STERKIANA

* *

NUMBER 36 COLUMBUS. OHIO DECEMBER 1969

* *

CONTENTS PAGE

EDITOR
Aurèle La Rocque
Department of Geology
Ohio State University
125 S. Oval Drive
Columbus 10, Ohio

ANNOUNCEMENT

STERKIANA is named after Dr. Victor Sterki (1846-1933) of New Philadelphia, Ohio, famed for his work on the Sphaeriidae, Pupillidae, and Valloniidae. It is fitting that this serial should bear his name both because of his association with the Midwest and his lifelong interest in non-marine Mollusca.

The purpose of STERKIANA is to serve malacologists and paleontologists interested in the living and fossil non-marine Mollusca of North and South America by disseminating information in that special field. Since its resources are modest, STERKIANA is not printed by conventional means. Costs are kept at a minimum by utilizing various talents and services available to the Editor. Subscription and reprint prices are based on cost of paper and mailing charges.

STERKIANA accepts articles dealing with non-marine Mollusca of the Americas in English, French, or Spanish, the three official languages of North America. Contributors are requested to avoid descriptions of new species or higher taxa in this serial as the limited distribution of STERKIANA would probably prevent recognition of such taxa as validly published. Papers on distribution, ecology, and revised checklists for particular areas or formations are especially welcome but those on any aspect of non-marine Mollusca will be considered.

STERKIANA will appear twice a year or oftener, as material is available. All correspondence should be addressed to the Editor.

SUBSCRIPTIONS: 50¢ per number; subscriptions may be entered for not more than 4 numbers in advance; please make checks and money orders payable to the Editor.

STERKIANA est une collection de travaux sur les Mollusques extra-marins des deux Amériques, distribuée par un groupe de malacologues du centre des Etats-Unis. STERKIANA publie des travaux en anglais, en français et en espagnol acceptés par le conseil de rédaction. Prière d'adresser toute correspondance au Rédacteur.

ABONNEMENT: 50¢ le numéro, par chèque ou mandat payable au Rédacteur.

STERKIANA es una coleccion de trabajos sobre los Moluscos extra-marinos viventes y fosiles de las dos Americas, editada por un grupo de malacólogos de los Estados Unidos centrales. Contenirá en el porvenir trabajos en inglés, francés, y español que serán acceptados por la mesa directiva. La correspondencia deberá ser dirigida al Editor.

PRECIO: 50¢ el número.

THE BIOLOGY OF *LYMNAEA STAGNALIS* L. (GASTROPODA: PULMONATA)

SHARON LEE CHALFANT McDONALD[1]

***Department of Wildlife and Fisheries**, School of Natural Resources, and Mollusk*
***Division, Museum of Zoology**, University of Michigan, Ann Arbor, Michigan*

CONTENTS

INTRODUCTION

Lymnaea stagnalis is a typical freshwater pulmonate gastropod belonging to the order Basommatophora and the family Lymnaeidae. As a member of the subclass Pulmonata, it is characterized by its detorsion, lack of a ctenidium, hermaphroditism, and transformation of the mantle cavity into a pulmonary cavity, with the concomitant for-

---

[1] Sponsored by a research grant from the National Institute of Allergy and Infectious Diseases, U.S. Public Health Service (5 T1 AI 41-11).

mation of a pneumostome. As a member of the order Basommatophora, it is characterized by the presence of eyes at the base of its one pair of non-invaginable tentacles, and by separate male and female gonopores. As a member of the family Lymnaeidae, it is characterized by the shape of its shell and its reproductive anatomy. *Lymnaea stagnalis* is the type species of the genus *Lymnaea* (Morton and Yonge, 1964; Hyman, 1967).

Lymnaea stagnalis has been extensively studied, not only morphologically but physiologically and ecologically as well. Its wide geographic range throughout the Holarctic Region, its frequent occurrence in quiet waters throughout this range, its relatively large size, and the ease with which it can be maintained and bred in the laboratory have made it a favored animal for field and laboratory studies.

The purpose of this paper is to provide an overview of the vast literature pertaining to *Lymnaea stagnalis*. While it does not pretend to be an exhaustive summary, it does seek to call attention to some of the major works and lines of investigation.

EXTERNAL ANATOMY

Shell

The shell of *Lymnaea stagnalis* is characterized by a long tapering spire of five to seven convex whorls. The body whorl constitutes two-thirds of the height of the shell (Germain, 1931: 484) which in an adult *L. stagnalis* typically ranges from 38 to 52 millimeters (Baker, 1911: 136). The sutures are distinct and sometimes impressed. The aperture is very large, constituting more than one-half of the height of the shell and varying in shape from broadly ovate to elongate ovate with a faint angulation toward the top. The outer lip is thin; the inner lip is reflected over the columellar region and is closely appressed to both the parietal wall and the columella, thus forming a heavy, oblique, ascending columellar plait. The umbilicus is either closed or with only a slight opening. The shell is normally dextral (Baker, 1911, 1928; Germain, 1931; Hubendick, 1951).

Sculpture on the shell is of two distinct types: 1) longitudinal growth lines and 2) spiral lines. The numerous, fine, impressed spiral lines are the result of the '... elevation of the growth lines to form an infinite number of small costae which are interrupted more or less regularly, these breaks between the ends of the costae giving the appearance of spiral impressed lines (Baker, 1911: 4).' The nucleus or protoconch, which in *L. stagnalis* includes the first 1¼ to 1½ whorls, is without sculpturing.

Lymnaea stagnalis is often difficult to distinguish on the basis of shell characteristics alone because of the wide range of variation in the shell throughout its geographic range (Hubendick, 1951). The radula, commonly used to distinguish gastropod species, is of no taxonomic value within the lymnaeids. The basis of species identification and relationships rests chiefly upon anatomical characteristics.

Soft parts

The head region is clearly distinguished from the foot and is characterized by the well-developed oral lappets surrounding the mouth and the long, flattened tentacles with paired eyes at their base. The foot occupies the entire ventral surface. With the exception of furrows on the foot, the body surface is smooth.

The shell is lined with the mantle, which is fused at the snail's neck to form the pulmonary cavity. The respiratory opening to the pulmonary cavity, the contractile pneumostome, is drawn out into a tube and occurs on the right side of the animal. The anus and the nephridia empty into the pulmonary cavity. The male and female genital apertures are located on the right side, and are widely separated, with the male gonopore behind the base of the right tentacle and the female gonopore at the base of the neck near the pneumostome (Baker, 1911, 1928; Hyman, 1967).

INTERNAL ANATOMY AND PHYSIOLOGY

Muscular system

The columellar muscle, which originates on the columella and branches to various parts of the body, is the main formed muscle. The foot is muscular but, with the exception of the foot retractors which attach to the columellar muscle, contains no formed muscle, only muscle fibers that intermingle with connective-tissue fibers. The major free muscles are the protractors and retractors of the radular apparatus and the protractors and retractors of the male copulatory organ (Baker. 1911; Hyman, 1967). Detailed descriptions of the muscles of the digestive system are given in Carriker (1946a). The muscles are mostly of smooth muscle fibers (Hyman, 1967).

Digestive system

Extensive work has been done on the morphology (Baker, 1911, 1928; Carriker, 1946a), function (Carriker, 1946b; Hubendick, 1957), and histology (Carriker and Bilstad, 1946) of the digestive system of *Lymnaea stagnalis*. The anterior region of the digestive tract consists of a mouth, bounded by oral lappets, which opens into the buccal cavity housing the tongue-like odontophore and the chitinous radula. The epithelium of the upper portion of the mouth is lined with a strong, horny organ, the superior jaw, which is fastened by cartilage and protruded and retracted by muscles. The epithelium of the sides of the mouth is lined by the lateral jaws which are also attached by cartilage (Baker, 1911; Carriker, 1946a). The radula, lying over the heavily muscularized odontophore, serves as a powerful abrasive tool to rasp and scrape food. Small pieces of food scraped off by the radula are passed into the buccal cavity where they are mixed with mucus which contains the digestive enzyme amylase (Carriker, 1946b) produced by the granular cells in the secretory ducts of the salivary glands (Boer, Bonga and van Rooyen, 1967). Six different cell types have been distinguished in the salivary glands of *L. stagnalis* (Gabe and Prenant, 1948) and studies of the ultrastructure of these cells (Boer, Bonga and van Rooyen, 1967) has revealed that, with the exception of a mixed cell type, each of the six secretory cell types produces its own granule type and hence its own secretion product, either mucus or serus.

Food particles pass from the buccal cavity through the esophagus and the crop (closely allied to the postesophagus) to the strongly muscular gizzard. The gizzard is kept full of sand, which functions as an effective tool for grinding the food into minute particles (Carriker, 1946a, 1946b). These particles are filtered out and passed through ciliated ducts into the bilobed hepatopancreas (midgut gland, digestive gland) for intracellular digestion. Extracellular digestion occurs in the lumen of the digestive tract. Indigestible material and large food particles are gathered into mucus strings which are carried into the ciliated intestine where they are compressed into pellets and passed through the anus to the exterior. The time required for passage of food from mouth to anus was found by Noland and Carriker (1946) to be about two hours.

The two main mechanisms responsible for the passage of food through the digestive tract are ciliary action and muscular contractions. With the exception of the anterior portion of the buccal cavity and the gizzard, both of which are lined with cuticle, the entire digestive tract is ciliated. The digestive tract has an extensive array of muscles, which are discussed in detail by Carriker (1946a: 41-56).

Excretory system

The excretory system begins in the wall of the pericardial cavity with a large nephrostome, and continues as a ciliated reno-pericardial canal that enters into the large nephridium (kidney sac) which occupies the greater part of the pulmonary cavity. A ureter leads from the nephridium to the anterior border of the pulmonary cavity, where it opens not far from the pneumostome (Grobben, 1891; Martin and Harrison, 1966).

In *L. stagnalis* as in other gastropods the production of urine is a process similar to that in vertebrates (cf. Potts, 1967, *in:* Bonga and Boer, 1969). The wall of the atrium, the reno-pericardial canal, the nephridium and the ureter are all probably involved in urine formation. The wall of the atrium may function as an ultrafilter (van Aardt, 1968) although its ultrastructure is unlike that of other known ultrafilters, such as the mammalian glomerulus (Bonga and Boer, 1969). Secretion of nitrogen containing waste products is a function of the nephridium (Spitzer, 1937). Reabsorption of water as well as solutes (van Aardt, 1968; Bonga and Boer, 1969) appears to occur in both the nephridium and the ureter.

That the excretory system may also function as a site to store the glycogen synthesized from the glucose which is reabsorbed in the ultrafiltrate is suggested by the presence of glycogen deposits in the epithelial cells of the reno-pericardial canal, the nephridium and in the cells of the ureter (Bonga and Boer, 1969).

Osmotic and ionic regulation

Lymnaea stagnalis, like all freshwater molluscs, maintains a higher concentration of ions in its blood than occurs in the water, and thus has the dual problem of excreting the excess inflow of water and of actively replacing, by absorption from a dilute medium, those ions which are lost by excretion and outward diffusion (Robertson, 1964). The excess inflow of water is compensated by the excretory system probably under the influence of an antidiuretic factor from neurosecretory cells within the pleural ganglia (Hekstra and Lever, 1960; Lever, Jansen and De Vlieger, 1961; Lever and Joose, 1961).

The active replacement, by absorption, of those ions lost by excretion and outward diffusion has been observed in *L. stagnalis*. If *L. stagnalis* is first depleted of its own salt content in distilled water, there will be an active uptake of chloride and sodium ions when the snail is placed in a hypertonic solution (Krogh, 1939). Moreover, even though the hemolymph of *L. stagnalis* contains 150-200 milligrams of calcium per liter, calcium will be actively taken up from a solution containing only five milligrams per liter (van der Borght, 1963; van der Borght and van Puymbroeck, 1964). Certain aspects of the epithelial cells of both the nephridium (kidney sac) and the ureter suggest that they are involved in the transportation of ions and water (Bonga and Boer, 1969).

Circulatory system

The circulatory system of *Lymnaea stagnalis* is an open system. The heart, consisting of a single auricle and a single ventricle, is enclosed within a pericardial cavity. From the ventricle, an arterial system of well-defined channels extends to capillary networks on the surface or in the interior of all organs. The capillaries, in turn, empty into the large venous sinuses of the body. From these sinuses the blood, or hemolymph, is transported into pulmonary arteries which branch into capillary networks in the top of the pulmonary cavity, where the blood is aerated. This capillary network continues into the pulmonary veins, which open into the auricle (Hill and Welsh, 1966; Hyman, 1967).

Hemolymph

The blood or hemolymph of *Lymnaea stagnalis* is alkaline in nature and does not coagulate on bleeding, although it contains protein which can be coagulated by boiling (Hyman, 1967). Müller (1956) has made an extensive study of the cell types of the hemolymph of *L. stagnalis* and their origin, and found that the hemolymph cells are formed continuously in connective tissue, particularly in the pulmonary cavity.

Lymnaea stagnalis has the ability to discharge a large amount of its hemocoelic blood through a hemal pore which lies at the edge of the renal aperture within the pulmonary cavity (Lever and Bekius, 1965). Such discharges of hemocoelic blood occur when the snail retreats far into its shell.

Respiratory system

Lymnaea stagnalis, although completely aquatic, lacks (like all pulmonates) ctenidia, the characteristic gills of freshwater gastropods. In *L. stagnalis,* respiration is of two forms: cutaneous, which occurs when the snail is submerged and depends upon the permeability of the skin to oxygen and upon a lower gas tension in the hemolymph than in the water; and aerial, which involves surfacing and use of the mantle cavity as a 'lung.' In *L. stagnalis,* Precht and Otto found that the proportion of cutaneous to aerial respiration is dependent upon the oxygen tension of the water. As the oxygen tension of the water falls, which occurs as the temperature of the water increases, the proportion of cutaneous respiration decreases. Thus at 13° C, cutaneous respiration for *L. stagnalis* was found to be 81 percent, while at 23° C it had dropped to 54 percent (Precht and Otto, 1950, *in:* Hyman, 1967: 640).

The 'lung' or pulmonary cavity is formed by the fusion of the edge of the mantle cavity with the snail's back, leaving only a contractile opening, the siphon-like pneumostome, which is closed when the snail is submerged. The roof of the pulmonary cavity is richly vascularized. *L. stagnalis* comes to the surface at intervals to renew the air in the pulmonary cavity; the length of time between surface visits depends upon the oxygen tension of the water (Füsser and Kruger, 1951; von Brand and Mehlman, 1953), the temperature and the season (Precht and Otto, 1950). In general, the oxygen consumption increases as the oxygen tension declines, which occurs as the temperature increases. Thus, von Brand and Mehlman (1953: 303) found that the oxygen intake of *L. stagnalis* into its pulmonary cavity in terms of cubic millimeters per gram of fresh weight per hour was more than twice as much (84.9 - 150) at 20° C than it was at 10° C (34.2 - 41.8).

Precht and Otto (1950) found that the length of time between surface visits averaged 50 minutes for a yearly cycle when the snails were kept at a constant 23° C, and averaged 175 minutes for a yearly cycle when kept at a constant 13° C. These results are reflected in the fact that after 60 minutes submersion the gas in the pulmonary cavity of *L. stagnalis* contained twice as much oxygen at 13° C (10.4 - 11.4 percent) as it did at 23° C (4.3 - 5.7 percent) (Precht and Otto, 1950, in Hyman, 1967: 641). Moreover, the length of time that *L. stagnalis* would stay submerged during the autumn and winter was twice that of the spring and summer for both temperatures. This seasonal variation in oxygen consumption is probably associated with some physiological activity of the snail (e. g. reproduction).

From the above results, it would appear that although *L. stagnalis* consumes twice as much oxygen at higher temperatures (20° C) than at lower temperatures (10°), it must nonetheless surface more than three times as often at the higher temperatures. This suggests that the duration of submersion between visits to the surface is dependent upon the degree of cutaneous respiration and the metabolism of the snail, both of which vary according to the temperature of the water.

Reproductive system

As most pulmonates, *Lymnaea stagnalis* is hermaphroditic and, as suggested by Crabb (1927a), its reproductive system may be thought of as comprising three distinct parts: 1) the true hermaphroditic part, which includes the ovotestis and the hermaphroditic duct; 2) the female part, which includes the oviduct and the uterus with its accessory glands: albumen, egg membrane, and egg mass membrane; the vagina, and the sperm receptacle; and 3) the male part which includes the vas efferens, prostate gland, vas deferens, and copulatory organ.

L. stagnalis is a simultaneous hermaphrodite in that in the follicles of the ovotestis, ovogenesis and spermatogenesis occur simultaneously. Like all of the Basommatophora and contrary to most pulmonates, it is believed that *L. stagnalis* cannot reciprocally copulate with exchange of sperm because the female and male apertures are too widely separated (Crabb, 1927a, b). The method of cross-fertilization thus involves one-sided copulation with one animal acting as male and the other as female. The factors determining which animal will assume the active male role have not, to the author's knowledge, been studied, although descriptions of the copulatory act (Barraud, 1957; Noland and Carriker, 1946) suggest that it may simply be dependent upon which animal, in the course of its travels, encounters another from behind, mounts it and, thus assuming the male copulatory position, attempts copulation (Noland and Carriker, 1946). This thought is substantiated by reports in the literature of *L. stagnalis* attempting to copulate with food containers, etc. (Noland and Carriker, 1946). After copulation, the snails will often reverse their roles and recopulate with each other or with different snails. Copulatory behavior is discussed in detail by Baker (1911), Noland and Carriker (1946), Bretschneider (1948a), and Barraud (1957).

The Lymnaeidae are probably the highest form of animal life in the evolutionary series in which self-fertilization occurs (Baily, 1931). There are many accounts in the literature of individuals of *L. stagnalis,* isolated since birth, laying viable eggs (Holzfuss, 1914; Crabb, 1927b; Noland and Carriker, 1946) and the author has observed this repeatedly in isolated *L. stagnalis* in the laboratory. It is interesting to note that paired *L. stagnalis* can begin laying eggs at such early ages as seven weeks (van der Steen, van den Hoven and Jager, 1969) and nine weeks (personal observation), but that isolated *L. stagnalis* are invariably older, about six months, when egg laying occurs (personal observation). Self-fertilization occurs in paired as well as isolated snails but breeding studies using an albino marker (Cain, 1956) have shown that, as suggested by Colton (1918) and contrary to the opinion expressed by Crabb (1927b), cross-fertilization is the dominating process in paired snails. Histological studies of the reproductive tract of *L. stagnalis* have been done by Holm (1946) and studies on gametogenesis have been conducted by Bretschneider and Raven (1951) and Joose, Boer and Cornelisse (1968).

Oviposition

Fertilization is internal, and the eggs are laid in gelatinous capsules which are attached to plants and other objects such as stones, other snails, or the sides of the aquarium. The capsules contain a variable number of eggs depending chiefly upon the age of the snail, the speed with which the eggs are deposited (Noland and Carriker, 1946) and such diverse environmental factors as water-change, atmospheric pressure change, quality and quantity of food, light-intensity and cycles, and temperature (van der Steen, 1967). The article by van der Steen (1967) on the influence of environmental factors on the oviposition of *L. stagnalis* is a vital acquisition for anyone concerned with the raising of any aquatic pulmonate—both in the information contained therein and in the extensive bibliography. The details of oviposition are given in Bretschneider (1948b), Noland and Carriker (1946: 481-486) and van der Steen (1967).

Embryology

Like other pulmonates, *Lymnaea stagnalis* lacks free-swimming larval stages. The stages which correspond to the trochophore and veliger are passed inside the egg case, and the young snails hatch anatomically complete except for their reproductive system. The rate of development is not the same for each snail in an egg mass, varying from 14 to 18 days at 20° C (Noland and Carriker, 1946: 487). When laid, the eggs are uncleaved. The approximate times for various stages at 20° C are as follows: first cleavage - four hours; 64-cell stage - 18 hours; trochophore stage - 100 hours; veliger stage - six days; creeping snail - 11 days (Noland and Carriker, 1946: 487). The creeping snail rasps first the inner surface of its egg case and then the gelatinous membrane case

case and then the gelatinous membrane case until it can crawl out. The egg case and the gelatinous membrane serve as sources both of protection and of food. The embryology of *L. stagnalis* has been studied by Raven (1945, 1946, 1967) and Regondaud (1964), and the literature has been reviewed by Raven (1964).

Nervous system

The central nervous system of *Lymnaea stagnalis* is of the detorted type, with the ganglia concentrated into a ring about the digestive tract. This ring is composed of nine ganglia: two cerebral, two pedal, two pleural, two parietal, and the unpaired visceral, as well as their commissures. The five latter ganglia, which form the ventral part of the ring, are further concentrated to form a visceral chain. In addition, there is a pair of buccal ganglia connected to the cerebral ganglia via connectives, and other minor nerve centers such as the osphradium, statocysts, etc. From the nine major ganglia, nerves radiate to all parts of the body (Baker, 1911; Hyman, 1967).

The anatomical roles of the various ganglia were ascertained through studies of their innervation (Baker, 1911; Elo, 1938; Carriker, 1964a, Joose, 1964), and are reflected in their names. More critical experiments to determine the physiological roles as well were performed by Hekstra and Lever (1960) through extirpation of the various ganglia. They found that extirpation of the cerebral ganglia prevented copulation, egg-laying, ventilation of the pulmonary cavity and feeding. Removal of the pleural ganglia (Lever, Jansen and De Vlieger, 1961) resulted in swelling due to intake of water; thus these must function in osmoregulation. Removal of the visceral and right parietal ganglia reduced feeding and crawling rates as well as the rate of ventilation of the pulmonary cavity. Extirpation of the left parietal ganglion increased egg production.

Morphologic (microscopic and ultramicroscopic) and histochemical investigations of the neurosecretory cells in the central nervous system of *L. stagnalis* have been intensively undertaken in the Zoological Laboratory of the Free University, Amsterdam and the reader is referred to the following papers: Lever, 1958; Lever, Kok, Meuleman and Joose, 1961; Joose, 1964; Boer, 1963, 1965; Brink and Boer, 1967; Boer, Douma and Koksma, 1968; Boer, Slot and van Andel, 1968.

Sense organs

In *Lymnaea stagnalis*, as in most gastropods, contact sensitivity to objects and chemicals is well-developed over that part of the body surface which is not covered by the shell. Contact sensitivity is particularly evident in those areas where neuro-sensory cells are most abundant: on the tentacles, the head, and the margins of the mantle and foot (Charles, 1966). De Vlieger (1968), in studies of the tactile system of *L. stagnalis*, has found evidence that suggests that there are, in fact, two tactile systems: one associated with exploration and creeping and the other with escape. Each system has its own specific sense cells and central pathways. The former system is stimulated by the repetition of weak tactile stimuli (e. g. a stationary object) which is the optimal stimulus for positive thigmotactic behavior. The latter system is the result of one strong stimulus (e. g. a sudden, strong touch) which is the optimal stimulus for negative thigmotactic behavior.

An osphradium in the form of an invaginated sac of ciliated sensory epithelium is present in *L. stagnalis*, as in all freshwater pulmonates, and serves as a chemoreceptor (Demal, 1954). That it may also function as a tactile receptor is suggested by Hulbert and Yonge (1937) and Charles (1966).

Although *L. stagnalis* has a pair of eyes located at the base of its tentacles, its visual sense is quite limited. Light intensities are discernible, but there is no evidence for form perception (Barraud, 1957). Liche (1934a, b), in some of the few experiments on color responses in gastropods, found that *L. stagnalis* could distinguish between red and blue wave lengths over a wide range of relative intensities and would avoid the red.

The senses of equilibrium and sound are centered in the paired ganglia known as statocysts. These organs consist of a fluid-filled sac in which are suspended several to many calcareous bodies, the otoliths, which are kept in a constant state of vibration by means of sensory hairs. A change in the position of the snail will alter the direction of the force exerted by the otolith on the sensory hairs. This results in a stimulation of those sensory cells which control the equilibrium of the snail (Baker, 1911; Charles, 1966). There is disagreement concerning the ability of any pulmonate to respond to sound as such, but it is evident that snails do show response to vibrations carried through the water, witness their extreme sensitivity to the presence of nearby moving objects (Barraud, 1957).

Orientation

Orientation of *Lymnaea stagnalis* with respect to gravity is dependent upon the paired statocysts and the condition of the pulmonary cavity with respect to oxygen tension (Lever and Geuze, 1965; Geuze, 1968). When the oxygen tension of the pulmonary cavity falls below 13.7 percent (Precht and Otto, 1950) the negative geotropic response obtains and the snail ascends to the surface. After the cavity is filled, the geotropic reaction becomes positive and the snail descends.

Locomotion

Locomotion in *Lymnaea stagnalis* consists chiefly of gliding or hunching, with the former the more common. Gliding is dependent upon the secretion of mucus and the beating of the cilia that cover the sole of the foot. It is not dependent upon pedal muscular contractions (Noland and Carriker, 1946). Gliding ceases if the ciliary action is eliminated by the addition of lithium chloride to the water; it is not affected by paralyzing the pedal muscles with curare (Hyman, 1967). *L. stagnalis* is not slow-moving for its size, and gliding rates up to 7.5 centimeters per minute have been reported. (Noland and Carriker, 1946: 476).

Hunching movements involve muscular contractions and appear to be limited to periods of stress (Hyman, 1967). Other movements involving pedal muscular contractions are the righting reaction, copulation, and retraction of the foot into the shell.

Lymnaea stagnalis, like almost all species of *Lymnaea*, can spin a thread of mucus and employ it as a locomotory aid. Thus *L. stagnalis* can be observed to hang suspended by a mucus thread from the surface film of the water or from an object, or to attach a mucus thread to the bottom and rise to the surface of the water on this thread and even to descend again on it (Baker, 1911).

ECOLOGY

Introduction

The freshwater pulmonates of the genus *Lymnaea* are familiar inhabitants of the waters of lakes, ponds, and slow-moving streams throughout the world. Their occurrence in a fairly wide range of habitats is dependent upon those certain environmental conditions which are necessary for growth and fertility. Among these environmental conditions, the most important are clean water, the presence of calcium, and the usual parameters of moderate temperature ranges, suitable food, and sufficient living space.

Clean water

That clean water is important to the growth of lymnaeids has been shown both in laboratory and field studies. Crabb (1929) showed that foul media and insufficient food were the most common growth-inhibiting factors in *L. stagnalis*. In the field, van der Schalie (personal communication, 1969) has noted that *L. stagnalis*, once abundant in most streams and lakes in southern Michigan, has disappeared owing most likely, to the increased fouling of these habitats by municipal and industrial waste. In studies currently under way in the Mollusk Division there is evidence that the elimination of *Lymnaea stagnalis* from areas in lower Michigan is related to the role of higher temperatures on the reproductive capacity of the snails. These studies are designed to improve understanding of the role of heat pollution in the biology and distribution of freshwater snails.

Presence of calcium

It is generally recognized that calcium is vital to the growth of the shell in all gastropods. Boycott (1936) found that a minimum of twenty milligrams per liter of calcium in the environment was necessary for the growth of the calciphilic lymnaeids and Macan (1950) verified this for *L. stagnalis*. Some argument exists in the literature as to the source of the calcium. Although most authors insist that the source is the water (Boycott, 1936; Macan, 1950; Tucker, 1958), Frömming (1956) stated that snails do not utilize the calcium of the water but rather that of their plant food. However, experiments by Klein and Trant (1961) involving the addition of radioactive calcium chloride to water show that it is calcium from water that is taken up by the snail and used in constructing its shell.

Lymnaea stagnalis normally lives in slightly alkaline water and, consequently, attempts have been made to relate their distribution directly with pH (Hunter, 1964). However, a clearer correlation is found with calcium content or total alkalinity (Boycott, 1936; Macan, 1950; Tucker, 1958), the alkalinity of the water owing to the presence of calcium carbonate.

Temperature

Lymnaea can, as a genus, be found living over a wide range of temperatures. Like most pulmonates, the lymnaeids are more sensitive to warm temperatures, usually not surviving continuous exposure to temperatures greater than 30° C, and less sensitive to cold, being able to withstand freezing. *L. peregra*, a highly resistant species has been found living in thermal waters of 45° C in the Pyrenees (Issel, 1908) and Weigmann (1936) found that *L. stagnalis* could be supercooled to - 3.5° to 4.5° C without freezing and subsequent death (In: Noland and Carriker, 1946: 489).

The above, however, are extremes, while the dominance of more moderate temperatures is of great importance in the life of *L. stagnalis* in controlling the rate of development, growth, and reproduction. Noland and Carriker (1946) successfully raised twenty generations of *L. stagnalis* at temperatures which ranged generally from 17° C to 21° C. A temperature drop to 15° C did not appear to harm the snails but did slow their rate of feeding, and growth and temperature drops to 10° C resulted in a growth check on the shell (Noland and Carriker, 1946: 471). In concurrence with these results, Vaughn (1953) found that growth would occur in *L. stagnalis* raised at constant temperatures ranging from 11.0° to 28.2° C with the lowest mortality occurring in those raised at temperatures between 15.7° and 20.1° C (Vaughn, 1953: 226). The optimum constant temperature for hatching of eggs and growth of young *L. stagnalis* was found, by Vaughn (1944), to be 20° C.

Light

Light does not appear to be of much importance in regulating growth and reproduction except indirectly as it affects the growth of plants. Frömming (1956) did note that young *L. stagnalis* grew faster when raised in the dark than in the light.

Food

Lymnaea stagnalis is, in general, herbivorous and obtains its plant food from three main sources: feeding on rooted submerged vegetation, raking small food particles from the surface film while gliding upside down under it, and scraping material from rocks and other such surfaces. It is interesting that no study has been conducted to determine if the food obtained in scraping material from submerged rocks is selectively periphyton or if it includes the entire Aufwüchs.

Lymnaea stagnalis has been observed in nature to feed on rotting fruit and vegetation (Baker, 1928) and green filamentous algae (Krehke, 1964), and in the laboratory to thrive (twenty generations) on a diet of lettuce and wheat cereal cooked with milk (Noland and Carriker, 1946) or simply on a diet consisting exclusively of loose, green leaf lettuce (Crabb, 1929; Baily, 1931; van der Steen, 1967; personal observation).

Lymnaea stagnalis has been known to attack living animals such as small fish (Baker 1911) and in a recent paper by Gorin (1966) the food spectrum of lymnaeids was widened to include the eggs of the fish Vimba.

Space

The amount of living space per snail has a definite effect on growth rates in *L. stagnalis*, but the cause of this effect is debated. Semper (1874) found that the more extensive the crowding, the smaller the shells. This conclusion is supported by the similar experiments of Forbes and Crampton (1942) on *L. palustris* and DeWitt (1958) on *L. columella*. Frömming (1956), however, claimed negative results with *L. stagnalis;* yet, in aquaria with one *L. stagnalis* in 350, 750, 1500, and 5000 ml. of water, he noted the least growth in the first aquaria and the greatest growth in the last (In: Hyman, 1967: 611), and attributed these results to increased plant growth with increased water quantity. Crabb (1929), while inclined to deny that overcrowding of *L. stagnalis* resulted in a decrease in growth rates, did concede that extreme crowding markedly retarded growth, but attributed this to insufficient food and fouling of the water. Legendre (1908) and Wright (1960) both concluded that the primary cause of stunting in overcrowded cultures was the accumulation of waste (cf. infra, p. 16).

A main problem to obtaining exact results in studies of overcrowding is that snails from the same batch of eggs vary greatly in growth rate, particularly when raised under crowded conditions. Frömming (1956), rearing 100 *L. stagnalis* from the same batch of eggs in one jar found shell lengths which ranged from 6.0 to 20.6 millimeters at the end of 90 days (In: Hyman, 1967: 612). Noland and Carriker (1946), with 2,589 eggs of *L. stagnalis* in a ten liter aquarium, got 30.5 percent survival (791 snails) at the end of 200 days. The range of shell lengths at 200 days was from 6.0 to 42 millimeters with the mode at 10 millimeters. In spite of extreme crowding, 136 snails were 20 to 30 mm. in length and 52 were 31 to 41 mm. in length (Noland and Carriker, 1946: 477). Snails stunted by overcrowding resumed normal growth when put in uncrowded conditions.

Parasites

Lymnaeids are important as vectors of parasites of man, domestic animals, and wild game. They are the intermediate hosts of the larval stages of at least fourteen medically important trematodes among which the most important are the liver flukes *Fasciola hepatica* and *F. gigantica* which have as their definitive hosts sheep, cattle, and other vertebrate hosts including man. *Lymnaea stagnalis* is not known to be an intermediate host of *Fasciola* but does serve as an intermediate host to *Schistosomatium douthitti* which has as its definitive host muskrats, deer and small rodents; and *Trichobilharzia ocellata* which has as its final host ducks and teals. These two species of trematodes, common in the United States and particularly so in Michigan, are important to man in that they are among those trematodes causing cercarial dermatitis in man (Malek, 1962).

Accounts of the effect of trematode infections on the intermediate host show that *L. stagnalis* infected with trematodes has a lowered oxygen consumption (Duerr,

1965) and that in *L. palustris* (Zischke and Zischke, 1965) and *L. stagnalis* (personal observation) the reproductive and digestive systems suffer irreversible damage. Moreover, the growth curves of *L. palustris* are notably affected, with a decrease in growth rate correlated with an increase in trematode infection (Zischke and Zischke, 1965).

There are several well documented cases of the annelid *Chaetogaster limnaei* von Baer commensal on *L. stagnalis* (Noland and Carriker, 1946; Comfort, 1949 Gruffydd, 1965a). This annelid has been found on all external parts of the snail and has been reported so abundant that 'the fleshy parts of the snail appeared hairy' (Noland and Carriker, 1946: 474-475). This commensal has also been found in the respiratory chamber (Noland and Carriker, 1946) and Gruffydd (1965a) noted that there were two distinct forms of *C. limnaei*, one living as an ectocommensal and the other inhabiting the kidney. Both Noland and Carriker (1946) and Comfort (1949) noted that *C. limnaei* caused no noted irritation to the snail.*

The degree to which the nonbloodsucking leeches of the genus *Glossiphonia* are predators or ectoparasites on lymnaeids is currently a point of debate. Dorier (1951) and Michelson (1957) consider the *Glossiphonia* as predators that reach into the retracted lymnaeid and suck it out. Gruffydd (1965b) considers that the leech, *G. heteroclita*, is probably an annual, living on the snail during the winter and becoming free-living during its breeding season.

The most serious predators of lymnaeids, and of aquatic snails in general, are the insects, particularly the Coleoptera and Diptera. Some insects, chiefly larval forms, such as the caddis larvae (Trichoptera) gnaw holes in the egg capsules of the snails. Other insects, such as the water beetles (Haliplidae) lay their eggs in the egg masses of the snails. Young and adult snails are preyed upon by dragonfly nymphs and adult beetles. The adult water beetle *Dytiscus marginalis* is, when present, a serious predator on young and adult *L. stagnalis* (Hyman, 1967). The most important single type of insect predator, however, is the larvae of the snail-killing dipteran family Sciomyzidae (Michelson, 1957; Foote, 1959, 1962; Berg, 1964).

Lymnaeids may also be preyed upon by carnivorous snails and by many groups of vertebrates: fish, salamanders, frogs, toads, lizards, snakes, birds, and small mammals (Pelseneer, 1935). The author has noted no studies which investigate the degree to which various predators regulate the size of lymnaeid populations in nature; the degree of predation upon lymnaeids by its predators, or the extent to which the lymnaeids constitute a food item in the food supply of its predators.

Life span

There is a certain disagreement in the literature concerning the normal life span of *Lymnaea*. Baker (1911: 51) states that 'The duration of life in the family Lymnaeidae is from three to four years, full maturity being reached in about two years.' Most observations in nature and in the laboratory, however, indicate that the normal life span of the lymnaeids is considerably less than the three to four years suggested by Baker (1911). The longest record for lymnaeids is that of two years by Berrie (1965) for *L. stagnalis* in Scotland, the northern limit of its range. However, as suggested by Berrie (1965: 293), *L. stagnalis* is most likely '... an annual but that under unfavorable conditions, such as are normally associated with marginal habitats, its life cycle becomes extended to include a second year.'

Observations on populations of *L. stagnalis* in Wisconsin by Brackett (unpublished, *in* Noland and Carriker, 1946) suggest that in nature these snails live about one year. The adults lay eggs in the latter part of the summer, the eggs hatch in the fall and the newly hatched snails survive the winter, resume growth and reach sexual maturity by the end of the summer.

---

* Continued page 17; two paragraphs omitted here by error. A.L.

With the onset of cold weather the adults die. This agrees with observations made by the author on the Au Sable River in Michigan.

Life spans for *L. stagnalis* under laboratory conditions range from nine months (Crabb, 1929) to fourteen months (Noland and Carriker, 1946) with reproduction continuing almost unstopped from the onset of sexual maturity to the end of the life cycle. The death of *L. stagnalis* in the laboratory and in nature, when not caused by predators, parasites, or other causes found in the environment, appears to be the result of expansion of the gonad and degenerative changes in those internal organs not directly concerned with reproduction (Noland and Carriker, 1946; Berrie, 1966).

Distribution

The Lymnaeidae constitute a relatively large family of forty genera (Taylor and Sohl, 1962) distributed in fresh water throughout the world particularly in the Holarctic Region. The major monographs dealing with the Lymnaeidae are Baker's (1911) *The Lymnaeidae of North and Middle America* and Hubendick's (1951) *Recent Lymnaeidae: their variation, morphology, taxonomy, nomenclature and distribution.*

Lymnaea stagnalis is Holarctic in its distribution occurring throughout Europe, the Palearctic area of Asia, North America north of the 37th parallel, and the northwesternmost part of North Africa. It does not appear to occupy much of the extreme regions of the Arctic north of the Arctic circle, nor is it to be found on Iceland or Greenland. *L. stagnalis* does not occur outside of the Holarctic Region except where it has been introduced secondarily, i.e. New Zealand (Baker, 1911; Hubendick, 1951).

Taxonomy

Generic names vary to some extent within the family Lymnaeidae, depending to a large degree upon whether the author of a work is taxonomically a lumper or a splitter. Some authors, essentially lumpers (e. g. Hubendick, 1951: 111) believe that '... a systematical division of Lymnaeidae into groups does not correspond to the natural conditions within the family,' and that characteristics are not sufficient to distinguish taxonomical units. Other authors, essentially splitters (e. g. F. C. Baker, 1911, 1928) recognize several distinct genera within the family Lymnaeidae and consider that lumping all species into the single genus *Lymnaea* '...obscures more than it reveals (Taylor, Walter and Burch, 1963: 239). Moreover, studies based on an immunological approach to lymnaeid systematics indicate that '...the species groups *Lymnaea, Bulimnea, Fossaria, Pseudosuccinea, Radix* and *Stagnicola* are each immunologically distinct' (Burch and Lindsay, 1968: 22). Still other authors, following the middle road (e. g. Hyman, 1967), consider that names, such as *Bulimnea, Galba, Radix,* and *Stagnicola* are best regarded as subgenera of *Lymnaea.*

Lymnaea stagnalis exhibits a wide range of shell differences as indicated by Hubendick (1951, fig. 299) in sketches of the shell variation in *L. stagnalis* obtained from Sweden. In Eurasia the more common varieties of *L. stagnalis* include *L. stagnalis armenica* (Westerlund), *L. stagnalis baltica* (Lindström), *L. stagnalis bodamica* (Clessin), *L. stagnalis fragilis* (Linné), *L. stagnalis lacustris* (Studer), *L. stagnalis raphidia* (Westerlund), and *L. stagnalis variegata* (Hazay). Many other varieties of *L. stagnalis* have been described in the literature. For a general discussion of the varieties of *L. stagnalis* found in Eurasia the reader is referred to Locard (1893: 17-20) and Germain (1931: 483-485).

The form of *L. stagnalis* most common in North America, but also present in Eurasia, is a form commonly referred to as *L. stagnalis appressa* (Say). This form has, in general, a less angulated body whorl, a more twisted axis and is more regularly fusiform than its counterpart in Eurasia, a form which should perhaps be referred to as *L. stagnalis stagnalis* (Hubendick, 1951).

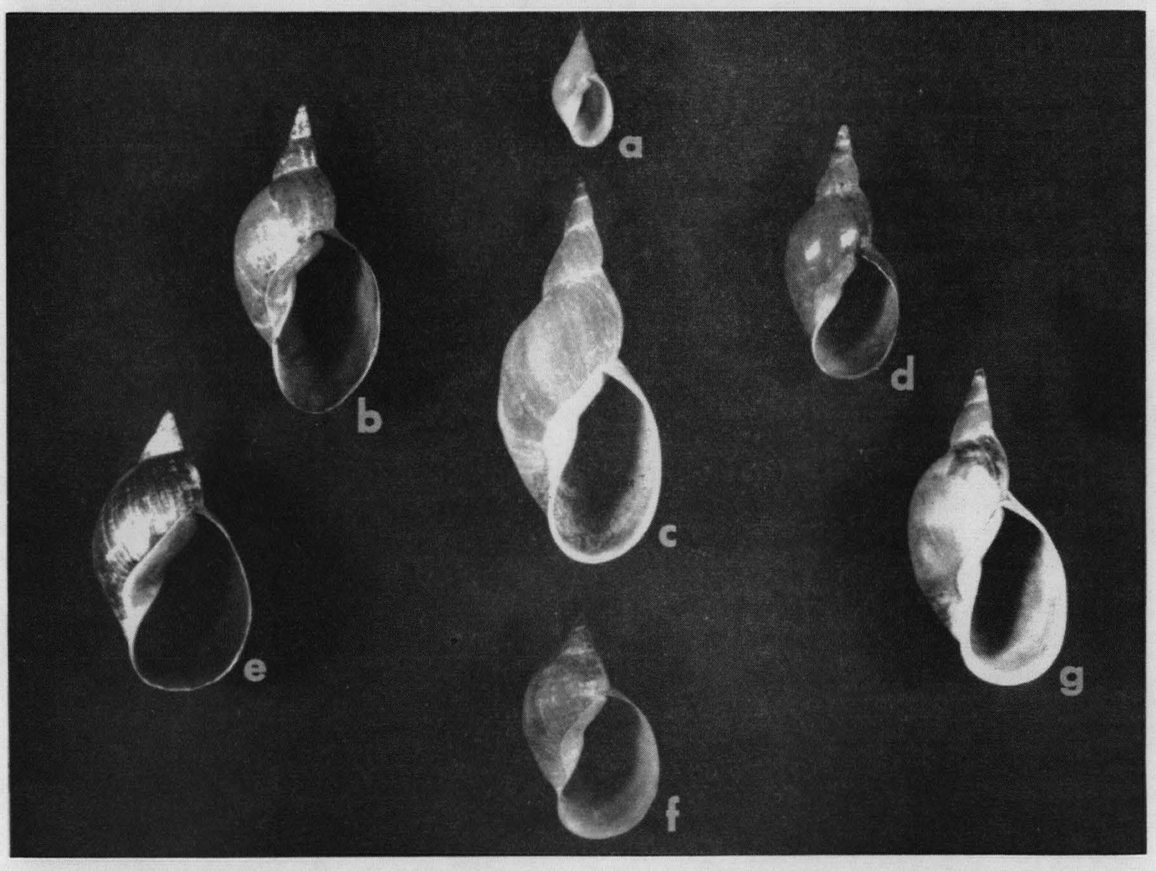

PLATE I. NORTH AMERICAN VARIETIES OF LYMNAEA STAGNALIS

a. *Lymnaea stagnalis goodrichi* (Walker). Lake Huron, Alcona County, Michigan.
b. *Lymnaea stagnalis sanctaemariae* (Walker). Lake Superior.
c. *Lymnaea stagnalis appressa* (Say). Crystal Lake, Benzie County, Michigan.
d. *Lymnaea stagnalis wasatchensis* (Hemphill). Swamp 1 mi west of Laketown, Rich County, Utah.
e. *Lymnaea stagnalis lillianae* (Baker). Siskiwit Lake, Isle Royale, Michigan.
f. *Lymnaea stagnalis occidentalis* (Hemphill). Lake Whatcom, Whatcom County, Washington.
g. *Lymnaea stagnalis perampla* (Walker). Bass Lake, Drummond Island, Michigan.

In North America many varieties of *L. stagnalis* have been recognized, the more common of which are shown in Plate I and include: *L. stagnalis goodrichi* (Walker), *L. stagnalis lillianae* (Baker), *L. stagnalis occidentalis* (Hemphill), *L. stagnalis perampla* (Walker), *L. stagnalis sanctaemariae* (Walker) and *L. stagnalis wasatchensis* (Hemphill). It is generally accepted that *L. stagnalis jugularis* (Say) is in reality *L. stagnalis appressa* (Say).

The ranges of variation in the above mentioned varieties of *L. stagnalis* in North America do not exceed the range of variation found for *L. stagnalis appressa* and do not in the opinion of Hubendick (1951) represent geographic races. As suggested by Hubendick, a cytological study—or immunological study of the problem —might help to answer some of the questions raised by these various forms of *L. stagnalis*.

APPENDIX: ANAESTHETIZATION TECHNIQUES

In order to conduct anatomical studies on either living or preserved specimens of *Lymnaea stagnalis*, it is necessary that the snails be completely relaxed. This is done either at the time of dissection when living or prior to fixation when preserved. The most commonly used relaxing agents for snails are sodium nembutal (van der Schalie, 1957) and menthol crystals. Two special techniques have been devised for relaxing freshwater snails in general and *L. stagnalis* in particular. The first of these (Joose and Lever, 1959) involves pretreatment with 0.08 percent nembutal for twenty to thirty minutes at 20-25° C. followed by immersion in a solution of 0.08 percent nembutal and 0.3 percent methansulphonate for ten minutes. The second technique for rapid and effective relaxing is similar to the first, but requires aerating a 0.1 percent nembutal solution at 20° C. (0.08 percent at 27° C.) with nitrogen for three minutes, immersing the snails, and after ten minutes transfering the snails to a mixture of 0.1 percent nembutal and 0.3 percent methansulphonate at 20° C. (0.07 percent methansulphonate at 27° C.) for five minutes (Lever, Jager, and Westerveld, 1964). Although both techniques are effective for anatomical studies, the latter is to be preferred for operations because of rapid recovery. The author suggests that those interested in using this latter technique consult both Lever, Jager, and Westerveld (1964) and van Aardt (1968: 261-269).

REFERENCES CITED

van AARDT, W.J. (1968) Quantitative aspects of the water balance in *Lymnaea stagnalis* (L.). -- Neth. J. Zool. 18: 253-312.

BAILY, J.L. (1931) Some data on growth, longevity, and fecundity in *Lymnaea columella* Say. -- Biol. Generalis 7: 407-428.

BAKER, F. C. (1911) The Lymnaeidae of North and Middle America. -- Chicago Acad. Sci., Special Publ. 3, 539 pp.

----- (1928) The Freshwater Mollusca of Wisconsin. I. Gastropoda. Pt. I, Bull. 70, Wis. Geol. and Nat. Hist. Survey.

BARRAUD, E.M. (1957) The copulatory behavior of the freshwater snail (*Lymnaea stagnalis* L.).-- Brit. Jour. Animal Behaviour, 5: 55-59.

BERG, C.O. (1964) Snail control in trematode diseases: the possible value of sciomyzid larvae snail-killing Diptera. -- Adv. Parasit. 2: 259-309.

BERRIE, A. D. (1965) On the life cycle of *Lymnaea stagnalis* (L.) in the west of Scotland. -- Malacol. Soc. London, Proc., 36 (5): 283-295.

----- (1966) Growth and seasonal variation in reproductive organs of *Lymnaea stagnalis* (L.). -- Malac. Soc. London, Proc., 37: 83-92.

BOER, H.H. (1963) A preliminary note on the histochemistry of the neurosecretory material (NSM) of the snail *Lymnaea stagnalis* (Basommatophora). -- Gen. Comp. Endocrin. 3 (6): 687--688.

----- (1965) A cytological and cytochemical study of neurosecretory cells in Basommatophora with particular reference to *Lymnaea stagnalis* L. -- Arch. Néerl. de Zool. 16 (3): 313-386.

BOER, H.H., BONGA, S.E. WENDELAAR & van ROOYEN, N. (1967) Light and electron microscopical investigations on the salivary glands of *Lymnaea stagnalis* L. --Z. Zellforsch. 76: 228-247.

BOER, H. H., DOUMA, E. & KOKSMA, J.M.A. (1968) Electron microscope study of neurosecretory cells and neurohaemal organs in the pond snail *Lymnaea stagnalis*. -- Symp. Zool. Soc. Lond. 22: 237-wty.

BOER, H. H., SLOT, J.W. & van ANDEL, J. (1968) Electron microscopical and histochemical observations on the relation between medio-dorsal bodies and neurosecretory cells in the basommatophoran snails *Lymnaea stagnalis, Ancylus fluviatilis, Australorbis glabratus* and *Planorbarius corneus*. -- Z. Zellforsch. 87: 435-450.

BONDENSEN, P. (1950) A comparative morphological-biological analysis of the egg capsules of freshwater pulmonate gastropods; Hygrophila, Basommatophora, Pulmonata. -- Natura Jutlandica 3: 1-208.

BONGA, S.E. Wendelaar & BOER, H.H. (1969) Ultrastructure of the reno-pericardial system in the pond snail *Lymnaea stagnalis* (L.). -- Z. Zellforsch. 94: 513-529.

van der BORGHT, O. (1963) Accumulation of radium-226 by the freshwater gastropod *Lymnaea stagnalis*. -- Nature 197 (4867): 612-613.

van der BORGHT, O. & van PUYMBROECK, S. (1964) Active transport of alkaline earth ions as physiological base of the accumulation of some radionuclides in freshwater molluscs. -- Nature 204 (4958): 533-534.

BOYCOTT, A. E. (1936) The habitats of fresh-water Mollusca in Britain. -- J. Animal Ecol. 5: 116-186.

von BRAND, T. & MEHLMAN, B. (1953) Relation between pre- and post-anaerobic oxygen consumption and oxygen tension in some freshwater snails. -- Biol. Bull. 104: 301-312.

BRETSCHNEIDER, L.H. (1948a) Insemination in *Lymnaea stagnalis* (L.). -- Proc. K. Ned. Akad. Wetensch. 51: 358-362.

----- (1948b) The mechanism of oviposition in *Lymnaea stagnalis* (L.). -- Proc. K. Ned. Akad. Wetensch. 51: 616-626.

BRETSCHNEIDER, L.H. & RAVEN, C.P. (1951) Structural and topochemical changes in the egg cells of *Limnaea stagnalis* L. during oogenesis. -- Arch. Néerl. de Zool. 10: 1-31.

BRINK, M. & BOER, H.H. (1967) An electron microscopical investigation of the follicle gland (cerebral gland) and of some neurosecretory cells in the lateral lobe of the cerebral ganglion of the pulmonate gastropod *Lymnaea stagnalis* L. --Z. Zellforsch. 79: 230-243.

BURCH, J. B. & LINDSAY, G. K. (1968) An immunological approach to lymnaeid systematics. --Ann. Rept. for 1968, Amer. Malacological Union: 22-23.

CAIN, G.L. (1956) Studies on cross-fertilization and self-fertilizwtion in *Lymnaea stagnalis appressa* Say.--Biol, Bull. 111: 45-52.

CARRIKER, M.R. (1946A) Morphology of the alimentary system of the snail *Lymnaea stagnalis appressa* Say. -- Trans. Wis. Acad. Sci. Arts Letters 38: 1-88.

CARRIKER, M.R. (1946b) Observations on the functioning of the alimentary canal of the snail *Lymnaea stagnalis appressa* Say. -- Biol. Bull. 91: 88-111.

CARRIKER, M. R. & BILSTAD, N. M. (1946) Histology of the alimentary system of the snail *Lymnaea stagnalis appressa* Say. -- Trans. Amer. Micros. Soc. 65(3); 250-275.

CHARLES, G.H. (1966) Sense organs (less Cephalopods). -- IN Wilbur, K.M. & Yonge, C.M., Physiology of Mollusca, v. II, Acad. Press: New York, pp. 455-522.

COLTON, H. S. (1918) Self-fertilization in the air breathing pond snail. -- Biol. Bull. 35: 48-49.

COMFORT, A. (1949) A commensal of *Lymnaea*. --Proc. Malac. Soc. London 27: 246.

CRABB, E. D, (1927a) Anatomy and function of the reproductive system in the snail *Lymnaea stagnalis appressa* Say. -- Biol. Bull. 53: 55-67.

----- (1927b) The fertilization process in the snail *Lymnaea stagnalis appressa* Say. -- Biol. Bull. 53: 67-97.

----- (1929) Growth of a pond snail *Lymnaea stagnalis appressa*, as indicated by increase in shell-size. -- Biol. Bull. 56 (1): 41-63.

DEMAL, J. (1954) Histologie comparée des organes chimorécepteurs des gastéropodes. -- Acad. Roy. Belg., Cl. Sci., Mém. in octavo, sér. 2, v. 29, fasc. 1.

DE VLIEGER, T.A. (1968) An experimental study of the tactile system of *Lymnaea stagnalis* (L.). -- Netherl. J. Zool. 18 (2): 105-154.

DE WITT, R.M. and SLOAN, W. C. (1958) The innate capacity for increase in numbers in the pulmonate snail, *Lymnaea columella*. -- Trans. Amer. Microsc. Soc. 77 (4): 290-294.

DORIER, A. (1951) Présence de *Glossiphonia heteroclita* sub. sp. *hyalina* dans la cavité palléale de *Limnaea stagnalis.* -- Trav. Lab. Hydrobiol. Grenoble, 46-47.

DUERR, F. (1965) The effect of digenetic trematode parasitism on the oxygen consumption of the fresh-water pulmonate snail, *Lymnaea stagnalis appressa.* -- Amer. Zool. 5: Abstract 393.

ELO. J. E. (1938) Das Nervensystem von *Lymnaea stagnalis* (L.). -- Ann. Zool Soc. Zool.-Bot. Fennica Vanamo 6: 4.

FOOTE, B.A. (1959) Biology and life history of the snail killing flies belonging to the genus *Sciomyza* (Diptera, Sciomyziday) -- Ann. Entomol. Soc. Amer. 52(1): 31-43.

----- (1962) Biology and immature stages of the snail killing flies belonging to the genus *Tetanocera* (Diptera, Sciomyzidae). -- Dissert. Abstracts 22.

FORBES, G.S., & CRAMPTON, H.E. (1942) The effects of population density upon growth and size in *Lymnaea palustris.* -- Biol. Bull. 83: 283-289.

FRÖMMING, E. (1956) Biologie der mitteleuropaischen Süsswasserschnecken. -- Berlin, Ducker & Humboldt.

FÜSSER, H. & KRUGER, F. (1951) Vergleichende Versuche zur Atmungsphysiologie von *Planorbis corneus* und *Limnaea stagnalis* (Gastropoda, Pulmonata). -- Z. vergleich. Physiol. 33: 14-52.

GABE, M. & PRENANT, M. (1948) Contribution a la cytologie de la glande salivaire de *Limnaea stagnalis.* -- Cellule 52: 18-34.

GERMAIN, Louis (1931) Faune de France 22 - Mollusques terrestres et fluviatiles (deuxième partie). -- Paris, Lechevalier, p. 479-893.

GEUZE, J. J. (1968) Observations on the function and the structure of the statocysts of *Lymnaea stagnalis* (L.). -- Neth. J. Zool. 18(2): 155-204.

GORIN, G. G. (1966) Vragi ikry rybtsa na nerestilishchakh rybotsovykh prudor. (The enemies of Vimba eggs on the spawning grounds in Vimba ponds). -- Tr. Azov. Nauch-Issled Inst. Rybn. Knoz. 8: 45-50. From Ref. Zh. Biol. 1966, no. 121188 (Translation) in Biol. Abstrscts (1968) no. 60292.

GROBBEN, C. (1891) Die Pericardialdruse der Gastropoden. -- Arb. Zool. Inst. Univ. Wien, 9: 35-56.

GRUFFYD, L. D. (1965a) Evidence for the existence of a new subspecies of *Chaetogaster limnaei* (Oligochaeta), in Britain. -- J. Zool., Proc. Zool. Soc. London 146: 175-196.

----- (1965b) Notes on a population of the leech, *Glossiphonia heteroclita,* infecting *Lymnaea pereger.* -- Ann. Mag. Nat. Hist. 8 (87/88): 151-154.

HEKSTRA, G. P., & LEVER, J. (1960) Some effects of ganglion extirpations in *Limnaea stagnalis.* -- Proc. K. Ned. Akad. Wetensch. 63: 271-282.

HILL, R. B. & WELSH, J.H. (1966) Heart, circulation, and blood cells. IN: Wilbur, K. M. & Yonge, C.M., Physiology of Mollusca, v. II, New York: Academic Press, pp. 126-174.

HOLM, L.W. (1946) Histological and functional studies on the genital tract of *Lymnaea stagnalis appressa* (Say). -- Trans. Amer. Micros. Soc. 65: 45-68.

HOLZFUSS, E. (1914) Selbstbefruchtung einer Süsswasserschnecken. -- Nachrichtsbl. Malakozool. Gesellsch. 1914: 67-73.

HUBENDICK, B (1951) Recent Lymnaeidae. Their variation, morphology, taxonomy, nomenclature, and distribution. -- Kungl, Svenska Vetenskapsakad. Handlingar 3: 1-223.

----- (1957) The eating function in *Lymnaea stagnalis* (L.). -- Arkiv Zool. 10(2): 511-521.

HULBERT, G.C.E.B. & YONGE, C.M. (1937) A possible function of the osphradium in the Gastropoda. -- Nature 139: 840.

HUNTER, W R. (1964) Physiological aspects of ecology in nonmarine molluscs. -- IN: Wilbur, K.M & Yonge, C.M., Physiology of Mollusca, v. I. New York: McGraw-Hill, 792 pp.

HYMAN, L. H. (1967) The Invertebrates, v. VI, Mollusca I. -- New York: McGraw-Hill, 792 pp.

ISSEL, R. (1908) Sulla biologia termale. -- Intern. Rev. Hydrobiol. 1: 29-36.

JOOSSE, J. (1964) Dorsal bodies and dorsal neurosecretory cells of the cerebral ganglia of *Lymnaea stagnalis* L. -- Arch. Néerl. de Zool. 16(1): 1-103.

JOOSSE, J., BOER, M. H., & CORNELISSE, C.J. (1968) Gametogenesis and oviposition in *Lymnaea stagnalis* as influenced by γ-irradiation and hunger. -- Symp. Zool. Soc. Lond., 22: 213-235.

JOOSSE, J. & LEVER, J. (1959) Techniques of narcotization and operation for experiments with *Limnaea stagnalis* (Gastropoda Pulmonata).--Proc. K. Ned. Akad. Wetensch. 62(2): 145-149.

KLEIN, U. & TRANT, W. (1961) Zur Herkunft der Schalenkalkes bei Süsswassermollusken. -- Internat. Rev. Gesamt. Hydrobiol. 46(3): 434-440.

KRENKE, G. (1965) Eksperimental'noe izuchenie pitaniya zhivotnykh, naselyayuschchikh nitchatye zelenye vodorosli v stoyachickh vodoemakh. (Experimental study of the food of animals living in filamentous green algae in stagnant bodies of water). -- Nauch. Dokl. Vyssh. Shkoly Biol. Nauk. 2: 19-23. From Ref. Zh. Biol., 1965, no. 5D205 (translation) in Biol. Abstr. 1968, no. 5251.

KROGH, A. (1939) Osmotic regulation in aquatic animals. -- New York, Cambridge Univ. Press, 242 pp.

LEGENDRE, R. (1908) Recherches sur le nanisme expérimental. Influence des excreta. -- Arch. Zool. Exptl. et Gén. sér. 8 (Notes et Revues no. 3): 77-84.

LEVER, J (1958) On the relation between the medio-dorsal bodies and the cerebral ganglia in some pulmonates. -- Arch. Néerl. de Zool. 13: 194-201.

LEVER, J. & BEKIUS, R. (1965) On the presence of an external hemal pore in *Lymnaea stagnalis* L. -- Experientia 21: 1-4.

LEVER, J. & GEUZE, J. (1965) Some effects of statocyst extirpations in *Lymnaea stagnalis*. -- Malacologia 2(3): 275-280.

LEVER, J., JAGER, J.C. & WESTERVELD, A. (1964) A new anaesthetization technique for fresh water snails, tested on *Lymnaea stagnalis*. -- Malacologia 1(3): 331-337.

LEVER, J., JANSEN, J. & DE VLIEGER, T. A. (1961) Pleural ganglia and water balance in the fresh water pulmonate *Limnaea stagnalis*.--Proc. K. Ned. Akad. Wetensch. 64(4): 531-542.

LEVER, J. & JOOSSE, J. (1961) On the influence of the salt content of the medium on some special neurosecretory cells in the lateral lobes of the cerebral ganglia of *Lymnaea stagnalis*. -- Proc. K. Ned. Akad. Wetensch. 64(5): 630-639.

LEVER, J., KOK, M., MEULEMAN, E. A. & JOOSSE, J. (1961) On the location of gomori-positive neurosecretory cells in the central ganglia of *Lymnaea stagnalis*. -- Proc. K. Nederl. Akad. Wetensch. 64(5): 640-647.

LICHE, H. (1934a) Les réactions photiques de la *Limnaea stagnalis* (L.). -- CR Acad. Cracovie 7: 5.

----- (1934b) Über die photischen Reaktionen bei der Schlammschnecke *Limnaea stagnalis* L. -- Bull. Intern. Acad. Polon. Sci., Classe Sci., Math. Nat., sér. B, II, (5-7): 233-249.

LO, C-T. (1967) Inhibiting action of ostracods on snail culture. -- Trans. Amer. Microsc. Soc. 86(4): 402-405.

LOCARD, A. (1893) Les coquilles des eaux douces et saumâtres de France. -- Paris: Baillière et Fils, 327 pp.

MACAN, T. T. (1950) Ecology of freshwater Mollusca in the English Lake District. -- Jour. Animal Ecol. 19: 124-146.

MALEK, E.A. (1962) Laboratory guide and notes for medical malacology. -- Minneapolis: Burgess, 154 p.

MARTIN, A.W. & HARRISON, F.M. (1966) Excretion.--IN: Wilbur, K.M. & Yonge, C.M., Physiology of Mollusca, v. II, New York: Academic Press, pp. 353-386.

MICHELSON, E.H. (1957) Study on the biological control of schistosome-bearing snails. Predators and parasites of freshwater Mollusca: a review of the literature. -- Parasitology 47: 413-426.

MORTON, J.E. & YONGE, C.M. (1964) Classification and structure of the Mollusca. -- IN: Wilbur, K.M. & Yonge, C.M., Physiology of Mollusca, v. I, 1964. New York, Academic Press, p. 1-58.

MÜLLER, G. (1956) Morphologie, Lebensablauf, und Bildungsort der Blutzellen von *Lymnaea stagnalis* L. -- Z. Zellforsch. 44: 519-556.

NOLAND, L.E. & CARRIKER, M.R. (1946) Observations on the biology of the snail *Lymnaea stagnalis appressa* during twenty generations in laboratory culture. -- Amer. Midland Nat. 36: 467-493.

PELSENEER, P. (1935) Essai d'éthologie zoologique d'après l'étude des Mollusques. -- Bruxelles, Acad. Royale Sci. Belgique, Publ. Fondation Agathon De Potter, No. 1, 662 pp.

POTTS, W.T.W. (1967) Excretion in molluscs. -- Biol. Rev. 42: 1-41.

PRECHT, H. & OTTO, E. (1950) Über die Atmung einiger Süsswasserpulmonaten und ihre Temperaturabhangigkeit. -- Zool. Anz. 145. (Cited by Hyman, not seen).

RAVEN, C.P. (1945) The development of the egg of *Limnaea stagnalis* L. from oviposition till first cleavage. -- Arch. Néerl. Zool. 7: 91.

----- (1946) The development of the egg

of *Limnaea stagnalis* L. from the first cleavage till the trochophore stage, with special reference to its 'chemical embryology.' -- Arch. Néerl. Zool. 7: 353.

----- (1966) Development. --In: Wilbur, K.M. & Yonge, C.M., Physiology of Mollusca, v. II, New York: Academic Press, pp. 165-195.

----- (1967) The distribution of special cytoplasmic differentiations in the egg during early cleavage in *Limnaea stagnalis*. -- Develop. Biol. 16(5): 407-437.

RÉGONDAUD, Jean (1964) Origine embryonnaire de la cavité pulmonaire de *Lymnaea stagnalis L.* Considerations particulières sur la morphogénèse de la commissure viscérale. -- Bull. Biol. France Belgique 98 (2): 433-471.

ROBERTSON, J.D. (1964) Osmotic and ionic regulation. IN: Wilbur, K.M. & Yonge, C. M., Physiology of Mollusca, v. I, New York: Academic Press, pp. 283-311.

van der SCHALIE, H. (1957) Nembutal as a relaxing agent for mollusks. -- Amer. Midl. Nat. 50: 511-512.

SEMPER, C. (1874) Über die Wachstumsbedingungen des *Lymnaea stagnalis*. -- Arb. Zool. Zootom. Inst. Würzburg, 1: 137-167.

SPITZER, J.M. (1937) Physiologisch-ökologische Untersuchungen über den Exkretstoffwechsel der Mollusken. -- Zool. Jb. 57: 457-496.

van der STEEN, W. J. (1967) The influence of environmental factors on the oviposition of *Lymnaea stagnalis* (L.) under laboratory conditions. -- Arch. Néerl. de Zool. 17(4): 403-468.

van der STEEN, W.J., van den HOVEN, N. P., & JAGER, J. C. (1969) A method for breeding and studying freshwater snails under continuous water change, with some remarks on growth and reproduction in *Lymnaea stagnalis* (L.). -- Netherlands J. Zool. 19(1): 131-139.

TAYLOR, D.W. & SOHL, N.F. (1962) An outline of gastropod classification. -- Malacologia 1(1): 7-32.

TAYLOR, D.W., WALTER, H.J. & BURCH, J.B. (1963) Freshwater snails of the subgenus *Hinkleyia* (Lymnaeidae: *Stagnicola*) from the western United States. -- Malacologia 1(2): 237-281.

TUCKER, D.S. (1958) The distribution of some fresh-water invertebrates in ponds in relation to annual fluctuations in the chemical composition of the water. -- Jour. Animal Ecol. 27: 105-123.

VAUGHN, C.M. (1944) The effects of temperature upon the hatching time and growth of *Lymnaea stagnalis appressa* Say. -- Summ. Doct. Diss. Univ. Wisc. 8: 80-82.

-----(1953) Effects of temperature on hatching and growth of *Lymnaea stagnalis*. -- Amer. Midland Nat. 49: 214-228.

WEIGMANN, R. (1936) Zur Kaltebestandigkeit poikilothermer Tiere. Untersuchung an Schnecken und Fischen. -- Biol. Zentbl. 56: 301-322.

WRIGHT, C.A. (1960) The crowding phenomenon in laboratory colonies of freshwater snails. -- Ann. Trop. Med. Parasit. 54: 224-232.

ZISCHKE, J.A. & ZISCHKE, D.P. (1965) The effects of *Echinostoma revolutum* larval infection on the growth and reproduction of the snail host *Stagnicola palustris*. -- Amer. Zoologist, 5: Abstract no. 402, p. 707-708.

Plate reproduced courtesy of Mollusk Division, Museum of Zoology, University of Michigan, Ann Arbor, Michigan.

Manuscript received and accepted for publication, October 20, 1969.

* * *

NOTE. The two paragraphs that follow were omitted on page 11 through an unfortunate error of the editor. AL

It must also be mentioned that there are many protozoans which infest lymnaeids among them ciliates and flagellates such as *Cryptobia limnorum* which inhabits the spermatheca of *L. stagnalis* (Hyman, 1967).

Predators

The types of animals which prey on lymnaeids are numerous and diverse. The rotifer *Proales gigantea* feeds on the egg masses of *Lymnaea* (Bondensen, 1950). Ostracods, while probably not a serious threat to lymnaeids in nature, are a major source of mortality if they become established in laboratory cultures (Lo, 1967). Physical contact of ostracods with the soft parts of lymnaeids is sufficiently irritating to cause the snails to retreat into their shells or to crawl out of the water (the possibility of chemical irritation, etc., has not been investigated, to the author's knowledge). Those snails which retreat into their shells may subsequently be consumed by the ostracods; those which crawl up the sides of the aquarium die from desiccation (Lo, 1967; personal observation).

ABBÉ LÉON PROVANCHER'S WRITINGS ON MOLLUSCA

Aurèle La Rocque
Ohio State University
Columbus, Ohio, 43210

One of the early pioneers of Canadian malacology was a Roman Catholic priest and scholar, Abbé Léon Provancher, whose ambition it was to describe the entire fauna of Canada in systematic fashion. He published several instalments of his work on the insects, relying on a tiny government grant which was given to him annually for some years. Finally, the Quebec government notified him that his grant had been cut off and he decided to await the availability of funds to continue the work on insects. He feared that the lack of funds would also mean the end of the *Naturaliste Canadien* which he had published for many years but fortunately, that publication managed to survive. It celebrated its 100th year of publication in 1968, with a magnificent volume of considerable size but, more important, of significantly important articles.

Provancher, almost in desperation, decided to begin publication of the Mollusca of Quebec, hoping to be able to finish their description before funds ran out. He did manage to publish the first part *'Les Mollusques de la Province de Québec. Première Partie. Les Céphalopodes, Ptéropodes et Gastropodes'* in the Naturaliste Canadien and separates of the entire work were assembled and published under the above title in 1891. It was thought that the manuscript for the second part, *'Lamellibranches'* had either been lost or had never been written.

Thanks to the diligent work of my friend Marcel Ouellet, who taught at Chicoutimi for a year or so, it is now known that the pelecypods were enumerated and keyed out in a manuscript now deposited in the Archives of the Séminaire de Chicoutimi. It is a pleasure to announce that this part of Provancher's work will soon be published in STERKIANA.

BOOK REVIEW

TREATISE ON INVERTEBRATE PALEONTOLOGY, Directed and edited by R. C. Moore and... Curt Teichert. Part N. Volumes 1 and 2 (of 3) Mollusca 6. Bivalvia. xxxviii and 951 p., illus. 1969. (Received November 20).

The volumes of the Treatise have been rolling off the presses at a steady rate since 1953 when Part G, Bryozoa, by R. S. Bassler, was first published. There were those who doubted that such an enormous undertaking as this could be brought to a successful conclusion. With the publication of each new volume, the doubters became fewer and hopes rose higher that the work would indeed end in triumphant completion. If so, it will be one of the greatest achievements of its kind, comparable to the great German and French synoptic works of this century.

Many malacologists of all parts of the world have been involved in this project, some of them from the very start, as the list of authors (p. viii - xi) will show.

The volume is dedicated to the late Leslie Reginald Cox who died August 5, 1965, after completing most of his assignment on the volume. In his long career at the British Museum (Natural History) Dr. Cox was a tower of strength to the paleontological fraternity and an inexhaustible source of information and wise counsel as the writer can testify by personal experience.

The name BIVALVIA was adopted by the commitee responsible for this volume after long and sometimes heated discussion by correspondence. It will come as a surprise to many, but the fact remains that Linnaeus adopted it in 1758 in the tenth edition of the *Systema Naturae*. Before objecting to the name as new, it would be well to read the wise summary of the matter by Cox (Treatise, pt. N, p. 3) for it turns out to be a restoration, not an innovation.

A. L.

SYNOPSIS METHODICA MOLLUSCORUM BY C. T. MENKE

WILLIAM J. CLENCH

Museum of Comparative Zoology, Cambridge, Mass. 02138

Two editions of this work by Menke appeared, the first in 1828 (Pyrmont, Germany, 12 + 91 pp.) and the second, 'Editio altera,' in 1830 (Pyrmont, Germany, 16 + 168 pp.). Both gave a list of species contained in his collection as well as descriptions of many new species. In the second edition, many additional species were described; unfortunately nearly all of the species which appeared in the 1828 edition were republished as new in the 1830 edition.

The 1828 edition is very rare; the 1830 edition is uncommon and is generally the one quoted as the origin of the new species. The numbers in the list below refer to the pages on which are described the new species in the original 1828 edition.

22 *Cyclostoma murrhinum*

24 *Rissoa decussata*

26 *Natica sigaretina*

33 *Buccinum terebrale*

34 *Purpura morum*

35 *Dolium costatum*

37 *Columbella variegata*

41 *Strombus laevilabris*

43 *Conus virgo fasciata*

44 *Oliva maura cinnamomea*

75 *Bulla obovata, Helix semilineata, H. subcarinata*

76 *H. hirta, Carocolla otomata, C. lonchostoma, Bulimus lateralis*

77 *B. cylindricus, B. fusiformis, B. bacillaris, Clausilia livida*

78 *C. orthostoma, Scarabus labrosus, S. fusiformis, Auricula pellucens*

79 *Physa striata, P. subarata, Helicina pyrrhostoma, H. flavida, H. subfusca*

80 *H. rotellaris, Paludina sulculosa, Melania ovularis, M. cruentata*

81 *M. angulosa, M. exarata, M. curta, M. plicata, M. sulcosa*

82 *M. ligata, M. fasciata, M. auriscalpium, Rissoa laevigata*

83 *R. tuberculata, R. mucronata, R. truncata, Turritella fascialis, Neritina venosa*

84 *N. turriculata, N. trifasciata, Ianthina bicolor, I. nitens*

85 *Monodonta fulminata, Trochus cingulatus, T. brasilianus, Scalaria notha, Cerithium nigrescens*

86 *C. lutosum, Harpa ligata, Cassis scrobiculata, C. muricata*

87 *C. laevigata, C. tenuilabris, Ranella lanceolata, Marginella glans*

88 *M. irrorata, M. apicina, Volvaria intermedia, V. tenera, Sigaretus cymba*

89 *Pileopsis paleacea, Crepidula squamosa, Calyptraea sella, Balanus imbricatus, Anatifa serrata*

90 *Mytilus prasinus, Unio rubens, U. rugatus*

91 *Chama mitrula, Cytherea fulminata*

Manuscript accepted for publication September 24, 1969

* * *

BOOK REVIEWS

DIE GASTROPODEN DER MADAGASSISCHEN BINNENGEWÄSSER. By Ferdinand Starmühlner. *Malacologia*, v. 8, nos. 1-2, p. 1-434, 570 text figs. Abstracts in German, p. 1, English, p. 412, French, p. 415, Spanish, p. 419, and Russian, p. 422.

The 1958 Austrian Expedition to Madagascar collected, among other things, an extensive suite of the non-marine Mollusca of the island. In this massive monograph, Dr. Starmuhlner has revised and described the freshwater gastropods with special attention to the shell, the gross and fine anatomy, ecology, and distribution of the 29 species recognized by him. Genera such as *Neritina, Radix, Bulinus, Anisus, Gyraulus*, and *Ferrissia*, will be familiar to the North American malacologist; in addition he will find some unusual and interesting forms, such as *Thiara* (figs., p. 209) which has spines similar to those of the North American *Io* but pointing upward instead of outward, and *Melanatria*, reminiscent of the Pleuroceridae of North America. Most of the species of Madagascar are related to African species, but the author points out relationships of *Melanatria* with *Doryssa* of South America, a possible indication of former connection of Madagascar with South America as well as Africa. There are some good data on ecology of all the species and the geographic distribution of each one has been carefully plotted on outline maps.

* * *

LAND MOLLUSKS AND NOXIOUS WEEDS OF THE CONNECTICUT VALLEY. By Milton Werner, Jr. *New York Shell Club Notes, No. 153, p.* 3-5, June-Aug. 1969.

Members of the New York Shell Club as a rule, write about marine mollusks and the 'Notes' contain frequent important records and ecological observations from many of the seas of the world. It is only infrequently that notes on non-marine forms appear in the 'Notes' but that is no reason for a specialist to disregard them, as witness this article which adds a number of species to our knowledge of the land snails of the Connecticut Valley. Such additions to our knowledge of the distribution of Mollusca, marine or non-marine, are a boon to the author of synoptic works; their publication should be encouraged.

DISTRIBUTION NOTES ON WESTERN AND SOUTHERN SNAILS

Branley A. Branson

Eastern Kentucky University
Richmond, Kentucky 40475

During the last several years I have accumulated a few gastropod records in my files which are probably of interest to students of the western fauna.

BRITISH COLUMBIA. *Arion ater* (Linnaeus), one specimen, 36.0 mm long, 12.0 mm wide, (contracted), 23 June 1963, Marine Drive, University of British Columbia, and three *Ariolimax columbianus* (Gould), 28.0-40 mm contracted length. *Lymnaea palustris* Muller, one specimen, 22 June 1963, Little Campbell Road, ditch pool, 5.3 miles south of Langley.

WASHINGTON. *Mudalia (Goniobasis) silicula* (Gould), two specimens, 20.0-28.5 mm long, 8.0-10.5 mm wide, 5-8 whorls, 25 June 1963, Satsop River, 1 mile north of Satsop, U.S. Highway 101; and one *Ariolimax columbianus,* 78.9 mm contracted length, from the bank. One each *Gyraulus vermicularis* (Gould) and *Physa ampullacea* Gould, 26 June 1963, near mouth of Lilliwaup River, Hoodsport. The next three species were collected at Spencer Park, U, S. Highway 101, Quilcene, 23 June 1963: one *Haplotrema sportella* (Gould), 12.8 mm wide, 6.8 mm in height, 3.3 mm umbilicus, 5 1/3 whorls; one *Prophysaon vanattae* Pilsbry, 25.0 mm contracted length; one *Prophysaon foliolatum* (Gould), 56.0 mm contracted length. In the last species, the body is reddish suffused with black, the mantle bears widely scattered black spots, and the pedal grooves are black. On 24 June 1963, three *Ariolimax columbianus,* 44.8-73.0 mm contracted length, and one *Prophysaon vanattae,* 26.9 mm contracted length, were secured at Sol Duc Falls.

NEVADA. The next five specimens were collected on 27 June 1963 at Salmon Falls Creek, 40.6 miles north of Wilkins: 112 *Aplexa hypnorum* Linnaeus, about one-half zebriated, 9.3-16.6 mm long; two *Physa ampullacea,* 16.0-23.0 mm long; five *Helisoma subcrenatum* (Cooper), 20.2-21.5 mm diameter, 9.0-10.3 mm height, 4-4 7/8 whorls; nine *Gyraulus vermicularis,* 2.0-3.5 mm diameter.

IDAHO. THE following were secured on 27 June 1963 from the Snake River, 16.5 miles west of Buhl: one *Physa ampullacea,* one *Parapholyx effusus* Lea, 7.5 mm diameter, 7.0 mm height, 4 1/3 whorls, and one *Valvata tricarinata* Say, 5.0 mm diameter, 4.0 mm height, 3½ whorls.

****

COMMENTS ON *ARION FASCIATUS* (NILSSON) FROM MINNESOTA

Branley A. Branson

Eastern Kentucky University
Richmond, Kentucky 40475

Dr. James T. Wallace, University of Pittsburgh, kindly donated the material upon which this note is based. The specimens were collected in April 1966, from beneath fallen logs and loose bark on the Carleton College campus, Northfield, Rice County, Minnesota. The 116 specimens secured from this habitat ranged from 5.0 to 22.5 mm in total contracted length, and measured 2.8 to 7.3 mm in width. The color pattern is more or less typical for the species. Associated with the *Arion* were 52 *Deroceras reticulatum* (Müller), 4 *Discus cronkhitei* (Newcomb), and 20 *Ventridens demissus* (Binney).

GLEBULA IN OKLAHOMA

Branley A. Branson

Eastern Kentucky University
Richmond, Kentucky 40475

For a long time, I have been expecting to secure specimens of *Glebula rotundata* (Lamarck) from Oklahoma, but from McCurtain County in the southeastern part of the state. Somewhat as a surprise, therefore, I eventually discovered a single specimen in Grand Lake, near Fairland, Ottawa County, on 14 January 1959. Grand Lake is an impoundment of the Neosho (Grand) River in the northeastern corner of Oklahoma. The pink-nacred, solid shell is 84.0 mm in greatest length and 61.0 mm in depth. The beaks are scarcely elevated above the general contour.

The Neosho River, inadequately collected by Isely (1925: Proc. Okla. Acad. Sci. 4: 43-118), is an interesting stream in several respects. Not only is the fish fauna (Branson, 1967 Amer. Midl. Nat. 78: 126-154) characterized by several species which have their nearest relatives in the Tennessee-Ohio river system, the molluscan assemblage quite reflects a relationship with the faunistically rich lower Mississippi River Drainage (Branson, 1963, Trans. Kansas Acad. Sci. 66: 501-512; 69: 242-294).

This relationship has come about through a rather complicated hydrographic history correlated with pre- and post-Pleistocene changes.

My thanks to Dr. David H. Stansbery, the Ohio State Museum, for verifying the diagnosis.

Manuscript accepted for publication October 25, 1969

* * *

BOOK REVIEWS

LIBBIE HENRIETTA HYMAN. AMNH Public Relations Release. New York Shell Club Notes, No. 154, September 1969, p. 2-3.

Dr. Hyman's treatise *'The Invertebrates'* has earned her the respect and admiration of all malacologists, amateur or professional. This short obituary includes some details not given elsewhere.

* * *

THE DISTRIBUTIONAL HISTORY OF THE BIOTA OF THE SOUTHERN APPALACHIANS. PART I: INVERTEBRATES. -- Virginia Polytechnic Institute, Blacksburg, Va., Research Division Monograph 1, 1969. Edited by Perry C. Holt and others. 8 and 295 p., illus.

At first glance, the only paper of interest to malacologists in this book is that by John B. BURCH, *Land Mollusks of the Southern Appalachians*, p. 247-264, 7 text figs., but three others deserve attention for various reasons. They are discussed below.

Dr. Burch's paper is a welcome summary of the land snails of the area illustrated by fine cuts drawn with consummate skill, to illustrate most of the species discussed.

The geology of the area, especially the events of the Cenozoic, are capably described by John T. HACK in *The Area, its Geology: Cenozoic Development of the Southern Appalachians*, p. 1-17. The section on stream capture should be noted.

Finally, the paper by Robert D. Ross, *Drainage Evolution and Fish Distribution Problems in the Southern Appalachians of Virginia* (p. 277 - 292) is of special interest to students of the Naiades.

Genus LEXINGTONIA Ortmann, 1914.

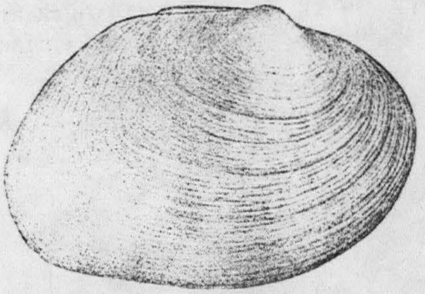

Fig. 160

"Shell subquadrate or subtrapezoidal, with slightly elevated beaks and well developed hinge teeth. Beaks not much anterior. Outer surface without sculpture. Epidermis lighter or darker brownish, with rather indistinct rays, which are narrower or wider and do not break up into blotches. Beak sculpture distinct, consisting of rather numerous (six to eight), rather crowded, subconcentric ridges, which form an indistinct, rounded angle upon the posterior ridge and are in front of this somewhat wavy and corrugated, but without showing any distinct zigzag pattern. Towards the disk, they disappear. Nacre whitish or pinkish."

Animal having only the outer gills marsupial and subcylindrical, red placentæ.

Type: *Unio subplanus* Con., fig. 160.

Genus ELLIPTIO Rafinesque, 1819.

Shell inequilateral, ovate to elongated, rounded in front and pointed or biangulate behind, with a more or less developed posterior ridge, often becoming slightly arcuate when old; beaks only moderately full, generally sculptured with coarse ridges, which run parallel with the growth lines or are somewhat doubly looped, sometimes broken and showing fine radiating lines behind; surface smooth, slightly concentrically ridged or pustulous; epidermis generally rather dull colored, rayless or fully rayed; hinge-plate narrow, two pseudocardinals and two laterals in the left valve and one pseudocardinal and one lateral in the right, with rarely a vestige of a second lateral; cavity of the beaks not deep or compressed. Marsupium occupying the whole length of the outer gills only, forming a thick, smooth pad when filled with young.

Key to the sections of *Elliptio*.

Shell spinose	*Canthyria.*
Shell smooth or feebly corrugated..............................	*Elliptio s. s.*

Section ELLIPTIO s. s.

Shell elongated, rhomboid or oval, usually more or less biangulate behind; beak sculpture consisting of a few rather strong ridges, which are nearly parallel to the growth lines or slightly doubly looped; the surface smooth or feebly corrugated.

Type: *Unio crassidens* Lam., fig. 161. Animal, fig. 162.

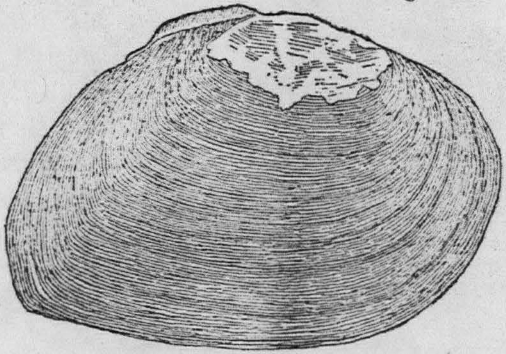

Fig. 161

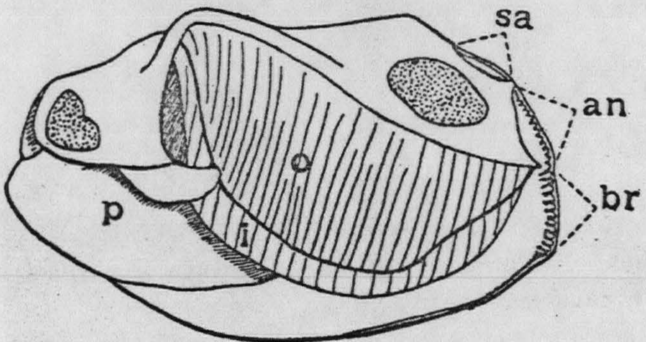

Fig. 162

Section CANTHYRIA Swainson, 1840.

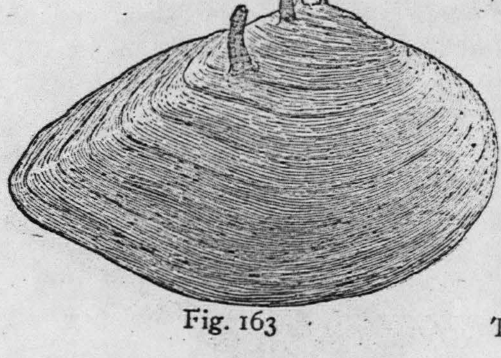

Fig. 163

Shell inflated, suboval, spinose, with a high, rather sharp posterior ridge, above which it is somewhat truncated; beaks rather compressed; epidermis smooth and shining, variegated with angular blotches; hinge sharply curved at the centre; pseudocardinals rather compressed; laterals short, remote; beak cavities rather deep.

Type: *Unio spinosus* Lea, fig. 163.

Genus UNIOMERUS Conrad, 1853.

Shell trapezoidal, with a rounded posterior ridge and pointed or feebly biangulate behind; beaks not prominent, sculptured with curved, rather strong, concentric ridges; epidermis generally rayless; pseudocardinals usually compressed, laterals delicate, slightly curved.

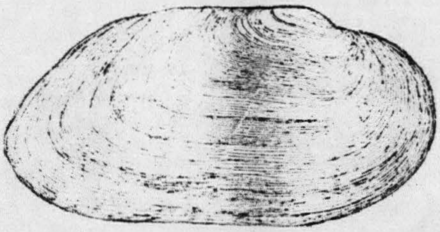

Fig. 164

Outer gills only marsupial.

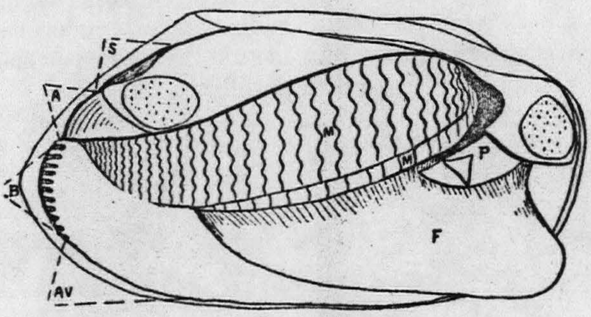

Fig. 165

Type: *Unio tetralasmus* Say, fig. 164. Animal, fig. 165.

Genus LASTENA Rafinesque, 1820.

Shell elongated, subsolid, inequilateral, generally wider in front, rounded and truncate at the anterior base, pointed at the post-basal region, and having a low posterior ridge, with one or more secondary ridges above it; beaks low, sculptured with a few coarse, irregular, longitudinal folds; epi-

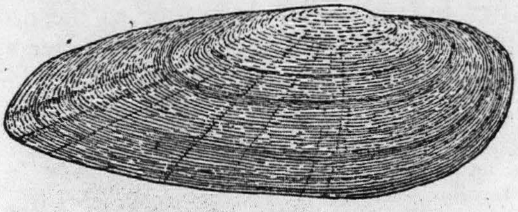

Fig. 166

dermis shining, often rayed; a single imperfect tooth in each valve and sometimes vestiges of laterals; nacre purplish shading to blue at the edge; pallial line radially ridged.

Animal having the foot very large, as long as the shell when extended, of a subcylindrical, compressed shape, with a distal swelling. The middle portion of the outer gills only marsupial. Glochidia semicircular, slightly oblique, inequivalve, without points or hooks.

Type: *Anodonta (Lastena) lata* Raf., fig. 166.

Genus GONIDEA Conrad, 1857.

Shell elongated, subtriangular, much narrowed in front, wide behind, inflated, subsolid, usually with a high, sharp posterior ridge; beaks rather sharp but not high, the sculpture consisting of a few, strong, concentric bars: epidermis rayless; hinge with a rudimentary pseudocardinal and lateral in each valve, though these are sometimes wanting; pallial line with a trace of a sinus behind; nacre lurid to purplish.

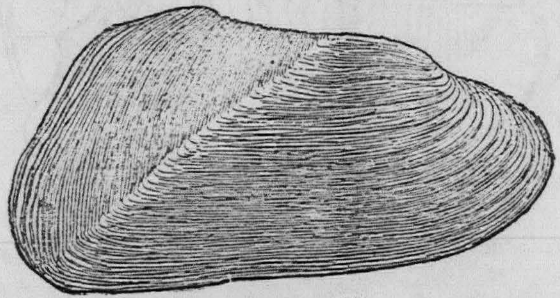

Fig. 167

Female having all four gills marsupial; with well developed septa, running parallel to the gill filaments and forming water tubes; septa not all continuous, but are often interupted, chiefly so toward the proximal (basal) part of the gill and, towards the edge, frequently shorter septa are intercalated. Glochidia subovate or nearly subcircular, without hooks.

Type: *Anodonta angulata* Lea, fig. 167.

Subfamily ANODONTINÆ Ortmann, 1912.

"Inner lamina of inner gill free from the abdominal sac, or more or less connected with it, rarely entirely connected; supra-anal opening well separated from the anal, sometimes the connection of the mantle separating it from the anal is very long and the supra-anal is quite short; branchial opening well defined, no papillæ or flaps in front of it on the edge of the mantle; marsupium formed by the outer gills in their length, distending, when charged, and the thickened tissue at the edge capable of stretching only in a direction transverse to the gill, but not beyond the edge (or only slightly so); water-tubes in the gravid female divided longitudinally into three tubes, with only the one in the middle used as an ovisac, and closed at the base of the gill; glochidium semicircular or triangular, with a spine (hook) in the middle of the ventral margin of each valve; shell generally very heavy, often thin, never round, but more or less elongated; color of epidermis generally bright and with color markings; sculpture of the beak double-looped or concentric, in the latter case often extremely heavy; hinge rarely complete and, if so, of peculiar structure; generally there is a distinct tendency toward the reduction of the hinge-teeth, and often they are completely absent; sexual differences in the shell very rarely present." (Ortmann.)

Key to the genera of *Anodontinæ*.

1.	Beak sculpture concentric	2.
	Beak sculpture double-looped	4.
2.	Beak sculpture fine	*Anodontoides.*
	Beak sculpture coarse	3.
3.	Pseudocardinals well developed	*Alasmidonta.*
	Pseudocardinals rudimentary	*Strophitus.*
4.	Hinge wholly edentulous	*Anodonta.*
	Hinge teeth more or less developed	5.
5.	Beak sculpture tubercular; surface tubercular or folded	6.
	Beak sculpture not tubercular; surface smooth except on posterior slope	7.
6.	Beak sculpture strong and continuous with tubercular surface sculpture	*Arcidens.*
	Beak sculpture poorly developed and not continuous with surface sculpture	*Arkansia.*
7.	Beak sculpture double-looped; pseudo-cardinals fully developed	*Lasmigona.*
	Beak sculpture open behind; a single pseudo-cardinal in each valve	*Simpsoniconcha.*

Genus STROPHITUS Rafinesque, 1820.

Shell elliptical to rhomboid, inflated, subsolid, pointed or biangulate behind, with a low posterior ridge, which is sometimes double; beaks full, sculpture consisting of a few, strong, concentric ridges, which curve sharply upwards behind; epidermis rayed or rayless, shining; hinge line incurved in front of the beaks; teeth rudimentary, a vestigial, compressed tooth in each valve, and sometimes a secondary tooth; laterals rarely present. Marsupium occupying the whole of the outer gills, consisting of short, horizontal ovisacs, which run directly across the gills.

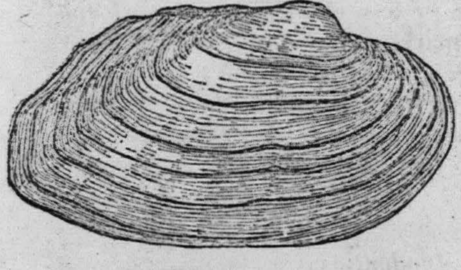

Fig. 168

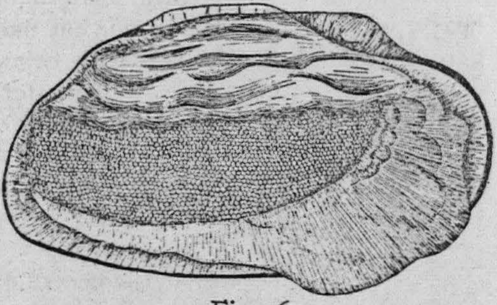

Fig. 169

Type: *Anodonta undulata* Say.
Example: *S. edentulus* (Say), fig. 168. Animal, fig. 169.

Genus ANODONTA Lamarck, 1799.

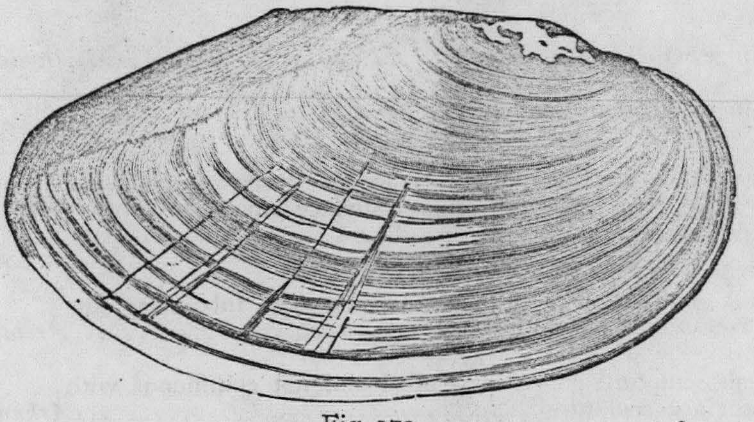

Fig. 170

Shell elliptical, thin, inflated, often slightly winged posteriorly; beak sculpture consisting of rather numerous, more or less parallel ridges, usually somewhat doubly looped and becoming slightly nodulous on the loops; surface generally smooth, shining; hinge edentulous, reduced to a mere line, regularly curved; nacre dull.

Marsupium occupying the whole outer gills, when filled forming a smooth, very thick, liver-colored pad.

Type: *Mytilus cygneus* L.

Example: *A. cataracta* Say, fig. 170. Animal, fig. 171.

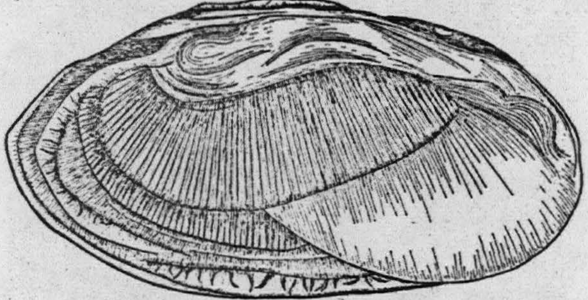

Fig. 171

Genus ANODONTOIDES Simpson, 1898.

Shell elliptical, inflated, thin, with a faint posterior ridge, sometimes constricted at the centre of the base; beaks rather full, with a few, not very coarse, subparallel, concentric ridges, which are curved up rather suddenly, behind and back of these are fine radiating ridges; epidermis smooth and shining, often rayed; hinge line slightly incurved in front of the beaks, edentulous or bearing the merest rudiments of teeth; nacre bluish-white. Marsupium occupying the outer gills only.

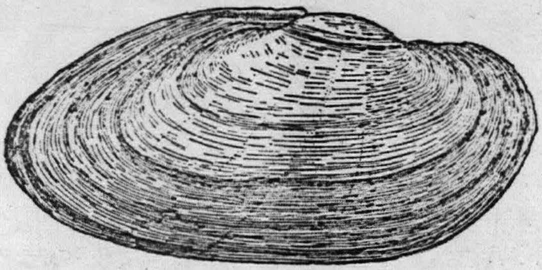

Fig. 172

Type: *Anodonta ferussaciana* Lea, fig. 172.

Genus ARCIDENS Simpson, 1900.

Shell subsolid, inflated, subrhomboidal, with full high beaks; beak sculpture very strong, consisting of irregular corrugations, which fall into two loops, at the base of which the ridges are swollen into knobs that continue out in two radiating rows on to the disk of the shell; in front of and behind the beaks are many fine, radial wrinkles, the posterior ones being zigzagged; surface of the shell covered with oblique folds and wrinkles; epidermis dark olive, shining; left valve with two elongated, compressed pseudocardinals, the posterior under the beak and curved upwards, cutting off the hinge plate in the right valve, which has a single, compressed pseudocardinal in front; laterals numerous, short, blurred; nacre white. Marsupium occupying the outer gills.

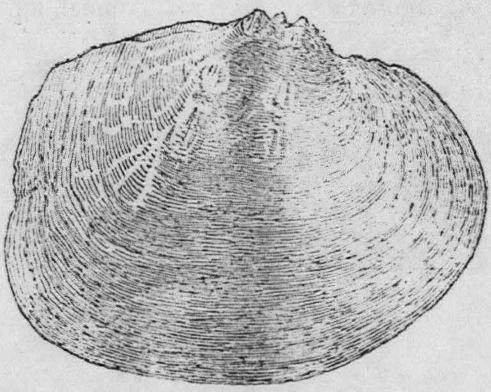

Fig. 173

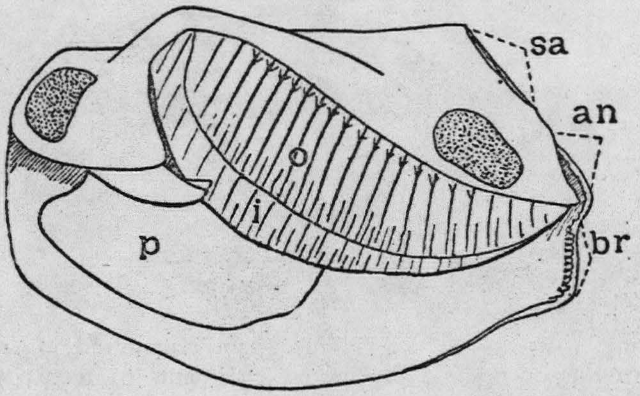

Fig. 174

Type: *Alasmodonta confragosa* Say, fig. 173. Animal, fig. 174.

Genus ARKANSIA Ortmann and Walker, 1912.

Shell moderately thick, subrotund to subovate or subrhomboidal, inflated, with full beaks. Disk sculptured with irregular, oblique folds, which are sometimes indistinct. Beak sculpture poorly developed, consisting of two to three double-looped bars, the loops slightly swollen or tubercular, disappearing toward the disk and not continuous with the sculpture of the latter. Hinge well developed, with strong pseudocardinals, a very strong interdental projection in the left valve and well developed, strong, but rather short laterals.

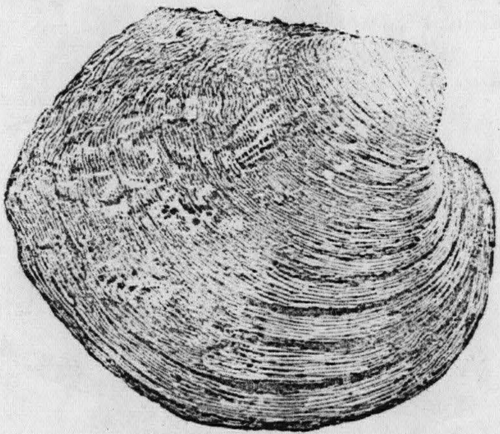

Fig. 175

Outer gills only marsupial.

Type: *Arkansia wheeleri* O. and W., fig. 175.

Genus LASMIGONA Rafinesque, 1831.

Shell elliptic-rhomboid, compressed; beaks low, their sculpture consisting of strong bars; one pseudocardinal in the right valve and two in the left, the hinder somewhat Λ-shaped, cutting off the hinge-plate in the right valve; laterals generally imperfect. Marsupium thick, padlike, filling the outer gills.

Key to the subgenera of *Lasmigona*.

1.	Shell corrugated on posterior slope	*Lasmigona s. s.*
	Shell smooth	2.
2.	Hinge teeth delicate	3.
	Hinge teeth very heavy	*Pterosyn*
3.	Lateral teeth compressed, moderately developed	*Platynaias.*
	Lateral teeth nearly or quite wanting	*Alasminota.*

Subgenus PLATYNAIAS Walker, 1917.

Shell smooth, subsolid, shining, rayed; beak sculpture sharply double-looped; teeth delicate; laterals compressed, moderately developed.

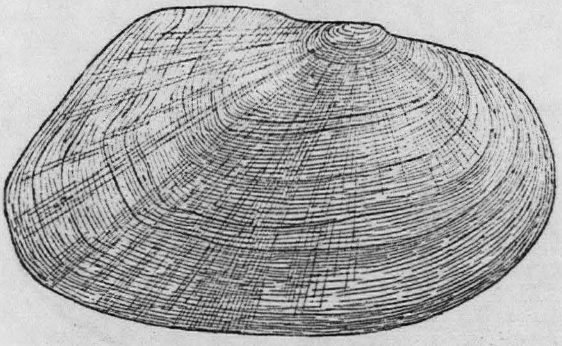

Fig. 176

Type: *Symphynota compressa* Lea, fig. 176.

Subgenus LASMIGONA s. s.

Shell subrhomboid, compressed, corrugated behind; beaks low, their sculpture consisting of several coarse ridges, which generally fall into two slight loops, and often with radiating ridges in front and behind; epidermis shining; laterals partly developed, consisting of blurred ridges, which slope diagonally downward and backward on the hinge-plate; cavities of the beaks shallow.

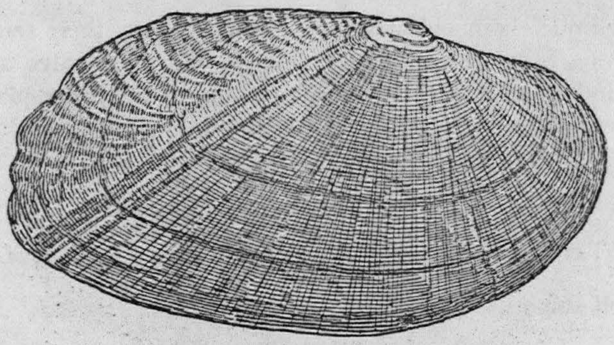

Fig. 177

Type: *Alasmidonta costata* Raf., fig. 177.

Subgenus ALASMINOTA Ortmann, 1914.

Shell elongated elliptical, rather small. Surface without sculpture. Pseudocardinals delicate; laterals nearly or quite wanting. Beak sculpture not heavy, consisting of four to six rather fine, sharp bars, the first one or two subconcentric, the following ones sharply double-looped, the posterior loop smaller, separated from the anterior by a deep, sharp, re-entering angle.

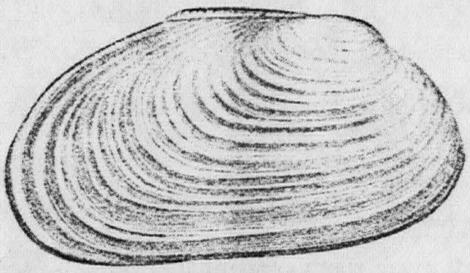

Fig. 178

Type: *Margaritana holstonia* Lea, fig. 178.

Subgenus PTEROSYNA Rafinesque, 1831.

Shell large, ovate-rhomboid, inflated in the post-basal region; beaks much compressed; their sculpture sharply and strongly doubly looped; epidermis dark, scarcely rayed; teeth very heavy.

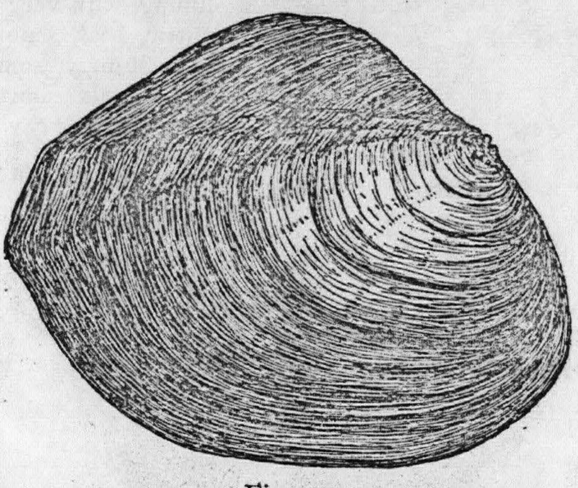

Fig. 179

Type: *Alasmodonta complanata* Bar., fig. 179.

Genus ALASMIDONTA Say, 1818.

Shell generally rhomboid, inflated, with a well developed posterior ridge, which ends in a point when it is single or a biangulation when double; beaks full and high, with coarse, concentric or slightly doubly looped bars; epidermis rayed, shining; hinge with two pseudocardinals in the left valve and one in the right; laterals usually wanting or imperfect, present in *Prolasmidonta*, cavity of the beaks deep; nacre bluish. Marsupium occupying the entire outer gills.

Key to the subgenera of *Alasmidonta*.

1.	Lateral teeth present	*Prolasmidonta.*
	Lateral teeth absent or obsolete	2.
2.	Shell solid, pseudocardinals solid, stumpy	3.
	Shell thinner, pseudocardinals compressed or imperfect	4.
3.	Shell ovate-rhomboid, inflated	*Alasmidonta s. s.*
	Shell smaller, compressed, very solid	*Pegias.*
4.	Posterior slope slightly corrugated	*Rugifera.*
	Posterior slope smooth	5.
5.	Shell rhomboid, posterior ridge low, rounded	*Pressodonta.*
	Shell subtriangular, posterior ridge high, sharp	*Bullella.*

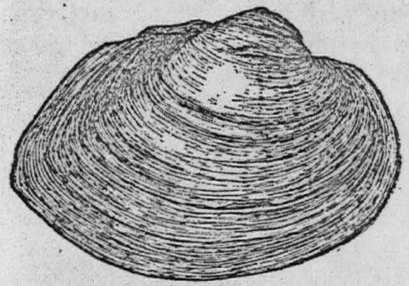

Fig. 180

Subgenus ALASMIDONTA s. s.

Shell ovate-rhomboid, solid, inflated, shining, with very strong, generally concentric, beak sculpture; pseudocardinals solid, stumpy, somewhat radiately ridged; laterals short, very imperfect or wanting; beak cavities deep, compressed.

Type: *Monodonta undulata* Say, fig. 180.

Subgenus PRESSODONTA Simpson, 1900.

Shell small, decidedly rhomboid, surface generally painted with unbroken rays; beak sculpture slightly corrugated; teeth compressed.

Type: *Unio calceolus* Lea, fig. 181.

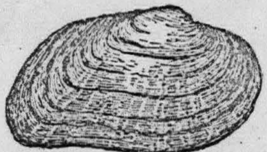

Fig. 181

Subgenus PROLASMIDONTA Ortmann, 1914.

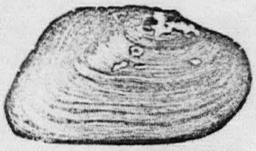

Fig. 182

Lateral hinge teeth present, but their number reversed, two in the right, one in the left valve. Beak sculpture moderately heavy, bars with an angle upon the posterior ridge and a slight sinus in front of it. Inner lamina of inner gills free. Female shell recognizable by a slight swelling in the region of the posterior ridge.

Type: *Unio heterodon* Lea, fig. 182.

Subgenus PEGIAS Simpson, 1900.

Fig. 183

Shell small, thickened in front, with a sharp posterior ridge, in front of which is a wide, radial impression, ending in a basal sinus; above this ridge is another, making the shell decidedly biangulate and truncate behind; beak sculpture consisting of sub-conic corrugations, generally swollen on the posterior ridge; epidermis decorticated, but showing a few, dark radial rays on the base of the shell; pseudocardinals rather solid; laterals wanting.

Type: ***Margaritana fabula*** **Lea, fig. 183.**

Subgenus RUGIFERA Simpson, 1900.

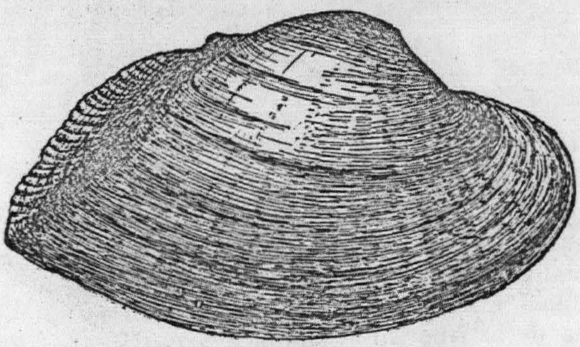

Fig. 184

Shell elongated, rhomboid, inflated, surface brilliantly painted with radiations which often break into dappled or splashed pattern of color; posterior slope slightly corrugated; teeth very imperfect; laterals wanting.

Type: *Alasmodonta marginata* Say, fig. 184.

Subgenus BULLELLA Simpson, 1900.

Shell thin, greatly inflated, somewhat triangular, with a high, sharp posterior ridge; beaks very full, having exceedingly strong, concentric sculpture, extending well on to the disk; pseudocardinals reflexed, compressed.

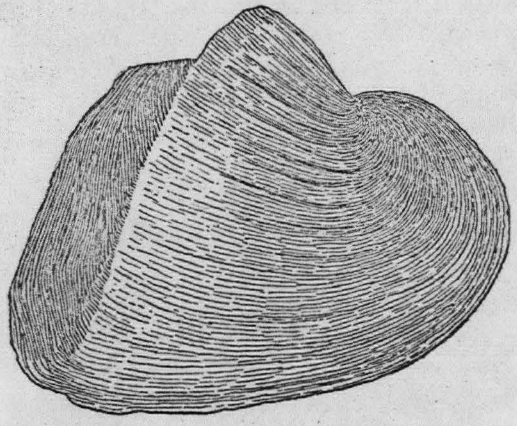

Fig. 185

Type: *Margaritana arcula* Lea, fig. 185.

Genus SIMPSONICONCHA Frierson, 1914.

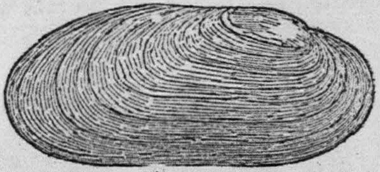

Fig. 186

Shell small, elongate elliptical, rounded in front and behind, often slightly incurved at the central base; beak rather sharp, but not full; sculpture consisting of fine parallel ridges which are looped up in the middle and open behind; epidermis brownish, rayless; teeth imperfect, a single, irregular, compressed tooth in each valve; laterals nearly or quite wanting; anterior end of the shell much thickened; nacre dull whitish. Marsupium occupying the whole of the outer gills.

Type: *Alasmodonta ambigua* Say, fig. 186.

Subfamily LAMPSILINÆ Ortmann, 1912.

"Inner lamina of inner gills rarely more or less free from the abdominal sac, generally connected with it throughout; supra-anal opening separated from the anal, rarely entirely closed; branchial openings well defined; edge of the mantle in front of the branchial opening smooth to crenulated or with peculiar papillæ or a flap; marsupium rarely formed by the whole outer gill, generally only by or within the posterior part of the outer gill; edge of marsupium, when charged, distending and bulging out beyond the original edge of the gill, generally assuming a beaded appearance; water-tubes simple in the gravid female; glochidium semicircular or semi-elliptic, without spine, rarely celt-shaped and with two spines; shell heavy or lighter, rounded, or oval to elongate; color of the epidermis rarely dull, mostly bright, with color markings; sculpture of the beak generally double-looped, but often obsolete, more rarely concentric; hinge generally complete, with well developed teeth, which only in rare cases show a tendency to become reduced; sexual differences more or less noticeable in the shell, often very strongly expressed." (Ortmann.)

Key to the genera of *Lampsilinæ*.

1. Male and female shells alike .... 2.
   Male and female shells different ....

2. Shell elongate-triangular .... *Ptychobranchus.*
   Shell rounded-triangular or oval .... 3.

3. Shell oval, with a medial row of large tubercles .... *Obliquaria.*
   Shell rounded-triangular, nodulously wrinkled or lachrymose .... 4.

4. Epidermis painted with delicate mottlings on a light ground, beak cavities shallow .... *Cyprogenia.*
   Epidermis painted with radiating hair-lines, beak cavities deep and compressed .... *Dromus.*

5. Female shell more or less expanded in the post-basal region ...... 6.
   Female shell slightly swollen just behind the middle of the base .... *Medionidus.*

6. Dorsal margin winged .... 7.
   Dorsal margin not winged .... 8.

7. Pseudocardinals perfect; glochidium celt-shaped, with two spines .... *Proptera.*
   Pseudocardinals rudimentary; glochidium semicircular, without spines .... *Paraptera.*

8. Pseudocardinals well developed, complete .... 9.
   Pseudocardinals divided into irregular laminæ .... *Glebula.*

9. Shell with a distinct posterior ridge, dorsal-slope smooth .... 10.
   Shell usually without a distinct posterior ridge, or when distinct, dorsal-slope radiately sculptured .... 11.

10. Hinge heavy and strong; hinge-plate wide and flat .... *Plagiola.*
    Hinge delicate; hinge-plate narrow .... *Amygdalonaias.*

11\. Marsupial expansion of the female shell of the same texture as the rest of the shell .... 12.
Marsupial expansion of the female shell of different texture from the rest of the shell and usually radiately sculptured .... *Truncilla.*

12\. Inner edge of the mantle in front of the branchial opening differentiated with papillæ or flaps .... 13.
Inner edge of mantle in front of branchial opening without papillæ or flaps .... 16.

13\. Shell smooth .... 14.
Shell strongly sculptured posteriorly .... *Lemiox.*

14\. Beak sculpture double-looped .... 15.
Beak sculpture concentric .... *Carunculina.*

15\. Inner edge of mantle in front of branchial opening in female distinctly papillate .... *Eurynia.*
Inner edge of mantle in front of branchial opening in female with a ribbon-like flap .... *Lampsilis.*

16\. Shell inflated, usually higher than long .... *Obovaria.*
Shell subcompressed, longer than high .... *Actinonaias.*

Genus PTYCHOBRANCHUS Simpson, 1900.

Shell triangular, solid, sometimes becoming arcuate in old specimens; umbonal region rather elevated; beak sculpture consisting of faint, somewhat broken ridges, which have a tendency to be doubly looped; posterior ridge rounded, but well developed; epidermis usually painted with wavy hair-like rays or broken, radiating bars, which show a tendency to form square spots; hinge-plate rather wide and flat; pseudocardinals small, low, triangular and roughened; laterals club-shaped, remote.

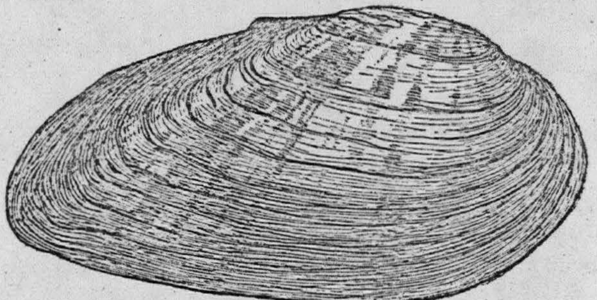

Fig. 187

Marsupium occupying the basal half of the entire length of the outer gills and having in front six to twenty beautiful folds; ovisacs distinct, each ending below in an enlarged, rounded bulb, which has a colored spot in the centre.

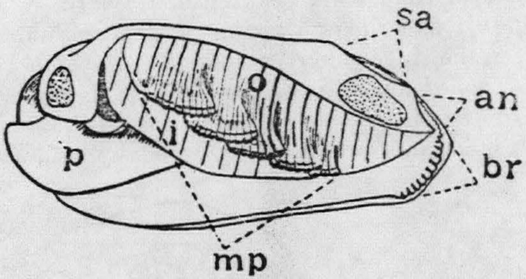

Fig. 188

Type: *Unio phaseolus* Hild., fig. 187. Animal, *P. subtentus* (Say), fig. 188.

Genus OBLIQUARIA Rafinesque, 1820.

Shell inflated, solid, oval, ending in a tolerably sharp point behind, having a row of large, compressed, longitudinal knobs running from the beaks to the centre of the base, those of one valve alternating with the knobs of the other, and a well developed posterior ridge, the space between the ridge and the knobs somewhat excavated; posterior slope and sometimes the entire shell more or less corrugately sculptured; beaks prominent, incurved and pointed slightly forward toward a tolerably well developed lunule; beak sculpture strong, consisting of four or five heavy, parallel ridges, which fall low in front, but are curved upwards behind; epidermis smooth, generally shining, painted with numerous, delicate, wavy, darker, broken rays; pseudocardinals strong, distinct and ragged; laterals short, nearly straight; front part of the shell very solid, suddenly becoming rather thin, just behind the knobs. Marsupium consisting of a few, distinctly marked ovisacs (4 to 7) occupying a position just behind the centre of the outer gills, projecting far below the rest of the branchiæ, their bases rounded.

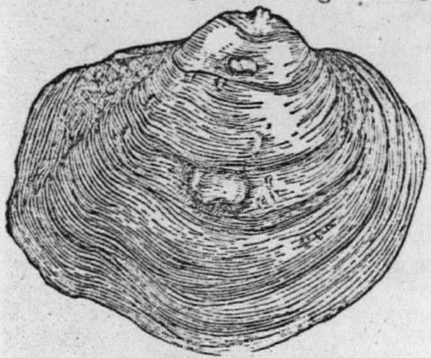

Fig. 189

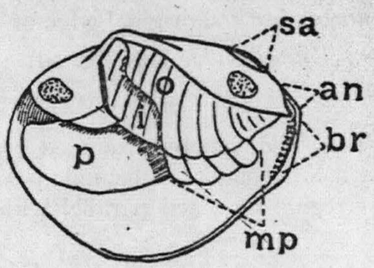

Fig. 190

Type: *O. reflexa* Raf., fig. 189. Animal, fig. 190.

Genus DROMUS Simpson, 1900.

Shell solid, rounded triangular; beaks well forward, rather high; beak sculpture consisting of fine ridges running parallel with the growth lines, the furrows between the ridges interrupted at the posterior ridge; posterior ridge distinct; a series of humps runs from the beaks down to the central part of the base of the shell, which is otherwise sculptured by irregular, concentric ridges; epidermis beautifully painted by undulated, radiating, broken hair-lines or fine maculations; hinge plate wide and flat; pseudocardinals triangular, small and low, ragged; laterals low, short, club-shaped; cavity of the beaks deep and compressed; front part of the shell very thick, suddenly becoming thinner at the row of humps. Marsupium occupying the base of nearly the whole outer gills in numerous narrow ovisacs, which extend beyond the original edge of the gill.

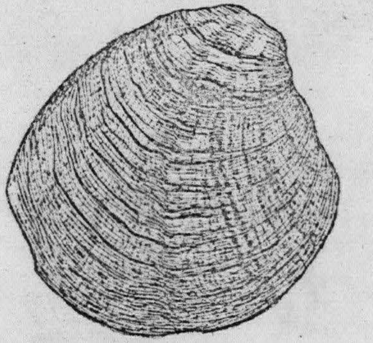

Fig. 191

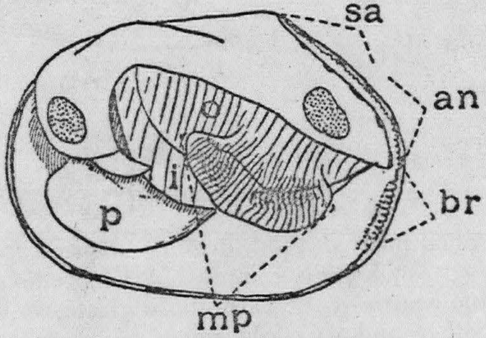

Fig. 192

Type: *Unio dromas* Lea, fig. 191. Animal, frontispiece, fig. 192.

Genus CYPROGENIA Agassiz, 1852.

Shell solid, inflated, rounded, triangular, sometimes slightly retuse, generally a little biangular behind; posterior ridge usually well developed; umbonal region flattened parallel with the axis of the shell, sometimes com-

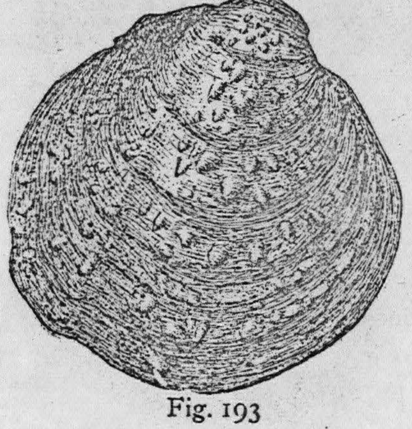

Fig. 193

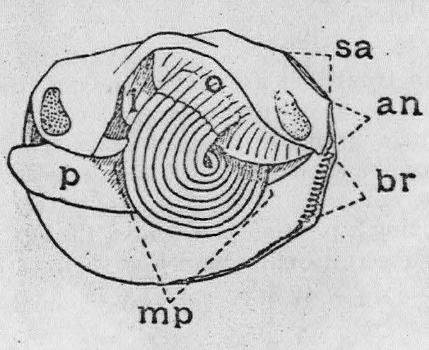

Fig. 194

pressed; beaks curved inward and forward, their sculpture very faint, consisting of slightly double looped ridges; sculpture of the shell nodular, radiately wrinkled or lachrymose; ligament black and conspicuous; lunule distinct, well developed; epidermis shining, painted with a delicate mottling on a light ground; hinge plate wide and flat; pseudo-cardinals heavy, triangular, blunt and ragged; laterals short, obliquely striated; cavity of the beaks not deep; nacre bright and silvery.

Marsupium consisting of from seven to twenty-three very long, purple ovisacs pendant from near the central base of the outer gills and formed into a close coil with the ends turned inward.

Type: *Unio irroratus* Lea, fig. 193. Animal, fig. 194.

Genus PLAGIOLA (Rafinesque, 1819), Agassiz.

Shell solid, surface irregularly, concentrically ridged; epidermis smoothish, but here and there wrinkled; painted with larger and smaller scattered rays, which are generally broken into irregular lunate or squarish blotches; hinge heavy and strong; hinge plate wide and flat; female shell smaller than the male, more inflated and swollen at the post basal region. Marsupium large, projecting far below the inner gills.

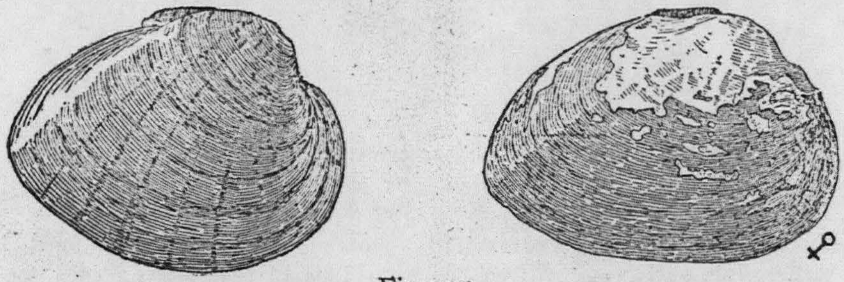

Fig. 195

Type: *Unio securis* Lea, fig. 195.

Genus AMYGDALONAIAS Fischer and Crosse, 1893.

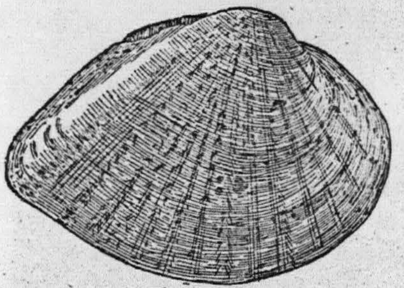

Fig. 196

Shell inflated, decidedly truncate at the posterior slope; surface slightly concentrically sculptured; posterior ridge sharp and well defined; epidermis shining, sometimes wrinkled, looped and painted with a beautiful pattern of broken or arrow-marked rays; area of the beaks flattened off in the direction of the axis of the shell, but not compressed; beak sculpture delicate, somewhat broken and doubly looped, the anterior loop rounded, the posterior sharp below, the ribs fading out where they cross the posterior ridge; hinge delicate; pseudo-cardinals rather compressed, high and ragged; hinge plate narrow; female shell very slightly swollen at the post-base. Marsupium consisting of numerous, distinct ovisacs and having a well marked sulcus extending around it at some distance above its base.

Type: *Unio cognatus* Lea.
Example: *P. elegans* (Lea), fig. 196.

Genus MEDIONIDUS Simpson, 1900.


Fig. 197

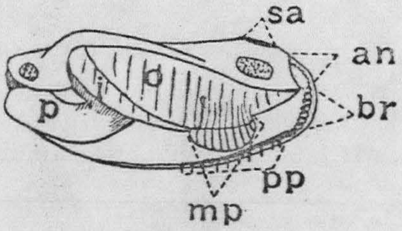

Fig. 198

Shell elongated, rather inflated, often arcuate when adult, sometimes having a posterior ridge; dorsal slope and occasionally the posterior portion of the shell plicately or nodulously wrinkled; epidermis smooth and bright, variagated with broken green rays and blotches; beak sculpture consisting of rather fine, subparallel, often broken ridges in two loops, the anterior rounded, the posterior somewhat angled, occasionally broken into zigzags; pseudo-cardinals small, stumpy and somewhat roughened; laterals rather short, slightly curved and club-shaped; female shell slightly swollen behind the middle of the base. Marsupium occupying the central posterior part of the outer gills, sometimes extending nearly their whole length.

Type: *Unio conradicus* Lea, fig. 197. Animal, fig. 198.

Genus GLEBULA Conrad, 1853.

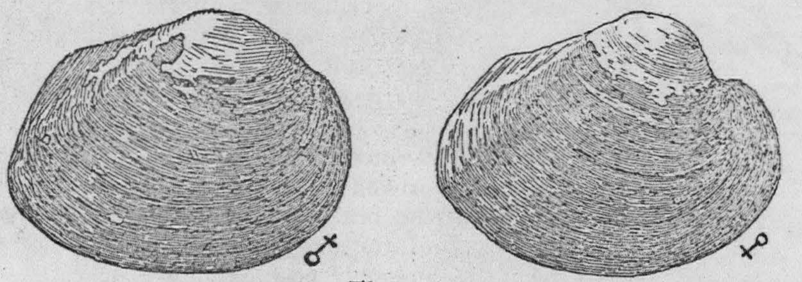

Fig. 199

Shell solid, much inflated, short, elliptical, bluntly pointed and slightly biangulate behind, with a low, posterior ridge; female shell swollen at the post-base; beaks compressed, sculpture unknown; epidermis brownish, cloth-like; pseudo-cardinals divided into irregularly radiating, granular lamina, sometimes to the number of a dozen or more in each valve; hinge-plate reduced to a mere rounded line behind the pseudo-cardinals; laterals short, remote. Ovisacs apparently separated from each other by a sulcus.

Type: *Unio rotundata* Lam., fig. 199.

Genus PROPTERA Rafinesque, 1819.

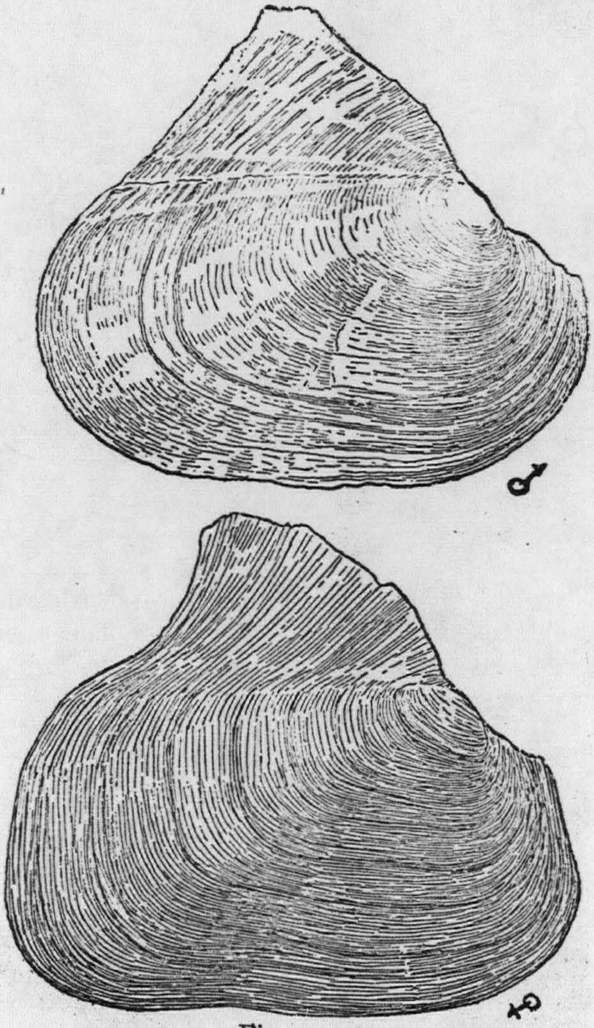

Fig. 200

Shell usually large, gaping at anterior edge and edge of dorsal slope, winged along the dorsal region when young and often when adult; beak sculpture feeble, consisting, when developed, of an anterior and posterior loop, the former often wanting; epidermis generally brown, often cloth-like when fresh, rayless or feebly rayed; teeth rather compressed, pseudo-cardinals frequently imperfect or nearly wanting; laterals remote. Marsupium kidney-shaped, consisting of numerous ovisacs occupying the posterior part of the outer gill; edge of mantle in female slightly lamellar in front of the branchial opening with granulations, but without papillæ. Glochidia celt-shaped, with two spines, one at each of the ventral corners.

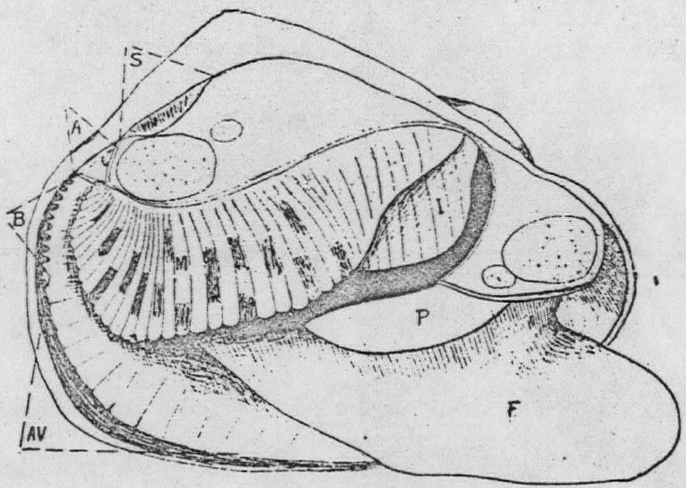

Fig. 201

Type: *Unio alatus* Say, fig. 200. Animal, fig. 201.

Genus PARAPTERA Ortmann, 1911.

Shell large, thin, elliptical or slightly obovate, more or less compressed, winged on the dorsal margin; beaks low; epidermis rather smooth, often feebly rayed, dull colored, but usually glossy; teeth compressed, pseudo-cardinals but feebly and often imperfectly developed; nacre purplish. Male and female shells nearly alike, the latter scarcely swollen at post-basal region.

Marsupium kidney-shaped, swollen, consisting of many ovisacs occupying the posterior part of the outer gill; mantle edge of the female slightly lamellar in front of the branchial opening, with crenulations, but not with papillæ. Glochidia very small, of suboval shape.

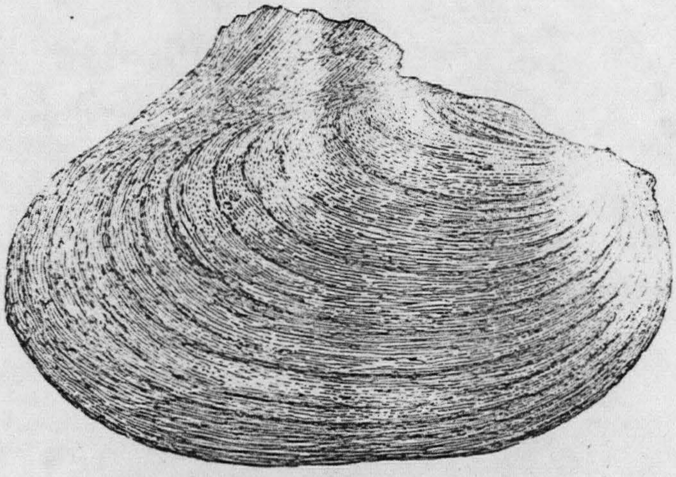

Fig. 202

Type: *Unio gracilis* Bar., fig. 202.

Genus OBOVARIA Rafinesque, 1819.

Shell short, oval, rounded or retuse, solid, inflated, thick in front, thinner behind, with high beaks, which are sculptured with very faint, irregular, often broken and slightly nodulous ridges, which show a tendency to fall into two loops, the posterior often open behind; epidermis dull, brownish, silky or cloth-like, rarely rayed, rays indistinct; female shell but slightly inflated in the post basal region, commonly having a shallow furrow or a flattened area at the posterior end; pseudo-cardinals solid; stumpy; laterals short, club-shaped. Marsupium kidney-shaped, projecting far below the edge of the gill and occupying the posterior portion of the outer gills.

Key to the subgenera of *Obovaria*.

Shell retrorse to short oval, beaks high and central........*Obovaria s. s.*
Shell elliptical, beaks anterior............................*Pseudoön.*

Subgenus OBOVARIA s. s.

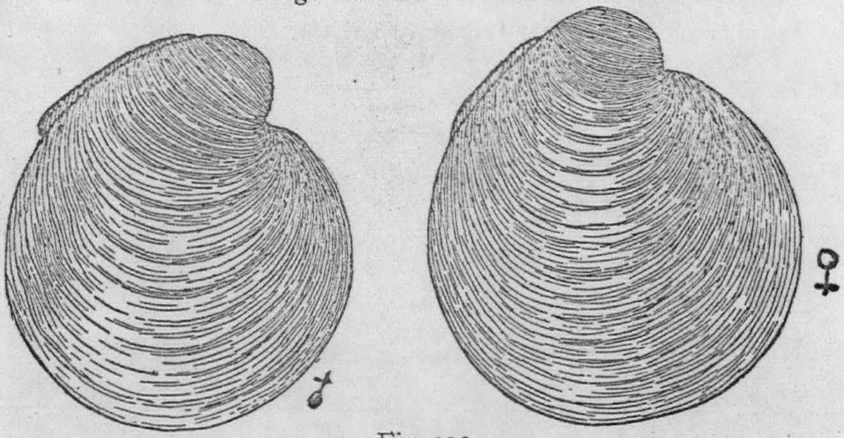

Fig. 203

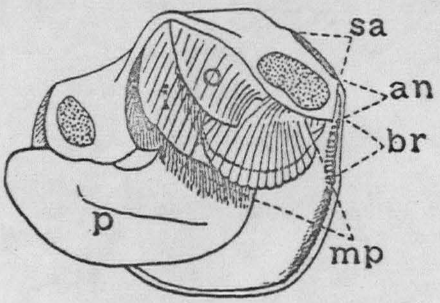

Fig. 204

Shell retrorse to short oval; beaks high, central; pseudo-cardinals rarely parallel with the laterals; cavity of the beaks deep, subcompressed; nacre bluish-white or purple. Marsupium as in the genus.

Type: *Unio retusa* Lam., fig. 203. Animal, fig. 204.

Subgenus PSEUDOÖN Simpson, 1900.

Shell elliptical, inflated, solid; that of the male slightly pointed at the upper posterior part; epidermis brownish or blackish, rayless or very feebly

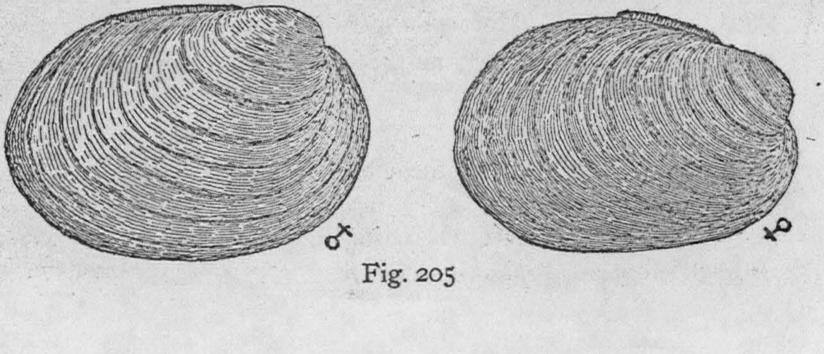

Fig. 205

rayed; beaks anterior; pseudo-cardinals solid, stumpy or slightly elongate in age, and showing a tendency toward being parallel with the laterals; nacre silvery, iridescent posteriorly. Marsupium kidney-shaped, not reaching to the posterior end of the outer gill, though extending quite well forward.

Type: *Unio ellipsis* Lea, fig. 205.

Genus ACTINONAIAS Fischer and Crosse, 1893.

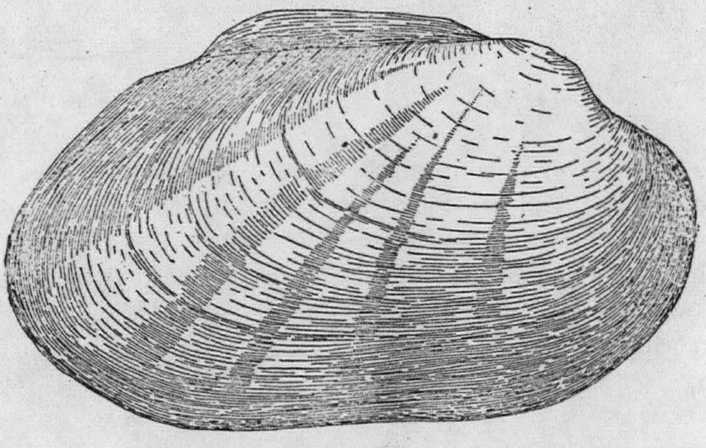

Fig. 206

"Shell ovate or subelliptical, distinctly longer than high, compressed or slightly inflated, without, or with, indistinct posterior ridge. Disk not sculptured. Beaks moderately anterior, never in the middle of the shell and never very near the anterior end. Beak-sculpture poorly developed, consisting of a few faint bars, which have a tendency to become double-looped, with the central part between the loops obliterated. Epidermis yellowish to greenish, generally with distinct rays. Male and female shells differing in shape, but the difference often hardly noticeable.

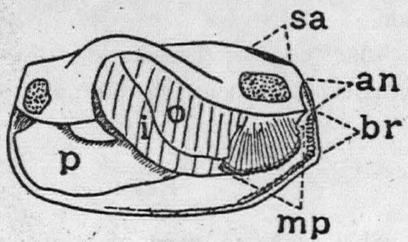

Fig. 207

Soft parts agreeing with those of Obovaria in every respect: the glochidia also of the same type." (Ortmann.)

Type: *Unio sapotalensis* Lea, (animal), fig. 207.

Example: *A. ligamentinus* (Lam.), fig. 206.

Genus CARUNCULINA Simpson, 1898.

Shell small, inflated, obovate, rather solid, with a thick dark epidermis, which is rayless or only feebly rayed; beak sculpture consisting of rather strong, concentric ridges, which form, as a general thing, only a single rounded loop in front and are strongly curved upward behind. Pseudocardinals compressed, smooth on the inside, generally reflected upward, somewhat torn on the edges. Shell quite commonly pointed posteriorly, that of the female truncated obliquely on the post-base. Marsupium kidney-shaped, formed by a few large ovisacs, projecting beyond the gill; female having a well developed caruncle on the inner edge of the mantle in front of the branchial opening.

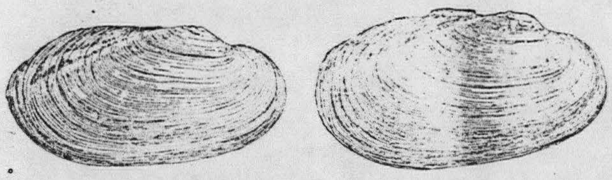

Fig. 208

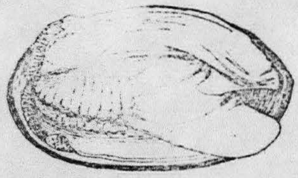

Fig. 209

Type: *Unio parvus* Bar., fig. 208. Animal, fig. 209.

Genus EURYNIA Rafinesque, 1820.

Shell oval to oblong; surface smooth; beak sculpture delicate, double-looped; female shell more or less expanded or swollen in the post-basal region.

Inner edge of the mantle in the female distinctly papillate. Marsupium kidney-shaped, ocupying the posterior part of the outer gill.

Key to the subgenera of *Eurynia*.

Shell elongate, more or less pointed behind.

Papillæ on inner edge of mantle regular, uniform, reaching to middle of lower margin............................*Eurynia s. s.*

Shell subovate or subelliptical, not much pointed behind.

Papillæ on inner edge of mantle irregular, not reaching to middle of lower margin..................................*Micromya.*

Subgenus EURYNIA s. s.

Shell usually of good size, subelliptical, elongated, more or less pointed behind; beak sculpture double-looped, the posterior loop often open behind.

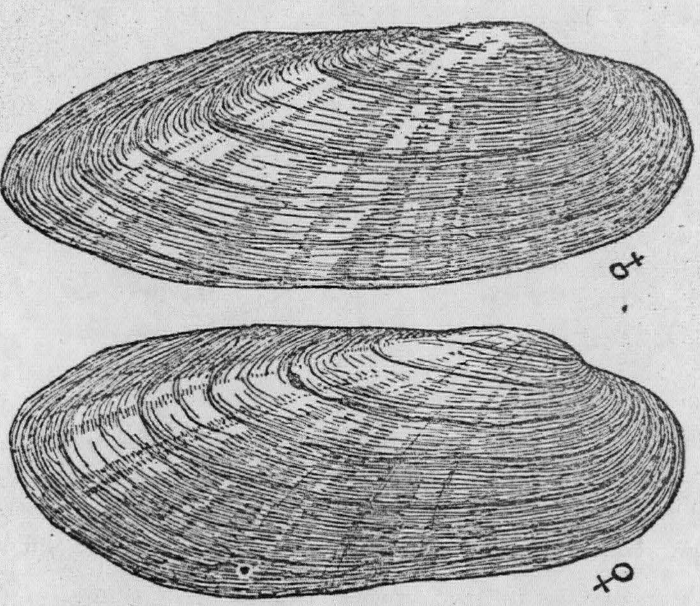

Fig. 210

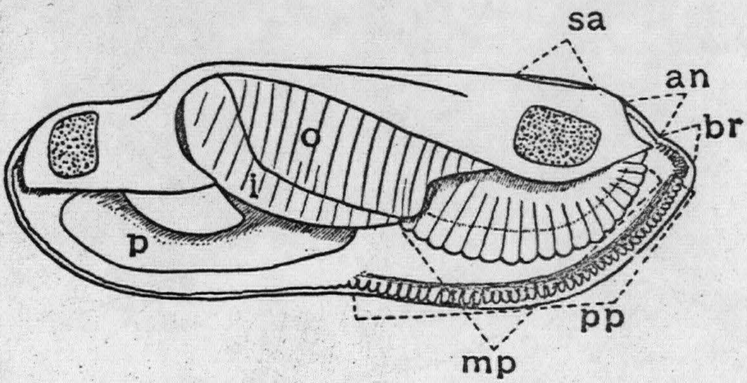

Fig. 211

Inner edge of the mantle in the female in front of the branchial opening with a long row of quite regular, uniform, subequal papillæ, reaching to about the middle of the lower margin.

Type: *Unio recta* Lam., fig. 210. Animal, fig. 211.

Subgenus MICROMYA Agassiz, 1852.

Shell small or of medium size, suboval or subelliptical, not very long and not much pointed behind; beak sculpture distinctly double-looped, but often obsolete, the posterior loop often showing a tendency to be open.

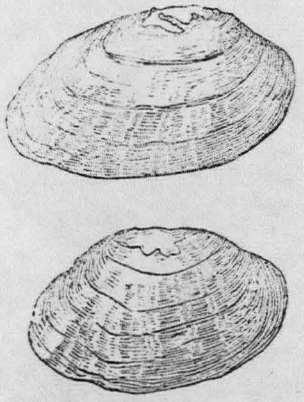

Fig. 212

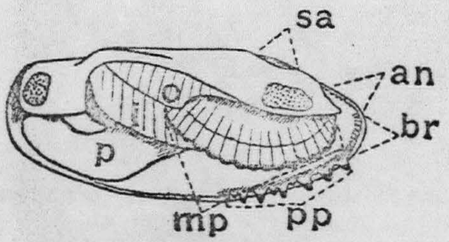

Fig. 213

Inner edge of the mantle of the female in front of the branchial opening with a shorter or longer row of rather irregular, larger and smaller papillæ, reaching not quite to the middle of the lower margin.

Type: *Unio fabalis* Lea, fig. 212. Animal, *E. iris* (Lea), fig. 213.

Genus LAMPSILIS Rafinesque, 1820.

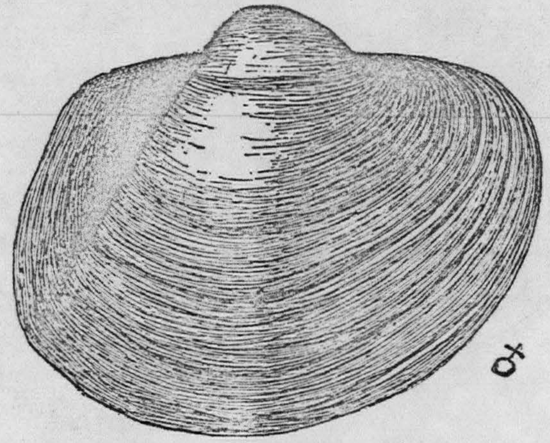

Fig. 214

Shell oval to elliptical, smooth or slightly, concentrically sculptured, usually without a posterior ridge; epidermis generally smooth and shining, often rayed; beak sculpture, consisting of double-looped, parallel ridges, sometimes the posterior loop open behind or the sculpture is obsolete; hinge