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Phylogeny of Eunicida (Annelida) based on morphology of jaws

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Abstract

Eunicida have a complex jaw apparatus with a fossil record dating back to the latest Cambrian. Traditionally, Eunicidae, Onuphidae, and Lumbrineridae were considered closely related families having labidognath maxillae, whereas Oenonidae with prionognath type maxillae were thought to be derived. Molecular phylogenies place Oenonidae with Eunicidae/Onuphidae, and Lumbrineridae as the most basal taxon. Re-evaluation of the jaw types based on morphology and ontogeny demonstrated that the labidognaths Eunicidae and Onuphidae have a closer relationship to the prionognath Oenonidae than was previously thought. Lumbrineridae are neither labidognath nor prionognath; therefore a new type, Symmetrognatha, is proposed. Homologies of jaw elements and considerations of functional aspects of the jaw apparatus are explored to present a hypothesis of the Eunicida phylogeny. The earliest fossils are of placognath and ctenognath types, lacking maxillary carriers. While the former are extinct, the latter are represented by the extant Dorvilleidae. The interpretation of relationships between the carrier-bearing families depends on whether the carriers are thought to have evolved once only or twice independently. The similarity of the carrier structure and their associated muscles suggests the former, placing the Lumbrineridae as sister to Eunicidae/Onuphidae and Oenonidae. However, the ontogeny of the eunicid/onuphid apparatus as well as its adult structure differ greatly from those of lumbrinerids, indicating that the lumbrinerid carriers may have evolved independently and earlier than in eunicids/onuphids and oenonids.

Key words: maxillae, mandibles, ontogeny, ctenognath, placognath, labidognath, prionognath, symmetrognath, fossils, scolecodonts

Introduction

A complex jaw apparatus consisting of ventral mandibles and dorsal maxillae is characteristic for polychaetes of the order Eunicida. The jaws are hardened cuticular structures, composed of calcium carbonate and/or scleroproteins. As a result of their durability they have a good fossil record. The earliest known eunicidan scolecodonts (isolated jaw pieces) are from the latest Furongian (latest Cambrian), but the Ordovician was the main period for their radiation, with more than 50 known genera belonging to 15–20 families (Hints & Eriksson 2007). The Recent fauna, in comparison, consists of about 100 genera in seven families (Paxton 2000).

Five different architectural types of maxillary apparatuses, based on their arrangement, number, and shape of elements, have been identified within the Eunicida (Paxton 2000: table 1.4). These types do not represent clades, but grades of evolution. The first two grades were named by Ehlers (1868) as Labidognatha (pincer-jaw) and Prionognatha (saw-jaw). Labidognatha was to include Eunicidae, Onuphidae, and Lumbrineridae, and was defined as having dissimilar maxillary elements on the two sides, and with the posterior two pairs of maxillae (MI and MII) of each side surrounded by a semicircle of smaller anterior elements. The position of Hartmaniellidae is unclear but has been

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considered to be labidognath (Carrera-Parra 2003). Prionognatha included the eunicidans now known as Oenonidae, and was defined as having more or less similar elements, positioned in two parallel rows. Histriobdellidae, a family of small crayfish and lobster parasites, is questionably included in the Prionognatha (Rouse & Pleijel 2001).

The designations Labidognatha and Prionognatha were adopted by Kielan-Jaworowska (1966) for fossil families. She further introduced Ctenognatha (comb-jaw) for the Recent Dorvilleidae and extinct Tetraprionidae, and Placognatha (plate-jaw) for several families that have no modern representatives. One other type of maxillary apparatus, Xenognatha (strange-jaw), was described by Mierzejewski & Mierzejewska (1975) and is known only for Archaeoprionidae from the Ordovician.

More recent phylogenetic hypotheses regarding the Eunicida based mainly on the jaws are those by Kielan-Jaworowska (1966), Kozur (1970),Tzetlin (1980), Edgar (1984), Orensanz (1990), and Szaniawski (1996), with these authors agreeing that the placognath and ctenognath type jaws are most ancestral. Orensanz (1990) gave the most complete treatment, considering extinct and extant eunicidan jaws, including the general morphology of extant forms. He stated that labidognaths evolved from a ctenognath ancestor and considered the Dorvilleidae as the most basal Recent taxon. The labidognath/prionognath types were generally accepted by neontologists and paleontologists. Oenonids were clearly prionognath, and eunicids and onuphids labidognath, while lumbrinerids did not fit either type completely and were already indicated as intermediates by Ehlers (1868) when he introduced the terms. Most authors considered the Lumbrineridae as labidognath, while Orensanz (1990) believed them to be sub-labidognath to prionognath, and placed them as a sister group of Oenonidae.

With the advent of phylogenies based on DNA analyses, members of Eunicida were included in several genetic studies (Struck *et al.* 2002a, b; 2005; 2006; 2007; Hall *et al.* 2004; Colgan *et al.* 2006; Rousset *et al.* 2007). The most comprehensive of these concluded that the Eunicidae/ Onuphidae and Dorvilleidae are the sister group to Oenonidae, and Lumbrineridae is the most basal taxon (Struck *et al.* 2006). The authors discussed the three architectural types of jaw apparatuses of Recent eunicidans in connection with their molecular results and concluded that the definition of both the labidognath and ctenognath jaw types does not address adequately the variation within Eunicida.

The present study is a re-evaluation of the three jaw types, in which the mandibles and aspects of the structure, function, and ontogeny of the maxillary apparatuses of so-called labidognaths, prionognaths, and ctenognaths were examined to determine whether the groupings are justified. A hypothesis of the phylogeny of Eunicida based on jaw elements of extinct and extant representatives, and new definitions of jaw types, are presented.

Materials and methods

Most of the specimens studied were collected intertidally at Port Adelaide, South Australia, obtained from an aquaculture facility near Lake Macquarie, New South Wales, or laboratory cultures. Material from other localities was examined in the Australian Museum, Sydney (AM) and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The following species were studied in depth:

Dorvilleidae: *Dorvillea australiensis* (McIntosh), Sydney (AM W.33880); *Ophryotrocha labronica* La Greca & Bacci laboratory culture strain PAX (AM W.33877); *Parougia bermudensis* (Åkesson & Rice) laboratory culture (AM W.33878); *Parougia nigridentata* (Oug), Lindaspollene, Norway (AM W.33879)

Eunicidae: *Marphysa* sp., Adelaide (AM W.33885)

Lumbrineridae: *Scoletoma gulielmi* (Benham), Adelaide (AM W.33884); *Ninoe nigripes* Verrill, Massachusetts, USA (USNM 30551)

Oenonidae: *Halla okudai* Imajima, Adelaide (AM W.33881)

Onuphidae: *Australonuphis parateres* Paxton, Sydney (AM W.33882); *Diopatra aciculata* Knox & Cameron, Aquaculture facility (AM W.33883)

The jaws of larger eunicidans are generally dissected from preserved animals and the adhering muscle tissue is carefully removed. A new method was developed during this study whereby deceased animals were not preserved but left to decompose for a few days submerged in water. Then the complete pharynx was pulled out through the mouth. The pharynx was kept in water until the desired state of decomposition was achieved, i.e., the muscles of the jaw apparatus were decomposed but the ligaments and cuticle were still intact (see Fig. 3), before the jaws were preserved.

Specimens were examined using scanning electron microscopy (SEM) and/or light microscopy. For SEM preparations jaws were left in water until the soft tissue was totally decomposed, then they were air dried, gold-coated and examined with a JEOL JSM-6480LA. Photographs were taken with an Olympus SZH stereo zoom system with Sony CFW-310C color digital camera while the jaws were submerged in water. Preserved specimens used for examination of larval and juvenile jaws were cleared in 10% KOH and mounted in diluted glycerin. Living specimens were anaesthetized in 6% magnesium chloride and mounted on a slide with glycerin added to the edge of the coverslip. All drawings were made with the aid of a camera lucida.The term ‘‘maxilla’’ is usually abbreviated to Mx or M. The individual elements are numbered with Roman numerals, starting with MI for the most posterior element with increasing numbers proceeding anteriorly, with MIL and MIR referring to the left and right first maxillae respectively. This is shown for Eunicidae/Onuphidae (Fig. 2A) and for Lumbrineridae (Fig. 2B). Maxillae of Oenonidae are labeled likewise. However, the first right element that is much smaller than the corresponding left one in some genera is generally referred to as MIR by neontologists (Fig. 2D), whereas paleontologists refer to it as the basal plate (Fig. 2E).

Results and discussion

Mandibles

The mandibles of eunicidans are exceedingly similar in structure, consisting of a more- or- less fused pair of proximal shafts widening distally into a cutting plate. Dorsally the mandibles display an overall smooth surface (Fig. 3B) while ventrally the cutting plates are typically slightly raised (Figs. 1, 3A). This basic pattern was already established in Ordovician fossils. Wolf (1980) described the structure and function of mandibles and Orensanz (1990) assigned the extant forms to three basic types.

Oenonid-dorvilleid type. These mandibles are black in color, unmineralized. In some dorvilleids the two parts appear totally free of each other while in others and oenonids they are connected by a thin ligament. In some dorvilleids there is no distinct ventral cutting plate (Fig. 1A) while it is typical in others (Fig. 1B–C) and oenonids (Fig. 1D). It has been stated that the dorvilleid mandibles have no growth rings (Orensanz 1990). However, in *Ophryotrocha* (Fig. 1B) and *Dorvillea* (Fig. 1C), growth rings are visible on the cutting plates as is typical for other eunicidans.

Lumbrinerid type. The mandibles are fused completely or partly along their length, including the cutting plates, producing a combined semi-circular plate (Fig. 1E). The structures are only lightly calcified, with the sclerotized growth rings visible through the calcium layer.

Onuphid-eunicid type. The shafts are hardly calcified while the ventral cutting plate is covered with a thick white layer (Figs. 1F, 3A–B).

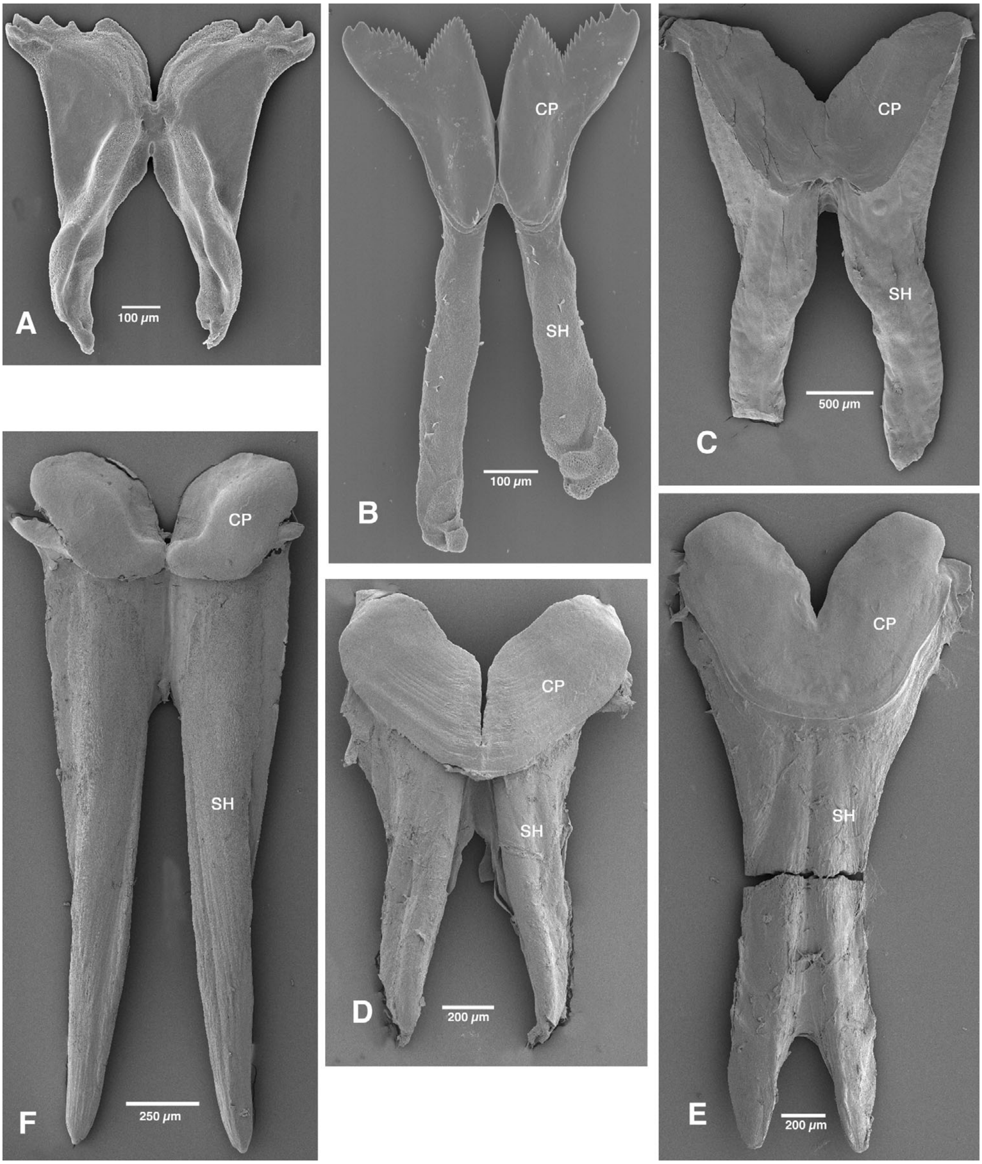

FIGURE 1. Mandibles, ventral view. A, *Parougia albomaculata* (Åkesson & Rice) (Dorvilleidae); B, *Ophryotrocha alborana* nom. nud. (Dorvilleidae); C, *Dorvillea australiensis* (McIntosh) (Dorvilleidae); D, *Halla okudai* Imajima (Oenonidae); E, *Scoletoma gulielmi* (Benham) (Lumbrineridae); F, *Marphysa* sp. (Eunicidae). Abbreviations: CP, cutting plate; SH, shaft; A, B by M.O. Macnaughton.

Re-evaluation of labidognath and prionognath types of maxillae

Detailed descriptions of the structure and function of two eunicid jaw apparatuses have been given by Hartmann-Schröder (1967) and Desière (1967), while Wolf (1980) studied a eunicid, a lumbrinerid, and two species of oenonids. This section discusses only aspects that have a bearing on the labidognath/prionognath condition to determine the status of the Lumbrineridae maxillary apparatus.

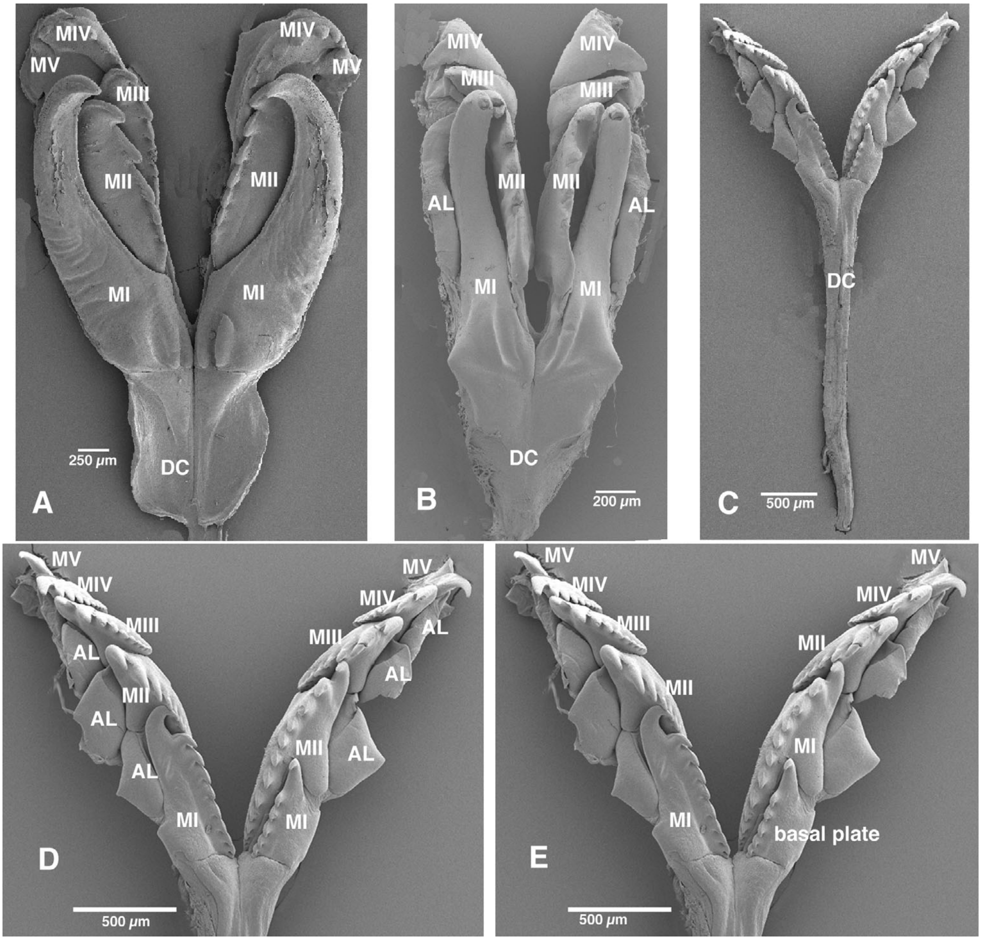

FIGURE 2. Maxillary apparatuses, dorsal view. A, *Australonuphis parateres* Paxton (Onuphidae); B, *Scoletoma gulielmi* (Benham) (Lumbrineridae); C, *Halla okudai* Imajima (Oenonidae); D, same, enlarged, labeled according to neontological convention; E, same, labeled according to paleontological convention. Abbreviations: AL, attachment lamella; DC, dorsal carrier; M, maxilla.

Original definition. Ehlers (1868) described the labidognath apparatus as having dissimilar elements. The eunicid/onuphid maxillae (Fig. 2A) clearly fit this description, as the MIII is present only on the left side and the right MIV is considerably larger than the left. However, the paired, symmetrical maxillae of a lumbrinerid (Fig. 2B) do not fit this definition. The second part of the definition, “MI and MII of each side surrounded by a semicircle of smaller anterior elements,” can be clearly seen in the onuphid jaw (Fig. 2A). Again, it does not apply for the lumbrinerid (Fig. 2B) where the anterior MIII and MIV are in a straight line, one in front of the other. Some lumbrinerid genera (e.g., *Lumbrineris* Blainville) have an edentate plate laterally to MIII or MIV, while it is absent in others. This plate has been regarded as MV by Orensanz (1990) and taken as representing the labidognath condition. I disagree with this interpretation. In my opinion it is not a maxillary plate but a lateral lamella. These lamellae are plesiomorphies, occur also in most oenonids and some dorvilleids, and will be discussed in more detail below.

The Prionognatha apparatus was described as having in each half more or less similar elements positioned in a row. The oenonid *Halla* Costa (Fig. 2C–E) with its small first right element does not quite fit the definition, but in the more common *Arabella* Grube the elements are more or less similar.

Dorsal carriers. Hartman (1944) added the possession of "carriers short, broad, embedded in pharyngeal tissue or absent" to the labidognath definition. These are present in all three families. They consist of two flat structures, connected by ligaments medially to each other and anteriorly to the MI. Except for the antero-median surface, which is covered only by a thin layer of connective tissue, the carriers serve as attachment site for a number of muscles, thus giving them mainly the function of an internal skeleton. Of importance is here the dorsal transverse carrier muscle (MTM 1 of Wolf 1980) which allows the dorsal folding of the carrier and therewith the spreading and closing of the maxillae. In Eunicidae and Onuphidae the carriers are short, rounded to heart-shaped, sometimes slightly longer than broad (Fig. 2A). At their anterior end, the carriers are closely linked to the forceps-like MI. The lumbrinerid carriers are of triangular shape, always longer than broad (Fig. 2B), sometimes longer than MI or with basal filiform extensions. The carriers are joined loosely, i.e., only the outer parts to the base of the MI, best seen in young specimens (Fig. 7D).

The dorsal carriers of prionognaths (Fig. 2C) are long and slender (Hartman 1944). The anterior parts are flat, medially joined by ligaments, forming more or less a triangle, that joins loosely with the MI. The posterior parts are long, slender shafts that are about four times as long as the MI. The prionognath apparatus lacks the dorsal transverse carrier muscle, so that the two carriers cannot fold dorsally. Their function is still to aid in the movement of the maxillae, but less in their spreading (Wolf 1980).

Ventral carrier. A third, flat carrier [also referred to as ventral unpaired piece (Hartman 1944); unpaired carrier (Wolf 1980); ventral ligament (Colbath 1989); median piece (Orensanz 1990)] is positioned ventral to the dorsal carriers, slightly above the ventral cavity of the pharynx. It originates at the posterior end of the dorsal cavity like the dorsal carriers, is generally of oval shape, about the width of the combined dorsal carriers but shorter. The ventral carrier ranges from unsclerotized to moderately sclerotized, never black in color like the dorsal carriers. This ventral carrier was considered as characteristic for the prionognath jaw type and thought to be present only in the Oenonidae (Hartman 1944). It has never been observed in fossil prionognaths which was ascribed to its delicate nature (Wolf 1980). Although the ventral carrier had never been reported to be present in eunicids, structures that could be interpreted as such have been described and labeled as tendon (Hartmann-Schröder 1967), epithelial blade (Desière 1967) and aponeurotic caudal extension of the maxillary fold cuticle or S-DM3 (Wolf 1980). The large maxillary retractor muscle [DM 3 of Wolf; *nappe musculaire* N1 of Desière] attaches to the lateral edges of this structure, i.e., the same muscle that attaches to the lateral edges of the ventral carrier of *Arabella* (see Wolf, 1980: fig. 13).

I am here confirming the presence of this structure in species of Eunicidae. I am identifying the structure as the ventral carrier, since it is of the same structure, position, and muscular insertion as the ventral carrier of Oenonidae. The ventral carrier is also present in Onuphidae, but not Lumbrineridae. The previous authors probably did not recognize the ventral carrier in eunicids as such because it is more deeply buried in the muscle than in oenonids and not sclerotized. My findings are the result of a new method of jaw preparation. Instead of removing the attached muscles by dissection, the worms were left to decompose before the pharynx was pulled out through the mouth. Structures that are normally deeply buried in muscle, such as cuticle, ligaments, aponeurotic filaments, and the ventral carrier became clearly visible (Fig. 3). In the ventral view of *Eunice* sp. (Fig. 3D) we see that the ventral carrier is a continuation of the maxillary folds. The ventral carrier of *Eunice* sp. appears as a fluted structure, while those of *Australonuphis parateres* Paxton (Fig. 3E–F) and *Marphysa* sp. (Fig. 3G–H) are flat, oval structures like in most oenonids.

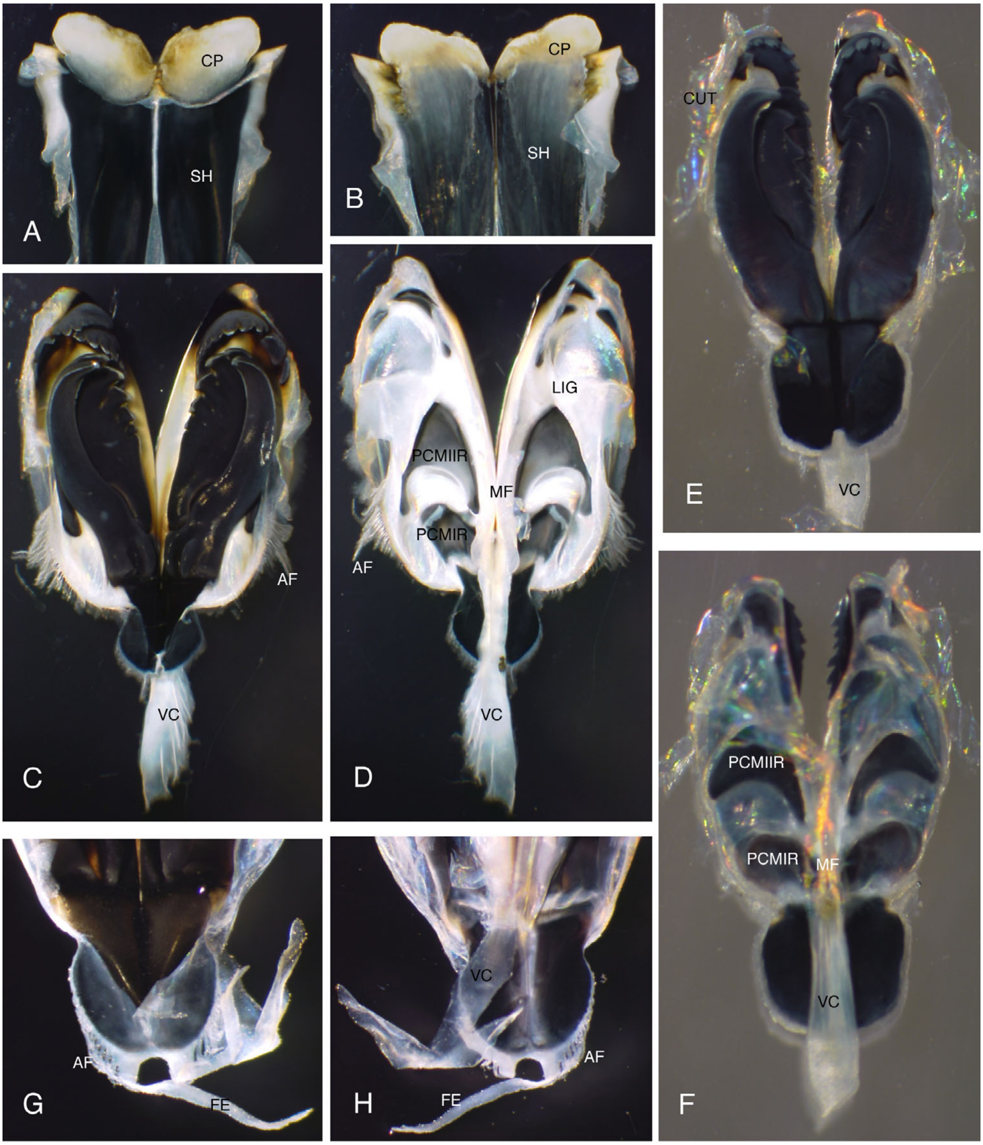

FIGURE 3. Jaws with ligaments intact. A, Upper part of mandibles of *Eunice* sp. (Eunicidae), ventral view; B, same, dorsal view; C, maxillary apparatus of *Eunice* sp. dorsal view; D, same, ventral view; E, same of *Australonuphis parateres* Paxton, dorsal view; F, same, ventral view; G, enlarged carrier area of *Marphysa* sp., dorsal view; H, same, ventral view. Abbreviations: AF, aponeurotic filaments; CP, cutting plate; CUT, cuticle; FE, filiform extension; LIG, ligament; PC, opening to pulp cavity; MF, maxillary fold; SH, shaft; VC, ventral carrier.

Wolf (1980: fig. 12A) indicated the S-DM 3 fold extension also for *Lumbrineris fragilis* Müller, positioned ventral to the dorsal carriers in a cross section. Inspection of the ventral side of the MI/carrier area of oenonids/eunicids/onuphids shows that the maxillary folds fuse at the MI/carrier junction to become the ventral carrier (Fig. 4A), while in the lumbrinerid they fuse more anteriorly and form only a short single ligament that terminates at the level of the MI/carrier junction (Fig. 4B). Another interesting difference between the pharynges of the eunicids and lumbrinerids that has not been previously mentioned is that the muscular bulb of the lumbrinerid is much shorter than that of the eunicid. While the eunicid pharynx extends almost the length of the entire jaw apparatus beyond the dorsal carriers, that of the lumbrinerid extends for less than the length of the carriers.

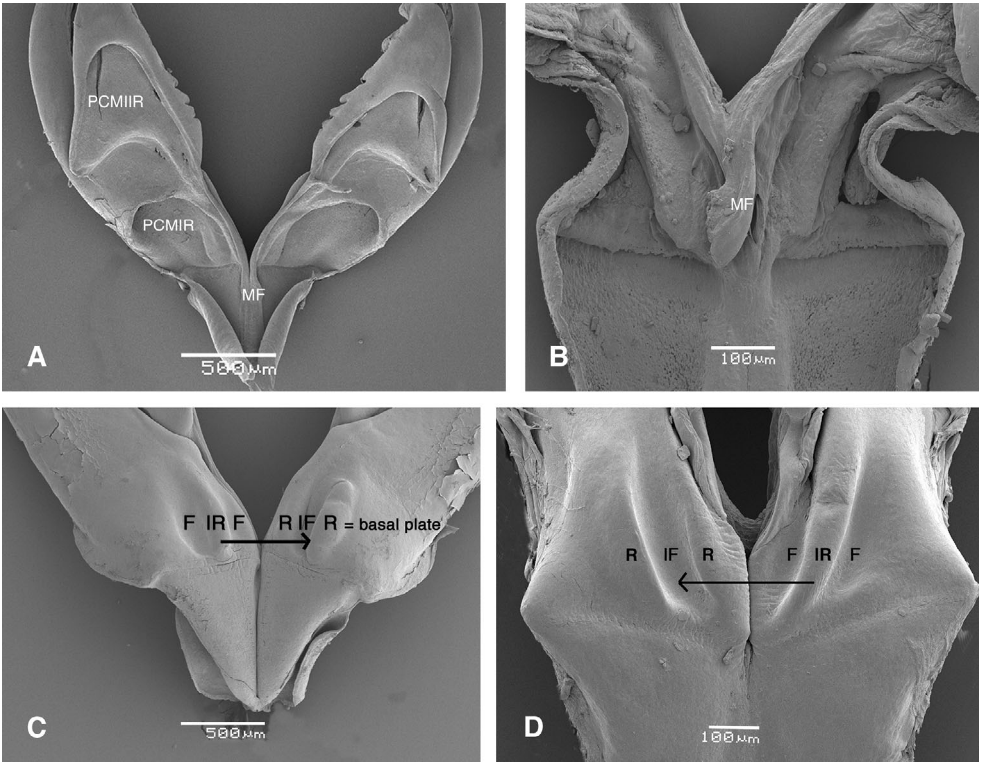

FIGURE 4. Maxillary apparatuses. A, *Australonuphis parateres* Paxton, ventral view; B, *Scoletoma gulielmi* (Benham), ventral view; C, *A. parateres*, area of MI locking system, dorsal view; D, *S. gulielmi*, same. Abbreviations: F, furrow; lF, large furrow; lR, large ridge; MF, maxillary fold; PC, opening to pulp cavity; R, ridge.

Filiform extensions of dorsal carriers. The new method of jaw preparation resulted in another discovery. The dorsal carriers of *Marphysa* sp. have unsclerotized filiform basal extensions that are slightly longer than the carriers themselves (Fig. 3G–H). Similar structures are absent in *Eunice* sp. and the distribution of this characteristic needs further investigation. However, the filiform extensions, indicating relic long dorsal carriers, together with the presence of ventral carriers and long pharyngeal bulbs indicate a much closer relationship between Eunicidae and Oenonidae than had previously been suggested based on morphological characters.

Maxilla I. The orientation of MI and MII is quite different among the so-called labidognaths. In the lumbrinerid (Fig. 2B) both pairs of these maxillae are directed dorsally, as they are in fossil placognaths and ctenognaths, while in the eunicid and onuphid (Fig. 2A) they are directed medially and only slightly dorsally, making it the derived state.

The MI is falcate in eunicids/onuphids (Fig. 2A) and lumbrinerids (Fig. 2B) and has a basal hinge structure that allows it to lock the left and right side. This is aided by the transverse muscle of the dorsal carriers. In the oenonids (Fig. 2C–E) the MI is dentate and lacks the locking system as well as the transverse carrier muscle. The locking system has been variously referred to as *Druckknopf* (snap)-*Struktur* (Hartmann-Schröder 1967), *Gelenk* (hinge)-*Struktur* (Wolf 1980) or interlocking ridge and furrow system (Colbath 1989). Since the locking system is present in typical labidognaths and lumbrinerids, it was considered as a characteristic for the labidognaths (Wolf 1980; Colbath 1989). However, on close examination, there are important differences in the systems of the eunicids/onuphids and lumbrinerids. In the former there are two furrows and a large ridge on the left side and two ridges and a large furrow on the right (Fig. 4C). The large ridge of the left side fits into the large furrow on the right side. In the lumbrinerids, however, there are two ridges and a large furrow on the left side and two furrows and a large ridge on the right side (Fig. 4D). Here the right large ridge fits into the left large furrow. This is not just a simple reversal. The ridges are not homologous. The right outer ridge of the eunicid/onuphid is the "basal plate" that will be discussed in detail below. In contrast, the large ridge of the right and the inner ridge of the left side of the lumbrinerid are the continuations of the cutting edge. This implies that while the maxillae I of so-called labidognaths may be derived from the same early eunicidan plates, the actual MI forceps evolved independently in the lumbrinerids and eunicids/onuphids.

Maxilla II and attachment lamellae. In the eunicid/onuphids, the maxilla II is cone-like and the pulp cavity is mainly enclosed, except for the basal opening (Fig. 5A). The maxilla II wraps around the MI, so that the two maxillae influence each other's movements. The oenonid MII (Fig. 5B) is cone-like to plate-like, with a wide- open ventral pulp cavity, wraps slightly around the MI with little cooperation between the two maxillae. The lumbrinerid MII (Fig. 5C) is plate-like, ventrally wide open, and does not touch the MI. The eunicid MII lacks lateral attachment lamellae, while both the oenonid and lumbrinerid have large ones. The oenonid MII is similar to the eunicid but at a simpler level, while the lumbrinerid has the simplest structure and function (Wolf 1980).

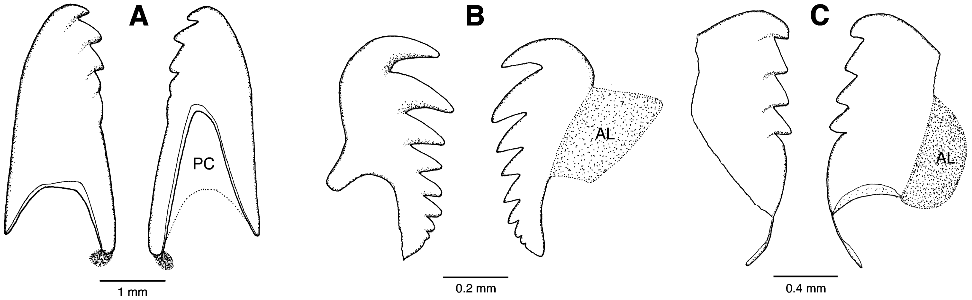

FIGURE 5. Maxilla II. A, *Marphysa* sp. (Eunicidae), dorsal and ventral view; B, *Halla okudai* Imajima (Oenonidae), outer and inner lateral view; C, *Scoletoma gulielmi* (Benham) (Lumbrineridae), same views. Abbreviations: AL, attachment lamella; PC, opening to pulp cavity.

Attachment lamellae are flat sclerotized plates that are either attached to maxillae as in the MII discussed above, or are separate lateral little plates that are called lateral lamellae. This terminology follows Wolf (1980), although the structures have also been referred to as callosities (Heider 1925; Desière 1967), paragnath plates (Orensanz 1990), accessory plates (Lu & Fauchald 2000), and bridles (associated with MI of lumbrinerids) (Orensanz 1990). Lateral plates and lamellae are difficult to represent in illustrations of maxillary apparatuses and therefore often neglected. Lateral plates have been reported for only one species of Dorvilleidae (Lu & Fauchald 2000). Onuphids and eunicids lack lateral lamellae, but have attachment lamellae associated with the MIII and MIV. Both attachment and lateral lamellae are prominent in oenonids and lumbrinerids and are very important for the propulsion of the jaw apparatus (Wolf 1980).

Hartmaniellidae. The enigmatic family Hartmaniellidae is represented by only a few Recent species and fossils from the Carboniferous to Triassic (Szaniawski & Imagima 1996). Its soft morphology is similar to Orbiniidae but it has a eunicidan jaw apparatus (Fig. 8J). Orensanz (1990) considered the maxillae of the labidognath type while Rouse & Fauchald (1997) interpreted the jaws as closer to Lumbrineridae and Oenonidae. The maxillae are almost symmetrical, except for two small elements constituting the left MIII (? and MIV), while on the right side there is only one element, about the size of the combined two left ones. Carrera-Parra (2003) interpreted this as an asymmetric maxillary apparatus of the labidognath type. I cannot concur with that interpretation. I consider the Hartmaniellidae maxillae as subsymmetrical and among Recent eunicidans as most closely related to Lumbrineridae.

Re-evaluation of ctenognath jaw type

The ctenognath jaw type holds a particular fascination for the evolutionary biologist. Although it is still uncertain whether it is the oldest known eunicidan fossil type (Hints & Eriksson 2007), it has been regarded as the most primitive living eunicidan (Orensanz 1990; Paxton 2000). These conclusions were based on morphological grounds but have been refuted by recent genetic studies (Struck *et al.* 2006). The Dorvilleidae are the Recent representatives of Ctenognatha. Iphitimidae has been proposed by Orensanz (1990) as a family for *Ophryotrocha* and related genera, but has not been widely accepted. The great diversity of dorvilleids has become obvious only during the past 30 years as the number of known genera has increased greatly, but the interrelationships are still unclear. Hilbig & Blake (1991) divided the Dorvilleidae into six informal groups of genera, while Eibye-Jacobsen & Kristensen (1994) carried out a phylogenetic analysis of the Dorvilleidae, Iphitimidae, and Dinophilidae, concluding that Iphitimidae represents a paraphyletic subgroup. Hilbig (1995) rejected Iphitimidae on the basis that some genera, e.g., *Anchidorvillea* would fall between the two families. The study of the anatomy and ultrastructure of the dorvilleid pharynx and jaws (Purschke 1987) and jaw growth and replacement in *Ophryotrocha labronica* Claparède & Mecznikow (Paxton 2004) have helped towards a better understanding of the ctenognath type of jaw to understand its intra- and interfamilial relationships.

Original definition. When Hartman (1944) revived Ehlers' (1868) labidognath and prionognath jaw types, she stated that the Dorvilleidae is of a third major type, but did not name it. Kielan-Jaworowska (1966) defined Ctenognatha as: “Jaw apparatus consisting of small, symmetrically arranged jaws in the posterior part and four rows of very numerous teeth in the anterior part, arranged in longitudinal series, extending for more than half the length of the apparatus. Carriers lacking. Jaws of the posterior part with gaping or narrowly open pulp cavities.”

The diversity of ctenognath jaw patterns is truly amazing and it is impossible to devise a definition that does justice to all. In this re-evaluation I am trying to isolate unifying themes that can be recognized in the different patterns.

Carrier-like structures. Carriers like those of the labidognaths and prionognaths are absent in ctenognaths. However, at least two different types of carrier-like structures are present. Some of the smaller bodied genera lack them completely, presumably due to secondary loss. The first type of structure occurs in *Dorvillea* Parfitt and related genera and has been referred to as carriers by neontologists (e.g., Fauchald 1970; Jumars 1974; Oug 1978) or carrier-like jaws (Wolf 1980) and basal and laeobasal plates by paleontologists (e.g., Kielan-Jaworowska 1966). The carriers or basal plates are positioned laterodorsally to the posterior maxillary plates, are dentate or smooth, separate or posteriorly united, and will be referred to as dorsal carrier-like structures. The extinct *Tetraprion* (Fig. 8C) and extant *Dorvillea* (Fig. 6A) belong to this group. Besides these dorsal carrier-like structures, the superior basal plates can also be fused basally, as in *Dorvillea (Schistomeringos) longicornis* Ehlers.

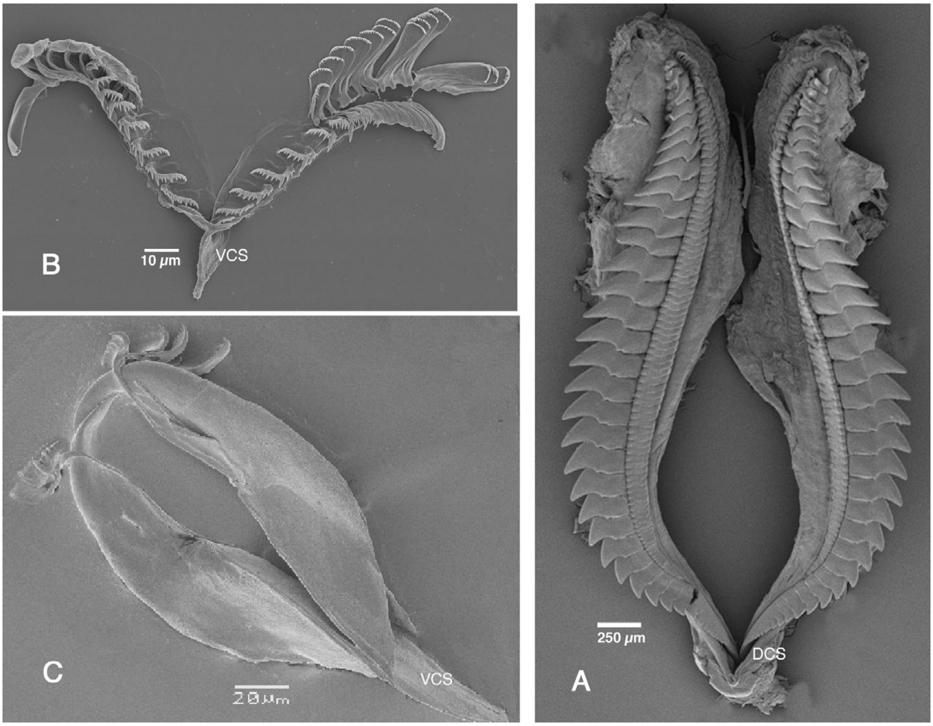

FIGURE 6. Dorvilleidae maxillary apparatuses, dorsal views. A, *Dorvillea australiensis* (McIntosh); B, *Parougia albomaculata* (Åkesson & Rice); C, *Ophryotrocha labronica*_La Greca & Bacci. Abbreviations: DCS, dorsal carrier-like structure; VCS, ventral carrier-like structure; A by M.O. Macnaughton.

Other genera, e.g., *Parougia* Wolf and *Ophryotrocha* Claparède & Mecznikow, lack the dorsal carrier-like structures but their basally fused maxillary plates continue as toothless structures that form another kind of carrier. These structures have been called carrier-like structures (Purschke 1987; Paxton 2004), or the combined structure as forceps composed of fused maxillary carriers and basal plates (Hilbig & Blake 1991). In his study of *Ophryotrocha gracilis* Purschke (1987: fig. 3B) has shown that the carrier-like structure is the continuation of the maxillary fold after the two sides have basally united, similar to the ventral carriers in oenonids/eunicids/onuphids and will here be referred to as ventral carrier-like structures.

The ventral carrier-like structures range from simple connections of the superior base plates as in *Anchidorvillea* (Hilbig & Blake 1991: fig. 24) to the vertical extension of the fused continuation in *Parougia* (Fig. 6B) to its most complex form found in *Ophryotrocha.* Here the large vertical plate is wedged between the posterior part of the forceps and extends beyond (Fig. 6C).

Base plates and anterior denticles. The major posterior maxillary elements of the *Dorvillea* group and the extinct *Tetraprion* Kielan-Jaworowska are referred to by neontologists as inferior and superior base plates following Fauchald (1970) and maxilla I and maxilla II by paleontologists as proposed by Kielan-Jaworowska (1966). Each of these elements is continued anteriorly by a row of anterior denticles. Species of the *Parougia* group lack the inferior base plate. The forceps element of *Ophryotrocha* is a derived structure and represents the fusion of the ventral carrier-like structure and the superior base plate. It has a reduced number of anterior denticles, typically consisting of three coarsely serrated superior and four finely serrated inferior denticles. Besides these most common types of dorvilleid jaws, there are genera that lack base plates and have varying numbers of rows of free denticles such as *Pettiboneia* (Hilbig 1995: fig. 13.7).

Histriobdellidae. The affinities of Histriobdellidae, tiny polychaetes with a eunicidan jaw apparatus that live as commensals on crustaceans, are still unclear (Orensanz 1990, Rouse & Pleijel 2001). Because of their long maxillary carriers Rouse & Fauchald (1997) considered the jaws of the prionognath type, while Tzetlin (1980) placed the family near Dorvilleidae. Since the histriobdellid jaws are unlike any of the recognized types, their relationship to other eunicidan families must await further study.

Xenognatha or Ctenognatha? Mierzejewski & Mierzejewska (1975) proposed the term Xenognatha for a symmetrical jaw apparatus consisting of two compound jaws and a pseudocarrier. The specimens came from the Upper Ordovician of Poland and were described as *Archaeoprion quadricristatus* Mierzejewski & Mierzejewska. Meanwhile they have been reported from the late Mid Ordovician to the Silurian (Hints & Eriksson 2007). When describing the new jaw type, the authors stated that the Archaeoprionidae represented a hitherto unknown phylogenetic line in polychaete evolution, and considered them as the most ancestral type of jaw development. The paired plates of *Archaeoprion* have four denticulated ridges each (Fig. 8D). The most posterior ridge has none or only a few teeth. The number of teeth increases in the next ridges to 16–20 in the fourth and terminal ridge, with the outermost teeth being the largest.The structure is remarkably similar to the superior base plates with fused ventral carrier-like structure of *Parougia* (Fig. 6B). Here the superior base plates consist of up to six fused denticulated ridges, each with a series of teeth, resembling the ridges of *Archaeoprion*. Just as in that genus, the most posterior ridges have the fewest teeth and the outermost ones are largest in *Parougia*. Mierzejewski & Mierzejewska (1975) stated that all elements of the apparatuses were yellow and transparent and only the teeth were brown. The same applies to *Parougia*. The dentate ridges are heavily sclerotized, while the remaining part of the base plate is almost clear. The single, long and vertical pseudocarrier of *Archaeoprion* appears very similar to the ventral carrier-like structures described above. Mierzejewski & Mierzejewska (1975) described it as wedged between the posterior parts of the jaw which they indicate in their drawing. However, judging from the photomicrograph of the actual specimen it could well have been a fused continuation of the jaws as we see in *Parougia.* I conclude that *Archaeoprion* represents the fused superior base plates and ventral carrier-like structure of a eunicidan jaw of similar architecture to the Recent *Parougia*, and thus of the ctenognath jaw type. *Archaeoprion* either did not have the free anterior denticles that are associated with the base plates of *Parougia*, or they have not been preserved.

Ontogeny

Larval development of eunicidans, and particularly the development of the jaw apparatus, has been studied for several onuphids, but only a few eunicids, lumbrinerids, and dorvilleids, while there is only anecdotal information on oenonids. Although the eunicidan mandibles grow throughout the life of the animal, the maxillary apparatus has to molt, or be replaced with a larger one, to keep up with the general growth of the animal (Paxton 2006). In all families studied, the first (larval) and second (juvenile) stages differ from each other and the final adult one, resembling in some ways their ancestral lineage, thus providing important clues to the phylogeny of the group, in a broad sense of the biogenetic law (Gould 1977; Nelson 1978).

Onuphidae. Larval and juvenile jaws have been reported for ten species of Onuphidae, although most of these reports were anecdotal (Paxton & Safarik 2008). The most complete studies are of *Kinbergonuphis simoni* Santos *et al.* following the development of larval to adult maxillae and confirming the replacement of larval maxillae by ‘’adult types’’ (Hsieh & Simon 1987), and of *Diopatra aciculata* Knox & Cameron, describing the developmental stages of the jaws, calculating the molt increments in maxillae and estimating size classes from fertilization to 45 days of age (Paxton & Safarik 2008).

The onuphid larval jaws are black like adult dorvilleids and oenonids, indicating that they are completely sclerotized. They consist of a single narrow carrier, a large serrated left fang-like element, a very small serrated right element, a large pair of serrated plates, and a distal pair of ridges (Fig. 7A). These larval jaws show no resemblance to the adult onuphid jaws and it has been remarked that they resemble dorvilleid jaws (Orensanz 1990). The carrier appears to be a tube-like structure and articulates with the left fang-like element and right small plate. The large left fang-like element is almost identical in its serration in all species so far studied. It has a large distal fang, several large teeth, and the proximal half is finely serrated. This kind of element is unknown in Recent eunicidan jaws but a single element of a similar structure has been reported as *Dualigenys erecta* Courtinat from the Jurassic of France and likened to the larval onuphid fang (Courtinat 1998). The tiny right element can be recognized in the very first report of an onuphid larval jaw by Krohn & Schneider (1867) while most other reports did not mention it. The large left and small right elements are here interpreted as maxillae I. A small right MI is known for oenonids, as for example *Halla* (Fig. 2C–E) and has been referred to by paleontologists as basal plate. The large pair of serrated plates has been considered as maxillae II (Hsieh & Simon 1987). The serrations appear like fused plates, reminiscent of extinct ctenognath and placognath elements. The small right MI on the other hand, points to a slightly younger evolutionary stage, and indicates a common ancestry with the oenonids.

The juvenile jaws are not black but transparent with the more sclerotized areas appearing light brown like in a small adult, indicating weak sclerotization and presumably some mineralization. They consist of adult-like carriers and four pairs of maxillae (Fig. 7B). The paired MI are not falcate as in adults but are basally dentate with a distal fang as found in the oenonid *Arabella.* The MII are large dentate elements like in the adult and are followed by MIV-like elements. The single left MIII, typical of adult onuphids, is absent. The juvenile maxillae I reconfirm the shared eunicid/onuphid/oenonid lineage.

Eunicidae. Only two illustrated descriptions of larval eunicid jaws are available. Borradaile (1901) studied *Marphysa borradailei* Pillai, and Herpin (1925) studied *Eunice harassii* Audouin & Milne-Edwards. Both are depicted like the onuphid larval jaws without the small right MI. In view of the overall similarity of the jaws and the delicacy of this element, I presume that it is present in the Eunicidae but has been overlooked. No juvenile eunicid jaws are known.

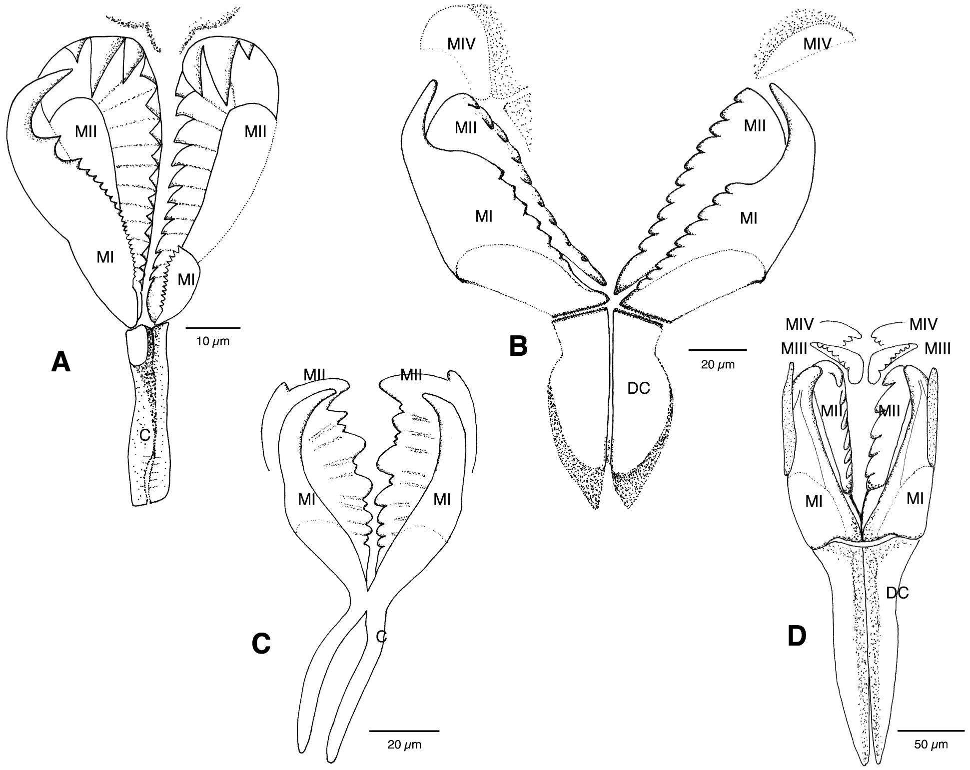

FIGURE 7. Developmental stages of maxillary apparatuses, dorsal views. A, Larval jaws of 4-chaetiger *Diopatra aciculata* Knox & Cameron (Onuphidae); B, juvenile jaws of 19-chaetiger of same; C, larval jaws of 8-chaetiger *Ninoe nigripes* Verrill (Lumbrineridae); D, juvenile jaws exuviae found in gut of 43-chaetiger of same. Abbreviations: C, carrier; DC, dorsal carrier; M, maxilla.

Oenonidae. Larval oenonid jaws have never been reported. Colbath (1989) observed juvenile jaws in four species of *Arabella*. Instead of the adult state of having basally dentate MI with a distal fang, the juvenile MI is dentate, with denticles projecting laterally rather than dorsally as in the adults. This indicates that jaws with dentate MI as in the fossil Polychaetaspidae (Fig. 8E) preceded the prionognath type of Atraktoprionidae (Fig. 8G), which is also supported by the timing of their records (Figs. 9–10).

Lumbrineridae. The reports of larval jaws of lumbrinerids agree that they are paired symmetrical structures consisting of carriers, MI and MII. Claparède & Mecznikov (1869) show the MI as falcate and MII as dentate, while Saint-Joseph (1888) described both MI and MII as dentate, MI with four and MII with six teeth, and also mentioned an additional pair of anterior elements with one tooth each. The larval jaws of *Ninoe nigripes* Verrill (Fig. 7C) were found to be very different from the onuphid jaws. The MI are symmetrical falcate structures that extend posteriorly into a pair of carriers. The MII are also paired large serrated plates but of a very different design from the onuphid ones. The teeth are rounded and alternate between large and small ones, and the left and right plates appear to interdigitate. There are also darker lines indicating fusion of plates but not as distinctly. This larval apparatus has similarities with the eunicids/onuphids in the symmetrical serrated MII with fusion lines, but differs greatly in the structure and symmetry of the MI and the carriers, suggesting a common early origin but evolution along a different line.

The figures of Fewkes (1885) and Okuda (1946) refer to juvenile jaws with short carriers, falcate MI, dentate MII and small MIII and MIV as in adults. The juvenile jaws of *N. nigripes* (Fig. 7D) differ slightly from adult jaws. They consist of the same type and numbers of elements but the dentation of MIII and MIV differs from the adult.

Dorvilleidae. The ontogeny of the dorvilleid jaw apparatus has been studied best for *Ophryotrocha*. In *O. labronica* and *O. puerilis* it goes through a distinct larval and juvenile stage before it reaches its adult K-jaw (Paxton 2004; Paxton & Åkesson 2007). It is known that in other genera the number of anterior denticles increases with consecutive molts (Jumars 1974), but I am not aware of any studies of the ontogeny of the jaw apparatus.

Symmetry and the basal plate concept

The maxillary apparatuses of Lumbrineridae are symmetrical (Fig. 2B) and those of the Dorvilleidae are nearly so (Fig. 6), but the majority of eunicidan jaws are asymmetrical. In the eunicids/onuphids (Figs. 2A, 3C, E) this is with respect to the left and right number of elements as well as with their proportions and shape. The left and right MI and MII are subsymmetrical, MIII is present only on the left, the right MIV is larger than the left, and only the small MV elements (and MVI when present) are alike. The presence of the larger right MIV and absence of MIIIR were considered by Hartman (1944) as the result of the fusion of the right MIII and MIV, a concept with which Kielan-Jaworowska (1966) disagreed. The Oenonidae (Fig. 2C–E) have a more diverse pattern. The number of left and right elements is equal but the counterparts are of a more or less different shape with the exception of *Drilonereis* Claparède which is symmetrical. In *Arabella* the MIR is usually smaller, and in *Halla* (Fig. 2C–E) and *Oenone,* the MIR is extremely reduced compared to the left.

This asymmetry can also be observed among the fossil eunicidans. Some placognaths have more right elements than left (Fig. 8B), and particularly in the early labidognaths (Fig. 8E) and prionognaths (Fig. 8G) the first right element is much smaller than the left one as we still find it in the oenonids *Oenone* and *Halla.* Kielan-Jaworowska (1966) referred to this plate as the basal plate. She referred to the paired plates lateral to the MI of placognaths (Fig. 8B) and ctenognaths (Fig. 8C) as laeobasal and basal plates for the respective left and right elements and developed the following concept. She speculated that the small first right element of early labidognaths and prionognaths is the homologue of the right basal plate while the laeobasal or left plate was lost. This concept is generally accepted by paleontologists but has not been followed by neontologists. In the early polychaetaspid labidognaths (Fig. 8E) this plate is about half the size of the MI, while in paulinitids it is much smaller. In the Paulinitidae we can observe over time how this small plate became more and more fused to the MIR until it was an integral part of maxilla I (Fig. 8F). Although totally fused, it can be observed as a pronounced ridge. And the same ridge is still present in Recent eunicids and onuphids. Actually, it is this ridge of MIR that forms part of the locking system. As to the Lumbrineridae, Kielan-Jaworowska (1966) assumed that they also evolved from the Paulinitidae (presumably before the basal plate was fused) and justified the symmetrical maxillae by the disappearance of one left element or the appearance of one extra right element, as well as the loss of both basal plates. Orensanz (1990) did not accept Kielan-Jaworowska's basal plate concept. He considered the small first right maxilla of *Oenone* and *Halla* as maxilla I, recognized its fusion with MI in Paulinitidae and stated that the first right element of extant eunicids and onuphids is the homologue of the left maxilla II. In agreement with Orensanz (1990) I believe that the basal plate concept is unnecessary. It requires some unparsimonious assumptions such as the loss of the laeobasal plate in eunicids/onuphids/oenonids, both plates in lumbrinerids, and does not explain the single MIIIL in eunicids/onuphids/oenonids.

Examination of homology/symmetry concept

The basal plates of the placognaths have been interpreted to be the result of division of the maxilla I (Kielan-Jaworowska 1966). This can be followed by comparing the secondary dentate rows on the MI of *Mochtyella* (Fig. 8A) with the free basal plates of *Pistoprion* (Fig. 8B). In the extinct ctenognath *Tetraprion* (Fig. 8C) there are similar plates lateral to the MI that are also considered as basal plates (Kielan-Jaworowska 1966), although there is no evidence as to their origin. Comparing the extant *Dorvillea* (Fig. 6A) to *Tetraprion*, it seems reasonable to consider the dorsal carrier-like structures of the former corresponding to the basal plates of the latter and presumably homologous.

The labidognaths and prionognaths have distinct flat carriers, but otherwise also markedly different patterns of design from the placognaths/ctenognaths. Most of the families are asymmetric, having an unpaired small first right element that was generally considered homologous to the right basal plate of the placognaths. Only Symmetroprionidae (Fig. 8H) was considered to have paired basal plates until Hints (1999) and Hints & Nolvak (2006) described symmetrical maxillary apparatuses from the Ordovician of Estonia. In *Kadriorgaspis* (Fig. 8I), typical labidognath carriers are attached to the MI. Hints (1999) noted that the conjungaspids display some characteristics common to placognaths and labidognaths, may be considered as intermediates and could represent a separate lineage (Hints & Nolvak 2006). Although Hints *in* Hints & Nolvak (2006) raised the question that the elements attached to the carriers of *Kadriorgaspis* might be homologous to the labidognath MI, he referred to them as laeobasal and basal plates.

The basal plate concept should be critically examined. There is no evidence that the elements connecting with the carriers in the conjungaspids and symmetroprionids are homologous to the basal plates of the placognaths. On the contrary, their position and articulation with the carriers characterize them more as maxillae I. Likewise, the more anterior pair resembles MII more than MI. Examining the labidognaths and prionognaths that have only the right basal plate makes the homology even more doubtful. In these labidognaths and prionognaths like *Atraktoprion, Oenone*, and *Halla* there are five elements on each side. Regarding the first right one as the basal plate we have to evoke the loss of the laeobasal plate and the gain of the left MIII or loss of the right MIII to account for all the elements. The basal plate concept becomes more dubious when we consider the ontogeny of the onuphid larval jaws. The first left element, large dentate forceps, the first right a small dentate element, presumably represent the first maxillary pair, or MI. The second elements are paired and dentate, appearing as MII. If this reasoning is correct, the same pattern would apply to early labidognaths such as *Oenonites* (Fig. 8E) and prionognaths such as *Atraktoprion* (Fig. 8G). The basal plate would be MIR, the present MIIR would be MIIIR etc. This means that the elements would all be paired, but would be asymmetric with their respective counterparts. The same would apply to paulinitids and extant eunicids/onuphids where the basal plate is fused with the MIR.

I am here presenting for consideration and reflection what I think is a more parsimonious concept of homology and symmetry of the eunicidan jaw elements. The families concerned in the neontological literature are the Eunicidae and Onuphidae where the right forceps are the homologue of the fused MIR and MIIR. I am advocating to acknowledge the evolutionary fact, but retaining the established terminology.

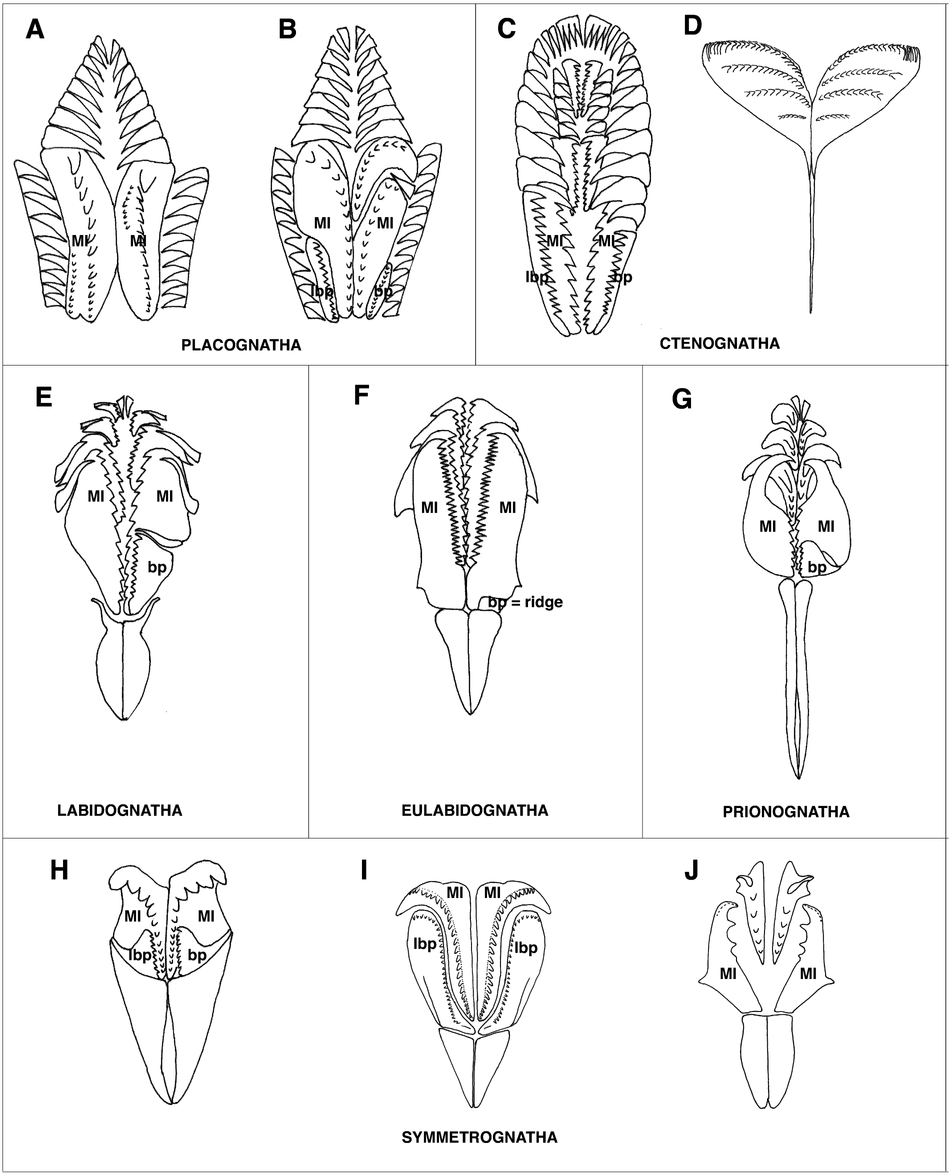

FIGURE 8. Maxillary apparatuses of fossils, dorsal view, labeled according to paleontological convention. A, *Mochtyella polonica* Kielan-Jaworowska (Mochtyellidae); B, *Pistoprion transitans* Kielan-Jaworowska (Mochtyellidae); C, *Tetraprion pozaryskae* Kielan-Jaworowska (Tetraprionidae); D, *Archaeoprion quadricristatus* Mierzejewski & Mierzejewska (Archaeoprionidae); E, *Oenonites wyszogrodensis* (Kozlowski) (Polychaetaspidae); F, *Kettnerites polonensis* (Kielan-Jaworowska) (Paulinitidae); G, *Atraktoprion cornutus* Kielan-Jaworowska (Atraktoprionidae); H, *Symmetroprion reduplicates* Kielan-Jaworowska (Symmetroprionidae); I, *Kadriorgaspis kaisae* Hints (Conjugaspidae); J, *Palurites jurassicus* (Hartmaniellidae). Abbreviations: lbp, laeobasal plate; bp, basal plate; M, maxilla; A—C, E—H, after Kielan-Jaworowska (1966: fig. 5), D after Mierzejewski & Mierzejewska (1975: fig. 1), I adapted from Hints & Nolvak (2006: plate II, figs. 5, 6), J after Szaniawski & Imajima (1996: fig. 1B).

Hypothesis of the phylogeny of Eunicida

The oldest known eunicidans are from the Late Cambrian (490 MYA) and had primitive placognath/ctenognath type jaws (Hints & Nolvak 2006). Recent discoveries of Early Ordovician (480 MYA) fossils showed that early eunicidans were more diverse than previously indicated but their abundance and diversity were still low compared to the Mid and Late Ordovician (Hints & Eriksson 2007). Although uncertainties still exist, I am here presenting a consideration of the eunicidan relationships, attempting to combine evidence from morphology, ontogeny, and fossil records of eunicidan jaws (Figs. 9–10). I am combining the cladogram with a time scale from the Upper Cambrian to the Lower Silurian as Hints & Nolvak (2006) stated that the 'advanced' forms are likely to have originated in the late Early or early Mid Ordovician.

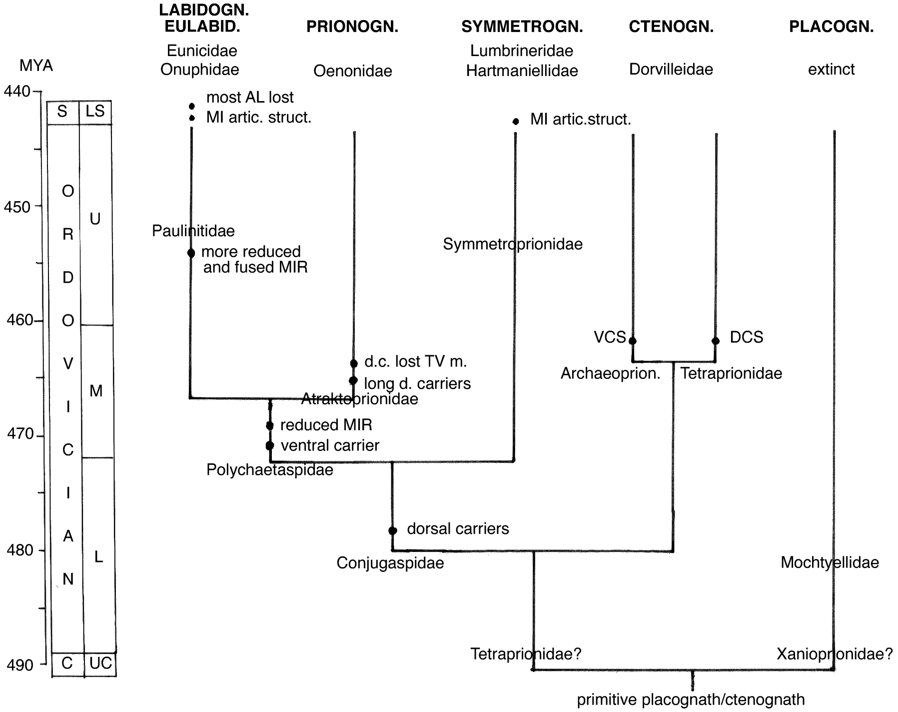

FIGURE 9. Hypothetical cladogram of Eunicida phylogeny based on assumption that dorsal carriers evolved only once. Abbreviations: AL, attachment lamellae; MI artic. struct., maxilla I articulation structure; d.c. lost TV m., dorsal carriers lost transverse muscles; DCS, dorsal carrier-like structure; VCS, ventral carrier-like structure; time scale after Webby et al. 2004.

The Eunicida is the only group of annelids with a jaw apparatus consisting of mandibles and maxillae. The mandibles of the different families are exceedingly similar (Fig. 1) and also similar to the earliest fossil mandibles. The similarity of early placognath, ctenognath, and symmetrognath maxillae (Fig. 8) is strong evidence of monophyly of the group. In the genetic analyses of Struck et al. (2006) monophyly of the Eunicida was not resolved in the 43-taxon 18S data set, but in the four-gene analyses with limited taxon sampling.

The probable ancestors may have been primitive placognath/ctenognath-like forms. Hints & Eriksson (2007) report Late Cambrian (490 MYA) questionable tetraprionids (ctenognath) and xanioprionids (placognaths). The earliest confirmed placognaths are mochtyellids from the Early Ordovician (480 MYA). They consisted of symmetrical plates with single dentate ridges that became compound and asymmetrical by the Mid Ordovician. They had small lateral and anterior teeth but lacked carriers (Fig. 8A). Placognaths became extinct by the end of the Permian.

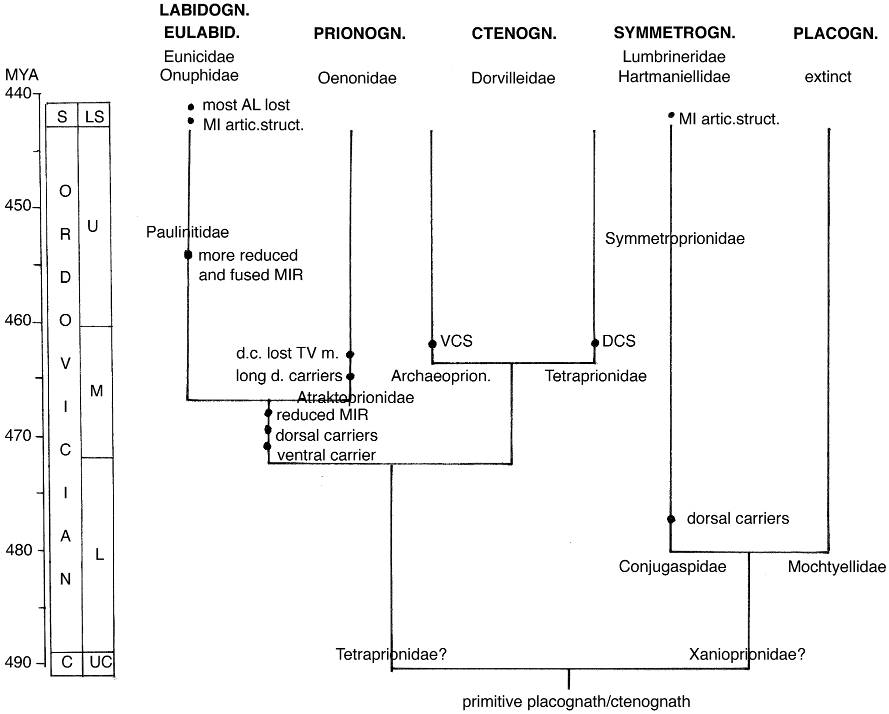

FIGURE 10. Hypothetical cladogram of Eunicida phylogeny based on assumption that carriers evolved twice independently. Abbreviations: AL, attachment lamellae; MI artic. struct., maxilla I articulation structure; d.c. lost TV m., dorsal carriers lost transverse muscles; DCS, dorsal carrier-like structure; VCS, ventral carrier-like structure.

The early ctenognaths appear to have given rise to the modern Ctenognatha and the remaining eunicidans (Fig. 9), although it is a curious fact that the earliest confirmed ctenognath *Tetraprion*, and *Archaeoprion*, considered here as ctenognath, have not been collected yet in strata older than latest Mid Ordovician (462 MYA). As discussed above, the ctenognaths fall into two lines: (1) the *Dorvillea* (Fig. 6A) line, possessing dorsal carrier-like structures, and including *Protodorvillea* etc. and probably deriving from *Tetraprion* and (2) the *Parougia* (Fig. 6B) line, lacking these carriers but having ventral carrier-like structures, and including *Ophryotrocha* etc. and perhaps deriving from *Archaeoprion*. These two lines are supported by genetic analyses (Struck et al. 2006: fig. 2) and represent the Dorvilleidae and Iphitimidae respectively. The architecture of the carrier-like structures and presence/absence of the inferior base plates demonstrates the distinctness of the two lines. The jaw structure and ancient separation of the two lines supports recognition of Iphitimidae. However, soft morphology of certain genera is not as clear cut (Hilbig 1995). This is best demonstrated by *Parougia*, clearly an iphitimid genus based on its jaws as defined here. However, its soft morphology is *Dorvillea*-like and was considered a dorvilleid by Orensanz (1990). Morphological revision and genetic analyses based on a greater number of taxa are needed to solve this question.

Early Ordovician eunicidans of a different jaw type were discovered recently (Hints & Nolvak 2006). *Kadriorgaspis* Hints (Fig. 8I) have a symmetrical maxillary apparatus and are the oldest known eunicidans with carriers (480 MYA). When Hints (1999) described the Conjugaspidae he considered their jaw type as uncertain as they appeared intermediate between the placognaths and labidognaths. I am proposing a new architectural jaw type, Symmetrognatha, for these and similar forms. Of the extant eunicidans, I consider the Lumbrineridae and Hartmaniellidae as part of this group (Table 1). As was demonstrated above, the Lumbrineridae are not of the labidognath type. It was shown that the falcate MI, the MII, and anterior elements of the lumbrinerids are structured differently from those of labidognaths. This is supported by the ontogeny of the jaws. In the lumbrinerid larval jaws the carriers are continuations of the MI, and the MII are symmetrical, while in eunicids/onuphids the respective structures are articulated and asymmetrical. The articular structure of the MI, allowing the forceps to lock, is an apomorphism of the Lumbrineridae that evolved independently of a similar structure in the eunicids/onuphids as was discussed above. The calcite mineralization of the maxillae was thought to be restricted to lumbrinerids and considered an apomorphy, while eunicids/onuphids were mineralized with aragonite (Colbath 1986). However, recent analyses showed that some eunicids and onuphids were mineralized with calcite, indicating that the type of mineralization may be due to environmental rather than genetic influences (Fauchald pers. com.). Assuming that dorsal carriers evolved once only, the Symmetrognatha are here considered the sister group of the asymmetric Labidognatha and Prionognatha. The earliest labidognaths are the Polychaetaspidae (Fig. 8E) from the early Mid Ordovician (469 MYA). The synapomorphies of the clade are the presence of a single ventral carrier (at least in Recent forms), and a very reduced right MI that has also been referred to as the basal plate. As discussed above, I view the small element as a reduction of the MIR rather than a homologue of the placognath basal plate. The asymmetry that we see in this extensive clade is thus caused by the realignment of the left and right side of the maxillary apparatus rather than the gain/loss of elements. The early members of this group with dentate MI appear more like prionognaths except for the short carriers.

The prionognaths developed the extremely long dorsal carriers and lost the transverse carrier muscles. The two events may have been connected for functional reasons. The earliest known prionognath, *Atraktoprion* (Fig. 8G), is from the Mid Ordovician (465 MYA) and looks remarkably like the Recent *Halla* (Fig. 3C). Species of the latter genus have not changed much over time, and are basically living fossils.

Traditionally, all jaws with short carriers have been treated as labidognath. When Ehlers (1868) established the designation he intended it for Recent forms with forceps-like maxillae I. Kielan-Jaworowska (1966) widened the term to include fossils with dentate MI for their short carriers. I am redefining the Labidognatha here (Table 1) by retaining the term for the fossil forms with reduced MIR and proposing Eulabidognatha for forms having an extremely small right MI that is more- or-less fused with the right forceps as in the Paulinitidae which are generally accepted as the ancestors of eunicids and onuphids (Kielan-Jaworowska 1966; Orensanz 1990). The oldest known fossil of this type is *Kettnerites* (Fig. 8F) from the Late Ordovician (454 MYA). Other apomorphies of the Recent eulabidognaths are the articular locking structure of the forceps and the loss of most attachment lamellae.

TABLE 1. Eunicidan architectural jaw types.

Jaw type	Definition	Age	Fossil families	Recent families
Placognatha	Symmetrical to asymmetrical; posterior elements plate-like; 2 anterior rows of denticles; carriers lacking	?Late Cambrian to Permian	Mochtyellidae Rhytiprionidae Xanioprionidae	—
Ctenognatha	Symmetrical to subsymmetrical; posterior elements plate-like; 4 or more rows of very small numerous denticles; carriers lacking	?Late Cambrian to present	?Archaeoprionidae Dorvilleidae ?Iphitimidae Tetraprionidae	Dorvilleidae ?Iphitimidae
Symmetrognatha	Symmetrical; posterior elements dentate to forceps-like; conical; 4 pairs of elements in 2 rows; short to moderately long carriers	Early Ordovician to present	Conjugaspidae Hartmaniellidae Symmetroprionidae	Hartmaniellidae Lumbrineridae
Labidognatha	Asymmetrical; posterior elements dentate; conical to plate-like; MIR reduced (basal plate); 5 pairs of elements in 2 rows; short to moderately long carriers	Mid Ordovician to Cretaceous	Hadrioprionidae Kalloprionidae Kielanoprionidae Polychaetaspidae Polychaeturidae Rhamphoprionidae	—
Eulabidognatha	Asymmetrical; posterior elements dentate to forceps-like; conical; surrounded in front by 2 semicircles of anterior elements; MIR very reduced/fused; 5-6 pairs of elements; short carriers	Late Ordovician to present	Paulinitidae	Eunicidae Onuphidae
Prionognatha	Asymmetrical; posterior elements dentate; conical to plate-like; MIR reduced (basal plate); 5 pairs of elements in 2 rows; long carriers	Mid Ordovician to present	Atraktoprionidae	Oenonidae ?Histriobdellidae
Xenognatha (see Ctenognatha)				

This phylogeny of Eunicida differs from the traditional proposals (Hartman 1944) by demonstrating that the Lumbrineridae are not of the labidognath jaw type and thus not closely related to the Eunicidae and Onuphidae. The sister group relationship of the Eunicidae/Onuphidae and

Oenonidae also differs greatly from the traditional view but is supported by the genetic 18S analysis and in slightly different configuration in the four-gene analysis proposed by Struck et al. (2006).

The remaining discrepancy with genetic analyses concerns the position of the Lumbrineridae and Dorvilleidae. Several genetic analyses place the Lumbrineridae at the most basal position (Struck et al. 2002a, b; 2006) or even outside the Eunicida (Rousset et al. 2007). This could be the result of some inherent problem with the analyses of these families. On the other hand, it may require some rethinking about the evolution of the jaws. For the above phylogeny (Fig. 9) I have assumed that the dorsal carriers evolved once only. This was based on their structure, muscle attachment, and function. Although the larval lumbrinerid carriers are very different from those of eunicids/onuphids, they are of a more primitive type that could have evolved into prionognath and labidognath carriers in turn. The fact that the lumbrinerid and oenonid adult carriers are attached only loosely at their outer edges to the MI, while the eunicids/onuphids are attached tightly across the total carrier/MI interface, supports this model. Although it seems unlikely, the carriers could have evolved twice, first in the symmetrognath *Kadriorgaspis* (Fig. 8I) and independently in the labidognath Polychaetaspidae (Fig. 8E). Such a scenario is depicted in Fig. 10. I would still expect the ancestor to have been a primitive placognath/ctenognath as this is supported by the fossil record. It is hoped that future advancements in genetic analyses and/or studies of morphology, ontogeny, and finds of early fossils will provide the answer to this conundrum.

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References

Borradaile, L.A. (1901) On the spawn and young of a polychaete worm of the genus *Marphysa*. *Proceedings of the Zoological Society London*, 2, 714–720.

Carrrera-Parra, L.F. (2003) Redescription of *Hartmaniella tulearensis* n. comb. (Amoureux, 1978) with comments on *Hartmaniella* sp. and affinities of the family (Polychaeta: Hartmaniellidae). *Journal of Natural History*, 37, 49–55.

Claparède, E. & Mecznikov, E. (1869) Beiträge zur Kenntnis der Entwickelungsgeschichte der Chaetopoden. *Zeitschrift für wissenschaftliche Zoologie*, 19, 163–205.

Colbath, G. K. (1986) Jaw mineralogy in eunicean polychaetes (Annelida). *Micropaleontology*, 32, 186–189.

Colbath, G. K. (1989) Revision of the family Lysaretidae, and recognition of the family Oenonidae Kinberg, 1865 (Eunicida: Polychaeta). *Proceedings of the Biological Society of Washington*, 102, 116–123.

Colgan, D.J., Hutchings, P.A. & Braune, M. (2006) A multigene framework for polychaete phylogenetic studies. *Organisms Diversity & Evolution*, 6, 220–235.

Courtinat, B. (1998) New genera and new species of scolecodonts (fossil annelids) with paleoenvironmental and evolutionary considerations. *Micropaleontology*, 44, 435–440.

Desière, M. (1967) Morphologie de l'organe buccal ventral de *Marphysa bellii* (Audouin & Edwards) (Polychète, Eunicidae). *Annales Societé Royale Zoologique Belgique,* 97, 65–90.

Edgar, D.R. (1984) Polychaetes of the Lower and Middle Paleozoic: a multi-element analysis and a phylogenetic outline. *Review of Palaeobotany and Palynology*, 43, 255–284.

Ehlers, E. (1868) *Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt.* Engelmann, Leipzig, 748 pp.

Eibye-Jacobsen, D. & Kristensen, R.M. (1994) A new genus and species of Dorvilleidae (Annelida, Polychaeta) from Bermuda, with a phylogenetic analysis of Dorvilleidae, Iphitimidae and Dinophilidae. *Zoologica Scripta*, 23, 107–131.

Fauchald, K. (1970) Polychaetous annelids of the families Eunicidae, Lumbrineridae, Iphitimidae, Arabellidae, Lysaretidae and Dorvilleidae from Western Mexico. *Allan Hancock Monographs in Marine Biology,* 5, 1–335.

Fewkes, J.W. (1885) On the development of certain worm larvae. *Bulletin of the Museum of Comparative Zoology Harvard*, 11, 168–208.

Gould, S.J. (1977) *Ontogeny and phylogeny.* Harvard University Press, Cambridge and London. 501 pp.

Hall, K. A., Hutchings, P.A. & Colgan, D.J. (2004) Further phylogenetic studies of the Polychaeta using 18S rDNA sequence data. *Journal of the Marine Biological Association of the U.K.,* 84, 949–960.

Hartman, O. (1944) Polychaetous annelids. Part V. Eunicea. *Allan Hancock Pacific Expeditions,* 10, 1–237.

Hartmann-Schröder, G. (1967) Feinbau und Funktion des Kieferapparates der Euniciden am Beispiel von *Eunice (Palola) siciliensis* Grube (Polychaeta). *Mitteilungen des Hamburgischen Zoologischen Institutes,* 64, 5–27.

Heider, K. (1925) Über *Eunice.* Systematisches, Kiefersack, Nervensystem. *Zeitschrift für wissenschaftliche Zoologie Leipzig,* 125, 55–90.

Herpin, R. (1925) Recherches biologiques sur la reproduction & le développement de quelques annelids polychètes. *Bulletin Société Scientifique Nationale de l'Ouest, ser. 4,* 5, 1–250.

Hilbig, B. (1995) Family Dorvilleidae Chamberlin, 1919. *In*: Blake, J.A., Hilbig, B. & Scott, P.H. (Eds.), *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and the Western Santa Barbara Channel.* Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 341–364.

Hilbig, B. & Blake, J. (1991) Dorvilleidae (Annelida: Polychaeta) from the U.S. Atlantic slope and rise. Description of two new genera and 14 new species, with a generic revision of *Ophryotrocha*. *Zoologica Scripta*, 20, 147–183.

Hints, O. (1999) Two new polychaete families from the Upper Ordovician of Estonia. *Palaeontology*, 42, 897–906.

Hints, O. & Eriksson, M. (2007) Diversification and biogeography of scolecodont-bearing polychaetes in the Ordovician. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 245, 95–114.

Hints, O. & Nolvak, J. (2006) Early Ordovician scolecodonts and chitinozoans from Tallinn, North Estonia. *Review of Palaeobotany & Palynology*, 139, 189–209.

Hsieh, H.-L. & Simon, J. L. (1987) Larval development of *Kinbergonuphis simoni*, with a summary of development patterns in the family Onuphidae (Polychaeta). *Proceedings of the Biological Society of Washington,* 7, 194–210.

Jumars, P. (1974) A generic revision of the Dorvilleidae (Polychaeta), with six new species from the deep North Pacific. *Zoological Journal of the Linnean Society*, 54, 101–135.

Kielan-Jaworowska, Z. (1966) Polychaete jaw apparatuses from the Ordovician and Silurian of Poland and a comparison with modern forms. *Palaeontologia Polonica*, 16, 1–152.

Kozur, H. (1970) Zur Klassifikation und phylogenetischen Entwicklung der fossilen Phyllodocida und Eunicida (Polychaeta). *Freiberger Forschungshefte,* Ser. C, 260, 35–81.

Krohn, A. & Schneider, A. (1867) Über Annelidlarven mit porösen Hüllen. *Archiv für Anatomie, Physiologie und wissenschaftliche Medicin,* 498–508.

Lu, H. & Fauchald, K. (2000) *Ophryotrocha lipscombae,* a new species and a possible connection between ctenognath and labidognath-prionognath eunicean worms (Polychaeta). *Proceedings of the Biological Society of Washington*, 113, 486–492.

Mierzejewski, P. & Mierzejewska, G. (1975) Xenognath type of polychaete jaw apparatuses. *Acta Palaeontologica*

Polonica, 20, 437–444.

Nelson, G. (1978) Ontogeny Phylogeny, Paleontology, and the biogenetic law. *Systematic Zoology*, 27, 324–345.

Okuda, S. (1946) Studies on the development of Annelida Polychaeta. Journal of the *Faculty of Sciences Hokkaido Imperial University*, 9, 115–219.

Orensanz, J. M. (1990) The Eunicemorph polychaete annelids from Antarctic and Subantarctic seas. *Biology of the Antarctic Seas XXI. Antarctic Research Series*, 52, 1–183.

Oug, E. (1978) New and lesser known Dorvilleidae (Annelida, Polychaeta) from Scandinavian and northeast American waters. *Sarsia*, 63, 285–303.

Paxton, H. (2000) Eunicida. *In:* Beesley, P. L., Ross, G.J.B. & Glasby, C.J. (Eds.), *Polychaetes and Allies: The Southern Synthesis. Vol. 4A: Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula.* CSIRO Publishing, Melbourne, pp. 89–106.

Paxton, H. (2004) Jaw growth and replacement in *Ophryotrocha labronica* (Polychaeta, Dorvilleidae). *Zoomorphology*, 123, 147–154.

Paxton, H. (2006) Replacement of adult maxillary jaws in Eunicida (Polychaeta). *Scientia Marina*, 70S3, 331–336.

Paxton, H. & Åkesson, B. (2007) Redescription of *Ophryotrocha puerilis* and *O. labronica* (Annelida, Dorvilleidae). *Marine Biology Research*, 3, 3–19.

Paxton, H. & Safarik, M. (2008) Jaw Growth and Replacement in *Diopatra aciculata* (Annelida: Onuphidae). *The Beagle, Records of the Northern Territory Museum of Arts and Sciences*, 24, 1–21.

Purschke, G. (1987) Anatomy and ultrastructure of ventral pharyngeal organs and their phylogenetic importance in Polychaeta (Annelida). IV. The pharynx and jaws of the Dorvilleidae. *Acta Zoologica (Stockholm)*, 68, 83–105.

Rouse, G. & Fauchald, K. (1997) Cladistics and polychaetes. *Zoologica Scripta*, 26, 139–204.

Rouse, G. & Pleijel, F. (2001) *Polychaetes*. Oxford University Press, Oxford. 354 pp.

Rousset, V., Pleijel, F., Rouse, G.W., Erséus, C. & Siddall, M.E. (2007) A molecular phylogeny of annelids. *Cladistics* 23, 41–63.

Saint-Joseph, A. de (1888) Les annelids polychètes des cotes de Dinard. Part 2. *Annales des Sciences Naturelles Paris, sér. 7*, 5, 141–338.

Struck, T.H., Hessling, R. & Purschke, G. (2002a) The phylogenetic position of Aeolosomatidae and Parergodrilidae, two enigmatic oligochaete-like taxa of the “Polychaeta,” based on molecular data from 18S rDNA sequences. *Journal of Zoological Systematic and Evolutionary Research*, 40, 155–163.

Struck, T.H., Westheide, W. & Purschke, G. (2002b) Progenesis in Eunicida (“Polychaeta”, Annelida) – separate evolutionary events? Evidence from molecular data. *Molecular Phylogenetics and Evolution*, 25, 190–199.

Struck, T.H., Halanych, K.M. & Purschke, G. (2005) Dinophilidae (Annelida) is most likely not a progenetic Eunicida: evidence from 18S and 28S rDNA. *Molecular Phylogenetics and Evolution*, 37, 619–623.

Struck, T.H., Purschke, G. & Halanych, K.M. (2006) Phylogeny of Eunicida (Annelida) and exploring data congruence using Partition Addition Bootstrap Alteration (PABA) approach. *Systematic Biology*, 55, 1–20.

Struck, T.H., Schult, N., Kusen, T., Hickman, E., Bleidorn, C. McHugh, D. & Halanych, K.M. (2007) Annelid phylogeny and the status of Sipuncula and Echiura. *BMC Evolutionary Biology*, 7, 57–64.

Szaniawski, H. (1996) Scolecodonts. *In:* Jansonius J.& McGregor D.C. (Eds.), *Palynology: Principles and applications.* American Association of Stratigraphic Palynologists Foundation, Vol. 1, pp. 337–354.

Szaniawski, H. & Imagima, M. (1996) Hartmaniellidae - living fossils among polychaetes. *Acta Palaeontologica Polonica*, 41, 111–125.

Tzetlin, A.B. (1980). *Ophryotrocha schubravyi* sp. n. and the problem of evolution of the mouth parts in the Eunicemorpha (Polychaeta). *Zoologicheskii Zhurnal*, 59, 666–670 (in Russian).

Webby, B.D., Cooper, R.A., Bergström, S.M. & Paris, F. (2004). Stratigraphic framework and time slices. *In*: Webby, B.D., Paris, F., Droser, M.L. & Percival, I.G. (Eds.), *The Great Ordovician Biodiversification Event.* Columbia University Press, New York, pp. 41–47.

Wolf, G. (1980) Morphologische Untersuchungen an den Kieferapparaten einiger rezenter und fossiler Eunicoidea (Polychaeta). *Senckenbergiana Maritima*, 12, 1–182.