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Two new and two poorly known autolytines (Polychaeta: Syllidae) from Madeira and the Mediterranean Sea

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Abstract

We describe *Proceraea albocephala*, new species, from Madeira, and *Erseia oligochaeta*, new genus and new species, from Istria, Croatia, and we provide redescriptions of *Proceraea madeirensis* (Nygren, 2004) from topotype material, and *Myrianida longoprimicirrata* (López, San Martín & Jimenéz, 1997) from material collected at Istria, Croatia, and Banyuls-sur-Mer, France. *Proceraea albocephala,* new species is morphologically separated from similar species by a prostomial white spot, and *E. oligochaeta*, new genus, new species is unique in having only a few (1–2) simple unidentate chaetae in all chaetigers, and a trepan with a single large and 25–28 smaller teeth. We assess the phylogenetic positions of the four species using nuclear 18SrDNA, together with mitochondrial COI and 16SrDNA. Our molecular data show that among the sequenced autolytines 1) *P. albocephala*, new species is most closely related to *P. nigropunctata* Nygren & Gidholm, 2001, *P. okadai* (Imajima, 1966), and *P. cornuta* (Agassiz, 1862), 2) *E. oligochaeta*, new genus, new species belongs within a clade together with *Procerastea nematodes* Langerhans, 1884, *Virchowia clavata* Langerhans, 1879, and *Imajimaea draculai* (San Martín & López, 2002), 3) *M. longoprimicirrata* is sister species to *M. pentadentata* (Imajima, 1966), and 4) *P. madeirensis* has a basal position within Procerini. The molecular data suggests that *Proceraea* Ehlers, 1864 as currently delineated is paraphyletic.

Key words: New species, new genus, redescriptions, nuclear data, mitochondrial data

Introduction

Autolytines are free-living syllid polychaetes that are from a few mm to several cm in length and usually much less than one mm in width. They inhabit shallow waters and are mostly associated to sedentary invertebrates such as hydroids, bryozoans, and sponges, animals which they apparently feed upon (see Nygren & Pleijel 2010 for references). Autolytines constitute both in morphological and molecular terms a well-delineated group of syllid polychaetes. Currently it includes 11 recognized genera divided in three major lineages, corresponding to different types of reproductive strategies (Nygren 2004; Nygren & Pleijel 2007); Procerini Nygren, 2004, where the members reproduce with anterior scissiparity (a single stolon is produced from behind chaetiger 13 or 14), *Epigamia* Nygren, 2004 where the members reproduce with epigamy (the main individual is transformed into an epitoke), and Autolytini Grube, 1850 where the members reproduce with gemmiparity (several stolons are produced in a row) or posterior scissiparity (a single stolon from a more posterior chaetiger is produced). Following Nygren (2004), and Nygren and Pleijel (2007) there are 21 autolytines known from the Mediterranean Sea and from Maderia. Four of these were originally decribed from Madeira by Langerhans (1879, 1884), while 13 are described originally from the Mediterranean Sea, mainly during two decades in the 19th century by Claparède (1864, 1868), Ehlers (1864), Grube (1860), and Marenzeller (1874, 1875). Later additions to the Mediterranean fauna includes species described by Cognetti (1953a, b), San Martín & Alós (1989), López *et al.* (1997), Nygren (2004), and Çinar and Gambi (2005). In this paper we redescribe one of Langerhans' species from Madeira, *Proceraea madeirensis* Nygren, 2004

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(new name for *Proceraea fasciata* Langerhans, 1879, junior homonym of *P. fasciata* Bosc, 1802), and the poorly known *Myrianida longoprimicirrata* (López, San Martín & Jiménez, 1997) described from Chafarinas Islands off the coast of Morocco. Neither of these two species have been reported since their original descriptions. We also describe two new autolytines, *Proceraea albocephala*, new species, from Madeira, and *Erseia oligochaeta*, new genus and new species, from Istria in Croatia. We assess their phylogenetic positions within Autolytinae using mitochondrial 16SrDNA and COI, and nuclear 18SrDNA, and estimate their intraspecific variation using COI and 16SrDNA.

Material and methods

Algae and gravel were put in tubs with sea-water, and emerging worms were collected. Live specimens were photographed with a Canon EOS 5D Mark II and a Canon MP-E65/2.8 1-5X macro lens. The specimens were then relaxed with magnesium chloride and then either 1) fixed in formalin (10%), rinsed in fresh water and transferred to 80% alcohol; 2) preserved directly in 90% alcohol for DNA-sequencing (entire or fragment); 3) squeezed between a microscope slide and cover glass while in $MgCl_2$, subsequently transferred to aquamount (Gurr) and saved as permanent slides. Origin of specimens, GenBank accession numbers, and deposition of vouchers are detailed in Table 1. DNA was extracted using DNAeasy Tissue Kit (Qiagen) following the protocol supplied by the manufacturer. We amplified 658 bp of COI, about 480 bp of 16S rDNA, and 1542–1771 bp of 18SrDNA. We used the primers 16SarL (CGCCTGTTTATCAAAAACAT) and 16SbrH (CCGGTCTGAACTCAGATCACGT) (Palumbi 1996) for 16SrDNA, PCR1F (AYCTGGTTGATCCTGCCAGT), PCR2F (TAAAGYTGYTGCAGTTAAA), PCR1R (TASGACGGTATCTGATCGTCTT), and PCR2R (ACCTTGTTACGACTTTTACTTCCTC) (Nygren & Sundberg 2003) for 18SrDNA, and LCO 1490 (GGTCAACAAATCATAAAGATATTGG) and HCO 2198 (TAAACTTCAGGGTGACCAAAAAATCA) (Folmer *et al.* 1994) for COI. PCR mixtures contained 21 µl ddH_20, 1 µl of each primer (10 µM), 2µl of DNA template, and puReTaq Ready-To-Go PCR Beads (Amersham Biosciences). The temperature profile was as follows: 96°C/240s–(94°C/30s–48-62°C/30s–72°C/60s)*45 cycles –72°C/480s. PCR products were purified with the E.Z.N.A. Cycle-Pure Kit (Omega Bio-tek). Sequencing was performed at Macrogen Inc. facilities (Seoul, Korea). Overlapping sequence fragments were merged into consensus sequences using Geneious 4.5.5 (Drummond *et al*. 2009). The protein coding COI was trivial to align, and the ribosomal genes were aligned using Clustal X (Thompson *et al*. 1997) with three different sets of gap/gap length penalties (20/2, 15/6, 30/8). We used the online GBlocks server v0.9b (Castresana 2002), using the option “Allow smaller final blocks”, to detect alignment-ambiguous sites that were subsequently excluded from the analysis (Gatesy *et al*. 1993; Castresana 2000; Talavera & Castresana 2007). Alignments are available at TreeBase, with study accession URL: http://purl.org/phylo/treebase/phylows/study/TB2:S10794. Initially we used a number of non-Autolytine syllid sequences from GenBank as outgroups, but as *P. albocephala*, new species, *P. madeirensis*, and *E. oligochaeta*, new genus, new species were all found to be members of the Procerini-clade, and *M. longoprimicirrata* was found to belong to the Autolytini-clade with strong support (posterior probability =1.0), we proceeded with autolytines belonging to the third main group, i.e. *Epigamia*, as outgroups, since this maximizes the number of alignable positions in the ribosomal genes, and increases the phylogenetic signal in the data set. The nuclear and the mitochondrial data sets were analysed separately and combined. In order to perform a sensitivity analysis (Wheeler 1995) we analysed all three different alignments for each data set and all possible combinations, which means for the mitochondrial data set the three different sets of 16SrDNA alignments together with COI, and for the nuclear data set the three different sets of 18SrDNA alignments, and for the combined data set we analysed all nine different combinations of these alternatives. We used MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) to conduct Bayesian analyses. The best-fit models were selected using the Akaike information criterion (AIC) in MrModeltest (Nylander 2004). For COI we used a General Time Reversible model with gamma distributed rate across sites with a proportion of the sites invariable (GTR+G+I) for all three codon positions, for 16SrDNA and 18SrDNA we also used a GTR+G+I model in all three sets of alignment parameters for each gene. The number of generations were set to between five and ten millions with four parallel chains (three hot, one cold), sample frequencies was set to 500, and numbers of runs were set to two. A quarter of the samples were discarded as burn in. Parameters were altered in the proposal mechanisms to acquire a span within 20–60% acceptance rates for the moves in the cold chain of each run (Gelman *et al*. 2009). Proposal rates were not changed. The tree files were analysed in AWTY (Are We There Yet) (Wilgenbusch *et al*. 2004; Nylander *et al*. 2008) to visually interpret if the analyses had reached the stationary phase. Numbers of haplotypes were determined in Geneious 4.5.5 (Drummond *et al*. 2009), and genetic variation was calculated in PAUP*4.0b10 (Swofford 2002) and Microsoft Excel 2004 for Mac, version 11.2.5. Museum abbreviations include GNM (Göteborgs Naturhistoriska Museum, Göteborg, Sweden), MNCN (Museo Nacional Ciencias Naturales, Madrid, Spain), and NHWM (Naturhistorisches Museum, Vienna, Austria). All voucher specimens and types are deposited at GNM.

TABLE 1. Sequenced taxa, locality, vouchers, and GenBank accession numbers.

	Locality	Voucher[1]	18S	16S	COI
Proceraea albocephala, new species sppm 1	Porto Moniz, Madeira	GNM Polychaeta 13194a, b	GU722646	GU722640	GU722607
Proceraea albocephala, new species spm 2	Porto Moniz, Madeira	GNM Polychaeta 13202		GU722641	GU722608
Proceraea albocephala, new species spm 3	Porto Moniz, Madeira	GNM Polychaeta 13203		GU722642	GU722609
Proceraea albocephala, new species spm 4	Porto Moniz, Madeira	GNM Polychaeta 13206			GU722610
Proceraea albocephala, new species spm 5	Porto Moniz, Madeira	GNM Polychaeta 13205a, b			GU722611
P. aurantiaca	Banyuls, France	SMNH 45837	AF474324	AF474278	GQ856160
P. cornuta	Koster, Sweden	SMNH 45830	AF474312	AF474266	-
P. fasciata	North Carolina, USA	GNM Polychaeta 13178	GQ856204	GQ856206	GQ856161
P. hanssoni	Friday Harbor, Washington, USA	SMNH 45832	AF474321	AF474275	GQ856162
P. madeirensis spm 1	Funchal, Madeira	GNM Polychaeta 13208	GU722645	GU722627	GU722617
P. madeirensis spm 2	Funchal, Madeira	GNM Polychaeta 13213		GU722628	GU722618
P. nigropunctata	Santa Catalina, California, USA	SMNH 45829	AF474320	AF474274	GQ856163
P. okadai	Friday Harbor, Washington, USA	SMNH 45828	AF474319	AF474273	GQ856164
P. paraurantiaca	Banyuls, France	SMNH 45838	AF474323	AF474277	GQ856165
P. picta	Banyuls, France	SMNH 45834	AF474317	AF474271	GQ856166
P. pleijeli	Cádiz, Spain	SMNH 5947	AF474318	AF474272	GQ856167
P. prismatica	Kaldbak, Faroe Islands	SMNH 45831	AF474311	AF474265	GQ856168
P. rubroproventriculata	Bahía de Paranagua, Brazil	SMNH 45835	AF474322	AF474276	GQ856169
P. scapularis	Banyuls, France	SMNH 45833	AF474316	AF474270	GQ856170
Virchowia clavata	Banyuls, France	AN	AF474314	AF474268	GQ856171
Procerastea nematodes	Santa Catalina, California, USA	AN	AF474315	AF474269	GQ856172
Erseia oligochaeta, new genus, new species spm 1	Rovinj, Croatia	GNM Polychaeta 13187a, b	GU722644	GU722635	GU722612

continued next page

TABLE 1. (continued)

	Locality	Voucher[1]	18S	16S	COI
Erseia oligochaeta, new genus, new species spm 2	Rovinj, Croatia	GNM Polychaeta 13191		GU722636	GU722613
Erseia oligochaeta, new genus, new species spm 3	Rovinj, Croatia	GNM Polychaeta 13192		GU722637	GU722614
Erseia oligochaeta, new genus, new species spm 4	Rovinj, Croatia	all material used for extraction		GU722638	GU722615
Erseia oligochaeta, new genus, new species spm 5	Rovinj, Croatia	all material used for extraction		GU722639	GU722616
I. draculai	Bratten area, Sweden	GNM Polychaeta 13167	GQ856205	GQ856210	GQ856176
Epigamia alexandri	Kaldbak, Faroe Islands	SMNH 45824	AF474308	AF474262	GQ856183
E. macrophtalma	Banyuls, France	SMNH 45827	AF474310	GQ856207	GQ856184
E. magna	Friday Harbor, Washington, USA	SMNH 45825	AF474309	AF474263	GQ856185
E. noroi	Santa Catalina, California, USA	SMNH 45826	AF474310	AF474264	GQ856186
Myrianida australiensis	Kaikora, New Zealand	GNM Polychaeta 13105	EF661838	EF661834	GQ856187
M. brachycephala	Kristineberg, Sweden	SMNH 45812	AF474926	AF474250	GQ856188
M. convoluta	Santa Catalina, California, USA	SMNH 45817	AF474303	AF474257	GQ856189
M. dentalia	Friday Harbor, Washington, USA	SMNH 45819	AF474301	AF474255	GQ856190
M. edwarsi	Kristineberg, Sweden	SMNH 45810	AF474294	AF474248	GQ856191
M. flava	Friday Harbor, Washington, USA	SMNH 45818	AF474300	AF474254	GQ856192
M. gidholmi	Carrie Bow Cay, Belize	GNM Polychaeta 13103	EF661839	EF661835	GQ856193
M. hesperidium	Banyuls, France	SMNH 45815	AF474305	AF474259	GQ856194
M. inermis	La Jolla, California, USA	SMNH 45821	AF474302	AF474256	GQ856195
M. irregularis	Friday Harbor, Washington, USA	SMNH 45822	AF474307	AF474261	GQ856196
M. langerhansi	Banyuls, France	SMNH 45813	AF474297	AF474251	GQ856197
M. longoprimicirrata spm 1	Banyuls, France	GNM 13214a, b	GU722643	GU722629	GU722619
M. longoprimicirrata spm 2	Banyuls, France	GNM 13215		GU722630	GU722620
M. longoprimicirrata spm 3	Banyuls, France	GNM 13216a, b		GU722631	GU722621
M. longoprimicirrata spm 4	Banyuls, France	GNM 13217a, b		GU722632	GU722622
M. longoprimicirrata spm 5	Rovinj, Croatia	GNM 13222a, b		GU722633	GU722623
M. longoprimicirrata spm 6	Rovinj, Croatia	GNM 13221			GU722624
M. longoprimicirrata spm 7	Rovinj, Croatia	GNM 13223a, b		GU722634	GU722625
M. longoprimicirrata spm 8	Rovinj, Croatia	all material used for extraction			GU722626
M. pachycera	Los Angeles California, USA	SMNH 45816	AF474304	AF474258	GQ856198

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TABLE 1. (continued)

	Locality	Voucher [1]	18S	16S	COI
M. pentadentata	La Jolla, California, USA	SMNH 45820	AF474299	AF474253	GQ856199
M. pinnigera	Cádiz, Spain	SMNH 45823	AF474298	AF474252	GQ856200
M. prolifera	Kristineberg, Sweden	SMNH 45811	AF474295	AF474249	GQ856201
M. quindecimdentata	Banyuls, France	SMNH 45814	AF474306	AF474260	GQ856202
M. rubropunctata	Ferrol, Spain	GNM Polychaeta 13106	EF661841	EF661837	GQ856203

[1] All vouchers are hologenophores (Pleijel *et al.* 2008). a=anterior end of specimen preserverd on slide, b=posterior end of same specimen preserved in alcohol.

Results

The COI data set consists of 658 aligned positions, of which 312 are parsimony-informative and 40 are variable but not parsimony-informative; the 16SrDNA data set consists, depending on alignment parameters used, of 365–381 (out of 490–494) unambiguously aligned positions, of which 137–155 are parsimony-informative and 27–29 are variable but not parsimony-informative; the 18SrDNA data set consists, depending on alignment parameters used, of 1626–1653 (out of 1880–1904) unambiguously aligned positions, of which 299–317 are parsimony-informative and 121–123 are variable but not parsimony-informative. The resulting phylogenetic trees from the nine different combinations of the mitochondrial and nuclear data sets have 31 out of 37 nodes in common, 26 of those have posterior probabilities (PP) ≥ 0.95 irrespective of alignment parameters used (Fig. 1). Twenty-eight of the 31 nodes found in the combined data set are in common with the results from either, or both, of the separate analyses of the mitochondrial and nuclear data sets, where 13 are unique for the nuclear and the combined data sets (Fig. 1, convex half circle, ◗), three are unique for the mitochondrial and combined data sets (Fig. 1, concave half circle, ◖), and 12 are found in both the mitochondrial and nuclear data sets as well as in the combined data set (Fig. 1, filled circle, ●). Three nodes in the mitochondrial data set have a posterior probabilitiy ≥ 0.95 in all three different alignments conflicting with the results from the combined data set (see taxa with an asterisk in Fig. 1). The mitochondrial data support a node where *M. rubropunctata* (Grube, 1860) is the sister species to a clade we may refer to as the *convoluta*-group, consisting of *M. convoluta* (Cognetti, 1953a), *M. australiensis* (Hartmann-Schröder, 1982), *M. gidholmi* Nygren & Pleijel, 2007, *M. pachycera* (Augener, 1913), *M. hesperidium* (Claparède, 1868) and *M. quindecimdentata* (Langerhans, 1884) (PP=0.99–1.0), while the topology based on the nuclear and the combined data sets depends on the alignment parameters used (Fig. 1). Further, a sister relationship of *M. pinnigera* (Montagu, 1808) and *M. langerhansi* (Gidholm, 1967) is suggested by the mitochondrial data (PP=0.95–0.99) while the nuclear data slightly favour a sister relationship for *M. pinnigera* with the *convoluta*-group mentioned above (PP=0.66–0.91), and a sister relationship between *M. langerhansi* and a group comprising *M. edwarsi* (Saint-Joseph, 1887), *M. prolifera* (O.F. Müller, 1788) and *M. brachycephala* (Marenzeller, 1874) (PP=1.0); in the combined analysis *M. pinnigera* is the sister species to a clade comprising *M. edwarsi*, *M. prolifera*, *M. brachycephala* and *M. langerhansi* (PP=1.0) (Fig. 1). Finally, a well-supported sister relationship between *Erseia oligochaeta*, new genus, new species and *Virchowia clavata* Langerhans, 1879 is identified by the mitochondrial data (PP=1.0), while the nuclear data favours a different topology where *E. oligochaeta*, new genus, new species and *Procerastea nematodes* Langerhans, 1884 are sister species (PP=0.64–0.93), and together with *V. clavata* and *Imajimaea draculai* (San Martín & López, 2002) constitute an unresolved trichotomy. The combined data set likewise support *E. oligochaeta*, new genus, new species and *P. nematodes* as sister taxa (PP=0.87–0.99), and also support a sister relationship between *I. draculai* and *V. clavata* (PP=0.52–0.86) (Fig. 1).

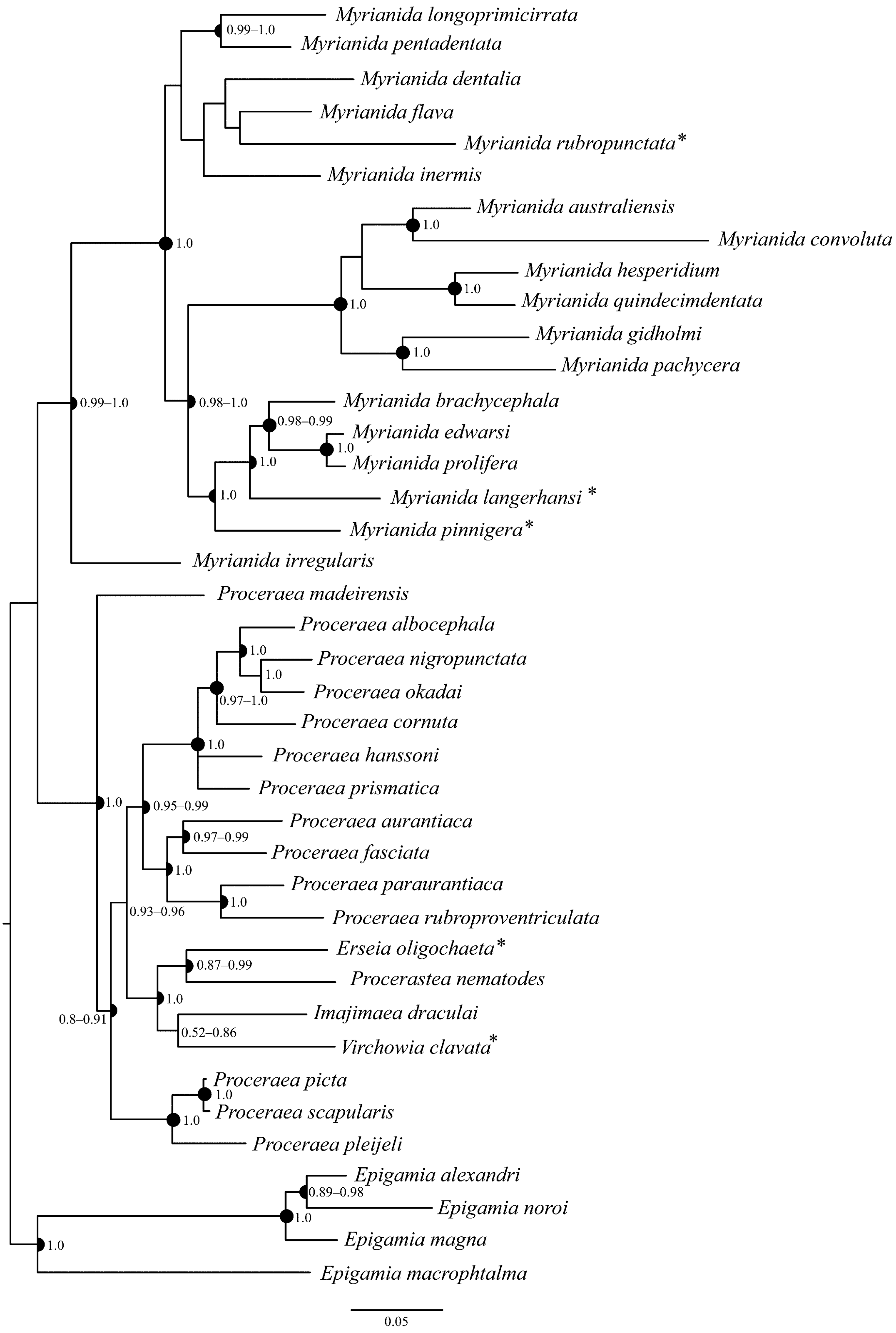

FIGURE 1. Majority rule consensus tree from the Bayesian analyses from the combined mitochondrial and nuclear data set with the gap/gap length penalites set to 15/6 for both 16SrDNA and 18SrDNA. Bayesian posterior probabilities are shown if the node is present in all nine possible data set combinations of alignments (see material and methods for further explanation). ◖: Node unique for the mitochondrial and combined data sets; ◗: node unique for the nuclear and combined data sets; ●: node present in mitochondrial, nuclear as well as in the combined data sets; *: taxa involved in conflicts between the mitochondrial data sets and the combined data sets with a posterior probability ≥ 0.95 in all three different alignments.

Discussion

To a high degree, our results are congruent with earlier phylogenetic studies of Autolytinae. In most parts they are stable and insensitive to the different alignment parameters herein applied. Contrasting with Nygren and Pleijel (2007) and Nygren and Pleijel (2010), but similiar to Nygren and Sundberg (2003) and Aguado *et al.* (2007), *Proceraea* Ehlers, 1864 is paraphyletic. As in Nygren and Sundberg (2003), the reason for this is that the type species *P. picta* Ehlers, 1864 together with *P. scapularis* (Claparède, 1864) and *P. pleijeli* (Nygren, 2004) form a basal sister group to a clade including the majority of the other *Proceraea*, together with a number of non-*Proceraea* taxa. Conversely, this recieves a rather high support in all our combined analyses (PP=0.93–0.96). In addition, the newly sequenced *P. madeirensis* is found to be the most basal taxon among the sequenced Procerini although with less support (PP=0.8–0.91). Consequently, there is good evidence that *Proceraea* should be delineated differently in order to keep it monophyletic, either by making *Proceraea* more inclusive and then, by and large, make it synonymous with Procerini, or introduce at least two new generic names, one for *P. madeirensis* and one for the remainder *Proceraea* that are not in the same, more inclusive clade as the type species *P. picta*. Among these two alternatives we would opt for the second one, but judge this choice premature as we only have molecular data for about half of the species referred to as *Proceraea* in Nygren (2004), and many of them would not be possible to allocate to correct “*Proceraea*”-group. Neither *P. madeirensis*, the *P. picta*-group or the group with the remainder *Proceraea* have unique and well-defined morphological characters that would make this task feasible. Accordingly, our new species with the epithet *albocephala* is also referred to *Proceraea* for the time being even though it does not belong to the type species clade.

On the other hand, we introduce a new generic name for *Erseia oligochaeta*, new genus, new species rather than describing it as a *Procerastea* Langerhans, 1884 or as a *Virchowia* Langerhans, 1879, despite that the former agreed with the nuclear and combined data sets, and the latter with the mitochondrial data set. From a morphological standpoint, *E. oligochaeta*, new genus, new species clearly resemble species in *Virchowia*. Possibly, some species now referred to *Virchowia* will also be shown to be more closely related to *E. oligochaeta*, new genus, new species than to *V. clavata*. The relation between *E. oligochaeta*, new genus, new species, *P. nematodes*, *I. draculai* and *V. clavata* is unstable, and somewhat unpredictable. When comparing our analyses in this study with those in Nygren & Pleijel (2010) we can observe some unsuspected differences. Both studies are based on the same three genes, but differ in number of taxa as several more taxa, among them *E. oligochaeta*, new genus, new species, are included in this study. In both studies, a clade of *V. clavata* and *I. draculai* is found in the combined analyses with PP=0.52–0.86 and PP=0.96 in this study and in Nygren & Pleijel (2010) respectively, the latter being only supported by the mitochondrial data (PP=0.97). In our mitochondrial phylogeny, a sister relationship between *V. clavata* and *E. oligochaeta*, new genus, new species is instead favoured (PP=1.0), and a close relationship between *V. clavata* and *I. draculai* is not found in any of the three alignments. In spite that we neither recovered a clade of *I. draculai* and *V. clavata* with the mitochondrial or the nuclear data set, the group still appears in the combined data, albeit with lower support than in Nygren and Pleijel (2010). Given that the phylogenetic position of *E. oligochaeta*, new genus, new species in some respects is uncertain and that it is unique in several morphological aspects (see below) we decided to describe it as a new genus. For further discussion see the Remarks sections below.

Systematics

Syllidae Grube, 1850

Autolytinae Grube, 1850

Procerini Nygren, 2004

Erseia, new genus

Etymology. *Erseia* is named in honour of Christer Erséus for his contributions to annelid phylogeny and taxonomy. The name is also intended as a "play on words", which is one of Erséus' distinguishing feature. Gender masculine.

Type species. *Erseia oligochaeta*, new genus, new species.

Diagnosis and description. Monotypic, see *E. oligochaeta*, new genus, new species.

Erseia oligochaeta, new genus, new species

(Fig 2A–D)

Material examined. *Holotype*. Croatia, Istria, 2 km west of Rovinj, 45°05.220'N 13°36.517'E, 27 m, sponges, hydroids, and *Holothuria* sp., Agassiz trawl, 17 Sept 2008, preserved in alcohol (GNM Polychaeta 13180). *Paratypes*. Same locality as holotype, four specimens preserved in formalin (GNM Polychaeta 13181–13184), two specimens preserved in alcohol (GNM Polychaeta 13185, 13186), seven specimens preserved on slides (GNM Polychaeta 13187a–13189a, 13190–13193), of which five rear ends preserved in alcohol, of which two are used up for DNA extraction (GNM Polychaeta 13187b–13189b). *Other material*. Same locality as holotype, two specimens preserved in alcohol, used up for DNA extraction, two specimens preserved on slides, rear ends preserved in alcohol.

Diagnosis. Procerini with only 1–2 unidentate simple chaetae in all chaetigers, and a trepan with single large, and 25–28 smaller teeth.

Description. Length 2.1–3.0 mm for 24–27 chaetigers, width at level of proventricle, excluding parapodial lobes, 0.2 mm. Live specimens pale gray, sometimes faintly reddish, without colour markings (Fig. 2A). Body shape, excluding parapodial lobes, cylindrical in transection, ventrally flattened. Body fairly constant in width, with tapering posterior end. Ciliation on nuchal epaulettes. Prostomium rounded rectangular. Four eyes with lenses, anterior pair larger, confluent in dorsal view; eye spots present. Palps small, invisible in dorsal view (Fig. 2A), not possible to evaluate degree of fusion. Nuchal epaulettes extending to anterior part of tentacular segment (Fig. 2A, indicated with arrow). Prostomium with three antennae; median antenna inserted medially on prostomium, lateral antennae on anterior margin. Tentacular cirri two pairs. Median antenna reaching chaetiger 4–5. Lateral antennae and first dorsal cirri about 2/3 as long as median antenna. Dorsal tentacular cirri half as long as median antenna, ventral tentacular cirri c. half as long as dorsal pair. Dorsal cirri from chaetiger 1 with following alternation in direction, where D=cirri pointing down and U=cirri pointing up: U DDU DU DDU followed by eight DU-groups. From chaetiger 2 dorsal cirri alternating in length; short cirri as long as 1–1.5 times body width, long cirri as long as 2–2.5 times body width. Cirrophores on tentacular cirri and all dorsal cirri. Cirrophores and cirrostyles alternating in length along the body; cirrophores and cirrostyles on short cirri c. half as long as its counterpart in long cirri; cirrophores on short cirri with thin base, cirrophores on long cirri with broad base; cirrophores shorter than parapodial lobes; cirrophores shorter than their cirrostyles. Antennae, tentacular cirri, first dorsal cirri, and short cirri cylindrical; long cirri, and anal cirri clavate (Fig. 2A, but note that most of the long cirri have been lost). Parapodial lobes of medium size, rounded. Aciculae 1–2 in all chaetigers (Fig. 2D). Chaetal fascicle with 1–2 unidentate simple chaetae in all chaetigers (Fig. 2C, D). Bayonet chaetae not observed. Pharynx with small sinuation in front of proventricle (Fig. 2A). Trepan in tentacular segment, with single large dorsal tooth and 25–28 small teeth in single ring (Fig. 2B). Basal ring present, infradental spines present. Proventricle as long as 1–1.5 segments in chaetiger 3–4 (Fig. 2A) with c. 23 rows of muscle cells. Length of anal cirri c. as long as body width.

Reproduction. Schizogamous reproduction by anterior scissiparity. One specimen with developing small antennae after chaetiger 13, and one specimen with newly regenerating posterior end after chaetiger 13.

Habitat. Sponges, hydroids, 25 m.

Distribution. Mediterranean, Adriatic Sea, only known from type locality.

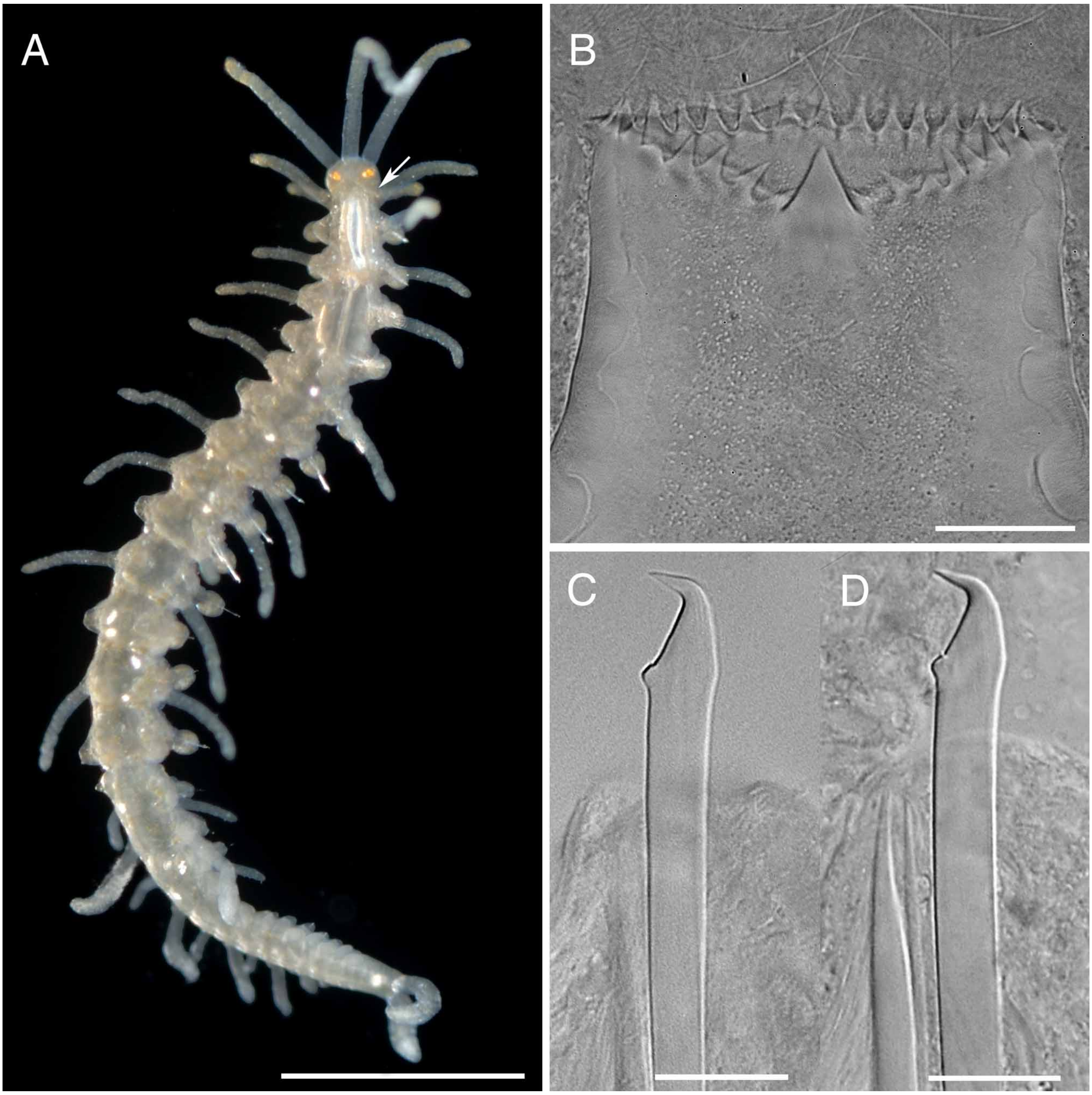

FIGURE 2. *Erseia oligochaeta*, new genus, new species. A. Holotype, dorsal view. B. Trepan, dorsal view (spm 2). C. Simple chaeta, chaetiger 2 (spm 2). D. Simple chaeta and aciculae, chaetiger 10 (spm 2). Scale lines A 0.5 mm, and B–D 10 µm.

Intraspecific genetic variation. Two haplotypes of COI separated by a single mutation, and a single haplotype of 16SrDNA were found in the five sequenced specimens.

Remarks. *Erseia oligochaeta*, new genus, new species is unique among autolytines in having a trepan with one large dorsal tooth and 25–28 smaller teeth, and only 1–2 simple unidentate chaetae in all chaetigers. These chaetae are reminiscent of those found in the anterior chaetigers of *Virchowia spirifer* (Augener, 1913) and *Imajimaea draculai*. However, both species have additional types of simple and/or compound chaetae, which are absent in *E. oligochaeta*, new genus, new species. In other morphological respects *E. oligochaeta*, new genus, new species is most similar to *Virchowia* species, with its alternating long clavate dorsal cirri and short cylindrical dorsal cirri, situated on unequally sized cirrophores. One character that *E. oligochaeta*, new genus, new species do not share with *Virchowia* (even though the situation for *V. pectinans* (Hartmann-Schröder, 1983) is uncertain) is the nuchal epaulettes which are not situated on outgrowths but instead extends on the dorsum.

Etymology. The species epithet *oligochaeta* is derived from the Greek oligos meaning few, and the Greek khaite meaning long hair, and refers to the few chaetae this species is provided with.

Proceraea Ehlers, 1864

Proceraea albocephala, new species

(Figs 3A, C, 5A, B)

?*Proceraea picta* Langerhans 1879: 577–578 (not *P. picta* Ehlers, 1864)

Material examined. *Holotype*. NW Madeira, East of Porto Moniz, 32°51.664'N 17°09.105'W, balanids with hydroids, SCUBA, 30 Sept 2009, preserved on slide (GNM Polychaeta 13194a), rear end preserved in alcohol (GNM Polychaeta 13194b). *Paratypes*. Same locality as holotype, six specimens preserved in formalin (GNM Polychaeta 13195–13200), three specimens preserved in alcohol (GNM Polychaeta 13201–13203), three specimens preserved on slides (GNM Polychaeta 13204a, 13205a, 13206), rear ends preserved in alcohol of which one is used up for DNA extraction (GNM Polychaeta 13204b, 13205b). *Other material*. Same locality as holotype, three specimens preserved in formalin, three specimens preserved in alcohol.

Diagnosis. *Proceraea* with a prostomial white spot and with two distinct and two faint longitudinal brown lines.

Description. Length 3.1–5.0 mm for 27–42 chaetigers, width at level of proventricle, excluding parapodial lobes, 0.1–0.15 mm. Live specimens with two distinct brown lines on dorsum, and two faint brown lines laterally along body (Fig. 3A, C); prostomium with mid-ventral white spot/gland (Fig. 3A, C). Body shape, excluding parapodial lobes, cylindrical in transection, ventrally flattened. Body fairly constant in width, with tapering posterior end. Ciliation on nuchal epaulettes. Prostomium rounded rectangular. Four eyes with lenses, anterior pair larger, almost confluent; eye spots absent. Palps in dorsal view projecting c. 1/4 of prostomial length, fused. Nuchal epaulettes extending to end of tentacular segment (Fig. 3A). Prostomium with three antennae; median antenna inserted medially on prostomium, lateral antennae on anterior margin. Tentacular cirri two pairs. Median antenna reaching chaetiger 10–12. Lateral antennae and dorsal tentacular cirri, c. half as long as median antenna. First dorsal cirri, c. 2/3 as long as median antenna. Ventral tentacular cirri and second dorsal cirri c. 1/3 as long as dorsal tentacular cirri. Alternation in direction of cirri not assessed due to observational difficulties. From chaetiger 3, all dorsal cirri equally long, 1/4–1/3 as long as body width. Cirrophores on tentacular segment and first dorsal cirri, otherwise absent. All appendages cylindrical. Parapodial lobes small, rounded conical. Single acicula in all chaetigers. Chaetal fascicle with 6–10 compound chaetae in anterior chaetigers, 3–7 in median and posterior chaetigers. Compound chaetae with small distal tooth, and serrated blade (Fig. 5A). Single thick bayonet chaetae (Fig. 5A), beginning on chaetiger 2–4. Pharynx with single sinuation anterior to proventricle (Fig. 3A). Trepan in chaetiger 1–2, with 18 unequal teeth in two rings, alternating 9 large with 9 smaller (Fig. 5B). Basal ring present, infradental spines absent. Proventricle as long as 1–2 segments, in chaetiger 5–6 (Fig. 3A), with c. 30 rows of muscle cells. Anal cirri as long as c. half body width.

Reproduction. Probably schizogamous reproduction by anterior scissiparity. One specimen with indication of a developing head after chaetiger 13.

Habitat. Among hydroids at 5–15 m.

Distribution. Madeira. Only known from type locality.

Intraspecific genetic variation. No genetic variation was found in the five sequenced specimens.

Remarks. In all our molecular analyses *P. albocephala*, new species comes out together with *P. cornuta* (Agassiz, 1862), *P. okadai* (Imajima, 1966) and *P. nigropunctata* Nygren & Gidholm, 2001. All these species are morphologically almost impossible to separate except for their colouration. *Proceraea nigropunctata* has seven dark brown spots in two transverse rows across each segment, while *P. cornuta* has only two faint brown longitudinal lines along the sides. *Proceraea albocephala*, new species resembles *P. okadai* in having two distinct and two faint longitudinal brown lines, but might be separated by the prostomial white spot that is absent in *P. okadai*. *Proceraea albocephala*, new species also seems smaller, and more delicate than *P. okadai*. According to our molecular data, *P. nigropunctata* and *P. okadai* are more closely related than either of them are to *P. albocephala*, new species. We found *P. albocephala*, new species only on the north coast of Madeira, but it is possible that the record of *P. picta* by Langerhans (1879) around Funchal (south coast) also refers to this species. If Langerhans overlooked the two faint lateral lines (which is easy), then his description fits better with *P. albocephala*, new species than with *P. picta*, which also has several brown squares and transverse white bands in addition to the longitudinal lines. However *P. scapularis* listed as a synonym to *P. picta* by Langerhans have two longitudinal brown lines only, but neither this species, nor *P. picta* were found by us at Madeira.

Etymology. The species epithet *albocephala* is derived from the Greek albus meaning white, and the Greek kephale meaning head, and refers to prostomial white spot found in this species.

Proceraea madeirensis **Nygren, 2004**

(Figs 3B, D, 5C–E)

Procereaea fasciata Langerhans, 1879: 581, fig. 33A–C Junior homonym of *Nereis fasciata* Bosc, 1802.
?*Autolytus (Proceraea) fasciata* Augener 1913: 264–265.
?*Proceraea fasciata* Westheide 1974: 323–325, figs 61–62; Hartmann-Schröder 1987: 44–45, figs 20–22.
Proceraea madeirensis nom. n. Nygren, 2004: 56–57, fig. 15A–B.

Material examined. *Holotype*. Madeira, NHMW 2512. *Other material*. NW Madeira, East of Porto Moniz, 32°51.664'N 17°09.105'W, balanids with hydroids, SCUBA, 30 Sept 2009, one specimen preserved in formalin (GNM Polychaeta 13207a), rear end preserved in alcohol (GNM Polychaeta 13207b); Madeira, Funchal, 32°38.130'N 16°55.815'W, 5–15 m, rocks with *Lithothamnion*, SCUBA, 21–25 Sep 2009, four specimens preserved in alcohol (GNM Polychaeta 13208–13211), two specimens preserved on slides (GNM Polychaeta 13212, 13213), rear ends preserved in alcohol, used up for DNA extraction.

Diagnosis. *Proceraea* with brown segmental bands; antennae, dorsal tentacular cirri, and dorsal cirri brown.

Description. Length 3.6–11 mm for 41–56 chaetigers, width at level of proventricle, excluding parapodial lobes, 0.2–0.3 mm. Live specimens with broad brown segmental bands on every segment, antennae, dorsal tentacular cirri and first dorsal cirri brown (Fig. 3B, D). Body shape, excluding parapodial lobes, cylindrical in transection, ventrally flattened. Body fairly constant in width, with tapering posterior end. Ciliation on nuchal epaulettes. Prostomium rounded rectangular. Four eyes with lenses, anterior pair larger, confluent in dorsal view (Fig. 3D); eye spots absent. Palps in dorsal view projecting c. 1/4 of prostomial length, fused. Nuchal epaulettes extending to middle of chaetiger 1 (Fig. 3D). Prostomium with three antennae; median antenna inserted medially on prostomium, lateral antennae on anterior margin. Tentacular cirri two pairs. Median antenna reaching chaetiger 14–15. Lateral antennae and dorsal tentacular cirri, c. half as long as median antenna. First dorsal cirri, c. 2/3 as long as median antenna, ventral tentacular cirri and second dorsal cirri c. 1/3 as long as dorsal tentacular cirri. Alternation in direction of cirri not assessed due to observational difficulties. From chaetiger 3, all cirri equally long, 1/4–1/3 as long as body width. Cirrophores on tentacular segment and first dorsal cirri, otherwise absent. All appendages cylindrical. Parapodial lobes small, rounded conical. Aciculae 1–3 in anterior chaetigers, 1 or 2 in median and posterior chaetigers. Chaetal fascicle with 6–9 compound chaetae in anterior chaetigers, 3–6 in median and posterior chaetigers. Compound chaetae in anterior 10–15 chaetigers with small distal tooth, then larger but still smaller than subdistal one (Fig. 5C, D); blade serrated. Single thick bayonet chaetae (Fig. 5C) beginning on chaetiger 4–15. Pharynx with single sinuation anterior to proventricle (Fig. 3D). Trepan in chaetiger 3, with 18 uneuqal teeth in two rings, alternating 9 large with 9 smaller (Fig. 5E). Basal ring present, infradental spines absent. Proventricle as long as 4–5 segments, in chaetiger 6–12 (Fig. 3D), with 55–60 rows of muscle cells. Anal cirri as long as c. half body width.

Reproduction. Unknown.

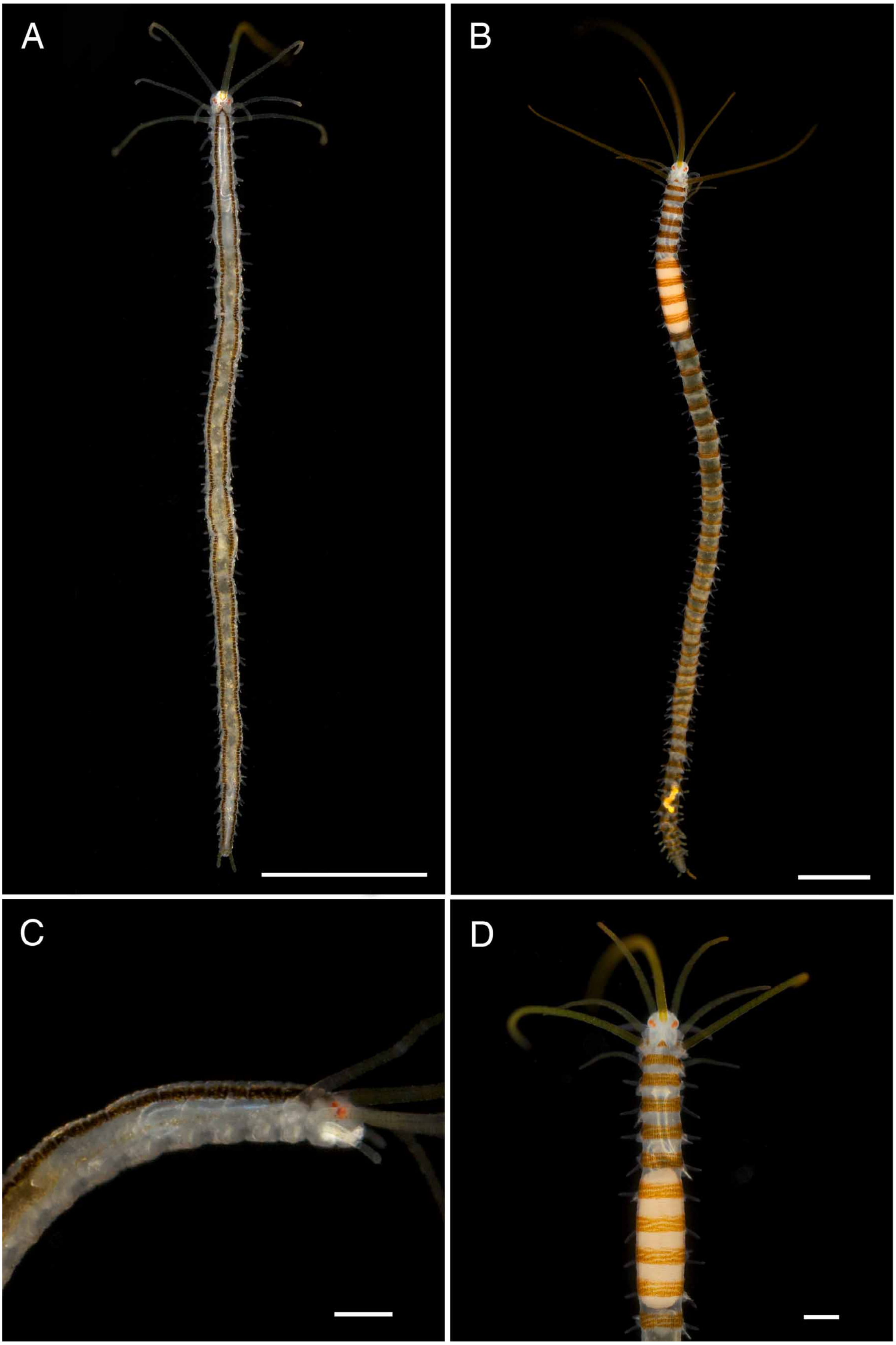

FIGURE 3. *Proceraea albocephala*, new species. A. Holotype, dorsal view. C. Holotype, lateral view, anterior end. *Proceraea madeirensis* (GNM Polychaeta 13211) B. Dorsal view, complete specimen. D. Dorsal view, anterior end. Scale lines A, B 1 mm, and C, D 0.1 mm.

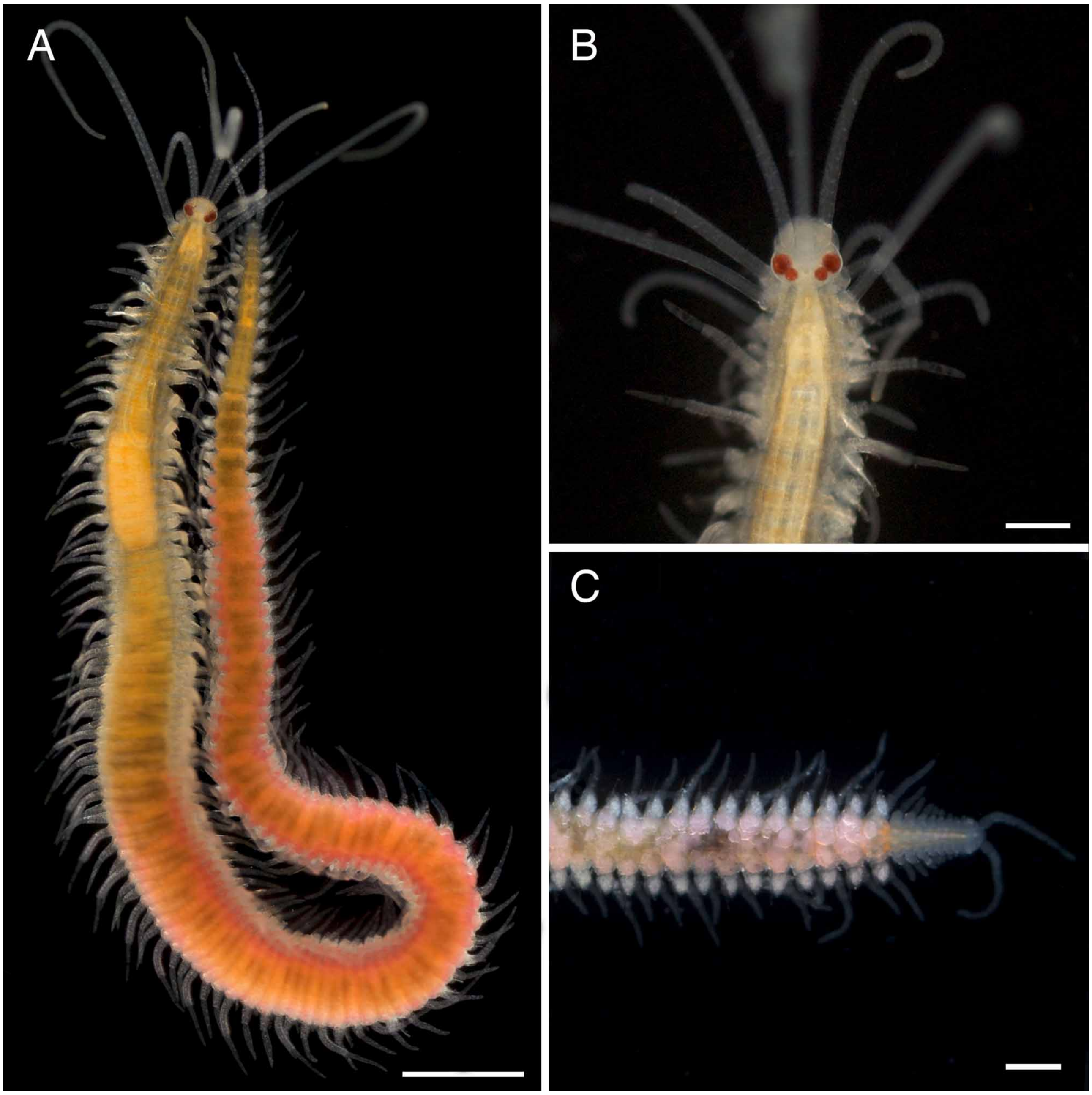

FIGURE 4. *Myrianida longoprimicirrata.* A. Dorsal view, compl.ete specimen (spm 5). B. Dorsal view, anterior end (spm 7). C. Ventral view, posterior end with regenerating segments (GNM Polychaeta 13219). Scale lines A 1 mm, and B, C 0.1 mm.

Habitat. Among hydroids on balanids, rocks with *Lithothamnion* and epifauna.

Distribution. Only known from Madeira.

Intraspecific genetic variation. No genetic variation was found in the two sequenced specimens.

Remarks. As discussed in Nygren (2004) the identity of Augener's (1913), Westheide's (1974) and Hartmann-Schröder's (1987) specimens as *P. madeirensis* is doubtful as Langerhans' holotype lacks the unidentate chaetae mentioned by these authors, and these chaetae are not present in the newly collected specimens in our study. According to our molecular data, *P. madeirensis* is the most basal taxon in Procerini among the sequenced taxa. As discussed above we believe new generic names should be introduced in order to keep *Proceraea* monophyletic. However we decided to postpone this awaiting more data and better taxon sampling. If a new generic name is introduced for *P. madeirensis*, then the original species epithet would be valid, as the homonomy with *P. fasciata* (Bosc, 1802) would cease.

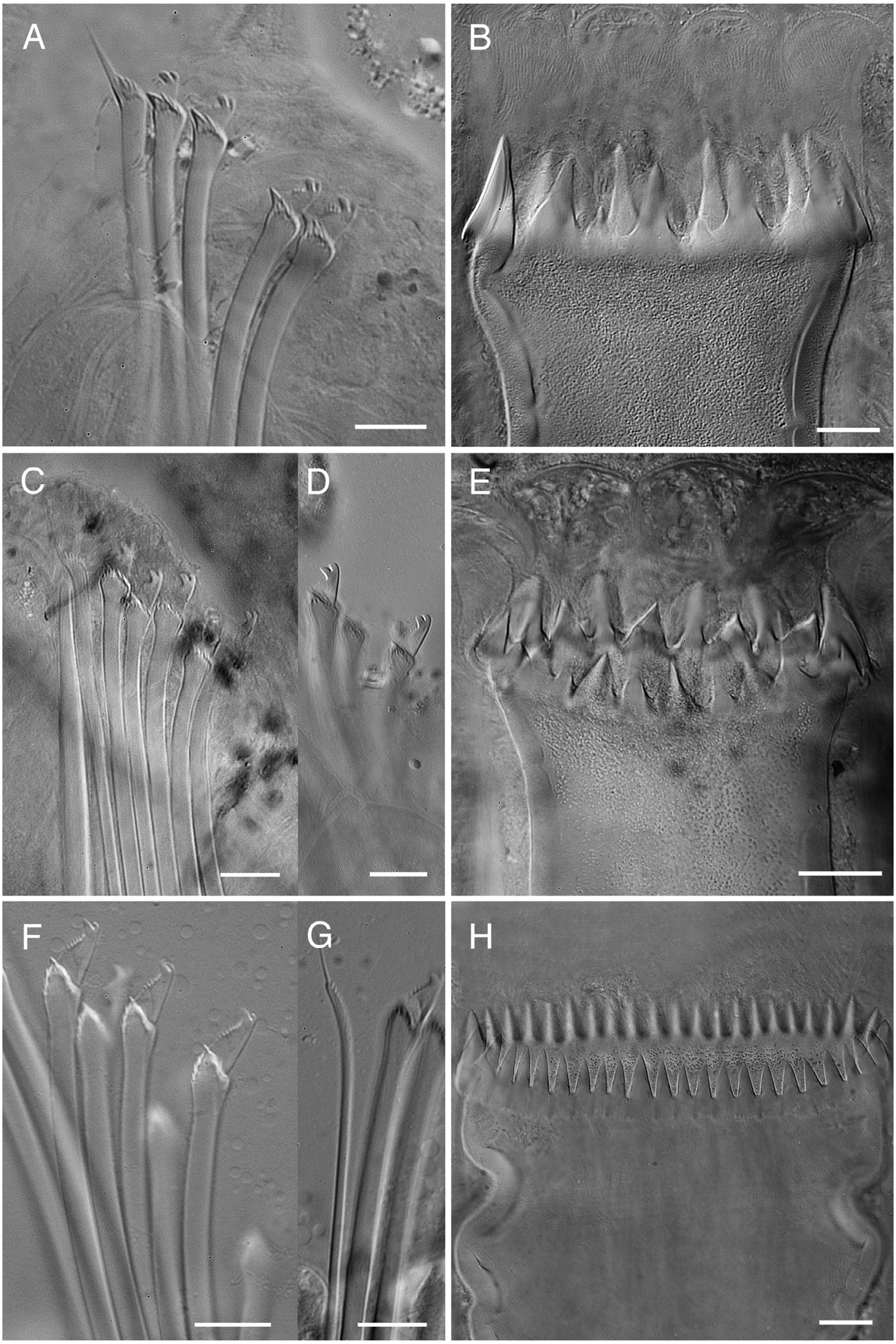

FIGURE 5. *Proceraea albocephala*, new species. A. Holotype, compound chaetae and bayonet chaeta, chaetiger 10. B. Trepan, dorsal view (spm 5). *Proceraea madeirensis*. C. Compound chaetae and bayonet chaeta, chaetiger 12 (spm 2). D. Compound chaetae, chaetiger 30 (spm 2). E. Trepan, dorsal view (spm 1). *Myrianida longoprimicirrata*. F. Compound chaetae, chaetiger 20 (spm 5). G. Bayonet chaeta, chaetiger 25 (spm 5). H. Trepan, dorsal view (spm 3). Scale lines A–H 0.1 mm.

Autolytini Grube, 1850

Myrianida Milne Edwards, 1845

Myrianida longoprimicirrata (López, San Martín & Jiménez, 1997)
(Figs 4A–C, 5F–H)

Autolytus longoprimicirrata López, San Martín & Jiménez, 1997: 296–298, fig. 2A–G; San Martín 2003: 492–494, fig. 271A–F.
Myrianida longoprimicirrata Nygren 2004: 141–142, fig. 69A–B.

Material examined. *Holotype*. Chafarinas Islands, 15 m, in *Cladocora caespitosa* blocks, 15 Sept 1992, MNCN 16–01/2122. *Paratypes*. Same locality as holotype, two specimens (MNCN 16–01/2122b). *Other material*. Croatia, Istria, Sv. Ivan, 45°02.755'N 13°37.422'E, 5–15 m, *Padina* and other algae, SCUBA, 19 Sept 2008, two specimens preserved on slides (GNM Polychaeta 13214a, 13215), rear ends preserved in alcohol, of which one is used up for DNA extraction (GNM Polychaeta 13214b); Croatia, Istria, Banjol, 45°04.442'N 13°36.664'E, 15–27 m, precoralligene, SCUBA, 23 Sept, 2008, two specimens preserved on slides (GNM Polychaeta 13216a, 13217a), rear ends preserved in alcohol (Polychaeta GNM 13216b, 13217b); Croatia, Istria, 2 km west of Rovinj, 45°05.220'N 13°36.517'E, 27 m, sponges, hydroids, and *Holothuria* sp., Agassiz trawl, 25 Sept 2008, two specimens preserved in alcohol (GNM Polychaeta 13218, 13219); Croatia, Istria, St Andrew's Island, 45°02.561'N 13°36.792'E, 10–16 m, precoralligene, SCUBA, 24 Sept 2008, one specimens preserved in formalin (GNM Polychaeta 13220); France, Banyuls-sur-mer, 42°29.94'N 03°08.46'E, 25 m, corraligene, SCUBA, 7 April 2009, two specimens preserved in alcohol of which one is used up for DNA extraction (GNM Polychaeta 13221), two specimens preserved on slides (GNM Polychaeta 13222a, 13223a), posterior ends preserved in alcohol (GNM Polychaeta 13222b, 13223b).

Diagnosis. *Myrianida* with long cirrophores on the long cirri from anterior chaetigers, and a trepan with 33–45 equal, or nearly equal, teeth.

Description. Length 4–14 mm for 43–124 chaetigers, width at level of proventricle, excluding parapodial lobes, c. 0.3 mm. Live specimens yellowish to orange, with more or less distinct bands of orange glands across each segment, giving an orange-banded impression (Fig. 4A). Body shape, excluding parapodial lobes, cylindrical in transection, ventrally flattened. Body fairly constant in width, with tapering posterior end. Ciliation on nuchal epaulettes and as a single ciliary troch per segment. Prostomium rounded rectangular. Four eyes with lenses, anterior pair larger, confluent in dorsal view (Fig. 4B); eye spots absent. Palps in dorsal view projecting c. half the prostomial length (Fig. 4B), fused. Nuchal epaulettes extending to between beginning of chaetiger 3 and end of chaetiger 5 (Fig. 4B). Prostomium with three antennae; median antenna inserted medially on prostomium, lateral antennae on anterior margin. Tentacular cirri two pairs. Median antenna reaching c. chaetiger 20. Lateral antennae, and dorsal tentacular cirri 1/3–1/2 as long as median antenna; first dorsal cirri as long as median antenna; ventral tentacular cirri and second dorsal cirri c. half as long as dorsal tentacular cirri. Dorsal cirri from chaetiger 1 with following alternation in direction, where D=cirri pointing down and U=cirri pointing up: U DDU DU DDU followed by eight DU-groups, 4 DDUU-groups, and up to 28 DDU-groups. From chaetiger 3 dorsal cirri alternating in length; short cirri as long as c. 4/5 of body width, long cirri as long as c. 1.2 times body width. Cirrophores on tentacular cirri and all dorsal cirri. Cirrophores alternating in length along the body; cirrophores on short cirri c. half as long as cirrophores on long cirri. Cirrostyles alternating in length in anterior and posterior chaetigers, but not in median chaetigers; cirrostyles on short cirri c. 1.5 times as long as cirrostyles on long cirri in anterior chaetigers, equally long in median chaetigers, and 2/3 as long in posterior chaetigers. Cirrophores on short cirri equal or slightly longer than parapodial lobes, cirrophores on long cirri longer than parapodial lobes. Cirrophores shorter than cirrostyles on short cirri, cirrophores longer than cirrostyles on anterior long cirri, equal in length in mid-body long cirri, and shorter in posterior long cirri (Fig. 4A). Parapodial lobes of medium size, rounded. Aciculae 2–3 in anterior chaetigers, 1or 2 in median and posterior chaetigers. Chaetal fascicle with 10–12 compounds in anterior chaetigers, 6–9 in median and posterior. Compound chaetae with small distal tooth

(Fig. 5F) and serrated blade. Single thin bayonet chaetae (Fig. 5G), beginning on chaetiger 20–31. Pharynx with sinuation mostly anterior to proventricle (Fig. 4A). Trepan in chaetiger 2–4, with 33–45 equal, or nearly equal, teeth (Fig. 5H). Basal ring present, infradental spines present. Proventricle as long as 4–6 segments, in chaetiger 10–20 (Fig. 4A) with 30–37 rows of muscle cells. Anal cirri as long as 1.5–3 times body width.

Reproduction. Probably with schizogamy. Three specimens have pink eggs from about chaetiger 40, one of them with a newly regenerating posterior end behind chaetiger 63 (Fig. 4C).

Habitat. Among *Cladocera caespitosa* blocks, *Padina* and other algae, and in coralligene, 15–30 m.

Distribution. Mediterranean, from Chafarinas Islands in Morocco, Istria in Croatia, and Banyuls-sur-Mer in France.

Intraspecific genetic variation. A single haplotype in the four specimens from Banyuls-sur-mer, and four haplotypes in the four specimens from Croatia were found in COI. The haplotypes from Croatia cluster together but are separated from each other with 1–4 mutational steps (uncorrected p = 0.41±0.16%). This group is in turn separated from the single Banyuls-sur-Mer haplotype with a minimum of six mutational steps (uncorrected p=1.11±0.18%). As for 16SrDNA, we found two haplotypes in the two Banyuls-sur-Mer specimens, and a single haplotype in the four Croatian specimens. The two Banyuls-sur-Mer haplotypes are separated from each other by a single mutational step, and the Croatian haplotype is separated by a single mutational step from the closest Banyuls-sur-Mer haplotype.

Remarks. *Myrianida longoprimicirrata* is a poorly known member of the genus, never recorded after the original description. The relationship between cirrophores and cirrostyles was not possible to assess in the original description or from the types. In the present material, the cirrophores are longer than cirrostyles on long anterior dorsal cirri and, then gradually become shorter towards the posterior end where they are shorter than cirrostyles. The only *Myrianida* which have cirrophores longer than cirrostyles on the long cirri are *M. dentalia* (Imajima, 1966), *M. langerhansi*, *M. pentadentata* (Imajima, 1966), *M. multidenticulata* (Westheide, 1974), *M. pulchella* (Day, 1953), and *M. rangiroaensis* (Imajima, 1966). We lack molecular data for the latter three species, but among the sequenced species *M. longoprimicirrata* is most closely related to *M. pentadentata*. Morphologically *M. longoprimicirrata* may be separated from all the aforementioned species by the 33–45 equal, or nearly equal, teeth, on the trepan, compared to a varied number and arrangement of distinctly unequal teeth in all species except *M. pentadentata* which has five equal teeth.

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