Zoosymposia 2: 265–295 (2009)
www.mapress.com/zoosymposia/

ISSN 1178-9905 (print edition)
ZOOSYMPOSIA
ISSN 1178-9913 (online edition)

Laonice (Annelida: Spionidae) from South and Central America

VASILY I. RADASHEVSKY[1,2,3] & PAULO DA CUNHA LANA[2]

[1] *A.V. Zhirmunsky Institute of Marine Biology of the Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, 690041, Russia. E-mail: radashevsky@mail.ru*
[2] *Centro de Estudos do Mar, Universidade Federal do Paraná, 83255-000, Pontal do Paraná, Paraná, Brasil.*
E-mail: lana@ufpr.br
[3] *Corresponding author*

Abstract

Laonice species from South and Central America are reviewed based on museum collections and new material collected in southern Brazil. An identification key is provided to 10 species including three previously described species, *L. antarcticae* Hartman, 1953, *L. weddellia* Hartman, 1978, *L. branchiata* Nonato, Bolívar & Lana, 1986, and three species represented by poor material, insufficient for final taxonomic diagnosis. Four new species, *L. petersenae* sp. nov., *L. aperata* sp. nov., *L. parvabranchiata* sp. nov., and *L. pinnulata* sp. nov. are described and illustrated. Earlier records of *L. cirrata* (M. Sars, 1851) from South America are not confirmed. The loss of neuropodial sabre chaetae and hooks until a certain size in terms of numbers of adult chaetigers is here used for the first time as a specific character with *Laonice* species.

Key words: taxonomy, morphology, Brazil, Chile, Costa Rica

Introduction

Laonice Malmgren, 1867 has never been defined in terms of phylogenetic relationships but appears to be an unambiguous monophyletic group of spionid polychaetes comprising 24 described species. Although well distinguished from other spionids, *Laonice* species are often difficult to identify when adults are encountered in benthic samples or larvae are caught in the plankton. Adult characters traditionally used for diagnostic purposes, such as shape of the prostomium and peristomium, length of the caruncle, arrangement of sabre chaetae, hooks, branchiae, lateral pouches, and number of pygidial cirri, vary a great deal among conspecific individuals of the same size (see Söderström 1920; Sikorski et al. 1988; Orrhage & Sundberg 1990; Sikorski 1999, 2003a–b) and, in addition, often change in the course of individual ontogenesis. This variability complicates the definition of individual species because there are few data on postlarval and juvenile morphology and on variability of adult morphology.

Very few *Laonice* species have been distinguished based on the presence of unique morphological features, such as appendages on branchiae or segments, while others are usually distinguished based on a combination of morphometric characteristics, such as caruncle length, arrangement of chaetae, branchiae, and lateral pouches. Variability in diagnostic characters resulted in the first described *Laonice* species, *L. cirrata* (M. Sars, 1851), originally collected in northern Norway, to be reported from all over the world in shallow to abyssal depths. A closer look at the morphology of specimens throughout the reported range of the species led Sikorski (2002) to suggest

Accepted by N. Maciolek: 20 Apr. 2009; published: 31 Aug. 2009

that *L. cirrata* was limited to the northern hemisphere and that more than one species was involved in previous reports.

Laonice cirrata has also been widely reported in South America. Hartmann-Schröder (1965) reported *L. cirrata* and also described two new subspecies, *L. cirrata praecirrata* and *L. cirrata postcirrata*, from Chile. The three taxa were distinguished on the basis of caruncle length and placement of the occipital antenna. Following an examination of Hartmann-Schröder's material, Foster (1971) was not able to separate these forms and placed these subspecies into synonymy with *L. cirrata*. This synonymy was followed by Carrasco (1974) in a study on Spionidae from Chile, by Blake (1983) in a review of South American spionids, and by Maciolek (2000) in a review of *Laonice* taxa. *Laonice cirrata* was also reported from the Straits of Magellan (Gambi & Mariani 1999; Bremec et al. 2000) and southern Brazil (Orensanz & Gianuca 1974; Bolívar & Lana 1987, 1988; Morgado & Amaral 1989; Paiva 1993). Two species, *L. antarcticae* Hartman, 1953 and *L. branchiata* Nonato, Bolívar & Lana, 1986 were described based on material from Brazil. In addition, *L. weddellia* Hartman, 1978 was reported from the Straits of Magellan (Blake 1983; Gambi & Mariani 1999; Bremec et al. 2000) and an unknown *Laonice* sp. was reported from off southern Chile (Blake 1983). The purpose of the present study is to review previous records of *Laonice* species from South and Central America and to document new material collected in Brazil by the authors.

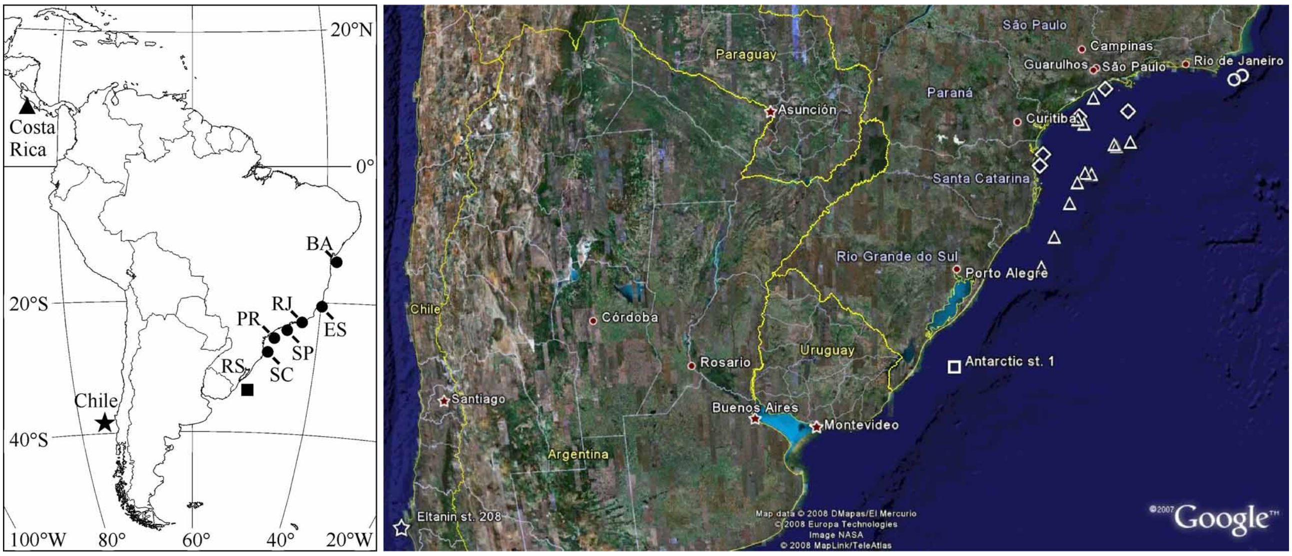

FIGURE 1. Sampling localities of *Laonice* material in Central and South America. Gulf of Nicoya in Costa Rica, the type locality of *Laonice pinnulata* sp. nov., is depicted by a filled triangle. The R/V *Eltanin* station off Chile, locality of *Laonice* sp. A, is depicted by a star. The R/V *Antarctic* station off Rio Grande do Sul, the type locality of *Laonice antarcticae*, is depicted by a square. Stations off the coast of Brazil sampled by the R/V *Almirante Saldanha* are depicted by rhombs; REVIZEE Score Sul-Bentos Programme, R/V *Prof. W. Besnard* are depicted by triangles; OCEANPROF are depicted by empty circles. BA—Bahia, ES—Espírito Santo, RJ—Rio de Janeiro, SP—São Paulo, PR—Paraná, SC—Santa Catarina, RS—Rio Grande do Sul.

Materials and methods

Field collections were made by the authors in Paranaguá Bay, Paraná, and in São Sebastião Channel, São Paulo, both in southern Brazil, from November 2000 through May 2004, and also in June 2007 (Fig. 1). Sediment samples were collected intertidally and in shallow water using grabs and by diving using SCUBA equipment. Samples were sieved in the field and polychaetes were removed from the residue under a stereomicroscope in the laboratory at the Centro de Estudos do Mar, Universidade Federal do Paraná, Pontal do Sul, Paraná, and Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, São Paulo. Adult worms were relaxed in isotonic magnesium chloride and examined alive with light microscopes.

Some material was collected earlier in the state of São Paulo, Brazil, by the *BIOTA/FAPESP* research program, *The Virtual Institute of Biodiversity* (http://www.biota.org.br); on the outer continental shelf and slope (60–808 m depth) of SE Brazil off the states of Rio de Janeiro south to Rio Grande do Sul by the *REVIZEE Score Sul - Bentos Programme* (Amaral et al. 2003; Amaral & Rossi-Wongtschowski 2004); and on the slope off the state of Rio de Janeiro by the *Campos Basin Deep Sea Environmental Project* (OCEANPROF) coordinated by CENPES/PETROBRAS. *Laonice* material deposited at the Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (UFRJ), Swedish Museum of Natural History (Naturhistoriska Riksmuseet), Stockholm, Sweden (SMNH), and United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM) was also examined.

Data on the length of the caruncle, arrangement of branchiae and excretory nephridia, number of pygidial cirri, and the first occurrence of lateral pouches, sabre chaetae, and hooded hooks were collected for statistical analysis. The first occurrence of paired structures, such as lateral pouches, sabre chaetae, and hooks, as well as the last branchiae and nephridia, was not always on the same chaetiger on both sides. Therefore, the anterior positions of pouches, sabre chaetae, and hooks were recorded as the first chaetigers bearing these structures on at least one side. The posterior positions of branchiae and nephridia were recorded as the last chaetigers bearing these structures on at least one side. Statements such as “lateral interneuropodial pouches starting from chaetiger 3” mean that the first pouch (or pair of pouches) is present between neuropodia of chaetigers 3 and 4.

Photos were taken on a Nomarski interference contrast microscope (Zeiss Axioskop 2) equipped with a digital camera (Nikon Coolpix 4500). Drawings were made using a camera lucida. After examination, worms were fixed in a 10% formalin solution, rinsed in fresh water, and transferred to 70% ethanol.

The examined material was deposited at the Centro de Estudos do Mar, Universidade Federal do Paraná, Brazil (MCEM); Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP); Museu de Zoologia da Universidade Estadual de Campinas, Campinas, São Paulo, Brazil (ZUEC POL); Museu Nacional, Rio de Janeiro, Brazil (MNRJ); Senckenberg Museum, Frankfurt-am-Main, Germany (SMF); and the Institute of Marine Biology, Vladivostok, Russia (IMBV). Information about samples is given below along with the description of species. The numbers of specimens in a sample is given in parentheses after the museum abbreviation and registration number.

Results

Spionidae Grube, 1850

Laonice Malmgren, 1867

Type species: *Nerine cirrata* M. Sars, 1851. By Malmgren 1867: 200.

Laonice Malmgren, 1867: 200. Söderström 1920: 220; Foster 1971: 69; Blake & Kudenov 1978: 204–205; Maciolek 2000: 533–536; Sikorski 2003a: 317.

Spionides Webster & Benedict, 1887: 735. *Fide* Söderström 1920: 227.

Aricideopsis Johnson, 1901: 413. *Fide* Hartman 1959a: 377.

Diagnosis. Up to 140 mm long and 5 mm wide for 160 chaetigers. Prostomium anteriorly rounded (frontolateral parts extended and resembling short horns in *L. japonica* Moore, 1907 and *L. parvabranchiata* sp. nov., see below), well separated to entirely fused with anterior part of peristomium. Peristomium small, forming low dorsolateral wings in some species. Two pairs of red eyes usually present. Occipital antenna usually present (absent in *L. brevicristata* Pillai, 1961 and *L. dayianum* Sikorski, 1997). Nuchal organs as U-shaped ciliary bands on sides of caruncle extending over a series of anterior segments. Segment 1 with capillaries and postchaetal lamellae in both rami. Hooks only in neuropodia (except *L. sarsi* having hooks in both rami), accompanied by alternating capillaries and inferior sabre chaetae throughout. Hooks generally tridentate (bi- and multidentate hooks occasionally present), with two upper teeth situated side by side above main fang, with only outer hood and slightly curved shaft without constriction. Branchiae from segment 2 on certain number of anterior segments. Dorsal crests present on postbranchiate segments in some species. Lateral pouches present between successive neuropodia (except *L. asaccata* Sigvaldadóttir & Desbruyères, 2003 and *Laonice aperata* sp. nov., see below). Pygidium with one pair of ventral cirri and variable number of dorsal cirri.

Laonice species from South and Central America:

1. *Laonice antarcticae* Hartman, 1953
2. *Laonice weddellia* Hartman, 1978
3. *Laonice branchiata* Nonato, Bolívar & Lana, 1986
4. *Laonice petersenae* sp. nov.
5. *Laonice aperata* sp. nov.
6. *Laonice parvabranchiata* sp. nov.
7. *Laonice pinnulata* sp. nov.
8. *Laonice* sp. A
9. *Laonice* sp. B
10. *Laonice* sp. C

Key to *Laonice* species from South and Central America*

1 Branchiae with appendages 2
– Branchiae smooth, without appendages.. 4
2(1) Branchiae with up to seven pinnules on outer basal part. Prostomium anteriorly fused with peristomium....... .... *Laonice pinnulata* sp. nov.
– Branchiae with single auricular lobes on frontal basal part. Caruncle to end of chaetiger 12 3
3(1) Prostomium anteriorly separated from peristomium. Lateral interneuropodial pouches from chaetiger 4 (probably from more posterior chaetigers in early juveniles). Sabre chaetae in neuropodia lost until chaetiger 38. Hooks in neuropodia lost until chaetiger 46. Branchiae until chaetiger 46. Dorsal crests in large individuals on 10–13 postbranchiate chaetigers, from chaetigers 45–48 to chaetigers 56–60. Pygidium with up to 12 cirri .... *Laonice branchiata*
– Prostomium anteriorly fused with peristomium. Lateral pouches between successive neuropodia and between noto- and neuropodia (?)invariably from chaetiger 3. Sabre chaetae in neuropodia lost until chaetiger 35. Hooks in neuropodia lost until chaetiger 42. Branchiae until chaetiger 42. Dorsal crests on about 8 postbranchiate chaetigers ....*Laonice* sp. C
4(1) Lateral pouches absent between neuropodia. Prostomium anteriorly wide, fused with peristomium .... *Laonice aperata* sp. nov.
– Lateral pouches present between neuropodia 5

5(4) Lateral pouches (?)invariably** from chaetiger 1. Caruncle over at least 50 chaetigers. Branchiae until chaetiger 42. Dorsal crests unknown.. *Laonice* sp. A

– Lateral pouches from more posterior chaetigers. Caruncle not exceeding chaetiger 30. Dorsal crests absent 6

6(5) Lateral pouches (?)invariably from chaetiger 4. Caruncle to end of chaetiger 12. Branchiae until chaetiger 31, very small on first 5–6 chaetigers and on succeeding chaetigers not exceeding notopodial lamellae. Sabre chaetae in neuropodia lost until chaetiger 24. Hooks in neuropodia lost until chaetiger 40 ....*Laonice antarcticae*

– Lateral pouches from more posterior chaetigers. Caruncle extending beyond chaetiger 12 (shorter in *Laonice parvabranchiata* sp. nov.). Branchiae longer than postchaetal lamellae at least on middle branchiate chaetigers 7

7(6) Prostomium anteriorly fused with peristomium. Caruncle to middle of chaetiger 26. Branchiae until chaetiger 35. Sabre chaetae in neuropodia lost until chaetiger 30. Hooks in neuropodia lost until chaetiger 36. Lateral pouches from chaetigers 3–17. Dorsal crests absent. Pygidium with up to 10 cirri .... *Laonice petersenae* sp. nov.

– Prostomium anteriorly separated from peristomium 8

8(7) Capillaries in noto- and neuropodia of about 15 anterior chaetigers numerous, arranged in at least 5 rows, with fascicles appearing dense and bushy. Caruncle to end of chaetiger 20. Branchiae until chaetiger 50. Sabre chaetae in neuropodia lost until chaetiger 13. Hooks in neuropodia lost until chaetiger 25. Lateral pouches from chaetigers 6–11. Pygidium with up to 8 cirri .... *Laonice weddellia*

– Capillaries in anterior parapodia few, arranged in three groups in each podium 9

9(8) Prostomium anteriorly entire, wide, with short frontolateral horns. One pair of large red eyes present. Caruncle to end of chaetiger 11. Branchiae until chaetiger 35. Sabre chaetae in neuropodia lost until chaetiger 28. Hooks in neuropodia lost beyond chaetiger 40. Lateral pouches from chaetigers 14–15 ....*Laonice parvabranchiata* sp. nov.

– Prostomium bell-shaped, anteriorly wide, with frontal margin concave to incised. One pair of small red eyes present or eyes absent. Caruncle to end of chaetiger 15. Branchiae until chaetiger 21. Sabre chaetae in neuropodia lost until chaetiger 20. Hooks in neuropodia lost beyond chaetiger 32. Lateral pouches from chaetigers 3–9...*Laonice* sp. B

* The loss of neuropodial sabre chaetae and hooks until a certain size in terms of numbers of adult chaetigers is here used for the first time as a specific character with *Laonice* species. Both types of chaetae first appear in late larvae from about chaetigers 9–10, probably in all *Laonice* species. As growth proceeds, these chaetae are lost from anterior neuropodia and their anteriormost position is shifted posteriorly until the final adult species-specific range is attained. The most posterior chaetigers (usually in the largest individual) for the start of sabre chaetae or hooks are specific characteristics and are used in the above identification key. Use of these characteristics depends on whether the largest individuals of the species were studied, thus, an ambiguity always remains. The situation is also complicated in that adults of different species may have different growth rates and may ultimately reach different maximal sizes; thus, the comparisons between size-related characteristics are not always adequate. Fortunately, each species demonstrates a different range of size-related characteristics that can be used to differentiate them. The same observations also refer to the arrangement of lateral interneuropodial pouches and numbers of branchiae and pygidial cirri. The anterior position of lateral pouches is fixed and not size-related in some species, while in others it is variable, when the pouches are reduced on anterior segments and their anterior position is shifted posteriorly with growth. The numbers of both branchiae and pygidial cirri increase with age until a certain species-specific limit is attained. This means that a wide range of individuals, including large mature worms, should be examined for proper identification. Identification of small worms is usually ambiguous, unless they demonstrate unique morphological features.

** Uncertain characters are preceded by question marks in parentheses. The uncertainty arises from poor knowledge of variability of species.

Laonice antarcticae Hartman, 1953

Laonice cirrata antarcticae Hartman, 1953: 40–41.

Laonice antarcticae: Hartman 1965: 147–148; Blake 1983: 219–221, fig. 8; Maciolek 2000: 538.

Material. Brazil, off Rio Grande do Sul, Swedish Antarctic Expedition 1901–1903, R/V *Antarctic*, Sta. 1, 33°0′S, 51°10′W, 80 m, dark gray mud, 12 Dec 1901, SMNH 613 (2 syntypes).

Adult morphology. Up to 13 mm long and 2 mm wide for 60 chaetigers. Prostomium anteriorly entire, with frontolateral horns variously developed, well separated from peristomium. Caruncle extending to end of chaetiger 12. Sabre chaetae in neuropodia from chaetigers 23–24. Hooks in neuropodia from chaetigers 35–40. Branchiae up to 30 pairs, first 5–6 pairs very small and largely concealed by postchaetal lamellae, full-sized from about chaetiger 7 but not exceeding notopodial lamellae in length. Dorsal crests absent. Lateral pouches from chaetiger 4. Pygidium unknown.

Remarks. *Laonice antarcticae* was originally described by Hartman (1953) based on material collected by the Swedish Antarctic Expedition 1901–1903 onboard the research vessel *Antarctic*. Two individuals were collected at the first benthic station taken off the coast of Rio Grande do Sul, southern Brazil (Fig. 1; incorrectly reported by Hartman 1953 as off the coast of Uruguay) and named after the vessel, although no more specimens were found during the Expedition. The species name is misleading because it implies an Antarctic distribution, although the species was indeed later reported from Antarctica (Hartman 1978; Knox & Cameron 1998; Cantone et al. 2000; Cantone & Di Pietro 2001).

Maciolek (2000) reported *L. antarcticae* as widely distributed in the Western Atlantic, from off eastern North America (40°N) south to Surinam, Brazil, Argentina, and Antarctic and subantarctic seas, occurring at 27–3697 m. Such a wide distribution appears suspicious because the morphology of the species is poorly known and neither ontogenetic nor individual variability has been described. Our examination of specimens from Argentina (USNM 67531–67533), South Georgia (USNM 69391) and South Sandwich Islands (USNM 69392), all referred by Blake (1983) to *L. antarcticae*, revealed significant differences between this material and the types of the species in the length of caruncle, branchiae, and arrangement of chaetae in neuropodia. Reports of a wide distribution of the species also seem suspicious because no individuals entirely matching the diagnosis of *L. antarcticae* were identified in numerous benthic samples collected by the REVIZEE and CENPES/PETROBRAS Programs on the continental shelf and slope of Brazil, off the states of Rio de Janeiro south to Rio Grande do Sul (Radashevsky & Paiva unpublished). This may be due either to an incorrect diagnosis of the species based on poor material, or to the presence of more than one species in deep water along the Americas. It is plausible that the diagnostic characters of *L. antarcticae* adopted here such as length of the caruncle, arrangement of branchiae, sabre chaetae, hooks, and lateral pouches may be more variable than now believed and the species may really be widely distributed in deep water along the coast of Americas. In this case, at least some individuals referred here to *Laonice* sp. B (see below) might really belong to *L. antarcticae*. Additional material, preferably from the type locality, is needed to understand the morphological variability of *L. antarcticae* and unambiguously separate this species from closely related species.

Distribution. Western Atlantic; Antarctic and subantarctic seas.

Laonice weddellia Hartman, 1978

Laonice weddellia Hartman, 1978: 161–163, fig. 16. Blake 1983: 221–222, fig. 9; Hartmann-Schröder & Rosenfeldt 1988: 57; Gambi et al. 1997: 202; Gambi & Mariani 1999: 237; Bremec et al. 2000: 194; Hilbig 2001: 541.

Material. Antarctica, Weddell Sea, R/V *Glacier*, Sta. 8, 77°36.5′S, 42°30′W, 585 m, 2 Mar 1969, USNM 46700 (holotype), 46701 (10 paratypes). Brazil: off Rio de Janeiro, northern part of the Campos Basin, OCEANPROF Sta. 49B, 22°04.55′S, 39°54.19′W, 722 m, 30 Jun 2003, MNRJ (1). Off São Paulo, REVIZEE Sta. 6658, 25º11.89′S, 47º08.09′W, 157 m, sand, 16 Dec 1997, ZUEC POL 701 (5). Off Santa Catarina, REVIZEE Sta. 6779, 26º49.90′S, 46º47.79′W, 200 m, silt+clay, 13 Mar 1998, ZUEC POL 702 (1); REVIZEE Sta. 6784, 27°9.51′S, 47°4.85′W, 195 m, 14 Mar 1998, ZUEC POL 703 (1); REVIZEE Sta. 6792, 27º48.20′S, 47º18.17′W, 228 m, 16 Mar 1998, ZUEC POL 704 (1). Off Rio Grande do Sul, REVIZEE Sta. 6821, 29º49.49′S, 48º12.76′W, 232 m, silty sand, 24 Mar 1999, ZUEC POL 705 (2).

Adult morphology. Up to 34 mm long and 2.5 mm wide for 130 chaetigers. Prostomium rounded anteriorly, with a shallow notch on frontal margin in some individuals. Peristomium with low to moderately developed lateral wings. Caruncle extending to chaetiger 20. Capillaries in noto- and neuropodia of about 15 anterior chaetigers, up to 100 in each ramus, arranged in 4–5 rows per fascicle, with fascicles appearing dense and bushy. Sabre chaetae in neuropodia from chaetigers 11–13. Hooks in neuropodia from chaetigers 16–25. Branchiae up to 50 pairs. Dorsal crests absent. Lateral pouches from chaetigers 6–11. Pygidium with up to eight cirri.

Habitat. *Laonice weddellia* was identified in samples collected in Brazil on silty sand bottom at 195–722 m depth. Blake (1983) reported the species from depth of 44–3111 m.

Remarks. *Laonice weddellia* was originally described by Hartman (1978) from the Weddell Sea and redescribed by Blake (1983) based on extensive material from off southern South America and Antarctic seas. Blake (1983) reported that the species has an elongated narrow prostomium, three pairs of eyes, nuchal organs extending over 20 chaetigers, and lateral pouches starting from chaetigers 8–11.

Specimens from Brazil examined in the present study appear similar to the type material but differ slightly from Blake's (1983) description of *L. weddellia* in having the prostomium anteriorly straight to slightly wide, lateral pouches beginning from more anterior chaetigers in some individuals (between chaetigers 6–11 instead of 8–11), and in the dentition of the hooded hooks. Blake (1983: 222) reported that the bidentate and tridentate hooks have a "main fang surmounted by 1–2 apical teeth; when present, second apical tooth located in tandem with first." We found that one of the small upper teeth is often broken, giving the hook a bidentate appearance, and suggesting that hooks are typically tridentate, with two upper teeth situated side by side above the main fang, in the same manner as in most of other *Laonice* species.

Records from northern Brazil of this Antarctic-subantarctic species appear unusual and should be verified with additional material. At this point, we interpret differences observed between the Brazilian specimens and the type material as variability of the same species rather than the presence of two different species. Numerous (up to 100) short yellowish capillaries arranged in 4–5 rows in anterior parapodia are a characteristic feature of this species.

Distribution. Antarctica and adjacent seas; Strait of Magellan; Falkland Islands; South Orkney Islands; South Shetland Islands; southern Brazil.

Laonice branchiata Nonato, Bolívar & Lana, 1986

Figures 2 & 3

Laonice branchiata Nonato, Bolívar & Lana, 1986: 21–25, figs. 1–7.
Laonice cirrata: Bolívar & Lana 1987 (*Part*.): 118. Not *L. cirrata* M. Sars, 1851.

Material. Brazil: Rio de Janeiro: Sta. TBG2 C501, E.P. Omena, MZUSP 115 (3). São Paulo: BIOTA, Sta. 4, 13 Feb 2001, ZUEC POL 706 (4); Sta. 9, 14 Feb 2001, ZUEC POL 707 (2). Ilha São Sebastião, Pedras do Sino, 23°44.82′S, 45°20.9′W, 5 m, sandy silt, V.I. Radashevsky, 15 Apr 2004, MZUSP 113 (1). Off São Paulo: R/V *Almirante Saldanha*, Sta. 6140, 26°06′S, 46°10′W, 33 m, fine sand, P.C. Lana, 21 Aug 1982, MCEM 54 (2 paratypes). Paraná: Paranaguá Bay: Paranaguá Harbour, 15 m, silty sand, P.C. Lana, 7 Nov 1981, MCEM 52 (holotype). Mouth of Maciel River, 25°33.5′S, 48°25.5′W, 10 m, silty sand, V.I. Radashevsky, 11 Aug 1998, IMBV 17936 (1). Galheta, off Ilha do Mel, 25°32.5′S, 48°20.5′W, 8 m, silty sand, O.A. Negrello-Filho, 15 Mar 2001, MZUSP 116 (2), 7 Feb 2003, SMF 14005 (1); 25°28′S, 48°23′W, 5 m, muddy sand, V.I. Radashevsky, 5 Sep 2001, MZUSP 111 (50); 24 Oct 2001, MZUSP 114 (9); 24 Apr 2002, SMF 14012 (11). Off Santa Catarina: R/V *Almirante Saldanha*, Sta. 6077, 26°44′S, 48°25′8″W, 39 m, silty sand, P.C. Lana, 2 Aug 1982, MCEM 40 (3), MCEM 53 (2 paratypes), USNM 100451 (paratype).

Adult morphology. Up to 90 mm long and 3.0 mm wide for 160 chaetigers. Pigmentation absent in life; light grayish-violet pigment present in noto- and neuropodial postchaetal lamellae from chaetigers 7–10 to 20–40 and occasionally on ventral side of these chaetigers in formaldehyde-preserved specimens.

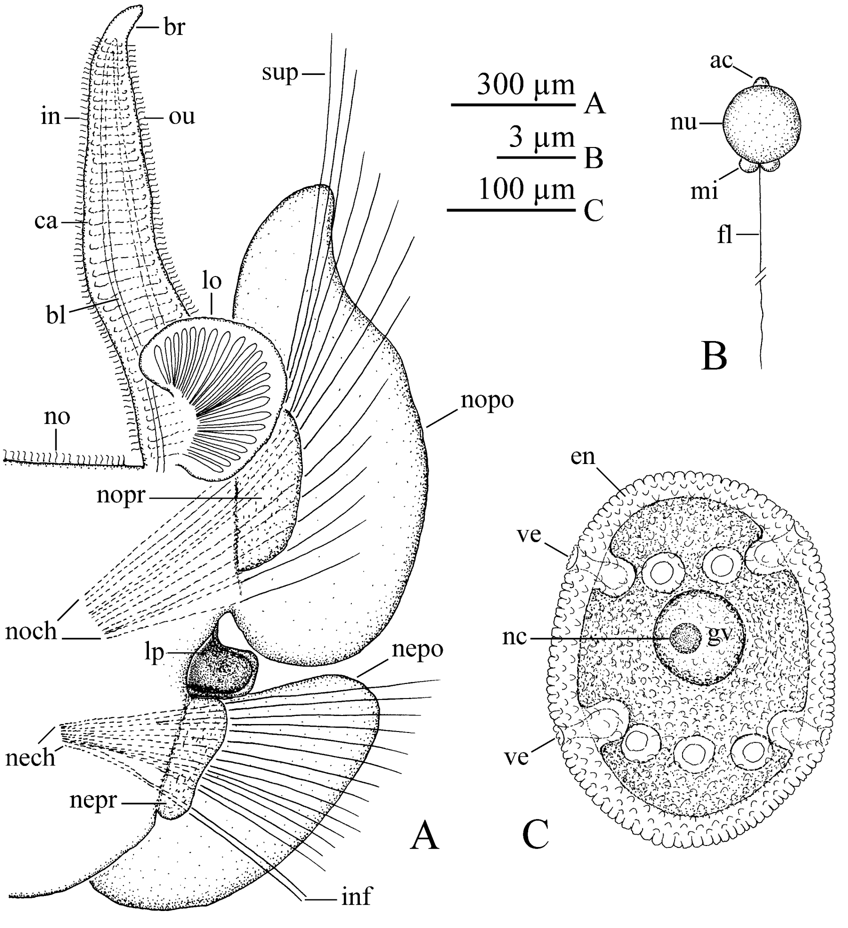

FIGURE 2. *Laonice branchiata* adult and gamete morphology. A, chaetiger 9, left half in frontal view, showing auricular lobe (*lo*) with blood capillaries on frontal basal part of branchia (*br*), notochaetae (*noch*), neurochaetae (*nech*), a tuft of long dorsal superior capillaries (sup), an inferior tuft of neurochaetae (*inf*), small notopodial (*nopr*) and neuropodial (*nepr*) prechaetal lamellae, larger notopodial (*nopo*) and neuropodial (*nepo*) postchaetal lamellae, lateral interneuropodial pouch (*lp*), nototroch (*no*), inner (*in*) and outer (*ou*) branchial ciliation, branchial blood loop (*bl*) and numerous circular capillaries (*ca*). B, spermatozoon, showing small subspherical acrosome (*ac*), spherical nucleus (*nu*), spherical mitochondria (*mi*), and flagellum (*fl*). C, intraovarian oocyte artificially released into sea water, showing large germinal vesicle (g*v*) with nucleolus (*nc*), thick envelope (*en*) with honeycombed external surface and large vesicles (*ve*) arranged in two parallel circles. A–C, MZUSP 111.

Prostomium anteriorly entire, wide and rounded, well separated from peristomium. Peristomium with moderate dorsolateral wings on lateral sides of prostomium. Occipital antenna distinct, finger-like on caruncle at level of chaetiger 1. Two pairs of red eyes usually present in small and middle-sized individuals, comprising one pair of small lateral eyes and one pair of very large median eyes situated posteriorly; only one pair of large median eyes usually prominent in large individuals. Caruncle low, extending to end of chaetiger 12, shorter in small individuals (Fig. 3A); large individuals with shallow median furrow all along length of caruncle. Nuchal organs U-shaped ciliary bands on either side of caruncle. Palps as long as 15–35 chaetigers, with deep frontal longitudinal groove lined with fine cilia and bordered by undulating edges.

Chaetiger 1 with well-developed capillary chaetae and postchaetal lamellae in both rami. Notopodia with only capillaries. Low prechaetal lamellae in noto- and neuropodia on anterior chaetigers. Postchaetal lamellae large, flat, ear-shaped on branchiate chaetigers (Fig. 2A), greatly reduced on posterior abranchiate chaetigers. Low dorsal crests joining notopodial postchaetal lamellae in large individuals on 10–13 postbranchiate chaetigers, from chaetigers 45–48 to chaetigers 56–60. Lateral interneuropodial pouches from chaetiger 10 in smallest 40-chaetiger individual, from chaetiger 4 in larger individuals (Fig. 3A), arranged through end of body.

Sabre chaetae in neuropodia from chaetigers 9–38, from more anterior chaetigers in small individuals (Fig. 3B), 1–2 in a tuft, 3–4 times longer than hooks, with weak granulations along shaft.

Hooks in neuropodia from chaetigers 14–46, from more anterior chaetigers in small individuals (Fig. 3B), up to 15 in a series, accompanied by up to five alternating capillaries and 1–2 inferior sabre chaetae throughout. Hooks tridentate, with two small upper teeth situated side by side above main fang. Alternating capillaries thin, with narrow limbation, 2–3 times longer than hooks.

Branchiae from chaetiger 2 to chaetiger 46, fewer in small individuals (Fig. 3A). Branchiae small anteriorly, gradually reaching full size on chaetigers 10–15, and decreasing again on posterior chaetigers, situated on basal part of notopodia, free from notopodial postchaetal lamellae, slightly flattened, with surfaces oriented perpendicular to body axis. Smallest, 40-chaetiger individual with branchiae very short on chaetiger 2, much longer from chaetiger 3. Fine longitudinal ciliation present along inner and outer edges of branchiae. Single auricular lobes with capillary blood vessels present on frontal surface of basal part of branchiae; lobes small on anterior branchiae, gradually increasing in size and fully developed from chaetigers 5–10. Afferent and efferent blood vessels of branchiae forming a loop and interconnected by numerous circular capillaries giving branchiae annulate appearance (Fig. 2A).

Nototrochs and intersegmental ciliation present in immature individuals, females, and males. Nototrochs from chaetiger 2, each composed of one row of small cells with short cilia. Nototrochs on anterior chaetigers interrupted by caruncle, on branchiate post-caruncle chaetigers extending from tip of one branchia to tip of opposite member; on posterior abranchiate chaetigers nototrochs extending onto inner edge of notopodial postchaetal lamellae; present on crest-bearing chaetigers on upper edges of crests. Short bands of intersegmental longitudinal cilia present on dorsolateral edges of chaetigers between notopodia, beginning from between chaetigers 2 and 3. Single transverse rows of cilia on anterior edge of branchiate chaetigers beginning from chaetiger 4.

Pygidium with one pair of ventral cirri and up to five pairs of dorsal cirri arranged in two vertical rows on sides of terminal anus. Dorsal cirri fewer in small individuals, thinner, and 3–4 times longer than ventral cirri.

Main dorsal blood vessel bifurcated at level of median eyes, giving rise to circumesophageal vessels. Palpal blood vessels arising from circumesophageal vessels, close to bifurcation point of main dorsal vessel. Main dorsal vessel giving rise to segmental vessels in chaetiger 2 to chaetigers 6–10 and transforming into intestinal sinus after chaetiger 10; no segmental vessels observed in chaetiger 1. Circumesophageal vessels joined ventrally in chaetiger 2 to form main ventral blood vessel extending length of body. Blood red, homogenous, without elements. Blood flow provided by sinuous constrictions of intestine.

Excretory metanephridia large, dark green, from chaetiger 4 to chaetigers 12–41, occupying all anterior sterile chaetigers (apart from chaetigers 1–3), fewer in small individuals (Fig. 3F).

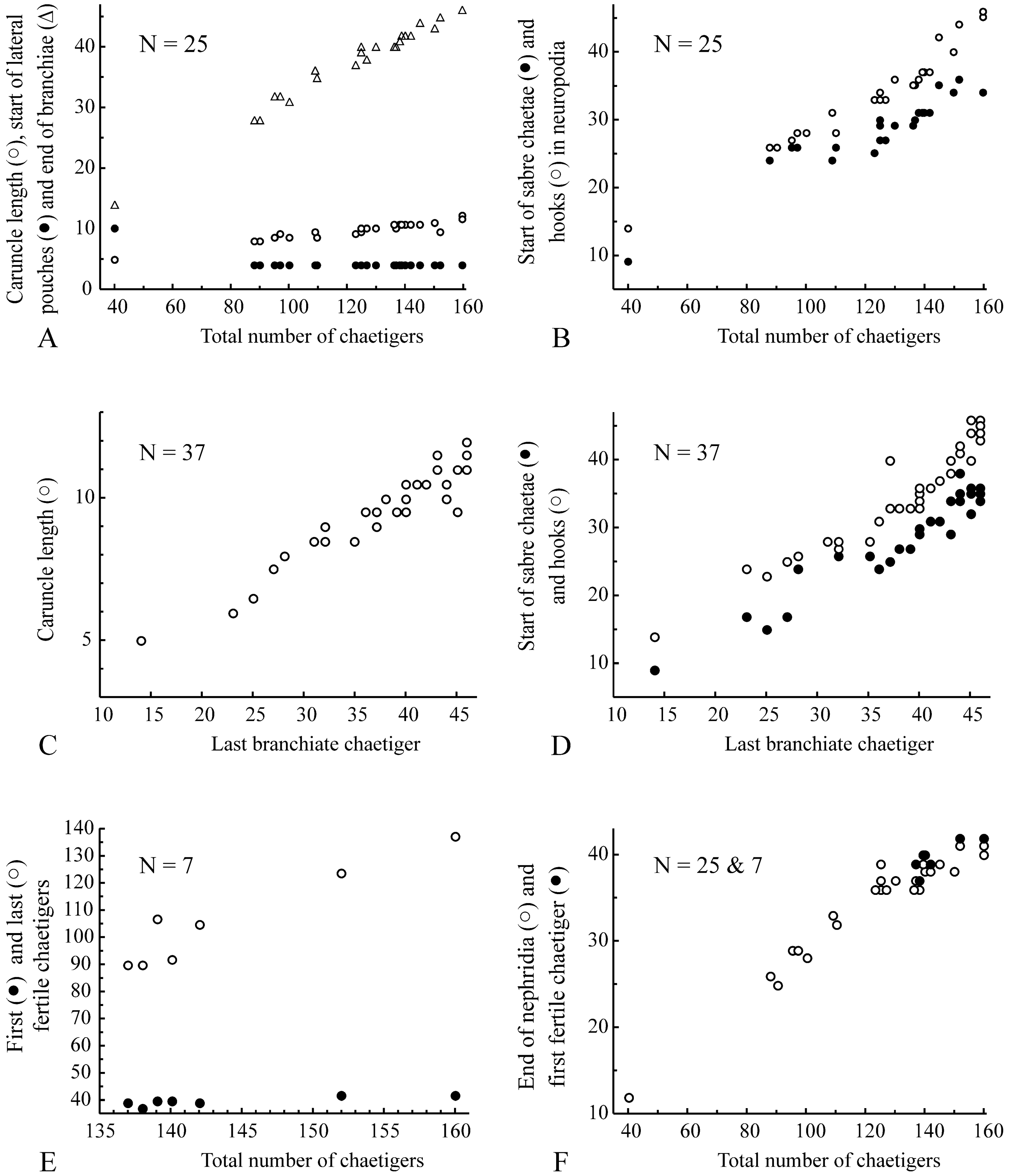

FIGURE 3. *Laonice branchiata* adult morphology. A, relationships between caruncle length (in chaetiger numbers) and total number of chaetigers in worm (empty circles), anterior position of lateral interneuropodial pouches (referring to number of the chaetiger in front of the first pouch) and total number of chaetigers in worm (filled circles), and distribution of branchiae (referring to number of the last branchiate chaetiger) and total number of chaetigers in worm (empty triangles). B, relationships between anterior position of sabre chaetae (referring to number of the first sabre-bearing chaetiger) and total number of chaetigers in worm (filled circles), and anterior position of hooks (referring to number of the first hook-bearing chaetiger) and total number of chaetigers in worm (empty circles). C, relationships between caruncle length (in chaetiger numbers) and distribution of branchiae (referring to number of the last branchiate chaetiger) in worm (empty circles). D, relationships between anterior position of sabre chaetae and distribution of branchiae in worm (filled circles), and anterior position of hooks and distribution of branchiae in worm (empty circles). E, relationships between anterior position of fertile segments (referring to number of the first chaetiger with gametes) and total number of chaetigers in worm (filled circles), and posterior position of fertile segments (referring to number of the last chaetiger with gametes) and total number of chaetigers in worm (empty circles). F, relationships between distribution of excretory metanephridia (referring to number of the last chaetiger bearing nephridiopores) and total number of chaetigers in worm (empty circles), and anterior position of fertile segments (referring to number of the first chaetiger with gametes) and total number of chaetigers in worm (filled circles).

Habitat. *Laonice branchiata* inhabits temporary burrows in sandy to silty sand bottoms at 5–39 m depth. Population density of the species reaches 100 individuals/m^2. In Paranaguá Bay, it co-occurs with *L. petersenae* sp. nov. (see below).

Reproduction. *Laonice branchiata* is gonochoristic. Of ten mature individuals examined, six were females and four were males. No external morphological differences were found between females and males. Both sexes reached a maximal size of 160 chaetigers. Gametes developed from chaetigers 37–42 to 90–137.

Spermatids were joined in tetrads. Spermatozoa were short-headed, with a small subspherical acrosome, a spherical nucleus 3.5±0.5 mµ in diameter, four spherical mitochondria, and a flagellum 71±2 µm long (Fig. 2B).

The largest 160-chaetiger female had 50–80 oocytes in each of 96 fertile segments (chaetigers 42–137, comprising 60% of total number of chaetigers), and about 7000 oocytes in total. The oocytes were in paired clusters, and the ovaries situated laterally in fertile segments. Each ovary was covered by a thin envelope, thus oogenesis was synchronous and probably entirely intraovarian, with oocytes entering the coelomic cavity shortly before spawning. Coelomic oocytes were flattened, of irregular shape, with a soft envelope. When artificially released from the body, oocytes gradually rounded up and acquired an oval to egg-like shape, measuring 190–200 × 250–270 µm (Fig. 2C). Individual oocytes had a germinal vesicle about 75 µm in diameter, a nucleolus about 25 µm in diameter, and an envelope about 20 µm thick with a honeycombed external surface and two rows of large encircling vesicles. Vesicles appeared as invaginations of the envelope into the ooplasm, with the embedded part about 34 µm in diameter and an external opening about 18 µm in diameter. The two parallel rows of encircling vesicles were oriented perpendicular to the long axis of the oocyte. About eight vesicles were present in one encircling row and ten vesicles were present in the other row. Gravid females and large individuals without gametes were found in September 2001; we assume that spawning occurred at that time.

Remarks. *Laonice branchiata* was originally described by Nonato et al. (1986) based on material collected from the SE coast of Brazil, off Rio de Janeiro south to Paraná. Hooded hooks were reported as bidentate in the original description of the species. The type material of *L. branchiata* was reexamined and the hooks were found to be tridentate.

Material reported by Bolívar & Lana (1987) as *L. cirrata* and deposited at MCEM was reexamined. One of the samples, MCEM 40, was reidentified as *L. branchiata* while the others were reidentified as *L. petersenae* sp. nov. and *L. aperata* sp. nov. (see below).

Laonice branchiata has been considered as unique among related species in having vascularized auricular lobes on the frontal surface of the basal part of the branchiae. However, similar lobes were found in specimens which may be another *Laonice* species (see *Laonice* sp. C below). The lobes probably serve to increase the respiratory surface of branchiae.

Distribution. Southern Brazil from Rio de Janeiro south to Santa Catarina.

Laonice petersenae sp. nov.

Figures 4–6

Laonice cirrata: Bolívar & Lana 1987 (*Part.*): 118. *Not L. cirrata* M. Sars, 1851.

Material. Type material. Brazil: São Paulo: São Sebastião, Praia do Saco Grande, 23°49.75′S, 45°25.53′W, 5 m, silty sand, V.I. Radashevsky, 10 Mar 2004, MZUSP 126 (**holotype**), MZUSP 118 (17 paratypes), 11 Apr 2004, MZUSP 121 (10 paratypes). Ilha São Sebastião, Pedras do Sino, 23°44.82′S, 45°20.9′W, 2 m, silty sand, V.I. Radashevsky, 24 Mar 2004, MZUSP 123 (paratype). Paraná: Paranaguá Bay: Galheta, off Ilha do Mel, 25°32.5′S, 48°20.5′W, 15 m, silty sand, F. Pleijel, 14 Aug 1998, IMBV (2 paratypes); 8 m, muddy sand, O.A. Negrello-Filho, 8 Oct 2002, MZUSP 124 (2 paratypes), 6 May 2003, MZUSP 117 (7 paratypes), SMF 13959 (paratype); 5–8 m, silty sand, V.I. Radashevsky, 13 Mar 2003, MZUSP 120 (5 paratypes), 30 Oct 2003, MZUSP 122 (4 paratypes), 19 Jun 2007, IMBV 18851 (paratype). Off Ilha Rasa da Cotinga, 25°31.8′S, 48°24′W, 3 m, silty sand, V.I. Radashevsky, 14 Mar 2001, MZUSP 125 (paratype). Mouth of Maciel River, 25°33.5′S, 48°25.5′W, 15 m, silty sand, V.I. Radashevsky, 17 Jul 2002, SMF 13960 (8 paratypes), 19 Jun 2007, IMBV 18850 (2 paratypes).

Representative material. Brazil: Bahia, coll. P.C. Paiva: Recife de Itacolomis, 16°53.2′S, 39°05.1′W, 5–10 m, 16 Feb 2000, UFRJ 179 (2); Recife de Timbebas, 17°30.4′S, 39°00.8′W, 15 m, 26 Feb 2000, UFRJ 180 (1); Recife da Corôa Vermelha, 17°57.3′S, 39°13.1′W, 3–6 m, 13 Feb 2000, UFRJ 181 (2); Recife de Viçosa, 17°59.8′S, 39°16.4′W, 8 m, 11 Feb 2000, UFRJ 182 (1). Off São Paulo: R/V *Almirante Saldanha*, Sta. 6125, 24°26′6″S, 46°36′8″W, 32 m, silty sand, 10 Aug 1982, MCEM 48 (2). Paraná: Seco do Limoeiro, Baixio Abrigado, 25°33.2′S, 48°18.6′W, 0.5 m, O.A. Negrello-Filho, 26 Sep 2002, MZUSP 119 (3).

Adult morphology. Up to 52 mm long and 2 mm wide for 120 chaetigers. Holotype complete male 42 mm long and 1.4 mm wide for 111 chaetigers. Pigmentation absent. Prostomium anteriorly rounded, entire, in small individuals weakly separated from peristomium, in large individuals anteriorly fused with peristomium, with anterior part of head appearing as a complete semicircle (Fig. 5A). Peristomium with moderate dorsolateral wings on sides of prostomium. Two pairs of red eyes usually present, comprising one pair of small anterior (lateral) eyes, and one pair of very large posterior (median) eyes. Anterior (lateral) eyes deeply embedded into prostomium and difficult to observe in large individuals, usually entirely obscured or reduced in individuals with more than 100 chaetigers. Distinct finger-like occipital antenna arising posterior to median eyes. Caruncle low, extending to middle of chaetiger 26 (to middle of chaetiger 25 in holotype), shorter in small individuals (Fig. 6A); shallow median furrow present along length of caruncle in large individuals. Nuchal organs U-shaped ciliary bands on either side of caruncle. Palps as long as 10–15 chaetigers, with deep longitudinal frontal groove lined with fine cilia and with undulating edges along sides; short compound non-motile cilia arising from palp surface bordering frontal groove and sparsely scattered on lateral and abfrontal surfaces on distal end of palps.

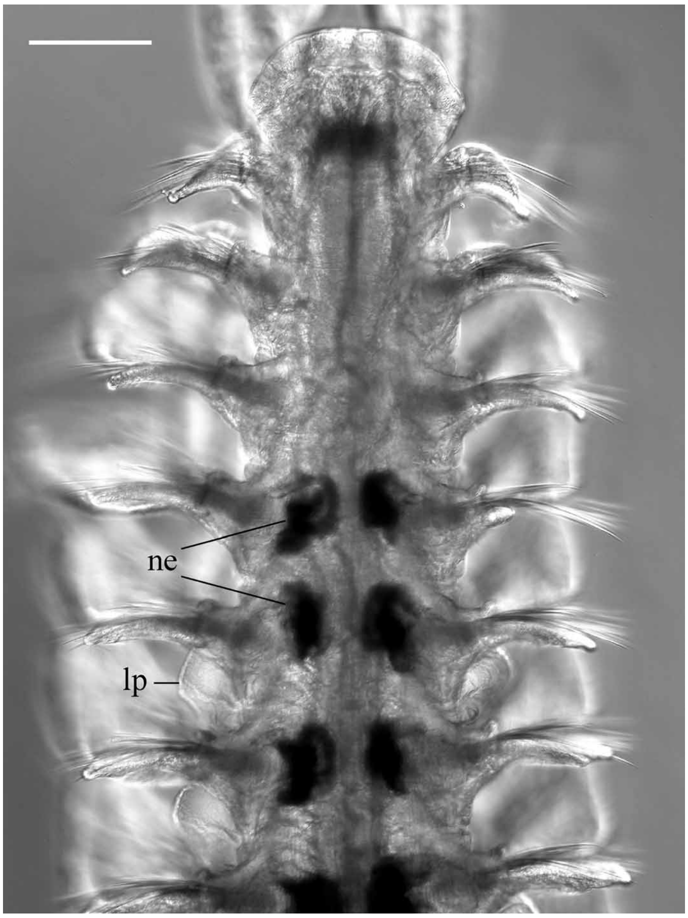

FIGURE 4. *Laonice petersenae* sp. nov. adult morphology. Anterior end, ventral view, showing excretory metanephridia (*ne*) and interneuropodial lateral pouches (*lp*). MZUSP 118 (paratype). Scale: 0.5 mm.

Chaetiger 1 with well-developed capillary chaetae and postchaetal lamellae in both rami. Notopodia with only capillaries. Low prechaetal lamellae present in noto- and neuropodia on anterior chaetigers after chaetiger 1. Postchaetal lamellae large, leaf-like on branchiate chaetigers (Fig. 5A), greatly reduced on posterior abranchiate chaetigers. Dorsal crests absent. Lateral neuropodial pouches from chaetigers 3–17 (chaetiger 5 in holotype) through end of body (Fig. 4). Anterior position of pouches weakly correlated with body size (Fig. 6A) and number of branchiae (Fig. 6C).

Sabre chaetae in neuropodia from chaetigers 13–30 (from chaetiger 20 in holotype), from more anterior chaetigers in small individuals (Fig. 6B), 1–2 in a tuft, 2–4 times longer than hooks, with weak granulations along shaft (Fig. 5E).

Hooks in neuropodia from chaetigers 16–36 (from chaetiger 32 in holotype), from more anterior chaetigers in small individuals (Fig. 6B), up to ten in a series, accompanied by up to eight alternating capillaries, and 1–2 inferior sabre chaetae throughout. Hooks tridentate, with two small upper teeth situated side by side above main fang (Fig. 5D). Alternating capillaries thin, with narrow limbation (Fig. 5C), 1.5–2 times longer than hooks, situated in upper part of row.

Branchiae from chaetiger 3 in juveniles with fewer than 60 chaetigers, from chaetiger 2 in larger individuals, up to 34 pairs (on chaetigers 2–32 in holotype), fewer in small individuals (Fig. 6A). Branchiae full-sized (2–2.5 times longer than notopodial lamellae) from chaetigers 4–6 and decrease in length on posterior branchiate chaetigers, on chaetiger 2 equal to or slightly longer than notopodial postchaetal lamellae (Fig. 5A). Branchiae situated on basal part of notopodia, free from notopodial postchaetal lamellae, slightly flattened, with surfaces oriented perpendicular to body axis, without additional appendages. Fine longitudinal ciliation present along inner and outer edges. Afferent and efferent blood vessels of branchia forming loop and interconnected by numerous circular capillaries giving branchiae annulate appearance.

Nototrochs and intersegmental ciliation present in immature individuals, females and males. Nototrochs from chaetiger 2, each composed of one row of small cells with short cilia. Nototrochs on anterior chaetigers interrupted by caruncle, on branchiate post-caruncle chaetigers extending from tip of one branchia to tip of the other; on posterior abranchiate chaetigers extending onto inner edge of notopodial postchaetal lamellae. Short bands of intersegmental longitudinal cilia present on dorsolateral edges of chaetigers between notopodia, from between chaetigers 2 and 3. Single transverse rows of cilia present on anterior edge of branchiate chaetigers beginning from chaetiger 4 (Fig. 5A).

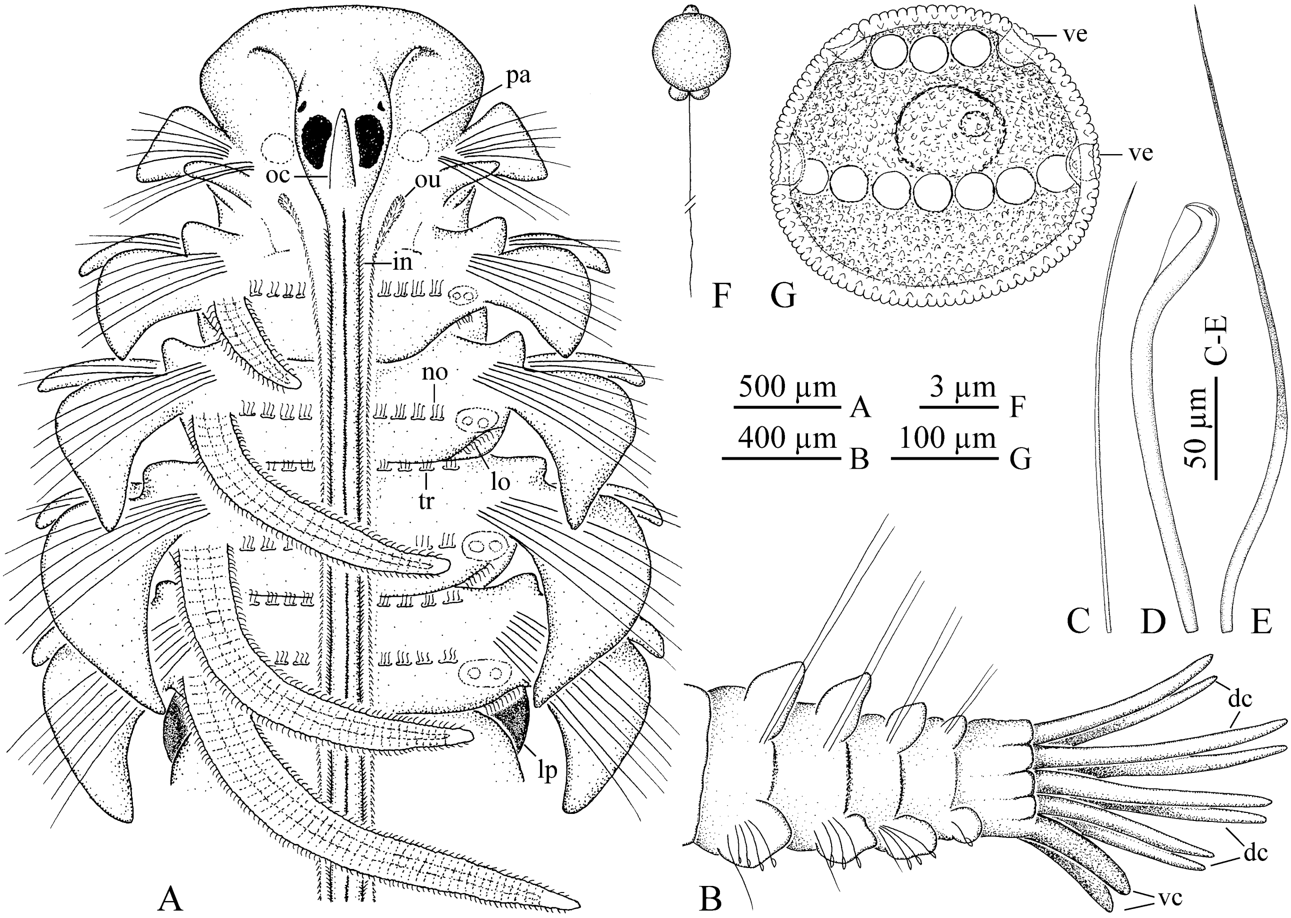

FIGURE 5. *Laonice petersenae* sp. nov. adult and gamete morphology. A, anterior end, dorsal view, showing palp scarves (*pa*), occipital antenna (*oc*), inner (*in*) and outer (*ou*) ciliary bands of paired U-shaped nuchal organs, nototrochs (*no*), intersegmental longitudinal (*lo*) and transverse (*tr*) ciliation, and interneuropodial lateral pouches (*lp*); branchiae on right side of chaetigers omitted, showing cross-sections of afferent and efferent arms of branchial blood loop. B, posterior end, left lateral view, showing four pairs of dorsal cirri (*dc*) arranged in two vertical rows, and one pair of ventral cirri (*vc*). C–E, chaetae from neuropodium of a middle chaetiger: C, capillary alternating with hooks; D, tridentate hooded hook, lateral view, with only one upper tooth visible; E, inferior sabre chaeta; F, spermatozoon; G, intraovarian oocyte artificially released into sea water, showing thick envelope with honeycombed external surface and large vesicles (*ve*) arranged in two parallel circles. A, MZUSP 126 (holotype); B–G, MZUSP 118 (paratypes).

Pygidium with one pair of short ventral cirri and up to four pairs (three pairs in holotype) of dorsal cirri arranged in two vertical rows on sides of terminal anus (Fig. 5B). Dorsal cirri thinner and up to two times longer than ventral cirri, fewer in small individuals.

Main dorsal blood vessel bifurcated at level of median eyes, giving rise to circumesophageal vessels. Paired palpal blood vessels arising from circumesophageal vessels, close to bifurcation point of main dorsal vessel. Main dorsal vessel giving rise to segmental vessels in chaetiger 2 to about chaetiger 10 and transforming into intestinal sinus after chaetiger 10; no segmental vessels observed in chaetiger 1. Circumesophageal vessels joined ventrally in chaetiger 2 to form main ventral blood vessel extending length of body. Blood red, homogenous, without elements. Blood flow provided by sinuous constrictions of intestine.

Excretory metanephridial organs large, dark green, from chaetiger 4 (Fig. 4) to chaetiger 29 (chaetigers 4–26 in holotype), fewer in small individuals. Number of nephridia increasing with age, thus occupying all anterior sterile chaetigers, apart from chaetigers 1–3 (Fig. 6F). Gonoducts in fertile segments short and transparent, hardly discernable in mature individuals, with inner funnel not evident, opening to exterior on lateral sides of chaetigers, in upper part of genital pouch; genital papillae lacking.

Regeneration. Two individuals, with 92 and 107 chaetigers, had 9 and 15 anterior chaetigers, respectively, that were distinctly smaller and more transparent than succeeding chaetigers. These chaetigers probably resulted from regeneration of the anterior end. The beginning of sabre chaetae and hooks, and arrangement of the branchiae and nephridia suggest that the number of regenerated chaetigers was equal to the number of lost chaetigers.

Habitat. *Laonice petersenae* sp. nov. inhabits temporary burrows in sandy to silty sand bottom at 0.5–32 m. Population density of the species reaches 100 individuals/m^2. In Paranaguá Bay, it co-occurs with *L. branchiata*.

Reproduction. *Laonice petersenae* sp. nov. is gonochoristic. Of 18 examined mature individuals, 13 were females and five were males. No external morphological differences were found between females and males. Both sexes reached a maximal size of 120 chaetigers. Gametes developed from chaetigers 27–29 to 70–96 (chaetigers 27–93 in male holotype).

Spermatids were joined in tetrads. Spermatozoa were short-headed, with small subspherical acrosome, spherical nucleus 3.5±0.5 mµ in diameter, four spherical mitochondria, and flagellum 65±5 µm long (Fig. 5F).

Largest 120-chaetiger female had 50–80 oocytes in each of 69 fertile segments (chaetigers 28–96, comprising 60% of total number of chaetigers), and about 4000 oocytes in total. The oocytes were in paired clusters, ovaries situated laterally in fertile segments. Each ovary was covered by thin envelop, thus oogenesis was synchronous and probably entirely intraovarian, with oocytes entering coelomic cavity shortly before spawning. Coelomic oocytes were flattened, of irregular shape, with soft envelope. When artificially released from the body, oocytes gradually rounded up and acquired oval to egg-like shape, measuring about 200 × 250 µm (Fig. 5G). Individual oocytes had envelope about 12 µm thick with a honeycombed external surface and two rows of large encircling vesicles. Vesicles appeared as invaginations of the envelope into the ooplasm, with embedded part about 30 µm in diameter and external opening about 15 µm in diameter. The two parallel rows of encircling vesicles were oriented perpendicular to the long axis of the oocyte. Nine to 16 vesicles were present in one encircling row and 16–21 vesicles were present in the other row.

Remarks. Adults of *L. petersenae* sp. nov. exhibit great ontogenetic and individual variability and have no unique morphological characters to readily distinguish them from related species. *Laonice petersenae* sp. nov. is similar to *L. cirrata* in the fusion of the anterior edge of the prostomium and peristomium, caruncle length, variable anterior position of lateral pouches, and absence of dorsal crests on segments. Adult morphological characters of the two species are compared in Table 2, including three characters introduced by Sikorski (2003a), such as difference between caruncle length and start of sabre chaetae (Ca-SS), start of hooks and sabre chaetae (HH-SS), and posterior position of branchiae and anterior position of sabre chaetae (Br-SS). The variation of all three characters in *L. petersenae* sp. nov. falls within the range of the variation of these characters in *L. cirrata*, which can be interpreted as due to a greater size range of examined individuals of the latter species.

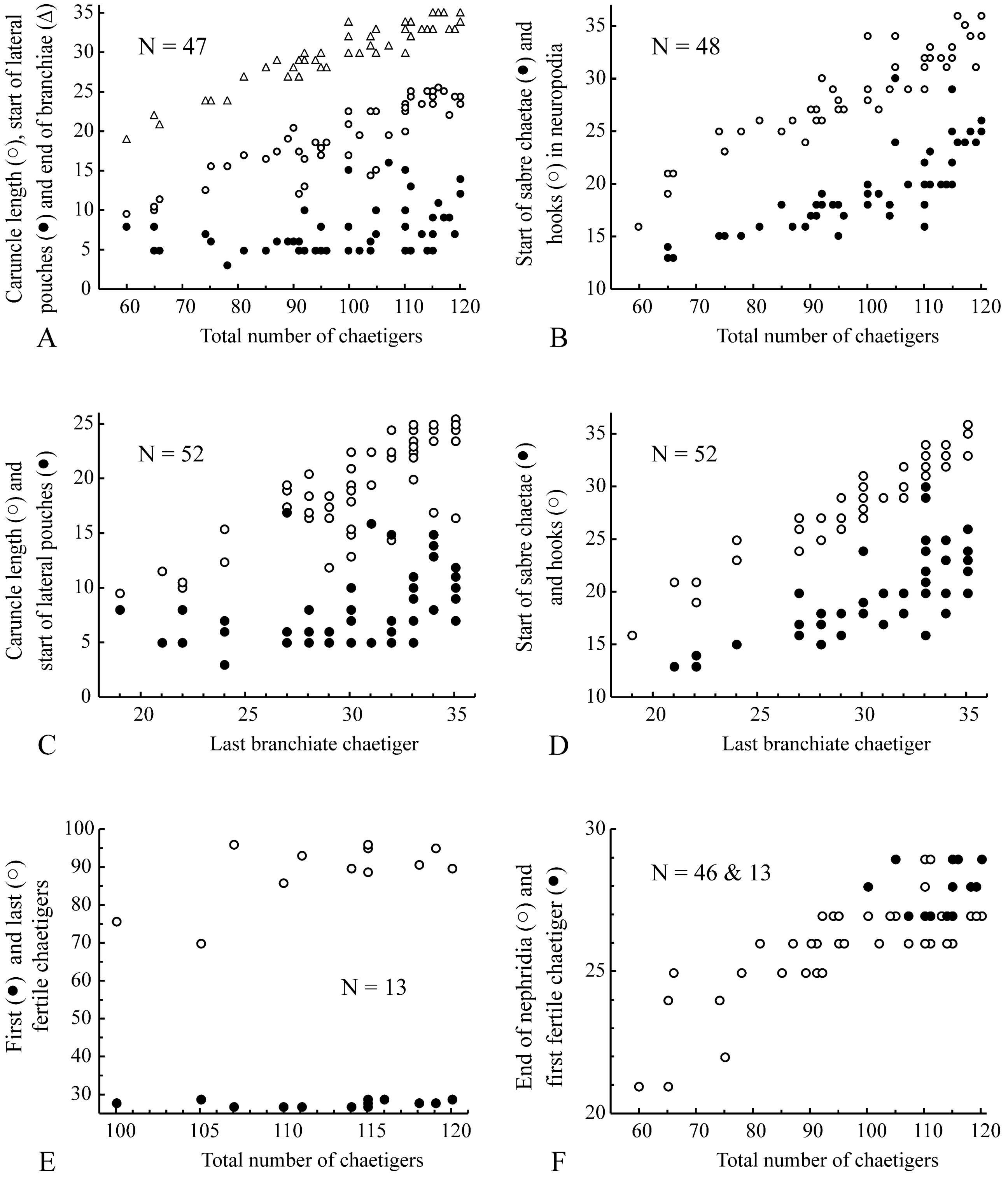

FIGURE 6. *Laonice petersenae* sp. nov. adult morphology. A, relationships between caruncle length (in chaetiger numbers) and total number of chaetigers in worm (empty circles), anterior position of lateral interneuropodial pouches (referring to number of the chaetiger in front of the first pouch) and total number of chaetigers in worm (filled circles), and distribution of branchiae (referring to number of the last branchiate chaetiger) and total number of chaetigers in worm (empty triangles). B, relationships between anterior position of sabre chaetae (referring to number of the first sabre-bearing chaetiger) and total number of chaetigers in worm (filled circles), and anterior position of hooks (referring to number of the first hook-bearing chaetiger) and total number of chaetigers in worm (empty circles). C, relationships between caruncle length (in chaetiger numbers) and distribution of branchiae (referring to number of the last branchiate chaetiger) in worm (empty circles), and anterior position of lateral interneuropodial pouches and distribution of branchiae (filled circles). D, relationships between anterior position of sabre chaetae and distribution of branchiae in worm (filled circles), and anterior position of hooks and distribution of branchiae in worm (empty circles). E, relationships between anterior position of fertile segments (referring to number of the first chaetiger with gametes) and total number of chaetigers in worm (filled circles), and posterior position of fertile segments (referring to number of the last chaetiger with gametes) and total number of chaetigers in worm (empty circles). F, relationships between distribution of excretory metanephridia (referring to number of the last chaetiger bearing nephridiopores) and total number of chaetigers in worm (empty circles), and anterior position of fertile segments (referring to number of the first chaetiger with gametes) and total number of chaetigers in worm (filled circles).

Material reported by Bolívar & Lana (1987) as *L. cirrata* and deposited at MCEM was reexamined. One of the samples, MCEM 48, was reidentified as *L. petersenae* sp. nov. while the others were reidentified as *L. branchiata* (see above) and *L. aperata* sp. nov. (see below).

Etymology. The species is named for Mary E. Petersen, marine biologist, polychaetologist, colleague, and friend for whom we both express our great sincere respect.

Distribution. Brazil: from Bahia south to Paraná.

***Laonice aperata* sp. nov.**

Figure 7A–E

Laonice cirrata: Bolívar & Lana 1987 (*Part.*): 118. Not *L. cirrata* M. Sars, 1851.

Material. Type material. Brazil: off São Paulo, R/V *Almirante Saldanha*, coll. P.C. Lana: Sta. 6127, 24°44′3″S, 45°55′W, 68 m, silty sand, 18 Aug 1982, MCEM 39 (**holotype**), MCEM 1495 (paratype); Sta. 6140, 24°06′S, 46°10′W, 33 m, silty sand, 21 Aug 1982, MCEM 41 (paratype); Sta. 6244, 25°55′4″S, 47°52´W, 50 m, silty sand, 17 May 1983, MCEM 43 (paratype). REVIZEE Score Sul - Bentos Programme, R/V *Prof. W. Besnard*: Sta. 6657, 25º17.30′S, 46º55.60′W, 60 m, sand, 16 Dec 1997, ZUEC POL 733 (4 paratypes); Sta. 6658, 25º11.89′S, 47º08.09′W, 157 m, sand, 16 Dec 1997, ZUEC POL 734 (paratype). Off Santa Catarina, R/V *Almirante Saldanha*, Sta. 6089, 26°22′1″S, 48°19′8″W, 48 m, silty sand, P.C. Lana, Nov 1982, USNM 100447 (paratype); REVIZEE Score Sul - Bentos Programme, R/V *Prof. W. Besnard*, Sta. 6807, 28º53.37′S, 47º48.50′W, 225 m, 22 Mar 1998, ZUEC POL 735 (paratype).

Representative material. Brazil: off Santa Catarina, R/V *Almirante Saldanha*, Sta. 6076, 26°29′5″S, 48°21′4″W, 38 m, silty sand, P.C. Lana, 1 Aug 1982, MCEM 42 (1).

Adult morphology. All specimens anterior fragments, largest about 33 mm long and 1.5 mm wide for 74 chaetigers. Pigmentation absent. Prostomium anteriorly entire, rounded, wide and fused with peristomium. One pair of small anterior eyes and one pair of very large posterior red eyes usually present in small individuals; large worms with anterior eyes deeply embedded in prostomium, reduced or even absent, thus only one pair of large posterior eyes usually visible;

indistinct crescent-shaped spots of red pigment present anterior to eyes in some large individuals. Low caruncle extending to middle of chaetiger 16, shorter in small individuals. Nuchal organs as U-shaped ciliary bands on sides of caruncle. Finger-like occipital antenna present. Palps missing.

Chaetiger 1 with short capillaries and small postchaetal lamellae in both rami. Capillaries in anterior chaetigers not exceeding in number those in succeeding chaetigers, arranged in two vertical rows and superior and inferior tufts in noto- and neuropodia, respectively. Prechaetal lamellae weakly developed to lacking on branchiate chaetigers. Notopodial postchaetal lamellae on branchiate chaetigers wide, thin and flattened, not enveloping chaetal fascicles; lamellae on chaetigers 2–7 with subtriangular distal part, those from chaetiger 8 onwards with rounded distal part. Dorsal crests absent. Lateral interneuropodial pouches absent in all specimens.

Sabre chaetae in neuropodia from chaetigers 21–31, up to four in a tuft, with fine granulation on distal end of shaft (Fig. 7E). Hooks in neuropodia from chaetigers 23–40, up to ten in a series, accompanied by 3–5 slender alternating capillaries and inferior sabre chaetae throughout. Hooks tridentate, with two small upper teeth situated side by side above main fang (Fig. 7A–B). Alternating capillaries with narrow limbation, equal to slightly longer than hooks (Fig. 7C).

Branchiae on chaetigers 2–36, up to 35 pairs, flattened, with surfaces oriented perpendicular to body axis, with ciliation along inner and outer edges. Branchiae on chaetigers 2 and 3 shorter than notopodial postchaetal lamellae in small individuals, but slightly longer than lamellae in large individuals; branchiae on succeeding chaetigers up to two times longer than postchaetal lamellae. Pygidium missing.

Habitat. *Laonice aperata* sp. nov. adults were found in samples collected on sandy to silty sand bottoms at 33–225 m. Population density of the species was less than 50 individuals/m^2.

Remarks. *Laonice aperata* sp. nov. is unique among South American *Laonice* species in the absence of lateral interneuropodial pouches in adults. Such pouches start on anterior branchiate chaetigers and are arranged through end of body in the majority of *Laonice* species, or are at least present on a series of anterior chaetigers in some species. In *L. aperata* sp. nov. lateral pouches were absent in the largest 74-chaetiger anterior fragment examined and no vestiges of lateral pouches were observed in other specimens. It is very plausible that pouches are completely absent in adults of this species. The only other *Laonice* species in which adults have no lateral pouches is *L. asaccata*, described by Sigvaldadóttir & Desbruyères (2003) from a hydrothermal vent on the Mid-Atlantic Ridge, close to the Azores Triple Junction. The two species differ in that *L. asaccata* has a prostomium separated from the peristomium, caruncle extending to end of chaetiger 4, sabre chaetae in neuropodia from chaetigers 20–23, hooks in neuropodia from chaetigers 30–32, and up to 30 pairs of branchiae, whereas *L. aperata* sp. nov. has the prostomium anteriorly fused with the peristomium, caruncle extending to middle of chaetiger 16, sabre chaetae in neuropodia from chaetigers 21–31, hooks in neuropodia from chaetigers 23–40, and up to 35 pairs of branchiae.

Material reported by Bolívar & Lana (1987) as *L. cirrata* and deposited at MCEM was reexamined. The samples MCEM 39, 41–43 were reidentified as *L. aperata* sp. nov. while the others were reidentified as *L. branchiata* and *L. petersenae* sp. nov. (see above).

Etymology. The species name is a compound word formed from *a*, lack of, and the feminine for Latin *pēra*, pouch. It refers to one of the characteristic features of adults, *i.e.*, absence of lateral pouches between successive neuropodia.

Distribution. Southern Brazil.

Laonice parvabranchiata sp. nov.

Figure 7F–G

Material. Type material. Brazil, REVIZEE Score Sul - Bentos Programme, R/V *Prof. W. Besnard*: off São Paulo, Sta. 6651, 25º53.58′S, 45º42.13′W, 256 m, silty sand, 15 Dec 1997, ZUEC POL 729 (**holotype**); Sta. 6652, 25º51.04′S, 45º47.30′W, 206 m, silty sand, 15 Dec 1997, ZUEC POL 730 (3 paratypes); Sta. 6685, 25º41.827′S, 45º11.686′W, 282 m, silty sand, 13 Jan 1998, ZUEC POL 731 (2 paratypes). Off Santa Catarina, Sta. 6778, 26º50.81′S, 46º33.95′W, 322 m, sandy silt, 13 Mar 1998, ZUEC POL 732 (paratype).

Adult morphology. All specimens anterior fragments, largest about 20 mm long and 2 mm wide for 42 chaetigers. Holotype about 6 mm long and 1 mm wide for 20 chaetigers. Pigmentation absent. Prostomium anteriorly entire, wide, with short frontolateral horns, separated from peristomium. Peristomium with low dorsolateral wings. One pair of large red eyes present. Caruncle low, extending to end of chaetiger 11, shorter in small individuals (to end of chaetiger 5 in holotype, Fig. 7G). Nuchal organs as U-shaped ciliary bands on sides of caruncle. Short cirriform occipital antenna present on caruncle (Fig. 7G). Palps missing.

Chaetiger 1 with short capillaries and postchaetal lamellae in both rami; postchaetal lamellae shorter than on succeeding chaetigers. Both noto- and neuropodial capillaries in anterior chaetigers not exceeding in number those in succeeding chaetigers, typically arranged in two vertical rows and superior and inferior tufts in noto- and neuropodia respectively. Prechaetal lamellae well developed in anterior chaetigers, better developed in notopodia than in neuropodia. Notopodial postchaetal lamellae thin, elongated, with subtriangular distal end from chaetiger 2 to chaetigers 5–7, flattened and rounded on succeeding branchiate chaetigers, reduced on postbranchiate chaetigers; lamellae not enveloping chaetal fascicles, without dark glandular cells. Dorsal crests absent. Lateral interneuropodial pouches from chaetigers 14–16 to end of fragments. Fine bands of intersegmental transverse ciliation situated along anterior edge of chaetigers and appearing similar to nototrochs.

Sabre chaetae in neuropodia from chaetigers 27–29, 1–3 in a tuft, with fine granulation on shaft and narrow limbation on distal part (Fig. 7F). Hooks in neuropodia absent in all fragments.

Branchiae from chaetiger 2 to chaetiger 35, up to 34 pairs, very short on first chaetigers, shorter than notopodial postchaetal lamellae until chaetigers 4–5; almost twice as long as postchaetal lamellae on middle branchiate chaetigers, then diminishing again. Branchiae situated on base of notopodia, free from postchaetal lamellae, slightly flattened, with surfaces oriented perpendicular to body axis, without appendages, with dense ciliation on inner and outer edges. Pygidium unknown.

Habitat. *Laonice parvabranchiata* sp. nov. adults were found in samples collected on sandy bottoms at 206–322 m. Population density of the species was about 100 individuals/m^2.

Remarks. *Laonice parvabranchiata* sp. nov. is unique among South American *Laonice* species in having short frontolateral horns on the prostomium. The species is similar to *L. nuchala* originally described from California by Blake (1996) in having the prostomium anteriorly broadened and well separated from the peristomium, the peristomium with dorsolateral wings, branchiae thin and short on the anterior chaetigers, and similar length of the caruncle. The two species differ in that *L. nuchala* has numerous capillaries arranged in at least five rows, with fascicles appearing dense and bushy in anterior chaetigers, hooks in neuropodia starting anterior to chaetiger 25, and lateral pouches beginning from chaetigers 7–9, while in *L. parvabranchiata* sp. nov. capillaries in anterior chaetigers are not more numerous than those on the following chaetigers, hooded hooks appear in neuropodia posterior to chaetiger 42, and lateral pouches occur from chaetigers 14–16.

Laonice parvabranchiata sp. nov. is similar to *L. blakei*, originally described from the Norwegian and Greenland seas, N Atlantic, by Sikorski & Jirkov (in Sikorski et al. 1988). It differs from the latter species in the more posterior start of the lateral pouches, from chaetigers 14–16 in *L. parvabranchiata* sp. nov. and chaetiger 3 in *L. blakei*. In addition, lateral pouches in *L. blakei* continue only through chaetigers 7–17, whereas in *L. parvabranchiata* sp. nov. they apparently continue through the end of body (i.e., to the end of the largest fragment examined), as in the majority of *Laonice* species.

Laonice parvabranchiata sp. nov. is similar to *L. japonica* originally described from Japan by Moore (1907) in having a prostomium that is wide anteriorly with frontolateral parts extended and resembling short horns. It differs from the latter species in having a more posterior start of the lateral pouches, from chaetigers 14–16 in contrast to chaetiger 4 as in *L. japonica*.

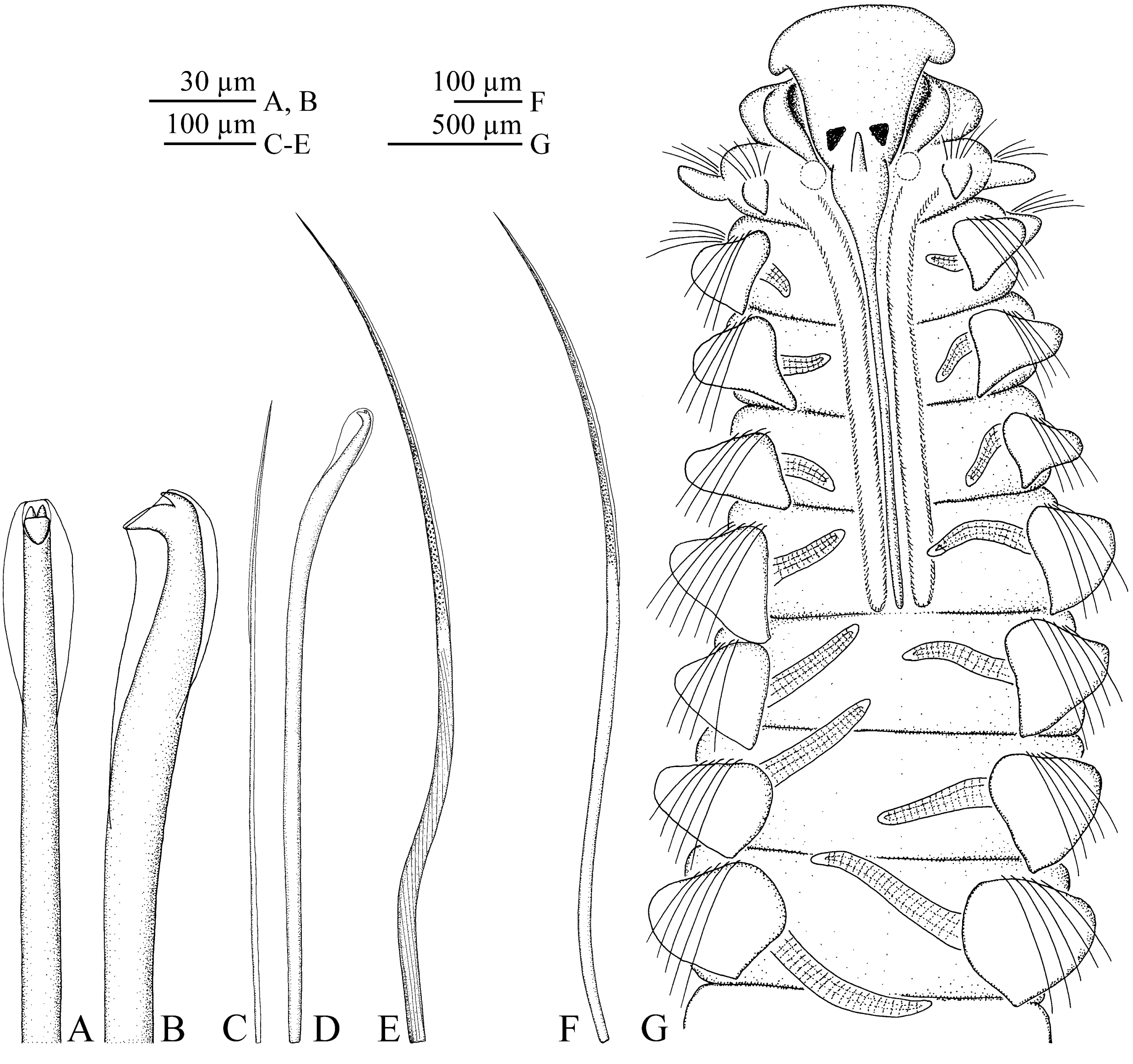

FIGURE 7. *Laonice* adult morphology. A–E, *Laonice aperata* sp. nov., chaetae from neuropodium of chaetiger 40. A, tridentate hooded hook, frontal view, showing lower main fang and two smaller upper teeth situated side by side; B, same, lateral view, with only one upper tooth visible; C, alternating capillary; D, hooded hook; E, inferior sabre chaeta; F–G, *Laonice parvabranchiata* sp. nov. F, anterior end, dorsal view; G, inferior sabre chaeta from neuropodium of chaetiger 35. A–E, ZUEC POL 735 (paratype); F, ZUEC POL 729 (holotype); G, ZUEC POL 732 (paratype).

Etymology. The species name is a compound word formed from the feminine for Latin *parvus*, small, and *branchiatus*, branchiate. It refers to one of the characteristic features of adults, i.e., presence of small branchiae on anterior chaetigers.

Distribution. Southern Brazil: from São Paulo south to Santa Catarina.

Laonice pinnulata **sp. nov.**

Figure 8A

Laonice antarctica [*sic*.]: Vargas et al. 1985: 337; Maurer et al. 1988: 48. Not Hartman 1953.
Laonice bassensis: Dean 1996: 75; 2004: 167. Not Blake & Kudenov 1978.

Material. Type material. Costa Rica, Gulf of Nicoya, R/V *Skimmer*: Sta. 1, 9º57′30″N, 84º53′W, 50 m, H.K. Dean, 10 Jul 1980, USNM 80283 (holotype); Sta. 31, Bahia Ballena, 9º44′N, 84º59′25″W, 22 m, H.K. Dean, 9 Jul 1980, USNM 80284 (paratype).

Adult morphology. Two anterior fragments with about 30 chaetigers each; holotype larger and in better condition, about 4 mm long and 0.7 mm wide. Body pigmentation absent. Prostomium anteriorly entire, wide and rounded, fused with peristomium on anterolateral sides. Peristomium with low dorsolateral wings on sides of prostomium. Two pairs of red eyes arranged in trapezoid, comprising one pair of small anterior eyes and one pair of large posterior eyes. Caruncle low, extending to end of chaetiger 7 in holotype, not distinct in paratype. Nuchal organs as U-shaped ciliary bands on either side of caruncle. Palps and occipital antenna missing.

Chaetiger 1 with well-developed capillary chaetae, postchaetal lamellae in both rami. Prechaetal lamellae not developed. Notopodial postchaetal lamellae on branchiate chaetigers thin, leaf-like with narrowed upper part. Neuropodial postchaetal lamellae rounded. Dorsal crests absent on segments. Lateral interneuropodial pouches from chaetiger 3 in both specimens.

Sabre chaetae in neuropodia from chaetiger 16 in holotype and from chaetiger 17 in paratype, 1–2 in a tuft, with fine granulation on distal part of shaft. Hooks in neuropodia from chaetiger 22 (paratype) or chaetiger 24 (holotype), up to 5 in a series, accompanied by 2–4 slender alternating capillaries and inferior sabre chaetae throughout. Hooks tridentate, with two small upper teeth situated side by side above main fang. Alternating capillaries about two times longer than hooks.

Branchiae from chaetiger 2 to end of each fragment. First pair of branchiae 3–4 times shorter than notopodial lamellae; branchiae on chaetiger 3 slightly shorter than notopodial lamellae; succeeding branchiae up to 1.5 times longer than notopodial lamellae. Branchiae situated on base of notopodia, free from notopodial postchaetal lamellae, slightly flattened, with surfaces oriented perpendicular to body axis, with fine ciliation on inner and outer edges. Afferent and efferent arms of branchial blood loop interconnected with circular capillaries giving branchiae annulate appearance. Up to seven pinnules forming characteristic pectinate structure on basis of each branchia from chaetiger 6 posteriorly (Fig. 8A). Branchial blood capillaries forming a loop in each pinnule. Pygidium missing.

Habitat. *Laonice pinnulata* sp. nov. adults were found in samples collected on muddy sand bottom at 22 and 30 m depth. Population density of the species was about 50 individuals/m^2.

Remarks. *Laonice pinnulata* sp. nov. is unique among *Laonice* species in having up to seven pinnules forming a pectinate structure on the bases of the branchiae from chaetiger 6 (Maciolek 2000: table 1). It is also one of only four described species having the anterior edge of the prostomium fused with the peristomium (Sikorski 2003a). Similar shorter appendages are present on the distal end of branchiae in *L. papillibranchiae*, which was described from Hawaii by Ward (1981).

The two species differ in that *L. papillibranchiae* has the prostomium anteriorly incised, lateral pouches from chaetiger 12, sabre chaetae in neuropodia from chaetigers 9–12, hooks in neuropodia from chaetigers 16–19, and dorsal crests from chaetiger 17, whereas *L. pinnulata* sp. nov. has the prostomium anteriorly entire, lateral pouches from chaetiger 3, sabre chaetae in neuropodia from chaetigers 16–17, hooks beginning in neuropodia from chaetigers 22–24, and dorsal crests not earlier than chaetiger 30, if present at all.

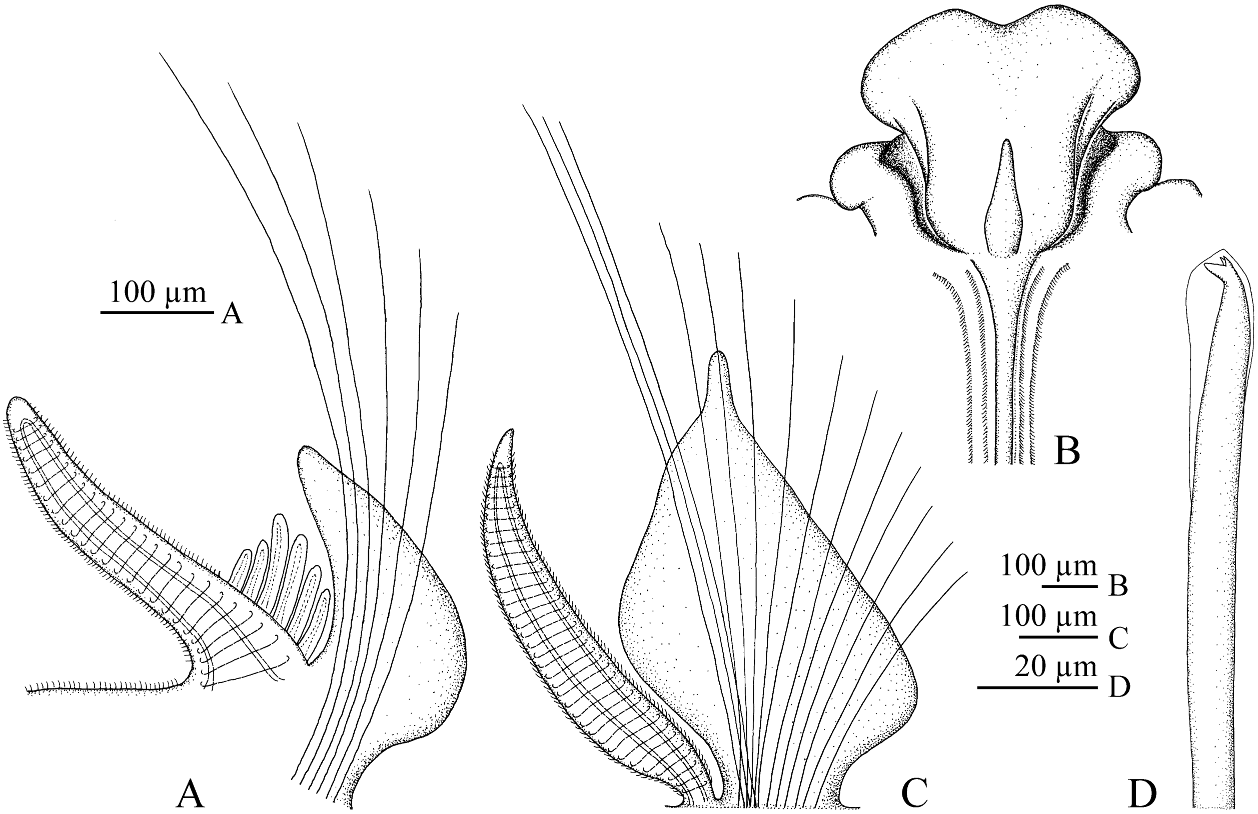

FIGURE 8. *Laonice* adult morphology. A, *Laonice pinnulata* sp. nov., chaetiger 7, left notopodium and branchia in frontal view, showing papillae on basal part of branchia. B–D, *Laonice* sp. B. B, head, dorsal view; C, chaetiger 3, left notopodium and branchia in frontal view; D, hooded hook from neuropodium of chaetiger 20. A,USNM 80283 (holotype); B–D, MNRJ.

The type material of *L. pinnulata* sp. nov. was reported earlier as *L. antarcticae* by Vargas et al. (1985) and Maurer et al. (1988), and then as *L. bassensis* Blake & Kudenov, 1978 by Dean (1996, 2004). Indeed, *L. pinnulata* sp. nov. is similar to *L. bassensis* described from Victoria, Australia, in the length of the nuchal organs and arrangement of the hooks in the neuropodia. The two species differ, however, in that *L. bassensis* has the prostomium anteriorly incised, branchiae smooth, without appendages, lateral pouches beginning invariably from chaetiger 2, and sabre chaetae in neuropodia from chaetigers 9–10, whereas *L. pinnulata* sp. nov. has the prostomium anteriorly entire, branchiae with pinnules, lateral pouches beginning from chaetiger 3, and sabre chaetae in neuropodia from chaetigers 16–17.

Etymology. The species name refers to one of the characteristic features of adults, i.e., the presence of pinnules on the bases of the branchiae.

Distribution. Pacific coast of Costa Rica.

Laonice sp. A

?*Laonice cirrata*: Hartman 1967 (*Part.*): 112. Not Sars 1851.
Laonice sp. A: Blake 1983: 224.

Material. Chile, off Eighth Region Del Bio Bio, R/V *Eltanin*, Sta. 208, 37°29´S, 73°55´W, 957 m, 11 Sep 1962, USNM 56389 (1).

Adult morphology. A 63-chaetiger anterior fragment of a large worm in bad condition. Prostomium wide anteriorly, probably fused with peristomium. Eyes absent. Caruncle posteriorly indistinct, extending at least to end of chaetiger 32. Prechaetal lamellae not developed. Capillaries in anterior chaetigers sparse, not numerous. Branchiae broken on anterior chaetigers, without appendages, posteriorly arranged at least until chaetiger 42. Lateral pouches from chaetiger 1.

Remarks. This single specimen from off southwestern Chile was questionably identified as *Laonice cirrata* by Hartman (1967). Blake (1983) noted that this specimen (incorrectly cited as USNM 56381) resembles *L. hermaphroditica* Blake & Kudenov, 1978 from Queensland, Australia, in having lateral pouches from chaetiger 1, and the caruncle prolonged over about 50 chaetigers. The Chilean specimen, however, appears different from *L. hermaphroditica* in having small and robust lateral pouches instead of large and delicate ones. It might represent a new species, but better material is needed for a final determination.

Distribution. Chile.

Laonice sp. B
Figure 8B–D

Material. Brazil, off Rio de Janeiro, OCEANPROF Project, 2002–2003 (station data will be provided in Radashevsky & Paiva, in preparation): Roncador: Sta. 4, 1335 m, MNRJ (3). Barracuda-Caratinga: Sta. 32H, 900 m, MNRJ (1); Sta. 43N, 1157 m, MNRJ (1). Northern part of the Campos Basin: Sta. 49A, 738 m, 24 Nov 2002, MNRJ (2); Sta. 49B, 722 m, 30 Jun 2003, MNRJ (2); Sta. 53, 1906 m, 27 Jun 2003, MNRJ (1); Sta. 54B, 698 m, 29 Jun 2003, MNRJ (1); Sta. 56, 1357 m, 25 Jun 2003, MNRJ (1); Sta. 59, 753 m, 29 Jun 2003, MNRJ (1); Sta. 61, 1372 m, 26 Jun 2003, MNRJ (1). Southern part of the Campos Basin: Sta. 64, 735 m, 22 Nov 2002, MNRJ (1); Sta. 75, 1039 m, MNRJ (1); Sta. 77, 1666 m, MNRJ (1); Sta. 78, MNRJ (3); Sta. 84, 1042 m, MNRJ (1); Sta. 87, 1931 m, MNRJ (2).

Adult morphology. All specimens anterior fragments of small and large individuals; largest fragment about 11 mm long and 2.5 mm wide for about 30 chaetigers; largest, almost complete specimen without pygidium 15 mm long and 1.2 mm wide for 71 chaetigers. Pigmentation absent. Prostomium bell-shaped, anteriorly wide, with frontal margin concave to incised, almost blunt in some individuals, separated from peristomium (Fig. 8B). Peristomium forming low dorsolateral wings on sides of prostomium. One pair of small red eyes usually embedded in prostomium; eyes absent in some individuals. Caruncle extending to end of chaetiger 15, shorter in small individuals. Prominent occipital antenna present on caruncle. Nuchal organs U-shaped ciliated bands on sides of caruncle. Palps with frontal longitudinal groove lined with fine cilia.

Chaetiger 1 with capillaries and postchaetal lamellae in both rami. Notopodial postchaetal lamellae on branchiate chaetigers with pointed distal tip. Dorsal crests absent. Lateral interneuropodial pouches from chaetigers 3–9 throughout body.

Sabre chaetae in neuropodia from chaetigers 6–20, 1–3 in a tuft, alimbate, with fine granulation on distal end. Hooks in neuropodia from chaetigers 15–32, up to 15 in a series, accompanied by 3–15 alternating capillaries and inferior sabre chaetae throughout. Hooks tridentate, with two small upper teeth situated side by side above main fang (Fig. 8D).

Branchiae on chaetigers 2–21, up to 20 pairs, fewer in small individuals, slightly shorter on chaetiger 2 than on chaetiger 3, flattened, with surfaces oriented perpendicular to body axis, with ciliation on inner and outer edges, free from notopodial lamellae. Branchiae equal to slightly longer than notopodial postchaetal lamellae on branchiate chaetigers (Fig. 8C).

Intersegmental transverse ciliation present on anterior edge of branchiate chaetigers. Pygidium missing.

Habitat. Polychaetes referred to here as *Laonice* sp. B were found at depths of 698–1939 m.

Remarks. The 22 specimens referred to *Laonice* sp. B perhaps represent more than one species. The material was too fragmentary and exhibited so much size-related and individual variability in the length of caruncle, arrangement of branchiae, sabre chaetae, hooks, and lateral pouches, that no distinct morphological patterns could be established to distinguish the species unambiguously. It is plausible that the diagnosis of *L. antarcticae* adopted here is incorrect and that at least some individuals referred to here as *Laonice* sp. B belong in fact to *L. antarcticae* (see Remarks on *L. antarcticae*).

Distribution. Southern Brazil: off Rio de Janeiro.

Laonice sp. C

Material. Brazil, Espírito Santo, Peroá Cangoá, 19°32′S, 39°35′W, 5–9 m, P.M. Costa, E. Calderon, & B.S. Ramos, 5 Feb 2002, UFRJ 407 (4).

Adult morphology. Anterior fragments of large worms in good condition. Prostomium anteriorly wide, rounded, fused with peristomium. One pair of large red eyes present. Caruncle extending to end of chaetiger 12. Palps missing.

Chaetiger 1 with capillary chaetae and postchaetal lamellae in both rami. Prechaetal lamellae well developed on branchiate chaetigers. Notopodial postchaetal lamellae of chaetiger 1 2–3 times shorter than those of chaetiger 2. Notopodial postchaetal lamellae from chaetiger 2 to chaetigers 5–7 with pointed to triangular distal tips; lamellae on succeeding chaetigers with rounded distal tips. Notopodial postchaetal lamellae large, foliose on branchiate chaetigers, gradually becoming reduced on postbranchiate chaetigers. Low dorsal crests joining notopodia on chaetigers 46–53. Lateral pouches between successive neuropodia and also between noto- and neuropodia from chaetiger 3 onwards in all specimens.

Sabre chaetae in neuropodia from chaetiger 35. Hooks in neuropodia from chaetiger 42; hooks tridentate, with two small upper teeth situated side by side above main fang.

Branchiae on chaetigers 2–42, small in the beginning, full-sized from chaetigers 10–15, almost same length as notopodial postchaetal lamellae. Branchiae on chaetiger 3 twice as long as those on chaetiger 2. Single auricular lobes present on frontal base of branchiae; lobes small on anterior branchiae, fully developed from chaetigers 5–7. Pygidium unknown.

Remarks. *Laonice* sp. C is similar to *L. branchiata* in having auricular lobes on the frontal base of branchiae and dorsal crests on postbranchiate chaetigers. The two species differ however in that adults of *L. branchiata* have lateral interneuropodial pouches beginning between chaetigers 4 and 5, whereas all four specimens of *Laonice* sp. C have pouches invariably beginning between chaetigers 3 and 4. These specimens are unique among known *Laonice* species in having folds resembling additional pouches between noto- and neuropodia and may represent a new species. The material is however too fragmentary to make a final taxonomic decision.

Distribution. Central Brazil: Espírito Santo.

Discussion

Of the ten species reported in the present paper, eight were collected along the coast of Brazil. This is due not only to a greater number of biological surveys conducted in this country but also to the high biodiversity in this part of South America. Recent studies on the outer continental shelf and slope off Brazil revealed that this biodiversity is not limited to the land and shallow water but extends into deep water as well (Lavrado & Ignacio 2006; Lavrado & Viana 2007).

The present paper is not a complete guide for the identification of *Laonice* species from South and Central America, but only a step towards the revision of this group of spionid polychaetes in this region. The material available for most of the reported species is insufficient to describe the range of specific variability, delineate biological limits, and distinguish these species unambiguously. Even previously reported species such as *L. antarcticae* and *L. weddellia* do not seem to be well characterized and delineated. The new species, *L. aperata* sp. nov., *L. parvabranchiata* sp. nov., and *L. pinnulata* sp. nov. are described based on poor material. More material is needed to resolve the taxonomy of the specimens referred to here as *Laonice* spp. A–C.

A part of the problem of gathering information about *Laonice* is that the adults have a thin fragile cuticle and become macerated unless properly treated soon after sampling. Another problem is that *Laonice* adults are soft-sediment dwellers with strong musculature, and even when carefully handled, complete individuals tend to fragment when fixed without relaxation. At the same time, morphometric characteristics such as correlations between length of caruncle, arrangement of chaetae, branchiae, lateral pouches, number of pygidial cirri, and the total number of chaetigers might be used as additional diagnostic characters (Söderström 1920; Orrhage & Sundberg 1990; Sikorski et al. 1988). To solve the problem of fragmented material, relationships between size-related characters and width of the specimens, and arithmetic differences between various numeric characters were suggested as additional diagnostic characteristics (Sikorski 2003a). It seems, however, that the arithmetic differences are useful to distinguish some pairs of species but not decisive in other pairwise comparisons (see Table 2).

A series of linear correlation analyses were carried out with morphometric and morphological variables taken from complete specimens of two species, *L. branchiata* and *L. petersenae* sp. nov. Variables included the total number of chaetigers (TCN, treated as independent), the number of the last branchiate chaetiger (BR), caruncle length (Ca), start of the sabre chaetae (SS) and hooks (HH), and the end of nephridia (Figs. 3, 6). Most variables, with the exception of the first chaetigers bearing lateral pouches (for both species) and sabre chaeta start and the last chaetiger bearing nephridia (for *L. petersenae* sp. nov.), are significantly correlated to TNC, as shown by high determination coefficients (Table 1). For both species, the number of the last branchiate chaetiger is clearly the best predictor of total number of chaetigers, whereas the first chaetigers bearing lateral pouches is a fixed (or almost fixed) feature and does not correlate with the other measures. These correlations are highly informative and useful for identification purposes and population studies, since anterior fragments in samples usually include the first chaetigers that bear branchiae, sabre chaetae or hooks or are overrun by the caruncle. Thus, in morphological and morphometric analyses of fragmented material, TNC can be replaced by BR or other variables without much loss of information. The correlations with TNC and BR treated as independent variables can be used as additional characteristics when no unique morphological feature is found in a species.

TABLE 1. Determination coefficients (r^2) between various morphological and morphometric characters, total number of chaetigers (TNC), and number of the last branchiate chaetiger (BR) in adults of *Laonice branchiata* and *L. petersenae* sp. nov. from Brazil. For additional details see Figures 3 and 6.

	Laonice branchiata **(n = 25)**		***Laonice petersenae*** **sp. nov. (n = 45)**	
Character	**TNC**	**BR**	**TNC**	**BR**
Lateral pouches start	0	0	0.1096	0.1446
Caruncle length	0.8978	0.8935	0.7727	0.6942
Branchiae end	0.9733	—	0.9047	—
Sabre chaetae start	0.8429	0.8518	0.5730	0.5222
Hooks start	0.9487	0.9203	0.8499	0.9101
Nephridia end	0.9008	0.9748	0.5789	0.6913

The anterior position and arrangement of lateral interneuropodial pouches is widely used for diagnoses of *Laonice* species. Little is known, however, about the modifications of this character in individual ontogenesis. Two major kinds of pouch “behavior” can be distinguished in adult *Laonice*. In some species, the pouches consistently start between certain neuropodia and retain their position throughout the life of an individual. In others, the pouches are gradually reduced on anterior chaetigers as growth proceeds; thus, their anteriormost position shifts backwards in ontogenesis. In the former group of species, the pouches in adults of all sizes start from one of the seven anterior chaetigers—the specific chaetiger being fixed and species-specific. However, information about the development of pouches in early ontogenesis of these species is not available and we do not know whether the pouches develop directly in the “adult” place or their fixed adult position is acquired at a certain period of ontogenesis. For example, in the 40-chaetiger juvenile of *L. branchiata*, the smallest specimen examined, pouches started from chaetiger 10, while in larger individuals with more than 88 chaetigers, the pouches invariably started from chaetiger 4. If this is not an aberrance, it means that in *L. branchiata* the anteriormost position of pouches shifts forward in early ontogenesis and reaches its “fixed” start from chaetiger 4 in a period of growth between 40 and 80 chaetigers.

The anterior position of pouches from chaetiger 4 has been reported as a diagnostic character of *L. antarcticae*, based on a few type individuals of the species. Whether this start of the pouches is fixed or variable remains uncertain. Two *Laonice* species, *L. asaccata* and *L. aperata* sp. nov., are distinguished by the absence of lateral pouches in the adults. Whether the absence of pouches in these two species is due to ontogenetic loss (only large adults of both species were studied) or if this represents an evolutionary loss in their nearest common ancestor is unknown. It also remains unknown whether the presence of pouches is an apomorphic character of the *Laonice* taxon or of a more inclusive group of spionid polychaetes (similar pouches are also present in some *Prionospio*, *Paraprionospio*, and *Spiophanes* species).

Another uncertain character used for the diagnosis of *Laonice* species is the dentition of hooded hooks. Bidentate and tridentate hooks with one main fang and two upper teeth situated either side by side or one above another have been reported for different species and also as present in individuals of the same species. However, it should be noted that (1) the upper teeth in *Laonice* hooks are usually tiny, situated close to one another, and often broken, and (2) the hooks are flattened laterally and on preparations usually appear in lateral view; thus, only one of two side-by-side upper teeth can be observed. The real number of upper teeth can be revealed only in frontal (or rear) view using light microscopy or, even better, SEM. Another problem is that, in at least one species, *L. cirrata*, the first hooks to develop in late larvae are bidentate (see Hannerz 1956: fig. 6E; Radashevsky unpublished). When the change from bidentate to tridentate hooks happens in ontogenesis is unknown.

TABLE 2. Morphological characteristics of *Laonice* species. Number of observations is given in the parentheses after range values of parameters.

Character	**Species**							
	antarcticae	***weddellia***	***branchiata***	***petersenae* sp. nov.**	***aperata* sp. nov.**	***parvabranchiata* sp. nov.**	***pinnulata* sp. nov.**	***cirrata***[1]
Length: max. (mm)	13	34	90	52	33*	20*	4*	140
No. chaetigers: max.	60	130	160	120	74*	42*	30*	160
Lateral pouches: start	4	6–11	4, 10	3–17	—	14–16	3	3–52
Caruncle length: max. (Ca)	12	20	12	25.5	16	11	7	4–40
Sabre chaetae: most posterior starting chaetiger (SS)	24	13	38	30	31	29	17	30
Hooks: most posterior starting chaetiger (HH)	40	25	46	36	40	After 42*	24	55
Branchiae: most posterior final chaetiger (Br)	31	51	46	35	36	35	After 30*	58
Dorsal crests: start	—	—	45–48	—	—	—	—	—
Dorsal crests: end	—	—	56–60	—	—	—	—	—
Dorsal crests: number	—	—	12–13	—	—	—	—	—
Pygidial cirri: max. no.	?	8	14	10	?	?	?	16
Gametes: start			37–42	27–29				27–40**
Ca-SS			-27.5– -4 (36)	-9–7 (52)				-14–18 (260)
HH-SS			0–12 (36)	0–16 (52)				-7–31 (275)
Br-SS			2–14 (36)	3–17 (51)				-11–33 (252)
Specific features	—	Up to 100 short yellowish capillaries arranged in 4–5 rows in anterior parapodia	Auricular lobes on base of branchiae	—	Lateral interneuro podial pouches absent in adults	Small branchiae on anterior chaetigers	Up to seven pinnules on base of branchiae from chaetiger 6	—

[1] after Sikorski (2003a); *only fragments were studied; **Radashevsky unpublished (based on material from the Sea of Japan).

Adults of some *Laonice* species have dorsal transverse crests joining notopodial postchaetal lamellae on certain postbranchiate chaetigers (see Maciolek 2000: table 1). The crests are fragile epithelial structures which can easily be destroyed and overlooked in poorly preserved material. Similar crests are also present in some *Prionospio* (see Maciolek 1985; Sigvaldadóttir 1998) and *Paraprionospio* (see Yokoyama 2007) species. Whether these dorsal crests in *Laonice*, *Prionospio*, and *Paraprionospio* species are homologs or evolved independently in different taxa remains unknown.

Gamete morphology and internal anatomy have not been considered as diagnostic characteristics and are not mentioned in taxonomic studies of *Laonice* species. Such information is nevertheless relevant for inferring hypotheses about the relationships of generic taxa of Spionidae (Söderström 1920; Blake & Arnofsky 1999; Blake 2006). Gradual development of excretory metanephridia in anterior sterile segments in the course of ontogenesis of *L. branchiata* and *L. petersenae* sp. nov. (Figs. 3F, 6F) and the presence of circular capillaries interconnecting afferent and efferent arms of the branchial blood loop in *Laonice* adults are documented here for the first time for spionid polychaetes.

Branchial circular interconnecting capillaries have been described in Flabelligeridae (Spies 1973), Orbiniidae (Claparède 1869, 1873), Paraonidae (Strelzov 1973), and some other polychaetes but never in Spionidae. An annulate appearance of branchiae in *Aonides oxycephala* (Sars, 1862) was reported by Claparède (1864: p. 507, pl. 3, figs. 3μ,φ, as *A. auricularis*), but it was interpreted as due to the presence of muscular fibers. Later, being under the influence of discovering non-interconnected branchial blood loops in *Nerine cirratulus* (=*Scolelepis squamata* (Müller, 1806)), Claparède (1873: p. 107) reported that his earlier figure of a branchia of *A. oxycephala* was "une coupe théorique" and that the annulations were due to "une illusion d'optique." In fact, afferent and efferent arms of the blood loop in the branchiae of *Aonides* adults are interconnected by circular capillaries (Radashevsky unpublished), the same as in branchiae of *Laonice* adults, but the arms of the branchial blood loop in *Scolelepis* adults are not interconnected by capillaries. Providing information on these characters along with the description of external morphology would allow formulation of hypotheses on the relationships and phylogeny of Spionidae taxa.

Acknowledgements

Antonia Cecília Zacagnini Amaral, Alvaro Esteves Migotto and Paulo Cesar de Paiva provided valuable material and generous support for this study. Elin Sigvaldadóttir and Tim Worsfold reviewed and commented on the manuscript after submission to the journal. Nancy Maciolek and James A. Blake provided valuable comments and final essential editorial assistance. To all these persons we express our sincere gratitude. Financial support to the first author was provided by the Ministério da Educação do Brasil through the Universidade Federal do Paraná, Curitiba (Contract 125/2000); State of São Paulo Research Foundation (FAPESP), Brazil within the BIOTA/FAPESP – The Biodiversity Virtual Institute Program (www.biota.org.br) (proc. nº 1998/07090-3; 2003/08688-0); CENPES/PETROBRÀS, Brazil (in 2007); Russian Foundation for Basic Research (RFBR Project 09-04-01235); Far East Branch of the Russian Academy of Sciences (FEB RAS Project 09-III-A-06-209).

References

Amaral, A.C.Z., Lana, P.C., Fernades, F.C. & Coimbra, J.C. (2003) *Biodiversidade bêntica da região sul-sudeste da costa brasileira. REVIZEE Score Sul - Bentos*. São Paulo, 156 pp.

Amaral, A.C.Z. & Rossi-Wongtschowski, C.L.D.B. (Eds.) (2004) *Biodiversidade bentônica da região sudeste-sul do Brasil, plataforma externa e talude superior (Série Documentos Revizee - Score Sul),* Instituto Oceanográfico da USP, São Paulo, 216 pp.

Blake, J.A. (1983) Polychaetes of the family Spionidae from South America, Antarctica, and adjacent seas and islands. *Biology of the Antarctic Seas XIV. Antarctic Research Series*, 39, 205–288.

Blake, J.A. (1996) Family Spionidae Grube, 1850. Including a review of the genera and species from California and a revision of the genus *Polydora* Bosc, 1802. *In*: Blake, J.A., Hilbig, B. & Scott, P.H. (Eds.), *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Volume 6. The Annelida Part 3 - Polychaeta: Orbiniidae to Cossuridae*, Santa Barbara Museum of Natural History, Santa Barbara, California, 81–223.

Blake, J.A. (2006) Spionida. *In*: Rouse, G. & Pleijel, F. (Eds.), *Reproductive Biology and Phylogeny of Annelida. Vol. 4. Reproductive Biology and Phylogeny*, Science Publisher, Enfield, NH, 565–638.

Blake, J.A. & Arnofsky, P.L. (1999) Reproduction and larval development of the spioniform Polychaeta with application to systematics and phylogeny. *Hydrobiologia*, 402, 57–106.

Blake, J.A. & Kudenov, J.D. (1978) The Spionidae (Polychaeta) from southeastern Australia and adjacent areas with a revision of the genera. *Memoirs of the National Museum of Victoria*, 39, 171–280.

Bolívar, G.A. & Lana, P.C. (1987) Spionidae (Annelida: Polychaeta) do litoral do Estado do Paraná. *Nerítica, Pontal do Sul, PR*, 2, 107–148.

Bolívar, G.A. & Lana, P.C. (1988) Padrões de distribuição de Spionidae e Magelonidae (Annelida: Polychaeta) do litoral do Estado do Paraná. *An. Sem. Reg. Ecol.*, 6, 247–267.

Bremec, C., Elías, R. & Gambi, M.C. (2000) Comparison of the polychaete fauna composition from the Patagonian Shelf and the Strait of Magellan. Preliminary results from cruises Shinkai Maru IV, V, X, and XI (1978–1979) and second Italian oceanographic cruise (1991). *Bulletin of Marine Science*, 67, 189–197.

Cantone, G., Castelli, A. & Gambi, M.C. (2000) Benthic polychaetes off Terra Nova Bay and Ross Sea: species composition, biogeography, and ecological role. *In*: Faranda, F.M., Guglielmo, L. & Ianora, A. (Eds.), *Ross Sea Ecology*, Springer-Verlag, Berlin Heidelberg, 551–561.

Cantone, G. & Di Pietro, N. (2001) Benthic littoral Polychaeta "Sedentaria" of Terra Nova Bay (Ross Sea, Antarctica). *Antarctic Science*, 13, 3–8.

Carrasco, F.D. (1974) Spionidae (Polychaeta) provenientes de la Bahía de Concepción y lugares adyacentes. *Boletín de la Sociedad de Biología de Concepción*, 48, 185–201.

Claparède, E. (1864) Glanures zootomiques parmi les Annélides de Port-Vendres (Pyrénées Orientales). *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève*, 17, 463–600.

Claparède, E. (1869) Les Annélides Chétopodes du Golfe de Naples. Seconde partie. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève*, 20, 1–225.

Claparède, E. (1873) Recherches sur la structure des Annélides Sédentaires. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève*, 22, 1–199.

Dean, H.K. (1996) Subtidal benthic polychaetes (Annelida) of the Gulf of Nicoya, Costa Rica. *Revista de Biología Tropical*, 44, 69–80.

Dean, H.K. (2004) Marine biodiversity of Costa Rica: Class Polychaeta (Annelida). *Revista de Biología Tropical*, 52, 131–181.

Foster, N.M. (1971) Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea. *Studies on the Fauna of Curaçao and other Caribbean Islands*, 36, 1–183.

Gambi, M.C., Castelli, A. & Guizzardi, M. (1997) Polychaete populations of the shallow soft bottoms off Terra Nova Bay (Ross Sea, Antarctica): distribution, diversity and biomass. *Polar Biology*, 17, 199–210.

Gambi, M.C. & Mariani, S. (1999) Polychaetes of the soft bottoms of the Straits of Magellan collected during the Italian oceanographic cruise in February–March 1991. *Scientia Marina*, 63, 233–242.

Hartman, O. (1953) Non-pelagic Polychaeta of the Swedish Antarctic Expedition 1901–1903. *Further Zoological Results of the Swedish Antarctic Expedition 1901–1903*, 4, 1–83.

Hartman, O. (1965) Deep-water benthic polychaetous annelids off New England to Bermuda and other North

Atlantic areas. *Allan Hancock Foundation Publications, Occasional Paper*, 28, 1–378.

Hartman, O. (1967) Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic Seas. *Allan Hancock Foundation Monographs*, 2, 1–387.

Hartman, O. (1978) Polychaeta from the Weddell Sea Quadrant, Antarctica. *Biology of the Antarctic Seas VI. Antarctic Research Series*, 26, 125–223.

Hartmann-Schröder, G. (1965) Zur Kenntnis des Sublitorals der chilenischen Küste unter besonderer Berücksichtigung der Polychaeten und Ostracoden. (Mit Bemerkungen über den Einflub sauerstoffarmer Strömungen auf die Besiedlung von marinen Sedimenten). Teil II: Die Polychaeten des Sublitorals. *Mitteilungen aus dem hamburgischen zoologischen Museum und Institut*, 62, 59–305.

Hartmann-Schröder, G. & Rosenfeldt, P. (1988) Die Polychaeten der "Polarstern"-Reise ANT III/2 in die Antarktis 1984. Teil 1: Euphrosinidae bis Chaetopteridae. *Mitteilungen aus dem hamburgischen zoologischen Museum und Institut*, 85, 25–72.

Hilbig, B. (2001) Deep-sea polychaetes in the Weddell Sea and Drake Passage: First quantitative results. *Polar Biology*, 24, 538–544.

Knox, G.A. & Cameron, D.B. (1998) The marine fauna of the Ross Sea: Polychaeta. *NIWA Biodiversity Memoir*, 108, 1–125.

Lavrado, H.P. & Ignacio, B.L. (Org.) (2006) *Biodiversidade bentônica da região central da Zona Econômica Exclusiva brasileira*. Museu Nacional - UFRJ, Rio de Janeiro, 389 pp.

Lavrado, H.P. & Viana, M.S. (Org.) (2007) *Atlas de invertebrados marinhos da região central da Zona Econômica Exclusiva brasileira*. Museu Nacional - UFRJ, Rio de Janeiro, 258 pp.

Maciolek, N.J. (1985) A revision of the genus *Prionospio* Malmgren, with special emphasis on species from the Atlantic Ocean, and new records of species belonging to the genera *Apoprionospio* Foster and *Paraprionospio* Caullery (Polychaeta, Annelida, Spionidae). *Zoological Journal of the Linnean Society, London*, 84, 325–383.

Maciolek, N.J. (2000) New species and records of *Aonidella*, *Laonice*, and *Spiophanes* (Polychaeta: Spionidae) from shelf and slope depth of the western north Atlantic. *Bulletin of Marine Science*, 67, 529–547.

Malmgren, A.J. (1867) Annulata polychæta Spetsbergiæ, Grönlandiæ, Islandiæ et Scandinaviæ hactenus cognita. *Öfversigt af Konglingar Vetenskaps-Akademiens Förhandlingar, Stockholm*, 24, 127–235.

Maurer, D., Vargas, J. & Dean, H. (1988) Polychaetous annelids from the Gulf of Nicoya, Costa Rica. *International Revue der gesammten Hydrobiologie*, 73, 43–59.

Moore, J.P. (1907) Descriptions of new species of spioniform annelids. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 59, 195–207.

Morgado, E.H. & Amaral, A.C.Z. (1989) Anelídeos poliquetos da região de Ubatuba (SP) - padrões de distribuição geográfica. *Revista Brasileira de Zoologia*, 6, 535–568.

Nonato, E.F., Bolívar, G.A. & Lana, P.C. (1986) *Laonice branchiata*, a new species of Spionidae (Annelida; Polychaeta) from the southeastern Brazilian coast. *Nerítica, Pontal do Sul, PR*, 1, 21–25.

Orensanz, J.M. & Gianuca, N.M. (1974) Contribuição ao conhecimento dos anelídos poliquetas do Rio Grande do Sul, Brasil. I. Lista sistemática preliminar e descrição de três novas espécies. *Comunicações do Museu de Ciências da PUCRGS, Porto Alegre*, 4, 1–37.

Orrhage, L. & Sundberg, P. (1990) Multivariate analysis of morphometric differentiation within the *Laonice cirrata*-group (Polychaeta, Spionidae). *Zoologica Scripta*, 19, 173–178.

Paiva, P.C. (1993) Anelídeos poliquetas da plataforma continental norte do Estado de São Paulo: I - Padrões de densidade e diversidade específica. *Boletim do Instituto Oceanografico, Universidade de São Paulo*, 41, 69–80.

Sars, M. (1851) Beretning om en i Sommeren 1849 foretagen zoologisk Reise i Lofoten og Finmarken. *Nyt Magazin for Naturvidenskaberne, Oslo*, 6, 121–211.

Sigvaldadóttir, E. (1998) Cladistic analysis and classification of *Prionospio* and related genera (Polychaeta, Spionidae). *Zoologica Scripta*, 27, 175–187.

Sigvaldadóttir, E. & Desbruyere, D. (2003) Two new species of spionidae (Annelida: Polychaeta) from Mid-Atlantic ridge hydrothermal vents. *Cahiers de Biologie Marine*, 44, 219–225.

Sikorski, A.V. (1999) Redescription of *Laonice appelloefi* (Polychaeta, Spionidae). *Zoologichesky Zhurnal*, 78, 1465–1467. (In Russian with English Summary).

Sikorski, A.V. (2003a) *Laonice* (Polychaeta, Spionidae) in the Arctic and the North Atlantic. *Sarsia*, 88, 316–345.

Sikorski*, A.V. (2003b) On the fauna of the genus *Laonice* (Polychaeta, Spionidae) in the northern Pacific. *Zoologichesky Zhurnal*, 82, 1179–1190. (In Russian with English Summary).

Sikorski, A.V. (2002) On distinguishing the morphologically close species, *Laonice cirrata* and *L. bahusiensis* (Polychaeta, Spionidae). *Zoologichesky Zhurnal*, 81, 406–419. (In Russian with English Summary).

Sikorski, A.V., Jirkov, I.A. & Tsetlin, A.B. (1988) The genus *Laonice* (Polychaeta, Spionidae) in the Arctic Ocean: weighing the taxonomic characters and species composition. *Zoologichesky Zhurnal*, 67, 826–838. (In Russian with English Summary).

Söderström, A. (1920) *Studien über die Polychätenfamilie Spionidae. Inaugural-Dissertation*. Almquist & Wicksells, Uppsala, 1–286, 1 plate.

Spies, R.B. (1973) The blood system of the flabelligerid polychaete *Flabelliderma commensalis* (Moore). *Journal of Morphology*, 139, 465–490.

Strelzov, V.E. (1973) *Polychaete worms of the family Paraonidae Cerruti, 1909 (Polychaeta, Sedentaria)*. USSR Academy of Sciences, Leningrad, 1-170. (In Russian. Translated into English in 1979. India: Oxonian Press, New Delhi).

Vargas, J.A., Dean, H.K., Maurer, D. & Orellana, P. (1985) Lista preliminar de invertebrados asociados a los sedimentos del Golfo de Nicoya, Costa Rica. *Brenesia*, 24, 327–342.

Ward, L.A. (1981) Spionidae (Polychaeta: Annelida) from Hawaii, with descriptions of five new species. *Proceedings of the Biological Society of Washington*, 94, 713–730.

Yokoyama, H. (2007) A revision of the genus *Paraprionospio* Caullery (Polychaeta: Spionidae). *Zoological Journal of the Linnean Society*, 151, 253–284.

* The name *Sikorski* has been spelled inconsistently in various publications, apparently due to different translations from the Russian. It is normalized and used consistently throughout this paper.