

ON *SOLAROPSIS* BECK: NEW ANATOMICAL DATA AND ITS SYSTEMATIC POSITION WITHIN THE HELICOIDEA (PULMONATA: STYLOMMATOPHORA)

MARIA GABRIELA CUEZZO

ABSTRACT

New anatomical data for three species of the genus Solaropsis Beck, 1837, is provided. The descriptions were based on gross-morphological studies of the genital, pallial, digestive and nervous systems. Based on the present descriptions and the published anatomical information of different species of the genus, their relationships within the Helicoidea are discussed. Psadara Miller, 1878, a formerly described subgenus of Solaropsis, later considered as a different genus, is currently not considered a natural group. The results of this study support the idea that Solaropsis should be included within the Camaenidae.

KEYWORDS: Anatomy, Systematics, *Solaropsis*, Camaenidae, Helicoidea, South America

INTRODUCTION

The genus *Solaropsis* was created by Beck in 1837 (Type species: *Solaropsis undata* (Lightfoot, 1786) = *S. pellisserpentis* (Chemnitz, 1795) = *S. cicatricata* Beck, 1837; see Tillier (1980)). Originally located within the

Camaenidae was posteriorly excluded from them by Wurz (1955) in his revision of the "American Camaenidae". He considered that *Solaropsis* was erroneously included in the Camaenidae, being a representative of a very ancient stock which affinities were not known. This idea was also sustained by Solem (1966). From that moment the systematic position of *Solaropsis* has remained problematic. Due to the insufficient knowledge on this group, Nordsieck (1986) considered that *Solaropsis* had to be placed in a different family, establishing Solaropsidae to include not only *Solaropsis* but also *Psadara*. Later Tillier (1989) retained *Solaropsis* traditional taxonomic position among the Camaenidae.

In 1878 Miller created the subgenus *Psadara*, later elevated to the category of genus. *Psadara* included all the *Solaropsis* species with small, fragile and depressed shell. The genus *Psadara* was rejected by Pilsbry (1890) but posteriorly revalidated by von Ihering (1900) and followed by Tillier (1980, 1989). Other authors (Weyrauch, 1956; Zilch, 1960; Haas, 1966) considered that *Psadara* is actually a subgenus of *Solaropsis*.

Richardson (1985) catalogued the Camaenidae including a list with a total of 44 species under *Solaropsis* Beck without distinction of the genus *Psadara* Miller. The systematic confusion around the *Solaropsis* group is probably due to the lack of information on the anatomies of the different species and the tradition of describing new species based only on shell characters. The works of von Ihering (1900, 1912) and Tillier (1980, 1989) resume all the knowledge on the anatomies of 4 out of 44 species of *Solaropsis* currently known.

The aim of this work is to provide new anatomical descriptions of certain species of *Solaropsis*. This information will contribute to a better understanding of the genus and will be the base of a future cladistic analysis of the Camaenidae.

MATERIAL AND METHODS

The material used in this study belong to the following Institutions: FML= Instituto-Fundación Miguel Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina. FMNH(=CNHM)= Field Museum of Natural History, Chicago, Illinois, USA. INBP= Inventario Biológico Nacional, Museo Nacional de Historia Natural del Paraguay, Asunción, Paraguay. NKC= Museo de Historia Natural "Noel Kempff Mercado", Santa Cruz de la Sierra, Bolivia. MLP= Museo de La Plata, La Plata, Buenos Aires, Argentina.

Material of other species than the present described, observed or dissected for character comparison:

Solaropsis (Psadara) monile Broderip

FMNH 173054: Ecuador. Dept. Pichincha. Santo Domingo de los Colorados. B.Malkin. Col. 4-7/6/71.

Solaropsis rosarium (Pfeiffer)

FMNH 126564: Brazil. Caninde, Rio Gurupi, Para. 6/7/63. Boris Malkin Col.

Solaropsis braziliana Deshayes

FMNH 173056: Ecuador. Dept Pastaza, Cushuene, Rio Cushuene. B.Malkin Col. 1971.

The specimens mentioned above were not described in the present study because of the availability of previous detailed descriptions published in the literature. Specimens of *S. angulifera* Haas and *S. heliaca* (d'Orbigny) were collected, drowned in water, fixed in 95% ethanol and later transferred into 70% ethanol. Specimens of the other species were available from malacological collections from the above cited Museums. All specimens used in this work were dissected under a Nikon SMZ-10 microscope. Illustrations were made with the aid of a camera lucida. No measurements of organs were included due to the modifications in size that the soft parts of the body normally suffer when the animal is washed and fixed. The terminology for the description of the different systems follows Tompa (1984) and Tillier (1989).

A Jeol Scanning electron microscope 35CF was used for the description of radulae and jaw. Standard procedures were used for radulae preparation (see Ploeger & Breure, 1977). Descriptions on the shell were not carried out because detailed descriptions are already published (Pilsbry, 1890). In the case of *S. gibboni* neither the digestive nor the central nervous systems were described because the state of preservation of the material used did not allow a good description.

RESULTS

Anatomical descriptions: *Solaropsis angulifera* Haas 1955 Haas, Fieldiana 34(35): 370-372.

External morphology: Head-foot of the animal light brown. Two dorsal, parallel, cephalic grooves extend from mantle collar towards inner side of tentacles. Both grooves limbed by wide dark-brown pigmented bands. Middorsal pedal groove well marked. Basal sole not divided. Suprapedal grooves well differentiated.

Pallial System: Pallial complex composed of lung, kidney and heart (Fig. 1). Lung roof bifurcated by a ramificated venous system. Fine black spots lined veins giving a dark appearance to roof. Lung extends proximally beyond top of kidney (approximately 5 mm) and distally limits with mantle collar. Venation abundant not only in area between kidney and rectum but also in area to left side of kidney. Lung floor or diaphragm thin, opaque, with muscular fibers in transverse and longitudinal disposition. Kidney located in proximal left side of lung roof; extending longitudinally 70-80% of pulmonary roof surface. Internally, kidney presents longitudinal, parallel, undulating lamellae, thinner and less pronounced distally, close to kidney pore. In proximal portion of kidney lamellae thicker and deeper. Internally kidney not divided in different regions, with one type of sculpture. Primary ureter runs along right side of kidney to top of lung roof turning down along rectum as secondary ureter. Secondary ureter closed until mantle collar where it splits into two grooves, adrectal and abrectal branches delimiting a deeply excavated ureteric interramus (Fig. 2). Main pulmonary vein runs parallel to kidney and rectum splitting in numerous minor transverse and oblique veins before reaching mantle collar. No pallial gland differentiated.

Digestive System: Radula: Central tooth tricuspid, laterals bicuspid with high mesocone. Edges of laterals and marginals teeth with fine denticulation. Marginals tricuspid with high mesocone.

Jaw: Arcuate, very thin and with 10 well marked ribs.

Buccal mass muscular (Fig. 3, 4), spheroidal to ovoid. Oesophagus short, cylindrical. Internally with longitudinal ridges along its length (Fig. 3). Oesophageal crop wide with thin, transparent wall. Body of salivary glands fused over proximal part of oesophageal crop. Oesophageal crop separated from stomach by a portion of duct, thinner than oesophagus in diameter. Stomach round. Typhlosole running from anterior digestive gland duct opening, longer than typhlosole running from posterior digestive gland opening (Fig. 5). Intestine lying along columellar side of digestive gland, followed by rectum. Rectum runs parallel to the pulmonary roof and ends in mantle collar.

Reproductive System (Fig. 6-8): Ovotestis (hermaphroditic gonad) composed of round to ovoid alveoli that conform a single, compact mass. Ovotestis embedded in columellar side of digestive gland. Hermaphroditic duct or ovotestis duct runs along columellar side of digestive gland, ending in distal portion of albumen gland. No fertilization pouch-spermathecal complex (FPSC = talon according to Wurz, 1955) differentiated. Distal portion of hermaphroditic duct reflexed over itself before entering carrefour zone. Albumen gland variable

in size with typical elongated, curved shape (Fig. 6). Female glandular portion of spermoviduct composed of transversal sacculations. Prostate tubular running parallel to feminine portion. Distally, transversal sacculations of uterus became oblique. Bursa copulatrix ovoid with short stalk, 1 1/2 length of bursal sac, running parallel to distal portion of spermoviduct (Fig. 7). Thin, long diverticulum, about three times the length of bursa copulatrix, splits at base of bursa copulatrix's duct. Diverticulum runs parallel to spermoviduct reaching its proximal portion distal zone of albumen gland (Fig. 6). Internal sculpture of both sac and stalk of bursa copulatrix consists of longitudinal, parallel ridges. Vas deferens rises at distal portion of prostate, runs to terminal genitalia, along free oviduct and vagina, passes through peni-oviducal angle, then runs parallel to penis and inserts in proximal portion of epiphallus (Fig. 6). Vas deferens attaches by connective tissue at peni-oviducal angle. Vas deferens regular in diameter not swelled at point of insertion. Free oviduct cylindrical and short. Vagina as long as penis or even a little longer. Internally, it presents seven to eight longitudinal parallel, deep ridges along its entire length. Atrium short with internal thick columns of lappets overlapped (Fig. 6, 8). Penial complex composed of penis, epiphallus and flagellum (Fig. 8). Penis cylindrical, long, completely wrapped by thin opaque sheath. Internally, penis presents several undulating longitudinal folds separated at regular intervals and a dorsal pilaster composed of round to quadrate lappets overlapping one to another. Verge short located in proximal penis with penial-epiphallus pore laterally positioned. External sculpture of verge consisting of transversal rows of lappets. Epiphallus cylindrical, as long as half of penis length. Epiphallus reflexed over itself (Fig. 8). Penial retractor muscle inserts in medial zone of epiphallus forming a ring that surrounds completely epiphallus. Proximal portion of epiphallus externally lined laterally by two folded projections. Epiphallus continued by flagellum with a very unusual form, composed of three projections, two lateral and a central one.

Central nervous System (Fig. 9): Entirely contained in pedal cavity forming a ring around proximal portion of oesophagus. Cerebral commissure short, both cerebral ganglia almost contiguous. Cerebro-pedal connectives thick and short, connecting both cerebral ganglia with visceral chain. Visceral chain conformed by visceral ganglion, parietal, pleural and pedal ganglia. Visceral ganglion fused with left parietal and positioned to left of pedal ganglia's median plane. Both parietal ganglia in close contact with pleural ganglia. Pedal ganglia round, positioned anterior to pleural ganglia.

Material examined: FML 14238: Bolivia. Depto Santa Cruz de la Sierra, Prov. Manuel Caballero. Yungas de Mairana. 20/4/93. Dominguez, E. Col.

CNHM 50730: Bolivia, Region Chapare, 400 mts alt. R. Zischka leg. 1951. TYPE.

Solaropsis heliaca (d'Orbigny) 1835 d'Orbigny, Guerin's Mag.Zool. 5(61): 4.

External morphology: Head-foot of animal dark brown to black. Two well marked bands parallel to longitudinal axis of foot. Sole without divisions. Head-foot when extended extremely thin. Genital orifice on right side of the head below ocular tentacle.

Shell as described by Pilsbry (1890: pg.185)

Pallial System: As in *S. angulifera* except for differences in length (Fig. 10)(see above description).

Digestive System: Radula (Fig. 14-17): Central tooth tricuspid, lateral teeth bicuspid with high mesocone, some showing a dorsal curved, triangle spine also present in dorsal surface of marginal teeth. Edges of lateral and marginals teeth with fine denticulation even in newest lines of teeth. 43-1-43 x 140 .

Jaw: Arcuate, very thin and with 10 well marked ribs.

Rest of system as described for *S. angulifera*.

Reproductive System (Fig. 11, 12): Ootestis and hermaphroditic duct as in *S. angulifera*. Albumen gland pale yellow, same shape than in *S. angulifera*. Female portion of spermoviduct plicated longitudinally except in distal portion, where folds became transverse to oblique (Fig. 11, 12). Free oviduct cylindrical, as long as vagina. Bursa copulatrix stalk short, double in length of free oviduct. Sac, round to oval, extends until distal portion of spermoviduct (Fig. 12). Proximal portion of sac attached to spermoviduct through thin strands of connective tissue. Thin diverticulum, arise from basal portion of bursa copulatrix, runs parallel to one side of bursal duct until it reaches top of sac.

Vas deferens narrow, surrounds free oviduct, attaches to peni-oviducal angle by connective tissue (Fig. 11). It inserts between limit of epiphallus and flagellum. Vagina shorter than penis, about half its length. Internally with parallel, thin, deep ridges continuous within free oviduct where became undulating and deeper. Short muscular strands connects vagina with right lateral body wall. Atrium short with internal bifurcated ridges. Genital pore located in head under right ocular tentacle. Penis long, tightly bound to epiphallus by connective tissue. Basal portion of epiphallus reflexed over last portion of penis. Thick penial

sheath cover penis. Internally, penis divided into two portions by its different sculpture. Proximal portion with zig-zag parallel ridges that became straight and thinner in distal region. Proximal portion of penis more swollen in diameter than distal one. Verge absent. Internal sculpture of epiphallus consists of three wide columns of shallow zig-zag ridges. Flagellum thick and short. Penial retractor muscle thin attached to diaphragm, inserts in upper region of epiphallus. Right ocular nerve pass through peni-oviducal angle.

Central Nervous System (Fig. 13): As described for *S. angulifera*, but cerebro-pedal connectives longer than in former species, although this could be interpreted as an artifact of fixation.

Material examined: FML 5109: Paraguay: Carumbe, Depto. San Pedro. 10/3/65. Golbach Col. FML 14237: Argentina: Formosa. Estancia "El Bagual", Pte. Irigoyen.5/3/93. Cuezco, F. Col.

INBP Paraguay: Dpto. Amambay. P.N. Cerro Cora. 2-8/6/82. Kochalka, J.! INBP Paraguay: Dpto. Alto Paraguay: Bahia Negra: Estancia Doña Julia. 28/9/84. Silva, L. Col.

MLP 978: Paraguay. Schiller, W. Col. MLP 992: Argentina: Picada Guaycuru, Chaco. 11/1942. Biraben, M. Col.

NKC 1: Bolivia: Departamento Santa Cruz, Santo Corazón. 2/1997. Fernandez, I. Col.

Solaropsis gibboni (Pfeiffer) 1846 Pfeiffer, Symb.Helic. 3: 37.

Pallial System (Fig. 18): Pulmonary roof extremely long. Kidney almost triangular, located in upper left side of pulmonary cavity. Kidney length about 1/4 of pulmonary roof length. Pericardium half length of kidney. Pulmonary roof proximally extends about 1 cm beyond top of kidney. Secondary ureter open from proximal to distal portion of lung. Pulmonary vein softly marked, rest of roof almost without any vein. Ureteric interramus deeply excavated.

Reproductive System (Fig. 19, 20): Ootestis composed of round alveoli conforming a single mass. Hermaphroditic duct convoluted inserting in distal part of albumen gland. Spermoviduct as long as penial complex. Oviducal portion of spermoviduct with longitudinal folds. Free oviduct three times vagina's length. Bursa copulatrix sac ovoid, with long, thin stalk. Diverticulum shorter than bursal stalk and thicker than in *S. heliaca* and *S. angulifera* (Fig. 19). Vagina short, with longitudinal, parallel internal ridges. Atrium short. Penis longer than vagina, about two times vagina's length, with a short and round blind sac or

penial appendix in its medial zone. Internally, a constriction marked penial appendix level (Fig. 20). Proximal part of penis with two pilasters. Distal part of penis with longitudinal internal ridges in zig-zag. Penial retractor muscle thick, basally splitting in short branches before attaching penis. Vas deferens wrapped to penis wall by connective tissue. Epiphallus long, with two internal pilasters thinner in proximal region. Verge absent. Flagellum thick and short.

Material examined: FMNH 115800: Colombia, San Andres, Santander, Quebrada de Pangote, 1400 mts. P.E. Acosta Col. 26/6/60.

DISCUSSION

The systematic position of the genus *Solaropsis* as well as the internal subdivisions into subgenera are problematic. The relationships of *Psadara* as a subgenus of *Solaropsis* or as a different genus are not well established.

According to Tillier (1980) characters that identified *Solaropsis* are the bifurcated spermatheca (=bursa copulatrix duct in the present work), the existence of a penial appendix, a penial retractor muscle sometimes bifurcated and the presence of an epiphallus and a flagellum. However, it was found in the present work that the last two characters are only present in *Solaropsis gibboni* being absent in the rest of the studied species.

In the present study a set of characters are proposed as important in *Solaropsis* definition: "bursa copulatrix bifurcated", the "spermiduct groove extending through the free oviduct" and the a lung surface extending beyond the top of the kidney". However, it is necessary to state that only through a cladistic analysis, it would be possible to test if those characters are really synapomorphies of the genus.

Tillier (1980) stated that *Psadara* differs from *Solaropsis* by having a closed secondary ureter, character that justified, according to him, its separation in a different genus. Other characters such as the presence of a long kidney and a short spermatheca (= bursa copulatrix in the present work) in *Psadara*, were used by Tillier in the same study to differentiate *Psadara*'s species from *Solaropsis*.

The species of the *Psadara* group analyzed in the present paper: *S. mamartensis*, *S. monile*, *S. angulifera* and *S. rosarium* do not seem to conform a unit based on Tillier's (1980) definition. No unique character was found that could justify the separation of those species from the rest of the *Solaropsis*'s ones. Indeed, the presence of a long kidney and a closed secondary ureter, characters that supposedly diagnosed *Psadara*, are also present in some *Solaropsis* species such as *S. heliaca* and *S. braziliiana*. With respect to the

systematic position of *Psadara*, Tillier himself changed his mind in 1989, when he state that *Psadara* should be classified within the Cepolinae because "the arrangements of the organs in *Cepolis maynardi* looked very much like that in *Psadara*". In concordance with Pilsbry (1890), the results of this work supports the idea that the species analyzed form a series too close related to admit the division proposed by Miller (1878). At the present moment, with the scarce availability of anatomical studies, it is not possible to clearly differentiate *Solaropsis* from *Psadara* or admit *Psadara* as a valid genus since there are no characters that could properly define it.

Solaropsis shares with *Labyrinthus* Beck, 1837, and *Isomeria* Albers, 1850, genera of the Camaenidae which distributions partially overlap by the presence of a reflexed penis-epiphallus, the absence of a FPSC, and a typhlosole from the anterior duct opening of the digestive gland more developed than the one from the posterior duct. Those characters, plus the distribution, could justify the relocation of *Solaropsis* within the Camaenidae. The creation of Solaropsidae to include *Solaropsis* was not clearly justified and well supported with characters by Nordsieck (1987).

In conclusion:

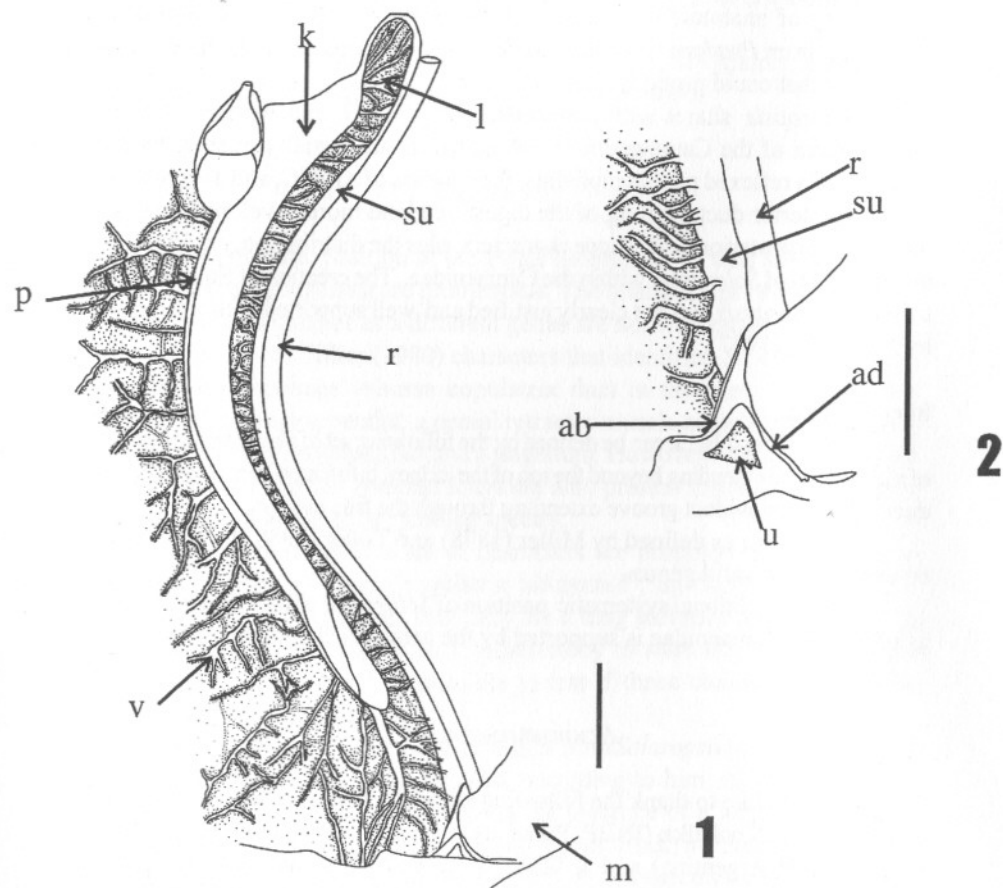
1) *Solaropsis* Beck can be defined by the following set of characters: presence of a lung surface extending beyond the top of the kidney, bifurcated bursa copulatrix's duct, and spermoviduct groove extending through the free oviduct.

2) *Psadara* as defined by Miller (1878) and Tillier (1980, 1989) can not be considered a valid genus.

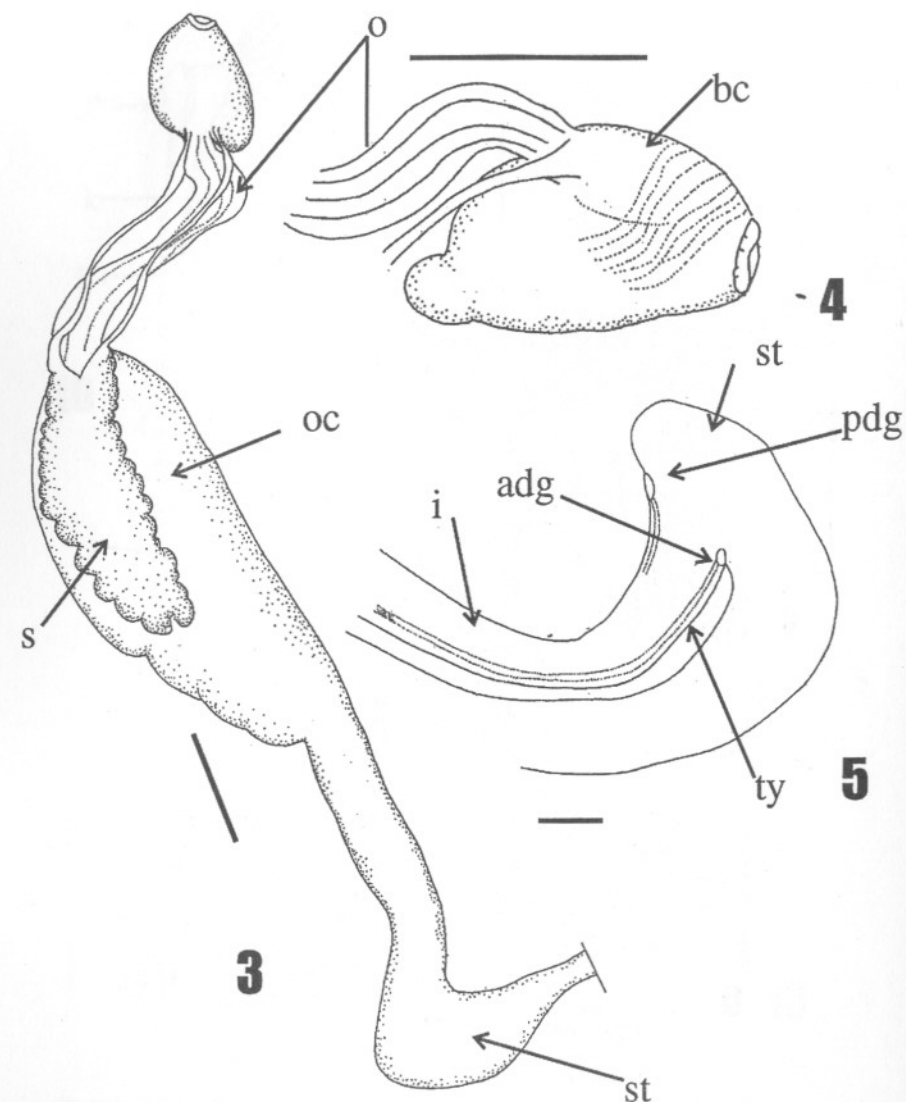
3) The traditional systematic position of *Solaropsis* within the Helicoidea as part of the Camaenidae is supported by the anatomical data presented.

ACKNOWLEDGEMENTS

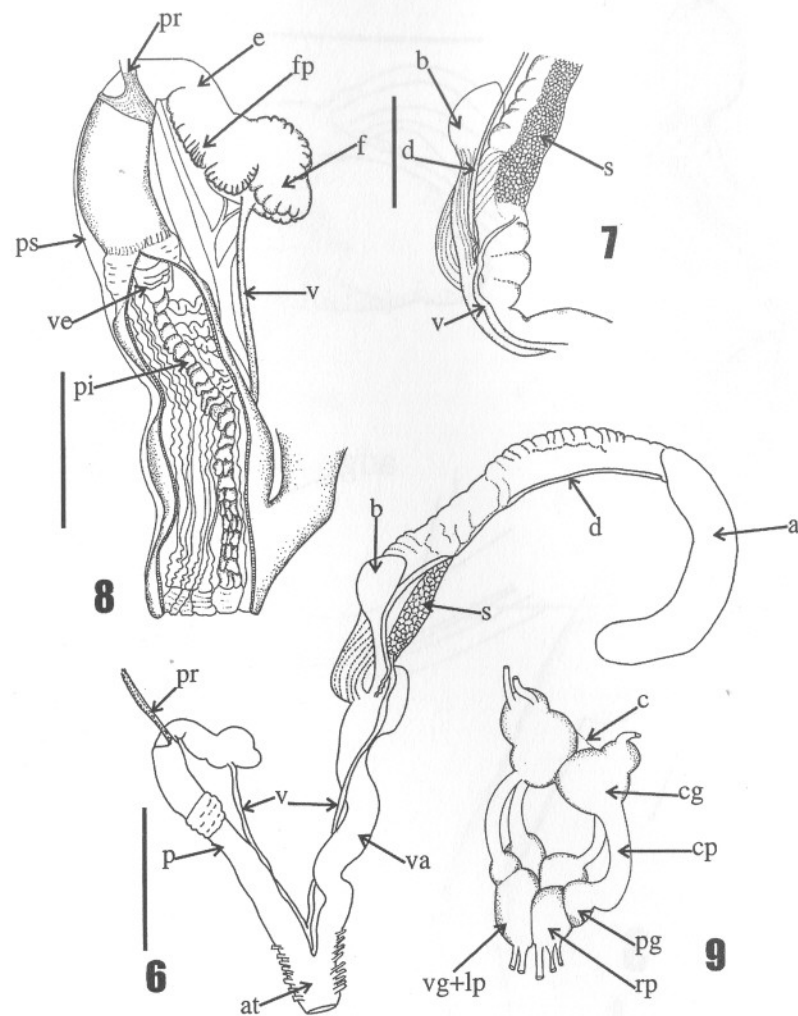
I would like to thank the following persons and Institutions for the loan of material: J. Kochalka (INBP, Paraguay); I. Fernandez (NKC, Bolivia); C. Ituarte (MLP, Argentina) and J. Slapcinsky and R. Bieler (FMNH, USA). Thanks are extended to A. Andrada of the EM facilities from LAMENOA (UNT-CONICET) for his technical assistance. This research was supported by the Argentine Council of Scientific Research (CONICET).



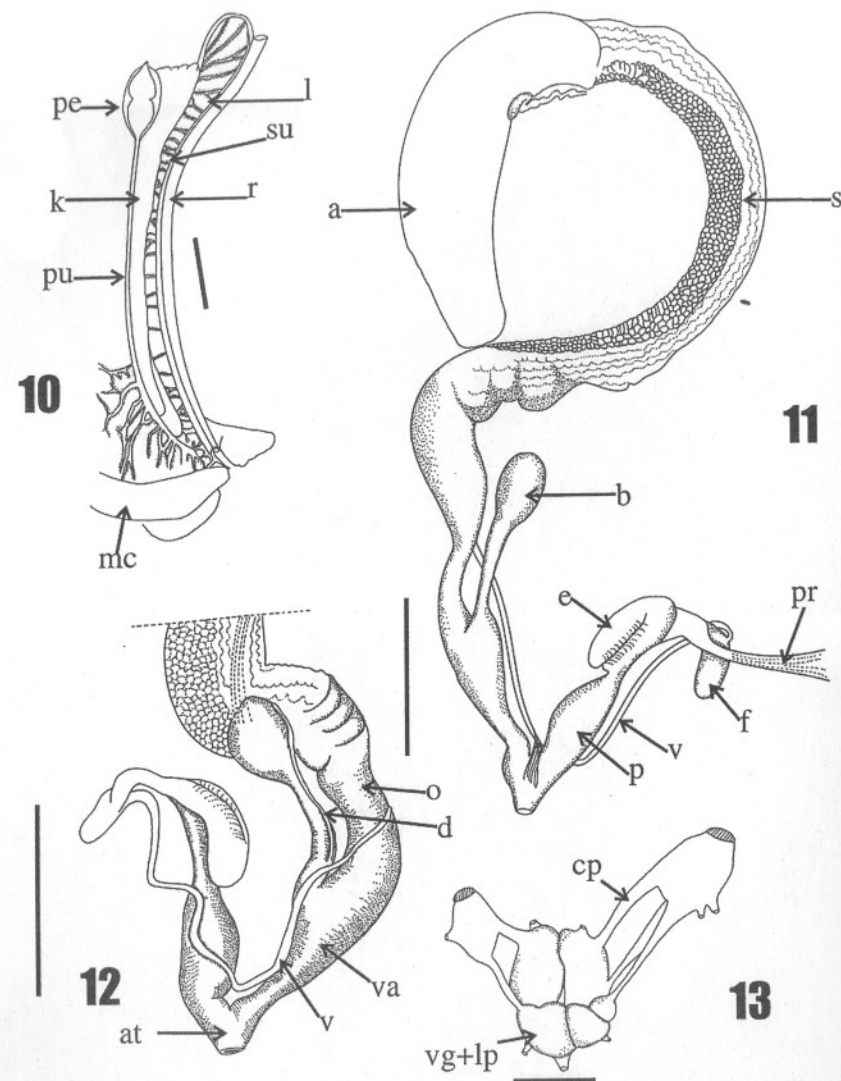
Solaropsis angulifera. Figure 1. Pallial complex in ventral view with excretory and part of circulatory systems; scale bar= 5 mm. Figure 2. Detail of the ureteric interramus zone; scale bar= 3 mm. Abbreviations: ab, abrectal groove; ad, adrectal groove; k, kidney; l, lung roof; m, mantle collar; p, main pulmonary vein; r, rectum; su, secondary ureter; u, ureteric interramus; v, general venation.



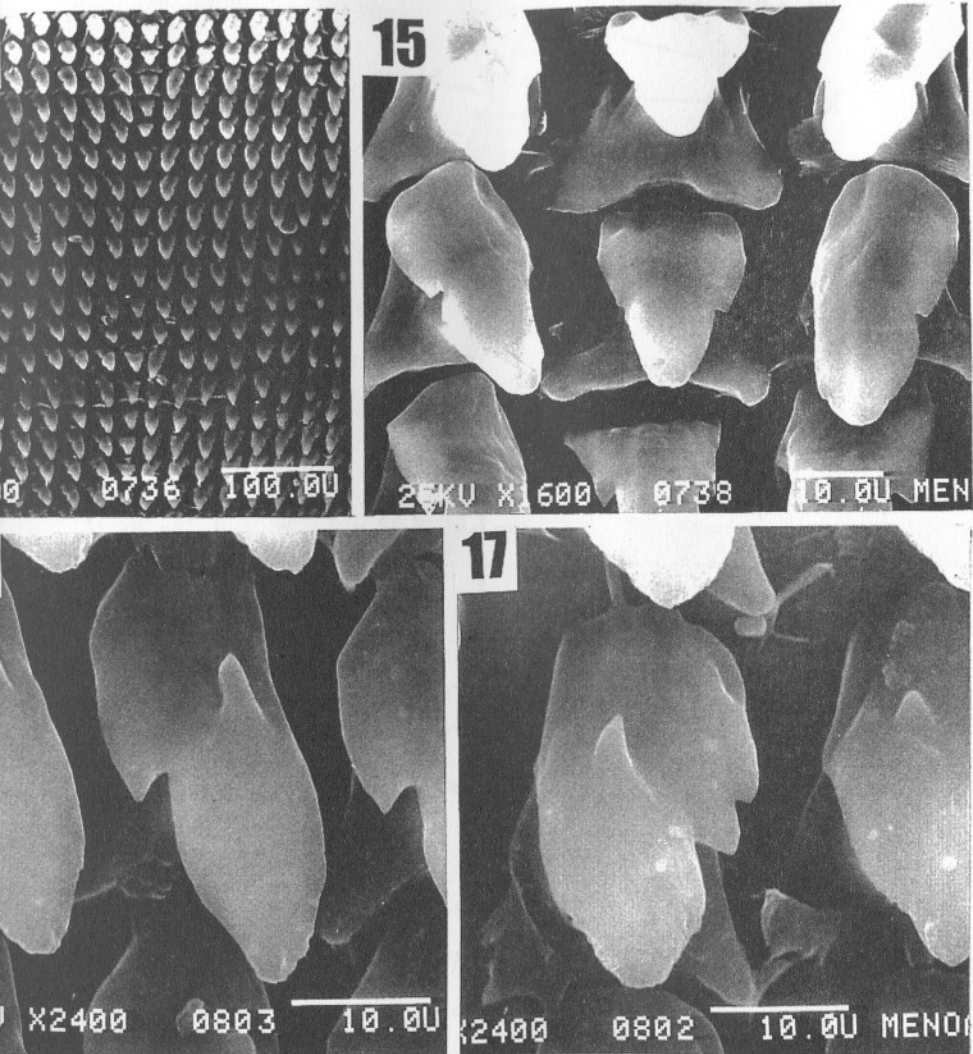
Solaropsis angulifera. Figure 3. Proximal portion of digestive system from buccal mass to stomach in dorsal position; scale bar= 5 mm. Figure 4. Buccal mass in lateral position; scale bar= 1 mm. Figure 5. Portion of stomach with internal typhlosoles extending from anterior and posterior digestive glands openings; scale bar= 5 mm. Abbreviations: adg, anterior digestive gland duct opening; bc, buccal mass; i, intestine; o, oesophagus; oc, oesophageal crop; pdg, posterior digestive gland duct opening; s, salivary glands; st, stomach; ty, typhlosole.



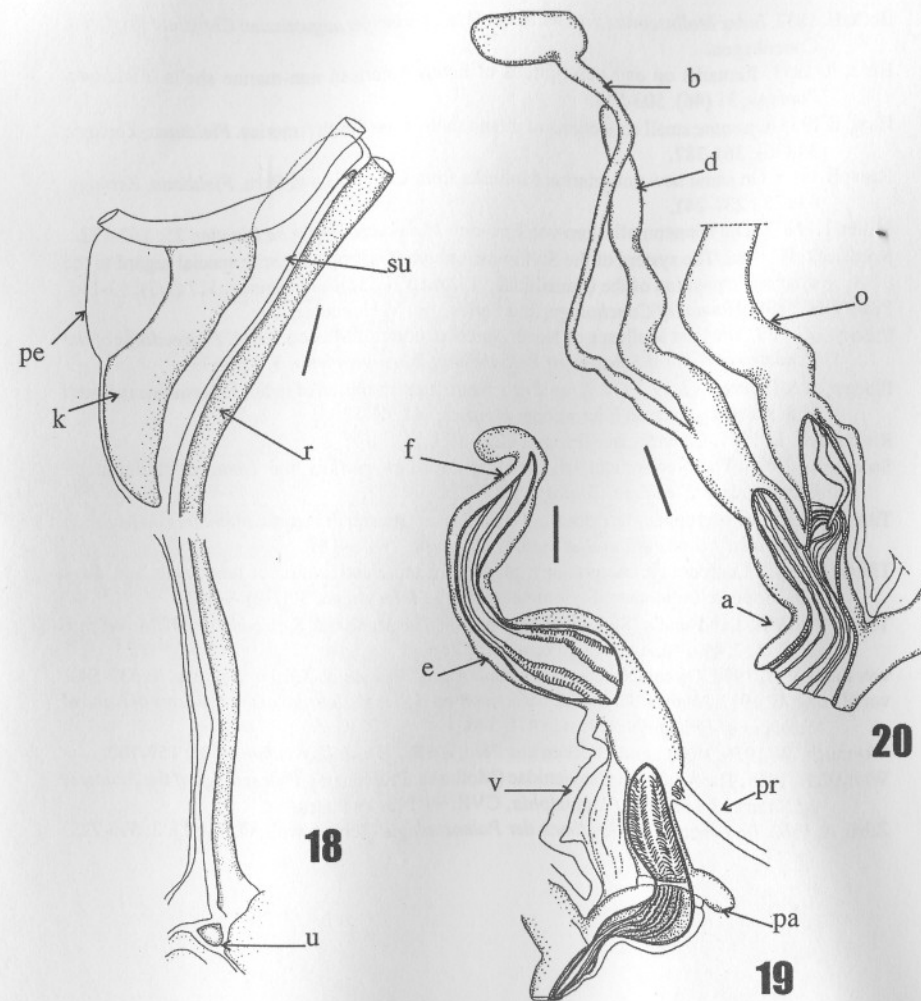
Solaropsis angulifera. Figure 6. General aspect of reproductive system in dorsal position, ovotestis and hermaphroditic duct not illustrated; scale bar= 5 mm. Figure 7. Detail of the bursa copulatrix and insertion of diverticulum and vas deferens; scale bar= 5 mm. Figure 8. Penial complex and internal sculpture of penis; scale bar= 5 mm. Figure 9. Central nervous system; scale bar= 1 mm. Abbreviations: a, albumen gland; at, atrium; b, bursa copulatrix; c, cerebral commissure; cg, cerebral ganglia; cp, cerebro-pedal connectives; d, diverticulum; e, epiphallus; f, flagellum; fp, folded projections; lp, left parietal ganglia; p, penis; pd, pedal ganglia; pg, pleural ganglia; pi, pilaster; pr, penial retractor muscle; ps, penis sheath; rp, right parietal ganglia; s, spermoviduct; v, vas deferens; va, vagina; ve, verge; vg, visceral ganglion.



Solaropsis heliaca. Figure 10. Pallial system in ventral view; scale bar= 5 mm. Figure 11. General morphology of the reproductive system, ventral view; scale bar= 5 mm. Figure 12. Detail of the terminal genitalia in dorsal view; scale bar= 5 mm. Figure 13. Central nervous system; scale bar= 1 mm. Abbreviations: a, albumen gland; at, atrium; b, bursa copulatrix; cp, cerebro-pleural connective; d, diverticulum; e, epiphallus; f, flagellum; k, kidney; l, lung roof; lp, left parietal ganglia; mc, mantle collar; o, free oviduct; p, penis; pe, pericardium; pr, penial retractor muscle; pu, main pulmonary vein; r, rectum; s, spermoviduct; su, secondary ureter; v, vas deferens; va, vagina; vg, visceral ganglion.



Solaropsis heliaca. Figure 14. Radula: General view; scale bar= 100μm; Figure 15. Central and lateral teeth; scale bar= 10μm. Figure 16. Detail of the lateral teeth; scale bar= 10μm. Figure 17. Dorsal view of the marginal teeth; scale bar= 10 μm.



Solaropsis gibboni. Figure 18. Pallial system; scale bar= 5mm. Figure 19. Penial complex in ventral position; scale bar= 5 mm. Figure 20. Detail of terminal genitalia; scale bar= 5 mm. Abbreviations: a, atrium; b, bursa copulatrix; d, diverticulum; e, epiphallus; f, flagellum; k, kidney; o, free oviduct; pa, penial appendix; pe, pericardium; pr, penial retractor muscle; r, rectum; su, secondary ureter; u, ureteric interramus; v, vas deferens.

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