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A phylogenetic analysis of the genus *Eunice* (Eunicidae, polychaete, Annelida)

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Species of *Eunice* are distributed worldwide, inhabiting soft and hard marine bottoms. Some of these species play significant roles in coral reef communities and others are commercially important. *Eunice* is the largest and most poorly defined genus in Eunicidae. It has traditionally been subdivided in taxonomically informal groups based on the colour and dentition of subacicular hooks, and branchial distribution. The monophyly of *Eunice* and of its informal subgroups is tested here using cladistic analyses of 24 ingroup species based on morphological data. In the phylogenetic hypothesis resulting from the present analyses *Eunice* and its subgroups are paraphyletic; the genus may be divided in at least two monophyletic groups, *Eunice s.s.* and *Leodice*, but several species do not fall inside these two groups. Most of the traditional characters used in the taxonomy of *Eunice* are homoplasies; however, characters used for the first time in this study, such as certain jaw characters and characters derived from a close examination of chaetal variation along the body, are promising sources of phylogenetic signal. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **150**, 413–434.

ADDITIONAL KEYWORDS: branchial distribution – Eunicida – jaw – Leodice – mandible – maxillae – phylogeny – subacicular hooks.

Eunice Cuvier, 1817 is the most species rich of the ten genera of the family Eunicidae, comprising around 220 species. It is distributed worldwide, but it is most common in shallow tropical waters (Fauchald, 1992). Species of *Eunice* inhabit soft and hard marine bottoms, many burrow into hard corals and calcareous algae or live in their crevices, and play significant roles in coral reef communities as bioeroders (Hutchings, 1986), but possibly also in assembling those communities (Roberts, 2005). *Eunice* includes some commercially important species used as bait in commercial and leisure fishing (Gambi *et al*., 1994). Sexually mature *Eunice* specimens have a large size range, varying from a few mm to 6000 mm in length (Fauchald, 1992), and both very large and very small species have been described without adequate knowledge of ontogenetic variation.

The taxonomy within *Eunice* is difficult because of the poor knowledge of ontogenetic and intraspecific variation of characters (Steiner, Nogueira & Amaral, 2002). In addition, many species have been described based on incomplete specimens (Miura, 1986), and several species are known just from type specimens (Fauchald, 1992). Furthermore, definition of the genus is problematic as it is based on the following plesiomorphies: presence of three antennae, a pair of palps, a pair of peristomial cirri, and a complete set of chaetal types (limbate, pectinate, aciculae, compound, and subacicular hooks) (Orensanz, 1990); features

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that are also present in the well-defined eunicid genus *Euniphysa* (Lu & Fauchald, 2000) and in another eunicean family, Onuphidae.

The poor definition of *Eunic*e and the insufficient understanding of character variation led to the description of genera such as *Leodice* Lamarck, 1818, and *Nicidion* Kinberg, 1865, both of which were later considered junior synonyms of *Eunice*. *Leodice*, named for *Leodice antennata* Lamarck, 1818, was not clearly differentiated from *Eunice*, and both names were used interchangeably through the first third of the 20th century (Hartman, 1944). *Nicidion* included *Eunice* species lacking branchiae, a character not considered acceptable at either the generic (Hartman, 1944) or subgeneric levels (Fauchald, 1970) because it is highly variable, and individuals within the same '*Nicidion*' species may or may not lack branchiae.

Currently *Eunice* is subdivided into taxonomically informal groups based on colour and dentition of subacicular hooks (Ehlers, 1868; Hartman, 1944) and branchial distribution patterns (Fauchald, 1970). Miura (1986) suggested that the *Eunice* informal groups based on the characteristics of subacicular hooks could correspond to genera or subgenera; he also suggested that the presence of few branchial filaments present along the whole body was the ancestral branchial distribution pattern in *Eunice*.

The monophyly of *Eunice* is currently disputed. Studies on the phylogeny of the order Eunicida using molecular data resulted in paraphyletic *Eunice* and Eunicidae (Struck, Westheide & Purschke, 2002; Struck, Purschke & Halanych, 2006). Fauchald (1992) attempted a phylogenetic analysis of *Eunice* based on morphological features of the type specimens to test the relationships within the genus. His results were generally inconclusive and the only consistent clade in all trees was a group that included all species with yellow hooks.

The purposes of the present study are to test the monophyly of the genus *Eunice*, as well as of its informal groups, based on colour and dentition of the subacicular hooks and branchial distribution patterns, and to provide a hypothesis of phylogeny for *Eunice* that can be used as a framework for future studies on *Eunice* and Eunicidae in general. For this we used an expanded morphological character set, compared with the one used by Fauchald (1992), and better preserved material than represented by the types.

MATERIAL AND METHODS

Taxonomic sampling

We examined 24 *Eunice* species (Table 1) representing all taxonomically informal groups (Table 2) and the morphological diversity within these. Outgroup taxa to test the monophyly of *Eunice* and/or root the phylogenetic analyses were species of other eunicid genera, *Marphysa*, *Palola*, and *Lysidice*, members of the other four best known families of the order Eunicida, Onuphidae, Dorvilleidae, Lumbrineridae, and Oenonidae, and members of Amphinomida, a probable sister group to Eunicida (Rouse & Fauchald, 1997; but see Struck *et al*., 2006 for a discussion) (Table 3).

Each specimen was examined under stereo and compound microscopes. Specimens were dissected as described by Day (1967) in order to code the characters of the buccal apparatus. To determine chaetal variation along the body, six parapodia of each specimen were examined, one from the first and last 2.5% (determined by number of chaetigers) of the body, respectively, and four from the median chaetiger of each quarter of the body. We quantified branchial distribution as the percentage of continuous chaetigers in which branchiae are present, as used by Fauchald (1992).

Specimens

The material examined in this study came from the following institutions: ECOSUR, Colecion de Referencia ECOSUR, Chetumal, Mexico; IBUFRJ, Departamento de Zoologia, Instituto de Biologia, UFRJ, Rio de Janeiro, Brazil; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; SMNH, Swedish Museum of Natural History, Stockholm, Sweden; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Phylogenetic analyses

We coded two different character matrices, one with composite characters (composite analyses) and another with reductive characters (reductive analyses) (*sensu* Strong & Lipscomb, 1999), to check the sensitivity of our data set to the coding methods, which differ in the number of inapplicable characters and in the underlying assumptions about primary hypotheses of homology.

A matrix of 59 composite (74 reductive; Appendix 1) morphological characters coded for 37 taxa (24 *Eunice* ingroup taxa plus 13 outgroup taxa) (Table 4; Appendix 2) was analysed under maximum parsimony optimization criteria. Eleven characters (20 in the reductive matrix) are uninformative autapomorphies or polymorphisms; however, these were included in the analyses because they have been observed in other species of the appropriate genus or family (J. Zanol & K. Fauchald, pers. observ.) not included here because of the limited taxonomic sampling. Alternatively, some of these characters represent polymorphic variation that is uninformative because of the way current analytic

Table 1. Ingroup taxa examined in the present study (see Table 2 for a description of the groups)

Group	Species	Number, collection, and locality of specimens examined
A1	*Eunice pennata* (Müller, 1776)	2 (USNM 97393) from Norway, Storskjan, Oslofjorden
		1 (USNM 3862) from USA, 42°01′N 68°01′W
	Eunice cf. *semisegregata* Fauchald, 1969	2 (USNM 22436) from USA, California, 33°49′N 119°24′W
	Eunice websteri Fauchald, 1969	1 (USNM 51134) from USA, North Carolina
		1 (USNM 090042) from USA, Florida
A2	*Eunice harassii* Audouin & Milne Edwards, 1833	1 (IBUFRJ 341) from UK, Plymouth
		1 (IRSNB 10910) from 24°13′N 15°44′W
		1 (SMNH 28277) from UK
B1	*Eunice dubitata* Fauchald, 1974	2 (IBUFRJ 342) from Norway, Rödberg
B2	*Eunice aphroditois* (Pallas, 1788)	2 (USNM 96453) from Indonesia
		1 (USNM 100202) from Japan, Kamagawa Prefecture
	Eunice denticulata Webster, 1884	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
	Eunice frauenfeldi Grube, 1866	1 (IBUFRJ 347) from Brazil
	Eunice cf. *grubei* Gravier, 1900	1 (SMNH 28294) from Western Australia
	Eunice norvegica (Linnaeus 1767)	3 (IBUFRJ 348) from Norway, Rödberg
	Eunice cf. *flavopicta* Izuka, 1912	1 (IBUFRJ 349) from Papua New Guinea, Mandang
	Eunice thomasiana Augener, 1922	1 (IBUFRJ 350) from Brazil, Bahia, 18°01′S 35°53′W
	Eunice cf. *torquata* Quatrefages, 1866	3 (IBUFRJ 351) from Panama, Bocas Del Toro
B3	*Eunice cariboea* Grube, 1856	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
C1	*Eunice* cf. *atlantica* Kinberg, 1865	1 (SMNH 28301) from Madagascar, Amborovy
	Eunice atlantica Kinberg, 1865	1 (IBUFRJ 356) from Brazil, Bahia, Salvador
		1 (IBUFRJ 357) from Brazil, Bahia, Salvador
		1 (IBUFRJ 358) from Brazil, Bahia, Salvador
	Eunice miurai Carrera-Parra & Salazar-Vallejo, 1998	1 (IBUFRJ 359) from Brazil, 00°28′N 45°32′W
	Eunice unifrons (Verrill, 1900)	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
	Eunice vittata (Chiaje, 1829)	2 (IRSNB 10910) from Senegal, 14°40′N 16°15′W
C2	*Eunice antennata* (Lamarck, 1818)	3 (USNM 96434) from Red Sea, Gulf of Suez, Zeit Bay
	Eunice rubra Grube, 1856	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
	Eunice stigmatura (Verrill, 1900)	1 (IBUFRJ 368) from Brazil, 26°46′S 40°05′W
		1 (IBUFRJ 369) from Brazil, 22°55′S 41°13′W
		1 (IBUFRJ 370) from Brazil, 19°45′S 39°31′W
D	*Eunice fucata* Ehlers, 1887	1 (IBUFRJ 371) from Brazil
		1 (IBUFRJ 372) from Brazil
		1 (IBUFRJ 373) from Brazil, 20°36′S 35°51′W
	Eunice sebastiani Nonato, 1965	2 (IBUFRJ 374) from Brazil, São Paulo, São Sebastião

Table 2. Taxonomically informal groups employed in the subdivision of the genus *Eunice* (adapted from Hartman, 1944; and Fauchald, 1970), used in the present study in the choice of the species to be examined. Branchial distribution was quantified as the percentage of continuous chaetigers in which branchiae is present, as used in Fauchald (1992)

Groups	Characteristics	Total of species*	Number of species in this study
A1	Subacicular hooks light bidentate. Branchiae present on less than 55% of the body.	27	3
A2	Subacicular hooks light bidentate. Branchiae present in most of the body (more than 65%).	10	1
B1	Subacicular hooks dark bidentate. Branchiae present on less than 55% of the body.	22	1
B2	Subacicular hooks dark bidentate. Branchiae present in most of the body (more than 65%).	94	8
B3	Subacicular hooks dark bidentate. Branchiae absent.	9	1
C1	Subacicular hooks light tridentate. Branchiae present on less than 55% of the body.	34	5
C2	Subacicular hooks light tridentate. Branchiae present in most of the body (more than 65%).	24	3
D	Subacicular hooks light to dark unidentate.	8	2
	Total	228	24

*Approximate total.

Table 3. Outgroup taxa examined in the present study

Family	Species	Number, collection, and locality of specimens examined
Amphinomidae	*Amphinome rostrata* (Pallas, 1766)	1 (USNM 51511) from Trinidad and Tobago, Matura Beach
Oenonidae	*Oenone fulgida* (Savigny, 1818)	1 (USNM 53751) from, USA, Florida, Conch Key
Lumbrineridae	*Lumbrineris fragilis* (Müller, 1776)	1 (USNM 30097) from USA, Massachusetts
	Lumbrineris latreille Audouin & Milne Edwards, 1834	1 (USNM 53018) from USA, North Carolina
Dorvilleidae	*Dorvillea sociabilis* (Webster, 1879)	1 (USNM 33830) from USA, Virginia
Onuphidae	*Diopatra tridentata* Hartman, 1944	1 (IBUFRJ 375) from Brazil, Bahia
	Kinbergonuphis tenuis (Hansen, 1882)	1 (IBUFRJ 376) from Brazil, Bahia
Eunicidae	*Palola brasiliensis* 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
	Palola cf. *viridis* Gray, in Stair, 1847	1 (SMNH 28292) from Western Australia
	Lysidice ninetta Audouin & Milne Edwards, 1833	1 (ECOSUR Euni-2) from Mexico
		1 (IBUFRJ 383) from France, Dinard
	Marphysa sanguinea (Montagu, 1807)	3 (IBUFRJ 377) from UK, Plymouth Sound
	Marphysa cf. *sanguinea* (Montagu, 1807)	1 (IBUFRJ 378) from Brazil, Paraná
	Marphysa cf. *atlantica* Kinberg, 1865	1 (IBUFRJ 379) from Brazil, Rio de Janeiro, 22°55′S 44°10′W
	Marphysa sp.	3 (IBUFRJ 380) from Brazil, Espírito Santo

Table 4. Composite coding character matrix

Species/characters	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	555555555 123456789
Amphinome rostrata	0001???311	1101100200	0---------	-0-020214-	4010000001	---0----0
Oenone fulgida	01000---11	2000--3001	1010-44000	-11310100-	0--0000000	1102101014
Lumbrineris fragilis	00000---00	---0--3101	1121133100	010100100-	0--0000000	0000----1
Lumbrineris latreille	01000---00	---0--2101	1121133100	010100200-	0--0002000	1100----1
Dorvillea sociabilis	01000---012	1201104101	200?-?????	-11011103-	0--0001100	1100----1

Table 4. *Continued*

Species/characters	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	555555555 123456789
Diopatra tridentata	00002--011	0121121011	1221011101	11111?0021	3101010000	110210101
Kinbergonuphis tenuis	21002--111	0121121011	1221011101	11111?0021	2111010000	110210101
Lysidice ninetta	0000101-11 1	1110--1101 2	1221001101	0313120121 2	0--1001100	000200001 11 11
Palola brasiliensis	0000101211 11 2	0111111111 2	1221022101	0212120220	1220001100	0100----1
Palola cf. *viridis*	0000102011	0111112111	1221022101	0212120220	1220001100	0100----1
Marphysa sp.	0100100111 1	0111111101 2	1221001101	1111110221	2211001100	000201001
Marphysa sanguinea	1000101111 1	0111112101	1221001101	1111110211	2211100010	000200001 11
Marphysa cf. *atlantica*	1010101111	0111112101	122100l1?1	1111100211	2211101100	000201001
Eunice aphroditois	0100102111 1 1	0011011111 1 1	1221000111	1111110211 2	2111001100	000201000 1 1
Eunice denticulata	0100100111 2	0111011111 1 2	1221000111	1111110110 2222	2211001100	000201001 1
Eunice cf. *flavopicta*	0100102111	0111112111	1221000111	1111110110	2111001100	000201000
Eunice norvegica	0100102111 1	0111112111	1221001111	1111110221	2111001100	000201000 1
Eunice cariboea	0000100111 1 1 2	0111111111 2	1221001101	1111100221	0--1001100	000201000 1
Eunice frauenfeldi	0100101011	0111111111	1221001111	1111110221	2211001100	000201000
Eunice cf. *grubei*	010010?011	?111112111	1221001111	1111120221	2011001100	010201000
Eunice thomasiana	0100101011	0211211111	1221001111	1111112121	2111001100	010201000
Eunice dubitata	0100101011	0111112111	1221001111	1111112121	2001001100	010201000
Eunice cf. *torquata*	0000101011 1	0211212111	1221001111	1111112121	2011001100	010201000
Eunice fucata	0100101011 2	0111111111 2	1221001111	1111110221	2101001100	010101100
Eunice sebastiani	0100101111	0?11?12111	1221001111	1111112111	2111001100	010111110?
Eunice harassii	0100101011 12	0111111111 2	1221001111	1111110121 22	2111001100	110200100
Eunice antennata	0100101011 1	0211211111 2	1221011101	1111110021 2	2111001200	110300101
Eunice rubra	0100100011 111 2	0211211111	1221011101	1111110121 22	2111001200	110300101 1
Eunice miurai	0100101011	0211211111	1221011101	1111112121	2101001200	110300100 1
Eunice websteri	0000112011 1 1	0111111111	1221011101	1111110221	2001001100	110210101
Eunice vittata	0100112011	0111111111	1221011101	1111110221	2001001100	110310101
Eunice atlantica	0100110011 2	0111112111	1221011101	1111110221	2001001100	110300101
Eunice unifrons	0100112011 1	0111111111 2	1221011101	1111110221	2001001100	110300101
Eunice pennata	0100100011	0111112111	1221011101	1111110221	2001001100	110200101
Eunice cf. *semisegregata*	0100101011 1	0111112111	1221011111	1111110111 2 2	2001001100	110200101
Eunice cf. *atlantica*	0000100011	0111112111	1221011101	1111100221	2001001100	110300101
Eunice stigmatura	0100102011 1	0111112111	1221011101	1111110221	2011001100	110300101

programs treat polymorphic characters (Wiens, 2000); however, information about this variation is certainly useful for understanding, for example, allometries caused by growth and other kinds of variation.

Trees were rooted using the outgroup method. Characters were treated as unordered and equally weighted; polymorphic characters were coded as such. The tree search was heuristic, using the option TBR (tree bisection and reconnection) + TBR in NONA (Goloboff, 1999). Analyses started with a stepwise addition tree with taxa randomly added in 2000 replicates and 100 trees held on each step of the TBR. During the search branches were collapsed when the minimum branch length was zero.

Parsimony analyses results were summarized in strict, 50% majority rule and Adams consensus of all most parsimonious trees. Branch support was calculated using bootstrap (Felsenstein, 1985) (2000 replicates, ten search replicates and max TBR) and Bremer support (Bremer, 1988). We used Winclada (Nixon, 2002) and NONA (Goloboff, 1999) to construct the matrices, run parsimony and bootstrap analyses and examine trees. Bremer support was calculated using PAUP*4.0b10 (Swofford, 2001) and TreeRot (Sorenson, 1999). We used ACCTRAN optimization to examine character evolution, but only unambiguous optimized characters (those that have the same optimization under ACCTRAN or DELTRAN) are considered as support synapomorphies for clades.

In order to determine how much longer trees are when traditional taxonomically informal groups (Table 2), *Eunice*, and Eunicidae are constrained as monophyletic, we ran additional parsimony analyses (using the composite matrix and the same settings as described above) constraining these groups as monophyletic.

DESCRIPTION OF CHARACTERS

Only composite characters are described here (see Appendix 1 for a list of reductive characters). Uninformative characters are underlined.

1. Shape of cross section of body: 0, circular; 1, dorsoventrally flattened; 2, ventrally convex.
2. Body shape: 0, cylindrical, abruptly tapering anteriorly and posteriorly; 1, evenly tapering from anterior-median chaetigers.
3. Relative width and length of chaetigers: 0, at most ten times wider than long; 1, more than ten times wider than long.
4. Posterior extension of prostomium (caruncle): 0, absent; 1, present.
5. Frontal lips (*sensu* Paxton, 1998): 0, frontal edge entire; 1, separated frontally by a narrow notch (Fig. 1A–C); 2, separated frontally by a distinct space (Fig. 1D).
6. Frontal lips separated by a narrow notch anteriorly: 0, round (Fig. 1A, B); 1, truncate (Fig. 1C). This character refers to the shape of the anterior end of the frontal lips in dorsal view of the specimen.
7. Frontal lips separated by a narrow notch, dorsally: 0, inflated (Fig. 2A); 1, flat (Fig. 2B); 2, dimpled (Fig. 2C). This character refers to the dorsal shape of the frontal lip in frontal view of the specimen. Characters 6 and 7 are linked to character state 1 of character 5.
8. Arrangement of prostomial appendages: 0, antennae and palps evenly spaced (Fig. 1C, D); 1, median antenna isolated by a gap from the other antennae and palps (Fig. 1A); 2, palps isolated by a gap from the antennae (Fig. 1B); 3, head appendages on conspicuously different regions of the prostomium, median antennae on the caruncle.
9. Median antennae: 0, absent; 1, present.
10. Lateral antennae: 0, absent; 1, present.
11. Antennal styles: 0, digitiform, tapering, or clavate (Fig. 3A–C); 1, medially inflated (fusiform) (Fig. 3D); 2, button shaped (Fig. 3E). Fauchald (1992) distinguished digitiform, tapering, and clavate states; further study has shown that there is a continuous gradation among these 'states' making differentiation impossible. Hartman (1944) and Miura (1977) suggested that the different shapes of styles are of little taxonomic significance.

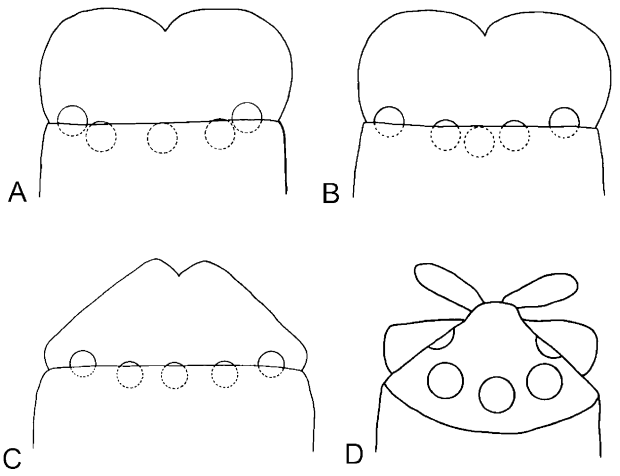

Figure 1. Schematic drawing of the dorsal view of the prostomium and anterior end of peristomium; circles and semicircles represent the arrangement of prostomial appendages (antennae and palps). A, round frontal lips separated by a narrow notch, median antennae isolated by a gap from the other antennae and palps. B, round frontal lips separated by a narrow notch, palps isolated by a gap from the antennae. C, truncate frontal lips separated by a narrow notch, antennae and palps evenly spaced. D, frontal lips separated by a distinct space, antennae and palps evenly spaced.

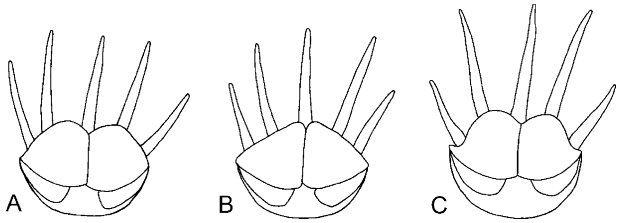

Figure 2. Schematic drawing of the frontal view of specimens that have frontal lips separated by a narrow notch. A, frontal lips dorsally inflated. B, frontal lips dorsally flat. C, frontal lips dorsally dimpled.

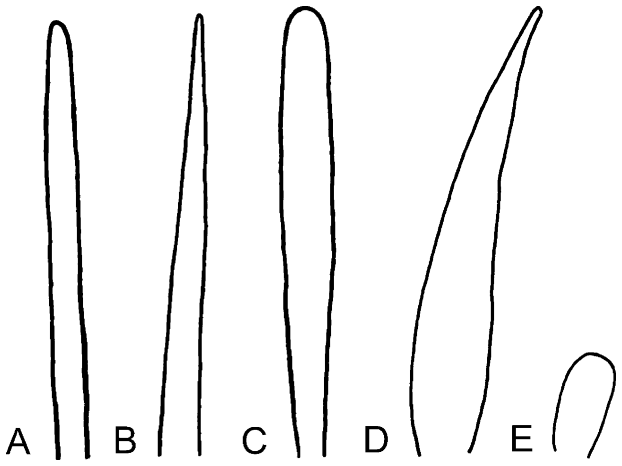

Figure 3. Schematic drawing of the shape of prostomial appendages. A, digitiform. B, tapering. C, clavate. D, fusiform. E, button shaped.

12. Articulations of antennal styles: 0, absent; 1, short or long cylinders (Fig. 4A); 2, moniliform (Fig. 4B). In many specimens the styles are strongly wrinkled and distinction between wrinkles and true articulations may be difficult (Day, 1967 e.g. *Marphysa fragilis* Treadwell, 1911; *Eunice mucronata* Moore, 1903 in Fauchald, 1992). Styles were considered truly articulated only if they had at least one complete groove visible on all sides of the style. When articulations were present along the whole style, scoring was based on the shape present in the basal–median region of the style.

13. Antennal ceratophore: 0, absent; 1, short, usually ring-shaped; 2, relatively long, usually articulated. Shape (character 11), articulations (character 12), and ceratophores (character 13) of median and lateral paired antennal styles are coded in the same character because the two kinds of antennae do not appear to be morphologically independent. The presence of both kinds of antennae is a clearly independent feature, but they are always of the same kind in these characters when both are present.

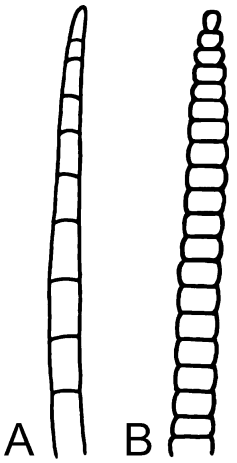

Figure 4. Schematic drawing of the shape the articulations of prostomial appendages. A, short or long cylinders. B, moniliform.

14. Palpal styles: 0, absent; 1, digitiform, tapering, or clavate (Fig. 3A–C). We considered the palps as the missing prostomial appendages in *Lysidice ninetta* Audouin & Milne Edwards, 1833 and *Oenone fulgida* Savigny, 1818. Antennae and palps used to be considered as the same structures (e.g. Chamberlin, 1919; Treadwell, 1921), and the nature of the missing appendages in the genera *Lysidice* and *Nematonereis*, as well as in members of the family Oenonidae, was not a concern. Orrhage (1995) demonstrated that the innervation of the palps differed from that of the three antennae, thus corroborating an idea first put forward by Binard & Jeener (1928) of separating the five head appendages in *Eunice* into three antennae and an outer pair of palps (called AI in Fauchald, 1992). In the genus *Lysidice* in which only three head appendages are present it is still not clear how these should be considered in relation to the appendages present in other eunicids. Here the lateral appendages are considered antennae, because of their placement between the eyes on the posterior region of the prostomium. However, Steiner (2000) considered the paired appendages in the specimen of *L. ninetta* she examined as palps, because of their position in front of the eyes.

15. Palpal styles articulations: 0, absent; 1, short or long cylinders (Fig. 4A); 2, moniliform (Fig. 4B).

16. Palpophores: 0, absent; 1, short, usually ring-shaped; 2, relatively long, usually articulated.

17. Peristomial ventrolateral lips: 0, absent; 1, set off by distinct grooves; 2, visible only as elevated surfaces; 3, scoop shaped; 4, medially short, about half as long as lateral side of the peristomium.

18. Peristomium: 0, a single ring; 1, two rings distinct at least dorsally; 2, reduced to region around the mouth.

19. Peristomial cirri: 0, absent; 1, present.
20. Mouth: 0, extending to the ventral side of anterior chaetigers; 1, restricted to peristomium.
21. Number of rows of maxillary plates: 0, absent; 1, one pair; 2, two or more pairs.
22. Calcium carbonate mineralzing jaws: 0, absent; 1, calcite; 2, aragonite.
23. Maxillary carrier: 0, ctenognath; 1, prionognath; 2, labidognath. We describe the shape of the maxillary carriers using the terminology generally used to group the jaws. This is because of both the debate about the ctenognath carrier (e.g. Paxton, 2004) and the consistent shape of the carriers in prionognaths and labidognaths (Colbath, 1989). Prionognath carriers are narrow, many times narrower than the posterior end of maxillae I (MxI), longer than the remaining maxillary apparatus anterior to it, not covered by muscles, and not attached to MxI. Labidognath carriers are wide, with the anterior end almost as wide as the posterior end of MxI, narrowing towards the posterior end, never longer than the remaining jaw apparatus, covered dorsally by a thin muscle layer, and attached to MxI.
24. MxI: 0, dentate; 1, fang shaped.
25. Fang shaped MxI: 0, facing each other; 1, facing dorsal side of the body.
26. Shape of MxIII: 0, dentate, front end part of distal arc with left MxIV (Fig. 5A–G); 1, dentate, at least in part located behind MxII (Fig. 5B); 2, edentate, behind MxII (Fig. 5D, E); 3, dentate, triangular; 4, dentate, with teeth arranged anterior to posterior, most anterior longest. Both Orensanz (1990) and Fauchald (1992) suggested that the shape of MxIII and its position in relation to other maxillae could be taxonomically informative.
27. Left MxIV: 0, wider than long with teeth on less than half of the plate, often only two teeth present (Fig. 5A); 1, wider than long with teeth on more than half of the plate, always more than two teeth present (Fig. 5B, C, F); 2, longer than wide often with just one tooth (Fig. 5D, E); 3, triangular, edentate, or with few teeth at the tip; 4, teeth decreasing in size from anterior to posterior, anteriormost tooth longest. The width and length of MxIV are defined here, respectively, as the axis in which it is attached to the body and the axis that it projects from the attachment into the lumen of the pharyngeal bulb.
28. MxV: 0, fang shaped; 1, plate like, a small tooth may be present.
29. MxVI: 0, absent; 1, present (Fig. 5A).
30. Right MxIII: 0, present; 1, absent.
31. Relative length of labidognath maxillary carrier: 0, longer than half the length of MxI; 1, shorter than half the length of MxI.
32. Mandibles: 0, absent; 1, flat (Fig. 6A); 2, strongly curved, forming an open scoop, plates fused anteriorly, anterior end strongly calcified (Fig. 6B, C); 3, curved, plates separated in a V shape at the anterior end, not strongly calcified (Fig. 6D, E). Although the mandibles of both *Lysidice* and *Palola* are curved, we prefer to consider them as different character states, because of the obvious differences between them, instead of assuming that the presence of the curved state is a homology. In addition to the differences described above, in *Palola* the strongly calcified anterior end is present beyond the organic matrix, whereas in *Lysidice* calcification closely follows the matrix.
33. Mandibles: 0, fused medially; 1, attached by ligaments.
34. Placement of the muscle fibre complex F1 + F2 (Desière, 1967) on the pharyngeal bulb: 0, absent; 1, posterior to mandible carriers (Fig. 7A); 2, above mandible carriers (Fig. 7B); 3, between mandible carriers (Fig. 7C).
35. Notopodia: 0, absent; 1, reduced to notopodial cirri; 2, complete chaetal lobe.
36. Neuropodia in mid-body distally: 0, round; 1, truncate; 2, pointed.
37. Neuropodial prechaetal lobes in mid-body: 0, absent; 1, longer than acicular lobes; 2, about as long as acicular lobes.
38. Neuropodial postchaetal lobes in mid-body: 0, longer than acicular lobes; 1, about as long as acicular lobes; 2, shorter than acicular lobes.
39. Ventral cirri: 0, absent; 1, tapering or digitiform in first few chaetigers, thereafter basally inflated; 2, tapering or digitiform in anterior and posterior chaetigers, basally inflated in median chaetigers; 3, digitiform, bases not inflated anywhere along the body; 4, tapering, bases not inflated anywhere along the body.
40. Shape of the inflated region of ventral cirri: 0, ventral ridge; 1, scoop shaped, rounded.
41. Shape of the branchiae: 0, absent; 1, single filaments; 2, filaments linearly arranged; 3, spiraled; 4, bushy. In both pectinate and palmate branchiae filaments are linearly arranged on a stem. The difference between these shapes is in the relative length between the stem and filaments (Fauchald, 1992); this may be difficult to distinguish as an almost continuous variation between extremes may be present; consequently, character state 2 unites both pectinate and palmate branchiae.
42. Branchiae start: 0, on chaetiger 3; 1, between chaetigers 4 and 9; 2, start late (after chaetiger 10).
43. Branchial distribution: 0, mostly limited to the first third of the body (present on less than 55% of the body segments); 1, in most of the body (present on more than 65% of the body); 2, mostly limited to the second third of the body (present on less than 55% of the body segments). Percentages refer to number of chaetigers in which branchiae are continuously present in relation to the total number of chaetigers in the body.

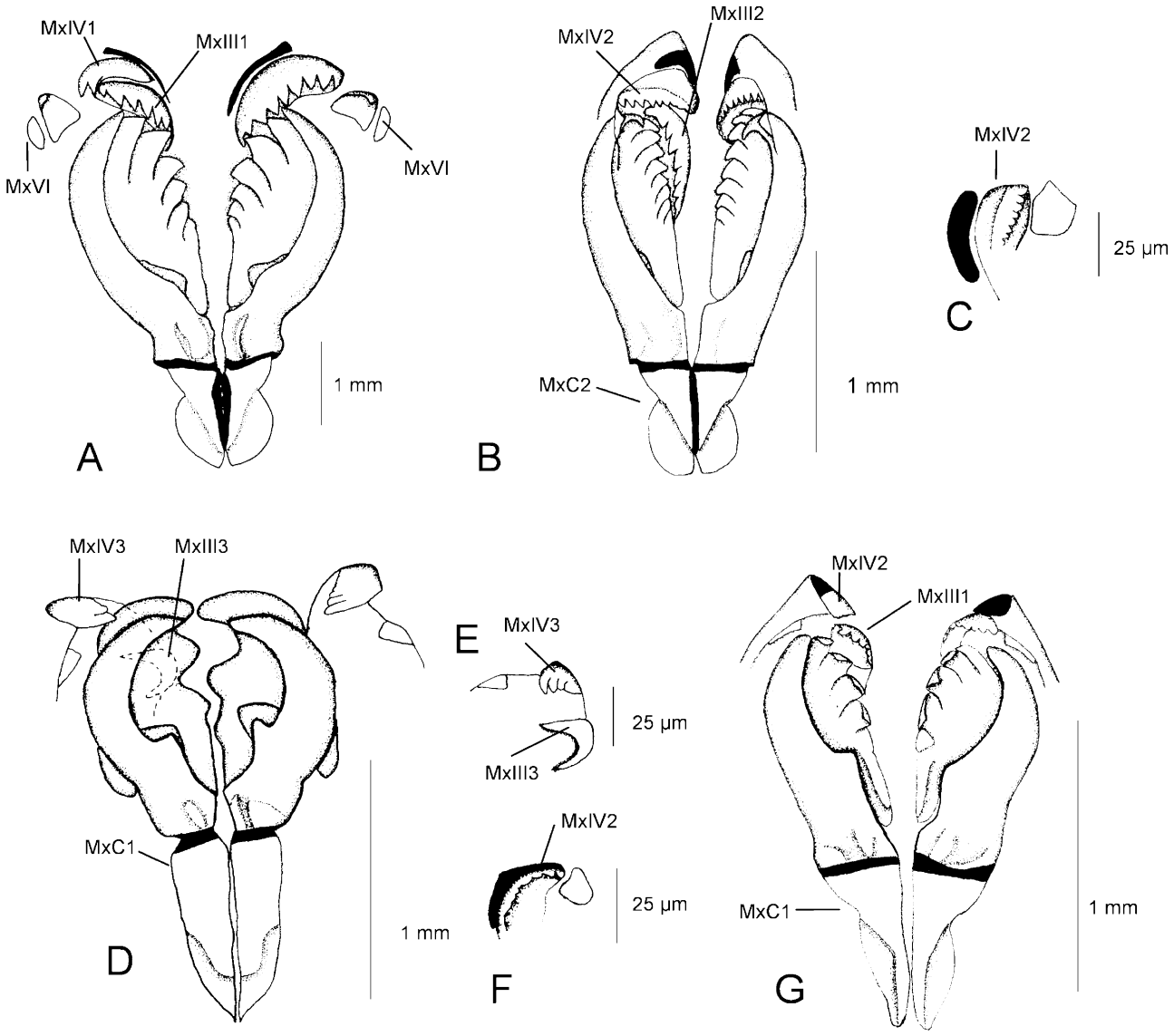

Figure 5. Maxillae. A, *Eunice denticulata* Webster, 1884 dorsal view. B, C, *Eunice rubra* Grube, 1856 dorsal view, and detail of maxillae IV (MxIV) and MxV. D, E, *Palola brasiliensis* Zanol, Paiva & Attolini, 2000 dorsal view, and detail of MxIII, MxIV, and MxV. F, G, *Lysidice ninetta* Audouin & Milne Edwards, 1833 detail of MxIV and MxV, and dorsal view. MxIII1, front end of MxIII as part of the distal arc; MxIII2, MxIII at least in part located behind MxII; MxIII3, MxIII edentate behind MxII; MxIV1, MxIV with teeth in less than half of the plate; MxIV2, MxIV with teeth in more than half of the plate; MxIV3, MxIV longer than wide, most of the time just with one tooth; MxVI, maxillae VI; MxC1, maxillary carrier greater than half of MxI; MxC2, maxillary carrier smaller than half of MxI.

44. Narrow, long pectinate chaetae: 0, absent; 1, present.
45. Spatula-shaped pectinate chaetae (short, wider than acicula with wide teeth): 0, absent; 1, present (Fig. 8A, B). When present these are usually found in the middle and posterior regions of the body.
46. Pseudocompound falcigers or spinigers: 0, absent; 1, present in a limited number of anterior chaetigers.
47. Distal end of compound falcigers (present in most of the body): 0, absent; 1, bidentate; 2, multidentate.
48. Distal ends of compound falcigers in the 2.5% posteriormost chaetigers: 0, absent; 1, all bidentate; 2, bi- and tridentate. Percentage refers to total number of chaetigers present.
49. Compound spinigers: 0, absent; 1, present.
50. Calcareous chaetae: 0, absent; 1, present.

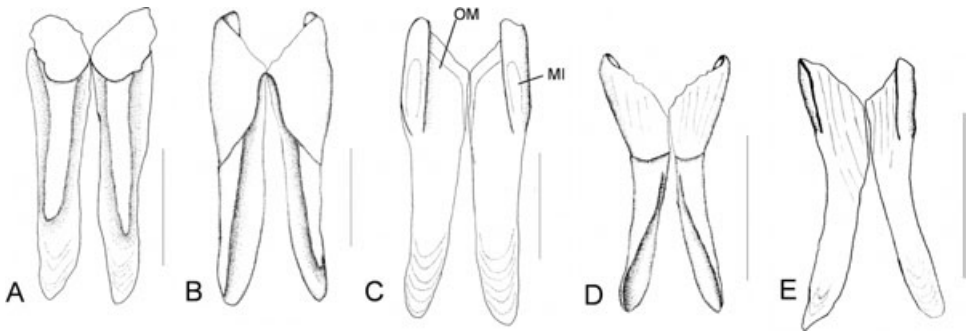

Figure 6. Mandibles. A, *Eunice rubra* Grube, 1856 ventral view. B, C, *Palola brasiliensis* Zanol, Paiva & Attolini, 2000 ventral, and dorsal views. D, E, *Lysidice ninetta* Audouin & Milne Edwards, 1833 ventral, and dorsal views. MI, muscle insertion; OM, outline of the organic matrix. Scale bars = 1 mm.

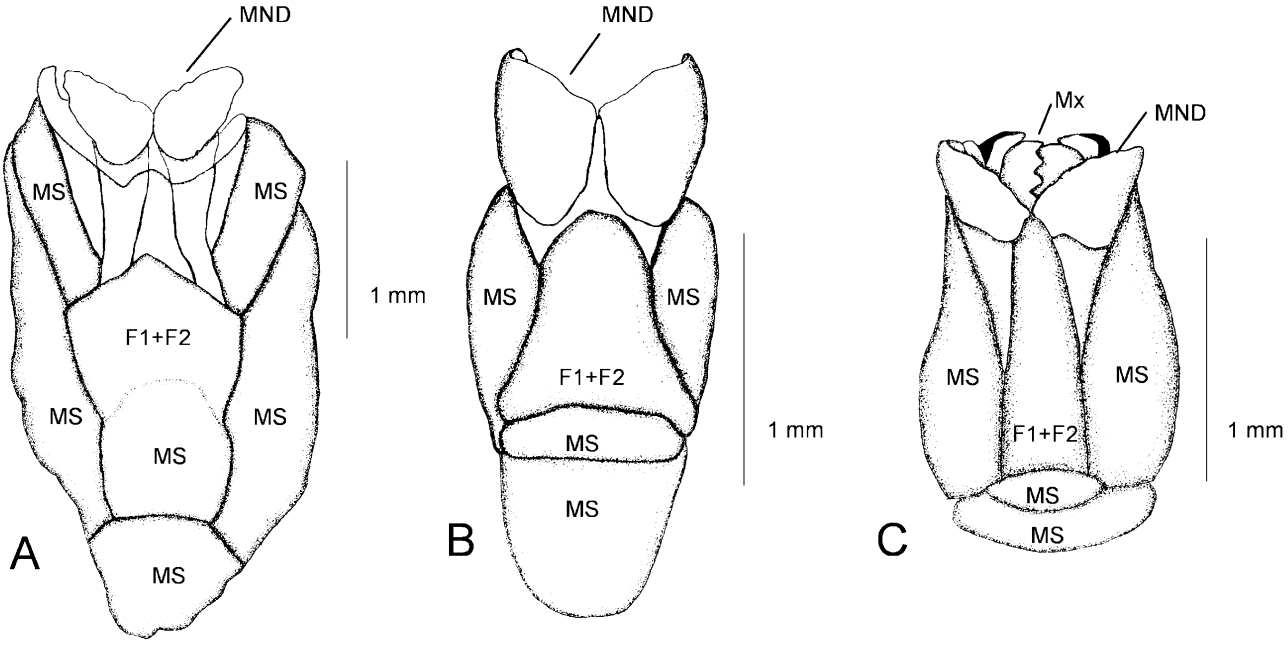

Figure 7. Pharyngeal bulb musculature, ventral view. A, *Eunice* cf. *torquata* Quatrefages, 1866. B, *Palola brasiliensis* Zanol, Paiva & Attolini, 2000. C, *Lysidice ninetta* Audouin & Milne Edwards, 1833. F1 + F2, muscle fibre complex F1 + F2 (Desière, 1967); MND, mandibles; MS, muscle; Mx, maxillae.

51. Color of neuropodial acicula: 0, dark (brown, dark brown or black); 1, light (nearly clear or yellow).
52. Color pattern of neuropodial acicula: 0, sheath and core with distinctly different colours; 1, sheath and core with similar colour.
53. Distal ends of neuropodial acicula: 0, blunt-tipped, conical or irregularly knobbed; 1, hammer-headed or bidentate.
54. Distal ends of subacicular hooks: 0, absent; 1, falcate; 2, bidentate; 3, tridentate; 4, spinigererous. Subacicular hooks are the ventralmost chaetae, usually not parallel to the remaining chaetae, but emerging at a more or less distinct angle to them, and inserted in the parapodium in front of the chaetal bundle.
55. Number of subacicular hooks per parapodium: 0, always single, except for replacements; 1, at least paired. The presence of multiple subacicular hooks was not included as a separate state because the information we have in the present analysis is insufficient to distinguish them consistently; however, distinguishing paired from multiple subacicular hooks may be informative in a larger group of species. Some of the species with multiple subacicular hooks have them arranged in a fan; others have them in irregular bundles. This arrangement may also be an informative character and will be considered in a future analysis.
56. Color of subacicular hooks: 0, light (nearly clear or yellow); 1, dark (brown, dark brown, or black).

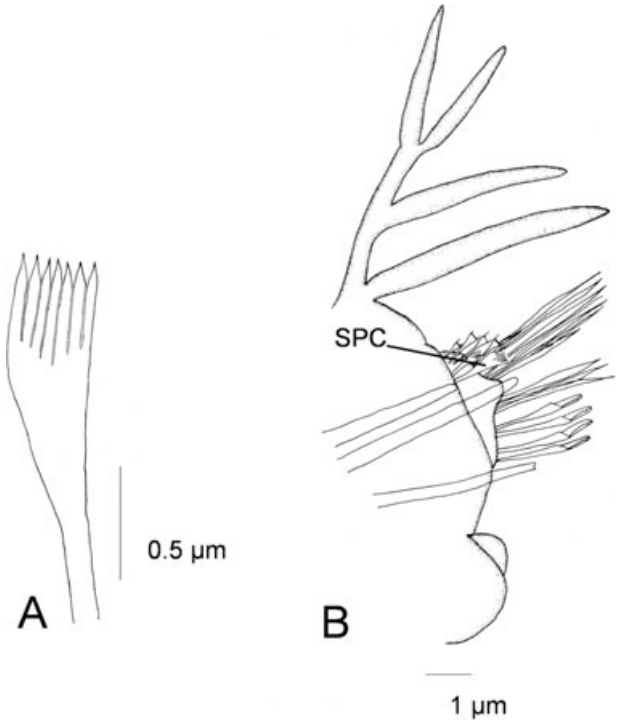

Figure 8. *Marphysa* cf. *atlantica* Kinberg, 1865. A, spatula-shaped pectinate chaetae. B, parapodium of chaetiger 109, left side. SPC, spatula-shaped pectinate chaetae.

57. Color pattern of subacicular hooks: 0, sheath and core with distinctly different colours; 1, sheath and core with similar colour.
58. Distribution of subacicular hooks: 0, present in every, or nearly every segment after first occurrence; 1, may be missing irregularly, sometimes in many segments.
59. Ventral pygidial cirri: 0, absent; 1, present.

Most polymorphic characters are soft-body features. This variability may be a result of size differences among specimens examined, but may also be caused by different fixation procedures or the condition of the preserved specimens (Treadwell, 1911; Hartman, 1944; Nonato & Luna, 1970; Steiner *et al*., 2002). Polymorphism in characters like 53 and 54 are caused by variation along the body of the specimens.

RESULTS

We concentrate on the results of the analyses of composite characters because these analyses yielded a more resolved strict consensus tree; the major differences between the results of the two matrices are caused by the ambiguous placement of *Palola* and Onuphidae.

Composite analyses

Unconstrained parsimony analyses yielded 200 most parsimonious trees (MPT) (length = 172 steps; consistency index = 0.57; retention index = 0.74). The Eunicidae/Onuphidae clade and Onuphidae were both monophyletic, but Onuphidae was deeply nested within Eunicidae, making the later paraphyletic (Figs 9, 10A, B). The Eunicidae/Onuphidae clade (Fig. 9, clade 6) excluding *Palola* had low support, and a monophyletic Eunicidae was present in trees just one step longer than the unconstrained MPT. All putative exclusive synapomorphies for Eunicidae, such as dorsal lips separated by a narrow notch, and short ring-shaped ceratophores and palpophores, supported the whole Eunicidae/Onuphidae clade in unconstrained MPT (Fig. 9, clade 7) and could not be unambiguously optimized on trees constraining Eunicidae to be monophyletic. When we constrained Eunicidae as monophyletic, the strict consensus of the MPT showed almost no resolution within the family. In this constrained analysis the only eunicid clades present were the ones with bootstrap support higher than 50% in the unconstrained analysis, and the clade (*Eunice norvegica* (Linnaeus, 1767) (*Eunice aphroditois* (Pallas, 1788) (*Eunice denticulata* Webster, 1884; *Eunice* cf. *flavopicta* Izuka, 1912))).

Onuphidae was sister to *Eunice websteri* Fauchald, 1969 in most MPT and to clade 1 (Fig. 9) in the remaining trees. The clade in which Onuphidae is nested in most MPT (Fig. 10A, B) was supported by homoplastic characters; many of these are polymorphic in several species and may be inapplicable in Onuphidae. However, the clade ((Onuphidae, *E. websteri*) *Eunice vittata* (Chiaje, 1829)) is supported by having peristomial ventrolateral lips set off by distinct grooves and by the presence of at least two subacicular hooks per parapodium: characters that are generally present in Onuphidae.

The monophyly of *Eunice* and most of its taxonomically informal groups was rejected in the present results: they were paraphyletic in all MPT (Figs 9, 10A, B). The group bearing dark unidentate hooks (group D), represented by *Eunice fucata* Ehlers, 1887 and *Eunice sebastiani* Nonato, 1965, was the only informal subgroup monophyletic in some unconstrained MPT. The monophyly of all other informal groupings required the trees to be between three and eight steps longer than the MPT (Table 5). The dark coloured subacicular hooks had a unique origin, but the *Eunice* informal subgroup based on this character was paraphyletic because the genera *Marphysa* and *Lysidice* were nested within the same clade (Fig. 9, clade 4); species of these two genera also have dark coloured subacicular hooks, although some species may be polymorphic for this feature.

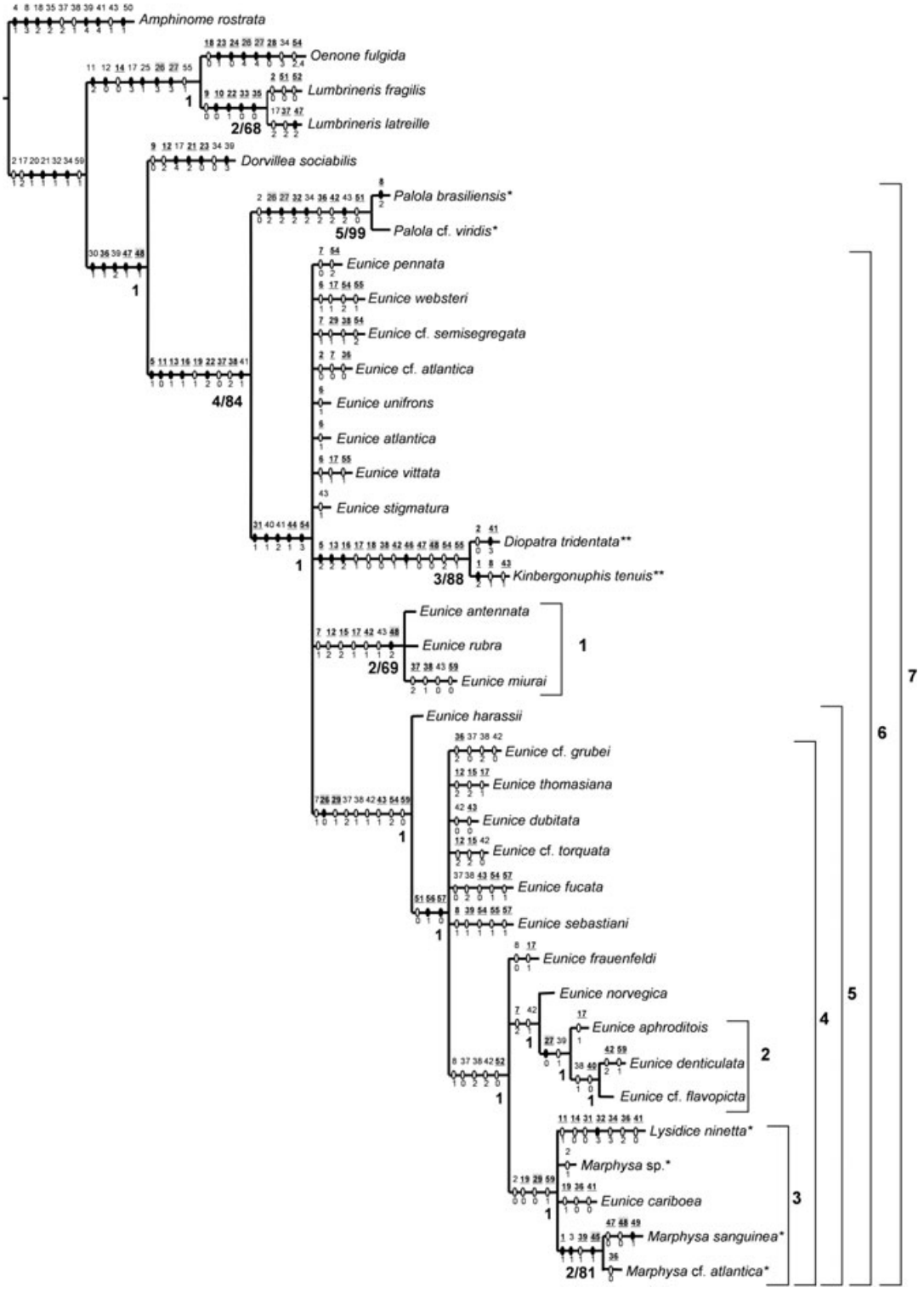

Figure 9. Strict consensus tree of 200 most parsimonious trees resulting from composite analyses. Tree statistics: length = 200 steps; consistency index = 0.49; retention index = 0.65. Characters optimized on nodes under ACCTRAN, unambiguous characters in bold face and underlined. Characters used for the first time in this study and promising sources of phylogenetic signal are shaded in grey. White and black hashmarks represent homoplasious and non-homoplasious characters, respectively. Bold numerals below branches are Bremer support/Bootstrap values; single numerals refer to Bremer support. Numerals beside square brackets are clade numbers. *Eunicidae outgroup species; **Onuphidae species.

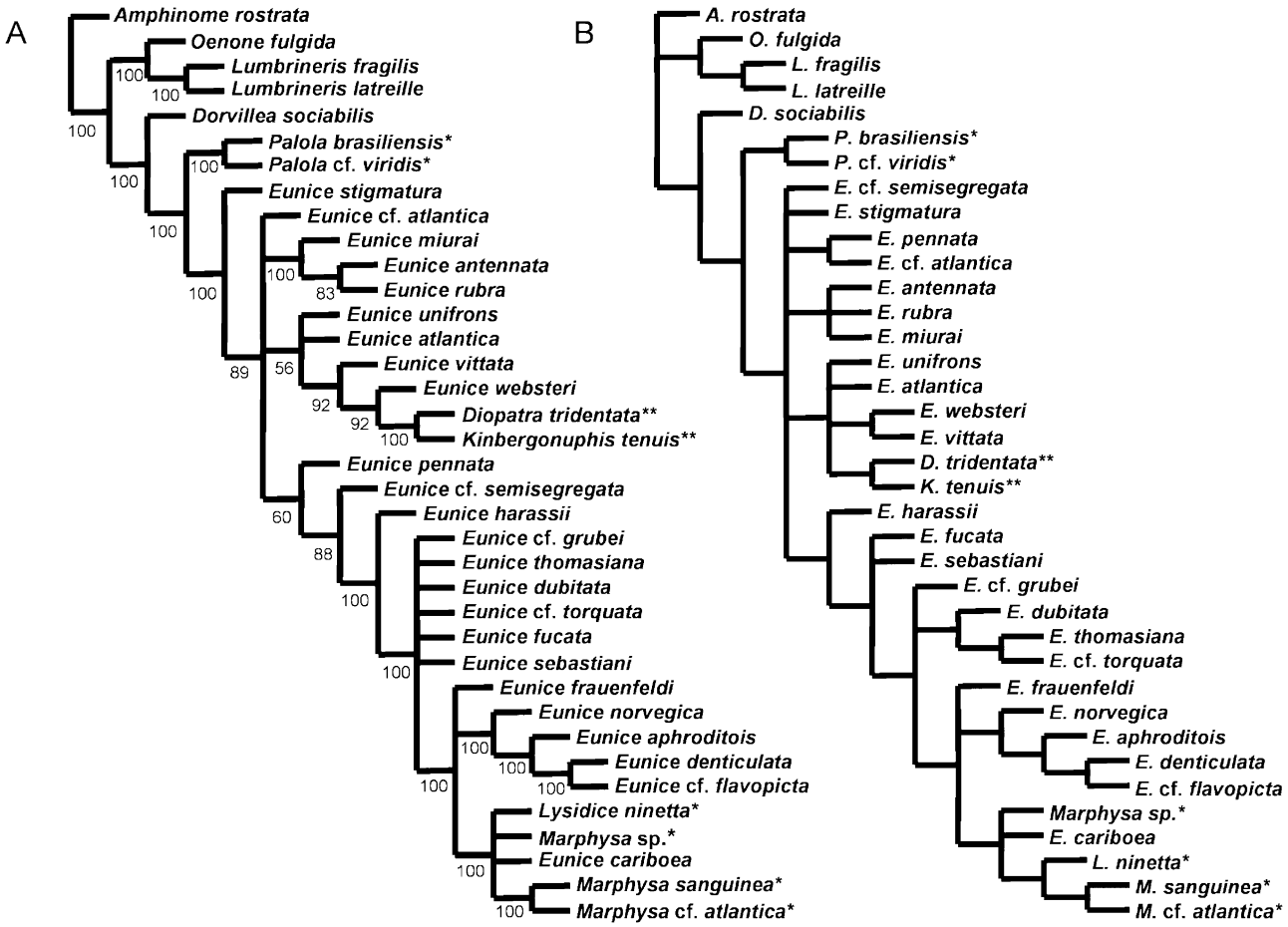

Figure 10. Consensuses of 200 most parsimonious trees resulting from composite analyses. A, 50% majority rule consensus, numerals below branches represent the percentage of the most parsimonious trees in which the clade is present. B, Adams consensus. *Eunicidae outgroup species; **Onuphidae species.

Two clades of *Eunice* species were present in all MPT. In one clade, *Eunice antennata* (Lamarck, 1818)/*Eunice rubra* Grube, 1856/*Eunice miurai* Carrera-Parra & Salazar-Vallejo, 1998, all species have yellow tridentate hooks, and compound falcigers of posteriormost chaetigers are bi- and tridentate. This clade was also present in all strict consensus trees resulting from constrained analyses in which its members had not been constrained to different clades. The other clade, clade 5 (Fig. 9), groups species in which MxIII is part of a distal arc with left MxIV and is placed side by side with right MxIV. The *Eunice* species of clade 5 were grouped in a similar clade even when *Marphysa* and *Lysidice* species were forced out of it, in the constrained analyses forcing *Eunice* to be monophyletic. *E. aphroditois* is the sister taxon to (*E. denticulata*, *E.* cf. *flavopicta*) in all MPT of unconstrained and constrained analyses.

The basal polytomy in the clade Eunicidae/Onuphidae in the strict consensus (Fig. 9) resulted from the 'wild-card' (Nixon & Wheeler, 1992) behav-

Table 5. Summary of results of constrained analyses (see Table 2 for descriptions of groups). Unconstrained analyses resulted in 200 most parsimonious trees, length = 172 steps. A, number of most parsimonious trees; B, difference in length (steps) from unconstrained most parsimonious trees

Constrained clades	A	B
Eunicidae	804	+1
Eunice	24	+6
Eunice, yellow hooks	962	+5
Eunice, dark hooks	6	+3
A group	163	+7
B group	192	+3
C group	184	+3
D group	100	±0
A1 group	8	+3
B2 group	1170	+5
C1 group	1560	+8
C2 group	2	+3

iour in the MPT of *Eunice* cf. *semisegregata* Fauchald, 1969; *Eunice pennata* (Müller, 1776), *Eunice* cf. *atlantica* Kinberg, 1865, and clade 1, which have conflicting placement among the MPT because they lack synapomorphies to resolve their relationships either with each other or with other species.

Most of the MPT did not support the monophyly of *Marphysa* based on the traditional characters, i.e. the absence of peristomial cirri, combined with the presence of five prostomial appendages. The two *Marphysa* sister species were grouped based on the flattened shape of the body and the presence of spatula-shaped pectinate chaetae; characters not widely or clearly described in previous studies.

The genus *Palola* is the basalmost clade in the Eunicidae/Onuphidae clade because of its lack of subacicular hooks and pectinate chaetae, and because of the presence of maxillary carriers longer than half of MxI. *Palola* is the only eunicid genus included in the analyses not nested within *Eunice*.

REDUCTIVE ANALYSES

Parsimony analyses yielded 858 MPT (length = 177 steps; consistency index = 0.56; retention index = 0.73), see Figure 11 for consensus trees. A monophyletic Eunicidae with Onuphidae as its sister group is supported in some MPT (Fig. 11B). In the MPT in which Eunicidae is paraphyletic, Onuphidae has the same sister-group relationships as in the composite analyses. *Palola* is the basalmost eunicid when the Eunicidae is paraphyletic, and is nested within *Eunice* when Eunicidae is monophyletic. *Palola* is sister to *Lysidice* or *E.* cf. *atlantica* when nested within *Eunice*. Clade 5 (Fig. 9) of the composite analyses collapses in the strict consensus of the reductive analyses (Fig. 11A) because of the uncertain placement of *Palola*. When *Palola* is removed from the reductive analyses clade 5 (Fig. 9) is present in the strict consensus tree.

DISCUSSION

The discussion concentrates on the results of the strict consensus tree of the composite analyses, and character numbers refer to composite coding.

PHYLOGENETIC RELATIONSHIPS AND TAXONOMY

Eunice and its informal taxonomic groups were found to be paraphyletic in this study, supporting results

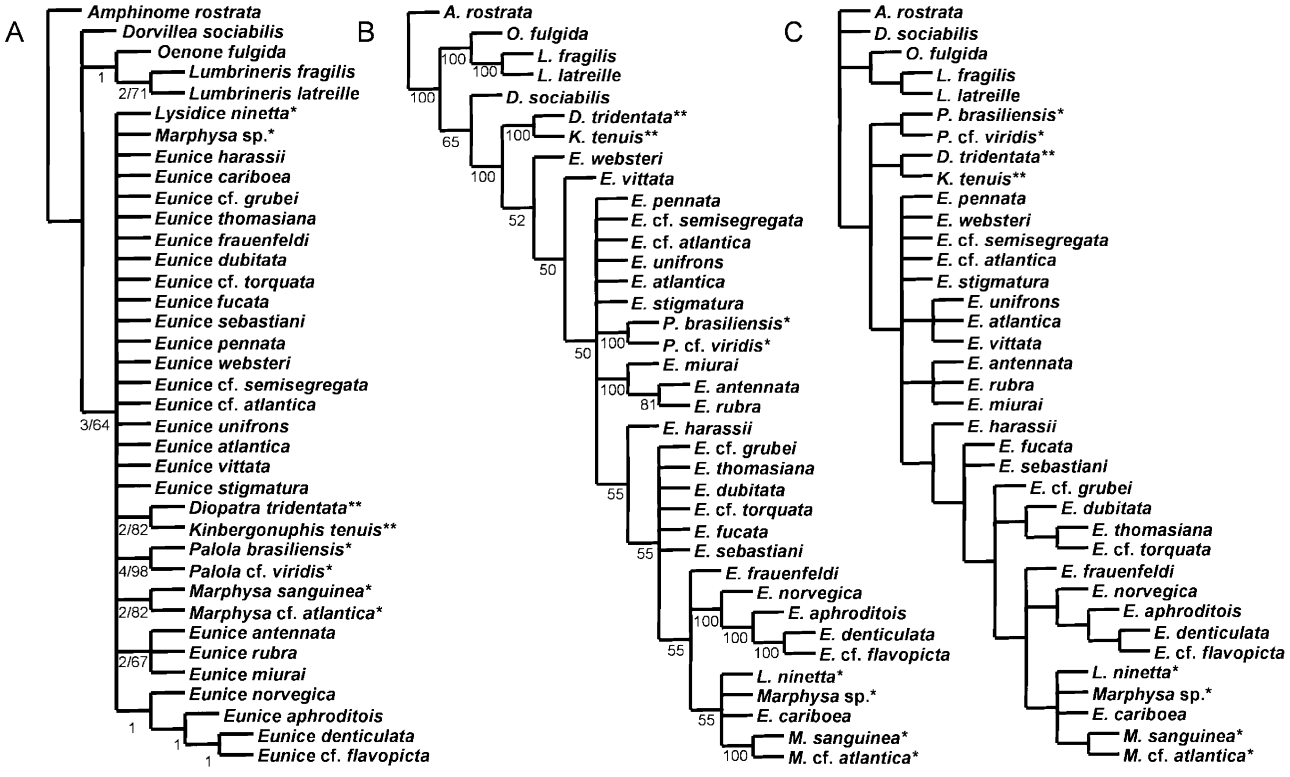

Figure 11. Consensuses of 858 most parsimonious trees resulting from reductive analyses. A, Strict consensus, numerals below branches are Bremer support/Bootstrap values; single numerals refer to Bremer support. B, 50% majority rule consensus, numerals below branches represent the percentage of the most parsimonious trees in which the clade is present. C, Adams consensus. *Eunicidae outgroup species; **Onuphidae species.

from previous phylogenetic analyses that included *Eunice* species (e.g. Struck *et al*., 2006). A consistent characteristic revealed for the first time in all trees resulting from the present analyses was the placement of *E. aphroditois*, type species of *Eunice s.s.*, and *E. antennata*, type species of the now defunct *Leodice*, in different clades (Figs 9, 11). This implies that as currently defined the genus *Eunice* could be split into at least two monophyletic groups, one representing *Eunice s.s.* and the other *Leodice*, each with its original type species. However, analyses with more resolved results are necessary before one can justify dividing *Eunice*. In the current results the species composition of each of these monophyletic groups, their characterizing synapomorphies, and the monophyletic group placement of most of the included *Eunice* species cannot be established with confidence because of the lack of basal resolution and the low support of clades.

The ambiguous placement of species with yellow bidentate hooks and the unique origin of black bidentate hooks in the present results contrasted with the results in Fauchald (1992), in which the yellow-hook clade was the only consistent one in all trees, and species with black hooks had conflicting arrangements among all trees. The analyses in Fauchald (1992) included a broader taxonomic sample than the present one. However, his results were flawed in that the analyses did not find all MPT and did not include characters that can be shown to be important in resolving the present trees (e.g. characters 26, 29, 48, and 59).

Marphysa and *Lysidice* were grouped with *Eunice cariboea* Grube, 1856 within *Eunice s.l.* (Fig. 9, clade 3). The synapomorphies supporting this clade are either reversals to the Eunicidae/Onuphidae plesiomorphic states (characters 29 and 59) or reversals within this clade (character 19). If descriptions in the literature are accurate, the absence of MxVI (character 29) and the presence of the ventral pygidial cirri (character 59) may be more variable within clade 3 (Fig. 9) than is represented by our taxa sample. Orensanz (1975) described *Marphysa* as having either only dorsal or both dorsal and ventral pygidial cirri. Furthermore, both Aiyar (1931) and Treadwell (1921) mentioned the presence of MxVI in *Marphysa* and *Lysidice*. The synapomorphies corroborating this clade are likely to have been produced by the lack of understanding and under-representation of the variability described above, and/or by error induced by paedomorphic evolution (e.g. Wiens, Bonnet & Chippindale, 2005; T. Struck, pers. comm.) as all the species in this clade have paedomorphic features. Juvenile traits in *Eunice* include absence of palps, as in *Lysidice*, absence of peristomial cirri, as in *Marphysa* and *Lysidice*, and branchiae either absent or poorly developed, as in *E. cariboea* and *Lysidice* (e.g. Giangrande, 1989; Lu & Fauchald, 1998; Nogueira, Steiner & Amaral, 2001).

The paraphyletic Eunicidae present in all MPT yielded by the composite analyses, but present in just some of the MPT from the reductive analyses, makes the idea of a monophyletic Eunicidae even more problematic. The molecular phylogenies of the order Eunicida are inconsistent on this issue (Struck *et al*., 2002, 2006); however, the taxa sample of Onuphidae and Eunicidae in that study was not large enough to address the relationships either within or among them adequately. In the present phylogeny Onuphidae is always sister to species with yellow hooks. In contrast, in the 18S rDNA phylogeny of the order Eunicida (Struck *et al*., 2006) Onuphidae is sister to a clade equivalent to the present dark-coloured subacicular hook one (Fig. 9, clade 4).

Character evolution

The low resolution among *Eunice* species at the base of the tree was caused in part to the fact that many of the characters commonly used in *Eunice* taxonomy are homoplasies. Among others, these characters include the shape of articulation of prostomial appendages, and the branchial shape and distribution. Most exclusive synapomorphies within clade 6 (Fig. 9), other than the dark colour of the subacicular hooks, were characters used for the first time in this study, such as the jaw characters (e.g. characters 26, 27, and 29) and characters derived from close examination of chaetal variation along the body (e.g. characters 45 and 48). Both types of characters, as well as other features of the buccal apparatus, appear to be promising sources of phylogenetic signal. To date, however, they have been poorly documented and their variation has not been properly taken into account.

Miura's (1986) hypothesis of branchial distribution evolution and the evolution of the dentition of subacicular hooks could not be tested by our results. The basalmost polytomy in clade 6 (Fig. 9) biased the plesiomorphic state. However, it is clear that unidentate subacicular hooks were derived from bidentate ones (Fig. 12A) as suggested by Orensanz (1990). Both species that bear unidentate hooks, *E. fucata* and *E. sebastiani*, are nested within clade 5 (Fig. 9) in which the plesiomorphic state of subacicular hooks is bidentate (Fig. 12A).

The dark colour of subacicular hooks was derived once from the plesiomorphic light-colour condition and reversed to this condition twice independently (Fig. 12B). The reversals occurred in *L. ninetta* and *Marphysa sanguinea* (Montagu, 1807), which showed polymorphism for this character. The colour variation and pattern of colours of subacicular hooks

are not well understood, but they may vary with size of the specimen and with the position along the body of the segment examined (Day, 1967; Fauchald, 1992).

The colour and the dentition of subacicular hooks are considered important features in the taxonomy of the family Eunicidae, mainly in the genus *Eunice* (e.g. Hartman, 1944; Fauchald, 1992). Miura (1986) considered them conservative enough to suggest that they could be used to divide the genus *Eunice* in groups, perhaps corresponding to subgeneric- or generic-level taxa. However, based on the present results, these groups are paraphyletic and most similarities in hook colour and dentition are homoplasies.

CONCLUSION

Eunice s.l. and its informal subgroups are paraphyletic. *Eunice* may consist of at least two monophyletic groups, *Eunice s.s.* and *Leodice*. However, the diagnostic features of these groups, their species composition, and the monophyletic group placement of most other species of *Eunice* remains unresolved. This study provides the first analytical hypotheses of phylogeny for *Eunice*, and it is a step towards a better understanding of the phylogeny of *Eunice* and also of Eunicidae.

Additional information is needed in order to obtain a more stable hypothesis of phylogeny, and future analyses should focus on the whole family Eunicidae and include a wider sample of Onuphidae species. Besides the inclusion of more species in the analyses, other characters that might have phylogenetic importance should be added and molecular data considered. Some sources of probable informative morphological characters may be found in the ontogeny (Åkesson, 1967), internal anatomy (Müller, 2006), and electronic microscopy (e.g. Hayashi & Yamane, 1994).

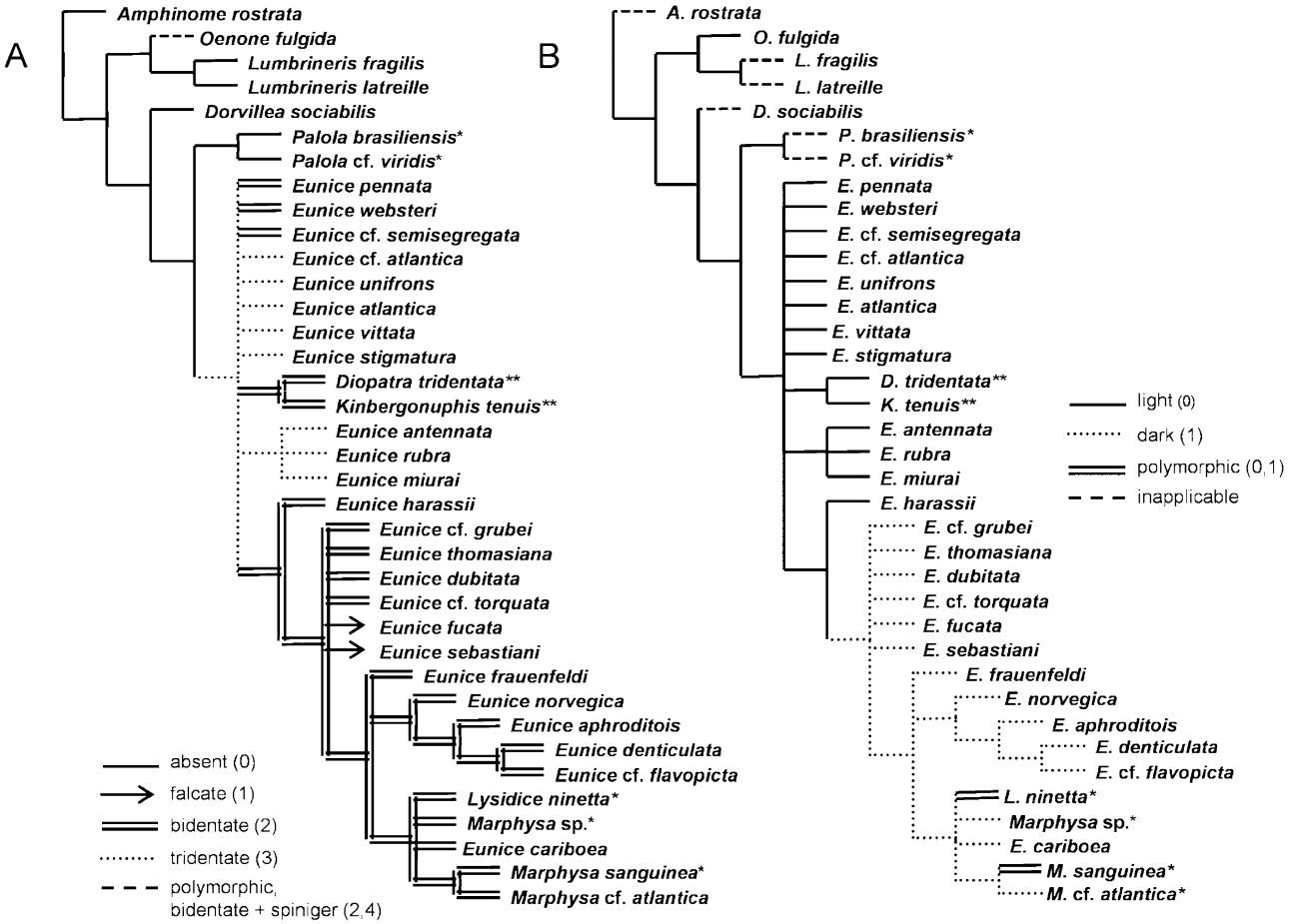

Figure 12. Evolution of subacicular hook. A, B, dentition (character 54) and colour (character 56). Characters optimized on the strict consensus of most parsimonious trees resulting from composite analyses, both characters are unambiguously optimized. *Eunicidae outgroup species; **Onuphidae species.

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APPENDIX 1

REDUCTIVE CHARACTERS: UNINFORMATIVE CHARACTERS UNDERLINED

1. Shape of cross section of body: 0, circular; 1, dorsoventrally flattened; 2, ventrally convex.
2. Body shape: 0, cylindrical, abruptly tapering anteriorly and posteriorly; 1, evenly tapering from anterior-median chaetigers.
3. Relative width and length of chaetigers: 0, at most ten times wider than long; 1, more than ten times wider than long.
4. Posterior extension of prostomium (caruncle): 0, absent; 1, present.
5. Frontal lips (*sensu* Paxton, 1998): 0, separated frontally by a narrow notch (Fig. 1A–C); 1, separated frontally by a distinct space (Fig. 1D); 2, frontal edge entire.
6. Frontal lips separated by a narrow notch anteriorly: 0, round (Fig. 1A, B); 1, truncate (Fig. 1C).
7. Frontal lips separated by a narrow notch, dorsally: 0, inflated (Fig. 2A); 1, flat (Fig. 2B); 2, dimpled (Fig. 2C).
8. Arrangement of prostomial appendages: 0, antennae and palps evenly spaced (Fig. 1C, D); 1, median antenna isolated by a gap from the other antennae and palps (Fig. 1A); 2, palps isolated by a gap from the antennae (Fig. 1B); 3, head appendages on conspicuously different regions of the prostomium, median antennae on the caruncle.
9. Median antennae: 0, absent; 1, present.
10. Antennal styles: 0, digitiform, tapering, or clavate (Fig. 3A–C); 1, medially inflated (fusiform) (Fig. 3D); 2, button shaped (Fig. 3E).
11. Articulations of antennal styles: 0, absent, 1, present.
12. Shape of articulations of antennal styles: 0, short or long cylinders (Fig. 4A); 1, moniliform (Fig. 4B).
13. Antennal ceratophore: 0, absent; 1, present.
14. Shape of antennal ceratophore: 0, short, usually ring shaped; 1, relatively long, usually articulated.
15. Lateral antennae: 0, absent; 1, present.
16. Palpal styles: 0, absent; 1, digitiform, tapering, or clavate (Fig. 3A–C).
17. Palpal styles articulations: 0, absent; 1, present.
18. Shape of palpal styles articulations: 0, short or long cylinders (Fig. 4A); 1, moniliform (Fig. 4B).
19. Palpophores: 0, absent; 1, present.
20. Shape of palpophores: 0, short, usually ring shaped; 1, relatively long, usually articulated.
21. Peristomial ventrolateral lips: 0, absent; 1, present.
22. Shape of peristomial ventrolateral lips: 0, set off by distinct grooves; 1, visible only as elevated surfaces; 2, scoop shaped; 3, medially short, about half as long as lateral side of the peristomium.
23. Peristomium: 0, a single ring; 1, two rings distinct at least dorsally; 2, reduced to region around the mouth.
24. Peristomial cirri: 0, absent; 1, present.
25. Mouth: 0, extending to the ventral side of anterior chaetigers; 1, restricted to peristomium.
26. Maxillary plates: 0- absent; 1- present.
27. Number of rows of maxillary plates: 0, one pair; 1, two or more pairs.
28. Calcium carbonate mineralizing jaws: 0, absent; 1, present.
29. Calcium carbonate mineralizing jaws: 0, calcite; 1, aragonite.
30. Maxillary carrier: 0, ctenognath; 1, prionognath; 2, labidognath.

31. MxI: 0, dentate; 1, fang shaped.
32. Fang-shaped MxI: 0, facing each other; 1, facing dorsal side of the body.
33. Shape of MxIII: 0, dentate, front end part of distal arc with left MxIV (Fig. 5A, G); 1, dentate, at least in part located behind MxII (Fig. 5B); 2, edentate, behind MxII (Fig. 5D, E); 3, dentate, triangular; 4, dentate, with teeth arranged anterior to posterior, most anterior longest.
34. Left MxIV: 0, wider than long with teeth on less than half of the plate, often only two teeth present (Fig. 5A); 1, wider than long with teeth on more than half of the plate, always more than two teeth present (Fig. 5B, C, F); 2, longer than wide often with just one tooth (Fig. 5D, E); 3, triangular, edentate, or with few teeth at the tip; 4, teeth decreasing in size from anterior to posterior, anteriormost tooth longest.
35. MxV: 0, fang shaped; 1, plate like, a small tooth may be present.
36. MxVI: 0, absent; 1, present (Fig. 5A).
37. Right MxIII: 0, present; 1, absent.
38. Relative length of labidognath maxillary carrier: 0, longer than half the length of MxI; 1, shorter than half the length of MxI.
39. Mandibles: 0, absent; 1, present.
40. Shape of mandibles: 0, flat (Fig. 6A); 1, strongly curved, forming an open scoop, plates fused anteriorly, anterior end strongly calcified (Fig. 6B, C); 2, curved, plates separated in a V shape at the anterior end, not strongly calcified (Fig. 6D, E).
41. Mandibles: 0, fused medially; 1, attached by ligaments.
42. Muscle fibre complex F1 + F2 (Desière, 1967) on the pharyngeal bulb: 0, absent; 1, present.
43. Placement of the muscle fibre complex F1 + F2 (Desière, 1967) on the pharyngeal bulb: 0, posterior to mandible carriers (Fig. 7A); 1, above mandible carriers (Fig. 7B); 2, between mandible carriers (Fig. 7C).
44. Notopodia: 0, absent; 1, present.
45. Notopodia: 0, reduced to notopodial cirri; 1, complete chaetal lobe.
46. Neuropodia in mid-body distally: 0, round; 1, truncate; 2, pointed.
47. Neuropodial prechaetal lobes in mid-body: 0, longer than acicular; 1, about as long as acicular lobes; 2, lobes absent.
48. Neuropodial postchaetal lobes in mid-body: 0, longer than acicular lobes; 1, about as long as acicular lobes; 2, shorter than acicular lobes.
49. Ventral cirri: 0, absent; 1, present.
50. Shape of ventral cirri: 0, tapering or digitiform in first few chaetigers, thereafter basally inflated; 1, tapering or digitiform in anterior and posterior chaetigers, basally inflated in median chaetigers; 2, digitiform, bases not inflated anywhere along the body; 3, tapering, bases not inflated anywhere along the body.
51. Shape of the inflated region of ventral cirri: 0, ventral ridge; 1, scoop shaped, rounded.
52. Branchiae: 0, absent; 1, present.
53. Shape of the branchiae: 0, single filaments; 1, filaments linearly arranged; 2, spiraled; 3, bushy.
54. Branchiae start: 0, on chaetiger 3; 1, between chaetigers 4 and 9; 2, start late (after chaetiger 10).
55. Branchial distribution: 0, mostly limited to the first third of the body (present on less than 55% of the body segments); 1, in most of the body (present on more than 65% of the body); 2, mostly limited to the second third of the body (present on less than 55% of the body segments).
56. Narrow, long pectinate chaetae: 0, absent; 1, present.
57. Spatula-shaped pectinate chaetae (short, wider than acicula with wide teeth): 0, absent; 1, present (Fig. 8A, B).
58. Pseudocompound falcigers or spinigers: 0, absent; 1, present in a limited number of anterior chaetigers.
59. Compound falcigers: 0, absent; 1, present.
60. Distal end of compound falcigers (present in most of the body): 0, bidentate; 1, multidentate.
61. Compound falcigers in the 2.5% posteriormost chaetigers: 0, absent; 1, present.
62. Distal end of compound falcigers in the 2.5% posteriormost chaetigers: 0, all bidentate; 1, bi- and tridentate.
63. Compound spinigers: 0, absent; 1, present.
64. Calcareous chaetae: 0, absent; 1, present.
65. Color of neuropodial acicula: 0, dark (brown, dark brown, or black); 1, light (nearly clear or yellow).
66. Color pattern of neuropodial acicula: 0, sheath and core with distinctly different colours; 1, sheath and core with similar colour.
67. Distal end of neuropodial acicula: 0, blunt-tipped, conical, or irregularly knobbed; 1, hammer-headed or bidentate.
68. Subacicular hooks: 0, absent; 1, present.
69. Distal end of subacicular hooks: 0, falcate; 1, bidentate; 2, tridentate; 3, spinigererous.
70. Number of subacicular hooks per parapodium: 0, always single, except for replacements; 1, at least paired.
71. Color of subacicular hooks: 0, light (nearly clear or yellow); 1, dark (brown, dark brown, or black).
72. Color pattern of subacicular hooks: 0, sheath and core with distinctly different colours; 1, sheath and core with similar colour.
73. Distribution of subacicular hooks: 0, present in every, or nearly every, segment after first occurrence; 1, may be missing irregularly, sometimes in many segments.
74. Ventral pygidial cirri: 0, absent; 1, present.

APPENDIX 2

REDUCTIVE CODING CHARACTER MATRIX

	1234567891 0	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	7777 1234
Amphinome rostrata	0001???311	100-11100-	0-2000----	--------0-	-0-1101113	-13010000-	0-01---0--	---0
Oenone fulgida	01002---12	0-0-10----	12001100-1	0-44000-10	112100000-	-0---0000-	0-00110111 3	0101
Lumbrineris fragilis	00002---0-	----00----	1210110102	1133100010	0100-0000-	-0---0000-	0-000000--	---1
Lumbrineris latreille	01002---0-	----00----	1110110102	1133100010	0100-0100-	-0---00011	0-001100--	---1
Dorvillea sociabilis	01002---00 2	110-11100-	13101110-0	?-?????-10	10-1010012	-0---00010	10001100--	---1
Diopatra tridentata	00001--010	1011111011	1001110112	1011101110	11010?2011	122101010-	0-00110111	0101
Kinbergonuphis tenuis	21001--110	1011111011	1001110112	1011101110	11010?2011	111111010-	0-00110111	0101
Lysidice ninetta	0000001-11 1	101010----	1010110112 1	1001101012	1121022111 2	10---10010	1000000110 11	0001 11
Palola brasiliensis	0000001210 11 2	1010111010	1011110112 1	1022101011	1111022211	0102200010	10000100--	---1
Palola cf. *viridis*	0000002010	1010111010	1111110112	1022101011	1111022211	0102200010	10000100--	---1
Marphysa sp.	0100000110 1	1010111010	1010110112 1	1001101110	1101012211	1112110010	1000000110	1001
Marphysa sanguinea	1000001110 1	1010111010	1110110112	1001101110	1101012210	111211100-	0-10000110	0001 11
Marphysa cf. *atlantica*	1010001110	1010111010	1110110112	10011?1110	1101002210	1112111010	1000000110	1001
Eunice aphroditois	0100002110 1 1	0010111010 1	1011110112	1000111110	1101012210 1	1111110010	1000000110 1	1000 1
Eunice denticulata	0100000110 2	1010111010	1011110112 1	1000111110	1101011110 222 1	0112110010	1000000110 1	1001
Eunice cf. *flavopicta*	0100002110	1010111010	1111110112	1000111110	1101012110	0111110010	1000000110	1000
Eunice norvegica	0100002110 1	1010111010	1111110112	1001111110	1101012211	1111110010	1000000110	1000 1
Eunice cariboea	0000000110 1 1 2	1010111010	1011110112 1	1001101110	1101002211	10---10010	1000000110	1000 1

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APPENDIX 2 *Continued*

	1234567891 0	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	7777 1234
Eunice frauenfeldi	0100001010	1010111010	1011110112	1001111110	1101012211	1112110010	1000000110	1000
Eunice cf. *grubei*	010000?01?	1010111010	1111110112	1001111110	1101022211	1110110010	1000010110	1000
Eunice thomasiana	0100001010	1110111110	1011110112	1001111110	1101011111	1111110010	1000010110	1000
Eunice dubitata	0100001010	1010111010	1111110112	1001111110	1101011111	1110010010	1000010110	1000
Eunice cf. *torquata*	0000001010 1	1110111110	1111110112	1001111110	1101011111	1110110010	1000010110	1000
Eunice fucata	0100001010 2	1010111010	1011110112 1	1001111110	1101012211	1111010010	1000010100	1100
Eunice sebastiani	0100001110	1?1011??10	1111110112	1001111110	1101011110	1111110010	1000010101	110?
Eunice harassii	0100001010 12	1010111010	1011110112 1	1001111110	1101011111 22	1111110010	1000110110	0100
Eunice antennata	0100001010 1	1110111110	1011110112 1	1011101110	1101012011 2	1111110010	1100110120	0101
Eunice rubra	0100000010 111 2	1110111110	1011110112	1011101110	1101011111 22	1111110010	1100110120 1	0101
Eunice miurai	0100001010	1110111110	1011110112	1011101110	1101011111	1111010010	1100110120 1	0100
Eunice websteri	0000012010 1 1	1010111010	1011110112	1011101110	1101012211	1110010010	1000110111	0101
Eunice vittata	0100012010	1010111010	1011110112	1011101110	1101012211	1110010010	1000110121	0101
Eunice atlantica	0100010010 2	1010111010	1111110112	1011101110	1101012211	1110010010	1000110120	0101
Eunice unifrons	0100012010 1	1010111010	1011110112 1	1011101110	1101012211	1110010010	1000110120	0101
Eunice pennata	0100000010	1010111010	1111110112	1011101110	1101012211	1110010010	1000110110	0101
Eunice cf. *semisegregata*	0100001010 1	1010111010	1111110112	1011111110	1101011110 2 1	1110010010	1000110110	0101
Eunice cf. *atlantica*	0000000010	1010111010	1111110112	1011101110	1101002211	1110010010	1000110120	0101
Eunice stigmatura	0100002010 1	1010111010	1111110112	1011101110	1101012211	1110110010	1000110120	0101

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