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New Phylogenetic Analysis of *Paraprionospio* Caullery (Polychaeta: Spionidae), with Description of a New Species from the Gulf of Mexico

Víctor H. Delgado-Blas¹ and Luis F. Carrera-Parra^{2,*}

¹Universidad de Quintana Roo, División de Ciencias e Ingeniería, Chetumal, Quintana Roo, 77010, México. E-mail: blas@uqroo.edu.mx ²El Colegio de la Frontera Sur. Depto. Sistemática y Ecología Acuática. Estructura y Función del Bentos. Chetumal, Quintana Roo,

México

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Victor H. Delgado-Blas and Luis F. Carrera-Parra (2018) A cladistic analysis of *Paraprionospio* was conducted based on the revision of some type materials and the original descriptions of some species. The phylogenetic reconstruction of *Paraprionospio* using parsimony analysis of 45 morphological characters yielded one most parsimonious tree (CI = 0.45, RI = 0.54). Herein, thirteen *Paraprionospio* species were considered to be valid, and one new species was described: *Paraprionospio pinnata* (Ehlers, 1901), *P. inaequibranchia* (Caullery, 1914), *P. africana* (Augener, 1918), *P. alata* (Moore, 1923), *P. treadwelli* (Hartman, 1951), *P. lamellibranchia* Hartman, 1974, *P. coora* Wilson, 1990, *P. tamaii* Delgado-Blas, 2004, *P. yokoyamai* Delgado-Blas, 2004, *P. cordifolia* Yokoyama, 2007, *P. oceanensis* Yokoyama, 2007, *P. patiens* Yokoyama, 2007, *P. cristata* Zhou, Yokoyama and Li, 2008, and *P. dibranchiata* sp. nov. This species is characterized by having two pairs of branchiae on chaetigers 1-2, the first pair pinnate with few pinnules, the second one cirriform; and with a long filament at the base of third notopodial lamella on chaetiger 3. Also, *P. alata*, *P. treadwelli* and *P. inaequibranchia* were redescribed based upon type material, and several morphological features were included to clarify the taxonomic status of *P. treadwelli*, *P. tamaii* and *P. yokoyamai*, which were previously considered synonyms of *P. alata*. A taxonomic key to all *Paraprionospio* species is provided.

Key words: Annelida, Polychaetes, Cladistic, Spionids, Morphology, Redescription.

BACKGROUND

Paraprionospio was established as a subgenus of *Prionospio* by Caullery (1914) to include *Prionospio pinnata* Ehlers, 1901, which has the first pair of branchiae on chaetiger 1. Later, Foster (1971) recognized *Paraprionospio* as a separated genus due to its well-developed parapodium of chaetiger 1, hood formed by the fusion of peristomium and the achaetigerous first segment, and three pairs of branchiae on chaetigers 1-3. Furthermore, Foster included *Prionospio (P.) inaequibranchia* Caullery, 1914, *P.*

africana Augener, 1918, *P. alata* Moore, 1923, *P. tribranchiata* Berkeley, 1927, *P. plumosa* Treadwell, 1931, *P. treadwelli* Hartman, 1951, and *P. ornata* Berkeley and Berkeley, 1961 as junior synonyms of *P. pinnata*. As a consequence, *Paraprionospio* was considered as a monospecific genus. Since then, *Paraprionospio* has been widely recognized as an independent genus (Fauchald 1972; Blake and Kudenov 1978; Maciolek 1985; Yokoyama and Tamai 1981; Wilson 1990; Delgado-Blas 2004; Yokoyama 2007; Zhou et al. 2008). Hartman (1974) studied material from the Mozambique Channel and used it to describe *P. lamellibranchia*.

^{*}Correspondence: E-mail: lcarrera@ecosur.mx

Posteriorly, Yokoyama and Tamai (1981) introduced additional features for *Paraprionospio* species and recognized various morphological variations. Wilson (1990), in his study of spionids from southern Australia, included the description of a new species of *Paraprionospio*. Delgado-Blas (2004) reported two new species, *P. tamaii* and *P. yokoyamai*, from the Grand Caribbean Region, and provided a taxonomic key to seven *Paraprionospio* species.

The last revision of Paraprionospio was made by Yokoyama (2007). He provided a new diagnosis for Paraprionospio based on a cladistic analysis, which was defined by having a prostomium fusiform with rounded, truncated or bluntly pointed anterior end; peristomium fused with an achaetigerous segment forming large lateral wings which enclosing the prostomium, and three pairs of branchiae on chaetigers 1-3. All branchiae with lamellar plates densely packed, attached serially on the inner posterior face of the shaft, except in the basal and distal end. Yokoyama (2007) also described three new species: Paraprionospio cordifolia, P. oceanensis, and P. patiens. Furthermore, he considered P. treadwelli, P. tamaii and P. yokoyamai as junior synonyms of P. alata, and redescribed P. africana, P. lamellibranchia, and P. inaequibranchia. Additionally, he included a taxonomic key to nine species: P. cordifolia, P. oceanensis, P. patiens, P. alata, P. africana, P. lamellibranchia, P. inaequibranchia, P. cora, and P. pinnata. The most recent Paraprionospio species was described from Chinese waters by Zhou et al. (2008) as P. cristata.

Herein, we provide a new phylogenetic analysis of *Paraprionospio* species, a revision of four species, and a description of a new species from the southern Gulf of Mexico. Furthermore, we provided evidence to refute the synonymies of *P. treadwelli*, *P. tamaii* and *P. yokoyamai* with *P. alata*.

MATERIALS AND METHODS

The type material of the following species was also examined: syntypes of *Prionospio pinnata inaequibranchia* deposited at the Zoologisch Museum, Universiteit van Amsterdam (ZMA); holotype of *Prionospio alata* and holotypes and paratypes of *Prionospio plumosa*, which are deposited at the Smithsonian National Museum of Natural History (USNM). The specimens of the new species were collected off the coast of Veracruz, Mexico with a grab at depths ranging from 63 to 185 m. Samples were sieved using a mesh size of 0.5 and 1 mm, fixed in 10% formalin and later preserved in 70% ethanol. All specimens were examined in alcohol or glycerol under a stereomicroscope or a compound microscope and scanning electron microscopy. For the observation of several features, specimens were stained with methyl green solution saturated in 70% alcohol. The drawings were made using a camera lucida. Measurements of body width refer to the distance between the most distal points of the parapodia seen dorsally on chaetigers 3-5 (not including chaetae).

The holotype and one paratype of *Paraprionospio dibranchiata* sp. nov. were deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); paratypes were also deposited in El Colegio de la Frontera Sur, Unidad Chetumal (ECOSUR).

For scanning electron microscopy (SEM), specimens were dehydrated via graded ethanol series, critical point dried using carbon dioxide, coated with gold-palladium, and examined with a Topcon SM-510 in El Colegio de la Frontera Sur, Tapachula, Chiapas.

The ingroup for the phylogenetic analysis includes the fourteen *Paraprionospio* species that are validated in this study. Following Sigvaldadóttir et al. (1997) we include as part of the outgroup *Laubieriellus grasslei* Maciolek, 1981, and *Prionospio steenstrupi* Malmgren, 1867, which are members of the *Prionospio*-complex and considered closely related to *Paraprionospio*, and also included *Streblospio benedicti* following the previous phylogenetic hypothesis of Yokoyama (2007).

The data matrix was edited in MacClade 4.08 (Maddison and Maddison 2001) and analyzed in PAUP 4.0b10 (Swofford 1998). Tree selection was carried out by Branch and Bound tree search using PAUP with default settings, character optimization by ACCTRAN, the multistate characters were treated as non-additive (unordered), and all characters carried equal weight. Inapplicable states are coded as "-" and treated as equivocal in the analysis. Missing data are coded as "?". Autapomorphies were included during the analysis, but were excluded from reported consistency indices (CI). The resulting trees and the trace of character state transformation were analyzed in MacClade.

The character matrix consisting of 45 morphological features was constructed based

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on Yokoyama (2007). Its character 5 was split (5-6 herein), and a character state was added in its character 15 (character 28 in this study). Furthermore, the following characters were added: 9, 12-18, 26-27, 30-32, 40-43, and 45 (see below and Table 1).

Information of some *Paraprionospio* species was obtained from the original descriptions, or the most recent redescriptions (Wilson 1990; Delgado-Blas 2004; Yokoyama 2007) and information provided herein. The morphological characters are described below and summarized in tables 1 and

Table 1. Characters and character states. Numbers correspond to those in table 2 and figure 6. NoPL: notopodial postchaetal lamellae; NuPL: neuropodial postchaetal lamellae; PBr; Branchial pinnules

Characters	Character states
1. Shape of prostomium	Triangular (0); rectangular (bottle-shaped) (1); spindle-shaped (2)
2. Caruncle reaches	Posterior segment 2 chaet. 2-3 (0); segment 1 (1)
3. Prostomial peaks	Absent (0); present (1)
4. Basal sheath of palp	Absent (0); present (1)
5. Peristomial wings	Absent (0); present (1)
6. Peristomial wings development	Moderate (0); conspicuous (1)
7. Fusion of segment 1 and peristomium	Partly (0); completely (1)
8. Notochaetae segment 1	Present (0); absent (1)
9. Neurochaetae segment 1	Present (0); absent (1)
10. Postchaetal lamellae segment 1	Well developed (0); absent (1); reduced (2)
11 NuPL segment 2 (chaet. 1)	Rounded (0); triangular (1); oval (2); subtriangular (3)
12. NuPL segment 3 (chaet. 2)	Rounded (0); subtriangular (1); oval (2); triangular (3)
13. NuPL segment 4 (chaet. 3)	Rounded (0); subtriangular (1); cordate (2); oval (3); triangular (4)
14. NuPL segment 5 (chaet. 4)	Rounded (0); triangular (1); cordate (2); oval (3); reniform (4)
15. NoPL segment 2 (chaet. 1)	Rounded (0); subtriangular (1); oval (2); foliaceous (3); triangular (4)
16. NoPL segment 3 (chaet. 2)	Subtriangular (0); rounded (1); oval (2); foliaceous (3); triangular (4)
17. NoPL segment 4 (chaet. 3)	Subtriangular (0); rounded (1); foliaceous (2); triangular (3)
18. NoPL segment 5 (chaet. 4)	Subtriangular (0); rounded (1); reniform (2); foliaceous (3); triangular (4)
19. NoPL middle segments	Digitiform (0); rounded (1); triangular (2); subtriangular (3)
20. NoPL last segments	Reduced (0); conspicuous (1)
21. Ventral crest segment 9	Absent (0); present (1)
22. Dorsal crests	Anterior to segment 22(0); posterior to segment 21 (1); absent (2)
23. Semitransparent dorsal cuticle	Absent (0); present (1)
24. Interparapodial pouches	Absent (0); present (1)
25. Number of branchial pairs	Four (0); one (1); three (2); two (3)
26. Branchiae on segment 1	Present (0); absent (1)
27. Branchiae on segment 2	Present (0); absent (1)
28. PBr on segment 2	Absent (0); digitiform (1); flabellate (2); bifoliated (3); unifoliated (4)
29. Branchiae on segment 3	Present (0); absent (1)
30. PBr on segment 3	Absent (0); digitiform (1); flabellate (2); bifoliated (3)
31. Branchiae on segment 4	Present (0); absent (1)
32. PBr on segment 4	Absent (0); bifoliated (1); flabellate (2)
33. Processes on 1st branchia	Absent (0); present (1)
34. Ridge between branchial base	Absent (0); segment 2 (1); segment 2-4 (2)
35. Filament segment 4	Absent (0); present (1)
36. Neuropodial capillaries segment 10	Non-limbate (0); limbate (1)
37. Neuropodial hooks start	Segment 7-13 (0); segment 15-17 (1)
38. Secondary hood	Absent (0); present (1)
39. Notopodial hooks	Absent (0); present (1)
40. Secondary teeth pairs, notopodial hook	Up to 6 pairs (0); up to 4 (1); up to 3 pairs (2); up to 2 pares (3)
41. Secondary teeth pairs, neuropodial hook	Up to 3 (0); up to 4 (1); up to 6 (2); up to 5 (3); up to 2 (4)
42. Single medial tooth over main tooth	Absent (0); present (1)
43. Single medial tooth over accessory teeth	Present (0); absent (1)
44. Number of anal cirri	Three (0); cero (1); one (2)
45. Dorsum with transverse series of slightly raised ridges	Absent (0); present (1)

2).

Description of morphological characters

1. Prostomial shape is highly variable within the complex-*Prionospio*. It varies from triangular (0) as in *Laubieriellus grasslei*, to rectangular (bottle-shaped) (1) in *Prionospio steenstrupi*, and *Streblospio benedicti*. All *Paraprionospio* species have a spindle-shaped prostomium (2).

2. The caruncle is a posterior extension of the prostomium, sometimes reaching the posterior end of segment 2 (chaetigers 2-3) (0) in *L. grasslei*, and *P. steenstrupi*, or segment 1 (1) as in *S. benedicti* and all *Paraprionospio* species.

3. The prostomial peaks can be absent (0) as in the outgroup and almost all *Paraprionospio* species, or can be present (1) as in *P. treadwelli*.

4. All spionids have paired peristomial palps; in some of them, a basal sheath is present on the palps. In this study, it is absent (0) in the outgroup; or present (1) in many of the *Paraprionospio* species, excepting in *P. africana*, *P. cristata*, *P. dibranchiata* sp. nov., *P. inaequibranchia*, *P. lamellibranchia*, *P. treadwelli* which lack information about it.

5-6. Peristomium forming large lateral membranous wings enclosing prostomium. The peristomial wings can be absent (0) as in *L. grasslei* and *P. steenstrupi*, or can be present (1) as in *S. benedicti* and all *Paraprionospio* species. When present, the development of the peristomial

wings varies in their length; it can be moderate (0) as in *S. benedicti* or conspicuous (1) as in all *Paraprionospio* species.

7. In adult of many *Prionospio* and some other species, the peristomial dorso-lateral wings are completely fused to the first notopodial postchaetal lamellae forming prominent earshaped structures. In adults of *Paraprionospio* and *Streblospio* species, the peristomium is completely fused ventrally and laterally with the following segment, which is achaetous and apodous, so that the dorsal part of their peristomial hood is formed by the peristomium and the first segment. The segment 1 is partly fused with the peristomium (0) in *L. grasslei*, *P. steenstrupi*, and completely fused (1) in all *Paraprionospio* species and *S. benedicti*.

8-9. The notochaetae and neurochaetae of segment 1 are present (0) in species of the outgroup, while these kind of chaetae are absent (1) in all *Paraprionospio* species.

10. Anterior postchaetal lamellae are usually well developed and foliate, gradually reducing in size on middle and posterior segments. The postchaetal lamellae of segment 1 can be well developed (0) as in *L. grasslei* and *P. steenstrupi*, or can be absent (1) as in *P. africana*, *P. alata*, *P. cordifolia*, *P. cristata*, *P. dibranchiata* sp. nov., *P. inaequibranchia*, *P. pinnata*, *P. tamaii*, *P. treadwelli*, and *P. yokoyamai*; also can be reduced (2) as in *S. benedicti*, *P. coora*, *P. lamellibranchia*, *P. oceanensis* and *P. patiens*.

Notopodial (15-18) and neuropodial (11-14)

	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45
L. grasslei	00000	-0000	00000	00000	00000	10000	00000	?000-	00000
P. steenstrupi	10000	-0000	11101	00111	00000	10101	00000	?1110	20100
S. benedicti	11001	01002	00000	11110	00001	01-1-	1-000	?010-	40110
P. africana	210?1	11111	13421	3232?	01102	10303	01021	10112	301?1
P. alata	21011	11111	13441	00221	01102	10202	02010	10112	00101
P. coora	21011	11112	22334	43400	02012	10202	02110	10113	40101
P. cordifolia	21011	11111	13404	43120	12112	10202	02011	00112	10101
P. cristata	210?1	11111	13004	43121	11102	10303	01011	00112	00101
P. dibranchiata	210?1	11111	31101	00031	02013	10400	1-011	001??	001?1
P. inaequibranchia	210?1	11111	13004	43021	01112	10202	02011	10112	001?1
P. lamellibranchia	210?1	11112	13411	00111	01112	10303	01?11	10112	00101
P. oceanensis	21011	11112	13403	32311	02112	10202	02111	00111	10121
P. patiens	21011	11112	13414	03121	01102	10303	01011	10112	10101
P. pinnata	21011	11111	10001	00121	02102	10202	02010	00111	00101
P. tamaii	21011	11111	13302	20201	01102	10202	02010	10112	01101
P. treadwelli	211?1	11111	31004	4302?	01102	10202	02?10	00013	401?1
P. yokoyamai	21011	11111	13204	43001	01102	10202	02010	10111	10101

Table 2. Character matrix. Character numbers correspond to table 1 and cladogram in figure 6. "?" denotes lack of data, "-" denotes inapplicable data. *L. grasslei*, *P. steenstrupi*, *S. benedicti* were defined as outgroup

postchaetal lamellae of chaetigers 2-5 are well developed, and Delgado-Blas (2004) used as useful features to recognize species. The different neuropodial lamellae shapes are rounded, oval, triangular, subtriangular, and cordate; while, the different notopodial lamellae shapes are rounded, oval, subtriangular, triangular, foliaceous, and reniform. All these shapes are easily observed when they are stained with methyl green (see Material and Methods section). Also, it includes the shape of notopodial lamellae of middle segments (19) and the size of parapodial lamellae of last segments (20).

11. Neuropodial lamella shape of segment 2 (chaetiger 1) is highly variable. It varies from rounded (0) as in *L. grasslei* and *S. benedicti*, triangular (1) as in most of *Paraprionospio* species; oval (2) as in *P. coora*; and subtriangular (3) as in *P. dibranchiata* sp. nov. and *P. treadwelli*.

12. The neuropodial lamella of segment 3 (chaetiger 2) is rounded (0) in *L. grasslei*, *S. benedicti* and *P. pinnata*; subtriangular (1) in *P. steenstrupi*, *P. treadwelli* and *P. dibranchiata* sp. nov.; oval (2) in *P. coora*; and triangular (3) in the rest of the species.

13. The neuropodial lamella of segment 4 (chaetiger 3) is rounded (0) in *L. grasslei*, *S. benedicti*, *P. cristata*, *P. inaequibranchia*, *P. pinnata*, and *P. treadwelli*; subtriangular (1) in *P. steenstrupi*, *P. dibranchiata* sp. nov.; cordate (2) in *P. yokoyamai*; oval (3) in *P. coora*, *P. tamaii*; and triangular (4) in *P. africana*, *P. alata*, *P. cordifolia*, *P. lamellibranchia*, *P. oceanensis*, and *P. patiens*.

14. Neuropodial lamella of segment 5 (chaetiger 4) is rounded (0) in species of the outgroup, *P. alata*, *P. cordifolia*, *P. cristata*, *P. dibranchiata* sp. nov., *P. inaequibranchia*, *P. oceanensis*, *P. pinnata*, *P. tamaii*, *P. treadwelli*, and *P. yokoyamai*; triangular (1) in *P. lamellibranchia*, and *P. patiens*; cordate (2) in *P. africana*; oval (3) in *P. coora*; and reniform (4) in *P. alata*.

15. Notopodial lamella of segment 2 (chaetiger 1) is rounded (0) in *L. grasslei* and *S. benedicti*; subtriangular (1) in *P. steenstrupi*, *P. africana*, *P. alata*, *P. dibranchiata* sp. nov., *P. lamellibranchia* and *P. pinnata*; oval (2) in *P. tamaii*; foliaceous (3) in *P. oceanensis*; and triangular (4) in *P. coora*, *P. cordifolia*, *P. cristata*, *P. inaequibranchia*, *P. patiens*, *P. treadwelli* and *P. yokoyamai*.

16. Notopodial lamella of segment 3 (chaetiger 2) is subtriangular (0) in *L. grasslei*, *P. steenstrupi*, *P. alata*, *P. dibranchiata* sp. nov., *P. lamellibranchia*, *P. patiens*, and *P. pinnata*; rounded (1) in *S. benedicti*; oval (2) in *P. tamaii*; foliaceous (3) in *P. africana* and *P. oceanensis*; and triangular (4) in *P. coora*, *P. cordifolia*, *P. cristata*, *P. inaequibranchia*, *P. treadwelli*, and *P. yokoyamai*.

17. Notopodial lamella of segment 4 (chaetiger 3) is subtriangular (0) in *L. grasslei*, *P. steenstrupi*, *P. alata*, *P. dibranchiata* sp. nov., *P. lamellibranchia*, *P. pinnata*, and *P. tamaii*; rounded (1) in *S. benedicti*; foliaceous (2) in *P. africana* and *P. oceanensis*; and triangular (3) in *P. coora*, *P. cordifolia*, *P. cristata*, *P. inaequibranchia*, *P. patiens*, *P. treadwelli*, and *P. yokoyamai*.

18. Notopodial lamella of segment 5 (chaetiger 4) is subtriangular (0) in *L.* grasslei, *P. cristata*, *P. dibranchiata* sp. nov., *P.* inaequibranchia, *P. treadwelli*, and *P. yokoyamai*; rounded (1) in *P. steenstrupi*, *S. benedicti*, *P.* cordifolia, *P. lamellibranchia*, *P. patiens*, and *P.* pinnata; reniform (2) in *P. alata* and *P. tamaii*; foliaceous (3) in *P. africana* and *P. oceanensis*; and triangular (4) in *P. coora*.

19. Notopodial lamellae of middle segments are digitiform (0) in *L. grasslei*, *P. coora*, *P. tamaii*, and *P. yokoyamai*; rounded (1) in *P. steenstrupi*, *S. benedicti*, *P. lamellibranchia*, and *P. oceanensis*; triangular (2) in *P. africana*, *P. alata*, *P. cordifolia*, *P. cristata*, *P. inaequibranchia*, *P. patiens*, *P. pinnata*, *P. treadwelli*; and subtriangular (3) in *P. dibranchiata* sp. nov.

20. Parapodial lamellae of last segments can be reduced (0) as in *L. grasslei*, *S. benedicti*, *P. coora*, and *P. cordifolia*; or can be conspicuous (1) as in the rest of species.

21. The ventral crest of segment 9 is absent (0) in almost all *Paraprionospio* species and the species of outgroup; while it is present (1) in *P. cordifolia* and *P. cristata*.

22. Dorsal crests are considered present when the postchaetal notopodial lamellae are connected over the dorsum forming crests. These crests may be restricted to some chaetigers. Crests present anterior to segment 22 (chaetiger 21) (0) as in *L. grasslei*, *P. steenstrupi*, *S. benedicti*; crest posterior to chaetiger 21 (1) as in *P. africana*, *P. alata*, *P. cristata*, *P. inaequibranchia*, *P. lamellibranchia*, *P. patiens*, *P. tamaii*, *P. treadwelli*, and *P. yokoyamai*; or can be absent (2) as in *P. coora*, *P. cordifolia*, *P. dibranchiata* sp. nov., *P. oceanensis*, and *P. pinnata*.

23. Semitransparent dorsal cuticles are absent (0) in *L. grasslei*, *P. steenstrupi*, *S. benedicti*, *P. coora*, and *P. dibranchiata* sp. nov.; and are present (1) in the rest of the species.

24. Interparapodial pouches are absent

(0) in all species of outgroup and in some *Paraprionospio* species; and the pouches are present (1) in *P. coora*, *P. cordifolia*, *P. dibranchiata* sp. nov., *P. inaequibranchia*, *P. lamellibranchia*, and *P. oceanensis*.

25. Most spionid genera have many pairs of branchiae. Some species have four pairs branchiae (0) as in *L. grasslei* and *P. steenstrupi*; one pair (1) as in *S. benedicti*. The *Paraprionospio* species have been characterized by having three pairs of branchiae (2), excepting the new species *P. dibranchiata* sp. nov. which has only two pairs (3).

In some spionid genera, the branchiae may start on the first of the second, and these branchiae have various branchial appendages on the shaft. Digitiform pinnules are the most common kind of branchial appendages in *Prionospio* and related taxa. The pinnules are arranged along one of the branchial edges or in both. Flattened, stacked, plate-like are characteristic of *Paraprionospio* species.

26. Branchiae on segment 1 are present (0) in *S. benedicti*, or absent (1) in all other species.

27. Branchiae on segment 2 (chaetiger 1) are present (0) in all *Paraprionospio* species, *L. grasslei*, and *P. steenstrupi*; or absent (1) in *S. benedicti*.

28. Pinnules of the branchiae on segment 2 (chaetiger 1) can be absent (0) as in *L. grasslei*; digitiform (1) as in *P. steenstrupi*; flabellate (2) as in *P. alata*, *P. coora*, *P. cordifolia*, *P. inaequibranchia*, *P. oceanensis*, *P. pinnata*, *P. tamaii*, *P. treadwelli*, *P. yokoyamai*; bifoliated (3) as in *P. africana*, *P. cristata*, *P. lamellibranchia*, and *P. patiens*; or unifoliated (4) as in *P. dibranchiata* sp. nov.

29. Branchiae on segment 3 (chaetiger 2) can be present (0) as in *L. grasslei*, *P. steenstrupi* and all *Paraprionospio* species; or absent (1) as in *S. benedicti*.

30. Pinnules of branchiae on segment 3 are absent (0) in *L. grasslei* and *P. dibranchiata* sp. nov.; digitiform (1) as in *P. steenstrupi*; flabellate (2) as in *P. alata*, *P. coora*, and *P. cordifolia*; or bifoliated (3) as in *P. africana*, *P. cristata*, *P. lamellibranchia*, and *P. patiens*.

31. Branchiae on segment 4 (chaetiger 3) are present (0) in *L. grasslei*, *P. steenstrupi* and almost all *Paraprionospio* species; or absent (1) as in *S. benedicti* and *P. dibranchiata* sp. nov.

32. Pinnules of branchiae on segment 4 are absent (0) in *L. grasslei*, *P. steenstrupi*; bifoliated (1) as in *P. africana*, *P. cristata*, *P. lamellibranchia*, and *P. patiens*; or flabellate (2) as in the rest of *Paraprionospio* species.

33. Processes on first branchia are absent (0) in species of outgroup and almost all *Paraprionospio* species, excepting in *P. coora* and *P. oceanensis* when processes are present (1).

34. The ridge is an elevation of the body wall on chaetiger 1. Ridge between branchial bases is absent (0) in species of outgroup; present in the segment 2 (1) as in almost all *Paraprionospio* species, excepting in *P. africana* when the ridge is present on segments 2-4 (2).

35. Filament of segment 4 is absent (0) in species of outgroup, *P. alata, P. coora, P. pinnata, P. tamaii, P. treadwelli, and P. yokoyamai; whereas it is present (1) in P. africana, P. cordifolia, P. cristata, P. dibranchiata n. sp., <i>P. inaequibranchia, P. lamellibranchia, P. oceanensis, and P. patiens.*

36. Neuropodial capillary chaetae on segment 10 (chaetiger 9) are alimbate (0) in *P. cordifolia*, *P. cristata*, *P. dibranchiata* sp. nov., *P. oceanensis*, *P. pinnata*, and *P. treadwelli*; and limbate (1) in *P. africana*, *P. alata*, *P. coora*, *P. inaequibranchia*, *P. lamellibranchia*, *P. patiens*, *P. tamaii* and *P. yokoyamai*.

The hooks are specialized chaetae, generally small, stout, with the main tooth and one or more distal teeth, either with or without a hyaline hood. This hood is called outer or primary hood, and some spionids have another small hood beneath the main tooth called inner or secondary hood; in some species, the hooks have both kinds of hoods. The neuropodial hooded hooks are similar in shape to those of the notopodia; however, they start in different segments.

37. Neuropodial hooks start on segments 7-13 (0) in *L. grasslei*, *S. benedicti*, and all *Paraprionospio* species; and on segments 15-17 (1) in *P. steenstrupi*.

38. The secondary hood is absent (0) in *L. grasslei* and *P. treadwelli*; while it is present (1) in *P. steenstrupi*, *S. benedicti* and all other *Paraprionospio* species.

39. Notopodial hooks are absent (0) in *L. grasslei* and *S. benedicti*; and present (1) in *P. steenstrupi* and all *Paraprionospio* species.

40. Most spionid genera have hooks with many pairs of teeth. The number of accessory pairs of teeth in notopodial hooks are with up to 6 pairs (0) in *P. steenstrupi*; up to 4 pairs (1) in *P. oceanensis*, *P. pinnata*, and *P. yokoyamai*; up to 3 pairs (2) in *P. africana*, *P. alata*, *P. cordifolia*, *P. cristata*, *P. inaequibranchia*, *P. lamellibranchia*, *P. patiens*, and *P. tamaii*; and up to 2 pairs (3) in *P. coora* and *P. treadwelli*.

41. The number of accessory pairs of teeth

in neuropodial hooks is with up to 3 pairs (0) in *L. grasslei*, *P. alata*, *P. cristata*, *P. dibranchiata* n. sp., *P. inaequibranchia*, *P. lamellibranchia*, *P. pinnata*, and *P. tamaii*; up to 4 pairs (1) in *P. cordifolia*, *P. oceanensis*, *P. patiens*, and *P. yokoyamai*; up to 6 pairs (2) in *P. steenstrupi*; up to 5 pairs (3) in *P. africana*; and up to 2 pairs (4) in *S. benedicti*, *P. coora*, and *P. treadwelli*.

42. A single, medial tooth above the main tooth is absent (0) in species of outgroup and almost all *Paraprionospio* species, excepting in *P. tamaii* when it is present (1).

43. A single, medial tooth above the accessories teeth is present (0) in *L. grasslei*; whereas it is absent (1) in *P. steenstrupi*, *S. benedicti* and all *Paraprionospio* species.

44. The pygidium is characterized by having a variable number of anal cirri. The number of anal cirri is three (0) in *L. grasslei*, *P. steenstrupi*, and almost all *Paraprionospio* species; zero (1) in *S. benedicti*; and one (2) in *P. oceanensis*.

45. Dorsum with transverse series of slightly raised ridges is absent (0) in species of outgroup, and present (1) in all *Paraprionospio* species.

RESULTS

SYSTEMATICS

Family Spionidae Grube, 1850 Genus *Paraprionospio* (Caullery, 1914), emended

Type species: Prionospio pinnata Ehlers, 1901, designated by Caullery 1914: 358.

Diagnosis: Prostomium fusiform with rounded, truncate to slightly rounded or bluntly pointed anterior end, occasionally with slight medial peaks; with a raised, narrow ridge on the posterior region of the prostomium; caruncle absent. Eyes present or absent. Peristomium fused with first achaetous segment, forming large lateral membranous wings enclosing prostomium. A pair of grooved palpi with membranous basal sheath. Eversible bilobate proboscis. Muscular gizzard present. Chaetiger 1 well developed, distinct from preceding segments. Two or three pairs of branchiae. When three pairs of branchiae are present, these are on chaetigers 1-3, all with densely packed lamellar plates attached serially on inner to posterior face of shaft, excepting in the basal region and distal tips. When two pairs of branchiae are present, these are located on chaetigers 1-2; first pair of branchiae pinnate with few plate-like pinnules or lamellae, the second one cirriform. Each branchia entirely free from notopodial lamella. Two threadlike filaments at the base of third notopodium present in some species. Distinct transverse ridge between branchial bases of chaetiger 1 or chaetigers 1-3 as in P. africana. Dorsal ridges in middle segment present. Interparapodial pouches present or absent. Notopodial and neuropodial capillaries limbate and granulated in anterior chaetigers, replaced by alimbate, slender capillaries without granulation in middle and posterior chaetigers. Sabre chaetae starting from chaetiger 9. Neuropodial multidentate hooded hooks from chaetiger 9. Notopodial hooded hooks appearing from middle body region. Notopodial and neuropodial hooks with conspicuous striated secondary internal hooded, absent in some species. Shallow ventral furrow presents longitudinally from middle to the end of the body. Dorsal crest present or absent. Pygidium with one long and thin mid-dorsal cirrus, and two shorter ventrolateral cirri present in some species.

Paraprionospio alata (Moore, 1923) (Fig. 1A-N)

Prionospio alata Moore 1923: 185-186. Paraprionospio alata Yokoyama 2007: 257-264, partim.

Type material: Holotype *Prionospio alata*, USNM 17369, off Point Pinos Lighthouse, Monterey Bay, California, 102 m.

Redescription: Holotype incomplete with 50 chaetigers, 29 mm long, 1.6 mm wide. Color in alcohol opaque white. Prostomium fusiform-shaped, frontal rounded (Fig. 1A), without peaks, extending posteriorly as a low raised ridge almost to chaetiger 1. Eyes not visible. Palps lost. Peristomium well developed, prolonged forward nearly to the tip of prostomium (Fig. 1A-B), with conspicuous, thin, translucent lateral wings (Fig. 1B) with rounded margins which conceal almost all prostomium. Posterior margin of each peristomial wing without a small papilla.

Branchiae present on chaetigers 1-3 (Fig. 1C, D, G). First pair of branchiae joined basally by prominent dorsal ridge; first pair longest, third pair shortest; first two basal branchial lamellae like plates; thereafter all lamellae flabellate. Without processes along anterior face of first branchiae, neither slender filament at the base of third branchiae.

Notopodial postchaetal lamellae well

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Fig. 1. *Paraprionospio alata* (Moore, 1923) Holotype USNM 17369. (A) Anterior region, dorsolateral view. (B) Anterior region, lateral view. (C) Parapodia of chaetigers 2-3. (D) Neuropodial lamellae, chaetigers 2-5. (E) Parapodia of chaetigers 6-8. (F) Parapodia of chaetigers 9-14. (G) Anterior region, lateral view. (H) Parapodia, posterior chaetigers. (I) Capillary notochaeta, anterior chaetiger. (J) Capillary neurochaeta, anterior chaetiger. (K) Neuropodial hooded hook. (L) Capillary neurochaeta, middle chaetigers. (M) Sabre chaetae, chaetiger 10. (N) Notopodial hooded hook, chaetiger 50. Scale bars: A, B, C, G = 1000 μm; D, E, F, H, L, N = 100 μm; I, J, K = 20 μm; M = 50 μm).

developed, elongate, subtriangular on chaetigers 1-3 (Fig. 1C-D), with rounded edge basally and middle on chaetigers 2-3; reniform on chaetigers 4-7 (Fig. 1E); lamellae longest on chaetigers 2-4 diminishing progressively in size to chaetiger 8 becoming rounded (Fig. 1F), thereafter becoming triangular (Fig. 1H) on middle and posterior chaetigers of the fragment. Dorsal crest on chaetigers 21-28, accompanied by a semi-transparent dorsal cuticle bearing circular concavities. Notopodial prechaetal lamellae well developed, elongate and fused in both edges of postchaetal and prechaetal lamellae on chaetigers 2-4 (Fig. 1C-E). On chaetigers 5-6 partially fused to postchaetal lamellae (Fig. 1F), posteriorly both lamellae free, diminishing progressively in size on middle and posterior chaetigers of the fragment.

Neuropodial postchaetal lamella triangular (Fig. 1D) on chaetiger 1, acuminate on chaetigers 2-3, distally more pointed on chaetiger 2 (Fig. 1D); rounded on chaetigers 4-12 (Fig. 1E-F), diminishing progressively in size to chaetiger 13, thereafter becoming like a small rounded lobe (Fig. 1H). Neuropodial prechaetal lamellae low, rounded. Interparapodial pouches absent. Ventral crest absent on chaetiger 8.

Anterior capillary bilimbate, long, thick with granulations (Fig 1I-J); posterior ones alimbate, long, thin, without granulations. Neuropodial chaetae (Fig. 1J) shorter and thinner than notopodial chaetae (Fig. 11). Chaetiger 1 with notopodial chaetae arranged in two rows, on chaetigers 2-11 arranged in three rows, on chaetigers 12-30 in two rows, chaetae of first row shortest; thereafter arranged in one row. Chaetigers 1-22 with neurochaetae (Fig. 1J) arranged in two rows, chaetae of first row shortest, replaced by hooded hooks (Fig. 1K), posterior ones with slender alimbate capillaries (Fig. 1L). Sabre chaetae in neuropodia from chaetiger 9, with up to two per fascicle, big, thick, heavily granulated, without limbation (Fig. 1M). Neuropodial hooded hooks very small, from chaetiger 9, up to 10 per fascicle; hooks with three pairs of accessory teeth above the main tooth, and a big striated secondary hood (Fig. 1K); a big primary hood covers more of the half of the shaft (Fig. 1K). Notopodial hooded hooks from chaetiger 46, with up to 2 per fascicle, hooks with 3 pairs of accessory teeth above main tooth, and a big striated secondary hood (Fig. 1N).

Pygidium unknown.

Distribution: Southern California.

Remarks: Foster (1971) synonymized five species previously described as *Prionospio*

africana Augener, 1918, Prionospio alata Moore, 1923, Paraprionospio tribranchiata Berkeley, 1927, Prionospio treadwelli Hartman, 1951 (new name for Prionospio plumosa Treadwell, 1931, which was preoccupied by Prionospio plumosa Sars, M in Sars, GO, 1872), and Prionospio ornata Berkeley and Berkeley, 1961, and a subspecies Prionospio pinnata inaequibranchia Caullery, 1914 with Paraprionospio pinnata (Ehlers, 1901); as a consequences, she considered Paraprionospio a monospecific genus. However, Fauchald (1972) provided morphological evidence to consider that Paraprionospio pinnata, P. inaequibranchia, P. africana, P. alata, and P. treadwelli should be retained as valid species.

Recently, Delgado-Blas (2004) described two new species, Paraprionospio tamaii and P. yokoyamai, from the Grand Caribbean Region. However, Yokoyama (2007) concluded that P. treadwelli, P. tamaii and P. yokoyamai are synonymies of Paraprionospio alata based on the shape of the branchial lamellae, and the presence of the dorsal crests. He redescribed Paraprionsopio alata, mixing the morphological features of the types specimens of P. alata, P. plumosa (formally P. treadwelli), P. yokoyamai and P. tamaii. Due to this, we consider necessary the redescription of P. alata and P. plumosa based upon type material, and also the revision of the type materials of P. yokoyamai and P. tamaii to clarify the supposed synonymies of these species. After that, we found some useful features to distinguish those species as valid (see Table 3).

Paraprionospio alata differs from P. treadwelli. P. tamaii, and P. yokoyamai by having well developed lateral wings touching each other dorsally at the posterior end, while in the other three species the lateral wings are shorter. Of these species, *P. treadwelli* is the only species that has prostomial peaks - a new feature described in this study (see below) - and lacks secondary hood in neuro- and notopodial hooks. Paraprionospio alata and P. tamaii differ from P. treadwelli and P. *yokoyamai* by having the notopodial postchaetal lamellae reniform on chaetigers 4-6, whereas the other species have a subtirangular shape on the same chaetigers. However, P. alata differs of all these species by having the neuropodial postchaetal lamella reniform on the same chaetiger instead of rounded. Furthermore, P. tamaii is the only species with an unpaired accessory tooth at the distal end of the noto- and neuropodial hooded hooks, while the other species have always paired accessory teeth.

Paraprionospio dibranchiata sp. nov.

(Figs. 2A-E; 3A-D) urn:lsid:zoobank.org:act:B384511A-F4DD-45B0-8B09-0CE375C9C82E

Type material: Holotype, USNM 1187918, Gulf of Mexico, off Coatzacoalcos, Veracruz, Mexico, 18°39.8'N, 94°13.1'W, E16, 147 m, mud, coll. F.E. Donath Hernández, 10 August, 1984. Paratypes: ECOSUR 0198, 5 specimens, off Coatzacoalcos, Veracruz, Mexico, 18°40.2'N, 94°25'W, E15, 185 m, muddy, coll. F.E. Donath Hernández, 10 August 1984. ECOSUR 0199, 1 specimen, 18°31'N, 94°36'W, E12, 63 m, coll. F.E. Donath Hernández, 10 August 1984.

Additional material: ECOSUR-SEM; E15, 185 m, 10 August 1984, 18°40.2'N, 94°25'W, muddy, coll. F.E. Donath Hernández.

Description: Holotype incomplete with 29 chaetigers, 7 mm long, 0.4 mm wide. (Paratypes all incomplete with 20-27 chaetigers, 4.5-6 mm long, 0.3-0.4 mm wide). Color in alcohol pale yellow. Prostomium fusiform, frontally truncate to slightly rounded, projecting slightly beyond peristomium (Fig. 2A), continuing as a narrow caruncle posterior to chaetiger 1. Eyes absent.

 Table 3.
 Some taxonomic characters of four *Paraprionospio* species. NoPL: notopodial postchaetal lamellae; NuPL: neuropodial postchaetal lamellae

Characters	P. alata	P. treadwelli	P. tamaii	P. yokoyamai
Type locality	off Point Pinos Lighthouse, Monterey Bay, California. 102 m depth	Chesapeake Bay. 7-48 m depth	Lake Worth, Florida. 2.5-13 m depth	between Dry Tortugas National Park and Naples, Florida, 16- 100 m depth
Prostomium peaks	Absent	Present	Absent	Absent
Peristomium size	Large, prolonged forward nearly to the tip of prostomium, lateral wings touching each other	Moderate. Lateral wings partly enclosing the prostomium	Large. Lateral wings partly enclosing the prostomium	Large. Lateral wings partly enclosing the prostomium
Anterior NoPL				
a. Chaetiger 1	a. subtriangular	a. triangular	a. oval	a. triangular
b. Chaetiger 2	b. subtriangular	b. triangular	b. oval	b. triangular
c. Chaetiger 3	c. subtriangular	c. triangular	c. subtriangular	c. triangular
d. Chaetiger 4	d. reniform	d. subtriangular	d. reniform	d. subtriangular
e. Chaetiger 5	e. reniform	e. subtriangular	e. reniform	e. subtriangular
f. Chaetiger 6	f. reniform	f. subtriangular	f. reniform	f. subtriangular
Middle and posterior NoPL Anterior NuPL	triangular	rounded	cirriform	cirriform
a. Chaetigers 1	a. triangular	a. subtriangular	a. triangular	a. triangular
b. Chaetiger 2	b. triangular	b. subtriangular	b. triangular	b. triangular
c. Chaetiger 3	c. triangular	c. rounded	c. oval	c. cordate
d. Chaetiger 4	d. reniform	d. rounded	d. rounded	d. rounded
e. Chaetiger 5	e. reniform	e. rounded	e. rounded	e. rounded
f. Chaetiger 6	f. reniform	f. rounded	f. rounded	f. rounded
Anterior notochaetae capillary	Bilimbate	Unilimbate	Slightly limbate	Slightly limbate
Anterior neurochaetae capillary	Bilimbate	Alimbate	Slightly limbate	Slightly limbate
Neuropodial hooded hooks				
a. Accessory teeth	a. 3 pairs	a. 2-3 pairs	a. 3 pairs and a single,	a. 3-4 pairs
b. Secondary hood	b. Present	c. Absent	medial tooth at distal end b. Present	b. Present
Notopodial hooded hooks				
a. Accessory teeth	a. 3 pairs	a. 2 pairs	a. 3 pairs and a single,	a. 3-4 pairs
b. Secondary hood	b. Present	b. Absent	medial tooth at distal end b. Present	b. Present

Palps lost. Peristomium moderately developed, collar-like, surrounding the prostomium, distinct from chaetiger 1, with small lateral wings (Fig. 2A-B), without marginal papillae.

Two pairs of branchiae present on chaetigers 1-2 (Fig. 3A); first pair longest, joined basally by

a small dorsal ridge, with few and small pinnules plate-like (Fig. 3A); the most basal branchial lamellae consisting of one rounded plate, lamellae on middle and distal regions thick, blunt and arranged along the posterior margins of the branchial shaft (Fig. 3A); without basal accessory



Fig. 2. Paraprionospio dibranchiata sp. nov. ECOSUR-SEM. (A) anterior region, lateral view; (B) anterior region, dorso-lateral view; (C) anterior and middle region, dorsal view; (D) anterior region, lateral view; (E) interparapodial pouches.

lamellae. Second pair of branchiae cirriform, with smooth surface, and scarce lateral ciliation (Figs. 2A-B; 3A), extending to chaetiger 4 (one specimen missing all branchiae). Chaetiger 3 with a long thin filament at base of third notopodial lamellae; filament twice longer than notopodial lamellae and lightly longer that of second pair of branchiae (Figs. 2A-C; 3A).

Notopodial postchaetal lamellae on chaetigers 1-4 subtriangular; first smallest; largest on chaetigers 2-3 (Fig. 2B); on chaetigers 5-11 becoming smaller, rounded with a small projection at central edge (Fig. 2C); from chaetiger 27 lamellae becoming longer, with subtriangular ligules. Thin glandular fields or rings absent. Notopodial lamellae from chaetiger 23 until last segment expanded towards dorsum, forming a small dorsal fold, without dorsal cuticle. Ventral and dorsal edges of notopodial and neuropodial lamellae not touching each other on anterior chaetigers (Fig. 2C). Notopodial prechaetal lamellae short in branchial region (Fig. 2D), inconspicuous thereafter.

Neuropodial postchaetal lamellae subtriangular on chaetigers 1-3 (Fig. 2B); largest on chaetigers 2-3; rounded with small central projection providing a subtriangular appearance on chaetigers 4-5; from chaetiger 6 entirely rounded, diminishing progressively in size, becoming a small round lobe in most posterior chaetigers (Fig. 2C). Neuropodial prechaetal lamellae very small (Fig. 4A), rudimentary throughout. Interparapodial pouches from chaetigers 6-28 (smallest paratypes, 0.2 mm wide, including parapodia, from chaetigers 5 to 20; in largest paratypes (up to 0.3 mm wide) from chaetiger 7 to about chaetigers 23-25) (Figs.



Fig. 3. Paraprionospio dibranchiata sp. nov. Holotype USNM 1187918. (A) anterior region, lateral view; (B) ventrolateral interparapodial pouches; (C) sabre chaeta; (D) neuropodial hooded hook. Scale bars: A = 200 μm; B = 64.28 μm; C, D = 0.5 μm.

2C, E; 3B). Ventral crest on chaetiger 8 absent.

Capillary chaetae in anterior region thick, moderately granulated, without limbation, arranged in two rows, chaetae of first row shortest, with fine granulations on shaft. Capillary chaetae of posterior region thin, lacking granulations. Sabre chaetae from chaetiger 9 (Figs. 2E; 3C), small, thin, moderately granulated, without limbation; one per neuropodium (Fig. 2E). Neuropodial hooded hooks from chaetiger 9, with 8-9 hooks per neuropodium, alternating with capillary chaetae (Fig. 2E); hooded hooks with three pairs of small accessory teeth above main fang, secondary hood striated (Fig. 3D). Notopodial hooded hooks not observed in fragments. Shallow furrow on ventral side of body beginning from chaetiger 15 to the end of the fragment.

Pygidium unknown.

Type locality: off Coatzacoalcos, Veracruz, Mexico (18°39.8'N, 94°13.1'W).

Distribution: Paraprionospio dibranchiata sp. nov. occurs in the SW Gulf of Mexico, off Coatzacoalcos, Veracruz, Mexico, from depths of 63-185 m on muddy bottoms.

Etymology: The species name, *dibranchiata*, refers to the number of pairs of branchiae.

Remarks: The presence of one filament at the base of the third notopodial lamellae is similar to *Paraprionospio inaequibranchia* and some species described by Yokoyama (2007), with which this species was compared. However, the consistency of taxonomic characters of *Paraprionospio dibranchiata* sp. nov. over the number and shape of branchiae is different to all other known *Paraprionospio* species. All specimens of *P. dibranchiata* sp. nov. have two pairs rather than three pairs of branchiae; the first pair is pinnate and the second one cirriform.

Foster (1971) and Yokoyama (1981) mentioned that in some instances, during the branchial regeneration, branchiae are entirely smooth in Paraprionospio pinnata. Also, Carrasco (1976) reported that the first pair of branchiae is bipinnate and the second pair cirriform in the larval stage of *P. pinnata*. However, all specimens studied in this study are juvenile or adult specimens. Further, the specimens were collected in three stations from the Gulf of Mexico at different depths (63-185 m), and all specimens have the same shape and number of branchiae regardless of its size. Therefore, we consider that the shape and the number of branchiae of these specimens do not correspond to branchiae in regeneration process or larval specimens.

Paraprionospio inaequibranchia (Caullery, 1914) (Figs. 4A-R)

Prionospio pinnata inaequibranchia Caullery 1914: 356-358, fig. 2.

Paraprionospio inaequibranchia Yokoyama 2007: 267-270, partim.

Type material: Four syntypes. Southern Africa: Siboga-Expeditie: ZMA 1568 (1), Sta. 2, Java Sea, 37 m; ZMA 1566 (1), Sta. 51, Java Sea, 69 m; ZMA 1571 (1), sta. 181, Ambon, Banda Sea, 54 m; ZMA 1688 (1), sta. 261, Banda Sea, 27 m. One of them designated as lectotype (ZMA 1688), the other are designated as paralectotypes (ZMA 1568, ZMA 1566, ZMA 1571).

Redescription: Lectotype (ZMA 1688) incomplete specimen with 35 chaetigers, 13 mm long, 1.5 mm wide. A gravid female with ova in chaetigers 10-35. All paralectotypes incompletes with 21-35 chaetigers (11-13 mm long, 1.5-2.0 mm wide). Any variation found on paralectotypes is given in brackets. Color in alcohol yellowish-brown with no obvious patterns.

Prostomium frontally truncated to rounded, projecting slightly beyond peristomium, extending posteriorly to chaetiger 1 as a narrow caruncle (Fig. 4A). Eyes absent. Palps lost. Peristomium long, forming large lateral wings which enclosing completely the prostomium (Fig. 4B), distinct from chaetiger 1; posterior margin of peristomial wings without papillae.

Three pairs of branchiae present on chaetigers 1-3. First pair of branchiae joined basally by a prominent dorsal ridge (Fig. 4A); first two pairs of branchiae of similar length, the third one shortest. All branchiae with densely packed of flabellate lamellae (Fig. 4C-E) over most of branchial length, decreasing slightly in size distally; branchial shaft bare distal and basally; the lamellae distribution of the three pair similar as the other: first pair basally with several triangular lamellae on anterior surfaces, without anterior basal accessory lamellae; middle and distal region with flabellate lamellae enclosing lateral and posterior surfaces (Fig. 4C). Second (Fig. 4D) and third pair of branchiae basally with few triangular lamellae (Fig. 4E); thereafter all lamellae flabellate, continuing to the distal end. First pair of branchiae as wide as half the body width, second pair narrower, and third pair thinner, half as wide as second branchiae. Filament present at base of third pair of branchiae (Fig. 4E).



Fig. 4. *Paraprionospio inaequibranchia* (Caullery, 1914). Lectotype ZMA1688. (A) anterior region, dorsal view; (B) anterior region, dorso-lateral view; Paralectotype ZMA1568. (C) first branchia; (D) second branchia; (E) third branchia and filament; (F) parapodium of chaetiger 1; (G-I) parapodium of chaetigers 2-4; (J-L) parapodium of chaetigers 7-9; (M) parapodium of chaetiger 13; (N) capillary notochaeta, chaetiger 2; (O) capillary neurochaeta, anterior chaetiger; (P) sabre chaeta, chaetiger 10; (Q) neuropodial hooded hook, chaetiger 11; (R) notopodial hooded hook, chaetiger 34. Scale bars: A-I = 571.2 μm; J-L = 571 μm; M = 200 μm; N-R = 50 μm.

Anterior notopodial postchaetal lamellae well developed, triangular (Fig. 4B), basally wider and rounded, distally pointed on chaetigers 1-6 (Fig. 4F-I); longest over chaetigers 2-4 (Fig. 4B); oval and smaller on chaetigers 7-9 (Fig. 4J-L), posteriorly becoming subtriangular at least until chaetiger 13 (Fig. 4M), from posterior chaetigers rounded, smallest. Dorsum of chaetigers 13-17 with transverse series of three slightly raised ridges. Dorsal crests on chaetigers 21-26 (two paralectotypes with dorsal crest missing). Ventral and dorsal edges of notopodial and neuropodial lamellae touching on chaetigers 1-2 (Fig. 4F-G). Notopodial prechaetal lamellae very large in anterior chaetigers (Fig. 4B), basal and middle edges fused with notopodial postchaetal lamellae (Fig. 4B, G-I), with fold or cup-shaped appearance becoming more pronounced on more anterior chaetigers when lamellae increase its size, with dorsolateral edge becoming more curved (Fig. 4G-I).

Neuropodial postchaetal lamella triangular on chaetiger 1 (Fig. 4F), triangular on chaetiger 2 (Fig. 4G), becoming wider and rounded with a small central projection on chaetiger 3 (Fig. 4H), rounded on chaetigers 4-9 (Fig. 4I-L), diminishing progressively in size to chaetiger 9; thereafter becoming a small triangular lobe (Fig. 4M). Neuropodial prechaetal lamellae very small (Fig. 4B, F-I), rudimentary throughout. Interparapodial pouches on chaetigers 9-19 (paralectotypes on chaetigers 11/17-18/28). Ventral crest absent on chaetiger 8.

Chaetae of first five chaetigers arranged in three rows, thereafter arranged in two rows, with chaetae of posterior row longest. All notopodial chaetae unilimbate, smooth (Fig. 4N), larger than those of neuropodia. Anterior neuropodial chaetae smooth, weakly bilimbate, anterior row broadest, (Fig. 4O), and shorter than those of posterior row. Sabre chaetae from chaetiger 9, with up to three per neuropodium, each chaeta stout, strongly granulated, without limbation (Fig. 4P). Neuropodial hooded hooks (Fig. 4Q) from chaetiger 9, with up to 15 per neuropodium, alternating with long, slender, alimbate chaetae. Notopodial hooded hooks (Fig. 4R) from chaetiger 30 (paralectotypes on 30-33), with up to three per notopodium, alternating with long and thin capillary chaetae. All hooded hooks, with three pairs of apical teeth above main fang and striated secondary hood (Fig. 4Q-R); with long, slightly curved shaft.

Posterior segments missing from all specimens.

Distribution: Herein, we restring the distribution of this species to the region of the Banda Sea and Java Sea.

Remarks: Prionospio pinnata inaequibranchia was described by Caullery (1914) based on specimens collected off Southern Africa from 54 to 1000 m depth. Recently, Yokoyama (2007) redescribed Paraprionospio inaequibranchia based on the syntypes and a specimen from Gadavari estuary, India, reported as P. lamellibranchia by Hartman (1974) and specimens collected from Malaysia. Yokoyama (2007) noted that the shape of the notopodial postchaetal lamellae is elongate, subtriangular on chaetigers 1-3, becoming low rounded and shorter from chaetiger 4 to about chaetiger 11. However, Yokoyama did not provide details on the notopodial lamellae which are anteriorly curved or folded, tapering dorsally with a gently curving at the dorsolateral border. The fold or cup-shaped appearance becomes more pronounced on more anterior chaetigers when the lamella is larger, with the dorsolateral edge becoming more curved. This cup result from the fusion of the medial edges of the pre- and postchaetal lamellae rather than folds in the postchaetal lamellae. Also, Yokoyama (2007) reported two pairs of dark-brown eyes in trapezoidal arrangement, neuropodial hooks with 4-5 pairs of accessory teeth, and notopodial hooks with 4 pairs. However, the presences of these eves and the number of the apical teeth are based on the specimens from Malaysia and India. None of the type specimens have eyes and all noto- and neuropodial hooks have three pairs of accessory teeth. We do not consider the specimens from Malaysia and India as belonging to Paraprionospio inaequibranchia.

Paraprionospio treadwelli (Hartman, 1951) (Fig. 5A-I)

Prionospio plumosa Treadwell 1931: 3-5, fig. 3. non Sars M. in Sars G.O. 1872.

Prionospio treadwelli Hartman 1951: 84-85 (new name for *P. plumosa* Treadwell, 1931).

Type material: Holotype *Prionospio plumosa*, USNM 19598, sta. 8881, Chesapeake Bay.

Additional material: Topotypes specimens, 7 specimens from the same station of holotype; 1 specimen, sta. 8882, in bad condition (anterior fragment with 12 chaetigers).

According to Treadwell (1931), the material was collected ranging through the lower middle

bay from the mouth of the Patuxent River to the mouth of the Rapphannock River, in depths of from 7.32 to 47.58 m, August 22 to October 19, 1920.

Redescription: Holotype incomplete with 46 chaetigers, 15 mm long, 0.6 mm wide. Median and posterior chaetigers in bad condition. Topotype specimens incomplete, with 38-62 chaetigers, 7-16 mm long, 0.5-0.8 mm wide. Color in alcohol dark. Prostomium spindle-shaped, small, frontally rounded (Fig. 5A), with two small peaks on ventrolateral position (one specimen with four peaks), one on each side of prostomium (Fig. 5B). The prostomium extends posteriorly as a low raised ridge until chaetiger 1 (Fig. 5A). Eyes not visible in holotype, some specimens with two pairs of dark-brown eyes in trapezoidal arrangement. Palps lost. Peristomium not fused with chaetiger 1; extending dorsally as a pair of lateral wings of moderate size, which partially enclose the prostomium, (Fig. 5C). Posterior margins of peristomial wings without pigment spots neither marginal papilla.

Branchiae present on chaetigers 1-3, all with flabellate lamellae (Fig. 5A, C); because of the condition of holotype, the description is based on topotype specimens. First pair largest, joined basally by a small dorsal ridge, without processes along anterior edge neither slender filament.

Notopodial postchaetal lamellae of chaetigers 1-3 elongate, triangular (Fig. 5C); longest on chaetiger two; lamellae of chaetigers 4-7 subtriangular (Fig. 5C), gradually reduced on the following segments, becoming rounded (Fig. 5D) near to the end of the fragments. Dorsal crests on chaetigers 21-28 (in holotype those chaetigers in bad conditions), accompanied by



Fig. 5. *Paraprionospio treadwelli* (Hartman, 1951). Holotype USNM 19598 (C), Topotype (A-B, D-I). (A) anterior region, dorsal view; (B) prostomium, lateral view; (C) anterior region, lateral view; (D) middle region, lateral view; (E) capillary notochaeta, anterior chaetiger; (F) capillary neurochaeta, anterior chaetiger; (G) sabre chaeta, chaetiger 10; (H) neuropodial hooded hook, chaetiger 11; (I) notopodial hooded hook, chaetiger 46. Scale bars: A, C, D = 500 μm; B = 90 μm; E-I = 0.5 μm.

a semitransparent dorsal cuticle. On anterior chaetigers, ventral edge of notopodial lamellae does not touch the dorsal edge of neuropodial lamellae (Fig. 5C). Notopodial prechaetal lamellae short in branchial region, inconspicuous thereafter.

Neuropodial postchaetal lamellae small, rounded through (Fig. 5C), except on chaetigers 1-2, subtriangular (Fig. 5C); becoming wider, rounded (Fig. 5C) on chaetigers 3-10, decreasing progressively in size, thereafter becoming as a small rounded lobe (Fig. 5D). Neuropodial prechaetal lamellae very small on anterior chaetigers (Fig. 5C), inconspicuous on median and posterior chaetigers. Interparapodial pouches and ventral crest on chaetiger 8 absent.

Capillary chaetae in anterior region thick, densely granulated (Fig. 5E-F); arranged in two rows, chaetae of first row shortest, with granulations on shaft; notochaetae unilimbated (Fig. 5E), and more granulated than neurochaetae; neurochaetae alimbates (Fig. 5F). Capillary chaetae of posterior region long, thin, without limbations neither granulations; neurochaetae shorter and thinner than notochaetae. Sabre chaetae from chaetiger 9, stout, heavily granulated, without limbation (Fig. 5G); with up to 2 per neuropodium. Neuropodial hooded hooks (Fig. 5H) from chaetiger 9, with up to 10 hooks per neuropodium, accompanied with small and thin capillary chaetae; hooded hooks with 2-3 pairs of small accessory teeth above main tooth (Fig. 5H). Notopodia hooded hooks (Fig. 5I) from chaetiger 45 (topotypes specimens 41-45), accompanied with long capillary chaetae, without granulations and alimbated; hooded hooks with 2 pairs of small accessory teeth above main fang (Fig. 51). All hooks with main hood striated (Fig. 5H-I), neuropodial hooks with main hood bigger than notopodial hooks, covering more than half of the hooks shaft; all hooks without secondary hood.

Pygidium unknown.

Distribution: Chesapeake Bay, USA. From 7 to 48 m depth.

Remarks: Treadwell (1931) described *Prionospio plumosa* based on specimens collected from the Chesapeake Bay. Hartman (1951) gave a new name for this species as *Prionospio treadwelli* because the specific name was preoccupied by *Prionospio plumosa* M. Sars in G.O. Sars, 1872. However, she described the species based on specimens collected from Louisiana, Gulf of Mexico, and stated the presence of four pairs of branchiae on those specimens. As we noted above and previously other authors (Foster 1971; Yokoyama 2007) the species only have three pairs of branchiae. Because of the presence of four pairs of branchiae on Hartman's specimens, these specimens correspond to a different species of *Prionospio*. Yokoyama (2007) considered *Paraprionospio treadwelli* similar to *Paraprionospio alata* in that both have three pairs of branchiae and a membranous dorsal crest on chaetigers 21-28. Due to these similarities, he suggested that both species are conspecific. However, *P. treadwelli* differs from *P. alata* in many features, as was noted above in the remark section of *P. alata* and table 3.

Phylogenetic analysis

The Branch-Bound search yielded one most parsimonious tree of 191 steps, with a consistency index (CI) of 0.45, excluding uninformative characters, and a retention index (RI) of 0.54 (Fig. 6).

Our result shows *Paraprionospio* characterized by a prostomium spindle-shaped, Peristomial wings conspicuous; notochaetae and neurochaetae of first segment absent; Postsetal lamellae of first segment well developed; Notopodial lamellae of middle segments triangular; with three pairs of branchiae (excepting *P. dibranchiata* sp. nov.); Pinnules branchial on segment 2 flabellated; Ridge between branchial bases on segment 2; with dorsum with transverse series of slightly raised ridges; Caruncle reach segment 1; peristomial wings present; peristomium and segment 1 completely fused. All characters, except the last three, are non-homoplastic.

In the analysis, the basal species is P. dibranchiata sp. nov., which is mainly characterized by having two pairs of branchiae, the first pair with unifoliated branchial pinnules, and notopodial lamellae of middle segments subtriangular; all these characters are autapomorphies. The following species is P. pinnata followed by a major clade including all other Paraprionospio species. The major clade is characterized by having dorsal crest posterior to segment 21, and with up to 3 pairs of secondary teeth in notopodial hooks. This clade is subdivided into another two subclades; the first one, identified by two homoplastic characters (triangular neuropodial lamellae on segment 3, and neuropodial capillaries on segment 10 limbate) include the species P. africana, P. lamellibranchia, P. patiens, P. alata and P. tamaii. In this group of species, P. africana, P. lamellibranchia, and P. patiens constitute a clade with P. africana basal to the sister species *P. lamellibranchia* and *P. patiens*;

while, *P. alata* and *P. tamaii* constitute a clade characterized by having one non-homoplastic character, the notopodial lamellae segment 5 reniform.

The second subclade is characterized by one non-homoplastic character (triangular notopodial lamellae of segment 3), and three homoplastic characters (triangular notopodial lamellae of segment 2 and 4, subtriangular notopodial lamellae of segment 5). This subclade is divided in another two clades, the first one including the species *P. treadwelli* as basal species of the sister species *P. coora* and *P. yokoyamai*. The second one, identified by two homoplastic characters (lanceolate neuropodial lamellae of segment 3 and filament of segment 4 present) includes *P. cristata* as the basal species followed by *P. inaequibranchia* as sister species of *P. cordifolia*



Fig. 6. Most parsimonious tree. Numbers in plain text are the characters and the superscript number is the character state occurring at the internode; filled rectangles represent no homoplasy, blank rectangles represent homoplasy, double lines represent reversal.

and P. oceanensis.

The result of this analysis confirms our idea that *P. treadwelli*, *P. tamaii* and *P. yokoyamai* are not synonymies of *P. alata* as Yokoyama suggested (2007). We found that the shape of noto- and neurolamellae are very useful features for recognizing the species.

Taxonomic key to all Paraprionospio species

1.	A filament present at base of third branchia
2(1)	With two pairs of branchiae: peristomium with small
2(1)	lateral wings: anterior notochaetae capillary alimbate
	<i>R</i> dibranchiata sp. pov
	With three poins of bronchies, periotemium with his or
-	with three pairs of branchiae, peristonium with big of
	moderate lateral wings, antenor notochaetae capillary
2(2)	uni- or bilimbate
3(2)	Interparapodial pouches present
-	Interparapodial pouches absent
4(3)	Dorsal crests present on postbranchial segments
-	Dorsal crests absent
5(4)	Small papilla on posterior margin of peristomial wing
	absent; anterior neuropodial postchaetal lamellae on
	chaetigers 3-4 rounded; anterior notochaetae capillary
	unilimbate <i>P. inaequibranchia</i> (Caullery, 1914)
-	Small papilla on posterior margin of peristomial wing
	present; anterior neuropodial postchaetal lamellae on
	chaetigers 3-4 triangular; anterior notochaetae capillary
	bilimbate P. Iamellibranchia Hartman, 1974
6(4)	Ventral crest present; small papilla on posterior margin of
	peristomial wing absent; anterior notopodial postchaetal
	lamellae on chaetigers 1-3 triangular
	P. corditolia Yokoyama, 2007
-	ventral crest absent; small papilla on posterior margin of
	peristomiai wing present; anterior notopodiai postchaetai
	lameliae on chaetigers 1-3 foliaceous, distally pointed
7(0)	With angle and active an estation meaning of pariotamic
7(3)	with small papilla on posterior margin of peristomial
	Wing P. patiens Yokoyama, 2007
-	Vittout papilia on posterior margin of peristomial wing 8
8(7)	ventral crest present; ridge between branchial base on
	chaetigers 2-3 absent; notopodial lamella on chaetigers
	1-3 triangular, on chaetiger 4 rounded; neuropodial
	lameliae on chaetigers 3-4 rounded
	P. cristata Zhou, Yokoyama and Li, 2008
-	ventral crest absent; ridge between branchial bases of
	chaetigers 2-3 present; notopodial lamellae on chaetiger
	r elongate subtriangular, on chaetigers 2-4 follaceous;
	neuropodial lameliae on chaetiger 3 triangular, cordate
0(1)	on chaetiger 4 P. arricana (Augener, 1918)
9(1)	interparapodial pouches present; with small papilia
	on posterior margin of peristomial wing; dorsal crests
	absent P. coora vviison, 1990
-	interparapodial pouches absent; without papilla on
	posterior margin of peristomial wing; dorsal crests
10(0)	present on postbranchial segments
10(9)	Prostomium peaks present; peristomium small; middle
	and posterior notopodial postchaetal lamellae rounded;
	nooks without secondary nood
	P. treadwelli (Hartman, 1951)

⁻ Prostomium peaks absent; peristomium large; middle

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	and posterior notopodial postchaetal lamellae triangular
	or cirriform; hooks with secondary hood 11
11(10)	Peristomium with large lateral wings almost enclosing
	all the prostomium; anterior neuropodial postchaetal
	lamellae on chaetiger 3 triangular, on chaetigers
	4-6 reniform; notopodial prechaetal lamellae basally
	fused with notopodial postchaetal lamellae on anterior
	chaetigers P. alata (Moore, 1923)
-	Peristomium with lateral wings of moderate size, never
	enclosing prostomium; anterior neuropodial postchaetal
	lamellae on chaetiger 3 rounded or cordate, on
	chaetigers 4-6 rounded; notopodial prechaetal lamellae
	not fused with notopodial postchaetal lamellae on
	anterior chaetigers 12
12(11)	Anterior notopodial postchaetal lamellae on chaetigers
	1-2 oval, on chaetigers 4-6 reniform; all hooks with 3
	pairs and a single medial tooth at distal end
	P. tamaii Delgado-Blas, 2004
-	Anterior notopodial postchaetal lamellae on chaetigers
	1-2 triangular, on chaetigers 4-6 triangular or
	subtriangular; nooks with 3-4 pairs, without a single
40(40)	medial tooth
13(12)	Dorsal crests absent; anterior neuropodial postchaetal
	lameliae on chaetigers 2-3 rounded
	<i>P. pinnata</i> (Ehlers, 1901)
-	Dorsal crests present; anterior neuropodial postchaetal
	amenae on chaeliger 2 mangular, cordate on chaeliger
	з P. уокоуата Deigado-Blas, 2004

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Availability of data and materials: The specimens are deposited in the National Museum of the Natural History, Smithsonian Institution, Washington (USNM); Zoologisch Museum, Universiteit van Amsterdam (ZMA); and the Collection of Benthos (ECOSUR) of El Colegio de la Frontera Sur, Chetumal, Mexico. Consent for publication: Not applicable.

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REFERENCES

- Augener H. 1918. Polychaeta. Beitrage zur Kenntnis der Meeresfauna Westafrikas. Herausgege- ben von W. Michaelsen (Hamburg). L. Friederichsen & Co., Hamburg 2:67-625, 6 pls.
- Blake JA, Kudenov JD. 1978. The Spionidae (Polychaeta) from southeastern Australia and adjacent areas with a revision of the genera. Mem Nat Mus Victoria **39**:171-280.
- Berkeley E. 1927. Polychaetous annelids from the Nanaimo district, 3. Leodicidae to Spionidae. Contr Can Biol Fisheries **3**:407-423.
- Berkeley E, Berkeley C. 1961. Notes on Polychaeta from California to Peru. Can J Zool **39:**655-664.
- Carrasco FD. 1976. Larvas de la Familia Spionidae (Polychaeta) en el plancton de la Bahía de Concepción, Chile. Gayana Zool **38:**1-63.
- Caullery M. 1914. Sur les Polychètes du genre *Prionospio* Malgren. B Soc Zool Fr **39**:355-361.
- Delgado-Blas VH. 2004. Two new species of *Paraprionospio* (Polychaeta: Spionidae) from the Grand Caribbean region and comments of the genus status. Hydrobiologia **520**:189-198. doi:10.1023/B:HYDR.0000027719.31685. d3.
- Ehlers E. 1901. Die Polychaeten des magellanischen und chilenischen Strandes. Ein faunistischer Versuch. Festschrift zur Feier des hundertfünfzigjährigen Bestehens der königlichen Gesellschaft der Wissenschaften zu Göttingen, Abhandlungen der Mathematisch-Physikalischen Klasse. Weidmannsche Buchhandlung, Berlin, Germany.
- Fauchald K. 1972. Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the eastern Pacific Ocean. Allan Hancock Monogr Mar Biol 7:1-575.
- Foster NM. 1971. Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea. Stud Fauna Cur **36**:1-183.
- Grube AE. 1850. Die Familien der Anneliden. Arch Naturg Berlin 16:249-364.
- Hartman O. 1951. The littoral marine annelids of the Gulf of Mexico. Pub Inst Mar Sci **2:**7-124.
- Hartman O. 1974. Polychaetous annelids of the Indian Ocean, including an account of species collected by members of the International Indian Ocean Expeditions, 1964-65 and

a catalogue and bibliography of the species from India. J Mar Biol Ass India 16:191-252.

- Maciolek NJ. 1981. A new genus and species of Spionidae (Annelida: Polychaeta) from the North and South Atlantic. Proc Biol Soc Wash **94**:228-239.
- Maciolek NJ. 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). Zool J Linn Soc **84:**325-383.
- Madisson DR, Maddison WP. 2001. MacClade 4: Analysis of Phylogeny and Character evolution. version 4.08 (Computer program and Manual), Sinauer Associates, Sunderland, Massachusetts.
- Malmgren AJ. 1867. Annulata Polychaeta: Spetsbergiae, Groenlandiae, Islandiae et Scandinaviae. Hactenus Cognita Kong Vetensk Akad Förhandl **1867**:127-235.
- Moore JP. 1923. The polychaetous annelids dredged by the USS "Albatross" off the coast of southern California in 1904. IV, Spionidae to Sabellariidae. Proc Acad Nat Sci Philadelphia **75**:179-259.
- Sars GO. 1872. Diagnoser af nye Annelider fra Christianafjorden, efter M. Sars efterladte Manuskripten. Forhandlinger i Videnskabsselskabet i Kristiania **1871:**406-417.
- Sigvaldadóttir E, Mackie ASY, Pleijel F. 1997. Generic interrelationships within the Spionidae (Annelida: Polychaeta). Zool J Linn Soc **119:**473-500. doi:10.1006/ zjls.1996.0074.
- Swofford DL. 1998. PAUP: Phylogenetic Analysis Using Parsimony, Version 4.0. Sunderland, MA: Sinauer Associates.
- Treadwell AL. 1931. Three new species of polychaetous annelids from Chesapeake Bay. Proc USNM **79:**1-5.
- Wilson RS. 1990. *Prionospio* and *Paraprionospio* (Polychaeta: Spionidae) from Southern Australia. Mem Nat Mus Victoria **50**:243-274.
- Yokoyama H. 1981. Larval development of a spionid-Polychaete Paraprionospio pinnata (Ehlers). Pub Seto Mar Biol Lab 26:157-170.
- Yokoyama H. 2007. A revision of the genus *Paraprionospio* Caullery (Polychaeta: Spionidae). Zool J Linn Soc **151:**253-284. doi:10.1111/j.1096-3642.2007.00323.x.
- Yokoyama H, Tamai K. 1981. Four forms of the genus *Paraprionospio* (Polychaeta: Spionidae) from Japan. Pub Seto Mar Biol Lab **26**:303-317.
- Zhou J, Yokoyama H, Li X. 2008. New records of *Paraprionospio* (Annelida: Spionidae) from Chinese waters, with the description of a new species. Proc Biol Soc Wash **121**:308-320. doi:10.2988/08-10.1.