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A new mesopelagic larvacean, *Mesochordaeus erythrocephalus*, sp. nov., from Monterey Bay, with a description of its filtering house

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Abstract. A new species in the genus *Mesochordaeus* is described from 25 specimens collected by a remotely operated vehicle at mesopelagic depths in Monterey Bay, California. *Mesochordaeus erythrocephalus* is a large species (tail length up to 50 mm, trunk length up to 7 mm) characterized by large crescent-shaped spiracles, digitate lips, a bifurcate tail and bright red pigmentation of the digestive system. The filtering 'house' is large, 4–5 times the tail length of the animal, and its structure is most similar to that of another large mesopelagic larvacean, *Bathochordaeus*. This description confirms the distinctness of this recently erected genus, but raises questions as to its taxonomic affiliation.

Introduction

With the increased utilization of manned and unmanned submersible vehicles in the past two decades, our knowledge of soft-bodied zooplankton has increased substantially (e.g. Hamner and Robison, 1992; Mills, 1995; Robison *et al*., 1998). Many such animals (e.g. ctenophores, larvaceans, medusae, siphonophores) are too fragile to survive collection with traditional plankton nets and can only be collected intact by *in situ* techniques (e.g. Hamner *et al*., 1975; Harbison, 1983; Fenaux, 1992). Despite their fragility, soft-bodied zooplankton are important components of marine zooplankton. The larvaceans, for example, are often the second or third most abundant group in plankton samples (e.g. Gorsky and Fenaux, 1998; Hopcroft and Roff, 1998). In the past decade, a number of new larvacean species have been collected and described, primarily from submersible collections (Fenaux and Youngbluth, 1990, 1991; Fenaux, 1992, 1993). As with their near-surface counterparts, members of such 'new' mesopelagic species may be surprisingly common (B.H.Robison and R.R.Hopcroft, unpublished data).

The genus *Mesochordaeus* (Fenaux and Youngbluth, 1990) has been erected within the family Oikopleuridae, subfamily Bathochordaeinae, based on a single specimen, *Mesochordaeus bahamasi*, collected off the Bahamas. Here we describe an additional member of this genus, *Mesochordaeus erythrocephalus*. The structure of the external mucilaginous feeding filter (the 'house') is also described from *in situ* observations and compared to other oikopleurids. This is the first in a series of papers describing new mesopelagic larvacean species and their ecology, from Monterey Bay, California.

Description

Mesochordaeus erythrocephalus sp. nov. (Figure 1A–F).

Material

In situ observations and collections were conducted by the ROV 'Ventana' (Robison, 1993) from a station of 1600 m depth at 36°42′N, 122°02′W located along the axis of the Monterey Submarine Canyon. Over the past decade, hundreds of specimens have been documented. They are most commonly observed between 300 and 500 m depth, where the temperature typically ranges between 5.5 and 8°C (Figure 2). Individuals have been observed as shallow as 200 m and as deep as 750 m, and show some seasonality of occurrence.

Descriptions are based on 20 specimens collected between 1991 and 1996 and preserved in 2% glutaraldehyde, plus five live specimens collected in 1997 and later preserved in 5% formalin. All specimens were collected with 'detritus' (Youngbluth, 1984) or suction samplers. Video footage of >50 individuals was examined to describe house structure and its size in relation to the animal. Juveniles (specimens with no gonadal development) are not represented in these collections; however, we believe our smallest immature individual is close to the transition between developmental stages. All measurements presented are based on preserved specimens, while drawings are based on combinations of both live and preserved material. Deviations between live and preserved material are noted. The holotype (CASIZ #117308) and six paratypes (CASIZ #117309–117314) have been deposited at the California Academy of Sciences.

Trunk

In dorsal view, the trunk is roughly 'skull' shaped. The anterior oikoplastic region is narrower than the remainder of the trunk, with a pair of lateral lobes formed by the transition between these two regions. For the specimens collected, the trunk ranged in length from 2190 to 7312 μm and in width from 1483 to 5047 μm (Table I). In lateral view, the maximum trunk height ranged from 893 to 3635 μm, narrowing dorsally at the junction of the anterior oikoplastic region and posterior trunk. The average length to width to height ratio was 1.5:1:0.7 for preserved specimens. After several months of preservation in formalin, shrinkage was ~10–15%, with the trunk subject to considerable distortion during shrinkage. To reduce variability caused by preservation, the oral lips have been excluded from the trunk's length—their inclusion would add ~8% (range 5–12%) to the trunk length.

Pharyngeal region. Although nearly terminal in position, the mouth originates on the anterodorsal surface of the trunk. When the mouth is fully open, the lips may extend forward of the trunk, thus appearing terminal in position. The mouth is surrounded by four fleshy lips. The anterior lip is largest and is subdivided into three lobes, with a medial digitate lobe bordered by relatively blunt sublobes. The

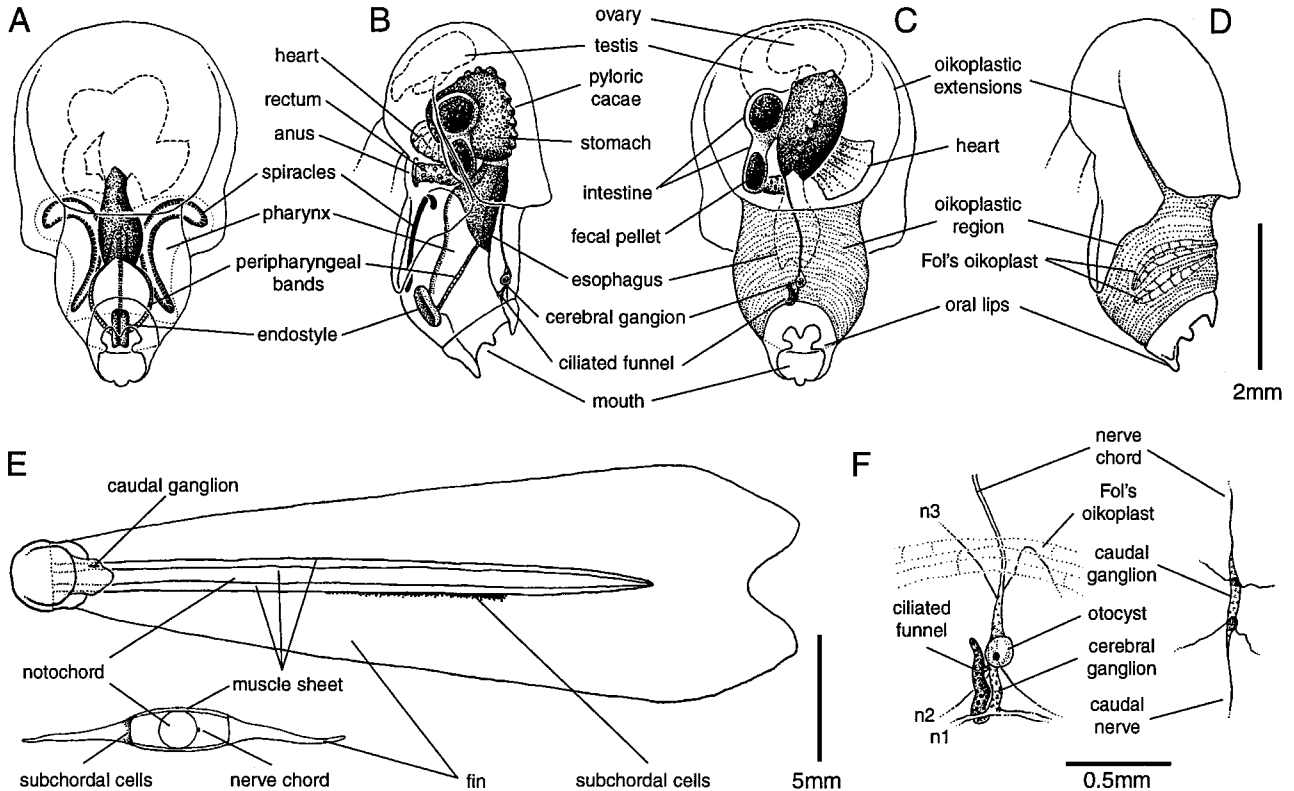

Fig. 1. Composite drawing of a live, immature *M.erythrocephalus*. (**A**) Dorsal view illustrating the pharyngeal cavity. (**B**) Lateral internal anatomy and illustration of the pharyngeal cavity. (**C**) Dorsal view indicating the arrangement of oikoplastic region and internal anatomy, ignoring the pharyngeal cavity. (**D**) Lateral external view indicating the arrangement of the oikoplastic region and the cells in Fol's oikoplast. (**E**) Whole animal, with cross-section of the tail through the anterior region of subchordal cells. (**F**) Dorsal view of the cerebral and caudal ganglia (drawn to the same scale).

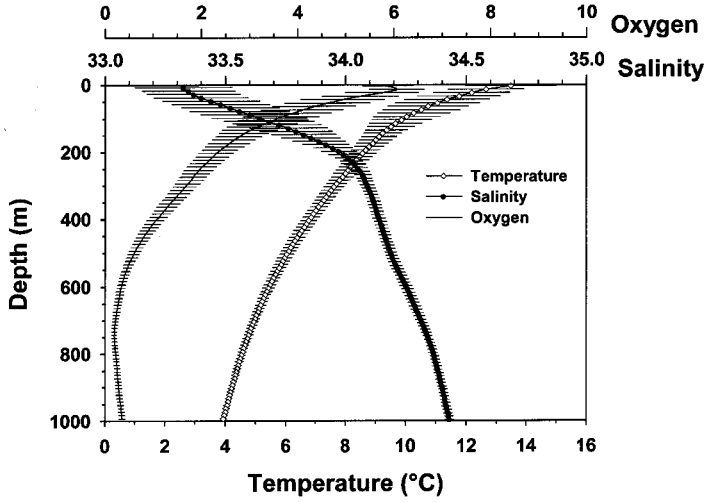

Fig. 2. Average temperature, salinity (PSU) and oxygen (mg m^{-3}) profiles for the upper 1000 m at the site of sample collection based on 5 years of weekly estimates from January 1989 to December 1994. Standard deviations for the data set are indicated.

posterior and lateral lips of the mouth are digitate distally. The distal end of each digitate lobe is populated by 10–30 tiny papillae, presumably of sensory function. In larger specimens, these papillae are of ~20 μm length, with width less than one-fourth of their length.

The endostyle lies midway between the mouth and spiracles, and is often partially visible through the mouth in dorsal view. The endostyle has a deep longitudinal cleft medially (under dark-field illumination, it has an unusual iridescent quality) and is a golden yellow–orange in color. Its length to width to height ratio was 2.0:1:0.8 (Table I). The ciliated peripharyngeal bands begin on the dorsal quarter of the endostyle, travel obliquely around the inner margin of the pharyngeal cavity, then each ends along an anterolateral lobe of the esophagus. These ridges typically transport the pharyngeal mucus feeding filter produced by the endostyle to the esophagus. An additional ciliated track begins on the medial dorsal surface of the endostyle and travels posteriorly on the medial floor of the pharyngeal cavity, until reaching the posteromedial edge of the esophagus.

A pair of equal-sized elongate spiracles begin level with the posterior half of the endostyle and curve outward in smooth tightening arcs that end behind the anus. The posterior pharyngeal cavity is expanded ventrolaterally to communicate with these spiracles. The spiracles occupy 37% of the trunk length, but, if straightened, each spiracle would traverse ~52% of the length of the trunk. The spiracular rings are lined with a dense continuous ciliature that is shallowly recessed from the body surface. In several of the preserved specimens, the spiracles appear almost level with the body surface, or they are enlarged with their edges variably scalloped or 'pleated'. These distortions are presumably due to

Table I. Morphometrics of preserved *M.erythrocephalus* collected from the Monterey Submarine Canyon. Gonadal development is ranked as mature (M) and immature (I). For the spiracle ratios, the values represent the proportion of the sagittal axis traversed in natural orientation (linear) and the proportion if straightened (edge). For the subchordal ratios, values represent the proportion of the notochord length at which subchordal cells begin and end, plus the proportion of tail width occupied by muscle sheets in the distal region of subchordal cells. Missing values indicate cases where damage or preservation artifacts prevented reliable measurement. All measurements are in micrometers

	Trunk			Endostyle			Tail			Trunk		Spiracles		Tail		Endostyle		Subchordal		
	Length	Width	Depth	Length	Width	Depth	Length	Notochord	Max-W	L:W	D:W	Linear	Edge	Trunk	L:W	L:W	D:W	Start	End	Muscle
I	2190	1483	893	293	167	119	14 824	12 122	3148	1.48	0.60	0.32	0.47	6.77	4.71	1.75	0.71	0.39	0.59	0.16
I	3025	2152	1640	457	234	178	24 304	21 843	6500	1.41	0.76	0.32	0.44	8.03	3.74	1.95	0.76	0.40	0.64	0.21
I	3104	1991	1329	425	213	164	21 040	18 680	4921	1.56	0.67	0.34	0.50	6.78	4.28	2.00	0.77	0.47	0.66	0.23
I	3120	2085	1411	432	210	190	23 795	20 070		1.50	0.68	0.35	0.47	7.63		2.06	0.90	0.41	0.57	0.26
I[c]	3434	2253	1532	430	220	168	20 485	18 408	5946	1.52	0.68	0.42	0.56	5.97	3.45	1.95	0.76	0.42	0.64	0.20
I[ab]	3889	2442	1896	506	232	205	30 210	25 856	6900	1.59	0.78	0.39	0.54	7.77	4.38	2.18	0.88	0.40	0.66	0.23
I	4159	2317	1717	578	268	225	31 490	27 382	8710	1.79	0.74	0.44	0.58	7.57	3.62	2.16	0.84	0.44	0.63	0.24
I	4378	2859	2290	533	264	212	28 560	25 549		1.53	0.80	0.35	0.53	6.52		2.02	0.80	0.44	0.62	0.24
I[c]	4480	2891	2015	525	294	202	30 316	26 499	9100	1.55	0.70	0.40	0.59	6.77	3.33	1.79	0.69	0.39	0.61	0.19
I	4632	3380	2462	566	295	226				1.37	0.73	0.35	0.47			1.92	0.77			
I[a]	4881	3168	2114	655	335	320	39 500	36 000		1.54	0.67	0.43	0.61	8.09		1.96	0.96	0.44	0.67	0.24
I	4931	3133	2104	582	273	230	32 450	27 843	10 364	1.57	0.67	0.36	0.52	6.58	3.13	2.13	0.84	0.41	0.62	0.20
I[ac]	5239	3273	2300	673	343	290		36 000		1.60	0.70	0.33	0.48			1.96	0.85			0.26
M	5541	4167	2723	651	302	259	40 156	34 277		1.33	0.65	0.34	0.56	7.25		2.16	0.86	0.35	0.62	0.25
M	5556	3787	3016	677	341	261	40 687	35 237		1.47	0.80	0.37	0.52	7.32		1.99	0.77	0.43	0.63	0.29
M[ac]	5600	3763	2487	732	359	340	42 595	39 000	9142	1.49	0.66	0.38	0.48	7.61	4.66	2.04	0.95	0.44	0.69	0.31
M[c]	5901	3655	2638	638	305	217		31 458		1.61	0.72	0.37	0.52			2.09	0.71			0.28
M				718	354	302	42 700	36 803								2.03	0.85	0.46	0.65	
M[c]	6705	4427	3097	729	312	270	41 402	36 273	12 080	1.51	0.70	0.36	0.56	6.17	3.43	2.34	0.87	0.40	0.61	0.24
M	6858	4634	3635	751	335	268	44 000	37 000	13 000	1.48	0.78	0.35	0.49	6.42	3.38	2.24	0.80	0.36	0.61	0.21
M	7312	5047	3306	729	331	289	44 520	36 960	15 301	1.45	0.66	0.37	0.53	6.09	2.91	2.20	0.87	0.42	0.62	0.17
M[a]				757	400	275	49 016	42 250	12 617						3.88	1.89	0.69	0.37	0.60	0.22
Mean		4747	3145	2230	593	290	237	33 792	29 786	9056	1.52	0.71	0.37	0.52	7.02	3.76	2.04	0.81	0.41	0.63
0.23																				
SE	309	217	159	28	13	12	2253	1787	984	0.02	0.01	0.01	0.01	0.17	0.16	0.04	0.02	0.01	0.01	0.01

Preservative was 2% glutaraldehyde, with the exception of several individuals preserved in 5% formalin ([a]).
[b]Holotype.
[c]Paratypes.

contraction of pharyngeal muscles during fixation, as they were never observed in live specimens.

Digestive region. The ciliated esophagus is funnel shaped with a pair of small anterolateral lobes where it receives the peripharyngeal bands of the pharyngeal cavity. The esophagus narrows to a strong sphincter valve as it meets the anterodorsal edge of the stomach, on the sagittal plane of the body. Viewed dorsally, the stomach leans to the right at 20–30°. A ridge of small bulbous pyloric cecae often encircles the laterally compressed stomach, beginning posterodorsally, continuing around the posterior margin, and ending ventrally on the anterior margin of the stomach.

The short intestine arises from the right side of the stomach, often widening into a globular bulb, then passes horizontally as a narrower tube that ends level with the anterior edge of the stomach. The intestine joins a narrower rectum that opens on the sagittal plane, slightly forward of the tail and slightly forward of the posterior borders of the spiracles. In profile, the rectum appears to descend vertically from the intestine. Numerous isolated spherical cells project into the rectum from its walls.

In life, the entire esophagus is a bright opaque red, while the stomach and proximal intestine vary from red to orange in color. After preservation, these rich colors are lost, typically leaving behind a less opaque, dull cream color. The intestine often appears distinctly darker than the stomach after preservation, due to increased visibility of its densely packed contents through the increased transparency of the intestinal walls.

Genital region. Gonadal development appears to begin at ~2 mm trunk length as a small plate at the posterior margin of the trunk. Both ovary and testis develop simultaneously, moving forward into the trunk as they enlarge (Figure 3). In early development, they form an almost continuous plate, with the bilobed ovary surrounded by the right and left lobe of the testis. The lobes of the testis connect dorsally as a tubular structure, but are separated ventrally. During development, the outer edges of the testis migrate forward faster than the ovary, such that in mature specimens the testis forms a ribbon that encircles the entire posterior trunk, obscuring most of the digestive tract.

In mature specimens (i.e. trunk length > 5.5 mm), the right and left lobes of the testis remain connected dorsally as a tube, while midventrally the lobes meet and pass inward where the intestine and stomach join. At maturity, the ovary hangs almost vertically in the trunk, immediately behind the stomach, as a bilobed plate almost reaching the testis at its margins. These lateral lobes drop anteroventrally, further obscuring the digestive tract. Although relatively opaque in preserved material, both gonads are almost transparent in live, immature specimens. As an individual nears maturity, the testis becomes increasingly opaque and develops an orange–yellow color.

Nervous system. The cerebral ganglion lies dorsally on the sagittal plain just behind the posterior lip of the mouth (Figure 1). Because of the animal's size,

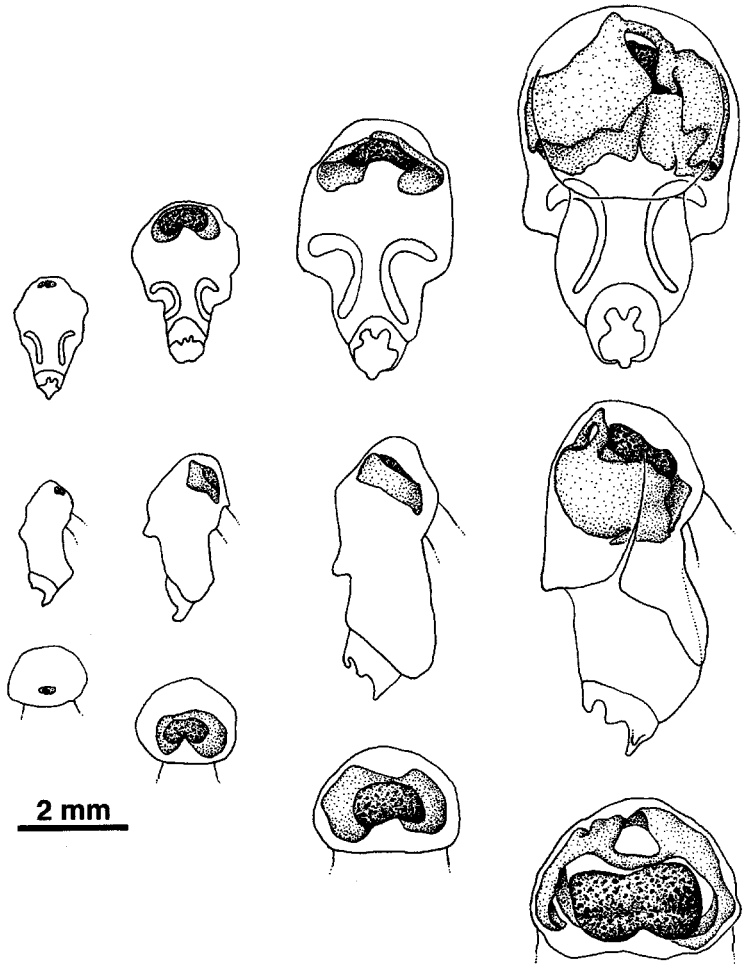

Fig. 3. Developmental series of gonads in *M.erythrocephalus*. Ovary denoted by darker, more granular stippling than testis. All drawings are based on preserved material.

many features of the nervous system can be discerned. The associated spherical otocyst and ciliated olfactory tube are clearly visible in most specimens. The ganglion splits anteriorly, at the margin of the lips and the oikoplastic layer, into two connectives that spread outward at right angles (cerebral nerve 1; Bone, 1998b). A pair of finer nerves (cerebral nerve 2) originate mid-ventrally from the ganglion near the otocyst. As the cerebral ganglion narrows posteriorly, it first gives rise to a branch on the right, then on the left (cerebral nerve 3), that appears to innervate the pharynx and/or spiracles. The main nerve chord continues to travel dorsally, slightly to the animal's right, passes the junction of the stomach

and intestine, then travels downward toward the tail, passing along the margin of the heart.

The nerve chord enters the tail medially, then shifts to the left as it enters the tail along the lateral edge of the notochord. A caudal ganglion can be observed proximally at a level near the endostyle when the tail is folded against the head. The caudal ganglion is about half the size of the cerebral ganglion with numerous small nerves leaving the ganglion and innervating the caudal muscles. The caudal nerve can generally be traced to the end of the tail muscles, suspended along the left edge of the notochord. Pairs of small ganglia can be observed along the caudal nerve's length, each of which gives rise to a small nerve innervating one side of the caudal musculature. The Langerhan's receptors could not be located.

Heart. The heart is a simple flattened sac-like structure that varies from one-half to one-fourth the width of the trunk. The heart is located ventrally, to the left of the sagittal plain; it lies near the insertion of the tail, between the posterior margin of the left spiracle and the anterior margin of the stomach. The outer, ventral side of the heart is convex and relatively immobile, across which an inner, dorsal, motile surface is stretched. Approximately 15–25 distinct muscle cells can usually be observed on this inner surface. Peristaltic contractions of the motile side pump fluid through the heart. This pumping action appears to propel fluid down the lumen of the tail directly beneath it, with return flow up the lumen on the opposite side of the tail.

Oikoplastic layer. Oikoplastic cells cover the anterodorsal region of the trunk, forming a pattern roughly encircling the mouth. This highly sculptured region ends dorsally and laterally where the trunk expands. Dorsally, this region ends prior to the level where the esophagus meets the stomach, then extends laterally in broad arcs that reach the posterior lateral edges of the trunk, level with the posterior margin of the pharynx. The oikoplastic region then extends anteroventrally to encircle the mouth, anterior to the spiracles. Thin, straight dorsolateral extensions of the oikoplastic region reach posteriorly to the level of the stomach–intestinal junction. Oikoplastic cells also thinly encircle the spiracles, connecting to the main oikoplastic region through short, broad channels at the anterolateral edges of the spiracles.

Fol's oikoplasts are large, consisting of two rows of giant cells anteriorly and three rows of large cells posteriorly. These two cell groups are separated by three rows of smaller cuboidal cells. There is an arch of large cells (of unknown function) midway between the Fol's oikoplasts and the posterior margin of the oikoplastic region. This is followed by a pair of ovoid giant cells of unknown function that occur mediodorsally just forward of the posterior margin of the oikoplastic region. Eisen's oikoplasts are absent.

Tail

The tail is long and widens from its origin to the bluntly bifurcated distal end. Tail length varied from ~15 to 50 mm with an average length to maximum width ratio

of 3.8 ± 0.2 (Table I). The average trunk length to tail length ratio was 7.0 ± 0.2. The tail is covered by an epithelium of large thin polygonal cells up to 100 μm in diameter. The tail musculature is composed of dorsal and ventral sheets of striated muscle that enclose a flattened tube. In cross-section, this tube is divided into three chambers by the inner central notochord. The notochord is closely applied to the striated muscle sheets dorsally and ventrally, while the other two sides appear as longitudinal septa located inward from the lateral margins of the musculature by approximately one-fifth of the muscle's width.

Hundreds of small subchordal cells are scattered along the right side of the tail, but only along the lateral edge of the muscle layer. These spindle-shaped cells begin proximally at 41% and end distally at 63% of the tail length, being more numerous distally. The caudal musculature is 23% of the width of the tail at the midpoint of the subchordal cells, and ends smoothly prior to the end of the tail. The notochord loses its turgor and shrinks 5–10% in length following preservation. The outer, non-muscular margins of the tail are relatively fragile, and undergo considerable shrinkage and distortion during preservation. This shrinkage typically narrows the apparent width of the tail, often masks its bifurcate shape and contributes to high variability in the ratios from tail morphometrics (Table I).

House

The external filtering structure is large, 4.7 ± 0.1 SE times the tail length (n = 17), and is roughly ovoid in shape (Figure 4). This corresponds to 30–35 times the trunk length and a physical length of up to 30 cm. The house is dominated by an inner food-concentrating filter that, despite its size, is extremely transparent in comparison to many other co-occurring species. The food-concentrating filter is closely surrounded by a mucous envelope that is only visible due to the adhesion of particles on its surface. This outer envelope may, or may not, be analogous to the outer house boundary of other oikopleurids.

The house does not appear to have any consistent orientation in the water, although that of Figure 4 is common. Owing to its large size and fragile composition, we doubt that the house is actively propelled through the water. Terms of orientation within the house thus become problematic, and although reference orientation for houses based on a ship analogy has been proposed (Flood and Deibel, 1998), it is not entirely appropriate for *Mesochordaeus*. For the following description, the animal has been oriented with the trunk forward, mouth pointing down, and the tail stretching horizontally 'aft'.

The animal is situated slightly above the inner food-concentrating filter. Just above, and slightly forward of the animal's trunk, two dorsal depressions can be discerned in the outer house envelope where water is presumably drawn into the house. The pre-filter characteristic of most oikopleurids has not been observed in these depressions. The tail beats slowly (2.35 ± 0.10 s beat^{-1}, n = 21), pushing water aft into an enlarged tail chamber that branches into two lateral supply passages. These passages expand and continue forward past the animal, then narrow as they turn down, back and inward toward the animal. Each of these

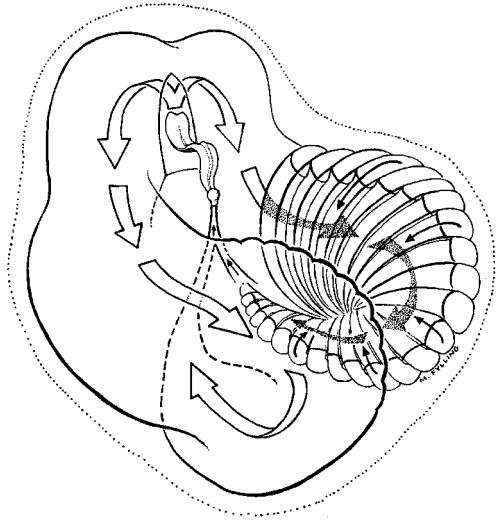

Fig. 4. Gross morphology of the filtering house structure of *M.erythrocephalus*. Flutes indicated for the left (far) arm only. Arrows indicate the direction of inferred water flow based on *in situ* video recordings.

lateral 'arms' consists of a large inner supply passage that feeds a series of smaller ribbed 'flutes' that encircle the supply passage. The flutes begin approximately medially on only the 'outer side' of each supply passage, and move inward toward the animal's mouth. The flutes narrow as they converge near the head, finally joining to form the buccal tube attached to the mouth.

Etymology

The specific name *erythrocephalus* refers to the bright red color of the 'head' in live specimens.

Diagnoses

The genus *Mesochordaeus* is readily separated from all other Oikopleuridae by its large spiracles (Fenaux, 1998b). *Mesochordaeus erythrocephalus* is most easily distinguished from its sibling species, *M.bahamasi*, by its crescent-shaped spiracles, digitate lips surrounding the mouth, and the notched tail. In living specimens (Figure 5A), the animal is virtually transparent with the exception of the gonads and the digestive system. The red pigmentation of the digestive system is characteristic, easily distinguishing it from all other larvaceans during *in situ* observation. The shape and large size of the house (Figure 5B) can also be used to separate this genus from all other species.

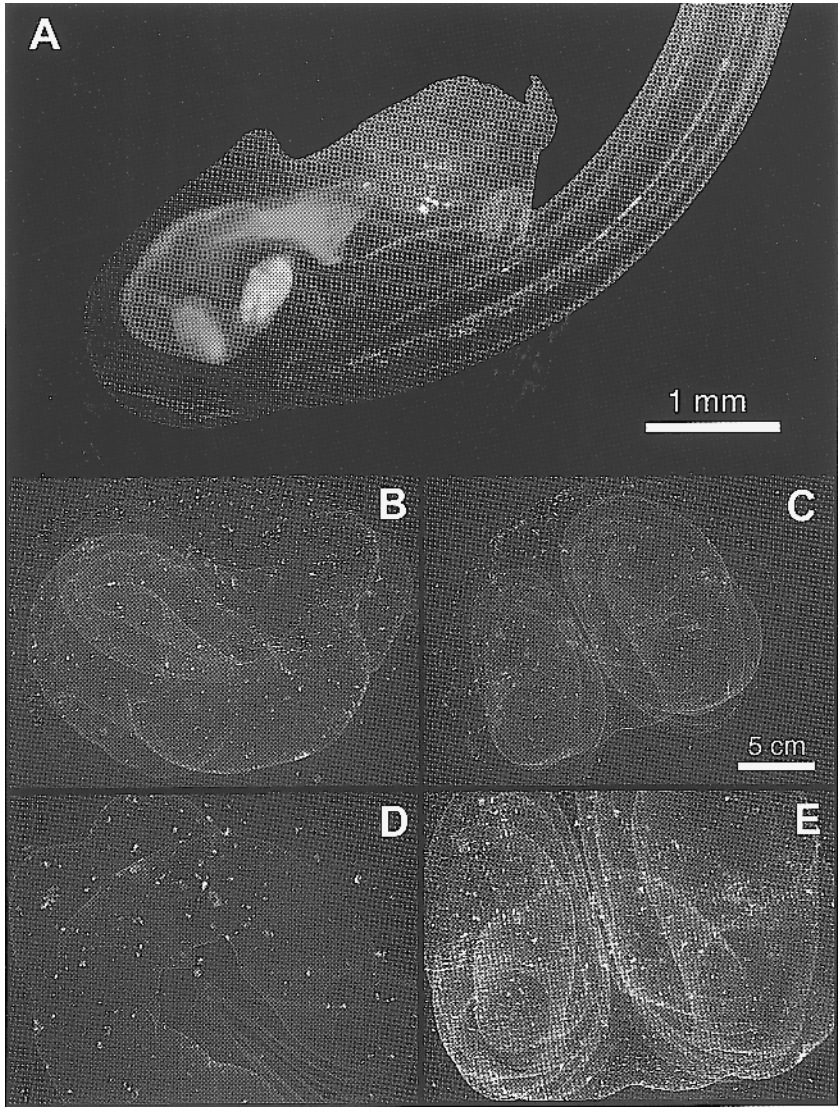

Fig. 5. *Mesochordaeus erythrocephalus*. (**A**) Photograph illustrating the general transparency of the live organism and the striking pigmentation of the digestive system (beige coloration is an artifact of lighting). *In situ* video frame grabs of animal and house structure: (**B**) dorsolateral view; (**C**) anterior view; (**D**) ventral view showing the tail chamber splitting into lateral arms and buccal tube attachment to the animal. (B–D) are to the same approximate scales. (**E**) Anterior view similar to (C) zoomed to show greater detail. Red pigmentation of the animal's trunk is apparent in all frames.

Discussion

In general, the anatomy of *Mesochordaeus* is consistent with that of most oikopleurids (Bone, 1998a,b; Fenaux, 1998a). Our description of *Mesochordaeus* confirms the distinctness of this recently erected genus. Although we are inclined to ally this genus most closely to *Bathochordaeus*, we note several features that raise questions with regard to its placement within the subfamily Bathochordaeinae (represented only by the genus *Bathochordaeus*) as opposed to the Oikopleurinae. First, the mouth is very nearly terminal in position. Second, the spiracles are extremely large. Third, although gonadal development begins posteriorly, like the Oikopleurinae, the flattened plate-like ovary and anterior migration of the testis into a ribbon-like organ in mature specimens, are more similar to *Bathochordaeus*. Fourth, the extent of the oikoplastic region is intermediate between the Oikopleurinae and *Bathochordaeus*. Finally, while the lateral lobes of the trunk are more similar to those observed in *Bathochordaeus* than those in most Oikopleurinae, the recently described *Oikopleura inflata* (Fenaux, 1998b; Fenaux and Youngbluth, 1991) also has similar lobes. As the features originally selected to place this genus in the Bathochordaeinae (i.e. large spiracles, 'dorsal' mouth) are somewhat arbitrary, it is likely that true taxonomic affinity will need to be established by molecular techniques.

Larvacean taxonomy rarely considers house structure, but this feature is also capable of supplying information on taxonomic affinity. The house of *M.erythrocephalus*, and particularly the inner food-concentrating filter, is large in comparison to the animal. Not surprisingly, the house of *M.bahamasi* is quite similar to that of *M.erythrocephalus* (M.Youngbluth, personal communication). In contrast, epipelagic Oikopleurinae houses are generally much smaller, only 6–15 times that of the trunk (Alldredge, 1977; Deibel, 1986), and likewise for the mesopelagic *Oikopleura villafrancae* (R.R.Hopcroft, personal observation).

The structure of the *M.erythrocephalus* house inner filter, and the orientation of the animal to it, are very similar to that described for *Bathochordaeus* (Hamner and Robison, 1992). Both differ significantly from that of the Oikopleurinae (Flood and Deibel, 1998). In particular, the food-concentrating filter is positioned more forward in the house. Perhaps the best explanation for this difference is that the normal forward/aft axis of the Oikopleurinae house (i.e. Flood and Deibel, 1998) has been compressed such that the apparent forward and aft of the Bathochordinae house correspond to the Oikopleurinae house's upper and lower surfaces, respectively. The apparent lack of the pre-filter, characteristic of most Oikopleurinae houses, is consistent with the absence of the Eisen's oikoplasts that are normally the sites of pre-filter secretion.

Despite their similarity, the house of *Mesochordaeus* differs significantly from that of *Bathochordaeus* in two important respects: the relative size of the animal to the 'inner' filter (smaller) and the relative size of the 'inner' house to the 'outer' house or mucus sheet (larger; cf. Hamner and Robison, 1992). Perhaps as a consequence of the *Mesochordaeus* filter's larger relative size, we note that the inner filter of *Mesochordaeus* is much more fragile and more transparent than that of *Bathochordaeus*. Additionally, we note that *Mesochordaeus* is less

reluctant to abandon its house than *Bathochordaeus*. Unlike the inner and outer house components of *Bathochordaeus*, which can be readily separated (Hamner and Robison, 1992), the two elements of the *Mesochordaeus* house are tightly linked.

Interestingly, despite the high similarity of *Bathochordaeus* and *Mesochordaeus* house structure, and the corresponding similarity in arrangement of cells in Fol's oikoplasts, the arrangement of most remaining oikoplastic cells differs significantly. The overall arrangement of oikoplastic cells in *Mesochordaeus* is more reminiscent of that for the Oikopleurinae, rather than the unique arrangement of giant cells outside the Fol's oikoplasts displayed in *Bathochordaeus* (Garstang, 1937; R.R.Hopcroft, personal observations). Perhaps these 'unassigned' fields of giant cells behind Fol's oikoplasts and on the 'chin' of *Bathochordaeus* are responsible for the production of the huge 'outer house' (Hamner and Robison, 1992) characteristic of only that genus.

At present, we know relatively little about the ecology of this animal and its relative importance in mesopelagic communities. *Mesochordaeus erythrocephalus* is typically found at depths below those normally inhabited by *Bathochordaeus* and occurs at lower densities (0.03×10^{-3} m^{-3}, maximum 1.6×10^{-3} m^{-3}, compared to 0.14×10^{-3} and 5.8×10^{-3} m^{-3} for *Bathochordaeus*). The houses of both species represent important oases for both metazoans (Steinberg *et al*., 1994, 1997) and protozoans (Davoll and Silver, 1986; Davoll and Youngbluth, 1990). Based on body size alone (Deibel, 1998), the volume of water filtered daily by these giant larvaceans must be substantial.

The heavy pigmentation of the digestive tract in *M.erythrocephalus* may be a mechanism for masking bioluminescent prey, that might otherwise make this larvacean visible to its own predators. This tactic is common among a broad range of mesopelagic taxa (Marshall, 1979). Preliminary examination of *Mesochordaeus* stomach contents (B.H.Robison, unpublished) reveals remains of tintinnids, Foraminifera, copepod eggs, copepod nauplii and unidentifiable remains of larger crustaceans amongst material most likely of detrital origin. The absence of a house pre-filter is consistent with the large size of particles observed in the gut.

Abandoned *Mesochordaeus* houses are readily recognized and distinguishable from those of *Bathochordaeus*. Both appear to contribute significantly to the downward flux of large particles in Monterey Bay (Davoll and Silver, 1986; Hamner and Robison, 1992). The global significance of larvaceans in oceanic flux is only now beginning to be realized (see the review by Gorsky and Fenaux, 1998). Ongoing research is directed at establishing filtering rates, the size spectra and composition of resources utilized, and the rates of house production by mesopelagic larvaceans in order to ascertain their full ecological importance.

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