

SYSTEMATIC POSITION AND ANATOMY OF DREPANOSTOMELLA TUCMA HYLTON SCOTT, 1948 (STYLOMMATOPHORA: SCOLODONTIDAE)

MARIA GABRIELA CUEZZO¹ & MARIA JOSE MIRANDA²

¹ CONICET-Facultad de Ciencias Naturales, Universidad Nacional de Tucumán, Miguel Lillo 205, 4000 Tucumán, Argentina.

² Fundación Miguel Lillo-Facultad de Ciencias Naturales, Universidad Nacional de Tucumán, Miguel Lillo 205, 4000 Tucumán, Argentina.

Abstract We redescribe *Drepanostomella tucma* Hylton Scott, 1948 and discuss the possible affinities of the genus. This is the first published report on the anatomy of a species of the genus *Drepanostomella* Bourguignat, 1889 since this taxon was previously known only on the basis of its shell morphology and radula. *Drepanostomella* was traditionally classified within *Systrophiidae* (now *Scolodontidae*), a widely distributed family in the Neotropical region. *D. tucma* is characterized by its deep sunken spire in a nautiloid shell, smooth protoconch, nacreous periostracum and an acute incision at parietal angle of the aperture. The animal has a holopod foot, while most of the other genera components of the family have an aulacopod foot. The radula has a central small tooth with the first lateral tooth smaller than the second one. Noteworthy is the presence of papilla regularly arranged with slightly recurved corneous hooks over the inner penis wall. Similar protuberances with corneous hooks have been already described in *Hirtudiscus* Hylton Scott, 1948. *Drepanostomella* shows shell similarities mainly with *Hirtudiscus* and *Guestieria* Crosse, 1872. On the base of its radula morphology, its condition of "egg retainer" and the course of the right ommatophoral retractor passing between penis and vagina, *Drepanostomella* should be classified within the *Scolodontinae* (sensu Tillier, 1980). Differences and similarities of *Drepanostomella* with *Happia* Bourguignat, 1889, *Systrophia* Pfeiffer, 1855, *Entodina* Ancey, 1887 and *Systrophiella*, Baker, 1925, the rest of the *Scolodontinae* genera (sensu Tillier, 1980), are discussed. However, more anatomical studies and a cladistic analysis are necessary to further test these proposed affinities.

Key words South America, *Scolodontidae*, *Systrophiidae*, radula, genitalia.

INTRODUCTION

The *Scolodontidae* Baker, 1925 (= *Systrophiidae* Thiele 1927) have a complicated taxonomic history and represent one of the less studied families of the South American malacological fauna. This family of land snails has a mainly Neotropical distribution with other occurrences in Central America and the Caribbean islands. About 150 species classified in eleven genera have been described so far (Hausdorf, 2006). Most of the species of *Scolodontidae* were previously classified among the *Streptaxidae*. Baker (1925a) proposed an arrangement of the American *Streptaxidae* based on characters of the radula and shell. He listed all together the genera included in the *Streptaxidae* and *Circinariidae*, some of them currently classified into the *Punctidae*, *Scolodontidae* (= *Systrophiidae*), *Haplotrematidae* and *Polygyridae*. In following publications, Baker (1925b, 1926) divided *Streptaxidae* into two families, the *Scolodontidae*, where he included *Austroselenites* Kobelt, 1905, *Happia*, *Drepanostomella*, *Scolodonta* Doering, 1875, *Miradiscops* Baker, 1925 and *Tamayoa* Baker, 1925 and the *Streptaxidae* with *Rechartemon*

Baker, 1925 and *Streptaxis* Gray, 1837. Later, Thiele (1927) studying the American streptaxids (including Baker's *Scolodontidae*) concluded that based on radular characters these taxa represented more than one family and for this reason created the *Systrophiidae*. The generic classification of *Systrophiidae* was published by Thiele (1931). Zilch (1959-60) mentioned *Systrophia*, *Happia*, *Miradiscops*, *Tamayoa*, and *Guestieria* as the genera comprising the *Systrophiidae* and considered that *Drepanostomella* was a subgenus of *Happia*. *Scolodonta* was classified among the *Streptaxidae* and *Austroselenites* among the *Haplotrematidae*. After Thiele (1931) and Zilch (1959-1960), the family name *Systrophiidae* was used replacing Baker's *Scolodontidae*. Tillier (1980) gave further details and a diagnosis of *Systrophiidae* splitting the group into two tribes, the *Systrophiini* and *Tamayoini* on the basis of anatomical characters. Nordsieck (1986) considered that *Haplotrematidae* and *Systrophiidae* are sister groups with vicariant distributions, the *Haplotrematidae* occurring in the western Neartic and northern Neotropical region and the *Systrophiidae* in the Neotropical region.

The first cladistic analysis of the *Systrophiidae* was carried out by Ramirez

(1993) who, on the basis of her phylogenetic analysis, made a generic arrangement into nine genera in two subfamilies: Tamayoinae with *Tamayoa* and *Happiella* Baker, 1925 and Systrophiinae with *Drepanostomella*, *Guestieria*, *Happia*, *Wayampia* Tillier, 1980, *Systrophia*, *Zilchistrophia* Weyrauch, 1860 and *Miradiscops*. She classified all the above mentioned genera within the family Systrophiidae. Although the analysis was based on anatomical characters of only fourteen species in total, the classification obtained represents a testable hypothesis and the only available cladistic analysis of the family.

Bouchet and Rocroi (2005) stated that if the anatomically unknown *Scolodonta* belongs to the family usually called Systrophiidae, then the name Scolodontidae has priority over Systrophiidae. For this reason, Hausdorf (2006) studied the anatomy of *Scolodonta semperi* Doering, 1875, the type species of *Scolodonta*, and concluded that this genus effectively belongs to the Systrophiidae not to the Streptaxidae. Thus, this family has to be called Scolodontidae Baker, 1925 under the principle of priority.

The genus *Drepanostomella* is composed of ten nominal species and is widely distributed in Central and South America (Ramirez, 1993). Anatomical information, especially concerning the morphology of the genitalia of the species is lacking except for an unpublished species described in a master thesis (Ramirez, 1993).

The objective of this paper is to describe for the first time the anatomy of *Drepanostomella tucma*, and to discuss the systematic position of the genus *Drepanostomella* within Scolodontidae.

MATERIAL AND METHODS

Specimens of *Drepanostomella tucma* were collected at different elevations (700 to 1200 m) in Parque Sierra de San Javier, a protected area of the Tucumán National University, Tucumán, Northwestern Argentina. Additional specimens from other localities of Salta Province (northwestern Argentina) were also examined. The animals were collected in summer and autumn seasons (November to May) in rainforest areas. They were active under humid tree logs on the floor. Adult specimens were fixed in 96% etha-

nol and later transferred to 70% ethanol. Other specimens were maintained alive in small terraria to observe their reproductive activities. The different anatomical systems were dissected from alcohol fixed specimens, observed and drawn under a Leica MZ6 stereoscopic microscope with the aid of a camera lucida. Shells were measured with calipers. Shell and radula were observed and photographed with a Jeol Scanning Electron Microscope 35 CF. Preparation procedures followed were as described by Ploeger and Breure (1977). Terminology for the anatomical descriptions follows Tompa (1984). Terms proximal and distal refer to position in relation to the ovotestis. All the material collected was deposited in the Fundación Miguel Lillo-UNT Malacological Collection, Tucumán, Argentina. Abbreviations used in the text: D maj: shell major diameter; D min: shell minor diameter; H: shell height; Ap D: shell apertural diameter; dept: Political Department division; idem: the same, used in the case when the locality is the same than in previous material, to avoid repetitions; leg.: collected by; det.: taxonomically identified by; Prov.: province. (AM): alcohol preserved material; (DM): dry material.

INSTITUTIONAL ABBREVIATIONS

FML Fundación Miguel Lillo, Tucumán, Argentina
MLP Museo de Ciencias Naturales, La Plata, Buenos Aires, Argentina.

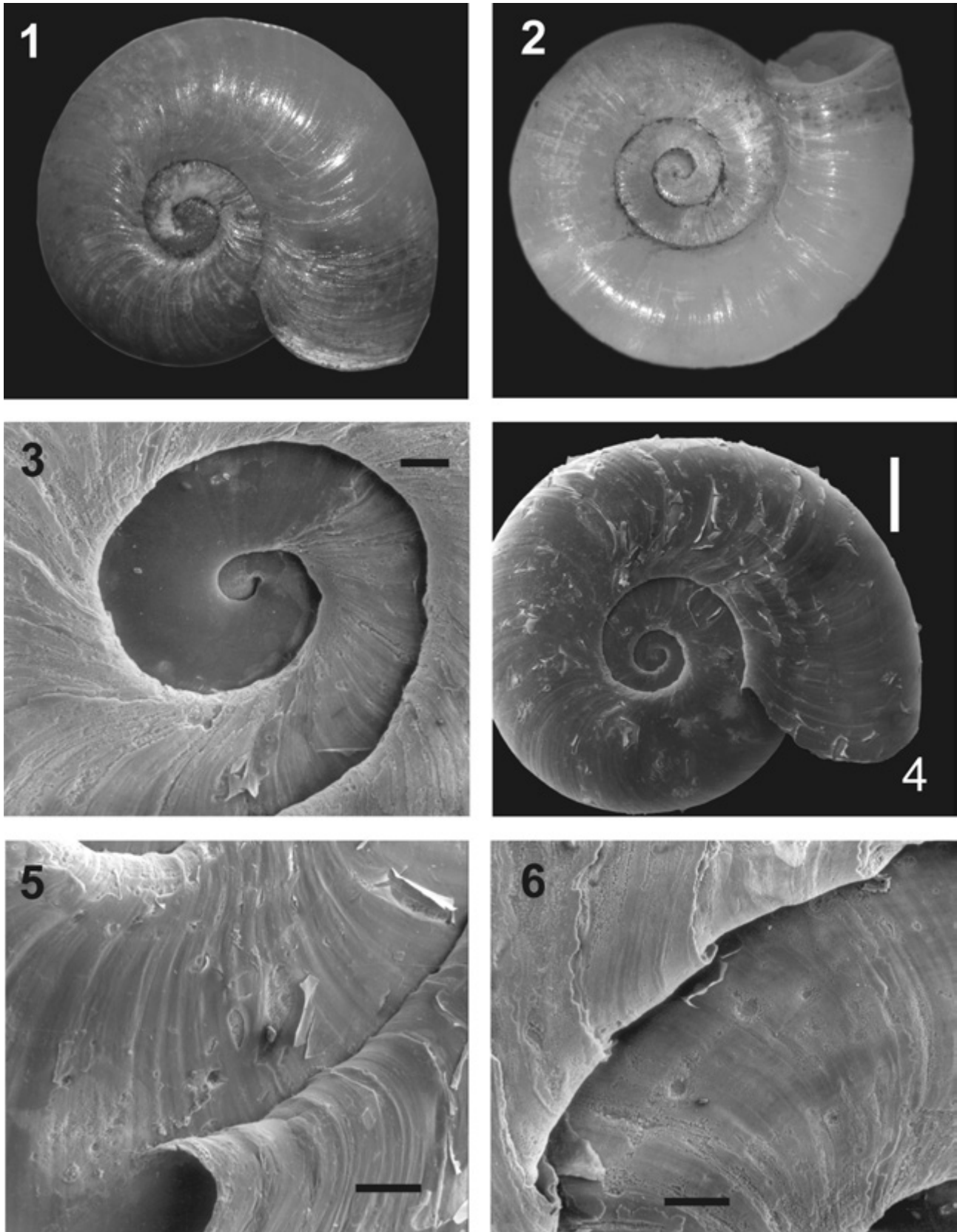
TAXONOMIC DESCRIPTION

Clade *Stylommatophora*
Superfamily Rhytidoidea Pilsbry, 1893
Family Scolodontidae Baker, 1925

Genus *Drepanostomella* Bourguignat, 1889

Type species: *Helix ammoniformis* d'Orbigny, 1835: 5 (by subsequent designation).

Distribution of the genus Costa Rica, Guatemala, Panama, Colombia, Venezuela, Ecuador, Peru, Bolivia, Paraguay, northern Argentina and southern Brazil.



Figs 1-6 *Drepanostomella tucma* 1 Shell in dorsal view. 2 Shell in ventral view. Note the wide umbilicus. 3 Detail of the sunken spire with smooth protoconch. Scale bar= 200µm. 4 Dorsal view of shell with loose periostracum. Note the acute incision of the aperture. Scale bar= 1000 µm. 5 Detail of body whorl showing incision at parietal angle of the aperture. Scale bar= 200 µm. 6 Suture between body whorl and previous whorl. Scale bar= 200 µm.



Figs 7-8 *Drepanostomella tucma* living specimen. Note the partially loose shell periostracum, a common condition in living snails of the present species.

Drepanostomella tucma Hylton Scott, 1948
(Figs. 1-12)

Streptaxis ammoniformis Parravicini, 1894: 1-2.

Happia (Drepanostomella) ammoniformis Ancey, 1897: 2.

Drepanostomella tucma Hylton Scott, 1948: 264-266.

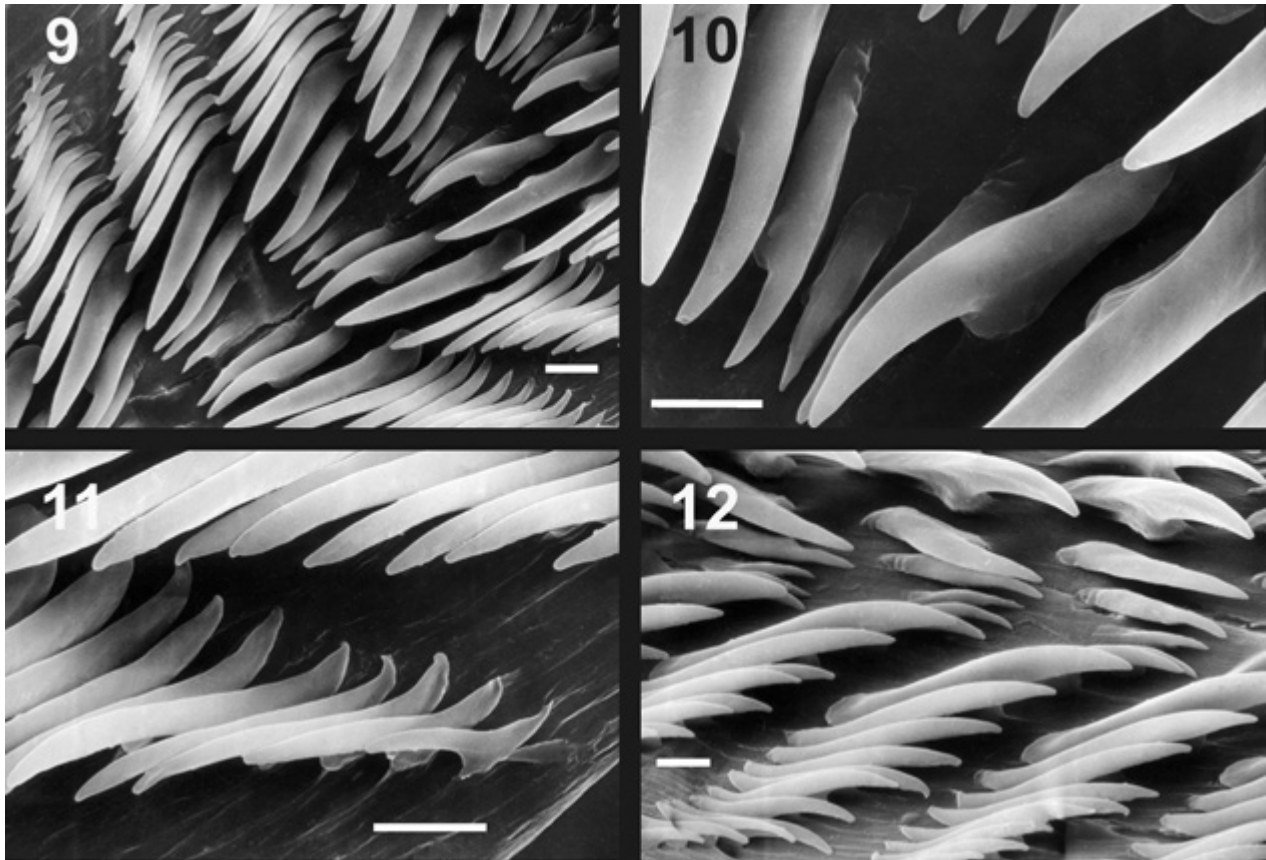
Holotype FML 473.

Paratypes FML 470, same locality as holotype. FML 472, idem. MLP 11103, Argentina, Tucumán, Yerba Buena dept., Naranjal, 27/9/1929, Hylton Scott det.

Type locality Argentina, Tucumán Prov., Yerba Buena dept. Alrededores de Tucumán, 27/XI/1929, Hylton Scott det.

Material examined *Drepanostomella tucma* MLP 8523 (DM): Argentina, Tucumán Prov., Yerba Buena dept. Horco Molle, 1960, Biraben & Hylton Scott leg. FML 14773A (AM): Argentina, Tucumán Prov., Yerba Buena dept. San Javier Park, close to Horco Molle, Senda rápida, 770 m, S 26° 46' 24" W 65° 20' 03", 19/04/2005, Cuezco, M.G. & Miranda, M.J. leg. FML 14779 A (AM): Argentina, Tucumán Prov., Yerba Buena dept. San Javier Park, close to Horco Molle, Senda rápida, 800 m, S 26° 46' 13" W 65° 20' 24", 19/04/2005, Cuezco, M.G. & Miranda, M.J. leg. FML 14778 A (AM): Argentina, Tucumán Prov., Tafi Viejo dept., San Javier Mountains, on the road to Nina, 975-1100 m, S 26° 43' 11" W 65° 17' 35", 1/11/1995, Cuezco, M.G. & Salas Oroño, E. leg. FML 14909 (DM): Argentina, Tucumán Prov., Trancas dept., route 364 on the road to Gonzalo, 1360 m, S 26° 19' 35" W 65° 32' 21", 7/05/2002, Cuezco, M.G. leg. FML 14906 A (AM): Argentina, Tucumán Prov., Yerba Buena dept, Puerta del Cielo road, 26°36' 27" S 65° 13' 44" W, 28/04/2006, Miranda, M. J. leg. FML 14907 A (AM): Argentina, Tucumán Prov. Yerba Buena dept., Horco Molle, Sierra de San Javier Park, Puerta del Cielo road, 795-920 m, S 26° 36' 27" W 65° 13' 44", 8/03/2006, Miranda, M.J. leg. FML 14911 (ex WW 444) (DM): Argentina, Tucumán Prov., Burruyacu dept., Altos de Medina, 18/09/1960, Willink, A. & Tomsic, Z. leg., Hylton Scott, M.I. det. FML 14910 (ex WW 455) (DM): Argentina, Tucumán Prov., Trancas dept., San Pedro de Colalao, October 1958, Hylton Scott, M.I. det., Ajmat de Toledo, Z. leg. FML 525 (DM): Argentina, Tucumán Prov., Burruyacu dept., Altos de Medina, 1400 m, 18/02/1962, Weyrauch, W. leg. FML 14905 (DM): Argentina, Tucumán Prov., Chicligasta dept., Los Alisos National Park, on the road to the university house, 1640 m, S 27° 13' 06" W 65° 55' 46", 21/09/2006, Cuezco, M.G. leg. FML 14772A (AM): Argentina, Salta Prov., La Caldera dept., route 9 Km 1638, S 24° 30' 52" W 65° 20' 31", 20/01/1997, Cuezco, M.G. leg.

Drepanostomella circumscripta Hylton Scott: MLP 11102 (Holotype) (DM): Argentina, Salta Prov., Orán dept., Urundel, 16/05/1947, M. Birabén leg. MLP 11101 (Paratypes) (DM): Argentina, Salta Prov., Orán dept., Urundel, 16/05/1947, M. Birabén leg. MLP 8509 (DM): Argentina, Salta Prov., Orán dept., Urundel, 11/12/1954, M. Birabén leg. MLP 8508 (DM): Argentina, Salta Prov., Pocitos, M. Birabén leg, R. Ramírez



Figs 9-12 *Drepanostomella tucma* 9 Radula. Note the slightly V-shaped disposition of the radular teeth. Scale bar= 10 μ m. **10** Detail of the central tooth plus the three lateral teeth at each side of the central. Scale bar= 10 μ m. **11** Most outer teeth in a row. Note the small size of the last tooth in comparison with previous teeth in a row. Scale bar= 10 μ m. **12** Lateral view of half of a radula showing the increase in size of lateral teeth of a row until the fifth lateral. From that point there is a progressive decrease in tooth length towards the thirteenth lateral that is smaller in size than the central tooth. Scale bar= 10 μ m.

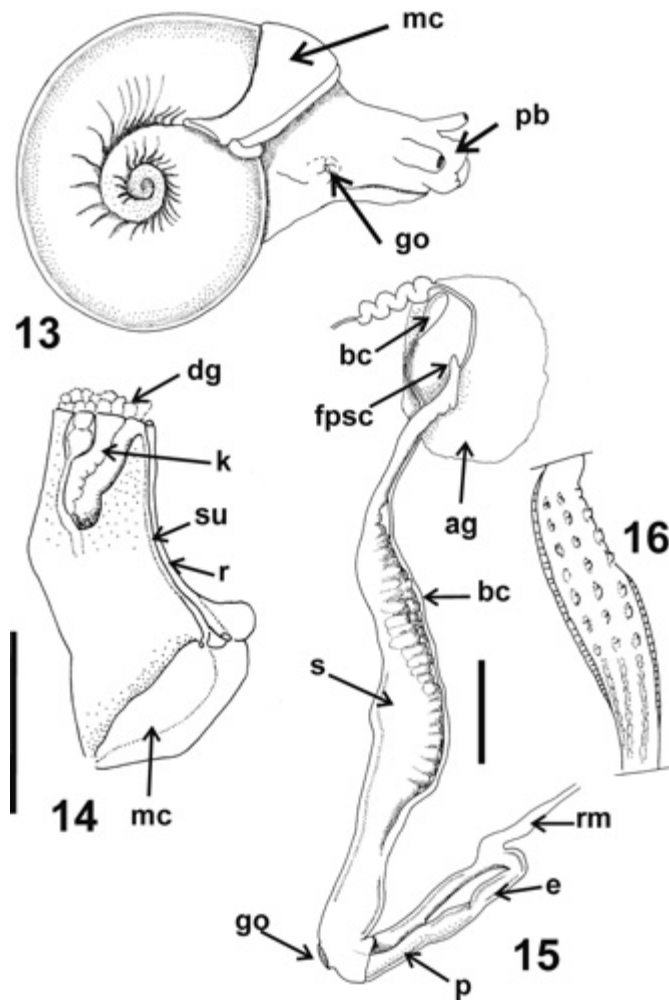
det. FML 14916: Argentina, Tucumán Prov., Burruyacu dept., Villa Padre Monti, 1000m, 14/09/1963, Weyrauch, W. leg.

Drepanostomella ammoniformis d'Orbigny: FML 14914 (ex WW 1298): Peru, Quita Sombrero, Río Rimac, 2100 m, Ticac, A. leg. FML 14918 (ex WW631) Perú, Quillabamba, 1000 m, W.Weyrauch leg. FML 14912 (ex WW 631-D): Peru, San Mateo, Río Rimac, 3200 m, W. Weyrauch leg. FML 14915 (ex WW 631-B): Peru, Andahuaylas, 3100 m, W. Weyrauch leg. FML 14917 (ex WW 631-A): Peru, Abancay, 2400 m, W.Weyrauch leg.

Diagnosis *Drepanostomella tucma* is characterized by a deep sunken spire in a nautiloid shape shell, smooth protoconch, nacreous periostracum, an acute incision at parietal angle of the aperture, holopod foot, radula with central small tooth and first lateral smaller than second one.

Radular teeth unicuspid. Regularly distributed papilla with recurved hooks in the inner penis wall. Flagellum absent.

Shell (Figs. 1-6) Nautiloid, depressed, whitish-pearl to pale cream, $3 \frac{1}{4}$ convex whorls (Figs.1-2). Spire sunken. Protoconch smooth to rugose surface (Fig. 3). Teleoconch with growth wrinkles or with delicate growth lines more marked in body whorl. Periostracum thin and easily lost in adult specimens (Fig. 4). Body whorl larger than previous whorls, not descending behind aperture. Suture deeply impressed, in some specimens crenulated aspect (Figs. 5-6). Acute incision at parietal angle of the aperture. Aperture roundish with granulose parietal wall inside aperture. Peristome sharp. Umbilicus wide (Fig. 2).



Figs 13-15 *Drepanostomella tucma* 13 General view of a living snail. Note that the mantle collar is overlapping the peristome. The cephalic region is prolonged in a short proboscis. Abbreviations: go: genital orifice; mc: mantle collar; pb: proboscis. 14 Pallial complex. Abbreviations: dg: digestive gland; k: kidney; mc: mantle collar; r: rectum; su: secondary ureter. Scale bar= 5 mm. 15 Genital system. Abbreviations: ag: albumen gland; bc: bursa copulatrix; e: epiphallus; fpSC: fertilization pouch-spermathecal complex; go: genital orifice; p: penis; rm: penis retractor muscle; s: spermoviduct. Scale bar= 2 mm. 16 Detail of inner sculpture of penis wall. Note the disposition of papilla with recurved hooks.

Shell Measurements Holotype: D maj: 7.2; D min: 6.1; D umbilicus: 3.1; H: 2.5; D/H: 2.88. Additional specimens: FML 14773A (n=10): D maj: 5.8-6.9 (Mean= 6.4); D min: 5.1-6.2 (Mean= 5.6); D umbilicus: 2.2-3.0 (Mean= 2.6).

External Features (Fig. 7- 8, 13) Animal body homogeneously yellowish to pale cream (Fig. 7, 8). Cephalic region with a snout (Fig. 13). Genital

orifice opening on right side of the cephalic region behind dorsal ocular tentacles, close to mantle collar. A portion of the mantle collar overlaps the apertural border of the shell in living animals (Fig. 13). Tail without distinct caudal pit or caudal horn, not truncated, sole homogeneous, not divided. Holopod foot.

Pallial system (Fig. 14) Composed of kidney, pulmonary cavity, pericardial cavity, rectum and ureters. Pulmonary roof mostly smooth with very few minor pulmonary veins. Main pulmonary vein short ending close to kidney. Kidney triangular, short, longer than wide, about a quarter of length of pulmonary roof. Primary ureter wide, bordering kidney along its length. Secondary ureter thin, closed until mantle collar. Mantle collar thick and wide, projecting over border of shell aperture.

Digestive system Jaw absent. Radula (Fig. 9) narrow and long with dagger-like teeth in V-shaped rows. Central tooth small, triangular, unicuspid with round to ovoid basal plate (Fig. 10). 10 to 13 teeth at both sides of the central tooth in each row (Figs. 9, 12). First lateral unicuspid slightly smaller than second laterals with cuspids pointed to center of radula (Figs. 9-10). Lateral teeth from first to fifth progressively increasing its length. From fifth lateral tooth length progressively decreasing towards the margins of the radula. Outermost teeth in a row smaller and shorter than central tooth (Fig. 11-12). Buccal mass cylindrical, very elongated. Two salivary glands with separated efferent ducts, elongated, distally attached to each other. Oesophageal crop absent.

Genital system (Fig. 15) Ovostestis of several bunches of acini, totally embedded in digestive gland. Hermaphroditic duct divided into three regions: proximal and distal thin and elongated, central region convoluted with enlarged diameter. Hermaphroditic duct ending at Fertilization pouch-Spermathecal complex (FPSC), finger-like, short, closed to albumen gland/spermoviduct junction. Albumen gland roundish irregularly outlined, pale cream, in close contact to digestive gland. Spermoviduct long, proximal portion thinner than distal portion. Bursa copulatrix oval, small with long, thin duct. Sac of bursa neatly delimited from duct. Bursa copulatrix natural

position level with seminal vesicle of hermaphroditic duct or slightly longer due to its long duct. Vagina short, a quarter of spermoviduct length, muscular, thick in diameter. Vas deferens running parallel to vagina overlapped by thin tissue. Penial complex formed by penis and epiphallus, flagellum absent. Right ocular muscle passing through penis-vagina angle. Vas deferens inserting terminally in epiphallus. Epiphallus reflexed over penis. Epiphallus as long as penis, with inner longitudinal straight ridges. Penis slightly thicker than epiphallus. Internally penis wall sculpture consisting in a distal portion with three to four straight thin pilasters continuous with papilla regularly arranged with slightly recurved corneous hooks. Proximal portion of penis with papilla more spaced between each other, less regularly distributed. Verge absent. Penial muscular retractor thick running from diaphragm to distal epiphallus. Penis sheath (=Penial tunica) short, thin, ensheating distal penis and proximal portion of epiphallus.

Biology The present species is an egg-retainer. Specimens collected during autumn and winter did not present eggs in the uterine portion of the spermoviduct. Specimens collected in summer had two to three eggs within the spermoviduct.

Derivation of name The specific epithet refers to the occurrence of the present species in Tucumán Province.

Distribution *Drepanostomella tucma* is mainly distributed in Tucumán Province with some scarce records in Salta Province, northwestern Argentina. It inhabits rainforest regions between 600 and 1500 m above sea level.

Remarks *Drepanostomella tucma* differs from *D. ammoniformis*, the type species of the genus, in its smaller shell diameter (*D. tucma*: major diameter of 7.2 mm in holotype, *D. ammoniformis*: major diameter of 14 mm) with one less shell whorl than *D. ammoniformis* as it was already pointed by Hylton Scott (1948). It also differs in its more pronounced suture and more sunken spire. The incision at the parietal angle of the aperture is acute but less pronounced in *D. ammoniformis* (Hylton Scott, 1948). *D. tucma* lacks of papillae on the shell surface that had also been

described for *D. ammonoceras* (Pfeiffer) (Baker, 1925). In both species the jaw is lacking. Shape of radular teeth is similar but in the case of *D. ammoniformis* 19 lateral teeth occur at both sides of the central tooth in each row (Hylton Scott, 1948). In *D. tucma* no more than 13 lateral teeth were observed in the present study. *D. tucma* differs from *D. circumscripta*, a species that shares part of its area of distribution with *D. tucma*, in that *D. circumscripta* is smaller in shell diameter (D maj: 3.80 mm; D min: 3, 28 in the holotype) than *D. tucma*. The shell surface in *D. circumscripta* is smooth or with fine growth lines and its mantle collar shows small pigmented spots (Hylton Scott, 1948). Concerning its radula, *D. circumscripta* has a smaller central tooth than *D. tucma*, which according to Hylton Scott (1948) can also be vestigial. In *D. circumscripta* as well as in *D. tucma* the length of the first lateral tooth is smaller than the second lateral. Unfortunately, Hylton Scott (1948) did not provide more anatomical features than shell characters, mandible and radula in her original description of *D. circumscripta*. For this reason no other comparison is currently possible.

DISCUSSION ON THE SYSTEMATIC POSITION OF *DREPANOSTOMELLA* BOURGUIGNAT, 1889

Drepanostomella is a genus scarcely studied. *D. ammoniformis* is the type species of the genus but has received little attention; even its anatomy is still unknown. The anatomy of only one *Drepanostomella* species has been previously figured but not described in an unpublished Master thesis (Ramirez, 1993). However, the illustration of that species, collected in Madre de Dios, Peru, is not sufficiently detailed to allow a comparison with *D. tucma* here described. For this reason, all comparisons between *D. tucma* and the rest of the species of the genus are restricted to shell and radular characters.

Tillier (1980) recognized two groups within Scolodontidae based mainly on the shape, size and disposition of the radular teeth. In the first group, organized into the tribe Systrophiini (now Scolodontinae) (*Systrophia* s.s., *Systrophiella* Baker, *Entodina* Ancey and *Happia*) the central tooth is smaller than the laterals and the first lateral is smaller than the second. In the second group,

organized into the Tamayoini (*Drepanostomella*, *Happiella*, *Prohappia* Thiele, *Tamayoa* and *Tamayops* Baker) the central tooth is more developed than in the first group, still smaller than the first lateral, but the first lateral is not bigger than the second one. Tillier (1980) also mentioned that in the case of *Drepanostomella* the shape of the central tooth is more important than the laterals having a "circular shape". Our results show that the central tooth in *D. tucma* is smaller than the first lateral, and that the first lateral is also smaller than the second one, because there is a progressive increase in length towards the fifth lateral teeth. Most outer laterals in a row are smaller than the central tooth or of similar size to it. The base of the central and lateral teeth is rounded to ovoid.

Hausdorf (2003) sustained that the radular characters used by Tillier (1980) to include *Drepanostomella* within Tamayoini are probably symplesiomorphies of Scolodontidae and that Tillier had missed the fact that *D. ammonoceras* is ovoviviparous (Baker, 1925). Hausdorf (2003) assumed that ovoviviparity is an autapomorphy of the subfamily Scolodontinae and that for this reason *Drepanostomella* should be transferred to the Scolodontinae. However, the ovoviviparity in *Drepanostomella* is not confirmed by new biological information. Although Baker (1925 a) had noted that *D. ammonoceras* is ovoviviparous, it was very common in anatomical works of these years to conclude that a snail was ovoviviparous when eggs were found in the reproductive organs during a dissection. However egg retention observed in one species does not imply that this genus is certainly ovoviviparous. It could happen that the eggs are retained inside the reproductive tract for a while but the embryos inside eggs hatch outside the parental body. This would be only an "egg retainer" snail. According to Tompa (1979a, b) all animals which are ovoviviparous *sensu stricto* are egg retainers, but not all egg retainers are ovoviviparous in the strictest sense of the word, only *sensu lato*. In this way ovoviviparity has been probed neither in *Drepanostomella* nor in Scolodontinae. On the basis of the radula morphology, the course of the right ommatophoral retractor passing between penis and vagina and its condition of "egg-retainer", *Drepanostomella* should be classified within the Scolodontinae, as diagnosed by Tillier (1980).

Drepanostomella shows shell similarities mainly with *Hirtudiscus* and *Guestieria*. The only cladistic analysis available for the family Scolodontidae where *Drepanostomella* is classified was done by Ramirez (1993). On the basis of her phylogenetic analysis, she made a generic arrangement into nine genera in two subfamilies, Tamayoinae with *Tamayoa* and *Happiella* and Systrophiinae (now Scolodontinae) that included *Drepanostomella*, *Guestieria* Crosse, 1872, *Happia*, *Wayampia*, *Systrophia*, *Zilchistrophia* and *Miradiscops*. According to her hypothesis, *Drepanostomella* form a clade together with *Guestieria* supported by the shape of the generating curve of the shell. However, *Guestieria*, a genus with seven species described, is also hardly known with its anatomy unexplored. Shared morphology in some shell characters such as a nautiloid form, size, and its condition of sympatry with *Drepanostomella* need further studies. *Guestieria* differs from *Drepanostomella* in that its central tooth is absent and lateral teeth are multicuspid (Ramirez, 1993). Another possible sister group of *Drepanostomella* is *Hirtudiscus* as proposed by Hausdorf (2003). *Hirtudiscus* was not included in Ramirez's (1993) cladistic analysis. According to Hausdorf, the peculiar suture and the incision at the parietal angle of the aperture might be synapomorphies of *Hirtudiscus* and *Drepanostomella*. *Hirtudiscus* is also very similar to *Drepanostomella* in its general shell shape and in the penis internal sculpture. *Hirtudiscus* differs from *Drepanostomella* in several aspects: the hairs, the smaller central teeth, higher number of teeth per row of the radula and the presence of a vaginal appendage.

In comparison to *Happia*, *Systrophia*, *Entodina* and *Systrophiella*, the rest of the genera comprising Scolodontinae (*sensu* Tillier, 1980), *Drepanostomella* differs from them mainly in shell shape and size and in its condition of holopod. *Drepanostomella* also lacks of any digitiform appendage in the terminal foot, structure usually present in *Happia* species (Baker, 1925). *Drepanostomella* is similar to *Happia* and to *Systrophiella* in their radular morphology, both having oblique rows and the first lateral teeth smaller than the second (Baker, 1925, Hylton Scott, 1948). However, Hylton Scott (1948) figured the central tooth of the radula of *Happia skiaphila* (d'Orbigny) as tricuspid. *D. tucma* is also similar to *H. skiaphila* in the external morphology of the penial complex having a vas deference inserted terminally in the epiphallus

and lacking of a flagellum (Hylton Scott, 1948). *Systrophia* is similar to *Drepanostomella* in radular morphology but differs from it in that their species are aulacopod and have an opaque, discoidal shell with numerous tightly coiled whorls of similar sizes. A flat or sunken spire is also characteristic of the *Systrophia* species. Anatomically, *Systrophia* as well as *Entodina* are not sufficiently known to allow a comparison with *Drepanostomella*. Besides the similarities in radula structure, the genera of Scolodontinae *Hirtudiscus*, *Happia*, *Drepanostomella*, *Systrophia* and *Systrophiella* all share the character of having a very long bursa copulatrix duct with a small terminal sac (Baker, 1925; Hylton Scott, 1948; Ramirez, 1993; Hausdorf, 2003) both exceeding the spermiduct length.

At this point we think that similarities in shell and radular characters exist specially between *Drepanostomella*, *Hirtudiscus*, *Systrophia* and *Happia* that suggest a close relationship among them. However, more material and morphological studies are clearly necessary before establishing any well supported subdivision within Scolodontidae or to perform a new cladistic analysis of the genera within the family.

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