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Análise filogenética de espécies selecionadas do
gênero *Eunice* (Eunicidae, Polychaeta)

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“Sábio o que se contenta
com o espetáculo do mundo
E ao beber nem recorda
que já bebeu na vida
Pra quem tudo é novo
E imarcescível sempre”

Fernando Pessoa

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Resumo

Em estudos anteriores sobre o gênero *Eunice*, a maioria dos espécimes examinados estava incompleta. O que acarreta problemas na taxonomia do gênero, um grande número de caracteres indetermináveis nas análises cladísticas e resultados inconclusivos. Nesse estudo, espécimes completos de 23 espécies de *Eunice* foram examinados e uma análise cladística realizada, com o objetivo de definir grupos monofiléticos dentro do gênero *Eunice* que pudessem ser usados na divisão desse em “novos” gêneros, já que em uma análise anterior esse foi demonstrado ser parafilético. Alguns dos caracteres codificados foram usados pela primeira vez, a maioria características do aparelho bucal. *Eunice sensu lato* foi dividido em três clados e os gêneros *Marphysa*, *Lysidice* e *Palola* inseridos dentro dele. Uma característica comum ao presente resultado, aos preliminares e ao de um estudo anterior é a constante separação das espécies *Eunice aphroditois* e *Eunice antennata* em clados diferentes. Um deles talvez corresponda ao antigo gênero *Leodice*, já que inclui *E. antennata*, sua espécie tipo. O clado que inclui *E. aphroditois*, espécie tipo do gênero *Eunice*, provavelmente poderá ser considerado como *Eunice sensu stricto*. O terceiro clado, possivelmente é resultado de uma subamostragem da diversidade das espécies do gênero e provavelmente não estará presente em futuras análises. Os grupos geralmente utilizados na divisão do gênero, baseados na distribuição branquial, cor e dentição dos ganchos subaciculares, resultaram como parafiléticos.

Abstract

Most specimens examined in previous studies of the genus *Eunice* have been incomplete. This lead problems in the taxonomy of the genus, large amount of missing characters in cladistic analyses and inconclusive results. In this study, complete specimens of 23 species of *Eunice* were examined and a cladistic analysis was performed. The purpose was to define monophyletic groups within *Eunice* that could be used to divide this genus into “new” genera, since it has been shown to be paraphyletic in a previous analysis. Some of the coded characters were used for the first time, most of them features of the buccal apparatus. *Eunice sensu lato* was divided in three clades, and the genera *Marphysa*, *Lysidice* and *Palola* fell inside it. A common feature to the present, preliminary and former results was the placement of *Eunice antennata* and *Eunice aphroditois* in clades apart. Perhaps one corresponds to the old genus *Leodice*, since it includes *E. antennata*, its type species. The clade including *E. aphroditois*, type species of the genus *Eunice*, may be considered as *Eunice sensu stricto*. The third group, which may be the result of a misrepresentation of the diversity of species, will most probably turn out to be invalid in future analyses. The groups usually used to subdivide the genus *Eunice*, based on the color and dentition of the subacicular hooks and branchial distribution, were shown to be paraphyletic.

Introdução

O gênero *Eunice* foi descrito por Cuvier (1817) dentro do grande grupo dos Nereidae, ao qual a maioria dos Polychaeta era referida na época. A família Eunicidae é uma das mais antigas entre as famílias de Polychaeta. Sua concepção surgiu em Lamarck (1818) (apud Fauchald, 1992), na mesma época em que outros gêneros foram descritos para a família, como o gênero *Leodice* Lamarck, 1818. As definições de *Eunice* e *Leodice* não eram explícitas e a distinção entre esses gêneros não era clara. Os dois nomes foram usados simultaneamente até o começo do século XX, o uso de um ou de outro variava com a preferência de cada autor (Hartman 1944). Devido a essa inconsistência e ambigüidade na definição desses gêneros, *Leodice* foi sinonimizada a *Eunice*.

A maioria das espécies de *Eunice* foi descrita até o começo do século XX, mas ainda se sabe pouco sobre elas. Essas espécies estão presentes em todos os ambientes marinhos e em todos os oceanos. São particularmente comuns em águas rasas tropicais e subtropicais em manguezais, associadas a corais e algas calcáreas (Paxton 2000), mas também são encontrados em praias, costões rochosos e associados a esponjas. Algumas espécies aparentemente não apresentam especificidade de habitat, como *Eunice rubra* Grube, 1856 que teve sua presença reportada em sedimento arenoso e em corais (Steiner *et al.* no prelo); e a espécie *Eunice conglomerans* Ehlers, 1887 que pode construir seu tubo dentro da esponja *Ircinia* sp. ou sob pedras (Paiva comunicação pessoal). A produção de tubo por espécies desse gênero é comumente registrada e pode ocorrer tanto em substratos inconsolidado (e.g. Bettoso *et al.* 1998) quanto em consolidado (e.g. Winsnes 1989), mas nem todas as espécies produzem tais estruturas. O tamanho das espécies de *Eunice* pode variar de poucos centímetros a 3 metros (Hartman 1944). As espécies do gênero foram classificadas por Fauchald e Jumars (1979) como primariamente carnívoras, mas não exclusivamente.

A superfamília Eunicea, à qual pertence a família Eunicidae, é um dos poucos grupos de Polychaeta a apresentar registro fóssil. As estruturas do aparelho bucal típicas desta superfamília são abundantes no registro fóssil dos períodos Ordoviciano e Devoniano (Colbath 1986). O aparelho bucal desse grupo é composto por uma forte musculatura (Fig. 1A), um par de mandíbulas ventrais (Fig. 1B) e maxilas labidognatas (Fig. 1C) – primeiro par de placas maxilares em forma de fórceps ligado a um par de

suportes cobertos por uma fina camada de músculos transversais dorsais, e outras placas distintas, grandes e geralmente pareadas – (Fauchald 1992). Nos Eunicidae e Onuphidae – família irmã da Eunicidae (Rouse e Fauchald 1997) –, as mandíbulas e maxilas são formadas por uma matriz de escleroproteína e mineralizados com aragonita (Colbath 1986). Essas estruturas surgem quando o espécime ainda é jovem (e.g. Akesson 1967). As mandíbulas têm crescimento contínuo (Colbath 1987) e as maxilas são substituídas durante a ontogenia dos espécimes (Hsieh e Simon 1987; Cassai 1996 apud Cassai e Prevedelli 1998). O crescimento de novas peças do aparelho bucal ocorre também durante regeneração da região anterior (Colbath 1987).

As espécies da família Eunicidae têm grande capacidade de regeneração das regiões anterior e posterior (Orensanz 1975) e de autotomia de partes do corpo. A habilidade de autotomia permite que algumas espécies na época reprodutiva epitoquem, o que na família Eunicidae geralmente ocorre com a liberação da região posterior cheia de gametas na coluna d'água pelos espécimes férteis simultaneamente (e.g. Clark e Hess 1940) num evento previsível e provavelmente controlado por fatores ambientais (Caspers 1984). A autotomia ocorre também em situações de stress, como coleta (observação pessoal) e transporte de indivíduos vivos (Karageorgopoulos comunicação pessoal). Essa característica e o corpo frágil dos espécimes dessa família que se quebra involuntariamente durante a coleta, triagem, fixação e manuseio resultam em uma grande porcentagem de indivíduos incompletos (Giangrande 1989). Para a identificação em nível específico de espécimes da família Eunicidae e codificação de alguns caracteres considerados importantes na filogenia de Eunicidae, em especial do gênero *Eunice*, é necessário, portanto, o exame de indivíduos completos (e.g. Orensanz 1975; Fauchald 1992).

Miura (1986) sugeriu que fosse feita uma revisão de todas as espécies do gênero *Eunice*, pois muitas das descrições originais são muito restritas ou baseadas em exemplares incompletos. Essa revisão foi feita por Fauchald (1992), usando espécimes tipo. A revisão incluiu um total de 205 redescições, dessas 122 foram baseadas no holótipo, mas desses apenas 69 estavam completos. Nesta revisão foi efetuada uma análise cladística do gênero, porém com resultados inconclusivos, devido ao grande número de espécimes incompletos, o que acarretou muitos caracteres indetermináveis, impossibilitando o estabelecimento de uma topologia. Esse tipo de caracter pode

esconder os sinais dos caracteres bem codificados, resultando em um grande número de cladogramas mais parcimoniosos e na falta de resolução dos cladogramas (Kitching *et al.* 1998).

Outro problema existente na taxonomia da família Eunicidae é a variação de caracteres taxonômicos durante a ontogenia das espécies (Parapar *et al.* 1993). Durante o desenvolvimento de algumas espécies, estas passam por fases nas quais seus caracteres são característicos de outros gêneros da família, tanto que o nome dado a cada uma dessas fases é o nome do gênero a que ela corresponde, *Nematonereis*, *Lysidice* e *Marphysa* (Orensanz 1990). Atento a essas variações, Orensanz (1990) incluiu uma nota no início de sua chave de identificação dos gêneros, advertindo que aquela só deve ser usada para indivíduos adultos. Mas algumas vezes a distinção entre jovens e adultos não é clara. Enquanto em algumas espécies de Eunicidae o adulto tem poucos centímetros de comprimento, como por exemplo *Eunice harassii* Audouin e Milne Edwards, 1833 (Giangrande 1989); em uma espécie do gênero *Marphysa*, o jovem com aproximadamente 4,8 centímetros de comprimento apresenta apenas três apêndices no prostômio (antenas e/ou palpos) (Aiyar 1931) (Fig. 2A) – característica do adulto do gênero *Lysidice* e comumente usada na identificá-lo – ao invés dos cinco apêndices característicos do adulto de *Marphysa*. Por causa dessas variações dos caracteres e de tamanho, provavelmente jovens de alguns gêneros foram descritos como adultos de outros gêneros.

Pouco se sabe sobre a reprodução e o desenvolvimento das espécies de *Eunice*. Alguns estudos (e.g. Miura 1986) observaram que importantes caracteres na identificação específica do gênero *Eunice*, como distribuição das brânquias e o começo dos ganchos subaciculares, são alguns dos caracteres que variam com o tamanho do espécime. Essas variações dos caracteres dificultam a definição de quais são intraespecíficas e quais são interespecíficas.

A família Eunicidae é dividida em sete gêneros considerados válidos pela maioria dos autores e dois descritos recentemente *Fauchaldius* Carrera-Parra e Salazar-Vallejo, 1998 e *Aciculomarphysa* Hartmann-Schröder e Zibrowius, 1998, todos formados a partir de partes do gênero *Eunice* (Fauchald 1992). Apenas três destes nove gêneros são definidos por caracteres derivados: *Euniphysa*, *Nauphanta* e *Palola*. Porém este sistema genérico tem se mantido bastante estável (Orensanz 1990). O gênero *Eunice* é

parafilético (Fauchald comunicação pessoal) e definido pelas seguintes plesiomorfias: três antenas (Fig. 2A), dois palpos (Fig. 2A), um par de cirros peristomiais (Fig. 2A) e um conjunto completo de cerdas (limbadas, pectinadas, falcíferas e gancho subacicular) (Fig. 2B). Hartman (1944) e Fauchald (1970) usaram os caracteres distribuição das brânquias, cor e denteção dos ganchos subaciculares para dividir o gênero *Eunice* em subgrupos. Miura (1986) sugeriu que os dois últimos caracteres seriam suficientemente conservativos para talvez corresponderem a níveis genéricos ou subgenéricos.

Entretanto, apenas a combinação de caracteres não deveria ser usada na definição dos clados, pois essa combinação pode não identificar grupos naturais (Sundberg e Pleijel 1994). O nome dos clados deveria se referir apenas a grupos monofiléticos, (de Queiroz e Gauthier 1992) e a definição deles deveria ser baseada no ancestral comum (Sundberg e Pleijel, 1994), para que seja produzida uma classificação natural consistente com as relações filogenéticas (evolutivas) dos grupos (Brooks e McLennan 1991). Estes princípios produzem uma taxonomia mais estável e universal, já que não é baseada em idéias pessoais de parentesco (de Queiroz e Gauthier 1994).

Como o gênero *Eunice* é parafilético, o objetivo do presente estudo é tentar determinar clados monofiléticos, dentro deste gênero, que possam ser usados para dividi-lo em “novos” gêneros que correspondam a grupos naturais.

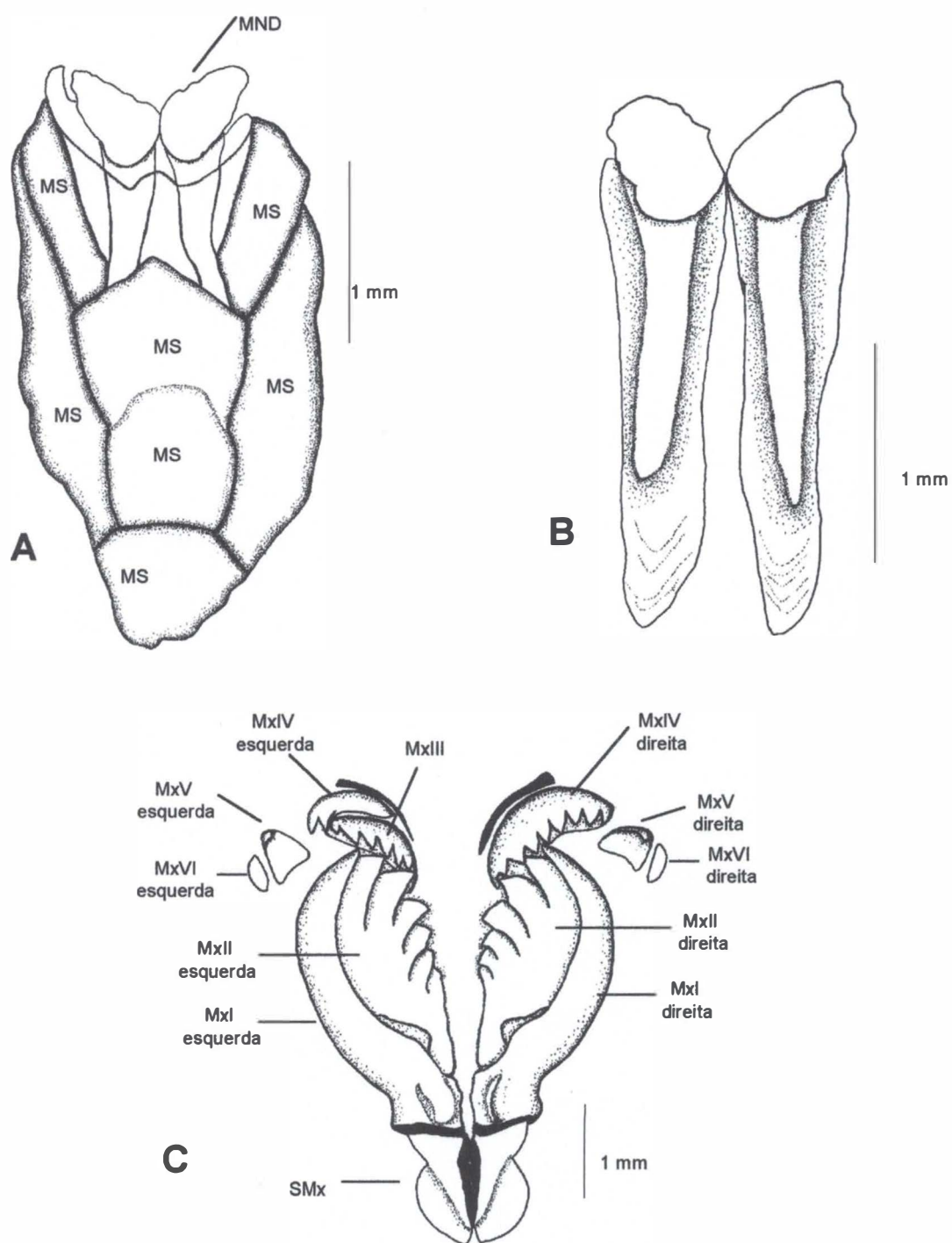


Figura 1 Aparelho bucal do gênero *Eunice*. –A. Vista ventral do bulbo faringiano, *Eunice cf. torquata*. –B. Vista ventral da mandíbula, *Eunice rubra*. –C. Vista dorsal da maxila, *Eunice conglomerans*. Abreviações: MND, mandíbula; MS, músculo; Mx, maxila; SMx, suporte maxilar.

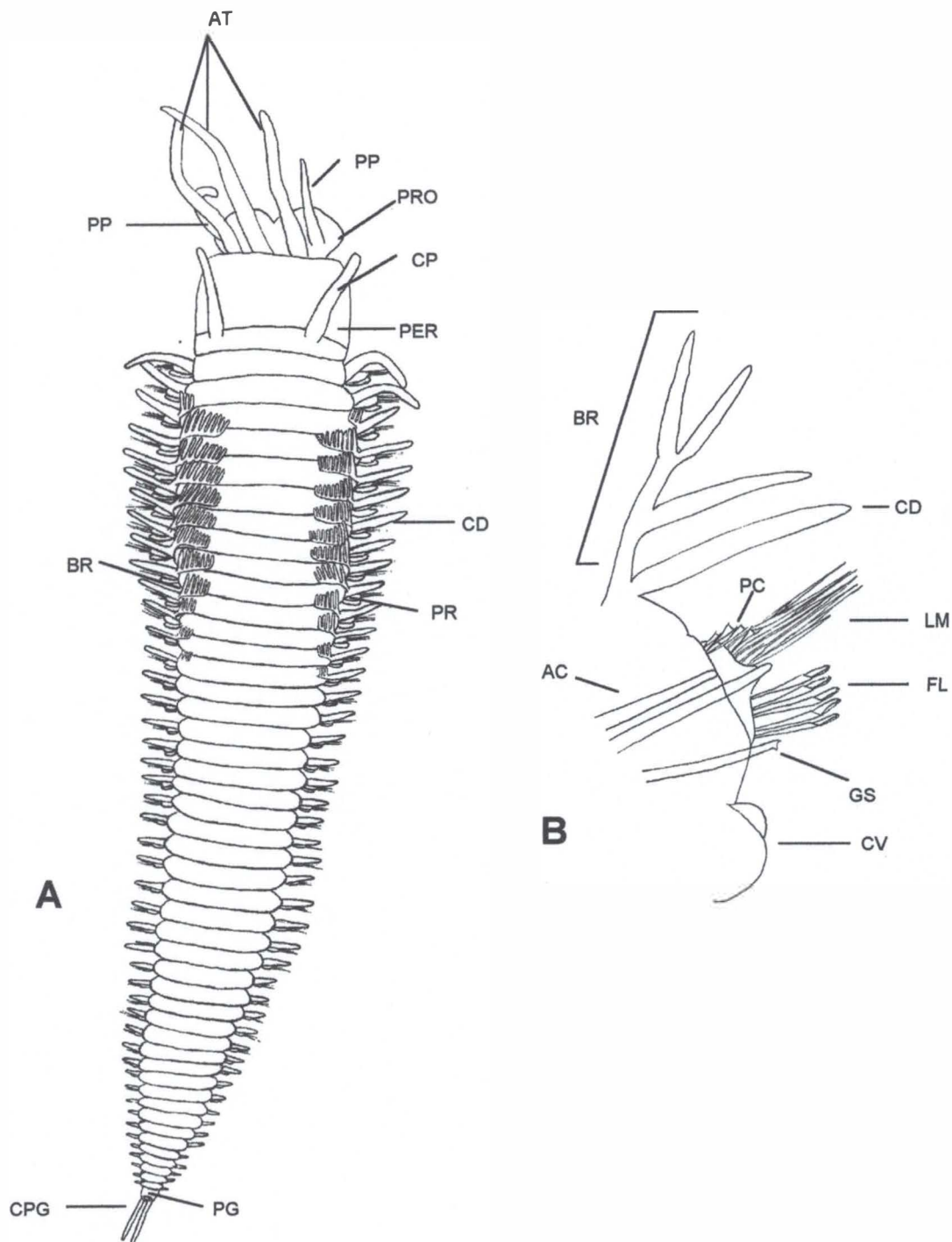


Figura 2 Esquema dos caracteres morfológicos da família Eunicidae e do gênero *Eunice*. –A. Espécime completo do gênero *Eunice*. –B. Vista anterior do parapódio mediano. Abreviações: AC, acículo; AT, antena; BR, brânquia; CD, cirro dorsal; CP, cirro peristomial; CPG, cirro pigdial; CV, cirro ventral; FL, cerda falcigera; GS, gancho subacicular; LM, cerda limbada; PC, cerda pectinada; PER, peristômio; PG, pigídio; PP, palpo; PR, parapódio; PRO, prostômio.

Phylogenetic analysis of selected species of the genus *Eunice* (Eunicidae, Polychaeta)

Joana Zanol, Kristian Fauchald and Paulo Cesar Paiva

Abstract

Most specimens examined in previous studies of the genus *Eunice* have been incomplete. This lead problems in the taxonomy of the genus, large amount of missing characters in cladistic analyses and inconclusive results. In this study, complete specimens of 23 species of *Eunice* were examined and a cladistic analysis was performed. The purpose was to define monophyletic groups within *Eunice* that could be used to divide this genus into “new” genera, since it has been shown to be paraphyletic in a previous analysis. Some of the coded characters were used for the first time, most of them features of the buccal apparatus. *Eunice sensu lato* was divided in three clades, and the genera *Marphysa*, *Lysidice* and *Palola* fell inside it. A common feature to the present, preliminary and former results was the placement of *Eunice antennata* and *Eunice aphroditois* in clades apart. Perhaps one corresponds to the old genus *Leodice*, since it includes *E. antennata*, its type species. The clade including *E. aphroditois*, type species of the genus *Eunice*, may be considered as *Eunice sensu stricto*. The third group, which may be the result of a misrepresentation of the diversity of species, will most probably turn out to be invalid in future analyses. The groups usually used to subdivide the genus *Eunice*, based on the color and dentition of the subacicular hooks and branchial distribution, were shown to be paraphyletic.

Introduction

The genus *Eunice* was described by Cuvier (1817) in the family Nereidae, as were most of the polychaete in those days. The family Eunicidae is one of the oldest polychaete families; its concept was first used by Lamarck (1818) (after Fauchald 1992a). About the same time, other genera were described to the family, as the genus *Leodice* Lamarck, 1818. The definition of *Eunice* and *Leodice* and the distinction between them were not clear. Both names were used in the same manner until the beginning of the 20th century. The choice of the name to be used was made by the authors of the studies (Hartman 1944). Due to this inconsistency and lack of definition *Leodice* was synonymized to *Eunice*. Although most of the species of *Eunice* were described until the beginning of the 20th century, they remain little known.

Miura (1986) suggested that a review on all species of the genus should be done, since many of the original descriptions are short or based on incomplete specimens, a common condition to the specimens of Eunicidae present in collections. This review was done by Fauchald (1992a) using only type specimens. It included 205 descriptions, among these, 122 were based on the holotype, however, only 69 were complete. In this review, a cladistic analysis of the genus was accomplished, but the results were inconclusive owing to the large number of incomplete specimens (for the scoring of many characters it is necessary to have the whole body), which resulted in many unscored characters. This kind of characters, usually coded as question marks, may induce the generation of many most parsimonious cladograms and lack of resolution by hiding the signal given by the scored data (Kitching *et al.* 1998).

Another problem on the taxonomy of the family Eunicidae is the variation of taxonomic characters during ontogenesis (Parapar *et al.* 1993). Some species during their development go through phases in which the states of their characters resemble diagnostic characteristics of other genera of the family, such as that the name given to each phase is the name of the genus they resemble, *Nematonereis*, *Lysidice* and *Marphysa* (Orensanz 1990). Careful with this changes, Orensanz (1990) put a note on the beginning of the key to the genera of the family Eunicidae, warning that it should only be used to adult specimens. Due to these changes on the characters, some juveniles belonging to genera *Eunice* and *Marphysa* may have been described as adult of other genera. Little is known about reproduction and development within the species of the family Eunicidae. Important characters in the identification of the species of *Eunice*, as the distribution of branchiae along the body and the first chaetiger where subacicular hooks appear, have been shown to vary with the size of the specimen (e.g. Miura 1986). These characters changes generate obstacles in the definition of which changes are intraspecific and which are interspecific.

The family Eunicidae is divided in seven genera considered valid in the latest studies and two recently described *Fauchaldius* Carrera-Parra & Salazar-Vallejo, 1998 and *Aciculomarphysa* Hartmann-Schröder & Zibrowius, 1998. Among these nine genera just three are well defined by derived characters, *Euniphysa*, *Nauphanta* and *Palola*, however this generic system has been fairly stable (Orensanz 1990). The genus *Eunice* is paraphyletic (Fauchald, personal communication), defined by the following

plesiomorphies: three antennae, two palps, a pair of peristomial cirri and a complete set of chaetal types. Hartman (1944) and Fauchald (1970) used the characters color and dentition of subacicular hooks and branchial distribution to divide the genus *Eunice* in informal subgroups. Miura (1986) suggested that the former two characters are conservative enough and the groups based on them might correspond to genus or subgenus level.

Nevertheless, just the combination of characters should not be used as the definition of clades, since this may not identify natural groups (Sundberg & Pleijel 1994). The name of the clades should refer only to monophyletic groups (de Queiroz & Gauthier 1992) and their definition based on the common ancestor (Sundberg & Pleijel 1994), in order to produce a natural classification consistent with the phylogenetic (evolutionary) relationships (Brooks & McLennan 1991). These principles yield a more stable and universal taxonomy, since it is not based on personal ideas of relationship (de Queiroz & Gauthier 1994).

Since the genus *Eunice* is paraphyletic, the aim of this study is to try to define monophyletic clades within this genus that could be used to divide it in “new” genera which correspond to natural groups.

Material and methods

Taxa

To define monophyletic groups within the genus *Eunice* a cladistic analysis was run with complete specimens of 23 species of the genus (Table 1). These were chosen in order to represent the diversity of branchial distribution, color and dentition of the subacicular hooks in the genus *Eunice* (Table 2), based on the groups used by Hartman (1944) and Fauchald (1970), with some modifications. Branchial distribution was quantified over the percentage of the body in which they are present, less than 55% or more than 65% of the body (Fauchald 1992a). Since would not be possible to examine all species of the genus we attempted to get as wide morphological representation as possible. We are aware that the few species examined may not have represented the genus accurately.

The amount of species from each group to be used in this study (Table 2) was initially defined by the logarithm on the base 2 of the total of species of each group. In

most of the groups it was not possible to examine the number of species planned due to the unavailability of complete specimens of such species. *Eunice* cf. *atlantica* was identified as “cf.” and kept separately from the other specimens of this species in the analysis since it is from Madagascar (Africa) and shows some differences when compared to the specimens from Brazil, type locality.

Table 1 Ingroup taxa examined in the present study.

Group	Species	Specimens examined	
A1	<i>Eunice pennata</i> (Muller, 1976)	2 (USNM 97393) from Norway, Storskjan, Oslofjorden 1 (USNM 3862) from United States, 42°01'N 68°01'W	
	<i>Eunice</i> cf. <i>semisegregata</i> Fauchald, 1969	2 (USNM 22436) from United States, California, 33°49'N 119°24'W	
	<i>Eunice websteri</i> Fauchald, 1969	1 (USNM 51134) from United States, North Carolina 1 (USNM 090042) from United States, Florida	
A2	<i>Eunice harassii</i> Audouin & Milne Edwards, 1833	1 (IBUFRJ 341) from England, Plymouth 1 (IG 10910) from 24°13'N 15°44'W 1 (SMNH 28277) from England	
B1	<i>Eunice dubitata</i> Fauchald, 1974	2 (IBUFRJ 342) from Norway, Rödberg	
B2	<i>Eunice aphroditois</i> (Pallas, 1788)	2 (USNM 96453) from Indonesia 1 (USNM 100202) from Japan, Kamagawa Prefecture	
	<i>Eunice conglomerans</i> Ehlers, 1887	1 (IBUFRJ 343) from Brazil, Espírito Santo 1 (IBUFRJ 344) from Brazil, 22°18'S 40°48'W 1 (IBUFRJ 345) from Brazil, 04°32'N 50°18'W 2 (IBUFRJ 346) from Brazil, Bahia, 17°57'S 38°42'W 1 (IBUFRJ 347) from Brazil	
	<i>Eunice frauenfeldi</i> Grube, 1866	1 (SMNH 28294) from Western Australia	
	<i>Eunice</i> cf. <i>grubei</i> Gravier, 1900	3 (IBUFRJ 348) from Norway, Rödberg	
	<i>Eunice norvegica</i> (Linnaeus, 1767)	1 (IBUFRJ 349) from Papua New Guinea, Mandang	
	<i>Eunice cf. flavopicta</i> Izuca, 1912	1 (IBUFRJ 350) from Brazil, Bahia, 18°01'S 35°53'W	
	<i>Eunice thomasi</i> Augener, 1922	3 (IBUFRJ 351) from Panama, Bocas Del Toro	
	<i>Eunice cf. torquata</i> Quatrefages, 1866	2 (IBUFRJ 352) from Brazil, Bahia, 17°57'S 38°42'W 1 (IBUFRJ 353) from Brazil, Bahia, 17°57'S 38°42'W 2 (IBUFRJ 354) from Brazil Bahia, Salvador 1 (IBUFRJ 355) from Brazil, 25°44'S 48°22'W	
	B3	<i>Eunice insularis</i> Nogueira, Steiner & Amaral, 2001	1 (SMNH 28301) from Madagascar, Ambovo 1 (IBUFRJ 356) from Brazil, Bahia, Salvador 1 (IBUFRJ 357) from Brazil, Bahia, Salvador 1 (IBUFRJ 358) from Brazil, Bahia, Salvador 1 (IBUFRJ 359) from Brazil, 00°28'N 45° 32'W
		<i>Eunice miurai</i> Carrera-Parra & Salazar-Vallejo, 1998	2 (IBUFRJ 360) from Brazil, 21°41'25''S 40°20'46''W 1 (IBUFRJ 361) from Brazil, 18°34'S 38°04'W 1 (IBUFRJ 362) from Brazil, Bahia, Salvador
	C1	<i>Eunice cf. atlantica</i> Kinberg, 1865	1 (IBUFRJ 362) from Brazil, Bahia, Salvador
		<i>Eunice atlantica</i> Kinberg, 1865	2 (IG 10910) from Senegal, 14°40'N 16°15'W 3 (USNM 96434) from Red Sea Gulf of Suez, Zeit Bay 1 (IBUFRJ 363) from Brazil, 23°50'S 45°56'W 1 (IBUFRJ 364) from Brazil, Espírito Santo, Guarapari 1 (IBUFRJ 365) from Brazil, São Paulo, São Sebastião 2 (IBUFRJ 366) from Brazil, Bahia, Salvador 1 (IBUFRJ 367) from Brazil, Bahia, Salvador
<i>Eunice vittata</i> (Chiaje, 1829)		1 (IBUFRJ 368) from Brazil, 26°46'S 40°05'W	
<i>Eunice antennata</i> (Lamarck, 1818)		1 (IBUFRJ 369) from Brazil, 22°55'S 41°13'W	
<i>Eunice rubra</i> Grube, 1856		1 (IBUFRJ 370) from Brazil, 19°45'S 39°31'W	
C2	<i>Eunice stigmatura</i> (Verrill, 1900)	1 (IBUFRJ 371) from Brazil 1 (IBUFRJ 372) from Brazil 1 (IBUFRJ 373) from Brazil, 20°36'S 35°51'W 2 (IBUFRJ 374) from Brazil, São Paulo, São Sebastião	
	<i>Eunice fucata</i> Ehlers, 1887		
	<i>Eunice sebastiani</i> Nonato, 1965		

Table 2 Groups employed in the sub division of the genus *Eunice* (adapted from Hartman 1944 and Fauchald 1970), utilized in the present study in the choice of the species to be examined. *approximated total

Groups	Characteristics	Total of species*	Log ₂	Number of species in this study
A1	Subacicular hooks light bidentate. Branchiae present on less than 55% of the body.	27	5	3
A2	Subacicular hooks light bidentate. Branchiae present in most of the body (more than 65%).	10	3	1
B1	Subacicular hooks dark bidentate. Branchiae present on less than 55% of the body.	22	5	1
B2	Subacicular hooks dark bidentate. Branchiae present in most of the body (more than 65%).	94	7	8
B3	Subacicular hooks dark bidentate. Without branchiae.	9	3	1
C1	Subacicular hooks light tridentate. Branchiae present on less than 55% of the body.	34	5	4
C2	Subacicular hooks light tridentate. Branchiae present in most of the body (more than 65%).	24	5	3
D	Subacicular hooks light to dark unidentate.	8	3	2
	Total	228	36	23

Complete specimens from the Eunicidae genera, *Marphysa*, *Palola* and *Lysidice*, and from the family Onuphidae (Table 3) were used as outgroup taxa in order to polarize the cladistic analysis. The onuphids were included in the outgroup since they have been shown to be the closest relatives of the eunicids in previous studies (Rouse & Fauchald 1997). Karageorgopoulos (submitted) has demonstrated that molecularly the only true populations of *Marphysa sanguinea* among the ones he studied are present in the type locality (Plymouth, England) and in the North of France. *M. cf. sanguinea* is a Brazilian specimen but it does not show any significant morphological difference when compared to the type locality specimens, for this reason it is identified as “cf.”.

The following institutions provided the specimens examined in the present study: Colecion de Referencia ECOSUR, Mexico; Departamento de Zoologia, Instituto de Biologia, UFRJ, Brazil (IBUFRJ); Institut Royal Des Sciences Naturelles de Belgique, Belgium (IG); National Museum of Natural History, Smithsonian Institution, USA (NMNH); and Swedish Museum of Natural History (SMNH).

Table 3 Outgroup taxa examined in the present study.

Family	Species	Specimens examined
Onuphidae	<i>Diopatra tridentata</i> Hartman, 1944	1 (IBUFRJ 375) from Brazil, Bahia
	<i>Kinbergomuphis tenuis</i> (Hansen, 1881)	1 (IBUFRJ 376) from Brazil, Bahia
Eunicidae	<i>Marphysa sanguinea</i> (Montagu, 1807)	3 (IBUFRJ 377) from England, Plymouth sound
	<i>Marphysa cf. sanguinea</i> (Montagu, 1807)	1 (IBUFRJ 378) from Brazil, Paraná
	<i>Marphysa regalis</i> Verrill, 1900	1 (IBUFRJ 379) from Brazil, Rio de Janeiro, 22°55'S 44°10'W
	<i>Marphysa</i> sp.	3 (IBUFRJ 380) from Brazil, Espirito Santo
	<i>Palola brasiliensis</i> Zanol, Paiva & Attolini, 2000	1 (IBUFRJ 381) from Brazil, 20°40'26"S 37°42'36"W
		2 (IBUFRJ 382) from Brazil, 17°48'01"S 35°52'52"W
	<i>Palola cf. viridis</i> Gray, in Stair 1847	1 (SMNH28292) from Western Australia
	<i>Lysidice ninetta</i> Audouin & Milne Edwards, 1833	1 (ECOSUR Euni-2) from Mexico
	1 (IBUFRJ 383) from France, Dinard	

Characters

Most of the characters are based on the traditional characters used to describe taxa in the family as summarized in Fauchald (1992a) and Carrera-Parra & Salazar-Vallejo (1998). The characterset is vastly simplified over the one presented by Fauchald (1992a), basically by excluding many of the details associated with the various kinds of chaetae and decreasing the number of character states. Some characters were used for the first time. Most of them are related to the buccal apparatus morphology.

Characters and characters states are the following:

1. Shape of the body's cross-section: 1- circular, 2- dorsoventrally flattened, 3- ventrally convex.
2. Body shape: 1- cylindrical abruptly tapering anteriorly and posteriorly, 2- evenly tapering from chaetigers 10-15.
3. Chaetigers: 1- at most 10 times as wide as long, 2- more than 10 times as wide as long.
4. Dorsal lips: 1- separated frontally, wide, 2- distinctly separated frontally, cirriform.
5. Dorsal lips: 1- rounded, 2- truncate.
6. Dorsal lips: 1- inflated, 2- flattened, 3- with thickened lateral margin (dimpled).
7. Vento-lateral lips: 1- distinct (set off by distinct grooves), 2- visible only as elevated surfaces.
8. Antennae and palps: 1- evenly spaced, 2- median antennae isolated by a gap, 3- palps isolated by a gap.

9. Antennae: 1- median present, 2- both median and laterals present.

10. Antennal ceratophores: 1- short, usually ring-shaped, 2- relatively long, usually articulated.

11. Antennal styles: 1- digitiform, tapering or clavate, 2- medially inflated (fusiform). The shapes digitiform, tapering and clavate were united in the same state due to the continuous variation within them, what makes their differentiation difficult. Hartman (1944) and Miura (1977b) suggested that the different shapes of the styles might have little taxonomic significance. These remarks are also true for the palpal styles.

12. Shape of the antennal styles articulations: 1- absent, 2- short or long cylinders, 3-moniliform. In many specimens antennal styles are strongly wrinkled and the distinction between wrinkles and true articulations may be dubious (Day 1967; e.g. *Marphysa fragilis* in Treadwell 1911; *Eunice mucronata* in Fauchald 1992a). Antennal styles were considered truly articulated when they had at least one complete groove around them. When articulations were present along the whole style, the scoring of this character was based on the shape present in the basal-median region of the style. These remarks are also true for the palpal styles

13. Palpal styles: 1- absent, 2- digitiform, tapering or clavate. Palps were considered as the missing prostomium appendage in the specimens of *Lysidice ninetta*. Although some disagreements, historically these appendages have been considered as the same structure (e.g. Chamberlin 1919a; Treadwell 1921), and the information about which appendages are missing on the genera *Lysidice* and *Nematonereis* was not a concern. Orrhage (1995) corroborated the idea first stated by Binar & Jeener (1928, after Orrhage 1995) differentiating by innervation the five appendages of a *Eunice* species in three internal antennae and a pair of palps, which used to be named A-I (Fauchald 1992a). However for the genus *Lysidice* it is still not clear which of the appendages are present. Herein the appendages present were considered as being the three antennae, due to its placement between the eyes on the posterior region of the prostomium. However this consideration can be contradictory. Steiner (2000) suggested that the paired appendages present in the specimens of *L. ninetta* examined by her were palps, due to their localization in front of the eyes.

14. Palpal ceratophores: 1- short, usually ring-shaped, 2- with relatively long,

usually articulated ceratophores.

15. Shape of the palps styles articulations: 1- absent, 2- short or long cylinders, 3- moniliform.

16. Peristomium: 1- single ring, 2- two rings distinct at least dorsally.

17. Peristomial cirri: 1- absent, 2- present.

*18. Maxilla VI (MxVI): 1- absent, 2- present (Fig. 1C).

*19. Relative size of the maxillary carrier: 1- greater than half of maxilla I (MxI) (Fig. 1D, G), 2- smaller than half of MxI (Fig. 1A, C).

*20. Left maxilla IV (MxIV): 1- with teeth in less than half of the plate, often only two present (Fig. 1C), 2- with teeth in more than half of the plate (Fig. 1A, B, E), 3- plate longer than wide most of the time just with one tooth (Fig. 1F, G).

*21. Maxilla III (MxIII): 1- front end as part of distal arc (Fig. 1C, D), 2- at least in part located behind maxilla II (MxII) (Fig. 1A), 3- edentate behind MxII (Fig. 1F, G). Orensanz (1990) and Fauchald (1992a) suggested that the shape of MxIII and its relation to other maxillae could be taxonomically informative.

*22. Paired mandibles: 1- flat (Fig. 2A), 2- strongly curved, forming an open scoop, plates united until the anterior end, which is strongly calcified (Fig. 2B, C), 3- curved, plates separated in a V shape at the anterior end, not strongly calcified (Fig. 2D, E). Even though *Lysidice* and *Palola* mandibles are curved, the existing differences seem enough to consider them as different character states. Beside the differences described on the character-states, on the genus *Palola* the strongly calcified anterior end is present beyond the organic matrix, while on the genus *Lysidice* calcification closely follows the matrix. At first sight the insertion of muscle fibers F4 (Desiére 1967) in the mandibles may look distinct in *Palola*, in which it ends in the middle of the cutting edge (Hartmann-Schröder 1967) approximately on the same point as the matrix (Fig. 2C), instead of going on until the anterior end as in *Lysidice* (Fig. 2E). However at a closer look it is possible to notice that the muscular insertion seems to follow the presence of the organic matrix as in all other examined genera of the families Eunicidae and Onuphidae (personal observation).

*23. Placement of the muscle fibers complex F1 + F2 (Desiére 1967) on the pharyngeal bulb: 1- posterior to the mandible carrier (Fig. 3A), 2- over the mandible carrier (Fig. 3B), 3- between the mandible carrier (Fig. 3C).

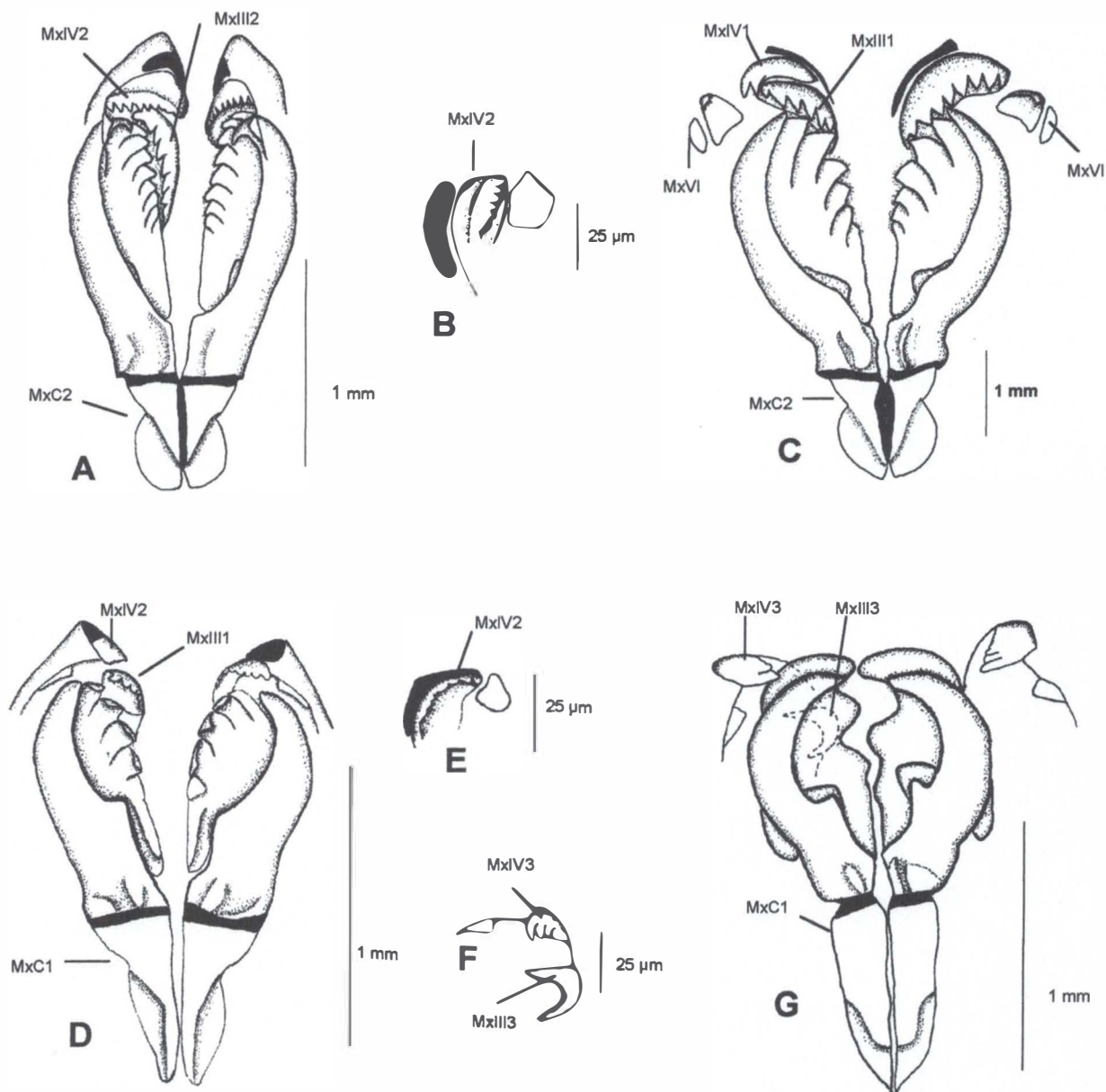


Fig. 1 Maxillae (dorsal view) of the genera *Eunice*, *Palola* and *Lysidice*. –A. *Eunice rubra*. –B. *E. rubra*, detail of MxIV and MxV. –C. *Eunice conglomerans*. –D. *Lysidice ninetta*. –E. *L. ninetta*, detail of MxIV and MxV. –F. *Palola brasiliensis*, detail of MxIII, MxIV and MxV. –G. *P. brasiliensis*. Abbreviations: MxIII1, front end of maxilla III as part of the distal arc; MxIII2, maxilla III at least in part located behind maxilla II (MxII); MxIII3, maxilla III edentate behind MxII; MxIV1, maxilla IV with teeth in less than half of the plate; MxIV2, maxilla IV with teeth in more than half of the plate; MxIV3, maxilla IV longer than wide most of the time just with one tooth; MxVI, maxilla VI; MxC1, maxillary carrier greater than half of maxilla I (MxI); maxillary carrier MxC2, smaller than half of MxI.

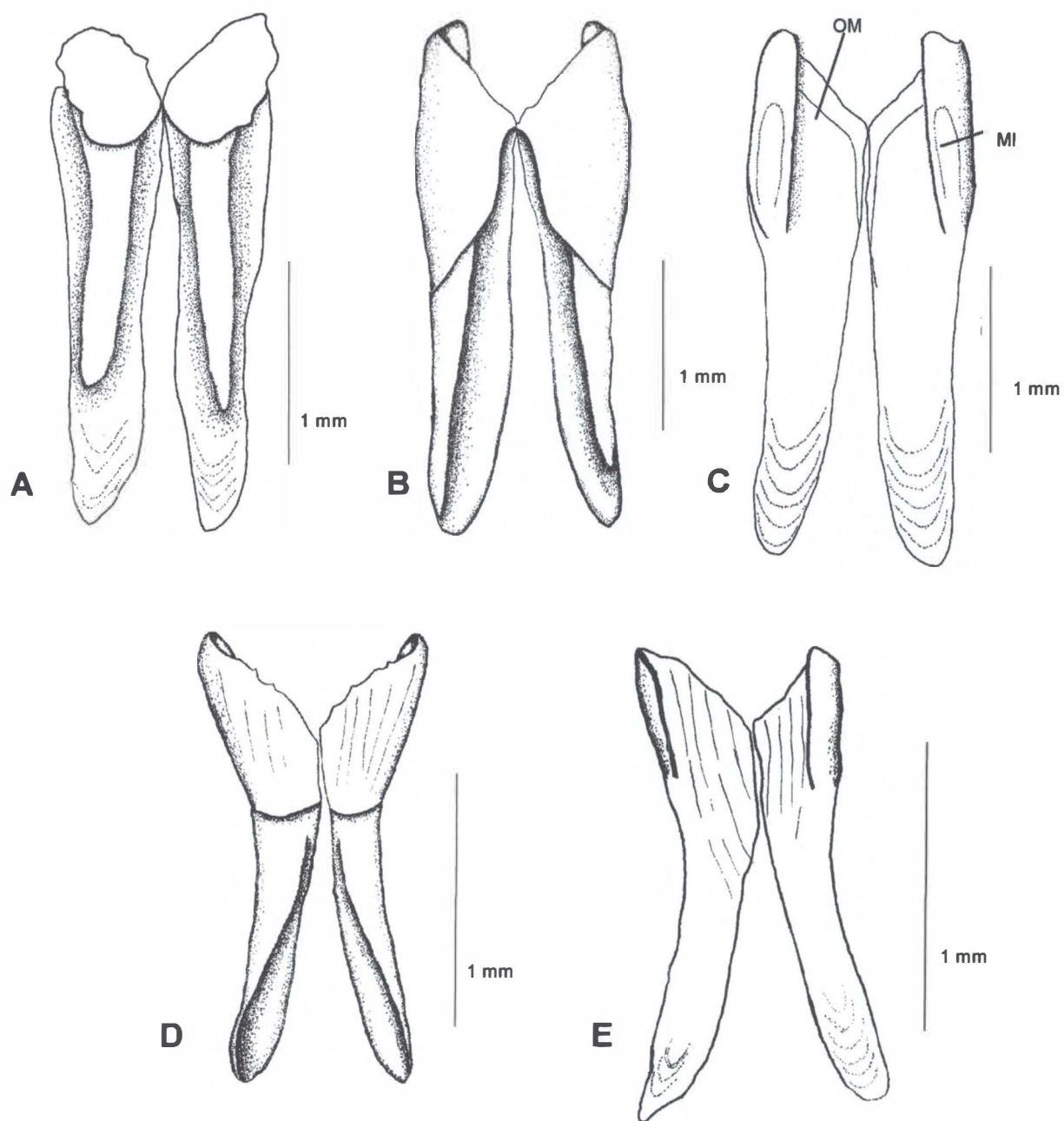


Fig. 2 Mandibles of the genera *Eunice*, *Palola* and *Lysidice*. –A. *Eunice rubra*, ventral view. –B. *Palola brasiliensis*, ventral view. –C. *P. brasiliensis*, dorsal view. –D. *Lysidice ninetta*, ventral view. –E. *L. ninetta*, dorsal view. Abbreviations: MI, place of muscle insertion; OM, outline of the organic matrix.

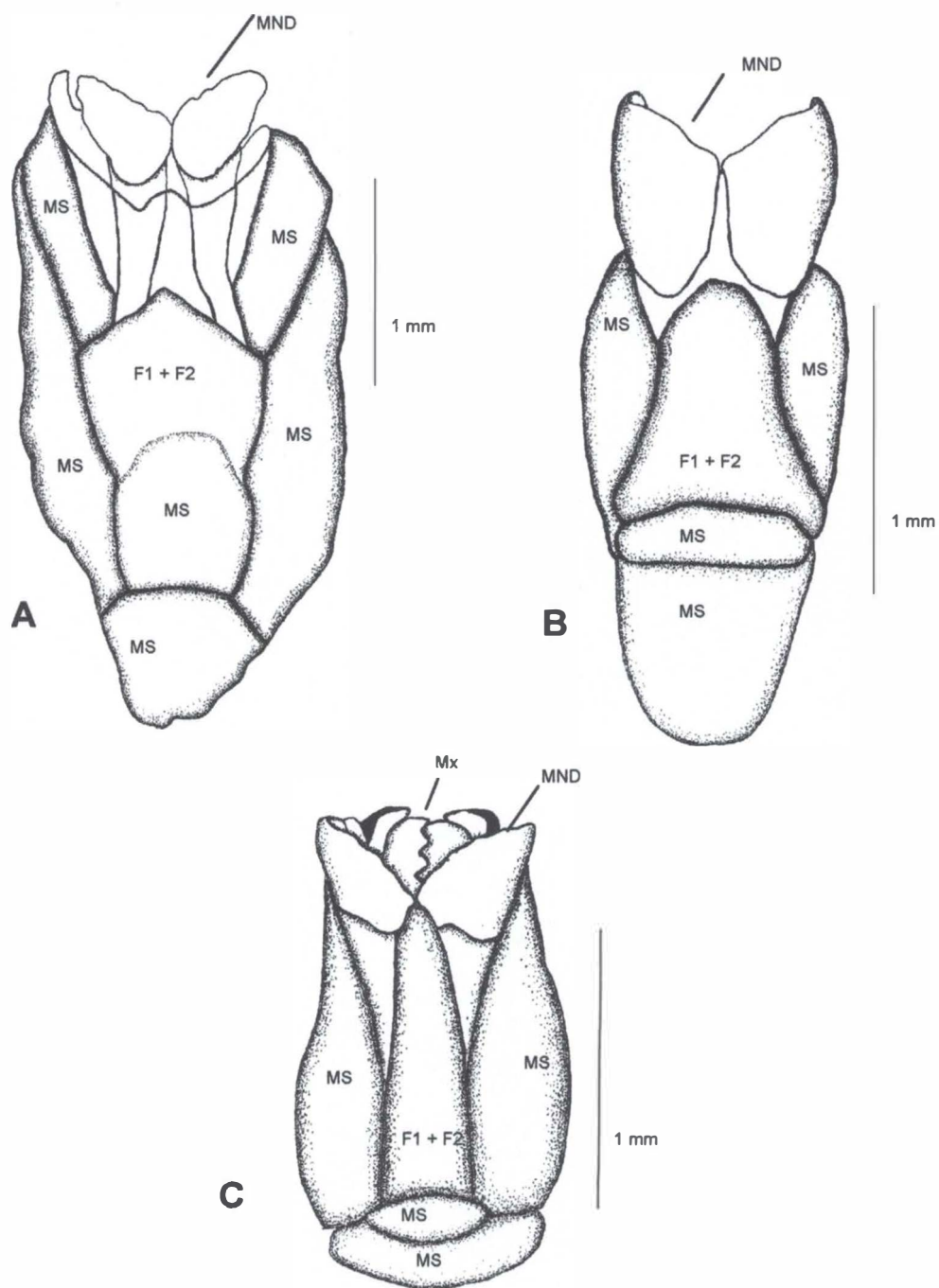


Fig. 3 Pharyngeal bulb (ventral view) of the genera *Eunice*, *Palola* and *Lysidice*. –A. *Eunice cf. torquata*. – B. *Palola brasiliensis*. –C. *Lysidice ninetta*. Abbreviations: F1 + F2, muscle fibers complex F1 + F2 (Desiére 1967); MND, mandibles; MS, muscle; Mx, maxillae.

24. Neuropodia in mid-body: 1- rounded, 2- truncate, 3- pointed.

25. Prechaetal lobes in mid body: 1- longer than acicular lobes, 2- about as long as acicular lobes, 3- absent except in anteriormost chaetigers.

26. Postchaetal lobes in mid body: 1- longer than acicular lobes, 2- about as long as acicular lobes, 3- shorter than acicular lobes

27. Ventral cirri: 1- tapering or digitiform in first few chaetigers, thereafter basally inflated, 2- tapering or digitiform in anterior and posterior chaetigers, inflated in median chaetigers.

28. Shape of the ventral cirri: 1- ventral ridge, 2- scoop shaped, rounded.

29. Branchiae: 1- absent, 2- single filaments, 3- filaments linearly arranged, 4- spiraled. In both pectinate and palmate branchiae, filaments are linearly arranged on a stem. What differentiates them is the size of the stem in relation to the size of the filaments (Fauchald 1992a). The distinction between these shapes is often not clear due to continuous variation among the extremes. Therefore, character state three is the combination of these shapes.

30. Branchiae start: 1- on chaetiger 3, 2- between chaetigers 4 and 9, 3- start late (after chaetiger 10).

31. Branchiae: 1- limited presence (less than 55% of the body), 2- present in most of the body (present in more than 65% of the body).

32. Pectinate chaetae thin and usually long: 1- absent, 2- present.

*33. Spatula shaped pectinate chaetae (short, wider than the acicula with very wide teeth): 1- absent, 2- present. It is present in middle and posterior regions of the body (Fig. 4A, B).

34. Pseudocompound falcigers or spinigers: 1- absent, 2- present in a limited number of anterior chaetigers.

35. Compound falcigers: 1- absent, 2- bi- or tridentate.

36. Compound spinigers: 1- absent, 2- present.

37. Acicula: 1- dark (brown, dark brown or black), 2- light (nearly clear or yellow). The codified color was the darkest one present on the specimen.

38. Acicula: 1- with distinctly differently colored sheath and core, 2- without distinctly differently colored sheath and core.

39. Acicula distally: 1- blunt-tipped, conical or irregularly knobbed, 2- hammer-

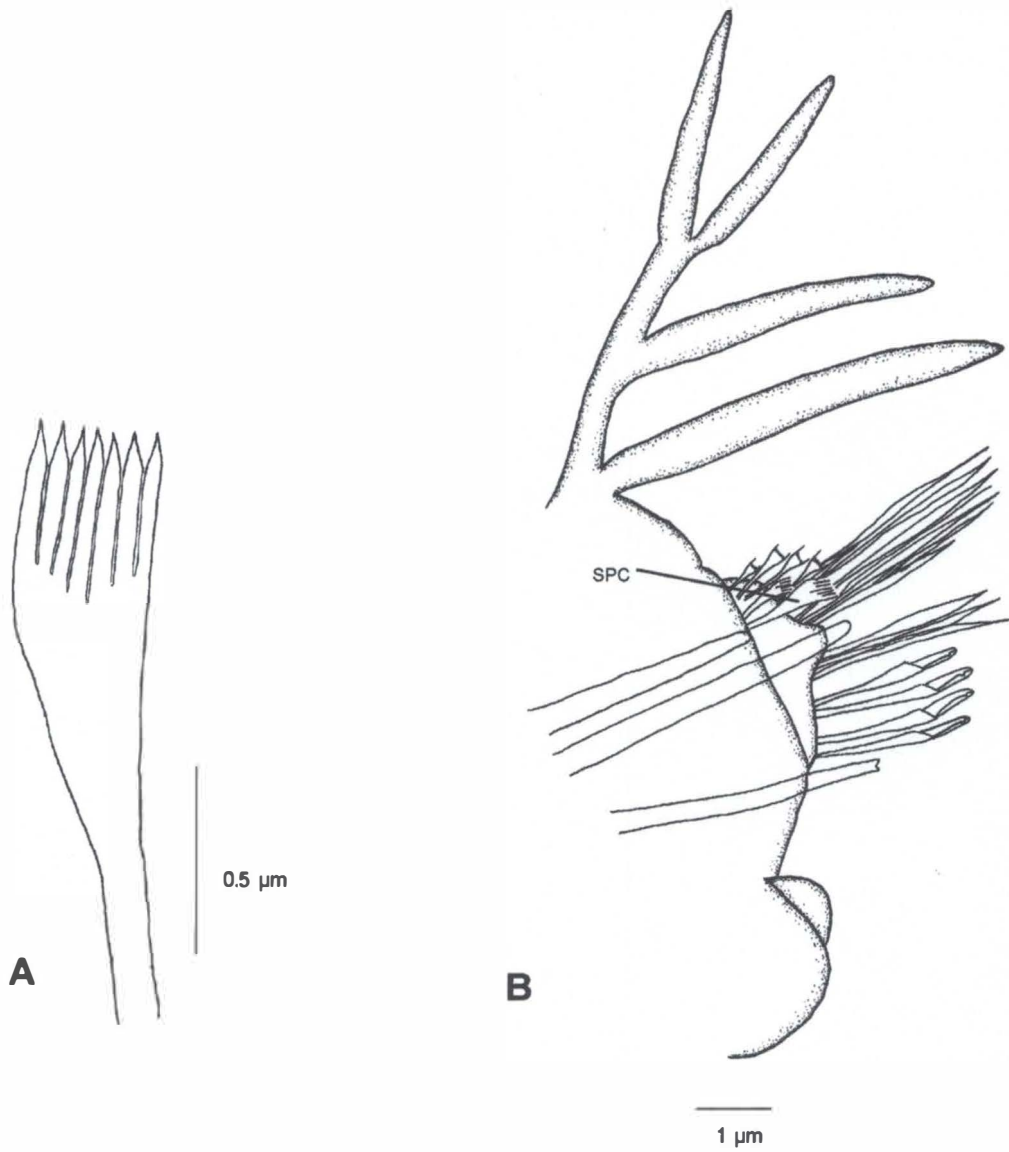


Fig. 4 Spatula shaped pectinate chaetae. –A. *Marphysa regalis*, spatula shaped pectinate chaetae. –B. *M. regalis*, parapodium 109 left. Abbreviation: SPC, spatula shaped pectinate chaetae.

headed or bidentate.

40. Subacicular hooks: 1- absent, 2- falcate, 3- bidentate, 4- tridentate.

41. Subacicular hooks: 1- light (nearly clear or yellow), 2- dark (brown, dark brown or black). The codified color was the darkest one present on the specimen.

42. Subacicular hooks: 1- distinctly differently colored core and sheath, 2- without distinctly differently colored core and sheath.

43. Subacicular hooks: 1- present in every or nearly every segment after first occurrence, 2- may be missing irregularly, sometimes in many segments.

44. Subacicular hooks: 1- always single, except for replacement, 2- at least paired.

*45. Ventral pygidial cirri: 1- absent, 2- present.

The symbol * on some characters means these were used for the first time in the present study.

The variation of the soft body characters 1, 2, 3, 5, 6, 7, 8, 12, 15, 24, 25 and 26, may be subject to size difference of specimens, different fixation procedures as well as the condition of preserved specimens (Treadwell 1911; Hartman, 1944; Nonato & Luna 1970; Steiner *et al.* in press).

For the codification of characters each specimen was examined under stereo and compound microscopes. The stereomicroscope was a Zeiss SV6 equipped with camera lucida and the compound microscope was a Zeiss Axiolab. Specimens were dissected in a similar method to the one described by Day (1967), and the pharyngeal bulb extracted in order to codify the characters of the buccal apparatus. To be able to observe some of the chaetal variation along the body, in each specimen six parapodia were examined, two from the first and last 2.5% of the body respectively and 4 from the median chaetiger of each fourth of the body.

Polymorphic characters were coded as such; all character states present on a certain species, due to intraspecific variation, were coded. *Eunice websteri* is polymorphic on character 40 due to variation within one specimen. Although this species usually holds only bidentate subacicular hooks (Fauchald 1969), tridentate ones were also coded in one of the examined specimens.

Question marks “?” denote unknown and inapplicable characters.

Cladogram construction

All characters had the same weight during the analysis and were treated as unordered. Characters in species coded as polymorphic were not considered while constructing the cladograms, PAUP* (Swofford 1998) assigns the most parsimonious state of these characters to the species a posteriori (Wiens 2000).

The outgroup specimens were not identified as such before running the analysis; they were left to be polarized by the analysis.

The final cladograms was determined by strict consensus of the most parsimonious cladograms resulting of the heuristic search. On this search taxa were randomly added on 1000 replicates and 100 trees were held at each step of the TBR (Tree Bisection and Reconnection) swap. The analysis was run using PAUP* 4.0b8 for Windows (Swofford 1998) and cladograms on the publication are modified from the ones produced by TreeView (Page 1996).

Nomenclature

We are aware of the discussions around the phylogenetic taxonomy and agree that the Linnaean nomenclature does not reach the necessities and is not consistent with a taxonomy based on the evolutionary history of groups. Nevertheless for the time being we decided to use the Linnaean nomenclature in the present study, since the PhyloCode (Cantino & de Queiroz 2000) is not yet in operation and the currently code in use is the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999). For a discussion on this subject we refer to de Queiroz & Gauthier (1990, 1992, 1994), Lee (1999) and Pleijel & Rouse (2000).

Results

Forty-eight trees resulted from the heuristic search, each with a consistency index (CI) of 0.73, a retention index (RI) of 0.78 and a length of 169 steps. The strict consensus tree (Fig. 5) is one step longer than the most parsimonious trees, with a CI of 0.72 and a RI of 0.77. In the present analysis, measurements of data fit (CI and RI) and size of the cladograms are over and underestimated, respectively, due to the exclusion in their calculation of the transformation of characters coded as polymorphic in some species.

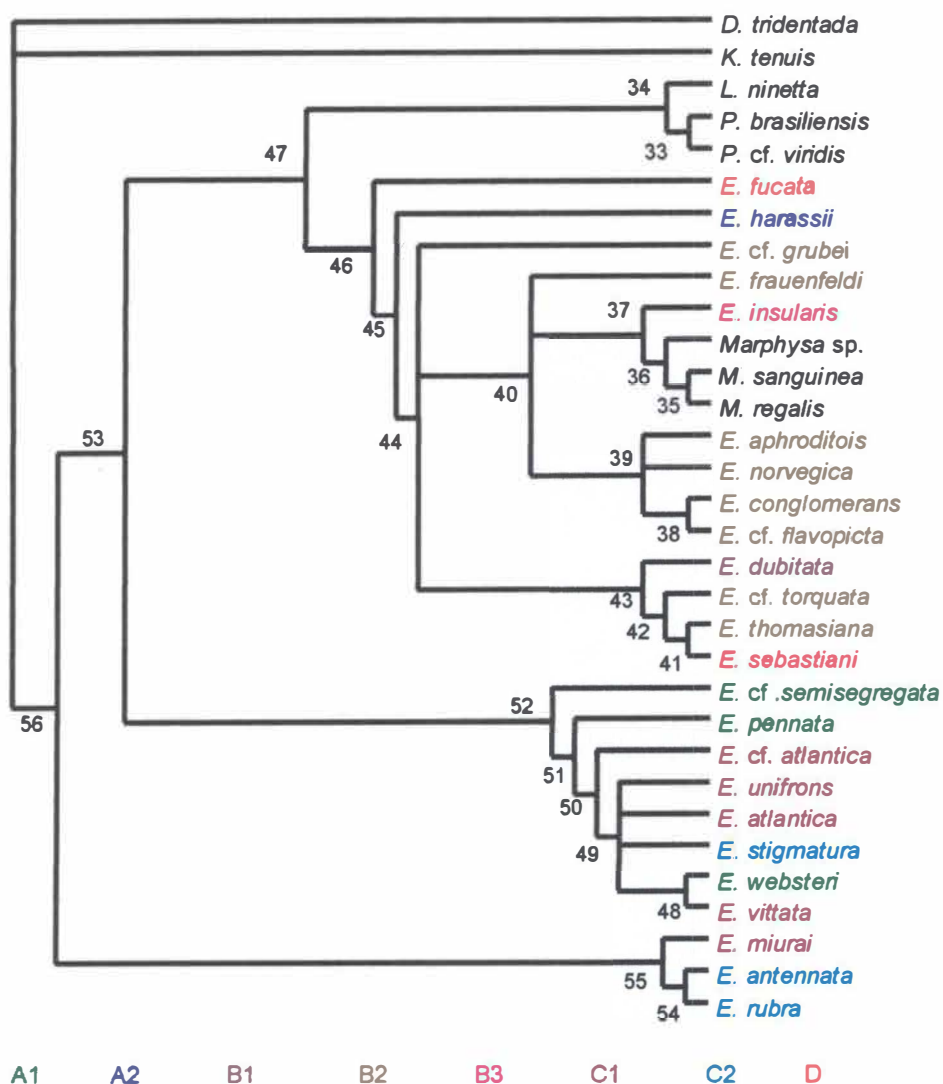


Fig. 5 Strict consensus tree of the most parsimonious trees. Length= 170 steps. CI= 0.72. RI= 0.77. All nodes are numbered and correspond to the numbers used in Appendix II to indicate character-state changes at each node. Different colors correspond to the groups modified from the ones defined by Hartman (1944) and Fauchald (1970).

Three of the 48 most parsimonious cladograms are shown in the figure 6. Some of the differences within these trees and between them and the strict consensus are present in the relationship of *Eunice cf. grubei*, *Eunice frauenfeldi*, *Eunice aphroditois* and *Eunice norvegica* with their neighbor species or clades. All their possible relationships are presented in figure 6. Besides these, the other conflict present is the arrangement among the species *Eunice atlantica*, *Eunice stigmatura*, *Eunice unifrons* and their interaction with the clade, which comprehends *E. websteri* and *Eunice vittata* (Fig. 6). But in all trees *E. unifrons* is always a sister species to the clade *E. websteri* and *E. vittata*.

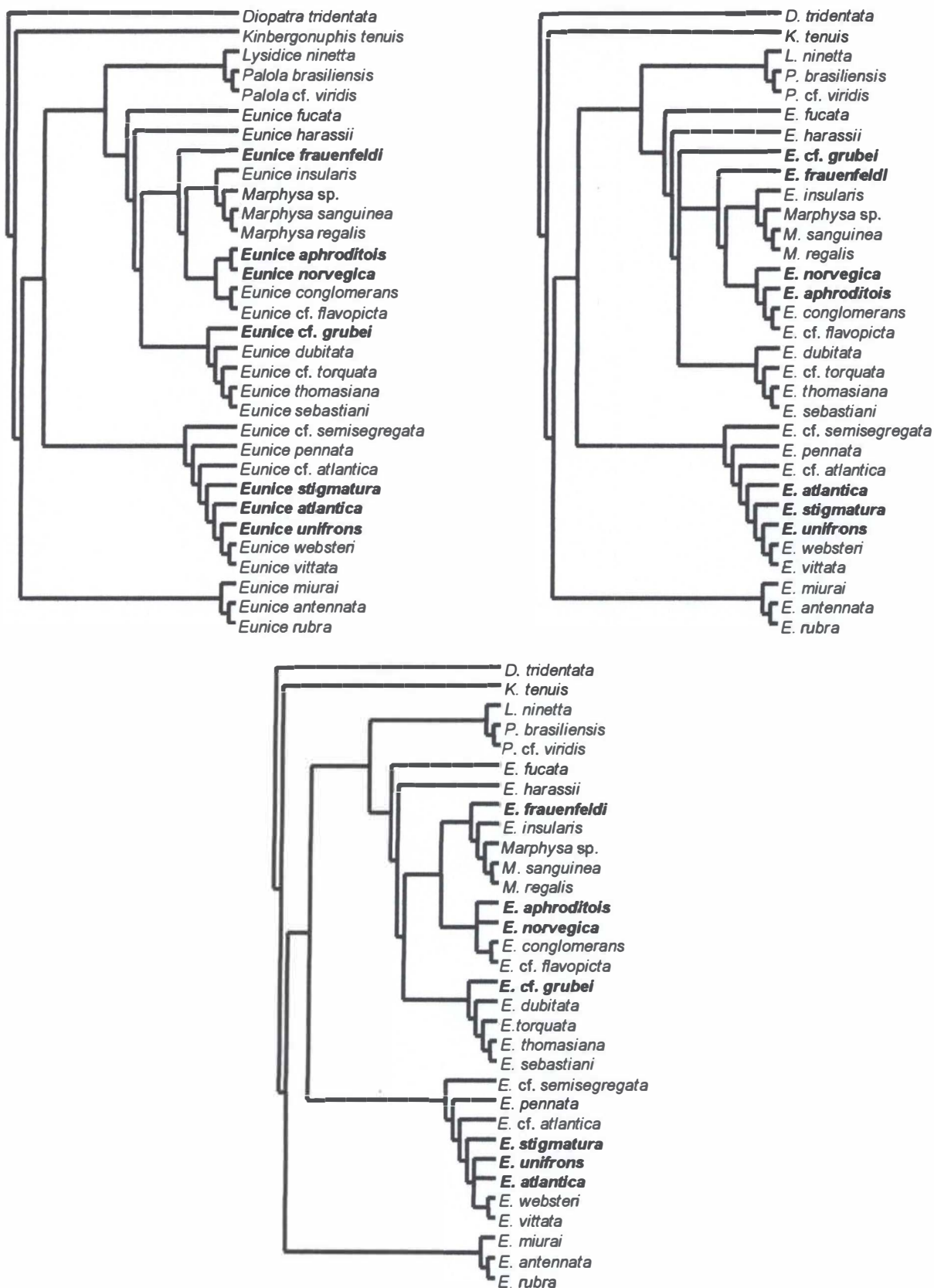


Fig. 6 Three of the 48 most parsimonious trees. Length= 169. CI= 0.73. RI= 0.78. Species in bold are divergences within most parsimonious trees and between them and strict consensus tree.

Although the specimens of *Diopatra tridentata* and *Kinbergonuphis tenuis* had not been defined as outgroup, they are consistently apart from the species of the genus *Eunice* on the trees. In contrast this is not true for the other genera of the family Eunicidae. All of them fell inside of what is considered to be the genus *Eunice*.

The analysis expressed three main monophyletic clades inside the genus *Eunice* (Fig. 5, nodes 46, 52 and 55). The first clade and most basal is formed by *Eunice antennata*, *Eunice rubra* and *Eunice miurai* (Fig. 5, node 55). It is a sister clade to the remainder of *Eunice*, *Lysidice*, *Palola* and *Marphysa*. This group is supported only by homoplastic synapomorphies (Fig. 5, Appendix II). *E. miurai* is the sister species to the *E. antennata* and *E. rubra* clade, which is supported by homoplastic characters, presence of branchiae in most of the body and dorsal lips, both rounded and truncate.

The monophyletic group uniting the remainder of *Eunice*, *Lysidice*, *Palola* and *Marphysa* (Fig. 5, node 53) is sustained just by ventral-lateral lips visible only as elevated surfaces (character 7), a homoplastic synapomorphy (Appendix II), polymorphic in many taxa (Appendix I).

The second main clade of *Eunice* species is delineated by *Eunice* cf. *semisegregata* and *E. vittata* (Fig. 5, node 52). It is weakly corroborated by the homoplastic synapomorphy start of the branchiae on the third chaetiger (Fig. 5, Appendix II). This clade congregates species with light colored bidentate – the two most basal species – and tridentate subacicular hooks – the clade from *E. vittata* to *E. cf. atlantica*. *E. websteri* is joined to *E. vittata* in a monophyletic group, which is arranged in a polytomy with *E. unifrons*, *E. atlantica* and *E. stigmatura*.

The last main clade, which includes *Eunice* species, also includes all *Marphysa* species (Fig. 5, node 46). It is sister group to the clade combining the genera *Lysidice* and *Palola* (Fig. 5, node 34). The monophyletic group formed by the combination of these two clades (Fig. 5, node 47) is supported by two synapomorphies (Appendix II), one of them is a unequivocal character, MxIII with front-end part of the distal arc.

Eunice fucata and *Eunice sebastiani* delineate the clade on node 46 (Fig. 5). It combines species with light bidentate, light falcate, dark bidentate and dark falcate subacicular hooks. It is corroborated by two homoplastic synapomorphies, MxVI present and ventral anal cirri absent. *E. fucata* and *Eunice harassii* are in the base of this

clade mainly due to their light colored subacicular hooks without distinctly differently colored core and sheath, plesiomorphies.

The remaining *Eunice* and all *Marphysa* species are arranged in a clade (Fig. 5, node 44) supported by the dark color of subacicular hooks with distinctly differently colored core and sheath, and branchiae starting on the third chaetiger.

This clade is a polytomy of three monophyletic groups. In the first of them (Fig. 5, node 43), *E. sebastiani* and *Eunice thomasiana* are united by the start of branchiae between chaetigers 4 and 9 in a clade, which is sister-group to *Eunice cf. torquata*. The moniliform shape of the palpal and antennal styles articulations holds these three species together. *Eunice dubitata* is the sister species to these species and the most basal one of the clade. The homoplastic synapomorphies, pre and pos chaetal lobes about as long as chaetal lobes, support this whole clade on node 43 (Fig. 5).

The second clade (Fig. 5, node 44) is formed just by *E. cf. grubei* and held by the pointed shape of the neuropodia in the mid-body.

Finally, the third clade (Fig. 5, node 40) expresses a trichotomy made up by *Marphysa* species and *Eunice insularis* clade (Fig 5, node 37); *E. aphroditois*, *E. norvegica*, *Eunice cf. flavopicta* and *Eunice conglomerans* clade (Fig. 5, node 39); and *E. cf. frauenfeldi* clade.

The genus *Marphysa* and *E. insularis* are supported in the same clade by the absence of MxVI and the presence of the anal cirri, reversals of the characters that hold together the monophyletic group of *Eunice* and *Marphysa* species in which they are included (Fig. 5, node 46, Appendix II). Species of *Marphysa* are held together by the character normally used to differentiate this genus from *Eunice*, the absence of peristomial cirri (Fauchald 1977).

Dorsal lips dimpled and branchiae starting between chaetigers 4 and 9 are the homoplastic synapomorphies, which corroborate the clade *E. aphroditois*-*E. cf. flavopicta*. Within this clade *E. conglomerans* and *E. cf. flavopicta* are combined in a monophyletic group supported by four synapomorphies, three homoplastic (Fig. 5, Appendix II) and one unequivocal character, teeth present in less than half of the left MxIV.

Lysidice and *Palola* are placed in the same clade by a series of synapomorphies (Fig. 5, Appendix II). Among them, three unequivocal characters are found, but two of

them transform in *Lysidice*: the placement of the muscle fibers complex F1 + F2 and the shape of the mandibles; which are two of the autapomorphies of this genus. The relative size of the maxillary carrier is the only one with the same state, greater than half of MxI, on both *Lysidice* and *Palola*. The clade of *Palola* species has five unequivocal characters among the synapomorphies that support it. These are: MxIII edentate behind MxII, left MxIV longer than wide most of the time with just one tooth, branchiae with single filaments, absence of pectinate chaetae and subacicular hooks.

All characters transformations for this hypothesis of phylogeny are shown in Appendix II, except character 9, which resulted as uninformative. All characters used in the selection of the species of *Eunice* to be included in the analysis – dentition of the subacicular hooks (character 40), color of these (character 41) and branchial distribution along the body (character 31) – were shown to be homoplasies, among many others (Appendix II). Both falcate and tridentate shapes of subacicular hooks have two parallel origins and the latter suffers a partial reversal to bidentate in *E. websteri* (Fig. 7). Dark hooks also have two parallel origins and in *M. sanguinea*, a polymorphic species for this character, a partial reversal to light colored hooks occurs (Fig. 8). Branchiae distributed in most of the body (more than 65%) has four different origins in the present phylogeny and reverts to the state branchiae present in less than 55% in *E. dubitata* (Fig. 9).

Discussion

In the description of *Eunice*, Cuvier did not define the type species; it was designated by Hartman (1959, after Fauchald 1992a) as *Nereis aphroditois* Pallas, 1788 (for more information on the definition of the type species for the genus *Eunice* see Fauchald 1992a). Lamarck (1818) on the description of the genus *Leodice* elected *E. antennata* as the type species of such genus. The definition and synonymization of these two genera was based on plesiomorphic similarities instead of on the evolutionary history of the group, a common situation caused by the absence of knowledge about the phylogenetic relationships and the traditional definition of taxon names (de Queiroz 1990; Lee 1999).

The paraphyletism of the genus *Eunice*, on its current definition, is clear in the hypothesis of phylogeny resulted from this study. A common characteristic revealed in

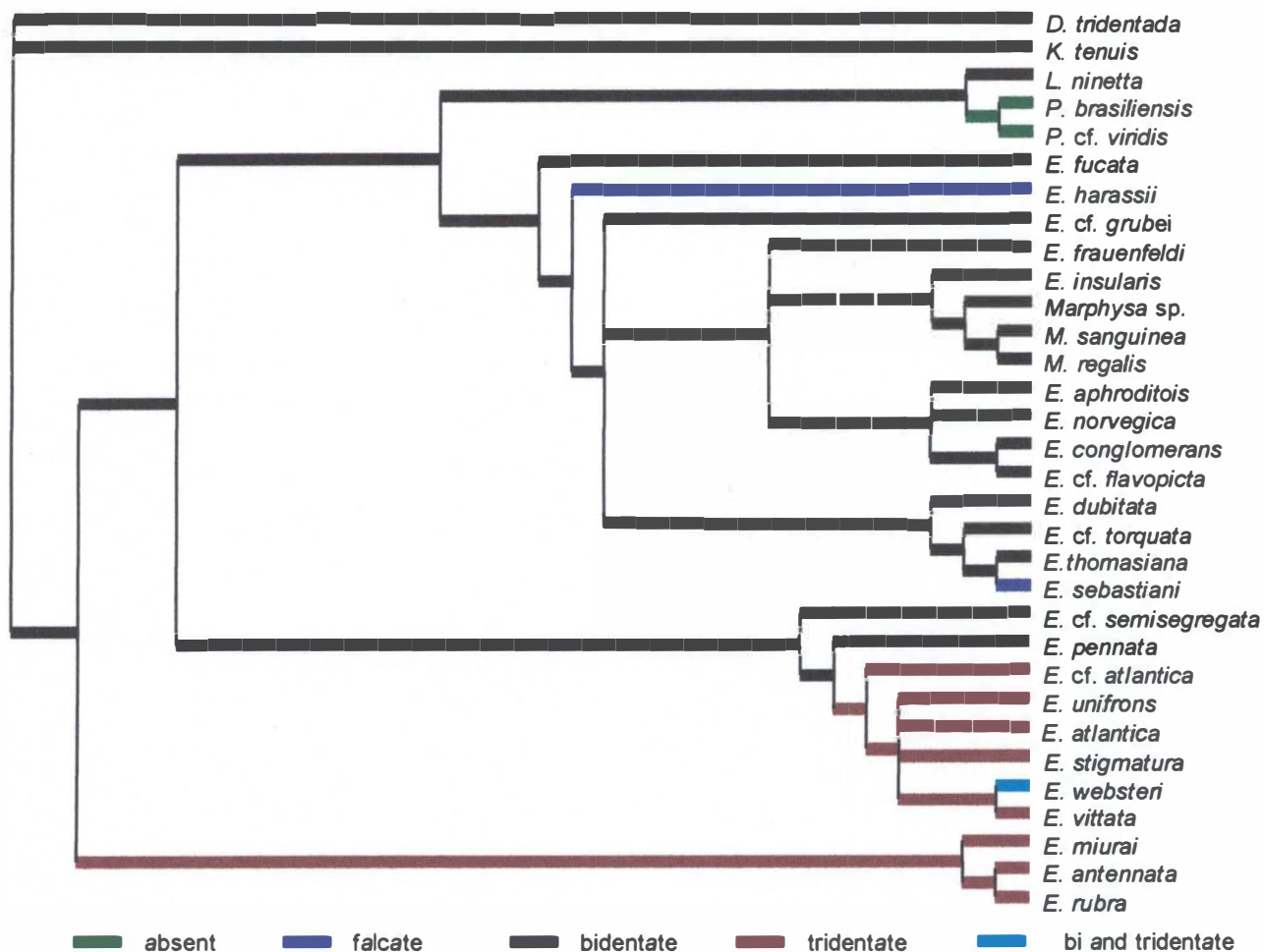


Fig. 7 Changes in the shape of the subacicular hooks (character 40) along the strict consensus tree.

almost all preliminaries analyses, in the final analysis of this study and also in the one in Fauchald (1992a) is the placement of the species *E. aphroditois* and *E. antennata* in different clades. This implies that the current genus *Eunice* can be split in at least two monophyletic genera, *Eunice sensu stricto* and *Leodice*, each with its original type species and boundaries delimited by its synapomorphies.

On the present phylogeny, *E. antennata* is held in the same clade of two other species with tridentate subacicular hooks and moniliform articulation on both antennae and palps, homoplastic synapomorphies of the clade. The differentiation between the shapes of the articulations of these appendages (antennae and palps) may be difficult (Gustus 1972). What, at some extent, can be caused by its probable dependence on the state of preservation of the specimens and on the degree of contraction of the appendages (Longbottom 1972, Fauchald 1992a). These three species are the only ones

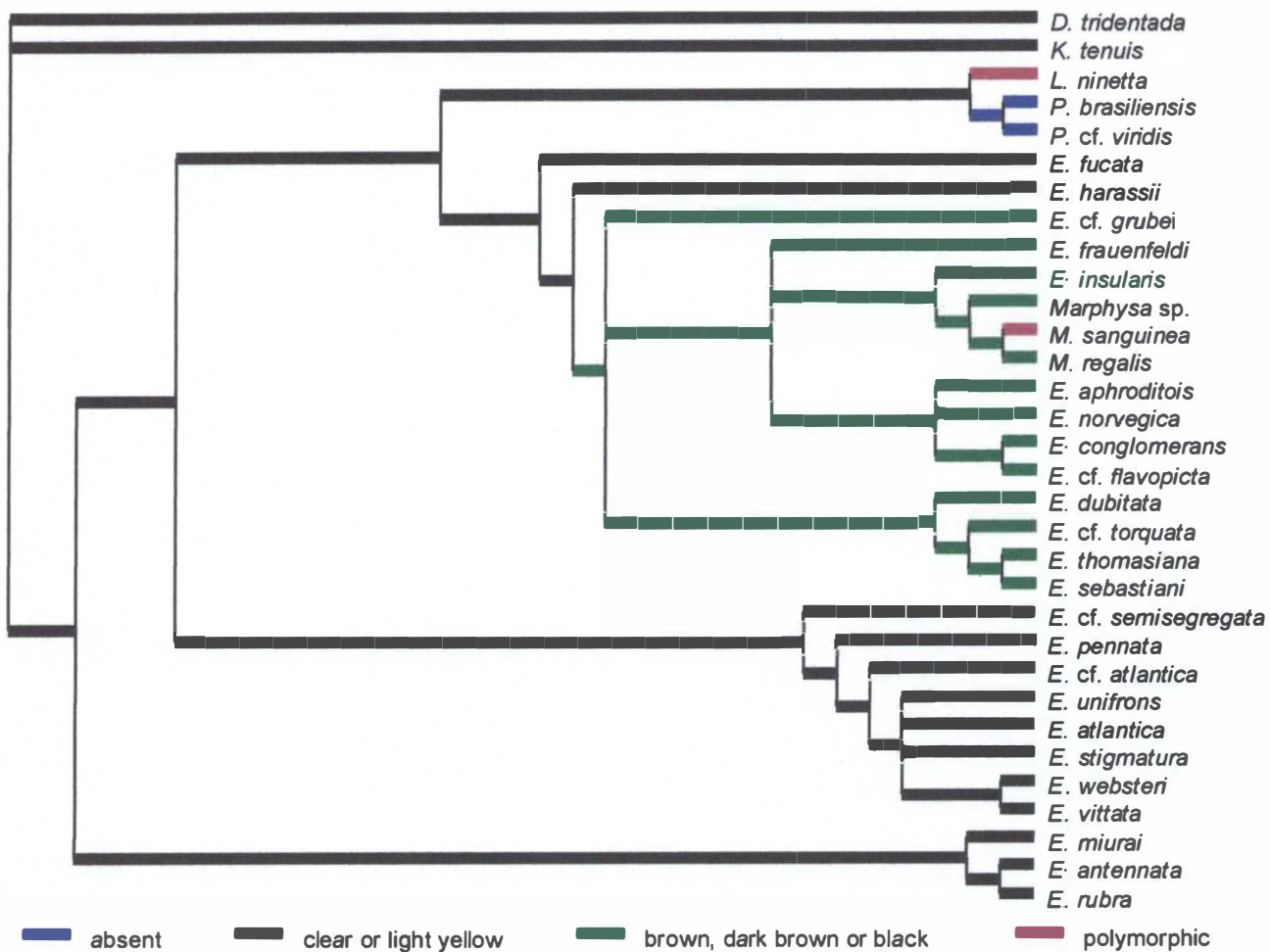


Fig. 8 Changes in the color of the subacicular hooks (character 41) along the strict consensus tree.

in the analysis to have tridentate falcigers chaetae in addition to the bidentate ones in the last 2.5% of the body. The presence of this uncommon type of falcigers might be an unequivocal character and a synapomorphy for this clade, which possibly represents the species “with a tendency toward tridentate falcigers”, as stated by Hartman (1944). All the species which had tridentate falcigers reported in Fauchald (1992a), also have tridentate subacicular hooks and branchiae starting on chaetigers six or eight; as the species of the *E. antennata* clade.

The clade *E. cf. semisegregata*-*E. vittata* is supported just by the start of branchiae on the third chaetiger. It may have been established as the result of a misrepresentation of the variety of starts of the branchiae existing in the species close to the ones present in this clade. For example, *Eunice prayensis* Kinberg, 1865, which has its branchiae starting on the fifth chaetiger, was considered by Hartman (1948) such a close species to *E. vittata* that she suggested the former was a probable synonym of the

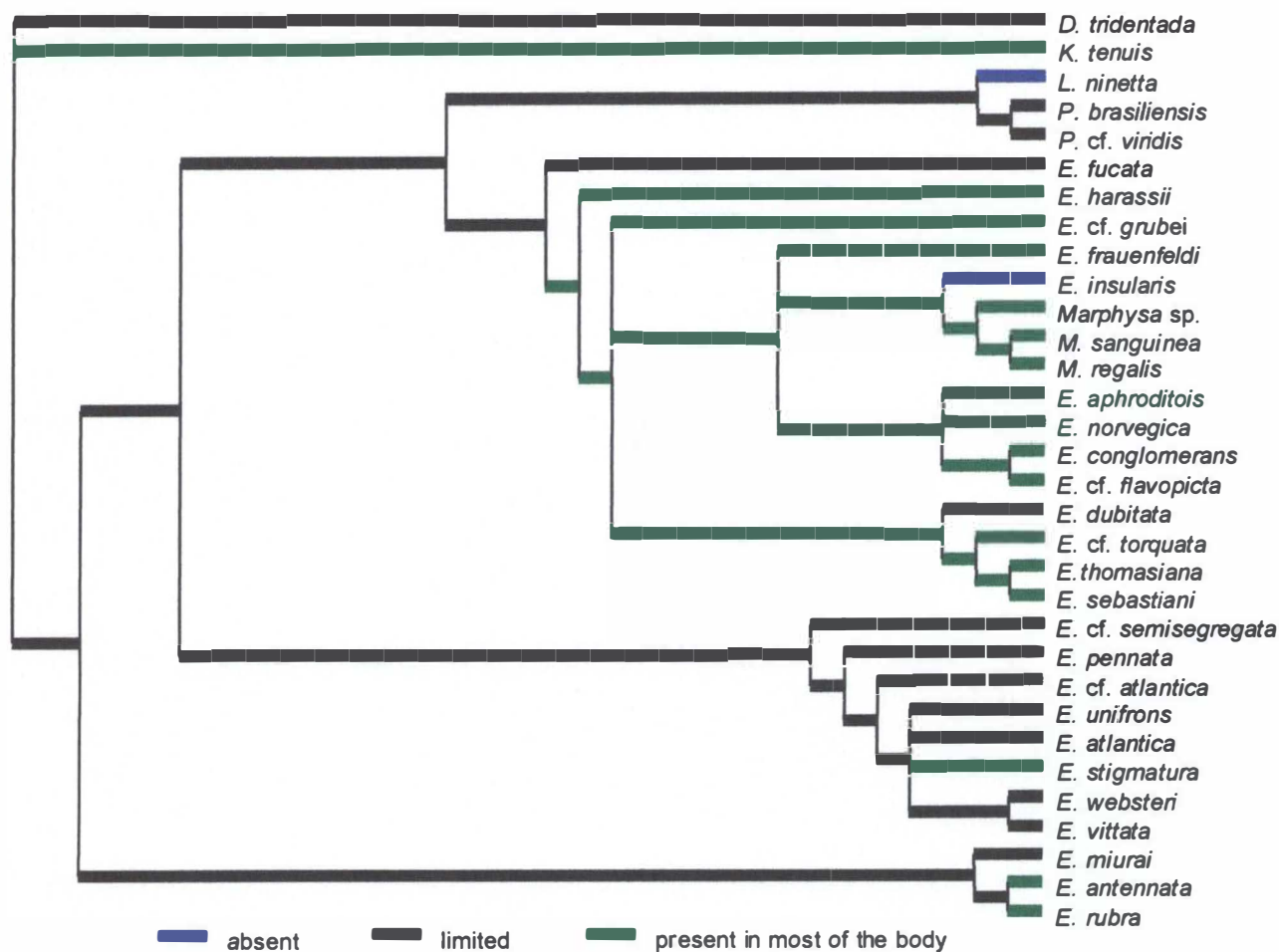


Fig. 9 Changes in the branchial distribution (character 31) along the strict consensus tree.

latter. All the support of the relationships within this clade is based on homoplastic synapomorphies (Fig. 5, Appendix II) and most of them have a great amount of intraspecific variation (Appendix I), perhaps due to their soft body characteristic, which, as mentioned above, may vary due to contraction, size, fixation procedure and condition of the preserved specimen. In addition to these poorly supported internal relationships, this clade is weakly corroborated and therefore it will most likely not be present in future analysis with more species and other characters included.

E. websteri is grouped within this clade with yellow tridentate subacicular hooks species owing to its polymorphic status for this character on the present analysis. Although all examined specimens of *E. stigmatura* had only tridentate subacicular hooks, Fauchald (1992a) reported some specimens bearing bidentate, others tridentate and some bearing both dentition of subacicular hooks. This indicates a close relationship within some bi and tridentate subacicular hook species. The partial reversal

from tri to bidentate subacicular hook showed in the present phylogeny (Fig. 7) points that the bidentate condition in some species can be a secondary change. But this reversal may also be a product of the exclusion of polymorphic characters during cladogram construction (see Wiens 1995, 2000).

E. aphroditois clade (Fig. 5, node 46), which may represent *Eunice sensu stricto*, is supported by two synapomorphies used for the first time in this study. One of them is the absence of the ventral pygidial cirri. The presence and absence of these cirri seem to have a high level of intraspecific variation, but it has not been widely described in the literature mainly because of the incompleteness of examined specimens. Winsnes (1989) reported the presence of the ventral pygidial cirri in the species *E. dubitata* and *E. norvegica*, which in the present study had this character coded as absent and polymorphic, respectively. In *E. insularis* this character is also polymorphic. Miura (1977a, 1986) described the presence of the ventral pygidial cirri in species that based on other characters would fit this clade even though this character is divergent, as happened to *E. conglomerans* in the present hypothesis of phylogeny. Outside of this clade the absence of the ventral pygidial cirri was observed in *E. miurai* and on the original description of *Eunice annulicirrata* Miura, 1986, both species have tridentate falcigers and subacicular hooks. For these reasons and the fact that clades should not be constructed based on common absences, due to the impossibility to observe and test the similarities within them (Lu & Fauchald 2000), this character should not be considered as a valuable synapomorphy on the definition of the clade.

The other synapomorphy is the presence of MxVI (Fig. 10); which is absent within this clade in the species of *Marphysa* and *E. insularis*. This character is a homoplasy owing to its presence in *E. cf. semisegregata*, which is the only species in the analysis outside of this clade to have this maxillary plate (Fig. 10). In the literature, the descriptions of this maxillary plate must be looked at with caution. MxVI is a small plate and nearly always lacks teeth. Probably it has been overlooked in several descriptions (e.g. *Eunice semisegregata* in Fauchald 1992a) as also may have happened to MxV (e.g. *Eunice valens* in Chamberlin 1919b, after Fauchald 1992a).

In the examined literature there are few accounts of the presence of MxVI in species of the family Eunicidae, which would not belong to the *E. aphroditois* clade or are not considered close to the species *E. cf. semisegregata*. Among the consulted

studies, the presence of MxVI in species with tridentate subacicular hooks was recorded just once, in Ehlers (1887). He described this maxillary plate in *E. rubra* and *Eunice tibiana* (Pourtalès, 1867). However the presence of MxVI is not registered in none of the other examined descriptions of these species (e.g. Fauchald 1992a; Steiner *et al.* in press). Although in the introduction about the genus *Palola*, Fauchald (1992b) described the maxillae of the genus with MxVI either absent or present, in all of the species in which he describes the maxillae, MxVI is absent. On the other consulted descriptions of *Palola* species, Hartmann-Schröder (1967) is the only one to register the presence of MxVI. In the genera *Marphysa* and *Lysidice*, the only found records of the presence of MxVI are in Aiyar (1931) and Treadwell (1921), respectively.

If these patterns observed on the literature about the family Eunicidae reflect the truth about these synapomorphies (absence of the ventral pygidial cirri and presence of MxVI) both of them are highly homoplastic on the present hypothesis of phylogeny. Hence, the *E. aphroditois* clade will probably not be held together in more complete analysis, as long as no other synapomorphy is defined for the group. However, these species are most likely to be kept apart from the other *Eunice* species by the MxIII part of the distal arc, an unequivocal character and a synapomorphy, which corroborates the more basal clade in which they are included (Fig. 11).

Reversals of the two synapomorphies just discussed that support the *E. aphroditois* clade are the synapomorphies holding the species of *Marphysa* and *E. insularis* together. Although in none of the examined *Marphysa* species the absence of the ventral pygidial cirri was codified, the genus *Marphysa* has been described as having either only dorsal pygidial cirri or both dorsal and ventral (Orensanz 1975). For this reason and the polymorphic condition of this character in *E. insularis* it will possibly not be a synapomorphy of this clade in other analyses. The absence of MxVI is at some point confusing as mentioned above. But its absence in *E. insularis* is consistent in all *Eunice* species without branchiae, which had their maxillary formula reported (Fauchald 1992a; Hartmann-Schröder & Zibrowius 1998; Nogueira *et al.* 2001). Although this clade is weakly corroborated by a synapomorphy most likely produced by a misrepresentation of variability and an absence, it is at least interesting that species with pedomorphic features were united in the same clade. Since combination of the presence of five prostomial appendages and the absence of the peristomial cirri in some

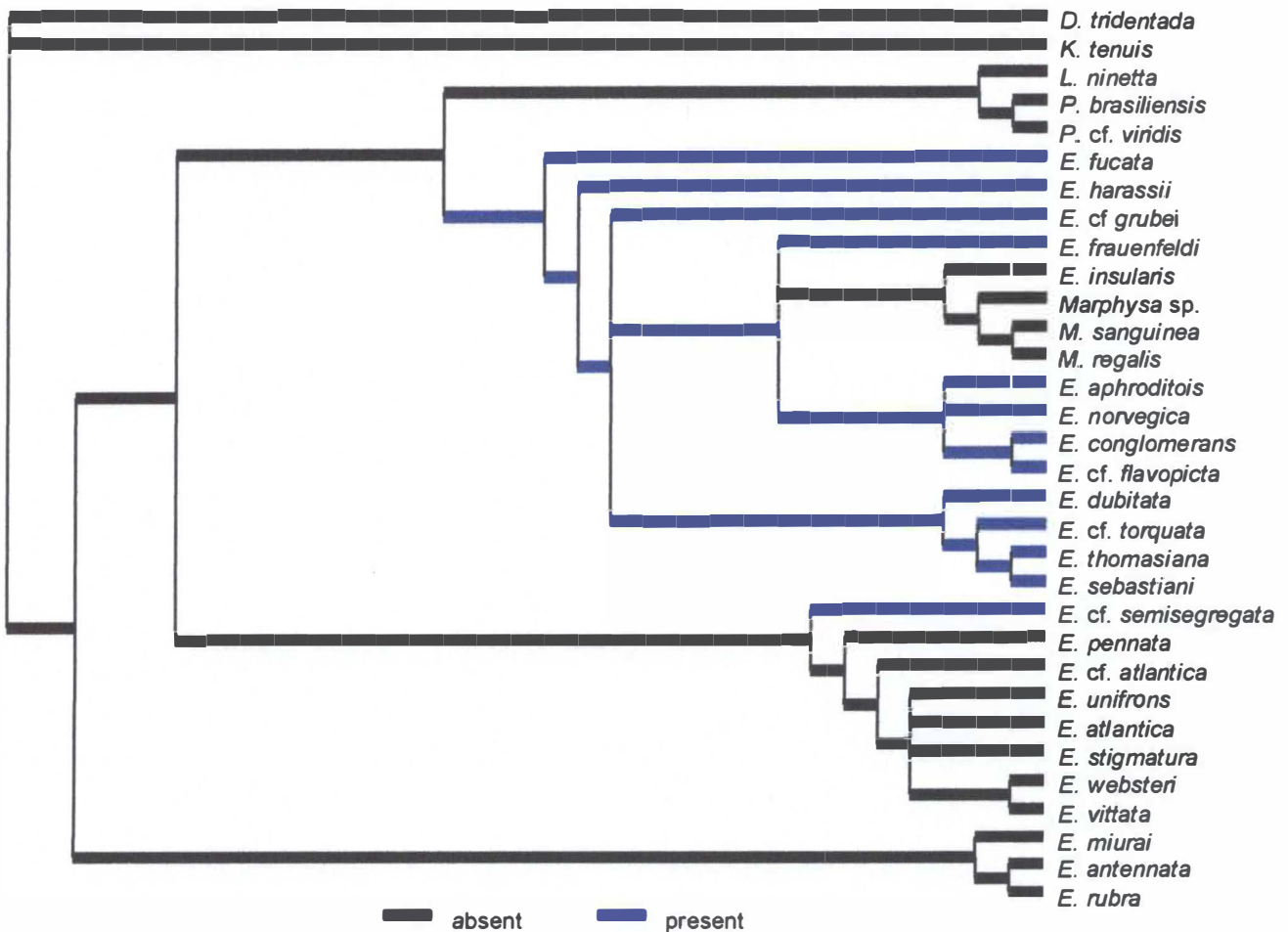


Fig. 10 Absence and presence of MxVI (character 18) along the strict consensus tree.

species of *Eunice* seem to be a juvenile tract (e.g. Nogueira *et al.* 2001), as well as the absence or presence of few branchial filaments (e.g. Giangrande 1989; Lu & Fauchald 1998), as happens in *E. insularis*.

The character holding the species of *Marphysa* together is the one used to differentiate it from *Eunice*: absence of peristomial cirri (Fauchald 1977). In the present phylogeny, the placement of *Marphysa* species within a clade of *Eunice* species showed that this character is not enough to differentiate these two genera. Besides, it is an absence and it is difficult to define clades just by them. Therefore, if this result remains in future analyses, *Marphysa* should be synonymized with *Eunice sensu stricto* in order to make this a monophyletic genus.

The character presence of spatula shaped pectinate chaetae, used for the first time in the present study, turn out to be an unequivocal character and one of the synapomorphies that support the clade *M. sanguinea-Marphysa regalis*. This kind of chaetae has also been reported to the species *Marphysa aenea* (Blanchard, 1849) in

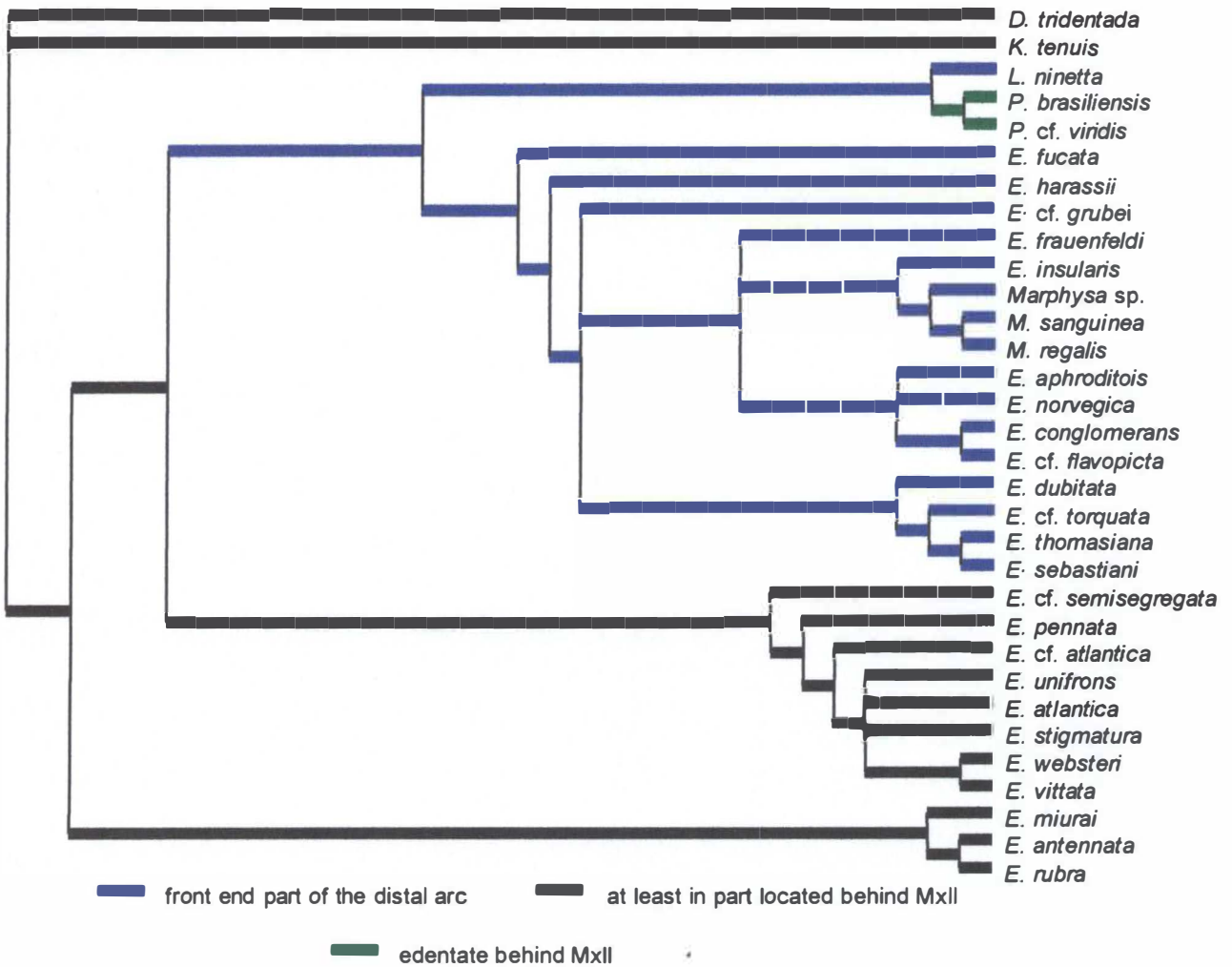


Fig. 11 Changes of MxIII (character 21) along the strict consensus tree.

Orensanz (1990). Since the monophyly of *Marphysa* is weakly corroborated by an absence, Orensanz (1990) suggested that this group is polyphyletic and considered the shape of pectinate chaetae, within other characters, as probable apomorphies of the monophyletic groups in which it possibly may be divided.

Other characters used for the first time in this study were features of the buccal apparatus. Just one of the six characters included in the analysis about this structure had been used before (character 22), but an additional state was added to it. Only some descriptions of species of Eunicidae include description of the jaws (maxillae and mandible). In 1885 McIntosh had already realized that the number of teeth in the maxillary plates have intraspecific variation, what was confirmed by Aiyar (1931), Hartman (1944) and Winsnes (1989). This and the necessity of specimen dissection to examine the jaws are probably the reasons for the low number of jaw descriptions, even

tough some authors (e.g. Hartman 1944; Nonato 1965; Carrera-Parra & Salazar-Vallejo 1998) have suggested that the buccal apparatus of the eunicids may have some important taxonomic information and it has a recognized importance on the distinction of some genera of the family Lumbrineridae (Orensanz 1973 after Carrera-Parra & Salazar-Vallejo 1998), close relative of the eunicids (Rouse & Fauchald 1997).

The characters about the buccal apparatus yielded good results, mainly on defining synapomorphies for the clade *Palola-Lysidice* and for both of these genera. Teeth in left MxIV present in less than half of the plate turn out to be an unequivocal character that is one of the synapomorphies corroborating the terminal clade *E. conglomerans-E. cf. flavopicta*. This kind of teeth distribution has been also registered at least in the species *Eunice notata* (Treadwell, 1921); *Eunice denticulata* sensu Treadwell, 1921 not Webster, 1884; *Eunice spongicola* (Treadwell, 1921); and *E. marconii* Nogueira *et al.*, 2001. These last three species are considered close to *E. conglomerans*.

Hanley (1986) and Miura (1987) recorded in *Eunice metatropos* Hanley, 1986 and *Eunice palauensis* Okuda, 1937, respectively, an uncommon trait for the Eunicidae, symmetric maxillary apparatus, feature normally asymmetric (Fig. 1) and considered invariable in descriptions of the family (e.g. Hartman 1944). These species seem to be close relatives based on the authors' description; both are present in Eastern seas – Australia and Japan. This and detailed descriptions of the buccal apparatus (e.g. Desiére 1967; Hartmann-Schröder 1967) suggest that perhaps some more information may be codified on it.

The genera *Palola* and *Lysidice* have been considered as close genera due to the curved mandibles (Orensanz 1990). Even though the mandibles of these genera were considered different states, in the present study this hypothesis of relationship was corroborated in the present phylogeny, since the arrangement of the states showed that the mandible of the genus *Lysidice* derived from the one on the genus *Palola*. That implies that the curved structure of their mandibles had the same origin, as suggested by earlier authors, and the present differences are latter divergences.

The hypothesis that the clade *Palola-Lysidice* is derived from species currently considered *Eunice* confirm Fauchald (1992a) suggestion that the genus *Palola* could fall within *Eunice*, as currently defined, and agrees with the ideas of pedomorphic

evolution of the genus *Lysidice* (e.g. Steiner 2000). This genus had its existence questioned by some authors (Salazar-Vallejo & Carrera-Parra 1998), since the presence of only three prostomial appendages and the absence of peristomial cirri, characters used to define the genus, are also present in juveniles of *Eunice* and *Marphysa* (e.g. Giangrande 1989; Aiyar, 1931). Its existence was supported by the description of sexually mature specimens (e.g. MacDonald 1857; Hofmann 1973; Miura 1977b) and by the presence of curved mandibles. The definition of *Palola* and *Lysidice* by apomorphies resulted from the present hypothesis of phylogeny (Appendix II) possibly confirm their status of monophyletic group as well as its generic status when considering the Linnaean Nomenclature. Characters states described for the genus *Nematonereis*, another genera of the family Eunicidae also considered as a pedomorphic taxon, in the consulted literature (e.g. Day 1967; Steiner 2000) are the same as in the examined specimens of *Lysidice*. Most likely, if the genus *Nematonereis* had been included in the analysis, it would have been grouped with *Lysidice* in a terminal clade and they would be separated only by the absence of the lateral antennae in *Nematonereis*.

The examined specimens of *L. ninetta* and *M. sanguinea* showed polymorphism for the character color of the subacicular hooks, which is a homoplasy in the present phylogeny. The color of these hooks may vary owing to size variation of the specimen and its placement along the body (Day 1967; Fauchald 1992a). These hooks are chaetae, hence its structure is composed by chitin fibers glued together by scleroprotein (Specht 1988, after Fauchald & Rouse 1997) and not much is known about the change of color of this kind of structure once it is fixated in formalin and preserved in ethanol, chemicals usually used in polychaetes. Day (1967) recommended caution when dealing with this character.

The color and the dentition of subacicular hooks have been considered as important features on the taxonomy of the family Eunicidae and mainly of the genus *Eunice* (e.g. Hartman 1944; Fauchald 1992a). Miura (1986) considered them conservative enough to suggest that they could be used to divide the genus *Eunice* in groups, perhaps correspondent to genera or subgenera. However, on the present hypothesis of phylogeny, all of these groups are paraphyletic. The distribution of branchiae also was shown not to be useful in the grouping of monophyletic clades in the

genus *Eunice* (Fig. 9). Therefore the groups defined by Hartman (1944) and Fauchald (1970) are assemblies of species by similarity, most likely without any evolutionary meaning (Fig. 5).

The distribution of branchiae is a homoplastic feature probably due to its adaptative characteristic. Its modifications may be a result of different requirements for more effective gas and ion exchange with minimum effort in diverse environments or habitats (Miura 1986). Branchial distribution and the amount of branchial filaments also change during ontogenesis (Fauchald 1992a). In the species *E. harassii* its development can also be influenced by the degree of contamination of the seawater (Walker 1977, after Winsnes 1989).

This study is a step towards a better understanding of the phylogeny of the genus *Eunice*. Its incompleteness allowed the results to yield just a general hypothesis of the outline of the evolutionary history of the genus, with some inconsistencies. Some other steps have to be taken in order to obtain a more stable hypothesis of phylogeny. Besides the inclusion of more species in the analysis, other characters that might have phylogenetic importance should be added and molecular data considered. Some sources of probable informative morphological characters could be ontogeny of species (Akesson 1967), internal anatomy (Fauchald & Rouse 1997) and electronic microscopy (e.g. Hayashi & Yamane 1994).

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Appendix II

Character-state changes along the cladogram and apomorphies of the clades. Internodes intervals are represented by the last node of the interval. Nodes correspond to those in Fig. 5. Character 9 is absent since it is uninformative. See next page for taxa labels and end of the table.

Node/ Taxon	1	2	3	4	5	6	7	8	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45												
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Taxa labels: T1- *Diopatra tridentata*; T2- *Kinbergomphus tenuis*; T3- *Eunice miurai*; T4- *Eunice antennata*; T5- *Eunice rubra*; T6- *Eunice cf. semisegregata*; T7- *Eunice pennata*; T8- *Eunice cf. atlantica*; T9- *Eunice atlantica*; T10- *Eunice unifrons*; T11- *Eunice stigmatura*; T12- *Eunice vittata*; T13- *Eunice websteri*; T14- *Eunice fucata*; T15- *Eunice harassii*; T16- *Eunice cf. grubei*; T17- *Eunice dubitata*; T18- *Eunice cf. torquata*; T19- *Eunice thomastana*; T20- *Eunice sebastiani*; T21- *Eunice frauenfeldi*; T22- *Eunice aphroditois*; T23- *Eunice norvegica*; T24- *Eunice conglomerans*; T25- *Eunice cf. flavopicta*; T26- *Eunice insularis*; T27- *Marphysa sp.*; T28- *Marphysa sanguinea*; T29- *Marphysa regalis*; T30- *Lysidice ninetta*; T31- *Palola brasiliensis*; T32- *Palola cf. viridis*.

Conclusões

A parafilia do gênero *Eunice sensu lato* foi confirmada. De acordo com a presente hipótese de filogenia, ele pode ser dividido em pelo menos dois grupos monofiléticos e os gêneros *Palola*, *Lysidice* e *Marphysa* – outros gêneros da família Eunicidae – estão incluídos nele. Estes dois grupos monofiléticos correspondem provavelmente aos gêneros *Eunice sensu stricto* Cuvier, 1817 e *Leodice* Lamarck, 1818, já que as espécies tipo destes, *Eunice aphroditois* e *Eunice antennata*, estão separadas em clados diferentes. O que diferencia estes dois gêneros, que foram sinonimizados anteriormente com base em plesiomorfias. Os grupos baseados na distribuição branquial, cor e denteção dos ganchos subaciculares, usualmente usados na divisão de *Eunice sensu lato*, são parafiléticos. Por isso não são grupos naturais e sim agrupamentos por similaridade, sem nenhum valor evolutivo aparente. A inclusão das espécies de *Marphysa* no clado que provavelmente corresponde ao gênero *Eunice sensu stricto* demonstrou que apenas a ausência do cirro peristomial não é suficiente para considerá-los gêneros diferentes.

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