these very shallow areas reached high levels, often over 30° and sometimes 35° C.

P. gyrina occupied something of a continuum of types of habitat from stagnant ponds to the wave-washed rocky shores of lakes which latter were also characteristic for *P. integra*. In the lake shore habitat and in the pond, the snails were within easy reach of the surface for aerial breathing. In most other respects, notably wave action, type of substratum, the relative scarcity of living and particularly of decaying vascular plant material, and more moderate and stable temperature conditions, the lake shore differs greatly from the pond. The *P. gyrina* of the 2 habitats were themselves different; as has already been noted (p 118), the lake shore *P. gyrina* had a consistently greater width-length ratio than did the 2 pond populations of the same species; these differences were statistically significant.

While *P. integra* populations can often be found in offshore vegetated areas of lakes in water 3 m or more deep, those of *P. gyrina* (at least in summer populations) appear to be completely absent from depths greater than 1 m, and are largely restricted to depths of only a few centimeters.

In summary, *P. gyrina*, although a characteristic pond species, may also be found on rocky shores of lakes in company with *P. integra*, as well as in habitats of an intermediate type. In depth distribution, however, *P. integra* is considerably less restricted than is *P. gyrina*.

Quantitative Samples

Quantitative samples were made in certain selected habitats in order to determine relative densities, and hence perhaps when and where the optimum conditions for survival and reproduction have been reached.

Techniques

In shallow water (wading depth), quantitative samples were taken using a sheet metal cylinder enclosing an area of 1/4 m^2. This "sampling cylinder" was used in lake shore and in pond habitats. The cylinder was placed upon, or if possible pushed into, the substratum; then all materials which it enclosed (stones, weed stems, etc.) were carefully removed and sorted for the snails which they contained. The snails were later counted and preserved for future study. Where densities of snails were low, a larger area of 1 m^2 was sampled. No very satisfactory technique was developed for securing data on densities

TABLE 2. Depth distribution of *Physa integra* in Center Lake (West Shore)

Depth	0-15 cm	50 cm	100 cm
Distance from shore	0-.5 m	2 m	5 m
Substratum	Cobbles (algae-covered)	Cobbles & gravel	Gravel, some mud
Number of snails / 1/4 m^2	835	210	46

TABLE 3. Depth Distribution of *Physa* in Spirit Lake (Big Stoney Point)

Depth	0-10 cm	10-35 cm
Distance from shore	0-.5 m	2 m
Substratum	(Boulders & cobbles throughout)	
Number / 1/4 m^2		
P. gyrina	185	17
P. integra	50	8

in the vegetated offshore zone, although a rough volumetric measure of the quantity of vegetation in a sample was of some value in this connection.

Density Related to Depth and Distance from Shore

Densities of both physid species were highly variable both spatially and temporally. Several factors may be involved in these variations. Most consistent and predictable among these is the fact that densities of both species decrease with depth. Two examples will serve to illustrate this relationship.

(1) On the rocky west shore of Center Lake (Fig. 1) in June of 1961, a very dense population of *P. integra* (but no *P. gyrina*) could be found. Table 2 summarizes data on density related to depth, distance from shore and substratum characteristics. The rapid decrease in numbers with increasing depth can readily be seen. Substratum changes may also have been a factor in this density-distribution pattern.

(2) At Big Stoney Point on the east shore of Spirit Lake (Fig. 1), both *P. gyrina* and *P. integra* could be found, in the summer of 1961, in large numbers. This shore again is rocky, with considerable exposure to wave action. Table 3 summarizes data collected in July 1961, along one side of Big Stoney Point. Again there was a decided decrease in density with increased depth and distance from shore, and in this case substratum changes could not have been a factor as there were none.

These 2 examples serve to illustrate what appeared to be a general pattern of distribution among all summer populations of *P. gyrina* and many of *P. integra*. Comparable results were obtained in other quantitative samples of one or both species from a variety of lake and pond habitats. These confirm the general impression that populations of both species are concentrated in shallow water close to shore. This distribution pattern is probably related to the surfacing behavior and respiratory habits of these pulmonate snails, at least as these phenomena apply to the larger adults of the 2 species.

Other Factors Associated with Density

Substratum, available food and pro-

tection for the young snails are all factors which may be of importance in explaining the densities of one or both snail species in their various habitats. To these may be tentatively added the factor of light. All are to some degree interrelated, though none could be isolated for separate investigation in the field.

Dense populations of *P. integra* are usually associated with the absence of, or an opportunity to avoid, a substratum of sand or silt. In rocky shore areas, such a substratum is absent, and in offshore areas the snails avoid these substrata by clinging to the vegetation. In the rocky shore areas, a dense "Aufwuchs" on the stones also appears to be essential, which in turn is dependent on considerable exposure to sunlight. Young snails must avoid or escape the impact of wave shock, which they can do in rocky shore habitats where there are rock pools or interstices among the stones which afford such protection.

Substratum appears not to be critical for *P. gyrina*. Dense populations of this species are usually associated with plentiful quantities of food, which may vary greatly with the type of habitat. In a pond, dead and partially decaying plant material, or perhaps fungi or algae associated with them, seem to be especially favored (DeWitt, 1955). Ponds heavily shaded with *Typha* or other large emergent plants, however, contain few *P. gyrina*. In the rocky lake shore habitat, *P. gyrina* appears to have the same needs, for food and protection for the young, as does *P. integra*.

Seasonal Changes in Local Distribution, Little Miller's Bay, West Okoboji Lake

The desirability of a year-round study on the locations of populations of the 2 physid species in relation to shore is suggested by the work of Cheatum (1934). Cheatum studied seasonal migrations of snails in Douglas Lake, Michigan, including 2 species of *Physa*. He found that as the water temperature declines in the fall, these snails migrate from the littoral zone to deeper water, where they overwinter. As the temperature rises in late spring and early summer, the snails move shoreward from the deeper water. By these seasonal migrations, the snails avoid being trapped in the ice cover in winter, and can easily reach the surface for aerial breathing in the summer; thus this behavior appears to have definite adaptive value. The question therefore arose: do *P. gyrina* and *P. integra*, in the Lake Okoboji area, have a similar seasonal migratory behavior?

Little Miller's Bay on West Okoboji Lake (Fig. 5) was chosen as the site for this year-round study. This small bay is mostly surrounded by land and therefore protected from heavy wave action. It is shallow, not more than 2 m deep, has a mud bottom, muddy or in some places sandy shores, and a dense growth of submerged vegetation (*Ceratophyllum* dominant; also *Myriophyllum*, aquatic *Ranunculus*, and several *Potamogeton* species). It is bordered with trees interspersed with meadow, and this terrestrial vegetation contributes allochthonous material to the bay.

An interesting pattern of distribution of the 2 *Physa* species occurred there during 1961 and 1962. *P. gyrina* populations were concentrated (in summer) around the periphery of the bay where the conditions were essentially pond-like, with emergent vegetation of a variety of kinds, and often much dead and decaying plant material; water was usually quiet, and daytime summer temperatures often reached 30° C or higher. By contrast, *P. integra* populations were found year-round in the offshore submerged vegetation, where temperatures rarely rose above 25° C.

Methods

Several stations along a transect, extending from the shore of the sand spit to a point 60 m westward into Little Miller's Bay (see Fig. 5), were sampled for snails at regular monthly intervals, from March 1962 to February 1963. Procedures already described for quali-

TABLE 4. Little Miller's Bay transect area*

Station No.	Depth in cm	Distance from shore in m	Substratum	Summer vegetation
1	0–10	0–0.5	Sand	Dead weed stems, leaves, sticks, debris.
2	50	6	Sand	Some green vegetation; debris.
3	100	12	Muddy sand	Moderate growth of submerged vegetation; outer edge of emergent zone.
4	150	25	Mud	Moderate growth of submerged vegetation.
5	180	60	Mud	Dense growth of submerged vegetation.

*See Fig. 5.

tative sampling (p 130) were also followed here.

Findings

Table 4 shows the locations of the 5 stations in terms of depth and distance from shore; information on substratum and summer vegetation conditions is also included. Station 5 (see also Fig. 5), 60 m from shore, is essentially similar to much of the central part of the bay, in substratum and vegetation characteristics as well as in the character of its snail population.

P. gyrina, whenever found (April through November), was concentrated in the extreme littoral area of the bay (station 1). Water temperatures during this period fluctuated between a low of 6° and a high of 31° C (as measured at times of sampling). No snails of this species were found at any station during the winter period of ice cover (December to April) when the surface was frozen solid to a depth of 50 cm or more. The findings of Cheatum (1934) and DeWitt (1955) suggest, however, that those snails which survived had migrated to depths of 1 m or more.

A dense population of *P. integra* was found throughout the year in the vegetated offshore zones, where temperatures ranged from 1° C under the ice to a 26° C maximum in the summer. During the winter of 1961-62, green submerged vegetation was scarce to absent within a range of 25 m or more from shore in the transect area, and few *P. integra* were found there. They were abundant, however, at station 5, 60 m from shore in water 1.8 m deep, on the *Ceratophyllum* which was green even under 25 cm of snow and 60 cm of ice; a dissolved oxygen content of 5 ppm was also present (March 1962). As the submerged vegetation near the margin of the bay grew and became progressively denser during the late spring and early summer of 1962, *P. integra* became more abundant also toward the shore, being well represented at station 2 (50 cm deep, 6 m from shore) by June. Although they came close, very few of the snails of this species actually reached the extreme littoral, pond-like shore area where *P. gyrina* were most abundant. During the winter of 1962-63, in contrast to the previous winter, *Ceratophyllum* remained healthy and abundant at station 3 (1 m deep, 12 m from shore), and *P. integra* were abundant at this station in a February collection.

In summary, it seems likely that there

are seasonal changes in the distribution pattern of *P. gyrina* in the Okoboji area; and there was a spread of the *P. integra* population toward the shore as spring and summer growth of the submerged vegetation progressed, but it did not culminate in the arrival of the species in the shore area, or in its disappearance from the vegetated offshore area.

For data on seasonal changes in shell size and periods of reproduction in the Little Miller's Bay populations of *P. gyrina* and *P. integra*, see Figs. 6 and 7.

SPECIFIC ANALYSES OF ENVIRONMENTAL FACTORS

The purpose of this section is to attempt to explain, in terms of food, behavior and physiological tolerances, why the 2 species are found in different kinds of habitats.

Food

Techniques

Two quite different approaches were made to the problem of determining the types of food used by the 2 species. One was an attempt to measure food preferences. Starved snails of each species were put into an environment containing a choice of materials which might conceivably be used as food, and behavior of the snails was observed. The second approach was an attempt to determine the different kinds and relative amounts of various materials actually consumed by the snails; stomach analyses were performed on a series of snails which had been killed and fixed shortly after being collected in the field. The second and more fruitful method will be discussed first.

Stomach Analyses

Analyses were made on the stomachs (i.e., crop plus gizzard) of 23 snails of each species, all from rocky shore habitats in either Spirit Lake or Center Lake. Stomachs of both *P. integra* and *P. gyrina* were found to contain a wide variety of materials, many of them recognizable. These included: diatoms, shreds of filamentous algae, other green and blue-green algae; rotifers; small crustaceans such as ostracods and cladocerans; parts of amphipods, Diptera (tendipedid) larvae, and other arthropods; chaetae of freshwater oligochaetes; small amounts of vascular plant tissues; and sand grains. An unidentified gelatinous material (possibly mucus secreted outside the body and later consumed) completely filled the stomachs of several *P. gyrina*, and formed a substantial part of the stomach contents of other snails of both species. As for relative proportions of different foods, the largest part consisted (in these habitats) of detritus, algae of all kinds, and the gelatinous material mentioned above; animal and vascular plant tissues formed only a minor portion. A rather striking difference in the algal flora of the 2 lake habitats was indicated in these analyses: stomachs of Spirit Lake snails of both species tended to contain a preponderance of diatoms; those from Center Lake yielded very few diatoms, but had a very large proportion of colonial bluegreen algae such as *Microcystis*.

The results of these analyses indicate that both species consume a great variety of types of materials, determined chiefly by what is available and can be scraped loose and ingested in any particular habitat where the snails are found. The 2 species apparently do not have appreciably different food habits, although the possibility of a difference has not been completely ruled out.

Food Preference Experiments

When starved snails of either species were introduced into a trough containing stones alternately with and without an algal coating, the majority always accumulated eventually on the stones covered with algae. Table 5 shows the cumulative results of a series of 20 experimental trials in each of which 10 *P. gyrina* or *P. integra* - i.e., cumulative total of 100 animals of each species - were released in the center of a small trough. For each replicate of 10 snails,

the trough contained lake water and 3 barren and 3 algae-covered stones, spaced alternately through the length of the trough. Positions of all snails relative to the stones were recorded at regular time intervals; the data given (Table 5) are the cumulative total number (= %) of snails found on algae-covered stones, barren stones, and elsewhere in the trough, as recorded at intervals during a total time of 60 minutes. The results are essentially the same for the 2 species. The very gradual accumulation of the snails on the stones covered with algae suggests random movements which cease when the animals chance to meet favorable environmental conditions (in this instance, food). These findings are similar to those of Bovbjerg (1957, 1965) on the freshwater mussel *Lampsilis siliquoidea* and the snail *Stagnicola reflexa*. That feeding was indeed taking place was indicated by radular motions; later examination of fecal material provided further confirmation.

When dead *Carex* stems from a pond were introduced into a container with starved snails, both species accumulated upon them, much as they had upon stones with an algal coating.

Extensive laboratory observations indicated that when snails of both species were given a "choice" between stones coated with algae and dead weed stems, the choice was neither clear-cut nor consistent for either species.

When *Ceratophyllum demersum* or *Myriophyllum exalbescens*, vascular plants characteristic of the offshore vegetated habitats of *P. integra*, were introduced as the "food" material, both species behaved indifferently toward these materials, even though they had been deprived of food previously for a week or longer. A similar indifference to the filamentous alga *Cladophora* was apparent for both species.

Laboratory populations of both *P. gyrina* and *P. integra* have been reared successfully using a mixture of dried maple leaves and green lettuce as the primary food sources. Both species accumulate upon and readily consume these materials.

In none of these experiments and observations have I been able to establish that there is a difference between the 2 species, even though some materials are quite characteristic of the habitat of one species and not of the other. On the basis of present evidence, therefore, it must be concluded that differences in the local distribution of the 2 species are based upon factors other than food preference and food consumption.

Dispersal Behavior and Factors Influencing Dispersal

Rates of Dispersal

Observations in the field and laboratory gave the impression that *P. gyrina* was a considerably more active snail than *P. integra*. Thinking this feature might have some significance in the distribution pattern of the 2 species, I designed laboratory and field experiments in an attempt to compare dispersal rates of the 2 species.

Laboratory experiment:

(1) Technique: The experimental chamber was an aluminum trough 68 cm long, 7 cm wide and 4 cm deep. Its length was marked with an 8 cm "release" area in the center, and at 5 cm intervals from this central area toward each end. The trough was filled with lake water to a depth of 2 1/2 cm for each experiment. Overhead fluorescent lights provided uniform lighting, and water temperatures ranged from 20° to 23° C. At the beginning of each of 20 replicate experiments, 10 *P. gyrina* or *P. integra* were released in the central starting area. Positions of all snails were recorded, to the nearest 5 cm, after 2, 5, 10, 15 and 20 minutes, and from these positions the mean distribution of each species was calculated for each time interval, to give a comparative measure of dispersal rate. Because some *P. gyrina* had reached the end of the trough after 5 minutes, useful data are limited to the first 5 minutes, and these alone will be presented below.

(2) Results (Fig. 12): Although there

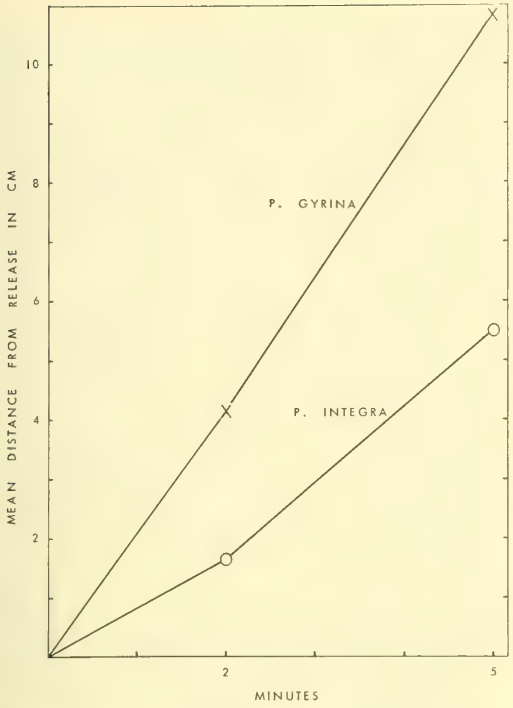

FIG. 12. Mean dispersal rates of *Physa gyrina* and *P. integra*, in a linear chamber in the laboratory. Data recorded in cm from release after 2 and 5 minutes. Based on 20 replicate experiments, using 10 snails in each. After 2 minutes, $P < .01$. After 5 minutes, $P < .05$ (for standard deviations, see text).

was considerable variability in the dispersal rates of both species, the average rate of dispersal of *P. gyrina* was twice that of *P. integra*. After 2 minutes, *P. gyrina* had moved 4.2 ± 2.2 cm (standard deviation, SD), while *P. integra* had moved only 1.7 ± 1.1 cm. After 5 minutes, *P. gyrina* had moved 10.9 ± 5.5 cm, and *P. integra* 5.5 ± 3.9 cm. Under these laboratory conditions, *P. gyrina* disperses at a significantly faster rate than does *P. integra* ($P < .01$ after 2 minutes, $P < .05$ after 5 minutes).

Field experiment:

Snails (130) of each species were marked on the upper surface of the shell with fingernail polish of a conspicuous hue - red for *P. gyrina*, pink for *P. integra*. They were then released on a substratum of cobbles near the west shore of Center Lake (July 1962). At intervals the area in the vicinity of release was searched for the marked snails, and their positions, as distances from release, were recorded. The first search took place 2 hours after the time of release; the last took place 3 weeks later.

The results of this experiment are summarized briefly in Table 6. They indicate that *P. gyrina* dispersed much more rapidly, and widely, in this experiment than did *P. integra*. However, as there was considerable local variability in the environment as to substratum, depth and other conditions, factors in addition to differential rates of movement in the 2 species may have been operating to produce these results.

Dispersal of both species, under natural conditions, may be passive as well as active. The laboratory experiments, and probably the one in the field, involved only active dispersal. Passive dispersal, through wind and wave action in lakes and currents in streams, may play an important role in dispersing snails to new habitats. Other animals (for example, aquatic birds which may carry young snails on their feet) may also play such a role. The exact nature and extent of these roles are not known.

Movements in Response to Temperature Changes

P. gyrina is often found in ponds and pond-like margins of lakes, where daytime temperatures rise to 30° C or higher during the summer. *P. integra* is nearly always absent from these habitats. It was therefore thought that behavior in response to temperature (and also tolerance to high temperature, for which data are given on p 144 and in Fig. 14) would help to explain this distribution.

Technique: A temperature gradient chamber was set up. It consisted of a horizontally placed glass tube, 4 cm in diameter and 120 cm long, filled half full of water and corked at both ends, and containing 3 thermometers, one at each end and one in the middle. In testing the response of the snails to

TABLE 5. Location of snails in trough containing algae-covered and barren stones*

Minutes after release	No. (=%) *P. gyrina*			No. (=%) *P. integra*		
	On algae-covered stones	On barren stones	Elsewhere in trough	On algae-covered stones	On barren stones	Elsewhere in trough
5	19	1	80	12	2	86
10	27	3	70	23	2	75
20	52	2	46	46	5	49
30	65	4	31	57	8	35
40	69	5	26	59	7	34
60	77	3	20	74	3	23

*See p 137-138 for further details.

TABLE 6. Field dispersal experiment, Center Lake, July 1962

Days after release	Species of *Physa*	No. snails located*	Mean distance from release m	Greatest distance from release m
1	*P. gyrina*	40	1.7	6.5
	P. integra	44	1.3	3.5
7	*P. gyrina*	34	3.9	18.5
	P. integra	25	2.2	6.5
14**	*P. gyrina*	18	4.3	12.5
	P. integra	15	1.7	4.5

*130 snails of each species were released at the beginning of the experiment.

**After 21 days, 8 *P. gyrina* and 6 *P. integra* were located, too few to yield meaningful data on mean and maximum distances from release.

cold, one end of the gradient was cooled with "Dry Ice" (solid CO_2) and the other end warmed above a beaker of hot water. Separate experiments were used to test the response to heat, by heating one end of the gradient strongly above boiling water and cooling the other slightly with ordinary ice. In the first set of experiments the cooled end of the gradient averaged 11° C; in the second set the heated end was maintained at 38°-40° C. Fifteen marked snails of each species were introduced into the gradient chamber for each replicated experiment. The positions, to the nearest 10 cm, of all snails of both species, were recorded at least 4 times at 15 minute intervals while the gradient was maintained. The

4 (or more) readings were averaged to reflect the distribution during the experiment as a whole. Seven such experiments, involving 105 snails and over 400 position recordings of each species, were done using the cold stimulus, and 7 more using the heat stimulus. A series of 10 control experiments were also done; in these, the above procedures were followed, except that the temperature was kept uniform throughout the chamber.

Results: The outcome of the temperature preference experiments is illustrated in Fig. 13. Both species moved away from the cold end of the gradient (middle figure). They both showed some tendency, though not consistently, to move toward but not into the heated end (at 38° - 40° C). Neither species showed great sensitivity to these differences in temperature; they moved around quite freely through a wide range of temperatures. There was no significant difference between the species in any of this behavior; on the contrary, they responded in much the same manner (see figure legend for probabilities). Temperature preferences, therefore, cannot be considered a factor controlling the different distributions of the 2 species in nature.

During the winter, when ice formed overnight in aquaria kept on a window sill in the laboratory, nearly all snails of both species clustered on the bottom and sides away from the site of ice formation. These snails again became more randomly distributed after the ice had melted. This adaptive response on the part of both species is suggestive of what probably occurs in nature.

Movements by Adult Snails in Response to Wave Shock

When wave shock was extremely heavy in the field, as it was frequently at Big Stoney Point on Spirit Lake, few if any snails could be seen on the upper exposed surfaces of stones, but both species could be found readily on the lower or otherwise protected surfaces of boulders and cobbles. When wave action was light or moderate, however, numerous snails of either species were seen on the exposed surfaces of the stones.

Respiratory Behavior

In the laboratory, *P. gyrina* and *P. integra* came regularly to the surface for aerial breathing. This also appeared to be true of pond *P. gyrina* and of shore-dwelling lake populations of both species during the warmer seasons. It seemed doubtful, however, that this surfacing behavior occurred in *P. integra* in the deeper water (1 - 3 m or more) farther from shore. Hunter (1953), studying offshore populations of *Physa fontinalis* in Loch Lomond, Scotland, found that in these snails the mantle cavity is invariably filled with water. I applied Hunter's method of direct microscopic examination in the field (from a boat), immediately after collection and before the snails had opportunity to come to the surface, in investigating the mantle cavity contents of a summer (August 1964) population of *P. integra*. This snail population was located in offshore vegetation (mainly *Potamogeton* spp) at a depth of 2.5 - 3 m in Spirit Lake, near Big Stoney Point. Samples of vegetation bearing the snails were pulled up gently from the substratum with a grappling hook, but kept continuously submerged in water in a large plastic container while the snails, a few at a time, were transferred under water to a dish, then immediately examined (before they crawled to the water surface) under a stereoscopic microscope. An air bubble in the mantle cavity, if present, could be detected easily by this method through the thin shell of any of these snails. Some 50 *P. integra* 4-9 mm long - and many more of smaller size - were collected and examined in this manner, and all had the mantle cavity filled with water. Egg masses and many young snails were present in the habitat at the same time. This evidence strongly indicates that the *P. integra* of these offshore habitats can complete their entire life cycle without coming to the surface and with the mantle cavity remaining filled with water. Respiratory needs would appear to be satisfied by direct

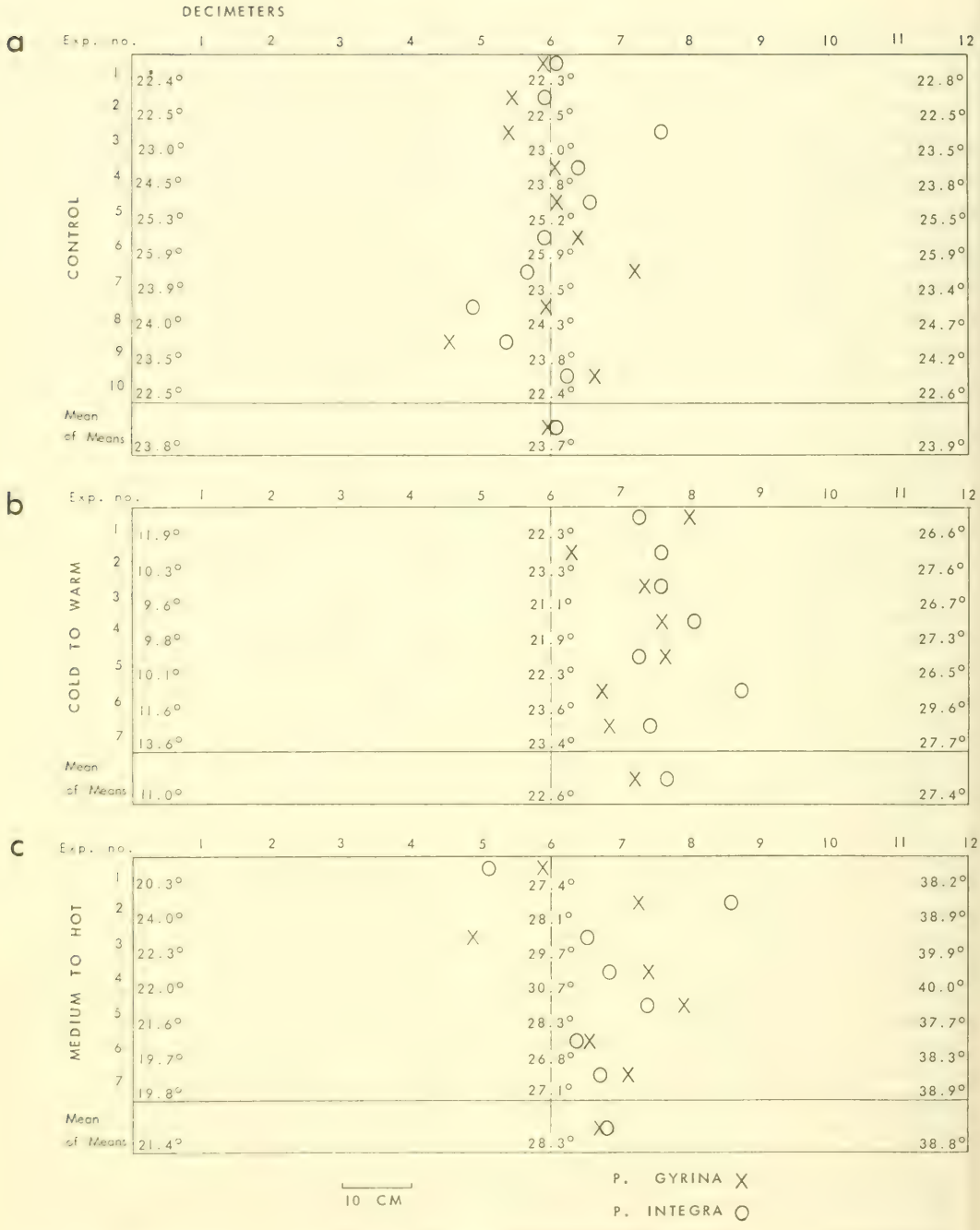

FIG. 13. Temperature preference of *Physa gyrina* (x) and *P. integra* (o). The symbols x and o represent the mean distribution within the temperature gradient chamber of a population of 15 snails of each species, in 3 series of experiments. a, Control experiments. Temperatures were kept uniform throughout the "gradient" chamber. Note that the mean distribution of both species lies, as expected, very near the mid-point in the chamber (for both species, $P > .80$). b, Response to cold temperatures. One end (left) of the gradient was chilled (to 11.0° C average), and

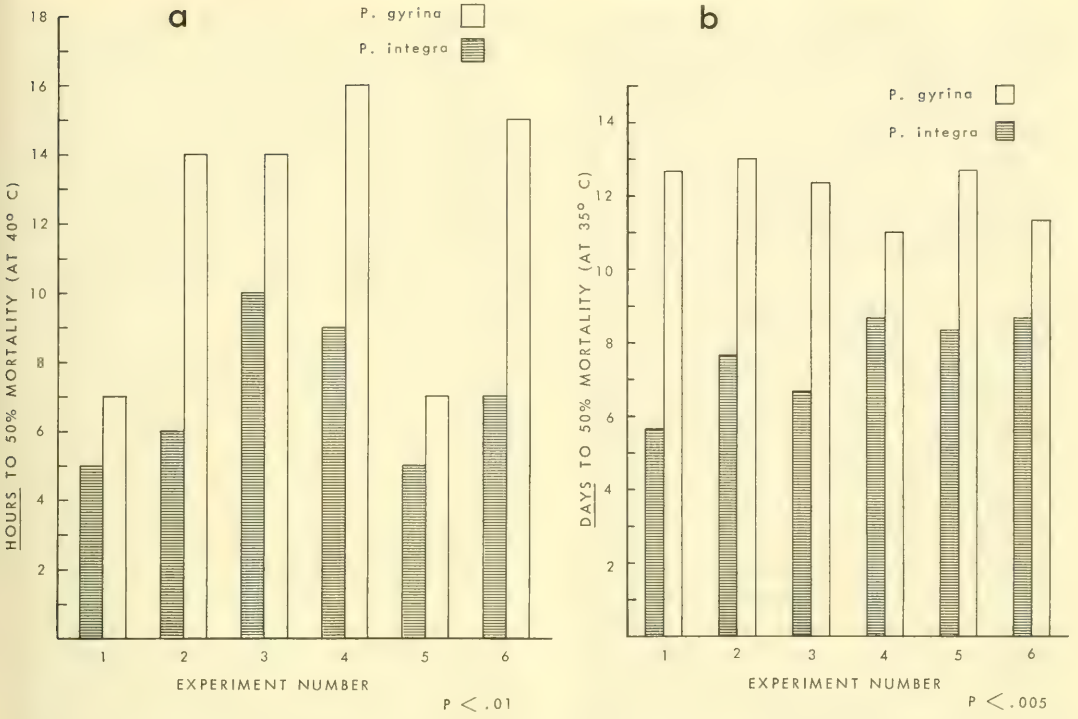

FIG. 14. Relative tolerance of *Physa gyrina* (white) and *P. integra* (shaded) to lethally high temperatures: a, Number of hours to 50% mortality in each species, at 40° C, from a series of 6 experiments, each involving an average of 25 snails of each species, collected from several localities. The difference between species is significant ($P < .01$). b, Number of days to 50% mortality, at 35° C, from 6 experiments, each with 20 snails of each species, all collected from Lower Gar Lake. Again, the difference between species is significant ($P < .005$).

diffusion of gases through the integument. Evidence of comparable behavior in *P. gyrina* is lacking, and the absence of these snails from deeper water may be tentatively explained (at least in part) on this basis.

Tolerances

Heat

Technique: Experiments were designed to measure tolerance to high, ultimately lethal temperatures. Snails of both species were first acclimatized for one week or more to laboratory room temperatures averaging 23-25° C. In one set of 6 experiments, the snails were then placed in an aquarium which was rapidly heated (in about 4 hours) from room temperature to 40° C. The experiment was checked and dead snails (those showing no sign, macroscopically, of muscular activity) were removed at 2-hour intervals, until at least 50% of both species of snails were dead. Each

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the opposite end (right) warmed (to 27.4° C average). Note the consistent displacement of the mean distribution of both species to the right of the mid-point. In both species, this displacement is significant; $P < .001$. Difference between species: $.20 > P > .10$, considered of doubtful significance. c, Response to heat. One end (right) of the gradient was heated (to 38.8° C average) and the opposite end (left) cooled slightly (to 21.4° C average). Note some (not consistent) displacement of mean distribution of both species to the right (toward the heated end) of the mid-point. For both species, $.20 > P > .10$; considered of doubtful significance.

of the 6 experiments involved 20 - 30 snails of each species, some 300 snails being tested in all. In a second set of 6 experiments, the aquarium was heated only to 35° C and snail mortality was checked at 8-hour intervals. All of the snails of both species were in this case collected from the same habitat (the rocky west shore of Lower Gar Lake; see Fig. 1). Twenty snails of each species were tested in each experiment, 240 snails in all.

Results (Fig. 14): In both sets of experiments, *P. gyrina* consistently tolerated the high temperature conditions for a longer period than did *P. integra*. At 40° C (Fig. 14 a), the range for the former species, until 50% mortality occurred, was 7 - 16 hours; for the latter species, only 5 - 10 hours. Considering the results of each experiment as a unit, the difference between species is significant ($P < .01$). At 35° C (Fig. 14 b), both species survived many times longer than at 40° C; 50% mortality was reached in 11 - 13 days (264-312 hours) in *P. gyrina* and in 5.7 - 8.7 days (136-208 hours) in *P. integra*. Again, the difference between species is significant ($P < .005$). Differential tolerance to high temperatures may therefore be a factor helping to explain the presence of *P. gyrina* in ponds and the absence of *P. integra* from such habitats.

Drying

P. gyrina has been reported from temporary as well as from permanent ponds (De Witt, 1955), habitats confirmed in this writer's experience, while *P. integra* is apparently absent from both. Because of the possible significance of desiccation in determining the distribution in temporary ponds, experiments were designed to measure the influence of this factor.

Technique: The experimental chamber was a large (30 x 60 cm) aquarium inverted over slightly moistened cheesecloth, supported in turn by a heavy screen placed on bricks whose bases stood in water to help maintain slightly humid conditions in the chamber. At the start of each experiment, 40 adult snails of each species (alive and apparently healthy) were placed at random on the cheesecloth. At 3-day intervals, the aquarium was removed and the snails were all removed to dishes of water. Those still alive nearly always showed signs of activity within a few minutes; these were returned to the experimental chamber. The experiment was continued until at least 50% of both species were dead. Four experiments were performed involving 160 snails of each species, all of which were collected from the rocky west shore of Lower Gar Lake (Fig. 1).

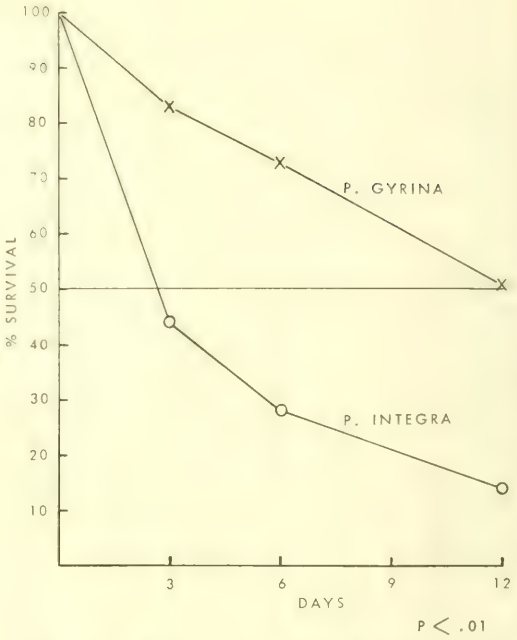

FIG. 15. Relative tolerance of *Physa gyrina* and *P. integra* to desiccation. Percent of survival after 3, 6 and 12 days, from a series of 4 experiments, each using 40 snails of each species. The difference between species is significant ($P > .01$).

Results (Fig. 15): *P. gyrina* showed considerably greater tolerance to drying than did *P. integra*. After 3 days, the percentage of survival in *P. gyrina* was 83 ± 11% (SD) while that in *P. integra* was 44 ± 17%; after 6 days: *P. gyrina*

73 ± 10% and *P. integra* 28±12%; and after 12 days: *P. gyrina* 51 ± 14% and *P. integra* 14 ± 14%. In *P. integra*, 50% mortality was reached in 3 days, but in *P. gyrina* not until 12 days. These differences between species are considered significant ($P < .01$). Limited tolerance to drying is probably, therefore, an important factor helping to explain the absence of *P. integra* from temporary ponds.

Data from a comparable set of experiments involving *P. integra* collected at Big Stoney Point on Spirit Lake and *P. gyrina* from 2 ponds in the area were more highly variable, but tended to confirm the above conclusions. They also suggest that considerable intraspecific variation occurs among populations of both species; in these 50% mortality occurred after an average of 10 days in *P. integra* and 23 days in *P. gyrina*.

Field data: Clear Creek Pond, near Iowa City (also discussed above, p 124), previously well-populated with *P. gyrina*, gradually dried out during a period of drought during late summer and early fall of 1962. In late September, at a time when the pond had held no free water for perhaps 2 weeks, an intensive search was made for live *P. gyrina*. A small number (totalling 19 during a search of at least 1 hour) were finally found. These were nearly all on the flat bottom mud near the center of the pond, the mud having gradually dried and cracked at intervals. These snails were fairly small (5 - 11 mm long), and all were oriented with the apertures facing down into the mud. The edges of the shell of each snail were buried very slightly below the surface, and the dorsal side of the shell protruded above the mud. The snail body had in each case retracted well into the shell, and there was usually an epiphragm, i.e., a small layer of dried mucus slightly behind the aperture. When placed in water, these snails, within a very few minutes, emerged and became active. A rainy period in early October temporarily improved moisture conditions in the pond. More dry weather was in turn succeeded by frost, and by the end of October nearly all of the snails had apparently been killed. An hour's search on October 29, 1962, yielded 1 live *P. gyrina*. Mortality at this time was, I believe, the direct result of freezing rather than of drying. That some of the snails survived through the winter has already been mentioned, p 124.

A small roadside pond about 3 miles (5 km) southwest of the Iowa Lakeside Laboratory on West Okoboji Lake was the focus of other observations on desiccation and survival in *P. gyrina*. During a dry period in the summer of 1964, the water gradually receded in this mud-bottomed pond (a good habitat for *P. gyrina*) so that by late July practically no standing water remained. On July 29, what was thought to be an intensive search for *P. gyrina* in the pond - on the partly dried mud, amongst the stems and leaves of *Typha*, *Carex* and other pond plants, and in the little remaining standing water - revealed no live specimens of this species. Then on the night of July 30, a 10-cm rainfall drenched the area. On again visiting the pond, now filled with water, I found rather to my surprise that live *P. gyrina* of adult size were quite numerous; 75 specimens were collected in less than half an hour. The possibility that these snails burrow in the mud as a temporary pond dries up (affirmed by DeWitt, 1955), tentatively rejected on the basis of the experience at Clear Creek Pond, had to be reconsidered. This problem warrants further investigation.

CONCLUSIONS

Apart from differences in size, there appear to be no morphological differences between the 2 species which would help to explain their differential distribution. But the size at maturity may be critical. A shell length of 7 mm is about the minimum size at which *P. gyrina* becomes sexually mature (DeWitt, 1955); 5 mm is the corresponding figure

for *P. integra*. The greater absolute size of *P. gyrina*, and the resulting decrease in the ratio of surface to volume, coupled with the respiratory needs of the animal, may be important in restricting this species, in summer populations, to very shallow water where snails have ready access to the surface for air-breathing. Conversely *P. integra* is less restricted, and its smaller size may be responsible, for corresponding reasons. In the vegetated offshore areas where this species is plentiful, the mantle cavity is filled with water; respiratory needs would thus appear to be satisfied, through the entire life cycle, by direct diffusion of gases through the integument. This parallels the situation described by Hunter (1953, 1964) for offshore populations of *Physa fontinalis* in Loch Lomond, Scotland. The available evidence suggests that the need for aerial oxygen may be limiting for *P. gyrina*, but not for *P. integra*.

The slower rate of growth of *P. integra*, and potentially, the more extended period of reproduction, could mean that this species needs relatively more stable conditions in order to survive and reproduce than does *P. gyrina*. These include food, temperature, oxygen and permanence of water; a larger body of water, such as a lake, provides such stability to a degree which a pond does not.

Because the food of both species is so varied, it is probably not limiting for either species in most habitats where they might otherwise be found. Appropriate foods may conceivably be in short supply, however, for *P. integra* in the vegetated offshore areas; stomach analyses performed on a few *P. integra* from such a habitat (Little Miller's Bay) indicate that the food is restricted largely to detritus and algae and that no vascular plant material is consumed. Hunter (1961b) attributed the smaller sizes and poorer reproduction in offshore populations of *P. fontinalis* in part to poorer feeding conditions in these areas. Growth rate differences in the 2 species suggest the possibility of a difference in food utilization rate; it is possible that *P. gyrina* requires a greater quantity of food than does *P. integra*, but again, a knowledge of the diverse types of food which both species may consume leads to the conclusion that food rarely limits their distribution.

The 2 species showed different rates of dispersal, but other behavioral attributes that were tested (movements in response to temperature and to wave shock) were not found to be different. Whether the slower rate of dispersal of *P. integra* serves to limit the distribution of this species is doubtful. However, it seems plausible that with the more stable conditions of lakes than of ponds, in food supply and in other factors, less of a premium would be placed on mobility. It may be that *P. integra* finds itself in a suitable microhabitat most often by staying where it is, while *P. gyrina* in a pond moves about at random and thereby discovers new and suitable microhabitats as they develop and change (see Bovbjerg, 1957).

The data on temperature tolerance indicate that temperature probably is limiting for *P. integra* in that it will not survive high environmental temperatures. This species is probably excluded from ponds, of all types, partly for this reason. The greater tolerance of *P. gyrina* to lethally high temperatures indicates that temperature is less likely to be limiting for this species.

Drying also is probably a limiting factor for *P. integra*, and effectively excludes the species from temporary ponds. Small size may be a disadvantage in this connection, too. *P. integra* may dry out more rapidly than does *P. gyrina*, eventually to the point of no recovery, partly because of the smaller initial size and therefore greater relative surface area for evaporation.

Adults of both species can tolerate fairly heavy wave shock, but the young need protection. Without the success of a new generation, a population on a rocky lake shore cannot long endure. There-

fore heavy wave shock, in the absence of protection for the young (i.e., without rock pools or interstices among the stones), acts as a limiting factor on populations of both species in rocky, wave-washed, lake shore habitats.

Several questions which remain unanswered, or are revealed by this study, include the following: how much genetic plasticity is there in both species, as suggested by morphological differences (width-length ratios) in *P. gyrina* and size differences in different populations of *P. integra?* As for O_2 requirements, could winter reduction of oxygen tensions in ponds prevent their habitation by *P. integra* while allowing such habitation by *P. gyrina?* The tolerance of some *P. gyrina* to drying followed by freezing in the pond is very striking, and leads to the question: how do they survive? Do those that survive do so primarily because of position or because of their inherent hardiness? What is the migration pattern in winter? This point is no clearer for shore populations of *P. integra* than for *P. gyrina.* What in fact prevents the habitation by *P. gyrina* of the offshore lake habitats where *P. integra* is common? Is there continuity, and therefore gene flow, between the offshore populations of *P. integra* and those along the shore, or is there isolation, and thus the opportunity for speciation? What are the effects of the intensity and the duration of periods of light on the growth and on the reproductive patterns of the 2 species? What are the effects of predation and parasitism on their distribution and abundance? Finally, is there competition between species in the lake shore habitats where the 2 species are found together? These questions await further study.

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RÉSUMÉ

ECOLOGIE COMPARÉE DES GASTROPODES *PHYSA GYRINA* ET *PHYSA INTEGRA* (BASOMMATOPHORA: PHYSIDAE)

P. T. Clampitt

Une étude comparée a été faite sur 2 mollusques pulmonés d'eau douce, *Physa gyrina* Say et *P. integra* Haldeman, dans la région du lac Okoboji, Comté de Dickinson, Iowa, pour reconnaître la distribution locale de chaque espèce et ses causes.

P. integra a été trouvé comme habitant caractéristique des berges rocheuses du lac et des zones de végétation aquatique jusqu'à des profondeurs de 3 m au moins, mais se trouve totalement absent des mares. Des populations denses de *P. gyrina* ont été

trouvées dans les mares, sur les berges rocheuses du lac et dans les habitats de type intermédiaire, mais toujours de faible profondeur d'eau. Dans les populations naturelles des 2 espèces la croissance et l'activité reproductrice est la plus forte au printemps (d'avril à juin); il y a une très forte mortalité en été et la croissance est faible en hiver. *P. gyrina* a une croissance notablement plus rapide dans la nature et au laboratoire, mais, élevée en laboratoire, l'espèce *P. integra* atteint généralement la maturité sexuelle légèrement plus tôt (souvent moins de 2 mois). Au laboratoire, les 2 espèces produisent une moyenne de 200-300 oeufs par individu par mois, durant la période de pointe de la reproduction (4 mois chez *P. gyrina*, 6 mois chez *P. integra*).

Des analyses d'estomac et des expériences poussées au laboratoire sur les préférences alimentaires, font penser que les 2 espèces consomment une large variété de matériaux nutritionnels, dont le choix est surtout dû au fait qu'ils peuvent être désagrégés par râclage et ingérés. Les taux de dispersion de *P. gyrina* sont significativement plus élevés que ceux de *P. integra* au laboratoire et dans la nature. Les 2 espèces se comportent de la même manière dans les circonstances suivantes: dans une chambre à gradient thermique, elles se déplacent du pôle froid (11° C) en direction mais non à l'intérieur du pôle chaud (38°-40° C); toutes deux se déplacent librement dans un large champ de températures. Quand l'action des vagues est importante sur les berges, elles se déplacent en profondeur ou à l'abri des pierres. Elles viennent régulièrement en surface pour respirer l'air quand elles sont en eau peu profonde. *P. integra* cependant, en eau profonde, a la cavité palléale pleine d'eau et peut demeurer immergée toute sa vie.

P. gyrina peut résister à des hautes température (35° et 40° C) et aussi aux effets de sécheresse, pendant une période significativement plus longue que *P. integra*. En partie pour cette raison, *P. integra* est exclue des mares. La grande taille et le taux rapide de croissance de *P. gyrina* a pour résultante un besoin d'oxygène atmosphérique, ce qui limite cette espèce en été aux eaux très peu profondes, tandis que *P. integra*, plus petite et plus lente de croissance n'est pas aussi limitée. *P. integra* peut être restreinte aux conditions plus stables des lacs (par rapport aux mares) en partie à cause de sa croissance plus lente, de sa période de reproduction potentiellement plus longue et de son taux de dispersion plus lent en réponse aux changements de conditions de milieu.

A. L.

RESUMEN

ECOLOGIA COMPARADA DE *PHYSA GYRINA* Y *PHYSA INTEGRA* (BASOMMATOPHORA: PHYSIDAE)

P. T. Clampitt

Este estudio comparativo, sobre dos caracoles pulmonados *Physa gyrina* Say y *P. integra* Haldeman en el área del lago Okoboji, condado de Dickinson, Iowa, fué hecho para investigar la distribución local y sus causas, de cada especie.

P. integra resulta ser un habitante caracteristico de las margenes rocosas del lago y de la vegetación sumergida a profundidades 3 metros por lo menos, pero totalemente ausentes en charcos. En cambio, densas poblaciones de *P. gyrina* se encontraron en charcos, pero también en orillas rocosas o habitats de tipo intermedio, pero siempre en aguas de poca profundidad. En poblaciones silvestres de ambas especies, crecimiento y actividad reproductiva fueron mayores en la primavera (de Abril a Junio); hubo mortalidad considerable durante el verano y el crecimiento fué poco notable en invierno. *P. gyrina* fué, consistentemente, la especie de crecimiento más rápido ya en

el campo o en laboratorio, pero las *P. integra* desarrolladas en el laboratorio alcanzaron madurez reproductora un poco antes (con frecuencia a los dos meses). En laboratorio, ambas especies produjeron un término medio de 200-300 huevos por individuo en un mes durante el período culminante de reproducción (4 meses en *P. gyrina*, y 6 meses en *P. integra*).

Analisis estomacales y observaciones extensivas en el laboratorio sobre las preferencias alimenticias, sugieren que ambas especies consumen una amplia variedad de materiales, determinados principalments por lo que puedan escarbar e ingerir al alcance; hábitos alimenticios no mostraron apreciable diferencias. Dispersión de *P. gyrina* fue significativamente mayor que la rápidez de dispersion en *P. integra* en el laboratorio como en el campo. Las 2 especies tuvieron comportamientos similares bajo las siguientes circunstancias: En una cámara de temperatura gradiente se movieron desde el extremo frío (11° C) con tendencia hacia, pero no internandose, en el extremo cálido (38°-40° C); ambas se movieron libremente dentro de amplios límites de temperatura. Cuando la acción del oleaje era fuerte en las áreas rocosas se trasladaron a zonas más profundas o bajo la protección de las rocas. Cuando se encuentran en aguas de poca profundidad suben regularmente a la superficie para respirar. Sin embargo, *P. integra* en aguas hondas, tiene la cavidad paleal llena de agua y puede permanecer sumergida a través de todo el ciclo vital.

P. gyrina puede soportar altas temperaturas (35°-40° C) y también los efectos de la sequía por un período mucho más largo que *P. integra*. Por esta razón, particularmente, *P. integra* esta excluída de los charcos. El tamaño grande y el crecimiento rápido de *P. gyrina* con la resultante necesidad de oxígeno atmosférico, puede limitar la especie en verano a aguas muy superficiales, mientras que la más pequeña y de lento crecimiento, *P. integra*, no está tan restringida. *P. integra* puede estar limitada sin embargo a las condiciones de lagunas mas estables (en relación a charcos) parcialmente por su menor rapidez de crecimiento, un período de reproducción potencialmente más largo, y una rapidez de dispersión menor en respuesta a los cambios ambientales.

J. J. P.

АБСТРАКТ

СРАВНИТЕЛЬНАЯ ЭКОЛОГИЯ МОЛЛЮСКОВ *PHYSA GYRINA* И *PHYSA INTEGRA* (*BASOMMATOPHORA, PHYSIDAE*)

Ф. Т. КЛЕМПИТТ

В озере Окоборжи, Дикинсон, штат Айова, проводилось сравнительное исследование двух пресноводных моллюсков из *P. integra Haldeman* и *Pulmonata -Physa gyrina Say* с целью изучить их локальное распространение и причины его обусловливающие. *P. integra* оказалась характерным обитателем каменистых берегов озера и его заросших открытых частей, на глубине до 3м; в прудах полностью отсутствовала.

Плотные поселения *P. gyrina* были найдены в прудах, на каменистых берегах озера и в местообитаниях промежуточного характера, но всегда в очень мелких местах.

У диких популяций обоих видов рост и репродуктивная активность были наибольшие весной (с апреля по июнь); в течение лета наблюдалось их значительное отмирание, а самый слабый рост был зимой. *P. gyrina* - это наиболее быстрорастущий вид, как в полевых, так и в лабораторных условиях. *P. integra*, выращенная в лаборатории, обычно достигает половозрелости не-

много скорее (часто менее, чем через 2 месяца). В лабораторных условиях каждая особь обоих видов продуцирует, в среднем, по 200-300 яиц в месяц в период наиболее интенсивного размножения (4 месяца у *P. gyrina* и 6 месяцев у *P. integra*). Анализ желудков и обширные лабораторные наблюдения по предпочтению моллюсками той или иной пищи, позволили предположить, что оба вида потребляют самую разнообразную пищу. Ее состав определяется главным образом тем, что может быть легко соскоблено и заглочено. Образ питания у обоих видов сходный.

Дисперсность *P. gyrina* (как в лаборатории, так и в поле) значительно выше, чем у *P. integra*.

Оба вида в определенных условиях ведут себя сходным образом. Так, в камере градиентов температуры, они уходят от холодной стороны камеры (11°C) и имеют тенденцию находиться ближе к теплой стороне камеры (38°C-40°C), не входя, однако, в нее. Оба вида свободно двигаются в довольно широких пределах колебаний температуры. При сильном волнении воды у каменистых берегов озера, моллюски опускаются по камням ниже или уходят в более защищенные части.

На мелководьях они регулярно выходят на поверхность для воздушного дыхания. Однако, у *P. integra*, обитающей в более глубоких местах, мантийная полость наполнена водой, и они могут оставаться погруженными в течение всего жизненного цикла. *P. gyrina* может выдерживать высокую температуру (35-40°C) и осыхание гораздо дольше, чем *P. integra*. Частично поэтому *P. gyrina* не встречается в прудах. Большие размеры и более быстрый темп роста *P. gyrina* и, как следствие этого, потребность в атмосферном кислороде, возможно, ограничивают распространение этого вида летом, когда он приурочен лишь к очень мелководным районам. Местообитание более мелкой и медленно растущей *P. integra* не так сильно ограничено. Она, возможно, ограничена более устойчивыми (по сравнению с прудами) условиями обитания в озерах, частично благодаря ее более медленному росту, потенциально более длинному периоду размножения и более медленной скорости расселения при изменении условий обитания.

Z. A. F.

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STUDIES ON AQUATIC PULMONATE SNAILS IN CENTRAL AFRICA

I. FIELD DISTRIBUTION IN RELATION TO WATER CHEMISTRY

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ABSTRACT

The aim of this study was to determine if there was any relationship between the distribution and relative densities of 5 common aquatic snails and the calcium bicarbonate concentration of the aquatic environment. Fourteen stations were selected within a 50-mile radius of Salisbury, Rhodesia, to cover a wide range of calcium and bicarbonate concentration. These stations were classified as follows: "Soft water" - less than 5 mg/1 Ca and less than 20 mg/1 bicarbonate as $CaC0_3$; "medium water" - 5 to 40 mg/1 Ca and 20 to 200 mg/1 bicarbonate as $CaC0_3$; "hard water" - above 40 mg/1 Ca and above 200 mg/1 bicarbonate as $CaC0_3$. Monthly quantitative snail samples and water analyses were obtained from all stations for at least a 12-month period. Highest snail densities were found in the "medium water" stations; densities in the "soft water" stations were low.

Four distributional patterns were found: *Gyraulus* spp. (mainly *G. costulatus*) were found only in soft and medium water; *Bulinus* (*B.*) *tropicus* was restricted to medium water; *Biomphalaria pfeifferi* was found only in medium and hard water; *Bulinus* (*Physopsis*) *globosus* and *Lymnaea natalensis* were continuous in their distribution and were found in all water types, although densities were lower in soft water.

Much concern has been expressed over the lack of detailed information on the ecology of freshwater snails, particularly those species which act as intermediate hosts of the schistosomes of man (World Health Organization, Tech. Rep., 1957). One of the most important ecological problems is the unexplained irregular distribution of snails in unpolluted aquatic habitats. Many workers have attempted to correlate the preference of freshwater snails for particular types of habitats with physical and chemical factors, and to discover the range within which the snails can establish themselves.

Ayad (1956), Boycott (1936) and Watson (1958) have shown that important factors involved are the amount of available food, penetration of sunlight, current strength and nature of the substratum. The available data, however, are too scanty for assessment of the individual importance of these factors.

Boycott (1936), Andrade (1954), Andrade, Santos & Oliveira (1955), Gohar & El Gindy (1960) and Harry, Crumbie & Martinez de Jesus (1957) have suggested that some degree of correlation exists between the distribution of snails in various habitats and the chemistry of the water. In contrast to these views, Alves (1958), De Meillion, Frank & Allanson (1958), Frömming (1938), Marrill (1958) and Deschiens (1954, 1957) have all concluded that the distribution

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is independent of the water chemistry.

The irregular type of distribution of freshwater snails occurs in the Salisbury area of Rhodesia, which is typical of high ground in Central Africa. The main species concerned are *Biomphalaria pfeifferi* (Krauss), the intermediate host of *Schistosoma mansoni*, *Bulinus* (*Physopsis*) *globosus* (Morelet), the host of *Schistosoma haematobium*, *Lymnaea natalensis* (Krauss), the host of *Fasciola gigantica*, *Bulinus* (*Bulinus*) *tropicus* (Krauss), and *Gyraulus* spp. Many of the latter were examined by Mr. C. C. Cridland and were all found to be *Gyraulus costulatus* (Krauss); nevertheless, all specimens could not be checked and the possibility remains that other species were present. In addition species of *Ferrissia* appeared occasionally in samples, but, as the sampling and handling techniques used were not considered suitable for this snail, these records have not been included in this study.

METHODS

Fourteen field stations were chosen in the Salisbury area covering a wide range of chemical conditions, and monthly snail and water samples were taken over a period of a year. At some stations collecting began in December, 1961 and at others in January, 1962, or a month or 2 later. At a few stations the water sampling programme was continued for a further year.

Biological samples.

The samples were taken with a modified drag scoop, Hairston, et al. (1958). This consisted of an elongated aluminum box, with cross section dimensions 30 cm by 30 cm, attached to a long handle, open at the proximal end and with the distal end covered with metal gauze of 10 mesh/cm and mesh holes of 0.8 mm across. The lower edge of the scoop was equipped with a cutting hacksaw blade. The scoop was pulled over the substratum, thereby collecting specimens clinging to stout aquatic plants, those on and in the top layer of mud, and those floating on the surface in shallow water. It was most effective in fairly loose vegetation, but could not be used in rocky or stony areas. Samples were taken by pulling the scoop a distance of 2 metres through vegetation; this was done twice on each monthly visit.

Biological samples were preserved in the field with 4% formalin and later subdivided into 2 parts in the laboratory using a sieve with 8 mesh/cm. The large snails retained by the sieve were removed and sorted by eye and the rest of this portion, the "macrosample", was scanned for further snails under a dissecting microscope. The portion passing through the sieve, the "micro-sample", was retained in a fine net; as it was usually very bulky, it was sub-sampled by the method of Allanson & Kerrich (1961), and juvenile snails were identified and counted under a dissecting microscope. Finally, the results were combined and the composition of the snail fauna was calculated.

Water samples.

Four litres were collected in polythene bottles for chemical analyses following the techniques outlined in the American Public Health Association's Standard Methods (1960). The electrical conductivity of the water and the pH values were determined in the field using a "Dionic" conductivity meter and a "Lovibond" comparator respectively. The pH values were checked occasionally by glass electrode measurements. The alkalinity, acidity, chlorides, sulphates, calcium, magnesium, sodium and potassium contents were determined according to Standard Methods (1960). The phosphates and copper were determined by the methods presented by Murphy & Riley (1958) and Somer & Garraway (1957) respectively. Turbid waters during the wet season were centrifuged to remove suspended solids before analyses were made.

Field stations.

The annual rainfall in the Salisbury area is from 30 to 35 inches and is confined to the warm season extending from about November to April; thus dilution of dissolved substances occurs during this time. The rest of the year is dry, allowing concentration through evaporation.

Many small streams, ponds and farm dams dry up completely during this period, but the sampling station for this study were all perennial. The sites were chosen because of their water chemistry and are numbered in the ascending order of the bicarbonate and calcium concentrations. All sampling stations were within a 50-mile radius of Salisbury, Rhodesia, and lay at altitudes between 1000 m and 1450 m above sea level, experiencing much the same temperature regimes. Shiff (1964a,b) gives an account of the range of water temperatures in the region.

DESCRIPTION OF FIELD STATIONS

Stations 1 and 2 (31° 15'E, 17° 35'S) were pools in a small stream running over soils derived from granite formations, the depth varying from a few cms in the dry season to 30 cms during the "rains". Station 3 (31° 14'E, 17° 53'S) was on a quiet backwater of a similar small stream. At these 3 stations, fast flowing water during the rainy season prevented the establishment of many aquatic plants in the main stream, but emergent vegetation flourished in the quiet pools and backwaters of the sampling sites. The depth varied from about 30 cm to over 1 metre. Stations 4 and 5 (31° 9'E, 17° 51'S) were on the shore of an old and supplementary reservoir, the 1st being at the spillway and the 2nd at the upper reaches of the reservoir where the feeding streams entered; Stations 6 and 7 (31° 30E, 18° 1'S) were situated in a fairly large conservation dam which had its catchment area lying on soils derived from granite formations. Stations 8 and 9 (30° 47'E, 17° 52'S) were on the south shore of Lake McIlwaine, which is the main water supply to Salisbury. The lake is approximately 10 miles long and 2 to 3 miles wide. Station 10 (30° 35'E, 17° 46'S) was a small pool in a perennial stream where a concrete ford crossed the stream. Most of the catchment area was granite, but some basement series formations were included; thus the drainage waters contained more calcium salts than the former stations. The depth of water at this station varied from about 30 cm during the dry season to about 1 metre during the wet season, although flash floods sometimes raised the water level up to 2 metres for short periods. Station 11 (31° 3'E, 17° 46'S) was in a permanently flooded borrow pit which collected drainage water from the metavolcanic basement series. Stations 12, 13 and 14 (31° 31'E, 17° 20'S) were small pools in a stream which flowed for a few weeks only, during the middle of the wet season. For the rest of the year it consisted of a series of more or less permanent pools in a swampy area. The catchment was situated in a region characterised by metasedimentary rocks with some limestone; the water of this series of pools was the hardest encountered in the area.

At all the stations there was much emergent vegetation present, and often submerged aquatic plants as well.

RESULTS

1. Water Chemistry.

Table 1 summarises the results of the chemical analyses of the water from the field stations over a sampling period of 2 years, and shows the mean values of calcium, magnesium, sodium, potassium and bicarbonates, which are the ions associated with hardness and alkalinity. The salt present in the greatest concentration and common to all the field stations was calcium bicarbonate, and

consequently the field stations are arranged in an ascending order of concentration of this salt in Table 1. The stations were also classified as soft, medium and hard water types according to their calcium bicarbonate content. Soft waters contained <5 mg/1 Ca^{++} and <20 mg/1 HCO_3^-; medium water, 5 to 40 mg/1 Ca^{++} and 20 to 200 mg/1 HCO_3^-, and hard water >40 mg/1 Ca^{++} and >200 mg/1 HCO_3^-.

Amongst other ions investigated were the phosphates, since they influence algal growth which constitutes part of the snail's diet; sulphates, because their low concentrations might have limiting effects on the snail distribution; and copper, since it is a known snail poison and is mined in the sampling area. The copper, sulphate, phosphate and chloride concentrations have, however, about the same range of values from Stations 1 to 14. They are thus unlikely to affect the abundance and consequently the distribution of the snails.

2. General distribution of snails

The summary analysis of the snails collected from the field stations is shown in Table 2. The next to the last column shows the total catches of snails at each station, and in the final column these catches are shown as percentages of the total snails recovered from all stations. The results are shown graphically in Fig. 1. The ionic concentrations increase progressively from Station 1 to 14, and the ratio of Ca^{++} to HCO_3^- ions is relatively constant at all stations. Any increase in the calcium ion concentration thus has a proportional increase in the alkalinity. This graph and the histograms (Fig. 2) relate the field results to the calcium ions only, but similar results would be obtained using the bicarbonate concentration.

It can be seen from Table 2 and Fig. 1 that when the total of all snail species is considered, numbers were low in soft water, rose to a maximum in medium water, and declined again in hard water; the ratio in the 3 types of water, expressed as a percentage of the total snails, was 11% 67% and 22% respectively.

3. Specific distribution patterns.

Table 3 presents the total number of snails of each of the individual species in each of the 3 water types (soft, medium and hard), as a percentage of the total snails of all species collected. This allows a comparison of the abundance of each species to be made in the different water types, and also allows a comparison of the total abundance of each species throughout the whole range of water chemistry.

Fig. 2 presents the number of snails of each individual species found in a particular water hardness range. As there were different numbers of stations per "water type", figures here have been adjusted as if there were 6 stations in each, and expressed as a percentage of the new total number of snails of that species found throughout the whole area. It can be seen that there are 4 distribution patterns. The first, represented by *Gyraulus* spp. (probably mostly *G. costulatus*), is a discontinuous one, for this species was absent from hard waters. Of their total numbers, 94% were recovered from medium water, and the remaining 6% were taken in the soft water range.

A 2nd type of distribution pattern, although again discontinuous, is shown by *Bulinus* (*B.*) *tropicus*. This species was even more restricted than *Gyraulus* spp., and was found only in medium type waters.

A 3rd type of distribution pattern, represented by 2 species, *Lymnaea natalensis* and *Bulinus* (*Ph.*) *globosus*, is of the continuous kind. Both species exist in the 3 types of water; *L. natalensis* attained its maximum population level in the medium water concentrations, but also tolerated soft and hard waters. *B.* (*Ph.*) *globosus* showed a

TABLE 1. Summary analyses of chemical results

		Stations											
		1	2	3	4, 5	6, 7	8	9	10	11	12*	13*	14*
Conductivity in micromhos	Max.*	48	39	53	40	75	108	155	290	245	650	700	870
	Mean	30	25	28	34	50	95	89	163	165	486	328	492
	Min.	18	14	20	30	20	86	56	87	206	48	85	87
pH	Max.	7.1	7.0	7.0	7.4	7.5	9.3	7.5	7.7	8.3	8.2	8.2	8.3
	Mean	6.9	6.8	6.9	7.1	7.1	8.0	6.9	7.2	7.8	7.7	7.7	7.9
	Min.	6.7	6.7	6.8	6.8	6.8	7.2	6.7	7.0	7.4	7.0	7.4	7.0
Carbonates, mg/1 as $CaCO_3$	Max.	-	-	-	-	-	12	-	-	-	-	-	-
	Mean												
	Min.	-	-	-	-	-	2	-	-	-	-	-	-
Bicarbonates, mg/1 as $CaCO_3$	Max.	28	21	33	26	45	43	100	190	142	470	469	557
	Mean	17	14	16	20	23	38	42	90	113	308	234	317
	Min.	12	9	10	17	18	20	27	51	90	30	37	37
Chlorides as mg/1 Cl	Max.	2.1	2.1	2.3	2.0	2.6	10.5	8.2	2.6	7.0	5.5	3.3	21.5
	Mean	1.3	1.4	1.3	1.1	1.3	4.5	3.2	1.7	3.1	2.4	2.1	4.4
	Min.	0.8	0.7	0.6	0.6	0.6	0.4	0.3	1.0	0.3	0.9	0.9	1.2
Phosphates as mg/1 PO_4	Max.	0.12	0.12	0.08	0.08	0.1	0.15	0.1	0.14	0.17	0.16	0.12	0.10
	Mean	0.08	0.07	0.06	0.07	0.07	0.09	0.09	0.10	0.12	0.12	0.09	0.08
	Min.	0.06	0.04	0.05	0.06	0.05	0.07	0.06	0.09	0.08	0.10	0.08	0.06
Magnesium as mg/1 Mg	Max.	2.5	2.2	6.6	1.2	4.1	3.4	4.0	13.5	27.9	44.0	43.0	64.0
	Mean	1.2	0.9	1.8	1.0	1.8	2.0	2.6	8.7	12.7	26.9	24.4	38.9
	Min.	0.3	0.5	0.4	0.5	0.1	0.4	0.9	3.1	9.0	0.1	3.5	14.0
Calcium as mg/1 Ca	Max.	2.9	3.7	8.4	6.1	7.1	11.3	24.6	32.4	31.1	101.0	93.0	95.0
	Mean	2.1	2.0	3.4	3.0	5.0	7.4	12.0	16.0	22.0	56.0	45.0	58.0
	Min.	0.9	0.8	0.9	0.6	2.9	4.9	4.4	6.9	17.0	6.2	11.0	22.0
Sodium as mg/1 Na	Max.	8.0	7.2	19.0	6.7	9.4	14.0	13.6	25.3	15.0	46.0	48.0	102.0
	Mean	4.7	4.7	7.5	4.9	7.0	12.0	9.9	16.8	12.0	34.0	29.0	53.0
	Min.	2.9	3.0	3.0	4.2	3.0	9.4	7.0	3.4	8.0	13.0	5.0	12.0
Potassium as mg/1 K	Max.	4.6	2.4	2.4	2.3	1.0	6.1	2.3	5.4	2.9	8.1	12.8	18.3
	Mean	1.6	1.2	1.7	1.4	0.8	3.6	1.5	2.6	1.9	5.5	6.8	8.6
	Min.	0.5	0.1	0.5	0.6	0.2	2.3	1.0	0.7	0.9	2.8	2.8	2.8
Copper as mg/1 Cu	Max.	0.07	0.05	0.02	0.04	0.01	0.08	0.08	0.04	0.02	0.08	0.2	0.09
	Mean	0.04	0.03	0.02	0.03	0.005	0.04	0.04	0.03	0.02	0.03	0.01	0.04
	Min.	0.02	0.02	0.01	0.03	0.002	0.02	0.02	0.02	0.01	0.006	0.006	0.02
Sulphates as mg/1 SO	Max.	7	8	5	2	3	9	6	6	7	6	8	20
	Mean	3.1	3.2	2.2	1.5	2	4	3	2	3	4	6	12.0
	Min.	1	1	1	1	1	1	1	1	1	1	1	1
Water type		Soft	Soft	Soft	Medium	Medium	Medium	Medium	Medium	Medium	Hard	Hard	Hard

*The very low minima for these stations persisted for periods of a few weeks during exceptionally heavy flooding. After floods had subsided values rose very rapidly and for 10 months of the year did not drop much below the mean values given.

**Max. = maximum; min. = minimum.

TABLE 2. Summary analyses of field results

Station No.	Water type	Annual total *B. (Ph.) globosus*	As % all *B. (Ph.) globosus*	Annual total *B. pfeiffferi*	As % all *B. pfeiffferi*	Annual total *Gyraulus* spp.	As % all *Gyraulus* spp.	Annual total *L. natalensis*	As % all *L. natalensis*	AAnnual total *B. (B.) tropicus*	As % all *B. (B.) tropicus*	Total snails	As % all snails
1	Soft	42	3.3	--	--	5	0.2	90	1.2	--	--	137	0.8
2	Soft	70	5.4	--	--	85	2.9	--	--	--	--	155	1.0
3	Soft	62	4.8	--	--	32	1.1	118	1.6	--	--	212	1.3
4	Soft	54	4.2	2	0.06	4	0.2	614	8.4	--	--	674	4.1
5	Soft	160	12.4	1	0.03	13	0.4	389	5.3	--	--	563	3.4
6	Medium	1	0.8	187	5.3	334	11.3	272	3.7	79	6	873	5.3
7	Medium	151	11.7	115	3.3	981	33.3	1785	10.7	460	35.8	2492	15.2
8	Medium	66	5.1	39	1.1	99	3.4	2988	40.8	268	20.9	3460	21.2
9	Medium	91	7.1	53	1.5	3	0.1	833	11.4	131	10.2	1111	6.8
10	Medium	289	22.4	1083	30.7	1268	43.0	410	5.6	35	2.7	3085	18.9
11	Medium	--	--	1124	31.9	122	4.1	--	--	312	24.3	1558	9.5
12	Hard	68	5.3	125	3.5	--	--	50	0.7	--	--	243	1.5
13	Hard	90	7.0	468	13.3	--	--	721	9.9	--	--	1279	7.8
14	Hard	145	11.3	331	9.4	--	--	40	0.6	--	--	516	3.2
Total		1289	100%	3528	100%	2946	100%	7310	100%	1285	100%	16,358	100%

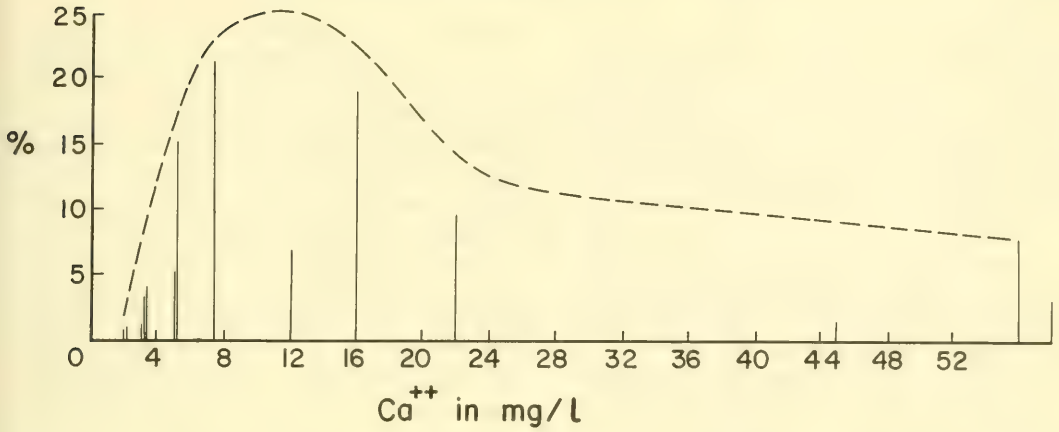

FIG. 1. Distribution of aquatic pulmonates in relation to calcium concentrations. The annual total of snails per station is expressed as a percentage of all snails collected from all stations.

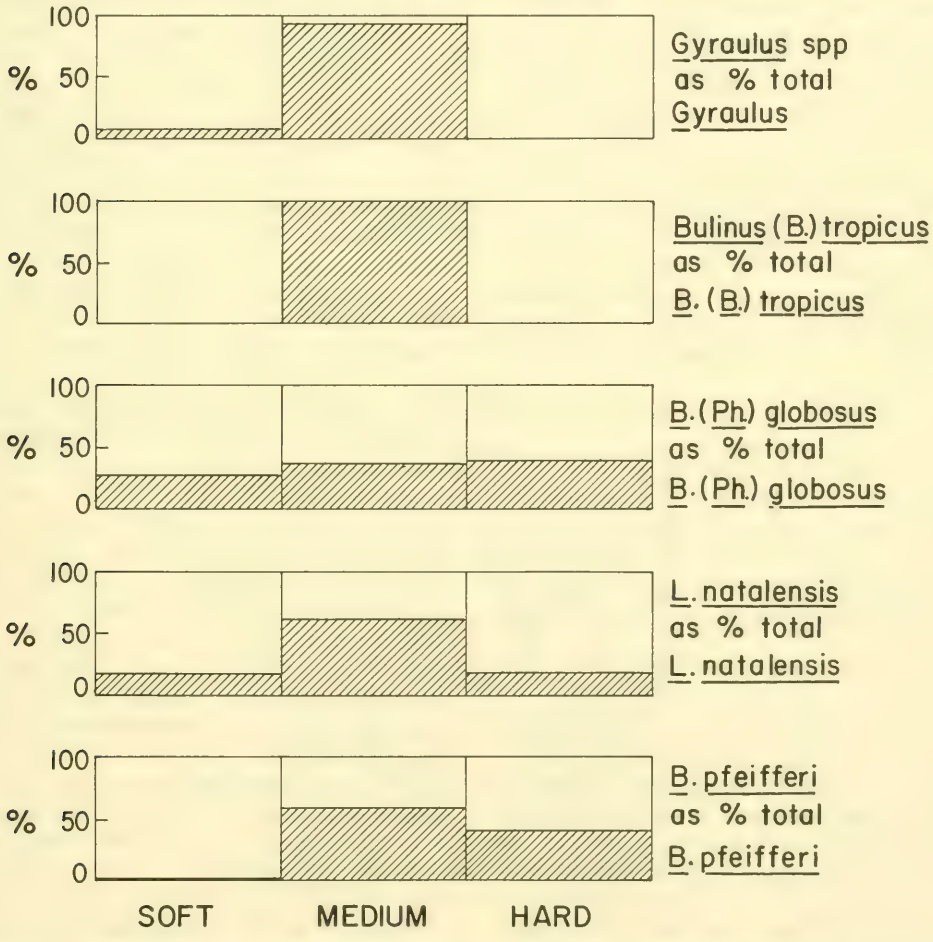

FIG. 2. Distribution of snails in relation to calcium concentrations. Figures have been adjusted for an equal number of snails per water type.

TABLE 3. Percentage distribution of all snails in relation to alkalinity and hardness

Chemical characteristic		Snail species									
Ca^{++} in mg/l.	HCO_3^- in mg/l.	*B. (Ph.) globosus*		*B. (B.) tropicus*		*B. pfeifferi*		*Gyraulus* spp.		*L. natalensis*	
		Nos.	As % all snails	Nos.	As % all snails	Nos.	As % all snails	Nos.	As % all snails	Nos.	As % all snails
0–5 (soft water)	0.–20	388	2.4	–	–	3	0.02	139	0.9	1211	7.4
5–40 (medium water)	20–200	598	3.7	1285	7.9	2601	16.0	2807	17.2	5288	32.3
Over 40 (hard water)	Over 200	303	1.9	–	–	924	5.7	–	–	811	5.0
Total %			8.0		7.9		21.7		18.1		44.7

more even distribution, but with a tendency to fall off in soft water.

A 4th and last type of distribution pattern, illustrated by *Biomphalaria pfeifferi*, was again of the discontinuous kind. This species obviously cannot live successfully under soft water conditions; only 3 specimens were collected in these waters during the sampling period. Of the total *B. pfeifferi* population, 58% was found in the medium range, but this species can also thrive well in hard water, where the remaining 41% were taken.

DISCUSSION

Both lentic and lotic habitats were included in the soft and medium water types. The 3 hard water stations were running for a few weeks during the height of the wet season, but at other times they could be considered to be ponds. The general distribution pattern of all snail species, irrespective of the habitat type was: low densities in soft waters and maximum densities in medium waters. From the more limited results available from hard water stations, there appeared to be a tendency for densities to be lower than in medium water. These hard water results are treated with more caution because of the close proximity of the stations, and because there were only 3 hard water stations; nevertheless, from other aspects, they would all have appeared to have been very suitable snail habitats as flood scour during the rainy season was minimal and the pools contained much aquatic vegetation and a rich invertebrate fauna. Harrison & Mason (1967) studied another hard water stream in the same district, which had been treated with molluscicide; when molluscicide was discontinued a similar snail fauna developed.

The specific distribution pattern shows that *Lymnaea natalensis* was more abundant in soft and medium water concentrations than any of the other 4 species, and it was also the most abundant snail species in the field, forming nearly 45% of the total snail collection. The fact that it is well distributed throughout the whole water hardness range is of economic importance, since it is the intermediate host of the liver fluke, *Fasciola gigantica*.

Biomphalaria pfeifferi was found to be the 2nd most abundant species in the area, forming 20% of the total snails, but it had a more limited range of distribution, being largely restricted to medium and hard water types, and it was less tolerant of soft water. This species was, however, the most abundant snail in the hard water range.

Bulinus (*Ph.*) *globosus* was found in all types of water, but formed only 8% of the total catch. These results are reflected in epidemiological studies of schistosomiasis, for although *Bulinus* (*Ph.*) *globosus*, the host of *Schistosoma haematobium*, forms only 8% of the total catch, its wide distribution results in a similar wide distribution of the parasite. On the other hand, *Schistosoma mansoni*, found in *Biomphalaria pfeifferi*, has a more restricted range, similar to its snail.

ACKNOWLEDGEMENTS

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RÉSUMÉ

ETUDES SUR LES MOLLUSQUES PULMONÉS AQUATIQUES D'AFRIQUE CENTRALE I. DISTRIBUTION NATURELLE EN RELATION AVEC LA NATURE CHIMIQUE DES EAUX

N. V. Williams

Le but de cette étude est de vérifier s'il y a une relation entre la distribution et la densité relative de 5 pulmonés aquatiques communs d'une part et la concentration du milieu aquatique en carbonate de calcium d'autre part. Quatorze stations ont été sélectionnées à l'intérieur d'un rayon de 50 miles autour de Salisbury, Rhodésie, de façon à recouvrir une large échelle de concentration en calcium et bicarbonate. Ces stations ont été classées comme suit: "eaux douces" - moins de 5 mg/l Ca et moins de 20 mg/l de bicarbonate exprimé en $CaCO_3$; "eaux moyennes" - de 5 à 40 mg/l Ca et de 20 à 200 mg/l de bicarbonate exprimé en $CaCO_3$; "eaux dures" - plus de 40 mg/l Ca et plus de 200 mg/l de bicarbonate exprimé en $CaCO_3$. Chaque mois des relevés quantitatifs de mollusques et des analyses d'eau ont été faits dans toutes les stations et ceci pendant une période d'au moin 12 mois. Les plus fortes densités de mollusques ont été trouvées dans les stations d' "eaux moyennes"; les densités dans les stations d' "eaux douces" étaient faibles.

Quatre modes de distribution ont été distingués: *Gyraulus* spp. (surtout *G. costulatus*) se trouvent seulement dans les eaux "douces" et "moyennes"; *Bulinus* (*B.*) *tropicus* est cantonné dans les eaux "moyennes"; *Biomphalaria pfeifferi* ne se rencontre que dans les eaux "moyennes" et "dures"; *Bulinus* (*Physopsis*) *globosus* et *Lymnaea natalensis* sont constantes dans leur distribution et se rencontrent dans tous les types d'eaux, bien que leurs densités soient plus faibles dans les eaux "douces".

A. L.

RESUMEN

ESTUDIOS SOBRE PULMONADOS ACUATICOS EN AFRICA CENTRAL I. DISTRIBUCION EN RELACION A LA QUIMICA DEL AGUA

N. V. Williams

El propósito de este estudio fué el de determinar la posible relación entre la distribución y densidad relativa de población, de 5 cinco especies de caracoles dulceacuícolas comunes, y la concentración de carbonato de calcio en el ambiente. Se eligieron 14 estaciones dentro de un radio de 50 millas de Salisbury, Rodesia, para cubrir un vasto campo de concentración de carbonato de calcio. Las estaciones se clasificaron como sigue: "Aguas blandas" (de menor concentración) con menos de 5 mg/l Ca y menos de 20 mg/l bicarbonato como $CaCo_3$; "aguas intermedias", con 5 a 40 mg/l Ca y 20 a 200 mg/l bicarbonato como $CaCo_3$; "aguas duras" con más de mg/l Ca y más de 200 mg/l bicarbonato como $CaCo_3$. Muestras cuantitativas mensuales de caracoles y analisis de aguas se sacaron por un periodo de por lo menos 12 meses. La mayor densidad de caracoles se encontró en aguas intermedias; en las aguas blandas la densidad fue la menor.

Pudieron establecerse cuatro patrones distribucionales: *Gyraulus* spp. (principalemente *G. costulatus*) se encontró solamente en aguas blandas y medianas; *Bulinus* (*B.*) *tropicus* restringido a las aguas medianas; *Biomphalaria pfeifferi* solamente en aguas medias y duras; *Bulinus* (*Physopsis*) *globosus* y *Lymnaea natalensis* en todos los tipos de agua, aunque la densidad fué más bien menor en las aguas blandas.

J. J. P.

АБСТРАКТ

ИЗУЧЕНИЕ ВОДНЫХ УЛИТОК PULMONATA ИЗ ЦЕНТРАЛЬНОЙ АФРИКИ
I. РАСПРОСТРАНЕНИЕ МОЛЛЮСКОВ В ПРИРОДЕ В СВЯЗИ
С ХИМИЗМОМ ВОДЫ

Н. В. ВИЛЬЯМС

Целью настоящей работы было: определить имеется ли какая-нибудь связь между распространением и относительной плотностью поселений 5 обычных водных моллюсков и концентрацией бикарбоната кальция в воде. Было выбрано 14 станций в радиусе 50 миль от Солсбери, Родезия, чтобы охватить более широкий диапазон изменений концентраций кальция и бикарбонатов. Эти станции были классифицированы следующим образом: "мягкая вода"-менее 5 мг/л Са и менее 20 мг/л бикарбонатов ($CaCO_3$); "средняя вода"-около 5-40 мг/л Са и 20-200 мг/л бикарбонатов ($CaCO_3$); "жесткая вода"-более 40 мг/л Са и более 200 мг/л бикарбонатов. В течение 12 месяцев ежемесячно на всех станциях брались количественные пробы моллюсков и анализы воды. Самая высокая концентрация моллюсков наблюдалась на станциях в "средних водах", а самая низкая-в "мягких водах".

Было отмечено 4 типа их распространения: *Gyraulus* spp. (главным образом, *G. costulatus*) были найдены только в мягких и средних водах; *Bulinus* (*B.*) *tropicus* придерживается средних вод; *Biomphalaria pfeifferi* была найдена только в средних и жестких водах; *Bulinus* (*Physopsis*) *globosus* и *Lymnaea natalensis* имели распространение непрерывное и были найдены в водах всех типов, хотя плотность их поселений в мягких водах была ниже.

Z. A. F.

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STUDIES ON AQUATIC PULMONATE SNAILS IN CENTRAL AFRICA

II. EXPERIMENTAL INVESTIGATION OF FIELD DISTRIBUTION PATTERNS

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ABSTRACT

These experimental studies followed field studies on the distribution of aquatic snails in the region of Salisbury, Rhodesia, in which the distribution and relative density of 5 species had been shown to bear some relationship to the calcium and bicarbonate concentrations of the aquatic environment. Two species were selected for confirmatory laboratory experiments: *Bulinus (Physopsis) globosus*, which had been present in waters containing very low concentrations of calcium bicarbonate to waters containing high concentrations, and *Biomphalaria pfeifferi*, which had been shown to be limited to waters with medium to high concentrations of calcium bicarbonate.

The 2 species were cultured in the laboratory in media designed to cover a wide range of calcium and bicarbonate concentrations, at a constant temperature of 25 C and with other controllable factors kept as constant as possible. Age specific fecundity and survivorship rates were determined for each test culture medium, and the mean generation time (MGT), the finite rate of increase (R) and the intrinsic rate of natural increase (r_m) were estimated.

The r_m values obtained for *Biomphalaria pfeifferi* showed that there were distinctly higher increase rates of experimental populations at medium concentrations of bicarbonate and calcium ions than at the upper and lower extremes. In addition, the r_m values were directly proportional to the relative density of this species at the different concentrations in the field, suggesting that its discontinuous distribution was partly due to its limited tolerance to the extremes of the calcium bicarbonate concentration range occuring in the Salisbury region, notably the lower extreme.

The r_m values obtained for *Bulinus (Ph.) globosus* also indicated that the highest population increase occurred at medium concentrations of calcium bicarbonate. However, the range of r_m values, obtained from the lowest to the highest ionic concentrations, was much smaller for this species than for the previous one, and no significant relationship was found between these values and the relative densities found in the field. This suggests that its continuous field distribution is due, in part, to its wider tolerance of calcium bicarbonate concentrations.

Field studies on 5 species of aquatic pulmonate snails in the Salisbury region of Rhodesia, Central Africa, have shown that the distribution of at least 3 of them is influenced by the ionic composition of the natural waters. Because of the complicated surface geology of the region, there was great variation in the composition of run-off water and it was found that these could be classified into 3 main types according to the calcium and bicarbonate concentrations: "soft" - <5 mg/l Ca^{++} and <20 mg/l HCO_3^-, as $CaCO_3$; "medium" - 5 to 40 mg/l Ca^{++} and 20 to 200 mg/l HCO_3^- as $CaCO_3$; and "hard" - >40 mg/l Ca^{++}

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and >200 mg/l HCO_3^- as $CaCO_3$. The field distribution of some species could be related to the distribution of these water types.

The aims of this experiment were to culture the snails in the laboratory in test waters covering these ranges of calcium and bicarbonate concentrations and to determine the effects on the life histories. It was hoped that the results might help to explain the field distribution patterns. Two species were chosen for the experiment, *Biomphalaria pfeifferi* (Krauss), the intermediate host of the "human" schistosome, *Schistosoma mansoni*, and *Bulinus* (*Physopsis*) *globsus* (Morelet), the intermediate host of *Schistosoma haematobium*. The field survey had shown that the first snail was restricted to waters of the "medium" and "hard" types, and the second had been shown to occur in all three types.

METHODS

Experimental parameters.

It was assumed from the field work that the effects of the different levels of calcium and bicarbonate concentrations on the snail life histories would be a subtle one, so that some parameter more sensitive than growth rate, egg-laying rate or death rate would have to be used.

Shiff (1964a) and Shiff & Garnett (1967) were able to demonstrate a relationship between different constant temperature levels in the culture medium and the intrinsic rate of natural increase (the biometric parameter r_m) of these 2 species of snails. Since values for r_m are obtained from a formula combining figures for survivorship and fecundity, it was decided to use this concept in the interpretation of these experimental studies.

The use of this parameter in ecology derives from Lotka's (1925) work on human populations. Andrewartha & Birch (1954) emphasize the importance of the biometric parameter r_m, "the innate capacity for increase," which they define as "the maximal rate of increase attained at any particular combination of temperature, moisture, quality of food, and so on, when the quantity of food, space and other animals of the same kind are kept at an optimum and other organisms of different kinds are excluded from the experiment." Nevertheless, they give sound reasons for introducing Lotka's concept of "stable age-distribution" into the definition and point out that his "intrinsic rate of natural increase " is the same as their "innate capacity for increase". The precise value for r_m may be obtained by solving the equation:

$$\int_0^\infty e^{-r_m x} \, l_x m_x \delta_x = 1$$

where x is the time interval considered
l_x is survivorship at time x
m_x is the number of female births at "pivotal age" x
e is the base of natural logarithms
r_m is the intrinsic rate of natural increase.

Andrewartha & Birch (1954) point out that r_m is a statistic which summarises those physiological qualities of an animal that are related to its capacity for increasing, qualities which are truly "innate" and which make r_m as characteristic of a species as its morphology.

Using the summation rather than the integral, it is possible to use experimentally obtained $l_x m_x$ data and to arrive at a solution for r_m. This is ordinarily done by a process of trial and error, as described by Andrewartha and Birch, using the equation:

$$r_m = \frac{\log_e \sum l_x m_x}{T}$$

T being the mean generation time of the population.

The experiments described below were designed to obtain survivorship (l_x) and

fecundity (m_x) data for the estimation of r_m values at different levels of calcium and bicarbonate concentrations, keeping all other controllable factors as constant and optimal as possible. It should be pointed out that both species of snails are hermaphrodites and are truly female during most of their reproductive lives, thus all births (i.e., fertile eggs) and deaths had to be taken into account.

The time intervals, x, used in the experiment were periods of 2 weeks, or a fortnight, and the "pivotal ages," when l_x and m_x values were calculated, were the middle points of these periods, 0.5x, 1.5x etc., to 13.5x.

Snail Culture.

The composition of the culture media for the 12 experiments carried out is given in Table 1. Natural waters were used for experiments 2 and 7; an entirely artifical, calcium-free solution was used for experiment 1; and the rest were built up from natural water 7 by adding deionised water and analytical reagents.

To study the effects of different levels of bicarbonates, solutions with values from 0 to 800 mg/l of bicarbonates, as $CaCO_3$, were prepared, this range being greater than the range encountered in natural environments during the field studies. The bicarbonate anions were built up with the sodium, magnesium and potassium salts, keeping these and the calcium levels at values consistent with the values found in the medium and hard waters in the field.

In a similar fashion, artifical snail culture solutions of calcium were prepared from 0 to 50 mg/l, as Ca, using the sulphate and chloride salts. The bicarbonate values were kept consistent with medium water levels in the field. The required amounts of ions for the various levels were theoretically computed, and the solutions analysed every 2 to 3 days to check the concentrations.

Tap water, which had been allowed to mature in a small outside concrete pond to eliminate the chlorine introduced by the municipal chlorination process, was used for the control experiments (7). At no time during the experiments were the various ratios of sodium, magnesium, potassium, sulphates and chlorides in the culture solutions, allowed to exceed the ratio of these salts found in the natural waters.

The culture of both *Biomphalaria pfeifferi* and *Bulinus* (*Ph.*) *globosus* was essentially similar. The eggs of both species are laid in oval to round capsules, the 1st species having 20 to 30 eggs per capsule and the 2nd having a larger number, usually up to 40 eggs per capsule. Since about 50 individuals are necessary for a suitable sized "cohort" for the establishment of a life table, 2 to 3 capsules were used per culture. The initial size of the cohorts was between 39 and 68 individuals, but most were between 50 and 60.

Individual stock tanks, containing unparasitised snails originating from individuals netted from Lake McIlwaine near Salisbury, were kept at 25°C ± 0.5°C in constant temperature cabinets. This was the temperature at which Shiff (1964a) obtained maximum "r_m" values for these snail species. Both species were kept in separate tanks and laid their egg capsules on the glass walls. These egg capsules were removed with clean razor blades when they were 4 to 5 days old. Those capsules showing live embryos were placed in 500 ml of the various artificial culture solutions contained in small plastic dishes, and were placed in the constant temperature cabinets.

Biomphalaria pfeifferi were fed after hatching with small pieces of boiled lettuce leaves. These leaves had been previously boiled and dried, the 2nd boiling ensuring the removal of air and further softening of the plant tissues. A small piece about 1 sq. cm was placed on the bottom of each container in an attempt to ensure that

searching for food by the young snails was kept to a minimum.

Bulinus (*Ph.*) *globosus* did not thrive very successfully when fed immediately on lettuce. Faeces from adult snails were therefore introduced into the media during the first week after hatching and the young snails fed on their algal content. When *Biomphalaria pfeifferi* and *B.* (*Ph.*) *globosus* reached a diameter of 1 to 2 mm, they were transferred to crystalising dishes of 1 litre capacity, and reared in these until they were 6 weeks old. They were finally transferred to large aquaria containing 12 litres of solution. The population of *B. pfeifferi* was maintained at a density of 1 to 1.5 snails per litre and that of *B.* (*Ph.*) *globosus* at 1 snail per litre of solution. Shiff (1964b) shows that the growth rate of the latter species is retarded at densities in excess of this. The aquaria were maintained in an aquarium room at a constant temperature of 25°C ± 1.0°C; the room received some daylight which was supplemented during the day with fluorescent light. Faeces and detritus were pipetted out of the aquaria every 2 or 3 days and fresh, dried lettuce was added daily. The culture solutions were tested at the same time as the tanks were cleaned, and their concentrations were adjusted if necessary. Make-up water was added to keep the volume constant. A few *Ceriodaphnia* spp. and *Simocephalus* spp. were introduced into the tanks to reduce the bacterial growth; this resulted in clear solutions and healthy snails.

The survivorship, fecundity and speed of development of the snails was recorded over a period of 13.5 fortnights (27 weeks) and the data used to calculate the values of r_m, its natural antilog R (the ratio of increase per unit time) and the mean generation time, MGT. For *Biomphalaria pfeifferi* values were obtained for all concentrations, but for *Bulinus* (*Ph.*) *globosus*, the parameters were not obtained at bicarbonate concentrations of 600 and 800 mg/l (experiments 11 and 12), or for experiments 1 and 2. Experiment 7 was considered to be in the nature of a control, since tap water was used; this water lay in the "medium" range with a bicarbonate concentration of 35 mg/l as $CaCO_3$. It originated from Lake McIlwaine, which was also the source of the laboratory colonies of the 2 snail species.

In the calcium experiments, solutions were prepared with concentrations of 0, 2, 12 and 50 mg/l as Ca. It was found, however, that some of the bicarbonate experiments had calcium ion levels which could be fitted into this series.

RESULTS

Bicarbonate concentrations.

Biomphalaria pfeifferi: Fig. 1 relates the values obtained after 13.5 fortnights for the experimental parameters, r_m, R and MGT, to the bicarbonate concentrations of the culture media. This species showed a positive r_m value in all concentrations, but the values varied widely from 0.298 to 0.719, a difference of 0.42. The variation was not haphazard, because a pattern emerged in that the highest values were obtained from the "medium" waters, and lower values were obtained from both "soft" and "hard" waters. The mean generation time varied reciprocally.

Bulinus (*Physopsis*) *globosus:* Fig. 2 gives the results for this species. Although similar relationships were found between the parameter values and the bicarbonate concentrations, the range of r_m values was less than for the previous species, viz., 0.345 to 0.513, a difference of only 0.17. These results are taken to indicate that *B.* (*Ph.*) *globosus* is tolerant of a wider range of bicarbonate concentrations that *Biomphalaria pfeifferi*.

Calcium concentrations.

Fig. 3 and 4 relate the parameter

TABLE 1. Ionic composition of experimental culture media

Ions	Experiments*											
	1	2	3	4	5	6	7	8	9	10	11	12
Ca^{++}, mg/l as Ca	0.0	2.0	2.4	9.0	10.5	13.0	12.0	51.0	36.0	39.0	80.0	106
Mg^{++}, mg/l as Mg	2.5	1.0	3.0	3.0	3.3	2.8	2.0	1.6	4.0	21.0	46.0	60
Na^{+}, mg/l	6.0	3.5	5.0	5.0	5.0	6.0	4.0	4.0	16.0	42.0	73.0	100
K^{+}, mg/l	2.5	1.0	3.0	2.0	2.0	2.5	2.0	2.0	4.8	23.0	26.0	38
HCO_3^{-}, mg/l as $CaCO_3$	26.0	15.0	30.0	0.0	5.0	15.1	35.0	66.8	150.5	300.0	608.0	829
Cl^{-}, mg/l	--	1.5	0.5	15.0	15.0	9.0	2.0	36.0	1.0	1.0	0.8	0.4
SO_4^{--}, mg/l	--	2.0	0.5	25.0	25.0	26.0	2.0	25.0	1.0	1.0	0.8	0.4

*Experiments 4, 5, 6, 7, 9, 10 and 12 were designed to test bicarbonate concentrations; 1, 2, 3, 7 and 8 formed the "calcium series," although some of the other experiments fitted in as well. Experiment 7 used matured tap water from Lake McIlwanie and Experiment 2 used water from a naturally soft stream.

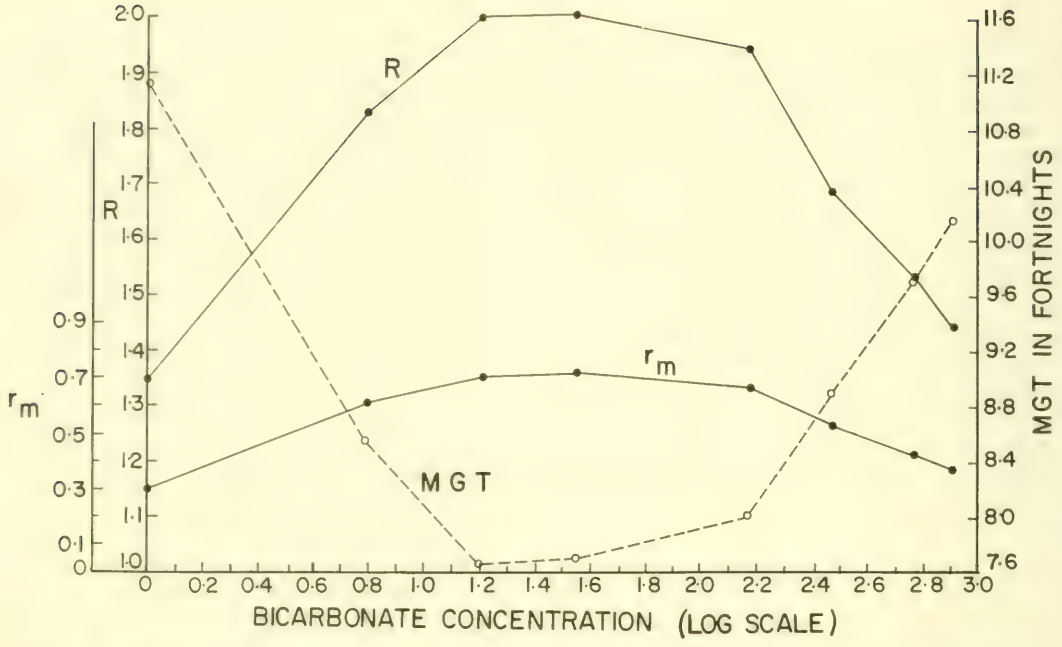

FIG. 1. The effect of bicarbonate concentration on r_m, R and MGT of *Biomphalaria pfeifferi*, obtained after 13.5 fortnightly periods.

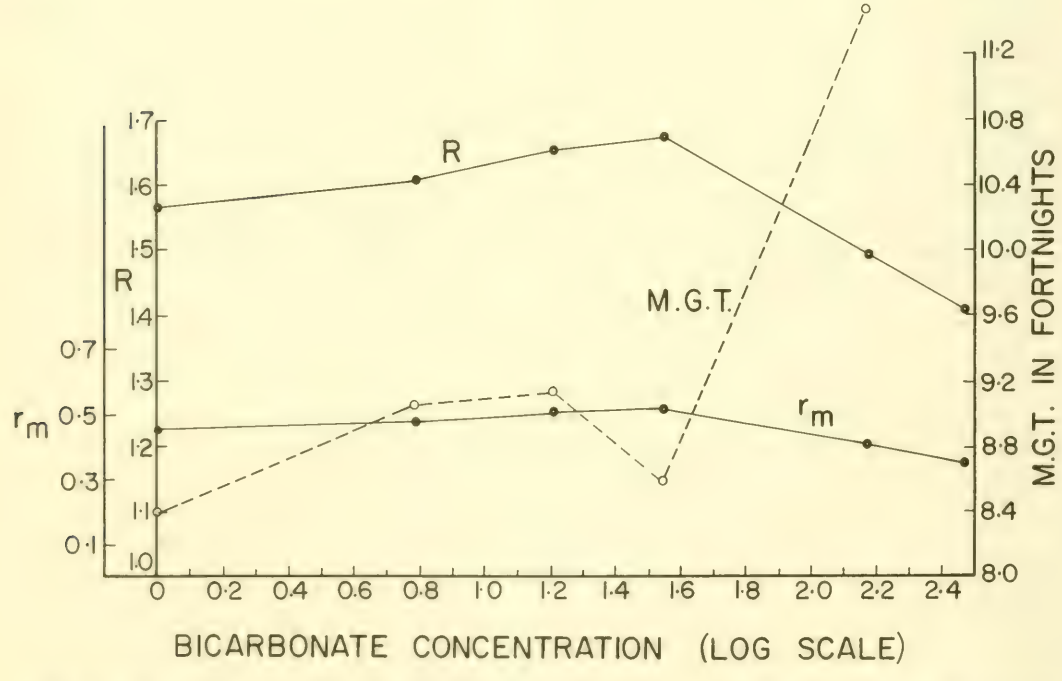

FIG. 2. The effects of bicarbonate concentration on r_m, R and MGT of *Bulinus (Physopsis) globosus*, obtained after 13.5 fortnightly periods.

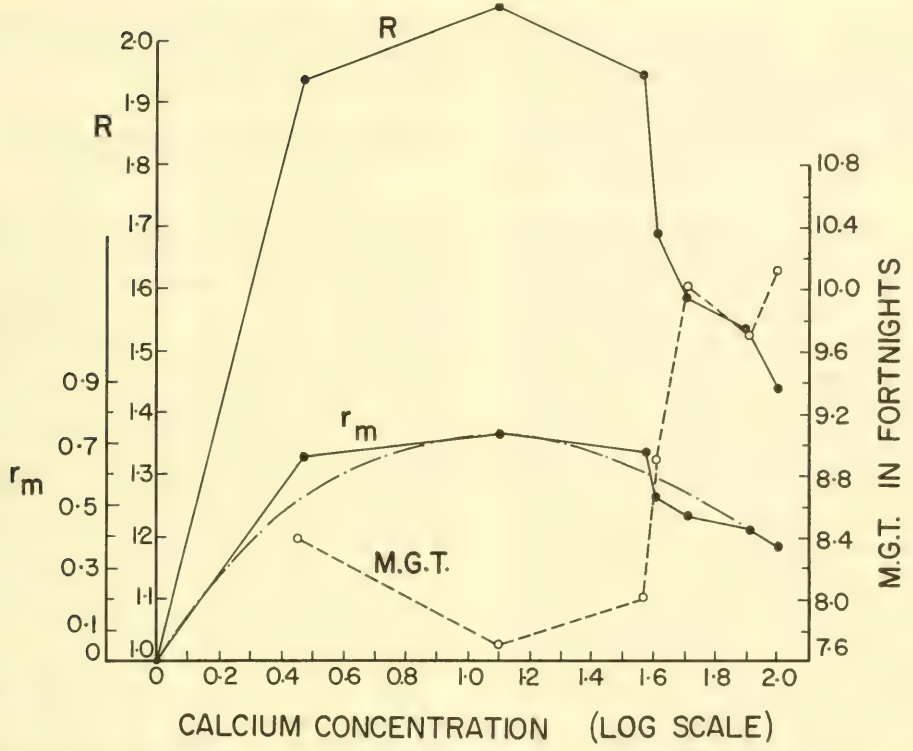

FIG. 3. The effects of calcium concentration on r_m, R and MGT of *Biomphalaria pfeifferi*, obtained after 13.5 fortnightly periods.

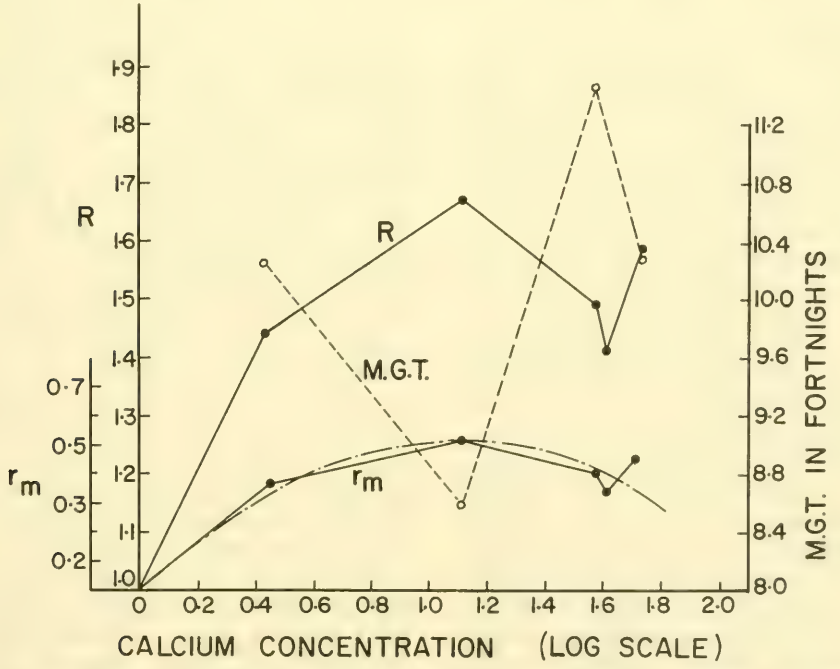

FIG. 4. The effects of calcium concentration on r_m, R and MGT of *Bulinus (Physopsis) globosus*, obtained after 13.5 fortnightly periods.

values for the 2 species to the calcium concentrations. Again *B. pfeifferi* showed a greater range of r values than did *B. (Ph.) globosus*. The latter species is then probably more tolerant of a wider range of calcium concentrations.

The validity of these experiments hinges, to some extent, on the time period of 13.5 fortnights within which they were carried out. It is possible to keep individuals of both species alive and laying eggs for much longer periods than this. In both species, egg-laying usually started between the 4th and the 6th fortnight, and it might seem necessary to run the experiments for more than 13.5 fortnights. Tables 2 and 3 show the values of r_m, R and MGT over the last 4 fortnights of the experimental runs for both species. It will be seen that the values for these parameters changed little over this period, so that contributions of further fortnightly periods would be negligible.

Fig. 5 summarizes the position regarding the r_m values obtained for both species in all experiments. Experiments 4 to 7 are of particular importance, because the calcium ion concentrations were very similar whereas the bicarbonate concentrations increased slowly from 0 to 35 mg/1. In these the maximum difference in r_m values for *Bulinus (Ph.) globosus* was only 0.07, while for *Biomphalaria pfeifferi* it was 0.4, showing the importance of bicarbonate concentrations (as divorced from differences in calcium) for the latter species. Since the bicarbonate concentrations must be responsible for the buffering capacity of natural waters, the small differences for *B. (Ph.) globosus* again indicate that it has a greater tolerance to changing chemical conditions. A comparison of the results of experiments 2 and 3 is interesting. In experiment 2, *B. pfeifferi* was cultured in a "soft" natural stream water with a calcium value similar to that of experiment 3. The main difference was the low bicarbonate concentration in expt. 2, a normal adjunct to low calcium values in the field. The r_m value was much lower in 2 than in 3.

COMPARISON OF LABORATORY AND FIELD DATA

The field results (Williams, 1970) demonstrated that *Bulinus (Ph.) globosus* has a wide tolerance to chemical conditions and is well distributed throughout the whole range, whilst *B. pfeifferi*, is restricted to medium and hard ranges of natural water.

In the present experimental study, the wide tolerance of *Bulinus (Ph.) globosus* is suggested by the relatively constant r_m values over the whole range of bicarbonate and calcium ion concentrations, while the more limited tolerance of *Biomphalaria pfeifferi* may be due to the wider range of r_m values over the same experimental conditions.

The total number of snails of both species recovered at each sampling station was known from the field studies, as was the corresponding average calcium ion concentration. The r_m values for both species were known for certain calcium ion concentrations from the experimental results, whilst other values could be interpolated. The 2 sets of data had thus a common factor, the calcium concentrations. In the case of *Biomphalaria pfeifferi*, the comparison of field and laboratory data by regression analysis (Snedecor, 1962), showed that the relationship between r_m and the log field numbers (Fig. 6) was significant at the 5% confidence level ($P > 0.05 < 0.025$). The regression of *Bulinus (Ph.) globosus* numbers on the experimental r_m values was not significant ($P > 0.4 < 0.2$), the regression line being almost horizontal (Fig. 7). A slight increase in r_m values produces a slight increase in field snail numbers, but this is not statistically significant.

The significant positive correlation between the field abundance of *Biomphalaria pfeifferi* and the laboratory determined r_m values suggest that the

TABLE 2. Laboratory determined values of r_m, R and MGT for *Biomphalaria pfeifferi* reared at a constant temperature of 25° C ± 0.5° C

Experiment	Ca^{++} in mg/l, Ca	HCO_3^- in mg/l as $CaCO_3$	Age											
			10.5x*			11.5x*			12.5x*			13.5x*		
			r_m	R	MGT	r_m	R	MGT	r_m	R	MGT	r_m	R	MGT
1	0	26												
2	2	15										0.3908	1.478	7.94
3	2.4	30										0.6595	1.934	8.388
4	9	0	0.2422	1.274	9.898	0.2752	1.317	10.415	0.2911	1.338	10.804	0.2986	1.348	11.116
5	10	5	0.5976	1.818	7.733	0.6010	1.824	8.073	0.6026	1.827	8.350	0.6027	1.829	8.540
6	13	15	0.6970	2.008	7.184	0.6986	2.011	7.381	0.6991	2.012	7.535	0.7001	2.014	7.660
7	12	35	0.7168	2.048	7.084	0.7183	2.051	7.347	0.7188	2.052	7.544	0.7193	2.053	7.703
8	50	66	0.4422	1.556								0.4632	1.589	10.074
9	36	150	0.6606	1.936	7.279	0.6632	1.941	7.579	0.6647	1.944	7.852	0.6653	1.945	8.014
10	40	300	0.5128	1.670	7.969	0.5188	1.680	8.358	0.5224	1.686	8.694	0.5243	1.689	8.922
11	83	600	0.4087	1.505	8.638	0.4166	1.517	8.968	0.4226	1.526	9.310	0.4266	1.532	9.713
12	108	830	0.3420	1.408	8.695	0.3577	1.430	9.180	0.3667	1.443	9.779	0.3667	1.443	10.153

Experiment 1: snails all died before laying eggs.

Experiments 2, 3 and 8: calculations were not made for all fortnights.

*Pivotal age x in fortnights.

TABLE 3. Laboratory determined values of r_m, R and MGT for *Bulinus (Ph.) globosus* reared at a constant temperature of 25° C ± 0.5° C

Experiment	Ca^{++} in mg/l, Ca	HCO_3^- in mg/l as $CaCO_3$	Age											
			10.5x*			11.5x*			12.5x*			13.5x*		
			r_m	R	MGT	r_m	R	MGT	r_m	R	MGT	r_m	R	MGT
1	0	26												
3	2.4	30										0.3618	1.436	10.262
4	9	0	0.4415	1.555	8.063	0.4441	1.559	8.218	0.4447	1.560	8.278	0.4460	1.562	8.393
5	10	5	0.4613	1.586	7.936	0.4663	1.594	8.256	0.4730	1.605	8.832	0.4748	1.608	9.064
6	13	15	0.4916	1.635	8.333	0.4953	1.641	8.536	0.5008	1.650	9.008	0.5014	1.651	9.142
7	12	35	0.5038	1.655	7.731	0.5086	1.663	8.070	0.5104	1.666	8.325	0.5134	1.671	8.594
8	50	66										0.4580	1.581	10.306
9	36	150							0.3846	1.469	10.891	0.3995	1.491	11.470
10	40	300	0.3450	1.412	8.154									

Experiment 1: snails all died before laying eggs.

Experiments 3, 8 and 9: calculations were not made for all fortnights.

Experiment 10: snails did not survive beyond the 11th fortnight.

*Pivotal age x in fortnights.

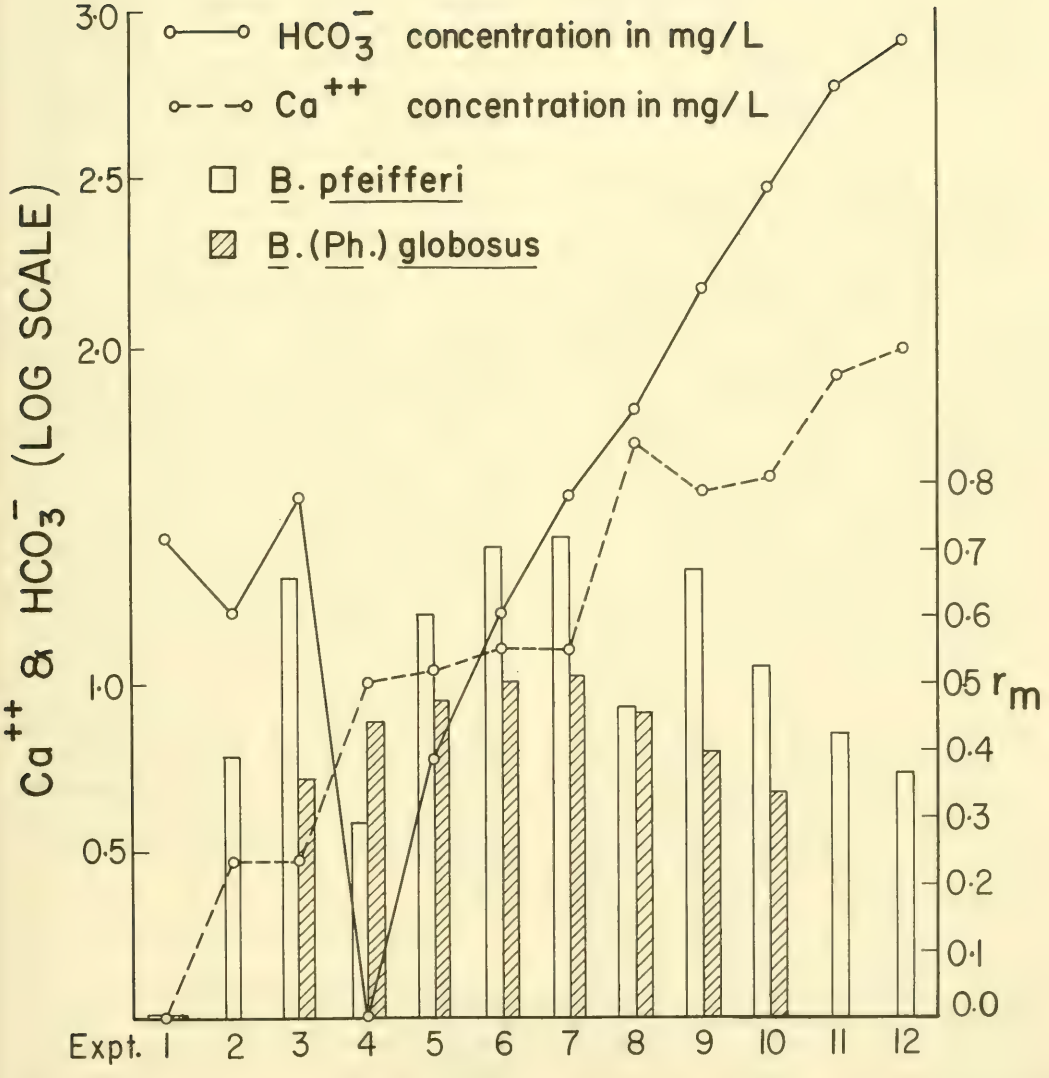

FIG. 5. Relationship between the intrinsic rate of natural increase (r_m) obtained experimentally, and calcium and bicarbonate concentrations. Consult Table 1 for actual concentrations.

abundance of this species in the field is controlled to some extent by the calcium concentration, in this case mostly calcium bicarbonate. It therefore follows that the distribution will also be determined in part by the ionic composition of the water. In the case of *Bulinus* (*Ph.*) *globosus*, since no significant correlation was found between the field abundance and the laboratory determined rates of increase, it appears that the ionic composition of the water does not significantly affect the field abundance, and consequently the distribution, of this species.

DISCUSSION

In considering the value of the biometric parameter r_m in laboratory investigations, it is well to consider the ways in which it may be used. First, is the commonly accepted method of using r_m as a means of demonstrating the rate of growth of a population under optimum constant conditions. It has also been used when the effects of survivorship, speed or development and fecundity are combined as a single response to some environmental factor. A 3rd use is the interspecific comparison of the ability of similar animals to adapt themselves to changes in environmental conditions, thus providing an insight into problems of abundance and distribution in the natural environment.

Andrewartha & Birch (1954) state that the intrinsic rate of natural increase (r_m), when calculated under ideal conditions, is as characteristic of the species as any distinct morphological feature. It is difficult however to evaluate experimental conditions in these terms, because it has been shown in this laboratory that slightly different culture techniques produce different estimations of the parameter r_m. Optimum laboratory conditions of temperature, food, space and water chemistry may be approached, but the "ideal condition" of Andrewartha & Birch (1954) may not be reached, and in consequence, the experimental r_m values may be slightly below the hypothetical "absolute" ones for any particular set of environmental conditions. An important point is that the experimenter may be much more successful in producing near-optimal conditions for one species than for another, so that interspecific comparison of actual r_m values will lead to erroneous conclusions. Nevertheless, comparable experimental regimes will allow optimal value for a variable, such as calcium concentration, to be determined for any one species, irrespective of the fact that the determined r_m values may be slightly lower than the absolute ones.

Any environmental factor which has a quantitative effect on either the speed of development, survivorship or fecundity of a species will cause changes in the r_m values. In this study, emphasis has been placed on water chemistry, but it is obvious, however, that the effect of other factors may be studied in this way. It has been possible to compare the values of r_m within one species under different conditions, but these values have not been used to compare one species with another. The range of r_m values, however, has been used for this interspecific comparison; the large range of r_m values of *Biomphalaria pfeifferi*, in contrast to the small range of *Bulinus* (*Ph.*) *globosus*, has been taken to indicate that the former tolerates a narrower range of chemical conditions. This lack of tolerance appears to be one of the factors affecting the abundance and distribution of *B. pfeifferi* in the natural environment.

ACKNOWLEDGEMENTS

Grateful thanks are due to Dr. A. D. Harrison, now at the University of Waterloo, Waterloo, Ontario, Canada for advice and useful criticism during the course of this study, and to my wife for her untiring assistance in the main-

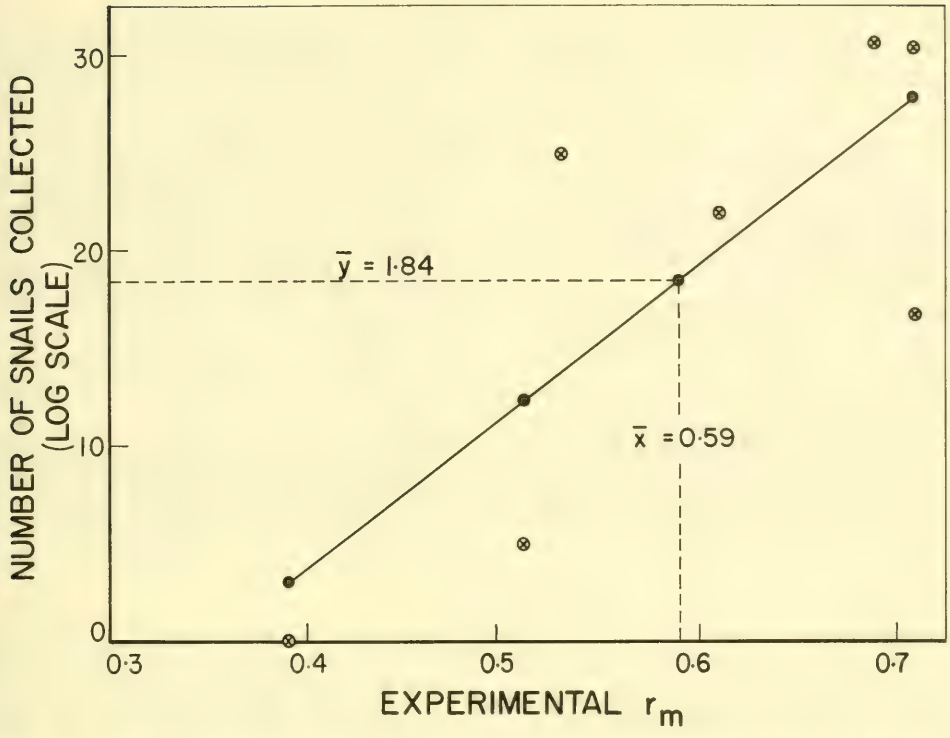

FIG. 6. Regression of experimental values of r_m on numbers of *Biomphalaria pfeifferi* collected in the field.

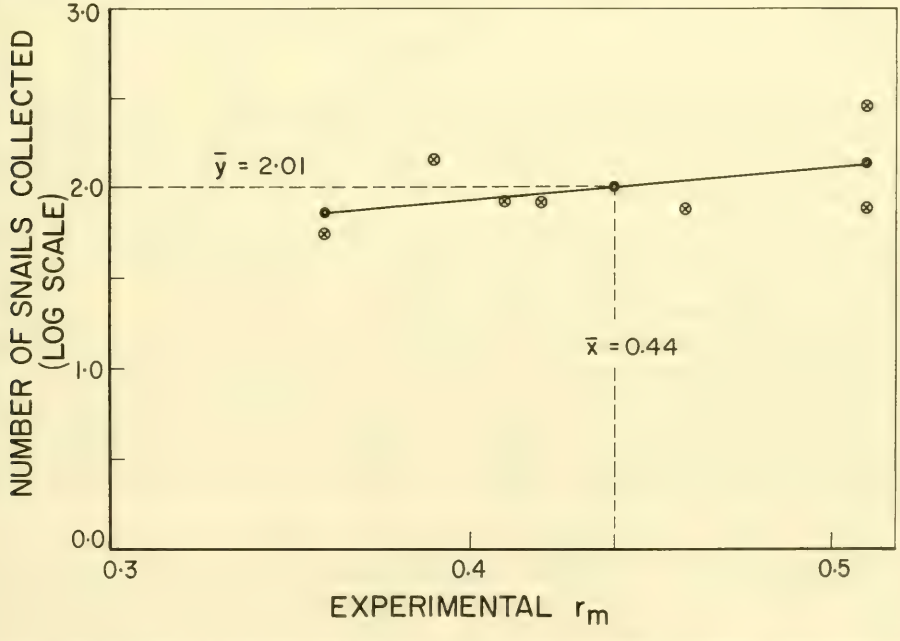

FIG. 7. Regression of experimental values of r_m on numbers of *Bulinus (Physopsis) globosus* collected in the field.

tenance of the large numbers of snail cultures. This project was financed by the Rockefeller Foundation of New York, U.S.A.

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RÉSUMÉ

ETUDES SUR LES MOLLUSQUES PULMONÉS AQUATIQUES D'AFRIQUE CENTRALE II. ANALYSE EXPÉRIMENTALE DES MODES DE DISTRIBUTION DANS LA NATURE

N. V. Williams

Ces expérimentations font suite à des études dans la nature sur la distribution de mollusques aquatiques dans la région de Salisbury, Rhodésie, dans lesquelles on a montré que la distribution et la densité relative de 5 espèces avaient une certaine relation avec les concentrations en calcium et bicarbonate du milieu aquatique. Deux espèces ont été retenues pour confirmation par expérimentation: *Bulinus* (*Physopsis*) *globosus*, qui se rencontre aussi bien dans les eaux à fortes qu'à faibles concentrations en bicarbonate de calcium, et *Biomphalaria pfeifferi* qui se limite aux eaux à moyennes et fortes concentrations en bicarbonate de calcium.

Les deux espèces ont été élevées en laboratoire dans des milieux calculés pour recouvrir une large variation de concentrations en calcium et bicarbonate, ceci à une température constante de 25°, les autres facteurs contrôlables étant maintenus aussi constants que possible. On a déterminé l'âge spécifique de fécondité et les taux de survivance pour chaque lot de culture, et estimé le temps moyen d'une génération (MGT), le taux limité d'accroissement (R) et le taux intrinsèque d'accroissement naturel (r_m).

Les valeurs du r_m obtenues pour *Biomphalaria pfeifferi*, montrent qu'il y a des taux d'accroissement des populations expérimentales, qui sont plus forts à des concentrations moyennes d'ions calcium et bicarbonate qu'à des concentrations basses ou élevées. En plus, les valeurs du r_m sont directement proportionnelles aux densités relatives de cette espèce selon les différentes concentrations observées dans la nature, ce qui suggère que la distribution discontinue de l'espèce est en partie

due à sa faible tolérance pour les concentrations extrêmes de bicarbonate de calcium existant dans la région de Salisbury, notamment les plus basses.

Les valeurs du r_m obtenues pour *Bulinus (Ph.) globosus* indiquent aussi que les plus forts accroissements de populations interviennent pour les concentrations moyennes de bicarbonate de calcium. Cependant, l'échelle des valeurs de r_m obtenues des plus hautes aux plus basses concentrations ioniques, sont plus faibles pour cette espèce que pour la précédente, et l'on n'a pas trouvé de relation significative entre ces valeurs et les densités relatives rencontrées dans la nature. Ceci suggère que sa distribution continue dans la nature est due, en partie, à sa grande tolérance vis-à-vis des concentrations en bicarbonate de calcium.

A. L.

RESUMEN

ESTUDIOS SOBRE PULMONADOS ACUATICOS EN AFRICA CENTRAL II. INVESTIGACION EXPERIMENTAL DE LOS PATRONES NATURALES DE DISTRIBUCION

N. V. Williams

Estos experimentos continuaron aquellos estudios realizados en el campo, acerca de la distribución y densidad relativa de 5 especies de caracoles de agua dulce en la región de Salisbury, Rodesia, cuya relación con la concentración de carbonato de calcio en el ambiente quedó demostrada. Dos especies se eligieron para experimentos confirmatorios en el laboratorio: *Bulinus (Physopsis) globosus*, presente en aguas que contienen una concentración baja de carbonato de calcio, y *Biomphalaria pfeifferi*, la cual esta limitada a los ambientes con concentraciones medianas y altas.

Las 2 especies fueron cultivadas en el laboratorio en una forma designada a cubrir una considerable latitud en la concentración del carbonato de calcio, a temperaturas constantes de 25° C y con otros factores controlables guardados en la forma más constante posible. Edad, fecundidad específica y proporción de sobrevivientes se determinaron para cada prueba de cultivo, y se calculó el término medio de generación-tiempo (MGT), la proporción definida de aumento (R), la proporción intrínsica del aumento natural (r_m).

Los valores r_m obtenidos para *Biomphalaria pfeifferi* distintamente indicaron aumento mayor en las poblaciones experimentales de concentración media de carbonato de calcio, que en los altos o bajos extremos. También, los valores r_m fueron directamente proporcionales a la densidad relativa de la especie con los diferentes tipos de concentración en el campo, sugiriendo que su distribución discontinua se debió en parte a la limitada tolerancia a los extremos de concentración del bicarbonato de calcio que existen en la región de Salisbury, notablemente en el extremo bajo.

En *Bulinus (PH.) globosus*, los valores r_m también indicaron que el mayor aumento de población ocurre en concentraciones medias. Sin embargo, la latitud de esos valores, obtenidas desde las más bajas a las más altas concentraciones iónicas, fué más reducida para esta especie que para la precedente, y no se encontró relación significativa entre esos valores y los que se encontraron en el campo. Esto sugiere que su continua distribución natural, se debe, en parte, a su más amplia tolerancia de concentración de carbonato de calcio.

J. J. P.

АБСТРАКТ

ИЗУЧЕНИЕ ВОДНЫХ УЛИТОК PULMONATA ИЗ ЦЕНТРАЛЬНОЙ АФРИКИ
II. ЭКСПЕРИМЕНТАЛЬНОЕ ИССЛЕДОВАНИЕ РАСПРОСТРАНЕНИЯ
ГРУППИРОВОК МОЛЛЮСКОВ В ЕСТЕСТВЕННЫХ УСЛОВИЯХ

Н. В. ВИЛЬЯМС

Эти экспериментальные работы сопровождали полевые исследования водных улиток в районе Солсбери, Родезия по распространению и относительной плотности поселений 5 видов моллюсков в связи с количеством кальция и концентрацией бикарбоната в природных водах.

Два вида были выбраны для подтверждения этого в лабораторных условиях: *Bulinus (Physopsis) globosus*, обитающий в водах как с низкой концентрацией бикарбоната кальция, так и в водах с высоким его содержанием; второй вид - *Biomphalaria pfeifferi*, которая придерживалась вод со средней и высокой концентрацией бикарбоната Са.

Эти два вида культивировались в лаборатории в водах с широким диапазоном концентрации кальция и его бикарбоната, при постоянной температуре 25°С и с другими, возможно более постоянными факторами, поддающимися контролю.

Для каждой культуры моллюсков определялась возрастная плодовитость, выживаемость и средняя скорость образования генераций 5 (MGT), конечная скорость их увеличения (R) и свойственная им скорость естественного увеличения (r_m).

Величина r_m для *Biomphalaria pfeifferi* показала, что наблюдается заметно большая скорость увеличения популяции в эксперименте при средней концентрации бикарбоната и ионов кальция, чем при высоких и низких их концентрациях. Кроме того, величины r_m были прямо пропорциональны относительной плотности поселений данного вида при различных их концентрациях в природных водах, если предположить, что непрерывное распространение этих видов определяется частично их ограниченной выносливостью к крайним величинам бикарбоната кальция, встречающимся в районе Солсбери, особенно к низким. Величины r_m полученные для *Bulinus (Ph.) globosus* также указывают на то, что самые плотные популяции этих моллюсков наблюдаются при средних концентрациях бикарбоната кальция. Однако, колебания величин r_m, полученных при самых низких и при самых высоких концентрациях этих ионов, были гораздо меньше для *B. globosus*, чем для предыдущего вида; не было найдено значительной связи между этими величинами и относительной плотностью поселений моллюсков в природных условиях. Поэтому можно думать, что его непрерывное распространение частично обуславливается его большой толерантностью к концентрациям бикарбоната кальция.

Z. A. F.

MALACOLOGIA, 1970, 10(1): 181-223

SOME GASTROPODS FROM MADAGASCAR AND WEST MEXICO [1]

Eveline du Bois-Reymond Marcus[2] and Ernst Marcus[3]

ABSTRACT

This paper deals with 43 species of marine gastropods, mostly opisthobranchs (but also 1 lamellariacean and 3 onchidiaceans) from Madagascar and from the Gulf of California. Anatomical descriptions are given for the various species. Three species were recognized to be common to both collections; these represent taxa occurring in circumtropical-warm seas. The following new species are described: *Smaragdinella kirsteueri, Stiliger (Stiliger) erbsus, Hypselodoris regina* and *Noumeaella isa* (from Madagascar), and *Elysia vreelandae* (from West Mexico). The new name *Stiliger (S.) raorum* substitutes *S. (S.) nigrovittatus* Rao & Rao, 1963. The opisthobranchs of Madagascar belong to the rather homogeneous Indo-Pacific reef fauna, while those from the Gulf of California live in areas largely devoid of coral reefs, but containing an admixture of Panamic and American temperate Pacific faunal elements.

INTRODUCTION

The present paper treats 30 species from Madagascar as Part XI of the Austrian Indo-west Pacific Expedition 1959/1960, and 13 species from the Gulf of California. Five new species are described, of which 4 are from Madagascar.

Benthonic animals of shallow water from these regions are separated by Ekman's East Pacific Barrier (Emerson, 1967). Only 3 species, which occur in all warm seas, are represented in both collections. Comparative morphological studies of opisthobranchs indicate that many species, especially nudibranchs, have extensive geographical ranges. Several species are known to occur in more than one zoogeographical province and some species of nudibranchs are apparently circumtropical in distribution. Therefore, a combined publication of zoologically allied, though geographically separate collections, facilitates faunal comparisons. The opisthobranchs of Madagascar belong to the rather homogeneous Indo-Pacific reef fauna, but those from the Gulf of California live in areas largely devoid of coral reefs. There, species of restricted or wide distribution in the Panamic faunal province meet with others of the American temperate Pacific fauna. The Panamic province is related to the Caribbean, and the American temperate Pacific fauna includes Japanese elements.

Although most of the species in the present collections are opisthobranchs, the first species treated belongs to the Lamellariacea. These are traditionally collected and studied together with opisthobranchs. Our 4 last species are Onchidiacea. Van Mol (1967) re-established the subclass Pulmonata in a recent study of the cerebral ganglion in Basommatophora, Stylommatophora, and

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[1] Published with the cooperation of the Institute of Malacology.

[2] Address: Caixa Postal 6994, São Paulo, Brazil.

[3] Professor Emeritus of Zoology, University of São Paulo. Deceased June 30, 1968.

Soleolifera, so the Onchidiacea are separated from the Opisthobranchia again, if one follows that author.

The types and some of the other material in this article are deposited in the Department of Living Invertebrates of The American Museum of Natural History.

MATERIALS

Collecting stations from Madagascar, 1959 (Ernst Kirsteuer)

viii Tanikely, *Porites* cf. *iwayamaensis*, 2.5 meters, June 25.
ix Tanikely, *Seriatopora angulata*, 2 meters, June 26.
x Tanikely, *Porites* cf. *iwayamaensis*, 2.5 meters, June 27.
xi Tanikely, *Seriatopora angulata*, 2.5 meters, June 29.
xiii Tanikely, *Seriatopora angulata*, 2.5 meters, July 1.
xiv Tanikely, *Seriatopora angulata*, 3 meters, July 2.
xvi Tanikely, *Seriatopora angulata*, 4 meters, July 4.
xviii Tanikely, tide pool, coarse sand and fragments of coral, under stones, 0.2 meter, June and July.
xix Tanikely, *Millepora tenella*, 4.5 meters, July 8.
xxi Tanikely, *Acropora corymbosa*, 2.5 meters, July 13.
xxii Tanikely, *Acropora corymbosa*, 2 meters, July 14.
xxiv Tanikely, *Acropora pharaonis*, 3 meters, July 16.
xxvi Nossi Iranja, southwest coast, under stones and dead coral, low intertidal zone, Nov. 24.
xxvii Tanikely, *Acropora pharaonis*, 2 meters, Dec. 3.
xxviii Tanikely, *Acropora corymbosa*, 3 meters, Dec. 4.
xxix Tanikely, *Acropora corymbosa*, 2.5 meters, Dec. 5.
xxx Tanikely, *Seriatopora angulata*, 2 meters, Dec. 6.
xxxi Tanikely, *Seriatopora angulata*, 2 meters, Dec. 7.
xxxii Tanikely, *Millepora tenella*, 2 meters, Dec. 8.
xxxiii Tanikely, *Porites* cf. *iwayamaensis*, 3.5 meters, Dec. 10.
xxxvi Tanikely, *Gracilaria* species, 3 meters, Dec. 13.
xxxvii Tanikely, *Millepora tenella*, 4 meters, Dec. 14.
xliii Nossi Be, Bay of Ambanoro, in front of the institute, sand under stones, low intertidal zone, Dec.
xlv Nossi Be, Bay of Ambanoro, mud with sand, 20 meters, Dec. 29.

Collecting stations from Mexico, Gulf of California

i Mexico, Sonora, Puerto Peñasco
ii Mexico, Sonora, San Agustin = El Sahuaral
iii Mexico, Sonora, Guaymas, latitude 27° 59' N, longitude 110° 58' W.
iv Mexico, Baja California, Cabo Pulmo, latitude 23° 22' N, longitude 109° 28' W.

SYSTEMATIC ACCOUNT

List of species

Prosobranchia, Monotocardia, Mesogastropoda, Lamellariacea, Lamellariidae

1. *Coriocella nigra* Blainville 1824

Euthyneura, Opisthobranchia, Cephalaspidea, Bullacea, Atyidae

Atys spec. juv.

Cephalaspidea, Philinacea, Smaraginellidae

2. *Lathophthalmus smaragdinus* Rüppell & F. S. Leuckart 1828
3. *Smaragdinella kirsteueri*, spec. nov.

Philine spec., juv.

Cephalaspidea, Philinacea, Aglajidae

4. *Chelidonura punctata* Eliot 1903
5. *Chelidonura inermis* (Cooper 1862)

Anaspidea, Aplysiidae

6. *Aplysia* (*Pruvotaplysia*) *parvula* Mörch 1863
7. *Dolabella auricularia* (Solander 1786)
8. *Dolabrifera dolabrifera* (Rang 1828)
9. *Stylocheilus longicauda* (Quoy & Gaimard 1824)

Ascoglossa, Elysiacea, Stiligeridae

10. *Stiliger* (*Stiliger*) *erbsus*, spec. nov.

Ascoglossa, Elysiacea, Elysiidae

11. *Elysia vreelandae*, spec. nov.

Notaspidea, Pleurobranchacea, Pleurobranchidae

12. *Berthellina cuvieri* (Bergh 1898)

Doridoidea, Eudoridacea, Cryptobranchia, Doridiidae, Conualevinae

13. *Conualevia marcusi* Collier & Farmer 1964

Doridoidea, Eudoridacea, Cryptobranchia,

Doridoidea, Eudoridacea, Cryptobranchia, Doridiidae, Chromodoridinae
14. *Chromodoris quadricolor* (Ruppell & F. S. Leuckart 1828)
15. *Chromodoris norrisi* Farmer 1963
16. *Hypselodoris regina,* spec. nov.

Doridoidea, Eudoridacea, Cryptobranchia, Doridiidae, Aldisinae
17. *Rostanga pulchra* MacFarland 1905

Doridoidea, Eudoridacea, Cryptobranchia, Doridiidae, Archidoridinae
18. *Atagema osseosa* (Keelart 1859)
19. *Trippa intecta* (Keelart 1858)

Doridoidea, Eudoridacea, Cryptobranchia, Doridiidae, Discodoridinae
20. *Taringa aivica timia* Marcus 1967
21. *Tayuva ketos ketos* Marcus 1967

Doridoidea, Eudoridacea, Cryptobranchia, Doridiidae, Halgerdinae
22. *Asteronotus cespitosus* (van Hasselt 1824)

Doridoidea, Eudoridacea, Cryptobranchia, Doridiidae, Platydoridinae (=Arginae)
23. *Platydoris scabra* (Cuvier 1804)

Doridoidea, Eudoridacea, Phanerobranchia, Nonsuctoria, Gymnodorididae
24. *Gymnodoris bicolor* (Alder & Hancock 1864)

Doridoidea, Porostomata, Dendrodorididae
25. *Dendrodoris nigra* (Stimpson 1855)
26. *Dendrodoris rubra* (Keelart 1858)
27. *Dendrodoris pudibunda* (Bergh 1879)

Doridoidea, Porostomata, Phyllidiidae
28. *Phyllidia (Phyllidia) varicosa* Lamarck 1801
29. *Dermatobranchus (Dermatobranchus) striatus* van Hasselt 1824

Eolidoidea, Pleuroprocta, Flabellinidae
30. *Coryphellina rubrolineata* O'Donoghue 1929

Eolidacea, Cleioprocta, Favorinidae
31. *Favorinus mirabilis* Baba 1955
32. *Pteraeolidia janthina* (Angas 1864)
3. *Noumeaella isa,* spec. nov.

Eolidacea, Cleioprocta, Aeolidiidae
34. *Aeolidiella indica,* Bergh 1888

Soleolifera, Onchidiacea, Onchidiidae
35. *Peronia peronii* (Cuvier 1804)
36. *Peronia verruculata* (Cuvier 1830)
37. *Hoffmannola hansi* Marcus 1967
38. *Onchidella hildae* (Hoffmann 1928)

Lamellariacea

Coriocella nigra Blainville 1824 (Figs. 1-9)

Coriocella nigra Blainville, 1824, p 259; 1825, p 466, pl. 42, fig. 1.

Range: Mauritius.

Collecting station: Madagascar; xxviii, 1 male.

Description: In life, the present specimen was 15 to 18 mm long, 8 to 10 mm broad, smooth, and uniformly black with whitish-yellow, granulated tentacles. In the preserved specimen a little pigment is present in the folds of the mantle, near the snout, and from the under side of the mantle onto the back of the foot. The surface of the mantle has about 5 bosses, evidently produced by contraction of the cutaneous muscles. One of the bosses lies over the apex of the shell (ax). The conchinous shell has about 3 whorls; the measurements are: length 10 mm, breadth 6.3 mm, length of aperture 8.5 mm. The blackish calcareous layer of the shell is shivered as generally in preserved *Coriocella.*

The inhalant siphon (er) lies in the middle. The triangular tentacles are smooth, not furrowed. They bear the brown eyes in a knob near the base. The anterior border of the foot is transversely grooved (vo). The mantle skirt is thin, its epidermis rich in gland cells. The osphradium (om) has at least 30 leaflets of equal length on either side of the broad rhachis. The food in the gut contains alcyonarian sclerites. The penis is rudimentary, only a hemispherical wart, 930 μ high and 200 μ in diameter at its base. The seminal duct (d), 35 μ in diameter, courses straight within the muscle layers of the body wall. In Bergh's much larger snails (1886, p 222, 225) it serpentines.

The jaws measure 1.4 by 1 mm. The radula has 48 rows. The left limb of the rhachidian tooth is 230 μ long, the right one 155 μ; the cusp is either median or inclined to the right or left. On either side it bears 4 to 6 denticles. The laterals are 380 μ high, their cusp has 3 to 6, generally 4, coarse teeth on the inner side, 6 to 12 (sometimes up to 17) finer teeth on the outer side.

Remarks: For synonomy and range we limit ourselves to Bergh (1886, p 176) who called the species *Chelyonotus tonganus* var. *mauritiana,* and synono-

mized *Marsenia berghi* from Mauritius and Réunion with it. Later (1908b, p 107) he united the latter with *C. semperi*, considered an independent species in 1886 and 1905b. In 1908b Bergh questioned the specifity of *C. semperi*.

Vayssière's *Chelyonotus niger* (1912, p 118) possibly belongs to the present species in which case its distribution would extend to the Gulf of Aden. But the symmetrical rhachidian tooth of Vayssière's material differs from that in ours. Whether or not Adam & Leloup's "? *Lamellaria* (*Coriocella*) *mauritiana* Bergh" (1938, p 141) from the Aru Islands belongs to *C. nigra* cannot be judged.

Scaphandracea
Atys species, juvenile
(Figs. 10-15)

Collecting station: Madagascar; xxvii.

Description: The living snail was 1.5 to 2 mm long, 1 mm thick. Its narrow head shield was 0.8 mm long and slightly notched behind. The parapodia lay to the sides of the head shield and touch a little distance behind it, like in other species of *Atys* (Ostergaard, 1955, fig. 1; Macnae, 1962b, fig. 1). In the present juvenile only a small part of the shell, as well as the posterior mantle lobe, projected from the parapodia. The living specimen was bluish-white. On the head shield, parapodia and mantle lobe there were opaque snow-white spots, in the region of the shell brown dots. The light yellowish-brown Hancock's organs, the gizzard of the same color behind the head shield, and the dark eyes are recognizable in the drawing of the collector.

In the preserved snail the head shield and parapodia are contracted forward, and the shell stands out behind. In front the jaw plates project from the mouth. The notch of the head shield is deepened. Under the head shield lie the inconspicuous transverse folds of the Hancock's organs, whose hind ends are united by a fold over the back. On the right side runs the seminal groove; the penis is not developed yet. The sole is not set off from the parapodia; a transverse fold in its anterior $\frac{1}{3}$ is probably due to contraction. The general color of the preserved snail is brown, the digestive gland is green. The shell which lies on the mantle border is completely decalcified. The preserved conchinous layer, 1 mm long, shows a protruding sinistral larval shell of 1 whorl. The following dextral whorl is widened to the front and backward; the growth lines run parallel to the border, whose outer lip is slightly concave in the middle. The hind lobe beyond the larval shell is strong. The absence of spiral lines does not permit a judgment of the full grown shell, in, e.g., *Micromelo undata*, the structure of the shell changes rather late.

From the mantle border a lobe hangs over the mantle opening behind the gill. It corresponds to the "squamiform lamella" of *Acteon* and *Aplustrum* (Perrier & Fischer, 1911, p 26, 65), but is bigger. The inner side of the lobe bears cilia (zo), 40 μ long, which are the beginning of the dorsal ciliated ridge, the "raphé supérieur" of Perrier & Fischer. The lower mantle lobe is smaller than in *Acteon*. The gill (k) is small.

The jaw plates, about 100 μ by 50 μ, are composed of 8 to 10 rows of short pegs whose surfaces bear 3 to 6 short denticles at their broadest sides. The radula has 27 rows of teeth, and in the present young snail there are 4 lateral teeth on either side. The rhachidian tooth has a broad short cusp and a base widened toward the sides. The laterals are hooks without denticles; the innermost and outermost are shorter than the 2 middle ones. The 3 brown gizzard plates measure 300 μ by 140 μ; they bear at least 21 straight ribs, each with one row of pointed spines. The connectives of the nerve ring are short.

Remarks: Apart from the limitations of a decalcified shell, a snail so young cannot be classified beyond the genus. In *Atys obovatus* Bergh (1908a, p 156) the ribs of the gizzard plates bear

similar spines as in the present animal, but the ribs form an angle on the crest of the plate. In *A. xarifae* Marcus (1960a, figs. 9, 10) the ribs are straight and spiny, but less numerous than in the present, smaller specimen. Also, the smooth elements of the jaw plates distinguish *A. xarifae*. The gizzard plates of *A. naucum* and *A. cylindricus*, both without spines, are very different from each other.

Philinacea

The genera of the Smaragdinellidae

The name Ophthalmidae Bergh (1905a, p 35) cannot be applied to this family because this name is not derived from one of the genera of the family. Thiele (1931, p 387) used Cryptophthalminae, but *Cryptophthalmus* Ehrenberg, 1831, has been replaced by *Lathophthalmus* (Pruvot-Fol, 1931, p 748). In a list, Thiele (1925, p 265) mentioned Smaragdinellinae, and this name appears in Pruvot-Fol (1934, p 29), Habe (1952, p 144), Zilch (1959) and Marcus & Burch (1965, p 236). Pruvot-Fol (1934, p 30) is inclined to unite the 2 genera with internal shell, *Lathophthalmus* and *Phanerophthalmus* Adams, 1850.

In *Smaragdinella* Adam & Reeve, 1848, the shell is mainly external (Fischer, 1887, p 557, 565; Pilsbry, 1893-1895, p 258; 1895-1896, p 36). The shell of *Nona algira* (Hanley) is similar to that of the type species of *Smaragdinella*, but as it is internal, *Nona* cannot be a subgenus of *Smaragdinella*.

An internal shell may appear to be external, when the mantle is very thin (Eales, 1938, p 82, 83). In *Phanerophthalmus* there is no mantle foramen; the mantle foramen of *Lathophthalmus* varies in diameter without relation to age; and that of *Aplysia* varies with age (Eales, 1960, p 280). When it is large (Baba, 1936, p 5), the exposed shell looks like an external shell, partly embedded in the mantle (Vayssière, 1912, p 8). In Ehrenberg's figure of *L. smaragdinus* (Pilsbry, 1895-1896, pl. 6, fig. 30) the mantle foramen shows when the parapodia are spread.

Bergh (1901, p 235) examined 2 specimens from Ehrenberg's collection without entering into the matter of the position of the shell. Previously (1900a, p 164) and later on (1901, p 301) he united 1 specimen from Mauritius and 1 from Fiji with Ehrenberg's species and described an external shell over the mantle. These animals do not belong to *Lathophthalmus*, but possibly to *Smaragdinella*. Some years later Bergh (1905a, p 36, 39) observed the internal shell and the mantle foramen of *Lathophthalmus*, but did not correct his earlier statement.

Evidently Thiele (1931, p 387) based his diagnosis of *Cryptophthalmus* upon Bergh's first characterization of the genus (1900a). Therefore he called the shell for the most part external, and Hoffmann (1934, p 363) and Zilch (1959, p 44) repeated this.

Lathophthalmus smaragdinus (Rüppell & Leuckart 1828) (Figs. 16-22)

Lathophthalmus smaragdinus, Marcus, 1960a, p 886-890, figs. 14-25.

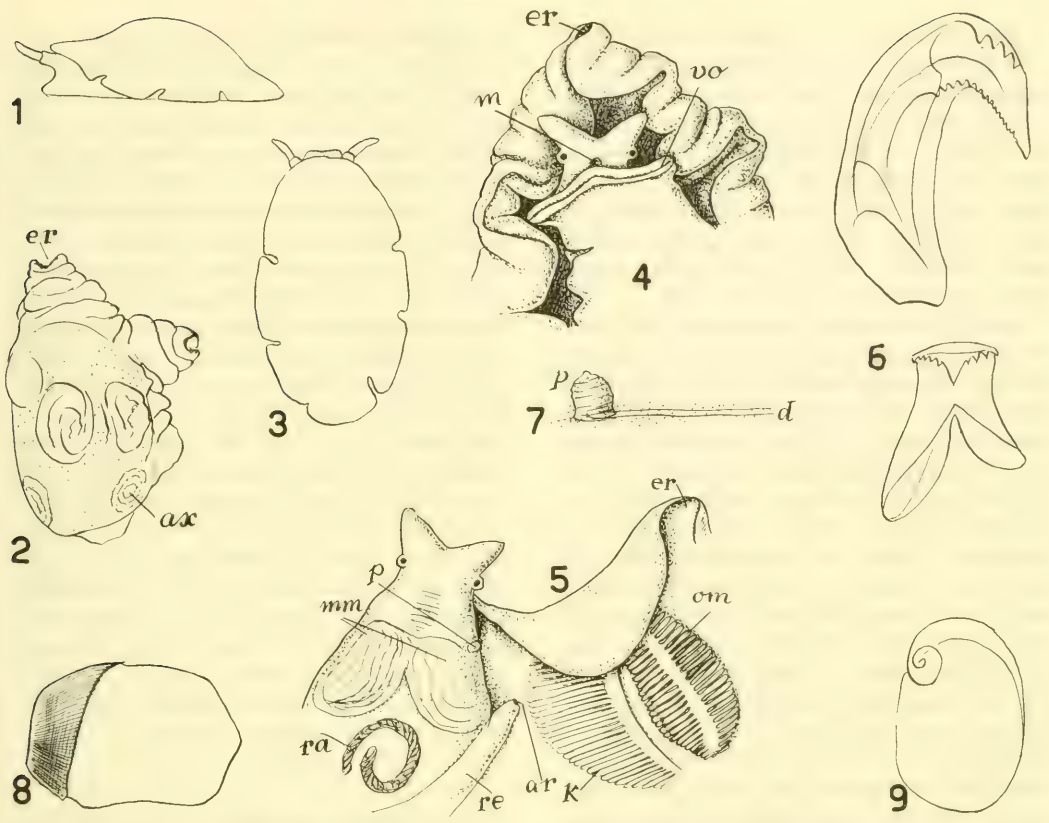
Range: From the Red Sea to the Ryukyu and Marshall Islands. (The *"Lathophthalmus"* specimens of Bergh (1901, p 301), cited by Marcus & Burch (1965, p 238), do not belong to this genus.) According to the aforesaid, not Fiji Islands (Marcus & Burch, 1965, p 238).

Collecting stations: Madagascar; xviii, xxvii, xxxiii, xliii, 25 snails.

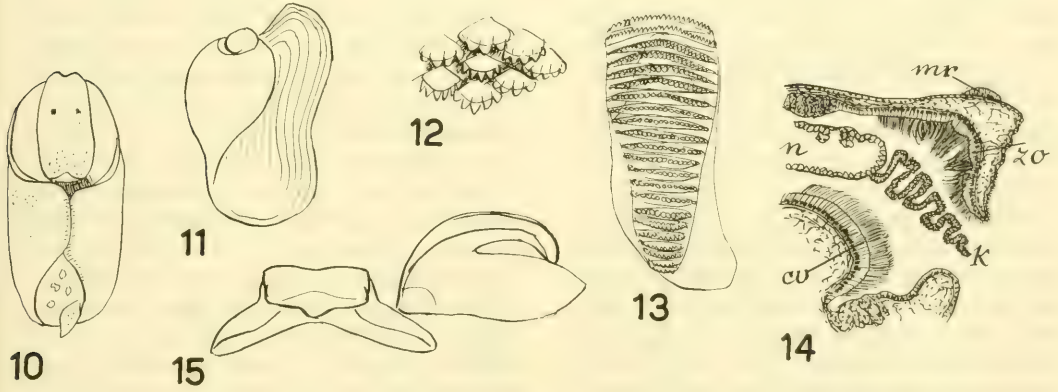
Description: The living snails were 20 to 22 mm long, 5 mm broad. The color is yellowish-green with fine dark spots. The rims of the head shield and parapodia are light bluish-green. In a photograph by Dr. Kirsteuer the black eyes and the yellow-brown pharynx are seen. The dark green digestive gland shines through the integument. .The preserved snails are light olive with a greenish liver.

KEY TO LETTERING IN FIGURES

a	ampulla
ag	albumen gland
am	male atrium
ao	aorta
ar	anus
as	ascus
au	allosperm duct
ax	apex
b	bursa copulatrix
cc	buccal ganglia
co	strand of connective tissue
cr	cerebral ganglion
cs	head shield
cv	ventral ciliated ridge
d	seminal duct
ea	pedal ganglion
er	inhalant siphon
eu	hermaphrodite duct
fa	female aperture
g	common genital opening
go	gastro-oesophageal ganglion
h	Hancock's organ
i	intestine
ia	digestive gland and its ducts
io	inner oviduct
k	gill
m	mouth
ma	male aperture
mm	foliate stomach
mo	mantle foramen
mr	gland of mantle border
mu	female gland mass
n	kidney
ne	nephroproct
ni	nidamental duct
no	notal gland
nx	pharynx
o	oesophagus
oc	oesophageal pouch
om	osphradium
on	opening of notal gland
oo	blood space
ov	ovotestis
p	penis
pg	penial appendage
q	prostate
r	retractormuscle
ra	radula
re	rectum
ri	rhinophore
ro	oral tube
sa	salivary gland
sc	spermatocyst
sd	gland of spine
so	stomach
sr	seminal groove
ss	spine sac with spine
t	spermatheca
uc	buccal gland
ui	thin part of male duct
um	sheathed part of male duct
us	blood gland
v	vagina
ve	vestibulum
vo	anterior border of foot
vs	seminal receptacle
xs	accessory prostate
xv	vestibular gland
y	eye
z	hyponotal glands
za	hyponotal pore
zi	perinotal glands
zm	transverse fold
zo	dorsal ciliated ridge
zu	ductule of hyponotal gland



FIGS. 1-9. *Coriocella nigra*. Fig. 1, Side view of living snail, from sketch by Dr. E. Kirsteuer. Fig. 2, Dorsal view of preserved snail. Fig. 3, Dorsal view of living snail, from sketch by Dr. E. Kirsteuer. Fig. 4, Ventral view of fore end. Fig. 5, Anterior part of body with opened mantle cavity. Fig. 6, Radular teeth. Fig. 7, Penis and seminal duct. Fig. 8, Jaw plate. Fig. 9, Shell.



FIGS. 10-15. *Atys* species, juvenile. Fig. 10, Living snail, from sketch by Dr. E. Kirsteuer. Fig. 11, Shell. Fig. 12, Jaw elements. Fig. 13, Gizzard plate. Fig. 14, Transverse section of opening of mantle cavity. Fig. 15, Radular teeth.

In life the head shield is slightly notched in front and has 2 short lobes behind; the eyes are equally far from the anterior border and from each other, but nearer to the sides. The border of the left parapodium is covered by the right one. The body is narrowest at the beginning of the parapodia, widest near the hind end. The skin is smooth, the sole not set off.

In the preserved specimens the borders of the parapodia touch each other. Under the head shield (cs), but standing out behind are the Hancock's organs (h), which consist of 18 vertical leaves. Their wavy upper borders are united by a transverse fold (zm) behind the head shield. In the anterior part of the back the silky fibers of transverse muscles are seen. The hind part bears the shell, covered by the mantle and decalcified by preservation in Bouin's fluid. The mantle aperture (mo) is of different widths, generally round, but sometimes triangular. The shell of a 6 mm snail measures 2.4 by 1.5 mm. The somewhat curved apex lies to the left near the middle. The growth lines run parallel to the right border, whose tip projects into the right mantle lobe.

The crescent-shaped jaw plates consist of short thick elements whose tips each bear 2 to 3 strong points on their broader sides. The radula has 38 rows of 14.1.14 teeth. The rhachidian tooth has a single cusp and is broadest at its base; all laterals are blunt-ending hooks, the outermost the smallest. The blackish-brown gizzard plates are 780 μ long. They have about 100 ribs, up to 10 μ broad, bearing a row (sometimes 2 rows) of pointed denticles.

From the seminal groove (sr) a closed male duct, more than 12 mm long, runs inwardly. Its innermost glandular tube, the prostate (q), is 2.5 mm long and contains sperm. Outwardly it follows as a sheathed muscular tube (um), which extends to the left until under the shell. A portion only 24 μ thick (ui) leads to the penial sac, which is 1.3 mm long and through which the male duct courses as a groove between 2 high folds.

Remarks: Only in the original material (Bergh, 1901, p 235) and in the present specimen are described the thin duct between the penial sac and the inner parts. Dissected reproductive organs, clarified ones, and those described by reconstruction from sections often result in rather different descriptions and alone do not justify specific separation. The length of the median cusp of the rhachidian tooth, small (Bergh, 1901, pl. 19, figs. 31-33) or great (Baba, 1936, fig. 1 C, a) depends upon the position on the slide (cf. figs. 18 and 19). The sharp borders of a pit in the base of the rhachidian tooth simulate lateral denticles of the cusp (Bergh, 1905a, pl. 10, fig. 12; Marcus, 1960a, fig. 19). The greater size of Ehrenberg's animals (Pilsbry 1895-1896, p 37) explains the large number of radular teeth (Bergh, 1901, p 236), greater than in Vayssiere's (1912), Baba's (1936), our first (Marcus, 1960a) and the present specimens.

Smaragdinella kirsteueri, new species
(Figs. 23-27)

Collecting stations: Madagascar; xxxi, xxxii, 2 specimens.

Diagnosis: The dark green-brown animals, up to 40 mm long, differ from the congeneric species by the short, posteriorly notched head shield, the denticulate jaw elements, and details of the radula. Holotype and paratype: AMNH (American Museum of Natural History) 140583.

Description: The living snails were 35 to 40 mm long, 9 to 10 mm broad, and uniformly dark green-brown with greyish-yellow shell. The surface of the parapodia of the perserved specimens is smooth. The head shield is short, in life slightly notched in front, bilobed behind. The border of the right parapodium covers the left, even when preserved. The large eyes are visible only after dissection; the sole is not set off. The Hancock's organs consist of

24 complete and several incomplete folds; they are united behind as in the preceding species. The head shield occupies about ¼ of the body length in life, the shell 1/7. Between both lies a stripe of the back, 6 mm long, with distinct transverse muscle fibers.

The shell of the larger specimen is completely decalcified; only in the smaller snail are its size (5 to 3.1 mm), position and approximate shape discernible. The shell lies free on the roof of the mantle, whose border is thickened by glands. The growth lines are parallel to the right shell border. The border is rolled in slightly near the middle on the left side, and a little wider in front than behind. If it had an inner columellar process, this would not be recognizable in the decalcified shell. The hind border of the mantle is prolonged into a short lobe on the right.

The jaw elements are thick columns, up to 80 μ high, with a surface 40 μ by 25 μ, whose narrow border bears 1 to 3 pointed denticles. The radula of the larger specimen has 57 rows and 37 teeth on either side of the rhachidian tooth. The latter measures 30 μ by 30 μ, is a little narrower basally, and has a denticle on the sides of the cusp, at least simulated by the structure of the tooth. The bases of the uniform lateral teeth measure 50 μ to 60 μ and are rough in the inner half of the row. The cusp of the 1st tooth is 50 μ long, the following ones increase to 80 μ, outwardly they decrease to 30 μ on the outermost tooth. The 3 equal gizzard plates, 2.7 to 1.6 mm long, bear numerous ribs, which are 28 μ broad, with several rows of knobs. The ribs are angled at the crest and inclined obliquely backwards.

The male copulatory organ, 7.2 mm long, extends backwards beyond the nerve ring. From the seminal groove a 2 mm tube courses inwards and widens (p) to a folded sac, 1.5 by 1.0 mm. On the bottom of the sac inserts a thick retractor muscle (r); a thin one inserts at the entrance of the tube. Entally to the sac follows a thin connecting tube, 2 mm long, to the glandular prostate (q), 1.7 by 0.65 mm, which contains sperm.

The species is named for the collector, Dr. Ernst Kirsteuer.

Remarks: The head shield of *Smaragdinella calyculata* (see Marcus & Burch, 1965, p 237), its mandibular rodlets and male organ are different from the present species. Also the radula (*ibid.*, fig. 4) is different, but cannot be used as distinctive character, if the synonymy (*ibid.*, p 236) is adopted.

Risbec's *Smaragdinella viridis* (1951, p 139) differs from *S. kirsteueri* mainly by the jaw elements, rhachidian tooth, and especially by the large shell; *S. andersoni* (see Pilsbry, 1893-1895, p 260) differs by the shape of the shell. Pilsbry called the parapodia of this species expansions of the mantle; Habe (1952, p 146) united the species with the unfigured *S. sieboldi* Adams, 1864. Bergh's *Cryptophthalmus olivaceus* (1900a, p 164) from Fouquets Reefs, with an external shell (hence not Ehrenberg's species, but probably a *Smaragdinella*), is similar to *S. kirsteueri* in the body size, measurements of the shell, formula of the radula and perhaps jaw platelets. Differences are the indistinct Hancock's organ and the rounded, hardly notched hind end of the head shield. The rhachidian tooth and the male organ of Bergh's animals were not described.

Philine species, juvenile
(Fig. 28)

Collecting station: Madagascar; xxvii, 1 snail.

Description: The living animal measured 3 by 1 to 1.5 mm and was whitish-yellow with the brownish liver shining through the skin. The strongly shortened head shield gives the preserved snail an odd appearance; its shell is decalcified. The radula has 13 rows of 2.1.0.1.2 teeth. The inner lateral tooth has a strong outer process and about 18 pointed denticles on the inner side. The 2 marginals are smooth hooks

whose cusp is larger than the base. The outer marginal is smaller than the inner one. There are no gizzard plates; the muscle layer of the gizzard is thickened. A penis is not yet developed.

Remarks: We only know *Philine caledonica* Risbec (1951, p 134) as an Indo-Pacific species of the genus without gizzard plates and with a radula of the same type as the present specimen. Its inner lateral tooth is, however, much broader (*loc. cit.*, fig. 8) than that shown in our Fig. 28. As our specimen has no shell remaining, we cannot compare it with the Atlantic *P.* (*Ossiania*) *quadrata*, also without gizzard plates and with the same radular formula.

Chelidonura Adams 1850

The 2 genera of the Aglajidae with elongated head shield and long mantle lobes, *Chelidonura* and *Navanax* Pilsbry, 1895, should be united (Bergh, 1905a, p 42). As in *Aglaja*, the shell can be used only for the separation of the species.

The cephalic sense organs of *Chelidonura* and *Navanax* are of the same type. On either side of the mouth there is a protrusible thickening beset with many tufts of cilia. In most cases the thickening is vertically bipartite, so that an outer, sometimes larger knob and an inner one are formed (Marcus, 1955, fig. 8). In preserved slugs the thickening is often retracted and hidden under the head shield, so that the bipartition and the size of the knobs are difficult to judge. If they can be analyzed they are useful specific characters.

The long and smooth penis papilla, considered as a generic character of *Navanax* (Marcus, 1961a, p 8), occurs also in certain species of *Chelidonura*.

Chelidonura punctata Eliot 1903 (Figs. 29-31)

Chelidonura hirundinina var. *punctata* Eliot, 1903c, p 336, pl. 13, fig. 2.

Range: Zanzibar.

Collecting station: Madagascar; xxxi, 1 specimen.

Description: The living snail was 40 to 45 mm long, 8 to 10 mm broad, bluish-black with scattered brown-orange spots of different size on the head shield, back, parapodia and under side. The head shield, parapodia and caudal lobes have a very narrow white rim. Also the seminal groove is white.

The tail lobes are pointed. To the sides of the mouth the inner and outer knobs are beset with tufts of sensory cilia. The Hancock's organs are only a row of pits. The shell, 7 by 4 mm, is nearly as long as the mantle shield. Its front part is shivered; around the aperture it is solid and silvery. The right border of the outer lip penetrates into the right tail lobe. Between the outer lip and the apex there is a deep sinus. The columella has a thick callus which is obliquely furrowed.

When the animal is opened ventrally, the foremost organ is the white foot gland, 2 mm long. Its surface is rough, the hind border slightly notched. Dorsal to the foot gland lies the small pharynx, 2.5 by 1.5 mm, with the cerebral ganglia apposed to its hind end. To the right is situated the male organ, 2.2 mm long. The peritoneum is stippled with melanophores.

The penis corresponds to "type 2" of *Aglaja* (Marcus, 1966, p 165). The seminal groove enters the atrium. Two slightly lobed prostatic tubes of different length go out from the bottom of the atrium. Between them there is a small lobe of the large cells. The pointed penial papilla is broad at its base and projects into the atrium.

Remarks: Quoy & Gaimard's original material of *Chelidonura hirundinina* (1833) was not uniform in color and pattern (Pilsbry, 1895-1896, p 35; Pruvot-Fol, 1934, p 29). Therefore, striped and spotted snails were classified as *C. hirundinina* (Pilsbry, 1895-1896, pl. 2, figs. 31, 32) or called var. *elegans* and var. *punctata* (Bergh, 1900b, p 213). The

penes of the species of *Chelidonura* should be better known before such combinations can be justified. The penis of *C. punctata* differs from that of *C. elegans*, and also from that of west Atlantic animals which we previously determined as *hirundinina* (due to their agreement with Baba's figures (1949, pl. 2, fig. 4; 1958, frontispiece)).

Baba & Abe (1959, p 280) stress the similarity of their *Chelidonura tsurugensis* with *C. punctata*, but the sole of the Japanese species has no spots, and the parapodia are not rimmed. The short right tail lobe is rounded in all specimens of *C. tsurugensis*. The head shield bears a triangular white area on either side of the midline (Abe, 1964, pl. 2, fig. 7).

Chelidonura inermis
(Cooper 1862)

Navanax inermis, Marcus, 1967, p 149, fig. 11.

Range: From Monterey Bay to the Gulf of California.

Collecting station: Mexico; iv, Dec. 26, 1966 (Paula Vreeland), 1 specimen.

Remarks: Alive the animal was 30 mm long. The bluish-grey under side of the photograph shows golden yellow dots. In part these are still recognizable in the preserved specimen, whose back has dark streaks.

Anaspidea
Aplysia (*Pruvotaplysia*) *parvula*
Mörch 1863

Aplysia (*Pruvotaplysia*) *parvula*, Eales, 1960, p 287-291, figs. 10-11.

Range: In all warm and warm-temperate seas, from about latitude 40° N to 40° S; not in the Mediterranean.

Collecting stations: Madagascar; xxix, 1 specimen.

Mexico: ii, Nov. 12, 1966 (Paula Vreeland), algae on rocks in the intertidal zone, 1 specimen.

Remarks: The living animal from Madagascar was 8 to 10 mm long and 3 to 4 mm broad. It was dark green with whitish-yellow spots and yellow tips of the tentacles and rhinophores, and dark brown rings around the eyes. The parapodia are rimmed with dark brown and joined high up.

The specimen from the Gulf was 18 mm long when living, colored reddish-brown with whitish blotches. The parapodia were rimmed with dark blue. The tips of the light outer parts of the tentacles and rhinophores were blue.

Dolabella auricularia
(Solander 1786)
(Fig. 35)

Dolabella scapula, Engel, 1942, p 199, 207-234, figs. 6-16.

Dolabella auricularia, Marcus, 1965, p 266.

Dolabella californica, MacFarland, 1966, p 32-37, pl. 6, fig. 14, pl. 8, figs. 26-32, pl. 9, figs. 13, 14.

Range: Indo-Pacific, from the Red Sea to Japan, Easter Island, Ecuador and the Gulf of California.

Collecting stations: Madagascar; xxvi, 1 specimen.

Mexico: iv, Dec. 26, 1966 (Paula Vreeland), 1 specimen.

Remarks: The snail from Madagascar was 100 mm long alive and 50 to 60 mm broad. It was green-brown with lighter and darker spots and whitish grey, mottled borders of the parapodia. The parapodia are beset with short, pointed papillae.

The Californian specimen was 95 mm long and had green spots similar to MacFarland's specimen 26.

Dolabrifera dolabrifera
(Rang 1828)

Dolabrifera dolabrifera, Engel, 1936, p 29-43, fig. 16; Kay, 1964, p 184, 185.

Range: Circumtropical and circumsubtropical, but not recorded yet from the American Pacific coast.

Collecting station: Madagascar; xviii, 3 specimens.

Remarks: The largest specimen was 40 mm long alive, 12 to 15 mm broad.

The ground color was a light green-brown, the border of the foot whitish-grey. On the back there were whitish-grey papillae and dark brown spots.

Stylocheilus longicauda
(Quoy & Gaimard 1824)

Stylocheilus longicauda, Engel, 1936, p 57-72, figs. 24-43; Kay, 1964, p 182-184, pl. 8, fig. 4; Marcus, 1967, p 159, figs. 16, 17.

Range: Circumtropical.

Collecting stations: Madagascar; xxxvi, 5 specimens.

Mexico: iv, Dec. 26, 1966 (Paula Vreeland), rocks, intertidal zone, 1 specimen.

Remarks: The preserved slugs from Madagascar are up to 22 mm long. They have wart-shaped and ramified papillae, black streaks and the ocellar spots visible as white dots, as in Engel's material from Barbados Reef (1936, p 61). In the hind gizzard we found only 3 cuticularized warts.

The Mexican specimen was 14 mm long, 10 mm high and 9 mm broad when alive. It has the longitudinal streaks and ocellar spots which distinguish the species from *Stylocheilus citrinus* (Rang, 1828, p 71; Marcus, 1962b, p 16, 1967, p 40). Radula, gizzard plates and penial spines do not furnish clear-cut diagnostic characters.

Ascoglossa

Stiliger (*Stiliger*) *erbsus*, new species
(Figs. 32-34)

Collecting station: Madagascar; xxii, 1 specimen.

Diagnosis: Small, whitish-yellow, with green granules in the liver branches, the hind ends of which anastomose. In the cerata the hepatic diverticula are unbranched. Holotype: AMNH 140585.

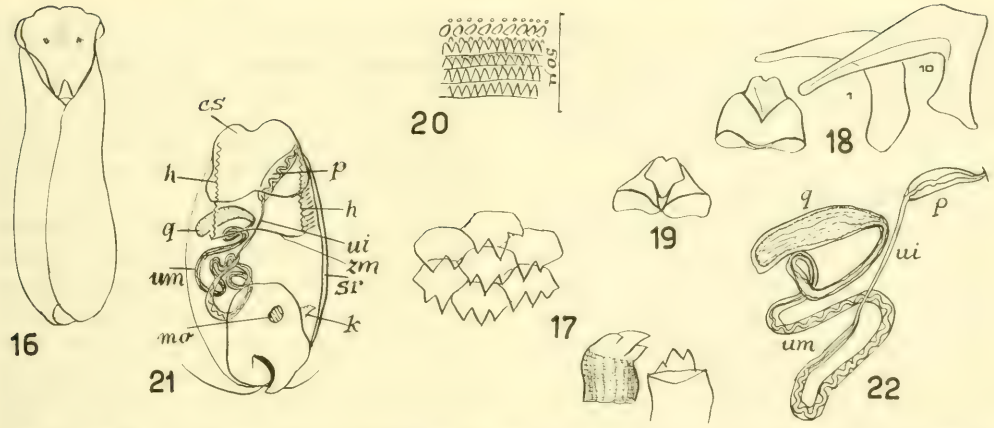
Description: The slug was 3 mm long and 1 mm broad when alive. The main liver stems are slightly ramified. The anterior foot border, lips and rhinophores are whitish and transparent; on the rhinophores there is a dorsal stripe of graphite-black. Further skin pigments are a dark brown irregular middorsal area, and melanophores between the cerata and the foot border.

The preserved animal measures in mm: length 2.5, breadth 0.55, tail 0.4, rhinophores 0.5, longest cerata 0.5, distance between the eyes 0.25; diameter of eyes 0.05. The cerata stand in a row on either side, about 12 large and many small ones. The head stands out over the thick lips. The rhinophores are blunt, round in transverse section, and narrowed at the base. The anterior foot border is notched, with short and round lateral angles. Two transverse folds of the sole are probably produced by contraction. The border of the sole is distinctly set off from the sides. The tail is limited by an anastomosis of the liver branches between the hindmost cerata.

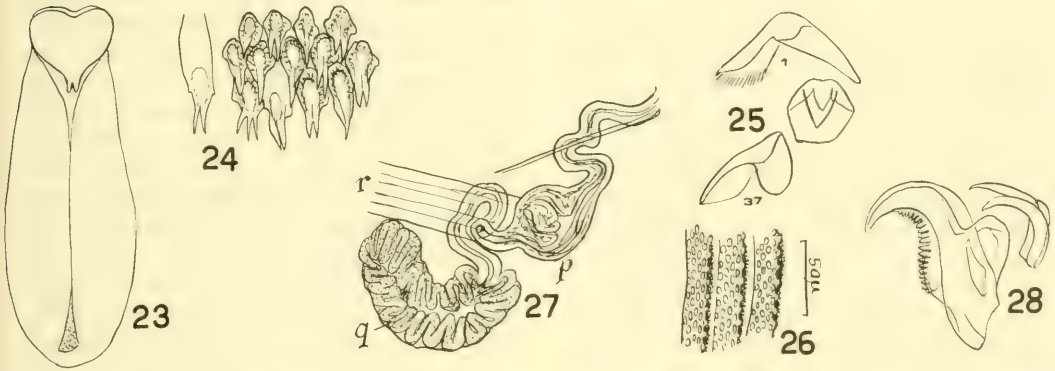
The blunt cerata contain an unbranched hepatic diverticulum, but no tube of the albumen gland. Large subepidermal gland cells, especially near the tip of the cerata, are irregular, not arranged in stripes. The short pharynx lies between the eyes. The anus is situated in the midline in the anterior part of the pericardial eminence, which extends to the middle of the body. The short penial stylet is curved.

The radula has about 6 teeth in the ascending limb, 6 in the descending limb, and 4 smaller ones heaped in the ascus. The teeth are 104 μ long, the base 39 μ; the tip is broad and round. The upper side of the tooth is bipartite by a pit, the borders of the hollow underside are smooth, even when viewed with high power.

Remarks: *Stiliger erbsus* differs from all other species of the genus. Avoiding a discussion of the synonymy of the European species, we mention only the Indo-Pacific ones. Those of the subgenus *Ercolania* Trinchese, 1872, differ from the new species by their rhinophores flattened or grooved on the outer side. These species are: *S.* (*E.*) *akkeshiensis* Baba (1935a, p 116); *S.* (*E.*) *illus* Marcus (1965, p 267); *S.* (*E.*)

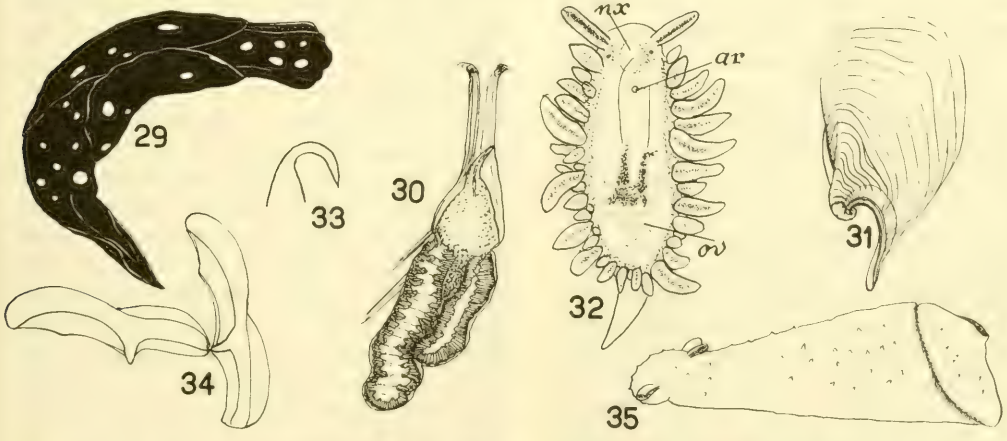


FIGS. 16-22. *Lathophthalmus smaragdinus*. Fig. 16, Living snail, from color photo. Fig. 17, Jaw elements. Fig. 18, Radular teeth. Fig. 19, Rhachidian tooth of other specimen. Fig. 20, Ribs of gizzard plate. Fig. 21, Male duct *in situ*. Fig. 22, Male duct.



FIGS. 23-27. *Smaragdinella kirsteueri*. Fig. 23, Living snail, from sketch by Dr. E. Kirsteuer. Fig. 24, Jaw elements. Fig. 25, Radular teeth. Fig. 26, Three ribs of the gizzard plate. Fig. 27, Male duct.

FIG. 28. *Philine* species, juvenile. Radular teeth.



FIGS. 29-31. *Chelidonura punctata*. Fig. 29, Living snail, from color photo. Fig. 30, Male duct. Fig. 31, Shell.

FIGS. 32-34. *Stiliger erbsus*. Fig. 32, Preserved slug. Fig. 33, Penial stylet. Fig. 34, Radular teeth.

FIG. 35. *Dolabella auricularia*. Living snail, from sketch by Dr. E. Kirsteuer.

noto Baba (1959, p 330); *S.* (*E.*) *smaragdinus* Baba (1949, p 32, 129); *S.* (*E.*) *vancouverensis* (O'Donoghue, 1924b, p 19); *S.* (*E.*) *zanzibaricus* (Eliot, 1903a, p 256); and *S.* (*E.*) *zosterae* Baba (1959, p 331).

Among the Indo-Pacific species with round rhinophores, the following species differ from *Stiliger* (*S.*) *erbsus* by a branched or lobed hepatic diverticulum in the cerata: *S.* (*S.*) *boodleae* Baba (1938, p 129), *S.* (*S.*) *evelinae* Marcus (1959, p 22), *S.* (*S.*) *gopalai* Rao (1937, p 435), *S.* (*S.*) *nigrovittatus* Rao & Rao (1963, p 232), *S.* (*S.*) *pica* Anandale & Prashad (1922, p 700) and *S.* (*S.*) *varians* Eliot (1904, p 290). *Stiliger varians*, it is true, has longitudinal lines on the cerata (Eliot, 1903b, pl. 32, figs. 9, 10), not hepatic branches. Such lines also distinguish *S.* (*S.*) *subviridis* Baba (1959, p 328) from *S.* (*S.*) *erbsus*.

The location of the anus in front of the pericardial hump, or behind it, separates *Stiliger* (*S.*) *fuscovittatus* Lance (1962, p 32) and *S.* (*S.*) *felinus* Hutton (Eliot, 1907, p 330) respectively from *S.* (*S.*) *erbsus*.

In *Stiliger* (*S.*) *berghi* Baba (1937, p 222) 7 to 9 large and small cerata alternate on either side; in *S.* (*S.*) *irregularis* Eliot (1904, p 291) and *S.* (*S.*) *pusillus* Baba (1959, p 328) the hindmost cerata are the largest.

Stiliger (*S.*) *ornatus* Ehrenberg, 1831, (not *modestus* (Bergh, 1872, p 139; 1878a, p 812)) and *S.* (*S.*) *viridis* (Kelaart, 1859, p 492; Eliot, 1906, p 686, pl. 46, fig. 3) differ from *S.* (*S.*) *erbsus* by the great number of cerata.

Prolonged anterior foot corners occur in *Stiliger* (*S.*) *formicarius* Baba (1959, p 329) [later transferred to *Costasiella*] and in *S.* (*S.*) *tentaculatus* Eliot (1917, p 179) [of doubtful generic position].

Stiliger viridis (Kelaart, 1859) has priority over the Mediterranean *S. viridis* (A. Costa, 1866), whose first synonym, *nigrovittatus*, must replace *viridis*. Therefore, *S.* (*S.*) *nigrovittatus* Rao & Rao, 1963, must be renamed. Therefore, we introduce the new name, *S.* (*S.*) *raorum*.

Elysia vreelandae, new species
(Figs. 36-40)

Collecting station: Mexico; ii, Nov. 12, 1966 (Paula Vreeland), on *Codium*, 4 specimens.

Diagnosis: A small, dark olive-green species with lighter borders of the parapodia and blue dots. The hepatic tubes are very thin near the stomach. Epithelial tubules form a penial appendage. There is a single female aperture. Holotype and paratype: AMNH 140586.

Description: The animals were about 10 mm long when living; preserved they are up to 8 mm. A preserved animal with almost fully spread parapodia is 7 mm long, 5 mm broad. The color is dark olive-green with lighter borders of the parapodia and the blue dots. A colorless crescent around the posterior border of the pericardial hump lies over the white kidney. Farther behind, the back is yellowish-brown in color. The small hepatic terminations containing the chloroplasts of the alga form a dense pattern on the head, neck and outer side of the parapodia; on the inner side they are coarser and less ramified. The inner side of the rhinophores (ri) and a minute halo around the eyes (y) are white, the sole is only a little lighter than the outer side of the parapodia.

Two longitudinal vessels run along the back. A single melanophore lies on either side of the mouth. The pharynx (nx) is very small, 400 μ by 400 μ. The radula has 8 teeth in the dorsal limb, 14 in the ventral limb, and many heaped up in the ascus (as). The teeth are up to 120 μ long, their furrow is 80 μ, the base 34 μ; 10 μ embrace 6 of the small denticles. The short oesophagus (o) bends to the left, bears a muscular pouch (oc) and passes gradually to the stomach (so). The oesophagus and the cardia are wide dorso-ventrally, and the stomach is wide antero-posteriorly, even when empty. The epithelium of the oesophagus, pouch, and stomach is ciliated; the cilia in the stomach are es-

pecially strong. The digestive gland (ia) has 6 ducts. The foremost duct supplies the head and enters the rhinophores; it opens far in front into the ventral wall of the stomach. The following 3 ducts come from their regions in front and on the right side, bend to the left, and turn to the stomach. The hindmost ducts course over the borders of the sole and open into the stomach from both sides. The hepatic tubes are very thin near the stomach, widen in the middle and decrease in width, again peripherally where they touch the skin. The stomach narrows gradually into the intestine, which is 100 μ long. The anus (ar) lies between the right parapodium and the pericardium.

The female germ cells occupy the ental half of the hermaphrodite follicles (ov); the male cells occupy the ectal part. The ciliated ampulla (a) lies about in the middle of the hermaphrodite duct (eu). The seminal duct (d) and the inner oviduct (io) receive the more central prostatic (q) and the more lateral albumen gland (ag) tubes, respectively. The crowded prostatic cells are claviform with homogeneous secretion; their diameter is 15 to 20 μ. The albumen gland cells measure about 25 μ and contain granules measuring 6 μ. The deep male atrium (am) is bent backwards and contains the conical penis (p), 3 times as long as broad. Epithelial tubules form a possibly glandular appendage (pg) in front, at the root of the penis. The male aperture (ma) lies under the right rhinophore (ri).

Clusters of glands open between the cells of the inner oviduct (io). This part corresponds to a membrane gland (Ghiselin, 1965, p 337). Where the oviduct passes into the mucus gland (mu) there are some small pouches (vs) with sperms not fastened to the wall. They correspond to a seminal receptacle. The low epithelium of the mucus gland has long cilia and invaginated saccules of glands which make the surface brambly. The vaginal duct leading to the bursa copulatrix (b) goes out from the nidamental duct (ni). The single female aperture (fa) lies 1 mm behind the male pore, the anus (ar) 100 μ behind it, and the renal pore (ne) still farther behind and farther dorsal.

The species is named for the collector, Mrs. Paula Vreeland.

Remarks: The atrial diverticula of *Elysia lobata* (Marcus, 1958, fig. 40, 3), *E. maoria* (Reid, 1964, figs. 7 A, B, d), and *E. hedgpethi* (Fig. 41) are farther behind than that in *E. vreelandae*.

Elysia hedgpethi Marcus (1961a, p 13) ranges from the State of Washington to the Gulf of California (Lance, 1966, p 71). It is up to 29 mm long when preserved. Its penis is twice as long as broad, with a diverticulum near the inner end of the atrium. The openings of the vagina and the oviduct are far apart. *Elysia bedeckta* MacFarland (1966, p 50) from Monterey to Newport Bay is synonymized to *E. hedgpethi* by Sphon & Lance (1968: 79) though it differs slightly by the position of the vaginal pore close to the male aperture and the anus on the right anterior side of the pericardial hump. The teeth of *E. bedeckta* reach 330 μ, those of *E. hedgpethi*, 170 μ. The mentioned characters separate *E. hedgpethi* from *E. vreelandae*.

Notaspidea
Berthellina cuvieri
(Bergh 1898)
(Figs. 42-48)

Pleurobranchus cuvieri, Bergh, 1898, p 129-131, pl. 11, figs. 19-27.

Range: Mauritius; possibly Ceram.

Collecting stations: Madagascar; xi, xiii, xiv, xvi, xix, xliii, 7 specimens.

Description: The animals were 35 to 40 mm long when alive, 15 to 17 mm broad, and uniformly light orange. The veil, and the membrane which unites the rhinophores at half their length, were transparent. The snails measure 13 to 19 mm when preserved; the longest is 14 mm high and 13 mm broad. The mantle border is rolled in, the foot border wavy. In the smooth, gelatinous

notum lie opaque, invaginated epidermal glands (up to 0.5 mm long) in different stages, as in *Berthellina granulata* (Hill, 1963, fig. 1). We found neither spicules nor organic traces of such; some sponge spicules stuck in the skin.

The shell measurements in mm are: 9 by 5.5 (body 13 mm); 5.5 by 2 (body 14 mm); 8.5 by 5 (body 15 mm); 6 by 2.5 (body 16 mm); 6.5 by 2.4 (body 19 mm). The growth lines are distinct. The spiral sculpture consists of rows of dots which do not reach the anterior border; on the shell of snails 13 to 16 mm long, it extends over $\frac{1}{3}$ of the shell, in the 19 mm specimen over $\frac{2}{3}$. The fact that a small snail had the biggest shell is fortuitous. The periostracum is colorless.

The furrowed anterior foot border, the veil and the rhinophores show no peculiarities. The last quarter of the gill is free. Animals of 15, 14 and 19 mm have 20, 24 and 26 branchial leaves, respectively.

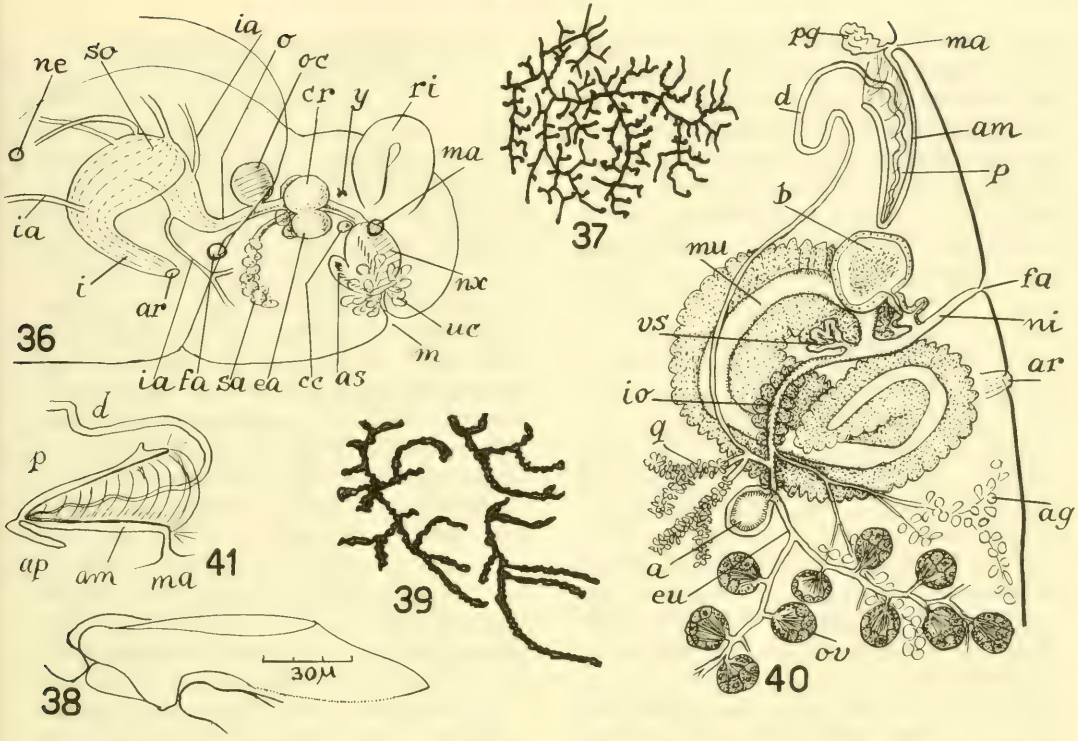
The jaw plates are 3.5 by 1.5 mm (14 mm snail) and 4.5 by 2 mm (15 mm snail). The elements (80 μ by 22 μ) are generally unicuspidate, but sometimes they have a secondary point on one or both sides of the cusp. The radulae of a 14 mm and a 15 mm snail measure 3.5 by 3.2 mm and 3.33 by 3.33 mm, respectively. They have 80 and 90 rows, 150 and 200 teeth per half-row, respectively. The largest teeth are 180 μ and 170 μ long, respectively. The teeth of both specimens have 12 to 19 denticles; the innermost teeth have the fewest denticles, those in the middle the greatest number of denticles. On the outer teeth the denticles are longest.

At the outlet of the long and narrow ampulla (a), filled with sperm, the sperm-oviduct divides into an inner oviduct (io) and a seminal duct, which is glandular at its beginning (q). The acinous prostate is apposed to the spermatheca (t). Into the succeeding part of the male duct there opens a coiled, glandular tube, the accessory prostate (xs). The heavily muscular seminal duct (d) enters the male atrium (am), dilated by a strong penial papilla (p). A retractor muscle (r) inserts at the bottom of the atrium.

Beside the male aperture (ma) lies the wide opening (fa) in common for vagina (v) and nidamental duct (ni). The vagina leads into the soft spermatheca (t) containing black residues of sperm and prostatic secretion. From the vagina a thin duct courses to the spermatocyst (sc) full of orientated sperm. The wall of the spermatocyst is connected with the mucus gland by a strand of connective tissue, whose position corresponds to an allosperm duct (perhaps it is a rudimentary duct).

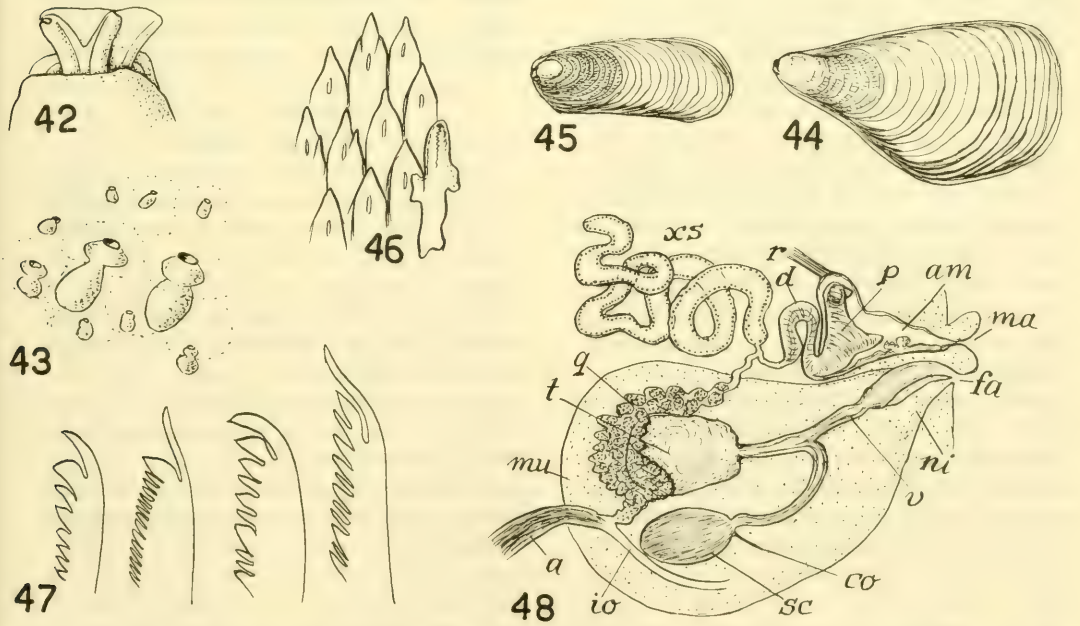
Remarks: Vayssière's *Berthellina brocki* (1896, p 120; 1898, p 256) and Bergh's *B. cuvieri* are from the same locality and collection, but Vayssière's name and description refer also to specimens from Amboina, Java, and New South Wales, Jervis Bay. Later, its range was extended to Easter Island (Odhner, 1921, p 248). The reproductive organs of *B. brocki* agree with those of our animals, while they are incompletely known for *B. cuvieri*. The spiral shell sculpture reaches the anterior border in *brocki*, but not in the present material. Possibly Vayssière's specimens from Jervis Bay are identical with *Pleurobranchus punctatus* Quoy & Gaimard, 1832, (Pruvot-Fol, 1934, p 34, 35). Therefore, Macnae (1962a, p 172) called his snails from Madagascar and southern Mozanbique *Berthellina punctata*. The position of the prostate and the allosperm duct in Macnae's figure differ from our Fig. 48.

Burn (1962, p 138) united *Berthellina brocki*, *B. punctata* and other species with *B. citrina* (Rüppell & Leuckart, 1828). In living animals of this species the cutaneous glands produce a reticulation of the notum, but not always, see Gohar & Abul-Ela, 1957, pl. 1. The spiral sculpture reaches the anterior border of the shell. The jaw elements are short and have 1 or several secondary cusps (Vayssière, 1906). The radula comprises 60 rows and up to 140



FIGS. 36–40. *Elysia vreelandae*. Fig. 36, Diagram of digestive tract. Fig. 37, Ramification of liver on back of animal. Fig. 38, Radular tooth. Fig. 39, Ramification of liver on inner side of parapodia. Fig. 40, Diagram of reproductive organs.

FIG. 41. *Elysia hedgpethi*. Penis.



FIGS. 42–48. *Berthellina curieri*. Fig. 42, Head of living snail, from color photo. Fig. 43, Notal skin, preserved. Fig. 44, Shell of 13 mm animal. Fig. 45, Shell of 16 mm animal. Fig. 47, Tips of radular teeth. Fig. 48, Diagram of reproductive organs.

teeth per half-row. The teeth are up to 160 μ long (Gohar, 1957); their denticles are coarser than in *B. brocki* (Vayssière, 1898, p 260). Though the reproductive organs of animals called *B. citrina* (Risbec, 1951, fig. 14, 2; Burn, 1962, fig. 3) agree with our Fig. 48, we consider it premature to use this name for the present specimens.

Eudoridacea
Conualevia marcusi
Collier & Farmer 1964
(Fig. 49)

Conualevia marcusi Collier & Farmer, 1964, p 381-383, figs. 1, C-H, pl. 2 on p 386.

Range: Gulf of California, west coast of northern part.

Collecting station: Mexico; ii, Nov. 12, 1966 (P. Pickens), rocky intertidal, 1 specimen.

Descriptive notes: The preserved slug is 8 mm long; alive it was 16 mm long. The body and the rhinophores are white, the 16 unipinnate gills retracted. The notum is finely papillose with opaque glands to the sides of the gills and farther in front. There are no ridges around the rhinophoral and branchial pits. The rhinophores are quite smooth, the stout tentacles rectangular. Translucent bundles of muscles produce striae in the hyponotum. No spicules are recognizable. The radula consists of 42 rows and 59 teeth per half-row. The teeth are simple hooks up to 60 μ high. Their aspect depends on their position on the slide. For further information on the alimentary and reproductive organs, we refer to the original paper (Collier & Farmer, 1964).

Remarks: The present slug has fewer rows and teeth in the radula than the original diagnosis. But as Collier and Farmer counted only 1 of their specimens, the taxonomic value of this difference cannot be judged.

Chromodoris quadricolor
(Rüppell & Leuckart 1828)
(Figs. 50-53)

Chromodoris quadricolor, Marcus, 1960a, p 899-901, fig. 42.

Glossodoris quadricolor, Engel & van Eeken, 1962, p 23, 24, fig. 1; Engel & Nijssen-Meyer, 1964, p 27-32, figs. 1-5, color plate, figs. 1-3.

Range: Red Sea; Indo-west Pacific, from the east coast of Africa to New Caledonia; possibly (Engel & Nijssen-Meyer, 1964) also Japan, Hachijojima and Sagami Bay (Baba, 1949, p 140).

Collecting station: Madagascar; xxxi, 1 specimen, together with *Hypselodoris regina* (Figs. 54-59).

Remarks: The living animal was 40 to 50 mm long, 8 to 10 mm broad, orange with 3 bluish-black longitudinal dorsal stripes bordered with whitish-blue, and a white rim around the notum. The tentacles are yellow and the 8 unipinnate gills are reddish-orange. On the sides of the foot there are 2 black lines. The salivary glands are long tubes with pointed ends. Our Figs. 52, 53 and 57, 58 show the differences between the labial armatures and the radular teeth of *Chromodoris quadricolor* and *Hypselodoris regina*, respectively.

Chromodoris norrisi
Farmer 1963

Chromodoris norrisi Farmer, 1963, p 81-84, figs. 1a-1e, pl. 1a; Marcus, 1967, p 170, figs. 21-24.

Range: Pacific coast of Baja California; Gulf of California, western and eastern coasts.

Collecting station: Mexico; iii, July 30, 1966 (A. Kerstitch), rocky intertidal, 3 specimens.

Remark: The present slugs have the same color pattern as the type specimens.

Hypselodoris regina, new species
(Figs. 54-59)

Collecting station: Madagascar; xxxi, 1 specimen together with *Chromodoris quadricolor* (Figs. 50-53).

Diagnosis: This is a species of *Hypselodoris* of the *H. semperi* group with straight stripes, similar to *H. nigrostriata* (Eliot), whose stripes are curved and branched. Eliot's species is much smaller than *H. regina*, has more gills and radular rows, but fewer teeth per half-row. Holotype: AMNH 140582.

Description: The living slug had an orange back with 3 bluish-black longitudinal stripes bordered with light blue and not raised. The pattern of light blue and black is shown in the Figs. 54-56; the rhinophores, gills and tip of the tail are orange. Only brown bands and the orange color were retained in the preserved specimen (August 1967). The measurements in mm were: alive, 40 to 50 mm long, 8 to 10 broad, preserved, 22 long, 7 broad, 9 high. The notal border is broad in front, narrow on the sides and behind, and has many globular glands, increasing in size backwards. The tentacles are short and grooved on the outer side. The bilabiate foot border is not notched. The rhinophores have 14 leaves; there are 7 unipinnate gills.

The labial rodlets are up to 60 μ high, 9 μ in diameter, unicuspidate or with 2 slight secondary cusps. The radula has 62 rows, a narrow naked rhachis, and 90 teeth per half-row. The teeth are bicuspidate, the innermost is tricuspidate by a strong inner and an outer denticle. Up to tooth 75, the outer denticle gradually moves downwards; farther to the side the teeth decrease in length, the cusps become blunt and the ventral border nodular. The salivary glands are flat with a broad middle portion and a pointed end.

The ampulla (a) is spherical, the spermoviduct is long; the seminal duct begins tubular, then forms a broad, flat, coiled prostate (q), more than twice as long as the following muscular section (d), which ends with an acrembolic, unarmed penis (p). Beside the penis open the vagina (v) and the nidamental duct (ni) independently; there is no vestibular gland. From the wide vagina 2 canals of equal length go to the spermatheca (t) and the spermatocyst (sc). At the same point begins the long, winding allosperm duct (au).

Remarks: According to its teeth, *Hypselodoris regina* belongs to Eliot's first group (1904, p 385), whose species are generally spotted. *H. nigrostriata* (Eliot 1904, p 394; 1905, p 247) is striped, but differs from *H. regina* by color pattern and teeth. Eliot's *Chromodoris ?magnifica* Quoy & Gaimard, var. (1904, p 397) is not Quoy and Gaimard's species, now united with *C. quadricolor* (Pruvot-Fol, 1934, p 72), but a *Hypselodoris*. It differs from *H. regina* by the radular teeth with 3 to 5 denticles under the terminal cusps, as in *H. hilaris* (Marcus & Burch, 1965, fig. 26).

Atagema osseosa
(Kelaart 1859)
(Figs. 60-64)

Doris osseosa Kelaart, 1859, p 298; Alder & Hancock, 1864, p 121, pl. 28, figs. 10, 11.

Doris carinata (non Quoy & Gaimard, 1832); Alder & Hancock, 1864, p 122, pl. 29, figs. 5, 6.

Sclerodoris osseosa, Eliot, 1903a, p 380; 1908, p 114; 1910, p 420.

Range: East Africa; Coetivy (latitude 7° 15' S, longitude 56° 24' E); Ceylon; coast of the Bay of Bengal.

Collecting station: Madagascar; xviii, 1 specimen.

Description: The living animal was hard, 40 mm long and 30 mm broad, with a folded notal border. The rough surface bears dorsal papillae which stand on a net of ridges. The meshes in between are flat. The papillae are small on the margins of the notum, the rhinophoral sheaths, and on a median ridge. This ridge begins behind the rhinophores and ends in front of the

gills. The ground color is ocher, the papillae are white. The meshes are light brown on the sides, dark brown or blackish-green in the region over the viscera; their pigment is traversed by lines of the ground color. The rhinophores are ocher; their high sheaths have finely scalloped borders.

The preserved animal is 30 mm long (35 mm when measured over the back) and has a 7 mm broad notum. The tentacles are pointed triangles; the rhinophores have 20 leaves. A hump in the cardiac region was not salient in the living slug. The branchial pit has 3 large anterior and 2 smaller posterior lobes; between these the 5 multipinnate gills and the anal papilla project backward. The notum covers the foot, which is 20 mm long. In front, the foot is deeply bilabiate; it is pointed behind.

The papillae contain projecting spicules and are connected by tracts of spicules. Further tracts run from the dorsal to the ventral side, where they form a coarse net. The spicules are smooth, blunt on both ends, and generally straight. The biggest were 700 μ long, 35 μ thick. Globular melanophores, 200 μ to 30 μ in diameter, lie in the connective tissue. The eyes are small; the central nervous system is similar to that of *Austrodoris* (Odhner, 1934, fig. 27). The blood glands are whitish-yellow.

The labial cuticle has no rods or platelets, but bears some colorless soft points. The salivary glands are ribbon-like. The radula, 4.8 by 3 mm, has 17 rows with 30 teeth per half-row. The 6 inner teeth are simple spines, whose size increases from 46 μ to 210 μ. The succeeding teeth are hooks. Their length increases from 300 μ to 500 μ. From the 24th outwards the size decreases; the 2 outermost teeth are 95 μ and 60 μ long. The stomach lies free over the liver, the caecum on the left.

The autosperms in the ampulla and the allosperms in the seminal reservoirs show that the specimen is mature. The inner oviduct (io) and the seminal duct separate at the exit of the longish ampulla (a). The prostatic part (q) is the dilated inner section of the male duct; the outer one (d) is narrower. It opens without a papilla into a strongly muscular male atrium and functions as an acrembolic penis (p).

Between the nidamental duct (ni) and the penis, a short vagina (v) runs to the seminal reservoirs, the large spermatheca (t) and the small spermatocyst (sc). The spermatheca contains irregularly heaped sperms, the spermatocyst parallelly arranged ones. The topography of the reservoirs and their ducts corresponds to the vaginal type. The allosperm duct (au) leads from the the spermatocyst to the inner region of the female gland mass (mu), where the rising allosperms meet the eggs descended through the inner oviduct (io).

On the genus *Atagema* Gray 1850

The holotype of *Doris carinata* Quoy & Gaimard 1832, from New Zealand has dried (Pruvot-Fol, 1934, p 64). Therefore Bergh's description of a similar specimen from New Zealand (1904, p 39-41), which he called *Atagema carinata* (Quoy & Gaimard, 1832), is acceptable to settle the type. *Petelodoris* Bergh (1882, p 227) and *Sclerodoris* Eliot (1903a, p 361) cannot be separated from *Atagema*. The 2 known species of *Peronodoris* Bergh, 1904, however, have a penial stylet. This genus cannot be united with *Sclerodoris*, as did Thiele (1931, p 435), Allan (1947, p 451) and Iredale & McMichael (1962, p 93), but should be maintained separate (Eliot, 1908, p 113, 114; Odhner, 1926, p 54).

The species of *Atagema* have a hard and rough notum; those of *Halgerda* Bergh, 1881, a leathery or stiff, jelly-like one. Due to the texture of the notum, *Doris apiculata* Alder & Hancock (1864, p 122) was removed from *Sclerodoris* Eliot (1903a, p 361), i.e., *Atagema*, to *Halgerda* (id., 1906, p 645, 1002; 1908, p 113). The strong prostate, an internal character of *Halgerda*, was found in *H. apiculata* by Eales (1938, p 404).

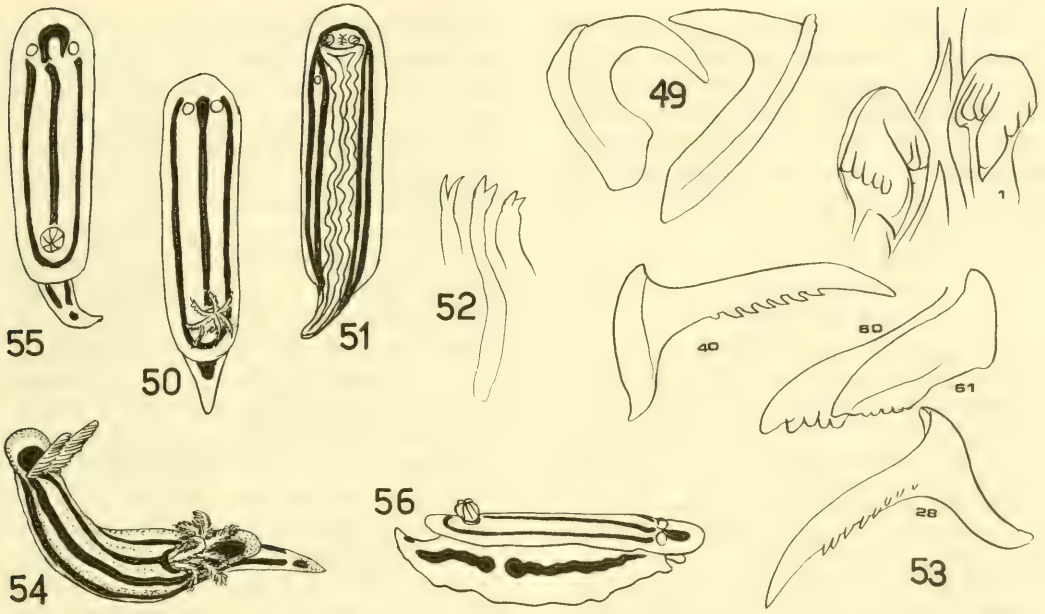
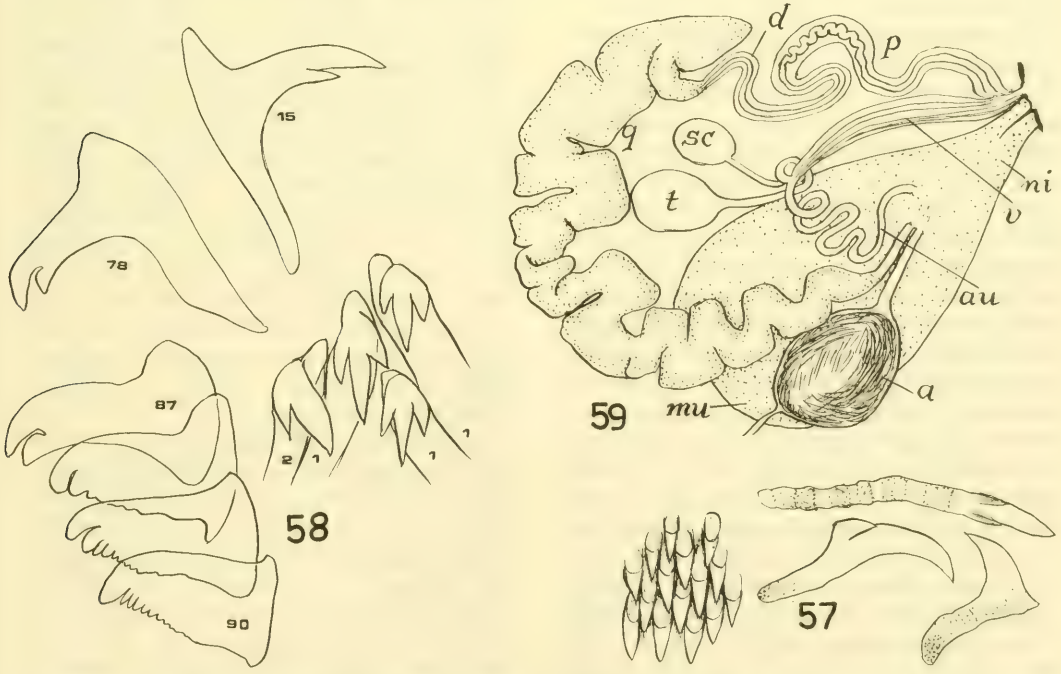


FIG. 49. *Conualevia marcusi*. Radular teeth.

FIGS. 50-53. *Chromodoris quadricolor*. Fig. 50, Dorsal view of preserved slug. Fig. 51, Ventral view of same. Fig. 52, Labial rodlets. Fig. 53, Radular teeth.

FIGS. 54-56. *Hypselodoris regina*. Fig. 54, Living slug, from color photo. Fig. 55, Preserved slug, dorsal view. Fig. 56, Side view of same.



FIGS. 57-59. *Hypselodoris regina*. Fig. 57, Labial rodlets. . Fig. 58, Radular teeth. Fig. 59, Diagram of reproductive organs; prostate laid apart.

The range of *Atagema* comprises the west coast of Africa (Pruvot–Fol, 1953); the Mediterranean (Pruvot-Fol, 1951); the western Indic from the east coast of Africa to the Bay of Bengal; New Zealand; Japan, Enoshima (latitude 35° 18' N, longitude 139° 22' E); California, San Diego (Collier, 1963).

Trippa intecta
(Kelaart 1859)
(Figs. 65, 66)

Doris intecta Kelaart, 1859, p 302.

Goniodoris erinaceus Angas, 1864, p 57, pl. 5, fig. 5.

Trippa ornata Bergh, 1905a, p 129-131, pl. 1, fig. 6, pl. 15, fig. 37; Risbec 1928, p 97.

Trippa affinis Bergh, 1905a, p 131-133, pl. 15, figs. 38, 42.

Trippa intecta, Eliot, 1909, p 83-85; Baba, 1949, pl. 24, fig. 89. Yu & Si, 1965, pl. 3, fig. 2.

Trippa erinaceus, Allan, 1947, p 450, pl. 42, fig. 8.

Range: Ceylon; Malaysia; South China Sea; middle Japan; New South Wales; New Caledonia.

Collecting station: Madagascar; xviii, 1 specimen.

Description: The slug was 40 to 50 mm long, 30 mm broad when alive; preserved, it is 30 mm long. The notum, hyponotum and sides were reddish-brown, the sole whitish-grey. The dark middle part of the back bore an ocher-brown stripe in the posterior $^2/_3$. The notum is covered with large tubercles with thin black papillae on their tops. These contain sparse spicules, some of which stand out. On the sides of the foot are small tubercles; larger ones are on its wavy black border. The connection from head to foot (Bergh, 1877a, pl. 58, fig. 3) was not seen, as part of the mantle border had been autotomized. The rhinophores are black with white tips and have about 25 leaves. The 5 tripinnate gills are black. The high rhinophoral sheaths and the borders of the branchial pit bear tubercles and papillae. The anterior foot border is bilabiate and notched.

The labial cuticle is smooth. The radula has 24 rows and 40 to 43 teeth per half-row. From the innermost tooth, 100 μ high, the succeeding teeth increase rapidly to 280 μ and remain large till far outwards, where they decrease to 85 μ. The large stomach and the caecum are free.

The winding ampulla (a) is continued in a short spermoviduct which divides into a seminal duct and inner oviduct (io). The tubular prostate (q) is very long. The muscular portion of the seminal duct winds in a sheath and is widened in its penial termination (p). From the vestibule the wide vagina (v) leads to a spherical spermatheca (t). Immediately beside the entrance of the vagina the allosperm duct (au) leaves the spermatheca and, near its origin, bears the spermatocyst (sc) filled with orientated sperm. The opening of the allosperm duct into the gland mass (mu) is near the entrance of the inner oviduct. The nidamental duct (ni) opens behind the vestibule (ve).

Remarks: Narrower inner teeth of the radula (Bergh, 1877a, pl. 58, fig. 5; Baba, 1949, p 64, fig. 78 a) or thicker ones (Bergh, 1905a, pl. 15, fig. 38, a) have no systematic value. Regular differences of the teeth within the row, as, e.g., in *Diaulula hispida* (Odhner, 1926, fig. 56), are specific. The light middle stripe or crest of *Trippa intecta* occurs also in material (Bergh, 1890, p 905) allotted to *T. affinis* (id. 1905a, p 131). Also the numbers of the rows and teeth of the radula do not furnish clear-cut differences in the descriptions by Bergh, Eliot and Risbec, so that *T. affinis* cannot be maintained.

Trippa monsoni Eliot (1903a, p 371) from the east coast of Zanzibar, probably identical with the Ceylonese *T. leoparda* (Kelaart, 1859, p 294), differs from *T. intecta* by characters of color and radula.

Rostanga pulchra
MacFarland 1905

Rostanga pulchra, MacFarland, 1966, p 165-169, pl. 25, fig. 7, pl. 29, figs. 7-10, pl. 35, figs. 1-16.

Range: From the Vancouver Island region to the Gulf of California (Farmer & Collier, 1963, p 62); South Chile, Chiloé.

Collecting station: Mexico; i, Oct. 29, 1966 (Mary Anne Hill), rocky intertidal on a red sponge, 2 bright red specimens.

Remark: The Indo-west Pacific *Rostanga arbutus* (Angas, 1864) differs from *R. pulchra* by the radula, but not always by the color (Marcus, 1959, p 36, 37).

Taringa aivica timia
Marcus 1967

Taringa aivica timia Marcus, 1967, p 189, figs. 47-51.

Range: Gulf of California, Sonora.

Collecting station: Mexico; i, Oct. 15, 1966 (Mary Anne Hill), rocky intertidal, 1 specimen.

Remarks: The specimen was transparent light brown with darker rhinophores and spots on the notum and gills. The latter form 2 circles, the right one with 7 normal plumes and a single minute one, the left with 3 large and 1 small plume. The pits of both circles are separated by a perineum. The terminal section of the intestine bifurcates, so that an anal opening occurs in the center of either circle. Probably the rectal anomaly caused that of the gills. Risbec (1928, p 108) mentioned 2 branchial pits in another doridid.

Tayuva ketos ketos
Marcus 1967

Tayuva ketos Marcus, 1967, p 192, figs. 52-56.

Range: Gulf of California, Sonora.

Collecting station: Mexico; i, July 18, 1966 (Mary Anne Hill), rocky intertidal, 1 specimen.

Remarks: The present animal, about 25 mm long when alive, is young and less intensely colored than the original material. The radula has 21 rows and 25 teeth per half-row. The 2 hindmost plumes of the 6 tripinnate gills are largest. The vestibule, though already wide, does not yet contain the characteristic cuticular spicules. Also, the penial papilla is shorter.

Two slugs from Curaçao differ principally by a carrot-shaped penial papilla, and will be described under a new subspecific name.

Asteronotus cespitosus
(van Hasselt 1824)
(Figs. 68-70)

Asteronotus cespitosus, Bergh, 1890, p 917-921 (synonymy), pl. 86, figs. 7, 8; 1905a, p 141 (synonyms), pl. 1, fig. 5; Baba, 1936, p 32 (references), pl. 1, fig. 2; Kenny, 1960, p 224; Yu & Si, 1965, pl. 3, fig. 9.

Asteronotus hemprichii Ehrenberg, 1831; Bergh, 1877b, p 161-173 (including the synonym *A. bertrana* Bergh), pls. 1, 2; Eliot, 1903a, p 384; 1908, p 116; 1910, p 428; Pruvot-Fol, 1933, p 120, 121, pl. 1, fig. 1; 1934, pl. 1, fig. 19.

? *Asteronotus fuscus* O'Donoghue, 1924a, p 551, 552, pl. 28, figs. 12, 13.

Asteronotus brassica Allan, 1932, p 93-95, Figs. 1, 2 (on p 104), pl. 5, figs. 12-14.

Range: Red Sea; western and eastern Indic; South China Sea; Ryukyu Islands; ?Western Australia; Queensland; New South Wales; Palau and Fiji Islands; Samoa.

Collecting station: Madagascar; xxvi, 1 specimen.

Description: The slug was 70 mm long and 40 mm broad when alive. The back and the warts on the notal bulges are blackish-green, the median crest, the bulges, and the rims of the rhinophoral and branchial pits greenish-brown, the margins of the notum ocher to reddish-brown. Preserved, the dark pigment is visible through the notal border on the under side. Inwards to this dark zone follows a dense light stripe and one with epidermal pigment. Also, the sole is pigmented. The peritoneum and the vestibule are grey. The rhinophoral sheaths have a median spur. The branchial pit is surrounded by 2 anterior and 3 posterior lobes. The smooth labial cuticle is folded. The radula has 38 rows with 45 smooth,

hooked teeth per half-row. The stomach has thick walls.

The hermaphrodite duct forms a tubular ampulla (a) at the exit of which the oviduct and the seminal duct separate. The latter begins with a clustered prostatic part (q), followed by a smooth, massive one. The winding sperm duct (d) ends with a coil in the muscular penial pouch (p), which opens into the deep, folded vestibule (ve). Opposite to the penial pouch there is a voluminous vestibular gland (sd), the follicles of which have a common muscular duct. This ends with a spine (ss) lodged in a muscular sac. The vagina (v) courses from the vestibule to the spermatheca (t) containing residues of sperm and prostatic secretion. Beside the entrance of the vagina the allosperm duct (au) leaves the spermatheca. The duct communicates with the broad lobed spermatocyst (sc) filled with sperm, and joins the inner oviduct at its entrance into the gland mass. The nidamental duct (ni) opens behind the aperture of the vestibule.

Remarks: The reproductive organs of our specimen agree with Bergh's descriptions (1878b, p 641-644; 1890, p 920, 921), which refer to animals from Malaysia and the Palau Islands. These organs are somewhat different in Eales' specimen (1938, p 104, fig. 120) from the Gulf of Aden, which measured 32 mm long preserved and was possibly immature.

Asteronotus fuscus, listed above, is probably a young *A. cespitosus*. Mrs. Joyce Allan related *A. brassica* to *A. mabilla* (Abraham, 1877, p 249) a synonym of *cespitosus*, by a handwritten note in her reprint of 1932, sent in 1954.

Asteronotus madrasensis O'Donoghue (1932, p 158) has considerably more radular teeth than *A. cespitosus*. *Asteronotus* sp. (Eales, 1938, p 105-107) is similar to *A. madrasensis*, but immature. *A. wardianus* Allan (1932, p 95) does not belong to *A. cespitosus*. *A.* (*Tumbia*) *trenberthi* Burn (1962, p 161) is not an *Asteronotus*. Risbec (1928 and later) called *Discodoris boholiensis* Bergh (1877a, p 519) *Asteronotus b.*, but it is the type species of *Discodoris*, whose species have labial rodlets.

Platydoris scabra (Cuvier 1804)

Platydoris scabra, Marcus, 1960a, p 907-911 (synonymy), figs. 55-57; 1965, p 277.

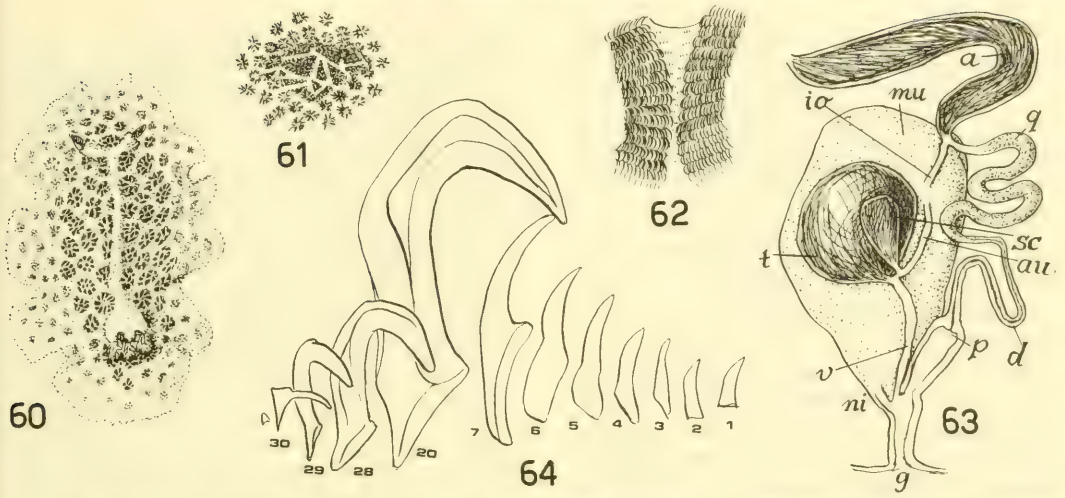
Range: Red Sea; Indo-west Pacific, from the east African coast to the Carolines, Marshall and Tonga Islands; Samoa.

Collecting station: Madagascar; xxvi, 2 specimens.

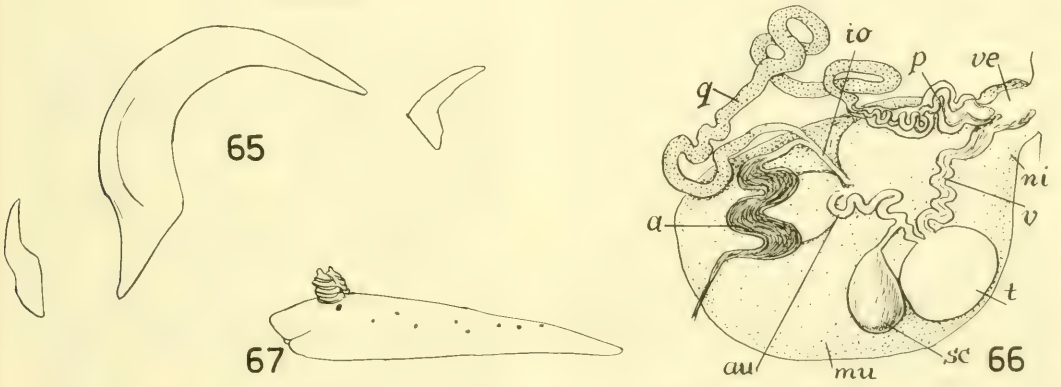
Descriptive notes: The living animal was 100 mm long, 50 mm broad. The notum is light brown with a broad marginal region of white blotches in its 3 posterior fourths. The rhinophores and the gills are grey; the former have orange-yellow terminal knobs, the latter have dark vessels. The digitiform tentacles are flecked with black and tipped with yellow. Also, the rim of the branchial pit and the border of the sole are yellow. The sole itself is white; the sides of the foot are rusty brown.

The radula has 50 rows of teeth with 98 to 100 teeth per half-row. In some of the innermost teeth the cusp arises from a shoulder-like angle of the base, as in Bergh's fig. 18 (1884, pl. 2). The salivary glands have narrow fundi, with an inner wide and an outer thin portion of the ducts.

Remarks: The salivary glands in the present specimen are as in the animal from the Red Sea (Marcus, 1960a); in other descriptions the terminal narrow part is much longer (Bergh, 1884, pl. 3, fig. 11, a) or the wide middle portion is absent (White, 1950, p 98). As in other species of the genus the ejaculatory duct and the vagina have different cuticular structures. The latter bears thick folds as in most descriptions; only once are prominent rounded bosses mentioned (Bergh, 1905a, p 138). The male duct contains spiny discs.

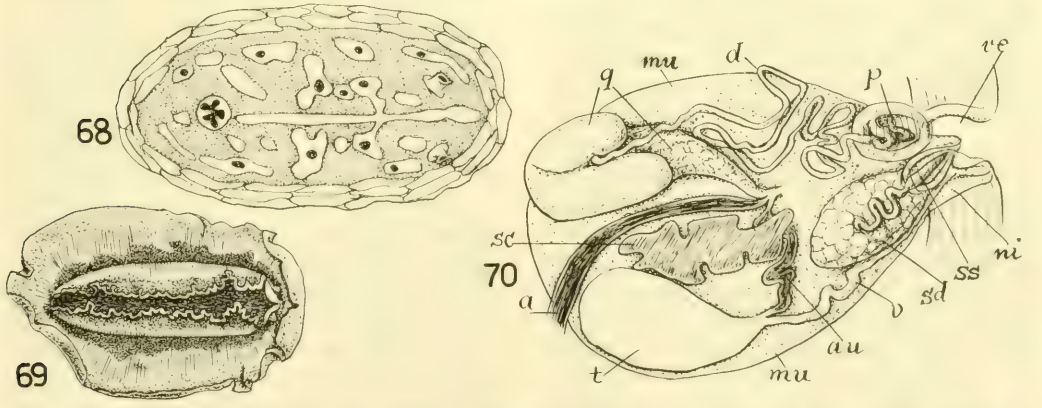


FIGS. 60-64. *Ategema osseosa*. Fig. 60, Dorsal aspect, combined from color photo and preserved slug. Fig. 61, Detail of sculpture. Fig. 62, Radula. Fig. 63, Diagram of reproductive organs. Fig. 64, Radular teeth.



FIGS. 65-66. *Trippa intecta*. Fig. 65, Innermost, middle, and outermost teeth. Fig. 66, Diagram of reproductive organs.

FIG. 67. *Gymnodoris bicolor*. Living slug, from sketch by Dr. E. Kirsteuer.



FIGS. 68-70. *Asteronotus cespitosus*. Fig. 68, Dorsal view of living slug, from sketch by Dr. E. Kirsteuer. Fig. 69, Ventral view of preserved slug. Fig. 70, Diagram of reproductive organs.

Gymnodoris bicolor
(Alder & Hancock 1864)
(Fig. 67)

Gymnodoris bicolor, Macnae, 1958, p 358 (synonymy); Marcus & Burch, 1965, p 249, 250 (range).

Range: Indo-west Pacific, from Zanzibar and Mozambique to middle Japan, New Caledonia, and Samoa.

Collecting station: Madagascar; xxvii, 1 specimen.

Remarks: The living animal was 2.5 mm long, yolk-yellow, with small orange spots. The 11 radular rows have 4 to 7 teeth per half-row, of the shape characteristic for the species. The slug has no gills yet around the anus that lies in the posterior $\frac{1}{3}$ of the back. This was examined in sections which still have yolk in the digestive gland.

Porostomata
Dendrodoris nigra
(Stimpson 1855)
(Fig. 74)

Dendrodoris nigra, Marcus & Burch, 1965, p 250 (references).

Range: Red Sea; Indo-west Pacific to west, south, and east Australia (Burn, 1966, p 349); north to Japan, Mutsu Bay (latitude 41° N.); east to Gilbert Islands and New Caledonia.

Collecting stations: Madagascar; xviii, xxii, xxiv, xxxiii, xliii, 5 specimens.

Remarks: The color of the present specimens is black with small whitish-yellow dots in 2 longitudinal rows or distributed irregularly. A liver-brown ground color with or without dots occurs in this species too. The body shape varies from broad with undulate borders to narrow with nearly smooth borders. Specimens of *Dendrodoris nigra* with an outermost black line are separated externally from the west Atlantic and east Pacific *D. krebsii* Bergh, but a white notal border without black rim occurs also in *D. nigra* (Baba, 1935b, pl. 6, fig. 2). Such animals differ from *D. krebsii* by the short penial pouch (Marcus, 1957, fig. 152, ei). The length of the seminal duct between the prostate and the pouch varies in *D. krebsii* (Marcus, 1967, figs. 62, 63). In the present *D. nigra* this part is long.

A grey or black blood gland characterizes *Dendrodoris nigra;* in *D. krebsii* it is unpigmented or contains only few pigment granules. The cerebro-buccal connectives are 3 times as long as the diameter of the pharynx in *D. krebsii* from the Gulf of California; in the present *D. nigra* they are quite short. Characters of these two species which differ by degree are the concentration of the central nervous system, higher in *D. krebsii,* and the more coalesced oral glands in that species.

Dendrodoris rubra
(Kelaart 1858)
(Figs. 71-73)

Doriopsis rubra, Alder & Hancock, 1864, p 126, pl. 31, figs. 1, 2; Collingwood, 1881, p 135, pl. 10, fig. 8; Bergh, 1902, p 190, 191, pl. 2, fig. 16.

Doridopsis rubra, Eliot, 1904, p 279; 1905, p 255; 1908, p 118, 119; 1909, p 95.

Dendrodoris rubra, O'Donoghue, 1929, p 731; White, 1951, p 250, fig. 20.

Range: Red Sea; Zanzibar and coast of the mainland; Mozambique, Inhaca Island; west and east coast of India; Ceylon; Singapore; Siam; Viet Nam (Risbec, 1956, p 26).

Collecting stations: Madagascar; xxi, xliii, 5 specimens.

Description: The living slugs were pink, a little darker in the middle of the back, with red spots. The shaft of the rhinophores was pink, the 16 leaves red, and the knob white. The gills were red. The largest of the preserved slugs is 30 mm long, measured over the back, 15 mm broad and 13 mm high. We dissected the most stretched specimen, which measured 12 by 8 mm. The skin is smooth without papillae or spicules. The tentacles are folds between the mouth pore and the anterior foot border, which is furrowed and notched. The hyponotum is folded in front, but the

aspect varies in the present 5 slugs. The 2 hindmost of the 6 multipinnate gills are the largest, and are bifurcate. The anal papilla lies in the center of the branchial circle. The rhinophoral ganglia are set off from the cerebral ones (cr). The pigment cups of the eyes (y) are big, 140 μ in diameter; the lens is not very large. The buccal gland (uc) consists of 2 roundish lobes and has a short and thick duct. The angled salivary glands (sa) are separate and lie behind the buccal ganglia (cc). The fore gut comprises the oral tube (ro), the pharynx (nx), the oesophagus (o), a spherical dilatation, and the digestive gland with a wide lumen, the stomach. The roundish blood gland is composed of small follicles which roughen the surface.

The spermoviduct leaves the spherical ampulla (a) beside the entrance of the hermaphrodite duct (eu). The short, thin seminal duct (d) is followed by the loop of the prostate (q) and a short muscular portion, 3 mm by 0.19 mm. In a 15-mm slug the penial spines were developed. The short inner oviduct (io) passes to the outer oviduct between the albumen (ag) and mucus gland (mu). In the young dissected slug which had copulated, the gland mass is small and opens into the common vestibule (ve) by a short nidamental duct (ni). Between the penis and the oviduct begins the vagina (v) first wide, then narrow and winding. It enters the longish spermatheca (t) beside the exit of the allosperm duct (au). The globular spermatocyst (sc) filled with sperm is joined by a short canal to the allosperm duct, which opens into the gland mass near the entrance of the inner oviduct. The 3 examined specimens had no vestibular gland.

Remarks: *Dendrodoris rubra nigromaculata*, frequent in Japanese seas, and the possible synonyms of *D. rubra* (Eliot, 1905, p 254; Pruvot-Fol, 1934, p 62), were not considered in the range. The description of *D. rosea* (Vayssière, 1912, p 82), whose hyponotum bears similar folds, does not allow for identification with *D. rubra* nor for separation from it. In Bergh's 18 mm specimen the seminal duct ectal to the prostate was "thin and highly wound"; in White's (1951) figure of a 36-mm animal it is short.

Dendrodoris pudibunda
(Bergh 1879)
(Figs. 75-79)

Doriopsis pudibunda Bergh, 1879, p 33, 34; 1889a, p 844, 845.
Doridopsis pudibunda, Eliot, 1904, p 274.

Range: Zanzibar; Mauritius, Fouquets Reefs; Philippines Sea.

Collecting station: Madagascar; xxvi, 1 specimen.

Description: The living animal was 80 to 90 mm long, and 30 to 35 mm broad. The color was light brown in the middle of the back, with 6 dark brown spots on either side; the sides of the notum were whitish-grey with yellowish-brown spots near the wavy border. The rhinophores were grey; the gills white with grey plumes. The notal papillae are soft bosses when preserved, smaller and more numerous toward the sides than in the middle. Their tops are covered with high glandular cells. In the big bosses the center of the glandular area is invaginated. The noval connective tissue is traversed by many nerves with nerve cells, as noted by Bergh (1879, p 34). There are no spicules.

The tentacles are small. The rhinophores have 25 leaves and smooth bordered pits. The circle of the 8 multipinnate gills is completed behind by the anal papilla, nearly as high as the gills. The eyes have small pigment cups, 80 μ in diameter, and lenses 120 μ high. As in all *Dendrodoris*, the central nervous system is highly concentrated. The cerebral (cr) and pleural ganglia are distinguished by the different size of the nerve cells. The buccal ganglia (cc) lie apposed to the limit of the pharnynx (nx) and oesophagus (o), between the small salivary glands (sa), which coalesce

behind them. The mouth tube (ro) projects into the buccal cavity and receives the thin, winding duct of the buccal gland (uc). The 2 lobes of the latter are fused. The mouth tube bends to the left before passing through the nerve ring. Behind this follows the long, muscular pharynx (nx) looping first to the left, then to the middle. Its lumen is triangular. The glandular oesophagus (o) forms a globular dilation before entering the stomach. At the beginning of the intestine there is a small caecum. The aorta (ao) courses through the bipartite, coarsely lobed blood gland (us). There is no pigment in the mouth tube, the inner organs, or the peritoneum.

The spermoviduct leaves the pear-shaped ampulla (a) some distance from the entrance of the hermaphrodite duct (eu). The seminal duct (d) widens suddenly to form the prostatic portion (q) and passes abruptly to the following narrow part (ui), 100 μ in diameter. This section uncoiled would be at least 10 mm long. The short muscular tube, the acrembolic penis (p), is wide and bears a few cuticular spines. Where it opens into the folded common vestibule (ve) inserts a retractor muscle (r), which lodges a small gland among its fibers. There is a long, clustered vestibular gland (xv). The inner oviduct (io) enters the gland mass between the albumen gland (ag) and the mucus gland (mu). The short nidamental duct (ni) opens into the vestibule (ve) beside the wide beginning of the vagina (v), and continues as a winding duct to the spherical spermatheca (t). Close to its entrance leaves the long, winding allosperm duct (au), to which the spermatocyst (sc) is connected by a long, straight duct. The spermatocyst contains oriented sperms.

Remarks: When the species was first mentioned (Bergh, 1876, p 387), it was neither described nor figured. The penial spines are scarse in specimens from the western Indic; in the original animal from the Philippines they were called "as usual." The thick-walled seminal duct of that slug, 2.5 mm long, does not agree with our specimen. The above mentioned different length of the seminal duct in *Dendrodoris rubra* shows that this character is systematically useless.

Dendrodoris clavulata (Alder & Hancock, 1864, p 127), not the *D. clavigulata* (Eliot, 1904, p 278) that is widely distributed in the Indo-west Pacific (Risbec, 1953, p 24), has spots on the border of the notum as *D. pudibunda*, but its colors are brighter and the bosses stronger.

Phyllidia (*Phyllidia*) *varicosa* Lamarck 1801

Phyllidia (*Phyllidia*) *varicosa*, Marcus, 1960a, p 911-913 (references, range), fig. 58; 1965, p 277, 278.

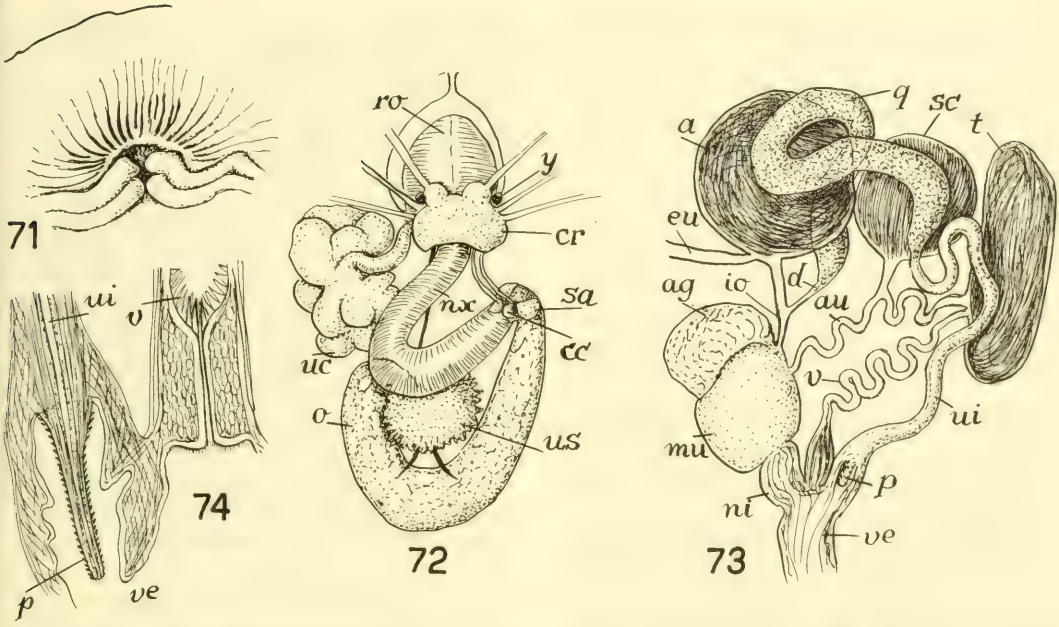
Range: Red Sea; tropical Indo-west Pacific, from the east coast of Africa to the Ryukyu Islands and east to Micronesia, Gilbert Islands.

Collecting station: Madagascar; viii, 4 specimens.

Descriptive notes: The living animals are up to 70 mm long and 40 mm broad, black with bluish-grey ridges, yellow papillae, and graphite-grey sides and sole. The connections of the tentacles with the foot (Bergh, 1869, pl. 14, fig. 6; Pruvot-Fol, 1952, fig. 3) are distinct. There are 150 branchial leaves; the genital aperture lies at the level of the 13th gill. The folds of the pericardium, an important feature of the Porostomata (Bergh, 1892b), were drawn in their natural position by Risbec (1956, fig. 85).

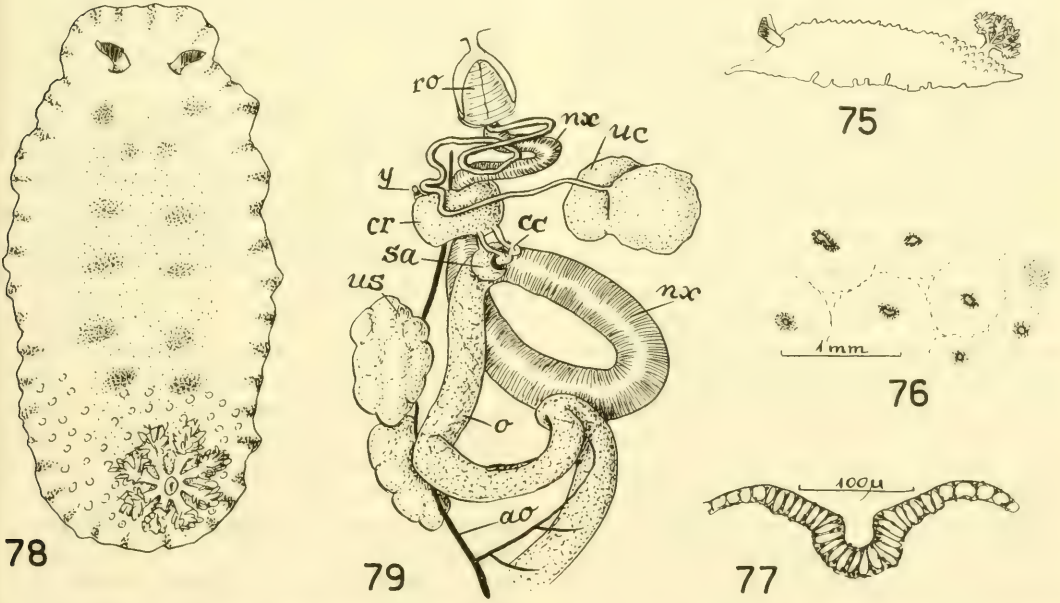
Remarks: The gastro-oesophageal ganglia (Bergh, 1869, p 380, 401, pl. 16, fig. 4) were confounded with salivary glands in early publications (Bergh, 1889a, p 857; 1892a, p 1126; 1897, pl. 12, fig. 13). This was repeated in Hoffmann's treatise (1938, p 947). Risbec (1956, p 23) described the 2 pairs of ganglia correctly.

Risbec's *Fryeria pustulosa* from Madagascar (1929) is *Phyllidia varicosa;* in



FIGS. 71-73. *Dendrodoris rubra*. Fig. 71, Head of preserved slug. Fig. 72, Anterior part of gut. Fig. 73, Diagram of reproductive organs.

FIG. 74. *Dendrodoris nigra*. Section of penis and vagina.



FIGS. 75-79. *Dendrodoris pudibunda*. Fig. 75, Side view of living slug, from sketch by Dr. E. Kirsteuer. Fig. 76, Skin. Fig. 77, Section of skin. Fig. 78, Dorsal view of living slug, from sketch by Dr. E. Kirsteuer. Fig. 79, Anterior part of gut.

his fig. 1 the dorsal anus is seen at the end of the dorsal crest.

Arminoidea
Dermatobranchus (*Dermatobranchus*) *striatus*
van Hasselt 1824

Pleuroleura striata, Bergh, 1905a, p 209, 210, pl. 4, fig. 22, pl. 19, figs. 7-9.
Dermatobranchus striatus, Baba, 1937, p 316, 317, fig. 12, pl. 2, fig. 1.
Dermatobranchus (*Dermatobranchus*) *striatus*, Baba, 1949, p 73, 157, 158, fig. 83, pl. 29, fig. 109.

Range: Malay Archipelago, coasts of Japan.

Collecting station: Madagascar; xxi, 2 specimens.

Descriptive notes: The slugs were 20 to 25 mm long when living, 5 to 7 mm broad. The ground color was yellow-ocher with whitish-grey ridges and dark brown blotches near the wavy borders. The rhinophores are furrowed longitudinally, whitish-grey peppered with black, and have a greenish-yellow top. In the borders of the notum lie the saccules, which are not cnidophores. In the middle of the notum there are 3 longitudinal ridges, which multiply irregularly backwards. On the border they run parallel to the contour in one specimen and fan out in the other. The notum is deeply notched in front and covers the pointed tail behind. Ventrally to the anterior border lie the frontal veil and the buccal folds. The foot is bilabiate and notched. The thick edge of the foot is frilled, the sole narrow. The genital opening lies to the right in the anterior third. The notal ridges do not contain diverticula of the digestive gland, contrary to the lateral lamellae of *Armina* (Marcus, 1960b, p 172). Nor are the ridges provided with especially numerous blood lacunae, so that a respiratory function is not evident.

The thin, light brown jaws have denticulate masticatory borders. The radula has 32 rows with 16 teeth on either side of the rhachidian. The innermost lateral is much broader than the succeeding ones, as shown in the figures of Bergh (pl. 19, fig. 9) and Baba (1937, fig. 12; 1949, fig. 83). The succeeding laterals are smooth hooks.

Remarks: The Red Sea is not included in the range of *Dermatobranchus* (*D.*) *striatus*, though a specimen from there was published under this name (Eales, 1938, p 111-113). The radular formula, as already noted by the author, and the shape of the central and the innermost lateral teeth (loc. cit., fig. 24) are incompatible with *D.* (*D.*) *striatus*. Eales' species does not agree with any of the 17 species of *Dermatobranchus*, not even with *D. glaber* (Eliot, 1908, p 88) from the Red Sea.

The genus can be expected to occur in deep water in low latitudes, because 1 species is known from the Arctis.

Eolidoidea
Coryphellina rubrolineata
O'Donoghue 1929
(Fig. 81)

Coryphellina rubrolineata O'Donoghue, 1929, p 798-802, fig. 219; Baba, 1955, p 26, 27, 51, figs. 40, 41, pl. 13, fig. 37; Marcus, 1961b, p 224-227, figs. 1-10; Burn, 1962, p 107; Abe, 1964, pl. 30, fig. 107.

Range: Suez and entrance of the Canal; Australia, Port Phillip heads; Japan, Sagami Bay, Toyama Bay; Brazil, entrance of the Bay of Santos.

Collecting station: Mexico; ii, Nov. 12, 1966 (Paula Vreeland), rocky intertidal, 1 specimen.

Descriptive notes: The living slug was 13 mm long. Measurements of the preserved specimen are in mm: length 8; tentacles 2.5; rhinophores 2.0; foot corners 1.0; cnidosacs 0.4. The body is pinkish-orange with orange inner organs. Tentacles, rhinophores, foot corners, tail and cerata bear red rings, which were violet in life. The long white tips of the cerata were powdered with yellow. A median line on the pointed tail was silvery white.

The shaft of the rhinophores is short. The back of the long club is beset with 12 oblique rows of about 15 high and blunt papillae each. The consistent,

slender cerata form 11 groups of 3 to 4 cerata each; the 3 first groups of the posterior liver contain 7, 6 and 5 cerata. The flange between the back and the side of the body reaches the posterior cerata.

The genital openings lie under rows 3 and 4, the anus under the flange in the interhepatic space.

The masticatory process of the jaws bears several rows of rough denticles. The radula has 34 rows of 1.1.1 teeth. The median tooth has 7 denticles on each side and a longer median cusp beneath them. The lateral teeth have 5 to 7 denticles on the inner side, which leave the tip free.

Remarks: The number of the rhinophoral papillae is highly variable, but the essential characters of the specimens from all localities do not evidence clear-cut differences. The zoogeographic aspect of *Coryphellina rubrolineata* is that of a species recently distributed on ships' bottoms. The larva of the neighboring *Coryphella rufibranchialis*, though better adapted for a pelagic life than the larvae of several other Eolidoidea (Thorson, 1946, p 269, 270), cannot survive long-distance transport by ocean currents (see Thorson, 1961, fig. 3). All previous records are from ports with much traffic. *C. rubrolineata* was possibly brought to the present Sonoran locality by the Japanese fishing fleet in the area of Guyamas (Steinbeck & Ricketts, 1941, p 247).

Favorinus mirabilis
Baba 1955
(Figs. 83-85)

Favorinus mirabilis Baba, 1955, p 30, 53, fig. 50, pl. 17, fig. 46.

Range: Japan, Sagami Bay, 50 to 60 meters.

Collecting station: Madagascar; xxix, 1 specimen.

Description: The living slug was 5 mm long and 1.2 mm broad. The ground color is transparent light grey with white flecks over the whole body, especially on the pericardial hump. The claviform grey cerata have a subapical brown spot. The head is light greenish-yellow, the tentacles grey; the brown rhinophores bear few yellow spots, between them lies a brown triangle. The preserved specimen is 3.5 mm long. The tentacles are longer than the rhinophores, the latter longer than the foot corners. The tail is pointed. The rhinophores have 8 to 9 leaves. The cerata stand in 8 groups in single rows, the 4 anterior ones are arches with 7, 7, 5 and 4 cerata. In the 5th group there are 2 cerata, the posterior groups each have 1 ceras. The genital opening lies under the 1st arch, the anus in the 2nd.

There are several rows of pointed denticles on the masticatory border of the jaws. The 15 radular teeth have strong cusps and no denticles.

Remarks: The type specimen was larger, 15 mm, and had correspondingly more (12) groups of cerata and 21 teeth. Only the 1st 3 groups are arches, the rest slanting rows, but our single specimen does not justify a specific separation. Foliate rhinophores occur also in *F. perfoliatus* Baba (1949, p 109, 177). It differs from the present species by short foot corners, slender cerata without a subapical spot, and only 2 groups of horseshoe-shaped cerata.

Pteraeolidia ianthina
(Angas 1864)

Flabellina ianthina Angas, 1864, p 65, pl. 6, fig. 6.

Pteraeolidia semperi (Bergh), Marcus, 1960a, p 921, fig. 77; 1965, p 280.

Pteraeolidia ianthina (Angas, 1864), Burn, 1965, p 89, 90.

Range: From the Red Sea and the east coast of Africa to middle Japan; New South Wales; east to New Caledonia and Micronesia, Carolines.

Collecting station: Madagascar; Tanikely, 1 specimen.

Remarks: The preserved animal is 40 mm long and has 18 pairs of tufts of cerata. Living slugs up to 75 mm long have been recorded.

Noumeaella isa, new species
(Figs. 86-89)

Collecting station: Madagascar; xxx, 1 specimen.

Diagnosis: This first *Noumeaella* from the western Indic is characterized by an opaque white net all over the body, and the radular tooth whose cusp is flanked by 2 small inner and 4 larger outer denticles. Holotype: AMNH 140854.

Description: The living animal was 5 mm long, 2.5 mm broad, semitransparent white, with an opaque white network over the whole body. Also, the yellowish-white cerata have this net, as well as brownish-yellow granules at their base. The pointed foot corners are about as long as the tentacles. The pointed rhinophores stand far behind the latter; on their posterior side they have a brush of papillae standing in rows. The small black eyes show at the base of the rhinophores. The slender cerata stand in 5 uniseriate arches. The 1st has 8 cerata. The groups following contain 8, 6, 4 and 2 cerata. In the interhepatic space lies the strong genital papilla; the anus lies in the first arch of the right posterior liver. The furrow of the anterior foot border is continued onto the angles.

The shape of the jaws is similar to that in *Noumeaella curiosa* Risbec and *N. rehderi* Marcus. No denticles were seen on the masticatory border. The radula has 16 horseshoe-shaped teeth with long limbs. The cusp is flanked by 2 small inner and 4 larger outer denticles on either side.

The male organs are a thin seminal duct which arises at the exit of the ampulla (a), a thick prostatic part (q) curving to the left and connected with the muscular terminal part (p) by a thin duct (d). The thick and long penis bears a cuticular stylet. The bursa (b) contains orientated sperm. A vaginal canal (v) isolated from the oviduct lies far inwards, but folds separate the path of the allosperms from the path of the eggs farther outwards. Insemination may be presumed near the opening of the vaginal canal.

Remarks: The 2 other species of the genus (Risbec, 1937, p 163; Risbec, 1953, p 158; Marcus, 1965, p 282) have a single strong median cusp flanked by 6 to 8 smaller denticles. The denticulate masticatory border of these species contrasts with the probably smooth one of the present species.

Aeolidiella indica
Bergh 1888
(Figs. 90, 91)

Aeolidiella indica Bergh, 1888, p 781-783, pl. 78, figs. 1, 2.

Range: Mauritius.

Collecting station: Madagascar; xlv, 1 specimen.

Description: The slug was 5 mm long, 1.5 mm broad, both when alive and preserved. Its buccal mass was pressed out. The longest cerata are 0.8 mm with 0.2-mm cnidosacs. The color was whitish-yellow with dark brown spots on the rhinophores, the middle of the back, and the anterior face of the cerata. The eyes are largest in the antero-posterior direction (140 μ). The tentacles are longer than the smooth rhinophores. The foot is narrower than the body, its furrowed anterior border has short angles. The tail is short.

The claviform cerata are cylindrical and pointed. The liver diverticula are smooth tubes in the present juvenile specimen. The cerata stand in 12 slanting rows. The 4 anterior ones bear 7 cerata each, followed with 2 with 5, 3 with 4, 1 with 3, and 2 with 2 cerata. Through the opaque skin the ramifications of the liver are not visible. The anus lies between the 4th and 5th rows.

The brownish jaws have growth lines parallel to the border. The radula has 13 light brown teeth. The strong median cusp is sometimes oblique. On either side of it stand 19 to 21 denticles; in the oldest teeth there are 10 to 14 denticles. The breadth of the teeth in micra is as

follows: 80 in front, 146 behind; the height of the teeth in micra is 52 and 110, respectively, including the denticles, which are 20 μ and 26 μ long.

There is only a primordium of the male reproductive organ.

Remarks: *Aeolidiella faustina* Bergh (1900b, p 235; 1904, pl. 1: *A. pacifica*) has a minute central cusp on the tooth; *A. orientalis* Bergh (1889b, p 673) has rounded anterior foot corners (Eliot, 1908, p 96). The adult specimen of *A. drusilla* Bergh (1900b, p 33) has especially short anterior rows of cerata, and its anus lies between the 5th and 6th row. Also the young specimens allotted to *A. drusilla* with reservation (Bergh, 1905a, p 222) have 3 to 4 cerata in the anterior rows; the tooth has 15 lateral denticles. Our young slug, not completely concordant with the preserved 8 mm long original animals of *A. indica*, agrees with them regarding the teeth and the numerous cerata in the anterior rows.

Onchidiacea

Peronia peronii
(Cuvier 1804)

Peronia (Peronia) peronii, Marcus, 1960a, p 877-881 (references), figs. 1-5.

Range: Red Sea (Labbé, 1934, p 190); Indo-west Pacific, from southern Mozambique and Madagascar (Odhner, 1919, p 42) to the west Pacific: Fiji, Tonga Islands, Samoa.

Collecting station: Madagascar; xxvi, 1 specimen.

Remarks: We consider the genera *Peronia* Blainville, 1824, and *Paraperonia* Labbé, 1934, at most as subgenera, because the definable character (Marcus, 1960a, p 876) of *Paraperonia* suffers exceptions (Labbé, 1934, p 202), while the other characters (ibid., p 196) are rather vague.

The examined slug was 90 by 80 mm when living. Arborescent tubercles occur over the whole notum, and more than 30 of them bear eyes. In life the ground color was a dark green, the tubercles were slightly lighter, brownish-green. The copulatory organs are very small, evidently malformed, as reported for other Onchidiacea (Plate, 1893, p 180; Labbé, 1934, p 195). The retractor of the penis originates beside the nerve ring, corresponding to Plate's 1st type (1893, p 148, 170, note 1), occurred generally in *Peronia peronii* (ibid., p 173). Hoffmann (1928, p 105) indicated the 2nd type for *P. peronii*, an origin beside the pericardium. We found the latter condition in a specimen from the Maldive Islands (Marcus, 1960a, p 480), but in a 2nd animal from there we now noted the 1st type.

Peronia verruculata
(Cuvier 1830)

Onchidium verruculatum, Hoffmann, 1928, p 44, 72, 106 (references, range); Awati & Karandikar, 1948, p 1-53 (anatomy, embryology, bionomics); Baba, 1948, p 20, 144.

Range: From Suez through the Indic and western Pacific to Hawaii and Japan, Shimoda (latitude 34° 40' N, longitude 138° 55' E).

Collecting station: Madagascar; xliii, 1 specimen.

Remarks: The living animal was 45 mm long, 20 mm broad, greyish-green above, with a hue of yellow towards the borders, and densely set tubercles of the same color as the back. The hyponotum is yellow with a slight green tint, the sole yellow-green. About 25 branched tubercles occur in the posterior 6th of the strongly contracted preserved animal. The peritoneum is slightly pigmented, the penial gland large, the penial retractor originates in the posterior angle of the body cavity (i.e., as in Plate's 3rd type (1893, p 170, note 1)). The intestinal loops are as in Plate's 2nd type (1893, p 119), uncommon in *Peronia verruculata*, but not unprecedented (Labbé, 1934, p 193). *Peronia anomala* Labbé (1934, p 195) has the same type of intestine; his species is probably a synonym of *P. verruculata*. A further species quite close to *P. veruculata* is *P. branchifera*

(Plate, 1893, p 183). The papilla of the penial gland of *Peronia gaimardi* Labbé (1934, p 194, fig. 8) is evidently not a specific character, but an evaginated muscular sac (Marcus, 1960a, fig. 1, es). Therefore, *P. gaimardi* also might be a synonym of *P. verruculata*.

Hoffmannola hansi
Marcus 1967
(Figs. 92, 93)

Hoffmannola hansi Marcus, 1967, p 232, figs. 87-95.

Range: Gulf of California, San Agustin, probably also Angel de la Guarda Island.

Collecting station: Mexico; ii, Nov. 12, 1966 (P. Pickens), on rocks, 7 specimens.

Remarks: The Onchidiacea can be separated into the Onchidiidae with the male pore situated to the left of the right tentacle, and the Onchidellidae with the male pore or pores (*Peronina* Plate, 1893) to the right of the right tentacle. *Watsoniella* Hoffmann, 1928, replaced by *Hoffmannola* Strand, 1932, belongs to the Onchidiidae, contrary to Labbé's indication (1934, p 238).

Hoffmann's material of *Hoffmannola lesliei* (Stearns, 1892) had been collected in 1852 and was histologically defective (Hoffmann, 1928, p 57). Therefore he could not understand an "organ of unknown function" (p 64) which lies between the big notal glands (no) and the body cavity. He observed the blood spaces (oo) and the hyponotal pores (za) connected with the organ in *H. lesliei*, and pondered a respiratory function. Thanks to Professor Pickens, who preserved material of *H. hansi* for histological purposes, the organ can be defined as composed of parcels of glands (z) embedded in diagonal fibers of the body musculature. The secretion is led out by ductules (zu) which unite to wider ducts. These also receive canals from the perinotum which drain clusters of small gland cells (zi).

In the outer part of the hyponotum the epidermal cells bear cuticular cones (Fig. 92), and some sensorial knobs, whose aspect and location suggest reception of mechanical stimuli.

Onchidella hildae
(Hoffmann 1928)

Onchidella hildae, Marcus, 1967, p 230-231, figs. 84-86.

Range: Ecuador, Puna Island; Panama, Pacific coast; Mexico, Sonora, Puerto Peñasco.

Collecting stations: Mexico; ii, Nov. 12, 1966 (P. Pickens), rocky intertidal, 6 specimens; iv, Dec. 26, 1966 (Paula Vreeland), rocks, 1 specimen.

Remarks: Measured over the back, the preserved animals are 8 to 25 mm long. Two specimens have 18 marginal papillae, 4 have 19, and 1 has 20 papillae. The slugs of the original material, up to 25 mm long, had 16 papillae. The radula of the smallest specimen has 48 rows of 52 teeth without denticles per half-row. The muscular wall of the efferent duct in its free part equals the diameter of its lumen. The hyponotal line near the foot distinguishes *Onchidella hildae* from *O. binneyi* Stearns, 1893, which occurs also at Puerto Peñasco (Marcus, 1967, p 227).

ACKNOWLEDGMENTS

We owe much of our information about the specimens from Madagascar to the collector, Dr. Ernst Kirsteuer of the American Museum of Natural History. He kindly sent us his drawings of the living animals accompanied by notes on colors and sculpture. The material from the Gulf of California was collected by Prof. Peter E. Pickens of the University of Arizona and his collaborators. Some specimens were illustrated by photographs of the living animals in natural colors, and continue Professor Pickens' previous collections, published by the Institute of Marine Science, Miami (Marcus, 1967).

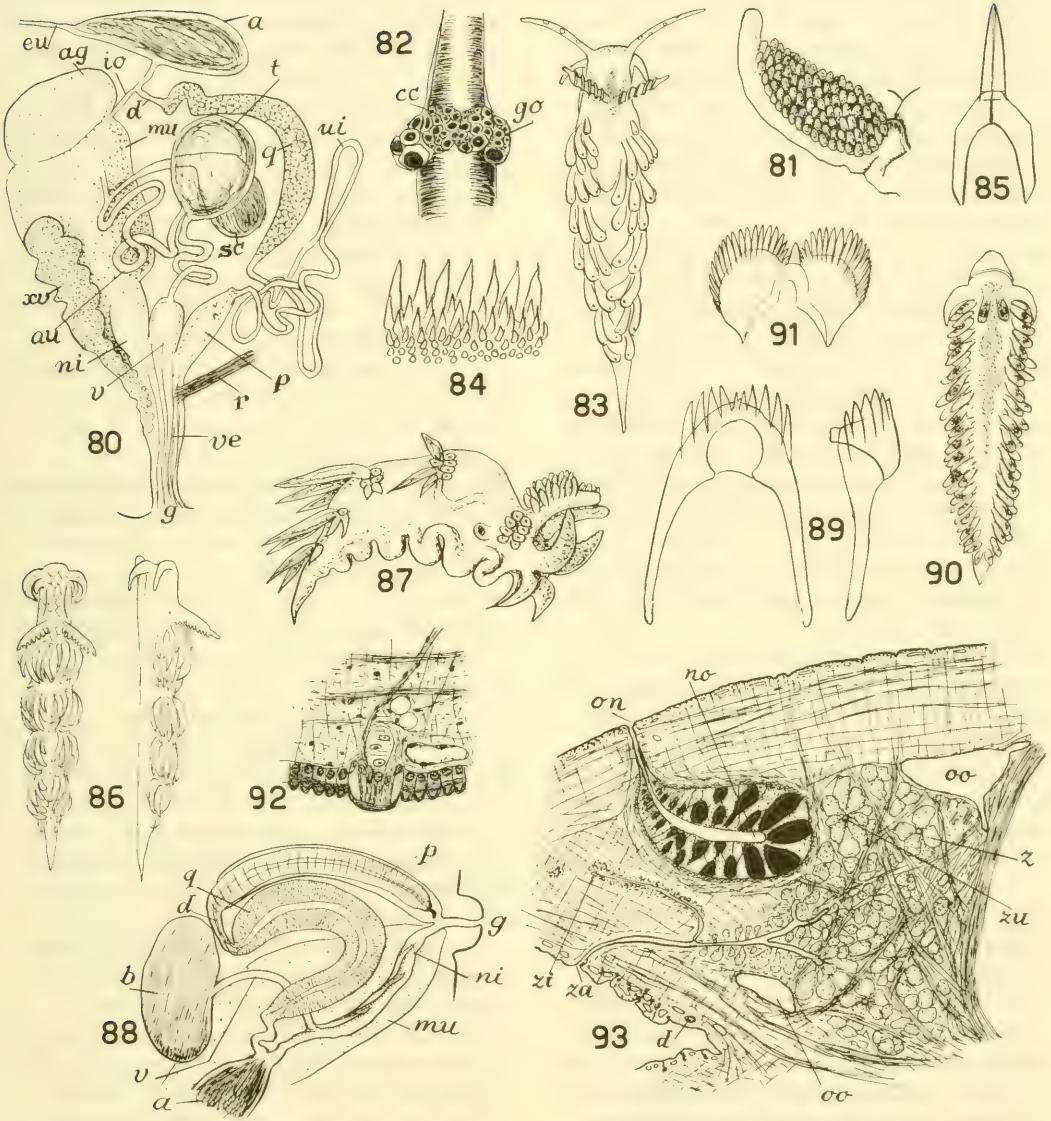


FIG. 80. *Dendrodoris pudibunda*. Diagram of reproductive organs.

FIG. 81. *Coryphellina rubrolineata*. Rhinophore of preserved slug.

FIG. 82. *Phyllidia varicosa*. Oesophagus with buccal and gastro-oesophageal ganglia.

FIGS. 83-85. *Favorinus mirabilis*. Fig. 83, Living slug, from sketch by Dr. E. Kirsteuer. Fig. 84, Denticles of masticatory border. Fig. 85, Radular tooth.

FIGS. 86-89. *Noumeaella isa*. Fig. 86. Dorsal and left side view of living slug, from sketches by Dr. E. Kirsteuer. Fig. 87, Preserved slug with partly plucked cerata. Fig. 88, Diagram of reproductive organs. Fig. 89, Radular tooth from above and from the side.

FIGS. 90-91. *Aeolidiella indica*. Fig. 90, Living slug, from sketch by Dr. E. Kirsteuer. Fig. 91, Radular tooth.

FIGS. 92-93. *Hoffmannola hansi*. Fig. 92, Section of outer part of hyponotum. Fig. 93, Section of notal and hyponotal glands.

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ADDENDUM

Since the present paper was completed in 1967, I received some opisthobranchs from Komodo by the kindness of Dr. Brian K. McNab-Gainesville. These were one specimen of *Trippa intecta*, two of *Atagema osseosa*, and one of a *Gymnodoris* with the innermost radular tooth twice the length of the second tooth, hence corresponding to the descriptions of the well-classified *G. citrina* (Bergh, 1877). The brown color of the innermost tooth agrees with that in the material from Eniwetok (Marcus and Burch, 1965: 249), at that time classified as *G. bicolor* (Alder and Hancock, 1864), later transferred to *citrina* (Marcus, 1970, Opisthobranchs from the Southern Tropical Pacific. Pacific Science 24: 155-179, on p 169).

RÉSUMÉ

QUELQUES GASTROPODES DE MADAGASCAR ET DE L'OUEST DU MEXIQUE

E. du Bois-Reymond et E. Marcus

Cet article traite de 43 espèces de gastropodes marins, surtout Opisthobranches (mais aussi 1 Lamellariacea et 3 Onchidiacea) de Madagascar et du golfe de Californie. Des descriptions anatomiques sont données pour les diverses espèces. Trois espèces ont été reconnues comme communes dans l'une et l'autre série; elles représentent des taxa qui se rencontrent dans les mers chaudes circumtropicales. Les nouvelles espèces suivantes ont été décrites: *Smaragdinella kirsteneri*, *Stiliger* (*Stiliger*) *erbsus*, *Hypselodoris regina* et *Noumeaella isa* (de Madagascar), et *Elysia vreelandae* (de l'Ouest du Mexique). Les Opisthobranches de Madagascar appartiennent à la faune récifale indo-pacifique, qui est assez homogène; au contraire, ceux du golfe de Californie vivent dans des zones largement dépourvues de récifs coralliens, mais contenant un apport d'éléments faunistiques du Pacifique tempéré américain et panaméen.

A. L.

RESUMEN

ALGUNOS GASTROPODOS DE MADAGASCAR Y MEXICO OCCIDENTAL

Marcus y Marcus

Se tratan 43 especies de gastropodos marinos, la mayoría opistobranquios (pero también 1 lamelariáceo y 3 onquidiacéos) de Madagascar y del Golfo de California. Se da la descripción anatómica para varias de las especies. Se reconocieron 3 especies comunes en ambas colecciones que representan taxa de mares circumtropicales. Se describen las siguientes especies nuevas: *Smaragdinella kirsteureri*, *Stiliger* (*Stilliger*) *erbsus*, *Hypselodoris regina*, y *Noumeaella isa* (de madagascar), *Elysia vreelandae* (del oeste de Mexico). Los opistobranquios de Madagascar pertenecen a una fauna Indo-Pacífica más bien homogenea, de los arrecifes, mientras que los del Golfo de California viven en areas donde no existen arrecifes de coral, pero que contienen una mezcla de elementos faunisticos de la zonas de Panamá y templadas del Pacífico.

J. J. P.

АБСТРАКТ

О НЕКОТОРЫХ БРЮХОНОГИХ С МАДАГАСКАРА И ЗАПАДНОЙ МЕКСИКИ

Э. ДЮБУА-РАЙМОН-МАРКУС И Э. МАРКУС

В работе рассматривается 43 вида морских брюхоногих моллюсков, главным образом заднежаберных (но также 1 представитель Lamellariacea и 3 представителя Onchidiacea) с Мадагаскара и из Калифорнийского залива. Приведены анатомические описания различных видов. Три вида оказались общими для обоих мест сборов; они представляют собой таксоны, встречающиеся в циркумтропическо-теплых морях. Описаны следующие новые виды: *Smaragdinalla kirsteueri, Stiliger* (*Stiliger*) *erbsus, Hypselodoris regina* и *Noumeaella isa* (с Мадагаскара) и *Elysia vreelandae* (из Западной Мексики). Заднежаберники с Мадагаскара принадлежат к более или менее однородной Индо-пацифической рифовой фауне, в то время как моллюски из Калифорнийского залива живут в областях, в значительной степени лишенных коралловых рифов, но содержащих примесь панамских и американских умеренных пацифических элементов фауны.

Z. A. F.

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THE MANTLE FLAP IN THREE SPECIES OF *LAMPSILIS* (PELECYPODA: UNIONIDAE)

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ABSTRACT

The purpose of this study was to review the morphological and general activity bases of mantle flapping in the North American unionid subfamily Lampsilinae and to explore experimentally some factors that may account for this striking activity: flapping mussels resemble small swimming fish. Morphological studies (chiefly on preserved material of *Lampsilis ventricosa* and *L. fasciola*), occasional field studies (in several counties in northwest Arkansas), and prolonged aquarium studies on living *L. ventricosa, L. siliquoidea* and *L. brevicula brittsi* were carried out from 1962 to 1965. It was found that the mantle flaps which are an extension of the inner lobe of the mantle edge just anteroventrad to the branchial siphon, are a permanent feature of the mature female. Among the flaps of these 3 species, there exist structural similarities (presence of eyespot, innervation by branches of pallial nerves from the visceral ganglion) as well as differences in shape and pigmentation.

Flap movements are initiated by paired pulses which produce contractions starting at the tail base and move toward the eyespot ends of the flaps. A recovery phase follows, in which the flaps assume their former position, with the tails floating horizontally.

Flapping behavior also involves the coordinated function of foot, marsupia, valves and siphons to such an extent that the supposed normal spatial relationships between body and shell are much altered. For different species flapping involves different behavioral complexes as well as different relevant stimuli (in particular light intensity for *Lampsilis ventricosa* and water waves and jarring of substrate for *L. siliquoidea*).

Flaps occur only in mature female specimens, although juveniles and males have flap rudiments, and flap movements have been seen only in gravid, never in non-gravid females. Flapping occurs in prolonged periodical spells throughout the summer months and has been seen to accompany the gradual emptying of the ovisacs, and the shedding of conglutinates. Flapping has not been observed after spawning of glochidia.

Two earlier hypotheses concerning the function of flap movements in the Lampsilinae, i.e., the roles of the moving flaps as "lures" for host fish to the mussels' glochidia, and as aerators for the gills and marsupia, seem now to be only partly plausible. Because of the differences in aspect, in speed of flapping and in responsiveness to environmental stimuli among the different species, it is here suggested that these differences are possible adaptations to habits of peculiar host species of fishes. The bellows-like movement created by the paired pulses of all flap movements, regardless of species or of flapping frequency, might help the glochidia to remain suspended in the water for a period of time, and thus facilitate the vitally necessary contact with a host fish.

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[1]Adapted from a dissertation submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy at the University of Michigan.

INTRODUCTION

Only a few genera of freshwater mussels, all in the American subfamily Lampsilinae[2] within the large and worldwide family Unionidae, are known to possess mantle flaps. These flaps (F) are appendages of the mantle, that are located anteroventrad to the branchial siphon (BS, Fig. 1). During late spring and through the summer months, female animals possessing such well-developed flaps may upend themselves in the substrate. Their mantle flaps are then extended (Fig. 2) and moved in a series of rhythmic pulsations. To the human observer they strongly suggest a small fish, complete with pigmented eyespots, stationary in the current and waving its flanks and tail.

Ortmann (1911) was the first to record observations of flap movements which he had seen best in *Lampsilis ventricosa* and *L. multiradiata* (*L. fasciola*). Studies on the natural history of freshwater mussels undertaken early in the century (e.g., Wilson & Clark, 1912; Coker et al., 1921) contain occasional references to lampsilid flap movements. Taxonomic treatments of the Unionidae (e.g.,

[2]The Lampsilinae are the only unionid subfamily entirely confined to North and Central America.

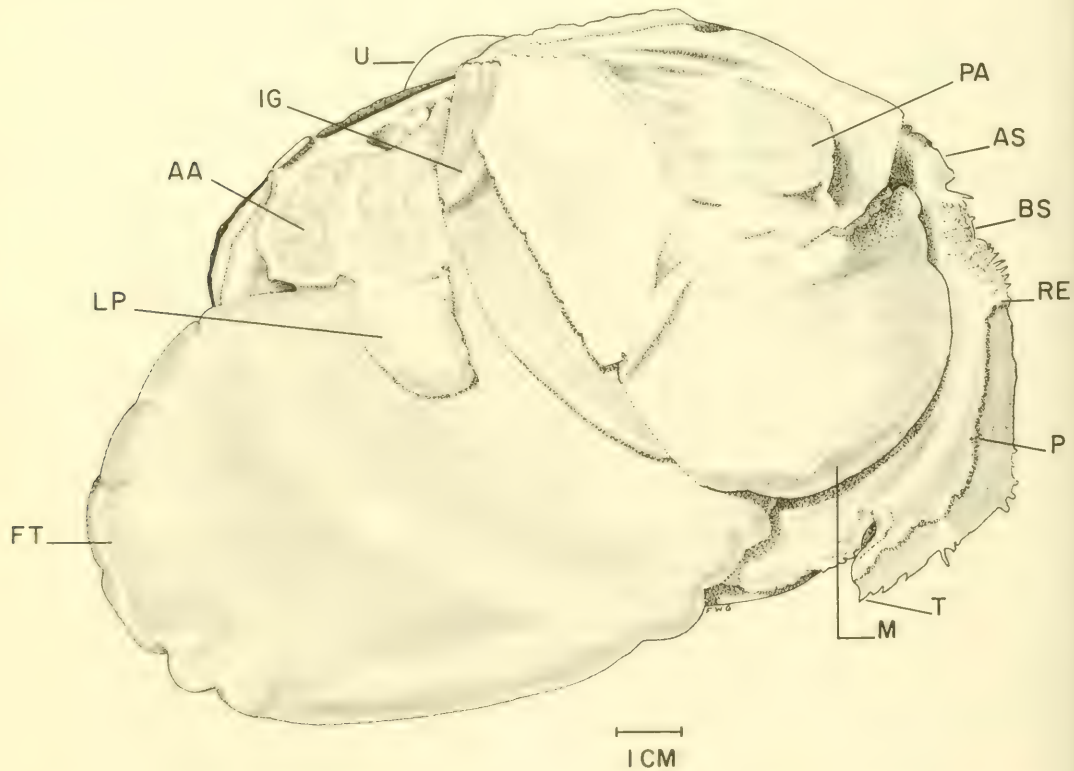

FIG. 1. *Lampsilis ventricosa* (Barnes). Drawing of preserved specimen, seen from the left side. Left valve and most of left mantle removed. Specimen collected from River Raisin, above Sharon Hollow, Washtenaw Co., Michigan, 1963. (For abbreviations, see p 228).

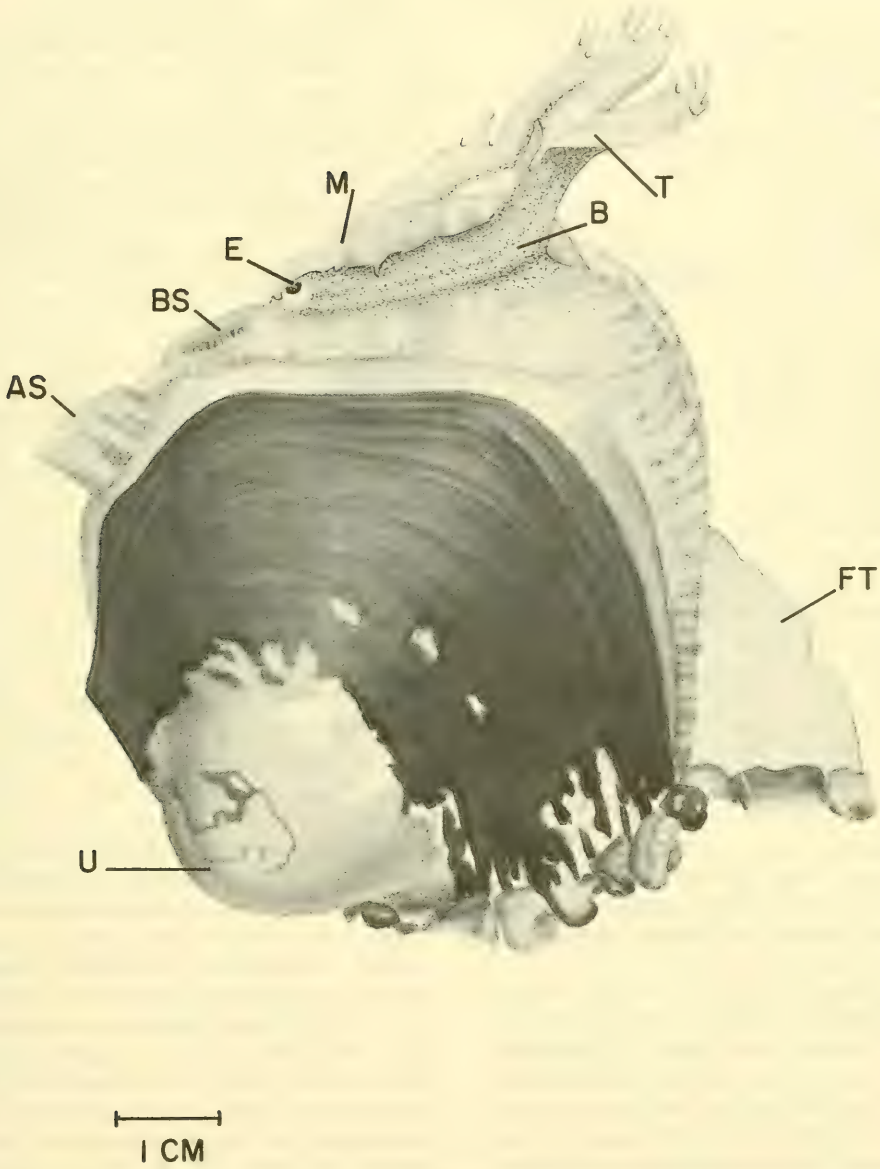

FIG. 2. *Lampsilis ventricosa* (Barnes) in typical "headstand" position (rotated by 90°) during flapping behavior, drawn from the left side. Specimen collected from War Eagle Creek, Benton County, Arkansas, June 14, 1964. (For abbreviations, see p 228).

Scammon, 1906; Ortmann, 1911; Simpson, 1914; Walker, 1918) provide brief descriptions of the flaps' appearance.

Some authors (Ortmann, 1911; Howard & Anson, 1922; Welsh, 1933) have speculated that the unique lampsilid flaps and flap movements may be involved in fish-host relationships. Welsh (1933) carried out a brief experimental study of the mantle flaps with *Lampsilis nasuta* (*Ligumia nasuta*) in which he discovered

LIST OF ABBREVIATIONS

AA	anterior adductor muscle
AE	"anterior" or eyespot end of flap
AS	part of mantle modified as anal siphon
B	base of flap
BS	part of mantle modified as branchial siphon
BT	basal tentacle
CG	conglutinates
DEF	distal edge of flap
DM	distal edge of marsupium
E	eyespot
ERF	edge of right flap
ESH	edge of shell
ET	empty tube
F	mantle flap
FT	foot
G	glochidia
H	hinge region
ISH	inner shell layer
IG	inner gill
L	ligament
LBS	location of branchial siphon
LF	left mantle flap
LM	left marsupium
LP	labial palp
LT	left mantle flap's "tail"
LV	left valve
M	marsupium (modified posterior portion of outer gill)
MA	mantle
OSH	outer shell layer
OV	ovisac (water tube) of exposed marsupium
P	line of pigment on inner surface of mantle flap
PA	posterior adductor muscle
PE	periostracum
PG	pedal gape
PO	pore
PS	pigment spot
RE	region which corresponds with location of eyespot on outer surface of right mantle flap
RF	right mantle flap
RM	right marsupium
RT	right mantle flap's "tail"
RV	right valve
SAS	supra-anal-siphon
SG	secretory groove
SP	siphonal partition
T	"tail" of mantle flap
TE	tentacle
U	umbo

a correlation between frequency of flap movements and decreasing light intensity. Lack of sufficient live material prevented Welsh from conducting further experiments.

The foregoing constitutes the slender bulk of work which has been published to date on lampsilid mantle flaps. The precise nature of the flap movements, their possible role in the mussel's life history, and in the distribution and speciation of the Lampsilinae, were unexplored. A feeling of some urgency accompanied the present study, because freshwater mussel populations are vanishing at an alarming rate in the U.S. (H. & A. van der Schalie, 1950). Living Lampsilinae are increasingly difficult to find, and may be unobtainable for such studies a decade hence.

It is the purpose of this communication (1) to describe flap movements of *Lampsilis ventricosa* (Barnes), as well as the species' characteristic "flapping behavior" complex (which is ostensively related to its general behavior inventory; (2) to summarize results of experimental studies of possibly relevant stimuli to flapping behavior in *L. ventricosa;* (3) to report comparative studies of *L. siliquoidea* (Barnes) and *L. brevicula brittsi* (Call), which reveal striking differences from *L. ventricosa* in flap morphology, in flapping behavior, and in stimuli relevant to that behavior; (4) to present evidence in support of certain conclusions which I have reached regarding the role of flapping behavior in the life history of these species; and (5) to suggest further hypotheses.

BACKGROUND

1. Taxonomic position of the Lampsilinae

Mantle flaps and flap movements are peculiar to the Lampsilinae, a subfamily

that has long been considered to contain the most advanced forms. As Walker (1917: 10) pointed out, the evolution of the Unionidae "has all been centered around the adaptation of the gills of the female for the care of the eggs until they are hatched." Evidence for Walker's generalization is patent in the distinguishing characteristics of the 3 subfamilies of the Unionidae: (1) the Unioninae are short-term breeders in which water tubes of all 4 gills serve as containers or ovisacs for glochidia; (2) the Anodontinae are long-term breeders in which only modified midsections of the water tubes of the outer gills serve as ovisacs (Ortmann, 1911); and (3) the Lampsilinae are long-term breeders in which only the posterior portion of each outer gill serves as a marsupium, the ventral borders of the latter extending below the distal edge of the inner gills, and often having a "beaded" appearance. Water tubes which become ovisacs in the Lampsilinae remain undivided, the whole tube serving as ovisac.

Ortmann (1911) believed that the Lampsilinae were the most highly evolved of the unionid subfamilies, not only because of the restriction of the marsupium to part of each outer gill, but also because of the prominent expression of sexual dimorphism in the shell, and the characteristic presence of special structures just in front of the branchial siphon: (1) the distinct, often large, conical papillae (or tentacles) found in *Ligumia* and *Villosa* (TE, Fig. 3) and (2) a lamellar keel or ribbonlike flap (the mantle flaps mentioned above), better developed in the female than in the male.

2. Mantle movements in other bivalves

Though mantle flap movements have been seen only in the Lampsilinae, generalized rhythmic movements of the mantle, independent of shell movements, occur in other bivalves. Redfield (1917: 233) investigated rhythmic mantle movements in at least 9 different species of lamellibranchs, and observed that in *Mya arenaria*, for example, a wave of contraction is seen to start at the distal end of the extended siphon, and to "move forward ending with the rise and fall of the mantle," about once a minute, in a freshly collected specimen. Pelseneer (1935) and Franc (1960) contended that such mantle movements favor circulation of water in the pallial cavity.

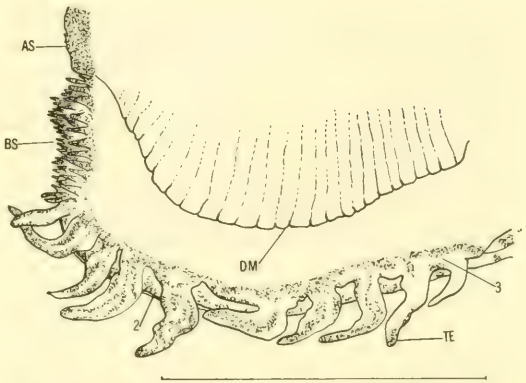

FIG. 3. *Villosa* (Lampsilinae); posterior left mantle edge, showing tentacles of unknown function anterior to branchial siphon (drawn from fresh specimen). 2, middle or second fold of mantle edge; 3, inner or third fold of mantle edge. Scale = 1 cm.

3. Modified mantle structures in other bivalves

Though mantle flaps per se are peculiar to the Lampsilinae, modified mantle structures are known in other bivalves, and include: eyes which rim the mantle of pectinid species and stud the siphonal tentacles of *Cardium;* a crown of tactile papillae around the branchial siphon (*Tapes, Corbula, Poromya*); and tactile papillae edging mantle borders (*Solenomya, Lepton, Pecten*). Among the Unionidae, in the Lampsilinae, there occur modified mantle structures of unknown function near the branchial siphon, such as "caruncles" or fleshy protuberances (*Carunculina*), and conspicuous tentacles and papillae (*Ligumia, Villosa*).

4. Factors which affect spawning in other bivalves

In the present study, the possible relationship of flaps, and flap movements of the Lampsilinae, to spawning of

glochidia will be considered. For freshwater mussels as a whole, direct experimental evidence of factors which affect spawning is slight, though some efforts have been made to study them (Utterback, 1931). For marine bivalves, especially for several commercially valuable species, a number of factors have been implicated (Table 1).

5. Review of general neuroanatomy and sensory structures of *Lampsilis*

Since the present paper deals with a form of bivalve behavior, and since "... an organism's behavior is an expression principally of the capabilities of its nervous system" (Dethier & Stellar, 1964: 3), there follows a brief review

TABLE 1. Factors implicated in spawning* in some marine bivalves

Presumed spawning factor	Species	Investigator
Condition ("ripeness" of bivalve prior to spawning)	*Mytilus californicus*	Young, 1945
Spawning movements (shell)	*Ostrea* (♀)	Galtsoff, 1938a
Temperature (above 27° C, spawning appears to be inhibited)	*Ostrea edulis* *Crassostrea virginica*	Loosanoff & Engle, 1940
Lunar periodicity (uncertain whether light or water pressure is critical factor)	*Ostrea edulis* (♀)	Korringa, 1947
Sex of bivalve (differences in latent period between stimulus and spawning: ♂ are generally more responsive to stimulus than ♀)	*Ostrea* *Gryphea* (= *Crassostrea*) *virginica*	Galtsoff, 1938a Nelson & Allison, 1940
Sperm cells in surrounding water	*Mytilus californianus* *Ostrea* (*Crassostrea*) *virginica*	Young, 1945
Diantlin (an active principle in sperm cells of some bivalves)	Oysters *Mytilus californianus* *Tridacna*	Nelson & Allison, 1940 mentioned by: Fretter & Graham, 1964
Thyroxin, theelin (injections followed by emission of sperm)	*Ostrea gigas* (♂)	Galtsoff, 1940
Extracts of *Ulva*, a green alga, induces shedding of sperm	*Ostrea gigas* (♂)	Miyazaki, 1938
Neurosecretions (as suggested by effects of extirpation of cerebropleural and visceral ganglia)	*Mytilus edulis* *Chlamys varia*	Lubet, 1956
Mechanical stimulation (scraping and pulling of byssus; water turbulence)	*Mytilus californianus* *Cumingia tellinoides*	Young, 1945 Grave, 1927
Repeated stimuli (no response to 1st application of stimulus but to later ones)	*Mytilus californianus*	Young, 1945

*Spawning refers to emission of sperm or eggs

of the neuroanatomy of *Lampsilis*. The organization of the nervous system of *Lampsilis* closely resembles that of *Anodonta* (described by Simpson, 1884).[3]

Members of the genus *Lampsilis* possess a bilateral nervous system that includes the 3 pairs of ganglia characteristic of bivalves. A pair of cerebropleural ganglia are located on either side and slightly posterior to the mouth and to the anterior adductor and protractor muscles, where they are embedded in the tissue of the foot. Nerves from the cerebropleural ganglia extend into the mantle, viscera, anterior muscles, muscles of the foot and to the statocysts. A conspicuous connective passes under the esophagus and joins the 2 cerebropleural ganglia. Connectives extend from each cerebropleural ganglion to the fused pedal ganglia, deep in the muscle of the foot. Prominent connectives from each cerebropleural ganglion emerge posteriorly from the visceral mass, and approach each other just behind the posterior retractor muscle, where they shortly join the fused visceral ganglia.

The visceral ganglia are closely joined by a wide commissure to form a single large, butterfly-shaped ganglion (hereafter referred to as the visceral ganglion), located just under the superficial epithelium covering the ventral surface of the posterior adductor muscle. From this ganglionic complex arise many nerves which I have traced into the osphradia, gills, kidneys, pericardial cavity, posterior adductor muscle, rectum, inner and outer surfaces of the mantle in general, and by way of many branches and anastomoses into the siphons and flaps.[4]

As in other bivalves, sense organs, such as statocysts[5] and osphradia are found in *Lampsilis*. The statocysts are 2 tiny spherical cavities (each of which contains a sizeable statolith) at the ends of the statocyst nerves, deep in the foot tissue. The osphradia are 2 small patches of specialized epithelia next to the branchial nerve, just dorsal to the gills and ventral to the visceral ganglion.[6]

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[3]The summary which follows here is based on dissections made for this study, as described in "Materials and Methods," under "Anatomical Studies" (p 232).

[4]No attempt was made in this study to follow nerve fibers through the ganglia. Friedenfelt (1904) described much of the fine structure of the visceral ganglion in *Anodonta;* but Rawitz (1887) was the only investigator whom I found to have described pathways of nerve fibers through this ganglion (in *Mytilus*). Since Rawitz' work was done with primitive techniques, one is inclined to believe, with Bullock & Horridge (1965: 1396) that especially with reference to the cerebropleural and pedal ganglia, "the whole matter of pathways. . . must be regarded as requiring investigation *de novo*."

[5]Statocysts have been experimentally implicated as organs of equilibrium (Buddenbrock, 1913, for *Chlamys varia*).

[6]The assertion (by Rawitz, 1887; Pelseneer, 1906) that the innervation of the osphradia is by way of connectives from the cerebropleural ganglia through the visceral ganglion, has recently been questioned (Bullock & Horridge, 1965). That osphradia function as chemoreceptors in bivalves has often been maintained (e.g., Pelseneer, 1906; Allen, 1923); but this claim has not, to my knowledge, been experimentally demonstrated. Bailey & Laverack (1963) reported that action potentials in the branchial nerve of a snail followed chemical stimulation of its osphradium. Aiello & Guideri (1964) suggest that regulation of water flow through the mussel (*Mytilus edulis*) may be due to a possible physiological connection between chemical stimulation of the animal's osphradia and subsequent nervous control of ciliary activity on the lateral epithelia of the gills.

Specialized photoreceptors have not been identified in the Unionidae, despite the fact that several species (including those of *Lampsilis*) are light, i.e., "shadow" sensitive (skioptic). Photoreceptors are known in some marine bivalves (reviewed by Franc, 1960).[7]

Tactile sensitivity in bivalves (noted in *Lampsilis*, too) is particularly localized in the siphonal papillae and in the anterior part of the foot. The innervation of such papillae has been studied in other species (e.g., by Galtsoff, 1964, in *Crassostrea virginica*). Franc (1960) reported that the siphons of *Mya* are sensitive to a pressure of 1 mg per 1 mm^2 of siphonal surface (Pieron, 1941) and noted that the foot of the Unionidae orients itself into the weakest of currents, being sensitive to the slightest differences in friction on either side of the foot.

MATERIALS AND METHODS

Field Collections: From the summer of 1962 through the summer of 1965, occasional collections were made of *Lampsilis ventricosa*, *L. siliquoidea* and *L. brevicula brittsi*, chiefly in the White River and its tributaries, in Washington County, northwest Arkansas (see Fig. 4). *L. ventricosa* exhibiting flapping behavior were observed on several occasions in June, 1962, and in June, 1963, in the White River. The best collection site was in that river near the Wyman Community. Very large (over 20 cm long) old specimens of *L. ventricosa* of both sexes were not difficult to find there prior to serious depletion of 2 fine shoals, apparently through drought and sewage pollution late in the summer of 1963. Other shoals which served as collection sites are now inundated by the backing up of the White River behind Beaver Dam. In no instance were *Lampsilis* abundant. Several hours of searching would turn up 2-3 gravid females. Young individuals were seldom found. Specimens were collected usually on shoals of sand and gravel, in swift and in sluggish currents, in water ranging from clear to very turbid, and from depths of 1-3.5 feet.

Anatomical Studies: Dissections were made of fresh specimens of *Lampsilis ventricosa*, *L. siliquoidia*, *L. brevicula brittsi* as they became available, largely in the summer months. The neuroanatomy of preserved *L. ventricosa* and *L. fasciola* and of methylene blue preparations of fresh *L. ventricosa* was examined in some detail. Preliminary studies of flap and nerve histology were also made.

Aquarium Studies: For purposes of observation some mature female *Lampsilis* were maintained in aquaria throughout most of the year from the summer of 1962 through the summer of 1965. Individuals were held in aquaria in a variety of environments for as long as 12 months. Female mussels were kept in various ways: solitary, with others of the same sex, with males of the same species, with specimens of other species, and with fish of various kinds, including the black crappie, largemouth bass, and madtom. The aquaria used were of various sizes ranging from 2 to 50 gallons in capacity. Water temperature in some aquaria was allowed to fluctuate with normal room temperatures, but was held constant in others. Light conditions were varied from no daylight with only occasional artificial light (i.e., incandescent or fluorescent light) to natural daylight only. It was not possible for me to feed the animals adequately. In many instances, algae were allowed to grow on the sides of the tank, and were then periodically suspended in the water

[7]Kennedy (1960) was able to demonstrate photoreceptive activity of the pallial nerve in *Spisula*, although he was not able to identify pertinent photoreceptor pigments there. (Photoreceptive function has not been demonstrated for cytochrome h, the hemoprotein he actually found present in high concentration in the pallial nerve of *Spisula*).

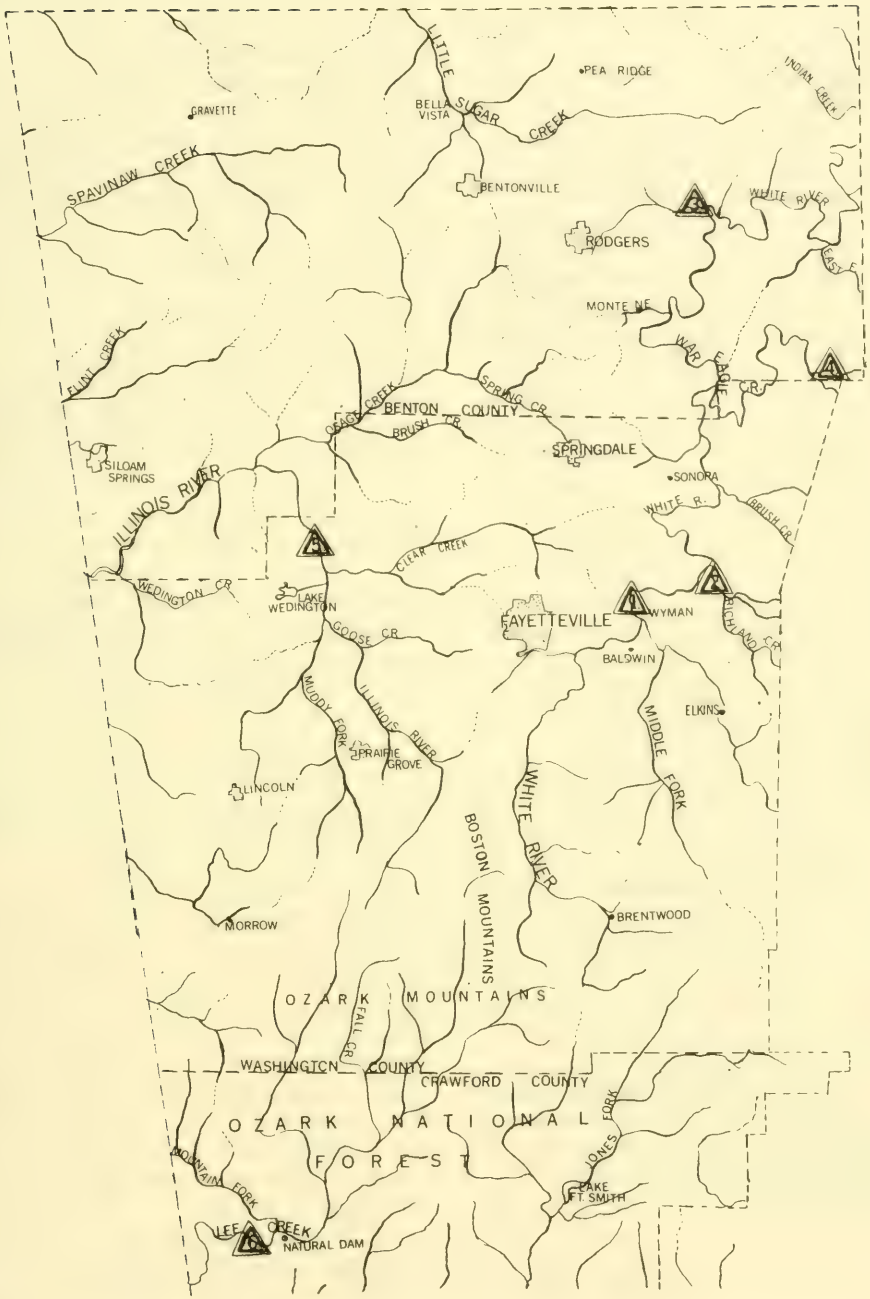


FIG. 4. Chief collection sites (triangles) in northwest Arkansas, for specimens used in this study. Map is from Arkansas Highway Dept., 1963. Scale shown here: 1 inch = approx. 10 miles.

by scraping the tank walls with a clean piece of nylon net.

Light Studies: *Lampsilis ventricosa*, *L. siliquoidea* and *L. brevicula brittsi* were subjected to initial exploratory light studies by means of a 3-way bulb (30, 70 and 100-Watts) suspended approximately 50 cm above the water surface. Changes in flapping behavior which accompanied change in light intensity were noted. Results of these studies coupled with data on diurnal flapping behavior (frequency of flap movements, response of flaps to natural light change at dusk and at dawn, etc.) in these same species indicated that *Lampsilis ventricosa* would be the most suitable animal for additional investigation. Subsequent light studies were carried out with a device (Variac) attached to a Weston AC voltmeter, which was used to vary the voltage through 200- and 300-Watt white frosted GE bulbs situated directly over the water surface at a distance of one meter. *Lampsilis ventricosa* were exposed both to successive increments and to successive decrements of light intensity at a variety of illuminations.

The preliminary studies with artificial light were partly made at natural fluctuating temperatures and partly at constant temperatures of 19-21° C. All of the later studies with *Lampsilis ventricosa* were performed at controlled temperatures (19-21° C). Almost all light studies were carried out at night, after dark, the later ones (reported in Table 14) between 7:30 and 11:30 p.m., from July 25 to August 16, 1965.

For convenience of measuring rapid flapping rates, and for ease of comparison, the frequency of flap movements has been expressed not as the number of moves per unit time, but as the duration of a fixed number of moves. The number was set at 30 after extended preliminary observations had indicated that a smaller number would not allow for the animal's occasional spontaneous alterations of flap movement rate.

During prolonged observations of flapping behavior in the dark, a safelight (a red 25-Watt bulb) was used. A penlight or small torch was employed occasionally just to check on the occurrence of flap movements in the dark.

BEHAVIOR INVENTORY OF *LAMPSILIS*

Familiarity with the various categories of "normal" behavior such as locomotion, siphoning, adductor rhythms, responses to several kinds of external stimuli and spawning is indispensable to an evaluation of the flapping behavior in *Lampsilis*. In an attempt to apply to these mollusks a holistic approach - a regular part of the technique of the vertebrate ethologist - a behavior inventory, summarizing normal activities, is presented in Table 2, before the highly specialized attributes of flapping behavior are considered in detail.

A. FLAPPING BEHAVIOR IN *LAMPSILIS VENTRICOSA*

1. General morphology and location of the mantle flaps

Characteristic morphological features of *Lampsilis ventricosa* mantle flaps are shown in Fig. 5a, b. In this species, as in others of the Lampsilinae, mantle flaps are extensions of the mature female's anal and branchial siphon edges. In transverse section, the bivalve mantle edge is generally understood to consist of 3 lobes,[8] Fig. 6. Like the siphons, the mantle flaps are part of the inner lobes of the mantle edge (shown as lobe 3 in Figs. 7 and 8).

All 3 lobes of the mantle edge are modified in the flap region. This modification accompanies sexual dimorphism

[8]This may be an arbitrary generalization. See Hillman's (1964: 8) article on "The functional morphology of the fourth [*sic*!] fold of the mantle of the Northern Quahog, *Mercenaria mercenaria*."

TABLE 2. Summary, behavior inventory of adult female *Lampsilis* (as examined in *L. ventricosa* and *L. siliquoidea*)[a]

Activity	Sub-categories	Observed Phenomena	Anatomical Basis, etc.
Adductor rhythms: (opening and closing of valves)	Tonic (slow) rhythm	Valves kept partly agape or completely closed, both for long periods. Less characteristic of gravid female just prior to spawning, than of juvenile or adult male during same period. Frequency of occurrence not influenced by light or temperature, except when animal is engaged in flapping.[b]	Muscle tissue: anterior and posterior adductor muscles which hold valves together, contain (1) tough, white smooth fibers which produce tonic rhythm; and (2) soft gray, translucent fibers ("fast" fibers) now known to be smooth fibers with peripheral twisted fibrils (reviewed by Hoyle, 1964, for *Anodonta*).
	Phasic (fast) rhythm	Quick closures, slower relaxations.[c] Active shell movements are altered, depending upon whether mussel is in increased state of excitability from rising water temp., accumulated metabolites in stagnant water, or whether it is a gravid female, spawning.[e]	Nervous control:[d] Control of both slow and fast rhythms appears to be intrinsic in the nerve ganglia, independent of peripheral stimulation. Rapid rhythm is controlled in each adductor by its nearest ganglion. Slow rhythm is controlled in each adductor muscle by combined effect of (1) the nearest ganglia which produce a tonus, and (2) the cerebropleural ganglia (which inhibit that tonus at intervals (Barnes, 1955).
Locomotion: (horizontal, or burrowing movement with foot in substrate)	Patterns of locomotion: (a) horizontal, valves at right angle to substrate, ligament dorsal; (b) burrowing: valves may be buried in substrate; only siphons' edges visible.	Elements of both horizontal[f] and burrowing movement are similar: (1) milky white foot is thrust out and forward between the valves; (2) foot's posterior, now heel-shaped portion is produced; (3) foot is then expanded, penetrates substrate, forms turgid hold; (4) valves open, close, mussel hunches, rocking down or forward into substrate.[g]	(According to Dawson, as described by Morton, 1964): for stages indicated in column #3: (1) external and internal anterior retractor muscles and transverse muscle fibers within the foot contract, compressing and lengthening the foot's blood sinuses; (2) further extension and heel formation is effected by contractions of the posterior retractor muscles; (3) expansion of the foot's volume occurs through massive blood flow into the foot's sinuses, and distal relaxation of the internal and external posterior retractor muscles.[h]

(See p 236 for footnotes a-h).

Table 2 (contd.)

Activity	Sub-categories	Observed Phenomena	Anatomical Basis, etc.
	Coincident conditions: (a) Substrate	In the absence of a yielding substrate (in aquarium), there may be keel-like protrusion of foot onto container's smooth bottom; foot then is further extended and expanded; but large animals cannot thus move into upright position, or complete the forward phase of locomotion. After a few days, foot is seldom extended; and the mussel may live thus for 4 months or more without attempting locomotion.	

[a]Applies to all unionids observed by author.

[b]I have noted periods of continuous rapid rhythm lasting 7-10 days, among gravid female lampsilid mussels maintained at ordinary room temperatures from April through September. Following spawning, however, a prolonged period of quiescence (7+ days) was always noted. Galtsoff (1964) noted a similar post-spawning characteristic for *Crassostrea virginica*.

[c]In *Anodonta cygnea* (Barnes, 1955) the sequence may be repeated 20 times an hour. My observations of *Lampsilis* are similar. The figure may be considerably higher during periods of flapping activity.

[d]The neurophysiological basis for the adductor rhythms is still unclear. To date, excitatory and inhibitory mechanisms have been found in mollusks only by stimulating whole nerve trunks or ganglia. Hoyle (1964: 327-328) commented that it "...has not been possible to make a nerve-muscle preparation of any molluscan muscle and feel sure that no synaptic junction in addition to the neuromuscular ones intervene."

[e]Galtsoff (1964) characterized these and additional subcategories of the rapid adductor rhythm for *Crassostrea virginica*, each accompanied by figures of kymograph recordings.

[f]The ligament (which dorsally joins the 2 valves of the shell) also functions in this context (Trueman, 1954).

[g]Fraenkels (1927) terms for locomotion in *Ensis* suggest a pattern similar to that observed in *Lampsilis* and in other unionids: (1) Grabschritt (digging step), initial movements of the foot, consisting of 3 stages: (a) Keilform (wedge-like extension of the foot), (b) Hakenform (heel shape) i.e., further extension and downward thrust of foot into substrate and (c) Schwellform (turgid state) i.e., swelling of the foot as blood sinuses fill: and (2) Grabstufe (digging stage) the downward movement, which brings the animal further into the substrate.

[h]Such movements are not inefficient. A mature lampsilid mussel can accomplish the circuit of a 10-gallon aquarium (about 5 feet) in 5 hours.

Table 2 (contd.)

Activity	Sub-categories	Observed Phenomena	Anatomical Basis, etc.
Locomotion, extensive (min. distance of 6 in.) by gravid female:	(b) Time of day:	*L. ventricosa* was observed to travel mostly at night. Several specimens were observed a number of times daily from May into August; 29 of 35 travels occurred during the dark. *L. siliquoidea* showed a different pattern: of 31 such travels, 18 were between dusk and dawn, as against 13 in daylight.	
	(c) Temperature:	Temperature did not seem to be a factor. One specimen of *L. ventricosa,* kept at a constant temp. of 19° C, made 12 lengthy moves in a 3-month period, all between dusk and dawn.	
Siphoning: (water current flows into branchial and out of anal siphon)	Discharge: of material from rectum and cloaca via anal siphon. Intake: of water and suspended material through branchial siphon, over gills where cilia sort particles, etc.	In siphoning animal, steady current of water into branchial siphon, and out of anal siphon. Particles move from a.s. in steady stream or in sudden "sneezes." Siphoning stops when siphons close or withdraw in response to shadows, tactile or chemical stimuli (see below). In usual erect posture (ligament dorsal), siphons protrude (e.g., 1/2 cm in 15 cm-long animal) parallel to substrate.	Posterior edges of mantle, inner lobe of left and right mantle edges joined laterally, not medially, except for superficial fusion with suprabranchial septum. Innervated by branching siphonal nerves from visceral ganglion. No nerves pass directly from one side of siphon to other. (Both siphons are striped and mottled with orange and black pigments. Branchial siphon usually most brightly colored with 3+ rows of papillae within the lumen. Largest papillae, located in innermost row, are sensitive to tactile stimuli).
Responses to sensory stimuli:	Response to shadows	Siphons, especially anal siphon, close quickly, then open.[i] See also Table 3.	Little information available. Siphons and foot with ample nerve supply. Neurophysiological mechanisms unknown.
	Response to tactile stimuli	Foot, especially anterior end, withdraws. Siphons, especially when papillae within branchial siphon are stimulated, close.[j]	

(See p 238 for footnotes i-j).

Table 2 (contd.)

Activity	Sub-categories	Observed Phenomena	Anatomical Basis, etc.
	Response to sudden jarring of substrate:	Siphons or siphons and foot withdraw, valves may close.[k]	
	Response to various chemicals:	Siphonal closure or withdrawal response, usually. See studies of Allen (1923, on *Lampsilis* and other unionids) and Hopkins (1931, on oysters).	
Spawning: (discharge of reproductive products).[l]	In male: discharge of sperm into water.	Discharge of sperm in clusters which exhibit rotary motion in water, described by Utterback (1931) for *L. ventricosa*.	
	In female: Discharge of glochidia, usually preceded and accompanied by flap behavior.	Discharge of glochidia from marsupia of female in clusters (conglutinates) having shape of ovisac, or singly. (Details in body of this paper).	

[i]Buddenbrock (1930) investigated the shadow reflex of *Arca, Pecten,* and especially of barnacles, and was concerned with the reflex as it relates to the shadow's intensity, to "adaptation," and to summation in response to a rapid succession of shadows.

[j]A sequence described by Allen for a number of unionid species (1923: 62) may be verified by repeatedly touching the inner circle of papillae with a fine probe: (1) Ventral siphon strongly stimulated. Both siphons close vigorously. Both reopen together. (2) Stimulus repeated soon. Both siphons close. Ventral reopens, then dorsal. (3) Stimulus again repeated. Dorsal siphon closes. Ventral not entirely closed, and reopens at once.

[k]The response described here presents problems in experiments with mussels. E.g., Wenrich (1916: 298) wrote for *Anodonta,* "...precautions against vibrations to which the animals are very sensitive, were taken by supporting the experimentation-box by another box on the cement floor of a basement room, and placing wads of paper under the lower box, between the two boxes, and under the jar containing the animals."

[l]Latter (1891) described shedding of eggs from oviducts of *Anodonta,* the only account I have seen of this process. He recorded that eggs pass singly, in a steady stream through the oviduct and out of the genital aperture, their passage being aided by contractions of intrinsic foot muscles and ciliated lining of the oviduct itself. In about 50 seconds an egg would have moved to the posterior edge of the visceral mass, meeting the stream of eggs from the other side of the body, and then would pass back through the suprabranchial cavity to the cloaca. From the cloaca the eggs are moved forward into the "latticed recess" of the outer gills. Latter estimated the number of eggs thus passed in 10 days at about 500,000.

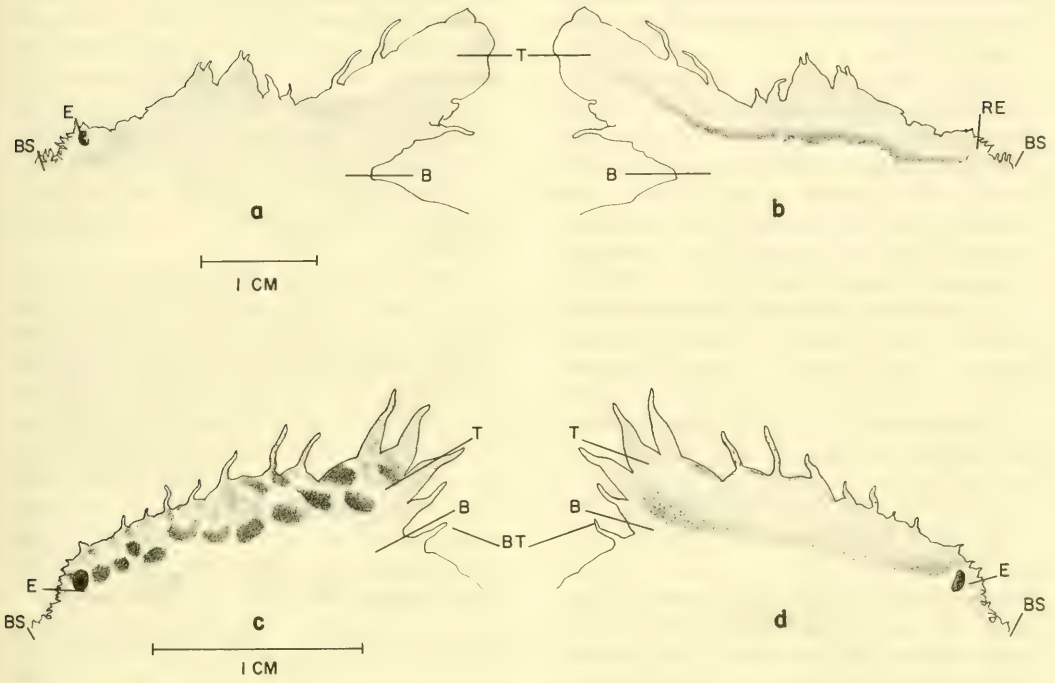
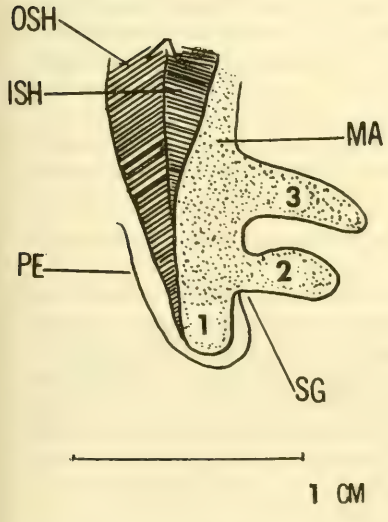


FIG. 5. Mantle flaps in 2 species of *Lampsilis,* drawn from preserved material. a, b, *L. ventricosa;* c, d, *L. fasciola*. The illustration shows the characteristic features of the outer (a, c) and inner surfaces (b, d) of the flap. Note the rather uniform pigmentation of outer surface, eyespot visible only on outer surface, and relatively narrow, truncated tail of *L. ventricosa*. Compare with many pigment spots on external surface, eyespot visible on both external and internal surface, and rather broad tail comprised of a number of large tentacles, in *L. fasciola*.



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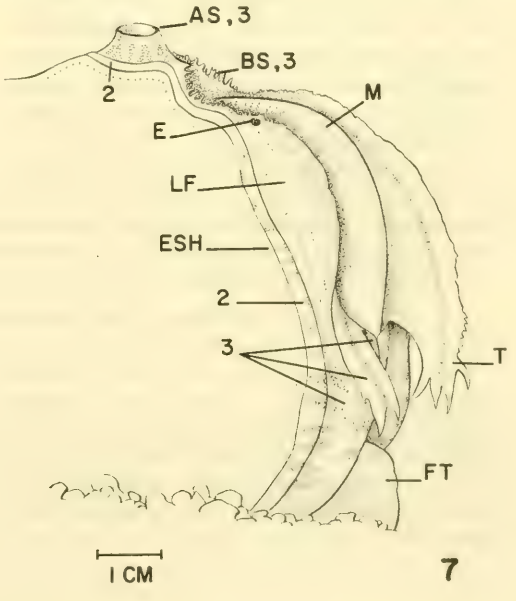

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(See p 240 for legends to Fig. 6 and Fig. 7).

of the valves, whereby the rotundity of the female shell accomodates the marsupia as well as the thickened posterior mantle edges.

In the living, mature female animal, the outer mantle lobe (Fig. 6, 1) is much thickened in the siphonal and flap region, and is almost completely covered by the shell. The middle lobe (2) is very thin at the base of the anal and branchial siphons, but is evident as a rounded pigmented ridge, near the flaps (Figs. 7, 8). The inner lobes (3) not only form the flaps, but their protruding apposition under the flaps' "tails" is seen (especially in a rear view of flapping *L. ventricosa*, Fig. 8, B3) to cause an elevation of the tails.

2. Orientation of *Lampsilis ventricosa* to the substrate during flapping behavior [9]

When the mussel is engaged in flapping, its appearance is much altered from "normal" (Figs. 9a, b) by: (1) forward tilting of valves (a rotation of about 90°); (2) exaggerated posterior extension of foot; and (3) extreme protrusion of flaps, inner mantle lobes and marsupia (Fig. 9c).

Flapping behavior configuration alters not only the position of the animal relative to its substrate, but to the valves of its shell as well. The "anatomical correspondence" areas defined by Stasek (1963) for a number of bivalves, would not apply to *L. ventricosa* during flapping. (See Fig. 10).

For the foregoing reasons, conventional designations of "anterior," "posterior," "dorsal" and "ventral," become misleading; and thus terms which are meaningful within the special context of flapping behavior (as shown in Fig. 11) will be used in this paper. A summary contrasting orientation of *L. ventricosa* to its substrate during flapping behavior and during normal activity is presented in Table 3.

The typical position of flapping *L. ventricosa* illustrated in Fig. 9c is the only one I have noted for this species under natural conditions. Ortmann (1911) and Grier (1926) have presented general descriptions of this position. However, I have often observed that *L. ventricosa* in aquaria may exhibit flap movements when its valves are tilted up no more than 45° (Fig. 7), although such flap movements are slow, and occur at low light intensities.

3. Analysis of flap movements in *Lampsilis ventricosa*

Ortmann (1911), Wilson & Clark (1912), Grier (1926) and others noted that flap movements are very rhythmic and rapid in *L. ventricosa*. In the course of prolonged observations of flapping animals in aquaria during spring and summer months and from analysis of 16 mm moving pictures of some of these animals, I have determined that there are at least 2 principal categories of flap movements: (1) regular movements, observed at high flapping frequencies of

[9] Orientation of animal to substrate only is discussed here. Field observations (my own, 1962, 1963, and those of Ortmann, 1911) indicate that the flapping animals may orient themselves into the current. Present studies have not included an investigation of this factor.

FIG. 6. Diagram of transverse section of bivalve mantle edge. 1, outer lobe; 2, middle lobe; 3, inner lobe (from Morton, 1960). Scale shown indicates approximate size of a transverse section through posterior mantle edge of *Lampsilis ventricosa*, ♀, in a specimen 15 cm long.

FIG. 7. Semi-diagrammatic view of *Lampsilis ventricosa*, during slow flap movements in aquarium, from left rear side, indicating lobes of mantle edge. 2, middle lobe; 3, inner lobe and structures arising from it. Note that valves here are tilted by only 45°; the inner mantle lobes are pushed out against each other.

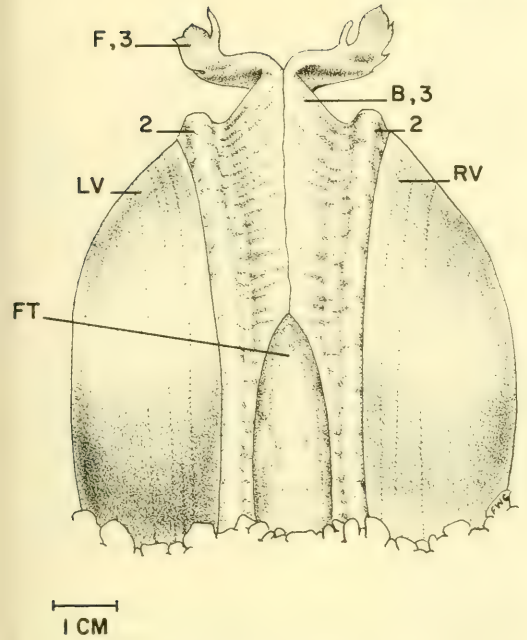


FIG. 8. Flapping in mature female *Lampsilis ventricosa*. Rear view during flap movements. Drawn from living animal. 2, 3, middle and inner lobes, respectively, of mantle edge. Note that the inner lobes below the mantle flaps are pushed tightly together.

60 or more moves per minute, and (2) slow movements, seen at rates of less than 30 moves per minute. The mantle flaps exhibit other types of movements too, though less often. All spontaneous flapping movements involve both mantle flaps.

Regular flap movements (Figs. 12, 13): Before the regular movement is begun, the tails of the flaps are spread apart, to float horizontally in the water, inner surface dorsal. The "anterior" ends (see Fig. 11) of the flaps, with white-rimmed black "eyespots"[10] on the external surface, are held together; or, if the marsupium protrudes, flaps are held close to the sides of the marsupium.[11] The movement starts with a quick strong contraction at the base of the flaps. The tails are thereby turned upward, and often clap together over the exposed edge of the marsupium. Now a pulse[12] moves from just in front of each of the tails, forward to the anterior, eyespot ends of the flaps. A lateral bulge is thus simultaneously produced in each flap; and as the pulse moves along, it increases in amplitude and causes each flap to be turned downward and outward. Finally the pulse reaches the eyespot end of each flap, pushing the whole flap-pair forward, and snapping the eyespot ends outward.[13] The slower recovery stroke of the regular movement now occurs. The tails relax and float out horizontally,

[10]The eyespot's function as a photoreceptor has not been demonstrated. Sufficient material for adequate pigment analysis was not available in this study, but chromatograms made from a couple of eyespots from very large (20 cm) specimens showed pink fluorescence above pigment sample, and dark, probably UV absorption spots 5-7 cm above pigment sample (Whatman #1 paper, butidine solvent). Presence of porphyrins (characteristic for photosensitive pigments) may be indicated. Because no photoreceptive function has yet been demonstrated for the "eyespot," the term is inappropriate. It will be used throughout this study, however, because it is established in the literature, and because many lampsilids possess numerous other pigment spots.

[11]Because frequently one marsupium only protrudes during flapping behavior, the term "marsupium" rather than "marsupia" will be used in much of this description, although both of the marsupia protrude from time to time.

[12]A pulse is a superposition of sine waves of different frequencies, analogous to the motion generated by pushing up, then pulling down on a taut rope's end - not a wave or undulation, which would advance at a constant speed and amplitude.

[13]When one observes a flapping *L. ventricosa* in a turbid stream, the completion of the forward movement of the pulse is striking. On the internal surface of the flaps in this species, at a point corresponding with external location of the eyespots, there is a patch of white. To the human observer, the flash of the white patches is the most eye-catching part of the regular flap movements.

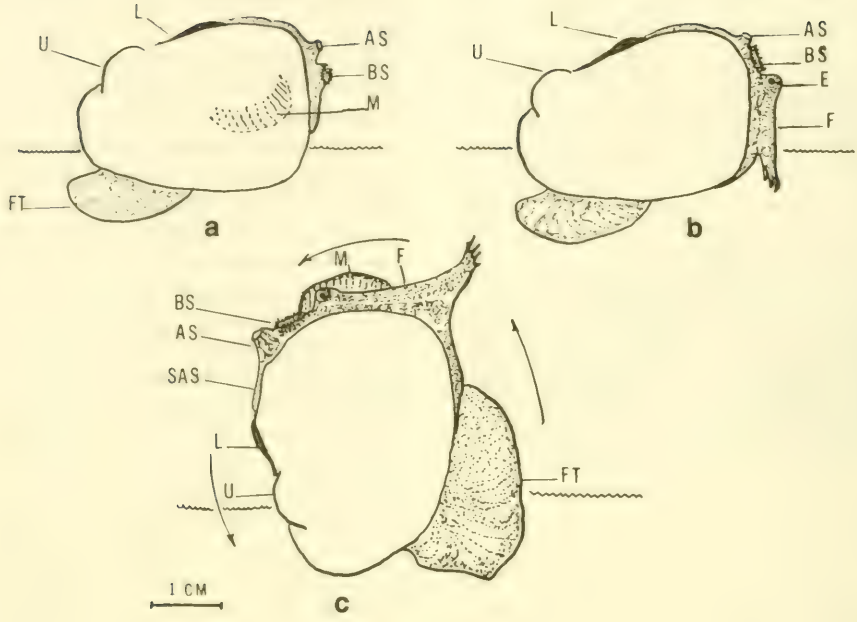


FIG. 9. Flapping in mature female *Lampsilis ventricosa*. Diagrams showing appearance while anchored in substrate, from the left side, a, during normal activity, flaps withdrawn; b, flaps visible; and c, during flapping behavior, showing "headstand" position with tilted valves, foot as prop, flaps and marsupium broadly protruding. Note "normal" position of marsupium (dotted) under shell in a.

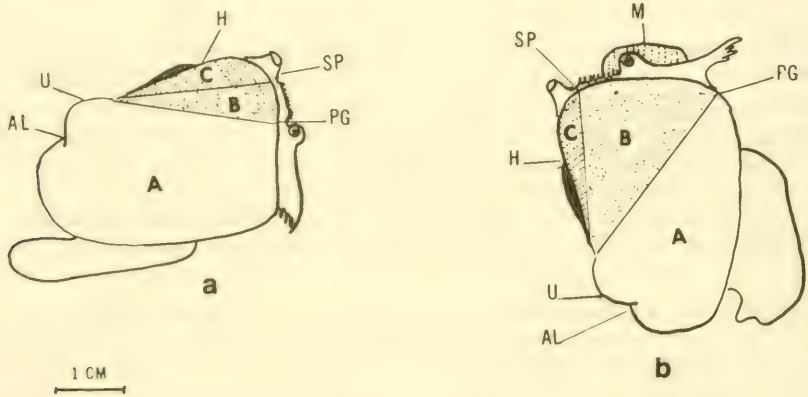


FIG. 10. Flapping in mature female *Lampsilis ventricosa*. Diagrams showing "anatomical correspondence" areas, defined by Stasek (1963) for bivalves, as they might be applied to *Lampsilis ventricosa* during: a, "normal" activity, and b, during flapping behavior. A, pedal margins, which extend from anterior limit (AL) of the infra-branchial chamber near the mantle isthmus of the animal to its pedal gape (PG); B, the inhalent aperture, extending from the pedal gape to siphonal partition (SP); and C, the exhalent aperture which extends from the siphonal partition to the limit of the suprabranchial chamber near the hinge (H).

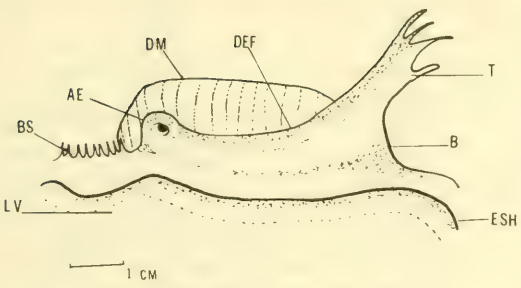


FIG. 11. Flapping in mature female *Lampsilis ventricosa*. Diagram of flap region showing terminology used in text (p 228) in analyzing movements of mantle flaps during flapping behavior. Note that the distal edge of marsupium and distal edge of flap is now "dorsal," while the eyespot end is "anterior" and the tail of the flap is "posterior."

the anterior ends move up against each other (or against the protruding marsupium), and both flaps are simultaneously pulled back and together.

Regular flap movements resemble swimming motions of a little fish, a resemblance first noted by Coker et al. (1921), and later by Howard & Anson (1922). This resemblance has prompted Welsh (1933) to refer to the flaps as "lures" for possible fish hosts to the mussel's glochidia. Regular flap movements have been observed at frequencies varying from 60 or slightly less to as much as 180 per minute. At 1 per second frequency, each recovery stroke requires about 0.6 seconds.

The slow movements (Figs. 14, 15): I have observed slow movements usually at low light intensities, and at frequencies of from 30 per minute down to less than one in 30 minutes. Before the slow movement starts, flaps are spread wide apart, the entire length of each floating out horizontally, inner sides uppermost in the water. The marsupium may not, but more often does, protrude between the flaps. When the movement begins, there is a contraction at the flap base; the tails move up and may touch medially; then a pulse moves forward from in front of the tails, which draws the eyespot ends of the flaps upright, together, and backward.

In recovery, first the tails, then gradually the rest of the flaps relax and float out horizontally once more. At the end of the recovery stroke, the flaps have moved forward slightly, again.

Whereas it has been speculated that the minnow-like aspect produced by the rapid ("regular") movements of the flaps might attract possible fish hosts, and that these movements may serve to aerate the glochidia, slow movements of the flaps seem unqualified for either role. The slow movements can go on for hours at very low light intensities and obviously contribute little to aerate glochidia, nor do they give the impression of a swimming fish.

A prominent feature of the mussel's slow movements is the accompanying, broad exposure of the marsupium.

Other flap movement patterns: Other movement patterns noted in this study for *L. ventricosa* are: "fluttering" movements, "weak, regular" movements, and, rarely, "double" movements. The first 2 are described here.

Fluttering movements may be observed during periods of very low flapping frequency. They consist of slight, rapid contractions which course from eyespot to tail and from tail-base to eyespot, and involve just the distal, gray-pigmented parts of the flaps. Their passage along the flap is accompanied by minute darkenings of the pigment, and bendings of delicate papillae which fringe the free surface of each flap.

Weak regular movements may be seen during periods of prolonged, high flapping frequency (1 move/sec.). Initial contractions at flap-base, and the pulse subsequently generated, are much less strong than in the regular movements. The pulse does not cause the eyespot ends of the flaps to be thrust forward and to snap apart. The recovery stroke does not bring the flap edges upright and together. The effect of these weak regular movements is to produce a rhythmic, gentle "waving" of the flaps.

TABLE 3. Orientation of *Lampsilis ventricosa* during "normal" activity, contrasted with position during flapping behavior (compare with Fig. 9)

Body structure	Position during "normal" (non-flapping) activity	Position during flapping behavior
Valves	"Upright," i.e., umbones and ligament on top (dorsal).	Tipped (rotated anteriorly), often in "headstand," i.e., umbones are now near substrate, ligament vertically above umbones or even in a line forming an acute angle with substrate in front of the animal.
Foot	Used chiefly during locomotion: foot extended at front, then back, valves then hunching forward.	Posterior part of foot much extended to make wedge-shaped prop for animal's up-tilted valves.
Anal siphon	Dorsal and posterior; line ligament - anal siphon nearly parallel with substrate.	Dorsal to anterodorsal. Line ligament - anal siphon vertical to substrate.
Branchial siphon	Posterior, ventral to anal siphon. Distal edges projecting parallel to substrate (papillae may be touching medially).	Dorsal, posterior to anal siphon, distal edges may be turned medially, papillae touching.
Mantle flaps	If visible, located ventral to branchial siphon, not extending far from valves. Tails may or may not be hanging free, and ventral to rest of flap.	Dorsal, posterior to branchial siphon. Eyespot, "anterior" flap portion just posterior to branchial siphon. Tail, posterior portion, floating free, the whole flap pushed out from valves.
Inner lobe (3), at base of flaps	Distal edges touching medially, or withdrawn between the valves. If withdrawn, mantle flaps are not extended or visible.	Distal edges projecting at least 2 cm from valves (in specimen 10 cm long, touching each other medially at 60° angle to form peak under flap tails (see Fig. 8).
Marsupia (posterior portion of outer gills)	Ventral to posterior adductor and rectum. Kept within pallial cavity.	Pushed out between flaps, protruding 2 cm; distal edges dorsal. Posterior tubes of marsupium now anterior because of 90° rotation of animal. Marsupia may move "up" and "down" between flaps according to light intensity and frequency of movements.

4. Behavior accompanying initiation of flap movements

Lampsilis ventricosa often begins flap movements at dawn, with a characteristic behavior sequence (Table 4), the consequences of which are: (a) mussel has assumed "headstand"; (b) foot is prominently displayed as a luminous white heel, or prop, for uptilted valves; (c) flap movements markedly increase in frequency (from 30 moves/5-10 minutes, to 30 moves/30 seconds or less, i.e., they become from 10-30 times as fast, see Fig. 16), and (d) one marsupium or both marsupia protrude between flaps.

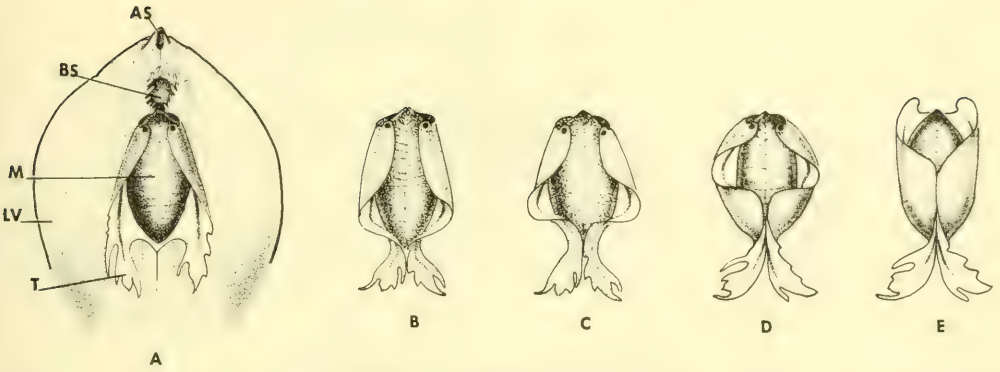


FIG. 12. Elements of the regular flap movements of *Lampsilis ventricosa*, viewed from above (semidiagrammatic). A, position at end of recovery stroke (tails floating out, eyespot ends against sides of marsupium); B, pulse begins near base of tails, outer margins fold over and meet at centerline; C, pulse (bulge) moving toward anterior eyespot end of each flap; D, pulse nearing eyespot ends of flaps; E, pulse at eyespot ends of flaps, pushing them outwards and forward horizontally.

TABLE 4. Summary of sequence of events in initiation of flap movements in gravid female of *Lampsilis ventricosa*

Step	Behavioral event	Approximate duration in minutes
1	Mussel in normal position (ligament dorsal).	--
2	Flaps are extended, until free edges of tails are exposed.	5-10
3	Flaps hang limply, ventral to branchial siphon.	5
4	Fluttering movements occur.	2
5	Pause.	2
6	Animal completely withdraws flaps; mantle lobes in siphonal region are squeezed together; mussel extends foot out and slightly backward in substrate and tips valves forward, toward umbones.	1
7	Valves open slightly; flaps are re-extended.	2
8	Repetition of steps 4 through 7, approx. 3 times.	20

Whenever flaps are withdrawn, the marsupium is moved down into the pallial cavity. The flaps then are re-extended, and move vigorously for 1-2 minutes before marsupium protrudes fully again.

Grier (1926) described an increase in flapping frequency in *L. ventricosa*, but not in the context of the animal's response to increasing daylight. He observed (:112): "At first the rate is quite slow, as if the creature were 'warming up' but rapid acceleration occurs to a maximum rate . . ." I have found that the rate of acceleration in flapping frequency is not always rapid, and that the "maximum" rate varies with each animal from

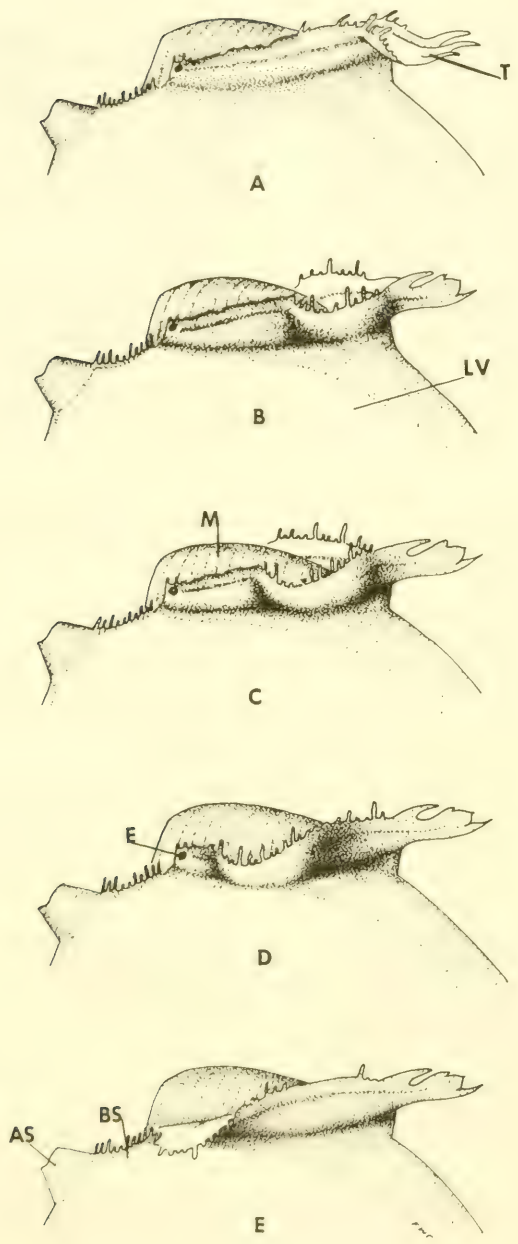


FIG. 13. Semidiagrammatic view of the regular flap movements of *Lampsilis ventricosa,* from the left side. Compare stages with Fig. 12. A, end of recovery phase (tails out, horizontally); B, beginning of "forward" pulse (note that it begins at base of tails); these are then brought upward and seem to clap together medially, over the protruding marsupium; C, pulse moves along each flap, causing a lateral bulge; D, pulse nears "anterior" eyespot end of flaps; E, pulse is at each flap end, pushes them outward and horizontally, also thrusting the flap-pair forward.

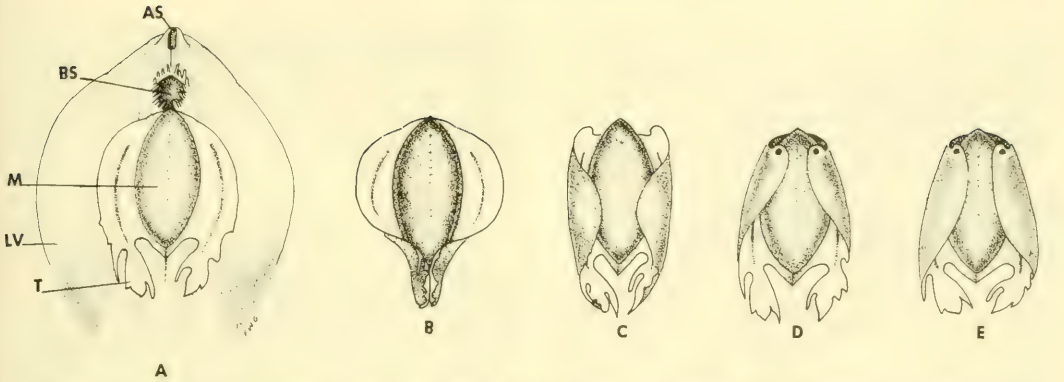


FIG. 14. Elements of the slow flapping movements of *Lampsilis ventricosa*, viewed from above. A, position of flaps at end of recovery stroke (flaps wide apart, floating horizontally, entire inner surfaces uppermost, marsupium widely exposed); B, pulse begins at base of flaps, bringing tails together medially; C, pulse moves forward, bringing mid-portion of flaps up medially; D, pulse nears eyespot ends of flaps, bringing them up close together with their anterior ends pulled back a little; E, end of forward pulse, most of flaps up, together and still backward.

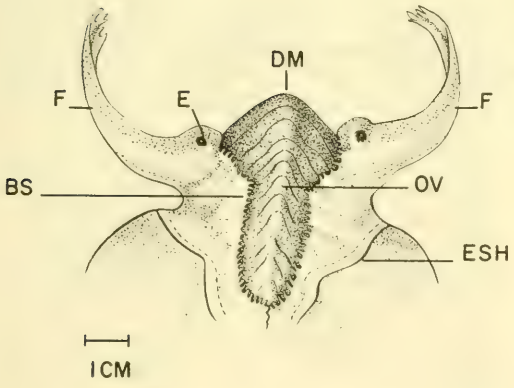


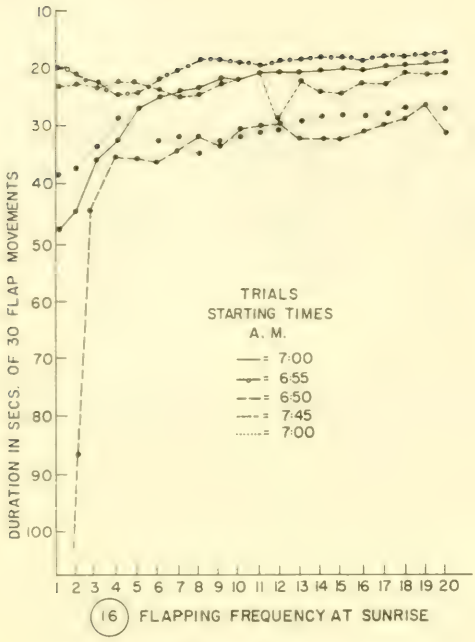
FIG. 15. "Head-on" view of flaps of *Lampsilis ventricosa* during slow movements; drawn from an animal in headstand position, looking from branchial siphon toward the flaps. Eyespot ends of flaps in foreground, free-floating flap-tails in rear. Note widely exposed marsupium. Only one marsupium is visible, the other one held within the branchial cavity.

one day to another (as well as from one time of day to another).

Variation in the daily time of onset of flap movements was noted in this study. Occasionally an animal would not initiate flap movements until mid-afternoon, even on a sunny day. Water temperature did not appear to be an immediate stimulus for initiation of flap movements. No differences were observed between specimens of *L. ventricosa* maintained in aquaria at normal, fluctuating temperatures, and others kept at a constant temperature of 19° C, in the lengths of their flapping periods, in the daily time of onset, or in behavior at onset of flap movements.

5. Behavior accompanying cessation of flap movements

This process may be observed in an undisturbed animal just before sundown (see Fig. 17), in rapidly fading daylight, when the mussel virtually reverses the warming up behavior it exhibited at sunrise (see Table 4). As the rate of flapping decreases from 1 movement/sec. to 1 movement/2 secs., there is a shift from the regular to the slow type of flap movement, the latter broadly exposing the marsupium. Flaps are drawn together, then withdrawn between the valves, as the animal gradually changes its angle of headstand orientation by hunching back down into the substrate. Flaps float out again and movements continue at the reduced rate. After a



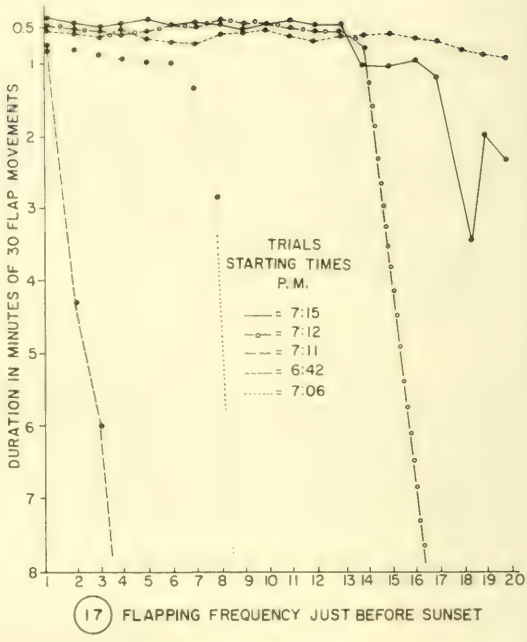
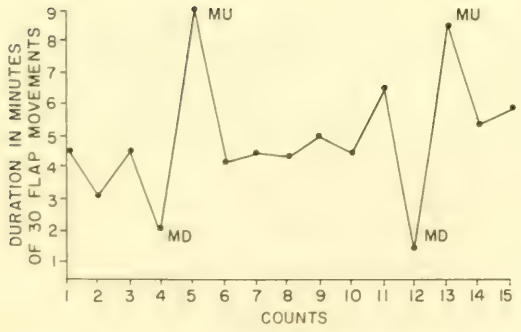


FIG. 16, 17. Flapping frequency of *Lampsilis ventricosa* at sunrise and sunset from 5 trials each, on different days in July and August, 1965. Each trial consisted of up to 20 consecutive counts (given in seconds in Fig. 16; in minutes in Fig. 17). Each of the large black dots represents a count, that is, the time span for 30 flap movements. Note that in 2 of the trials at sunset, movements did not cease, though movements perceptibly slowed in one of them.



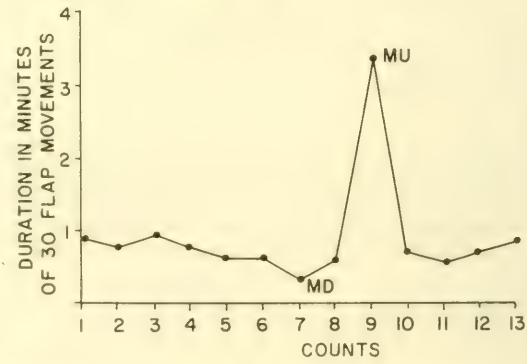


FIG. 18, 19. Alteration of flapping frequency (duration in minutes of 30 flap moves) which accompanies movements of marsupia in *Lampsilis ventricosa*. Trials comprised of 15, 13 consecutive counts in Figs. 18, 19 respectively. A count is the duration of 30 flap movements. Trials started at 3:40 p. m. on August 1, 1965 (Fig. 18) and at 10:45 a. m. on July 11, 1965 (Fig. 19). MD, marsupia moved down into pallial cavity; MU, marsupia moved up to protrude between flaps.

few minutes, flap withdrawal, valve closure, hunching down and flap re-extension are repeated. Finally, the flaps remain withdrawn, and the animal has assumed a normal siphoning position in the substrate.

6. Behavior accompanying diminution of flapping frequency (see Fig. 17)

Often the mussel maintains a headstand while its flap movements decrease in frequency with the oncoming dusk. Flap movements change to the slow pattern; the marsupia continue to protrude; and the flaps are spread more and more widely apart as daylight fades.[14]

7. Role of marsupia in flapping behavior of *Lampsilis ventricosa*

The marsupia of *L. ventricosa* affect flapping behavior in at least 4 ways:

(a) As a necessary condition for flapping behavior. The marsupia must contain glochidia. Among more than 40 living mature female *L. ventricosa* observed at length in this study, flap movements were seen only in gravid, though not in all gravid specimens.

(b) In increasing prominence of display. In the course of the 3- to 4-month summer season of flapping, *L. ventricosa* will, the first few weeks, show one marsupium or the other (seldom both) protruding just slightly between the flaps whereas in later weeks, one or both marsupia project prominently from between the flaps throughout the daily flapping periods. When both marsupia are exposed, one is invariably thrust out more than the other, occupying a position closer to the siphons. The appearance of the 2 marsupia is neither quite side-by-side, nor quite one-behind-the-other (see Figs. 20, 21).

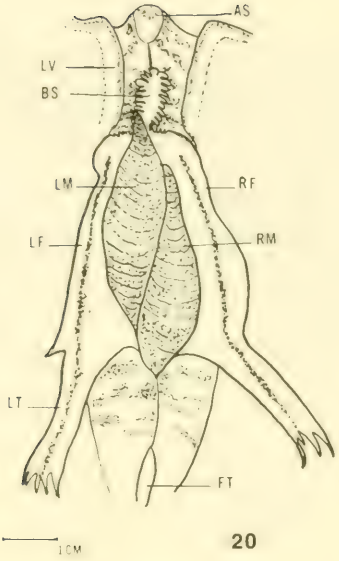
(c) In sharply altering frequency of flap movements (Figs. 18 and 19). The marsupia are occasionally spontaneously moved down into the pallial cavity and subsequently up between the flaps, during flapping movements. The downward movement is accompanied by a slight pause, then an increase in flapping frequency. Re-emergence of the marsupium is typically accompanied by a noticeable slowing of flap movements.

(d) In spawning of glochidia. Toward the end of several months of intermittent flapping behavior, a tiny hole appears in the distal margin of each visible ovisac (charged water tube in a marsupium); and within a week or less, the ovisacs are emptied of glochidia, ostensibly through these openings, during lengthened periods of flapping. Alternatively, the edge of one (or more) of the ovisacs may rupture, and the entire contents are shed as a conglutinate.[15] Figs. 20 and 21 show marsupia protruded (in the manner typically observed late in the season of flapping behavior). Location of pores in the ovisacs is shown in Fig. 22, and the gradual emptying of ovisacs, or spawning, is shown in Fig. 23. Because the ovisacs are transparent, and because individual ovisacs may have contents of different appearance,[16] it is

[14]The animal may remain thus for hours in the dark. I have watched these movements for long periods at night, with a safe-light (a red, 25-Watt bulb). Slowest flapping rate recorded in this context: 30 flap movements in 36 minutes and 18.3 seconds (August 13, 1965).

[15]The conglutinate or mass of embryos expelled as a whole still has the shape of the ovisac. Conglutinates of *Lampsilis ventricosa* are the size, shape and color of a slivered almond. All those examined in this study consisted of well-developed glochidia, each larva usually still surrounded by its own membrane. Lampsilinae do not seem to abort conglutinates as readily as some other unionids. *Pleurobema*, for example, frequently shed many tiny, bright pink, splinter-shaped conglutinates within an hour after collection. These often consist largely of immature embryos.

[16]Differences in color and texture of ovisac contents are not as marked in *Lampsilis ventricosa* as they are in *Pleurobema* and other unionids (Lefevre & Curtis, 1910) where there can be brightly colored stratification of unfertilized eggs among the glochidia in the tubes of each marsupium.



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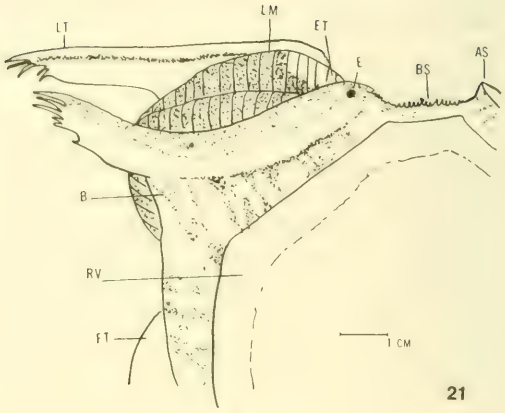

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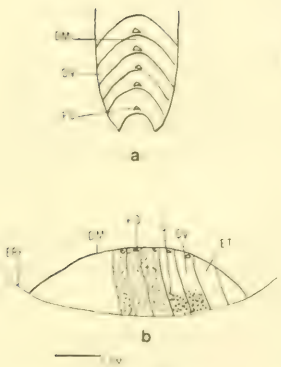
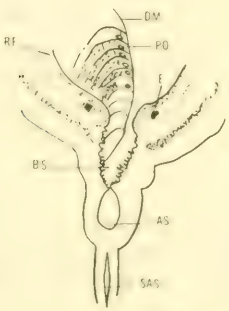
FIGS. 20-23. Marsupia of gravid female *Lampsilis ventricosa*.

FIG. 20. Protrusion of both marsupia, dorsal view (sketched on August 5, 1964, 10:30 p. m. artificial light (75 Watt incandescent bulb).

FIG. 21. Protrusion of both marsupia seen from right side (sketched on August 15, 1964, 8:00 a. m. in natural light). Several water tubes (ovisacs) in left marsupium, near branchial siphon (BS) looked partly empty.





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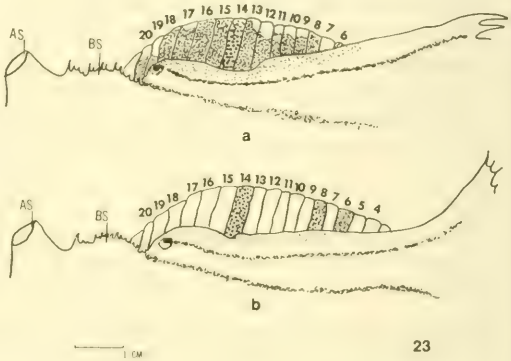

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FIG. 22a, b, c. Location of pores in ovisacs (water tubes of posterior portion of outer gill). a. "Anterior" part of exposed marsupium, showing "edge-on" view of marsupial border; ovisacs empty. Orientation as in Fig. 15. b. Lateral view, slightly tipped to show pores on border. c. Exposed marsupium of flapping animal, sketched from anterior (eyespot) end of flaps.

FIG. 23. Spawning. Left mantle flap and exposed right marsupium, seen from left side, on 2 successive days. Ovisacs are numbered to show that between time when upper sketch was made, (6:30 a. m., Sept. 2, 1964) and time of lower sketch (8:30 p. m., Sept. 3, 1964), a number of water tubes (serving as ovisacs) had discharged their glochidia, probably via pores (not sketched here). No conglutinates were shed during that time.

possible to observe the emptying of various tubes in a marsupium, from day to day (Fig. 23).

8. Characteristic flapping periodicities

The times when *Lampsilis ventricosa* exhibits flapping may be summarily categorized as follows:

(a) Flapping season: extends for about 4 months from late spring onwards through the summer. I have records for a few Arkansas specimens which exhibited flapping behavior intermittently from June through September while in aquaria (see Tables 13 & 14).

(b) Flapping period: consists typically of a week or less in which the mussel exhibits flapping behavior at least part of every day. I have observed 6-8 such periods in individual specimens kept in aquaria at normal temperatures throughout a flapping season. A flapping period is frequently preceded by extensive locomotion, i.e., the mussel makes a circuit or two of the aquarium, before tilting up to a headstand (flapping position). Flapping periods are separated by several days to several weeks or more when no flapping occurs.

(c) Flapping day: is a day of flapping activity, which often begins at dawn; the flap movements finally cease or radically diminish in frequency just before sundown. Table 5 is a record, for one specimen of *Lampsilis ventricosa*, of 4 flapping periods, including a total of 18 flapping days, during which the animal was checked continually for flap movements. These data seem typical for *L. ventricosa*, in that they indicate the following: (1) frequency of flap movements varies throughout the day, and from one day to another; (2) flapping frequency does not increase or decrease uniformly through the day; (3) a flapping day is usually inaugurated at sunrise and tapers off just before sunset (Graph, Fig. 24, taken from Table 5).

I have further observed (at controlled and uncontrolled temperatures) that during any day of a flapping period, *Lampsilis ventricosa* is more likely to exhibit flapping activity at sunrise or just before sunset than at any other times of the 24 hour day.

B. EFFECT OF PHOTIC STIMULI ON THE FLAPPING BEHAVIOR OF *LAMPSILIS VENTRICOSA*

Early studies of the general (non-flapping) behavior of *Lampsilis ventricosa* included observation of the marked response of both siphons, but especially of the anal siphon to sudden shadows (skioptic response). Table 6 shows a typical series of responses by the anal siphon of a specimen of (non-flapping) *L. ventricosa* to repeated shadows. The anal siphon soon becomes "habituated" to the shadow stimulus. That is, the anal siphon shows a waning response to the repeated stimulus, not evidently occasioned by sensory adaptation or muscular fatique, inasmuch as the "habituated" siphon is still responsive to other (e.g., tactile) stimuli.

Later studies of the flapping behavior of *Lampsilis ventricosa* indicated the flapping animal's evident sensitivity to photic stimuli. Table 7 contrasts the observable responses of mantle flaps to photic stimuli (as well as to tactile stimuli, local water waves, jar of substrate, and temperature fluctuations) during flapping behavior, with responses of siphons during normal activity. The reader is reminded of the fact that both siphons and mantle flaps are part of the third (inner) lobe of the mantle edge, and that both are innervated by nerves from the visceral ganglion.

Simple preliminary experiments revealed that *Lampsilis ventricosa* can apparently be induced to increase its flapping frequency in response to light of increasing intensity.[17]

A series of experiments was then

[17] *Lampsilis ventricosa* does alter its flapping frequency in apparent response to sudden, artificial changes in light intensity. The following is taken from notes made on July 7, 1964, regarding an aquarium specimen maintained at normally fluctuating temperatures: "A hot (100° F) sunny day. Water temperature up to 33° C. Mussel had been flapping in extreme headstand all through the day. Movements very rapid (up to 10 sec. for 30 movements). (Contd. on p 252).

TABLE 5. Average flapping frequency* for one specimen of *Lampsilis ventricosa* at various times of day in natural light only, at a constant water temperature of 19° C, during 4 flapping periods, from July 2 to August 18, 1965

Flapping periods	Date 1965	Duration in seconds of 30 movements at different hours							
		6-8 h	8-10 h	10-12 h	12-14 h	14-16 h	16-18 h	18-20 h	20-22 h
	7/2								20.0
1	7/8		15.2	17.2	19.7 17.6	17.8 18.1 17.5	18.0	54.6	
	7/9	25.2	16.8		16.5	24.6 19.9		32.9 105.8	
	7/10	19.9		46.7 28.7	26.4		30.5	36.5	
	7/11	21.5 21.6		56.0		332.3			
	7/12	43.7		486.8(3)				479.0	
2	7/27	23.1	27.5	27.0		30.7	2:39.5		
	7/28							481.2(4)	
	7/29	29.7		32.4	34.6	44.4	46.4	170.4(3)	
3	8/1	33.2		125.3		347.3		900.9(3)	
	8/2	24.6	25.4					39.3	
	8/3	93.9		108.4				605.3(1)	
	8/4							464.0(1)	
4	8/12					29.7 26.7		293.0(1)	
	8/13	22.5		22.0	22.7	23.3	30.7	401.1(1)	
	8/14	30.6	25.6	24.6		31.1	34.7	1110.0(1)	
	8/15	30.8		35.5	38.4	303.4(4)			
	8/16							131.6(9)	
	8/17	42.8							

*Frequency is expressed as average duration of 30 flap movements in a series of 20 trial counts. In 11 instances fewer counts (10) were made (superscripts in parentheses).

[17](contd.) Still flapping at 8:00 p.m. Turned on light over aquarium at 9:00 p.m. Mussel had tilted back down toward normal position in substrate. No flap movements. Marsupia withdrawn. 9:30 p.m., animal in headstand, flapping rapidly. (30 movements in 10 seconds)." I later found an evident correlation between the beginning, continuation and termination of a flapping period, and the proclivity of a mussel for exhibiting such artificially induced movements.

TABLE 6. Successive responses of anal siphon of a gravid *Lampsilis ventricosa* to a sequence of shadows (1 sec. each). Total time for all trials tabulated, 7 minutes

Trial	Shadow* sec.	Siphon closure	Recovery time** in seconds
1	1	Immediate, complete	26.1
2	1	Immediate, complete	23.5
3	1	Immediate, complete	15.9
4	1	Immediate, complete	23.3
5	1	Immediate, complete	30.3
6	1	Immediate, complete	37.3
7	1	Immediate, complete	15.1
8	1	Immediate, complete	18.6
9	1	Immediate, partial	8.5
10	1	Immediate, partial	8.1
11	1	Immediate, partial	7.5
12	1(x3)	Delayed, partial	16.3
13	1(x3)	Delayed, complete	21.1
14	1(x3)	Delayed, complete	16.8
15	1(x4)	More delayed, partial	15.5
16	1(x8)	Still more delayed, partial	9.3
17	1(x20)	No response. Anal siphon remained open	

*Shadows were presented more than once (numbers in parentheses) in trials 12-16 before siphon closed.

**Recovery time is period between closure of anal siphon in shadow response and re-opening.

carried out, (a) to test the assumption that photic stimuli can alter mantle flap behavior in *L. ventricosa*, and, if photic stimulation could be experimentally demonstrated, (b) to examine certain parameters of the photic response.

The experiments covered a considerable range of light intensities (0.3-22.5 foot candles). They were performed at night, with a single light source (see Materials and Methods), and at a constant water temperature of 19° C. Observations included short time checks (10 timed counts or less of 30 movements each), and long ones (20-such trial counts). They were conducted when the animal was in a headstand or almost a headstand position; after days of vigorous flapping, and after days of flapping inactivity; and at the beginning, middle, and end of flapping periods. Preconditions of 8 experiments are summarized in Table 8. Table 9 is a summary of the results of the 8 experiments.

At light intensities greater than 3.7 foot candles, alterations of flapping frequencies in response either to increments or decrements of light were not consistent. In the light intensity interval from 2.3 foot candles to 0.8 foot candles, flapping frequencies were consistently altered, increasing in response to small or large increments of light (Fig. 25), decreasing in response to small or large decrements of light (Fig. 26). The above experimental results make it seem likely that the "warm-up" and "slow-down" character of flapping behavior typically exhibited by *L. ventricosa* at sunrise and just before sundown, respectively (compare Figs. 16 & 17), is a photic response.

C. COMPARATIVE STUDIES WITHIN THE GENUS *LAMPSILIS*

Comparative studies were made of the flapping behavior of *Lampsilis siliquoidea* and *L. brevicula brittsi* in order

TABLE 7. Comparison of responses to various stimuli of mantle flaps (during flapping behavior) and of siphons (during normal activity) in *Lampsilis ventricosa*

Stimulus	Response of Mantle Flaps	Response of Siphons
Photic		
a. Repeated shadows (sudden light decrements)	Shadow response present, as slight pause (0.1 sec.) in flap movements (some indication that shadow response may be inhibited at a high flapping frequency).*	Shadow response present, especially for anal siphon, except after repeated responses to shadows (Table 6).
b. Gradual decrement (as at sundown)	"Headstand" maintained, moves slow, change from "regular" to "slow" pattern, flaps are spread wide apart, marsupia exposed; OR: headstand abandoned, flapping slows, then ceases; flaps and marsupia withdrawn.	No consistent observable response to natural gradual increments or decrements of light intensity. Siphons may be wide open, or closed, in dim or in bright light, day or night.
c. Darkness	If flapping, moves are in "slow" pattern, marsupium (-ia) exposed.	
d. Gradual increment (as at sunrise)	Assumption of headstand, extension of flaps, onset of flap movements, change from "fluttering" to "slow" to "regular" pattern (the last a protective configuration, i.e., marsupia mostly covered by flaps).	
Tactile		
Stroking of relevant structures with fine probe	Negligible; flapping frequently unaltered, even when moving flaps are touched.	Anal siphon: negligible; branchial siphon: innermost row of papillae in lumen sensitive, siphon may close.
Local water waves	No observable response in *L. ventricosa* (marked response in *L. siliquoidea* and *L. brevicula*).	No observable response.
Sudden jarring of substrate	Animal may pause and then either continue or withdraw flaps, then siphons, abandon "headstand" and stop altogether.	Siphons may close, then withdraw; foot may also withdraw, and valves may close.
Temperature fluctuations		
Diurnal variations vs. constant temperature	None noted (although Grier, 1926, claimed temperature response for this species).	None noted.

*I have made several observations of *L. ventricosa* during periods of very high flapping frequency (as high as 3 movements per second), when the mussel gave no recognizable response to shadows. One such observation was made on June 22, 1963, in the White River near Wyman, Washington County, Arkansas, on a large (20 cm long) gravid female, angled in a headstand, into the current, and flapping in full mid-afternoon sun, in approx. 18 in. of water. For more than an hour, I made repeated attempts to induce the shadow reflex in the flapping animal, There was, however, no closure of siphons nor any apparent diminution of flapping frequency. Such observations as these indicate that high flapping frequency may inhibit the siphonal shadow reflex.

to distinguish elements of flapping behavior common to these 2 species and to *L. ventricosa*, as well as to determine any flapping characteristics peculiar to one or more of these species.

Flaps and Flapping Behavior in *Lampsilis siliquoidea*

1. Flapping position and gross flap morphology

In *L. siliquoidea*, flapping position in characteristically a rotation of only about 50°; the flaps are heavily pigmented, with less conspicuous eyespots than those of *L. ventricosa*, and with elaborate development of flap tail portions (Table 10; Figs. 27, 28).

2. Flap movements in *L. siliquoidea*

These are similar to the "regular" movements of *L. ventricosa*. The moves begin with contractions at the base of each flap's tail, and progress as paired pulses toward the eyespot. The pulse pulls the eyespot end of each flap laterally. Recovery phase of the movement brings first the eyespot ends, then the rest of the flaps together once more. Flap movements in this species differ from those of *L. ventricosa* as follows:

a. There are no movements comparable in configuration to the "slow" movements of *L. ventricosa* in the flapping behavior repertoire of *L. siliquoidea*.

b. Frequency of flap movements is much lower in *L. siliquoidea* than in *L. ventricosa*. I have recorded rates up to 180 per minute for *L. ventricosa*, compared with a maximum for *L. siliqoidea* of 29.7 per minute.[18] *L. ventricosa*, also, exhibits a much greater range of flapping frequencies.

c. Spontaneous flap moves in *L. siliquoidea* are preceded by definite, twitching contractions of basal tentacles (BT, Figs. 27, 28) just under the flap tails, followed by a slight pause.

d. Spontaneous flap moves typically occur in pairs in *L. siliquoidea*. Howard & Anson (1922: 71) also noted this characteristic of *L. siliquoidea* flap movements, describing them as ". . .regular undulations [*sic*!] of two rapidly succeeding waves lasting 2 seconds, each taking approximately a second to pass from the anterior ventral lobes to the eyespots."[19]

e. A single flap movement (i.e., a simultaneous movement of both flaps) may be readily induced in *L. siliquoidea* (but not in *L. ventricosa*) by sudden jarring of the substrate or by water waves in the immediate vicinity of the flaps, such as can be caused by fin movements of a fish.[20] Such flap responses cannot be induced by stroking the flaps with a fine probe. The single flap movement occurs when the flaps are extended and either moving rhythmically,[21] or not moving. These mechanically induced flap movements are thus readily distinguished from spontaneous movements (Table 11).

3. Characteristic flapping periodicities of *Lampsilis siliquoidea*

a. Flapping season lasts through the spring and summer months. My earliest

---

[18]The most extensive recordings of daily flapping frequency for a single specimen of *L. siliquoidea*, cover the period from April 25 to July 23, 1963. Average number of movements per minute for 10 minute counts were tabulated several times daily. Average flapping frequency throughout this period was between 4 and 5 moves per minute.

[19]"Anterior ventral lobes" are the tails of the flaps. The speed these authors record is faster than that I measured for *L. siliquoidea*.

[20]An attempt to measure the stimulus causing this response was unsuccessful. Tuning forks (512, 384 and 324 cycles per second) set to vibrating in and near the aquarium containing flapping *L. siliquoidea* did not stimulate the single flap movement response described above.

[21]If the single flap move is induced during spontaneous movements, their rhythm is broken. Further, ability of flaps to respond to water waves or to jarring with the single flap movement diminishes with prolonged stimulation, then ceases, so that several minutes must elapse before the single-flap-move response can be induced again.

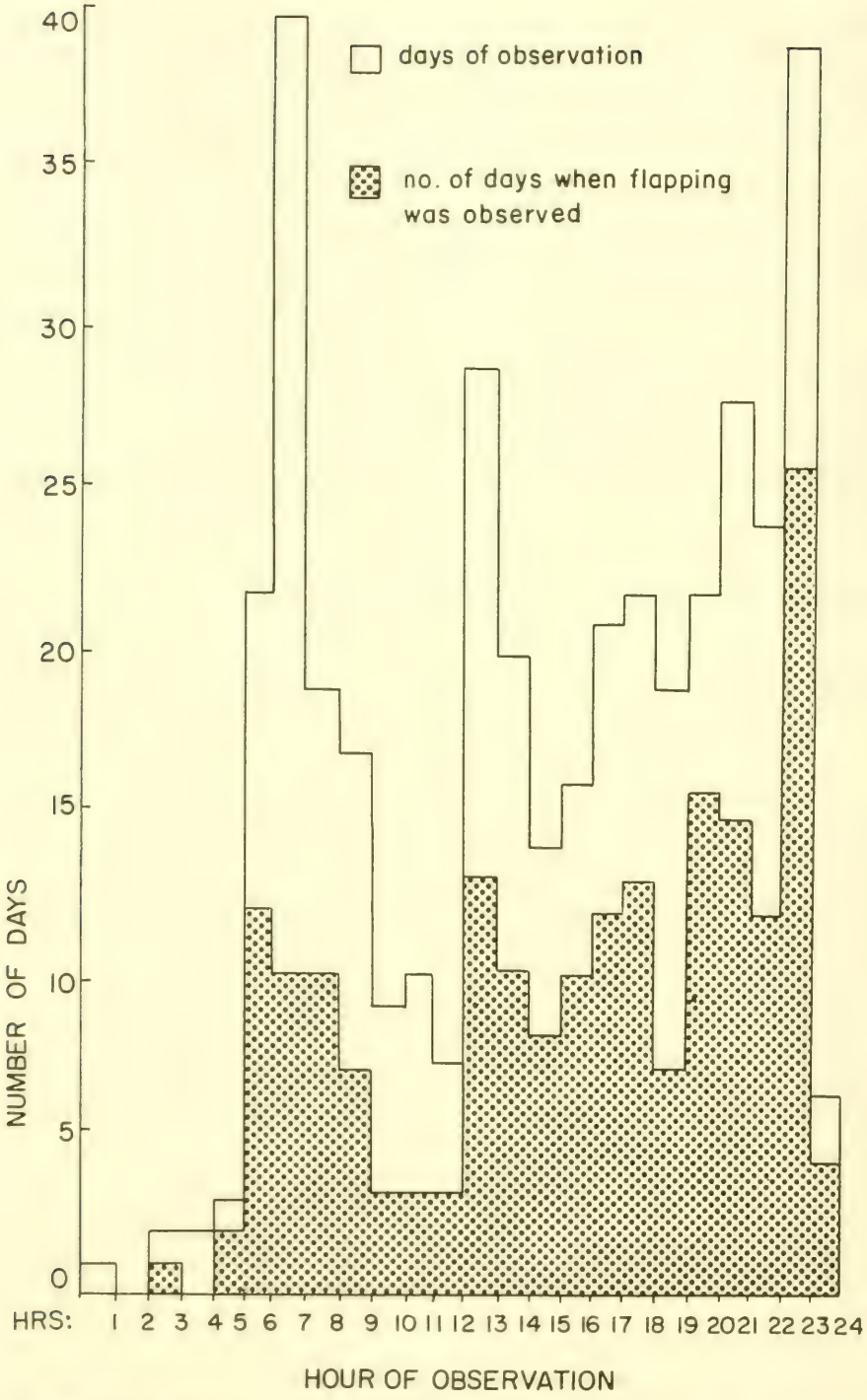

FIG. 24. Flapping activity of *Lampsilis ventricosa*. Times of 24-hour day, during 4 flapping periods (compare with Table 5), when flap movements occurred. Constant water temperature of 19° C.

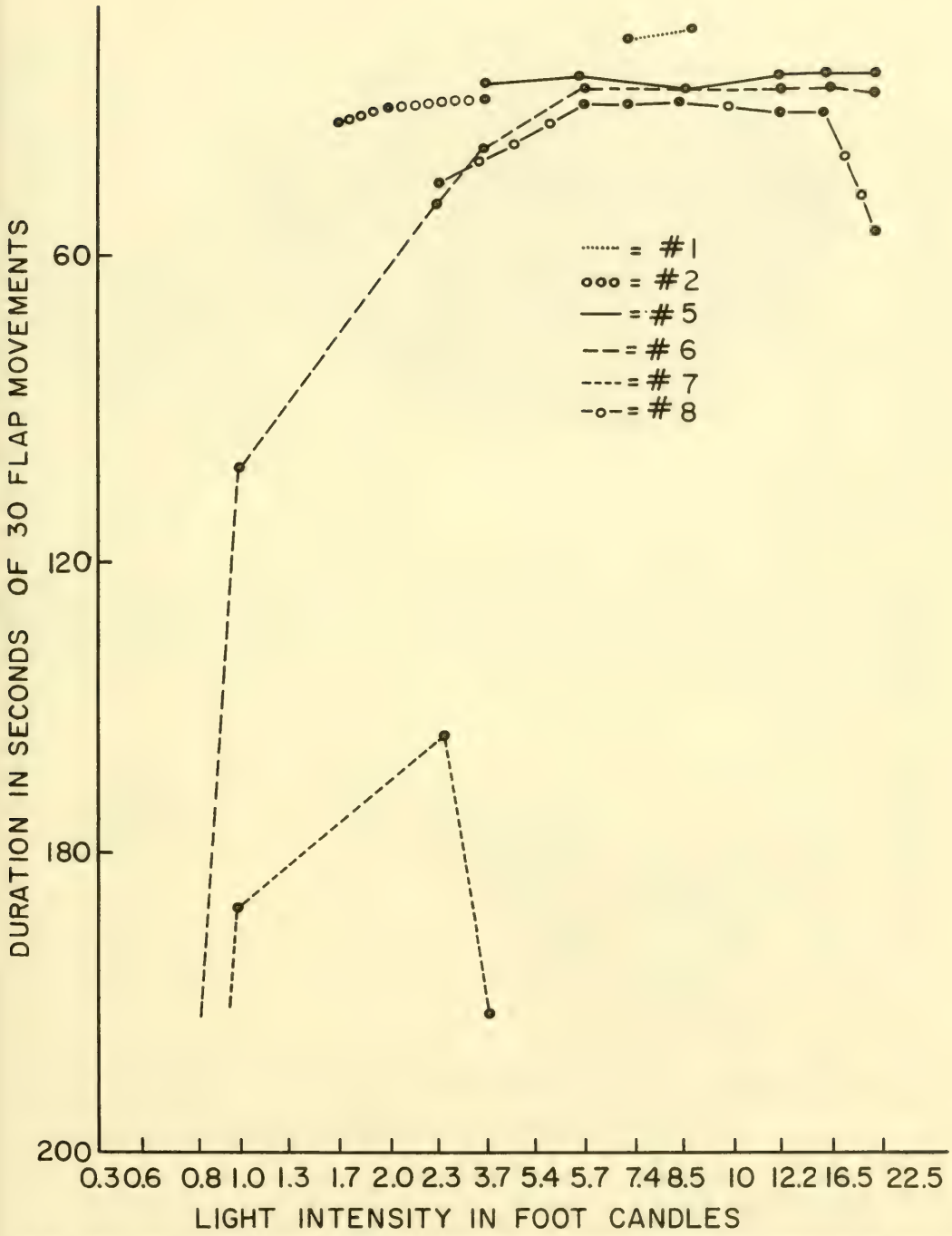

FIG. 25. Response of mantle flap movements of *Lampsilis ventricosa* to increasing light intensities. Data taken from experiments recorded in Tables 8 and 9. At low light intensities (between 0.8 and 2.3 foot candles) flapping frequency increased in response to light increments (compare with speedup of activities at sunrise, Fig. 16).

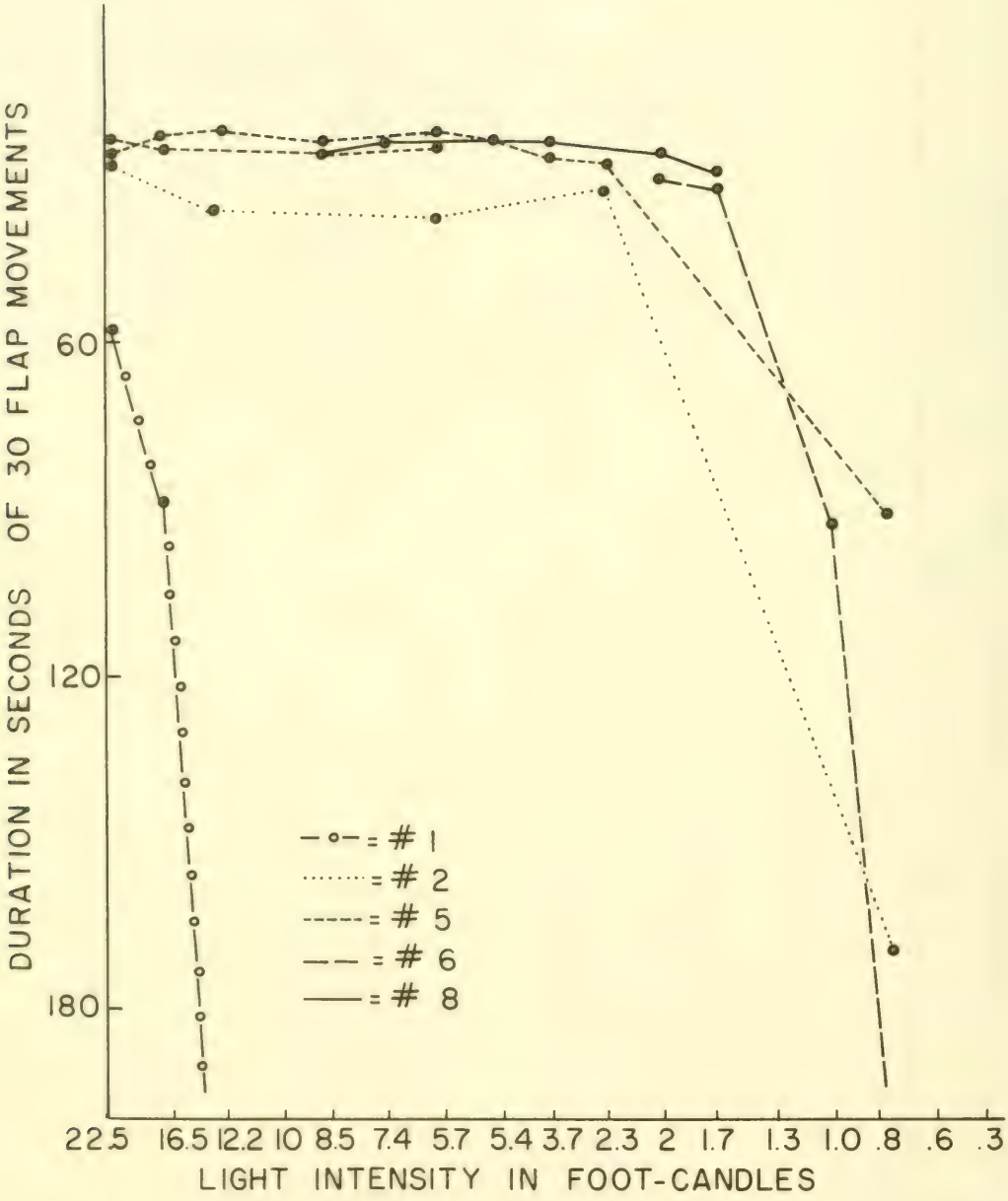

FIG. 26. Response of mantle flap movements of *Lampsilis ventricosa* to decreasing light intensities. Data taken from experiments recorded in Tables 8 and 9. At low light intensities (between 2.3 and 0.8 foot candles) flapping frequency decreased in response to light decrements (compare with slowing or stoppage of activity at sunset, Fig. 17).

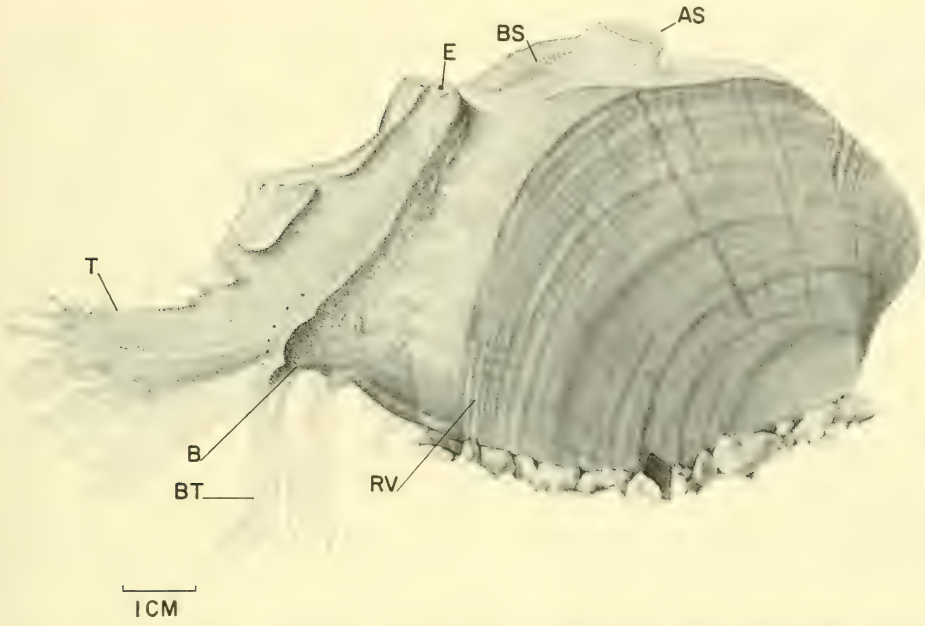

FIG. 27. *Lampsilis siliquoidea*, during flapping behavior, drawn from the right side. Note the position of the animal in a typical flapping stance: while the valves are somewhat tilted forward, the animal is not in the headstand so often seen in *L. ventricosa*. Note also that the edges of the branchial siphon (BS) are held horizontally and not vertically as in *L. ventricosa*.

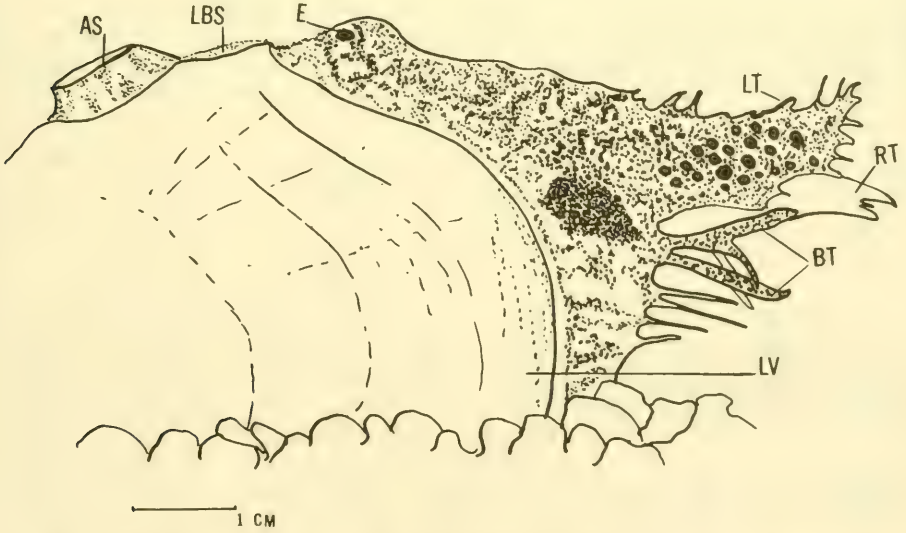

FIG. 28. *Lampsilis siliquoidea* in flapping position, seen from the left side, showing typical, ornate pigmentation especially in tail region of flaps. Branchial siphon not visible from this angle. Specimen from War Eagle Creek, Benton County, Arkansas, July 5, 1964.

TABLE 8. Summary of conditions under which 8 experiments on photic stimulation of flap responses by artificial light were carried out during July and August, 1965*

Experiment	Date (1965)	Time relative to flapping period	Prior: Locomotion	Prior: Headstand	Prior: Flapping speed in natural light (in min. for 30 moves)	Duration of experiment (p.m.)	Sequence of light intensities in foot candles (read across page)	No. of trial counts at each light intensity
1	7/25	2 days before onset	yes	yes	none	8:05-11:00	8.5 7.4 5.4 3.7 2.0 1.7	20
2	7/28	during 2nd day	yes	yes	10	7:50-11:00	1.7 1.7 2.0 1.7 1.0	20
							.6	10
3	7/29	near end	no	yes	15	8:00-11:00	.6	10
							.3	2
4	7/31	1 day before onset	no	45^{o} angle	none	8:10-11:00	10.0	20
							10.0	10
5	8/12	1st day	yes	yes	4	7:30-11:30	22.5 16.5 12.2 8.5 5.7 3.7 5.7 8.5 12.2 16.5 22.5 16.5 5.7 2.3	20
							.8	10
6	8/13	2nd day	no	yes	6	7:15-10:50	.8 1.3 2.3 3.7 5.7 8.5 12.2 16.5 22.5 12.2 5.7 2.3 .8	10
7	8/14	3rd day	no	yes	18	7:30-11:00	.8 1.3 2.3 3.7	10
8	8/16	before last day	no	yes	10	7:50- 9:50	2.3 3.7 5.7 8.5 12.2 16.5	10
							22.5	8
							1.65	10
							12.2	2

record for flapping activity in this species is April 25, and the latest record August 15.

b. Flapping periods are not as distinct in *L. siliquoidea* (Table 12) as they are in *L. ventricosa* (Tables 13 and 14). For example, in 69 days of daily observations of a specimen of *L. siliquoidea* (maintained in an aquarium at naturally fluctuating temperature and light conditions), intermittent flapping activity was recorded during 52 days.

c. A flapping day. *L. siliquoidea*, unlike *L. ventricosa*, may often start or stop flapping activity several times a day. In a series of recorded observations (Table 12) the start-stop pattern was noted on 43 out of 52 days (or 84.6% of the time during which flapping was observed). Such a pattern was seen less than 50% of the time in similar series of observations on *L. ventricosa* (Tables 13 and 14).

Flapping activity in *L. siliquoidea* occurred much less often in the morning than in the mid-afternoon (2-5 p.m.) or late evening from 10-11 p.m. (see Fig. 29).[22] Characteristics of a flapping day for *L. siliquoidea* as contrasted with *L. ventricosa* are summarized in Table 15. Table 16 presents a few records of occasions on which I timed an animal's flapping frequency for 10 consecutive minutes in very dim light and for a like period in bright light.

Flaps and Flapping Behavior in *Lampsilis brevicula brittsi*[23]

1. Flapping position and gross flap morphology

L. brevicula brittsi is a small, thin-shelled species. Externally the flap is little (2.5 cm long in a specimen 6 cm long), dark gray, has inconspicuous eyespot and an elaborate tail which has a number of tentacles and a prominent pigment spot (Fig. 30). Marsupia protrude between the flaps, their dorsalmost edges scalloped, uneven (not smooth as in *L. ventricosa*). Flapping position is less than a headstand (i.e., rotated only by 45° - 75° instead of 90°) and the animal is typically dug deeper into the

[22]Late evening observations were made by means of a 25-Watt red bulb or with a penlight. Of 130 recorded observations between midnight and noon, flapping was noted 50 times (31%). Of 260 observations made between noon and midnight, flapping was observed 146 times (56%). As regards observations made on 39 days between 10-11 p.m., the animal was flapping vigorously 66.6% of the time.

[23]Flap movements of this species were observed through spring and summer of 1964 only, whereas flapping individuals of *L. ventricosa* were alanyzed through 4 seasons, and those of *L. siliquoidea* through 3 seasons.

*General conditions of the experiments which are summarized in Table 8.

a. Water temperature 19°C throughout.

b. Length of experimental periods was limited naturally: at high light intensities, though without measurable increase in water temperature, prolonged exposure would bring about pause in regular flap movements, then fluttering movements, finally a halt. At low light intensities, moves slowed to negligible rate. Movements were considered to have stopped if there was a pause longer than 10 minutes between movements.

c. Experiments were all conducted at night, to control light conditions. Animal could not be moved to a darkroom because of its sensitivity to "jarring"; such a move might have stopped its flap movements, which may then not have been resumed for days.

d. The number of counts made (time for 30 moves) was large because the animal's response to altered light intensities by marsupial movements is often accompanied by alteration in flapping.

e. Observations concern a single animal because, even with 8-10 mature females kept, there was seldom more than one animal flapping for long periods. This same animal's flapping behavior, when not exposed to artificial illumination constituted the control. Movements in the darkness were observed with a red 25-Watt safelight.

TABLE 9. Average flapping frequency* of a specimen of *Lampsilis ventricosa* at various light intensities

Experiment no.	Light intensity (in foot candles)															
	22.5	16.5	12.2	10.0	8.5	7.4	5.7	5.4	3.7	2.3	2.0	1.7	1.3	1.0	.8	.6	.3
1					25.0 ← 26.3 → 24.6	114.6 36.8	→ 24.7		→ 25.2	→ 27.2	→ 30.1						
2											32.4 ← 34.4 → 34.9	53.0	→	94.5	→	292.6	
3																568.0	→ 1728.1
4				104.0 140.2													
5	33.2 25.1 → 24.5 → 24.2 ← 24.4 → 25.3		23.7 ← 24.1		→ 25.5 ← 26.7		→ 24.8 ← 25.0 → 25.4		→ 26.5	→ 28.4					→ 92.2		
6	28.1 ← 26.9 → 36.9		← 27.8		← 27.0		← 27.1 → 38.3		← 40.4 → 33.8	← 50.2		← 104.6			52.3 2178.3 ← 255.6 → 171.0		
7									279.3	← 110.9		← 201.6			← 572.2		
8	58.7 ← 89.6	33.0 ←	33.3 ← 427.7		← 30.6		← 30.8		← 29.9	← 47.6							

*Frequency is expressed as average duration of 30 movements; time is expressed in seconds, the numbers are averages from up to 20 consecutive counts of 30 moves each.

Arrows indicate whether a particular frequency followed an increment (←) or a decrement (→) of light.

TABLE 10. Comparison of flapping position and gross flap morphology in *Lampsilis siliquoidea* and *L. ventricosa*

Flapping feature	*L. siliquoidea*	*L. ventricosa*
Position		
valves:	typically not a headstand; animal usually tilted (i.e., rotated forward) at 45° angle. (Figs. 27, 28)	typically a headstand, especially at higher flapping frequencies. Animal tilted (rotated anteriorly) at 90° angle to substrate. Foot serves as prop. (Fig. 2)
branchial siphon:	edges often held horizontally	edges not often held horizontally
marsupia:	do not protrude prominently between the flaps	do protrude prominently between the flaps, especially later in flapping season, at time of regular moves with high flapping frequency, and at times of very "slow" flap movements; marsupia may move up and down with changes in light intensity
Appearance (in flapping animal)		
tail:	long, broad, prominently fringed with many basal tentacles	truncated, with few or no basal tentacles
eyespot:	raised, dark, not prominent on external surface of flap; visible though smaller on internal surface	prominent, often raised, dark, and surrounded by white ring; not visible on internal surface of flap
outer flap surface:	often dark, reddish brown, with rows of dark brown spots. Prominent dark spots near tail base and on tail	uniform, medium-light gray; not spotted. Line of pigment on inner surface shows through
inner flap surface:	a rosy peach, especially in tail region of flap. Line of pigment, extending from eyespot to tail, may be present	pale gold to pink, with prominent black line of pigment extending from just behind area corresponding to exterior location of eyespot to tail tip

substrate.

2. Flap movements

They resemble those of *L. siliquoidea*, beginning as a pair of pulses at the base of the flap tails, moving simultaneously toward the eyespots, causing the eyespot portions of the flaps to turn laterally. Recovery stroke brings first the eyespot ends, then the rest of the flaps together in apposition once more.

Movements occur in groups of 2 or more, the flaps moving at slightly higher frequencies than those of *L. siliquoidea*.

TABLE 11. Comparison of spontaneous "regular" flap movements with mechanically induced movements in *Lampsilis siliquoidea*

Spontaneous movements	Mechanically induced movements
normal flap movements as described for *L. ventricosa*	the same aspect for individual move
preceded by twitching of basal tentacles	not so preceded
occur typically in pairs (less often triple, rarely single moves)	are single
--	produced in response to jarring of substrate or to local water waves
--	provokable in absence of spontaneous flapping

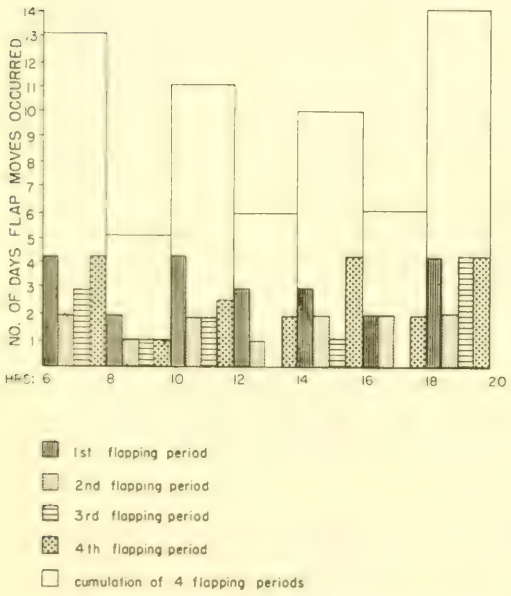

FIG. 29. Diurnal flapping activity in *Lampsilis siliquoidea*.

Flap movements may be mechanically induced in *L. brevicula brittsi*, as they are in *L. siliquoidea*. The fortuitous observation described below indicates how flap movements induced mechanically (e.g., by water waves) may facilitate mantle flap activity by *L. brevicula brittsi*.

On August 11, 1964, a specimen of *L. brevicula brittsi* had come to a position not more than 5 cm away from a specimen of *L. siliquoidea*, in one of my aquaria. At 11:00 a.m., both animals were exhibiting flap movements, almost flap-tail to flap-tail.[24] The very regular alternation of movements, first by one animal then the other, caused me to time several flapping sequences of the 2 animals (Table 17).

L. brevicula brittsi maintained a flapping frequency about twice that of *L. siliquoidea* throughout. Neither the characteristic twitching of the basal tentacles which precedes spontaneous flapping in *L. siliquoidea*, nor the typical paired movements were observed at that time. It seemed probable that the movements of *L. siliquoidea* were being mechanically stimulated by the movements (local water waves) of *L. brevicula brittsi* nearby. *L. brevicula brittsi*, in turn, may have been responding at least

[24] Two mature female specimens of *Lampsilis ventricosa*, at the opposite end of the same aquarium, exhibited no flap movements at that time.

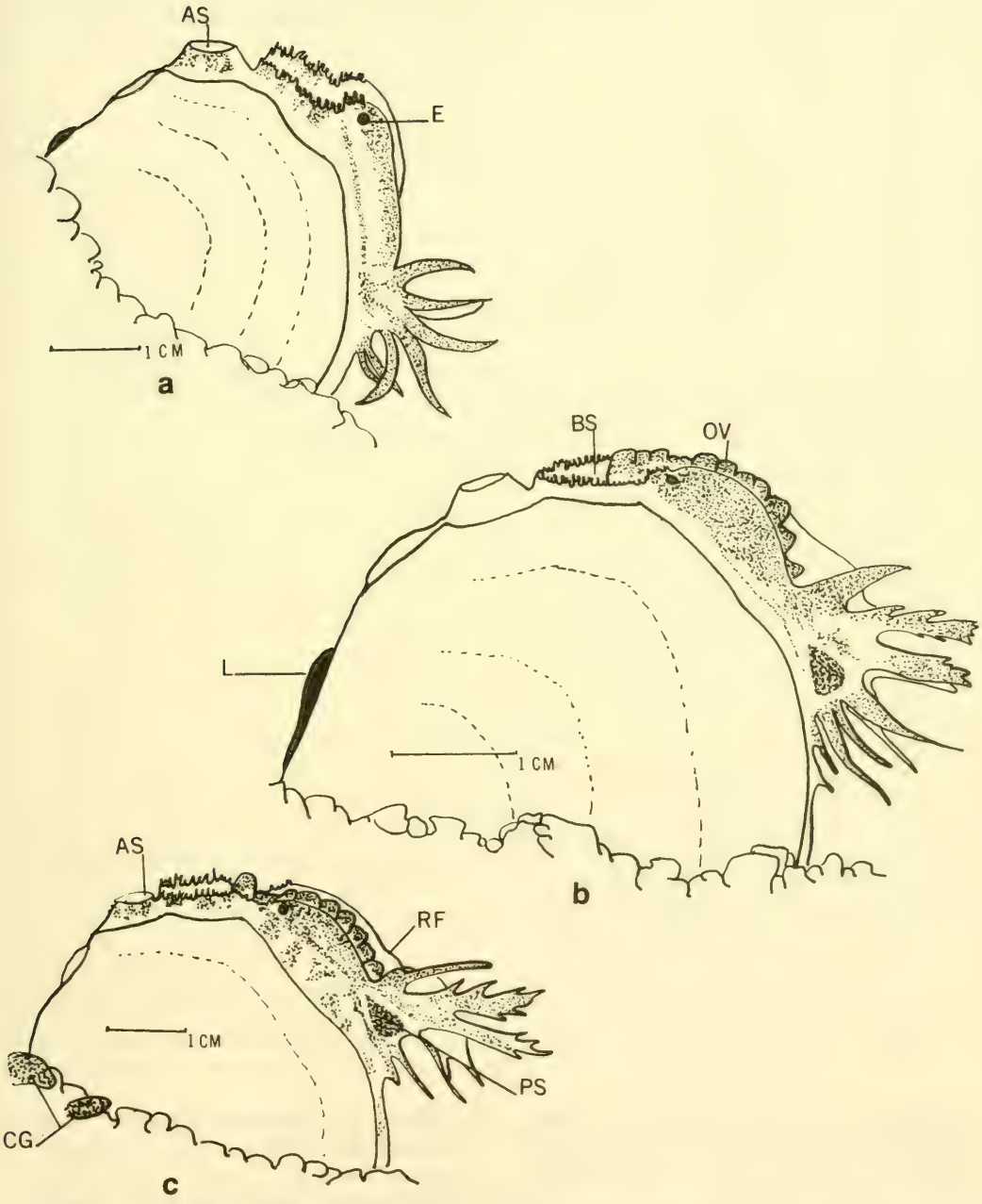

FIG. 30. Various flapping positions in *Lampsilis brevicula brittsi*. Specimen collected from War Eagle Creek, Washington County, Arkansas, on July 5, 1964. Sketched: a, August 4, at 7:00 a.m.; b, August 5, at 6:30 a.m.; c, August 1, at 11:00 a.m.

TABLE 12. Diurnal flapping activity of a specimen of *Lampsilis siliquoidea* at seasonal fluctuating temperatures and natural light[X], from April 25 to July 2, 1963

Date (1963)	Hour of the day																							
	24	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
4/25																					*			
26							*														*		*	
27						*																*	*	
28														*		*	*			*			*	
29																				*			*	
30																				*		*	*	
5/ 1																								
2																								
3																	*	*						
4													*		*			*	*			*		
5														*	*	*	*			*	*		*	
6																	*	*	*		*		*	
7					*																			
8																				*			*	
9			*				*	*					*		*			*						
10													*			*		*		*				*
11																					*		*	
12																		*			*		*	
13						*	*	*												*	*		*	
14																*								
15																								
16																								
17																							*	
18																								
19																								
20																								
21																								
22																								
23																						*		
24																								
25							*	*	*	*		*	*								*	*		*
26									*			*		*		*				*			*	
27														*			*			*			*	
28																				*		*		
29																				*			*	
30																		*				*		*
31						*							*											
6/ 1														*									*	
2																			*				*	
3									*		*		*											

part of the time to the movements of its neighbor. The animals did not then seem to be maintaining independent spontaneous mantle flap rhythms.[25]

3. Time of flapping activity of *L. brevicula brittsi*

The flapping season lasts through the

[25]This behavior continued through the day. Another series of 20 minute-count trials was made beginning at 10:30 p.m. on the same date, with results much the same as those recorded in Table 17.

Table 12. (Contd.)

Date (1963)	Hour of the day																							
	24	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
6/ 4	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´
5	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´
6	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´
7	´	´	´	´	´	´	´	´	´	´	´	´	*	*	´	´	*	´	*	´	*	´	*	´
8	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	*	´	´
9	´	´	´	´	´	*	´	´	´	´	´	´	´	´	´	´	´	´	´	*	´	´	*	´
10	´	´	´	´	´	*	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´
11	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´
12	´	´	´	´	´	*	*	*	*	´	´	´	´	*	´	´	*	*	´	´	*	´	*	´
13	´	´	´	´	*	´	*	*	*	´	´	´	*	´	*	´	´	´	*	´	*	´	*	´
14	´	´	´	´	´	*	´	*	´	´	´	´	´	*	*	´	*	´	´	´	*	´	*	´
15	´	´	´	´	´	*	´	*	´	´	´	´	´	´	´	´	´	´	´	´	´	´	*	*
16	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´
17	´	´	´	´	´	´	´	´	´	´	´	´	´	*	´	*	´	´	´	*	´	´	*	´
18	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´
19	´	´	´	´	´	*	´	´	´	´	´	´	´	´	*	´	*	´	*	*	´	´	*	´
20	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	*	´	´	´	´	´	´	´
21	´	´	´	´	´	´	´	*	´	´	´	´	*	´	´	*	´	*	´	*	*	´	*	´
22	´	´	´	´	´	´	*	*	*	´	*	´	´	´	´	´	´	´	´	´	´	´	´	´
23	´	´	´	´	´	´	´	´	´	´	´	´	´	*	´	*	*	´	´	´	´	´	´	´
24	´	´	´	´	´	´	´	´	´	´	´	´	*	´	´	*	´	*	´	*	*	´	*	´
25	´	´	´	´	´	´	´	´	´	´	´	´	´	´	*	´	´	´	*	´	´	*	´	´
26	´	´	´	´	´	*	´	´	´	´	´	´	´	´	*	´	´	*	´	´	*	´	´	´
27	´	´	´	´	´	´	´	´	´	´	´	´	*	´	´	´	*	´	´	*	´	*	´	´
28	´	´	´	´	´	´	*	´	´	*	´	*	´	´	´	´	´	*	´	´	´	*	´	´
29	´	´	´	´	´	*	´	´	´	´	´	´	*	´	´	*	´	*	´	´	´	´	*	´
30	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´	´
7/ 1	´	´	´	´	´	*	´	´	*	´	*	´	´	´	´	´	´	´	´	´	´	´	´	´
2	´	´	´	´	´	´	´	´	´	´	´	´	*	´	´	´	´	´	´	´	´	´	´	´
Summary																								
Flapping	0	0	1	0	2	12	10	10	7	3	3	3	13	10	8	10	12	13	7	16	15	12	26	4
Not flapping	1	0	1	2	1	10	30	9	10	6	7	4	16	10	6	6	9	9	12	6	13	12	13	2
Total	1	0	2	2	3	22	40	19	17	9	10	7	29	20	14	16	21	22	19	22	28	24	39	6

´ = No flapping occurred.

* = Flap movements occurred.

x = After dark observations were made with a small penlight.

spring and summer months. For a single specimen my earliest record of flapping activity was June 5, and the latest, September 3. There is not enough information at the present time for meaningful comparisons of eventual "flapping periods" of *L. brevicula brittsi* with those of other species. Specimens of *L. brevicula brittsi*, like *L. siliquoidea*, however, are capable of vigorous flapping in the dark (as seen with a 25-Watt safelight).

A Note on Flaps and Flapping Behavior in *Lampsilis fasciola* Rafinesque

L. fasciola is of interest, because, as H. & A. van der Schalie (1963) have

TABLE 13. Diurnal flapping activity[x] of a specimen of *Lampsilis ventricosa* maintained at seasonal, fluctuating temperatures, from June 29 to September 11, 1964, with some observations in artificial light

Date (1964)	Hour of the day																		
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
6/29														*					
7/ 3			*																
8					*											*			#
9		*	*	*	*	*	*	*	*	*	*	*	*	*	*				
10																			#
11	´	´	´																
12	´																		
13		´																	
14-22																			
23					*														
26											*								
28		*																	
29		´																	
30		´																	
31		´																	
8/ 1		´																	
2			*	*	*	*	*	*	*	*	*	*	*	*	´	´			
4		*	*	*	*	*	*	*	*	*	*	*	*	*	´	#			´ #
5	*	*													´ #	# ´		´	
7		´																	
8		´																	
9		´																	
10		´																	
11		´																	
15				*	*	*	*	*		*					´ #	#			
16				*	*	*	*	*	*				*	´	´				
17		*																	
18		´																	
19		*						´											
28			*	*															
31		*	*																
9/ 1			*				*	*	*	*	*	*	*						
2		*	*	*	*	*	*	*	*	*	*	*							
3																#			
10								(conglutinates shed)											
11								(conglutinates shed)											

[x]No observations were made between midnight and 5 a. m.

*Flap movements occurred, in natural light (after dark observations were made with a small penlight).

´Flap movements did not occur, in natural light.

[+] The same animal as that used in the previous light experiments.

[x] No observations were made between midnight and 6 a. m.

* Flap movements occurred, in natural light (after dark, checks were made with 25-Watt red safelight).

´ No flap movements occurred, in natural light (after dark, checks were made with 25-Watt red safelight).

Flap movements occurred, in artificial light (incandescent bulb, at different light intensities).

IR Flap movements occurred, in dim natural light plus artificial infra-red source. These preliminary studies with infra-red light were insufficient to yield conclusive results.

TABLE 14. Flapping activity of a specimen of *Lampsilis ventricosa*[+] maintained at 19° C under varying conditions of light, from July 2 to August 24, 1965[X]

Date (1965)	Hour of the day																	
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
7/ 2																	*	
3					´		´			´	´	´						
5									´	´	´							
6					´				´						´	´		
8					*				*	*	*	*	*	*	*	*	*	
9	´	*		*				*	*				*	´	´			
10	*				*	*								*				´#
11		*			*	*			*	*	´			´	´	´	´	
12	*		*	´	*	´	´			´	´			*		´	´	
13	´	´		´					´				´					
14		´		´		´	´			´	´					´		
15		´		´	´		´						´		´			
16		´						´	´				´					
17		´			´	´	´	´						´				
18		´							´									
19	´				´		´						´					
20		´			´	´	´						´					
21		´			´	´	´							´	´			
22		´		´	´	´	´						´	´	´			
23		´			´	´	´			´	´			´	´			
24		´								´		´						
25			´											´#	#	#	#	
26	´			´						´				´	´	´		
27		*		*	*	*			*	*	*	*		´	´			
28	´				´						´	´		*	#	#	#	#
29	*				*	*	*			*	*	*		*	#	#	#	
30	´		´		´	´	´				´			´				
31	´				´	´	´				´			´	´	#	#	#
8/ 1		*			*					*					*	#	#	
2	*			*	IR	IR	IR	IR	IR	IR			*´					
3	*			*	*	*	*	*	*	*	*		*					
4	´			´						´	*			*	#	#		
5	´									´				´				
6	´			´					´					´				
7	´						´						´					
8	´				´	´	´							´	´			
9	´						´				´			´	´	´	´	
10		´			´	´				´				´	´	´	´	´
11		´								´							´	
12		´						´		*				*				
13		*			*	*	*	*	*	*	*	*		*	#	#	#	#
14		*		*	*	*	*		*	*	*	*		*	#	#	#	#
15		*			*	*	*		´	´	*		´					
16		´			´	´	´		´	´	´			*	#	#		
17		*		´		´	´		´	´	´	´		´	´	´		
18	´				´	´	´			´	´			´				
19	´					´							´					
20		´			´	´	´			´	´	´		´	´			
21		´			´	´				´	´			´	´	´	´	
22	´				´	´	´			´	´			´	´	´	´	
23	´																	
24	´				´	´	´			´	´				´			

TABLE 15. Characteristics of a flapping day for *Lampsilis siliquoidea* and for *L. ventricosa*

Flap activity	*L. siliquoidea*	*L. ventricosa*
Time of onset	any time of day	often at dawn
Pattern through daylight hours	starts, stops, starts; often 3 or more times a day	starts, speeds up flap movements at dawn, flaps through day, slows down or stops at dusk
Pattern after dark	may show more vigorous flap moves (especially from 10-11 p.m.) than in daylight	if flapping, moves are of slow pattern
Response to experimental light conditions	no consistent definite responses noted*	consistently, at low illuminations flapping frequency slows in response to light decrements and speeds up with light increments

*Limited experimental efforts only were made to check the effect of various light intensities on flap movements of *L. siliquoidea* (see Table 16).

pointed out, it has a curiously circumscribed distribution in some areas of Michigan. This species exhibits fairly rapid, regular mantle flap movements. I had the opportunity to observe a number of *L. fasciola* in the River Raisin, upstream from Sharon Hollow, Washtenaw County, Michigan (see also footnote 40), in August, 1962. The 9 flapping females seen at that time were all clearly visible in the main channel at water depths from 1.5 to 2 feet. Movements of their flaps were such that all must have been in a headstand position. The movements were rapid and regular. In appearance, the flaps (Figs. 5c, d) are similar to those of *L. siliquoidea* (Figs. 27, 28), with elaborate pigmentation and many basal tentacles.

DISCUSSION AND CONCLUSIONS

In the course of this study, it has been found that:

(1) Mantle flaps in *Lampsilis ventricosa*, *L. siliquoidea*, *L. brevicula brittsi* and *L. fasciola* have common structural features:[26] (a) all are extensions of the third or inner lobe of the posterior mantle edge anteroventrad to the branchial siphon; (b) all possess the same general configuration with a pigmented spot (the eyespot) just posterior to the branchial siphon, and a free-hanging tail; (c) pigmentation of the external flap surface is generally more elaborate and always different from that of the internal surface; (d) innervation of the mantle flaps (examined in *L. ventricosa* and

[26]These morphological characteristics are found also in *Lampsilis cariosa*, of which a number of preserved specimens were examined for this study.

TABLE 16. Flapping frequency averages (average No. of moves/min. for 10 min.) in dim light and in bright (incandescent) light for *Lampsilis siliquoidea*

Date: April 1964	Time P. M.	Frequencies/min.	
		dim light	bright light
26	8:30	4.4	5.3
27	9:15	6.1	1.3
	10:30	13.8	10.8
28	7:30	5.1	5.4
29	7:10	3.5	3.5
30	7:15	1.1	0.8
	9:30	2.2	2.3

L. fasciola) is by way of branches of pallial nerves extending from the visceral ganglion.

(2) Mantle flaps in the above species differ morphologically in (a) external pigmentation, which may be a uniform gray (*L. ventricosa*), or heavily spotted (*L. siliquoidea*, *L. brevicula brittsi* and *L. fasciola*); (b) development of the tail, which may be truncated and slender, as in *L. ventricosa*, or broad and elaborately fringed with tentacles, as in the other 3 species; (c) appearance of the eyespot, which may be prominent, ringed with white, and confined to the external flap surface (*L. ventricosa*), or inconspicuous and visible on external and internal flap surfaces (as in the other 3 species).

(3) Flap movements as studied in *L. ventricosa*, *L. siliquoidea* and *L. brevicula brittsi* all comprise (a) paired pulses which are initiated as contractions at each tail base and move toward the eyespot ends of the flaps; and (b) a recovery phase in which the flaps assume their former position, often with tails floating free and horizontally in the water.

(4) Flapping behavior in the above 3 species is not limited to flap movements, but involves the coordinated function of many body structures, to such an extent that the supposed normal relationships between body and shell are much altered.

(5) Flapping involves different behavioral complexes in different species, e.g., headstand (upending by 90°), regular and slow flap movements, spontaneous marsupial movements, changes in flapping frequencies at dawn and dusk, and diurnal flapping pattern in *L. ventricosa* - contrasted with not so pronounced a headstand (forward rotation of 50°), regular double flap movements, no slow movements, no noticeable spontaneous marsupial movements, crepuscular to nocturnal flapping pattern in *L. siliquoidea*.

(6) Flapping behavior in these species involves different stimulus modalities, especially light for *L. ventricosa*, and water waves and jarring of substrate for *L. siliquoidea*.

(7) The special characteristics of flap movements in the species studied here, fit into the larger context of the total behavior repertoire of the non-flapping animal: (a) mantle movements independent of shell movements do exist in various bivalve genera (as found by Redfield, 1917, for *Mya*, *Modiolus*, *Mytilus*, *Solenomya*, *Ensis*, *Cumingia* and *Yoldia*); (b) extreme heel formation of the foot, in serving as a prop for some flapping lampsilids, can logically be viewed as an exaggeration of a phase of normal bivalve locomotion (the *Hakenform* and *Schwellform* of Fraenkel, 1927); (c) alterations of flapping frequency in response to alterations of light intensity show similarities to the animal's general skioptic (shadow) sense, which mediates siphon withdrawal in many bivalves; (d) marked response of extended or moving mantle flaps of mussels such as *L. siliquoidea* to jarring of substrate and to water waves is more difficult to identify although bivalves are notoriously sensitive to jar, the most widely observed response being siphon withdrawal and valve closure.

(8) Despite the fact that mantle flaps respond to different stimuli in different species and that flap movements can occur for a whole season previous to

TABLE 17. Sequence and number of flap movements during 20 1-min. periods for 2 specimens of *Lampsilis* whose moving flaps were approximately 5 cm apart; in aquarium, at natural temperatures. Trials started at 11:00 a.m. on August 11, 1964

Trial	Species*	Consecutive flap movements during 1 minute**	Total flap movements
1.	L.b.	/ / / / /	5
	L.s.	/ /	2
2.	L.b.	/ / / / / /	6
	L.s.	/ / /	3
3.	L.b.	/ / / / / /	6
	L.s.	/ / /	3
4.	L.b.	/ / / / / /	6
	L.s.	/ /	2
5.	L.b.	/ / / / / /	6
	L.s.	/ / /	3
6.	L.b.	/ / / / /	5
	L.s.	/ / / /	4
7.	L.b.	/ / / / / /	6
	L.s.	/ /	2
8.	L.b.	/ / / / / /	6
	L.s.	/ / /	3
9.	L.b.	/ / / / / / /	7
	L.s.	/ / / /	4
10.	L.b.	/ /	2
	L.s.	/ / /	3

spawning, they apparently do accompany spawning of glochidia in all species in which the movements have been observed. The foregoing statement is supported by the following evidence from this study: (a) flaps occur only in mature female specimens, whereas juveniles and males have flap rudiments; (b) flap movements have been seen only in gravid, never in non-gravid females (although not all gravid females maintained in aquaria for months showed flap movements); (c) flap movements have been seen in association with gradual emptying of the ovisacs and with shedding of conglutinates; (d) flap movements have not been observed after shedding of glochidia.

* * *

Grier (1926) and Welsh (1933) are the only previous investigators known to me to have undertaken experiments with flapping Lampsilinae. Grier contended he had induced increasing frequency of flap movements in a specimen of *Lampsilis ventricosa* by experimentally increasing water temperature. My own observations do not support his finding.

Welsh (1933) made a brief series of

Table 17. (contd.)

Trial	Species*	Consecutive flap movements during 1 minute**	Total flap movements
11.	L.b.	/ / / / / / /	7
	L.s.	/ / /	3
12.	L.b.	/ / / / /	5
	L.s.	/ / /	3
13.	L.b.	/ / / / /	5
	L.s.	/ / / /	4
14.	L.b.	/ / / / /	5
	L.s.	/ /	2
15.	L.b.	/ / / /	4
	L.s.	/ / /	3
16.	L.b.	/ / / / / /	6
	L.s.	/ /	2
17.	L.b.	/ / / / /	5
	L.s.	/ / /	3
18.	L.b.	/ / / / / /	6
	L.s.	/ /	2
19.	L.b.	/ / / / / /	6
	L.s.	/ / / /	4
20.	L.b.	/ / / / /	5
	L.s.	/ /	2

*L.b. = *Lampsilis brevicula brittsi*; L.s. = *Lampsilis siliquoidea*.

**/ = one flap movement.

determinations of the time required for 10 flap movements in a specimen of *Lampsilis nasuta* (*Ligumia nasuta*) over a range of 9 decreasing light intensities, as a consequence of which he observed (1933: 755) that ". . .light did play an important role in determing the frequency of these rhythmical contractions." Though his graph plotting frequency of flap moves against light intensity (here reproduced as Fig. 31) looks as though the animal had increased its frequency in response to increasing light intensity, it had in fact decreased its flapping frequency in response to decreasing light intensity, the data being arranged in inverse order. His numerical data (:755) are here reproduced (Fig. 32). Welsh found (:756) that the flapping rhythm of his specimen "was interrupted at low light intensities and ceased entirely [*sic*!] after a short exposure to an illumination of about 0.2 foot-candles." My own prolonged observations of *Lampsilis ventricosa* would indicate that *Ligumia nasuta* may actually possess a far more complex response to light than Welsh was able to discover

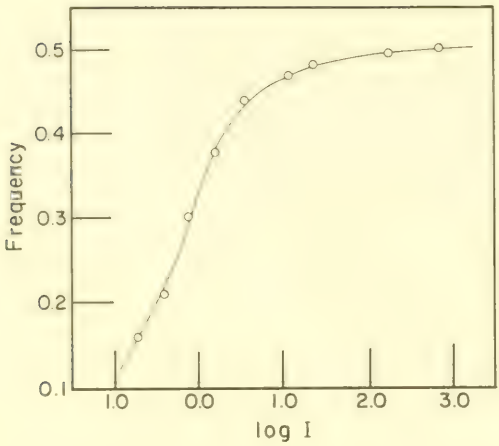

FIG. 31. Frequency of flapping in "*Lampsilis*" (= *Ligumia*) *nasuta* from Welsh (1933: 755-756. Note that exposure was in reverse order, i.e., with decreasing light intensity, as indicated by his explanation of the graph: "Plot of data showing frequency of movement (number of movements per second) of the mantle flaps of *Lampsilis nasuta* plotted against the logarithm of the light intensity. Observations were begun at the highest illumination."

from his more limited opportunity for study.

Two hypotheses have been advanced by other investigators concerning the probable functions of flapping in these animals. First, the speculation by Ortmann (1911) and others (e.g., Coker et al., 1921) who followed him, that the flap movements help to aerate the glochidia, and second, the hypothesis subscribed to by Coker et al. (1921), Howard & Anson (1922), and Welsh (1933), that the moving flaps are in effect mimicking minnows and serve as lures to host fish. The first hypothesis seems, in the light of the study presented here, to be qualifiedly plausible. Regular movements of *Lampsilis ventricosa* (carried on intermittently for several months during the summer) especially those at high frequencies, do appear to create a lively water current over the bulging marsupia, though the slow movements certainly do not. But in species such as *L. siliquoidea*, in which flapping movements are much slower, and the marsupia do not commonly protrude, the relation of flapping to gill or marsupial aeration would hardly seem to be of much consequence.

The second hypothesis is an intriguing idea, but it has many shortcomings. Admittedly, to the human observer watching rapid regular movements of an upended *L. ventricosa*, particularly on an eye-level with the eyespots of the flaps, the resemblance of the moving flaps to some small fish is striking. However, a flapping *Lampsilis ventricosa* exhibiting slow movements does not present a fish-like appearance, neither does a mussel such as *L. siliquoidea*, which does not characteristically assume a headstand, does not commonly protrude its marsupia (suggesting the rounded body of a fish), does not flap in a fish-like fashion, and does not have prominent eyespots.

It seems most plausible to reason that if host fishes are attracted to the flaps, it would be movements per se, rather than a fish-like appearance which might attract them. All of the species observed at length in this study (*L. ventricosa*, *L. siliquoidea*, *L. brevicula*), have been maintained from time to time with possible host fish such as the largemouth bass (*Micropterus salmoides*) and the black crappie (*Pomixis nigromaculatum*). The crappies upon occasion would make darting movements toward the tails of the moving flaps. At other times, a fish would loiter nearly motionless for hours in the vicinity of the tails of the moving flaps. If the fish were attracted by the flapping (though their presence always seemed merely fortuitous to me) the presence of the fish in the neighborhood of the moving flaps would insure their exposure to any glochidia discharged.

The differences between mussel species in flapping postures, appearance, optimal time of flapping activity [27] and

[27] Such differences might coincide with periods of activity of potential fish hosts, such as described by Davis (1962).

Times in Seconds for Ten Movements of the Mantle Flaps of Lampsilis with Their Averages, and the Frequency (Number of Movements per Second) at Each of Several Intensities of Illumination. Temp. 21.3°C.

Intensity (Foot-candles)	0.20	0.41	0.83	1.66	3.6	12.0	23.0	180.0	689.0
Time (secs.) for 10 movements	65.0	48.0	28.6	24.5	22.5	21.2	21.0	20.1	20.0
	61.0	46.8	30.5	25.8	22.3	20.9	20.8	20.1	20.0
	62.0	49.2	32.2	27.4	22.2	21.4	20.8	20.1	20.2
	63.5	48.6	35.2	26.6	22.1	21.5	20.6	20.1	20.4
	61.8	46.7	33.0	26.4	21.9	21.8	20.9	20.5	20.1
			32.5	27.6	22.6	21.5	20.9	20.2	19.7
			30.8	27.6	23.4	21.2	21.0	20.4	19.6
			35.0	27.4	23.6	21.5	20.6	19.9	19.8
			36.0	27.0	23.3	21.0	20.6	20.4	20.0
			38.0	25.6	23.6	21.2	21.2	20.1	19.8
Averages	62.66	47.86	33.18	26.59	22.75	21.32	20.84	20.19	19.96
Frequency	0.159	0.210	0.301	0.376	0.439	0.469	0.481	0.495	0.502

FIG. 32. Numerical data from Welsh (1933).

the manner in which they respond to environmental stimuli suggests possible adaptations (still in need of much study) to habits of peculiar fish-host species.[28]

I would like to suggest another explanation for the flapping movements of lampsilids. A simple if partial hypothesis for the flap movements may be suggested by the diagram (Fig. 33) here. It shows an aquarium which Lefevre & Curtis (1910) constructed for the purpose of infecting host-fish with glochidia. The tank has a cross-hatched arrangement of perforated connecting pipes on the bottom, which were fed by a vertical inlet pipe of similar diameter. The purpose of this apparatus was to prevent glochidia, when introduced into the tank, from settling helplessly on the bottom, and to keep them suspended in the water, so that they might more readily come into contact with fish-hosts already in the tank. Similarly, I suggest, the bellows-like movement created by the paired pulses of all flap movements, regardless of species or flapping frequency or regularity, would help the glochidia to remain suspended in the water for a period of time, and thus facilitate the vitally necessary contact with a host fish. Regrettably, I did not experiment with the adequacy of flap generated currents to sustain glochidia in a mid-water position. This certainly should be done.

Ancillary problems arising from this

[28]However, I am loathe to subscribe to anthropomorphic generalizations: what looks like fish to us need not necessarily do so to fish themselves. Further, empirical evidence - some almost paradoxical in the light of earlier hypotheses - should not be ignored. *L. ventricosa,* flapping at high speed in full sun in the stream or in the aquarium has never been observed in the course of this study to "attract" any local creatures, any more than any other piece of the scenery. Also, this animal flaps very slowly for long periods in the dark. Under such circumstances, the nature of the "attraction" for a fish-host would be difficult to imagine. *Lampsilis siliquoidea,* which flaps in a similar manner day and night (i.e., with its own characteristic slower but "regular" movements), responds quickly to any local water movement including the movement of a fish's fin by interrupting its regular flap movements, with no detectable response by the fish. *Lampsilis fasciola* studied for a week in the River Raisin, July, 1967 repeatedly ceased flapping movements in response to movements of fish or crayfish in the immediate vicinity of the flaps.

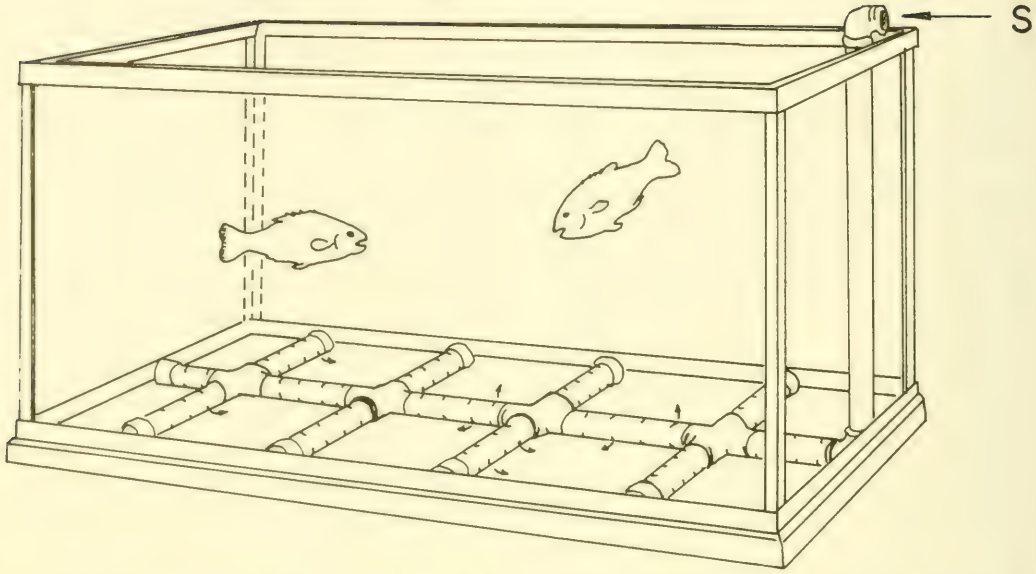

FIG. 33. Apparatus designed by Lefevre & Curtis (1910: 166) "for keeping glochidia suspended in water while fish are being exposed to them for gill infections." The force of the tap water entering at S and issuing in fine jets from perforations in the bottom grid is so regulated as to insure an even distribution of glochidia within the water, while preventing them from rising to the top and escaping with the overflow.

study fall into 2 groups, those related to mechanisms within flapping Lampsilinae, primarily, and those of broader taxonomic ramification such as species distribution, and fish-host relationships. In the first group would be included:

(a) The study of microscopic anatomy of the flaps, combined with neuroanatomical studies of the animal. Such studies, including a search for neurosecretory material, are in progress.

(b) Physiological studies of the mechanism whereby increasing light at low illuminations can increase or induce flapping behavior, and decreasing light at low illuminations can slow down or inhibit flapping behavior, as is the case in *L. ventricosa*. Particularly light (shadow) sensitive areas should be searched for in the mantle flaps and in neural entities such as the visceral ganglion or pallial nerve. Relationships between the siphonal shadow reflex and mantle flap response to altered light intensity might be investigated and measured in a single species. Careful efforts could be made to extract pigments (especially from eyespots of *L. ventricosa*) and perhaps to ascertain the reaction spectrum of the mantle flaps.[29]

(c) Neurosecretory substances known to control spawning in other organisms could be injected into the mussels, such as the "shedding substance" investigated by Chaet et al., (1964) from radial nerves of starfish, in order to determine whether flapping behavior could thus be induced in *Lampsilis*.

(d) The mechanism whereby some lampsilids alter their flapping behavior

[29]Conly-Dillon (1965: 346) in his work on spectral sensitivity of eyes of the scallop *Pecten maximus*, injects a word of caution into an analysis of his findings: ". . . the possibility is not excluded that other light-sensitive structures, perhaps located directly within the nervous system itself, may be contributing to the spectral sensitivity of the animal."

in response to jarring of substrate or to water waves, should be investigated, along with the relationship between this response and the general bivalve response to jarring.

In the second group would be included:

(a) Tests of the hypothesis that flap movements help to keep glochidia afloat, employing lighting techniques (Westphal, 1965) to make the glochidia visible, and devising means to collect larvae at varying distances above the flapping animal.

(b) Further field studies, perhaps on a species such as *Lampsilis fasciola*, for which some living material is still available.

(c) Systematic fish host studies, especially with a view toward matching the flapping behavior repertoire of a given species of *Lampsilis* (time of maximum flapping frequency, etc.) with the behavior of the fish species.

(d) Further comparative studies among the species here investigated (*Lampsilis ventricosa* was contrasted with *L. siliquoidea* and *L. brevicula brittsi*) and other Lampsilinae, to discover the parameters of relevant flapping stimuli within the subfamily as a whole.

There is urgency in making these studies because of the decline of mussel populations so often noted in American streams. The urgency is accentuated by the need for substantial numbers of experimental and sacrificial mussels if the experimental analyses are to be adequately replicated in well designed, statistically significant studies.

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RÉSUMÉ

LE VOILE PALLÉAL CHEZ 3 ESPÈCES DE LAMPSILIS (PELECYPODA, UNIONIDAE)

L. R. Kraemer

L'objet de cette étude est de passer en revue les bases morphologiques et d'activité générale des battements des voiles palléaux chez les unionides d'Amérique du Nord, de la sous-famille des Lampsilinae, et d'explorer expérimentalement certains facteurs qui peuvent compter pour cette activité frappante: les mollusques battant leurs voiles ressemblent à des poissons en train de nager. Les études morphologiques (principalement sur du matériel fixé de *Lampsilis ventricosa* et de *L. fasciola*) les études occasionnelles dans la nature (dans plusieurs régions du Nord-Ouest de l'Arkansas), et les études prolongées en aquarium sur *L. ventricosa*, *L. siliquoidea* et *L. brevicula brittsi* ont été menées de 1962 à 1965. On a trouvé que les voiles palléaux, qui sont une extension du bourrelet interne du bord du manteau antéroventral au siphon branchial, sont un fait permanent chez les femelles matures. Parmi les voiles de ces 3 expèces, il existe des similitudes de structure (présence de tâches "oculaires" pigmentées, innervation par les branches des nerfs palléaux en provenance du ganglion viscéral), aussi bien que des différences dans la forme et la pigmentation.

Les mouvements des 2 voiles débutent par des pulsations couplées qui produisent des contractions partant de la base des franges et se propagant vers l'extrêmité où se trouvent les tâches pigmentées. Il s'ensuit une phase de repos, pendant laquelle les voiles reprennent leur position initiale, avec les franges flottant horizontalement.

Le comportement du battement entraine aussi des fonctions coordonnées du pied, du marsupium, des valves et des siphons, à un point tel que les relations spatiales que l'on peut considérer comme normales entre le corps et la coquille, sont profondément altérées. Pour les différentes espèces, le battement nécessite différents types de comportements de même que différents stimuli adéquats (en particulier, intensité lumineuse pour *Lampsilis ventricosa* et agitation de l'eau et tremblement du substrat pour *L. siliquoidea*).

Le voile n'existe que chez les femelles matures, bien que les juvéniles et les mâles en aient des rudiments; les mouvements du voile n'ont été observés que chez les exemplaires gravides, jamais chez les non-gravides. Le battement se produit périodiquement tout au long des mois d'été et on l'a vu accompagner le vidage graduel des ovisacs et le rejet de larves glochidium conglutinées. Le battement n'a pas été observé après l'émission des larves.

Deux anciennes hypothèses concernant la fonction des mouvements du voile en mouvement agissant soit comme leurre pour les poissons qui sont les hôtes des larves glochidium, soit comme aérateurs des branchies et du marsupium, semblent maintenant n'être que partiellement plausibles. Compte-tenu des différences existantes dans l'aspect, dans la vitesse de battement et dans la réponse aux stimuli chez les diverses espèces, on pense pouvoir suggérer que ces différences sont des adaptations possibles aux modes de vie d'espèces particulières de poissons-hôtes. Le mouvement de soufflet, créé par des pulsations couplées pour tout battement du voile, quelles que soit les espèces et la fréquence de battement, pourrait aider les larves glochidium à demeurer en suspension dans l'eau pendant un certain temps et ainsi leur faciliter le contact vital nécessaire avec un poisson-hôte.

A. L.

RESUMEN

EL REPLIEGUE PALEAL EN LAS ESPECIES DE *LAMPSILIS* (PELECYPODA: UNIONIDAE)

L. R. Kraemer

El propósito de este estudio fué revisar las bases morfológicas y de actividad general del repliegue y aleteo del manto en las especies norteamericanas de uniónidos de la subfamilia Lampsilinae, y explorar experimentalmente algunos factores que pueden contarse en esa actividad: el aleteo del manto simula un pequeño pez nadando. Estudios morfológicos, (principalmente de material conservado de *Lampsilis ventricosa* y *L. fasciola*), estudios ocasionales en el campo (en algunos condados del noroeste de Arkansas), y prolongados estudios en acuarios sobre individuos vivos de *L. ventricosa*, *L. siliquoidea* y *L. brevicauda brittsi*, se realizaron desde 1962 a 1965. Se comprobó que los repliegues alígeros del manto, que son una expansión del lóbulo interno del borde paleal anteroventral al sifón, constituyen un caracter permanente de las hembras maduras. Entre los repliegues de las 3 mencionadas especies existen similaridades estructurales (presencia de manchas oculares, ramificación de nervaduras paleales del ganglio visceral) así como diferencias en forma y pigmentación.

El aleteo se inicia en pulsaciones pares que producen contracciones, empezando en lo que correspondería a una base caudal y moviéndose hacia la terminación del repliegue con manchas oculares. Sigue una fase de reposo, en la que el repliegue asume su posición anterior, con la cola flotando horizontalmente.

El comportamiento envuelve también la función coordinada del pie, marsupia, valvas y sifones en forma tal que las supuestas relaciones espaciales normales entre el cuerpo y la concha estan muy alteradas. En diferentes especies el aleteo implica diferentes complejos de comportamiento, así como tambien los diferentes estímulos pertinentes (en particular intensidad luminosa para *Lampsilis ventricosa*, y sacudidas del substrato por los movimientos del agua en *L. siliquoidea*).

Los repliegues aparecen solamente en ejemplares de hembras maduras, aunque las juveniles y los machos presentan rudimentos; los movimientos del repliegue se han observado sólo en la hembras grávidas, nunca en las no grávidas. El aleteo ocurre por turnos periódicos durante el verano y se ha visto que acompañan la descarga gradual de los ovisacos y el derrame de conglutinados. No se observaron después de la liberación de las gloquidias.

Dos previas hipótesis concerniente a la función de estos movimientos del repliegue paleal de los Lampsilinae, que indicaban ser ya un cebo para peces que hospedan las gloquidias, o un sistema ventilador para las bránquias y marsupia, sólo en parte parecen ser verosímiles. Las diferencias en aspecto, velocidad de aleteo, y respuesta a los estímulos ambientales en diferentes especies, sugiere posible adaptaciones a los hábitos de las especies particulares de peces huéspedes. Los movimientos como de fuelle que se crean en las pulsaciones de los repliegues del manto, sin tener en cuenta especies o frecuencia del aleteo, podrían ayudar a la gloquidia a permanecer suspendida en el agua por cierto tiempo, facilitando así el contacto vital necesario con el pez hospedador.

J. J. P.

АБСТРАКТ

МАНТИЙНЫЙ КЛАПАН У ТРЕХ ВИДОВ *LAMPSILLIS* (PELECYPODA: UNIONIDAE)

ЛУИЗА Р. КРЕМЕР

В настоящей статье дается обзор морфологии и деятельности мантийного клапана у северо-американских унионид из семейства Lamsilinae, а также приводятся данные экспериментального исследования некоторых факторов, которые могут объяснить эту интересную активность. Движение мантийного клапана несколько напоминает небольших плавающих рыбок.

Морфологические исследования (главным образом на фиксированном материале по *Lampsilis ventricosa* и *L. fasciola*), случайные полевые наблюдения (в некоторых районах северо-западного Арканзаса) и длительное аквариальное изучение живых *L. ventricosa, L. siliquoidea* и *L. brevicula brittsi* проводились в период с 1962 по 1965 гг.

Было найдено, что мантийные клапаны моллюсков, которые представляют собой выросты внутренней лопасти края их мантии и находятся антеро-вентрально от бронхиального сифона, всегда имеются у половозрелых самок. Среди клапанов указанных выше моллюсков, существуют как структурное сходство (наличие глазных пятен, иннервация ветвями мантийных нервов, отходящих от висцерального ганглия), так и различия (в общей форме и пигментации).

Движения этих клапанов вызываются парной пульсацией, благодаря их сокращениям, которые начинаются с их хвостовой части и идут вперед, к тем концам клапанов, где имеются глазные пятна. Затем следует обратная фаза, когда клапаны приходят в исходное положение, и концы их располагаются горизонтально.

Работа клапанов включает также координированные движения ноги, марзупиев, створок и сифонов, в той степени, в какой предполагаемое нормальное пространственное отношение между телом и раковиной наиболее выгодно. Для различных видов колебания клапанов связаны как с различными поведенческими комплексами у моллюсков, так и стимулами из внешней среды (особенно таких, как интенсивность света для *Lampsilis ventricosa* и движение воды или вибрация субстрата для *L. siliquoidea*).

Клапаны развиваются только у половозрелых самок, в то время как у молоди и у самцов бывают только их рудименты. Движения клапанов наблюдаются только у беременных самок. Движение клапанов может происходить длительно в течение всех летних месяцев и сопровождаться постепенным опорожнением яйцевых сумок и высеванием конглютинатов. После выхода глохидиев движение клапанов прекращается. Ранее высказанные гипотезы, относительно роли движения клапанов у Lampsilinae, видимо, справедливы лишь отчасти. Так, считалось, что движение клапанов служит "приманкой" для рыб-хозяев глохидиев и что это движение служит для аэрации жабр и марзупиев. Различие в скорости движения клапанов и в отношении к факторам среды у различных видов моллюсков предполагает возможность существования адаптаций жизнедеятельности моллюсков к особенностям образа жизни различных рыб-хозяев.

Движения, напоминающие работу мехов для раздувания, обусловленные парной пульсацией всего аппарата клапанов (вне зависимости от вида моллюска или от частоты колебаний клапанов), может помогать глохидиям оставаться в течение некоторого времени в воде во взвешенном состоянии и таким образом облегчать жизненноважную для них возможность контакта с рыбами-хозяевами.

Z. A. F.

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THE NEW ZEALAND SPECIES OF *POTAMOPYRGUS* (GASTROPODA: HYDROBIIDAE)

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ABSTRACT

In his revision of the genus, Suter (1905) recognized 6 species and 3 subspecies of *Potamopyrgus* from the 2 main islands of New Zealand, but the present study has shown that only 3 species exist. They are *P. antipodarum* (Gray, 1843), *P. pupoides* Hutton, 1882, and a previously unrecognized species **P. estuarinus** n. sp.

Potamopyrgus estuarinus and *P. pupoides* are oviparous, possess smooth, unornamented shells and are confined to brackish water, whereas *P. antipodarum* is ovoviviparous, highly variable in shell size, shape and ornamentation, and inhabits both fresh and brackish water. Populations of *P. antipodarum* may consist entirely of parthenogenetic females or contain varying numbers of sexually functional males. Rearing of *P. antipodarum* in the laboratory has shown that snails do not necessarily breed true with respect to shell ornamentation, and that shell shape and ornamentation are not controlled primarily by environmental factors. The shell of *P. estuarinus* is indistinguishable from shells of some *P. antipodarum*, but *P. pupoides* is easily recognized by its small, pupiform shell.

The radula, operculum, external morphology, body pigmentation and male reproductive system are similar in all species and do not provide useful taxonomic characters. In *Potamopyrgus antipodarum* the lower section of the female reproductive system is modified to form a brood pouch with the open sperm groove running along its floor. In *P. estuarinus* and *P. pupoides* the lower reproductive tract is dominated by the strongly developed capsule gland which is physically separated from the spermathecal duct below.

The diploid chromosome number of all 3 species is 24.

Ion-exchange chromatography of shell periostracal protein has disclosed no significant differences in amino acid composition between species, but considerable intraspecific variation is found.

Potamopyrgus antipodarum is abundant in permanent freshwaters of all kinds and has been found in water up to 26‰ salinity, although experimental work indicates that it is active only in water below 17·5‰ salinity. No clear relationship between shell morphology and type of habitat has been found. *P. estuarinus* is most abundant in tidal estuaries where considerable fluctuations in salinity are found, and where many snails are regularly exposed to the air for part of each tide cycle. *P. pupoides* occupies a similar habitat, but normally remains fully aquatic at all times. In the laboratory *P. estuarinus* and *P. pupoides* remained active at all salinities from fresh to sea water, but they have not been found in fresh water in the field.

Laboratory experiments have shown the existence of behavioural differences between species, which are associated with the different habitats occupied by them. *Potamopyrgus estuarinus* shows pronounced amphibious tendencies not found in *P. antipodarum* and was able to survive in a " dormant " state when exposed to the air for up to 70 days.

The *Potamopyrgus antipodarum* complex is examined in the light of current concepts of the species, and the high degree of variability found in this species is associated with

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the occurrences of ovoviviparity and parthenogenesis which allow a high degree of divergent evolution to occur independently in individual populations.

A comparison between *Potamopyrgus antipodarum* and the European species *P. jenkinsi* (Smith) shows that the 2 cannot be distinguished on anatomical grounds, and many features of their biology and ecology are similar. It therefore seems probable that the 2 are the same species, the European snails having been introduced from New Zealand (or Australia ?) in the 19th century.

INTRODUCTION

Two genera of Hydrobiidae, *Potamopyrgus* Stimpson 1865 and *Opacuincola* Ponder 1966 are recognised from New Zealand, the latter containing a single, recently discovered subterranean species (Ponder, 1966). The genus *Potamopyrgus* was erected for the New Zealand species *Melania corolla* Gould 1874, and was separated from other hydrobiid genera primarily on the basis of radular structure. This study has confirmed the generic distinctness of *Potamopyrgus*, but its relationships to other hydrobiid genera remain unclear. Taylor (1966) has suggested it may belong in his subfamily Littoridininae in which he places *Pyrgophorus* Ancey 1888, the other genus containing ovoviviparous, spiny-shelled snails, although differences in the verge of *Potamopyrgus* suggest that it is not close to the American hydrobiids familiar to him.

In 1882, Hutton assigned all the known New Zealand Hydrobiidae to *Potamopyrgus*, and in the most recent revision of the genus, Suter (1905) recognised 6 species and 3 subspecies, which he distinguished primarily on shell characters.

Suter's (1905) revision has remained the definitive systematic work on *Potamopyrgus* in New Zealand, but it is now clear that there is much greater variation in shell characteristics than was recognised by him. A thorough investigation of the systematics of *Potamopyrgus* in New Zealand has therefore been undertaken.

Snails were collected from 128 localities throughout the 2 main islands of New Zealand, and selected morphological, reproductive and biochemical factors, as well as environmental relationships have been examined.[2]

As a result of this study it is concluded that only 3 species can be recognised on the 2 main islands of New Zealand. In addition, 2 species, *Potamopyrgus dawbini* Powell 1955 and (?) *P. melvilli* (Hedley, 1916) have been described from the Auckland and Kermadec Islands respectively, and species probably referable to *Potamopyrgus* are found in southern and eastern Australia (Williams, 1968). A single species, *P. jenkinsi* (Smith) is widely distributed in Britain and Europe, and was probably introduced from Australasia in the late 19th century (Boettger, 1951; and this paper).

North American species formerly referred to *Potamopyrgus* are now placed in other genera (Morrison, 1939; Taylor, 1966) but the true generic status of central African snails placed in *Potamopyrgus* by Pilsbry & Bequaert (1927) remains problematical.

REVISED DIAGNOSIS OF *POTAMOPYRGUS*

Potamopyrgus Stimpson 1865

Type (Monotypy): *Melania corolla* Gould, 1847

Shell dextral; height less than 12 mm; shape variable ovateconical-cylindrical; up to eight whorls, ventricose-flat sided,

[2] The raw data on which this account is based may be found in the appendices to a thesis by the author deposited in the Massey University Library, Palmerston North, New Zealand.

smooth with or without shouldering and/or periostracal spines; body whorl over half height of shell; imperforate; aperture ovoid, continuous (in fully grown shells). Operculum ovate, thin, corneous, subspiral, usually possessing a calcareous smear. Radula taenioglossan; central tooth trapezoidal, inferior margin nearly straight, faintly trilobate, basal cups close to lateral margins; lateral tooth denticulate, shank 2–3 times length of subrhomboidal body which possesses no basal peg; marginals finely serrate, long and slender, shanks straight, sharply curved at free ends; cusp formula $\frac{(3–5)\ 1\ (3–5)}{(2–5)\quad (2–5)}$: (7–13): (14–32): (21–48). Animal with long pointed tentacles. Reproduction sexual or parthenogenetic, ovoviviparous or oviparous. Males with long, narrow non-lobate penis containing a single duct, normally coiled beneath the mantle edge and attached to the head on right of middorsal line; vas deferens strongly coiled; prostate imbedded in visceral mass. Ovoviviparous females possess a thin walled brood pouch, with the sperm channel (=ventral channel) incorporated in its floor; oviparous females with the spermathecal duct separated from the accessory glands above, and probably functioning as the pallial oviduct. Habitat, fresh and brackish water.

Synonymy

Until further anatomical information is available the synonymy of other genera with *Potamopyrgus* must be considered tentative. Such genera may include *Austropyrgus* Cotton 1942 and *Fluviopupa* Pilsbry 1911.

DIAGNOSTIC CHARACTERS OF THE NEW ZEALAND SPECIES

Potamopyrgus antipodarum (Gray, 1843)

Amnicola antipodanum, Gray, 1843, *in* Dieffenbach, E., *Travels in New Zealand*, 2: 241 (New Zealand; British Museum).

Amnicola antipodarum, Gray, 1844, *Rev. Zool.*, 7: 356.

Hydrobia antipodum, von Martens, 1873, *Mal. Blätter*, 19: 14.

Hydrobia antipodum, Smith, 1875, *Zool. Voy. "Erebus" & "Terror"*, 2: 3.

Bythinella antipoda, Hutton, 1880, *Man. N.Z. Moll.*, p 81.

Potamopyrgus antipodum, Hutton, 1882, *Trans. N.Z. Inst.*, 14: 145.

Potamopyrgus antipodarum, Hedley & Suter, 1893, *Proc. Linn. Soc. N.S.W.*, 7: 619.

Potamopyrgus antipodum, Suter, 1893, *J. Conchyliol.*, 41: 221.

Potamopyrgus antipodum, Suter, 1905, *Trans. N.Z. Inst.*, 37: 263.

Potamopyrgus antipodum zelandiae (Gray, 1843), Suter, 1905, *Trans. N.Z. Inst.*, 37: 263 (New Zealand; in British Museum).

Potamopyrgus corolla (Gould, 1847), Suter, 1905, *Trans. N.Z. Inst.*, 37: 260 (New Zealand; U.S. Nat. Museum).

Potamopyrgus badia (Gould, 1848), Suter, 1905, *Trans. N.Z. Inst.*, 37: 264 (Banks Peninsula, N.Z.; U.S. Nat. Museum).

Potamopyrgus egenus (Gould, 1848), Suter, 1905, *Trans. N.Z. Inst.*, 37: 265 (Banks Peninsula, N.Z.; U.S. Nat. Museum).

Potamopyrgus corolla salleana (Fischer, 1860), Suter, 1905, *Trans. N.Z. Inst.*, 37: 262 (New Zealand; collection of *J. de Conchyliologie*, Paris).

Potamopyrgus spelaeus (Frauenfeld, 1862), Suter, 1905, *Trans. N.Z. Inst.*, 37: 266 (caves, Collingwood, Nelson, N.Z.; K.K. Hofmuseum, Vienna).

Potamopyrgus subterraneus, Suter, 1905, *Trans. N.Z. Inst.*, 37: 267 (well, Ashburton, N.Z.; Dominion Museum, Wellington).

Holotype.—Deposited in the British Museum (Natural History).

Type Locality.—New Zealand, in fresh water.

A full account of all earlier synonymies and the nomenclatural histories of the species recognized by Suter (1905) is given in his paper and therefore is not repeated here. However, the full nomenclatural history of Suter's *Potamopyrgus antipodum* is given, as the valid spelling of the specific name has been in doubt. This is resolved as follows.

In his original description, Gray misspelled the specific name *antipodanum*. This was emended in a second description of the species the following year (Gray, 1844) and was also recognized as "an evident and accidental mis-spelling" by Hedley & Suter (1893). As Gray's original spelling was clearly an inadvertent error it should be corrected to *antipodarum*. The emendation of Gray's name to *antipodum* is not justified, and this spelling which has been followed by most subsequent authors should not be used.

Shell ovate-conic, height fully grown 3–12 mm; shape highly variable, slender and elongate to ventricose; spire long or short, loosely or tightly coiled, whorls 4–8 flattened to rounded, with or without shouldering and variable periostracal spination. Females ovoviviparous, the lower oviduct forming a brood pouch. Reproduction sexual or parthenogenetic, sex ratio variable. Inhabit fresh waters of practically every type and also brackish water, throughout New Zealand.

Potamopyrgus pupoides Hutton, 1882

Potamopyrgus pupoides, Hutton, 1882, *Trans. N.Z. Inst.*, 14: 146. (Heathcote estuary Christchurch; Canterbury Museum).
Potamopyrgus spelaeus pupoides (Hutton, 1882), Suter, 1905, *Trans. N.Z. Inst.*, 37: 266.

Holotype.—Deposited in the Canterbury Museum, Christchurch, New Zealand.
Type Locality.—Heathcote estuary, near Christchurch, New Zealand. In brackish water.

Shell height less than 2·5 mm, conic-cylindrical, obtuse in apical region; whorls 5, flat, smooth, never possessing spines or keels, suture often margined below. Reproduction sexual, females oviparous. Inhabits the brackish lower reaches of streams and rivers, and tidal estuaries, throughout New Zealand.

Potamopyrgus estuarinus n. sp.

Holotype: Deposited in Dominion Museum, Wellington, New Zealand.
Paratypes: Auckland, Dominion and Canterbury Museums, New Zealand; Naturhistoriska Museet, Goteborg, Sweden.
Type Locality: Small brackishwater stream, Bell Block, Taranaki, New Zealand.

Shell ovate-conic, height up to 7 mm; whorls 6–7, smooth, flattened; never possessing periostracal ornamentation; sutures sometimes margined below; apical whorls frequently eroded. Females oviparous, reproduction sexual. Rostral and mantle pigmentation always very dark. The ecological niche of this species is restricted and distinctive, snails inhabiting the lower tidal reaches of rivers, and particularly harbour mud flats adjacent to river mouths, where they are alternately exposed and covered by water of varying salinity.

The animals of dried specimens labelled *Amnicola antipodarum* in the U.S. National Museum were examined by Morrison (1939), who reported that the males possessed a long, simple, geniculate verge and the females were oviparous. This description indicates that they were my *Potamopyrgus estuarinus*. However, examination of a photograph of the holotype of *A. antipodarum* in the British Museum shows that it is definitely not *estuarinus* as it possesses a large, heavily built shell unlike that found in the latter and this is confirmed by Dr. R. K. Dell (pers. comm.) who has examined the type.

COMPARATIVE SYSTEMATIC ACCOUNT

Methods

Shell

Three shell parameters, height, width and height of aperture (Fig. 1a) were

measured to the nearest 0·1 mm, with a linear eyepiece micrometer inserted in a stereoscopic microscope at magnifications of ×12·5 and ×32. For comparative purposes, ratios of shell height to shell width (h/w) and shell height to aperture height (h/ap h) were employed, as well as direct comparisons of measurements. Shells of fully grown snails only were used in comparative studies. The number of snails measured from each population was determined partly by numbers available and in all cases was sufficient to give a thorough indication of the full range of variation found within the population. In most cases 10–20 snails were measured.

Whorl counts were made to the nearest complete whorl. Because the apex of many shells was eroded accurate whorl counts could not always be made.

Some shell characters such as convexity and shouldering of whorls, and degree of ornamentation cannot be expressed conveniently as measurements and so do not lend themselves to biometric examination. Comparisons of such characters were made from camera lucida tracings.

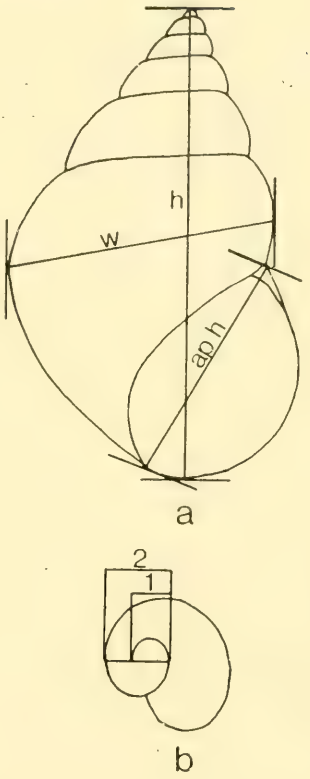


FIG. 1. Measurements made in the study of shell variation. **a.** Fully grown shell. **b.** Embryonic shell. h, shell height; w, shell width; ap h, aperture height; 1, width of tip of apical whorl; 2, diameter of first whorl.

Embryo shell

Embryos were taken from the brood pouches of individuals of *Potamopyrgus antipodarum* and camera lucida tracings of shell outlines were made at a magnification of ×120. From the shell tracings the width of the tip of the apical whorl, and the diameter of the first whorl were measured (Fig. 1b).

Operculum

Opercula were removed from snails and cleaned in a weak solution of oxalic acid. Permanent mounts were made in polyvinyl alcohol (PVA), and examined with a binocular microscope using both top and bottom lighting. Slides were placed on a dark background so that calcification within the operculum would be visible.

Radula

Radulae were extracted in boiling 4% KOH, stained in picric acid and permanently mounted in PVA. Some radulae were mounted intact, whereas the teeth of others were teased apart. Duplicate counts of cusps, denticles and serrations were made on at least 3 lateral, inner and outer marginal teeth from each radula. All measurements were made with a linear eyepiece micrometer at magnifications of ×100 and ×400.

Internal anatomy

Anatomy was examined by dissection and serial sections. The most successful dissections were carried out on fresh

material. Snails to be sectioned were fixed in Bouin's fluid, sections were cut at 5–10 μ, stained with Ehrlich's haematoxylin and counterstained with eosin.

Chromosome numbers

Chromosome numbers were determined using a squash technique.

Shells of freshly obtained snails were cracked and tissues were examined immediately without fixation, or were fixed for 24 hours at 4°C in Carnoy's fluid (ethyl alcohol: glacial acetic acid: chloroform, 6:1:3, v/v/v), and stored in 70% alcohol in a refrigerator until required.

Small pieces of testis and ovary (plus digestive gland) were separated and stained in acetic-orcein (1% orcein in 45% acetic acid) for 10–15 minutes on a cavity slide. Material was transferred to a plain microscope slide in a minimum of stain, gently squashed under a cover slip and examined microscopically using oil immersion at $\times 1000$ magnification.

Laboratory rearing of *Potamopyrgus antipodarum*

Potamopyrgus antipodarum was kept in the laboratory in transparent plastic boxes ($14 \times 11 \times 6$ cm) with loose fitting lids. Boxes were half filled with tap water, and each contained several grams of finely sieved pond mud and pieces of *Elodea canadensis*. No artificial aeration of the water was required. Water levels were maintained and small quantities of pond mud were added at infrequent intervals. Under these conditions growth of snails was continous and fairly rapid (minimum generation time 6 months), and embryos were released by large numbers of adult snails.

Amino acid composition of shell periostracal protein

The method of Ghiselin *et al.* (1967) was used for preparation and analysis of shell material. Snails were completely removed from their shells, or in some cases the animal was separated after decalcification, and the shells were thoroughly cleaned. Shells were decalcified in the presence of 10% trichloracetic acid solution by HCl, and the periostracum remaining was removed, washed and hydrolysed with 6N HCl at 110°C for 24 hours under vacuum. All samples consisted of periostracal material pooled from a number of snails. Amino acids were analysed using a Beckman/Spinco Model 120 amino acid analyser.

Salinity relations

Snails were kept in the laboratory at 11 salinities, 0, 10, 20—100% sea water, made up by diluting freshly collected sea water with distilled water. Salinities were checked by titration with silver nitrate. Ten fully-grown individuals of *Potamopyrgus estuarinus*, 10 of *P. pupoides* and 20 of *P. antipodarum*, half from freshwater and half from water of fluctuating salinity, were placed in glass bowls containing 200 ml of water, at each salinity. Snails were transferred direct to the experimental salinity from water taken from their natural habitats. All experiments were run at 18–20°C for 24 hours. At the end of an experiment all inactivated snails were transferred to water with a salinity of 3·5‰ and examined again after a further 24 hours. All experiments were run in duplicate.

Amphibious behaviour

Laboratory experiments were designed to compare the behaviour of *Potamopyrgus antipodarum* and *P. estuarinus* when offered a choice between submerged and exposed substrata. The experimental apparatus consisted of a rectangular plastic box ($20 \times 10 \times 7$ cm) with a cardboard floor covered in a layer of river mud forming a sloping "ramp". The floor was subdivided into 3 zones, a lower submerged section, an upper zone of

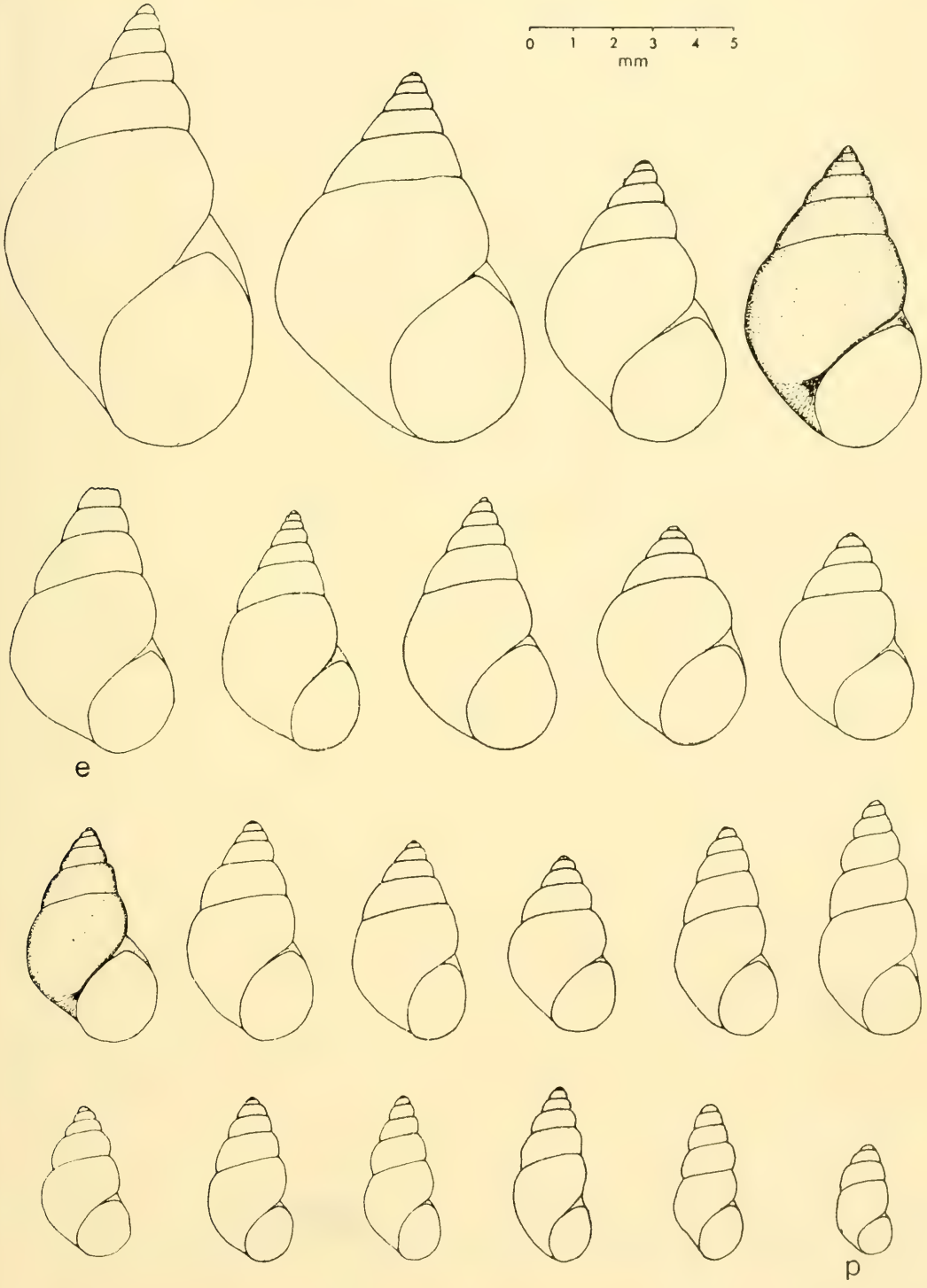


FIG. 2. Outline tracings of fully grown shells of *Potamopyrgus antipodarum* from 19 populations showing variations in size and shape. Typical shells of *P. estuarinus* (e), and *P. pupoides* (p) included for comparison.

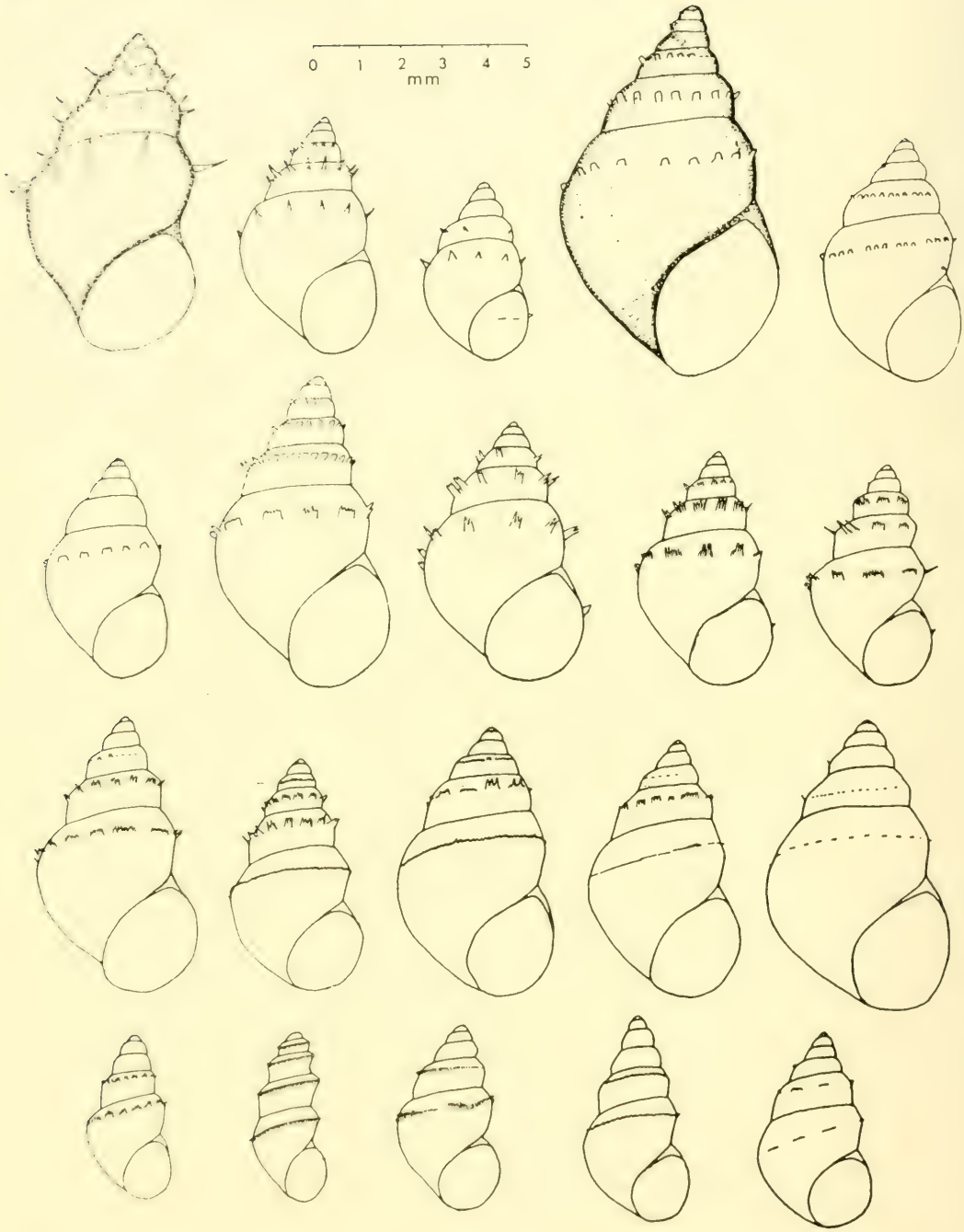


FIG. 3. Outline tracings of fully grown, ornamented shells of *Potamopyrgus antipodarum* from 20 populations, showing variations in size, shape and form of ornamentation.

slightly damp, exposed mud, and a middle zone of saturated mud also exposed to the air. One hundred snails were used in each experimental run. Tap water

was employed in experiments on both species and sea water was also used with *P. estuarinus*. The different salinities did not affect the responses of *P. estuarinus* in the experimental situation. All experiments were carried out at 18–20°C.

Effects of desiccation and starvation

(1) To determine the time snails can exist in a dry atmosphere before death occurs, experiments similar to those of van der Schalie & Getz (1963) were carried out. Shells of experimental snails were dried thoroughly with filter paper and placed in open, 9 cm diameter petri dishes which were kept in a desiccator containing calcium chloride as desiccant. The apparatus was maintained at 20–22°C

Fifty specimens of *Potamopyrgus estuarinus* and *P. antipodarum*, and 20 of *P. pupoides* were used in each experiment. Five individuals of each species were removed from the desiccator every hour for the first 3 hours, and then at 6 hour intervals until all were dead. A snail was considered dead if it showed no sign of movement within an hour of being placed in a shallow container of water.

(2) A permanently saturated atmosphere was produced in 9 cm covered petri dishes, by placing 6 thicknesses of water-soaked filter paper on the floor of each dish. As the petri dish lids were loose fitting, they permitted adequate gaseous exchange with the outside atmosphere. Dishes were kept at 20–25°C. In each experiment 40 individuals of each species were employed. Snails were examined daily to determine whether they were dead or alive, until all had died, or for 56 days in the case of *Potamopyrgus estuarinus*, and then after 70 days. Death was not easy to determine towards the end of the experiment, as with an increase in time the snails gradually withdrew further into their shells, until in many cases the operculum could no longer be seen. A snail was considered dead when no withdrawal reaction was elicited upon prodding the operculum firmly with a needle, or when signs of putrefying tissue were visible around the aperture of strongly withdrawn individuals.

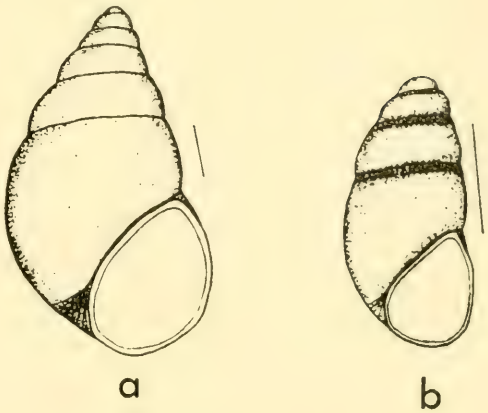


FIG. 4. Outline tracings of typical shells of **a**, *Potamopyrgus estuarinus* (from the type locality) and **b**, *P. pupoides*.

Results

Shell

Shells of the New Zealand species of *Potamopyrgus* are small and plain (apart from periostracal ornamentation), and offer few useful taxonomic characters. Shells of *P. antipodarum* are illustrated in Figs. 2 and 3, and of *P. estuarinus* and *P. pupoides* in Fig. 4.

Size and shape

Shell size, shape and variability within and between populations were examined biometrically by measuring shell height, shell width, aperture height and whorl number. It was reasoned that by comparing these parameters from a large number of populations, the nature of the shell variation, i.e., whether continuous or discontinuous variation existed, within

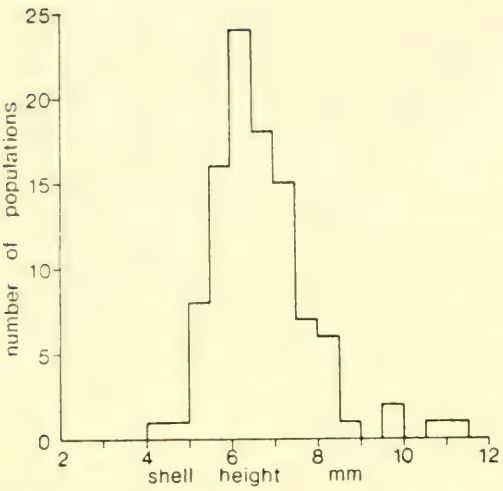


FIG. 5. Maximum height of shells in 100 populations of *Potamopyrgus antipodarum*.

the *Potamopyrgus* complex could be determined. Any discontinuities thus found might be indicative of separate lower taxonomic units which could be investigated further.

Maximum shell height in populations of *Potamopyrgus antipodarum* ranged from 4–11·5 mm. When the frequency of these heights is plotted (Fig. 5), the distribution is approximately normal and possesses a single peak at 6–6·6 mm, 72% of the values lying between 5·5–7·5 mm. By contrast, shells of the other 2 species are more uniform in height, those of *P. estuarinus* ranging from 5·5–7·5 mm and those of *P. pupoides*, 2·5–3 mm.

Shell ratios (h:aph, h:w) from selected populations of the 3 species are compared in Figs. 6 and 7. The populations are arranged in order of increasing mean h:aph ratios, and little correlation between aperture height and shell width is apparent. Mean shell ratios for all populations of *Potamopyrgus antipodarum* are plotted in Fig. 8, and the range of variation of these ratios within populations is shown in Fig. 9. Although the shells of some populations of *P. antipodarum* are so unlike that they could be considered sub-specifically different (Mayr *et al.*, 1953), it is clear that continuous variation in shell shape is found within this species. By comparison, only limited variability is exhibited by the shells of *P. estuarinus* and *P. pupoides*.

Numbers of whorls in fully-grown shells from 100 populations of *Potamopyrgus antipodarum* are shown in Table 1. Again there is considerable variation between populations but no clear division into discrete groups is found. As a general rule, the taller the shell, the more whorls developed.

To summarize, measurement of shell parameters has not provided evidence of clearcut morphological groups existing within the *Potamopyrgus antipodarum* complex, but rather has shown the existence of continuous variation of size and shape within this species. *P. pupoides* is distinguished by its small, pupiform shell, but the shell of *P. estuarinus* is indistinguishable from those of some forms of *P. antipodarum*.

Ornamentation

The presence or absence of spines or keels has been considered important in the separation and identification of the New Zealand species of *Potamopyrgus* (Suter, 1905). However, field observations made during the course of this study have shown that within the *P. antipodarum* complex considerable variation in degree and nature of shell ornamentation is found, even, in many cases, within a single population (Fig. 10). Ornamentation is purely periostracal, and no calcium is found in the spines.

Potamopyrgus antipodarum was reared in the laboratory in order that shell form and ornamentation of progeny of known parent snails could be examined. Some investigators (Dell, 1953; Hunter, 1961) have considered that much shell variation

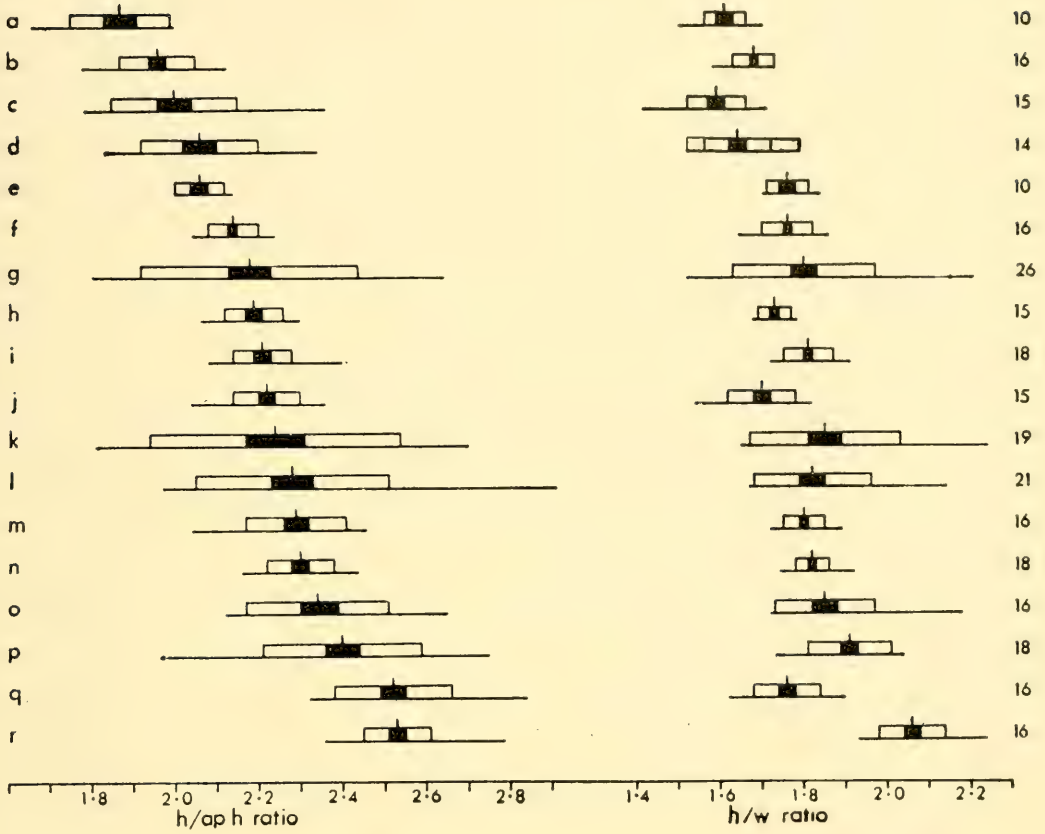


FIG. 6. Variation in shell height: shell width (h:w) ratio, and shell height: aperture height (h:aph) ratio in 18 populations of *Potamopyrgus antipodarum*. horizontal bar=range; open rectangle=1 SD; closed rectangle=1 SE; vertical bar=mean; numbers at right are sample sizes.

is the result of exposure to different environmental conditions, and this was observed in *Lymnaea tomentosa* reared in the laboratory under different conditions (Boray & McMichael, 1961).

In this study the experimental situation was reversed, and snails taken from differing environments were reared in the laboratory under identical conditions. Experimental populations were maintained for up to 3 years.

In the first series of rearings 711 progeny of 32 parthenogenetic snails from 12 populations were examined. Of 14 smooth-shelled parent snails, 9 produced totally smooth young, and 5 both smooth and spiny young. No smooth parent produced only spiny progeny. Of 18 spiny adult snails, however, only 3 produced all spiny young, 3 produced both smooth and spiny young, and 12 produced smooth young. In all cases, snails from natural populations consisting solely of smooth-shelled snails bred true in the laboratory, but this did not always hold for spiny-shelled snails.

As snails from different populations were reared under identical laboratory

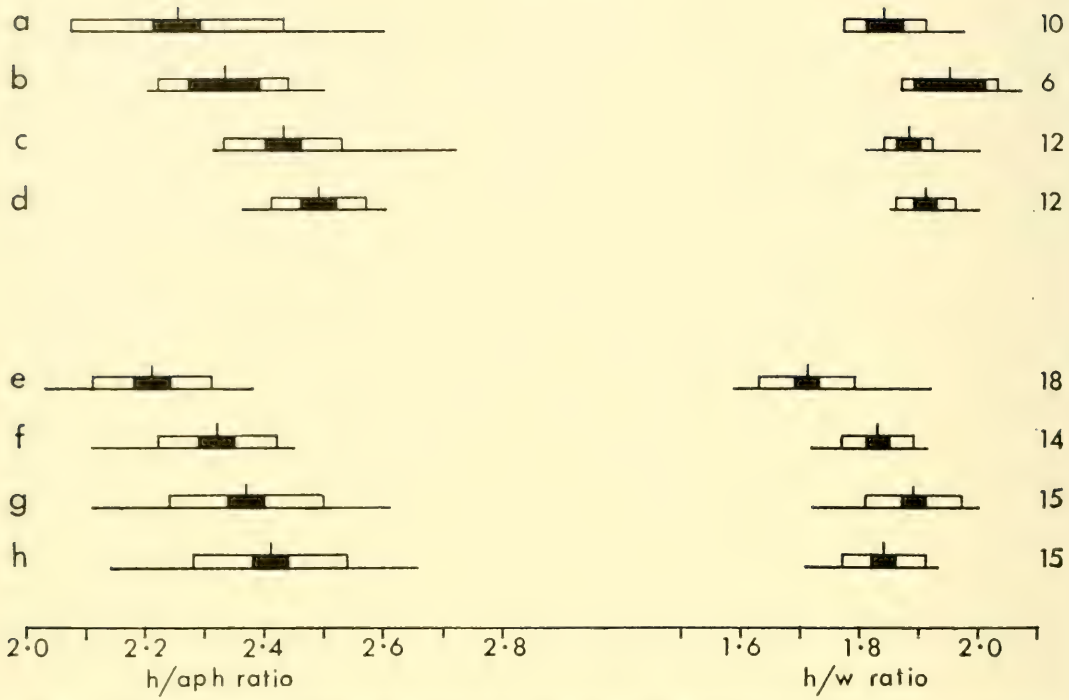


FIG. 7. Variation in shell height: shell width ratio, and shell height: aperture height ratio in populations of *Potamopyrgus pupoides* (a–d) and *P. estuarinus* (e–h).

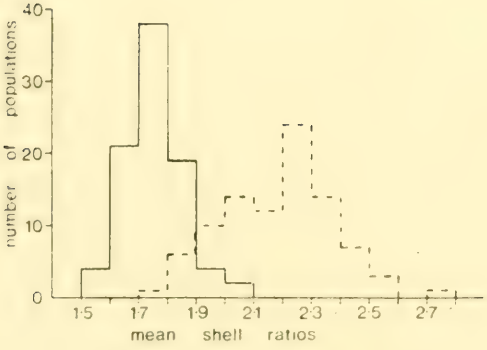


FIG. 8. Mean shell height : shell width ratios, and mean shell height : aperture height ratios in populations of *Potamopyrgus antipodarum*. Broken line=h: aph ratio; solid line=h: w ratio.

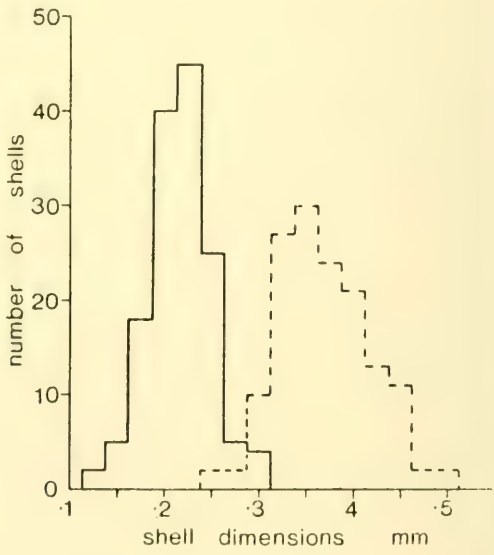


FIG. 9. Range of variation in shell height: shell width ratio, and shell height: aperture height ratio in 95 populations of *Potamopyrgus antipodarum*. Broken line=h:aph ratio; solid line=h:w ratio. A minimum of 10 shells were measured in all populations.

Erratum

The figure shown for Fig. 9 (p 294) is incorrect. The correct figure is shown below.

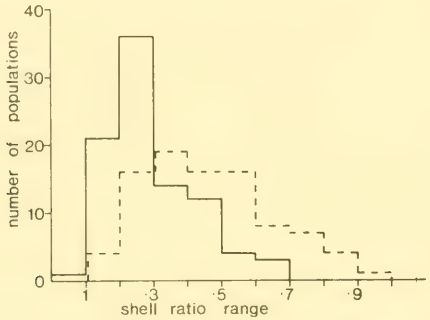


FIG. 9. Range of variation in shell height : shell width ratio, and shell height : aperture height ratio in 95 populations of *Potamopyrgus antipodarum*. Broken line = h:aph ratio; solid line = h:w ratio. A minimum of 10 shells were measured in all populations.

The figure shown for Fig. 19 (p 315) is incorrect. The correct figure is shown below.

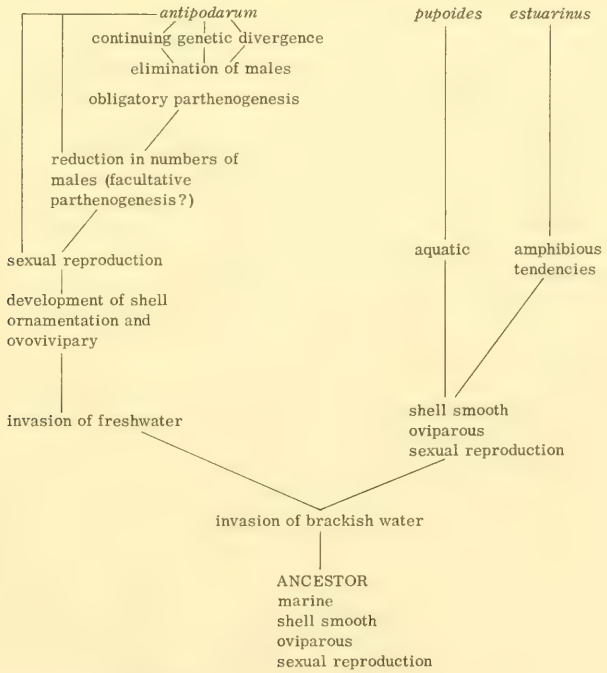


FIG. 19. Postulated steps in the evolution of the New Zealand species of *Potamopyrgus*.

TABLE 1. Numbers of whorls in fully-grown shells from 100 populations of *Potamopyrgus antipodarum*.

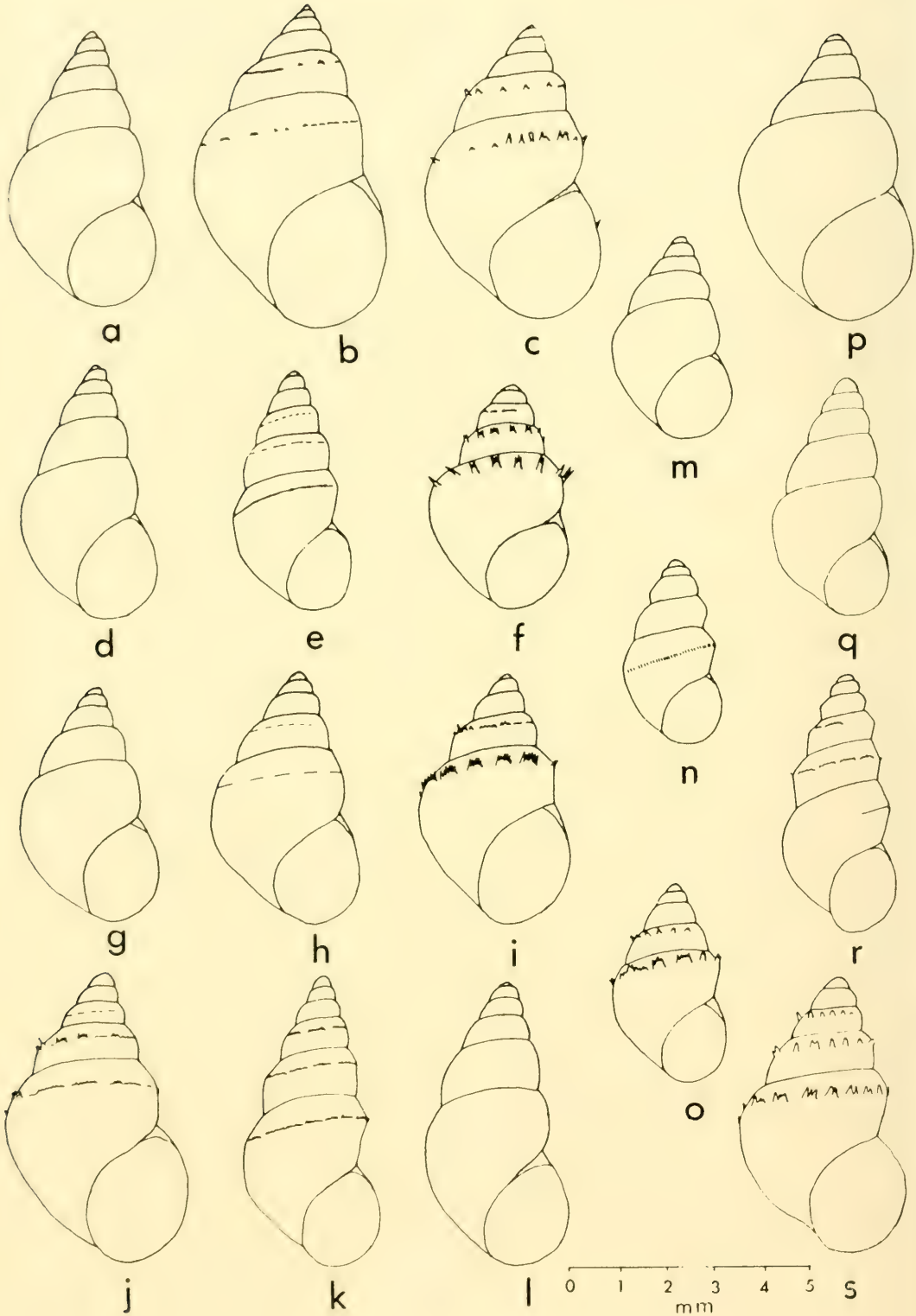
Shell height in mm	No. of Whorls					Totals
	4	5	6	7	8	
3–3·9	1	13	1	...	...	14
4–4·9	...	23	30	1	...	54
5–5·9	1	4	15	2	...	22
6–6·9	...	1	5	1	...	7
7–7·9	...	...	1	...	...	1
8–8·9	...	...	...	...	1	1
Totals	2	41	52	4	1	100

TABLE 2. Results of rearings from parthenogenetic individuals of *Potamopyrgus antipodarum* obtained from a pond at Massey University.

P_1*	F_1*		P_2*	F_2		P_3	F_3	
	Smooth	Spiny		Smooth	Spiny		Smooth	Spiny
Smooth	4	1	Smooth	35	0	...	...	
			Smooth	0	37	Spiny	2	3
						Spiny	0	10
						Spiny	0	22
			Smooth	43	0			
			Spiny	4	20	Spiny	0	33
						Spiny	0	10
						Spiny	0	16
Spiny	21	20	Smooth	43	0			
			Smooth	12	0			
			Smooth	5	0			
			Smooth	6	0			
			Smooth	20	0			
Spiny	56	3						
Smooth†	92	0	Smooth	25	0	Smooth	11	0
			Smooth	24	0			
			Smooth	35	0			
			Smooth	27	0			
			Smooth	20	0			
			Smooth	8	0			

*P=parent; F=offspring.

†4 snails kept together.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mm

conditions, it is impossible to infer environmental influences as the only factors determining shell ornamentation. This must therefore have a genetic basis.

A longer term experiment was carried out using parthenogenetic snails taken from a pond at Massey University, Palmerston North, in which smooth and spiny shelled snails were present in approximately equal numbers. All generations were kept under identical experimental conditions but again a considerable amount of variation in shell ornamentations was found between the progeny of siblings, and between generations (Table 2).

A possible genetic basis for shell polymorphism in *Potamopyrgus jenkinsi* and *P. antipodarum* is suggested as follows. Ornamentation may be under polygenic control rather than determined by a single pair of alleles, and the expression of different degrees of shell ornamentation could result from interaction between environmental factors and the genomes of shell secreting cells in the mantle. Characteristically, only a part of a cell's genome is manifest at any one time, and environmental changes could modify and direct gene function producing phenotypic differences, e.g., inducing spine development, when the correct genes were active. Such a mechanism could account for the intra-specific variation in shell ornamentation which is frequently found and which cannot be explained in simple Mendelian terms or as solely environmentally controlled changes of the phenotype.

In contrast to shell ornamentation, the shell shape, height, whorl convexity and ratios of shell parameters of progeny in all laboratory populations closely resembled those of the parent. Range of shell variation between daughter snails was slight, and less than that found in samples of randomly selected adult snails from the original habitats.

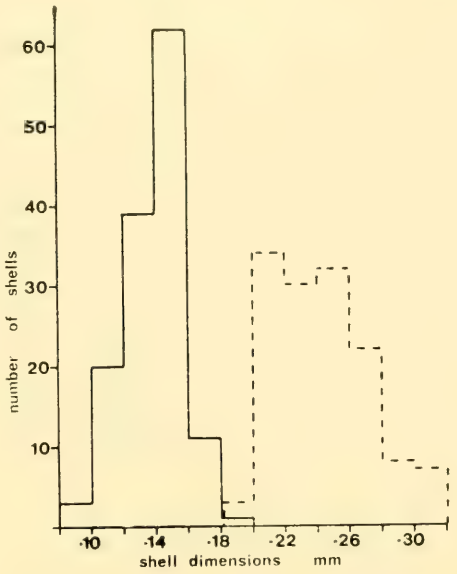

FIG. 11. Whorl measurements of 136 embryonic shells from 19 populations of *Potamopyrgus antipodarum*. Broken line=diameter of first whorl; solid line=width of tip of apical whorl.

Embryonic shell

The shells of embryos contained in the brood pouch of *Potamopyrgus antipodarum* are semi-transparent and possess no ornamentation, although transverse growth rings are visible (Fig. 12 c-e). The embryonic shell possesses 1·5 whorls when released from the brood pouch, and in older snails these whorls cannot be differentiated from later developed shell.

The width of the tip of the apical whorl and the diameter of the first whorl of 136 embryonic shells from 19 populations of *Potamopyrgus antipodarum* are plotted in Fig. 11. No indication of the presence of distinct size groups is found.

FIG. 10. Variation in shell shape and ornamentation in 6 populations of *Potamopyrgus antipodarum* 1, a–c; 2, d–f; 3, g–i; 4, j–l; 5, m–o; 6, p–s.

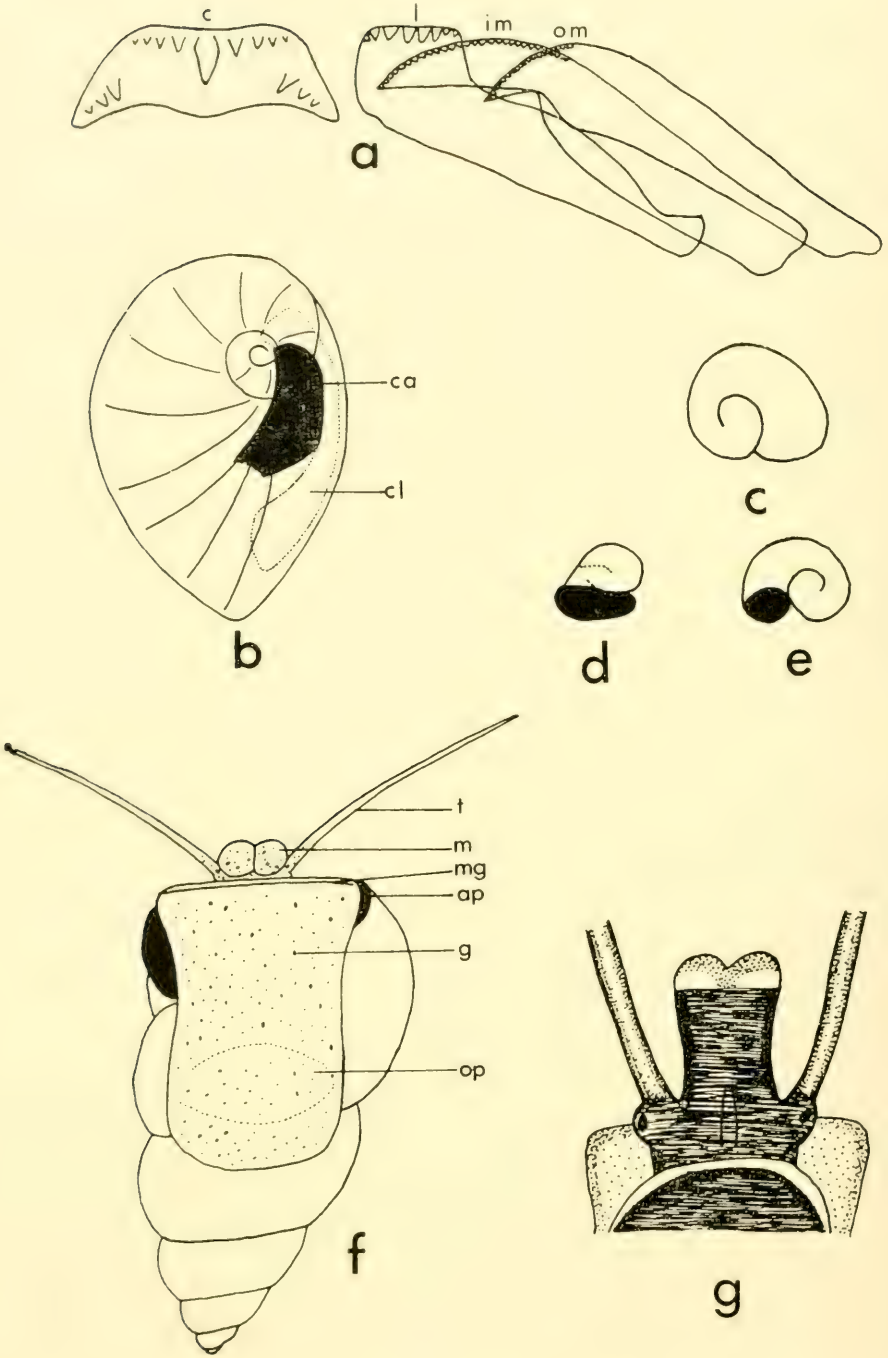

FIG. 12. Externals and radula of *Potamopyrgus antipodarum*. **a**, Radular teeth. **b**, Operculum (outer side). **c–e**, Embryonic shells from brood pouch. **f**, Animal extended (ventral). **g**, Head pigmentation. c=central; l=lateral; im=inner marginal; om=outer marginal; ca=calcareous smear; cl=clear area; t=tentacle; m=mouth lobe; mg=mucous groove; ap=aperture; g=granule; op=position of operculum.

TABLE 3. Variation in whorl dimensions of embryonic shells from 4 populations of *Potamopyrgus antipodarum*.

Locality	No. of shells measured	Width of apical tip (mm)	Diameter of 1st whorl (mm)
Lake Rotoiti	10	0·10—0·13	0·21—0·23
Lake Pupuke	10	0·11—0·16	0·21—0·23
Mt. Wharite	10	0·09—0·16	0·20—0·27
Lindis Pass	10	0·13—0·16	0·25—0·31

The range of variation in whorl measurements found in embryonic shells from 4 populations is given in Table 3. Clearly intrapopulation size variations can be almost as great as variations between populations.

Operculum

Stimpson (1865) described the operculum of *Potamopyrgus* simply as corneous, and Suter (1913) did not elaborate further. The following more detailed description is based on an examination of opercula from 30 populations of *P. antipodarum*, 3 of *P. estuarinus* and 3 of *P. pupoides*.

The ovoid operculum (Fig. 12b) is semi-transparent, its colour ranging from yellow to brown. The nucleus is subcentral, subspiral growth lines are clearly visible and there is no distinct marginal area. The muscle insertion area is indistinct but a narrow, clear, quasicrescentic area extending over half the length of the operculum is present close to the inner margin. The clarity of this area is somewhat variable. A small, irregularly shaped, calcareous smear is usually present to the right of the nucleus. The extent and degree of calcification is also variable but is clearly visible when the operculum is viewed with top lighting against a dark background. The operculum is of no value in distinguishing the New Zealand species of *Potamopyrgus*.

Radula

The radula of *Potamopyrgus* is taenioglossan. No important differences in general tooth shape are found between species, and representative teeth are illustrated in Fig. 12a. Within populations, slight variations may be found in the positions of the teeth on the radular ribbon with respect to one another. Some individuals have a clear space between the central and lateral teeth, but in others, no gap is found. Radular length generally increases with snail size (Fig. 13).

In all 3 species radulae of fully grown individuals examined possessed 62–93 rows of teeth. The rows are closer together in *Potamopyrgus pupoides* than in *P. antipodarum* or *P. estuarinus* (Fig. 14).

Cusp formulae for the 3 species are given below. These are based on an examination of snails from 28 populations of *Potamopyrgus antipodarum*, 3 of *P. pupoides* and 3 of *P. estuarinus*.

P. pupoides

$$\frac{(4\text{–}5)\text{—}1\text{—}(4\text{–}5)}{(4\text{–}5)\ \text{—}\ (4\text{–}5)} : 9\text{–}11 : 21\text{–}25 : 29\text{–}30$$

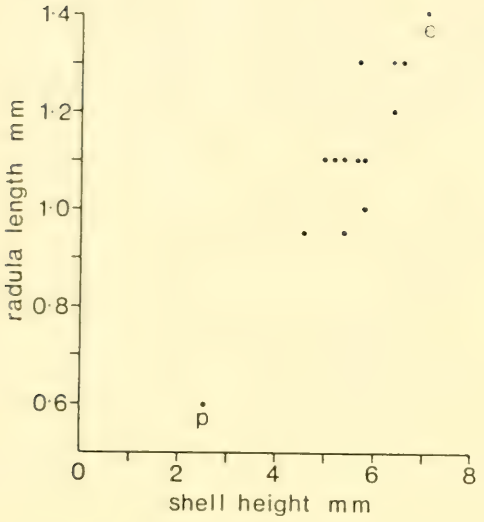

FIG. 13. Radular length plotted against shell height in 14 populations of *Potamopyrgus*. p=*P. pupoides*; e=*P. estuarinus*; other points=*P. antipodarum*.

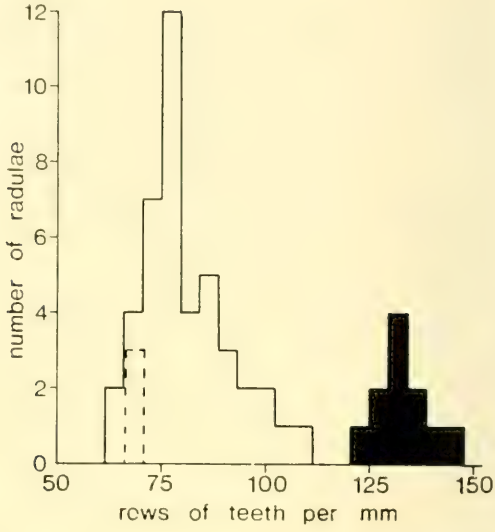

FIG. 14. Numbers of rows of teeth per mm of radular ribbon in the 3 species of *Potamopyrgus*. Broken line=*P. estuarinus*; solid line=*P. antipodarum*; solid histogram=*P. pupoides*.

P. estuarinus

$$\frac{(3\text{–}4)\text{—}1\text{—}(3\text{–}4)}{3\ \text{—}\ 3} : 8\text{–}\ 9 : 14\text{–}19 : 21\text{–}35$$

P. antipodarum

$$\frac{(3\text{–}5)\text{—}1\text{—}(3\text{–}5)}{(3\text{–}5)\ \text{—}\ (3\text{–}5)} : 7\text{–}13 : 15\text{–}32 : 24\text{–}48$$

Results of a study of cusp variation in 3 populations of *Potamopyrgus antipodarum* are presented in Table 4. Cusp formulae vary considerably and in *P. antipodarum* this variation appears to be independent of variations in shell characteristics. *P. pupoides* can be distinguished using radular characters, (smaller, and the rows of teeth are closer together), but *P. estuarinus* and *P. antipodarum* possess sufficient variability in shape, cusp formulae and radula length: shell length ratios to prevent specific differences from being defined.

Hutton's (1882) cusp formulae for 4 New Zealand "species" cannot be given the diagnostic importance he gave them. The minor variations in tooth shape shown in his figures appear to have been produced by orientation of the radulae for illustration rather than by true structural differences and the dimensions he provided are far too large. Ponder's (1967) figure of the radula of "*Potamopyrgus antipodum*" (actually *P. estuarinus*; Ponder, pers. comm.) is also inaccurate.

Externals of animal

The external appearance of the 3 species is identical (Fig. 12 f, g) except for differences in size and intensity of head and mantle pigmentation. The following description therefore applies to all 3 species.

The tentacles are long and slender, clear, with black pigment distributed as in Fig. 12g. The eyes have prominent pigment cups and are located in bulges at the bases of the tentacles. They are not borne on prominent tubercles as described by Morrison (1939). Rostral pigment is distributed in fine transverse

TABLE 4. Variation in numbers of cusps, denticles and serrations on the radular teeth of *Potamopyrgus antipodarum* from 3 populations.*

Locality	Central	Lateral	Inner Marginal	Outer Marginal
Massey University	(4–5)–1–(4–5) / (3–4)–(3–4)	9–11	20–25	31–47
Tiritea Stream	5–1–5 / (3–4)–(3–4)	9–11	25–35	32–45
Makara	(4–5)–1–(4–5) / (3–4)–(3–4)	9–11	21–29	32–42

* Examination of 12 snails per population making duplicate counts of cusps, denticles and serrations on at least 3 teeth per row per radula.

bands, is dark and evenly dispersed in *Potamopyrgus pupoides* and *P. estuarinus*, but is often lighter and more variable in *P. antipodarum*. The mouth lobes are white and normally have grey, crescentic markings dorsally. Pigmentation of the head behind the level of the eyes is always dark and the buccal mass is often visible dorsally near the base of the rostrum. The broad, grey foot has a stippled appearance, is rounded posteriorly and truncated anteriorly. The anterior margin is nearly straight, and the antero-lateral angles are somewhat auriculated. The anterior mucus slit is prominent and extends the width of the foot. The mantle skirt is black, with a well defined, pale, anterior margin. Large numbers of shiny white " granules " are found in the foot and mantle edge, and frequently in the mouth lobes and tentacles close to the eyes.

Although both Fretter & Graham (1962) and Muus (1963) consider that head pigmentation is distinctive in different species of European Hydrobiidae, and a useful aid in identification, no consistent differences in pigment distribution have been found between the New Zealand species of *Potamopyrgus*. Also, no correlation has been found between pigment intensity and shell form in *P. antipodarum* as has been suggested may occur in *P. jenkinsi* (Warwick, 1952).

Reproduction

Sex ratio

Morrison (1939) found that the specimens of " *Amnicola antipodarum* " he examined possessed sexual reproduction and were oviparous, and he assumed that all the New Zealand species of *Potamopyrgus* reproduced in this way. Later writers, however, apparently unaware of Morrison's study, have assumed them all to be viviparous (Marples, 1962; Dell, 1969), and apart from *P. pupoides*, parthenogenetic (Ponder, 1966).

The present investigation has shown that none of the New Zealand species consists solely of parthenogenetic females, and that males are relatively common in all 3 species.

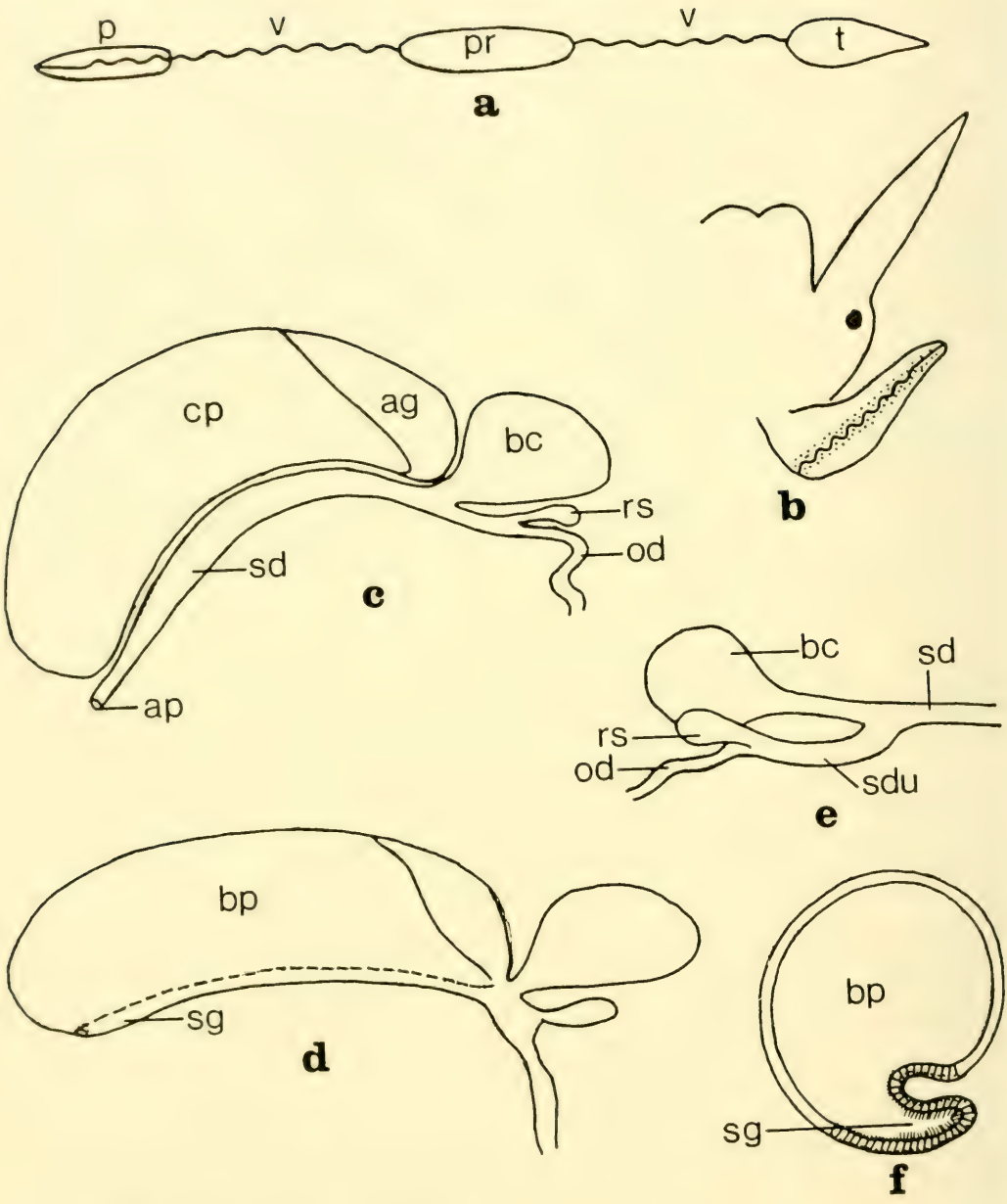

FIG. 15. Reproductive system. **a**, diagramatic representation of male system. **b**, penis. **c**, diagramatic representation of female system of *Potamopyrgus estuarinus* and *P. pupoides*. **d**, diagramatic representation of female system of *P. antipodarum*. **e**, arrangement of ducts in region of the bursa in *P. estuarinus*. **f**, Transverse section of empty brood pouch of *P. antipodarum* showing position of sperm groove. p penis; pr prostate; t testis; v vas deferens; ag albumen gland; ap female opening to pallial cavity; bc bursa copulatrix; bp brood pouch; cp capsule gland; od oviduct; rs receptaculum seminis; sd=spermathecal duct; sdu=sperm duct; sg=sperm groove.

TABLE 5. Dimensions of sperms of New Zealand species of *Potamopyrgus* compared with those of 2 species of European Hydrobiidae.

Species	Total length (microns)	Head length (microns)	Reference
P. antipodarum	110	3	Present study
P. estuarinus	140	3	Present study
P. pupoides	110–120	3	Present study
P. jenkinsi	40	4–6	Patil (1958)
Hydrobia ulvae	100	?	Patil (1958)

An initial investigation into the occurrence of males was made by examining 6–10 individuals from each of 63 populations of *Potamopyrgus antipodarum*, 5 of *P. estuarinus* and 3 of *P. pupoides*. Males were found in all populations of the 2 latter species and in 24% of *P. antipodarum* populations.

In a more comprehensive study, 50–200 snails were examined from selected populations. Males were found in 9 out of 24 populations of *Potamopyrgus antipodarum*, and in 7 of these they constituted less than half of the total sample. (In populations in which males occurred they represented 2–52%, mean=29%, of snails examined.) In *P. estuarinus* 36–58% of population samples were males, and in *P. pupoides* males constituted 10–28% of population numbers.

Male reproductive system

The gross anatomy of the male reproductive system is identical in all 3 species (Fig. 15a) and closely resembles that of *Potamopyrgus jenkinsi* as described by Patil (1958). The testis lies in the upper whorls of the shell on the columella side, and from it arises the vas deferens, a narrow, highly convoluted tube with a thin, muscular wall. It passes through a large prostate gland embedded in the tissues of the visceral mass at the posterior end of the body whorl, and finally runs forward on the head, close to the skin, to the penis, opening at its tip. No proximal dilation of the vas deferens, as described in *P. jenkinsi* by Patil, was found. In all 3 species the vas deferens of mature individuals is normally packed with living sperm throughout its entire length and consequently has a conspicuous white appearance.

Sperms have slender, conical heads and long, lash-like tails, and are all of the one kind. Their dimensions (living) are given in Table 5 in which comparisons are made with the sperm of *Potamopyrgus jenkinsi* and *Hydrobia ulvae*.

The sperms of the New Zealand species are comparable in length to those of *Hydrobia ulvae* but are 2–4 times as long as those described for *P. jenkinsi*. As the sperm of *P. jenkinsi* was observed in sectioned material, however, it is possible that the dimensions given are not a good indication of their length in life.

The penis (Fig. 15b) is situated on the right side of the head beneath the mantle edge. It is simple in form, tapering at its tip and bears no accessory lobes. In life

it is colourless and semi-translucent, the vas deferens being visible within. It is capable of considerable contraction and expansion, and when contracted the walls near its base have a telescopic appearance. In preserved specimens the shape and orientation of the penis tend to vary considerably, and usually it becomes somewhat coiled, especially towards the tip.

The penis is of no value as a taxonomic character for differentiating between New Zealand species of *Potamopyrgus*.

Female reproductive system

The structure of the female reproductive system divides the New Zealand species of *Potamopyrgus* into 2 distinct groups which possess major differences in the form of the lower section of the oviduct, and its associated glands.

(1) *Potamopyrgus antipodarum* (Fig. 15d)

The ovary is situated on the columellar side of the digestive gland in the apical whorls, and reaches almost to the tip of the spire. It has a white, rather lumpy appearance when mature, and contrasts strongly in colour with the brownish digestive gland which has a stippled appearance. The oviduct leading from it is slender and thin walled, but its walls become greatly thickened in the region of the bursa copulatrix and receptaculum seminis. Anteriorly, the reproductive system consists of the pallial oviduct which has a prominent, clearly demarcated groove, the sperm channel, on its ventral surface (Fig. 15f). In immature individuals the thin walled lower oviduct is circular in cross section but in mature snails it becomes greatly enlarged and distended to form a brood pouch within which over 100 embryos in various stages of development may be found. The sperm channel leads directly to the very large bursa copulatrix and via the sperm duct to the smaller receptaculum seminis. Both normally function to store sperm (Fretter & Graham, 1962), but must have lost this function in parthenogenetic individuals. Fretter and Graham have suggested that the well developed bursa copulatrix of *Potamopyrgus jenkinsi* may act as a waste dump for excess egg capsule secretions. Surrounding the posterior wall of the brood pouch are a prominent albumen gland and a mucus (shell) gland. The single opening of the pallial oviduct is situated close to its anterior extremity. The condition found in *P. antipodarum* agrees well with that described for *P. jenkinsi* by Patil (1958), and Fretter & Graham.

(2) *Potamopyrgus estuarinus* and *P. pupoides* (Fig. 15e)

In these 2 species the form of the female system is identical and differs markedly from that of *Potamopyrgus antipodarum* in the structure and function of the lower section which is dominated by the strongly developed capsule gland. The ovary, oviduct, bursa copulatrix and receptaculum seminis are similar in size, shape and position to those of *P. antipodarum*, and in fertilized individuals the receptaculum seminis has a vivid, white appearance, given to it by masses of sperm packed inside. Both the diverticulae communicate with the spermathecal duct, a straight tube with a muscular wall, which opens to the anterior of the mantle cavity and is completely separate from the capsule gland above. This is unlike the condition found in *Hydrobia*, where the capsule gland forms the pallial oviduct, with the spermathecal duct running along its ventral surface only partially separated by longitudinal folds of tissue. Immediately in front of the bursa copulatrix is the albumen gland whose lumen is continuous with that of the capsule gland. Although the exact course of the eggs through the system has not been established it seems probable that the capsule

gland does not function as a pallial oviduct. Evidence from dissections and serial sections indicates that it has no anterior opening to the mantle cavity, nor any major connection with the spermathecal duct or oviduct (Fig. 15e) and developing eggs have never been found in its lumen. It is assumed, therefore, that eggs pass into the spermathecal duct which would act as the pallial oviduct as proposed by van der Schalie & Getz (1962) for *Pomatiopsis cincinnatiensis*.

The eggs of *Potamopyrgus estuarinus* and *P. pupoides* are spherical with a granular appearance, possess a thick (15 μ), striated shell, have no organs of attachment, and are laid singly. Eggs of *P. estuarinus* have a diameter of about 200 μ, whereas those of *P. pupoides* are larger, with a diameter of about 370 μ.

Gametogenesis has been observed in collections of *Potamopyrgus estuarinus* made in January, May, August, September and December and it seems probable therefore that it occurs throughout the year. Less is known regarding *P. pupoides* but females containing developing ova have been observed in spring and summer.

Chromosome numbers

Squashes of male and female gonads from the 3 species, including *Potamopyrgus antipodarum* from parthenogenetic and sexually reproducing populations, were examined to determine chromosome numbers. Interpretation of ovarian material was difficult but testis squashes included cells at various stages of spermatogenesis and could be readily interpreted. Chromosomes could be distinguished with some difficulty in early prophase and were most clearly counted in late prophase and metaphase. In all 3 species the diploid number 2n=24 was found and male gametes possessed the haploid complement n=12.

As a rule, chromosome numbers in the Prosobranchia tend to be conservative (Patterson, 1967), and this is clearly the case in *Potamopyrgus*.

Amino Acid Composition of Shell Periostracal Protein

The use of amino acids from molluscan shell protein for phylogenetic and taxonomic purposes is a very recent development, and preliminary studies have indicated that it could be a useful taxonomic technique (Degens, 1967; Ghiselin *et al.*, 1967). The molluscan shell is produced by secretion of precursors from the epithelial tissue in specialized areas of the mantle, and may consist of several layers. The outer layer or periostracum is not calcified and consists of over 95% protein (Degens, 1967). The inner layers of the shell are calcareous and include a proteinaceous matrix which represents less than 1% of the mineralized shell layers in the Gastropoda (Hare & Abelson, 1965).

As a species is defined, in part, by its distinct genetic composition differing from that of other species, and as proteins are genetically determined, genetic divergence between species will be displayed by differences in protein composition. In this investigation, amino acid analyses of periostracal protein have been made using ion exchange chromatography. Periostracum was chosen for two main reasons:

(*a*) It is easy to obtain relatively large quantities of material compared with minimal amounts of matrix protein.

(*b*) Shell ornamentation is periostracal, and comparisons of amino acid composition of smooth and spiny shells is of interest.

Snails from 2 populations of *Potamopyrgus estuarinus*, 1 of *P. pupoides* and 4 of *P. antipodarum* were examined (Table 6) and the results of analyses are presented in Table 7. Reproducibility of results was tested on 2 samples of *P. estuarinus*

TABLE 6. Material used for shell protein analysis.

Sample	Species	Locality	Shell form
1	*P. pupoides*	Wananaki B*	Smooth
2 a	*P. estuarinus*	Huia B	Smooth
2 b, c	*P. estuarinus*	Huia B	Smooth
3	*P. estuarinus*	Heathcote B	Smooth
4	*P. antipodarum*	Dannevirke	Smooth
5	*P. antipodarum*	Lake Pupuke	Spiny
6	*P. antipodarum*	Whangarei	Smooth & spiny
7	*P. antipodarum*	Lake Tutira	Smooth
8	*P. antipodarum*	Lake Tutira	Spiny

* B=brackish water.

from Huia (Table 7, 2a, 2b, 2c). When 2 identical runs were made on the sample (2b, 2c) the mean variation between amino acid values was 0·26% (range 0·01–0·63%). The mean variation between the same amino acids from 2 different samples from the same locality (2a, 2b) was 0·71% (range 0·11–2·8%). This variation incorporates differences between specimens, and errors introduced by decalcification, chromatography and data handling.

Marked differences in amino acid concentrations were found between Huia and Heathcote samples of *Potamopyrgus estuarinus*, glycine, proline, tyrosine and phenylalanine being greatly reduced in the latter, whereas most others showed corresponding increases in proportions. Values for *P. pupoides* corresponded closely to those of *P. estuarinus* from Huia, apart from a lower proportion of tyrosine. A wide range of variation was found in *P. antipodarum*, and no relationship between amino acid concentration and shell ornamentation was apparent. This is clearly demonstrated by comparing the extreme shell forms represented by Lake Pupuke and Dannevirke samples. In these, with the exception of tyrosine, relative proportions of amino acids are of a similar order. The presence of increased tyrosine in spiny shells is probably of no significance however, as high concentrations are also found in the smooth shells of *P. estuarinus*. Clearly, the New Zealand species cannot be distinguished by comparing the proportions of amino acids in shell periostracum as a high degree of intra-specific variation is found, paralleling the wide range of variation in macroscopic shell morphology.

The presence of considerable variation in the proportions of amino acids in the periostracum of *Potamopyrgus* species reinforces similar findings obtained in other studies. Hare (1963) found that periostracum showed more variation in amino acid composition than any other structural unit of the shell, and showed

TABLE 7. Ratios of periostracal amino acids in the 3 species of *Potamopyrgus*, expressed as percent total amino acids.

Amino acid	*P. pupoides*	*P. estuarinus*				*P. antipodarum*				
	1	2a	2b	2c	3	4	5	6	7	8
Aspartic acid	12·1	12·9	11·5	10·9	14·9	13·3	12·7	11·5	11·7	9·9
Threonine	4·4	3·5	3·2	3·2	4·5	4·6	4·4	3·2	4·8	5·5
Serine	5·3	4·4	4·1	4·0	5·3	4·7	4·4	3·5	5·1	6·7
Glutamic acid	7·0	6·8	6·1	6·4	8·6	7·4	7·6	5·2	7·4	8·5
Proline	4·8	4·7	5·4	5·8	2·2	2·4	2·3	3·6	4·5	5·4
Glycine	32·9	35·7	34·2	34·2	26·6	31·9	28·9	40·1	26·9	20·5
Alanine	7·0	5·7	5·4	5·2	7·7	4·4	7·1	4·1	8·7	11·0
1/2 Cystine	T*	T	T	T	T	T	T	T	T	T
Valine	4·5	4·1	4·4	4·0	6·0	5·6	5·0	3·4	4·4	6·2
Methionine	0·7	0·7	0·5	0·5	0·8	0·8	0·6	0·2	0·5	1·0
Isoleucine	2·5	2·3	2·1	2·1	2·8	2·7	2·8	1·8	3·0	3·7
Leucine	4·6	4·3	4·0	4·0	5·4	5·8	5·7	4·0	5·5	6·0
Tyrosine	2·4	6·2	6·9	7·1	3·7	4·1	6·4	4·8	3·2	3·2
Phenylalanine	5·5	4·5	4·1	4·7	4·3	5·4	5·1	6·4	5·5	4·6
Lysine	2·7	2·1	4·9	4·3	3·4	3·2	2·9	3·4	4·4	3·7
Histidine	0·4	0·2	0·3	0·2	0·1	0·6	0·2	1·1	0·7	0·3
Arginine	3·2	1·6	2·7	3·3	3·6	3·1	3·9	3·8	3·5	3·7

* T=trace.

that samples from the growing edge, around the periphery of a single specimen of *Mytilus californianus* may vary 10–15% in numbers of residues of many amino acids. Clearly defined differences in amino acid composition of periostracum between individuals of the brachiopod *Laqueus californianus* have also been demonstrated by Jope (1967).

An important source of amino acid variation may be protein heterogeneity, i.e., more than 1 protein may contribute to the periostracum as suggested by Hare (1963), Degens *et al.* (1967) and Jope (1967). Ghiselin *et al.* (1967) found that environmentally controlled variation in the amino acid composition of periostracum is sufficient to mask genetic differences in many cases. Recently, Hare & Meenakshi (1968) have reported that changes occurred in the proportions of periostracal amino acids of *Potamopyrgus jenkinsi* raised in the laboratory at different salinities. In particular they found an increase in the ratio of glycine to the acidic amino acids with decreasing salinity. However, no similar relationship was evident when the brackish water species *P. estuarinus* and *P. pupoides* were compared with *P. antipodarum* from fresh water.

Environmental Relationships

Distribution and general ecology

(1) *Potamopyrgus estuarinus.*

Potamopyrgus estuarinus has a clearly circumscribed habitat, and is confined to brackish water. Commonly it is found near the mouths of streams and rivers entering harbours, where the water is of fluctuating salinity. Frequently, the snails live a semi-terrestrial existence on mud flats or muddy banks adjacent to river

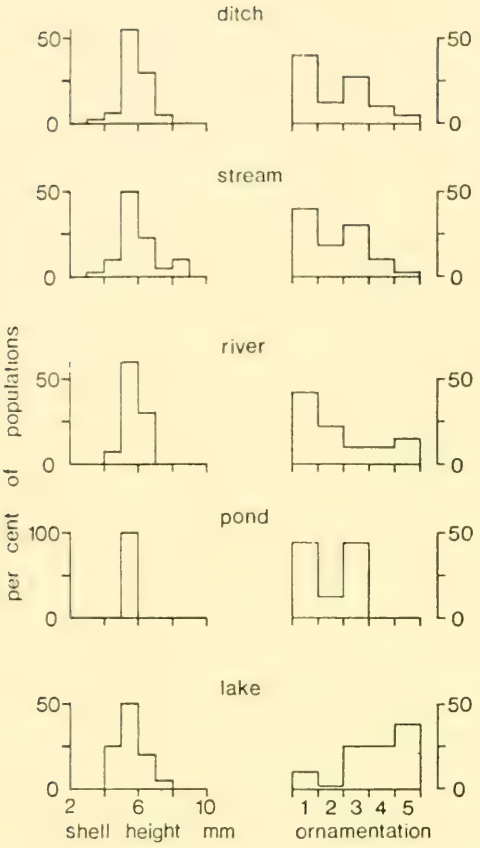

FIG. 16. Relationship between shell size, ornamentation and habitat in 97 populations of *Potamopyrgus antipodarum*. Key to shell ornamentation classes: 1—all snails smooth shelled; 2—most smooth; 3—half smooth, half spiny; 4—most spiny; 5—all spiny.

channels, or in harbour backwaters and salt swamps. In these situations they may lie exposed to the air for over half a tide cycle, and for the other half live in water of high salinity. The snails are inactive when exposed on mud flats, and may lie on the surface of the mud, be partially buried, or be grouped gregariously alongside or under stones, wood, etc. Snail densities of up to 884,000 per m^2 have been recorded in the Heathcote estuary.

Other snails remain immersed throughout the tide cycle, and may occupy various substrates including sand, mud, the upper and lower surfaces of stones, and clumps of weed. In river estuaries, snails are normally most abundant towards the seaward end, where salinities remain high.

Many past reports of the finding of *Potamopyrgus antipodarum* in brackish water undoubtedly refer to *P. estuarinus*.

(2) *Potamopyrgus pupoides*.

Potamopyrgus pupoides is confined to brackish water, and is frequently found in association with *P. estuarinus* in river estuaries, but is less frequently found on mud flats where it would be exposed to the air for regular periods of time. *P. pupoides* exhibits no marked substrate preferences and is found on stones, mud, and among living and decaying vegetation. Frequently, it is abundant in estuaries on a substrate of smooth, clean sand.

(3) *Potamopyrgus antipodarum*.

Potamopyrgus antipodarum occurs throughout New Zealand in a wide variety of habitats, including lowland rivers, stony streams, creeks, ditches, estuaries, ponds, lakes, springs, wells and permanent seepage. One of the few freshwater habitats it seems unable to colonize is the temporary pond as the snails apparently lack resistant stages capable of carrying them over long dry seasons.

Within the *Potamopyrgus antipodarum* complex a number of relationships between particular shell forms and geographical or ecological distribution are evident, but none of these relationships appears to be so well circumscribed, or clearly defined, as to warrant taxonomic recognition of the populations concerned. The main trends found are:

(*a*) Many snails at high altitudes, and/or in relatively oligotrophic waters, have a much smaller adult size than most low-

TABLE 8. Salinity ranges at which the 3 species of *Potamopyrgus* have been found living.

Species	Salinity o/oo		Maximum Diurnal Range
	Maximum	Minimum	
P. antipodarum	26·4	0	17·7
P. pupoides	32·3	2·7	,,
P. estuarinus	34·8	2·7	,,

land populations. These snails are predominantly smooth shelled.

(*b*) Snails in many, but not all, populations north of Auckland attain a very large size, their shells sometimes exceeding 10 mm in height. This size increase is produced by an increase in the number of whorls, rather than by an increase in size of the whorls.

(*c*) There is a tendency for the shells of spiny shelled snails in many lakes and rivers to be more slender and strongly shouldered in the South Island than in the North.

Although laboratory rearing work has indicated that shell form is not a simple phenotypic response to environment, in some instances small size may be the result of reduced growth at low temperatures, or under poor food conditions. Conversely, higher temperatures may permit an increase in the rate and amount of growth, resulting in the attainment of large size.

No clear relationship between shell height or ornamentation, and different habitat types was found (Fig. 16), although many lake populations tend to consist predominantly of spiny snails, whereas smooth shelled snails are more abundant in running water.

Salinity relations

All 3 species of *Potamopyrgus* are found over a wide range of salinities, but only *P. antipodarum* is found in fresh water (Table 8).

In order to determine the range of salinities tolerated by each species, the responses of snails kept in water at 11 different salinities ranging from 0–33‰ salinity, were examined in the laboratory.

After 24 hours in the experimental situation all individuals of *Potamopyrgus estuarinus* and *P. pupoides* exhibited normal acitivity at all experimental salinities, 0–33‰ salinity, and *P. antipodarum* from fresh and brackish waters was active at up to 17·5‰ salinity. Some reduced movement of *P. antipodarum* was found at 21‰ salinity but in more saline water all snails withdrew completely into their shells, their opercula acting as physical barriers to exclude the water. After a further 24 hours in water of 3·5‰ salinity, all previously inactivated snails resumed normal activity.

In the field, the highest salinity at which *Potamopyrgus antipodarum* has been found living is 26·4‰, slightly higher than the greatest salinity at which activity occurred under experimental conditions. It is possible that some intraspecific variation is found in *P. antipodarum* with respect to salinity tolerance as was found in *P. jenkinsi* by Duncan & Klekowski (1967). Although *P. estuarinus* and *P. pupoides* have not been found in fresh water in the field, they were able to exist

in it for several months in the laboratory. Perhaps they are unable to reproduce or develop in freshwater.

The ability to tolerate a wide range of salinities is clearly advantageous to all 3 species, as rapid changes in salinity are regularly encountered in the estuarine reaches of rivers frequently inhabited by them.

Amphibious behaviour

Apart from inhabiting waters of different salinities, *Potamopyrgus antipodarum* and *P. estuarinus* are frequently found in contrasting physical environments. *P. estuarinus* is often abundant on high-tidal mud flats bordering streams where snails may be exposed to the air for an appreciable period of each tide cycle, whereas *P. antipodarum* always remains in the water. Laboratory experiments were carried out to compare the behaviour of the 2 species when a choice of 3 substrata, submerged mud, exposed water saturated mud, and slightly damp mud, was offered to them.

Results of experiments are shown in Fig. 17. In Experiment 1 snails were distributed evenly throughout the box at the start of the experimental period and a single examination of their subsequent distribution was made after 17 hours. In Experiment 2 all snails were placed in the submerged section of the box on commencing the experiment, and their distribution was examined after 1, 2, 24 and 72 hours. Similar results were obtained in both studies. A clear behavioural difference between the 2 species was apparent, the majority of *Potamopyrgus estuarinus* finally selecting the driest substrate, whereas almost all *P. antipodarum* remained in the water, or were buried in the water-saturated mud of the middle zone. Movement of *P. estuarinus* from the water to the dry upper zone is clearly shown in Experiment 2 (Fig. 17).

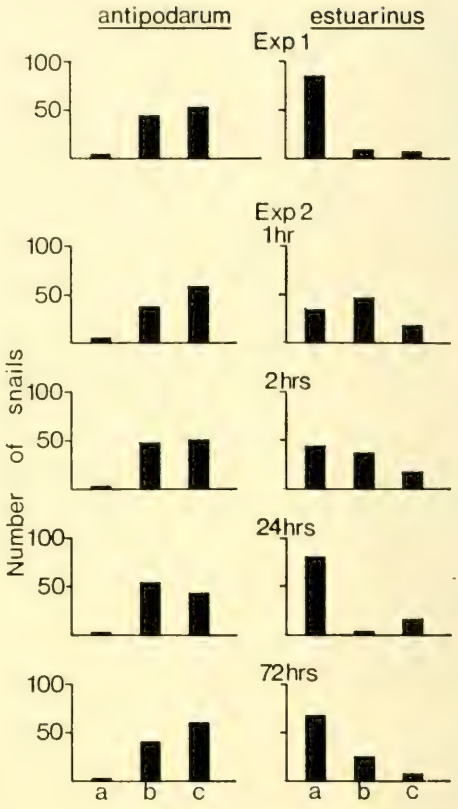

FIG. 17. Selection of submerged and exposed substrata by *Potamopyrgus estuarinus* and *P. antipodarum* in laboratory experiments. Expt. 1, snails initially distributed throughout box; examined after 17 hours; Expt. 2, all snails initially submerged. Substrata: a=damp, exposed mud; b=saturated mud; c=submerged mud.

The relatively large numbers of *Potamopyrgus antipodarum* occupying the middle zone of water-saturated mud, is probably explained by the presence of favourable respiratory conditions at the air-water interface in this zone. A similar situation is regularly found in still water laboratory cultures lacking vegetation, in which the majority of snails move up the sides of the containers and settle immediately beneath the surface film.

Although in the experimental situation most *Potamopyrgus estuarinus* remained

TABLE 9. Time survived by snails in a still, dry atmosphere, and on a dry substratum.

Species	All alive (hours)	First death occurs (hours)	All dead (hours)
P. antipodarum	0–6	6–12	30
P. estuarinus	0–6	6–12	42
P. pupoides	0–6	6–12	24

permanently in the dry zone and exhibited no active movement back to the water, in their natural habitat they do not normally remain exposed to the air for more than a few hours at a time, as tidal movements ensure they will be covered at regular intervals. It is essential that the habitat should be submerged regularly as snails cannot move about and feed when the substrate is dry. One consequence of this positive movement out of water could be to prevent colonization of permanent river channels, and so effectively isolate populations of *P. estuarinus* and *P. antipodarum* in many areas where their ranges overlap.

Effect of desiccation and starvation

Associated with the colonization of a non-aquatic habitat is the problem of preventing desiccation. This is likely to be of considerable importance to a primarily aquatic species such as *Potamopyrgus estuarinus* which is periodically exposed to the air. *P. antipodarum* although strictly aquatic, sometimes inhabits bodies of fresh water with fluctuating water levels, or which can be drained by natural or artificial means. In such situations, if the snails are unable to withstand exposure to air, whole populations may be quickly destroyed.

Laboratory experiments were designed to examine the effect of desiccation and starvation on the 3 species, (*a*) in dry air and on a dry substratum, and (*b*) on a damp substratum in moisture saturated air.

The time survived by the 3 species in a still, dry atmosphere is shown in Table 9. Similar responses were obtained from all species.

Survival times of snails in a moisture-saturated atmosphere, and on a damp substrate is shown in Fig. 18.

Direct observations indicated that snail tissues did not become rapidly desiccated under these conditions, and that at all times some moisture was maintained within the shells of the snails. On a damp, but non-submerged substrate, however, movement, and consequently feeding, cannot occur and therefore death probably results from starvation combined with desiccation. Deaths of *Potamopyrgus antipodarum* and *P. pupoides* are therefore attributed to the combined effects of desiccation and starvation. However, the situation was very different for *P. estuarinus* which apparently entered a state of dormancy or aestivation, and had a high survival rate over a long period. Individuals which remained dormant up to 50 days resumed activity when transferred to a vessel of water.

Little is known about aestivation in the Prosobranchia although short term aestivation does occur in some Pomatiasidae

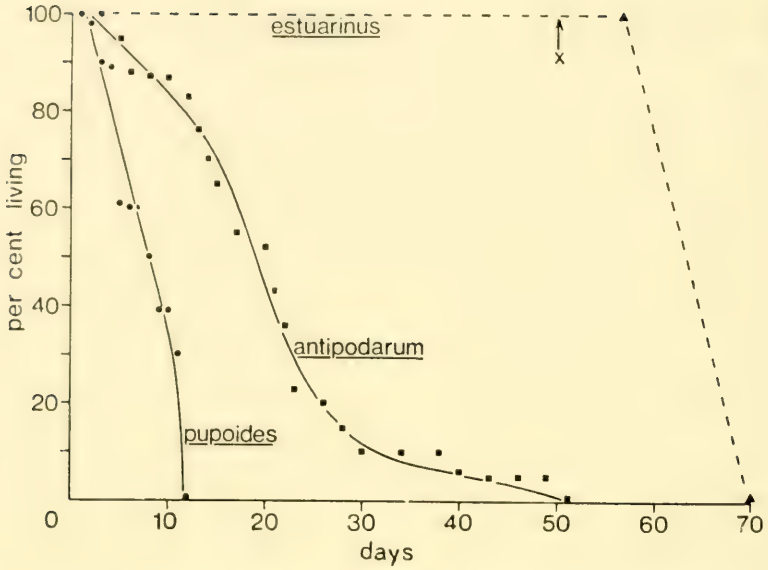

FIG. 18. Survival time of snails on a damp substratum at 20–25° C. Circles = *Potamopyrgus pupoides*; squares = *P. antipodarum*; triangles and broken line = *P. estuarinus*. X–10 snails placed in water (all resumed activity).

(Hunter, 1964) and Hydrobiidae (Dundee, 1957). Quick (1920) found that *Hydrobia* spp. could withstand long periods of exposure and survive in an apparently desiccated state, and Dundee (1957) has noted that dormancy occurs in the amphibious *Pomatiopsis lapidaria* in very cold or hot and dry weather. This evidently ensues when there is a lack of sufficient available moisture, the snails lying with their opercula inserted well into the shell apertures during the inactive period, and becoming reactivated with the onset of rain. Clearly the ability to withstand long periods of exposure out of water is advantageous to snails such as *P. lapidaria* and *P. estuarinus* which possess an amphibious way of life, and may suffer prolonged periods of exposure.

DISCUSSION

The species problem

As a result of this study, 3 species of *Potamopyrgus* are now recognized in New Zealand. Two of these, *P. pupoides* and *P. estuarinus*, are clearly distinguished using morphological, reproductive, and ecological evidence, but *P. antipodarum* contains a heterogeneous assemblage of forms embracing all the purely freshwater populations. It includes a wide range of morphological variants, as well as differing reproductive forms, and is found under diverse environmental conditions. In the past, many of the forms included in this species have been considered morphologically distinct enough to be recognized as separate species, or to have had restricted geographical distributions allowing them subspecific recognition. This study has shown that continuous morphological variation exists within the complex, and that discrete geographical distributions of taxonomic subgroups, consistent with the definition of the subspecies (Mayr, *et al.*, 1953) are difficult to find. A gradation in reproductive forms, through populations with few males, to total parthenogenesis is also

found, and the possession of these different states, apparently unassociated with particular morphological forms, or the occupation of particular habitats adds further to the difficulty of discriminating distinct taxonomic units within the complex.

The possession of a parthenogenetic mode of reproduction by a large proportion of the populations of *Potamopyrgus antipodarum* is perhaps the major factor responsible for so much of the taxonomic uncertainty that has occurred in the past, and it has permitted the formation of many reproductively isolated clones in which divergent evolution has been able to occur. Furthermore, Struhsaker (1968) in a discussion of shell variation in *Littorina* spp. suggested that species which are viviparous could be expected to have more intra-specific variation because of decreased distribution (dispersal) and restricted mating. This would result in isolated populations, whereas strictly oviparous populations with widespread larvae should be least variable. This contention is supported by the findings in the present study, the 2 oviparous species, *P. estuarinus* and *P. pupoides* possessing limited morphological variability compared with the extreme plasticity of the ovoviviparous *P. antipodarum*.

Reproduction by parthenogenesis also poses nomenclatural problems. The biological species definition (e.g. Mayr, 1963, " Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups "), applies only to sexually reproducing organisms, and it is generally accepted that the taxonomy of obligatory parthenogens therefore must be arbitrary. In the past it has been based primarily on morphological, ecological and biogeographic evidence. The occurrence of sexual reproduction and parthenogenesis in the *Potamopyrgus antipodarum* complex poses further problems. White (1954) and Mayr (1963) have pointed out that it is illogical to recognize parthenogenetic and bisexual " races " of the same species, irrespective of the morphological resemblances between the genotypes, and they considered that such forms were better recognized as sibling species, if they were indistinguishable by ordinary taxonomic criteria. On the other hand, Mayr *et al.*, (1953) have agreed that it is unjustifiable to give nomenclatural recognition to forms with temporary or facultative parthenogenesis. In *P. antipodarum*, sexually reproducing and parthenogenetic forms are connected by intermediates possessing limited numbers of males, and it seems likely that in such populations both parthenogenesis and sexual reproduction may occur.

In view of this lack of a sharp division between reproductive types, and the presence of continuous morphological variation within the complex, it seems most sensible to consider the whole range of intergrading populations as a single species.

The suitability of an evolutionary species concept such as that of Simpson (1961); " An evolutionary species is a lineage evolving separately from others and with its own unitary evolutionary role and tendencies ", which is not hampered by the static restrictions of genetical (biological) definitions, is evident in a situation of this kind.

Parthenogenesis and evolution in *Potamopyrgus*

Parthenogenesis was first discovered in molluscs by Boycott (1919), in *Potamopyrgus jenkinsi*, and later in the American viviparids *Campeloma rufum* and *C. decisum* by van Cleave & Altringer (1937) and Medcof (1940), and in 4 species of Melaniidae by Jacob (1957). Parthenogenesis in all these species is thelytokous (female diploid parthenogenesis) and of the apomictic type, (i.e., it is ameiotic and

neither chromosome reduction nor fusion of nuclei takes place in the egg). In many animals, parthenogenesis is frequently accompanied by polyploidy (Suomalainen, 1950), and of the molluscs examined, 3 species of *Melanoides* are polyploid and 1 species is diploid (Jacob, 1957). It has been stated that *P. jenkinsi* exists as 2 distinct genotypes, a diploid race in Europe (2n=20–22) and a tetraploid race in Great Britain (2n=36–44) (Sanderson, 1940), but Suomalainen (1950) and Patterson (1967) consider that this needs reinvestigation.

In the *Melanoides* species, parthenogenesis is obligatory, although small numbers of sexually non-functional males are found in 2 species (0·01–3·0% of populations). Obligatory parthenogenesis has been considered the rule in *P. jenkinsi* also, although a single male has been found by Patil (1958). Males occur sporadically in populations of *C. rufum* (about 1%) and are scarce or rare in 3 other species of *Campeloma* about whose reproduction little is known (Mattox, 1938; van der Schalie, 1965).

In *Potamopyrgus antipodarum* parthenogenesis is apomictic (2n=24) and polyploidy has not been observed in any snails examined. In populations where males are present, they are always sexually functional and male gametes possess the haploid chromosome number (n=12). Circumstantial evidence therefore suggests that parthenogenesis is not necessarily obligatory in all populations of *P. antipodarum*, and that where it is not, and fertilization occurs, a reduction in the chromosome number of ova must occur, so as to maintain the diploid number and not produce a triploid form. Perhaps the stimulus bringing about meiosis in the developing egg is the occurrence of copulation, or the presence of the sperm in the female system. A situation closely paralleling that found in *P. antipodarum* has been described by Robertson (1966) in chrysomelid beetles of the genus *Calligrapha*. These possess extremely variable sex ratios, ranging from 1:1, to all female populations, and parthenogenesis in at least one species, *C. scalaris*, is facultative.

The origin of parthenogenesis in all cases examined is considered to be from sexually reproducing forms, i.e. it is a secondarily derived condition (Mayr, 1963; Suomalainen, 1961), and Mayr has stated, that with the apparent exception of the bdelloid Rotifera, virtually every case of parthenogenesis in the animal kingdom is probably of very recent origin. A recent origin for parthenogenesis in *Potamopyrgus antipodarum* is indicated by the continued presence today of bisexual as well as parthenogenetic populations, and by the retention of the sperm channel, bursa copulatrix and receptaculum seminis in the reproductive system of parthenogenetic females. A parallel situation is found in parthenogenetic species of *Calligrapha* which retain a non-functioning spermatheca (Robertson, 1966).

The advantages parthenogenesis gives to a species have been discussed by several workers (White, 1954; Mayr, 1963; Tomlinson, 1966), who have concluded that it is particularly advantageous to animals inhabiting temporary or marginally suitable habitats where population densities are often low. In these situations it permits a single individual to commence breeding without requiring a mate and the reproductive capacity of the clone will be doubled as all individuals will be egg producing females. Thus, parthenogenesis increases productivity by allowing rapid build up of populations, and therefore it can be of definite, short term advantage to forms possessing it. Because no exchange of genes is possible, a parthenogenetic species frequently will continue to diverge as different mutations establish in different lines of descent. Thus, a high degree of variability will

ultimately result within many parthenogenetic species, variability which will not necessarily be correlated with geographic distribution in the same way as in a sexually reproducing form. This is what is found in *Potamopyrgus antipodarum*. Suomalainen (1961, 1962) has speculated on the ways in which mutations may be expressed in apomictic parthenogenetic animals, and his theoretical mechanism could possibly apply in the present situation. He argues that increasing heterozygosity will occur between more and more gene pairs (because elimination of recessive mutations by natural selection is impossible) until the 2 chromosome sets can no longer be considered diploid or polyploid in a genetic sense. This will reduce obstacles to the expression of the mutations present in them, and may thus, in part, even allow the formation of morphologically divergent biotypes. Further, with a continuous increase in the degree of heterozygosity, an apomictically parthenogenetic form gets an ever increasing chance to benefit from heterosis (hybrid vigour). This may therefore provide the basis for the apparently great adaptiveness and dispersive ability of many parthenogenetic forms (e.g., *P. antipodarum*), although it is in direct contrast with the widely held view that parthenogenesis leads to a lack of adaptability, and long term disadvantage (White, 1954).

Probable steps in the evolution of *Potamopyrgus* are shown in Fig. 19. *P. estuarinus* and *P. pupoides* possess the primitive features, smooth shell, sexual reproduction and oviparity, and are confined to brackish water, whereas in *P. antipodarum* shell ornamentation, parthenogenesis and ovoviviparity have developed, probably concurrently with the invasion of fresh water. Further divergent evolution has occurred and is occurring within isolated parthenogenetic populations of *P. antipodarum*, resulting in a high degree of genetic and phenotypic variability.

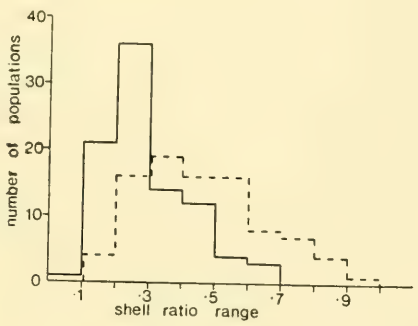

FIG. 19. Postulated steps in the evolution of the New Zealand species of *Potamopyrgus*.

The relationship of *Potamopyrgus antipodarum* to the European species *P. jenkinsi*

Potamopyrgus jenkinsi made a sudden appearance in Europe, first being described by E. A. Smith in 1889, although it may have been present as early as 1859. Its origin is uncertain and has been the subject of considerable speculation which has been reviewed by Adam (1942), Bondeson & Kaiser (1949) and Fretter & Graham (1962). The subsequent distribution of *P. jenkinsi* through Europe has also been discussed by these authors and others, e.g., Hubendick (1950).

Attempts to explain the sudden appearance of *Potamopyrgus jenkinsi* in Europe have been made by various authors, and 2 possible explanations have been suggested; (*a*) that it arose by mutation (Steusloff, 1927; Boettger, 1949), and (*b*) that it had been introduced from elsewhere. Bondeson & Kaiser (1949) have hypothesized a possible Australian origin on account of the close resemblance to the Australian species (?) *P. pattisoni*, and Boettger (1951) has suggested a New Zealand origin for *P. jenkinsi* as he considered its shell characters identical with those of *P. badia* (=*P. antipodarum*) from the South Island of New Zealand.

As a result of the present study on the New Zealand species of *Potamopyrgus*, it is possible to make a more critical comparison with *P. jenkinsi* than has been possible in the past. In doing this, information contained in the literature has been evaluated, and in addition, living and preserved material of *P. jenkinsi* from Scotland has been examined.

The shells of *Potamopyrgus jenkinsi* are variable in shape, size and ornamentation, although not as variable as those of *P. antipodarum* (T. Warwick, pers comm.), and cannot be differentiated from those of some *P. antipodarum*. Ornamentation is purely periostracal, and exists in many degrees of strength, from a faint line to a well marked spinous keel (Warwick, 1944; Fretter & Graham, 1962). Rearing experiments (Boycott, 1929; Robson, 1926; Warwick, 1944), have shown that as in *P. antipodarum* shell ornamentation of progeny does not necessarily follow that of the parent, but despite considerable speculation the mechanism controlling shell ornamentation remains unknown (Warwick, 1944; 1952; Bondeson & Kaiser, 1949).

The radula of *Potamopyrgus jenkinsi* has been described by Woodward (1892) and Krull (1935), and new material has been examined in this study. The shape of the teeth, cusp formulae, radular length, and number of rows of teeth lie within the ranges found in *P. antipodarum*.

Potamopyrgus jenkinsi exhibits considerable variability in colour and pigmentation of the head and mantle (Robson, 1920), and it cannot be separated from *P. antipodarum* on this basis, or on the structure of the operculum, or the form of the female reproductive system. Both species are ovoviviparous, and *P. jenkinsi* is considered to be parthenogenetic like many populations of *P. antipodarum*. A single male of *P. jenkinsi* has been described by Patil (1958), and it is possible that a situation similar to that found in *P. antipodarum* in which variable numbers of males occur in some populations, also exists in *P. jenkinsi*. The anatomy of the male reproductive system in the solitary male *P. jenkinsi* was identical to that of *P. antipodarum*, apart from one minor difference, the presence of a small swelling in the upper vas deferens, described as the seminal vesicle by Patil. No such swelling has been found in *P. antipodarum*. Both species reproduce throughout the year, an unusual condition in freshwater Mollusca (Fretter & Graham, 1962), and although a maximum of only 35–40 embryos has been recorded in the brood pouch of *P. jenkinsi*, compared with over 100 in some individuals of *P. antipodarum*, this is unlikely to be of systematic significance. Rather, it is probably a function of the size of the snail (and therefore the brood pouch) as *P. jenkinsi* rarely exceeds about 5 mm in shell height, whereas *P. antipodarum* may attain a height greater than 10 mm.

Considerable variation in ecology is also found in the 2 species. *Potamopyrgus jenkinsi* was initially found in brackish water (1889) and has since colonized inland waters throughout Europe and the British Isles, first having been recorded in fresh water in England in 1893 (Hunter & Warwick, 1957). *P. antipodarum*, similarly, is found in fresh and brackish water, although it is primarily a freshwater species and has certainly been established in that environment for a much longer period than has *P. jenkinsi*. Salinity records and experimental work have shown that both species possess a high degree of euryhalinity and can tolerate considerable and rapid changes in salinity. Maximum salinities at which *P. jenkinsi* can reproduce, 12–18‰, (Duncan & Klekowski, 1967) correspond closely to the value of 17·5‰, obtained in this study at which normal activity of *P. antipodarum* ceases and the snails withdraw into their shells. Both species tolerate waters with

high and low calcium content, and live in a variety of still, and running water habitats, on hard and soft substrates, and amongst vegetation.

To conclude, no significant morphological or biological differences between the 2 nominal species have been found to date, and the evidence available therefore suggests that they are the same. However, the systematics of the Australian hydrobiids, some of which are or have been placed in *Potamopyrgus* and related genera, are not clear at present and their relationship to the New Zealand species and to *P. jenkinsi* cannot be clarified until after comprehensive morphological and biological studies have been carried out on them. The presence of related genera and species in Australia (Williams, 1968) and in the South Pacific (Hubendick, 1952), indicates that New Zealand is near the centre of *Potamopyrgus* evolution, however, and it seems most likely that the European snails have been introduced from the Australasian region.

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RÉSUMÉ

LES ESPÈCES DE *POTAMOPYRGUS* DE NOUVELLE-ZÉLANDE

(Gastropoda: Hydrobiidae)

M. Winterbourn

Dans sa revision du genre, Suter (1905) reconnaît 6 espèces et 3 sousespèces de *Potamopyrgus* dans les deux principales îles de Nouvelle-Zélande, mais l'étude présente a mis en évidence qu'il n'y a seulement que 3 espèces. Ce sont: *P. antipodarum* (Gray 1843), *P. pupoides* Hutton 1882 et une espèce précédemment non reconnue **P. estuarinus** n. sp.

Potamopyrgus estuarinus et *P. pupoides* sont ovipares, possédant des coquilles lisses non ornementées et se confinent aux eaux saumâtres, tandis que *P. antipodarum* est ovovivipare, a une coquille extrêmement variable par sa taille, sa forme et son ornementation et habite aussi bien les eaux douces que saumâtres. Les populations de *P. antipodarum* peuvent comprendre uniquement des femelles parthénogénétiques ou contenir un pourcentage variable de mâles sexuellement fonctionnels. L'élevage de *P. antipodarum* au laboratoire a montré que les individus ne conservent pas forcément d'une génération à l'autre les caractères ornementaux de la coquille et que la forme et l'ornementation de la coquille ne dépendent pas à l'origine des facteurs du milieu. La coquille de *P. estuarinus* est indistingable de certaines coquilles de *P. antipodarum*, mais *P. pupoides* est facilement reconnaissable par sa petite coquille pupiforme.

La radula, l'opercule, la morphologie externe, la pigmentation du corps et l'appareil reproducteur mâle sont semblables dans toutes les espèces et n'apportent pas de caractères taxonomiques utilisables. Chez *Potamopyrgus antipodarum* la section inférieure de l'appareil reproducteur femelle est modifié pour former une poche incubatrice, sur le plancher de laquelle s'étend le sillon spermatique ouvert. Chez *P. estuarinus* et *P. pupoides* la partie inférieure du tractus génital est dominé par la glande nidamentaire fortement développée qui est effectivement séparée du conduit spermatique situé au-dessus.

Le nombre diploïde de chromosomes est de 24 pour les trois espèces.

La chromatographie des protéïnes du périostracum de la coquille n'a pas permis de distinguer de différences significatives entre les espèces en ce qui concerne la composition en amino-acides, mais a mis en évidence de considérables variations intraspécifiques.

Potamopyrgus antipodarum est abondant dans les eaux douces permanentes de toutes sortes et a été trouvé dans une eau atteignant 26‰ de salinité, bien que les expérimentations montrent qu'il n'est actif que dans une eau de salinité inférieure à 17,5‰. On n'a pas établi une nette relation entre la morphologie de la coquille et le type d'habitat; *P. estuarinus* est surtout abondant dans les estuaires de marées où existent d'importantes fluctuations de la salinité et où beaucoup d'individus sont régulièrement exposés à l'émersion entre chaque marée. *P. pupoides* occupe un habitat semblable, mais normalement demeure toujours immergé. Au laboratoire *P. estuarinus* et *P. pupoides* demeurent actifs à toutes les salinités, depuis l'eau douce jusqu'à l'eau de mer, mais ils n'ont pas été trouvés en eau douce dans la nature.

Des expériences de laboratoire ont montré l'existence de différence le comportement entre les espèces, qui sont en relation avec leurs différences d'habitat. *Potamopyrgus estuarinus* montre des tendances amphibies prononcées qui n'existent pas chez *P. antipodarum* et se révèle capable de survivre dans un état " dormant " quand il est exposé à l'air pendant 70 jours.

Le complexe *Potamopyrgus antipodarum* est examiné à la lumière des conceptions actuelles sur la notion d'espèce, et le haut degré de variabilité qu'on a trouvé dans cette espèce est à mettre en relation avec l'existence de l'ovoviviparité et de la parthénogénèse qui permettent à un haut degré d'évolution divergente d'apparaître indépendamment dans des populations individuelles.

Une comparaison entre *Potamopyrgus antipodarum* et l'espèce européenne *P. jenkinsi* (Smith) montre que les deux ne peuvent être distinguées sur des bases anatomiques et que de nombreux faits de leur biologie et de leur écologie sont semblables. Il semble par conséquent probable que les deux sont la même espéce, les spécimens européens ayant été introduits de Nouvelle-Zélande (ou d'Australie?) au cours du 19 eme siècle.

A. L.

АБСТРАКТ

НОВОЗЕЛАНДСКИЕ ВИДЫ *POTAMOPYRGUS* (GASTROPODA: HYDROBIIDAE)

М. ВИНТЕРБОУРН

В своей ревизии рода *Potamopyrgus*, Suter (1905) различал в нем 6 видов и 3 подвида, обитающих на двух основных островах Новой Зеландии; однако в настоящей работе указывается, что имеется лишь три вида: *P. antipodum* (Gray 1843), *P. pupoides* (Hutton 1882) и ранее неизвестный вид- *P. estuarinus n.sp.*

P. estuarinus и *P. pupoides* откладывают яйца, имеют гладкую без узоров раковину и связаны в своем обитании с солоноватыми водами, в то время как *P. antipodum* является яйцекладуще-живородящей, сильно изменчивой по размерам, очертаниям и орнаментации раковины и живет как в пресной воде так и в солоноватой. Популяции *P. antipodum* могут состоять только из партеногенетических самок или содержать различное количество особей, функционирующих как самцы. Разведение *P. antipodum* в лабораторных условиях показало, что эти моллюски не обязательно дают орнаментированные раковины и что форма раковины и ее орнамент не зависят от факторов среды. Раковина *P. estuarinus* не отличима от раковин некоторых *P. antipodum*, однако *P. pupoides* легко отличается от них своей маленькой раковиной. Радула, крышечка, наружная морфология, пигментация тела и половая система самцов сходны у всех видов и не имеют таксономического значения. У *P. antipodum* нижняя часть женской половой системы модифицирована в выводковую камеру с открытым желобком для спермы, проходящим по ее дну.

У *P. estuarinus* и *P. pupoides* нижний репродуктивный проток имеет вид сильно развитой капсульной железы, отделенной от лежащего ниже протока сперматеки.

Диплоидное число хромосом у всех трех видов равно 24. При помощи ионно-обменной хроматографии белков из периостракa раковины не было установлено различий в составе аминокислот у всех видов, однако отмечена его внутривидовая изменчивость.

P. antipodum изобилует в постоянно-пресных водах всех типов и был найден также при солености 26‰, хотя эксперименты показывают, что эти моллюски активны лишь при солености ниже 17,5‰. Не было найдено никакой ясной корреляции между морфологией раковины и характером их местообитания.

P. estuarinus наиболее обилен в эстуариях литоральной зоны, где наблюдаются значительные колебания солености и где многие брюхоногие моллюски регулярно подвергаются осушению во время приливно-отливного цикла.

P. pupoides занимает сходное местообитание, но обычно всегда находится под водой. В лабораторных условиях *P. estuarinus* и *P. pupoides* остаются активными при разной солености, начиная от пресной воды до морской, однако в природе они в пресных водах до сих пор не встречались.

Лабораторные опыты указывают на существование различий в поведении различных видов, которые связаны с различиями в условиях их обитания. *P. estuarinus* имеет ясно выраженную тенденцию к амфибионтности (чего не наблюдается у *P. antipodum*) и может выживать на воздухе в "сонном" состоянии в течение 70 дней.

Комплекс *P. antipodum* исследовался в свете современных теорий о виде; высокая степень изменчивости этого вида связана с наличием у него то откладки яиц и живорождения, то партогенеза, которые сопровождаются высокой степенью дивергентной эволюции и наблюдается независимо у различных популяций.

Сравнение между *P. antipodum* и европейским видом *P. jenkinsi* (Smith) показывает, что они не могут быть отличимы по анатомическим признакам и что многие черты их биологии и экологии сходны. Поэтому кажется вполне вероятным, что оба они являются одним и тем же видом, поскольку европейские улитки были интродуцированы из Новой Зеландии (или Австралии?) в XIX столетии.

Z.A.F.

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DESCRIPTION OF THE JUVENILE FORM OF THE ANTARCTIC SQUID *MESONYCHOTEUTHIS HAMILTONI* ROBSON[1]

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ABSTRACT

The juvenile form of *Mesonychoteuthis hamiltoni* Robson is fully described and figured from 4 specimens captured by the U.S. Naval Ship ELTANIN in Antarctic waters. Measurements and indices are given. This constitutes the first full description of the species. The validity of the genus is reaffirmed, but relationships to other genera within the family Cranchiidae are not yet clear.

In 1925 Robson described a new species of squid, *Mesonychoteuthis hamiltoni*, from 2 large brachial crowns taken from the stomach of a sperm whale captured near the South Shetland Islands. He was uncertain of the systematic position of the species represented by these fragments, but tentatively placed it between the Onychoteuthidae and Enoploteuthidae (Robson, 1925: 272). The principal features mentioned by Robson in this paper were the presence of hooks in the central portion of the arms, and the supposedly distinctive structure of the tentacular hooks. Clarke (1966) includes the species in his systematic review, with the statement "*M. hamiltoni* is a taonine cranchiid which attains giant size" (Clarke, 1966: 240). Clarke further states that the genus *Mesonychoteuthis* is monotypic and is "characterized by hooded hooks in the middle of each arm." The only other reference to the genus found in the literature is Clarke's (1962) discussion of the mandibles.

Among the Antarctic cephalopod collections made by the National Science Foundation's research ship ELTANIN are 4 small cranchiid squids which bear hooded hooks in the central portion of the arms, and must be referred to Robson's species. The following description of these juvenile specimens constitutes the first full description of the species.

The writer would like to thank Dr. G. L. Voss of the Institute of Marine Sciences for his comments and criticisms of the manuscript. Dr. R. E. Young of the Department of Oceanography, University of Hawaii, materially aided the writer by offering many helpful suggestions and critically read the manuscript. The specimens on which the description is based were collected by the University of Southern California's biological sampling program aboard the U.S.N.S. ELTANIN. The terminology used in describing the mandibles is after Clarke (1962) and Mangold & Fioroni (1966). The illustrations were executed by my wife Constance.

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Mesonychoteuthis hamiltoni Robson, 1925
Figs. 1–3

Mesonychoteuthis hamiltoni Robson, 1925, p. 272, figs. 1, 2.

Material examined:

1 Specimen, mantle length 86 mm. ELTANIN Sta. 142. 60°04'S, 65°15'W. 10 Aug. 1962. 3 m IKMT, 0–1850 m.
1 Specimen, mantle length 68 mm. ELTANIN Sta. 929. 70°12'S, 110 17'W. 19 Jan. 1964. 3 m IKMT, 0–1098 m.
1 Specimen, mantle length 59 mm. ELTANIN Sta. 941. 69°56'S, 98°31'W. 23 Jan. 1964. 3 m IKMT, 0–2562 m.
1 Specimen, mantle length 59 mm. ELTANIN Sta. 946. 67°39'S, 90°27'W. 26 Jan. 1964. 3 m IKMT, 0–1711 m.

Description

The mantle is short and wide (MWI=35·0), tapering smoothly to the middle of the fins, where it abruptly narrows to closely sheath the gladius. Only the integument continues over the conus. The mantle is thin and leathery, and is fused to the head at the dorsal midline and ventrally to each side of the funnel. At each ventral fusion there is a 5 or 6-pointed cartilaginous tubercle, and at the dorsal fusion point there is a single small, conical tubercle. The gladius is distinctly visible through the integument along the dorsal midline. The fins measure 20–30% of the mantle length and are almost semicircular (FLI, FWI=21·0). The funnel is broad at the base and tapers rapidly, extending nearly to the base of the ventral arms. It is fused to the head dorsally. The dorsal member of the funnel organ has the shape of a rounded, inverted V, with the two legs of the V directed slightly outward at the tips. At the apex there is a long conical tubercle surmounted by a narrow flap of tissue. The height of this tubercle is $\frac{1}{3}$ to $\frac{1}{2}$ the total length of the dorsal member. At the posterior end of each leg of the V, there is a smaller, rounded tubercle. The ventral pads are fanshaped, with the apex directed anteromedially. There is no trace of a funnel valve.

The head is small, with large globular eyes. The total width, including the eyes, is less than the mantle width (HWI=25·0). The eyes are directed outward at an angle of about 45° from the longitudinal axis. The eyes have a large, wide, crescent-shaped light organ applied to the ventral surface, and extending upward almost half the circumference. A smaller, oblong light organ lies inside the concavity of the crescent, close to the pupil. There is a very small anterior notch in the rim of the eye opening. The stalk of the "olfactory papilla" is very short, and the organ is closely applied to the posterior surface of the eye capsule, well below the midline.

The arms range from 20–30% of the mantle length in smaller specimens and from 30–40% in the larger specimens. They are round in cross section, with the formula 4.3.2.1. Protective membranes and trabeculae are fairly well developed on the ventral side of all the arms, and consist of a low, scalloped fringe on the dorsal side. A weak swimming keel is present on the third arms, and a stronger lateral keel on the ventral arms. The suckers are arranged in 2 rows with small suckers proximally, becoming larger to about the mid-point of the arms, where they are replaced by prominent hooks. On the largest specimen, these hooks are initially much larger than any of the suckers, becoming the same size distally. On the smaller specimens, the proximal hooks are about equal in size to the preceding suckers. The distal portion of the arms again bears suckers, the most proximal of these being slightly smaller than

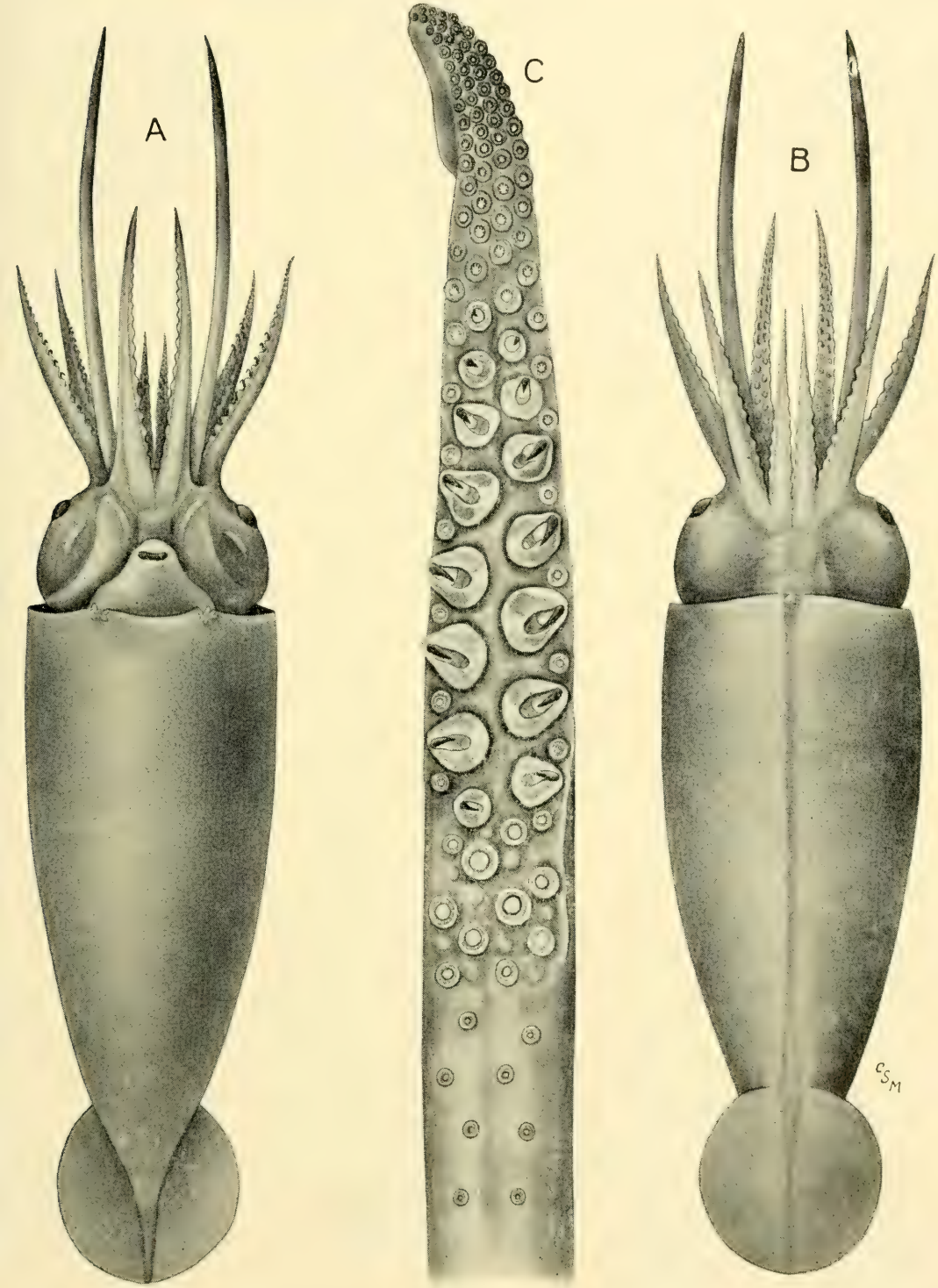

FIG. 1. *Mesonychoteuthis hamiltoni* Robson. Mantle length 86 mm (ELTANIN Sta. 142). **A.** Ventral view. **B.** Dorsal view. **C.** Tentacular club.

TABLE 1. Measurements (in mm) of 4 juvenile specimens of *Mesonychoteuthis hamiltoni* Robson.

Character	ELTANIN Sta. 142	ELTANIN Sta. 929	ELTANIN Sta. 941	ELTANIN Sta. 946
Mantle length	86	68	59	59
Head width	27	17	15	15
Eye diameter	15	10	8	8
Fin length	22	14	11	11
Fin width	21	14	11	11
Arm length: I	25	13	11	10
II	29	18	13	11
III	31	20	16	14
IV	33	24	18	16
Tentacle length	60	44	46	37
Club length	15	12	10	9

the last sucker proximal to the hooks. Table 3 lists the numbers of proximal suckers and hooks. The number of suckers distal to the hooks ranges from 8–10 in the smaller specimens to 25–30 in the largest specimen. Dentition is apparent on the first few suckers distal to the hooks. This consists of incisions in the most distal quarter of the inner ring to form 1 to 5 irregular teeth.

The tentacles are moderately long and slender, oval in cross section and slightly flattened on the oral surface. The diameter is nearly constant, with the club tapering evenly to the tip. The only demarcation between the stalk and club is a slight constriction across the aboral surface. The club comprises one-quarter of the total tentacle length and is bordered by a very low and indistinct protective membrane on either side. There is a very small dorsal keel at the extreme tip. The club bears 4 longitudinal rows of suckers, with from 22 (dorsal row) to 24 (ventral row) suckers. The first 6 to 8 suckers in the two central rows are modified into hooks. The suckers of these rows, distal to the hooks, decrease in diameter toward the tip, while those of the marginal rows are small suckers of nearly constant diameter throughout. The club suckers are armed with small teeth around the inner circumference, with those in the distal quarter better developed. The carpal apparatus consists of 10 suckers, without teeth, and 10 pads on each tentacle. The stalk carries 22 to 23 pairs of small suckers, alternating with pads, and extending almost to the base of the tentacle.

The buccal membrane has 7 lappets. The connectives attach dorsally to arms I and II, and ventrally to arms III and IV.

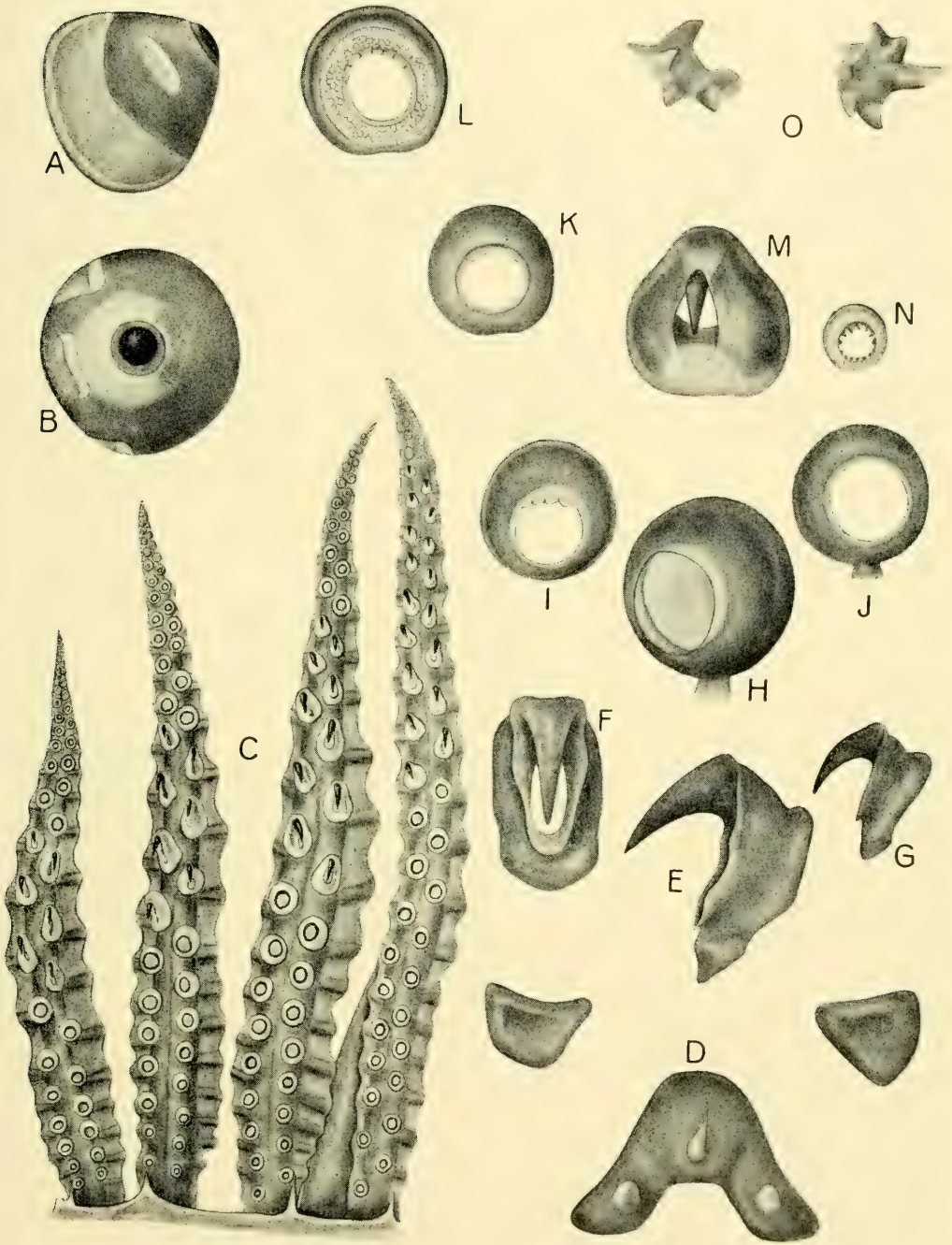

FIG. 2. *Mesonychoteuthis hamiltoni* Robson. (A–K, M–O, ELTANIN Sta. 142. L, ELTANIN Sta. 929). **A.** Ventral, and **B.** Lateral view of eye capsule, showing light organs. **C.** Left arms I–IV. **D.** Funnel organ. **E, F.** Hook, arm III. **G.** Hook, arm IV. **H.** 1st sucker proximal to hooks, arm III **I.** 1st sucker distal to hooks, arm III. **J.** 1st sucker proximal to hooks, arm IV. **K.** 2nd sucker distal to hooks, arm II. **L.** 2nd sucker distal to hooks, arm I. **M.** Tentacular hook. **N.** Dactylus sucker. **O.** Cartilaginous tubercles at mantle-funnel fusion points.

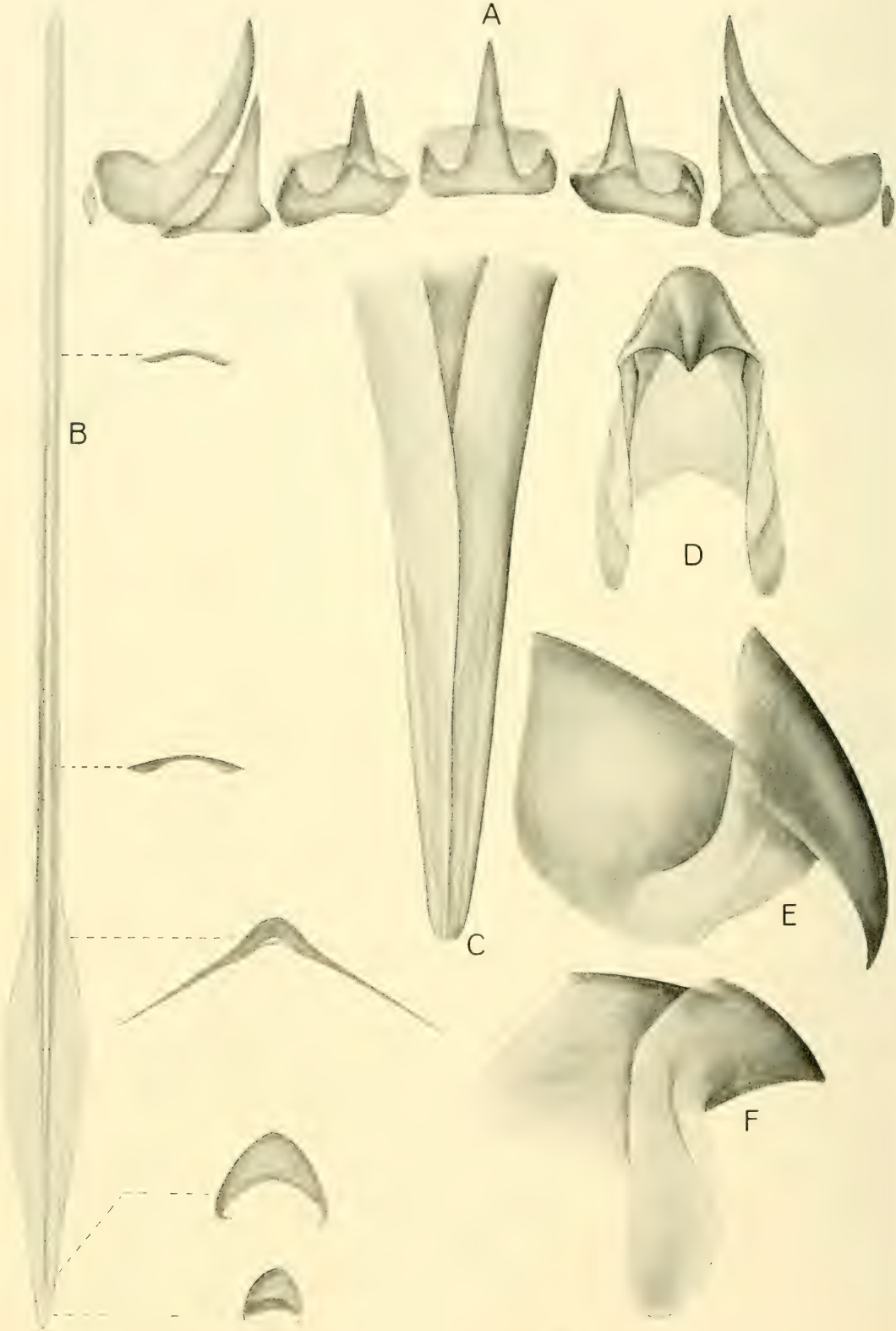
A
B
C
D
E
F

TABLE 2. Indices of bodily proportions of 4 juvenile specimens of *Mesonychoteuthis hamiltoni* Robson. All indices are the indicated measurement expressed as a percentage of the mantle length.

Character	ELTANIN Sta. 142	ELTANIN Sta. 929	ELTANIN Sta. 941	ELTANIN Sta. 946
Mantle width index (MWI)	35·0	31·0	34·0	36·0
Head width index (HWI)	31·0	25·0	25·0	25·0
Fin length index (FLI)	26·0	21·0	19·0	19·0
Fin width index (FWI)	26·0	21·0	19·0	20·0
Arm length index (ALI): I	29·0	19·0	19·0	17·0
II	34·0	26·0	24·0	20·0
III	36·0	29·0	30·0	26·0
IV	38·0	35·0	32·0	27·0
Club length index (CLI)	17·0	18·0	17·0	17·0

The hood of the upper mandible is slightly flattened dorsally and forms rounded angles dorso-laterally. These dorso-lateral angles join near the tip of the rostrum to form a dorsal ridge. The line of the inner edge of the rostrum continues posteriorly across the wing as a distinct ridge. Above this ridge, the lateral surfaces of the hood are slightly concave. The wings extend downward to the lower angle of the lateral wall. There is a wide area of fusion between the lateral wall and the wing, forming a slightly projecting shoulder. The jaw angle is about 90°, and is somewhat recessed. The hood length is approximately $\frac{3}{4}$ of the crest length.

The lower mandible has the obtuse jaw angle partially obscured by an overlapping lateral bulge of the wing. The wing extends downward beyond the lower margin of the lateral wall. The hood length is slightly more than $\frac{1}{2}$ the crest length.

The radula has a tricuspid rachidian tooth with a long median and small outer cusps. The first lateral tooth has a broad base, with a moderately long inner cusp and a small outer cusp. The second lateral is simple, broad and thick at the base, and somewhat longer than the first lateral. The third lateral is simple, strongly curved, and longer than the other teeth. The marginals are very small, unarmed plates.

The gladius is narrow, with the vanes bordering the posterior third of the rachis. The anterior $\frac{2}{3}$ of the rachis is very narrow, of nearly uniform width, and slightly concave ventrally. In the region of the vanes, it is thickened and

FIG. 3. *Mesonychoteuthis hamiltoni* Robson (A, B, D, E, F, ELTANIN Sta. 142;) C, ELTANIN Sta. 946). **A,** Radula. **B,** Gladius. **C,** Conus of gladius; ventral view **D, E,** Upper mandible. **F,** Lower mandible.

TABLE 3. Numbers of proximal suckers and hooks on arms of juvenile specimens of *Mesonychoteuthis hamiltoni*. Question marks indicate missing hooks at end of series.

Character	ARM	ELTANIN Sta. 142	ELTANIN Sta. 929	ELTANIN Sta. 941	ELTANIN Sta. 946
Proximal	I	13/14	13/13	14/15	14/14
Suckers (Right/Left)	II	15/14	13/13	15/15	15/15
	III	17/17	16/16	19/19	18/18
	IV	20/20	19/20	22/22	22/21
	I	6/6	6/5	7/7	5/5
Hooks (Right/Left)	II	7/8	8/7	8?/9?	6/6
	III	10/9	9/9	10/10	7/8
	IV	16/16	13/14	10+/12?	8/7

steeply ridged along the midline. At the posterior tip the vanes overlap ventrally, but are not fused. This portion of the gladius of a 59 mm specimen (ELT 946) is illustrated in Fig. 3C. All others had the vanes broken away in this region.

DISCUSSION

It is difficult to compare the present material with Robson's original description, even without considering the disparity in size. Some of the features which he mentioned as being characteristic were most probably the result of the action of the digestive process. However, some conclusions can be drawn.

The arms present the feature of greatest interest, namely the series of hooks in the central portion. As *Mesonychoteuthis* is the only cranchiid known to possess hooks on the arms, it is not surprising that this armament, coupled with the tentacular hooks, led Robson to ally the species with the enoploteuthids and onychoteuthids. The presence of the hooks in these juvenile specimens is of utmost importance, as it accentuates the value of this feature as a generic character. This character makes *Mesonychoteuthis* easily separable from *Galiteuthis*, which it resembles in the possession of tentacular hooks. The writer has examined a mature specimen of *Galiteuthis* and found well developed suckers present along the full length of the arms.

In Robson's specimens, the suckers were missing in the distal portion of the arms, with the stumps remaining. He considered that this was the result of atrophy rather than accident (Robson, 1925: 273). The fact that in the present material the suckers extend to the tips of the arms indicates that in Robson's specimens these suckers were probably lost accidentally or through digestion.

Robson considered the "swivel-movement" of the tentacular hooks to be a feature characteristic of only a few species (1925: 275). After an examination of

specimens of most of the genera which have tentacular hooks, it is apparent that all are capable of some degree of swivel-motion, probably much more so in life than is indicated in preserved animals. The principal difference between species seems to be in the degree of freedom of movement, although differences are not really great. It is doubtful that this feature has particular significance in *Mesonychoteuthis*. The tentacular club of Robson's specimen was probably broken, as he mentions a " very short hand " and states that it lacked suckers (1925: 275). It is possible that the proportions of the club change with growth, but it seems probable that the extreme condition reported by Robson was the result of damage or digestion, or both. The lack of differentiation between the tentacular stalk and the comparatively long club is a distinctive feature of the specimens described above.

Robson described the row of suckers and pads on the tentacular stalk as being " unique among these forms " (1925: 276). What is meant by " these forms " is unclear, but this conformation is common among cranchiid squids, while it does not occur in either of the families to which he supposed *Mesonychoteuthis* was most closely related.

The eyes are completely sessile in the present material, giving no indication of a stalked condition, although it is very likely that younger forms pass through such a stage. This has been shown to be the case in *Desmoteuthis* (=*Megalocranchia*) by Muus (1956), and has been observed by the writer in specimens of *Taonius* and *Galiteuthis*. No features observed in the present material could be considered larval characters.

The light organs of the eye, although well-formed in the largest specimen, are probably not completely developed. In the smaller specimens, the small light organ at the inside of the ventral crescentic organ is only partially formed, consisting of a narrow, thickened ridge. In the larger specimens, this ridge is bordered by an area of thin, dark tissue. These organs may in time become crescent-shaped also, or oval.

The mandibles show some differences from Clarke's (1962) description of a much larger example. The significance of these differences cannot be determined without a series bridging the gap in size. The principal differences are in the concave lateral surfaces of the hood, and the ridge across the midpoint of the wing.

The radula shows a considerable difference from Robson's illustration (1925, fig. 1), but the differences can probably be explained by both the difference in size of the specimens and the angle at which the drawings were made. In Robson's figure, the third lateral tooth is shown as nearly straight, although Robson states (1925: 276) that it is slightly curved. This indicates that the drawing was made without flattening the ribbon, which could account for other differences, as in the relative height of the cusps. Robson also overlooked the marginal plates, which are extremely small.

These specimens show similarities to other genera in some respects, notably to *Megalocranchia* in general appearance, and to *Galiteuthis* in possession of tentacular hooks. However, this resemblance is only superficial, as is shown by most of the principal characters. It would be premature at this time to speculate on relationships within the family.

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RÉSUMÉ

DESCRIPTION DE LA FORME JUVÉNILE DU CALMAR ANTARCTIQUE *MESONYCHOTEUTHIS HAMILTONI* ROBSON

E. S. McSweeny

La forme juvénile de *Mesonychoteuthis hamiltoni* Robson est entièrement décrite et figurée à partir de quatre spécimens capturés par le U.S.N.S. Eltanin dans les mers antarctiques. Des mensurations et des indices sont donnés. Cela constitue la première description complète de l'espèce. La validité du genre est réaffirmée, mais la relation avec les autres genres de la famille des Cranchiidae n'est pas encore claire.

A. L.

RESUMEN

DESCRIPCION DE LA FORMA JUVENIL DEL CALAMAR ANTARTICO *MESONYCHOTEUTHIS HAMILTONI* ROBSON

E. S. McSweeney

La forma juvenil de *Mesonychoteuthis hamiltoni* Robson, se describe en forma completa y se ilustra con 4 ejemplares que fueron capturados por el U.S.N.S. ELTANIN en aguas antarticas. Todo esto constituye la primera descripción total de la especie. Se confirma la validez del género *Mesonychoteuthis*, aunque su relación con otros en la familia Cranchiidae no resulta todavía muy clara.

J. J. P.

АБСТРАКТ

ОПИСАНИЕ ЮВЕНИЛЬНОЙ ФОРМЫ АНТАРКТИЧЕСКОГО КАЛЬМАРА *MESONYCHOTEUTHIS HAMILTONI* ROBSON

Э. С. МЭКСВИНИ

Ювенильные формы *Mesonychoteuthis hamiltoni* Robson описаны и изображены по 4 экземплярам, пойманным на корабле "Илтенин" в водах Антарктики. Приводятся данные измерений и индексы, что дополняет первое полное описание этого вида. Подтверждается валидность рода, однако его взаимоотношения внутри семейства Cranchiidae еще не ясны.

Z. A. F.

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A RE-EVALUATION OF THE RECENT UNIONACEA (PELECYPODA) OF NORTH AMERICA

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ABSTRACT

Recent higher classifications of freshwater mussels, based principally on shell characters, do not reflect the phylogenetic relationships of these animals which may be interpreted from reproductive features. Although these 2 types of characters are not consistently mutually exclusive, there is comparatively little overlap. Shell characters have received emphasis in the classification of naiades on a world-wide basis because of convenience of study and because they can be employed in investigations of fossil material. Unfortunately, too little information on reproductive morphology and habits is presently available to permit a wide-scale classification based on these features, and it may prove difficult to relate fossil forms to such a scheme should one eventually be proposed. The choice of one system (*i.e.*, either shell or soft-parts) demonstrates parallel evolution of characters in the other system. It is considered here that a system based on aspects of reproduction, with parallelism in the shell features, more accurately reflects natural, evolutionary affinities than does a system which reverses the emphasis.

In order to stimulate further investigation (particularly of non-Nearctic groups), a revised system of affinities of North American naiades at the familial and subfamilial levels, derived from anatomical and related aspects of reproduction, is presented here. This system concerns such features as (*a*) the number of marsupial demibranchs (4 or 2), (*b*) the location of the marsupial demibranchs (only the inner 2, or only the outer 2), (*c*) specific regions of the marsupial demibranchs which incubate the developing larvae (the entire demibranchs, only the posterior portion, only the central portion, *etc.*), (*d*) the morphology of the marsupial demibranchs (simple or subdivided septa and water-tubes; continuous or interrupted septa and water-tubes), (*e*) the duration of incubation of the larvae (short- or long-term), (*f*) the nature of the glochidial shell (hooked or hookless), and (*g*) other anatomical aspects more subtly related to reproduction in terms of water currents (completeness and composition of the diaphragm; presence/absence of a supra-anal opening).

These characters indicate that Recent representatives of the Margaritiferidae, Amblemidae and Unionidae occur in North America. A fourth family, the Hyriidae, is known from the Nearctic Region only in fossil form; living species are presently confined to South America and Australasia. Nearctic subfamilies and their characters are delineated for these 3 Recent families, and the North American genera of each group are listed. Three new subfamilies are proposed: **Cumberlandinae** (Margaritiferidae), **Megalonaiadinae** (Amblemidae) and **Popenaiadinae** (Unionidae). Notes on related unionacean groups in the Neotropical, Palearctic, Ethiopian, Oriental and Australasian regions are provided.

A suggested relationship of the Mutelacea to the Unionacea is included, and phylogenetic affinities of the families and subfamilies of Nearctic unionaceans are interpreted from reproductive data. The presently-Holarctic Margaritiferidae, the most primitive group of unionaceans, is considered to have independently given rise to the hyriid-mutelacean stock and to the Amblemidae. The Amblemidae, present in all areas but South America and the Australasian Region, in turn is described as ancestral to the Unionidae. The unionids have reached greatest diversification in North America and comprise the vast majority of Nearctic mussels. The more primitive Pleurobeminae (presently confined to North and Central America) is suggested to have given rise inde-

pendently to (*a*) the Popenaiadinae of the southern United States, Mexico and Central America, (*b*) the Anodontinae of the Northern Hemisphere, and (*c*) the Lampsilinae of North and Central America. The Unioninae s.s. of Eurasia is thought to have been derived from anodontine stock. The Pleurobeminae is considered to be ancestral to the primitive lampsiline stock which subsequently diverged along several lines through specializations of the marsupial demibranchs.

The evolutionary trends in advancement and/or specialization of the Nearctic unionaceans include (*a*) reduction from 4 to 2 (principally the outer pair) marsupial demibranchs, with greatest diversification occurring in present groups in the Northern Hemisphere, (*b*) development of continuous interlamellar septa and water-tubes, (*c*) morphological adaptations of the marsupial demibranchs which reach greatest specialization by restricted regionalization of ovisacs in the unionid Lampsilinae, (*d*) a tendency toward a complete diaphragm formed entirely by the ctenidia, and (*e*) a general change from short-term to long-term incubation of the larvae. Most unionaceans possess hookless glochidia, and the hooked larvae are considered to have evolved independently in the hyriids and in the unionine-anodontine stock.

INTRODUCTION

Modell (1942, 1949, 1964), Morrison (1955, 1966, 1967), McMichael & Hiscock (1958), and Haas (1969a, 1969b) have altered the taxonomic treatment and presented new impressions of the phylogenetic affinities (?) of freshwater mussels of the families Margaritiferidae, Mutelidae and Unionidae as formerly interpreted by Simpson (1896, 1900a, 1914), Ortmann (1910a, 1911a, 1912a, 1921a) and Frierson (1927). However, the work of Parodiz & Bonetto (1963) has demonstrated the necessity of a re-evaluation of these other recent reports and has consequently prompted this extension of their findings.

Modell originally (1942) emphasized beak sculpture as the principal character which he considered to reflect phylogenetic relationships; other shell characters (e.g., form and hinge aspects), anatomical features, and larval type were relegated to secondary importance. Later (1949), Modell fruitlessly attempted to support his concepts with morphological information. His most recent report (1964) shows few digressions from his previous considerations.

While Ortmann's (1910a) system of the "Unionidae," widely followed by North American workers, consists of but 3 subfamilies (viz., Unioninae, Anodontinae and Lampsilinae), Modell's latest (1964) scheme includes the following higher taxa which include Nearctic representatives:

Family Elliptionidae Modell, 1942
- Subfamily Pleurobeminae[1] Modell, 1942
- Subfamily Elliptioninae Modell, 1942
- Subfamily Ambleminae[2] Modell, 1942
- Subfamily Alasmidontinae[2] Frierson, 1927
- Subfamily Lampsilinae von Ihering, 1901

Family Unionidae[2] Fleming, 1828
- Subfamily Quadrulinae von Ihering, 1901
- Subfamily Rectidentinae Modell, 1942
- Subfamily Anodontinae[2] Swainson, 1840

Morrison (1955) restored Modell's Ambleminae to familial rank (as Refinesque, 1820, employed it) and included in it the subfamilies Ambleminae

[1] This taxon was first employed by Hannibal in 1912.

[2] These taxa were originally proposed by Rafinesque in 1820.

s.s. and Lampsilinae. As Morrison (1967) also pointed out, the family Quadrulidae Hannibal, 1912, and its subfamily Quadrulinae von Ihering, 1901, are synonyms of the Amblemidae and Ambleminae, respectively.

McMichael & Hiscock (1958) recognized the importance of soft-part and reproductive features, but they persisted in subscribing to Modell's scheme based principally on shell characters.

Haas (1969a, 1969b) presents more conservative systems which include the Recent North American unionaceans in the Margaritiferidae and Unionidae (and its subfamilies Unioninae s.s., Quadrulinae, Anodontinae, Alasmidontinae, Lampsilinae and Hyriinae).

In our opinion most classifications of freshwater mussels have (1) overemphasized shell sculpture, paleontological data and seemingly zoogeographic relationships, and (2) only superficially interpreted anatomical features. While Frierson (1909, p 107) stated that "beak sculpture and manner of carrying ova in the gills are not correlated," he preferred to use shell features as the basis of classification. However, as Hannibal (1912, p 117) and Ortmann (1912a, p 230) have pointed out, respectively, shell characters are of "secondary importance in the recognition of groups more comprehensive than genera," and are "unfit to be used for the distinction of the larger groups." Modell's (1942, p 164) suggestion that most anatomical characters "gehen Hand in Hand mit Umbildungen der Schale" would be considered by Hannibal and Ortmann (and by us) to be fallacious.

A number of different schemes of classification of freshwater mussels have been proposed (see McMichael & Hiscock, 1958), each seeming to stress a different combination of characters and/or rearranging the member groups. Van der Schalie (1952) has provided a most informative paper which reviews (1) some of the systems that earlier workers devised, and (2) the personalities of several of these taxonomists/systematists.

Sterki (1898, 1903) indicated that the classification of these mollusks should include their reproductive features, e.g., the number and location of the marsupial demibranchs, the regions of these demibranchs which incubate the developing larvae, the morphology of the marsupial demibranchs, the duration of gravid periods (= "breeding season" of authors), and the nature of the glochidial larvae. Simpson (1900a) created a number of divisions (based upon distinctive marsupial demibranch features) within the subfamilies of the "Unionidae." Ortmann subsequently subscribed to the initial findings of Sterki and Simpson and extended their work in more detail.

In viewing Modell's most recent phylogenetic scheme (1964, figure on p 122), one can immediately detect the composite nature of the families Elliptionidae and Unionidae. In the Elliptionidae (comprising elements of Ortmann's 1910a Unioninae, Anodontinae and Lampsilinae!) are the Lampsilinae and Alasmidontinae which are for the most part bradytictic (i.e., "long-term breeders," retaining developing glochidial larvae except in the Nearctic summer), while others are tachytictic (i.e., "short-term breeders," carrying glochidia only in the Nearctic summer: Pleurobeminae, Elliptioninae and Ambleminae). The Alasmidontinae contains species with hooked glochidia, while the other members of this family Elliptionidae possess hookless larvae. Animals of the Elliptionidae have seven different marsupial gill conditions which Simpson (1900a) termed tetragenae, homogenae, diagenae, heterogenae, mesogenae, eschatigenae and ptychogenae. Modell also included in the "family Unionidae" groups with (1) the tetragenous condition, short-term

breeding and hookless glochidia, and (2) the homogenous condition, long-term breeding and hooked glochidia. Furthermore, groups with hooked glochidia, the homogenous condition and long-term breeding were placed in 2 different unionid subfamilies (Rectidentinae and Anodontinae), and genera with these same features were included in the Alasmidontinae of the Elliptionidae. Finally, Modell's Rectidentinae contains (1) *Rectidens* Simpson which is tetragenous and has hookless glochidia, and (2) *Arnoldina* Hannibal, *Utterbackia* Baker and *Pyganodon* Crosse & Fischer[3] which have the homogenous condition and hooked glochidia. These few examples should suffice to demonstrate the shortcomings of Modell's classification.

Hass (1969a, 1969b) has provided the most recent conchological systems, and he lists 6 subfamilies (compared to Modell's 12), in the Unionidae: Unioninae, Quadrulinae, Anodontinae, Alasmidontinae, Lampsilinae and Hyriinae. However, his scheme (1) does not consistently separate tetragenous and homogenous groups, (2) maintains a distinction between the Anodontinae and the Alasmidontinae, and (3), like Modell, retains the Hyriinae[4] in the Unionidae.

In these previous examples we have attempted to show the limited value of using principally (or entirely) shell characters in the classification of freshwater mussels. Ortmann's work remains today as a model of the anatomical/reproductive approach. He recognized, however, that his provisional interpretations could be subject to change in the light of additional information. In addition, he was interested in the natural relationships of these mussels, not just in their nomenclature. We will attempt to follow Ortmann's lead and hopefully extend our knowledge of the evolution of this large and diverse group of animals. To do so, however, requires a re-evaluation of his concept of the unionid subfamilies, particularly the Unioninae (see Ortmann, 1910a, 1912a). His consideration of this group includes several genera with 4 marsupial demibranchs as well as others with only the outer 2 demibranchs marsupial (although all except *Megalonaias* Utterback (tetragenae) and *Popenaias* Frierson (homogenae) are short-term breeders, and all North American groups possess hookless glochidia). His (1910a) Anodontinae (s.l.) encompasses the Alasmidontinae (s.s.) as defined by Rafinesque (1820), Swainson (1840), Frierson (1927), Modell (1942, 1949, 1964) and Haas (1969a, 1969b). Since all species of these 2 groups possess marsupial demibranchs (homogenae in all genera but *Strophitus*, which has the diagenous condition) with secondary interlamellar septa and secondary water-tubes, they are more correctly considered as a single group unlike any other subfamily. Ortmann's (1910a) Lampsilinae (an extension of von Ihering's 1901 taxon) is retained by Modell (1942, 1949, 1964) and Morrison (1955), but is removed to the Elliptionidae and Amblemidae, respectively.

It appears to us that the aforementioned reproductive characters are more significant than Modell, Morrison, McMichael & Hiscock, and Haas have considered, and we find their systems artificial and untenable. Consequently, we recommend a consideration of what we feel are more distinctive features, and we offer here a revised higher classification of the North

[3] These 3 taxa are actually subgenera of *Anodonta* Lamarck which Modell correctly places in the Anodontinae.

[4] McMichael & Hiscock (1958) included the Hyriinae in the Mutelidae (Mutelacea), but Parodiz & Bonetto (1963) correctly restored it to familial rank and placed it in the Unionacea.

American naiades. Unlike numerical taxonomists who use all characters and give them equal weight, we have subjectively elected to ignore one entire array of characters (i.e., conchological features) and to suggest soft-part anatomy and reproductive habits as pre-eminent in describing phylogenies. There is regretably little specific evidence to support our contention that shell features are the less conservative characteristics. However, ecophenotypic variation in the shell is well documented, and it is difficult (if not impossible) to interpret the possible genetic adaptation(s) of different forms of beak and disc sculpture. Besides, although the shell features of these mussels are indeed convenient, they have not adequately been demonstrated to be more conservative than any other set of characters. Consequently, we have preferred to emphasize reproductive aspects in the manner that systematic botanists favor flowers (i.e., reproductive organs) to such vegetative characters as leaves. Nevertheless, it is hoped that when more information on naiades from other regions becomes available the shell and reproductive features can be correlated into a more meaningful system which more accurately defines the parallel evolution in either or both set(s) of characters on a worldwide basis.

The anatomy and reproductive habits of mussels of the Ethiopian, Oriental and Australasian Regions are still poorly known. While we have provided notes on some species/genera from these areas, we cannot at this time adequately interpret their characters in terms of our proposed system. Future investigations of naiades in these areas will provide information which may well modify the views and concepts presented here. Our objective is to present a format to which future studies (hopefully to be stimulated by this paper) may be compared.

We have listed in this paper the commonly-used generic designations of the different families and subfamilies of the Nearctic unionaceans. However, we wish to stress that a critical re-evaluation of these alleged genera is needed. This is indicated in particular by the presence of some 18 monotypic genera among the 48 genera listed for North America. Superscript numbers in the following section refer to corresponding comments under Notes, which appear at the end of this paper (p 345).

CLASSIFICATION

SUPERFAMILY UNIONACEA
(Fleming, 1828) Thiele, 1935

Freshwater pelecypods with schizodont hinge dentition; ovoviviparous animals, the larvae (= glochidia[1]) being incubated in all 4 or in only some (either the inner or the outer pair) of the demibranchs; glochidia of most species temporarily parasitic on the gills or fins of fishes[2]; for additional features see Thiele (1935, p 815).

Family 1. MARGARITIFERIDAE
Haas, 1940[3]

Type genus: *Margaritifera* Schumacher, 1816[4] (type species: *Mya margaritifera* Linnaeus, 1758). All 4 demibranchs marsupial; glochidia hookless but with irregular small teeth at ventral margin of the valves (Ortmann, 1912a, p 232); interlamellar connections of demibranchs irregularly scattered or forming irregular oblique rows, or incomplete septa which run obliquely to the direction of the gill filaments; ctenidia lacking water-tubes; posterior margins of mantle not united, lacking even a tendency to form anal and branchial siphons; supra-anal opening lacking; diaphragm separating branchial and suprabranchial cavities

incomplete, formed only by the ctenidia; bradytictic. Present distribution: North America and Eurasia.

Subfamily Margaritiferinae s.s. (Modell, 1942[5])

Type: same as for the family. Interlamellar connections discontinuous, irregularly scattered or falling into oblique rows. Represented in the United States by *Margaritifera margaritifera* (Linnaeus), *M. falcata* (Gould) and *M. hembeli* (Conrad).

Subfamily **Cumberlandinae,** new subfamily

Type genus : *Cumberlandia* Ortmann, 1912b (for *Unio monodonta* Say, 1829). Interlamellar connections of the demibranchs scattered and in interrupted rows, but developed as continuous septa which run obliquely forward. The monotype, *Cumberlandia monodonta* (Say), is confined to the Tennessee, Cumberland and Ohio River systems in the United States.

Family 2. AMBLEMIDAE Rafinesque, 1820

Type genus: *Amblema* Refinesque, 1820 [type species: *Amblema costata* Rafinesque, 1820 = *A. plicata* (Say, 1817)]. All 4 demibranchs marsupial (= tetragenae); glochidia hookless[6]; interlamellar connections usually developed as continuous septa (interrupted in *Gonidea*), parallel to the gill filaments; undivided water-tubes present, either continuous or interrupted (*Gonidea*), but always parallel to the gill filaments; posterior margins of mantle not united but drawn together by the diaphragm, thus separating the branchial and anal siphons; anal siphon closed above, leaving a separate supra-anal opening; diaphragm complete, formed entirely by the ctenidia; principally tachytictic (except in the Megalonaiadinae). Present distribution in the Nearctic Region[7]: principally in the United States, a few species ranging into southern Canada.

Subfamily Gonideinae Ortmann, 1916

Type genus : *Gonidea* Conrad, 1853, for *Anodonta angulata* Lea, 1838. Septa incomplete, interrupted and perforated by subcircular holes so that the water-tubes communicate with each other[8]; tachytictic. The monotype, *Gonidea angulata* (Lea), is presently found in western North America from southern British Columbia into southern California.

Subfamily Ambleminae s.s.

[=Quadrulinae (von Ihering, 1901) Hannibal, 1912]

Type: same as for the family. Septa and water-tubes well-developed and continuous, not perforated; tachytictic. Recent genera in the Nearctic Region are:

Amblema Rafinesque, 1820
Elliptoideus Frierson, 1927
Fusconaia Simpson, 1900a
Plectomerus Conrad, 1853
Quadrula Rafinesque, 1820[9]
Quincuncina Ortmann, 1922
Tritogonia Agassiz, 1852

Subfamily **Megalonaiadinae,** new subfamily

Type genus : *Megalonaias* Utterback, 1915, for *Unio crassus* var. *giganteus* Barnes, 1823. Septa and water-tubes well-developed and continuous; bradytictic. *Megalonaias* Utterback currently ranges from north-central United States into Central America.

Family 3. HYRIIDAE (Swainson, 1840) Parodiz & Bonetto, 1963

Type genus: *Prisodon* Schumacher, 1817, for *Prisodon obliquus* Schumacher, 1817. Only the 2 inner demibranchs marsupial; glochidia with hooks; marsupial demibranchs with septa-like, interrupted interlamellar connections forming incomplete (discontinuous) water-tubes which run parallel to the gill filaments; distinct branchial and anal openings present, but lacking a separate supra-anal opening; diaphragm complete: anterior part formed by the ctenidia (perforated), posterior part formed by union of the posterior mantle margins; duration of larval incubation little known[10]. Recent species are confined to South America and Australasia, although *Diplodon* is known from the Triassic of Texas and Pennsylvania in the United States (Parodiz & Bonetto, 1963).

Family 4. UNIONIDAE Rafinesque, 1820 [11]

Type genus: *Unio* Philipsson, 1788 [12] (type species: *Mya pictorum* Linnaeus, 1758). Only the 2 outer demibranchs marsupial; glochidia hooked or hookless[13]; interlamellar connections developed as continuous septa; water-tubes usually uninterrupted [14] (but divided in the Anodontinae s.l.); septa and water-tubes parallel to gill filaments except in *Strophitus* (Anodontinae); posterior margins of mantle not united but drawn together by the diaphragm, thus separating the branchial and anal siphons; anal siphon closed above, leaving a separate supra-anal opening[15]; diaphragm complete, formed entirely by the ctenidia; tachytictic or bradytictic. Recent species occur in the Nearctic, Neotropical, Palearctic, Ethiopian, Oriental and Australasian Regions.

Subfamily Unioninae s.s.[16]

Type: same as for the family. Marsupial demibranchs: homogenae (entire outer demibranchs forming smooth pads externally); glochidia usually with hooks[17]; septa and water-tubes (parallel to the gill filaments) undivided, lacking secondary septa and secondary water-tubes; tachytictic. Ortmann (1912a, p 273) suggests that *Unio* of Europe is not equivalent to the similar forms (i.e., Pleurobeminae) of North America, principally because of the presence of hooked glochidia and differences in beak sculpture. Present distribution: Palearctic, Ethiopian, Oriental, and Australasian Regions; absent from the Nearctic and Neotropical Regions.

Subfamily Pleurobeminae (Hannibal, 1912) Modell, 1942

Type genus: *Pleurobema* Rafinesque, 1820 (type species: *Pleurobema mytiloides* Rafinesque, 1820=*Unio clava* Lamarck, 1819). Marsupial demibranchs: homogenae; glochidia lacking hooks; septa and water-tubes (parallel to gill filaments) undivided, lacking secondary septa and secondary water-tubes; tachytictic. Recent genera are known from southern Canada and the United States (listed below), and the northern Neotropical Region (Central America[18]).

Cyclonaias Pilsbry, 1922
Elliptio Rafinesque, 1820
Hemistena Rafinesque, 1820
Lexingtonia Ortmann, 1914
Plethobasus Simpson, 1900a
Pleurobema Rafinesque, 1820
Uniomerus Conrad, 1853

Subfamily **Popenaiadinae,** new subfamily [19]

Type genus: *Popenaias* Frierson, 1927 (type species: *Unio popei* Lea, 1843).

Marsupial demibranchs: homogenae; glochidia lacking hooks; septa and water-tubes (parallel to gill filaments) undivided, lacking secondary septa and secondary water-tubes; bradytictic. Presently known only from peninsular Florida (*P. buckleyi* (Lea)) and Texas (*P. popei* (Lea)) in the United States; Mexico and Central America.

Popenaias Frierson, 1927
Cyrtonaias Crosse & Fischer, 1893, in Central America

Subfamily Anodontinae (Rafinesque, 1820) Ortmann, 1910a

Type genus : *Anodonta* Lamarck, 1799, for *Mytilus cygneus* Linnaeus, 1758. Marsupial demibranchs: homogenae, or diagenae (in *Strophitus* only: marsupia filling the entire outer 2 demibranchs, with ovisacs subdivided into compartments which are transverse to the demibranchs); glochidia hooked; septa divided from front to rear by secondary septa, producing secondary water-tubes which are parallel to the demibranchs (except in *Strophitus*); bradytictic.[20] Principally North American forms, but also occurring in Central America, Eurasia and the Oriental Region.

Alasmidonta Say, 1818
Anodonta Lamarck, 1799 [21]
Anodontoides Simpson, 1898
Arcidens Simpson, 1900a
Arkansia Ortmann & Walker, 1912
Lasmigona Rafinesque, 1831
Simpsoniconcha Frierson, 1914
Strophitus Rafinesque, 1820

Subfamily Lampsilinae [22] (von Ihering, 1901) Ortmann, 1910a

Type genus: *Lampsilis* Rafinesque, 1820 (type species: *Unio ovatus* Say, 1817). Marsupia represented by ovisacs confined to varying restricted regions of the outer 2 demibranchs: (*a*) longenae=ventral part of entire demibranchs, (*b*) heterogenae=posterior part, (*c*) mesogenae=central part, (*d*) eschatigenae=lower part of posterior region, demibranchs not folded, and (*e*) ptychogenae=lower part of demibranchs which are composed of vertical folds; ovisacs marked externally by sulci, marsupia not forming smooth pads as in tetragenae, homogenae and diagenae; glochidia hookless, or axe-head shaped (*Proptera*); septa and water-tubes undivided, both running parallel to the gill filaments; bradytictic, except *Obliquaria* which is tachytictic; widespread sexual dimorphism in the shell [23] and in the development (in females) of flaps, papillae or caruncles in the mantle below the branchial opening. Recent genera, confined to North and Central America, are:

heterogenae:

Actinonaias Crosse & Fischer, 1893
Carunculina Simpson, 1898
Dysnomia Agassiz, 1852
Ellipsaria Rafinesque, 1820 [24]
Glebula Conrad, 1853
Lampsilis Rafinesque, 1820
Lemiox Rafinesque, 1831 [25]
Leptodea Rafinesque, 1820
Ligumia Swainson, 1840
Medionidus Simpson, 1900b
Obovaria Rafinesque, 1819
Pachynaias Crosse & Fischer, 1893
Proptera Rafinesque, 1819
Truncilla Rafinesque, 1819
Villosa Frierson, 1927

mesogenae:

Cyprogenia Agassiz, 1852
Obliquaria Rafinesque, 1820

eschatigenae:

Dromus Simpson, 1900a [26]

ptychogenae:

Ptychobranchus Simpson, 1900a

longenae:[27]

Friersonia Ortmann, 1912a

DISCUSSION

Hannibal (1912), Ortmann (1912a) and Walker (1917) have concluded that the primitive condition of the freshwater mussels is the tetragenous marsupial condition in which all 4 demibranchs incubate the developing glochidial larvae for a short (i.e., tachytictic) duration. Of the 2 groups which exhibit this feature, the Amblemidae is more advanced than the Margaritiferidae because of the typical presence in the former of (*a*) continuous interlamellar septa and water-tubes, (*b*) distinct branchial, anal and supra-anal openings (="siphons"), and (*c*) a complete diaphragm. While Hannibal and Ortmann derive the Mutelidae and Unionidae (both *sensu lato*) from the Margaritiferidae, Modell (1964) has proposed that the Mutelidae (i.e., his opinion of the superfamily Mutelacea) gave rise independently to the composite Unionidae and to the Margaritiferidae, from which the composite Elliptionidae evolved.

It seems more probable that the tetragenous condition of the Margaritiferidae gave rise to the tetragenous condition of the Amblemidae, and through the loss of the marsupial function of the outer demibranchs also gave rise to the unionacean Hyriidae and to the Mutelacea (Fig. 1). The nature of such a divergence is obscure, particularly concerning the larvae (glochidia in the Unionacea, lasidial forms in Mutelacea). Indeed, our conjecture is in contrast to the view of Parodiz & Bonetto (1963, p 185) that "The two different types of larvae, i.e., glochidium and lasidium, cannot be considered to be derived from any hypothetical direct ancestry."

Through loss of the marsupial function of the inner demibranchs, the tachytictic Amblemidae could account for the origin of the tachytictic Unionidae which could have independently given rise to the subfamilies Unioninae s.s., Anodontinae and Pleurobeminae by adaptations in the larvae (some developing hooks), a tendency toward a bradytictic habit, and morphological changes in the marsupial demibranchs (Anodontinae). The Lampsilinae is considered here to have evolved from the Pleurobeminae through a change in the duration of incubation and in the morphological specialization of the marsupial demibranchs (Fig. 2). Our suggested relationships within the Lampsilinae are outlined in Fig. 3.

Gonidea angulata (Lea) has usually been associated with the family Unionidae *sensu lato*: in the Unioninae s.l., by Ortmann (1916), Frierson (1927), Thiele (1935) and Haas (1969a, 1969b); in the Anodontinae s.l. by Hannibal (1912). Modell (1964), however, saw fit to place it in the margaritiferid subfamily Pseudodontinae Frierson, 1927, which in turn Thiele (1935) considered part of the Unionidae (Unioninae *sensu lato*). Ortmann (1916) investigated the anatomy of this monotypic genus and found some features suggesting the Margaritiferidae (interlamellar septa and water-tubes present, but not continuous) and some recalling the Amblemidae (complete diaphragm; supra-anal opening present), while other aspects were common to both groups (tetragenous gill condition; data suggesting a tachytictic habit). We consider Ortmann's subfamily Gonideinae a valid taxon and place it in the Amblemidae below the more advanced Ambleminae (see Fig. 1).

A number of other peculiarities and exceptions have been previously mentioned (e.g., the bradytictic *Megalonaias* and *Popenaias*, the allegedly ultra-tachytictic *Anodonta imbecilis*, and the tachy-

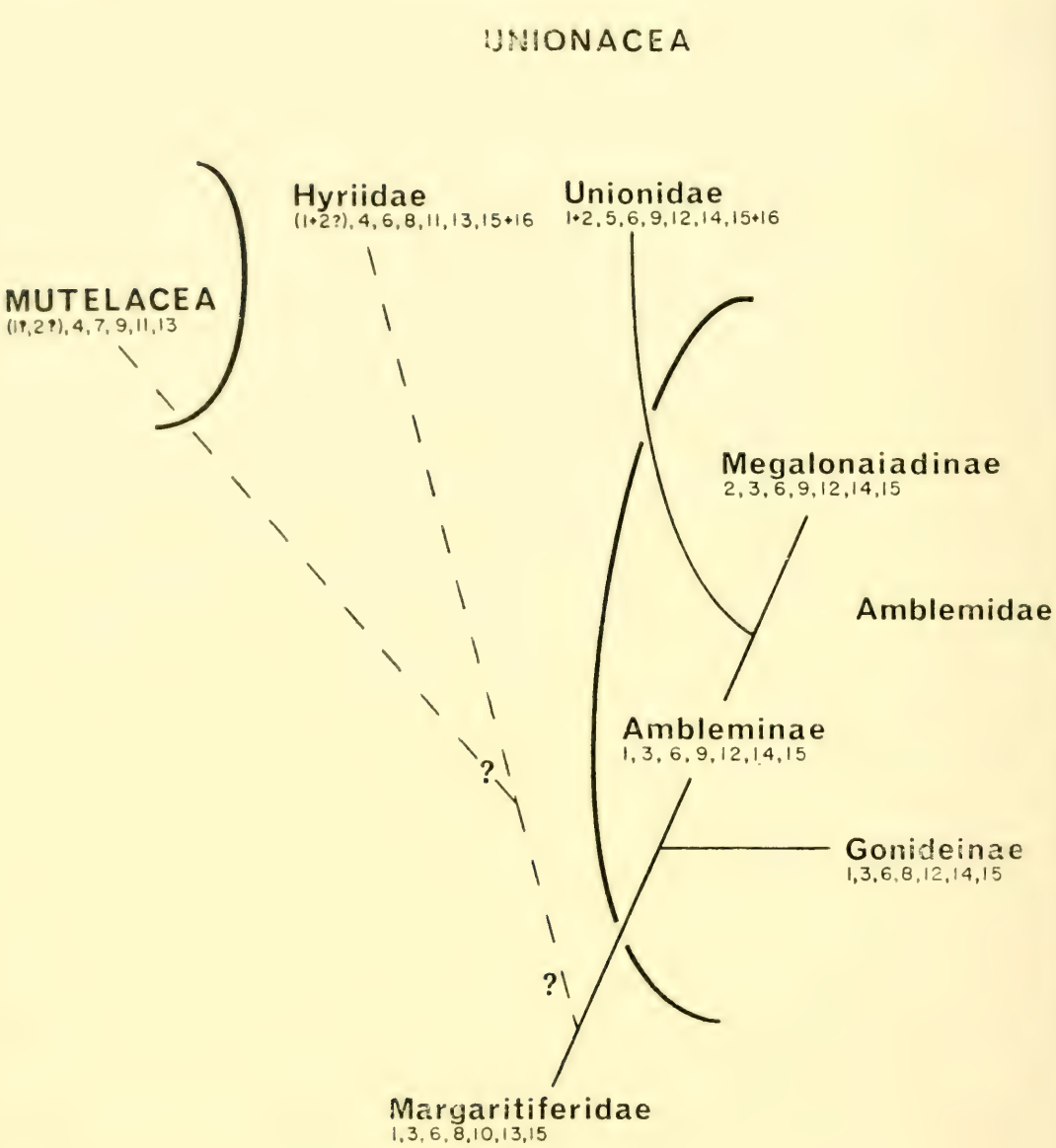

FIG. 1. Proposed affinities of the families of the Unionacea, and the suggested relationship of the Mutelacea to the Unionacea. 1, tachytictic (short-term incubation); 2, bradytictic (long-term incubation); 3, tetragenae (all 4 demibranchs marsupial); 4, only the inner 2 demibranchs marsupial; 5, only the outer 2 demibranchs marsupial; 6, possessing glochidial larvae; 7, possessing lasidial or lasidial-like larvae; 8, interlamellar septa and water-tubes interrupted; 9, interlamellar septa and water-tubes continuous; 10, diaphragm incomplete; 11, diaphragm complete, composed of gill and mantle tissues; 12, diaphragm complete, formed by gills only; 13, supra-anal opening absent; 14, supra-anal opening present; 15, glochidia hookless; 16, glochidia with hooks.

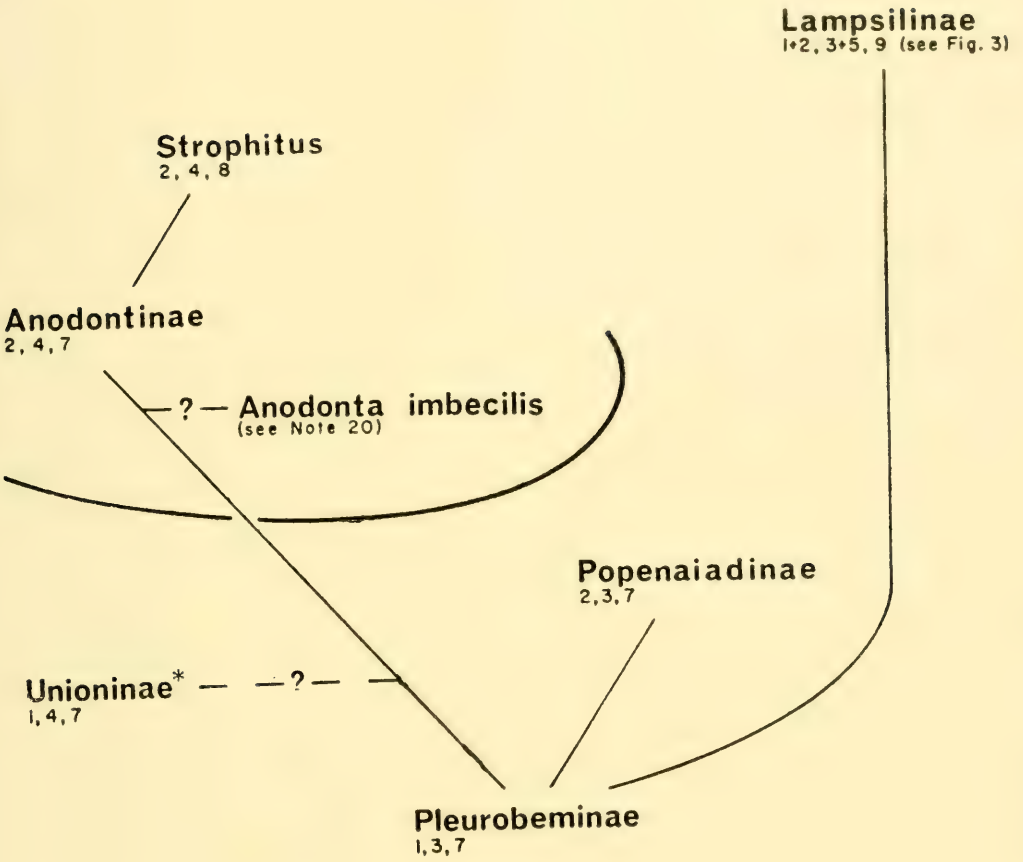

FIG. 2. Proposed affinities of the subfamilies of the Unionidae. *For the Unioninae Ortmann (1912a, p 273), however, suggests that (*a*) *Unio* and the Pleurobeminae arose independently from a tetragenous marsupial condition, and (*b*) the subtriangular hooked glochidium " somewhere near *Unio* was the starting point for the development of the subfamily Anodontinae." 1, tachytictic; 2, bradytictic; 3, glochidia hookless, semielliptical; 4, glochidia hooked, subtriangular; 5, glochidia hookless, axe-head shaped; 6, tetragenae; 7, homogenae; 8, diagenae; 9, marsupial demibranchs other than tetragenae, homogenae or diagenae.

tictic *Obliquaria*). Our interpretation of their phylogenetic affinities is shown in Figs. 2 and 3.

The taxonomy and relationships of most freshwater mussels is still poorly known. Of the 54 genera of the Unio-

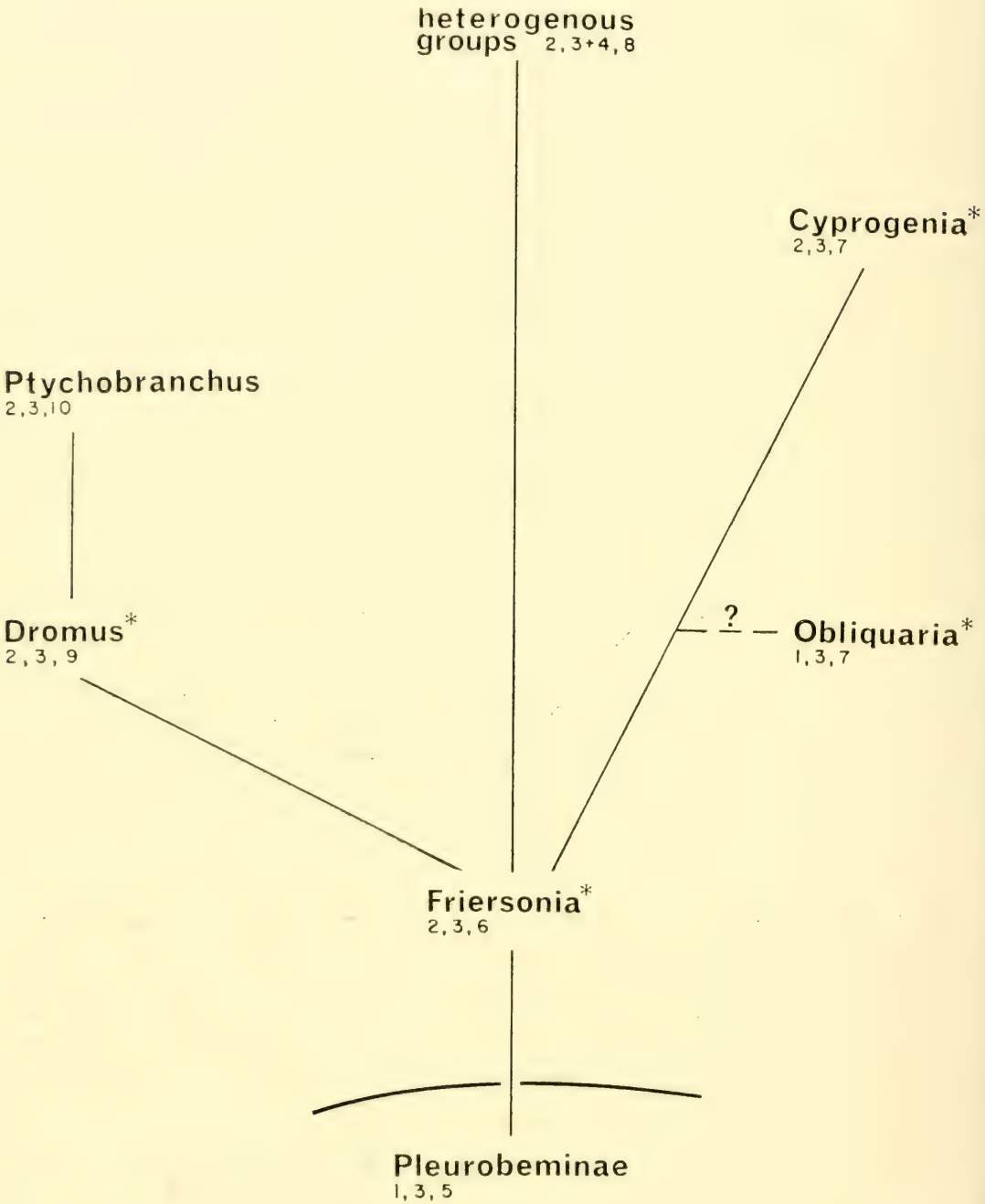

FIG. 3. Possible relationships in the unionid subfamily Lampsilinae. **Cyprogenia*, *Dromus*, *Friersonia* and *Obliquaria* are monotypic genera. 1, tachytictic; 2, bradytictic; 3, glochidia semielliptical; 4, glochidia axe-head shaped (in *Proptera*); 5, homogenae; 6, longenae; 7, mesogenae; 8, heterogenae; 9, eschatigenae; 10, ptychogenae.

ninae *sensu lato* discussed by Thiele (1935), 24 are listed as " Tier unbekannt; " and of the morphological accounts available, many are superficial. Thiele was able to provide only inconsistent information from the previous literature in his review of the Unioninae. Such information, because it is incomplete, is confusing and at present it is impossible to relate it adequately to our classification.

In our system of the Nearctic freshwater mussels we have attempted to employ with consistency what we feel are the most pertinent features which characterize the various groups. The superfamilies are distinguished principally according to the larval type produced. The families of the Unionacea are separated primarily on the basis of (*a*) the number and location of the marsupial demibranchs, and (*b*) the morphology of these demibranchs. The subfamilies have been characterized largely by the (*a*) morphology of the marsupial demibranchs (i.e., the anatomical conditions of the ovisacs), (*b*) hooked/hookless nature of the glochidia,[5] and (*c*) duration of larval incubation.

Although further studies of soft-part morphology are desirable, continued investigation of the shell features (e.g., beak and disc sculpturing, hinge dentition) and their critical evaluation in the definition of genera, subgenera and species (and their geographic and temporal distribution) is also needed. Chromosome and electrophoretic studies on the Nearctic unionaceans are currently underway in several laboratories, and it is hoped that these approaches will also provide greater insight into a natural classification of these freshwater mussels and allow a better understanding of their evolutionary relationships.

NOTES

[1] The superfamily Mutelacea Parodiz & Bonetto (1963) is characterized principally by the production of lasidial (Mycetopodidae Gray, 1840) or lasidial-like (Mutelidae Gray, 1847) larvae which (like the unionacean Hyriidae) are incubated in the inner two demibranchs.

[2] In the Unionidae s.s., *Anodonta imbecilis* Say and *Strophitus undulatus* (Say) (both Anodontinae s.l.) nave been reported to undergo direct development in the marsupia without a parasitic stage (Howard, 1914, and Lefevre & Curtis, 1911, respectively). However, Tucker (1927, 1928) has shown that the glochidia ot *A. imbecilis* are facultatively parasitic, utilizing the fish *Lepomis cyanellus* Rafinesque as the host. *Simpsoniconcha ambigua* (Say), also in the Anodontinae s.l., utilizes a salamander [*Necturus maculosus* (Rafinesque)] as the glochidial host. In the hyriid genus *Diplodon* Spix, the subgenus *Diplodon* s.s. possesses parasitic glochidia while the larvae of the subgenus *Rhipidonta* Mörch undergo direct development (Parodiz & Bonetto, 1963).

[3] Official List Name No. 202 (see Flemming, 1958a); =Margaritanidae Ortmann, 1911a.

[4] Official List Name No. 1236 (see Flemming, 1958b); =*Margaritana* Schumacher, 1817 (Official Index Name No. 1082; see Flemming, 1958c).

[5] Margaritiferinae Modell, 1942 = Margaritaninae Ortmann, 1910a (Official Index Name No. 233; see Flemming, 1958d).

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[5] The number of species of *Unio* Philipsson with glochidia possessing/lacking hooks is presently unknown. If the number of species with hooked glochidia is small in relation to the number lacking hooks, the provisional distinction of the subfamilies Unioninae s.s. and Pleurobeminae would seem artificial. If further investigations demonstrate this possibility, the Pleurobeminae might best be considered synonymous with the Unioninae s.s.

[6] Thiele (1935) cites *Rectidens* Simpson (southeast Oriental Region) as having tuberculated glochidia.

[7] According to Bloomer (1931a, 1931b, 1932, 1933, 1946, 1949), Haas (1924, 1954), von Martens (1900), Morrison (1967), Ortmann (1910b, 1911b, 1917), Prashad (1918, 1919a, 1919b) and Thiele (1935), additional tetragenous species occur in Central America and in the southern Palearctic, Ethiopian and/or Oriental Regions: *Balwantia* Prashad, *Brazzaea* Bourguignat, *Caelatura* Conrad, *Contradens* Haas, *Ensidens* Frierson, *Indonaia* Prashad, ? *Lamellidens* Simpson, *Lamprotula* Simpson, *Nitia* Pallary, *Parreysia* Conrad, *Potomida* Swainson, *Pseudodon* Gould, *Psilunio* Stefanescu, *Rhombunio* Germain, *Rectidens* Simpson and *Trapezoideus* Simpson.

However, several discrepancies and/or unusual features may be noted: (1) Bloomer (1931a) reported that *Brazzaea anceyi* Bourguignat from Africa is tetragenous, has a distinct supra-anal opening, and has continuous but perforated septa (except in the inner demibranchs of males). He consequently suggested removing the genus *Brazzaea* from the Mutelidae (Haas, 1969a, nevertheless retained it there as a subgenus of *Aspatharia* Bourguignat; he later, 1969b, removed it to the Unioninae s.l. as a subgenus of *Caelatura* Conrad) and placing it in Ortmann's Unionidae/Unioninae. This taxon would appear to belong to our concept of the amblemid subfamily Gonideinae. (2) *Contradens cambojensis* (Sowerby) from Siam had previously been grouped in the Unionidae s.l. by Ortmann (1917). (3) *Lamellidens* Simpson was cited by Thiele (1935) as containing embryos either in all 4 or only the outer 2 demibranchs, although Prashad (1918, 1919a) and Bloomer (1931b) found that in *L. marginalis* (Lamarck) from India only the outer demibranchs were marsupial. Bloomer (1931b) also noted discontinuous, perforated septa in this species. *Lamellidens consobrinus* (Lea) from India was previously grouped in the Unionidae s.l. by Ortmann (1911b). (4) Thiele (1935) placed *Potomida* Swainson in the Margaritiferidae as a subgenus of "*Margaritana*," although Haas (1969a, 1969b) considers *Potomida* to be a member of the Quadrulinae of the Unionidae s.l. (5) *Pseudodon salwenianus* (Gould) was reported by Prashad (1919a) to be tetragenous, to lack a separate supra-anal opening, and to possess a complete diaphragm formed by the ctenidia only. These features suggest that this species is an amblemid which has secondarily lost the supra-anal opening. (6) "*Psilunio*" *sinuata* (Lamarck), which Haas (1940) listed in the unionid Quadrulinae, was previously demonstrated by Ortmann (1912b) to be a margaritiferid. Haas, (1969a, 1969b) eventually concurred and placed this species (as *Pseudunio sinuata*) in a subgenus of *Margaritifera*.

Although no living species of the Amblemidae (?) possessing radial beak sculpture are currently found in North America, a variety of presumably related fossil forms (*Proparreysia* Pilsbry, 1921) have been reported from Cretaceous deposits in Wyoming, Montana, Colorado and New Mexico in the United States. Henderson (1935) placed this group in the subfamily Parreysiinae of the Unionidae s.l.

[8] Perforated marsupial septa are also known in *Brazzaea anceyi* Bourguignat (Bloomer, 1931a), *Caelatura aegyptiaca* (Cailliaud) (Bloomer, 1932, 1949) and *Parreysia acuminata* (H. Adams), *P. bakeri* (H. Adams), *P. ruellani* (Bourguignat) and *P. stuhlmanni* (von Martens) (see Bloomer, 1932), all in the Amblemidae; in *Contradens cambojensis* (Sowerby) and *Hyriopsis* Conrad (see Ortmann, 1917) and *Lamellidens thwaitesii* (Lea) (Bloomer, 1931b), all in the unionid Pleurobeminae (?); and even in *Grandidieria burtoni*

(Woodward) in the Mutelidae (Bloomer, 1933).

[9] Frierson (1927) listed a number of seemingly meaningless subgeneric names for *Quadrula* Rafinesque and described additional new ones. Morrison (1966) elevated several of these taxa to generic rank.

[10] The 4 Australasian subfamilies of the alleged Mutelidae listed by McMichael & Hiscock (1958) were relocated on anatomical grounds in the family Hyriidae by Parodiz & Bonetto (1963). These groups should be re-examined, and perhaps re-defined, however, particularly in terms of (*a*) the characteristic portion(s) of the inner demibranchs which are marsupial, and (*b*) the gravid periods. It is of special interest that among members of *Hyridella* Swainson (Hyridellinae Iredale) " Breeding apparently seasonal, from spring through summer " (McMichael & Hiscock, 1958, p 439). This time would correspond to the Nearctic fall and winter. Dr. Juan J. Parodiz (of the Carnegie Museum, Pittsburgh, Pennsylvania, U.S.A.) has kindly provided us with unpublished data from his observations on South American hyriids (pers. comm., 1969): " *Diplodon charruanus* (d'Orb.) begins [*incubation*] in summer (Dec., Jan.); maturation in fall (May) to early spring (Sept.). *D. rhuacoicus* (d'Orb.), the same as in *charruanus*. *D. burroughianus* (Lea), spring and summer (Sept. to Feb.), sometimes continues until next fall (May). *D. hylaeus* (d'Orb.), spring and summer (Oct. to Jan.), lasts all winter; maturation next spring. This species lives in rather warmer areas than the others mentioned. *D. delodontus* (Lam.), begins in summer, maturation in fall to next spring and cont.; probably all year around."

[11] Unionidae Fleming, 1828 =Official List Name No. 201 (see Flemming, 1958a). However, as Bowden and Heppell (1968, Note 48, p 250) pointed out, Rafinesque should receive authorship through previous usage.

[12] Official List Name No. 1235 (see Flemming, 1958b). *Unio* Philipsson, 1788=" *Unio* Retzius, 1788 " (see Simpson, 1900a, p 679).

[13] Morrison (1955) erroneously listed hooked glochidia, as well as divided water-tubes, as a feature of the entire family Unionidae. *Acuticosta* Simpson from China was cited by Thiele (1935) as having tuberculated glochidia.

[14] In *Lamellidens consobrinus* (Lea) (Pleurobeminae) from India most marsupial septa are continuous, although some are incomplete (temporarily, becoming continuous during gravidity?) (Ortmann, 1911b).

[15] The supra-anal opening is secondarily lost in *Cyclonaias tuberculata* Rafinesque (Pleurobeminae) and in *Carunculina parva* (Barnes) (Lampsilinae). A similar condition occurs in *Mutela kamerunensis* (Walker) (Mutelidae) and in *Pseudodon salwenianus* (Gould) (Amblemidae).

[16] Ortmann's, 1910a, Unioninae s.l. encompasses the subfamilies Unioninae s.s. and Pleurobeminae of the Unionidae as well as the entire family Amblemidae as employed here.

[17] Ortmann (1918) reported the absence of hooks on the glochidia of *Unio caffer* Krauss from Africa. However, Ortmann's material may have been comparatively immature. McMichael & Hiscock (1958) have demonstrated that *Velesunio ambiguus* (Philippi) from Australia does indeed possess hooked glochidia (the hooks appear only late in larval development), although this species was considered earlier by Hiscock (1951) to have hookless larvae. A re-examination of *U. caffer* Krauss (the type of Simpson's, 1900a, Section *Cafferia* which Modell, 1964, considered to be a genus in the unionid subfamily Rectidentinae; Haas, 1969a and 1969b, placed it in the Unio-

ninae s.l.) in terminal stages of larval incubation is therefore desirable.

[18] The Central American "genera" *Cinicula* Swainson, *Psoronaias* Crosse & Fischer and *Sintoxia* Rafinesque, which Morrison (1967) listed in the Amblemidae, may belong to the Pleurobeminae.

[19] Ortmann (1912a) noted that "*Elliptio*" *popei* (Lea) from Mexico is gravid in December and January, and Frierson (1913) observed that "*Unio* (*Nephronaias*)" *ortmanni* Frierson from Guatemala is gravid in February. Ortmann (1921c) further reported that 3 other species from Guatemala (viz., "*Elliptio*"[6] *calamitarum* (Morelet), *E. yzabalensis* (Crosse & Fischer) and *E. ravistellus* (Morelet)) are gravid in January and/or February. Finally, Morrison (1967) has indicated that "*Elliptio*" *opacatus* (Crosse & Fischer) and an unidentified species of *Barynaias* Crosse & Fischer from Mexico are gravid in December, and he further suggested that "*Cyrtonaias* mussels may also have a short breeding season in the cool summer months."

Ortmann (1912a: 272) stated for *E. popei* that "Here we would have a so-called summer breeder which breeds in mid-winter. But we know now, that not the season of the year, but the shortness of the breeding season is important, and according to all analogies, *E. popei* should be a form with a short breeding season" (i.e., tachytictic). However, recent investigations have confirmed 1 species with the homogenae type of marsupial demibranchs to be bradytictic, and circumstantial evidence suggests that other such species in Texas, Mexico and Central America undergo winter breeding.

In 1965 six bi-monthly collections of what is commonly known as *Elliptio buckleyi* (Lea) (=*Unio buckleyi* Lea, 1843), endemic to the Florida peninsula, were made by the senior author from the Myakka River at the Myakka River State Park, 17 miles southeast of Sarasota, Sarasota Co., Florida. The January, March, May, September and November collections contained gravid females; gravid animals were lacking in the July collection (each collection contained more than 100 animals). Although Ortmann (1912a) implied that *E. popei* is tachytictic, it is probable that this species, as well as *E. ortmanni*, *E. calamitarum*, *E. opacatus*, *E. yzabalensis* and *E. ravistellus* (and conceivably others), does not exhibit latitudinal, seasonal variation from the more northern summer-breeding groups but is also bradytictic.

"*Elliptio*" *buckleyi*, *E. calamitarum*, *E. ortmanni*, *E. popei*, *E. ravistellus* and *E. yzabalensis* display the homogenae structure which is found in the species of the pleurobeme genera previously listed. The extended (=winter) breeding habit is the principal character which distinguishes this group from the related tachytictic species of the Pleurobeminae. The occurrence of bradyticy in this group warrants providing these species with a generic designation distinct from those given to their tachytictic allies. The only available name for any of these species is *Popenaias* Frierson, 1927 (p 38).[7] This taxon was originally proposed as a subgenus of *Elliptio* Rafinesque; the type is *P. popei* (Lea) by original designation (p 10). Future taxonomic re-evaluation may necessitate the inclusion of other

[6] Ortmann considered all Central American naiades with the anatomy of *Elliptio* to belong to that genus.

[7] Haas (1969a, 1969b) considers *Popenaias* (homogenae, bradytictic) to be a subgenus of *Nephronaias* Crosse & Fischer, but the anatomy and breeding habits of the type of *Nephronaias* (*Unio plicatulus* Charpentier) are entirely unknown. Although Haas originally (1969a) placed *Elliptoideus* (tetragenae, tachytictic) as a subgenus of *Elliptio* (homogenae, tachytictic), he later (1969b) included it as a subgenus of *Nephronaias*. This example again demonstrates the misleading value of shell characters.

species and/or genera in this bradytictic-homogenae group of unionids.

This group of bradytictic, subtropical and tropical, homogenae-unionids with undivided septa and water-tubes is more advanced than the related species of the Pleurobeminae and is here placed in a new subfamily, the Popenaiadinae, which is characterized by long-term gravidity.

[20] Allen (1924) has postulated a very short (3-week), repetitive reproductive habit in *Anodonta imbecilis* Say.

[21] *Anodonta* Lamarck has been divided into several subgenera, one of which (*Arnoldina* Hannibal, 1912) Modell (1964) placed as a genus in the subfamily Rectidentinae, family Unionidae. The type, *Rectidens* Simpson, 1900a, was placed in the Unioninae s.l. by Thiele (1935), who stated that all 4 demibranchs contain glochidia, and by Haas (1969a, 1969b).

[22] Hannibal (1912) raised the Lampsilinae to familial rank, including in it only some of the typical lampsiline genera.

[23] Sexual dimorphism in the shell is noted among the other subfamilies only in *Tritogonia verrucosa* (Rafinesque) of the Ambleminae (Amblemidae).

[24] *Ellipsaria* Rafinesque, 1820 = *Plagiolopsis* Thiele, 1935 = *Plagiola* Rafinesque, 1819 (see Baker, 1964a).

[25] *Lemiox* Rafinesque, 1831 = *Conradilla* Ortmann, 1921b, *fide* Thiele (1935).

[26] *Conchodromus* Haas, 1930 = *Dromus* Simpson, 1900a, *fide* Baker (1964b).

[27] Longenae is a new term (consistent with Simpson's, 1900a, terminology) to describe the nature of the comparatively primitive marsupial demibranchs of *Friersonia* Ortmann, 1912a.

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RÉSUMÉ

UNE REÉVALUATION DES UNIONACES (PELECYPODA) ACTUELS D'AMÉRIQUE DU NORD

W. H. Heard et R. H. Guckert

Les principales classifications récentes des bivalves d'eau douce, basées essentiellement sur le caractère de la coquille, ne reflètent pas les relations phylogénetiques de ces animaux, alors que ces relations peuvent être interprétées à partir de caractéristiques de reproduction. Bien que ces 2 types de caractères ne soient pas en toute logique mutuellement exclusifs, ils se recoupent relativement peu souvent. Les caractères de la coquille ont été exagérés dans la classification des moules d'eau douce dans l'ensemble du monde, d'une part parce qu'ils peuvent être employés dans les recherches sur matériel possible, d'autre part à cause de la facilité d'étude. Malheureusement il y a trop peu d'informations sur le fonctionnement et la morphologie de l'appareil reproducteur pour permettre d'établir, à l'échelle mondiale, une classification basée sur ces caractéristiques, et il serait difficile de mettre en évidence les relations des formes fossiles avec un tel système si jamais on le proposait. Le choix d'un système unique (c.a.d. soit la coquille, soit les parties molles) montre une évolution parallèle des caractères dans l'autre système. D'où l'on considère qu'un système basé sur les aspects de la reproduction, en parallèle avec les caractèristiques de la coquille, reflète les affinites naturelles et évolutives avec plus de précision que ne le ferait un système qui se limiterait à exagérer un autre caractère.

Dans le but de stimuler de nouvelles investigations (en particulier pour les groupes non-Néoarctiques) on présente ci-aprés un systéme revisé des affinités des moules d'eau douce d'Amérique du Nord, en le situant au niveau des familles et sous-familles et en le basant sur l'anatomie et les aspects de la reproduction. Ce système tient compte de caractéristiques telles que (*a*) le nombre de chambres marsupiales (4 ou 2), (*b*) la localisation des chambres marsupiales (seulement les 2 internes ou seulement les 2 externes), (*c*) les régions spécifiques de la chambre interbranchiale qui sert á l'incubation des larves (la chambre entiére, ou seulement la portion centrale etc. . .) (*d*) la morphologie des chambres marsupiales (septa et canaux simples ou subdivisés, septa et canaux continus ou interrompus), (*e*) la durée de l'incubation des larves, (*f*) la nature de la coquille du glochidium (avec ou sans crochet), et (*g*) les autres aspects anatomiques plus subtilement en relation avec la reproduction en matière de courant d'eau (forme et composition du diaphragme, présence/absence d'une ouverture supra-anale).

Ces caractères indiquent que les représentants actuels des Margaritiferidae, Amblemidae et Unionidae se rencontrent en Amérique du Nord. Une 4ème famille, les Hyriidae,

est connue de la région Néoarctique seulement sous forme fossile, les espèces vivantes actuelles sont actuellement confinées à l'Amérique du Sud et l'Australie. Les sous-familles Neoarctiques ont été caractérisées pour ces 3 familles et la liste des genres de chaque groupe a été établie. Trois nouvelles sous-fammilles sont proposées: **Cumberlandinae** (Margaritiferidae), **Megalonaiadinae** (Amblemidae) et **Popenaiadinae** (Unionidae). Des indications sur less roupes d'Unionacés ont été fournies pour les régions Néotropicales, Paléarctiques, Ethiopiennes, Orientales et Autralasiennes.

Un parenté des Mutelacea aux Unionacea a été suggérée et les affinités phylogénétiques des familles et sons-familles d'Unionacés Néoarctiques sont interprétées d'aprés des données de la reproduction. Les Margaritiferidae Holarctiques actuels, le plus primitif des groupes d'Unionacés, est considéré comme ayant donné naissance independamment d'une part au stock mutelacés-hyriidés, d'autre part aux Amblemidae. Les Amblemidae, présents dans toutes les aires sauf de Sud-Amérique et d'Australasie, sont à leur tour décrits comme ancêtres des Unionidae. Les Unionides ont atteint leur plus grande diversification en Amérique du Nord et comprennent la grande majorité des moules d'eau douce Néoarctiques. Les plus primitifs Pleurobeminae (actuellement confinés à l'Amérique du Nord et du Centre) ont, pense-t-on, donné naissance indépendamment (*a*) aux Popenaiadinae du Sud des U.S.A., du Mexique et de l'Amérique Centrale, (*b*) aux Anodontinae de l'hemisphere Nord et (*c*) aux Lampsilinae d'Amerique du Nord et du Centre. Les Unioninae S. S. d'Eurasie ont, semble-t-il, dérivé du stock des Anodontinae. Les Pleurobeminae sont considérés comme les ancêtres du stock primitif des Lampsilinae qui, en conséquence, se separent en plusieurs lignees selon la specialisation du marsupium.

Les tendances évolutives dons la progression et/ou la spécialisation des Unionacés Néoarctiques comprend (*a*) la réduction de 4 à 2 (surtout la paire externe) chambres marsupiales, avec la plus grande diversification apparaissant dans les groupes actuels de l'hémisphère Nord, (*b*) le développement de septa et canaux interlamellaires continus, (*c*) les adaptations morphologiques des marsupiums qui atteignent la plus grande spécialisation par restriction spaciale des ovisacs chez les Lampsilinae, (*d*) une tendance à avoir un diaphragme complet formé entièrement par les cténidies et (*e*) un passage général d'une incubation des larves du court terme au long terme. La plupart des Unionacés possèdent des larves glochidium sans pointes, et les larves à pointes sont considérées comme ayant évolué indépendamment d'une part chez les Hyriidae et d'autre part chez les Unioninae-Anodontinae.

A. L.

АБСТРАКТ

РЕВИЗИЯ СОВРЕМЕННЫХ UNIONACEA (PELECYPODA)
СЕВЕРНОЙ АМЕРИКИ

В. ХЕРД и Р. ГУККЕРТ

Современные классификации пресноводных моллюсков на уровне высоких таксонов, основанные, главным образом, на характере строения раковины, не отражают филогенетических отношений этих моллюсков, которые могут быть освещены при учете характера их размножения. Хотя эти два типа особенностей моллюсков не исключают друг друга, но они перекрываются сравнительно мало. На характер раковины особенно обращается внимание в классификации наядид. Эти признаки широко известны, благодаря удобству их применения как на живых, так и на ископаемых раковинах. К сожалению, имеется слишком мало данных по морфологии размножения и по образу жизни личинок, чтобы можно было создать крупно-масштабную классификацию, основанную точно на этих признаках. Если бы такая схема и была предложена, возникают трудности установления родственных связей между современными и ископаемыми формами. При выборе какой-нибудь одной системы (т.е. по морфологии раковины или по морфологии мягких частей тела) выяснилось бы наличие параллельной эволюции признаков.

Авторы считают, что система, основанная на характере размножения, с параллельным учетом признаков строения раковины, точнее отражает естественную эволюцию и близость форм, чем любая другая система.

Чтобы стимулировать дальнейшие исследования (особенно среди не-неоарктических групп), в настоящей статье авторы представляют пересмотренную систему признаков северо-американских наядид на уровне семейств и подсемейств, учитывая анатомические признаки и родственные черты в характере размножения.

Эта система охватывает такие признаки, как: а) количество полужабр с марзупиями (4 или 2); б) расположение полужабр с марзупиями (только 2 внутренних или только 2 внешних); в) особые места, где инкубируются развивающиеся личинки (вся полужабра, или лишь задняя ее часть, или только центральная и т.д.); г) морфология марзупиальной полужабры (простая или разделенная септа и водяные трубки, непрерывная или прерывистая септа и водяные трубки); д) продолжительность инкубации личинок (кратко- или долговременная); е) природа раковины глохидия (с крючками или без них); ж) другие анатомические аспекты, более тонко связанные с характером размножения, например, токи воды (полнота и строение диафрагмы, наличие или отсутствие супра-анального отверстия).

Эти признаки указывают на то, что современные представители семейств Margaritiferidae, Amblemidae и Unionidae встречаются в Северной Америке. Четвертое семейство-Hyriidae, известно из неоарктического района лишь в ископаемом виде. Современные же приурочены к Южной Америке и к австрало-азиатскому району. Для этих трех современных семейств устанавливаются неоарктические подсемейства и указываются их признаки, а также даются списки северо-американских родов для каждой группы. Предлагаются три новых подсемейства: Cumberlandinae (Margaritiferidae), Megalonaiinae (Amblemidae) и Popenaiinae (Unionidae). Приводятся замечания о родственных группах унионид в неотропическом, палеарктическом, эфиопском, восточном и австрало-азиатском районах. Рассматриваются предполагаемые родственные связи между Mutelacea и Unionacea, а также филогенетическая близость семейств и подсемейств неоарктических унионид, которые интерпретируются исходя из особенностей их размножения. Margaritiferidae (самая примитивная группа из унионид), являющаяся в настоящее время холарктической, рассматривается как представляющая собой независимую ветвь от Hyriidae-Mutelacea к Amblemidae. Последние, распространенные во всех областях, кроме Южной Америки и ав-

страло-азиатского района, рассматриваются в свою очередь как предки унионид, которые достигли наибольшего разнообразия в Северной Америке и составляют большую часть неоарктических моллюсков.

Предполагается, что наиболее примитивные **Pleurobeminae** (в настоящее время приуроченные к Северной и Центральной Америке) восходят непосредственно к а) **Popenaiinae** из южных районов США, Мексики и Центральной Америки; б) к **Anodontinae** северного полушария и в) к **Lampsilinae** Северной и Центральной Америки.

Считается, что **Unioninae s.str.** Евразии произошли от **Anodontinae. Pleurobeminae** рассматриваются как предки примитивных лампсилин, которые постепенно разделились на несколько линий путем специализации марзупиальных полужабр. Эволюционные тенденции в развитии и/или в специализации неоарктических унионид включает: а) редукцию с четырех до двух (главным образом, на внешней паре) марзупиальных полужабр, при этом самое большое разнообразие встречается у современных форм в северном полушарии; б) развитие непрерывной интерламеллярной септы и водяных трубок; в) морфологическую адаптацию марзупиальных полужабр, достигающую наибольшей специализации путем усиления локализации яйцевых мешков у **Lampsillinae**; г) тенденцию к образованию полной диафрагмы, целиком за счет ктенидиев; д) общее изменение периода инкубации личинок с кратковременной на долговременную. Большинство унионид имеют глохидий без крючков, а крючконосые личинки рассматриваются как возникшие независимо у **Hyriidae** и у унионид-анодонтид.

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SYMBIOSIS IN SACOGLOSSAN OPISTHOBRANCHS: SYMBIOSIS WITH ALGAL CHLOROPLASTS

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ABSTRACT

The green bodies responsible for the color of 4 species of sacoglossan opisthobranchs (Mollusca: Gastropoda) were investigated and were found to be chloroplasts derived from the animals' algal food. The chloroplasts were invariably restricted to digestive cells of the digestive diverticula in each species.

Chloroplasts in the tissues of *Elysia hedgpethi* and *Placida dendritica* are derived either from *Codium fragile* or *Bryopsis corticulans*. The plastids in the tissues of *Placobranchus ianthobapsus* are derived from an unidentified siphonaceous green alga. In the 3 cases above, the chloroplasts were found to be retained in the animals in a symbiotic condition.

The 4th species investigated, *Hermaeina smithi*, was found to ingest chloroplasts of *Chaetomorpha aerea* and *Cladophora trichotoma*, but the plastids are apparently rapidly degraded.

It is suggested that symbiosis between algal chloroplasts and sea slugs of the Order Sacoglossa may be the rule rather than the exception.

INTRODUCTION

Unicellular algae living in symbiotic associations with a variety of animal hosts have been known since the 19th century. Since that time much work has been done on relationships of algae symbiotic with protozoans, coelenterates and platyhelminths, but comparatively little has been done on molluscs (see reviews by Droop, 1963; McLaughlin & Zahl, 1966; and Yonge, 1957). As early as 1895, it was known through the work of Hecht that opisthobranch molluscs could exist in symbiotic relationships with unicellular algae, specifically zooxanthellae. Naville (1926) showed that the nudibranch *Aeolidiella alderi* contained zooxanthellae intracellularly in its digestive gland. He further showed that the zooxanthellae were derived from the tissues of the actinian, *Heliactis bellis*, upon which the nudibranch fed. It was Naville's belief that the zooxanthellae reproduced within the nudibranch's tissues, but Graham (1938) was unable to observe this.

Buchner (1965) listed 5 species of nudibranchs which reportedly contained zooxanthellae in their tissues. Those species are: *Aeolis glauca*, *Favorinus albus*, *Melibe rangii*, *Phyllirhoe* sp. and *Spurilla neapolitana* which contain zooxanthellae within the cells of the digestive gland in the dorsal appendages, and *Doridoeides gardineri* which apparently contains zoochlorellae, or green algae. It is supposed that in all cases, the algal cells are ingested along with the food.

Yonge & Nicholas (1940) described

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zooxanthellae in the tissues of *Tridachia crispata*, a sacoglossan opisthobranch from Jamaica. This statement was, however, ultimately retracted for lack of evidence (Yonge, 1966).

Kawaguti (1941) reported that another sacoglossan, *Placobranchus ocellatus* from Palao, contained unicellular green algae in its body. He demonstrated that when maintained in the light, the animal/algal association produced more oxygen than it consumed. In 1965, Kawaguti, Yamamoto & Kamishima reported a similar association in *P. ianthobapsus* from Hawaii. On the basis of pigment extracts and observations with the electron microscope, the green bodies were interpreted as unicellular blue-green algae living within the cells of the animal's digestive gland. The present study presents evidence to show that these bodies are not unicellular algae, but algal chloroplasts.

In the same year, Kawaguti & Yamasu (1965) identified the green bodies in the digestive gland cells of *Elysia atroviridis* as chloroplasts of the alga, *Codium fragile*, on the basis of structural similarities revealed with the electron microscope. Taylor (1967) reported finding chloroplasts in the digestive gland cells of five additional sacoglossan slugs: *Elysia viridis*, *Hermaea bifida*, *H. dendritica*, *Acteonia senestra* and *Limapontia capitata*. In a more complete report, Taylor (1968) demonstrated the similarity between the chloroplasts found in the tissues of *Elysia viridis* and those from the alga, *Codium tomentosum*, upon which the animal feeds. The tentative identity of the chloroplasts was established by use of the electron microscope and comparisons of plant pigment extracts. By incubating animals in sea water containing $^{14}CO_2$ and doing radio-autography, he was able to establish that the chloroplasts within the animal's cells fix ^{14}C in the light.

More recently, Trench, Greene & Bystrom (1969) have re-examined *Tridachia crispata* (see also Trench, 1969) and, in addition, have investigated *Tridachiella diomedea* from the Gulf of California and *Placobranchus ianthobapsus* from Hawaii. Chloroplasts have been found in the cells of the digestive diverticula in all 3 species. Exposure of the animals to $^{14}CO_2$ in the light, with subsequent radioautography of the animal tissue has revealed ^{14}C in the chloroplasts.

It is now evident that the occurrence of algal chloroplasts within the tissues of sacoglossan opisthobranchs is a widespread phenomenon.

In the present study, the green bodies in the digestive gland cells of *Placobranchus* have been examined in detail and evidence will be offered to establish their identity not as blue-green algae, but as algal chloroplasts. In addition, chloroplast-animal symbioses are described in two species of sacoglossans from southern California: *Elysia hedgpethi* and *Placida dendritica*. A third sacoglossan from California, *Hermaeina smithi*, was also investigated and was found to lack chloroplast symbionts in its tissues.

MATERIALS AND METHODS

Experimental animals

Four species of animals were used in the present study, and all belong to the Order Sacoglossa (Mollusca: Opisthobranchia).

Elysia hedgpethi Marcus was collected at Flat Rock, Palos Verdes, Los Angeles County, California. *Elysia* was found on fronds of *Codium fragile* Hariot or on filaments of *Bryopsis corticulans* Setchell along with another sacoglossan, *Placida dendritica* Alder & Hancock. Collections were made from low intertidal to about 5 m below low water neaps.

Hermaeina smithi Marcus was collected at Leo Carillo Beach State Park, Los Angeles County, California. This species

was found in the mid-tide region in the rocky tide pools containing either *Cladophora trichotoma* Kützing, or more commonly, *Chaetomorpha aerea* Kützing. *Hermaeina* was not observed on any other algal substrate.

Placobranchus ianthobapsus Gould was collected from reef-flats in Kaneohe Bay, Oahu, Hawaii. The animals were invariably found crawling in the silty white sand which makes up the sediment on the reef-flat. No animal was ever collected from, or observed on, an alga in the field, although the red alga, *Acanthophora* sp., was abundant at the collecting site. Most specimens used in this study were collected from water about 1 m in depth.

Species from California were maintained in large holding tanks in the recirculating sea water system at the Zoology Department of the University of California at Los Angeles. The temperature was maintained at 13°C. The local species were given constant access to their natural algal food.

Placobranchus was maintained in plastic tubs (27 × 32 × 13 cm) at room temperature (about 22°C). Since the algal food of this species is not known, the animals were not fed in the laboratory.

Histology

Whole animals were fixed in Clark's fixative, Bouin's solution made up in sea water, or Fleming's fixatives with and without acetic acid (see Weesner, 1960). Best results were achieved with Clark's and Bouin's fixatives. Fixation times ranged between 1 and 24 hours after which the tissues were transferred directly to 70% ethanol. All animals were dehydrated through serial dilutions of ethanol (1 hour in each solution), cleared in xylene, and embedded in paraffin (56–58°C). Sections were cut at 7 or 10 μ and were stained with Ehrlich's haematoxylin and eosin Y, Mallory triple stain, toluidine blue (Weesner, 1960) or periodic acid-Schiff (PAS) (Lillie, 1965). Materials fixed in Fleming's fixatives were left unstained.

Electron microscopy

Small pieces of tissue (1 mm²) were fixed in 3% glutaraldehyde (with glucose and monosodium phosphate) for 1 hour at 25°C. They were rinsed completely in 3·4% sodium chloride solution and were post-fixed in 1% osmium tetroxide (with glucose and monosodium phosphate) for 1 hour at 25°C (J. Lauritis, pers. comm.). The tissues were then dehydrated through a series of ethanol concentrations and were embedded in Araldite (Luft, 1961).

Sections were cut on a Porter-Blum MT-2 ultra-microtome, then stained with uranyl acetate and lead citrate, and viewed and photographed with an Hitachi 11B electron microscope.

Plant pigment analysis (F.T. Haxo, pers. comm.)

Photosynthetic pigments were extracted from the various plant and animal tissues in the cold (3–4°C) under nitrogen gas with absolute methanol. The pigments in the methanolic extract were transferred to diethyl ether in a separatory funnel and 10% sodium chloride was added to effect phase separation. The diethyl ether phase was further washed with the salt solution to remove any remaining methanol. Petroleum ether (b.p. 60–80°C) was added to the diethyl ether, and was washed with distilled water. The resulting petroleum ether-diethyl ether extract was transferred to a small flask and the remaining traces of water removed by the addition of anhydrous sodium sulfate. The extract was then concentrated by evaporation under nitrogen gas. All extraction procedures were conducted in a darkened room, and the flasks containing

the pigments were wrapped in aluminum foil to shield the extracts from direct light. The dried extracts were taken back into solution in diethyl ether and were spotted on precoated silica-gel sheets (Eastman Chromagram, Type K301R2). The thin layer sheets were then developed in the dark with 15% petroleum ether in diethyl ether.

Comparisons were made between whole extracts from the animals and plants, as well as between separate pigment bands eluted from the thin layer chromatograms. Absorption spectra were read on a Cary 15 Recording Spectrophotometer in diethyl ether unless otherwise specified.

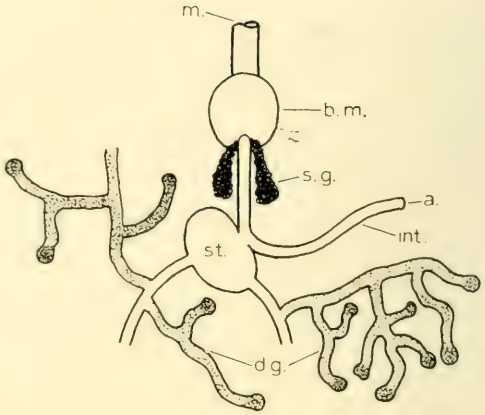

FIG. 1. Diagrammatic representation of a generalized sacoglossan gut. a, anus; b.m., buccal mass; d.g., digestive gland; int, intestine; m., mouth; s.g., salivary gland; st., stomach.

RESULTS

Gross anatomy

A diagrammatic representation of a typical sacoglossan gut appears in Fig. 1. A short oral tube leads from the mouth to the muscular buccal mass which houses the radula. The esophagus runs posteriorly from the buccal mass to the stomach, an outpocketing at the junction of the esophagus and intestine. The stomach receives tubules from the digestive diverticula which branch extensively throughout the body. It is the character of the cells of the digestive diverticula which is of interest in the present study.

Histology of the digestive diverticula

In Elysioid sacoglossans (*Elysia* and *Placobranchus*) the digestive diverticula ramify throughout the entire body of the animal. Sections taken at random through the animals invariably include many sections through digestive tubules (see Fig. 2). In cross-section, the tubules are composed of 5 or 6 cells surrounding a central lumen. These cells, in the living animal, are dark green in color. They stain darkly in tissues fixed in solutions containing osmium tetroxide, indicating the presence of lipid. Such cells appear granular when observed under the light microscope (Fig. 3). The granular bodies, 2–3 μ in diameter and roughly spherical, seem similar to the "Spherules" described in the digestive cells of *Elysia viridis* by Fretter (1941) and Taylor (1968). The spherical bodies are strongly eosinophilic. Evidence presented below will establish these bodies in *Placobranchus* as algal chloroplasts.

Eolidiform sacoglossans (*Placida* and *Hermaeina*) show a slight variation on the pattern described above. The stomach in species of this group is a large, thin-walled sac. The digestive gland sends branches into each of the cerata and is generally less branched than in the elysioid forms. In *Placida*, the digestive diverticula extending into the cerata are very similar in appearance to the digestive tubules in elysioid sacoglossans. The lumen is small compared with the size of the diverticulum. The cells surrounding the lumen are large and rounded. In stained preparations the 2–3 μ spherules are inside the cells. In *Hermaeina*, on the other hand, the

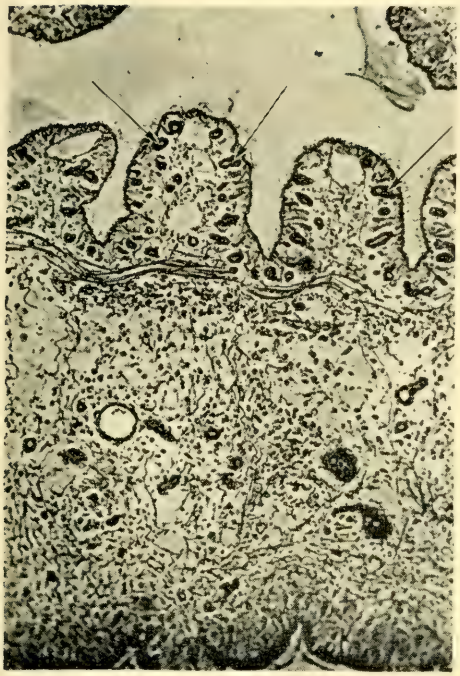

FIG. 2

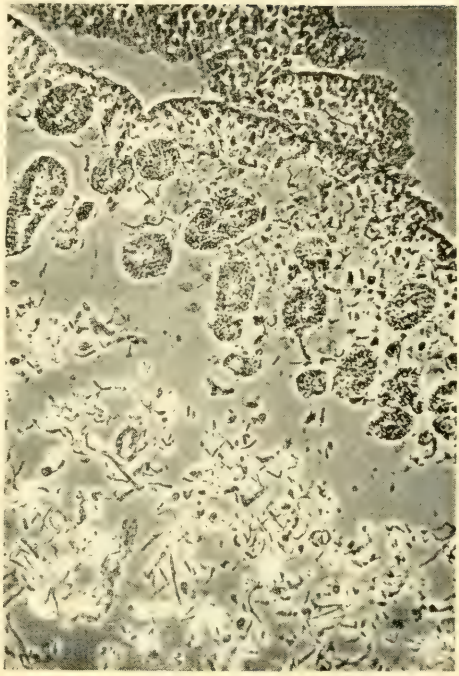

FIG. 3

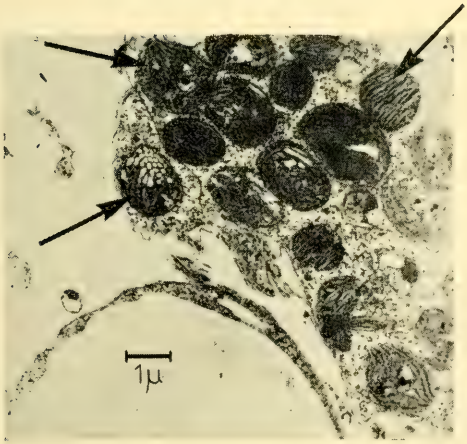

FIG. 4

FIG. 5

FIG. 2. Photomicrograph of transverse section through the middle of the body of *Placobranchus*. Clark's fixative, stained with hematoxylin and eosin Y. Arrows indicate digestive gland tubules. 50X.

FIG. 3. Photomicrograph of digestive gland cells of *Placobranchus* showing 2 3 μ granules. Tissue was fixed in Fleming's fixative with acetic acid, and was left unstained. 125X.

FIG. 4. Electron micrograph showing chloroplasts (arrows) within digestive gland cells of *Placobranchus*. 36,500X.

FIG. 5. Electron micrograph showing chloroplasts in cells of *Placobranchus* 75,000X. Animal cell nucleus is designated by " N ".

cells lining the diverticulum are long and narrow. The lumen in this species is large compared with the diameter of the diverticulum, and granules are not visible within the gland cells.

The egg masses and veliger larvae of *Elysia*, *Placida* (= *Hermaea*) and *Hermaeina* have been described elsewhere (Greene, 1968), as have those of *Placobranchus* (Ostergaard, 1950). In no case has it been possible to identify bodies resembling the 2–3 μ plastids described above in the eggs or larvae. This implies that the plastids are not transmitted via eggs or sperm, but are newly acquired by each individual sometime after the late veliger stage.

Electron microscopy

Symbiosis with algal chloroplasts has already been described for species of *Elysia* (Kawaguti & Yamasu, 1965; Taylor, 1967, 1968) and for *Placida* (= *Hermaea*) (Taylor, *loc. cit.*). In the preceding reports, the symbionts have been likened to chloroplasts of species of *Codium*, the alga upon which the animals feed.

The spherical bodies within the digestive cells of *Placobranchus*, however, have been previously identified as unicellular green algae (Kawaguti, 1941) and blue-green algae (Kawaguti *et al.*, 1965). Fig. 4 is an electron micrograph showing lamellar bodies within the cells of the digestive gland of *Placobranchus*. The same bodies appear in Fig. 5 at still higher magnification.

The interior of these bodies is almost completely occupied by lamellae formed of varying numbers of thin membranes. There is no nuclear material in evidence and no cell wall. The bodies are always intracellular and are present only in the digestive cells of the diverticulae. Plastoglobuli are commonly found within the lamellar system of the bodies and are highly osmiophilic.

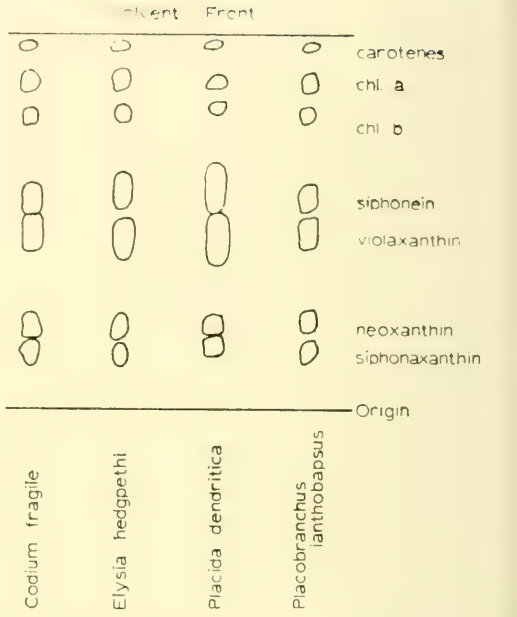

FIG. 6. Thin-layer chromatogram comparing methanolic extracts of *Elysia*, *Placida* and *Placobranchus* with pigments of the alga, *Codium fragile*.

These lamellar bodies are identical with the granular bodies described in the previous section and have now been identified as algal chloroplasts on the basis of the above observations and the following information on pigment extracts.

Pigment analyses

The results of the various pigment analyses appear in Figs. 6 and 7. The animals which normally feed on species of siphonaceous algae (i.e., *Elysia*, *Placida* and *Placobranchus*) are shown together with pigments extracted from *Codium fragile*, the algal substrate of *Elysia* and *Placida*. Each pigment band corresponds to a band in each of the other extracts (Fig. 6). The unique feature of all of these pigment extracts is the presence of siphonein (A_s maxima in petroleum ether, 450 and 475 nm) and siphonaxanthin (A_s maxima in petroleum

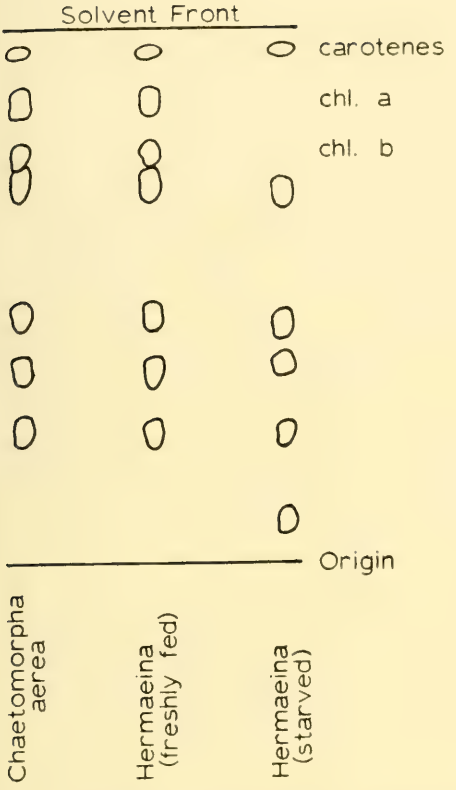

FIG. 7. Thin-layer chromatogram of methanolic extracts of *Hermaeina* (fed and 24 hr.-starved) and its algal food, *Chaetomorpha aerea*.

ether, 450 and 480 nm), 2 pigments characteristic of siphonaceous green algae (Strain, 1965). Although *Placobranchus* has not been observed feeding on algae in the field, the pigment extract conformed to the pattern characteristic of a siphonaceous alga. Thus, on the basis of the pigment analysis, it may be concluded that the chloroplasts in the tissues of *Placobranchus* are derived from an alga belonging to the Order Siphonales. A similar conclusion was drawn from investigations on *Tridachia crispata*, a sacoglossan opisthobranch from Jamaica (Trench, 1969; Trench, Greene & Bystrom, 1969). Pigment extracts from the animal and the siphonaceous alga, *Caulerpa racemosa*, were identical, suggesting that the chloroplasts were originally derived from some species of siphonaceous alga. No attempt has been made in either case to identify the alga.

Pigment extracts of *Hermaeina smithi* were compared with extracts from *Chaetomorpha aerea* (Order Cladophorales), the alga upon which the animal is found. The results are found in Fig. 7. In animals starved one day prior to extraction, the carotenoid pigments show the same mobility as those from the algal food, while the chlorophylls do not. The latter effect may be due to pigment degradation by the animal. In freshly fed animals, extracted pigments were indistinguishable from pigments from *Chaetomorpha*.

DISCUSSION

All of the data presented in the previous section are consistent with the interpretation that the green bodies in the digestive gland cells of *Placobranchus ianthobapsus* are algal chloroplasts. Furthermore, information derived from the separation of the plastid pigments permits the assignment of the chloroplasts to an alga belonging to the Order Siphonales (Chlorophyta). Unfortunately, it is not possible to identify the source of the plastids more completely, since the animals have not been found in close association with any species of alga in the field. Kawaguti *et al.* (1965) identified the bodies in *Placobranchus* as blue-green algae. However, my pigment data (Fig. 6) do not support this interpretation. The presence of chlorophylls *a* and *b* and the xanthophylls, siphonein and siphonaxanthin in the extract establish the symbiont's identity among the siphonaceous green algae (Strain, 1965). If the bodies were blue-green algae, chlorophyll *b* would not be present in the pigment extracts.

Chloroplasts symbiotic with digestive gland cells of species of the genus *Elysia*

have already been described. Kawaguti & Yamasu (1965) found chloroplasts in the tissues of *E. atroviridis* from Japan. In this case the chloroplasts were derived from the green alga, *Codium fragile*. In 1968, Taylor reported finding chloroplasts of *Codium tomentosum* within the digestive cells of *E. viridis* from Great Britain. The present report extends these accounts to include *E. hedgpethi* from California. This species obtains its chloroplasts from either *Codium fragile* or *Bryopsis corticulans*, both siphonaceous green algae.

Another species of sacoglossan which has been discussed in this regard is *Placida dendritica* (Taylor, 1967, 1968). *Placida* from the coast of California has now also been found to contain chloroplasts. Again, the chloroplast source is either *Codium* or *Bryopsis*, whichever happens to be abundant.

A close relative of *Placida*, *Hermaeina smithi*, differs from the other sacoglossans studied. *Hermaeina* shows no sign of chloroplasts within the cells of the digestive gland. Indeed, pigment separations from this species indicate that chloroplasts are ingested, but are rapidly degraded (digested?). In animals starved for very short periods, it can be determined that the chlorophyll pigment from the plastids has been destroyed (Fig. 7). Preliminary studies involving incorporation of $H^{14}CO_3^-$ show that *Hermaeina* is incapable of fixing any more carbon in the light than it can in the dark, inferring that the chloroplasts are no longer photosynthetic. Thus, it must be concluded that a symbiotic association does not exist in the case of *Hermaeina*. Functional aspects of the chloroplasts symbiotic in *Elysia*, *Placida* and *Placobranchus* will be presented elsewhere (Greene, in prep.).

The occurrence of chloroplasts in animal cells raises many questions. Symbiosis between sacoglossan opisthobranchs and algal chloroplasts is an example of an hereditary symbiosis in which the symbiont is not transmitted from one generation to the next through the egg (as in anemones and corals). Each generation must acquire its chloroplasts anew and most hosts must be assured a continuous supply of new chloroplasts to maintain their association (Greene, 1968, and in prep.). In other hosts, the chloroplasts may replicate. The actual mode of primary infection of the animal by the chloroplasts remains unknown, though it seems logical that they are acquired through feeding by the adult and enter the cells of the digestive gland by phagocytosis.

The highly specialized feeding habits exhibited by the Sacoglossa (Fretter, 1941) have generally limited each species within the group to a single species of alga which can be used for food. Some sacoglossans, however, may feed on 2 or 3 species of closely related algae (e.g., *Elysia* on *Codium* or *Bryopsis*). Table 1 shows the results of a food preference survey of 38 sacoglossan species from all over the world. It is significant that 56% of the slugs surveyed fed exclusively on green algae of the Order Siphonales. The question immediately arises as to the nature of the attractant quality of the algae involved in these associations. Evans (1953) and Kay (1968) have mentioned the possible importance of the chemical nature of the food, while MacNae (1954) was more concerned with the structural peculiarities of the algae in question. It is difficult to assess the former possibility since appropriate information on the metabolism of marine algae is unavailable. The idea that the structure of the algal species is an important factor is more easily examined.

First, it is necessary to consider whether or not the animal will be capable of feeding on the alga considering the modified nature of the buccal apparatus.

TABLE 1.* Algae commonly taken as food by sacoglossan opisthobranchs.

Algae**	Per cent of total plant species
Division Clorophyta	
Order Cladophorales	(14·6)
Chaetomorpha	2·1
Cladophora	6·2
Rhizoclonium	2·1
Urospora	2·1
Unspecified Cladophorales	2·1
Order Siphonales	(56·2)
Boodlea	2·1
Bryopsis	2·1
Caulerpa	18·7
Codium	20·8
Halimeda	12·5
Division Xanthophyta	
Order Vaucheriales	(8·3)
Vaucheria	8·3
Division Phaeophyta	
Order Dictyotales	(6·3)
Dictyota	2·1
Padina	4·2
Order Fucales	(2·1)
Sargassum	2·1
Division Rhodophyta	
Order Ceramiales	(8·4)
Delesseria	2·1
Griffithsia	2·1
Laurencia	2·1
Polysiphonia	2·1
Order Gigartinales	(4·2)
Gracilaria	2·1
Gracilariopsis	2·1

* Data compiled from a review of the literature.
** Classification follows the scheme of Dawson (1966).

The algal species best suited for the animals would be those with large cells that could be easily punctured by the radular teeth. Indeed, the algal genera listed in Table 1 reflect this requirement for the most part, and are characterized by having large cells. Algae in the Order Siphonales (Chlorophyta) are coenocytic, or " acellular ", and would, therefore, yield large amounts of cell sap to an animal exerting little energy in feeding.

The other point is the ability of the animals involved to ingest the chloroplasts of the various algal species. Once again

the genera in Table 1 show a general similarity with regard to their chloroplasts. With the exception of the members of the Order Cladophorales, the algal species fed upon have large numbers of small chloroplasts in their cells. In the Cladophorales each cell contains a single, reticulate chloroplast of large size, which at first would seem impossible for a liquid feeder to ingest. However, under certain conditions this type of chloroplast does fragment into numerous discoid pieces (Smith, 1951), especially after mechanical disruption of the cells. It is these pieces which are ingested by *Hermaeina smithi* (pers. observ.). It was pointed out above that *Hermaeina* did not possess functional chloroplast symbionts since the latter did not fix $^{14}CO_2$. It was assumed that the chloroplasts were degraded shortly after ingestion. My preliminary experiments show that the fragments from disrupted *Chaetomorpha* and *Cladophora* are quite capable of photosynthetic fixation of $^{14}CO_2$ (Greene, unpubl.).

The probability is great that chloroplast-sacoglossan symbiosis is a widespread phenomenon. Of 86 sacoglossan species surveyed for body color, 82% were described as green. Those species that were not green had been collected from non-green algal species, and Taylor (1967) has already shown that at least two of these contain plastids from red algae in their tissues. Thus, it appears that symbiosis with algal chloroplasts may be nearly universal among the Sacoglossa.

In light of information now available, it would seem that Kay's (1968) hypothesis regarding the evolution of feeding habits among sacoglossans must be re-evaluated. The hypothesis, as it stands, states that primitive forms fed on species of *Caulerpa* which supplied a nutrient not available in other algal genera. Then, drawing on the older literature describing symbionts in various sacoglossans as zooxanthellae and zoochlorellae, it is assumed by Kay that the presence of algal symbionts freed the slugs from the *Caulerpa* " habit ". Since, in all cases investigated, the symbionts are now known to be chloroplasts derived from the animal's algal food, the Sacoglossa must now be even more firmly associated with those algal species whose chloroplasts they bear.

ACKNOWLEDGEMENTS

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RÉSUMÉ

SYMBIOSE CHEZ DES OPISTHOBRANCHES SACOGLOSSES SYMBIOSE AVEC DES CHLOROPLASTES D'ALGUES

R. W. Greene

Les corpuscules verts responsables de la couleur de quatre espèces d'Opisthobranches Sacoglosses (Mollusca; Gastropoda) ont été étudiés et l'on a trouvé que les chloroplastes dérivent de l'alimentation en algues de l'animal. Les chloroplastes sont invariablement limités aux cellules des diverticules digestifs dans chaque espèce.

Les chloroplastes des tissus d'*Elysia hedgpethi* et *Placida dendritica* dérivent soit de *Codium fragile* soit de *Bryopsis corticulans*. Les plastes des tissus de *Placobranchus ianthobapsus* dérivent d'une algue verte siphonée non identifiée. Dans les trois cas précédents, on a trouvé que les chloroplastes sont maintenus dans l'animal dans les conditions de symbiose.

La quatrième espèce étudiée, *Hermaeina smithi*, ingère des chloroplastes de *Chaetomorpha aerea* et *Cladophora trichotoma*, mais les plastes sont apparemment vite dégradés.

On pense que la symbiose entre les chloroplastes d'algues et les Opisthobranches de l'ordre des Sacoglosses est peut-être la règle, plutôt que l'exception.

A. L.

RESUMEN

SIMBIOSIS EN OPISTOBRANQUIOS SACOGLOSOS: SIMBIOSIS CON CLOROPLASTOS ALGACEOS

R. W. Greene

Se investigaron los cuerpos verdes causantes de ese color en cuatro especies de opistobranquios sacoglosos, descubriendo que son cloroplastos derivados de la alimentación algácea del molusco, y estan invariablemente restringidos a los divertículos digestivos en cada especie.

Cloroplastos en los tejidos de *Elysia hedgpethi y Placida dendritica*, derivan de *Codium fragile* odde *Bryopsis corticulans*. En los tejidos de *Placobranchus ianthobapsus* derivan de un alga sifonácea verde de especie no identificada. En esos tres casos los cloroplastos estaban retenidos por los animales en condición simbiótica.

La cuarta especie investigada, *Hermaeina smithi*, demostró haber ingerido cloroplastoa de *Chaetomorpha aerea* y *Cladophora trichotoma*, pero aparentemente los plástidos degradaron muy rápido.

Se sugiere que la simbiosis entre cloroplastos algáceos y esas "babosas marinas" del orden Sacoglossa pueda ser la regla en vez de la excepcion.

L. L. D.

АБСТРАКТ

СИМБИОЗ У МОЛЛЮСКОВ SACOGLOSSAN OPISTHOBRANCHS: СИМБИОЗ С ХЛОРОПЛАСТАМИ ВОДОРОСЛЕЙ

Р. ГРИН

Были изучены зеленые тельца, создающие окраску тела у четырех видов Sacoglossa (Mollusca, Gastropoda, Opisthobranchia). Оказалось, что происхождение у них этих хлоропластов связано с питанием моллюсков водорослями. Хлоропласты всегда располагались в пищеварительных клетках пищеварительных дивертикул всех видов моллюсков. Хлоропласты в тканях *Elysia hedgpethi* и *Placida dendritica* происходили или от *Codium fragile* или от *Bryopsis corticulans*. Пластиды в тканях *Placobranchus ianthobapsus* были связаны с неопределенной зеленой водорослью из Siphonacea. В трех случаях, из указанных выше, хлоропласты находились в животных как симбионты. Четвертый из изученных видов- *Hermaeina smithi* получил хлоропласты от заглоченных ею *Chaetomorpha aerea* и *Cladophora trichotoma*, но пластиды, видимо, быстро деградировали.

Предполагается, что симбиоз между хлоропластами водорослей и морскими моллюсками из отряда Sacoglossa может быть скорее правилом, чем исключением.

Z.A.F.

MALACOLOGIA, 1970, 10(2): 369–380

SYMBIOSIS IN SACOGLOSSAN OPISTHOBRANCHS: TRANSLOCATION OF PHOTOSYNTHETIC PRODUCTS FROM CHLOROPLAST TO HOST TISSUE

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ABSTRACT

Two species of sacoglossan slugs, *Elysia hedgpethi* and *Placobranchus ianthobapsus* (Mollusca: Opisthobranchia), were studied in order to determine whether or not the chloroplasts present in their tissues were leaking organic compounds to the animal tissues. Animals were incubated with $H^{14}CO_3^-$ in the light and dark for varying periods of time. Radioautographs of tissue sections indicated rapid translocation of ^{14}C–labeled material to the animals' mucus glands, and renopericardial tissue. Separation of chloroplast-bearing from chloroplast–free tissues in *Placobranchus* afforded an independent assay for translocation, and showed that after 36 hrs., over 20% of the total ^{14}C fixed by the chloroplasts was leaked to the animal tissue.

Chloroplasts isolated from *Codium fragile*, *Elysia's* algal food, were incubated with $H^{14}CO_3^-$ and the suspending medium was analysed by radiochromatography. A single leakage product was found in the medium which was identified as glycolic acid and which accounted for about 16% of the total carbon-14 fixed.

INTRODUCTION

One of the most frequently discussed features of symbiotic relationships between autotrophs and heterotrophs is the question of translocation of nutrient substances from the symbiont to the host. Muscatine & Hand (1958) presented the first radioautographic evidence for the translocation of ^{14}C-labeled materials from zooxanthellae to their sea anemone host, *Anthopleura elegantissima*. Since that time studies have been carried out on a variety of organisms harboring algal symbionts in their tissues in an attempt to establish translocation of materials (Goreau, Goreau & Yonge, 1965; von Holt & von Holt, 1968; Muscatine & Lenhoff, 1963). These studies all demonstrated the translocation of materials produced by the algal symbiont to the tissues of an animal host.

More recently, attention has focused on *in vitro* studies of symbiotic algal strains in order to elucidate the nature of compounds being excreted to the external medium. Work in this area has been reviewed by Smith, Muscatine & Lewis (1969). The carbohydrates most commonly released by symbiotic algae to their animal hosts are glycerol, glucose or maltose depending on the association investigated. Algal symbionts in lichens have also been studied and have been found to release sorbitol, ribitol, erythritol and glucose (Smith *et al.*, 1969).

Similar questions have now been raised concerning symbioses between algal chlo-

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roplasts and sacoglossan opisthobranchs. Since the first report of this phenomenon (Kawaguti & Yamasu, 1965), it has become apparent that animal-chloroplast associations are widely distributed (Taylor, 1967, 1968; Greene, 1968, 1970; Trench, 1969; Trench, Greene & Bystrom, 1969). The papers of Taylor (1968), Trench (1969) and Trench *et al.* (1969) all present radioautographic evidence for the translocation of ^{14}C-labeled materials from symbiotic chloroplasts to host animal tissue.

The present study gives evidence for the translocation of material in 2 species of chloroplast-bearing sacoglossan slugs, using ^{14}C as a tracer. Studies on the algal chloroplasts *in vitro* show that glycolic acid is excreted to the external medium under the experimental conditions.

MATERIALS AND METHODS

1. Experimental Organisms

(*a*) *Animals.* Two species of sacoglossans (Mollusca: Opisthobranchia) were used. *Elysia hedgpethi* Marcus was collected from Flat Rock, Palos Verdes, Los Angeles County, California. The specimens were obtained intertidally on the green alga, *Codium*, which is abundant in the collecting area. The other species, *Placobranchus ianthobapsus* Gould, was collected from reef-flats in Kaneohe Bay, Oahu, Hawaii, at a depth of about 1 m.

Specimens of *Elysia* were maintained in large holding tanks in the recirculating sea water system in the Zoology Department at the University of California at Los Angeles. The animals were kept in constant light, and water temperature was maintained at 13°C. While in captivity, *Elysia* was supplied with fresh *Codium* continuously.

Placobranchus was kept in plastic tubs (27×32×13 cm) containing sea water at room temperature (about 22°C) and in constant light. Since the algal food of this species is unknown, the animals were not fed in captivity. Experimental animals were used within 5 days of their collection in Hawaii.

(*b*) *Algae.* The alga used in this study was *Codium fragile* Hariot (Chlorophyta: Siphonales). It was obtained at Flat Rock, Palos Verdes, Los Angeles County, California, intertidally. The alga was maintained in holding tanks with recirculating sea water at 13°C in constant light.

2. Experimental Procedures

(*a*) *Incubation of Animals with* ^{14}C. Animals were incubated in 25 ml Erlenmeyer flasks containing Millipore-filtered sea water (porosity 0·45 μ) to which had been added $NaH^{14}CO_3$ (Calbiochem, sp. act. 35 mc/mM) to achieve an initial specific activity of 10 μc/ml. Experimental animals were placed in the light from 15 minutes to 5 hours for *Elysia* and to 60 hours for *Placobranchus*. The light source consisted of 4 photoflood lamps (C.E. 150W., 115V.) controlled by a rheostat. Light intensity was maintained at 500 foot candles measured at the bottom of the incubation flasks (Weston Illumination Meter, Model 756). Temperature was maintained constant during incubations by immersing the flasks in a running water bath (14°C for *Elysia*, 22°C for *Placobranchus*). Following incubation, animals were rinsed twice with about 5 ml fresh Millipore-filtered sea water to remove excess isotope prior to further analysis.

(*b*) *Radioautography.* Whole animals incubated as in (*a*) above were fixed in Clark's fixative for 1 hour. Specimens were transferred directly into 70% ethanol and were dehydrated through a series of ethanol solutions. Tissues were cleared in xylene, and embedded in paraffin

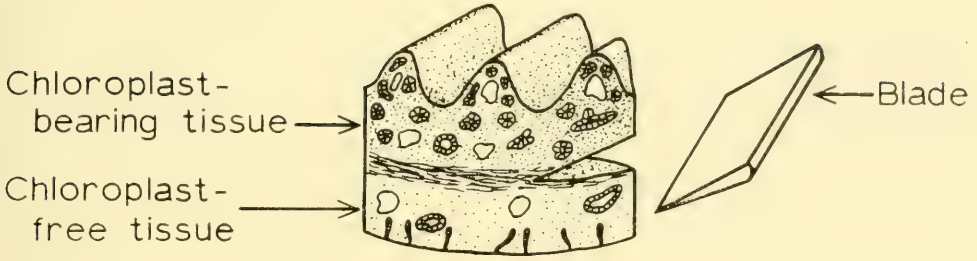

FIG. 1. Diagrammatic representation of the tissue separation technique as applied to samples of *Placobranchus* showing the appearance of the tissue cylinders (see *Methods*).

(m.p. 56–58°C). Sections were cut at 7 μ and were mounted on glass microscope slides. Slides were dipped in Kodak nuclear track emulsion (Type NTB2), and sections were allowed to expose for 1–2 weeks. Dark control animal tissues were treated similarly. Development was carried out according to the manufacturer's directions.

(*c*) *Tissue Separations.* This technique was only possible with specimens of *Placobranchus.* Animals were incubated with isotope as described above, and 4 specimens were sampled at each 12 hour interval up to 60 hours. The animals were frozen on dry ice in an extended position, and cylindrical sections were cut from the animals' parapodia by use of a 3/16″ diameter cork borer. The frozen cylinders which resulted contained an upper region of chloroplast-bearing tissue, and a lower region of chloroplast-free tissue (see Fig. 1). By careful trimming with a sharp blade, the 2 layers could be separated and assayed for radioactivity. Separated tissues were ground with a glass rod in hot 1N NH_4OH to produce a homogeneous suspension. Aliquots of 0·1 ml were plated on preweighed planchets, acidified with 1·0N HCl to drive off unbound $^{14}CO_2$, and dried under an infrared lamp. The planchets were weighed again to determine the weight of tissue deposited, and radioactivity was assayed by counting with a transistorized Nuclear Supplies scaler (Type SA–250) with a thin end-window G.M. tube (LND Inc., No. 733).

(*d*) *Isolation of Chloroplasts.* Approximately 10 g fresh *Codium* were placed in a Waring Blender with a serological head. Fifty ml of Millipore-filtered sea water (0°C) were added and the material was blended for 5 seconds. The suspension was immediately poured through glass wool into tubes for centrifugation. The material was centrifuged for 50 seconds at high speed (International Clinical Centrifuge, Model CL) and the supernatant removed. The pellets were resuspended in fresh Millipore-filtered sea water and then recentrifuged. This washing process was repeated 3 times. Observation of the pellets with an oil immersion lens (930X) showed particulate contamination by algal cell nuclei and unidentifiable material. In proportion to the chloroplasts in the preparation, the contamination was judged to be negligible.

(*e*) *Incubation of Chloroplasts.* Chloroplasts were incubated as in section (*a*) except that the initial specific activity used was 20 μc/ml, and the incubation period was shortened to 10 minutes. The chloroplasts were centrifuged, the medium was saved, and alcohol soluble materials were extracted from the pellet in a series of hot ethanol dilutions.

(*f*) *Paper Chromatography.* Materials to be analyzed by paper chromatography

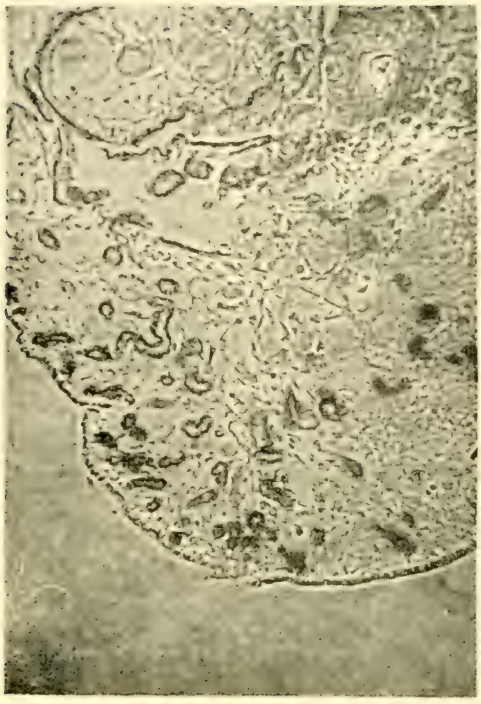

FIG. 2

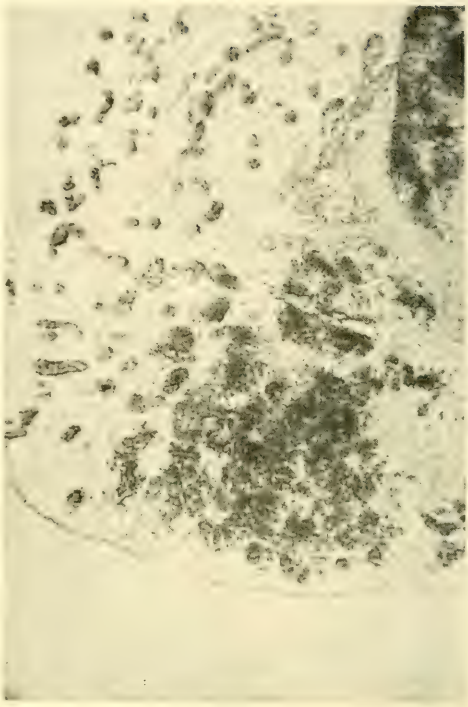

FIG. 3

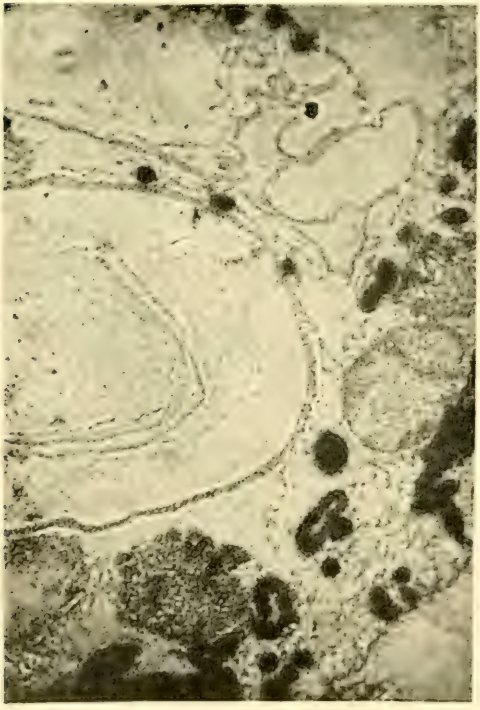

FIG. 4

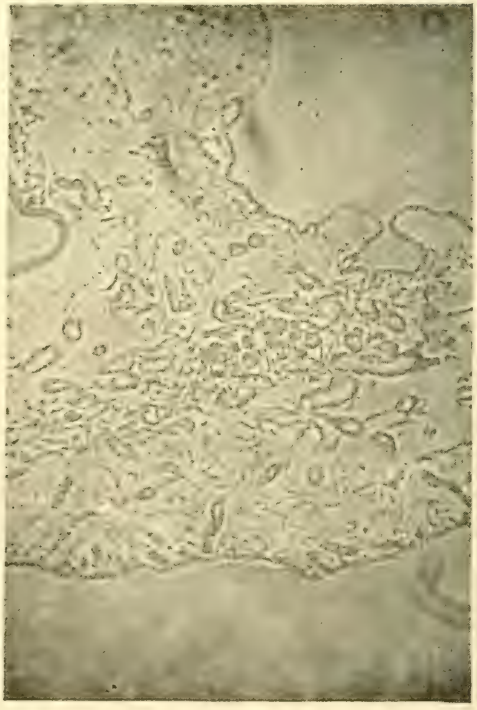

FIG. 5

were first desalted by evaporation to dryness *in vacuo* (Rotary Evapomix), and resuspension in dry absolute ethanol. The material was placed at the origin on Whatman No. 4 chromatography paper (46×57 cm) and was developed in 2 dimensions. The solvent in the first dimension was phenol-water (100:39, w/v) (PW), and in the second dimension was n-butanol: propionic acid: water (142:71: 100, v/v/v) (BPAW). Radioactive spots were located by exposing the paper to Kodak single-coated, blue-sensitive medical X-ray film (Bassham & Calvin, 1957). Films were developed according to the manufacturer's specifications.

(*g*) *Identification of Unknowns.* Radioactive spots were cut from chromatograms, and the compounds were eluted with a small volume of distilled water. In the present study, glycolic acid was tentatively identified in the following manner. The unknown material was co-chromatographed in 2 dimensions (PW: BPAW) with authentic glycolic acid (Calbiochem). Tolbert & Zill (1956) report that no other acid moves with the Rf values (39, 63) in the PW:BPAW solvent system. The unknown was also co-chromatographed with authentic material in a single dimension developed with ethyl acetate - acetic acid - water (3:3:1, v/v/v). Specific identifications of other compounds of less importance will be discussed elsewhere (Greene & Muscatine, in prep.).

RESULTS

1. Radioautography

In order to detect the translocation of ^{14}C-labeled materials from chloroplast-bearing tissues to chloroplast-free tissues of sacoglossans, animals were incubated in $NaH^{14}CO_3$ for varying periods of time, sectioned and exposed to liquid nuclear-track emulsion. Fig. 2 shows a section through a specimen of *Elysia* which was incubated in isotope for 15 minutes in the light. The exposed silver grains are generally limited to areas directly over the tubules of the digestive gland which contain the symbiotic chloroplasts.

In specimens incubated with ^{14}C for 60 minutes in the light (Fig. 3), labeled material appears in the mucus glands. At the same time, the number of exposed silver grains lying over digestive gland has increased markedly.

After 90 minutes incubation in the light, the digestive diverticula and mucus glands appear heavily labeled (Fig. 4). The reno-pericardial complex also shows, signs of high activity. In general, reduced silver grains appear over all parts of the tissue.

Control animals incubated in the dark for 90 minutes elicited very little silver grain reduction (Fig. 5). That radioactivity which is present could be the result of heterotrophic fixation by the animal tissue. It must be remembered

FIG. 2. Radioautograph of tissue of *Elysia* following incubation in $H^{14}CO_3^-$ in the light for 15 minutes. The tissue was unstained. 50X.

FIG. 3. Radioautograph of tissue of *Elysia* following incubation in $H^{14}CO_3^-$ in the light for 60 minutes. The tissue was unstained. 50X.

FIG. 4. Radioautograph of tissue of *Elysia*following incubation in $H^{14}CO_3^-$ in the light for 90 minutes. The tissue was unstained. 50X.

FIG. 5. Radioautograph of tissue of *Elysia* following incubation in $HC^{14}O_3^-$ in the dark for 90 minutes. The tissue was unstained. 50X.

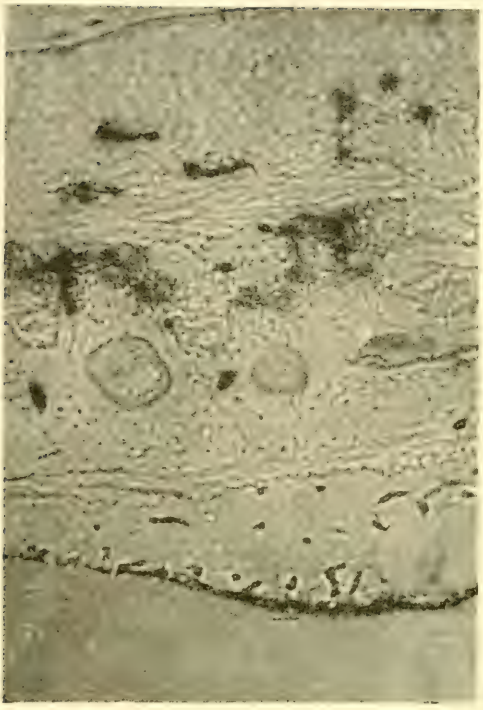

FIG. 6. Radioautograph of tissue of *Placobranchus* following incubation in $H^{14}CO_3^-$ in the light for 180 minutes. The tissue was unstained. 50X.

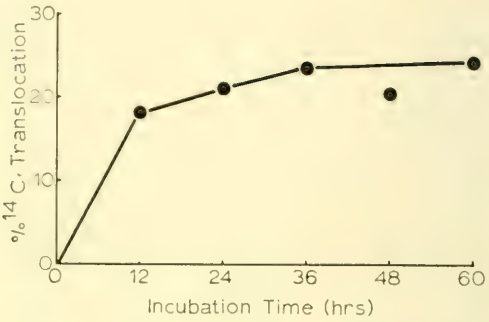

FIG. 7. Translocation of ^{14}C-labeled photosynthate from chloroplast-bearing tissues to chloroplast-free tissues of *Placobranchus*. The values were derived from the tissue-separation experiment and are expressed as % of total ^{14}C fixed present in the chloroplast-free fraction.

that in the above procedure, only radioactive materials in the animal tissue which are not soluble in water, alcohol or xylene are detected. It has been previously demonstrated that a minimum of 39% of the total ^{14}C fixed is extracted from a sea slug during dehydration and embedding (Trench *et al.*, 1969). Comparable extraction values were obtained during the present study.

Studies involving specimens of *Placobranchus ianthobapsus* incubated in $NaH^{14}CO_3$ follow the same pattern of labelling as in *Elysia*. Fig. 6 shows a radioautograph of an animal incubated with isotope for 180 minutes in the light, in which the animal tissue is nearly uniformly labeled. Reduced silver grains are especially abundant over the digestive gland tubules which contain the chloroplasts and over the mucus glands. Dark-control specimens of *Placobranchus* showed negligible silver grain reduction.

The appearance of reduced silver grains over chloroplast-free regions of tissue in *Elysia* and *Placobranchus* indicates that there has been translocation of ^{14}C-labeled material from the symbiotic chloroplasts to the animal tissue. Since animals incubated with isotope in the dark showed negligible radioactivity in their tissues, it may be concluded that the observed ^{14}C in the tissues of light incubated animals is mainly the result of photosynthesis by the chloroplasts.

2. Assay of Translocation by Tissue Separation

Since chloroplast-bearing and chloroplast-free tissues may be separated relatively easily in *Placobranchus*, an independent assay for translocation of ^{14}C-photosynthate was possible. Animals were incubated with $NaH^{14}CO_3$ in the light and dark for varying periods of time. Tissues were then frozen, sepa-

TABLE 1. Tissue separation data showing the translocation of ^{14}C-labeled photosynthate from chloroplast-bearing tissues to chloroplast-free tissues of *Placobranchus*. Data represent cpm/mg dry weight.

Sample		LIGHT			DARK		
		chloroplast-bearing (cpm)	chloroplast-free (cpm)	translocated (%)	chloroplast-bearing (cpm)	chloroplast-free (cpm)	translocated * (%)
12 h.	a	8966	1257	12·2	97	36	27·0
	b	3789	1135	23·0	187	59	23·9
24 h.	a	3199	654	16·9	144	93	39·2
	b	3678	1321	26·4	137	93	40·4
36 h.	a	831	396	32·2	104	50	32·4
	b	7475	1219	14·0	61	40	39·6
48 h.	a	4012	1320	24·7	84	85	50·2
	b	5314	1024	16·1	51	32	38·5
60 h.	a	4702	1433	23·3	59	90	60·4
	b	3792	1229	24·4	106	64	37·6

* see Results section.

rated and assayed as described above. Table 1 shows the data derived from the tissue separations. This information shows that considerable radioactive material was found in the chloroplast-free tissue at every sampling time. Data for animals incubated in the dark show that small amounts of ^{14}C are heterotrophically fixed by the animal tissue. The values for translocation occurring in dark-incubated animals are presented for comparison of ^{14}C-distribution only, since the activity was probably fixed *in situ* in these tissues rather than translocated from the chloroplast-bearing tissue. Fig. 7 shows the percentage of the total ^{14}C fixed by the animal in the light which appeared in the chloroplast-free tissue fraction. The data are averages from the 2 groups of animals incubated (see Table 1). These values must all be considered to be minimum values since, unavoidably, there is chloroplast-free tissue assayed with the chloroplast-bearing tissue.

From the data presented above, it is evident that after 36 hours of exposure to isotope in the light, over 20% of the total ^{14}C fixed by the animal has been passed to the chloroplast-free tissue. It is significant to note that all of the activity found in the animal tissue is insoluble in water and hot ethanol.

3. Release of ^{14}C-labeled Products by Chloroplasts *in vitro*

To determine the identity of the compound(s) released to the animal tissues in the previous experiments, chloroplasts isolated from the alga, *Codium fragile*, were incubated with $NaH^{14}CO_3$ in the light, and the suspending medium was

FIG. 8. Radiochromatogram of the aqueous medium in which isolated chloroplasts of *Codium* were incubated with $H^{14}CO_3^-$ for 10 minutes in the light. The solvent system used was phenol-water (1) and n-butanol-propionic acid-water (2). The (O) shows the position of the origin.

FIG. 9. Radiochromatogram of an ethanol extract of isolated chloroplasts of *Codium* following 10 minutes incubation with $H^{14}CO_3^-$ in the light. Solvents as in Fig. 8. The notation (Glu/Gal) indicates the presence of both glucose and galactose, inseparable in these solvents.

analyzed by paper chromatography. Fig. 8 is a radiochromatogram of this material showing that a single radioactive compound was leaked to the medium by the chloroplasts under the experimental conditions. In order to demonstrate that the compound in Fig. 8 was not the result of chloroplast disruption, the incubated chloroplasts were extracted with ethanol and the resultant material was chromatographed (Fig. 9). If plastid disruption had occurred during the isolation procedure or incubation, the radiochromatograms would be identical.

The material released from the chloroplasts under the experimental conditions previously described has been provisionally identified as glycolic acid. This, presumably, is the compound leaked to the animal tissues during photosynthesis by the plastids. The amount of glycolic acid excreted represents about 16% of the total ^{14}C fixed by the chloroplasts in the light, while the glycolic acid within the chloroplasts accounts for 26% of the total radioactivity extracted.

DISCUSSION

In the present study radioautographic evidence was presented to establish translocation of ^{14}C-labeled photosynthetic material from symbiotic chloroplasts to the tissues of the sacoglossan slugs, *Elysia hedgpethi* and *Placobranchus ianthobapsus*. In both species the mucus glands and renopericardial tissues became rapidly labeled. In very short incubations with isotope, only the areas associated with digestive diverticula show evidence of radioactivity. This was to be expected since the chloroplasts occur solely within the cells of the diverticula. In dark-incubated controls, reduction of silver grains over animal tissue was negligible. The material released by chloroplasts of *Codium fragile* incubated *in vitro* was identified as glycolic acid.

It is well known that algae symbiotic with a variety of invertebrate hosts are capable of selectively releasing compounds derived from photosynthesis to the host tissue. Muscatine & Lenhoff (1963),

working with green hydra, showed that between 10–12% of the photosynthetically-fixed ^{14}C was translocated to the host tissues, and that about half of this material was incorporated into protein. In 1965, Goreau, Goreau & Yonge demonstrated that when the giant clam, *Tridacna*, was incubated with $^{14}CO_2$, label rapidly appeared in the mucus glands, crystalline style and pericardium. Von Holt & von Holt (1968) showed that after 3 hours of photosynthesis by the symbionts of various coelenterates, 24–40% of the total photosynthate was found in the tissues of the animals.

In 1968, Taylor presented electron radioautographic evidence for the translocation of ^{14}C-labeled photosynthate from chloroplast symbionts to the tissues of the sacoglossan slug, *Elysia viridis*. Trench, Greene & Bystrom (1969) used light radioautography to demonstrate the movement of labeled photosynthate from the chloroplasts symbiotic with *Tridachia crispata*, to the animal tissues. Carbon-14 labeled material appeared in the pedal mucus gland, the reno-pericardium and in the sheath associated with the cerebral ganglia.

The occurrence of labeled material in the mucus glands and pericardial tissue of *Elysia* and *Placobranchus* is consistent with the findings of Goreau *et al.*, (1965) and Trench *et al.* (1969). In both cases the regions may be assumed to have high metabolic requirements, and, in the case of the mucus glands, a high turnover rate of materials due to secretory activity.

The excretion of glycolic acid by intact algae to the suspending medium both *in vivo* and *in vitro* is well known. Allen (1956) reported the excretion of glycolic acid into the medium by species of *Chlamydomonas*. Nalewajko, Chowdhuri & Fogg (1963) showed that planktonic *Chlorella* liberated glycolic acid, and they discussed some aspects of glycolate in aquatic habitats. In 1965, Fogg, Nalewajko & Watt surveyed phytoplankton samples and again demonstrated the excretion of glycolic acid to the surrounding waters. Hellebust (1965) studied 22 species of marine algae and was able to show glycolate excretion by most species, albeit in small amounts.

Among species of algae found in symbiotic relationships, glycolic acid is commonly found to be excreted to the medium when incubations are carried out *in vitro* (Muscatine, 1965; Muscatine, Karakashian & Karakashian, 1967). Excretion of glycolic acid has also been reported from studies on isolated chloroplasts (Jensen & Bassham, 1966; Bassham, Kirk & Jensen, 1968).

In the present study 16% of the total ^{14}C incorporated by the chloroplasts was released to the suspending sea water as glycolic acid. This value is well within the limits described in the foregoing papers dealing with intact algal cells. In contrast to the work of Bassham *et al.* (1968), however, glycolic acid was the sole product excreted by *Codium* chloroplasts under the experimental conditions. The chloroplasts from spinach (Bassham *et al.*, 1968) " leaked " several compounds to the medium.

Muscatine (1965) has already suggested the " adventitious utilization " of excreted glycolic acid by an animal acting as host to algal symbionts. Glycolic acid may easily enter the tricarboxylic acid cycle through glyoxylic acid and then combination with succinic acid to form isocitric acid (Bassham & Calvin, 1957). From this point, it is able to enter the metabolic pathways of the animal cell.

It should be noted that excretion by the chloroplasts *in vitro* does not necessarily represent the *in vivo* situation. Although the chloroplasts isolated from *Codium* leaked glycolic acid into the suspending medium, one cannot be certain that the same occurs when the plastids are in the tissues of *Elysia*.

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RÉSUMÉ

SYMBIOSE CHEZ LES OPISTHOBRANCHES SACOGLOSSES: TRANSFERT DES PRODUITS DE PHOTOSYNTHÈSE DU CHLOROPLASTE AU TISSU DE L'HÔTE

R. W. Greene

Deux espèces de Sacoglosses, *Elysia hedgpethi* et *Placobranchus ianthobapsus* (Mollusca: Opisthobranchia), ont été étudiés afin de déterminer si oui ou non les chloroplastes présents dans leurs tissus cédent des composés organiques aux tissus animaux. On a inoculé aux animaux du H $^{14}CO_3$- pendant des temps variables, en lumière et à l'obscurité. La radioautographie des coupes de tissus ont montré un transfert rapide du ^{14}C marqué dans les glandes à mucus de l'animal et dans le tissu péricardique. La séparation des tissus porteurs de chloroplastes des tissus non porteurs chez *Placobranchus*, a permis de réaliser un test de transfert et a montré qu'après 36 heures, plus de 20% du ^{14}C total fixé par les chloroplastes avait migré dans les tissus de l'animal.

Des chloroplastes isolés de *Codium fragile*, nourriture algale d'*Elysia*, ont été mis au contact de H $^{14}CO_3$-, puis le milieu de suspension a été analysé par radiochromatographie. Un seul produit migran ta été mis en évidence dans le milieu; on l'a identifié comme étant un acide glycolique qui correspond à environ 16% du total de carbone 14 fixé.

A. L.

RESUMEN

SIMBIOSIS EN OPISTOBRANQUIOS SACOGLOSOS: TRANSPOSICIÓN DE PRODUCTOS FOTOSINTÉTICOS, DE CLOROPLASTOS A TEJIDOS HUÉSPEDES

R. W. Greene

Se estudiaron dos especies de moluscos opistobranquios sacoglosos, las " babosas marinas " *Elysia hedgpethi* y *Placobranchus ianthobapsus*, para determinar si los cloroplastos presentes en los tejidos, eran o no productos de derrame de los compuestos orgànicos." Los animales fuer on incubados con $H^{14}CO_3$- a la luz y en la obscuridad por varios periodos. Radioautografías de cortes histólogicos indicaron cambios rápidos en la ubicación de los materiales marcados como ^{14}C a las glándulas mucosas y renopericardicas del animal. Separación de los tejidos, conteniendo cloroplastos y otros sin ellos, en *Placobranchus*, permitieron probar la transposición independiente, mostrando también que despues de 36 horas, más del 20% del total del ^{14}C de los cloroplastos habia entrado por derrame al tejido animal.

Cloroplastos aislados de *Codium fragile*, que es el alimento algófilo de *Elysia*, se incubaron con $H^{14}CO_3$ y el medio de suspensión fue analizado por radiocromatografía. Un producto único de derrame se encontró en el medio, el cual fué identificado como ácido glicólico, e importaba a un 16% del total fijo de Carbón 14.

J. J. P.

АБСТРАКТ

СИМБИОЗ У SACOGLOSSA OPISTHOBRANCHIA: ТРАНСЛОКАЦИЯ ПРОДУКТОВ ФОТОСИНТЕЗА ИХ ХЛОРОПЛАСТОВ В ТКАНЯХ ХОЗЯЕВ

Р. ГРИН

У двух видов улиток Sacoglossa- *Elysia hedgpethi* и *Placobranchus ianthobapsus* (Mollusca, Opisthobranchia)выяснилось, имеются ли хлоропласты в их тканях и отдают ли последние органические соединения в ткани животного. Моллюски инкубировались при $H^{14}CO_3$ на свету и в темноте в течение различного времени. Радиоаутография срезов тканей показала быстрый перенос помеченных C^{14} веществ к выделяющим слизь железам моллюсков и к почечно-перикардильным тканям. Разделение несущих хлоропласты тканей от тканей без них у *Placobranchus* при независимых попытках выяснить перенос показало, что после 36 часов более 20% общего количества C^{14}, связанного хлоропластами проникало в ткани моллюсков; хлоропласты, выделенные из *Codium fragile* (растительная пища *Elysia*) инкубировались при $H^{14}CO_3$, после чего среда анализировалась при помощи радиохроматографии. Единично попавшие туда вещества были определены как гликогеновые кислоты, составляющие около 16% от общего количества веществ, помеченных C^{14}.

Z. A. F.

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FIELD STUDIES ON LIFE HISTORY, GONADAL CYCLE AND REPRODUCTIVE PERIODICITY IN *MELAMPUS BIDENTATUS* (PULMONATA: ELLOBIIDAE)[1]

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ABSTRACT

Melampus bidentatus is found in the high littoral zone of semi-enclosed salt marshes along the Atlantic Coast from New Brunswick, Canada, to Texas, U.S.A. Observations and work from 1964 through 1968 on a population inhabiting Little Sippewisset Marsh, Falmouth, Massachusetts, U.S.A., emphasizes ecological and physiological aspects of life-cycle, gonadal cycle, and reproductive periodicity. A 3 to 4 year life-cycle is evident in this population, with usual maximum shell length of about 10·5 mm. Reproductive maturity (when gametogenesis first occurs) is reached at a size of approximately 5 mm shell length with individuals from 2 age groups participating in annual reproductive periods. The winter growth rate is only one-fifth of the spring-summer growth rate which in turn is nearly twice the growth rate of snails during the breeding season. Annual reproductive periods last 6 weeks sometime during late May, June, and early July each year. Each annual period consists of 3 cycles of oviposition at 2 week (semilunar) intervals correlated with spring tides. A consistently predictable pattern of behavior during these semilunar cycles of reproduction involving aggregation, copulation, oviposition and dispersion exists throughout the population. Egg masses are small, gelatinous, and without a tough outer envelope, each containing a mean of 850 eggs. Free-swimming veligers hatch after 13 days if egg masses are covered by water at that time. Veligers then spend a period of 2 to 6 weeks as planktonic larvae. Settled spat have been found no earlier than 6 weeks following hatching. Using measures such as total organic carbon or tissue dry weight, it was found that growth extends through nearly 6 orders of magnitude during the 3 to 4 year life span.

M. bidentatus is a true simultaneous hermaphrodite in contrast to all reports or assumptions of protandry throughout the family Ellobiidae. Assessments of gonad volume showed an 11-fold increase in volume from wintering to breeding snails, with a tripling of volume during the week preceding the first cycle of oviposition. Systematic decreases in gonad volume, oocyte numbers, and relative sperm content of gonads were found to coincide with periodicity of copulation and oviposition throughout the breeding cycles. A mean of 39 egg masses (850 eggs/mass) per individual per breeding season corresponds to 33,150 eggs per standard snail per year. This indicates a selection ratio of about 50,000:1 assuming any individual need replace itself only once during its lifetime.

Adaptations of *M. bidentatus* to survive the alternating exposure to marine and to nearly terrestrial conditions include a unique combination of physiological and behavioral factors. Of particular importance is the semilunar correlated occurrence of oviposition, hatching, and settlement with spring tides, as is manifested in the Sippewisset population.

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INTRODUCTION

The salt marsh snail, *Melampus bidentatus* Say, is a member of the family Ellobiidae, order Basommatophora, and has been regarded as one of the more primitive living pulmonates. The habitat of *M. bidentatus* is primarily that of semi-enclosed salt marshes from New Brunswick, Canada, to the gulf coast of Texas, U.S.A. These snails inhabit the high littoral zone of salt marshes and consequently are exposed to a unique combination of terrestrial and marine conditions. Frequent exposure to both has resulted in a reproductive facies essentially characteristic of marine forms but adapted for accommodation of the rigors of a semi-terrestrial environment.

Although *Melampus bidentatus* occurs frequently on the Atlantic seaboard and in many salt marshes as the dominant organism, surprisingly little work has been done on its physiology or ecology. Observations of life-cycle and life history of *M. bidentatus* have been made by Hausman (1932, 1936), Holle & Dineen (1957), and Morrison (1958). Morton (1955b) includes a consideration of *M. bidentatus* within an evolutionary study of the ellobiids. Russell-Hunter & Apley (1966) and Apley, *et al.* (1967) have reported preliminary work involving aspects of life history and reproductive turnover in a population of *M. bidentatus*. The work and observations reported herein involves the same population of snails in Little Sippewisset Marsh, Falmouth, Massachusetts, U.S.A. (41° 35′ N 70° 40′ W).

OBSERVATIONS AND RESULTS

Only in a few instances have individuals with a shell length greater than 11·5 mm been observed in the Sippewisset Marsh population. The more typical maximum size is about 10·5 mm. The usual minimum reproductive size (at time of onset of first gametogensis) is at a shell length of approximately 5 mm, which the majority of snails reach before or during their second spring. This population of *Melampus bidentatus* is represented in Fig. 1 in terms of generations on the ground through a representative year. As shown in this figure, the life span of *M. bidentatus* extends over a period of 3 to 4 years. Included within Fig. 1 are generation mean size, standard deviation, size range, and growth. The data in Fig. 1 are for the year 1966, including data from 22 samples taken through the year (bi-monthly, for the most part). Regular samples were collected (all snails in any 1 area were collected until a total of approximately 150 was reached), shell length determined, and number of individuals per class mark of 0·1 mm expressed as per cent of sample. Generations were apparent upon expressing the above data as histogram percentages showing frequency per class mark. In some instances observations of shell erosion and growth lines were used to verify generation divisions. The samples are a part of a continuous sampling program extending from 1964 to 1967.

Some notes have already appeared (Russell-Hunter & Apley, 1966; Apley, *et al.*, 1967) reporting attempts to express these growth rates as measures of actual organic biomass. As noted elsewhere (Russell-Hunter, *et al.*, 1968), the ash-free dry weight (or tissue dry weight without shell) in *Melampus* is closely related to the total organic carbon, and thus to calorific value. The mean size measurements (see Fig. 1) for different samples of the " 1964 " generation at Sippewisset can be converted to mean wet weights and then to ash-free dry weights. Typical values are: 1900 μg (June 28, 1965), 5400 μg (October 18, 1965), 6600 μg (March 9, 1966), 9200 μg (May 9, 1966), and 10,300 μg (June 28, 1966). This generation of

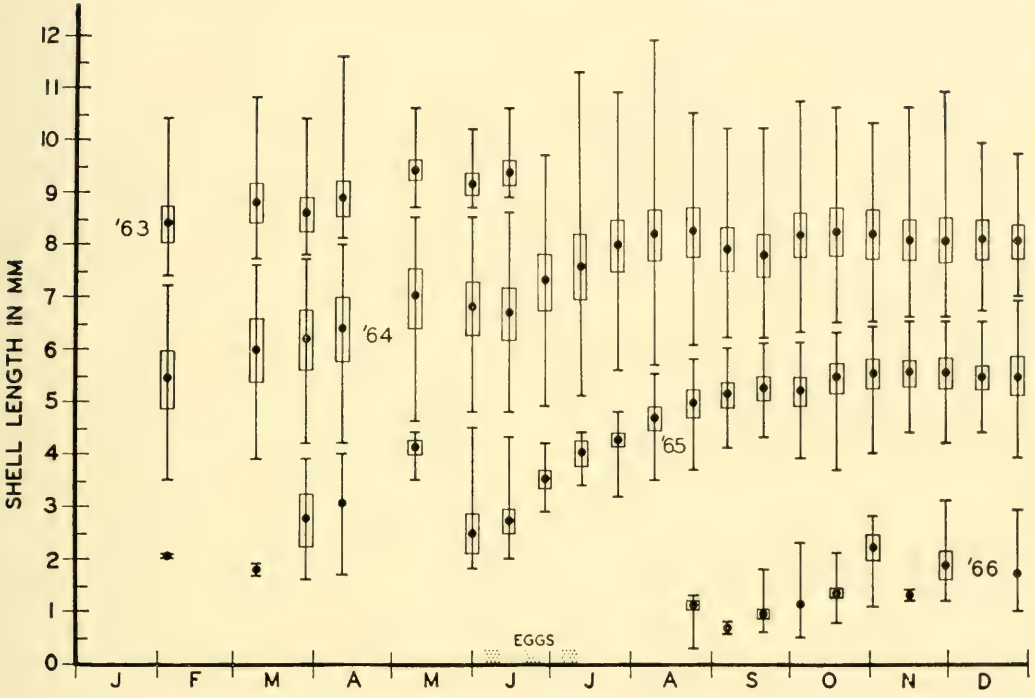

FIG. 1. Shell "lengths" of *Melampus bidentatus* in Sippewisset Marsh throughout 1966 (mostly bimonthly samples). Means ●, ranges I, and standard deviations □ are shown for samples of each generation with egg-laying cycles represented at bottom of figure. Generations are labelled according to the year of their hatching. The growth rate is indicated by the gradually increasing means within generations. Occurrence of new individuals ('66 generation) and dying out of older individuals ('63 generation) is also apparent. The means shown for the 1965 generation from January through May are not representative and should be treated with caution. Biased sampling resulted in disproportionately small numbers of lower-size groups being collected in these months. Additional information concerning this figure is given in Table 1 and in the text.

snails is the principal contributor (Apley, 1967) to the 1966 reproductive period which was most closely studied. When the increments of dry weights are made proportional to the elapsed times involved, the following rates can be expressed as increment per year (in mg dry weight): 11·4 (late summer), 3·08 (winter), 15·6 (spring-summer) and 8·03 (reproductive period in late May-early July), and with an annual average value of 8·4. Thus it can be seen that the growth rate (expressed in biomass terms) is reduced nearly two-fold during the reproductive period, but is still 2·6 times the overwinter growth rate. These rates will be discussed below in relation to measures of the reproductive output.

Oviposition occurs in cycles varying from year to year between late May and the first part of July. Egg masses measure from 1 to 2 mm in diameter (approximately 0·5 mm thick in the center) and appear as convex gelatinous mounds. Deposition of the masses occurs most commonly upon the ground surface, where they are soon covered by detritus and suspended material due to the action of tides. Egg masses may also be deposited on grass stems or leaves and have been observed on the shells of *M. bidentatus*. Counts of individual egg masses

TABLE 1. Quantitative aspects of eggs, veligers, spat and adults of *Melampus bidentatus*.

	Shell-length (mean values)	Wet weights (mean values)	Dry weights (mean values)	Tissue dry weight (ash free) (mean values)	Shell calcium carbonate (mean values)	Organic carbon (mean values)
Individual eggs		4·72 μg	354 nano-g			109 nano-g
Veligers	127 μ	494 nano-g	129 nano-g	ca. 116 nano-g	<13 nano-g	33·4 nano-g
Spat (newly settled —ca. 6 weeks after hatching)	383 μ	14·6 μg	6·0 μg	1·8 μg	4·3 μg	
Spat	675 μ	65·0 μg	23·2 μg	11·3 μg	11·9 μg	5·03 μg
Adult	5·8 mm	36·1 mg	17·4 mg	4·3 mg	13·1 mg	1·86 mg
Adult	10·1 mm	176·0 mg	81·0 mg	18·2 mg	62·8 mg	7·4 mg
Adult	12·3 mm (indiv. value)	312·0 mg (indiv. value)				14·6 mg (indiv. value)

revealed a mean number of 850 eggs per mass. Observations of egg masses, maintained on moist filter paper in petri dishes at a room temperature comparable to a field temperature, indicated that eggs hatch in 13 days, but only if they are submerged in water at that time. Newly hatched veligers measure 127 μ (mean length), are free-swimming, and assume a planktonic existence. Veligers were collected on outgoing tides at times of hatching with a small plankton net in the tidal inlet area. The veligers are planktonic for at least 2 but almost certainly not more than 6 weeks. The earliest that newly settled spat were found in the adult habitat was 6 weeks after oviposition. These spat had a mean length of 383 μ. Spat snails frequently occur around the bases of grass stems, in cavities of the plant, organic matter, and surface soil matrix. Before their first winter, most young snails reach a length between 1·0 and 2·0 mm. The life-cycle then follows the pattern already discussed (see Fig. 1). Russell-Hunter & Apley (1966) provide a more quantitative approach to the life history of *M. bidentatus*, and their data on biomass values for eggs, veligers and spat are relevant to consideration of fecundity. These data plus corresponding data for adult snails are presented in Table 1. The ratio of organic carbon in μg per mg wet weight changes from 23·1 (egg), 67·6 (veliger), 77·4 (spat) to 51·5 through 42·1 (in adult growth).

In *Melampus*, using any *real* measure such as total organic C or TDW (total dry weight), growth extends through 3 orders of magnitude in the first 3 months of life, and through nearly 6 orders of magnitude in the 3- to 4-year life span. In contrast, most freshwater or land pulmonates hatch from relatively large eggs and increase only 2 to 3 orders of magnitude in their life span (e.g., *Physa*

heterostropha from 36 μg to 5·3 mg C; Russell-Hunter, unpublished).

The adults in the population studied live in the upper 1/3 of the littoral zone of a semi-enclosed salt marsh. This is mainly in the zone of growth for the sedge, *Juncus gerardi*, and the grass, *Distichlis spicata*, with some *Spartina alterniflora* in lower regions. The marsh at this level is normally flooded for 1½–3 hours at times of spring tides and may remain dry for a few days during neap tides in each lunar cycle. Snail activity is normally at a maximum preceding the rising tides. Such populations of *M. bidentatus* are generally found to be inactive through periods of high temperature during the day in summer, and over a period of a few months during low winter temperatures. Snails may be found in groups and partially buried in moist sand during the summer when temperatures reach a daily and seasonal maximum. At this time they are frequently in whatever shade may be available and are usually inactive. Overwintering specimens of *M. bidentatus* are found especially accumulated in the holes of fiddler crabs at the same tidal level.

Studies of the genital tracts of ellobiids have been infrequent, and those that exist are inadequate in some aspects. The only work specifically referring to *Melampus bidentatus* is that of Morton (1955b), which is based only on fixed specimens and is somewhat limited. Koslowsky (1933) reported on the genital system of the European *M. boholensis*. In work on *M. coffeus* collected in Brazil, Marcus & Marcus (1965) briefly discuss the reproductive tract. Berry, *et al.*, (1967) reported on the genital systems of 3 ellobiids, *Pythia*, *Cassidula*, and *Auricula*, all collected from Malayan mangrove swamps.

As in all pulmonate snails, the reproductive system in *Melampus* is hermaphroditic with a single gonad or ovotestis and largely distinct male and female duct systems. The present studies have shown that unlike other ellobiids, *M. bidentatus* is a true simultaneous hermaphrodite, i.e., with ova and spermatozoa produced in the ovotestis synchronously. The ovotestis, shaped as a flattened hollow cone, overlies the digestive gland posteriorly and fits under the apex of the shell (see Fig. 2). Considerable increases in gonad volume occur just before and during the reproductive period (see Fig. 4). The ovotestis consists of many acini (which produce both ova and sperm), some of which anastomose, but are basically radial in orientation. At times the lumina of the acini were observed to be distended by densely packed sperm (ova were not observed in this location). Acinar walls vary in thickness, depending on the number and size of oocytes produced and retained. The lesser or little hermaphroditic duct extends from the center of the underside of the ovotestis to the albumen gland. This duct is opaque-white in color, highly convoluted and varies considerably in diameter depending on the stage of the reproductive period. It is packed with masses of sperm at times during each reproductive cycle. At times other than the reproductive period it is empty, and its lumen is of 5–10% its capacity during the reproductive phase. The lumen is enlarged distally and receives the centripetal lumina of the acini of the ovotestis. The greater hermaphroditic duct runs from the albumen gland to the mucous gland at which point it is joined by the duct of the bursa copulatrix. In contrast to most other ellobiids the greater hermaphroditic duct is short and is not glandular (see Morton, 1955b). This duct is incompletely divided into male and female ducts by a longitudinal fold. The albumen gland and mucous gland are separate diverticula of the genital tract, although in *M. bidentatus* they are in much closer proximity

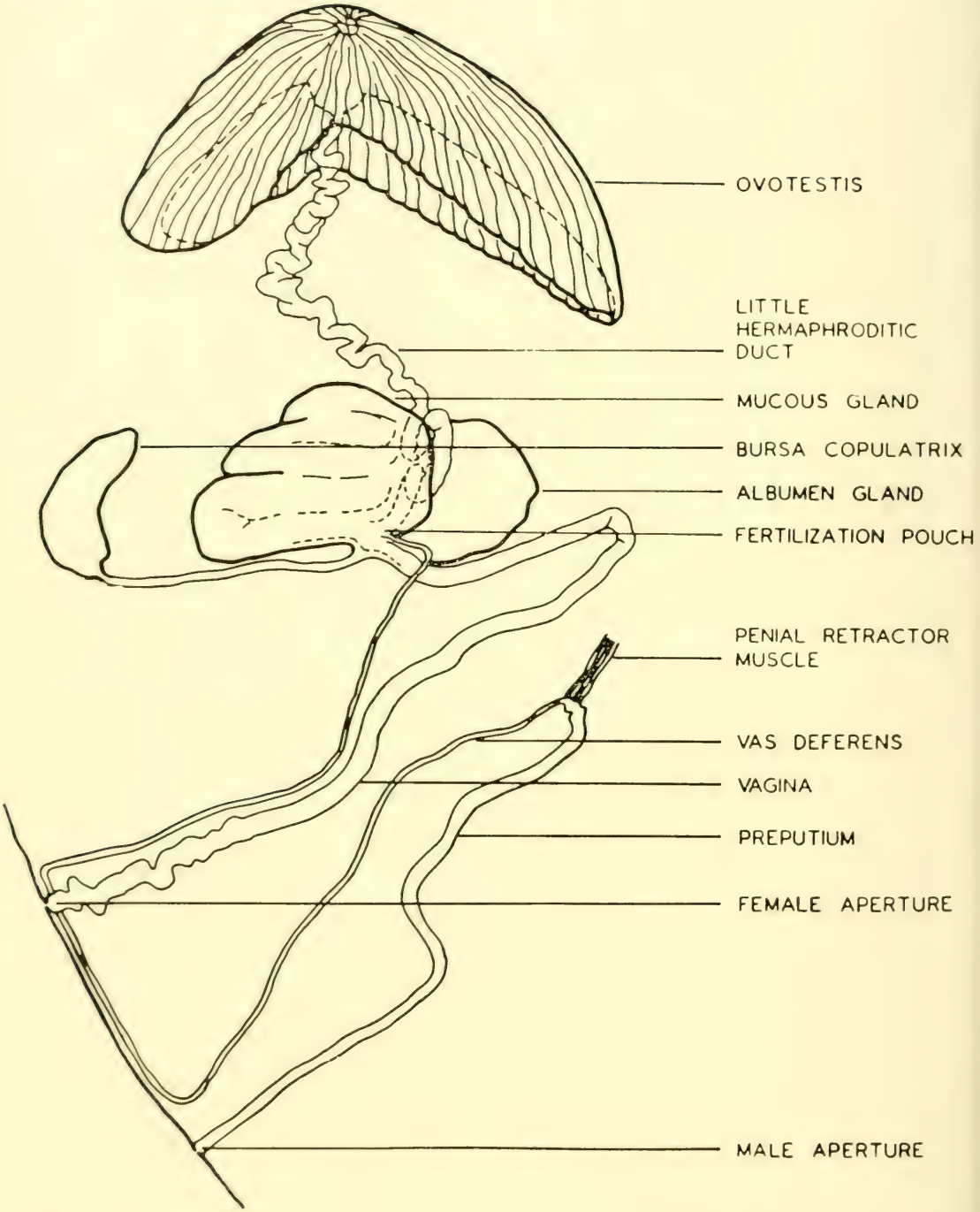

FIG. 2. The reproductive tract of *Melampus bidentatus* as drawn from dissection and from histological observations, proportionately enlarged.

than in most pulmonates. The gametes follow separate pathways after leaving the lesser hermaphroditic duct. Spermatozoa are evidently passed directly into the vas deferens which branches from the anterior portion of the lesser hermaphroditic duct. Foreign sperm are stored in the bursa copulatrix following copulation. Presumably, fertilization occurs in this vicinity. However, foreign sperm have not been positively identified as such in any of the sections studied. In this same region a duct from the albumen gland unites with the greater hermaphroditic duct. Morton (1955b) suggests that the material within the egg capsule is supplied by the albumen gland at this point in the reproductive tract of most ellobiids. This is supported by the work of Berry, *et al.* (1967) on *Pythia*, *Cassidula* and *Auricula*. These authors also suggest that the mucous gland or glands then produces the egg capsule itself and at least some of the embedding mucous. Histological sections of the single mucous gland in *M. bidentatus* reveal a channel, parts of which are ciliated, running through the gland. The lumen of this channel is also visible in the mucous gland of entire genital tracts cleared and lightly stained for low power observation. This would suggest that the ova traverse the mucous gland during the process of egg formation. Berry, *et al.* (1967) have also proposed this in *Pythia*, *Cassidula* and *Auricula* as being the actual pathway. Marcus & Marcus (1965) believed that the pathway of eggs was through the mucous gland in their work on *M. coffeus*. In the present work (and in all these other cases) the evidence is circumstantial, and in no case have the eggs been observed on their way through the mucous gland in any ellobiid. It seems most likely that Morton (1955b) was in error in his deduction that, in *Melampus*, the mucous-secreting region is not traversed by sexual products. No one suggests that the albumen gland is so traversed. From the base of the mucous gland the oviduct transports the eggs to the vagina and to the female genital aperture laterally located on the right side of the foot, roughly above the transverse pedal groove. Prior to egg-laying, the intromittent organ of the copulatory partner is introduced through the vaginal opening and into the vagina. The vas deferens, with a considerably smaller lumen, runs parallel to the vagina as far as the vaginal opening, and then turns anteriorally to the male aperture. From here it loops back into the body cavity and into the distal portion of the preputium at the point of attachment of the penial retractor muscle. The male aperture is located below and behind the right tentacle. A true retractile penis is not present in *M. bidentatus*. At copulation, the relatively undifferentiated intromittent organ consists of the everted muscular wall of the preputium. Oviposition occurs soon after copulation.

In contrast to more random behaviour at non-reproductive times (or throughout most of the rest of the year), the days preceding, during, and just following egg-laying in *Melampus bidentatus* are behaviorally patterned. A pronounced reproductive or sexual aggregation of the snails occurs, starting 2 to 3 days prior to copulation. At this time, aggregations of snails may frequently cover areas totalling up to 1/3 of a square meter, with densities (counted per 10 cm^2 plots) reaching 124. It is worth noting here that non-aggregated snails generally avoid contact with each other. Within these reproductive aggregations snails are generally active and do not exhibit this usual avoidance reaction.

Egg masses have always been found within 1 day of the first observation of copulation in both field and laboratory populations. In approximately 90% of the instances where copulating pairs were observed and separated, copulation was

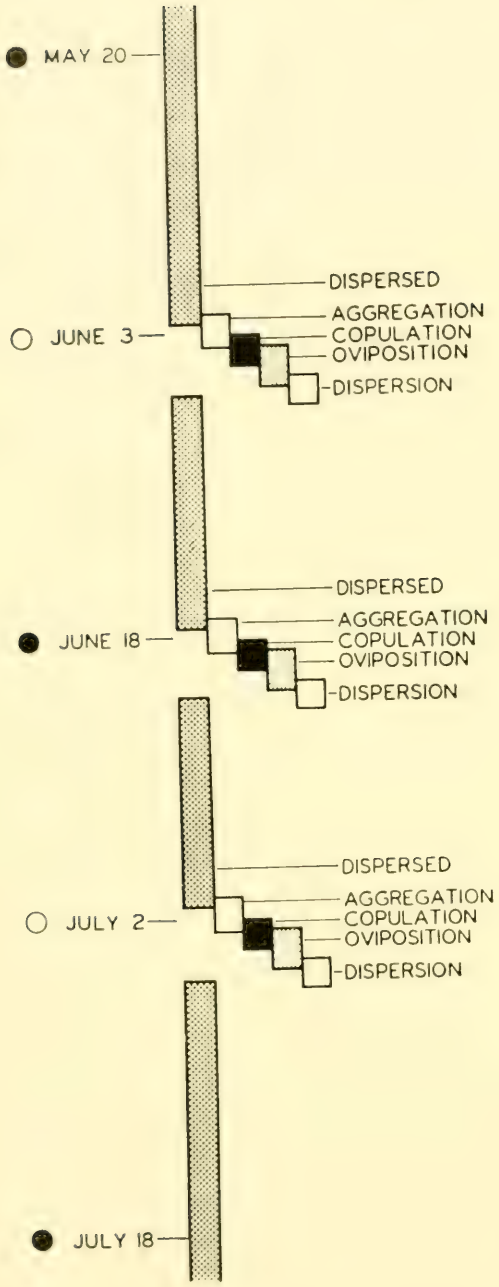

FIG. 3. Sequence and duration of behavioral phases of reproductive cycles as observed during 1966. See text for further discussion.

found to be unilateral rather than reciprocal. Frequency of copulating pairs is highest during the first to second day of egg-laying. It seems probable that copulation occurs randomly and more than once, with each individual acting as both male and female at some time during the reproductive cycle. However, it remains possible that only one effective sperm transfer is involved. Frequency of contact with other individuals increases preceding copulation. Tentacles and oral lobes are involved in an exploration of the head and anterior pedal portions by opposite members of the potential copulatory pair. Subsequently the pair becomes orientated with right frontal body regions in contact with each other (i.e., with the male genital opening of each animal opposite the vaginal opening of the other). The whole process requires minutes rather than hours. However, successful entrance of the intromittent organ does not always follow exploration and orientation of a pre-copulatory pair. The highest rate of egg-laying occurs late the second day or early the third day after the onset of copulation. Egg-laying is usually completed within 4 days. Dispersion of the aggregations begins to occur about the fourth day of egg-laying and is complete by the seventh to eighth day following the beginning of copulation. These observations have been repeated and found to be consistent over the 4 summers of 1965–68. These behavioral aspects of the reproductive cycle are presented in Fig. 3.

Observations on the field population during the years 1965 through 1968 revealed a definite semilunar periodicity in reproduction. The behavioral sequence, as defined in the preceding section, is repeated in phase with the spring tides in late May, June or the first part of July. Not only are oviposition and related behavior patterned to the diurnal and lunar sequence, but also the annual reproductive period covers parallel weeks in May, June, or July from year to year.

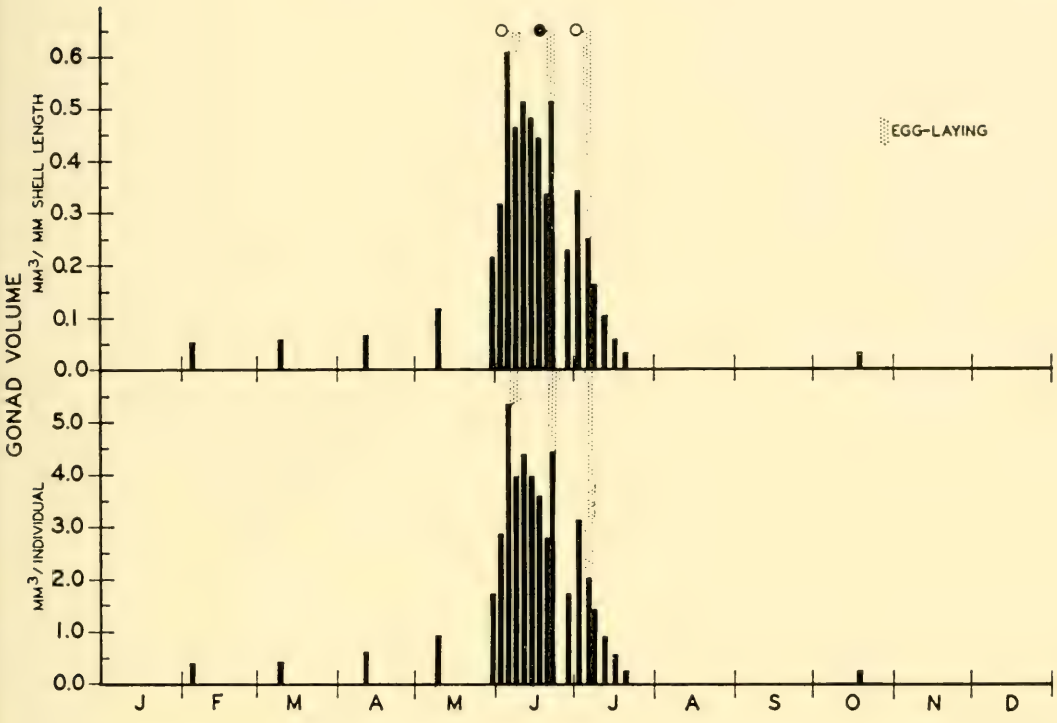

FIG. 4. Changes in mean gonad volume per individual (lower graph) and changes in mean gonad volume related to shell-length (upper graph) at intervals in 1966. Times of egg-laying are represented. Lunar changes preceding egg-laying are shown by ○ for full moon and ● for new moon. General decrease in gonadal volume occurs with progression through the breeding period as shown in the graphs. Also shown is the volume increase just before or early into egg-laying.

The data for 1966 are most complete with oviposition occurring at times related to spring tides around June 3, June 18, and July 2 (see Fig. 3). During the summer of 1967, oviposition was again correlated with the spring tides, this time around June 8, June 22, and July 7. In 1968, May 27, June 10, and June 25 were times at which oviposition was correlated with occurrence of spring tides. Oviposition at Sippewisset Marsh in 1965 was noted twice, at times corresponding with spring tides of June 14 and July 13. Examination of histologically-fixed collections taken for growth studies indicated that there was also oviposition in conjunction with the spring tides of June 29, 1965.

Gonad volume for individuals throughout the year was assessed. Simple gross dissections of fixed specimens demonstrate a rather rapid increase in gonad size preceding egg-laying, as well as a rapid size decrease that accompanies and follows egg-laying (Fig. 4). Individuals were selected at size ranges within each mature generation and fixed in neutral formalin at 2- to 5-day intervals throughout the reproductive period in 1966. Shell lengths were recorded and used as an indication of age and as the basis for comparison of results. The shell was then carefully removed by cracking through gradual application of pressure with a screw clamp and the ovotestis separated from the rest of the snail by first peeling away the mantle and then loosening the ovo-

testis around the edges and lifting it away. Each ovotestis was serially sectioned working from the posterior to the anterior at 9 micra and stained by Masson's hematoxylin. Each tenth section was marked, starting with the fifth section in which gonad material appeared. Each marked section was projected at a known magnification using an ocular prism. The projected image was traced in outline and the area was estimated in terms of a system of grid squares calibrated to the magnification. A set of about 15 to 17 tracings of area were then converted to give the estimated gonad volume. These volumes are plotted with reference to annual life-cycle in Fig. 3. In general there is an 11-fold increase in gonad volume from wintering to breeding snails. An approximate tripling of gonad volume occurs within the week just prior to the first egg-laying. A nearly 10-fold decrease in gonad volume occurs over the six weeks which follow the first oviposition. Apley, *et al.* (1967) noted that biomass values for gonads show systematic decreases during this period. Values were obtained immediately before breeding started (A), after the first cycle of egg-laying (B), and after the third cycle had concluded the annual reproductive period (C). Mean wet weights of individual gonads change from 6·32 mg (A) to 6·95 mg (B) and to 1·09 mg. (C). Dry weights are less variable, as are the organic carbon values, mean carbon being 698 μg C (A), 845 μg C (B) and 151 μg C (C). Depletion of organic nitrogen is pronounced and uniform with mean values falling from 110 μg (A) and 114 μg (B) to 10 μg (C) In 1966, observed groups totalling 244 snails laid 219×10^4 eggs, then 345×10^4 eggs, and finally 254×10^4 eggs. Therefore, the overall fecundity totalled 818×10^4 eggs, corresponding to 33,150 eggs per standard snail per year. (The standard snail of 8·5 mm shell length was calculated from all data used in work on ovotestis volume and contents. This was done to eliminate any small variations involved due to differences in the mean size for each sample group.) Mean biomass values for individual eggs are dry weight=354 nano-g and organic C=109 nano-g. This average total egg output per individual corresponds to 7·3 mg of dry organic material annually, while mean depletion of "standing biomass" in the gonads corresponds to 99·8 μg N or 920 μg of dry organic material. These values can be related to the mean growth increments for *M. bidentatus* presented earlier. It would appear that 87% of the non-respired assimilation (N–RA) was directed to reproduction during the reproductive period. This corresponds to 46% of the total N–RA, or to 32% N–RA if spring pre-breeding growth rates could be sustained throughout the year (Apley *et al.*, 1967). Total oocyte numbers (all developing oocytes and ova visible under 100× magnification) were determined from the same serial sections used for ovotestis volume. Oocytes were individually counted in 3 marked sections for each specimen, one centrally located and one evenly spaced on each side. Oocyte counts were made over the entire section at 100× magnification. Results are presented in Fig. 5 in terms of total oocytes per mm^3 of gonad per standard snail, and are plotted for time and stage in the reproductive cycle (the actual data on oocyte counts were presented in Appendix A in Apley, 1967). By measuring each individual oocyte with an ocular micrometer, in a number of sections of specimens at different reproductive stages, a natural discontinuity in size of oocytes was evident, usually at an approximate volume between 1×10^{-3} and 1×10^{-4} mm^3. As total oocyte counts were made, each oocyte was included in 1 of the 2 size categories so defined (although no attempt was made to classify these according to the various stages of oogensis), and total numbers are shown

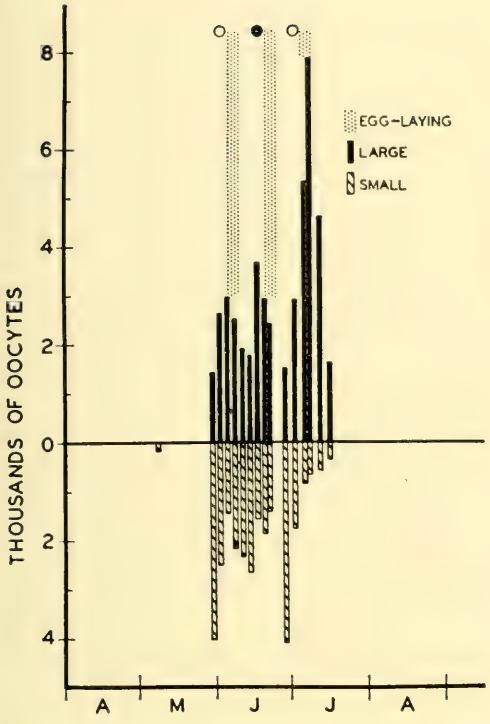

FIG. 5. Oocytes (all potential female gametes visible with 100X magnification) per mm^3 of gonad per standard snail (see text) in field collected specimens for times during the breeding period of 1966. Numbers of small oocytes are represented below the midline and numbers of large oocytes are shown above the line. Changes in the ratio of large to small oocytes occur in the progression of each breeding cycle. See text and Fig. 4 for further information in relation to changes illustrated.

in Fig. 5. The relation of size distribution in terms of time and reproductive cycle is obvious and these results can be correlated with the total fecundity.

Changes in the amount and distribution of spermatozoa in gonads are much more difficult to quantitify than are similar assessments of oocytes. Of several approaches tried, quantitative changes of spermatozoa (assessed relative to overall gonad volume) primarily related to thickness of acinar walls yielded reproducible results. The lumina or spaces within the acini of the gonad of *Melampus bidentatus* are the regions where sperm accumulate when they reach maturity. Categories were devised on the basis of changes in the proportional width of the lumina as compared to the double thickness of the acinar walls. The same slides of gonads used for other studies of the natural reproductive cycle were used here. At June 4, June 19 and July 3 (times just preceding copulation) the acinar walls were distended by dense masses of sperm in the lumina (specific data are presented in Apley, 1967; see Appendix A and Figs. 8–13, 16). There is a considerable decrease in the relative amounts of mature sperm free in the gonad during the subsequent part of each of the 3 reproductive cycles following copulation. There is an increase in thickness of acinar walls, reflecting an increase in the production and retention of oocytes just preceding egg-laying. The cyclic activities of copulation and oviposition at 2 week (semilunar) intervals through the normal breeding period of about 7 weeks are thus again reflected in the changing relationship of lumina width to acinar wall thickness.

DISCUSSION

The life-cycle of *Melampus bidentatus* is of 3 to 4 years with annual reproductive periods from late May or early June into the first part of July, and with a semilunar reproductive periodicity involving patterned behavioral responses. The correlation of egg-laying, hatching, and settlement with the incidence of spring tides is clearly adaptively significant. Sequence of patterned behavior and of gonadal changes in experimental specimens maintained in the laboratory and within field collected specimens was closely comparable. An account of experimental work demonstrating controls of reproductive period and cycles depending on day length and

semilunar changes is given elsewhere (Apley, 1971).

Melampus bidentatus is a simultaneous hermaphrodite and not a protandrous hermaphrodite as are other ellobiids which have been investigated and from which the assumption (Morton, 1955b) of protandry in all ellobiids was evidently derived.

Contrary to the early assumption of a biennial cycle being general in pulmonates (Pelseneer, 1906, Baker, 1911) or to the annual cycles reported by Russell-Hunter (1957, 1961), a 3 to 4 year life-cycle is evident at Sippewisset (Fig. 1; and Russell-Hunter & Apley, 1966; Apley, *et al.*, 1967). Such a life-cycle is much more common in marine and nonmarine littoral prosobranchs such as *Littorina littorea* (Moore, 1940) and *Viviparus contectoides* (Van Cleave, 1934). The usual minimum reproductive size lies between 5 and 6 mm shell length. Two reproductively mature generations are therefore present in the population through the June and early July reproductive period. The participation of 2 different generations of snails during the annual reproductive period is advantageous to the population. This would buffer the population against lasting effects resulting from 1 reproductively unsuccessful year.

The habitat occupied by *Melampus bidentatus* is probably close to that in which the family has evolved (as the Subclass Pulmonata itself has). This habitat in the high littoral or intertidal zone offers a number of advantages and disadvantages. Essentially, *M. bidentatus* is an amphibious organism, capable of living either terrestrially or submerged (for at least short periods of time), as are other pulmonates of similar habitats (*Lymnaea truncatula*, and *Succinea pfeifferi*, both of which drown if kept continuously submerged, see Russell-Hunter, 1953 and 1964, respectively). Regarding respiration, *M. bidentatus* is a true land pulmonate with pneumostome and air-filled mantle cavity. From the viewpoint of reproductive physiology, *M. bidentatus* is a primitive aquatic gastropod, producing large numbers of small unprotected eggs. Such animals living in the high littoral zone can either lay eggs only during the short periods when water is present, or migrate into deeper water at their reproductive periods. Of course, a number of littoral animals have internal fertilization and subsequently lay small numbers of large eggs with more-or-less direct development to the adult. In the majority of littoral animals a number of larval stages intervene between hatching and the assumption of the adult forms and habitat. *Melampus* falls in the latter category, producing large numbers of small eggs which hatch directly as veliger larvae. However, there is no migration into deeper water.

The problem of ensuring survival of gelatinous egg masses without resistant outer cases and containing many small eggs (mean of 850 eggs/mass) is overcome very effectively and in some respects quite simply. Throughout the course of these investigations (1965-68) a semi-lunar periodicity of egg production has been observed. Eggs are laid only through 4 days at the time of spring tides. This helps prevent immediate desiccation of freshly laid egg masses, but more importantly, it covers the egg masses with detritus and organic debris which collect and maintain moisture through the ensuing neap tides. In the field the detritus helps maintain better conditions for the survival and development of eggs through the period of nonsubmersion until the next spring tide occurs. At this time, approximately 13 days later, veligers have developed, ready to break from the egg masses, and take up a temporary planktonic existence. Eclosion is triggered by submersion in sea water. This was seen in all observations of egg masses kept in

moist conditions as well as in those observations of desiccated egg masses. (These were egg masses which appeared to be completely dried out, but from which veligers emerged when covered by sea water. These eggs were all relatively far along in development before desiccation occurred.)

Thus in the field, the eggs hatch only upon the inundation by the spring tides, approximately 13 days after being deposited. The free-swimming veligers which emerge are, of course, aquatic animals moving by ciliary means. Since both eggs and larvae are highly water-dependent, reproduction is made possible in these semi-terrestrial conditions by this significant semi-lunar correlation of egg-laying and hatching with the occurrence of spring tides. The time of settlement of larvae back into terrestrial marsh conditions is not yet clear, but must occur after 2 but before 6 weeks of planktonic life. Settled spat have not yet been observed earlier than 6 weeks after hatching. Partially successful laboratory rearing of larvae of *M. bidentatus* indicate that the veligers have at least 2 weeks of normal planktonic life.

Settlement appears to be correlated with the time of spring tides, the only time at which spat snails would be capable of reaching habitat conditions similar to those of their parental stock. This semilunar synchrony of egg-laying, hatching and settlement of spat is of primary importance for the survival of these high littoral populations. It is not difficult to conceive of the kinds of selection pressures which would create and fix these rhythms of behavior and reproduction. The occurrence of more than one egg-laying cycle is significant, especially in terms of species survival and distribution. The density of newly settled spat at times following appropriate spring tides varies, and this reflects the extent or success of settlement corresponding to each reproductive cycle. The slight variations observed in intensity of egg-laying with each reproductive cycle could not alone account for the much greater variation in density at spatfall. Multiple periods of intensive oviposition increase the likelihood of adequate spatfall.

Egg masses of *Melampus* have been reported at different times along the Atlantic coast of North America. Holle & Dineen (1957) reported egg masses on June 20 in 3 marsh areas north of Cape Cod. This compares with the May, June or early July periodicity reported for snails of Sippewisset Marsh by Russell-Hunter & Apley (1966), Apley, *et al.* (1967), and within the present report. Morrison (1958) reports egg masses by August 20 in the vicinity of Cape Hatteras, North Carolina. At the time of the observations of Holle & Dineen (1957) and Morrison (1958), there was no appreciation of a semilunar periodicity of reproduction as was briefly discussed in Russell-Hunter & Apley (1966), Apley, *et al.* (1967), and amplified in Apley (1971) and herein. Such reproductive dates cited before 1966 may be isolated observations of only a single reproductive cycle in each case, other cycles of that year's reproductive period not having been observed or suspected. There was no regularity of field observations in these earlier studies, and their extent is unknown. Holle & Dineen (1957) did report egg-laying in specimens which they took into the laboratory during late spring and early summer of 1955. Examination of their reported dates show no simple correlation of egg-laying with lunar cycles.

Scattered individual observations by Morrison (1958) suggested a progression of egg-laying dates from north to south through the summer, which he regarded as in "apparent anticipation of winter seasons." Observations of a population of *Melampus bidentatus* at Fort Macon, North Carolina (34° 43′ N 76° 41′ W), during the summer of 1968 revealed 3

periods of oviposition with a semi-lunar periodicity during the last part of August and in September. Through the year a progressively later onset of reproduction as one moves northward is most usual in marine littoral animals (see Hutchins, 1947, and Jenner, 1956). Experimental work reported elsewhere (Apley, 1971) suggests that there may be several alternative explanations of these data. The possibility exists of a greater number of egg-laying cycles extended over a longer period of time in some more southern populations. The occurrence of physiological races in mollusks has been reported and/or hypothesized in a number of instances. These include Korringa (1957), Loosanoff (1960), Russell-Hunter (1961), and Russell-Hunter, *et al.* (1967). Existence of physiological races of *M. bidentatus* is quite possible (and perhaps even probable).

As stated, eggs produced by *Melampus bidentatus* are small and numerous. Counts of egg masses from groups of snails maintained in the laboratory indicate a mean of 39 egg masses per individual per breeding period, corresponding to $3{\cdot}3 \times 10^4$ eggs (derived from data in Apley, 1967). Estimates of egg numbers in *M. bidentatus* compare with approximate egg numbers reported by Fretter & Graham (1964) of 4×10^3 in *Littorina littorea*, 13×10^3 in *Nassarius reticulatus*, both examples of marine prosobranchs. This figure for *M. bidentatus* can be compared with egg numbers of 100–130 in *Lymnaea stagnalis*;[3] 20–42 in *Planorbarius corneus*;[3] 60–90 in *Helix pomatia*[4] (all from Fretter & Graham, 1964); and 150 in *Achatina fulica*[4] (Mead, 1961), all of which are non-marine pulmonates. Assuming no great differences within natural populations of *M. bidentatus* over periods of several years, one would conclude that only a small percentage of the eggs produced resulted in settled spat and an even smaller percent in adults. Since it is likely that each adult snail need only replace itself during its lifetime, the ratio of selection would therefore be about 50,000:1 in *M. bidentatus*. This would compare with selection ratios reported by Russell-Hunter (1957) of 1,400:1 in *Lymnaea peregra* and 46:1 in *Ancylus fluviatilis*, both of which are freshwater pulmonate snails.

No data concerning overall fecundity in other ellobiid pulmonates are available, and there are few such data for other snails. Thorson (1950) reports egg numbers ranging from a few thousand to several hundred thousand per female per breeding season in marine bottom invertebrates with planktonic larvae. Marcus & Marcus (1965) report egg masses in *M. coffeus* similar in form and number of eggs to *M. bidentatus*, but no overall figures. Egg masses enclosed in protective cases with smaller numbers of eggs than in *Melampus* have been reported by Morton (1955a, 1955c) for *Leucophytia*,[5] *Ovatella*,[5] and *Carychium*.[4] The most complete adaptation to terrestrial life is shown by the large eggs with calcareous shells found in *Strophocheilus* (Russell-Hunter, 1955) or *Achatina* (Mead, 1961), which are physiologically cleidoic and resemble those of higher vertebrates. Thus, *Melampus*, though a genus of air breathers with appropriate behavioral responses for life in the semiterrestrial conditions of the highest littoral, has an egg size (and total number) closely corresponding to true marine snails. Many of the peculiarities herein reported of ecology and physiology in *M. bidentatus* are related to this " amphibian " pattern of aquatic reproduction.

[3] Aquatic.
[4] Terrestrial.
[5] " Amphibious ".

ACKNOWLEDGEMENTS

The author would like to express his gratitude to Dr. W. D. Russell-Hunter for his advice and concern throughout this work. Appreciation is also extended to Dr. David C. Grant who kindly made regular collections during many of the winter months, to Jay Shiro Tashiro for his assistance in numerous ways, including many calculations and measurements, and to Eric W. Lindgren for his observations and collection of samples of a North Carolina population.

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RÉSUMÉ

ÉTUDES DANS LA NATURE SUR LE MODE DE VIE, LE CYCLE SEXUEL ET LA PÉRIODE DE REPRODUCTION CHEZ *MELAMPUS BIDENTATUS* (PULMONATA: ELLOBIIDAE)

M. L. Apley

Melampus bidentatus (Ellobiidae, Pulmonata) se rencontre dans la zone supralittorale de lagunes saumâtres à demi fermées le long de la côte atlantique depuis le Nouveau Brunswick, Canada, jusqu'au Texas, U.S.A. Des observations et des études qui ont duré de 1964 à 1968 sur une population habitant la lagune de Little Sippewisset, Falmouth, Massachusetts, U.S.A., a montré les aspects écologiques et physiologiques du cycle vital, du cycle sexuel et de la période de reproduction. C'est l'évidence que, dans cette population, le cycle vital dure 3 à 4 ans, avec généralement une longueur maximale de la coquille d'environ 10,5 mm. La maturité sexuelle (quand la gamétogenèse a lieu pour la première fois) est atteinte quand la taille de la coquille est d'environ 5 mm chez des individus qui appartiennent à deux groupes d'âge. Le taux de croissance hivernal est seulement le 1/5 du taux de printemps-été qui est lui-même le double de celui des mollusques pendant la saison de reproduction. La période annuelle de reproduction dure quelque fois 6 semaines, en fin mai, juin, début juillet. Chaque période annuelle de reproduction comporte 3 cycles de ponte à intervalle de 2 semaines (semilunaires) en corrélation avec les marées de vives eaux. Il y a, dans cette population, toute une gamme de comportements bien prévisibles pendant ces cycles semilunaires de reproduction comprenant les rassemblements sexuels, la copulation, la ponte et la dispersion. Les pontes sont petites, gélatineuses, et dépourvues d'une enveloppe externe dure; chacune contient une moyenne de 850 oeufs. Les véligères nageuses éclosent après 13 jours si les pontes sont couvertes d'eau à ce moment là. Ensuite les véligères sont planctoniques pendant 2 à 6 semaines. On n'a pas trouvé de larves benthiques plus tôt que 6 semaines après l'éclosion. En utilisant des mesures de carbone organique total ou de poids secs des tissus on a trouvé que la croissance couvre presque 6 ordres de grandeur pendant la durée de vie de 3–4 ans.

M. bidentatus est un véritable hermaphrodite simultané contrairement aux observations ou présomptions de protandrie qui ont été faites dans la famille des Ellobiidae. Les valeurs du volume de la gonade augmente de 11 fois quand on passe du mollusque hivernant au mollusque en reproduction, avec un triplement du volume pendant la semaine précédent le premier cycle de ponte. Les diminutions systématiques du volume de la gonade, du nombre d'oocytes et de la quantité relative de sperme des gonades se sont trouvées être en coïncidence avec les périodes de copulation et de ponte tout au long des

cycles sexuels. Une moyenne de 39 pontes (180 oeufs par pontes) par individu par saison de reproduction correspond à 33.150 oeufs par mollusque standard, par an. Ceci montre un taux de sélection d'environ 50,000–1 assurant le remplacement de tout individu une fois seulement au cours de sa vie.

Les adaptations de *M. bidentatus* pour survivre au fait d'être exposé alternativement à des conditions tantôt marines et tantôt presque terrestres, sont le résultat d'une combinaison unique de facteurs physiologiques et éthologiques. Les périodes semilunaires de ponte, d'éclosion et de passage à la vie benthique, en corrélation avec les marées de vives eaux sont à ce propos d'une toute particulière importance, comme on le voit dans la population de Sippewisset.

АБСТРАКТ

ПОЛЕВЫЕ ИССЛЕДОВАНИЯ ЦИКЛА РАЗВИТИЯ ГОНАД И ПЕРИОДИЧНОСТИ РАЗМНОЖЕНИЯ У *MELAMPUS BIDENTATUS* (PULMONATA: ELLOBIIDAE)

М. Л. ЭПЛИ

Melampus bidentatus (Ellobiidae, Pulmonata) был найден в верхней части литоральной зоны в полузамкнутых районах соленых болот, вдоль берегов Атлантики от Нью-Брунсвика, Канада до Техаса, США. В наблюдениях и исследованиях, проводившихся в 1964-1968 гг. на популяциях этих моллюсков, обитающих в болотах Литтл Сиппивиссет, Фальмут, Массачусетс, США, обращалось внимание на экологический и физический аспекты жизненного цикла, на цикличность в развитии гонад и периодичность размножения моллюсков. Для этой популяции установлено 3-4-х годичный цикл при наиболее обычной максимальной длине раковины около 10,5 мм. Половозрелость (когда впервые наблюдается гаметогенез) наступает при длине раковины около 5 мм у индивидуумов из двух возрастных групп, принимающих участие в годовом периоде размножения. Зимняя скорость роста составляет лишь 1/5 от весенне-летней скорости роста, которая в свою очередь почти в 2 раза больше, чем темп роста моллюсков во время периода размножения. Годовой период размножения длится 6 недель, захватывая конец мая, июнь и начало июля ежегодно. Каждый годовой период состоит из 3 циклов откладки яиц с 2-х недельным интервалом (половина лунного месяца) и коррелируется с сизигийными приливами. Устойчивые, предсказуемые особенности поведения моллюсков в течение этих полумесячных циклов размножения (включая их агрегации, копуляцию, откладку яиц и дисперсию) наблюдаются у всех популяций.

Яйцевые пачки небольшие, слизистые, без плотной внешней оболочки; каждая из них содержит в среднем 850 яиц. Свободно плавающие личинки-велигер выходят через 13 дней, если яйца в это время покрыты водой. Затем в течение 2-3 недель велигеры ведут планктонный образ жизни. Осевшие личинки (спат) были отмечены не ранее, чем через 6 недель после выклева. При помощи определения количества органического углерода или сухого веса тканей было найдено, что в течение первых 3-4 лет жизни моллюсков наблюдается их прирост почти в 6 раз.

M. bidentatus- настоящий одновременный гермафродит, в противоположность представлениям о протандрии всего семейства Ellobiidae. Измерение объема гонад показало их увеличение в 11 раз у размножающихся моллюсков, по сравнению с зимующими; объем гонад увеличивается в 3 раза в течение недели перед первым циклом откладки яиц. Систематическое уменьшение объема гонад, количества ооцитов и относительного содержания спермы в гонадах совпадает с периодичностью копуляции и откладки яиц в течение цикла размножения. В среднем 39 пачек яиц (из 850) на одну особь за сезон размножения соответствует 33 150 яйцам на стандартного моллюска в год. Это указывает на скорость отбора примерно в отношении 50 000:1, допуская, что каждая особь должна сменить себя 1 раз за свою жизнь.

Адаптация *M. bidentatus* к выживанию при смене морских условий на почти сухопутные включает единую комбинацию физиологических факторов и условий среды. Особое значение имеет полумесячная корреляция откладки яиц, выклева и оседания личинок с сизигийными приливами, как это было установлено на популяциях моллюсков из Сиппевиссета.

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ASPECTS OF THE GROWTH OF THE SNAIL *LYMNAEA PALUSTRIS* (MÜLLER)

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ABSTRACT

Analysis of weekly population samples of overwintering *Lymnaea palustris* (Müller) revealed that the spring and early summer growth of this snail was rapid, following an almost linear pattern, but that little growth occurred before April 15 or after early July. There was no concentrated spring egg-laying activity in Arkell pond, although some spring-hatched snails were present in Pond 2. Smaller *L. palustris* overwintered best, and in Arkell pond almost all the spring and summer population is derived from snails ovipositing the previous year, in late summer or autumn. Unlike some pulmonates, no spring population turnover was observed. Up to maturity, the reproductive system is slender and shows no pronounced change in general form, but after maturity it undergoes great expansion. The growth rate (k) of the reproductive system is not constant, but gradually declines with age. After a shell length of 11 or 12 mm, growth of individual reproductive organs (albumen gland, oöthecal gland, uterus and muciparous gland, and prostate) in relation to shell length, is linear. Beyond 8 mm the same is true for gizzard growth. All these structures develop very slowly during the first few millimeters of shell growth. Great fluctuation in size occurs with the albumen gland, and this is probably related to reproductive activity. The growth rate of the oöthecal gland is fastest and that of the prostate slowest.

INTRODUCTION

Detailed life histories of many gastropods are already well known, although it is only in recent years that some have been investigated extensively. Among the basommatophoran pulmonates it has been found, at least in temperate climates, that a number of them have a life span of around 1 year, with oviposition and hatching of young particularly evident in the spring and early summer months. Growth is most rapid during a period lasting from spring until late fall. With the onset of winter temperatures, the growth velocity of all snails decreases, and weeks or months may pass when sampling methods reveal little or no change (excepting possibly for deaths) in population structure (Duncan, 1959; McCraw, 1961). After a rise in temperature following winter conditions, growth resumes, often resulting in a quickly changing population picture and sometimes even an almost complete population turnover (Hunter, 1953; DeWitt, 1955; Geldiay, 1956; McCraw, 1961).

It is the purpose of the present study to investigate closely the spring and early summer growth of the pulmonate, *Lymnaea palustris* (Müller). As little work has been carried out on the growth of internal organs that accompanies an increase in shell size, it seemed desirable to follow also the development

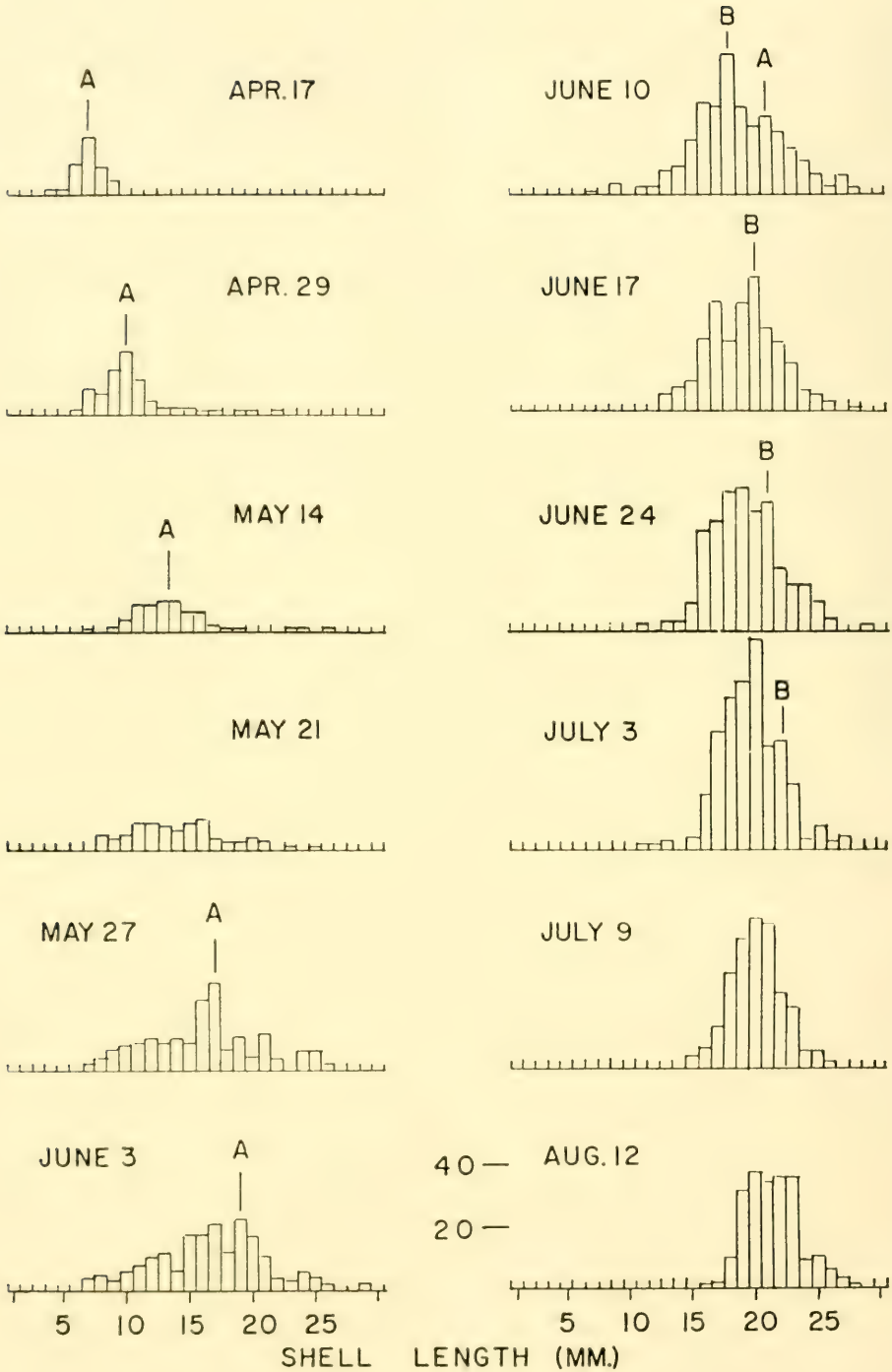

FIG. 1. Collections of *L. palustris* from Arkell pond plotted according to the number falling within mm size classes.

of some of these internal structures, especially the reproductive system, during this spring and early summer period.

MATERIALS AND METHODS

Collections of *Lymnaea palustris* were made at approximately weekly intervals from 2 small semi-permanent ponds near Guelph, Ontario, Canada. Shell dimensions of smaller snails were measured with an ocular micrometer calibrated to a stereoscopic microscope; for larger snails calipers were used.

Snails used for growth analysis of internal organs were relaxed in nembutal and menthol (McCraw, 1958) and fixed in 10% formaldehyde. The various organs were weighed on a B. T. L. " Empire " aperiodic projection balance. The combined weight of the following structures, taken while still unseparated from one another, was measured: the albumen gland, prostate, uterus and muciparous gland, oöthecal gland and vagina. This measurement will be referred to as the total weight of the reproductive system. However, it excludes the male copulatory organ, ovotestis and the seminal receptacle. The weight of the latter structure in mature snails depended largely upon the amount of sperm present in it. The ovotestis is thoroughly embedded in the digestive gland making a clean dissection exceedingly difficult. The following organs were weighed individually: the gizzard, albumen gland, oöthecal gland and prostate gland. Structures to be weighed were dissected from snails stored in formaldehyde and whose shells were decalcified (in 10% formaldehyde containing 10% hydrochloric acid) just before dissection. To remove excess surface moisture immediately before weighing, each organ was gently rolled over on filter paper several times until no more moisture was absorbed. Growth data were analyzed by computer to determine the predicted weight of the reproductive system, as well as the weights of various organs of the reproductive system from shell length (Snedecor & Cochran, 1967).

RESULTS AND DISCUSSION

Fig. 1 shows the results of approximately weekly samples of *Lymnaea palustris* taken from Arkell pond between April 17 and July 9, 1959. On May 6 snails were very difficult to find, and the number collected on that date was too small to warrant plotting. Before April 17 no snails were observed, probably because of low water temperatures. As only slight movement of *L. palustris* is observed in water temperatures between 7° and 9·5°C, it is likely that these snails were inactive until about April 13 when the water temperature first reached 10°C. The sample of April 17 was unimodal, and the shift in this mode was relatively easy to follow in frequency plots until June 3 (' A ' in Fig. 1). On June 10 a new mode was detected (' B ') and this one could be followed until July 3. From July 9 on, throughout the remaining summer weeks little change in the population picture was evident. The spring and early summer growth of this snail is more clearly revealed by plotting modes (Fig. 2). Shifts in the first mode (' A ') resulted in a striking linearity for the spring growth of *L. palustris*. In a second pond, Pond 2, where both *Aplexa hypnorum* (L.) and *L. palustris* were present, structural changes in the population of both these snails were followed for comparison. Unfortunately, with *L. palustris* distinct modes which could be followed at weekly intervals were not present. However, clearly defined modes for *A. hypnorum* were found

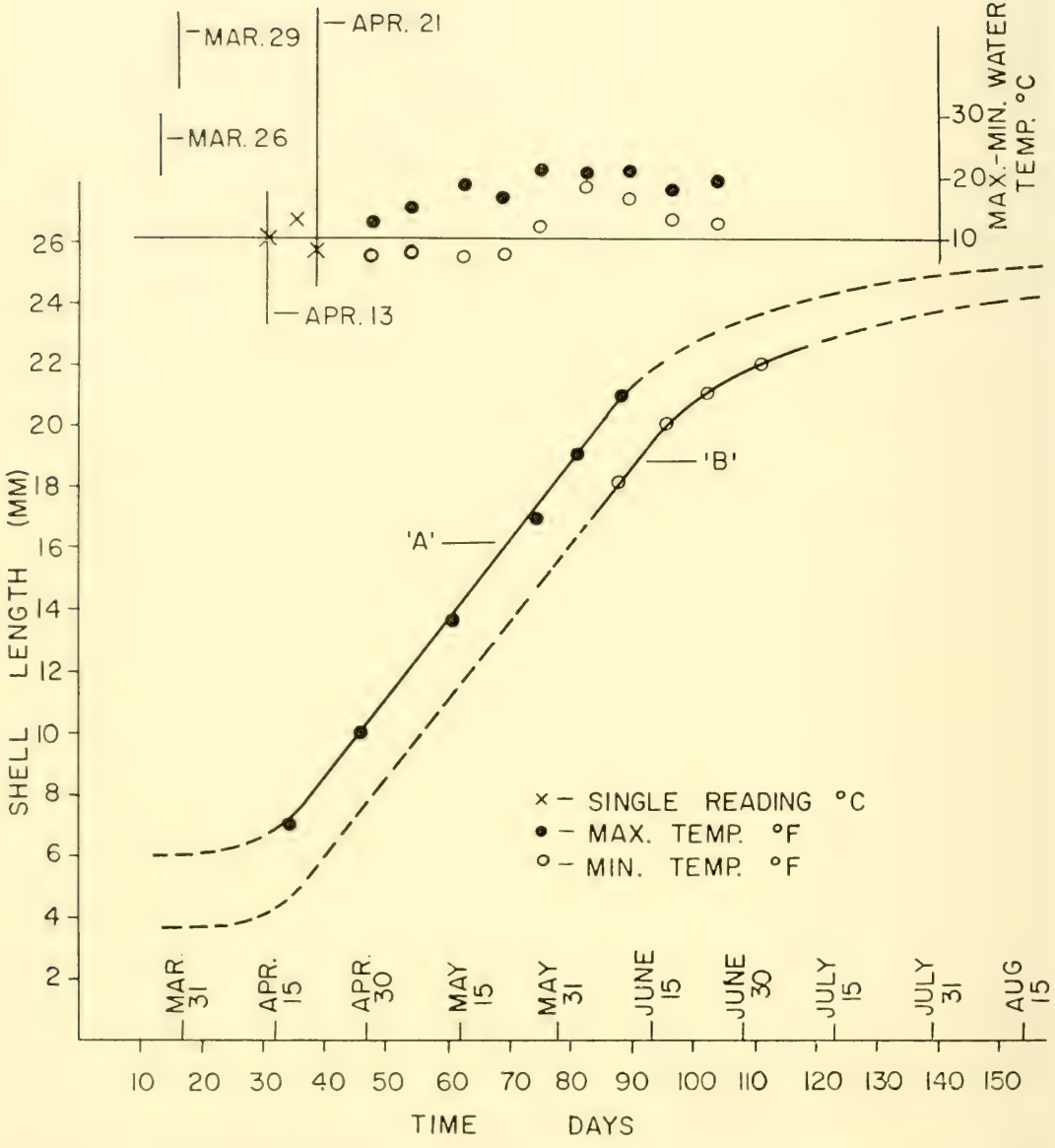

FIG. 2. Plots of modes, labelled A and B in Fig. 1, to illustrate the spring and early summer growth of *L. palustris* in Arkell pond. Broken lines indicate estimated growth.

(Fig. 3) and these also displayed a remarkably linear pattern for the spring growth of this snail (Fig. 4). These observations are consistent with the growth pattern of laboratory-reared *Physa gyrina* Say, which increases in size quickly during the first few weeks after hatching (12·0 mm at 8th week; 13·6 at 52nd week) (DeWitt, 1954). Similar results were obtained by Chernin & Michelson (1957a; 1957b) for the growth of *Australorbis* (= *Biomphalaria*) *glabratus* raised

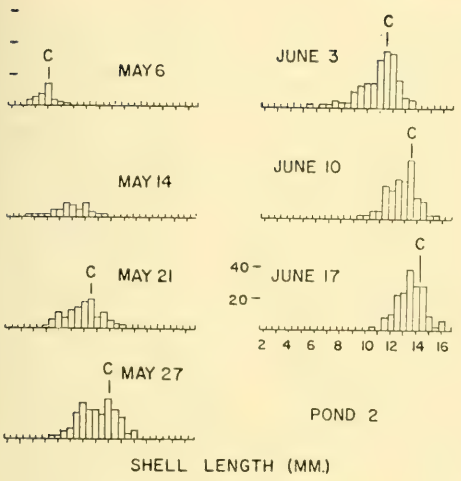

FIG. 3. Collections of *A. hypnorum* from Pond 2 plotted according to the number falling within mm size classes.

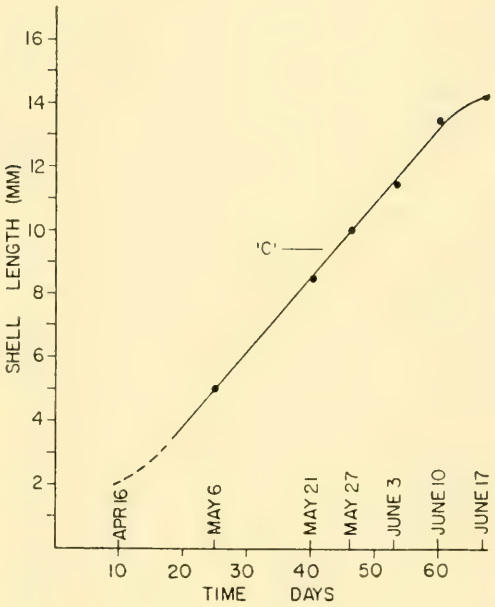

FIG. 4. Plots of modes, labelled C in Fig. 3, to illustrate the spring growth of *A. hypnorum*. Broken line indicates estimated growth.

in aquaria. In addition, these authors found that the growth velocity of *A. glabratus* was markedly influenced by crowding which, when severe, effected considerable retardation.

There was probably very little growth of snails in both of these ponds prior to the middle of April. According to Vaughn (1953) *Lymnaea stagnalis appressa* Say will develop and hatch at a temperature as low as 9·9°C and growth of young occurs between 11°C and 28·2°C. Oviposition (and presumably growth) in *Physa gyrina* Say does not occur below water temperatures of 10 or 12°C (DeWitt, 1955), while Duncan (1959) found that *Physa fontinalis* (L.) resumed growth at a slightly lower water temperature (7°C). An estimate of the amount of growth of *L. palustris* before April 17 is shown in Fig. 2. Plots of the second mode 'B' (Fig. 1) which could be followed in 4 consecutive samples showed a decline in growth velocity (Fig. 2). After July 9, the population structure stabilized, and, except for an accumulation of 22 and 23 mm size classes, the sample of August 12 was little changed from that of July 9 (Fig. 1). These findings suggest, therefore, that after about June 15 an inhibiting phase of growth set in with a gradual levelling of the growth curve occurring throughout the summer (Fig. 2). No snails were observed in Pond 2 before May 6. On June 24, 1959 this pond was beginning to dry with the snail fauna clustered into an isolated pocket and a slight decline in growth velocity of *Aplexa hypnorum* was evident beginning June 17 (Fig. 4).

Ritchie *et al.* (1963) showed that size at the onset of laying of *Australorbis glabratus* varied with the growth rate, i.e., a rapidly growing snail would reach a larger size before laying than one that grew slowly. On the other hand, stunting is known to be accompanied by a decrease in the rate of gonadal maturation. Reduced growth of *Oncomelania* spp. results in a lack of development of sex organs as

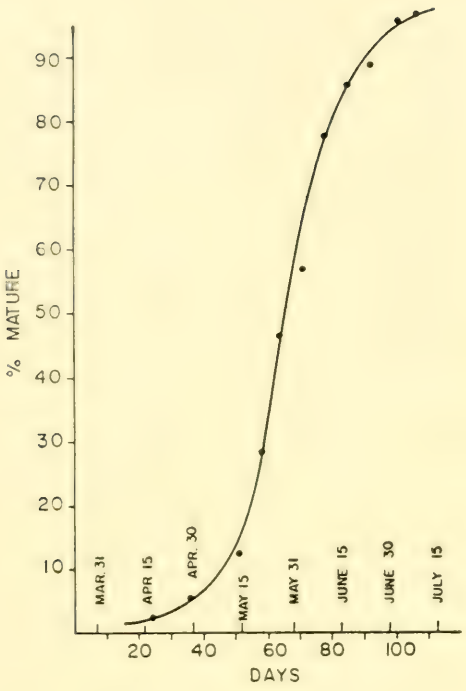

FIG. 5. The increase in the percent mature *L.palustris* in Arkell pond during spring and early summer.

well as an increase in mortality (van der Schalie & Davis, 1965). However, Ritchie *et al.* (1963) concluded that when a near-maximum growth rate occurs, both size and age correlate well with the onset of oviposition; otherwise size is a better criterion of maturity. There was no field evidence that *Lymnaea palustris* was not growing normally and the smallest field-collected snail to oviposit in the laboratory was 14·85 mm in shell length; of a series of snails collected and observed in aquaria, the mean shell length at which oviposition began was 16·25 mm. Fig. 5 illustrates the rapid rise in the per cent of mature animals (16·25 mm and over) present in samples taken from Arkell pond during spring and early summer, 1959. The increase was especially great between May 15 and June 15. From these facts, a burst of egg-laying might have been expected toward the end of May with the appearance of large numbers of young by June 15 (based on a 10-day hatching period for most egg masses in aquaria). No recently hatched young were seen at that time and no rapidly growing juveniles were found on successive collecting days (Fig. 1). A check on this observation was made the following year (1960) in Arkell pond, and on June 1 only one *L. palustris* as small as 4·5 mm was found; the smallest found on June 9 was 7 mm, on June 17 and 23, 8 mm, and on June 30, 9 mm. On the other hand, larger forms were abundant during this time. Although some spring egg-laying must occur (one 4·5 mm snail taken on June 1), the results of two years observation have indicated that in Arkell pond concentrated egg production does not occur in the spring months. Some spring-hatched *L. palustris* were present in Pond 2, but again there was no pronounced burst of spring reproductive activity. This behavior is in sharp contrast to that of the amphibious *L. humilis* Say which produces great numbers of eggs during several weeks in spring, as soon as water and air temperatures are favorable, resulting in a large new population of spring juveniles (McCraw, 1961). A similar spring juvenile population was found for *Physa gyrina* (DeWitt, 1955), and during the month of May, Duncan (1959) observed many egg capsules of *P. fontinalis* with a corresponding abundance of young (up to 5 mm) the following month.

A remarkable feature of the snails in both ponds studied was that the smaller ones survived winter conditions in greatest numbers. In Arkell pond at the time the water temperature first permitted the resumption of growth the majority of over-wintering *Lymnaea palustris* would have been somewhat less than 7 mm in length (Fig. 1). These findings

are consis- tent with the fact that smaller *L. humilis* were found to withstand the change from autumn to winter conditions better than larger ones (McCraw, 1961).

While no eggs were found in spring and early summer in Arkell pond, they were present by mid-summer (August 12). Spring growth of snails which were very small in the middle of April continued in a linear fashion until a shell length of 20 or 21 mm was attained (Fig. 2). To account for the 19 to 21 mm groups of August 12 (assuming a linear growth velocity) one might have expected size classes of 10 to 13 mm or smaller to be present on or about July 9 (Fig. 1). The absence of those size classes on July 9 suggests that the 19 to 21 mm snails of August were not late spring broods, but groups which had over-wintered either as very small snails or perhaps as larval forms in egg masses. While it may be difficult not to include some contribution to the late-summer *Lymnaea palustris* population of Arkell pond from egg masses laid in spring or early summer, analysis of weekly samples would indicate that the bulk of adult molluscs of 1 year is derived from the previous year. Since very few dead snails were observed in July and August, the molluscs of this over-wintering population must normally live throughout the summer, giving a life span for *L. palustris* of about 1 year.

Unlike what has been observed with *Lymnaea palustris* in Arkell pond, recent life cycle studies of several other pulmonates have shown that a spring population turnover of these snails is a common occurrence. Results of a study of DeWitt (1955) showed that in April nearly all *Physa gyrina* were mature, and that most of this generation died during this month after a period of active egg-laying. During May the population was composed almost exclusively of newly-hatched snails. Similar findings are recorded for *P. fontinalis* (Duncan, 1959) and *Ancylus fluviatilis* Muller (Hunter, 1953). Following continuous egg-laying for at least 6 weeks, over-wintering *L. humilis* populations, which were composed of 95% mature snails in April, were found to die off promptly in late May or early June (McCraw, 1961). However, rapid onset of senility followed by death is evidently not a sequel to the spring reproduction of the lymnaeid *Acella haldemani* (" Desh." Binney), which lives until mid summer (Morrison, 1932).

Fig. 6–11 show the changes that occur in the size and shape of the reproductive system of *Lymnaea palustris* with shell lengths of 23·0, 16·3 and 10·8 mm. Marked differences in appearance are evident between the slender reproductive system of the juvenile (10·8 mm) and the bulky organs of a large mature animal (23·0 mm). The oöthecal, muciparous and albumen glands displayed great expansion with age, particularly after the onset of maturity. However, up to the time of maturity, there was no pronounced change in the general form of the male and female reproductive tracts.

An interesting relationship was observed between growth of snails in the field and sexual maturity. The inhibiting phase of snail growth (June 15 onwards, Fig. 2) corresponded to a time at which approximately 85 per cent of *Lymnaea palustris* were mature (Fig. 5) suggesting that a decline in growth velocity is related to sexual maturity.

It has long been appreciated that the different parts of an organism do not always grow at the same rate. Although several approaches to the problem of growth analysis have been followed (Clark & Medawar, 1945), perhaps one of the most widely used is that proposed by Huxley (1924, 1932). According to this approach, the relation between the size

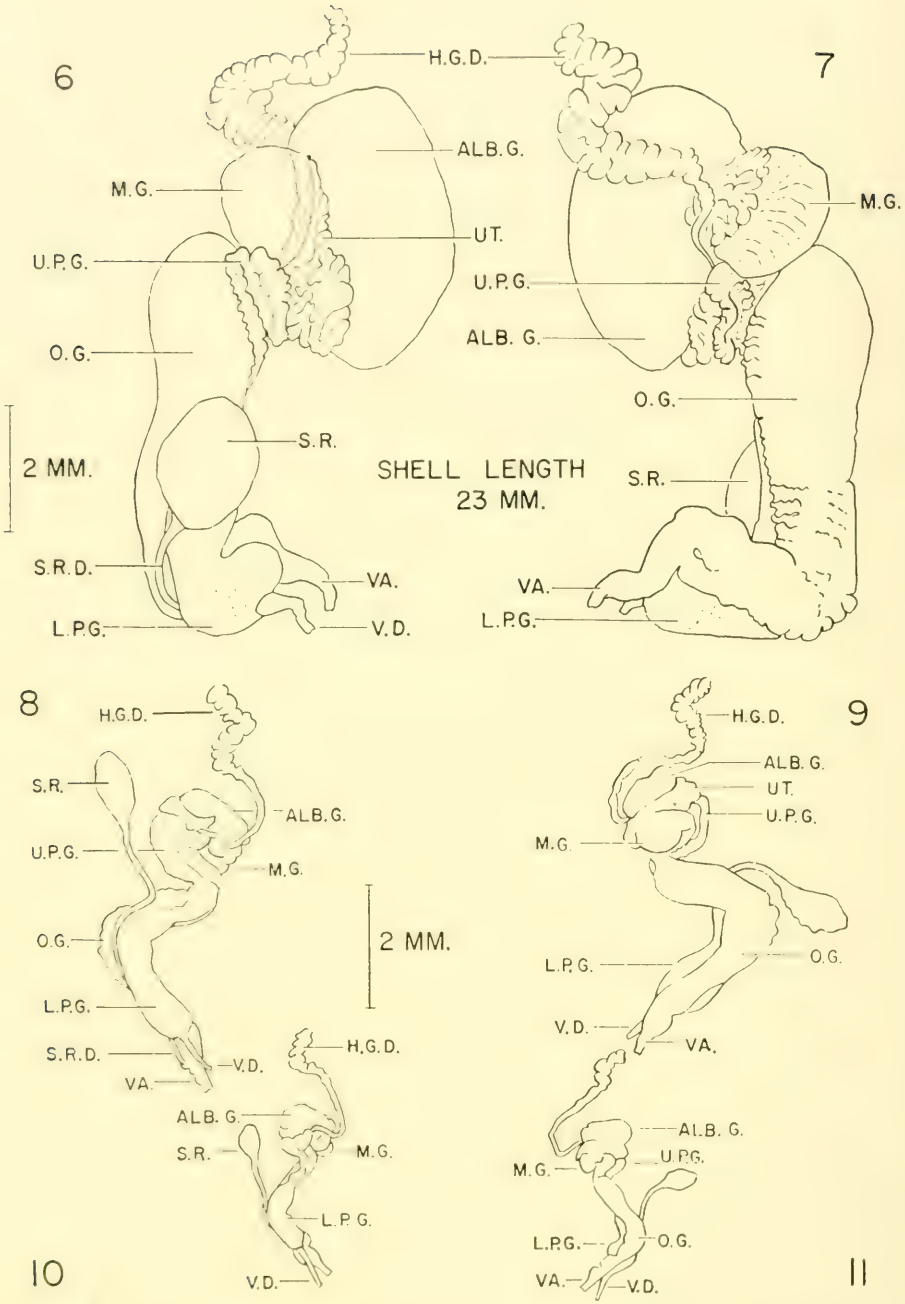

FIG. 6, 7, 8, 9, 10 and 11. Changes in the size and morphology of the reproductive system of *L. palustis* with an increase in shell length.

Figs. 6 and 7 from a snail with a shell length of 23 mm, Figs. 8 and 9 from one of 16.3 mm shell length, and Figs. 10 and 11 from one of 10·8 mm shell length.

Abbreviations : ALB. G., albumen gland; H.G.D., hermaphrodite gland duct; L.P.G., lower prostate gland; M.G., muciparous gland; O.G., cothecal gland; S.R., seminal receptacle; S.R.D., duct of seminal receptacle; U.P.G., upper prostate gland; UT., uterus; VA., vagina; V.D., vas deferens.

of the whole organism (x) and that of some part of it (y) can often be described by the equation

$$y = bx^k.$$

This equation is usually referred to as the allometry equation; however, other terminologies have been applied to describe growth when k is greater or less than unity, or merely unequal to 1 (Richards & Kavanagh, 1945). The parameter b is the value of y when x is o and the value of this parameter in turn depends on the measuring scales used (Richards & Kavanagh, 1945). These authors attribute no biological significance to it and even consider comparisons between values of b extremely hazardous. The value k is the slope of the line when the equation is in the form $log\ y = log\ b + k\ log\ x$ or the ratio of the 2 specific growth rates, $dy/ydt : dx/xdt$. The exponent k may be a true constant, or as Richards & Kavanagh (1945) point out, it may not actually be one but may remain so while the specific growth rates are themselves changing in such a manner as not to affect their ratio. On the other hand, k may show a gradual change in slope reflecting a continuous or nearly continuous adjustment of this value. Such a changing value of k was found for a plot of the total weight of the reproductive system against shell length of *Lymnaea palustris* (Fig. 12). Using the data of Miller & Hoy (1939), Richards & Kavanagh (1945) found a similar relationship between the length of the second antenna and body width in the isopod *Asellus californicus*. A gradual decline in the ratio of the specific growth rates of reproductive system and shell of *L. palustris* was evident, with the tendency more pronounced in larger animals. Since few living snails were found over 25 mm in length, this more rapid decline in larger animals is probably indicative of

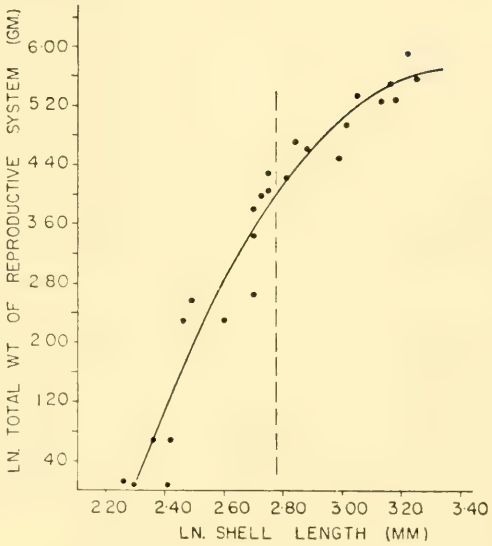

FIG. 12. A changing value of the exponent k in the relationship between the growth of the reproductive system and shell length of *L. palustris*. Broken line indicates the onset of maturity (16·25 mm). (Ln. Y=—51·97+34·43 (Ln. X)—5·14 (Ln. X_1)^2.

senile changes. It is therefore clear that although the form of the reproductive system of a juvenile is not in general the same as that of an adult (Fig. 6, 7, 10, 11), there is certainly no sudden change in the ratio of the specific growth rates of this system and shell length that can be attributed to any biological phenomenon, such as the onset or cessation of reproduction.

While the allometry formula describes the relationship between the reproductive system as a unit and shell length, the growth activities of separate organs or regions and shell length followed a linear relationship within the limits of the measurements made (Fig. 14–17). The same situation also prevailed for gizzard size (Fig. 13). All these organs, especially the reproductive structures, develop very slowly during the first few mm of shell growth. In *Lymnaea*

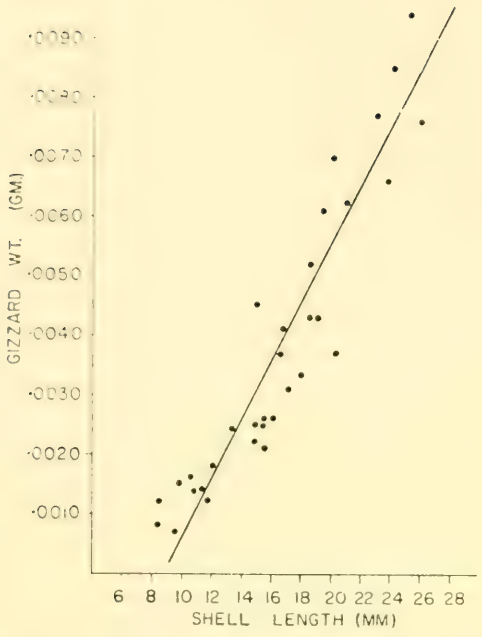

FIG. 13. The relationship between gizzard weight and shell length of *L. palustris*. (Y = ·0005X— ·0044; r^2 = ·874).

palustris smaller than 10 mm, the albumen' oöthecal and prostate glands each weighed much less than .0001 g while in a 25 mm animal these glands weighed .0099, .0134 and .0056 g respectively. Moreover, the mean weight of the entire reproductive system of six *L. palustris* averaging 9.60 mm was only .0001 g whereas in a 25 mm or larger snail this figure may reach well over .0250 g. For the mean shell length at which oviposition began (16.25 mm), the predicted total weight of this system is .0055 g. Beyond a shell length of about 10 mm various parts of the reproductive system undergo a sudden increment in growth velocity (Fig. 14–17).

The albumen gland showed great variation in weight (r^2 = ·618)[1]. Very often in a snail of 20 mm it may be no larger than in a snail of 12 mm (Fig. 14). In addition, its % weight (relative to the total weight of the reproductive system) showed no consistent change with an increase in shell length (Table 1). These findings indicate that the size of this organ is dependent not only upon overall animal size, but to a large measure upon the reproductive state of an individual snail. With the prosobranch *Rissoa parva* Da Costa, Gostan (1958) stated that there was not always correspondence between the development of the reproductive system and growth of the shell, and she suggested seasonal factors, especially temperature, as a possible reason. With the exception of the albumen gland, correspondence between these 2 parts in *Lymnaea palustris* was for the most part good, and only one animal with a stunted reproductive system was observed. Duncan (1958) observed that the albumen gland of *Physa fontinalis* (L.) varied seasonally and was small and difficult to detect during the period October to February. Berrie (1966) noted a similar seasonal reduction in the size of the albumen gland of *L. stagnalis* (L.). The variation recorded here for *L. palustris* occurred during late spring and early summer. Fluctuations in the magnitude of the albumen gland of *L. palustris* were especially noticeable around the time of maturity.

A closer relationship was found between the growth of the remaining structures of the reproductive system and shell length than for the albumen gland and shell length (r = ·92 and above; r^2 = ·851 and above) (Fig. 15–17). The % weights

[1] Snedecor & Cochran (1967) state that "r^2 may be described as the proportion of the variance of Y that can be attributed to its linear regression on X. When r is 0.5 or less, only a minor proportion of the variation in Y can be attributed to its linear regression on X. At r = 0.7, about half the variance of Y is associated with X, and at r=0.9, about 80%."

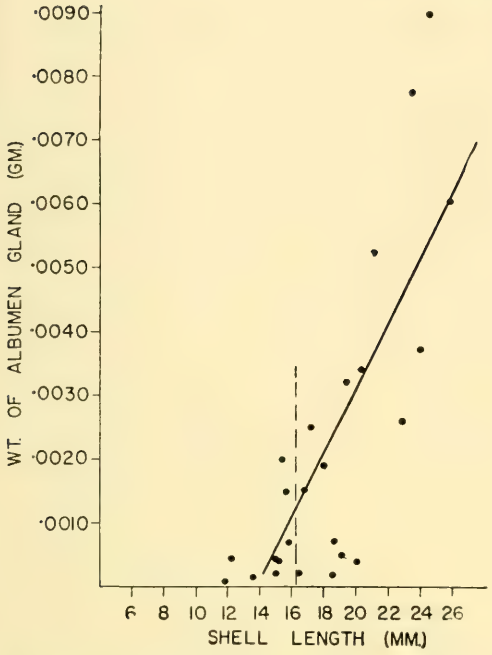

FIG. 14. The relationship between albumen gland weight and shell length of *L. palustris*. Brokenine indicates the onset of maturity (16.25 mm). (Y=.0005X—.0069; r^2=.618).

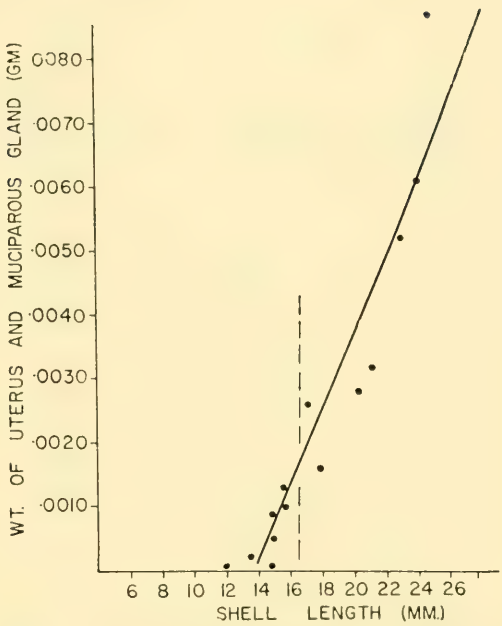

FIG. 15. The relationship between the weight of the uterus (including the oviduct) and muciparous gland, and shell length of *L. palustris*. Broken line indicates the onset of maturity (16.25 mm). (Y=.0006X—.0082; r^2=.891).

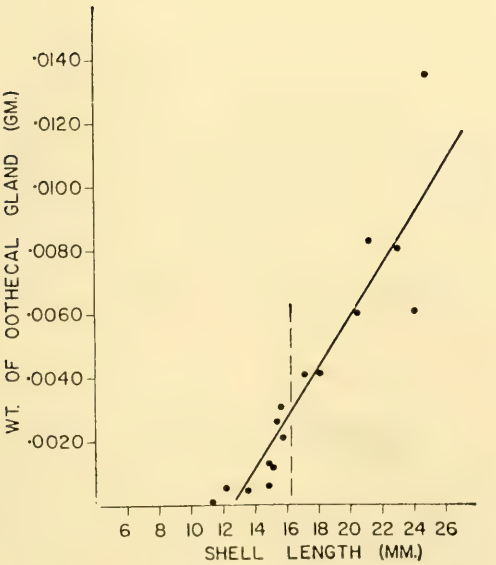

FIG. 16. The relationship between the weight of the oöthecal gland (including the vagina) and shell length of *L. palustris*. Broken line indicates the onset of maturity (16.25 mm). (Y=.0008X —.0100; r^2=.856).

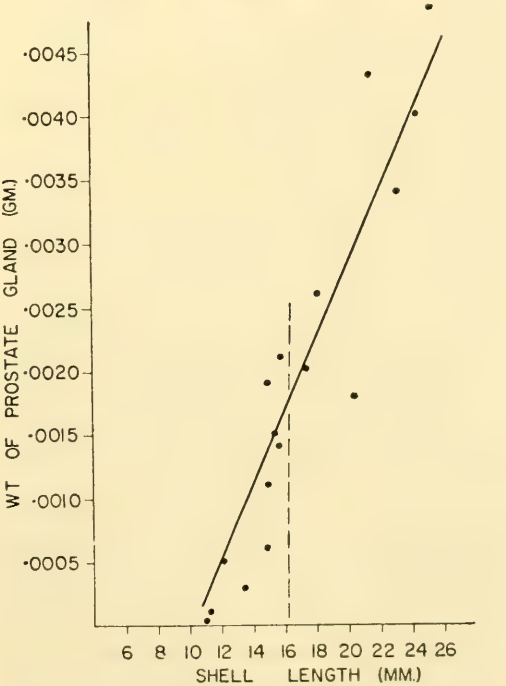

FIG. 17. The relationship between the weight of the prostate gland and shell length of *L. palustris*. Broken line indicates the onset of maturity (16.25 mm). (Y=.0003X—.0031; r^2=.851).

TABLE 1. Weights of various parts of the reproductive system of *L. palustris* expressed as per cents of the total weight of the reproductive system. Data arranged according to increasing shell length.

Shell Length (mm)	Total Wt. of Reproductive System* (g)	Albumen Gland Per cent Total Wt.	Oviduct, Uterus, Muciparous Gland Per cent Total Wt.	Oothecal Gland Per cent Total Wt.	Prostate Gland Per cent Total Wt.
11·7	·0010	10·0			
12·0	·0014	28·6	0	35·7	35·7
13·5	·0010	10·0	20·0	40·0	30·0
14·9	·0014	14·3	0	42·8	42·8
14·9	·0032	12·5	15·6	37·5	34·4
14·9	·0045	8·8	20·2	28·8	42·2
15·6	·0073	20·5	17·8	42·5	19·2
15·7	·0059	11·9	16·9	35·6	35·6
16·7	·0069	21·7			
17·1	·0112	22·3	23·2	36·6	17·9
17·9	·0103	18·4	15·6	40·8	25·2
20·0	·0091	4·4			
20·3	·0141	24·1	19·8	43·3	12·8
21·1	·0210	24·8	15·2	39·5	20·5
22·9	·0193	13·5	26·9	42·0	17·6
23·7	·0246	31·3			
24·0	·0199	18·6	30·7	30·7	20·1
25·0	·0376	26·3	23·2	35·6	14·9
25·8	·0269	22·3			
		Range % 4·4–31·3	Range % 0–30·7	Range % 28·8–43·3	Range % 12·8–42·8

*Includes only those values from which percents are calculated.

of the oviduct-uterus muciparous gland complex, oöthecal and prostate glands are shown in Table 1.

The phase of initial slow growth is more prolonged for the reproductive organs than in the case of gizzard growth. In the former it lasts until a shell length of 11 or 12 mm is attained, 5 or 6 mm before oviposition begins. After the phase of rapid growth has set in, there is no spectacular difference in the ratios of the absolute growth rates for gizzard growth on the one hand (Fig. 13), and the glandular structures on the other (Fig. 14–17). However, of the individual organs it is worth noting that the growth rate of the oöthecal gland is fastest and that of the prostate slowest. These 2 rates may reflect a difference in glandular activity or in the nature of the secretions of these structures. The oöthecal gland is to a large degree mucus-secreting, while secretory droplets are a prominent feature of the prostate follicles (Holm, 1946; Duncan, 1958).

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RÉSUMÉ

ASPECT DE LA CROISSANCE CHEZ *LYMNAEA PALUSTRIS* (MÜLLER)

B. M. McCraw

L'analyse d'échantillons hebdomadaires d'une population posthivernale de *Lymnaea palustris* (Müller) a révélé que la croissance de printemps et du début d'été a été rapide suivant une courbe presque linéaire, mais qu'il n'y a eu qu'une faible croissance avant le 15 avril et après le début juillet. Il n'y a pas eu une activité de ponte de printemps intense dans l'étang d'Arkell, bien que quelques lymnées nées du printemps aient été présentes dans l'Etang 2. Les plus petits *L. palustris* hivernent bien et dans l'étang d'Arkell presque toute la population de printemps et d'été dérivait d'animaux nés l'année précédente en fin d'été ou d'automne. Contrairement à certains pulmonés, il n'y a pas eu renouvellement de la population au printemps. Jusqu'à la maturité, l'appareil reproducteur est mince et ne montre pas de changement notable dans sa forme générale, mais après maturité il subit une grande extension. Le taux de croissance (k) de l'appareil reproducteur n'est pas constant, mais décline graduellement avec l'âge. Après une taille de coquille de 11 ou 12 mm, la croissance de chaque organe reproducteur (glande de l'albumen, oothèque, utérus et glande nidamentaire, et prostate) en relation avec la longueur de la coquille, est linéaire. Au-dessous de 8 mm la même chose est vraie pour le gésier. Toutes ces structures se développent très lentement pendant les premiers millimètres de croissance de la coquille. Une grande fluctuation de taille se manifeste pour la glande à albumen, ce qui est probablement en relation avec l'activité reproductrice. Le taux de croissance de l'oothèque est le plus rapide et celui de la prostate le plus lent.

A. L.

RESUMEN

ASPECTOS DEL CRECIMIENTO DEL CARACOL *LYMNAEA PALUSTRIS* (MÜLLER)

B. M. McCraw

Anàlisis semanales de muestras de poblaciones de *Lymnaea palustris* (Müller) después de invernada, revelaron que en primavera y principio del verano el crecimiento de los caracoles fué màs rápido, pero antes del 15 de Abril o después del principio de Julio no se registro crecimiento. No hubo desove concentrado en la pequeña laguna Arkell,– aunque algunos caracoles que habian hecho eclosión en primavera estaban presentes en la laguna 2. Caracoles pequeños invernaron mejor, y en Arkell toda la población de primavera-verano derivó de individuos que desovaron el año anterior al fin del verano o en otoño. Antes de alcanzar madurez, el sistema reproductor és delgado sin mostrar cambio pronunciado en la forma general, pero después experimenta gran expansión. El crecimiento del sistema reproductor no és constante sino que declina con la edad. Despues que la concha alcanza a 11 o 12 mm, el crecimiento individual de los organos reproductores (glándula albuminoidea, ooteca, útero, glándula mucipora y prostata) es lincar en relación a la longitud de la concha. Desde los 8 mm, lo mismo ocurre en el crecimiento del estómago. La glándula albumimoidea ofrece gran fluctuación en el crecimiento y esto probablemente està relacionado a la actividad reproductiva. El crecimiento más rápido se observó en la glandula ootecal y el más lento en la prostata.

J. J. P.

АБСТРАКТ

О РОСТЕ РАКОВИНЫ УЛИТКИ *LYMNAEA PALUSTRIS* (MULLER)

Б. МЭКРОУ

Изучение еженедельных проб популяций перезимовавших *Lymnaea palustris* (Muller) указывает на то, что рост этих моллюсков весной и в раннее летнее время происходит быстро, сопровождаясь линейными отметками.

Ослабленный рост наблюдается вплоть до 15 апреля или даже до начала июля. Концентрированная весенняя кладка яиц в пруде Аркелл отсутствовала, хотя молодь улиток весеннего выклева наблюдалась в пруде № 2. Лучше всех перезимовывали более мелкие *L. palustris;* в пруду Аркелл почти все улитки весенней популяции происходили от особей, отложивших яйца в предыдущем году-в конце лета или осенью. Не в пример некоторым Pulmonata у них не наблюдалось круговорота весенней популяции. Вплоть до наступления половозрелости, их репродуктивная система была развита слабо и в ней еще не наблюдалось заметных изменений общей формы; после наступления половозрелости гонады заметно увеличиваются.

Темп роста (К) половой системы не постоянен, но постепенно затухает с возрастом, и после увеличения размера раковины до 11-12 мм у отдельных особей рост половой системы (альбуминовой железы, оотеки, матки, слизистой железы и простаты) по отношению к длине раковины происходит линейно. У особей менее 8 мм тоже самое верно в отношении роста желудка. Все эти структуры развиваются очень медленно при росте раковины на первые несколько мм. Большие колебания размера наблюдаются также у альбуминовой железы, что может быть связано с размножением. Темп роста железы оотеки наиболее быстрый, а у простаты-самый медленный.

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THE SHELL STRUCTURE OF *ASTRAEA OLFERSI* (GASTROPODA: TURBINIDAE)[1]

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ABSTRACT

A study of 30 shells of *Astraea olfersi* Troschel *in* Philippi, 1846, concerned especially with their structural design and crystallographic arrangement, shows the presence of 2 layers: an outer one, with homogeneous-foliate structure consisting of aragonite and traces of calcites and an inner one, with nacreous structure consisting of aragonite only. After corrosion, the structural design is foliate in both layers. A review of the literature shows that several Recent and Tertiary species of *Turbo* and *Astraea* possess this type of aragonite structure.

Examination of a polished section of a molluscan shell often shows that the external and internal parts of a layer seem to have the same appearance. This may be observed in the crossed lamellar and prismatic structures. In some instances, on the contrary, the 2 parts are quite different. This happens in the nacreous structure, the external part of which is iridescent, whereas the internal one shows sinuous superposed lines without iridescence after exposure to corrosion. Based on this fact, and adopting Böggild's (1930) terminology, I introduce the expression " structural design " to signify the figure produced by any weak corrosion process. The results obtained are expected to be of use in studies of systematics and paleontology, as they bring additional details to the description of structural components of shells and to the comparison between Recent and fossil forms.

MATERIAL AND METHODS

The shell of the turbinid prosobranch *Astraea olfersi* Troschel *in* Philippi, 1846, was studied by means of corrosion of surfaces, replicas in polyester (Araldite-Ciba), staining with alizarin, Phloxin, cotton blue in acetic acid (Ranson, 1952), ultra-violet examination (Jurberg & Barth, 1964) and X-ray diffraction (Swamy Rama, 1935).

The diagrams were made by the powder method, in a Norelco diffractometer. The powder was obtained by scraping off separately each layer of the shell. The specimens were collected alive and left to die in jars at room temperature so as to allow decomposition of the organic material to take place. This procedure prevents aragonite from turning into calcite during the preparation of the material, as pointed out by Davies & Hooper (1963).

About 30 specimens were used in this study. They were collected from calm sea between the middle littoral and the infralittoral zones (Pérès, 1961), at Arraial do Cabo, Praia do Forno, State of Rio de Janeiro, Brazil.

[1]Work carried out in the Instituto Oswaldo Cruz and the Instituto de Pesquisas de Marinha, and supported by a grant from the Conselho Nacional de Pesquisas, Brazil.

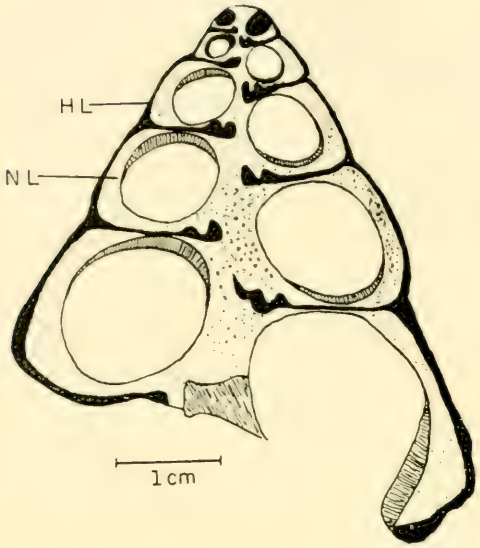


FIG. 1. Section longitudinal to the columellar axis, showing the distribution of the homogeneous (HL) and nacreous (NL) layers.

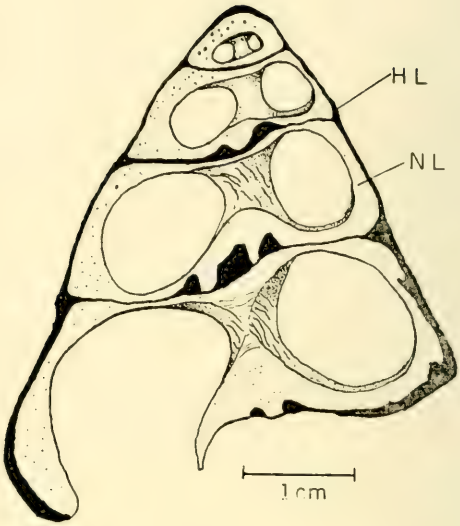


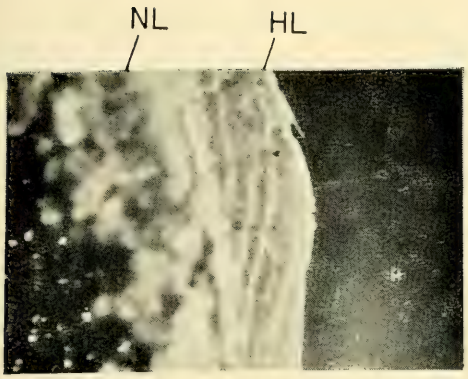
FIG. 2. Same section seen from the opposite side.

THE SHELL OF *ASTRAEA OLFERSI*

The shell of *Astraea olfersi* shows 2 clearly visible layers, even with macroscopic observation (Figs. 1–2). The most careful examination did not reveal any periostracal layer, even in specimens collected alive.

A thick polished section of the outermost layer shows no textural arrangement and, on this account, it should be considered a "homogeneous structure". However, after corrosion its structural design was disclosed as a foliate pattern of sinuous superposed lines (Fig. 3). It could be regarded as a transition from the homogeneous to the foliate structure, and this is why I find it appropriate to name it, with Böggild (1930), the "homogeneous-foliate structure". This outer layer spreads all over the external surface of the shell and extends beneath some inclusions into the underlying layer. It did not take the above-mentioned dyes and showed no fluorescence under ultraviolet light, owing probably to its low content of organic material. The presence of calcite in this layer seems difficult to understand. Theories on the determinism of $CaCO_3$ formation in the molluscan shell are still contradictory as pointed out by Wilbur (1964).

The innermost layer has a nacreous aspect and covers all the internal surface of the shell. After corrosion it shows a foliate structure (Fig. 4) much more conspicuous than that in the outer layer. Excellent corrosion images were obtained with cotton blue acetic acid. This layer also differs from the outer one in taking comparatively well some dyes such as picric acid, phloxin and alizarin. Microscopical observation showed, however, that the stain was not evenly distributed throughout the section surface, owing perhaps to the action of the dyes on the organic material largely found in the nacreous layer. Under ultraviolet light the shell sections displayed an intense green fluorescence confined to the inner layer and similar to that observed in the outer surface of shells that have a super-



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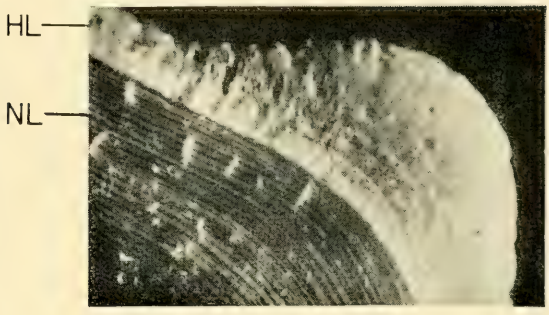

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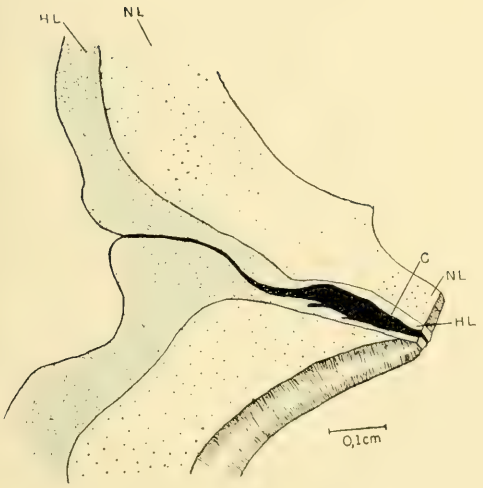

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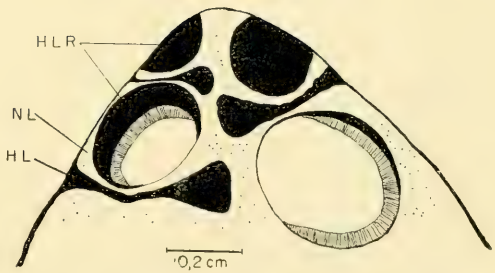

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FIG. 3. Cross section showing the corrosion figure in the outer layer and the sinuous lines NL, nacreous layer; HL, homogenous layer.

FIG. 4. Cross section showing the corrosion figure and the sinuous lines of the nacreous (inner) layer.

FIG. 5. Cross section showing the cement (C) between two contiguous whorls.

FIG. 6. Longitudinal section of the apex, showing the first whorls filled with material similar to that of the outer layer. HLR = homogeneous layer reinforcement.

ficial conchiolin layer, such as *Thais haemastoma* (Linné, 1767) and *Olivancillaria brasiliana* (Lamarck, 1811). This property may be attributed to the large quantity of organic material in the nacreous layer. X-ray diffraction showed that the inner layer is made up of aragonite distributed in lamellae parallel to the basal plane. This lamellar arrangement was evidenced by the reflection 2·85 Å

TABLE 1. Forms of $CaCO_3$ crystallization in Recent and fossil Turbinidae, as shown by the X-ray powder diffraction method.

Species	Calcite	Arago-nite	Geologic age	Locality	Authors
Turbo rhectogrammicus Dall			Pliocene	Florida, USA	Grandjean, Grégoire & Lutts 1964.
Astraea of C. A. phoebia Röding		·	Pleistocene?	Florida, USA	Idem.
Turbo marmoratus L.			Recent		Roche, Ranson & Eysseric-Lafon 1951.
Turbo sp.		·			Swamy 1935.
Turbo sp.		·			Grégoire 1957.
Turbo sp.					Lutts, Grandjean & Grégoire 1960.
Turbo sp.		·			Grégoire 1961.

(Muller's index 002), which revealed greater intensity than did the ASTM 5–0453 standard reflection; the corrosion figures confirmed the lamellar structure showed by the diffraction process. Taking into account the external iridescent aspect of this layer, its structural design and the form of its $CaCO_3$ crystals, it can be considered a "nacreous structure", following Böggild's terminology.

At the points of connection between 2 contiguous whorls there forms a layer of moderate thickness surrounded by the homogeneous outer layer which is reflected over it (Fig. 5). It seems to be a cement of organic origin, because it stains much more intensely than the other 2 layers with the same dyes.

A section longitudinal to the columellar axis shows, near the apex of the shell, a homogeneous layer which stains less intensely than the outer layer (Fig. 6). Its material makes up the bulk of the apical whorls, and its function seems to be to reinforce the walls of those whorls.

The structural design just described is the same for each layer in all parts of the shell, and may be observed whatever the angle of section through the shell.

DISCUSSION

Those who have studied shell structure in Recent and fossil Turbinidae have confined themselves either to the external appearance, or to the structural design,

or to the crystallographic arrangement of $CaCO_3$, without considering such aspects together.

Gray (1833), Carpenter (1848) and Böggild (1930) agreed that the Turbinidae possess a nacreous layer. Gray (1833) observed that the Haliotidae and Turbinidae have a "foliate structure". As concerns the Turbinidae, I cannot be sure that Böggild's (1930) foliate structure is equivalent to Grégoire's (1957) calciostracum. Such a doubt arises from the fact that Böggild (1930) described 2 analogous structures—the foliate and the nacreous structures—the former differing from the latter in having calcite instead of aragonite (common to the nacreous structure), and in being less iridescent. Both structures show the same design, namely, superposed sinuous lines.

Böggild (1930) examined Recent and Tertiary species of *Turbo*, stating that "the lower layer is nacreous and the upper one homogeneous and at the same time irregularly prismatic or grained".

Grégoire *et al.* (1955) studied the protein network in nacre and referred to the following species of Turbinidae as possessing a nacreous structure: *Turbo canaliculatus* Gmelin, *T. cidaris* Gmelin, *T. chrysostomus* Linné, *T. tessellatus* Kiener, *T. setosus* Gmelin, *T. coronatus* Gmelin, *T. undulatus* Martyn, *Astraea unguis* (Wood), *A. rugosa* (Linné) and *A. olivacea* (Wood).

Table 1 shows the different forms under which $CaCO_3$ crystallizes in the Turbinidae, according to the data from several authors, in some cases without species identification.

The only references to calcite in the Turbinidae are those by Lutts *et al.* (1960) and Grégoire (1961), in undetermined species of *Turbo*. Grégoire (1961) noticed this discrepancy and tried to explain it in Böggild's (1930) words: "calcite may occur quite unexpectedly in one or a few members of a genus otherwise consisting entirely of aragonite". The possibility of a wrong taxonomic identification should be considered, since Lutts *et al.* (1960) and Grégoire (1961) referred to the occurrence of prisms in a genus in which, according to the literature, they otherwise are lacking.

CONCLUSIONS

1. The expression "structural design" is introduced to signify the figures obtained by weak corrosion, a method that permits a more complete study of shell structure.

2. The shell of *Astraea olfersi* consists of 2 layers: an outer one, with an apparently homogeneous structure, and an inner one, with a typical nacreous structure. The structural design of the outer layer shows a homogeneous foliate structure (following Böggild's terminology) consisting of aragonite and traces of calcite, without iridescence. The inner layer, as revealed by corrosion, is made up of aragonite in superposed sinuous lines, with interposed organic material.

3. Other species of *Astraea* and *Turbo* are said to be similar in structure. However, the systematic value of shell structure in the Turbinidae will be settled only after examination of more specimens of different species at different stages of development.

4. Recent and Tertiary turbinid shells are made up of aragonite, the only exceptions being pointed out in the text.

ACKNOWLEDGMENTS

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RÉSUMÉ

LA STRUCTURE DE LA COQUILLE DE *ASTRAEA OLFERSI* (GASTROPODA: TURBINIDAE)

P. Jurberg

L'étude de 30 coquilles d'*Astraea olfersi* Troschel in Philippi, 1846, concernant leur agencement structural et leurs caractères cristallographiques, montre la présence de deux couches: une externe, à structure homogène feuilletée constituée d'aragonite et de traces de calcite et une interne, à structure nacrée constituée d'aragonite seulement. Après corrosion, l'agencement structural est feuilleté dans les deux couches. Une revue de la littérature montre que plusieurs espèces de *Turbo* et d'*Astraea*, actuelles et du Tertiaire, possèdent ce type de structure avec aragonite.

A. L.

RESUMEN

ESTUDIO CONCHOLOGICO ESTRUCTURAL DE *ASTRAEA OLFERSI* TROSCHEL (GASTROPODA, TURBINIDAE)

P. Jurberg

El estudio de la estructura y composición cristalográfica en 30 ejemplares, de la concha de *Astraea olfersi* Troschel *in* Philippi, 1846, mostró la presencia de dos capas: una externa homogenea y foliada consistente de aragonita y trozos de calcita, y otra interna, nacarífera, con aragonita solamente. Cuando corroídas, ambas capas son foliadas. Una revisión de la literatura al respecto reveló que varias especies del Terciario y Reciente, de *Turbo* y *Astraea*, poseen este tipo estructural de aragonita.

J. J. P

АБСТРАКТ

СТРУКТУРА РАКОВИНЫ *ASTRAEA OLFERSI* (GASTROPODA: TURBINIDAE)

П. ЮБЕРГ

Исследование 30 раковин ***Asrtaea olfersi*** **Troschel** (в **Philippi, 1846**), касающееся их структуры и кристаллографического строения, показало наличие двух слоев: наружного, гомогенно-листоватой структуры, состоящего из арагонита и следов кальцита, и внутреннего, перламутрового, состоящего только из арагонита. При коррозии строение обоих слоев становится листоватым. Просмотр литературы показал, что некоторые современные и третичные виды ***Turbo*** и ***Astraea*** обладают таким же типом арагонитовой структуры раковины.

Z.A.F.

MALACOLOGIA, 1970, 10(2): 423–439

STUDIES ON SHELL FORMATION: MEASUREMENT OF GROWTH IN THE GASTROPOD *AMPULLARIUS GLAUCUS*[1]

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ABSTRACT

Calcium deposition in various shell regions of *Ampullarius glaucus* was measured over periods of 4–24 hours using Ca^{45}. The rate of calcium deposition was highest near the shell aperture (7×10^{-4}mg/cm^2/hr) and decreased very markedly and progressively with increasing distance from the aperture within the body whorl. The calcium deposition rate decreased with increasing shell weight. The relation between linear growth rate of the mantle and calcium deposition rate by different mantle areas results in an increasing shell thickness as the whorls develop. After 10 days without food, the mean calcium deposition rate decreased 50%. In darkness, mean linear growth was reduced sharply, whereas the reduction of calcium deposition rate was not significant.

The shell has a cross lamellar structure in which the crystals are made up of crystallites 500 Å—600 Å in thickness. In rapidly growing snails, 36 layers may be deposited each day.

INTRODUCTION

Shell growth in molluscs has commonly been studied by following linear or weight changes over weeks or months (Wilbur & Owen, 1964). Other methods permit growth measurements during shorter periods. These include fluorescent shell marking following tetracycline injection (Nakahara, 1961); incorporation of Ca^{45} into the shell (Wilbur & Jodrey, 1952); external shell marking with later microscopic examination (Kenny, unpub.); and measurements of distances between daily growth lines (Choe, 1963; Clark, 1968).

Two of these methods—Ca^{45} deposition and external shell marking with microscopic observations—have been employed in the present study with the purpose of examining their usefulness in growth studies of very short periods in gastropods. The rate of calcium deposition occurring in several hours in the snail *Ampullarius glaucus* was found to be easily measurable using Ca^{45}. This method was then used to measure the rate of calcium deposition (1) in various shell regions, (2) as a function of size, (3) in the absence of food, and (4) in the absence of light. As a complement to the Ca^{45} method, shell marking with microscopic obser-

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vation was used to measure linear growth over short periods. With the information gained from the 2 methods, it has been possible to analyze certain aspects of calcium deposition and shell morphology as the animal increases in size.

Observations of the growing shell edge with the light microscope and the scanning electron microscope demonstrated that *Ampullarius glaucus* forms shell by depositing alternating layers differing in crystal orientation. During active growth a large number of crystal layers is formed each day.

MATERIALS AND METHODS

Animals and maintenance

Specimens of *Ampullarius glaucus* were collected from Laguna Campoma, approximately 85 km east of Cumana, Venezuela. They were maintained in aquaria 52 cm × 29 cm × 27 cm containing 15 liters of aerated tap water and fed lettuce every other day. Laboratory lighting during daylight hours was natural and fluorescent illumination. There was no lighting at night except during the course of occasional experiments.

Isotope procedures

Prior to exposure to radioactive solutions, the animals were cleaned, dried, and coated with nail polish to prevent uptake of Ca^{45} by the outer shell surface (Wilbur & Jodrey, 1952). They were then returned to tap water for several hours to remove all traces of solvent.

Single snails were placed in 250 ml of tap water in plastic boxes 6 cm × 8 cm × 8 cm without food. Although certain plastics may have a toxic effect on snails, no evidence for this was found in the present study in snails reared in plastic boxes up to 3 months. When movements were observed to be normal, the tap water was exchanged for Ca^{45}—tap water with an activity of 3×10^6 counts per minute per liter. The Ca^{45} was carrier-free and thus did not appreciably increase the total calcium content of the water. The temperature throughout the experimental period ranged from 24·5° to 25·5°C.

At the end of the exposure periods of 4 hours to 24 hours in Ca^{45}—tap water, snails were removed from the shell with forceps after cutting the columellar muscle. Pieces of shell 5 mm × 5 mm were cut from various regions (Fig. 1, insert) with a Dremel power tool with a steel cutting blade and washed with a stream of distilled water from a wash bottle to remove adhering radioactive material.

Radioactivity was measured with a gas flow counter with a window thickness of 1·5 mg/cm². The amount of calcium deposited on the inner shell surface was calculated from the following relation (Wilbur & Jodrey, 1952):

$$D = \frac{A_s}{A_w} \times C,$$

where D is mg/Ca deposited/cm²; A_s is counts/min/cm² of shell; A_w is counts/min/liter medium; and C is mg Ca/liter tap water. Calcium content of the tap water ranged from 22 to 26 mg per liter during the experimental period.

To estimate radioactivity due to exchange, empty shells were exposed to radioactive solutions under the same conditions used for living animals. The values obtained for living animals were corrected for exchange in each case.

Methodology relating to the use of isotopes for measuring shell growth in molluscs has been discussed previously (Wilbur & Jodrey, 1952).

Starvation experiments

In studies of the effects of starvation, snails were maintained as described above

but no food was given. After various periods up to 10 days the animals were exposed for 16 hours to Ca^{45}—tap water with an activity of 3×10^6 c/min/l. The rate of calcium deposition was determined near the shell aperture (Fig. 1, insert, A).

Light-dark experiments

Individual snails were placed in Ca^{45}—tap water in plastic boxes without food as described under isotope procedures. Some animals were maintained in complete darkness. Others were exposed to constant illumination from a 40-watt incandescent lamp at a distance of approximately 2 feet. All experiments were started between 8:00 and 9:00 a.m. At the end of a 24-hour period in Ca^{45}, the deposition of Ca^{45} near the shell aperture was measured.

The effect of light on linear growth was studied on groups of 15 snails of similar size range placed in each of three plastic tanks containing 28 liters of aerated water. One tank was kept dark by means of black cloth. Two other tanks were each supplied with two 20-watt fluorescent lamps, 60 cm in length, placed approximately 30 cm above the water. The light intensity at water level was 1500 lux in the center, with minimum intensities of 875 and 950 lux at the edges of the two tanks. One tank was illuminated continuously. The other tank was exposed to a 12-hour light—12-hour dark cycle regulated automatically. The maximum temperature variation in the three tanks was 22·3°–25·0°C. The experiments ran for 5 days and 6 days.

The consumption of lettuce by each group of snails was determined by providing weighed amounts of carefully blotted lettuce and reweighing the lettuce after each 24-hour period.

Measurements of linear growth

For measuring linear growth, the edge of the shell aperture was very carefully ringed with nail polish or India ink (Pelican Brand) and the snails returned to aquaria. After various intervals, a random group of snails was removed and a piece of the newly deposited shell 5 mm wide was carefully cut out with a fine-tooth triangular file. The pieces were mounted in water between a slide and coverslip and growth rings were counted using transmitted light with a stereomicroscope at magnifications of 250 and 500 diameters. Linear growth was measured with compass-type calipers.

Handling of the animals and addition of nail polish quite possibly retarded growth temporarily. Any initial disturbance of growth was minimized by maintaining the animals for growth periods of 5 to 30 days without handling.

Transmission electron microscopy

Pieces of shell edge were dehydrated in a series of concentrations of ethanol (3 changes, 5 minutes each in 50%, 70% and 90%; 4 changes, 15 minutes each in 100%), rinsed in 1:1 mixture of propylene oxide and 100% ethanol, and soaked in two changes of propylene oxide, 30 minutes each. They were left overnight in 1:1 mixture of propylene oxide and Vestopal H in a vacuum desiccator, followed by constant agitation for 2 hours in Vestopal H. They were then placed in gelatin capsules with fresh Vestopal H and left in an oven at 60°C for 2 days. Thin sections were cut with a diamond knife and observed with an Hitachi HU-11 electron microscope operated at 75 KV. Some sections were decalcified in 1% aqueous solution of uranyl acetate for the observation of organic matrix.

Scanning electron microscopy

Shell fragments were treated with 5·25% sodium hypochlorite for a few seconds to remove the organic covering of the shell

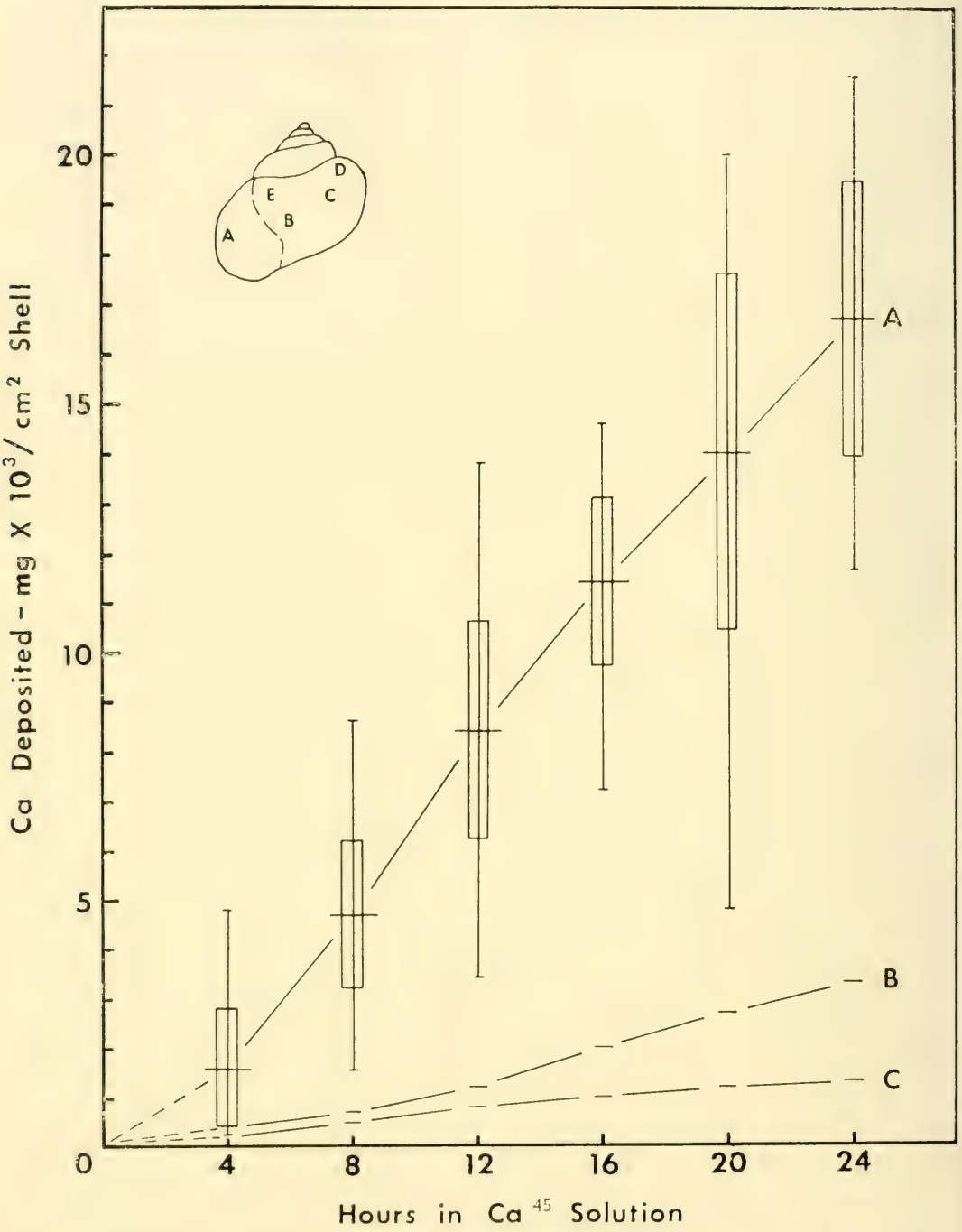


FIG. 1. Calcium deposition in 3 areas of the shell of *Ampullarius glaucus*. Insert shows regions where measurements were made. Areas D and E are on the opposite side of the shell from A, B and C. Vertical lines represent range, horizontal lines the means, and vertical bars the standard deviations of the amounts of calcium deposited by 15 snails 20–25 mm long (from tip of spire to base of body whorl) at each time interval.

and washed in distilled water. They were mounted on specimen holders, coated with gold under vacuum, and observed with a Stereoscan Scanning Electron Microscope.

RESULTS

Calcium deposition

The rate of shell formation as indicated by deposition of Ca^{45} was measured in normal specimens of *Ampullarius* near the aperture (Fig. 1, insert, A) and at various distances from the aperture (B, C, D, E). The amount of deposition in regions A, B, and C after various periods of immersion in Ca^{45} is given in Fig. 1, curves A, B, and C. Each horizontal bar through the curves represents the mean of 15 specimens. The deposition rates of two other areas, D and E (Fig. 1, insert), have also been measured, but are not included in Fig. 1. The relative rates of deposition for the 5 areas measured over 24 hours were: A=14·3; B=2·7; C=1·0; D=0·3; and E=0·1. The values show that the rate of calcium deposition was highest at the mantle periphery corresponding to region A and decreased markedly and progressively centrally.

Calcium deposition increased linearly with time after the first 4 hours. The linear nature of curve A (area near aperture) demonstrated that the deposition of Ca^{45} reflected total calcium deposition even at the highest deposition rate. As deposition continued to increase, the radioactivity first deposited would be absorbed by overlying layers of $CaCO_3$ and the slope of the curve would be expected to decrease due to self-absorption. This did not occur during a 24-hour period. The mean rate of calcium deposition in the aperture region was $0{\cdot}7 \times 10^{-3}$ mg/cm²/hr. The range in individual calcium deposition rates was great (Fig. 1, vertical bars and lines), a finding commonly observed in molluscan growth studies (see, for example, Wilbur & Jodrey, 1952).

Extrapolation of the curves in Fig. 1 toward zero time indicates a change in rate of deposition during the first 4 hours. This is not surprising since time would be required for the Ca^{45} of the medium to come into equilibrium with the mantle. The time for mantle equilibrium in the fresh-water bivalves *Anodonta lauta* and *Hyriopsis schlegelii* has been estimated at 24 hours and 40 hours respectively (Kado, 1960). Obviously, equilibrium is more rapid in *Ampullarius*. In addition to the time for calcium equilibrium, an initial disturbance of growth probably resulted from changing solutions at the beginning of the experiment.

Exchange between the radioactive solution and empty shell was low and amounted to 0·81% of the mean deposition rate at the aperture as measured at 24 hours and 0·69% and 0·78% in areas B and C, respectively. Exchange *in vivo* may not be the same as in the case of empty shells because of differences in conditions at the crystal surfaces in the 2 situations. The extent of exchange in the living animal could be evaluated only if the composition of the extrapallial fluid in contact with the shell surface in the living animal were known, and this has not been studied.

Calcium deposition rate and shell size

The rate of calcium deposition (mg Ca/cm²/hr) decreased with increasing shell weight (Fig. 2). The decrease was marked as small animals grew to a medium size; and the change was less as the animals attained larger size. The total decrease in calcium deposition rate was some four-fold over the size range studied.

Although the rate of calcium deposition decreases as the animal becomes larger,

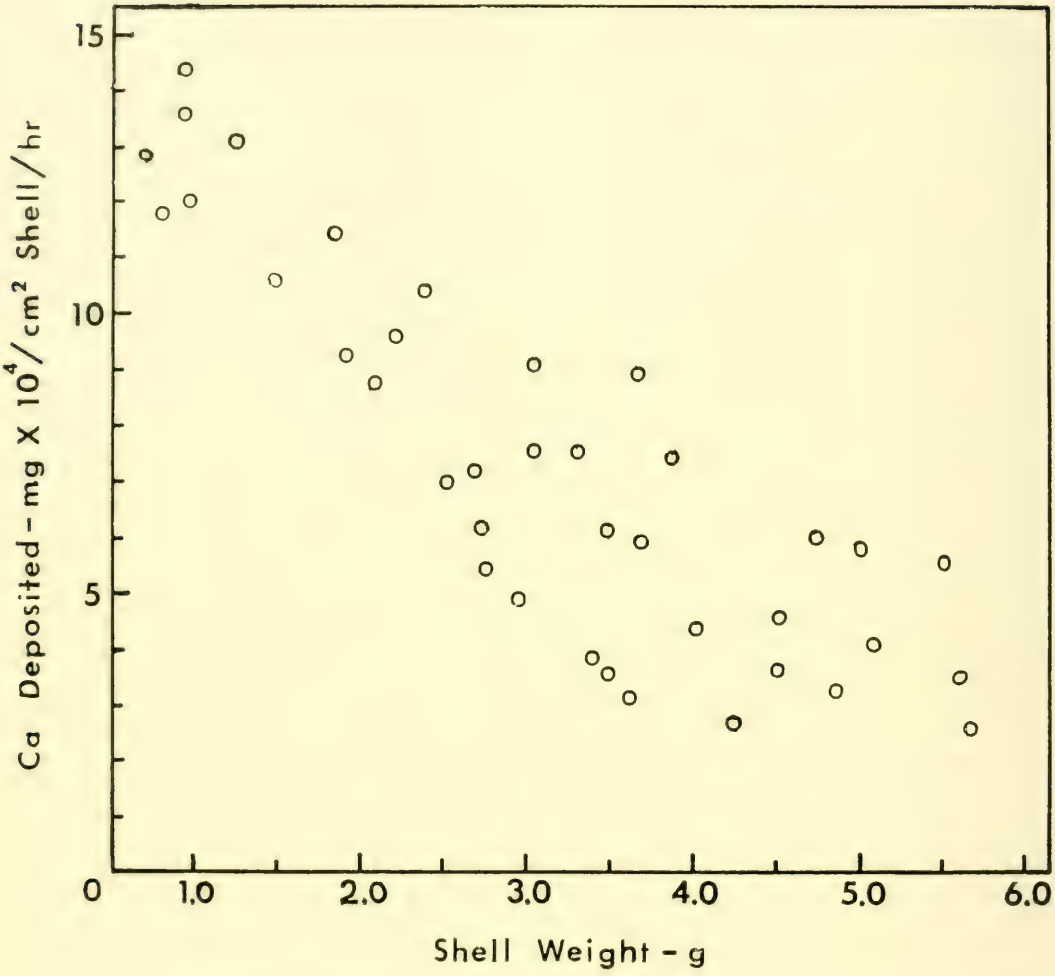


FIG. 2. Rates of calcium deposition as a function of shell weight in *Ampullarius glaucus*. Animals were exposed to Ca^{45} for 24 hours. Measurements were made adjacent to the outer edge of the aperture (area A, see Fig. 1, insert).

the thickness of the shell increases. This was shown by measuring shell thickness in 2 areas (Fig. 1, insert, A and C). Thickness increased linearly with shell length (Fig. 3). Older snails may form thickened ridges in the shell, as shown by the points falling well above the line. Linear increase in shell thickness with size was also found in another gastropod *Marisa cornuarietis* (Fig. 4). In this species, thickness was measured at 6 points along the whorls and plotted as a function of the diameter at the point of measurement (see Fig. 4, insert).

Calcium deposition in starved animals

The rate of calcium deposition was measured in specimens of *Ampullarius* maintained for various periods without food (Fig. 5). After 6 days, the mean

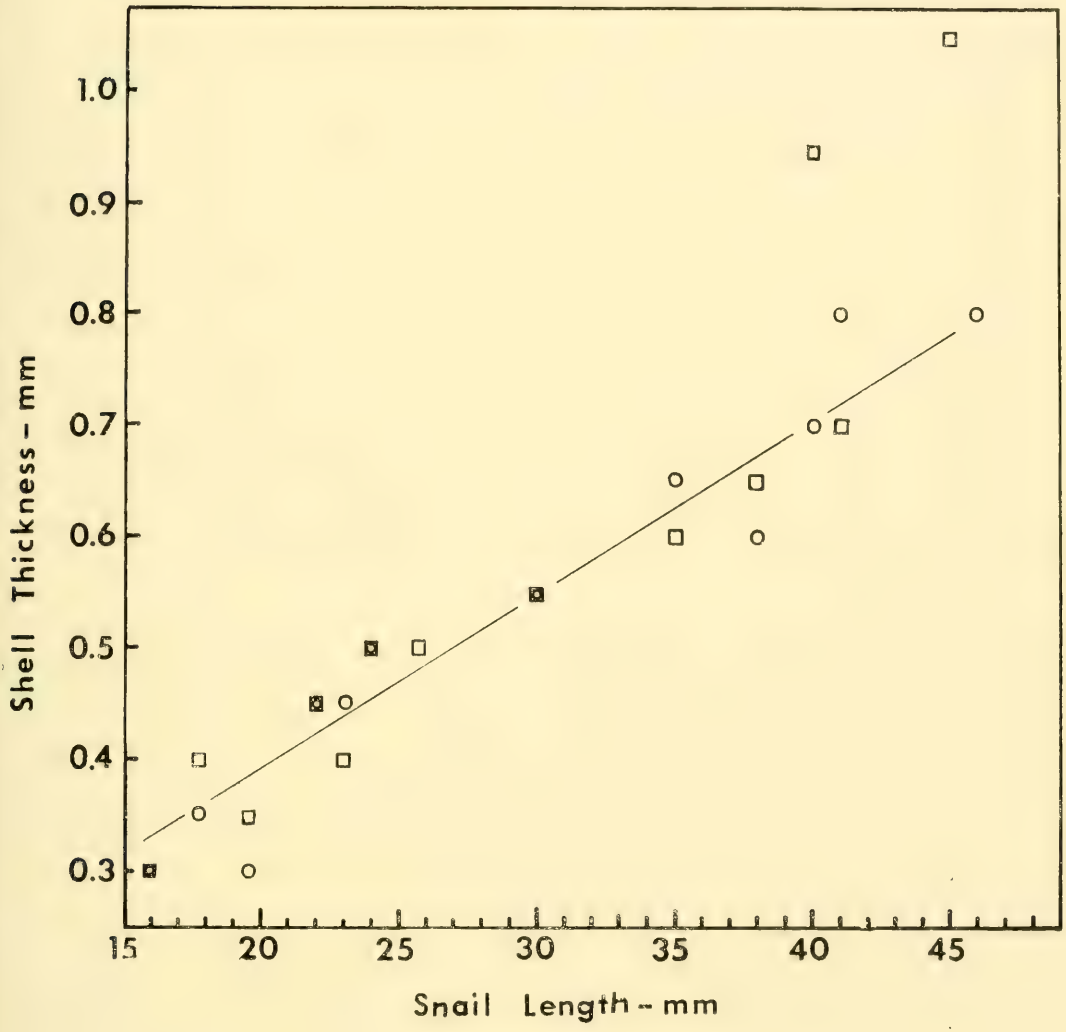
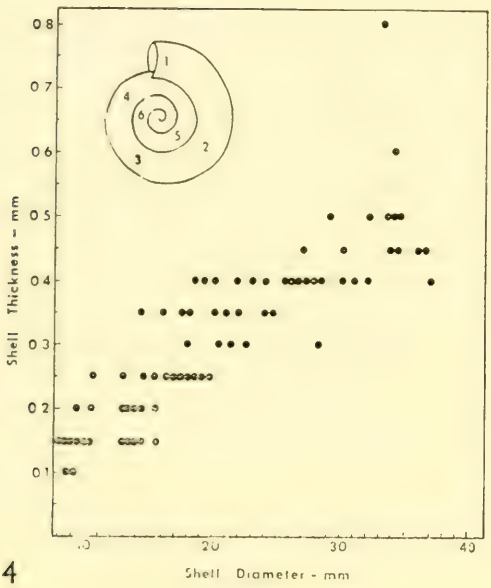


FIG. 3. Shell thickness as a function of shell length in *Ampullarius glaucus*. Length is the distance from tip of spire to base of body whorl. Squares represent the measurements at edge of aperture (area A, Fig. 1, insert); circles represent the measurement approximately midway around body whorl (area C). Line, drawn by inspection, shows the trend of majority of points.

decrease in calcium deposition rate was 10%. After 10 days starvation, the rate had decreased to 50% of that of feeding animals. A more rapid and more marked decrease in rate with starvation has been observed in the marine snail *Purpura patula* (Zischke, unpub.).

Calcium deposition in light and darkness

Measurements of rates of calcium deposition in the marine gastropod *Purpura* indicated decreased deposition in darkness (Zischke, unpub.). Comparable measurements have been carried out with *Ampul-*



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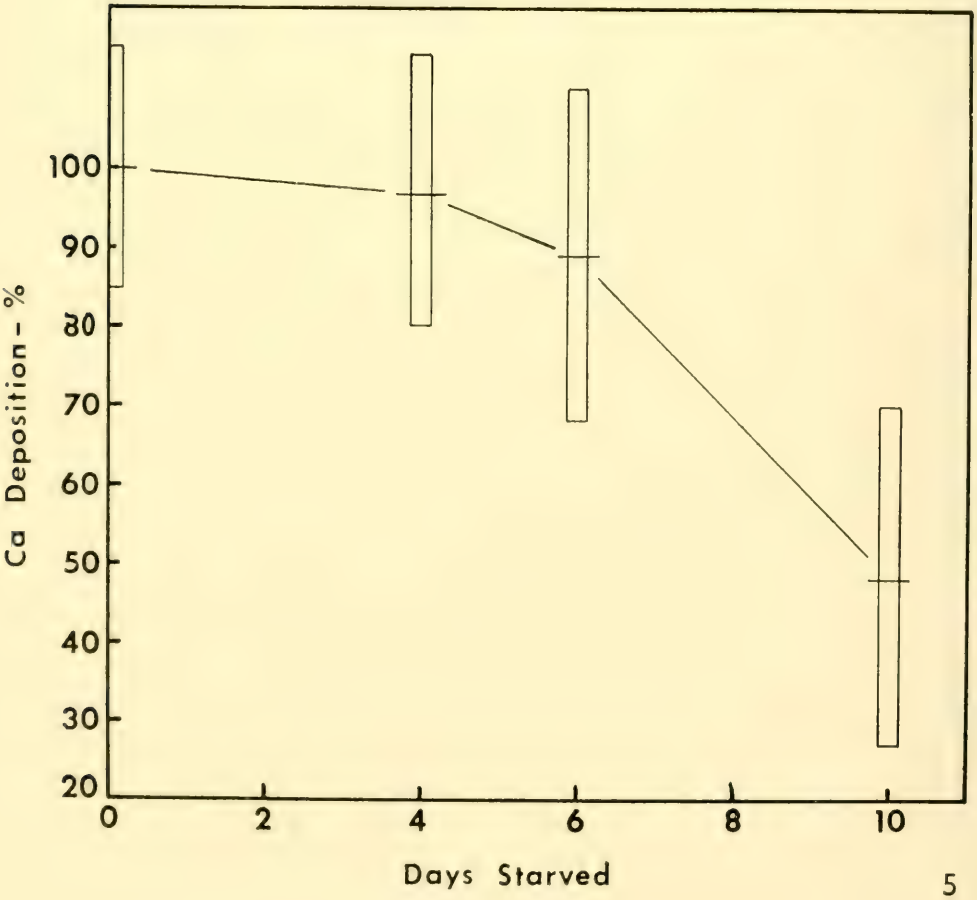
larius by measuring Ca^{45} deposition under constant illumination and darkness over a 24-hour period. The mean deposition rate in darkness was 82% that with illumination. Because of the spread of values for individual animals, this difference was not significant statistically ($P<0{\cdot}1$). The general form of the curve of deposition as a function of time in darkness resembled Fig. 1, A.

Linear growth

The experiments described to this point have related to shell growth as measured by calcium deposition per unit area. We now will consider shell growth in terms



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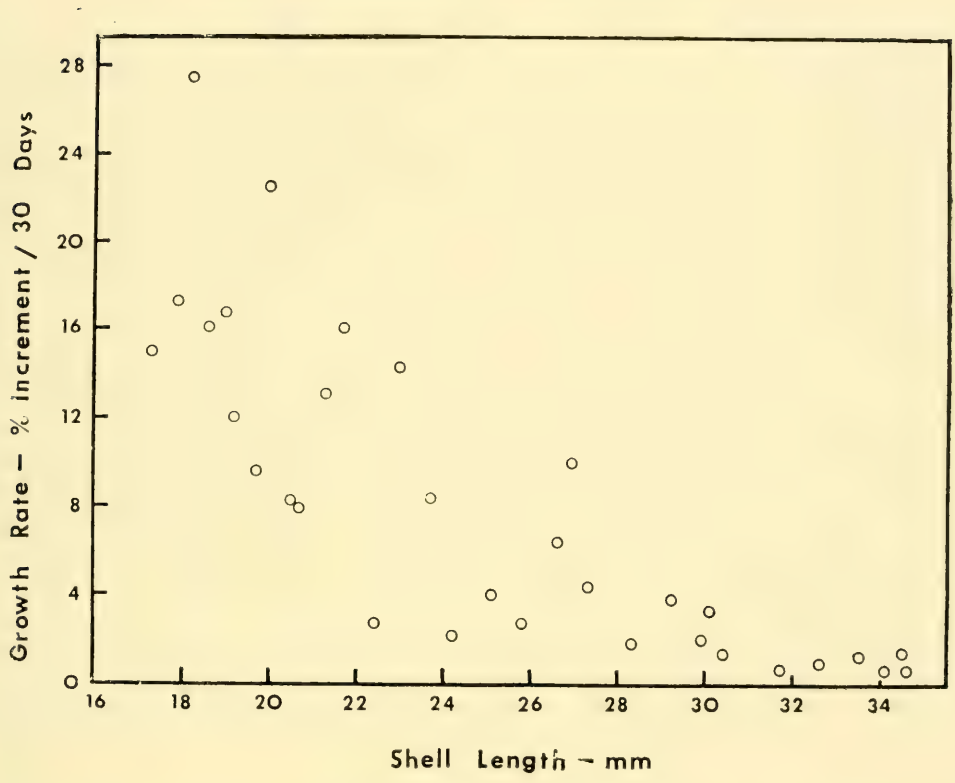


FIG. 6. Linear growth rate as a function of shell size. Linear growth of the shell at the aperture was measured in marked animals. Shell length was measured from the tip of the spire to the base of the body whorl.

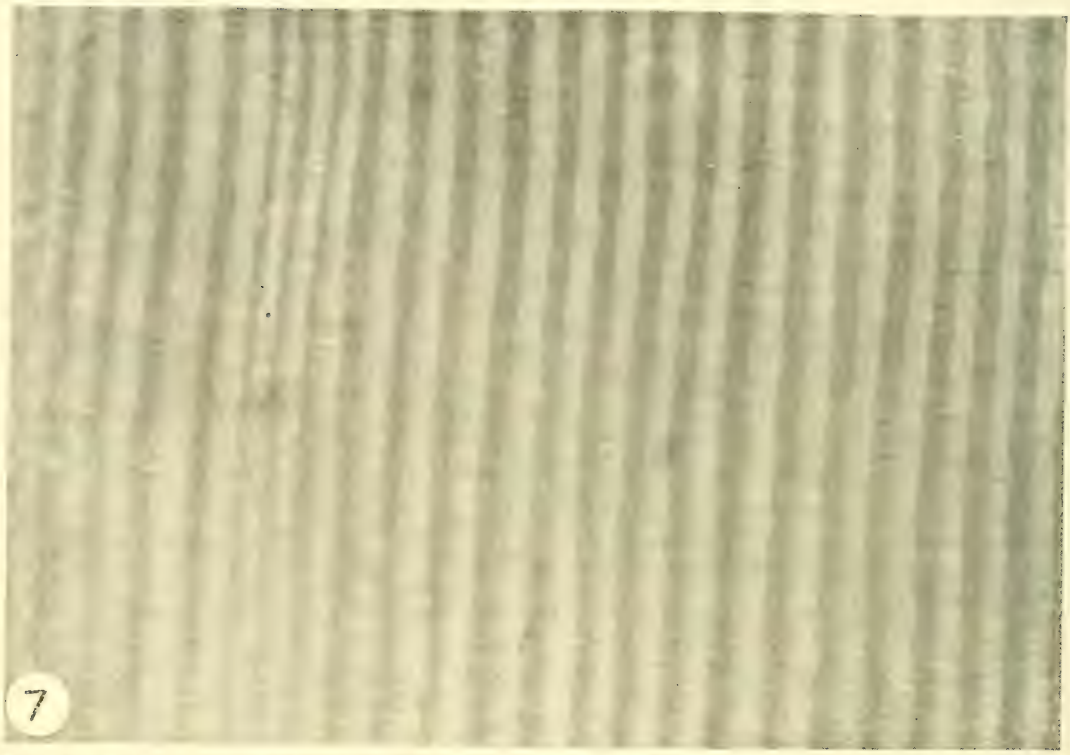
of linear increase.

Linear growth was measured in snails differing in size. The growth rate decreased with increasing size (Fig. 6). It will be seen that a snail 18 mm in length may grow 10 or 15 times more rapidly than one 35 mm in length. The variation in growth rate between individuals of similar size was considerable, as observed with calcium deposition.

Linear growth rate was also studied under 3 conditions of illumination: con-

FIG. 4. Shell thickness in *Marisa cornuarietis*. Thirteen snails having diameters between 31 and 37 mm were each cut in two along a mid-sagittal plane. Measurements were made to the nearest 0·5 mm at the 6 points indicated in the sketch and plotted as a function of the diameter at that point.

FIG. 5. Rate of calcium deposition during starvation. The rate is expressed as percentage of rate in feeding snails. Horizontal lines represent means, and vertical bars show standard deviations of the rates of calcium deposition in 15 snails 20–25 mm long (from tip of spire to base of body whorl). Animals were exposed to Ca^{45} for 16 hours.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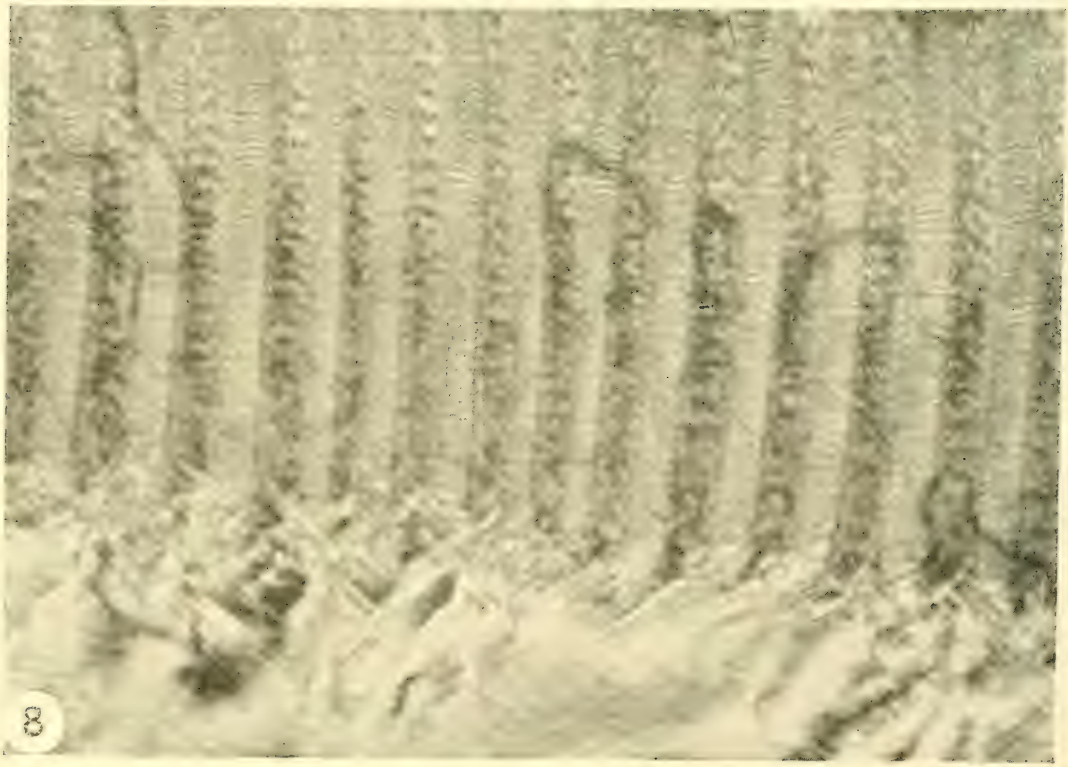
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TABLE 1. Linear growth in *Ampullarius glaucus* under different light conditions.

Exp.	I Conditions	II Duration	III Size Range (mm)	IV Mean Growth (mm)	V Probability	VI Double * Bands/mm	VII Food Consumed (gm)
1	24 hr. light	5 days	11·0—20·0	2·8±1·8		43·4± 7·3	0·39
					< 0·1		
	24 hr. dark	5	10·4—17·7	1·4±1·7		43·3± 3·8	0·27
					< 0·7		
	12 hr. light-12 hr. dark	5	12·0—19·3	1·9±1·5		41·4± 8·3	0·39
2	24 hr. light	6 days	11·1—20·0	1·3±0·9		43·3± 6·5	—
					< 0·01		
	24 hr. dark	6	11·0—19·0	0·5±0·7		34·2± 9·3	—
					< 0·1		
	12 hr. light-12 hr. dark	6	10·6—20·8	1·1±1·0		37·1±11·0	—

* Based on growing specimens

stant light, constant darkness, and a cycle of 12-hours light—12-hours darkness. The size range for the 3 groups was similar (Table 1, column III). The rate was reduced in darkness as compared with constant illumination (Table 1, column IV). The difference was statistically significant in 1 experiment and borderline in the other (column V). Whereas 7% of the snails failed to grow in constant light and with a light-dark cycle, 28% showed no growth in darkness. The mean food consumption was somewhat less in animals maintained in darkness (Table 1, column VII). The growth rate under the light-dark cycle was intermediate between that in constant light and constant darkness. The difference in rate between animals on the light-dark cycle and those in darkness was not

FIG. 7. Outer surface of a shell edge of *Ampullarius glaucus* showing light and dark bands. Photomicrograph. ×160.

FIG. 8. Ground section of a shell edge. The outer layer (vertical structure in the picture) has a cross lamellar structure composed of alternating bands of crystals differing in orientation. The bands correspond to those shown in Fig. 7 (see also Fig. 9). A portion of the second layer is seen at the bottom. Crossed nicols. Photomicrograph. ×500.


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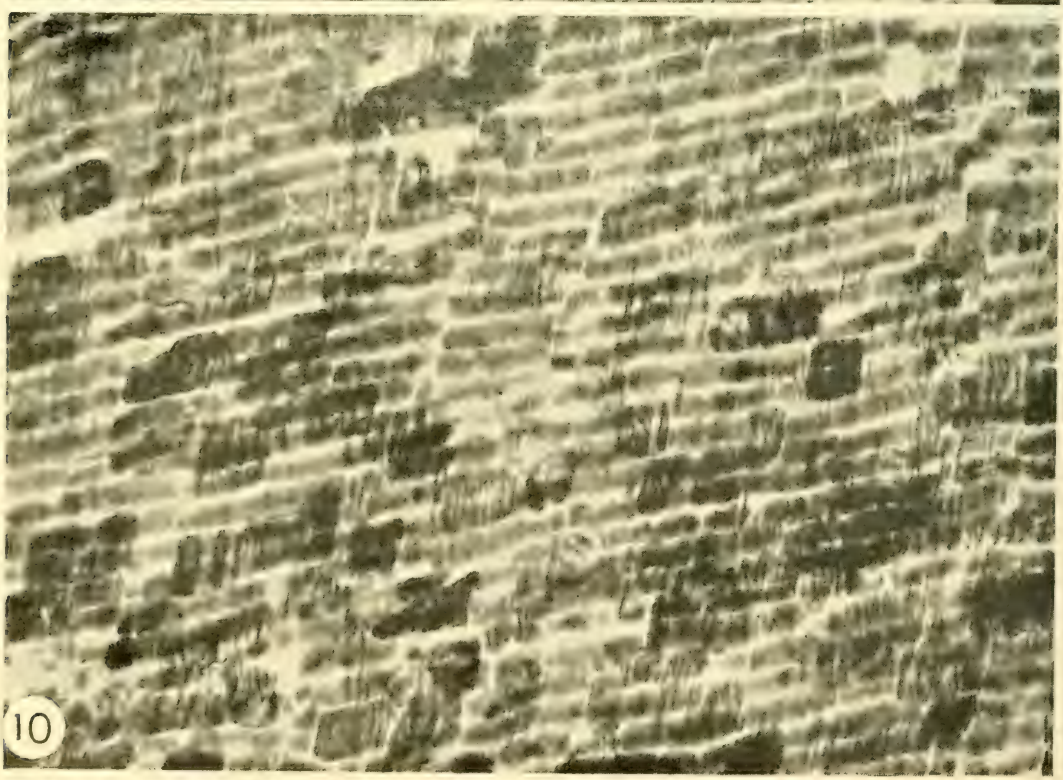
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statistically significant in one experiment and of border line significance in a second experiment (Table 1, column V).

Band formation

The shell surface at the growing edge is seen under the light microscope to be made up of alternating light and dark bands (Fig. 7). The width of the bands was similar throughout the body whorl and averaged about 12 microns, or about 40 double bands per mm, in snails of medium size. In animals less than 15 mm in length, the band width was less. The band width may remain constant with changes in linear growth (Table 1, Exp. 1, column VI) or it may be altered (Table 1, Exp. 2, column VI).

Ground sections and fracture surfaces showed an outer shell layer at the growing edge which was underlain proximally by a second layer (Fig. 8, bottom). The outer layer was composed of alternating bands of crystals differing in orientation (Fig. 8). The crystal bands correspond to the bands seen on the shell surface (Fig. 7). Fig. 9 shows 4 bands as seen in a fracture surface with the scanning electron microscope. In the 2 vertical bands, crystals made up of elongate units are shown. In the other bands, the fractured ends of similar crystals oriented differently and composed of smaller units are seen. Thin sections viewed in the transmission electron microscope show that the crystals consist of rows of crystallites 500 Å—600 Å thick (Fig. 10). A crystal band 12 microns in width would comprise more than 200 rows of small

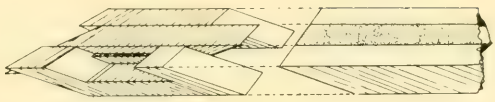

FIG. 11. Schematic drawing of the cross lamellar structure in *Ampullarius glaucus* showing 3 bands of crystals with alternating directions of orientation.

crystallites. The presence of organic matrix throughout the crystalline material was observed in decalcified sections. In summary, 3 orders of crystals are evident in the outer shell layer: large crystals which are the width of the band and arranged in cross-lamellar structure (Fig. 11); elongate units of which the large crystals are composed; and small crystallites arranged in rows. Since the crystals of alternate bands are oriented at a different angle, the difference in light refraction produces light and dark bands as seen in the light microscope.

The second shell layer is also cross-lamellar in structure. In contrast to the outer layer, the bands are tapered, giving an appearance of interdigitation. The structural details of this layer have not been studied.

DISCUSSION

Shell formation can be viewed in terms of 2 activities of the mantle: *linear growth*, which governs the increase in shell area, and *secretion*, which results in both mineral and organic shell deposition.

FIG. 9. Scanning electron micrograph of a vertical fracture surface of the outer layer. The 2 vertical bands are crystals made up of elongated units. In the horizontal structure, the fractured ends of crystals oriented differently are seen. ×3,500.

FIG. 10. Transmission electron micrograph of a thin section of the outer layer. The area corresponds to the horizontal structure seen in Fig. 9, and shows rows of crystallites 500 Å—600 Å thick. ×65,000.

Units of shell growth

Linear growth and the increase in shell area in *Ampullarius* are represented by bands composed of crystals. The bands can be considered growth units. Whether the mantle which forms the shell growth units also grows in units, we do not know. From the rate of linear growth and the number of bands formed per millimeter, one can calculate that a rapidly growing snail forms a band about every 40 minutes on the average. The actual time required to form the band may be less than this, of course. The thickness of the individual crystal layers is quite uniform, indicating a well controlled mechanism of deposition. The crystals have 2 orientations which alternate as successive bands are formed. The mechanisms which determine layer thickness and crystal orientation are largely unknown, although possible factors have been suggested (Wilbur & Simkiss, 1968; Bevelander & Nakahara, 1969).

Banding and cross lamellar structure similar to that in *Ampullarius* have been described by MacClintock (1967). However, the crystallites of 500 Å to 600 Å in width which make up the crystals in *Ampullarius* (Fig. 10) and in bivalves (Watabe, 1965) were not detectable by MacClintock and others who have studied cross lamellar structure with optical microscopes.

Shell thickness

The thickness of the shell in any region will depend upon the rate and period that inorganic ions and organic material pass from the mantle to the site of shell deposition. From the data on Ca^{45} deposition, it is clear that the deposition rate depends upon the mantle region and the size of the animal. Shell thickness, which increases as the animal becomes larger, will also depend upon a third factor—the rate of linear mantle growth. Each of these factors will now be considered briefly. In our discussion it will be convenient to imagine the spiral shell stretched to a straight tube whose wall thickness increases as it increases in length and diameter.

The rate of calcium deposition was highest near the aperture and decreased progressively centrally. For shell of medium size, the difference in deposition rate within the body whorl was more than 100-fold. Because of an extremely low deposition rate in the older shell regions, the shell does not become markedly thickened, even though the time factor would favor increase in thickness.

The rate of calcium deposition was found to decrease with increasing size, the decrease being 4 or 5-fold over the size range examined. While the quantitative relation between size and age is not known, older individuals certainly deposit calcium less efficiently than younger animals (see also Wilbur & Owen, 1964).

As the shell grows forward, each shell region becomes displaced centrally relative to the more recently formed portions. As an animal becomes larger, any given shell region will increase in thickness at a decreasing rate both from the regional effect and the age effect.

The relation between shell thickness and linear mantle growth rate can be illustrated in terms of the mantle periphery, which is the part most active in deposition. As the mantle grows forward, the total amount of calcium deposited will obviously depend in part upon the length of time that the mantle periphery covers a particular shell region. If the mantle grows forward rapidly, there will be less shell thickening at any given deposition rate than with slow forward growth. Now linear growth becomes slower as the size of the animal increases (Fig. 6), favoring an increased thickness

of shell in the aperture region. The thick ridges seen in some shells, particularly in large specimens, may indicate that the ratio of shell deposition to mantle growth rate was temporarily increased in those shell areas.

In summary:

1. The decrease in calcium deposition rate with increasing size will favor a decreased shell thickness toward the aperture.
2. The decreased linear mantle growth rate with increasing size will favor an increased shell thickness toward the aperture.

The effect of these factors acting together and integrated over the age of each shell region is to increase shell thickness as the animal becomes larger. In other species the resultant of the 2 factors may be different, as in some bivalves in which shell thickness remains essentially uniform with increasing size.

Starvation

Starvation reduced the calcium deposition rate. A possible cause may be a less active movement of calcium into the animal and through the mantle to the site of deposition. We cannot say whether a deficiency of organic material secreted by mantle occurs and also reduces the deposition of calcium carbonate. The effects of starvation on calcium movement and secretions of organic material could be determined using Ca^{45} and labelled compounds, respectively.

Light and linear growth

Linear growth was reduced in darkness as compared with continuous illumination. The effect was clearcut in 1 experiment and of borderline statistical significance in another (Table 1). R. Kenny (per. comm.) observed that shell growth in the limpet *Acmaea* was essentially stopped in the absence of light. The somewhat decreased food consumption in *Ampullarius* in darkness does not appear a probable explanation.

The inhibitory effect of darkness on linear growth appeared to be greater than on calcium deposition. Since the linear growth measurements were carried out over 5–6 days and calcium deposition over 1 day, a strict comparison cannot be made.

ACKNOWLEDGEMENTS

We thank Mr. Freddy Losada and Miss Julia K. Hiott for technical assistance, Mr. Rafael Martinez for aid in collecting specimens and Dr. Mary E. Rice and Dr. William Banta for preparing thin sections of shells. Dr. Ernesto Medina kindly furnished counting equipment. We are grateful to the Engis Equipment Company, Morton Grove, Illinois for the use of the Stereoscan Scanning Electron Microscope and to Miss Donna Letzring for taking photographs with this instrument.

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RÉSUMÉ

ÉTUDES SUR LA FORMATION DE LA COQUILLE: MESURE DE LA CROISSANCE CHEZ LE GASTROPODE *AMPULLARIUS GLAUCUS*

J. A. Zischke, N. Watabe F. Losada et K. M. Wilbur

Le dépôt de calcium dans divers endroits de la coquille d'*Ampullarius glaucus* a été mesuré sur des périodes de 4 à 24 heures, par utilisation du Ca^{45}. Le taux de dépôt de calcium est le plus élevé près de l'ouverture de la coquille (7×10^{-4} mg/cm²/h) et décroît progressivement et notablement depuis l'ouverture jusqu'aux tours de spires. Le taux de dépôt de calcium décroît quand le poids de la coquille augmente. La relation entre le taux de croissance linéaire du manteau et le taux de dépôt de calcium par différents secteurs du manteau a pour résultat une augmentation de l'épaisseur de la coquille à mesure que les tours de spire se développent. Aprés 10 jours sans nourriture, le taux moyen de dépôt de calcium décroît de 50%. Dans l'obscurité, la croissance linéaire moyenne est réduite brusquement, tandis que la réduction du taux de dépôt de calcium n'est pas significative.

La coquille a une structure transversale lamellaire dans laquelle les cristaux sont constitués de cristallites de 500 Å à 600 Å d'épaisseur. Chez les mollusques à croissance rapide, il peut y avoir dépôt de 36 couches par jour.

A. L.

RESUMEN

ESTUDIOS SOBRE LA FORMACION DE LA CONCHA: MEDIDAS DE CRECIMIENTO EN EL GASTROPODO *AMPULLARIUS GLAUCUS*

J. A. Zischke, N. Watabe y K. M. Wilbur

La deposición de calcio en varias regiones de la concha de *Ampullarius glaucus* fue medida durante períodos de 4 a 24 horas usando Ca^{45}. La tasa de deposición de calcio fue mayor cerca de la abertura (7×10^{-4} mg/cm²/hr), decreciendo muy marcada y progresivamente a medida que en una determinada región de una espira del cuerpo, aumenta la distancia de la abertura. También hubo disminución de esta tasa en relación con el aumento del peso de la concha. La relación entre la tasa de crecimiento linear del manto y la tasa de deposición de calcio para diferentes areas del manto resulta en un engrosamiento de la concha a medida que la espira se desarrolla. Despues de 10 días sin alimento, la tasa de deposición de calcio decreció, en promedio, en un 50%. En la obscuridad, el crecimiento linear promedio se redujo marcadamente, mientras que no hubo disminución significativa en la tasa de deposición de calcio.

La concha tiene una estructura laminar cruzada en la cual los cristales están formados de cristales muy pequeños con un grosor de 500 Å—600 Å. En caracoles que crecen rápidamente pueden depositarse 36 capas por día.

F. LOSADA

АБСТРАКТ

ИССЛЕДОВАНИЕ ОБРАЗОВАНИЯ РАКОВИНЫ: ИЗМЕРЕНИЕ РОСТА РАКОВИНЫ *AMPULLARIUS GLAUCUS* (GASTROPODA)

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Измерялось отложение кальция в различных частях раковины *Ampullarius glaucus*; измерения длились в течение 4-24 часов с помощью Ca^{45}. Скорость отложения кальция была наибольшей в области устья раковины ($7x10^{-4}$мг/см^2/час), заметно и постепенно уменьшаясь по мере увеличения расстояния от устья раковины к ее завиткам. Скорость отложения кальция уменьшается по мере увеличения веса раковины. Соотношение между линейной скоростью роста мантии и скоростью отложения кальция различными участками мантии выражается в увеличении толщины раковины по мере развития ее оборотов. При отсутствии пищи в течение 10 дней, средняя величина отложения кальция падает на 50%. В темноте средний линейный прирост раковины резко уменьшается, в то время как редукция скорости отложения кальция незначительна.

Раковина имеет поперечно-пластинчатую структуру, в которой кристаллы состоят из кристалликов 500-600Å толщиной. У быстро растущих моллюсков в раковине ежедневно могут образовываться 36 слоев.

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THE FUNCTION OF THE ODOUR OF THE GARLIC SNAIL *OXYCHILUS ALLIARIUS* (PULMONATA: ZONITIDAE)

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ABSTRACT

The pungent garlic odour of *Oxychilus alliarius* has been investigated. It had been presumed by previous authors to be a defensive adaptation. The possibilities of a sex attractant or antibiotic have been shown to be very unlikely. An experiment with hedgehogs as predators showed that the garlic snail was statistically significantly rejected, the 3 other British species of *Oxychilus* being favoured.

INTRODUCTION

The garlic snail *Oxychilus alliarius* (Miller) is characterised, as its name suggests, by the production of a pungent odour indistinguishable from that of garlic. This feature has been noted many times by naturalists; for example Macgillivray (1843) states that the odour from a very small specimen is so strong that it may be noted from a distance of several feet. The snail emits the odour on irritation throughout the year. There appears to be no particular season for its production, nor any time of increased pungency. The odour is even produced in newly hatched animals.

Some authors (Step, 1945; Rimmer, 1880; Taylor, 1914) state that the possession of a garlic odour is not characteristic of *O. alliarius*, but is also found in related species. It is possible that this is a result of misidentification, as there has been considerable confusion in the identification and taxonomy of these very similar snails. Recent authors (Janus, 1965; Frömming, 1954) attribute the garlic odour only to *O. alliarius* and I am in complete agreement with this.

Garlic odour is recorded from 1 other group in the Animal Kingdom. Perkins (1919) notes that 3 species of solitary bees produce such an odour, but no work appears to have been done on it. Much work has in contrast been performed on the various odours and extracts from the genus *Allium*, especially those from garlic and onion. These plants have well documented antibiotic properties which are linked, in part, to volatile tissue components (Hatfield, Walker & Owen, 1948).

Fischer (1948) has suggested that the slime from some snails is antiseptic, and Campion (1961) performed experiments to see whether this is so in *Helix aspersa*. She obtained clearly negative results. An antibiotic has been shown to be secreted by the stomach and salivary glands of *O. cellarius* by Tercafs (1960), working with a cavernicolus population which catches and preys upon Lepidoptera.

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The function of the antibiotic here is to prevent fungal and bacterial decomposition of half-eaten prey.

In this laboratory it was noted that the appearance of the odour was coincidental with the production of a characteristic viscous, brown mucus from the mantle region. On separation from the snail this mucus continued to emit the garlic odour for several hours. Step (1945) concluded that the odour of *Oxychilus alliarius* is most probably a defensive secretion as it is only produced on irritation of the snail. Urbanski (1937) suggests that it may well be a defense mechanism against the predatory *O. draparnaldi*, although Frömming (1954) criticises this, saying that *O. draparnaldi* does not prey on *O. alliarius* but rather on *O. cellarius*. Taylor (1914) notes that *O. alliarius* is the only mollusc to be found alive in the vicinity of wood ants' nests.

Peculiar odours and distasteful secretions are found in many species of molluscs. Kjerschow-Agersborg (1921) has described the odour of *Melibe leonina* as being like that of oil of bergamont and he presumed it to have a defensive function. André (1900) noted that the North African snail *Hyalinia* (=*Oxychilus*) *cheliella*, produced a very strong characteristic odour on irritation. He likened it to the odour of the caterpillar of *Cossus ligniperda*. Thompson (1959, 1960a, b) has shown that the acidic defensive secretions of a number of marine opisthobranchs cause them to be distasteful to fish, and Edmunds (1968) has described similar secretions in several species of Doridacea. Binot (1965) has worked on the histology and histochemistry of repugnatory glands in *Oncidiella celtica*, and Renault (1966) has described a defensive gland in the mantle of *Cassidula labrella*. Experiments to determine the possible sex-attractant, antibiotic or defensive function of the odour of *Oxychilus alliarius* are described in the present paper.

MATERIALS AND METHODS

Sex Attraction

A semi-circular, air-tight, wooden box (90×45×6 cm) with a glass lid was lined with moist filter paper. Air was extracted from the centre of the base of the box by a vacuum pump. Air was allowed to enter at 5 points on the circumference (Fig. 1). The sucked-in air first had to pass through the small chambers (*a*) before entering the main box (*b*). In 1 of these chambers, chosen at random, 10 stimulated snails were placed so that the draught picked up the garlic odour. In the main body of the box were placed 100 snails, and the air current was maintained for 5–6 hours. The experiment was repeated several times, each with fresh snails, in both daylight and total darkness. The air current was also varied by altering the strength of the vacuum pump.

Antibiotic

Experiments with mucus were performed similar to those described by Campion (1961) on *Helix aspersa*.

Mucus was taken from *O. alliarius* and also from *O. cellarius*. The latter does not produce a garlic odour and was used as a control. Sterile Petri dishes of nutrient agar (Oxoid) were streaked with slime as follows: (a) *O. alliarius* mucus; (b) *O. cellarius* mucus; (c) Mucus from both species.

An identical series was streaked and then innoculated with *Neurospora*, and finally a third series was streaked onto plates already carpeted with *Neurospora*. All plates were incubated at 28° C for 3–4 days.

Defense

A laboratory experiment was performed to ascertain whether hedgehogs (*Erinaceus europaeus*), when feeding, exhibited any

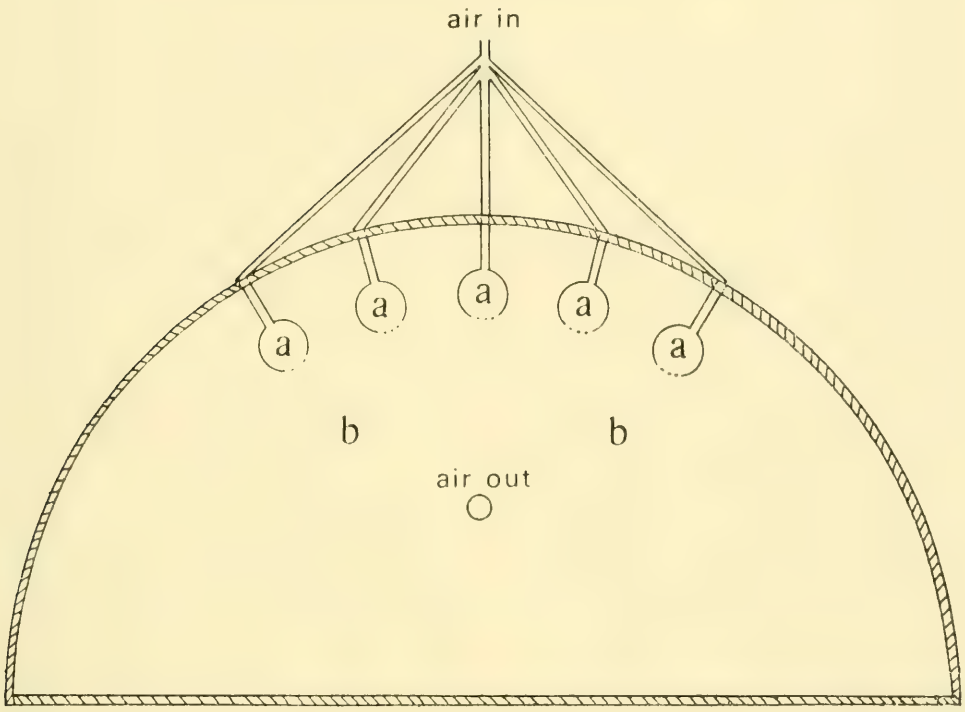

FIG. 1. Apparatus to test for the possible attractive function of the garlic odour. a=small chambers; b=main box.

discrimination between the 4 British *Oxychilus* species.

An enclosure of approximately 30 sq. feet was erected in the laboratory and on the floor were fixed 16 plastic Petri dishes arranged in 4 rows of 4. One snail was placed in each dish, 4 specimens of each species being used in each test. To overcome the possibility that the hedgehogs might learn the distribution of the snail species, the positions of the various species were frequently altered during the course of the experiment. In order to randomise the snails' distributions the 4 rows of 4 latin square patterns of Fisher & Yates (1953) were adopted.

The observations, 15 in all, were carried out on 4 successive nights, using 3 hedgehogs which had been previously exercised for 2–3 hours. The feeding hedgehogs were filmed by time lapse ciné-photography. By using a wide aperture it was possible to photograph with flashlights at half-strength. It soon became apparent that the flashes did not affect the hedgehogs; they continued walking and eating uninterrupted. The photographs were taken at 15 second intervals over a period of 15 minutes. At the end of the experiment the remaining snails were noted. The developed film was viewed through a microscope and the positions of the hedgehogs every 15 seconds was noted.

RESULTS

Sex Attraction

The positions of the 100 unstimulated snails at the end of each run was noted. It was found that on each occasion they were randomly distributed all over the

TABLE 1. This shows the number of visits by a hedgehog to each species of snail as observed on film, the number of snails eaten during the experiment, and calculated from these data the number of snails taken per visit, and the square of this number.

	O. alliarius				*O. helveticus*				*O. cellarius*				*O. draparnaldi*			
Test No.	No. of Visits	Nos. Taken	Nos. Taken per Visit	Square	No. of* Visits	Nos. Taken	Nos. Taken per Visit	Square	No. of Visits	Nos. Taken	Nos. Taken per Visit	Square	No. of Visits	Nos. Taken	Nos. Taken per Visit	Square
1	2	2	1	1	7	4	0·571	0·326	4	4	1	1	6	4	0·667	0·445
2	7	3	0·429	0·184	3*	4	1·333	1·777	2*	4	2	4	5	3	0·6	0·36
3	2	2	1	1	2*	4	2	4	3*	4	1·333	1·777	2*	3	1·5	2·25
4	1	1	1	1	2	2	1	1	6	2	0·333	0·111	6	3	0·5	0·25
5	2	0	—	—	6	4	0·667	0·445	3	2	0·667	0·445	6	3	0·5	0·25
6	3	1	0·333	0·111	4	4	1	1	6	4	0·667	0·445	4	4	1	1
7	3	1	0·333	0·111	4	4	1	1	3	3	1	1	5	4	0·8	0·64
8	1	1	1	1	2	2	1	1	2	2	1	1	3	2	0·667	0·445
9	4	1	0·25	0·062	4	3	0·75	0·562	2	2	1	1	7	2	0·286	0·082
10	0	0	—	—	3	3	1	1	1	1	1	1	1	0	—	—
11	1	0	—	—	3	2	0·667	0·445	1	1	1	1	4	2	0·5	0·25
12	7	2	0·286	0·082	6	4	0·667	0·445	4	3	0·75	0·562	5	3	0·6	0·36
13	9	1	0·111	0·012	7	4	0·571	0·326	5	1	0·2	0·04	7	4	0·571	0·326
14	6	1	0·167	0·028	10	4	0·4	0·16	7	3	0·429	0·184	4	3	0·75	0·562
15	6	0	—	—	9	2	0·222	0·049	5	3	0·6	0·36	7	3	0·429	0·184
Totals	54	16	5·909	4·59	72	50	12·85	13·54	54	39	12·98	13·92	72	43	9·37	7·404

Mean number taken per visit:

$\frac{16}{54}=0\cdot296$ $\frac{50}{72}=0\cdot694$ $\frac{39}{54}=0\cdot722$ $\frac{43}{72}=0\cdot597$

* "No. of visits" refers to the number recorded by 15-second, time-lapse photography. Some visits to Petri dishes were missed, but the error so introduced is considered to be insignificant in view of the duplication (15 %) of the experiments.

TABLE 2. Statistical analysis of the number of snails taken by hedgehogs.

	O. alliarius	*O. helveticus*	*O. cellarius*	*O. draparnaldi*	Total
Observed	16	50	39	43	148
Expected (total/4)	37	37	37	37	148
O—E	—21	13	2	6	—
$(O—E)^2$	441	169	4	36	—
$\frac{(O—E)^2}{E}$	11·92	4·57	0·108	0·973	17·571

moistened floor of the box. Some appeared to have moved only about 5 cm or less, whilst others had wandered to the circumference of the box. However, no obvious migration towards the source of odour was observed.

Antibiotic

In all cases a negative result was obtained, and no distinction could be observed between the effects of the slime from the 2 species. In the first set of plates bacterial colonies developed, presumably derived from the bacteria already present in the snails' slime. In the second and third series no inhibition of germination or of growth of the fungus was observed.

Defense

It was first decided to perform a simple X^2 test on the total of each species taken during the entire experiment (Table 1). The null hypothesis assumed was that there was no difference in the predation on the 4 snail species. The results of this analysis are shown in Table 2.

In the tables of the distribution of X^2 (Fisher & Yates, 1953) with 3 degrees of freedom $X^2=16.266$ at a probability of $p=0.001$. In the above experiment the calculated $X^2=17.571$. This means that if all the species were equally preferred (null hypothesis) one could expect such a large deviation of the observed from the expected in less than 0.1% of cases. Therefore there is quite clearly a significant difference between the 4 species, and the greatest contribution (11.92) to this comes from *O. alliarius*.

A " t " test was then performed on the numbers taken per visit for each species.

Comparing pairs of species:

alliarius with *helveticus* " t "=11.09
alliarius with *cellarius* " t "= 9.45
alliarius with *draparnaldi* " t "= 5.17
cellarius with *helveticus* " t "= 1.06
helveticus with *draparnaldi* " t "= 1.42
cellarius with *draparnaldi* " t "= 1.70

In the tables of the distribution of " t " (Fisher & Yates, 1953) with 28 degrees of freedom (2n-2), " t "=3.674 at a probability of $p=0.001$. In the comparisons between the non-odourous species the calculated " t " is less than the tabular " t ", whilst comparing the garlic snail with the others in each case the calculated " t " exceeds the tabular " t ". Therefore at the 0.1% level there is no significant difference between the means of the non-odourous species, whilst the mean value obtained for *O. alliarius* differs significantly from the others and this difference

cannot be accounted for by random chance. The conclusion is that there is a definite rejection of *O. alliarius* in favour of the other species.

DISCUSSION

Odourous pheromones are sometimes used in the Animal Kingdom as a means of sexual attraction. Thus it was necessary to perform an experiment to see whether this might be the function of the garlic snail odour. There is no clearly defined breeding season in this snail. Rigby (1963) states that the breeding time in *O. cellarius* is from January to August, and whilst no record has been found in the literature, personal observation in the field indicates a similar duration in the case of *O. alliarius*. These experiments were performed in the early springtime.

The results tend to disprove an attractant function for the garlic odour, although they do not rule out an aphrodisiac function acting when the snails are in contact. There are a number of reasons why both of these possibilities are unlikely. Firstly, the odour is produced all the year round, and there appears to be no correlation with any breeding cycle. The odour is only emitted on irritation of the snail, and whilst this would not rule out contact attraction, it would certainly argue against attraction from a distance. Finally the odour is produced even by the very newly hatched snails well before they have reached sexual maturity.

The negative results for the antibiotic experiment confirm those obtained by Campion (1961) for *Helix aspersa*. Campion in fact obtained increased growth of microorganisms on and around the slime. She suggested 3 possible explanations; the stickiness of the mucus retained spores settling on it, or the mucus offered extra nutrients to the microorganisms, or thirdly there was the possibility of growth-promoting substances in the mucus.

The general conclusions that may be drawn from the preceding experiments are that the odour does not seem to be a sex attractant, nor is it concerned with antibiotic activity, but that it seems most probably to be a defensive adaptation. This confirms the subjective opinions of several previous authors (Taylor, 1914; Urbanski, 1937; Step, 1945).

The predators of terrestrial snails such as the oxychilids are quite numerous. The major predators are probably other molluscs, various insects, such as glow worm larvae and carabid beetles, birds and small mammals.

When the possible defensive function of the garlic snails' odour was considered it seemed that small mammals would be the best subjects for experiment. They are predators which hunt, partly at least, by sense of smell. Hedgehogs were chosen as experimental subjects, chiefly because they are probably the easiest of the available small mammals to keep in captivity, and most amenable to the rigours of laboratory experiments.

Dimelow (1963a, b) has described the best way to keep hedgehogs in captivity, and has also determined their food preferences within a large range of common invertebrates. She found that whilst they ate most of the animals which she offered, they consistently selected some species. Dimelow (1963b) and previous workers (Brockie, 1959, Rothschild, 1961) have shown that hedgehogs are affected considerably by odours emitted by their prey. The odours either repel the hedgehogs, as in the case of the ladybird, *Adalia*, (Rothschild, 1961), or aid the hedgehog in finding prey such as certain millipedes (Brockie, 1959). Brockie even found that hedgehogs persistently nosed leaves which had been partly eaten by odourous millipedes since removed. With molluscs Dimelow (1963b) found that copious slime

did not deter hedgehogs from readily eating the slugs *Milax budapestensis* and *Arion hortensis*. They tended to reject *Arion ater*, *A. fasciatus* and *A. subfuscus*, a possible deterrent here being the tough skin, and the thick-shelled snails *Helix* sp., *Cepaea* sp., *Discus rotundatus*, *Pomatias elegans* and *Hygromia striolata*. With oxychilids Dimelow (1963b) found that *O. draparnaldi* was most strongly preferred, although she notes that *O. alliarius* was also taken despite its garlic odour.

In the filmed tests with hedgehogs, *Oxychilus alliarius* was also taken, but the statistical analysis shows that it was the least favoured. The " t " tests, however, show no significant difference between the remaining 3 species. Dimelow (1963b) mentions that the relative sizes of the prey may play a part in determining the hedgehogs' preference. This was allowed for in the present experiment by using half-grown specimens of the non-odourous species which were more or less equal in size to the adult garlic snails.

This experiment was limited in that hedgehogs were the only snail predators used. Most certainly there are many more common predators of oxychilids, and it is expected that experiments with some of these would confirm the defensive advantage of *Oxychilus alliarius* odour. Previous authors have remarked upon the degree of immunity from attack which *O. alliarius* seems to possess against certain predators, e.g., wood ants (Taylor, 1914), and *O. draparnaldi* (Urbanski, 1937, Frömming, 1954). Experiments with these 2 predators would be a useful extension of the hedgehog experiment.

Unfortunately very little is known of the general ecology of oxychilids. Often one finds within a local woodland a small area dominated by just 1 or 2 of the species, whilst other species dominate adjacent areas. Alternatively one may find all 4 species in seemingly equal numbers within the same area, even under the same stone or log. This creates an anomalous situation when the marked defensive advantage which *Oxychilus alliarius* seems to possess over the other species in laboratory experiments is considered.

The predator/prey relationships are obviously very complex, and an ecological investigation of them would be of considerable value.

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RÉSUMÉ

LA FONCTION DE L'ODEUR D'AIL DU GASTROPODE *OXYCHILUS ALLIARIUS* (MILLER) (PULMONATA: ZONITIDAE)

D. C. Lloyd

La violente odeur d'ail de l'*Oxychilus alliarius* a été analysée. Des auteurs précédents avaient présumé de son adaptation à la défense. On a montré qu'il n'était pas possible de la considérer comme ayant un rôle d'attirance sexuelle ou d'antibiotique. Une expérience avec des hérissons comme prédateurs a montré que les mollusques à odeur d'ail étaient statistiquement significativement rejetés; les trois autres espéces britanniques d'*Oxychilus* étant préférées.

A. L.

RESUMEN

LA FUNCION ODORIFERA EN EL CARACOL DE AJO *OXYCHILLUS ALLIARIUS* (MULLER) (PULMONATA: ZONITIDAE)

D. C. Lloyd

El pungente olor a ajo de *Oxychillus alliarius*, había sido indicado por previos autores como una adaptación defensiva. La investigación demuestra que las posibilidades de que sea un atractivo sexual o antibiotico son muy remotas. Experimentos hechos con él predator puercoespín resultaron en el rechazo, estadisticamente significante, de los caracoles; otras especies britanicas de *Oxychillus* fueron acceptadas por el animal.

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АБСТРАКТ

ФУНКЦИЯ ЗАПАХА У ЧЕСНОЧНОЙ УЛИТКИ *OXYCHILUS ALLIARIUS* (MILLER), (PULMONATA: ZONITIDAE)

Д. К. ЛЛОЙД

Был исследован острый чесночный запах у улитки *Oxychilus alliarius*. Работы ряда прежних авторов показали, что этот запах представляет собой защитную адаптацию моллюска. Возможность привлечения моллюсков другого пола или наличие антибиотиков кажутся маловероятными. Эксперименты с ежами, как хищниками, статистически показали, что чесночные улитки ими обычно отбрасываются, три же других вида *Oxychilus* предпочитаются.

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THE COMPOSITION OF THE ODOUR OF THE GARLIC SNAIL *OXYCHILUS ALLIARIUS* (PULMONATA: ZONITIDAE)

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ABSTRACT

Direct injection into a gas liquid chromatograph shows that the principal volatile compound produced by *Oxychilus alliarius* (Miller), on irritation, is n-propyl mercaptan. This is probably responsible for the pungent garlic-like odour peculiar to this species.

INTRODUCTION

The garlic-like odour produced by *Oxychilus alliarius* when it is irritated is a marked feature of this snail. It has been shown that it is a defense mechanism (Lloyd, 1970), and originates from a small group of cells in the mantle close to the pneumostome.

The obvious point at which to begin an attempt at identifying a garlic-like odour is to look at what causes the odour of the garlic and onion plants. The chemistry of the odourous compounds from *Allium* spp. has been studied in considerable detail (Jones & Mann, 1963). Garlic, *Allium sativum*, contains an odourless water soluble amino acid called alliin which is acted upon, on injury, by the enzyme allinase to yield allicin, the characteristic, sulphur containing, antibacterial, odourous compound of freshly crushed garlic tissue. This is however unstable and breaks down to yield the odourous constituents of garlic oil. Whilst garlic oil contains mainly allyl sulphur compounds, onion oil, *Allium cepa*, yields methyl and propyl compounds, and this probably explains the difference in aroma and flavour between garlic and onion.

Semmler (1892) reported that onion oil consisted mainly of allyl-n-propyl disulphide, and this finding was accepted for many years. In 1949 Challenger & Greenwood demonstrated n-propyl mercaptan, and Niegisch & Stahl (1956) using mass spectrometry also identified n-propyl mercaptan and a trace of n-propyl disulphide. No allylic disulphides were demonstrated. Carson & Wong (1961) have analysed the volatile components of onions by gas chromatography. They tried 2 methods of isolation; carbon adsorption followed by Soxhlet extraction in ether, and isopentane extraction of steam distillates. Their work yielded a variety of volatile constituents including several methyl and propyl disulphides, trisulphides and mercaptans.

Thus it seems clear that in *Allium* spp. the characteristic odours are the result of the liberation, especially on injury, of a variety of volatile sulphur derivities of the lower alcohols. It is most likely that similar chemicals are concerned in the odour of *Oxychilus alliarius*.

There are a few records in the literature of similar volatile sulphur compounds

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occurring in animals. The odour of the North American skunks consists principally of butyl mercaptan (Blackburn & Challenger, 1938). Ronald & Thomson (1964) identified dimethyl sulphide as being responsible for the odour of fresh Pacific oysters *Crassostrea gigas*. Here it is possible that the odour is the result of bacterial action. Bacterial decomposition of these oysters certainly results in an increase of dimethyl sulphide and also the production of a variety of other volatile sulphur compounds. Motohiro (1962) has shown that the " petroleum odour " of tinned Pacific chum salmon is mainly dimethyl sulphide liberated on cooking from dimethyl-β-propiothetin (DMPT). This compound has been traced through the food chain. It is first found in the phytoplankton (Ackman, Tocher & McLachlan, 1966). DMPT appears in abnormally high concentrations in the pteropod *Limacina helicina*, which is the principal food of the salmon at the time of year when the petroleum odour is noticed. Dimethyl sulphide is also responsible for the " blackberry " problem in the atlantic salmon (Sipos & Ackman, 1964), although the links in the food chain are unknown. DMPT has also been found in penguins' stomachs, derived from krill, which in turn grazes on the phytoplankton.

The purpose of this paper is to identify the chemical(s) responsible for the very interesting defensive odour of the garlic snail.

MATERIALS AND METHODS

1. Grote test for disulphide and sulphydryl compounds (Walsh & Merritt, 1960).

Adult snails were obtained from woodland in the Bangor (Caern., U.K.) area. Air was passed over 100 snails stimulated by agitation of their container, and bubbled through a mixture of 10 drops of 95% ethanol plus 2 drops of a mixture of 5% potassium cyanide and 1% sodium hydroxide. Then 5 drops of 1% sodium nitroprusside were added and any colour change noted.

2. Carbon adsorption.

Air was passed over 100 stimulated snails and through a tube of activated charcoal. This was then Soxhlet extracted with diethyl ether for several hours. The solvent was then gently evaporated in a warm water bath down to about 1 ml, and an aliquot injected into a gas liquid chromatography column.

3. Gas liquid chromatography.

Nitrogen was passed over about 50 snails. They were stimulated by repeated agitation of their container and the volatiles which they produced were condensed in a liquid nitrogen trap. After one hour's collection the contents of the trap were introduced into a Pye series 104 gas chromatograph via a Pye gas sampling valve. The carrier gas was nitrogen, flowing at a rate of 40 ml per minute. Five foot columns packed with 10% polyethylene glycol adipate adsorbed onto 60–80 celite were used. The separations were carried out at 80°C, and the fractions detected by hydrogen flame ionization. Some difficulty was encountered with the gas sampling valve. On allowing the volatiles to warm up preparatory to injection into the carrier gas stream there was an increase in pressure in the collecting coil so that when the valve to the column was opened the detector flame was snuffed out. Thus it became necessary to add to the sampling valve a second collecting tube which remained uncooled and took up most of this increased pressure.

Glass and stainless steel apparatus was used throughout in the collecting and injection system. On the completion of each run the system was flushed with

nitrogen for an hour and then a blank collection was made, i.e., with nothing in the snail chamber. Only when this collection resulted in a blank record from the chromatograph was the next experimental run performed. Reference chromatograms were also produced under the same conditions with as many alkyl sulphides, disulphides and mercaptans as were commercially available. Finally for confirmation the nitrogen stream from the snail chamber was bubbled through a trap containing either mercuric chloride or mercuric cyanide solutions before being condensed in the liquid nitrogen trap. Identical runs were performed with 3 other species of *Oxychilus* which are non-odourous.

RESULTS AND DISCUSSION

The Grote test, although it is sensitive to 50 μg of these compounds, did not show the red colour indicating disulphide and sulphydryl compounds. This would suggest that any such compounds, if present, occur in minute quantities. Skunk odour, butyl mercaptan, is detectable by man down to a concentration of 1 part in 10^{10}. This perhaps gives some indication of the sensitivity of mammals to these sulphurous compounds and may explain why the apparently pungent odour from *Oxychilus alliarius* was nevertheless not detected by this fairly sensitive Grote test.

The carbon adsorption and solvent extraction also yielded nothing. Carson & Wong (1961) needed about 140 pounds of onions to produce 8·7 gm. of distillate of onion oil, representing 75 parts per million of the fresh weight. Probably therefore any attempt to concentrate such compounds from *Oxychilus alliarius* odour after solvent extraction would result in the loss of the majority of these volatile compounds if they were only present in minute amounts. Further attempts at solvent extraction methods were therefore abandoned. It was decided that only by direct injection into a highly sensitive instrument such as a gas liquid chromatograph would it be possible to demonstrate the presence of specific components in the odour. Fig. 1 shows the traces obtained from this investigation. Chromatograms of *O. alliarius* odour are characterised by a large peak which has a short retention time. The time corresponds to that of n-propyl mercaptan. This peak is absent from chromatograms obtained from the other 3 species. There were several smaller peaks obtained whose retention times did not correspond with any of the available reference compounds. Whether these in fact contain sulphur groups could only be demonstrated for certain by mass spectrometry. It is quite clear that the major peak obtained from *O. alliarius* is n-propyl mercaptan and that any other volatiles present are in very small amounts.

Folkard & Joyce (1963) have shown that if disulphides are passed through 3% aqueous mercuric chloride solution they form complexes whilst mercaptans are unaffected, and *vice versa* with 4% aqueous mercuric cyanide. Prior passage of the *Oxychilus alliarius* vapour through these solutions showed that mercuric cyanide removed the main peak whilst mercuric chloride did not. This is confirmation that the peak is mercaptan. Challenger (1959) gives the following formula for the complex produced when propyl mercaptan is passed through mercuric cyanide:

$$Hg(CN)_2 + CH_3 \cdot CH_2 \cdot CH_2 \cdot SH \longrightarrow Hg(S \cdot CH_2 \cdot CH_2 \cdot CH_3)_2 + 2HCN$$

(mercury di-thio-n-propoxide)

All the peaks from extracts of non-garlic species of *Oxychilus*, plus the minor peaks in *O. alliarius*, were removed in both the cyanide and chloride solutions; this would suggest that they are neither disulphides nor mercaptans.

ACKNOWLEDGEMENTS

The author wishes to thank Dr. N. W. Runham for considerable advice and criticism, and Dr. J. Turvey for his patient aid and advice in the gas chromatographic work. Acknowledgement is also due to Professor F. W. Rogers Brambell, C.B.E., Sc.D., F.R.S., in whose department part of the study was carried out. The work was supported by an S.R.C. Research Studentship grant.

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RÉSUMÉ

LA COMPOSITION CHIMIQUE DE L'ODEUR D'AIL DU MOLLUSQUE *OXYCHILUS ALLIARIUS* (MILLER) (PULMONATA: ZONITIDAE)

D. C. Lloyd

Par la méthode de chromatographie en phase gazeuse on a montré que le principal produit volatile émis par *Oxychilus alliarius*, en état d'irritation, est le n-propyl mercaptan. C'est probablement lui qui est responsable de la violente odeur d'ail particulière à cette espèce.

A. L.

RESUMEN

LA COMPOSICION DEL OLOR DEL "CARACOL DEL AJO" *OXYCHILUS ALLIARIUS* (MILLER), (PULMONATA: ZONITIDAE)

D. C. Lloyd

La principal esencia volátil producida por *Oxychilus alliarius*, cuando es irritado, es n-propyl mercaptan. A esto probablemente se debe el penetrante olor a ajo peculiar de esta especie.

J. J. P.

АБСТРАКТ

СОСТАВ ЗАПАХА У ЧЕСНОЧНОЙ УЛИТКИ *OXYCHILUS ALLIARIUS* (MILLER), (PULMONATA: ZONITIDAE)

Д. К. ЛЛОЙД

Прямая инъекция в газово-жидкостной хромотограф показала, что главное летучее вещество, продуцирующееся при раздражении *Oxychilus alliarius*, является n-пропилмеркаптаном. Возможно, он дает тот острый запах, столь характерный для этого вида моллюска.

Z.A.F.

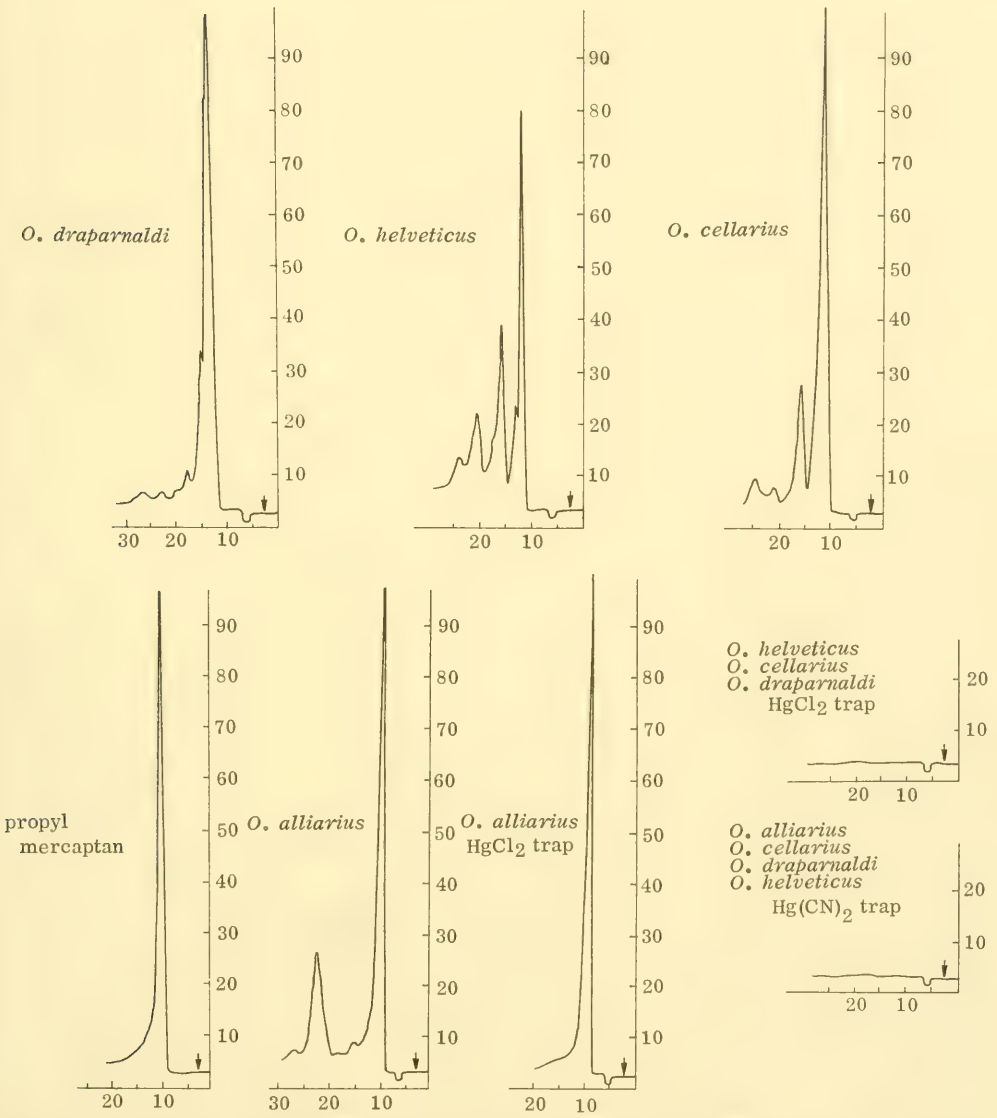

FIG. 1. Gas liquid chromatographs of n-propyl mercaptan and *Oxychilus* spp. volatiles, injected directly, and also after having been passed through mercuric chloride or cyanide traps. The injection point is marked by an arrow.

ACKNOWLEDGEMENTS

The author wishes to thank Dr. N. W. Runham for considerable advice and criticism, and Dr. J. Turvey for his patient aid and advice in the gas chromatographic work. Acknowledgement is also due to Professor F. W. Rogers Brambell, C.B.E., Sc.D., F.R.S., in whose department part of the study was carried out. The work was supported by an S.R.C. Research Studentship grant.

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АБСТРАКТ

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Д. К. ЛЛОЙД

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Z.A.F.

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