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The ontogeny of parapodia and setae in *Laeonereis culveri* (Webster) (Polychaeta: Nereididae)

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Abstract

The ontogeny of parapodia on the first four larval trunk segments was followed toward maturity in the nereidid *Laeonereis culveri*. The morphologies ultimately attained by the parapodia include cephalic, uniramous, and biramous forms. Setal types and arrangements were also determined for all setigers present on discrete life history stages from larva to adult. The results showed pronounced differences in parapodial morphology and setation between larvae, postlarval juveniles, and adults. These differences stem from the sequential development of parapodial processes and setae. Taxonomists rely heavily on adult setation and parapodial morphology to characterize nereidid species, but since these features vary ontogenetically, their adult states cannot be used to distinguish species during earlier life history phases.

Key words: polychaete, parapodial morphology, setal succession, tentacular cirri

Introduction

Parapodia and setae have morphological features characteristic of species in the Nereididae. Ontogenetic changes in these features occur during life histories but are seldom documented. This account provides such documentation for *Laeonereis culveri* (Webster), a coastal species ranging from southern New England to eastern South America (Pettibone 1971) and adds to previously published observations on the reproduction and development of the species (Mazurkiewicz 1975).

Materials and methods

The study is based on microscopic examinations and camera lucida illustrations of excised parapodia from worms of a Connecticut population cultured in the laboratory (Mazurkiewicz 1975), including nectochaete larvae (3–7setigers), postlarval juveniles, and adults.

The external development of parapodia originating on the first four larval trunk segments was followed to adulthood. Throughout this report they are designated according to their respective larval segments as the first, second, third and fourth parapodia. Additionally, setal types and arrangements were recorded for select life history stages in a search for successional patterns.

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Results

Parapodia

The first four larval trunk segments and their parapodia have different ontogenetic fates. The first segment ultimately forms an apodous tentacular segment, the parapodia modified into a pair of tentacular cirri (Mazurkiewicz 1975). The second and third segments are then established as the first and second setigers; and their parapodia gradually change from biramous to uniramous forms. The fourth segment, in turn, becomes the third setiger. Its parapodia and subsequent ones that arise posteriorly remain biramous, reaching fullest maturity in the anterior region of the adult.

The morphology of a mature biramous parapodium is presented below, followed by details on how the fourth parapodium attains such a form. Finally, descriptions are provided on how the first, second and third parapodia deviate during their development from the basic biramous condition. The terminology is taken from Pettibone's (1971) revision of *Laeonereis culveri*.

The adult biramous parapodium. A mature adult biramous parapodium (Fig. 1) bears dorsal (dC) and ventral (vC) cirri and the notopodium and neuropodium are each subdivided into three processes. Those of the notopodium include an upper triangular ligule (noLi1), a lower rounded ligule (noLi2), and a medial presetal lobe (prL1) containing the notoacicula (noAc). The neuropodium also has an acicular presetal lobe (prL2), situated above a ligule (neLi) and behind a postsetal lobe (poL).

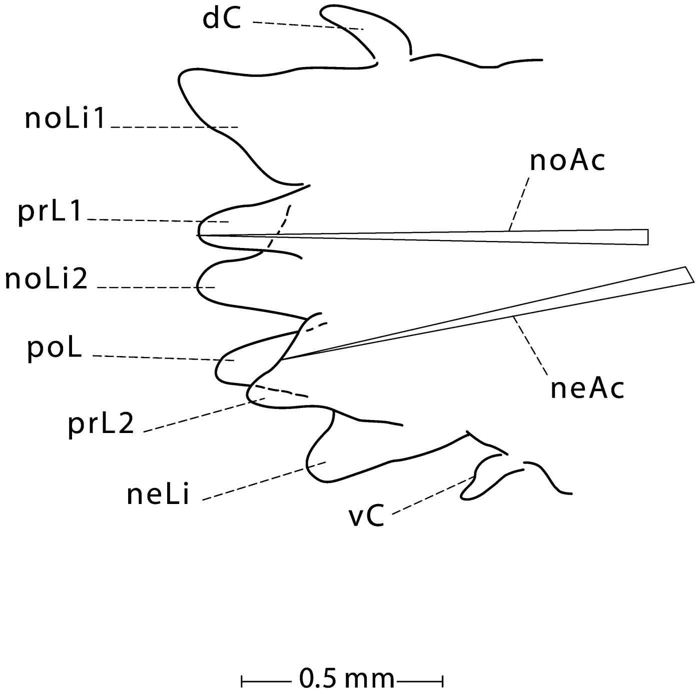

FIGURE 1. Adult morphology of the tenth right parapodium, anterior view, setae omitted. Abbreviations: dC, dorsal cirrus; neLi, neuropodial ligule; noLi, notopodial ligule; poL, postsetal lobe; prL, presetal lobe; vC, ventral cirrus.

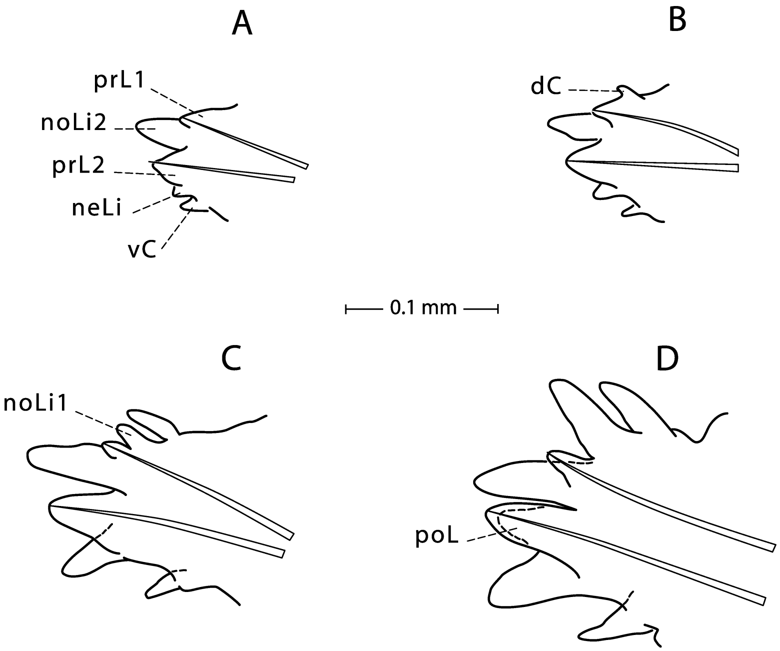

FIGURE 2. Fourth right parapodium, anterior view from select life-history stages, setae omitted. A, 4-setiger larva; B, 5-setiger larva; C, 11-setiger juvenile; D, 19-setiger juvenile. See Fig. 1 for abbreviations.

Development of the fourth parapodium. The ligules, lobes, and cirri of the fourth parapodium develop sequentially from larval to adult biramous states as summarized in Table 1 and depicted in Fig. 2. The definitive number of processes and cirri is not present until the 19-setiger stage. Upon further growth, they differentiate into adult forms.

TABLE 1. Developmental sequences of ligules, lobes and cirri on parapodia originating from the first four larval trunk segments of *Laeonereis culveri*. References to specific figures included. Capital letter next to life history stage refers to position on specified figure. In B–D, the parapodial process listed is the one that appears at the stage listed. See Fig. 1 for locations of the full complement of processes on a biramous parapodium.

Development of fourth parapodium (Fig. 2)
A. 4-setiger larva : single lobe > bilobed (prL1 + prL2) > noLi2 > neLi + vC
B. 5-setiger larva: dC
C. 11-setiger juvenile: noLi1
D. 19-setiger juvenile: poL

Development of second and third parapodia (Fig. 3)
A. 3–4-setiger larva: single lobe > bilobed (prL1 + prL2) > noLi2 > neLi + vC
B. 6-setiger larva: dC
C. 9-setiger juvenile: poL

Development of first parapodium (Fig. 4)
A. 3–4-setiger larva: single lobe > bilobed (prL1 + prL2)
B. 5-setiger larva: noLi2
C. 7-setiger larva: ptC (= noLi2)

Development of the second and third parapodia. The second and third parapodia develop identically. Their elements appear in the same sequence as those of the fourth parapodium, though at different life history stages (Table 1, Fig. 3). The upper notopodial ligule (noLi1) moreover, never develops. The definitive complement of processes is present in the 9-setiger juvenile (Fig. 3C). Also at this stage, notosetae have sloughed off and the notoacicula is slightly smaller than the neuroacicula. The notoacicula ceases to elongate and gradually recedes into the base of the parapodium (Fig. 3D) persisting as a remnant in the adult (Fig. 3E). Concurrently, the presetal lobe of the notopodium (prL2) atrophies and disappears in the adult. The second and third parapodia thereby become uniramous, each with a notopodium reduced to the lower notopodial ligule.

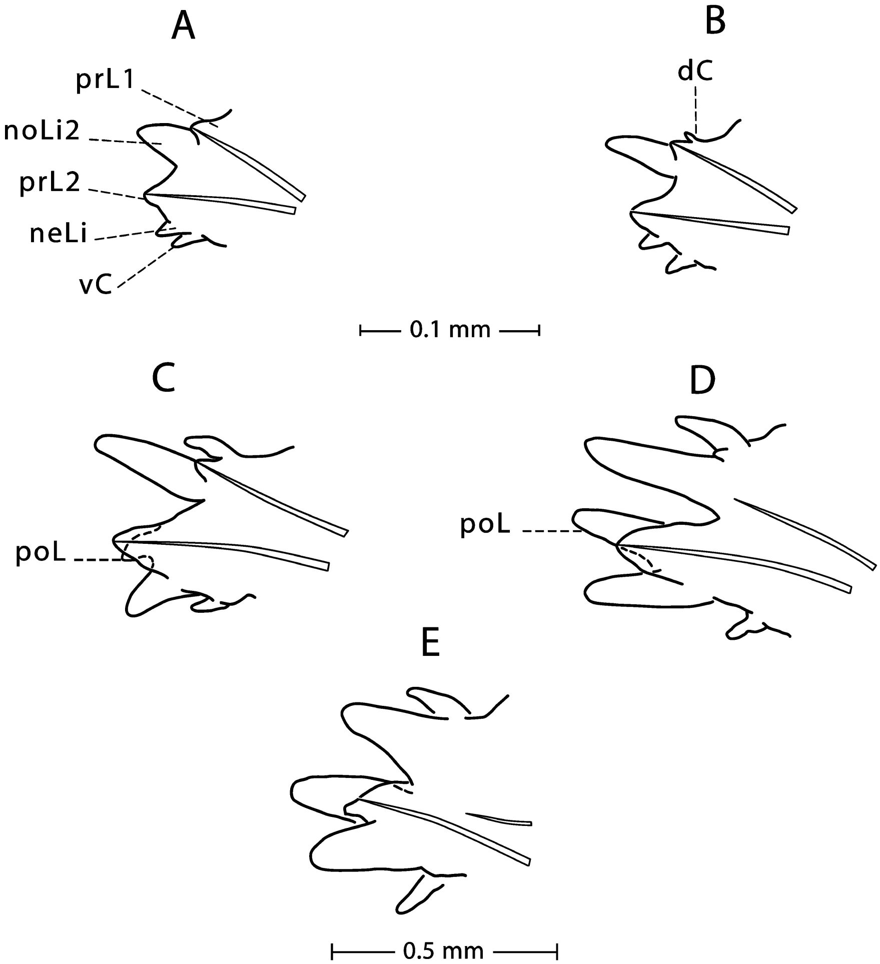

FIGURE 3. Second right parapodium in anterior view from select life history stages, setae omitted. A, 4-setiger larva; B, 6-setiger larva; C, 9-setiger juvenile; D, 19-setiger juvenile; E, 103-setiger adult. See Fig. 1 for abbreviations.

Development of the first parapodium. The first parapodium develops initially like the second, third and fourth parapodia (Table 1) but forms only two lobes, one ligule and no cirri. It is bisected into acicular presetal lobes in the 4-setiger larva (Fig. 4A). The lower notopodial ligule (Fig. 4B) arises as a digitate lobe medial to the presetal lobes of the 5-setiger larva and elongates greatly as the larva advances to the 7-setiger stage (Fig. 4C).

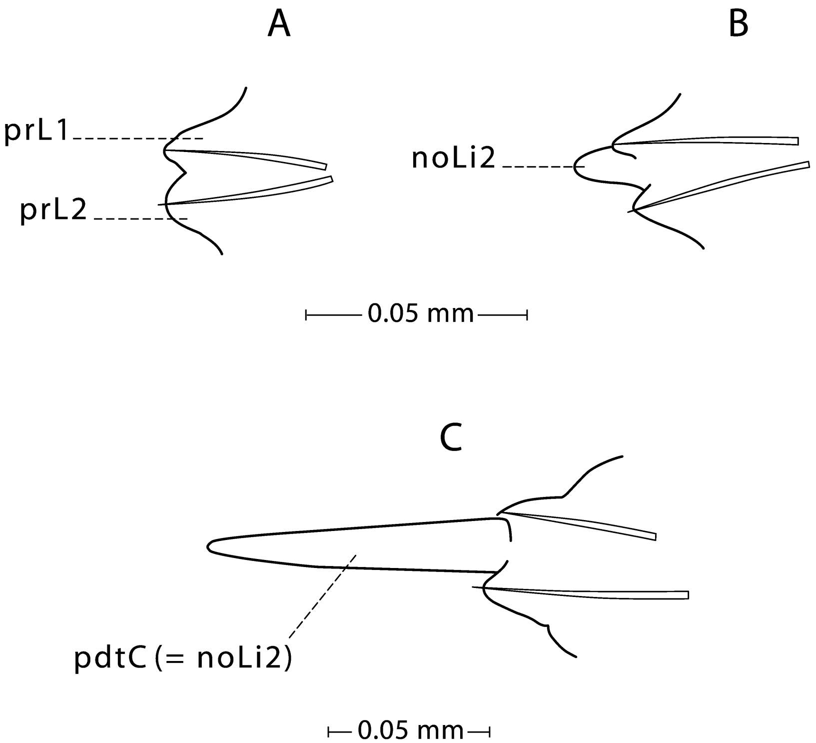

FIGURE 4. First right parapodium in anterior view from select life history stages. A, 4-setiger larva; B, 5-setiger larva; C, 7-setiger larva. Abbreviations: pdtC, posterodorsal tentacular cirrus, others as noted in Fig. 1.

When an eighth trunk segment is added, the first parapodium is reduced to an asetigerous base supporting the elongated notopodial ligule, now fully established as the posterodorsal tentacular cirrus (pdtC, Fig. 5). The parental trunk segment serves as an apodous tentacular segment. Acicular presetal lobes have atrophied but the aciculae persist within the base of the cirrus, gradually receding into the tentacular segment where they may continue to be present in the adult.

A posteroventral tentacular cirrus (pvtC, Fig.5) originates as a rudimentary bud inferior to the base of its dorsal mate in the late 7-setiger postlarval juvenile and is not derived from a parapodial process. The anterodorsal (adtC) and anteroventral tentacular cirri (avtC) arise from the head during embryogenesis (Mazurkiewicz 1975) and though of metameric descent (Ackermann et al. 2005), they too, cannot be identified as homologues of specific parapodial processes.

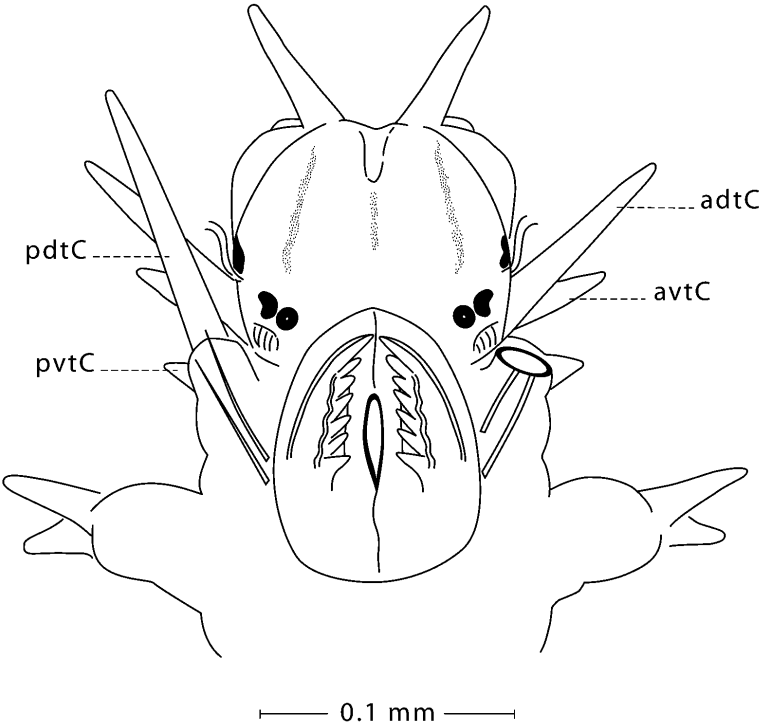

FIGURE 5. Head, tentacular segment and first setiger of a 7-setiger juvenile displaying tentacular cirri; right posterodorsal tentacular cirrus removed. Abbreviations: adtC, anterodorsal tentacular cirrus; avtC, anteroventral tentacular cirrus; pdtC, posterodorsal tentacular cirrus; pvtC, posteroventral tentacular cirrus.

TABLE 2. The distribution of setae in select life history stages of *Laeonereis culveri*. Numbers refer to setigers bearing parapodia with the specified setae; 0 = absent. Setigers numbered consecutively from anterior to posterior.

	Notosetae		**Neurosetae**	
Life history stage	**Spinigers**	**Falcigers**	**Spinigers**	**Falcigers**
5-setiger larva	0	1–5	0	1–5
6-setiger larva	4–5	1–6	4	1–6
7-setiger larva	4–6	2–7	2–5	1–7
9-setiger larva	3–7	3–8	1–6	1–9
11-setiger juvenile	3–10	7–10	1–7	1–11
19-setiger juvenile	3–16	11–18	1–13	1–19
31-setiger juvenile	3–30	19–24	1–31	1–30
35-setiger juvenile	3–35	0	1–35	1–32
44-setiger juvenile	3–44	0	1–44	3–34
75-setiger juvenile	3–75	0	1–75	10–65
104-setiger adult	3–104	0	1–104	13–84

Setae: ontogenetic changes in forms and arrangements

Setae include homogomph falcigers and spinigers (Fig. 6A–D) that change in their patterns of development and distribution during the life history of the species (Table 2). These changes entail a gradual shift in predominance from falcigers to spinigers as the worm grows.

Only falcigers are present in 3- to 5-setiger larvae, arranged in noto- and neurosetal bundles. The falcigers have 12–30 µm long serrate blades with slightly thickened, hooked distal tips (Fig. 6A–B).

Spinigers first appear among notosetae and neurosetae in the fourth and fifth parapodia of the 6-setiger larva. A serrate blade tapering gradually to a fine tip characterizes each spiniger. The blade is identical in form to that of an adult spiniger (Fig. 6D) and measures 48–55 µm in length. Notosetal and neurosetal falcigers meanwhile continue to occupy all parapodia.

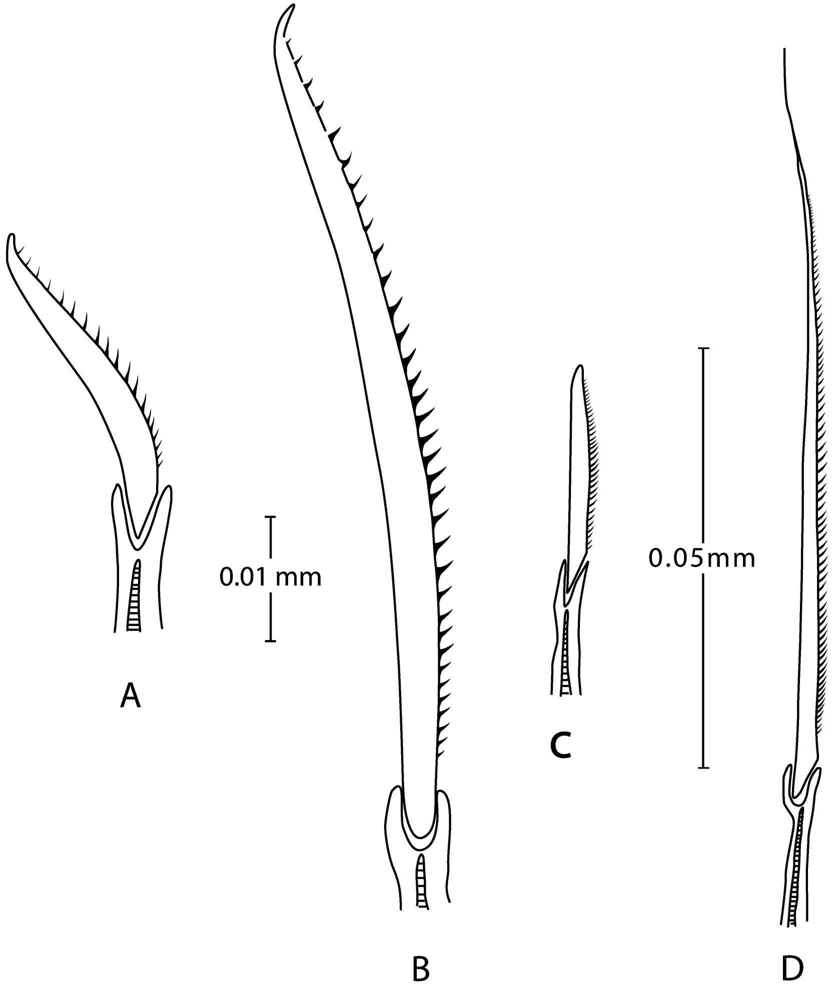

FIGURE 6. Setal types. A–B, homogomph falcigers with short and long blades from a 3-setiger larva; C, adult homogomph falcigers; D, adult homogomph spiniger. A–B scaled to 0.01 mm bar; C–D scaled to 0.05 mm bar.

In subsequent life history stages, spinigers steadily expand in distribution among the setigers. There is also a shift in the timing of spiniger development in newly formed posterior parapodia, first evident in the 31-setiger juvenile. At this stage, spinigers arise first, followed by falcigers as the posterior parapodia mature, a pattern retained into adulthood. Just the reverse is evident in earlier life history stages, i.e., falcigers being the first setae to form during maturation of the posterior parapodia.

Falcigers, in contrast to spinigers, become more restricted in distribution as the worm grows. This results from losses and the delayed development on posterior parapodia as previously noted. By the 35-setiger stage, notosetal falcigers have completely sloughed off to be replaced by spinigers. With the addition of further setigers, there is even a gradual loss of neurosetal falcigers from the anterior parapodia. This leads to the adult pattern in which spinigers have completely replaced falcigers on the most anterior 12–15 setigers, followed by parapodia with falcigers limited to lower neurosetal bundles, just 1–4 falcigers per bundle. Finally toward the rear of the body, immature parapodia are found bearing solely spinigers. The adult falcigers (Fig. 6C) have thick, serrated knoblike blades 38–60 µm long while the spinigers (Fig. 6D) have finely serrated, tapering blades 60–240 µm long.

Discussion

Parapodial processes. The sequential development of parapodial processes has been described for *Hediste (=Nereis) diversicolor* by Dales (1950) and for *Nereis virens* by Bass & Brafield (1972). The sequences differ significantly from each other and from *L. culveri*. There is no common pattern as to when and in what order ligules, lobes and cirri form during a life history. Furthermore, the definitive complements appear in 19-, 31-, and 40-setiger juveniles of *L. culveri*, *H. diversicolor*, and *N. virens*, respectively. Unfortunately comparable studies are lacking for other species.

Posterodorsal tentacular cirri. Gilpin-Brown (1959) and Bass & Brafield (1972) review early literature on the ontogeny of the posterodorsal tentacular cirri and add their own observations, which concur with those given for *L. culveri*. Nine species are now known in which a lobe medial to the acicular lobes gives rise to these tentacular cirri; the present study is the first to identify the medial lobe as the lower (second) notopodial ligule. On the other hand, in four additional species, the dorsal cirrus is claimed to be the anlage of the posterodorsal tentacular cirrus. This view, originating with Langerhans (1879), is mistakenly assumed by many polychaetologists to be the norm, but clearly that is not so.

Setation. Larval setae in the Nereididae may include simple capillaries, spinigers (homo- and heterogomphs), falcigers (homo- and heterogomphs), and forms intermediate between spinigers and falcigers. Species differ in the types of larval setae present, their spatial arrangements, and subsequent patterns of succession during ontogeny (Hempelmann 1911; Herpin 1925; Wilson 1932; Dales 1950; Banse 1954; Reish 1954; Gilpin-Brown 1959; Bass & Brafield 1972). For instance, in the case of *N. virens*, adult setation is not achieved until 90 setigers have developed and successional changes have taken place among four setal types (Bass & Brafield 1972). This contrasts with *L. culveri* in which succession involves just two types of setae with adult arrangements arising by the 44-setiger juvenile stage, except for a subsequent gradual loss of anterior neurofalcigers.

Concluding remarks

Species in the Nereididae are described on the basis of adult characteristics, with heavy emphasis on setation and parapodial morphology. Since these characteristics undergo sequential patterns of development toward maturity, their adult states cannot be used to identify immature worms to species. Our knowledge about these patterns is grossly incomplete. They require further documentation to be of use in species recognition (Zottoli & Long, 1998) and comparative morphology.

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