LYMNAEA DIAPHANA: A STUDY OF TOPOTYPIC SPECIMENS  
(PULMONATA: LYMNAEIDAE)  

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A description of the species Lymnaea diaphana King, 1830 is presented, on the basis of material collected at its type-locality, San Gregorio, on the north coast of the Strait of Magellan, in the Chilean province of Magallanes. It may be identified by the following characters taken together: adult shell over 10 mm in length, whorls inflated, regularly convex, separated by a well-marked suture, aperture ovate occupying about half the shell length; renal organ forming an approximately right angle with the ureter; pouch of the oviduct well noticeable high on the right ventral surface and on the right side of the nidamental gland; uterus bent to the right into an approximately right angle; body of the spermatheca projected into the pulmonary cavity and adhered to the pericardium and to the roof of the pulmonary cavity; spermiduct highly sinuous, folding dorsalward between the left half of the oviduct and the left shoulder of the nidamental gland, and then winding on ventralward to reach the prostate on the middle line; prostate voluminous, convex on the left, pushed in on the right, with a deep dorsal furrow corresponding to a fold which projects into the prostatic lumen and is more developed at the fore half of the organ; apical end of the penial sheath with about six minute protuberances corresponding to inner chambers; prepuce from about as long to about twice as long as the penial sheath, with some variation beyond those limits; lateral teeth of the radula basically tricuspid, with a usually simple ectocone which may show a bifid or trifid point.

A diagnosis between Lymnaea diaphana and three other lymnaeids which also occur in South America and were previously studied by the author — L. columella, L. viatrix and L. rupestris — is presented.

Among the molluscs collected by Spix in Brazil there is a nominal species, Limnaeus papyraceus, with a shell about 32 mm long by 11 mm wide, from the “Provincia Sebastianopolitana loco natali non indicato” (Wagner, 1827:17, Pl.X, Fig. 5). In this context, “Provincia Sebastianopolitana” refers to the city of Rio de Janeiro (in full, São Sebastião do Rio de Janeiro, colloquially shortened to Rio). So large a lymnaeid has never been subsequently found in Brazil, and Kriechbaumer (1866), after examining the type of Limnaeus papyraceus, concluded that it is really a young specimen of Bulimus goniosomata Férussac.

Since Spix’s species is not valid, the oldest name of a South American lymnaeid comes to be Lymnaea diaphana King, 1830. By the way, Lymnaea columella Say, 1817 is considered a Nearctic species which secondarily spread to South America.

L. diaphana was briefly described as follows (King, 1830: 344, not figured): “L. testa turritâ, transversim substratâ, anfractibus ventricosis; long. 15,16 mm; lat. 5,16 mm; poll. = Habitat ad fretum Magellanicum. (Cape Gregory.) Mus. Brit., nost., Brod.

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This shell was found in the fresh-water ponds in the neighbourhood of Cape Gregory, which is on the continental side of the eastern end of the Strait of Magalhaens.

In October 1982, I collected 75 specimens of *Lymnaea diaphana* from a pond and a single one from a drainage ditch at its type-locality, San Gregorio (neighborhood of Cape Gregory), in the Chilean province of Magallanes (about 49°00'S, 70°38'W), which are studied in this paper.

MATERIAL AND METHODS

The collected specimens were narcotized in a 0.05% solution of nembutal in tap water for about 4 hr. They were then killed by plunging into hot water at 70°C for about 40 sec and transferred to cool water. Each specimen (under water) was gently pulled by the foot with a tweezer, so as to disconnect the attachment of the columellar muscle to the shell. The whole animal was drawn out of the shell and fixed in modified Ralliet-Henry’s fluid: distilled water 930 ml, sodium chloride 6 g, formalin 50 ml, acetic acid 20 ml. The radulae were separated from the buccal mass by digestion, for about 2 hr, in a vial with 10% NaOH immersed in gently boiling water, then rinsed in tap water and mounted in Turtox non-resinous medium.

Ten adult and three young specimens from the pond sample and one (adult) from the drainage ditch were dissected under the stereomicroscope.

*Lymnaea diaphana* — Figs. 1, 2: shells of specimens from San Gregorio, Magallanes province, Chile. Fig. 3: type; portion of outer wall of body whorl separated, not represented; specimen from British Museum (Natural History) 1950-5-16-1. Fig. 4: roof of pulmonary cavity (he = heart, mc = mantle collar, pv = pulmonary vein, rt = renal tube, rv = renal vein, se = septum between pulmonary and hypopelplar cavities, ur = ureter).
DESCRIPTION

The largest shell (Fig. 1) is 14.6 mm long and 8.8 mm wide, and has 5 whorls increasing rapidly in diameter. The whorls are inflated, regularly convex and separated by a deep suture. The surface is marked by thin growth lines. The aperture is ovate, 8.5 mm in length by 6.5 mm in width, occupying a little more than half the length of the shell; its inner lip is broadly reflected, covering to a variable extent the umbilical chink. Some degree of variation may be appreciated between specimens of Figs. 1 and 2, the latter being comparatively slenderer and with a more rounded aperture occupying a little less than half the shell length. The specimen of Fig. 2 resembles more closely the type-specimen deposited in the collection of the British Museum (Fig. 3).

The cephalopedal mass is diffusely grayish. The roof of the pulmonary cavity shows a grayish to black pigmentation with interspersed unpigmented spots. The renal organ (Fig. 4, rt) is a straight tube that tapers distalward to open behind the pneumostome through a right-angled ureter (Fig. 4, ur).

The genital system is shown in Fig. 5. The ovotestis (ot), which looks like a piece of ginger rhizome, is a cluster of lobulate acini pressed against each other around a collecting canal (cc) which continues into the ovispermic duct. The latter has a short and very thin proximal portion (od₁) which continues into the seminal vesicle (sv), a bosselated swelling of the ovispermic duct which narrows distally (od₂) to empty into the carrefour (ca).

The albumen gland (not represented in Fig. 5) shows no special features, and partly covers the oviduct, the pouch of the oviduct and the spermicduct. The oviduct (ov₁) has a wrinkled outer surface, and follows a convoluted course from left to right between the albumen and nidamental glands. Near its distal end (ov₂), at a point hidden by its terminal folds, it is connected with a wrinkle-walled pouch, the pouch of the oviduct (po), which projects from its right side, and then ends in the nidamental gland (ng). This is a bulky, oblong to approximately hemispherical mass of ribbed surface, with a dorsal convexity and a shallow ventral concavity occupied by the spermicduct and the prostate. The nidamental gland continues into the uterus (Fig. 9, ut), which gradually narrows distalward and bends to the right, ending in the vagina (Figs. 5, 9, va). The spermatheca has an egg-shaped body (Fig. 5, sp) and a duct about twice as long as the body; the duct, very slender at its origin (Fig. 5), gradually widens toward a markedly swollen basis (Figs. 9, sp). The body of the spermatheca projects into the pulmonary cavity, pushing around itself a fold of the membrane that covers the dorsal surface of the visceral mass and adhering through it to the pericardial membrane and to the roof of the pulmonary cavity, so that care must be taken on dissection not to sever the body from the duct.

The spermicduct emerges from the carrefour as a flattened tube (Fig. 5, sd₁) of irregular width that follows a very tortuous course in contact with the upper ventral surface of the nidamental gland and the middle portion of the oviduct, some of its coils appearing on the dorsal side of the specimen (Fig. 8, sd). After folding into several pleats, the spermicduct approaches the middle line (Fig. 5, sd₂) and tapers down to end in the prostate. The prostate (pr) is voluminous, convex on the left, irregularly creased in on the right, and has a deep dorsal furrow corresponding to a fold which projects into the lumen of the organ and is more developed at the fore prostatic half (Fig. 7). The vas deferens (vd) emerges from the cephalic end of the prostate and, as usual in pulmonates, descends, embedded in the neck wall, to a point on the margin of the male opening where, after interweaving with the surrounding tissue, it bends backward into a long loop to end in the penial sheath. The penial sheath (ps) is a little expanded at the apical end, which shows about six minute but well-defined protuberances corresponding to inner chambers communicating with the sheath lumen. The prepuce (pp) is from about as long to about twice as long as the penial sheath and somewhat wider, and has a well-developed saccobulum responsible for the expanded condition of its apical end. In most specimens the
Lymanea diaphana — Fig. 5: genital system; albumen gland removed, protractor muscles of prepuce not represented (ag = opening of albumen gland into carrefour, ca = carrefour, cc = collecting canal of ovotestis, cm = branch of columnellar muscle, ng = nidamental gland, od₁ = proximal portion of ovispermic duct, od₂ = distal portion of ovispermic duct, ot = ovotestis, ov₁ = initial portion of oviduct, ov₂ = terminal portion of oviduct, po = pouch of oviduct, pp = propus, ppc = protractor muscles of penial complex, pr = prostate, ps = penial sheath, rpc = retractor muscles of penial complex, rpp = retractor muscles of propus, sd₁ = initial portion of spermic duct, sd₂ = terminal portion of spermic duct, sp = spermitheca, sv = seminal vesicle, va = vagina, vd = vas deferens). Fig. 6: penial complex of another specimen, with less invaginated penial sheath (ppp = protractor muscles of propus; other abbreviations as in Fig. 5). Fig. 7: cross-section through fore half of prostate. Fig. 8: dorsal view of upper genital organs showing sd = coils of spermic duct between ov₁ = initial portion of oviduct and ng = nidamental gland; ov₁ = distal portion of oviduct, po = pouch of oviduct. Fig. 9: distal female genital organs (ng = nidamental gland, sp = wide base of spermitheca, ut = uterus, va = vagina). Fig. 10: radular teeth; small numbers indicate tooth position in transverse row (c = central; 1, 2, 7 = laterals; 9 = intermediate; 10, 20, 30 = marginals). Fig. 11: variation of lateral teeth in a transverse row (c = central; 1, 2 = first and second laterals). — Except in Figs. 10 and 11, bar = 1 mm.

Penial sheath is more or less deeply invaginated in the propus, preventing an accurate measurement being taken and distending the surrounding portion of the preputial wall. The extrinsic muscles of the penial complex are arranged as shown in Figs. 5 and 6: a common retractor (rpc) arising from the columnellar muscle and splitting, at a variable distance from its origin, into two branches, one of which attaches to the top of the penial sheath whereas the other attaches to the top of the propus (the two branches may be apparently independent throughout their length); a common protractor (ppc) arising from the tissue that surrounds the distal portion of the propus, and also splitting into
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a wider and a thinner branch which attach to the top of the penial sheath and of the prepuce, respectively; and a number of exclusively preputial retractors (rrp) and protrac-
tors (ppp, not depicted in Fig. 5), connecting the wall of the prepuce to the columellar
muscle and to the head wall, respectively.

The radula of the largest specimen has 114 transverse rows of teeth and its
formula is 30-1-30. Some teeth are shown in Figs. 10 and 11. The central tooth has a
small cusp and a minute cusplet high on its left. There are 8 laterals, 2 intermediates and
20 marginals. The laterals are tricuspid, with a small entocone, a long wide mesocone and
a medium-sized ectocone; the ectocone, usually simple, may be two- or three-pointed,
as in both first laterals in Fig. 11. The ectocone of the first left lateral is simple at trans-
verse rows 1 to 35, 38 to 41, 55 to 73; two-pointed at rows 36, 37, 42 to 54. The ectocone
of the first right lateral is simple at rows 46 to 49, 61, 62, 65 to 68; two-pointed at rows
1 to 34, 37 to 40, 42 to 45, 50 to 54, 56 to 60, 63, 64, 69 to 73; three-pointed at rows
35, 36, 41, 55. The increasingly worn teeth at rows 74 to 114 were disregarded. The same
kind of variation is observed in laterals other than the first one, but its frequency decreases
in farther laterals. Fig. 11 is an example of variation of laterals in the same transverse row.
The radulae of the remaining specimens agree in general with the foregoing description.

COMPARISON WITH RELATED SPECIES

The following comparison will involve Lymnaea diaphana and three species
previously studied by myself (L. viatrix, L. rupestris and L. columella), so the reader
is referred to the respective papers (Paraense, 1976, 1982, 1983).

The shell of diaphana differs from that of columella in its longer spire, less
developed outer whorl and smaller aperture, which occupies about half the shell length
(about two thirds in columella). Compared with rupestris, it has less convex, not shoul-
dered whors which are tightly coiled and, therefore, separated by a shallower suture.
As to viatrix, its shell so closely resembles that of diaphana that separation of the two
species can only be made by anatomic characters.

The following anatomic differences are observed: 1) the ureter has a double
flexure in columella, and is only bent to the right in the other three species; 2) the ovo-
testis of columella looks comparatively more compact and smaller in proportion to the
bulk of the genital system than in the other three; 3) the pouch of the oviduct, clearly
visible on the right of the oviduct in columella, diaphana and viatrix, is rudimentary and
nearly imperceptible in rupestris; 4) the uterus is curved rightward in columella, diaphana
and viatrix, abruptly bent caudalward in rupestris; 5) the body of the spermatheca lies in
contact with the esophagus in columella; in diaphana, viatrix and rupestris it projects into
the pulmonary cavity, pushing around itself a fold of the membrane that covers the dorsal
surface of the visceral mass and adhering through it to the pericardial membrane and to
the roof of the pulmonary cavity; 6) the spermiduct is approximately straight in columella
and viatrix, moderately sinuous in rupestris, highly sinuous in diaphana, 7) the prostate
is from thread-like to ribbon-like and about as wide as the widest portion of the spermid-
duct in columella, expanded into an oblong, more or less ovoid and somewhat flattened
body wider than the widest portion of the spermiduct in the other species; 8) in cross-
section the prostate shows a simple, slit-like lumen in columella and rupestris, and an
inward fold in viatrix and diaphana; 9) the penial sheath of columella seems to be devoid
of the minute apical protuberances present in diaphana, viatrix and rupestris; 10) the
prepuce is about two to six times as long as the penial sheath in columella, about as long
in *rupesstris*, from about as long to thrice as long in *viatrix*, and from about as long to twice as long in *diaphana*; these proportions are subject to appreciable variation and overlap, being in themselves unreliable as an isolated diagnostic character; quite striking, however, is the impression of smallness of the penial complex in comparison with the bulk of the genital system in *columella*, not so marked when observing the other species; 11) the first lateral tooth of the radula is tricuspid in *columella* and *diaphana*, bicuspid (tricuspid in a number of first laterals of some specimens) in *viatrix* and *rupesstris*.

The shells of Figs. 1 and 2, collected at the type-locality of *L. diaphana*, somewhat differ from the type-specimen (Fig. 3), which is slenderer than that of Fig. 1, although not so much in comparison with that of Fig. 2. Such difference is of common occurrence in populations of any *lymnaeidae* species and has been recorded by many authors who have dealt with adequately sized samples. The type-specimen, measuring in reality 17.5 mm in length, is represented in its present condition, without a portion of its outer whorl which is broken apart. No attempt was made to recompose it for fear of additional damage to that invaluable specimen collected during the first voyage of the "Beagle".

Anatomic studies of *L. diaphana* are scarce and lack important details. Pillsbry (1911:523-524, Fig. 2) examined the radula of specimens from Rio Chico, on the west of the Argentine province of Santa Cruz, about 500 km to the north of San Gregorio. His description reads as follows: "There are about 30, 7, 1, 7, 30 teeth. The central tooth is wider than usual in *Lymnaea*, unicusp. The lateral teeth are bicuspid, the broad inner cusp becoming bifid on the transition teeth. The inner margins have the mesocone and entocoone split into four to six small cusps, the entocoone remaining simple. Further out the margins become transversely lengthened, their cusps lie parallel to the long axis of the tooth, and are split into a comb-like series of denticles. The marginal teeth of *L. diaphana* differ from those of typical *Lymnaea* by their prostrate position, the cusp of one tooth overlying the basal plate of the succeeding one in the same transverse row, and also by the comb-like cusps. In typical *Lymnaea* (*L. stagnalis*, Fig. 3) the cusp stands obliquely erect, its cutting edge transverse to the long axis of the tooth." Differing from Pillsbry’s description and illustration, Fig. 10 of the present paper shows an asymmetric bicuspid central, tricuspid laterals and oblique marginals.

The specimens studied by Hubendick (1951) were collected at Punta Arenas, about 120 km by road westward from San Gregorio, at Valparaiso, about 2,500 km northward, at Falkland Islands, and at two probably misspelled South American localities (Rio Pescao and Rinto). Among the described characteristics, only three (internally folded prostate, length of the prepuce twice that of the penial sheath, and tricuspid condition of the lateral teeth of the radula) have diagnostic value, but are not decisive in identifying a *lymnaeidae* species. In fact, those characteristics may be found together at least in specimens of *L. diaphana* and *L. viatrix*. Hubendick (1951:90) states that in his material the radula has the same structure as described by Pillsbry (1911), but his illustration (Fig. 297, No. 20), representing a specimen from the Falkland Islands, shows a bicuspid (not unicusp) central, two tricuspid (not bicuspid) laterals and a nearly vertical (not transversely lengthened) marginal.

The anatomic description of *L. diaphana* presented by Castellanos & Landoni (1981) is a condensation of Pillsbry’s (1911) and Hubendick’s (1951) descriptions of the radula and distal genitalia, respectively.

RESUMO

É apresentada uma descrição da espécie *Lymnaea diaphana* King, 1830, baseada em material coletado na sua localidade-tipo, San Gregorio, na costa norte do Estreito de Magalhães, província chilena de Magallanes. Sua identificação específica pode ser feita pelo seguinte conjunto de caracteres: concha do adulto acima de 10 mm de comprimento,
giros inflados, regularmente convexos e separados por sutura bem marcada, abertura ovóide ocupando cerca de metade do comprimento da concha; órgão renal formando com o ureter um ângulo aproximadamente reto; bolsa do ouvido bem visível no alto da parte ventral direita e do lado direito da glândula nidamental; útero defletido em curva formando um ângulo aproximadamente reto para a direita; corpo da espermatoza projetado na cavidade pulmonar e aderido ao pericárdio e ao teto da cavidade pulmonar; espermídio muito sinuoso, formando voltas na direção dorsal entre a metade esquerda do ouvido e o ombro esquerdo da glândula nidamental, e depois voltando na direção ventral até atingir a próstata na linha mediana; próstata volumosa, convexa à esquerda, variavelmente côncava à direita, com uma ranhura dorsal correspondente a uma pega que se projeta na luz prostática e é mais desenvolvida na metade cefálica do órgão; ápice da bainha do pênis com cerca de seis minúsculas protuberâncias correspondentes às câmaras internas; comprimento do prepúcio de mais ou menos igual a duas vezes maior que o comprimento da bainha do pênis, podendo entretanto variar além desses limites; rádula com dentes laterais basicamente tricúspides, podendo o ectocone, simples na grande maioria dos laterais, apresentar a ponta bifurcada ou trifurcada.

São indicadas as diferenças entre os caracteres diagnósticos da concha, do órgão renal, do sistema genital e da rádula da L. diaphana e de outros três limneídeos que ocorrem na América do Sul, previamente estudados pelo autor – Lymnaea columella, L. viatrix e L. rupestris.

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