

# Morphological comparison between *Doryteuthis pleii* and *D. sanpaulensis* (Cephalopoda, Myopsida, Loliginidae) from Brazil

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**Abstract.** The distinction of squid species in the genus *Doryteuthis* is not easy due to their morphological similarity, lack of conspicuous specific characters, and overlap geographical occurrence. This difficulty has leading to an almost exclusive molecular approach, and a premature neglect of the morpho-anatomy. To emphasize that the squid phenotypic features can be useful to identify, as well as to perform any comparative analyses (such as taxonomy and phylogeny), two close species were selected as outset. *Doryteuthis pleii* and *D. sanpaulensis* are common sympatric squids in Brazilian waters, commonly used in fisheries, not so difficult to distinguish by external features of the adult specimens. The samples were analyzed from biometric data to dissections, and the found most expressive characters to distinguish them are the mantle-fin ratio; morphology of the tentacle club, its ratio compared to the mantle length; hectocotylus morphology and nidamental gland morphology.

**Key-Words.** Anatomy; Characters; Squid; Sympatric; Taxonomy.

## INTRODUCTION

Loliginidae is a widely distributed squid family of economic importance, extensively targeted as fishery products and with a relevant role in an intricate marine food web (Fields, 1965; Anderson, 2000; Vecchione & Young, 2010a; Granados-Amores *et al.*, 2014). It comprises 47 species distributed in 10 genera, all of which are pelagic (Jereb & Roper, 2010; Vecchione & Young, 2010a; Granados-Amores *et al.*, 2014). Loliginids usually have the posterior end of the fins connected to the mantle and four rows of suckers on the tentacular club [except for *Pickfordiateuthis* (Voss, 1953) (see Brakoniecki, 1996; Vecchione & Young, 2010a)]. Initially, two of the commonest species in Brazilian coast, *Doryteuthis pleii* (Blainville, 1823) and *D. sanpaulensis* (Brakoniecki, 1984), were placed in the genus *Loligo*, a genus that is now restricted to the Eastern Atlantic (Vecchione *et al.*, 2005).

There is eight species of *Doryteuthis*, which are sometimes misidentified due to their morphological similarity, the lack of conspicuous, indubitable specific characters to define them, and their overlapped geographical distribution (Vecchione *et al.*, 1998; Vecchione & Young, 2010b).

Nowadays, detailed studies on squid anatomy are scarce, even though morphological data have proved to be very useful in producing phylogenetic hypotheses and defining relationships within mollusk groups (*e.g.*, Simone, 2011; Couto *et al.*, 2015; Dornellas & Simone, 2015). There are more recent papers about molecular analyses than morphological studies. Still, most morphological studies on squids are focused on external characters, barely taking into account the internal anatomy.

Therefore, considering that *D. pleii* and *D. sanpaulensis* are relatively locally common, have economic importance in Brazilian waters, and are sympatric, the main purpose of this study is to clarify the differences between these two species, which are commonly misidentified, focusing on both internal and external characters, a more practical approach to determine the species from laboratories to fishmongers. It is not the intention of this paper to perform any statistical analysis, an approach already done elsewhere (Juanicó, 1979), focusing, here, the morpho-anatomical features only. The pioneer study by Juanicó (1979) is commonly used to base the identification of *D. pleii* and *D. sanpaulensis* (then called *Loligo brasiliensis* Blainville, 1823), and has a comprehensive morphometric analysis of the external features and of the gladius.

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However, a detailed comparison of the internal anatomy of both species is still inedited, a gap fulfilled herein.

## MATERIAL AND METHODS

The material examined belongs to the Malacological Collection of the Museu de Zoologia da Universidade de São Paulo (MZSP). Specimens preserved in 70% ethanol were measured following the standards of \_ENREF\_4, Roper & Voss (1983), Laptikhovskiy *et al.* (2009) and Vecchione *et al.* (2015) and dissected through usual procedures.

Biometric data were clustered in a table and only the mantle length (ML), fin length (FL), arms length (AI, All, AIII, AIV – counted dorsally to ventrally), eye diameter (ED) and hectocotylus length (HtL) were used in order to describe and compare the species. Some morphological characters (*e.g.*, tentacle length) are prone to alterations during fixation and therefore were not listed here (Vecchione *et al.*, 2015). All the arms were measured and average values were taken for each arm pair. Some measurements were converted to percentage of the mantle length (after Vecchione *et al.*, 2015) in order to standardize the values, allowing for the comparison between *D. pleii* and *D. sanpaulensis*. In total, 40 specimens of each species were measured. Drawings were made with the aid of a camera lucida. Radulae of both species were manually extracted and prepared by immersion in KOH and further ultrasonic cleaning, followed by immersion in distilled water, prior to Scanning Electron Microscope (SEM) examination.

**Abbreviations in the figures:** aa, anterior aorta; ad, adductor muscle; ag, accessory nidamental gland; ah, anterior head retractor nerve; am, anterior mass; an, anus; ap, posterior aorta; ar, arm; at, aortic trunk; ba, branchial artery; bh, branchial heart; bl, blood vessel; bm, buccal bulb; br, branchial muscle; bv, branchial vein; ca, caecum; cg, capillaries of the gill; cn, collar nerve; es, esophagus; ey, eye; fi, fin; fn, funnel; fu, mantle-funnel locking apparatus; gi, gill; gs, stellate ganglion; he, head; ib, interbranchial commissure; ik, ink sac; ki, kidney (nephridium); lv, lateral nephridial vessel; ma, mantle aorta; mm, middle mass; mt, muscular mantle; ni, nidamental gland; ns, Needham sac; oc, inferior anterior oculomotor nerve; og, oviducal gland; ol, optic lobe; oy, ovary; pe, penis; pm, posterior mass; pn, pallial nerve; po, post-orbital nerve; pv, posterior vena cava; rt, rectum; sh, systemic heart; sk, skull; so, superior posterior oculomotor nerve; sp, spermatophoric gland; st, stomach; sy, statolith; te, tentacle; ts, testis; vg, vagina.

## RESULTS

### *Doryteuthis pleii* (Blainville, 1823) (Figs. 1, 3, 5, 6)

**Synonymy see Cohen (1976). Complement:**

*Loligo plei* [sic]: Cohen, 1976: 341 (figs. 25-26); Whitaker, 1980: 39; Hanlon *et al.*, 1983: 638 (fig. 4); Roper

*et al.*, 1984: 98; Haimovici & Perez, 1991: 227; Costa & Fernandes, 1993: 753 (tab. 1); DiMarco & Hanlon, 1997: 93 (fig. 2); Anderson, 2000: 606 (tab. 2); Jackson & Forsythe, 2002: 677; Perez *et al.*, 2002: 271 (tab. 2); Pineda *et al.*, 2002: 71 (tab. 1); Cardoso *et al.*, 2005: 373 (tab. 4); Martins & Perez, 2006: 24 (fig. 1); Perez *et al.*, 2006: 750 (fig. 1); Rodrigues & Gasalla, 2008: 634 (tab. 1).

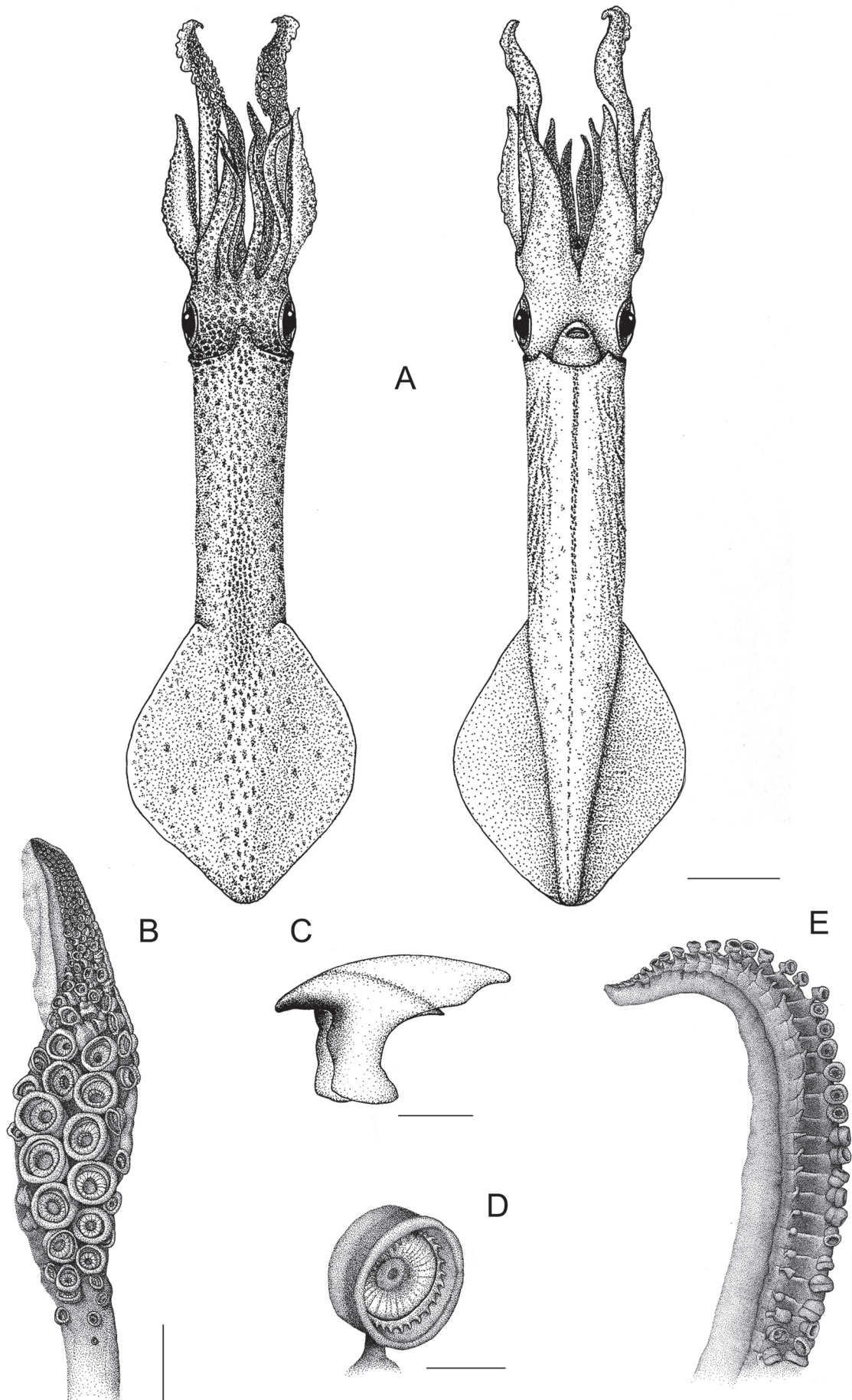
*Doryteuthis plei* [sic]: Brakoniecki, 1984: 436; Haimovici & Andriquetto, 1986\_ENREF\_13: 5 (fig. 1); Grassi *et al.*, 1990: 260; Vecchione *et al.*, 2005: 25 (tab. 2); Jereb & Roper, 2010: 55 (fig. 83); Marian, 2010\_ENREF\_20: 2 (fig. 1); de Pasquier & Carroz, 2012: 37 (fig. 4); de Aguiar *et al.*, 2012: 17 (tab. 1); Marian, 2012: 250 (figs. 1-21); Marian & Domaneschi, 2012: 93 (figs. 1-20); de Luna Sales *et al.*, 2013: 294 (fig. 1); Barcellos & Gasalla, 2014: 3 (figs. 1, 2, 3 and 6).

*Doryteuthis pleii*: Allcock *et al.*, 2015: 18 (tab. 2); Willems *et al.*, 2015: 28 (tab. 2).

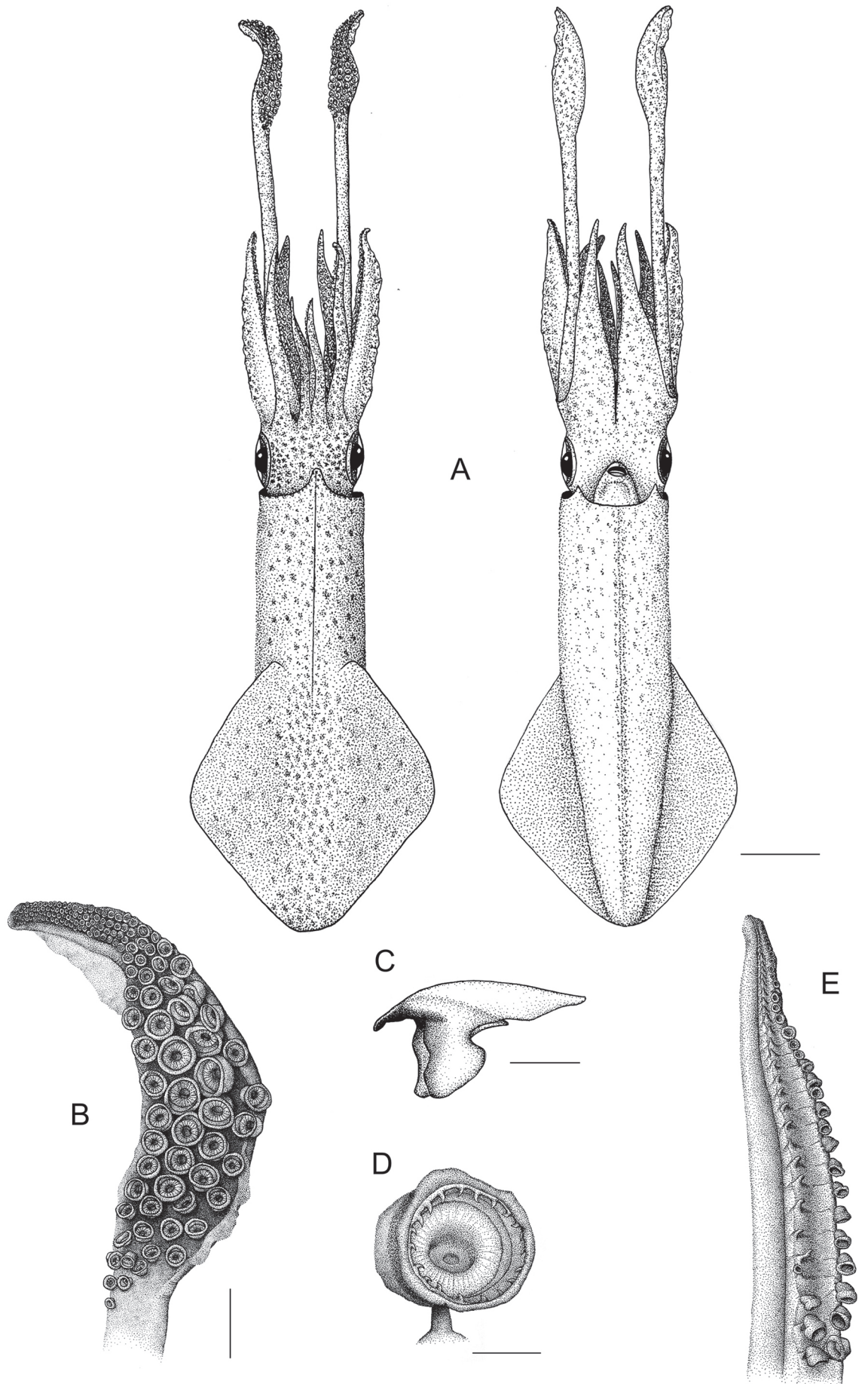
**Type locality:** Martinique, West Indies, western North Atlantic Ocean.

**Holotype:** Muséum National d'Histoire Naturelle, Paris [despite the label of the specimen thought to be the holotype is missing (Cohen, 1976)].

**Material examined: Brazil; Rio de Janeiro:** off São João da Barra, MZSP 15294, 24 spm. ("Exp. Dep. Zool." coll., July 1963). off Farol de São Thomé, 22°08'S, 41°00'W, MZSP 27095, 22 m, 1 spm. (R/V "W. Besnard" coll., 12 March 1971). off Cabo Frio, 22°51'S, 41°52'W, MZSP 27092, 48 m, 17 spm. (R/V "W. Besnard" coll., 01 December 1970). 22°59'S, 42°06'W, MZSP 102761, 25-33 m, 2 spm. (1 June 1987). off Saquarema, 23°02'S, 42°37'W, MZSP 101893, 50-62 m, 1 spm. (19 November 2007). off Niterói, 23°05'S, 43°06'W, MZSP 110029, 30-50 m, 2 spm. (Mendonça Jr. coll., 05 December 2012). off Angra dos Reis, Vila Velha Beach, MZSP 27063, 1 spm. ("Exp. Dep. Zool." coll., 21 July 1966). off Paraty, 23°11'S, 44°38'W, MZSP 58954, 2 spm. (Simone coll., 12 January 2006). MZSP 27061, 13 spm. (July 1983). MZSP 32965, 2 spm. (Fishermen coll., March 2001). **São Paulo:** off Ubatuba, MZSP 27076, 8 spm. (Boffi coll., 08 February 1970). MZSP 101892, 1 spm. (Caires coll., 2011). MZSP 27084, 2 spm. (Local fishermen coll., 12 March 1970). Lázaro Beach, MZSP 27087, 2 spm. (Sazima coll., 04 April 1970). off Maranduba, 23°39'S, 45°05'W, MZSP 27101, 28-32 m, 4 spm. (R/V "W. Besnard" coll., 05 December 1970). off Santos, MZSP 90936, 2 spm. (Cunha coll., March 2009). MZSP 27097, 42 m, 4 spm. (R/V "W. Besnard" coll., 05 December 1970). MZSP 86427, 8 spm. (R/V "Miragem Boat" coll., March 1988). off Praia Grande, Boqueirão, 24°01'S, 46°25'W, MZSP 80342, 1 spm. (Simone coll., 1997). 24°05'S, 46°20'W, MZSP 110145, 2 spm. (10 April 2012). off São Sebastião, Alcatrazes archipelago. 24°07'S, 45°40'W, MZSP 102400, 46 m, 3 spm. (Amaral coll., 04 October 2011). 24°07'S, 45°40'W, MZSP 102401, 46 m, 2 spm. (Amaral coll., 04 October 2011). 24°24'S, 46°05'W, MZSP 27159, 52 m, 25 spm. (R/V "W. Besnard"



**Figure 1.** *Doryteuthis pleii* general features. (A) Dorsal (left) and ventral (right) whole view of a male, scale = 20 mm; (B) Tentacular club, scale = 5 mm; (C) Upper beak, scale = 2 mm; (D) Sucker from tentacular club, scale = 1 mm; (E) Left ventral arm showing hectocotylyzed portion, scale = 5 mm.



**Figure 2.** *Doryteuthis sanpaulensis* general features. (A) Dorsal (left) and ventral (right) whole view of a male, scale = 20 mm; (B) Tentacular club, scale = 5 mm; (C) Upper beak, scale = 2 mm; (D) Sucker from tentacular club, scale = 1 mm; (E) Left ventral arm showing hectocotyized portion, scale = 5 mm.

coll., 21 January 1971). off Itanhaém, 24°24'S, 46°18'W, MZSP 27093, 45 m, 13 spm. (R/V "W. Besnard" coll., 05 March 1971). off Peruíbe, 24°20'S, 46°49'W, MZSP 27094, 79 m, 28 spm. (R/V "W. Besnard" coll., 06 March 1971). 24°38'S, 45°05'W, MZSP 27102, 102 m, 6 spm. (R/V "W. Besnard" coll., 06 March 1971). off Barra do Una, 24°40'S, 46°49'W, MZSP 27096, 38 m, 10 spm. (R/V "W. Besnard" coll., 06 December 1970). off Cananéia, Castilho Island – ESEC Tupiniquins, 25°00'S, 47°55'W, MZSP 83165, 5 spm. (Guimarães, Lima & Amaral coll., 24 January 2007). 25°26'S, 45°35'W, MZSP 27091, 125-128 m, 10 spm. (R/V "W. Besnard" coll., 05 July 1970). 25°44'S, 46°37'W, MZSP 27089, 111 m, 6 spm. (R/V "W. Besnard" coll., 04 March 1971). **Paraná:** off Pontal do Sul, 25°36'S, 47°30'W, MZSP 27104, 50 m, 2 spm. (R/V "W. Besnard" coll., 07 December 1970). 25°59'S, 47°15'W, MZSP 27105, 77-82 m, 4 spm. (R/V "W. Besnard" coll., 07 December 1970). **Santa Catarina:** São Francisco do Sul Island, 26°17'S, 48°22'W, MZSP 27162, 10 spm. (R/V "W. Besnard" coll., February 1977). off Itajaí, MZSP 92949, 51 m, 2 spm. (R/V "NPq Soloncy Moura" coll., 09 November 2009). off Imbituba, 28°18'S, 48°34'W, MZSP 27090, 50 m, 12 spm. (R/V "W. Besnard" coll., 01 March 1971). **Rio Grande do Sul:** off Balneário Pinhal, 30°37'S, 49°25'W, MZSP 27058, 150 m, 4 spm. (GEDIP Project coll., 05 August 1972).

**Distribution:** Cape Hatteras (36°N) to northern Argentina (35°S) usually associated with Brazilian warm current. Also including Gulf of Mexico, Caribbean Sea, Bermuda and Bahamian and Caribbean islands (Jereb & Roper, 2010).

## Description

**Mantle:** Cylindrical; muscular (~ 91 mm; Table 1); usually long and slender (Fig. 1A), ~ 4-times longer than wide.

**Head:** Eye diameter approximately 13% of mantle length (Table 2). Width similar to length values.

**Chromatophores:** Widely distributed, with higher densities on dorsal region including head (around eyes), dorsal midline of mantle (highly concentrated beginning of fins), fins and arms/tentacles. Mature males presenting striped pattern along ventral surface of mantle (Fig. 1A).

**Fins:** Rhomboid, slightly ovate comprising ~ 48% ML (Table 2), connected posteriorly to posterior end of mantle (Fig. 1A).

**Arms:** Muscular, broad at base and gradually tapering into thin tips; formula III>IV>II>I (~ lengths: 33 mm, 30 mm, 29 mm, 23 mm); biserial suckers. Hectocotylized portion ~ 39% of left ventral arm length reaching arm's tip (Table 2), only left row of suckers modified into small peduncles. Bar between row of peduncles and row of suckers connecting them in ladder pattern (Fig. 1E).

**Tentacle:** Club long and thin, ~ 28% ML (Table 2), carpus, manus and dactylus easily defined; 4 rows of suckers diagonally distributed along club, more visible at manus and dactylus regions; 2 central rows at manus region much bigger than other suckers. Each sucker with small chitin ring of teeth inside. Longitudinal muscle around sucker visible (Figs. 1B, 1D).

**Circulatory system:** Normal Loliginidae form (Fig. 6A). One central systemic croissant-shaped heart; two smaller peripheral branchial round hearts associated to gills. Two aortae: (i) anterior aorta delivering blood to head, arms and tentacles; (ii) posterior aortic trunk, divided in: (a) visceral aorta, sending blood to posterior part of mantle and visceral organs; (b) mantle aorta, distributing blood to anterior region of mantle. Blood return to heart (i) from posterior vena cava and (ii) from lateral nephridial vessel, both ending in a branchial heart. Branchial artery leaving branchial heart, and ending in gills complex; after this, returning to heart through branchial vein (Fig. 3A).

**Digestive system (Figs. 5, 6):** Pigmented tip of upper beak short and robust (Fig. 1C). Radula usual for the family; rachidian and first lateral teeth bearing primary large projection and secondary smaller one(s) (Fig. 4A). Usual digestive system for Loliginidae: buccal bulb occupying ~ half of inner head volume. Esophagus narrow, running straight posteriorly along ~ 1/3 of mantle length. Stomach spherical, wall weakly muscular, occupying ~ 20% of visceral volume, located in middle level of visceral sac; posterior caecum wide, extending up to posterior mantle space. Intestine narrow, originating in YY region of stomach, performing simple loop in anterior region of visceral sac. Anus with two papillae, located in middle level of pallial cavity, preceded by short flexible stalk. Digestive gland wide and located between four retractile muscles of head and funnel. Esophagus passing through digestive gland ventro-dorsally.

**Male genital system:** Normal genital system for Loliginidae, including characters of penis, Needham sac, spermatophoric gland and a single testicle (Figs. 6A, 6B). Hectocotylus described above.

**Female genital system:** Normal genital system for Loliginidae, including characters of vagina, oviduct, oviducal gland, ovary, a pair of nidamental glands and pair of accessory nidamental glands (Fig. 5). Nidamental glands more uniform, with no slender tip (Fig. 5B).

**Central nervous system (Fig. 3B):** Central mass slightly divided into anterior and posterior regions. Giant fibers running from posterior end, along dorsal portion of mantle; stellate ganglion visible beneath gills. One pair of optic lobes mushroom-shaped, flanking central mass on each side. Several nerves running anteriorly towards arms and tentacles, forming ring around buccal bulb (Fig. 3B: ib).

**Table 1.** Biometric measurements of *Doryteuthis pleii*. ML: mantle length (mm); FL: fins length (mm); ED: eye diameter (mm); AI, AII, AIII, AIV: arms length dorsally to ventrally (mm); HtL: hectocotylus length (mm); CL: tentacular club length (mm).

Individual	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Sex	♂	♀	♀	♀	♀	♂	♂	♂	♀	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♂
<b>ML</b>	165	124	122	147	92	87	88	39	72	80	61	49	55	50	53	112	79	101	82	111
<b>FL</b>	87	64,6	60,2	78,1	53,8	51,4	45,5	20,4	40,8	46,4	31,9	26,1	27,2	24,3	25,7	54,5	32,3	44,7	32,5	51,5
<b>ED</b>	14,6	13,8	14	15,3	11,1	10,3	10,3	7,5	8,7	10,3	10	7,3	8	7,6	9,4	12,6	9	12,2	9,4	11
<b>LEFT AI</b>	34,6	32,6	31,4	35,1	25,3	26,4	26,5	14	22,6	22,6	21,9	14,2	16	18,7	18,8	26,5	19,1	26,4	20,6	30,7
<b>AII</b>	40,5	36,2	37,1	40,8	34,5	32,9	32,4	16,2	27,8	26,9	23,9	17,1	23,8	10,5	21,4	31,3	20,3	30,4	23	36,6
<b>AIII</b>	43,4	38,7	37,3	45,5	39,1	36	36,4	20,9	32,4	37,1	27,7	22,9	26,5	24,9	26	35,5	27,3	34,8	30,1	39,8
<b>AIV</b>	40,4	36,6	30,9	42,1	32,7	33,9	33,2	19,1	28,6	33,1	27	20,8	21,4	23,7	23	33	22,1	32,8	25,2	37,1
<b>HtL</b>	15,8	—	—	—	—	10,8	13	5,2	—	13,9	9,4	9,5	8,6	9,4	—	—	—	—	—	18,7
<b>CL</b>	25,2	27,3	26,3	32	34,5	24,9	22,8	12,8	20,4	24,8	21,6	16,5	18,5	15,7	24	28,2	18,2	28,8	23,8	25,4
<b>RIGHT AI</b>	34,6	31,1	30,4	28,7	28,5	27	24,2	13,4	21,1	28,4	20,1	14,5	16,3	18,6	17	27	18,8	26,4	20,6	31,5
<b>AII</b>	39,6	37,4	34,6	41	33,9	34,2	29,6	16,5	26,6	31,1	27,2	21,4	20,8	21,7	13,2	32,9	25,4	28,6	25,3	39,3
<b>AIII</b>	42,9	38,2	38,1	43	41,2	38,7	33,5	22,3	33,1	37,5	28,5	23,4	25	20,1	25,1	38,5	27,6	33,7	29,5	41,3
<b>AIV</b>	36,9	37,4	31,8	40,1	37,8	32	34,5	19,3	31	34,1	28,9	22,3	15,9	24	23,8	34,8	26,4	34,2	26,5	34
<b>CL</b>	24,6	27,9	25,9	32,8	35,3	25,5	23,5	13,3	22,3	25,3	22,1	15,8	17,5	15,4	24,9	27	18,4	28,7	21,1	24,3
Individual	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Sex	♂	♂	♀	♂	♀	♀	♀	♀	♀	♂	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
<b>ML</b>	117	90	136	104	84,4	67,2	65	66,3	60,1	62,8	72	74,5	151	175	121	80,1	70,4	87,4	102	77
<b>FL</b>	47,7	40,1	72,8	54,4	33	28,9	23,7	26,6	25,3	26,3	40,9	40	75	90	62	35	32	36,4	46	30,5
<b>ED</b>	10,9	10,9	12,6	10,5	12,9	10,7	11,4	10,9	10,9	11,9	11,3	10,6	15,5	15,7	13,5	12,2	11	11,5	13	10
<b>LEFT AI</b>	29,1	25,6	31,1	—	21,2	19,7	18,6	19,9	19,5	18,3	18,1	21	—	—	31,7	24,2	19,2	21,7	22,8	16,3
<b>AII</b>	34,4	31,9	28,5	34,6	29,5	28	21,9	26,4	24,4	23,5	29	31,3	—	—	39	29,9	26	27,5	28,4	19,9
<b>AIII</b>	39,7	36,1	43,6	38,5	33	27,4	27,2	26,8	25,8	25	35,3	33	—	—	43	31,9	27,2	29,5	37,6	25
<b>AIV</b>	36,4	30,6	34,8	37,7	34,2	24,9	30,1	24,8	26,3	26	35,4	34	—	—	42,8	30,4	26,3	29	32	26
<b>HtL</b>	15,9	11,8	—	16,3	—	—	—	—	—	8,2	—	—	—	—	—	—	—	—	—	—
<b>CL</b>	25,5	22,9	31,5	24,3	20,3	21,6	22,4	23,4	19,8	20,1	19,6	22,2	33,4	35,2	30,7	25,4	18,8	23,1	25,5	19,5
<b>RIGHT AI</b>	30,3	26,9	32	30,9	22	20,6	18,6	19,9	19,6	19,4	20,5	21	—	—	32	24,2	20	22	25,6	16
<b>AII</b>	34,6	33,5	25,4	37,3	30,8	26,8	22,7	24,6	25,8	26,2	28,7	30	—	—	39,7	27	27	26	25,7	20
<b>AIII</b>	30,9	35,2	42,3	40,3	33	26,9	29,4	29,7	25,8	28	33	35	—	—	45,5	32	27,3	31	35	25,3
<b>AIV</b>	37,2	35,1	40,4	39,2	33	21,8	27,9	27,4	26,8	24	33,2	34	—	—	42	—	27,1	30	31,7	25,8
<b>CL</b>	25,1	22,6	31,2	24,2	20,1	21,5	22,3	23,5	19,9	20	19,8	22,3	33,4	35,2	30,5	25,6	18,7	23,3	25,3	19,6

**Table 2.** Proportions between characters of *Doryteuthis pleii*. FL-ML: Proportion between fin length and mantle length (%); ED-ML: Proportion between eye diameter and mantle length (%); HtL-Lft AIV: Proportion between hectocotylized portion and left ventral arm length (%). CL-ML: Proportion between tentacular club length and mantle length (%).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	♂	♀	♀	♀	♀	♂	♂	♂	♀	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀	♂
<b>FL-ML</b>	52,7	52,1	49,3	53,1	58,5	59,1	51,7	52,3	56,7	58	52,3	53,3	49,5	48,6	48,5	48,7	40,9	44,3	39,6	46,4
<b>ED-ML</b>	8,85	11,1	11,5	10,4	12,1	11,8	11,7	19,2	12,1	12,9	16,4	14,9	14,5	15,2	17,7	11,3	11,4	12,1	11,5	9,91
<b>HtL-Lft AIV</b>	39,1	—	—	—	—	31,9	39,2	27,2	—	42	34,8	45,7	40,2	39,7	—	—	—	—	—	50,4
<b>CL-ML</b>	15,1	22,3	21,4	22	37,9	29	26,3	33,5	29,7	31,3	35,8	33	32,7	31,1	46,1	24,6	23,2	28,5	27,4	22,4
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
	♂	♂	♀	♂	♀	♀	♀	♀	♀	♂	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
<b>FL-ML</b>	40,8	44,6	53,5	52,3	39,1	43	36,5	40,1	42,1	41,9	56,8	53,7	49,8	51,4	51,4	43,7	45,5	41,6	45,1	39,6
<b>ED-ML</b>	9,32	12,1	9,26	10,1	15,3	15,9	17,5	16,4	18,1	18,9	15,7	14,2	10,3	8,97	11,2	15,2	15,6	13,2	12,7	13
<b>HtL-Lft AIV</b>	43,7	38,6	—	43,2	—	—	—	—	—	31,5	—	—	—	—	—	—	—	—	—	—
<b>CL-ML</b>	21,6	25,3	23,1	23,3	23,9	32,1	34,4	35,4	33	31,9	27,4	29,9	22,2	20,1	25,4	31,8	26,6	26,5	24,9	25,4

***Doryteuthis sanpaulensis* (Brakoniecki, 1984)**  
(Figs. 2, 3, 5, 6)

**Synonymy see Brakoniecki (1984). Complement:**

*Loligo sanpaulensis* Brakoniecki, 1984: 441-446 (figs. 3-4); Roper *et al.*, 1984: 102; Haimovici & Perez, 1991: 227; Costa & Fernandes, 1993: 753 (tab. 1);

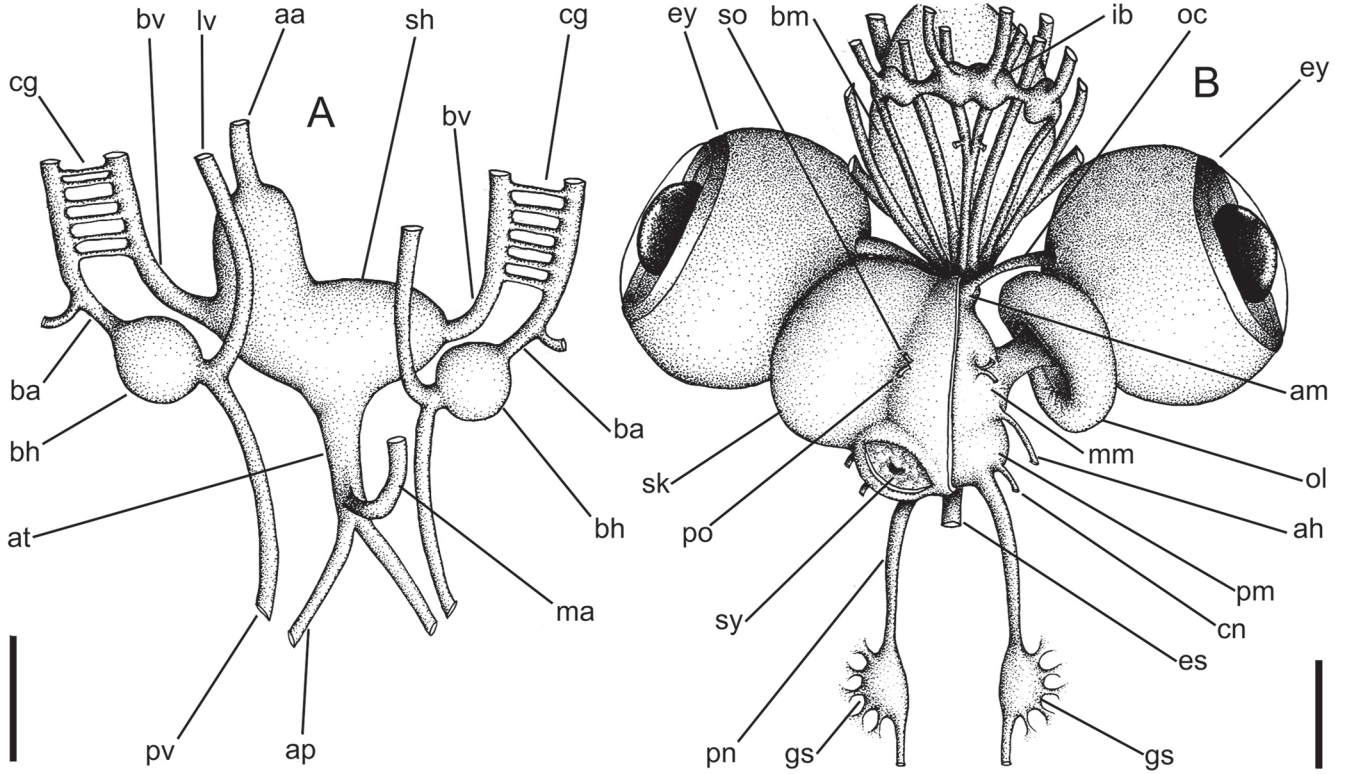
Andrighetto & Haimovici, 1996: 444; Pineda *et al.*, 1996: 88 (fig. 5); Sanchez *et al.*, 1996: 540 (fig. 17); Anderson, 2000: 606 (tab. 2); Barón & Ré, 2002: 270 (figs. 1 and 5); Herke & Foltz, 2002: 106 (tab. 1); Pineda *et al.*, 2002: 71 (tab. 1); Barón, 2003a: 222 (fig. 1); Barón, 2003b: 1350 (figs. 4, 6 and 8); Rodrigues & Gasalla, 2008: 634 (tab. 2); Vidal *et al.*, 2010: 1348 (tab. 1).

*Doryteuthis sanpaulensis*: Vecchione *et al.*, 2005: 25 (tab. 2); Jereb & Roper, 2010: 69 (fig. 97); de Aguiar *et al.*, 2012: 17 (tab. 1); de Luna Sales *et al.*, 2013: 294 (fig. 1); Crespi-Abril *et al.*, 2014: 15 (tab. 1).

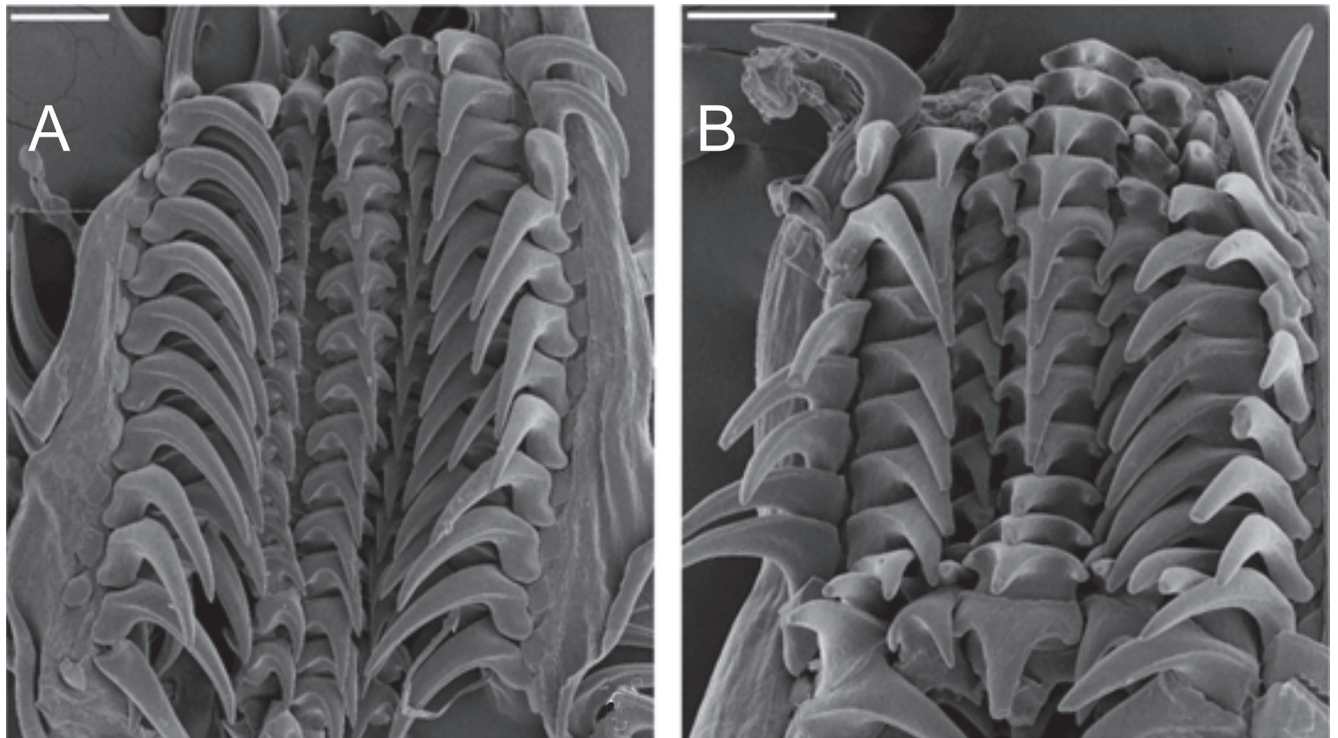
**Type locality:** San Matias Gulf, Argentina, 41°47'S, 63°35'W.

**Holotype:** USNM 815464.

**Material examined:** **Brazil; Rio de Janeiro:** off Farol de São Thomé, MZSP 101894, 1 spm. (Nunan coll., 26 January 2007). off Maricás Island, 23°01'S, 42°50'W, MZSP 101891, 44-50 m, 1 spm. (17-18 November 2002). off Niterói, 23°05'S, 43°06'W, MZSP 110019, 30-50 m, 1 spm. (Mendonça Jr



**Figure 3.** (A) Central vascular system representing both species, ventral view; (B) Central nervous system representing both species, ventral view. Scales: = 5 mm.



**Figure 4.** Radulae in SEM: (A) *Doryteuthis pleii*; (B) *Doryteuthis sanpaulensis*. Scales: = 200 µm.

coll., 05 December 2012). 23°05'S, 43°06'W, MZSP 110025, 30-50 m, 20 spm. (Mendonça Jr coll., 05 December 2012). off Paraty, MZSP 32966, 2 spm. (Fishermen coll., March 2001). **São Paulo:** off Ubatuba, Itaguá Beach, MZSP 26409, 2 spm. (Figueiredo coll.). MZSP 27083, 19 spm. (Monfouchet coll., 12 March 1970). off São Sebastião, Alcatrazes Island, MZSP 27075, 2 spm. (16 March 1964). 24°02'S, 44°42'W, MZSP 27160, 80-90 m, 25 spm. (R/V "W. Besnard" coll., 11 August 1970). MZSP 47280, 2 spm. off Santos, MZSP 34506, 10-15 m, 6 spm. (Cunha coll., May 1998). MZSP 34645, 130-150 m, 1 spm. (Cunha coll., February 2002). MZSP 47289, 18 m, 13 spm. (R/V "Emília" coll., November 1976). MZSP 91389, 3 spm. (Cunha coll., June 2009). MZSP 107571, 20 m, 30 spm. (Cunha coll., June 2009). off Boqueirão, 24°01'S, 46°25'W, MZSP 80343, 11 spm. (Simone coll., 1997). MZSP 27321, 6 m, 3 spm. (Simone coll., 10 January 1990). off Iguape, 25°10'S, 46°45'W, MZSP 18639, 7 spm. (R/V "W. Besnard" coll., 30 May 1970). **Santa Catarina:** off Itajaí, MZSP 92950, 51 m, 11 spm. (R/V "NPq Soloncy Moura" coll., 09 November 2009). off Florianópolis, 27°09'S, 47°41'W, MZSP 27135, 115 m, 2 spm. (R/V "W. Besnard" coll., 16 August 1970). 27°56'S, 48°29'W, MZSP 18680, 8 spm. (R/V "W. Besnard" coll., 17 December 1970). off Laguna, 28°32'S, 48°11'W, MZSP 18638, 4 spm. (R/V "W. Besnard" coll., 03 June 1970). off Balneário Gaivota, 29°13'S, 49°35'W, MZSP 27133, 20 m, 2 spm. (R/V "W. Besnard" coll., 31 January 1972). 29°13'S, 49°35'W, MZSP 27148, 19 m, 10 spm. (R/V "W. Besnard" coll., 06 April 1972). 29°16'S, 49°14'W, MZSP 27143, 51 m, 3 spm. (R/V "W. Besnard" coll., 30 January 1972). 29°23'S, 49°16'W, MZSP 27137, 50 m, 4 spm. (R/V "W. Besnard" coll., 06 April 1972). **Rio Grande do Sul:** off Arroio do Sal, 29°52'S, 48°41'W, MZSP 18603, 4 spm. (R/V "W. Besnard" coll., 05 March 1969). off Capão da Canoa, 29°58'S, 49°18'W, MZSP 27144, 92 m, 5 spm. (R/V "W. Besnard" coll., 29 January 1972). off Tramandaí, MZSP 26410, 3 spm. (Phonlor coll., 1974). off Cidreira, MZSP 26411, 10 m, 1 spm. (Phonlor coll., July 1974). MZSP 26408, 10 m, 1 spm. (Phonlor coll., 08 October 1974). off Balneário Pinhal, 30°16'S, 50°09'W, MZSP 27138, 22 m, 2 spm. (R/V "W. Besnard" coll., 28 January 1972). 30°22'S, 49°36'W, MZSP 18589, 18 spm. (R/V "W. Besnard" coll., 05 December 1968). 30°27'S, 49°48'W, MZSP 27130, 71 m, 6 spm. (R/V "W. Besnard" coll., 28 January 1972). off Solidão, 30°47'S, 50°28'W, MZSP 27145, 17 m, 8 spm. (R/V "W. Besnard" coll., 26 January 1972). 30°53'S, 50°16'W, MZSP 27132, 60 m, 2 spm. (R/V "W. Besnard" coll., 26 January 1972). off Mostardas, 31°09'S, 50°43'W, MZSP 27131, 20 m, 12 spm. (R/V "W. Besnard" coll., 07 August 1972). 31°12'S, 50°35'W, MZSP 27141, 59 m, 5 spm. (R/V "W. Besnard" coll., 29 January 1972). off Tavares, 31°30'S, 51°00'W, MZSP 27139, 22 m, 13 spm. (R/V "W. Besnard" coll., 25 January 1972). off Rio Grande, 32°13'S, 50°35'W, MZSP 27136, 84 m, 2 spm. (R/V "W. Besnard" coll., 22 January 1972). 32°20'S, 51°22'W, MZSP 27128, 52 m, 8 spm. (R/V "W. Besnard" coll., 21 January 1972). 32°28'S, 51°07'W, MZSP 27155, 61 m, 5 spm. (R/V "W. Besnard" coll., 03 November 1972). 32°28'S, 52°15'W, MZSP 47314, 15 m, 10 spm. (R/V "W. Besnard" coll., 20 January 1972). MZSP 47292, 2 spm. (R/V "W. Besnard" coll., 17 August 1968). MZSP 18579, 3 spm. (R/V "W. Besnard" coll., 22 August 1968). off Curral Alto, 33°13'S, 51°58'W, MZSP 27150, 51 m, 2 spm. (R/V "W. Besnard" coll., 02

November 1972). 33°16'S, 52°05'W, MZSP 18601, 4 spm. (R/V "W. Besnard" coll., 13 December 1968). 33°32'S, 52°18'W, MZSP 18619, 2 spm. (R/V "W. Besnard" coll., 13 March 1969). MZSP 27158, 20 spm. (No additional information).

**Distribution:** Southwestern Atlantic Ocean; usually from southern Brazil (20°S) to northern Patagonia, Argentina (46°S) (Jereb & Roper, 2010).

### Description

**Mantle:** Cylindrical and muscular ranging to about 89 mm (Table 3; Fig. 2A); ~ 3 times longer than wide.

**Head:** Eye diameter approximately 12% ML (Table 4). Length and width very similar to each other.

**Chromatophores:** Distributed throughout body, especially on dorsal region including head (around eyes); dorsal midline of mantle forming an expressive solid line in region free from fins; few chromatophores clustering in middle of fins and at arms/tentacles (Fig. 2A). Mature males do not present stripped chromatophores along ventral portion of mantle.

**Fins:** Rhomboid, posteriorly connected to mantle, slightly ovate and moderately long, comprising ~ 59% ML (Table 4; Fig. 2A).

**Arms:** Muscular, thick at base and distally tapering into slender tips; formula III>IV>II>I (~ lengths: 41 mm, 38 mm, 36 mm, 28 mm); two rows of suckers. Hectocotylus consists of ~ 40% of left ventral arm length extending to arm tip (Table 4). Left row of suckers modified into a simple peduncle whereas right row remaining as suckers. No connection between modified row and suckers, forming valley pattern throughout hectocotylus (Fig. 2E).

**Tentacle:** Club long and broad, ~ 37% ML (Table 4). Carpus, manus and dactylus uniformly distributed, with boundaries not very sharp, hindering their definition (especially between manus and dactylus); 4 diagonal rows of suckers along club as stated for *D. pleii*; 2 central rows at manus not so different in size from other suckers (Fig. 2B). Each sucker with small ring of teeth apparently at surface of sucker's aperture. Longitudinal muscle around suckers present (Fig. 2D).

**Circulatory and central nervous system:** Similar to preceding species. No apparent morphological differences (Fig. 3A).

**Digestive system:** Pigmented tip of upper beak is long and slender (Fig. 2C). Remaining structures similar to preceding species.

**Male genital system:** Similar to preceding species. No apparent morphological differences (Figs. 6A, 6B) except for hectocotylus above described.



**Table 3.** Biometric measurements of *Doryteuthis sanpaulensis*. ML: mantle length (mm); FL: fins length (mm); ED: eye diameter (mm); AI, AII, AIII, AIV: arms length dorsally to ventrally (mm); HtL: hectocotylus length (mm); CL: tentacular club length (mm).

Individual Sex	1 ♀	2 ♂	3 ♂	4 ♀	5 ♀	6 ♀	7 ♂	8 ♂	9 ♂	10 ♀	11 ♂	12 ♀	13 ♀	14 ♀	15 ♀	16 ♀	17 ♀	18 ♂	19 ♂	20 ♂
<b>ML</b>	92	116	110	92	102	95	94	77	82	74	85	75	70	75	75	70	74	55	145	149
<b>FL</b>	55,1	70,1	64,9	53,2	63,6	56,2	56,1	43,1	47,3	43,4	51,2	45,1	42,3	42,8	45,8	42,6	42,1	32,3	86,1	90,6
<b>ED</b>	10,9	10,7	10,9	10	11,1	10,2	10,1	9,7	10,9	9,8	10,5	8,7	8,7	8,3	11	11,5	8,6	8,3	12,2	12,4
<b>LEFT AI</b>	31,1	33,5	30,5	29,2	37	25,6	26,7	27,8	27	25	29,6	25,5	22,8	26,4	31,3	33,3	22	17,7	30,9	40
<b>AII</b>	38,5	44,1	40,8	38,1	49,2	37,8	38,6	32,4	36,5	32,2	39,2	33,4	32,9	30,8	40,3	29,3	27,8	24,5	51,6	50,3
<b>AIII</b>	43,4	49,6	41,4	46,1	55,1	35,9	44,4	35,4	38,2	39	40,5	38,7	35,7	37,2	46,7	53,5	24,8	26	57,9	55,4
<b>AIV</b>	43,1	38,2	47,3	10,3	49,2	38,7	40,8	31,4	31,1	35,5	29,9	33,5	33,1	34,6	47,2	49,3	30,3	24,8	45,2	52,9
<b>HtL</b>	—	17,8	15,8	—	—	—	15	12,6	15,2	—	12,8	—	—	—	—	—	—	9,9	21,3	17,8
<b>CL</b>	34,4	38,7	36	33,5	43,9	30,3	32,1	22,8	28	29,8	27,2	35,2	30,2	30,2	32,5	34,4	27,7	22	38	46,6
<b>RIGHT AI</b>	29,9	22,2	29,7	30,8	34,3	28,5	26,1	25,7	28,3	25,8	27,2	27,2	23,1	25,3	31,5	24,9	21,4	19	38	42,5
<b>AII</b>	38,6	44,2	32,7	39,6	50,5	34,9	38,7	32,6	37,2	32,2	38,4	32,1	34,5	32,4	41,8	45,4	27,8	22,2	46,4	49,5
<b>AIII</b>	45,8	48,7	45,1	45,9	54,2	37,6	44,6	35,8	38,9	34,6	39,4	42,2	36,2	35,9	47,7	55,4	32,2	27,4	51,5	53,3
<b>AIV</b>	40,3	40,1	44,9	44,2	51,4	39,6	39,4	31,8	34,5	36	35,2	35	33,3	34,1	47,8	47,1	31,1	24,5	50,5	55,1
<b>CL</b>	19,8	34,9	35,5	33,5	46,9	31,5	32,3	23	28,5	29	30,2	35,1	30,7	35,9	33,3	32,9	29,2	22,7	38,6	48,3
Individual Sex	21 ♂	22 ♂	23 ♀	24 ♂	25 ♀	26 ♀	27 ♀	28 ♂	29 ♀	30 ♂	31 ♀	32 ♀	33 ♂	34 ♀	35 ♂	36 ♀	37 ♀	38 ♂	39 ♂	40 ♀
<b>ML</b>	115	107	111	78,7	70	71,8	69	85,3	98,2	146	96,1	75,9	75,4	84,3	62	75,8	98	84,3	71,8	74
<b>FL</b>	70,4	63,2	66,2	47	41,6	37,4	39	50	61,8	87,2	55	41,7	42,3	52	36	43	59	51,7	43	43,3
<b>ED</b>	11	9,9	10,4	9,6	9,4	9,8	9,4	8,1	12,8	14	13,3	10,9	10	13,9	11	11,3	12,6	12,6	11	11,4
<b>LEFT AI</b>	35,6	34,8	34,4	22,5	20,3	23,2	22,5	22,6	—	32,6	30	25,4	25,7	—	21,5	23,3	29,6	27,4	25	—
<b>AII</b>	46,6	42,8	41,8	26,3	26,8	31,9	26,8	28	—	35,8	36	32,3	33,9	—	26,4	29,1	41,8	34,7	34,3	—
<b>AIII</b>	49,6	49	48,9	30,6	33	35,8	33,5	32,4	—	50,9	46,5	39	36,8	—	32	33,2	44,5	36,6	38,7	—
<b>AIV</b>	48	41,8	46,8	29,7	31,7	32,4	31,9	32,3	—	51,2	45,9	38	32	—	31	36,5	42	35,3	32,7	—
<b>HtL</b>	19,1	16,8	—	11,1	—	—	—	12,9	—	19,5	—	—	13,9	—	14	—	—	12,3	11	—
<b>CL</b>	34,3	41,1	41	30,8	33,6	31,2	29,7	29,8	32,1	45,9	30,6	29,4	28,8	31,5	28,7	31,1	38,4	30,6	28,9	29,9
<b>RIGHT AI</b>	34,5	34,1	33,7	22	21	22,4	22,8	22,6	—	32,8	31,1	24,3	27,5	—	21	23,3	29,6	27,2	25	—
<b>AII</b>	41,2	35,5	45,3	26,1	28,4	30,8	28,9	27,9	—	35	35,9	32	33,5	—	26	28,7	41,8	34,7	34	—
<b>AIII</b>	44,7	46,7	54,2	32	33,1	32,8	33,5	31,8	—	51,4	45	38,8	36,8	—	31,8	34,4	44,5	36,5	38,6	—
<b>AIV</b>	52,5	45,7	50,6	30,7	31,3	33,1	33,3	30,3	—	56	44,8	37,6	33,6	—	29,8	33,4	42	35	33,4	—
<b>CL</b>	42	41,5	41,5	30,6	32,9	31,7	30,3	29,9	31,5	45,3	31,2	30,1	28,5	32	29,1	32	38,3	31,2	28,8	29,8

**Table 4.** Proportions between characters of *Doryteuthis sanpaulensis*. FL-ML: Proportion between fin length and mantle length (%); ED-ML: Proportion between eye diameter and mantle length (%); HtL-Lft AIV: Proportion between hectocotylized portion and left ventral arm length (%). CL-ML: Proportion between tentacular club length and mantle length (%).

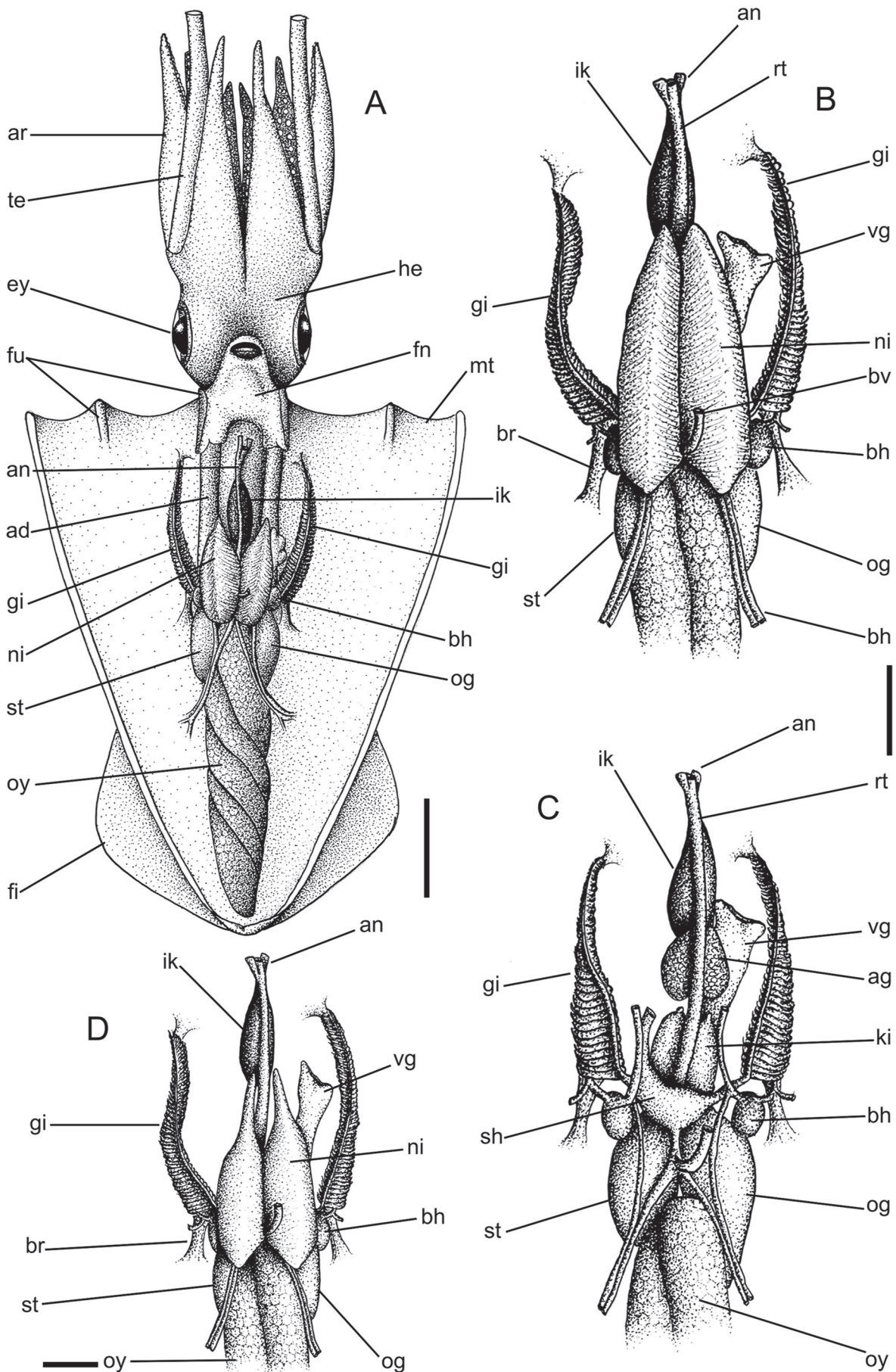
	1 ♀	2 ♂	3 ♂	4 ♀	5 ♀	6 ♀	7 ♂	8 ♂	9 ♂	10 ♀	11 ♂	12 ♀	13 ♀	14 ♀	15 ♀	16 ♀	17 ♀	18 ♂	19 ♂	20 ♂
<b>FL-ML</b>	59,9	60,4	59	57,8	62,4	59,2	59,7	56	57,7	58,6	60,2	60,1	60,4	57,1	61,1	60,9	56,9	58,7	59,4	60,8
<b>ED-ML</b>	11,8	9,22	9,91	10,9	10,9	10,7	10,7	12,6	13,3	13,2	12,4	11,6	12,4	11,1	14,7	16,4	11,6	15,1	8,41	8,32
<b>HtL-Lft AIV</b>	—	46,6	33,4	—	—	—	36,8	40,1	48,9	—	42,8	—	—	—	—	—	—	39,9	47,1	33,6
<b>CL-ML</b>	29,5	31,7	32,5	36,4	44,5	32,5	34,3	29,7	34,5	39,7	33,8	46,9	43,5	44,1	43,9	48,1	38,4	40,6	26,4	31,8
	21 ♂	22 ♂	23 ♀	24 ♂	25 ♀	26 ♀	27 ♀	28 ♂	29 ♀	30 ♂	31 ♀	32 ♀	33 ♂	34 ♀	35 ♂	36 ♀	37 ♀	38 ♂	39 ♂	40 ♀
<b>FL-ML</b>	61,2	59,1	59,6	59,7	59,4	52,1	56,5	58,6	62,9	59,8	57,2	54,9	56,1	61,7	58,1	56,7	60,2	61,3	59,9	58,5
<b>ED-ML</b>	9,57	9,25	9,37	12,2	13,4	13,6	13,6	9,5	13	9,6	13,8	14,4	13,3	16,5	17,7	14,9	12,9	14,9	15,3	15,4
<b>HtL-Lft AIV</b>	39,8	40,2	—	37,4	—	—	—	39,9	—	38,1	—	—	43,4	—	45,2	—	—	34,8	33,6	—
<b>CL-ML</b>	33,2	38,6	37,2	39	47,5	43,8	43,5	35	32,4	31,3	32,2	39,2	38	37,7	46,6	41,6	39,1	36,7	40,2	40,3

**Female genital system:** Similar to preceding species except for nidamental glands with prominent thin tip (Fig. 5D).

## DISCUSSION

*Doryteuthis pleii* and *D. sanpaulensis* are really similar to each other, sometimes difficult to separate in the field

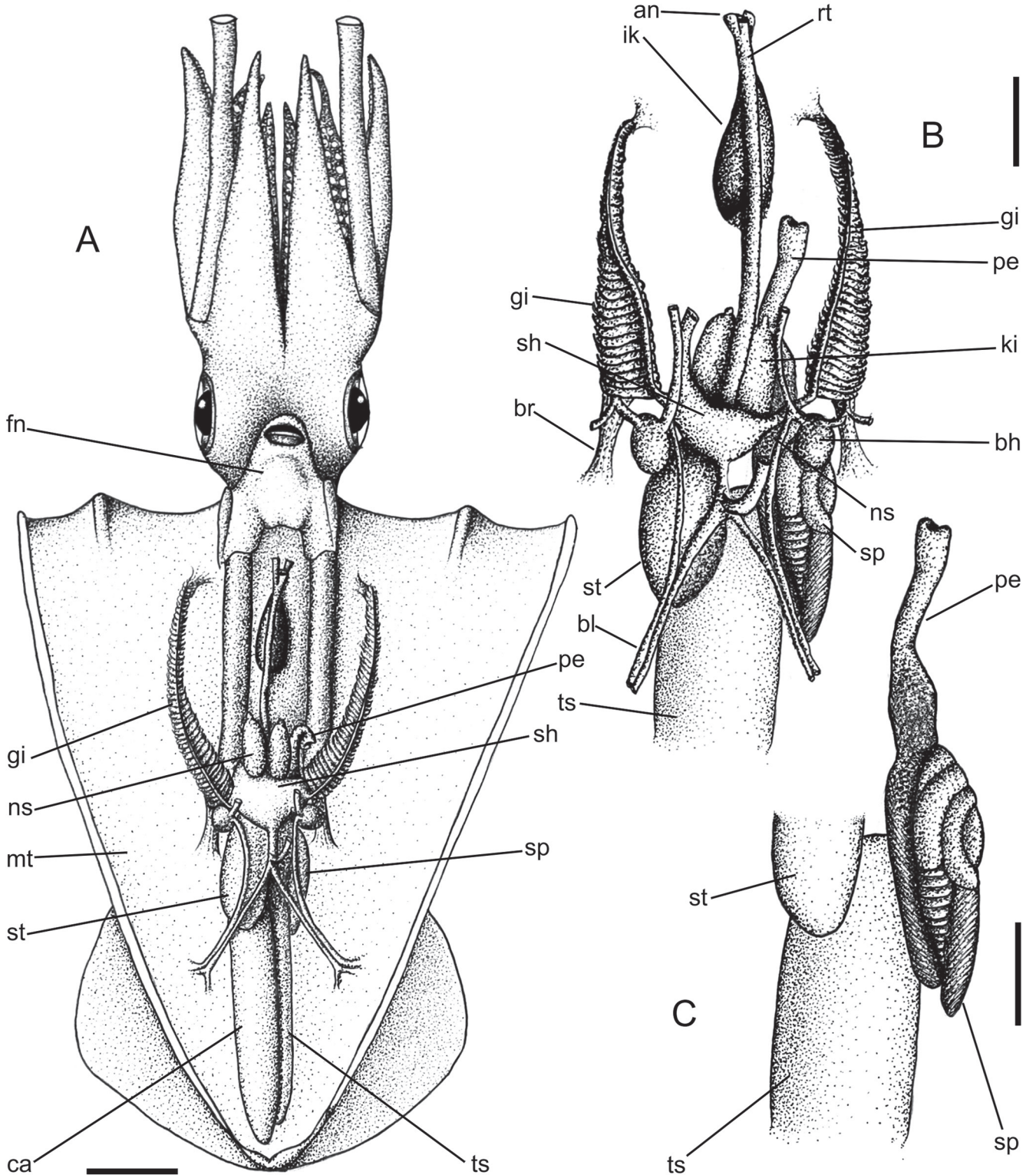
and in preserved samples. The main differences between them resides in the glacial features and in external proportions (Juanicó, 1979; Brakonieccki, 1984). However, the overall anatomy of both species described herein showed additional distinguishing characters. The tentacular club of *D. pleii* has two central rows of suckers larger than the marginal ones (Fig. 1B), whereas *D. sanpaulensis* has four similarly sized rows of suckers (Fig. 2B), where the marginal rows are just slightly smaller than the central ones.



**Figure 5.** (A) Female, representing both species, ventral view, mantle opened longitudinally, scale = 20 mm; (B) *Doryteuthis pleii* female reproductive system, ventral view, scale = 10 mm; (C) Female reproductive system representing both species nidamental gland removed, scale = 10 mm; (D) *Doryteuthis sanpaulensis* female reproductive system, ventral view, scale = 10 mm.

Furthermore, the relation between the club length and mantle length is different between these species. For *D. pleii*, the ratio is around 28% of mantle length, which was also found by Cohen (1976), who stated that the club of *D. pleii* is 19-29% of ML. While for *D. sanpaulensis*, the ratio is around 37%, which is larger possibly due to the similar size of the suckers along the club, which increases its overall size.

The mantle itself does not have large differences between these species. However, the mantle-fin ratio in *D. pleii* usually reaches approximately 40-50%, hardly no more than 1/2 of mantle length (Fig. 1A), while in *D. sanpaulensis* this ratio usually stays around 60% or more (Fig. 2A). Additionally, Brakonieccki (1984) stated that the mantle-fin ratio of *D. pleii* are more similar to *D. gahi* than to *D. sanpaulensis*.



**Figure 6.** (A) Male, representing both species, ventral view, mantle opened longitudinally, scale = 20 mm; (B) Detail of male reproductive system representing both species, ventral view, scale = 10 mm; (C) Male reproductive system isolated, representing both species, ventral view, scale = 10 mm.

Cohen (1976) stated that the hectocotylized portion of *D. pleii* is no more than  $\frac{1}{2}$  of the left ventral arm length, which was confirmed here. The hectocotylized portion is practically the same for these two specimens, comprising 39–40% of the left ventral arm length. However, the morphology of the hectocotylus differs between them. *Doryteuthis pleii* shows a bar connecting the modified and unmodified row, forming a ladder pattern (Fig. 1E), whilst *D. sanpaulensis* does not have any kind of structure connecting the rows, forming a valley between the rows (Fig. 2E).

The eye diameter of *D. pleii* has been referred as about 14–19% of mantle length (Brakoniecki, 1984); however, this study has obtained the eye diameter of around 13%. This difference has been interpreted as a variation in the southern population. As evidenced herein, the eye diameter in *D. sanpaulensis* is around 12% ML.

The statistical morphometric analyses done by Juanicó (1979) already showed the distinction between both species, including ontogenetic and dimorphism variation. The preliminary results of the data of the present paper greatly coincided with those of Juanicó (1979), which was also partially included in Perez *et al.* (2002), dispensing the need of additional analyses. This paper remains, then, focused on the visible morpho-anatomical features of adult specimens.

The internal anatomy does not show significant differences between these two species. The circulatory and the nervous systems have practically the same features in the two species (Fig. 3). Regarding the digestive system, only the beak structure has shown some differences. The pigmented tip of the upper beak of *D. pleii* is short and robust (Fig. 1C), whereas that of *D. sanpaulensis* has a long and slender tip (Fig. 2C). Moreover, the radulae also did not have expressive differences to distinguish the species (Fig. 4). *Doryteuthis pleii* and *D. sanpaulensis* have typical squid radulae: rachidian and first lateral teeth with a primary large projection and secondary smaller one(s) (Fig. 4).

As for the genital system, the nidamental glands are more uniform in *D. pleii* females, without a slender tip (Fig. 5B), whilst in *D. sanpaulensis* females, the nidamental glands have a more prominent, thin anterior tip (Fig. 5D). On the other hand, there were no significant differences between the male genital system of both species (Fig. 6). In the case of the male genital system, spermatophores are good sources of distinguishing characters, since they are highly complex and a key structure to differentiate species (Marian & Domaneschi, 2012; Marian, 2012).

The genus *Doryteuthis* is divided into three subgenera: (i) *Amerigo* (Brakoniecki, 1986) that comprises *D. gahi* (D'Orbigny, 1835), *D. ocula* (Cohen, 1976), *D. opalescens* (Berry, 1911), *D. pealeii* (Lesueur, 1821) and *D. surinamensis* (Voss, 1974), (ii) *Doryteuthis* s.s. (Naef, 1912), encompassing *D. pleii* (type species) and *D. roperi* (Cohen, 1976) and (iii) the undescribed subgenus of *D. sanpaulensis* (*sensu* Vecchione *et al.*, 2005; Jereb & Roper, 2010). *Amerigo* and *Doryteuthis* are separated by differences in the glacial structure and in the hectocotylized portion in the left ventral arm (Jereb & Roper, 2010; Vecchione & Young, 2010b).

Even though there are interesting characters listed in this study that can be used to further distinguish *D. pleii*

from *D. sanpaulensis*, there are also some characteristics that might bring them phylogenetically closer. This is the case of the size of hatchlings and eggs (Barón, 2003b); the slightly exclusive internal anatomy; and the morphology of the hectocotylus [Brakoniecki (1986) once clustered *D. pleii* and *D. sanpaulensis* together using this character]. The key to the subgenus *Doryteuthis*, as proposed by Vecchione *et al.* (2005), is based on the hectocotylized portion extending to the arm tip, and on the thickened gladius vane for *Doryteuthis*; a character absent in *Amerigo*; for *D. sanpaulensis*, the hectocotylized portion is similar to those in the *Doryteuthis* s.s. Therefore, the undescribed subgenus of *D. sanpaulensis* might be phylogenetically closer to *Doryteuthis* than to *Amerigo*. Certainly, more studies are required to clarify this relation among *Doryteuthis* species as well as a complete study to describe the subgenus of *D. sanpaulensis*, or to consider it definitively as *Doryteuthis*.

As the separation between *Loligo* and *Doryteuthis* has been essentially based on molecular results, another intention of this paper is furnishing additional, morphological subsidies for genus' definition. Possibly further studies on more species of these two taxa in the same level as described here can supply identification by simply inspection, dispensing laboratorial procedures or morphometric analyses. On the other hand, it is recognized that the relative uniformity of the internal anatomy of both species herein studied cannot resist to further investigation, such as more details of the digestive system (*e.g.*, odontophore and beak muscles), of the brain, etc. These details are still being developed, and are not the present scope.

## CONCLUSIONS

- 1) *Doryteuthis pleii* and *D. sanpaulensis* are really close taxa, and possibly belong to the same subgenus (*Doryteuthis* s.s.).
- 2) Despite their similarities, at least details and proportions of the mantle color and form, mantle-fin ratio, tentacular club, hectocotylus, gladius, and eye, can provide relative easy identification between these both sympatric species.
- 3) The internal anatomy, in the present level of details, is relatively uniform between both species; significant differences are found in beak and nidamental glands.

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