

Re-description of genitalia of *Stephacharopa* and description of a new Peruvian genus

(Gastropoda, Stylommatophora, Charopidae)

Sergio Eduardo Miquel & Juan Francisco Araya

Miquel, S. E. & Araya, J. F. 2022. Re-description of genitalia of *Stephacharopa* and the description of a new Peruvian genus (Gastropoda, Stylommatophora, Charopidae). *Spixiana* 45(1): 1–7.

The genital apparatus of *Stephacharopa testalba* is re-described from Argentinian specimens and recorded in Chile for the first time. *Stephadiscus madreiosensis*, a species currently restricted to the Peruvian Amazon, is transferred to the newly established genus *Perucharopa* based on differences of morphology, dimensions and structure of their embryonic and adult shells in comparison with South American charopids.

Sergio Eduardo Miquel, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Avda. Ángel Gallardo 470, C1405DJR, Ciudad Autónoma de Buenos Aires, República Argentina; Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET); e-mail: semsnail@yahoo.com.ar

Juan Francisco Araya, Museo del Mar, Universidad Arturo Prat, Iquique, Chile; e-mail: jfaraya@u.uchile.cl; <https://orcid.org/0000-0002-4087-9641>

Introduction

South American Charopidae (Gastropoda, Stylommatopora) show a wide variety of shell sculpture, from simple growth lines to very different and complex sculptures on both protoconch and teleoconch. Historically, many Charopidae species were originally allocated in just a few genera, following gross teleoconch morphology (v.g., *Helix* L., 1758; *Zonites* Montfort, 1810; *Pyramidula* Fitzinger, 1833; *Patula* Held, 1837) (Pilsbry 1893) – with many of these genera subsequently transferred to several other families (Bank, 2017). Characteristics of morphology, including coloration and the form of the aperture and umbilicus, were used in the description of early described species in genera *Amphidoxa* Albers, 1850; *Stephanoda* Albers, 1860; *Flammulina* Martens, 1873 and *Payenia* Rochebrune & Mabilie, 1889 (Pilsbry 1893). *Radiodiscus* Pilsbry & Ferriss, 1906 was the first genus erected from characteristics of the shell sculpture of both protoconch and teleoconch (Pilsbry & Ferriss 1906, Hylton Scott 1970).

Regarding the complexity of shell structure, Hylton Scott (1981) erected the genus *Stephadiscus*, based on species which have embryonic shells with radial ribs, designating *Helix lyratus* Couthouy in Gould, 1846 as its type species. The author included several previously described species in the new genus (*Stephanoda celinae* Hylton Scott, 1969; *S. perversa* Hylton Scott, 1969; *S. distincta* Hylton Scott, 1970; *S. testalba* Hylton Scott, 1970; *S. antarctica* Hylton Scott, 1973 and *S. rumbolli* Hylton Scott, 1973), all of them formerly considered within the genus *Stephanoda*, and she further added also *Stephadiscus striatus striatus* Hylton Scott, 1981 from Argentina and *S. striatus caribeus* Hylton Scott, 1981 from Venezuela to her new genus. Between 1981 and 2011 two new *Stephadiscus* species were described from disjunct areas from South America: *S. stuardoi* Miquel & Barker, 2009 (southern Chile) and *S. madreiosensis* Miquel & Ramírez, 2011 (Peruvian Amazonas). A re-examination of several of these taxa allowed to describe a new genus, *Stephacharopa* Miquel & Araya, 2013, where three Argentinian-Chilean species were

allocated: *Stephacharopa calderaensis* Miquel & Araya, 2013 (type species), *S. testalba* and *S. distincta*. More recently, the genus *Neoparyphantopsis* Miquel & Araya, 2015 was created to accommodate a species from the Juan Fernández Archipelago, off central Chile, which has a nepionic radial sculpture.

In the present contribution, we re-describe the genital system of *Stephacharopa testalba*, which is also recorded for the first time in Chile, and propose the new genus *Perucharopa* for *Stephadiscus madrediosensis* from Peru.

Material and methods

Abbreviations used are: ANSP, Academy of Natural Sciences of Philadelphia; MACN-In, Museo Argentino de Ciencias Naturales (Invertebrates Division) (Ciudad Autónoma de Buenos Aires); MLP, Museo de La Plata (La Plata); MNHNCH, Museo Nacional de Historia Natural de Chile (Santiago); MUSM, Museo de la Universidad San Marcos (Lima). Figures 1a and 1b were taken at the scanning electron microscope in MACN; some Argentine specimens of *Stephacharopa testalba* were also dissected (MACN-In 42752).

Results

Genus *Stephacharopa* Miquel & Araya, 2013

This genus includes four species: *Stephacharopa calderaensis*, *S. distincta*, *S. testalba* (recorded for the first time in Chile) and *S. paposoensis* Araya & Miquel, 2018. *Stephadiscus perversus* was originally described as *Stephanoda perversa*, later transferred to *Stephadiscus* by Hylton-Scott (1981), and herein in this work we transfer this species to genus *Stephacharopa*, and thus it is now *Stephacharopa perversa* (nov. comb), due to the similar characteristics of proto- and teleoconch of *Stephacharopa* (see Miquel & Barker 2009).

Stephacharopa testalba (Hylton Scott, 1970)

Figs 1a–b, 2a–c, Table 1

Stephanoda testalba Hylton Scott 1970: 284, fig. 4(1, 2); Fernández 1973: 46.

Stephadiscus testalbus Hylton Scott 1981: 125; Miquel et al. 2003: 236.

Stephadiscus testalba Fonseca & Thomé 1993: 72.

The shell of this species was described and illustrated by Hylton Scott (1970), but a re-examination of the genital system is necessary due to several particular characteristics observed in the drawing and comments of that author. At the moment, this is the only species of *Stephacharopa* whose soft parts are partially known.

Type locality: Area of Mascardi Lake, Nahuel Huapi National Park, Argentina.

Distribution. Argentina: Chubut (Futaleufú, Los Alerces National Park); Neuquén (Lanín National Park); Río Negro (Bariloche, Nahuel Huapi National Park). Chile: Concepción (Concepción, Hualpén Botanical Park), Región del Biobío; Cajón del Maipo, Región Metropolitana de Santiago.

Re-description of the genital apparatus

The genital apparatus of this species (Fig. 2a–b) was first described by Hylton Scott (1970), although the illustrations seem to correspond to a contracted individual, with a male genital tract folded in on itself, which is noticeable when comparing the original drawing by Hylton Scott with figures of this work, where its structure appears unfolded (Fig. 2c). The genital tract (Fig. 2a) presents a small gonad (G) and a short hermaphrodite duct (HD); a short spermiduct with an albumen gland (AG) with a small caecum (AGC), and a small prostate; the female tract continues in a thick oviduct (OV), at the base of which an oviduct caecum (OC) opens. Of greater length and thickness and somewhat twisted is the free oviduct (FO); vagina (V) ends in a feminine aperture (FA); spermatheca (SPE) is small and globular with a long duct (SPED), most of which runs adhered between the albumen gland and the prostate, inserting itself in the free oviduct, near the caecum major.

The male tract (Fig. 2b) presents a complex penis, with a thick epiphallus (EP), at the free end of which the vas deferens (VD) and the retractor muscle (RM) are inserted; the penis itself is a thick organ, wider in its distal portion, with translucent walls, which reveal areas of denser tissue, like muscle pads (MP). Before opening into the short atrium through its masculine aperture (MA), the penis presents a thickened structure, with thick walls and a “ringed” surface (apparently a sphincter), in which a long and translucent penial caecum (PC) opens at its free end. This structure could be considered as a “stimulating organ” (STO).

Comparisons with genital systems of other genera of Charopidae

The genital tract of *Stephacharopa testalba* (Fig. 2a–c), shows greater complexity than that described for other South American Charopidae, due to the presence of structures interpreted as caeca (dependent on the albumen gland, the oviduct, and the penis), of unknown function. The more complex structure and solidity of the penis is significant in relation to those of the other species described. The female via of *S. testalba* (Fig. 2b–c) presents two caeca, depend-

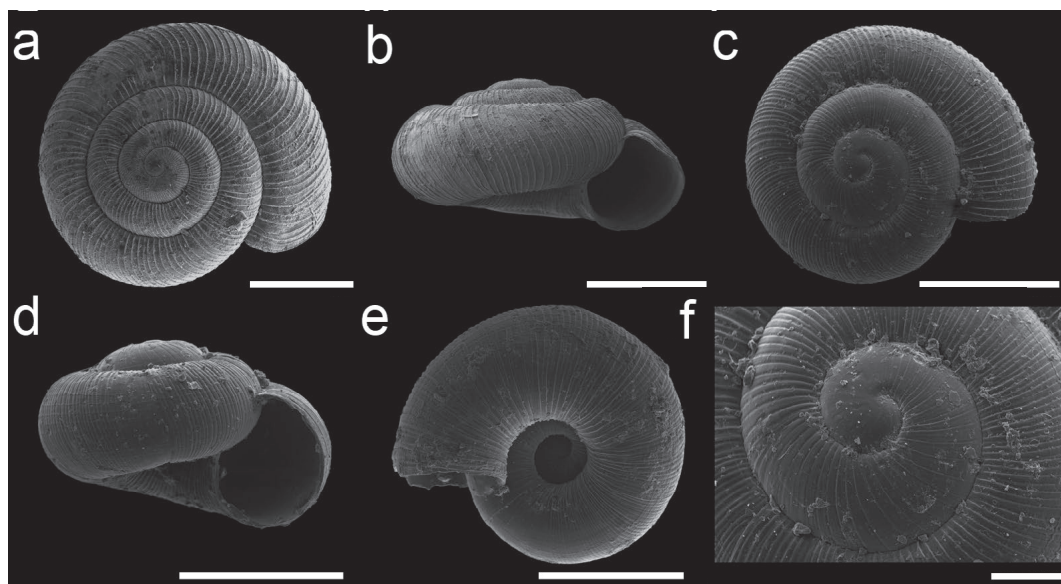


Fig. 1. a–b. *Stephacharopa testalba* (Hylton Scott, 1970), MACN-In 42755, Chile, Santiago, San José de Maipo. a. Apical view. b. Apertural view. c–f. *Perucharopa madreiosensis* (Miquel & Ramírez, 2011), holotype, MUSM 4.238a. c. Apical view. d. Apertural view. e. Umbilical view. f. Detail of protoconch. Photos c–f © Senckenberg Gesellschaft für Naturforschung (by permission). Scale a–b = 1 mm, c–e = 0.5 mm, f = 0.1 mm.

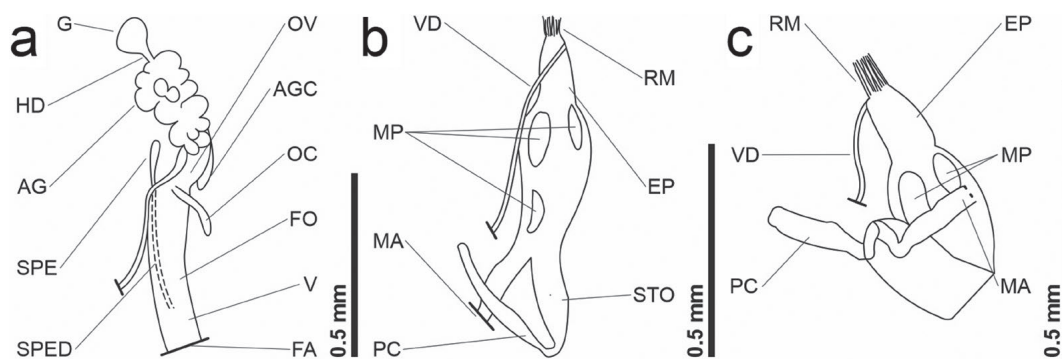


Fig. 2. *Stephacharopa testalba* (Hylton Scott, 1970), MACN-In 42752, Argentina, Nahuel Huapi National Park, route 258, Mascardi Lake. a. Male genital tract folded on itself, according to the original drawing by Hylton Scott (1970); and b. current morphological interpretation. c. Genital apparatus relaxed. AG, albumen gland; AGC, albumen gland caecum; EP, epiphallus; FA, feminine aperture; FO, free oviduct; G, gonad; HD, hermaphrodite duct; MA, masculine aperture; MP, muscle pads; OC, oviductal caecum; OV, oviduct; PC, penial caecum; RM, retractor muscle; SPE, spermatheca; SPED, duct of spermatheca; STO, “stimulating organ”; V, vagina; VD, vas deferens. Total length: feminine tract: 0.90 mm, masculine tract: 0.80 mm. Scale = 0.5 mm.

ent on the albumen gland and the oviduct, absent in the other two species, while the penis has muscle pads on its internal surface, not described for those two species mentioned above. In comparison with *Zilchogyra costellata* (d’Orb., 1835) and *Stephadiscus lyratus*, species with known soft anatomy (Hylton Scott 1970, Cuezco et al. 2021), the former has a long

and thin epiphallus and penis, while the latter lacks a stimulating and blind organ; *Stephadiscus lyratus*, in contrast, has an epiphallus with a caecum and a retractor muscle that attaches to it and to the penis. In another micromollusc studied, *Flammulina festiva* Hylton Scott, 1970, only a thick “accessory organ” appears (of unknown internal structure and func-

tion), related to the female section (Cádiz & Gallardo 2008), not present in *S. testalba*.

The features of the genital tract described for *S. testalba* allow a more complete differentiation of *Stephacharopa* from *Stephadiscus*, a genus that includes species that were formerly classified as *Stephadiscus* (Miquel & Barker 2009, Miquel & Araya 2013, Araya & Miquel 2018).

Studied material. Holotype MLP 10511: Mascardi Lake area, Coll. M. Birabén, 1942; MACN-In 35366: Lanín National Park, route 63, Neuquén, Argentina, dry, open scrubland, Coll. Barker-Miquel, 17-X-1996, 1 spm; MACN-In 21754: Llao Llao, Nahuel Huapi National Park, 1 spm; MACN-In 36103: Lanín National Park, route 63, dry, open scrubland, Coll. Barker-Miquel, 17-X-1996, 3 sppm; MACN-In 36112: Hualpén Botanical Park, Concepción, Chile, Coll. Barker-Miquel, 13-X-1996, 1 spm, Broadleaf gulley forest, adjacent to lake; MACN-In 36113: Nahuel Huapi National Park, route 258, Gutiérrez Lake, *Nothofagus* forest, Coll. Barker-Miquel, 16-X-1996, 1 spm; MACN-In 36114: Futalaufquen Lake (Los Alerces National Park), Coll. S.E. Miquel, 1994, 1 spm; MACN-In 42752: Argentina, Nahuel Huapi National Park, route 258, Mascardi Lake; MACN-In 42753: Argentina, Nahuel Huapi National Park, route 231, Las Flores; MACN-In 42754: Argentina, Nahuel Huapi National Park, route 258, Cañadón de la Mosca; MACN-In 42755: Chile, Santiago, San José de Maipo, Coll. J.F. Araya and J.A. Aliaga, 20 sppm.; MACN-In 43255: Laguna El Barco, Isla El Barco (37°55'56.6" S, 71°16'45.4" W), comuna de Alto Bío-Bío, Región del Biobío, Chile central, a pocos km de la frontera con Argentina, Coll. N. Zambrano, 28-II-2018, En humus, 3 sppm; MLP 10509 (214): Frías lagoon, Coll. Pérez Moreau, 1940, 1 spm.; MLP 10511 (173): Mascardi Lake, Nahuel Huapi National Park, Río Negro, 1944, 2 sppm; MLP 12042-1: López Bay, Nahuel Huapi. Coll.

Scott-Birabén, 1 spm.; MLP 12047: Llao-Llao Peninsula. Coll. Rapoport, 5-III-1959, 1 spm.; MLP 12048: Lago Lacar, Coll. Rapoport, 20-III-1959, 1 spm; MLP 12053: Lago Puelo National Park, Coll. Rapoport, 10-III-1959, 1 spm; FMNH 308211/4: Chile, Prov. Concepción, camino a Ramuntcho, Coll. T. Cekalovic, 2-XI-1986 [Tc-178].; FMNH 308212/1: Chile, Prov. Concepción, Cerro Caracol, Coll. T. Cekalovic, 17-VIII-1996 [482]; FMNH 308.230/7: Chile, Prov. Concepción, Estero Nonguen, Coll. T. Cekalovic, 8-XII-1993 [Tc-371]; FMNH 312444(ex 308219)/1: Chile, Prov. Concepción, Fundo El Manzano, Coll. T. Cekalovic, 7-XII-1996 [Tc507].

Table 1 shows differences among South American genera with axial ribs on the surface, mainly regarding size and number of ribs on proto and teleoconch. These distinctive features allow distinguishing *Stephadiscus madreiosensis* as belonging to a new genus, with a distribution restricted, so far, to the Amazon basin, while *Amphidoxa*, *Stephacharopa* and *Stephadiscus* are chiefly austral charopids.

Perucharopa gen. nov.

Fig. 1c–f, Table 1

Diagnosis. Shell minute, orbicular, of convex whorls; ornamentation of proto- and teleoconch differentiated, with numerous low and flat, ribbon-like, axial ribs; some spiral threads irregularly distributed; protoconch with 1.75 whorls.

Description

Shell minute, orbicular, of 3.50 whorls; with a moderately elevated spire; convex whorls; marked sutures; subcircular and descendent aperture; um-

Table 1. Comparative measurements of South American species of Charopidae. AP, aperture; H, height; MD, main diameter; RPC, protoconch ribs; RTW, ribs of all shell whorls; UMB, umbilicus; W, whorls; *, in the original diagnosis 90–95 axial ribs on teleoconch.

Taxa	MD	H	AP	UMB	W	RTW/RPC
<i>Perucharopa madreiosensis</i> n. comb. (Miquel & Ramírez 2011) MUSM 4.238a – Holotype	0.93	0.50	0.43×0.27	0.27	3.25	300/30
<i>Perucharopa madreiosensis</i> n. comb. MACN-In 31.721 – Paratype	1.04	0.52	0.32×0.26	0.45	3.25	250/40
<i>Stephacharopa calderaensis</i> Miquel & Araya, 2013 MNHCL 7.593 – Holotype	2.10–3.00	1.10	–	0.80–1.00	4.50	90/50*
<i>Stephacharopa perversa</i> n. comb. (Hylton Scott, 1969) MACN-In 27.329	5.90	3.30	2.50×1.30	1.30	4.50	300/70
<i>Stephacharopa testalba</i> (Hylton Scott, 1970) MACN-In 42.755	2.60	1.70	1.30×0.65	0.90	4.50	250/60
<i>Stephadiscus lyratus</i> (Gould, 1846) MACN-In 27.225	6.00	3.20	–	0.20–0.25	4.00	320/120
<i>Amphidoxa marmorella</i> (L. Pfeiffer, 1845) ANSP 130.443	2.80	1.50	1.25×1.10	0.56	3.25	65/–

bilicus perspective; ornamentation of proto- and teleoconch undifferentiated, with numerous low and flat axial ribs (like a ribbon); teleoconch with 250–300 axial ribs, last whorl with 110–120; intercostular spaces smooth; spiral threads irregularly distributed; 10 spiral cords on umbilical face; protoconch with 1.75 whorls, and about 30–40 low and flat axial ribs; translucent white; 1 mm. Soft parts unknown.

Etymology. Genus masculine, in honour to Peru, the country with the type locality for the genus. The suffix *Charopa*, in reference to the type genus of the family Charopidae.

Type species: *Stephadiscus madreiosensis* Miquel & Ramírez, 2011 (p. 51, figs 2–6).

Distribution. Peru, Madre de Dios department; 200–360 m a.s.l. *Perucharopa* gen. nov. is an isolated taxon from the remaining Charopidae species described for Peru (Ramírez et al. 2007) and Brazil (Simone 2006) (Fig. 3).

Comparisons. *Perucharopa* differs from all other South American Charopidae with nepionic radial sculpture by its diminutive size in comparison to the number of whorls, by the presence of smooth rib interspaces, and by the fine spiral cords, irregularly distributed on the shell. The number of radial ribs in the protoconch is about a sixth of the total number of radial ribs in all the whorls, while in similar charopids this relationship (RTW/RPC) does not exceed a factor of 4 (Table 1). With a few exceptions, South American Charopidae have adult shells with a diameter exceeding 2 mm, while adults *Perucharopa* reach 1 mm.

Regarding the number and density of ribs present on protoconch and teleoconch, *Perucharopa* is characterized by having a protoconch where the number of ribs is tripled on the second whorl (Table 1), a characteristic which is unique among charopids. Just a few species possess such a high number of axial ribs,



Fig. 3. Geographic localities of examined species.

v.g., *Stephadiscus lyratus*, *Stephacharopa calderaensis*, and *S. perversa* (Table 1) from Southern Argentina and from Chile. However, they show a slow increase in the density of ribs and also have larger shells and more whorls. Regarding *S. calderaensis*, this species has about 90–95 axial ribs (indicated, incorrectly, as 60 in the original description) (Table 1).

With respect to its small size, the new genus is similar to *Araucocharopa gallardoi* Miquel & Cádiz Lorca, 2008 from southern Chile, but this latter differs



Fig. 4. *Amphidoxa marmorella* (L. Pfeiffer, 1845), ANSP 130.443. A. Apical view. B. Apertural view. C. Umbilical view. Scale = 1 mm.

by its trochoid shell, a protoconch with spiral lirae and a teleoconch with few axial ribs and a very small umbilicus. *Amphidoxa marmorella* (L. Pfeiffer, 1845) and *Neoparyphantopsis crusoana* Miquel & Araya, 2015 are differentiated by having nautiloid shells, and by having larger shells sculptured by considerable fewer ribs. Analysing non-type specimens, Odhner (1922) and Solem (1983) re-described the shell of *A. marmorella*, the specimen herein illustrated was revised by the first author (Fig. 4a–c, Table 1). The record of this species by Miquel & Araya (2015) is erroneous, and it corresponds to a *Stephadiscus* species, possibly an undescribed species. In the same matter, the generic allocation of *Amphidoxa hasselae* Hylton Scott, 1969, from southern Chile must be revised; in this case, proto- and teleoconch differ strongly from the generic description of *Amphidoxa*, exhibiting a completely smooth protoconch (Hylton Scott 1969).

Studied material. *Perucharopa madrediosensis*: Paratypes MACN-In 31.716, 1 spm; MACN-In 31.720, 1 spm; MACN-In 31.721, 1 spm.

Stephadiscus lyratus: MACN-In 27.220, Laguna Escondida, Tierra del Fuego, Coll. M. Birabén, II-1965, 20 sppm; MACN-In 27.225, Fagnano Lake, Tierra del Fuego, Coll. M. Birabén, 9-II-65, 13 sppm.; MACN-In 27.226, Lapataia, Tierra del Fuego. Coll. M. Birabén, 22-II-65, 13 sppm.

Stephacharopa celinae: Holotype MACN-In 27.275.

Stephacharopa perversa: MACN-In 27.329, Argentina, Nahuel Huapi National Park, Puerto Blest, Coll. E. Rapoport, 6-III-1959, 1 spm [although labelled by the autor as “Tipo” (=type), the author excluded it from the type series in the last paragraph of her paper].

Stephadiscus striatus striatus: Holotype MLP 11.486, paratype MLP 11.487.

Stephadiscus striatus caribeus: Syntypes MACN-In 31.132, 38.977, 39.043.

Acknowledgements

We are thankful to A. G. Rosenberg, P. Callomon and K. Seizova (ANSP) for the photographs of *Amphidoxa* spp., among them the specimen herein illustrated, and to the Director of the Senckenberg Gesellschaft für Naturforschung for the permission for re-use of images of *Perucharopa madrediosensis*.

References

- Araya, J. F. & Miquel, S. E. 2018. A new *Stephacharopa* (Gastropoda: Punctoidea: Charopidae) from Paposo, northern Chile. *Journal of Conchology* 43(11): 1–5.
- Bank, R. A. 2017. Classification of the Recent terrestrial Gastropoda of the World. *MolluscaBase* (last update: July 16th, 2017), www.molluscabase.org [accessed 20 September 2022].
- Cádiz, F. J. & Gallardo, C. S. 2008. Morphological and anatomical features of *Flammulina festiva* Scott, 1970 (Stylommatophora; Charopidae) from southern Chile, with notes on its natural history. *Gayana* 72(1): 1–8.
- Cuezzo, M. G., Medina, R. G. & Nieto, C. 2021. Geographic distribution modelling and taxonomy of *Stephadiscus lyratus* (Couthouy in Gould, 1846) (Charopidae) reveal potential distributional areas of the species along the Patagonian Forests. *PeerJ* 9: e11614. doi:10.7717/peerj.11614
- Fernández, D. 1973. Catálogo de la malacofauna terrestre argentina. Monografías 4, 197 pp., La Plata (Comisión de Investigaciones Científicas).
- Fonseca, Á. L. M. da & Thomé, J. W. 1993. Classificação das espécies neotropicais de micromoluscos dos géneros *Stephanoda* Albers 1860, *Stephadiscus* Scott 1981 e *Ptychodon* Ancey 1888 (Charopidae, Endodontoidea, Stylommatophora, Gastropoda). *Acta Biológica Leopoldensia* 15(2): 65–76.
- Hylton Scott, M. I. 1969. Endodóntidos neotropicales IV (Moll. Pulm.). *Neotropica* 15(47): 59–63.
- 1970. Endodóntidos de la región austral cordillerana (Gastropoda-Pulm.). *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Zoología* 10(18): 267–296.
- 1973. Endodóntidos neotropicales IV (sic) (Gastropoda-Pulmonata). *Neotropica* 19(59): 104–109.
- 1981. Referencia al género *Stephanoda* Albers, 1860 y la creación del género *Stephadiscus* n. gen. (Mollusca Endodontidae). *Neotropica* 27(78): 123–126.
- Miquel, S. E. & Araya, J. F. 2013. A new Charopidae from Chile and Argentina, *Stephacharopa calderaensis* gen. et sp. nov., with remarks on the taxonomy of the genus *Stephadiscus* Hylton Scott 1981 (Mollusca Gastropoda Pulmonata). *Archiv für Molluskenkunde* 142(2): 227–235.
- & Araya, J. F. 2015. New records of terrestrial molluscs of the Juan Fernández Archipelago (Chile), with the description of a new genus and species of Charopidae (Gastropoda: Stylommatophora). *Archiv für Molluskenkunde* 144(2): 155–167.
- & Barker, G. M. 2009. New Charopidae from Chilean–Argentine Patagonia (Mollusca: Gastropoda: Stylommatophora). *Archiv für Molluskenkunde* 138(1): 1–9.
- & Cádiz Lorca, J. F. 2008. *Araucocharopa gallardoi* gen. et sp. n. de Charopidae (Mollusca: Gastropoda: Stylommatophora) del sur de Chile. *Revista del Museo Argentino de Ciencias Naturales, Nueva Serie* 10(2): 329–340.
- & Ramírez, R. 2011. First records of actual and fossil *Stephadiscus* outside of Patagonia, and the description of a new Amazonian species (Mollusca: Pulmonata: Charopidae). *Archiv für Molluskenkunde* 140(1): 49–56.
- , Ramírez, R. & Thomé, J. W. 2003. Análisis cualitativo de la distribución de Punctoidea en áreas de forestas de América del Sur. P.236 in: *Livro de Resumos, 18º Encontro Brasileiro de Malacologia, Sociedade Brasileira de Malacologia*, 21–25 de julho de 2003, Rio de Janeiro, 302 pp.

- Odhner, N. H. J. 1922. Mollusca from Juan Fernandez and Easter Island. Pp.219-254, pls 8-9 in: Skottsberg, C. (ed.). The natural history of Juan Fernandez and Easter Island, Vol. 3 Zoology. Uppsala (Almqvist & Wiksells).
- Pilsbry, H. A. 1893-1895. Manual of conchology, Ser. 2 Pulmonata, Vol. 9, Helicidae Vol. 7, Guide to the study of Helices. 366pp., 71 pls, Philadelphia (Conchological Section, Academy of Natural Sciences).
- & Ferris, J. H. 1906. Mollusca of the southwestern States II. Proceedings of the Academy of Natural Sciences of Philadelphia 58: 123-175, pls 5-9.
- Ramírez, R., Miquel, S. E., Medina, N., Romero, P., Borda, V., Peceros, F., Chumbe, A. & Ramírez, J. 2007. Micromoluscos de la reserva Los Amigos y el primer registro de *Stephadiscus* fuera del extremo sur de América. P.173 in: Resúmenes, XVI Reunión Científica ICBAR, Instituto de Investigación de Ciencias Biológicas Antonio Raimondi, Facultad de Ciencias Biológicas, Universidad Nacional Mayor de San Marcos, 27-29 de Agosto de 2007, Lima.
- Simone, L. R. L. 2006. Land and freshwater molluscs of Brazil. 390pp., São Paulo (EGB, Fapesp).
- Solem, A. 1983. Endodontoid land snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra). Part 2: Families Punctidae and Charopidae, Zoogeography. 336pp., Chicago (Field Museum of Natural History).