

## Phylogenetic analysis of *Petaloproctus* (Maldanidae: Polychaeta), with description of a new species from southeastern Brazil

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**SUMMARY:** We used morphological data for a phylogenetic analysis of the genus *Petaloproctus* (Maldanidae: Polychaeta). We found three most parsimonious phylogenetic trees with length = 37, CI = 0.89 and RI = 0.92. The genus *Petaloproctus* is monophyletic, and is supported by a strongly arched prostomium, pinnate capillary setae, and an anal cup with a reduced dorsal border. Our proposal for the systematisation of the subgroups of *Petaloproctus* is ((*P. tenuis* (*P. terriculus* + *P. neoborealis*)) (*P. ornatus* (((*P. cirratus* + *P. dentatus*) (*P. macrodentatus* (*P. borealis* (*P. vallejo* n. sp. + *P. socialis*)))))). We also regard Nicomachinae as a monophyletic group with the following synapomorphies: prostomium short and arched; nuchal grooves short and curved; cephalic plate lost; anal pore opening on margin of anal plate. Monophyly of *Micromaldane* and *Nicomache* was also supported in the analysis. *Petaloproctus vallejo* n. sp. has 19 setigerous and one asetigerous pre-anal segment. The prostomium is rounded, forming a keel with curved laterals. Nuchal grooves are short and deep, strongly curved outwards. Each neuropodium has one acicular spine on setigers 1-3. The pygidium has a large ventral border, and a reduced dorsal border. The anus is terminal, and close to the margin of the anal plate, surrounded by divergent folds.

**Keywords:** phylogeny, maldanids, Nicomachinae, *Petaloproctus*, coast of São Paulo, southeastern Brazil.

**RESUMEN:** ANÁLISIS FILOGENÉTICO DE *PETALOPROCTUS* (MALDANIDAE: POLYCHAETA) CON LA DESCRIPCIÓN DE UNA NUEVA ESPECIE EN EL SURESTE DE BRASIL. – En este estudio se utilizaron datos morfológicos para realizar un análisis filogenético del género *Petaloproctus* (Maldanidae: Polychaeta). Se establecieron los tres árboles filogenéticos más parsimoniosos, con tamaño = 37, CI = 0.89 y RI = 0.92. El género *Petaloproctus* es monofilético, y es soportado por un prostomio arqueado; cerdas capilares pinadas y un copo anal con borde dorsal muy reducido. Nuestra propuesta de sistematización para los subgrupos de *Petaloproctus* es ((*P. tenuis* (*P. terriculus* + *P. neoborealis*)) (*P. ornatus* (((*P. cirratus* + *P. dentatus*) (*P. macrodentatus* (*P. borealis* (*P. vallejo* n. sp. + *P. socialis*)))))). También se recomienda Nicomachinae como un grupo monofilético con las siguientes sinapomorfias: prostomio corto y arqueado; órganos nucales cortos y curvados; sin placa cefálica; poro anal abriéndose en el margen de la placa anal. Los análisis realizados soportan la monofilia de *Micromaldane* y *Nicomache*. *Petaloproctus vallejo* n. sp. se describe para el litoral sureste del Brasil. Esta especie nueva posee 19 segmentos setígeros y 1 segmento asetígero preanal. El prostomio es redondeado anteriormente y forma una quilla con los bordes laterales curvados. Los órganos nucales son cortos y profundos, ligeramente curvados hacia fuera. Posee una espina acicular en los setígeros 1-3. El pigidio con el borde ventral grande y un borde dorsal reducido. El ano es terminal, central, e incluido en la placa, con varios pliegues divergentes.

**Palabras clave:** filogenia, maldánidos, *Petaloproctus*, costa de São Paulo, sureste de Brasil.

## INTRODUCTION

Maldanids are sedentary, tube-builder polychaetes, commonly known as bamboo worms because of the elongate median segments with globose tori at the extremities (Fauchald and Rouse, 1997). There are no head appendages, but some species may have a cephalic plate. The keel-shaped prostomium is completely fused to the peristomium. The pygidium may be cone-shaped and bear a truncate plate, or this plate may be within the anal cup (Day, 1967; Hartmann-Schröder, 1971; Fauchald, 1977; Imajima and Shiraki, 1982).

Maldanids are found from the intertidal region to the deep sea (Arwidsson, 1907; Chamberlin, 1919). Their tubes are constructed both horizontally, with sand and shell fragments under rocks, or vertically, in sandy bottoms with fine and hyaline sand (De Assis *et al.*, 2007a, b).

The subfamily Nicomachinae was proposed by Arwidsson (1907) to include three genera: *Micromaldane* Mesnil, 1897, *Nicomache* Malmgren, 1865 and *Petaloproctus* Quatrefages, 1865.

The genus *Petaloproctus* Quatrefages, 1865 has nine valid species (De Assis *et al.*, 2007b). The main characters conventionally used to separate species are the form of the anal plate and of the funnel. Three of the currently known species have a smooth anal border and the other six have a cirri-rimmed anal plate (De Assis *et al.*, 2007a).

The aim of the present study is to propose the first phylogenetic analysis of *Petaloproctus* and to describe *P. vallejoi* n. sp. from shallow shelf waters off the coast of São Paulo, southeastern Brazil. We also tested the monophyly of the subfamily Nicomachinae, and its genera.

## MATERIAL AND METHODS

All information was obtained from the literature, from observations of the new species described herein, and from examination of the following species:

1. El Colegio da la Frontera Sur (ECOSUR) - *Euclymene coronata* (Verrill, 1900), *Axiiothella mucosa* Andrews, 1891, *Axiiothella somersi* (Verrill, 1900), *Micromaldane ornithochaeta* Mesnil, 1897, and *Nicomache (Nicomache) antillensis* Augener, 1922.

2. Centro de Estudos do Mar, Universidade Federal do Paraná (CEM-UFPR) - *Axiiothella brasiliensis* (Mangum, 1966), *Clymenella dalesi* Mangum,

1966, and *Petaloproctus borealis* Arwidsson, 1907.

3. Universidade Federal da Paraíba (UFPB) - *Axiiothella brasiliensis* (Mangum, 1966); *Clymenella dalesi* Mangum, 1966, *Clymenella zonalis* (Verrill, 1874), *Isocirrus papillatus* (Berkeley and Berkeley, 1939), *Nicomache (Nicomache) brasiliensis* De Assis *et al.*, 2007b, *Nicomache (Nicomache) lanai* De Assis *et al.*, 2007b; *Nicomache (Nicomache) lumbri-calis* (Fabricius, 1870).

We used illustrations available in the primary literature in order to compare homologous structures throughout the clade.

The analysis was carried out using MacClade 3.05 (Maddison and Maddison, 1992) for editing the data matrix. The trees were constructed with the program Phylogenetic Analysis Using Parsimony – PAUP version 3.1.1. (Swofford, 1993). Heuristic tree searches were executed with PAUP default settings, with TBR, and using the closest stepwise addition sequence with 50 replicates. Zero-length branches were collapsed, MULPARS was activated, and ACCTRAN was used for character-state optimisation.

Six characters were coded as having two successive states, and eleven were treated as absent/present. Three characters were coded as having more than two states. All characters were treated as unordered (non-additive). Character polarisation was obtained with multiple outgroups (Ax, 1987; Nixon and Carpenter, 1993; Christoffersen and Araújo-de-Almeida, 1994; Von Sternberg, 1997; Amorim, 2002). Non-applicable states were coded as “-”.

We used a species of Euclymeninae, *Euclymene coronata*, and four other species of Nicomachinae, *Micromaldane ornithochaeta*, *Micromaldane bispinosa* Hartmann-Schröder, 1960, *Nicomache (Nicomache) lanai* and *Nicomache (Loxochona) personata* Johnson, 1901, as outgroups in order to test the monophyly of Nicomachinae and its genera, as suggested by Barriel and Tassy (1998).

Specimens to the new species were collected off the coast of São Paulo, in southeastern Brazil. The material was anaesthetised with menthol, fixed in 10% formalin and preserved in 70% alcohol. The animals were observed with a Zeiss stereoscopic microscope. The setae, rostral hooks and acicular spines were observed with an Olympus BX41 compound microscope. All illustrations were made with a camera lucida. Measurements are in millimetres.

We propose synapomorphies for the subfamily Nicomachinae, and for the genera *Micromaldane*, *Nicomache* and *Petaloproctus*. In the taxonomic

remarks we compare the new species to all previously known species. Specimens are deposited in the reference collection of invertebrates at the Centro de Estudos do Mar, Universidade Federal do Paraná, Brazil (MCEM-UFPR).

### Characters

01. Anterior end of the prostomium (keel): (0) rounded; (1) pointed.

A rounded prostomial anterior is a plesiomorphic character state found in most species of the outgroup and in some species of *Petaloproctus* (De Assis *et al.*, 2007a). The apomorphic condition of this character is shared by the species *P. neoborealis*, *P. ter-riculus* and *P. tenuis*.

02. Size of the prostomium in relation to the head: (0) long; (1) short.

The prostomium is always very long in the Euclymeninae, all along the cephalic plate. The shorter prostomium is an apomorphic state for the Nicomachinae.

03. Shape of the prostomium: (0) straight; (1) slightly arched; (2) strongly arched.

The prostomium is keel-shaped and fused to the peristomium in the maldanids (Day, 1967; Fauchald, 1977; Imajima and Shiraki, 1982; De Assis *et al.*, 2007a, b). This keel is straight in the most basal maldanids, and mainly in those with a cephalic plate. The plate is lost and the keel becomes arched. In *Petaloproctus* the keel is more arched than in *Micromaldane* and *Nicomache*. In this paper, this strongly arched keel is interpreted as an apomorphic condition for the genus (Arwidsson, 1907; Imajima and Shiraki, 1982; De Assis *et al.*, 2007a).

04. Two clusters of eyespots: (0) absent; (1) present.

This is an apomorphic character for the *Micromaldane* (Rouse, 1990).

05. Shape of nuchal grooves: (0) straight (1) slightly curved; (2) strongly curved.

Straight nuchal grooves are an important character for defining Euclymeninae. In Nicomachinae, they are always curved, forming slightly curved and deep lines (Day, 1967; Imajima and Shiraki, 1982; Rouse, 1990; Gherardi, *et al.*, 2002; De Assis *et al.*, 2007a, b). Within *Petaloproctus*, *P. vallejo*, *P. socialis*, *P. borealis* and *P. macrodentatus* have the

nuchal grooves strongly curved outwards, representing a synapomorphy for these species.

06. Size of nuchal grooves in relation to the prostomial keel: (0) long; (1) short.

In maldanids the nuchal grooves are usually of the same length as the prostomium. Their reduction represents an apomorphic state for the genus *Petaloproctus* (De Assis *et al.*, 2007a).

07. Cephalic plate: (0) absent; (1) present.

This is an apomorphic character for the subfamilies with anal plate: Notoproctinae Detinova, 1985; Maldaninae Arwidsson, 1907 and Euclymeninae Arwidsson, 1907. However, this character is reverted in Nicomachinae, herein treated as a secondary loss.

08. Acicular spines on setigers 1-3: (0) absent; (1) present.

The presence of these spines is a synapomorphy for Euclymeninae, *Nicomache* and *Petaloproctus* (De Assis *et al.*, 2007a, b), but it is reverted in the *Micromaldane*.

09. Shaped of acicular spine: (0) curved; (1) slightly curved; (2) straight.

In Euclymeninae only *Clymenella* Verrill, 1873 and *Euclymene* Verrill, 1900 have acicular spines with a strongly curved apex, looking like a hook. In *Nicomache* and most species of *Petaloproctus* the acicular spines are slightly curved. The straight form is found in *P. vallejo* n. sp. + *P. socialis* + *P. borealis* + *P. cirratus* + *P. ornatus* + *P. dentatus* + *P. macrodentatus*.

10. Distal end of the acicular spines: (0) sharp; (1) obtuse.

The acicular spines are modified setae, usually found in the first setigerous segments, in most members of maldanids. This represents an important character for the taxonomy of the family. Acicular spines with obtuse points are an apomorphic character for species *P. vallejo* n. sp. + *P. socialis* + *P. borealis* + *P. cirratus* + *P. dentatus* + *P. macrodentatus* (Day, 1967; Imajima and Shiraki, 1982; Lee and Paik, 1986).

11. Rostrate uncini strongly curved in all setigers (0) absent; (1) present.

The rostrate hooks strongly curved in all setigers is an apomorphy for *Micromaldane* (Rouse, 1990; Gherardi, *et al.*, 2002; De Assis *et al.*, 2007a).

12. Helicoidal capillary setae: (0) without or (1) with bifurcated tips.

Helicoidal capillaries are only found in the *Nicomache* (Day, 1967; Imajima and Shiraki, 1982; Lee and Paik, 1986; De Assis *et al.*, 2007a, b).

13. Pinnate and very long capillary setae: (0) absent; (1) present.

Pinnate capillaries are only found in the *Petaloproctus* (Day, 1967; Imajima and Shiraki, 1982; Lee and Paik, 1986; De Assis *et al.*, 2007a).

14. Ruffled base of the spinous capillaries: (0) absent; (1) present.

Spinous capillaries are found in most species of the Euclymeninae and Nicomachinae. However, their bases are always smooth. In *Petaloproctus vallejoi* n. sp. + *Petaloproctus socialis*, the capillaries basis are ruffled; this is a synapomorphy for both species (De Assis *et al.*, 2007a, b).

15. Preanal asetigers: (0) 1-2; (1) 0.

Most species of *Petaloproctus* have 1 or 2 asetigerous preanal segments. Their absence is interpreted as a secondary loss for the *P. terriculus* + *P. neoborealis* (Day, 1967; Hartman, 1969; De Assis *et al.*, 2007a, b).

16. Anal cup with reduced dorsal border: (0) absent; (1) present.

The anal cup is an apomorphy for the Euclymeninae and Nicomachinae. However, the reduction of the anal cup is the most important apomorphic character for genus *Petaloproctus* (Arwidsson, 1907; Day, 1967; De Assis *et al.*, 2007a). *Petaloclymene* Green, 1997 (Euclymeninae) presents a slightly reduced dorsal border of the anal cup, which is laterally flattened (Green, 1997). Notwithstanding, the species in this genus have a cephalic plate, an apomorphy to Notoprocetinae, Euclymeninae and Maldaninae, and herein is interpreted as loss in the Nicomachinae. The homology relationship for this character is represented in Figure 1.

17. Ornamentation of the border of anal cup: (0) absent; (1) present.

This character has been often used to separate species of *Petaloproctus*. This character is interpreted as homoplastic condition arising in *P. vallejoi* n. sp. + *P. socialis* + *P. borealis* and for *P. neoborealis*

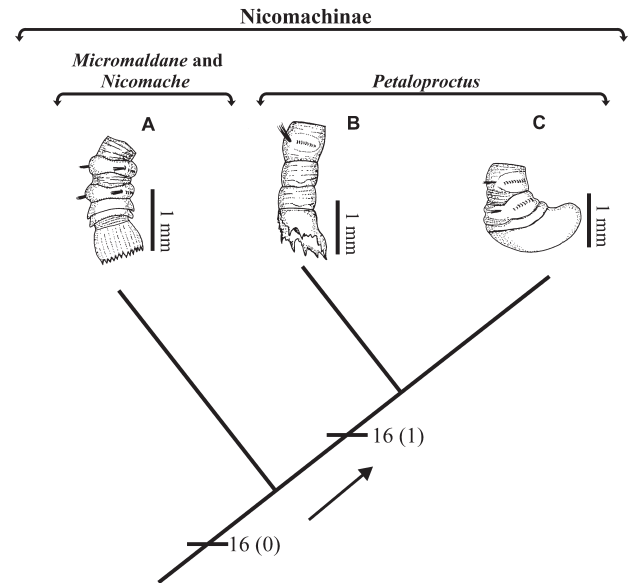


FIG. 1. – Phylogenetic hypothesis for the reduction of the dorsal border of the pygidium in *Petaloproctus*. A, *Nicomache (Nicomache) lanai*, posterior end in dorsal view; B, *Petaloproctus* sp., posterior end in lateral view; C, *Petaloproctus vallejoi* n. sp., posterior end in lateral view.

(Imajima and Shiraki, 1982; Lee and Paik, 1986; De Assis *et al.*, 2007a).

18. Ornamentation of the anal cup: (0) with cirri; (1) crenulated.

This character is an apomorphic condition for *Micromaldane*, which has no anal cirri (Rouse, 1990).

19. Anal cirri symmetric and very small (saw-shaped): (0) absent; (1) present.

In the genus of analysis, the anal cirri always vary in length. However, in *P. dentatus* and *P. cirratus* the anal cirri is of very small. The border is saw-like. Imajima and Shiraki (1982) compare the two species, agreeing that they are closely related on the basis of the form of the anal cirri, but differ nevertheless because the first has 29 triangular cirri and the second has only 15.

20. Anal pore: (0) opening at apex of anal cone; (1) opening on margin of anal plate.

Most maldanids taxa are diagnosed by characters related to the pygidium. In Euclymeninae and Nicomachinae, both having an anal cup, the anus is terminal on the anal cup. However, in Euclymeninae the anal pore is projected beyond the anal plate. In most genera, the anal pore is inserted on a short projection, but in the *Maldanella* McIntosh, 1885, *Microclymene* Arwidsson, 1907 and *Praxillella* Verrill, 1881, the anal pore is inserted on a large projection and becomes



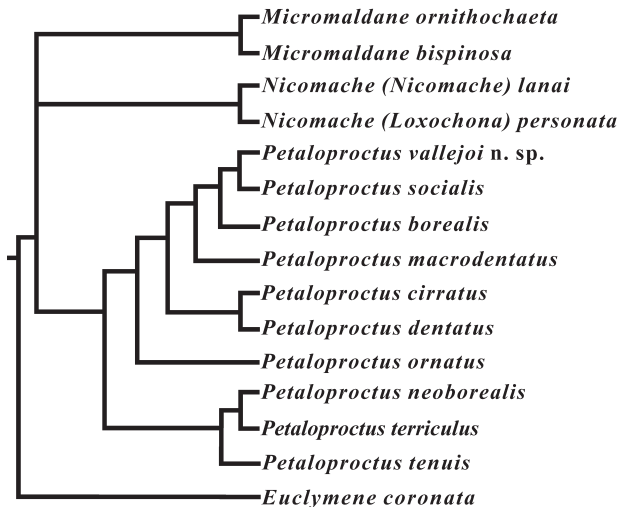


FIG. 2. – Strict consensus of three most parsimonious phylogenetic trees with equal weighting (tree length = 37 steps, CI = 0.89; RI = 0.92).

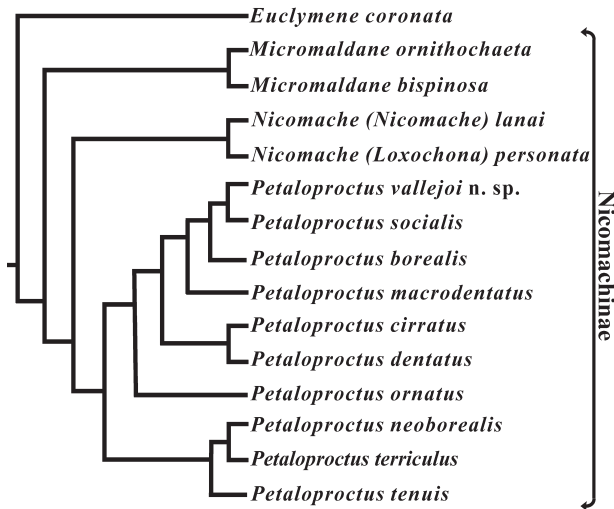


FIG. 3. – Most resolved phylogeny of Nicomachinae (tree length = 37 steps, IC = 0.89, RI = 0.92).

exposed beyond the anal cup (Day, 1967; Imajima and Shiraki, 1982; Lee and Paik, 1986; Fauchald, 1977). In the Nicomachinae, the anal pore is placed close to the margin of the anal plate, representing an apomorphic condition of this subfamily.

RESULTS

Phylogenetic analysis

We analysed 20 morphological characters, treated as non-ordered and with equal weighting. Characters resulted in three most parsimonious trees with length = 37, CI = 0.89, and RI = 0.92. The first tree represents the strict consensus (Fig. 2), in which the ingroup was well-supported in all trees. The second tree represents one of the three trees of same length and same indices, accepted as representative of the phylogeny of genus *Petaloproctus* (Fig. 3). Character coding is presented in Table 1. Our proposal for the systematisation of *Petaloproctus* into subgroups is ((*P. tenuis* (*P. terriculus* + *P. neoborealis*)) (*P. ornatus* (((*P. cirratus* + *P. dentatus*) (*P. macrodentatus* (*P. borealis* (*P. vallejoi* n. sp. + *P. socialis*)))))).

Systematics

Family MALDANIDAE Malmgren, 1867  
 Subfamily NICOMACHINAE Arwidsson, 1907

References: Day, 1967; Rouse, 1990; De Assis et al., 2007a.

*Emended diagnosis* (apomorphic characters in bold type). Nuchal grooves slightly curved or ellip-

TABLE 1. – Character matrix for phylogenetic analysis of *Petaloproctus*. (0, plesiomorphic state; 1-2, successively apomorphic states).

Taxa	Characters																			
	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20
<i>Euclymene coronata</i>	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0
<i>Micromaldane ornithochaeta</i>	0	1	1	1	1	1	0	0	-	-	1	0	0	0	1	0	1	1	-	1
<i>Micromaldane bispinosa</i>	0	1	1	1	1	1	0	0	-	-	1	0	0	0	1	0	1	1	-	1
<i>Nicomache (Nicomache) lanai</i>	0	1	1	0	1	1	0	1	1	0	0	1	0	0	1	0	1	0	0	1
<i>Nicomache (Loxochona) personata</i>	0	1	1	0	1	1	0	1	1	0	0	1	0	0	1	0	1	0	0	1
<i>Petaloproctus vallejoi</i> n. sp.	0	1	2	0	2	1	0	1	2	1	0	0	1	1	1	1	0	-	-	1
<i>Petaloproctus socialis</i>	0	1	2	0	2	1	0	1	2	1	0	0	1	1	1	1	0	-	-	1
<i>Petaloproctus borealis</i>	0	1	2	0	2	1	0	1	2	1	0	0	1	0	1	1	0	-	-	1
<i>Petaloproctus neoborealis</i>	1	1	2	0	1	1	0	1	1	0	0	0	1	0	0	1	0	-	-	1
<i>Petaloproctus terriculus</i>	1	1	2	0	1	1	0	1	1	0	0	0	1	0	0	1	1	0	0	1
<i>Petaloproctus tenuis</i>	1	1	2	0	1	1	0	1	1	0	0	0	1	0	1	1	1	0	0	1
<i>Petaloproctus cirratus</i>	0	1	2	0	1	1	0	1	2	1	0	0	1	0	1	1	1	0	1	1
<i>Petaloproctus ornatus</i>	0	1	2	0	1	1	0	1	2	0	0	0	1	0	1	1	1	0	0	1
<i>Petaloproctus dentatus</i>	0	1	2	0	1	1	0	1	2	1	0	0	1	0	1	1	1	0	1	1
<i>Petaloproctus macrodentatus</i>	0	1	2	0	2	1	0	1	2	1	0	0	1	0	1	1	1	0	0	1

tical; **cephalic plate lost**; pygidium as a foliaceous plate, with central anus, and **anal pore opening on margin of anal plate**, sunken into a funnel, crenulated, rimmed with cirri or smooth; neuropodial hooks always in single row.

Genus *Petaloproctus* Quatrefages, 1865

Type species: *Petaloproctus terriculus* Quatrefages, 1865

References: Arwidsson, 1907; Day, 1967; Fauchald, 1977; Imajima and Shiraki, 1982; Wolf, 1984; De Assis *et al.*, 2007a.

*Emended diagnosis* (apomorphic characters in bold type). Prostomium forms a well-developed cephalic keel; **nuchal grooves strongly curved**; acicular spines on setigers 1-3; notopodia with three kinds of chaetae: a) limbate or bi-limbate capillaries, b) spinulose capillaries, and c) **a very long filamentous pinnate capillary**; setiger 4 with rostrate uncini in a single row; pygidium forms an anal plate with well-developed ventral border, while the **dorsal border is reduced**.

*Petaloproctus vallejo* n. sp.  
(Figs. 4 and 5)

*Material examined*: Holotype MCEM-638, St. 6407, Op. Sueste III, RV "Almirante Saldanha" (Diretoria de Hidrografia e Navegação), Paulo Lana col., 26 March 1984, 24°06'S, 46°10'W, off São Paulo coast (southeastern Brazil), 30 m, muddy sand. Paratype: MCEM-639, St. 6407, Op. Sueste III, RV "Almirante Saldanha" (Diretoria de Hidrografia e Navegação), Paulo Lana col., 26 March 1984, 24°06'S, 46°10'W, off São Paulo coast (southeastern Brazil), 30 m, muddy sand.

*Diagnosis*. Body with 19 setigerous segments and one preanal asetigerous segment; prostomium rounded anteriorly, forming a keel arched, slightly curved on the lateral borders; nuchal grooves short strongly curved outwards; one acicular spine on setigers 1-3; beginning on fourth setiger, neuropodia with a row of rostrate hooks; hooks with six teeth on the main flange; notopodia with setae of three types: limbate capillaries, spinulose capillaries, and very long, filamentous and pinnate capillaries; pygidium with a large anal plate, with smooth ventral border; anus at centre of plate, with many divergent folds.

*Description*. Holotype complete, with 19 setigerous segments and one asetigerous preanal segment. Total body length, 65 mm. Paratype represented by a posterior fragment measuring 3.7 mm in length. Head 1.5 mm long (Fig. 4A). First setiger very short, 1.5 mm long and 2 mm wide. Fourth setiger 4 mm

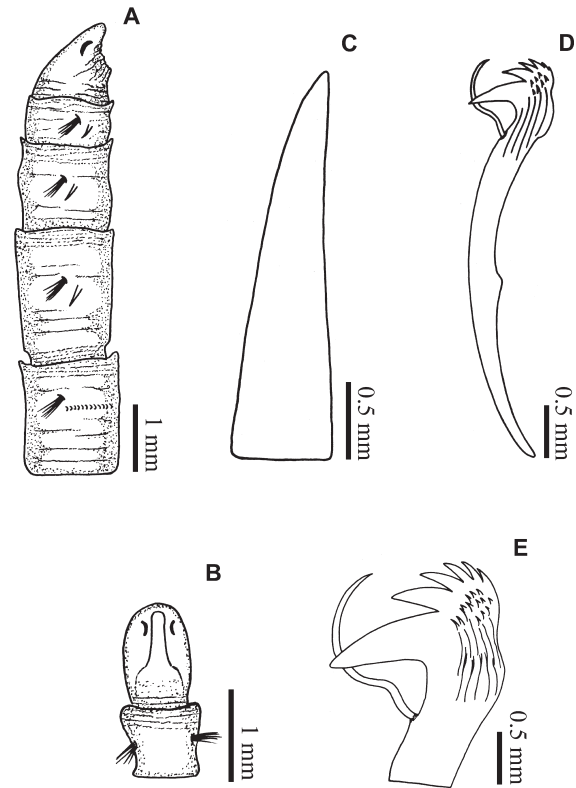


FIG. 4. – *Petaloproctus vallejo* n. sp. A, anterior end of holotype, lateral view; B, head, dorsal view; C, acicular spine from setiger 1; D, rostrate uncinus from setiger 15; E, distal end of middle uncinus.

long and 2 mm wide; setigers 5-16 measure 6 mm long and 2 mm wide. Remaining segments decrease gradually in size. Posterior region formed by an preanal asetigerous segment and a funnel with a completely reduced dorsal border. The pygidium is 2 mm long and 3 mm wide.

Prostomium fused to peristomium, forming a well-defined head. Prostomium rounded anteriorly, forming a keel arched, with slightly curved sides (Fig. 4A). Nuchal grooves short, deep, and slightly curved outwards. Peristomium with many transverse folds, that become expanded behind the prostomium (Fig. 4B). Mouth located ventrally, with well-developed and rugose lips.

Setigers 1-3 without a collar. Neuropodia of setigers 1-3 with a strong acicular spine, which is obtuse and honey-coloured (Fig. 4C). Posterior to setiger 3, neuropodia have a row of rostrate hooks, which are present up to setiger 19. Each hook has a rostrum and five teeth on the main fringe. A single thick barbule, bent upwards, present below the rostrum (Fig. 4D, E). Each hook is perpendicular to the body wall, with a long and curved posterior shaft, and a prominent manubrium on the posterior half. The tori have

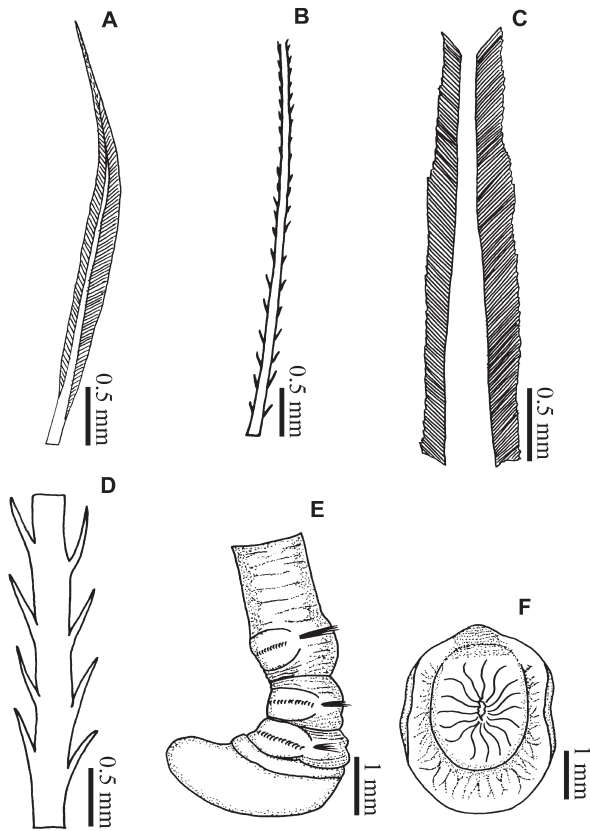


FIG. 5. – *Petaloproctus vallejoi* n. sp. A, bilimbate capillary chaeta from setiger 4; B, spinous capillary chaeta; C, ruffled base of the spinous capillary chaeta; D, very long, filamentous and pinnate capillary chaeta; E, posterior end of holotype; F, anal plate, frontal view.

a variable number of rostrate hooks (4: 10, 5: 17, 6: 22). Anterior setigers have glandular bands with short borders (4, 5, 6, and 7).

Notopodia of setigers 1-19 with tufts of long and fine capillary setae. These setae have a short base and are of three types: bilimbate capillary setae, with fine points (Fig. 5A); spinous capillary setae, with a ruffled base (Fig. 5B, C); very long, filamentous and pinnate capillaries (Fig. 5D).

Preanal asetigerous segment short. Anal plate with reduced dorsal border and long and smooth ventral border (Fig. 5E). Anus terminal, central and close to anal plate, surrounded by divergent folds (Fig. 5F).

**Tubes.** Tube fragments composed of fine sand grains and gravel.

**Habitat.** At 30 m depth, in sand-muddy sediment.

**Etymology.** The species is named after Dr. Sergio I. Salazar-Vallejo, who has contributed so much to

the knowledge of maldanid polychaetes from the Gulf of Mexico.

**Remarks.** *P. socialis* Andrews, 1891 differs from *P. vallejoi* n. sp. by having a dorsoventrally flattened, pointed prostomium, 23 setigers, 2 preanal asetigerous segments, rostrate hooks with 3-4 teeth on the main flange and a smooth region opposite to the rostrum (Andrews, 1891; De Assis *et al.*, 2007a). *P. borealis* Arwidsson, 1907 differs from *P. vallejoi* n. sp. by having 21 setigers, 1-2 acicular spines on setigers 1-3, a hook with up to 5 teeth on the main flange and numerous barbules, and 2 preanal asetigerous segments (Hartman, 1948; Uschakov, 1955; Imajima and Shiraki, 1982; Buzhinskaja, 1985). *P. neoborealis* Hartman, 1969 differs from *P. vallejoi* n. sp. by having a truncate, long and ventrally pointed prostomium, J-shaped nuchal grooves, 20-21 setigers, 1-2 acicular spines on setigers 1-4, only two types of setae: hairs-like capillaries and simple capillaries, and no preanal asetigerous segment (Hartman, 1969; De Assis *et al.*, 2007a). *P. terriculus* Quatrefages, 1865 differs from *P. vallejoi* n. sp. by having divergent nuchal grooves, 22 setigerous segments, 4-5 teeth over the main flange, the border of the anal plate with numerous teeth, and no preanal asetigerous segment (Fauvel, 1927; Day, 1967; Rullier, 1965; De Assis *et al.*, 2007a). *P. tenuis* Thèel, 1879 differs from *P. vallejoi* n. sp. by having 20-21 setigers, 2-3 acicular spines on setigers 1-3, and the border of the anal plate with numerous cirri (Hartman, 1942, 1948; Berkeley and Berkeley, 1952; Rullier, 1965; Amoureux, 1982; Buzhinskaja, 1985). *P. cirratus* Monro, 1937 differs from *P. vallejoi* n. sp. by having uncini with 2 teeth on the main flange, and 15 marginal cirri on the anal border (Monro, 1937; De Assis *et al.*, 2007a). *P. ornatus* Hartman, 1969 differs from *P. vallejoi* n. sp. by having an anteriorly truncate prostomium, 22 setigers, and 22 marginal cirri on the anal border (Hartman, 1969; De Assis *et al.*, 2007a). *P. dentatus* Imajima and Shiraki, 1982 differs from *P. vallejoi* n. sp. by having a frontally flattened prostomium, long nuchal grooves, 22 setigers, 2-3 acicular spines on setigers 1-3, 2 preanal asetigerous segments, and 29 cirri along the anal border (Imajima, 2001; De Assis *et al.*, 2007a). *P. macrodentatus* Lee and Paik, 1986 differs from *P. vallejoi* n. sp. by having 20 setigers, 2 preanal asetigerous segments and 10 marginal cirri along the anal border (Lee and Paik, 1986; De Assis *et al.* 2007a).

## DISCUSSION

De Assis *et al.* (2007a) reviewed Nicomachinae, and recognised seven species for *Micromaldane*, sixteen valid species for *Nicomache*, and only nine valid species for *Petaloproctus*. In this last genus, *Petaloproctus crosnieri* Rullier, 1965 was excluded because of the absence of the posterior part of the body. *Petaloproctus crenatus* Chamberlin, 1919 was considered *incertae sedis*, since complete specimens are unknown.

The phylogenetic analysis, based on 20 morphological characters, shows that the subfamily Nicomachinae, and the genera *Micromaldane*, *Nicomache* and *Petaloproctus* are monophyletic taxa. Nicomachinae was supported by the following synapomorphies: prostomium short and arched (characters 2, 3); nuchal grooves curved and short (characters 5, 6); cephalic plate lost (character 7), anal pore opening on margin of the anal plate (character 20). Euclymeninae is a more basal group and herein considered the sister-group of Nicomachinae (Figs. 2-3).

Bleidorn *et al.* (2005) conducted a molecular phylogenetic analysis based on three genes, mitochondrial 16SrRNA, nuclear 18SrRNA and a small fraction of nuclear 28SrRNA, with the aim of testing the monophyly of Maldanidae and Arenicolidae and of the genera of Arenicolidae. Both families were considered monophyletic. The genera of Maldaninae appeared as basal and as the sister-group of Euclymeninae. Among the genera of Euclymeninae, *Nicomache* sp. appeared as the sister-group of *Clymenura clypeata* (Saint-Joseph, 1894).

The synapomorphies of the genus *Micromaldane* are two clusters of eyespots on anterior end of the head (character 4), rostrate uncini strongly curved in all setigers (character 11), and the anal cup with crenulated border (character 18) (Rouse, 1990; De Assis *et al.*, 2007a).

*Nicomache* has also been supported as a monophyletic taxon, with the following synapomorphy: helicoidal capillaries with bifurcated tip in all setigers (character 12). This kind of seta has not been found in other maldanid polychaetes (Day, 1967; Imajima and Shiraki, 1982; Lee and Paik, 1986; De Assis *et al.*, 2007a, b). Although not resolved in the strict consensus, *Nicomache* is considered as a sister-group of the *Petaloproctus* because of the presence of acicular spines on the first three setigers (character 8) (De Assis *et al.*, 2007a).

Finally, the genus *Petaloproctus* is herein treated as a valid group in the analysis, having been well supported by three apomorphies: prostomium strongly arched (character 3(2)), capillaries long and pinnate (character 13), and an anal cup with dorsal border reduced (character 16) (Day, 1967; Imajima and Shiraki, 1982; De Assis *et al.*, 2007a) (Figs. 2-3).

The most basal clade of *Petaloproctus* is formed by the species *P. terriculus*, *P. tenuis*, and *P. neoborealis*, which are grouped by the anteriorly pointed prostomium (character 1). The plesiomorphic condition of this character is a rounded prostomium, found both in the outgroup and in the majority of maldanids. The synapomorphy of the clade formed by *P. terriculus* and *P. neoborealis* is the loss of the pre-anal asetigers (character 15).

The next more derived clade was supported by the presence of straight acicular spines (character 9). Some genera of Euclymeninae have strongly curved acicular spines, hook-like. In *Nicomache* and in the most basal species of *Petaloproctus*, these spines become slightly curved, and in the clade formed by species *P. ornatus*, *P. dentatus*, *P. cirratus*, *P. macrodentatus*, *P. borealis*, *P. socialis*, and *P. vallejo* n. sp. the acicular spines become straight, a derived condition not observed in other species of maldanids (Day, 1967; Imajima and Shiraki, 1982; Lee and Paik, 1986; De Assis *et al.*, 2007a).

A more nested clade is formed by the species *P. dentatus*, *P. cirratus*, *P. macrodentatus*, *P. borealis*, *P. socialis* and *P. vallejo* n. sp., having as an apomorphy acicular spines with obtuse points (character 9(2)). Both in the outgroups, with the exception of *Micromaldane*, that does not have acicular spines, and the most basal species of *Petaloproctus*, these spines have fine tips (Imajima and Shiraki, 1982; Lee and Paik, 1986).

A distal end of the acicular spines with obtuse points (character 10) is only present in *P. vallejo* n. sp., *P. socialis*, *P. borealis*, *P. cirratus*, *P. dentatus* and *P. macrodentatus*, representing a synapomorphy uniting these species (Day, 1967; Imajima and Shiraki, 1982; Lee and Paik, 1986).

The acicular spines are modified setae with a single tooth, usually found in the first setigerous segments in most members of maldanids. This is an important character for the taxonomy of the family.

The ornamentation of the border of the anal plate (character 17) is a character that has been used to differentiate many species. In our analysis,



this character is interpreted as homoplastic for *P. vallejoi* n. sp. + *P. socialis* + *P. borealis* and for *P. neoborealis* (Imajima and Shiraki, 1982; Lee and Paik, 1986; De Assis *et al.*, 2007a). However, many species of Euclymeninae and Nicomachinae have cirri of different sizes and forms. We hypothesise that crenulations represent reduced cirri, which retain the same sensory function. These cirri are further reduced to a crenulated border in *Micromaldane* (Rouse, 1990).

The clade formed by species *P. cirratus* and *P. dentatus* was supported by the diminute, symmetrical, saw-like, anal cirri (character 19 (1)).

The clade containing species *P. macrodentatus*, *P. borealis*, *P. socialis*, and *P. vallejoi* n. sp. was sustained by the presence of strongly curved nuchal grooves (character 5(2)) (Hartman, 1969; Imajima and Shiraki, 1982; Lee and Paik, 1986; De Assis *et al.*, 2007a), herein considered to represent an apomorphic character. In species of *Micromaldane* and *Nicomache*, and the most basal species of *Petaloproctus*, the nuchal organs form slightly curved sinuous lines, sometimes with hooks on anterior and posterior ends.

The derived clade containing the species *P. borealis*, *P. socialis*, and *P. vallejoi* n. sp. is supported by the absence of ornamentation on the ventral border of the anal cup. This character is considered to be homoplastic for *P. neoborealis*, *P. socialis* and *P. vallejoi* n. sp. are unique within Maldanidae for having the base of the spinulous setae ruffled (character 14).

We chose the most resolved topology among our three phylogenetic trees of equal length, CI, and RI, as representative of the phylogeny of the Nicomachinae (Fig. 3). The relationships among the species of *Petaloproctus* are identical to those appearing in the strict consensus phylogenetic tree (Fig. 2).

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#### REFERENCES

- Amorim, D.S. – 2002. *Fundamentos de Sistemática Filogenética*. Holos Editora, Ribeirão Preto.
- Amoureux, L. – 1982. Annelides polychètes recueillies sur la pente continentale de la Bretagne à l'Irland, Campagne 1973 de la "Thalassa" (suite et fin) avec la description de quatre espèces nouvelles pour la science. II. Inventaire taxonomique annoté de toutes les polychètes sédentaires. *Cah. Biol. Mar.*, 23: 179-213.
- Andrews, E.A. – 1891. Report upon the Annelida Polychaeta of Beaufort, North Carolina. *Proc. U. S. Nat. Mus.*, 14: 277-301.
- Arwidsson, I. – 1907. Studien über die Skandinavischen und Arktischen Maldaniden nebst Zusammenstellung der bis jetzt bekannten Arten dieser Familie. *Zool. Jahrb. Suppl.*, 9: 1-308.
- Ax, P. – 1987. *The phylogenetic system: the systematization of organisms on the basis of their phylogenesis*. John Wiley and Sons, New York.
- Barriel, V. and P. Tassy. – 1998. Rooting with multiple outgroups: consensus versus parsimony. *Cladistics*, 14: 193-200.
- Berkeley, E. and C. Berkeley. – 1952. Annelida, Polychaeta Sedentaria. *Can. Pac. Faun.*, 9: 1-139.
- Bleidorn, C., L. Vogt. and T. Bartolomaeus. – 2005. Molecular phylogeny of lugworm (Annelida, Arenicolidae) inferred from three genes. *Mol. Phylogenet. Evol.*, 34: 673-679.
- Buzhinskaja, G.N. – 1985. Polychaeta of the shelf off South Sakhalin and their ecology. *Issl. Faun. Mor. SSSR*, 30(38): 72-224.
- Chamberlin, R.V. – 1919. Pacific coast Polychaeta collected by Alexander Agassiz. *Bull. Mus. Comp. Zool. Harv. Univ.*, 63: 251-270.
- Christoffersen, M.L. and E. Araújo-De-Almeida. – 1994. A phylogenetic framework of the Enterocoela (Metameria: Coelomata). *Rev. Nord. Biol.*, 9(2): 173-208.
- Day, J.H. – 1967. *A monograph on the Polychaeta of southern Africa*. Part 2 Sedentaria. British Museum Natural History, London.
- De Assis J.E. C. Alonso and M.L. Christoffersen. – 2007a. A catalogue and taxonomic keys of the subfamily Nicomachinae (Maldanida, Polychaeta) of the world. *Zootaxa*, 1657: 41-55.
- De Assis, J.E., C.A. Samiguel and M.L. Christoffersen. – 2007b. Two new species of *Nicomache* (Polychaeta: Maldanidae) from the Southwest Atlantic. *Zootaxa*, 1454: 27-37.
- Fauchald, K. – 1977. The polychaete worms. Definitions and keys to the orders, families and genera. *Nat. Hist. Mus. Los Ang. Count. Sci. Ser.*, 28:1-188.
- Fauchald, K. and G.W. Rouse. – 1997. Polychaete systematics: past and present. *Zool. Scr.*, 26: 71-138.
- Fauvel, P. – 1927. *Polychètes sédentaires. Addenda aux Errantes, Archannelides, Myzostomaires*. Faune de France vol. 16. Librairie de la Faculté des Sciences Paul Lechevalier, Paris.
- Green, K.D. – 1997. *Petaloclymene pacifica*, a new genus and species of Maldanidae (Annelida: Polychaeta). *Bull. Mar. Sci.*, 60(2): 235-239.
- Gherardi, M., M.F. Gravina and A. Giangrande. – 2002. Note Tassonomiche ed Ecologica su *Micromaldane ornithochaeta* (Polychaeta, Maldanidae), Rinventura Lungo Le Costa Italiane Meridionale. *Thal. Sal.*, 26: 133-143.
- Hartman, O. – 1942. A review of the types of polychaetous annelids at the Peabody Museum of Natural History, Yale University. *Bull. Bingham Ocean. Coll.*, 89: 1-98.
- Hartman, O. – 1948. The polychaetous annelids of Alaska. *Pac. Sci.*, 2(1): 1-58.
- Hartman, O. – 1969. *Atlas of the sedentary polychaetous annelids from California*. Allan Hancock Foundation, California.
- Hartmann-Schröder, G. – 1971. Annelida, Borstenwürmer, Polychaeta. *Tierw. Deut.*, 58: 1-594.
- Imajima, M. – 2001. Deep-Sea benthic polychaetous annelids of Tosa Bay, Southwestern Japan. *Monogr. Nat. Sci. Mus. Tokyo*, (20): 31-100.
- Imajima, M. and Y. Shiraki. – 1982. Maldanidae (Annelida: Polychaeta) from Japan. Part 1. *Bull. Nat. Sci. Mus. Tokyo*, 8: 7-46.
- Lee, J.H. and E.I. Paik. – 1986. Polychaetous annelids from the Yellow Sea III: Family Maldanidae (Part 1). *Ocean. Res.*, 8(1): 13-25.
- Maddison, W.P. and D.R. Maddison. – 1992. *Mac Clade version 3.05. Analysis of phylogeny and character evolution*. Sinauer Associates, Inc., Sunderland, Massachusetts.

- Monro, C.C.A. – 1937. Polychaeta. The John Murray Expedition. *Scient. Rep.*, 4(8): 243-321.
- Nixon, K.C. and J.M. Carpenter. – 1993. On outgroups. *Cladistics*, 9(4): 413-426.
- Rouse, G.W. – 1990. Four new species of *Micromaldane* (Polychaeta: Maldanidae) from Eastern Australia. *Rec. Austral. Mus.*, 42: 209-219.
- Rullier, F. – 1965. Contribution à la faune des annélides polychètes de l'Australie. *Pap. Univ. Queensl.*, 2(9): 163-201.
- Swofford, D.L. – 1993. *PAUP – Phylogenetic analysis using parsimony, version 3.1.1*. Illinois: Illinois Natural History Survey, Champaign.
- Uschakov, P. – 1955. Monogoshchetinkovye chervi' dal nevostochnykh morei SSSR [Polychaeta of the Far Eastern Seas of the USSR]. *Akad. Nauk. Zool. Inst. Opred. Faun. SSSR.*, 1: 1-445.
- Von Sternberg, R. – 1997. Cladistics of the freshwater crab family Trichodactylidae (Crustacea: Decapoda); appraising the reappraisal. *J. Comp. Biol.*, 2: 49-62.
- Wolf, P.S. – 1984. Family Maldanidae Malmgren 1867. In: Uebelacker M, Johnson PG. (eds.), Chapter 15. *Taxonomic guide to the Polychaetes of the Northern Gulf of Mexico*. Barry A. Vittot & Associates, Alabama.

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