Crepidula argentina (Gastropoda: Calyptraeidae), a new species from the littoral of Argentina

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ABSTRACT

Crepidula argentina, a new species of gastropod of the family Calyptraeidae, is described from the littoral of Mar del Plata, province of Buenos Aires, Argentina. The new species is conchologically similar to *C. protea* d'Orbigny from southern Brazil. *Crepidula argentina* has a larger, subcircular shell and lower convexity than *C. protea.* Anatomical characters that allow differentiation from this latter species are: larger lateral shell muscle and very weak dorsal shell muscle; kidney proportionally smaller, with a characteristic arrangement of inner folds of dorsal lobe; presence of a renal vessel edging rectum and working as adrectal sinus; connection between odontophore muscle pairs m7 and m11; longer salivary gland; four ducts to digestive gland in stomach (instead of two); distinctive arrangement of folds in inner surface of stomach between esophageal aperture and posterior pair of ducts to digestive gland; seminal vesicle of males broad and few coiled; penis and papilla long and narrow; vaginal tube running closely attached to capsule gland. The reproductive biology is also distinctive. *Crepidula argentina* new species has a very well defined seasonal reproductive cycle. Females brood between 1 and 46 egg capsules per spawn. The average total number of embryos per spawn is 5600. The uncleaved, laid egg diameter is 170 µm and the number of eggs per egg capsule is about 320. All eggs develop, there are no nurse eggs. Larvae hatch as planktotrophic veligers. The new species is compared with other members of the genus *Crepidula* from the southern Atlantic coast of South America.

Additional key words: Crepidula protea, anatomy, reproduction, littoral.

INTRODUCTION

Most species of mollusks described from the southern Atlantic coast of South America are based on specimens collected by nineteenth century expeditions. *Crepidula* species are no exception. Alcide d'Orbigny (1841) described *Crepidula protea* for the first time on his large work "Voyage dans l'Amérique Méridionale". This book was published in several parts in different dates. According to Sherborn and Woodward (1901), Sherborn and Griffin (1934), and Keen (1966) the page (465) with the *C. protea* description (with no illustration) was published on 1841. A year later in the French edition of the Atlas of R. de la Sagra's "Histoire . . . de la I´Île de Cuba", d'Orbigny published a plate (pl. 24, figs. 30-32) with three illustrations of C. *protea* and no description (A description was published in 1846 in the Spanish edition of the same work.) It seems clear that the intention of d'Orbigny was to publish the chapter of mollusks in Sagras work before his "Voyage", because he cited that other book despite its later publication. *Crepidula protea* was described without mention of a distinct type locality. A label at The Natural History Museum, London (BMNH) states only "Patagonia' without further geographic details. The examination of the type specimens did not suggest any precise locality nor were there shell characters that could reveal which population they had came from.

D'Orbigny s description and illustration of *Crepidula protea* clearly groups at least two different species. First Dall (1889), and later Hoagland (1977), pointed out that *C. plana* Say, 1822, and *C. unguiformis* Lamarck, 1822, might be included within his concept of *C. protea.* According to d'Orbignys illustrations and description this seems to be possible.

Parodiz (1939) studied the species of *Crepidula* from Argentina with particular emphasis on the shell and, for the first time, on the radula. Based on a large number of lots from different localities Parodiz described and illustrated the radula and shell of five previously known species and two new subspecies. The subspecies are now considered to be geographical forms. Despite that, Parodiz (1939) is still the most authoritative paper on the genus *Crepidula* from southern Atlantic coast of South

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America. Unfortunately, no anatomical descriptions or reproductive features were described in that work. The specimens examined by Parodiz are still housed at the Museo Argentino de Ciencias Naturales (MACN) and were re-examined in this paper. Since Parodiz's pioneering work no further articles on *Crepidula* from Argentina have been published.

Hoagland (1977) published a comprehensive study of living and fossil species of *Crepidula.* Although her work was basically restricted to North America and the eastern Pacific, she included descriptions and pictures of C. *protea* and *C. dilatata* as well as a few other southern species. Hoagland (1983) described several specimens from Brazil of what she concluded was *C. protea.* She recognized *C. protea* as a species distinct from *C. plana* and *C. unguiformis* and studied d'Orbignys type material of *C. protea.* In the same paper, Hoagland described the larval development of *C. protea* based on specimens from the southeastern Brazilian coast. Here we consider the specimens she studied to represent actual *C. protea* mainly because they are conchologically similar to the lectotype and paralectotypes.

In an annotated list of several type specimens from the coast of Argentina, Aguirre (1993) designated a lectotype for *C. protea.* Unfortunately, she selected the only complete specimen in d'Orbignys collection at BMNH. She seems to have been unaware of the differences among the southern species of this genus. Aguirre (1993) mentioned only 4 syntypes when the count is actually 16, arranged in two lots of 5 and 11 specimens respectively (BMNH 1854.12.4.573 and 574) (Hoagland, 1983).

Gallardo (1977, 1979) and Brown and Olivares (1996) described several new species of *Crepidula* from Chile with distinctive reproductive patterns as diagnostic characters. These authors led the way in the search for new characters in this variable genus, showing that in several cases the shell lacks real taxonomic value at the specific level.

Hoagland (1983) and Rios (1985) pointed out that *Crepidula protea* occurs from Rio de Janeiro, Brazil, south to Miramar, in the province of Buenos Aires. However, studies on different population samples along this range revealed that more than one pattern of reproductive strategy and anatomical characters are found, indicating the presence of an unnamed species.

In this paper we describe this new species of *Crepidula* and provide the groundwork for a future revision of the group in the southwestern Atlantic. The new species was originally recognized first by its distinctive reproductive pattern and second through detailed anatomical studies. Comparison with several known species from South America is presented. The study of reproductive biology in the new species is the main topic of another paper (Cledón and Penchaszadeh, submitted.).

MATERIALS AND METHODS

Fresh specimens of *Crepidula argentina* new species used in this study were collected by commercial fish trawlers at Mar del Plata (38°00′ S, 57°33′ W) and Puerto Quequén (38°35′ S, 58°42′ W) along the coast of the province of Buenos Aires, Argentina. Types and material examined are deposited at: Museu Oceanográfico de Rio Grande, Rio Grande do Sul, Brazil (FURG); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN); Museo Nacional de Historia Natural, Montevideo, Uruguay (MHNM); Museu de Zoologia, Universidade de Sao Paulo (MZSP); National Museum of Natural History, Smithsonian Institution, Washington (USNM). The type material of C. *protea* was studied at The Natural History Museum, London (BMNH).

Specimens were fixed in formalin for at least 24 hours and preserved in 70% ethanol. They were not relaxed. All observations were made on preserved material. Dissections were performed on 3 males and 13 females using standard techniques under a stereomicroscope with the specimens immersed on 70% ethanol. Radulae were prepared (two specimens of *C. argentina* new species of 32.2 and 35 mm length and two of C. *protea* of 18.5 and 17.4 mm) according to the method described by Solem (1972) and observed and illustrated using a LEO 440 scanning electron microscope (SEM) at the National Museum of Natural History, Washington.

Shell measurements including convexity index, were done using the parameters established by Hoagland (1977). Most photographs were taken using a Nikon N70 with a 60 mm Nikkor macro lens. These images were latter scanned from black and white 35 mm negatives using a Nikon Coolscan III slide scanner. All images and plates were processed with the software Photoshop 5.02.

In the figures and text, the following abbreviations are used: aa, anterior aorta; ab, auricle region beyond ventricle connection; ac, anterior extremity of gill on mantle border; ag, albumen gland; **an,** anus; au, auricle; **bb,** bulged part of br; bg, buccal ganglion; br, subradular membrane; **bv,** mantle blood vessel inserting in kidney; **cg,** capsule gland; cv, ctenidial vein; da, aperture of duct to digestive gland; **dd,** duct to digestive gland; **dg,** digestive gland; dm, dorsal shell muscle; **dp,** posterior duct to digestive gland; ea, esophageal aperture; en, endostyle; es, esophagus; fd, dorsal surface of foot; fg, food groove; fl, female papilla; fp, female pore; ft, foot; gd, gono-pericardial duct; gi, gill; gs, gastric shield; hg, hypobranchial gland; in, intestine; ir, insertion of m4 in tissue on radula preceding its exposed (in use) portion; iu, U-shaped loop of intestine on pallial roof; kd, dorsal lobe of kidney; **ki,** kidney; kv, ventral lobe of kidney attached to intestine; 11, left lateral expansion (flap) of neck; 1m, lateral membrane restricting pallial cavity; ml to m14, odontophore muscles; mb, mantle border; **mj,** muscles of jaws and mouth; ml, mantle region restricting pallial cavity; mo, mouth; mr, mantle reinforcement; mt, mantle; ne, nephrostome; **nr,** nerve ring; ns, neck "sole"; oc, odontophore cartilage; os, osphradium; ov, pallial oviduct; oy, ovary; **pc,** pericardium; pd, penis sperm groove; **pe,** penis; pg, pedal gland anterior furrow; **pp,** penis papilla; **pr,** propodium; **pt,** pallial sperm

Table 1. Shell morphometrics of *Crepidula argentina* new species. Linear measurements in mm.

Specimen #	Total length	Height	Width	Diameter	Septum length	Septum free area	Convexity D/L
1	31.5	6.3	25	37	13.4	17.9	1.17
2	35.7	7.7	24.7	41	15.1	19.8	1.14
3	32.8	8.6	23.1	39	17.6	17.5	4.18
4	35.8	8.9	25	42	17	19.4	1.17
5	33.8	8.8	27	43	13.7	21.8	1.27
6	28.1	7.1	21.7	36	11.8	16.4	1.28
7	32.6	7.3	22.5	39	13.3	17.6	1.23
8	30	7.3	23.4	37	13.3	16.8	1.14
9	29.8	7.1	23.9	34	12.3	16.3	1.14
10	33	9.3	28	41	14.4	19.3	1.24

groove; **ra,** radula; **rl,** right lateral expansion (flap) of neck; **rn,** radular nucleus; **rs,** radular sac; **sc,** subradular cartilage; **sg,** salivary gland; **sn,** snout-proboscis; **sp,** aperture of *vas deferens* into pallial cavity; **ss,** style sac; **st,** stomach; **sv,** seminal vesicle; **te,** cephalic tentacle; **tm,** net of transversal muscles of haemocoel; **to,** tissue covering middle region of radula before its exposed part; **ts,** testis, **vc,** visceral connection with haemocoel; **ve,** ventricle; **vg,** vaginal duct; **vm,** visceral mass; **vo,** visceral oviduct; **vs,** vesicles of pallial oviduct.

SYSTEMATICS

Class Gastropoda Cuvier, 1797
Subclass Orthogastropoda Ponder and Lindberg, 1996
Superorder Caenogastropoda Cox, 1960
Order Sorbeoconcha Ponder and Lindberg, 1997
Family Calyptraeidae Lamarck, 1809
Genus *Crepidula* Lamarck, 1799

Crepidula argentina new species
Figures 1-21, 28–46

Crepidula protea: Parodiz, 1939: 702, fig. 8, pl. 1, fig. 6 (not d'Orbigny, 1841).

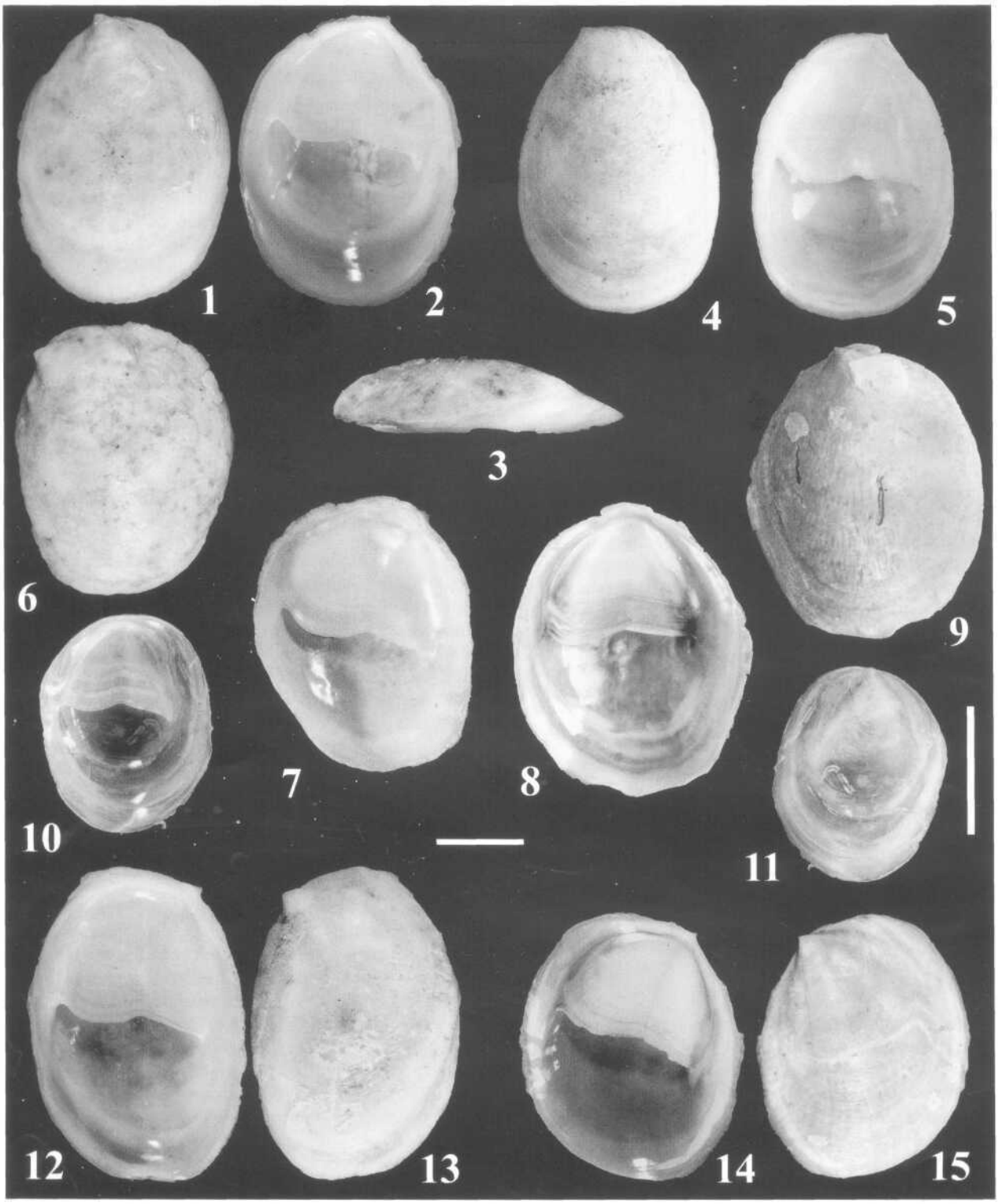
Diagnosis: *Shell:* Large and wide, slightly convex. Protoconch smooth, with 1¾ whorls. Aperture elliptical. Beak solid, very small. Septum planar, septum margin with sulcus on left side and clear notch in center. Muscle scars absent. Shell externally opaque white, internally white porcelanaceus. Periostracum absent.

Anatomy: Large lateral shell muscle. Dorsal shell muscle weak. Kidney proportionally small, with characteristic arrangement of inner folds of dorsal lobe, renal vessel edging rectum. Connection between odontophore muscle pairs m7 and m11. Long salivary glands. Four gastric ducts to digestive gland, distinctive arrangement of folds (sorting area) in inner surface of stomach between esophageal aperture and posterior pair of ducts to digestive gland. Seminal vesicle broad and few coiled. Penis and its apical papilla long and narrow. Vaginal tube running attached to capsule gland.

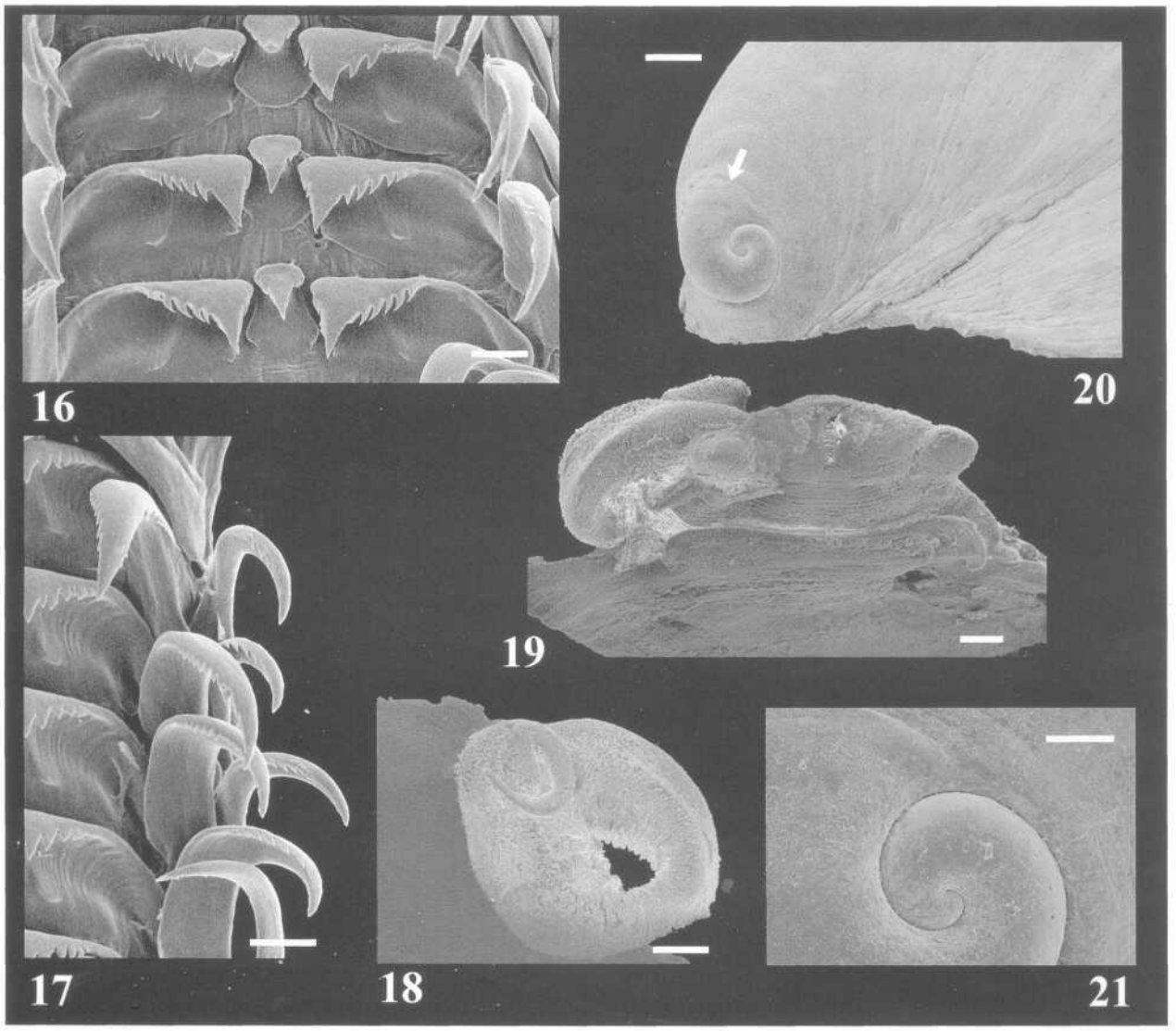
Description: *Shell (Figures 1-15, 20, 21):* Large (up to 40 mm in length) and wide, thin (0.35–0.45 mm in thickness), slightly convex, convexity = 1.20 (see table 1 for other measurements), male specimens very thin, brittle, transparent, planar shells. Protoconch smooth, with 1¾ whorls, transition to teleoconch clearly defined. Aperture elliptical or subcircular. Beak solid, very small, turned to right on females, almost central on males, at level of or only slightly above margin, in males never reaching margin, in females never extended beyond it. Septum planar (never convex), with central ridge almost imperceptible but present, margin of septum with sulcus on left side and clear notch in center, covering less than half of aperture, color bright white with translucent edge. Muscle scars absent. Growth lines covering entire shell. Shell externally opaque-white, internally porcelain-white; some specimens externally with diffuse radial orange lines and/or internally with radial brownish lines. Males always translucent-white externally and bright-white internally. Periostracum absent.

Head-foot (Figures 28, 30, 34, 43): Head protruded, at the end of long (about same length as foot), dorso-ventrally flattened, neck region. Snout short and cylindrical, able to retract and partially invaginate for about half of its length within haemocoelic cavity. Tentacles long, stubby, tip somewhat rounded. Eyes dark, situated on low ommatophores about midway on lateral margin of tentacles. Neck region with pair of lateral, flattened expansions (nuchal lobes); right nuchal lobe bears shallow food groove along its limit with head (figure 28). Sperm groove of males (described below) running externally along food groove (figure 43). Ventral surface of neck region forming an additional, anterior "sole" (figure 30). Foot very ample (occupies about ¾ of shell aperture), dorso-ventrally flattened. Shell septum defining dorsal limit of foot. Mantle fusing with dorsal surface of foot and protruding beyond its borders. Furrow of pedal glands transversal, located on central region of anterior margin of foot (about 1/3 of its width); a small, pointed expansion present on each side of furrow (figure 30). Anterior margin of foot covering ventrally posterior region of neck "sole". Columellar muscle very reduced, small flap contouring anterior border of shell septum, only evident on right side. Inner haemocoelic cavity narrow, running approximately along center of neck region, almost entirely filled by mass of salivary glands (described below) and numerous, transversal, very slender muscle fibers (figure 34); these fibers connect ventral surface of dorsal haemocoelic wall with dorsal surface of its ventral wall.

Mantle organs (Figures 29, 31–33, 44): Mantle border very thick, edging entire ventral margin of shell, free on its anterior half and attached to foot edge on its posterior half. Mantle border without appendages, but entirely covered by a series of minute glands. Mantle border with

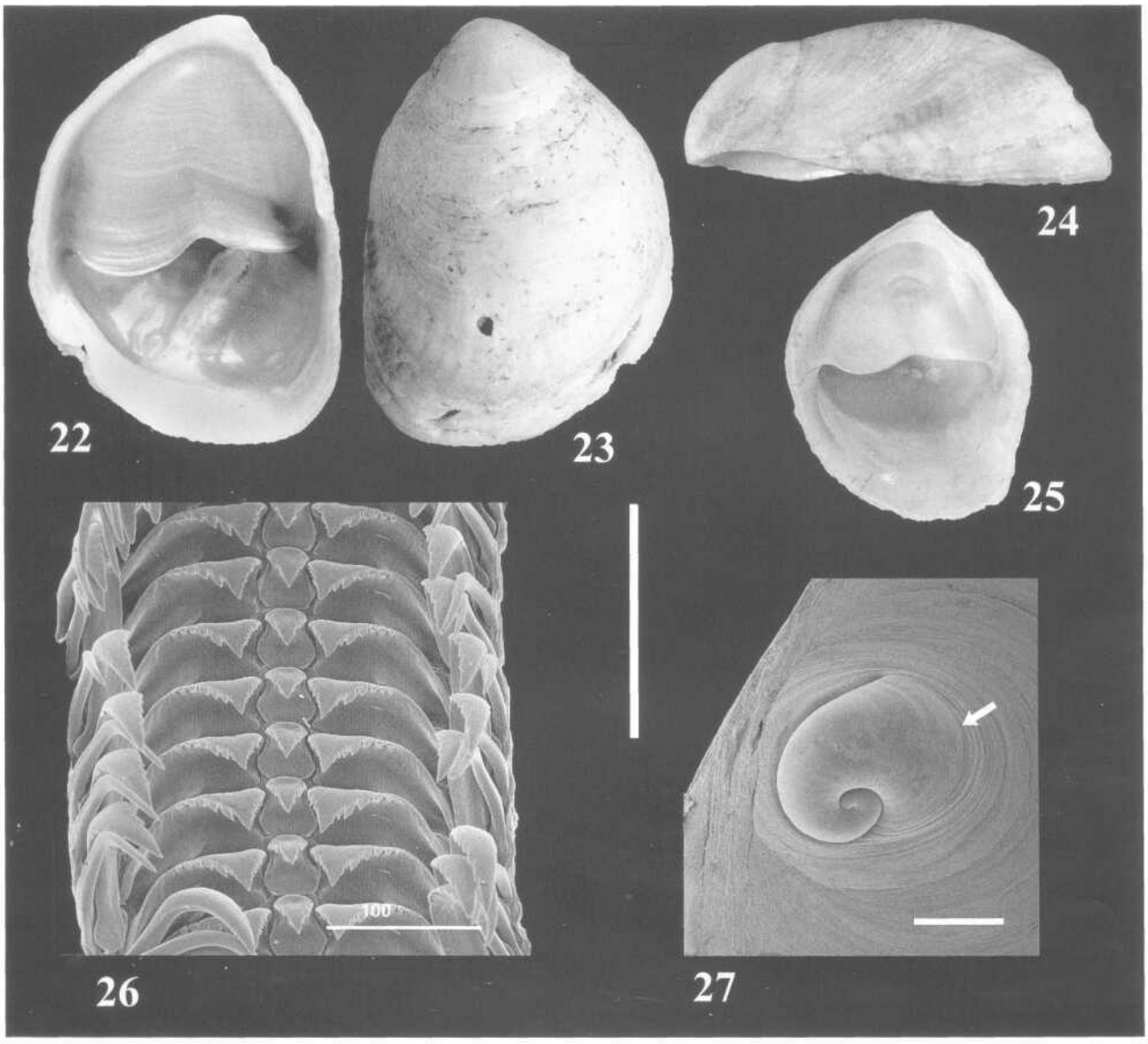


Figures 1-15. Shells of *Crepidula argentina* new species. **1-3.** Holotype, MACN 34508, Mar del Plata, Buenos Aires, Argentina. 4-5. Paratype, MACN 34509, Mar del Plata, Buenos Aires, Argentina. **6-7.** Paratype, MACN 34509, Puerto Quequén, Buenos Aires, Argentina. 8-9. Paratype. **10-11.** Paratype, MACN 34509, male specimen, scale bar on right side of figure 11 = 0.5 mm (for figures 10 and 11). **12-13.** Paratype, MACN 34509 **14-15.** Paratype, MACN 34509. Scale bar under figure 8 = 1 cm for all specimens, except figures 10 and 11.



Figures 16–21. *Crepidula argentina* new species. **16–17.** Radula. 16. Radula, frontal view. Scale bar = 30 µm. 17. Radula, marginal teeth, scale bar = 30 µm. **18-19.** Penis, critical-point dried. 18. Dorsal view. Scale bar = 200 µm. 19. Ventral view. Scale bar = 200 m. **20-21.** Protoconch. 20. Dorsal view. Scale bar = 300 µm. 21. Detail of figure 20. Scale bar = 100 m.

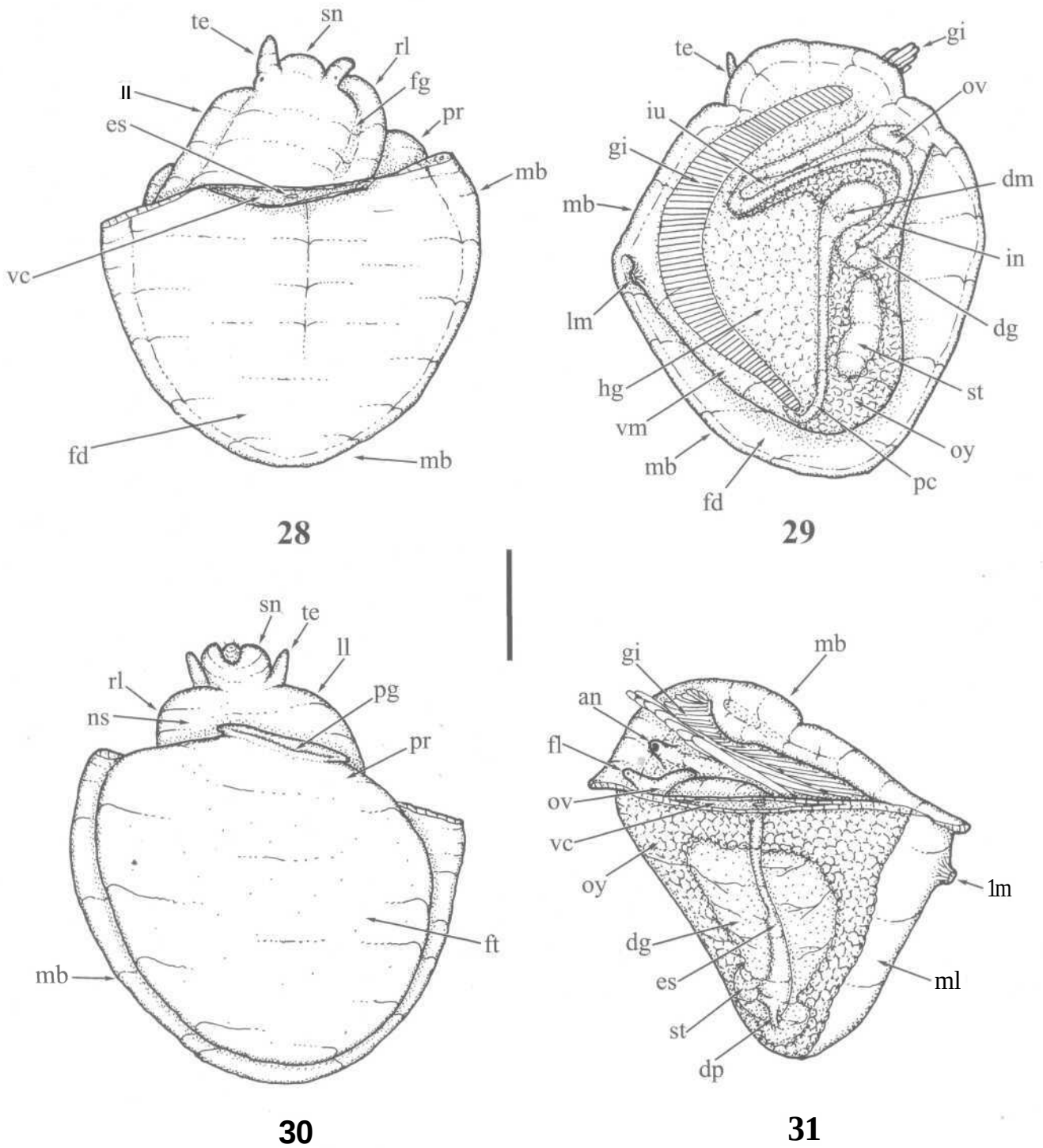
characteristic arrangement of folds along central region of aperture of pallial cavity (figure 33), a broad furrow beginning on anterior extremity of gill, running toward left side, and ending at about right third of osphradium; this thick fold presents broad central furrow. Dorsal shell muscle apparently lacking in most specimens, very reduced and difficult to observe in others (figure 29). Lateral shell muscle well developed, inserting broadly in left lateral region of mantle border and region posterior to it, originating shortly in inner shell surface in region close to left anterior edge of shell septum. Pallial cavity aperture occupying about 2/3 of anterior half of shell border, turned to right (drawing an analogy between shell in dorsal view and a clock, with head occupying 12:00, pallial aperture occupies a sector beginning at 9:00 and ending at 2:00). Pallial cavity deep, broad, triangular, arched and flattened dorso-ventrally (figure 29). Anterior extremity of pallial cavity slightly larger than its aperture due to constriction on left and right extremities produced by fusion of mantle and foot (figures 31, 44). Pallial cavity narrows gradually in posterior direction, penetrating left side of visceral mass (described below); cavity length about 3/4 of total length of animal. Osphradium (figure 33) long, monopectinate, located between anterior region of gill and mantle border, occupying about middle region of pallial aperture, somewhat perpendicular to longitudinal axis of animal, compressed between gill and mantle border. Osphradium length slightly exceeding 1/5 of pallial aperture length. Osphradium leaflets long, somewhat thick, closely packed, with rounded tip. Gill very large, with somewhat narrow base, edging anterior and left margin of pallial cavity along almost its entire length; anterior extremity of gill in anterior and left region of pallial cavity aperture, near its



Figures 22-27. *Crepidulaprotea* d'Orbigny, 1841. **22–24.** Shell, MACN 34511, off Ubatuba, Sao Paulo, Brazil, 23°30′ S, 44°54′ W, 42 m, dorsal, ventral, and lateral views of the same specimen. 25. Shell, MACN 34511, other specimen in lot, ventral view. Scale bar = 1 cm for all shells. 26. Radula, frontal view. Scale bar = 100 µm. 27. Protoconch, dorsal view. Scale bar = 300 µm.

right limit, on thick mantle border; posterior extremity of gill in posterior end of pallial cavity (figure 32). Base of gill filaments triangular. Gill filament with very long, almost straight, stiff rod extending to right; rods extend for about twice as long as their triangular, membranous base; these rods begin in region of ctenidial, in left margin of cavity roof, touching food groove of head-foot, in right margin of cavity floor. Rod apex rounded and preceded by a thicker region. Gill filaments connected to each other by cilia, mainly along their thicker apical region, which helps maintain somewhat gill structure. Gill filaments longer in central region of gill, shortening gradually toward both extremities. Anterior extremity of gill with short filaments, abruptly turning forwards, ending at mantle border (figure 33). Ctenidial vein cylindrical. Endostyle well developed, yellowish (a somewhat narrow glandular ridge located on ventral surface of ctenidial vein and present along its entire length) (figure 33). Hypobranchial gland whitish, low, slightly developed, occupying surface between gill and visceral mass (figures 1, 5). About 1/3 of visceral mass encroaches on pallial cavity roof, occupying about 1/3 of posterior and right sectors of this region; pericardium and kidney located in posterior part; long intestinal loop, anus, and pallial oviduct in anterior part (described below).

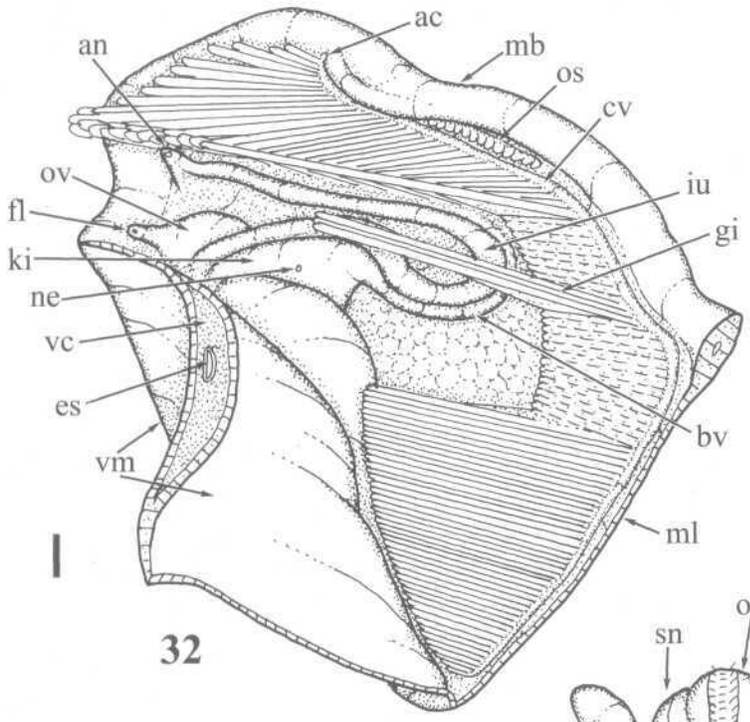
Visceral mass (Figures 29, 31, 32, 44): A dorso-ventrally flattened cone lying in shell chamber produced by septum. Thin calcareous septum separating visceral mass from dorsal surface of foot. Left and anterior region of



Figures 28-31. Anatomy of *Crepidula argentina* new species. 28. Female animal with shell, visceral mass, and pallial cavity removed, dorsal view. 29. Same animal, whole, dorsal view. 30. Same, ventral view. 31. Isolated visceral mass and pallial cavity, ventral view. Scale bar = 5 mm.

visceral mass occupied by pallial cavity (figures 31, 44). Remaining region of visceral mass with stomach as central structure, immediately and almost completely surrounded by digestive gland (except in some ventral and dorsal parts). Gonad surrounding digestive gland externally.

Visceral mass encroaching on right and posterior regions of pallial cavity roof. Anterior extremity of visceral mass (ventral to posterior pallial cavity region) covering columellar muscle just posterior to anterior border of shell septum.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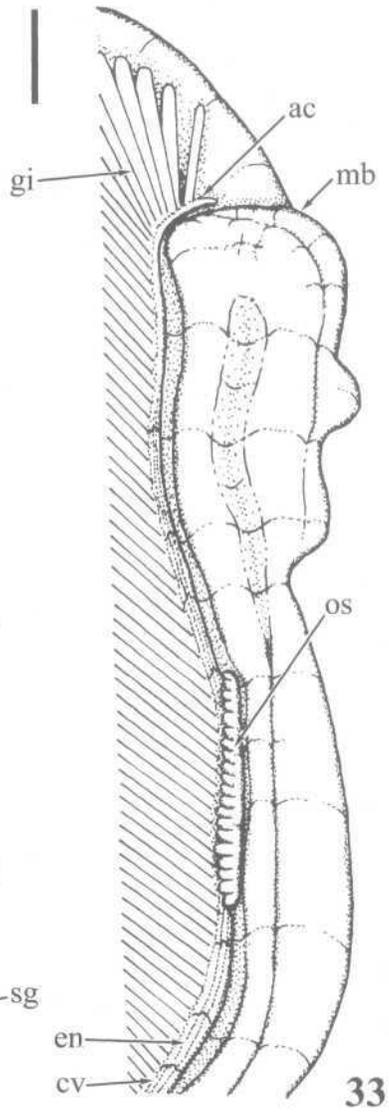
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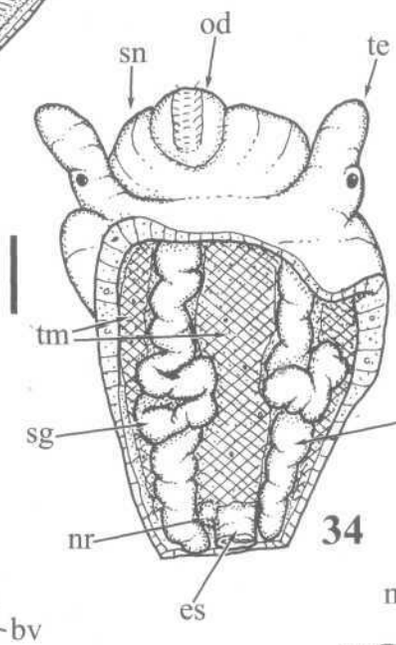
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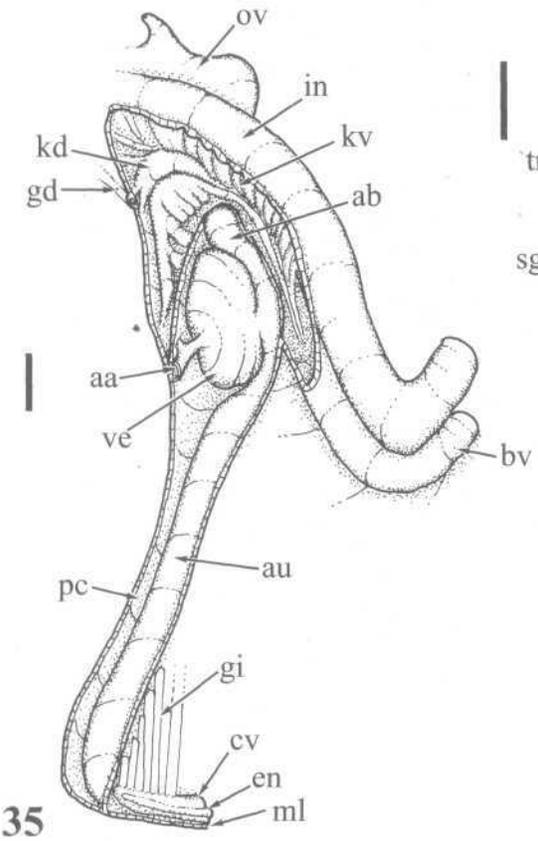
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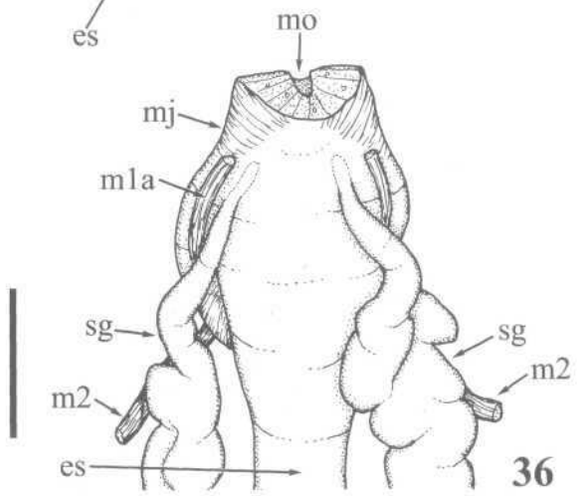
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Circulatory and excretory systems (Figures 29, 35): Pericardium very long, somewhat perpendicular to longitudinal axis of animal (figure 29); very narrow in posterior extremity of gill (posterior and left end of pallial cavity); running along anterior margin of visceral mass where it encroaches on pallial roof, enlarging gradually and ending at about middle level of this region of visceral mass, near its median line. Pericardium circumscribes (1) pallial cavity in anterior and ventral direction, (2) visceral mass (mostly gonad) in posterior direction, (3) mantle in dorsal direction, and (4) kidney to right. Auricle thin-walled and very long, running long entire pericardium length, attached to its anterior and dorsal inner surfaces; auricle connects with ventricle approximately along its middle and right thirds; auricle portion beyond connection with ventricle represented by broad bind sac. Ventricle elliptical, very muscular, its connection with auricle located about middle region of its anterior surface; aortas originating in opposite side. Anterior aorta broad, directed away from posterior aorta. Anterior aorta directed toward right, edging posterior inner surface of pericardium. Anterior aorta penetrates head haemocoel. Kidney small, occupying about 1/4 of area of visceral mass when projected on inner surface of pallial cavity. Kidney circumscribes (1) mantle in dorsal direction, (2) pallial cavity in ventral and left lateral direction, (3) visceral mass (mostly gonad) in posterior and right direction, (4) pericardium in posterior and left direction, (5) an intestinal loop in anterior direction, (6) intestine and oviduct (when present) in lateral right direction. Kidney mostly hollow, with pair of very irregularly shaped lobes. Ventral lobe with several, slight narrow transverse folds attached to posterior surface of adjacent intestine. Dorsal lobe occupies most of dorsal and lateral surfaces, bearing several irregular folds in left direction; part of lobe covering ventral surface around nephrostome. *Nephridial gland thin, present along boundary between kidney and pericardium, bearing series of transverse, narrow folds connected with dorsal renal lobe. Nephrostome a very small slit in left region of ventral wall. A broad vessel connected with left extremity of kidney and running along external pallial loop of intestine for about ¾ of its length.

Digestive system (Figures 29, 31, 32, 34–42): Mouth longitudinal, in center of anterior surface of snout (figure 34). Buccal mass very large, occupying most of inner space of snout. Buccal mass capable of some protraction and invagination. Dorsal wall of buccal mass with pair of broad and thin jaw plates. Pair of dorsal folds broad and low, connected to jaws in posterior direction. Odontophore large, consisting of most of volume of buccal mass. Odontophore muscles (figures 36-38, 40, 41): (m1) jugal muscles, several very narrow muscles connecting buccal mass to adjacent wall of snout, more concentrated anteriorly around mouth; (m1a) pair of dorsal protractor muscles, narrow, thin and superficial, with origin in antero-dorsal region of mouth, close to its median line, insertion in posterio-dorsal and lateral region of odontophore; (mj) jaws and peribuccal muscles, somewhat thick, surrounding lateral and dorsal wall of buccal mass, with origin around mouth, insertion in middle region of lateral and dorsal wall of odontophore; (m2) pair of retractor muscles of buccal mass (retractor of pharynx), broad, with origin in latero-ventral region of haemocoel just posterior to snout, running in anterior direction, with insertion in postero-lateral and dorsal region of odontophore cartilages; (m2a) pair of dorsal tensor muscles of radula, continuation of m2 after insertion in cartilages, running in anterior direction, with insertion in subradular cartilage in middle region of its dorsal inner surface; (mt) dorsal transversal muscle or ventral approximator muscle of cartilages, connecting dorsally posterior-dorsal and lateral surface of both cartilages, lying between superficial membrane that covers odontophore and tissue on middle region of radula (to); (m4) pair of median dorsal tensor muscles of radula, very large and thick, with origin in ventral-central and posterior region of odontophore cartilages, running along their middle region, contouring meso-ventral surface of cartilages, running along their dorsal surface, with insertion in dorsal-posterior and medial extremity of subradular cartilage; (m5f) pair of median radular tensor muscles, thick, with origin in meso-posterior and dorsal regions of odontophore cartilages, just adjacent to m2 insertion and m2a origin, crossing middle region of m4, running toward medial region of m4, with insertion along radular sac on both sides (each branch of m5 runs along a side of radular sac, medially and dorsally); (m6) horizontal muscle, very thin, uniting anterior half of odontophore cartilages, with insertion on their dorsal margin; (m7) pair of ventral tensor muscles of radula, thin and narrow, with origin in meso-anterior margin of m4, running in posterior direction adjacent to subradular membrane, bifurcating in posterior region of odontophore, median branch connecting with that of other member of pair and inserted in meso-posterior region of radular sac, lateral branch connecting with m11; (m8) pair of strong muscles with origin in postero-dorsal and lateral region of odontophore cartilages just adjacent to insertion of m2, running along and attached to dorsal margin of odontophore car-

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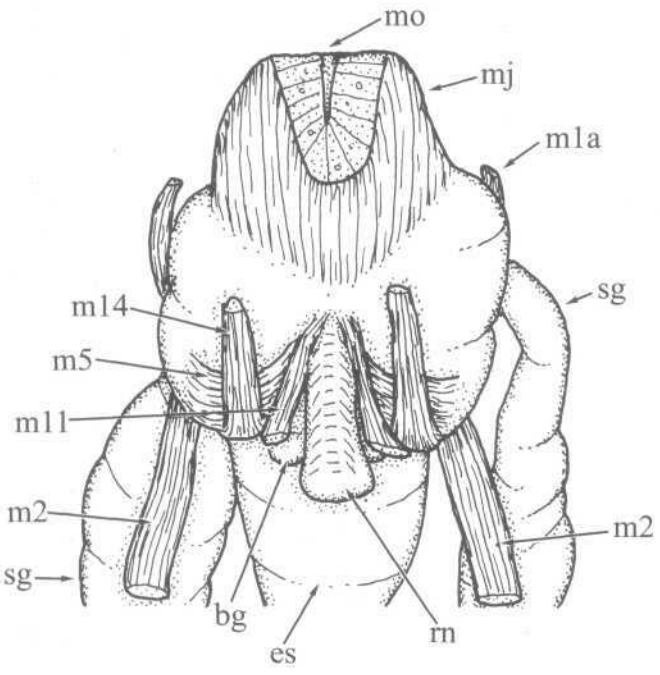
Figures 32-36. Anatomy of *Crepidula argentina* new species. 32. Pallial cavity, ventral view, part of visceral mass deflected, some gill filaments of central part of gill removed. 33. Detail of mantle border and pallial cavity at anterior extremity of gill. 34. Head and haemocoel, ventral view, foot and neck "sole" removed. 35. Detail of visceral mass at border of pallial cavity, adjacent to pericardial structures, ventral view, ventral surface of pericardium and kidney membranes removed. 36. Buccal mass, dorsal view. All scale bars = 1 mm.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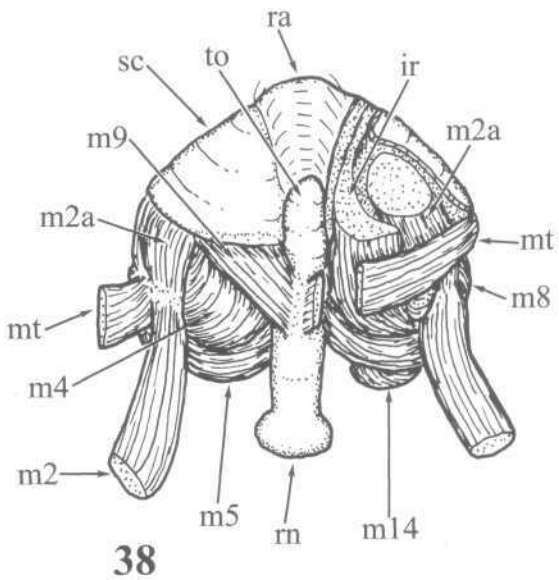
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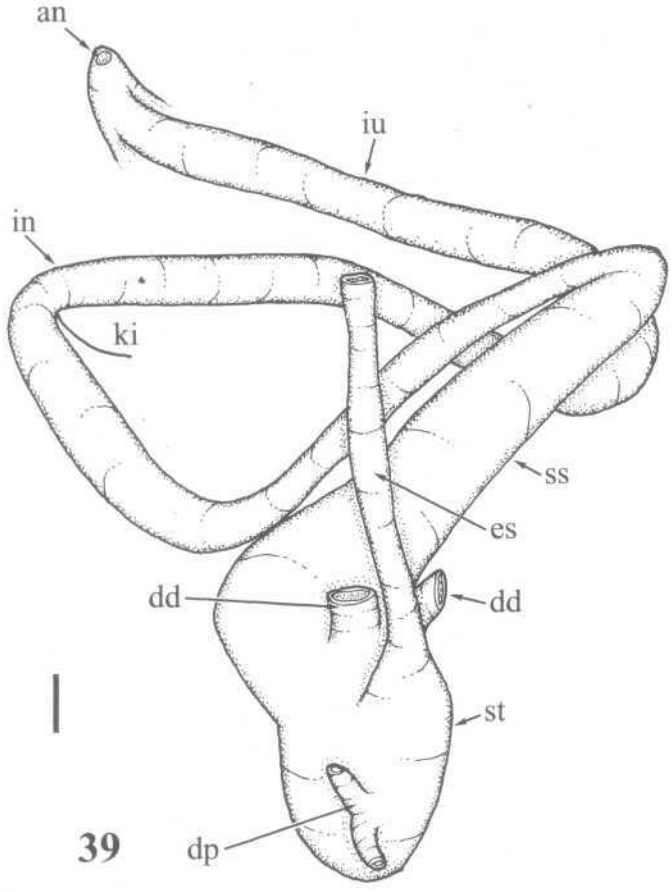
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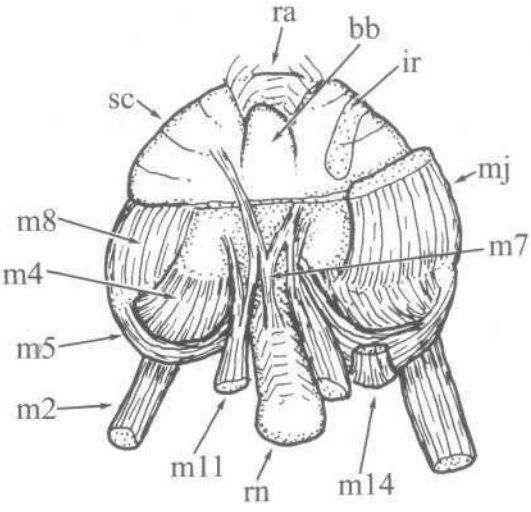
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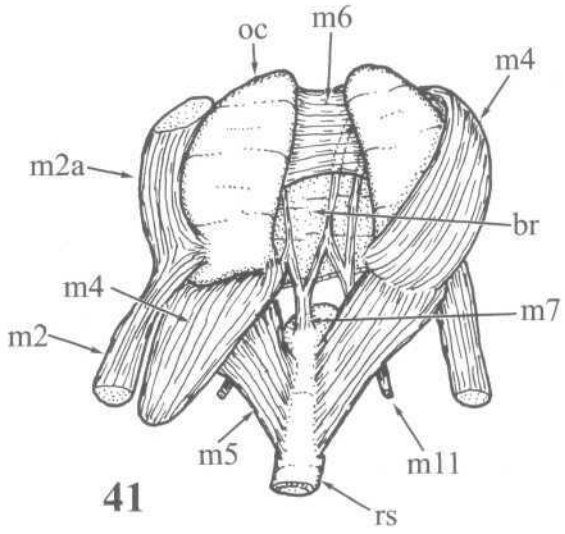
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tilages, with insertion in their antero-dorsal region adjacent to horizontal muscle (m6); (m9) pair of dorso-medial tensor muscle of radula, broad and thin, with origin along meso-dorsal surface of radular sac (in its region internal to odontophore), crossing to dorsal surface, with insertion in dorso-ventral margin of subradular cartilage; (m11) small, narrow pair of muscles, with origin in meso-ventral region of mouth, running in posterior direction along its median line, penetrating in median region of odontophore, running between m7 and m4, with insertion in anterior region of subradular membrane; (m14) pair of broad and thin muscles, with origin in postero-dorsal region of odontophore, close to origins of m2 and m5, running in antero-ventral direction, with insertion in inner ventral surface of snout at about middle region of odontophore; to) tissue covering middle region of radula within odontophore, along its dorsal surface; br) subradular membrane, covering ventral surface of subradular cartilage and some neighboring areas.

Radula taenioglossate, short, measuring little more than odontophore length (figures 37, 38). Rachidian tooth tall, narrow with curved, convex base, central cusp very large and sharp, at least two weak denticles on each side decreasing in size toward lateral teeth, no basal cusps but pair of lateral reinforcements present along borders. Lateral tooth broad (about 3 times rachidian width), curved inward, with conspicuous apical cusp turned toward rachidian line and 5—7 short, triangular denticles along edge on marginal side and 2−3 very weak denticles on edge on rachidian side, denticles decreasing in size in both directions, disappearing at about middle region of tooth, only a thickened border remaining. Marginal teeth long, curved, tall, tip sharply pointed, with serrate inner margin (at least 7 denticles); inner marginal tooth broad, about twice as wide as outer marginal tooth.

Pair of buccal ganglia large, close together near median line (figure 37), situated between buccal mass and adjacent esophagus. Salivary glands very long, tubular, coiled (about 3 times longer than haemocoel length when straightened) (figure 34). Several narrow transverse muscles unite internally dorsal and ventral surfaces of haemocoel, passing both sides of salivary glands, esophagus, and aorta (figure 34). Salivary glands not passing through nerve ring. Ducts of salivary glands thick, running to dorsal surface of buccal mass, penetrating adjacent wall of buccal mass; apertures small, close to site of penetration, located in anterior region of dorsal folds of buccal mass (figure 36).

Esophagus narrow and long (figure 39). Inner surface of anterior esophagus with a pair of broad folds. Middle esophagus with pair of narrow folds (continuation from those of anterior esophagus) and moderately spacious glandular chamber. Inner surface of posterior esophagus with 4−5 longitudinal, narrow, folds of similar dimensions. Stomach (figures 39, 42) large, slightly conical, occupying about half of visceral mass; esophagus inserting in left side of its posterior region of stomach, adjacent to region of shell apex. Four ducts to digestive gland present: anterior pair narrow, inserted in ventral surface, between insertion of esophagus and posterior gastric end, one turned in anterior direction and other to opposite side; posterior pair of ducts thick, located in middle region of ventral and left surface of stomach, one at considerable distance from other. Stomach gradually narrows in anterior and left direction, close to left and posterior extremity of pallial cavity. Stomach inner surface (figure 42) with pair of narrow and long folds, both with origin adjacent to insertion of esophagus, lining posterior surface of stomach, gradually disappearing in direction posterior to apertures of anterior ducts to digestive gland. Gastric shield thin, presenting transversal folds marking a somewhat elliptical, concave area. Anterior half of stomach with a pair of slight tall, longitudinal folds; posterior region between both folds smaller than anterior region; smaller region as intestinal branch of stomach; broader (anterior) region as style sac. Digestive gland pale-brown in color, surrounding stomach except for some spots in dorsal and ventral surfaces.

Intestine very narrow and sinuous (figure 39); running from left to right adjacent to anterior border of stomach, running up near median line to right and anterior extremity of visceral mass; in this region and toward left, it surrounds right and anterior border of kidney, turning suddenly to right and running parallel to preceding loop; both loops exposed along pallial roof (figures 29, 32, 35, 39). Anus small, slightly siphoned, situated in right region of pallial cavity close to mantle border (figures 31, 32, 39). Last loops of intestine contain numerous, small, somewhat elliptical fecal pellets.

Male genital system (Figures 43, 44, 46): Only small specimens (up to 9 mm) are functional males. Testis situated in anterior region of visceral mass, color orange. Seminal vesicle convoluted, very thickened, color cream, situated in anterior and right region of visceral mass, where it abruptly narrows, becoming very slender and opening in postero-ventral and right region of pallial cavity. A shallow groove runs from this aperture to penis base, on pallial floor near right margin of head. Sperm groove better defined and deeper in anterior direction. Penis long (about 3 times tentacle length), curved, orig-

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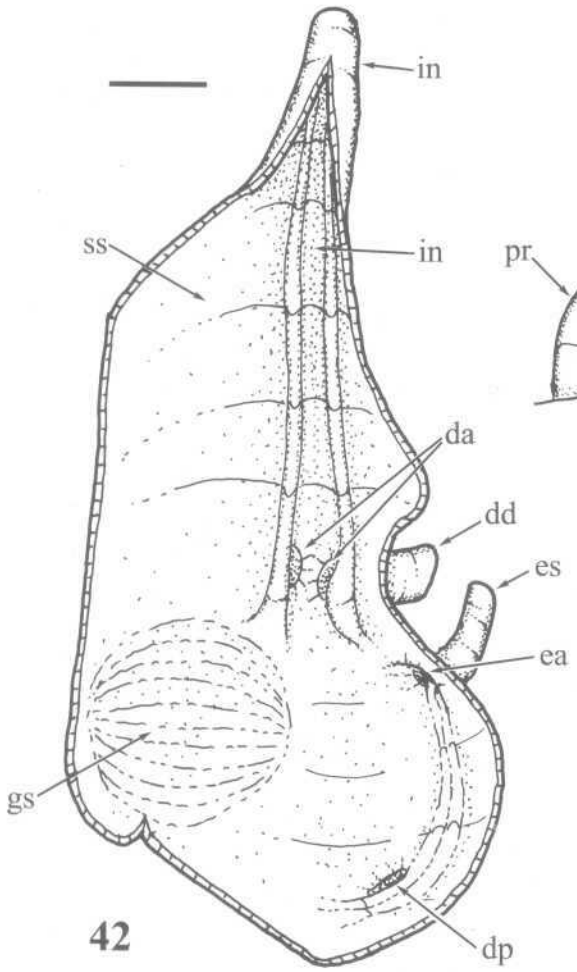
Figures 37–41. Anatomy of *Crepidulaargentina* new species. 37. Buccal mass, ventral view. 38. Odontophore, dorsal view, some muscles sectioned and deflected, part of right region of subradular cartilage removed to show muscular insertions in it. 39. Digestive tubes seen *in situ* with visceral mass as a transparent structure, ventral view. 40. Odontophore, ventral view, superficial membrane and muscles removed, right mj (left in figure) also removed. 41. Odontophore, ventral view, radular sac deflected and only partially shown, odontophore cartilages deflected from each other, right m4 (left in figure) deflected downward. All scale bars = 1 mm.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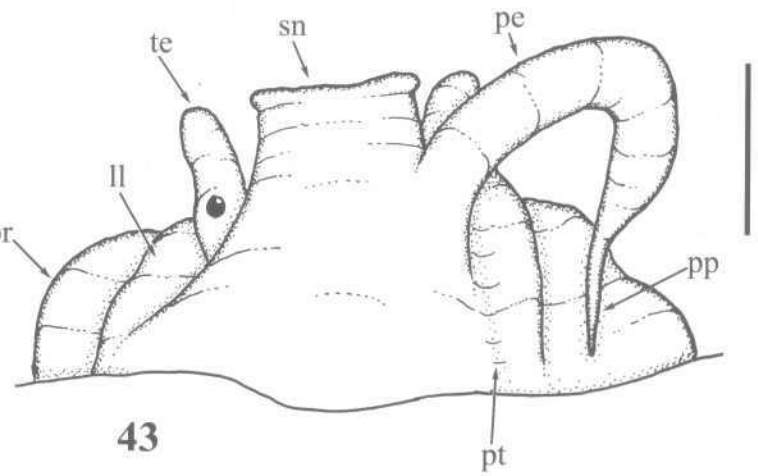
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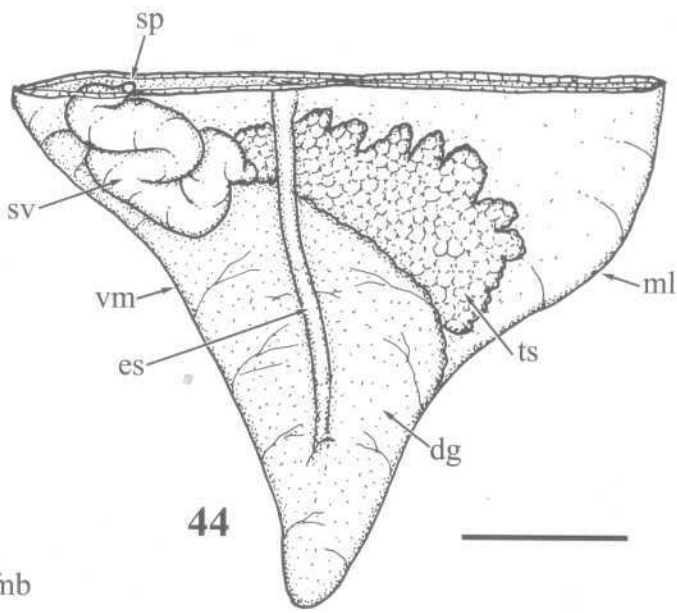
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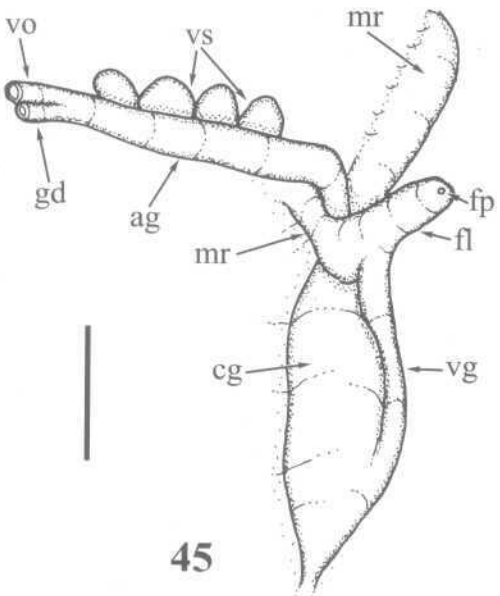
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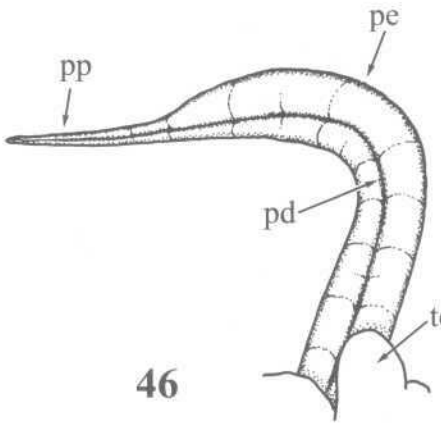
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inating dorsally to right tentacle. Papilla on penis tip, very long, about half of penis length. Penis duct opened, running along middle region of ventral surface of penis to tip of papilla.

Female genital system (Figures 29, 31, 32, 35, 45): Ovary pale brown, surrounding digestive gland, denser in anterior region of visceral mass (figures 29, 31). Visceral oviduct very narrow, running from left to right in anterior border of visceral mass. Gonopericardial duct well developed, slightly thicker than visceral oviduct, with origin in ventral and right extremity of pericardium (figure 35); running along visceral glands encroached in pallial cavity; inserted in posterior extremity of pallial oviduct where it joins insertion of visceral oviduct. Albumen gland long, moderately thick, whitish; walls thick, glandular; situated in anterior and right extremity of visceral mass; 3 to 4 seminal receptacles inserted along right surface of albumen gland. Capsule gland a continuation of albumen gland, marked by sudden increase of secretory tissue in wall and by turn toward left; walls irregular, thick, glandular. Vaginal tube moderately narrow, originating in posterior region of capsule gland, running attached to this latter up to its right limit, where it abruptly turns in ventral direction to form tall genital papilla. Papilla with pair of low folds running along its posterior side, from base almost to tip; folds close to each other with narrow furrow in between. Female genital pore situated in tip of papilla (figures 31, 32, 45) slit-like, transversal, with posterior and anterior edges slightly projected.

Etymology: The specific epithet, a noun in apposition, refers to the name of the country where the species occurs, Argentina.

Type locality: Mar del Plata, Buenos Aires, Argentina in 35-50 m, on shells of *Mytilus edulis platensis* d'Orbigny, 1846.

Type material: Holotype, MACN 34508; 20 paratypes, MACN 34509 (10 dry specimens) and MACN 34510 (10 specimens preserved in ethanol); 6 paratypes, MLP 5578; 16 paratypes (3 males, 13 females) MZSP 32152; 6 paratypes USNM 2016009 (1 specimen preserved in ethanol); MHNM, 6 specimens without number; 6 paratypes MHNM 15105; all from type locality.

Additional material examined: MACN 18504, 39 specimens, Puerto Quequén, Buenos Aires; MACN 8887, 9 specimens, off Mar del Plata, in 46 m; MACN 11367, 36 specimens; MACN 9361–49, 5 specimens; MACN 18374, 2 specimens; MACN 8653, 4 specimens; MACN 11586, 27 specimens; all from Mar del Plata; MACN 20529-1 more than 60 specimens, mouth of Rio Negro.

Literature records: Due to similarities with *C. protea,* most literature records should be re-checked from now on. Records cited by Parodiz (1939) were revised and are included in the material examined.

Distribution: Province of Buenos Aires, Argentina, from Mar del Plata to the mouth of Rio Negro, on banks of *Mytilus edulis platensis,* 35-50 m depth. Records from Uruguay and Brazil need to be confirmed.

Reproductive pattern: *Crepidula argentina* new species is a protandrous hermaphrodite that undergoes complete sex change. Males mature at about 4 mm length. Sex change begins when individuals reach approximately 9 mm and is completed when the first previtelogenic ovocites appear, usually at around 11 mm length. The smallest brooding female we found was 15.0 mm length and the largest 39.0 mm.

The new species has a well-defined seasonal reproductive cycle. Between September and March more than 30% of the females are brooding, with maximum brooding in January (57%). In June and July brooding is uncommon (0-10%). Females brood 1−46 egg capsules per spawn. The average number of embryos per spawn is 5600. There is no correlation between size of the female and number of egg capsules or eggs per spawn. However, female size, capsule size, and the average number of embryos per capsule are positively correlated (Cledón and Penchaszadeh, submitted). Uncleaved egg diameter is 170 μm and there are about 320 eggs per egg capsule. All eggs develop, there are no nurse eggs, and the only extra-embryonic nutritional source is the intracapsular liquid. There is no record of cannibalism in early or advanced stages of development. The embryos hatch as planktotrophic veliger larvae.

DISCUSSION

Crepidula argentina new species is usually found on the posterior edge of living shells of *Mytilus edulis platensis* d'Orbigny, 1846, typically in association with *Calyptraeotheres garthi* (Fenucci, 1975) (Crustacea: Brachiura). Mytilid banks, distributed all around the coast of Argentina (Penchaszadeh, 1971a) are a suitable habitat for *Crepidula argentina.*

Crepidula argentina was included by different authors (Parodiz, 1939; Hoagland, 1977; 1983, in part) in *C. protea* and referred to as *C. unguiformis* by Penchaszadeh (1971b: 480). The type specimens of *C. protea* were examined by Hoagland (1983). At BMNH, there are two lots with 5 and 11 syntypes under the numbers 1854.12.4.573 and 574 respectively Aguirre (1993) designated and illustrated the only whole specimen as lectotype plus two paralectotypes, with no mention to

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Figures 42–46. Anatomy of *Crepidula argentina* new species. **42.** Stomach, ventral view, inner surface exposed by means of a longitudinal incision. 43. Head of male, dorsal view. **44.** Visceral mass and adjacent part of pallial cavity, male, ventral view; **45.** Pallial oviduct, ventral view. **46.** Penis, ventral view. All scale bars = 1 mm.

Hoagland's paper or d'Orbigny's (in Sagra) illustrations. Most of the type specimens are smaller than 30 mm and have the conchological attributes of what Hoagland described for *C. protea* from Brazil. In terms of shell characters, *C. protea* and C. *argentina* new species are similar. Measurements of C. *argentina* in Table 1 are identical to those given to C. *protea* by Hoagland (1977). However, in a later paper, Hoagland (1983) mentioned that the largest specimen of *C. protea* was 20 mm long. Therefore, we suspect that both species were combined under the name *C. protea* in her 1977 paper. *Crepidula argentina* is larger and wider, particularly in young specimens. *Crepidula protea* has an elliptical aperture with a thicker and more convex shell, while the new species has a subcircular aperture and a thinner and flatter shell. Both species differ primarily in their anatomical features and reproductive strategy. Further anatomical study of *C. protea* is provided in another paper (Simone, submitted); some data from that paper are here discussed for comparative purposes. *Crepidula argentina* differs morphologically from *C. protea* in that *C. argentina* has: 1) a more developed lateral shell muscle, 2) a poorly developed dorsal shell muscle, 3) the kidney proportionally smaller and with a different arrangement of inner folds of dorsal lobe, 4) presence of a renal vessel edging rectum and working as adrectal sinus, 5) a connection between odontophore muscle pairs m7 and m11, 6) a longer salivary gland, 7) four ducts to digestive gland in stomach, instead of two, 8) different arrangement of folds in inner surface of stomach between esophageal aperture and posterior pair of ducts to digestive gland, 9) seminal vesicles of males broader and less coiled, 10) penis and papilla longer and narrower, and 11) vaginal tube running closely attached to capsule gland.

, Embyological features of *Crepidula argentina* are very distinct from those of C. *protea (fide* Hoagland, 1983). The total number of embryos per spawn and per egg capsule and the size range of brooding females are the most remarkable differences. Furthermore, Hoagland (1986) described later stages of developing embryos (veliger stage) as pinkish in color and embedded in a sticky gelatinous matrix in which the embryos did not move freely. We never observed this in pre-hatching stages of *C. argentina.*

It is possible to differentiate several species of *Crepidula* along the southern Atlantic coast of South America. Parodiz (1939) cited five species of *Crepidula* for the Argentine coasts: C. *dilatata* Lamarck; *C. aculeata* (Gmelin); *C. protea* d'Orbigny; *C. onyx* Sowerby and C. *unguiformis* Lamarck. Specimens of *Crepidula unguiformis* were described by Parodiz as usually associated with hermit crabs. The distribution of *C. unguiformis* is given by Hoagland (1977) as restricted to the Mediterranean Sea and Northern Africa. It is probable that "C. *unguiformis" sensu* Parodiz is a distinct, perhaps unnamed, species. *Crepidula onyx* from the northern Pacific was cited by Parodiz (1939) as living in northern Patagonia. However, Hoagland (1977) based on Parodiz s drawing of the radula of *C. onyx* presumed that "C. *onyx" sensu* Parodiz is a different species: C. *aplysioides* Reeve, 1859. The latter species was cited as a synonym of C. *onyx* by Parodiz (1939). Hoagland (1977) described *C. aplysioides* as a different species ranging from Grenada south to Brazil and Argentina. Reeve s types were not examined. This type material includes four specimens and is housed at the BMNH (Reg. Number: 1977137). As far as we know, there is no species similar to *C. aplysioides* Reeve on the coast of Argentina.

The study of the family Calyptraeidae and the genus *Crepidula* in particular is less than finished for the region in study. It is expected that additional new species will be detected and described following detailed studies on anatomy and reproductive biology of these mollusks.

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