Genus	Vol. 9 (1): 1-93	Wrocław, 30 IV 1998

European species of the family *Lymnaeidae* (*Gastropoda*: *Pulmonata*: *Basommatophora*)

MARIA JACKIEWICZ
Department of Animal Taxonomy and Ecology, Adam Mickiewicz University, Szamarzewskiego 89/91, 60-569 Poznań, Poland

ABSTRACT. The book presents the general data regarding freshwater snails of the order *Basommatophora* as well as detailed knowledge of the lymnaeid morphology, anatomy, biology, ecology and taxonomy. The book contains a key to species identifications and author's views on the phylogeny and the relationships within the family *Lymnaeidae*. The book is addressed to malacologists and to hydrobiologists, teachers, students and amateur-malacologists.

Key words: malacology, monograph, Europe, *Gastropoda*, *Lymnaeidae*.

The book is dedicated to Professor Dr hab. Jarosław URBAŃSKI's memory.

[1]The studies were partially supported by a grant within the research programme of the Zoological Institute, Polish Academy of Sciences, Warsaw, project CPBP 04.06.05.1.12.1 „*Lymnaeidae* (*Gastropoda, Pulmonata*) of Poland".

CONTENTS

I. INTRODUCTION

Lymnaeid shells display a wide variability. Almost 1800 lymnaeid species and forms have been described on the basis of shell morphology. HUBENDICK (1951) estimates the number of recent world species, that are significantly different in anatomical structures, at about 40. It is currently known that the anatomical structure of the lymnaeid reproductive organs is of much more taxonomic value than the shell. Moreover, it plays a fundamental role in the recognition of phylogenetic relationships of these snails.

On the basis of anatomical structure of their reproductive organs, eleven lymnaeid species have been found to exist in Europe. They belong to the family *Lymnaeidae*, which comprises one of the basic groups of the order *Basommatophora* in the subclass *Pulmonata.*

On the other hand, species described in recent years in European parts of the former U.S.S.R. have not been taken into consideration in this paper. Opinions of Russian malacologists on the lymnaeid taxonomy, as well as on that of other snail and bivalve groups, raised great doubts and are not accepted by all European specialists.

There is a considerable discrepancy in the literature on the systematics of the family *Lymnaeidae*. GEYER (1927) distinguished 6 genera in this family: *Lymnaea* LAMARCK, 1799, *Radix* MONTFORT, 1810, *Stagnicola* LEACH, 1830, *Leptolymnaea* SWAINSON, 1840, *Galba* SCHRANK, 1803 and *Amphipeplea* NILSSON, 1822. EHRMANN (1937) listed 5 genera: *Lymnaea* LAMARCK, 1799, *Stagnicola* LEACH, 1830 (with subgenera *Stagnicola* s. str. and *Omphiscola* BECK, 1837), *Radix* MONTFORT, 1810, *Galba* SCHRANK, 1803 and *Myxas* SOWERBY, 1822. According to HUBENDICK (1951), all lymnaeid species belong to one genus, that is *Lymnaea* LAMARCK, 1799. Only some North American lymnaeid species are included in a separate genus *Lanx* CLESSIN, 1882. The genus constitutes a different group, sometimes elevated to subfamily (*Lancinae*) or even to family (*Lancidae*) rank.

Taking into account the structure of the reproductive organs, particularly the praeputium and prostate, I have distinguished 2 genera in the family *Lymnaeidae*: *Omphiscola* BECK, 1837 and *Lymnaea* LAMARCK, 1799, with 5 subgenera: *Galba* SCHRANK, 1803, *Radix* MONTFORT, 1810, *Myxas* SOWERBY, 1822, *Stagnicola* LEACH, 1830 and *Lymnaea* s. str. (JACKIEWICZ 1993b).

There is a relatively high number of papers on lymnaeids in Polish. Some of them only list species recorded from particular regions. Many malacologists have however extended their studies through anatomy, systematics and zoogeography. Publications of FALNIOWSKI (1980a, 1980b, 1981), FELIKSIAK (1938) and PIECHOCKI (1969, 1975, 1979a, 1979b) belong to the latter category. Among Polish authors, ROSZKOWSKI (1914a, 1914b, 1914c, 1923, 1925, 1926, 1927, 1928, 1929), and ROSZKOWSKI and ŻEBROWSKA (1915) have contributed the largest share to the knowledge of the family *Lymnaeidae*. They were the first to appreciate the value

of anatomical characters. The outstanding Swedish malacologist, Bengt HUBENDICK, continued their studies. His comprehensive monograph, published in 1951, is dedicated to the world distribution of lymnaeid species, their variability, anatomy, systematics and nomenclature. The anatomy and systematics of lymnaeids, particularly of those occurring in Germany, have been a subject of FALKNER's studies (1984, 1985, 1990) for the last few years.

II. GENERAL PART

1. CHARACTERISTICS OF LYMNAEIDS

Shells of snails of the family *Lymnaeidae* are dextrous (except some sinistrous species from Oceania), turriform, sometimes low-spired and with a greatly expanded body whorl. The body is massive, the head with wide snout lobes is shortly set. The tentacles are triangular and the eyes are located internally at their basis. The pneumostome as well as male and female gonopores are situated on the right side of the snail body. The foot is wide, sharply truncated in front, and rounded at the rear. The jaws are threefold. The central tooth of the radula is narrow with one small cusp. The lateral teeth are large with 2-3 cusps. The marginal teeth are smaller with many cusps. The reproductive organs split into male and female parts as early as at the end of the hermaphroditic duct.

The lymnaeid geographic distribution is wide. They inhabit large areas of almost all continents (HUBENDICK 1951). They are absent from circumpolar areas, northern parts of South America, and almost all Sahara, partially from the Arabian Peninsula as well as from western Australia and probably some Pacific islands. They are treated as a cosmopolitan group. The greatest number of species is found in Western Europe (11), eastern parts of North America (10) and on the Hawaiian Islands (5) (JACKIEWICZ 1991). Some species are widely distributed, for example *Lymnaea stagnalis* (L.), *L. truncatula* (O.F.MÜLL.) and *L. auricularia* (L.). The ranges of other species, like *Omphiscola glabra* (O.F.MÜLL.), are limited.

According to HUBENDICK (1951), lymnaeids have their „roots" in North America, as the number of species found there is high. He shared ROSZKOWSKI's (1928) opinion that the migration *Lymnaea* from one area to another took place through the transpacific bridge.

However, an analysis of the world distribution of the genus *Lymnaea* throws new light on this problem. Most of the lymnaeid species occur in western Palaearctic (11) and in eastern Nearctic (10) areas. Lymnaeids could arise and disperse from the areas which formed, according to Wegener's continental drift theory, one land in the past and were later separated into Western Europe and eastern parts of North America. This is evidenced by the amphiatlantic concentration of a large number of species and the great diversity of their internal

structure, particularly of the prostate, as well as by the fact that the genus *Lymnaea* has been known since Malm (JACKIEWICZ 1991).

The analysis of the structure of the reproductive organs of 11 European lymnaeid species (see: species descriptions and Table 1) allowed me to modify the systematic arrangement of the family *Lymnaeidae*. The differences in the structure of the reproductive organs of *Omphiscola glabra* are so great in relation to the other species, that it is necessary to distinguish two genera, as mentioned in the introduction: *Omphiscola* BECK, 1837 and *Lymnaea* LAMARCK, 1799. Five subgenera are distinguished in the genus *Lymnaea*.

2. DIAGNOSES OF GENERA AND SUBGENERA

Genus *Omphiscola* Beck, 1837

Lack of any fold inside prostate, proximal prostate part of the same width as its distal part or wider, one longitudinal fold inside praeputium, frequently with short additional fold, lack of papillary fold (velum), prolonged lumen of papilla (sarcobelum) (Figs 48-55).

Shell small, very narrow, slender, cylindrically turriform, with the spire height much greater than the aperture height, body whorl slightly wider than the penultimate one (Plate I.2).

Genus *Lymnaea* Lamarck, 1799

One or several folds inside prostate, proximal prostate part always narrower than its distal part, two longitudinal folds inside the praeputium, papillary fold (velum) present, round lumen of papilla (sarcobelum) (Figs 63A-C, E, 77E).

Shell characters are discussed in the descriptions of particular subgenera.

Subgenus *Galba* Schrank, 1803

Penis short and smooth (Fig. 61D), shell small, ovately conical, with the spire height usually greater than the aperture height or equal to it, and the body whorl much expanded (Plate I.1).

Subgenus *Radix* Montfort, 1810

Penis long and thin, resembling vas deferens (Fig. 63D), shell ovate or spherically ovate, large or medium, spire usually low, with the body whorl most frequently greatly expanded (Plates II, III).

Subgenus *Myxas* Sowerby, 1822

Penis long and thin (Fig. 67D), shell big and spherical, spire very low, with the body whorl very strongly expanded (Plate I.3), shell covered externally with greatly developed mantle.

Subgenus *Stagnicola* Leach, 1830

Penis long and thick with or without a narrowing, or very long (Figs 69D, 71D, 73D), shell large, ovately or cylindrically turriform, spire height frequently greater than the aperture height, with the body whorl greatly expanded (Plates IV-VI).

Subgenus *Lymnaea* s. str.

Penis short with a ring-shaped swelling (Fig. 75D), shell large or very large, ovately conical, spire height lower than the aperture height as a rule, with the body whorl greatly expanded (Plates VII-IX).

3. SYSTEMATIC INDEX OF EUROPEAN LYMNAEIDS

Family: *Lymnaeidae*

Genus: *Omphiscola* Beck, 1837

1. Species: *Omphiscola glabra* (O. F. Müller, 1774)

Genus: *Lymnaea* Lamarck, 1799

Subgenus: *Galba* Schrank, 1803

2. Species: *Lymnaea* (*Galba*) *truncatula* (O. F. Müller, 1774)

Subgenus: *Radix* Montfort, 1810

3. Species: *Lymnaea* (*Radix*) *peregra* (O. F. Müller, 1774)
4. Species: *Lymnaea* (*Radix*) *auricularia* (Linnaeus, 1758)

Subgenus: *Myxas* Sowerby, 1822

5. Species: *Lymnaea* (*Myxas*) *glutinosa* (O. F. Müller, 1774)

Subgenus: *Stagnicola* Leach, 1830

6. Species: *Lymnaea* (*Stagnicola*) *palustris* (O. F. Müller, 1774)
7. Species: *Lymnaea* (*Stagnicola*) *turricula* (Held, 1836)
8. Species: *Lymnaea* (*Stagnicola*) *occulta* (Jackiewicz, 1959)

Subgenus: *Lymnaea* s. str.

9. Species: *Lymnaea* (*Lymnaea*) *vulnerata* Küster, 1862
10. Species: *Lymnaea* (*Lymnaea*) *corvus* (Gmelin, 1791)
11. Species: *Lymnaea* (*Lymnaea*) *stagnalis* (Linnaeus, 1758)

4. SHELL

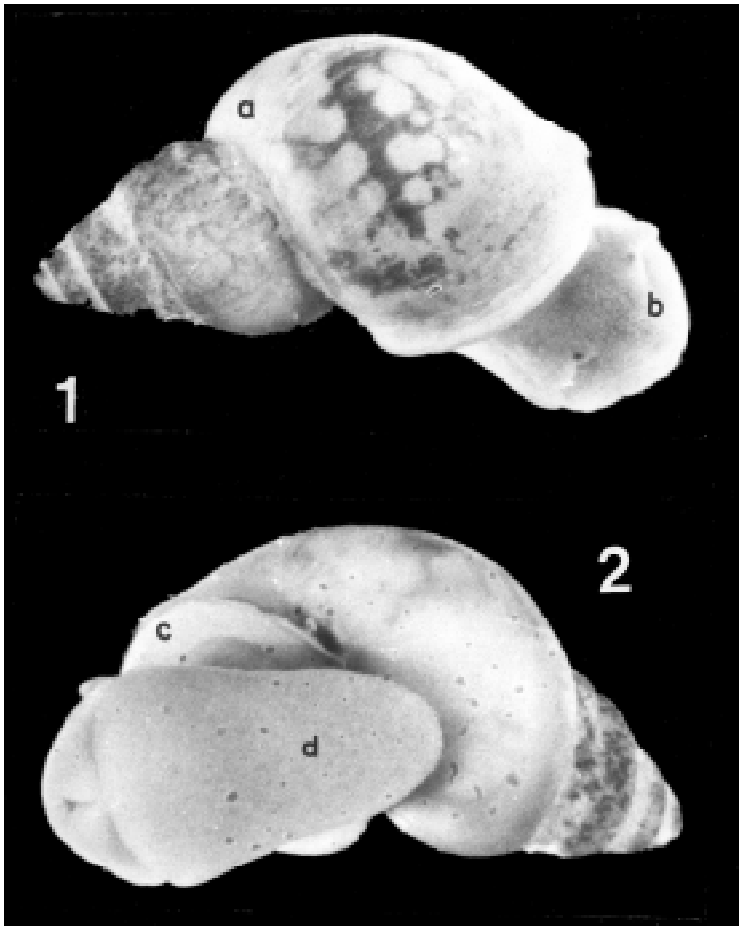
The lymnaeid body, particularly its visceral mass, is covered with a shell (Figs 1, 2) that secures its protection. When water reservoirs are drying, or in danger, a snail may also retract its head and foot into the shell.

Lymnaeid shells (Plates I-IX) are dextral and helical (turbospiral). The number of whorls (*anfracti*) ranges from 4 to 8. They are separated from one another by a suture of varying suture. The depth depends on the degree of whorl convexity. The first whorls, which are embryonic (protoconch), form the apex of the shell. The youngest whorl is always the largest and most frequently it is larger than all the previous whorls combined. This is best visible in *Lymnaea glutinosa* (Plate I.3). The internal wall of the shell, coiled spirally along the main axis, creates the axial column called a columella. The lumen of this column is very small and opens with a narrow, fissured axial pit called the umbilicus. It is almost completely covered with a columellar fold. This fold is usually thin, of lighter colour than the shell and close to the columellar margin of the shell aperture. Only the fold in *Lymnaea occulta* is wide, thick and chalky white (Plate VI). The last whorl ends with the aperture, usually ovate in shape. The external aperture margin is sharp. The shell part over the aperture is termed a spire. The shell walls in general are thick and strong. Only in *Lymnaea glutinosa* the shell is very thin, fragile and transparent. Shell colour varies from whitish to dark brown. Sometimes the shell is eroded which is visible as damaged shell surface. This happens most often to the shells of *Lymnaea occulta*. As a result of the partial destruction of the dark-coloured horny shell layer (periostracum), pale erosion spots of the calcareous layer become visible. The erosion may be caused by mechanical factors, for example rubbing against gravel or sand grains, or by chemical compounds dissolved in water which may react with the shell built of calcium carbonate (PIECHOCKI 1979a).

The lymnaeid shells are characterized by a simple structure but they are of wide intraspecific variability both within particular populations and between them. Moreover, the shells of different species may be very similar or even identical, for example those of *Lymnaea palustris* and *L. turricula* (Plate IV, V). This great variability of the shell means that often particular species can be correctly identified only on the basis of anatomical structure of reproductive organs, which are are not as seriously affected by external conditions. Their taxonomic value is therefore higher.

The surface sculpture of the lymnaeid shell is relatively poorly differentiated. The shell sculpture of *Lymnaea peregra* (Fig. 3) and *L. glutinosa* (Fig. 4) consists of growth striae, running parallel with the aperture margin, that is transversely to the whorls. On the shells of the remaining lymnaeid species, there are tiny lamellae on the growth striae. They are arranged into several regular rows running spirally, i.e. along the whorls. The rows of lamellae are separated from one another with grooves of different width and depth. The length of lamellae, their thickness and curvature are characteristic of particular species. For exam-

ple, there are very short (0.07 mm), very convex lamellae in *Lymnaea occulta* (Fig. 5) but those in *L. stagnalis* (Fig. 6) are thick and up to 0.5 mm long, or longer (JACKIEWICZ and KORALEWSKA-BATURA 1995). There is a clearly visible reticulate sculpture on the shell surface of some species. It is called „hammering", as it looks like traces of hammer blows. It is made of thicker, intersecting transverse and spiral striae.

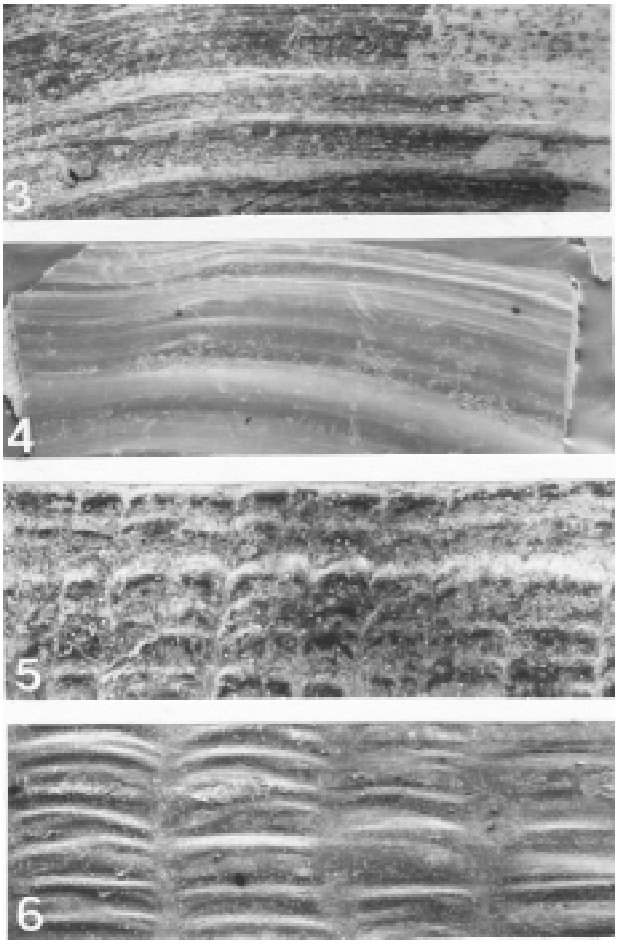


1, 2. *Lymnaea (Galba) truncatula.* Orientation of the shell in relation to the snail body: Fig. 1. - dorsal view; Fig. 2 - ventral view; a - shell, b - head, c - mantle collar, d - foot. 25x. (Original).

5. SOFT PARTS

E x t e r n a l a p p e a r a n c e. The lymnaeid body consists of a head, a foot and a visceral mass covered with a shell (Figs 1, 2).

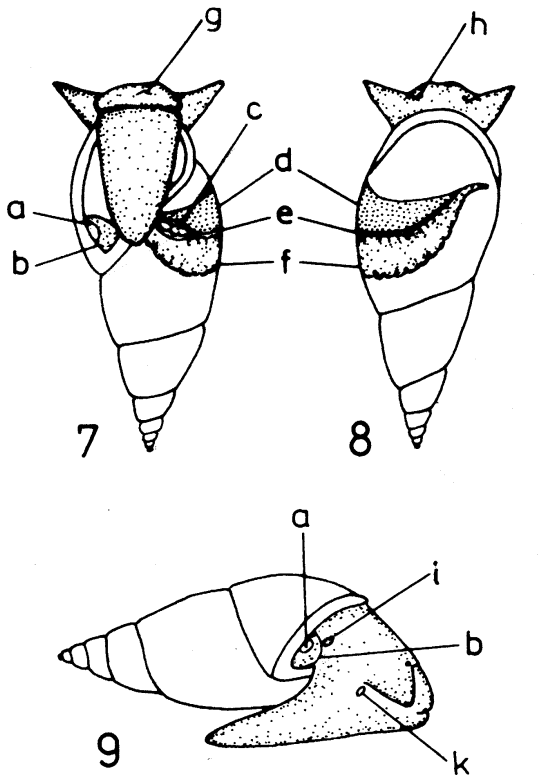
The head is large and shortly set. It bears a pair of lobate, triangular tentacles. The eyes are located internally at their basis. The front of the head passes into two snout lobes. The mouth is located ventrally between them. It is small and triangular, slightly elongated to the end. The male gonopore is located on the neck near the right tentacle. The female gonopore is also situated on the right side, just near the base of the mantle collar (Figs 7-9).



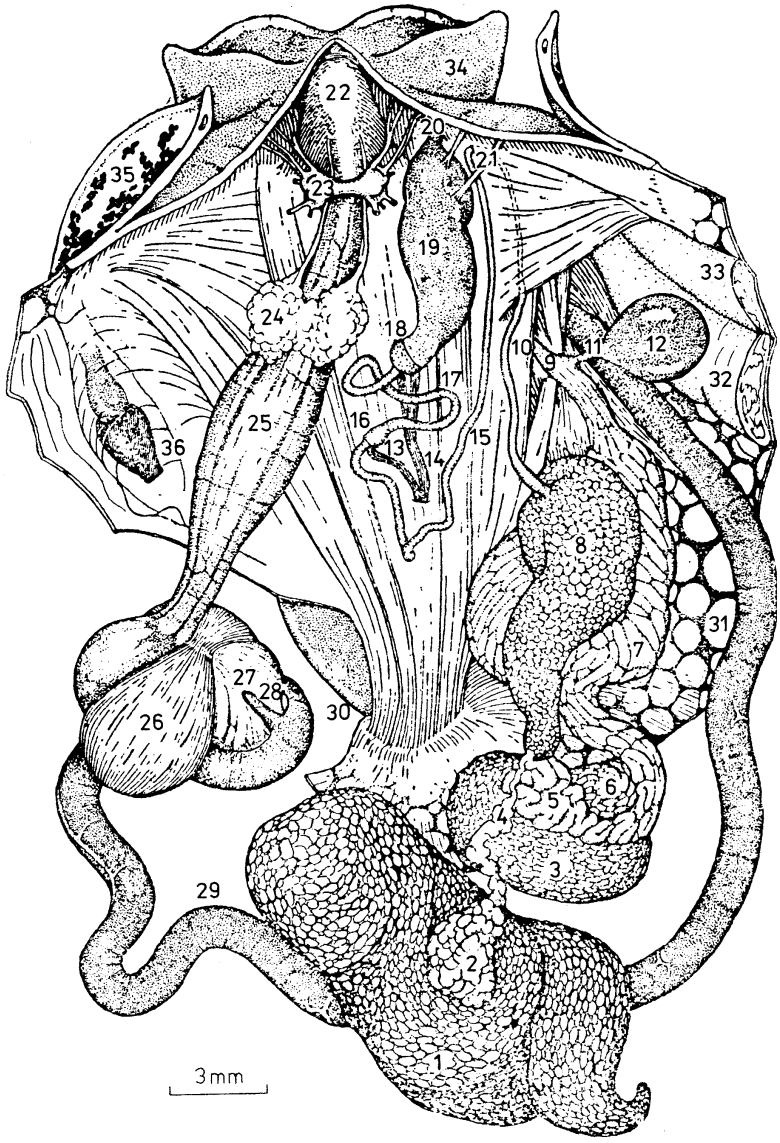
3 - 6. Surface sculpture of the lymnaeid shells: 3 - *Lymnaea (Radix) peregra*; 4 - *Lymnaea (Myxas) glutinosa*; 5 - *Lymnaea (Stagnicola) occulta*; 6 - *Lymnaea (Lymnaea) stagnalis*. SEM, 202x (after JACKIEWICZ and KORALEWSKA-BATURA).

The foot is a rather wide massive organ, truncate in front, and rounded at the back. The foot is particularly wide in specimens living in rapid streams, for example *Lymnaea peregra* f. *ampla* (HARTM.). The adhesiveness of its sole to substratum is increased in this way.

The spirally coiled visceral mass is covered with a skin tunica. In the last whorl this tunica becomes thicker creating a mantle (pallium) that turns into a wide fold called the mantle collar, finished with a thickened ridge. Almost the whole shell of *Lymnaea glutinosa* is covered externally with greatly developed mantle. There are characteristic colour patterns on the mantle which is covered with dark pigment (Plate X). These patterns usually show great diversity, being similar in some species only. The mantle pattern is therefore of little taxonomic value for identification of the lymnaeid species. It is a good diagnostic feature only for the separation between *Lymnaea peregra* and *L. auricularia* (Plate X. 6, 7), sometimes also *L. glutinosa* (Plate X.5) (JACKIEWICZ 1993a).

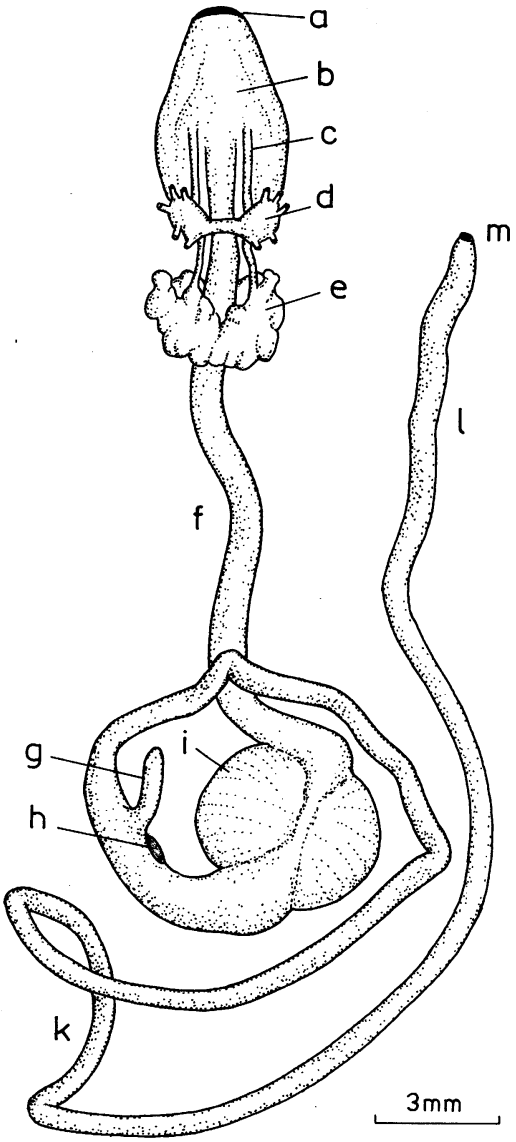


7-9. Position of the reno-pericardial system of *Lymnaea (Stagnicola) palustris*: 7 - ventral view; 8 - dorsal view; 9 - lateral view: a - pneumostome, b - lower pulmonary valve, c - heart, d - lung, e - vena cava, f - kidney, g - mouth, h - eye, i - female gonopore, k - male gonopore. (Original).



10. Internal organs of *Lymnaea (Radix) peregra*: 1 - liver, 2 - hermaphroditic gland, 3 - albumen gland, 4 - hermaphroditic duct with the seminal vesicles, 5 - uterus, 6 - nidamental gland, 7 - pyriform body, 8 - prostate, 9 - vagina, 10 - female gonopore, 11 - spermathecal duct, 12 - spermatheca, 13 - retractor of the penis sheath, 14 - retractor of the praeputium, 15 - vas deferens, 16 - bulbous termination of the penis sheath, 17 - penis sheath, 18 - bulbous termination of the praeputium, 19 - praeputium, 20 - male gonopore, 21 - protractor, 22 - buccal mass, 23 - cerebral ganglia, 24 - salivary glands, 25 - oesophagus, 26 - stomach, 27 - caecum, 28 - liver duct outlet, 29 - intestine, 30 - foot, 31 - mantle, 32 - kidney, 33 - lung, 34 - tentacle, 35 - mantle collar, 36 - heart. (After JACKIEWICZ, slightly modified).

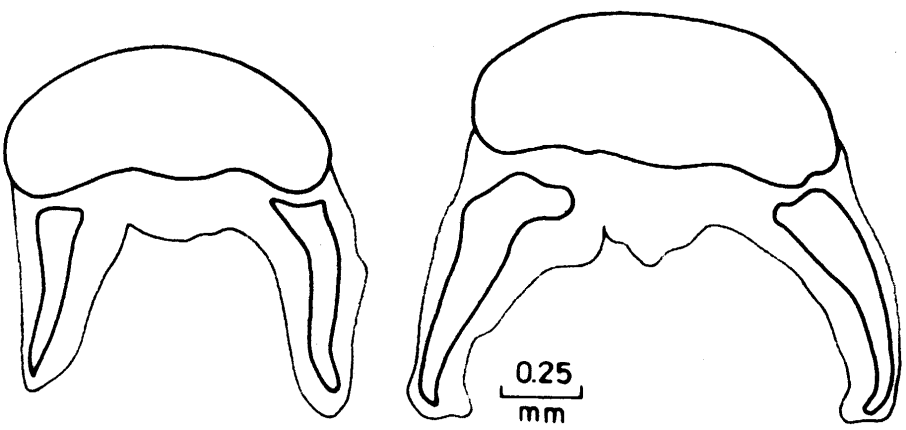
The lymnaeid head with appendices, and the foot is homogeneously coloured from pale yellow through grey to almost black tints.



11. Digestive tract in a natural position of *Lymnaea (Stagnicola) palustris*: a - jaw, b - buccal mass, c - salivary gland ducts, d - cerebral ganglia, e - salivary glands, f - oesophagus, g - caecum, h - liver duct outlet, i - stomach, k - small intestine, l - rectum, m - anus. (Original).

D i g e s t i v e t r a c t. The lymnaeid digestive tract (Figs 10, 11) is similar to that of other pulmonate snails. Like in other basommatophorans, it is relatively short. For example, it is twice as long as the shell of the adult *Lymnaea stagnalis* with a typical shell (BOETTGER 1944).

The mouth opening leads to an oral cavity. It contains jaws (Fig. 11a) built of conchiolin, produced by epithelial cells of the oral cavity. The jaw is used first and foremost for cutting off larger fragments of food. It consists of one large,



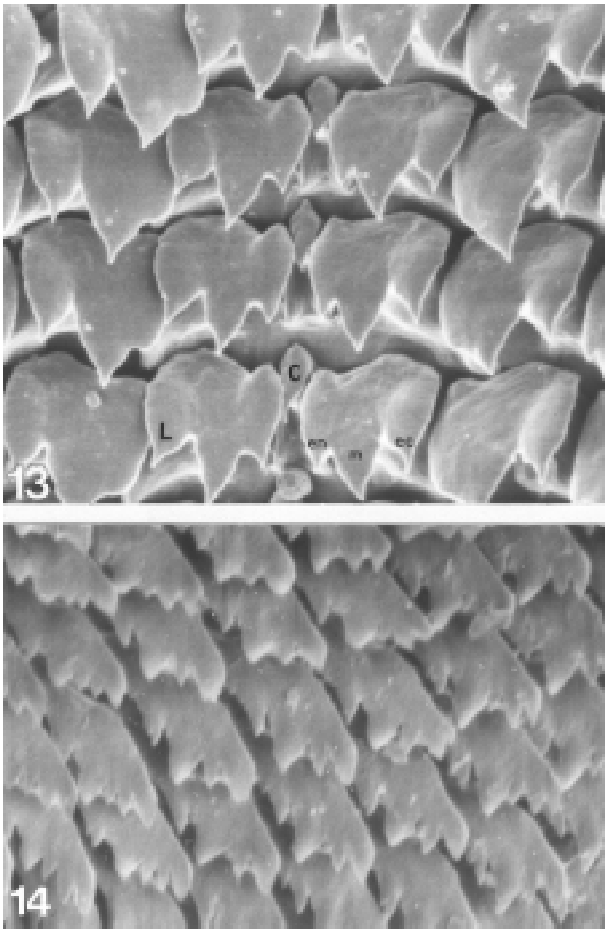
12. Jaw structure of *Lymnaea (Stagnicola) palustris*. (Original).

thick upper plate, usually with three knobs at the cutting edge. There are two narrow, soft lateral plates at each side of the upper one (Fig. 12). Each jaw part is brown in colour.

The oral cavity expands next into a barrel-shaped buccal mass (*pharynx*) (Fig. 11b). It is strongly muscled and lined with cylindrical ciliated epithelium. There are thick layers of longitudinal and circular muscles under the epithelium. The lumen of the buccal mass is formed by a big central channel that is divided into several smaller branches at its both ends. The shape of this channel is different in particular parts of the buccal mass. A large flexible oblique lamina, the so called tongue, is situated inside the buccal mass. Several muscles attached to the tongue enable its movements in different directions. The tongue is covered with a radula towards the oral cavity.

The radula (*radula*) is of an extended spatula shape. It is composed of basal lamina covered with many chitin teeth. The part of the radula, inserted in a radular sac, is rolled up in the form of a tube, cells (odontoblasts) producing the basal radular lamina and its teeth are also situated there. The teeth of the proximal part of the radula, more or less towards its centre, are rubbed off during feeding so that their cusps are mildly rounded. The teeth growing from behind form new

rows of teeth with dagger cusps, and they progressively move towards the front. The radular teeth are arranged in regular longitudinal rows and in slightly arcuated transversal rows. The number of the transversal rows is always much larger than that of the longitudinal rows. One row of central teeth (*dentes centrales*) runs medially through the radula (Figs 13, 14). On its both sides, several rows of lateral teeth (*dentes laterales*) are situated. There are also several rows of marginal teeth (*dentes marginales*) located externally of the lateral rows. The left and right sides of the radula are usually symmetrical, i.e. there is the same number of teeth on both sides of the central tooth in particular transversal rows. However, this symmetry is sometimes disturbed. Each tooth consists of a

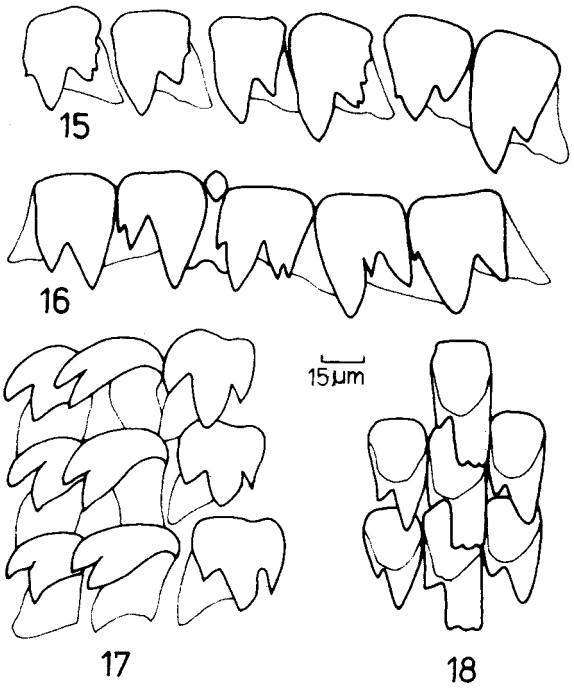


13-14. Radular teeth of *Lymnaea (Lymnaea) vulnerata* (approximately in the middle of the radula): 13 - Lateral tooth (L) and central tooth (C); 14 - Marginal teeth. m - mesoconus, en - endoconus, ec - ectoconus. SEM 3000x. (Original).

basal plate, lying on the basal lamina, and of a cutting plate, directed backwards, used for food scraping. There are three types of cusps on the free dental edges: one central (*mesoconus*) and two lateral: internal (*endoconus*) and external (*ectoconus*) (Fig. 13). The central teeth are undoubtedly only slightly involved in scraping of food. This is testified to by their soft structure. They are narrow, usually with one small cusp and frequently they are partially covered by the neighbouring lateral teeth. The latter are large and usually have three, well developed cusps. The central cusp is the best developed. The internal cusp often disappears, partially or even completely, in several rows of lateral teeth, so these teeth become bicuspid. The marginal teeth are weakly developed. Their structure is irregular. The number of cusps may be 1 to 6, sometimes even more. The radular formula in *Lymnaea corvus* can be presented as follows:

$$\frac{32}{3\text{-}5}\ \frac{11}{2\text{-}3}\ \frac{C}{1}\ \frac{11}{2\text{-}3}\ \frac{32}{3\text{-}5} = 43 - C - 43$$

The length and the width of this radula are 4.27 mm and 1.93 mm, respectively. There are 87 longitudinal and 118 transversal rows. The shell height and width were 31.83 and 14.00 mm, respectively. Radula size is directly proportional to the specimen size.



15-18. Abnormal lateral teeth of the lymnaeid radula. (15-17 originals, 18 after JACKIEWICZ).

Anomalies in radular structure (Figs 15-18) are relatively rare. For example, spatulate teeth or additional cusps sometimes occur. Considerable change in tooth shape or even a fusion of particular teeth may also happen.

Lymnaeids move forward while feeding. They perform arcuate movement of their heads. Feeding trails on the substratum are characteristic of particular species. Nevertheless, the feeding trails of specimens of one species or even various trails of the same specimen may be different. It depends on the kind of food, and satiation of the specimen or even on its age (BOETTGER 1944).

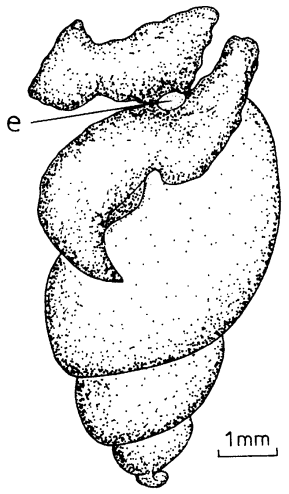
The lymnaeid radula is without diagnostic value for species identification. It is of similar structure in all species of the family *Lymnaeidae*. Some differences can be found in the number and size of cusps on the lateral teeth, particularly in some first longitudinal rows (JACKIEWICZ 1959).

Two big lobate salivary glands (*glandulae salivales*) (Fig. 11e) lie close to the buccal mass. They are made of several vesicles, built of two types of cells, like in *Acicula polita* (HARTM.) (JACKIEWICZ 1967). Large vesicular cells with ovate nucleus predominate among them. Their cytoplasm is of a soft frothy structure. Cells of the other type are fewer. They are much smaller than the former ones. Their nucleus is ovate as well, but their cytoplasm is more condensed. Most researchers mention two types of cells of salivary glands. However some of them suggest that they only represent different secretory stages of one cellular type. This opinion is stressed by WÄCHTLER (1929). On the other hand, WIKTOR (1989) writes about *Limacoidea*: „The gland is built of cells of several different types". The salivary glands produce mucus, that surrounds portions of food, and enzymes, that partially digest them. Salivary mucus is secreted to the buccal cavity by long tubular ducts of the salivary glands (Fig. 11c). The cells of these ducts are not ciliated.

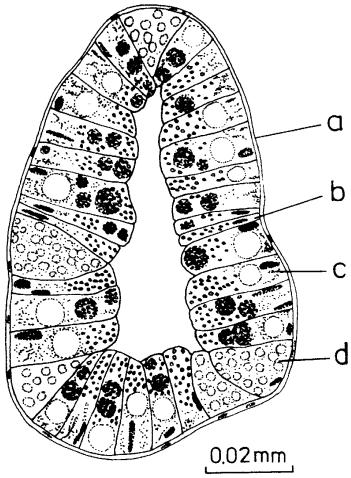
The oesophageal duct (*oesophagus*) is tubular, rather long and thin (Fig. 11f). It is slightly narrowed where it is surrounded by cerebral ganglia (Fig. 11d). The terminal part of the oesophagus is gradually widened and leads into the stomach. The wall of the oesophagus is relatively thin. Its cells are ciliated which makes the movement of food towards the stomach possible.

The stomach (*ventriculus*) is large (Fig. 11i) and well muscled. The musculature consists of several, alternating layers of longitudinal and circular muscles. The inner wall of the stomach is covered by ciliated epithelium. There is a layer of connective tissue between the epithelium and the muscles (DROZDOWSKI and ZAWIEJA 1993). There is a lot of small sand grains in the stomach contents, ingested with food.

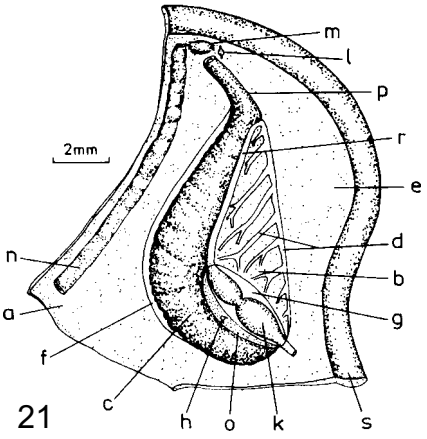
A very large digestive gland (*hepatopancreas*) is also called the liver (Fig. 19). Food digestion and absorption take place in it. The gland is built of two lobes. One is quite small but the other is very big. The latter is coiled spirally around the hermaphroditic gland and reaches the apex of the visceral mass. Both lobes of the gland open with a common duct at the posterior part of the stomach (Fig. 11h). The liver is coloured with brown-green to intensively brown shades.



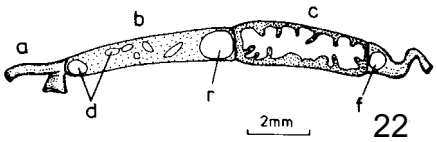
19



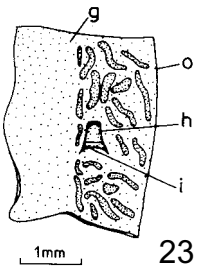
20



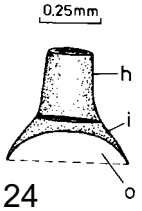
21



22



23



24

19-20. Structure of the liver of *Lymnaea (Stagnicola) palustris*: 19 - Liver lobes in natural position; 20 - Transverse section through the liver sac. a - connective tissue sheath, b - absorption cells, c -secretory cells, d - calcium cells, e - liver duct opening. 21. Pallial complex of *Lymnaea (Stagnicola) palustris* in natural position (as seen from the inside): a - mantle, b - lung, c - kidney, d - pulmonary veins, e - mantle collar, f - renal portal vein, g - pericardium, h - reno-pericardial duct, i - nephrostome, k - heart, l - osphradium, m - upper pulmonary valve, n - intestine, o - part of the pericardium adjacent to the kidney, p - kidney duct, r - vena cava, s - ridge. 22-24. Components of the pallial complex of *Lymnaea (Stagnicola) palustris*: 22 - Transverse section of the lung and the kidney; 23 - Fragment of the pericardium and the kidney with the reno-pericardial duct; 24. The reno-pericardial duct. (Original). For lettering see Fig. 21.

There are three types of cells in the epithelium of particular liver lobules (Fig. 20) covered externally by a very thin connective tissue sheath. The majority of liver cells are broad cylindrical secretory cells with a large vacuole, a nucleus at the base and several spherical concretions consisting of tiny particles. There is a relative shortage of absorption cells. They are very narrow, also with a nucleus at the base, but without any vacuole. There are also few calcium cells of a trapezoidal shape. Their nucleus, barely visible, is situated at the base. There are very numerous spherical calcareous grains within their cytoplasm. Other researchers, among them ABOLINŠ-KROGIS (1961), also distinguish three types of cells of the liver epithelium. However some of them, e.g. ROSENBAUM and DITZION (1963), mention only two types of cells, namely secretory-absorption and calcium cells. On the other hand, WALKER (after WIKTOR 1989) mentions four types of cells in the liver of *Deroceras reticulatum* (O.F. MÜLL.). Finally, some other workers maintain that the presence of different types of liver cells is connected with various functions of the tissue during a cyclic process that takes place in this organ (HESCHELER 1900, MCGEE-RUSSELL 1955 and others).

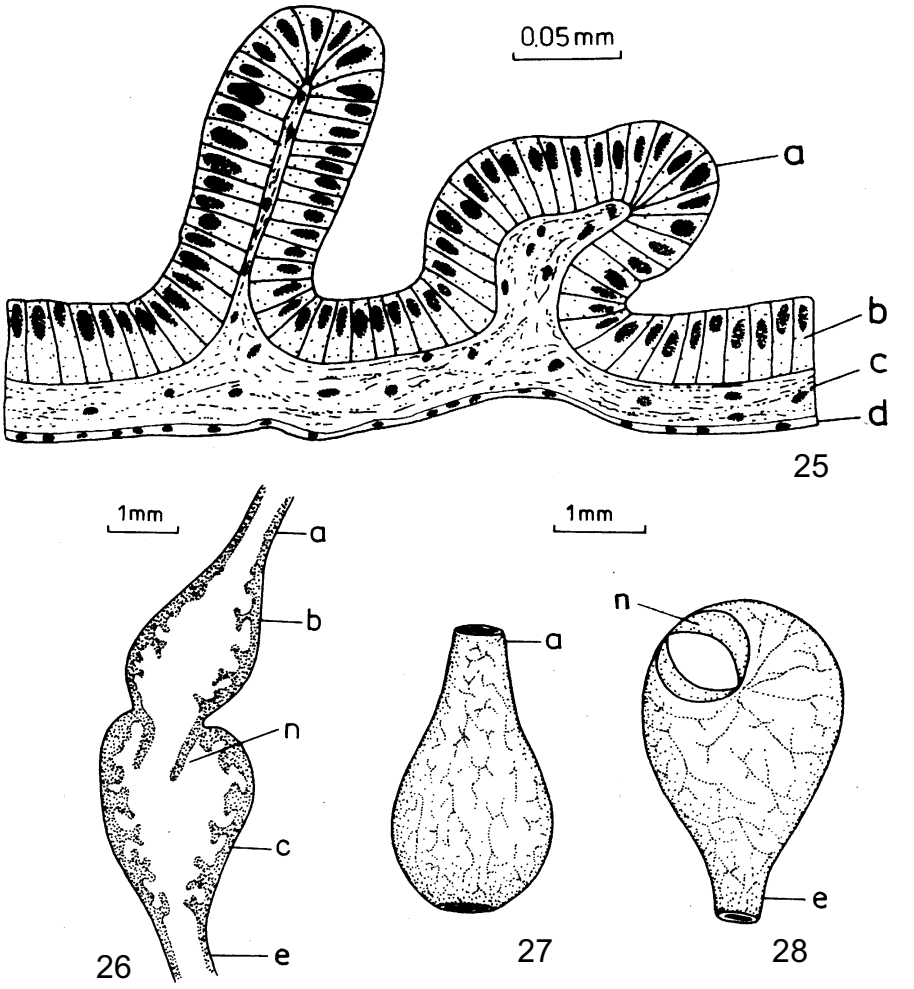
There is a blind finger-like appendix, called a caecum (Fig. 11g) with an unknown function near the entrance of the liver to the stomach (Fig. 11h).

A small intestine (*intestinum*), sharply separated from the stomach, is a long thin duct of almost constant diameter (Fig. 11k). Initially it runs around the stomach, then leads towards the liver, and encircles its surface with a big loop, then slowly going up, it gradually passes into a wider rectum (Fig. 11l). This part of the intestine is of almost the same length as the oesophagus. It ends with an anus (Fig. 11m).

P a l l i a l c o m p l e x (Fig. 21). It is composed of mantle organs which, independently of topographic movements during the gastropod phylogeny, always form a complex and are located next to each other. The complex includes: a lung, a kidney, a heart and the terminal parts of the alimentary tract and the reproductive organs. These organs are covered externally with thin body integument, constituting the so called mantle. There is a broad mantle (or lung) cavity between the mantle and the snail body. Near the pneumostome, there are openings of the rectum and the renal duct. An osphradium also lies there, embedded in the tissue of the mantle collar.

E x c r e t o r y s y s t e m. The kidney (*nephridium*) (Figs 21c, 22c) is a large sac-like organ of spongy structure. There are numerous folds reaching deep inside the wide cavity of the organ (Fig. 22c). The kidney is easily visible through the thin body integument. It is located together with the lung and the pericardium in the last whorl of the visceral mass (Figs 7, 8). The kidney lies closely along the walls of the lung and the pericardium. A kidney duct (*ureter*), situated just behind the lung, is usually strongly narrowed and always markedly curved. Its pore is big and located close to the pneumostome, opposite to the anus. The kidney duct wall near the pore is whitish, slightly thickened, forming a distinct papilla.

The kidney is connected with the pericardium by a reno-pericardial duct, lying along the medial part of the pericardium that adheres to the kidney (Fig. 21h). This duct starts with a funnel of nephrostome (Figs 23i, 24i). The funnel has its own wall only against the pericardium lumen. The rest of its wall is formed by the pericardium walls (Fig. 21o). In this way, something like a pouch 0.5 mm wide is developed. The duct (Figs 23h, 24h) looks like a short narrow tube 0.3 mm long, with fine lamellae visible in its lumen. It is slightly narrowed, so it is 0.2 mm wide near the opening and its colour is yellow as a rule. The above dimensions refer to the reno-pericardial duct of *Lymnaea stagnalis*.



25. Kidney structure of *Lymnaea (Stagnicola) palustris*: a - fold of the kidney, b - kidney cells, c - connective tissue, d - epithelium. 26-28. The structure of lymnaeid heart: 26 - Longitudinal section through the heart; 27 - auricle; 28 - ventricle. (Original). For lettering see Fig. 29.

The kidney is covered with the mantle epithelium. There is a thick layer of connective tissue just under the epithelium. The connective tissue also fills up the recesses between the folds. The epithelium of the kidney lumen is built of high, cylindrical cells with apically lying nuclei (Fig. 25).

R e s p i r a t o r y s y s t e m. A part of the mantle surface of pulmonate snails is covered with a network of blood vessels. It builds a lung, so that the mantle cavity has turned into a lung cavity. To create it, the mantle border of the last whorl fused with the snail body, leaving only a small, open slit on the right side, used as a respiratory opening (pneumostome). When a snail swims up, from time to time, to the water surface, gas exchange between the air and the lung cavity takes place through this opening. The part of the mantle that is not fused with the body creates a broad fold called mantle collar. It is much thickened, particularly near the border. The collar is much wider on the dorsal side of the snail than on the ventral side. There is a spacious area between the collar and the cephalic part of the body.

The lung (*pulmo*) (Figs 21b, 22b) is unpaired. It is located in the lung cavity under the mantle. It is triangular in shape and runs along the kidney so they adhere close together. The lung is relatively small, with a poorly developed network of vessels. The vesicular connective tissue fills the space between the lung epithelium and the blood vessels. The respiratory opening, leading to the lung cavity, is situated on the right side of the collar. It is surrounded by two valves: a small upper valve (Fig. 21m), invisible externally, and a large, clearly visible, lower valve (Figs 7b, 9b). It is located where the upper collar part turns into the ventral one. The lower valve of *Lymnaea palustris* looks like a large tonguelet assuming a tubular shape. The lower valve of *Lymnaea auricularia* is also large but it is circular in shape.

Larger lungs and a denser blood vessel network are found in large active snail species (Drozdowski 1970). As lymnaeids have rather poorly developed lungs, the gas exchange through their skin meets a part of oxygen requirements. There are divergent opinions on the role of the skin in respiratory processes. Skin respiration alone is sufficient only in lymnaeids living in well oxygenated waters (Boettger 1944). Some lymnaeid species, staying all their life at greater depths, take oxygen from the water which fills up their lung cavity (Hescheler 1900, Roszkowski 1914a).

C i r c u l a t o r y s y s t e m. The lymnaeid circulatory system is open like in other snails. It consists of a heart, that is the central organ for blood pumping, and blood vessels. Blood both circulates in the blood vessels and flows into the sinus system, so that it bathes different internal organs. The blood moves with vessels from the sinuses to the lung where it is oxygenated and then it returns to the heart.

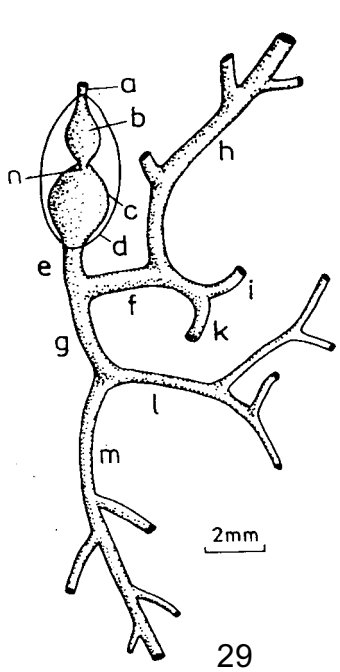
The heart (*cor*) is located on the left side of the snail's body between the kidney and the anterior part of the lung (Fig. 7). It lies just under a thin mantle

integument so it is quite visible from the outside. The heart consists of an auricle (*atrium*) and a ventricle (*ventriculus*). It is surrounded by a broad pericardium filled with fluid.

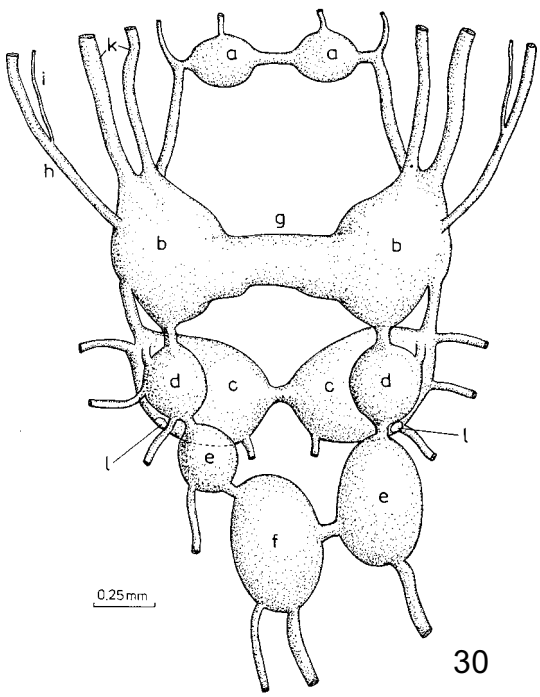
The walls of the auricle and the ventricle are well muscled (Fig. 26). Tiny muscle fibres are visible as a subtle network on the heart surface (Figs 27, 28). There are two big semicircular valves on the border line between the auricle and the ventricle (Figs 26n, 28n) with several thicker fibres, arranged radially, visible at the point where the valves meet. On the other hand, there is a lack of valves on the border line between the ventricle and the aorta. There is only a conspicuous concentration of connective tissue and muscle fibres.

The pulmonary veins (Fig. 21d) are weakly branched. There is the main vein (*vena cava*) between the lung and the kidney (Fig. 21r) and a renal portal vein on the other side of the kidney (Fig. 21f).

The main aorta (Fig. 29e) runs out of the heart ventricle backwards and soon divides into an anterior aorta (*aorta anterior*) and a posterior one (*aorta poste-*



29



30

29. Circulatory system of *Lymnaea (Stagnicola) palustris*: a - vena cava, b - auricle, c - ventricle, d - pericardium, e - main aorta, f - anterior aorta, g - posterior aorta, h - head artery, i - genital artery, k - internal visceral artery, l - external visceral artery, m - liver and gonad artery, n - valves.
30. Central nervous system of *Lymnaea (Stagnicola) palustris*: a - buccal ganglia, b - cerebral ganglia, c - pedal ganglia, d - pleural ganglia, e - parietal ganglia, f - visceral ganglion, g - cerebral commissure, h - tentacular nerve, i - optic nerve, k - nerves running to the oral lobes, l - statocysts. (Original).

rior). The anterior aorta (Fig. 29f) goes slightly deeper into the body, giving off two arteries. One of them, the head artery (Fig. 29h), is very long and runs anteriorly. Its numerous branches reach the head, the foot and the distal part of the reproductive organs. The other artery is short and is soon divided into a genital artery (*arteria genitalis*) (Fig. 29i) that branches to the proximal part of the reproductive organs and into an internal visceral artery (Fig. 29k). The vessels originating in this artery are particularly branched on the stomach surface. The posterior aorta (Fig. 29g) also branches into two arteries: an external visceral artery (Fig. 29l) and a liver-gonad artery (Fig. 29m) which runs up to the apex of the visceral mass. The external visceral artery also produces numerous vessels on the stomach surface but on its opposite side to the internal visceral artery (Fig. 29k).

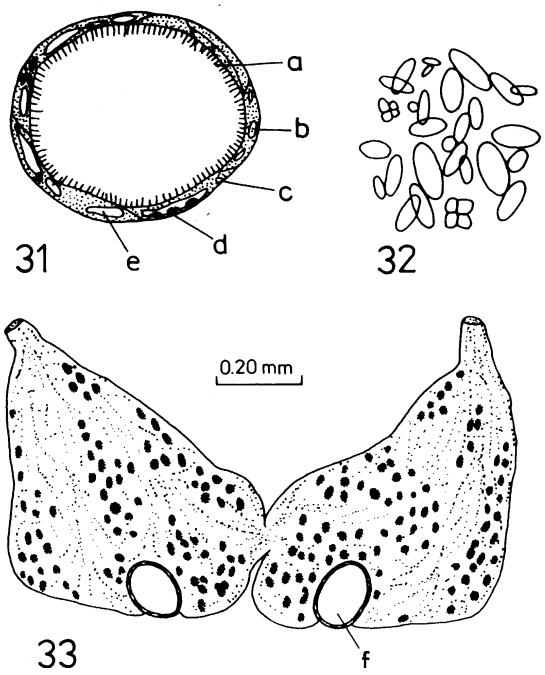
N e r v o u s s y s t e m. A central nervous system of lymnaeids (Fig. 30) consists of paired brain or cerebral ganglia (*ganglia cerebralia*), foot or pedal ganglia (*ganglia pedalia*), lateral or pleural ganglia (*ganglia pleuralia*), parietal ganglia (*ganglia parietalia*) and oesophageal or buccal ganglia (*ganglia buccalia*) as well as unpaired visceral ganglion (*ganglion viscerale*). The cerebral ganglia are large. They are connected by a transverse commissure (*commisura*) while the cerebral ganglia are connected with the pedal as well as with the pleural ganglia by short longitudinal connectives (*connectiva*). On the other hand, very long connectives link them with the buccal ganglia. Three nerves lead from each cerebral ganglion. Two of them (Fig. 30k) run toward the oral lobe, while the third (Fig. 30h) runs to the tentacle. A very thin optic nerve starts with this last nerve (Fig. 30i). The pedal ganglia are also large and connected with a short commissure. These ganglia give off several nerves running toward the sole. There are roundish shiny statocysts (Fig. 30l) visible in the middle of the lower part of these ganglia. The pleural ganglia are connected by short connectives both with the pedal and the parietal ganglia. The parietal ganglia are linked with the unpaired, much larger visceral ganglion. Several nerves start asymmetricaly with this ganglion. The buccal ganglia lie slightly over a circumoesophageal ring, in the recess near the outlet of the buccal mass to the oesophagus.

The lymnaeid central nervous system shows partial asymmetry which is expressed by localization of ganglia and by their size. The ganglia are slightly shifted in relation to each other. Moreover the ganglia on the right side are better developed than those on the left side. The right pleural ganglion is, for example, slightly larger than the left one, however the right parietal ganglion is much larger than the left one. There is a considerable concentration of the nervous system but the particular ganglia have not fused. They are clearly separated and connected by shorter or longer connectives. This testifies to the primitive condition of the nervous system.

Simplified or partial descriptions of the structure of the lymnaeid central nervous system, specially of *Lymnaea stagnalis*, were given by BOETTGER (1944) and GÖTTING (1974). ELO (1938) presented a very detailed description of the

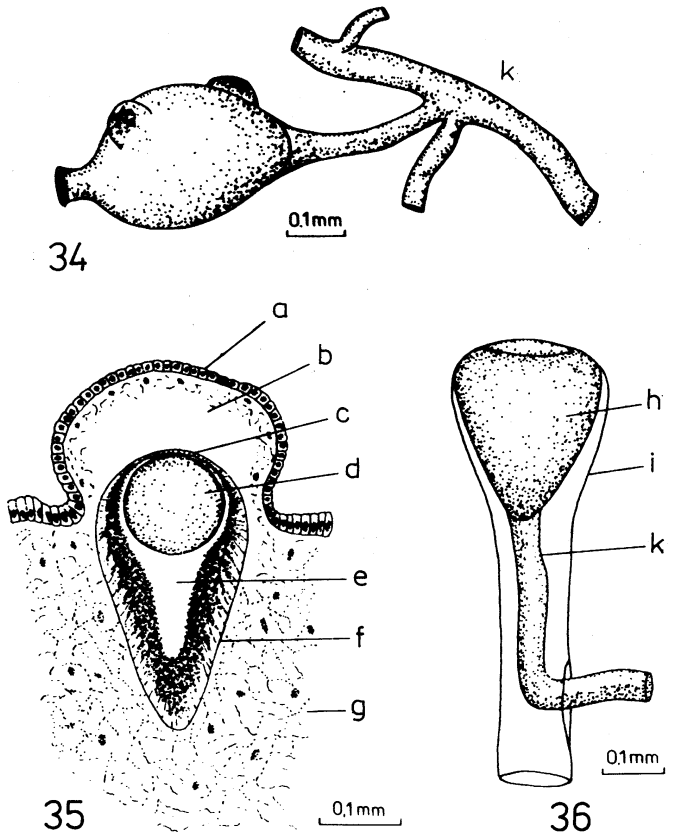
structure of particular nervous ganglia, however without completing the whole picture. The lymnaeid nervous system was frequently a subject of physiological and neurosecretory studies (JOOSSE 1964, RUNHAM and HUNTER 1970, BULLOCH and RIDGWAY 1995).

S e n s e o r g a n s. Two s t a t o c y s t s constitute a lymnaeid sense organ of the labyrinthine type. They are enclosed in a theca of connective tissue. There is a single layer of the sensory epithelium inside them. According to SCHMIDT (1912) and BOETTGER (1944) the statocyst is built of three types of cells: syncytial, giant and vesicular, covered with cilia (Fig. 31). KILIAS (1960) states that the statocyst wall in *Helix pomatia* (L.) is also built of these three types of cells. The statocyst interior is filled with fluid (statolymph) and numerous statoliths, even as many as 700, are suspended in it. They are usually elliptical (Fig. 32). The statocysts are situated in a hollow in the lower part of the pedal ganglia (Figs 30l, 33) but they are innervated by the cerebral ganglia. As stated by BOETTGER (1944), this nerve consists of several fibres that surround the statocyst from all sides and innervate its particular cells.



31-33. Lymnaeid sense organs: 31 - Statocyst, 300x; 32 - Statoliths, 1000x; 33 - Pedal ganglia with the statocysts: a - cilia, b - giant cells, c - syncytial cells, d - vesicular cells, e - vacuoles, f - statocyst. (31 after SCHMIDT from BOETTGER; 32, 33 original).

An o s p h r a d i u m (Fig. 34) is an organ of chemical (smell) sense. It lies near the pneumostome. The osphradium is barrel-shaped with two lateral outgrowths. Its cells, according to BOETTGER (1944), are higher than the neighbouring cells and covered with cilia. The organ base is surrounded by a nervous ganglion. It is innervated by a nerve going from the right parietal ganglion.



34-36. Lymnaeid sense organs: 34 - Osphradium; 35 - Internal structure of the eye; 36 - Eye: a - cornea externa, b - sinus, c - cornea interna, d - lens, e - vitreous body, f - retina, g - connective tissue, h - eye-vesicle, i - sheath, k - nerve. (34 original; 35, 36 after JACKIEWICZ).

Like in all pulmonate snails, lymnaeid e y e s are well developed. They are situated at the base of the tentacles, on their inner side. The eye lies in a small lacuna with smooth walls. It is pear-shaped and is uniformly dark coloured (Figs 35, 36). The optic nerve (*nervus opticus*) runs to its basal part. This nerve (Fig. 36n) is a branch of the tentacular nerve, going out the cerebral ganglion. It runs to the eye from the external side, that is on the tentacle side. Near the eye it turns at

an angle of 90° and crossing quite a big opening in the sheath it penetrates the eye base. The sheath, covering the eye and the part of the nerve, looks like a transparent tube. Its part that surrounds the eye is much widened. The sheath length is variable. It probably depends on the degree of its contraction. A uniform sheath wall may be sometimes divided into several strips. The base of the sheath is fused with the bottom of the lacuna. Moreover, tiny fibres, often branched, join the sheath with the lacuna wall. They undoubtedly serve to stabilize the vertical position of the sheath. An external cornea (*cornea externa*) lies rather far above the eye itself (Fig. 35). It is built of smaller cells than the neighbouring body epithelium. A thin layer of connective tissue adheres to it. There is a spacious sinus between the external cornea and the eye. It is filled with liquid that doubtless protects the eye against injuries. An inner cornea (*cornea interna*) creates the anterior colourless eye wall. Its structure is barely visible. It is usually built of a monolayer epithelium (BOETTGER 1944, JACKIEWICZ 1967, 1990). The largest part of the eye is occupied by a retina (*retina*). There is a thick layer of cells, forming a cup around the lens. It is built of two types of cells: visual and supporting ones. The former cells usually do not contain any pigment. There is a lens inside the eye, spherical in shape, which strongly refracts light rays. It adheres to the inner cornea. The eye interior is filled with a vitreous body which is mostly located at the bottom of the eye. The eye is surrounded externally by connective tissue.

R e p r o d u c t i v e s y s t e m. Lymnaeids are hermaphroditic. Each specimen contains a complete set of both female and male reproductive organs. This system is built according to one scheme for all lymnaeid species. Some interspecific differences in its structure concern details that are sometimes very important for the taxonomy of this snail group. Within particular species, the reproductive organs usually show small variability.

The reproductive system (Figs 10, 47) begins with an unpaired hermaphroditic gland (*glandula hermaphroditica*), called also gonad. It is embedded in liver tissue that occupies the anterior part of visceral mass. The gland is large, consisting of very many sacs (*acini*). Through efferent ducts (*vassa efferentia*) they are connected with a hermaphroditic duct (*ductus hermaphroditicus*). There are seminal vesicles (*vesiculae seminales*) in its mid part. There is a small fertilization pocket just at the outlet of the hermaphroditic duct, near the base of the uterus (*uterus*) and albumen gland (*glandula albuminalis*). This is the place where eggs are fertilized. Further organs of the reproductive system are divided into a male and a female part.

The female reproductive organs begin with a long, ribbon-like, strongly folded uterus. Its folds are close to the albumen gland. This gland opens through a very short duct into the uterus. The albumen gland is very large and is usually bean-shaped. The uterus passes into a short tubular duct that forms the proximal part of the oviduct (*oviductus* I). A roundish nidamental gland (*glandula*

nidamentalis) opens in this place. Further on the oviduct is much widened, forming a so called pyriform body (*corpus pyriforme*). This organ is big, usually ovate and greatly swollen. It passes quite clearly into a distal part of the oviduct (*oviductus* II). This part of the oviduct has a different shape in each particular species. A vagina (*vagina*) is a final part of the female reproductive organs. Both its shape and its size vary. A duct of spermatheca (*ductus bursae copulatricis*) is connected with the vagina usually on one side. It may be long and thin, or short and much wider, also widened into a funnel near the outlet. The duct is absent in *Lymnaea peregra* only. The spermatheca (*bursa copulatrix*) is frequently large, spherical or ovate in shape, rarely more elongated, usually brightly orange in colour. A jelly-like substance containing the mating partner's spermatozoa gets to the spermatheca during copulation. It stays there some time. The spermatheca secretion activates the spermatozoa which next go up to the insemination pocket, where they fertilize the eggs. The vagina terminates with a female gonopore. It lies in a small papilla near the pneumostome at the mantle collar base on the right side of the snail body (Fig. 9i).

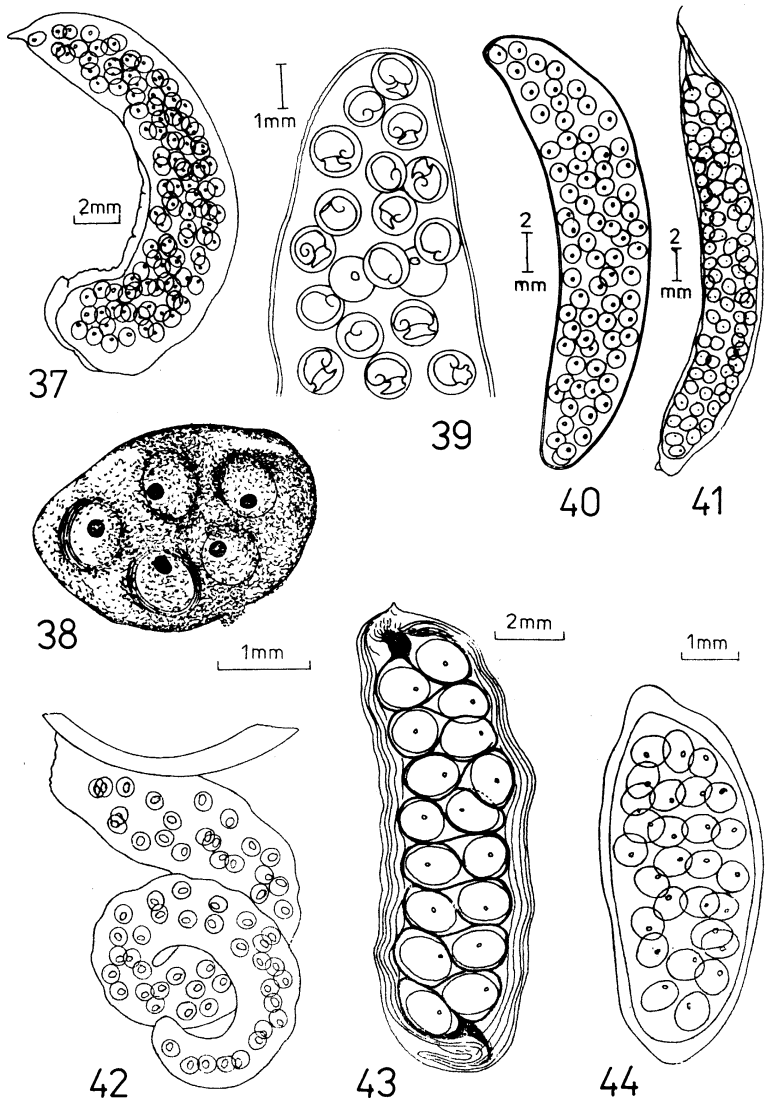
The prostate is the first part of the male reproductive organs. Spermatozoa arrive here from the gonad through the hermaphroditic duct. The prostate structure is characteristic in each particular lymnaeid species. Its proximal part is usually narrower than the widened, greatly swollen, distal part. There is one (Fig. 63E) or many (Fig. 79E) folds inside the prostate, usually in its widened part. Their sutures are well visible externally in all species except *Omphiscola glabra*. The prostate wall of *O. glabra* does not form any folds (Fig. 49). The prostate is almost completely covered with the pyriform body. A long thin duct (vas deferens) departs from the prostate on its apical side or slightly lower. At first, it runs along loosely in the body cavity, then near the female gonopore it enters the snail body wall, running parallel to the praeputium. It leaves the body wall near the male gonopore, then forms several loops and falls into the penis sheath. The length of the penis sheath is variable. It is very short in some lymnaeid species or it is very long, similar to the vas deferens, in others. The sheath basis is more or less widened, forming a so called bulbous termination. There is a penis inside the sheath. Its length is related to the sheath length. Sometimes the penis may also resemble vas deferens (Figs 67D, 71D) or it may be of a more complicated structure (Fig. 79D). The penis sheath passes into a praeputium. This is a large organ, usually club-shaped, with one (Figs 51, 52) or two (Figs 56, 57) longitudinal folds. There is a disk at the bottom of the praeputium. It is made of a papillary fold (*velum*) and a papilla (*sarcobelum*) with a central opening (Figs 58, 59). There is no papillary fold in *O. glabra* (Fig. 50). The basal praeputium part where the mentioned disk is located is called a bulbous termination of the praeputium. Externally it is not always well separated however. Special muscles are attached to the penis sheath and the preputium. These are retractors. The retractor of the penis sheath serves for retraction of the penis as well as its sheath into the interior of the body after they have been everted during copulation. The penis eversion is

a result of an increase in pressure of snail body fluids. Each retractor is built of one or several muscle strands. The retractors are very thick in some species but in others they are subtle, thin and long. Both retractors join the columellar muscle (*musculus columellaris*). Moreover, some other tiny muscles are inserted on the praeputium wall. They are called protractors, used for attachment of the praeputium to the snail body wall. The male gonopore lies on the right side of the snail body, near the base of the tentacle (Fig. 9k). Anomalies in the structure of lymnaeid reproductive organs are found very rarely. Among hundreds of specimens I examined, there was only one that had only the male part of the reproductive organs developed, while the female parts were completely absent.

6. BIOLOGY

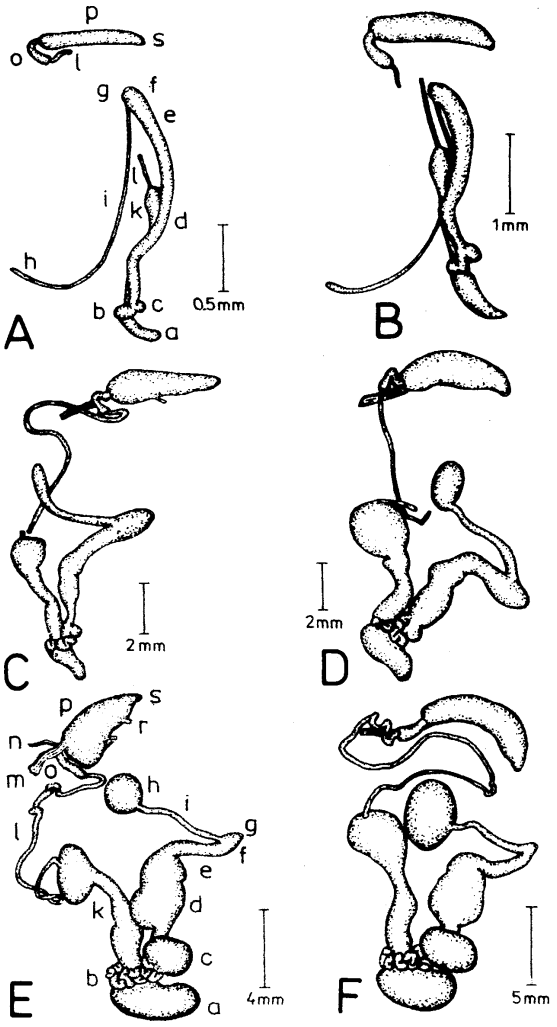
R e p r o d u c t i o n. The lymnaeid reproductive season is long. It starts in spring (March - April) and lasts till late summer. As many as three generations appear during a year. The lymnaeids are hermaphroditic. Two specimens usually mate. One of them plays a male role, the other behaving like a female. Self-fertilization is very rare. The lymnaeids are characterized by internal fertilization. During copulation, spermatozoa of one specimen are placed in the female reproductive organs of its partner. The sperm is transferred in liquid but quite cohesive form (JACKIEWICZ 1986b). The fertilization takes place in the insemination pocket. The fertilized egg cell (zygote) contains nutritious substances produced by the albumen gland. It is surrounded by an internal membrane (*membrana interna*) and an external one (*membrana externa*) when it passes through the farther parts of the female reproductive ducts. Thin egg filaments (*fila ovi*) stick out of the latter membrane. Next, the eggs are completely covered with a gelatinous substance. This substance forms the egg capsule interior. The wall (*theca interna*) of the egg capsule is also built there. The egg capsule is covered externally with a thin mucus layer (*pallium gelatinosum*) (PIECHOCKI 1975, 1979a). The egg capsule is usually cylindrical and swollen (Figs 37, 40-44) but it is spherical in *Lymnaea truncatula* (Fig. 38). The shape and size of the egg capsules are characteristic of each particular species. Moreover, the number of eggs in egg capsules may vary both between and within species. For example, in *L. corvus* the length and width of 6 egg capsules ranged from 12 to 24 mm and from 3 to 4 mm, respectively. The number of eggs was 43-100. According to CZAPSKI (1977) egg capsule length of *L. occulta* ranged between 20 and 35 mm but its width was 4 mm. These egg capsules contained from 11 to 72 eggs. The egg capsules are attached to plants, stones or other submerged objects. The embryonic development takes place inside the egg membranes (Fig. 39). The egg development depends on temperature and lasts 2-4 weeks on average. Specimens of *L. corvus* collected in the field and kept in an aquarium laid egg capsules after 4 days. The water temperature was 21°C. Six days later, the embryos had a shell, eyes, heart and radula. After three more days, some young specimens left the eggs and crept

onto the substratum. According to BOETTGER (1944), the process of leaving egg membranes lasts 1-3 days, exceptionally one week. Within one egg capsule, the development time of individual embryos is different, moreover some embryos die in early developmental stages and they are eaten by their siblings.



37-44. Lymnaeid egg capsules: 37 - *Lymnaea (Radix) peregra*; 38 - *Lymnaea (Galba) truncatula*; 39 - Fragment of an egg capsule of *Lymnaea (Lymnaea) corvus,* with embryos; 40 - *Lymnaea (Lymnaea) corvus*; 41 - *Lymnaea (Lymnaea) stagnalis*; 42 - *Lymnaea (Stagnicola) occulta* (20-35 x 4 mm); 43 - *Lymnaea (Myxas) glutinosa*; 44 - *Lymnaea (Stagnicola) palustris*. (37, 38, 41, 44 after PIECHOCKI; 39, 40 original; 42 after CZAPSKI; 43 after BONDESEN from PIECHOCKI).

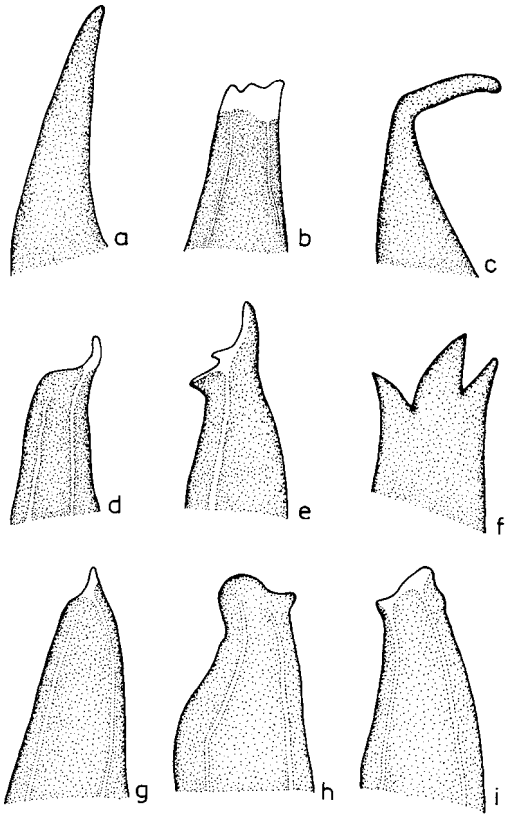
P o s t e m b r y o n i c d e v e l o p m e n t. Lymnaeid snails mature within about 3 months, that is before their shell growth has been completed. The lymnaeid reproductive system (Fig. 45) in the early stages of postembryonic development is weakly developed and tape-like. It gradually develops as the specimen reaches adulthood, and its particular parts progressively assume their



45. Postembryonic development of the reproductive organs of *Lymnaea (Lymnaea) stagnalis* (shell sizes of particular stages: A. 4 - 8 mm; B. 7-16 mm; C. 11-26 mm; D. 18-31 mm; E. 24-32 mm; F. 31-60 mm): a - albumen gland, b - uterus, c - nidamental gland, d - pyriform body, e - oviduct, f - vagina, g - female genital pore, h - spermatheca, i - spermathecal duct, k - prostate, l - vas deferens, m - retractor of the praeputium, n - penial nerve, o - penis sheath, p - praeputium, r - protractor, s - male genital pore. (After JACKIEWICZ and ZBORALSKA).

characteristic shape. It should be stressed that the spermathecal duct and retractors are almost the same in length in each developmental stage, they only become thicker. In the beginning, both male and female reproductive organs of young specimens develop at the same rate. Later, the male organs develop faster than the female ones. Taking this fact into account, it should be assumed that a smaller specimen with well developed male reproductive organs plays a male role in mating. Such a situation may be frequently observed. It has also been found that shell size is no guide in estimating a snail's maturity. UMIŃSKI (1975) draws attention to a similar situation in *Vitrinidae*. Sometimes the reproductive organs of larger specimens are less developed than those of smaller specimens (JACKIEWICZ and ZBORALSKA 1994).

T e n t a c l e r e g e n e r a t i o n. Lymnaeids are capable of regenerating lost body parts, especially tentacles. They may often be bitten off by various aquatic animals, usually by fish (BOETTGER 1944). It has been found experimen-



46. Normal tentacle (a) and various forms of regenerated tentacles (b - i) of *Lymnaea* (*Lymnaea*) *stagnalis*. 6x. (Original).

tally that regeneration of completely amputated tentacles lasts longer in adult specimens than in younger ones, on average about 48 days and 34 days, respectively (RUCH 1979). Regenerated tentacles (Fig. 46b-i) are very different from normal ones (Fig. 46a). Most frequently the top of the regenerated tentacle may be either bifurcate or serrated, also lobate, either sharpened or rounded. Similar endings of lymnaeid tentacles were observed in the field by BOETTGER (1944). This suggests that such abnormal tentacles develop most frequently as a result of damage and very rarely as an ontogeny disturbance (JACKIEWICZ 1969).

S h e l l r e g e n e r a t i o n. Repair of mechanically damaged shells is a very frequent phenomenon both in land and aquatic snails. On the other hand, a completely destroyed shell is never regenerated (BOETTGER 1944). The shell shape is not changed after repair of small damage. However, regeneration of larger shell losses results in an atypical pattern and the regenerated fragment is different from the normal part of the shell (Plate XI.6).

Abnormal shells are very rarely found in lymnaeid species. Among hundreds of specimens kept in my collection, there are only a few with atypically developed shells (JACKIEWICZ 1972).

The „scalariform" shell of *Lymnaea stagnalis* (Plate XI.3) undoubtedly seems to be the most interesting one. The shell of *L. auricularia* with a big malformation of its body whorl may be another example. A large pouch-shaped protuberance has been developed there (Plate XI.1). Moreover, a deep sinus has been created at the outer aperture margin of the same shell (Plate XI.2). A similar pouch (Plate XI.4), although much smaller, may be seen between the body and the penultimate whorl of the shell in *L. corvus*.

There are different opinions among malacologists regarding reasons for the development of abnormal shells. BOETTGER (1944) maintains that „scalariform" shells are caused by the attachment of a foreign body, such as duckweed (*Lemna*) or a snail egg, to the shell. The „scalariform" shells that are formed during the growth of their owners, the author calls „phenotypic detorsion" in contradistinction to „genotypic detorsion". KOVANDA (1956) stresses the role of parasites in the development of „scalariform" shells. According to other authors, this phenomenon may be a result of damage to the columellar muscle (GEYER 1927) or a break in the columella (ROTORIDES and SCHLESCH 1951).

The shell shape also depends on the environment in which the snail lives. Shells of specimens living in the breaker zone of large lakes are characterized by curved outer margins of the body whorl, that bend like a claw into the shell interior (JAECKEL, 1953). This facilitates attachment to the reeds. A shell of *L. stagnalis* found in the Charzykowskie lake is shown as an example (Plate XI.5).

F e e d i n g. Lymnaeids feed on aquatic vascular plants. They eat live tissues but prefer those macerated tissues which are of greater nutritive value, due to development of saprophytic bacteria and fungi (KORNIJOW et al. 1995). Moreover

they feed on algae, debris and slime, pollen, diatoms and bacteria. They also eat animal matter, such as dead vertebrates and invertebrates, amphibian spawn, snail egg capsules, sometimes even of their own species. Animal proteins positively affect snail growth and fertility, as well as the life span (FRÖMMING 1956). Lymnaeids may live up to 5 years. They are resistant to a lack of food and may starve for several months.

7. PARASITES

Larvae of many trematode (*Trematoda*) species are the most frequent parasites of lymnaeids. BERTMAN and WOJCIECHOWSKA (1974) state that *Lymnaea stagnalis* from the vicinity of Wrocław is an intermediary host of 7 trematode species. The intensity of invasion with trematode larvae is sometimes very high. For example, I found about 80% infected specimens among *L. auricularia* collected in a small water body in a gravel-pit near the Wielkopolski National Park. There were almost 100% infected specimens of *L. corvus* among those found in a pond at Dębina near Poznań. Several hundred cercariae can develop in the body of one snail specimen. This causes a high mortality in some populations. CZAPSKI's studies (1977) show that *L. occulta* may play a great role as an intermediate host for the liver fluke (*Fasciola hepatica* L.), being in this respect even more important than *L. truncatula*. Other lymnaeid species are much more rarely intermediate hosts for this parasite. Lymnaeids are also attacked by oligochaets (*Oligochaeta*), mainly by a commensal species like *Chaetogaster limnaei limnaei* K. BAER and *Ch. limnaei vaghini* GRUFFYDD, living in the kidney or kidney duct of these snails (PIECHOCKI 1979). I found *Glossiophiona heteroclita* in the mantle cavity of *L. palustris* as the only case among a huge number of studied specimens. This indicates that the leech is an accidental parasite. A rotifer *Proales giganta* (GLASSCOTT), entering egg capsules, as well as larvae of several dipteran species (*Diptera*), mostly *Parachironomus varus limnaei* GUIBÉ, which consume liver blood of their snail host, are other parasites of lymnaeids.

Moreover, lymnaeids are often eaten by caseworm larvae, aquatic coleopterans, fish, aquatic birds and some rodents.

8. ECOLOGICAL REMARKS

Lymnaeids are freshwater snails, though some species may live in brackish water. They develop dwarf forms in unfavourable conditions. Lymnaeids inhabit permanent water reservoirs where they usually appear in large numbers (CZAPSKI 1977). They, especially *Lymnaea glutinosa*, most often spend time among dense inshore vegetation. They find there not only food and shelter but also suitable substrata for lying egg capsules, usually on the underside of leaves or on macrophyte stems. They may be also found on various submerged objects. Species of *Radix* MONTFORT, 1810 usually creep along the sandy, muddy or stony bottom of water reservoirs.

It is assumed that forms of very wide foot are developed in rivers with a strong current or in turbulent lakes. This ensures a better attachment to the substratum. However, this is not confirmed by the observation on *L. vulnerata* living in the rapid current of the Cetina river (Dalmatia). It has a foot no wider than those of other specimens of the same species living in still waters.

Lymnaeids are resistant to drying. In natural conditions, they may spend many months in anabiotical state. They dig themselves in bottom deposits, creep into crevices in the soil or hide under vegetation covering the bottom of a water body. Some species (*Lymnaea truncatula*, *L. occulta*) may live in water reservoirs which are periodically dry, or spend life amphibiotically (*L. peregra*, *L. vulnerata*).

Environmental temperatures of 20 to 25°C are the most favourable for lymnaeid vital processes such as feeding, development and reproduction. They stop when the water reservoirs freeze completely.

Lymnaeids migrate to deeper parts of lakes during late autumn but they are still active (for example *L. peregra*).

Lymnaeids serve as indicators of water purity within the saprobic system - division of waters into saprobic zones *i. e.* the zones of pollution with organic compounds. The number of snails, among them lymnaeids, is low or very low in alpha-mesosaprobic waters (MICHAŁKIEWICZ 1993). However, they live in rather pure waters, that is in beta-mesosaprobic ones. This is the zone of final mineralization of organic materials. The oxygen level most frequently reaches values of 5.0 to 9.0 mg O_2/dm^3. Lymnaeid respiration is mostly based on atmospheric oxygen. Therefore oxygen shortage in aquatic environments is not essential for them. Excessive quantities of hydrogen sulphide, amino acids, ammonia and nitrites limit their occurrence. Carbon dioxide dissolved in water causes shell erosion.

Calcium plays an important role in lymnaeid life. Calcium carbonate is the main component of the snail shell. It is ingested with food, but not directly from the substratum. The hardness of the water does not directly affect the snail occurrence (FRÖMMING 1956).

Lymnaeids tolerate a wide range of pH between 5.6 and 8.5, and thus can live in slightly acid to slightly alkaline waters. The level of calcium salts has a profound effect on the concentration of hydrogen ions. As a result of hydrolysis of those salts, free OH^- ions appear, and develop an alkaline reaction in the water.

III. DETAILED DESCRIPTION

The shells of some lymnaeid species are very similar. The key to their identification is therefore based both on the morphological features of the shells and on the anatomical structure of the reproductive organs. The anatomical structure in some species is the only diagnostic feature that permits their unambiguous identification. In other cases, it makes it possible to verify the conchological determinations.

1. KEY TO THE IDENTIFICATION OF GENERA AND SUBGENERA

1. Shell cylindrically turriform (Plate I.2), aperture small, about 1/3 shell height, prostate without any fold, praeputium with one fold, sometimes with a short additional fold ..... *Omphiscola* BECK, 1837
-. Shell of different shape (Plate I.1, 3), aperture much larger, prostate with one, two or many folds, praeputium with two folds (*Lymnaea* LAMARCK, 1799) ..... 2.
2. Spire much lower than the aperture, penis long, thin ..... 3.
-. Spire equal to or higher than the aperture, penis different ..... 4.
3. Mantle does not cover the shell externally ..... *Radix* MONTFORT, 1810
-. Mantle covers the shell externally ..... *Myxas* SOWERBY, 1822
4. Shell small, whorls very convex, „stair-like", penis short, smooth .... *Galba* SCHRANK, 1803
-. Shell large, whorls not so convex ..... 5.
5. Spire higher than the aperture, turriform, body whorl not very expanded, penis either very long, or long and smooth, or long with a narrowing .... *Stagnicola* LEACH, 1830
-. Spire lower than the aperture, conical, body whorl greatly expanded, penis short with ring-like swelling ..... *Lymnaea* s. str.

2. KEY TO THE IDENTIFICATION OF SPECIES

1. Spire as high as aperture or higher (Plate IX) ..... 2.
-. Spire much lower than aperture (Plate II) ..... 9.
2. Body whorl very greatly expanded, spire slender and tapered .... *Lymnaea* (*Lymnaea*) *stagnalis* (L.) (page 69)
-. Body whorl less expanded, spire not so slender ..... 3.
3. Shell small (to 15 mm in height) ..... 4.
-. Shell much larger ..... 5.
4. Shell stocky, whorls very greatly convex, „stair-like", aperture usually as high as spire ..... *Lymnaea* (*Galba*) *truncatula* (O.F. MÜLL.) (page 38)
-. Shell slender and cylindrically turriform, whorls slightly convex, aperture much lower smaller than spire ..... *Omphiscola glabra* (O.F. MÜLL.) (page 35)
5. Shell ovately conical, aperture usually equal to or higher than spire ..... 6.
-. Shell of different shape ..... 7.
6. Prostate with two large folds inside .... *Lymnaea* (*Lymnaea*) *vulnerata* KÜSTER (page 63)
-. Prostate with many folds inside..... ..... *Lymnaea* (*Lymnaea*) *corvus* (GMELIN) (page 66)
7. Shell cylindrically turriform, whorls weakly convex, columellar fold large, thick and chalky white ..... *Lymnaea* (*Stagnicola*) *occulta* (JACK.) (page 60)

-. Shell ovately turriform, whorls very convex, columellar fold narrow, thin and whitish ..... 8.
8. Praeputium length to penis sheath length ratio 1:1 .... *Lymnaea* (*Stagnicola*) *palustris* (O.F. MÜLL.) (page 53)
-. Ratio of praeputium length to penis sheath length 1:3-5 .... *Lymnaea* (*Stagnicola*) *turricula* (HELD) (page 57)
9. Shell spherical, very thin and fragile, spire low and flattish, broad mantle covers the shell externally .... *Lymnaea* (*Myxas*) *glutinosa* (O.F. MÜLL.) (page 50)
-. Shell ovate, spherically ovate, spire conical, elevated, shell thicker and stronger, mantle does not cover the shell ..... 10.
10. Spire widely conical, blunt, columellar fold straight, spermatheca with or without a short duct ..... *Lymnaea* (*Radix*) *peregra* (O.F. MÜLL.) (page 42)
-. Spire narrow conical, tapered, columellar fold severely bent, spermatheca with a long duct ..... *Lymnaea* (*Radix*) *auricularia* (L.) (page 47)

3. DESCRIPTION OF PARTICULAR SPECIES

***Omphiscola glabra* (O.F. MÜLLER, 1774)**

Figures 47-55; Plates I.2, X.1.

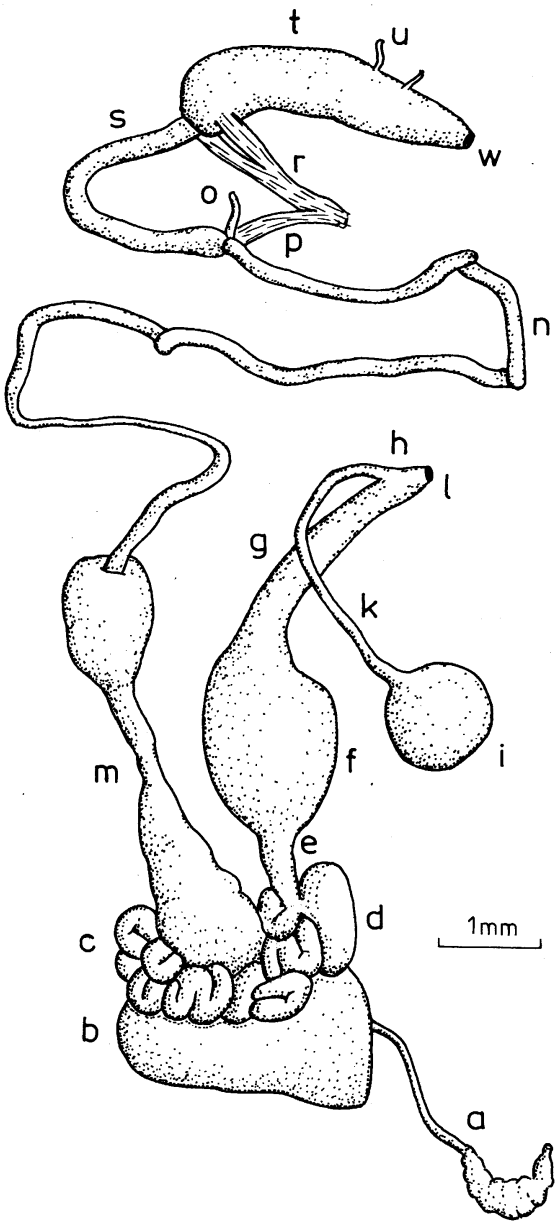
Buccinum glabrum O.F. MÜLLER, 1774; Ver. terr. II, p. 135, no. 328.

Locus typicus: Frederiksdal near Copenhagen (Denmark).

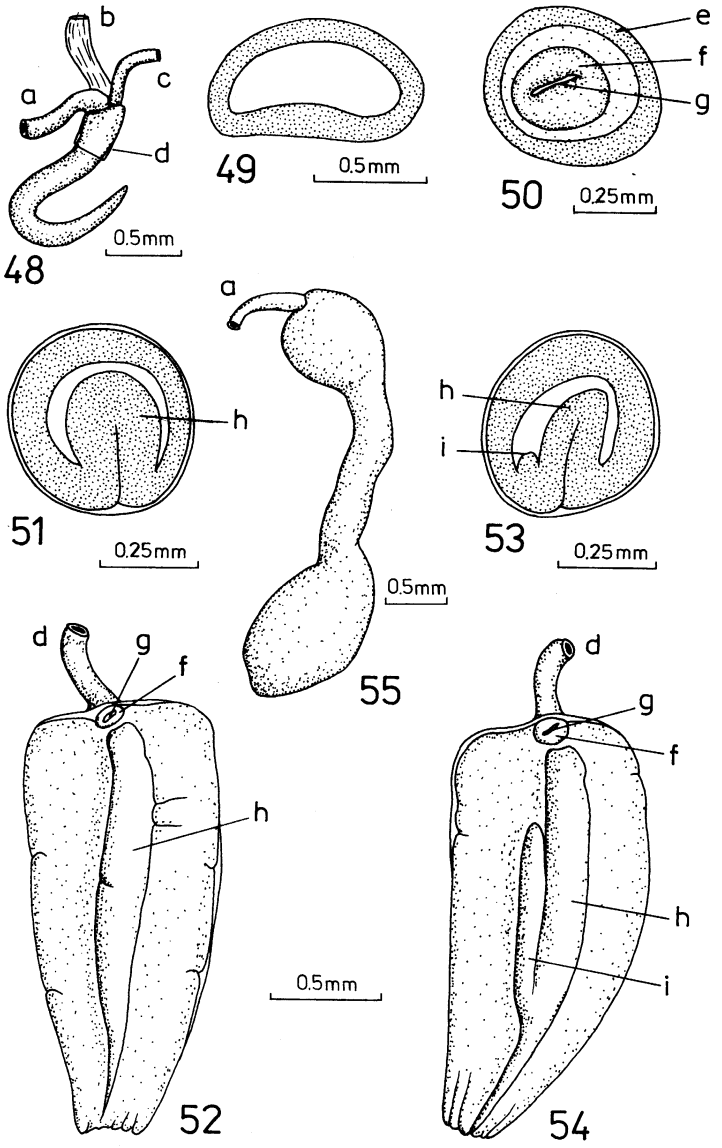
Synonyms: *Lymnaea glabra* (O.F. MÜLLER, 1774); *Leptolymnaea glabra* (O.F. MÜLLER, 1774); *Stagnicola glabra* (O.F. MÜLLER, 1774); *Galba glabra* (O.F. MÜLLER, 1774); *Bulimus leucostoma* POIRET, 1801; *Limneus elongatus* DRAPARNAUD, 1805.

S h e l l (Plate I.2) very narrow, slender, cylindrically turriform, quite thin. Up to 8 slightly convex whorls, slowly and evenly increasing. Body whorl slightly wider than the penultimate one. Spire very high, bluntly terminated. Aperture small, equal to 1/3 shell height. Lower part of columella slightly coiled, its fold thin but distinct. Umbilicus narrow, fissured and often completely covered. Shell colour from bright yellow to rusty-brown. Fold and shell interior are brighter, usually whitish, often with white lamella inside the aperture. Shell up to 15 mm high and up to 5.5 mm wide.

M a n t l e (Plate X.1) brownish-black, covered with small pale yellow spots. They may be roundish, elliptical or oblong and evenly scattered on the whole mantle surface. There is no dark stripe over the pneumostome that is visible in all



47. Reproductive organs of *Omphiscola glabra*: a - hermaphroditic duct with the seminal vesicles, b - albumen gland, c - uterus, d - nidamental gland, e - oviduct I, f - pyriform body, g - oviduct II, h - vagina, i - spermatheca, k - spermathecal duct, l - female gonopore, m - prostate, n - vas deferens, o - nerve of the penis, p - retractor of the penis sheath, r - retractor of the praeputium, s - penis sheath, t - praeputium, u - protractor, w - male gonopore. (Original).



48-55. Main features of the reproductive organs of the genus *Omphiscola*: 48 - Penis; 49 - Transverse section through the distal part of the prostate; 50 - Bulbous termination of the praeputium as seen from the inside; 51 - Transverse section through the praeputium with a single fold; 52 - Praeputium (inside a longitudinal fold is visible); 53 - Transverse section through the praeputium with an additional fold; 54 - Praeputium (inside an additional longitudinal fold is visible); 55 - Prostate: a - vas deferens, b - retractor of the penis sheath, c - nerve of the penis, d - cut off penis sheath, e - wall of the cut off praeputium, f - papilla (sarcobelum), g - lumen of the papilla, h - longitudinal fold, i - additional longitudinal fold. (After JACKIEWICZ).

other species. Mantle collar whitish-yellowish, finished with a fairly wide, slightly darker ridge. Other body parts yellowish-grey.

R e p r o d u c t i v e o r g a n s (Fig. 47). Praeputium club-shaped. Retractor inserted on one side of its basal part (bulbous termination). Praeputium wall invaginated into its interior as a single, well developed longitudinal fold (Figs 51h, 52h). There is often an additional fold, thinner and half as long (Figs 53i, 54i). Fairly large, thick disk at the praeputium bottom (Fig. 50). Sometimes it looks like two lips, one of them is usually larger than the other. A fissured disk aperture connects the lumen of the penis sheath with the praeputium lumen. According to HUBENDICK (1951), this disk corresponds only with a papilla (*sarcobelum*) but not with a papillary fold (*velum*) of other lymnaeid species. Nevertheless it resembles the papillary fold more than the papilla. The penis sheath is cylindrical and fairly thick with the ratio of the penis sheath length to the praeputium length of 1:1 (Fig. 47s, t). The penis is inside the sheath and is slightly pointed at the end (Fig. 48). The proximal and distal parts of the prostate are of almost the same width, although sometimes the proximal part is wider (Fig. 55). There is no fold inside the prostate. The wall of the distal prostate part is slightly thicker on one side only (Fig. 49). Vas deferens leaves the prostate at the centre. Pyriform body ovate. A very long, tubular oviduct II leaves the pyriform body, and passes into a short but relatively wide vagina. The spermathecal duct is also very long and thin with a large, spherical spermatheca (Fig. 47).

B i o n o m i c s. *Omphiscola glabra* is usually found in shallow, still waters with dense vegetation. It is a rare, even very rare, species. According to other authors, for example GEYER (1927), it appears mostly in spring, and is resistant to dry conditions. Its anatomy is best known but its bionomics and ecology are almost unknown.

D i s t r i b u t i o n. In Poland, it was found in 1929 by HAAS at Gronowo near Leszno in the vicinity of the so called „Napoleon's Table". GEYER (1927) recorded it from East Prussia. It has not been found since then in either of these places although it has been intensively searched for. No other localities have been reported in the Polish territory. *O. glabra* is a north-west European species. Many localities are found in Germany and Sweden. Its distribution is not precisely known, as it is often confused with small forms of *Lymnaea palustris* and *L. turricula*.

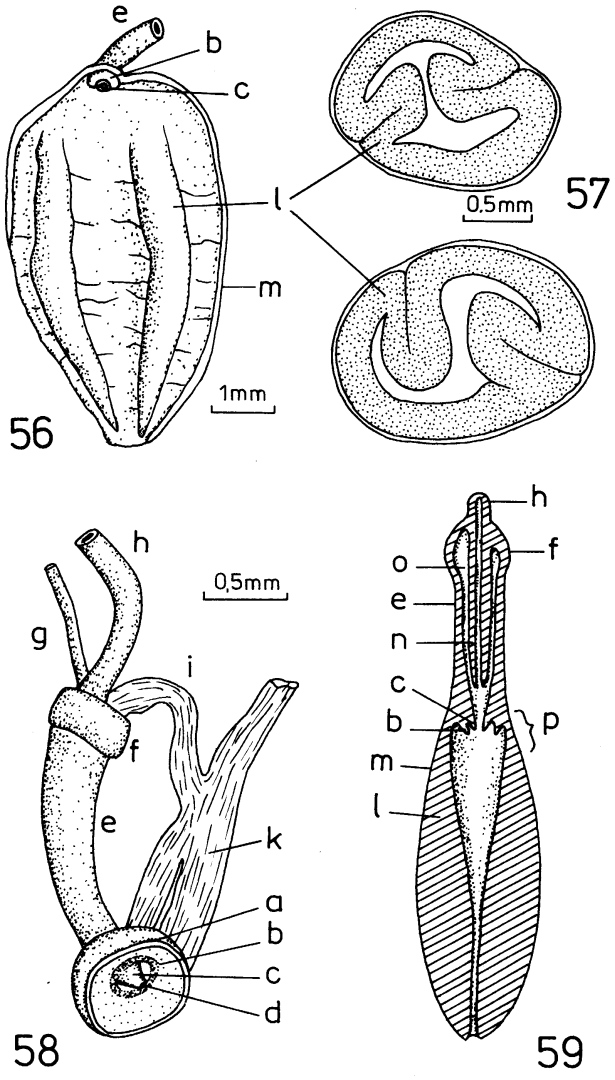
***Lymnaea* (*Galba*) *truncatula* (O.F. MÜLLER, 1774)**

Figures 1, 2, 38, 60, 61; Plates I.1, X.2.

Buccinum truncatulum O.F. MÜLLER, 1774; Verm. terr. II, p. 130, no. 325.

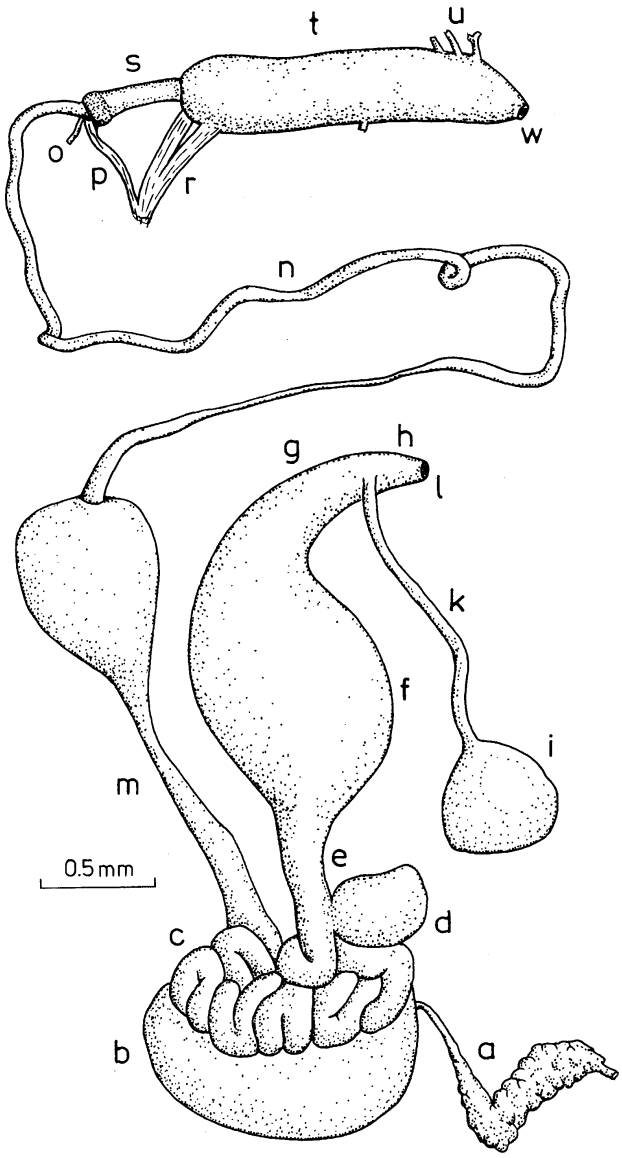
Terra typica: Denmark.

Synonyms: *Fossaria truncatula* (O.F. MÜLLER, 1774); *Limneus minutus* DRAPARNAUD, 1801.



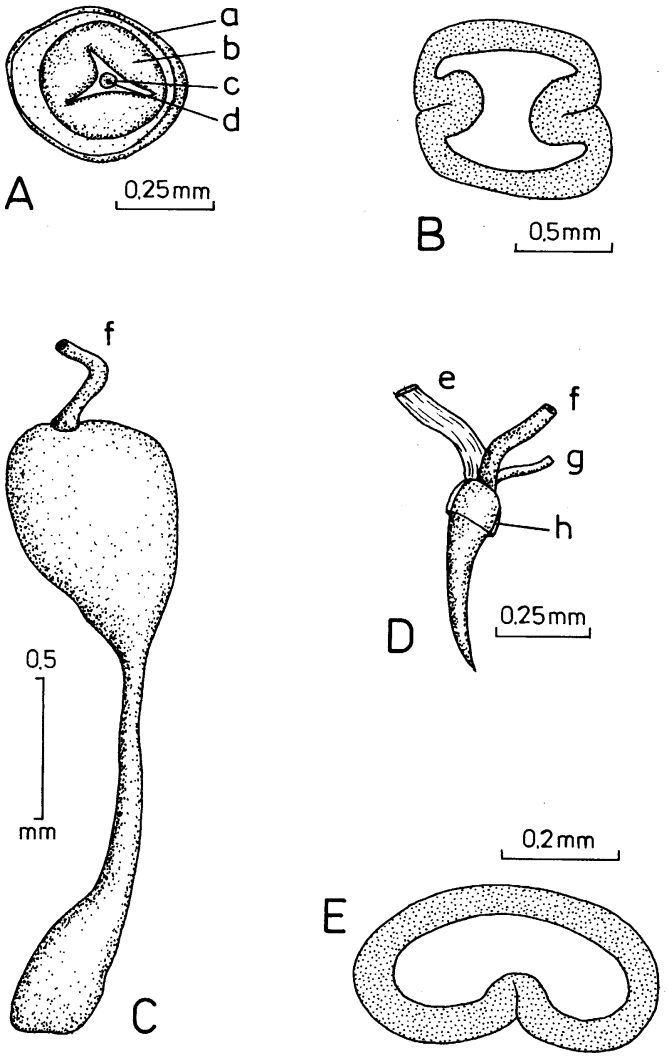
56-59. Main features of the reproductive organs of the genus *Lymnaea*: 56 - Praeputium (inside two longitudinal folds are visible); 57 - Transverse sections through the praeputium (arrangement of two longitudinal folds is visible); 58 - Bulbous termination of the paeputium as seen from the inside; 59 - Diagrammatic longitudinal section through the penis sheath and the praeputium: a - wall of the cut off praeputium, b - papillary fold (velum), c - papilla (sarcobelum), d - lumen of the papilla, e - penis sheath, f - bulbous termination of the penis sheath, g - penial nerve, h - vas deferens, i - retractor of the penis sheath, k - retractor of the praeputium, l - longitudinal folds, m - praeputium, n - penis, o - glandular cavity, p - bulbous termination of the praeputium. (After JACKIEWICZ).

S h e l l (Plate I.1) small, ovately conical and relatively thin. Up to 6, very convex, almost „stair-like", whorls, separated with deep suture. They grow quite evenly but the body whorl is the largest and sometimes much expanded. The spire may be slender or widely conical, and bluntly terminated. The aperture ovate, is



60. Reproductive organs of *Lymnaea (Galba) truncatula*. (Original). For lettering see Fig. 47.

usually big and equals 1/2 shell height. The lower columellar part is almost straight. Its fold is fairly thick and most frequently of the same shade as the rest of the shell. Fissured umbilicus usually quite visible. Shell horny-yellowish. Up to 11 mm high (exceptionally more), up to 6 mm wide.



61. Structure of the male reproductive organs of *Lymnaea (Galba) truncatula*: A. Bulbous termination of the praeputium as seen from the inside; B. Transverse section through the praeputium; C. Prostate; D. Penis; E. Transverse section through the distal part of the prostate: a - wall of the cut off praeputium, b - papillary fold (velum), c - papilla (sarcobelum), d - lumen of the papilla, e - retractor of the penis sheath, f - vas deferens, g - penial nerve, h - cut off penis sheath. (after JACKIEWICZ).

M a n t l e (Plate X.2). The pigmentation of the mantle in *L. truncatula,* as opposed to other lymnaeid species, is relatively invariable. The mantle is uniformly black, with small clearly outlined spots of different sizes, shaped like little irregular yellow-grey stars with very short beams. A long wide black stripe, lying above the pneumostome, almost merges with the dark mantle background. The mantle collar is grey or yellow-grey with a few spots of dark pigment. The ridge is fairly narrow and pale yellowish-grey. The head with tentacles and foot are grey.

R e p r o d u c t i v e o r g a n s (Fig. 60). Praeputium sac-like. Retractor inserted on its bulbous termination, somewhat shifted to one side. The praeputium wall develops two small longitudinal folds inwards (Fig. 61B), so there is a relatively big lumen inside this organ. The papillary fold, located at the praeputium bulbous termination bottom, is built of several small beefy lips that make a small disk. It surrounds a very small finger-like papilla with a small opening in the centre (Fig. 61A). Tubular penis sheath is slightly widened at the base into a so called bulbous termination. The ratio of the praeputium length to the penis sheath length is 3:1 (Fig. 60s, t). The short penis (Fig. 61D) quickly tapers off and becomes wedge-shaped. Proximal prostate part narrow but its distal part much wider and swollen. There is a single weakly developed fold inside this gland (Fig. 61E) therefore its lumen is very broad. Vas deferens leaves almost at the top of the prostate (Fig. 61C). Pyriform body much elongated. It passes unnoticeably into a short wide oviduct II, terminating with a large vagina. The spermathecal duct is long and thin. The spermatheca rather large and spherical (Fig. 60).

B i o n o m i c s. *Lymnaea truncatula* lives in small shallow water bodies of still water, such as drainage ditches, pools, puddles, ruts, watering-places and also in springs. It also appears in slow streams, moreover in oxbows and shallower parts of rivers and lakes. It often crawls out on wet waterside stones and plants. It is an intermediate host of the liver fluke (*Fasciola hepatica* L.). Since it lives in water reservoirs in the neighbourhood of human habitations, it facilitates the expansion of the fluke disease among cattle and sheep.

D i s t r i b u t i o n. This species lives on the plains of Poland and also often appears in the mountains where it may reach considerable altitudes. A Holarctic species inhabiting Europe, W and N Asia, as well as NW Africa.

Lymnaea (*Radix*) *peregra* (O.F. Müller, 1774)

Figures 3, 10, 37, 62, 63; Plates II, X.6.

Buccinum peregrum O.F. Müller, 1774; Verm. terr. II, p. 130, no. 324.

Locus typicus: Frederiksdal near Copenhagen (Denmark).

Synonyms: *Radix limosa* (Linnaeus, 1758), *Radix baltica* (Linnaeus, 1758), *Radix lagotis* (Schrank, 1803), *Radix ovata* (Draparnaud, 1805), *Radix neglecta* (C.R. Boettger, 1944).

S h e l l (Plate II) very variable, most frequently ovate or spherically ovate, fairly thick and strong or thin and fragile, slightly translucent, glittering, rarely „hammered". 3 - 5 convex whorls, the body whorl most often greatly or very greatly expanded. Spire turriform, usually low, and bluntly terminated, of 1/4 - 2/5 shell height. A large aperture reaches up even higher than the shell apex, its margin sometimes turned inside out. Lower columellar part straight or only slightly twisted with a small fold, usually thin and lighter than the shell. Umbilicus fissured and well visible under the columellar fold. Shell interior often lighter and glittering. The shell height and width may reach 40 mm.

M a n t l e (Plate X.6) deep black. Whitish round spots with a regular border are clearly outlined. There is a long fairly wide stripe of black pigment near the pneumostome. Many irregular black pigment spots are spread against the whitish background of the mantle collar. The collar is encircled by a clearly marked pale beefy ridge. The head with appendices and foot of yellowish-grey colour. The mantle pattern of this species is a good diagnostic feature, so it is easily distinguishable from the closely related *Lymnaea auricularia*.

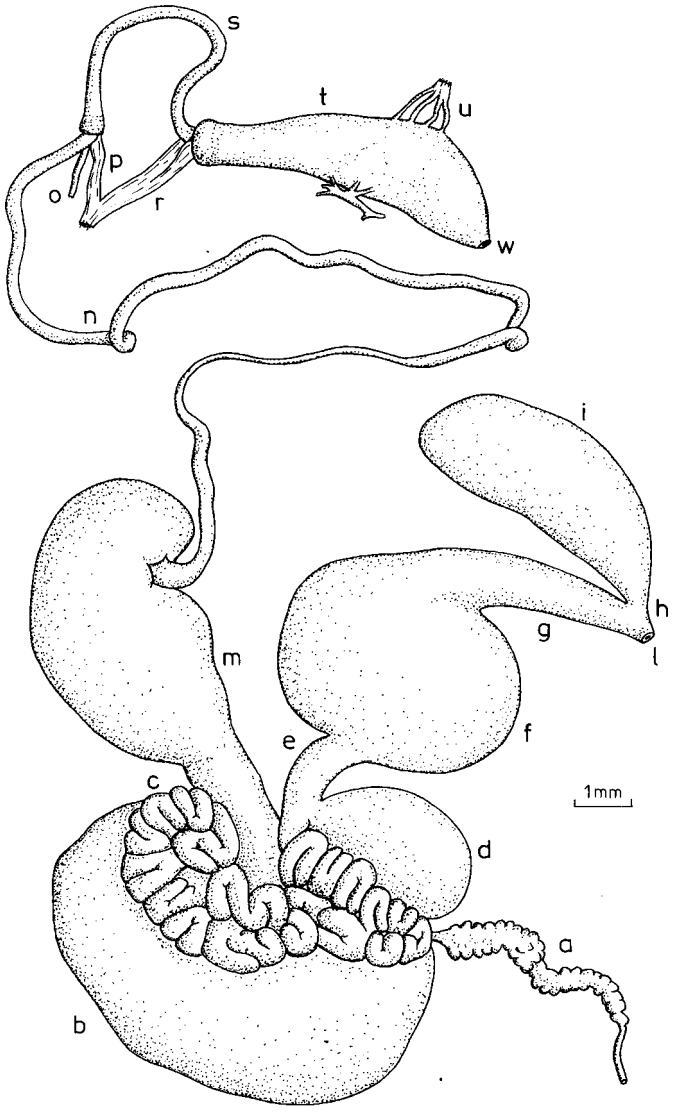
R e p r o d u c t i v e o r g a n s (Fig. 62). The praeputium is club-shaped and narrowed in its proximal part where a bulbous termination is well developed. The retractor is inserted at this point, just next to the penis sheath. Two longitudinal folds are visible inside the praeputium (Fig. 63B) originating as an invagination of the praeputium wall. A big domed papilla with a very small opening on its top lies at the praeputium bulbous termination bottom. It is surrounded with a large beefy papillary fold, usually composed of something like two lips (Fig. 63A). The praeputium sheath is long and very thin, with a faintly developed bulbous termination. The ratio of the praeputium length to the penis sheath length is 1:1 (Fig. 62s, t). The penis (Fig. 63D) is very long and becomes narrower towards its end. The proximal prostate part is thick and passes unnoticeably into a large swollen distal part (Fig. 63C). There is one very large fold in that part of the gland, so there is relatively little lumen between the fold and the prostate wall (Fig. 63E). The vas deferens leaves from the side of the distal part of the prostate. The pyriform body is very large and spherical and passes upwards into a long oviduct II which gradually narrows and extends to a short vagina. The spermathecal duct is very short or, most frequently, completely missing, then the spermatheca opens directly to the vagina. In such cases it is called „a sitting spermatheca" (Fig. 62). Its shape and size are very variable.

Sometimes it is difficult to distinguish *Lymnaea peregra* from the related *L. auricularia* on the basis of shell features only. The length of the spermathecal duct and the spermatheca shape are the most important characters that distinguish these two lymnaeids. Furthermore, the pattern of the mantle surface pigmentation may be useful.

Former malacologists who took into account shell features only, distinguished 6 species and about 50 varieties of lymnaeid *Radix* MONTFORT, 1810 group. It was found, on the basis of the structure of their reproductive organs, that

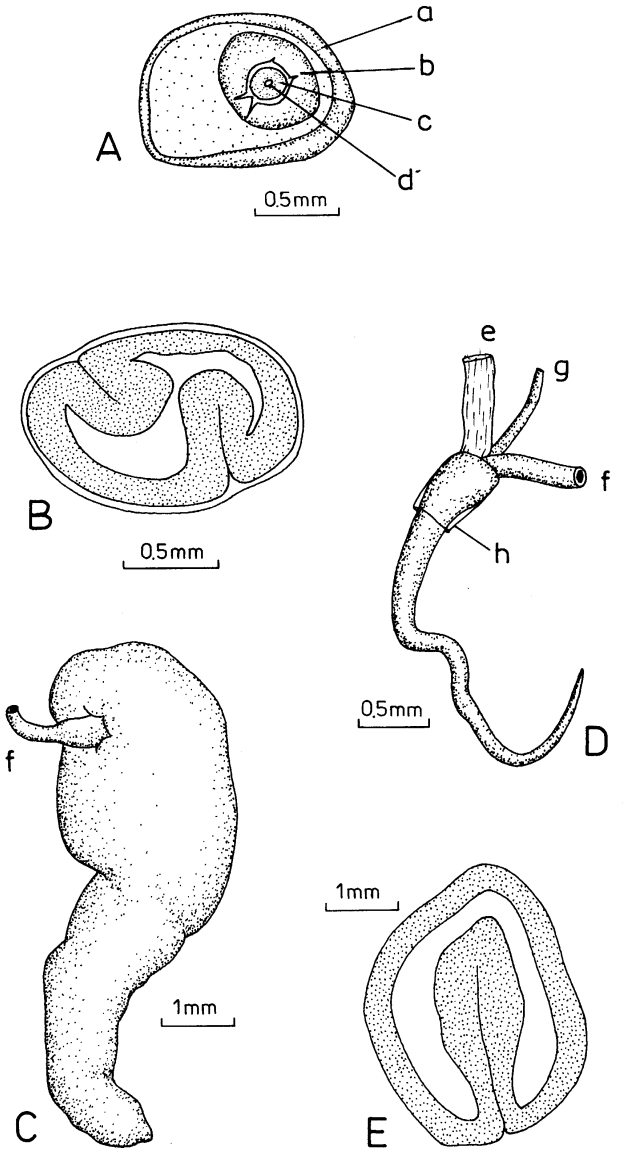
only *Lymnaea peregra* and *L. auricularia* are valid distinct species. All other names were given to different shell forms of these two species (HUBENDICK 1945, 1951, JACKIEWICZÓWNA 1954).

Some forms of *L. peregra,* listed below, are noteworthy. They differ in shell shape only but their reproductive organs are identically built.



62. Reproductive organs of *Lymnaea (Radix) peregra*. (Original). For lettering see Fig. 47.

The shell of the form called *typica* (O.F.MÜLLER, 1774) (Plate II.1) is elongate ovate. Its spire reaches even 1/2 shell height. The shell wall is quite thick and strong, pale brown or horny in colour with four to five convex whorls. The ovate aperture is quite large and narrowed upwards. The shell reaches a height of up to 22 mm and a width of up to 13 mm.



63. Structure of the male reproductive organs of *Lymnaea (Radix) peregra*. (After JACKIEWICZ). For lettering see Fig. 61.

This form is usually found in small muddy water reservoirs (puddles, marshes, drainage ditches). It may spend its life amphibiotically, crawling up the banks. It is found in extreme conditions both in cold mountain reservoirs and in hot springs. The form from the latter habitat is called *geysericola* BECK. The *typica* form lives in waters of pH 5.8-8.8 and is resistant to drying. It is the most widespread form of *L. peregra* (URBAŃSKI 1957, PIECHOCKI 1979a).

The form *o v a t a* (DRAPARNAUD, 1805) is characterized by an ovate shell (Plate II.2). The shell spire height can equal 1/4 shell height. The shell wall is thin, faintly translucent and slightly glittering, with a pale yellow to horny colour. There are 4-4.5 weakly convex whorls and the body whorl is the largest and greatly expanded. The aperture is large and ovate. The shell is up to 30 mm high and 20 mm wide.

It lives in lakes, ponds, rivers and oxbows, and also in meadow floods or peatbogs. It prefers reservoirs rich in vegetation.

The shell of the form *l a g o t i s* (SCHRANK, 1803) is ovate. Spire quite high, up to 1/3 shell height. The shell wall is thin and fragile, somewhat translucent and glittering. Four to five very convex whorls, separated by a deep suture, the body whorl being greatly expanded. Aperture ear-shaped, shifted to one side. Shell up to 25 mm hegh and 20 mm wide.

It inhabits clean stagnant or flowing waters.

The shell of the form called *a m p l a* (HARTMANN, 1921) (Plate II.3) is spherically ovate. Its spire is very low and turriform. There are 3-3.5 rather convex whorls, the body whorl is the largest and greatly expanded. The aperture is very large, and sometimes may reach up over the apex. The shell at times is strong, slightly translucent and glittering, with a whitish-yellow to horny colour. It may be „hammered". Up to 40 mm high and wide.

It may be found crawling on muddy or sandy bottoms of lakes, flowing waters as well as in lake breaker zones.

It should be emphasized that populations of *L. peregra* with shell characters intermediate between the above forms may exist.

FALKNER (1990) is of opinion that the form *ampla* (HARTMANN, 1921) is a distinct species. The form *ovata* (DRAPARNAUD, 1805) is also sometimes treated as a good species (FALKNER 1990, GLÖER and MEIER-BROOK 1994).

B i o n o m i c s. *Lymnaea peregra* inhabits all kinds of water reservoirs. It enters pretty far brackish waters of the Baltic and North Sea.

D i s t r i b u t i o n. The species is one of most common and most widespread snails in Poland. *L. peregra f. typica* lives both in the lowlands and in the mountains, and reaches altitude of 1400 m a.s.l. in the Tatra Mountains and the

Babia Góra Mount. *L. peregra f. ovata* lives mostly in the lowlands but it may be also found in lower parts of the Beskidy Mts and the Sudetes. *L. peregra f. ampla* also inhabits lowland parts of Poland and lower mountain altitudes but it is rare in the latter localities (North Sudetes, East Beskidy Mts). *L. peregra f. lagotis* is the rarest form. Its few localities were reported from the Mazurian Lakeland, lowlands Nizina Mazowiecka and Nizina Wielkopolsko-Kujawska, Lower Silesia, Wyżyna Małopolska upland, Nizina Sandomierska lowland, West Sudetes and the East Beskidy Mountains. The general range of distribution of this Palaearctic species covers almost all of Europe as well as large areas of north and west Asia.

***Lymnaea* (*Radix*) *auricularia* (LINNAEUS, 1758)**

Figures 64, 65; Plates III, X.7, XI.1, 2.

Helix auricularia LINNAEUS, 1758; Syst. nat., p. 774, no. 617.

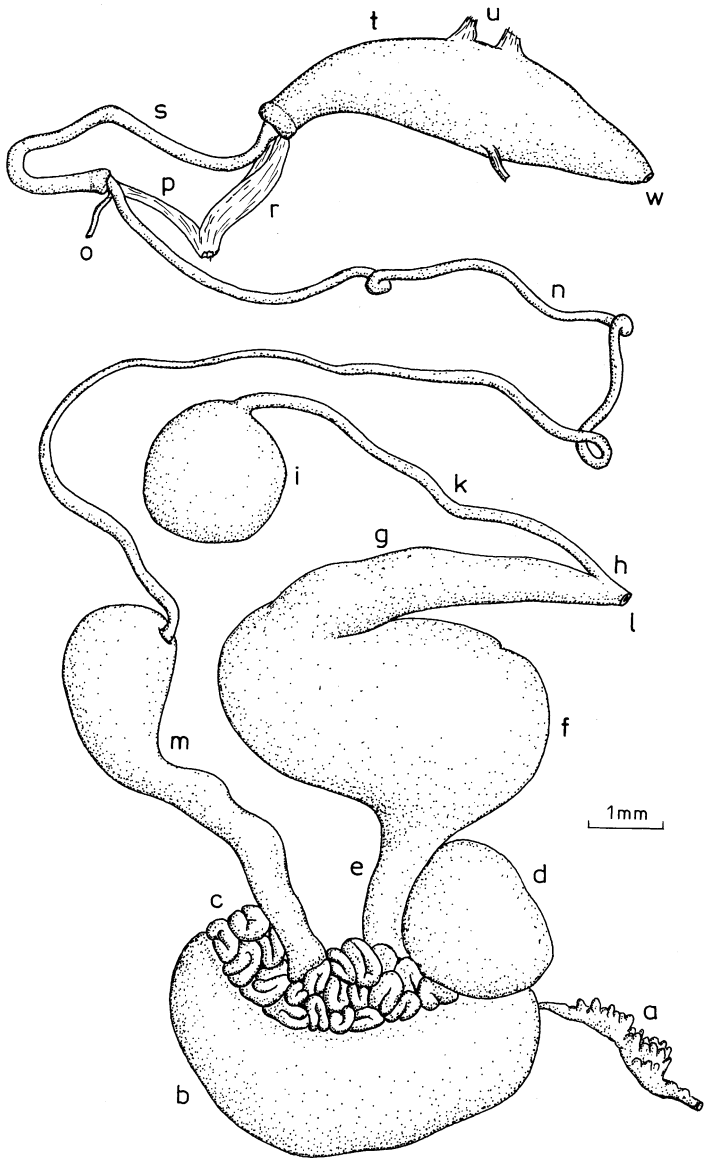
Terra typica: Sweden.

S h e l l (Plate III) slightly variable. Ovate or spherically ovate in shape, relatively thin-walled and fragile. „Hammering" sometimes visible on its surface. 4 - 4.5 weakly convex whorls. Spire low, conical and sharply terminated, with the body whorl greatly expanded. Aperture very large, widely ovate. Its outer margin sometimes slightly turned inside out. Lower columellar part strongly twisted (taxonomic feature). Its fold quite wide and thin. Umbilicus narrow, fissured and often covered. Shell colour from whitish-yellow to brown. Shell height, usually the same or almost the same as its width, reaches 30 mm.

M a n t l e (Plate X.7) is not as deep black as in *L. peregra*, with some big whitish spots of circular shape with subtly rough edges. There is a long stripe of dark pigment above the pneumostome, much narrowed in one place. The mantle collar is pale grey, almost whitish, with large elliptical black spots. In adults, border spots merge together into a wide black stripe at the collar edge. The mantle collar is finished with a well outlined whitish ridge. On this ridge, small grains of black pigment are irregularly distributed. Such grains cover also the whole yellowish-grey snail body as well as its internal organs. All this makes the pattern of the mantle pigmentation a good diagnostic feature. Therefore it is easy to distinguish *L. auricularia* from *L. peregra.*

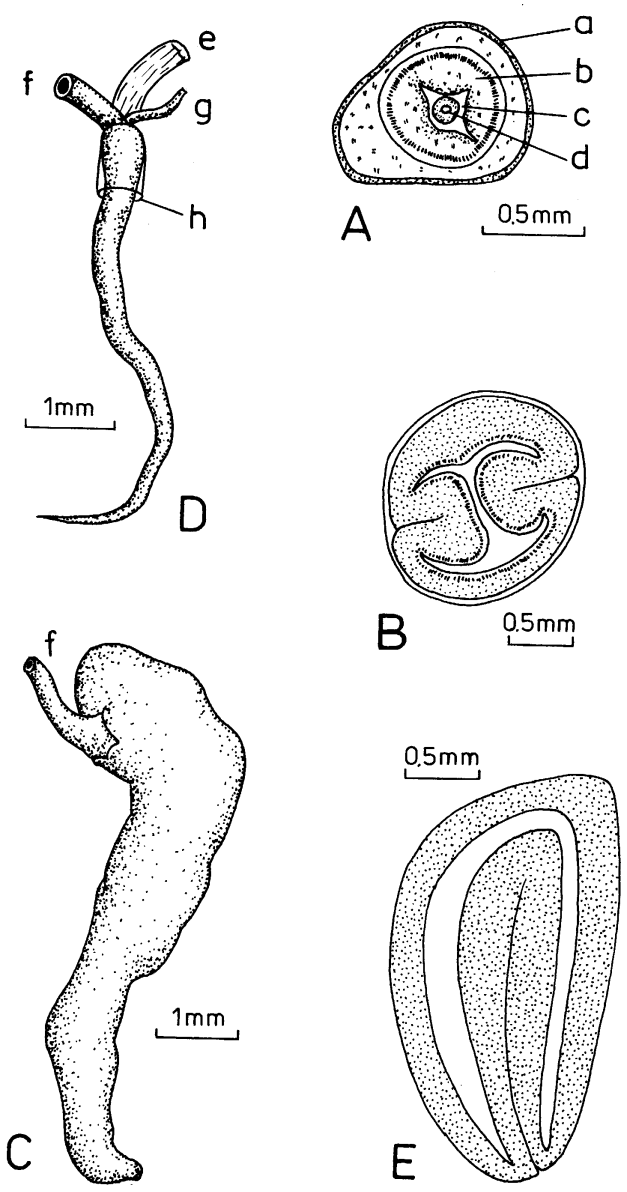
R e p r o d u c t i v e o r g a n s (Fig. 64). The praeputium is fusiform, with a well outlined bulbous termination. Its wall forms two, internally facing, longitudinal folds. They usually lie opposite one another (Fig. 65B) but they may be shifted. There is a papillary fold inside the praeputium, at the bottom of its bulbous termination (Fig. 65A). It looks like a large flat disk. There are small grains or even rods of dark pigment at the outer margin of this fold. There is a small convex papilla with a tiny opening on its top in the disk centre. The penis sheath is long and thin. The ratio of the praeputium length to the penis sheath length is 1:1 (Fig. 64s, t). The penis (Fig. 65D) is thin and long so that it

resembles the vas deferens. The proximal prostate part is relatively wide and gradually turns into the wider and swollen distal part (Fig. 65C). The wall of the distal prostate part invaginates making a single large fold, so a very narrow lumen is left around it (Fig. 65E). The vas deferens runs out from one side of the distal



64. Reproductive organs of *Lymnaea (Radix) auricularia*. (Original). For lettering see Fig. 47.

part of the prostate. The pyriform body is big and more or less ovate. The relatively long oviduct II starts here. The vagina is very small and short. A very long thin duct of spermatheca opens to the vagina. It terminates with a large, always roundish spermatheca (Fig. 64).



65. Structure of the male reproductive organs of *Lymnaea (Radix) auricularia*. (After JACKIEWICZ). For lettering see Fig. 61.

B i o n o m i c s. This species inhabits lakes, ponds and oxbows. It lives also in brackish waters of the Baltic Sea but only in the coastal zone. It prefers still waters, where the typical form characterized by a fairly high spire and an ear-like aperture lives. A form similar to *L. peregra f. ampla* lives in waters of rapid current and strong waves. It has a very wide foot which facilitates attachment to the substratum. The shell of this form is more massive, with a lower spire and a large round aperture. Specimens living on reeds are noteworthy. Their feet are also wide to hold to the reed culms but there is a grooved hollow in the border of the shell aperture, at the point where the shell adheres to the culm.

D i s t r i b u t i o n. *Lymnaea auricularia* is common and widespread in the lowlands, especially in still waters. Singule localities are scattered in the West Sudetes, the East and West Beskidy Mountains. The occurrence in the Tatra and Pieniny Mountains is not sure (PIECHOCKI 1979a). This is a Palearctic species, distributed in almost all of Europe and in large areas of Asia as well as of North America where it was introduced (HUBENDICK 1951).

Lymnaea (*Myxas*) *glutinosa* (O.F. MÜLLER, 1774)

Figures 4, 43, 66, 67; Plates I.3, X.5.

Buccinum glutinosum O.F. MÜLLER, 1774; Verm. terr. II, p. 129, no. 323.

Terra typica: Denmark.

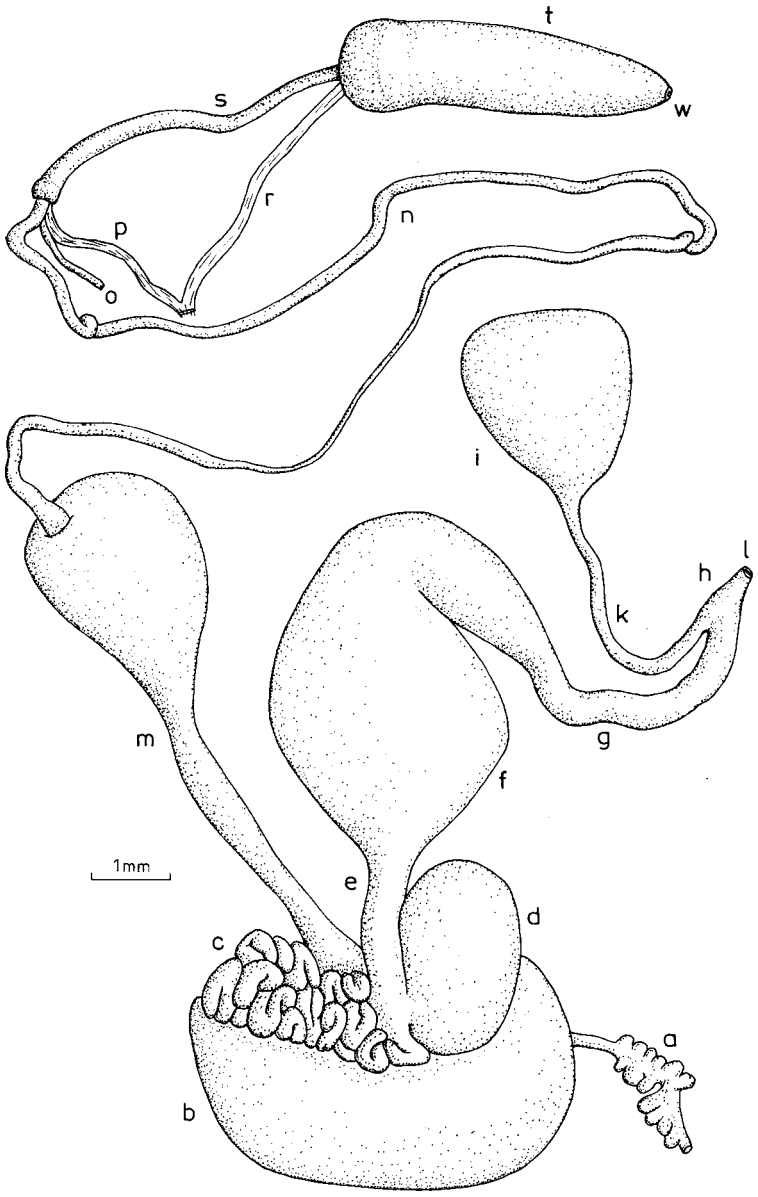
Synonyms: *Amphipeplea glutinosa* (O.F. MÜLLER, 1774); *Radix glutinosa* (O.F. MÜLLER, 1774)*; Myxas glutinosa* (O.F. MÜLLER, 1774).

S h e l l (Plate I.3) spherical, very thin, translucent, smooth, glittering. Up to 3 - 3.5 whorls. Spire very low and flattish. Body whorl greatly expanded, in fact it forms the whole shell. Aperture large and widely ovate. Lower columellar part slightly twisted. Its fold narrow and subtle, tightly adhering to the shell. Umbilicus completely covered. Shell pale horn in colour. Up to 15 mm high and to 13.5 mm wide. In live snails, a greatly developed mantle covers externally a large part of its shell or sometimes even all of it.

M a n t l e surface of the last whorl marbled (Plate X.5) with big round yellow spots of rough edges placed against the black background. Collar yellowish. It is covered with irregular spots of black pigment separated with the larger bright intervals. Some spots may be merged into an almost uniform stripe that adheres to the yellowish ridge. Moreover, there are two long narrow black stripes near the pneumostome. The rest of the body is olive-grey. The pattern of the mantle pigmentation may also be a good diagnostic feature.

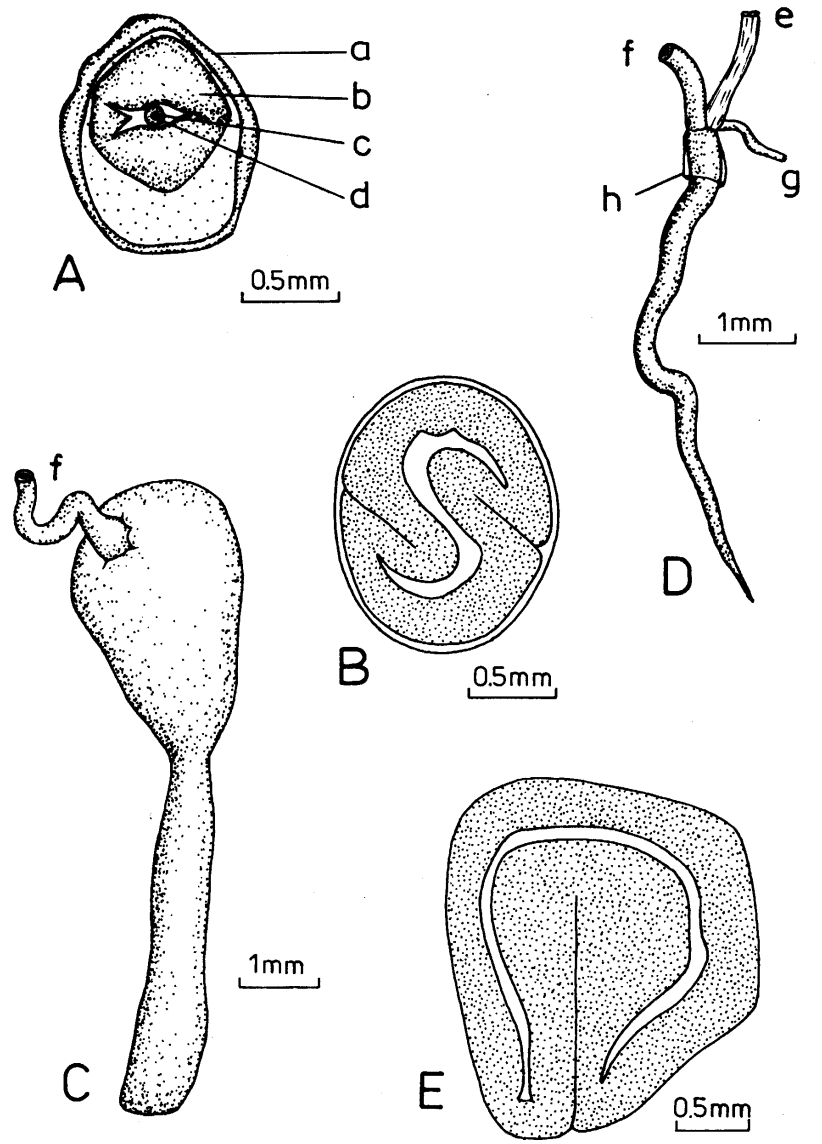
R e p r o d u c t i v e o r g a n s (Fig. 66). The praeputium is club-shaped. Its basal part, the so called bulbous termination, is much widened. There are two longitudinal folds inside the praeputium (Fig. 67B). They are shifted relative to each other, so that the lumen of the organ resembles the letter S. The position of these folds may vary a little. There is a very large, relatively thick papillary fold

at the bottom of the praeputium bulbous termination (Fig. 67A). It is built of two beefy lips of equal size. The papillary fold surrounds a very small papilla of conical shape. The opening on its top is also very small. The penis sheath is very



66. Reproductive organs of *Lymnaea (Myxas) glutinosa*. (Original). For lettering see Fig. 47.

thin and long. The ratio of the praeputium length to the penis sheath length is 1:1 (Fig. 66s, t). The penis (Fig. 67D) is very thin and long. It is wavy inside the penis sheath which is very thin. The proximal prostate part is long and usually wide. It suddenly passes into a greatly widened and swollen distal part (Fig. 67C). There is also one large fold in this part which fills the interior of the gland (Fig. 67E).



67. Structure of the male reproductive organs of *Lymnaea (Myxas) glutinosa*. (After JACKIEWICZ). For lettering see Fig. 61.

The vas deferens leads from one side of the distal part of the prostate. The pyriform body is ovate and greatly swollen. It passes quite rapidly into a very long oviduct II which is gradually narrowed towards the opening to the short narrow vagina. The spermatheca is large, ovate or more elongated. Its duct is thin and fairly long (Fig. 66).

B i o n o m i c s. This lymnaeid lives in stagnant or more rarely in flowing waters. It may be found in overgrown ponds, old riverbeds, river sandbanks or peatbogs where it dwells among plants or crawls on the substratum.

D i s t r i b u t i o n. *L. glutinosa* is quite a widespread species in the lowlands of Poland, though it is not common. It is entirely absent in many regions, particularly in the mountains. It is generally distributed in north-western Palaearctic areas.

***Lymnaea* (*Stagnicola*) *palustris* (O.F. MÜLLER, 1774)**

Figures 7-9, 11, 12, 19-25, 29, 30, 44, 68, 69; Plates IV, X.4.

Buccinum palustre O.F. MÜLLER, 1774; Verm. terr. II, p. 131, no. 326.

Locus typicus: Frederiksdal near Copenhagen (Denmark).

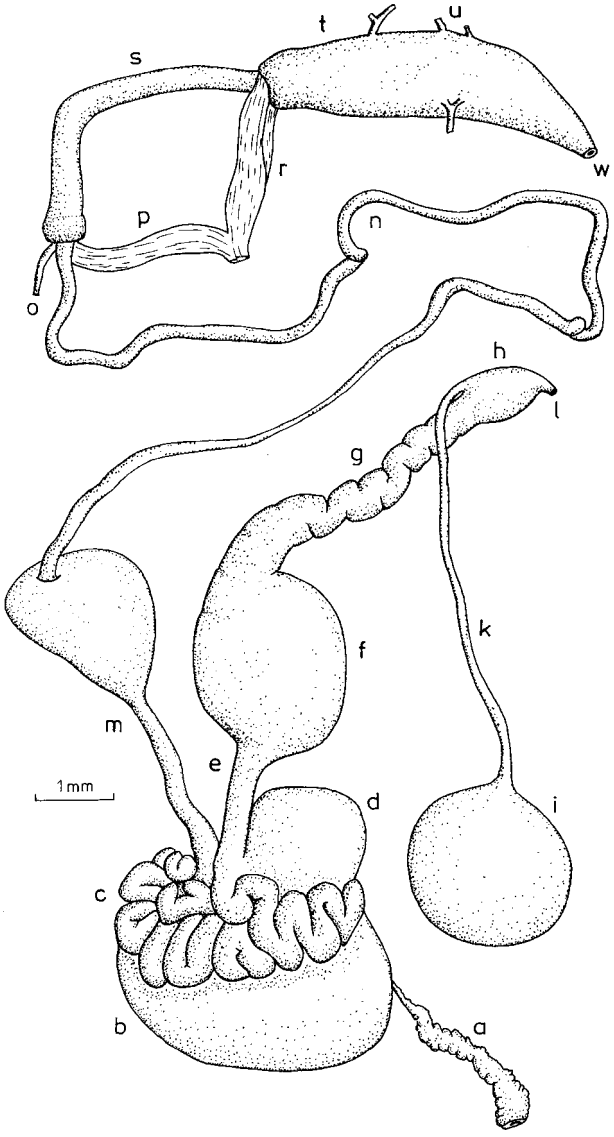
Synonyms: *Stagnicola palustris* (O.F. MÜLLER, 1774) - partim; *Galba palustris* (O.F. MÜLLER, 1774) - partim; *Stagnicola palustris f. turricula* (HELD, 1836); *Galba palustris f. turricula* (HELD, 1836); *Galba turricula* (HELD, 1836).

S h e l l (Plate IV) slender and ovately turriform. An irregular net, called „hammering" is sometimes created by thicker striae running transversely and spirally. The very convex whorls, 6-7 in number, are separated with quite a deep suture. The whorls increase almost regularly but the body whorl is big and fairly expanded. The spire is high, turriform and sharply terminated. The aperture is large, most often clearly lower than half of the shell height. The columella is twisted in its lower part, with a thin narrow columellar fold, adhering to the shell wall and usually much lighter than the shell. The umbilicus is very narrow and fissured, almost completely covered. The shell colour varies from pale to dark brown. Its interior is darker, glittering, frequently with a red-brown lamella that runs parallel with the aperture border. The shell is of up to 30 mm hig and up to 15 mm wide.

M a n t l e surface (Plate X.4) grey-black or even entirely black, with many whitish-yellowish spots. They are tiny, ovate and usually with a dark rim. There is a relatively short wide black stripe near the pneumostome. The mantle collar is dark grey, usually without any spots. The collar ridge is narrow and pale grey. The mantle pattern is very variable. Other body parts are grey or yellowish grey. Single specimens or even whole populations are often uniformly black.

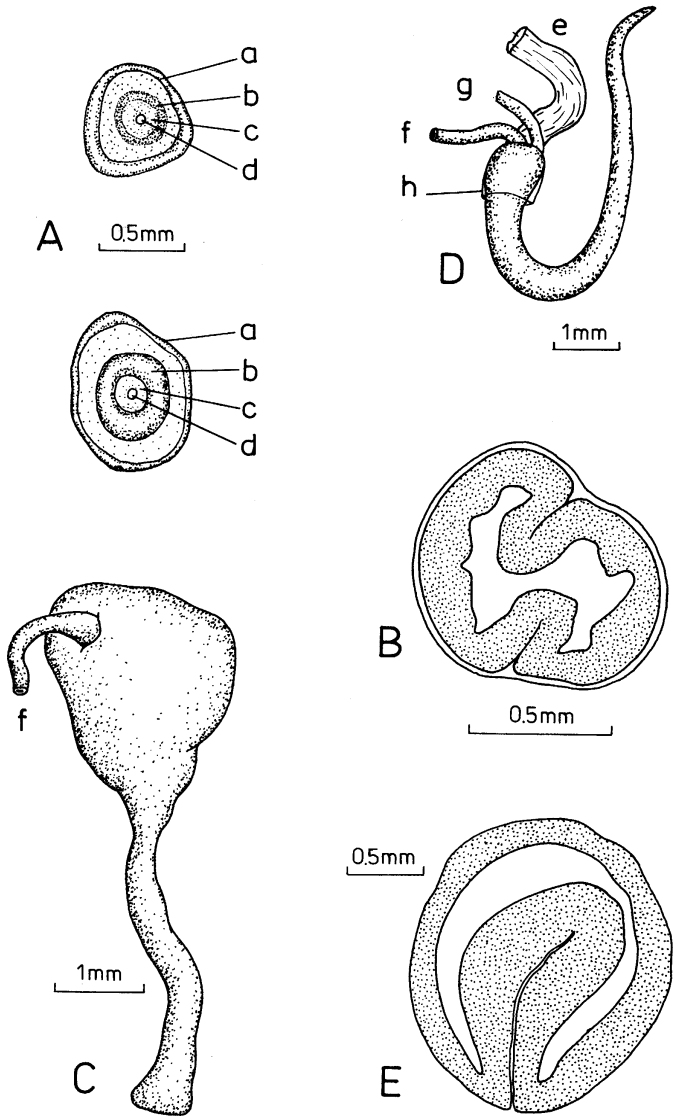
R e p r o d u c t i v e o r g a n s (Fig. 68). The praeputium is fusiformly club-shaped, with two longitudinal folds inside (Fig. 69B), one of them may be slightly smaller. These folds are shifted relative to each other so that the lumen of

the organ resembles the letter S. The papillary fold (Fig. 69A), situated inside the praeputium, may occur in two forms: it may be narrow and subtle or much wider but also delicate. The papilla is always big and conical with a small opening at its top. The penis sheath is long, cylindrical and quite thick, with a well developed bulbous termination. The ratio of the praeputium length to the penis sheath length



68. Reproductive organs of *Lymnaea (Stagnicola) palustris*. (Original). For lettering see Fig. 47.

is 1:1 (Fig. 68s, t). The penis (Fig. 69D) is also long and thick, it tapers slowly towards the end. The proximal prostate part is narrow, suddenly passing into the big pear-shaped distal part. Both prostate parts are almost equal in length (Fig. 69C). There is one large fold deeply entering the distal part of this gland (Fig. 69E). The vas deferens leads from the distal part, slightly to one side. The



69. Structure of the male reproductive organs of *Lymnaea (Stagnicola) palustris*. (After JACKIEWICZ). For lettering see Fig. 61.

pyriform body is large and round in outline. The oviduct II is very long and usually strongly plicate. The vagina is barrel-shaped, hard and swollen. The spermathecal duct that opens to the vagina is very long and thin. The spermatheca is spherical and very large (Fig. 68).

B i o n o m i c s. It inhabits mostly lakes of mesotrophic character, moreover forest and meadow ditches, marshes, peatbogs and oxbows, rarely ponds. It also lives in brackish waters. According to some authors (GEYER 1927) it develops dwarf forms.

D i s t r i b u t i o n. *L. palustris* is a common species in the lowland part of Poland. It has also been found in lower parts of the Western Sudetes and Eastern Beskidy Mountains. On the basis of the modern studies, taking into account the anatomical structure of the reproductive organs, it has been reported from the Netherlands (VELDE 1984), Germany (FALKNER 1984) and Sweden (JACKIEWICZ and PROSCHWITZ 1991). Despite intense search I found it neither in the former Yugoslavia nor in the former Czechoslovakia. Thus the range of its distribution is not precisely known.

The anatomical studies performed by JACKIEWICZ (1959) revealed that *Lymnaea palustris* (O.F. MÜLL.) (= *Galba palustris* (O.F. MÜLL.)) was a complex species, including three distinct species. Two of them were called *Galba corvus* GMEL. and *Galba turricula* HELD. They had been known for years as shell forms of *Stagnicola* (*Galba*) *palustris* (O.F. MÜLL.). The third species, new to the science, was called *Galba occulta* JACKIEWICZ.

None of these species received the common name *Stagnicola palustris* (O.F. MÜLL.). This species was described by O.F. MÜLLER (1774) so vaguely that it was impossible to draw a conclusion which of its many forms served as the type for the description.

FALKNER (1984) studied the structure of reproductive organs of lymnaeids identified as *Stagnicola palustris* (O.F. MÜLL.) and collected at the type locality, that is at Frederiksdal in Denmark. It became evident that the reproductive organs of these lymnaeids were built in the same manner as those of *Galba turricula* HELD sensu JACKIEWICZ (1959). There is no doubt that *Stagnicola palustris* (O.F. MÜLL.) from the type locality and *Galba turricula* HELD sensu JACKIEWICZ (1959) are conspecific. The name *Stagnicola palustris* (O.F. MÜLL.) is an older name. Therefore, according to the priority rules, *Galba turricula* HELD (1836) sensu JACKIEWICZ (1959) is its junior synonym (JACKIEWICZ 1989b).

In his 1992 paper KILIAS questioned the specific distnctness of *L. palustris*, *L. turricula*, *L. occulta*, *L. vulnerata* and *L. corvus*. Unfortunately, his studies raised serious objections that have been presented in a separate paper (JACKIEWICZ 1996).

***Lymnaea* (*Stagnicola*) *turricula* (HELD, 1836)**

Figures 70, 71; Plates V, X.3; Map 1.

Limnaea turricula HELD, 1836; Isis (OKEN), 278.

Locus typicus restrictus: Regensburg (Germany) (FALKNER 1985).

Synonyms: *Stagnicola palustris* (O.F. MÜLLER, 1774) - partim; *Galba palustris* (O.F. MÜLLER, 1774) - partim; *Lymnaea palustris* (O.F. MÜLLER, 1774) - partim; *Stagnicola vulnerata* (KÜSTER, 1862) sensu JACKIEWICZ, 1962.

S h e l l (Plate V). It is of identical structure as in *Lymnaea palustris* (Plate IV), however the „hammering" effect occurs more often on its surface. The largest specimen in my collection is 24 mm high and 9 mm wide. The above two species can not be distinguished on the basis of conchological features alone. The structure of their reproductive organs is the only good diagnostic feature (Fig. 68, 70).

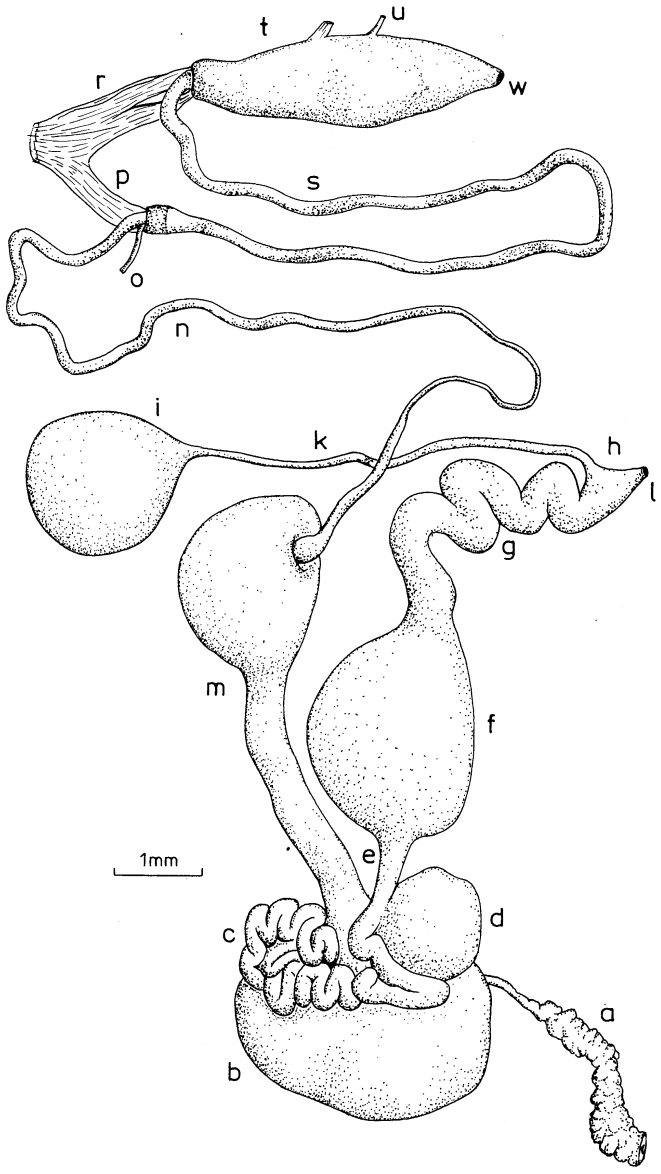
M a n t l e (Plate X.3) grey-black or even almost black. Many tiny whitish spots on it are roundish and of variable size. Sometimes a dark rim is visible around them. There is a black stripe, usually short and wide, near the pneumostome. The mantle collar is uniformly dark grey with a grey-brown ridge. The foot and the head with its appendices are dark grey. Completely black specimens may be also found. The mantle pattern of this species is identical to that of *Lymnaea palustris* (Plate X.4). It testifies to their close relationship, evidenced also by their shell morphology and the anatomical structure of the reproductive system.

R e p r o d u c t i v e o r g a n s (Fig. 70). The praeputium is fusiform (Fig. 70t). Its wall develops two relatively small longitudinal folds inwards (Fig. 71B). The papillary fold and the papilla (Fig. 71A), occurring internally at the bottom of the praeputium bulbous termination, are shaped in the same way as in the previous species. The penis sheath is cylindrical and very long, almost as thin as the vas deferens. The ratio of the praeputium length to the penis sheath length may be 1:3 or even 1:5 (Fig. 70s, t). This is the longest penis sheath among the lymnaeid species that I know. The penis (Fig. 71D) is also very long and thin so it looks like the vas deferens. The proximal prostate part is relatively narrow but the distal one is large, pear-like and swollen (Fig. 71C). The proximal prostate part is much longer than its distal part. There is one large fold inside the distal part (Fig. 71E). The vas deferens leads from this part, slightly to one side. The pyriform body is large, ovate and swollen. The oviduct II is very long and strongly plicate. The vagina is triangular in outline, hard and swollen. A thin, very long duct of spermatheca enters the vagina from its apical side. The spermatheca is large and spherical (Fig. 70).

The reproductive organs of *L. turricula* and *L. palustris* differ significantly in the ratio of the praeputium to the penis sheath length. Moreover, they differ in their prostate shapes, specially in the length ratio of its proximal part to the distal one.

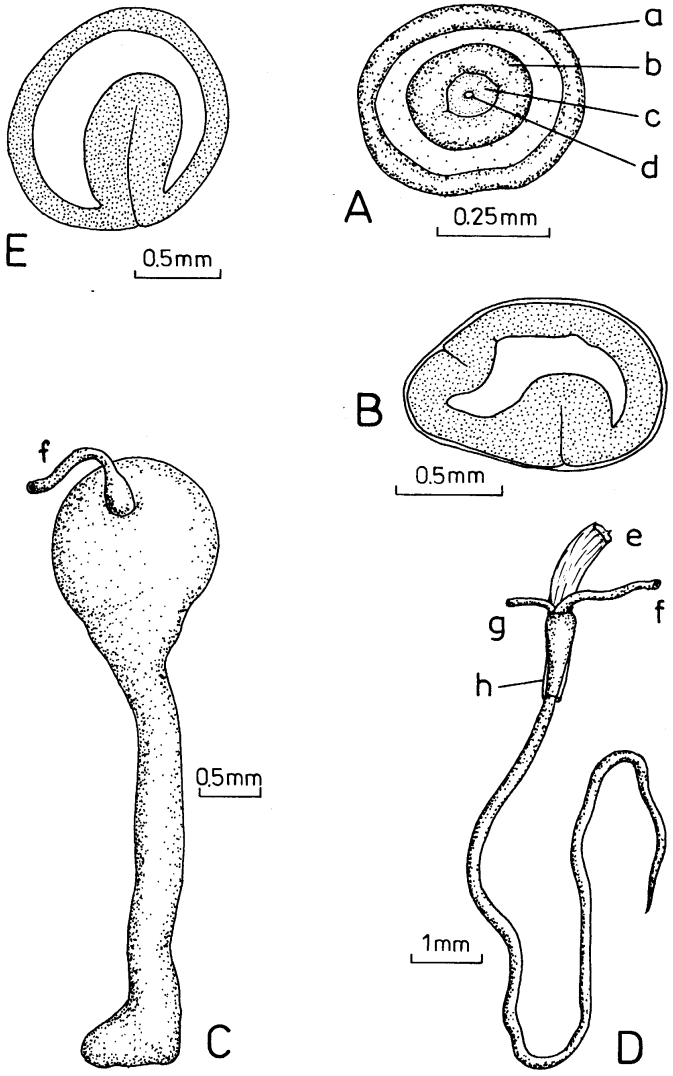
B i o n o m i c s. *L. turricula* lives in various waters like large lakes and ponds, rivers and streams, ditches, floods and peatbogs.

D i s t r i b u t i o n. In Poland, *L. turricula* was found in the Bieszczady Mountains and at Brzezina Polska near Nysa in Lower Silesia (JACKIEWICZ 1988a).



70. Reproductive organs of *Lymnaea (Stagnicola) turricula*. (Original). For lettering see Fig. 47.

General distribution of this species is not precisely known because it has been confused with *L. palustris*. It occurs in the areas of the former Czechoslovakia (HUDEC and BRABENEC 1966) - these authors incorrectly determined the species as *Stagnicola turricula* sensu JACKIEWICZ 1959 (= *Lymnaea palustris*), in Germany and Austria (FALKNER 1985) as well as in Bulgaria and Hungary (JACKIEWICZ 1962, 1992a) - see: Map 1.



71. Structure of the male reproductive organs of *Lymnaea (Stagnicola) turricula*. (After JACKIEWICZ). For lettering see Fig. 61.

Lymnaea (*Stagnicola*) *occulta* (JACKIEWICZ, 1959)

Figures 5, 42, 72, 73; Plates VI, X.9; Map 2.

Galba occulta JACKIEWICZ, 1959; Pr. Kom. mat. przyr. Pozn. TPN, p. 39.

Locus typicus: Siemianice near Kępno (Poland).

S h e l l (Plate VI) cylidrically turriform, quite thin. 5 - 6 whorls, slightly convex and separated with a shallow suture. Spire usually high, with regular growth. Its top bluntly terminated. Body whorl slightly expanded. Aperture small, usually equal to 1/3 shell height. Columella almost straight in its lower part, its fold wide and strongly turned inside out, usually white (this is the most characteristic shell feature of this species). Umbilicus narrow, fissured and well visible. Shell colour pale brown to brown. Its interior whitish or of shell colour, glittering. In some places, the horny layer of the shell frequently falls away exposing a whitish calcareous layer. Shell height of up to 21 mm, width of up to 9 mm.

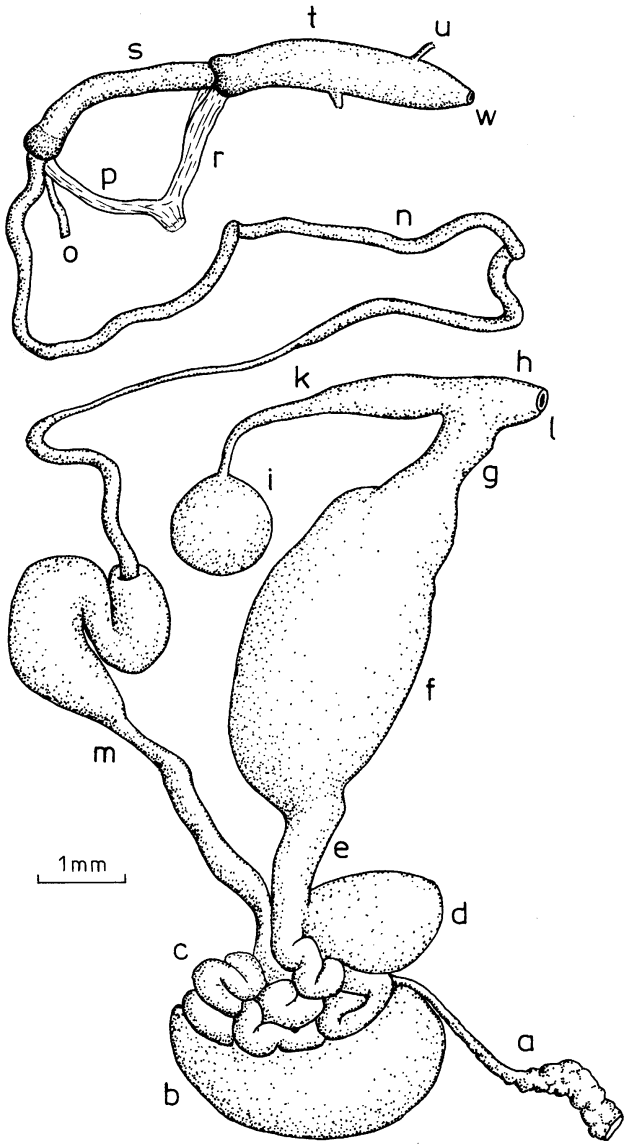
M a n t l e (Plate X.9). It is dark grey and is much darker, covered with whitish spots over a kidney and a hindgut. The spots are closely dispersed, usually ovate in shape with an irregularly rough border. There is a large spot over the pneumostome, instead of the stripe found in other species. The mantle collar is also dark grey with quite a wide pale brown ridge. The other body parts are yellowish or grey brown.

R e p r o d u c t i v e o r g a n s (Fig. 72). The praeputium is narrow and cylindrical, with a clearly separated bulbous termination. There are two longitudinal folds inside this organ (Fig. 73B). The papillary fold, lying at the bottom of the praeputium bulbous termination, is wide and flat. It surrounds a fairly large, conical papilla with a small opening in the centre (Fig. 73A). The penis sheath is quite thick and cylindrical, its bulbous termination is well separated. The ratio of the praeputium length to the penis sheath length is 1:1 (Fig. 72s, t). The penis (Fig. 73D) is rather long with a smaller or greater narrowing near its centre. It divides the organ into the thicker, usually longer, basal part and the thinner shorter distal part. The proximal prostate part is long and rather thin. Its dark ligulate enlargement is the most characteristic feature. The distal part is much wider and usually plicate (Figs 72m, 73C) with one large fold inside (Fig. 73E). The vas deferens starts almost in its centre. The pyriform body is very large and very elongated. It passes into a short tubular oviduct II, terminating with a short vagina. The spermathecal duct is rather short and strongly funnel shaped at the opening into the vagina. The spermatheca is small and usually spherical (Fig. 72).

B i o n o m i c s. Specimens of this species occur chiefly in drying forest or sometimes meadow ditches, also in neglected drying nursery ponds, moreover in shallow streams and in bogs. In winter, such water bodies most often freeze up to the bottom but they dry out in summer. *L. occulta* is peculiar in its high resistance to the lack of water. It may survive unfavourable conditions in anabiotic state for a long time. It digs itself in the bottom deposits or under a layer of rotting

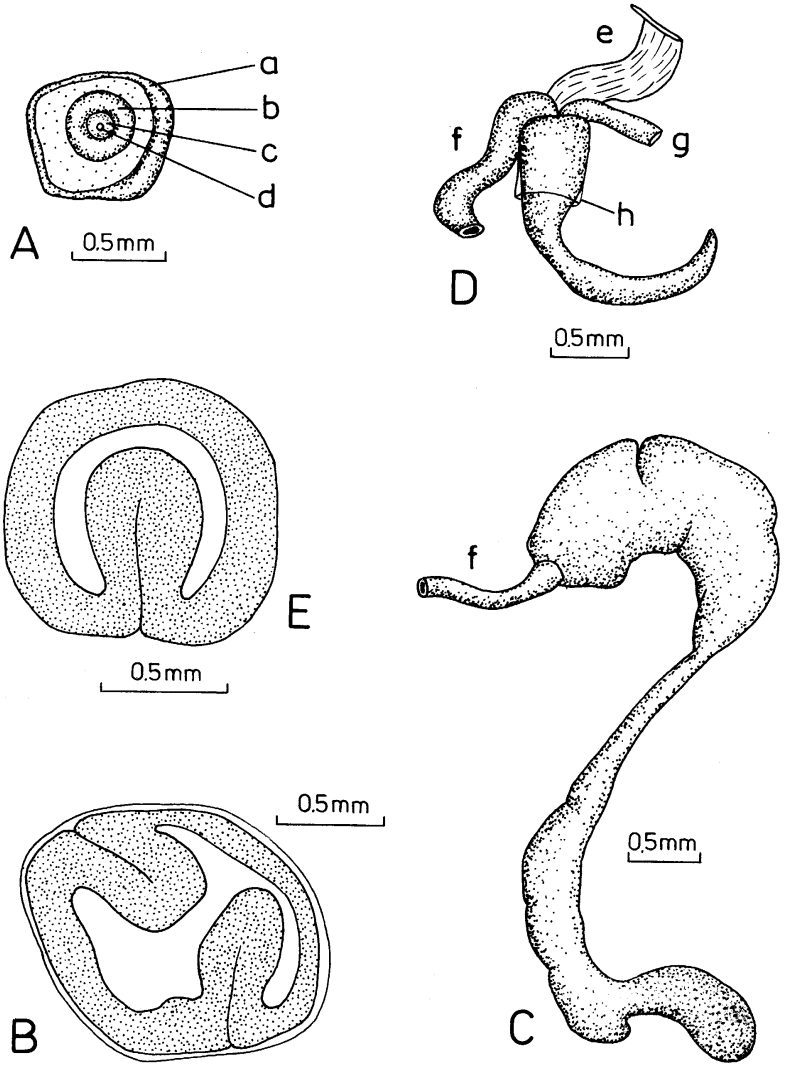
vegetation at the bottom of water basins. This species, like *L. truncatula*, is an intermediate host of the liver fluke (CZAPSKI 1965).

D i s t r i b u t i o n. *L. occulta* is known from the western part of Poland, especially from Wielkopolska (BERGER 1961, JACKIEWICZ 1959, KORALEWSKA 1979, KORALEWSKA-BATURA 1992), from the region of Wrocław (BERGER 1961, KOSIŃSKA



72. Reproductive organs of *Lymnaea (Stagnicola) occulta*. (Original). For lettering see Fig. 47.

1979) as well as from several localities in the Koszalin and Szczecin provinces (CZAPSKI 1973, 1977). It occurs in the Świętokrzyskie Mountains, too (PIECHOCKI 1979b). It was also reported from the former Czechoslovakia (HUDEC and BRABENEC 1966) - see: Map 2, and from Ukraine (STADNIČENKO 1968) as well as Siberia (JACKIEWICZ 1992b). It lives in former Yugoslavia (JACKIEWICZ 1997). Moreover, it occurs in Sweden, where I found it only as shells in the collections of the Natural History Museum of Göteborg (JACKIEWICZ and PROSCHWITZ 1991).



73. Structure of the male reproductive organs of *Lymnaea (Stagnicola) occulta*. (After JACKIEWICZ). For lettering see Fig. 61.

Lymnaea (*Lymnaea*) *vulnerata* KÜSTER, 1862

Figures 13, 14, 74, 75; Plates VII, X.8; Map 3.

Limnaeus vulneratus KÜSTER, 1862; Martini u. Chemnitz, Syst. Con. Cab.

Locus typicus: Cetina river near Omiš in Central Dalmatia (Croatia).

! Non: *Stagnicola vulnerata* (KÜSTER): JACKIEWICZ, 1962: 47-62, pl. 1-2, figs 1-7.

Synonym: *Stagnicola fuscus* (C. PFEIFFER, 1821) (GLÖER and MEIER-BROOK 1994).

S h e l l (Plate VII) ovately conical, not very thick but strong. Rather coarse, transverse and spiral striae run sparsely on its surface giving an effect called „hammering". There are usually 6 rather convex whorls which are separated with a well outlined suture. The stocky spire increases slowly. The sharp apex is usually red brown in colour. This was the reason for the specific name of this lymnaeid. The aperture is wide and ovate, usually equal to or lower than half of the shell height. The columella is almost straight in its lower part. Its fold narrow, lighter in colour than the rest of the shell. The umbilicus is fissured and well covered. The shell is pale brown, internally glittering, often with a red brown lamella near the aperture. The largest shell in my collection was 25 mm high and 11.5 mm wide.

M a n t l e (Plate X.8). It is brown-black. The whitish roundish (more frequently elliptical), sharply bordered spots are visible on it. It appears that the elliptical spots are characteristic of the specimens more withdrawn into shells, i.e. more contracted. There is a dark usually arched stripe over the pneumostome. The collar is uniformly grey-yellow, with several brown spots, finished with a rather yellowish ridge. The head with appendices and the foot are yellowish grey.

R e p r o d u c t i v e o r g a n s (Fig. 74). The praeputium is sac-like, with two longitudinal folds inside (Fig. 75B). A small conical papilla with a tiny opening at the top lies at the bottom of the weakly developed praeputium bulbous termination. A wide papillary fold surrounds it (Fig. 75A). The penis sheath is short and tubular, with a well separated bulbous termination. The ratio of the praeputium length to the penis sheath length is 3:1 (Fig. 74s, t). The short penis (Fig. 75D) is well widened in its basal part but becomes gradually narrower in the distal part. A ring-like swelling lies in the middle of its length or nearer to the penis opening. It may be more or less developed. The prostate (Fig. 75C) is a large gland, especially strongly swollen in its distal part. There are two longitudinal folds, lying side by side, inside this part (Fig. 75E). There are no folds in the proximal part. The vas deferens leaves apically the distal part of the prostate. The pyriform body is large and ovate. The oviduct II is wide and long. The vagina is short and triangular. The spermathecal duct is narrow and very long. It opens into the vagina with a narrow funnel-shaped widening. The spermatheca is big and spherical (Fig. 74).

B i o n o m i c s. In the Cetina river (Dalmatia) which is characterized by a rapid current, this species lives mostly in the water but also on low wet river

banks. It also occurs in the dead-end arm of the Rhine (Germany), densely covered with duckweed (*Lemna*). There are no data on the waters in Sweden where it also lives.

D i s t r i b u t i o n. *L. vulnerata* occurs in Dalmatia (Croatia) (JACKIEWICZ 1988c), in Germany (JACKIEWICZ and GERBER 1990) as well as at many localities in

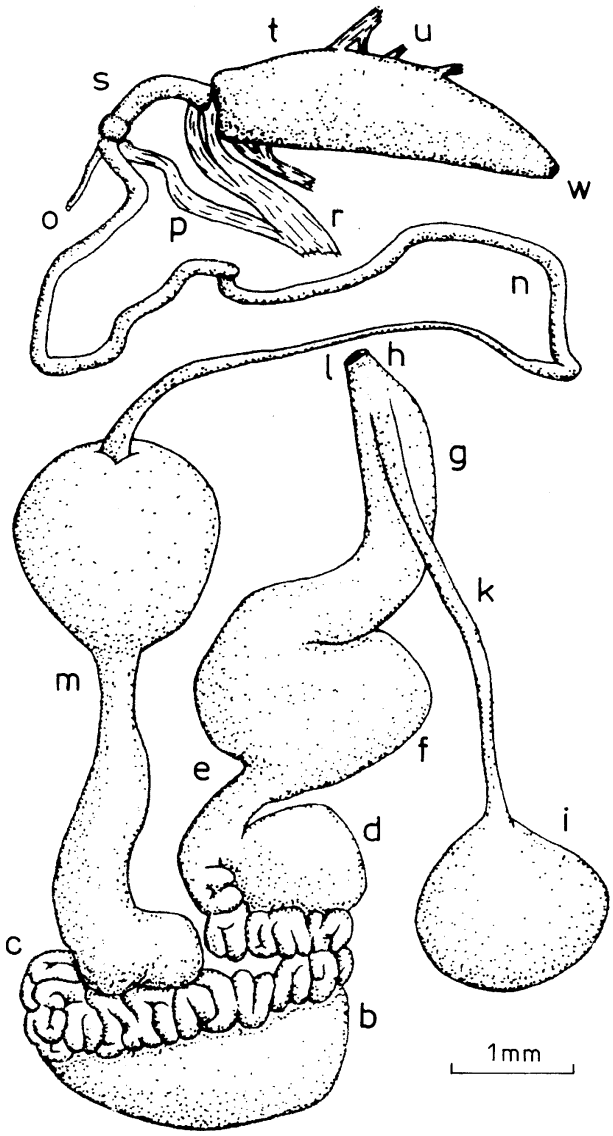
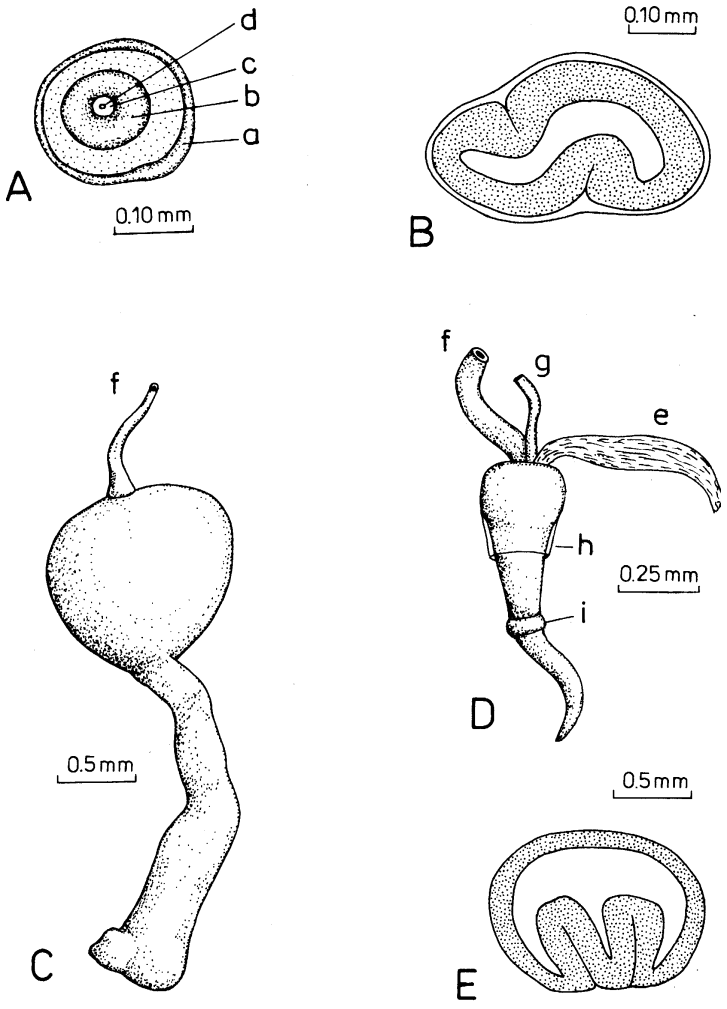


Fig. 74. Reproductive organs of *Lymnaea (Lymnaea) vulnerata*. (After JACKIEWICZ). For lettering see Fig. 47.

Sweden (JACKIEWICZ and PROSCHWITZ 1991). This lymnaeid, along with *L. palustris*, is the most common and widespread species in Sweden. The prostate cross-section of *L. palustris* is shown in LARAMBERGUE's paper (1928). However it shows two folds inside the prostate and this is characteristic of *L. vulnerata* only. The prostate structure as well as the other features clearly suggest that LARAMBERGUE (1928) dealt with *L. vulnerata*, not with *L. palustris.* Therefore it may be assumed that this species lives also in France (Toulouse). The above data suggest that *L. vulnerata* may be widely distributed in western Europe (Map 3).



75. Structure of the male reproductive organs of *Lymnaea (Lymnaea) vulnerata*. (After JACKIEWICZ). For lettering see Fig. 61, and: i - ring-like swelling.

Lymnaea (*Lymnaea*) *corvus* (GMELIN, 1791)

Figures 39, 40, 76, 77; Plates VIII, X.10, XI.4.

Helix corvus GMELIN, 1791; Syst. nat. p. 3665.

Terra typica: Thuringia (Germany).

Synonyms: *Stagnicola palustris* (O.F. MÜLLER, 1774) - partim; *Galba palustris* (O.F. MÜLLER, 1774) - partim; *Stagnicola palustris f. corvus* (GMELIN, 1791); *Galba palustris f. corvus* (GMELIN, 1791); *Galba corvus* (GMELIN, 1791).

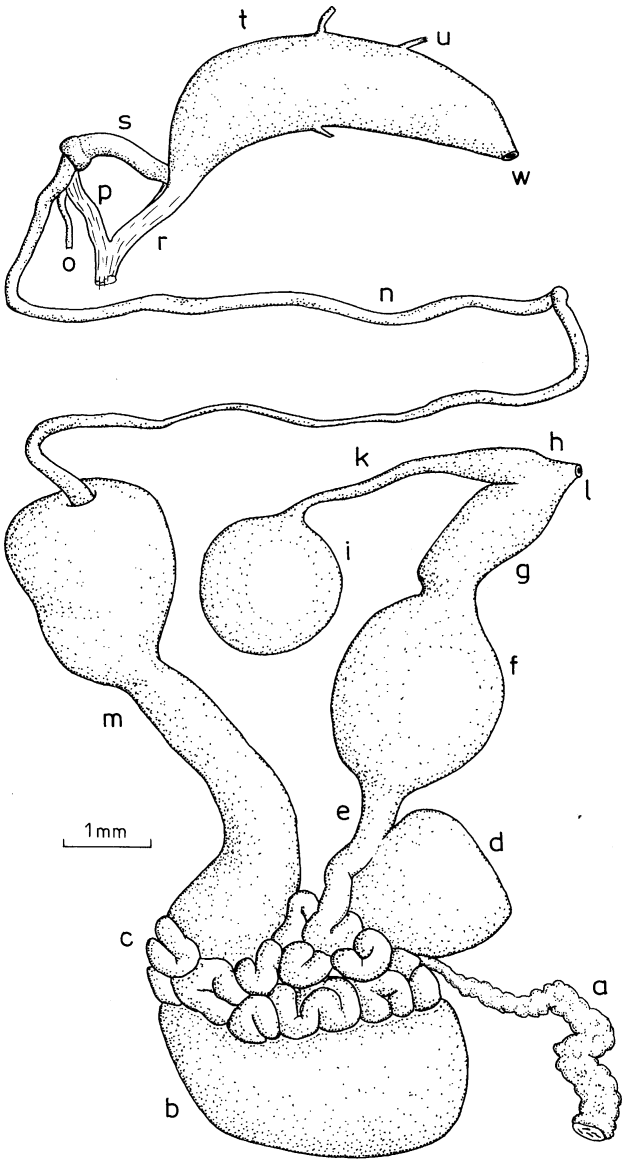
S h e l l (Plate VIII) ovately conical, rather thick-walled and strong. The „hammering" effect is clearly visible on its surface. Six to seven weakly convex whorls are separated by a shallow suture. They increase unevenly, so that the body whorl is large and much expanded. The spire is high, conical and sharply terminated. The aperture is narrowly ovate, equal to or larger than half of the shell height. The columella is strongly twisted in its lower part. The thin narrow columellar fold firmly adheres to the wall of the body whorl and is lighter in colour than the rest of the shell. The umbilicus is very narrow, fissured, usually completely covered. The shell is horny to intensely brown in colour. Its interior is usually darker, glittering, most often with a red-brown lamella parallel to the aperture margin. The shell height is up to 40 mm (sometimes to 45 mm), the width up to 16 mm.

M a n t l e (Plate X.10). There are many light roundish spots of different size visible against the grey-black or even completely black mantle background. They are darkly stellate rimmed. There is a long wide stripe of dark pigment near the pneumostome. The mantle collar is dark grey, with a few irregular darker spots. Its ridge is pale and very narrow. The head, tentacles and foot are grey, dark grey or, along with the mantle, completely black.

R e p r o d u c t i v e o r g a n s (Fig. 76). The praeputium sac-shaped, with two internal longitudinal folds (Fig. 77B). The papilla is conically domed with a small opening on its top. It is surrounded by a subtle papillary fold that may be quite narrow or much wider (Fig. 77A). The penis sheath is short and tubular, with a well developed bulbous termination. The ratio of the praeputium length to the penis sheath length is 3:1 (Fig. 76s, t). The penis (Fig. 77D) is also short but rather thick, especially at its base. A very characteristic ring-like swelling on the penis may be well developed or barely marked. Behind this swelling, the penis is wedge-shaped. The prostate (Fig. 77C) is big, particularly its strongly swollen distal part. There are internal folds along the whole gland (Fig. 77E, F). They are numerous and thick, frequently with secondary folds in the distal part of the prostate. The vas deferens leaves this part apically. The pyriform body is large and ovate. The oviduct II is also large but may be either wide or much narrower. The spermathecal duct that opens into the small vagina is short and strongly funnel-shaped at the end. The spermatheca is big and spherical (Fig. 76).

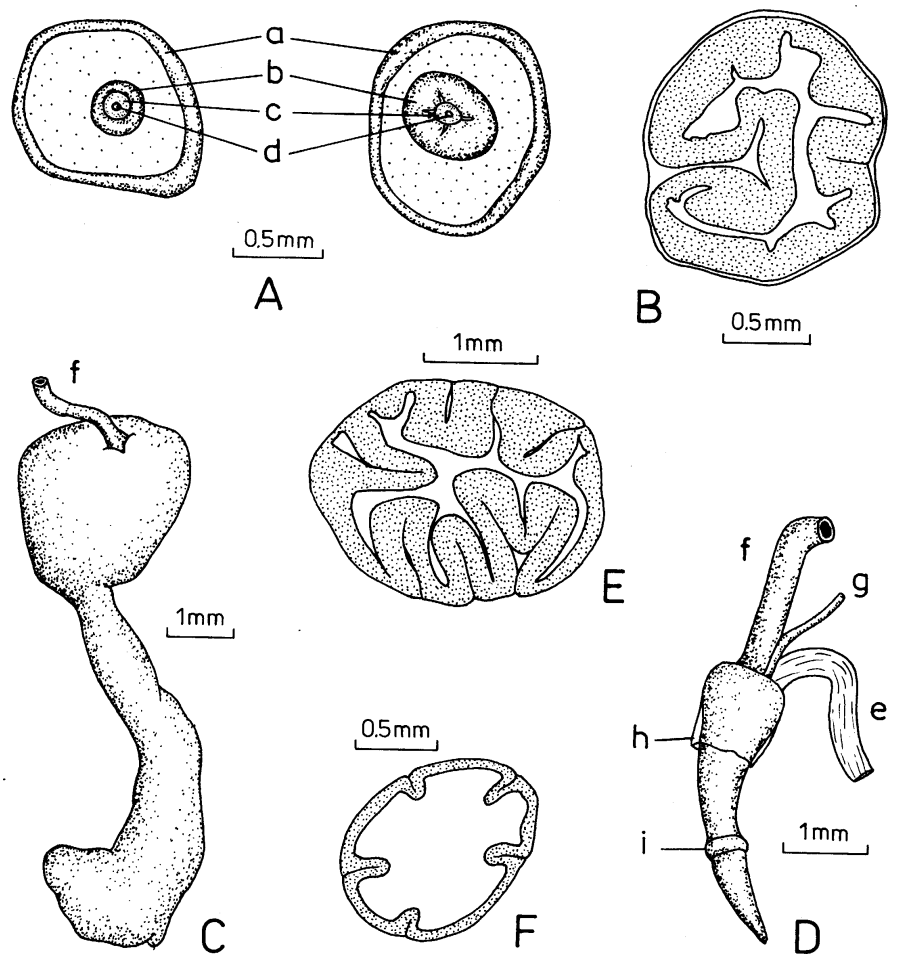
B i o n o m i c s. *L. corvus* lives in relatively small, eutrophic, meadow ponds, sometimes in forest ponds as well as in ditches and peatbogs. It also occurs in lakes and oxbows.

D i s t r i b u t i o n. *L. corvus* belongs to the most common and widespread freshwater snails of Poland. It is relatively rare in the lowlands and at lower altitudes in the mountains but is completely absent in higher mountains. The general geographic distribution of this species should be verified. The species has



76. Reproductive organs of *Lymnaea (Lymnaea) corvus*. (Original). For lettering see Fig. 47.

been separated from the species complex *Galba palustris* (page). On the basis of the specimens that were verified anatomically, it was reported from the former Czechoslovakia (HUDEC and BRABENEC 1966) and from the Netherlands (Velde 1984). It was found by JACKIEWICZ in Yugoslavia and Hungary and, moreover, in Sweden but only on the basis of typical shells (JACKIEWICZ and PROSCHWITZ 1991). The hitherto studies suggest that *L. corvus* is characterized by a larger range of distribution than *L. palustris*.



77. Structure of the male reproductive organs of *Lymnaea (Lymnaea) corvus*. (After JACKIEWICZ). For lettering see Fig. 61, and: F. Transverse section through the proximal part of the prostate (Original), and: i - ring-like swelling.

Lymnaea (*Lymnaea*) *stagnalis* (LINNAEUS, 1758)

Figures 6, 41, 45, 46, 78, 79; Plates IX, X.11, XI. 3, 5, 6.

Helix stagnalis LINNAEUS, 1758; Syst. nat. p. 774, no. 612.

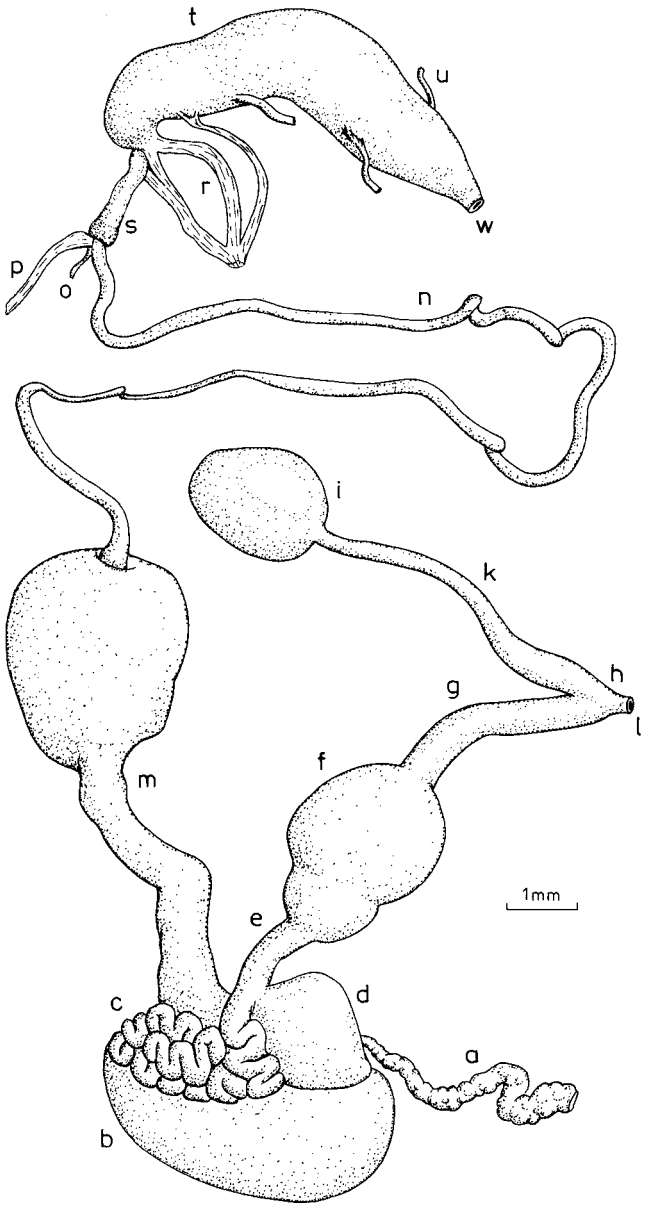
Terra typica: Sweden.

S h e l l (Plate IX). It is very large, ovately conical, relatively thin and fragile, slightly glittering. Its surface is sometimes „hammered". The whorls, 6 - 8, increase slowly and are strongly flattish. The body whorl is large and very much expanded. The spire is slender, high and very sharply terminated. The aperture is large and ovate, usually equal to half of the shell height. The columella is clearly twisted in its lower part with the wide but thin columellar fold, firmly adhering to the shell. The umbilicus is usually completely covered. The columellar fold and the shell interior are intensely glittering and most often of paler colours than the shell. Shell colour is variable, from whitish to dark horn shade. The initial whorls are darker. The shells of young specimens are usually pale and very slender. Their body whorls are not so much expanded. The shell height reaches 60 mm (sometimes more), its width 30 mm.

M a n t l e (Plate X.11). It is grey to deep black. There are many large, irregularly roundish, grey spots over the mantle. There is a subtle bright area or a tiny whitish dot visible in the centre of each spot. The mantle edge is covered with a lot of greyish little dots. A long wide stripe of black pigment is located near the pneumostome. The mantle collar is grey, densely covered with irregular black spots forming transverse zigzag bands. The ridge is rather wide and pale. The head with appendices and the foot are grey-black. The mantle pigmentation is unstable and may be easily obliterated even by a soft touch that often changes the typical pattern.

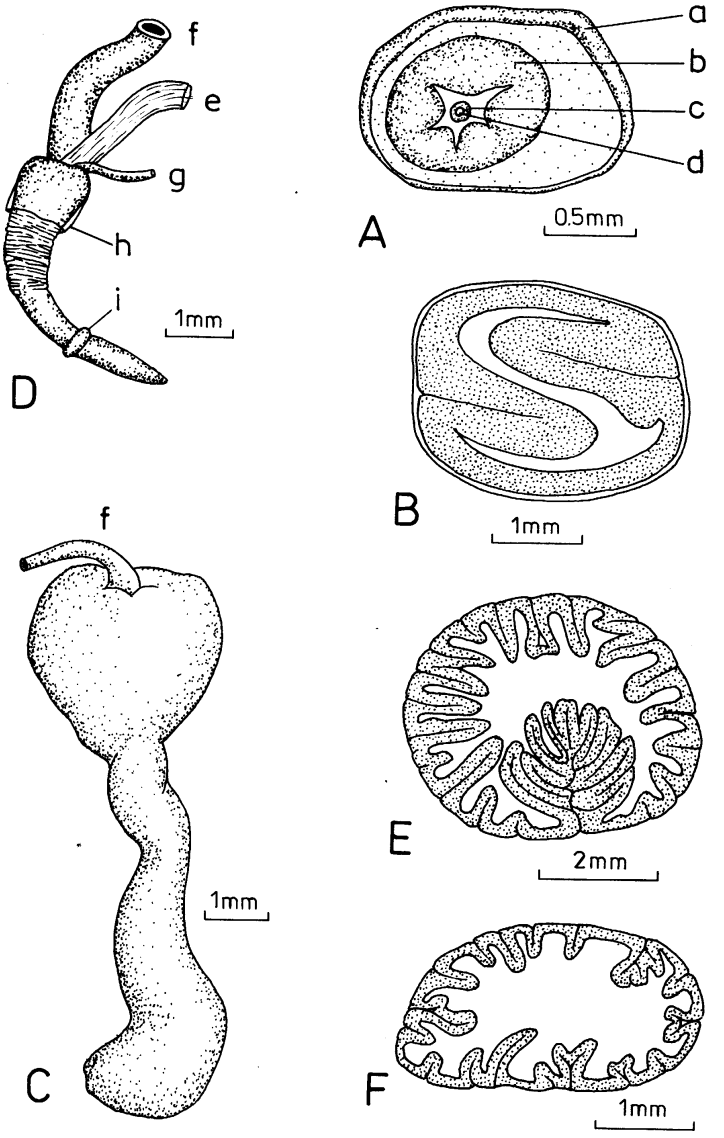
R e p r o d u c t i v e o r g a n s (Fig. 78). The praeputium is like a greatly elongated sac with a faintly separated bulbous termination. There are two internal longitudinal folds in it (Fig. 79B). A large wide, relatively flat, papillary fold lies at the bulbous termination bottom of the praeputium (Fig. 79A). It surrounds a minute papilla. It is of more or less conical shape, sometimes even finger-like. There is a small opening on its top. The penis sheath, like in the preceding species, is short and tubular with a well developed bulbous termination. The ratio of the praeputium length to the penis sheath length is 3:1 (Fig. 78s, t). The penis (Fig. 79D) resembles that of *L. corvus* (Fig. 77D), as it is short and rather thick, especially at its base. A ring-like swelling is visible in the centre of the penis but sometimes it is poorly developed. Behind the swelling, the penis becomes dagger- or wedge-shaped. There are very characteristic miniature folds on the surface of the penis. The prostate (Fig. 79C) is big and strongly swollen in its distal part. Internally, there are many small folds along the whole gland (Fig. 79E, F) but they are particularly well developed in its distal part. The vas deferens leaves apically this prostate part. The pyrifom body is relatively small, as if composed of two: a smaller and a larger part. The distal part is usually smaller. It

passes into a thin narrow oviduct II, terminating with a very small vagina. The spermathecal duct is rather long and widened like a funnel at the opening to the vagina. The spermatheca is big and ovate (Fig. 78).



78. Reproductive organs of *Lymnaea (Lymnaea) stagnalis*. (Original). For lettering see Fig. 47.

B i o n o m i c s. *L. stagnalis* is very common in the lowlands of Poland. It occurs both in stagnant and flowing waters, especially at places with dense vegetation. It also lives in the low-salinity parts of the Baltic Sea. Depending on the water body type, the species develops forms of different shell shapes (Plate



79. Structure of the male reproductive organs of *Lymnaea (Lymnaea) stagnalis*. (After JACKIEWICZ). For lettering see Fig. 61. and: F. Transverse section through the proximal part of the prostate (Original), and: i - ring-like swelling.

IX). They were formerly treated as varieties or even as subspecies. However the reproductive organ structure in all those forms is the same which indicates that the shell is affected by the external conditions. The typical form of the high spire and ovate aperture lives in still waters. A form with the much shortened spire and a much expanded aperture occurs in great lakes in turbulent zones. Specimens crawling on reeds have a wide foot to hold to the reed culm and the outer margin of the shell aperture is often recurvate inwards. *L. stagnalis* inhabits waters with either muddy or sandy, or even stony bottom. It survives well temporary drying of water reservoirs.

D i s t r i b u t i o n. *L. stagnalis* belongs to the most common species found in Poland. It is a Holarctic species. Its wide range of distribution covers almost all of Europe, a larger part of Asia, northern Africa and North America.

IV. PHYLOGENY AND SPECIES RELATIONSHIPS

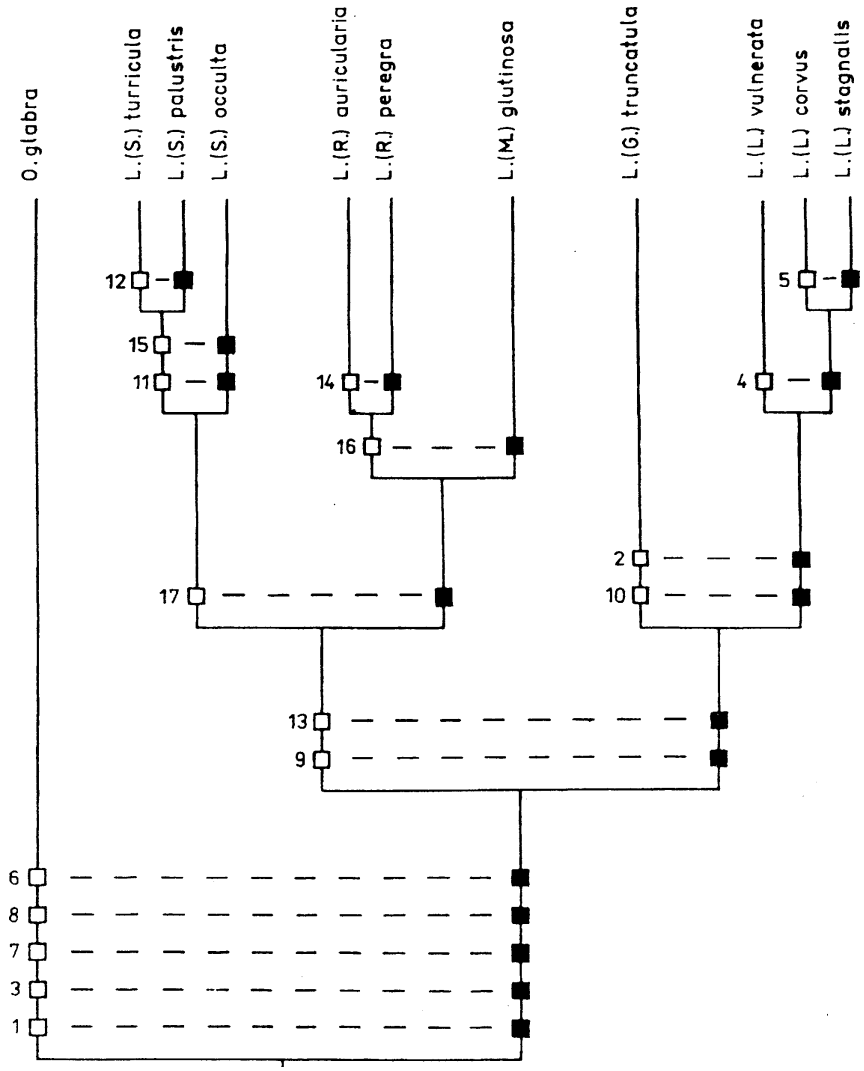
Studies on the structure of the lymnaeid reproductive system have allowed a reconstruction of the evolutionary trends of some organs of this system. Very important information is provided by the structure of the praeputium and its bulbous termination, as well as of the penis and the prostate.

The p r a e p u t i u m of *Omphiscola glabra* should be recognized as the most primitive form of the praeputium. It is characterized by a single longitudinal fold (Fig. 52h) with a poorly developed additional fold that occurs quite frequently (Fig. 54i). There is a papilla (*sarcobelum*) with a fissured lumen at the bottom of the praeputium bulbous termination (Fig. 50).

There are two well developed folds inside the praeputium of all other lymnaeid species (Fig. 56l). There is also a papilla (*sarcobelum*) at the bottom of its bulbous termination (Fig. 58) but there is an oval opening on the top. The papillary fold (*velum*) surrounding the papilla is an additional structure (JACKIEWICZ 1989a, 1993b).

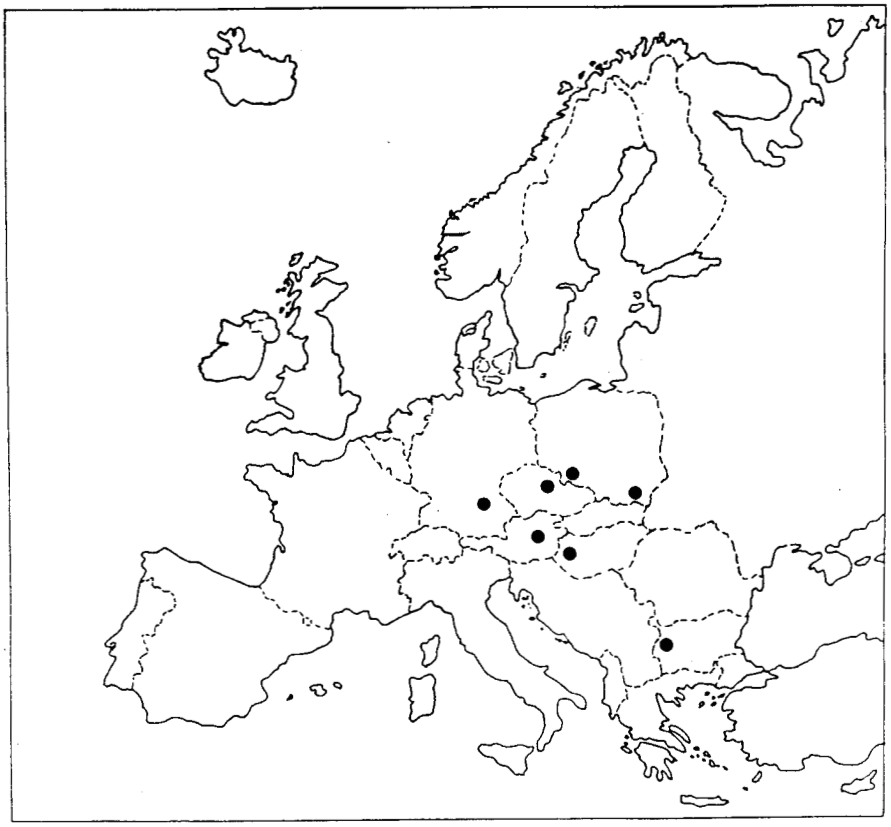
The tendency for a p e n i s shortening as well as a complication of its structure is clearly visible in the phylogenetic development of lymnaeids, especially of the genus *Lymnaea* LAMARCK, 1799. The most primitive penis, resembling a vas deferens in shape, is very long and thin, like in *Lymnaea turricula* (Fig. 71D) or long, like in *L. peregra* (Fig. 63D), *L. auricularia* (Fig. 65D) and *L. glutinosa* (Fig. 67D). It is about 14-20 times longer than the width of its own bulbous termination. The penis in *L. palustris* (Fig. 69D) and *L. occulta* (Fig. 73D) is thicker and much shorter. It is about 5-8 times longer than the width of its bulbous termination. The penis of the latter species is narrowed more or less in the centre. Further shortening of the penis takes place in *L. truncatula* (Fig. 61D) and also in *L. vulnerata* (Fig. 75D), *L. corvus* (Fig. 77D) and *L. stagnalis* (Fig. 79D). It is only 4 times longer than the width of its bulbous end. The penis of the last three species is thick and is characterized by a ring-like swelling (JACKIEWICZ 1986a, 1988b).

The p r o s t a t e, particularly the internal structure of its distal part, permits a clear view on the development of this gland during the lymnaeid phylogeny (JACKIEWICZ 1992c). It leads from very simple to more and more complicated forms. This opinion is also confirmed by ROSZKOWSKI (1927) and HUBENDICK (1951). The prostate without a fold (Fig. 49) is the most primitive form. From this form, the following forms have been later developed: one with a single small fold



80. Cladogram of *Lymnaea*. Plesiomorphic character states marked by white squares, apomorphic character states marked by black squares. Explanations of the numbers (characters) in the text (p. 82).

(Fig. 61E), one with a large fold (Fig. 63E), one with two folds (Fig. 75E) and one with many folds (Fig. 77E). The complication of the prostate structure leads to the formation of an increasingly higher number of folds, which increases the internal surface of the prostate. The development tendency of the prostate could also go another way. It may be assumed that the prostate with one well developed fold (species of subgenera *Radix, Myxas* and *Stagnicola*) is the most primitive form. This fold has been reduced either completely in small species like *Omphiscola glabra* or partially, like in *Lymnaea truncatula*. On the other hand, two folds of the same size have been developed in larger species, for example *L. vulnerata.* Many folds have come into existence in *L. corvus* and *L. stagnalis*, that is in the largest species. Folds in the proximal prostate part have also been developed in the last two species. In both developmental tendencies of the prostate, its size and the number of folds are correlated with the size of particular species.

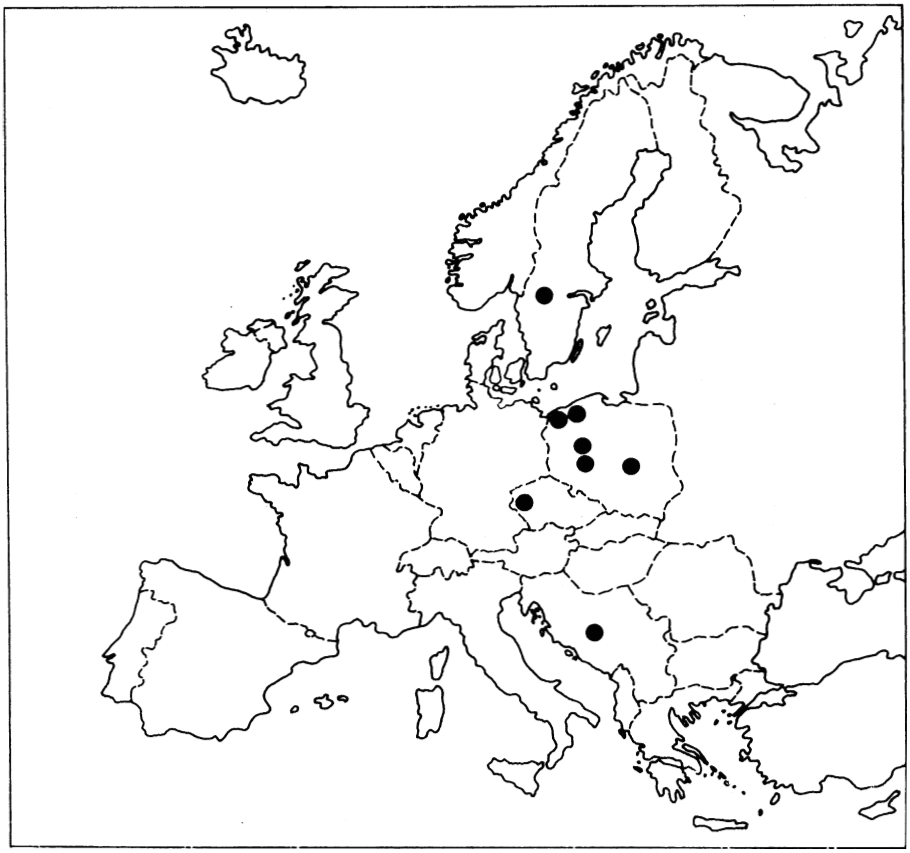


Map 1. Records of *Lymnaea (Stagnicola) turricula.*

I have attempted to reconstruct the phylogeny and relationships of the species that belong to the family *Lymnaeidae* by means of a cladogram (Fig. 80). It has been based on differences in the structure of the reproductive organs and on some other selected features of 11 studied species of the family *Lymnaeidae*.

A lack or a lower number of structures in some organs is assumed to be plesiomorphic, while a higher number of those structures and a more complex structure is treated as an apomorphy.

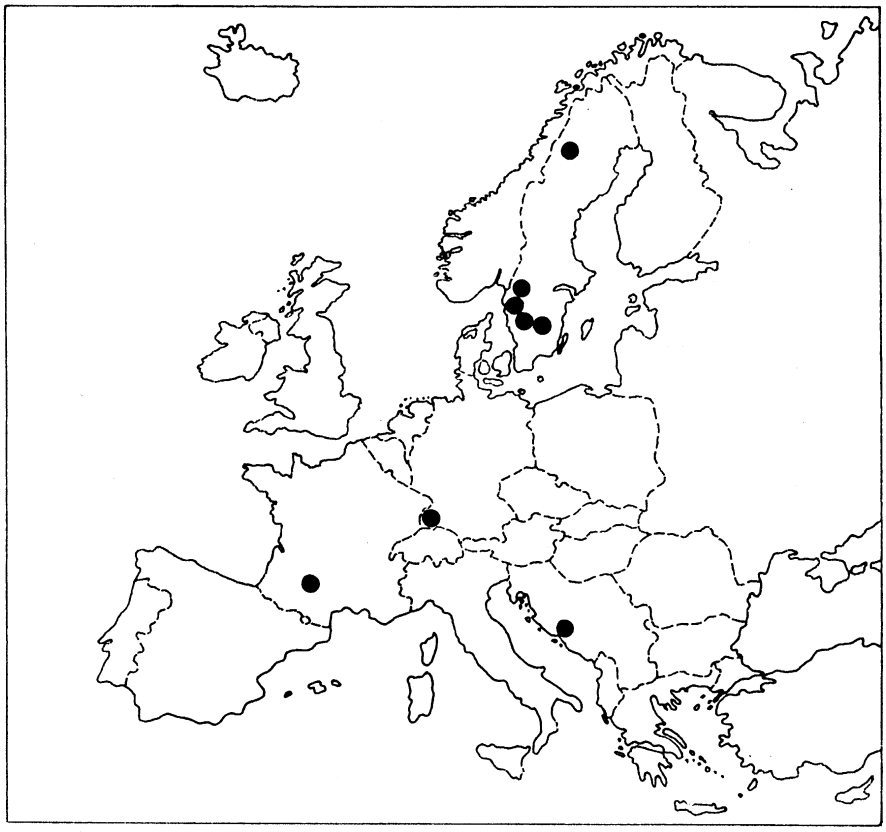
Cladistic analyses justify the changes in the classification system of the family *Lymnaeidae* suggested by me on the basis of the analysis of anatomical structure of the reproductive system. They also show significant differences between the genera and the subgenera, and the species included in them. They define close relationships between some taxa as well as the evolutionary pathways in this group of pulmonate snails (JACKIEWICZ 1993b). The reproductive system of *O. glabra* is undoubtedly the most primitive in the structure of all the



Map 2. Records of *Lymnaea (Stagnicola) occulta* (excluding localities in Ukraine and Siberia).

organs except penis. The more advanced condition of the reproductive organ structure of other lymnaeid species may be derived from this primitive system.

Regarding the reproductive organs, *O. glabra* is the most distinct species among lymnaeids. Some features of *L. truncatula* (prostate and praeputium structures) are to some extent similar to the situation characteristic of *O. glabra.* However, some other features (short penis) link it with *L. vulnerata, L. corvus* and *L. stagnalis*. A distinct group includes *L. palustris*, *L. turricula* and *L. occulta*, though rather large differences in the structure of their reproductive organs make their systematic position and their relationships unclear. *L. peregra, L. auricularia* and *L. glutinosa* are very closely related. The strongly developed mantle that externally covers the shell in *L. glutinosa* is the only feature which determines its distinct systematic position. *L. vulnerata*, *L. corvus* and *L. stagnalis* constitute the most coherent group with the highest degree of uniformity in the structure of their reproductive system.



Map 3. Records of *Lymnaea (Lymnaea) vulnerata.*

REFERENCES

ABOLINŠ-KROGIS, A., 1961. The histochemistry of the hepatopancreas of *Helix pomatia* (L.) in relation to the regeneration of the shell. Ark. Zool. Stockholm, **13** (2-3): 159-201.

BERTMAN, M., WOJCIECHOWSKA, K. 1974. Fauna cerkarii ślimaków słodkowodnych zbiorników wodnych Wrocławia i okolic. Prz. Zool. Wrocław **18**: 354-359.

BERGER, L., 1961. Mięczaki pogranicza Wielkopolski, Śląska i Jury Krakowsko-Wieluńskiej. Pr. Kom. mat. przyr. Poz. TPN. Poznań **25**(1): 1-124.

BOETTGER, C. R., 1944. *Basommatophora*: Tierwelt der Nord- und Ostsee, **9**, Leipzig. 241-478.

BULLOCH, A. G. M., RIDGWAY, R. L., 1995. Comparative aspects of gastropod neurobiology. The Nervous System of Invertebrates: An Evolutionary and Comparative Approach ed. by O. BREIDBACH and W. KUTSCH, Birkhauser Verlag. Basel 89-113.

CZAPSKI, Z., 1965. Z badań nad biologią *Galba occulta* JACK., 1959 - nowego żywiciela pośredniego *Fasciola hepatica* L. Wiad. Parazyt. Warszawa, **11**, suppl. 1-2: 273-277.

-. 1973. Nowe stanowiska *Galba occulta* JACK. na zachodnich obszarach Polski. Mat. 11 Zjazdu PTP, p. 16.

-. 1977. Biologiczne aspekty epidemiologii fasciolozy. AWF w Poznaniu, Seria: Monografie. Poznań **95**: 143 pp.

DROZDOWSKI, A., 1970. Vergleichende Studien über die Lungenmorphologie bestimmter Schneckenarten (*Gastropoda, Pulmonata*). Zool. Pol. Wroc aw 20: 217-256.

DROZDOWSKI, A., ZAWIEJA, E., 1993. Influence of hibernation on the histological structure of alimentary ductus of *Lymnaea stagnalis* (L.). Stud. Soc. Sci. tor. Toru **10**(6): 1-12.

ELO, J. E., 1938. Das Nervensystem von *Limnaea stagnalis* (L.) LAM. Ann. zool. Soc. zool.-bot. fenn. „Vanamo" Helsinki **6**(4): VI+40 pp.

EHRMANN, P., 1937. *Mollusca*. In: BROHMER P., EHRMANN P., ULMER G. Die Tierwelt Mitteleuropas, **2**, 1. Leipzig. 264 pp.

FALKNER, G., 1984. *Stagnicola palustris* (O. F. MÜLLER) vom Originalfundort (Basommatophora: Lymnaeidae). Heldia. München **1**(1): 15-21.

-. 1985. *Stagnicola turricula* (HELD) - eine selbständige Art neben *Stagnicola palustris* (O. F. MÜLLER). Heldia. München **1**(2): 47-50.

-. 1990. Binnenmollusken: FECHTER R., FALKNER G. Weichtiere. Europäische Meeres- und Binnenmollusken. Steinbach's Naturführer, Mosaik Verlag. München **10**: 112-280.

FALNIOWSKI, A., 1980a. Pigmentation of the mantle border in Polish representatives of the subgenus *Radix* (*Lymnaeidae, Basommatophora, Gastropoda*). Basteria **44**: 3-8.

-. 1980b. Podrodzaj *Radix s. str.* (*Gastropoda, Basommatophora*) w Polsce. I. Pigmentacja i anatomia. Opis *Lymnaea peregra roszkowskiana* subsp. nov. Zesz. Nauk. UJ, Prace Zoologiczne. Kraków **26**: 67-108.

-. 1981. Podrodzaj *Radix s. str.* (*Gastropoda, Basommatophora*) w Polsce. II. Muszla i jej zmienność. Zesz. Nauk. UJ, Prace Zoologiczne. Kraków **27**: 113-141.

FELIKSIAK, S., 1938. Badania biologiczno-morfologiczne nad otułką [*Radix glutinosa* (O. F. MÜLLER)]. Arch. Nauk biol. TNW. Warszawa **7**(2): 56 pp.

FRÖMMING, E., 1956. Biologie der mitteleuropäischen Süsswasserdchnecken. Berlin 311 pp.

GEYER, D., 1927. Unsere Land- und Süßwasser-Mollusken, 3. Aufl. Stuttgart XI+224 pp.

GLÖER, P., MEIER-BROOK, C., 1994. Süsswassermollusken. Ein Bestimmungsschlüssel für die Bundesrepublik Deutschland. 11 erw. Aufl. Hamburg 136 pp.

GÖTTING, K. J., 1974. Malakozoologie. Stuttgart X + 320 pp.

HAAS, E., 1929. Liste einiger Süsswassermollusken aus der Provinz Posen. Senckenbergiana. Frankfurt a. M. **11**(3): 108-110.

HESCHELER, K., 1900. Lehrbuch der vergleichenden Anatomie der wirbellosen Tiere. 1. *Mollusca*. Jena VIII + 509 pp.

HUBENDICK, B., 1945. Die Artabgrenzung bei den schwedischen Lymnaeiden der *Radix*-Gruppe. Arkiv. Zool. Stockholm **37A**(10).

-. 1951. Recent *Lymnaeidae* their Variation, Morphology, Taxonomy, Nomenclature, and Distribution. Svenska Vetensk. Akad. Handl. Stockholm **3**(1): 223 pp.

HUDEC, V., BRABENEC, J., 1966. Neue Erkenntnisse über die Schnecken der Gesamtart *Galba palustris* (Müll., 1774) aus der Tschechoslowakei. Folia Parasit. Praha **13**(2): 132-143.

JACKIEWICZÓWNA, M., 1954. Z badań anatomiczno-porównawczych nad niektórymi gatunkami z rodzaju *Radix* MONTFORT na terenie Wielkopolski. Pr. Kom. mat. przyr. Pozn. TPN. Poznań **15**(3): 20 pp.

JACKIEWICZ, M., 1959. Badania nad zmiennością i stanowiskiem systematycznym *Galba palustris* O. F. MÜLL. Pr. Kom. mat. przyr. Pozn. TPN. Poznań **19**(3): 86 pp.

-. 1962. Wiederbeschreibung der Schlammschnecke *Limnaeus vulneratus* KÜSTER, 1892 = *Limnaea berlani* BOURGUIGNAT, 1870 (*Mollusca, Gastropoda*). Bull. Soc. Amis Sci. Lett. Poznań Sér. D. **3**: 47-62.

-. 1967. Badania anatomiczne i histologiczne nad *Acicula polita* (HARTM.) z uwzględnieniem innych gatunków *Acicula* HARTM. (*Mollusca, Prosobranchia*). Pr. Kom. mat. przyr. Pozn. TPN. Poznań 32(3): 76 pp.

-. 1969. Interesujący przypadek anormalności czułka u *Physa acuta* DRAP. (*Mollusca, Basommatophora*). Fragm. faun. Warszawa **15**(11): 199-207.

-. 1972. Anormalności w budowie skorupki niektórych mięczaków wodnych. Prz. zool. Wroc aw **16**(1): 95-98.

-. 1986a. Formy prącia u *Lymnaea stagnalis* (L.) (*Gastropoda, Pulmonata*). Prz. zool. Warszawa-Wrocław **30**(3): 357-359.

-. 1986b. Pakiet plemników *Lymnaea corvus* (GMELIN) (*Gastropoda, Basommatophora*). Prz. zool. Warszawa-Wrocław **30**(1): 121-122.

-. 1988a. *Stagnicola turricula* (HELD, 1836) (*Gastropoda, Lymnaeidae*) - gatunek błotniarki nowy dla Polski. Prz. zool. Warszawa-Wrocław 32(2): 203-205.

-. 1988b. The penis as a valuable diagnostic feature in lower taxonomic units of the family *Lymnaeidae* (*Gastropoda*, *Pulmonata*). Malak. Abh. Mus. Tierkd. Dresden **13**(2): 23-26.

-. 1988c. Anatomy and taxonomic status of *Lymnaea vulnerata* (KÜSTER 1862) (*Mollusca, Gastropoda*). Bull. Soc. Amis Sci. Lett. Pozna Sér. D. **26**: 125-128.

-. 1989a. Innenstruktur der Prostata und des Praeputiums bei *Omphiscola glabra* (O. F. MÜLL.) (*Gastropoda, Basommatophora*: *Lymnaeidae*). Malak. Abh. Mus. Tierkd. Dresden **14**(2): 7-13.

-. 1989b. *Galba turricula* HELD sensu JACKIEWICZ, 1959 als jüngers Synonym von *Stagnicola palustris* (O. F. MÜLL.) (*Gastropoda, Basommatophora: Lymnaeidae*). Malak. Abh. Mus. Tierkd. Dresden **14**(1): 1-5.

-. 1990. Die Struktur des Auges bei Schlammschnecken (*Gastropoda, Pulmonata: Lymnaeidae*). Malak. Abh. Mus. Tierkd. Dresden **15**(5): 51-54.

-. 1991. Die Verbreitung der Gattung *Lymnaea* und die Innenstruktur der Prostata (*Gastropoda, Pulmonata*). Proc. Tenth Intern. Malacol. Congress (Tübingen 1989) 583-586.

-. 1992a. Neue Erkenntnisse über *Stagnicola turricula* (HELD, 1836) (*Gastropoda, Pulmonata, Lymnaeidae*). Proc. Ninth Int. Malac. Congress (Edinburgh 1986). Leiden 180-184.

-. 1992b. *Lymnaea* (*Stagnicola*) *occulta* (JACKIEWICZ 1959) (*Gastropoda: Pulmonata*) in Sibirien. Mitt. dtsch. malakozool. Ges. Frankfurt a. M. **49**: 13-16.

-. 1992c. Morphologische reihenfolge des Innenbaues der Prostata bei den Schlammschnecken (*Gastropoda, Pulmonata*, *Lymnaeidae*). Proc. Ninth Int. Malac. Congress (Edinburgh 1986). Leiden 185-186.

-. 1993a. Die Mantelpigmentation als Diagnosemerkmal bei Schlammschnecken (*Gastropoda, Pulmonata: Lymnaeidae*). Malak. Abh. Mus. Tierkd. Dresden **16**(19): 165-172.

-. 1993b. Phylogeny and Relationships within the European Species of the Family *Lymnaeidae* (*Gastropoda: Pulmonata: Basommatophora*). Folia Malacologica. Kraków **5**: 61-95.

-. 1996. Concerning Hungarian populations of „*Galba palustris*" studied by KILIAS (1992) (*Gastropoda: Pulmonata: Lymnaeidae*). Malak. Abh. Mus. Tierkd. Dresden **18**(6): 60-67.

-. 1997. New European locality of *Lymnaea* (*Stagnicola*) *occulta* (JACKIEWICZ, 1959) (*Gastropoda*, *Pulmonata*: *Basommatophora*). (in press).

JACKIEWICZ, M., GERBER, J., 1990. Eine für die Bundesrepublik Deutschland neue Schlammschnecke: *Lymnaea vulnerata* KÜSTER 1862 (*Gastropoda: Pulmonata*). Mitt. dtsch. malakozool. Ges. Frankfurt **47**: 1-5.

JACKIEWICZ, M., KORALEWSKA-BATURA, E., 1995. The shell surface sculpture of *Lymnaeidae* (*Gastropoda*: *Pulmonata*: *Basommatophora*). Malak. Abh. Mus. Tierkd. Dresden **17**(17): 191-197.

JACKIEWICZ, M., PROSCHWITZ, T. von, 1991. *Lymnaea* (*Stagnicola*) *occulta* (JACK.), *Lymnaea* (*Lymnaea*) *vulnerata* KÜST. und *Lymnaea* (*Lymnaea*) *corvus* (GMEL.) - drei für Schweden neue Schlammschneckenarten (*Gastropoda, Basommatophora: Lymnaeidae*). Malak. Abh. Mus. Tierkd. Dresden **15**(14): 125-132.

JACKIEWICZ, M., ZBORALSKA, H., 1994. Postembryonal development of reproductive organs of the selected species of families *Lymnaeidae* and *Succineidae* (*Gastropoda, Pulmonata*). Bull. Soc. Amis Sci. Lett. Pozna Sér. D. **30**: 63-68.

JAECKEL, S. H., 1953. Die Schlammschnecken unserer Gewässer. Die Neue Brehm-Bücherei. Leipzig 30 pp.

JOOSSE, J., 1964. Dorsal bodies and dorsal neurosecretory cells of the cerebral ganglie of *Lymnaea stagnalis* L. Arch. néerl. Zool. Leiden **16**: 103 pp.

KILIAS, R., 1960. Weinbergschnecken. Ein Überblick über Biologie und wirtschaftliche Bedeutung. Berlin 94 pp.

-. 1992. Vergleichend-anatomische Untersuchungen an „*Galba palustris* (O. F. MÜLLER)" von ungarischen Fundorten als beitrag zur *palustris*-Problematik (*Gastropoda, Basommatophora: Lymnaeidae*). Malak. Abh. Mus. Tierkd. Dresden **16**(4): 25-29.

KORALEWSKA, E., 1979. Ślimaki (*Gastropoda*) Ziemi Wrzesińskiej. Bad. fizjogr. Pol. zach., Poznań **32**: 105-113.

KORALEWSKA-BATURA, E., 1992. Mięczaki (*Mollusca*) Wielkopolski. Wyd. nauk. UAM, Ser. Zool. Poznań **18**: 41 pp.

KORNIJÓW, R., GULATI, R. D., OZIMEK, T., 1995. Food preferences of freshwater invertebrates: comparing fresh and decomposed angiosperm and filamentous alga. Freshwater Biology **33**: 205-212.

KOSIŃSKA, M., 1979. Mięczaki Wrocławia. Acta Univ. Wratislaviensis, 437. Prac. zool. Wrocław **9**: 13-40.

KOVANDA, J., 1956. O skalaridnich a anomálnich formách ulit některých našich plžů. Vesmir. Praha **35**: 139-141.

LARAMBERGUE, M., 1928. Étude de l'appareil génital de quelques Limnées; ses rapports avec la systématique. Bull. Soc. zool. France. Paris 33.

MCGEE-RUSSELL, S. M., 1955. A new reagent for the histochemical and chemical detection of calcium. Nature. London **175**, 311 pp.

MICHAŁKIEWICZ, M., 1993. Mięczaki (*Mollusca*) jako składnik makrozoobentosu wybranych jezior Wielkopolski i ich rola w ocenie stopnia zanieczyszczenia wód powierzchniowych (unpublished Ph. D. thesis).

PIECHOCKI, A., 1969. Mięczaki (*Mollusca*) rzeki Grabi i jej terenu zalewowego. Fragm. Faun. Warszawa **15**: 111-191.

-. 1975. Beobachtungen über den Bau von Laichen und die Fortpflanzung von Süsswasserschnecken aus den Familien: *Physidae, Lymnaeidae* und *Planorbidae*. Fragm. Faun. Warszawa **20**(14): 223-232.

-. 1979a. Mięczaki (*Mollusca*). Ślimaki (*Gastropoda*). Fauna słodkow. Pol. **7**. Warszawa-Poznań 187 pp.

-. 1979b. *Lymnaea* (*Galba*) *occulta* (JACK.) (*Gastropoda, Basommatophora*) w Górach Świętokrzyskich. Prz. zool. Wrocław **23**(3): 246-248.

ROSENBAUM, R. M., DITZION, B., 1963. Enzymic histochemistry of granular components in digestive gland cells of the Roman snail, *Helix pomatia.* Biol. Bull. Lancaster **124**(2): 211-224.

ROSZKOWSKI, W., 1914a. Contribution a l'étude des Limnées du Léman. Rev. suisse Zool. Geneve **22**: 457.

-. 1914b. Note sur l'appareil génital de *Limnaea auricularia* L. et *Limnaea ovata* DRAP. Zool. Anz. Leipzig **44**(4): 175.
-. 1914c. Przyczynek do znajomo ci anatomii narządów płciowych u błotniarki podrodzaju *Gulnaria* LEACH. Spraw. TNW. Warszawa **7**(1).
-. 1923. Przyczynki do poznania rodziny *Lymnaeidae*. 4. Aparat płciowy *Galba truncatula* (MÜLL.). Arch. Nauk biol. TNW. Warszawa **1**(5).
-. 1925. Z badań nad otułką *Amphipeplea* NILSS. Univ. Warsz. Rozp. **1**. Warszawa 45 pp.
-. 1926. Contributions to the study of the Family *Lymnaeidae.* 7. The structure of the prostate of the *Lymnaeidae*. Ann. Mus. zool. polon. (Hist. nat.) Warszawa **5**(1): 14 pp.
-. 1927. Contributions to the study of the Family *Lymnaeidae.* 8. The Genus *Pseudosuccinea* from South Brazil. Ann. Mus. zool. pol. (Hist. nat.). Warszawa **6**(1): 33 pp.
-. 1928. The distribution of Lymnaeids in Europe and in North America, with relation to Wegener's theory. Ann. Mus. zool. pol. (Hist. nat.). Warszawa **7**(2-3): 85-94.
-. 1929. Contribution to the Study of the Family *Lymnaeidae*. 1. On the Systematic Position and the Geographical Distribution of the genus *Myxas* J. SOWERBY. Ann. Mus. zool. pol. (Hist. nat.). Warszawa **8**(2): 64-97.
ROSZKOWSKI, W., ŻEBROWSKA, A., 1915. O budowie pochewek prącia u błotniarek (*Limnaea* LAM.). Prace TNW. Warszawa **9**: 24 pp.
ROTARIDES, M., SCHLESCH, H., 1951. Regeneration of the shell and related phonomena in the family *Clausiliidae*. Acta biol. Acad. Sci. hung. Budapest **2**(1-3): 55-117.
RUCH, M., 1979. Regeneracja czułków u *Lymnaea stagnalis* L. (*Mollusca, Pulmonata, Basommatophora*) (unpublished Master's thesis).
RUNHAM, N. W., HUNTER, P. J., 1970. Terrestrial slugs. London 184 pp.
SCHMIDT, W., 1912. Untersuchungen über die Statocysten unserer einheimischen Schnecken. Inaug. Diss. Jena.
STADNIČENKO, A. P., 1968. *Galba occulta* JACKIEWICZ, 1959 (*Gastropoda, Pulmonata*) novyj vid fauny SSSR. Zool., Moskva **47**(6): 942-944.
UMIŃSKI, T., 1975. Reproductive maturity in some *Vitrinidae* (*Mollusca, Gastropoda*) from Poland. Ann. zool. Warszawa **32**(16): 357-373.
URBAŃSKI, J., 1957. Krajowe ślimaki i małże. Warszawa 276 pp.
VELDE, G. van der, 1984. Anatomical evidence for the occurrence of *Lymnaea* (*Galba*) *palustris* (O. F. MÜLLER, 1774) and *L.* (*Galba*) *corvus* (GMELIN, 1778) (*Gastropoda: Lymnaeidae*) in the Netherlands. Zool. Meded. Leiden **58**(22): 341-352.
WÄCHTLER, W., 1929. Anatomie und Biologie der augenslosen Landlungenschnecke *Caecilioides acicula* MÜLL. Z. Morphol. Ökol. Berlin **13**(3-4): 359-462.
WIKTOR, A., 1989. *Limacoidea et Zonitoidea nuda.* Ślimaki pomrowiokształtne (*Gastropoda: Stylommatophora*). Warszawa, 207 pp.

Table 1. The most important anatomical features of the reproductive organs of the lymnaeid species

feature / species	proximal part of the prostate	distal part of the prostate	folds in the proximal part of the prostate	number of folds in the distal part of the prostate	length ratio of the praeputium to the penis sheath	number of the praeputium folds	swelling on the penis	pyriform body	oviduct II	duct of the spermatheca	distal part of the spermatheca duct
Omphiscola glabra	wide	usually of the same width like proximal	absent	absent	1 : 1	1	absent	ovate	long	long	narrow
Lymnaea truncatula	narrow	wide	absent	1 small	3 : 1	2	absent	ovate	short	long	narrow
Lymnaea peregra	rather wide	wide	absent	1 big	1 : 1	2	absent	ovate	short	very short or absent	narrow
Lymnaea auricularia	narrow	narrow	absent	1 big	1 : 1	2	absent	ovate	long	long	narrow
Lymnaea glutinosa	narrow	wide	absent	1 big	1 : 1	2	absent	ovate	long	long	narrow
Lymnaea palustris	narrow	wide	absent	1 big	1 : 1	2	absent	ovate	very long	very long	narrow
Lymnaea turricula	narrow	wide	absent	1 big	1 : 3 to 1 : 5	2	absent	ovate	very long	very long	narrow
Lymnaea occulta	narrow with ligula	narrow plicate	absent	1 big	1 : 1	2	absent	strongly elongated	very short	short	funnel shaped
Lymnaea vulnerata	rather wide	wide	absent	2 big	3 : 1	2	present	ovate	long	long	narrowly funnel shaped
Lymnaea corvus	rather wide	wide	present	many wide	3 : 1	2	present	ovate	short	short	funnel shaped
Lymnaea stagnalis	rather wide	wide	present	many narrow	3 : 1	2	present	ovate dichotomous	long	long	funnel shaped

Explanations of the charcters used in the cladogram

Plesiomorphic character state	Apomorphiccharacter state
1. One fold of praeputium	Two folds of the praeputium
2. Two small folds of the praeputium	Two big folds of the praeputium
3. Folds of the prostate absent	Folds of the prostate present
4. Two folds of the prostate	Numerous folds of the prostate
5. Numerous big folds of the prostate	Numerous small folds of the prostate
6. Proximal and distal prostate parts identical width	Proximal prostate parts narrower than its distal parts
7. Papillar fold (velum) absent	Papillar fold (velum) present
8. Lumen of the papilla longitudinal	Lumen of the papilla round
9. Penis long or very long	Penis short
10. Penis without a ring swelling	Penis with a ring swelling
11. Penis without a narrowing	Penis with a narrowing
12. Penis thin, very long	Penis thicker, long
13. Length ratio of the praeputium to the penis sheath is 1:1, or even 1:5	Length ratio of the praeputium to the penis sheath is 3:1
14. Spermathecal duct long	Spermathecal duct short or absent
15. Spermathecal duct without a funnel--shaped widening	Sparmathecal duct with a funnel--shaped widening
16. Shell not covered with a mantle	Shell covered with a mantle
17. Shell turriform with high spire	Shell ovate with low spire

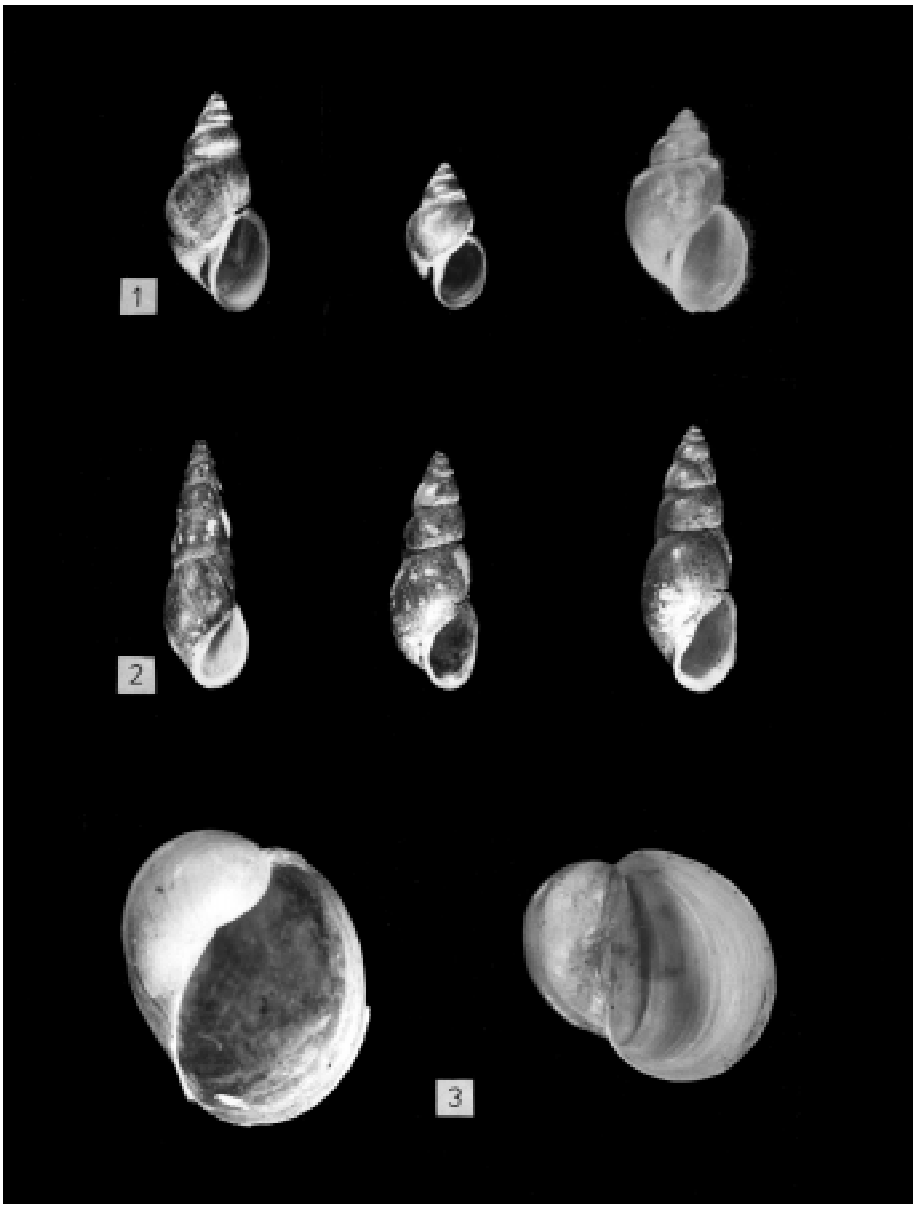


Plate I. Shells of *Lymnaea*: 1 - *Lymnaea (Galba) truncatula*; 2 - *Omphiscola glabra*; 3 - *Lymnaea (Myxas) glutinosa*. 5x. (Original).

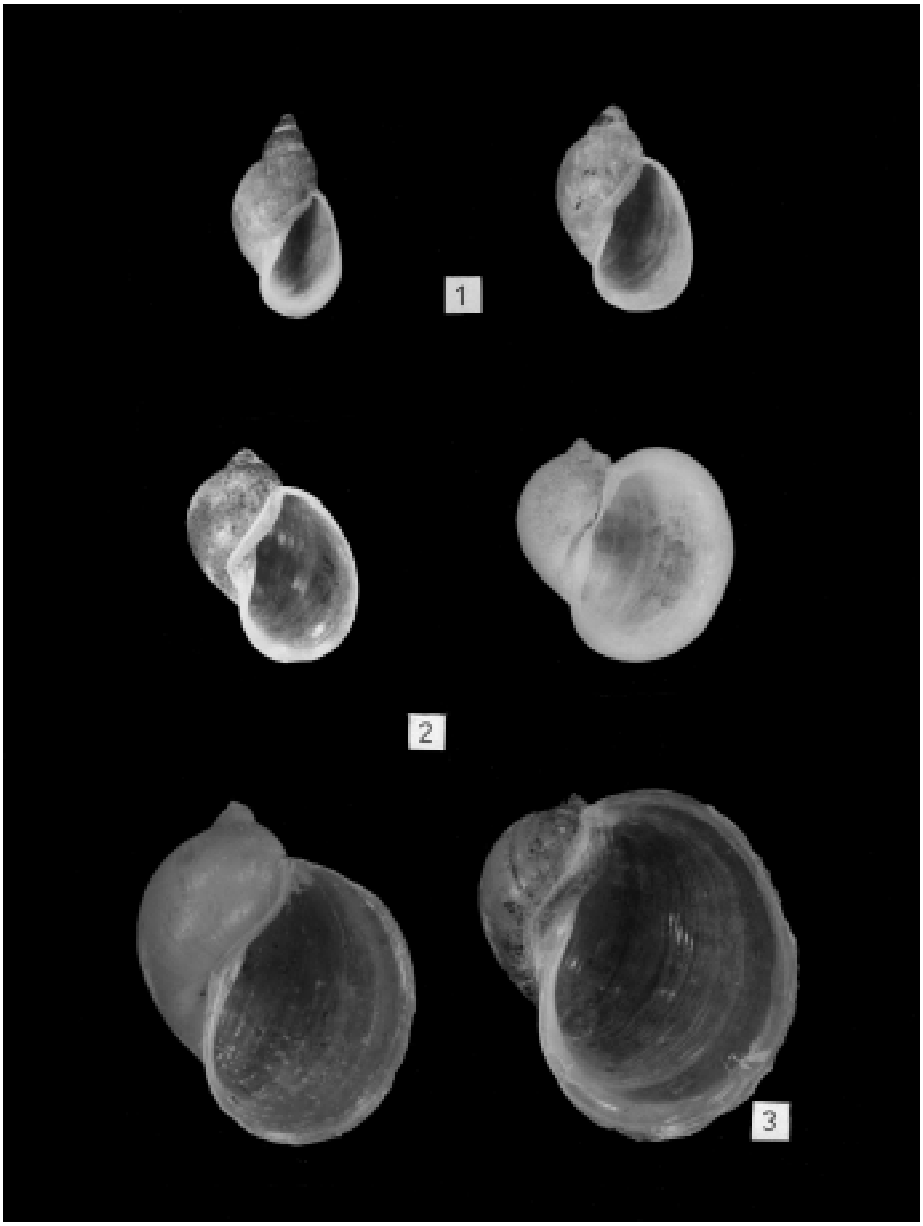


Plate II. Shells of *Lymnaea (Radix) peregra*: 1 - *Lymnaea (Radix) peregra* f. *typica*; 2 - *Lymnaea (Radix) peregra* f. *ovata*; 3 - *Lymnaea (Radix) peregra* f. *ampla*. 2x. (Original).

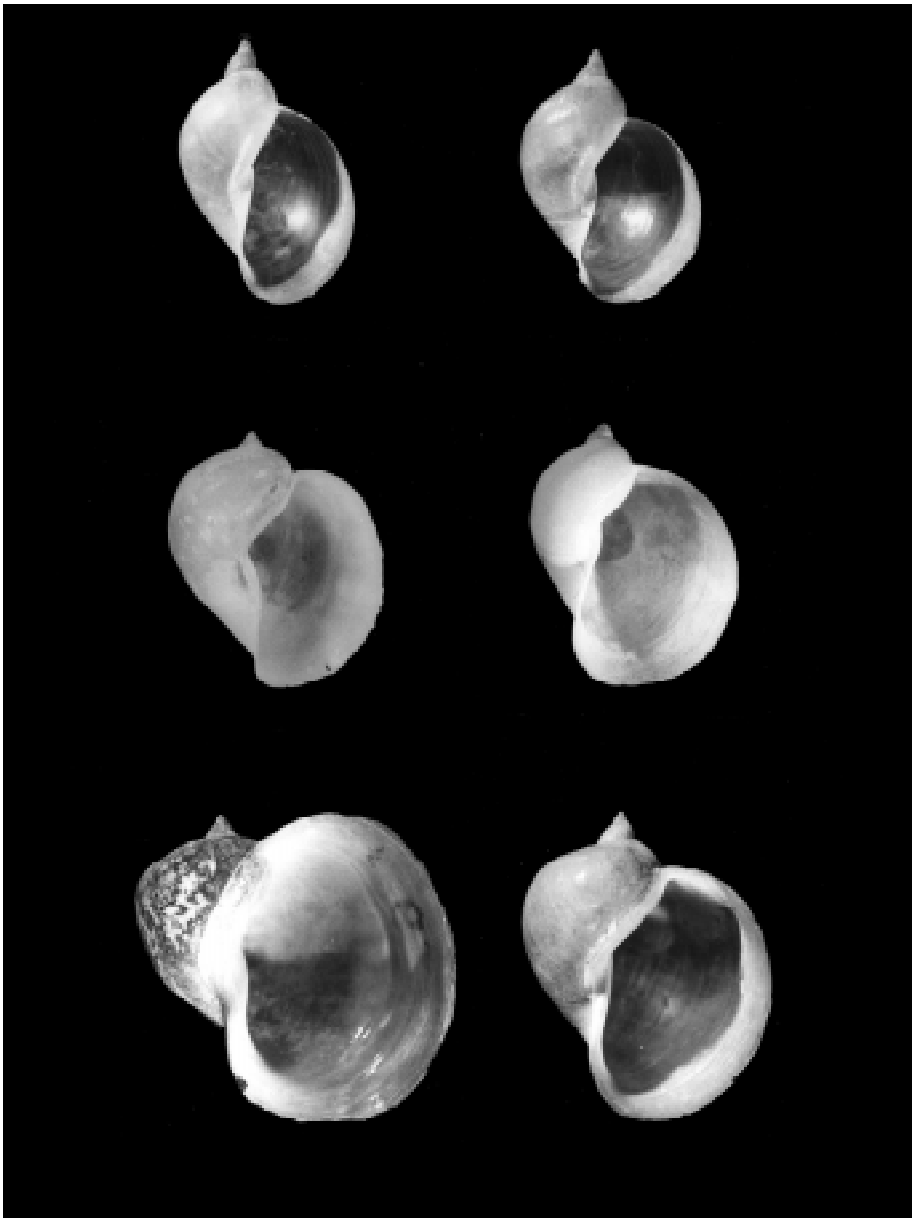


Plate III. Shells of *Lymnaea (Radix) auricularia* 2x. (Original).

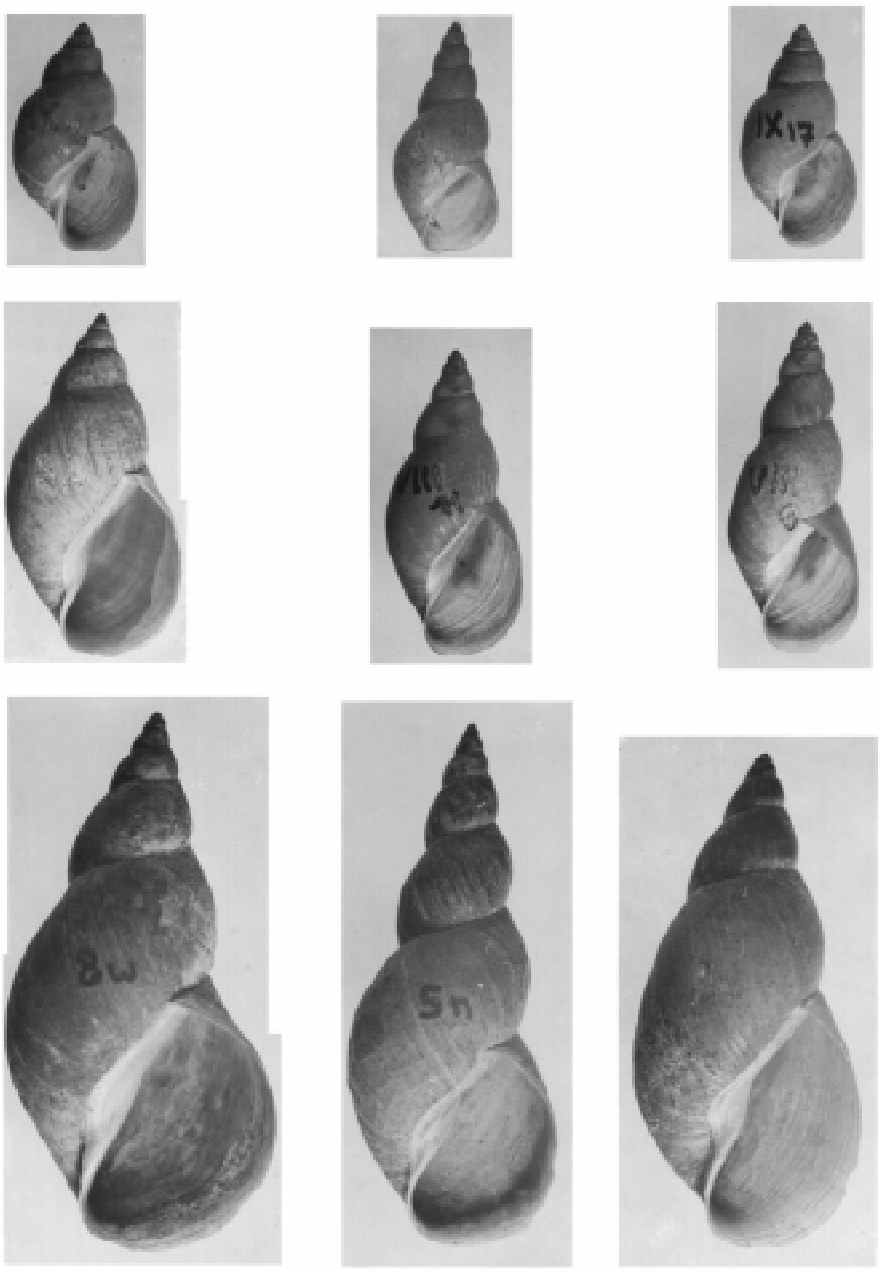


Plate IV. Shells of *Lymnaea (Stagnicola) palustris* 3x. (After JACKIEWICZ).

Plate V. Shells of *Lymnaea (Stagnicola) turricula* 3x. (After JACKIEWICZ).

Plate VI. Shells of *Lymnaea (Stagnicola) occulta* 3x. (After JACKIEWICZ).

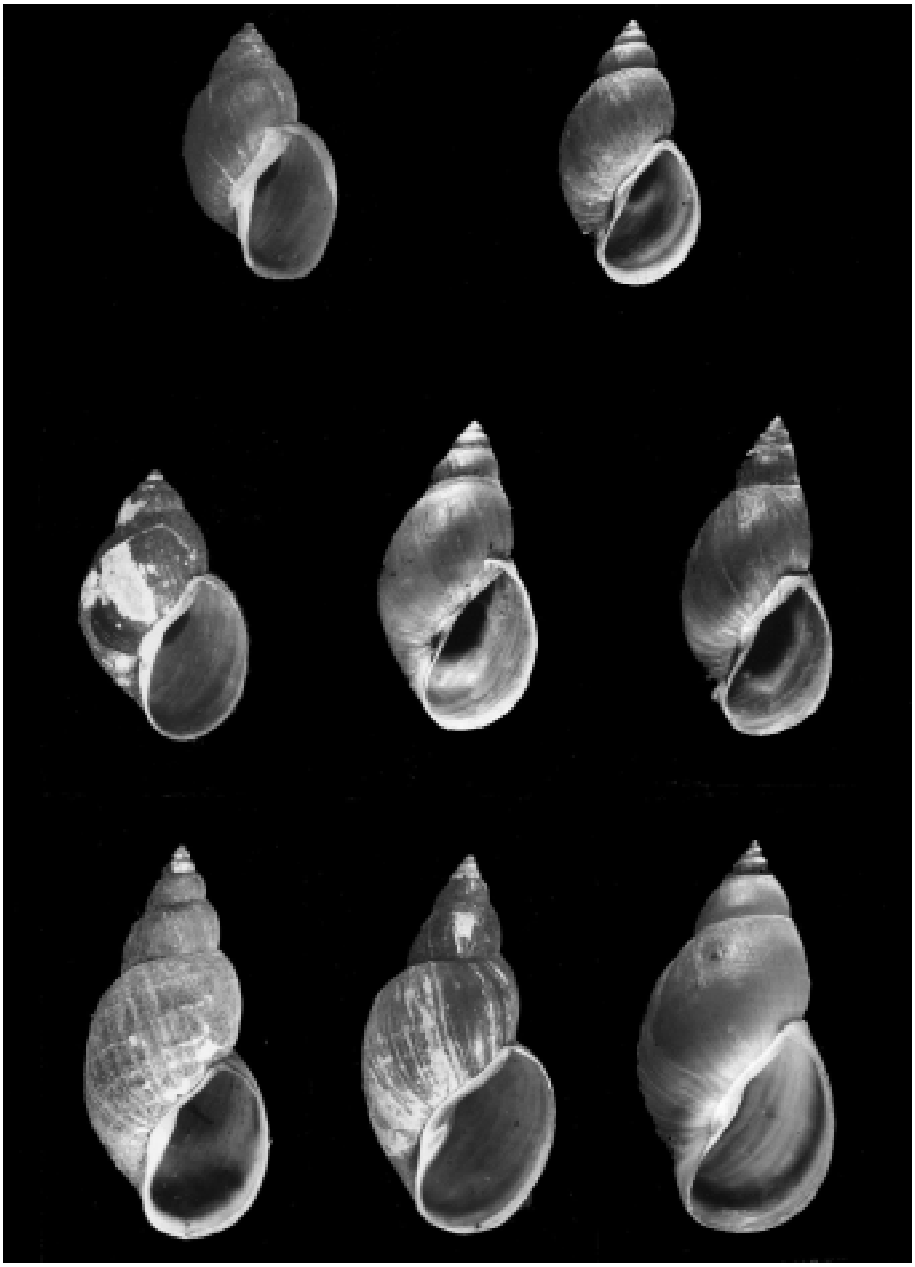


Plate VII. Shells of *Lymnaea (Lymnaea) vulnerata* 3x. (After JACKIEWICZ).

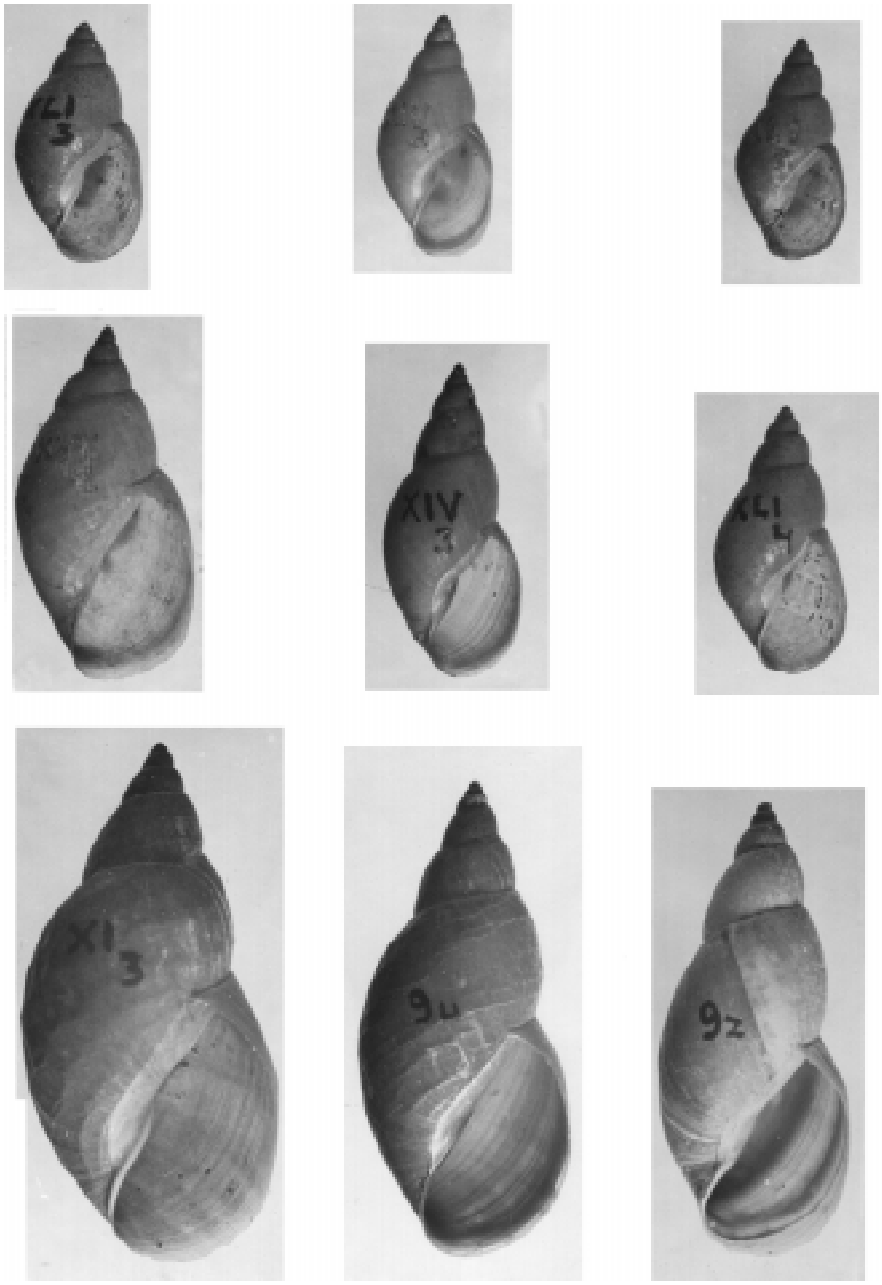


Plate VIII. Shells of *Lymnaea (Lymnaea) corvus* 3x. (After JACKIEWICZ).

Plate IX. Shells of *Lymnaea (Lymnaea) stagnalis* 1.3 x. (Original).

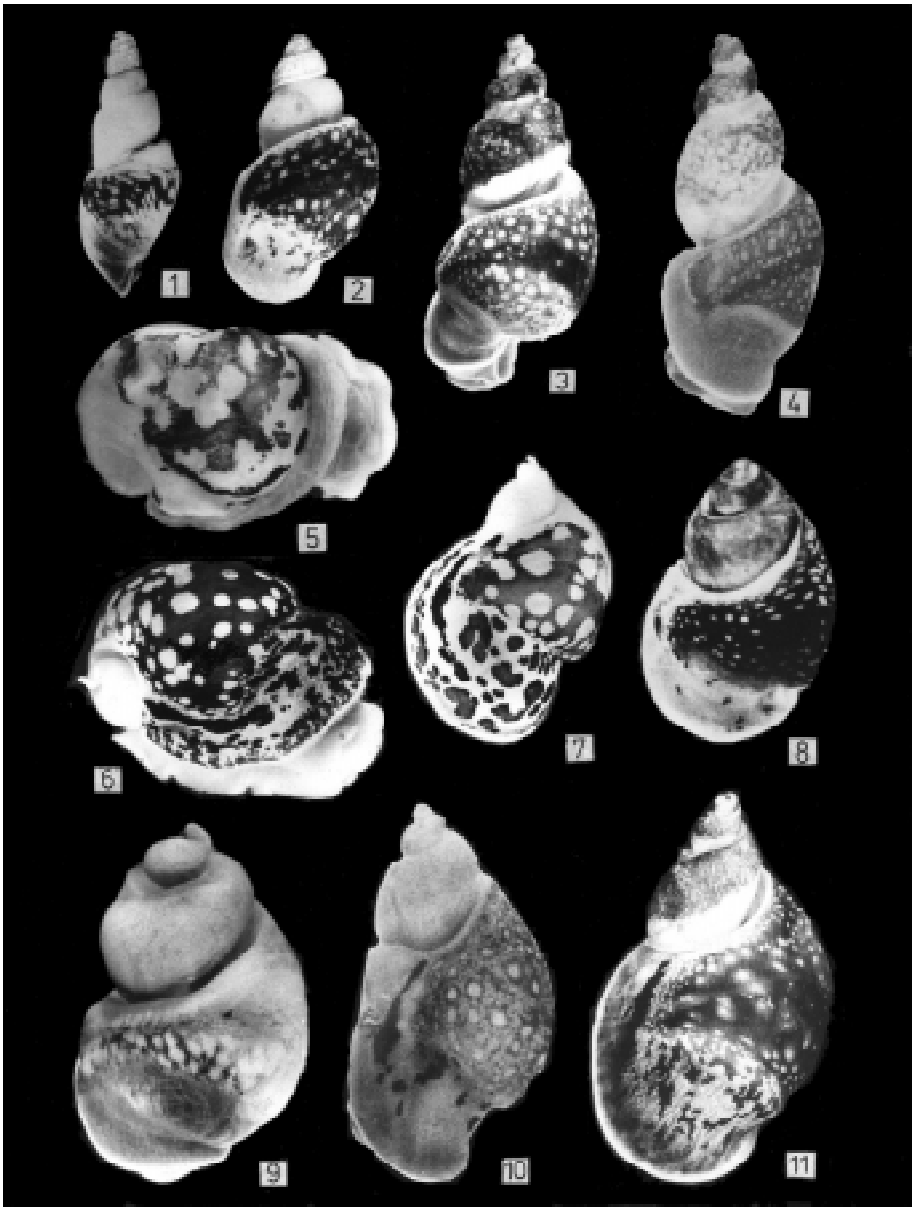


Plate X. Mantle pigmentation of *Lymnaea*: 1 - *Omphiscola glabra* (8 mm); 2 - *Lymnaea (Galba) truncatula* (6 mm); 3 - *Lymnaea (Stagnicola) turricula* (22 mm); 4 - *Lymnaea (Stagnicola) palustris* (24 mm); 5 - *Lymnaea (Myxas) glutinosa* (11 mm); 6 - *Lymnaea (Radix) peregra* (19 mm); 7 - *Lymnaea (Radix) auricularia* (21 mm); 8 - *Lymnaea (Lymnaea) vulnerata* (17 mm); 9 - *Lymnaea (Stagnicola) occulta* (19 mm); 10 - *Lymnaea (Lymnaea) corvus* (25 mm); 11 - *Lymnaea (Lymnaea) stagnalis* (28 mm). (After JACKIEWICZ).

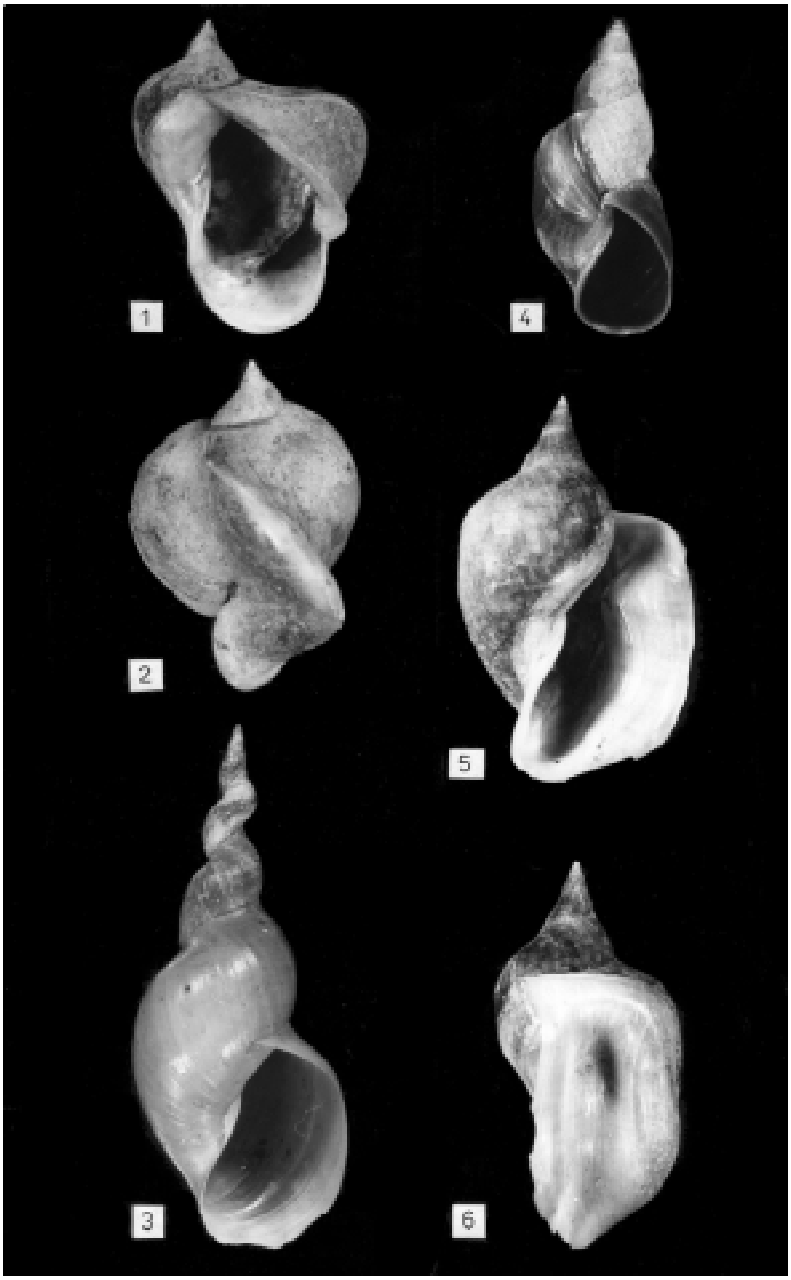


Plate XI. Abnormal shell structure of *Lymnaea*: 1, 2 - *Lymnaea (Radix) auricularia*; 3, 5, 6 - *Lymnaea (Lymnaea) stagnalis*; 4 - *Lymnaea (Lymnaea) corvus*. 2 - 2.5 x. (1-5 after JACKIEWICZ; 6 original).