

PHYLOGENY AND RELATIONSHIPS WITHIN EUROPEAN SPECIES OF THE FAMILY LYMNAEIDAE (GASTROPODA: PULMONATA: BASOMMATOPHORA)

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ABSTRACT: Anatomical studies of the reproductive organs were carried on 11 lymnaeid species, collected in Europe: *Omphiscola glabra* (O. F. Müller, 1774), *Lymnaea (Galba) truncatula* (O. F. Müller, 1774), *Lymnaea (Radix) peregra* (O. F. Müller, 1774), *Lymnaea (Radix) auricularia* (Linnaeus, 1758), *Lymnaea (Myxas) glutinosa* (O. F. Müller, 1774), *Lymnaea (Stagnicola) palustris* (O. F. Müller, 1774), *Lymnaea (Stagnicola) turricula* (Held, 1836), *Lymnaea (Stagnicola) occulta* (Jackiewicz, 1959), *Lymnaea (Lymnaea) uulnerata* Küster, 1862, *Lymnaea (Lymnaea) corvus* (Gmelin, 1788) and *Lymnaea (Lymnaea) stagnalis* (Linnaeus, 1758). Special attention was paid to the structure of the praeputium and its head lumen termination, and to the structure of the penis, and habitus and internal organization of the prostate. Basing on the above characters, two genera were distinguished within the family: *Omphiscola* Beck, 1837 and *Lymnaea* Lamarck, 1799, the latter including five subgenera: *Galba* Schrank, 1803, *Radix* Montfort, 1810, *Myxas* Sowerby, 1822, *Stagnicola* Leach, 1830 and *Lymnaea* s. str. Besides, a view on relationships and ways of evolution of lymnaeids are presented.

KEY WORDS: Lymnaeidae, classification, genera, subgenera, reproductive system, structure, phylogeny

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Phylogeny and Relationships within the European Species of the Family *Lymnaeidae* (*Gastropoda: Pulmonata: Basommatophora*)

1. Introduction

The systematics of the gastropods from the family *Lymnaeidae* until recently was based on the shell morphology solely, although the shell often shows considerable variability. Not much attention was paid to the reproductive organs structure, whose taxonomic usefulness is higher than in case of the shell.

Basing on the shell morphology, nearly 1,800 species and forms of the *Lymnaeidae* have been already described. HUBENDICK (1951) determined the number of recent species as higher than 40.

Earlier authors, like GEYER (1927) or EHRMANN (1937) distinguished the following genera within the *Lymnaeidae*: *Lymnaea* LAMARCK, 1799, *Galba* SCHRANK, 1803, *Radix* MONTFORT, 1810, *Myxas* SOWERBY, 1822, *Stagnicola* LEACH, 1830 and *Leptolimnaea* SWAINSON, 1840 (Table 5 - 6). HUBENDICK (1951) included all the lymnaeid species into one genus *Lymnaea* LAMARCK, 1799 (Table 7), which was followed by some other authors.

For several years I have carried on detailed anatomical research of the reproductive organs of 11 lymnaeid species known to me, and collected in the territory of Europe. There are: *Omphiscola glabra* (O. F. MÜLLER, 1774), *Lymnaea* (*Galba*) *truncatula* (O. F. MÜLLER, 1774), *Lymnaea* (*Radix*) *peregra* (O. F. MÜLLER, 1774), *Lymnaea* (*Radix*) *auricularia* (LINNAEUS, 1758), *Lymnaea* (*Myxas*) *glutinosa* (O. F. MÜLLER, 1774), *Lymnaea* (*Stagnicola*) *palustris* (O. F. MÜLLER, 1774), *Lymnaea* (*Stagnicola*) *turricula* (HELD, 1836), *Lymnaea* (*Stagnicola*) *occulta* (JACKIEWICZ, 1959), *Lymnaea* (*Lymnaea*) *vulnerata* KÜSTER, 1862, *Lymnaea* (*Lymnaea*) *corvus* (GMELIN, 1788) and *Lymnaea* (*Lymnaea*) *stagnalis* (LINNAEUS, 1758).

In present paper I do not consider the species described recently from the European part of the late Soviet Union. The drawings of the reproductive organs of those species, presented in numerous papers, are schematic, slightly accurate and do not show details of the structures, therefore they are useless in my considerations.

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In presented research I was paid special attention to the structure of the praeputium and its head distalmost part, to the structure of the penis, and habitus and internal organization of the prostate. The structure of the organs listed above supported me with many new and important data concerning the phylogeny and relationships of lymnaeids.

The analysis of the reproductive organs structure of the species listed above, carried by me on, enabled to change the divisions of the *Lymnaeidae* into lower taxa, used till now. The new system of the family is presented in Table 8 and in the end of this paper.

2. Material and methods

I had at my disposal about 50 specimens of *Omphiscola glabra*, collected at three localities: Toollarp in der Nähe von W. Wröm (Sweden), 3rd of July 1878, leg. W. Lilljeborg; Mönchbruch-Wiesen (Germany), 1st of May 1958, ex coll. Dr A. Zilch; Krefeld-Hülserberg, Niederrhein (Germany), 1958, leg. Dr Miegel. On the other hand, 43 specimens of *Lymnaea (Lymnaea) vulnerata* I collected in October 1979 in Yugoslavia from the *locus typicus*: River Cetina near Omis, 30 km S of Split. They occurred at the left bank of the river, between the town Omis and Radmanove Mlinice village. The material of the other nine species are mainly from the territory of Poland, but also from Czechoslovakia, Hungary, Bulgaria and Sweden. Only adult specimen were studied, collected from various populations and in various time. The gastropods were fixed in 75% ethanol.

3. Description of the shell and reproductive organs

Omphiscola glabra (O. F. MÜLLER, 1774)

Galba glabra (O. F. MÜLLER, 1774); *Stagnicola glabra* (O. F. MÜLLER, 1774);

Leptolimnaea glabra (O. F. MÜLLER, 1774)

The shell (Pl. I.1) is roller-shaped, with the surface delicately striated. Shell colour from pale to dark brown. Whorls, 6 - 8 in number, grow regularly, the body whorl is then only somewhat broader than the penultimate one. The spire very high, smoothly terminated. The mouth small, oval, its height equals half of the spire height. Shell height up to 15 mm, shell breadth up to 5.5 mm.

Praeputium (Fig. 1: r) is relatively narrow, clavate in shape. To the praeputium, somewhat laterally, is inserted the retractor. Inside the praeputium there is one well developed longitudinal fold (Figs 15 and 18). Another, accessory longitudinal fold, thinner and twice shorter than the former one, often runs along it (Figs 16 and 19).

At the bottom of bulbous termination of praeputium there is relatively big and fleshy shield (Figs 14, 18 and 19: h), circular in shape. One part of this structure is usually bigger, and the second one - somewhat smaller. Sometimes the shield is thicker and forms a sort of two lips. Its crevice-shaped lumen juncts directly the lumen of the penis sheath and of the praeputium. After HUBENDICK (1951) the shield is homologous with the papilla (sarcobelum) of the other lymnaeids. However, it resembles rather papillar fold (velum) than the papilla (sarcobelum) of the other lymnaeid species (Fig. 21: c, d).

The penis sheath (Fig. 1: p) is tapering, cylindrical, rather long and thick. Its breadth equals approximately half of the breadth of the praeputium. The length ratio between the praeputium and penis sheath equals usually 1: 1 (Fig. 1: r, p). The penis (Fig. 12) is rather long (seven times longer than its breadth at its base). It narrows slowly to its sharp tip.

The proximal part of the prostate (Fig. 17) is broader or as broad as its distal part, there is no fold inside the organ. However, the wall of the terminal part of the prostate is somewhat thicker dorsally (Fig. 13). According to ROSZKOWSKI (1927) and HUBENDICK (1951) the prostate with no fold is the most primitive type of the prostate in lymnaeids.

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

Fossaria truncatula (O. F. MÜLLER, 1774); *Limnaeus minutus* DRAPARNAUD, 1801

Shell (Pl. I, 2) is small, ovally turritiform, horny in colour. It consists of 5 - 6 strongly convex whorls, arranged "steppy" one to another. The whorls grow slowly, the body whorl is the biggest and sometimes markedly broadened. The spire usually rather high, terminated blunt. The mouth oval, its height not much less than the height of the spire. Shell height up 11 mm, shell breadth up 6 mm.

Praeputium (Fig. 2: r) is roller-shaped and somewhat flattened. Similarly as in *Omphiscola glabra*, its retractor is inserted somewhat laterally. Inside the praeputium there are two longitudinal folds, developed better in the praeputium's distal part. The folds are not big, so there is relatively big space between them. In the other species the folds are much bigger (Fig. 22).

The papillar fold is situated at the bottom of bulbous termination of praeputium, similarly as in other lymnaeids. The fold consists of a few small, fleshy lips forming a small shield. The papilla situated in the centre of this shield is very small, finger-shaped; the circular opening on its tip is also very small (JACKIEWICZ 1984).

Penis sheath (Fig. 2: p) is short and rather thick. Its breadth equals nearly half of the praeputium breadth. The length ratio between the praeputium and penis sheath equals usually 1 : 1/3 (Fig. 2: r, p). The penis (Fig. 31) is oval, like in all the lymnaeids, and it is short (4 times longer than its breadth at its base). It narrows rather abruptly to its markedly sharp tip, wedge-shaped.

The wall of the distal part of the prostate forms one fold, very slightly developed. The lumen of the gland is therefore very spacious (Fig. 25). The vas deferens runs nearly from the middle of the prostate.

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

Radix peregra (O. F. MÜLLER, 1774); *Radix limosa* (LINNAEUS, 1758); *Radix balthica* (LINNAEUS, 1758); *Radix ovata* (DRAPARNAUD, 1805); *Radix neglecta* (C. R. BOETTGER, 1944)

The shell (Pl. I, 3) is very variable. Its shape may be oval, circularly-oval or ovaly-turritiform. Its colour is from whitish yellowish to dark brown. There are 3 - 5 whorls, the body whorl is often markedly swollen. The spire usually very low, turritiform and blunt terminated. The mouth usually very big. The height and breadth of the shell sometimes reaches 40 mm.

The praeputium (Fig. 3: r) resembles an elongated sac in shape and is proximally markedly narrower. Its retractor is inserted to its head, closely to the penis sheath leaving the praeputium. The latter is characteristic of all the lymnaeid species described below as well. The wall of the praeputium, similarly as in other species (Figs 20 and 22) forms two longitudinal folds, well developed already. There are as big as there is only restricted space of the lumen between them, which shows the pattern of "S" or amphidisc which depends on the arrangement of the folds one to another.

At the bottom of bulbous termination of praeputium there is a big papilla, cupolated in shape. The opening on its top is very small. Around the cupola there runs a big and fleshy papillar fold, often in the form of two lips (JACKIEWICZ 1984).

The penis sheath (Fig. 3: p) is very narrow and long, its head is poorly developed. The length ratio between the praeputium and penis sheath equals 1 : 1 (Fig. 3: r, p). The penis, like in *L. (R.) auricularia* (Fig. 35) is very long (14 times longer than its breadth at its base). It resembles much the vas deferens in its shape and length.

In the distal part of the prostate, similarly as in *L. (S.) palustris* (Fig. 26) and some other species, there is one, very big fold. It fills nearly completely the lumen of the gland. The vas deferens outlet is situated somewhat laterally.

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

Radix auricularia (LINNAEUS, 1758)

The shell (Pl. I, 4) of the species is less variable than the one of *L. (R.) peregra*. It may be oval or circularly-oval in shape. Its colour is from whitish, through yellow, to various shades of brown. There are 4 - 4.5 whorls. Initially the whorls are slightly convex. The body whorl is most often very big and swollen. The spire very low, conical and sharply terminated. The mouth is also very big, broadly oval in shape. The shell height and breadth may approach 30 mm.

The praeputium (Fig. 4: r) is fusiform in shape. Inside it there run, similarly as in *L. (R.) peregra*, two longitudinal folds. They are situated opposite one to another, but their position in relation one to the other is not constant.

The papillar fold is in the form of a big and flat shield. There is a dark pigment close to its border, arranged in a form of small grains or even clubs. The cupola-shaped papilla is rather big, while its aperture is small (JACKIEWICZ 1984).

The penis sheath (Fig. 4: p) is very narrow and long, like in *L. (R.) peregra*. The length ratio between the praeputium and penis sheath also equals 1 : 1 (Fig. 4: r, p). The penis (Fig. 35) is also very narrow and long (14 times longer than its breadth at its base), and also resembles the vas deferens.

Within the distal part of the prostate there is also only one big fold (Fig. 26). Relatively unspacious lumen of the gland is situated nearly regularly around the fold.

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

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

The shell (Pl. I, 5) is circular in outline. It is thin-walled, very delicate and fragile, yellowish in colour. There are 3 - 4 whorls. However, the spire of this lymnaeid is very low, flattened. The body whorl is very thin and strongly swollen; it constitutes, in fact, all the shell. The mouth is very big as well, widely oval in shape. The strongly developed mantle covers nearly all the shell in living specimens. The shell height and width approaches 15 mm.

The praeputium (Fig. 5: r) is apparently club-shaped. Its proximal part is markedly broadened. Inside the organ there run also two longitudinal folds. Their arrangement in relation one to another is such, that the lumen of the praeputium shows a pattern of "S".

The papillar fold situated at the bottom of bulbous termination of praeputium is very big and thick. It is formed by the two big and fleshy lips identical in size. In the middle of the fold there is a very small, conical papilla. The aperture at its tip is also very small (FELIKSIK 1938, JACKIEWICZ 1984).

Penis sheath (Fig. 5: p), similarly as in the two *Lymnaea (Radix)* species discussed above, is very thin and long. The length ratio between the praeputium and penis sheath also equals 1 : 1 (Fig. 5: r, p). The penis (Fig. 35) is also narrow and long (14 times longer than its breadth at its base). There can be seen through the thin wall of the penis sheath that the penis runs undulately.

The wall of the distal part of the prostate forms one big fold (Fig. 26), similarly as in *L. (R.) peregra* and *L. (R.) auricularia*.

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

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) sensu JACKIEWICZ 1959

The shell (Pl. II, 6) ovally-turritiform, its colour from light brown to dark brown. On its surface there may occur sometimes irregular depressions, so called "hammering", formed by the riblets running perpendicularly and parallelly to the mouth edge. There are 6 - 7 whorls. They are usually convex and grow rather regularly. The body whorl is the biggest one and usually slightly swollen. The aperture is big, but usually smaller than the half of the shell height. It is ovally- or ovally-elongated-shaped. The shell height up 43 mm, the shell breadth up 16 mm.

The praeputium (Fig. 6: r) is club-shaped. Inside the organ there are also two longitudinal folds (Figs 20 and 22). Sometimes one of them is somewhat bigger. Unspacious lumen, situated between the folds, is most often S-shaped.

The papillar fold may show two different patterns: it may be narrow and delicate, or markedly broader but still showing delicate structure. The papilla is always big, conical, with small opening on its tip (Figs 21 and 23: b, c, d).

The penis sheath (Fig. 6: p) is long, cylindrical and rather thick. Its breadth equals 1/3 of the breadth of the praeputium. The length ratio between the praeputium and penis sheath equals 1 : 1 (Fig. 6: r, p). The penis (Fig. 32) is long (8 times longer than its breadth at its base) and rather thick. It narrows gradually to its sharpened tip.

The wall of the lateral part of the prostate forms one well developed fold (Fig. 26), squeezing deeply into the lumen of the gland. The proximal and distal part of the prostate are equally long (Fig. 6: k).

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

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

The shell (Pl. II, 8) of this species has identical organization as the shell of *L. (S.) palustris* (Pl. II, 6). Therefore I omit its description. There is impossible to distinguish those two species basing on the shell characters, but only basing on the anatomical structure of the reproductive organs.

The praeputium (Fig. 7: r) is fusiform in shape. Inside the organ there are also two longitudinal folds (Figs 20 and 22).

At the bottom of bulbous termination of praeputium there are the same structures as in the previously described species (Figs 21 and 23).

The penis sheath (Fig. 7: p) is very long, cylindrical, not much thicker than the vas deferens. The length ratio between the praeputium and penis sheath equals 1 : 3, or even 1 : 5 (Fig. 7: r, p). No one lymnaeid known to me showed such wide variability of the length of those two organs. The penis (Fig. 34) is very long (up 20 times longer than its breadth at its base), thin, it resembles the vas deferens very much.

Inside the prostate there is also one big fold (Fig. 26). The proximal part of the gland is markedly longer than its distal part (Fig. 7: k).

There are only two characters of the reproductive organs structure that distinguish *L. (S.) turricula* from *L. (S.) palustris*. There are: the length ratio between the praeputium and penis sheath, and the length ratio between the proximal and distal part of the prostate.

Lymnaea (Stagnicola) occulta (JACKIEWICZ, 1959)

Galba occulta JACKIEWICZ, 1959

The shell (Pl. II, 7) is ovate-turritiform. Its colour may be yellowish brown or brown. There are usually 5 - 6 whorls. The whorls are separated by a shallow suture, so they are slightly convex. The spire is usually high, regularly growing, with the apex blunt. The aperture relatively small, oval. Its height usually less than the height of the spire. The fold of the columellar lip is especially worth of attention. It is thick, flanged and usually whitish. The height of the shell up 21 mm, the breadth up 9 mm.

The praeputium (Fig. 8: r) is narrow, roller-shaped, with its head slightly marked. Inside the organ there are two folds (Figs 20 and 22), running along it. There may be moved in relation one to another and then the lumen of the praeputium forms S, or they may be situated opposite one to another and then the lumen approaches a shape of amphidisc (Fig. 22).

The papillar fold, situated at the bottom of bulbous termination of praeputium, is broad and flat. It surrounds rather big, conical papilla, the latter terminated with a small opening (JACKIEWICZ 1984).

The penis sheath (Fig. 8: p) is rather thick, cylindrical, with well marked head. The length ratio between the praeputium and penis sheath equals 1 : 1 (Fig. 8: r, p). The penis (Fig. 33) is rather long (5 times longer than its breadth at its base). There is visible more or less developed narrowing on the penis, approximately in the middle of its length. It divides the organ into a thicker and usually longer proximal section and thinner and shorter distal section.

The proximal part of the prostate is long, narrow and begins with a dark, very characteristic ligulate broadening. The distal part is much broader and often folded externally (Fig. 8: k). The wall of the gland forms one big internal fold (Fig. 26).

Lymnaea (Lymnaea) vulnerata KÜSTER, 1862

The shell (Pl. II, 9) is ovally-conical, its colour is dark brown. The apex is often reddish. There are five slightly convex whorls, separated by the shallow suture. The spire relatively low, growing slowly. The body whorl is markedly swollen. The aperture oval, nearly as high as the spire. The shell height, of the biggest specimen in my collection, is 13 mm, its breadth 7 mm.

The praeputium (Fig. 9: r) is club-shaped. Its head is slightly marked. The wall of the organ forms two big inner folds (Figs 20 and 22).

At the border between the praeputium and the penis sheath there is inside not big papilla, conical in shape, with a small opening at its tip. There runs around it a rather broad papillar fold (JACKIEWICZ 1984).

The penis sheath (Fig. 9: p) is in a form of short tube. Its proximal part, so called head, is well marked. The length ratio between the praeputium and penis sheath equals 3 : 1 (Fig. 9: r, p). The penis, as in the two next species, is short (4 times longer than its breadth at its base). It is the broadest at its proximal part, and then it narrows gradually. Approximately in the middle of its length, or somewhat closer to its outlet, there is a ring-like swelling, circling the penis around. The swelling is often poorly or very poorly visible. The terminal part of the penis is stylet-shaped.

The proximal part of the prostate is broad and somewhat flattened. Its distal part is oval, big and strongly swollen (Fig. 9: k). Inside this part of the prostate there are two big folds, situated one along the other (Fig. 27). The vas deferens outlets apically from the prostate.

Lymnaea (Lymnaea) corvus (GMELIN, 1788)

Stagnicola palustris (O. F. MÜLLER, 1774) - partim; *Galba palustris* (O. F. MÜLLER, 1774) - partim; *Stagnicola palustris f. corvus* (GMELIN, 1788); *Galba corvus* (GMELIN, 1788)

The shell (Pl. II, 10) big, ovally-conical. Its colour may be light horny, but also even intensively brown. On the shell surface there are visible riblets, running parallelly and perpendicularly to the shell mouth edge and forming a net of irregular, rectangular meshes, so called "hammering". There are 6 - 7 slightly convex whorls, separated by a narrow suture. They grow irregularly, and the body whorl is the biggest and strongly swollen. The spire big, conical, rather sharply terminated. The aperture oval, big and usually bigger than the spire, or at least as high as the latter. The shell height up 45 mm, the breadth up 16 mm.

The praeputium (Fig. 10: r) is also club-shaped, and there are two well developed longitudinal folds inside it (Figs 20 and 22).

At the bottom of bulbous termination of praeputium a conical or more cupolar in shape papilla, terminated with small opening, is visible. The papilla is surrounded by a delicate papillar fold, that may be narrow or much broader. A wide variability of this structure is observed (JACKIEWICZ 1984).

The penis sheath (Fig. 10: p), similarly as in previously described species, in a form of short tube with well marked head. The length ratio between the praeputium and penis sheath equals 3 : 1 (Fig. 10: r, p). The penis (Fig. 36) is also short (4 times longer than its breadth at its base), rather thick, especially at its base. Its well distinguishable terminal part is wedge-shaped. A characteristic feature is ring-shaped swelling, that may be well developed or hardly marked.

The prostate (Fig. 10: k) is big. There are numerous and thick folds, especially inside its distal part (Fig. 28). Some of them are secondarily folded. The vas deferens outlets apically from the gland.

Lymnaea (Lymnaea) stagnalis (LINNAEUS, 1758)

Lymnaea stagnalis (LINNAEUS, 1758)

The shell (Pl. II, 11) is ovally-conical in shape, its colour is from whitish yellow to dark brown. Its surface is covered by a net of irregular meshes, in a form of so called "hammering". The latter occurs first of all on the body whorl. The whorls are slightly convex, usually 6 - 8 in number. The body whorl is very big and strongly swollen. The spire is usually very big and slender, exceptionally sharply terminated. The aperture is big, oval, most often as high as the spire. This is the biggest species within the lymnaeids, and the height of its shell may approach 60 mm, while the breadth 30 mm.

The praeputium (Fig. 11: r) is in the shape of strongly elongated, narrow sac. Its wall forms, by invagination, two big longitudinal folds filling a considerable part of the lumen of the organ (Figs 20 and 22).

The papillar fold, situated at the bottom of bulbous termination of praeputium, is big and broad, but relatively flat. The papilla the latter surrounds is very small, more or less conical, sometimes digitate, with a big opening at its tip (JACKIEWICZ 1984).

The penis sheath (Fig. 11: p), similarly as in the two previously described species, is short, tube-shaped, also having a well marked head. The length ratio between the praeputium and penis sheath equals 3 : 1 (Fig. 11: r, p).

The penis (Fig. 36) is similarly organized as in *L. (L.) vulnerata* and *L. (L.) corvus*. It is short (4 times longer than its breadth at its base) and rather thick. Its terminal part, situated distally from the ringlike swelling is stylet-shaped or wedge-shaped. The characteristic feature of this penis are tiny folds occurring at its surface, especially at the proximal section (JACKIEWICZ 1988).

The prostate (Fig. 11: k) is big and strongly swollen at its distal part. Especially inside this part there are very numerous and tiny folds (Fig. 29). The vas deferens outlets also apically from the prostate.

4. Conclusions

The anatomical studies carried on showed univocally that *Omphiscola glabra* basically differs in its reproductive organs' structure from the other lymnaeid species. In *O. glabra* there is only one well developed longitudinal fold inside the praeputium (Figs 15 and 18). Along the fold there is often a second, accessory one (Figs 16 and 19), but the latter is much thinner and shorter. At the praeputium head lumen termination there is a papilla (sarcobelum) having crevice-shaped lumen (Figs 14, 18, and 19: g, h). The papillar fold (velum) is lacking. The proximal and distal parts of the prostate are approximately identically broad (Fig. 17). There is no fold inside the prostate. The wall of the prostate is often only somewhat thicker dorsally (Fig. 13).

Among the other ten lymnaeid species the reproductive organs show higher degree of organization. The latter may be easily derived from the more primitive organization of the organs in *O. glabra*.

There are two well developed longitudinal folds inside the praeputium (Figs 20 and 22). Inside, at the praeputium head lumen termination, there is a centrally situated papilla (sarcobelum) with an oval opening at its tip, surrounded by a papillar fold (velum: Fig. 21: c, d). The proximal part of the prostate is markedly narrower than its distal part (Fig. 30). Inside the distal part of the gland being usually strongly swollen there may occur one or two folds, or numerous foldings (Figs 26 - 29).

The differences in the reproductive organs structure between *O. glabra* and the other studied lymnaeids are as profound, as to justify the distinguishing within the family *Lymnaeidae* two separate genera, they are: *Omphiscola* BECK, 1837 and *Lymnaea* LAMARCK, 1799, the latter with five subgenera. The most important characters of the genera are presented in Table 1.

The penis organization (Figs 31 - 36 and Table 2) is an important character, having high value in the lower level systematics of the family. Basing on the character, within the genus *Lymnaea* there can be distinguished the following subgenera: *Galba* SCHRANK, 1803, *Radix* MONTFORT, 1810, *Myxas* SOWERBY, 1822, *Stagnicola* LEACH, 1830 and *Lymnaea s. str.* The distinguished taxa differ one to the other in the shell characters as well (Plates I and II and Table 3).

The subgenus *Galba* seems to be the most primitive within the genus *Lymnaea*. In *L. (G.) truncatula* the lateral attachment of the retractor to the praeputium head (in the other species attached to the base of the head), as well as poorly developed folds inside the praeputium and the fold inside the prostate, resemble to some degree to the pattern we can see in *Omphiscola glabra*.

The characters of the reproductive organs structure of the representatives of the subgenera *Radix* and *Myxas*, as well as the habitus of their shells indicate their close relationship. Only the occurrence of a spacious mantle, covering in *L. (M.) glutinosa* the outer side of the shell, is decisive in classifying the species in separate subgenus.

The profound differences in the reproductive organs structure of the species belonging to the subgenus *Stagnicola* indicate that the systematic status and relationships are not clear. Undoubtedly, the subgenus has to be acknowledged as a complex taxon. The future studies may, perhaps, solve the problem.

The highest organization of the structure of the reproductive organs there show the representatives of the subgenus *Lymnaea s. str.* Their penis is short and its structure more complicated. Inside the prostate there is more than one fold. It is a group characterized by a very uniform morphological structure of those organs.

There are 11 lymnaeid species known at present from the territory of Europe. The most important characters of their anatomical organization are given in Table 4.

The profound interspecific differences in the reproductive organs structure in 11 studied lymnaeid species have tended me to try to reconstruct the phylogeny and relationships within the family *Lymnaeidae*, by means of a cladogram (Fig. 37).

An absence or lower number of structures of some organs of the reproductive system is interpreted as plesiomorphy, while the higher number of the structures and more complex structure as apomorphy, so reached later.

The cladogram presented (Fig. 37) confirms the validity of the changes in the systematic division within the family *Lymnaeidae* proposed by me. It displays important differences between the genera and subgenera, and the species belonging to them. Moreover, it determines close relationships between some taxa. The analysis of differences and similarities in character states was given in the beginning of this chapter.

Moreover, I have carried on, by means of diagram of CZEKANOWSKI (Fig. 38), a taxonomical analysis of the anatomical characters of 11 studied lymnaeid species. A method used by KOWAL (1965) in plant taxonomy was applied in the analysis. In the method all the characters are treated as equally important. The method enables the presentation of similarities of studied objects in a graphic form. In the taxonomical analysis the following characters of the reproductive organs were considered:

- number of the folds of the praeputium (1, 2 small, 3 big) - 3 characters;
- point of the attachment of the retractor to the praeputium head (laterally, at the head base) - 2 characters;
- praeputium head lumen termination (papilla, papilla and fold) - 2 characters;
- lumen of the papilla (elongated, circular in shape) - 2 characters;
- habitus of the prostate (proximal part as broad as the distal one, narrower) - 2 characters;
- vas deferens outlet from the prostate (laterally, apically) - 2 characters;
- number of the prostate folds (none, 1 small, 1 big, 2 folds, numerous thick, numerous narrow) - 6 characters;
- length ratio between the praeputium and penis sheath (1 : 1, 1 : 3 - 5, 3 : 1) - 3 characters;

- length of the penis (long and thick, long and narrow, very long and narrow, long with narrowing, short and smooth, short with ring-shaped swelling)
- 6 characters;
- the duct of spermatheca (long, rather long, short, lacking) - 4 characters;
- broadening of the duct of spermatheca (absent, present, small, big)
- 4 characters.

Explanations of the symbols used in the cladogram

Plesiomorphic character state	Apomorphic character state
1. One fold of the 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 part of the prostate identically broad	Proximal part of the prostate narrower than its distal part
7. Papillar fold (velum) absent	Papillar fold (velum) present
8. Lumen of the papilla elongated	Lumen of the papilla circular
9. Penis long or very long	Penis short
10. Penis with no ring-shaped swelling	Penis with ring-shaped swelling
11. Penis with no narrowing	Penis with narrowing
12. Penis narrow, very long	Penis thicker, long
13. Length ratio between the praeputium and penis sheath equals 1 : 1, or even 1 : 5	Length ratio between the praeputium and penis sheath equals 3 : 1
14. The duct of spermatheca long	Duct of spermatheca short or absent
15. The duct of bursa with no broadening	The duct of bursa with broadening
16. The shell not covered with the mantle	The shell covered with the mantle
17. The shell turritiform with high spire	The shell oval with low spire

In total of 36 characters were considered in this manner. When the per cent values of similarities or differences are given, the number has to be acknowledged as 100%. In the analysis of similarities and differences the results reached were converted into graphic symbols.

A distinct group consist the following species: *Lymnaea (Lymnaea) vulnerata*, *L. (L.) corvus* and *L. (L.) stagnalis*. A coherent group, as well, constitute *L. (Radix) peregra*, *L. (Myxas) glutinosa* and *L. (Radix) auricularia*, and *L. (Stagnicola) palustris*. The latter group shows also a strong relation with *L. (S.) turricula*, and somewhat less strong with *L. (S.) occulta*. The relations of the group with *L. (Galba) truncatula* are much weaker. From the listed species differs most *Omphiscola glabra*. In respect of the studied characters, the latter is the most isolated species.

Statistical analysis, concerning biological objects, is undoubtedly of auxilliary application/character/use/importance. It enables to put in order, according to the mathematical rules, some/particular/given assemblage of the studied objects .

As well the cladogram, as the diagram of CZEKANOWSKI confirmed the results received from the analysis of the anatomical studies. They contributed to more extensive determination of the hierarchy of similarities, relationships and evolutionary ways of the lymnaeids.

The systematics of the family *Lymnaeidae* presented below is based on the characters of the anatomical structure of the reproductive organs and morphology of the shell.

- Family: *Lymnaeidae*
- Genus: *Omphiscola* BECK, 1837
- Species: *Omphiscola glabra* (O. F. MÜLLER, 1774)
- Genus: *Lymnaea* LAMARCK, 1799
- Subgenus: *Galba* SCHRANK, 1803
- Species: *Lymnaea (Galba) truncatula* (O. F. MÜLLER, 1774)
- Subgenus: *Radix* MONTFORT, 1810
- Species: *Lymnaea (Radix) peregra* (O. F. MÜLLER, 1774)
- Species: *Lymnaea (Radix) auricularia* (LINNAEUS, 1758)
- Subgenus: *Myxas* SOWERBY, 1822
- Species: *Lymnaea (Myxas) glutinosa* (O. F. MÜLLER, 1774)
- Subgenus: *Stagnicola* LEACH, 1830
- Species: *Lymnaea (Stagnicola) palustris* (O. F. MÜLLER, 1774)
- Species: *Lymnaea (Stagnicola) turricula* (HELD, 1836)
- Species: *Lymnaea (Stagnicola) occulta* (JACKIEWICZ, 1959)
- Subgenus: *Lymnaea s. str.*
- Species: *Lymnaea (Lymnaea) vulnerata* KÜSTER, 1862
- Species: *Lymnaea (Lymnaea) corvus* (GMELIN, 1788)
- Species: *Lymnaea (Lymnaea) stagnalis* (LINNAEUS, 1758)

Table 1.

Main anatomical characters of the genera *Omphiscola* and *Lymnaea*

Character	Genus	
	<i>Omphiscola</i> 1	<i>Lymnaea</i> 2
Number of folds of the praeputium	absent	present
Papillar fold (velum)	elongated	circular
Lumen of the papilla (sarcobelum)	yes	no
Proximal part of prostate as broad as distal one	absent	1 - many

Table 2.

Main anatomical characters of the subgenera of the genus *Lymnaea*

Character	Subgenus				
	<i>Galba</i>	<i>Radix</i>	<i>Myxas</i>	<i>Stagnicola</i>	<i>Lymnaea s.str.</i>
Penis short, smooth	+	-	-	-	-
Penis long, narrow	-	+	+	-	-
Penis long and thick, with or without narrowing, or very long	-	-	-	+	-
Penis short with ring-like swelling	-	-	-	-	+

Table 3.

Shell characters of the genera and subgenera of the family *Lymnaeidae*

Taxon	Characters
Genus <i>Omphiscola</i>	Shell roller-shaped-turritiform, aperture small
Genus <i>Lymnaea</i>	Shell oval, circularly-oval, ovally-turritiform or ovally-conical, aperture big or very big
Subgenus <i>Galba</i>	Shell small, ovally-turritiform, whorls strongly convex, "stepped", aperture almost as high as the spire
Subgenus <i>Radix</i>	Shell oval or circularly-oval with low spire, body whorl strongly swollen, aperture very big
Subgenus <i>Myxas</i>	Shell nearly circular with very low spire, strongly developed mantle covers the shell from its outside, aperture very big
Subgenus <i>Stagnicola</i>	Shell big, ovally-turritiform, whorls strongly convex, aperture almost as high as the spire
Subgenus <i>Lymnaea s.str.</i>	Shell ovally-conical, whorls slightly convex, aperture as high as the spire or higher

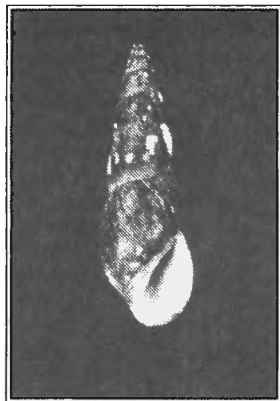
Table 4.

Characteristic anatomical features of the species of the family *Lymnaeidae*

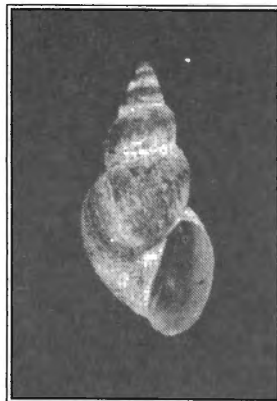
1. <i>Omphiscola glabra</i>	Praeputium with 1 fold, prostate with no fold
2. <i>Lymnaea (Galba) truncatula</i>	Praeputium with 2 small folds, prostate with 1 small fold
3. <i>Lymnaea (Radix) peregra</i>	Spermatheca with no duct or with very short duct
4. <i>Lymnaea (Radix) auricularia</i>	Duct of spermatheca long
5. <i>Lymnaea (Myxas) glutinosa</i>	Mantle covers shell from the outside
6. <i>Lymnaea (Stagnicola) palustris</i>	Penis as long as praeputium
7. <i>Lymnaea (Stagnicola) turricula</i>	Penis 3 - 5 times longer than praeputium
8. <i>Lymnaea (Stagnicola) occulta</i>	Penis as long as praeputium and with narrowing
9. <i>Lymnaea (Lymnaea) vulnerata</i>	Prostate with 2 folds
10. <i>Lymnaea (Lymnaea) corvus</i>	Prostate with numerous thick folds
11. <i>Lymnaea (Lymnaea) stagnalis</i>	Prostate with very numerous and small folds

Tables 5 - 8. Classification and relationships within the European *Lymnaeidae*

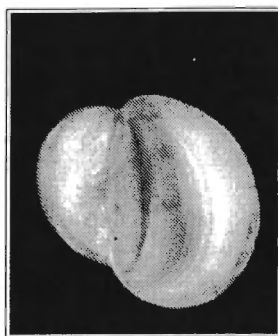
GEYER 1927			Table 5.
Genus	Subgenus	Species	
<i>Limnaea</i>		<i>L. stagnalis</i>	
		<i>R. auricularia</i>	
<i>Radix</i>		<i>R. ampla</i>	
		<i>R. ovata</i>	
		<i>R. peregra</i>	
<i>Stagnicola</i>		<i>S. palustris</i>	
<i>Leptolimnaea</i>		<i>L. glabra</i>	
<i>Galba</i>		<i>G. truncatula</i>	
<i>Amphipeplea</i>		<i>A. glutinosa</i>	
EHRMANN 1937			Table 6.
Genus	Subgenus	Species	
<i>Lymnaea</i>		<i>L. stagnalis</i>	
		<i>S. (S.) palustris</i>	
<i>Stagnicola</i>	<i>Stagnicola s. str.</i>	<i>S. (O.) glabra</i>	
	<i>Omphiscola</i>	<i>R. auricularia</i>	
		<i>R. ovata subsp. ampla</i>	
<i>Radix</i>		<i>R. peregra</i>	
		<i>R. tumida</i>	
		<i>R. lagotis</i>	
		<i>R. ovata</i>	
<i>Galba</i>		<i>G. truncatula</i>	
<i>Myxas</i>		<i>M. glutinosa</i>	
HUBENDICK 1951			Table 7.
Genus	Subgenus	Species	
		<i>L. stagnalis</i>	
		<i>L. auricularia</i>	
		<i>L. peregra</i>	
<i>Lymnaea</i>		<i>L. ovata</i>	
		<i>L. palustris</i>	
		<i>L. truncatula</i>	
		<i>L. glabra</i>	
		<i>L. glutinosa</i>	
JACKIEWICZ			Table 8.
Genus	Subgenus	Species	
<i>Omphiscola</i>		<i>O. glabra</i>	
	<i>Galba</i>	<i>L. (G.) truncatula</i>	
	<i>Radix</i>	<i>L. (R.) peregra</i>	
		<i>L. (R.) auricularia</i>	
<i>Lymnaea</i>	<i>Myxas</i>	<i>L. (M.) glutinosa</i>	
		<i>L. (S.) palustris</i>	
	<i>Stagnicola</i>	<i>L. (S.) turricula</i>	
		<i>L. (S.) occulta</i>	
		<i>L. (L.) vulnerata</i>	
	<i>Lymnaea s.str.</i>	<i>L. (L.) corvus</i>	
		<i>L. (L.) stagnalis</i>	



1



2



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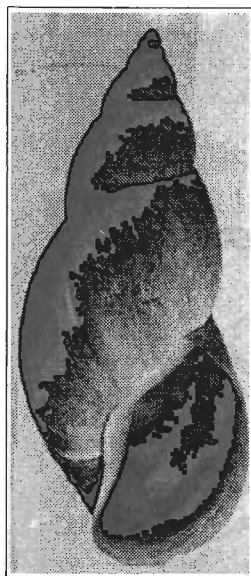


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4

Plate I. Shell of lymnaeids: 1 - *Omphiscola glabra*, 2 - *Lymnaea (Galba) truncatula*, 3 - *L. (Radix) peregra*, 4 - *L. (R.) auricularia*, 5 - *L. (Myxas) glutinosa*. The shells are approximately twice bigger than their natural size (after JACKIEWICZ 1989 - in part)



6



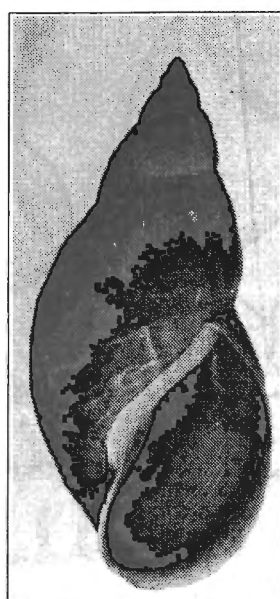
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Plate II. Shell of lymnaeids: 6 - *Lymnaea (Stagnicola) palustris*, 7 - *L. (S.) occulta*, 8 - *L. (S.) turricula*, 9 - *L. (Lymnaea) vulnerata*, 10 - *L. (L.) corvus*, 11 - *L. (L.) stagnalis*. The shells are approximately 2 - 3 times bigger than their natural size (after JACKIEWICZ 1959 - in part)

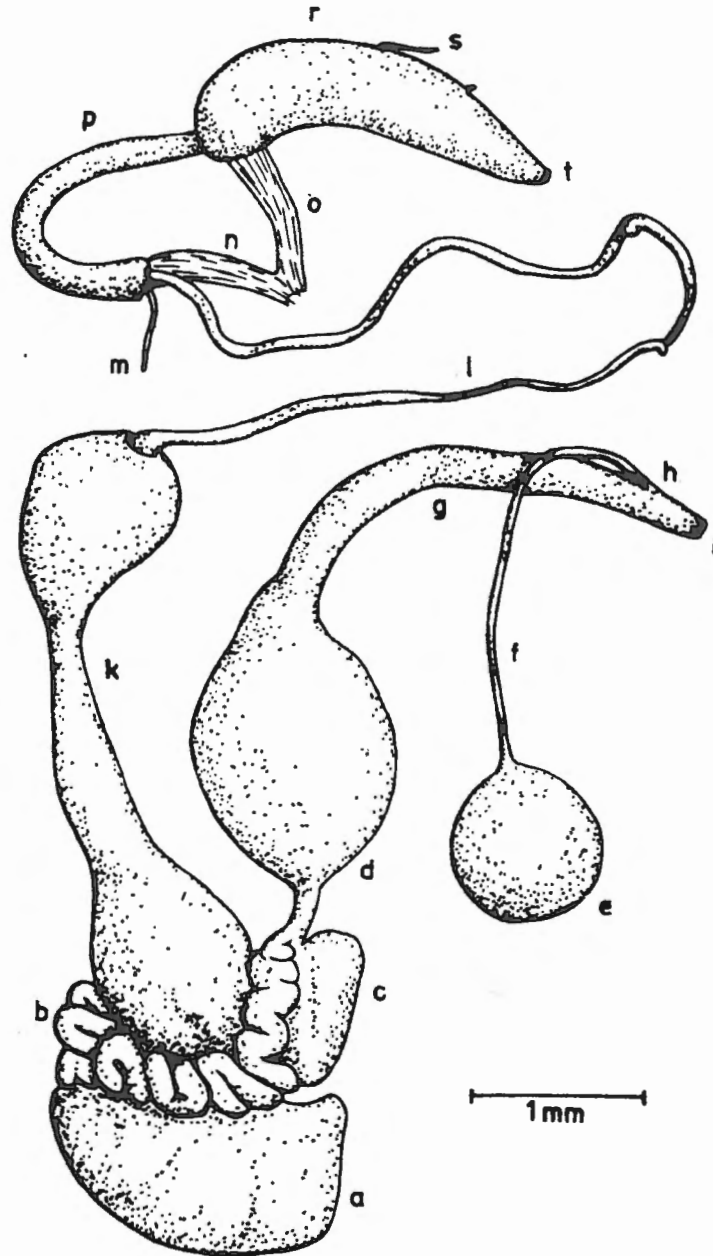


Fig. 1. Reproductive organs of *Omphiscola glabra*: a - albuminoid gland, b - uterus, c - nidamental gland, d - pyriform body, e - spermatheca, f - duct of spermatheca, g - oviduct, h - vagina, i - opening of female reproductive organs, k - prostate, l - vas deferens, m - nerve of penis, n - retractor of penis sheath, o - retractor of praeputium, p - penis sheath, r - praeputium, s - protractor, t - opening of male reproductive organs

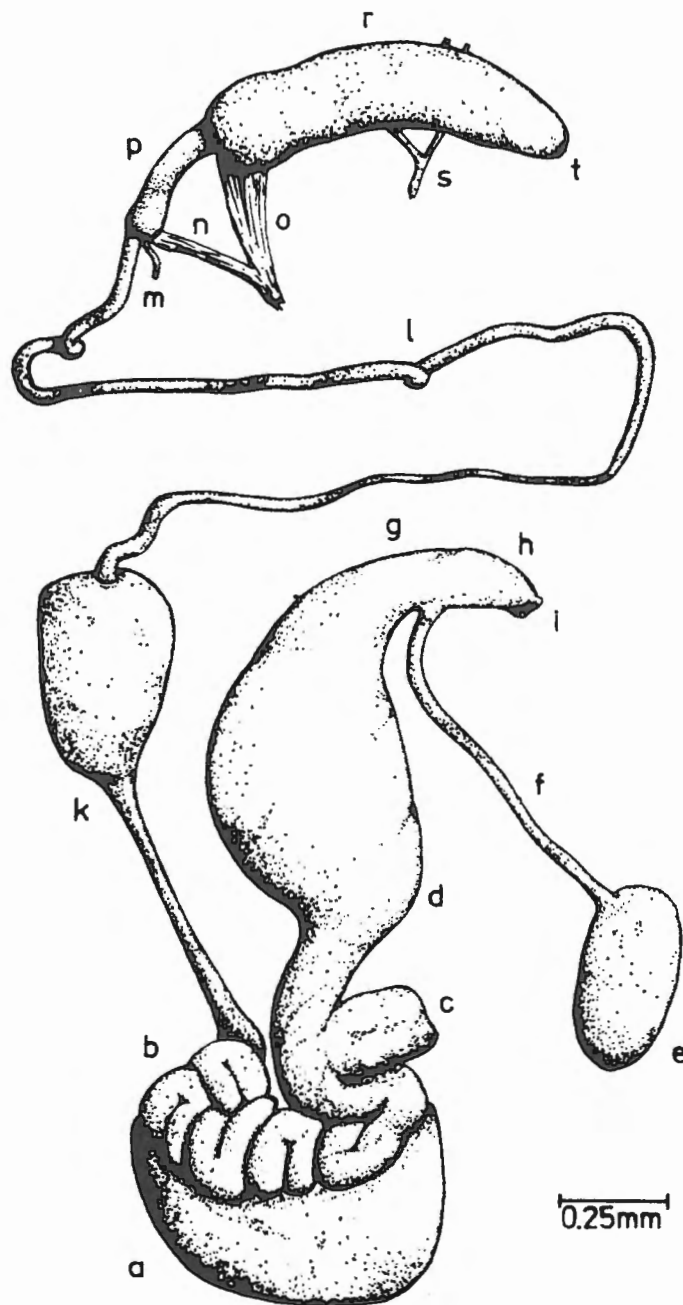


Fig. 2. Reproductive organs of *Lymnaea (Galba) truncatula* (lettering as in Fig. 1)

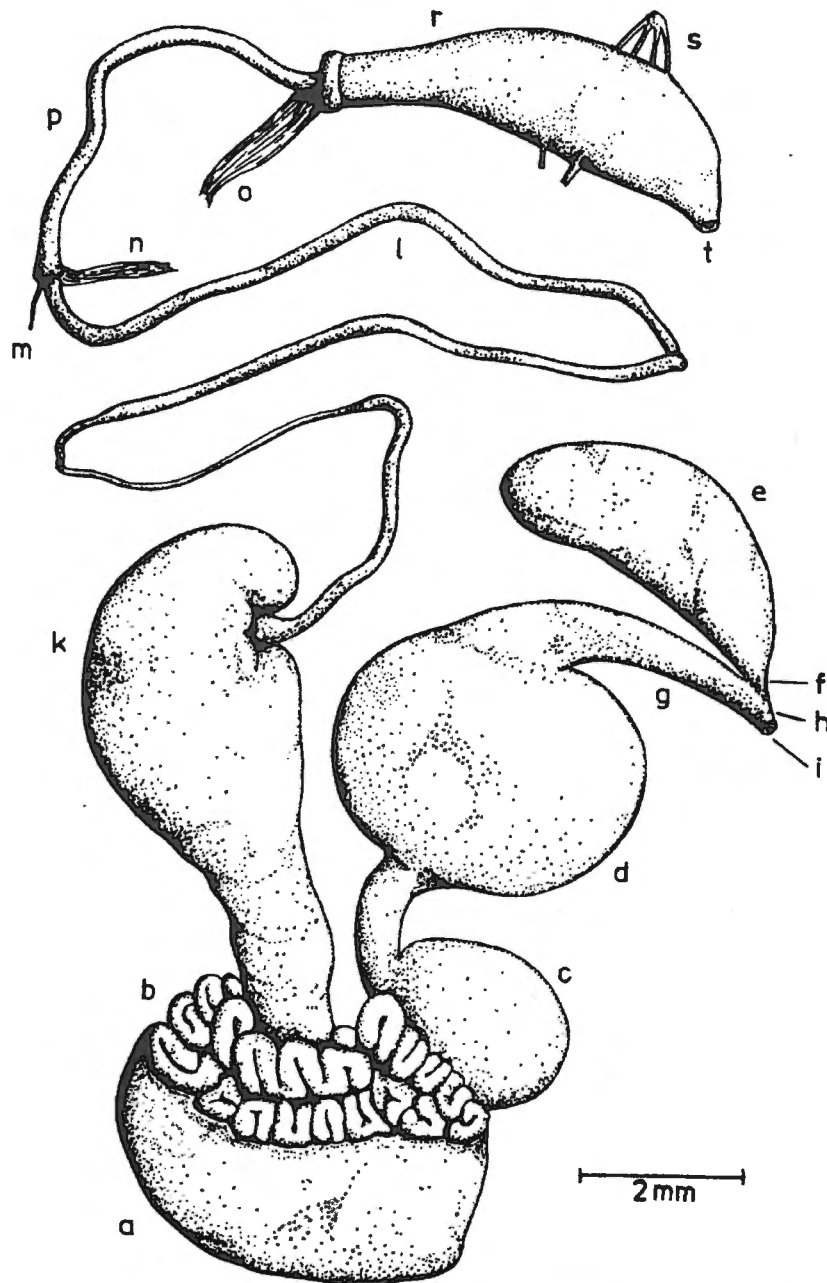


Fig. 3. Reproductive organs of *Lymnaea (Radix) peregra* (lettering as in Fig. 1)

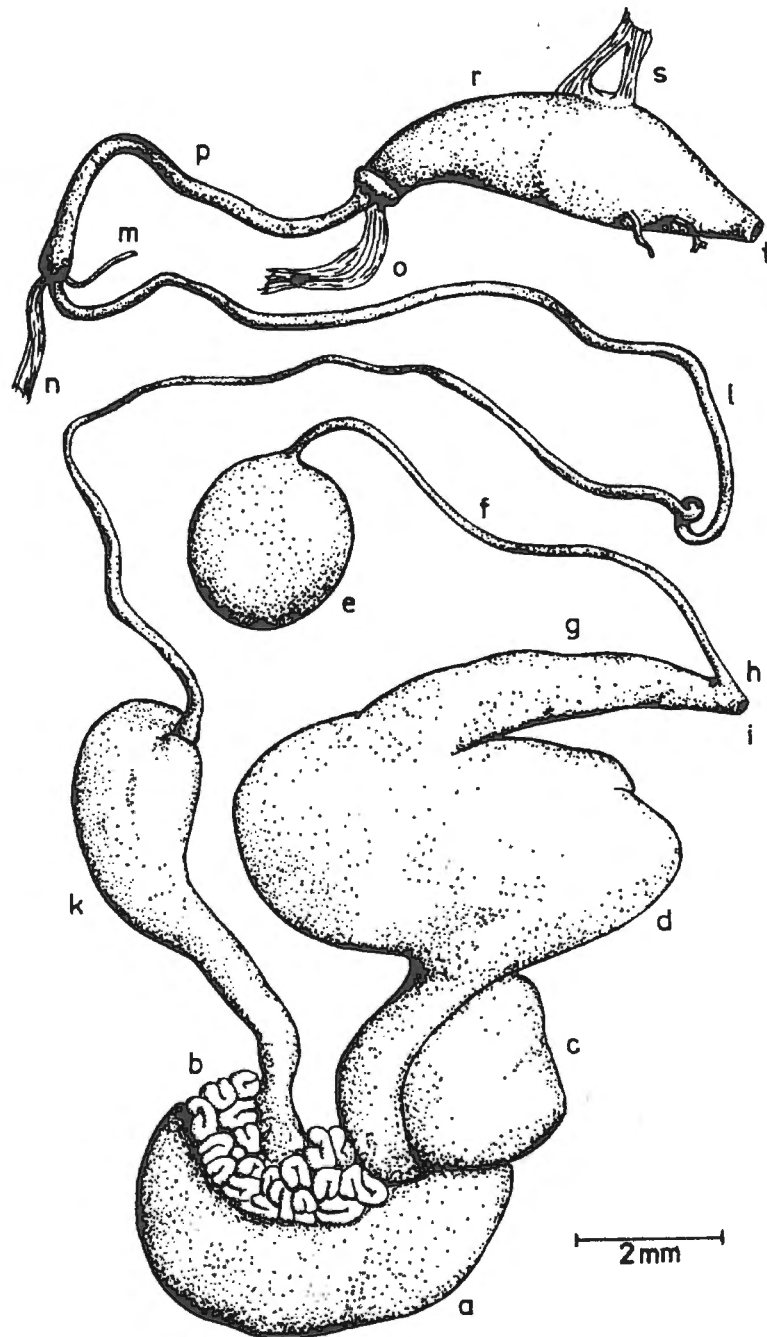


Fig. 4. Reproductive organs of *Lymnaea (Radix) auricularia* (lettering as in Fig. 1)

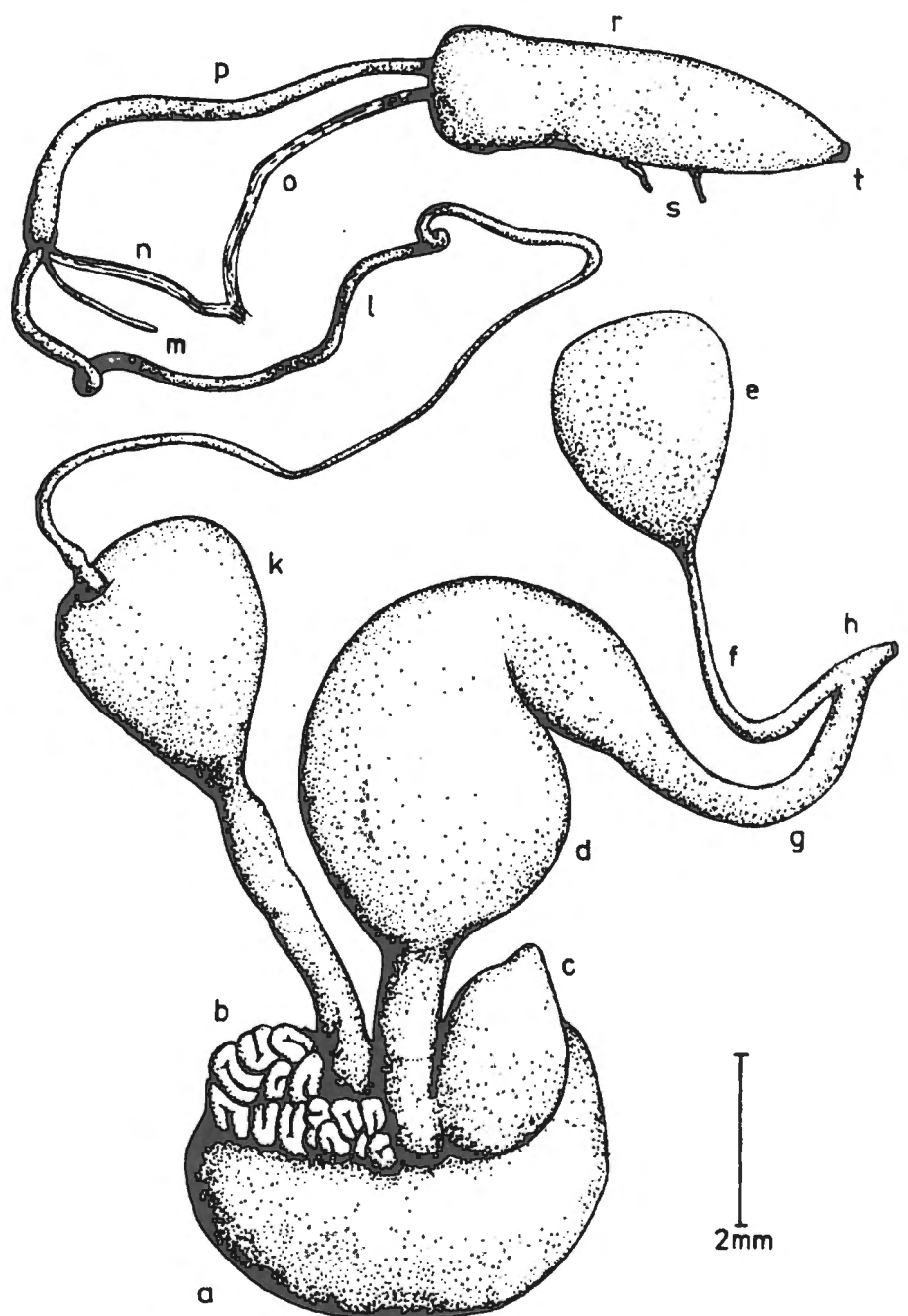


Fig. 5. Reproductive organs of *Lymnaea (Myxas) glutinosa* (lettering as in Fig. 1)

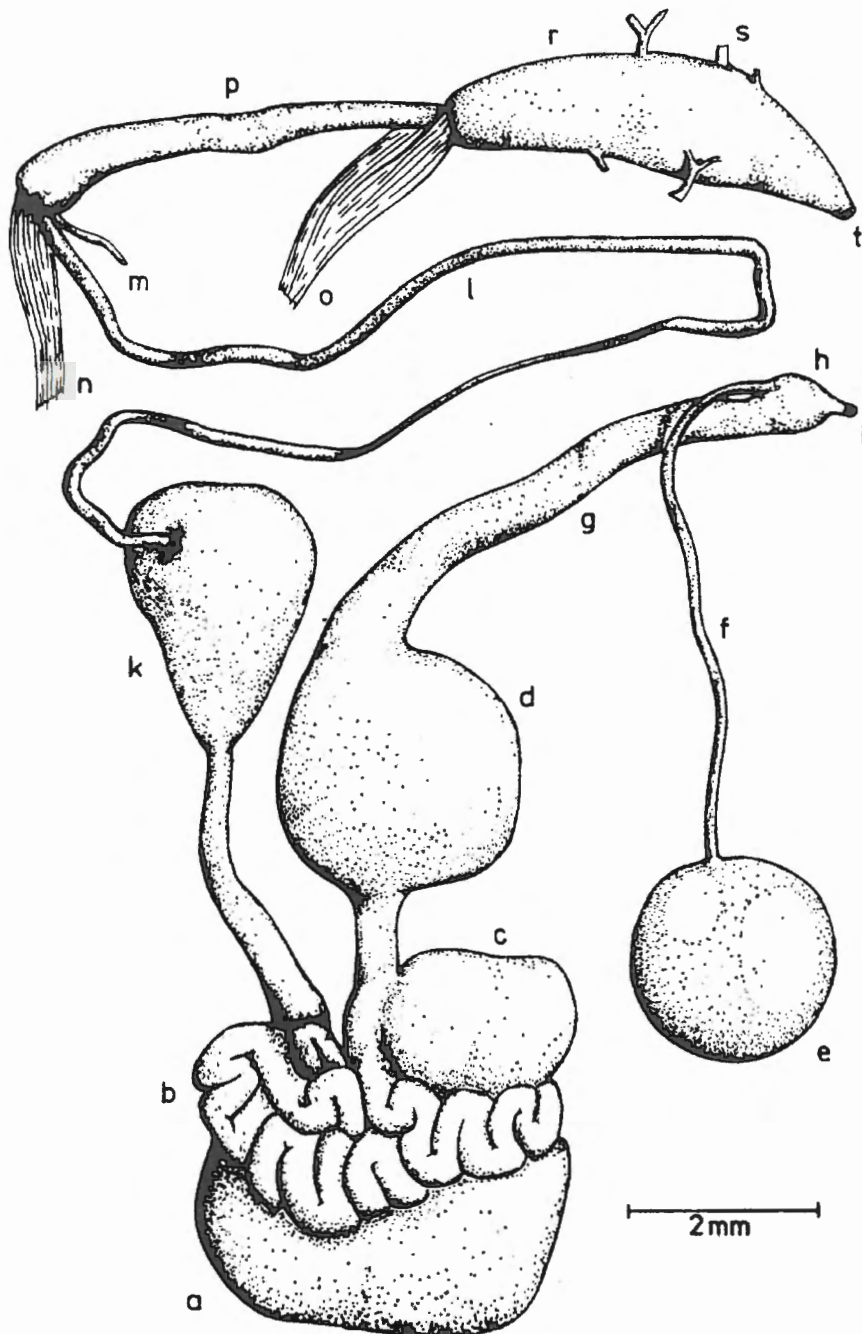


Fig. 6. Reproductive organs of *Lymnaea (Stagnicola) palustris* (lettering as in Fig. 1)

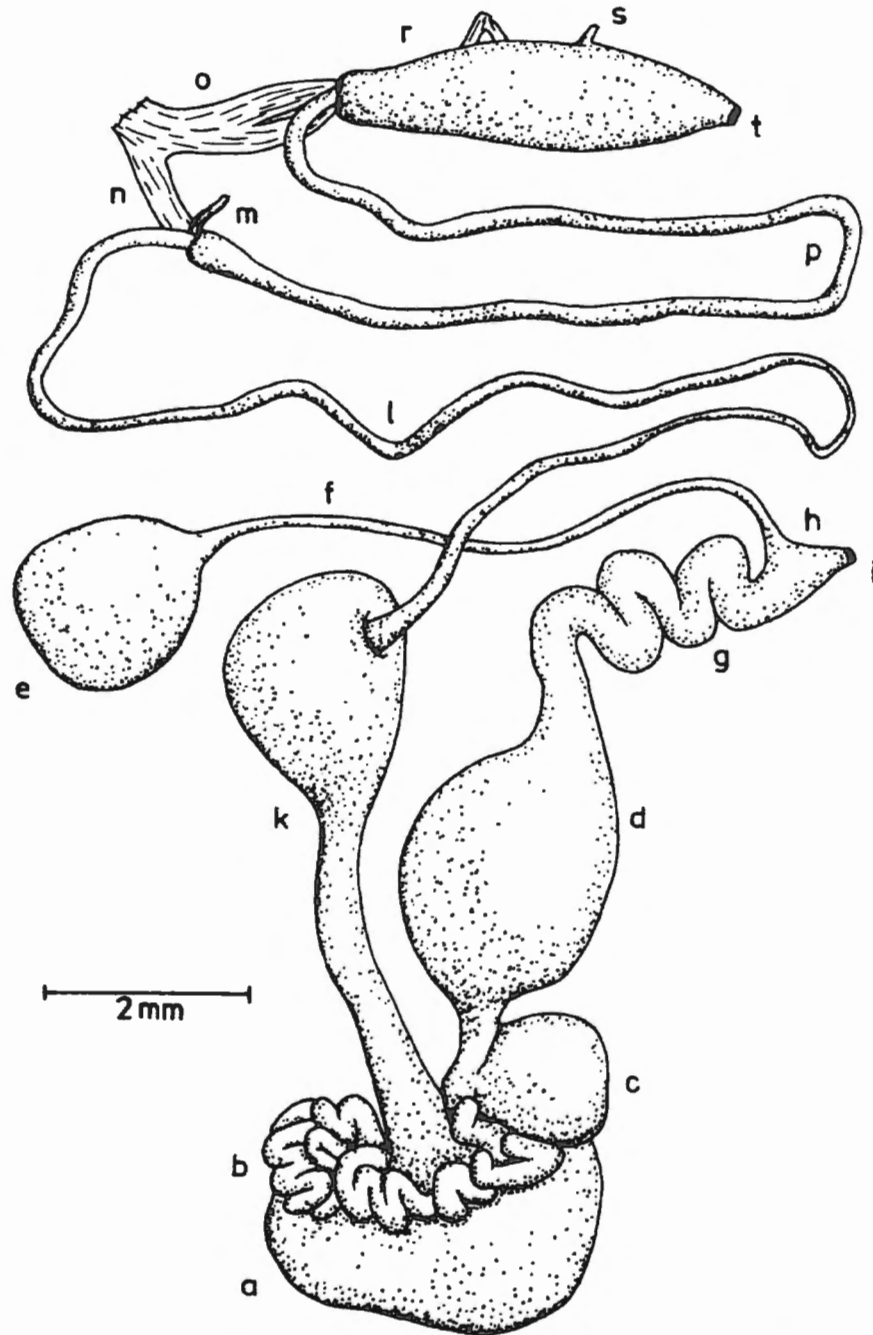


Fig. 7. Reproductive organs of *Lymnaea (Stagnicola) turricula* (lettering as in Fig. 1)

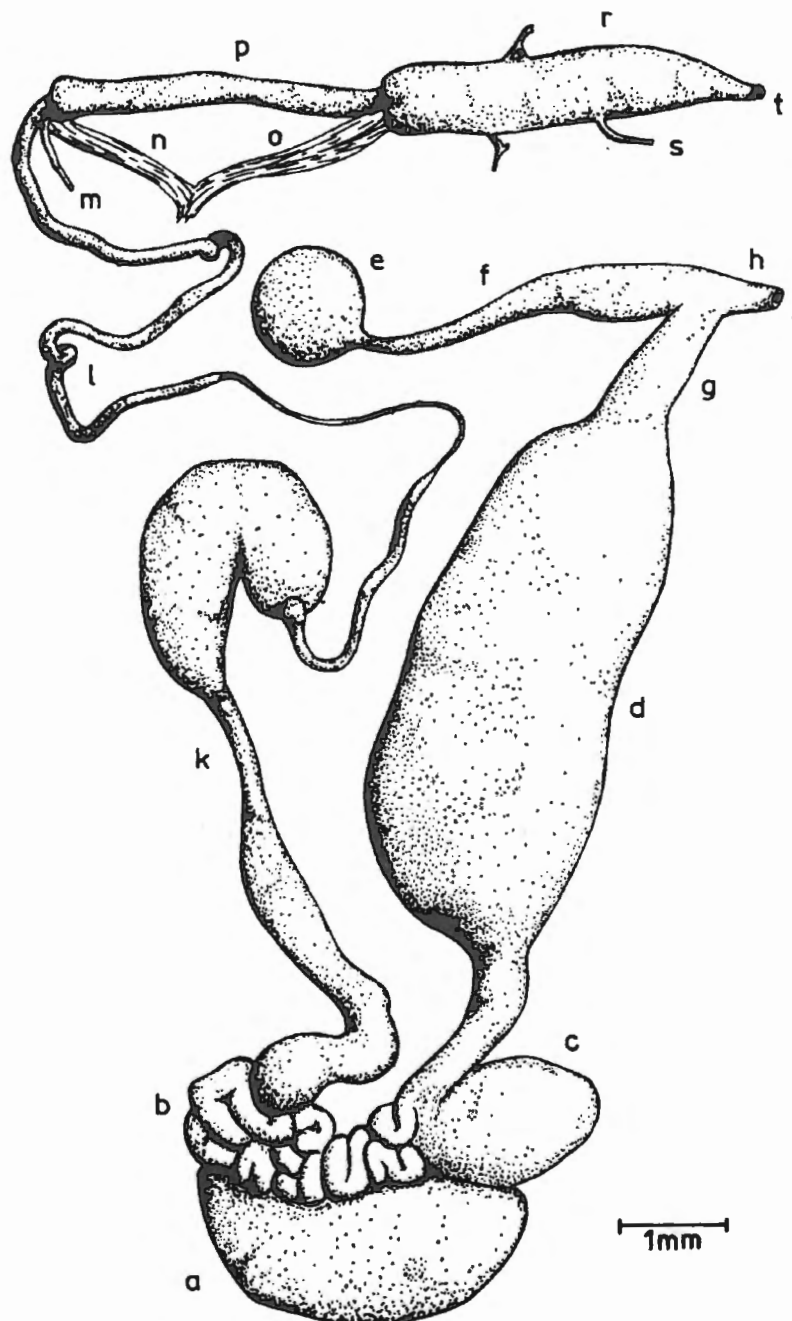


Fig. 8. Reproductive organs of *Lymnaea (Stagnicola) occulta* (lettering as in Fig. 1)

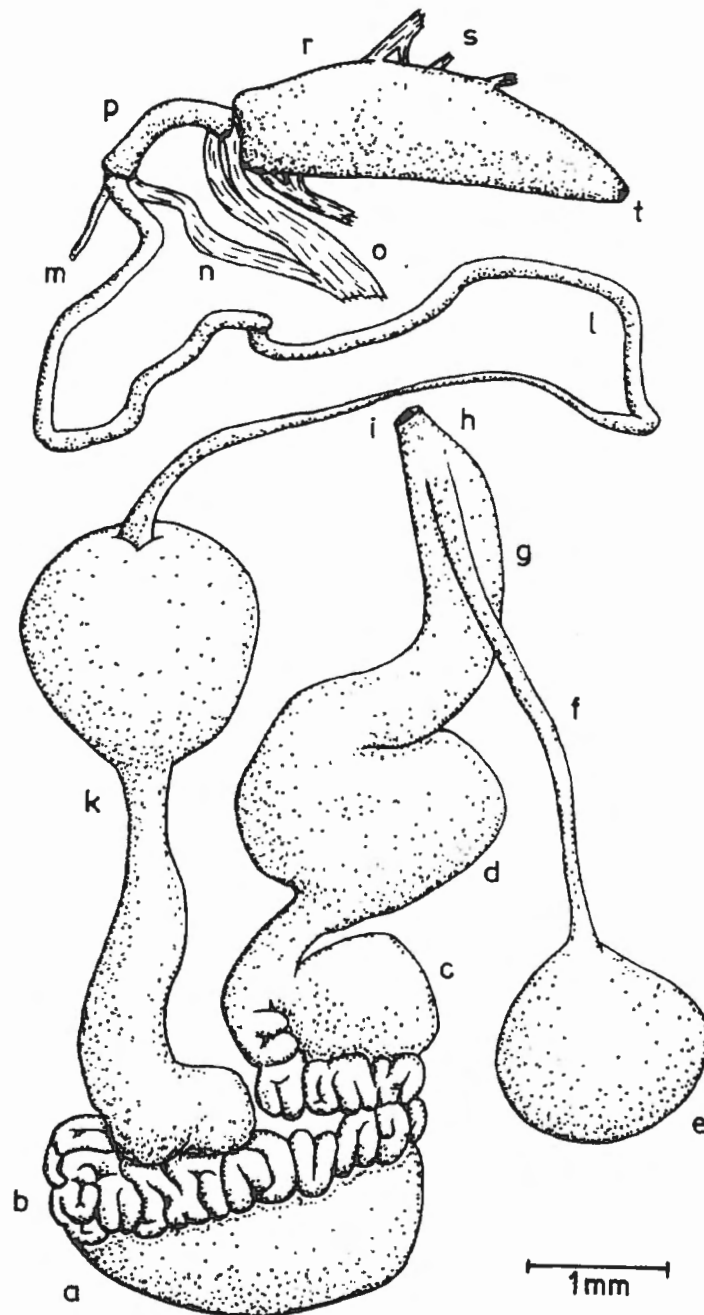


Fig. 9. Reproductive organs of *Lymnaea (Lymnaea) vulnerata* (lettering as in Fig. 1)

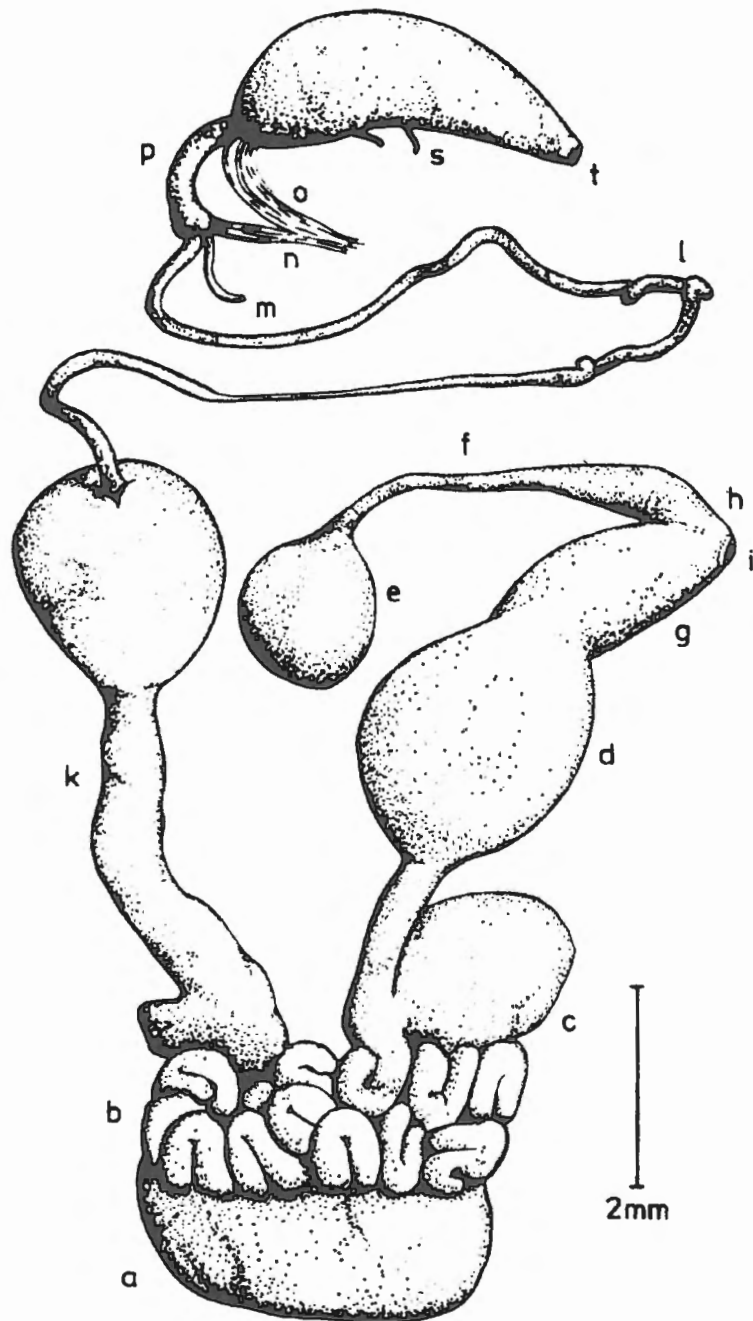


Fig. 10. Reproductive organs of *Lymnaea (Lymnaea) corvus* (lettering as in Fig. 1)

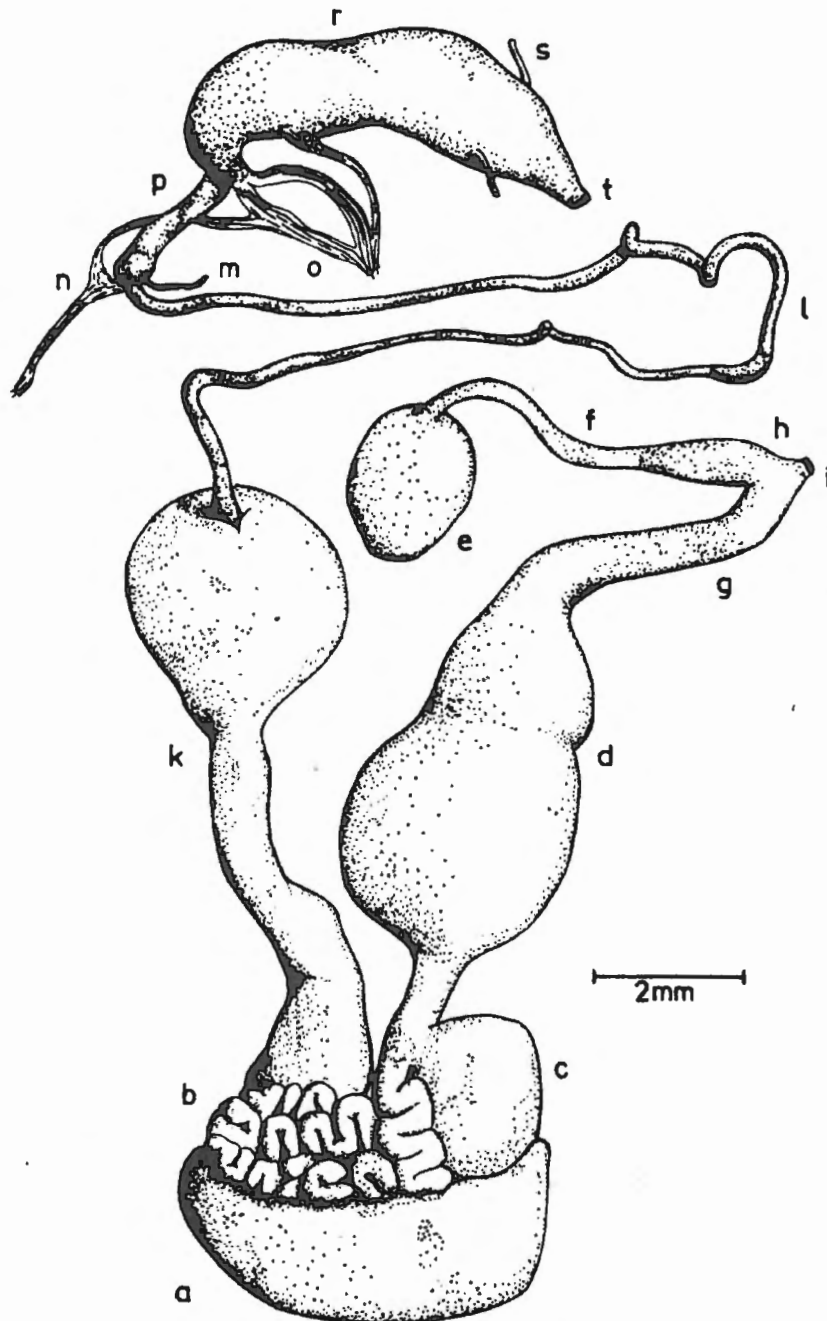
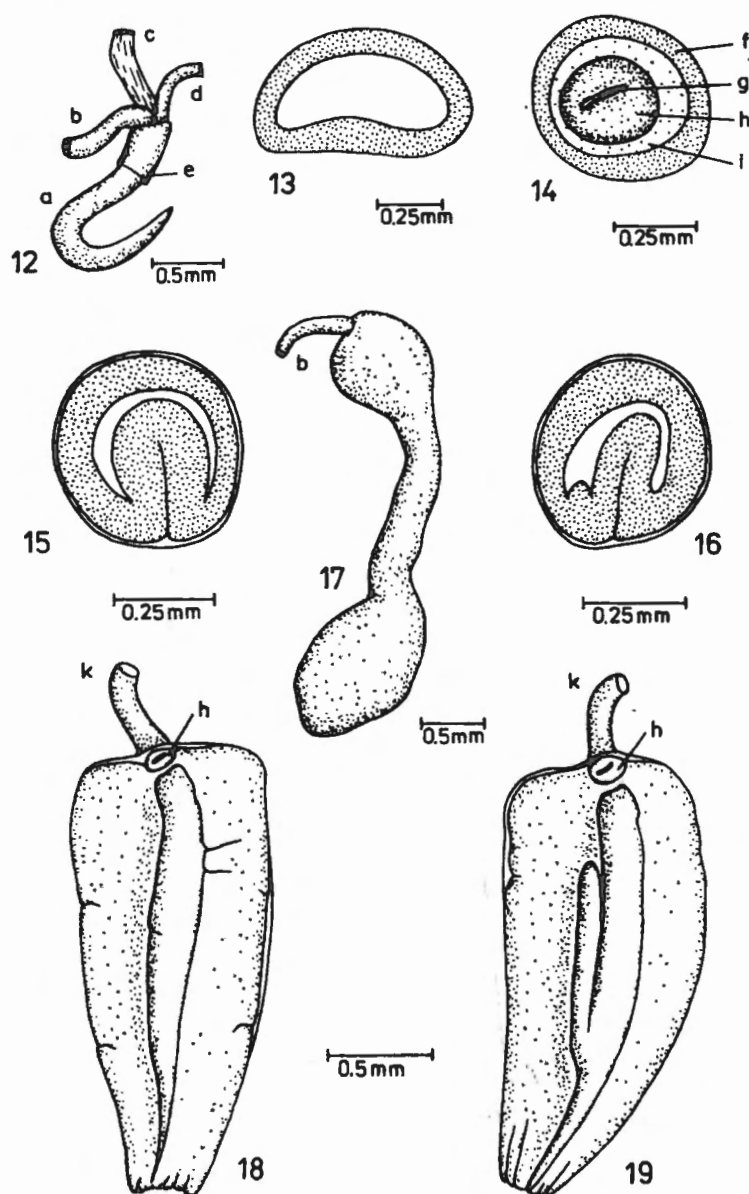
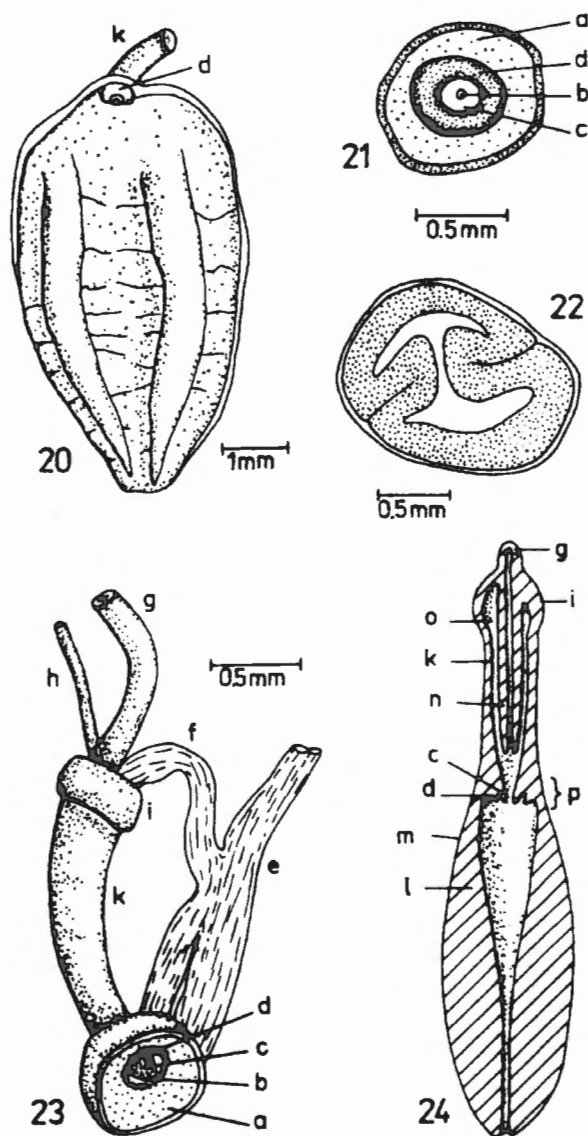


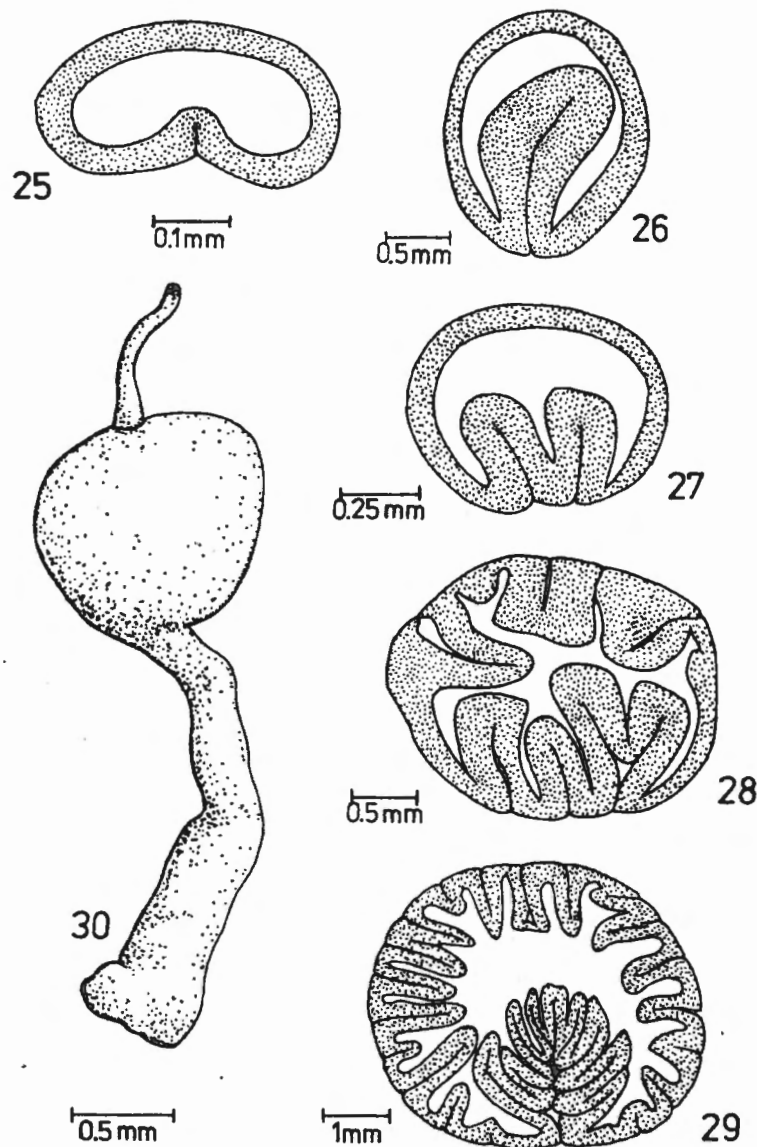
Fig. 11. Reproductive organs of *Lymnaea* (*Lymnaea*) *stagnalis* (lettering as in Fig. 1)



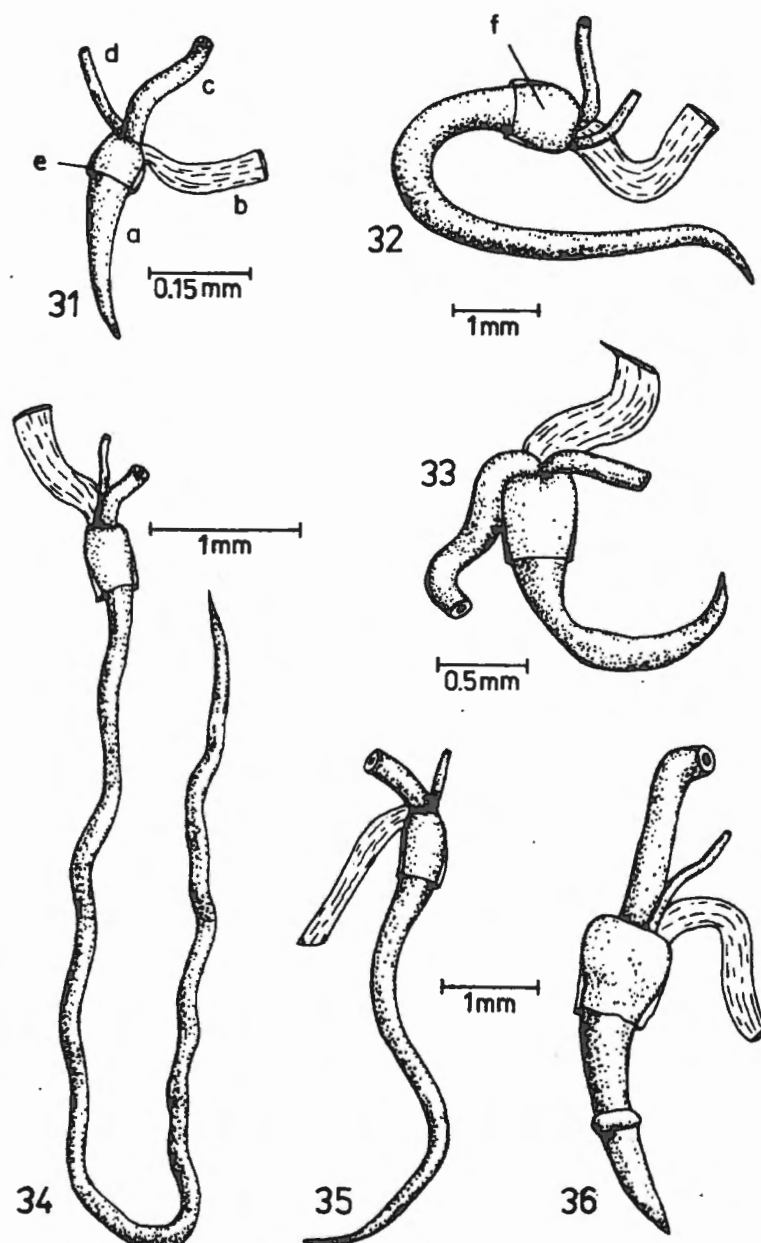
Figs 12 - 19. Characteristic features of genus *Omphiscola*: 12 - penis; 13 - transversal section of prostate; 14 - bulbous termination of praeputium seen from its lumen; 15 - 16 - transversal section of praeputium; 17 - prostate; 18 - 19 - praeputium, inside longitudinal folds are visible: a - penis, b - vas deferens, c - retractor of the penis sheath, d - nerve of the penis, e - wall of the cut-off penis sheath, f - wall of the cut-off praeputium, g - lumen of sarcobelum, h - sarcobelum, i - lumen of praeputium, k - part of penis sheath (after JACKIEWICZ 1984, 1988 and 1989)



Figs 20 - 24. Characteristic features of genus *Lymnaea*: 20 - praeputium, inside two longitudinal folds are visible; 21 - bulbous termination of praeputium seen from above; 22 - transversal section of praeputium; 23 - bulbous termination of praeputium, lateral view; 24 - schematic longitudinal section through penis sheath and praeputium: a - wall of the transversal cut praeputium (from inside), b - lumen of sarcobelum, c - sarcobelum, d - velum, e - retractor of praeputium, f - retractor of penis sheath, g - vas deferens, h - nerve of penis, i - bulbous termination of penis sheath, k - penis sheath, l - longitudinal folds, m - praeputium, n - penis, o - glandular cavity, p - bulbous termination of praeputium (after JACKIEWICZ 1959, 1984)



Figs 25 - 30. Characteristic features of genus *Lymnaea*: prostate and its transversal section: 25 - *L. (Galba) truncatula*, 26 - *L. (Stagnicola) palustris* [the same type of the prostate structure is characteristic of: *L. (Radix) peregra*, *L. (R.) auricularia*, *L. (Myxas) glutinosa*, *L. (Stagnicola) turricula* and *L. (S.) occulta*], 27 - *L. (Lymnaea) vulnerata*, 28 - *L. (L.) corvus*, 29 - *L. (L.) stagnalis*, 30 - *L. (L.) corvus* (similar habitus of the prostate is found in the other species of the genus *Lymnaea*) (after JACKIEWICZ 1959 and 1988, in part)



Figs 31 - 36. Characteristic features of subgenera: penis: 31 - *Galba*, 32 - 34 - *Stagnicola*, 35 - *Radix*, *Myxas*, 36 - *Lymnaea s. str.*: a - penis, b - retractor of penis sheath, c - vas deferens, d - nerve of penis, e - wall of the transversal cut penis sheath, f - bulbous termination of penis sheath (after JACKIEWICZ 1988 - in part)

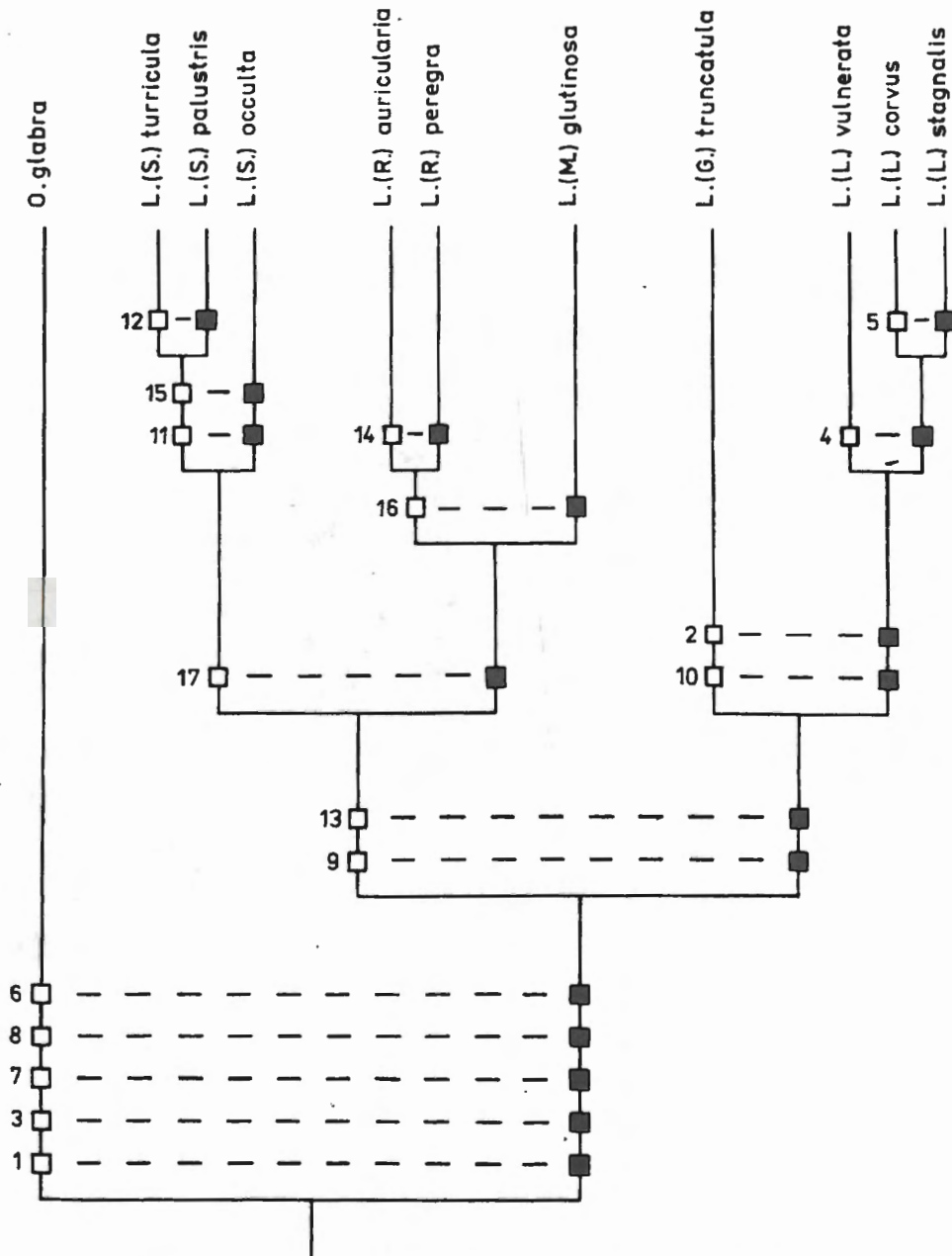


Fig. 37. Cladogram of *Lymnea* phylogenesis. Plesiomorphic character states marked by white squares, apomorphic character states marked by black squares. Explanations of numbers (characters) in the text

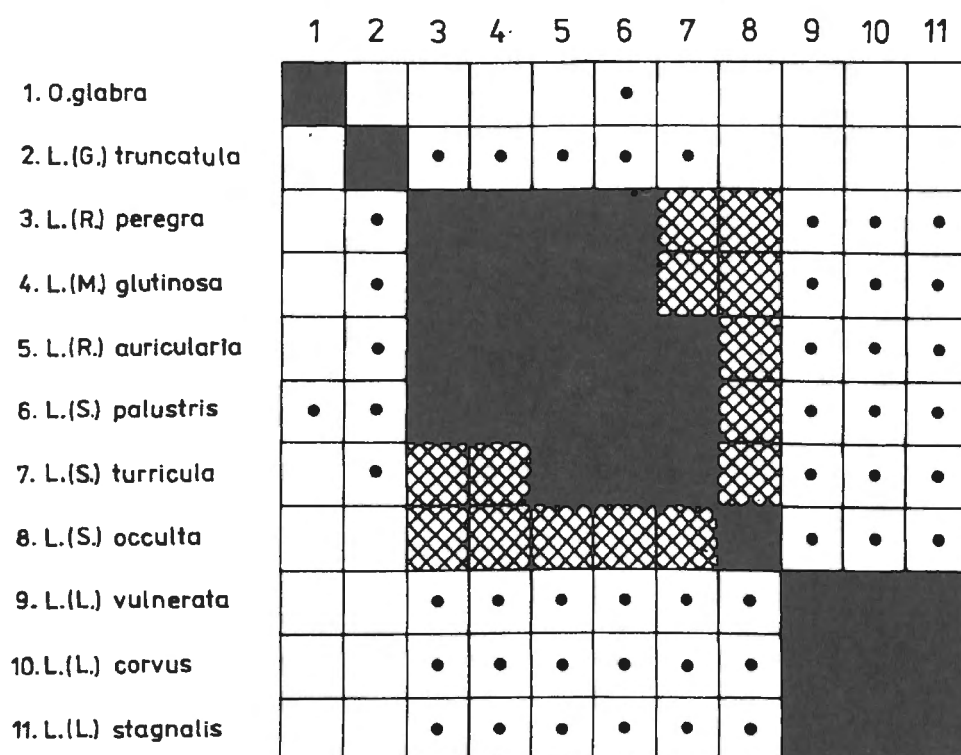


Fig. 38. Diagram of similarity of anatomical characters within the family *Lymnaeidae*: solid square - high degree of similarity, 32 or 34 common characters (89% - 100% similarity); shaded square - great similarity, 28 - 31 common characters (over 77% similarity); dots - medium similarity, 24 - 27 common characters (over 67% similarity); blank square - low degree of similarity, less than 23 common characters (66% or less similarity)

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