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Revision of the smiling worms, genera *Prosadenoporus* Bürger, 1890 and *Pantinonemertes* Moore and Gibson, 1981 and description of a new species *Prosadenoporus floridensis* sp. nov. (Prosorhochmidae; Hoplonemertea; Nemertea) from Florida and Belize

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The hoplonemertean genera *Prosadenoporus* Bürger, 1890 and *Pantinonemertes* Moore and Gibson, 1981 are revised and synonymized based on a morphological re-evaluation. We redefine *Prosadenoporus* Bürger, 1890 on the basis of characters held in common by the eight species: *Prosadenoporus agricola* (Willemoes-Suhm, 1874) comb. nov., *Prosadenoporus arenarius* Bürger, 1890, *Prosadenoporus spectaculum* (Yamaoka, 1940) comb. nov., *Prosadenoporus winsori* (Moore and Gibson, 1981) comb. nov., *Prosadenoporus enalios* (Moore and Gibson, 1981) comb. nov., *Prosadenoporus mooreae* (Gibson, 1982b) comb. nov., *Prosadenoporus mortoni* (Gibson, 1990) comb. nov. and *Prosadenoporus fujianensis* (Sun, 2001) comb. nov. We describe a new semi-terrestrial species *Prosadenoporus floridensis* sp. nov. from Belize and Florida and compare its morphology to other species of *Prosadenoporus*. The average sequence divergence of *P. floridensis* sp. nov. from other congeners is 9.15% (16S) and 10.65% (COI) and 7.8% and 10.3% respectively from the nearest sequenced congener *P. mortoni*.

Keywords: nemertea; *Prosadenoporus*; *Pantinonemertes*; Prosorhochmidae; semi-terrestrial

Introduction

Members of the hoplonemertean family Prosorhochmidae are distinguished by a crescent-shaped epithelial head groove – the ''prosorhochmid smile''. Like the majority of nemerteans, many prosorhochmids are marine, but some occupy semi-terrestrial, terrestrial or even arboreal habitats. The transition to terrestriality and the morphological adaptations that might have facilitated this are the subject of much discussion (Moore 1985; Moore and Gibson 1985; Gibson and Moore 1989). Established by Bürger (1895), the family Prosorhochmidae initially included three genera: *Prosorhochmus* Keferstein, 1862, *Geonemertes* Semper, 1863 and *Prosadenoporus* Bürger, 1890. Two features stand out in the original diagnosis – the enormously developed cephalic glands and hermaphroditism (Bürger 1895). At this time, hermaphroditism can no longer serve as a defining feature of the family because many prosorhochmids with separate sexes have been discovered. However, the massive cephalic glands and large frontal organ through which some of these glands discharge are characteristic of all prosorhochmids. Although the ''most terrestrial'' of the species actually do not have the prosorhochmid smile, it appears

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that the well-developed frontal organ and cephalic glands, associated with the smile in other prosorhochmids, might have played an important role in the conquest of land.

Over the years, the content of the family varied, and at one time Prosorhochmidae encompassed up to 19 different genera, including all known terrestrial and some of the freshwater forms (Gibson 1972, 1982a). Following the revision of the terrestrial nemerteans (Moore and Gibson 1981), and the genera *Prosorhochmus* Keferstein, 1862 (Gibson and Moore 1985) and *Prosadenoporus* Bürger, 1890 (Moore and Gibson 1988), the family was redefined based on the characters interpreted as being held in common by the four genera *Geonemertes* Semper, 1863, *Prosadenoporus* Bürger, 1890, *Prosorhochmus* Keferstein, 1862 and *Pantinonemertes* Moore and Gibson, 1981 (Moore and Gibson 1988, p. 85). As part of an ongoing revision of the family Prosorhochmidae (Maslakova et al. 2005; Maslakova and Norenburg 2008) here we revise the genera *Prosadenoporus* and *Pantinonemertes*.

The genus *Prosadenoporus* currently includes one species: *Prosadenoporus arenarius* Bürger, 1890 (Moore and Gibson 1988). The genus was established by Bürger (1890) for four briefly described species from Indonesia mainly distinguished by size and colour: *P. arenarius* Bürger, 1890, *P. badiovagatus* Bürger, 1890, *P. janthinus* Bürger, 1890 and *P. oleaginus* Bürger, 1890. Each description was based on a single preserved specimen. Punnet (1901) briefly described a fifth member of the genus, *P. buergeri*, based on a single specimen from a geographically distant area – the Laccadive Islands. None of the five species is sufficiently described to allow unambiguous identification and Bürger's material is almost certainly lost. Moore and Gibson (1988) re-evaluated Punnet's material deposited at the Cambridge Museum of Zoology: one tube labelled *Prosadenoporus buergeri*, which contained fragments of proboscis and posterior body insufficient for identification, and one tube labelled *Prosadenoporus* sp. from Kedah Province on Malay Peninsula with several preserved specimens which they sectioned and examined. Moore and Gibson (1988) invalidated four species as *nomina dubia*, retaining *Prosadenoporus arenarius* Bürger, 1890 as the type species of the genus. They provided a detailed description of the internal anatomy of the species, arguing that Punnet's Malaysian specimens cannot be distinguished from Bürger's description of *P. arenarius* from Indonesia and are, therefore, conspecific.

The genus *Pantinonemertes* currently includes nine valid species: *P. agricola* (Willemoes-Suhm, 1874), *P. spectaculum* (Yamaoka, 1940), *P. winsori* Moore and Gibson, 1981 (Figures 1B, 1E and 1F), *P. enalios* Moore and Gibson, 1981, *P. mooreae* Gibson, 1982b (Figures 1C and D), *P. californiensis* Gibson et al., 1982, *P. mortoni* Gibson, 1990, *P. daguilarensis* Gibson and Sundberg, 1992 and *P. fujianensis* Sun, 2001. It was first established for the taxon encompassing *Geonemertes agricola* (Willemoes-Suhm, 1874), *P. enalios* Moore and Gibson, 1981 and *P. winsori* Moore and Gibson, 1981, with the latter designated as the type species (Moore and Gibson, 1981). However, as pointed out by Chernyshev (1992), *Pantinonemertes* is a junior synonym of *Neonemertes* – the genus established by Girard (1893) for *Tetrastemma agricola* Willemoes-Suhm, 1874. Subsequently, *Tetrastemma spectaculum* Yamaoka, 1940 was re-described and transferred to *Pantinonemertes* (Gibson, 1990) and five new species were described, including two species whose affiliation with the genus is questionable: *P. californiensis* and *P. daguilarensis*.

We describe a new semi-terrestrial prosorhochmid species from Florida and Belize whose morphology closely resembles that of *Pantinonemertes* and *Prosadenoporus* (Figures 1A, 2A, 2B, 3–6 and 10I). To make a thorough comparison with the previously described species we re-evaluated all the available type and voucher material and recollected fresh specimens of as many species of both genera as possible for morphological and molecular study. In the process we came to recognize that the morphological differences between *Pantinonemertes* and *Prosadenoporus* are elusive and the two genera should be synonymized; in which case, according to the principle of priority (International Code of Zoological Nomenclature, Article 23), *Prosadenoporus* Bürger, 1890 takes precedence over both *Pantinonemertes* Moore and Gibson, 1981 and *Neonemertes* Girard, 1893. The following revision incorporates this change of generic names.

Material and methods

Specimen preparation

Characters of external appearance and stylet apparatus were documented in living specimens as described in Maslakova and Norenburg (2008). Measurements such as body length and width were taken on live specimens relaxed by gradual addition of 7.5% $MgCl_2$. For histology, specimens were relaxed in $MgCl_2$, fixed for 24 h in 4% formaldehyde made in local seawater, briefly rinsed in tap water and post-fixed in Hollande's cupri-picri-formal-acetic fluid for 48–72 h. After post-fixation specimens were transferred to 70% ethanol for long-term storage. Specimens were dehydrated in a standard alcohol series, embedded in Tissueprep Paraffin (56° C m.p.), serially sectioned at 8 µm and stained using Crandall's polychrome protocol – a combined variant of the Mallory, Gomori, Koneff and Gurr-McConail techniques (Frank Crandall, National Museum of Natural History, Smithsonian Institution, Washington, DC, personal communication to authors).

DNA extraction, amplification and sequencing

Tissue samples for molecular work were obtained for the following species: *Prosadenoporus mortoni* comb. nov., *Prosadenoporus mooreae* comb. nov., *Prosadenoporus winsori* comb. nov., *Prosadenoporus floridensis* sp. nov. and *Pantinonemertes californiensis* (Table 1). Specimens were preserved in 95% ethanol and stored at room temperature or $-20°C$ short-term and at $-80°C$ long-term. DNA was extracted using Qiagen DNeasy Kits. Partial sequences of genes encoding for cytochrome oxidase subunit I (COI), 658 bp long, and mitochondrial large subunit rRNA (16S), 458–467 bp long, were PCR-amplified using universal primers: 16sar-L [cgcctgtttatcaaaaacat] and 16sbr-H [ccggtctgaactcagatcacgt] from Palumbi et al. (1991) for 16S, and LCO1490 [ggtcaacaaatcataaagatattgg] and HCO2198 [taaacttcagggtgaccaaaaaatca] from Folmer et al. (1994) for COI. In addition, a pair of nemertean specific internal primers were designed for each gene to amplify fragments where DNA degradation appeared to be a problem: P2619-Nem16S-intF [acaagaagacccttttgagct] and P2620-Nem16S-intR [taaagct-caaaagggtcttctt] for 16S, and P2638-COIF3-nemert [gtctagraatrttgctcatgctg] and

P2683-COIR-nemert [ctyccagcatgwgcaayatt] for COI. PCR amplification was performed as described by us (Maslakova and Norenburg, 2008). The purified PCR products were sequenced on a 3100 ABI Capillary DNA Sequencer; both strands were sequenced at least once and proofread using Sequencher 4.1.4 (Gene Codes Corporation). Sequences are deposited with the GeneBank (see Table 1 for accession numbers).

Stylet measurements

To determine whether interspecific differences in the stylet and basis measurements were statistically significant we performed a one-way ANOVA correcting for multiple comparisons with Tukey–Kramer HSD method using the statistical software package JMP 6.0.3 (SAS Institute Inc.). Stylet measurements used in the analysis are presented in Table 2. Cases where individual measurements were not reported or where only a single data point was available could not be used in the analysis. However, these measurements were used to adjust the range of variation in species diagnoses. Data for statistical comparisons were only available for *Prosadenoporus winsori* comb. nov., *Prosadenoporus mooreae* comb. nov. and *Prosadenoporus floridensis* sp. nov.

Results

<div align="center">

Class: **HOPLONEMERTEA**
Order: **MONOSTILIFERA**
Family: **PROSORHOCHMIDAE** Bürger, 1895

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Diagnosis

Monostiliferous, marine, brackish-water, semi-terrestrial or terrestrial hoplonemerteans with rhynchocoel extending most or all the body length, body wall containing distinct outer circular and inner longitudinal muscle layers and a delicate layer of diagonal muscles between; longitudinal musculature may appear to be anteriorly divided (i.e. some of the proboscis insertion muscles may be oriented obliquely and longitudinally); four simple eyes; proboscis may be small or large, and sometimes used in locomotion; stylet basis in most species characteristically truncated; head in most species with characteristic dorsal horizontal epithelial fold (the prosorhochmid smile); cerebral sensory organs anterior or anterolateral to brain, with simple unbranched cerebral canals, in most species opening ventro-laterally via reduced cerebral organ furrows; cephalic glands well developed, with distinct granular proteinaceous components (orange-G and acidophilic glands) in addition to basophilic mucus lobules; frontal organ represented by an exceptionally well-developed tubular canal, typically with laterally specialized epithelium; middorsal blood vessel with a single vascular plug; typically gonochoric and oviparous, occasionally hermaphroditic and viviparous.

Composition

As a result of our proposed synonymization of *Pantinonemertes* Moore and Gibson, 1981 with *Prosadenoporus* Bürger, 1890 the family now contains three genera:

Table 1. GenBank accession numbers and specimen data for molecular analysis.

Species	Accession numbers	Collecting information (specimen numbers)
Pantinonemertes californiensis	EF157597, EF157585	Coll. Crandall, Tomales Bay, CA, USA (#4-15-92)
Prosadenoporus floridensis sp. nov.	EF157596, EF157583, EF157584	Coll. JLN, Link Port, FL, USA (#2-22-98-2); Coll. SAM, Twin Keys, Belize (#178-14-2-00-1)
Prosadenoporus mooreae comb. nov.	EF157595, EF157582	Coll. SAM, 21 March 2003, type locality in Picnic Bay and in Cockle Bay, Magnetic Island, Australia (#778-03-23-03-1,2,3)
Prosadenoporus mortoni comb. nov.	EF157593, EF157580	Coll. Sun, Nan Ao Island and Xiamen; Fujian Province; China (#910913, #990909-2B, #9909-1A)
Prosadenoporus winsori comb. nov.	EF157594, EF157581	Coll. SAM, 18 March 2003, type locality on the banks of Ross River, Townsville, Australia (#777-03-18-03-5)

Prosorhochmus Keferstein, 1862 (type genus), *Prosadenoporus* Bürger, 1890 (=*Pantinonemertes* Moore and Gibson, 1981 part, new synonymy) and *Geonemertes* Semper, 1863.

Geographic distribution

Atlantic coast of the British Isles, France, Spain, USA (FL and SC) and Bermuda; Caribbean (Belize); Adriatic Sea (coast of Italy and Croatia); Mediterranean Sea (coast of Italy, France, Chafarinas Islands); Black Sea (Russian coast); Pacific coast of USA (Puget Sound, WA to CA, Hawaii) and Chile; Hong Kong, China (Fujian Province), north-eastern coast of Australia (Queensland), Indopacific Islands (Noordwachter Is. off Sulawesi, Palau Bidan off Malay Peninsula, Papua New Guinea, Japan, Seychelles, Sri Lanka, Sulawesi, Pelew Is., Caroline Is., Samoan Is., Kei Is., Mauritius, Samarai, the Philippines), the West Indies (Dominica, Jamaica).

Prosadenoporus Bürger, 1890

Prosadenoporus Bürger, 1890.
Neonemertes Girard, 1893. New synonymy. Type species *Tetrastemma agricola* Willemoes-Suhm, 1874 by monotypy.
Pantinonemertes Moore and Gibson, 1981 (part). New synonymy. Type species *Pantinonemertes winsori* Moore and Gibson, 1981 by original designation.

Type species

Prosadenoporus arenarius Bürger, 1890, by subsequent designation (Moore and Gibson 1988).

Etymology

"Pro"=before, forward, in front of, L.; "adeno, adenos"=gland, G.; "poros"=hole, G. Likely refers to the presence of well-developed frontal organ [anterior pore] through which mucus cephalic glands discharge.

Table 2. Measurements of the stylet apparatus in *Prosadenoporus* species.

Species	Specimen	Body length (mm)	Stylet length (S; μm)	Basis length (B; μm)	S:B ratio	Source
P. floridensis sp. nov.	1	N/A	165	250	0.66	Collected JLN, Belize
P. floridensis sp. nov.	2	N/A	98	196	0.5	Collected JLN, Belize
P. floridensis sp. nov.	3	N/A	158	269	0.59	Collected SAM, Belize
P. floridensis sp. nov.	4	N/A	159	371	0.43	Collected SAM, Belize
P. floridensis sp. nov.	5	N/A	146	372	0.39	Collected SAM, Belize
P. floridensis sp. nov.	6	12	92	140	0.66	Collected JLN, Florida
P. floridensis sp. nov.	7	25	130	250	0.52	Collected JLN, Florida
P. floridensis sp. nov.	8	40	130	300	0.43	Collected JLN, Florida
P. floridensis sp. nov.	9	22	115	230	0.5	Collected JLN, Florida
P. floridensis sp. nov.	10	17	140	240	0.58	Collected JLN, Florida
P. floridensis sp. nov.	11	18	115	165	0.7	Collected JLN, Florida
P. floridensis sp. nov.	12	16	120	192	0.63	Collected JLN, Florida
P. mooreae comb. nov.	1	N/A	50	150	0.33	Gibson (1982b)
P. mooreae comb. nov.	1	N/A	130	140	0.92	Collected SAM, Magnetic Island, QLD, Australia
P. mooreae comb. nov.	2	N/A	120	130	0.92	Collected SAM, Magnetic Island, QLD, Australia
P. mooreae comb. nov.	3	N/A	120	160	0.75	Collected SAM, Magnetic Island, QLD, Australia
P. winsori comb. nov.*	N/A	N/A	200–250	950	NA	Moore and Gibson (1981)
P. winsori comb. nov.	1	180	220	850	0.26	Collected SAM, Magnetic Island, QLD, Australia
P. winsori comb. nov.	2	65	120	490	0.25	Collected SAM, Magnetic Island, QLD, Australia
P. winsori comb. nov.	3	N/A	360	720	0.5	Collected SAM, Magnetic Island, QLD, Australia

Table 2. (*Continued*).

Species	Specimen	Body length (mm)	Stylet length (S; μm)	Basis length (B; μm)	S:B ratio	Source
P. fujianensis comb. nov.	1	N/A	120	380	0.32	Sun (2001)
P. agricola comb. nov.*	N/A	N/A	80–95	75–90	NA	Coe (1904)
P. enalios comb. nov.	1	N/A	110	170	0.65	Moore and Gibson (1981)
P. mortoni comb. nov.	1	N/A	125	123	1	Collected Sun, Fujian province, China

Note: *Cases where individual measurements are not reported.

Diagnosis

Monostiliferous marine, brackish-water, semi-terrestrial or terrestrial hoplonemerteans with a horizontal cephalic epithelial fold (prosorhochmid smile) (Figures 1D, 1E and 2B). Four eyes (Figures 1A, 1D, 1E and 2B). Body-wall musculature well developed with a delicate layer of diagonal muscles between outer circular and inner longitudinal muscle layers (Figures 3A and 3B). Rhynchocoel full body-length, with wall composed of distinct outer circular and inner longitudinal muscle layers (Figure 3K). Proboscis small or massive, may be used for rapid locomotion. If massive, proboscis often with increased number of proboscis nerves and accessory stylet pouches, longer stylet (S) and basis (B) and decreased S:B ratio (Table 3). Tubular frontal organ is long and exceptionally well developed, with laterally differentiated epithelium (Figures 3C, 4I–L, 5G–I, 7A–I, 7L, 8A–D and 9C–F). Cephalic glands extensive, reaching into stomach-pylorus region and containing basophilic (mucus) components (Figure 3C) discharging through frontal organ and via improvised epidermal ducts and acidophilic (proteinaceous) components, staining red (red glands) (Figure 5H) and orange with Mallory trichrome and its modifications (orange-G glands) (Figures 5J, 6B and 6D). Proteinaceous cephalic glands discharge via improvised ducts scattered throughout epidermis. Cerebral sensory organs small, anterior or antero-lateral to brain, with simple un-forked canal, opening ventro-laterally into reduced cerebral organ furrows (Figures 2A, 5A, 5B and 5J). Neurochord cells and neurochords present in some species (Figures 5E, 5F, 7J, 8E, 8F and 9G), but not necessarily together. Lateral nerve cords without accessory nerves (e.g. Figures 4G and 7J). Oesophagus divisible into anterior region supplied with acidophilic glands (Figures 3F, 3I, 3J, 5J, 6A and 6B), and posterior non-glandular region (Figures 3G and 6C). Caecum long, anteriorly bifid, with numerous lateral diverticula on each side (Figure 6E). Blood system with three main longitudinal vessels, without transverse connectives; mid-dorsal blood vessel with single vascular plug (Figure 4F); cephalic vascular loop recurved. Extracellular matrix (parenchyma) may be very extensive, especially in large species. Excretory system well developed, with binucleate terminal nephridial cells reinforced by transverse support bars (Figures 5C, 5D and 7K), thin-walled canals and large number of inconspicuous nephridiopores. Gonochoric or hermaphroditic. Oviparous or viviparous.
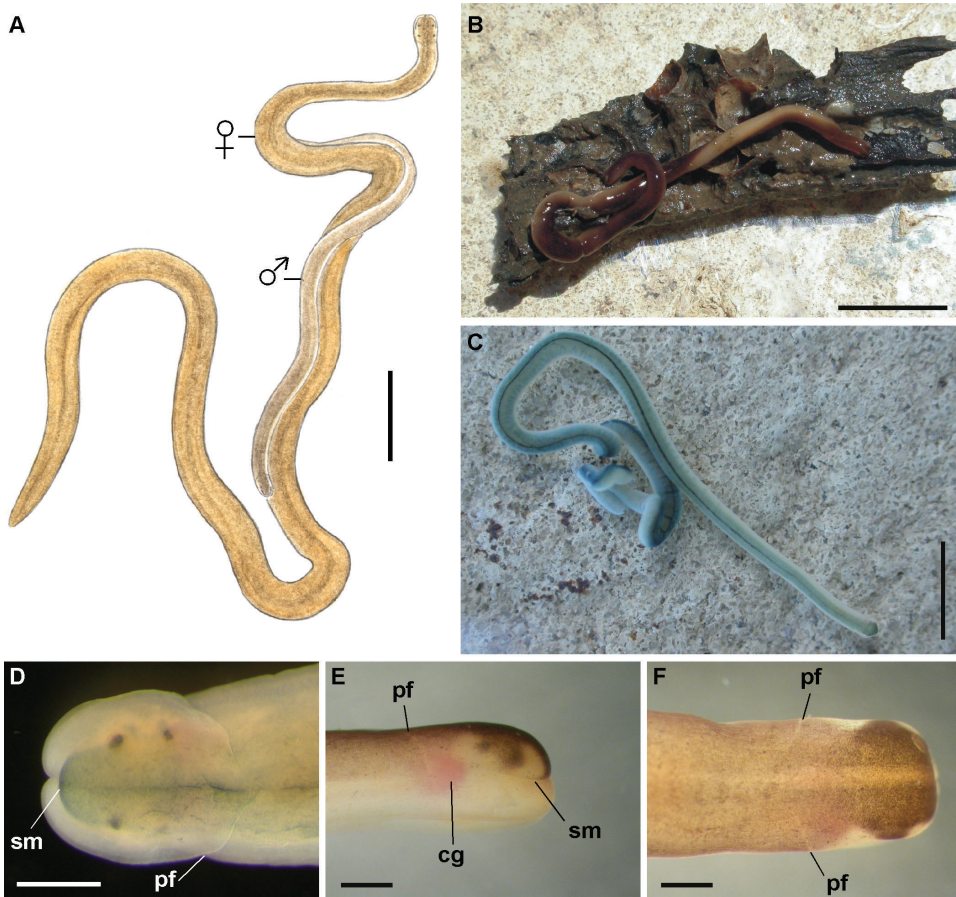
Figure 1. External appearance of members of *Prosadenoporus*. (A) Female and male of *Prosadenoporus floridensis* sp. nov.; (B) *Prosadenoporus winsori* comb. nov. on a piece of rotten mangrove penetrated by teredinid burrows (its natural habitat); (C–D) *Prosadenoporus mooreae* comb. nov.; (E–F) anterior end of *P. winsori* (E=lateral view; F=dorsal view). Notes: cg, cerebral ganglia; pf, posterior cephalic furrow; sm, prosorhochmid smile. Scales: (A and C), 3 mm; (B), 20 mm; (D), 0.5 mm; (E and F), 1 mm.

Composition

Prosadenoporus includes nine species: *P. agricola* (Willemoes-Suhm, 1874) comb. nov., *P. arenarius* Bürger, 1890, *P. spectaculum* (Yamaoka, 1940) comb. nov., *P. winsori* (Moore and Gibson, 1981) comb. nov., *P. enalios* (Moore and Gibson, 1981) comb. nov., *P. mooreae* (Gibson, 1982b) comb. nov., *P. mortoni* (Gibson, 1990) comb. nov., *P. fujianensis* (Sun, 2001) comb. nov., and *P. floridensis* sp. nov.

Geographic distribution

Atlantic coast of the USA (FL) and Bermuda; Caribbean (Belize); Pacific coast of USA (Puget Sound, WA to CA); Hong Kong, China (Fujian Province), north-eastern coast of Australia (Queensland), Indonesian Islands (Noordwachter

Island off Sulawesi and Ambon Island [Amboina]), Palau Bidan (Kedah Province) off Malay Peninsula, Laccadive Islands.

Prosadenoporus agricola (Willemoes-Suhm, 1874), new combination
(Figure 10F; Tables 2 and 3)

Tetrastemma agricola (Willemoes-Suhm 1874; Moseley 1879; Hubrecht 1887; Verrill 1902).

Neonemertes agricola (Girard 1893; Joubin 1894; Friedrich 1955).

Geonemertes agricola (Bürger 1895, 1897–1907, 1904; Coe 1904, 1905, 1929, 1939, 1940; Crozier 1917; Pantin 1947, 1961, 1969; Gibson 1972; Moore and Moore 1972; Moore 1973, 1975a, 1975b).

Pantinonemertes agricola (Moore and Gibson 1981; Gibson et al. 1982; Gibson 1982b; Gibson, 1990; Sundberg 1989; Gibson and Sundberg 1992; 2001; Moore et al. 2001; Sun 2001).

Etymology

The name reflects terrestrial habitat of this species (*agricola*=farmer, L).

Type material

Types were never designated. Original material almost certainly lost.

Material examined

Prosadenoporus agricola (Willemoes-Suhm, 1874) comb. nov. Series of sections of one mature and one juvenile specimen are held at the University Museum of Zoology, Cambridge, UK (coll. Boden, B. 1951, Bermuda).

Diagnosis

Prosadenoporus agricola comb. nov. differs from most other *Prosadenoporus* species in being hermaphroditic and viviparous (Table 3). It differs from *Prosadenoporus arenarius*, the only other hermaphroditic congener, whose life history is unknown, by having fewer proboscis nerves 12–15 (compared with 15–17) and possessing neurochord cells. Central stylet (S) 80–95 μm long, basis (B) rounded, pear-shaped or truncated 75–90 μm long, two accessory stylet pouches. It is not possible to determine mean S:B ratio because only ranges of stylet and basis lengths are available. Data at hand are insufficient to determine whether these metrics are significantly different from those of other species.

Habitat and distribution

Along the shores of mangrove swamps, under stones and logs on moist, silty soil or inside burrows of earthworms above high-water mark and, during wet season, on adjacent hillsides. Associated with a heteronemertean *Lineus* sp., earthworms, nematodes and, sometimes, insects. Smaller individuals also occur below the high-water mark. Found in Hungary Bay, Bayley's Bay, Walsingham Bay, on shores of Castle Harbor, near the "Causeway", at Hamilton Harbor and other localities on Bermuda Island. Once common on Bermuda (Coe 1904, p. 532), this species had last been collected in 1966 during an extensive search of the islands by Dr B. Boden, which yielded very few specimens, all obtained from a remote place. More recent commercial

Table 3. Morphological characteristics of *Prosadenoporus* species.

Species	Habitat	Body colour in life	Sex/life history	Neuro-chords	Neuro-chord cells
P. floridensis sp. nov.	Semi-terrestrial	Light yellowish, orange-brown, olive-tan or greenish-brown dorsally, darkest in the dorsal midline, off-white to yellowish cream ventrally	Gonochoric, oviparous	Absent	Present
P. arenarius	?	Unknown, preserved specimens uniformly dull brown	Hermaphroditic, presumably oviparous	Absent	Absent
P. agricola	Semi-terrestrial, terrestrial	Varies from uniform milk-white or grayish-white to orange, rosy, greenish-brown or grayish-brown dorsally, and pale gray or whitish ventrally	Hermaphroditic, viviparous	Absent	Present
P. winsori	Semi-terrestrial	Purplish-brown dorsally with a narrow, pale mid-dorsal longitudinal stripe anteriorly, pale cream to grayish-white ventrally, intensifying to pale reddish-brown posteriorly	Gonochoric, presumably oviparous	Present	Present
P. fujianensis	Semi-terrestrial	Grayish-black dorsally, pale whitish ventrally, dark pigment concentrated along the dorsal midline forming a narrow stripe	Gonochoric, presumably oviparous	Absent	Present
P. mooreae	Marine intertidal	Dorsal colour grayish-green with a dark-green to black narrow longitudinal stripe, ventral side cream to pale greenish	Gonochoric, presumably oviparous	Absent	Absent
P. mortoni	Marine intertidal	Dorsal colour olive-green with a dark-green narrow longitudinal stripe, ventral side yellowish-white	Gonochoric, presumably oviparous	Absent	Absent
P. enalios	Marine intertidal	Pale fawn-brown, orange-brown or orange dorsally, deepest pigmentation appearing over anterior pair of eyes, ventrally cream, off-white or pale orange	Gonochoric, presumably oviparous	Absent	Absent
P. spectaculum	Semi-terrestrial	Off-white to creamy-brown, speckled with dark-brown? dorsally and laterally, more densely toward dorsal midline; characteristic spectacle-shaped pattern of dark-brown around eyes		Absent	Present

Table 3. (*Continued*).

Species	Shape of stylet basis	Stylet length (S; μm)	Basis length (B; μm)	S:B ratio	Number of accessory stylet pouches	Number of proboscis nerves
P. floridensis sp. nov.	Truncated	92–165 (mean 130.7)	140–372 (mean 247.9)	0.39–0.7 (mean 0.55)	2	11–14
P. arenarius	?	?	?	?	?	15–17
P. agricola	Rounded, pear-shaped or truncated	80–95	75–90	?	2	12–15
P. winsori	Truncated	200–360 (mean 233.3)	490–850 (mean 686.7)	0.25–0.5 (mean 0.34)	6–9	22–24
P. fujianensis	Truncated	120	380	0.32	5	19–20
P. mooreae	Elongated, narrow and rounded	50–130	130–160 (mean 145)	0.33–0.92 (mean 0.73)	2	15–16
P. mortoni	Elongated, narrow and rounded	125	123	1.0	?	14
P. enalios	Truncated	110	170	0.65	?	14–16
P. spectaculum	?	?	?	?	2	18–22

development has left very little suitable habitat and the species has apparently not been found since (Moore et al. 2001; W. Sterrer, personal communication to SAM).

Remarks

Coe's (1904) anatomical account of the species mentions 13–15 proboscis nerves. SAM observed 12 proboscis nerves in the available voucher specimen in the collection of University Museum of Zoology, Cambridge, UK.

Prosadenoporus arenarius Bürger, 1890

Prosadenoporus arenarius (Bürger 1890, 1895, 1904; Moore and Gibson 1988).

Etymology

The species name means ''living in sand'' (L).

Type material

Type material almost certainly does not exist; not known from the most likely repositories – Museum für Naturkunde, Berlin; Zoologisches Institut, Universität Göttingen; Stazione Zoologica, Naples.

Material examined

Prosadenoporus arenarius Bürger, 1890. Series of transverse sections (slides 1–3) of hermaphroditic specimen from Punnett's collection (Palau Bidan off Malay Peninsula) held at the University Museum of Zoology, Cambrige, UK.

Diagnosis

Prosadenoporus arenarius differs from all other *Prosadenoporus* species except *Prosadenoporus agricola* comb. nov. by being hermaphroditic (Moore and Gibson 1988, p. 81) and from the Bermudan *P. agricola* by having 15–17 proboscis nerves (compared with 12–15) and by lacking neurochord cells (Table 3). Characters of the proboscis armature are unknown.

Habitat and distribution

Habitat is unknown, except in as much as the name of the species implies. Found in Java Sea (Noordwachter Island off northwestern Sulawesi) and Palau Bidan (Kedah Province, off Malay Peninsula).

Remarks

As mentioned above, Bürger's material is almost certainly lost. A tube with several specimens labelled ''*Prosadenoporus* sp.'' from Punnett's collection from Palau Bidan (Kedah Province, Malay Peninsula) was deposited at the University Museum of Zoology in Cambridge, UK. Moore and Gibson (1988) sectioned some of these specimens and re-described *Prosadenoporus arenarius* Bürger, 1890, arguing that Punnett's specimens fit the original (very brief) description of *P. arenarius*. However,

some evidence suggests that Bürger's *P. arenarius* from Indonesia and Punnet's *Prosadenoporus* sp. from Malaysia might represent different species.

First, the specimen described by Bürger (1890) from the Noordwachter Island off Sulawesi had a broad dark-brown, mid-dorsal stripe on a grayish-green background, while Punnett's specimens were uniformly dull brown (Moore and Gibson 1988). Second, and more important, Bürger's diagnosis of the genus mentions neurochord cells and neurochords. Moore and Gibson (1988) report about Punnett's specimens that "few neurochord cells are present, located near the inner margins of the dorsal cerebral lobes and neurochords can be traced in the main nerve cords" (p. 80). However, their figure 10 (Moore and Gibson 1988, p. 78, fig. 10) suggests that they mistake the type III neurons for neurochord cells, both defined by Bürger (1895). Our reinvestigation of Punnett's material showed no traces of neurochord cells or neurochords. Finally, Bürger's specimen had 12 proboscis nerves, while there are 17 proboscis nerves in Punnett's material. Although we have little confidence that Bürger's description and Punnett's material belong to the same species, lack of the type or other informative material thwarts resolution of the question.

Moore and Gibson (1988, p. 82) provided an amended diagnosis of the genus *Prosadenoporus*. The main difference between *Pantinonemertes* Moore and Gibson, 1981 and *Prosadenoporus* Bürger, 1890 is the presence of a second cephalic vascular loop described for *Prosadenoporus* by Moore and Gibson (1988, p. 81, fig. 18). However, the two authors of the present paper, as well as Frank Crandall (National Museum of Natural History, Smithsonian Institution, personal communication), independently confirmed the presence of a single cephalic vascular loop upon re-examining Punnett's material. This eliminates the main distinction between the two genera and provides grounds for synonymizing *Prosadenoporus* Bürger, 1890 and *Pantinonemertes* Moore and Gibson, 1981.

Prosadenoporus enalios (Moore and Gibson, 1981), new combination
(Figures 7A–C and 10E; Tables 2 and 3).

Pantinonemertes enalios (Moore and Gibson 1981; Gibson 1982b, 1990; Gibson et al. 1982; Sundberg 1989; Gibson and Sundberg 1992; Sun 2001).

Etymology

The species name reflects the fully marine habitat of the species; (*enalios*=in the sea, G).

Type material

Prosadenoporus enalios (Moore and Gibson, 1981) comb. nov. Sections of holotype W5900 and paratype W5899 are held at the Australian Museum, Sydney, Australia.

Material examined

Prosadenoporus enalios (Moore and Gibson, 1981) comb. nov. Holotype W5900, paratype W5899. Additional sectioned specimen 1978-12-3, coll. by R. Gibson from Magnetic Island, Queensland, Australia held at the Natural History Museum, London, UK.

Diagnosis

Prosadenoporus enalios comb. nov. differs from *P. fujianensis*, *P. winsori* and *P. spectaculum* by paler colouration and the absence of neurochord cells. Additionally, it differs from *P. winsori* in lacking neurochords. It differs from *P. agricola* and *P. arenarius* by being gonochoric, and from *P. mortoni* and *P. mooreae* by lacking characteristic greenish striped colouration and by having a truncated basis of central stylet (Figure 10E). It differs from *P. floridensis* sp. nov. by the absence of neurochord cells and having 14–16 proboscis nerves (compared with 11–14). Number of accessory stylet pouches unknown. Central stylet (S) 110 µm long, basis (B) truncated 170 µm long, S:B ratio 0.65 (Moore and Gibson 1981). Data at hand are insufficient to determine whether these metrics are significantly different from those of other species.

Habitat and distribution

In silty mud beneath rocks and coral boulders, mid- to lower-shore, intertidal. Nelly Bay and Picnic Bay on Magnetic Island, Queensland and on Pelorus Island, Palm Island Group, Great Barrier Reef, Australia.

Remarks

Original description mentions 14–15 proboscis nerves (Moore and Gibson 1981). However, we observed 16 nerves in the holotype. Although it appears to have been abundant at the time of original description, SAM failed to re-collect any from the type locality and other localities nearby in March 2003 despite the successful recollection of *P. mooreae* from the same area.

Prosadenoporus floridensis, new species
(Figures 1A, 2A, 2B, 3–6 and 10I; Tables 1–4)

Etymology

The species is named after Florida, its type locality.

Type material

Type specimens are deposited at the US National Museum of Natural History (NMNH), Smithsonian Institution, Washington, DC, USA. The holotype – mature female USNM 1098692 consists of two series of transverse sections of anterior and posterior body regions in addition to unsectioned proboscis and a fragment of midbody in 70% ethanol (coll. JLN, May 1992, type locality in FL, USA). Paratypes – mature male USNM 1098693 (two series of transverse sections of anterior and posterior, coll. JLN, May 1992, Link Port, FL, USA) and mature female USNM 1098696 (a series of longitudinal frontal sections of the anterior and a series of transverse sections of the posterior, coll. C. Glasby, 1986, Twin Cays, Belize). Additional voucher specimens (sectioned and unsectioned) are stored at the NMNH and assigned the following catalog numbers USNM 1098701, 1098702, 1098713, 1098714, 1014302–1014306, 1098694, 1098695, 1098697–10987000, 1098703–1098712.
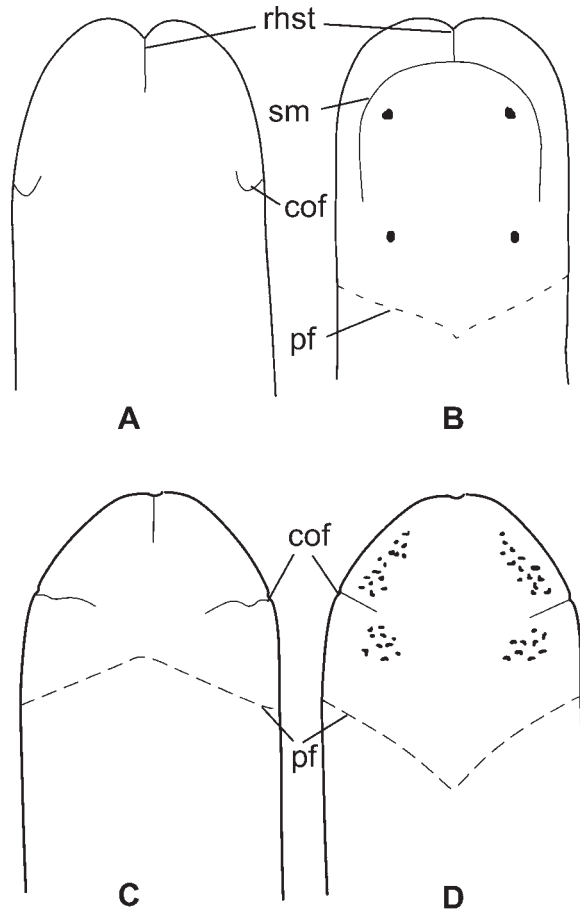
Figure 2. (A–B) Diagrams of anterior end of *Prosadenoporus floridensis* sp. nov. (A=ventral view; B=dorsal view); (C–D) *Pantinonemertes californiensis* (C=ventral view; D=dorsal view). Notes: cof, cerebral organ furrow; pf, posterior cephalic furrow; rhst, rhynchostome; sm, prosorhochmid smile.

Material examined

Holotype and paratypes USNM 1098692, 1098693 and 1098696. Sections of voucher specimens from Belize and Florida USNM 1098701, 1098702, 1098713, 1098714, 1098697–109869700, 1098704, 1098706, 1098708–1098710 and 1098712.

Diagnosis

Prosadenoporus floridensis sp. nov. is not known to possess any morphological apomorphies. It differs from *P. arenarius* in being gonochoric and from *P. agricola* in being gonochoric and oviparous. It differs from *P. winsori* by paler colouration (compare Figures 1A and 1B) and by lacking neurochords (Figures 4G and 7J). It differs from both *P. winsori* and *P. fujianensis* by having but a single pair of accessory stylet pouches (Table 3), and from *P. mooreae* and *P. mortoni* by lacking characteristic greenish striped colouration (compare Figures 1A and 1C) and by

having a truncated basis of central stylet (Figures 10A, 10B and 10I). It differs from *P. enalios* by having neurochord cells (Figures 5E and 5F) and fewer proboscis nerves (11–14 compared with 14–16), and from *P. spectaculum* by lacking a distinct spectacle head colour pattern and by having 11–14 proboscis nerves (compared with 22–24). Two accessory stylet pouches. Central stylet (S) 92–165 μm long, average=130.7 μm, basis (B) truncated 140–372 μm long, 247.9 μm average, S:B ratio 0.39–0.7, average=0.55. All three stylet metrics are significantly different from those of *P. winsori* ($p=0.05$) and the S:B ratio is significantly different from that of *P. mooreae* ($p=0.05$). Data for other species are insufficient to make the statistical comparisons. The average sequence divergence between *P. floridensis* and other *Prosadenoporus* species is 9.15% (16S) and 10.65% (COI) (Table 4).

Type locality, habitat and distribution

Prosadenoporus floridensis is common underneath and on the under surface of large rocks partially embedded in coarse moist sand in the supra-littoral zone in the type locality, locally known as Link Port, near Harbor Branch Oceanographic Institution in Fort Pierce, Florida, USA on the shore of the Indian River Lagoon (27°32′6.18″N, 80°20′47.14″W). Nemerteans were found from the top of oligochaete zone up into wrack zone (a vertical distance of about 20 cm). Additional specimens were collected from Twin Cays, Belize (16°49′27.93″N, 88°6′12.63″W) from a similar habitat, underneath large logs embedded in moist sand in the supra-littoral zone at the edge of mangroves.

Description

External appearance. Prosadenoporus floridensis is a relatively large species with maximum recorded length of reproductive specimens 70–75 mm and width up to 1.2 mm. Females tend to be larger than males. The colour in life ranges from light yellowish, orange-brown to olive tan or greenish-brown dorsally and from off-white to deeper yellowish-cream ventrally. The colour is darkest in the dorsal midline, sometimes creating an appearance of a very faint median stripe (Figure 1A). There is a rather sharp lateral transition from darker dorsal to paler ventral colouration. The body is broadest in the middle part, slightly narrower at the anterior and gradually tapering toward the posterior to end in a bluntly rounded tip. The dorsal surface is vaulted, so that the body is oval to round in cross-section, similar to other semi-terrestrial members of the genus – for example, *P. winsori*.

The head is blunt with a characteristic vertical anterior notch giving it a somewhat bilobed appearance, otherwise not demarcated from the body (Figures 2A and 2B). A dorsal horizontal epidermal fold anterior to the eyes separates two ventral apical lobes from a median dorsal lobe, forming the characteristic prosorhochmid "smile" (Figure 2B). The four large dark-brown to black eyes are situated at the anterior margin of the brain in a rectangle; the anterior pair is slightly larger than the posterior. The distance between the eyes of the anterior pair and those of the posterior pair is about the same as the distance between the two pairs (Figure 2B). The rudimentary cerebral organ furrows appear as a pair of inconspicuous latero-ventral, whitish, semi-circular grooves between the anterior and posterior pairs of eyes; these are not visible from the dorsal side (Figures 2A and B). The faint posterior cephalic

furrow forms a shallow, dorsal, posteriorly directed ''V'' immediately behind the brain (Figure 2B). The rhynchostome opening is subterminal.

Body wall, musculature and parenchyma. Epidermis is of typical hoplonemertean structure (Figure 3A). Dermis is represented by a thin layer of extracellular matrix. Body-wall musculature consists of an outer circular layer and an inner longitudinal layer. Diagonal (oblique) muscle fibres situated between the circular and long-itudinal musculature of the body wall form a very delicate but distinct layer best visualized in longitudinal tangential sections (Figure 3B).

The proboscis insertion comprises mostly longitudinal and oblique muscle fibres, which form a more or less separate inner layer of longitudinal muscles that joins the outer longitudinal muscle layer behind the brain. A radial component of the proboscis insertion is weakly developed or absent. In other words, precerebral septum is not well defined and the longitudinal musculature is anteriorly split into an inner layer composed of proboscis insertion muscles and outer layer – the body-wall longitudinal muscles proper (Figures 3C and 4I). Individual fibres from the inner portion of the longitudinal musculature continue into the head as cephalic retractors.

Dorso-ventral muscles are well developed (Figure 3D). Isolated muscle fibres oriented dorso-ventrally, obliquely and horizontally are found in the precerebral region (Figure 3E). The longitudinal muscle fibres surrounding rhynchodeum continue posteriorly as an almost continuous thin sheet of muscles surrounding foregut (Figure 3F); these are often referred to as the ''splanchnic musculature''. At the brain level the foregut muscles are reinforced by longitudinal muscle fibres originating at the proboscis insertion. Foregut or splanchnic muscles continue as a delicate, sometimes indistinct layer of fibres surrounding the stomach (Figure 3H). The amorphous extracellular matrix, the so-called ''parenchyma'', is very sparse but is otherwise unremarkable.

Proboscis apparatus. The proboscis pore opens at the tip of the head (Figures 2A and 2B) and leads into a short, thin-walled rhynchodeum lined with squamous epithelium. It was not possible with light microscopy to determine whether rhynchodeal epithelial cells are ciliated. The rhynchodeal musculature comprises a delicate layer of longitudinal and circular muscle fibres. There is no localized concentration of circular muscle fibers representing a distinct rhynchodeal sphincter. The rhynchocoel reaches 75–100% of body length. Its wall is of typical distromatonemertean (Thollesson and Norenburg 2003) structure and contains separate outer circular and inner longitudinal muscle layers (Figure 3K). The thickness of the layers changes dramatically with the state of contraction of the animal.

The proboscis is thin, longer than the body, cream-coloured, and used in escape reaction. Anteriorly the proboscis wall consists of a non-glandular epithelium, a thin layer of circular muscles and a thick layer of longitudinal muscles supplied with proboscis nerves (Figures 3L and 4A). Further posteriad, the wall of the anterior chamber is composed of a tall glandular epithelium, arranged into conical papillae, a thin layer of extracellular matrix, an outer circular muscle layer, a longitudinal muscle layer divided into two concentric layers by the neural sheath, a delicate layer of inner circular muscles, and a thin endothelium (Figures 4B and 4C). The neural sheath bears 11–14 proboscis nerves (Figure 4B).
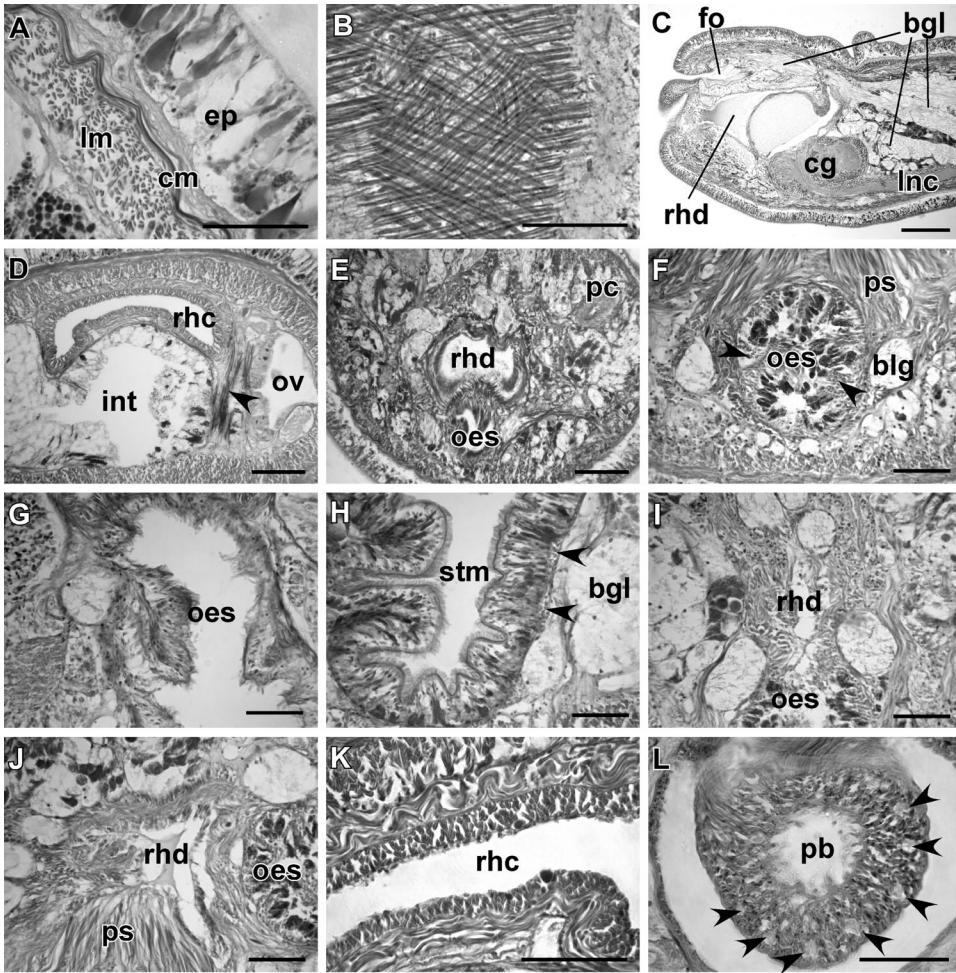
Figure 3. Histological sections of *Prosadenoporus floridensis* sp. nov. (dorsal=up; ventral= down unless otherwise noted). (A) Transverse section through the body wall; (B) longitudinal (tangential) section through the body wall showing diagonal muscle fibres; (C) longitudinal saggital section through the head (anterior to the left) showing frontal organ, cerebral ganglia and voluminous basophilic cephalic glands; (D) transverse section showing well-developed dorso-ventral musculature in the midgut region (arrowhead); (E) transverse section through precerebral region showing rhynchodeum, oesophagus and an ocellus; (F) transverse section through the anterior oesophagus showing acidophilic oesophageal glands and "splanchnic" musculature (arrowheads); (G) transverse section through the posterior oesophagus showing ciliated oesophageal epithelium lacking acidophilic glands; (H) transverse section through the stomach showing "splanchnic" musculature (arrowheads); (I) transverse section through the anterior rhynchodeum; (J) transverse section through the rhynchodeum at the level of the proboscis insertion (ventral to the right); (K) transverse section through the rhynchocoel wall (L) transverse section through anterior-most portion of proboscis (near proboscis insertion) showing distinct proboscis nerves (arrowheads). Notes: bgl, basophilic cephalic glands; cg, cerebral ganglia; cm, circular muscles; ep, epidermis; oes, oesophagus; fo, frontal organ; int, intestine; lm, longitudinal muscles; lnc, lateral nerve cord; ov, ovary; pb, proboscis; pc, ocellus; ps, proboscis insertion muscles; rhc, rhynchocoel; rhd, rhynchodeum; stm, stomach. Scales: (A, B), (F–L), 50 μm; (D–E), 100 μm; (C), 200 μm.
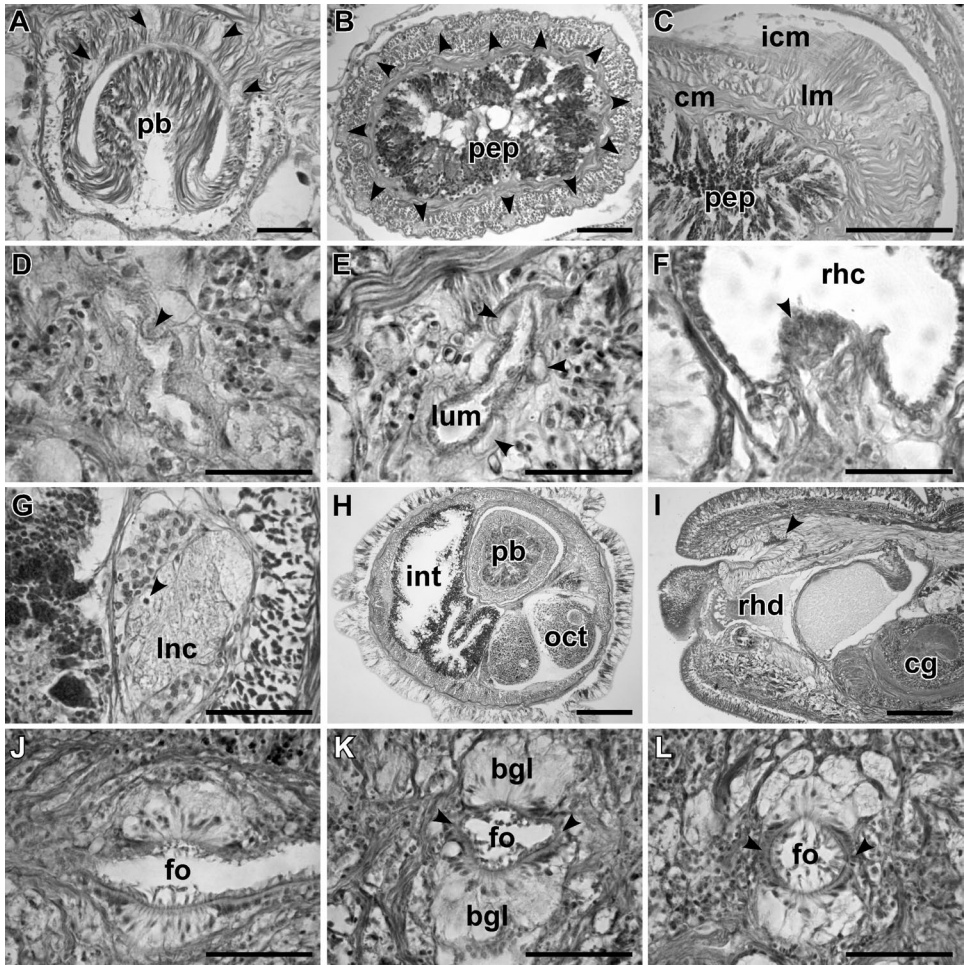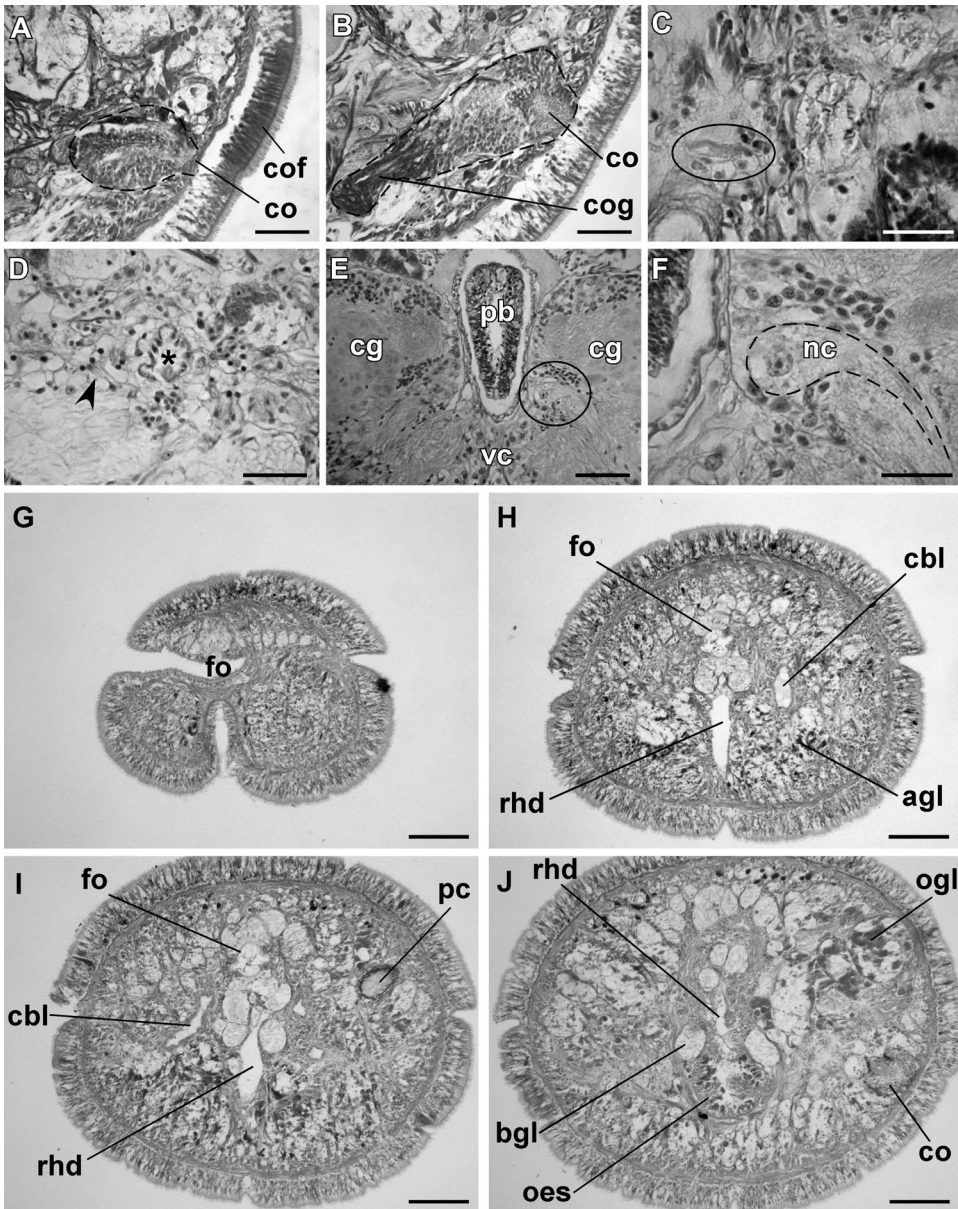
Figure 4. Histological sections of *Prosadenoporus floridensis* sp. nov. Transverse sections through (A) the proboscis insertion, and (B) anterior proboscis showing proboscis nerves (arrowheads); (C) transverse section through the proboscis showing inner circular muscles; (D–E) transverse sections through the cephalic blood vessels, demonstrating "valves" and "pouches" (arrowheads); (F) transverse section through the vascular plug (arrowhead); (G) transverse section through the lateral nerve cord showing nerve cord muscles (arrowhead); (H) transverse section through the midgut region of a mature female showing large oocytes in the ovary; (I) longitudinal (sagittal) section through the frontal organ (arrowhead) and precerebral region (anterior to the left); (J–L) a series of transverse sections through the anterior (J), middle (K) and posterior (L) portions of the frontal organ showing lateral acidophilic regions (arrowheads). Notes: bgl, basophilic cephalic glands; cg, cerebral ganglia; cm, circular muscles; fo, frontal organ; icm, inner circular musculature; int, intestine; lm, longitudinal musculature; lnc, lateral nerve cord; lum, blood vessel lumen; oct, oocytes; pb, proboscis; pep, proboscis epithelium; rhc, rhynchocoel; rhd, rhynchodeum. Scales: (D–F), 25 μm; (A, B, C, G and J–L), 50 μm; (H–I), 200 μm.

The proboscis armature consists of a central stylet, mounted on a character-istically truncated basis (Figure 10I) and two pouches each containing 2 or 3 accessory stylets. The length of the central stylet (S) varies from 98 to 165 μm, average = 130.7 μm; basis length (B) ranges from 140 to 372 μm, average = 247.9 μm (n = 13). S:B ratio varies from 0.39 to 0.7, average = 0.55 (Tables 2–3). The wall of the posterior chamber of the proboscis consists of strongly basophilic glandular

epithelium organized into papillae, outer longitudinal muscle layer, thin inner circular muscle layer, and a delicate endothelium.

Alimentary canal. The oesophagus opens into the rhynchodeum in front of the proboscis insertion (Figure 3E). It is enclosed by longitudinal muscle fibres, which are confluent with the rhynchodeal musculature and continue posteriorly as the musculature of the stomach (Figures 3F and 3H). As in all other species of *Prosadenoporus*, the anterior portion of oesophageal epithelium is richly supplied with finely granular acidophilic gland cells, staining deep red with Crandall's trichrome technique (Figures 3F, 3J, 5J, 6A and 6B). Posteriorly the oesophageal epithelium is ciliated and conspicuously lacks acidophilic or basophilic glands (Figures 3G and 6C). This part sometimes is referred to in the literature as the anterior stomach (see, for example, Moore and Gibson 1981, p. 184); however, it more resembles oesophagus in morphology.

The stomach is of typical hoplonemertean structure with densely ciliated, deeply folded epithelium, containing numerous basophilic and acidophilic glands (Figures 3H and 6D). The intestinal caecum is well developed, anteriorly bifid and bears numerous lateral diverticula throughout its length (Figure 6E). The anterior caecal diverticula reach the posterior portion of the dorsal cerebral ganglia. Intestinal diverticula are lobed.

Blood system. The blood system comprises paired lateral and an unpaired mid-dorsal blood vessel, joined precerebrally via a suprarhynchodeal loop and posteriorly via a supra-anal loop. As is characteristic of *Prosadenoporus*, the suprarhynchodeal (cephalic) loop in *P. floridensis* sp. nov. is recurved: i.e., the lateral blood vessels run forward into the tip of the head before curving up and backward to anastomose in the midline just behind the posterior chamber of the frontal organ. The mid-dorsal blood vessel originates near the ventral cerebral commissure from the right cephalic vessel (traced in two specimens) and immediately penetrates the rhynchocoel floor to form a single vascular plug. The wall of the vascular plug consists of thickened endothelium of the blood vessel, a thin layer of extracellular matrix and a modified

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Figure 5. *Prosadenoporus floridensis* sp. nov. (A) Slightly oblique transverse section through the cerebral organ furrow and anterior portion of the cerebral organ (outlined) showing cerebral organ gland; (B) transverse section through the posterior portion of the cerebral organ (outlined) showing posterior lobe of the cerebral organ gland; (C) transverse section through the terminal region of nephridia showing a particularly distinct binucleate flame cell (circled); (D) transverse section through the cephalic blood vessel (asterisk) showing the nephridial tubules and flame cells (arrowhead) crowded around the blood vessel; (E and F) transverse sections through the brain, showing a neurochord cell (E circled; F outlined); (G–J) a series of slightly oblique transverse sections from anterior tip to oesophagus: (G) the prosorhochmid smile; (H) the frontal organ, (I) the anterior eye and cephalic blood vessel, (J) one of the cerebral organs and anterior oesophagus. Notes: agl, acidophilic cephalic glands; bgl, basophilic cephalic glands; cbl, cephalic vascular loop; cg, cerebral ganglia; co, cerebral organ; cof, cerebral organ furrow; cog, cerebral organ gland; oes, oesophagus; fo, frontal organ; nc, neurochord cell; ogl, orange-G cephalic glands; pc, ocellus; pb, proboscis; rhd, rhynchodeum; vc, ventral brain commissure. Scales: (C and F), 20 μm; (D), 30 μm; (A, B and E), 50 μm; (G–J), 100 μm.

rhynchocoel endothelium (Figure 4F). No transverse connectives linking mid-dorsal and lateral blood vessels in the intestinal region were found by us. The blood vessels are thin-walled with few "valves" and "pouches" (Figures 4D and 4E).

Nervous system. As in other nemerteans, the brain consists of two ventral and two dorsal ganglia, joined by ventral (subrhynchocoelic) and dorsal (suprarhynchocoelic) commissures, respectively (Figures 3C, 4I, 5E, 6B and 6C). The dorsal ganglia are more widely separated than the ventral. A thin, but distinct outer neurilemma encloses the brain as a whole, but there is no inner neurilemma dividing the fibrous and ganglionic tissues. Notably, there is a pair of large and conspicuous neurochord cells close to the inner side of the ventral cerebral ganglia in vicinity of the ventral cerebral commissure (Figures 5E and 5F). However, no neurochords are found in the lateral nerve cords (Figure 4G).

The lateral nerve cords contain a single fibrous core throughout their length, i.e. there are no accessory nerve cords. As observed in most monostiliferans studied in the last three decades, each lateral nerve cord contains a single delicate muscle bundle, consisting of 3–7 fibres and running within or adjacent to the fibrous core, near its dorsal border. In addition, there are several less conspicuous muscle fibres running along the inner lateral side of the fibrous core (Figure 4G). Muscle fibres associated with the lateral nerve cords can be traced to their origin near the proboscis insertion. Numerous cephalic nerves lead anteriorly from the brain lobes to supply various structures of the head. A pair of stout nerves originating from the ventral brain lobes supplies the cerebral sensory organs. Paired proboscis nerve trunks originate from the ventral brain lobes near the ventral cerebral commissure and branch before entering the proboscis (Figure 4A).

Frontal organ. The well-developed frontal organ opens at the tip of the head. Its elongated ciliated canal, about 200–400 μm long, extends about half way to brain (Figures 3C and 4I) and is lined by regionally differentiated epithelium. The ventral and dorsal walls as well as the posterior extremity of the canal, through which the basophilic mucus cephalic glands discharge, have a vacuolated appearance and bear long, sparsely distributed cilia. The lateral walls of the canal, sometimes bearing a more or less distinct groove, comprise strongly acidophilic epithelium clad in short densely arranged cilia (Figures 4L and 5G–I). The acidophilic appearance results from the densely arranged elongated nuclei of the ciliated cells. Unlike some other species of the genus, such as *P. winsori*, *P. mooreae* and *P. spectaculum*, the frontal organ canal does not exhibit any noticeable "twisting" (compare Figures 4J–L, 5G–I to 7A–C, 7F–I, 8A–D and 9C–F).

Cephalic glands. Cephalic glands are extremely well developed. As in other *Prosadenoporus*, they include three types of cells: basophilic lobules with vacuolated appearance (mucus glands), coarsely granular proteinaceous gland cells staining golden-yellow to brown with Mallory trichrome or orange with Crandall's method (orange-G glands), and finely granular proteinaceous acidophilic cells, staining red with Mallory or Crandall's technique (acidophilic or red glands).

Mucus glands open into the frontal organ (Figures 3C and 4I), as well as through the epidermis via multiple improvised ducts. Mucus glands are found precerebrally around the frontal organ: organized into more compact lobes dorsally and ventrally

and interspersed with the orange-G glands laterally (Figures 3C, 3F, 3H–J, 4I–L and 5H–J). Two major ventro-lateral lobes of the mucus gland descend closely on both sides of the rhynchodeum and run posteriad ventro-lateral to the foregut (Figures 3F, 3I, 5J and 6A–D). At the level of proboscis insertion dorsal lobes of mucus glands abound above the rhynchodeum (Figures 5J and 6A). Numerous smaller lobes are found between the body wall and internal organs laterally. In the cerebral region, mucus glands occupy the dorso-medial region between the dorsal body wall and rhynchocoel, as well as the region ventro-lateral to the brain ganglia. Ventro-lateral mucus tracts are very prominent postcerebrally (Figure 6D). Further posteriad, ventro-lateral lobes gradually become displaced by the caecal diverticula, while dorso-lateral lobes remain prominent (Figure 6E). Mucus glands gradually decrease in number toward the posterior and disappear at the end of pylorus.

Acidophilic glands are well developed and, for the most part, restricted to the ventro-lateral precerebral region (Figures 5H and 5I). Individual acidophilic gland cells are found dorsally in the precerebral region directly underneath the body wall interspersed with the mucus cephalic glands (Figures 5H–J). Ventral acidophilic glands largely disappear posterior to the proboscis insertion, while the scattered dorsal gland cells can be found in the cerebral region.

Orange-G glands are extremely well developed. Overall, they present a distribution typical for the genus. Two dorso-lateral tracts of orange-G glands first appear at the level of the frontal organ and reach as far back as the end of the pylorus. In the precerebral region, orange-G glands are found laterally between the ventral acidophilic glands and dorsal mucus glands, and dorso-laterally, where they intersperse with mucus glands (Figure 5J). The orange-G glands are very abundant postcerebrally above the lateral nerve cords where they are interspersed with the mucus glands (Figure 6D).

Cerebral organs. The compact paired cerebral organs are situated in front of the brain between the anterior and posterior pairs of eyes. Each organ opens ventro-laterally into a reduced anterior cephalic furrow (Figure 2A). The latter are shallow semi-circular grooves lined by strongly acidophilic ciliated epithelium (Figure 5A). Cerebral organ canals are not branched. Two types of gland cells can be distinguished in the cerebral organs. The coarsely granular cells, staining dark reddish-brown with Crandall's method are found at anterior face of the cerebral organ (Figure 5A). The second type of cell is finely granular, stains less intensively red to brownish purple and forms a single lobe on the posterior face of each organ (Figure 5B). This posterior glandular lobe of cerebral organs may extend under the brain.

Excretory system. The collecting tubules of the excretory system are thin-walled and inconspicuous. Terminal flame cells are small, binucleate and reinforced by five to seven very thin and indistinct transverse support bars. Flame cells are typically observed embedded in the extracellular matrix in the vicinity of blood vessels, and are particularly numerous around the cephalic blood vessels (Figures 5C and 5D). Collecting tubules open to the outside via numerous inconspicuous thin-walled nephridioducts. With effort, few flame cells and nephridioducts can be detected past foregut region, but it is impossible to determine the full extent of the nephridial system in this species with light microscopy.
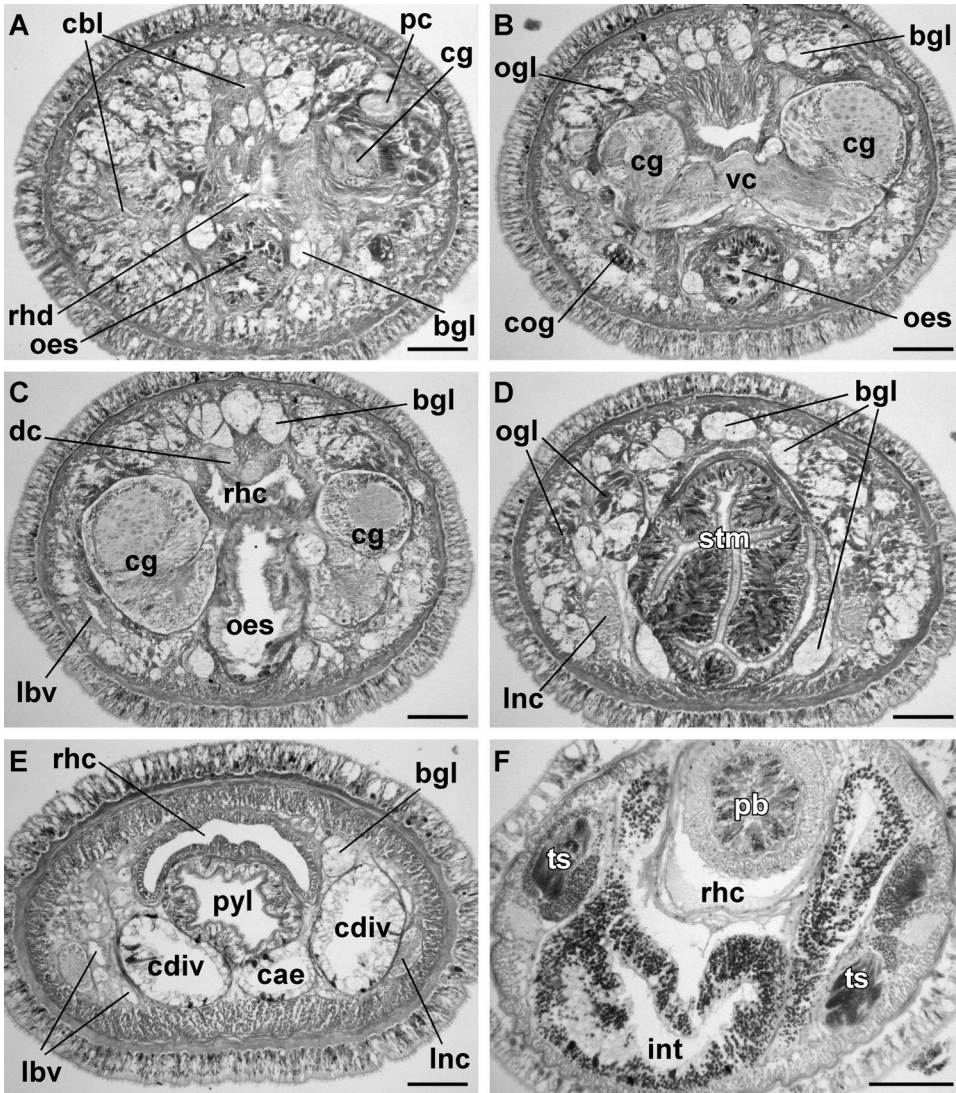
Figure 6. (A–E) A series of slightly oblique transverse sections of *Prosadenoporus floridensis* sp. nov. from precerebral region to pyloric region (proboscis is missing in this individual): (A) Section through the posterior eyes immediately in front of cerebral ganglia; (B) cerebral ganglia, ventral cerebral commissure and anterior oesophagus; (C) cerebral ganglia and posterior oesophagus; (D) stomach; (E) pylorus and caecum. (F) transverse section through the midgut region of another specimen showing ripe testes. Notes: bgl, basophilic cephalic glands; cae, caecum; cbl, cephalic vascular loop; cdiv, caecal diverticulum; cg, cerebral ganglia; cog, cerebral organ gland; dc, dorsal cerebral commissure; oes, oesophagus; int, intestine; lbv, lateral blood vessel; lnc, lateral nerve cord; ogl, orange-G cephalic glands; pb, proboscis; pc, ocellus; pyl, pylorus; rhc, rhynchocoel; rhd, rhynchodeum; stm, stomach; ts, testis; vc, ventral brain commissure. Scales: (A–F), 100 µm.

Reproductive system and life history. Sexes are separate. All sectioned sexually mature individuals possessed either ovaries (Figure 4H) or testes (Figure 6F) and never mixed gonads. Reproductive males and females were observed from January to May in Florida. Males and females can be distinguished by the colour of mature gonads: testes are whitish, while the ovaries are pinkish-orange, due to the colour of mature oocytes. Males also tend to be smaller than females. Mature ovaries contain three to seven oocytes each. Mature egg is about 380 μm in diameter, very yolky, pinkish-orange to brownish-orange and enclosed within an egg envelop approximately 430 μm in diameter. In captivity, several females laid clutches of 100–150 eggs on walls of glass or plastic containers above the water line.

Development is encapsulated. Gastrulation occurs on the second day of development (approximately 36 h) and ciliation is obvious on the third day. Large and yolky cells of epidermis, possibly corresponding to the transitory larval epidermis, described in some other hoplonemertean larvae (Maslakova and Malakhov 1999; Maslakova and von Döhren 2007), are apparent on the sixth day of development. Yolky, teardrop-shaped to vermiform juveniles about 2 mm long hatch from the egg envelopes in about 6–10 days, after which they may remain crawling within the mucus clutch for a few more days. Two-week old juveniles have brain, ocelli and proboscis with a central stylet on a basis.

Prosadenoporus fujianensis (Sun, 2001), new combination
(Figures 8F and 10D; Tables 2 and 3)

Pantinomertes fujianensis (Sun 2001)

Etymology

The species is named after the place of discovery – Fujian province of China.

Type material

Prosadenoporus fujianensis (Sun, 2001) comb. nov. Holotype DH07 and paratypes DH08 and DH09 are deposited with the College of Fisheries, Ocean University of Qingdao, China.

Material examined

Prosadenoporus fujianensis (Sun, 2001) comb. nov. Holotype DH07, paratypes DH08 and DH09.

Diagnosis

Prosadenoporus fujianensis comb. nov. differs from all the other species of the genus except *P. winsori* by having multiple pouches of accessory stylets. It differs from *P. winsori* by lacking the pale mid-dorsal stripe and the neurochords, and by having fewer proboscis nerves (19–20 compared with 22–24) and fewer accessory stylet pouches (5 compared with 6–9) (Table 3). Central stylet (S) 120 μm long, basis (B) truncated 380 μm long, S:B ratio 0.32. Data at hand are insufficient to make statistical comparison of the stylet metrics with other species.

Habitat and distribution

Semi-terrestrial; in mud not soaked with water in the mangrove area in the estuary of Jiulong Jiang River, Fugong, Longhai County, Fujian Province, China.
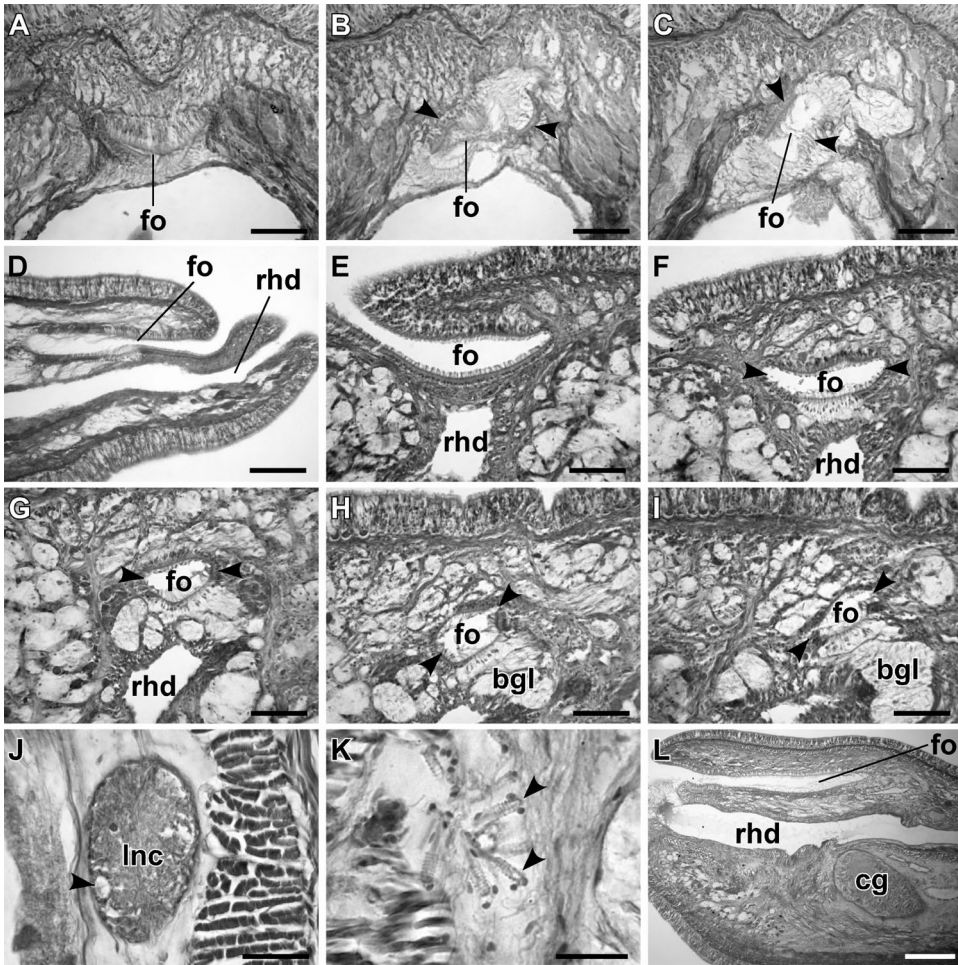
Figure 7. Microscopic anatomy of *Prosadenoporus* species. (A–C) A series of transverse sections through the frontal organ of *Prosadenoporus enalios* comb. nov.; relative position of the lateral acidophilic regions (arrowheads) indicate a noticeable twist of the frontal organ canal; (D) a longitudinal sagittal section through frontal organ of *Prosadenoporus mooreae* comb. nov. (anterior to the right); (E–I) a series of slightly oblique transverse sections through the frontal organ of *P. mooreae* comb. nov.; lateral acidophilic regions of the frontal organ (arrowheads), note the twisting of the frontal organ canal; (J) transverse section through lateral nerve cord of *Prosadenoporus winsori* comb. nov. showing the tentative neurochord (arrowhead); (K) binucleate terminal cells of nephridia (flame cells) of *P. winsori* comb. nov. (arrowheads); (L) a longitudinal sagittal section through the frontal organ of *P. winsori* comb. nov. (anterior to the left). Notes: bgl, basophilic cephalic glands; cg, cerebral ganglia; fo, frontal organ; lnc, lateral nerve cord; rhd, rhynchodeum. Scales: (A–C), and (E–I), 50 µm; (D), 100 µm; (J), 30 µm; (K), 20 µm; (L), 200 µm.

Remarks

The original description mentions 19 proboscis nerves in all three specimens, however, our re-investigation showed that the paratypes have 19 and the holotype has 20 proboscis nerves. Morphologically, this species most resembles another mangrove-dwelling species – *P. winsori* from Queensland, Australia. Unfortunately,

Table 4. Percentage sequence divergence between species of *Prosadenoporus* species and *Pantinonemertes californiensis* (%, 16S/COI).

	P. winsori	*P. mooreae*	*P. mortoni*	*P. floridensis* sp. nov.
P. winsori	–	–	–	–
P. mooreae	7.8/10.2	–	–	–
P. mortoni	7.9/10.6	2.4/4.1	–	–
P. floridensis sp. nov.	10.3/10.8	7.8/10.3	8.6/10.4	–
P. californiensis	7.3/13.1	7.6/12.6	7.6/12.8	9.9/11.1

tissue for molecular analysis was not available to us to compare the sequence divergence between the two species.

Prosadenoporus mooreae (Gibson, 1982b), new combination
(Figures 1C, 1D, 7D–I and 10B; Tables 1–4)

Pantinonemertes mooreae (Gibson 1982b, 1990; Sundberg 1989; Gibson and Sundberg 1992; Sun 2001)

Etymology

The species is named after Dr Janet Moore of the Department of Zoology, University of Cambridge, as a tribute to her work on the terrestrial nemerteans of the world.

Type material

Prosadenoporus mooreae (Gibson, 1982b) comb. nov. Sections of holotype W5903 and paratype W5904 are held at the Australian Museum, Sydney, Australia.

Material examined

Prosadenoporus mooreae (Gibson, 1982b) comb. nov. Holotype W5903 and paratype W5904. Several additional specimens (most sectioned) collected by SAM in March 2003 from Picnic Bay and Cockle Bay, Magnetic Island, Queensland, Australia held at the National Museum of Natural History in Washington, DC, USA (USNM 1087356, 1087357, 1087359–1087361, 1087358). One unsectioned specimen from the same collecting trip G20028 is held in 70% ethanol at the Museum of Tropical Queensland, Townsville, Queensland, Australia.

Diagnosis

Prosadenoporus mooreae comb. nov. does not have any known morphological apomorphies. It differs from all other species of the genus except *P. mortoni* by having a distinct greenish colour pattern with a dark-green to black mid-dorsal longitudinal stripe (Figures 1C and 1D). Similar to *P. mortoni*, *P. mooreae* has a very slender rounded stylet basis (Figure 10B). With the exception of the number of

proboscis nerves (15–16 vs. 14) these two species are morphologically indistinguishable (Table 2, 3) and represent the closest molecular pair in the genus, exhibiting sequence divergence of 2.4% (16S) and 4.1% (COI) (Tables 1 and 4). Two accessory stylet pouches. Central stylet 50–130 μm long, average=105 μm, basis (B) rounded 130–160 μm long, average=145 μm, S:B ratio 0.33–0.92, average=0.73. All three stylet metrics are significantly different from those of *P. winsori*. The S:B ratio is significantly different from that of *Prosadenoporus floridensis* (*p*=0.05). Data at hand are insufficient to make the statistical comparisons with other species.

Habitat and distribution

In silty mud beneath rocks and coral boulders, mid- to low-shore, intertidal. Picnic Bay and Cockle Bay, Magnetic Island, Queensland, Australia.

Remarks

Two specimens were collected originally in Picnic Bay by R. Gibson in 1975. SAM collected nine additional specimens from the nearby Cockle Bay in March 2003, and two from Picnic Bay. Gibson (1982b) reported only one measurement for the stylet apparatus (S:B ratio=0.33), which is very different from that observed by SAM (average S:B for three specimens=0.86). With the data at hand it is not possible to determine whether the difference is statistically significant. We pooled our measurements with Gibson's and adjusted the means for the species accordingly. Contrary to Gibson's observations, SAM found that *P. mooreae* uses its proboscis for rapid locomotion. Upon the slightest contact the worm everts its

Figure 8. (A–D) A series of transverse sections through the frontal organ of *Prosadenoporus winsori* comb. nov.; relative position of the lateral acidophilic regions (arrowheads) indicate a noticeable twist of the frontal organ canal; (E) Neurochord cell of *P. winsori* comb. nov. (circled, insert); (F) Neurochord cell of *Prosadenoporus fujianensis* comb. nov. (circled, insert). Notes: bgl, basophilic cephalic glands; cg, cerebral ganglia; fo, frontal organ; pb, proboscis. Scales: (A–F), 100 μm; inserts, 50 μm.

proboscis and quickly draws it back in, pulling itself into a crevice and out of reach of the collector.

Prosadenoporus mortoni (Gibson, 1990), new combination
(Figure 10A; Tables 1–4)
Pantinonemertes mortoni (Gibson 1990; Gibson and Sundberg 1992; Sun 2001)

Etymology

The species is named in honour of Professor Brian Morton, as a tribute to his considerable involvement in furthering the knowledge of the marine flora and fauna of the Hong Kong region.

Type material

Prosadenoporus mortoni (Gibson, 1990) comb. nov. Sections of the holotype 1987-4-54 are deposited at the Natural History Museum in London, UK (coll. P. G. Oliver and A. S. Y. Mackie. Starfish Bay, Hong Kong).

Material examined

Prosadenoporus mortoni (Gibson, 1990) comb. nov. Holotype 1987-4-54. Additional material coll. by Dr Shichun Sun, Nan Ao Island and Xiamen, Fujian Province, China; sectioned and deposited at the National Museum of Natural History in Washington, DC, USA (USNM 1020576–1020577).

Diagnosis

Prosadenoporus mortoni comb. nov. does not have any known morphological apomorphies. It differs from all other species of the genus except *P. mooreae* by having a distinct colour pattern with a greenish-black mid-dorsal longitudinal stripe. *P. mortoni* shares with *P. mooreae* the characteristic slender rounded basis of central stylet (Figure 10A) and is nearly indistinguishable from it morphologically. The two species represent the closest molecular pair in the genus exhibiting sequence divergence of 2.4% (16S) and 4.1% (COI) (Tables 1 and 4). Number of accessory stylet pouches unknown. Central stylet (S) 125 µm long, basis (B) rounded 123 µm long, S:B ratio 1.0. Data at hand are insufficient to make the statistical comparisons of stylet metrics with other species.

Habitat and distribution

Under rocks on coarse sand, lower shore; Starfish Bay, Hong Kong; Xiamen and Nan Ao Island, Fujian Province, China.

Remarks

The original description is based on a single specimen from Hong Kong and has no account of the stylet apparatus. Dr Shichun Sun kindly provided three additional specimens collected and identified by him from Fujian Province in China, used here

for morphological and molecular comparisons. Dr Sun also provided his sketches of the stylet apparatus, which is very similar to that of *Prosadenoporus mooreae* comb. nov. (compare Figures 10A and 10B).

Prosadenoporus spectaculum (Yamaoka, 1940), new combination
(Figures 9C–I; Table 3)

Prostoma spectaculum (Yamaoka 1940).
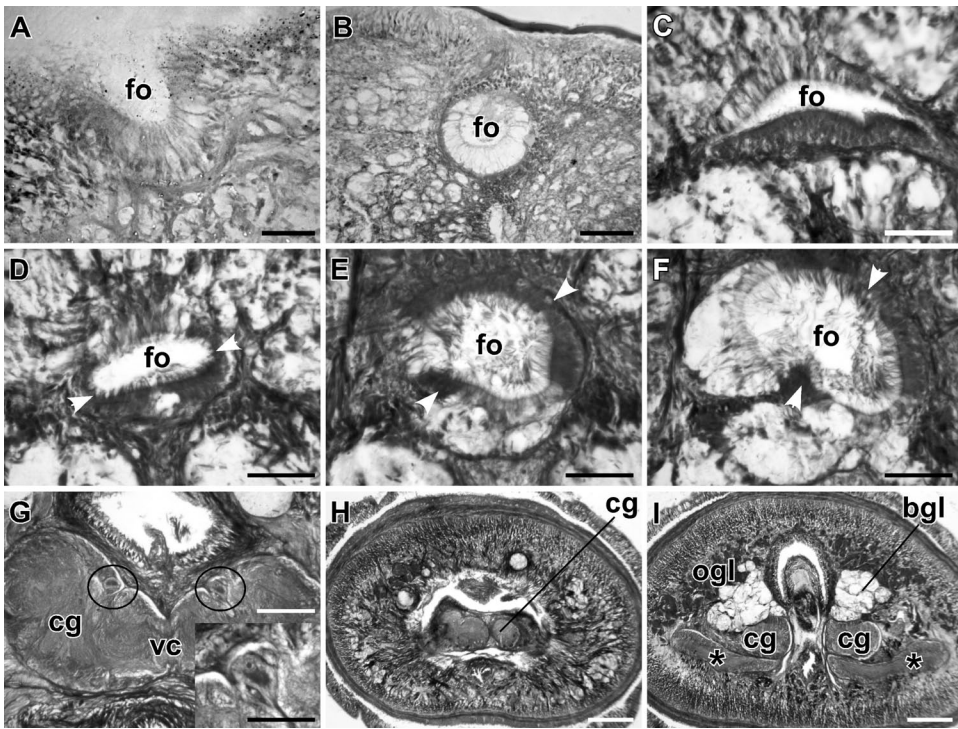*Pantinonemertes spectaculum* (Gibson 1990; Gibson and Sundberg 1992; Sun 2001).

Figure 9. (A–B) Transverse sections through the frontal organ of *Pantinonemertes californiensis*; (C–I) *Prosadenoporus spectaculum* comb. nov.: (C–F) a series of transverse sections through the tip of the head showing frontal organ twisting; lateral acidophilic regions of the frontal organ marked with arrowheads; (G) transverse section through the cerebral ganglia showing two neurochord cells (circled, insert); (H) transverse section through the proboscis insertion and anterior portion of cerebral ganglia showing contracted proboscis insertion muscles; (I) transverse section through the posterior region of brain showing beginning of the lateral nerve cords (asterisks) which appear sectioned longitudinally, presumably because of the severe contraction of the specimen during fixation. Notes: bgl, basophilic cephalic glands; cg, cerebral ganglia; fo, frontal organ; ogl, orange-G cephalic glands; vc, ventral brain commissure. Scales: (A–F), 50 µm; (G), 100 µm (insert, 50 µm); (H–I), 200 µm.

Etymology

The name reflects the unique spectacle-shaped pattern of pigmentation on the head of this species.

Type material

Type material almost certainly lost.

Material examined

Prosadenoporus spectaculum (Yamaoka, 1940) comb. nov. Two sectioned specimens 1987-2-43 and 1987-2-42 held at the Museum of Natural History, London, UK.

Diagnosis

Prosadenoporus spectaculum comb. nov. is distinguished from other species in the genus by the characteristic spectacle or helmet-shaped pattern of pigmentation on the head. Additionally, *P. spectaculum* differs from *P. winsori* in lacking neurochords and from both *P. winsori* and *P. fujianensis* by having a single pair of accessory stylet pouches. It differs from *P. mooreae*, *P. mortoni*, *P. enalios* and *P. arenarius* by having neurochord cells (Figure 9G) and from *P. agricola* and *P. floridensis* by having more proboscis nerves (18–22 compared with 11–14 in *P. floridensis* and 12–15 in *P. agricola*). The shape and size of stylet and basis are not known.

Habitat and distribution

Originally described from Naha and Tinen, Riukiu Islands, Japan; habitat unknown. Three specimens on which the re-description by Gibson (1990) is based were collected from rock crevices and clefts just below high tide level in Starfish Bay and Tai Mong Tsai, Hong Kong.

Remarks

Gibson (1990) stated that one of the diagnostic features of this species is presence of the split precerebral septum (Kirsteuer 1974). Our re-investigation of one of the Hong Kong specimens deposited at the British Museum of Natural History revealed that the structure of the precerebral septum (i.e. proboscis insertion muscles) in this species is the same as in other members of the genus; that is there is no distinct precerebral septum. However, we observed that the voucher specimen is severely contracted – as evident from the position of lateral nerve cords – which causes longitudinal muscle fibres in the proboscis insertion to appear as radial, giving the impression of the "split precerebral septum" (Figures 9H and 9I).

Prosadenoporus winsori (Moore and Gibson, 1981), new combination
(Figures 1B, 1E, 1F, 7J–L, 8A–E, 10G and 10H; Tables 1–4)
Pantinonemertes winsori (Moore and Gibson 1981).

Etymology

The species is named after Dr Leigh Winsor, who first drew attention to the species.

Type material

Prosadenoporus winsori (Moore and Gibson 1981) comb. nov. Sections of the holotype W5895 and paratype W5896 are deposited at the Australian Museum, Sydney, Australia.

Material examined

Prosadenoporus winsori (Moore and Gibson, 1981) comb. nov. Holotype W5895, paratype W5896. Additional sectioned specimen deposited at the Museum of Natural History in London 1978-12-2 (coll. R. Gibson, Townsville, Queensland, Australia) and five specimens collected by SAM in March 2003 from the type locality near Townsville, Queensland, Australia, four of which are partly sectioned and held at the National Museum of Natural History in Washington, DC, USA (USNM1087362–1087364, 1087366). The unsectioned specimen in 70% ethanol deposited at the Museum of Tropical Queensland, Townsville, Queensland, Australia (G20043).

Diagnosis

Prosadenoporus winsori comb. nov. is the only species in the genus to possess neurochords (Figure 7J). It differs from all other species of the genus except *P. fujianensis* in having multiple accessory stylet pouches. It additionally differs from *P. fujianensis* by the presence of a pale midline stripe on the dorsal surface of living specimens and by having 22–24 proboscis nerves (compared with 19–20) and more accessory stylet pouches (6–9 compared with 5–6). Central stylet=200–360 µm long, average=233.3 µm, basis (B) truncated, 490–850 µm long, average=686.7 µm, S:B ratio=0.25–0.5, average=0.34. All three stylet metrics are significantly different from those of *P. floridensis* and *P. mooreae* (p=0.05). Data at hand are insufficient to make statistical comparisons with other species. Average sequence divergence between *P. winsori* and other sequenced *Prosadenoporus* species is 8.7% and 10.5% for 16S and COI respectively (Tables 1 and 4).

Habitat and distribution

Semi-terrestrial or upper intertidal. Beneath bark or in cavities and burrows of teredinid bivalves in rotting fallen mangrove timber (*Avicennia marina* (Forsk.), *Ceriops tagal* (Perr.)); associated with polychaetes, teredinid bivalves, crustaceans (especially the grapsid decapod *Sesarma erythrodactyla* Hess), polyclad flatworms, coleopteran larvae and ants. In estuaries of Ross River (south bank) and Three Mile Creek, near Townsville, Queensland, Australia.

Remarks

Number of accessory stylet pouches is not mentioned in the original description (Moore and Gibson 1981). We investigated stylet armature in four out of five specimens collected by SAM from the type locality in March 2003 – two had six, one had seven and one had nine accessory stylet pouches.

Pantinonemertes californiensis Gibson et al., 1982, *incertae sedis*
(Figures 2C, 2D, 9A, 9B and 10C; Tables 1 and 4)

Pantinonemertes californiensis (Gibson et al. 1982; Gibson and Sundberg 1992; Sun 2001).

Type material

Type material deposited at the Museum of Natural History in London, UK consists of sections of the holotype (female) 1981.1.2 and paratype (male) 1981.1.3.

Material examined

We examined sectioned specimens from the personal collection of Frank Crandall (National Museum of Natural History, Smithsonian Institution, Washington DC, USA) collected from Millerton Creek marsh between Hwy 1 and the bay just opposite the Hwy 1 gate to the Borello ranch, Tomales Bay, CA, USA (FC031, FC034–37, FC085, FC112) and sections of one specimen collected by F. Crandall in July 1981 from the Bolsa Chica Ecological Reserve, CA, USA (a California State

Figure 10. Central stylets: (A) *Prosadenoporus mortoni* comb. nov. (a sketch of stylet apparatus provided by Dr Shichun Sun); (B) *Prosadenoporus mooreae* comb. nov. (specimen from the type locality coll. by SAM); (C) *Pantinonemertes californiensis* (after Gibson et al. 1982, p. 471, fig. 3b); (D) *Prosadenoporus fujianensis* comb. nov. (redrawn from Sun 2001, p. 205, fig. 23); (E) *Prosadenoporus enalios* comb. nov. (redrawn from Moore and Gibson 1981, p. 183, plate III, fig. c); (F) *Prosadenoporus agricola* comb. nov. (redrawn from Coe 1904. p. 571. plate 23, fig. 3); (G–H) *Prosadenoporus winsori* comb. nov. (specimen from the type locality coll. by SAM); (I) *Prosadenoporus floridensis* sp. nov. Note: Scales: (A, B, E, F), 100 µm; (C, D, G, H, I), 500 µm.

designated area near Huntington Beach) (FC102–104, FC 109–111). We anticipate these to be deposited with the NMNH. We also examined additional specimens collected by F. Crandall from Tomales Bay, CA, USA deposited at the NMNH: USNM 64138 (70% ethanol) and USNM 1076584–1076587 (slides).

Pantinonemertes daguilarensis Gibson and Sundberg, 1992, *incertae sedis*
Pantinonemertes daguilarensis (Gibson and Sundberg 1992; Sun 2001).

Type material

Pantinonemertes daguilarensis Gibson and Sundberg, 1992. Sections of the holotype 1990-7-5, and paratypes 1990-7-6 and 1990-7-7 are deposited at the Museum of Natural History in London, UK.

Material examined

Pantinonemertes daguilarensis Gibson and Sundberg, 1992. Holotype 1990-7-5, paratypes 1990-7-6 and 1990-7-7.

Discussion and conclusions

Synonymization of **Pantinonemertes** and **Prosadenoporus**

According to the amended diagnosis of the currently monotypic genus *Prosadenoporus* by Moore and Gibson (1988, p. 82), the main difference between the *Pantinonemertes* Moore and Gibson, 1981 and *Prosadenoporus* Bürger, 1890 is the presence of a second cephalic vascular loop, described for *Prosadenoporus* by Moore and Gibson (1988, p. 81, fig. 18). We re-examined sections of the voucher specimen of the only valid species of *Prosadenoporus* – *P. arenarius* Bürger, 1890 and were not able to confirm the presence of a second cephalic vascular loop. We also could not find any other morphological characters that could distinguish *Prosadenoporus* from *Pantinonemertes*. Therefore, we propose to synonymize *Prosadenoporus* Bürger, 1890 and *Pantinonemertes* Moore and Gibson, 1981. According to the principle of priority (ICZN Art. 23), *Prosadenoporus* Bürger, 1890 takes precedence over *Pantinonemertes* Moore and Gibson, 1981.

Prosadenoporus floridensis *sp. nov. – a new semi-terrestrial prosorhochmid*

We describe a new semi-terrestrial prosorhochmid species from Florida and Belize. The presence of the prosorhochmid smile, reduced cerebral organ furrows, extremely well-developed frontal organ with laterally differentiated epithelium, well-developed cephalic glands including basophilic, acidophilic and orange-G glands and truncated stylet basis support the prosorhochmid affinity of this species. However, these characters are shared by *Prosadenoporus* and *Prosorhochmus* species. Characters that distinguish this species from *Prosorhochmus* and support its position within *Prosadenoporus* include: thin-walled nephridial canals; extreme multiplication of the nephridiopores; binucleate flame cells reinforced by transverse support bars; presence of acidophilic glands in the anterior esophagus; elongated shape of the frontal organ; and recurved cephalic vascular loop.

Prosadenoporus floridensis differs from the closest geographical congener, a semi-terrestrial species from Bermuda *P. agricola*, by being gonochoric and oviparous. The average sequence divergence between *P. floridensis* and other *Prosadenoporus* species is 9.15% (16S) and 10.65% (COI) and 7.8% (16S) and 10.3% (COI) from the nearest sequenced congener *P. mortoni*, which is comparable to the sequence divergence between other sequenced species of *Prosadenoporus* (Tables 1 and 4).

Two species of uncertain taxonomic affinity

Pantinonemertes daguilarensis, a fully marine species from Hong Kong, reaches a maximum length of 200 mm and width of 0.75 mm. Colour in life varies from light grey with a brown tinge to pale pink; the posterior half of the intestinal region being darker gray or purplish-gray. Unlike all other *Pantinonemertes* (now *Prosadenoporus*) species, *P. daguilarensis* has a distinct cephalic lobe, numerous eyes situated in groups or rows, lacks orange-G cephalic glands and its frontal organ is a simple epithelial pit. Furthermore, it lacks the prosorhochmid smile and lateral differentiation of the epithelium in the frontal organ canal, has a planar (as opposed to recurved) cephalic vascular loop, forked cerebral organ canals, lacks acidophilic glands in the anterior esophagus, possesses an accessory nerve in the lateral nerve cords, has thick-walled nephridial canals, and only a few nephridiopores. Additionally, upon reinvestigation of the type and paratype specimens, we have not been able to find any terminal nephridial flame cells characteristic of *Prosadenoporus* species (confirmed by Frank Crandall, personal communication to authors), although they are described by Gibson and Sundberg (1992) even as having distinct support bars.

Pantinonemertes daguilarensis originally was placed in the genus *Pantinonemertes* by Gibson and Sundberg (1992) based on the presence of anteriorly split body-wall longitudinal muscle, simple cephalic vascular loop, presence of diagonal musculature in the body wall, lack of precerebral septum, cephalic retractor muscles derived only from the outer portion of the divided longitudinal musculature, and a rhynchocoel near full body length. We argue that these characters are not sufficient to justify placement of this species within *Prosadenoporus*. First, a diagonal muscle layer in the body wall is present in almost all monostiliferan species studied by us and it is easily missed when only cross-sections are investigated. It cannot serve as a diagnostic character. Simple vascular loop and rhynchocoel near full body length are so widely distributed among the monostiliferous hoplonemerteans that they most likely represent plesiomorphic similarity. It is the alternatives that are unusual and characteristic. Finally, anteriorly split longitudinal musculature, or something interpreted as such, is reported to occur in over 25 monostiliferan genera (Chernyshev 2002), and derivation of the cephalic retractor muscles is not a sufficiently well-studied character to be the sole basis for generic placement. Because the differences from other species of the genus are substantial and the only similarities are likely plesiomorphies, we argue that *Pantinonemertes daguilarensis* does not belong in *Prosadenoporus*. Until more data are available to clarify position of this species, it may be referred to as species *incertae sedis*.

Pantinonemertes californiensis, an oviparous, dioecious, semi-terrestrial species from the coast of California, reaches a maximum length of 265 mm and width of

3 mm. Dorsal colour in life is greenish-brown to grayish-green, shading to a lighter greenish-tan laterally; pigmentation is darker in the dorsal midline, forming a stripe of very dark green without clearly delimited margins; ventral surface is light cream to tan and head is almost the same colour. Mature oocytes are characteristically coral red, while testes show through the body wall as salmon pink or cream-coloured opaque masses.

Unlike other prosorhochmids, *Pantinonemertes californiensis* has numerous eyes situated in four groups or rows (compared with four simple eyes) (Figure 2D), oblique cerebral organ furrows (compared with reduced ventro-lateral arches) (Figures 2C and 2D) and a weakly developed frontal organ (Figures 9A and 9B). However, similar to other prosorhochmids, *P. californiensis* possesses well-developed cephalic glands, including basophilic and proteinaceous (red and orange-G) cells, reaching well into foregut region and some into intestinal region. Unlike species of *Prosadenoporus*, *P. californiensis* lacks the prosorhochmid smile (Figure 2D) and epithelial differentiation of the frontal organ canal (Figures 9A and 9B). In this species, the frontal organ is but a small undifferentiated ciliated pit at the tip of the head. *Pantinonemertes californiensis* resembles *Prosadenoporus* species in having binucleate flame cells reinforced by distinct support bars and thin-walled nephridial canals opening via a large number of nephridiopores.

Similar to the *Prosadenoporus* species occupying semi-terrestrial and terrestrial habitats, such as *P. winsori* and *P. fujianensis*, *Pantinonemertes californiensis* has a large proboscis with multiple accessory stylet pouches. Morphological cladistic analysis of the family Prosorhochmidae with several hoplonemertean outgroups places *P. californiensis* outside *Prosadenoporus*, while molecular analysis based on partial sequences of 16S and COI and the combined morphological and molecular analysis place it either as a sister clade to *Prosadenoporus* or outside of the Prosorhochmidae (Maslakova 2005). Average sequence divergence between *P. californiensis* and *Prosadenoporus* species is 8.1% for 16S and 12.4% for COI; comparable to, if slightly larger than, the sequence divergence between such species as *P. winsori* and *P. mooreae*. Until more data are available to clarify its position, this species also may best be treated as *incertae sedis*.

It had been argued previously that *Pantinonemertes* was erected invalidly because the monotypic *Neonemertes agricola* (Willemoes-Suhm, 1874) was among the originally included nominal species (Chernyshev 1992), rendering *Pantinonemertes* an objective junior synonym and unavailable. If *Pantinonemertes* is treated as valid, as it functionally has been since 1981, our action here would be to treat it as a junior subjective synonym and potentially available, except that we transfer the type species to *Prosadenoporus*. Thus, either way, *Pantinonemertes* is unavailable for *P. californiensis* and *P. daguilarensis*. With respect to these two species, we anticipate useful phylogenetic realignment and consequent taxonomic actions as DNA sequence data for other distromatonemerteans become available in the near future, but we see no practical or useful immediate options. This is especially so with respect to *P. californiensis*, which now is well known from California to Puget Sound and is the subject of a significant number of publications. For this reason, we can envision supporting, within the context of the ICZN, a proposal to make the name available. This latter route is preferable to creating new monotypic genera as an almost certain short-lived solution.

Acknowledgements

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