FOLIA MALACOLOGICA
Vol. 7(4): 197–240
ISSN 1506-7629
The Association of Polish Malacologists
& Faculty of Biology, Adam Mickiewicz University
Poznań 1999

HELIX LUTESCENS ROSSMÄSSLER, 1837 (GASTROPODA: PULMONATA: HELICIDAE) – ITS STRUCTURE, BIOLOGY AND ECOLOGY

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ABSTRACT: *Helix lutescens* Rossmässler, 1837 is a xerothermophilous species. It reaches its NW distribution border in SE Poland. The studies, carried out in 1990–1997, involved the distribution of *H. lutescens* in Poland, its biology and ecology. Besides, shell structure and internal organs were studied, with special reference to differences between *H. lutescens* and the related *H. pomatia* L. In *H. lutescens* the shell is roundish-conical, of a yellowish-white colour and much smaller than that of *H. pomatia*. The body is greyish and covered with numerous wrinkles and grooves; fine, whitish granules are located in the grooves, especially in those that form two delicate light streaks along the darker back of the animal; these streaks are characteristic of the species. The reproductive system of *H. lutescens* is of a structure similar to that in *H. pomatia*, but the duct of the gametolythic gland never bears a diverticle while flagellum, epiphallus and penis in adults are pigmented. The diurnal activity of *H. lutescens* varies seasonally, depending on environmental factors (air temperature and relative humidity in ground layer, and substratum humidity – dew point). The reproductive activity reaches its peak in May and June. Courtship and copulation are in accordance with the typical helicid pattern. The copulation lasts ca. 15 mins, and the entire mating process takes over 3 hrs. Eggs are laid in nests dug in the soil, the mean number of eggs per nest being 35. In two weeks young hatch and remain in the nest for ca. 16 days. The abundance and density of three age classes in a selected population of *H. lutescens* have been estimated on a permanent sampling plot, using marking-release-recapture method, with JOLLY-SEBER'S model for an open population. The results made it possible to trace seasonal changes in the abundance within the whole population. In Poland *H. lutescens*, because of its insular occurrence and the threat resulting from confusion with the edible *H. pomatia*, is a protected species.

KEY WORDS: *Helix lutescens*, Helicidae, land snails, distribution, reproduction, biology, ecology, population dynamics

CONTENTS

INTRODUCTION

Contrary to the common *Helix pomatia* Linnaeus, 1758, *H. lutescens* Rossmässler, 1837 was rarely an object of malacologists' interest. Till now it is among the least studied species in the fauna of Poland. Information on its occurrence in the country is contained in fairly numerous publications (e.g. POLIŃSKI 1917, 1919, 1927, GROCHMALICKI 1932, CZUBIŃSKI & URBAŃSKI 1933, URBAŃSKI 1937, 1947, 1948, 1957, 1964, 1973, 1977, RIEDEL 1954, 1988, BARGA-WIĘCŁAWSKA 1989, 1997, PIECHOCKI 1990, 1991, KORALEWSKA-BATURA 1993c), but its morphology and anatomy have been only poorly studied. Basic information on the species can be found in general publications dealing with European malacofauna, e.g. EHRMANN (1933), LIKHAREV & RAMMELMEIER (1952), GROSSU (1955, 1983), LOŽEK (1956, 1964), KERNEY et al. (1983), LISICKÝ (1991), and in some papers dealing with the gastropod fauna of Poland (BĄKOWSKI & ŁOMNICKI 1892, URBAŃSKI 1957). ROSSMÄSSLER (1837), based on few specimens, described the shell, radula and reproductive system, the latter in very general terms. POLIŃSKI (1924) discussed, in a cursory way, the structure of its circulatory system, and SHILEYKO (1978) gave a shell description and photograph. Recently, KORALEWSKA-BATURA (1993a, b, 1994a, 1997a) has studied shell biometrics in *H. lutescens*, its love dart, postembryonic development of the reproductive system and lung structure; the author has analysed the structure of radula, on the background of other helicid species (KORA-

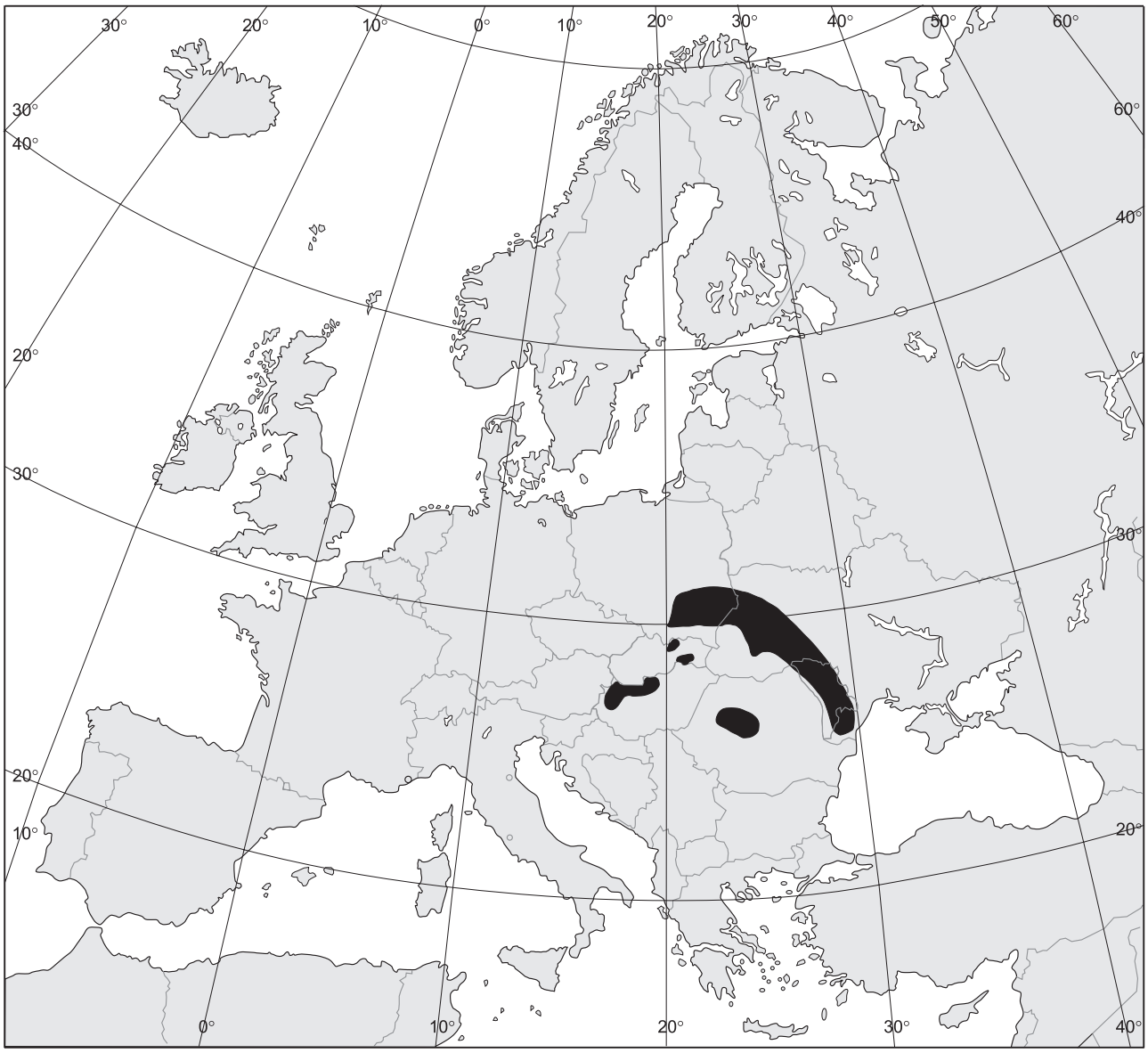


Fig. 1. Distribution of *H. lutescens* in Europe

LEWSKA-BATURA 1994b). A sinistral specimen of this species has also been described (KORALEWSKA-BATURA 1997b).

H. lutescens is a xero-thermophilous species. It inhabits localities of steppe character, dry shrubs, grasslands, sunny slopes, especially on calcareous substratum. It is very often found also in gardens and cemeteries where it lives among ruderal vegetation of sunny places, close to fences or walls of old buildings.

Zoogeographically, *H. lutescens* is a Dak-Podolian species (Fig. 1). POLIŃSKI (1919) reports that it "reaches from its Podolian motherland to the northern fringes of the Lublin and Małopolska uplands". According to URBAŃSKI (1948), the dry and rather warm Subboreal period affected favourably the dispersal of south-eastern, often xero-thermophilous, species. The presence of *H. lutescens* in south-eastern Poland would testify to its being a postglacial pseudorelict. Its distribution range is divided in two parts by the Carpathian range: a south-western part, including Spisz and Slovakian Karst, northern and western Hungary and the plains of inner Transylvania, and a north-eastern part comprising Moldavia, Besarabia, Podolia and southern uplands of Poland (RIEDEL 1988). According to the latter author *H. lutescens* is probably a receding species in Poland.

The very scanty knowledge of *H. lutescens* has induced me to attempt a more detailed and more extensive study, combined with summarizing the existing literature data with a view of producing a monograph of this species. My own studies included faunistic field survey of areas where the snail had been observed or its occurrence seemed likely, observations on the activity of adult individuals, their reproduction and population studies, as well as anatomical-histological studies in which special attention was paid to the reproductive and alimentary systems. The structure of the remaining systems, which mostly corresponds to that found in other members of the genus *Helix* (see below), even if not analysed in detail and based partly on literature data, was discussed for the sake of completness of this monograph. Attention was focused on the shell morphology and structure; morphology and anatomy of soft parts, including histological structure of the reproductive system; up-dating information on the distribution in Poland; diurnal and seasonal activity; reproductive biology; estimation of abundance and density of particular age classes on a constant study plot; seasonal changes of population density.

STUDY AREA

The faunistic survey included the whole distribution area of *H. lutescens* in Poland – south eastern part of the country i.e. uplands Wyżyna Małopolska and Wyżyna Lubelska, lowland Nizina Sandomierska and the foothills of the Beskid Wschodni mountains.

Behavioural and population studies were carried out on a study plot located in the north-eastern part of the town of Kielce next to Maria Konopnicka street, in the district of Szydłówek (Fig. 2). The habitat was a phytocoenosis of grassland character. The dominant grasses were: *Arrhenatherum elatius* (L.) P. B., *Poa angustifolia* L., *Agropyron repens* (L.) P. B. and *Dactylis glomerata* L. The plant community resembled a tall-herb community because of the abundant presence of *Tanacetum vulgare* L., on the other hand, it also resembled thermophilous xerothermic grassland of the class *Festuca-Brometea*, because of the presence of such species as *Poa compressa* L., *Euphorbia cyparissias* L., *Plantago media* L. and *Salvia verticillata* L. The vegetation was probably formed on an abandoned field, as indicated by the presence of weed the class *Stellarietea mediae*, representing a relict of agrophytocoenosis. Likewise, plants of the class *Artemisietea*, with *Artemisia vulgaris* L., *Cirsium arvense* (L.) Scop. and *Solidago serotina* Ait. indicated a synantropic nature of the syntaxon. The grassland character of the vegetation resulted from a dry, warm, calcium-rich substratum of pH 7.58. Chemical analysis of the soil revealed high quantities of calcium (4.64 mg/g), which favours calciphilous plants. As early as May they form a high and dense cover. The absence of trees results in a lack of shadow, which causes large fluctuations of temperature and air humidity (Figs 3, 4). The soils in Kielce are classified as rendzina formed of slowly eroding Devonian crystalline limestones and dolomites. They are skeletal soils, of a high content of $CaCO_3$ or $CaCO_3 \times MgCO_3$. The study plot is covered by anthropogenic soil, deeply dug and mixed, with an unformed profile.

In the regional division of climatic areas of Poland (OKOŁOWICZ & MARTYN 1979) the area is located in the Świętokrzyski climatic district, which is a part of the Silesian-Małopolska climatic region. Data on selected climatic elements of Kielce during the studies in 1993–1996 were obtained from the IMiGW weather station in Sułków near Kielce. The mean annual temperature is 9.1°C. In the summer, mild effects of continental climate prevail (mean temperature of July 18.7°C), and mild winters (mean temperature of January -2.3°C) testify to the effect of western oceanic climate. The mean annual precipitation in Kielce is 625 mm, with the maximum in August (91.6 mm) and the minimum in February (23.6 mm). Snowfall takes

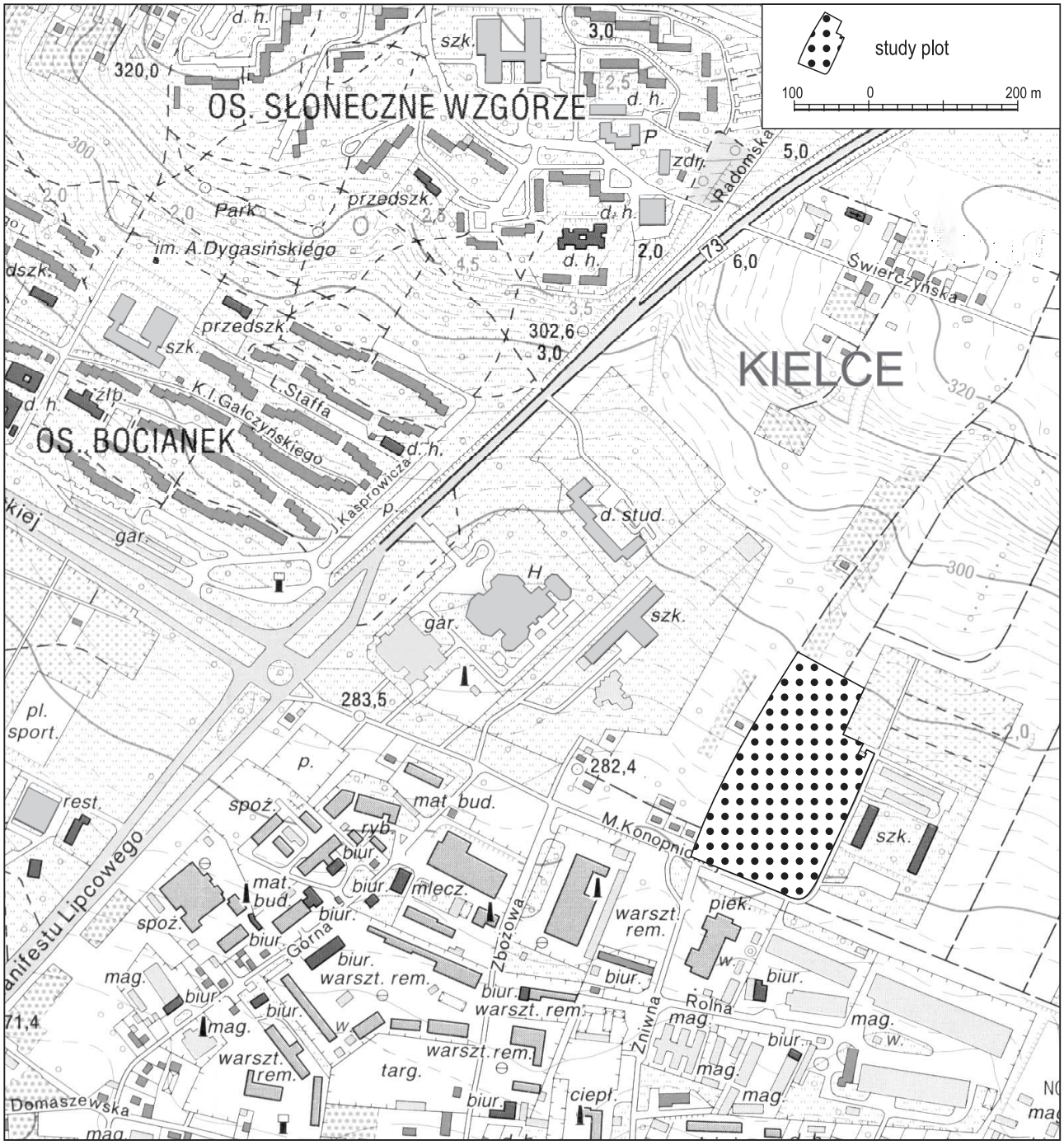


Fig. 2. A fragment of map of the town of Kielce; with study plot indicated

place from November till April, the mean being 68 days per year. Westerly, south-westerly and southerly winds prevail, and to a lesser extent south-easterly. The location of the city, in a wide valley opened to south-east and north-west, results in relatively few calm periods.

MATERIAL AND METHODS

Field and laboratory studies were carried out in 1990–1997. During the first three years I surveyed the current distribution of *H. lutescens* in Poland, special attention being paid to its typical habitats, such

as xerothermic grasslands, shrubs, copses, cemeteries and gardens. The aim was both finding new localities of the species and confirming its earlier records. The field studies involved the vegetation season, from the second half of April till the end of September.

In 1994, the field work involved estimation of abundance of a selected population of *H. lutescens*, and in 1995 – observations of diurnal and seasonal activity of adult individuals in the site in Kielce, described above. Earlier, two separate study plots had been established, which were subject to detailed observations. The first plot was 500 m^2 in area. For practical reasons, I divided it in 20 squares, 5×5 m (25 m^2) each. The squares made it possible to locate all the observed snails more precisely. The other study plot, of 25 m^2, was divided into 25 numbered squares, 1×1 m each. The plots and their component squares were marked with wooden poles or plastic plates stuck in the corners of squares.

The abundance of snails was studied from half of May till half of September 1994, at monthly intervals, on the larger of the two plots (500 m^2). The studies consisted in catching, marking, release and recapture of *H. lutescens*. During catches, I searched the squares thoroughly, inspecting the places below plants and partly uncovering the surface layer of soil.

During consecutive catches all the snails caught were marked and left where they had been found. The snails were marked on the suture between the body and penultimate whorls, with a waterproof, quick-drying marker, each time of different colour. The marker had no negative effect on the snails. Since during subsequent observations the paint was observed to wear off, I corrected the marks during subsequent marking. In each consecutive catch I found snails marked during the previous catches and unmarked individuals, and both categories were marked with a new colour. Based on the colour combination of individual snails, I could tell which had been caught earlier, when and how many times. Out of the total of 1,815 *H. lutescens* caught during the studies, 280 (15.4%) were caught and marked at least twice.

Based on measurements of shell diameter and the degree of development of genitalia, three age classes were distinguished:

D – adults, in which the shell growth had been terminated and lip was present, with fully developed genitalia;

M – young individuals (2 years and older), of shell diameter 10.1–21.0 mm, with incompletely developed genitalia;

J – yearlings and younger (including those just leaving their nests), of shell diameter up to 10.0 mm and only slightly developed genitalia.

The abundance was estimated independently for each age class, with JOLLY-SEBER'S model for an open population (JOLLY 1965, SEBER 1982, SUTHERLAND 1996). Calculations were made with the programme JOLLY–1989, considering the correction of the JOLLY-SEBER model (the so called JOLLY-SEBER B model) with the variable individual viability and variable probability of catch within consecutive time units.

The population abundance (N) was calculated with the formula:

$$N_i = M_i\ (n_i + 1)/(m_i + 1)$$

where:

M_i – number of marked individuals present in the population in the i^{th} catch $= m_i + (R_i + 1)z_i/(r_i + 1)$;

m_i – number of individuals marked during the preceding catch and present in the sample;

R_i – number of individuals left in the place where they had been found;

z_i – number of individuals caught before the i^{th} catch, not caught in the i^{th} catch but caught in any of the next catches;

r_i – number of individuals caught and left in the i^{th} catch, which were caught in any of the next catches;

n_i – total number of individuals caught in the i^{th} catch.

In 1995, at 2 week intervals, from May till half of September, I observed the activity of *H. lutescens* on the 25 m^2 plot. Only adult individuals were included. They were marked individually (waterproof marker), with numbers written on the body whorl. The marking made it possible to observe activities of particular individuals, and the division of the plot into squares enabled me to locate them precisely. In May 1995, I collected and marked 63 adult snails. The study plot was not fenced in any way, so that the marked snails could escape and return, while unmarked individuals could enter the plot at will. For this reason, during consecutive controls I numbered adult individuals that were found for the first time, and included them in further observations.

The diurnal activity of *H. lutescens* was observed regularly, irrespective from weather conditions, during eight observation sessions: May 11/12th and 25/26th, June 7/8th and 21/22nd, July 9/10th and 25/26th, August 10/11th and 24/25th 1995. Each observation session of 24 hrs started at 7.00 a.m., the observations being repeated every two hours, the last observation was at 5.00 next morning. During the observations I determined precisely the position of each marked snail within the study plots (squares) and the place where each individual stayed (e.g. on the ground, on vegetation etc.). At the same time I noted the state of activity of each snail (activity versus rest). The snails, which during the observations were crawling, feeding, displaying activity associated with court-

Fig. 3. A fragment of the study plot in the spring

Fig. 4. A fragment of the study plot in the summer

ship, copulation or egg-laying, were regarded as active. During the eight observation sessions, I observed a total of 84 marked individuals. The marked snails were the most numerous in the sample of May 11th 1995 (63 individuals), the fewest (12 individuals) in that of August 10th 1995. In ninth observation, on September 13th 1995, I found no adult specimen (marked and unmarked) within the whole study area.

During the observations, I measured the air temperature in the ground layer and the relative humidity (hair hygrometer, WSZ Kraków TŻ-7/48249) and noted the weather.

The snail activity was also observed outside the constant study plot, especially in the spring. These observations were aimed mainly at tracing the breeding biology of *H. lutescens*.

The analysis of diurnal activity of *H. lutescens* was based on mean values of observations at particular hours, repeated several times, depending on changes in the relative humidity and temperature of the ground layer, in the spring and summer.

Live specimens of *H. lutescens* for morphological, anatomical and histological studies were caught during faunistic trips. The specimens destined for morphological and anatomical examination were drowned in boiled water, cleaned of mucus and preserved in ethyl alcohol, of a concentration gradually increasing from 30 to 75%. For histological studies, I removed from the snails reproductive and alimentary systems under stereomicroscope (magn. 40×) and fixed them in BOUIN liquid. Serial histological sections of particular organs were stained with hematoxylin and eosin. Some sections were stained with MAYER'S method (detection of mucous substances), and VAN KOSS'S method (calcium detection). The statining procedures applied are described in detail in ZAWISTOWSKI (1975). Photographs were taken with AGFA 15 DIN films under light microscope.

The structure of shell walls of *H. lutescens*, and of its jaw, radula and love dart were examined mainly in scanning electron microscope Philips 515. Drawings were made based on photos, supplied with details observed during dissection. When estimating the size of shell, I considered such parameters as height, breadth and diameter. During measurements, especially of the diameter, I followed STĘPCZAK (1976) who first introduced this measurement.

All the basic statistics were calculated as described in SOKAL & ROHLF (1995); the nomenclature and significance level of the characteristics and tests are given in the respective parts of the text. Calculations were made with the programme Statistica for Windows. The programme JOLLY–1989 was made available by CEPE/CNRS, Montpellier Cedex, France.

The illustrations in the text are original, if not indicated otherwise.

RESULTS

A. MORPHOLOGY AND ANATOMY

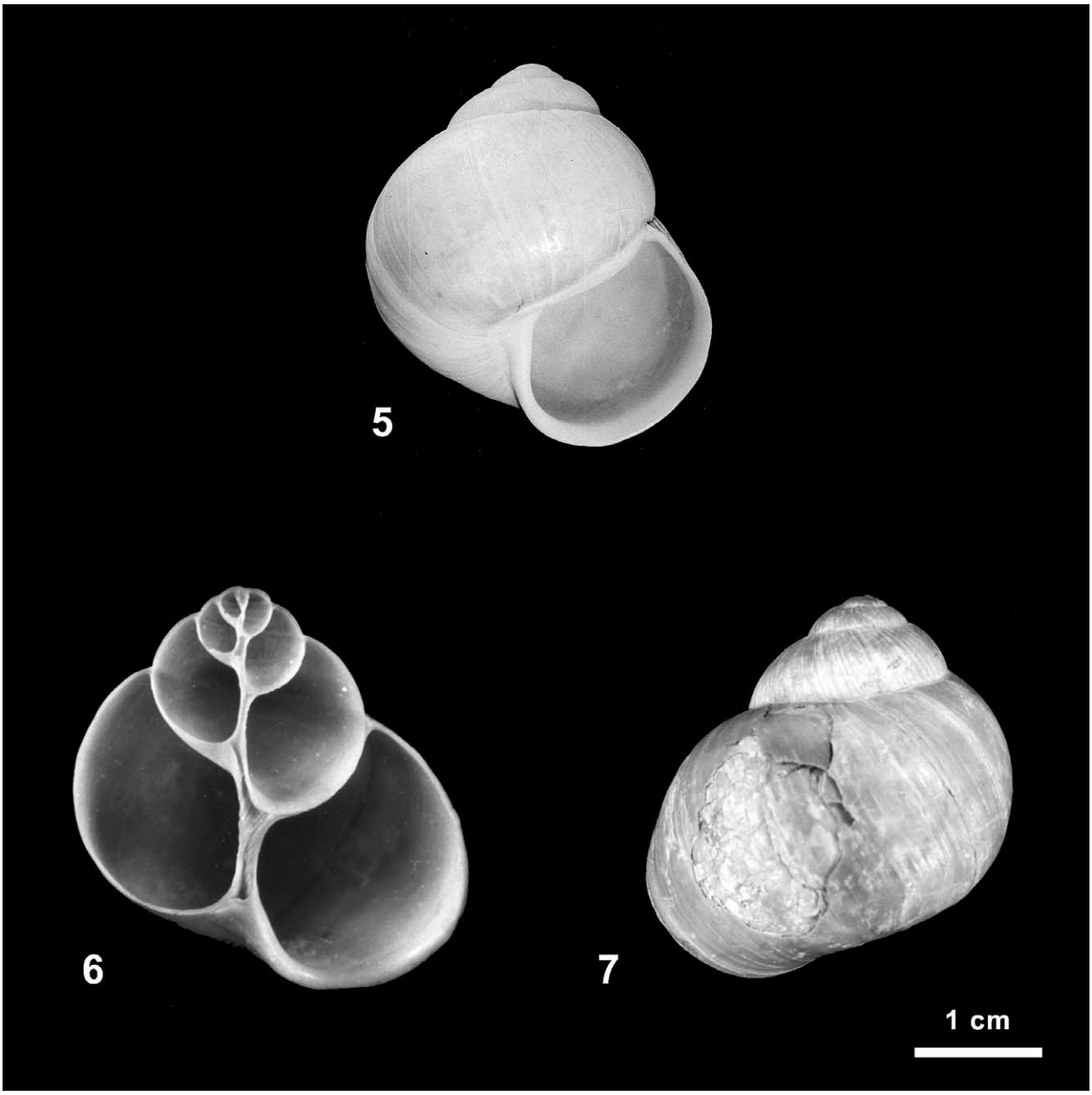
1. Shell

The shell of *H. lutescens* (Fig. 5) is sphaerical-conical, of 4–4.5 poorly convex whorls separated by a shallow suture. It is more conical than in *H. pomatia*. The protoconch (Fig. 8) has a wide apical part and quick increment. The border between the protoconch and the definitive whorls is fairly distinct. The surface of the protoconch at a low magnification is smooth; viewed at a higher magnification in SEM (Fig. 9) it is coarse-grained, with numerous, irregularly arranged grooves. Definitive whorls increase quickly. The aperture is large, roundish, in most cases slightly higher than wide. Its outer margin is usually developed as a poorly marked, whitish lip. The shell is, as a rule, unicolour, yellowish-white. The shell measurements in adult specimens are within 28.5–34.1 mm height, 26.9–32.1 mm breadth and 22.5–26.9 mm diameter. The shells are only slightly elongated, and the mean value of their height/breadth ratio is 1.06 which means that the mean shell height is not much larger than its mean breadth (KORALEWSKA-BATURA 1993a). All the examined adult *H. lutescens* had their shells much smaller than those of adult *H. pomatia*.

The internal structure of the shell of *H. lutescens* is shown in Figure 6. In juvenile individuals the umbilicus is partly visible; in adults it is completely covered while in *H. pomatia* it is usually partly open.

The macrosculpture of definitive whorls, analysed in SEM, is rather poorly distinct (Fig. 10). It consists of radial growth stripes of various width, resulting from uneven growth of the shell, and of spiral lines. The distinct growth stripes combined with very delicate spiral lines create an impression of grating. The macrosculpture is more delicate than in *H. pomatia*.

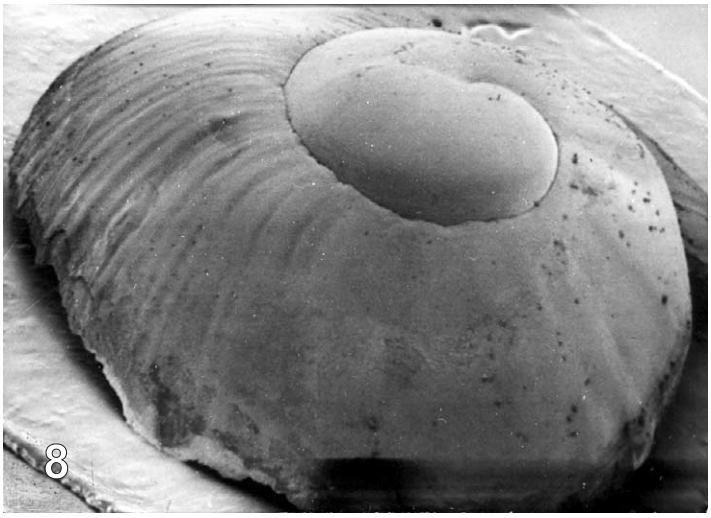
On shell fractures, perpendicular to its growth stripes, analysed in SEM, four layers can be distinguished, as reported by KILIAS (1960) for *H. pomatia*: periostracum, ectostracum, mesostracum and endostracum (Fig. 11). However, their relative thickness in these two species is different. The periostracum (Fig. 11a) is the thinnest layer, built of conchiolin, which in adult snails wears off against the substratum and vegetation. The remaining, calcareous layers, also contain conchiolin, but inorganic

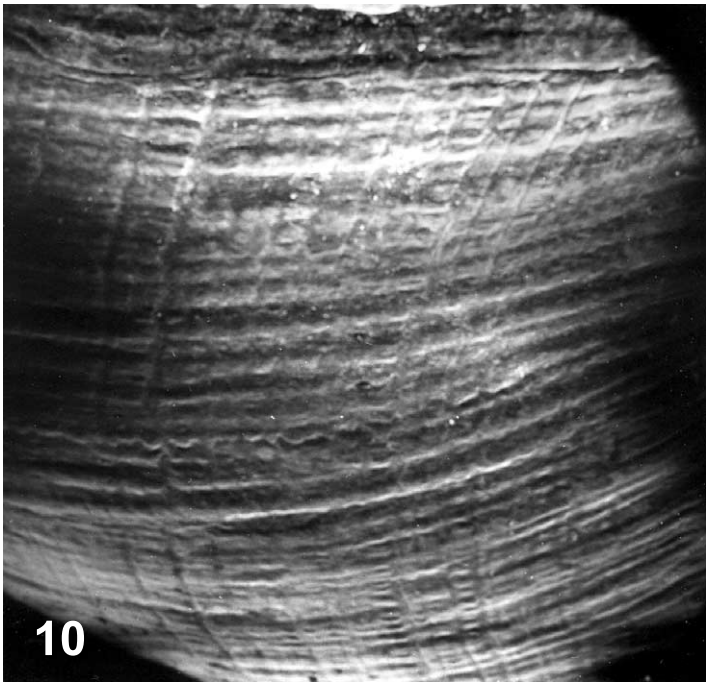


Figs 5–7. Shell of *H. lutescens*: 5 – front view, 6 – longitudinal section, 7 – regenerated shell

components, mainly calcium carbonate, constitute 90–99% shell weight (GREGOIRE 1972). The ectostracum – lamellate layer (Fig. 11b) in *H. lutescens* consists of lamellae of diagonal arrangement, running parallel to each other and at an angle relative to the main lamellar axis. The thickest, prismatic layer – mesostracum (Fig. 11c) is built of high, slender and very distinct prisms. Their arrangement is regular and their width varied. Sporadically found shorter prisms terminate sharply close to the middle of this layer. Most prisms are bluntly terminated and are well distinct from the fibrous layer – endostracum (Fig. 11d). The latter layer in *H. lutescens* has an arrangement of extensive, fibrous diagonal structures. They are arranged almost parallelly to the shell surface.

In *H. lutescens* damage to aperture margin is repaired through rebuilding of the missing fragments of a structure like that of normally built shell. Damage to older whorls is repaired by epithelium of the visceral sac, with inorganic substance alone, and no conchiolin (Fig. 7). According to WAGGE (1951) shell regeneration in *H. aspersa* O. F. Müller follows the same pattern. Deposition of calcareous layers (WILBUR & YONGE 1964, CHETAIL & KRAMPITZ 1982) is effected in the extrapallial chamber filled with the fluid which contains the shell-composing ions and





Figs 8–11. Shell structure in *H. lutescens*: 8 – protoconch, 43×; 9 – sculpture of protoconch, 4,650×; 10 – sculpture of body whorl, 46.5×; 11 – shell fracture perpendicular to growth lines, a – periostracum, b – lamellate layer, c – prismatic layer, d – fibrous layer, 1,725×

compounds. They are provided to the extrapallial fluid through diffusion and actively transported by amebocytes. Calcium is taken up with food and accumulated in calcium cells of the hepatopancreas and connective tissue. According to HELLER & MAGARITZ (1983), oxygen, carbon and probably also calcium originate from water absorbed through the skin from the surface layer of the soil. Calcium transport is enhanced by alkaline phosphatase, detected in most molluscs. The carbonate residue is derived from metabolic carbonic acid, while deposition of crystalline carbonates is enhanced by carbonic anhydrase (WILBUR & YONGE 1964). The ultimate deposition of calcium carbonate is extracellular.

2. External appearance

The external appearance of the body of *H. lutescens* does not depart from that found in other members of the genus *Helix*. The body is greyish-coloured and covered by numerous wrinkles and grooves. In the grooves there are fine, whitish granu-

Fig. 12. A crawling *H. lutescens*

lations. They are the most numerous in the grooves that form two light streaks along the darker back of the snail (Fig. 12), which are characteristic of the species. The sole of the large, strongly muscled foot, is yellowish-grey. A large pneumostome is surrounded by two large lobes and a flat disc whose whole free margin is rounded, while in *H. pomatia* the margin is straight (JACKIEWICZ & KORALEWSKA-BATURA 1999).

3. Musculature and body covers

The structure of the main retractor muscles of *H. lutescens* is shown in Figure 13; it does not differ from that of *H. pomatia*. In the foot there are numerous strands of longitudinally, transversely and dorsoventrally arranged muscles.

The body wall of the snail is built of a monolayer epithelium, whose cells are provided with numerous ciliae; the latter are the most numerous on the sole. Among them there are mucous glands. Around the mouth, on sole edges and on the tentacles there are also groups of sensory cells. The basal membrane of the epithelium is adjoined by a layer of connective tissue and strongly developed musculature of the body wall.

4. Alimentary tract

The alimentary tract of *H. lutescens* (Fig. 14) corresponds to such tract in *H. pomatia* with respect to its morphological, anatomical and histological structure.

The mouth (Figs 15a, 16), in the shape of a transverse slit, is located on the underside of the anterior part of head. It is bordered by the upper and the

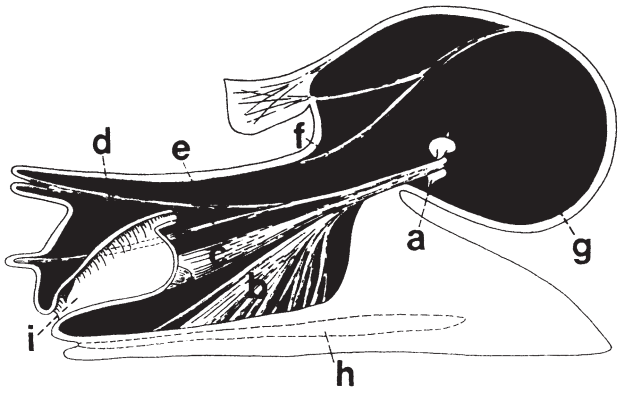


Fig. 13. Musculature of a snail: a – columella and columellar muscle, b – foot retractors, c – pharynx retractors, d – ommatophore retractors, e – lower tentacle retractors, f – penial retractor, g – visceral sac, h – pedal gland, i – pharynx (after TRAPPMANN, from KILIAS 1960)

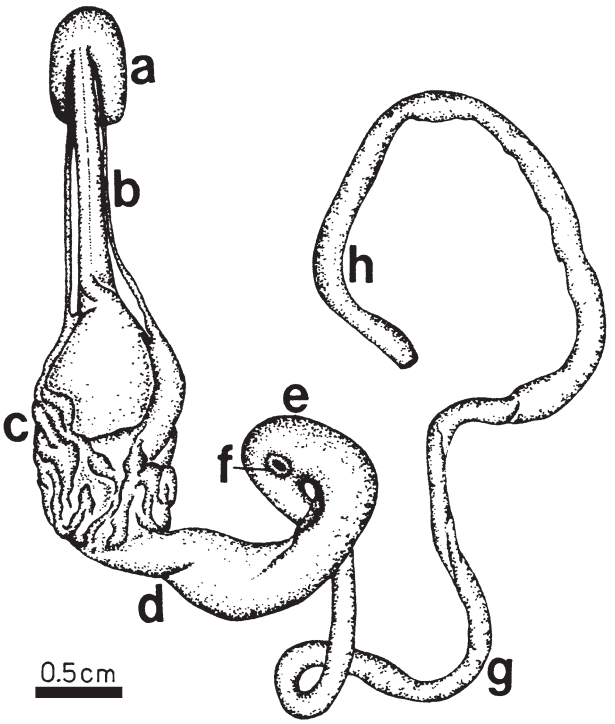


Fig. 14. Alimentary tract: a – pharynx, b – oesophagus, c – salivary glands and ducts, d – crop, e – stomach, f – outlet of smaller lobe of hepatopancreas to stomach, g – small intestine, h – rectum

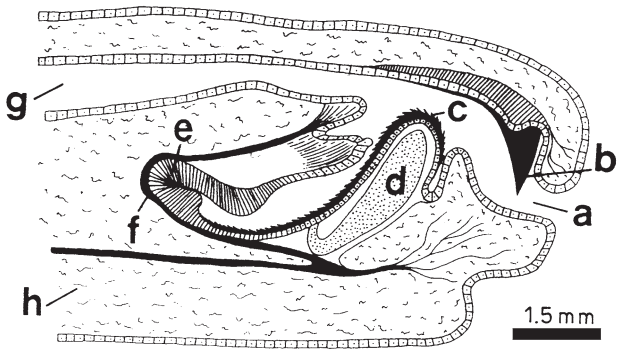


Fig. 15. Longitudinal section through mid portion of pharynx: a – mouth and oral cavity, b – jaw, c – radula, c – odontophore, e – odontoblasts, f – radular pocket, g – oesophagus, h – muscles and connective tissue

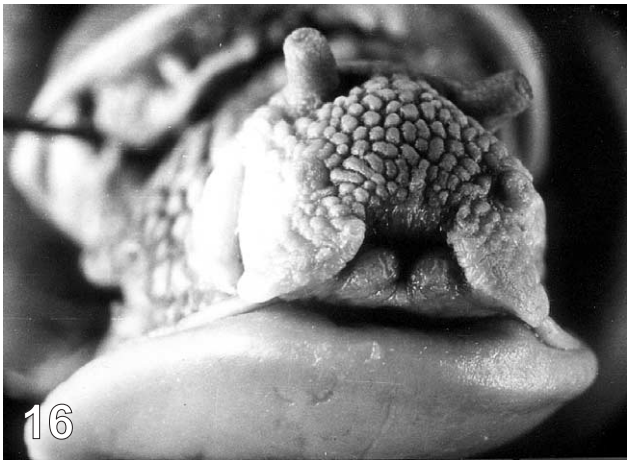
lower lip, on its sides there are two mouth lobes. Close to the mouth the walls of oral cavity are lined with cuticle which locally is strongly developed, to form a chitinous upper jaw (Figs 15b, 17). The jaw of *H. lutescens* resembles that of *H. pomatia* in its shape, but is smaller. In adults the mean jaw width is 3 mm, the height 1 mm. On its upper surface, there are 5 large transverse ridges. The jaw is strongly anchored in the pharynx with its chondrous part. Behind the jaw there is a short oral cavity, also lined with cuticle. It passes into the pharynx (Fig. 14a). In adult *H. lutescens* the mean length of radula (Figs 15c, d) is 8 mm, width 4 mm. A single tooth in lateral position is shown in Figure 18, and the arrangement of teeth in the radula in Figure 23. The tooth consists of a very thick, concave basal plate and the crown, covered by cusps. Teeth of each longitudinal row differ only in the degree of wear: in the anterior part of the radula they are blunted (Fig. 19), while those situated further are very sharp (Fig. 20). In the posterior part the teeth are young (Fig. 21), often still not fully formed. The teeth-producing odontoblasts in the radular sheath are shown in Figures 15e, f and 22, and the three types of teeth in the transverse row – in Figure 24. On both sides of the symmetrical central tooth there are lateral teeth, whose basal plates and crowns are asymmetrical. On their external side there are marginal teeth. Most often on each side of the central tooth there is the same number of teeth. Numerous radulae of *H. lutescens* examined in SEM make it possible to propose the following radular formula:

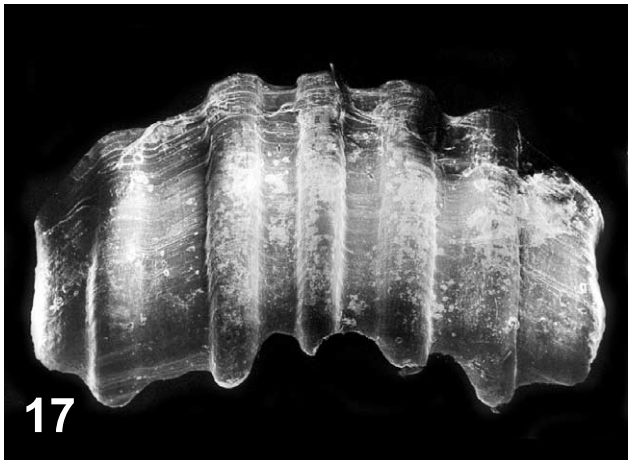
3-4/34 – 2/20 – 3/1 – 2/20 – 3-4/34 × 150

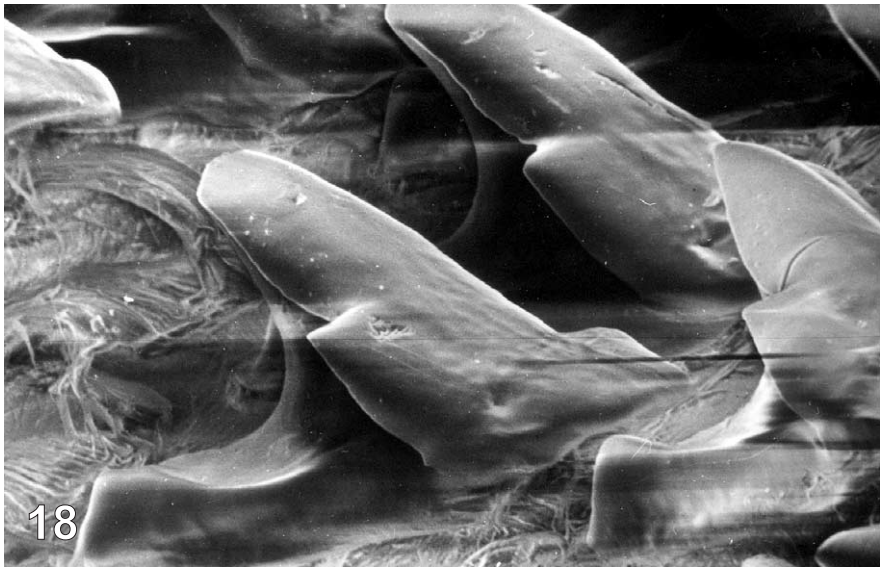
I have found, based on the structure of marginal teeth, that the radula of *H. lutescens* is of denticulate type (JUNGBLUTH et al. 1985), thus being typical of the ecological group of herbivorous snails. It should be stressed that radular teeth of other species of Helicidae and of species feeding on the same kind of food are fairly diverse (KORALEWSKA-BATURA 1994b). This would suggest that the structure of radula depends not only on the kind of food but also on other, perhaps also phylogenetic, factors.

A pair of salivary glands (Fig. 14c) opens, through salivary ducts that run within the oesophageal ring, to the posterior part of the pharynx on its dorsal side. The glands consist of two irregular lobes which anastomose with each other only in their posterior parts and tightly adjoin the crop. Among the gland cells (Fig. 25) large cells of vesicular shape prevail, with oval nuclei. Inside them a foam-like cytoplasm is visible. Between the cells there are fine canaliculi of the salivary glands which in each lobe join into a long efferent duct. The pharynx passes into a short, narrow and strongly muscled oesophagus (Fig. 14b). In *H. lutescens* it forms numerous, thick and high folds (Fig. 26). The oesophagus wall is lined with cylindrical epithelium (Fig. 27), covered with a thin cuticular layer. The nuclei of the epithelial cells are located at various levels, usually closer to the base. Among the epithelial cells there are glandular cells, characterized by a bottle-like shape with distinct "necks". Their nuclei are located basally, in their widest part. Below the epithelium there is connective tissue and muscle fibres.

The terminal part of the oesophagus widens gradually to form a crop (Fig. 14d) which in *H. pomatia* is often regarded as a part of the stomach (MEISENHEIMER 1912, KILIAS 1960, GÖTTING 1974). It follows from histological studies of GHOSE (1962)



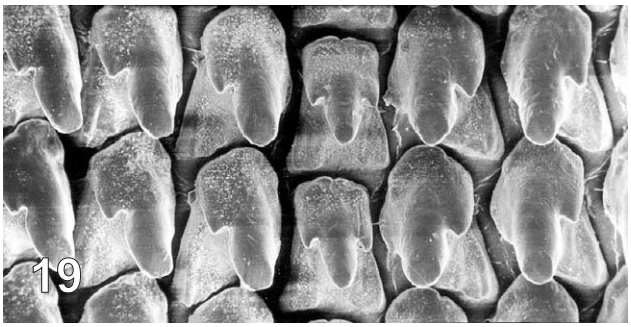


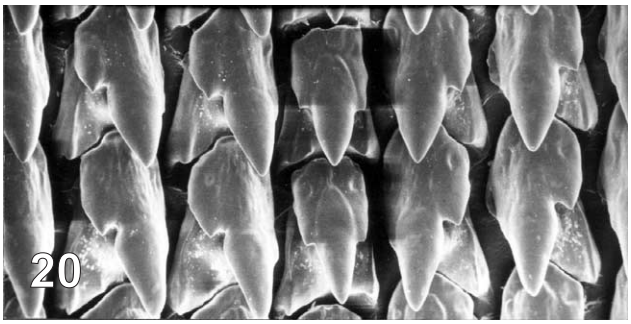


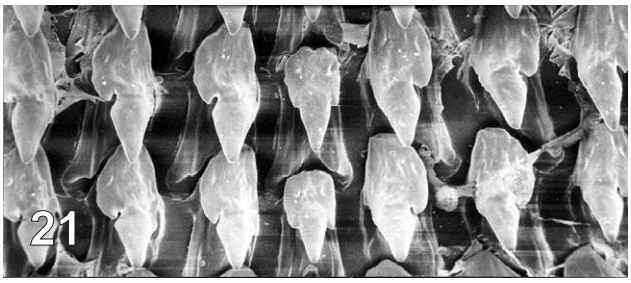
Figs 16–18. Head and details of mouthparts: 16 – head in front view, 17 – jaw, 73×, 18 – radular tooth (after KORALEWSKA-BATURA 1994b), 2,400×

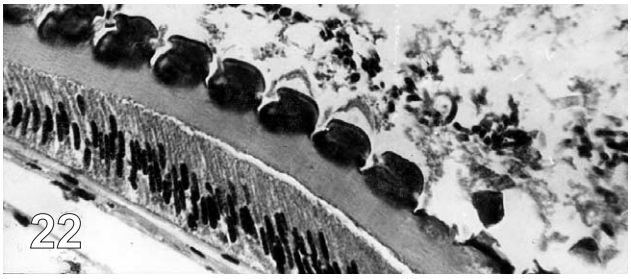
on *Achatina fulica* Bowdich that the crop originates from the anterior part of the stomach. Thus the crop of Stylommatophora can be regarded as a transformed part of the stomach. In *H. lutescens* it is a wide tube which widens considerably in its mid part. In its spacious lumen there are numerous folds which are lower than those in the oesophagus (Fig. 28). The crop wall is lined with cylindrical epithelium, which also contains glandular cells (Fig. 29). Below the layer of epithelial cells there is connective tissue interspersed with muscle fibres, that run in various directions. In the crop of *H. pomatia* the food is subject to preliminary enzymatic treatment (DROZDOWSKI & ZAWIEJA 1993).

The stomach (Fig. 14e) is the shortest part of the alimentary tract. It has a shape of a semicircular, somewhat flattened sac. A detailed analysis of stomach structure in *H. lutescens* has demonstrated that in its lumen, like in *H. pomatia* (KILIAS 1960, DROZDOWSKI & ZAWIEJA 1993) there are three large, very characteristic folds (Fig. 31). Two of them, one located in the dorsal and the other in the central part of the stomach, are much larger than the third. They form a gutter – typhlosole (Fig. 31d) running towards the intestine. The third fold is located between the two outlets of the hepatopancreas lobes. Between them, there are much smaller folds. The stomach wall is lined with a ciliated cylindrical epithelium with numerous glandular cells (Fig. 30). Below the epithelium there is connective tissue, its main component being lipid cells and relatively numerous muscle fibres. The stomach muscular layer is built of circular, longitudinal and oblique fibres. Two ducts of the hepatopancreas open to the stomach (Figs 32c, f). Digestion mechanisms in the stomach of pulmonate snails result in only the finest food particles, not exceeding 1 μm, getting into the hepatopancreas where they are absorbed (SUMNER 1965b, ZAWIEJA 1969). Larger particles are moved towards the intestine.

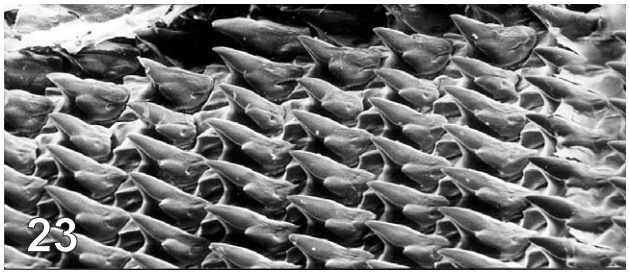


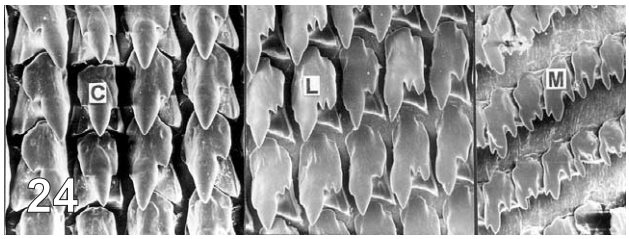






Figs 19–22. Radular teeth: 19 – blunted teeth, 20 – sharp teeth, 21 – young teeth (after KORALEWSKA-BATURA 1994b), 790×, 22 – a fragment of radular pocket with odontoblasts and a forming row of teeth, 245×

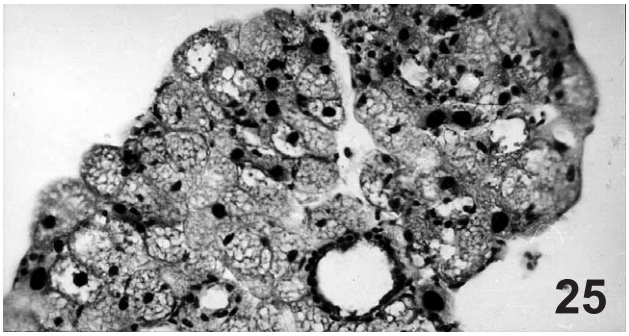


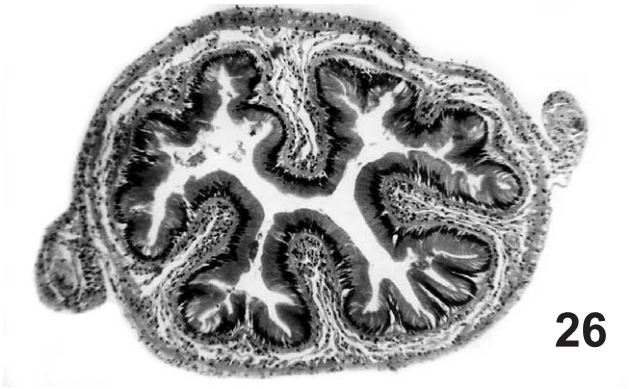


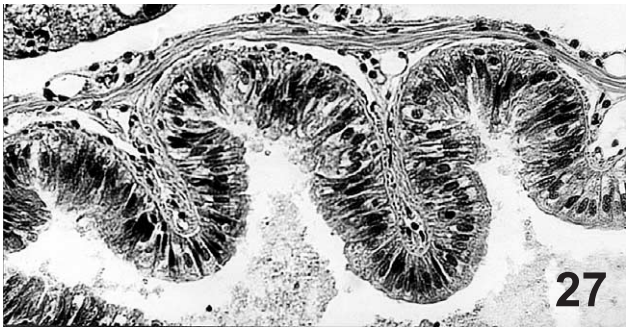
Figs 23, 24. Radular teeth: 23 – arrangement of teeth, 395×, 24 – a fragment of radula, C – central tooth, L – lateral teeth, M – marginal teeth (after KORALEWSKA-BATURA 1994b), 395×

The hepatopancreas in *H. lutescens* consists of two lobes of yellowish-greenish colour. The upper, smaller lobe fills 2–3 initial whorls of the visceral sac and surrounds the hermaphroditic gland. Its duct opens to the stomach close to the intestine (Fig. 32c). The second, larger lobe occupies further, larger whorls of the visceral sac and partly surrounds the albumen gland. This lobe opens to the stomach near the crop (Fig. 32d). The hepatopancreas is built of numerous lobules (Fig. 33) connected by canaliculi that open to the main ducts, and these in turn open to the stomach. The most abundant data on the structure and function of this gland come from the studies on *H. pomatia* (ABOLINS-KROGIS 1961, 1965, 1970a, b, SUMNER 1965a, b). Between the lobules and canaliculi of the gland, there is connective tissue. The canaliculi and ducts are lined with ciliated epithelium. In the epithelium of hepatopancreas lobules four types of cells are present. They are rectangular digestive cells which may also play an absorption role; secretory cells which are barrell-shaped; calcium cells of pyramidal shape which store calcium in the form of carbonates in the structures called calcospherites, built of concentrically arranged lamellae. Calcium cells in *Deroceras reticulatum* (O. F. Müller) contain also numerous lipid drops (BABULA & WIELIŃSKA 1988). The last type includes cells of not precisely known function, regarded by SUMNER (1965a) as undifferentiated cells that can transform into the remaining three types described above. In the snail hepatopancreas the activity of amylase, maltase and lactase (RAO 1975), as well as cellulase (OWEN 1966) was detected. It is also the place of absorption of digested food and accumulation of reserve materials e.g. glycogen whose quantity increases especially in the period preceding hibernation. According to HRYNIEWIECKA-SZYFTER (1966), within the canaliculi of the hepatopancreas of *H. pomatia*, copper is also present, which may suggest its participation in haemocyan synthesis. It has been also found that the hepatopancreas in *Arion ater* (L.) has an ability to accumulate inorganic ions – heavy metals (IRELAND 1982, after BABULA & SKOWROŃSKA-WENDLAND 1988).

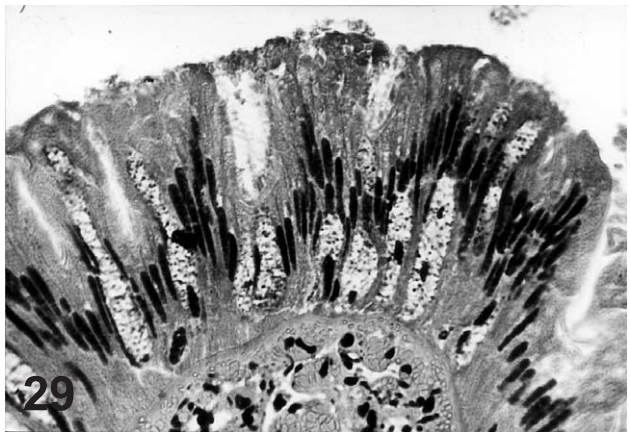
The stomach of *H. lutescens* passes into the intestine (Fig. 14g), consisting of the small intestine and rectum. Both these sections are lined with cylindrical epithelium with numerous glandular cells. The small

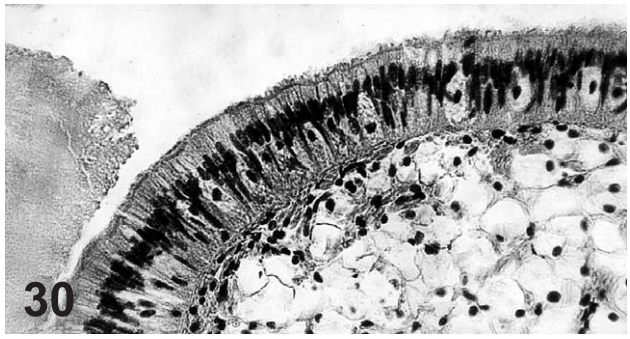






Figs 25–27. Sections through oesophagus and salivary glands: 25 – a fragment of salivary gland, 145×; 26 – transverse section through oesophagus with its numerous folds, 40×; 27 – a fragment of oesophagus wall lined with cylindrical epithelium with glandular cells, 170×





Figs 28–30. Transverse sections through crop and stomach: 28 – a fragment of folded crop wall, 75×; 29 – cylindrical epithelium with glandular cells, lining the crop wall, 295×; 30 – a fragment of stomach wall, lined with ciliated cylindrical epithelium with glandular cells, 205×

intestine on almost its whole length is a tube of equal diameter. Only its terminal, glandular part is somewhat wider. In the stomach-adjoining portion of the small intestine, besides low folds, there is a high fold which is a continuation of one of the stomach typhlosole folds. In the folds of the glandular part of the small intestine there occur very numerous glandular cells (Fig. 34). The mucus produced in this part of the alimentary tract facilitates defecation (MEISENHEIMER 1912). The small intestine runs in the gutter in the lower lobe of the hepatopancreas, surrounds it and passes into the rectum (Figs 14h, 35), whose essential function is removal of faeces. According to KILIAS (1985) individuals of *H. pomatia* preparing for hibernation remove their intestine contents.

5. Pallial complex

The pallial complex in *H. lutescens* includes, like in other pulmonates, the following organs: lung, heart surrounded by pericardium, kidney with ureter and the terminal section of alimentary canal (Fig. 36). A part of the mantle covered with a network of blood vessels forms lung. Below it, there is a spacious pallial cavity contacting with the outer world through a large pneumostome. The pneumostome is located on the right side of the body, close to the terminal part of the intestine and ureter. The kidney in *H. lutescens* is a

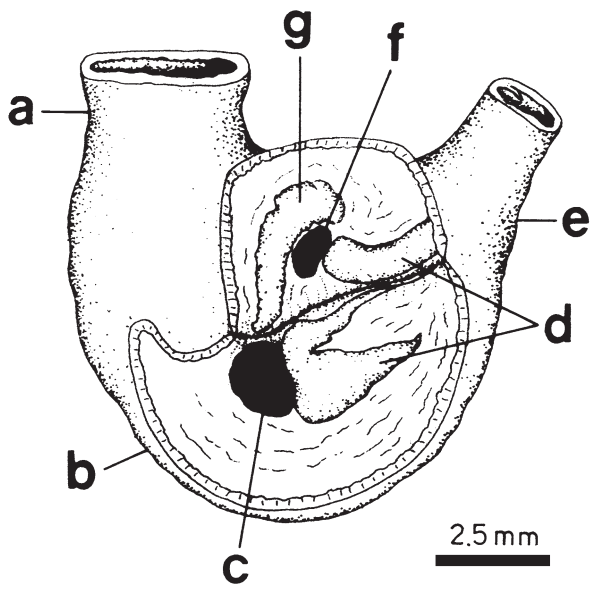


Fig. 31. Internal structure of stomach: a – crop, b – stomach, c – outlet of large lobe of hepatopancreas, d – two folds forming typhlosolis, e – small intestine, f – outlet of small lobe of hepatopancreas, g – fold between outlets of hepatopancreas lobes

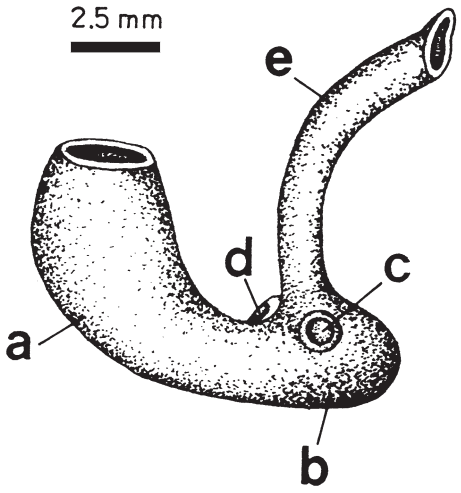
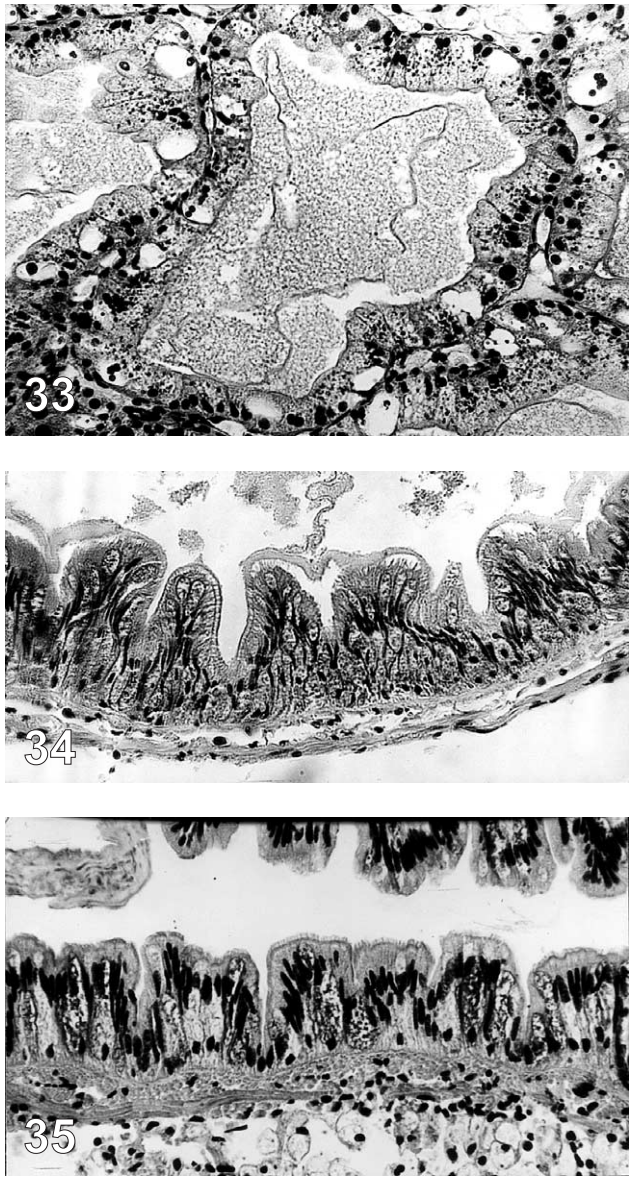


Fig. 32. Stomach and hepatopancreas outlet: a – crop, b – stomach, c – outlet of small lobe of hepatopancreas, d – outlet of large lobe of hepatopancreas, e – small intestine

large, sac-like organ of creamy colour (Fig. 36b). It is well visible through the thin body covers. With the heart and lung it lies in the last whorl of the visceral sac. Its outline, with the primary ureter, is an elongate triangle of different sides. The longest side is parallel to the rectum, located at a distance from it. The shortest runs close to the hepatopancreas, the third borders on the pericardium.



Figs 33–35. Sections through hepatopancreas and intestine: 33 – hepatopancreas lobules, 170×; 34 – a fragment of midgut with glandular cells visible, 170×; 35 – a fragment of rectum wall lined with ciliated cylindrical epithelium with glandular cells, 205×

6. Excretory system

The kidney communicates with the pericardium through a narrow reno-pericardial duct (Fig. 36a), located more or less in the middle of the part of pericardium that adjoins the kidney (Fig. 36b). The primary ureter departs from the apical part of the kidney (Fig. 36c). It bends sharply and, along its side, runs posteriad and gradually narrows to pass into the secondary ureter (Fig. 36d). The latter bends anteriad and, as a narrow duct, tightly adjoining the rectum, runs to the anterior part of pallial cavity. Near the anus it departs from the rectum and continues

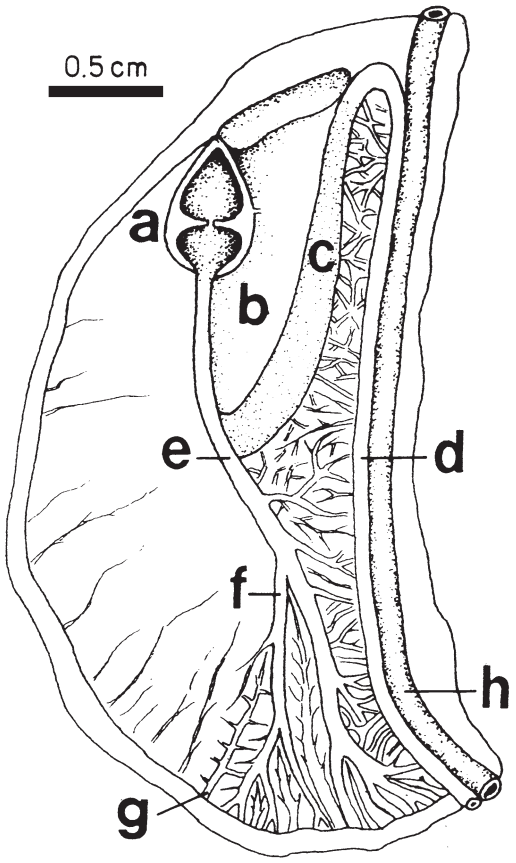


Fig. 36. Pallial complex: heart in pericardium and reno-pericardial duct, b – kidney, c – primary ureter, d – secondary ureter with excretory pore, e – pulmonary vein, f – efferent vessel, g – main artery, h – rectum with anus

as a wide, spacious bi-partite gutter which opens to the outside on the left of anus, close to the pneumostome.

The blood with metabolic wastes is brought to the kidney by the vein. The vein splits into numerous capillary vessels that enter the kidney folds. Probably nephrocytes pick up the metabolites and transfer them to the kidney cavity. After getting rid of the metabolites, the blood collects in vessels that join into a common kidney vein, which opens to the pulmonary vein next to its outlet to the heart auricle. In the primary ureter, the excretory products become concentrated due to secretion and resorption, and then they are removed through the secondary ureter. In *H. pomatia* the main excretory product is uric acid and it is removed in concentrated form (KILIAS 1960).

7. Circulatory system

The circulatory system in *H. lutescens* is very similar to that of other helicids, especially *H. pomatia*. The heart is composed of a thin-walled auricle (Fig. 37b) and a strongly muscled ventricle (Fig. 37c). It is sourrounded by a spacious pericardium (Fig. 37a) filled with a liquid. On the border between the auricle and ventricle, there are two semicircular valves, while on the border between the ventricle and the main aorta there is only one valve. The short main aorta leaves the heart chamber and runs posteriad (Fig. 37d). In *H. pomatia* the aorta is also present, but it was not mentioned e.g. by MEISENHEIMER (1912) or KILIAS (1960, 1985). It is divided into anterior (Fig. 37e) and posterior (Fig. 37f) aorta.

The anterior aorta is directed towards the cephalic part of the body. It is very long and passes through the

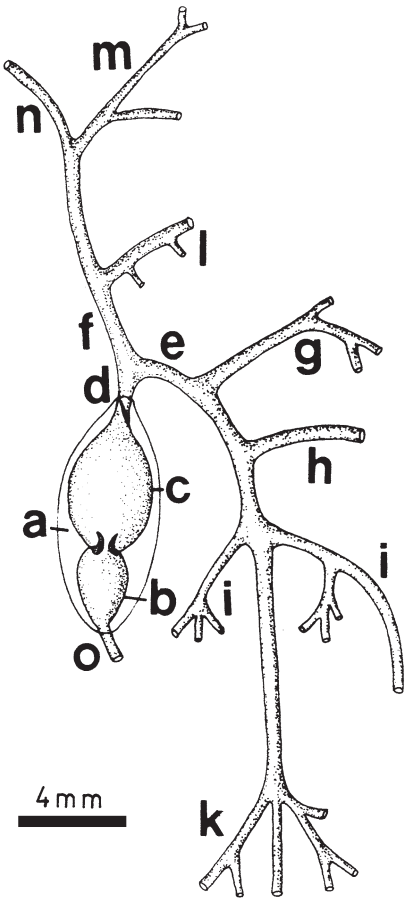


Fig. 37. Vascular system: a – pericardium, b – auricle, c – ventricle with valves, d – main aorta, e – anterior aorta, f – posterior aorta, g – genital artery, h – pedal artery, i – arteries of anterior section of alimentary tract, body walls and muscles, k – cephalic arteries, l – hepatopancreatic artery, m – gastro-intestinal artery, n – gonad artery, o – pulmonary vein

oesophageal ring. Its numerous branches reach the reproductive organs (Fig. 37g), foot (Fig. 37h), anterior part of the alimentary canal, body walls and muscles (Fig. 37i). In its terminal part, the anterior aorta gives off numerous branches that reach the head (Fig. 37k).

The posterior aorta is shorter than the anterior. A hepatopancreatic artery departs from it (Fig. 37l). In its terminal part the posterior aorta forks into the gastro-intestinal artery (Fig. 37m), and the gonad artery (Fig. 37n).

The only morphotic elements of snail blood are haemocytes. They play a role of phagocytes and transport, among others, calcium ions. Because of their great ability to aggregate, which increases in wounded animals, the haemocytes may be responsible for preventing haemolymph loss (ŻBIKOWSKA 1997). Besides, the haemolymph, filling some organs such as penis, makes them stiff, which is the condition of their functioning.

8. Respiratory system

The thick pulmonary vein (Fig. 36e) makes a gentle arch along the whole lung. The vein, especially close to the mantle collar, is fairly strongly branched. The branches are efferent blood vessels (Fig. 36f) which convey blood from the lung to the pulmonary vein. They are thin at the mantle margin but become gradually thicker towards their outlet to the pulmonary vein. Between the efferent vessels there are numerous delicate afferent vessels (Fig. 36g), which are located close to the efferent vessels. The afferent vessels are branches of the circular blood sinus which collects the deoxygenised haemolymph from all the body. The density of the blood vessel network in snails depends on their size and mobility (DROZDOWSKI 1970, 1977, WIKTOR 1989, KORALEWSKA-BATURA 1997a). In *H. lutescens*, compared to its body mass without shell, the lung area is smaller and the blood vessel network less branched than in the larger *H. pomatia*. DROZDOWSKI (1986, 1993) reports that the respiratory surface of the lung of *H. pomatia* and *Limax flavus* L. is lined with flat epithelium. The lung parenchyma is filled mostly with bundles of muscle fibres arranged in various planes, and a small quantity of connective tissue. Besides, there are numerous inter-tissue spaces playing a role of haemal canals. Their inner surface is not lined with endothelium. According to DROZDOWSKI (1986, 1993) they are haemal sinuses or canals and not blood vessels.

9. Nervous system and sense organs

Like in nearly all pulmonates, the central nervous system in *H. lutescens* is strongly concentrated. Some ganglia adjoin each other so tightly that the borders between them are almost completely blurred. They can be identified only based on the nerves that depart from them to respective body parts.

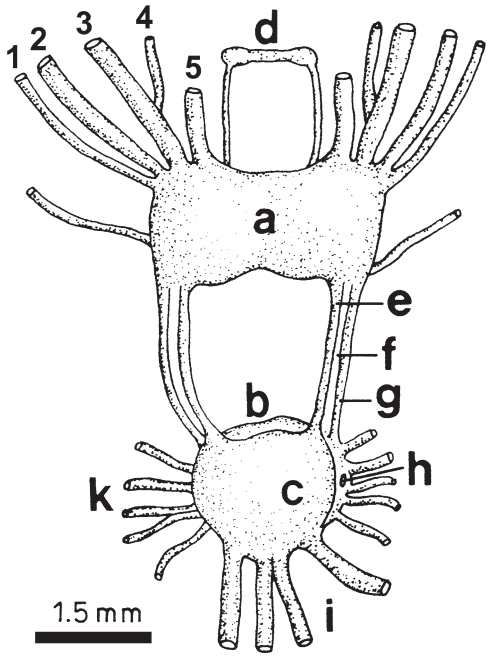


Fig. 38. Central nervous system: a – cephalic ganglia with their nerves, b – pedal ganglia, c – pleural and parietal ganglia with visceral ganglion, d – oesophageal ganglia connected by a commisure, e – cerebro-pleural connective, f – statocyst nerve, g – cerebro-pedal connective, h – statocyst, i – nerves running to body walls and visceral sac, k – nerves running to sole

The central nervous system in *H. lutescens* (Fig. 38) is very similar to that of *H. pomatia*: it consists of paired cerebral ganglia, pedal ganglia, pleural ganglia, parietal ganglia, buccal ganglia and a single visceral ganglion. The ganglia give off nerves that supply particular body parts and organs.

The cerebral ganglia (Fig. 38a) are large. They are connected with each other by a very short commisure, and with the pedal and pleural ganglia by connectives (Figs 38e, g). Each cerebral ganglion gives off anteriad five nerves (Fig. 38a). Four innervate the region of mouth, mouth lobe, tentacle, the upper part of ommatophore and the eye. The fifth nerve runs to the basis of ommatophore, and on the right part of the body its branch reaches the terminal parts of the reproductive organs. The pedal ganglia (Fig. 38b) are also large and connected by a very short commisure. They give off several nerves that go to the sole. On each pedal ganglion a shiny, roundish statocyst (Fig. 38h) is located. Despite its position, it is innervated by the corresponding cerebral ganglion with which it is connected by a long nerve (Fig. 38f) running between the cerebro-pleural and cerebro-pedal connectives.

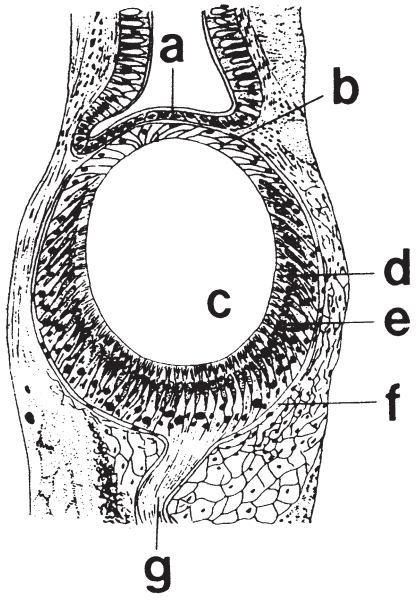


Fig. 39. Longitudinal section through ommatophore with retracted eye in *H. pomatia*: a – external cornea, b – internal cornea, c – lens, d – retina, e – retinal rod, f – basal membrane, g – optic nerve (after SIMROTH 1876 and BÄCKER 1903, from KILIAS 1985)

The parietal ganglia are connected by short connectives with the pedal and parietal ganglia. The latter are connected with the unpaired visceral ganglion. These three ganglia are so tightly connected (Fig. 38c) that the borders between them are completely obliterated. The visceral ganglion gives off several very long and asymmetrically arranged nerves which run to the body walls and the internal organs of the visceral sac (Fig. 38i). A pair of small buccal ganglia (Fig. 38d) is located above the oesophagus, in an invagination at the outlet of the pharynx to the oesophagus. They are connected with each other by a fairly long commisure and by long connectives with the cerebral ganglia. They innervate the pharynx, radula, oesophagus and salivary glands.

The morphology of neurohormonal system was described in some species of stylommatophoran snails, including the genus *Helix* (POKORA 1989). Large groups of neurosecretory cells were found in the mesocerebrum of these snails. They secrete substances of neurohormonal character which take part in the regulation of most reproductive processes.

The eye structure in *H. lutescens* corresponds to that in *H. pomatia* (Fig. 39). Above the eye vesicle, there is a translucent epithelium forming the external cornea. Below it there is, also colourless, internal cornea that forms the anterior wall of the eye vesicle. Its further part is retina, formed of optic and pigment cells. The latter surround the optic cells and form rods together with them. The bases of optic cells are reached by fibres of the optic nerve. In the middle of the vesicle there is a large, spherical lens.

The statocysts, situated on the pedal ganglia, are vesicles filled with a liquid (statolymph) in which oval, fine statolyths are submerged.

Like in other snails, all the body surface of *H. lutescens* is susceptible to mechanical and chemical stimuli. The main location of touch, taste and smell sense are tentacles, the region of mouth, sole edges and the mantle margin. However, the main role in receiving tactile stimuli is played by tentacles which can also receive smell stimuli. Taste stimuli are perceived thanks to chemoreceptors located in the lips, within the mouth cavity and also on the mouth lobes and on the anterior part of foot (PIECHOCKI 1979).

10. Reproductive system

The general structure of the reproductive organs in *H. lutescens* is the same as in other members of the family Helicidae, though it differs in details.

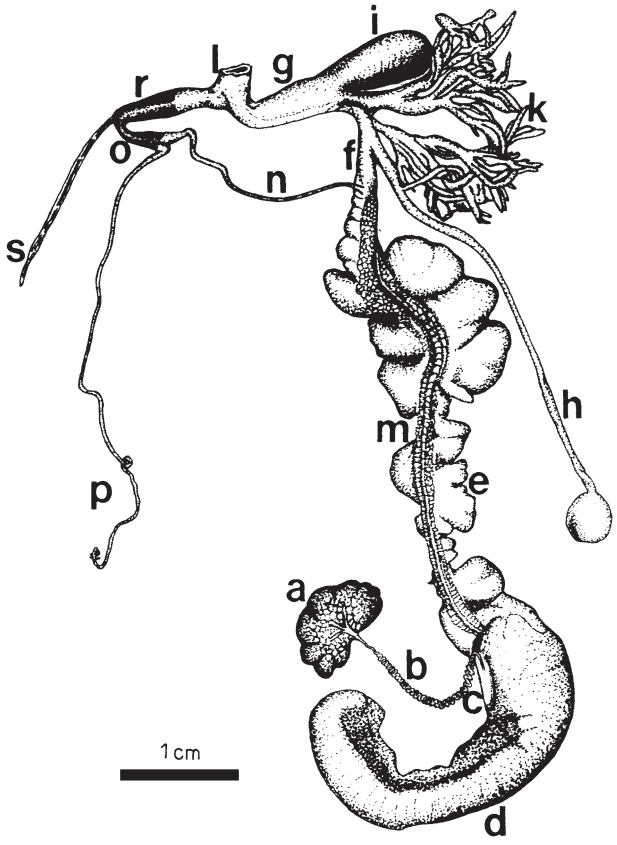
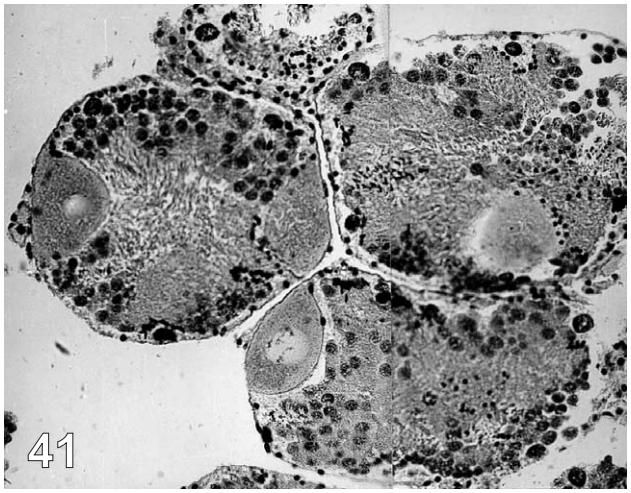
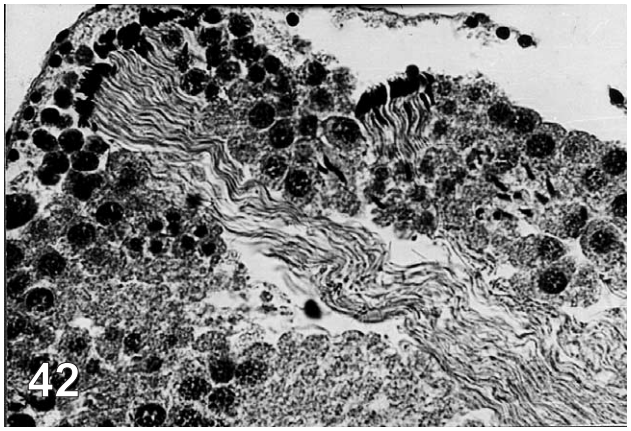
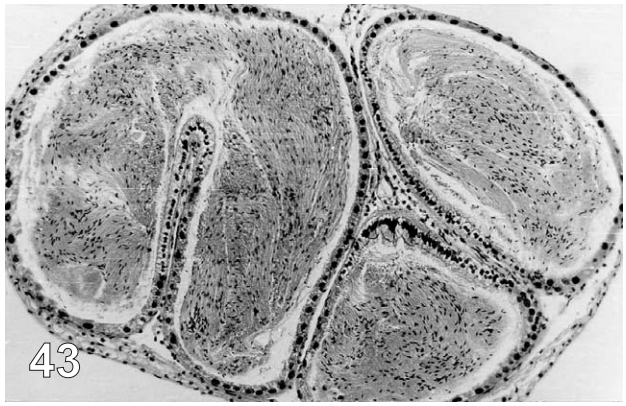


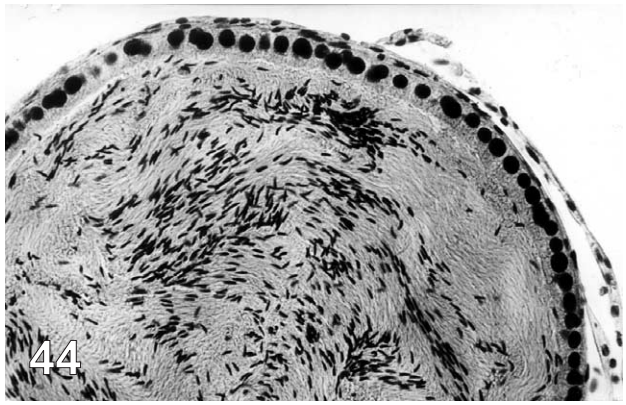
Fig. 40. Reproductive system: a – hermaphroditic gland, b – hermaphroditic duct, c – seminal vesicle, d – albumen gland, e – spermoviduct, f – oviduct, g – vagina, h – gametolythic gland and its duct, i – love dart sac, k – mucous gland, l – genital atrium, m – prostate gland, n – vas deferens, o – epiphallus, p – flagellum, r – penis, s – penial retractor muscle





Figs 41, 42. Sections through gonad: 41 – acini with visible ova, 135×; 42 – a fragment of acinus filled with spermatozoa at various development stages, 270×





Figs 43, 44. Transverse sections through hermaphroditic duct: 43 – folded section of hermaphroditic duct, 145×; 44 – a fragment of hermaphroditic duct filled with sperm, 370×

The unpaired gonad (Fig. 40a) is rather small, of beige colour, surrounded by the upper lobe of the hepatopancreas. It is built of numerous, single acini, separated by connective tissue (Fig. 41). The wall of each acinus is formed of a mono-layer squamous epithelium, laying on a basal membrane. Spermatozoa, ova and their accompanying cells differentiate from this epithelium. Spermatogenesis takes place in the lumen of the acinus (Fig. 42), where spermatogonia are located, as well as spermatocytes I, of large nuclei surrounded with a thin layer of cytoplasm; spermatocytes II, of smaller nuclei; spermatids, which are small cells of nuclei with condensed chromatin, and spermatozoa with a head and a short tail. The mature spermatozoa have a distinct elongate head, a neck and a long tail. The spermatocytes are concentrated around the SERTOLI cells, and remain in contact with them even after they have transformed into spermatozoa. The oogonia, increasing their volume, transform into oocytes I and II, and finally into mature ova. The ovum has a large nucleus surrounded by a thick layer of sponge-like ooplasm. The ova, like spermatozoa, are in permanent contact with their accompanying cells prior to leaving the acinus. The SERTOLI cells are immobile, forming a part of the acinus epithelium, while the accompanying cells leave the epithelium together with the mature gamete.

Fine efferent ducts drain particular acini of the gonad. They open into the common hermaphroditic duct (Fig. 40b). In *H. lutescens* the duct is thin, whitish, surrounded by a connective tissue sheath. It is strongly folded, hence on the transverse section more than one lumen is visible (Fig. 43). In the lumen of the hermaphroditic duct, I have found morphologically mature spermatozoa (Fig. 44). According to LIND (1973), the hermaphroditic duct in *H. pomatia* plays a part of a duct accumulating autosperm. The spermatozoa that have stayed in the hermaphroditic duct for a longer time disintegrate and are digested after getting into the gametolythic gland. Besides, BREUCKER (1964) reports that spermatozoa can also be absorbed by the epithelial cells of the hermaphroditic duct, especially in snails just leaving their winter shelters.

The hermaphroditic duct in *H. lutescens* opens to an elongate fertilization pocket. The latter passes into a fertilization pocket duct, which connects this pocket with the albumen chamber. Along the fertilization

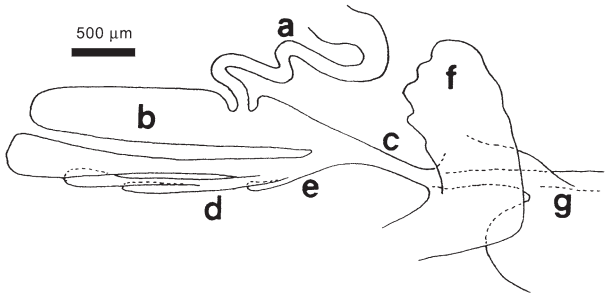
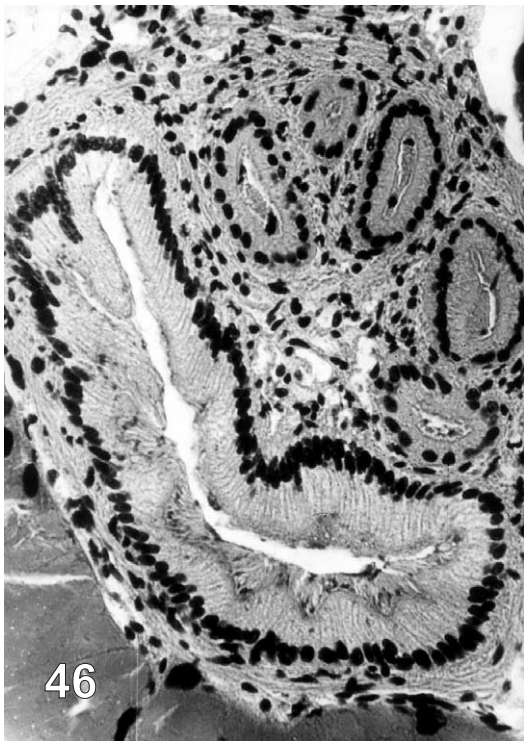
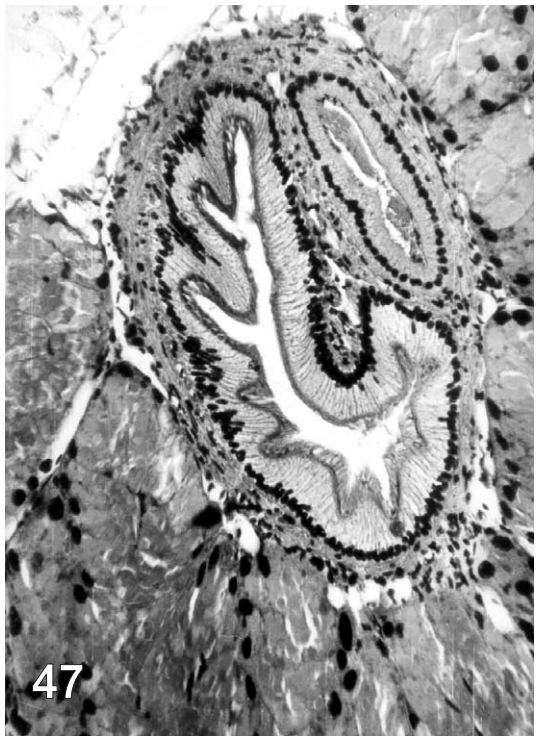
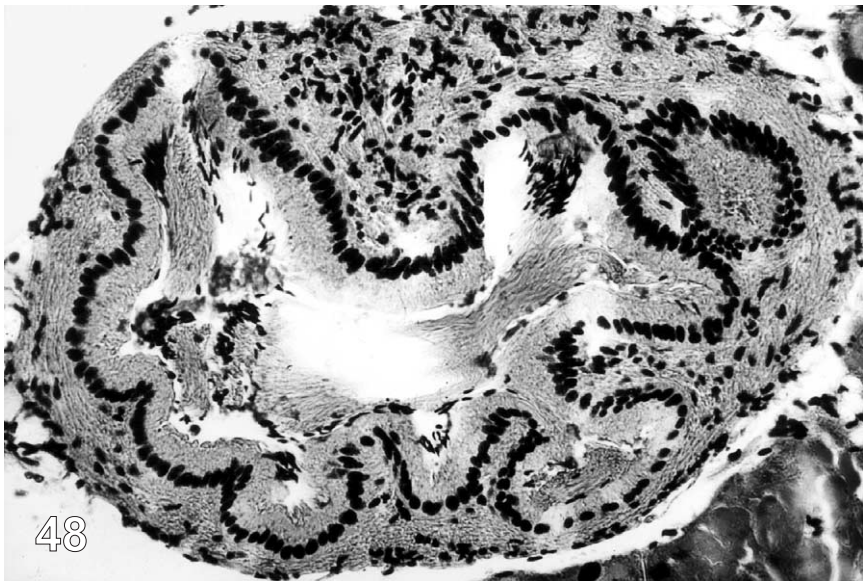


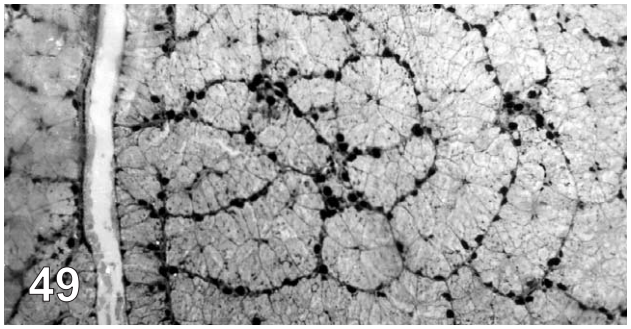
Fig. 45. Diagrammatic longitudinal section through fertilisation pocket and seminal vesicles in *Helix pomatia* L.: a – hermaphroditic duct, b – fertilisation chamber, c – duct of fertilisation chamber, d – seminal vesicles, e – duct of seminal vesicles, f – albumen chamber, g – spermoviduct (after LIND 1973)

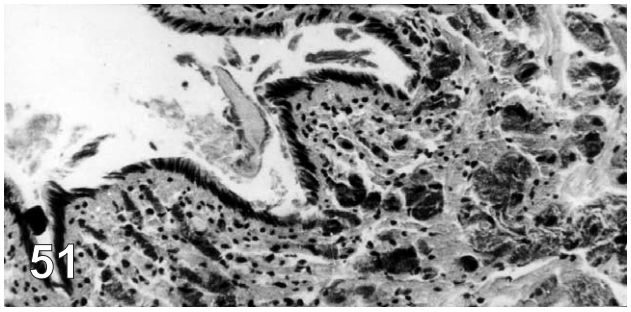


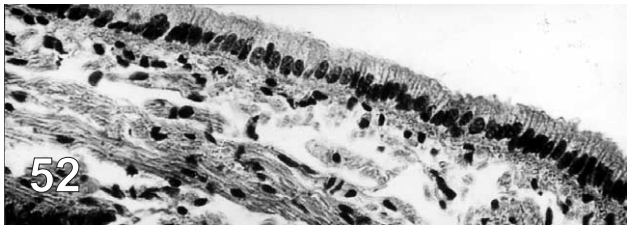




Figs 46–48. Transverse sections through fertilisation pocket and seminal vesicles: 46 – fertilisation pocket and five seminal vesicles, 175×; 47 – fertilisation pocket and seminal vesicle with ciliated cylindrical epithelium, 150×; 48 – seminal vesicle filled with spermatozoa arranged in packets, 230×







Figs 49–52. Sections through albumen gland, oviduct and vagina: 49 – albumen gland with its efferent duct, 95×; 50 – a fragment of oviduct wall lined with ciliated epithelium, 310×; 51 – vagina with numerous internal folds, 115×; 52 – a fragment of vagina wall, with well visible cylindrical epithelium, 230×

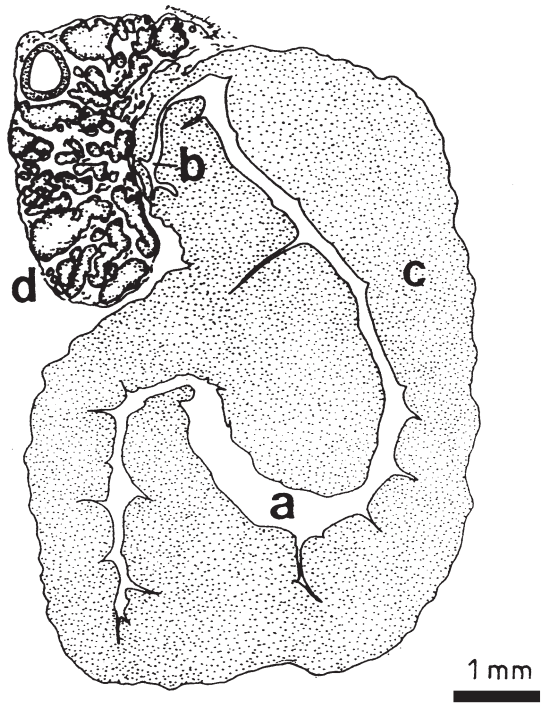
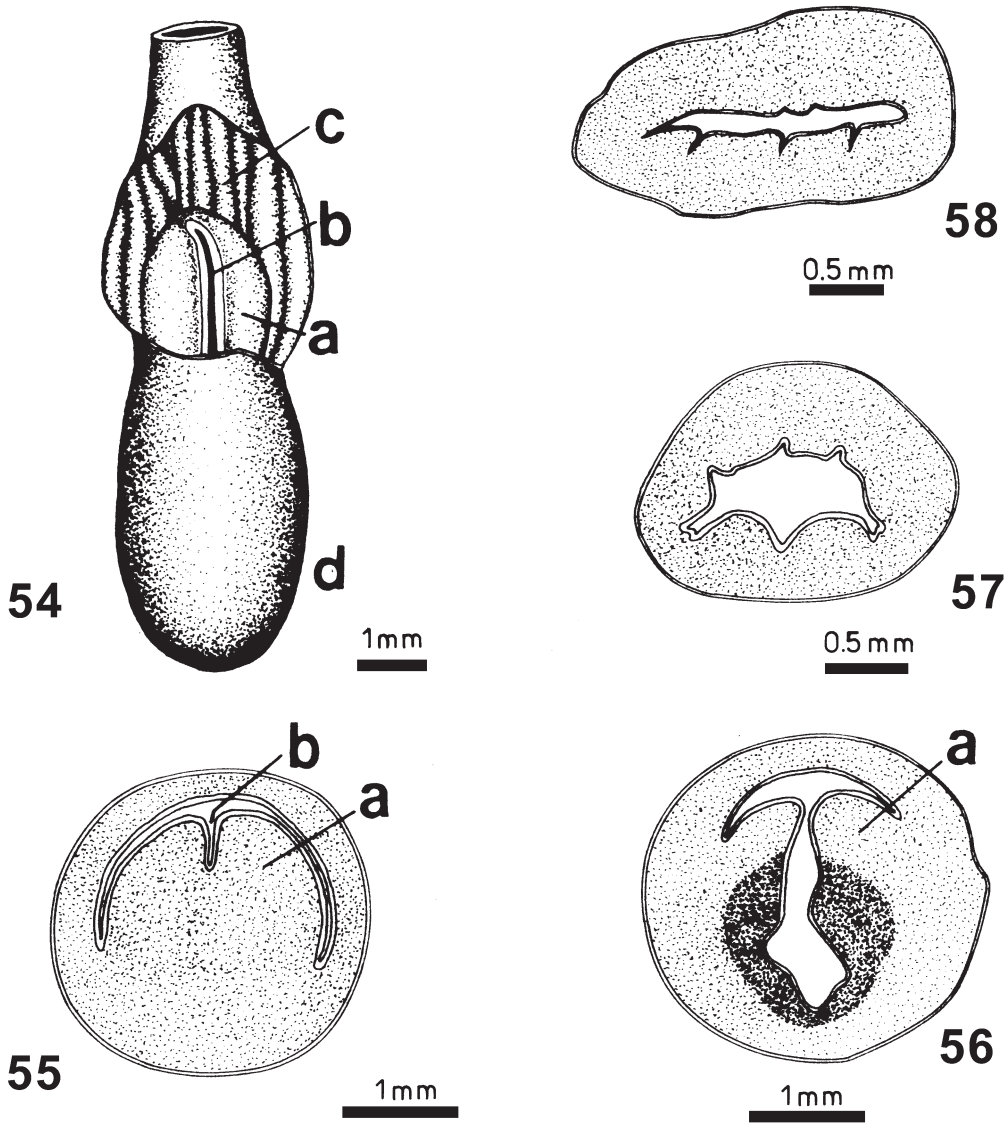


Fig. 53. Transverse section through spermoviduct: a – oviduct canal, b – glandular cells of oviduct, d – prostate gland

pocket, there are from one to five seminal vesicles of various size (Fig. 40c), which open jointly to the duct of the pocket. The above structures are located in the anterior part of the albumen gland and are the same as in *H. pomatia* (LIND 1973) (Fig. 45).

The fertilization pocket and the five seminal vesicles in *H. lutescens* are surrounded by a connective tissue sheath (Fig. 46). The walls of these structures are lined with cylindrical ciliated epithelium (Fig. 47). The nuclei of the epithelial cells are round and basally located. In the seminal vesicles spermatozoa are stored, arranged in packets (Fig. 48). According to LIND (1973), the spermatozoa come from the mating partner. In the duct of the fertilization pocket they wait for the ova to fertilize them.

The albumen gland (Fig. 40d) in *H. lutescens* is elongate, with a clearly bent posterior part. The gland consists of numerous lobules. Each lobule is built of secretory cells of a conical or cylindrical shape, whose apical parts limit the lumen of the acinus (Fig. 49). The acini open to the ciliated central duct, which in the anterior part of the albumen gland widens to form the so called albumen chamber, opening to the oviduct, as demonstrated by LIND (1973) in *H. pomatia*. According to NIELAND & GOUDSMIT (1969), in the acini of the albumen gland of *H. pomatia*, besides secretory cells, there are also the so called centrotubular cells. They are ciliated and probably take part in transporting the secretion along the lumen of the acini. The appearance of the secretory cells depends on their secretory cycle which changes with the phase of reproduction (RUDOLPH 1975). Besides, GOUDSMIT (1975) states that in the spring, when the snails prepare for reproduction, the secretory cells of albumen gland synthesize and accumulate galactogen and proteins, which are the main components of the so called perivitelline fluid. During the egg-laying, the perivitelline fluid fills the albumen chamber and directly surrounds each fertilized ovum. It constitutes the nutritive material for the developing embryo and later for the hatchlings during the first few days of their life; it forms one of the first

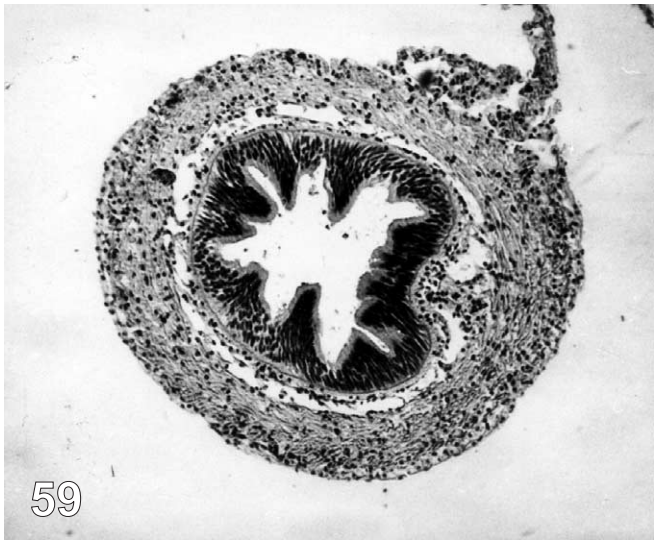


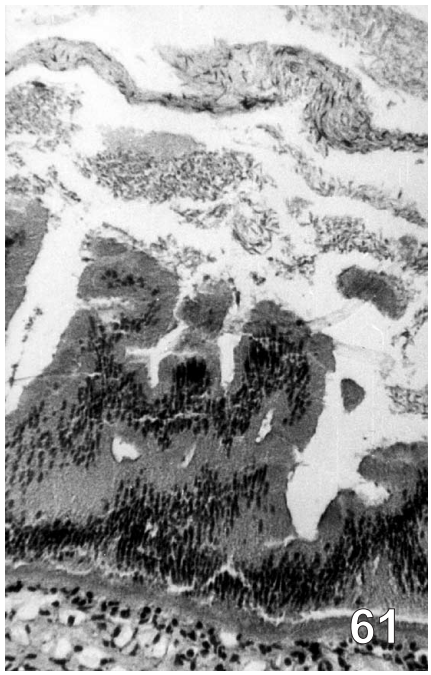
Figs 54–58. Vagina and genital atrium: 54 – internal structure of vagina; 55–57 – transverse sections through various parts of vagina; 58 – transverse section through genital atrium; a – two large folds of vagina, b – groove between two vaginal folds and love dart, c – numerous fine folds of vagina, d – love dart sac

layers of the secondary envelope. Prior to hibernation, the cells of the albumen gland in *H. pomatia* synthesize and accumulate glycogen which is a source of energy for the hibernating snail (MAY 1934, after GOUDSMIT 1975).

Where the duct of the fertilization pocket joins the albumen chamber, the spermoviduct starts (Fig. 40e). It is very long, strongly folded, yellowish-white, of mean length 30–37 mm and 5 mm thick. On its transverse section (Fig. 53), two parallel, contacting gutters are visible. One is the oviduct (Fig. 53a), the other spermiduct (Fig. 53b). Their contact in *H. pomatia* is stressed also by other authors, e.g. MEISENHEIMER (1912) and LIND (1973). They found that autosperm passed through the spermiduct gutter to the copulatory organ only during copulation, when the oviduct and spermiduct gutters were functionally separated by a transverse musculature of the oviduct wall. According to LIND (1973), the autosperm is often expelled from the hermaphrodite canal at other times, and not only during copulation. Then most spermatozoa pass from the spermiduct to the oviduct gutter, and through the terminal part of the oviduct to the gametolythic gland where their disintegration and digestion take place. The oviduct canal serves both eggs migrating downwards, and the allosperm.

The oviduct gutter (Figs 50, 53a) in *H. lutescens* is spacious, and its wall is strongly folded and lined with a ciliated epithelium. The cells of this epithelium have large, centrally located nuclei. A thick layer of the oviduct parenchyma is formed by glandular cells which provide the outer envelope for the fertilized





Figs 59–61. Gametolythic gland and its duct: 59 – transverse section through gametolythic gland duct, 79×; 60 – spermatophore and love dart in the lumen of duct, 4×; 61 – a fragment of gametolythic gland with spermatozoa at various stages of disintegration, 150×

eggs. The external envelope is the main source of calcium for the developing embryo. Where the spermoviduct ends, the oviduct canal passes into the free oviduct and then into the rather long vagina (Fig. 40f, g).

The internal structure of the vagina in *H. lutescens* is much varied. In its lumen, there are two large folds (Figs 54a – 56a). Between them, there is a fissure in which the terminal part of the love dart is located (Figs 54b – 55b). Towards the dart sac, the fissure-like lumen between the large vagina folds deepens into a common lumen of both these organs (Fig. 56). Closer to the genital atrium, on the vagina wall, there are numerous folds (Figs 51, 54c, 57). The vagina (Fig. 52) is lined with cylindrical epithelium whose cells have elongate, basally located nuclei. Below the epithelium there is a connective tissue layer, with single muscle fibres and glandular (mucous) cells embedded in it. The connective tissue is adjoined by a thick layer of bundles of variously arranged muscle fibres.

The duct of the gametolythic gland opens to the vagina (Fig. 40h). The mean length of the duct is 30 mm. I have found, as was reported by ROSSMÄSSLER (1837), that in *H. lutescens* it is always devoid of diverticle, which is present e.g. in the related *H. pomatia*. Like the vagina, the spermatheca duct on its

whole length is built of cylindrical epithelium and muscular layer. Based on this, LIND (1973) postulated that in *H. pomatia* it was a continuation of the vagina. The lumen of the gametolythic gland duct is narrow and irregular (Fig. 59). Some cells of its epithelium are higher, others lower, surrounded by a thin layer of circular muscle fibres. Below, there is a thick layer of longitudinal muscle fibres, interspersed with connective tissue. Following copulation, in the gametolythic gland duct of *H. lutescens*, the spermatophore and love dart are present (Fig. 60). According to LIND (1973), in *H. pomatia* strong unidirectional contractions of the muscular layer of the duct move the spermatophore to the gametolythic gland.

The gametolythic gland (Fig. 40h) in *H. lutescens* is spherical or oval, 3–4 mm in diameter and of red-brown colour. It is located just next to the kidney. In the lumen of the gland I found mucus and few spermatozoa at various stages of disintegration (Fig. 61). Following copulation, the whole spermatophore enters the gametolythic gland, and the unshot love dart may also enter it (Fig. 60). According to LIND (1973) the gland in *H. pomatia* is the place of disintegration of allosperm, excess of autosperm and of other products of the reproductive system. This is confirmed by the studies of HRYNIEWIECKA-SZYFTER & RĘDZINIAK (1976). LIND (1973) suggests that a part of the products decomposed in the gametolythic gland remains as a red mass composed of substances which are not absorbed by the epithelium and will never be removed from the gland. REEDER & ROGERS (1979) found that the gametolythic gland in the genus *Sonorella* Pilsbry was a storage, digestive and absorption organ.

The dart sac (Fig. 40i) opens to the vagina. In *H. lutescens* the sac is large, strongly muscled, of whitish colour, and its shape is sac-like. Its mean length is 5.0–5.5 mm, the diameter ca. 3 mm. On its longitudinal section (Fig. 62), a canal is visible, with a small papilla, built of a thick layer of muscles. It is separated by a very narrow lumen from the bottom sac wall. The inner surface of the sac and the papilla are lined with cylindrical epithelium (Figs 63, 64). The cells of this epithelium have elongate, basally located nuclei. Under the epithelium, there is a fairly thick layer of loose connective tissue. Then, there is a thick muscle layer, with circularly and longitudinally arranged fibres. Calcium concretions were found in the sac tissues. They are the most numerous in the papilla (Figs 63, 65), and much less so in the walls of the sac. DILLAMAN (1981) reports that in *H. aspersa* the love dart is formed as a result of the secretory function of the papilla epithelium and the inner surface of the sac. It is built of aragonite. The anterior part of the love dart in *H. lutescens* is set on the papilla. A more or less open calyx can be distinguished in it, which constitutes ca. 1/6 dart length (Fig. 66). The calyx consists of a base on which there are "petals" with delicately serrated margins. They are rather wide and sometimes overlap. The calyx passes gently into a slightly bent stem which, gradually narrowing, is strongly tapered at its end. On the stem there are four ribs. They start at the base of the calyx and continue almost to the end of the stem. Perhaps they play a role of reinforcing structures, as was observed by HUNT (1979). The terminations of the love dart ribs in *H. lutescens* are of different shape (Fig. 68). Two opposite ribs are club-shaped, and the remaining two are only delicately rounded at their ends. Inside the stem of the love dart there is a canal. It is spacious, rounded in outline. The surface of the love dart (Fig. 67) is rough, covered with numerous tubercles. The latter are the most numerous on the surface of the calyx base and undoubtedly also play a reinforcing role. FEDOSEEVA (1994) reports that in members of the Helicoidea the whole structure of the love dart increases its mechanical resistance. The mean length of the dart in *H. lutescens* is 6–7 mm, the width being 0.8 mm. It is almost by 1/3 longer than the sac lumen, so that its terminal part is located in the groove between the two large vaginal folds (Fig. 54a).

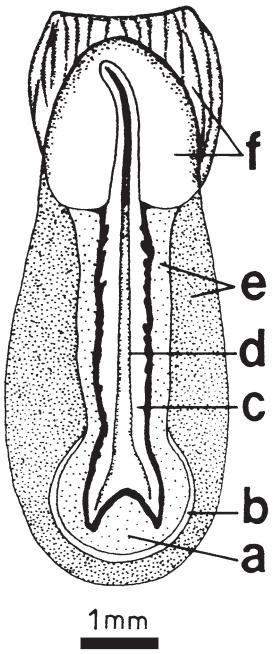
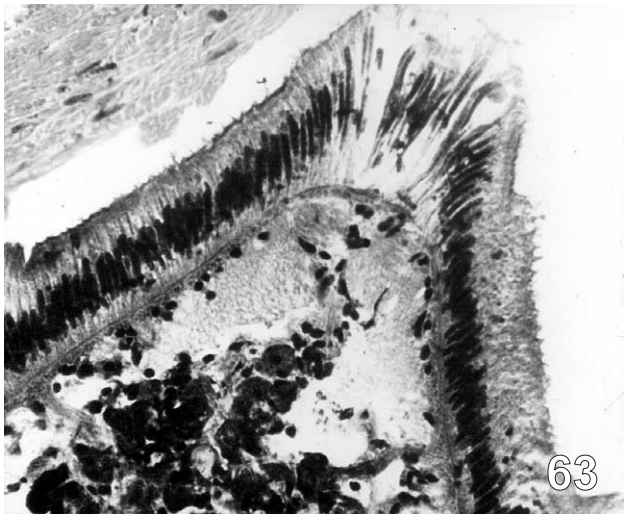
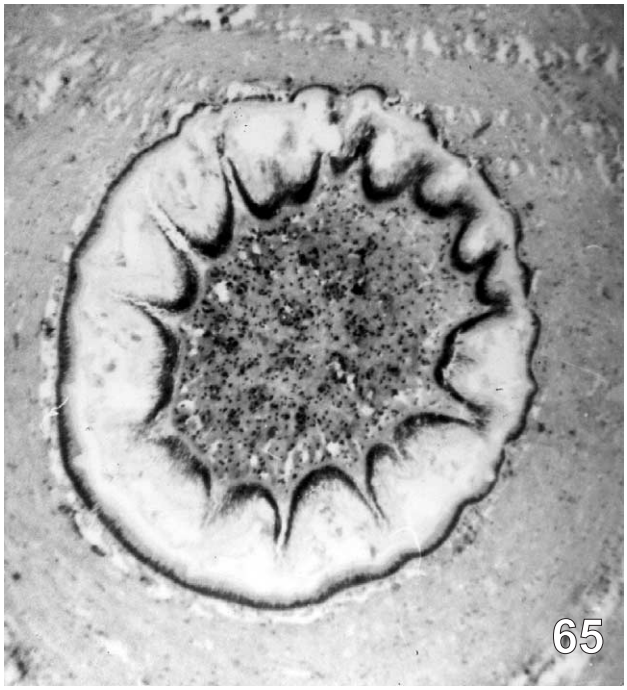
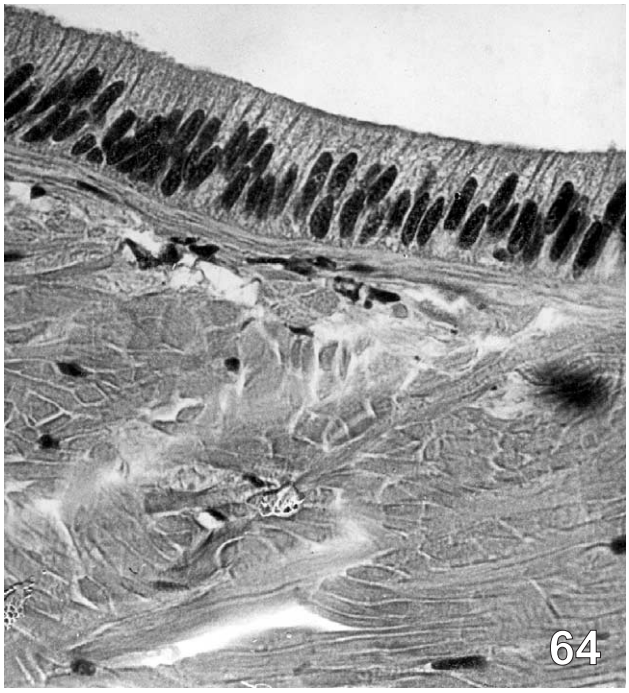


Fig. 62. Diagrammatic longitudinal section through love dart sac: a – papilla, b – lumen between the papilla and the bottom of the sac, c – sac canal, d – love dart, e – sac muscles, f – vaginal folds

Characteristic mucous glands (Fig. 40k) also open to the vagina. They are finger-shaped or tubular, of white colour. They are arranged in two bundles, left and right. The right bundle consists of an average of 61 finger-like branches and opens to the vagina through a thick trunk. The left bundle, of an average





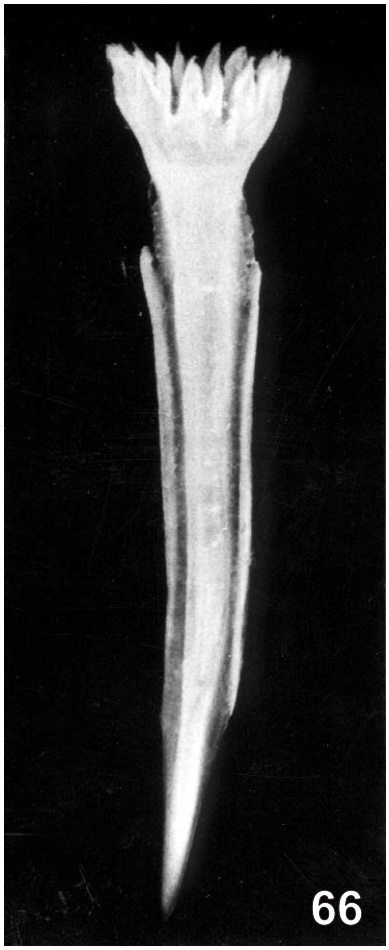


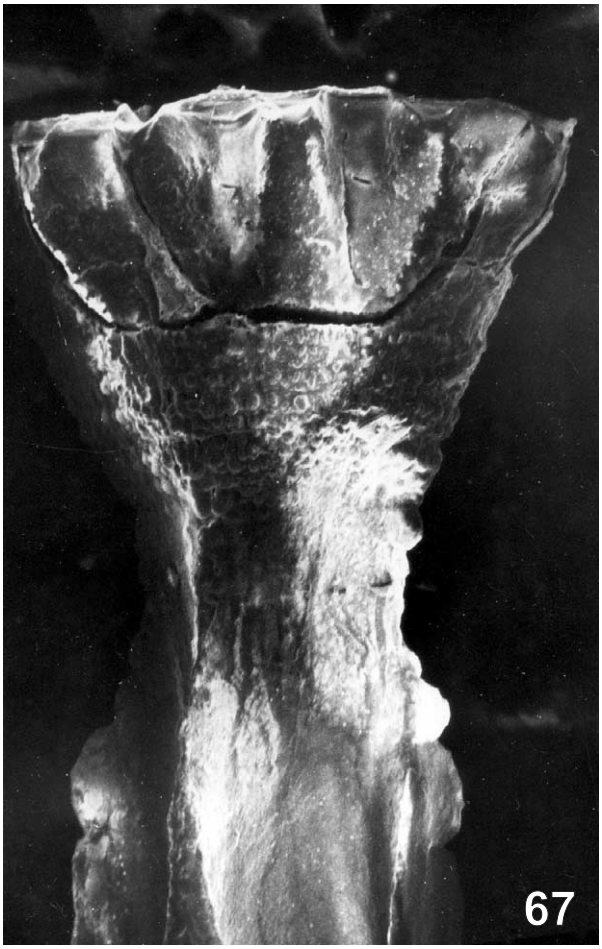
Figs 63–65. Sections through love dart sac: 63 – longitudinal section through sac papilla with cylindrical epithelium, 265×; 64 – a fragment of sac wall lined with cylindrical epithelium, 445×; 65 – transverse section through papilla with accumulations of calcium carbonate concretions, 53×

of 52 branches, opens to the vagina with a thinner trunk. The length of each bundle ranges from 10 to 15 mm. Each mucous gland has a spacious, circular lumen, filled with milky mucus (Fig. 69) and is built of cylindrical epithelium whose cells adhere closely. Their nuclei are large, round and basally located (Fig. 70). The epithelium of the mucous gland is surrounded by muscle fibres pressed into a wall built of connective tissue. GOMEZ et al. (1996) report that in the Helicoidea the cells of the mucous gland display a considerable development of organelles associated with secretion, and bear structural characters of transporting cells. The secretion of the mucous glands is transferred to the vagina pior to copulation. According to MEISENHEIMER (1912), in *H. pomatia* the mucus from the mucous glands facilitates movements of the love dart during its shooting. JEPPESEN (1976) found that snails with removed mucous glands were unable to receive the spermatophores donated during copulation. A stimulating role of the mucous secretion of these glands, transferred by the love dart during courtship in some species of the genus *Helix*, was stressed by DORELLO (1925) and BORNCHEN (1967). ADAMO & CHASE (1990) suppose that in *H. aspersa* the secreted mucus contains an active component (pheromone) which, when transmitted by the love dart to the partner's haemocoel, shortens the duration of courtship. However, JEPPESEN (1976) and LIND (1976) in *H. pomatia*, and GIUSTI & LEPRI (1980) and CHUNG (1986, 1987) in *H. aspersa* showed no stimulating influence of the shot dart on the behaviour of snails during courtship. According to LIND (1976), the shot dart has even an inhibitory effect on the receiver and clearly delays the copulation, which I have also observed in *H. lutescens*. JEPPESEN (1976) demonstrated that the presence/absence of the sac and love dart, and of mucous glands, had no effect on the sexual activity and the mating behaviour of snails.

The vagina opens into a short genital atrium (Fig. 40l). Its wall is very well muscled and strongly folded (Fig. 58). The genital atrium opens with the gonopore located on the right side of the body, just below the ommatophore.

The spermiduct gutter wall is lined with ciliated cylindrical epithelium (Fig. 71). The gutter is adjoined





Figs 66, 67. Love dart: 66 – love dart (after KORALEWSKA-BATURA 1993b), 17×; 67 – surface of love dart, 143×

by the prostate gland (Fig. 40m), with a well visible blood vessel (Fig. 72).

The prostate consists of glandular cells of large, basally located nuclei (Fig. 72). Its secretion products are found in the lumen of the spermiduct gutter. According to BREUCKER (1964), in *H. pomatia* the prostate is at a constant secretory phase during the whole activity period, and not only during mating.

Near the terminal part of the prostate in *H. lutescens*, the spermiduct gutter passes into a thin vas deferens (Fig. 40n). It runs freely in the snail's body, though at half its length it is suspended with connective tissue on the genital atrium wall. On transverse sections (Figs 73, 74) its inner wall is strongly folded and lined with ciliated cylindrical epithelium of large, centrally located nuclei. The ciliae of the epithelium are dense and so long, that they almost completely obliterate the spermiduct lumen (Fig. 73). In the region of the outlet of the spermiduct to the epiphallus, the ciliae get shorter (Fig. 74). Below the spermiduct epithelium, there is a rather thin layer of longitudinal muscle fibres, interspersed with connective tissue.

The vas deferens enters apically a short (3–4 mm) epiphallus (Fig. 40o). The latter structure is grey as a result of a strong pigmentation. Inside it (Figs 75b, 79) there are five large folds.

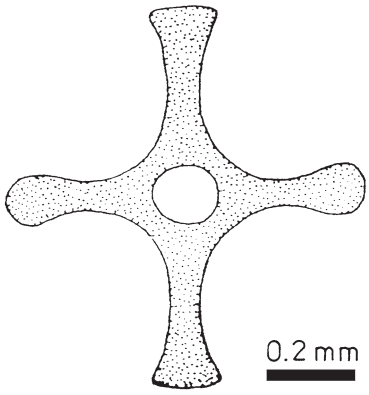
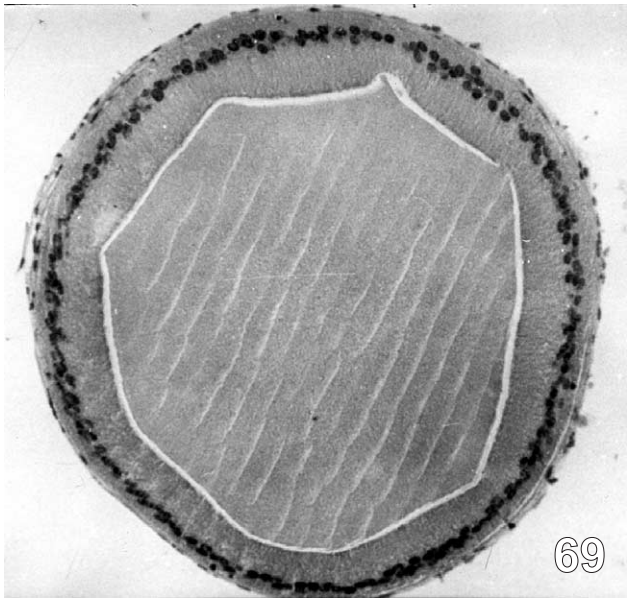
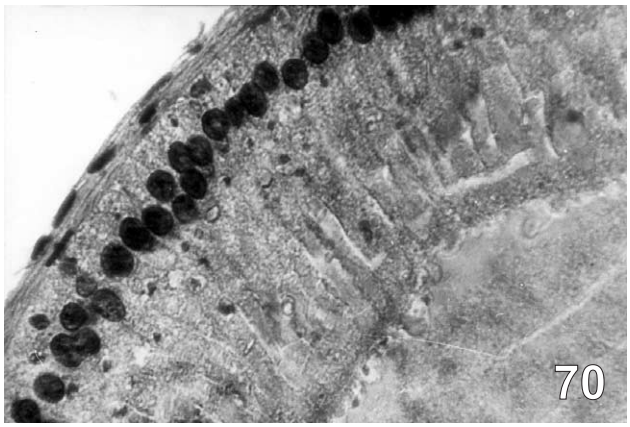


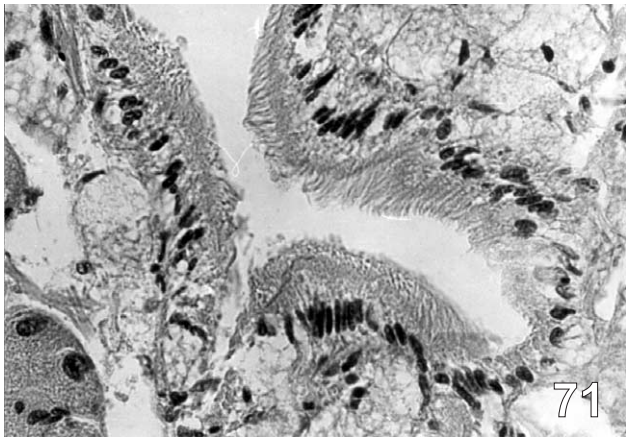
Fig. 68. Transverse section through love dart stem (after KORALEWSKA-BATURA 1993b)

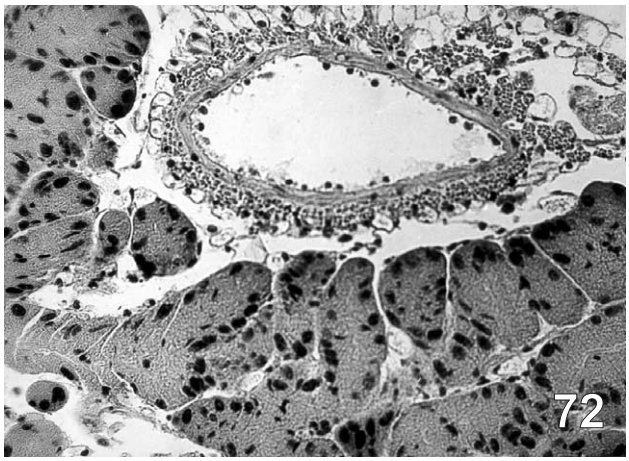
Also the flagellum opens to the epiphallus (Fig. 40p); it is delicately pigmented, of average length of slightly over 30 mm. Its lumen on its whole length is filled with a hook-shaped, longitudinal fold (Fig. 76).





Figs 69, 70. Mucous gland: 69 – transverse section through mucous gland, 150×; 70 – a fragment of gland wall lined with cylindrical epithelium, 550×

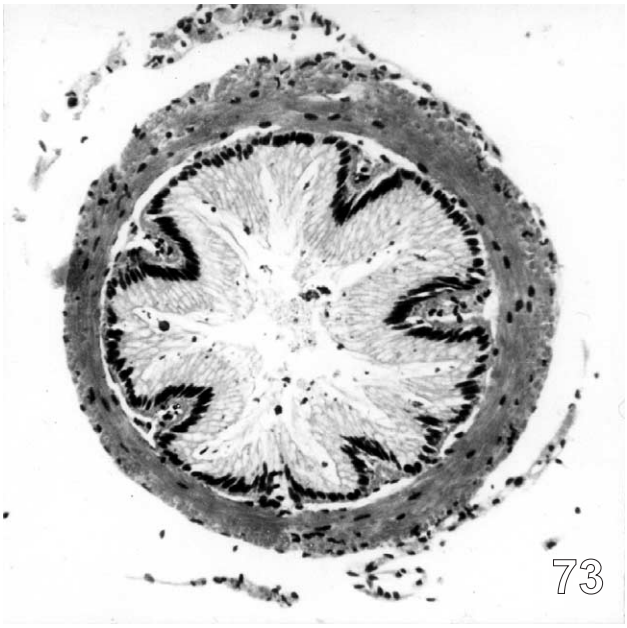


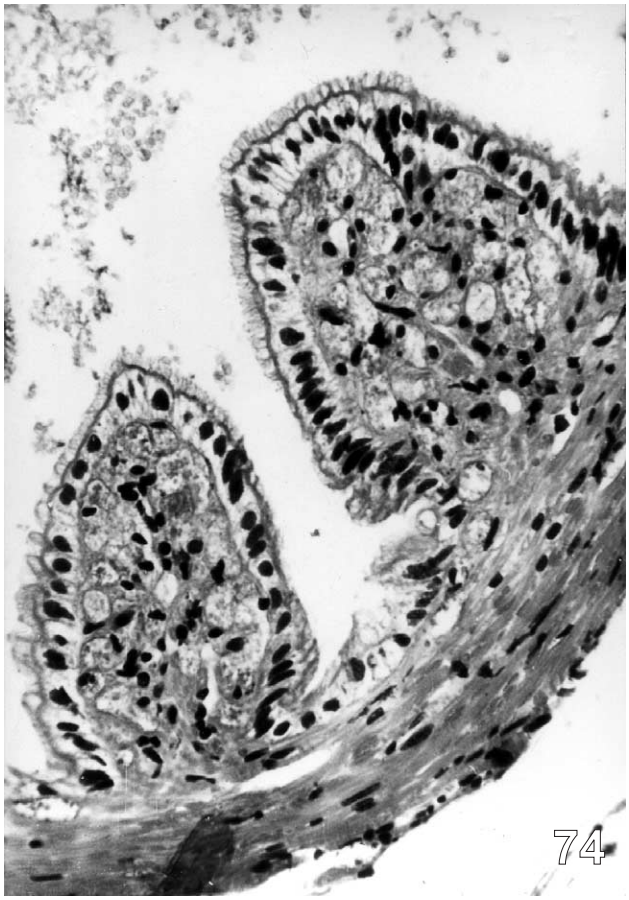


Figs 71, 72. Sections through sperm groove and prostate gland: 71 – sperm groove lined with ciliated cylindrical epithelium, 310×; 72 – prostate gland with visible blood vessel, 150×

The flagellum wall (Fig. 77) is lined with cylindrical epithelium of elongate, basally located nuclei. The epithelium is surrounded by muscle fibres. Among them, there are numerous glandular cells with mucous secretion. The epiphallus and the flagellum are spermatophore-producing organs. The spermatophore has a very delicate envelope of thin translucent walls, usually amber-yellow. The formation of the spermatophore sheath is initiated just after mating has started and before the spermatozoa reach the vas deferens. During copulation, spermatozoa are injected into the sheath to be exchanged between the partners as spermatophores.

The spermatophore in *H. lutescens* (Fig. 78) consists of a head, neck, body and tail and differs from that of *H. pomatia* only in a smaller size (MEISENHEIMER 1976). The head has a form of an elongate, slightly bulged tube. The head and neck combined are ca. 7 mm long. Along the head there run delicate convexities. They may increase its elasticity and resistance to the pressure of musculature of the vagina and gametolythic gland duct. The spermatophore body is formed in the epiphallus. It is ca. 3.8 mm long and consists of a densely and spirally packed thread of spermatozoa. In its anterior part, the body is closed, while its posterior part is directly connected with the tail. It is the longest and very delicate section of the spermatophore, of an average length of ca. 30 mm. A longitudinal fold of the flagellum results in the spermatophore's tail having a shape of an open canal corresponding to the lumen of the flagellum in which it is formed. In the tail's lumen there is a thread of spermatozoa, which is a prolongation of the contents of the spermatophore body. The direct connection between the posterior part of the spermatophore's body and its tail's lumen makes it possible for the spermatozoa to migrate from the body to the open canal of the tail. Only some of the spermatozoa leave the tail and pass to the oviduct, to reach the seminal vesicles. The remaining part of the spermatophore gets to the gametolythic gland to disintegrate and be digested.





Figs 73, 74. Sections through vas deferens: 73 – transverse section through vas deferens, 117×; 74 – a fragment of vas deferens wall lined with ciliated cylindrical epithelium, 270×

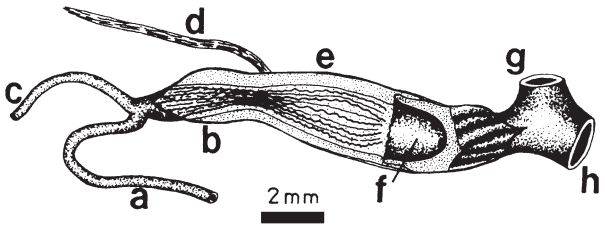
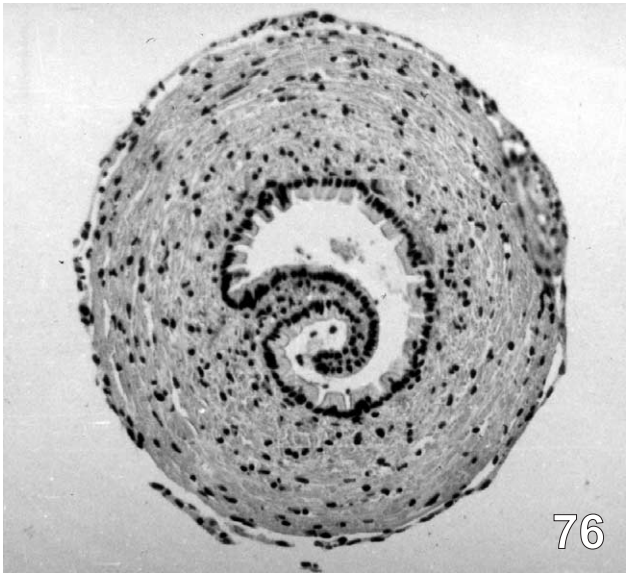
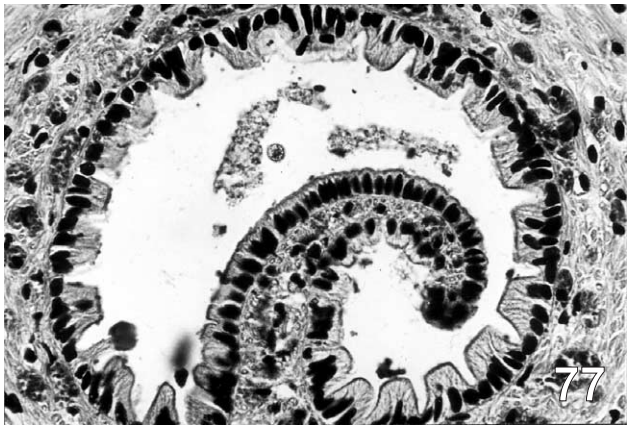


Fig. 75. Diagrammatic longitudinal section through the middle of penis and epiphallus: a – vas deferens, b – epiphallus, c – flagellum, d – penial retractor muscle, e – penis, f – papilla penis with opening at top, g – genital atrium, h – outlet of female reproductive tracts to the atrium





Figs 76, 77. Sections through flagellum: 76 – transverse section through flagellum with visible hook-like fold, 125×; 77 – wall of flagellum lined with cylindrical epithelium, 290×

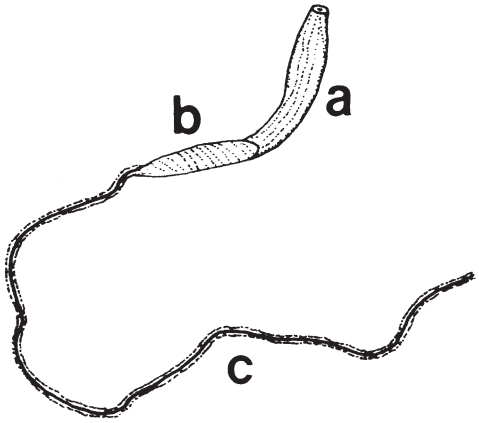
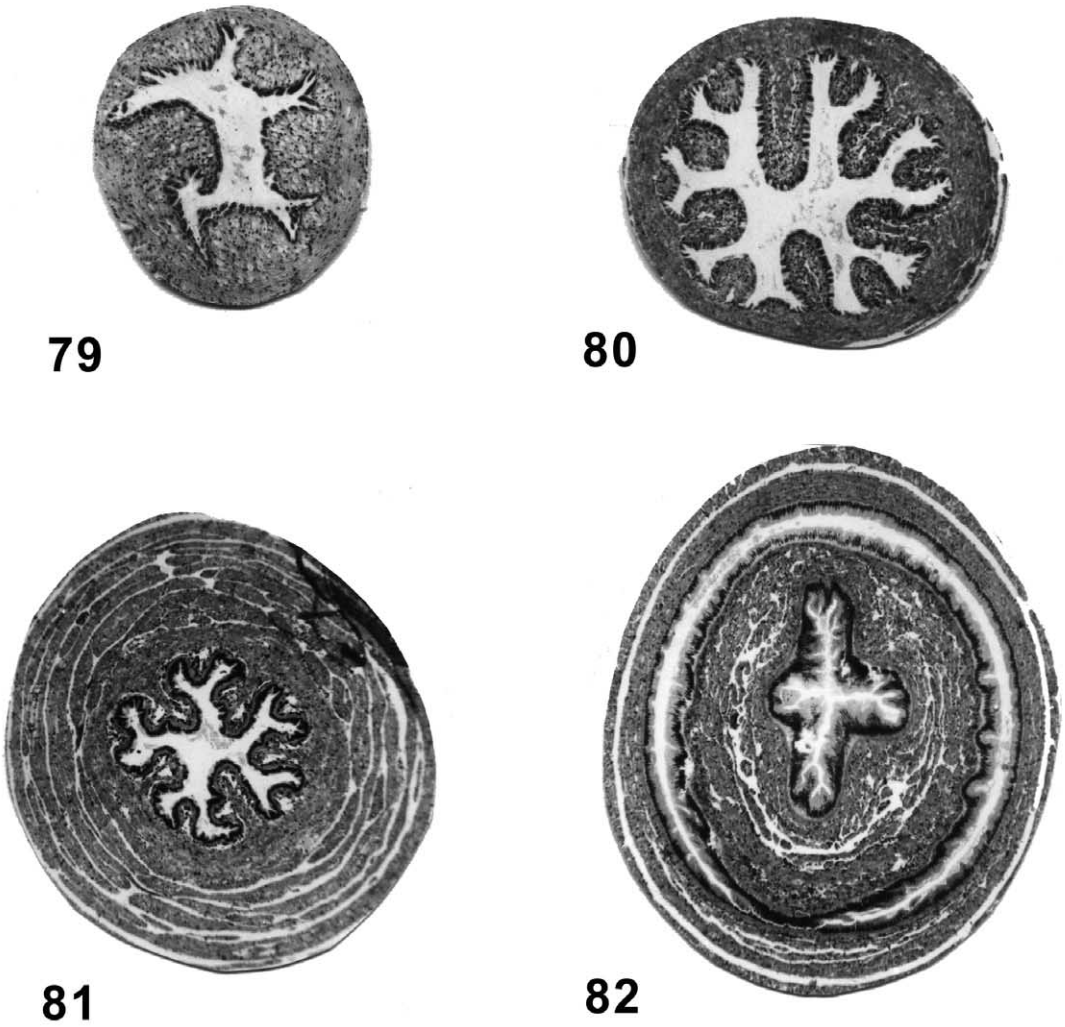


Fig. 78. Spermatophore: a – head and neck, b – body, c – tail; 3×

The epiphallus, narrowing considerably, passes into penis (Fig. 40r). In this place the penial retractor muscle is inserted (Fig. 40s). The penis is elongatedly tubular, of an average length of ca. 8 mm. Like the epiphallus, it is strongly pigmented, which is characteristic of adult individuals of *H. lutescens*. Inside the penis, there are numerous folds (Figs 75e, 80). Thicker folds are the continuation of the five epiphallial folds. The penial folds converge at the base of penial papilla, resulting in a decrease of the penis lumen (Fig. 81). The papilla is strongly domed (Fig. 75f) and, contrary to the pigmented part of penis, is whitish. On its top there is an irregular penial opening (Fig. 82). The penis and epiphallus pigmentation may be an additional diagnostic character to distinguish *H. lutescens* from the related *H. pomatia* in which the penis and epiphallus are always uniformly white. The penis, like the vagina, opens to the genital atrium (Fig. 75g), which is the terminal section of the



Figs 79–82. Transverse sections through terminal portion of male genitalia: 79 – epiphallus, 38×; 80 – mid portion of penis, 38×; 81 – base of papilla penis, 38×; 82 – terminal portion of penis, 38×

reproductive system. During copulation the penis and vagina of each partner are everted, and the penes are inserted into the vaginae simultaneously. This enables transfer of sperm in spermatophores which leave the snail's body through the opening at the top of the penial papilla.

B. DISTRIBUTION OF *H. LUTESCENS* IN POLAND

In Poland *H. lutescens* occurs only in the south-eastern part of the country: in Roztocze, the uplands Wyżyna Lubelska, Wyżyna Malopolska, the lowland Nizina Sandomierska and the foothills of the Beskid Wschodni mts (up to ca. 300 m a.s.l.). In the first half of this century, its distribution extended westward to the line Kraków-Busko-Kielce-Skarżysko Kamienna-Kazimierz Dolny, and northward to the northern egde of the upland Wyżyna Lubelska (RIEDEL 1988). In Poland *H. lutescens* reaches its north-western distribution border. Below I list its up-dated localities in Poland (Fig. 83), based on UTM grid system.

The following localities, listed in older literature and then regarded as doubtful, have been recently confirmed by me: Lubelskie voivodeship: FB 17 Abramowice near Lublin, EB 68 Janowiec – xerothermic hills, EB 68 Kazimierz Dolny – cemetery, FB 30 Zwierzyniec – parks, gardens; Podkarpackie voivodeship: FA 32 vicinity of Przemyśl; Świętokrzyskie voivodeship: DB 73 Kielce – cemetery, gardens, shrubs at the foot of Wietrznia, DB 61 Korytnica near Jędrzejów, DB 60 xerothermic hills between Pińczów and Skowronno.

Recently, BARGA-WIĘCŁAWSKA (1989) has found localities of *H. lutescens* in the Świętokrzyski National

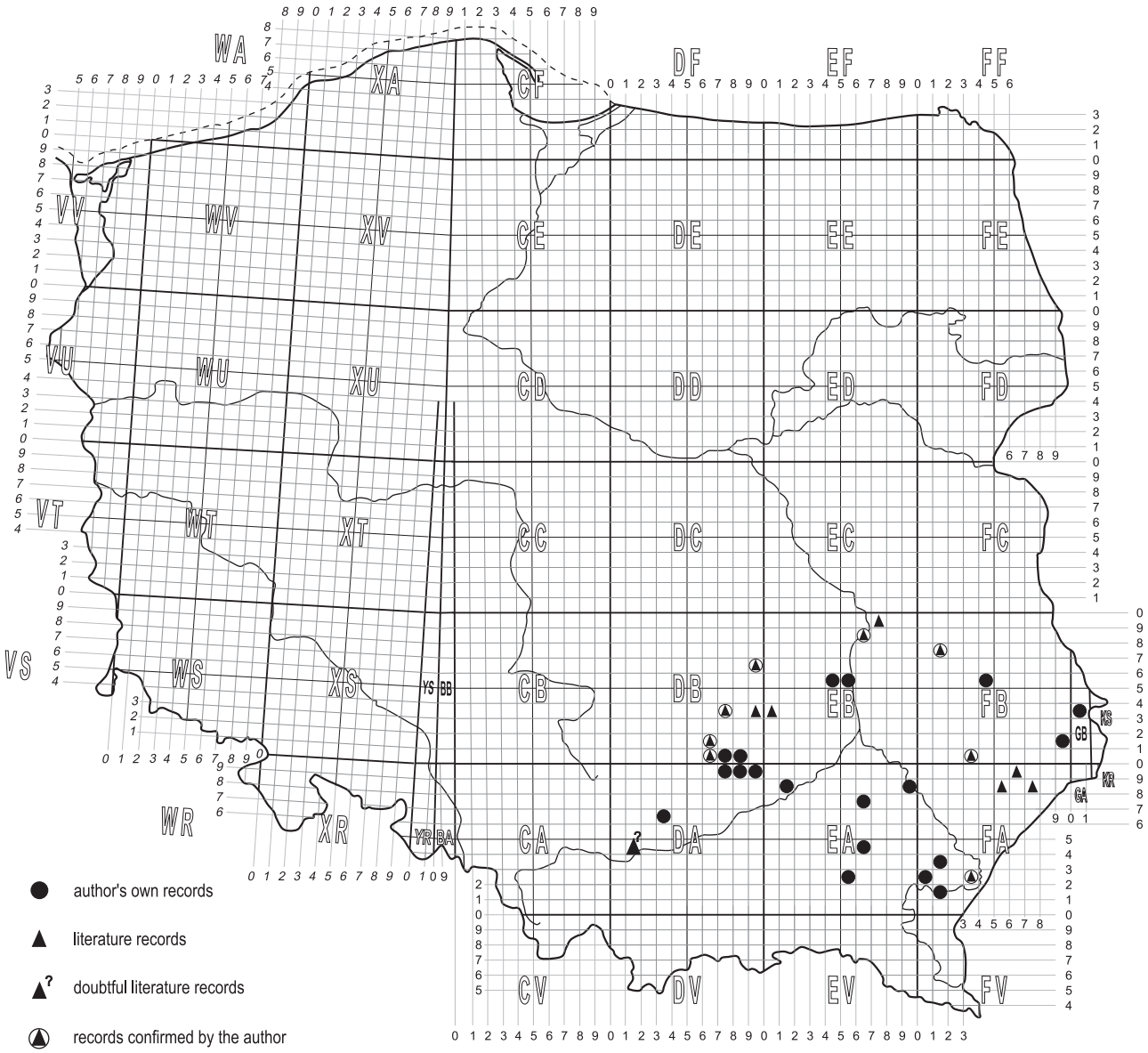


Fig. 83. Distribution of *H. lutescens* in Poland

Park and its protecting belt, i.e.: DB 93 Łysa Góra, EB 03 Baszowice, EB 03 Góra Chełmowa, EB 03 Rudki, EB 03 Serwis Dąbrowa and DB 73 Kielce – cemetery and gardens. Besides, PIECHOCKI (1990, 1991) lists the following localities in the Roztoczański National Park: FB 30 Zwierzyniec, FB 30 Tartaczna Góra near Zwierzyniec, FA 58 Rebizanty on the Tanew river, FA 58 Rybnica, FA 69 Góra Wapielnia, FA 78 Machniów near Lubycz Królewska.

New records of the snail, found by me, are the following: Lubelskie voivodeship: GB 03 Gródek – bushes at a field road to the river Huczwa, FB 45 Suchodoły – bushes in the park, FB 91 Tyszowce – cemetery; Małopolskie voivodeship: DA 36 Maszków near Słomniki; Mazowieckie voivodeship: EB 45 Czekarzewice – shrubs, EB 55 Józefów – bushes on the Vistula river; Podkarpackie voivodeship: FA 02 Babice – San river escarpment, FA 32 Buszkowice – bushes on the San river, FA 13 Bystrowice – roadside bushes, EA 98 Bystre – bushes, FA 11 – bushes between Krzywcza and Ruszelczyce, EA 67 Nowa Wieś Czudacka – bushes on a small river, EA 52 Ubieszyn – bushes on the San river, EA 64 Zwięczyca – bushes; Świętokrzyskie voivodeship: DB 73 Białogon near Kielce – xerothermic grassland, DA 89 Busko Zdrój – gardens, nature reserve Zimne Wody of limestone-gypsum substratum and steppe vegetation, DB 73 Kielce – area covered with grass vegetation, DB 70 Kije – cemetery, EA 18 Łubnice – bushes, DB 60 Pińczów – sunny slope, DA 89 Siesławice near Busko Zdrój – steppe vegetation on gypsum-limestone susbtratum, DB 96 Skarżysko Kamienna – cemetery, bushes on a drainage plot, DB 61 Sobków near Korytnica – cemetery, DB 60 Skowronno – roadside ditches, DA 99 Stopnica – garden, DA 89 Szczaworyż – Garb Pińczowski, DB 80 Śladków Mały – hills with rock outcrops, DA 79 Winiary near Pińczów.

I have never found *H. lutescens* to co-occur with *H. pomatia*.

The new records of *H. lutescens* from Poland do not shift its distribution border given by RIEDEL (1988). The latter author cites URBAŃSKI (1977) who reports that the snail has gone or is going extinct near Kraków (DA 14); likewise, my own studies have not confirmed the occurrence of *H. lutescens* in the region of Kraków. Contrary to what is reported by RIEDEL (1988), *H. lutescens* is not going extinct in the Świętokrzyskie Mts; in anthropogenic sites it forms there abundant insular populations (KORALEWSKA-BATURA 1993c, BARGA-WIĘCŁAWSKA 1997). Likewise, the populations of *H. lutescens* from Roztocze are not endangered. They are numerous and of high density (PIECHOCKI 1990).

Because of its distribution (north-western distribution border), insular occurrence and possibility of accidental collection for culinary purposes, *H. lutescens* is legally protected in Poland (WIKTOR & RIEDEL 1992).

C. BIOLOGY

1. Diurnal and seasonal activity of adult individuals

In the wild, *H. lutescens* is active only during the vegetation season. The snails spend the remaining part of the year buried in the soil ca. 6 cm deep. Their shells are then positioned with their apertures upwards, the aperture being closed with the calcified epiphragm. At the end of April and in the first days of May the snails reject their epiphragms and leave their winter shelters. The activity of adult *H. lutescens* includes seasonal behaviour: feeding, courtship and copulation, egg-laying and preparations to hibernate.

During rest, at a considerable air humidity, the snail's head is retracted into the shell, and the foot adheres to the substratum. With increasing humidity the snails may immediately get active. Low or high temperatures cause the snails to retract completely into the shell and lie on the ground. Fairly often, during drought, the snails form a membrane of solidified mucus, which attaches them to the substratum. At such times they do not react to tactile stimuli and are unable to regain activity immediately.

The diurnal activity of the snails in the spring is presented in Figure 84. The vertical section denotes standard deviation, for three observation sessions: on May 11/12th (Fig. 84a), 25/26th (Fig. 84b) and June 7/8th (Fig. 84c) 1995.

The curve of the diurnal activity indicates that in the spring the activity of the snails starts with the increase in relative humidity. The further increase in the proportion of active individuals is correlated with the increase in relative humidity to 100%, which is most often associated with a decrease in air temperature in the ground layer to the so called dew point. According to my observations, this usually fell on the hours from 15.00 to 11.00 next day. The percentage of active snails was the highest between 5.00 and 9.00. At noon and in the afternoon, from 11.00 till 15.00, at an increase of temperature till 26°C and relative humidity of 74%, the snail activity was close to zero.

The considerable standard deviation from the mean activity, between 17.00 and 3.00, is associated with rather widely varying weather conditions during the consecutive spring observations. Gusty winds and low temperatures in the night considerably decrease the snail activity (Fig. 84a). On a sunny day, a rapid increase in activity was associated with a passing rain of only several minutes duration (Fig. 84b). A gradual increase in relative humidity results in a slow increase in activity which gets more intense at the dew point, already at a temperature of 15°C (Fig. 84c).

H. lutescens has no permanent shelter to which it would return to rest; the snail ceases to be active and stays where it was during the final phase of its activity. However, the preferable resting places change sea-

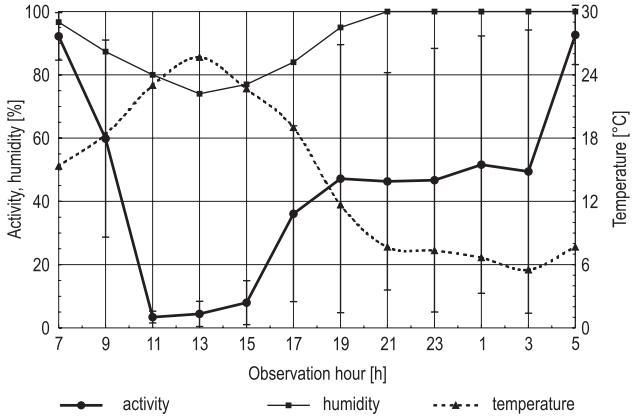


Fig. 84. Diurnal changes in the activity of snails depending on the relative humidity and temperature in the herb layer of the investigated phytocoenosis, calculated as mean values of three observation sessions in the spring 1995

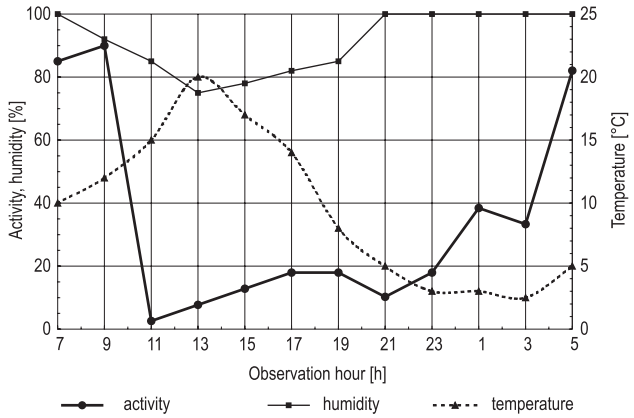


Fig. 84a. Activity of snails depending on the relative humidity and temperature in the herb layer of the investigated phytocoenosis, during a 24 hrs observation session of May 11/12th 1995 (N = 63)

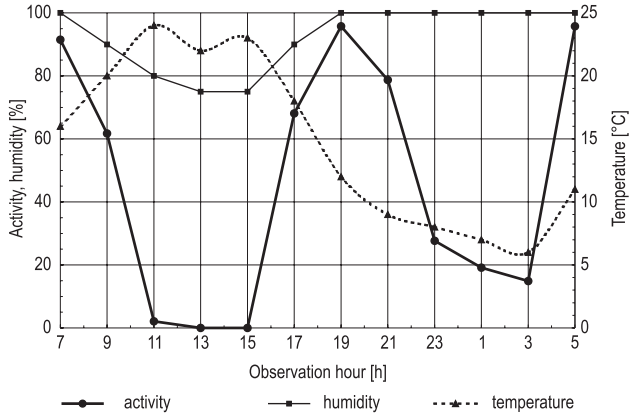


Fig. 84b. Activity of snails depending on the relative humidity and temperature in the herb layer of the investigated phytocoenosis, during a 24 hrs observation session of May 25/26th 1995 (N = 47)

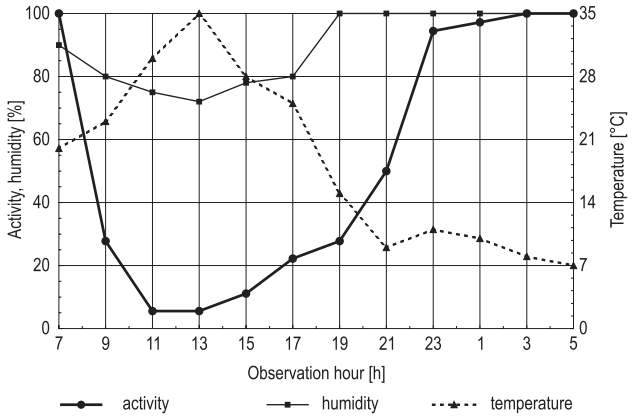


Fig. 84c. Activity of snails depending on the relative humidity and temperature in the herb layer of the investigated phytocoenosis, during a 24 hrs observation session of June 7/8th 1995 (N = 36)

sonally. On cool spring days adult snails rest in hollows in the ground, under leaves of herbaceous plants, fixed to the substratum with the foot, and for this reason they react to humidity so quickly. At the end of spring, more numerous snails rest above the ground on plants, and their reaction to changes in relative humidity is slower and gets more intense at the dew point. In the summer adult *H. lutescens* do not display a high activity and as a rule only few individuals remain on the ground.

The diurnal activity of snails during the summer was calculated based on observation sessions of June 21/22nd, July 9/10th and 25/26th, and August 10/11th 1995. The mean activity in the summer is presented in Figure 85. The curve generally corresponds to the spring activity, though there are some differences. They involve not only the number of active snails, but mainly consist in a shift of the hours of the activity and resting phases.

In the summer the snail activity started roughly at 17.00, with the increase in the relative humidity above 72%, i.e. several hours before dew appeared. In this case the maximum number of active snails was observed between 1.00 and 5.00, at 100% relative humidity. A complete cessation of activity in the summer took place much earlier, i.e. already at 9.00, and the inactivity continued till 17.00, at a temperature increased to 30°C and the minimum relative humidity of 68%. The standard deviation of the snail activity between 19.00 and 21.00 results from a longer time required for the snail to get active during the dry and hot summer 1995 (Figs 85a–c). At a minimum relative humidity of 49%, the beginning of activity was observed only at the dew point, at 21.00, at a temperature of 11°C (Fig. 85d).

During the period of the highest temperatures and at the same time the greatest drought, adult *H. lutescens* are hidden in the soil (estivation). Only few individuals rest high up on plants, fixed with mucus

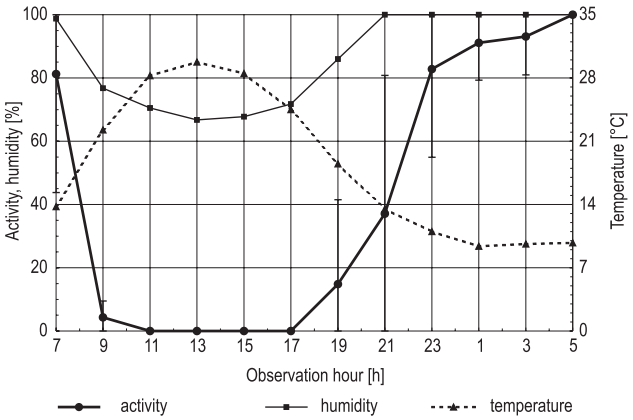


Fig. 85. Diurnal changes in activity of snails depending on the relative humidity and temperature in the herb layer of the investigated phytocoenosis, calculated as mean values of four observation sessions in the summer 1995

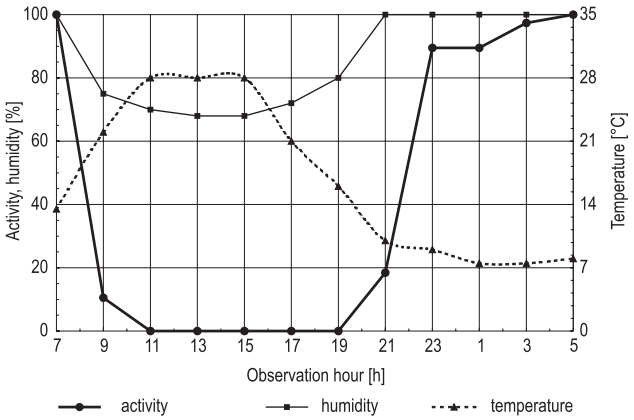


Fig. 85c. Activity of snails depending on the relative humidity and temperature in the herb layer of the investigated phytocoenosis, during a 24 hrs observation session of July 25/26th 1995 (N = 41)

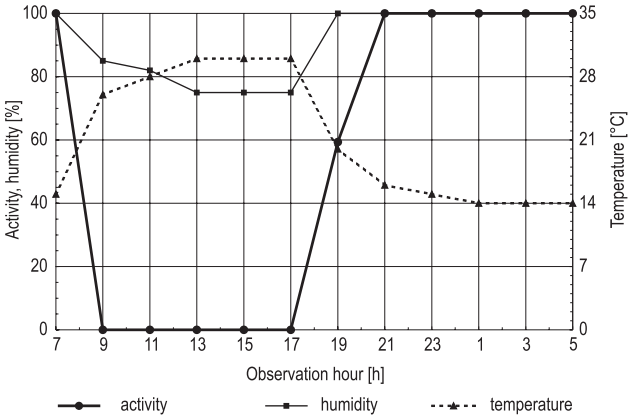


Fig. 85a. Activity of snails depending on the relative humidity and temperature in the herb layer of the investigated phytocoenosis, during a 24 hrs observation session of June 21/22nd 1995 (N = 44)

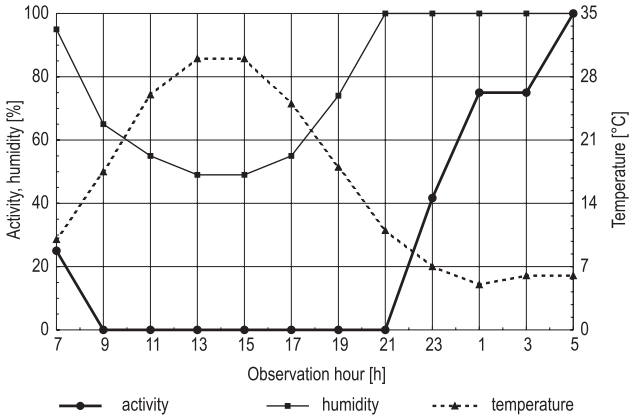


Fig. 85d. Activity of snails depending on the relative humidity and temperature in the herb layer of the investigated phytocoenosis, during a 24 hrs observation session of August 10/11th 1995 (N = 12)

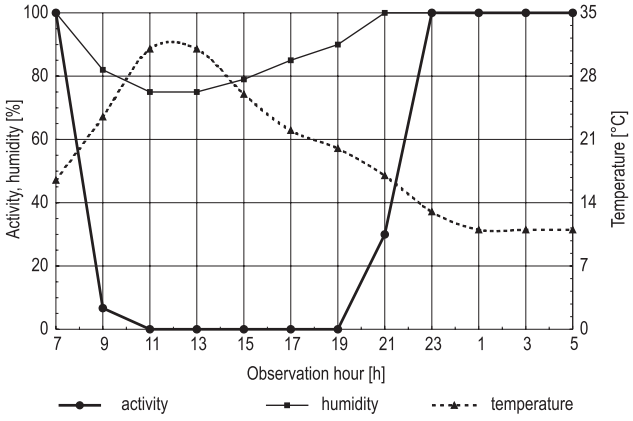


Fig. 85b. Activity of snails depending on the relative humidity and temperature in the herb layer of the investigated phytocoenosis, during a 24 hrs observation session of July 9/10th 1995 (N = 35)

membranes. They can remain in this state even up to several days. In this way the snails avoid the hottest air in the herb layer of the investigated phytocoenosis. Only a heavy rain causes an immediate restoring of activity (Fig. 86).

On rainy days, the snails can be active both during daytime and in the night, and the activity periods alternate with rest periods. Then the snails rest high up on live plants and on dry stems of the tansy (*Tanacetum vulgare* L.).

Copulation and egg-laying in *H. lutescens* are seasonal activities. A distinct peak of mating falls on May and the first half of June, though single copulating pairs were observed also in August, especially in the morning. Two weeks after copulation the snails dig nests and lay eggs. They do it most often in the morning, in the first days of June.

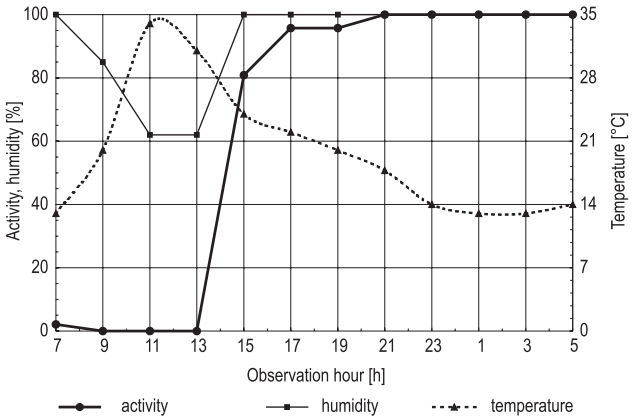


Fig. 86. Activity of snails depending on the relative humidity and temperature in the herb layer of the investigated phytocoenosis, during a 24 hrs observation session of August 24/25th 1995 (N = 46)

The diurnal activity cycle of *H. lutescens* includes two phases, whose timing is associated with circadian changes in environmental conditions, such as relative humidity, air temperature in the ground layer and humidity of the substratum (dew point). An effect of sunlight on the behaviour of the snails can not be excluded. In the spring, the snails are active at a relative humidity in the ground layer of 80–100%, and the temperature ranging from 5 to 23°C. In the summer, they are active when the relative humidity is within 86–100% and the temperature 8–18°C. A very high increase in their activity takes place after rainfall and at the dew point (water moistening the substratum). The activity phase in the spring falls between 15.00 and 11.00, and in the summer between 17.00 and 9.00 next day. Both in the spring and summer the peak of activity falls on early morning hours, just after sunrise. The rest phase falls usually on the remaining hours. In September, at a mean daily temperature of 12.4°C, the absence of adult individuals on the ground surface results from their preparation to hibernate in shelters.

According to many authors, among others GASPARD (1823), KÜHN (1914), FRÖMMING (1954), NIETZKE (1970), TISCHLER (1973, 1974) and STĘPCZAK et al. (1982), the hibernation in *H. pomatia* starts when temperature decreases in autumn. However, LIND (1988) reports that decreasing temperatures have no effect in the initial period of hibernation, which in *H. pomatia* starts as early as in the third week of August. According to that author, it is very likely that the initial period of hibernation is influenced by the change in photoperiod, as was earlier reported by JEPPESEN & NYGÄRD (1976) and JEPPESEN (1977). The latter authors are of opinion that cessation of hibernation depends on photoperiod, and also on relatively high temperatures, exceeding a threshold value and remaining at that level for a longer time. However, KÜHN (1914) and FISCHER (1931) suggest that varied tendencies of particular individuals to hibernate and resume activity are also an effect of the annual cycle of their physiological changes. The activity of the snails would be thus influenced by both external and internal, physiological, factors.

2. Courtship and copulation

The mating frequency in *H. lutescens* reaches its peak in May and the first half of June. At that time the snails perform a prolonged courtship and copulate, most often early in the morning, on warm, humid and windless days, and during thunder storms. They select places among herbaceous vegetation which shelters them from wind. The copulation in *H. lutescens* consists in transfer of sperm in spermatophores. Behaviour of both partners is identical but not always synchronised. Four consecutive phases of mating can be distinguished. In the first, preliminary, phase the partners assume a vertical position. The second phase involves behaviour associated with shooting love darts. In the third phase the snails assume a spiral position and copulate, while in the fourth phase they assume a characteristic post-copulation position.

The first phase is aimed at recognition of the partner, and probably involves both species identification and establishing the partner's readiness to copulate. Very often more than two snails are engaged in the initial phase of mating. Only two of them assume a vertical position and remain in further contact through their mouths, tentacles and raised anterior parts of their feet. The snails are supported on posterior parts of their feet and on their shells, most often stuck in concavities in dense herbaceous vegetation. Almost all the surface of their soles adheres closely, and the gonopores widen (Fig. 87). The snails tilt their heads to the left (right side of the partner), which makes it possible for their mouths and lower tentacles to mutually touch sole edges and genital atria which get partly everted. During this phase very often one of the snails resigns courtship.

The second phase involves behaviour associated with dart shooting (Fig. 88). The dart shooting is rapid but preparation for it is gradual. In this phase most often one of the partners is more active, its atrium and vagina are everted, with well-visible love dart. The dart is squeezed out with a dose of milky mucus from the mucous glands, and stuck into the partner's sole. Following the dart shooting, the snail relaxes completely, its exposed genitalia are gradually retracted, while the receiver of the dart slowly retracts into its shell and then slowly emerges again. Very often I observed *H. lutescens* to protrude its dart, which was not shot, but retracted into the vagina with retracting atrium, and then to the duct of the gametolythic gland (Fig. 61). During courtship snails often skipped the dart shooting phase, in spite of the presence of dart in the sac.

Figs 87–92. Courtship and copulation: 87 – phase I, vertical position; 88 – phase II, behaviour associated with love dart shooting; 89, 90 – phase III, spiral position and copulation; 91, 92 – phase IV, post-copulation position

In the third phase, the snails assume a spiral position (Fig. 89). That phase is preceded by resuming of vertical position by both partners, and then repeated tilting of the heads to the left and twisting anterior body parts clockwise, by 90°, the posterior sole part tightly adjoining the partner's sole. The head tilting and body twisting initially enables touching of the partner's exposed atrium with the lip and short right tentacle, till strongly everted genitalia touch each other. In the spiral phase the snails make attempts at copulation. However, for the copulation to be accomplished it is necessary for penes and vaginae to get everted; then the penes are mutually inserted into the vaginae (Fig. 90) which makes it possible to transfer spermatophores. In *H. lutescens* the copulation (transfer of spermatophores) lasts ca. 15 min, then the everted genitalia are retracted; in *H. pomatia* the copulation lasts only 5 minutes (LIND 1976). Very often attempts at copulation fail. The copulation is interrupted when both partners fail to insert their penes simultaneously and when the everting penes of the partners are misdirected. Following such failed attempts, the everted genitalia are quickly retracted, and in a short time another attempt is made.

Following copulation, the fourth phase starts during which the snails remain immobile and assume a post-copulation position. In this position the whole snail bodies contact except the heads which are now moved away from the partner. The soles become very wide and motionless, directed upwards and together forming a cup (Figs 91–92). Perhaps in this phase a part of sperm is released from the wholly transferred spermatophores, the sperm migrating then to the oviducts and to seminal vesicles. The remnants of spermatophores get to the gametolythic gland where they are disintegrated and digested. In *H. lutescens* the fourth phase lasts ca. 2 hrs, and the whole mating process ca. 3 hrs, depending on thermal conditions. The duration of the first two phases is very much variable.

3. Egg laying and hatching

Two weeks after copulation *H. lutescens* starts nest digging and egg laying. The intensity of these activities is the highest in June, the are sporadic in the first days of July. A high air humidity, preceded by a short period of intense rain, creates very good conditions for nest digging. The nests are located in places with loose soil and sparse vegetation, most often under the plants of tansy (*Tanacetum vulgare* L.) and in sheltered places. In such places the nest digging snails tend to gather in groups of several (Fig. 93). This results from a particularly good structure of the soil. The nest depth from the bottom to the soil surface is 4–6 cm and depends on the kind of substratum. During the egg laying, the snail buries its body in the nest, so that its shell is completely covered by the excavated soil (Fig. 94).

The eggs of *H. lutescens* (Figs 95–96) are spherical, with a pearl-like sheen, 4.0–4.5 mm in diameter. Their outer envelope is very delicate and calcified. The eggs are laid together with mucus, in groups of a few or about a dozen. The high viscosity of the mucus results in the eggs in the nest being arranged regularly, forming a cluster which tightly adjoins one of the nest walls. *H. lutescens* lays from 16 to 67 eggs (KARSZNIA 1997), and on an average 35 eggs per nest. Following the egg laying, the snail leaves the nest, closes its with mucus-glued soil and evens the soil surface thus masking the nest. The process lasts from two to three days.

Figs 93, 94. Egg laying: 93 – distribution of clutches in the study plot; 94 – nest digging

Figs 95, 96. Egg laying: 95 – arrangement of eggs in the nest; 96 – eggs taken out of the nest, ca. 3×

Fig. 97. Hatching, ca. 3×

Fig. 98. Hatchlings three days old, ca. 3×

Fig. 99. Juveniles upon leaving their nest, ca. 3×

In developing eggs of *H. lutescens*, already on the 14th day, shells of juvenile snails can be seen shining through, and the eggs become light yellow (Fig. 97). Young snails leave the egg shell thanks to its gradual resorption. The newly hatched snails stay in the nest and feed on the remnants of egg shells (Fig. 98). Earlier hatched juveniles may consume eggs and smaller juveniles; they eat also dead eggs. The egg cannibalism is common in some helicids, e.g. *H. pomatia* and *Arianta arbustorum* (L.) (BAUR 1988, 1990). From 14 to 16 days after hatching the snails emerge from the nest to the soil surface (Fig. 99). In favourable humidity conditions I found them on the soil as early as in the first days of July. The development of earlier laid eggs (first days of June) is favoured by the high humidity in the nest, remaining after winter. The mean mortality of eggs is 48.5% (KARSZNIA 1997). A drought preceding reproduction decreases chances for hatching, increasing the mean mortality of eggs up to over 70% (KARSZNIA 1997). The effect of humidity on egg development was observed also by POLLARD (1975) in *H. pomatia*. I have found that one of the reasons for destruction of whole clutches in *H. lutescens* is an excess of water in the substratum; then the egg shells break.

Natural enemies of *H. lutescens* and its eggs are ants and earthworms. The latter dig the eggs out which results in their drying. Ants attack and destroy eggs that were laid near ant hills.

D. ECOLOGY

1. Abundance and density

The mean abundance, its extreme values, as well as mean densities of the three age classes of *H. lutescens* on the study plot of 500 m^2, are presented in Table 1. The density of individuals aged one year and younger (just after leaving their nests), of shell diameter up to 10 mm and little advanced development of genitalia, is the highest. As a result of mortality of consecutive age classes, their number gradually decreases.

Table 1. Mean abudance and density of the three age classes in *H. lutescens* on the study plot

Age class	Mean abudance ±SE	Range (min–max)	Mean density per m^2
adult	573.3±124.4	329–817	1.15
young (2 years and older)	408.2±133.5	147–670	0.82
1 year and younger	1,988.8±946.3	134–3,844	3.98

Young individuals display a much lower density, on an average 0.82 individual per m^2. It seems likely that the snails become sexually mature in the fourth year of their life. Since adult individuals live a few years, this age class includes adults of various generations i.e. of varied age. Most probably this accounts for the high density of adults (1.15 indiv./m^2).

2. Changes in population abundance

Seasonal changes in abundance of the three age classes of *H. lutescens* are presented in Figure 100.

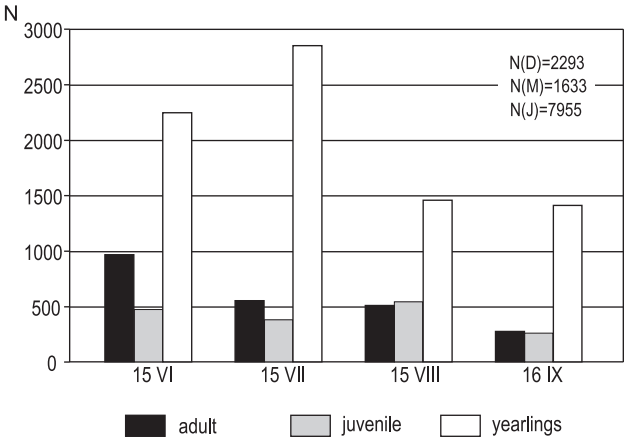


Fig. 100. Abundance of the three age classes of *H. lutescens* on the study plot during consecutive controls in 1994 (control: i = 0 of May 1994, whose values are given in the text, has been omitted from the graph)

In the control plot I took the first sample (in the model – sample i: 0) on May 15th 1994. I found and marked 236 adult, 142 young (two years and older) individuals and 126 yearlings. The analysis of the data with JOLLY-SEBER'S model indicates that the peak of population abundance fell on June and persisted till the end of July, with a marked decrease at half of September. Adult individuals were the most numerous in June. This resulted no doubt from their intense activity, which consisted in searching for a mating partner, copulation, selecting places for nest digging and egg laying. The decrease in abundance of adults and young in July was associated with drought. It can be supposed that in the study period high temperatures accompanied by drought, which persisted till half of August, caused adult individuals to hide in the soil. The abundance of yearlings, which was high already in June, reached its peak at half of July, thanks to emergence of juveniles (less than one year) from the nests. Already in August, quickly growing yearlings increased the abundance of the class of young snails. At the same time, the long draught resulted in a high mortality of snails of all the age classes. Yearlings and individuals of less than one year were active till half of September, when adult snails had already retired to their winter shelters.

CONCLUDING REMARKS

1. *Helix lutescens* Rossm. is a xero-thermophilous species. It inhabits steppe habitats, dry shrubs, grasslands, and sunny slopes, especially on calcareous substratum; it is often found in gardens and cemeteries. I have not found it together with *H. pomatia* in any of the studied localities. In Poland *H. lutescens* is found only in the south-eastern part of the country, where it reaches its north-western distribution border.
2. The shell of *H. lutescens* is spherical-conical, yellowish-white, of 4–4.5 poorly convex whorls separated by a shallow suture. It is more conical than in *H. pomatia*. The shell measurements in adults are 28.5–34.1 height, 26.9–32.1 width and 22.5–26.9 diameter, thus being considerably smaller than in *H. pomatia*. In adult *H. lutescens* the umbilicus is completely covered, while in *H. pomatia* it is partly open. The embryonic shell sculpture differs from that of definitive whorls, which consists of growth lines of various width and delicate spiral lines, resulting in a grating-like pattern.
3. The body of *H. lutescens* is greyish and covered with numerous grooves and wrinkles; in the grooves there are fine, whitish grains, which are the most numerous in the grooves forming two characteristic light streaks along the darker back. The character is species-specific.
4. In the reproductive system of *H. pomatia* it is noteworthy that the spermatheca duct never bears a diverticle, which is present in *H. pomatia*. Besides, the delicate pigmentation of the flagellum and intense pigmentation of the epiphallus and penis in adult *H. lutescens* is an additional diagnostic character to distinguish it from *H. pomatia* whose corresponding organs are always pure white.
5. The activity of adult *H. lutescens* is strictly associated with seasonal behaviour: crawling, feeding, mating and egg laying, as well as preparing for hibernation. The diurnal activity of *H. lutescens* includes two phases, their timing depending on seasonal fluctuations of environmental factors. In the spring, the snails are active at a relative humidity from 80 to 100% and a temperature of 5–23°C. In the summer they are active when the relative humidity is within the range of 86–100% and the temperature – 8–18°C. Their activity increases very much especially after a rain or at the dew point. The active phase in the spring falls between 15.00 and 11.00, and in the summer between 17.00 and 9.00 next day. Both in the spring and summer the peak of activity falls on early morning hours, just after sunrise. The resting phase usually includes the remaining hours. In September, at a mean diurnal temperature of 12.4°C, on the soil surface there are no adult individuals which results from their preparation to hibernate in winter shelters.
6. The highest frequency of mating in *H. lutescens* was observed in May and the first half of June. Four consecutive mating phases can be distinguished. The first, initial, phase involves probably recognition of the partner's species identity and its readiness to mate. During that phase the partners assume a vertical position and remain in contact. The second phase includes behaviour associated with love dart shooting, but this is often not accomplished, in spite of the presence of the dart in the sac. In the third phase, the snails assume a spiral position and copulate. The sperm is transferred in spermatophores and the process lasts ca. 15 min. Following sperm transfer, the fourth phase begins during which the snails remain motionless. The last phase lasts ca. 2 hrs, and the whole mating takes over 3 hrs and depends on temperature.
7. Two weeks from mating *H. lutescens* starts digging its nests and laying eggs. The eggs are spherical, of pearl-like lustre and 4.0–4.5 mm in diameter. The snail lays from 16 to 67 eggs, on an average 35 eggs per nest. In developing eggs, already 14 days from egg laying, shells of juvenile snails shine through. The juveniles leave the egg envelopes resorbing them gradually. The hatchlings remain in the nest and leave them most often in 14–16 days.
8. The mean densities of the three age classes of *H. lutescens* found in the constant study plot were the following: 1.15 individuals/m^2 (adults), 0.82 indiv./m^2 (two years and older) and 3.98 indiv./m^2 (one year and younger). The population abundance reached its peak in June and persisted till half of July, and a distinct decrease was observed at half of September. The adults were the most numerous in June. The abundance of the youngest age class, which was high already in June, reached its peak at half of July, due to the emergence of hatchlings from the nests. The individuals aged one year and younger, as well as few young individuals, were active till half of September when the adults had already sheltered for winter.
9. The new localities of *H. lutescens* in Poland do not change the distribution limits of the species reported by RIEDEL (1988). Contrary to RIEDEL'S (1988) data, the species is not going extinct in the Świętokrzyskie Mts: in anthropogenic sites it forms abundant insular populations (KORALEWSKA-BATURA 1993c, BARGA-WIĘCŁAWSKA 1997). Likewise, the Roztocze populations of *H. lutescens* are not endangered (PIECHOCKI 1990). In Poland, because of the north-western distribution border and the insular occurrence, as well as threat of unintentional collecting for culinary purposes, *H. lutescens* is a protected species (WIKTOR & RIEDEL 1992).

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received: July 5th, 1999
accepted: September 27th, 1999